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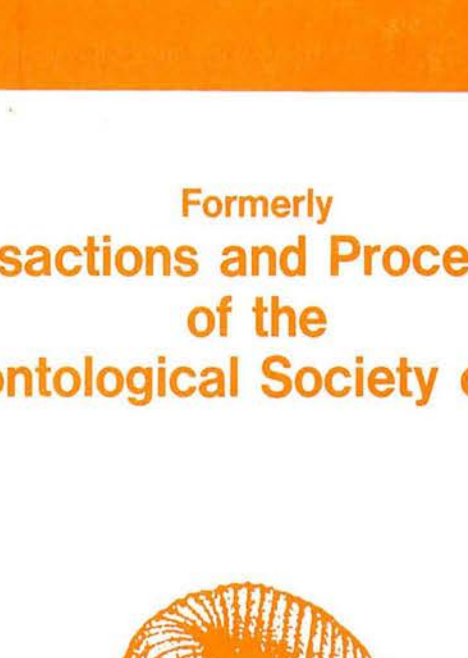

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Cover: Idealized sketch of *Nipponites mirabilis* Yabe, a Late Cretaceous (Turonian) nostoceratid ammonite. Various reconstructions of the mode of life of this species have been proposed, because of its curiously meandering shell form (after T. Okamoto, 1988).

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Two new species of Decapoda (Crustacea) from the Upper Cretaceous Izumi Group, Japan

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Abstract. Two new species of decapod crustacean, *Hoploparia miyamotoi* (Astacidea : Nephropidae) and *Callianassa masanorii* (Thalassinidea : Callianassidae), are described from the Upper Cretaceous Izumi Group of Osaka and Hyogo Prefectures, Japan. *H. miyamotoi* represents the first record for the genus from Cretaceous deposits of Japan and *C. masanorii* is the second of a callianassid known from the Japanese Cretaceous. The occurrence of *H. miyamotoi* extends the known geographic range of *Hoploparia* to the west side of the North Pacific.

Key words : Astacidea, Crustacea, Decapoda, Izumi Group, Japan, Thalassinidea, Upper Cretaceous

Introduction

The Upper Cretaceous (Campanian-Maastrichtian) Izumi Group is distributed for about 300 km from western Shikoku eastward to the Izumi mountains along the north side of the Median Tectonic Line, SW Honshu, Japan. It is a thick, submarine deposit mainly composed of alternating beds of conglomerate, sandstone and mudstone of a turbidite facies. This group contains a rich marine molluscan fauna which has been the subject of several paleontological studies, such as on pelecypods (Ichikawa and Maeda, 1958a, b, 1963 etc.), gastropods (Kase,1990) and cephalopods (Matsumoto and Morozumi, 1980 ; Morozumi, 1985 etc.). Besides these, well-preserved decapod crustaceans occur from several places.

Imaizumi (1978) first recorded, but did not figure, three species of decapod crustacean, *Callianassa ezoensis* Nagao, 1932 (Callianassidae), *Linuparus japonicus* Nagao, 1931 (Palinuridae) and *Plagiolophus ezoensis* Nagao, 1941 (Goneplacidae), from the Izumi Group (Upper Cretaceous) of Osaka and Hyogo Prefectures, Japan. Miyamoto (1992) figured *P. ezoensis* from Osaka Prefecture. Collins, Kanie and Karasawa (1993) redescribed *P. ezoensis* from Osaka and Hyogo Prefectures, and moved it from *Plagiolophus* Bell, 1857 to *Archaeopus* Rathbun, 1908 (Retroplumidae). The purpose of this paper is to describe two new species, *Hoploparia miyamotoi* (Nephropidae) and *Callianassa masanorii* (Callianassidae) from two new localities of the Izumi Group in Osaka and Hyogo Prefectures.

The specimens are housed in the Museum of Nature and Human Activities, Hyogo (D1-), 6 Yayoigaoka, Mita, Hyogo 669-1546, Japan, and the Mizunami Fossil Museum (MFM), Yamanouchi, Akeyo, Mizunami, Gifu 509-6132, Japan.

Systematic descriptions

Infraorder Astacidea Latreille, 1802
Superfamily Nephropoidea Dana, 1852
Family Nephropidae Dana, 1852
Subfamily Homarinae Huxley, 1879
Genus **Hoploparia** McCoy, 1849

Type species.—*Astacus longimanus* Sowerby, 1826 by subsequent designation of Rathbun, 1926.

Hoploparia miyamotoi sp. nov.

Figures 1, 2

Diagnosis.—Rostrum with small dorsolateral spines on distal half ; one supraorbital, one metaorbital and one postantennal spine present, all small ; abdominal somites with well developed lateral ridge, somites 3-5 bearing two marginal spines on pleura.

Description.—Carapace laterally compressed by deformation. Anterior half of carapace well preserved. Surface finely granulated and punctuated. Rostrum short, slender, slightly downturned proximally and slightly upturned over distal fourth, with four small, forwardly directed dorsolateral spines on distal half (Figures 1-1, 2-1). Orbit small, rounded, bordered by narrow, rounded ridge (Figure 1-1). Postcervical groove well defined, deep, broad, becoming shallower at junction with hepatic groove (Figures 1-2, 2-3). Cervical groove well defined, narrow, slightly arcuate, extending ventrally to join antennal groove (Figures 1-2, 2-3). Hepatic groove shallow, curving to join antennal and cervical grooves (Figures 1-2, 2-3). Antennal groove deep, arcuate, extending to anterior margin (Figures 1-2, 2-3). Gastro-orbital groove shallow (Figures 1-2, 2-3). One small, forwardly

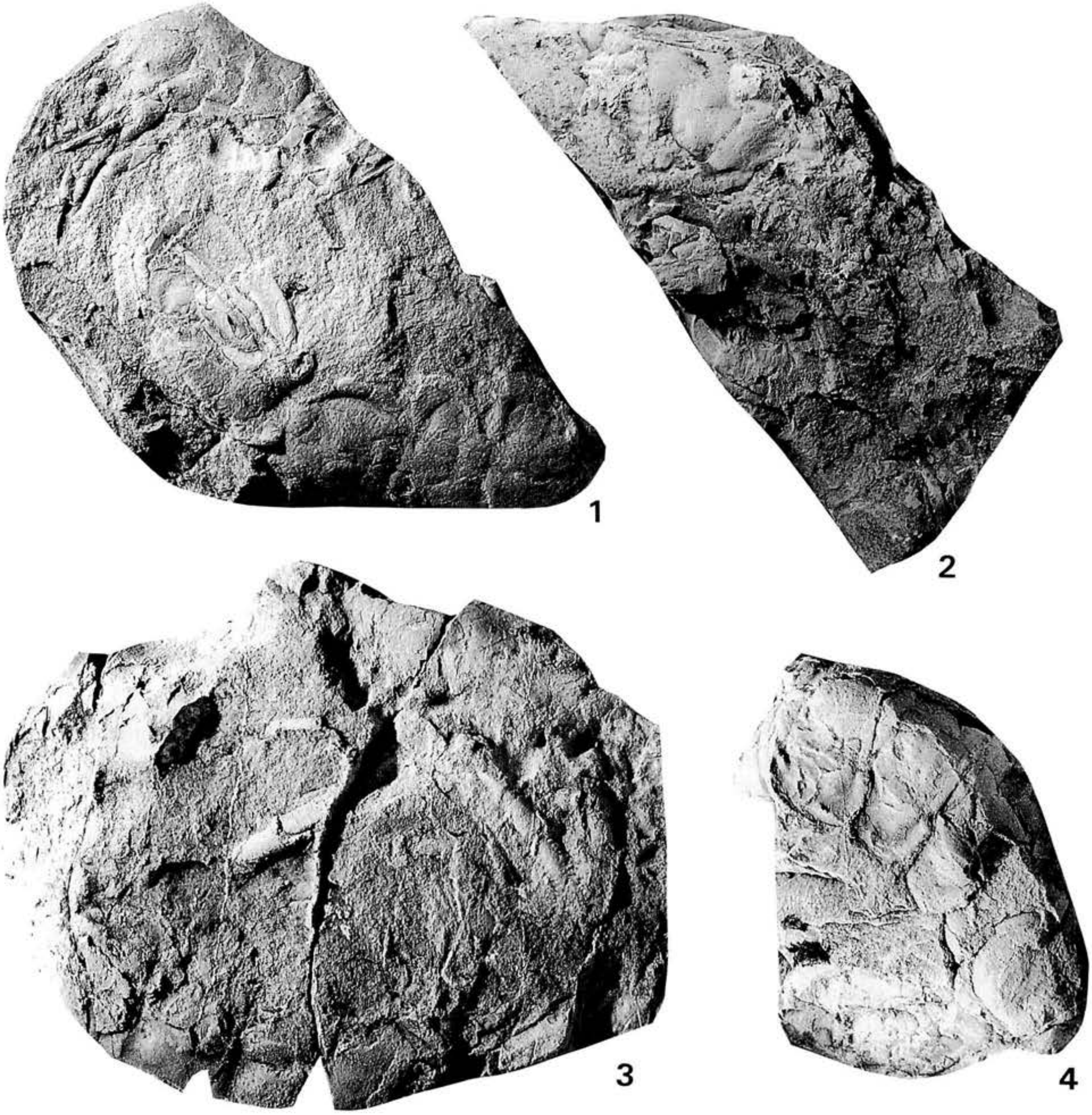

Figure 1. *Hoploparia miyamotoi* sp. nov. **1**, D1- 015001 (holotype), carapace, abdomen, telson and uropod, lateral view, ×1.8 ; **2**, MFM247,004 (paratype), carapace, pereiopods, lateral view, ×. 1.2 ; **3**, MFM247,006 (paratype), carapace, abdomen and pereiopods, lateral view, ×1.5 ; **4**, MFM247,005 (paratype), abdomen and uropod, lateral view, ×1.5.

directed supraorbital spine present (Figures 1-1, 2-1). Metaorbital spine small, forwardly directed, situated behind deepest part of orbit (Figures 1-1, 2-1). Antennal spine large, directed forward (Figures 1-2, 2-3) ; postantennal spine small (Figures 1-1, 2-1). Cornea of eye small (Figures 1-1, 2-3). Scaphocerite long, but shorter than rostrum (Figures 1-1, 2-1). Antennula, antenna, and maxilliped 3 preserved (Figures 1-1, 1-2, 2-1, 2-3).

All terga of abdominal somites finely punctuate ; somite 1 short ; somite 2 largest of all terga ; somites 3-5 decreasing in size. Terga and pleura of somites 2-5 separated from one another by well developed ridge (Figures 1-4, 2-4). Anterior margins of pleura of somites 2-5, nearly straight, ventral margins gently convex, anteroventral angles rounded, posterolateral angles with a small, posteroventrally directed spine, posterior margins of pleura of somites 3-5 gently convex with small, posteriorly directed spine on ventral third (Figures 1-1, 1-4, 2-1, 2-4). Pleuron of somite 6 reduced, convex anteriorly and ventrally, but concave posteriorly (Figures 1-1, 1-4, 2-1, 2-4). Surfaces of pleura finely punctate

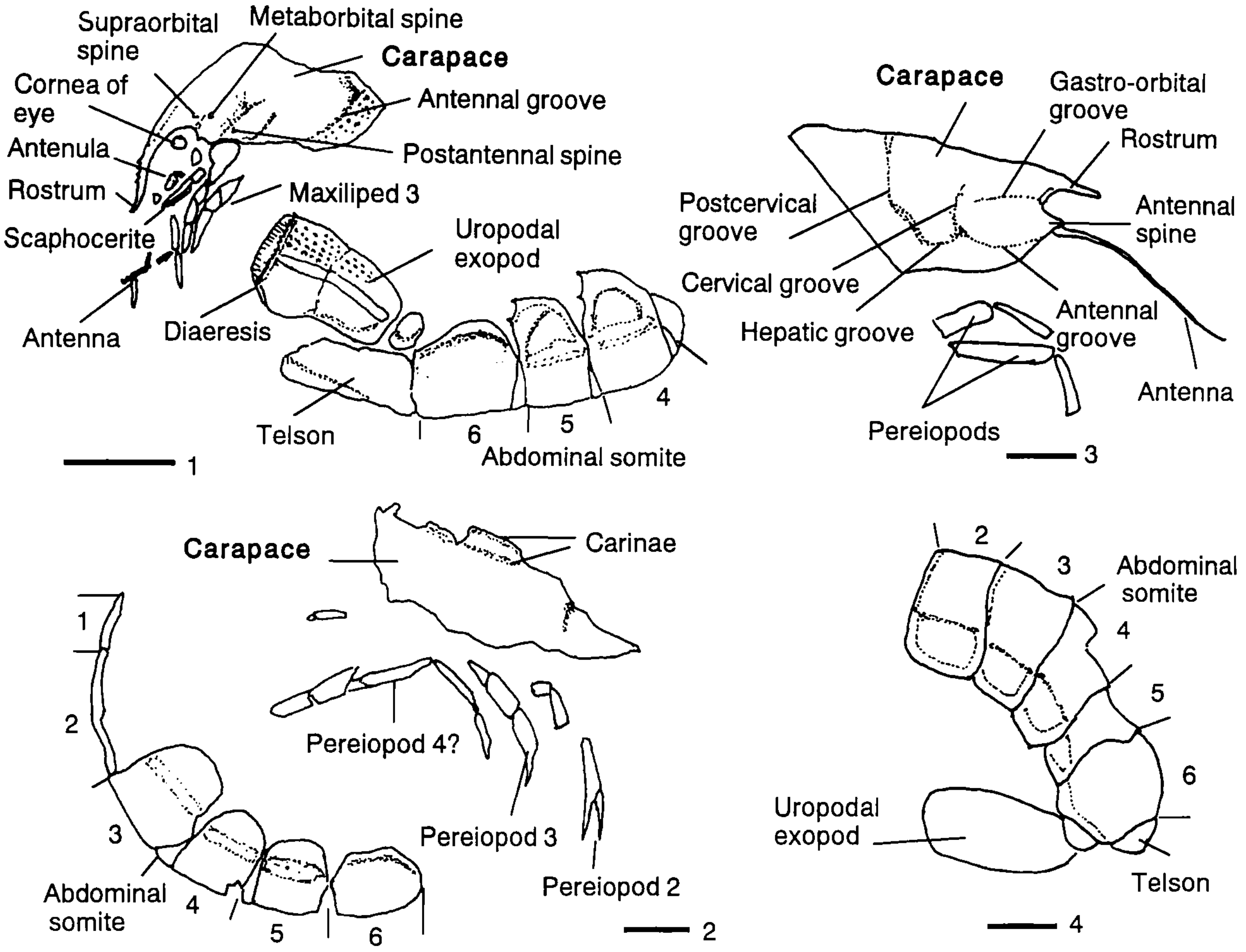

Figure 2. *Hoploparia miyamotoi* sp. nov. **1**, D1-015001 (holotype), carapace, abdomen, telson and uropod, lateral view; **2**, MFM247,006 (paratype), carapace, abdomen and pereiopods, lateral view; **3**, MFM247,004 (paratype), carapace, pereiopods, lateral view; **4**, MFM247,005 (paratype), abdomen and uropod, lateral view. Scale bar=1 cm.

with marginal furrow.

Telson longer than wide, narrowing posteriorly, surface punctuated with a median groove and a longitudinal groove diverging from mid-line posteriorly (Figures 1-1, 2-1). Uropodal exopod triangular in outline, bearing median ridge on dorsal surface, with weakly convex lateral margin (Figures 1-1, 2-1). Surface covered with small granules on outer half, diaeresis with 11 small spines on anterior margin and with fine radial ornament on posterior dorsal surface (Figures 1-1, 2-1).

Pereiopods preserved, slender; pereiopod 2 chelate (Figures 1-3, 2-2).

Discussion.—The present species is the first record of *Hoploparia* from Cretaceous deposits of Japan. *H. miyamotoi* resembles *Hoploparia bearpawensis* Feldmann *in* Feldmann, Bishop and Kammer, 1977 from the Bearpaw Shale (Campanian) of Montana, but differs by the presence of two marginal spines on the pleura of somites 3-5 and in the absence of the postcervical spine of the cardiac region and the median abdominal ridge. The species also resembles *Hoploparia buntingi* (Feldmann and Holland, 1971) from the Cannonball Formation (Paleocene) of North Dakota (Aguirre Urreta *et al.*, 1991), but differs in having a short rostrum, having short abdominal pleura and lacking a pit on pleura of somites 2-5. In *H. miyamotoi* only one postantennal spine is present, while *H. buntingi* has three spines.

Previously known species of *Hoploparia* have been recorded from Cretaceous-Palaeogene deposits in Europe, North America, Argentina, Australia, Antarctica and Madagascar (Aguirre Urreta, 1989), and New Zealand (Feldmann and Keyes, 1992). The discovery of *H. miyamotoi* shows that the genus had reached Japan—the west side of the North Pacific—by Maastrichtian time.

Etymology.—The name is dedicated to Junichi Miyamoto, who is now studying the paleontology of the Izumi Group.

Material examined.—Holotype (D1-015001), Mitsukawa, Sumoto City, Hyogo Prefecture, mudstone of the Kita-ama Formation of the Izumi Group (Lower Maastrichtian; *Nostoceras hetonaiense* Zone of Morozumi, 1985); 3 Paratypes, MFM247,004, Sobura, Kaizuka City, Osaka Prefecture, mudstone of the Shindachi Formation of Izumi Group (probably Lower Maastrichtian of Matsumoto and Morozumi, 1980); MFM247,005, MFM247,006, Mitsukawa, Sumoto City, Hyogo Prefecture, mudstone of the Kita-ama Formation of the Izumi Group (Lower Maastrichtian).

Infraorder Thalassinidea Latreille, 1831
Superfamily Callianassoidea Dana, 1852
Family Callianassidae Dana, 1852
Genus ***Callianassa*** Leach, 1814

Type species.—*Cancer (Astacus) subterraneus* Montagu, 1808 by monotypy.

"Callianassa" (s.l.) ***masanorii*** sp. nov.

Figure 3

Diagnosis.—Large-sized callianassid. *Linea thalassinica* present. Carapace with rostral spine; dorsal oval well defined, occupying about half length of dorsal carapace. Pereiopods 1 chelate, subequal, minor slightly smaller than major, dissimilar without meral hook.

Description.—Carapace well preserved, laterally compressed, height about half of length excluding rostral spine. Frontal margin with short, broadly triangular, downturned rostral spine and without lateral spines (Figure 3-5). *Linea thalassinica* well defined (Figure 3-5). Dorsal oval convex, about half of dorsal length (Figure 3-5). Cervical groove deep, joining *linea thalassinica* at posterior third of oval (Figure 3-5). Posterior margin evenly curved without lateral lobe (Figure 3-5).

Abdomen large; somite 1 short, trapezoidal in dorsal view, bearing dorsal transverse groove at anterior fourth, with divergent lateral margins (Figure 3-6). Somite 2 about 1.5 times as long as 1, lateral margin divergent posteriorly (Figure 3-6). Somites 3-5 diminishing in size posteriorly (Figure 3-6). Somites 2-5 with small setal pits posterolaterally (Figure 3-6). Telson and uropod unknown.

Pereiopods 1 chelate, subequal, dissimilar. Length of propodus of major cheliped about twice the height; fingers about 1/3 of propodus length, with smooth opposing margin; carpus short, about half as long as propodus, slightly shorter than high, dorsal margin nearly straight, ventral margin strongly curved; merus about equal to carpus length, rhomboidal in lateral view, dorsal and ventral margins strongly convex without ventral spine, lateral surface strongly vaulted with median ridge (Figures 3-1a, 2, 3, 7). Propodus of minor cheliped slightly smaller than major propodus, rather slender in outline; fingers about 2/5 of propodus length with smooth opposing margin; carpus short, about 1/3 of propodus length, convergent proximally, dorsal margin gently convex, ventral margin strongly curved; merus slightly longer than carpus, slightly convergent proximally without ventral spine, dorsal and ventral margins slightly convex, lateral surface gently vaulted (Figures 3-1b, 3).

Pereiopod 2 with fingers not gaping, cutting edges straight; dactylus slender, but fixed finger wide; palm about as long as high; merus narrowing distally (Figure 3-4).

Carpi and meri of pereiopods 3-4 preserved (Figures 3-1a, b, 2, 7).

Discussion.—*"C." masanorii* differs from another Japanese Cretaceous callianassid, *Callianassa ezoensis* Nagao, 1932 from the "Hakobuchi Sandstone" (Campanian to Maastrichtian) of Hokkaido in that pereiopods 1 have dissimilar chelipeds, smooth ventral margins of propodi, and a rhomboidal merus of the major cheliped.

It is noteworthy that the carapace, abdomen, and pereiopods 1-4 are preserved, although the fossil record of callianassids is usually confined to pereiopods 1.

Manning and Felder (1991) recognized two families, seven subfamilies and 21 genera for taxa previously assigned to the extant Callianassidae. Since then, four genera, *Gilvossius* Manning and Felder, 1992, *Corallichirus* Manning, 1992, *Poti* Rodrigues and Manning, 1992, and *Sergio* Manning and Lemaitre, 1993, have been described.

The present species is characterized by the carapace with a rostral spine, with a dorsal oval region, and without a cardiac prominence, also by the major cheliped without a meral hook. With these features it may be assigned to *Neocallichirus* Sakai, 1988 and *Sergio* Manning and Lemaitre, 1993 in the Callichirinae or *Cheramus* Bate, 1888 in the Cheraminae. It also has an affinity *Anacalliax* de Saint Laurent, 1973, which Poore (1994) moved to the Callianassidae from the Ctenochelidae, although it lacks a rostral carina and cardiac prominence of the carapace. The generic placement of the present species is obscure because of absence both of maxilliped 3 and the telson, until knowledge of these characters is at hand, it is considered best to place the species in *Callianassa* (s.l.).

"C." masanorii differs from all known species of *Protocallianassa* Beurlen, 1930 in the extinct subfamily Protocallianassinae Beurlen, 1930, in that the articulation between the carpus and propodus of the major cheliped lies at an angle of nearly 90° to the long axis of the propodus. In *Protocallianassa* the carpus-propodus joint of the major cheliped is inclined at about 120° to the long axis (Mertin, 1941, Vega *et al*., 1995, Feldmann *et al*., 1995). Nevertheless, in the carapace character, the species has a close affinity with the type *Protocallianassa archiaci* (A. Milne Edwards, 1860) from the Upper Senonian of England. Although in many extant callianassids the cervical groove of the carapace extends far back medially (Glaessner, 1969: R477), in species, *"C." masanorii* and *P. archiaci*, it is situated at the mid-length of the carapace. This character is also observed in the callianassid subfamily Eucallinae and the members of the Ctenochelidae.

Etymology.—The name is dedicated to Masanorii Tani, who collected the paratype specimen.

Material examined.—Holotype (D1-000495), 5 paratypes (D1-000506, D1-000507, MFM247,007-247,009), Mitsukawa, Sumoto City, Hyogo Prefecture, Mudstone of the Kita-ama Formation of the Izumi Group (Lower Maastrichtian; *Nostoceras hetonaiense* Zone of Morozumi, 1985).

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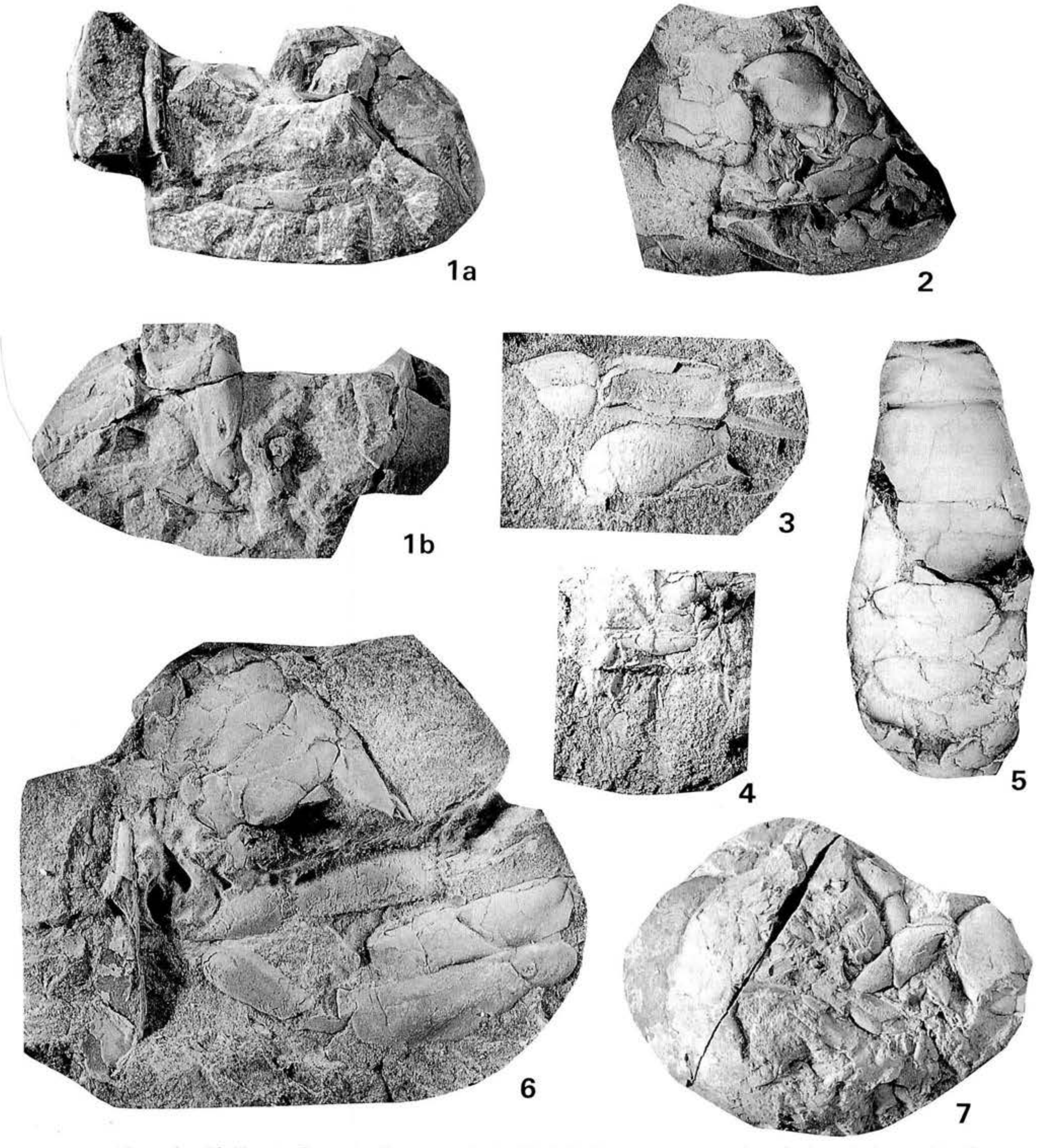

Figure 3. *"Callianassa" masanorii* sp. nov. **1a, b**, MFM247,007 (paratype), pereiopods, lateral view, ×1.5 ; **2**, D1-000507 (paratype), pereiopods, lateral view, ×1.5 ; **3**, D1-00506 (paratype), pereiopods 1, lateral view of right cheliped, mesial view of left cheliped, ×1.5 ; **4**, MFM247,008 (paratype), pereiopod 2, lateral view, ×1.5 ; **5**, D1-000495 (holotype), lateral view of carapace, mesial view of pereiopods 1, ×1.5 ; **6**, D1-000495 (holotype), abdomen, dorsal view, ×1.5 ; **7**, MFM247,009 (paratype), abdomen and pereiopods, lateral view, ×1.5.

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Formation of plications in the Miocene bivalve *Mytilus* (*Plicatomytilus*) *ksakurai* as a consequence of architectural constraint

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Abstract. A total of 68 specimens of thick-shelled, peculiarly shaped Miocene mytilids from Hokkaido and northern Honshu were examined from the viewpoint of constructional morphology. They have been treated as members of three species : *Mytilus* (*Plicatomytilus*) *ksakurai*, *M.* (*Tumidimytilus*) *tichanovitchi*, and *M.* (*T.*) *furanuiensis*, with different shell shapes, muscle scars and surface sculpture. *M. ksakurai* shows an abrupt increase in shell convexity during ontogeny, like that in *M. tichanovitchi*. It develops a few conspicuous plications just after this allometric change in shell convexity. Polished sections of the shell of *M. ksakurai* reveal that just after the abrupt change in shell convexity, the internal growth increments bend sharply toward the inside of the shell. This is associated with a remarkable thickening of the outer part of the fibrous prismatic layer of the shell. These facts suggest that in *M. ksakurai*, the mantle turned inward at the stage of the allometric change in shell convexity. Consequently, the diverging plications were formed by the wrinkled mantle as a result of the reduction in space across which the mantle extended.

Key words : allometric change, mantle bending, *Mytilus ksakurai*, plication, tablecloth wrinkle

Introduction

The tempo and mode of morphological evolution in fossil organisms can be inferred by analyzing changes in fossilized hard tissue through geologic time. Realization of the rule of constructional processes of hard tissue structures is important for better understanding their morphological evolution.

A number of works deal with pattern formation in molluscan shell sculpture from the viewpoint of constructional morphology (e.g., Seilacher, 1972) and theoretical morphology (e.g., Macomber and Macomber, 1983 ; Hayami and Okamoto, 1986 ; Gunji, 1991 ; Ackerly, 1992). However, little is known about how shell sculpture is formed, although several hypotheses have been proposed by previous authors (e.g., Cox *et al.*, 1969 ; Hayami, 1974 ; Seilacher, 1985). Hayami and Okamoto (1986) pointed out that the formation of striae in the shell of the scallop *Camptonectes* may be related to the direction of crystal growth of foliated calcite.

Divergent ribs are one of the characteristic features of bivalve shells. During Early to Late Miocene time, peculiarly shaped mytilids flourished in the North Pacific region. Among them were forms with a plication or several diverging plications, described under the subgenus *Mytilus* (*Plicatomytilus*) by Allison and Addicott (1976) (Figure 1-3, -4, and -5). During the same time interval, several non-plicated but similarly thick-shelled *Mytilus* species (Figure 1-1 and -2) occurred in the same paleozoogeographic realm. Kafanov (1984) proposed the subgenus *M.* (*Tumidimytilus*) for these forms. These plicated and non-plicated mytilids have been considered to be closely allied to each other phylogenetically (Noda and Hoyanagi, 1993).

The process and factors controlling formation of plications in *M.* (*Plicatomytilus*) are analyzed here on the basis of microscopic observations of shell cross-sections and biometric analysis of shell form. The paper focuses on how the plication is formed in relation to mantle behavior.

Materials

Lower and Middle Miocene marine strata in Hokkaido and northern Honshu yield abundant shallow cold-water molluscan fossils known as the Asahi and Chikubetsu faunas respectively (Chinzei, 1978). The faunas typically include thick-shelled, peculiarly shaped mytilids that have been classified as species of *Mytilus* (*Plicatomytilus*) and *M.* (*Tumidimytilus*). The following five species have been described from Sakhalin, Hokkaido, and northern Honshu : *M. tichanovitchi* Makiyama, 1934, *M. furanuiensis* Uozumi and Akamatsu, 1988, *M. ksakurai* Nomura and Hatai, 1936, *M.* (*P.*) *hidakensis* Suzuki, Sakai, and Uozumi, 1983, and *M.* (*P.*) *monbetsuensis* Uozumi and Akamatsu, 1988. Related species in these two subgenera are also known from the

Miocene of Kamtchatka, Alaska, and California, indicating that these mytilids were widely distributed throughout the North Pacific paleozoogeographic realm.

In this study, 68 specimens of these Miocene mytilids were analyzed from the viewpoint of constructional morphology. Specimens of three extant non-plicated *Mytilus* species, *M.* (*Mytilus*) *galloprovincialis*, *M.* (*M.*) *californianus* and *M.* (*Crenomytilus*) *grayanus* were also studied for comparison. Localities and stratigraphic horizons from which the samples came are listed in Table 1.

Specimens of *M.* (*Plicatomytilus*) were collected from outcrops exposed in the Katsura River, Aomori Prefecture, northern Honshu, and in the Kishimatsu-zawa River, southern Hokkaido. The Katsura River is the type locality of *Mytilus ksakurai*, and the Kishimatsu-zawa River that of *M. monbetsuensis*. According to the original description by Nomura and Hatai (1936), *M. ksakurai* is characterized by a thick, extremely convex shell without plications. Noda and Motoyama (1991) reported specimens referable to *M. hidakensis* from the type locality of *M. ksakurai*. *M. hidakensis* was described on the basis of specimens from Urakawa Town, Hidaka Province, southern Hokkaido. It is characterized by a thick, highly convex shell with three strong plications. Noda and Hoyanagi (1993) suggested that the specimens described as *M. ksakurai* are juvenile specimens of *M. hidakensis*. Subsequently, Noda (1994) interpreted *M. hidakensis* as a junior synonym of *M. ksakurai* based on the presence of a plication preserved in relief on the inner mold of the holotype of *M. ksakurai*, and assigned *M. ksakurai* to the subgenus *M.* (*Plicatomytilus*).

Uozumi and Akamatsu (1988) described *M. monbetsuensis* from a Middle Miocene outcrop in the Kishimatsu-zawa, a branch of the Kabari River, Monbetsu Town, Hidaka Province, Hokkaido. This species is similar to *M. hidakensis* but is distinguished from that species by having a single plication, weaker than the three in *M. hidakensis*, and a slightly concave dorsal margin. However, in the same way as does *M.* (*P.*) *gratacapi* described by Allison and Addicott (1976), specimens collected at localities in the Katsura and Kishimatsu-zawa Rivers exhibit wide variation in the number and strength of plications (Figure 1-3, -4, and -5, Figures 2 and 9), including morphotypes assignable to both *M. hidakensis* and *M. monbetsuensis* (see Figures 1-3, -4, and -5, Figures 2 and 9). These specimens are, therefore, regarded as belonging to a single species showing wide variation in shell morphology. They are classified as *M. ksakurai* in this paper.

All the specimens utilized are housed in the University Museum, University of Tokyo (UMUT).

Methods

For microstructural observation, single valves of both extant and fossil specimens were cut along the maximum growth axis. The sectioned surfaces were polished with graded series of carborundum and alundum, coated with clear nail vanish, and observed under a binocular microscope.

In all double scatter diagrams, 95% confidence intervals of the data are represented by horizontal and vertical bars.

This study focuses on four aspects of the shell of *Mytilus*. They are: a) morphological features of the commissure plane (generating curve), b) whorl expansion rate, c) secretion rate of the outer part of the fibrous prismatic layer, and d) degree of plication development.

To realize aspect a), four variables were measured. They are: 1) the shape of the generating curve (Raup and Michelson, 1965), that is, lengths of major and minor axes of the commissure plane approximated as an ellipse, 2) position of the break point on the commissure (explained below), 3) distance between the hinge axis and the break point on the commissure at which plications begin to appear, or at the stage of the allometric change in shell convexity, and 4) curvature of each segment of the commissure. 1) is utilized to understand the overall morphological characters of the commissure plane. 3) and 4) are utilized to understand the

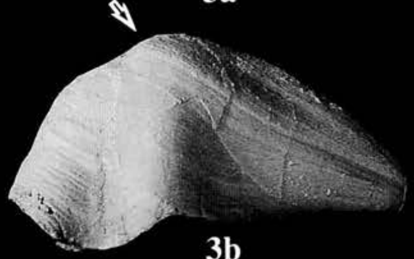
Table 1. List of the materials utilized. The numbers in parentheses represent the numbers of specimens used in measurements of all variables. Ages after Kimura and Tsuji (1992) for Takinoue Formation and Noda (1994) for Furanui and Isomatsu Formations.

