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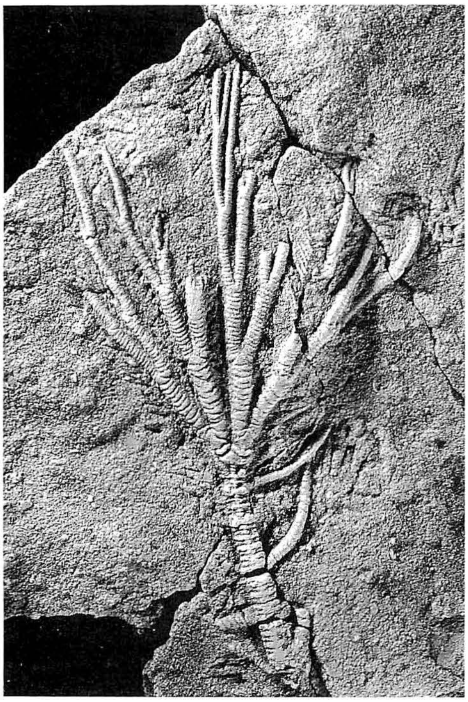

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The fossil on the cover is *Isocrinus* (*Chladocrinus*) *hanaii* Oji, an Early Cretaceous (Aptian) crinoid, which was described from the Hiraiga Formation exposed at Haipe, Tanohata-mura, Shimo-Hei County, Iwate Prefecture, Northeast Japan. (University Museum of the University of Tokyo coll. cat. no. ME6950, paratype specimen, length about 11 cm)

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968. *MEDIARIA MAGNA* YANAGISAWA, SP. NOV., A NEW FOSSIL RAPHID DIATOM SPECIES USEFUL FOR MIDDLE MIOCENE DIATOM BIOSTRATIGRAPHY*

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Abstract. A new fossil diatom species *Mediaria magna* Yanagisawa sp. nov. is described from the lower Middle Miocene Oidawara Formation in Mizunami area, Gifu Prefecture, Japan. Morphologic investigation by light and scanning electron microscopes has revealed that *Mediaria magna* is distinct from *Mediaria splendida* f. *splendida* and *M. splendida* f. *tenera* by its unique characteristics. *M. magna* is of great value in Neogene diatom biostratigraphy because it is easily identifiable even when fragmented and also because it is very short-lived, being restricted to the lower part of the early Middle Miocene *Denticulopsis lauta* Zone (NPD 4A) of the Neogene North Pacific diatom zone (Akiba, 1986). Scanning electron microscopy reveals the presence of a raphe in the genus *Mediaria* for the first time. The genus has a raphe of simple slit without fibulae and therefore it cannot be placed in the order Bacillariales Hendey. It is morphologically similar to some genera in the family Catenulaceae Mereschkowsky in the order Thalassiophysales Mann.

Key words. Diatom, fossil, *Mediaria*, Miocene, Neogene, biostratigraphy.

Introduction

The fossil pennate diatom genus *Mediaria* was erected by Sheshukova-Poretzkaya (1962) as a monotypic genus including only *Mediaria splendida* Sheshukova from the Neogene deposits of north Sakhalin of Far East Russia. About a decade later, Schrader (1973) described an additional member *M. splendida* f. *tenera* from DSDP Hole 173 off California. Since then, *Mediaria splendida* f. *splendida* and its forma *tenera* have been reported from a number of areas in the world, and used as important markers in Neogene diatom biostratigraphy (e.g. Barron, 1985a).

In the course of Neogene diatom biostratigraphic study, I have found another *Mediaria* species which is distinct from the two previously described taxa. In this paper, the new species *Mediaria magna* Yanagisawa sp. nov. is described from the lower Middle Miocene Oidawara Formation in Mizunami area, central Japan on the basis of detailed light and scanning electron microscopic observation. In addition, I have made a light and scanning electron microscopy on *M. splendida* f. *splendida* and *M. splendida* f. *tenera* for comparison. Moreover, the systematic position of the genus *Mediaria* is briefly discussed.

Materials and method

Samples used for this study are as follows:
(1) Samples Mzn 05, 06, 09, 11 and 14 from

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the Oidawara Formation in Mizunami area, Gifu Prefecture, central Japan (Figures 1, 2). The samples were collected by Fumio Yoshida of the Geological Survey of Japan. (2) Sample JDS-11833 from the lower part of the Taga Group, Kitaibaraki, Ibaraki Prefecture, Joban Coal field, northeast Japan, offered by Fumio Akiba of Japan Petroleum Exploration Co. Ltd. (3) Samples from Deep Sea Drilling Project Site 438 (Holes 438A and 438B) (Figure 1).

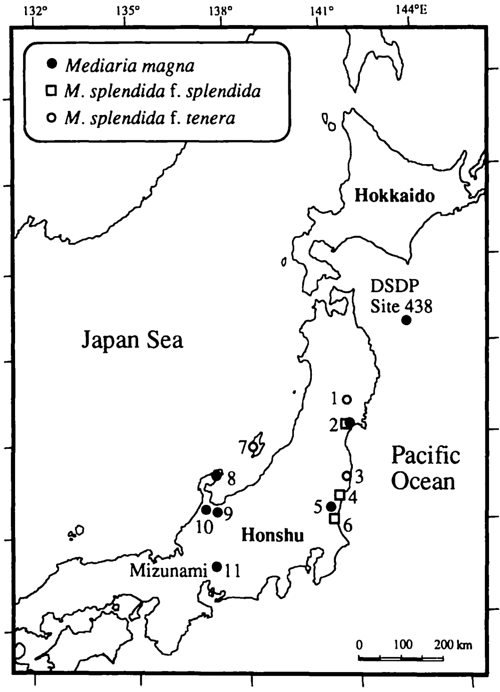


Figure 1. Map showing the locations of *Mediaria magna* Yanagisawa sp. nov., *M. splendida* Sheshukova f. *splendida* and *M. splendida* f. *tenera* Schrader in Japan. DSDP Hole 438 (this study); 1 : Shimokurosawa Formation, Ichinoseki area (Maruyama, 1984); 2 : Otsuka Formation, Matsushima area (Akiba *et al*., 1982); 3 : Taga Group, Tomioka, Futaba area (Yanagisawa *et al*., 1989); 4 : the lower part of the Taga Group, Kitaibaraki, Joban Coalfield (this study); 5 : Genjigawa Formation, Hitachi-ota area (Maruyama, 1984); 6 : Katta Formation, Nakaminato area (Maruyama, 1984); 7 : Nakayama Formation, Sado Island (Hasegawa, 1977); 8 : Hojuji Diatomaceous Mudstone and Awagura Formation, Suzu area, Noto Peninsula (this study); 9 : Higashibessho Formation, Yatsuo area (this study); 10 : Omine Mudstone, Iozen area (Ito, 1986); 11 : Oidawara Formation, Mizunami area (Mori, 1974; Akiba, 1979; this study).

Samples were processed following the method described in Koizumi (1985). A strewn slide for light microscopy (LM) was prepared for each sample on an 18×18 mm cover glass and the cover glass was mounted in Pleurax on a glass slide. For scanning electron microscopy (SEM), diatom valves were picked from dried samples and mounted on sample stages, using one hair of a tiny paint brush under a long-focused objective lens. SEM observation was performed with a JOEL T330A scanning electron microscope at the Geological Survey of Japan.

SEM observation was made on specimens obtained from the Oidawara Formation in Mizunami area. Stratigraphic distribution of this genus was examined in the sequence of Deep Sea Drilling Project Holes 438A and 438B. In this study, samples analyzed by Akiba *et al.* (1982), Maruyama (1984) and Akiba (1986), together with those deposited in DSDP Reference Center in National Science Museum (Tokyo) were re-examined with special attention to the genus *Mediaria*.

The Neogene North Pacific diatom zonation of Akiba (1986) and the classification system of Round *et al.* (1990) are utilized in this paper.

Observation and description

Genus *Mediaria* Sheshukova, 1962

Mediaria magna Yanagisawa sp. nov.

Figures 3-1—3, Figures 4-1—8.

Synonymy : *Mediaria splendida* Sheshukova-Poretzkaya, Mori, 1974, pl. 100, fig. 5; Akiba, 1979, pl. 3, fig. 23; Akiba *et al*., 1982, pl. 2, fig. 34, non pl. 2, fig. 35; Ito, 1986, pl. 3, fig. 9; *Mediaria splendida* Sheshukova-Poretzkaya (robust form), Maruyama, 1984, pl. 12, fig. 17, non pl. 12, fig. 16.

Description. — Valve robust, broadly lan-

Table 1. Characters in *Mediaria* taxa. Numbers in parentheses for *M. splendida* f. *splendida* and *M. splendida* f. *tenera* indicate measurement in original descriptions of the two taxa. Other numbers indicate measurement in this study.

