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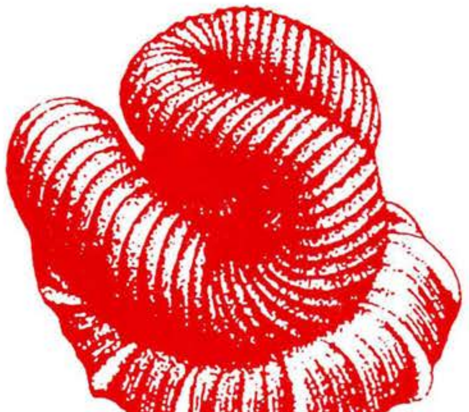

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Cover: Idealized sketch of *Nipponites mirabilis* Yabe, a Late Cretaceous (Turonian) nostoceratid ammonite. Various reconstructions of the mode of life of this species have been proposed, because of its curiously meandering shell form (after T. Okamoto,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

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PALAEONTOLOGICAL SOCIETY OF JAPAN
c/o Business Center for Academic Societies,
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Glyptostrobus rubenosawaensis sp. nov., a new permineralized conifer species from the Middle Miocene, Central Hokkaido, Japan

MIDORI MATSUMOTO[1], TAKESHI ASAKAWA OHSAWA[2], MAKOTO NISHIDA[3], and HARUFUMI NISHIDA[4]

[1] *Department of Earth Sciences, Faculty of Science, Chiba University, 1-33 Yayoicho, Inage-ku, Chiba, 263 Japan*
[2] *Laboratory of Phylogenetic Botany, Faculty of Science, Chiba University, 1-33 Yayoicho, Inage-ku, Chiba, 263 Japan*
[3] *Research Institute of Evolutionary Biology, 2-4-28 Kamiyoga, Setagaya-ku, Tokyo, 158 Japan*
[4] *Faculty of Science, Chuo University, 1-13-27 Kasuga, Bunkyo-ku, 112 Japan*

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Abstract. Anatomically well preserved fertile and vegetative remains of *Glyptostrobus rubenosawaensis* sp. nov. (Coniferae-Taxodiaceae) have been recovered from silicified lacustrine deposits of the late Middle Miocene Shimokawa Group near Shimokawa Town, Kamikawa district, Central Hokkaido. Vegetative remains include shoots bearing polymorphic leaves. Fertile remains include seed and pollen cones. The fossil remains closely resemble living *Glyptostrobus pensilis* (D. Don) K. Koch in gross morphology, but differ in possessing larger cones and a prominent abaxial projection of the bract.

Previous reports of fossil *Glyptostrobus* were limited to compression floras. This report is the first to use permineralized remains to reconstruct fossil *Glyptostrobus* and document the internal anatomical features of the genus to allow meaningful comparison with the living representative, *G. pensilis.*

Abundant remains of *Glyptostrobus* indicate wetland as the paleoecological setting, based on the co-occurrence of wetland taxa such as *Decodon* (Lythraceae), *Osmunda* and *Alnus*, and mountainous taxa such as *Picea* and *Tsuga*, and using permineralized plant fossils. We can reconstruct an ecological setting in a lake.

Key words : Anatomy, conifer, *Glyptostrobus*, Hokkaido, Miocene, permineralization

Introduction

In a number of previous reports, Matsumoto *et al.* (1994, 1995, 1996) and Nishida (1990) reported on the occurrence of permineralized leaves of *Picea* Dietrich and *Tsuga* (Endlicher) Carrière, seeds of *Decodon* Gmelin and *Osmunda* L. rhizomes from the late Middle Miocene sediments of the Shimokawa Group near Shimokawa town, Kamikawa district, Hokkaido, Japan. In addition, others such as Uemura (1991), Sato (1992), Tanai *et al.* (1992) and Igarashi *et al.* (1993) discussed the regional paleovegetation based on compression fossils or palynological remains from the Middle to Late Miocene deposits near our study area.

This is the third report on the permineralized conifers contained within the silicified lacustrine deposits of the Shimokawa Group. Here we describe a new species of fossil *Glyptostrobus* Endlicher. Extant *Glyptostrobus pensilis* (D. Don) K. Koch is monotypic and a rare endemic to southern Guangdong, northern and southern Fujian, southern Guangxi, and southeastern Yunnan provinces in China. Understanding of the ecological tolerance and attempting to determine the natural geographic distribution of *Glyptostrobus pensilis* have been made difficult because extensive deforestation throughout China has left few, if any, natural stands. Nevertheless, where present, *Glyptostrobus pensilis* occurs in small groves and is restricted to the subtropical and mixed mesophytic forests where climate is warm, humid, and rich in rainfall (Wang, 1961).

Fossil remains of *Glyptostrobus* have been found in the Cretaceous (Bell, 1949, 1957; Brown, 1962). Tertiary fossil remains of *Glyptostrobus* have been found in Eocene to Pliocene age deposits throughout the northern hemisphere (Florin, 1963). Its present distribution is probably a Plio-Pleistocene relict outpost with phylogenetic affinities to a much larger Late Tertiary Asian population (Florin, 1963). LePage and Basinger (1991, 1995), using features of seed cones, reported that some coniferous taxa such as *Larix* Mill and *Pseudolarix* Gordon were present as a high-latitude forest constituent during the early Tertiary. They provide insight into the early evolution and distribution of those two genera.

Conventional thought suggests that all fossil remains of *Glyptostrobus* are in fact representatives of living *G. pensilis* (Christophel, 1976; Endo and Okutsu, 1936; *etc.*). The discovery of *Glyptostrobus rubenosawaensis* sp. nov. provides significant data for interpreting the evolutionary history of this genus.

Geologic setting

The study site is located near the town of Shimokawa, 15 km east of Nayoro City, Kamikawa district, Central Hokkaido, Japan (Figure 1A). This area has been studied by Sako and Osanai (1955), Sako *et al.* (1960), Suzuki and Matsui (1975) and Yamaguchi *et al.* (1990). In the Shimokawa area the following three stratigraphically distinct units are recognized in an ascending order: (1) Sandstone, mudstone and chert rocks of the pre-Tertiary Hidaka Group; (2) Volcaniclastic rocks, lacustrine deposits of the Miocene Shimokawa Group; and (3) Volcanic rocks and fluvial deposits of Pliocene to Quaternary age (Figures 1A-C, 2). The boundaries between these units exhibit unconformable relation. As all specimens analyzed in this study were collected from the Shimokawa Group, we present further information about it.

The Shimokawa Group covers an area of approximately 600 km^2, extending 30 km wide in N-direction, and 20 km wide in E-direction. Its total thickness reaches 500 to 600 m. As *Glyptostrobus*-bearing beds occur in the eastern region, we make a brief stratigraphic description only in this region in an ascending order: the Sanru Lava, the Mosanru and the Ninohashi Formations (Suzuki and Matsui, 1975). The Sanru Lava is exposed widely and consists of volcaniclastic rocks; welded tuff, lava and voluminous pyroclastic flow. The Mosanru Formation is recognized as lacustrine deposits including conglomerate, sandy conglomerate, sandstone, and mudstone (Sako and Osanai, 1955; Sako *et al.*, 1960; Suzuki and Matsui, 1975). As the mudstone is strongly silicified, abundant macro- and micro-permineralized plants have been well preserved in it. The Ninohashi Formation consists of tuffaceous conglomerate containing gravels derived from underlying silicified rocks. The similar successions are also found in the southern and western regions. The main Formation names are summarized in Figures 1C and 2.

The *Glyptostrobus* specimens analyzed in this study were collected primarily from the western outcrop in the Mosanru Formation (Figures 1B, 3). Four silicified mudstone layers (S1-S4) and two agate mudstone layers (A1, A2) are found from the three outcrops of the Formation (Figures 1A, B, 3). The facies analysis of this lacustrine sediments indicates fining-upwards system (Figure 3). *Glyptostrobus rubenosawaensis* were collected at one horizon (S1) in the Mosanru Formation. The upper agate mudstone layers (A1, A2) do not contain plant mega-fossils but contain pollen grains and spores. As the grain size of this mudstone is very fine, their depositional condition seems to be that of topmost supernatant.

Fission track and K-Ar analysis indicate that the age of the volcaniclastic rocks such as the Furebetsu and the Futamata Volcanics, the Sakingawa and the Sanru Formations ranges from 11-13 Ma, while the age of upper volcaniclastic rocks, the Fureppu Lava is from 10-12 Ma (Table 1, Figure 2; Watanabe *et al.*, 1991; *etc.*). These data show

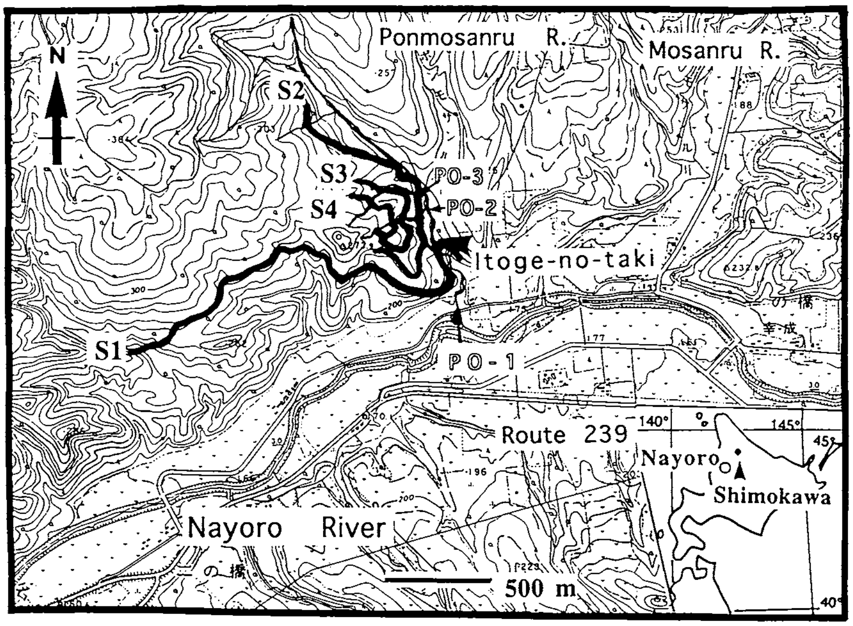


Figure 1A. Locality map of study area (using the topographical map "Shimokawa", scale 1 : 25,000 published by Geographical Survey Institute of Japan) showing the four silicified layers and study sites.

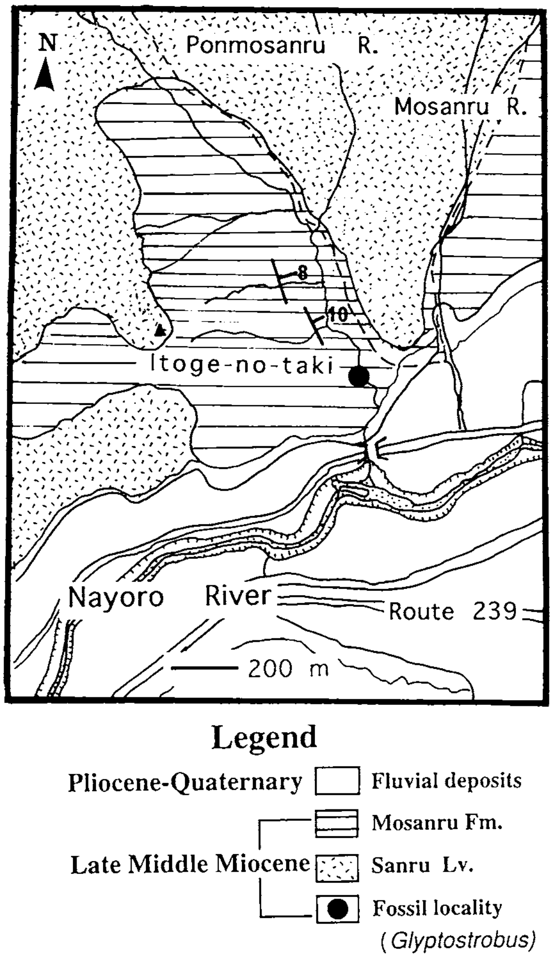


Figure 1B. Geologic map of Shimokawa district including the distribution of the plant-fossiliferous lacustrine deposits, in the Mosanru Formation, Shimokawa Group. Fm.: Formation, Lv.: Lava.

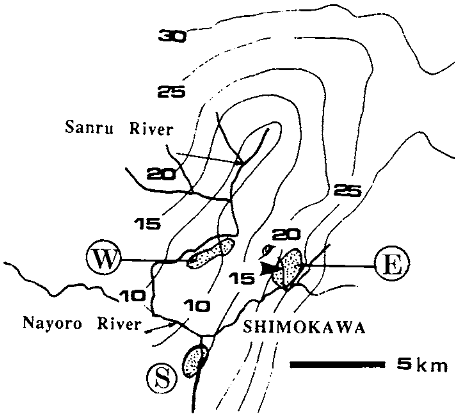


Figure 1C. Map showing the permineralized plant-bearing localities and gravity contours. Bouguer anomalies based on the Normal Gravity Formula (Yamaguchi *et al.*, 1990), which is assumed to be 2.0 g/cm^3. Contour intervals 5 milligals. E: Eastern region is mainly located along the Ponmosanru River, W: Western region is located along the Sanru River, S: Southern region is located along the Shimokawa Panke River

Age	*Stratigraphic Units			Main Lithology	Thickness
	Western R.	Eastern R.	Southern R.		
Quaternary - Pliocene				Fluvial deposits and volcanic rocks	>50m
Late Middle Miocene	Fureppu Lv.	Ninohashi Fm.		Lv., Pyroclastic rocks	ca.300m
	Penke Fm. Sanru Fm.	**Mosanru Fm.	Panke Fm.	Lacustrine deposits	ca.50-80m
	Sanru Lv. Sakingawa Fm.		Furebetsu Fm. Futamata V.	Welded Tf., Lv., Py-flow	ca.200m
Pre-Tertiary	Hidaka Gp.			Sandstone, mudstone, chert rocks	

Figure 2. Stratigraphic sequence of the pre-Tertiary, late Middle Miocene, Pliocene and Quaternary in the Shimokawa region. Three regions are referred to Figure 1C. Fm.: Formation, Gp.: Group, Lv.: lava, Py: pyroclastic, R: region, Tf: tuff, V.: volcanics, *: see to Suzuki and Matsui (1975) and Yamaguchi *et al.* (1990), **: this study

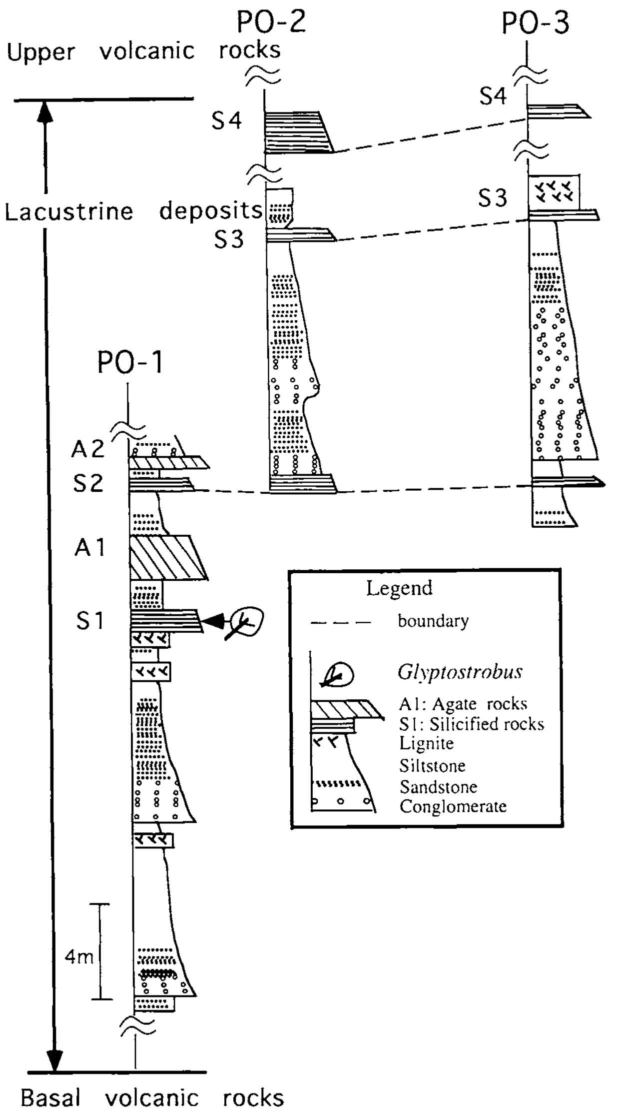


Figure 3. Columnar sections of the Mosanru Formation at Itoge-no-taki, in Shimokawa town.

that deposition of the Shimokawa Group probably occurred without significant interruption and that the age of the plant-bearing horizon is the late Middle Miocene.

Floristic setting

Based on the quality of preservation the plants grew and were preserved *in situ* under the low-energy condition associated with a swamp or lake (Yamaguchi *et al.*, 1990). Such depositional environments and preservational conditions are commonly associated with volcanic terrains (Tiffney, 1981; Cevalloz-Ferriz *et al.*, 1988). The deposits containing the plant fossils roughly correspond to a low-gravity area and a caldera lake is suggested as a possible depositional environment (Figures 1C, 4). Megafloral remains associated with the lacustrine deposits include *Picea, Tsuga, Glyptostrobus, Alnus* P. Miller, *Decodon*, and *Osmunda* (Nishida, 1990 ; Matsumoto *et al.*, 1994, 1995, 1996). This assemblage suggests a possible candidate for the sedimentary environment of the lacustrine deposits. Thus we offer a schematic drawing of the paleo-vegetation (Figure 4).

Throughout the high-latitude regions of the northern hemisphere *Glyptostrobus* was a common constituent of the warm-temperate forests (Budanstev, 1992). Extant *Glyptostrobus pensilis* is very sensitive to frost, requires high humidity during the winter months, and will not tolerate temperatures below 0°C. Similar conditions are inferred for Hokkaido during the late Middle Miocene.

Occurrence of fossil plants

The plants occur in a 1.0-1.5 m thick silicified mudstone (S1) that crops out near Itoge-no-taki, a small waterfall on the Ponmosanru River (also called Rubeno Sawa), a tributary of the Nayoro River (Figures 1A-C, 3). The columnar section (PO-1) of the outcrop is shown in Figure 3 and their strike and dip are N40°W and 10°N, respectively (Figure 1B). Another two columnar sections (PO-2, 3) are also indicated in Figure 3.

The rock consists largely of chalcedonic quartz and includes abundant anatomically and morphologically well-preserved plant remains (Figures 5A-C). Preserved shoots are commonly orientated perpendicular to the bedding plane,

Table 1. Ages of formations of the Shimokawa Group

Formation	Rock	Methods	Age (Ma)	References	
Fureppu Lv.	Andesite	K-Ar	12.8±0.6	Watanabe et al.	1988
Fureppu Lv.	Andesite	K-Ar	10.0±0.5	Watanabe et al.	1988
Furebetsu V.	Andesite	K-Ar	11.2±0.3	Sugawara et al.	1992
Sakingsawa Fm.	Andesite	K-Ar	11.2±0.5	Watanabe et al.	1988
Sanru Fm.	Altered volcanics	FT	11.3±0.7	Koshimizu et al.	1987
Sanru Fm.	Rhyolite, Dacite	K-Ar	12.1±0.6	Watanabe et al.	1988
Futamata V.	Basalt	K-Ar	12.1±0.7	Sugawara et al.	1992
Sakingawa Fm.	Altered volcanics	FT	12.1±0.9	Koshimizu et al.	1987
Futamata V.	Basalt	K-Ar	12.4±1.3	Watanabe et al.	1991
Sakingawa Fm.	Green tuff	FT	13.9±1.1	Koshimizu et al.	1986
Futamata V.	Basalt	K-Ar	15.2±1.6	Watanabe et al.	1991

Fm.: Formation, FT: fission track, Lv.: Lava, V.: Volcanics

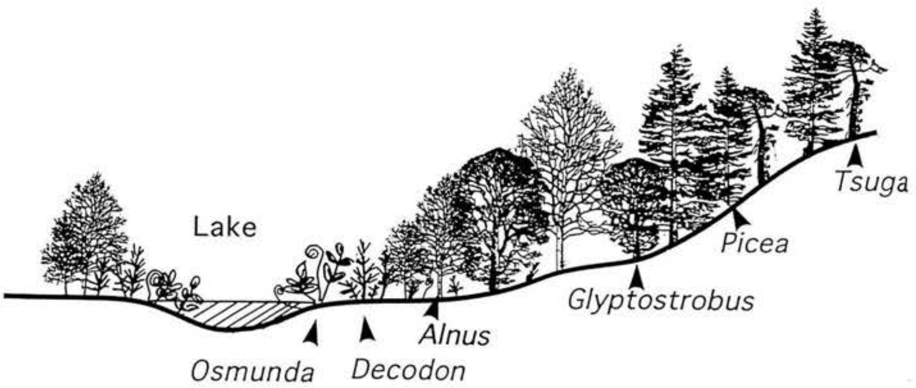


Figure 4. Generalized reconstruction of the region showing the environmental setting and inferred relationship of floristic constituents within a larger vegetational mosaic.

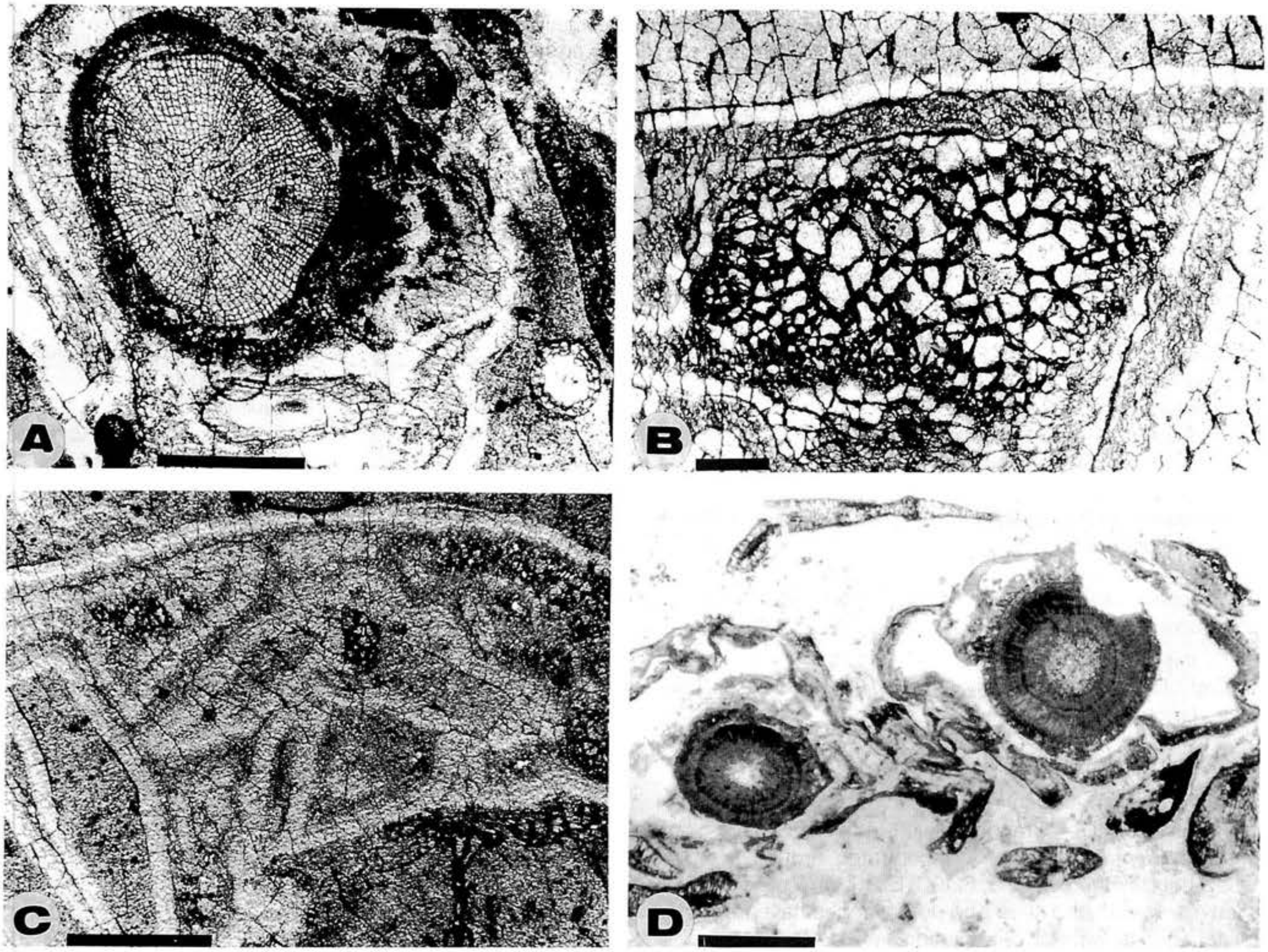


Figure 5. Hand-ground thin sectioned rock samples (A–C) from Itoge-no-taki (S1 layer, #95061501C), and peel section (D). **A, B.** Silicified rock and quartz vein enclosing plant fragments. **C.** Lowermost rocks from the plant bearing horizon. **D.** Peel of shoots and leaves of *Glyptostrobus rubenosawaensis* sp. nov. in transverse section (#93081402). Scale bars : A, C = 0.5 mm ; B = 0.1 mm ; D = 2 mm.

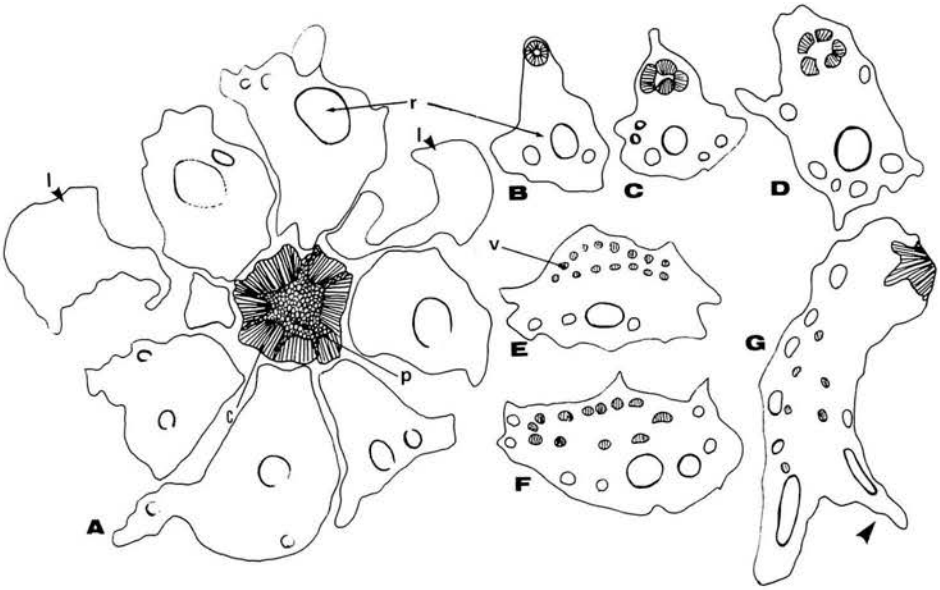


Figure 6-1. Camera lucida drawings showing the arrangement of the vascular bundles and resin canals within the bract-scale complexes of *Glyptostrobus rubenosawaensis* sp. nov. **A-F.** Transverse sections. **G.** Longitudinal section. Note the arrow showing the prominent bract. c : cortex, l : leaf, p : pith, r : resin canal, v : vascular bundle.

Table 2. Measurements (mm) of extant and fossil *Glyptostrobus* cones

Species	Cone		b-s complex		Measured no. of specimes	Locality
	Length	Diameter	Length	Width		
Glyptostrobus rubenosawaensis sp. nov.	26.2	18.8	20.1	7.0	22	Hokkaido, Japan
G. pensilis Endl.	20.9	17.5	11.5	5.5	11	Chiba, Japan
G. pensilis Endl.	22.4	16.8	16.5	6.2	103	Shizuoka, Japan
G. pensilis Koch.	21.0	16.0	11.5	4.8	?	Many places, Honsyu, Japan
G. pensilis Endl.	19.1	12.5	16.1	4.0	45	Aichi, Japan
G. orientalis Endo	16.0	10.5	10.5	6.0	1	Kyushin, Korea
G. nordenskioeldii (Heer) Brown	13.5	10.6	—	—	1	Axel Heiberg Island, Canada
G. nordenskioeldii (Heer) Brown	14.7	10.9	7.5	5.0	13	Smoky Tower, Canada
G. nordenskioeldii (Heer) Brown	10.0	10.0	—	—	?	Alberta, Canada
G. europaeus (Brong) Heer	24.0	19.0	—	—	1	Gifu, Japan
G. europaeus (Brong) Heer	17.0	12.3	—	—	3	Hokkaido, Japan
G. europaeus (Brong) Heer	18.0	14.0	8.0	4.0	1	Hokkaido, Japan
G. europaeus (Broug) Heer	22.0	16.0	—	—	2	Akita, Japan
G. europaeus (Brong) Heer	18.5	11.5	9.2	4.7	4	Germany

* : this paper ; ** : collector

Cret : Cretaceous, E : Early, L : Late, M : Middle, Pal : Paleocene, Eoc : Eocene, Mio : Miocene, Pli : Pliocene, U : Upper, b-s : bract-scale, Ex : Extant

indicating that plant burial and preservation was rapid and *in situ* (Figures 5A, D). Branches with attached leaves and cones of *Glyptostrobus* are concentrated around some of these shoots (Figures 7A, B, F, 10C-E). Many organs, such as leaves, shoots and seed and pollen cones have kept their original shapes without deformation.

Microscopic observations of thin-sectioned rocks show the textures of the well preserved shoots, branches and fragments of plants. Numerous quartz network veins surround the plant fragments preserving their structure (Figures 5A-C).

Materials and Methods

Twelve fossiliferous rocks (No. 903000, 903001, 903005, 931122, 94081401, 94081402, 94081403, 94081406, 94081407, 95052802, 95061501C, and 95071401) were collected by Isekichi Nakauchi of Shimokawa, Kamikawa district, Central Hokkaido, and the authors from the riverbeds of the Ponmosanru River, tributary of the Nayoro River (Figures 1A-C).

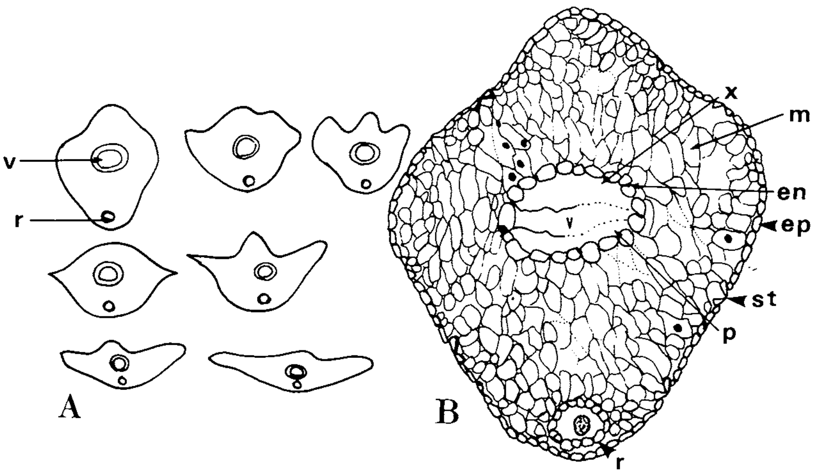


Figure 6-2. Camera lucida drawings showing the internal anatomy of leaves of *Glyptostrobus rubenosawaensis* sp. nov. in transverse section. **A.** Note that the shape of the leaf changes at different levels. **B.** Transverse section of a rhomboid-shaped leaf (#93081403). en : endodermis, ep : epidermis, m : mesophyll, p : phloem, r : resin canal, st : stomata, v : vascular bundle, x : xylem.

and bract-scale complex

Age	Source
Mio.	I. Nakauchi, M. Matsumoto & T. Ohsawa*
Ex	M. Matsumoto & T. Ohsawa*
Ex	M. Matsumoto*
Pli.	S. Miki (1950)
L. Mio.-Pli.	K. Uemura (1982)**
E. Mio.	S. Endo & H. Okutsu (1936)
Eoc.	J.F. Basinger (1991)
Pal.	D.C. Christophel (1976)
U. Cret.	W. Bell (1949)
M. Mio.	T. Tanai & N. Suzuki (1961)
M. Mio.	T. Tanai & N. Suzuki (1961)
M. Mio.	T. Tanai & N. Suzuki (1961)
E. Mio.	K. Huzioka (1964)
Tertiary	O. Heer (1855-59)

The fossils are preserved as silica permineralizations.

Rocks were sliced by a rock cutter, at intervals of 1-2 cm. All specimens were prepared using the cellulose acetate peel method which has been modified for silicifications with 25-45% hydrofluoric acid as the etching reagent (Joy *et al.*, 1956 ; Basinger, 1981). The peels were mounted in a xylene-soluble Canada balsam suitable for light microscopy. We also made thin sections of rocks for microscopic observation and examined textures.

With the exception of specimen No. 94081407, all specimens are housed in the Laboratory of Phylogenetic Botany, Faculty of Science, Chiba University, Japan. Specimen No. 94081407 is housed in the Board of Education Office, Shimokawa, Hokkaido, Japan.

Leaves, shoots and seed and pollen cones of extant *Glyptostrobus pensilis* were examined anatomically for comparison purposes. These specimens were collected from a number of localities throughout Japan (Table 2), fixed in FAA, and embedded in Palaplast. The leaves, shoots, and pollen cones were then sectioned with a rotary microtome in 12.0-20.0 μm thick, stained with safranine and fastgreen, and mounted on glass slides. The seed cones, both attached and detached, were either fixed with a glycerin-alcohol mixture or air dried, and sectioned by hand using a razor.

A number of fossil *Glyptostrobus* specimens were studied for comparative purposes (Table 2). Unfortunately, it was not possible to examine some of these specimens and the taxonomic information was, from necessity, obtained from the literature.

Description

Systematic treatment
Order Coniferae Jussieu, 1789
Family Taxodiaceae Warming, 1884
Genus **Glyptosrobus** Endlicher, 1847

Type species.—*Glyptostrobus pensilis* Endlicher, Syn. Conif., 1847

Glyptostrobus rubenosawaensis sp. nov.

Occurrence.—Itoge-no-taki ; S1 Bed of the Mosanru For-

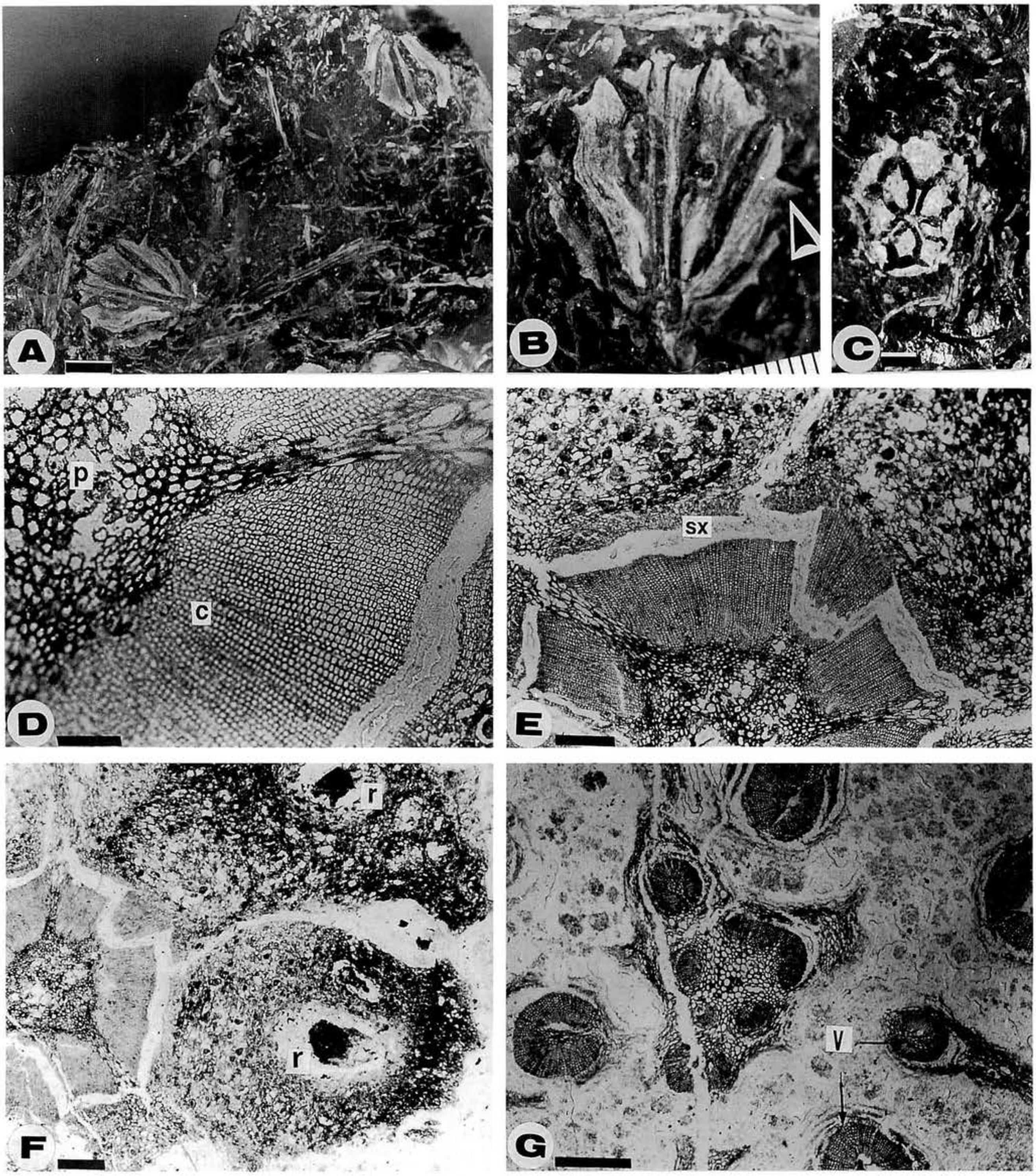


Figure 7. Transverse and longitudinal sections of the bract-scale complex of *Glyptostrobus rubenosawaensis* sp. nov. **A.** Seed cones in longitudinal section showing the individual bract-scale complexes (#94081407). **B.** Enlargement of specimen in Figure 7A. Note the prominent bract (arrow, #94081407). **C.** Cross section of seed cone (#95071401). **D.** Transverse section of cone axis showing pith (p), cortical tissues (c) (#94081403). **E.** Transverse section of cone axis showing pith, cortical tissues, and bract-scale complexes with large resin canals (#94081403). **F.** Transverse section of cone axis and bract-scale complex showing large resin canals (#94081403). **G.** Transverse section of cone axis showing cylindrical units (#94081403). c : cortex, p : pith, r : resin canal, sx : secondary xylem, v : vascular bundle. Scale bars : A, C=10.0 mm ; D=150 μm ; E-G=400 μm.

mation of the Shimokawa Group.