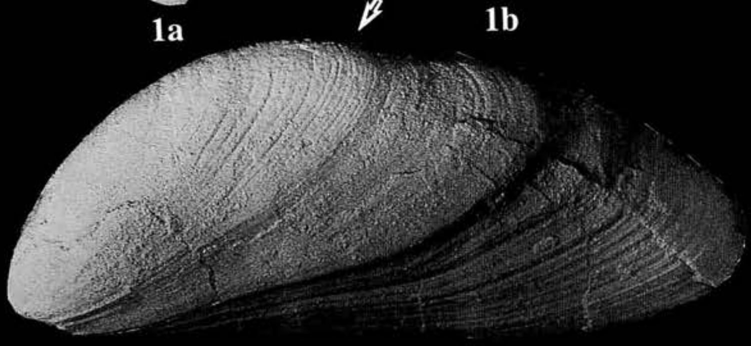
Species and related species	Number of specimens	Horizon and age	Locality
Mytilus (*Mytilus*) *galloprovincialis* Lamarck, 1819	7(6)	Recent	Nojima Coast, Yokohama City, Tokyo Bay, central Japan
M. (*M.*) *californianus* Conrad, 1837	4(3)	Recent	Pismo Beach, California, U.S.A.
M. (*Crenomytilus*) *grayanus* Dunker, 1853	7(6)	Recent	Samani Coast, Samani Town, Hidaka Province, southern Hokkaido, Japan
M. (*Tumidimytilus*) *tichanovitchi* Makiyama, 1934	8(7)	Takinoue Formation, lower Miocene	Asahi Town, Iwamizawa City, central Hokkaido, Japan
M. (*T.*) *furanuiensis* Uozumi and Akamatsu, 1988	6(5)	Furanui Formation, middle Miocene	Hirotomi, Monbetsu Town, Hidaka Province, southern Hokkaido, Japan
M. (*Plicatomytilus*) *ksakurai* Nomura and Hatai, 1936	22(7)	Isomatsu Formation, lower Miocene	Katsura River, Shiura Village Tsugaru Peninsula, Aomori Pref., northern Honshu, Japan
M. (*Plicatomytilus*) *ksakurai* Nomura and Hatai, 1936	32(9)	Furanui Formation, middle Miocene	Kishimatsu-zawa River, Monbetsu Town, Hidaka Province, southern Hokkaido, Japan
Crassostrea gigas (Thunberg, 1793)	1(0)	Recent	Goshiki-hama Coast, Iyo City, Ehime Pref., western Japan

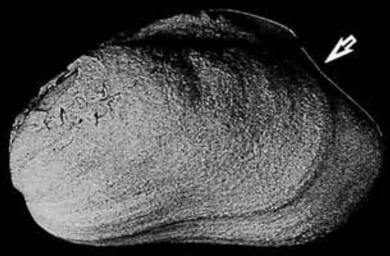

1a

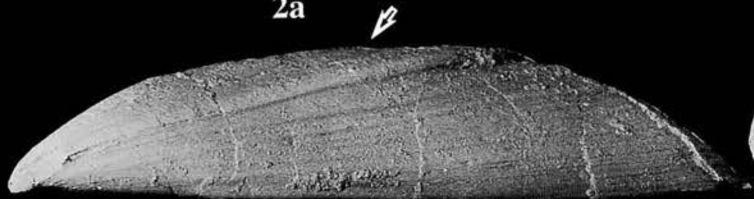

1b

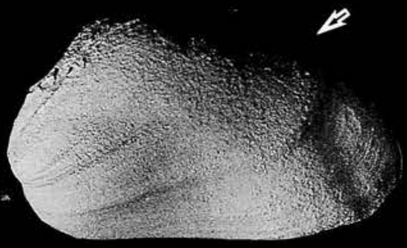

3a

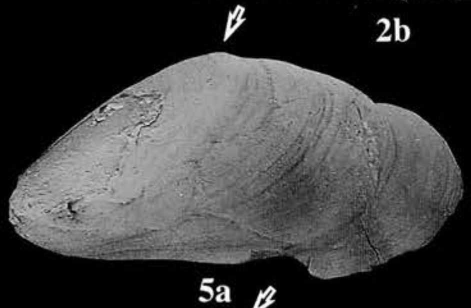

3b


2a


4a


2b


4b


5a


5b


6a


6b


7

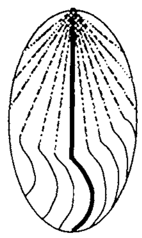
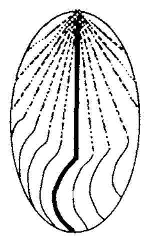
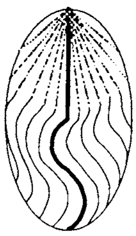
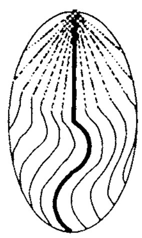
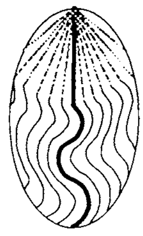
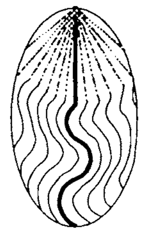
Number of plications	1		2		3	
Ventral view						
Katsura River	3	0	7	5	1	3
Kishimatsu-zawa River	7	4	9	9	0	3

Figure 2. Variation in plication pattern viewed from the ventral side in specimens of *M. ksakurai* from localities in the Katsura and Kishimatsu-zawa Rivers. The number of specimens of each plication type from the two localities is listed in the lower two rows.

detailed characters. 2) is utilized for the base of 3) and 4) to show the position on the commissure.

In this study, aspect b), the whorl expansion rate, is shown as the relationship between the area of the commissure plane (generating curve) and the revolving angle of the commissure plane about the hinge axis (coiling axis). This is not essentially different from the original description of whorl expansion rate in Raup and Michelson (1965). To show this parameter, two variables were measured, 5) revolving angle of the commissure plane about the hinge axis, and 6) area of the commissure plane.

Miocene mytilid species are characterized by their thick shells. Investigation of the change of shell thickness during growth is important to understand the process of their growth. In particular, the change of thickness of the outer part of the fibrous prismatic layer is important, because that is formed following the periostracum and consolidates the shell shape. However, the shell thickness is not useful for precise investigation, because it consists of several internal growth increments that do not all correspond to a single growth stage. Therefore, in this study, parameter c), the index of the secretion rate of the outer part of the fibrous prismatic layer is introduced. This is defined as the height of a quadrilateral that approximates an internal increment. This index corresponds to the relative secretion rate of an infinitesimal area of the mantle epithelium per one internal growth increment. This is measured as variable 7).

As mentioned above, *M. ksakurai* exhibits wide variation in the number and strength of plications. In this case, it is nonsense to focus only on the number of plications. It is necessary to introduce the index d) degree of plication development. It is natural that when the allometric relationship between the area of the commissure plane and the outline length of the commissure is expressed in a double scatter diagram, the slope of regression abruptly increases after the appearance of plication. The degree of plication development is defined by the angle between two regression lines before and after the plication appears. For this index, 8) outline length of the commissure is measured, and 9) degree of plication development is represented based on variables 6) and 8).

To make a biometric analysis, commarginal growth rings on the shell at different growth stages were marked by attaching narrow adhesive tapes to them. These commar-

Figure 1. Shell morphology of selected Miocene (1-5) and extant (6) mytilids, and *Crassostrea* (7). Lateral (a) and ventral (b) views for 1-6. All at natural size. Arrows point to the allometric critical point for the growth of shell convexity. **1.** *Mytilus* (*Tumidimytilus*) *tichanovitchi* Makiyama. Lower Miocene Takinoue Formation, Asahi Town, Iwamizawa City, central Hokkaido. UMUT CM 27606a. **2.** *Mytilus* (*Tumidimytilus*) *furanuiensis* Uozumi and Akamatsu. Middle Miocene Furanui Formation, Hirotomi, Monbetsu Town, Hidaka Province, southern Hokkaido. UMUT CM 27607a. **3, 5.** *Mytilus* (*Plicatomytilus*) *ksakurai* Nomura and Hatai. Middle Miocene Furanui Formation, Kishimatsu-zawa River, Monbetsu Town, Hidaka Province, southern Hokkaido. UMUT CM 27609a (3) and UMUT CM 27609b (5). **4.** *M. ksakurai* Nomura and Hatai. Lower Miocene Isomatsu Formation. Katsura River, Shiura Village, Tsugaru Peninsula, Aomori, North-East Japan. UMUT CM 27608a. **6.** *Mytilus* (*Mytilus*) *galloprovincialis* Lamarck. Recent. Nojima Coast, Tokyo Bay, central Japan. UMUT RM 27603a. **7.** *Crassostrea gigas* (Thunberg). Lateral view. Recent. Goshiki-hama Coast, Iyo City, Ehime Prefecture, western Japan. UMUT RM 27610.

ginal growth rings are chosen as narrowly as possible. The most distant point from the hinge axis, that is the coiling axis in Raup and Michelson (1965), was marked with a pen for each growth ring. Then, photographs were taken from different directions for each specimen: one from the lateral side, perpendicular to the last-formed commissure plane, one from the ventral margin, parallel to the last-formed commissure plane, and a series of photographs from directions perpendicular to the commissure plane at each growth stage.

Variables 1) to 9) mentioned above were measured. For variables 3) and 4), measurement data are normalized so that the commissure planes of all specimens have the same area as the last-formed commissure plane of the specimen of *M. galloprovincialis* (UMUT RM 27603b).

Detailed methods to obtain the above variables are described below:

1) *Lengths of major and minor axes of the commissure plane approximated to an ellipse.*—These lengths were measured in the specimens of *M. ksakurai* and *M. tichanovitchi*. First, photographs were taken perpendicular to the commissure plane at each growth stage. Images of commissure planes were approximated to an ellipse using the software NIH Image 1.53 (freeware). They were transmitted to a Macintosh computer via an image scanner, and the lengths of major and minor axes were measured using the software NIH Image 1.53 (freeware).

2) *The position of the break point on the commissure.* —The Miocene mytilids examined are generally flat in the juvenile stage, but the curvature of the shell increases abruptly during ontogeny, which causes an inflated shell form in the middle to later growth stages. The commarginal growth line at the stage of the allometric change in shell convexity was photographed for each specimen. On the enlarged photo, the commissure at this stage was divided by a number of chords of equal length (5 mm) using a compass, starting from the beak. The mid-point of each segment of commissure is called the break point (BP, Figure 3A). The position of the break point on the commissure is defined as the angle β between the hinge axis and the straight-line segment connecting a break point and the mid-point (P) of the hinge line (Figure 3-A). This angle was measured using a protractor. This variable is used as a signpost on the commissure in the graph of variables 3) and 4). The position on the commissure is represented as shown in Figure 3-B.

3) *The distance between the hinge axis and the break point on the commissure.*—This is defined as the perpendicular distance from a break point to the hinge line (d, in Figure 3-A). It is measured (using a slide caliper) from the point at which plications begin to appear, or at the stage of the allometric change in shell convexity.

4) *Curvature of each segment of the commissure.*—Curvature, R is generally defined as:

$$R = d\theta / dl \qquad (1)$$

where l is the arc length and θ is the angle between two unit normal vectors. Measurements on actual specimens were made in the following manner (see Figure 3-A).

On the enlarged photo used in the measurement of variable 2), the commissure was divided by a number of chords of equal length (5 mm), using a compass, starting from the beak. When this chord is sufficiently short, it approximates a segment of the commissure. The angle θ_a between each pair of bisectors (a_1 and a_2, in Figure 3-A) of the angles between neighboring chords (α_1 and α_2, in Figure 3-A) was measured using a protractor. It is regarded as θ in equation (1). Thus, the curvature (R) of each segment of the commissure (c, in Figure 3-A) was approximated by:

$$R = \theta_a / b$$

where b is the length of a chord.

5) *Revolving angle of the commissure plane about the hinge axis.*—This value at a given growth stage was obtained using the following formula (see Figure 3-C):

$$\varphi_{rot} = \arctan\left(\frac{z}{x}\right)$$

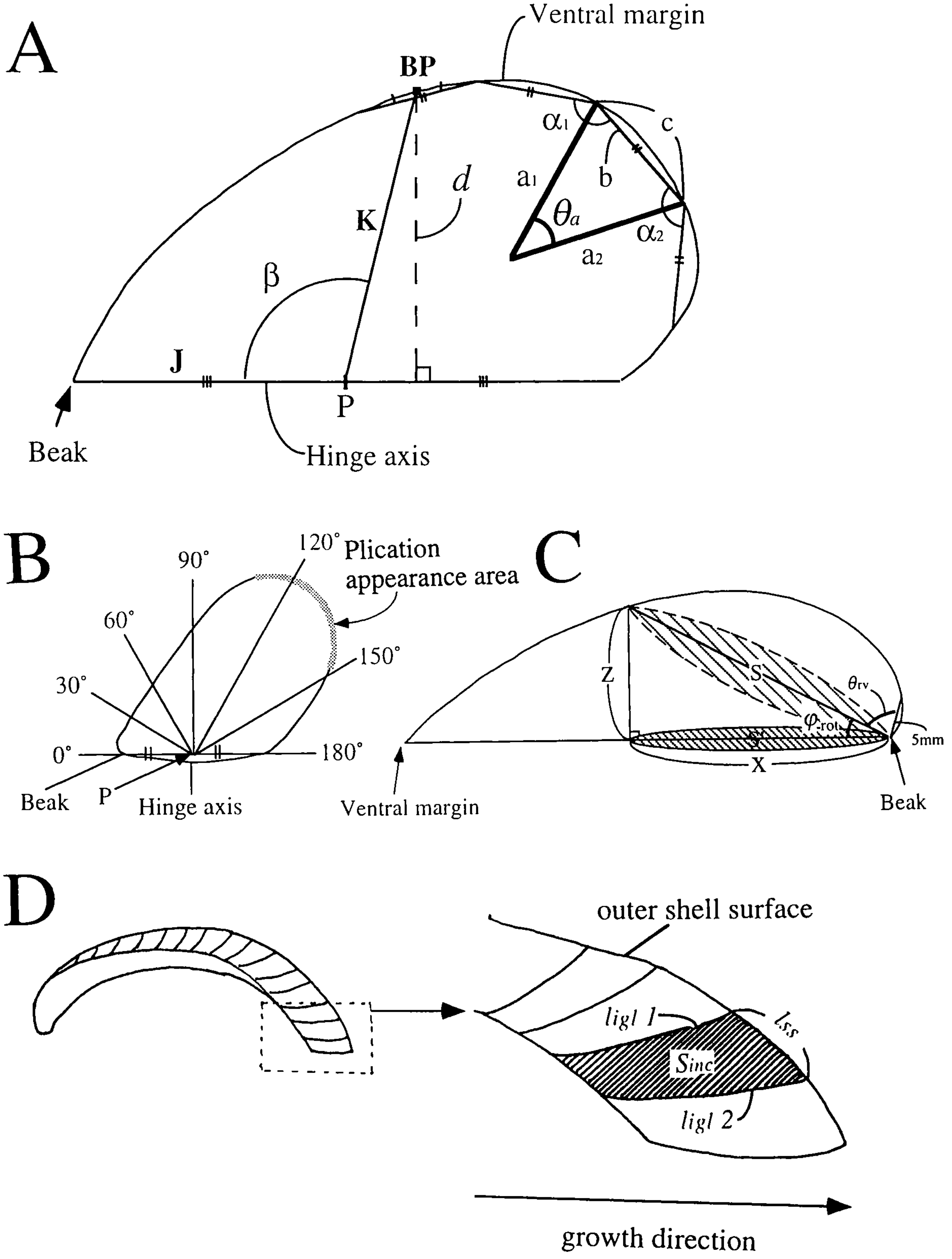
Figure 3. Diagrams showing the methods of measurements.

A: Schematic figure showing the measurements of curvature for each segment of the commissure, the distance from the hinge axis to break point on the commissure, and the position on the commissure. See text for details. This figure shows the shell outline viewed from a lateral direction. b: length of the chord, c: length of the segment of the commissure, BP: break point on the commissure, d: distance from the hinge axis to BP, P: the middle point of the hinge axis, α_1 and α_2: angles between two neighboring chords, a_1 and a_2: bisectors of α_1 and α_2, β: angle representing the position of BP on the commissure, J: segment connecting the beak and P, K: segment connecting P to MP.

B: Schematic diagram showing the position on the commissure. Position on the commissure is represented with the angle as shown in Figure 3-B. Shadowed portion represents the plication appearance area in the shell of *M. ksakurai* at the allometric critical point. P: the mid-point of the hinge axis.

C: Schematic diagram showing the measurement of the revolving angle of the commissure plane and the area of the commissure plane. φ_{rot}: the backward rotation angle from the last-formed commissure plane, z: the perpendicular distance between the last-formed commissure plane and the most distant point (marked point) from the hinge axis in each earlier commissure plane, x: the distance between the projection of that point to the last-formed commissure plane and the hinge axis, θ_{rv}: the revolving angle of the commissure plane, S: the real area of the commissure plane, S': the projected area of the commissure plane.

D: Schematic figures defining the index of the secretion rate of the outer part of the fibrous prismatic layer. The left figure is a sectioned valve cut along the maximum growth axis. The right figure is a closeup view of the internal growth increments near the ventral margin. $l_{igl}1$ and $l_{igl}2$: internal growth lines, l_{ss}: the length of the side of the shadowed area along the shell surface, S_{inc}: area of the shadowed area. The index of the secretion rate of the outer part of the fibrous prismatic layer is defined as the height of the quadrilateral approximating the shadowed area.


A
Ventral margin
BP
α_1
c
b
a_1
d
K
θ_a
α_2
a_2
β
J
P
Beak
Hinge axis
B
90°
120°
Plication appearance area
60°
30°
150°
0°
180°
Beak
P
Hinge axis
C
Z
S
θ_{rv}
φ_{rot}
S'
5mm
X
Ventral margin
Beak
D
outer shell surface
ligl 1
l_{ss}
Sinc
ligl 2
growth direction

where φ_{rot} is the backward rotation angle from the last-formed commissure plane, z is the perpendicular distance between the last-formed commissure plane and the most distant point (marked point) from the hinge axis in each earlier commissure plane, and x is the distance between the projection of that point to the plane of the last-formed commissure plane and the hinge axis. The values of z and x were measured on enlarged photographs using a slide caliper and then converted to natural size. The backward rotation angle (φ_{rot}) is finally converted to the revolving angle of the commissure plane (θ_{rv}) measured forward from the earliest shell at a shell length of 5 mm. Conversion from φ_{rot} to φ_{rv} has no biological significance.

6) *Area of the commissure plane.*—Each photographic image of the commissure plane was transmitted to a Macintosh computer using an image scanner, and the projected area of the commissure plane was calculated using the software NIH Image 1.53 (freeware). The projective area was calibrated by the following equation:

$$S=\frac{S'}{\cos\varphi_{rot}}$$

where S is the real area of the commissure plane, S' is the projected area of the commissure plane, and φ_{rot} is the backward rotation angle (Figure 3-C).

7) *Index of secretion rate of the outer part of the fibrous prismatic layer.*—The definition of this parameter has already been mentioned above. This is obtained as:

$$\frac{2S_{inc}}{(l_{igl}1+l_{igl}2)\times l_{ss}}$$

where S_{inc} is the area of the hatched portion in Figure 3-D; $l_{igl}1$ and $l_{igl}2$ are the lengths of two neighboring internal growth lines; and l_{ss} is the increment width on the outer shell surface (see Figure 3-D). S_{inc} was measured using the software NIH Image 1.53 (free ware). $l_{igl}1$, $l_{igl}2$, and l_{ss} were measured, using a slide caliper, on the photograph of the sectioned surface of the shell.

8) *Outline length of the commissure.*—The length of an adhesive tape attached to each major growth ring is defined as the outline length of the commissure. It was measured using a slide caliper.

9) *Degree of plication development.*—As already mentioned, this is defined by the angle between two regression lines before and after the plication appearance in the scatter diagram which represents the relationship between the area of the commissure plane and the outline length of the commissure. These two regression lines were calculated with the reduced major axis method.

Results

Morphology of the commissure plane

In *M. tichanovitchi, M. furanuiensis*, and *M. californianus*, the outline shape of the commissure plane consists of two straight portions (hinge axis and anterior half of ventral margin) and two sharply curved ones (beak area and rounded ventral end). In these species, the commissure plane approximates an elongated ellipse. The major axis of this ellipse is nearly parallel to the hinge axis. Therefore, the sharply pointed area with the largest curvature is located near the hinge axis (Figures 1-1a and -2a, and 4-B, C and F). In the later growth stage of *M. furanuiensis*, the ventral margin is curved and the sharply pointed area moves away from the hinge axis as the shell grows (Figure 1-2a). In *M. galloprovincialis* and *M. grayanus*, the sharply pointed area is much closer to the beak and much more distant from the hinge axis than in *M. tichanovitchi, M. furanuiensis, M. ksakurai* and *M. californianus* (Figures 1-6a, and 4-D, E). However, the curvature of each segment of the commissure of *M. galloprovincialis* and *M. grayanus* is smaller than in *M. tichanovitchi, M. furanuiensis, M. ksakurai*, and *M. californianus* (Figures 4D and E), indicating that the commissure plane in *M. galloprovincialis* and *M. grayanus* approximates to a short, wide ellipse. The outline shape of the commissure plane in *M. ksakurai* is intermediate between *M. galloprovincialis* and *M. tichanovitchi* (Figures 1-3a and 4-A). The sharply pointed area on the commissure plane in *M. ksakurai* is similar to but slightly closer to the beak than in *M. tichanovitchi* (Figure 4-A and B). The curvature of the sharply pointed area in *M. ksakurai* is slightly smaller than in *M. tichanovitchi*, although the range of this area in *M. ksakurai* is wider than in *M. tichanovitchi* (Figure 4-A and B). Therefore, the ellipse of the commissure plane in *M. ksakurai* is shorter and wider than in *M. tichanovitchi* (Figure 5). The outer shape of the commissure plane in *M. tichanovitchi* tends to be markedly elongated along the maximum growth axis, whereas the degree of shell elongation is weak throughout ontogeny in *M. ksakurai* (Figure 5).

Shell convexity

The Miocene mytilids examined exhibit diphasic shell growth (Figures 1 and 6, Table 2). In the juvenile stage, their shells are thin and weakly convex (having high whorl expansion rate) as in most extant mytilids. Juvenile shells of *M. tichanovitchi* and *M. furanuiensis* are more weakly convex than adult shells of extant mytilids and juvenile shells of *M. ksakurai* (Figure 6, Table 2). The juvenile shell form of *M. ksakurai* is as weakly convex as the adult shell forms of *M. galloprovincialis* and *M. grayanus*.

In the Miocene mytilids examined, shell convexity is low in their juvenile stages but begins to increase markedly in mid-ontogeny (Figures 1 and 6). This allometric change in shell convexity causes an unusually inflated shell form in later stage. This allometric change is very similar to "geniculation" in the Late Cretaceous inoceramid *Cremnoceramus* (Crampton, 1996). This allometric change is especially conspicuous in *M. tichanovitchi* and *M. ksakurai*, but it is only weakly developed and not abrupt in *M. furanuiensis* (Figure 1-2). The shell of *M. furanuiensis* is much less convex than those of *M. tichanovitchi* and *M. ksakurai* (Table 2). The shell convexity of *M. tichanovitchi* is similar to that of *M. ksakurai* (Table 2). However, the ontogenetic change of shell convexity is more conspicuous in the former species than in the latter (Table 2). In both species, conspicuous commarginal ribs resembling steps begin to develop soon after the allometric change in shell convexity (Figure 1-1～5).

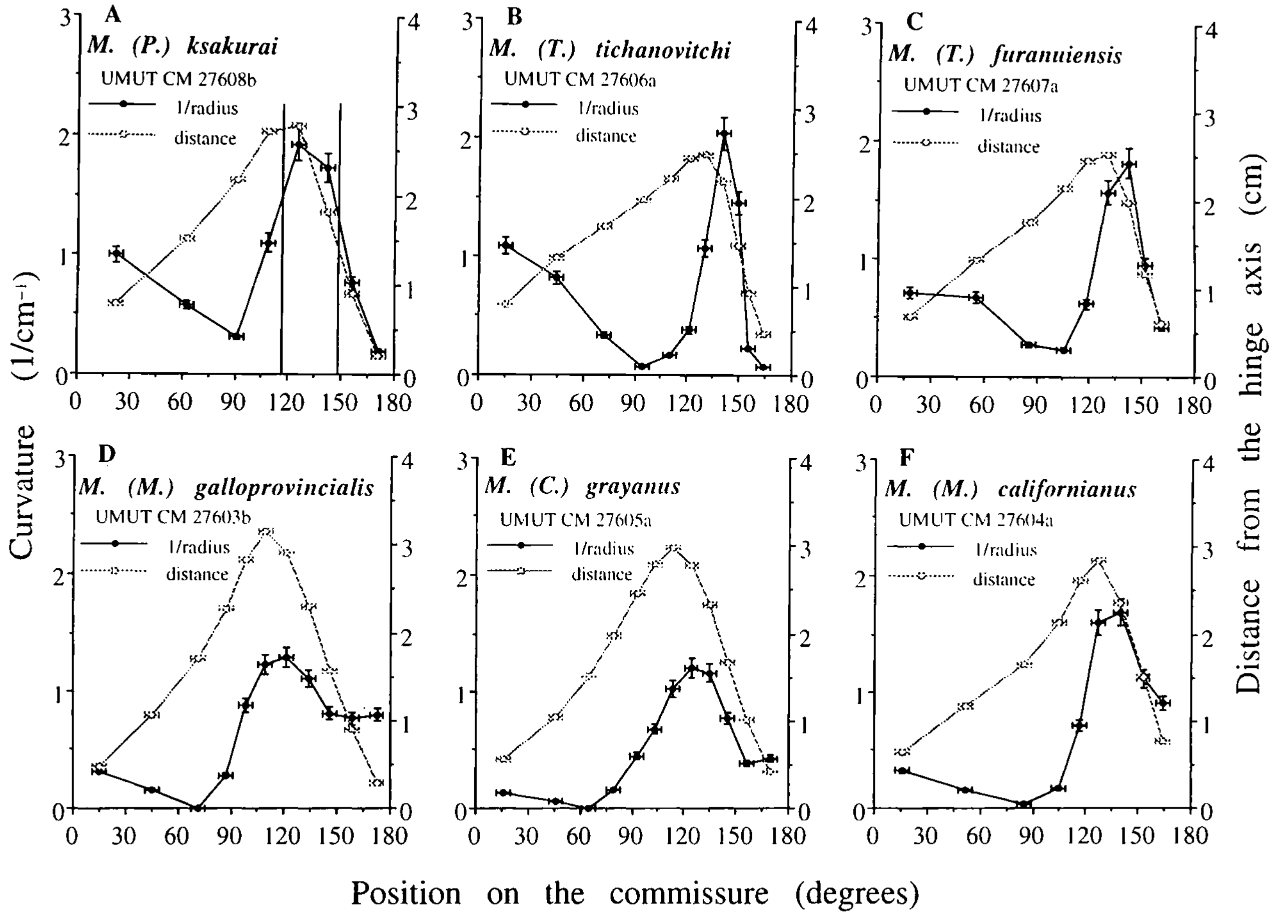


Figure 4. Relationship of the curvature of each segment of the commissure, and of the distance from the hinge axis to the commissure, compared with the position on the commissure in six species of *Mytilus*. The data are based on the measurements of a single specimen for each species. Two vertical lines in the case of *M. ksakurai* (A) represent the area where plications appear (from 117° to 148°).

Mode of shell secretion and expansion

In order to understand the relationship between increasing shell convexity and shell thickness, polished sections of selected specimens were observed under a microscope. In specimens of *M. grayanus* and *M. ksakurai*, each internal growth increment in the outer part of the fibrous prismatic layer is widest on the outer shell surface and narrowest just above the boundary with the inner part of the fibrous prismatic layer (Figure 7). *M. grayanus* does not exhibit any remarkable ontogenetic change in the growth pattern of internal growth increments (Figure 7-A). This is true also for *M. galloprovincialis* and *M. californianus*. In contrast, internal growth lines in *M. tichanovitchi*, *M. furanuiensis*, and *M. ksakurai* all bend toward the inside of the shell as if the pallial line were a fulcrum at the stage of the allometric change in shell convexity (Figure 7-B).

In *M. ksakurai*, the secretion rate of the outer part of the fibrous prismatic layer in the stage before the allometric change in shell convexity is low (index of shell secretion rate about 0.2, Figure 8-B). In this stage, the shell expands ventrally, maintaining low convexity (Figure 6-C). The index increases to 0.35 near the stage of allometric change in shell convexity and attains a maximum (0.55) at the stage of the allometric change (Figure 8-B). After the abrupt change in shell convexity, this index fluctuates between about 0.2 and 0.7 (Figure 8-A). This causes the development of steplike growth rings on the shell of *M. ksakurai* and in all the other Miocene mytilids examined here (Figure 1-1—5). In general, the index of the secretion rate is small in the juvenile stage but increases abruptly soon after the stage of the allometric change in shell convexity (Figure 8). The whorl expansion rate after the stage of the allometric change in shell convexity is much lower than before this allometric change (Figure 6, Table 2). This produces a thick, highly convex shell. In both *M. tichanovitchi* and *M. ksakurai*, the conspicuous ontogenetic change in inclination of microincrements corresponds to the stage of the allometric change in shell convexity. In contrast, in *M. furanuiensis*, the conspicuous change of inclination of microincrements occurs in later growth stage after the allometric change in shell convexity, following the initiation of the step-like commarginal ribs in cross section. Therefore, in this species, the allometric change in shell convexity is not so conspicuous and the shell form becomes markedly elongated and weakly inflated later in ontogeny

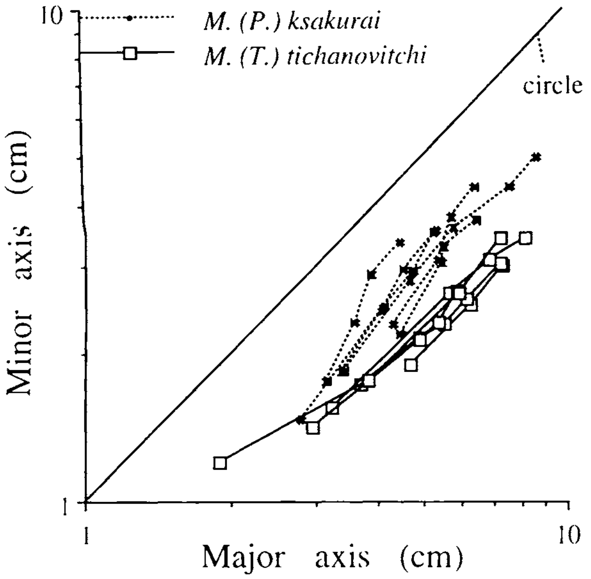


Figure 5. Ontogenetic allometric relationship between major and minor axes of the generating curve for selected specimens of *M. ksakurai* and *M. tichanovitchi*.

Table 2. Average of the slope of the regression line in double scatter diagram of the allometric relationship between the square root of the area of the commissure plane and the total revolving angle of the commissure plane.

species	stage	av	N	SD
M. (*T.*) *tichanovitchi*	juvenile	24.120	7	7.337
	adult	155.532	7	23.133
M. (*T.*) *furanuiensis*	juvenile	18.341	1	
	adult	101.838	4	42.570
M. (*P.*) *ksakurai*	juvenile	56.437	7	18.154
(Katsura River)	adult	114.987	7	35.927
M. (*P.*) *ksakurai*	juvenile	38.480	7	18.480
(Kishimatsu-River)	adult	157.530	9	49.623
M. (*C.*) *grayanus*		49.525	6	13.223
M. (*M.*) *galloprovincialis*		45.285	6	3.526
M. (*M.*) *californianus*		72.501	3	17.803

av : average of slope, N : number of specimens,
SD : standard deviation

(Figure 1-2).

Plication morphology

In *M. ksakurai*, the stage of the allometric change in shell convexity corresponds with the abrupt appearance of plications (Figure 1-3, -4, and -5). Large samples from localities in the Katsura and Kishimatsu-zawa Rivers show remarkable individual variation in the number of plications, and the pattern of undulations in the commissure is not uniform among specimens with the same number of plications (Figure 2). In general, the variation in the number of plications is regarded as a discrete distribution, because the number of plications is not a decimal but an integer. However, in view of the degree of plication development, plications show continuous variation (Figure 9). Therefore, continuous variation in excessive expansion of the mantle edge appears as discrete variation in the number and pattern of plications. In spite of the wide variation in their number, pattern, and degree of development, plications in *M. ksakurai* begin to appear in a restricted area on the commissure at the stage just before the allometric change in shell convexity (between 110° and 150° in the angle measured from the standardized point P in Figure 3-B ; see Figure 1-3a, -4a, and -5a). The index of shell secretion rate at a given shell size is measured in the portion of ridge and sulcus. In both portions, this index fluctuates between about 0.2 and 0.7 (Figure 8-A). The range of the fluctuation of this index in the portion of the ridge does not differ clearly from that in the portion of the sulcus. Therefore, it can be said that the index of shell secretion rate at a given shell size does not differ between ridge and sulcus (Figure 8-A).

Discussion

Several explanations have been proposed for the formation of patterns of radial and spiral sculpture in molluscs. Cox *et al.* (1969) and Hayami (1974) speculated that radial costae and striae in bivalves result from the enhanced secretion of calcium carbonate by groups of cells perpendicular to the mantle margin. According to their hypothesis, the shell sculpture would consist of thick ridges and relatively thin furrows. However, in the examined specimens of *M. ksakurai*, no significant difference in the index of the shell secretion rate occurs between ridge and sulcus (Figure 8A). This suggests the absence of perpendicular cells along the mantle margin.

Seilacher (1985) suggested that the divergent plications of ostreids, malleids, and anomiids are produced by excessive tangential growth of the mantle edge. The existence of divergent plications on the shell implies an excess of mantle in relation to shell edge. However, the plication of *M. ksakurai* is distinguished from that of ostreids and malleids by its association with allometric changes in shell convexity and a subsequent abrupt shell thickening (Figures 1-3, -4, and -5, and 7-B). In *M. ksakurai*, the development of plication is restricted to part of the shell margin (between 110° and 150° in the angle measured from the standardized point P in Figure 3-A, Figure 1-3a, -4a, and -5a), whereas in ostreids, malleids, and anomiids, plications are developed over the whole shell surface (Figure 1-7). Moreover, in extant Bivalvia, a relative increase of shell convexity is, in most cases, caused by a reduction in the mantle proliferation rate (Seed, 1968 ; 1980 ; Vermeij, 1990). Therefore, the mantle proliferation rate of *M. ksakurai* presumably decreased after the allometric change in shell convexity. In this species, excessive tangential growth of the mantle edge might not have occurred when plications appeared.