Mediaria taxa	Length (μm)	Width (μm)	Transapical striae in 10 μm	Longitudinal rows in 10 μm
M. splendida f. *splendida*	60- 87 (70-100)	13.5-17 (10-16)	13-14 (13-14)	11-12 (11-12)
M. splendida f. *tenera*	81-115 (70-100)	12-15 (6- 8)	14-15 (15-16)	11-13 (14-15)
M. magna	82-188	22-37	9.5-10	8-10*

* : areolae spacing in each transapical striae.

ceolate with elongate acute apices, 82-188 μm long, 22-37 μm wide (Figure 5, Table 1). Valve face strongly plicated with respect to apical axis ; raphe-bearing side convex, whereas rapheless side concave with the part near the transapical axis being raised (Figure 4-1). A small triangular area near each apex is hyaline and the rest of the valve face is covered with relatively coarse areolae. The areolae are arranged to form transapical striae, 9.5-10 in 10 μm, with areolae in each striae, 8-10 in 10 μm (Table 1). The striae are slightly curved, more radiating toward the apices. The areolae are also arranged in quincunxes on the midway of the valve, but near the raphe-bearing margin, are arranged in two or three longitudinal rows parallel to the margin. Around the transapical axis, the areolae are in an irregular arrangement with several minute areolae (Figure 4-7) Areolae circular or semicircular, somewhat elongated transapically, 0.5-0.65 μm in diameter. Each areola is occuluded by bars parallel to the apical axis, the bars being commonly 3-4 and rarely 5 (Figure 4-8). The areolae of the marginal row along the rapheless margin are conspicuously elongated transapically, 0.7-1.5 μm long, with 4-10 bars (Figure 4-6). Valve mantle is present only along the raphe-bearing side, about 8-9 μm in height. The valve mantle is covered with areolae arranged in four longitudinal rows, which gradually decrease in number toward the apices (Figures 4-1, 4). A raphe, consisting of two simple slits without internal fibulae (Figure 4-3), runs the length of the valve along the border between the valve face and valve mantle. A relatively large terminal pore of the slit, about 1 μm in diameter, opens near each apex (Figures 4-2, 5) and continues internally to form a tubelike structure curving to the valve interior (Figure 4-3). This tubelike structure is probably a kind of helictoglassa (Mann,

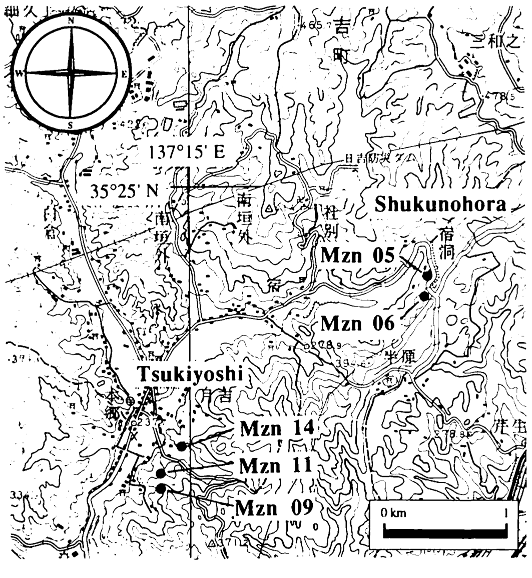


Figure 2. Map showing locations of samples in Mizunami area, Gifu Prefecture, Japan. Mzn 06 : the type locality of *Mediaria magna* Yanagisawa sp. nov. Topographic maps "Minokamo" (left) and "Ena" (right), 1 : 50,000 in scale, Geographical Survey Institute of Japan.

1977), a structure present at the internal raphe end near the pole in many raphe-bearing diatoms (Round *et al.*, 1990).

Holotype. — Figure 3-1 (GSJ F 14585, deposited in the Geological Survey of Japan).

Type sample.— Mzn 06, massive diatomaceous mudstone from the Oidawara Formation of the Mizunami Group, collected by Fumio Yoshida of Geological Survey of Japan from a small road-cut cliff near Shukunohora, Mizunami City, Gifu Prefecture (35°24′31.22″N, 137°16′17.80″E ; Figure 2). The diatom flora of this sample is assignable to the lower part of the Middle Miocene *Denticulopsis lauta* Zone (NPD 4A) of Akiba (1986).

Remarks. — This new species is mainly characterized by its broader and more robust valve as well as its relatively coarser areolation compared with *Mediaria splendida* f. *splendida* and *M. splendida* f. *tenera* (Figure 5, Table 1). The species also differs from the latter two taxa in having elongated and pointed apices, a plicated valve face, rounded areolae, quincunx arrangement of areolae on the valve face and three to five bars in each areola. In fossil samples, the species is commonly found as a small broken fragment, but it is easily identified and distinguished from *M. splendida* f. *splendida* and *M. splendida* f. *tenera* because of its larger areolae and more robust valve wall.

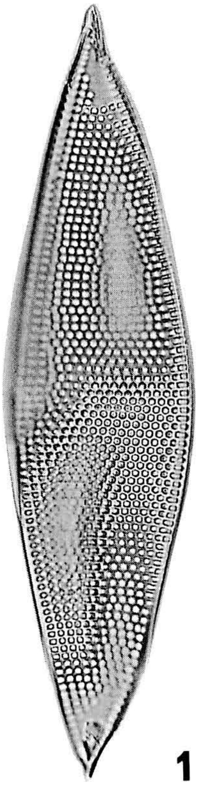
Mediaria magna has been figured previously by many researchers as *M. splendida* (Mori, 1974; Akiba, 1979; Akiba *et al.*, 1982; Maruyama, 1984; Ito, 1986). Among them, Maruyama (1984) was the first to note that this new species is a distinct form different from the more slender form of *M. splendida*. He illustrated this new species as *M. splendida* (robust form).

Stratigraphic occurrence. — *Mediaria magna* is a very short-lived species, with its occurrence confined within the lower part of the early Middle Miocene *Denticulopsis lauta* Zone (NPD 4A) of Akiba (1986) (Figure 6). In DSDP Hole 438A, the first occurrence of this species lies between the first occurrence of *Denticulopsis lauta* (Bailey) Simonsen and the last occurrence of *D. praelauta* Akiba et Koizumi (Figure 7). The last occurrence of *M. magna* approximates or is slightly below the first occurrence of *Cavitatus lanceolatus* Akiba et Hiramatsu. The same stratigraphic occurrence of *M. magna* has been recognized in the Otsuka Formation in Matsushima area, the Higashibessho Formation in Yatsuo area, and the Hojuji Diatomaceous Mudstone and the Awagura Formation in Suzu area (Yanagisawa, unpublished data). The first and last appearance datums of *M. magna* can be estimated at 15.65 and 15.4 Ma, respectively on the basis of the age calibration of Oda (1986) and the sediment accumulation curve in DSDP Hole 438A.

Mediaria magna will provide a most useful and reliable guide to the recognition of the lower part of the *D. lauta* Zone (NPD 4A) because of its limited stratigraphic range as well as its easily identifiable characteristics. This new species, coupled with *Cavitatus lanceolatus* (Akiba *et al.*, 1993) and *Denticulopsis lauta* and its related species (Yanagisawa and Akiba, 1990), can serve to improve the precision and resolution of the Middle Miocene diatom biostratigraphy in the North Pacific (See Figure 7).