Geologic age.—The late Middle Miocene.

Diagnosis.—Foliaged-bearing shoots bearing cryptomeroid, taxodioid, and cupressoid-like leaves (Figures 6-2A, 10D, E, 11A). Leaves bifacially flattened or four-sided, stomata present in two to three rows on all surfaces (Figures 6-2B, 11A). Epidermis one cell-layer thick and consisting of elliptical to rounded cells, 7.0-15.0 μm wide, 5.0-7.5 μm high. Hypodermis not discernible (Figure 11A). Endodermis composed of isodiametric parenchyma cells, 90.0-130.0 μm in diameter and forming a continuous sheath around the vascular bundle (Figures 6-2B, 11A). Single resin canal 40.0-65.0 μm in diameter located just on the abaxial surface near the epidermis and encircled by one layer of epithelial cells (Figures 6-2B, 11A). One single centrally located vascular bundle. Mesophyll undifferentiated, elliptic to isodiametric in shape, 10.0-25.0 μm long, 15.0-40.0 μm wide.

Seed cones obovate in outlook. Ovuliferous scale wedge-shaped and fused with bract basally; bract free apically. Free portion of the bract is up to 2.0 mm long, conspicuous, and forming a 90° angle with ovuliferous scale (Figures 6-1G, 7B, 9A). Bract-scale complex wedge-shaped, narrowing toward the basal part (Figures 6-1G, 7A, B, 8F, G, 9A). Bract width is about one half the length of the bract-scale complex.

Pollen cones composed of four to five microsporophylls, each bearing 4-8 microsporangia (Figures 11D-F). The arrangement of microsporophyll and subtending scale-leaves helical.

Type and deposition.—Specimen including leaves, seeds and pollen cones.

Holotype : Specimen No. 94081402

Paratypes : Specimens Nos. 903000, 903001, 903005, 931122, 94081401, 94081403, 94081404, 94081407, 95052802, 95061501C, and 95071401

Extant material : Specimen Nos. 950529 and 941125.

Etymology.—The specific epithet is named after this fossil locality, Rubeno-Sawa.

Detailed description

Descriptive terms.—The terminology used here concerning coniferous seed cones are after Miller (1975). The terms bract-scale complex, scale, and bract signify the cone-scale complex, ovuliferous scale, and bract-scale of Florin (1951), respectively. We describe the term cone as seed cone.

Shoots and leaves.—The leafy twigs bear cryptomeroid and taxodioid leaves distally and cupressoid leaves proximally (Christophel, 1976) (Figure 10E). Shape of leaf is acute-acuminate-obtuse or rotundate in cross section ; their width and thickness are various in size, ranging from 0.4-1.1 mm wide, 0.3-0.9 mm thick (Figures 6-2A, B, 10C-E, 11A).

The epidermis consists of a single layer of elliptical to rounded cells in cross section, 7.0-15.0 μm wide, 5.0-7.5 μm high, with cell walls 1.0-2.0 μm thick (Figures 6-2B, 11A).

Stomata are arranged in two to three rows on each face (Figures 6-2B, 11A). We did not examine the hypodermis on these specimens. Mesophyll cells are not differentiated into palisade and spongy tissues. These cells are elliptical to isodiametric in shape, with round corners in cross section and 10.0-25.0 μm thick, 15.0-40.0 μm wide with cell walls 1.0-2.5 μm thick (Figures 6-2B, 11A).

Cell of the endodermis are isodiametric, 90-130 μm in diameter, and form a single layer that completely encircles the vascular bundle (Figures 6-2B, 11A). Endodermal cells are not well preserved, about 20 cells in number. Details of their anatomy are obscured (Figures 6-2B, 11A). The diameter of endodermis is about 150-180 μm. The median vascular bundle is poorly preserved and details of its anatomy are obscured (Figures 6-2A, B, 11A).

A single resin canal 40.0-65.0 μm in diameter and encircled by one layer of epithelial cells is located on the abaxial surface near the epidermis. Epithelial cells are 10-16 in number (Figures 6-2A, B, 11A).

Cones.—The seed cones are obovate in outline, 26.2 mm long and 18.8 mm wide on average (Table 2, Figures 7A, B). Each cone is composed of approximately 15 bract-scale complexes arranged helically on a central cone axis. Seven to nine bract-scale complexes are visible in lateral view in longitudinal section (Figures 7A-C). The ovuliferous scale is fused with the bract basally, but free apically (Figures 7A, B). The shape and size of the cone scales vary with positions. Those near the base of the cone are spatulate, 3.5-6.7 mm wide, and 1.5-2.7 mm thick, those near the middle are peltate, 1.3-3.8 mm wide, and 1.9-4.4 mm thick, while those near the top are cuneate, 0.5-2.0 mm wide, and 1.9-2.4 mm thick (Figure 7B). The cone scales are wedge-shaped, narrow at the base and reaching a maximum width of 7.0-8.0 mm near the apex, and range from 17.0-23.0 mm in length (Figure 7B).

The centrally located cone scales diverge from the central axis at 22-26°, while the basal scales diverge from the central axis at 45-52° and turn upwards at a 20° angle (Figures 7A, B, 8F, G, 9A). The basal scales are somewhat furrowed and possess wavy margins (Figures 7A, B, 10A). The free portion of the bract is up to 2.0 mm long, conspicuous, and forming a 90° angle with the ovuliferous scale (Figures 6-1G, 7A, B, 8F, G, 9A). Bract width is about one half the length of the bract-scale complex (Figures 6-1G, 7B, 8F, G, 9A).

Cone axis.—The cone axis is 2.7-3.0 mm in diameter with a central vascular cylinder 0.5-0.6 mm in diameter (Figures 6A, 7D-F). The pith is 1.0-1.2 mm in diameter and composed of thick-walled isodiametric parenchyma cells, 25.0-50.0 μm in diameter and 100-125 μm in length (Figures 6-1A, 7D-F). The vascular cylinder is 2.2-2.4 mm in diameter and composed primarily of secondary xylem (Figures 6-1A, 7D-F). Secondary xylem tracheids are 8.0-15.0 μm in diameter. The primary xylem is endarch and located at the inner edge of the vascular cylinder (Figures 7D-F).

Cortex.—The cortex of the cone axis is 80.0-120.0 μm thick and composed of isodiametric parenchyma cells that are 10.0-15.0 μm in diameter and cell walls 2.0-2.5 μm thick (Figures 6-1A, 7E, F). Resin canals were not observed in the cortex or surrounding tissues ; however, tissues external to the cortex were not well preserved.

Bract-scale complex.—Tissues of the bract-scale complexes consist of epidermis, hypodermis, fundamental tissue, vascular trace and resin canals.

The vascular trace that supplies the bract-scale complex diverges from the central stele in the cone axis as a cylindrical unit (Figures 6-1B, 7G, 8A). A small strand diverges from the trace that enters the complex on the abaxial surface and enters the bract (Figures 6-1C, D, 8B-G). The trace then splits into 14-18 vascular strands in two horizontal rows that supply the scale (Figures 6-1E, F, 9C, 10A, B). Phloem associated with the adaxial vascular strands occurs on the adaxial surface, while that of the abaxial strands is found on the abaxial surface. In the distal part of the bract-scale complex the vascular bundle consists of 7-12 filed xylem cells and 5-7 filled phloem cells (Figure 9F).

Near the base of the bract-scale complex one resin canal, 0.5-1.4 mm in diameter, is present (Figures 6-1A, 7F). This large canal divides acropetally into 14-18 smaller resin canals, 0.1-0.4 mm in diameter, and arranged in two rows on the abaxial side (Figures 6-1A-G, 8A-G, 9A-C, 10A, B). The fundamental tissue consists of parenchyma cells and scattered fibers (Figures 8G, 9B-F). The parenchyma cells are isodiametric and 25.0-70.0 μm in diameter, while the fibers are round to polygonal and 50-90 μm in diameter, with walls 15.0-30.0 μm thick. The fibers are moderately abundant basally and become more prevalent in the apical part of the cone scales (Figures 9D-F).

The epidermis consists of a single layer of thick-walled, elliptical cells, 15.0-25.0 μm in diameter on the adaxial and lateral sides of the distal part of the complex (Figures 9D, G).

The hypodermis is composed of 2-5 layers of thin-walled, isodiametric parenchyma cells, 20.0-35.0 μm in diameter (Figures 9D, G). On the adaxial surface these cells are occluded by an unidentifiable black substances. Adaxially, trichomes are abundant (Figure 9D).

Pollen cones.—The pollen cones are subtended by 3-4 bracts and consist of 4-5 helically arranged microsporophylls bearing 4-8 peltate microsporangia. The microsporangia are 40.0-50.0 μm in diameter and arranged in two rows (Figures 11D-F). A longitudinal dehiscence zone occurs on the abaxial side.

Affinity and Discussion

Comparisons with extant genera of Taxodiaceae

Seed cones.—Taxodiaceous cones are separated into three distinct groups based on bract-scale morphology, the relative size of the ovuliferous scales and bracts, and arrangement of the vasculature traces within the bract-scale complex (Eames, 1913; Satake, 1934; Hirmer, 1936; Dallimore and Jackson, 1966; La Pasha and Miller, 1981).

The first group includes *Glyptostrobus, Cryptomeria* D. Don, and *Taxodium* Richard. The bract-scale complexes of this group are commonly cuneiform and non-peltate (although peltate in *Taxodium*) and possess small bracts. The vascular trace is of the open type (Satake, 1934; La Pasha and Miller, 1981).

The second group, which includes *Sequoia* Endlicher, *Sequoiadendron* Buchholz, and *Metasequoia* Hu et Cheng has peltate bract-scale complexes, equally sized scales and bracts, and possesses a circular trace to the bract-scale complex (Eames, 1913; Hirmer, 1936; La Pasha and Miller, 1981).

Group three consists of *Cunninghamia* R. Brown and *Taiwania* Hayata and possesses tapering non-peltate bract-scale complexes, large bracts, reduced scales and terete traces (Satake, 1934). *Athrotaxis* D. Don shows wide variation in these features and is commonly not considered in such analyses (Eames, 1913; Hirmer, 1936; Dallimore and Jackson, 1966).

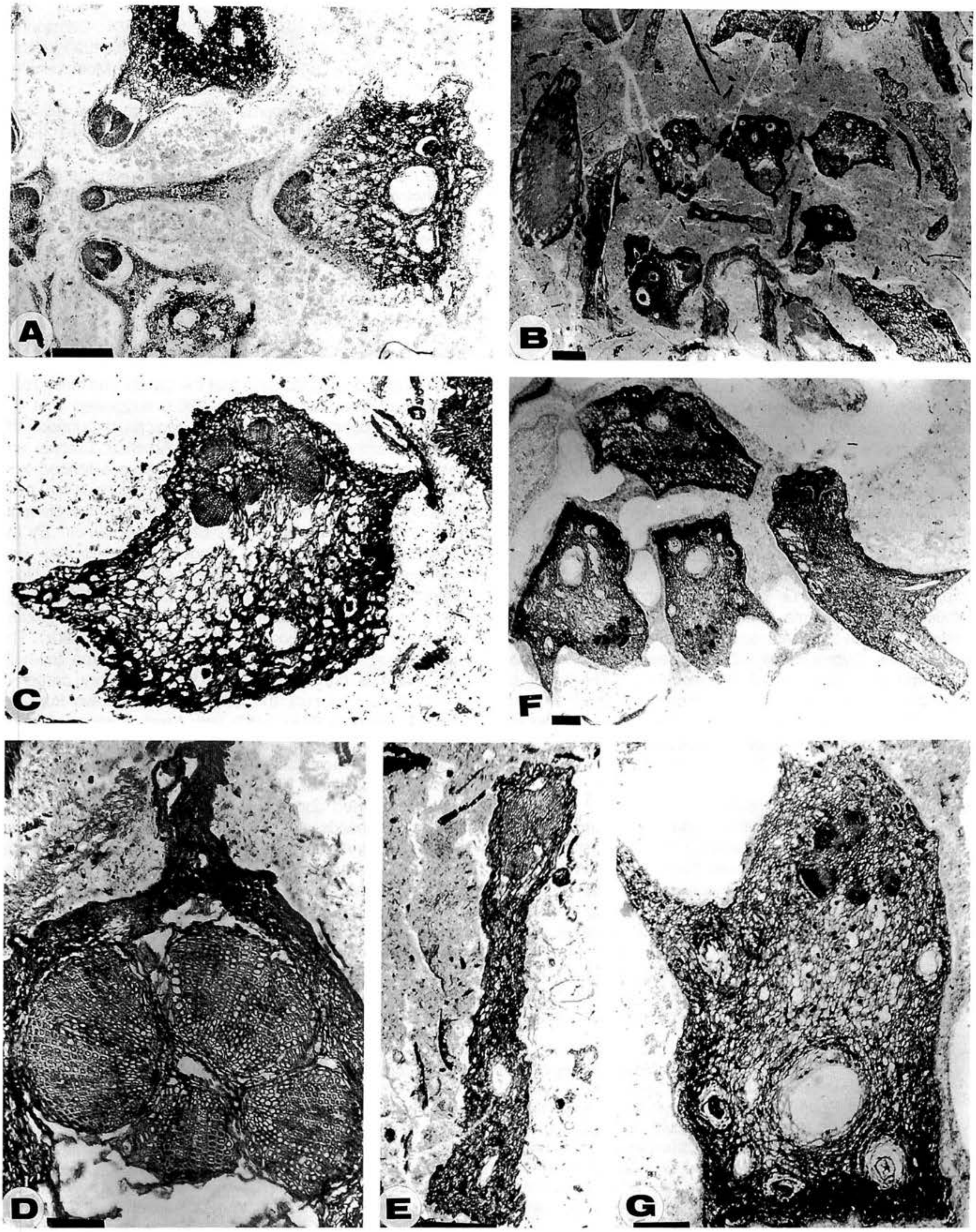
Based on gross morphological features, the shape and size of the bract, the small ovuliferous scale, and degree of fusion between the bract and scale, our fossil material most closely resembles the seed cones of *Glyptostrobus, Cryptomeria* and *Taxodium* (Satake, 1934; La Pasha and Miller, 1981).

Although *Cryptomeria* and *Taxodium* resemble our fossil specimens in some aspects, there are significant differences. *Cryptomeria* seed cones are globular, less than 15.0 mm in diameter, and possess wedge-shaped bract-scale complexes with deeply sculptured apical margins. Seed cones of *Taxodium* are ovoid to sub-globose with peltate cone scales.

Pollen cones.—Pollen cones of *Metasequoia* and *Taxodium* are also subtended by a number of bracts, but in *Metasequoia* the arrangement of the bracts, microsporophylls, and subtending scale leaves is decussate and only three microsporangia are present. In *Taxodium* there are 5-9 microsporangia per microsporophyll (Dallimore *et al.*, 1966; Rothwell *et al.*, 1979; Basinger, 1981); usually the microsporangia flattened on the abaxial side. However the microsporangia of *Glyptostrobus* are arranged in a double horizontal lines. The shape of the microsporophylls is peltate with a radial longitudinal downward curve at the abaxial side. Based on these features and comparison of our fossil specimens with those of living *Metasequoia* and *Taxodium* there is no doubt that our material is *Glyptostrobus*.

Shoots and leaves.—The shoots and leaves of *Glyptostrobus rubenosawaensis* are characterized by possession of helically arranged, four-sided, linear to acicular scalelike leaves with stomata on all surfaces. Internally, there is a single resin canal near the epidermis on the abaxial surface, no hypodermis, a single median vascular bundle, and mesophyll which has not been differentiated into palisade tissues or spongy mesophyll. Although *Cryptomeria* (Suzuki, 1979), *Athrotaxis* (Dallimore *et al.*, 1966), and *Taxodium* (Basinger, 1981) possess four-sided, linear to acicular scalelike leaves,

Figure 8. Transverse and longitudinal sections of the bract-scale complex of *Glyptostrobus rubenosawaensis* sp. nov. **A.** Transverse section showing a large and small resin canals (#94081403). **B.** Transverse section of a bract-scale complex (#903005). **C-E.** Enlargement of specimen of Figure 8B (#903005). **F.** Transverse and longitudinal section of bract-scale complex (#94081402). **G.** Enlargement of specimen of Figure 8G (#94081402). ep: epidermis, ph: phloem, r: resin canal, t: trichome, v: vascular bundle, x: xylem. Scale bars: A, B, F=800 μm; C, E, G=400 μm; D=150 μm.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with undifferentiated mesophyll, and a single resin canal and bear some similarity to those of *Glyptostrobus rubenosawaensis*, there are notable differences. Leaves of *Taxodium* are broader and possess sclerids abaxial to the vascular bundle. Leaves of *Cryptomeria* and *Athrotaxis* possess a single-layered hypodermis, and a resin canal which is closely associated with the vascular bundle sheath, but not in contact with the epidermis.

Thus our leaf specimens are not assigned to these three genera of Taxodiaceae but belong to *Glyptostrobus*.

Based on anatomical and morphological features of the seed and pollen cones, shoots and leaves our fossil specimens most closely resemble those of extant *Glyptostrobus pensilis* (extant *G. pensilis*: pollen cone- Figure 11C, leaf in cross section-Figure 11B).

Comparisons with extant and fossil *Glyptostrobus*

Specimens of *Glyptostrobus rubenosawaensis* were compared with *G. pensilis* and a number of previously described fossil *Glyptostrobus* (Table 2). *Glyptostrobus rubenosawaensis* differs from *G. pensilis* in having larger seed cones, longer bract-scales, and a prominent bract (Table 2; Figures 6-1G, 7B, 8F, G, 9A). The most obvious difference between *Glyptostrobus rubenosawaensis* and the other fossils is the larger cone size and prominent projection of the bract in *G. rubenosawaensis*. The North American *Glyptostrobus nordenskioeldii* (Heer) Brown and Asian *G. orientalis* Endo are significantly smaller, while those of *G. europaeus* Heer and *G. pensilis* are about 25% smaller. Although cone size may not necessarily be a diagnostic feature on which to base a new species, the prominent bract distinguishes *Glyptostrobus rubenosawaensis* from all other fossil and living species of *Glyptostrobus*. The bract of *Glyptostrobus rubenosawaensis* is more than twice as long and wide as in the extant species. This is a major reason why we describe *Glyptostrobus rubenosawaensis* as a new species.

Fossil records of *Glyptostrobus*

The first appearance of the genus *Glyptostrobus* was reported from the Upper Cretaceous of northwestern North America (Bell, 1949, 1957; Brown, 1962). The fossil record of this genus indicates that the genus was a common forest constituent throughout Europe, North America, Asia, and Japan from the Early Tertiary until the Late Pleistocene (Heer, 1855; Endo *et al.*, 1936; Shimakura, 1939; Miki, 1941, 1950, 1954, 1957; Endo, 1953; Hantke, 1954; Okutsu, 1955; Tanai, 1952, 1961, 1970, 1992; Tanai *et al.*, 1963, 1972, 1992; Wang, 1961; Huzioka, 1964, 1972; Ferguson, 1967; Matsuo, 1967, 1970a, b, 1971, 1972; Klipper, 1968; Murai, 1968; Pabst, 1968; Ishida, 1970; Schweitzer, 1974; Christophel, 1976; Basinger, 1981, 1991; Uemura, 1988, 1990; Ozaki, 1991; Budantsev, 1992; Yamakawa, 1993; Momohara *et al.*, 1993; Momohara, 1994a, b).

Although the fossil records of *Glyptostrobus* are relatively extensive, aspects of its evolutionary history and intergeneric relationships within the Taxodiaceae are poorly understood. While most of these reports are based on well-preserved, morphologically informative compression fossils, anatomical data are rare and limited to reports of leaves (Basinger, 1981) and wood (Watari, 1947; Suzuki *et al.*, 1989; Itoh, 1993). Based on data derived from immunological (Price and Lowenstein, 1989) and DNA analyses (Chase *et al.*, 1993), Ohsawa (1994) concluded that the genus probably first appeared sometime during the early Tertiary.

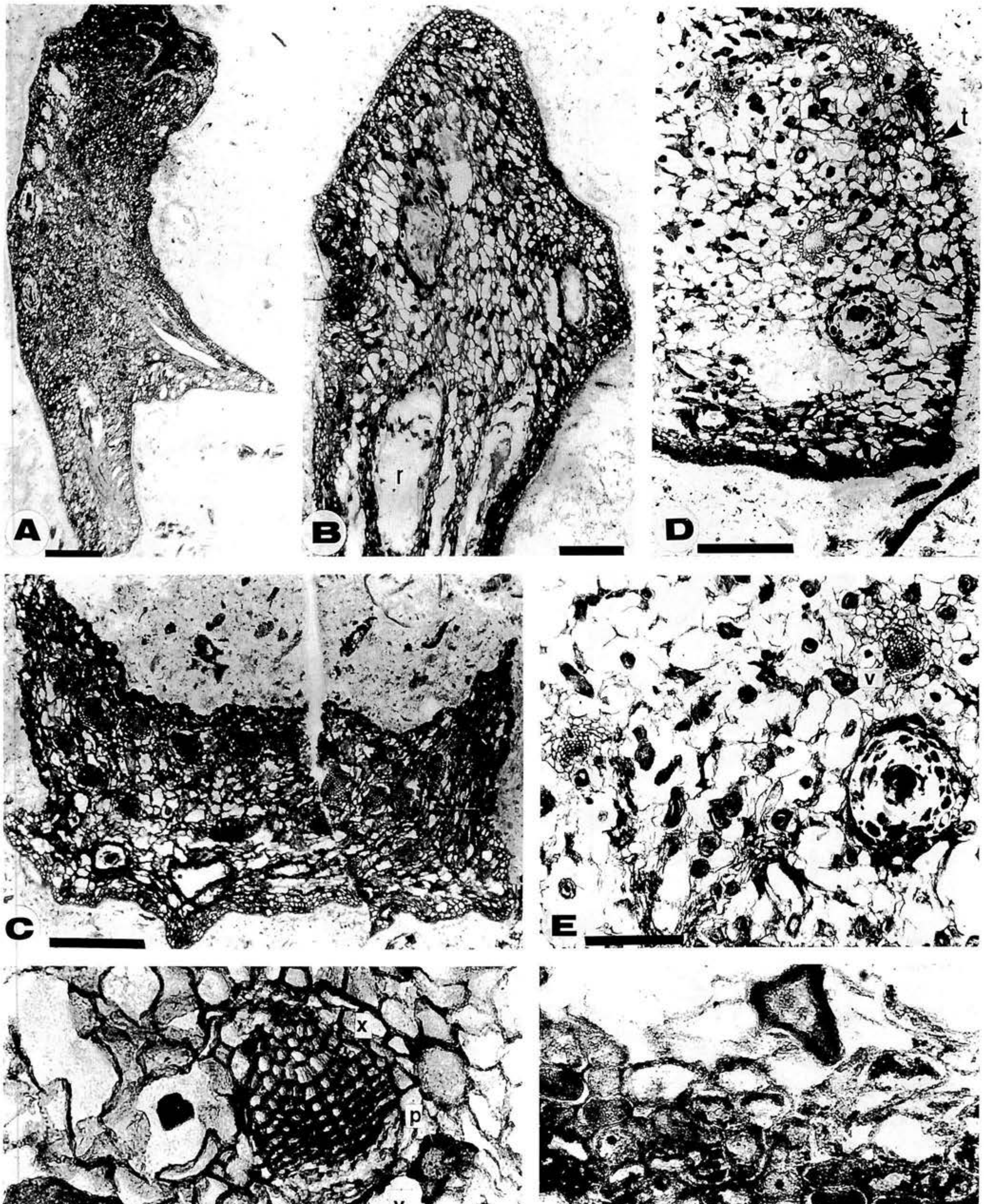
Evolutionary history of *Glyptostrobus*

The fossil records indicate that the genus was much more widespread than today. Florin (1963) suggested that the genus was concentrated in three regions throughout the northern hemisphere: western North America, Europe, and Asia. In western North America the genus extended from Montana to Alaska during the Upper Cretaceous to Lower Paleocene. This was thought to be the center of origin (Bell, 1949, 1957; Brown, 1962; Christophel, 1976). By the Late Paleogene and Early Neogene *Glyptostrobus* was widespread, but appears to have disappeared from North America by the end of the Miocene (Basinger, 1991).

In Eurasia, *Glyptostrobus europaeus* was widely distributed from the Eocene to Pliocene (Wolfe and Tanai, 1980). The Asian region, including southeastern Siberia, Korea, Sakhalin and Japan is considered to be the secondary center of distribution. In Japan, the genus is well known from the Pliocene deposits (Miki, 1957), with fossil representatives of *Glyptostrobus pensilis* becoming rare in the Early Pleistocene (Momohara *et al.*, 1993). The genus survived into the first warm interglacial of the Pleistocene (Florin, 1963).

We mentioned above that the Eurasian species *Glyptostrobus europaeus* was widely distributed in the northern hemisphere during the Tertiary, and is difficult to distinguish from the North American species, *G. nordenskioeldii* from the Oligocene to Miocene, which are represented by impressions or compressions of foliage and cones. We reconstruct generalized paleogeographic distribution of the genus *Glyptostrobus* in the northern hemisphere of the late Middle Miocene (Figure 12). Data on distribution of fossil and living *Glyptostrobus* include specimens referred to Florin (1963) and previous data.

Figure 9. Transverse and longitudinal sections of the bract-scale complex of *Glyptostrobus rubenosawaensis* sp. nov. **A.** Longitudinal section showing the angle of divergence between the bract and scale (#94081402). **B.** Enlargement of specimen in Figure 8A showing large resin canals and hypodermal cells (#94081402). **C.** Transverse section showing vascular strands arranged in two rows (#903005). **D.** Transverse section of the bract-scale complex showing epidermis, hypodermis, resin canals, vascular bundles, parenchyma, and trichomes (#94081404). Note the 2-5 layers of hypodermis and trichomes on the abaxial surface. **E.** Enlargement of specimen in Figure 9D (#94081404). **F.** Enlargement of specimen in Figure 9D showing vascular bundle. (#94081404). **G.** Enlargement of specimen in Figure 9C showing epidermis and hypodermis (#94081404). ep: epidermis, p: phloem, v: vascular bundle, x: xylem. Scale bars: A=800 μm; B-D=400 μm; E=200 μm; F, G=50 μm.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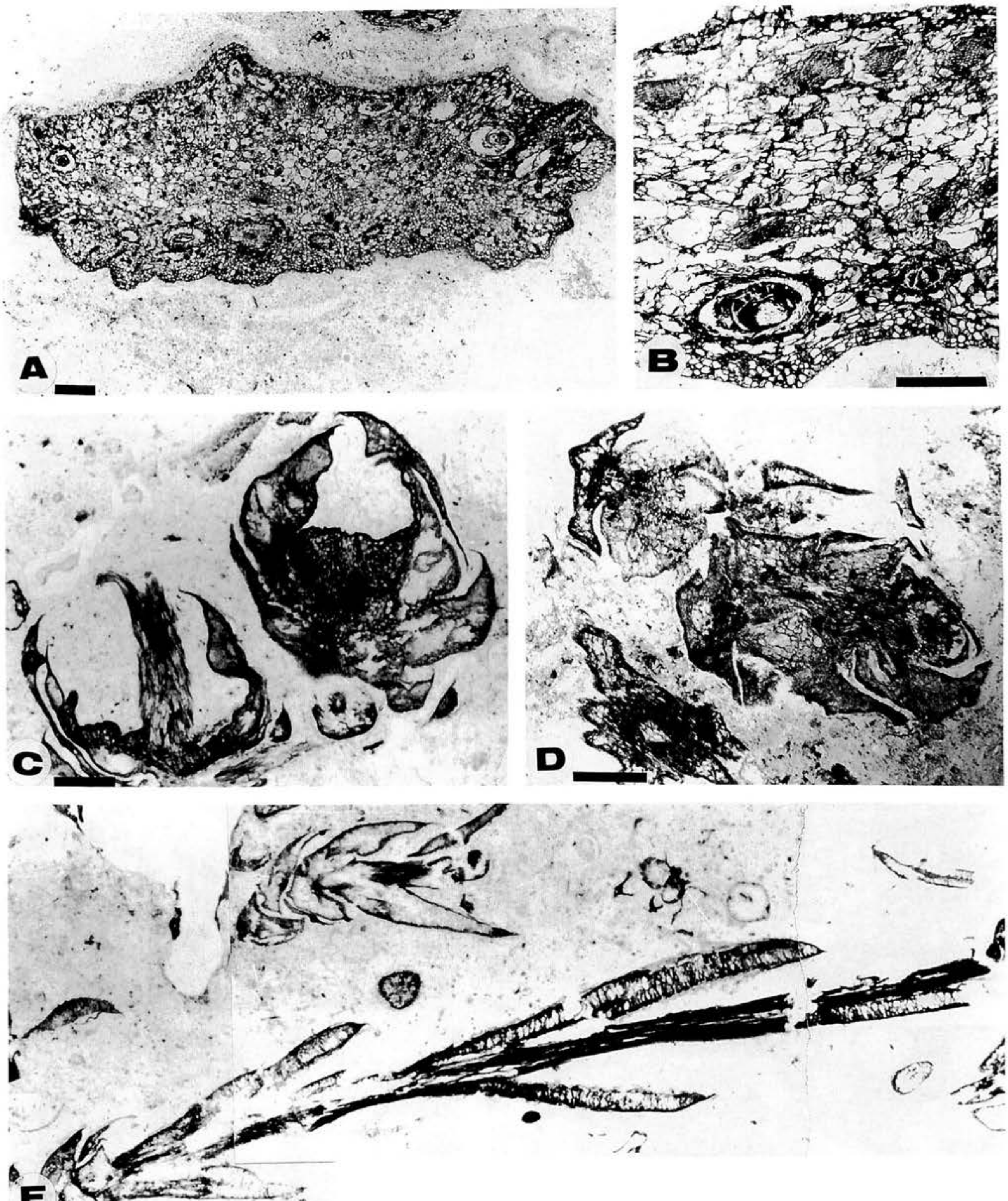

Figure 10. Transverse and longitudinal sections of seed cones and shoots of *Glyptostrobus rubenosawaensis* sp. nov. **A.** Cross section of cone scale showing vascular strands and resin canals on abaxial and adaxial surfaces (#94081402). **B.** Cross section of cone scale showing arrangement of vascular bundles and resin canals (#903005). **C.** Longitudinal section of the basal region of a cone scale (#94081402). **D.** Transverse section of the basal region of a cone scale (#94081402). **E.** Longitudinal and slightly oblique section of a cone scale and shoots (#94081402). Scale bars : A–D=400 μm ; E=800 μm.

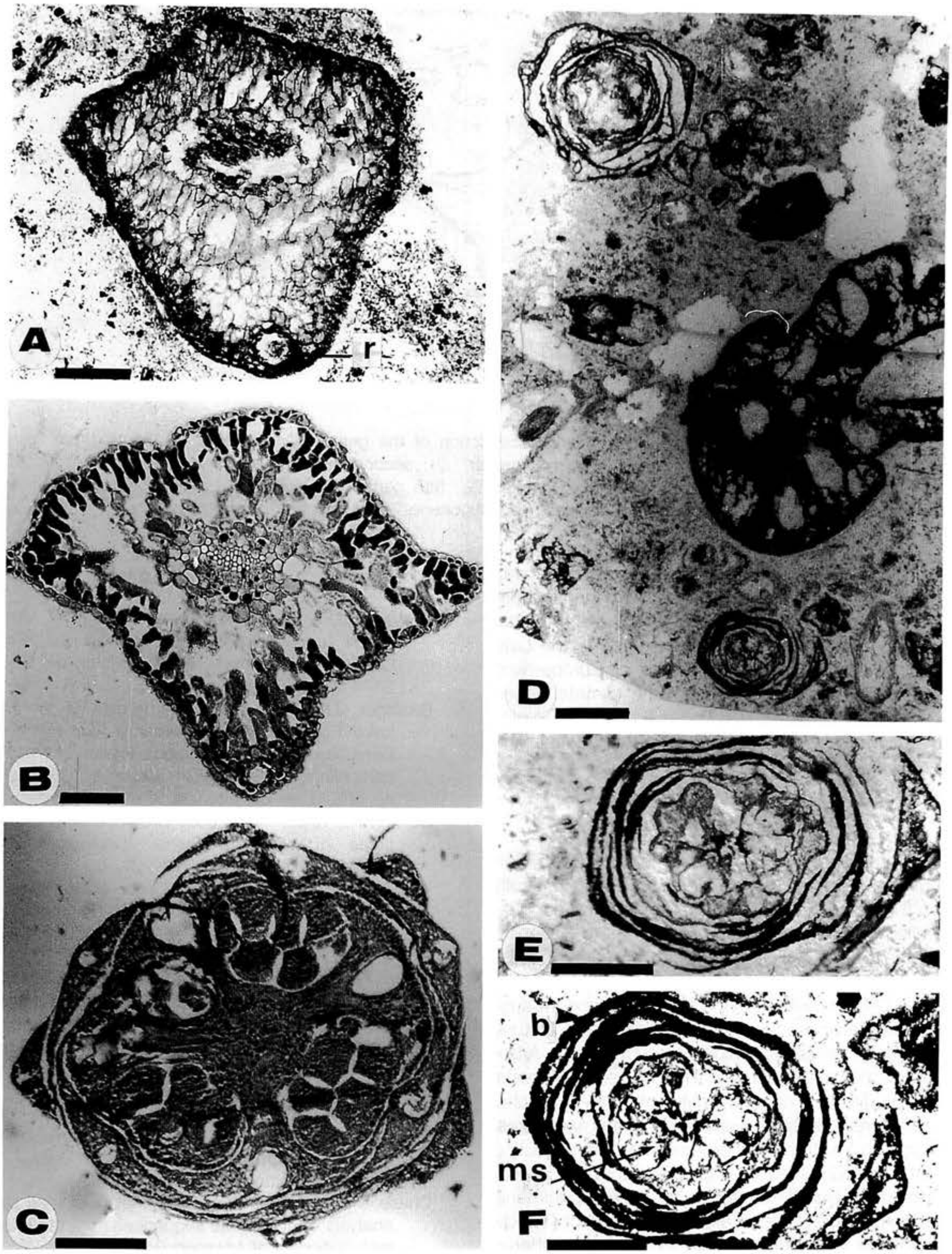

Figure 11. Transverse section of leaves and pollen cones of *Glyptostrobus rubenosawaensis* sp. nov. and leaf of *G. pensilis*. **A.** Leaf showing resin canal and vascular bundle (#94081402). Compare with Figure 11B. **B.** Leaf of living *Glyptostrobus pensilis* showing resin canal and vascular bundle (#950529). Compare with Figure 11A. **C.** Pollen cone showing the microsporophyll and microsporangia (#941125). **D.** Pollen cones. (#903000). **E-F.** Enlargement of specimens Figure D (#903000). b : bract, ms : microsporangia, r : resin canal. Scale bars : A, B=100 μm ; C, E=400 μm ; F=800 μm.