To generate the excess of mantle margin relative to the shell edge without acceleration of mantle proliferation, the space in which the mantle can be accommodated must be reduced. Internal growth lines conspicuously turn inward after the allometric change in shell convexity. This suggests a bending of the distal part of the mantle (Figure 7-B). If a curved surface or a plane with a curved perimeter is bent inward along its edge, the distal part of that plane surface

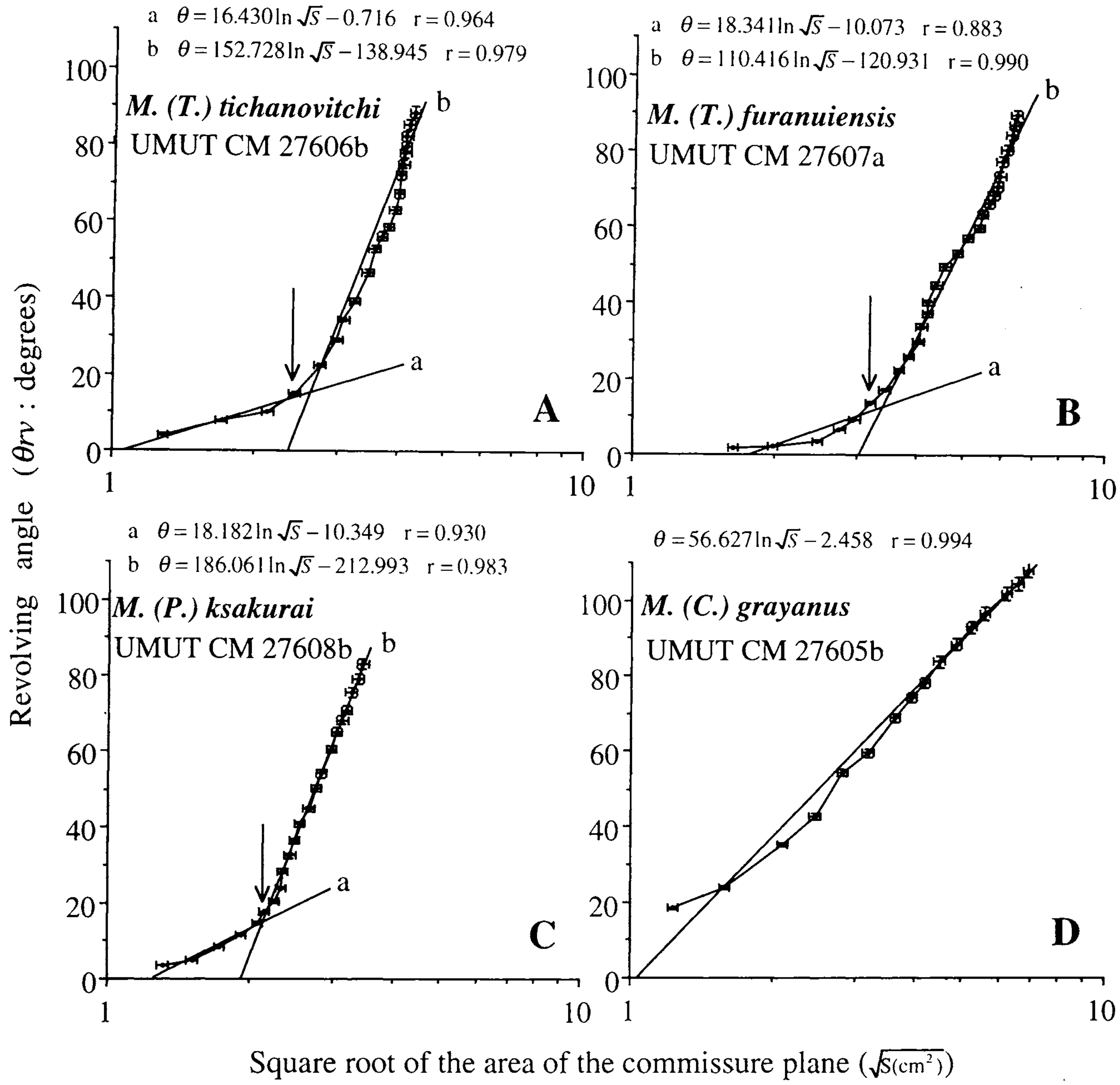


Figure 6. Ontogenetic allometric relationship between the area of the commissure plane and the revolving angle of the commissure plane in three Miocene mytilids (**A**-**C**) and one extant one (**D**). Each graph is based on a single specimen. Arrows in A-C point to the stage of the allometric change in shell convexity. Regression lines a and b were calculated by the least squares method.

must be deformed and wrinkled, because this portion, including the edge, is compressed into a narrower space. This leads to the prediction that the mantle edge will be deformed and wrinkled when the distal part of the mantle is bent. This type of plication is analogous to the wrinkles of the skirt of a tablecloth (Figure 10), so this model is called here "the tablecloth wrinkle model". This explanation has already been applied to plate tectonics under the name spherical shell tectonics (Bayly, 1982 ; Yamaoka, 1984, 1988). In the case of tablecloth wrinkles, the bending force is gravity. In the case of the mantle of *M. ksakurai*, it is inferred to be the adhesive force of the mantle to the inner shell surface. The changed direction of this force would result from abrupt shell thickening, due to a rapid increase in the rate of shell precipitation relative to the whorl expansion rate (Figures 7-B and 8-B).

In the case of a bivalve mantle, space reduction derived from mantle bending is greatest when 1) the mantle bending angle is large, or 2) the curvature of the margin of the commissure is large, or 3) the distance of the area of bending from the mantle edge (the distance from the mantle edge to the pallial line) is large (Yoshida, 1996). The mantle

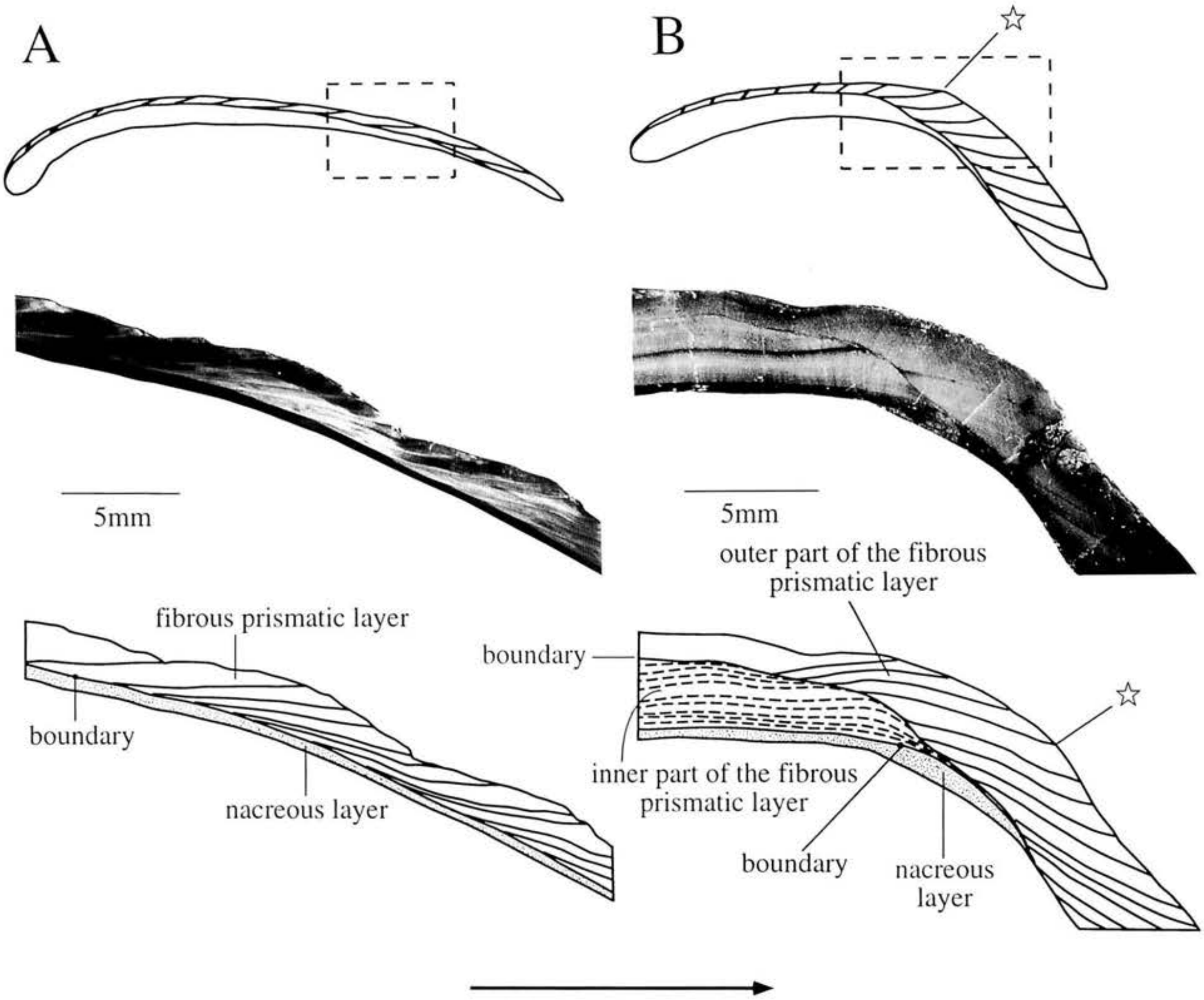


Figure 7. Photomicrographs and sketches of the middle shell portion cut along the maximum growth axis of *M. grayanus* (A : UMUT RM 27605c) and *M. ksakurai* (B) UMUT CM 27608c). The stars in B indicate the stage of the allometric change in shell convexity.

bending angle is large where there is a high shell secretion rate, because here shell thickness is large, and the mantle has to be bent inward at a large angle to adhere to the inner shell surface. In most bivalves, the shell secretion rate has to be in proportion to the distance from the hinge axis, because they could not otherwise close their shell completely. Therefore, the mantle bending angle is in proportion to the distance from the hinge axis. The condition 1) can also be expressed in the words, "when the distance from the hinge axis is large".

As already noted, plications do not appear in *M. furanuiensis* and the three extant mytilids examined. In these species, mantle bending may not occur because of the absence of a conspicuous allometric change in shell convexity. In *M. ksakurai*, plications appear in the area between the point most distant from the hinge axis and the point having the largest curvature (between 110° and 150° in rotation angle measured from the standardized point P) (see Figures 3-A and 4-A). Following the tablecloth wrinkle model, the mantle is pushed into a narrower space here than elsewhere. This model may explain the remarkable variation in the degree of plication in *M. ksakurai* (Figure 9), since it is determined mainly by the shape of the commissure plane and the degree of mantle bending, which may vary independently of one another. This model may also be applied to the nature of the variation of plication in *M. ksakurai*. Following this model, the pattern of plication is determined by the excess of mantle via the nonlinear process of buckling of the mantle. The excess of mantle derived from mantle bending may have a continuous variation. Therefore, in *M. ksakurai*, the degree of plication exhibits a continuous variation, although the pattern of plication has a descrete variation.

Under this model, growth of *M. tichanovitchi* should have involved a higher degree of space reduction than in *M. ksakurai*, in view of its more conspicuous allometric change in shell convexity (Figures 1 and 6, Table 2) and larger curvature of the ventral margin of the commissure (Figure 4).

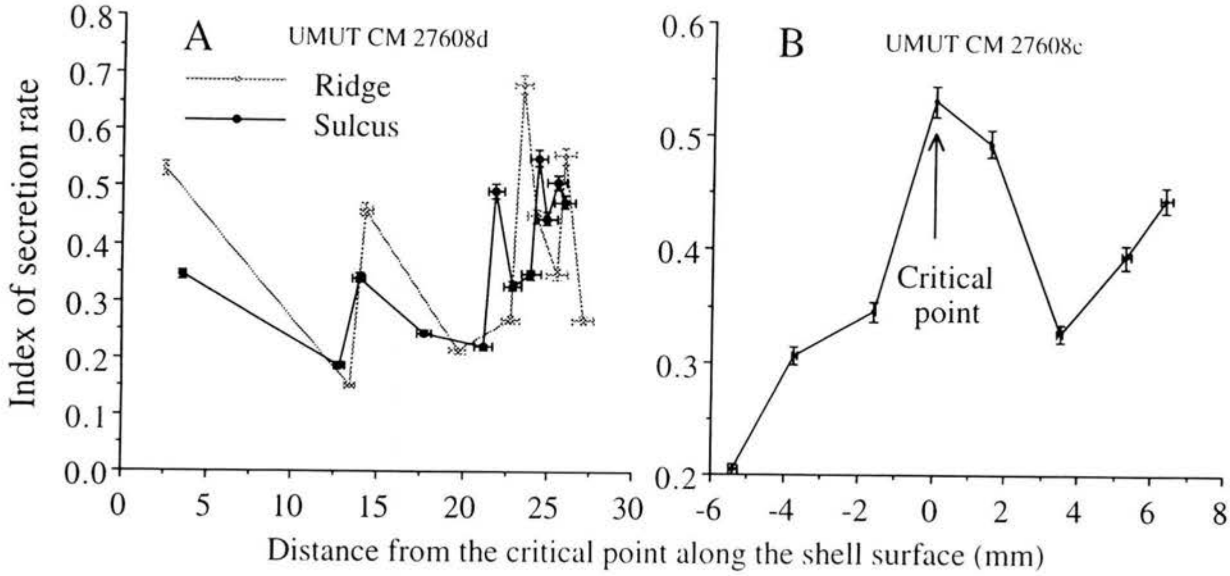


Figure 8. Index of shell secretion rate of the outer part of the fibrous prismatic layer in two specimens of *M. ksakurai*. **A**: Comparison between ridge and sulcus. UMUT CM 20608d from the lower Miocene in the Katsura River. **B**: Change of the index of secretion rate around the allometric critical point. UMUT CM 20608c (same specimen as shown in Figure 7B).

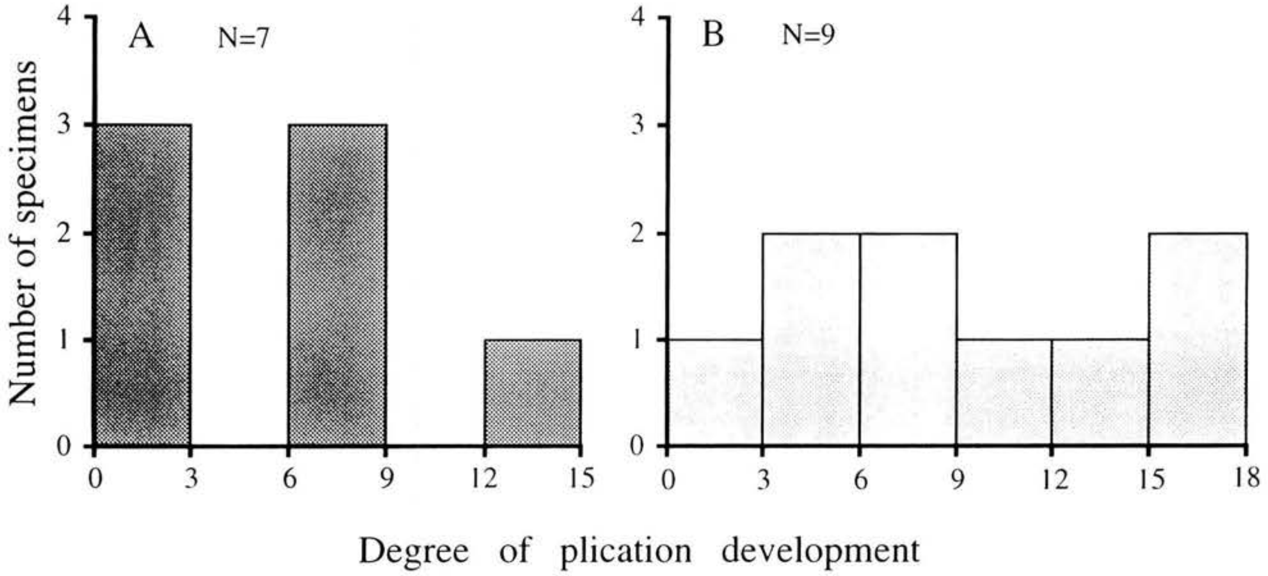


Figure 9. Variation of the degree of plication development in the samples of *M. ksakurai* from the localities in the Katsura (**A**) and Kishimatsu-zawa (**B**) Rivers. The variations of the two samples overlap each other.

In Yamaoka's (1984) experiments on transformation of a cylindrical elastic body, wrinkles with a large wave length are stable under a high degree of space reduction. A similar phenomenon appears to occur in the bending of the elastic bivalve mantle. In *M. tichanovitchi*, with a high degree of space reduction, a single large wrinkle (indicated by the bold line in Figure 11-A) is more stable than several small wrinkles (indicated by the dotted line in Figure 11-A). This produces a new force indicated by the arrow in Figure 11. The vector of this force is oriented obliquely to the commissure plane and roughly parallel to the hinge axis (see Figure 11B). The vector has components parallel to and perpendicular to the commissure plane. The perpendicular component of this vector makes the shell shape of *M. tichanovitchi* highly convex (Figure 1-1b, Figure 6, Table 2), whereas the parallel one makes it elongated and straight (Figures 1-1a, and 4, and 5). Therefore, the narrowly rounded posteroventral margin of *M. tichanovitchi* itself may represent a single large plication under the condition of a very high degree of space reduction.

The subgenus *M.* (*Plicatomytilus*) has been distinguished from other mytilid subgenera by differences in the patterns of retractor muscle scars (Allison and Addicott, 1976). How-

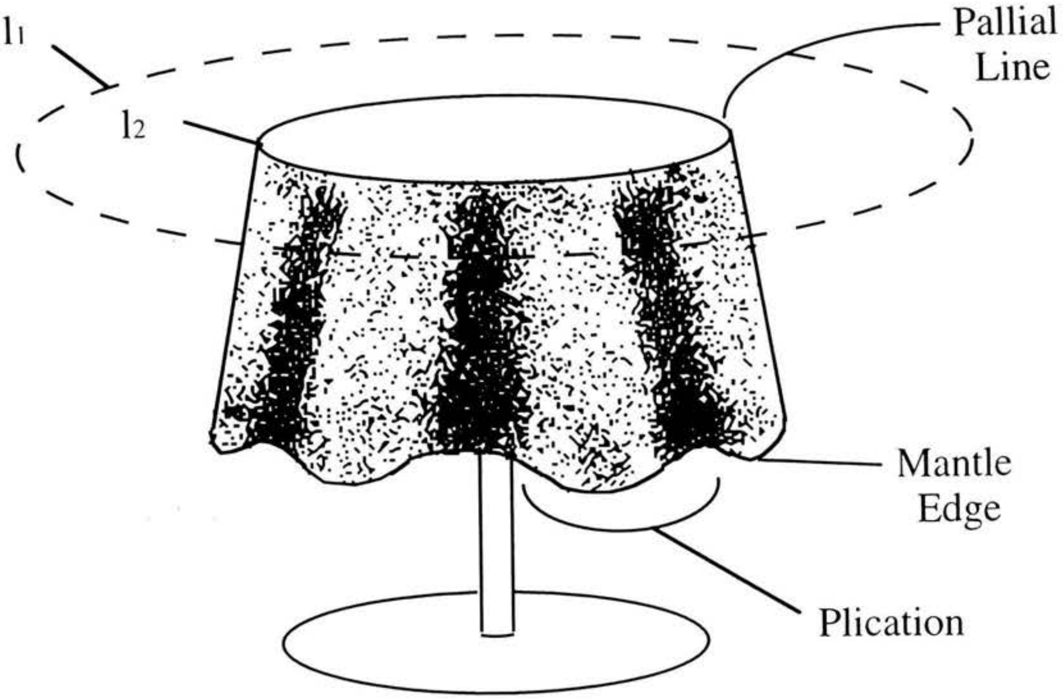


Figure 10. Schematic figure showing tablecloth bending. The tablecloth is bent by gravity along the table-edge. The larger circumference l_1 is pushed into the smaller circumference l_2, and as a result, the table cloth edge is transformed to a wrinkled state.

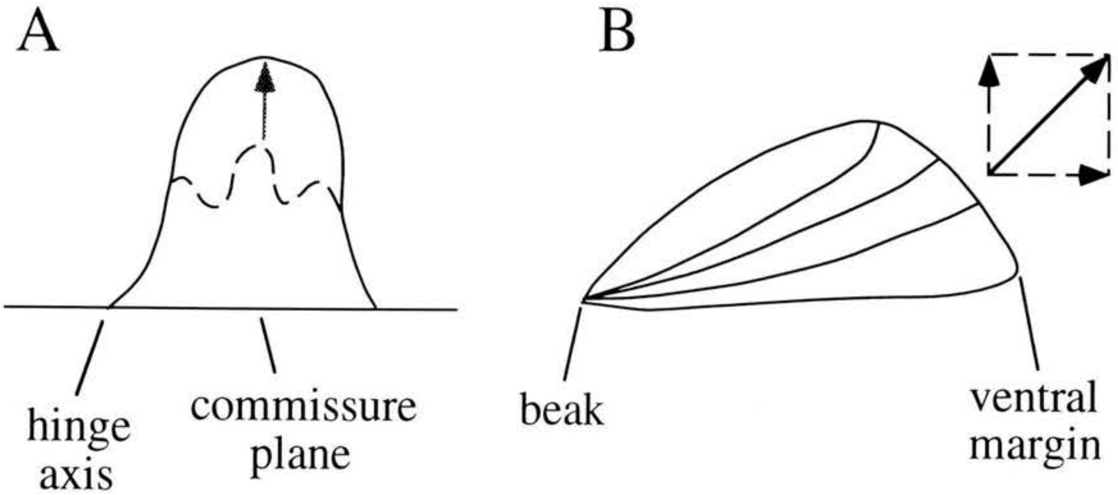


Figure 11. Schematic diagrams showing the effect of mantle bending in *M. tichanovitchi*. The solid arrows represent directions of force under the condition that a large single wrinkle is stable. The diagram **A** shows a posterior view of the valve. The vector represents the new force that occurs when the mantle shape undergoes a transition from the unstable several wrinkle state to the more stable single wrinkle state via the buckling process. As shown in **B**, this vector is divided into two directions that are parallel and perpendicular to the commissure plane (B).

ever, Noda and Hoyanagi (1993) suggested that *M.* (*Plicatomytilus*) is closely related to *M.* (*Tumidimytilus*) in the shape of its anterior byssal retractor muscle scars. If this is correct, the marked morphological discontinuity between the plicated form (*M.* (*Plicatomytilus*)) and nonplicated form (*M.* (*Tumidimytilus*)) appears to have originated from a slight change of geometric parameters during ontogeny.

As already mentioned, Seilacher (1985) pointed out that divergent plication in bivalves can be achieved by excessive tangential growth of the mantle margin. However, the tablecloth wrinkle model suggests that in *M. ksakurai*, the excess mantle margin arose from a reduction in space resulting from mantle bending. McGhee (1978) investigated a hypothetical shell growth model and said that changes in whorl expansion rate and increment magnitude along the shell margin should produce irregularity along the commissure margin. In the case of *M. ksakurai*, the irregularity along the commissure margin was produced as a result of the collapse of the equilibrium between the whorl expansion rate and the shell secretion rate.

This study shows that the development and wide variation of plication in the shell of *M. ksakurai* are constrained mainly by an architectural factor (Bautechnischer Aspekt: Seilacher 1970; structural factor: Raup, 1972; "Can the machine be built?": Thomas, 1979; fabricational factor: Seilacher, 1991) derived from mantle bending. The bivalve shell is built as if by stacking of layers in the revolving commissure plane (Lison 1949; Raup and Michelson, 1965; Bayer 1978). Likewise, plication in *M. ksakurai* is created by stacking of layers in a distorted commissure plane.

It is important in constructing theoretical models of morphology to conceive of hard tissue construction in relation to mantle behavior (Savazzi, 1995). This paper proposes a plausible geometric model for plication formation in *Mytilus* (*Plicatomytilus*), without discussing physical properties of the mantle such as elasticity or viscosity. Study of these properties of the mantle during the growth of living bivalves will provide a reliable biophysical basis on which to consider the morphogenesis of molluscan hard tissues.

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Two Permian lyttoniid brachiopods from Akasaka, central Japan

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Abstract. Two lyttoniid brachiopod species, *Coscinophora magnifica* Cooper and Grant, 1974 and *Leptodus nobilis* (Waagen, 1883) are described from the Middle and Upper Permian limestones in the Akasaka district, Mino Belt, central Japan. The Permian brachiopod fauna of Akasaka is characterized by a mixture of both Tethyan and North American elements. The fauna is considered to have occupied a mid-equatorial region of the Panthalassa Ocean in Permian time.

Key words: Akasaka, brachiopods, central Japan, *Coscinophora magnifica, Leptodus nobilis*, Mino Belt, Permian

Introduction

The Akasaka district, northwest of Ogaki City in the Gifu Prefecture is a famous, classical area for the Japanese Permian. The Permian marine invertebrate fossils of the Akasaka Limestone in this district have been studied by many authors since the pioneering works of Schwager (1883), Gottsche (1884) and Ozawa (1927). Brachiopods from the Akasaka Limestone were studied by Sato (1919), Ozawa (1927) and Hayasaka (1925, 1932), and ten species were described or listed: *Lyttonia richthofeni* Keyser (Sato, 1919; Hayasaka, 1925; Ozawa, 1927), *Enteletes akasakensis* Ozawa (Ozawa, 1927; Hayasaka, 1932), *Scacchinella* cf. *gigantea* Gemmellaro (Hayasaka, 1925, 1932), *Reticularia lineata* Martin, *R. waageni* Loczy, *R.* cf. *inaequilateralis* Gemmellaro, *Terebratuloidea*? sp. (Hayasaka, 1925), *Enteretes minoensis* Hayasaka, *E. suessi* Schellwien and *Geyerella* sp. (Hayasaka, 1932). Recently a lyttoniid species *Coscinophora magnifica* Cooper and Grant, from its lower part (*Parafusulina* Zone), was described and added to the list by Tazawa (1997b).

In this paper two lyttoniids from the Akasaka Limestone, *Coscinophora magnifica* Cooper and Grant, 1974 from its lower part (*Parafusulina* Zone) at Locality 1, Kinshozan, and *Leptodus nobilis* (Waagen, 1883) from its uppermost part (*Codonofusiella-Reichelina* Zone) at Locality 2, Hanaoka-yama, are described, and their palaeobiogeography is discussed. The fossil localities are shown on Figure 1. The first author (J.T.) is responsible for the systematic descriptions and discussion of Permian brachiopod palaeobiogeography, and the second and third authors (T.O. and M.H.) are responsible for field geology and collecting the specimens. All the specimens described here are stored in the Department of Geology, Faculty of Science, Niigata University.

Distribution of *Coscinophora* and *Leptodus*

The distribution of the genus *Coscinophora* is restricted stratigraphically and geographically. It has been described from only two regions, the Lower Permian (Wolfcampian) and Middle Permian (Leonardian) of west Texas, U.S.A. and the Middle Permian (*Parafusulina* Zone) of Akasaka, central Japan. *Coscinophora magnifica* Cooper and Grant has been known from the Middle Permian (Road Canyon Formation) of west Texas and the Middle Permian (lower part of the Akasaka Limestone) of Akasaka, central Japan (Sato, 1919; Hayasaka, 1925, 1932; Cooper and Grant, 1974; Tazawa, 1997b, this paper).

On the other hand, the genus *Leptodus* is widely distributed in the Lower to Upper Permian of the Tethyan and its neighboring regions. *Leptodus nobilis* (Waagen) is known from the Middle and Upper Permian of Hungary (Schréter, 1963), Croatia (Sremac, 1986), Serbia (Simic, 1933), Transcaucasia (Licharew, 1932; Sarytcheva, 1964; Ruzhentsev and Sarytcheva, 1965; Kotljar in Kotljar and Zakharov, 1989), Salt Range (Waagen, 1883; Noetling, 1904, 1905; Frech, 1911; Fredericks, 1916; Cooper and Grant, 1974) and Khisor Range (Grant, 1976) in Pakistan, Kumaon Himalayas (Diener, 1897), Kashmir (Diener, 1915), Cambodia (Mansuy, 1913, 1914; Termier and Termier, 1960; Chi-Thuan, 1961), Laos (Mansuy, 1912), Timor (Hamlet, 1928; Wanner and Sieverts, 1935), Port Keats in northern Australia (Thomas, 1957), Tibet (Zhan and

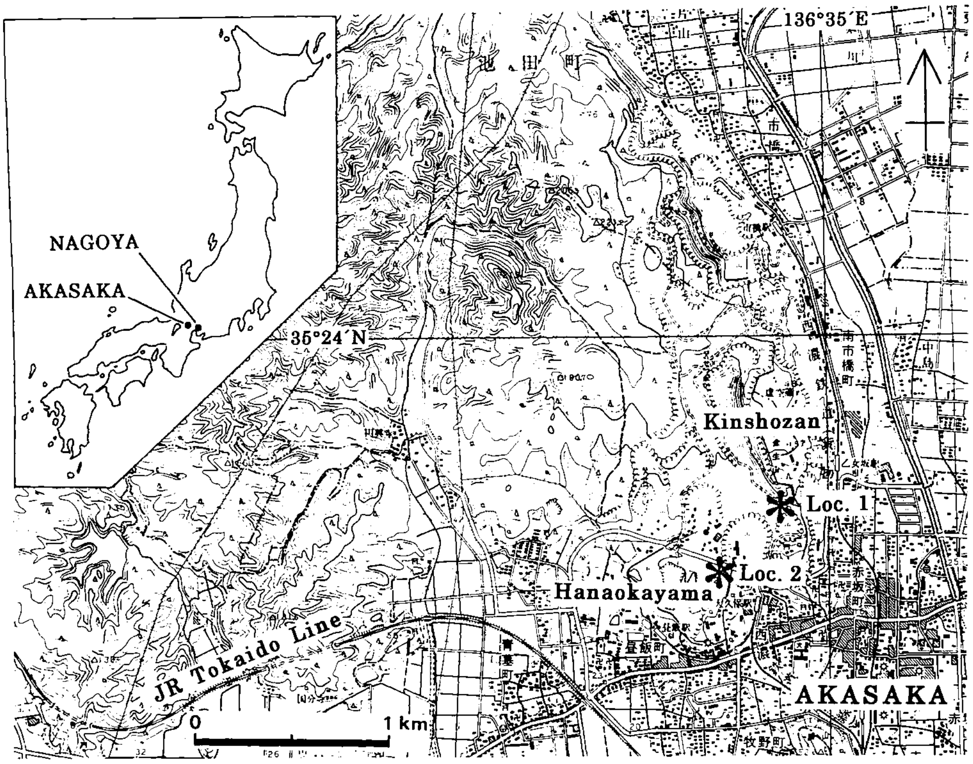

Figure 1. Map showing the fossil localities (using the topographical map of "Ogaki" scale 1 : 25,000 published by Geographical Survey of Japan).

Wu, 1982), Yunnan (Fang and Fan, 1994), Sichuan (Hayasaka, 1917, 1922b ; Huang, 1932), Guizhou (Hayasaka, 1917, 1922b ; Huang, 1932 ; Feng and Jiang, 1978), Guangxi (Huang, 1936 ; Yang *et al.*, 1977), Guangdong (Yang *et al.*, 1977 ; Zhan, 1979), Hunan (Yang *et al.*, 1977 ; Liao and Meng, 1986) and Hubei (Yang *et al.*, 1977 ; Yang, 1984) in South China, Jiangxi (Hayasaka, 1922b), Fujian (Wang *et al.*, 1982 ; Zhu, 1990) and Zhejiang (Liang, 1990) in East China, Gansu (Zhang *et al.*, 1983) and Qinghai (Jin *et al.*, 1979) in Northwest China, Inner Mongolia(Grabau, 1931 ; Lee and Gu, 1976 ; Lee *et al.*, 1980 ; Duan and Li, 1985 ; Gu and Zhu, 1985), Heilongjiang (Lee *et al.*, 1980) and Jilin (Lee *et al.*, 1980) in Northeast China, South Primorye in eastern Russia (Licharew and Kotljar, 1978), South Kitakami Belt (Yabe, 1900 ; Hayasaka, 1917, 1922a ; Tazawa, 1976, 1987 ; Minato *et al.*, 1979), Hida Gaien Belt (Tazawa, 1987 ; Tazawa and Matsumoto, 1998), Maizuru Belt (Mashiko, 1934 ; Shimizu, 1961) and Mino Belt (this paper) in Japan.

Permian reconstruction of the Akasaka Limestone

From the above data, it is clear that the genus *Leptodus* is a Tethyan element and the genus *Coscinophora* is a North American element, and the Permian brachiopod fauna of the Akasaka Limestone is a mix of Tethyan and North American elements.

The Akasaka Limestone is one of the limestone-greenstone blocks in the Jurassic melange of the Mino Belt in central Japan. The limestone-greenstone blocks are considered to have originated from reef-seamount complexes formed at the equatorial region of the Panthalassa Ocean in Permian time on the basis of palaeomagnetic (Hattori and Hirooka, 1977, 1979), sedimentological (Sano, 1988 ; Sano and Kanmera, 1996) and palaeontological data (Ishii *et al.*, 1985 ; Ozawa, 1987 ; Tazawa, 1991, 1992). However, none of these authors gave their opinion about the palaeolongitude of the Permian reef-sea mount complexes.

Tazawa (1997a, b) and Tazawa and Shen (1997) previously mentioned that these limestone-greenstone blocks were formed at the mid-equatorial region of Permian Panthalassa based on palaeobiogeographical studies of brachiopod faunas of the Hiyomo and Akasaka districts, Mino Belt. The occurrence of a typical Tethyan-type genus *Leptodus* together with a North American-type genus *Coscinophora* from the Akasaka Limestone strongly supports the above opinion.

Systematic descriptions

Order Productida Waagen, 1883
Suborder Strophalosiidina Waagen, 1883
Superfamily Lyttonioidea Waagen, 1883
Family Lyttoniidae Waagen, 1883
Subfamily Lyttoniinae Waagen, 1883
Genus ***Coscinophora*** Cooper and Stehli, 1955

Type species.—*Coscinophora nodosa* Cooper and Stehli, 1955

Coscinophora magnifica Cooper and Grant, 1974

Figures 2-3—5, 3

Coscinophora magnifica Cooper and Grant, 1974, p. 454, pl. 182, figs. 35, 36 ; pl. 184, figs. 1-8 ; pl. 185, figs. 1-17 ; pl. 186, figs. 1-13 ; pl. 187, figs. 1-11 ; pl. 188, figs. 15-22, 24 ; Tazawa, 1997b, p. 447, figs. 2-1—3.

Lyttonia richthofeni (Kayser). Sato, 1919, p. 276, text-fig. ; Hayasaka, 1932, p. 1.

Lyttonia sp. Hayasaka, 1925, p. 143, text-fig.

Material.—Three specimens, NU-B110-112, from the lower part (*Parafusulina* Zone) of the Akasaka Limestone at Locality 1, Kinshozan, Akasaka.

Description.—Shell large for genus, transversely subelliptical in outline ; length 56 mm, width 65 mm in the largest specimen (NU-B111). Pedicle valve slightly convex in lateral and anterior profiles except anterolateral margins which form steep slopes.

Pedicle valve interior with a median ridge and at least 12 lateral ridges, both of them consisting of a row of small beads. Lateral ridges rather regularly and symmetrically arranged on both sides of median ridge, nearly straight but slightly arched facing convexity towards front. Number and size of beads are obscure in the present material.

Brachial valve interior partly preserved in one specimen (NU-B110). Lateral lobes rather regularly and symmetrically arranged anteriorly on both sides of median lobe, but irregularly developed posteriorly. Each lateral lobe with a row of small, subrectangular holes, numbering 4 holes per 10 mm (Figure 3). Other internal structures not observed.

Remarks.—The present specimens are assigned to the genus *Coscinophora* on the basis of their pedicle valve moniliseptate, median and lateral ridges consisting of a row of beads, and their brachial valve median and lateral lobes consisting of a row of holes. These specimens are referred to *Coscinophora magnifica* Cooper and Grant, 1974, from the Road Canyon Formation of the Glass Mountains, west Texas, on account of the comparable size and shape of shell, and size and number of holes on the lateral lobes of the brachial valve.

The lyttoniid brachiopods collected from the lower part (Kasumi Zone of Wakimizu, 1902) of the Akasaka Limestone and reported as *Lyttonia richthofeni* (Kayser, 1883) (Sato, 1919, p. 276 ; Hayasaka, 1932, p. 1) and *Lyttonia* sp. (Hayasaka, 1925, p. 143) may be conspecific with the present species.