Geographic distribution. — At the present,

→ **Figure 3.** Light photomicrographs of *Mediaria*. Scale bar equals 10 μm. **1-3.** *Mediaria magna* Yanagisawa sp. nov., Oidawara Formation, Mizunami area; (1) Holotype, GSJ F14585, Sample Mzn 06, change of focus; (2) Sample Mzn 11; (3) GSJ F14586, Sample Mzn 06. **4, 5.** *Mediaria splendida* Sheshukova f. *splendida*, Sample JDS 11833, the lower part of the Taga Group, Kitaibaraki, Joban Coalfield; (4) GSJ F14589a, change of focus; (5) GSJ F14589b. **6-8.** *Mediaria splendida* f. *tenera* Schrader; (6) GSJ F14589c, Sample JDS 11833, the lower part of the Taga Group, Kitaibaraki, Joban Coalfield; (7) GSJ F14587, Sample Mzn 05, Oidawara Formation, Mizunami area; (8) GSJ F14588, Sample Mzn 05, Oidawara Formation, Mizunami area.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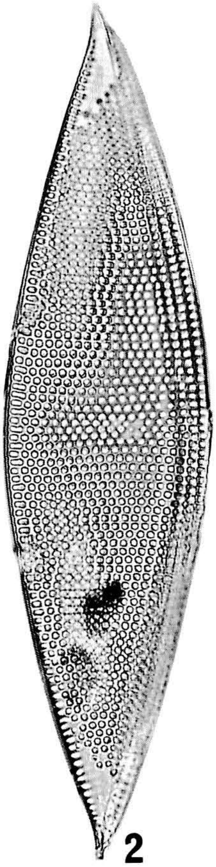
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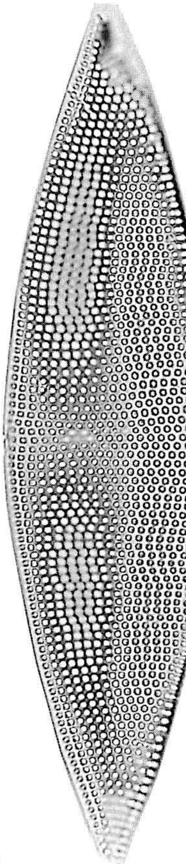
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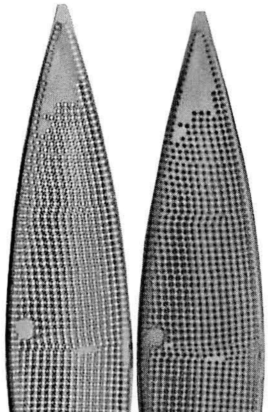
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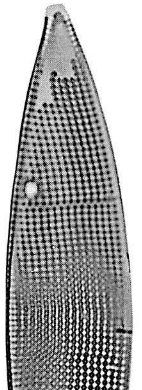
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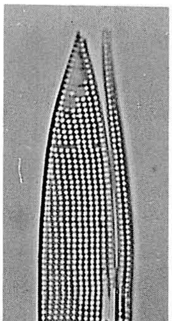
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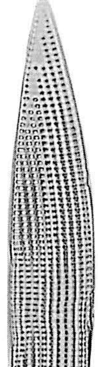
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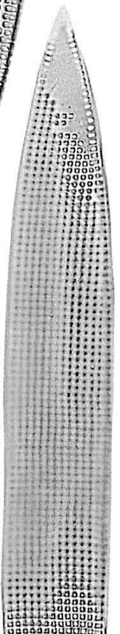
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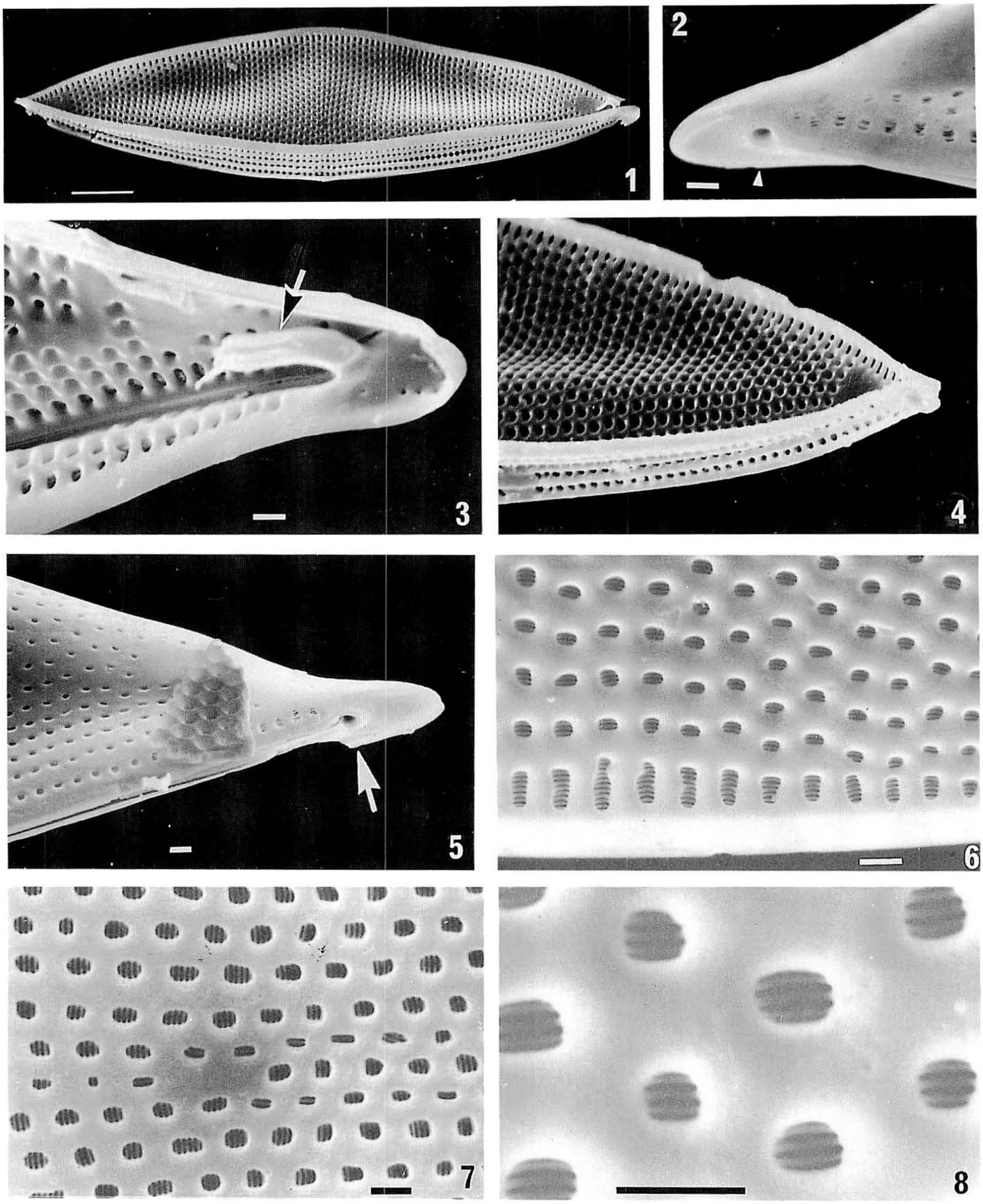

Figure 4. Scanning electron photomicrographs of *Mediaria magna* Yanagisawa sp. nov. Sample Mzn 06, Oidawara Formation, Mizunami area. Scale bars equal 10 μm in Figure 1 and 1 μm in Figures 2–8. **1.** Inner view of valve face and valve mantle. **2.** Outer view of valve apex, showing a terminal pore of raphe (arrow head). **3.** Inner view of valve apex, showing a tube-like structure of raphe (arrow). **4.** Inner oblique view of valve. **5.** Outer view of valve apex. Note a terminal pore of raphe (arrow). **6.** Inner valve surface. **7.** Irregular arrangement of areolae in the middle of the valve face. **8.** Areolae with bars on valve face.

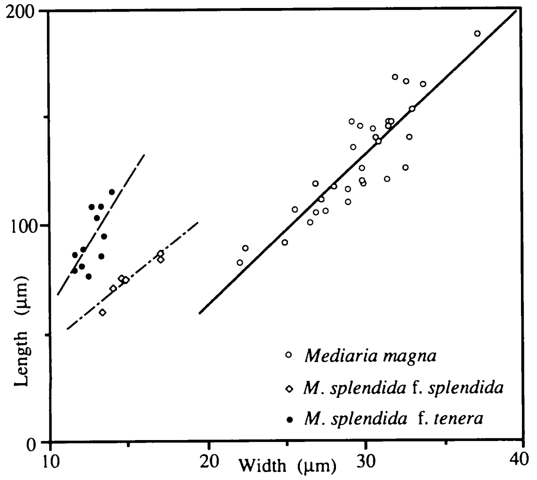

Figure 5. Scatter plot of valve width (W) versus valve length (L) in *Mediaria* taxa. Closed circles: *Mediaria splendida* f. *tenera* Schrader (L = 11.6W-53.1, r = 0.484); Open rhombuses: *Mediaria splendida* Sheshukova f. *splendida* (L = 5.8W-12.6, r = 0.887); Open circles: *Mediaria magna* Yanagisawa sp. nov. (L = 6.9W-75.8, r = 0.802). Specimens of *M. splendida* f. *tenera* and *M. magna* are from the samples Mzn 05, 06, 09, 11, 14 in the Oidawara Formation, Mizunami area, and those of *M. splendida* f. *splendida* are from the sample JDS-11833 in the lower part of the Taga Group, Kitaibaraki, Joban Coalfield.

M. magna has been found only in Middle Miocene sediments in Japan; DSDP Hole 438A (this study), the upper part of the Otsuka Formation in Matsushima area (Akiba *et al.*, 1982; this study), the Genjigawa Formation in Hitachi-ota area (Maruyama, 1984), the Oidawara Formation in Mizunami area (Mori, 1974; Akiba, 1979, this study), the Omine Mudstone in Iozen area (Ito, 1986), the upper part of the Higashibessho Formation in Yatsuo area (this study) and the Hojuji Diatomaceous Mudstone and the Awagura Formation in Suzu area (this study) (Figure 1). Since the genus *Mediaria* is broadly distributed in the world, *M. magna* will very likely be found outside Japan in the future.

Etymology. — The species name is derived from its large size.

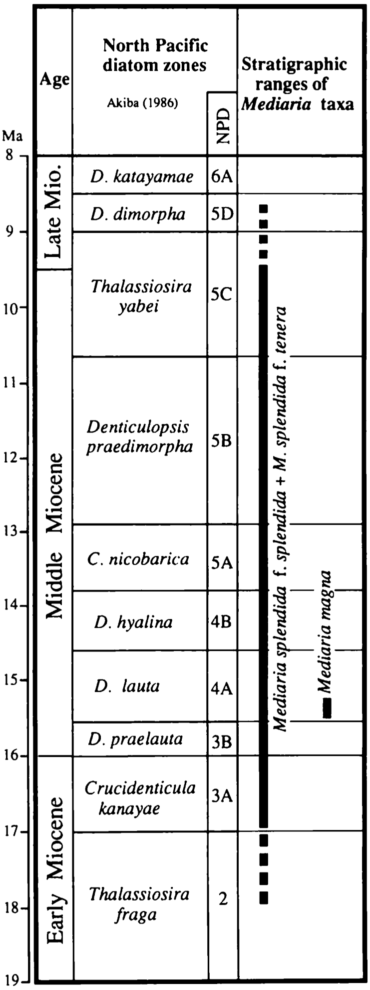

Figure 6. Stratigraphic ranges of *Mediaria* taxa in the western North Pacific.

Mediaria splendida Sheshukova, 1962 f. *splendida*

Figures 3-4, 5.