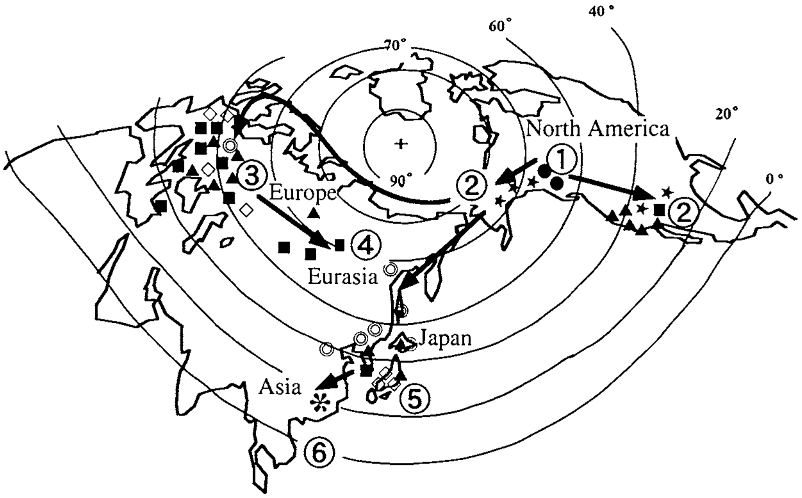

Figure 12. Generalized paleogeographic reconstruction of the genus *Glyptostrobus* in the northern hemisphere, showing the distribution orders. ①: first center, ②: second center, ③: third center through Thulian Route, ④: fourth center through Beringian Corridor, ⑤: fifth center, in Japan, ⑥: present distribution. ●: Upper Cretaceous, ★: Paleocene, ◎: Eocene, ■: Oligocene, ▲: Miocene, ◇: Pliocene, ＊: Present.

By the Miocene, the distribution of *Glyptostrobus* was becoming restricted as climate in the northern hemisphere cooled (LePage and Basinger, 1995). In North America, *Glyptostrobus* appears to have become extinct by the Late Miocene. *Glyptostrobus* became extinct in Europe and Japan at the end of the Pliocene when the climate turned more arid (Figure 12; Miki, 1957). The discovery of *Glyptostrobus rubenosawaensis* suggests diversification within the genus in the Tertiary.

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Moscovian (Carboniferous) orthoconic cephalopods from Guizhou and Guangxi, South China

SHUJI NIKO[1], **TAMIO NISHIDA**[2] **and YUKO KYUMA**[3]

[1]*Department of Environmental Studies, Faculty of Integrated Arts and Sciences, Hiroshima University, Higashihiroshima, 739 Japan*

[2]*Department of Earth Sciences, Faculty of Education, Saga University, Saga, 840 Japan*

[3]*Wakimisaki Elementary School, Nagasaki, 851-05 Japan*

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Abstract. Nine species of orthoconic cephalopods have been described from Moscovian (Carboniferous) limestone of the Guizhou and Guangxi region, South China. The fauna is composed of four orthocerids: *Bogoslovskya guizhouensis* sp. nov., *Mericoceras guangxiense* sp. nov., *Mericoceras* sp., and *Mimogeisonoceras*? sp. and five bactritids: *Bactrites faqingensis* sp. nov., *Bactrites* cf. *nagatoensis* Niko, Nishida and Kyuma, *Bactrites* sp., *Ctenobactrites*? sp., and *Sinobactrites wuae* gen. et sp. nov. The new parabactritid genus *Sinobactrites* is diagnosed by its relatively small angle of shell expansion, oval cross section, and abruptly recurved septal necks. It is noteworthy that the assemblage includes species closely related to some of the Akiyoshi fauna.

Key words: Bactritida, Moscovian, Orthocerida, South China

Introduction

During most of the Late Paleozoic Era, South China (Yangtze platform) was located in tropical to subtropical zones (Scotese and McKerrow, 1990; Zhang and Yan, 1993). A thick Carboniferous sequence, dominated by limestones and dolomites, is widely developed in the Yunnan, Guizhou, and Guangxi region, and has provided important information to biozonation schemes using fusulinids, brachiopods, corals (Wu *et al*., 1974), and ammonoids (Yang, 1978) in low-latitude waters. In contrast, knowledge of orthoconic cephalopods of South China has remained insufficient. As far as we know, only four (or five?) orthocerid species and a single species of actinocerid have been reported in Visean strata of the area (Lai, 1964; Liang and Zhu, 1988). It is the purpose of this report to describe Carboniferous orthoconic cephalopods from Faqing of the Riupansui area, Guizhou Province (see text-fig. 2 in Nishida *et al*., 1996) and Balai of the Riucai area, Guangxi Zhuangzu Autonomous Region (Figure 1). The cephalopods described herein occur in light-gray bioclastic limestone with the following associated fusulinids: *Fusulinella* cf. *pseudobocki* (Lee and Chen) in Faqing, and *Fusulinella bocki* Möeller and *F.* cf. *pseudobocki* in Balai. Nishida *et al*. (1996) stated that the cephalopod-bearing rocks belong to the Dala (Huanglong) Formation and can be correlated with strata of the lower Upper Carboniferous Moscovian Stage. The type specimens are deposited in the geological collections of Saga University (GS).

Systematic paleontology

Class Cephalopoda Cuvier, 1797
Subclass Nautiloidea Agassiz, 1847
Order Orthocerida Kuhn, 1940
Superfamily Orthocerataceae M'Coy, 1844
Family Orthoceratidae M'Coy, 1844
Subfamily Michelinoceratinae Flower, 1945
Genus **Bogoslovskya** Zhuravleva, 1978

Type species.—*Bogoslovskya perspicua* Zhuravleva, 1978.

Bogoslovskya guizhouensis sp. nov.

Figures 2—1-13

Diagnosis.—Species of *Bogoslovskya* with approximately 8-10 degrees angle of shell expansion, weak lateral compression in cross section, transverse lirae-ribs; adoral cameral ratio 2.8-3.9; minimum distance of central axis of siphuncle from shell surface per dorsoventral diameter approximately 0.22 in adoral shell.

Description.—Orthocones with rapid shell expansion for genus, angle ranges from 8.1 to 10.0 degrees; cross section of shell laterally compressed weakly, lateral/dorsoventral ratio 0.92 in holotype; largest specimen (GS.C145) of phragmocone reaches 15.1 mm in dorsoventral diameter; juvenile shells (up to 4-5 mm dorsoventral diameter) lack surface

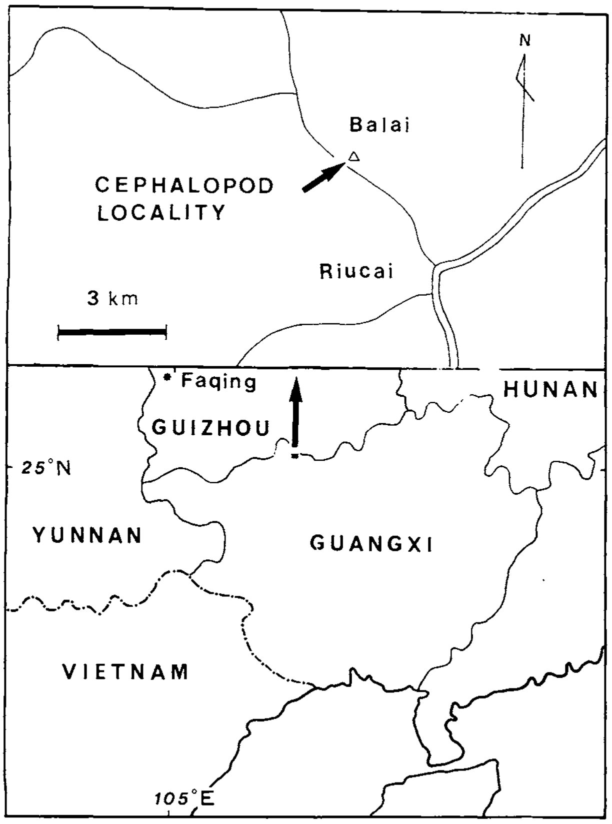

Figure 1. Index map of fossil locality on the southwestern foot of small conical mountain called Balai in Guangxi, South China.

ornamentation, then anti-siphuncular (dorsal ?) shell surface marks begin with straight, transverse but slightly oblique (toward aperture on anti-siphuncular side) lirae, which diminish toward siphuncular side and possess periodic, well prominent ridges; these ridges become distinct adorally, forming slightly sinuate ribs; however, ornamentation becomes faint again in most adoral shell (dorsoventral shell diameter approximately 15 mm); sutures straight, directly transverse to slightly oblique; septal curvature moderate; cameral length short for genus, 2.3-3.7 mm in adoral shell of holotype, cameral ratio (dorsoventral diameter/length) 2.8-3.9; siphuncle narrow, maximum diameter of septal neck/dorsoventral shell diameter approximately 0.06, submarginal position, minimum distance of central axis of siphuncle from shell surface per dorsoventral shell diameter ranges from 0.21 to 0.23 in holotype at dorsoventral shell diameter of approximately 10-12 mm; septal necks gently tapering orthochoanitic, forming funnel shape, neck length 1.0 mm at dorsoventral shell diameter of 12.3 mm of holotype; weak auxiliary deposits recognized in septal foramina; connecting rings not preserved; no cameral deposits detected.

Discussion.—*Bogoslovskya guizhouensis* sp. nov. is closely similar to *B. akiyoshiensis* Niko, Nishida and Kyuma (1995, figs. 1-1—14) described from the Moscovian of the Akiyoshi Limestone, Southwest Japan. It differs from the Akiyoshi species by the larger angle of shell expansion (approximately 8-10 degrees vs. approximately 7 degrees in *Bogoslovskya akiyoshiensis*), the well-developed surface ornamentation, and the less eccentric siphuncular position; *i.e.* ratio of the minimum distance of the central axis of the siphuncle from shell surface per the dorsoventral diameter is approximately 0.22 vs. 0.19 in *B. akiyoshiensis* in the corresponding shell diameter.

The surface ribs are also recognized in the Gzhelian to Asselian species *Bogoslovskya miharanoroensis* Niko and Ozawa (1997, figs. 2-1—9) from the Taishaku Limestone, Southwest Japan. However, *B. miharanoroensis* is evidently distinguished from the new species by the narrower shell (angle of shell expansion 4-5 degrees) and the well-developed ribs even in the adoral shell.

This new species is the most abundant cephalopod in the Dala (Huanglong) Formation. To date 44 specimens, which account for approximately 72 per cent of all examined orthoconic cephalopods, have been obtained. The swarmed occurrence is also known in *Bogoslovskya akiyoshiensis*.

Etymology.—The specific name is derived from the province name of the type locality, Guizhou.

Material and occurrence.—The holotype, GS.C128, is an incomplete phragmocone, 24.0 mm in length. The following 11 paratypes of fragmentary phragmocones are assigned: GS.C129, 144-147, 156-159, 167, 170. In addition, 32 reference specimens, GS.C127, 130-143, 148-155, 160-166, 168, 169, were also examined. All specimens were collected from Faqing.

Genus **Mericoceras** Zhuravleva, 1978

Type species.—*Mericoceras karagandense* Zhuravleva, 1978.

Mericoceras guangxiense sp. nov.

Figures 3-4—6

Diagnosis.—Species of *Mericoceras* with angle of shell expansion approximately 7 degrees; cameral ratio 2.2-2.4; siphuncle with weak constrictions at septal foramina.

Description.—Single orthoconic phragmocone with moderate to relatively rapid shell expansion, angle 7.3 degrees (reconstructed from slightly deformed shell) in adoral portion of shell; cross section of shell circular, reaches approximately 19 mm (reconstructed) diameter; surface ornamentation of reticulated pattern composed of transverse and longitudinal lirae, transverse lirae wider and more prominent than longitudinal lirae, form salients in adoral shell; sutures nearly transverse; septal curvature moderate to relatively deep; cameral length 6.1-7.4 mm in adoral shell, giving cameral ratio 2.2-2.4; siphuncle central in position, siphuncular diameter/corresponding shell diameter 0.13-0.15, free of endosiphuncular deposits; septal necks short, weakly recurved suborthochoanitic to orthochoanitic, 0.7-1.0 mm in length at shell diameter of approximately 18 mm (reconstructed), connecting rings thin, cylindrical with weak constrictions at septal foramina; cameral deposits not observed.

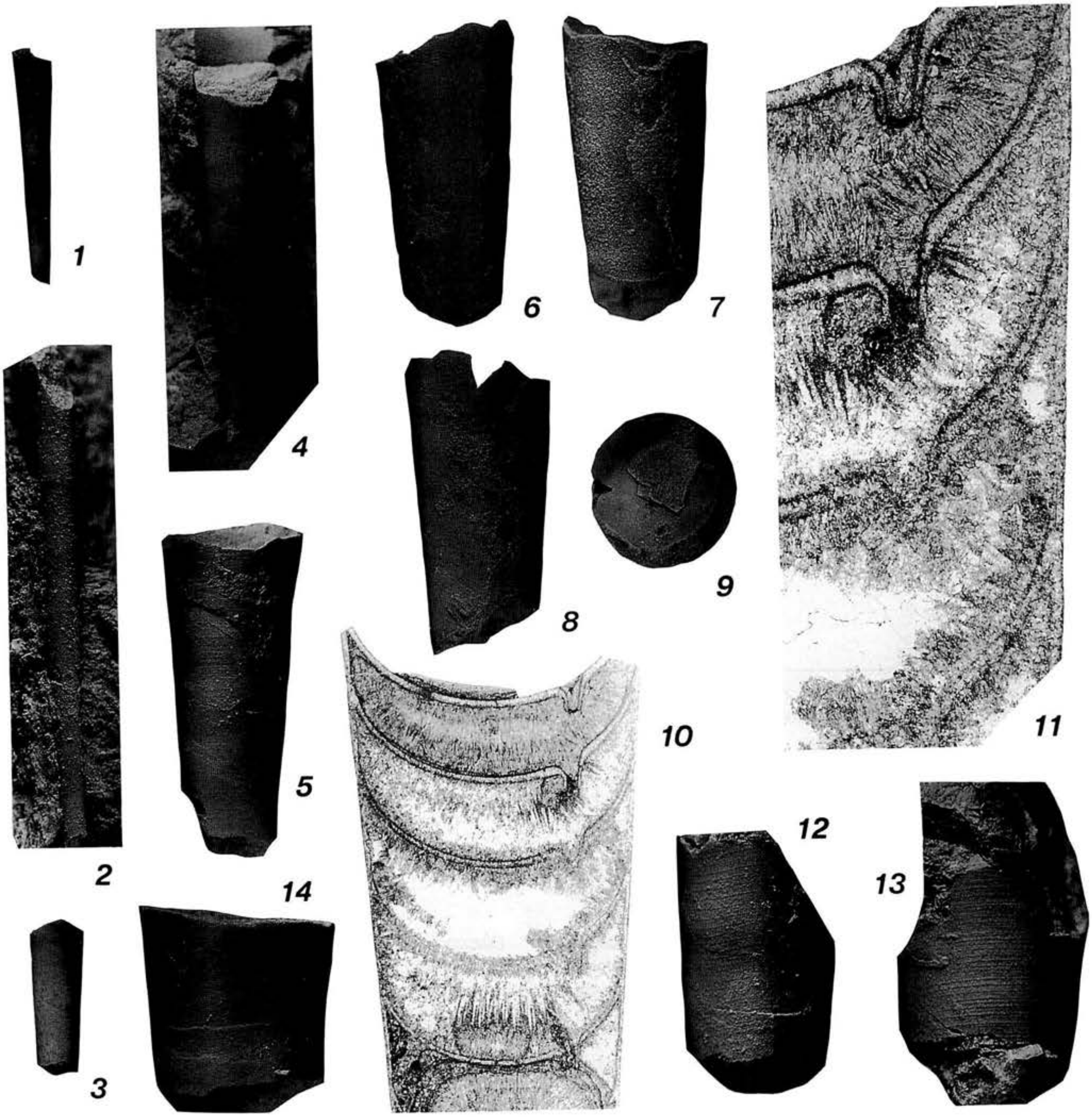

Figure 2. *Bogoslovskya guizhouensis* sp. nov. **1.** Paratype, GS.C146, side view of early juvenile shell. **2.** Paratype, GS.C147, side view of early juvenile shell. **3.** Paratype, GS.C167, lateral view of juvenile shell, siphuncular side on right. **4.** Paratype, GS.C144, lateral view of juvenile shell, siphuncular side on right. **5.** Paratype, GS. C157, anti-siphuncular view. **6-11.** Holotype, GS.C128, 6 : anti-siphuncular view, 7 : siphuncular view, 8 : lateral view, siphuncular side on right, 9 : septal view of adoral end, siphuncular side down, 10 : dorsoventral thin section, 11 : details of adoral siphuncle. **12.** Paratype, GS.C170, lateral view, siphuncular side on left. **13.** Paratype, GS. C156, anti-siphuncular view. **14.** Paratype, GS.C145, lateral view, siphuncular side on left. 1, 2, 10 = ×4, 3-9, 12-14 = ×2, 11 = ×10.

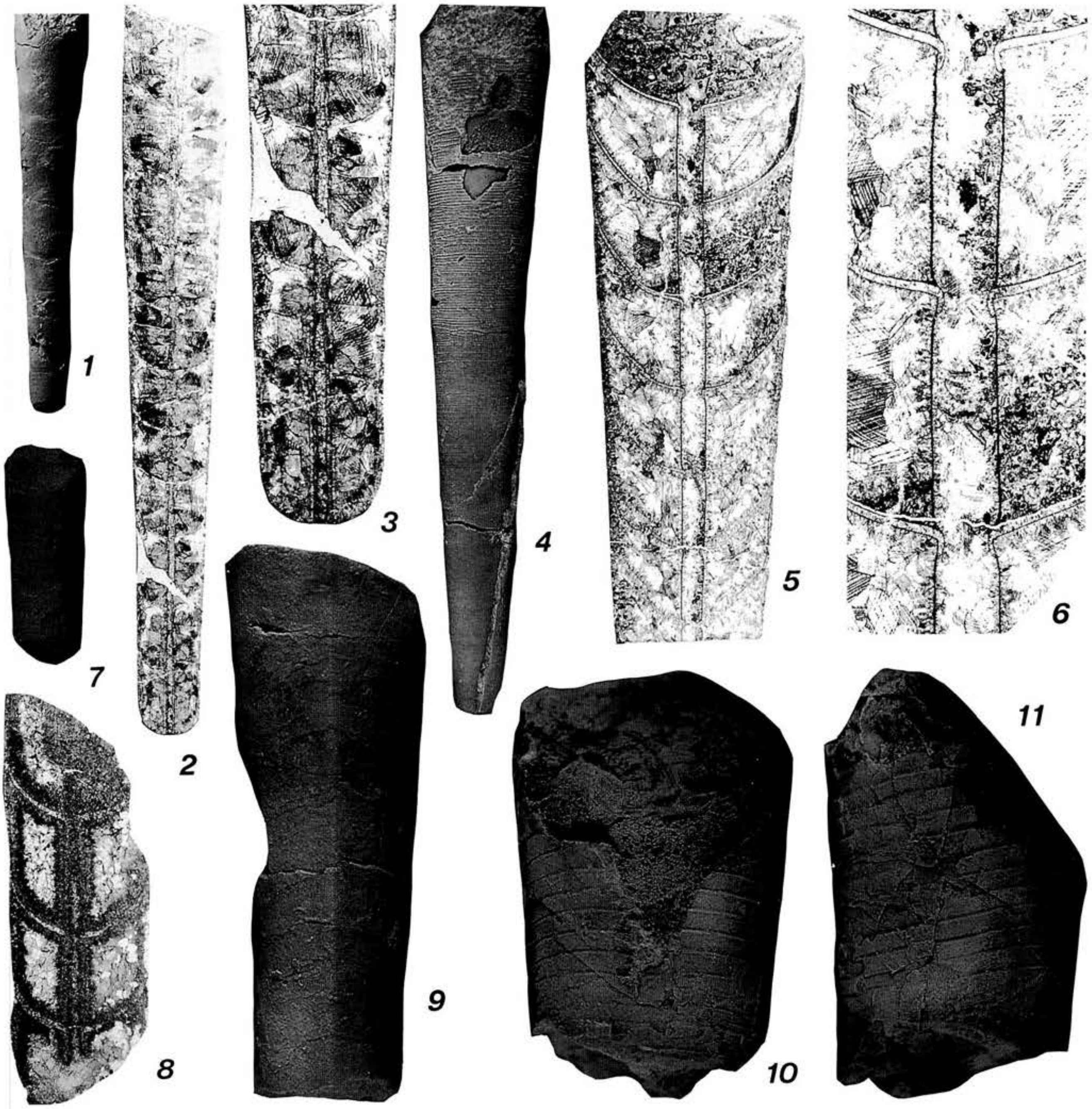

Figure 3. **1-3.** *Mericoceras guangxiense* ?, GS.C124, 1 : side view, 2 : longitudinal thin section, 3 : details of apical shell. **4-6.** *Mericoceras guangxiense* sp. nov., holotype, GS.C125, 4 : side view, 5 : longitudinal thin section of adoral shell, 6 : details of adoral siphuncle. **7, 8.** *Mericoceras* sp., GS.C126, 7 : anti-siphuncular view, 8 : dorsoventral thin section. **9.** *Bactrites* cf. *nagatoensis* Niko, Nishida and Kyuma, GS.C178, dorsal view. **10, 11.** *Ctenobactrites* ? sp., GS.C183, 10 : dorsal view, 11 : lateral view, venter on left. 1 = ×3, 2, 6 = ×5, 3 = ×10, 4, 10, 11 = ×1, 5, 7, 9 = ×2, 8 = ×4.

Discussion.—The possession of reticulate surface ornamentation consisting of lirae is relatively rare for orthoconic cephalopods, but recognized through several families, such as Orthoceratidae, Geisonoceratidae, and Pseudorthoceratidae. The siphuncular structure mentioned above suggests that the cephalopod is a species of the orthoceratid genus *Mericoceras* Zhuravleva (1978). The type species, *Mericoceras karagandense* Zhuravleva (1978, pl. 4, figs. 1-4), from the Famennian (Upper Devonian) of central Kazakhstan, was previously the only species definitely assigned to the genus. Slightly larger angle of adoral shell expansion (approximately 7 degrees vs. 4-6 degrees in *Mericoceras karagandense*) and the possession of weak constriction at septal foramina of the Carboniferous species are considered as difference of specific rank.

Etymology.—The specific name is derived from the Autonomous Region name of the type locality, Guangxi.

Material and occurrence.—The holotype, GS.C125, is an incomplete phragmocone, 108.5 mm in length. The specimen was collected from Balai.

Mericoceras guangxiense Niko, Nishida and Kyuma?

Figures 3-1—3

Discussion.—In addition to the holotype described above a phragmocone questionably assigned to *Mericoceras guangxiense* sp. nov. was also examined. The specimen is an orthoconic shell with circular cross section, reticulate surface ornamentation, *Michelinoceras*-like siphuncular structure and mural deposits. It may represent the juvenile portion of *Mericoceras guangxiense*. However, lack of intermediates between the holotype and this specimen prevents a positive assignment.

Internally and externally siphuncle of this specimen is covered with thin carbonate. Judging from position and uniform thickness of the deposits, we consider that they are of diagenetic origin.

Material and occurrence.—GS.C124 from Balai.

Mericoceras sp.

Figures 3-7, 8

Description.—Single incomplete phragmocone of orthoconic shell with circular cross section, weak reticulate surface ornamentation; angle of shell expansion approximately 4 degrees; siphuncle subcentral with orthochoanitic necks and cylindrical connecting rings; no cameral and/or endosiphuncular deposits detected.

Discussion.—The species differs from *Mericoceras guangxiense* sp. nov. in its subcentral siphuncular position, but this is insufficient for a specific identification.

Niko *et al.* (1987) illustrated an ill-preserved Moscovian orthocerid as *Striacoceras*? sp. from the Akiyoshi Limestone. The combination of reticulate surface ornamentation and the orthochoanitic septal necks suggests that the species probably falls within the genus *Mericoceras*. With the exception of the siphuncular position, both species share diagnostic morphology.

Material and occurrence.—GS.C126 from Faqing.

Genus ***Mimogeisonoceras*** Shimanskiy, 1968

Type species.—*Mimogeisonoceras ljubovae* Shimanskiy, 1968.

Mimogeisonoceras? sp.

Figure 4-11

Description.—Single incomplete phragmocone of orthoconic shell with circular cross section, gradual shell expansion; surface ornamentation of transverse, slightly sinuate grooves with very deep salient; siphuncular position central.

Discussion.—The species shares the characteristic ornamentation with *Mimogeisonoceras ljubovae* Shimanskiy (1968, pl. 1, fig. 3) from the Namurian of the Southern Urals, but the shell is more slender than that of *M. ljubovae*. It is represented by a single fragment of the probably juvenile portion. Thus, the generic assignment is tentative.

Material and occurrence.—GS.C171 from Faqing.

Subclass Bactritoidea Shimanskiy, 1951
Order Bactritida Shimanskiy, 1951
Family Bactritidae Hyatt, 1884
Genus ***Bactrites*** Sandberger, 1843

Type species.—*Bactrites subconicus* Sandberger, 1843.

Bactrites faqingensis sp. nov.

Figures 4-1—7

Diagnosis.—Species of *Bactrites* with approximately 7-8 degrees angle of shell expansion, circular cross section; surface ornamentation transverse dense lirae; cameral ratio 1.8-2.5.

Description.—Orthocones with relatively rapid shell expansion for genus, angle 7.1-8.4 degrees; cross section of shell circular; largest specimen (holotype) attains 16.6 mm in diameter at portion of last septum; preserved body chamber 29.9 mm in length; shell surface marked by transverse dense lirae that are slightly oblique towards aperture on dorsal side; excepting ventral lobe sutures directly transverse, straight; septa deeply concave with wide mural portion; cameral length moderate, 6.2-7.4 mm, its ratio 1.8-2.5 in holotype at shell diameter approximately 13-16 mm; siphuncular position ventral margin; septal necks orthochoanitic in dorsum, 1.0 mm in length at last septum of holotype; ventral septa attached to shell wall in dorsoventral section with weak projections at septal foramina; minimum diameter of septal foramen/shell diameter in holotype approximately 0.05; connecting rings not preserved; lacks cameral and/or endosiphuncular deposits.

Discussion.—This species is easily distinguished from most known Carboniferous species of *Bactrites* by its surface ornamentation of transverse dense lirae. Only *Bactrites costatus* Mapes (1979, pl. 31, figs. 7-9, 13), from the Virgilian of Texas, possesses similar surface ornamentation. However,

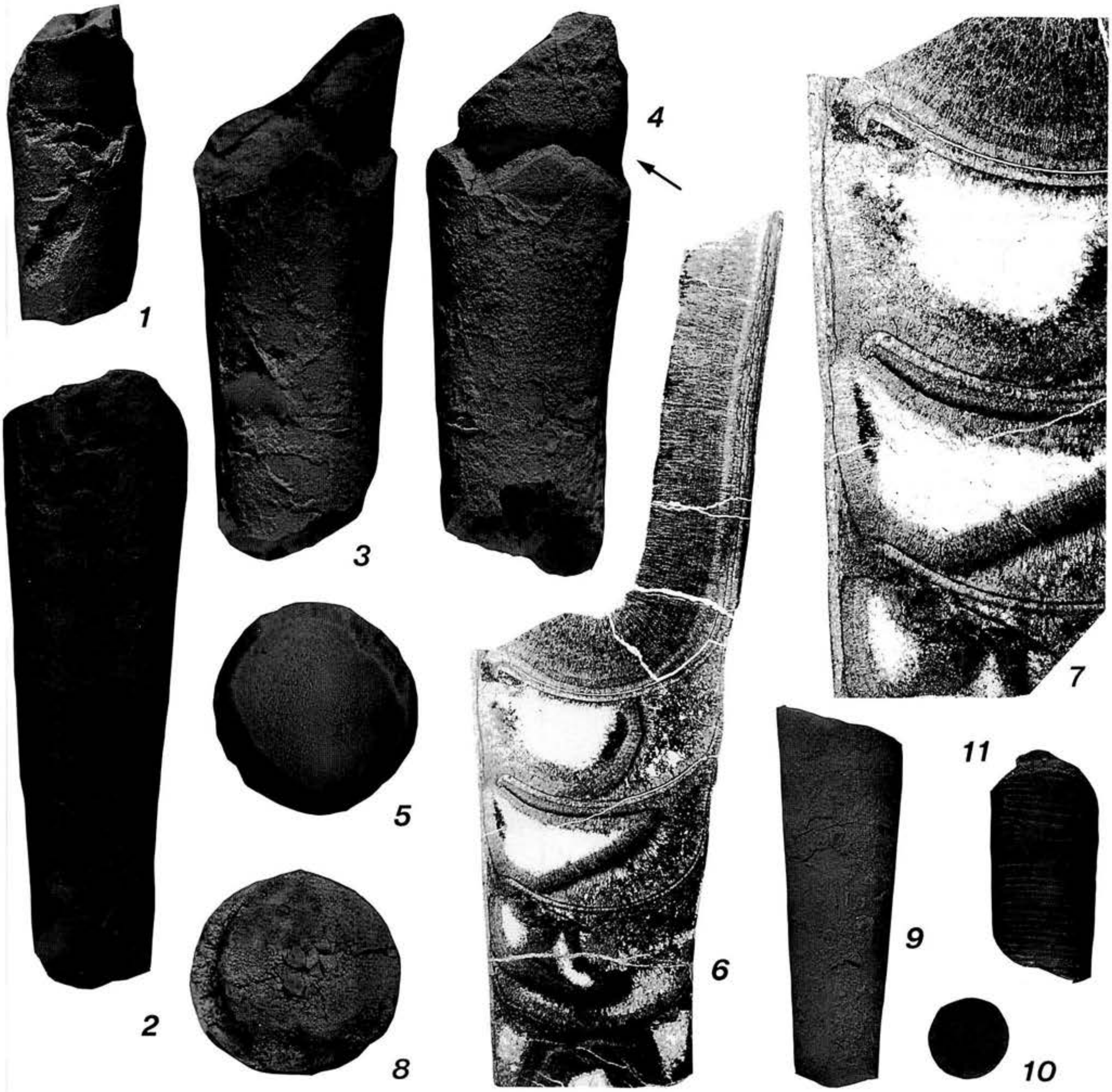

Figure 4. **1-7.** *Bactrites faqingensis* sp. nov., 1: paratype, GS.C174, lateral view, venter on left, 2: paratype, GS.C173, ventral view, 3-7: holotype, GS.C172, 3, lateral view, venter on left; 4, ventral view, arrow indicates position of the last septum; 5, septal view of the last septum, venter down; 6, dorsoventral thin section; 7, details of adoral siphuncle. **8.** *Bactrites* cf. *nagatoensis* Niko, Nishida and Kyuma, GS.C178, adoral end, venter down. **9, 10.** *Bactrites* sp., GS.C181, 9: lateral view, venter on right, 10: septal view of apical end, venter down. **11.** *Mimogeisonoceras* ? sp., GS.C171, side view. 1-5, 8-10 = ×2, 6 = ×2.5, 7 = ×5, 11 = ×4.

it has longer camerae (cameral ratio 1.2-1.7 vs. 1.8-2.5) and a somewhat narrower shell (angle of expansion 5-7 degrees vs. approximately 7-8 degrees) than does *Bactrites faqingensis*.

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

Material and occurrence.—The holotype, GS.C172, is an incomplete phragmocone with apical body chamber, 63.7 mm in length. The following two paratypes of incomplete phragmocones are assigned: GS.C173, 174. In addition, three fragmentary specimens, GS.C175-177, were also examined. All specimens were collected from Faqing.

Bactrites cf. ***nagatoensis*** Niko, Nishida and Kyuma, 1991

Figures 3-9; 4-8

cf. *Bactrites nagatoensis* Niko, Nishida and Kyuma, 1991, p. 715, figs. 2-1—10, 3-1—5.

Description.—Orthocones with moderate shell expansion, angle of expansion approximately 6 degrees; cross section of shell circular; largest specimen (GS.C179) attains approximately 22 mm (reconstructed) diameter; a single dorsal carina strongly developed, shell surface lacks other ornamentation; septal and siphuncular morphology not observed.

Discussion.—This species bears a close resemblance in its shell shape and ornamentation to *Bactrites nagatoensis* from the Moscovian (Kyuma and Nishida, 1992) of the Akiyoshi Limestone, but its internal structure needs to be examined.

Material and occurrence.—GS.C178, 179 from Faqing.

Bactrites sp.

Figures 4-9, 10

Description.—Orthocones with relatively rapid shell expansion, angle approximately 8 degrees; largest specimen (GS. C181) attains 9.8 mm in diameter; cross section of shell circular; shell surface lacks ornamentation; sutures transverse, but form weak sinuation and ventral lobe; siphuncular position ventral margin.

Discussion.—The specimens may represent immature shells. Inadequate knowledge of morphology prevents comparison at the specific level.

Material and occurrence.—GS.C180-182 from Faqing.

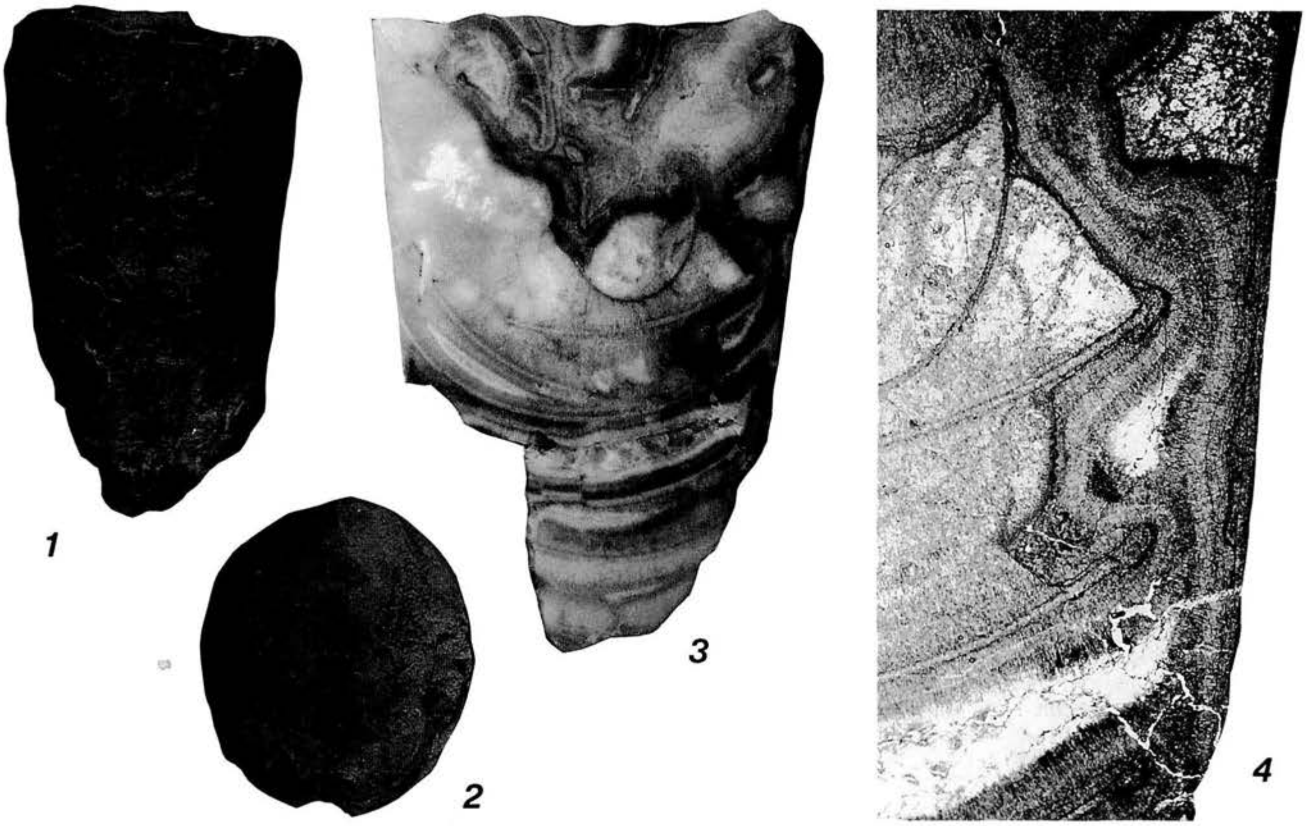

Figure 5. *Sinobactrites wuae* gen. et sp. nov., holotype, GS.C184. **1.** Lateral view, venter on right. **2.** Adoral end, venter down. **3.** Dorsoventral polished section, venter on right. **4.** Dorsoventral thin section, showing details of siphuncle. 1, 2=×1, 3=×1.5, 4=×4.

Genus **Ctenobactrites** Shimanskiy, 1951

Type species.—*Ctenobactrites costatus* Shimanskiy, 1951.

Ctenobactrites ? sp.

Figures 3-10, 11

Description.—Single large-sized orthocone with circular cross section, having maximum diameter of approximately 43 mm (reconstructed); shell surface ornamented by flat-topped wide ribs that form broad, but shallow ventral sinus and dorsal saddle, each rib ranges from 2.5 to 3.0 mm in width; grooves separating ribs narrow; septal and siphuncular morphology not observed.

Discussion.—The lack of internal structure of the present specimen hinders confident taxonomic assignment. However, the characteristic rib form suggests a relationship to *Ctenobactrites*. The surface ornamentation of this species somewhat resembles *Ctenobactrites* spp. from the Virgilian of Texas (Mapes, 1979, pl. 23, figs. 1, 2) and the Moscovian of the Akiyoshi Limestone (Niko *et al*., 1991, figs. 3-10, 11).