Genus ***Leptodus*** Kayser, 1883

Type species.—*Leptodus richthofeni* Kayser, 1883

Leptodus nobilis (Waagen, 1883)

Figures 2-1, 2-2, 4

Lyttonia nobilis Waagen, 1883, p. 398, pl. 29, figs. 1-3 ; pl. 30, figs. 1, 2, 5, 6, 8, 10, 11 ; Diener, 1897, p. 37, pl. 1, figs. 5-7 ;

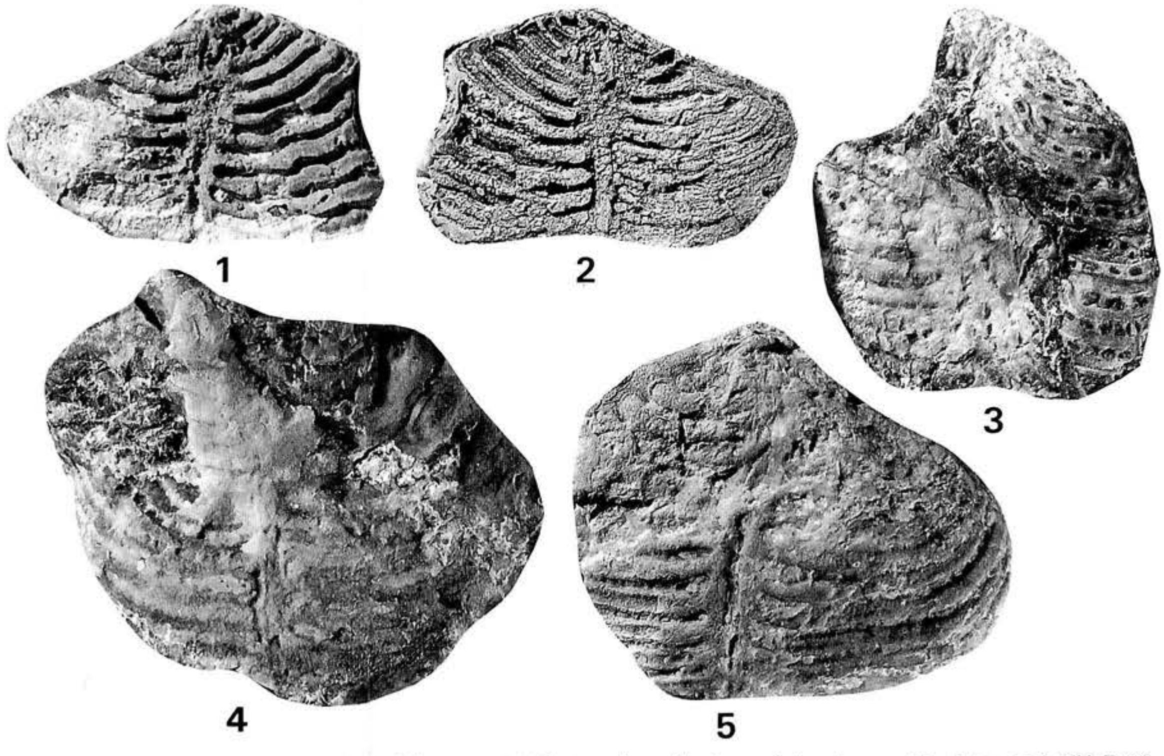

Figure 2. 1, 2. *Leptodus nobilis* (Waagen, 1883). Internal mould of a pedicle valve and the latex cast, NU-B128. **3-5.** *Coscinophora magnifica* Cooper and Grant, 1974. Internal moulds of three pedicle valves, 3 : NU-B110 ; 4 : NU-B111 ; 5 : NU-B112. (All figures are natural size)

Figure 3. A part of the brachial valve of *Coscinophora magnifica* Cooper and Grant, 1974, showing details of the lateral lobes, NU-B110. (×3)

Noetling, 1904, p. 112, text-figs. 4-7; Noetling, 1905, p. 140, pl. 17, figs. 1, 2; pl. 18, figs. 1-11, text-fig. 2; Mansuy, 1913, p. 123, pl. 13, fig. 10; Mansuy, 1914, p. 32, pl. 6, figs. 7a-d; pl. 7, figs. 1a-e; Diener, 1915, p. 99, pl. 10, fig. 15; Grabau, 1931, p. 285, pl. 28, figs. 4, 5 only; Huang, 1932, p. 89, pl. 7, figs. 9, 10; pl. 8, figs. 8, 9; pl. 9, figs. 1-8, text-figs. 8-11; Simic, 1933, p. 49, pl. 4, fig. 1.

Lyttonia tenuis Waagen, 1883, p. 401, pl. 30, figs. 3, 4, 7, 9.

Lyttonia sp. Yabe, 1900, p. 2, text-figs. 1, 2.

Lyttonia cf. *tenuis* Waagen. Mansuy, 1912, p. 19, pl. 4, fig. 4; pl. 5, figs. 1a-e; Huang, 1936, p. 493, pl. 1, fig. 6.

Oldhamina (*Lyttonia*) *richthofeni* var. *nobilis* Waagen. Fredericks, 1916, p. 76, pl. 4, fig. 2, text-fig. 22.

Lyttonia richthofeni (Kayser). Frech, 1911, p. 135, pl. 20, figs. 2a, b only; Hayasaka, 1917, p. 43, pl. 18, figs. 1-8; Hayasaka, 1922a, p. 62, pl. 11, figs. 1-6; Hayasaka, 1922b, p. 103, pl. 4, figs. 12, 13; Licharew, 1932, p. 56, 86, pl. 1, figs. 1-16; pl. 2, figs. 1, 2, 5, 7, 10, 12; pl. 3, figs. 2-7; pl. 4, figs. 1-17; pl. 5, figs. 1-4, 6; Mashiko, 1934, p. 182, text-fig.

Lyttonia (*Leptodus*) *richthofeni* Kayser. Hamlet, 1928, p. 31, pl. 6, figs. 1-4.

Lyttonia richthofeni forma *nobilis* Waagen. Licharew, 1932, p. 69, 96, pl. 2, figs. 13, 14; pl. 5, figs. 1-4, 6, text-fig. 3.

Leptodus nobilis (Waagen). Wanner and Sieverts, 1935, p. 249, pl. 9, figs. 27, 28, text-figs. 16-18; Termier and Termier, 1960, p. 241, text-pl. 3, figs. 1-10; Chi-Thuan, 1961, p. 274, pl. 1, figs. 1a, b; Schréter, 1963, p. 107, pl. 3, figs. 5-8; Sarytcheva, 1964, p. 65, pl. 7, figs. 5-8, text-fig. 1; Ruzhentsev and Sarytcheva, 1965, pl. 39, figs. 6-8; Cooper and Grant, 1974, pl. 191, figs. 8, 9; Grant, 1976, pl. 43, figs. 18, 19; Lee and Gu, 1976, p. 267, pl. 162, figs. 1, 2; Tazawa, 1976, pl. 2, fig. 8; Yang *et al*., 1977, p. 371, pl. 147, fig. 5; Feng and Jiang, 1978, p. 269, pl. 100, fig. 2; Licharew and Kotljar, 1978, pl. 14, figs. 13-15; Jin *et al*., 1979, p. 82, pl. 23, fig. 15; Minato *et al*., 1979, pl. 66, figs. 1, 4, 5: Zhan, 1979, p. 93, pl. 9, fig. 12; Lee *et al*., 1980, p. 389, pl. 172, figs. 15, 16; Wang *et al*., 1982, p. 229, pl. 95, fig. 20; Zhan and Wu, 1982, pl. 4, fig. 4; Zhang *et al*., 1983, p. 297, pl. 102, figs. 7, 8; Yang, 1984, p. 226, pl. 35, fig. 12; Gu and Zhu, 1985, pl. 1, figs. 31, 33, 34; Liao and Meng, 1986, p. 81, pl. 2, figs. 24, 25; Sremac, 1986, p. 30, pl. 10, figs. 1-2; Tazawa, 1987, fig. 1-11; Kotljar in Kotljar and Zakharov, 1989, pl. 20, fig. 6; pl. 23, fig. 12; Liang, 1990, p. 225, pl. 40, figs. 1, 5; Fang and Fan, 1994, p. 83, pl. 23, figs. 1-3; pl. 30, fig. 5; Tazawa and Matsumoto, 1998, p. 7, pl. 2, figs. 7-12.

Lyttonia cf. *nobilis* Waagen. Huang, 1936, p. 493, pl. 1, fig. 5.

Leptodus cf. *nobilis* (Waagen). Thomas, 1957, p. 177, pl. 20, figs. 1-6.

Leptodus richthofeni Kayser. Shimizu, 1961, pl. 18, figs. 14, 15; Schréter, 1963, p. 106, pl. 3, fig. 4; Sarytcheva, 1964, p. 65, pl. 7, figs. 2-4; Yang *et al*., 1977, p. 372, pl. 147, fig. 10; Yang, 1984, p. 226, pl. 35, fig. 11; Duan and Li, 1985, p. 119, pl. 35, figs. 17-19.

Leptodus ivanovi Fredericks. Minato *et al*., 1979, pl. 66, fig. 3.

Leptodus sp. Minato *et al*., 1979, pl. 66, fig. 2.

Leptodus tenuis (Waagen). Duan and Li, 1985, p. 119, pl. 35, figs. 14-16; Liang, 1990, p. 226, pl. 40, fig. 9; Zhu, 1990, p. 79, pl. 18, figs. 19-21; Fang and Fan, 1994, p. 83, pl. 23, figs. 4-5; pl. 30, fig. 6.

Leptodus sp. Tazawa, 1987, fig. 1-10.

Material.—One specimen, NU-B128, from the uppermost part (*Codonofusiella-Reichelina* Zone) of the Akasaka Limestone at Locality 2, Hanaokayama, Akasaka.

Description.—Shell medium to small for genus, transversely subtrigonal in outline, with flattened pedicle valve, having greatest width near anterior margin; length 31 mm, width 53 mm.

Pedicle valve interior with regularly and symmetrically arranged lateral septa on both sides of median septum. Median septum extended for whole length of pedicle valve with blunt, rounded edge. Lateral septa rounded, solid (Figure 4), nearly straight, but slightly arched toward front, numbering 11 in the pedicle valve. Other internal structures not observed.

Remarks.—This specimen is safely assigned to the genus *Leptodus* by its rounded and solid (solidiseptate) lateral septa in the pedicle valve. The Akasaka specimen may be an immature one of *Leptodus nobilis* (Waagen), originally described and figured by Waagen (1883, p. 398, pl. 29, figs. 1-3; pl. 30, figs. 1, 2, 5, 6, 8, 10, 11) from the Wargal and Chhidru Formations of the Salt Range, Pakistan.

The single lyttoniid specimen figured by Ozawa (1927, pl. 45, fig. 12) as *Lyttonia richthofeni* Kayser from the lower part (Same Zone of Wakimizu, 1902) of the Akasaka Limestone is clearly distinguished from the present species by its grooved (angustilobate) lateral septa in the pedicle valve, which is the diagnostic character of the genus *Eolyttonia* Fredericks,

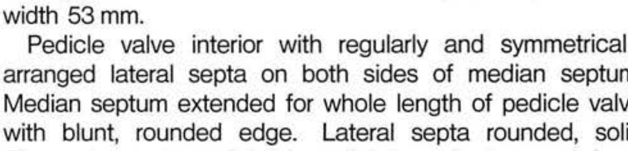

Figure 4. Longitudinal profile of the pedicle valve of *Leptodus nobilis* (Waagen, 1883). Right lateral view of a section of the latex cast, showing the lateral septa, NU-B128. (×2)

1924.

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A Miocene pseudodontorn (Pelecaniformes: Pelagornithidae) from the Ichishi Group of Misato, Mie Prefecture, Central Japan

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Abstract. Part of a right dentary of a pseudodontorn, bony-toothed bird, was newly found from the shell bed of the Kamimitsugano tuffaceous siltstone Facies of the Mitsugano Member in the Oi Formation (17.5-17 Ma), Ichishi Group in the Misato area, Mie Pref., Central Japan. This is the first record of a pseudodontorn bill from the Miocene of Japan. The discovery supplements the fossil record of pseudodontorns in Japan, which comprises the Early Oligocene to the Pliocene. The arrangement of the bony teeth corresponds to that of *Osteodontornis orri* Howard, 1957 known from the west coast of North America, and the specimen is provisionally identified as *Osteodontornis* sp.

Key words: Aves, Ichishi Group, Japan, Miocene, *Osteodontornis*, pseudodontorn

Introduction

The Miocene Ichishi Group, distributed in the Ichishi region of Mie Prefecture, Central Japan (e.g., Shibata, 1967), is famous for the abundant occurrence of fossils (Figure 1A). In particular, the shell beds in the Kamimitsugano tuffaceous siltstone facies of the Mitsugano Member in the Oi Formation (Shibata, 1967) yield a variety of vertebrate remains including sharks (Uyeno *et al.*, 1980), a bird (Diomedeidae; Davis, 1996) and marine mammals. These are recognized as important sources for Japanese Miocene fossil vertebrates.

A large dentary found by Fujio Sakakura from the outcrop in Misato area (Figure 1B) was first identified as that of a fish, but turned out to be the right dentary of a bony-toothed bird after chemical preparation with acetic acid by Fumio Ohe. This is the first and only example in which the arrangement of the bony teeth is preserved in the Miocene record of pseudodontorns from Japan. The bony tooth-like prominences borne by the tomia is a remarkable feature of pseudodontorns, and their arrangement is important for the taxonomy of this group. This paper aims to describe the Ichishi specimen in order to further the taxonomical evaluation of Japanese pseudodontorns and palaeo-geographical studies of the marine avifauna in the Pacific rim.

Systematic paleontology

Order Pelecaniformes Sharpe, 1891
Family Pelagornithidae Furbringer, 1888
Genus ***Osteodontornis*** Howard, 1957

Osteodontornis sp.

Figures 2, 3

Material.—A partial right dentary with bony teeth. Mizunami Fossil Museum, MFM28351, collected by Fujio Sakakura on February 13, 1994 (=the Ichishi specimen).

Locality.—Misato, Misato Village, Mie Prefecture, Japan (Figure 1).

Horizon and age.—Shell bed in the Kamimitsugano tuffaceous siltstone facies of the tuffaceous sandstone and shale Mitsugano Member, Oi Formation, Ichishi Group (Shibata, 1967). Late Early Miocene. 17.5-17 Ma. (Itoigawa and Shibata, 1992).

Description.—The specimen consists of part of a right dentary, missing both anterior and posterior ends (Figures 2, 3). Anteriorly, the mandible is slender and slightly curves dorsally. The bony teeth, sharp and conical prominences, stand vertically on the dorsal margin, which inclines somewhat to the external side, so that the vestibular margin of the bony teeth is continuous with the external surface of the mandible.

The bony teeth can be differentiated on the basis of size,

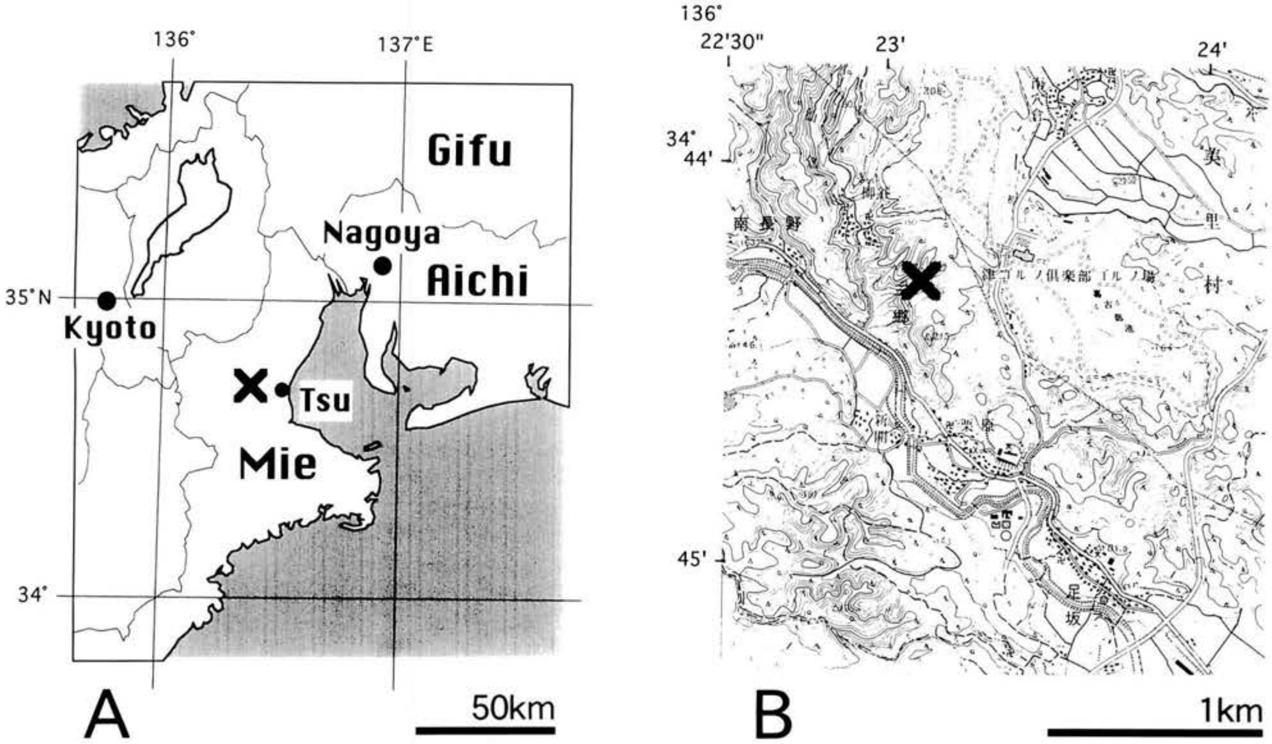

Figure 1. Locality maps for the pseudodontorn from Ichishi. **A.** The locality map in Central Japan. The locality is about 10 km west of the center of Tsu City, Mie Pref. **B.** The locality map showing Misato of Misato Village, based on the 1 : 25,000 scale topographic map of the Geographical Survey Institute of Japan, "Tsu-seibu".

into four types ; four large teeth (L1-L4), three medium teeth (M1-M3), five small teeth, and at least eight tiny processes (Figure 3). These size classes exhibit a repetitive pattern ; about midway between each pair of large teeth is a medium tooth, the pair of spaces between these two sizes each contains a small tooth, and, finally, a tiny process occupies the intervening space between each of these teeth (Figures 2, 3). A deep and round hole (h) occurs in front of the third large tooth (Figures 3 upper and lower). The distance between each of the large teeth increases anteriorly.

The external surface is almost flat and bears a deep, plain longitudinal sulcus, the mandibular groove (mg), that draws nearer to the ventral margin anteriorly (Figures 2A, 3 upper and lower). The internal surface is smoothly convex and a shallow sulcus with some nutrient foramina runs just above the ventral margin (Figures 2B, 3 middle).

Broken sections show that the mandible and the bony teeth are completely hollow and the inner surface of the bone wall is rough. The thickness of the bone wall is, at most, 2 mm.

Measurements.—See Table 1.

Comparison and remarks.—The pattern of size variation in the bony teeth of the Ichishi specimen is similar to that of *Osteodontornis orri* Howard, 1957 known from the Upper Miocene of California (Howard, 1957, Howard and White, 1962, reconstruction in Harrison and Walker, 1976), and also of the referred portion of a lower mandible of *Pseudodontornis longirostris* (Spulski, 1910), described from the Upper Oligocene (Olson, 1985) of South Carolina (figure 1A of Hopson, 1964 = the South Carolina specimen).

If we compare the Ichishi specimen with *Osteodontornis* and the South Carolina specimen, the relatively smaller sizes of bony teeth, which are diagnostic for the classification of pseudodontorns, link the Ichishi specimen to *Osteodontornis*. The South Carolina specimen, in which the heights of the large bony teeth are almost equivalent to the rest depth (height) of the mandible not including the bony teeth, has by far the largest and most robust bony teeth in comparison with the Ichishi specimen or *Osteodontornis*. Therefore, the Ichishi specimen is likely to be assigned to *Osteodontornis* species. In addition, the zoogeographical similarity of the Miocene of Japan and California, and the dissimilarity between the Pacific and the Atlantic, support this identification.

Compared with *Osteodontornis orri* Howard, 1957, the increasing rate of separation within each size variation pattern of the bony teeth in the Ichishi specimen corresponds exactly to part of the lower mandible of the former (Figure 4A), and the restored head of this animal, in its original state, is shown in Figure 4B. This indicates that the size of the Ichishi specimen is about two-thirds of the type specimen of *O. orri*. In addition, there is a gap of some millions of years between the older Ichishi specimen and the younger *O. orri*. In conclusion, we assume the Ichishi specimen is a species of *Osteodontornis*, but may not be the same species as *O. orri*.

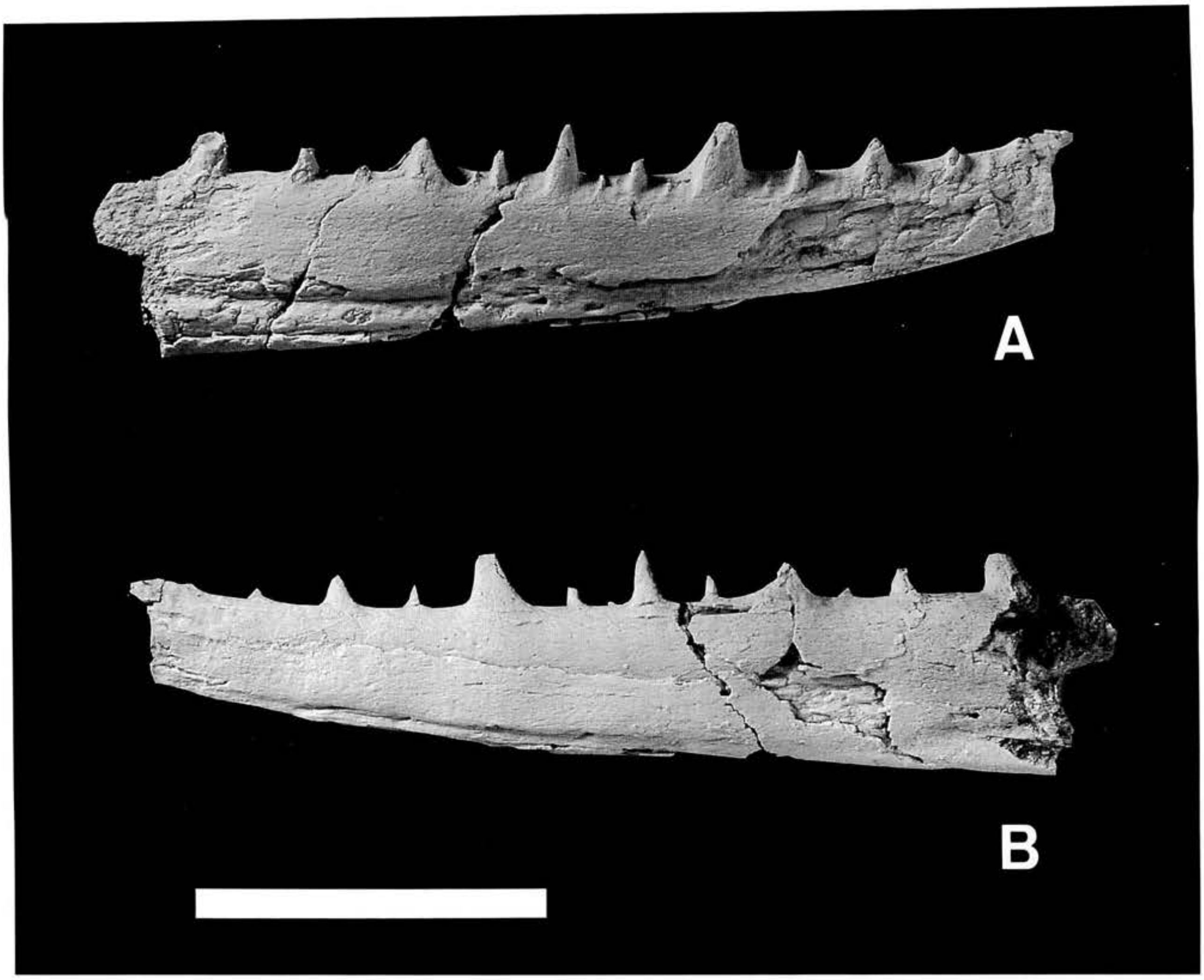

Figure 2. *Osteodontornis* sp., the Ichishi specimen, partial right dentary, MFM28351. **A.** The external surface. **B.** The internal surface. The scale bar is 50 mm long.

On the other hand, the confused taxonomy of pseudodontorns produces vexatious problems. Olson (1985) pointed out the possibility of synonymising *Osteodontornis* Howard with the earlier name *Cyphornis* Cope. All names of pseudodontorns, except the oldest name *Pelagornis* Lartet, may suffer from a similar problem, and this group is in need of comprehensive and sensible revision (Olson, 1985). So, we assign the Ichishi specimen to *Osteodontornis* sp., but emphasize that this is very provisional.

A brief review of pseudodontorn records from Japan

Several remains of pseudodontorns have been recorded from the marine Tertiary System of the Japanese Archipelago (Figure 5).

The oldest fossil is a rostrum tip that was excavated from the Lower Oligocene Iwaki Formation in Iwaki City, Fukushima Pref. (1 in Figure 5 ; Hasegawa *et al*., 1986 ; Ono and Hasegawa, 1991). In addition to the pseudodontorn, the Iwaki Formation has also yielded *Puffinus, Morus, Sula, Phalacrocorax*, plotopterids, accipitrids and alcids (Ono and Hasegawa, 1991). Though the taxonomic study of the Iwaki specimen is still under preparation, the cyclic pattern of the teeth, which consists of large (posterior) and medium and small (anterior) bony teeth, is different from that of *Osteodontornis orri*, as determinable from the published picture. Thus, the Iwaki specimen and the Ichishi specimen (*Osteodontornis* sp.) may represent different taxa.

Okazaki (1989) reported a slab bearing a humerus and some fragmentary wing elements from the Upper Oligocene Yamaga Formation, Ashiya Group, in Kitakyushu City, Fukuoka Pref. (2 in Figure 5). The locality of this specimen is only 1 km northwest of the locality of the "Orio specimen" (Hasegawa and Seki, 1979) of *Copepteryx hexeris* Olson and Hasegawa, 1996 (Plotopteridae).

Two records, other than the present report, are from the Miocene formations. Each of the three deposits is of similar age : middle Miocene. Ono (1989) described a

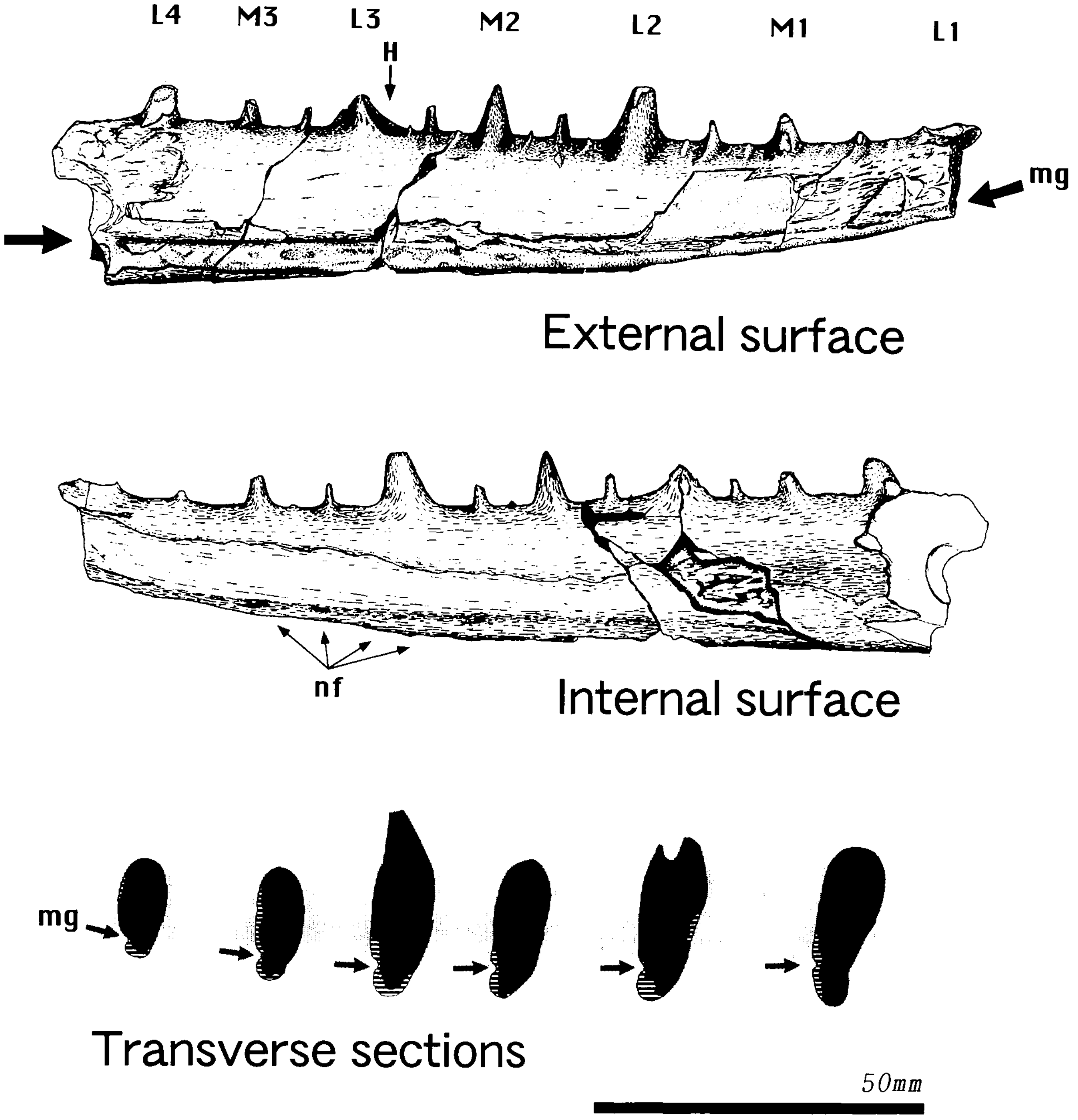

Figure 3. *Osteodontornis* sp. from Ichishi, MFM28351. External (upper), internal (middle) and transverse (lower) views from top to bottom respectively. Abbreviations: h, hole; L1-4 and M1-3, the 1st to 4th large bony tooth and the 1st to 3rd medium bony tooth respectively; mg, mandibular groove. The scale bar is 50 mm long.

pseudodontorn quadrate from the early Middle Miocene Nagura Formation, Chichibumachi Group of the Chichibu City, Saitama Pref. (5 in Figure 5), and identified it as *Osteodontornis* sp. Ono's identification was "very tentative" as he noted, but the occurrence of the Ichishi specimen may support his conclusion. The Nagura Formation has also yielded *Puffinus* and *Sula* besides the pseudodontorn (Ono and Sakamoto, 1991).

Ono (1989) mentioned pseudodontorn material form Mizunami (3 in Figure 5). Mizunami is one of the neighboring sedimentary basins to Ichishi, however, a detailed description of this material has not been published. The youngest known plotopterid, *Plotopterum* sp., was reported from the Mizunami group (Olson and Hasegawa, 1985).

The youngest pseudodontorns are Pliocene in age (Unwin, 1993), and their fossil record is thin (Olson, 1985). Two Pliocene records are known from Japan. Ono *et al.* (1985) reported on a humerus from the Lower Pliocene of Maesawa Town, Iwate Pref. (1 in Figure 5). It is very important as it is a certain record of Pliocene pseudodontorns.

Table 1. Measurement of MFM28351 (the Ichishi specimen) in mm.

Maximum length of the specimen	139.7
Maximum height of the mandible plus bony tooth	31.2+
Maximum height of the mandible not including the bony teeth	25.3
Minimum height of the mandible not including the bony teeth	14.2+
Maximum width of the mandible	10.1
Height of the mandible at the point of the 2nd large tooth	26.9+
Height of the largest bony tooth (2nd large tooth)	7.7+
Distance	
between the 1st large tooth and the 1st medium tooth	23.6
between the 1st medium tooth and the 2nd large tooth	22.2
between the 2nd large tooth and the 2nd medium tooth	22.2
between the 2nd medium tooth and the 3rd large tooth	20.3
between the 3rd large tooth and the 3rd medium tooth	16.6
between the 3rd medium tooth and the 4th large tooth	13.7

Ono *et al.* (1985) also referred a femur from the Upper Pliocene Dainichi Formation, Kakegawa Group of Shizuoka Pref. (7 in Figure 5), which was previously identified by Ono (1980) as "Diomedeidae, gen. et sp. indet.", to a pseudodontorn. Ono *et al.* (1985) compared the Kakegawa specimen with *Pseudodontornis stirtoni* of the Pliocene (Howard and Water, 1969); Harrison and Walker (1976) subsequently erected a new genus and species for this specimen: *Neodontornis stirtoni*. If the Kakegawa specimen is indeed a pseudodontorn, it is one of the youngest records of the family in the world.

Conclusion

The Ichishi specimen has the most diagnostic feature of Pelagornithidae, and was identified as a species of *Osteodontornis*. It supports evidence of the similarity of marine avifaunas of Japan and the west coast of North America. The pseudodontorn records of Japan range from the Early Oligocene to the Late Pliocene. Because of their stratigraphically continuous record, Japanese pseudodontorns form important materials for the zoogeographical and systematic study of this family. The Tertiary System of Japan, during which there was extensive development of marine deposits, is indispensable for the study of the evolution and palaeo-ecosystem of marine members of higher vertebrates.