Sheshukova-Poretzkaya, 1962, p. 210-211, text-fig. 5, plate-fig. 2; 1967, p. 306, pl. 47, fig. 14; pl. 48, fig. 8; Schrader, 1973, pl. 3, figs 14, 15; Koizumi, 1973, pl. 7, figs. 5, 6; Barron, 1976, pl. 1, fig. 21; Baldauf and Barron, 1982, pl. 7, fig. 15; Akiba *et al.*, 1982, pl. 2, fig. 35, non pl. 2, fig. 34; Maruyama, 1984, pl. 12, fig. 16, non pl. 12, figs. 15, 17; Barron, 1985a, p. 786, fig. 12.1; Gersonde and Burckle, 1990, pl. 4, fig. 14.

Synonymy: *Trachysphenia australis* Peit sensu

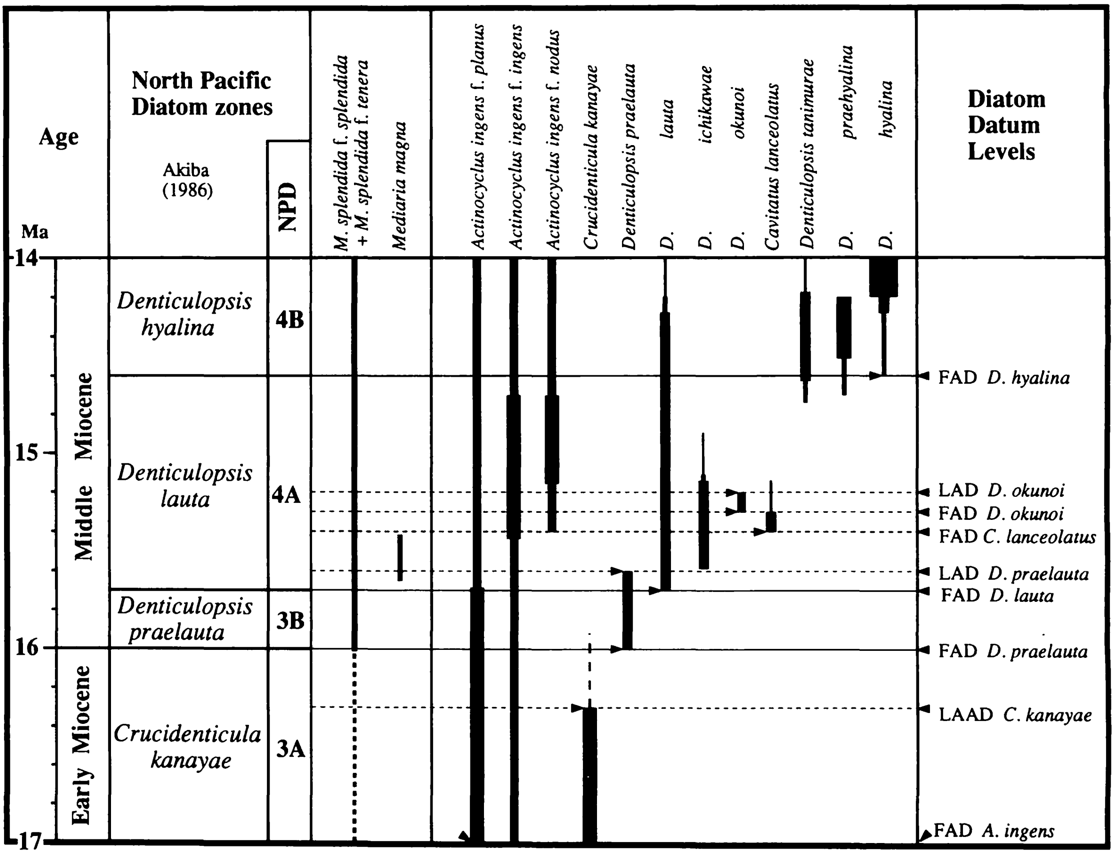

Figure 7. Stratigraphic occurrence of *Mediaria magna* Yanagisawa sp. nov. This figure is made on the basis of stratigraphic analysis of DSDP Holes 438A and 438B. Ages of zone boundaries after Oda (1986). Ages of other diatom datums were estimated by sediment accumulation curve in DSDP Holes 438A and 438B. FAD, LAD and LAAD indicate the first, last and last abundant appearance datums, respectively.

Jousé, 1959, pl. 3, fig. 1 ; 1963, pl. 10, fig. 13 ; *Rhizosolenia* sp. b, Mertz, 1966, p. 23, pl. 5, figs. 5-7.

Observation. — Valve lanceolate with acutely rounded apices. Valve face almost flat, but slightly concave at raphe side. Specimens observed in this study measure 60-87 μm long and 13.5-17 μm wide (Figure 5, Table 1). Valve face covered with fine areolae except for a small hyaline area near each apex. Areolae arranged in transapical rows forming striae, which are slightly curved and more radiating toward the apices. The areolae also form curved longitudinal rows parallel to the raphe-bearing margin. The transapical striae and the longitudinal rows are spaced, 13-14 in 10 μm and 11-12 in 10 μm, respectively (Table 1).

Although this species was not examined by electron microscopy in this study, its fine valve structures may be the same as those of the forma *tenera* described below, because of intimate morphologic similarities between the two taxa.

Remarks. — The forma resembles the forma *tenera*, but differs from the latter by its broader valve outline (Figure 5) and slightly coarser areolation (Table 1). However, the two taxa are hardly distinguishable when they are fragmented. *Mediaria splendida* f. *splendida* differs from *M. magna* by its more slender valve outline (Figure 5), finer areolation and non-quincunx arrangement of areolae.

Stratigraphic occurrence. — In DSDP Holes 438A and 438B, the first occurrence of this species may lie slightly above the base of the *Crucidenticula kanayae* Zone (NPD 3A) of Akiba (1986) (Figure 6). However, the species may range down to the upper part of the *Thalassiosira fraga* Zone (NPD 2) in the Lower Miocene sediments in Boso Peninsula, Japan (Akiba, personal communication, 1992). Its last consistent occurrence is in the *Thalassiosira yabei* Zone (NPD 5C) and its last occurrence lies in the *Denticulopsis dimorpha* Zone (NPD 5D).

Geographic distribution. — Reported occurrences of *M. splendida* f. *splendida* indicate that it is a middle- to high-latitude species (Barron, 1985a). The species has been mainly recorded from the middle-to high-latitude Northern Hemisphere; i.e. from Sakhalin (Jousé, 1959; Sheshukova-Poretzkaya, 1962, 1967), Japan (Barron, 1980, Akiba *et al.*, 1982, Maruyama, 1984), California (Schrader, 1973, 1974a; Barron, 1975, 1976, 1981; Baldauf and Barron, 1982) and the Norwegian Sea (Schrader and Fenner, 1976; Baldauf, 1987). It has also been reported from the Southern Ocean (Schrader, 1976; Ciesielski 1983; Gersonde and Burckle, 1990) and Peru (Mertz, 1966). However, this species has never been documented from tropical regions (e.g. Schrader, 1974b; Barron, 1983, 1985b).

Madiaria splendida f. *tenera* Schrader, 1973

Figures 3-6—8, Figures 8-1—7.

Schrader, 1973, p. 706, pl. 3, fig. 13; Gersonde and Schrader, 1984, p. 101-102, pl. 1, fig. 8.

Synonymy: *Mediaria splendida* Sheshukova-Poretzkaya, Barron, 1976, pl. 1, fig. 22; Schrader and Fenner, 1976, pl. 8, fig. 18; Hasegawa, 1977, p. 55, pl. 25, figs. 1-3; Abbott and Andrews, 1979, p. 246, pl. 4, fig. 2; Abbott and Ernissee, 1983, p. 301, pl. 13, fig. 4; Powers, 1988, pl. 6, fig. 6; Fourtanier and Macharé, 1988, pl. 3, fig. 32; Yanagisawa *et al.*, 1989, pl. 5, fig. 42; *Mediaria splendiaa* Sheshukova-Poretzkaya (slim form), Maruyama, 1984, pl. 12, fig. 15.

Observation. — Valve delicate, narrowly lanceolate with nearly parallel sides in the middle, and with acutely rounded apices (Figures 3-7, 8). Valve face almost flat, but somewhat concave at the raphe side (Figure 8-1). Specimens observed in this study measure 81-115 μm long and 12-15 μm wide (Table 1, Figure 5). According to Schrader's (1973) description, the transapical striae and the longitudinal rows are spaced, 15-16 in 10 μm and 14-15 in 10 μm, respectively, but those of my specimens are slightly coarser; the transapical striae and longitudinal rows are 14-15 in 10 μm and 11-13 in 10 μm, respectively (Table 1). Areolae except for marginal areolae are nearly quadrangular in shape, transapically elongated, ca. 0.2×0.4 μm in size. Each areola is occluded with a narrow bar parallel to the apical axis (Figures 8-5, 6). The areolae of the marginal rows along both margins are elongated transapically, occluded with 3-5 bars (Figures 8-5, 6). Valve mantle is present only at the raphe side (Figure 8-4), with two longitudinal rows of areolae of the same size at those on the valve face (Figures 8-1, 3, 7). A raphe occupies almost the whole valve length along the border between the valve face and valve mantle. It is interrupted at the middle (Figures 8-6, 7), consisting of two simple raphe slits without fibulae. A relatively large terminal pore (about 0.4 μm in diameter) opens near each apex (Figure 8-3), and continues internally to form a tubelike structure which curves to the valve center (Figures 8-2, 4).