Material and occurrence.—GS.C183 from Faqing.

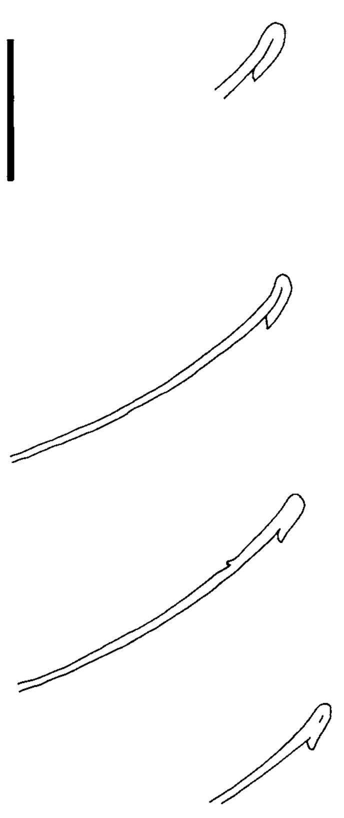

Figure 6. *Sinobactrites wuae* gen. et sp. nov., holotype, GS.C184. Camera lucida drawing of siphuncle, based on dorsoventral thin section. Scale bar=5 mm.

Family Parabactritidae Shimanskiy, 1951
Genus ***Sinobactrites*** gen. nov.

Type species.—*Sinobactrites wuae* sp. nov., by monotypy.

Diagnosis.—Breviconic orthocone with relatively small angle of expansion for family, approximately 15 degrees; cross section of shell laterally compressed; shell surface smooth; siphuncle marginal, relatively large; septal necks abruptly recurved, brims in contact with posterior surface of septa.

Etymology.—The generic name is derived from *Sino* (combining form of the Latin *Sinae*, meaning Chinese), and *Bactrites*.

Sinobactrites wuae sp. nov.

Figures 5-1—4, 6

Diagnosis.—As for the genus.

Description.—Single large-sized breviconic orthocone, angle of shell expansion relatively small for family, 14.8 degrees in dorsoventral plane; cross section of shell laterally compressed, oval; adoral end attains 41.6 mm in dorsoventral diameter and 35.1 mm in lateral diameter, giving form ratio 0.84; shell surface smooth, lacks conspicuous ornamentation; sutures rectilinear except for ventral lobe; septal curvature moderate to relatively deep for the family; camerae short, cameral ratio in dorsoventral section 0.2; siphuncular position ventral margin; siphuncle relatively large, minimum diameter of septal foramen/shell diameter in dorsoventral section approximately 0.07; dorsal septal necks abruptly recurved and septal brims in contact with posterior surface of septa, brim length 1.6-2.0 mm in approximately 31 (reconstructed)-38 mm in dorsoventral shell diameter; septa on ventral side of siphuncle in contact with shell wall in dorsoventral plane with weak projections at septal foramina; connecting rings not preserved; lacks any evidence of cameral and/or endosiphuncular deposits.

Discussion.—The abruptly recurved septal necks of *Sinobactrites wuae* gen. et sp. nov. are also recognized in *Belemnitomimus palaeozoicus* Shimanskiy (1954, pl. 12, figs. 1, 2; type species of the genus) from the Lower Permian of the Southern Urals. However, *Belemnitomimus* can be clearly distinguished from the new genus by its much greater shell expansion (approximately 30 degrees vs. approximately 15 degrees in *Sinobactrites wuae*), the circular cross section of the shell, and the well prominent ventral septa.

The Permian genus *Microbactrites* Shimanskiy (1954, type species, *Parabactrites scorobogatovae* Shimanskiy, 1948, fig. 2) from the Southern Urals has somewhat similar shell shape to *Sinobactrites*. Although the siphuncular structure of *Microbactrites* is not illustrated by Shimanskiy, the genus is clearly distinguished from *Sinobactrites* in having oblique folds in the shell surface.

The geographic distribution of parabactritids was previously restricted to the Southern Urals (Shimanskiy, 1948, 1954, 1968), Pamirs (Shimanskiy, 1993), and the Taishaku Limestone (Niko *et al*., 1993). Thus, the Chinese species extends the range of the family. In addition, pre-Permian undoubted records of parabactritids are exceedingly rare. Previously only a single Namurian species from the Southern Urals, *Aktastioceras* sp., has been recorded (Shimanskiy, 1968).

Etymology.—The specific name honors Dr. Wu Wangshi, in recognition of her contributions to the Carboniferous stratigraphy of South China.

Material and occurrence.—The holotype, GS.C184, is an incomplete phragmocone 66.7 mm in length. The specimen was collected from Faqing.

Acknowledgments

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Akiyoshi 秋吉, Balai 巴来, Dala 达拉, Faqing 発箐, Guangxi (Guangxi Zhuangzu Autonomous Region) 广西 (广西壮族自治区), Guizhou 贵州, Huanglong 黄龙，Riucai 六寨, Riupansui 六盘水, Taishaku 帝釈, Yangtze 楊子, Yunnan 云南

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Reexamination of the Sagara Fauna — Middle Miocene molluscan assemblage from the Sugegaya Formation, Sagara Group, Shizuoka Prefecture, Central Japan —

KEISUKE INOUE[1], **TOMOWO OZAWA**[1], **TAKAMI NOBUHARA**[1] **and SUSUMU TOMIDA**[2]

[1]*Department of Earth and Planetary Sciences, Nagoya University, Furo-cho, Chikusa-ku, Nagoya, 464-01 Japan*

[2]*Chukyo Gakuin University, Nakatsugawa, Gifu, 509-91 Japan*

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Abstract. The Sagara Fauna has been regarded as the Middle Miocene to Early Pliocene warm-water molluscan faunal unit in Southwest Japan. Descriptive works, however, have not been enough to discuss the faunal succession in the type section of the Sagara Fauna. This paper reports a molluscan assemblage from shell-concentrated beds in the lower part of the Sagara Group, Shizuoka Prefecture, giving systematic descriptions of the representative species. This assemblage is composed of molluscs transported from shelf depths, such as *Phos*, *Olivella*, *Megacardita*, and *Glycymeris*. The shell beds are placed in Zone N14 of Blow's planktonic foraminiferal zonal scheme in which the late Middle Miocene global warming condition has been recognized as the Climatic Optimum 2. The warming evidence in Japan is the appearance of tropical to subtropical molluscs from the Kukinaga Group in Tanegashima Island. The molluscan assemblage reported here represents a warm temperate molluscan fauna in the paleo-Kuroshio realm. Moreover, it is noteworthy that the last appearance of the Early to Middle Miocene relict elements and the first appearance of some living species are recognized in this assemblage. This supports a division of the so-called Sagara Fauna into the middle to late Middle Miocene Kukinaga Fauna and the Late Miocene to Early Pliocene Zushi Fauna.

We define the Sagara Faunule for the fossil assemblage from the lower part of the Sagara Group, which lived in the warm-temperate region in Southwest Japan during the Climatic Optimum 2.

Key words: Japan, Kukinaga Fauna, Middle Miocene, Molluscan fossils, Sagara Faunule, Sugegaya Formation

Introduction

The Middle Miocene to Early Pliocene Sagara Group has been regarded as one of the type sections of the Neogene warm-water molluscan faunal succession in Japan. Tsuchi (1961) studied the temporal change of the younger Neogene fauna in the Sagara-Kakegawa area, Shizuoka Prefecture, central Japan, and first proposed the Sagara Fauna for the fossil molluscs from the Sagara Group. In his stratigraphic range chart of molluscan fossils, the Sagara Fauna is characterized by the appearance of *Amussiopecten iitomiensis* and *Chlamys miurensis*. Subsequently, the term Sagara Fauna has been used to describe a warm-water fauna which flourished along the Pacific coast of Southwest Japan during the Middle Miocene to Early Pliocene (e.g., Chinzei, 1986). However, the fossil records from the Sagara Group were based on allochthonous poorly preserved specimens from some shell-beds. Moreover, no descriptive works has been done on the fossils, except for Yokoyama (1926b). He reported 16 species from the "Sagara Bed" but provided no data on the fossil localities or the modes of occurrence. In addition, Yokoyama (1926b) reported no characteristic species such as *Amussiopecten iitomiensis*. Therefore, paleontological and paleoecological basic data are not enough to discuss the faunal succession and paleobiogeography. The Sagara Fauna is used as a general term denoting a warm-water "linkage" fauna between the early Middle Miocene Kadonosawa Fauna and the Plio-Pleistocene Kakegawa Fauna.

Recently Ozawa *et al.* (1995) revised the outline of the Japanese Neogene warm-water molluscan faunas in relation to global climatic events. They divided the Sagara Fauna into the following two faunas: the Kukinaga Fauna in the middle to late Middle Miocene and the Zushi Fauna in the Late Miocene to Early Pliocene. The time intervals of the faunas correspond to the Climatic Optima 2 and 3 of Barron and Baldauf (1990), respectively. Concerning the later phase of the Sagara Fauna, Ozawa and Tomida (1992) reported the molluscan assemblages and their species composition, and clearly defined the Zushi Fauna. On the other hand, the details of the early phase of the Sagara Fauna remain unclear in the type section.

We obtained abundant molluscan fossils from the Sugegaya Formation, the lowermost part of the Sagara Group. This paper reports the molluscan assemblage, with systematic descriptions of the representative species. Paleobiogeographic significance is also discussed on the basis of the taxonomic data obtained in this study.

Geologic setting

We collected molluscan fossils from lenticular beds of granule-bearing sandstone of the Sugegaya Formation exposed in a cliff (lat. 34°43′23″N ; long. 138°11′22″E) near Tsuchizawa (Figure 1).

The Miocene Sugegaya Formation is the lowermost part of the Sagara Group (Figure 2). It consists of alternating beds of granule-sized conglomerate, sandstone and mudstone (Ujiié, 1962 ; Oda, 1971 ; Nakamori *et al.*, 1991 ; Tsukawaki, 1994). It is distributed on both flanks of the Megami anticline from Shirai north of Tsuchizawa to Iwachi. The total thickness is about 500 m (Oda, 1971). The Sugegaya Formation comes into fault contact with the lower Middle Miocene Megami Formation, and grades upwards into the Sagara Formation. Sedimentary facies analysis by Tsukawaki (1994) suggested that the Sugegaya Formation was deposited in submarine channels. The Sagara Group is estimated to have been deposited in the bathyal zone on the basis of benthic foraminifers (Ishigaki, 1991).

In the outcrop alternating beds of sandstone and siltstone show slumping structures and intercalate many lenticular beds of medium-grained sandstone (Figure 3). We recognized two fossiliferous beds which are separated by an about 4 m stratigraphic interval from each other. We found no differences in species composition between the two shell beds. Therefore, for convenience, we treated the specimens from the two shell beds as one sample.

This locality is the same as Loc. TZ 02 in the studies of planktonic foraminiferal biostratigraphy by Ibaraki (1986). She revealed that the horizon is assigned to Zone N14 of Blow's planktonic foraminiferal zonation in the late Middle Miocene (Figure 2). Oda (1971) listed seven molluscan species from this locality: *Glycymeris* sp., *Limopsis* sp., *Venericardia* sp., *Tectonatica janthostomoides, Mitra* sp., *Siphonalia* sp., and *Fulgoraria* sp.

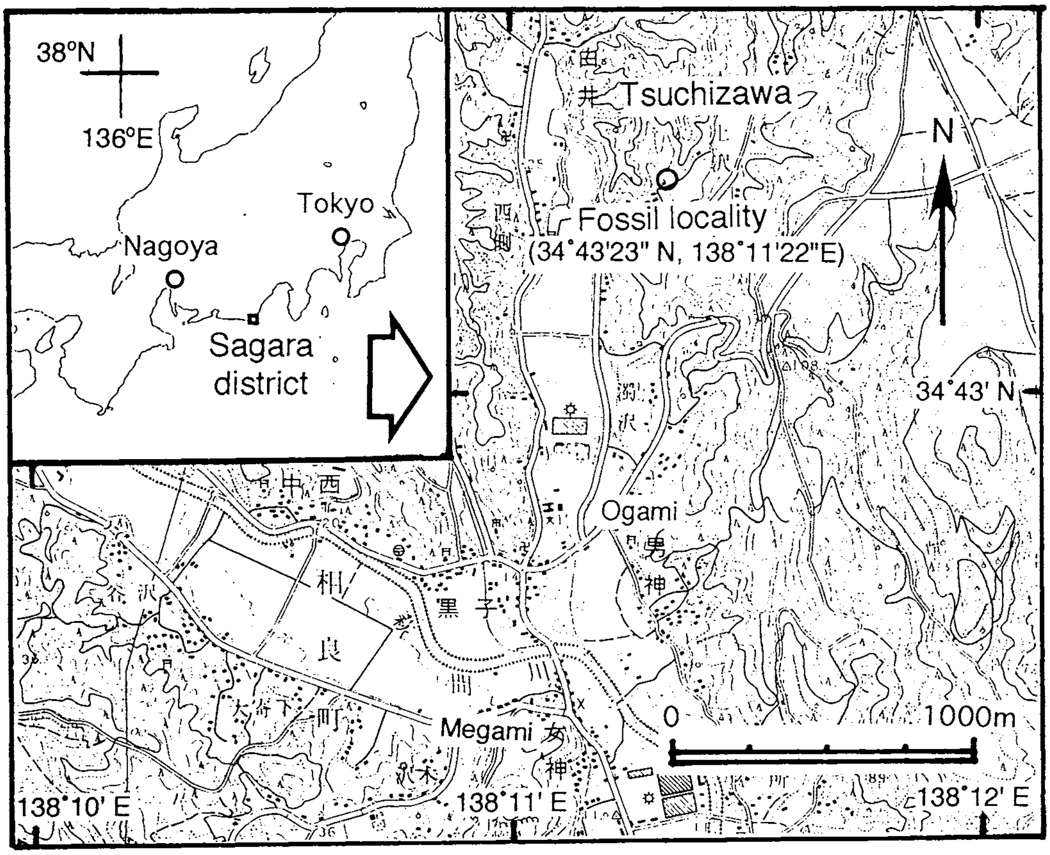


Figure 1. Index map and fossil locality plotted on the 1 : 25,000-scale topographic map, "Sagara" (Geographical Survey Institute of Japan).

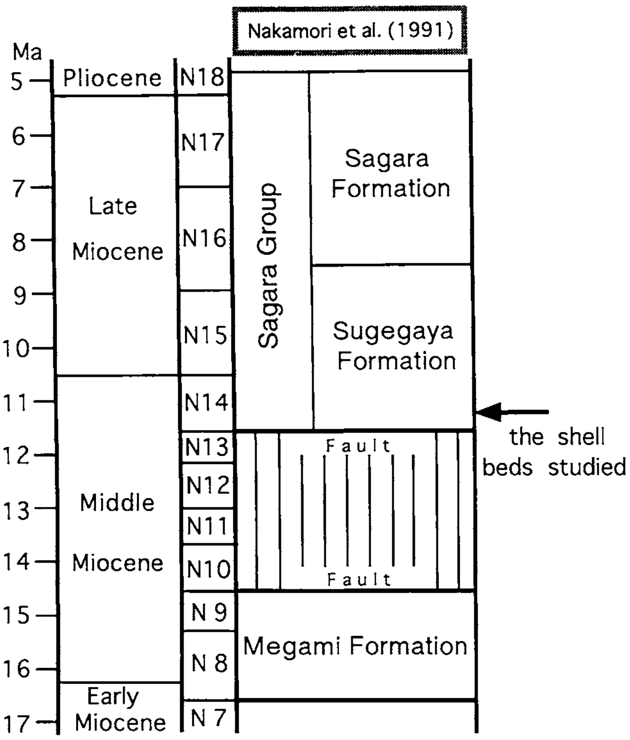


Figure 2. Stratigraphy of the Miocene formations in the Sagara district, showing the stratigraphic level of the fossil shell beds.

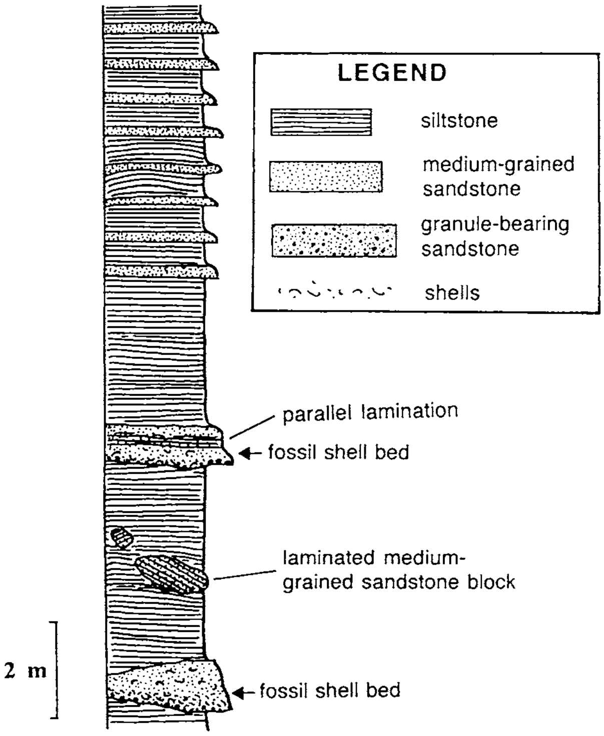


Figure 3. Columnar section of the Sugegaya Formation at the fossil locality in Tsuchizawa, Sagara Town.

Molluscan assemblage

The molluscan fossils were obtained from two granule-bearing sandstone beds about 50 cm thick, which grade laterally into fine-grained sandstone (Figure 3). No molluscan fossils were obtained from the siltstone. The shells are supported by matrix sediments. Most of the shells were disarticulated or fragmented and their shell surfaces were abraded.

We recognize 26 species of molluscs, as shown in Table 1. *Olivella fulgurata* is the dominant species. *Phos miyagiensis, Glycymeris idensis, Crenulilimopsis* sp. cf. *C. oblonga*, and *Megacardita ferruginosa* are also abundant. This assemblage contains seven living species. They are represented by three tidal to sublittoral dwellers (*Olivella fulgurata, Nipponocrassatella nana* and *Callista chinensis*), two sublittoral inhabitants (*Megacardita ferruginosa* and *Antalis weinkauffi*), and two eurybathyal ones (*Acila divaricata submirabilis* and *Anisocorbula venusta*). In addition, most of the extinct species were dwellers of tidal to sublittoral depths (e.g. *Glycymeris* and *Phos*). The mode of occurrence and species composition suggest that this assemblage was formed by the transportation of shells from littoral to sublittoral depths.

Table 1. List of fossil molluscs from the shell beds of the Sugegaya Formation. A ; abundant (more than 25 specimens), C ; common (11-25 specimens), F ; frequent (5-10 specimens), R ; rare (less than 5 specimens).

1.	*Acila divaricata submirabilis* (Makiyama)	C
2.	*Bathyarca* sp.	R
3.	*Glycymeris idensis* Kanno	A
4.	*Glycymeris izumoensis* Matsukuma and Okamoto	C
5.	*Crenulilimopsis* sp. cf. *C. oblonga* (A. Adams)	A
6.	*Nipponolimopsis* sp. cf. *N. azumana* (Yokoyama)	F
7.	*Nipponocrassatella nana* (A. Adams and Reeve)	F
8.	*Megacardita ferruginosa* (A. Adams and Reeve)	A
9.	*Laevicardium* sp.	R
10.	*Callista chinensis* (Holten)	F
11.	*Anisocorbula venusta* (Gould)	C
12.	*Cuspidaria* sp. cf. *C. nobilis* A. Adams	R
13.	*Otukaia* sp.	R
14.	*Solariella* sp.	R
15.	*Solariella (Machaeroplax)* sp.	F
16.	*Capulus*? sp.	R
17.	*Neverita coticazae* (Makiyama)	R
18.	*Primovula* sp. cf. *P. rhodia* (A. Adams)	R
19.	*Phalium yokoyamai* Nomura and Hatai	F
20.	*Shiponalia* sp.	F
21.	*Phos miyagiensis* Masuda and Takegawa	A
22.	*Olivella fulgurata* (A. Adams and Reeve)	A
23.	*Conus (Endemoconus)* sp. cf. *C. (E.) sieboldi* Reeve	R
24.	*Conus (Chelyconus) tokunagai* Otuka	R
25.	*Comitas* sp.	R
26.	*Antalis weinkauffi* (Dunker)	F

Marine climate and paleobiogeography: Reexamination of the Sagara Fauna

The species composition reflects the marine climate at shelf depths on the Pacific side of central Japan in N14. The occurrence of two *Conus* species suggests the influence of a warm current system from the south. Except for *Conus*, however, no tropical-subtropical elements are found in this assemblage. Most of the species have been commonly reported from the Neogene in Honshu or the present-day warm-temperate region along the Pacific coast (Boso Peninsula to Kyushu). Therefore, the marine climate may have been warm-temperate.

On the other hand, many tropical-subtropical elements such as *Telescopium telescopium* and *Tibia fusus* were reported from the Kukinaga Group, Tanegashima Island, which correlates with the Sugegaya Formation in age (Inoue, 1992, 1994). He proposed the Kukinaga Fauna for the tropical-subtropical assemblages and suggested that this fauna was established during the northward shift of the tropical-subtropical front in the Climatic Optimum 2 of Barron and Baldauf (1990). Many global warming events are recognized to correlate with the Climatic Optimum 2. For example, McGowran (1986) showed that the distribution of larger foraminifers expanded from the equatorial region to middle latitudinal zones in both hemispheres in N14. In Central to Northeast Japan, much evidence of warm-water influence has also been recognized, as follows: *Sinum yabei* from the Kubota Formation, Fukushima Prefecture (Iwasaki, 1970; Ogasawara, 1988), *Apollon sazanami*, *Nanaochlamys notoensis otutumiensis* and *Calliostoma* sp. cf. *C. simane* from the Ginzan and Utsuno Formations, Yamagata Prefecture (Hatai and Kotaka, 1959; Ogasawara and Sato, 1986), *Cryptopecten yanagawaensis* from the Nagaoka Formation,

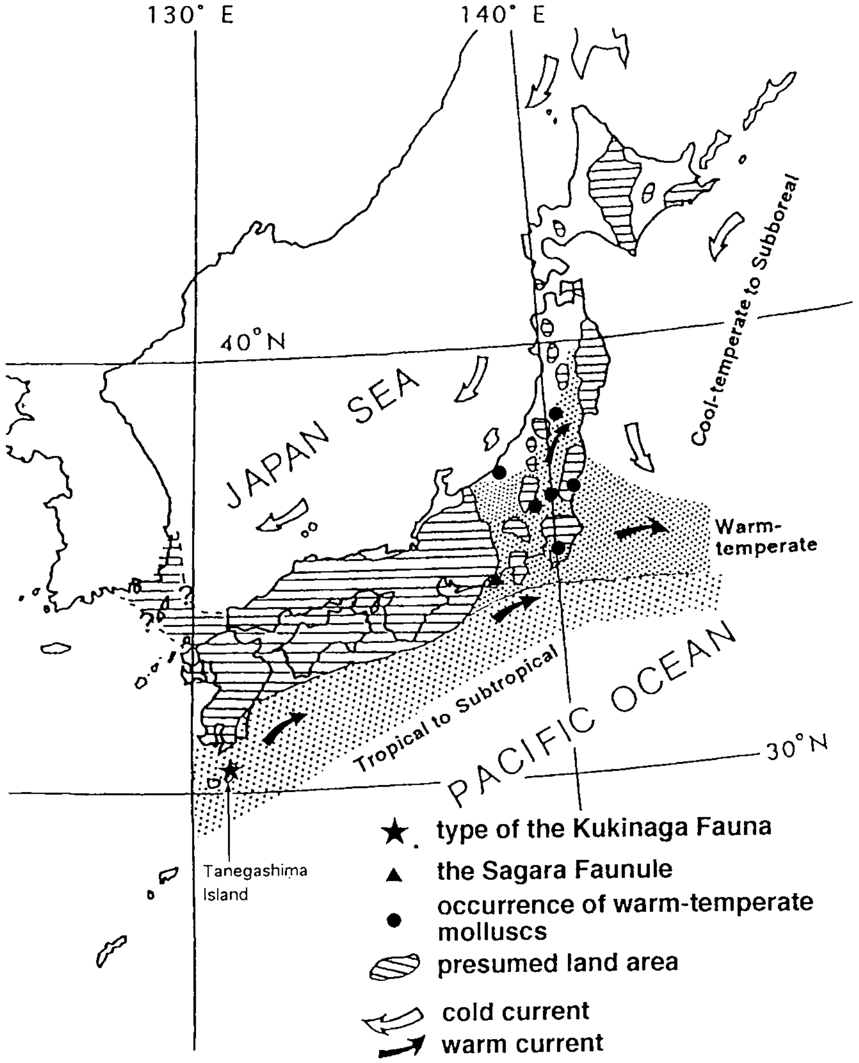


Figure 4. Paleobiogeographic map of the late Middle Miocene around the Japanese Islands modified from Maiya (1988).

Tochigi Prefecture (Sato, 1991), *Aturia formae* from the Kokozura Formation, Ibaragi Prefecture (Tomida, 1992), *Aturia cubaensis* from the Amatsu Formation, Chiba Prefecture (Tomida, 1992), *Mizuhobaris izumoensis* from the Teradomari Formation, Niigata Prefecture (Kobayashi and Yoshiwara, 1988). Figure 4 shows the paleobiogeographic map of Japan in the Climatic Optimum 2.

Next, we discuss the characteristics of the fossil assemblage reported here from the viewpoint of the faunal succession in Japan. The climatic fluctuations mentioned above have controlled the distribution of marine organisms and directly influenced faunal compositions, especially in mid-latitude areas. As noted in the introduction, Ozawa *et al.* (1995) divided the Sagara Fauna into two faunal units: the middle to late Middle Miocene Kukinaga Fauna and the Late Miocene to Early Pliocene Zushi Fauna. These fauna flourished under global warming conditions, i.e., the Climatic Optima 2 and 3 respectively. The assemblage from the Sugegaya Formation corresponds to the early phase of the Sagara Fauna in the type section.

This assemblage is composed of three elements, namely, 1) survivors from the Early to early Middle Miocene, 2) species confined in occurrence to the Middle to Late Miocene, and 3) living species which first appeared in this age. The survivors from the Early to early Middle Miocene are *Glycymeris izumoensis*, *Conus* (*Chelyconus*) *tokunagai*, and so on. These relic species make their first records in the upper Middle Miocene, as well as their last appearance. *Glycymeris idensis* and *Phos miyagiensis* have been reported only from the Middle to Late Miocene of Japan. Some living species such as *Olivella fulgurata*, *Nipponocrassatella nana*, and *Megacardita ferruginosa* occur for the first time in the late Middle Miocene of Japan. It is noteworthy that we obtained no specimens of the characteristic species of the Sagara Fauna, such as *Amussiopecten iitomiensis* or *Chlamys miurensis*, although they commonly occur in the Late Miocene of Japan (Ozawa and Tomida, 1992).

In conclusion, we redefine the molluscan assemblage from the lower part of the Sagara Group as the Sagara Faunule, which is a warm-temperate faunule in the warm-water Kukinaga faunal realm under the influence of the Climatic Optimum 2.

Systematic descriptions

All the specimens examined are deposited in the collection of the Furukawa Museum, Nagoya University (ESN).

Class Bivalvia Linnaeus, 1758
Order Nuculoida Dall, 1889
Family Nuculidae Gray, 1824
Genus ***Acila*** H. and A. Adams, 1858

Acila divaricata submirabilis (Makiyama, 1926)

Figure 5-3

Synonymy.—see Noda, Kikuchi and Nikaido (1993, p. 125, 126).

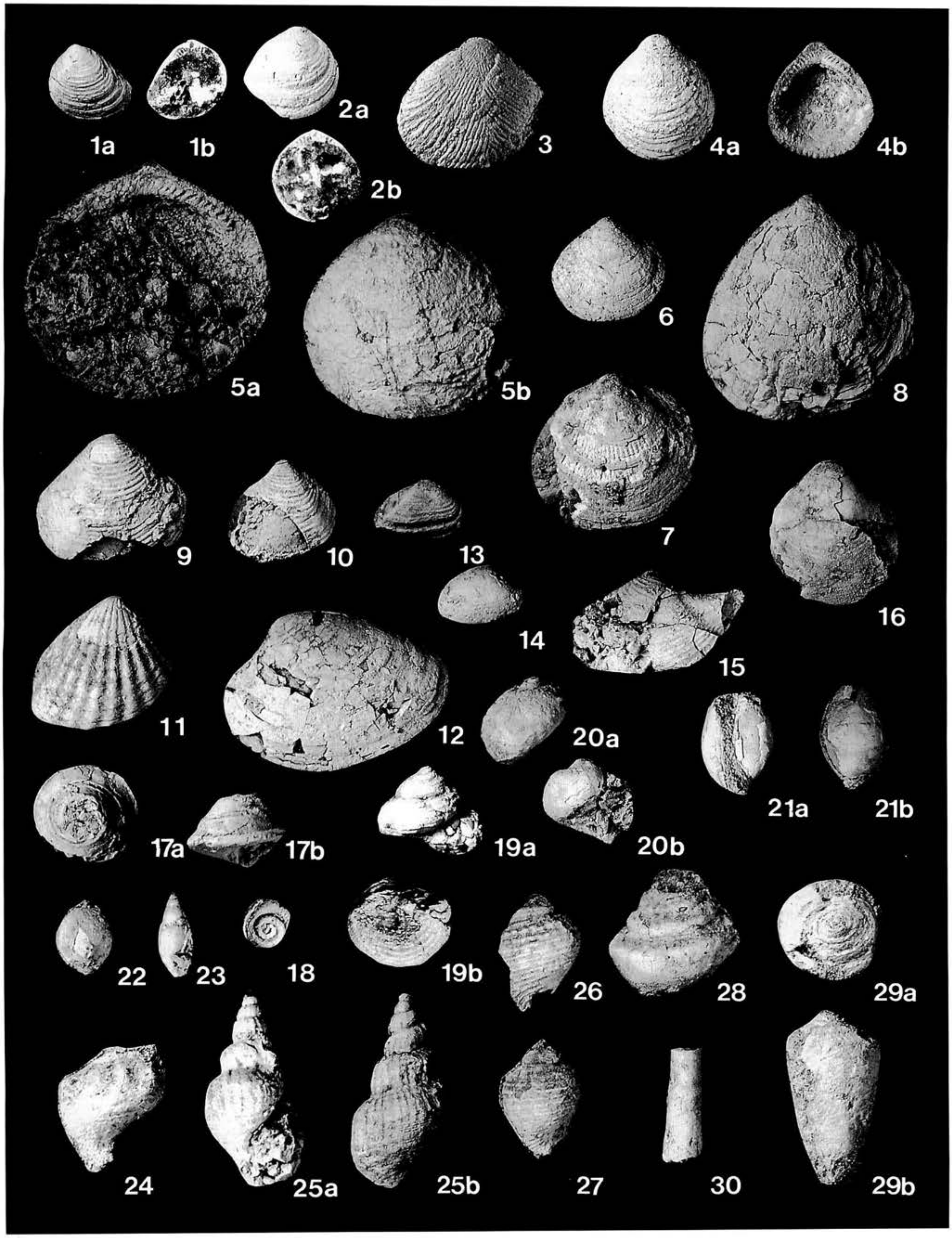
Descriptive remarks.—Seven poorly preserved specimens were obtained. The shells are medium-sized, thick and ovate in shape. The posterior margin is shortly rostrate. The outer surface is sculptured by divaricating radial ribs forming angles from the umbo to the midpoint of the ventral margin. The escutcheonal area is also decorated with radial sculpture. This is a diagnostic feature of *A. divaricata submirabilis*. *Acila divaricata* (s.s.) has no sculpture on the escutcheon. As mentioned by Noda, Kikuchi and Nikaido (1993), many Japanese specimens identified as *A. divaricata* need to be reexamined, paying attention to the escutcheon sculpture.

Dimensions (*in mm*).—Length 15.2, height 12.1 (ESN no. 2615)

Distribution.—Late Early Miocene to Recent.

Order Arcoida Stoliczka, 1871
Family Glycymerididae Newton, 1922
Genus ***Glycymeris*** Costa, 1778

Figure 5. Representative molluscan species of the Sagara Faunule. **1a, b.** *Nipponolimopsis* sp. cf. *N. azumana* (Yokoyama), left valve, ESN no. 2613, ×2. **2a, b.** *Crenulilimopsis* sp. cf. *C. oblonga* (A. Adams), right valve, ESN no. 2614, ×2. **3.** *Acila divaricata submirabilis* (Makiyama), left valve, ESN no. 2615, ×2. **4a, b, 8.** *Glycymeris izumoensis* Matsukuma and Okamoto. 4 : right valve, ESN no. 2616, ×1.5, 8 : right valve, ESN no. 2617, ×1.5. **5a, b, 6, 7.** *Glycymeris idensis* Kanno. 5 : left valve, ESN no. 2618, ×1.5, 6 : right valve, ESN no. 2619, ×1.5, 7 : left valve, ESN no. 2620, ×1.5. **9, 10.** *Nipponocrassatella nana* (A. Adams and Reeve). 9 : right valve, ESN no. 2621, ×1.5, 10 : left valve, ESN no. 2622, ×1.5. **11.** *Megacardita ferruginosa* (A. Adams and Reeve), right valve, ESN no. 2623, ×1.5. **12.** *Callista chinensis* (Holten), left valve, ESN no. 2624, ×1.5. **13, 14.** *Anisocorbula venusta* (Gould). 13 : right valve, ESN no. 2625, ×2, 14 : right valve, ESN no. 2626, ×2. **15.** *Cuspidaria* sp. cf. *C. nobilis* A. Adams, left valve, ESN no. 2627, ×1.5. **16.** *Laevicardium* sp., left valve, ESN no. 2628, ×2. **17a, b.** *Otukaia* sp. 17a : apical view, 17b : aperturral view, ESN no. 2629, ×2. **18.** *Solariella* sp., upper side view, ESN no. 2630, ×2. **19a, b.** *Solariella* (*Machaeroplax*) sp. 19a : apertural view, 19b : basal view, ESN no. 2631, ×2. **20a, b.** *Neverita coticazae* (Makiyama). 20a : adapertural view, 20b : apertural view, ESN no. 2632, ×2. **21a, b.** *Primovula* sp. cf. *P. rhodia* (A. Adams). 21a : ventral view, 21b : dorsal view, ESN no. 2633, ×2. **22.** *Capulus* ? sp., dorsal view, ESN no. 2634, ×2. **23.** *Olivella fulgurata* (A. Adams and Reeve), apertural view, ESN no. 2635, ×2. **24.** *Siphonalia* sp., adapertural view, ESN no. 2636, ×2. **25a, b.** *Phos miyagiensis* Masuda and Takegawa. 25a : apertural view, 25b : adapertural view, ESN no. 2637, ×2. **26, 27.** *Phalium yokoyamai* Nomura and Hatai. 26 : adapertural view, ESN no. 2638, ×1.5, 27 : adapertural view, ESN no. 2639, ×1.5. **28.** *Conus* (*Endemoconus*) sp. cf. *C.* (*E.*) *sieboldi* Reeve, lateral view, ESN no. 2640, ×1.5. **29a, b.** *Conus* (*Chelyconus*) *tokunagai* Otuka. 29a : apical view, 29b : adapertural view, ESN no. 2641, ×1.5. **30.** *Antalis weinkauffi* (Dunker), ESN no. 2642, ×1.5.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29b

Glycymeris idensis Kanno, 1956

Figures 5-5a, b, 6, 7

Glycymeris idensis Kanno, 1956, p. 267, 268, pl. 38, figs. 1-5; Masuda and Takegawa, 1965, pl. 1, figs. 2, 3; Mizuno, Sumi and Yamaguchi, 1969, pl. 28, fig. 10.

Glycymeris (*Glycymeris*) *idensis* Kanno. Amano, 1983, p. 41, pl. 2, fig. 7; Amano, 1986, p. 193-195, pl. 18, figs. 1a-2b, 4; Honda, 1988, p. 359, pl. 1, figs. 7-9.

Type.—Holotype (Institute of Geoscience, University of Tsukuba, Reg. no. TKD 5536; Kanno, 1956, pl. 38, figs. 1a, b) from the Middle Miocene Yoshigasawa Formation, Miyagi Prefecture, Northeast Japan.

Materials.—Three illustrated specimens (ESN nos. 2618, 2619, and 2620) and more than twenty poorly preserved specimens.

Description.—The shells are solid, small (less than 28 mm in length), longer than high, and moderately convex. They are equilateral and equivalve. The shell shape is subcircular to suboval. The beak is prominent and placed at nearly the midpoint of the dorsal margin. The outer surface is ornamented with rather obscure radial striae which are effeced near the anterior and posterior margins. The radial striae are crossed by wrinkled and fine concentric growth lines. The inner ventral margin is crenulated. The ligamental area is unknown owing to the poor preservation. The hinge teeth are strong and become smaller towards the middle. Nine to ten hinge teeth are radially arranged in the anterior and posterior series, respectively.