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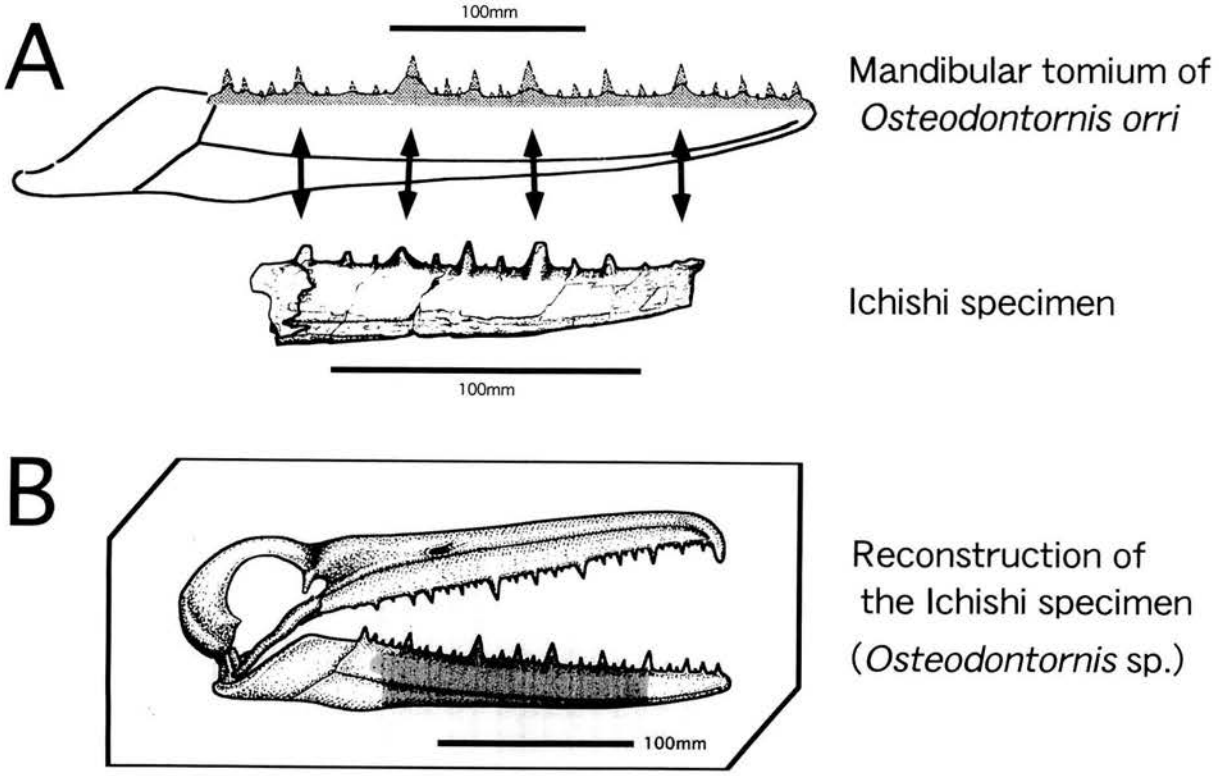
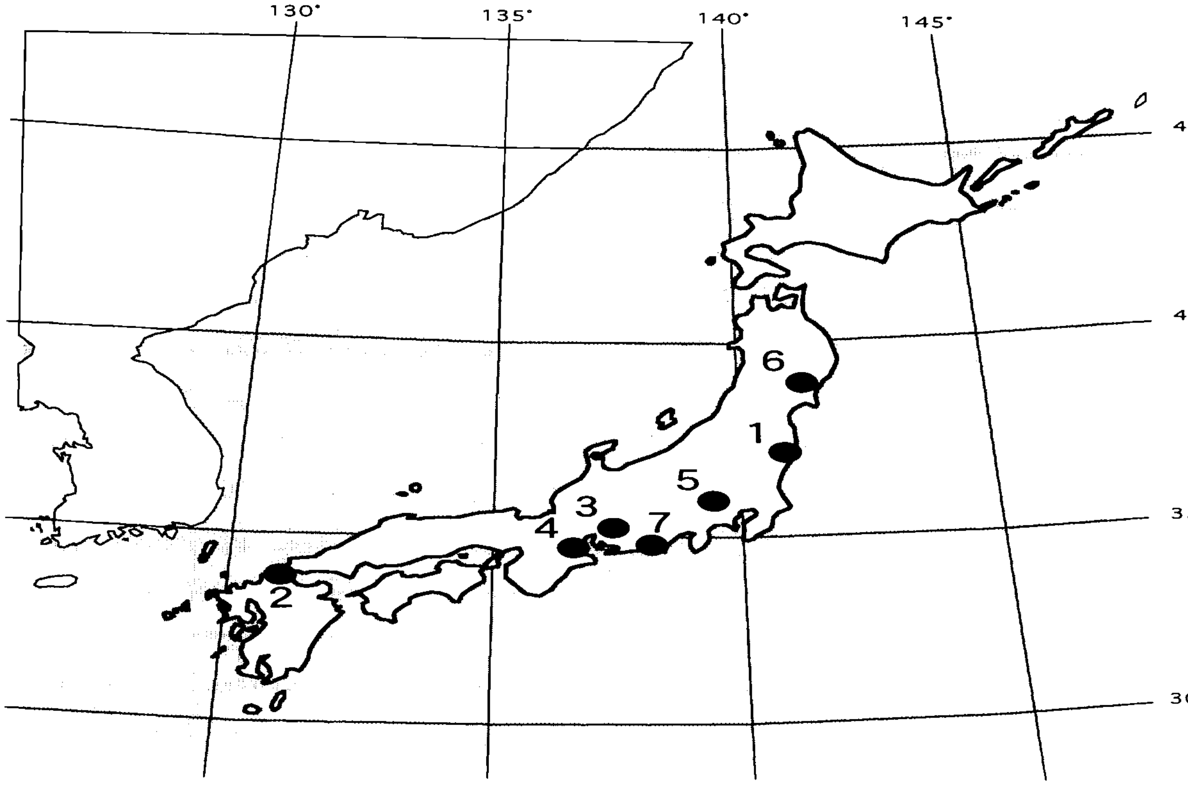


Figure 4. Restoration of *Osteodontornis* sp. from Ichishi. All scale bars represent a length of 100 mm. **A.** Correspondence between the arrangement of the bony teeth in the Ichishi specimen (below) and *Osteodontornis orri* Howard, 1957 (above: from Harrison and Walker, 1976). **B.** The original state of the Ichishi specimen. Both heads, of the Ichishi pseudodontorn (B) and *Osteodontornis orri* (A-above), are scaled by the shorter scale bar, and only the Ichishi specimen (A-below) is scaled by the longer scale bar. Note the size reduction necessary for *Osteodontornis orri* to match the Ichishi specimen, which implies a smaller size for the Ichishi pseudodontorn.



No. in map	Age	Locality	Horizon	Element	Reference
1	E. Oligocene	Ogawa-tyo, Iwaki, Fukushima.	Iwaki F., Shiramizu G.	Rostrum	Hasegawa et al., 1986 Ono and Hasegawa, 1991
2	L. Oligocene	Yoshida, Mizumaki, Fukuoka.	Yamaga F., Ashiya G.	Humerus (left)	Okazaki, 1989
3	late E. Miocene	Mizunami, Gifu.	Mizunami G.	- No report -	(Ono, 1989)
4	late E. Miocene	Sangou, Misato, Mie.	Oi F., Ichishi G.	Dentary (right)	Present report
5	early M. Miocene	Ohnohara, Chichibu, Saitama.	Nagura F., Chichibumachi G.	Quadrate (right)	Ono, 1989
6	E. Pliocene	Seibo, Maesawa, Iwate.	Yushima F. (=Tatsunokuchi F.)	Humerus (right)	Ono et al., 1985
7	L. Pliocene	Haranoya, Kakegawa, Shizuoka.	Dainichi F., Kakegawa G.	Femur (right)	Ono, 1980 Ono et al., 1985

Figure 5. Summary of pseudodontorn records of Japan. Locality numbers in above figure correspond to material listed in below in order of geological age. Abbreviations : E, Early ; M, Middle ; L, Late ; F, Formation ; G, Group.

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Calcareous nannoplankton from the Seoguipo Formation of Cheju Island, Korea and its paleoceanographic implications

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Abstract. Twenty species of calcareous nannofossils belonging to 11 genera are identified from the Seoguipo Formation in Cheju Island, Korea. On the basis of the marker species, the Seoguipo Formation is biostratigraphically assigned to the *Pseudoemiliania lacunosa* Zone (NN19), which corresponds to the combined zones of *Emiliania annula-Emiliania ovata* (CN13a-CN14a) of the latest Pliocene and Early Pleistocene. Generally, cold-water species are dominant in the lower part, and warm-water ones in the upper part. This suggests that the paleoceanographic condition of the study area changed from a cooling to a warm phase. The change in floral composition and abundance of specific species allows recognition of four ecostratigraphic zones in the Seoguipo Formation and the migration of an oceanographic frontal boundary. According to nannofossil distribution in the study area, the position of an oceanographic boundary between warmer water and cooler water appeared to have oscillated north-south over the Korea Strait and Cheju Island in response to glacial and interglacial cycles. The geologic time of the interpreted paleoceanographical changes determined by nannofossil biochronology agrees well with the results obtained from the Japan Sea (East Sea) and Japan-Sea side of Japan.

Key words : Bio- and ecostratigraphy, Cheju Island, Korea, nannoplankton, paleoceanography, Seoguipo Formation.

Introduction

Cheju Island, located 90 km off the southern coast of Korea at 33°12′-33°34′N, 126°10′-126°58′E, was formed by Late Cenozoic volcanic activity (Figure 1). The Seoguipo Formation, a highly fossiliferous marine formation, seems to have been deposited just before the onset of Quaternary volcanism, since it underlies Pleistocene volcanic rocks that cover most of the island (Table 1). The Seoguipo Formation is mainly composed of sandstone with a minor amount of interbedded conglomerate and mudstone. It is well developed at the subsurface level all over the island and is exposed only on the southern coast of the island at Seoguipo. The subsurface Seoguipo Formation is encountered in core samples of numerous bore holes drilled in the island.

Yokoyama (1923) first reported molluscan fossils from these sedimentary deposits, designating their geologic age as Upper Pliocene. Haraguchi (1931), who described diverse invertebrate faunas such as mollusks, brachiopods, echinoids, corals and fish teeth, named this fossiliferous sedimentary formation the Seikiho (Seoguipo) Formation of the Pleistocene epoch. After Haraguchi's research, numerous works including detailed field survey, paleontological, magnetostratigraphic, and sedimentological studies were carried out for determination of the geologic age, depositional environment, and stratigraphical zonation (Kim, 1972 ; Won, 1975 ; Lee, M.W., 1982a, 1982b ; Kim, 1984 ; Nomura, 1984 ; Yun *et al*., 1987 ; Min *et al*., 1986 ; You *et al*., 1987 ; Yoon, 1988 ; Tamanyu, 1990 ; Lee E.H., 1990 ; Yoon *et al*., 1995 ; Kang, 1995). However, no consensus was achieved for the geologic age of the Seoguipo Formation which was assigned to different ages from Pliocene to Pleistocene (Table 1). Several studies analyzed paleoclimate and paleoceanographic conditions of the Seoguipo Formation based on molluscan fauna and isotope data (Yoon, 1988 ; Amano, 1994 ; Park *et al*., 1994 ; Woo *et al*., 1995). The results for the water temperature are also contradictory, reporting warm or cold glacial environment during deposition of the formation.

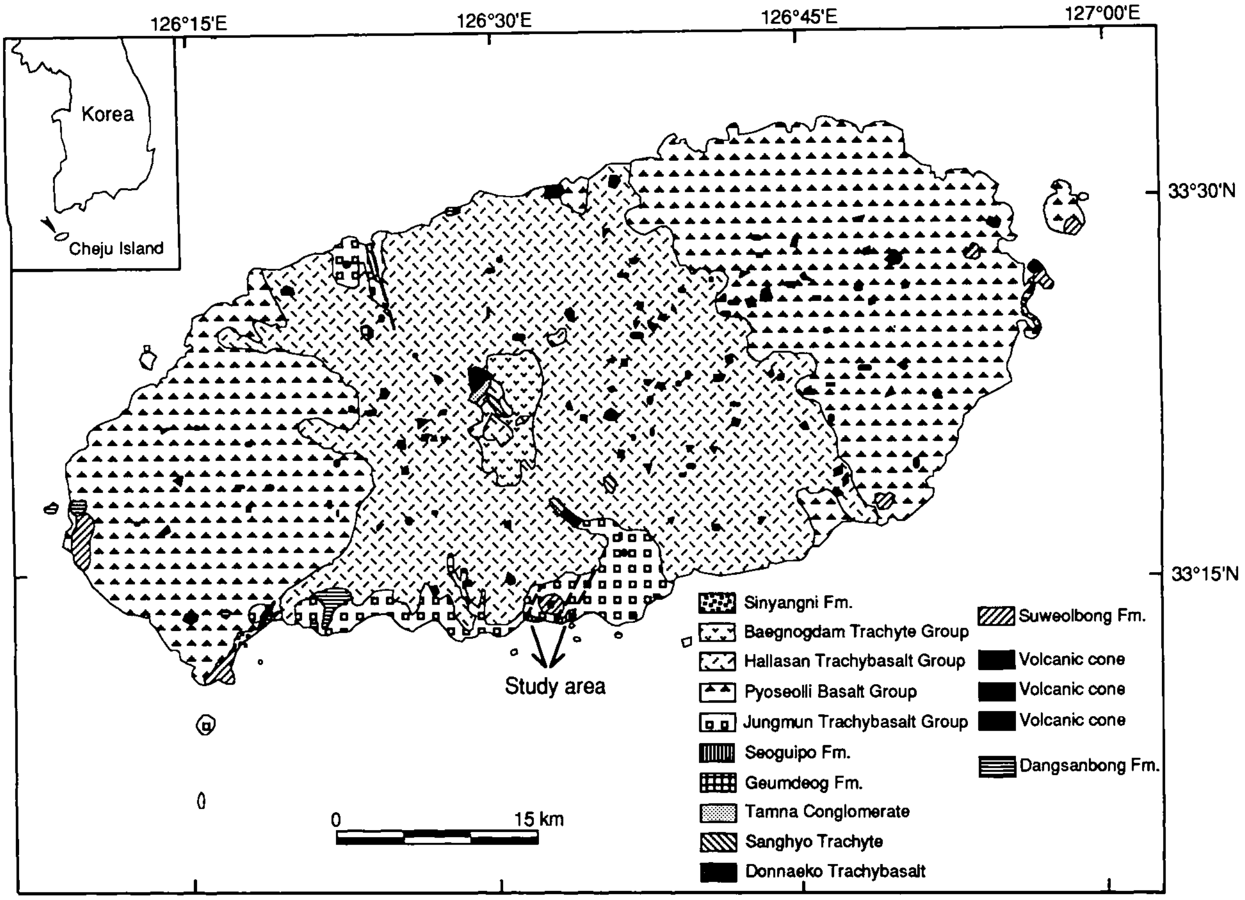


Figure 1. Geologic map of Cheju Island with sample locality (after Yoon *et al.*, 1995).

Cheju Island is located in the oceanic pathway to the Japan Sea. This area was paleoclimatologically and tectonically sensitive and often affected by small- or large-scale changes in the tectonic (Inoue, 1982) or climatological settings. The climatic or sea-level changes may cause subsidence or uplift which in turn affects the system of current and the biofacies. Therefore, a biofacies analysis may deductively provide a clue to the climatic and tectonic history of this area, which is not only important for the development of Cheju Island and the Korea Strait, but also for the evolution of the Japan Sea during the late Pliocene and Pleistocene (Muza, 1992 ; Rahman, 1992).

Analysis of calcareous nannofossil assemblage is the best means to resolve the debateble claims made concerning the geologic age and environment of the Seoguipo Formation, since it may enable fine zonation and reconstruction of the paleoenvironmental and geologic events. Therefore, our study primarily aims to establish a biozonation and ecostratigraphy based on nannoplankton, and to investigate the frequency and nature of paleoceanographic changes during deposition of the Seoguipo Formation. The results may help in interpretation of the paleoclimatic and tectonic history of Cheju Island and the neighboring area.

Geologic setting of the Seoguipo Formation

The Seoguipo Formation is divided into 7 distinctive lithologic units in ascending order (Lee, 1990 ; Figure 2). Litho-unit I of about 3.5 m thickness is composed of laminated yellowish gray siltstones in the lower part, and massive fine-grained gray sandstones with fossil shells and volcanic clasts in the upper part. Litho-unit II overlying the Litho-unit I with a diastem is about 5 m thick, and consists of alternating brownish medium-grained, parallel-stratified sandstones and thin-laminated mudstones. The upper part of this unit with a thickness of about 2 m is highly bioturbated and contains a few articulated bivalve shells. Litho-unit III with a thickness of about 15 m is relatively homogeneous. It is composed of poorly consolidated massive sandstones. The lower boundary of this unit nearly coincides with the Pliocene-Pleistocene boundary. Except for the middle part this unit is highly fossiliferous and bioturbated. Litho-unit IV with a thickness of about 2 m is composed of massive yellowish- gray fine-grained sandstones and highly bioturbated mudstones. Litho-unit V, which is about 10 m in thickness, overlies Litho-unit IV with a diastem. It is lithologically very variable showing cross-laminated shell conglomerate layers, medium- to coarse-grained sandstones intercalated with mudstones, and massive, poorly sorted gray

Table 1. Stratigraphic classifications of volcanics and sedimentary strata in Cheju Island (The sources of the radiometric ages ae indicated in brackets : a. Ahn *et al*., 1995 ; b. Yoon *et al*., 1995 ; c. Lee, 1994 ; d. Won *et al*., 1986 ; e. Sameshima *et al*., 1988).

Age		Haraguchi, K. (1931)	Won, C.K. (1975)	Lee, M.W. (1982)	Yun, S.K. *et al.* (1987)	Tamanyu, S. (1990)	Yoon, S. *et al.* (1995)
Holo.		Flood Deposits Shell-Sand Bed Wacke Bed	Shell-sand Formation Parasitic volcanic ejectas	1007, 1002 activities Groups of small basalt cones	1007, 1002 activities	1002, 1007 activities Shell and Formation Scoria vol. cones	Sinyangni Formation [4780±60 y.B.P.][e]
Pleistocene	Late	Gunzan Basalt Suikido Basalt Kanrasan Basalt Aphanitic Basalt Augite Basalt Feldspar Basalt Saishu Basalt Alkali-basalt Trachy-andesite	Baegrogdam Basalt Hanlasan Trachy-andesite Hanlasan Basalt Seongpanak Basalt Sihungri Basalt Beobjeongn Trachyte Hahyori Basalt Jeju Basalt	Sinyangri Formation Hanlasan Trachyte Hanlasan hawaiite Seonpanak hawaiite Sihungri hawaiite Beobjeongri mugearite Hahyori hawaiite Jeju hawaiite	Dongnam palaeosol Basalt flows along the flanks of Hanlasan [0.07±0.04−0.035±0.014 Ma] Sinyangri Formation	Paeknoktam Hawaiite [0.47±0.07 Ma] Hallasan Trachyte [0.07±0.01 Ma]	Baegnogdam Trachyte Group ┌ Baegnogdam Trachyte [0.025±0.008 Ma][d] └ Yeongsil Trachyte Hallasan Trachybasalt Group ┌ Hallasan Trachybasalt Seongpanag Trachybasalt └ Cheju Trachybasalt
	Middle	Hornblende-bearing Trachy-andesite Gyojoseigaku Lava Kakushugan Lava Sanbosan Lava	Sinyangri Formation	Hornblende mugearite Sanbangsan Trachyte	Hanlasan trachyte Tuff-rings (Songaksan, Ilchulbong, Suwolbong) Seoguipo trachyandesite [0.41±0.01 Ma] Tuff-rings (Dansan, Dusan) **Seoguipo Formation** Pyoseonri basalt [0.63±0.03 Ma]	Pyosonri Alkali Basalt [0.31±0.04 Ma] Hallasan Hawaiite [0.52±0.03 Ma] Sogwip'o Hawaiite [0.55±0.04 Ma]	Pyoseolli Basalt Group ┌ Siheungni Trachybasalt Pyoseolli Basalt [0.63±0.03 Ma][c] └ Seoguipo Trachybasalt
	Early	**Seikiho Formation**	Jungmun Trachyte ┌ Seongsanpo Fm. └ Hwasun Fm. Seoqwipo Trachyte Pyoseonn Basalt	Jungmun hawaiite Seonsanpo Formation Seoguipo hawaiite Pyoseonri alkali basalt	Tuff-rings (Hwasoon, Dansan) Sanbangsan Trachyte [0.87±0.13 Ma] marine sediments basalt (olivine augite basalt) [1.20±0.05 Ma]	Sanbangsan Trachyte **Sogwip'o Formation** Basal Basalt	Jungmun Trachybasalt Group ┌ Jungmun Trachybasalt Sanbangsan Trachyte [0.733±0.056 Ma][d] └ Gagsuam Trachyte [0.893±0.027 Ma][c]
Pliocene		Shinto Lava Johangaku Lava Gyojoseigaku Lava Kanrasan Lava Granite Blocks-bearing Volcanic Detritus Bed	**Seoqwipo Formation** Basal basalt	**Seoguipo Formation** Basal Basalt			Cheju Group ┌ **Seoguipo Formation** U Formation (uncemented sediment beds) Geumdeog Formation └ Tamna Conglomerate Sanghyo Trachyte Donnaeko Basalt Panpo Basalt [2.22±0.16 Ma][b]
Cret. (?)-Paleogene		Granite ?		Granite ?	Granite in the northern part Tuff in the eastern and southern part	Granite ?	Granite [58.14±1.4 Ma][a] Volcanic sandstones and mudstones Welded tuffs Lapilli tuffs

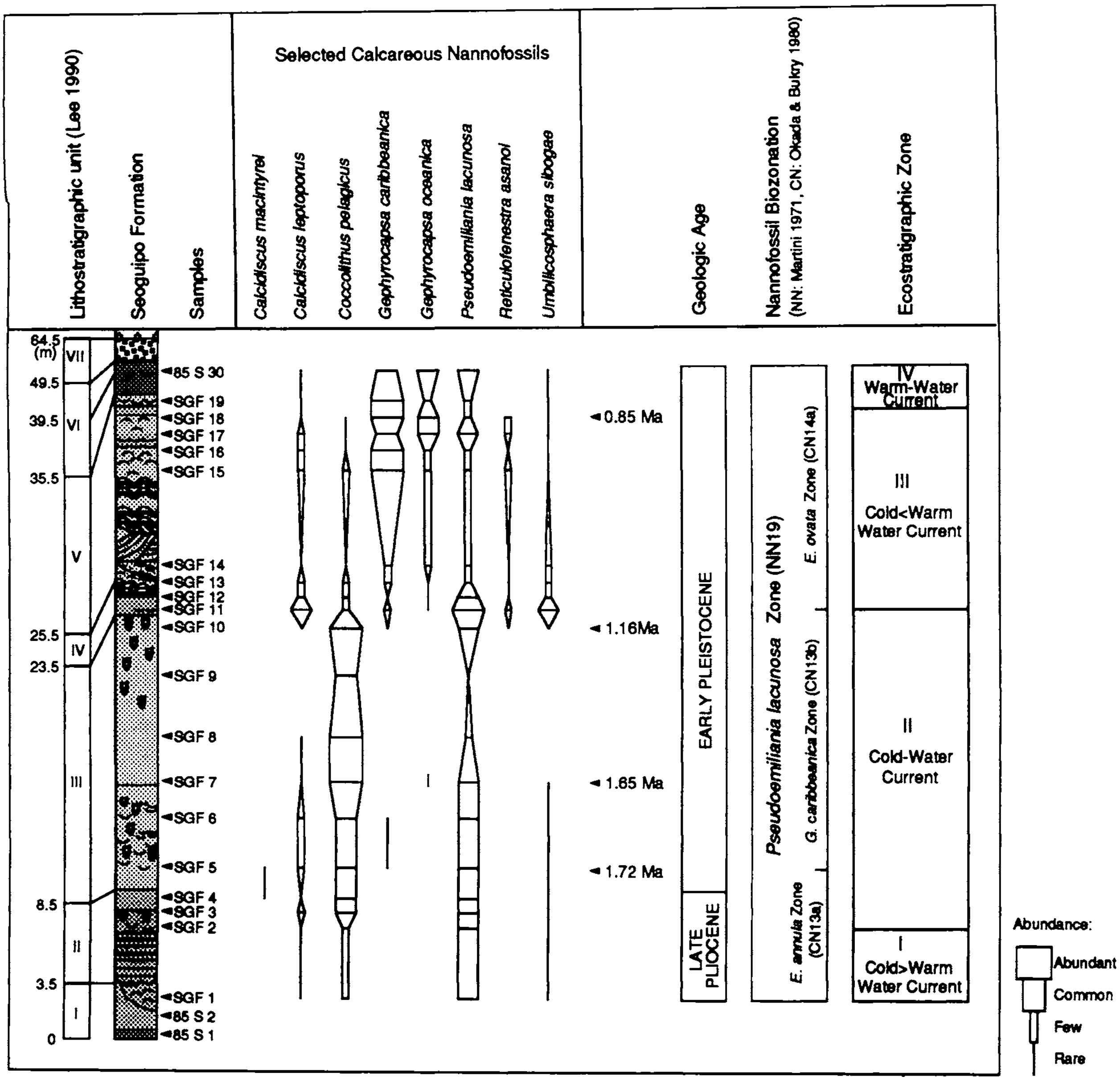


Figure 2. Biozonation and ecostratigraphic zones of the outcrop section of the Seoguipo Formation based on nannofossils.

medium to coarse sandstones. This unit is characterized by a variety of sedimentary structures such as ripple drift laminae, wavy bedding, flaser bedding, graded bedding, and convolute bedding. Litho-unit VI with a thickness of about 14 m is composed of semi-consolidated massive, light-gray siltstones and volcanic ash. Litho-unit VII of about 15 m thickness consists of volcanic conglomerate without any fossil remains. This unit is covered by a basalt flow.

Methods

Twenty-two samples were collected from the outcrop of the Seoguipo Formation (Figure 2, Table 2). Smear slides were prepared following the centrifuging method of Perch-Nielsen (1985, p. 330-331). Samples were crushed and centrifuged for 30 seconds at 2,000 r.p.m. Slides were examined with a light microscope at ×1,250 magnification and a scanning electron microscope. Preservation and abundance of nannofossils in each sample are denoted as follow: Abundant (A), 1-10 specimens/one field of view; Common (C), 1 specimen/2-10 fields of view; Few (F), 1 specimen/11-100 fields of view; Rare (R), 1 specimen/101-1,000 fields of view; Barren (B), no fossils observed; Good (G): specimens show little effects of dissolution or overgrowth; Moderate (M), specimens show some effects of dissolution or overgrowth.

Table 2. Stratigraphic occurrence of calcareous nannofossil from the Seoguipo Formation.

Geologic Age	Nannofossil zone		Ecostratigraphic Zone	Formation	Samples	Abundance	Preservation	*Braarudosphaera bigelowii*	*Calcidiscus leptoporus*	*Calcidisucs macintyrei*	*Ceratolithus cristatus*	*Coccolithus pelagicus*	*Coccolithus* sp.	*Gephyrocapsa caribbeanica* (3.5-4.0 μm)	*Gephyrocapsa oceanica* (>4.0 μm)	small *Gephyrocapsa* spp. (<3 μm)	*Helicosphaera carteri*	*Helicosphaera* sp.	*Pontosphaera japonica*	*Pontosphaera discopora*	*Pseudoemiliania lacunosa*	*Reticulofenestra asanoi*	small *Reticulofenestra* spp.	*Syracosphaera pulchra*	*Syracosphaera* sp.	*Umbilicosphaera hulburtiana*	*Umbilicosphaera sibogae*
PLEISTOCENE	Pseudoemiliania lacunosa Zone (NN19)	CN14a	IV	Seoguipo	85 S 30	A	G	•	R	•	•	•	•	A	C	A	R	•	R	•	C	•	C	R	•	F	R
					SGF 19	A	G	•	R	•	•	•	•	A	F	A	F	•	•	•	F	•	F	•	•	•	R
			III		SGF 18	A	G	R	R	•	R	R		A	C	A	R	•	R	•	F	F	F	R	•	•	R
					SGF 17	C	G	R	F	•	•	R	•	C	C	A	R	R	•	•	C	F	F	•	•	•	R
					SGF 16	A	M	•	F	•	•	R	•	A	F	A	R	•	•	•	F	R	F	•	•	•	R
					SGF 15	A	G	R	F	•	•	F	•	A	F	A	R	•	•	•	F	C	C	•	•	•	R
					SGF 14	F	M	•	R	•	•	R	•	F	F	F	•	•	•	•	F	R	F	•	•	R	F
					SGF 13	A	G	•	F	•	R	F	•	F	R	A	F	•	R	•	C	R	F	•	•	•	F
					SGF 12	A	G	•	F	•	•	F	R	R	R	A	R	R	R	R	A	F	C	•	R	•	F
					SGF 11	A	G	R	C	•	R	F	•	F	R	A	C	•	R	•	A	F	C	F	•	•	C
		CN13b	II		SGF 10	A	G	R	R	•	•	A	F	R	•	C	F	•	•	•	C	F	C	•	•	•	R
					SGF 9	C	G	•	•	•	•	C	•	•	•	•	R	•	•	•	R	•	•	•	•	•	•
					SGF 8	A	G	R	R	•	•	A	F	•	•	•	R	•	•	•	F	•	R	•	•	•	•
					SGF 7	A	G	R	R	•	•	A	F	•	R	F	R	•	R	•	C	•	C	•	R	•	R
					SGF 6	C	M	F	F	•	•	C	R	R	•	R	F	•	•	•	C	•	F	•	•	•	R
					SGF 5	C	M	R	F	R	•	C	R	R	•	R	F	•	R	•	C	•	F	•	•	•	R
PLIOCENE		CN13a			SGF 4	C	M	•	R	R	•	C	•	•	•	•	R	•	•	•	C	•	R	•	•	•	R
					SGF 3	C	M	•	F	•	•	C	R	•	•	F	R	•	R	•	C	•	R	•	•	•	R
			I		SGF 2	C	M	•	R	•	•	F	R	•	•	C	R		R	•	C	•	•	•	•	•	R
					SGF 1	A	G	•	R	•	•	F	R			A	R	•	R	•	C	•	C	•	•	•	R
					85 S 03	B		•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•
					85 S 02	B		•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•

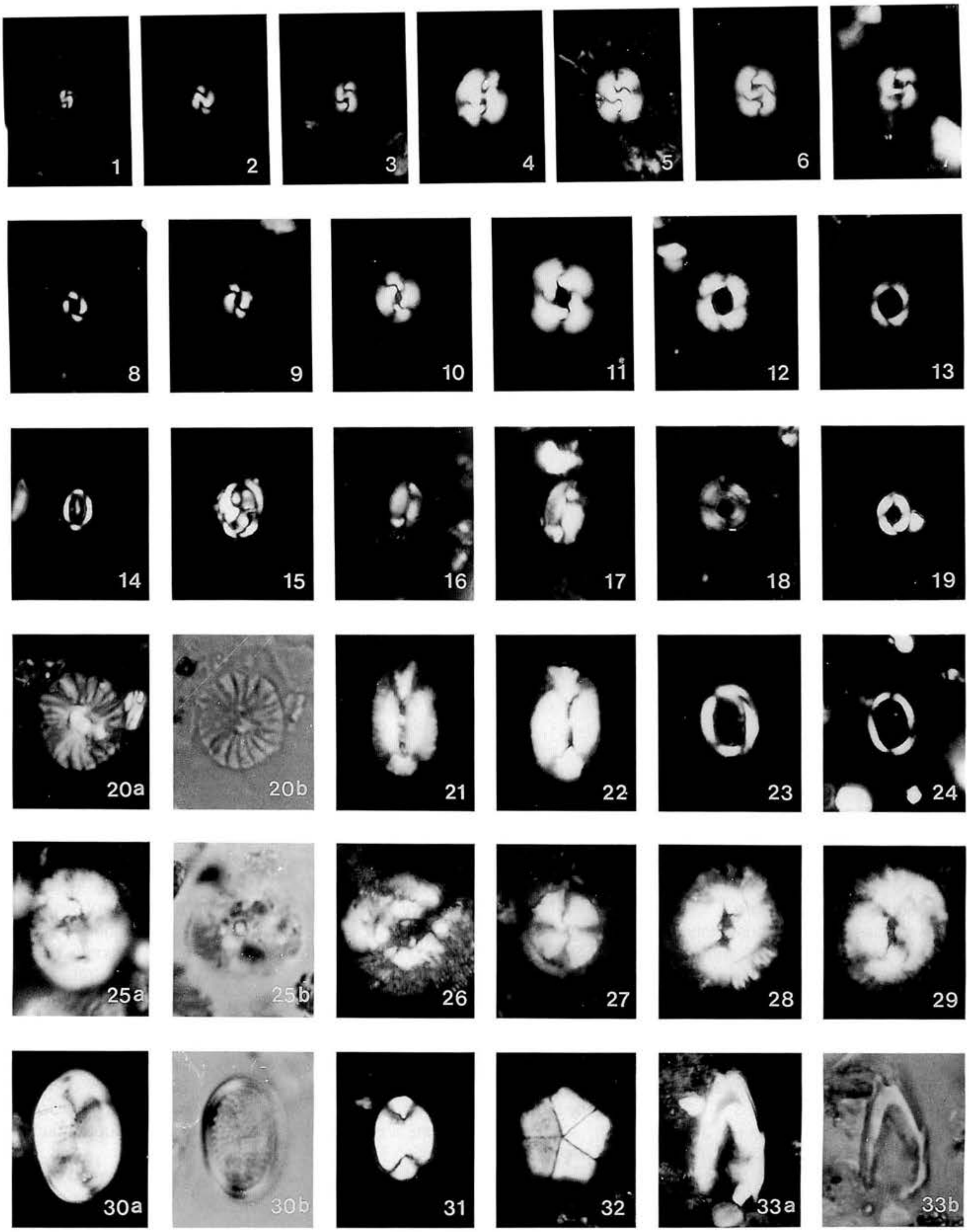
Results

1. Calcareous nannofossil flora

Twenty species of calcareous nannofossils belonging to 11 genera were identified from 22 samples from the Seoguipo Formation (Table 2). Nannofossils were generally common to abundant. However, some species changed their relative abundance throughout the formation. The dominant species are small *Gephyrocapsa* spp. (<3 μm ; Figures 3-1—3, 4-1, 2), *Pseudoemiliania lacunosa* (Figures 3-12, 13, 4-4, 5), *Coccolithus pelagicus* (Figures 3-28, 29, 4-15), small *Reticulofenestra* spp. (Figures 3-8—10, 4-3), *Gephyrocapsa caribbeanica* (3.5-4 μm ; Figures 3-4, 5, 4-7, 8) and *G. oceanica* (>4 μm ; Figures 3-6, 7, 4-9, 10) in ascending order in the formation. The minor species include *Braarudosphaera bigelowii* (Figure 3-32), *Calcidiscus leptoporus* (Figures 3-20a, b, 27, 4-12—14), *C. macintyrei* (Figures 3-25a, b, 26), *Ceratolithus cristatus* (Figures 3-33a, b), *Coccolithus* sp. (Figures 3-19, 23, 24, 4-11), *Helicosphaera carteri* (Figures 3-21, 22, 4-16), *Helicosphaera* sp. (Figures 3-16, 17), *Pontosphaera japonica* (Figures 3-30a, b, 31, 4-17), *P. discopora*, *Reticulofenestra asanoi* (Figure 3-11), *Syracosphaera pulchra* (Figures 3-15, 4-18), *Syracosphaera* sp. (Figure 3-14), *Umbilicosphaera hulburtiana* and *U. sibogae* (Figures 3-18, 4-6).

The nannoflora in the formation shows a transition from cold subpolar to warm subtropical assemblage. Abundance of the typical cold-water indicator *C. pelagicus* varies greatly within the formation. *C. pelagicus* is extremely abundant in the lower part of the formation and gradually decreases upward, becoming few to barren. Subtropical nannofossils such as *G. oceanica* (>4 μm), *C. leptoporus, U. sibogae, S. pulchra*, and *C. cristatus* are common in the upper part of the formation.

The assemblage characteristics change in response to the paleoceanographic conditions during deposition of the formation and hence allow recognition of four ecostratigraphic zones in the outcrop section of the Seoguipo Formation (Figure 2). Zone I (SGF 1-2) contains dominant small *Ge-*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phyrocapsa spp. (<3 μm), common *P. lacunosa* and small *Reticulofenestra* spp., and few *C. pelagicus*. The flora of these strata consists of mixtures of warm and cold-water species. Zone II (SGF 3-10) is characterized by a prominent peak in abundance of the cold-water species *C. pelagicus*. Zone III (SGF 11-18) shows an abrupt decrease of *C. pelagicus* and increase of subtropical to tropical species including *G. oceanica* (>4 μm), *C. leptoporus*, *U. sibogae*, *S. pulchra*, and *C. cristatus*. The change from a cold- to warmer-water flora and increase of the oceanic species took place at SGF 11. Zone IV (SGF 19, 85S30) reveals dominance of *G. oceanica* (>4 μm), *G. caribbeanica* (>3.5-4 μm), small *Gephyrocapsa* spp. (<3 μm), and *U. hulburtiana* and was barren of *C. pelagicus*.