Remarks. — This taxon is distinguished from *M. splendida* f. *splendida* by its more slender valve (Figure 5) and slightly finer areolation (Table 1). However, the differences are not so clear that it might be rather difficult to distinguish the two taxa when valves are fragmented to small pieces of punctated plates.

The valve structures of *M. splendida* f. *tenera* are almost the same as those of *M. magna* ; the both taxa have in common such structures as the lanceolate valve outline, the hyaline triangular area near each apex, areolae occuluded with bars, the large terminal pores of raphe and associated internal tubelike structures. However, *M. splendida* f. *tenera* is different from the latter species in having a more slender valve outline (Figure 5), smaller areolae (Table 1) and quadrangular shape of areolae occuluded with a single bar.

Stratigraphic occurrence. — Since *M. splendida* f. *splendida* and *M. splendida* f. *tenera* are hardly distinguishable from each other in moderately or poorly preserved fossil materials where specimens are fragmented, it was difficult to clarify the precise stratigraphic range of *M. splendida* f. *tenera* in DSDP Holes 438 A and 438B.

According to Schrader's (1973) occurrence chart of DSDP Hole 173, *M. splendida* f. *tenera* occurs in the interval from Cores 17-3 to 16-1. On the basis of re-examination of Hole 173 by Barron and Keller (1983), this interval can be placed from the middle part of the late Miocene *Denticulopsis hustedtii* Zone to the upper part of the *Thalassiosira antiqua* Zone of Barron (1981). As this forma has also been reported in the Lower Pliocene Trubi marls of Sicily (Schrader and Gersonde, 1978) and in Upper Miocene Messinian sediments from southwest Spain, Algeria and Sicily (Gersonde and Schrader, 1984), the last appearance of this forma may lie in the Early Pliocene. In Hole 438A, however, no *Mediaria* specimens are found in the Upper Miocene to Lower Pliocene interval. Thus the stratigraphic range of *M. splendida* f. *tenera* appears to be largely diachronous.

Geographic distribution. — This forma has been recorded from various areas in the middle to high latitudes ; DSDP Hole 173 off California (Schrader, 1973), the Monterey Formation in Upper Newport Bay section, California (Barron, 1976), the Shimokurosawa Formation in Ichinoseki area, Japan (Maruyama, 1984), the Taga Group in the Futaba area, Japan (Yanagisawa *et al*., 1989), the Nakayama Formation in Sado Island, Japan (Hasegawa, 1977), the Pisco Formation in Peru (Fourtanier and Macharé, 1988), the Hawthorn Formation of South Carolina and Georgia (Abbott and Andrews, 1979), the Pungo River Formation of North Carolina (Abbott and Ernissee, 1983), Messinian sediments in southwest Spain, Algeria and Sicily (Gersonde and Schrader, 1984), the Lower Pliocene Trubi marls of Sicily (Schrader and Gersonde, 1978), and DSDP Hole 348 in the Norwegian Sea (Schrader and Fenner, 1976).

Discussion

Despite the biostratigraphic utility of the genus *Mediaria,* the taxonomic status of the genus has long been obscure. Sheshukova-Poretzkaya (1962, 1967) reported the presence of a keel (canal raphe) on the valve shoulder of *M. splendida* and hence she placed the genus *Mediaria* in the family Nitzschiaceae Grunow. However, the presence of a keel (canal raphe) cannot be ascertained from her figures and no subsequent diatom study has recognized or mentioned the keel in the species. Probably for this reason, a precise

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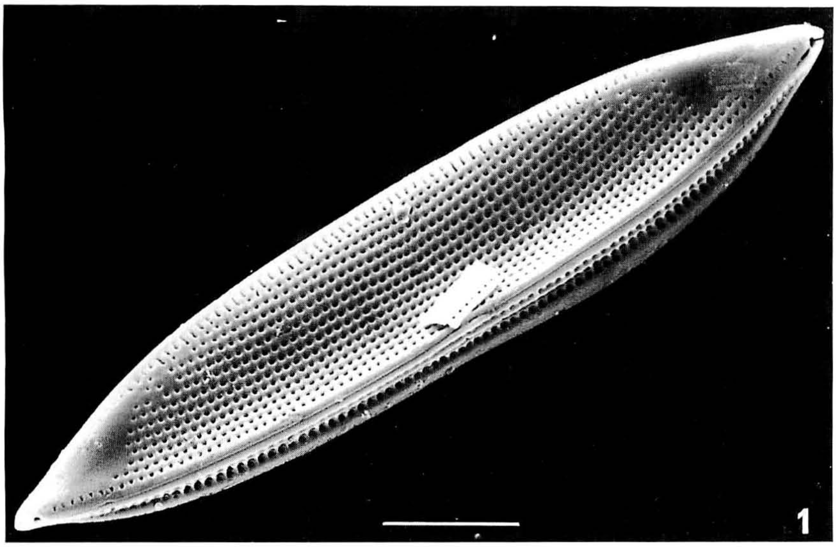
→ **Figure 8.** Scanning electron photomicrographs of *Mediaria splendida* f. *tenera* Schrader. Sample Mzn 06, Oidawara Formation, Mizunami area. Scale bars equal 10 μm in Figure 1 and 1 μm in Figures 2–7. **1.** Outer oblique view of valve. Note a raphe along the shoulder of the valve. **2.** Inner view of valve apex with detached mantle. Arrow head indicates a tube-like structure of raphe. **3.** Outer view of valve apex, showing a terminal pore of raphe (arrow head). **4.** Inner view of valve apex. Note a tube-like structure of raphe (arrow). **5.** Inner view of valve interior. **6.** Outer view of valve surface with interrupted raphe slit. Arrow head indicates the interruption of raphe at the middle. **7.** Outer view of valve face and valve mantle. Arrow head indicates the interruption of raphe at the middle.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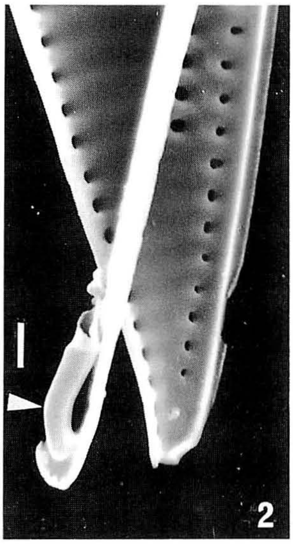
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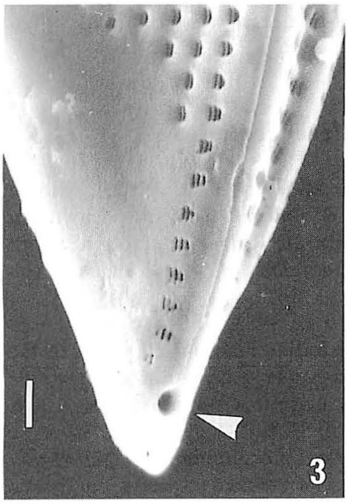
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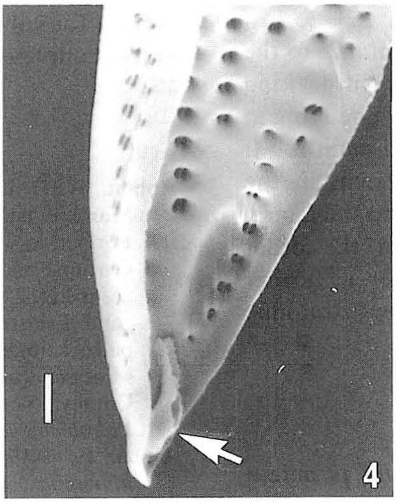
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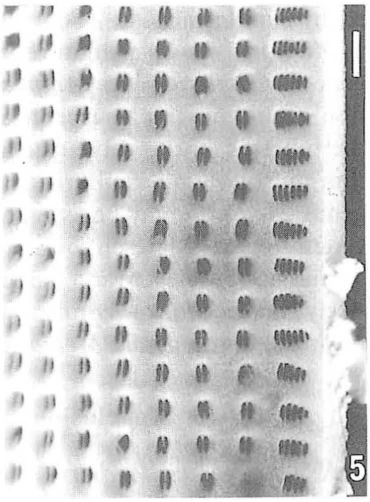
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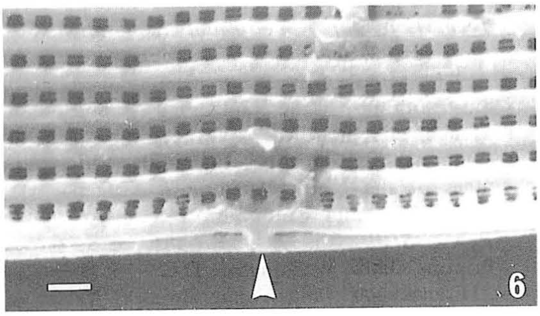
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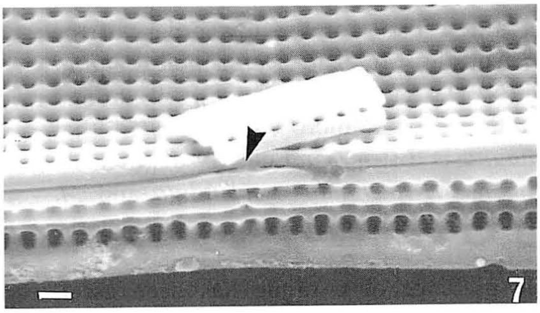
7

systematic position has not been given to this genus in recent diatom taxonomic syntheses (Simonsen, 1979; Round *et al*., 1990).