Dimensions (*in mm*).—

Specimens	Height	Length	Thickness	Valve
ESN no. 2618	25.6	27.4	6.1	left
ESN no. 2619	13.0	14.9	3.2	right
ESN no. 2620	18.9	—	5.2	left

Distribution.—The Middle to Upper Miocene in Central to North Japan. Middle Miocene: Atsunai Formation in Hokkaido (Mizuno, Sumi and Yamaguchi, 1969; Honda, 1988), Togeshita Formation in Hokkaido (Amano, 1983), Ishiizawa Formation in Hokkaido (Amano, 1986), Yoshigasawa Formation in Miyagi Prefecture (Kanno, 1956), Sugegaya Formation in Shizuoka Prefecture (present study). Upper Miocene: Kanagase Formation in Miyagi Prefecture (Masuda and Takegawa, 1965)

Glycymeris izumoensis Matsukuma and Okamoto, 1986

Figures 5-4a, b, 8

Glycymeris (*Glycymeris*) *izumoensis* Matsukuma and Okamoto, 1986, p. 95, 96, figs. 2A-C.

Type.—Holotype (Department of Zoology, National Science Museum, Tokyo, Reg. no. NSMT-Mo61507; Matsukuma and Okamoto, 1986, fig. 2C) from the Miocene Fujina Formation, Shimane Prefecture.

Species diagnosis.—see Matsukuma and Okamoto (1986, p. 96).

Materials.—Two illustrated specimens (ESN nos. 2616, 2617).

Description.—The shells are solid, small to moderate in size, compressed to moderately inflated, higher than long, and subequilateral equivalve. The shell shape is subtrigonal to oval. Both dorsal margins are almost straight. The posterior dorsal margin is more or less shorter than the anterior one. The anterior and ventral margins are gently rounded. The posterior margin is weakly angulated. An obtuse ridge runs from the beak to the posterior angulation. The outer surface is ornamented with regularly spaced periostracal radial striae. The beak is high, pointed, situated near midpoint of dorsal margin, and slightly opisthogyrate. The ligamental area is small trigonal, inequilateral and incised with narrow grooves. Nine to ten hinge teeth are arranged substraightly in the anterior and posterior series, respectively. The inner ventral margin is coarsely crenulated.

Dimensions (*in mm*).—

Specimens	Height	Length	Thickness	Valve
ESN no. 2616	15.0	13.6	5.0	right
ESN no. 2617	26.0	27.3	5.6	right

Remarks.—The specimens have shell characteristics nearly identical with the type specimens of *Glycymeris izumoensis* from the Fujina Formation.

Distribution.—This species is known only from the Middle Miocene of Japan; the middle Middle Miocene Fujina Formation in Shimane Prefecture (Matsukuma and Okamoto, 1986) and the upper Middle Miocene Sugegaya Formation (present study).

Family Limopsidae Dall, 1895

Genus ***Crenulilimopsis*** Kuroda and Habe, 1971

Crenulilimopsis sp. cf. ***C. oblonga*** (A. Adams, 1860)

Figures 5-2a, b

Descriptive remarks.—The shells are small and inflated. The outer surface is ornamented with fine concentric growth lines and obscure radial sculpture. The inner ventral margin is finely crenulated. These shell features are close to those of *Crenulilimopsis oblonga* living in the adjacent Sea of Japan (at depths of 50-2,000 m; Habe, 1977).

Genus ***Nipponolimopsis*** Habe,1951

Nipponolimopsis sp. cf. ***N. azumana*** (Yokoyama, 1910)

Figures 5-1a, b

Descriptive remarks.—More than nine specimens were examined. The illustrated specimen has a small and subtriangular shell which elongates posteriorly. The posterodorsal margin is nearly straight. The beak is anteriorly placed. The outer surface is ornamented with distinct and wavy concentric lines. The radial striae are recognized on the anterior outer surface. Five to six hinge teeth are arranged substraightly in the anterior and posterior series, respectively. *Nipponolimopsis azumana* which lives in Sagami Bay, central Japan, is distinguishable from the present species in having a more rounded shell.

Dimensions (*in mm*).—Length 7.4, height 7.3 (ESN no. 2613)

Order Veneroida H. and A. Adams, 1856
Family Carditidae Fleming, 1820
Genus **Megacardita** Sacco, 1899

Megacardita ferruginosa (A. Adams and Reeve, 1850)

Figure 5-11

Cardita ferruginosa A. Adams and Reeve, 1850, p. 76, pl. 21, fig. 29 (*non vidi*).

Venericardia kiiensis Sowerby, 1913, p. 238, pl. 3, fig. 14 (*fide* Kuroda, Habe and Oyama, 1971).

Venericardia cipangoana Yokoyama, 1920, p. 137-139, pl. 11, figs. 2a-c; Yokoyama, 1922, p. 162, pl. 13, fig. 4; Yokoyama, 1928, p. 86, 87, pl. 9, figs. 3-5.

Venericardia (*Megacardita*) *kiiensis cipangoana* Yokoyama. Taki and Oyama, 1954, p. 38, pl. 12, fig. 2. pl. 33, fig. 4.

Venericardia (*Megacardita*) *ferruginosa* (A. Adams and Reeve). Uozumi, 1953, p. 329, pl. 21, figs. 165, 165a; Ozaki, Fukuta and Ando, 1954, p. 170, pl. 31, fig. 34; Shuto, 1957, p. 86, pl. 22, fig. 13; Hayasaka, 1973, pl. 6, fig. 6; Oyama, 1973, p. 91, pl. 37, figs. 7, 11; Matsuura, 1985, pl. 35, fig. 16.

Megacardita ferruginosa (A. Adams and Reeve). Kuroda, Habe, Oyama, 1971, p. 602, pl. 87, fig. 5, p. 386; Habe, 1977, p. 157, pl. 29, figs. 7, 8; Kobayashi, 1986, pl. 21, fig. 16; Kobayashi, Yahata, Sugimoto and Iyoda, 1986, pl. 15, fig. 21; Yoon, 1988, pl. 1, figs. 38, 39; Mizuno and Amano, 1988, pl. 16, figs. 3, 4; Amano and Kanno, 1991, figs. 5-11.

Venericardia ferruginosa (A. Adams and Reeve). O'Hara and Ito, 1980, pl. 16, fig. 3; Baba, 1990, p. 273, pl. 32, fig. 3.

Descriptive remarks.—More than twenty specimens were obtained. The shells are solid, convex, rectangularly ovate in shape. The anterodorsal margin is short and steeply inclined, while the posterodorsal margin is long and slightly convex. The posterior end is obliquely truncated. The outer surface is ornamented with round-topped, 14-15 radial ribs. Interspaces between the ribs are shallow and form a wavy cross-section. These shell characters are identical with those of *M. ferruginosa*. *M. granulicostata* differs from this species in having granules on radial ribs. *M. panda* has deeper interspaces than this species.

Dimensions (*in mm*).—Length 18.2, height 15.6 (ESN no. 2623)

Distribution.—Upper Middle Miocene: Sugegaya Formation in Shizuoka Prefecture (present study). Upper Miocene: Senhata Formation in Chiba Prefecture (O'Hara and Ito, 1980), Tano Formation in Miyazaki Prefecture (Shuto, 1957). Pliocene: Setana Formation in Hokkaido (Uozumi, 1953), Nadachi Formation in Niigata Prefecture (Amano and Kanno, 1991), Kota Formation in Niigata Prefecture (Mizuno and Amano, 1988), Seoguipo Formation in South Korea (Yoon, 1988), "Byoritz Beds" in Formosa (Yokoyama, 1928). Pliocene to Lower Pleistocene: Haizume and Sawane Formations in Niigata Prefecture (Kobayashi, 1986; Kobayashi, Yahata, Sugimoto and Iyoda, 1986), Junicho Formation in Toyama Prefecture (Matsuura, 1985), Tajima Formation in Kagoshima Prefecture (Hayasaka, 1973). Upper Pliocene to Middle Pleistocene: Naganuma Formation in Kanagawa Prefecture (Yokoyama, 1920; Taki and Oyama, 1954; Oyama, 1973), Kazusa Group in Chiba, Tokyo and Kanagawa Prefectures (Baba, 1990). Middle to Upper Pleistocene: Shimosa Group in Chiba Prefecture (Yokoyama, 1922; Uozumi, 1953; Taki and Oyama, 1954; Oyama, 1973; Baba, 1990), Tokyo Formation in Tokyo (Ozaki, Fukuda and Ando, 1954). Living: The Western Pacific off the southern Boso Peninsula and the Japan Sea off the Noto Peninsula of Japan (at depths of 10-100 m; Habe, 1977).

Family Crassatellidae Ferussac, 1822
Genus **Nipponocrassatella** Kuroda and Habe, 1971

Nipponocrassatella nana (A. Adams and Reeve, 1850)

Figures 5-9, 10

Crassatella nana A. Adams and Reeve, 1850, p. 81, 82, pl. 23, fig. 2 (*non vidi*); Yokoyama, 1922, p. 164, 165, pl. 13, fig. 8; Yokoyama, 1927, p. 434, pl. 49, fig. 11; Baba, 1990, p. 276, pl. 32, fig. 12.

Crassatella loebbeckei Kobelt, 1886, p. 18, pl. 2, fig. 6, pl. 5, fig. 5 (*fide* Nomura, 1933); Yokoyama, 1931, p. 7 (*fide* Nomura, 1933).

Crassatella heteroglypta Pilsbry. Yokoyama, 1920, p. 141, 142, pl. 11, figs. 10, 11.

Crassatellites nanus (A. Adams and Reeve). Otuka, 1935, p. 889, pl. 56, figs. 146, 147; Nomura and Hatai, 1936, p. 122, 123, pl. 14, figs. 5, 6; Nomura and Zinbo, 1936, p. 239, pl. 11, figs. 6a, b; Takayasu, 1986, pl. 62, fig. 12.

Crassatellites (*Crassatellites*) *nanus* (A. Adams and Reeve). Taki and Oyama, 1954, p. 38, pl. 12, figs. 10, 11, pl. 33, fig. 8, pl. 46, fig. 11; Tanaka, 1961, p. 71, pl. 1, figs. 16, 17; Hayasaka, 1961, p. 36, pl. 3, figs. 3a, b.

Crassatellites (*Eucrassatella*) *nana* (A. Adams and Reeve). Oyama, 1973, p. 90, pl. 37, figs. 5, 8-10.

Crassatella (*Nipponocrassatella*) *nana* (A. Adams and Reeve). Matsuura, 1985, pl. 32, fig. 24.

Nipponocrassatella nana (A. Adams and Reeve). Yoon, 1988, pl. 1, figs. 22, 23; Masuda and Huang, 1994, pl. 1, fig. 19.

Eucrassatella (*Nipponocrassatella*) *nanus* (A. Adams and Reeve). Noda, 1991, p. 25, 27, figs. 11-1a, b, 4a, b.

Descriptive remarks.—Ten small specimens were examined. The shells are solid, compressed, trigonally ovate, shortly rostrate and truncated posteriorly. The surface is ornamented with concentric ribs. The trigonal shell shape and concentric ribs of the specimens are diagnostic features of *Nipponocrassatella nana*.

Dimensions (*in mm*).—Length 18.9, height more than 15.3 (lacking posterior corner) (ESN no. 2621); length 12.3, height 11.2 (ESN no. 2622).

Known distribution.—Middle Miocene: Moriya Formation in Nagano Prefecture (Tanaka, 1961). Upper Middle Miocene: Sugegaya Formation in Shizuoka Prefecture (present study). Upper Miocene: Kubota Formation in Fukushima Prefecture (Nomura and Hatai, 1936). Pliocene: Nakoshi Formation in Okinawa Prefecture (Nomura and Zinbo, 1936), Yonabaru Formation in Okinawa Prefecture (Noda, 1991), Seoguipo Formation in South Korea (Yoon, 1988), Chinsui Formation in Formosa (Masuda and Huang, 1994). Lower to Middle Pleistocene: Shibikawa Formation in Akita Prefecture (Takayasu, 1986), Narita Formation in Chiba Prefecture (Yokoyama, 1922; Taki and Oyama, 1954; Oyama, 1973; Baba, 1990), Tokyo Formation in Tokyo (Yokoyama, 1927), Naganuma Formation in Kanagawa Prefecture (Yokoyama, 1920; Taki and Oyama, 1954; Oyama, 1973; Baba, 1990), Tahara Formation in Aichi Prefecture (Hayasaka, 1961). Upper Pleistocene: Hiradoko Shell Beds in Ishikawa Prefecture (Otuka, 1935), Tarayama Shell Bed in Ishikawa Prefecture (Matsuura, 1985). Living: South China Sea and the adjacent Sea of Japan up to the Boso Peninsula on the Pacific side and Oga Peninsula on the Japan Sea side (intertidal to 100 m in depth; Habe, 1977).

Family Veneridae Rafinesque, 1815
Genus **Callista** Poli, 1791

Callista chinensis (Holten, 1803)

Figure 5-12

Venus chinensis Holten, 1803, p. 20 (*non vidi*).
Venus pacifica Dillwyn, 1817, p. 175 (*fide* Kuroda, Habe and Oyama, 1971).
Cytherea sinensis Sowerby, 1855, p. 624, pl. 131, figs. 80, 81 (*fide* Kuroda, Habe and Oyama, 1971).
Chione roscida Gould, 1861, p. 31 (*fide* Kuroda, Habe and Oyama, 1971); Johnson, 1964, p. 141, pl. 29, fig. 5.
Callista pacifica (Dillwyn). Otuka, 1935, p. 895, pl. 56, fig. 181.
Callista chinensis (Holten). Ozaki, Fukuta and Ando, 1954, p. 171, pl. 31, fig. 32; Kuroda, Habe and Oyama, 1971, p. 644, pl. 90, fig. 9, p. 417; Oyama, 1973, p. 101, pl. 45, figs. 1, 2; Takayasu, 1986, pl. 23, fig. 20, pl. 64, fig. 15.
Callista (*Callista*) *chinensis* (Holten). Taki and Oyama, 1954, p. 43, pl. 9, figs. 9, 10; Shuto, 1960, p. 131, pl. 13, fig. 2; Tanaka, 1961, p. 75, pl. 1, figs. 32, 33; Hayasaka, 1961, p. 43, pl. 4, figs. 10a, b; Kaseno and Matsuura, 1965, pl. 14, fig. 2; Hayasaka, 1973, pl. 6, fig. 8; Habe, 1977, p. 269, pl. 56, fig. 2; Aoki and Baba, 1980, fig. 18-18; Ogasawara, 1981, pl. 1, fig. 3; Itoigawa, Shibata, Nishimoto and Okumura, 1981, pl. 16, fig. 3; Matsuura, 1985, pl. 32, fig. 28, pl. 39, fig. 10, pl. 42, fig. 9; Okumura and Takei, 1993, pl. 39, fig. 9; Noda, Kikuchi and Nikaido, 1993, p. 163, 164, figs. 21-11a, b.
Callista sp. cf. *Callista chinensis* (Holten). Shibata in Itoigawa, Shibata and Nishimoto, 1974, p. 85, pl. 22, fig.4.

Descriptive remarks.—Only one specimen was obtained. The outer surface is smooth except for concentric ribs in a ventral part.

Dimensions (*in mm*).—Length 25.0, height 17.8 (ESN no. 2624).

Distribution.—Many fossil records have been reported from the Lower Miocene to the Quaternary of Japan. This species now lives in the coastal waters of Japan, Formosa, and South China. The northernmost limit of distribution is the Boso Peninsula on the Pacific side (Habe, 1977).

Order Myoida Stoliczka, 1870
Family Corbulidae Lamarck, 1818
Genus **Anisocorbula** Iredale, 1930

Anisocorbula venusta (Gould, 1861)

Figures 5-13, 14

Corbula venusta Gould, 1861, p. 25 (*non vidi*); Gould, 1862, p. 164 (*fide* Oyama, 1973); Tokunaga, 1906, p. 39, pl. 2, fig. 22a-b′; Yokoyama, 1920, p. 107, 108, pl. 7, figs. 4a-6.
Caryocorbula (*Anisocorbula*) *venusta* (Gould). Taki and Oyama, 1954, p. 49, pl. 8, figs. 4-6; Oyama, 1973, p. 116, pl. 55, fig. 5; Matsuura, 1985, pl. 39, fig. 14, pl. 41, fig. 16.
Anisocorbula venusta (Gould). Ozaki, 1958, p. 135, pl. 22, figs. 16, 17; Hayasaka, 1961, p. 63, pl. 5, figs. 7a, b, pl. 6, figs. 8a, b; Matsushima, 1969, pl. 11, fig. 14; Kuroda, Habe and Oyama, 1971, p. 707, pl. 102, fig. 15, p. 465; Itoigawa and Ogawa, 1973, pl. 5, fig. 9; Itoigawa in Itoigawa, Shibata and Nishimoto, 1974, p. 103, pl. 32, figs. 7a-8b; Habe, 1977, p. 282, pl. 59, fig. 9; Itoigawa, Shibata, Nishimoto and Okumura, 1981, pl. 21, figs. 3a-4b; Yasui and Kobayashi, 1985, pl. 1, fig. 10; Kobayashi, Yahata, Sugimoto and Iyoda, 1986, pl. 16, fig. 6; Takayasu, 1986, pl. 39, figs. 16a-c, pl. 55, figs. 10a-b, pl. 56, figs. 15, 16a-b, pl. 66, figs. 2, 8a-9b; Yoon, 1988, pl. 1, fig. 11.

Descriptive remarks.—More than ten specimens were obtained. The slightly convex posterodorsal margin and fine concentric sculpture on the outer surface are identical with those of *Anisocorbula venusta*.

Dimensions (*in mm*).—Length 7.9, height 5.1 (ESN no. 2625); length 7.5, height 5.0 (ESN no. 2626)

Distribution.—Upper Lower to lower Middle Miocene: Akeyo and Oidawara Formations in Gifu Prefecture (Itoigawa in Itoigawa, Shibata and Nishimoto, 1974; Itoigawa, Shibata, Nishimoto and Okumura, 1981). Upper Middle Miocene: Sugegaya Formation in Shizuoka Prefecture (present study). Pliocene: Annogawa Formation in Niigata Prefecture (Yasui and Kobayashi, 1985), Seoguipo Formation in South Korea (Yoon, 1988). Upper Pliocene to Lower Pleistocene: Sasaoka, Shibikawa and Nakazawa Formations in Akita Prefecture (Takayasu, 1986), Haizume Formation in Niigata Prefecture (Kobayashi, Yahata, Sugimoto and Iyoda, 1986), Zukawa Formation in Toyama Prefecture, Suginoya Formation in Ishikawa Prefecture (Matsuura, 1985). Middle Pleistocene: Katori Formation in Chiba Prefecture (Ozaki, 1958), Tahara Formation in Aichi Prefecture (Hayasaka, 1961), Sakishima Formation in Mie Prefecture (Itoigawa and Ogawa, 1973). Upper Pleistocene: Tokyo Formation in Tokyo (Tokunaga, 1906). Holocene: Sakuragicho Formation in Kanagawa Prefecture (Matsushima, 1969). Living: From South Hokkaido to Kyushu and South Korea (intertidal to 200 m in depth; Habe, 1977).

Class Gastropoda Cuvier, 1795
Order Archaeogastropoda Thiele, 1925
Family Trochidae Rafinesque, 1815
Genus ***Otukaia*** Ikebe, 1942

Otukaia sp.

Figures 5-17a, b

Descriptive remarks.—Two specimens were obtained. The apical part is missing. The shells are small and conical. Three spiral keels are on the body whorls. One is situated just below the suture and the others on the periphery. The base is abraded, but spiral cords with narrow interstices are recognized. These specimens resemble the young stage of *Otukaia kiheiziebisu*, but the species identification is difficult owing to the poor preservation.

Genus ***Solariella*** Wood, 1842

Solariella sp.

Figure 5-18

Descriptive remarks.—Two poorly preserved specimens were examined. The shells are small, low-spired and conical. Each whorl is rounded and ornamented with beaded spiral cords. The aperture is circular. The umbilicus is open and bounded by a beaded spiral rib. The conchological profile agrees well with *Solariella* (s.l.).

Subgenus ***Machaeroplax*** Friele, 1877

***Solariella* (*Machaeroplax*)** sp.

Figures 5-19a, b

Descriptive remarks.—Eight poorly preserved specimens were obtained. The shells are small (7-8 mm in height), relatively high-spired, and conical. The whorls have a narrow flat area just below the deep suture. The outer surface of the whorls is iridescent and ornamented with four beaded spiral cords. The base is also ornamented with many beaded cords. The umbilicus is open. These specimens resemble *Machaeroplax delicatus*, but the latter species has remarkable growth lines.

Order Mesogastropoda Thiele, 1925
Family Capulidae Fleming, 1822
Genus ***Capulus*** Montfort, 1810

Capulus ? sp.

Figure 5-22

Descriptive remarks.—Only one specimen was obtained. The shell is small, cap-shaped, and nearly symmetrical. The apex is posteriorly situated. The outer surface is smooth. The inner surface cannot be observed. This specimen also resembles *Crepidula*, but the genus has an apex strongly curved to the right side.

Family Naticidae Gray, 1840
Genus ***Neverita*** Risso, 1826

Neverita coticazae (Makiyama, 1926)

Figures 5-20a, b

Polinices (*Neverita*) *coticazae* Makiyama, 1926, p. 150, pl. 12, fig. 8; Nomura, 1939, p. 255, pl. 13, figs. 13a-14b.
Neverita coticazae (Makiyama). Kamada, 1962, p. 157, pl. 18, figs. 21a-22; Masuda and Takegawa, 1965, pl. 2, fig. 21; Masuda, 1967, p. 5, pl. 1, figs. 25a-26b; Kotaka and Noda, 1967, pl. 1, figs. 13, 16; Itoigawa in Itoigawa, Shibata and Nishimoto, 1974, p. 148, pl. 45, figs. 5, 10a, b; Taguchi, Ono and Okamoto, 1979, pl. 4, figs. 4, 5.
Polinices coticazae Makiyama. Kanno and Ogawa, 1964, pl. 2, fig. 12.
Neverita (*Glossaulax*) *coticazae* (Makiyama). Itoigawa, Shibata, Nishimoto and Okumura, 1981, pl. 34, figs. 2a-b.

Descriptive remarks.—One illustrated specimen (ESN no. 2632) and more than four poorly preserved specimens were examined. The shell is small and globular. Most of the shells are abraded, but in the illustrated specimen the appressed suture is preserved. The surface is smooth. The umbilical calus is transversely grooved.

Dimensions (in mm).—Height 10.9, diameter 11.5 (ESN no. 2632)

Distribution.—Upper Lower to lower Middle Miocene: Takinoue Formation in Hokkaido (Kanno and Ogawa, 1964), Kozai Formation in Miyagi Prefecture (Nomura, 1939), Akeyo and Oidawara Formations in Gifu Prefecture (Itoigawa in Itoigawa, Shibata and Nishimoto, 1974; Itoigawa, Shibata, Nishimoto and Okumura, 1981), Higashi-Innai Formation in Ishikawa Prefecture (Masuda, 1967), "lower formation" of Bihoku Group in Okayama Prefecture (Taguchi, Ono, and Okamoto, 1979), Mankodo Formation in North Korea (Makiyama, 1926). Upper Middle Miocene: Kokozura Formation in Ibaragi Prefecture (Kamada, 1962), Sugegaya Formation in Shizuoka Prefecture (present study). Middle to Upper Miocene: Ogawara Formation in Aomori Prefecture (Kotaka and Noda, 1967), Kanagase Formation in Miyagi Prefecture (Masuda and Takegawa, 1965).

Family Cassididae Latreille, 1825
Genus ***Phalium*** Link, 1807

Phalium yokoyamai Nomura and Hatai, 1933

Figures 5-26, 27

Galeodea (*Sconsia*) *japonica* Yokoyama, 1923a, p. 3, pl. 1, figs. 4a, b; Yokoyama, 1923b, p. 11; Yokoyama, 1923c, p. 11, pl. 1, fig. 10; Yokoyama, 1926a, p. 240; Yokoyama, 1926b, p. 342.
Tonna japonica (Yokoyama). Makiyama, 1927, p. 73, not *Tonna japonica* (Dunker).
Phalium yokoyamai Nomura and Hatai, 1933, p. 50, pl. 8, figs. 1, 1a, 3, 7, new name for *Galeodea japonica* Yokoyama; Otuka, 1936, p. 442, pl. 30, fig. 4; Otuka, 1937, p. 170.
Shichiheia yokoyamai (Nomura and Hatai). Hatai and Nisiyama, 1949, p. 93, 94, pl. 23, figs. 14, 15.
Doliocassis japonica (Yokoyama). Kamada, 1962, p. 162, 163, pl.

19, figs. 9, 10 ; Suehiro, 1979, p. 90, 91, pl. 16, figs. 3a-4b.

Liracassis yokoyamai (Nomura and Hatai). Moore, 1963, p. 30.

Phalium (*Mauicassis*) *yokoyamai* Nomura and Hatai. Abbott, 1968, p. 120, pl. 99, figs. 3-7.

Descriptive remarks.—Six immature specimens of *P. yokoyamai* were obtained. Illustrated specimens lack an apical part, outer lip, and siphonal canal. The whorls bear rounded shoulder. Twelve spiral cords are recognized on the body whorl with fine striae in the interspaces. The spiral cords that cross axial threads become tubercular, especially at the shoulder.

Distribution.—Upper Lower Miocene : Shirado Formation in Fukushima Prefecture (Otuka, 1937). Lower Middle Miocene : Sugota Formation in Akita Prefecture (Otuka, 1936 ; Moore, 1963), Susahara Formation in Toyama Prefecture (Hatai and Nisiyama 1949). Middle Middle Miocene : Fujina Formation in Shimane Prefecture (Yokoyama, 1923a ; Nomura and Hatai, 1933 ; Moore, 1963 ; Suehiro, 1979). Upper Middle Miocene : Kokozura Formation in Ibaragi Prefecture (Yokoyama, 1923c ; Kamada, 1962), Sugegaya Formation in Shizuoka Prefecture (present study). Upper Upper Miocene to Lower Pliocene : Embetsu Formation in Hokkaido (Yokoyama, 1926a). Upper Pliocene : Kakegawa Group in Shizuoka Prefecture (Yokoyama, 1923b, 1926b ; Makiyama, 1927).

Order Neogastropoda Thiele, 1929
Family Buccinidae Rafinesque, 1815
Genus **Siphonalia** A. Adams, 1863

Siphonalia sp.

Figure 5-24

Descriptive remarks.—Two specimens that preserved only body whorls were obtained. They resemble the body whorls of *Siphonalia declivis* in the form and ornamentation. We have postponed the species identification until well-preserved specimens are available.

Genus **Phos** Montfort, 1810

Phos miyagiensis Masuda and Takegawa, 1965

Figures 5-25a, b

Phos miyagiensis Masuda and Takegawa, 1965, p. 13, pl. 2, figs. 22a, b.

Type.—Holotype (Institute of Geology and Paleontology, Faculty of Science, Tohoku University, Reg. No. IGPS 90792 ; Masuda and Takegawa, 1965, pl. 2, figs. 22a, b) from the Miocene Kanagase Formation, Miyagi Prefecture.

Materials.—One illustrated specimen (ESN no. 2637) and more than twenty specimens.

Description.—The shells are rather thin, medium in size and fusiform, having an apical angle of about 35°. The shells are composed of 6 to 7 rounded whorls with a slightly angulated shoulder. The whorls are ornamented with axial ribs (30 on body whorl). The ribs are narrower than the interspaces and are crossed by many fine spiral threads. The aperture is nearly ellipsoidal and angulated posteriorly. These shell characteristics agree well with the original description.

Dimensions (*in mm*).—Height 15.3, diameter 8.5 (ESN no. 2637).

Remarks.—This species resembles *Phos iwakiana* and *P. nigroliratum*. *Phos miyagiensis*, however, has a higher shell, more rounded whorls and more numerous spiral threads than *P. iwakiana*. *P. nigroliratum* differs from *P. miyagiensis* in having distinct and deeper sutures, a smaller number of axial ribs and an outer lip with numerous denticles.

Known distribution.—The distribution is confined to the Middle to Upper Miocene of Japan : namely, the upper Middle Miocene Sugegaya Formation in Shizuoka Prefecture (present study) and the Upper Miocene Kanagase Formation in Miyagi Prefecture (Masuda and Takegawa, 1965).

Family Olividae Latreille, 1825
Genus **Olivella** Swainson, 1831

Olivella fulgurata (A. Adams and Reeve, 1850)

Figure 5-23

Oliva fulgurata A. Adams and Reeve, 1850, p. 31, pl. 10, fig. 12 (*non vidi*) ; Sowerby, 1871, p. 37, pl. 351, figs. 424, 425 (*fide* Kuroda, Habe and Oyama, 1971).

Oliva fabula Sowerby, 1871, p. 36, pl. 350, figs. 420, 421 (*fide* Kuroda, Habe and Oyama, 1971).

Olivella fulgurata (A. Adams and Reeve). Nomura and Zinbo, 1935, p. 173, pl. 15, figs. 21, 22 ; Yen, 1942, p. 235, pl. 24, fig. 173 ; Ozaki, 1958, p. 154, pl. 19, fig. 11 ; Kuroda, Habe and Oyama, 1971, p. 302, pl. 54, figs. 14, 15, p. 197 ; Takayasu, 1986, pl. 70, figs. 9a, b, 16, 17 ; Yoon, 1988, pl. 5, fig. 5 ; Tomida, 1989, pl. 13, fig. 9 ; Baba, 1990, p. 182, pl. 13, fig. 21 ; Okumura and Takei, 1993, pl. 30, fig. 12.

Olivella (*Olivella*) *fulgurata* (A. Adams and Reeve). Shuto, 1959, p. 180, pl. 14, figs. 7, 8, 13, 14 ; Tsuru, 1983, p. 77, pl. 19, figs. 3a, b ; Noda, Kikuchi and Nikaido, 1993, p. 184, figs. 24-15a-16b ; Noda, Watanabe and Kikuchi, 1995, p. 79, 81, fig. 16-11.

Descriptive remarks.—More than twenty specimens were obtained. The shell surface was dissolved in most of the specimens. The shell is small and fusiform, composed of 5 to 6 whorls. The body whorl is about 3/5 as long as the total shell length. In size and slender shell form, the specimens closely resemble those of *O. fulgurata*. The specimens from the Sugegaya Formation are also similar to one of the specimens of *O. iwakiensis* from the Miocene Kanagase Formation (Masuda and Takegawa, 1965, pl. 2, fig. 24). The relationship between *O. fulgurata* and *O. iwakiensis* needs to be reexamined taxonomically.

Dimensions (*in mm*).—Height 7.8, diameter 3.6 (ESN no. 2635)

Distribution.—Upper Lower to lower Middle Miocene : Yanagawa Formation in Fukushima Prefecture (Nomura and Zinbo, 1935), Togane Formation in Shimane Prefecture (Tsuru, 1983). Upper Middle Miocene : Sugegaya Formation in Shizuoka Prefecture (present study). Upper Miocene : Kawabaru Formation in Miyazaki Prefecture (Shuto, 1959), Senhata Formation in Chiba Prefecture (Tomida, 1989). Pliocene: Kume and Hitachi Formations in Ibaragi Prefecture (Noda, Kikuchi and Nikaido, 1993; Noda, Watanabe and Kikuchi, 1995), Ananai Formation in Kochi Prefecture (Okumura and Takei, 1993), Seoguipo Formation in South Korea (Yoon, 1988). Lower Pleistocene: Anden Formation in Akita Prefecture (Takayasu, 1986). Middle Pleistocene: Katori Formation in Chiba Prefecture (Ozaki, 1958), Mandano, Jizodo and Narita Formations in Chiba Prefecture (Baba, 1990). Upper Pleistocene: Miyata Formation in Kanagawa Prefecture (Baba, 1990). Living: South China Sea and the adjacent Sea of Japan up to the Boso Peninsula on the Pacific side and the Oga Peninsula on the Japan Sea side (intertidal to 20 m in depth; Higo and Goto, 1993).

Family Conidae Thiele, 1925
Genus **Conus** Linnaeus, 1758
Subgenus **Endemoconus** Iredale, 1931

Conus (Endemoconus) sp. cf. **C. (E.) sieboldi** Reeve, 1848

Figure 5-28

Descriptive remarks.—An incompletely preserved specimen was obtained. The shell surface was slightly dissolved. The sutural ramp is slightly concave to flat and the shoulder is broadly carinate without granules. These shell features are consistent with *C. sieboldi* which lives now at depths of 50 to 200 m from Kyushu to the Boso Peninsula (Higo and Goto, 1993).

Subgenus **Chelyconus** Moerch, 1852

Conus (Chelyconus) tokunagai Otuka, 1934

Figures 5-29a, b

Conus tokunagai Otuka, 1934, p. 632, pl. 50, figs. 83, 84; Kamada, 1962, p. 177, pl. 21, figs. 1a-c; Masuda, 1967, pl. 2, figs. 29a-30b; Nakagawa and Takeyama, 1985, pl. 24, figs. 7a, b; Ozawa, Nakagawa and Takeyama, 1986, pl. 13, fig. 7.

Descriptive remarks.—Two poorly preserved specimens were collected. The shell surface was slightly dissolved. The shell is moderate in size (about 21.2 mm high) and ventricosely conical in shape. The shoulder is subrounded, with granules. Fine striations are recognized in the sutural ramp. The shell features mentioned above agree with the original description of *Conus tokunagai*.

Distribution.—Upper Lower to lower Middle Miocene: Shiratori Formation in Iwate Prefecture (Otuka, 1934), Higashi-Innai Formation in Ishikawa Prefecture (Masuda, 1967), Shimo Formation in Fukui Prefecture (Nakagawa and Takeyama, 1985; Ozawa, Nakagawa and Takeyama, 1986). Upper Middle Miocene: Kokozura Formation in Ibaragi Prefecture (Kamada, 1962), Sugegaya Formation in Shizuoka Prefecture (present study).

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Frenelopsis pombetsuensis: a new cheirolepidiaceous conifer from the Lower Cretaceous (Albian) of Hokkaido, Japan

KEN'ICHI SAIKI

Department of Plant Science, Natural History Museum and Institute, Chiba, 955-2, Aoba, Chuo-ku, Chiba, 260 Japan

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Abstract. A new fossil conifer, *Frenelopsis pombetsuensis* sp. nov., is described on the basis of a single specimen obtained from the Lower Cretaceous (Albian) of Hokkaido, Japan. *Frenelopsis pombetsuensis* is similar to *F. choshiensis* from the Lower Cretaceous of Choshi, Kimigahama, in having two leaves at each node. The cuticular feature of *Frenelopsis pombetsuensis* is, however, rather more similar to that of *F. hoheneggeri* from the Lower Cretaceous of Poland than to *F. choshiensis*. The Late Jurassic to Early Cretaceous paleofloras of Japan have been divided into two distinct types: the Ryoseki and Tetori. However, attributions of the Early Cretaceous flora of Hokkaido have not been made because of its hitherto poorly-known fossil record. The genus *Frenelopsis* is one of the most important members of the Ryoseki-type floras and has never been found in the Tetori-type floras. The present fossil is the first record of characteristic taxon of the Ryoseki-type flora from the Lower Cretaceous of Hokkaido.

Key words: Albian, conifer, *Frenelopsis pombetsuensis*, Hokkaido, Middle Yezo Group, Ryoseki-type floras

Introduction

During Late Jurassic to Early Cretaceous time, two paleofloristic types flourished in Japan and its adjacent areas; the Ryoseki-type and Tetori-type floras (Kimura, 1961, 1975, 1987; Kimura and Ohana, 1992; Ohana and Kimura, 1995). The taxonomic compositions of these two paleofloristic types of floras are quite different. According to Ohana and Kimura (1995), the difference between the two floras is due to climatic factors. Based on the taxonomic compositions of the floras, and the morphological features of fossil plants, they estimate that the Ryoseki-type floras flourished under tropical-subtropical and rather arid climatic conditions, while the Tetori-type floras flourished under warm-temperate and rather humid conditions.

Although a number of fossil plants have been described from the Middle-Upper Yezo Group of Hokkaido (see Nishida, 1991), all of them, except for a single conifer seedling-like structure (Stockey *et al*., 1990), are dated as Late Cretaceous. Thus, no characteristic plant fossils of the Ryoseki-type or Tetori-type floras have previously been described from Hokkaido.

In the present paper, the author describes a new species of *Frenelopsis* from the Lower Cretaceous (Albian) of Hokkaido. *Frenelopsis* is an extinct conifer genus assigned to the family Cheirolepidiaceae. Frenelopsids, a group consisting of the genus *Frenelopsis* and the closely related genus *Pseudofrenelopsis*, have been used as an indicator of tropical or subtropical and arid climate (Alvin, 1982). In Japan, *Frenelopsis* is one of the characteristic taxa of the Ryoseki-type floras, thought to have flourished under tropical or subtropical and arid or semi-arid conditions (Kimura and Ohana, 1992; Ohana and Kimura, 1995).