2. Nannofossil biochronology

The Seoguipo Formation yields Pleistocene marker species such as *G. caribbeanica* (>3.5-4 μm), *G. oceanica* (>4 μm), *P. lacunosa*, *C. macintyrei*, and *R. asanoi* (Table 2, Figures 2, 3). Among them, the first appearance datum of *G. caribbeanica* (FAD : 1.72 Ma ; Sato and Kameo, 1996) has been used for the determination of the Pliocene-Pleistocene boundary. This species is first recognized in sample SGF 5. *G. oceanica* (FAD : 1.65 Ma ; Sato and Kameo, 1996), another important indicator for the Pliocene-Pleistocene boundary, occurs in sample SGF 7. *C. macintyrei* with the last occurrence datum (LAD) of 1.60-1.64 Ma (Shipboard Scientific Party, 1996) was encountered in sample SGF 5, although the total occurrence of *C. macintyrei* may not have been properly detected because of its rarity in the samples, and would be expected to occur also in somewhat younger samples. Compiling all these data, the Pliocene-Pleistocene boundary can be drawn between SGF 4 and SGF 5. Consequently, the lowermost part (SGF 1-4) can be presumed to be older than 1.72 Ma and thus belongs to the latest Pliocene.

The sample SGF 11 indicates the lower boundary of Zone CN14a defined by the reoccurrence of *G. oceanica* (>4 μm ; 0.94-1.02 Ma ; Shipboard Scientific Party, 1996). The presence of *P. lacunosa* (LAD : 0.41 Ma ; Sato and Kameo, 1996) indicates that the uppermost part of the formation is older than 0.41 Ma in age. Specimens of *R. asanoi*, with FAD of 1.16 Ma (Sato and Kameo, 1996), are first found in sample SGF 10 at the end of the cooling phase. Therefore, the upper section of sample SGF 10 is younger than 1.16 Ma. This species is last recorded in sample SGF 18, near the upper boundary of the formation, suggesting that this layer is older than the LAD of *R. asanoi* (0.85 Ma ; Sato and Kameo, 1996).

Thus, it is clear that the Seoguipo Formation comprises the latest Pliocene to Early Pleistocene nannofloras. The lower boundary is older than 1.72 Ma, while the upper one is slightly younger than 0.85 Ma. The calcareous nannofossil of this formation is assigned to the *P. lacunosa* Zone (NN19) (Martini, 1971), which corresponds to the combined zones *E. annula* to *E. ovata* (CN13a-CN14a ; Okada and Bukry, 1980) of the latest Pliocene to Early Pleistocene.

3. Paleoceanography

The four ecostratigraphic zones established on the basis of the floral composition reflect paleoceanographic conditions (Figure 2). The lowermost section, Zone I is characterized by co-existence of cold (subpolar) and warm (subtropical) water masses. The cooler-water influence increases upward reaching its peak in the middle part of the core (Zone II). It deteriorates toward the upper part (Zone III) until it is totally replaced in Zone IV under the influence of warmer water. This is interpreted as a cooling phase which began in Zone I, culminated in the Zone II, and finally faded out at the upper section (Zone III and IV). In view of the absence of any cold-water current in the present sea around the study area this would seem to be a reflection of the glacial-interglacial cycle rather than due to the local influence of a warm-water current. Comparing the cooling phase with biochronological data, it is certain that a glacial cycle in the study area started shortly before 1.72 Ma (FAD of *G. caribbeanica*) and halted around 0.94-1.02 Ma (reoccurrence of *G. oceanica*).

The distribution of calcareous nannofossils in the Seoguipo Formation also records the position of an oceanographic frontal boundary between warmer water derived from a branch of the Kuroshio Current as it entered the Japan Sea to the north and cooler water introduced into the western portion of the Japan Sea derived from the Liman Current. This oceanographic front oscillated back and forth in response to the ongoing cooling phase. It probably lay near Cheju Island during deposition of Zone I and Zone III, whereas it stood south and north of the island during formations of Zone II and Zone IV, respectively.

Figure 3. All illustrations are light micrographs. Abbreviations : XP=cross-polarized light, TR=transmitted light. Magnification= ×2,000. **1, 2.** small *Gephyrocapsa* spp., SGF 12, XP. **3.** small *Gephyrocapsa* spp., SGF 11, XP. **4.** *Gephyrocapsa caribbeanica*, SGF 5, XP. **5.** *Gephyrocapsa caribbeanica*, SGF 10, XP. **6.** *Gephyrocapsa oceanica*, SGF 7, XP. **7.** *Gephyocapsa oceanica*, SGF 30, XP. **8, 9.** small *Reticulofenestra* spp., SGF 10, XP. **10.** small *Reticulofenestra* spp., SGF 11, XP. **11.** *Reticulofenestra asanoi*, SGF 15, XP. **12.** *Pseudoemiliania lacunosa*, SGF 11, XP. **13.** *Pseudoemiliania lacunosa*, SGF 5, XP. **14.** *Syracosphaera* sp., SGF 12, XP. **15.** *Syracosphaera pulchra*, SGF 18, XP. **16.** *Helicosphaera* sp., SGF 12, XP. **17.** *Helicosphaera* sp., SGF 17, XP. **18.** *Umbilicosphaera sibogae*, SGF 11, XP. **19.** *Coccolithus* sp., SGF 16, XP. **20a, b.** *Calcidiscus leptoporus*, SGF 11, a : XP., b : TR. **21.** *Helicosphaera carteri*, SGF 11, XP. **22.** *Helicosphaera carteri*, SGF 12, XP. **23.** *Coccolithus* sp., SGF 7, XP. **24.** *Coccolithus* sp., SGF 1, XP. **25a, b.** *Calcidiscus macintyrei*, SGF 4, a : XP., b : TR. **26.** *Calcidiscus macintyrei*, SGF 5, XP. **27.** *Calcidiscus leptoporus*, SGF 3, XP. **28.** *Coccolithus pelagicus*, SGF 5, XP. **29.** *Coccolithus pelagicus*, SGF 7, XP. **30a, b.** *Pontosphaera japonica*, SGF 12, a : XP., b : TR. **31.** *Pontosphaera japonica*, SGF 7, XP. **32.** *Braarudosphaera bigelowii*, SGF 5, XP. **33a, b.** *Ceratolithus cristatus*, SGF 4, a : XP., b : TR.


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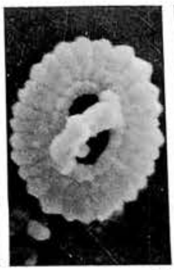
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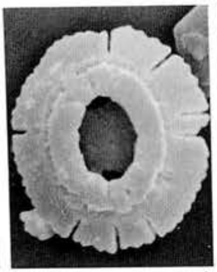
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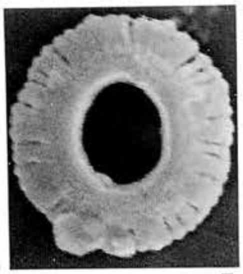
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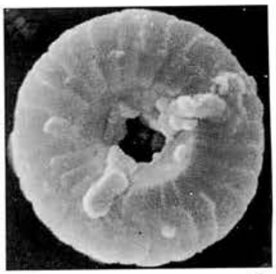
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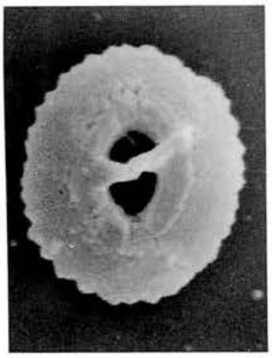
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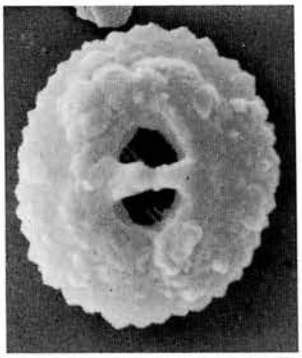
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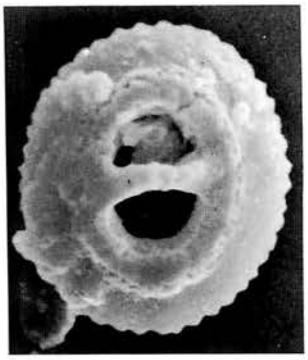
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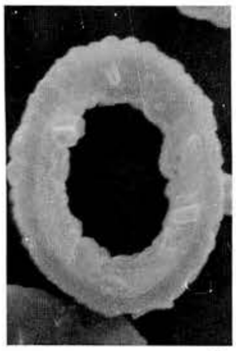
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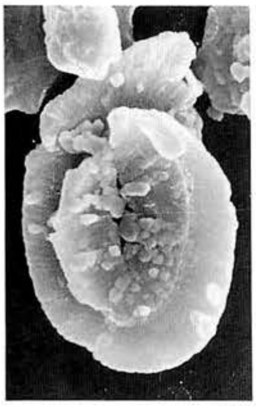
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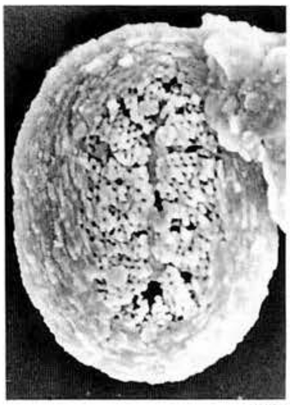
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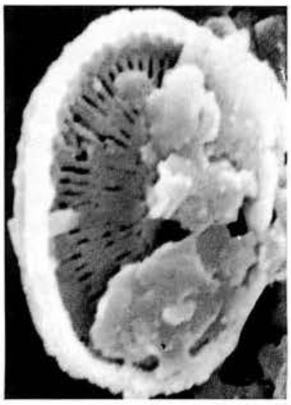
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Discussion

1. Stratigraphy

Although the exposure of the Seoguipo Formation above sea level measures about 50 m thick in the Seoguipo area, this formation is developed in the subsurface throughout Cheju Island except for the eastern area of a line connecting Bukchon and Pyoseon. The upheavals of the Seoguipo Formation at Seoguipo City indicate a 150 m uplift of this area at least (cf. Yoon, 1988). However, it is reasonable to suspect that the Seoguipo Formation was formed at a much lower level than where it is at present, since sea level dropped 85-130 m during intense global glacial periods (Muza, 1992).

Quaternary studies on the Seoguipo Formation reported that the outcrop of the Seoguipo Formation in Seoguipo stratigraphically differs from its subsurface strata (Yun *et al.*, 1987 ; Lee *et al.*, 1987). The above-mentioned researchers considered the age of the Seoguipo Formation to be Middle Pleistocene (0.60-0.41 Ma). They further insisted that subsurface marine sediments recovered from core are Lower Pleistocene (1.2-0.87 Ma) in age (Table 1). For the age determination of sedimentary bodies they applied the paleomagnetic data and radiometric age (K-Ar) of the volcanic rocks that they believed to underlie or overlie two different sedimentary sequences. However, the FAD and LAD of index nannofossils such as *G. caribbeanica* (3.5-4 μm), *G. oceanica* (>4 μm), *C. macintyrei*, *R. asanoi*, *P. lacunosa* and the characteristic nannoflora of the four ecostratigraphic zones recognized in the outcrop section are also observed in 20 cores of Cheju Island. These facts imply that the outcrop strata are to be stratigraphically correlated to subsurface ones. The ecostratigraphic zones and their order of appearance, cold-dominant transitional, cold, warm-dominant transitional, and warm phase from bottom to top can be used as a good stratigraphic tool in Cheju Island. The subdivision of these units largely coincides with that of lithostratigraphic units.

The geologic age and stratigraphic range of the Seoguipo Formation provide a clue in determining the stratigraphic position of comparable sedimentary deposits in Cheju Island and Japan. In previous molluscan studies *Turritella saishuensis*, which occur throughout the Seoguipo Formation, is regarded as an index species for the depositional period of the Seoguipo Formation. However, the lower boundary of this formation is ambiguous due to the absence of stratigraphic marker fossils that may be caused by an influence of cold-water current. Therefore, the FAD of *Turritella saishuensis* also could not be clearly delineated. Some recent paleontological works attempted to define the age of the Seoguipo Formation by paleoceanographic conditions in the Early Pleistocene, when the cold-water mass expanded and the southward migration of the boreal species proceeded further along the Japan Sea borderland (Lee, 1990 ; Kang, 1995 ; Woo *et al.*, 1995). However, there are two different results for the age of first occurrence of *Turritella saishuensis* in the Seoguipo Formation ; Pliocene or Pleistocene. The Pliocene to Pleistocene Omma-Manganzian fauna in Honshu Island of Japan is correlated with the Seoguipo fauna based on the *Turritella saishuensis* bioseries (Ogasawara, 1981, 1986, 1996 ; Yoon, 1988). Our result confirms the lower stratigraphic range of the Seoguipo Formation and extension of the FAD of *Turritella saishuensis* to the latest Pliocene. Consequently, the formations correlated to the Seoguipo Formation might be stratigraphically placed between upper Pliocene and Pleistocene (Yoon, 1988).

The paleomagnetic normal polarities of the Seoguipo Formation have been interpreted as the Gauss Normal Polarity Epoch of late Pliocene age (Min *et al.*, 1986) or the Brunhes Normal Polarity Epoch in the middle Pleistocene (Yun *et al.*, 1987). Referring to the reverse polarity of the unconformably overlying Sanbangsan Trachyte, the Seoguipo Formation was placed in the Matuyama Reverse Polarity Epoch of the early Pleistocene (Taneda *et al.*, 1970). However, in a recent paleomagnetic study of the Seoguipo Formation two reversals were recognized in the upper part of the Seoguipo outcrop (Lee, 1998).

2. Biochronology

Previous paleontological studies on the Seoguipo Formation suggested that it was deposited during the Late Pliocene (Yokoyama, 1923 ; Kim, 1972 ; Kim, 1984 ; Yoon, 1988), Pleistocene (Haraguchi, 1931 ; Lee, 1990 ; Kang, 1995) or around the Plio-Pleistocene boundary (Paik and Lee, 1984 ; You *et al.*, 1987).

Our study suggests the age of the upper boundary of the formation is slightly younger than 0.85 Ma based on the presence of *P. lacunosa* (Last Appearance Datum : 0.41 Ma) and LAD (0.85 Ma) of *R. asanoi* (Table 2, Figure 2). It is confirmed by the reoccurrence of *G. oceanica* (>4 μm ; e.g. medium *Gephyrocapsa*) whose acme zone is known to be 0.94-1.02 Ma, in the upper part of the formation. This age of the upper boundary coincides with the results of radiometric K-Ar age of overlying basalt rocks (Table 1 ; Sanbangsan Trachyte : 0.733±0.056 Ma [Won *et al.*, 1986], 0.87±0.13 Ma [Yun *et al.*, 1987] ; Gaksuam Trachyte : 0.893±0.027 Ma [Lee, 1994]). The boundary of the Pleistocene-Pliocene determined by the FAD of *G. caribbeanica* (1.72 Ma) is regarded to lie between Sample SGF 4 and SGF 5. The two samples (SGF 3 and 4) of cold-water environment below Sample SGF 5 are provisionally assigned to the Pliocene, because they may not contain the Pleistocene index taxa for environmental reasons. However, the lowermost part of the formation (Sample SGF1 and 2) definitely belongs to the

Figure 4. All illustrations are Scanning Electron Micrographs. Scale bar equals 2 μm. **1, 2.** small *Gephyrocapsa* spp., SGF 11. **3.** small *Reticulofenestra* spp., SGF 11. **4.** *Pseudoemiliania lacunosa*, SGF 30. **5.** *Pseudoemiliania lacunosa*, SGF 11. **6.** *Umbilicosaphera sibogae*, SGF 11. **7, 8.** *Gephyrocapsa cabibbeanica*, SGF 30. **9, 10.** *Gephyrocapsa oceanica*, SGF 30. **11.** *Coccolithus* sp., SGF 1. **12.** *Calcidiscus leptoporus*, SGF 11. **13.** *Calcidiscus leptoporus*, SGF 11. **14.** *Calcidiscus leptoporus*, SGF 11. **15.** *Coccolithus pelagicus*, SGF 5. **16.** *Helicosphaera carteri*, SGF 11. **17.** *Pontosphaera japonica*, SGF 30. **18.** *Syracosphaera pulchra*, SGF 30.

Pliocene in age, since its relatively warmer environment exclude the possibility of climatic effect on distribution of index taxa. This presumption is also supported by normal polarity (Olduvai Normal Polarity Subepoch) specifically obtained from the paleomagnetic analysis of samples SGF 1-SGF 4 (Lee, 1998).

3. Paleoceanography

1). **Paleotemperature.**—Most paleontological studies reported that the Seoguipo floras and faunas are composed of mixtures of warm- and cold-water elements (Paik and Lee, 1984; You *et al.*, 1987; Yoon, 1988; Lee, 1990; Kang, 1995). According to our results the Seoguipo sequence is characterized by a cooling phase in the lower part and a warm phase in the upper part, and by two transitional phases (Figure 2). Ecostratigraphic Zone I is a first transitional phase in the lowermost part of the formation before beginning of cooling phase. Zone II is characterized by abundant occurrence of *C. pelagicus* is the coldest zone among the eco-zones of the Seoguipo Formation. *C. pelagicus* is presently restricted to the subarctic and transitional waters in the North Atlantic (7°-14°C: McIntyre and Bé, 1967) and North Pacific (6°-14°C: McIntyre *et al.*, 1970). This fact indicates that the paleotemperature of the surface water during deposition of this zone was below 14°C. Zone III is the second transitional phase indicating turnover to the general warming trend. The remarkable bio-event during deposition of the Seoguipo Formation is the sudden emergence of warm-water taxa in this zone. The abundance of *C. pelagicus* abruptly decreases, whereas diversity and abundance of the warm-water elements of *C. leptoporus, U. sibogae, G. oceanica,* and *S. pulchra* (the first two being oceanic elements) increase substantially. *G. oceanica* is presently distributed within a temperature range of 18°-29°C (McIntyre *et al.*, 1970; Honjo, 1977) or 19°C-31°C (Brand, 1994, p. 44). *Umbilicosphaera sibogae* prefers moderately nutrient-rich, tropical water (Roth and Coulbourn, 1982; Brand, 1994). *S. pulchra* is also a characteristic species in tropical and subtropical environments (Roth and Coulbourn, 1982). Zone IV in the uppermost part of the Seoguipo Formation contains diverse and abundant warm-water taxa. This means that the paleotemperature of the surface water of Zone III and IV was slightly warmer than the average present temperature, 19.38°C (Kwak *et al.*, 1993).

Study of ostracods also revealed similar paleoclimatic patterns to our results in six established biotopes of the formation; cooling phase in the lower part of the formation and warming trend upward (Lee, 1990). Assemblage of biotope 1 and 2 (Eco-Zones I and II: SGF 1-SGF 10) in the lower part of the formation is dominated by cold-water elements such as *Normanicythere sogwipoensis* and *Kotoracythere paiki* which are completely replaced by the warm-water elements *Cytheropteron uchioi* and *Cytheropteron abnormis* at biotope 3 (basal part of the Eco-Zone III: SGF 11-SGF 12), and in biotopes 4 and 5 (middle part of the Eco-Zone III: SGF 13 - SGF 14) the cold-water elements slightly increase again. The upper part of biotope 6 (upper part of Eco-Zone IV and higher: SGF 15-SGF 19) is characterized by a decrease in the cold-water elements and the occurrence of several warm-water elements. The warm-water ostracods found in the Seoguipo Formation are presently distributed in the South China Sea, southern part of the Yellow Sea and Korean South Sea influenced by warm Kuroshio Current (Lee, 1990).

Amano (1994) investigated the surface temperature of the Japan Sea in the Pleistocene through molluscan assemblages from coastal areas of the Japan Sea of Hokkaido to Cheju Island. He estimated the paleotemperature of the Seoguipo Formation as 20°C warmer than the average present temperature, 18.5°C (Marine Environment Map by Japanese Marine Safety Agency).

Woo *et al.*, (1995) analyzed oxygen isotopes from calcareous skeletons of Mollusca. The paleotemperature of his lithologic Unit 4 (SGF 5-SGF 10) from the Seoguipo Formation is calculated to be 13°C. He considered his lithologic Unit 4 the coldest, and the warmest temperature for the entire sequence was 18°C. Paleotemperature of other Units 1, 9, 11, 13 varies from 14 to 17°C. Based on these data, he concluded that the whole sequence of the Seoguipo Formation was deposited during glaciation. His paleoclimatic interpretation coincides with our results for the lower part of the Seoguipo Formation influenced by cold water.

2). **Paleoceanographic front.**—The site of the Seoguipo Formation is now located in warm surface waters south of an oceanographic front. However, in response to Pleistocene glacial episodes in the last 1.8 m.y. the cold-water front may have migrated southward over Cheju Island as global climate cooled (Momohara, 1994), the sphere of cooler-water influence expanded, and the effect of the warm-water Kuroshio Current diminished (Muza, 1992). Then the Pleistocene nannofossil association in the Seoguipo Formation could record the oscillation or migration of the oceanographic front over Cheju Island as the Japan Sea and the Korea Strait responded to glacial-interglacial cycles. If this is the case, as the oceanographic front migrated southward over Cheju Island owing to global glaciation, cooler surface water would replace warmer water during the deposition of the Seoguipo Formation. This, in turn, may have resulted in a reduced calcareous nannoplankton diversity dominated by cooler-water forms such as *C. pelagicus* as shown in the lower part of the Seoguipo Formation. A lowering of the sea level around the Cheju area in response to the early Pleistocene glaciation is also expected.

Conversely, when the Seoguipo Formation was located south of the oceanographic front in warmer water, assemblage diversity may have been higher, dominated by warmer-water forms such as *G. oceanica*. Since glacial and interglacial cycles have been the primary influence on oceanography of the Japan Sea, Korea Strait, and the vicinity of Cheju Island during the last 1.8 m.y., the changing paleoceanographic conditions of the Seoguipo Formation indicated by the nannofossil assemblages are primarily interpreted as an expression of global climatic changes.

The migration of the oceanographic front is related to the influence of local warm-water currents and global glaciation in the Pleistocene. As a function of these two factors the oceanographic front migrates southward or northward. When global glaciation set about, the cooler-water front was built first in the Oki Ridge, Ishikawa-Toyama area and migrated southwards to Cheju Island and the Okinawa Trough about 1.8 Ma (Figure 5). It retreated from the Okinawa Trough at 1.60-1.64 Ma (LAD of *C. macintyrei*), from Cheju Island at 0.94-1.02 Ma (reoccurrence of *G. oceanica*), and from the Oki Ridge and the Ishikawa-Toyama area of Japan at 0.85 Ma. The duration of the cooling phase is shortest in the Okinawa Trough and longest in the Japan Sea. Generally invasion of cooler water took place abruptly in comparison to the relatively slow retreating process. Influence of cooler water that migrated southward is well documented in the samples of Oki Ridge, Ishikawa-Toyama area, Niigata area, Seoguipo Formation and Okinawa Trough (Kobayashi, 1990 ; Muza, 1992 ; Ogasawara, 1996 ; Yi *et al, in press*). Considering the geographic location and present-day oceanography only the Niigata area provides an exceptional case, since a cooling phase in this area appeared later and disappeared earlier than expected for its geographic location. The duration of the cooling phase in the Niigata area is also different from that of the neighboring Ishikawa-Toyama area. Therefore, the influence of a warm-water current (*G. inflata* bed No. 2) in this area is considered to be stronger than global glaciation effect in the Pleistocene.

Regarding the cooling phase and cold-water influence in the Seoguipo Formation that lasted from ca. 1.8 Ma to 0.94-1.02 Ma, it would appear that the Korea Strait never closed during the first Quaternary glaciation. Hence, the cold-water current could expand through the Korea Strait into the Okinawa Trough (Yi *et al., in press*).

3). **Paleobathymetry.**—The depositional environment of the Seoguipo Formation was interpreted as a littoral zone of shallow sea based on the foraminifera (Kim, 1972), Mollusca (Yoon, 1988) and brachiopods such as *Coptothyris grayi* and *Terebratalia coreanica* that are indicative of a depth of about 50 m (Kim, 1984). Ostracod studies from the Seoguipo Formation enabled a finer subdivision of six biotopes deposited in a shallow sea ranging from bay, through near-shore, to offshore environments (Lee, 1990). An investigation of molluscan fossils suggests the Seoguipo Formation has been formed under the environment of bay to open sea (Kang, 1995).

Among the nannofossil assemblage, neritic species such as *Braarudosphaera bigelowii, Gephyrocapsa oceanica*, and *Syracosphaera* spp. occur consistently throughout the formation except for the upper part (Sample SGF 11), where

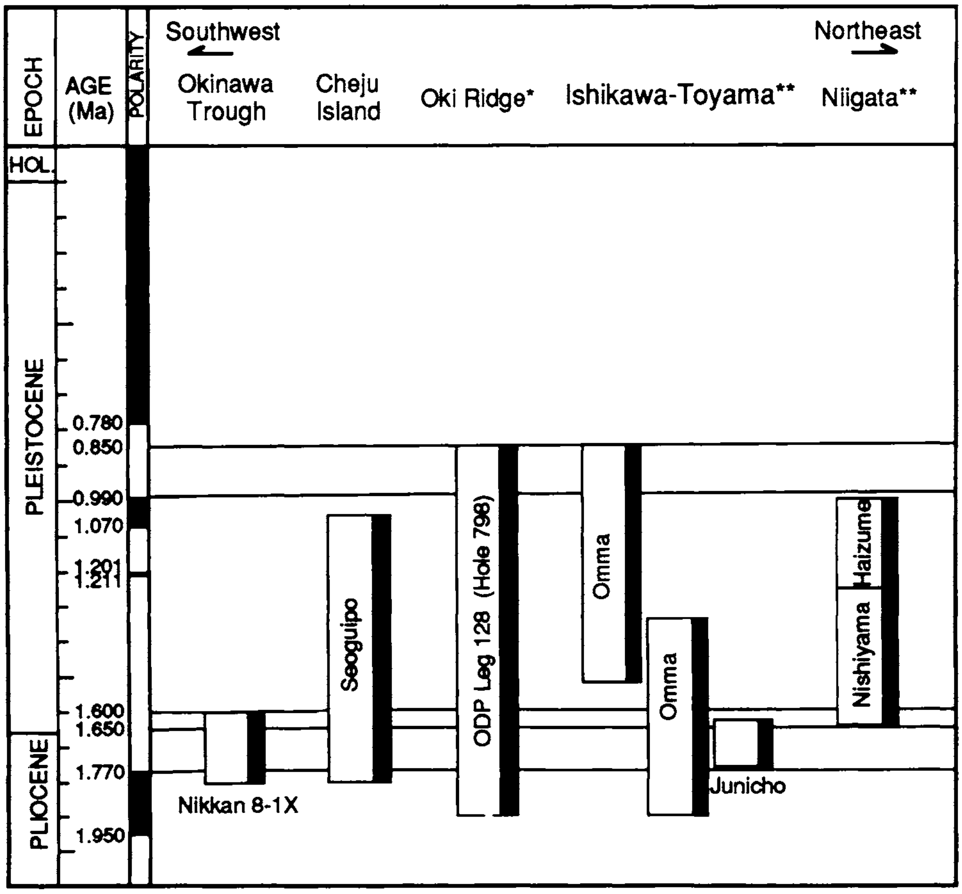

Figure 5. Correlation of Plio-Pleistocene cooling phases between the Okinawa Trough, Cheju Island, Oki Ridge, and Japan Sea (East Sea) borderland of Japan (Polarity : Cande and Kent, 1995 ; * : Muza, 1992 ; ** : Ogasawara, 1996).

oceanic species *Calcidiscus leptoporus* and *Umbilicosphaera sibogae* are common. Occurrences of the oceanic taxa in this upper part are accounted for the global warming trend and consequent rising of eustatic sea level. Ostracods from the sample of SGF 11 also indicate that this section was deposited in the outer shelf at depths from 50 m to 100 m.

It is also presumed that the Seoguipo Formation was uplifted after deposition, because its present altitude is above the presumed sea level in the Early Pleistocene glaciation.

Acknowledgements

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Anatomy of a complex trace fossil: *Phymatoderma* from Pliocene bathyal mudstone, northwestern Ecuador

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Abstract. An exceptionally well-preserved example of *Phymatoderma granulatum* from continental slope deposits within the Pliocene Upper Onzole Formation, coastal Ecuador, supports an important reinterpretation of this large, branching, subhorizontal burrow system. Traces such as this have been regarded simply as fodinichnia (the work of subsurface deposit feeders). However, we propose that the trace producer was capable of changing its feeding strategy as a probable adaptation to a variable trophic regime. Tunnels within the burrow system are filled with pelleted volcanic ash conveyed from the seafloor to subsurface storage areas, indicating surface deposit feeding; the same tunnels enclose secondary tunnels that rework the primary fill of pellets, pointing to recycling/restocking of fecal banks as another trophic behavior. Alternative feeding strategies represented in *P. granulatum* could be the reactions of the burrowing animal to a pulsed delivery of labile organic material at the ocean bottom (in this instance associated with large ashfalls).

Key words: Continental slope, deepsea paleoecology, Ecuador, ethology, *Phymatoderma*, Pliocene

Introduction

Unique, well-preserved fossil specimens have always been crucial in paleontology for working out the details of anatomy, function, ecologic properties, and genealogic relationships of every kind of organism, from protist to dinosaur. A newly discovered specimen, having all the skeletal elements intact, appendages still attached or the soft tissues preserved, is often more important than all the fragmentary remains of a particular species (or higher taxon) ever collected. The same thing is true for trace fossils: exceptional preservation can lead to breakthroughs in behavioral and ecologic interpretations.

In this paper we describe an exceptional example of *Phymatoderma granulatum* (Schlotheim, 1822) from Pliocene continental slope deposits of Ecuador (Figure 1), a specimen that allows a more comprehensive interpretation of this biogenic structure than was previously possible. *Phymatoderma* [identified by most authors as "*Zonarites*", "large *Chondrites*", or "pellet-filled *Chondrites*" (see Seilacher, 1954, 1958; Simpson, 1956; Sellwood, 1970; Chamberlain, 1977; Brenner and Seilacher, 1978; Pickerill *et al*., 1984; Savrda and Bottjer, 1989; Savrda *et al*., 1991)] is a distinctive, subhorizontal, branching burrow system consisting of clusters of radiating tunnels that converge and overlap near the center of the system. Such structures have been interpreted as fodinichnia (burrows produced by subsurface food-mining activity). However, we can show that the organism that produced the Ecuadorian specimen was involved in more complicated behavior than simply subsurface deposit feeding, and apparently was capable of changing its feeding behavior and controlling its trophic resources to some extent. Although traditional methods of description and structural analysis can be applied to such intricate burrow systems, the traditional ethologic classification of trace fossils does not accommodate this kind of behavioral complexity. This paper supports and extends previous work by Miller and Vokes (1998) on the same trace fossils.

The example of *P. granulatum* described and illustrated here has been deposited in the University of California Museum of Paleontology (UCMP 39901).

Geologic context

The example of *P. granulatum* that we document was part of a moderately rich ichnofauna occurring in green mudrocks of the Pliocene Upper Onzole Formation, exposed near the coastal city of Esmeraldas (Figure 2). Visible in extensive wave-cut platforms and seacliffs at Punta Gorda (Figure 3), the formation consists of over 300 m of mostly thick-bedded mud turbidites with mud pelagite, silt-sand turbidite, and comparatively light-colored volcanic ash interbeds. The ichnofauna is preserved at the tops of the mud turbidite beds. Other common ichnotaxa in the Upper Onzole at this location include *Alcyonidiopsis* ichnosp., *Chondrites intricatus, Phycosiphon incertum, Rorschachichnus amoeba*, and *Zoophycos* ichnosp. The ichnofauna has been described recently by Miller and Vokes (1998).

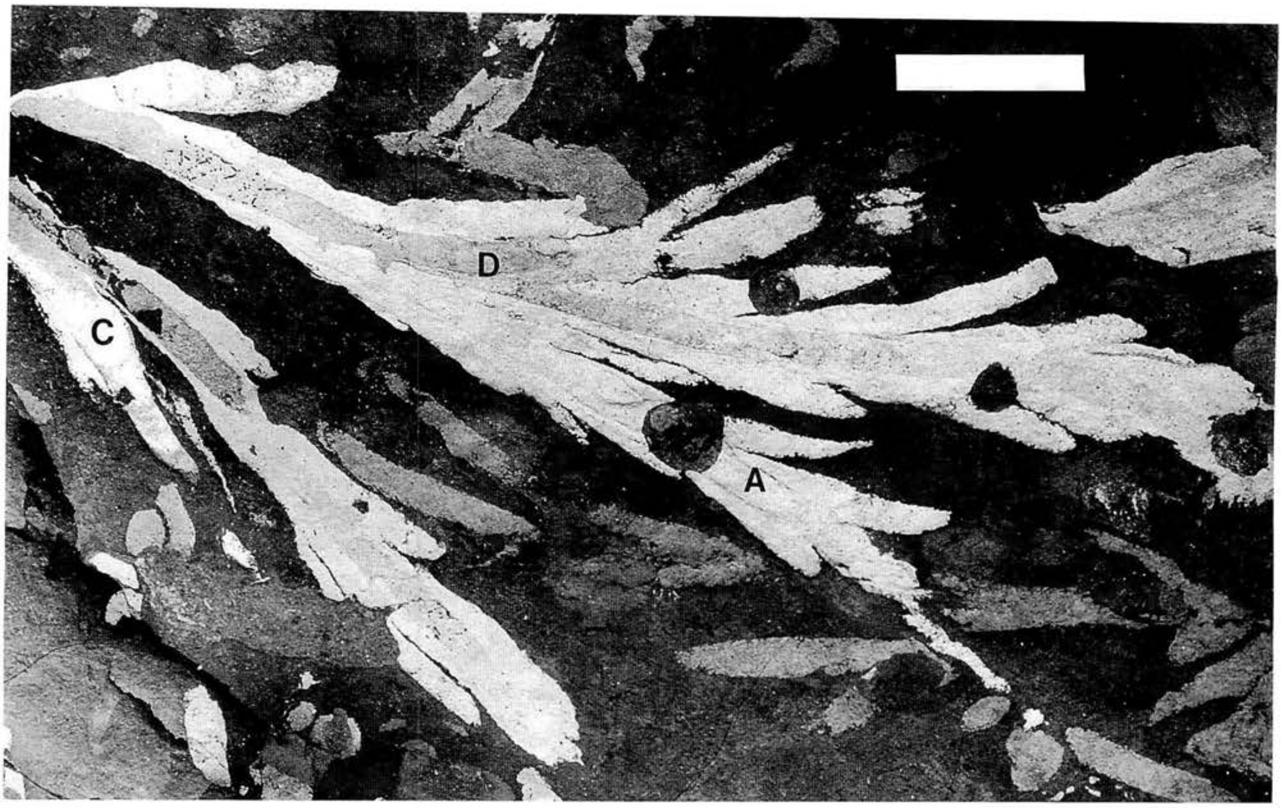


Figure 1. A large, well-preserved example of *Phymatoderma granulatum* from the Pliocene Upper Onzole Formation of northwestern Ecuador (UCMP 39901). Letters indicate locations of close views shown in Figure 5. Scale bar represents 4 cm.

Where the burrow systems occur below a volcanic ash, overall form and internal structure of the trace fossils have been preserved in extraordinary detail (Figures 4, 5). In this situation, burrows were filled either passively or by the trace producers actively conveying ash to subsurface tunnels or galleries, resulting in an ichnofauna that stands out in sharp contrast to the dark-colored matrix (Figures 1, 4B, 5). *Alcyonidiopsis, Zoophycos* and *Phymatoderma* all contain pellets made of the ash, indicating active filling of below-surface storage areas and suggesting that food caching or storage of fecal pellets was an important aspect of the behavior of animals that produced these varied structures. Kotake (1989, 1991, 1993, 1994) has described a strikingly similar pattern of ash-filled burrows occurring in Plio-Pleistocene bathyal deposits of Japan.