Scanning electron microscopy by this study has ascertained the presence of raphe in this genus for the first time. As mentioned above, Sheshukova-Poretzkaya (1962, 1967) placed the genus *Mediaria* in the family Nitzschiaceae Grunow (=the order Bacillariales Hendey in Round *et al*., 1990) because of the presence of keel (canal raphe). This study, however, has revealed that the raphe of *Mediaria* is not a canal raphe but a simple fissure without fibulae. Since the presence of fibulae in the raphe is the most characteristic feature of the Bacillariales (Round *et al*., 1990), the genus *Mediaria* can not be included in Bacillariales.

Madiaria shows a slight resemblance to the genera *Catenula* and *Amphora* in lacking fibulae and having an eccentric raphe lying at the junction of the valve face and mantle. If this morphologic similarity is essential, the genus *Mediaria* may be assigned to the family Catenulaceae Mereschkowsky in the order Thalassiophysales Mann. However, further study is needed to confirm the taxonomic position of the genus *Mediaria*.

Conclusion

A new species *Mediaria magna* is herein described, which is very short-lived and useful as an index fossil for the lower part of the early Middle Miocene *Denticulopsis lauta* Zone (NPD 4A) of Akiba (1986). Light and scanning electron microscopy revealed that *M. magna* is distinct and clearly distinguishable from *M. splendida* f. *splendida* and *M. splendida* f. *tenera* by its unique characteristics.

The presence of a raphe has been ascertained in this genus for the first time using scanning electron microscopy. The raphe of this genus is a simple slit without fibulae and therefore the genus cannot be assigned to the order Bacillariales Hendey. It rather resembles some genera in the family Catenulaceae Mereschkowsky in the order Thalassiophysales Mann.

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中期中新世珪藻層序学に有用な化石珪藻の 1 新種 *Mediaria magna* Yanagisawa sp. nov.：海生化石珪藻の 1 新種 *Mediaria magna* sp. nov. を，岐阜県瑞浪市付近に分布する中部中新統生俵層から記載した。また，本種および，常磐炭田の中新統多賀層群から産出した *Mediaria splendida* Sheshukova f. *splendida*，および生俵層から得られた *M. splendida* f. *tenera* Schrader について，光学・走査型電子顕微鏡による観察と形態の比較を行い，それぞれのタクサの特徴を明らかにした。*Mediaria magna* は大型で頑丈な殻を持ち，特有の形態的特徴により他の 2 タクサからは明瞭に区別される。この種は，層序学的産出範囲が中期中新世初期の *Denticulopsis lauta* Zone (NPD 4A) の下部に限定され，生層学的に極めて有用である。なお，*Mediaria* 属に縦溝 (raphe) が存在することが走査型電子顕微鏡による観察の結果，はじめて確認された。本属の縦溝は間板 (fibula) のない単純な構造であり，このことから本属は，間板を持つことを特徴とする Bacillariales 目に含めることはできない。本属はむしろ Thalassiophysales 目 Catenulaceae 科の幾つかの属に似ている。

柳沢幸夫

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969. TAXONOMIC STUDIES OF THE *NEOGONIOLITHON FOSLIEI* COMPLEX (CORALLINACEAE, RHODOPHYTA) IN THE RYUKYU ISLANDS*

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Abstract. Taxonomic studies of the "*Neogoniolithon fosliei* complex" are conducted on the basis of the Recent materials collected from reefs on Ishigaki-jima (Ishigaki Island), the Ryukyu Islands, southwestern Japan. Detailed morphological and anatomical examination reveals that nonarticulated coralline algae comprising the complex are classified into three species: *N. fosliei, N. tenuicrustaceum* sp. nov., and *Neogoniolithon* sp. A. The arrangement of bi-/tetrasporangia in the conceptacle chamber (across the floor or periphery only) or the presence or absence of the central columella is proved to be of potential taxonomic significance for distinguishing *Neogoniolithon* from *Spongites*.

Key words. Coralline algae, *Neogoniolithon, Spongites*, Ryukyu Islands.

Introduction

Neogoniolithon fosliei was first described by Heydrich (1897a) as *Lithothamnion fosliei* based on the specimens from El Tor, Red Sea, and was soon transferred to *Lithophyllum* (Heydrich, 1897b). Foslie assigned this species to *Archaeolithothamnium* (Foslie, 1898) and later to *Goniolithon* (Foslie, 1901). Setchell and Mason (1943) emended the highly confused generic circumscription of *Goniolithon* and differentiated *Neogoniolithon* from it. *Neogoniolithon fosliei* was selected as the type species of the genus *Neogoniolithon*. Lemoine (1911) considered that this species was referable to *Lithophyllum*, but later assigned it to *Neogoniolithon* (Lemoine, 1965, 1966). In these taxonomic studies, including the protolog of the present species, only a few figures were given to show anatomical features. Gordon *et al.* (1976) and Adey *et al.* (1982) gave detailed morphological-anatomical descriptions of *N. fosliei* based on materials from Guam and Hawaii, respectively, falling into disagreements about its outer appearances and internal structures. In the Ryukyu Islands are found nonarticulated coralline algae which can be identified as *N. fosliei sensu* Gordon *et al.* (1976) and *N. fosliei sensu* Adey *et al.* (1982). Moreover, in his experimental study on succession and growth rates of nonarticulated coralline algae, Matsuda (1989) found that *N. fosliei* covered an artificial sub-

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strate placed in an upper forereef environment off Ishigaki-jima. *Neogoniolithon fosliei* in his sense is apparently different from *N. fosliei sensu* Gordon *et al.* (1976) and that of Adey *et al.* (1982).

Consequently, there exists an "*N. fosliei* complex" which comprises *N. fosliei sensu* Gordon *et al.* (1976), *N. fosliei sensu* Adey *et al.* (1982), and *N. fosliei sensu* Matsuda (1989) in the Ryukyu Islands, and thus the question which arises is: Which of the three is *N. fosliei*? The aim of this paper is to clarify such ambiguity in the taxonomy of the *N. fosliei* complex.

Materials and Methods

All the specimens were collected at Ishigaki-jima, Ryukyu Islands (Figure 1). Some of them were dried and the others fixed and preserved in sea water with 8-10% formalin. Fractures of the dried material were coated with gold and then observed with a scanning electron microscope (JEOL-JSM-25SII). Pieces of the fixed materials were decalcified with a 5% trichloroacetic acid- or acetic acid-sea water mixture, dehydrated in a graded series of ethanol or ethanol-normal buthanol mixture, embedded in paraffin, and cut to 10 μm in thickness. Sections were stained in Delafield's haematoxylin and eosin. Permanent slides of *N. fosliei sensu* Matsuda on which the study of Matsuda (1989) was based were also re-examined. Epithallial cell dimensions were measured under an optical microscope and the other cell measurements were made on scanning electron micrographs. These measurements represent the size of cell lumens, not including cell walls. The specimens examined in this study (Table 1) are housed in the Institute of Geology and Paleontology, Faculty of Science, Tohoku University, Sendai (IGPS).

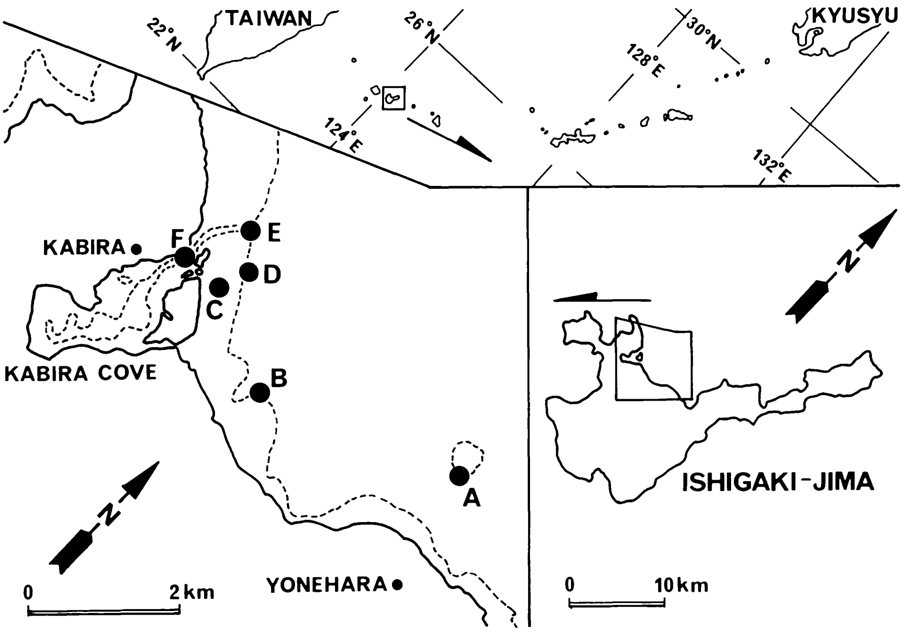


Figure 1. Map showing localities where specimens were collected.