Material and Methods

Material.—The compressed conifer shoot was found in the Pombetsu Valley about 60 km northeast of Sapporo City (Figure 1). The specimen was obtained from the mudstone bed of the uppermost strata of the Main part, Middle Yezo Group. Matsumoto (1965) described *Ammonoceratites yezoensis* (Yabe) from the same locality, indicating a middle?- upper Albian age.

Methods.—For the cuticle observation, fossil leaves were treated by Schulze's solution followed by diluted NaOH. Obtained cuticles were mounted in EUKITT for light microscope observation. For SEM observation, cuticles were coated by Pt-Pd with a HITACHI E-1030 ion sputter and photographed by HITACHI S-800.

The specimen is housed in the Mikasa City Museum, Ikushumbets-nishikicho, Mikasa, 068-21 Japan.

Systematic description

Order Coniferales
Family Cheirolepidiaceae Takhtajan, 1963
Genus **Frenelopsis** Schenk, 1869

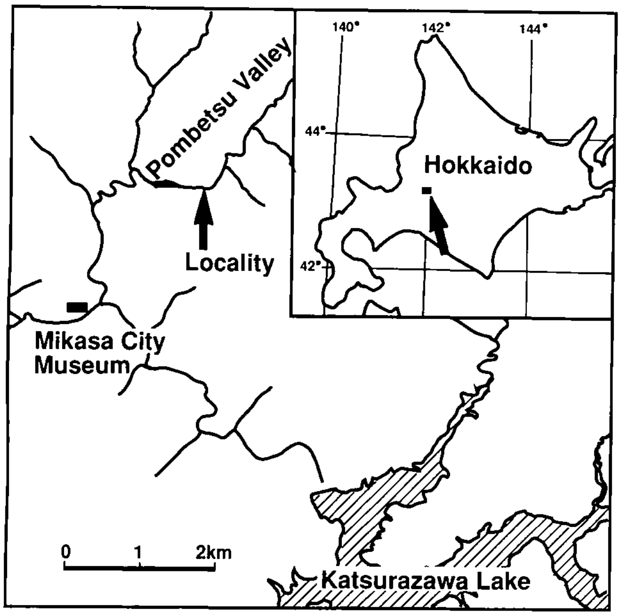

Figure 1. Locality map.

Frenelopsis pombetsuensis sp. nov.

Figures 2A-E, 3A-I

Material.—Holotype, MCM-A573.

Horizon.—Uppermost strata of the main part of Middle Yezo Group (Albian).

Type locality.—Pombetsu Valley, Mikasa City, Hokkaido (Figure 1 ; roughly 43°16′19″N, 141°59′48″E). The outcrop corresponds to locality no. Ik 2024 of Matsumoto (1965).

Diagnosis.—Internode at least 10 mm long and 1.4 mm wide (Figure 2A). Scale leaves two at each node (Figure 2B). Triangular part of leaf up to 1.5 mm high at a node (Figure 2B). Stomata about the same optical density as rest of cuticle ; arranged in longitudinal rows (Figures 2C, D). Subsidiary cells 4-5 in number (Figures 2D ; 3C, D).

Internode cuticle about 10 μm in total thickness, with outer periclinal epidermal wall about 3-4 μm thick (Figures 3A, D). Epidermal cells rectangular to polygonal in shape, 30-50 μm in diameter. Outer surface of cuticle smooth, non-papillate (Figure 3E). Hypodermal cells thin-walled, longitudinally arranged, elongate rectangular in shape, 20-40 μm wide (Figure 3I). Stomata arranged in rather irregular longitudinal rows in 100-150 μm interval, each row a single stoma wide ; stomata 30-40 per mm^2 in density (Figures 2C, D ; 3B, C). Non-stomatal zone 50-100 μm (2-3 cells) wide, consisting of longitudinally arranged epidermal cells. No dorsiventrality observed (Figures 2C, D).

Stomatal complex 65-80 μm in diameter, consisting of a pair of guard cells and 4-5 subsidiary cells (Figures 3C, D). Guard cells sunken about 7 μm below surface ; each cell 40-90 μm long and 30-40 μm wide (Figures 3D, G). Mouth of stomatal pit rectangular or polygonal in shape, bounded by a rather thick, lobed canopy (Figures 3E, F) ; lobes corresponding in number to subsidiary cells. Papillae in throat of pit short and wide ; equal in number with that of subsidiary cells (Figures 2E, 3G). Stomatal orientation most frequently transverse (Figure 3H).

Further description.—The branch system of *Frenelopsis pombetsuensis* and the whole length of the internode are uncertain because of fragmental preservation of the fossil.

External and cuticular observations of the specimen clearly indicate the absence of a groove or suture separating the basal cushions, as seen in living cupressaceous species.

The preservation of the cuticle of one side is poor, but is sufficient to observe the number, shape and size of stomata and other epidermal cells.

Comparison and Discussion.—Although the present specimen is frangmental, both external and cuticular features of the specimen correspond well with the diagnosis of *Frenelopsis* Schenk emended by Watson (1988). The opposite arrangement of leaves is similar to that of extant cupressaceous conifers and some cheirolepidiaceous conifer genera such as *Cupressinocladus* Seward. However the present specimen differs from these taxa in the absence of a groove or suture separating the basal cushions.

Among the species of *Frenelopsis* previously described, most have leaves in whorls of three. Only two exceptional species, *Frenelopsis teixeirae* and *F. choshiensis*, have two leaves at each node like the present specimen (Table 1). Of these two species, *Frenelopsis teixeirae*, described by Alvin and Pais (1978) from the Lower Cretaceous of Portugal, differs from the present specimen in its markedly thick cuticle and absence of a lobed ring around the mouth of the stomatal pit. The other species, *Frenelopsis choshiensis*, is described by Kimura *et al.* (1985) from the Lower Cretaceous of Choshi, Japan. *Frenelopsis choshiensis* is clearly distinguished from the present specimen in its large canopy covering the mouth of the stomatal pit, and the presence of a narrow groove surrounding the mouth.

Despite the presence of two leaves at each node, the cuticular features of the present specimen are more similar to *Frenelopsis hoheneggeri* (Ettingshausen) Schenk, having leaves in whorls of three, than to other *Frenelopsis* species with opposite decussate arrangement of leaves (Table 1). *Frenelopsis hoheneggeri* was redescribed in detail by Reymanóna and Watson (1976) based on specimens from the type locality in the Polish Carpathians. The present specimen is distinguished from *Frenelopsis hoheneggeri* only by the number of leaves and cuticle thickness. Despite their different external features, the cuticular features of the present specimen suggest its close relationship with *Frenelopsis hoheneggeri.*

Paleophytogeography.—Since Kimura (1961, 1975) divided the Late Jurassic-Early Cretaceous floras of Japan and its adjacent areas into the Ryoseki-type and Tetori-type floras, his distinction has been extended around Southeast Asia, with some modification (Kimura, 1980, 1987 ; Kimura and Ohana, 1992 ; Ohana and Kimura, 1995).

Stopes and Fujii (1910) described some fossil plants from the Upper Yezo Group (Upper Cretaceous) of Hokkaido and, since then, additional specimens have been described from the Upper Cretaceous part of the Yezo Group (see Nishida,

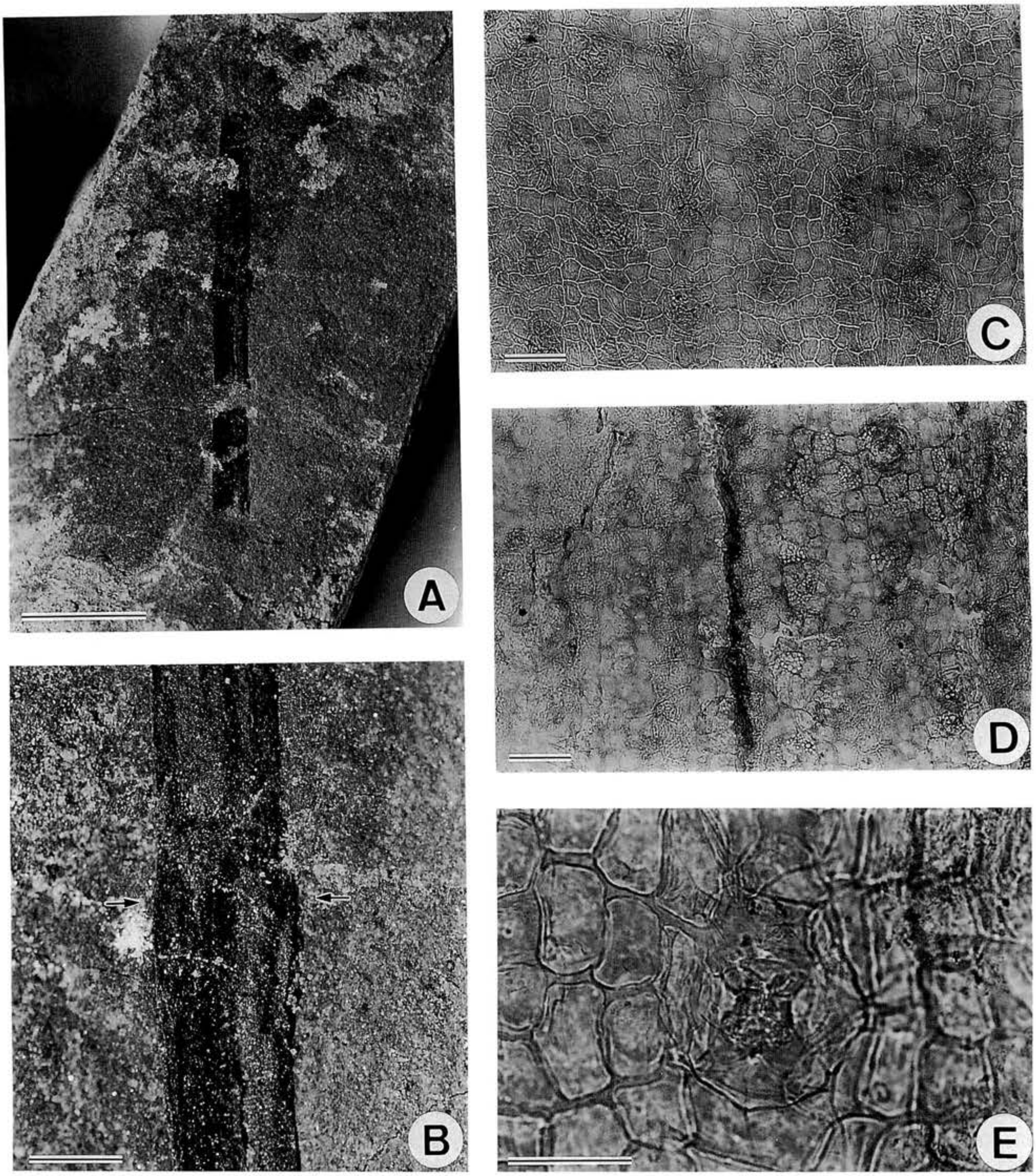

Figure 2. *Frenelopsis pombetsuensis* Saiki (MCM A-573). **A**: Holotype (MCM A-573). **B**: Arrows indicate a pair of leaves. **C**: Cuticle of internode, light microscope. **D**: Cuticle of internode, opposite side of Figure 2C. No dorsiventrality observed. **E**: Stoma, light microscope. Scale bars = 5 mm in A; 1 mm in B; 100 μm in C, D; 50 μm in E.

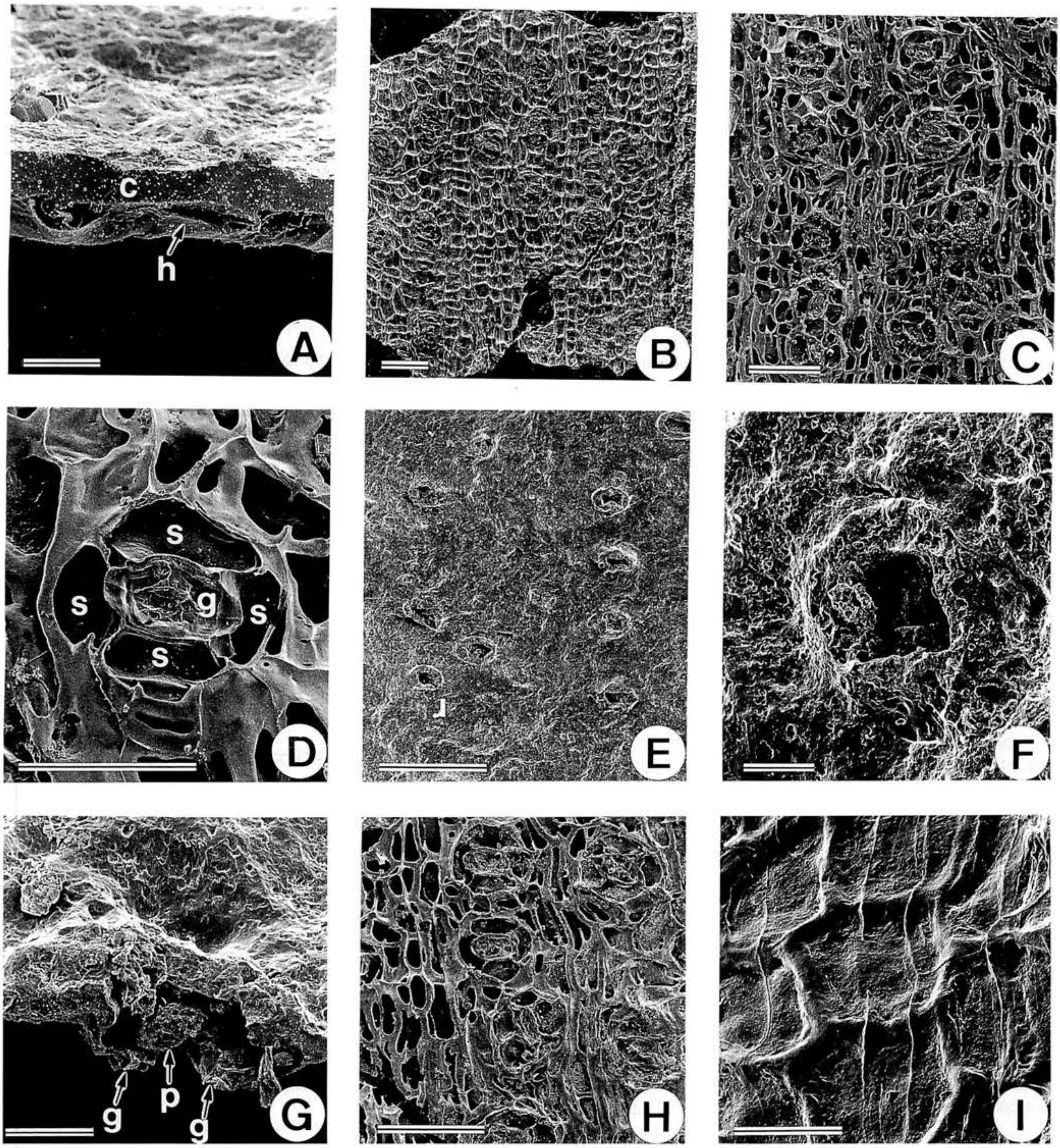

Figure 3. SEM micrographs of cuticle of *Frenelopsis pombetsuensis* Saiki (MCM A-573). **A**: Section of cuticle showing cutinized epidermis (c) and hypodermis (h). **B**: Cuticle of internode, showing longitudinally arranged rows of stomata. **C**: Internode cuticle seen from inside showing transversely oriented stomatal pit. **D**: Stomatal complex showing a pair of guard cells(g) and four subsidiary cells(s). **E**: Internode cuticle from outside showing mouth of stomatal pit. Surface of cuticle smooth, without any papillae or trichome. **F**: Single stoma from outside showing rectangular mouth of the stomatal pit and papillae in throat. **G**: Section of stoma showing guard cells(g), and papillae in throat of stoma (p). **H**: Internode cuticle. Epidermal layer covered by hypodermal layer in lower right of this photograph. **I**: Polygonal epidermal cells covered by longitudinally elongated hypodermal cells. Scale bars=10 μm in A, F, G; 100 μm in B, C, E, H; 50 μm in D, I.

Table 1. Comparative morphometrics of *Frenelopsis pombetsuensis* sp. nov. and related species. 1 : Kimura *et al.* (1985), 2 : Alvin and Pais (1975), 3 : Reymanówna and Watson (1976).

Characters\Species	*F. pombetsuensis*	*F. choshiensis*[1]	*F. teixeirae*[2]	*F. hoheneggeri*[3]
Internode length	at least 10 mm	4-4.5 mm	2.5-5 mm	8 mm
Internode width	1.4 mm	1.5-2 mm	1.5 mm	3 mm
Leaf number per node	2	2	2	3
Maximum length of free leaf	up to 1.5 mm	0.5 mm	—	1.5 mm
Leaf margin	—	hairs up to 4 μm	scarious	scarious
Total thickness of cuticle	10 μm	50 μm	50 μm	40 μm
Stomatal arrangement	ill defined rows	ill defined rows	ill defined rows	well defined rows
Density of stomatal row	7-9 per mm	—	—	10-12 per mm
Density of stomata	30-40 per mm^2	200 per mm^2	—	—
Diameter of stomatal complex	65-80 μm	45-75 μm	—	60-70 μm
Number of subsidiary cells	4-5	4-6, usually 4	5-6	4-6, usually 4
Orientation of stomatal aperture	horizontal	horizontal	—	horizontal
Surface around stomatal pit	thickened ring	grooved	slightly raised	thickened ring
Papillae in throat of stomatal pit	present	present	present	present
Trichomes on epidermal cells	none	none	—	none
Stratigraphic range	Albian	Barremian	Hauterivian-Barremian	Hauterivian

1991). All of these specimens have been obtained from Upper Cretaceous sediments. This marked absence of fossil plants from the Lower Cretaceous of Hokkaido, has prevented a comparison of the Early Cretaceous flora of Hokkaido with the Ryoseki- and Tetori-type floras. *Frenelopsis pombetsuensis* is therefore important because it is the first report of a characteristic taxon of the Ryoseki-type flora from the Lower Cretaceous (Middle Yezo Group) of Hokkaido.

Based on their distribution in the fossil record, frenelopsids are interpreted as thermophilous plants. Alvin (1982) plotted the Berriasian-Cenomanian distributions of frenelopsids on the paleogeographical maps. They seem to lie essentially at the edge of the tropical or subtropical and arid belt of low paleolatitudes. *Classopollis*, the pollen produced by cheirolepidiaceous conifers, also supports the thermophilous nature of frenelopsids. The occurrence of *Classopollis* corresponds well with estimated tropical or subtropical and arid paleoclimates (Vakhrameev 1970, 1980, 1981, 1991).

Although the thermophylly of the frenelopsids is not in dispute, their xerophytic or halophytic nature is certainly controversial (Alvin, 1982 ; Watson, 1988). Halophytic and xerophytic plants have evolved similar features to prevent excessive water loss due to high salinity. Frenelopsids have a distinctly succulent appearance which is sometimes compared with modern halophytic angiosperm plants such as *Salicornia* L. (Zeiller, 1882 ; Reymanóna and Watson, 1976). A relatively thick cuticle and a deeply sunken stoma surrounded by papillae are the characteristic features not only of xerophytes but also of halophytes. Moreover, sedimentological evidence clearly indicates a coastal habitat of some frenelopsids, such as *Frenelopsis harissii* Doludenko and Reymanóna and *Pseudofrenelopsis varians* (Fontaine) Watson (Alvin, 1982). Thus, it is inappropriate to use frenelopsids as an indicator of arid climates without any additional supporting evidence.

The Ryoseki-type flora is thought to have flourished under tropical-subtropical climatic conditions with a fairly long-term arid season in each year (Ohana and Kimura 1995). The occurrence of frenelopsids supports the presence of tropical-subtropical climate in Hokkaido area. However, the remarkably thinner cuticle of *Frenelopsis pombetsuensis* in relation to other frenelopsids, and the non-papillate surface of its cuticle, may also indicate rather humid conditions.

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Mantle kinematics and formation of commarginal shell sculpture in Bivalvia

TAKAO UBUKATA

Department of Earth Sciences, Shizuoka University, Otani 836, Shizuoka, 422 Japan

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Abstract. The geometry of the commarginal shell sculpture and internal microgrowth pattern in 82 species of the Bivalvia were analyzed both theoretically and empirically. Two major categories were recognized in the geometry of internal microgrowth increments ; 1) the regular type, which consists of regularly arranged curves, being mutually parallel in the sections and maintaining their morphology during growth independent of the sculpture pattern, and 2) the undulated type, with undulated microgrowth increments along the folds of prominent sculpture. For the former category, geometric patterns of the sculpture and increments of actual specimens were well reproduced by computer simulations under the condition that the sculpture is originated by mantle extension and shrinkage. In the latter case, mantle bulging or bending appears to produce a plicated shell folding, although sculpture formation cannot be simulated by the model adopted in this study.

Key words : Bivalves, microgrowth increments, shell sculpture, theoretical morphology

Introduction

The external shell sculpture of molluscs and brachiopods have been taken for granted not only as taxonomically useful, but also as functionally significant characters (Wrigley, 1948 ; Rudwick, 1968 ; Stanley, 1969, 1970 ; Seilacher, 1972, 1974 ; Savazzi *et al*., 1982 ; Signor, 1982 ; Savazzi, 1986). On the other hand, two-dimensional patterns of ornamentation on the external shell surface have attracted much attention from theoretical morphologists (Waddington and Cowe, 1969 ; Lindsay, 1982a, 1982b ; Hayami and Okamoto, 1986 ; Meinhardt, 1984 ; Meinhardt and Klinger, 1987 ; Gunji, 1990 ; Ackerly, 1992). However, only a few authors have focused on the role of the mantle (Carter, 1967 ; Checa, 1994). Analyzing the mantle kinematics during shell growth is necessary for understanding the mantle-shell relationship in which the mantle forms the shell and the shell constrains the shape of the mantle (Savazzi, 1990 ; Seilacher and Gunji, 1993). For such an analysis, the commarginal sculpture in bivalves is particularly suitable because it is geometrically simple and is widespread in many taxa.

Commarginal shell sculpture in bivalves consists of a series of conformable curves with a concentric direction on the outer shell surface determined by the former position of the shell. Cox (1969) suggested that the commarginal sculpturing resulted from a rhythmic change in the rate of secretion of shelly matter, while Seilacher (1985) assumed periodic bulging of the mantle edge for its origin. However, no attempts have yet been made to estimate parameters determining the sculptural patterns in general.

The present work analyzes the geometric pattern of radially sectioned bivalve shell and attempts to model the formation of the commarginal shell sculpture from the viewpoint of mantle kinematics. The relationship between internal microgrowth increments and the sculptural pattern is especially taken into consideration. The sequences of internal microgrowth increments have been regarded as the record of periodic time series in many cases (Pannela and MacClintock, 1968 ; Jones *et al*., 1978 ; Jones, 1985 ; Tanabe, 1988 ; Tanabe and Oba, 1988). Then the internal microgrowth increments are also the record of the mantle kinematics because the mantle is in contact with the inner surface of the shell during shell secretion.

Material and method

In order to clarify the microscopic features of the shell, microscopic observations in radial and vertical sections were made for all species examined. A total of 82 extant and fossil bivalve species listed in Table 1 were studied. Each species is represented by one or a few specimens. Most specimens were collected at various localities around the Japanese Islands and the Philippines by myself, but some specimens were selected from the collection of the University Museum, University of Tokyo. All the figured specimens are preserved in the University Museum, University of Tokyo (UMUT).

A single valve for each specimen was first cut using an electric saw vertical to the outer shell surface along the radial direction. Pieces of the sections were embedded in

Table 1. List of materials examined.

Family	species	locality
Arcidae	*Arca navicularis*	Shikanoshima, Fukuoka, western Japan
	A. boucardi	Morozaki, Aichi, Central Japan
	Barbatia amygdarumtortum	Iriomote Is., Okinawa, southwest Japan
	Anadara antiquata	Honda Bay, Palawan, southwest Philippines
Glycymerididae	*Glycymeris yessoensis*	Sarufutsu, Hokkaido, northern Japan
Mytilidae	*Mytilus grayanus*	Samani, Hokkaido, northern Japan
	M. galloprovincialis	Yokohama, Kanagawa, Central Japan
	M. californianus	Neah Bay, Washington, USA
	Septifer bilocularis	Turtlecove Is., Palau
	Modiolus modiolus	Samani, Hokkaido, northern Japan
Inoceramidae	*Inoceramus hobetsensis*	Obira, Hokkaido, northern Japan
	I. uwajimensis	Obira, Hokkaido, northern Japan
Pteriidae	*Pinctada margaritifera*	Ishigaki Is., Okinawa, southwest Japan
	P. fucata	Misaki, Kanagawa, Central Japan
Isognomonidae	*Isognomon perna*	Iriomote Is., Okinawa, southwest Japan
	I. isognomum	San Luice, Bathangas, Philippines
	I. legumen	Iriomote Is., Okinawa, southwest Japan
Malleidae	*Malleus regula*	Iriomote Is., Okinawa, southwest Japan
Pinnidae	*Pinna muricata*	Honda Bay, Palawan, southwest Philippines
	Atrina kinoshitai	Amakusa, Kumamoto, western Japan
Limidae	*Lima vulgaris*	Turtlecove Is., Palau
Ostreidae	*Crassostrea lineata*	Iriomote Is., Okinawa, southwest Japan
	Crassostrea gigas	Misaki, Kanagawa, Central Japan
Plicatulidae	*Plicatula muricata*	Misaki, Kanagawa, Central Japan
Pectinidae	*Cryptopecten vesiculosus*	Misaki, Kanagawa, Central Japan
	Chlamys swifti	Wakkanai, Hokkaido, northern Japan
	Patinopecten yessoensis	Wakkanai, Hokkaido, northern Japan
Spondylidae	*Spondylus squamosus*	Iriomote Is., Okinawa, southwest Japan
	S. barbatus	Sagami Bay, Kanagawa, Central Japan
Unionidae	*Inversidens reiniana*	Lake Biwa, Shiga, Central Japan
	Unio biwae	Lake Biwa, Shiga, Central Japan
	Lanceolaria grayana oxyrhyncha	Lake Biwa, Shiga, Central Japan
	Cristaria plicata	Lake Biwa, Shiga, Central Japan
	Lamprotula rochechoarti	Lake Tung-t'ing, China
	Lamprotula sp.	Lake Tung-t'ing, China
Trigoniidae	*Neotrigonia margaritacea*	French Is., Australia
Lucinidae	*Codakia tigerina*	Panglao Is., Cebu, southern Philippines
Carditidae	*Cardita leana*	Misaki, Kanagawa, Central Japan
	Beguina semiorbiculata	Honda Bay, Palawan, southwest Philippines
	Megacardita ferruginosa	Misaki, Kanagawa, Central Japan
Chamidae	*Chama brassica*	Honda Bay, Palawan, southwest Philippines
Astartidae	*Tridonta alaskensis*	Etorofu Is., Hokkaido, northern Japan
Cardiidae	*Fragum unedo*	Iriomote Is., Okinawa, southwest Japan
	Nemocardium samarangae	Misaki, Kanagawa, Central Japan
Tridacnidae	*Tridacna crocea*	Honda Bay, Palawan, southwest Philippines
Mactridae	*Mactra chinensis*	Wakkanai, Hokkaido, northern Japan
	M. veneriformis	Misaki, Kanagawa, Central Japan
	Pseudocardium sachalinense	Sarufutsu, Hokkaido, northern Japan
Tellinidae	*Tellina venulosa*	Sarufutsu, Hokkaido, northern Japan
Psammobiidae	*Solecurtus divaricatus*	Morozaki, Aichi, Central Japan
Glossidae	*Meiocardia tetragona*	Misaki, Kanagawa, Central Japan
Corbiculidae	*Corbicula sandai*	Lake Biwa, Shiga, Central Japan
Veneridae	*Venus foveolata*	Shima, Mie, Central Japan
	Periglypta puerpera	Honda Bay, Palawan, southwest Philippines
	Circe scripta	Sagami Bay, Kanagawa, Central Japan
	Gafrarium tumidum	Iriomote Is., Okinawa, southwest Japan
	Callanaitis disjecta	Australia
	Anomalocardia brasiliana	Brazil
	Placamen tiara	Shima, Mie, Central Japan
	Mercenaria stimponi	Wakkanai, Hokkaido, northern Japan
	M. cyprinoides	Danvers, Massachussetts, USA
	M. mercenaria	Danvers, Massachussetts, USA
	Protothaca euglypta	Misaki, Kanagawa, Central Japan
	P. jedoensis	Misaki, Kanagawa, Central Japan
	Timoclea micra	Shikanoshima, Fukuoka, western Japan
	Meretrix petechialis	Morozaki, Aichi, Central Japan
	Callista brevisiphonata	Sarufutsu, Hokkaido, northern Japan
	Saxidomus purpuratus	Morozaki, Aichi, Central Japan
	Ruditapes philippinarum	Misaki, Kanagawa, Central Japan
	Katelysia japonica	Iriomote Is., Okinawa, southwest Japan
	Paphia schnelliana	Sagami Bay, Kanagawa, Central Japan
	P. amabilis	Sagami Bay, Kanagawa, Central Japan
	P. euglypta	Sagami Bay, Kanagawa, Central Japan
	Phacosoma japonicum	Misaki, Kanagawa, Central Japan
	Clementia vatheleti	Shima, Mie, Central Japan
	Cyclina sinensis	Ariake, Saga, western Japan
Corbulidae	*Solidicorbula erythrodon*	Morozaki, Aichi, Central Japan
Hiatellidae	*Hiatella orientalis*	Misaki, Kanagawa, Central Japan
Pholadidae	*Zirfaea crispata*	California, USA
Cuspidariidae	*Cuspidaria hindsiana*	Misaki, Kanagawa, Central Japan
	C. nobilis	Misaki, Kanagawa, Central Japan

gypsum and polished with graded powder. The polished plane was etched with 5% acetic acid for several minutes, washed, and dried in air. For optical microscopy an acetate peel was prepared for each specimen by pressing a sheet of triacetylcellulose film (25 μm in thickness) onto the etched surface flooded with acetone (Kennish *et al.*, 1980). Thin sections were made for fossil specimens. The acetate peels and the thin sections were observed with an Olympus AHBT optical microscope. Polished and etched surfaces of selected specimens were coated with platinum vanadium using an Eiko IB-5 ion coater and examined with a Hitachi S-2400 scanning electron microscope operated at 15 kV.

For the computer simulation of the shell section, a program written in N-88 BASIC was carried out with a personal computer (NEC PC-9821Xp) interfaced with a CRT (SANYO CMT-B15M6) and an ink-jet printer (Canon BJC-600J).

Geometric pattern of shell section and remarks on sculpture formation

Internal microgrowth increments

In many species, internal microgrowth increments consist of regularly arranged straight lines with elliptic or sigmoid curves which are mutually parallel in sections (Figures 1-1, 1-2). They maintain a similar basic morphology during growth which is independent of the sculptural pattern. This type of microgrowth increments is tentatively called **the regular type.** In *Anodonta woodiana, Cristaria plicata, Chlamys swifti, Clementia vatheleti, Cuspidaria nobilis, Cuspidaria hindsiana, Inoceramus hobetsensis* (Figure 1-3), and *Inoceramus uwajimensis*, microgrowth increments prominently undulate along the plicated sculpture. Consequently, the shells of these species consist of prisms or lamellae which are not parallel to one another (Figure 1-4). This type of increment is here called **the undulated type.**

In *Inversidens reiniana* and *Pseudocardium sachalinense*, morphology of microgrowth increments is occasionally disturbed at a localized part in the outermost portion (Figure 1-5). Week undulation or disturbance of microgrowth increments was occasionally found in *Mytilus galloprovincialis* (Figure 1-6), *Mytilus californianus* and *Modiolus modiolus*. In *Tridonta alaskensis* (Figure 1-7), *Lamprotula rochechoarti* and *Solecurtus divaricatus*, microgrowth increments in the outer most shell layer slightly change their shape in the distal part during growth. They are sigmoid-shaped near the ridge of the sculpture, but such a feature disappears in the groove. The morphology of increments of these species mentioned above seems to be an intermediate between the regular and undulated types, but the undulation of the increments is generally weak, and this type essentially belongs to the regular type in substance.

If mantle deformation is restricted to lateral extension and shrinkage, and if the mantle does not heave or bend, internal microgrowth increments, which are trails of mantle movement, maintain their direction mutually parallel to one another. But if the mantle edge bulges or bends, the stacking pattern of microgrowth increments is disturbed and they change their direction in limited parts of the shell. The basic morphology of the regular-type microgrowth increments is maintained during growth, and is independent of sculptural pattern. From the above arguments, it is expected that in the species with the regular-type increments, the mantle deformation is restricted to lateral extension and shrinkage along the inner surface of the shell in substance. Conversely, in the case of the undulated type of increments, the mantle edge is considered to heave or bend.

Remarks on sculpture with undulated type of increments

In many bivalve species, wave phases of the ridges and furrows on a valve usually correspond to those of the other valve. However in *Anodonta woodiana*, *Cristaria plicata*, which have the undulated type of increments, folds alternately occur on the left and right valves, so that the ridges on one valve correspond to furrows on the opposite valve (see also Savazzi and Peiyi, 1992). In *Anodonta woodiana* and *Cristaria plicata*, ribs are often oblique to the commarginal growth lines on the external shell surface (Figure 2-4), namely the sculpture is not perfectly commarginal. In this case, a bivalve cannot close its valves tightly without phase difference of the plicae between both valves. The plicated fold of *Inoceramus hobetsensis* sometimes runs obliquely across the commarginal growth lines. In *Inoceramus hobetsensis*, it is presumed that the folds on one valve correspond to furrows on the opposite valve, even though no specimen of this species, which has slightly oblique ribs, with the valves conjoined was found.

It is evident that plicated folds with the undulated type of increments reflect the topography of the wavy mantle surface which acts as a template for shell formation. Slight obliquity of the sculpture in *Anodonta woodiana* (Figure 2-4), *Cristaria plicata* and *Inoceramus hobetsensis* suggests that the phase of topographic condition of the mantle waving shifts along the mantle margin during growth. In these three species, plicae are built alternatively on both valves. These

Figure 1. Photographs of the lateral view of the bivalve shell in radial sections. The outer surface of the shell is upward and the ventral side to the right. Arrows indicate the myostracum. **1.** Optical micrograph of peeled section of *Paphia schnelliana* from Sagami Bay, Kanagawa, Central Japan (UMUT RM 27340). Scale bar : 500 μm. **2.** Optical micrograph of peeled section of *Phacosoma japonicum* from Misaki, Kanagawa, Central Japan (UMUT RM 27341). Scale bar : 1 mm. **3.** Broken section of a giant shell of *Inoceramus hobetsensis* from Turonian (Cretaceous) bed in Obira, Hokkaido, northern Japan (UMUT MM 27342). Scale bar : 3 cm. **4.** Scanning electron micrograph of *Cuspidaria hindsiana* from Misaki, Kanagawa, Central Japan (UMUT RM 27343). Scale bar : 200 μm. **5.** Optical micrograph of peeled section of *Pseudocardium sachalinense* from Sarufutsu, Hokkaido, northern Japan (UMUT RM 27344). Scale bar : 1 mm. **6.** Optical micrograph of peeled section of *Mytilus galloprovincialis* from Misaki, Kanagawa, Central Japan (UMUT RM 27345). Scale bar : 1 mm. **7.** Optical micrograph of peeled section of *Tridonta alaskensis* from Etorofu Is., Hokkaido, northern Japan (UMUT RM 27346). Scale bar : 1 mm.