Mudrocks of the Upper Onzole Formation were deposited for the most part during planktic foraminiferid zones N. 19 and 20 (ca. 3-5 Ma), at bathyal depths on the inner trench slope (Evans and Whittaker, 1982; Whittaker, 1988). Aalto and Miller (*in press*) have proposed a trench-slope basin as the most likely depositional setting (Figure 2B). The basin received sediment chiefly in the form of successive, large-scale, muddy turbidity currents. Benthic ecosystems were continually reestablished on each newly deposited mud blanket; endobenthic populations produced distinctly tiered ichnoassemblages following recolonization (Figure 4A), of which *P. granulatum* is the most prominent component (Figure 4B). Thus, the Upper Onzole trace fossils represent the benthic ecosystems that existed in the basin "between" episodes of disturbance caused by the turbidity currents.

Paleoethologic classification and analysis

We are accustomed to the practice of equating an ichnotaxon to a single ethologic category or to one kind of organism-environment interaction. Most ichnologists employ the ethologic classification originally proposed by Seilacher (1953, figure 6), and subsequently modified to include additional categories (Ekdale *et al.* 1984; Frey and Pemberton, 1984; Ekdale, 1985; see recent summary in Bromley, 1996), to label the modal or most obvious behavior deduced for a particular biogenic structure. This classification has produced satisfactory results when applied to structurally simple traces that are essentially snapshots of a dominant habitat interaction or behavioral reaction, and has been used successfully in the analysis of stratigraphic successions and paleoenvironmental trends (Ekdale *et al.*, 1984; Pemberton, 1992). There have been problems created, however, by over-extending the scheme.

One unfortunate result has been to associate an ichnogenus (e.g., *Zoophycos*) exclusively with one of the standard ethologic categories (e.g., fodinichnia), even though the structures identified with that name could have been made at different times during the Phanerozoic by different kinds of

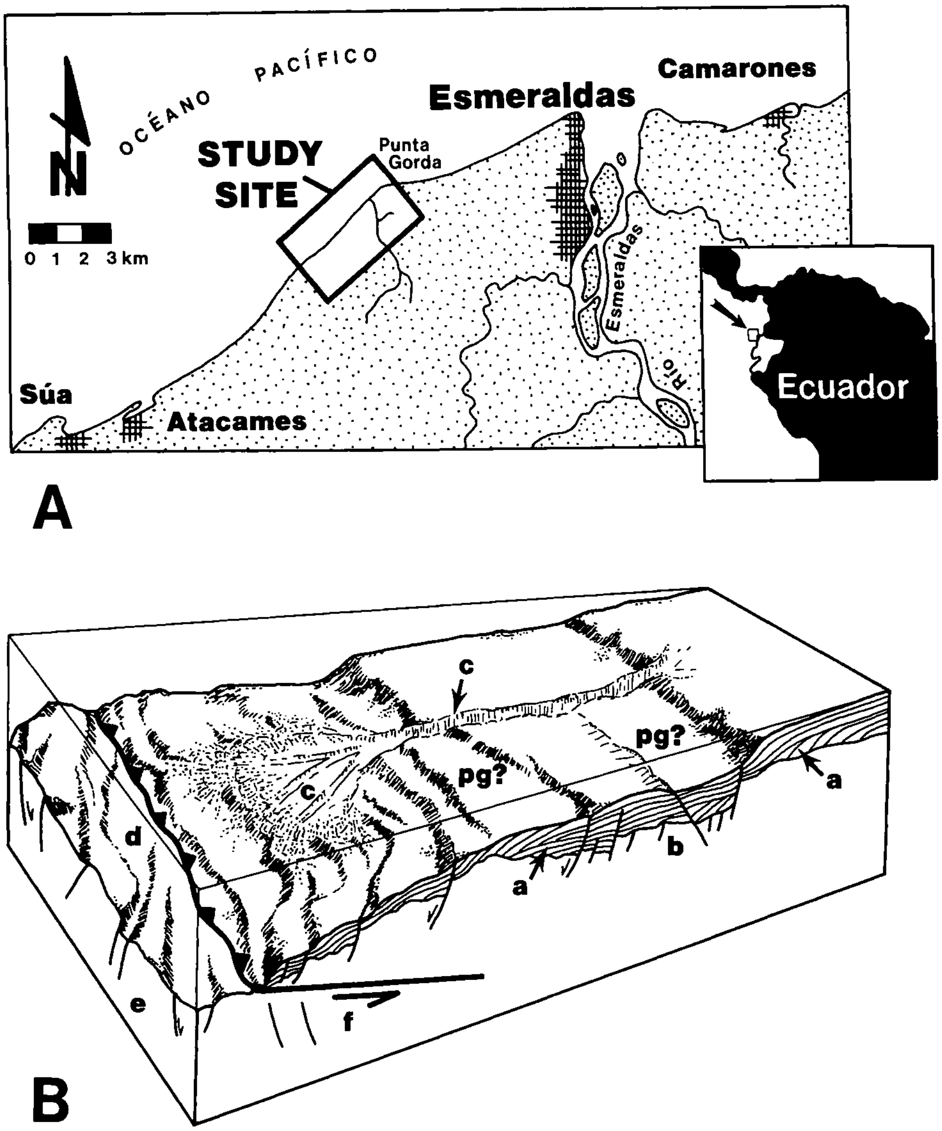


Figure 2. Location and paleogeographic reconstruction of the study site. (**A**) Location map. (**B**) Reconstruction of Pliocene continental margin of the Esmeraldas area showing possible position of study site on the inner trench slope (pg), Neogene trench-slope deposits and inboard equivalents (a), normal faults (b), Esmeraldas canyon-fan system (c), trench floor (d), oceanic crust (e), and subduction zone (f). Not drawn to scale; from Aalto and Miller (in press).

animals, possibly for different purposes. A more significant problem comes from the reevaluation of structurally elaborate traces (e.g., *Zoophycos, Paleodictyon, Ophiomorpha-Thalassinoides*, and other compound systems). These intricate burrow systems record long-term occupation in some cases (Bromley, 1996); variable behavior and possibly some form of habitat restructuring [including control of local environment, damping of disturbances, and active management of food supplies (see Hansell, 1984; Vander Wall, 1990; Jones *et al*., 1994)]; and "extended phenotypes" of the trace producers affecting their survival and fitness (Dawkins, 1989). Such animal artefacts contain evidence of complicated behavioral routines and subroutines involved in the construction, operation and maintenance of the structures. In this view, they are comparable to complex terrestrial artefacts like beaver dam-lodge-impoundment systems and termite "nests".

The traditional ethologic classification was not intended to accommodate this kind of complexity. Miller (1996a, b, 1998) has proposed that intricate biogenic structures preserving evidence of complex behavior, including some control of local environments, should be designated as "deliberate" trace fossils and receive special attention as rich sources of paleoethologic data; simpler, "incidental" structures (typically short-lived and preserving evidence of one kind of behavior or reaction) can still be accommodated in the

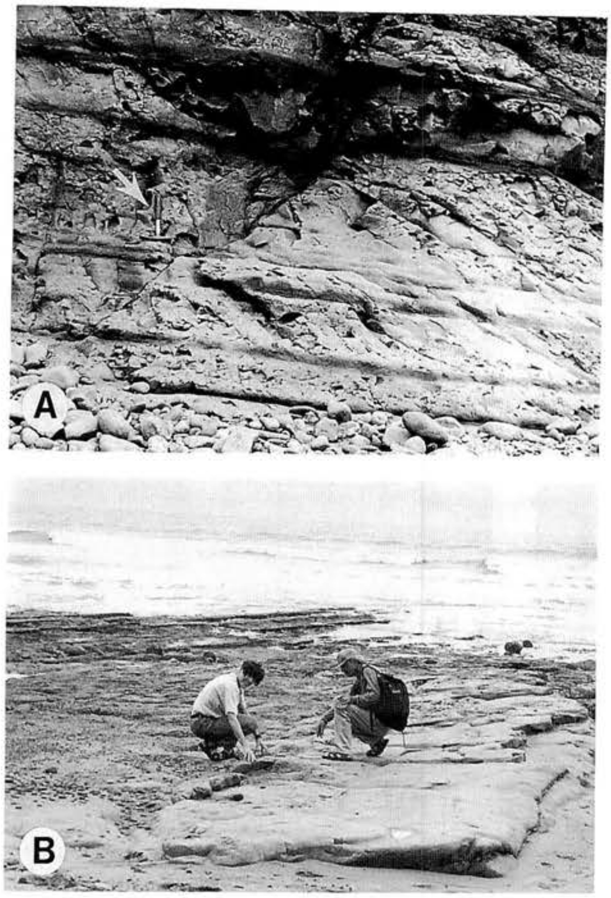


Figure 3. Punta Gorda outcrops of the Upper Onzole mudstone. (**A**) Seacliff consisting of thick muddy turbidites (hammer at arrow is 25 cm long). (**B**) Intertidal platform showing large, gently-dipping bedding surfaces (S. Walker and F. Cortez for scale).

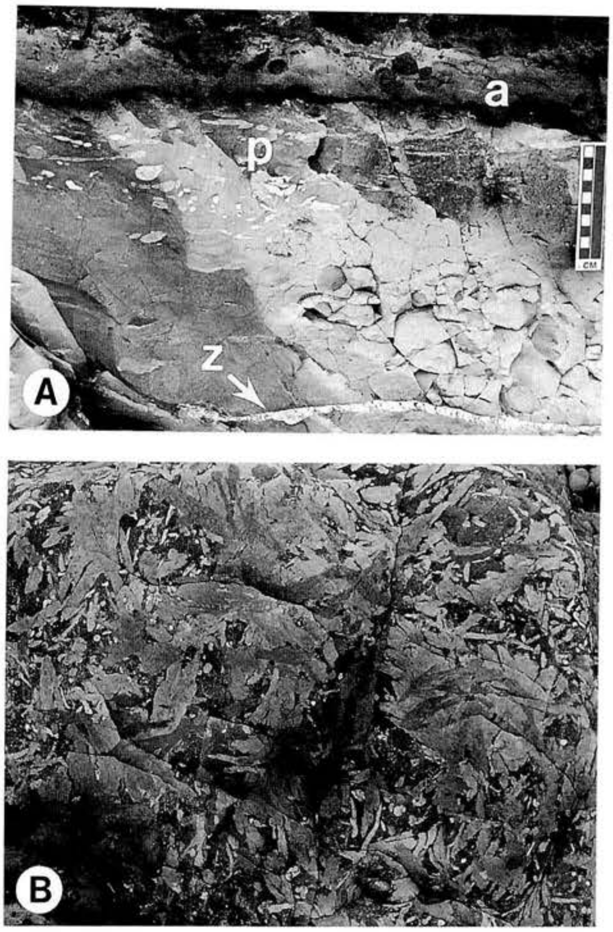


Figure 4. Punta Gorda trace fossils. (**A**) Tiered ichnoassemblage below a volcanic ash (a), with *Phymatoderma* (p) as the most prominent shallow burrow system and *Zoophycos* (z) as the deepest system. (**B**) Dense cluster of *Phymatoderma* on a bedding surface (field of view is approximately 0.5 m wide).

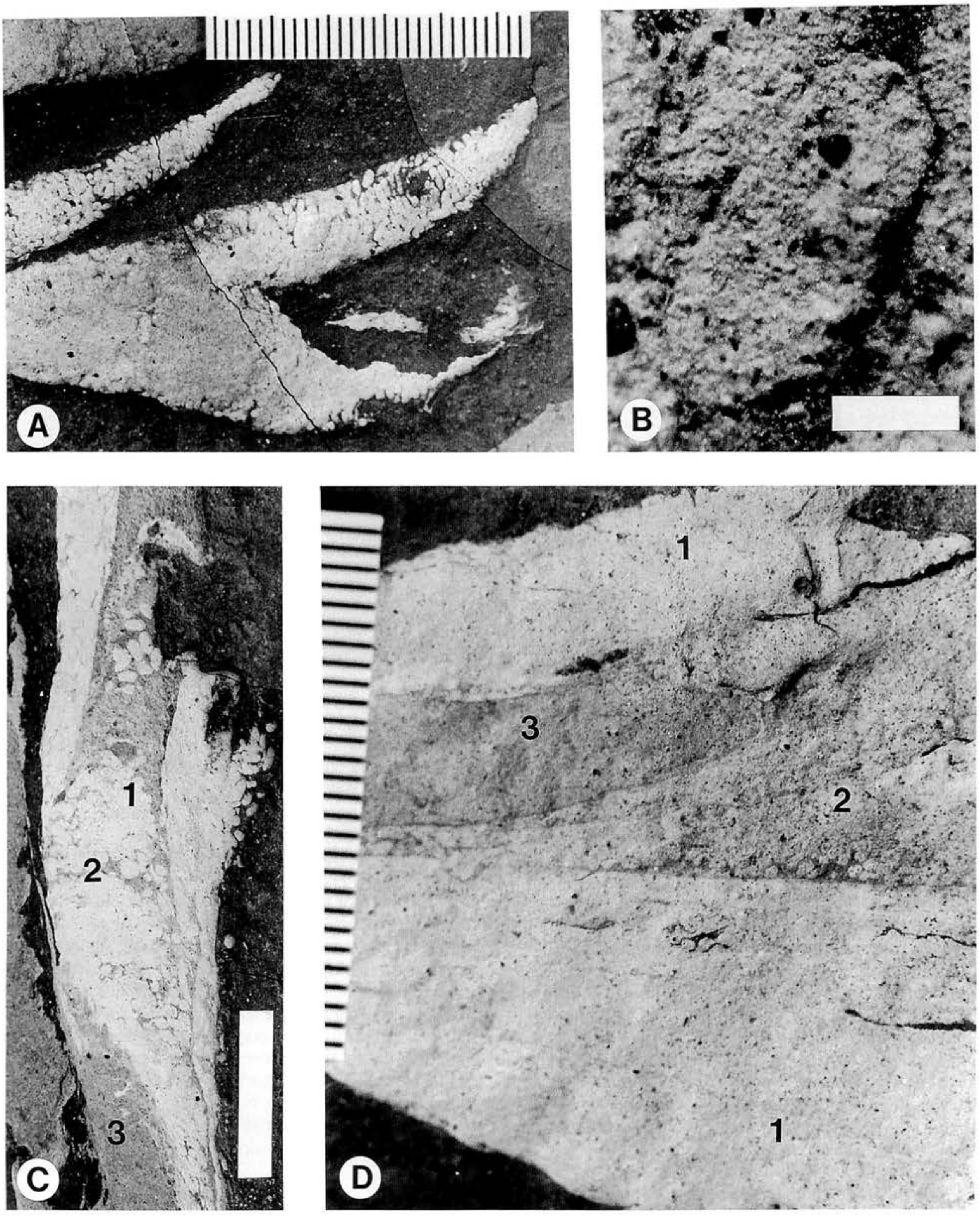
traditional classification. *Phymatoderma granulatum* is a complex burrow system and belongs in the former general category.

Paleoethologic analysis depends upon two sources of information: "morphology" (really a structural inventory) of trace fossils, and comparison with modern traces or trace-producing activity. This approach can be termed the "actualistic method" (reviewed in Seilacher, 1953; Schäfer, 1972; Frey, 1975; Frey and Seilacher, 1980; Ekdale *et al*., 1984; Frey and Pemberton, 1985; Pemberton, 1992; Bromley, 1996). The fundamental idea behind this form of analysis is that a fossilized "token" of behavior (e.g., branching pattern, wall structure, or the organization/composition of fill material of burrow systems) potentially can be matched to a modern structure produced by a particular kind of organism, or to a behavioral product made by different organisms having broadly similar adaptations. In cases where uniformitarian assumptions are tenuous or unsupported (as with interpretation of Vendian traces or with structures having unknown modern counterparts), description of structural elements, overall morphology, and size, together with very general comparison to trace-producing activity of modern organisms, still can yield plausible interpretations of biogenic structures. This is the method we have employed.

It is important to keep in mind that structural intricacy is related to behavioral complexity. The more complicated and varied the tokens of burrow fabrication, the more complicated is the behavior required to build, operate, and maintain a particular structure (Hansell, 1984; Dawkins, 1989). Thus, the behavior "visible" in a specimen of *Skolithos* or *Planolites* is simpler than that in *Zoophycos* or *Paleodictyon*, notwithstanding the fact that the entire behavioral repertoire of the trace producers is only partially recorded in these different structures. The obvious, but largely unappreciated, point to make here is that demonstrably complex structures are the records of complex behavior.

Ecuadorian *Phymatoderma*

General features: In the Punta Gorda exposures, *Phymatoderma granulatum* is a shallow-tier burrow system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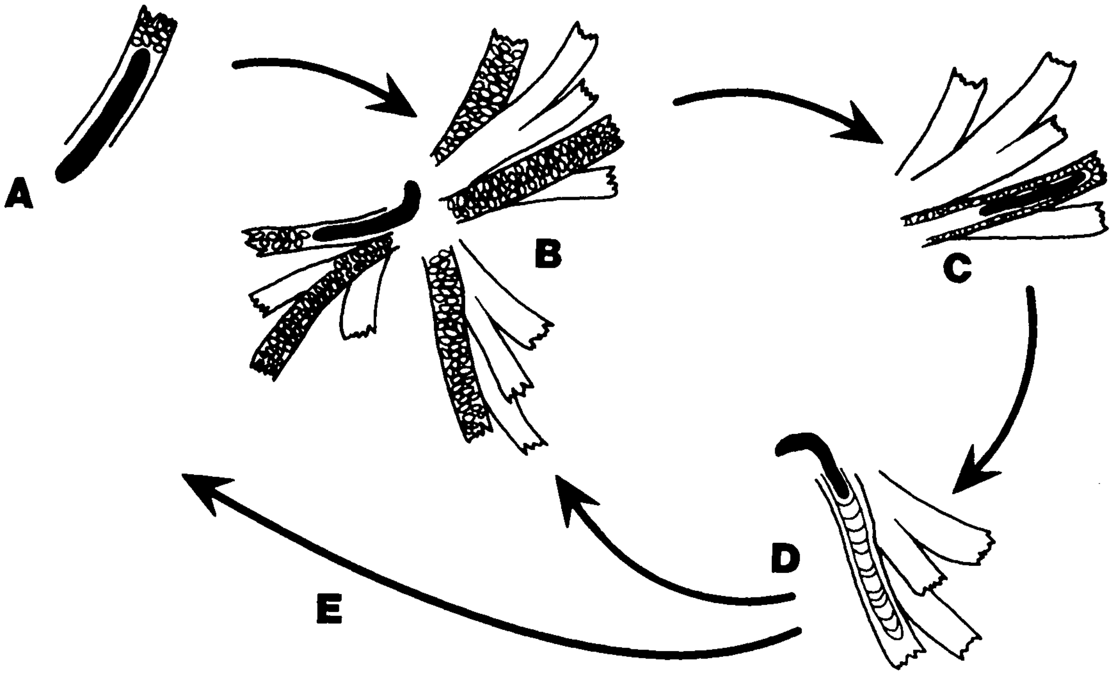

Figure 6. An "action cartoon" depicting the fabrication of Ecuadorian *Phymatoderma*. Successive parts include (**A**) initiation of structure, (**B**) construction and stocking of multiple tunnel bundles with pellets, (**C**) recycling of burrow contents, (**D**) withdrawal, and either (**E**) abandonment or (B again) restocking of structure. Only the most general features are shown.

occurring as clusters of large specimens (Miller and Vokes, 1998). The structures consist of bundles of radiating tunnels that overlap near the central region of the burrow system (Figures 1, 5). The tunnel bundles, or branches, extend outward 10 to 30 cm in typical specimens, but in a few instances the branches are >50 cm long. The branches themselves are organized in bundles that also diverge. Most of the structures were constructed at essentially one level below the seafloor; a few consist of multilevel systems. Estimated widths of the flattened tunnels vary from 3 mm to >1 cm within the same burrow system. Edges and terminations of tunnels are ragged, not uniformly smooth. Tunnels were originally unlined and filled with ellipsoidal pellets 1 to 2 mm in length.

These large burrows resemble some of the ichnospecies of *Chondrites*, but size, absence of uniformly smooth tunnel margins, subhorizontal orientation of the overall system, pelleted fill, and the overlapping tunnels allow recognition of *Phymatoderma* as a distinctive ichnotaxon. Fu (1991) has provided a taxonomic reevaluation of the ichnospecies of *Chondrites* and *Phymatoderma*, and we have adopted her concept of *P. granulatum here.*

Conveyed material: The contrast in color between the light-gray volcanic ash filling the tunnels and the enclosing dark-green mudstone is perhaps the most striking feature of the Ecuadorian burrows. The nearly pure ash in many of the tunnels originally occurred in the form of pellets made of material conveyed from the seafloor to subsurface storage areas. However, the primary pelleted fabric has been obliterated by reworking and possibly compaction in many specimens. In the example we illustrate (Figures 1, 4), one can see the original pelleted fabric preserved at tunnel margins and extremities; most of the pellets are oriented with their long axes perpendicular to the tunnel margins. Well-preserved pellets are composed chiefly of ash, but sometimes contain crystal fragments and planktic foraminiferid tests that are pyritized in some cases. It is notable that although the surrounding mudstone contains a rich assemblage of both benthic and planktic foraminiferids (Hasson and Fischer, 1986; Whittaker, 1988), the ash-rich

Figure 5. Anatomy of an exceptional specimen of *Phymatoderma granulatum* (example shown in Figure 1). (**A**) Distal parts of tunnels packed with light-colored pellets. (**B**) A pellet made mostly of volcanic ash and containing a pyritized planktic foraminiferid test (dark dot). (**C**) Proximal part of branch showing secondary tunnel and the results of recycling/restocking burrow contents, including reworked ash areas (1), muddy laminae (2), and darker, muddy pellets (3). (**D**) Reworking of burrow fill in successive stages; earliest stage (1) is light colored with pelleted fabric preserved at the margins of tunnels, intermediate stage (2) consists of blotchy ash-mud mixture, and latest stage (3) is dark colored and cross-cuts all other internal structures. Scale in A and D marked in millimeters; scale bar in B represents 0.5 mm, and in C represents 1 cm.

portions of the burrow fills of *P. granulatum* contain almost exclusively planktic globigerinaceans.

Pellet composition indicates that the behavior of the trace producer included nonselective "surface" deposit feeding and the storage of fecal material or possibly caching of food-ash mixtures in subsurface tunnels. The trace producer lavished so much attention on the ash probably because ash deposition coincided with pulsed delivery of food to the ocean floor (discussed by Miller and Vokes, 1998). The overlapping, outward-branching tunnels, as in the traditional interpretation, suggest some form of subsurface deposit feeding as part of the organism's behavior. In addition, the primary pelleted fabric was apparently disrupted by the trace producer in a systematic way.

Secondary tunnels: Our example is typical of *P. granulatum* from the Punta Gorda beds in having secondary tunnels positioned in the middle of the pellet-filled primary tunnels. These subsequent tunnels rework the pelleted fill, but do not extend beyond the limits of the original structure. Earliest generations of the secondary tunnels contain apparently structureless, pure ash; the latest reworkings contain darker-colored ash-mud mixtures (Figure 5D). The reworked areas in some specimens have a meniscate structure with the concave sides of laminae oriented toward the central region of the burrow system. These laminae consist of interlayered ash and mud-rich sediment; in some of the tunnels the latest generation of reworked burrow fill also is pelleted, suggesting possible restocking (Figure 5C). Although a quantitative inventory of the foraminiferid component of the burrow fill was not performed, as it would entail destruction of the specimen, globigerinaceans also appear to be the dominant foraminiferids in the later ash-mud mixtures. Thus, the trace producers seem to have systematically revisited these storage areas to practice autocoprophagy/utilize food caches and to restock tunnels with pellets.

Behavioral variability: This complicated pattern of burrow construction and utilization, over apparently long intervals of time (relative to life cycle of the trace producer), is evidence that the organisms responsible for *P. granulatum* could switch their trophic behavior from surface feeding (possibly in times of plenty) to other ways of feeding, including the reprocessing of pellet banks (in times of scanty food supply). This is precisely the behavioral adaptation required by relatively large, long-lived endobenthos exploiting a pulsed delivery of labile organic material to the seafloor (Jumars *et al.*, 1990). The seasonal or irregular supply of food to the deep ocean bottom, resulting from events such as plankton blooms, is now recognized as one of the most important processes controlling composition and structure of deepsea benthic ecosystems (reviewed by Gooday and Turley, 1990; Gage and Tyler, 1991; Smith, 1994). The pulsed delivery of food in this case was caused by, or coincident with, major volcanic ashfalls reaching the seafloor at the continental margin of northwestern South America (Miller and Vokes, 1998). Behavioral variability actually may have been greater than what we have suggested: initial construction of tunnels could have involved subsurface feeding and possibly the invasion of adjacent systems that were stocked with pellets; and repeated excursions into the pellet banks could have promoted bacterial or fungal growth on pellet surfaces (a kind of passive cultivation; cf. Fu and Werner, 1995). At least we can say that *P. granulatum* records alternation of feeding strategies, and that surface deposit feeding and pellet recycling probably were essential behavioral adaptations of the trace producer.

Implications

The most popular way to illustrate behavior inferred from trace fossils is to use "action cartoons", showing organisms in the various stages of building and utilizing their burrows or borings (Miller, 1996a, b, 1998). In an action cartoon, Ecuadorian *Phymatoderma* would have to be depicted as the result of variable behavior, not one dominant kind of behavior (Figure 6). But in order to account for the structural intricacy more comprehensively, a much more complicated diagram of behavior is required (Figure 7). The detailed depiction of burrow-related activity in a blueprint or systems diagram of this kind has been termed fabrication analysis by Miller and Vokes (1998, fig. 11 and p. 38) and includes the itemization of "(1) construction (primary fabrication involving excavation, probing, lining and initial filling of structures); (2) operation (secondary fabrication including all forms of structure utilization and 'normal' modification after construction); and (3) maintenance (secondary fabrication involving minor localized repairs, reoccupation of damaged structural elements, extensions to the seafloor following catastrophic burial events, and reestablishment of structures after a major physical or biogenic disturbance". Simply stated, a diagram depicting the full range of possible behaviors recorded in *P. granulatum* would be a complex pattern in its own right, not a simple cartoon.

A more general implication from our study, as well as from other reevaluations of elaborate marine burrow systems, from new work on complex terrestrial trace fossils, and from a renewed interest in compound ichnotaxa, is that the traditional ethologic classification has important limitations (Miller, 1998). Complex animal artefacts are not easily accommodated in the traditional scheme (already demonstrated in the controversy over the behavioral interpretations of *Zoophycos*; Bromley, 1991). Such biogenic structures deserve special treatment individually as records of elaborate, variable behavior. Complexity of Ecuadorian *Phymatoderma* is apparently related to changing trophic resources, probably the result of pulsed delivery of labile organic material to the deep ocean floor. In this case, the pulsed delivery of food was associated with major ashfalls. By merely allocating our burrow system to a single, traditional ethologic category, we would have failed to recognize the essential behavioral and ecologic properties of the trace and the organism that constructed it.

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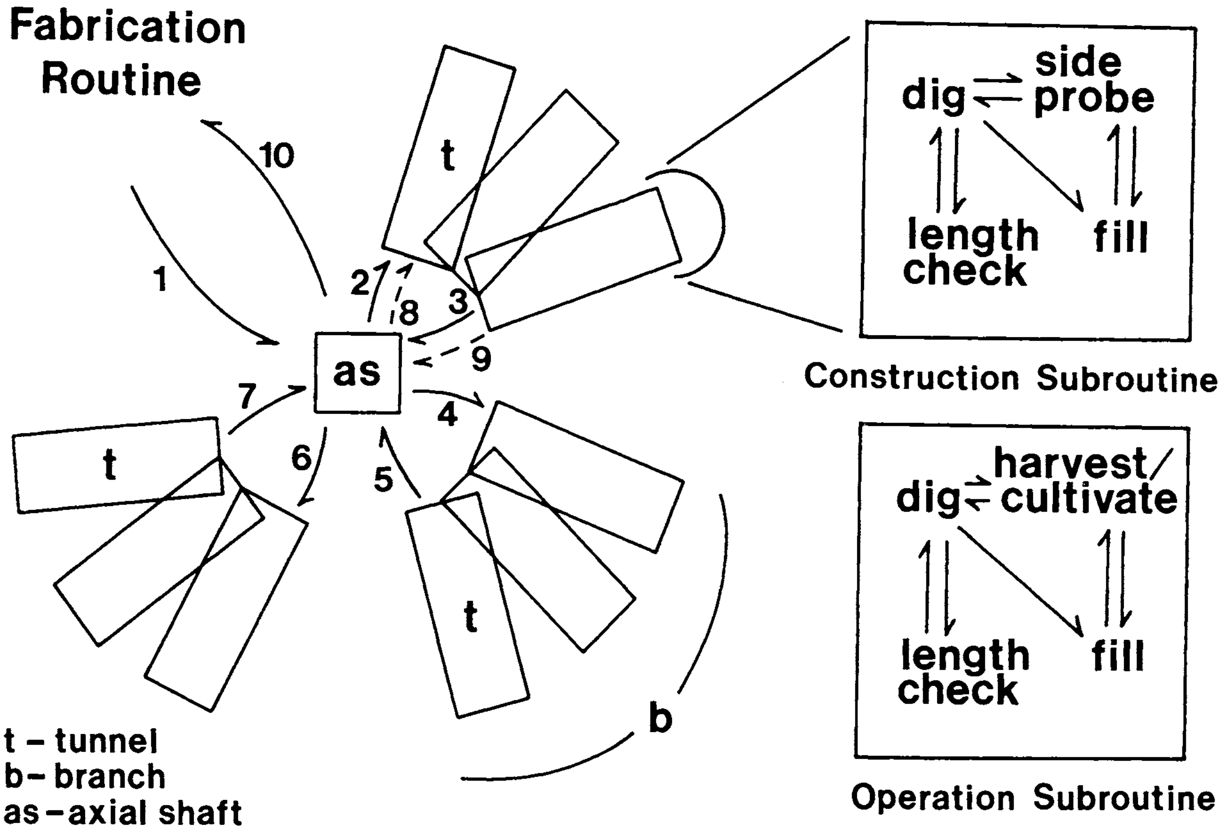

Figure 7. A possible blueprint of construction and utilization of Ecuadorian *Phymatoderma* that depicts burrow fabrication as a series of behavioral routines and subroutines—a more comprehensive summary than that shown in Figure 6. Fabrication sequence includes : (1) initiation of structure ; (2-7) tunnel construction and stocking ; (8-9) structural operation involving revisiting tunnels and recycling/restocking contents ; and (10) abandonment. Structures such as this are demonstrably more complex (in terms of diversity of behavioral tokens) than simpler burrows that do not record long occupation, deliberate modification of habitat, and active management of food resources by the trace producer. From Miller and Vokes (1998, figure 11).

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SHORT NOTES

Early Cretaceous frog remains from the Okurodani Formation, Tetori Group, Japan

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Abstract. The Early Cretaceous Okurodani Formation, Tetori Group, near Shokawa village, Gifu Prefecture, Japan, has yielded a mixed assemblage of terrestrial and aquatic small vertebrates, including the fragmentary remains of a frog (ilium, vertebra) and a salamander (vertebra). These are the first Mesozoic lissamphibians recorded from Japan, and some of the oldest from Asia. The ilium is of rather primitive form and suggests a frog of basal grade, that is outside the Discoglossanura.

Key words: Anura, Caudata, Cretaceous, Japan, Tetori Group.

Introduction

The early fossil history of frogs is limited to a relatively small number of specimens. The earliest recognised crown-group frog is the early Jurassic (Pliensbachian) *Prosalirus* (Shubin and Jenkins, 1995), with further Jurassic taxa recorded from Argentina (*Vieraella, Notobatrachus*, Baez and Basso, 1996), Britain (*Eodiscoglossus*, Evans *et al*., 1990), North America (Hecht and Estes, 1960; Evans and Milner, 1993), Kyrgyzstan (Nessov *et al*., 1994) and, possibly, India (Yadagiri, 1986). Early Cretaceous frogs have been recorded from Europe (Britain, Spain, Ensom *et al*., 1991; Fey, 1988; Hecht, 1970), Israel (Nevo, 1956, 1968), North America (Gardner, 1994; Winkler *et al*., 1990), Africa (Jacobs *et al*., 1990; Evans and Sigogneau Russell, pers. obs.) and Central Asia (Nessov, 1988; Rocek and Nessov, 1993). Thus the published early Mesozoic frog record of Asia is limited to an indet. ilium from India (Yadagiri, 1986), which was not part of Asia at this time, an indeterminate frog from the Middle Jurassic of Kyrgyzstan (Nessov *et al*., 1994) and a number of Aptian/Albian taxa from Central Asia (Rocek and Nessov, 1993). The recovery of Early Cretaceous (Neocomian, circa 135 mya) frog material from Japan, albeit fragmentary, is therefore of some interest.

Geology and materials

The three specimens described here were collected and prepared by Mr Ikoi Shibata, and are now deposited in the collections of the Museum of the Izumi Board of Education, Fukui Prefecture, Japan. The specimens were collected between 1992-1994 from a bone bed (designated the "KO2" locality, 36°03′N, 136°53′E, Locality No. 2 in Hasegawa *et al*., 1995) in the Okurodani Formation, Tetori Group, in the Kobudani Valley, near Shokawa village, Gifu Prefecture. The bone bed is a dark grey silty-sandstone with plant macrofossils at the base, overlain by a concentration of shell debris and bone, and then by the rarer articulated specimens (turtles, choristoderan reptiles); dinosaur teeth are found in the uppermost layers. Most of the specimens are disarticulated but unabraded, suggesting deposition under relatively low energy conditions (Cook *et al*., 1998). The most common vertebrate are aquatic ones: fish, turtles, choristoderes, although rare terrestrial elements (lizards, birds, dinosaurs, pterosaurs) are also known. In this environment, lissamphibian remains were not unexpected, although they are extremely rare. The available materials consisting of a single frog ilium, a frog vertebra and a vertebral centrum that is probably salamander.

Recent geological work by Chris Nicholas (University of Cambridge) suggests the KO2 locality may represent a flood plain environment close to a large river. The Okurodani and younger Bessantani Formations have been provisionally dated as around 140 to 120 Ma on the basis of fission track analysis (Gifu-Ken Dinosaur Research Committee, 1993). In addition, Nicholas' new work in the area has identified tuff bands both above and below the bone-bed horizon. New radiometric dating of these is now in preparation.

Descriptive paleontology

All specimens deposited in the Museum of the Izumi Board of Education carry the prefix IBEF VP.

Lissamphibia Haeckel, 1866
Anura Rafinesque, 1815

The two frog specimens recovered to date are a left ilium

(IBEF VP 28) and a presacral vertebra (IBEF VP 29).

IBEF VP 28 (Figure 1)
Description.—This represents the acetabular portion of a left ilium with the proximal part of the shaft. The preacetabular process is damaged but appears to have been small. There is little or no supraacetabular process. From the medial surface, it would appear that there was also no interiliac synchondrosis, although this surface bears a shallow triangular depression. The iliac shaft is long and recurved, mediolaterally compressed but becoming ovoid in cross-section distally. There is little development of a dorsal crest, although this border is sharp, while the anteroventral border is separated from the rest of the shaft by a marked groove. Proximally, the acetabular region is relatively smooth and grades smoothly into the shaft, i.e. there is no marked expansion of the proximal end nor waisting of the shaft above the acetabulum (probably a primitive feature).

A low ridge runs from behind the acetabulum to the dorsal margin but there is little development of a dorsal tubercle and no supraacetabular fossa. The acetabular rim is moderately expanded anteriorly but undeveloped posteriorly. There is, however, a marked notching of the posterior acetabular border. The sutural surface for the puboischiadic plate is damaged but there appears to be a posteromedial lip which may have helped to stabilise the connection.