Table 1. List of the specimens examined. All the specimens were collected by Y. Iryu and S. Matsuda, but the samples of IGPS Coll. Cat. Nos. 99310 and 99311 were collected by Y. Iryu and those of IGPS Coll. Cat. Nos. 102469 and 102470 by S. Matsuda.

Species	IGPS Coll. Cat. No.	Depth (m)	Loc.	Date y/m/d
N. fosliei sensu Gordon *et al.* (1976)	100957	8	St. A	1987/7/23
= *N. fosliei*	100958	15	St. A	1987/7/23
	100959	29	St. A	1987/7/23
	100963	29	St. A	1987/7/24
N. fosliei sensu Adey *et al.* (1982)	99310	17	St. A	1985/9/6
= *Neogoniolithon* sp. A	99311	18	St. E	1985/9/12
	99312	15	St. A	1985/9/11
	100964	1	St. C	1987/7/29
	100965	1	St. C	1987/7/22
	100966	5	St. A	1987/7/22
	100967	16	St. A	1987/7/23
	100968	1	St. C	1987/7/29
	100969	1	St. C	1987/7/30
	100970	1	St. C	1987/7/30
	100971	16	St. A	1987/7/23
	100972	5	St. A	1987/7/22
	100973	8	St. A	1987/7/23
	100974	5	St. A	1987/7/22
	100975	16	St. A	1987/7/23
	100976	5	St. A	1987/7/22
	100977	8	St. A	1987/7/23
	100978	1	St. C	1987/7/30
	100979	1	St. C	1987/7/30
	100980	1	St. C	1987/7/30
	100981	12	St. B	1987/7/21
	100982	5	St. A	1987/7/22
	100983	16	St. A	1987/7/23
	100984	16	St. A	1987/7/23
	100985	5	St. A	1987/7/22
	100986	8	St. A	1987/7/23
	100987	8	St. A	1987/7/23
	100988	?	St. A	1987/7/23
	100989	5	St. A	1987/7/22
	100990	5	St. A	1987/7/22
	100991	16	St. A	1987/7/23
	100992	16	St. A	1987/7/23
	100993	12	Sr.A	1987/7/23
	100994	16	St. A	1987/7/23
	100995	16	St. A	1987/7/23
	100996	5	St. A	1987/7/22
	100997	5	St. A	1987/7/22
	100998	8	St. A	1987/7/23
N. fosliei sensu Matsuda (1989)	100999	2	St. A	1987/7/25
= *N. tenuicrustaceum* sp. nov.	101000	2	St. A	1987/7/25
	102459	2	St. A	1987/7/24
	102460	2	St. A	1987/7/25
	102461	2	St. A	1987/7/25
	102462	2	St. A	1987/7/25
	102463	2	St. A	1987/7/24
	102464	2	St. A	1987/7/24
	102465	2	St. A	1987/2/25
	102466	2	St. A	1987/7/24
	102467	2	St. A	1987/7/25
	102468	2	St. A	1987/7/25
	102469	3	St. F	1979/5/14
	102470	3	St. D	1977/10/3

Observations

1. Nonarticulated coralline algae forming the *Neogoniolithon fosliei* complex

a. External appearance

Plants of *N. fosliei sensu* Gordon *et al.* (1976) are anchored to the substratum ventrally by cell adhesion (Figure 2-1). The degree of adhesion varies from full to localized. They consist of a crust, more or less conforming to the contour of the substratum, with a rather flattened to irregularly lobed dorsal thallus surface, never having protuberances or branches. They are thick (up to 5 mm) and extensive (exceeding 20 cm in diameter). The dorsal thallus surface is dull and pale gray to pale pink. The thallus margin is more or less smooth. Large, convex to conical, protruding conceptacles (1,200-1,700 μm in diameter) are scattered over the dorsal thallus surface except for the peripheral part of the thalli. With the scanning electron microscope (SEM) a number of polygonal concavities are observed on the dorsal thallus surface (Figure 2-5). These concavities, termed epithallial concavities (Garbary, 1978), are due to the collapse of epithallial cells during specimen preparation as noted for some other nonarticulated coralline species (Garbary and Veltkamp, 1980; Masaki *et al.*, 1984; Woelkerling *et al.*, 1985; Woelkerling and Irvine, 1986; May and Woelkerling, 1988). Epithallial concavities are evident, and each concavity is lined by ridges in some parts, whereas in the other parts where they are not so distinct very shallow hollows are barely recognized. A pinhole, a trace of the primary pit-connection, can be observed at the center of some concavities. Holes from which trichocyte hairs protruded are scattered among the concavities, not forming distinct fields or clusters.

Plants of *N. fosliei sensu* Adey *et al.* (1982) are firmly attached to the substratum ventrally by cell adhesion and crustose, with a flattened dorsal thallus surface (Figure 2-2). They are up to 3 mm in thickness and do not exceed 15 cm in diameter. The dorsal thallus surface is glossy and minutely rugulose. Color is light pink to pale orange on the vegetative surface, but attaining yellowish spots on conceptacle domes and white to pale yellowish brown patches or rings on scars caused by breaking out of conceptacles. The thallus margin is serrated. Convex to conical, protruding conceptacles (800-1,500 μm in diameter) are dispersed over the dorsal thallus surface. The number of conceptacles is highly variable from specimen to specimen. With the SEM, it is clear that dorsal thallus surface is characterized by numerous, rounded to polygonal epithallial concavities and ridges between the concavities (Figure 2-5). The epithallial concavities of these plants are much deeper and more distinct than those of *N. fosliei sensu* Gordon *et al.* (1976). Holes from which trichocyte hairs emerged are sporadically found among the concavities.

Plants of *N. fosliei sensu* Matsuda (1989) are tightly anchored ventrally to the substratum by cell adhesion (Figure 2-3). They form a crustose thallus less than 500 μm thick and up to 10 cm in diameter. The dorsal thallus surface is not glossy but dull, regulose, and pale yellow to orange yellow. The thallus margin is minutely serrated. Small conical conceptacles evenly scattered over the dorsal thallus surface are numerous, 600-760 μm in diameter. With the SEM, it is observed that the dorsal thallus surface is paved with numerous, polygonal to subrounded, flat, domed or slightly depressed, dorsal walls of epithallial cells, lacking epithallial concavities (Figure 2-6). Such a surface texture indicates that, as shown below, the dorsal walls of the epithallial cells here are much thicker than in the previous cases, which is why they evaded collapse during specimen preparation. A trace of the primary pit-connection is found as a pinhole at the center of some concavities. Holes from which trichocyte hairs emerged are dispersed on the dorsal thallus surface.

b. Anatomy

Thalli are organized in a dorsiventral manner in all cases, viz. *N. fosliei sensu* Gordon *et al.* (1976)., *N. fosliei sensu* Adey *et al.* (1982), and *N. fosliei sensu* Matsuda (1989). In fractures or vertical sections, three regions are easily discernible: epithallium, perithallium, and hypothallium, from dorsum to venter (Figures 3-1, 3-2 and 3-3.)

b-1. Epithallium

Epithallium of *N. fosliei sensu* Gordon *et al.* (1976) consists of a single layer of rounded, subisodiametric to laterally elongated cells with thickening dorsal lateral cell walls, which Adey *et al.* (1982) called cover cells (Figure 3-4). Cells are 6-10 μm long and 7-15 μm in diameter. In the field, it is frequently found, as noted by Gordon *et al.* (1976), that the epithallium of these plants is sloughed off and observed as a semitransparent membrane.

Neogoniolithon fosliei sensu Adey *et al.* (1982) has an epithallium composed of a single layer of cells. Cells are generally rounded and laterally elongated, 4-10 μm long and 7-17 μm in diameter, but they are subisodiametric where the shedding of epithallium and subsequent new cell formation occurs (Figure 3-5). Thickening of dorsal lateral cell walls is not observed and the cell walls are thinner than those of *N. fosliei sensu* Gordon *et al.* (1976) and *N. fosliei sensu* Matsuda (1989), resulting in the most distinct epithallial concavities of the three plants.

Epithallium of *N. fosliei sensu* Matsuda (1989) is formed of a single layer of rounded and laterally elongated cells (Figures 3-6 and 3-7). Cells are domed, with thick dorsal lateral cell walls (up to 10 μm in thickness) which forms convexities on the thallus surface observed with the SEM. The dorsal lateral cell walls are as thick as or thicker than the cell lumina, being up to 10 μm in thickness. Cells are 3-8 μm long and 7-14 μm in diameter.

b-2. Perithallium

Perithallium of *N. fosliei sensu* Gordon *et al.* (1976) is multilayered and its constituent filaments are straight (Figures 3-1, 3-4 and 4-1). Cells are rounded, subisodiametric to vertically elongated, 6-16 μm long and 5-13 μm in diameter. The vertical cell walls of older (=ventral) portions are thick (up to 8 μm) due to heavy calcification, which makes these cells more rounded than those newer (=dorsal) portions. Some cells contain floridean starch granules. Fusions between cells of adjacent filaments are commonly seen.