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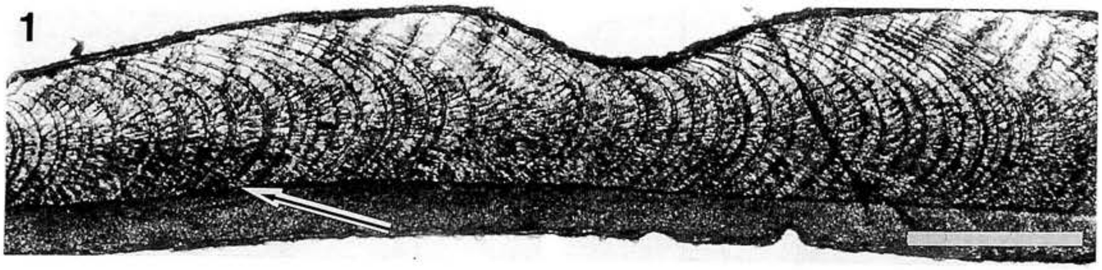

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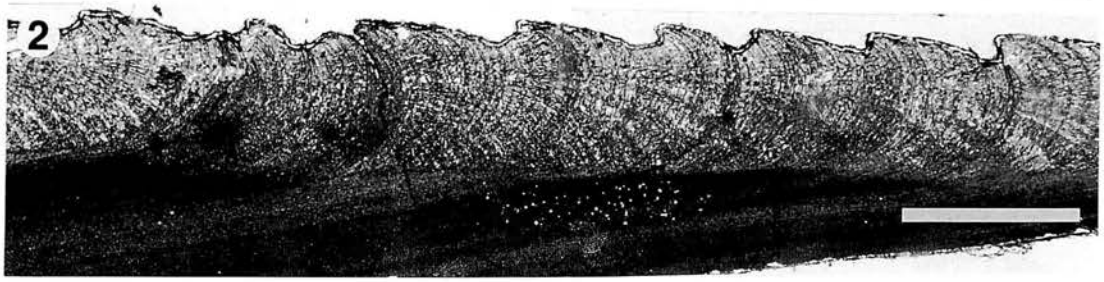

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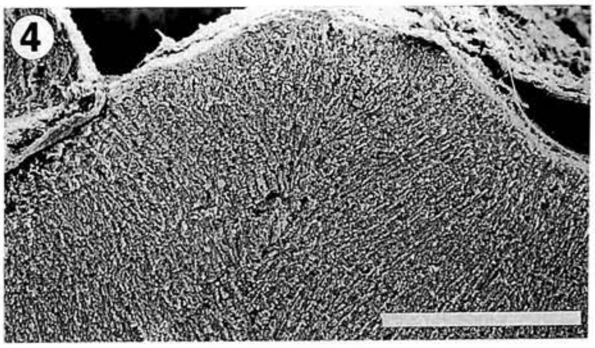

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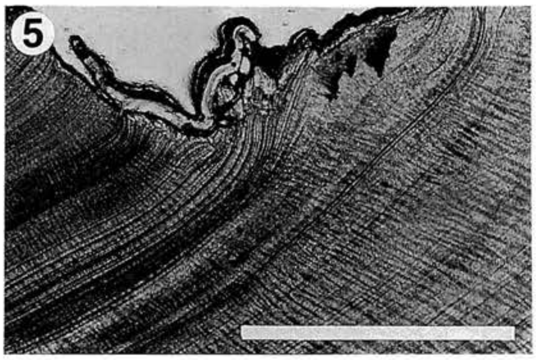

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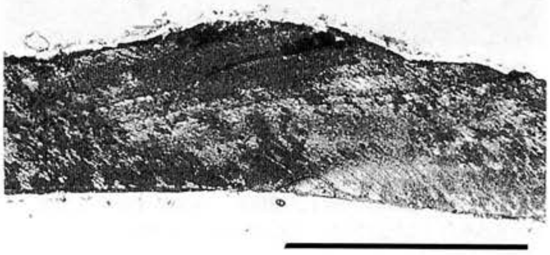

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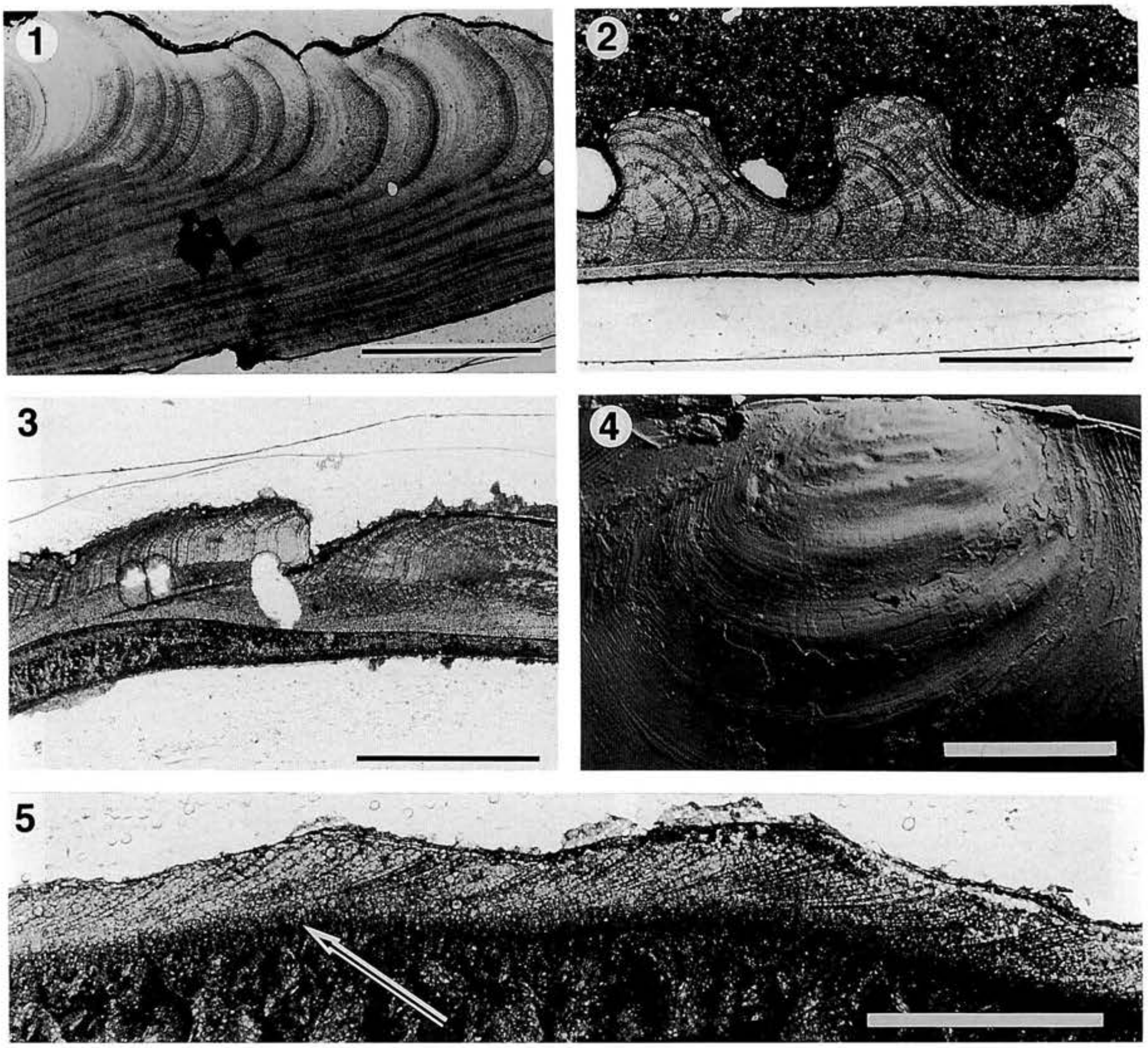

Figure 2. **1-3, 5.** Optical micrographs of radial peeled sections. The outer surface of the shell is upward and the ventral side to the right. Arrows indicate the myostracum. **1.** *Callista brevisiphonata* from Sarufutsu, Hokkaido, northern Japan (UMUT RM 27347). Scale bar : 2 mm. **2.** *Paphia amabilis* from Sagami Bay, Kanagawa, Central Japan (UMUT RM 27348). Scale bar : 1 mm. **3.** *Megacardita ferruginosa* from Misaki, Kanagawa, Central Japan (UMUT RM 27349). Scale bar : 2 mm. **4.** Lateral view of the valve of *Anodonta woodiana* from Lake Biwa, Shiga, Central Japan (UMUT RM 27350). Scale bar : 2 cm. **5.** *Meiocardia tetragona* from Misaki, Kanagawa, Central Japan (UMUT RM 27351). Scale bar : 1 mm.

facts indicate that mantles on the left and right sides bend in the same direction and that commarginal waves are formed on the mantles, namely, commarginal shell sculpture appears to originate from mantle bending on the left and right sides and the subsequent shell folding. On the other hand, in *Chlamys swifti*, *Clementia vatheleti* and *Cuspidaria* spp., each commarginal ridge on a valve matches that on the opposite valve, showing that bulging of the mantles on both sides or swelling of the visceral mass is the likely factor. In these four species, sculpture formation is explained by the bulging or rising of mantle edges on both sides.

Remarks on sculpture with regular type of increments

The accretionary pattern of regular type internal microgrowth increments is not always conformable to that of the sculpturing phase on the shell. For example, in *Tridonta alaskensis, Tridacna crocea, Meiocardia tetragona, Corbicula sandai, Circe scripta, Gafrarium tumidum, Anomalocardia brasiliana, Katelysia japonica, Paphia schnelliana* (Figure 1-1), *Paphia amabilis* (Figure 2-2), *Phacosoma japonicum* (Figure 1-2), and other many species, the increments are generally irregularly spaced and their periodic patterns appear to be independent of the sculptural pattern. The accretionary patterns of internal microgrowth increments in such species are considered to be affected by environmental factors

(Pannella and MacClintock, 1968 ; Lutz and Rhoads, 1977 ; Jones, 1985). In all probability, the effect of environmental fluctuations on shell precipitation seems to be not strong enough to build the sculpture in such species. If so, what growth components form the sculpture in such species?

On the contrary, in *Callista brevisiphonata* (Figure 2-1), *Pseudocardium sachalinense* and *Mytilus grayanus*, the regular-type increments tend to be densely arranged on the ventral side of the slope in going from the ridge to the furrow of the costae. An irregular and incidental furrow is occasionally accompanied by a condensed band of regular-type increments in *Arca navicularis, Glycymeris yessoensis, Megacardita ferruginosa* (Figure 2-3), *Solecurtus divaricatus, Timoclea micra* and *Protothaca euglypta*. Does fluctuation of the precipitation rate of calcium carbonate cause the sculpture formation in such cases?

In many species with the regular type of increments, the myostracum is generally smooth, independent of sculpturing (Figures 1-1, 1-7, 2-2). However, a weak undulation of the myostracum is occasionally found in *Barbatia amygdarumtortum, Megacardita ferruginosa, Meiocardia tetragona* (Figure 2-5), *Mytilus californianus* and *Modiolus modiolus*. What determines the geometry of myostracum through the sculpture construction?

Theoretical morphology of shell section with regular type increments

Modeling of growth kinematics

In order to recognize clearly growth components controlling the sculpture formation, and to estimate theoretical spectrum of geometric pattern of the shell section, the microscopic shell growth with the regular type of increments is modeled theoretically.

Let us consider the process of shell growth in Figure 3. The shell growth in radial sections during a short period of

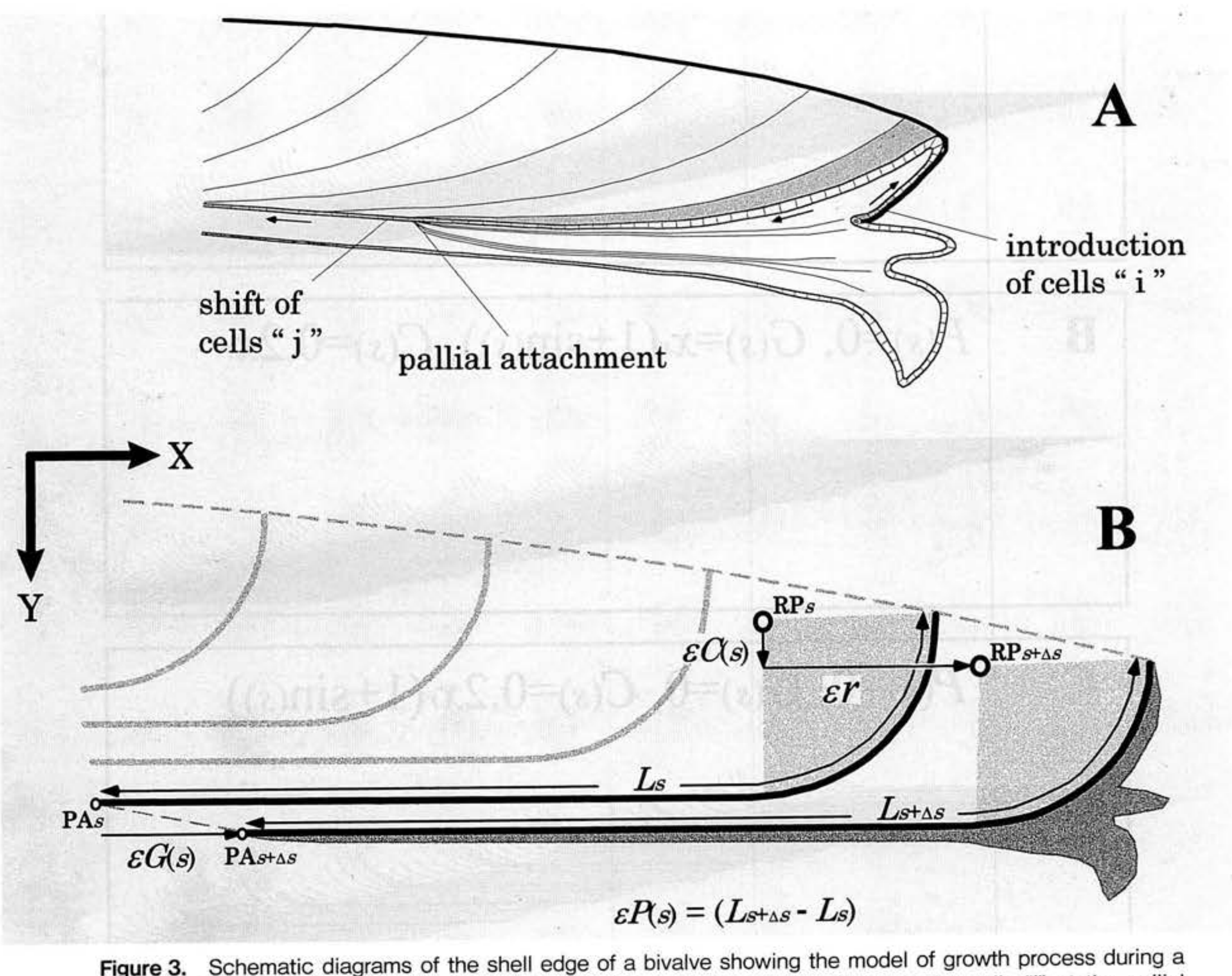

Figure 3. Schematic diagrams of the shell edge of a bivalve showing the model of growth process during a short period of time. **A.** In a growth stage, cells "i" arise from the mantle edge and the cells "j" at the pallial attachment shift by formation of cells "i", and the secretory product of the cells "j" alters from myostracum to inner shell layer. **B.** During a growth stage Δs, the reference point $\boldsymbol{RP}_s$ shifts by εr where r is equal to the radius of the circular arc of the increment curve, the pallial attachment point translates from $\boldsymbol{PA}_s$ to $\boldsymbol{PA}_{s+\Delta s}$ and the distal part of the mantle changes its length from L_s to $L_{s+\Delta s}$.

time is exhibited by kinematics of an internal microgrowth increment. Growth components are expressed as functions of growth stage *s*, rather than as functions of time, since the time scale of the growth process is hardly detected in many cases. The position of a microgrowth increment at a growth stage *s* is shown by the reference point $\boldsymbol{RP}_s(x_{rs}, y_{rs})$. On the ventral side to the reference point the morphology of a microgrowth increment is represented by a circular arc whose radius is expressed as *r*, while on the dorsal side it is exhibited by a straight line (Figure 3B). The translation of the internal microgrowth increment is described by the three growth parameters *C*(*s*), *G*(*s*) and *P*(*s*), defined below.

Over a short period of growth step Δs, the mantle secretes calcium carbonate on the inner surface of the shell giving rise to the stippled area in Figure 3A, an area which is analogous to Lison's (1949) matrix. If the reference point moves to the right by εr parallel to the X axis during the growth step, the reference point shifts below by $\varepsilon C(s)$ parallel to the Y axis, where ε is an arbitrary constant reflecting the magnitude of growth step. The value of $\varepsilon C(s)$ represents the amount of shell precipitation on the inner surface of the outer shell layer. Meantime the pallial attachment point $\boldsymbol{PA}_s$ (xa_s, ya_s) linearly shifts to $\boldsymbol{PA}_{s+\Delta s}(xa_{s+\Delta s}, ya_{s+\Delta s})$ (Figure 3B). Then we express the displacement of the X coordinate of $\boldsymbol{PA}_s$ over the growth step by $\varepsilon\boldsymbol{G}(s)$ which exhibits progression of the pallial attachment. While calcium carbonate is secreted, the mantle proliferates and changes its length by division of epithelial cells. The outer epithelial cells of the mantle mainly arise from the periostracal groove, and successive introduction of cells pushes the earlier produced cells out into the more proximal part of the mantle (Figure 3A). Then the function of the cells change from perios-

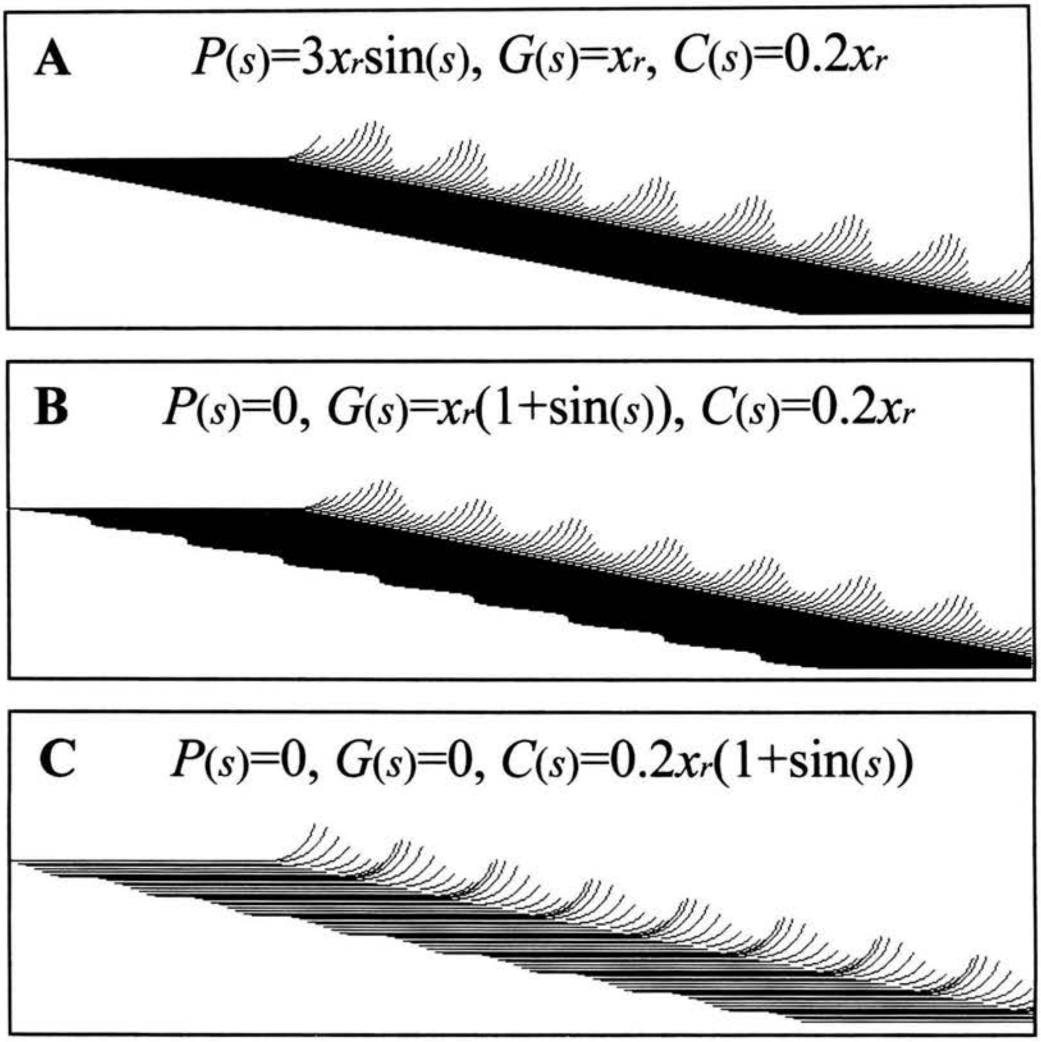

Figure 4. Computer simulations of the bivalve shell in radial sections, showing geometric patterns of microgrowth increments and external sculpture. Only the effect of oscillation of one parameter is considered. The value of x_r represents the X coordinate of the reference point. **A.** The effect of mantle extension and shrinkage is simulated. **B.** The effect of oscillation of mantle proliferation rates is simulated. **C.** The effect of fluctuation in shell precipitation rates is simulated.

tracum secretion to shell secretion or connection to the shell (Stasek and McWilliams, 1973). Consequently, for quite a short period of time, the proliferation of the mantle cells can be approximated by the progression of the pallial attachment from $\boldsymbol{PA}_s$ to $\boldsymbol{PA}_{s+\Delta s}$, even though the progression of pallial attachment represents the growth of visceral mass and is indeed slightly slower than the mantle growth rate throughout ontogeny. The mantle as a whole is a kind of hydroskeleton supported by blood pressure (Morita, 1991) and can be shrunk by the radial pallial muscle. Consequently, if we express the length from $\boldsymbol{PA}_s$ to the mantle edge along the increment by L_s, its value may be changed by mantle extension or shrinkage. Then, the value of $\varepsilon P(s)$ is defined by the difference of L_s during the growth step Δs. In general, three growth parameters are defined as follows:

$$C(s)=\frac{y_{rs+\Delta s}-y_{rs}}{\varepsilon},\quad G(s)=\frac{x_{rs+\Delta s}-x_{rs}}{\varepsilon},$$
$$P(s)=\frac{L_{s+\Delta s}-L_s}{\varepsilon}$$

The sculptural pattern of a bivalve shell in the radial sections is generally more or less periodic and originates by fluctuation of some parameters given by a periodic function. Then, a constant or a periodic function is given for each parameter. The formulation of the periodic function is considered to be variable depending on the physiological nature of a species and is arbitrarily chosen. In the present simulations, a sine curve function for the periodic oscillation of parameters is chosen. Although three parameters $C(s)$, $G(s)$ and $P(s)$ are incremental components and must increase with size of the whole animal, the zero growth of $P(s)$ is assumed for a limited part of the shell section, namely the mean of $P(s)$ is zero in this model.

Computer simulation of shell section

Firstly, a case was considered in which only one of the three parameters, $C(s)$, $G(s)$ and $P(s)$ oscillates, with the remaining two being fixed. Figure 4 shows computer-produced shell sections for three cases. The trail of the mantle edge during growth becomes wavy in each case, demonstrating that the commarginal sculpture can be produced in any of these conditions. In each case, topography of the shell surface, which varies depending on the given initial microgrowth increment morphology, is not a useful criterion for estimating the origin of the sculpture. But significant characters such as the trail of the pallial attachment, *i.e.*, myostracum, and the interval of microgrowth increments are different among the three cases. When $P(s)$

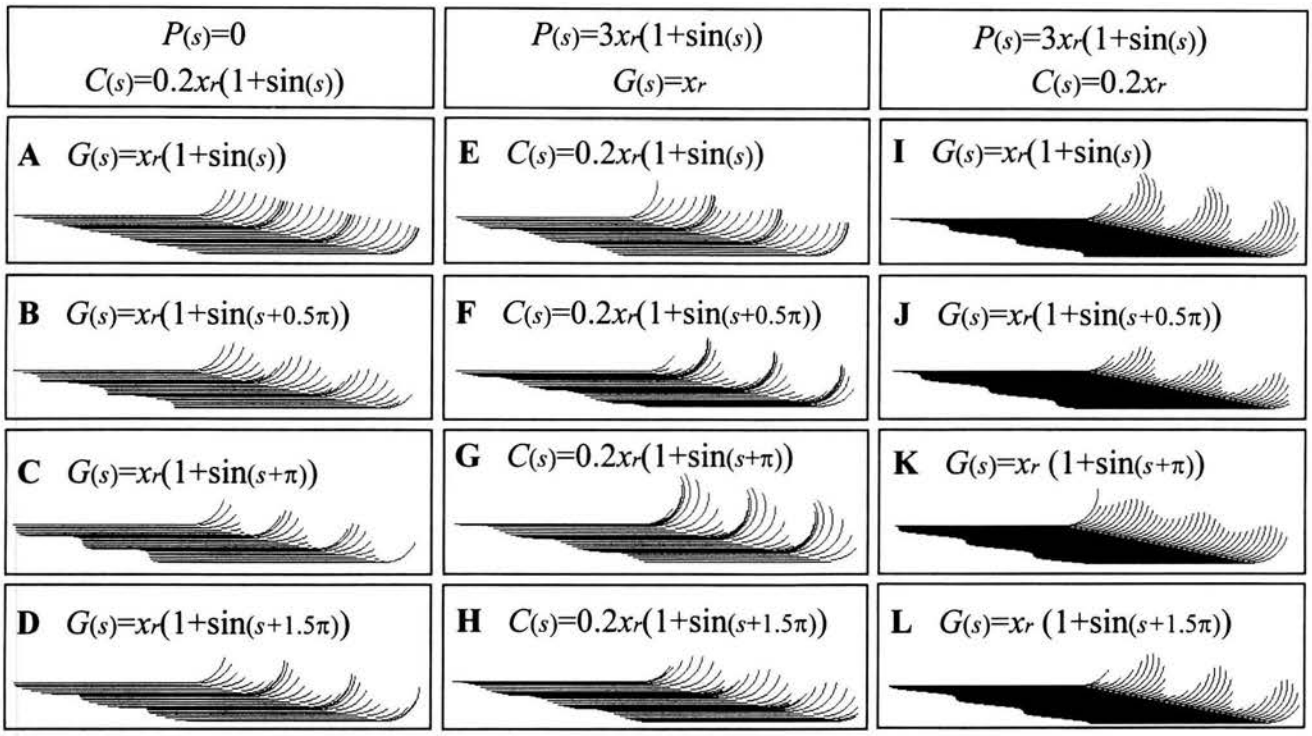

Figure 5. Computer simulations for external shell sculpture and internal microgrowth increments in radial sections as two parameters fluctuate by sine curve functions. This shows the effects of phase difference between two given sine-curve functions for two parameters. The value of x_r represents the X coordinate of the reference point. **A-D.** The progression rates of the pallial attachment and shell precipitation both oscillate, and mantle does not deform. **E-H.** Mantle extends and shrinks, rate of shell precipitation is changed, and the progression rate of the pallial attachment is fixed. **I-L.** Mantle extends and shrinks, the progression rate of the pallial attachment is fluctuated, and the rate of shell precipitation is constant.

oscillates and the other parameters are fixed, the myostracum does not undulate and the interval of increments remains unchanged (Figure 4A). When only *G*(*s*) oscillates, the interval of microgrowth increments is also unchanged, but the myostracum undulates (Figure 4B). When only *C*(*s*) oscillates, periodically narrowing microgrowth increments are inevitably produced (Figure 4C). In this case, microgrowth increments are densely arranged on the slope of the sculpture from a furrow to a ridge, i.e., on the dorsal side. The myostracum also undulates by *C*(*s*) oscillation because the pallial attachment does not translate linearly.

Secondly, let us consider the case when two parameters both oscillate by a sine curve function with a constant wavelength. Figure 5 shows some examples of computer-produced diagrams, illustrating the effects of changes in the phase difference between the two given sine curves for variable parameters. Morphology of the external sculpture is variable depending upon the phase difference. When external sculpture and undulation of myostracum originate by oscillations of *C*(*s*) and *G*(*s*), microgrowth increments tend to be crowded on the dorsal side of the sculptural slope (Figures 5B-D), while they do not conspicuously develop if the phase of oscillation of *C*(*s*) is the same as that of *G*(*s*) because effects of fluctuation of *C*(*s*) and *G*(*s*) are compensated by each other (Figure 5A). When *C*(*s*) and *P*(*s*) both oscillate and *G*(*s*) is fixed, the myostracum inevitably undulates and the sculpture is constructed (Figures 5E-H). Under this condition, microgrowth increments also tend to be crowded on the dorsal side of the sculptural slope (Figures 5F-H), but the sculpture becomes weak when the phase of *P*(*s*) is the same as that of *C*(*s*) because of compensating relationships between them (Figure 5E). When both *G*(*s*) and *P*(*s*) oscillate and contribute sculpture formation, the interval of microgrowth increments has a fixed value during growth and the myostracum always becomes wavy (Figures 5I-L). In this case, if the phase of *G*(*s*) lags 180° behind that of *P*(*s*), the sculpture becomes relatively weak because of the compensating relationship between them (Figure 5K).

Thirdly, let us consider the case in which all the three parameters oscillate by a sine curve with the same wave length. Figure 6 shows computer-produced figures illustrating the effects of phase lag of *P*(*s*), *G*(*s*) or *C*(*s*) behind the remaining two parameters whose fluctuation effects are compensated by each other. When *C*(*s*) and *G*(*s*) oscillate without a phase difference, the myostracum does not undulate because of compensating relationships between them (Figures 6A-E, J), the case in which sculpture originates by *P*(*s*) oscillation. In other cases, the myostracum becomes wavy by fluctuation effects of *C*(*s*) and *G*(*s*). When the phase of *P*(*s*) is the same as that of *C*(*s*), effects of fluctuation

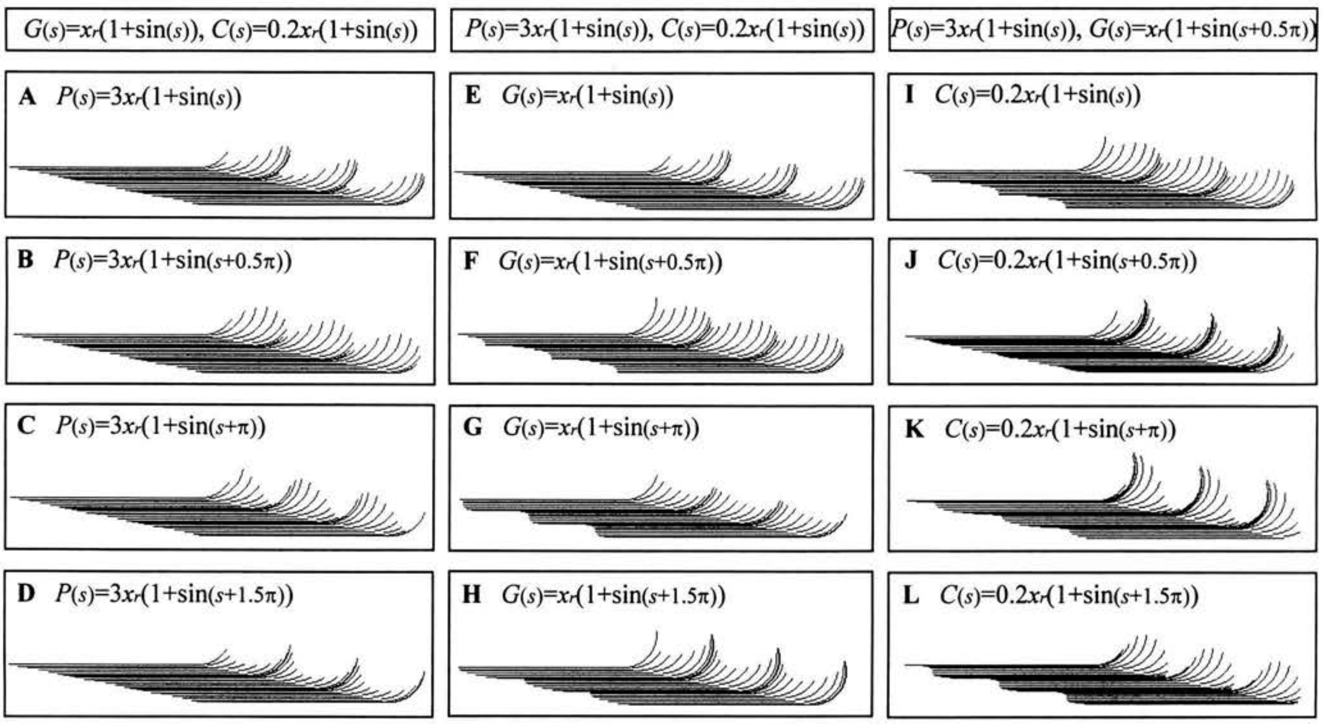

Figure 6. Computer simulations for shell sculpture and increments in the sections showing the effects of phase difference among three oscillating parameters by sine curve functions. The value of x_r represents the X coordinate of the reference point. **A-D.** The effect of *P*(*s*) oscillation is taken into consideration in the case of Figure 5A. Phase of *P*(*s*) fluctuation is deferred from the other two parameters. **E-H.** Fluctuation effect of *G*(*s*) is taken into consideration in the case of Figure 5E. Phase of *G*(*s*) oscillation is deferred from the other two. **I-L.** The effect of *C*(*s*) oscillation is taken into consideration in the case of Figure 5K. Phase of *C*(*s*) fluctuation is different from the others.

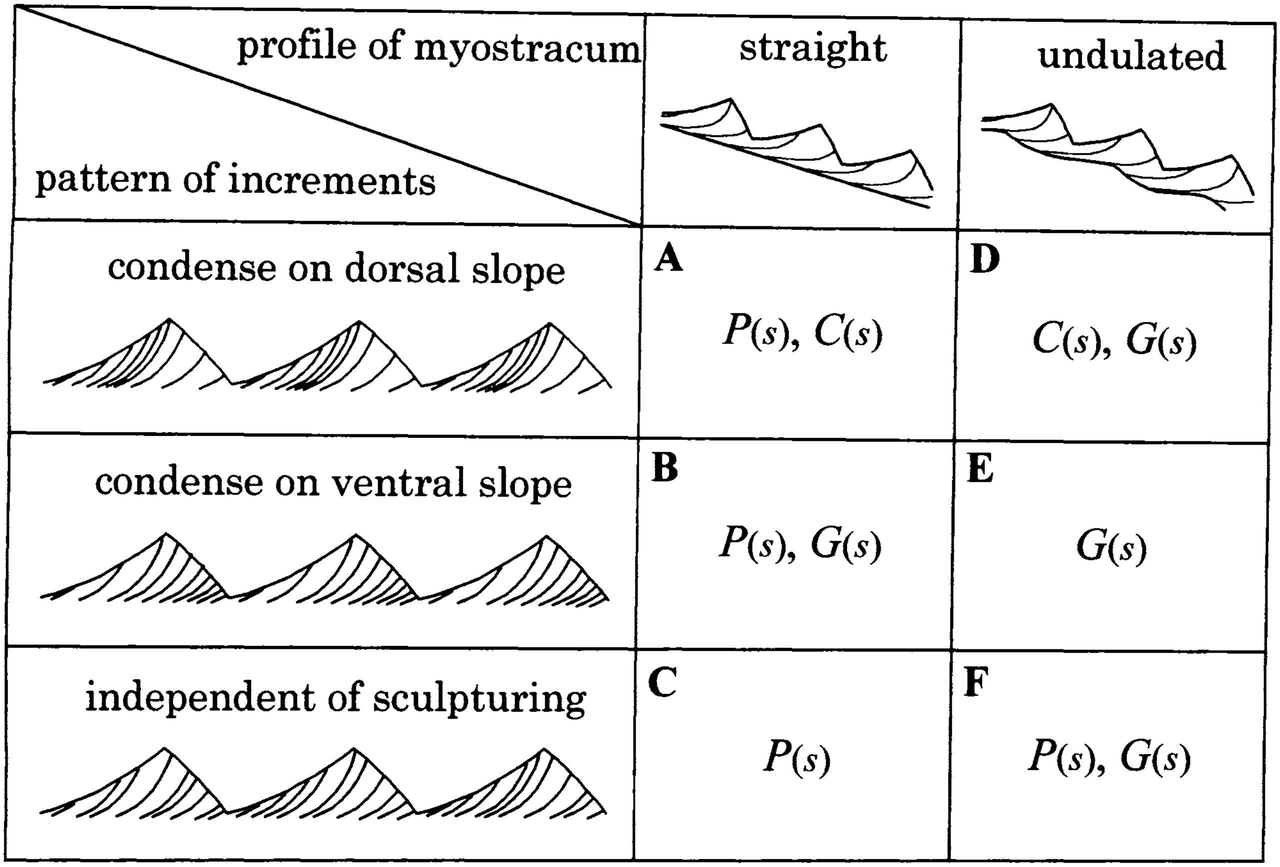

Figure 7. Summary of computer simulations showing what parameters may be effective in shell sculpturing. If myostracum is not wavy in its profile, fluctuation of *P*(*s*) is considered to be a main factor of sculpture construction (A-C), while oscillation of *G*(*s*) may be more effective in shell sculpturing when myostracum becomes wavy (D-F).

of these two parameters compensate each other and *G*(*s*) oscillation causes sculpture formation (Figures 6A, E-H, I). When *G*(*s*) lags 180° in phase behind that of *P*(*s*), effects of fluctuation of them also compensate for each other and fluctuation of *C*(*s*) is the origin of shell sculpturing (Figures 6B, F, I-L). However, in the case of Figure 6C or Figure 6K, the sculpture is regarded to originate by the interaction of *P*(*s*) and *C*(*s*) oscillations since fluctuation effect of *G*(*s*) compensates for those of remaining two parameters. For the same reason, in the case of Figure 6A or Figure 6E, the sculpture is regarded to be produced by the interaction of *P*(*s*) and *G*(*s*) oscillations. Microgrowth increments generally condense on the dorsal slope of the sculpture when phase of *P*(*s*) lags 180° behind that of *G*(*s*) (Figures 6I-L). In other cases, the relationship between the phase of commarginal sculpture and the pattern of microgrowth increments becomes variable and depends upon the phase lag of *P*(*s*) or *G*(*s*) behind the remaining two parameters (Figures 6A-D, E-H).

To sum up the results of the computer simulations, the theoretical spectrum of geometric pattern of the shell section is obtained, and we can identify effective factors on sculpturing for each case when the growth pattern of the microgrowth increment and the morphology of myostracum are given (Figure 7). When the myostracum does not undulate, oscillation of *P*(*s*) caused by mantle extension and shrinkage mainly contributes to sculpture construction (Figures 7A-C). If the myostracum is wavy, oscillation of *G*(*s*) mainly causes the sculpture (Figures 7D-F).