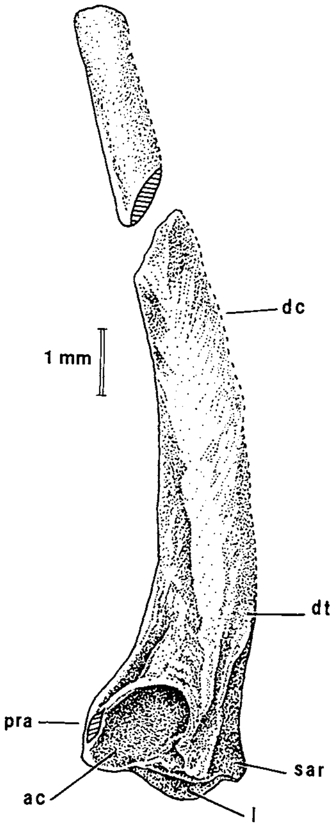

Figure 1. IBEF VP 28, left ilium in lateral view. ac, acetabulum; dc, dorsal crest; dt, area of weakly defined dorsal tubercle; l, lip-like flange, possibly for puboischiadic plate; pra, preacetabular region; and sar, supraacetabular region (same as in Figure 4).

IBEF VP 29 (Figure 2)
Description.—The single vertebra is probably a posterior dorsal. The transverse process is broken. There is a small posterior spine which suggests weak imbrication. Pronounced interspinous muscle attachment surfaces are present. The centrum is amphicoelous, apparently ectochordal and of simple type.

Caudata Oppel, 1811

Remarks.—Salamanders are represented in the Okurodani Formation by a single isolated centrum (IBEF VP 30) which is unfortunately undiagnostic. The centrum is deeply amphicoelous, heavily built (for a salamander) and moderately elongate. In all these respects it resembles the vertebrae of primitive taxa.

Systematic position of the Tetori Group anuran

In traditional frog classification (e.g., Duellman and Trueb, 1986), the most primitive living frogs were grouped into two families: the Leiopelmatidae (*Ascaphus* and *Leiopelma*) and the Discoglossidae (*Bombina, Barbourula, Alytes, Discoglossus*), together forming the Discoglossoidea. This arrangement has most recently been supported by Clarke (1988) and by Baez and Basso (1996), although the latter were concerned only with primitive frogs. However, in a recent

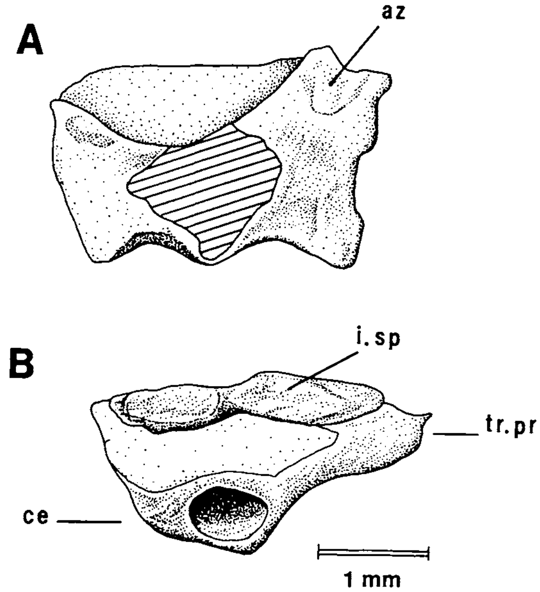

Figure 2. IBEF VP 29, anuran dorsal vertebra. **A**, dorsal view; **B**, posterior view. az, anterior zygapophysis; ce, centrum; i.sp, interspinous muscle attachment surface; tr.pr, transverse process.

cladistic review (Figure 3), Ford and Cannatella (1993) proposed an arrangement in which *Ascaphus* and *Leiopelma* form successive outgroups to higher frogs (Bombinanura). Within Bombinanura, *Barbourula* and *Bombina* are separated into a family Bombinatoridae which itself forms the sister taxon of Discoglossanura (Discoglossidae sensu stricto *Alytes, Discoglossus*) and crown group frogs-Pipanura). Few extinct taxa were included in the analysis.

Amphicoelous notochordal vertebrae are a primitive anuran character state found in Jurassic frogs such as *Prosalirus* (Pliensbachian, Arizona), *Vieraella* (Callovian/Oxfordian, Argentina), the living *Ascaphus* (Pacific rim of North America) and *Leiopelma* (New Zealand), the mid-late Cretaceous Asian gobiatines (Rocek and Nessov, 1993) and the Jurassic/Cretaceous *Eodiscoglossus*. The polarity of neural arch imbrication (overlap) is not clearcut. Full imbrication of the neural arches occurs in *Notobatrachus, Bombina* and *Discoglossus*, but also in *Triadobatrachus* ; weak imbrication occurs in *Vieraella* ; while the arches of *Ascaphus, Leiopelma* and *Alytes* are not imbricate. Thus the weak imbrication in the Tetori frog is not phylogenetically useful.

The characters of the Tetori ilium are also, for the most part, primitive, e.g., relatively small acetabulum ; unexpanded pre- or supraacetabular processes ; absence of an interiliac synchondrosis and a supraacetabular fossa ; little development of either a dorsal crest or a dorsal tubercle. The stem salientian *Triadobatrachus* (Early Triassic, Madagascar) has a protruberant dorsal tubercle, but this is lacking in *Ascaphus* and *Leiopelma*, and only weakly developed in *Bombina* and *Barbourula*. In the Jurassic *Notobatrachus* (Argentina), a low elongated prominence is described for some specimens (Baez and Basso, 1996), but there is no dorsal crest. The dorsal prominence is usually developed in discoglossids (sensu stricto, Ford and Cannatella, 1993), but the presence of a dorsal crest, supraacetabular fossa and interiliac synchondrosis is variable.

In *Ascaphus* and *Leiopelma* (SE, personal observations. and Barry Clarke personal communication.), the pre- and supraacetabular regions are of roughly equal size, creating a flared distal iliac shape with the expansions lying roughly symmetrically about a small hemispherical, centrally placed, acetabular fossa. In *Bombina* and *Barbourula* (Figure 4B), the preacetabular region is unexpanded and the acetabular surface lies very close to the anterior rim of the bone. The supraacetabular region is somewhat wider, though with only a very small supraacetabular expansion which does not extend to the dorsal limit of the ischium (Clarke 1988, character 71). This contrasts with the condition in *Alytes* (Figure 4C) and *Discoglossus* (Discoglossidae sensu stricto of Ford and Cannatella, 1993), where the supraacetabular expansion is much stronger and does extend to the dorsal limit of the ischium.

In these features, the Tetori frog matches the condition in the Bombinaturidae most closely (little or no dorsal tuberosity, anteriorly placed acetabular surface, weak development of the supraacetabular region, some mediolateral compression of the iliac shaft, in contrast to that of *Ascaphus* and *Leiopelma* in which the shaft is almost circular in cross-section). The Tetori frog differs from living bombinaturids in the absence of any waisting between the acetabular region and the shaft, but since this waisting is also seen in *Ascaphus* and *Leiopelma*, but not in the Jurassic *Notobatrachus*, it is difficult to determine whether the condition in the Tetori

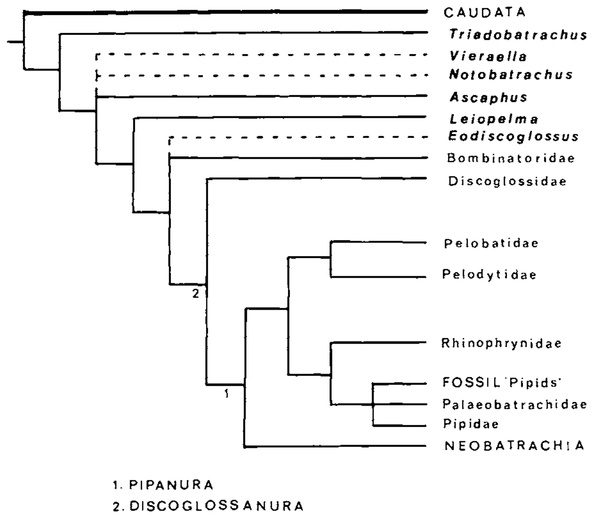

Figure 3. Phylogenetic relationships of Salientians (=*Triadobatrachus*+Anura) based on morphology as proposed by Ford and Cannatella (1993), but simplified from the original.

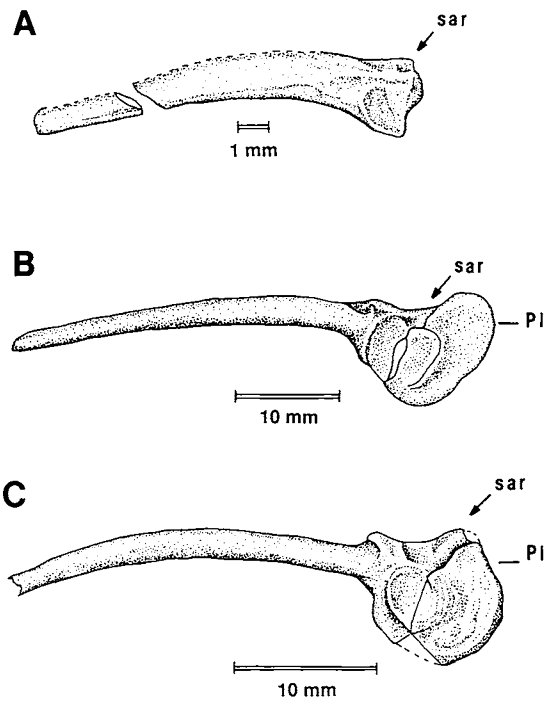

Figure 4. **A**, lateral view of IBEF VP 28, as compared to the ilium and pelvis of a recent **B**, *Barbourula busuangensis*, and **C**, *Alytes cisternasii*. B, C, redrawn from Clarke, 1988, figure 93, with permission from Clarke. PI, puboischiadic plate ; for others, see Figure 1.

frog is a specialisation in a bombinaturid grade frog, or a primitive feature of a late surviving stem anuran. More material is needed to answer this question.

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Devonian tentaculitids from Central and Northeast Japan

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Abstract. Two Lochkovian (Early Devonian) species, *Tractabilis* ? sp. and *Gotlandellites fukujiensis* sp. nov., from the Fukuji Formation, and an Eifelian (Middle Devonian) species, *Tentaculites* sp., from the Nakazato Formation, are described and comprise the first modern treatment of tentaculitids in Japan. This discovery of *Gotlandellites fukujiensis* extends the stratigraphic range of the genus, which was previously known from the Early Silurian.

Key words : Devonian, Fukuji Formation, *Gotlandellites fukujiensis* sp. nov., Nakazato Formation, tentaculitids.

Introduction

Tentaculitids from Japan have never previously received a modern taxonomic treatment. Only Minato *et al.* (1959) has earlier pointed out the occurrence of "*Tentaculites*" from the Devonian Nakazato Formation in the Southern Kitakami Mountains, Northeast Japan. The purpose of this paper is to describe certain tentaculitid species, namely, *Tractabilis* ? sp. and *Gotlandellites fukujiensis* sp. nov. from the Fukuji Formation and *Tentaculites* sp. from the Nakazato Formation, in order to provide taxonomic, biostratigraphic and paleobiogeographic base data. Thus, the present work initiates the up-to-date description of tentaculitid faunas in Japan.

The Fukuji species occur in Lochkovian (Early Devonian) calcareous shale at locality FH-4 and FH-5, for which geographic and stratigraphic information are given in Niko (1996), in Gifu Prefecture, Central Japan. Specimens examined from the Fukuji Formation are in the paleontological collections of the University Museum of the University of Tokyo (UMUT).

The present *Tentaculites* sp. is based on five specimens of external molds on a tuffaceous siltstone slab that was kept in the Ofunato City Museum (OCM), Iwate Prefecture. According to the accompanying label, this slab was collected as a float block in a tributary in the uppermost reaches of the Higuchi-zawa valley, Ofunato City, Iwate Prefecture, Northeast Japan. This slab is thought to be derived from the Eifelian (Middle Devonian) portion of the Nakazato Formation, based on its lithology and collecting site.

The classification and terminology of tentaculitids follows Larsson (1979).

Systematic paleontology

Phylum Incertae Sedis
Class Tentaculitoidea Ljashenko, 1957
Order Tentaculitida Ljashenko, 1955
Family Tentaculitidae Walcott, 1886
Genus ***Tentaculites*** Schlotheim, 1820

Type species.—*Tentaculites scalaris* Schlotheim, 1820.

Tentaculites sp.

Figures 1-1a, b, 2, 3a, b

Description.—Medium-sized for genus, straight conchs with circular cross sections, attaining 17.0 mm in length, 1.7 mm (slightly deformed) in distal diameter ; angle of conch expansion approximately 4-6° ; proximal conch up to 5.5 mm in length, with dense annulets, then closely spaced symmetrical rings with 0-4 (usually 1 or 2) alternating annulets recognized in more distal conch ; ring size and prominence increase progressively toward distal end, most distal rings have subtriangular profiles.

Discussion.—The present species is somewhat similar to *Tentaculites bellulus* Hall (1876, pl. 26, figs. 15-18 ; Hall, 1879, pl. 31, figs. 15-18 ; reillustrated by Fisher, 1962, figs. 55-1a, b ; redescribed by Yoder and Erdtmann, 1975, pl. 1, figs. 1-3, 6-8) from the Middle Devonian Hamilton Group in New York. This species, however, is represented by poorly preserved external molds, and knowledge of the interior of the conch is necessary to characterize the species.

Although "*Tentaculites*" (tentaculitid in Kato, 1979) was listed from the Nakazato Formation by Minato *et al.* (1959), this species is still undescribed.

Material and occurrence.—OCM G-SN02—06 from the


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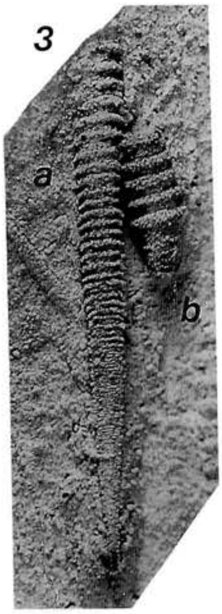
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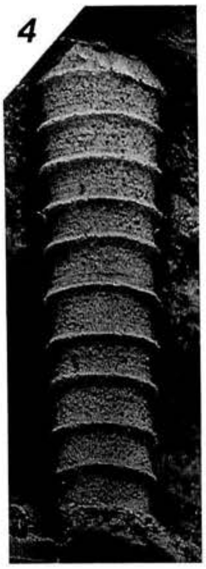
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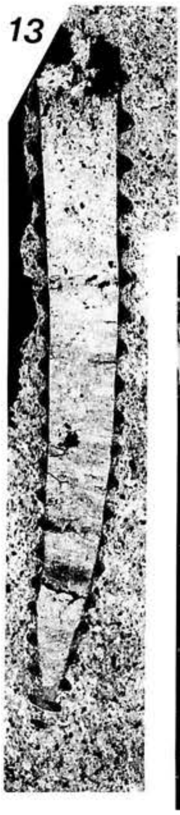
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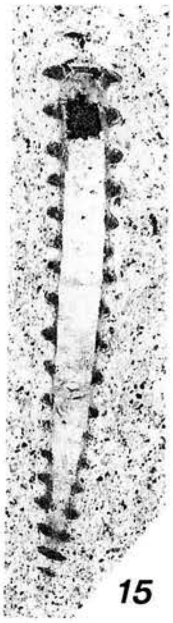
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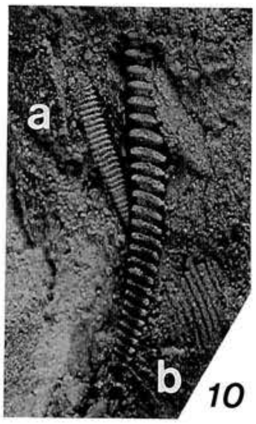
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Nakazato Formation.

Genus **Tractabilis** Ljashenko, 1969

Type species.—*Tractabilis arcticus* Ljashenko, 1969.

Tractabilis ? sp.

Figures 1-4, 10a

Description.—Single, straight conch, 6.9 mm in length, with circular cross section, diameter of distal end 1.8 mm; rings monotonous, strongly asymmetrical, proximal slopes steeper than distal ones, with wide interspaces; weak annulets consisting of fine striations in interspaces.

Discussion.—This species is represented by an external mold of a fragmentary specimen. The shape of the rings is similar to that of *Tractabilis arcticus* Ljashenko (1969, pl. 1, figs. 1-3) from the Middle Devonian of Novaya Zemlya, but accurate comparison is impossible owing to limited morphological data for the Fukuji specimen. In addition to this specimen, a small straight conch (2.1 mm in length, Figure 1-10a), that has asymmetrical rings and weak longitudinal lirae, was also examined. There is a possibility that the smaller specimen represents the proximal portion of the present *Tractabilis* ? sp.

Material and occurrence.—UMUT PW 27453 and another specimen, UMUT PW 27454, questionably assigned to this species, from Locality FH-5, in the Fukuji Formation.

Family Gotlandellitidae Larsson, 1979
Genus **Gotlandellites** Larsson, 1979

Type species.—*Gotlandellites visbyensis* Larsson, 1979.

Gotlandellites fukujiensis sp. nov.

Figures 1-5—9, 10b, 11—15

Diagnosis.—Species of large-sized *Gotlandellites* with approximate 5° angle of conch expansion; rings with rounded crests, their density relatively low for genus, 2-3 per corresponding conch diameter; annulets absent or rarely present in interspaces.

Description.—Large-sized for genus, curved conchs with circular cross sections, largest specimen (holotype) attains 7.4 mm in distance between ends of conch, 0.9 mm in diameter near distal end; angle of conch expansion ranges from 4.5° to 5.7°, usually approximately 5°; rings strongly prominent, monotonous, symmetrical; each ring slopes towards convex side of conch with annular slope of approximately 8-20°; crests round; density of rings relatively low for genus, 2-3 per corresponding conch diameter; interspaces flat to slightly concave, smooth or rarely bearing 1-2 annulets; minimum thickness of conch wall in interspaces 0.02-0.05 mm in sectioned paratypes (UMUT PW 27462, 27463); internal surface smooth or forms very shallow but wide annular concavities; conch wall impunctate; endocone and septal element not detected.

Discussion.—The curved conchs with monotonous and strongly prominent rings are characteristic of *Gotlandellites*, which has been reported only from the late Llandovery to early Wenlock (Early Silurian) of Baltica, Avalonia and Laurentia (Larsson, 1979). Among the known species of the genus, *Gotlandellites fukujiensis* sp. nov. most closely resembles *G. areolatus* Larsson (1979, figs. 66 A-F), from the early Wenlock of Gotland, specially in regard to proximal conch morphology. However, the present new species has a larger conch (7.4 mm vs. maximum observed length 4.7 mm) and a lower density of rings on the distal conch (2-3 vs. 6-7 per corresponding conch diameter). *Gotlandellites visbyensis* Larsson (1979, figs. 67 A-F) has a small conch, a triangular profile of the rings and well-developed annules.

Material and occurrence.—Holotype, UMUT PW 27489; paratypes, UMUT PW 27462, 27463, 27473, 27508, 27517, 27522, 27526, 27528, 27530. In addition, 76 other specimens (UMUT PW 27455-27461, 27464-27472, 27374-27488, 27490-27516, 27518-27521, 27523-27525, 27527, 27529, 27531-27539) were also examined. The locality for the specimens is as follows: FH-4 (UMUT PW 27455-27505), and FH-5 (27506-27539), both in the Fukuji Formation.

Etymology.—The specific name is derived from the type locality, Fukuji.

Acknowledgments

I thank E.L. Yochelson for suggestions on improving this paper. T. Kamiya helped collect the present tentaculitids from the Fukuji area. Thanks are also due to A. Kaneko and E. Sato for allowing me access to the Ofunato City Museum's collections.

Figure 1. 1a, b, 2, 3a, b. *Tentaculites* sp., 1a: OCM G-SN02, 1b: OCM G-SN05, ×3, 2: OCM G-SN04, ×3, 3a: OCM G-SN03, 3b: OCM G-SN06, ×3. **4, 10a.** *Tractabilis* ? sp., 4: UMUT PW 27453, ×10, 10a: UMUT PW 27454, ×10. **5-9, 10b, 11-15.** *Gotlandellites fukujiensis* sp. nov. 5: paratype, UMUT PW 27473, ×10, 6: paratype, UMUT PW 27517, ×10, 7: paratype, UMUT PW 27530, ×10, 8: paratype, UMUT PW 27526, ×10, 9: paratype, UMUT PW 27508, ×10, 10b: paratype, UMUT PW 27522, ×10, 11: paratype, UMUT PW 27528, ×10, 12: holotype, UMUT PW 27489, ×10, 13, 14: paratype, UMUT PW 27463, 13=×14, 14=×50, 15: paratype, UMUT PW 27462, ×14. 1-10, 12, silicone rubber casts, 11, internal mold, 13-15, longitudinal sections, 13, 15, negative prints.

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Fukuji 福地, Higuchi-zawa 樋口沢, Nakazato 中里, Ofunato 大船渡

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Survival of crinoid stalk fragments and its taphonomic implications: discussion

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Key words: Crinoids, survival strategies, taphonomy

The recent paper by Oji and Amemiya (1998), apart from being an important and, perhaps, unexpected input to crinoid paleobiology, also makes a notable contribution to the ongoing debate concerning how major accumulations of crinoid-derived material (mainly fragments of stalks) are formed (for a recent review of such "regional encrinites", see Ausich, 1997). Kidwell and Brenchley (1994) specifically did not include analysis or detailed interpretation of such crinoid-rich beds in their assessment of the temporal patterns of variation shown by shell accumulations during the Phanerozoic. Regional encrinites are recognised to have patterns of accumulation that are somewhat different from shell beds that are dominated by, for example, brachiopods, bryozoans or benthic molluscs. The determination that lengths of crinoid stalk that have disarticulated from the 'parent' organism, for whatever reason, can survive presumably by the direct absorption of nutrients (as is known to occur in other, unmutilated echinoderms; see Lawrence, 1987, for review) provides at least a partial explanation of why regional encrinites can be dominated by stalk fragments-that is, pluricolumnals-rather than a range of completely disarticulated ossicles from all parts of the skeleton.

The purpose of the present brief discussion is to provide data which support and supplement the observations and deductions of Oji and Amemiya (1998). Coincidentally, at about the same time that this paper was published, Donovan and Pawson (1998) described the rare occurrence in two extant species of the bourgueticrinid *Democrinus* of peculiar, root-like growths at the apex of the column (instead of a crown) (Table 1). The interpretation of these bizarre structures is that such specimens were decapitated by predation, but the remaining stem continued to survive by direct absorption of nutrients and, indeed, sealed the broken end by new stereom calcite growth, in most examples also producing short, root-like outgrowths. Thus, there is excellent evidence for survival of the detached stem in at least one other group of extant, stalked crinoids. The notable difference between isocrinids (such as *Metacrinus rotundus* Carpenter; Oji and Amemiya, 1998) and bourgueticrinids is the mechanism of stem detachment. Unlike isocrinids, bourgueticrinids do not include regularly-spaced autotomy planes within their column and a crownless specimen is therefore most likely to be generated by predation or, speculatively, autotomy immediately beneath the crown where articulations are synostosial or syzigial, rather than synarthrial (*Democrinus* stem morphology discussed by Donovan, 1997).

The different 'survival strategies' of the stalks in *Metacrinus* and *Democrinus* are probably related to the different functional morphologies of the column in isocrinids and bourgueticrinids. Oji and Amemiya (1998, p. 68) noted that "... there has been no record of apparent stalk regeneration in Recent stalked crinoids". However, such studies have concentrated on isocrinids, which have specialised articulations adapted for autotomy that are spaced regularly throughout the column (Emson and Wilkie, 1980). Autotomy at these articulations surely suggests that they are adapted to 'seal off' disarticulated lengths of column. I am not aware that an experimental study has ever observed what happens

Table 1. Locality data of 'regenerating', decapitated *Democrinus* spp. (based on Donovan and Pawson, 1998, appendix). All specimens in the National Museum of Natural History, Smithsonian Institution (USNM).

- USNM E11616. *Democrinus chuni* (Döderlein). South Atlantic Ocean, South Africa, Durban, 30°10′S, 32°9′E. 700 m. R/V ANTON BRUN. Identified by A.M. Clark.
- USNM E18604. *Democrinus brevis* (A.H. Clark). North Atlantic Ocean, Caribbean Sea, Los Testigos Island, Venezuela. 11°34′24″N, 62°10′42″W. 597-598 m. R/V PILLSBURY. Identified by D.B. Macurda, Jr.
- USNM E25870. *Democrinus brevis* (A.H. Clark). North Atlantic Ocean, Gulf of Mexico, Florida Keys, Straits of Florida. 24°14′00″N, 82°56′00″W. 641-686 m. R/V GERDA. Identified by D.L. Mayer.
- USNM E41940. *Democrinus brevis* (A.H. Clark). North Atlantic Ocean, Gulf of Mexico, south of Louisiana Point, Louisiana. 27°24′30″N, 93°17′54″W. 576-732 m. R/V GYRE.

if an isocrinid column is mechanically broken between autotomy planes, that is, in the middle of a noditaxis. Does it survive and can it seal the breakage with stereom? In *Democrinus*, which lacks autotomy planes, the column reacted to decapitation by regenerating at the apical end with all it 'knew' how to grow, that is, a root system. The same might be true of isocrinids if mechanically broken in mid-noditaxis position or, indeed, in any of the other groups of extant, stalked crinoid, none of which show particular adaptations to column autotomy.

Acknowledgments

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Survival of crinoid stalk fragments and its taphonomic implications: additional discussion

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Key words : Crinoids, regeneration, taphonomy

The discussion by Stephen K. Donovan (in this issue) on our paper (Oji and Amemiya, 1998) provided additional examples of extant and fossil stalked crinoids in which stalk elements have an ability to stay alive after they have lost their crowns. We are grateful for such information in other crinoid taxa. Such lines of evidence that crinoid stalk fragments (pluricolumnals), or a whole stalk, of many different taxa of crinoids can/could live for a considerable time, will certainly change our view that all incomplete body parts on the today's or ancient sea floor were completely dead at the time of burial.

We would like to mention one thing about the word "regeneration". In most cases, this word refers to the process in which the lost body part was repaired. There are a lot of records that crinoid arms, pinnules and visceral mass, if lost, can be regenerated, repaired, and often leave no traces of damage to the skeletons (Mladenov, 1983 ; Meyer, 1985 ; Schneider, 1988 ; Amemiya and Oji, 1992). On the other hand, the previous reports of stalk "regeneration" of 1) an Ordovician crinoid (*Lichenocrinus dubius*) by Ausich and Baumiller (1993), and 2) "regeneration" of extant *Democrinus* species by Donovan and Pawson (1998), are not true repair processes of the lost body parts but, as they described as "root-like growths", it may be called as an inaccurate regeneration on the proximal part of the stalk. The extant *Democrinus* and fossil Ordovician crinoid could not regenerate their lost crowns from the stalk alone.

With regards to the crinoid stalks, at least two different patterns of regeneration/overgrowth may be categorized as follows :

1. Regeneration—In this process the lost body parts are repaired as in the original morphology. This is observed only in the crinoid arms, pinnules, and visceral mass.
2. Overgrowth—Lost body parts are replaced by very incomplete growth of the skeleton, differing in morphology from the original. This process probably comes closer to the term "healing" rather than "regeneration". This overgrowth is documented in the proximal stalk in the decapitated specimens of extant *Democrinus* (Donovan and Pawson, 1998), Ordovician *Lichenocrinus dubius* (Ausich and Baumiller, 1993), Ordovician pluricolumnals (cited in the discussion by Donovan), and the distal end of the stalk (synostosis on the nodal facet) of some extant isocrinid species (*Endoxocrinus* and *Diplocrinus*).

In the sense as above, regeneration is only seen in the crown, and it has not been documented in the stalk (except for the cirri generation of a damaged or lost tip). On the other hand, overgowth is often seen in the stalks. The morphology of the stalk overgrowth, as Donovan pointed out, is very similar to the radicular cirri. This evidence seems to indicate that the stalk does not have the ability of regeneration as commonly understood. Therefore, in addition to the different functional morphologies and survival stragegies of the stalks in *Metacrinus* and *Democrius* as pointed out by Donovan, the response to stalk autotomy and/or breakage is also different between these two taxa.

The present note aims to clarify that there seems to be at least two different patterns in the repair process of crinoids, corresponding to their body parts. We have not started the test suggested by Donovan, if the stalk survives or regenerates after it is mechanically broken between the articulation, in the middle of a noditaxis. Further observations of such experiments will probably clarify if isocrinid stalks show different regrowth patterns from *Demoncrinus*, or if they are essentially the same. Also more work should be done on this subject in order to know the meaning of survival of such a stalk and its pluricolumnals. We thank Jay Schneider for the review of this note.

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The typical format for arrangement of systematic paleontology can be learned from current issues of the Journal. All descriptions of new taxa must include a diagnosis, and, as appropriate, stratigraphic and geographic indications, designation of a type or types, depository information, and specification of illustrations. In synonymies use an abbreviated form of the reference, consisting only of authors of reference, date of publication, and number of pages, plates, figures and text-figures referring to the organism or organisms in question.

References. Heading for the bibliography can be either "References cited" or "References." Entries are to be listed alphabetically. No abbreviations will be used in article and book titles. Journal titles are written out, not abbreviated. Series, volume, and number or part are to be given, with the appropriate word abbreviated in each case ("ser.", "vol.", etc. ; see the next page for examples).

Illustrations : All illustrations, including maps, geologic sections, and half-tone illustrations (including "plates") are to be called figures and must be numbered in the same sequence as they are first cited in the text. Citations of illustrations in the text are to be spelled out in full (e.g., Figure 2 or Figure 2.1). Figure captions are to be typed separately. Plan the illustrations so that they take up either the entire width of the printed page (170 mm) or the width of one column (80 mm). Originals should not be smaller than the final intended size for printing. No foldouts will be accepted. Mark all originals clearly with authors' names and figure number. Photographs of all specimens except sections must be illuminated from the upper left side, as is conventional.

Manuscripts on disk : Authors are encouraged to deliver final, revised manuscript copy on disk, but disks should be sent only after the paper has been accepted. 3.5 inch disk with the text in a recent version of Word Perfect or Microsoft Word is acceptable. Be sure to specify, in a covering note, the hardware and the word-processing package used.

Galley proofs and offprints : Galley proofs will be sent to authors about one month before the expected publication date and should be returned to the Editors within 3 days of receipt. The authors are responsible for reading the first galley proof. Minor changes submitted by the author will be permitted while a paper is in galleys, but a charge will be made for substantial alterations.

The authors receive free of charge 50 offprints without covers. Additional copies and covers can be purchased and should be ordered when the proofs are returned.

Charges: If a paper exceeds 24 printed pages, payment of page charges for the extra pages is a prerequisite for acceptance. Illustrations in color can also be published at the authors' expense. For either case, the Editors will provide information about current page charges.

Return of published figures: The manuscripts of the papers published will not be returned to the authors. However, figures will be returned upon request by the authors after the paper has been published.

Ager, D.V., 1963: *Principles of Paleoecology*, 371 p. McGraw-Hill Co., New York.

Barron, J.A., 1983: Latest Oligocene through early Middle Miocene diatom biostratigraphy of the eastern tropical Pacific. *Marine Micropaleontology*, vol. 7, p. 487-515.

Barron, J.A., 1989: Lower Miocene to Quaternary diatom biostratigraphy of Leg 57, off northeastern Japan, Deep Sea Drilling Project. *In*, Scientific Party, *Initial Reports of the Deep Sea Drilling Project*, vols. 56 and 57, p. 641-685. U.S. Govt. Printing Office, Washington, D.C.

Burckle, L.H., 1978: Marine diatoms. *In*, Haq, B.U. and Boersma, A. *eds.*, *Introduction to Marine Micropaleontology*, p. 245-266. Elsevier, New York.

Fenner, J. and Mikkelsen, N., 1990: Eocene-Oligocene diatoms in the western Indian Ocean: Taxonomy, stratigraphy, and paleoecology. *In*, Duncan, R.A., Backman, J., Peterson, L.C., *et al.*, *Proceedings of the Ocean Drilling Program*, *Scientific Results*, vol. 115, p. 433-463. College Station, TX (Ocean Drilling Program).

Koizumi, I., 1972: Marine diatom flora of the Pliocene Tatsunokuchi Formation in Fukushima Prefecture. *Transactions and Proceedings of the Palaeontological Society of Japan*, *New Series*, no. 86, p. 340-359.

Kuramoto, S., 1996: Geophysical investigation for methane hydrates and the significance of BSR. *Journal of the Geological Society of Japan*, vol. 11, p. 951-958. (*in Japanese with English abstract*)

Palaeontological Society of Japan (JSP) Standing Committee Actions

During its meeting on December 12, the JSP Standing Committee enacted the following changes to its membership.

New members elected;
Chisato Nishihara,
Shinji Kakihara,
Hideaki Nagamori,
Eiichi Kitamura,
Tomohiro Iwashita,
Hiroaki Ugai,
Yoichi Kondo,
Megumi Ichise,
Hidekatsu Mizoguchi,
Takanobu Yamaoka,
Kyohei Omaru,
Yuichiro Kashiyama.

Deceased member;
Mitsuo Noda.

List of reviewers

The coeditors are indebted to the following individuals who scientifically reviewed one or more of the papers included in Paleontological Research vol. 1 and 2.

Beu, A.,
Bockelie, F.,
Bogan, A.E.,
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Copper, P.,
Endo, K.,
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Farrell, J.,
Feldmann, R.M.,
Friis, E-M.,
Furutani, H.,
Gunji, Y.,
Hasegawa, S.,
Hayami, I.,
Hirano, H.,
Igo, Hh.,
Igo, Hy.,
Ikeya, N.,
Ingle, J.C. Jr.,
Kidwell, S.M.,
King, A.,
Lardeux, H.,
Kaiho, K.,
Karasawa, H.,
Kato, H.,
Kato, M.,
Kohno, N.,
Kotake, N.,
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Matsuoka, A.,
Noda, H.,
Oba, T.,
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Oji, T.,
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Setoguchi, T.,
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Smith, A.B.,
Thomas, R.D.K.,
Tomida, Y.,
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Wang, H.
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Yamanoi, T.,
Yanagida, J.,
Yao, A.

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Protoctista

Mollusca

Brachiopoda

Arthropoda

Bryozoa

Echinodermata

Conodonta

Vertebrata

Trace fossil

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Paleobotany

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Notes : Words listed are names of genus and species-groups which are described, discussed or illustrated in the articles in Paleontological Research, vol. 1, no. 1 to vol. 2, no. 4. Words in bold-type are names of newly proposed taxa.

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行事予定

◎1999年年会は1999年1月29日（金）～1月31日（日）に，「東北大学」で開催されます．シンポジウムとして1月29日に「復元の科学3，生物事変，世話人：海保邦夫，西　広嗣，大野照文」が行われます．

◎第148回例会は，1999年6月26日（土）～6月27日（日）に，「兵庫県立人と自然の博物館」で行われます．一般講演の申し込み締切は5月7日です．シンポジウムの企画をお持ちの方は，1998年12月末までに行事係までお申し込み下さい．

◎2000年年会・総会には現在の所「早稲田大学」から開催の申し込みがありました（決定ではありません）．シンポジウム企画の申し込み締切は1999年3月末日です．

◎第149回例会（開催予定時期：2000年の6月末頃）は，今の所開催申し込みがありません．開催を計画されている機関がありましたら，お申し込み下さい．

◎現在，常務委員会は2001年からの学会行事の変更を検討しております．2001年からは，従来とは異なった時期や開催形式で年会，例会，総会が開催される可能性があります．従いまして，第149回例会（2000年6月末に開催予定）までは，従来通り開催の申し込みを受け付けますが，2001年以降の開催申し込みは，しばらくの間見あわさせて頂きます．

講演の申し込み先：〒240-8501 横浜市保土ケ谷区常盤台79-2
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