Origin of commarginal shell sculpture with regular type of increments

Although the regular-type increments tend to be densely arranged on the ventral side of the slope or at the furrow of the sculpture in *Arca navicularis, Glycymeris yessoensis, Callista brevisiphonata, Paphia schnelliana, Megacardia ferruginosa* (Figure 2-3), *Solecurtus divaricatus, Timoclea micra* and *Protothaca euglypta*, the pattern of microgrowth increments such as shown in Figure 7 was not found in the specimens examined. The results of computer simulations show that the fluctuation of precipitation rates of the shell *C*(*s*) does not influence the sculpture formation. In addition, in many species with the regular-type increments, the myostracum does not prominently undulate. In this case we can identify the factor of sculpturing as the mantle extension-shrinkage and/or changes in progression rates of the pallial attachment (Figures 7B, C). The undulating myostracum, whose wavy phase corresponds to that of the sculpture, is only found in *Barbatia amygdarumtortum, Meiocardia tetragona* and *Mytilus californianus*. However, such an undulation is generally weak and is not enough to construct a prominent sculpture by itself. In this case, mantle extension-shrinkage movement surely contributes to the sculpture formation (Figure 7C).

In *Isognomon perna, Lamprotula* sp., *Tridonta alaskensis, Codakia tigerina, Mercenaria cyprinoides, Meretrix petechialis* and *Katelysia japonica*, all of which possess two sublayers of different shell microstructure or coloration in the outer shell layer, the boundary between the outermost and middle sublayers often oscillates (Figures 1-2, 1-7). This fact suggests that the relative position of epithelia secreting each sublayer is almost fixed on the mantle during a short period of time, and that the mantle extension-shrinkage movement causes swinging of the boundary between the two clusters of epithelial cells on the mantle edge.

Concluding remarks

From the comparison of the results of computer simulation with microscopic observation of actual specimens, it was made clear that in species with regular-type increments, the commarginal shell sculpture is mainly constructed by mantle extension and shrinkage by blood pressure and pallial muscle contraction, while fluctuations of shell precipitation rates do not affect sculpture formation. On the other hand, in species with undulated-type increments, the commarginal shell sculpture is produced by mantle heaving or bending, the pattern of which cannot be represented by computer simulation in this study. In any case, it is concluded that periodic state change of the mantle-shell relationship associated with sculpture formation originates in elastic deformation of the distal part of the mantle. The above discussion deals with the two-dimensional pattern of the microscopic feature in the radial shell section, but is essentially valid in three-dimensional morphology as far as the commarginal sculpturing is concerned. Since internal growth pattern of the shell is often preserved in fossils, constructional morphology of shell section could reveal the process of the microscopic-level growth and mantle movements of fossil bivalves.

The morphology of external shell sculpture is quite variable in actual specimens. They are strongly influenced by the shape and direction of each microgrowth increment which is constrained by the crystal growth in the shell (Ubukata 1994, 1997). For example, in *Codakia tigerina, Gafrarium tumidum, Anomalocardia brasiliana, Mercenaria stimpsoni, Periglypta puerpera, Fragum unedo*, and *Phacosoma japonicum* (Figure 1-2), ridges are prominently tilted and asymmetrical like saw teeth, and prisms or lamellae radiate from the central longitudinal axis in the outer shell layer (Carter and Clark, 1985; Carter *et al*., 1991); accordingly, a saw like thread is more easily formed in such species by mantle extension and shrinkage. On the other hand, in *Inoceramus uwajimensis, Pinctada margaritifera, Isognomon legmen, Malleus regula, Atrina kinoshitai, Anodonta woodiana*, and *Modiolus modiolus*, for instance, each microstructural unit of the outer shell layer grows from the periostracum to the mantle. In this case, it is easy to program imbricated lamellae by rhythmic mantle extension-shrinkage or plicated folds by periodic mantle bulging or bending (Figure 1-3). The saw like thread sculpture may be suitable for burrowing (Seilacher, 1974), while the imbricated lamellae are considered to resist burial movement but may serves a stabilizing function for shallow burrowers (Stanley, 1970). Plicated folds seem to provide mechanical strength for thin shells (Stanley, 1970). If a close relationship between the commarginal sculpture and habitat exist, functional morphology and diversity of the commarginal sculpture can be attained with variation of mantle behavior in bivalves.

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The enclosing latticed sphere of *Tuscaridium cygneum* (Murray), a eurybathyal phaeodarian Radiolaria, from the North Pacific

HSIN YI LING and STEVEN H.D. HADDOCK

Department of Geology, Northern Illinois University, DeKalb, Illinois 60115, U.S.A.

Marine Science Institute, University of California, Santa Barbara, California 93106, U.S.A.

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Abstract. **Specimens of *Tuscaridium cygneum* (Murray), the eurybathyal phaeodarian Radiolaria, from the eastern temperate North Pacific Ocean were enclosed in an intricate latticed sphere in *in situ* samples. Scanning electron microscopy revealed unique microstructures on the shells of individual radiolarians and on the spheres. Although the function and significance of the enclosing spheres are unknown, colonies of these deep-dwelling, bioluminescent phaeodarians may be common in the world's oceans.**

Key words : Enclosing latticed sphere, eurybathyal phaeodarian, North Pacific, Radiolaria, *Tuscaridium cygneum*

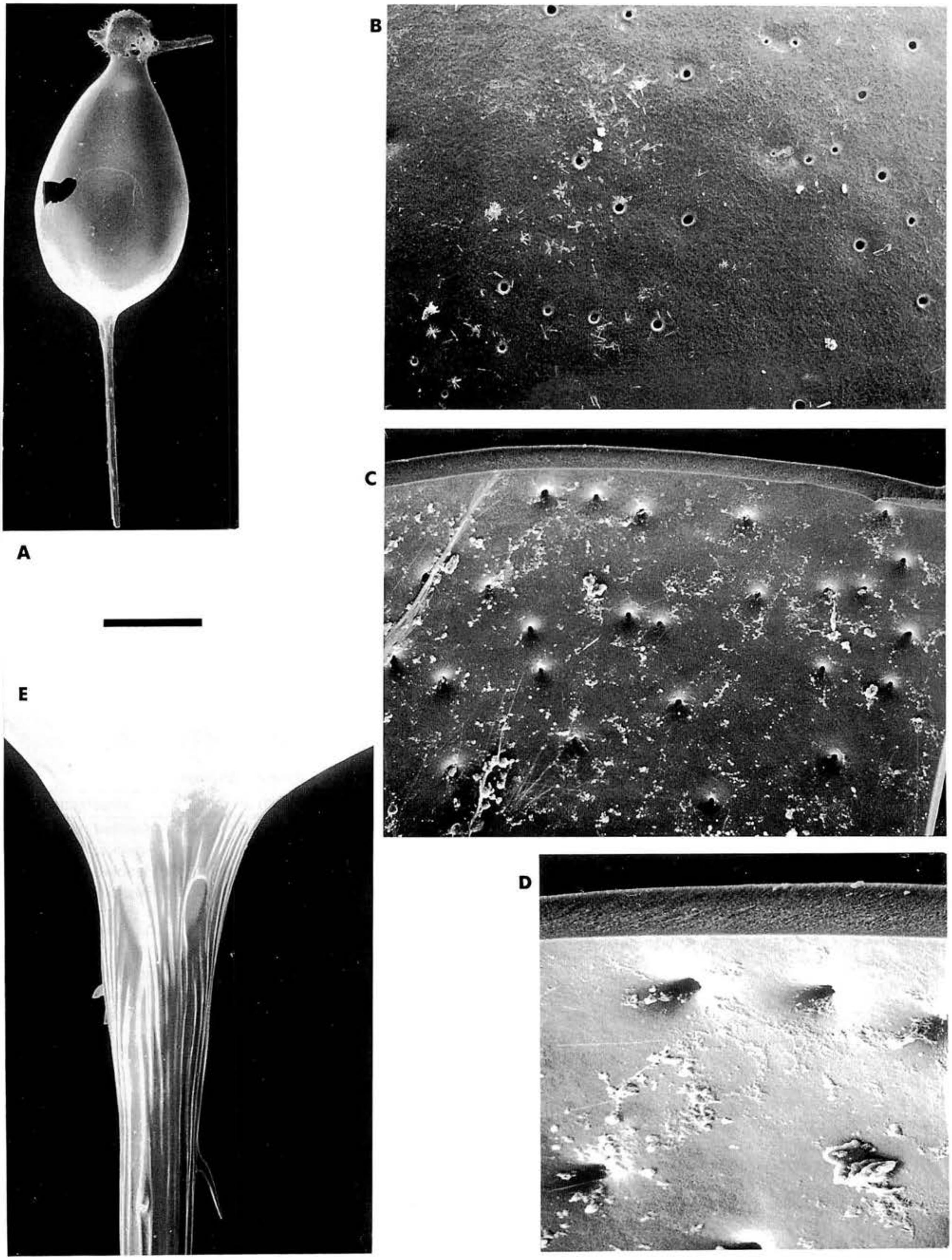
Introduction

The occurrence of phaeodarian radiolarians in the depths of the ocean has been well documented since 1885 (Murray, 1885 ; Haeckel, 1887 ; Haecker, 1904, 1908 ; Reshetnyak, 1966 ; Takahashi, 1987). Furthermore an association of phaeodarians with latticed spheres has been known since the beginning of this century. Haecker (1904, fig. 17 as *Tuscarusa chuni* ; 1908, figs. 222, 223) illustrated some individuals of *Tuscaretta globosa chuni* (Borgert) from the "Antarctic drift" which were attached to the surface of a "shell". He suggested that they were in colonies and that each individual hung to a "shell" of double-layered lattice network. Takahashi's photograph of *Tuscaridium cygneum* from the subarctic Pacific (1987, fig. 11g) shows that some of the 16 individuals associated with a sphere appear to attach to the sphere with their oral end, probably with their long oral spines. Here we report specimens of *Tuscaridium cygneum* which were completely enclosed in a latticed sphere collected off California.

Collection

Specimens were collected on cruises with Dr. James J. Childress, University of California, Santa Barbara, using an opening-closing 10-m^2 Tucker-trawl with a 30-liter thermally insulated closing cod end (Childress *et al*., 1978). Ship speed was kept below 1 knot during the horizontal trawls to minimize damage to specimens caused by the net. This system is effective in recovering fragile deep-sea organisms (e.g. Thuesen and Childress, 1994). Specimens examined in this study were collected in a 2,600 m deep trawl, approximately 160 km west of Point Conception, California (35°01′N, 122°50′W) in March, 1993. Additional specimens were obtained from a depth of approximately 900 m near the same location (34°55′N, 122°57′W). The specimens were always found to be colonial in nature and appeared to be alive when recovered, since upon mechanical stimulation in a shipboard darkroom they produced a blue bioluminescent glow characteristic of photoprotein-bearing radiolarians (Campbell and Herring, 1990 ; unpublished data). The specimens used for SEM were fixed in approximately 4% formalin. The radiolarians are identified as *Tuscaridium cygneum* (Murray).

Figure 1. Microstructure of *Tuscaridium cygneum* (Murray). **A.** A specimen with four incomplete radial tubes at the oral end and a caudal spine. Oral spines are broken off during the preparation. Scale bar = 556 μm. **B.** Outer shell wall with irregularly scattered holes which are the outer ends of the canals. Scale bar = 50 μm. **C.** Solid shell wall (top) and irregularly scattered holes which are the inner ends of the canals. Note elevated areas surrounding the holes. Scale bar = 50 μm. **D.** Details of the shell wall (top) showing the solid, porcellaneous and opaque nature of the wall and irregularly scattered holes which are the inner ends of canals. Note elevated areas surrounding the holes. Scale bar = 26 μm. **E.** Distal end of the shell and a caudal spine. Note lineate surface structure and scattered bristles on the surface. Two pedal pores are visible at the proximal end of the spine. Scale bar = 67 μm.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Taxonomy

Family Tuscaroridae Haeckel, 1887

Original description.—"Phaeodaria with an ovate, spindle-shaped, or nearly spherical shell exhibiting a peculiar solid porcellaneous structure ; with a few radial pores around the base of the hollow tubules, which are symmetrically arranged around the main axis and the mouth. Surface of the shell smooth or spiny, not tabulate nor panelled".

Remarks.—Haeckel (1887, p. 1703) further discussed "... a solid porcellaneous shell, which is perfectly opaque, milky-white or yellowish-white when dried and has a smooth surface (not tabulated or panelled). The shell wall is solid, but is pierced by innumerable very fine pores, which everywhere pierce the thick, apparently solid, fundamental substance of the shell wall".

Genus **Tuscaridium** Haeckel, 1887

Haeckel, 1887, p. 1709 ; Borgert, 1905, p. 108 ; Haecker, 1908, p. 225.

Type species.—T. cygneum (Murray, 1885).

Original description.—"Tuscarorida without radial aboral feet, but with a terminal axial caudal foot, and a variable number of circoral teeth".

Remarks.—Among the three genera of the Family Tuscaroridae, the genus *Tuscaridium* is characterized by its spindle-shaped (vs.ovate or subspherical) outline, its possession of an aboral (=terminal, axial, or caudal) spine (=foot), but the absence of radial aboral feet. (The genus *Tuscarora* bears three equidistant aboral radial feet, while *Tuscarusa* has four equidistant aboral radial feet.) In addition, *Tuscaridium* also possesses four radial tubes, dorsal and ventral pairs, at the oral end, which extend nearly horizontally. The mouth is prolonged into a cylindrical, spinulate proboscis which curves towards the ventral face of the shell (Haeckel, 1887).

Tuscaridium cygneum (Murray, 1885)

Figures 1, 2

Tuscarora cygnea Murray, 1885, p. 226, pl. A, fig. 20.
Tuscaridium cygneum (Murray) Haeckel, 1887, p. 1709-1710.
Tuscaridium lithornithium Haeckel, 1887, p. 1710, pl. 100, figs. 8, 8a.
Tuscaridium cygneum (Murray) Haecker, 1908, p. 226, pl. 26, fig. 204, pl. 32, fig. 243, pl. 33, fig. 254 ; Reshetnyak, 1955, p. 98 ; 1966, p. 163, pl. 1, fig. 3.

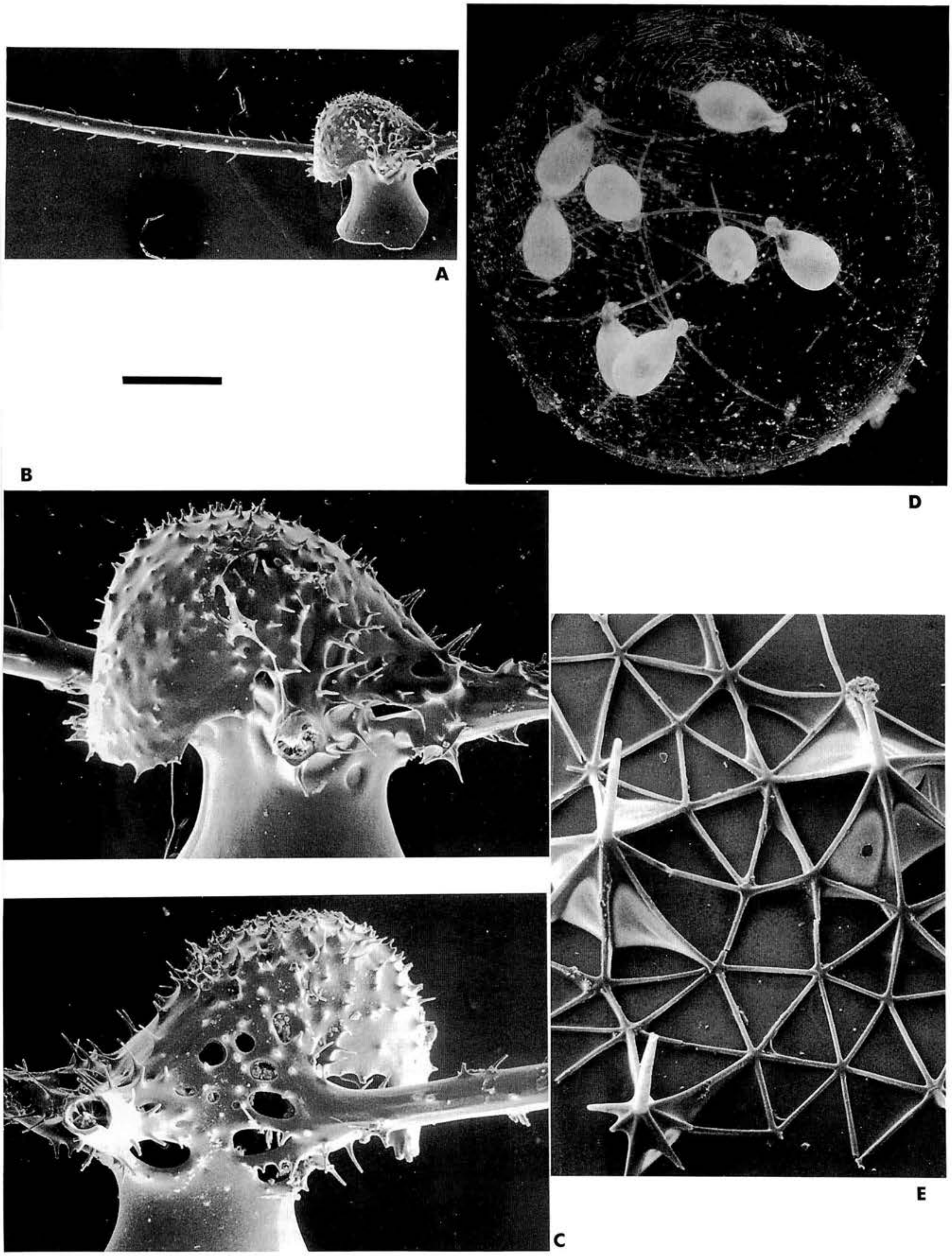
Original description.—"Shell spindle-shaped, twice as long as broad (in the transverse section circular) equally tapering towards both poles of the main axis. The aboral pole bears a thin, cylindrical, straight, caudal spine, placed in the prolongation of the main axis, and about half as long as the shell. Its base is pierced by two large opposite pedal pores. The anterior or oral pole bears a cylindrical peristome, similar to a bird's head, and curved towards the ventral face ; on both sides of its neck (at right and left) a series of three or four irregular, ovate, buccal holes. The neck bears four cylindrical, spinulate, radial tubes (two on each side), crossed nearly horizontally, and placed in two diagonal planes perpendicular one to another ; these planes correspond to those in which four feet of *Tuscarusa* medusa lie. The base of each tube is pierced by four dental pores".

Remarks.—Haeckel (1887) reported two species within the genus from his *Challenger* samples in the tropical Central North Pacific : *T. cygneum* from Station 250 and *T. lithor-*

Table 1. The occurrence and measurements of *Tuscaridium cygneum* (Murray).

Location	Depth (in m)	Length (in mm)	Width (in mm)	Investigator
central North Pacific	5,490	3.6	1.8	Haeckel (1887)
	5,582	3.2	1.6	Haeckel (1887)
equatorial South Atlantic	3,500	2.9-3.0		Heacker (1908)
Northwestern Pacific	50-200, 200-1,000, 1,000-2,000, 4,000-8,000			Reshetnyak (1966)
Okhotsk	3,395	1.43-1.46 (av. 1.44)		Reshetnyak (1966)
Indian Ocean	1,500			Reshetnyak (1966)
eastern Subarctic Pacific	4,200			Takahashi (1987)
off California	900, 2,600	2.70-2.79 (av. 2.74)	1.30-1.37 (av. 1.34)	this paper

Figure 2. Microstructure of *Tuscaridium cygneum* (Murray). **A.** Right ventral view of the cephalis and cylindrical radial tubes with scattered bristles. Scale bar=333 μm. **B.** Details of the oral part and bristly proboscis of the same specimen. Note that all the bristles are located on the top of a slight conical elevation thus appearing as an irregular surface. Also the distal end of the proboscis terminates in irregular scalloped edges and with some needle-like projections. Scale bar=111 μm. **C.** Dorsal left view of the oral part with helmet-like proboscis. Note that the proximal part of radial spines possesses a lineation and bristles on the surface. Scale bar=111 μm. **D.** A colony of eight specimens and the enclosing lattice sphere. Diameter of the sphere is 12.6 mm. **E.** Details of a single-layered geodesic latticed sphere. Note the short spines projecting outward from slightly elevated nodal points and the web among the silica rods. Scale bar=100 μm.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C

nithium from Station 264. Although their overall lengths are similar, *T. cygneum* and *T. lithornithium* differ in (a) the number of dental pores (4 vs. 6~8), (b) the number of pedal pores (2 vs. 4), and (c) the surface of the aboral and apical spines (smooth vs. spiny).

Haecker (1908) noted similarities between specimens he collected from the equatorial South Atlantic and *T. cygneum* described by Haeckel from the Pacific, especially in the exceptionally bristle nature of the peristome and the spine. Despite the small length of his Atlantic specimens as compared to those from the Pacific (2.9-3.0 mm vs. 3.2-3.6 mm), Haecker concluded that all the specimens should be considered conspecific.

Apparently the species has considerable length variations because in the Okhotsk Sea (Reshetnyak, 1966), it ranges from 1.43 to 1.46 mm (average 1.44 mm), while our California specimens range from 2.70 to 2.79 mm (average 2.74 mm : N=5) (Table 1). It also has a wide geographic distribution and is found at a variety of depths (Table 1).

Discussion

Microstructure

In our discussion below, we generally follow the terminology of Haeckel (1887) and Haecker (1908) except for the enclosing sphere (see below). New features recognized based on the present investigation are italicized hereafter. According to Haecker (1908), in the living organism the cephalis is located below while a long single caudal spine points upward. However, in the colony, individuals are apparently randomly oriented within the sphere.

Shells.—The shell is oval to pear-shaped in outline (Figure 1-A). Numerous holes are scattered irregularly all over the surface (Figure 1-B) of the porcellaneous and opaque shell wall (Figures 1-C, D). These are actually the outer ends of the canals which pierce through the solid wall and end as smaller holes on the inner wall with slight inward protrusions (Figures 1-C, D).

The cephalis is covered by an irregular surface with bristles at its top (Figures 2-A-C), which both Haeckel (1887) and Haecker (1908) described as "spiny". A helmet-like proboscis covers the mouth and its distal end terminates in irregular scalloped edges with needle-like projections at each cusp (Figures 2-B, C). Four long cylindrical radial tubes, the oral spines, are divided into right and left pairs. Numerous holes of different sizes are observed both on the peristome (buccal holes of Haeckel) and the proximal part (dental pores of Haeckel) of the tubes (Figures 2-B, C). The very end of the proximal part of the tubes shows lineate ridges but becomes smooth distally, and bristles are scattered along the surface of the tube.

At the aboral end of the specimen, the shell tapers into a long caudal spine with many distinct linear ridges (Figure 1-E) which extend all the way to the distal end. Four oval-shaped pedal pores (Figure 1-E) are located at its proximal end. The surface of the caudal spine is also covered with bristles, but compared to Haeckel's (1887, pl. 100, fig. 8) specimen from the Pacific, they are few in number.

The enclosing sphere.—The interest of the present study, aside from the unusually large size, unique shell structure and morphology, is that all of our specimens are found not individually but are completely enclosed in a latticed sphere (Figure 2-D). This is not only the first such report for the present genus in the California Current, but also the first time we have encountered this throughout our investigations of plankton samples.

For the enclosing sphere, we use the term "latticed sphere" instead of "latticed shell" (=Gitterschale, German of Haecker and Borgert) in order to differentiate the shell (=Schale, German) of an individual Radiolaria. The complete enclosing sphere measures 12.6 mm in diameter. It consists of a single-layered, geodesic-like sphere, formed by cylindrical rods, 0.1 mm in length, which connect into triangles of different sizes. Qualitative spot mode analysis with an energy-dispersing spectrometer indicates that the rods are made of silica, as expected. Short cylindrical spikes project outward from several elevated nodal points where silica membranes form a web among the rods (Figure 2-E).

Although shells of our California specimens are completely enclosed within a single-layered latticed sphere, some shells of this species from the eastern Subarctic Pacific (Takahashi, 1987) are located outside of the sphere with their oral ends toward the sphere.

Such an orientation of the oral end toward or penetrating inside the sphere, while the major part of the shell remains outside, has been observed in other phaeodarians. Haecker (1904, 1908) reported that all the shells of *Tuscaretta globosa* (Borgert) were outside of a double-layered latticed sphere. They attached by sticking both oral spines and the proximal part of their four strongly recurved aboral spines into the sphere (1904, fig. 17 ; 1908, figs. 222, 223) as is the case with *T. passercula* Haecker (1908, fig. 181).

The shells of our specimens are held in position within the sphere by their long spines. The sphere, although fragile, does not collapse if held out of the water (Takahashi, 1987). Because we do not know whether the sphere is filled with sea water or some other fluid, its contribution to the buoyancy of a colony has not been determined.

The mechanism by which the sphere is formed is also not known. Because radiolarians cannot get inside once the sphere has been made, either individuals of a colony are reproduced inside the sphere after its formation (for example, through fission), or the sphere is formed collectively by a group of individuals. The spherical shape of the latticed sphere appears incongruous with the asymmetry of the radiolarians themselves but its formation is probably affected by external physical constraints, just as pressure and surface tension determine the shape of a bubble.

Acknowledgements

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Paleontological Research, vol. 1, no. 2, pp. 150-152, 3 Figs., June 30, 1997

SHORT NOTES

An interesting mid-Cretaceous ammonite from Hokkaido

(Studies of the Cretaceous ammonites from Hokkaido and Sakhalin-LXXIX)

TATSURO MATSUMOTO and NAOKO EGASHIRA

c/o Department of Earth and Planetary Sciences, Kyusyu University, Fukuoka, 812-81 Japan
1353 Yoga-cho, Saga, 840 Japan

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Abstract. In this paper a fairly well-preserverd ammonite is shortly described to show its interesting characters. It is provisionally referred to *Bhimaites* and regarded as a new species. Since it is small even at the adult stage and has a probable trace of lappet, it may represent a microconch of a dimorphic pair. It was found solely from the upper part of the Albian in the Soeushinai area of Hokkaido. More material is, however, required to clarify the extent of variation, to confirm the idea of dimorphism and to know the stratigraphic range and geographic distribution of this species.

Key words: Ammonite, *Bhimaites*, dimorphic pair, Hokkaido, mid-Cretaceous

Introduction

Among a large collection of ammonites from the mid-Cretaceous strata of the Soeushinai area, northwestern Hokkaido, there is a small but interesting ammonite which has not been reported previously. This is a short note on it.

Before going further, we greatly appreciate Yoshitaro Kawashita for his keen sight and also for the generous supply of his acquisition to scientific research. Thanks are extended to Tamio Nishida, University of Saga, for his warm help during the course of field and indoor works related to this study; to C.W. Wright for his kindness in reading an earlier draft with linguistic improvement; to Kazuko Mori for her assistance in preparing the manuscript.

Palaeontological description

Genus ***Bhimaites*** Matsumoto, 1954

Type species.—Ammonites bhima Stoliczka, 1865 (by original designation, Matsumoto, 1954, p. 113).

Remarks.—Because of the degree of morphological similarity, *Bhimaites* could be ranked among the subgenera of *Puzosia* Bayle, 1878. It contains several species of Albian and/or Cenomanian age. A few species have been recorded from the Turonian and possibly from the Coniacian. From the standpoint of phylogenetic divergence, the generic status of *Bhimaites* is kept at least for the time being (see Matsumoto, 1988, p. 21)

Species of *Bhimaites* are rare in the Cretaceous of Japan. *B. takahashii* Matsumoto (1988, p. 107, fig. 47) was a sole example from the mid-Turonian *Inoceramus hobetsensis* Zone in the Obira area (northwestern Hokkaido). Here is another rare but interesting new species which is provisionally referred to *Bhimaites* with a query.

Bhimaites* ? *kawai sp. nov.

Figures 1-3

Material.—GK. H8490 (=YKC061111) from the laminated sandstone (feldspathic wacke) at locality R813 on the River Sounnai from the uppermost part of Member My2, Middle Yezo Group (see Nishida *et al.*, 1996, fig. 2 and fig. 10). This is the holotype. We have endeavored to get more material, but so far we have not been successful.

Diagnosis.—Shell small and discoidal, with moderate involution (about 3/5) and umbilical ratio (1/3). Whorls increasingly compressed with growth. Outer whorl narrowly oval in section with the maximum breadth at one third of height, from where the outer flanks converge gently to arched venter, while the inner flanks are bent abruptly to low but nearly vertical umbilical wall.

Phragmocone nearly smooth. Body chamber occupies about three-quarters of the last whorl. Constrictions fairly frequent on the body chamber, flexuous on the main part of the flank and much projected from the ventrolateral shoulder to the venter. On each interspace of the constrictions a few weak furrows may run roughly subparallel with the constrictions.

Suture rather simple; L as deep as E and rather asymmetric; U2 much smaller than L and tripartite; auxiliaries still smaller and regularly descending.

Specific name.—This species is dedicated to Kawa-san [Mr. Kawa], a friendly nickname of Yoshitaro Kawashita, who found the holotype.

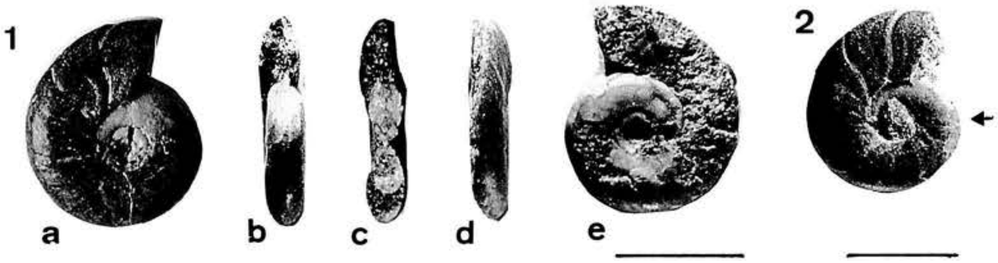

Figure 1. *Bhimaites* ? *kawai* sp. nov. Holotype. GK. H8490 [=YKC061111] from locality R813, Member My2 of the Soeushinai area. **1**. left lateral (a), frontal (b), sectional (c), back (d) and right lateral views, ×1.7. **2**. left lateral view of the same specimen in different light before cleaning the umbilicus, ×1.5 ; arrow : last septum. Bar scales : 10 mm for each of Figs. 1-1, 1-2.

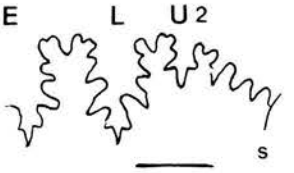

Figure 2. *Bhimaites* ? *kawai* sp. nov. The last third suture (external) of the holotype. E, L. U2 : external, lateral and 2nd umbilical lobes ; s : umbilical seam. Bar scale : 1 mm.

Dimensions.—See Table 1.

Observation.—The holotype is the sole material which is at present available for this species. Although its body chamber is fairly long, the actual apertural margin is not preserved. The trace of the faint furrow in front of the constriction shows a slightly more pronounced lateral convexity than that of the constriction. This seems to suggest the possible existence of a lappeted peristome. For the reason of the small size and the above observation, the holotype may represent a microconch. To confirm this presumption, examples of corresponding macroconchs should be searched out. It is noted that the holotype has a somewhat larger umbilical ratio (U/D) than that of the typical species of *Bhimaites*. This may be due to its small size, corresponding to a juvenile of a normal species of *Bhimaites*. Such a presumption should be examined by a find of macroconchs of this species.

Comparison and discussion.—In the previous literature, there is no species with which the present specimen can be

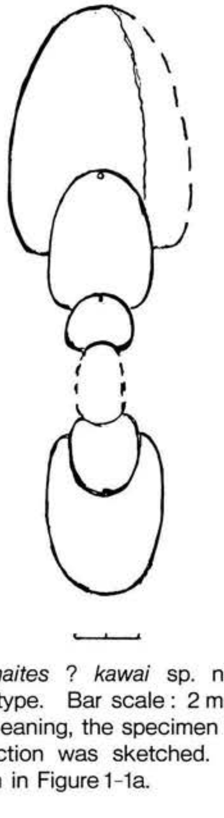

Figure 3. *Bhimaites* ? *kawai* sp. nov. Cross-section (sketch) of the holotype. Bar scale : 2 mm. While the umbilicus was under cleaning, the specimen was cross-cut into halves and the section was sketched. The trace of the fissure may be seen in Figure 1-1a.

Table 1. Measurements of *Bhimaites* ? *kawai*.

Specimen		D	U	U/D	H	H/D	B	B/D	B/H	H/h
Holotype	(E)	16.4	5.4	.33	6.8	.41	4.5	.28	.66	1.33
〃	(E-180°)	12.3	4.0	.33	5.1	.41	3.4	.28	.67	1.31

D=diameter, U=width of umbilicus, H=whorl-height, B=whorl-breadth, h=whorl-height at half a whorl adapical from H ; E=preserved end, E-180°=at half a whorl adapical from E. Measurements of linear dimensions are in mm.

identified. The specimen from the presumed Lower Cenomanian of England, described as *Puzosia* (? *Bhimaites*) sp. by Wright and Kennedy (1984, p. 59, pl. 4, fig. 4; text-fig. 2) has compressed whorls and prorsiradiate constriction. It is, hence, somewhat similar to the Hokkaido specimen described above. It is still septate at its preserved end at a larger diameter (nearly 30 mm) than ours and is less compressed (B/H=0.87 as compared with 0.67 of our holotype) despite its later growth stage. The illustrated suture of the British specimen is rather of a *Puzosia* pattern, whereas that of ours is dissimilar to it, showing a somewhat peculiar feature.

The holotype of *Puzosia decemsulcata* Collignon (1964, p. 56, pl. 332, fig. 1495), from the "Lower Cenomanian" of Madagascar, has frequent constrictions which are prorsiradiate and slightly flexuous on the main part of the flank and markedly projected from the ventrolateral shoulder to the venter. In this respect it is fairly similar to our species, but it is larger (still septate at D=90 mm) and has a larger ratio B/H [0.78] than that of our species. Collignon's species may be referable to *Bhimaites*, but a final conclusion should be deferred, until it is defined more clearly.

As in the case of *Microdesmoceras tetragonum* Matsumoto and Muramoto in the Desmoceratinae (see Matsumoto *et al*., 1972), this species might represent a progenetic dwarf offshoot of *Puzosia*, but we hesitate to propose a new subgenus for the reason of insufficient evidence.

Occurrence.—As for *Material*. Member My2 is referred to the upper part of the Upper Albian (see Nishida *et al*., 1996). The true stratigraphic range and geographic distribution of this species should be determined by further investigations.

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Fukuoka 福岡, Hokkaido 北海道, Obira 小平, Saga 佐賀, Soeushinai 添牛内, Sounnai 早雲内, Yoga-cho 与賀町

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Palaeontological Society of Japan (JSP) Standing Committee Actions

During its meeting on March 8, the JSP Standing Committee enacted the following changes to its membership.

New members elected;

Tuyahiko Fujimoto, Hiroaki Yoshikawa.

Resigned members;

Masayoshi Asaga, Hidehiko Asai, Yukimasa Oho,
Akira Okajima, Naomi Oyama, Kazuhisa Satomi,
Sadako Takeuti.

Deceased member;

Sotoji Imamura.

During its meeting on May 24, the JSP Standing Committee enacted the following changes to its membership.

New members elected;

Kohsaku Arai, Yoshimasa Date, Shinjiro Fujimoto,
Kazuhiko Fujita, Takao Inoue, Toshiyuki Kurihara,
Jianbo Liu, Yuriko Matsumura, Takao Mukuda,
Hiroyoshi Sano, Masahiro Shiraki, Yuji Soeda,
Hiroaki Tanaka, Bunji Tojo, Junichi Uchida,
Atsuko Uchino.

Resigned members;

Ikuo Fujita, Noriyuki Nishida, Morihiko Ofusa,
Japan Energy Development CO., LTD.

行事予定

◎日本地質学会第104年学術大会(福岡)は，日本古生物学会の参加した連合学術大会となります．日本古生物学会は10月10日にシンポジウム「タフォノミーと堆積過程—化石層からの情報解読—」(世話人：小笠原憲四郎，斎藤文紀，増田富士雄，近藤康生，下山正一) を実施いたします．詳細は今後のご案内をご覧下さい．

◎1998年年会・総会は1998年1月30日 (金) ～2月1日 (日) に，神奈川県立生命の星・地球博物館で開催予定です．一般講演の申し込み締め切りは12月5日です．

◎第147回例会は1998年6月に北海道大学で開催する予定です．

1998年年会からの申込先：〒240　横浜市保土ケ谷区常盤台79-2
横浜国立大学教育学部地学教室　間嶋隆一 (行事係)
問い合わせ先　間嶋隆一：Tel. 045-339-3349　Fax 045-339-3264
E-mail majima@ed.ynu.ac.jp
樽　創 (行事係幹事)：Tel. 0465-21-1515　Fax 0465-23-8846
E-mail taru@pat-net.or.jp

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