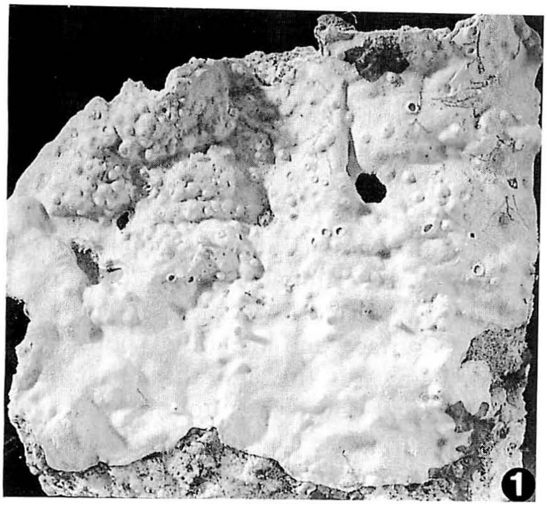
Neogoniolithon fosliei sensu Adey *et al.* (1982) has a multilayered perithallium consisting of undulated filaments (Figures 3-2, 3-5 and 4-2). Cells are somewhat rounded, sub-isodiametric to vertically elongated, 9-20 μm long and 7-15 μm in diameter. Floridean starch granules are contained in some cells. Cell fusions are common.

Perithallium of *N. fosliei sensu* Matsuda (1989) is multilayered and consists of rather straight filaments, cells of which are laterally elongated, subisodiametric or vertically elongated, 8-15 μm long and 5-13 μm in diameter (Figures 3-3, 3-6 and 4-3). Floridean starch granules are rarely found. Cell fusions are commonly seen.

b-3. Trichocytes

The trichocytes of *N. fosliei sensu* Gordon *et al.* (1976) are arranged in vertical columns at the thallus surface or within the perithallium, not forming lateral fields or clusters (Figures 3-1 and 3-4). The abundance of

→ **Figure 2.** Habit (1, 2, and 3) and scanning electron micrographs of thallus surfaces (4, 5, and 6). Note holes from which trichocyte hair cells emerged (arrow) and traces of primary pit connection, each of which is observed as a pinhole at the center of epithallial concavity (arrow head). **1**: *Neogoniolithon fosliei sensu* Gordon *et al.* (1976), IGPS Coll. Cat. No. 100958. **2**: *N. fosliei sensu* Adey *et al.* (1982), IGPS Coll. Cat. No. 99310. **3**: *N. fosliei sensu* Matsuda (1989), IGPS Coll. Cat. No. 102459. **4**: *N. fosliei sensu* Gordon *et al.* (1976), IGPS 100957. **5**: *N. fosliei sensu* Adey *et al.* (1982), IGPS Coll. Cat. No. 100966. **6**: *N. fosliei sensu* Matsuda (1989), IGPS Coll. Cat. No. 100999.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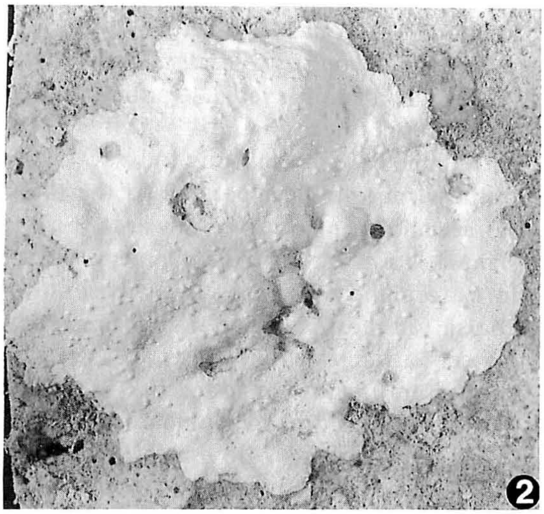
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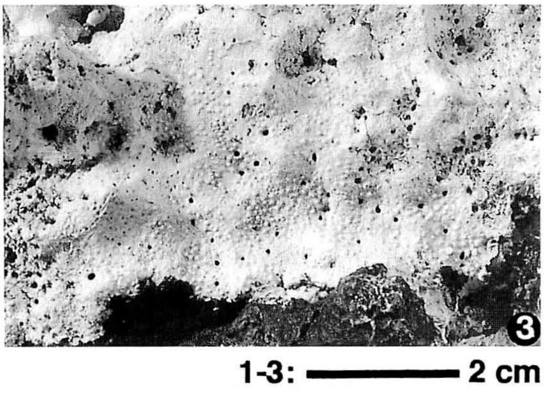
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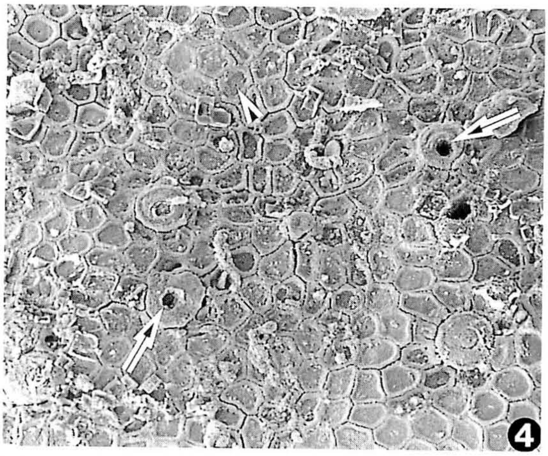
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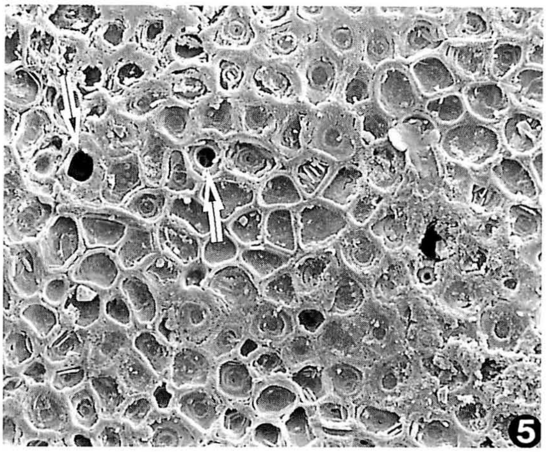
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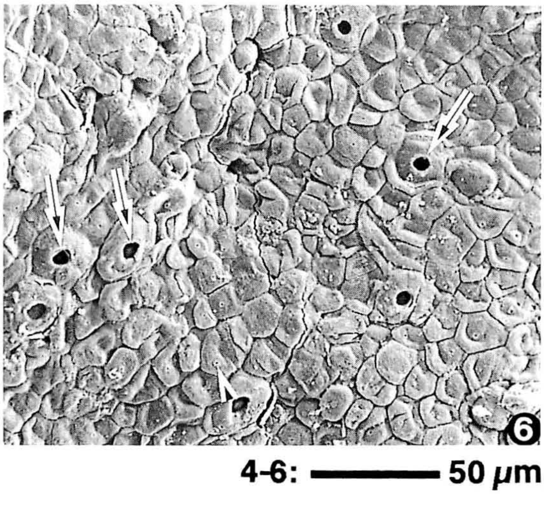
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1-3: 2 cm

4-6: 50 μm

trichocytes in the plants is variable from specimen to specimen, but they are found in all the specimens examined in this study. Up to 20 trichocytes are arranged in each column, the cell size of which is 6-27 μm length and 14-22 μm in diameter. A terminal trichocyte in the column is two-celled, vertically elongated, and larger in cell size than lower subisodiametric to laterally elongated cells, when observed at the thallus surface. It is evident in *N. fosliei sensu* Gordon *et al.* (1976) that the trichocytes persist after epithallial and perithallial cells are produced from them and after sinking into the perithallium they never degenerate or are filled with endogenously orginating filaments of perithallial cells, unlike *Neogoniolithon notarisii* (Foslie) Setchell et Mason (Cabioch, 1971).

Neogoniolithon fosliei sensu Adey *et al.* (1982) has trichocytes arranged in vertical columns at the thallus surface or within the perithallium (Figure 3-5). All the plants examined have trichocytes, although their abudance varies. Up to 10 trichocytes are arranged in a column. Each of the columns at the thallus surface consists of a terminal trichocyte which is two-celled and vertically elongated, and lower subisodiametric to laterally elongated cells, where the cell size of the terminal trichocyte is much larger than that of the lower cells. Cells are 4-34 μm long and 6-28 μm in diameter. Thichocytes persist after burial in the perithallial tissue.

All the plants of *N. fosliei sensu* Matsuda (1989) have trichocytes arranged in vertical columns, where up to 10 cells are observed (Figures 3-7 and 4-3). A terminal trichocyte in the column at thallus surface is two-celled, vertically elongated, and larger than those of lower subisodiametric to laterally elongated cells. Cells are 7-29 μm long and 12-29 μm diameter. Thichocyte hairs are multicelled, up to 80 μm long and ca. 5 μm in diameter (Figure 3-7). Trichocytes persist after sinking into the perithallium.

b-4. Hypothallium

Hypothallium of *N. fosliei sensu* Gordon *et al.* (1976) is multilayered and up to 400 μm in thickness (Figures 3-1 and 4-4). In longitudinal section, the proximal portions of filaments are more or less parallel to the thallus surface and the distal portions are curved upwards (towards the dorsal thallus surface) and downwards (towards the ventral thallus surface). The filaments form recumbent, convexly arching tiers of cells (coaxial). Cell fusions are common. Cells are 4-35 μm long and 8-15 μm in diameter.

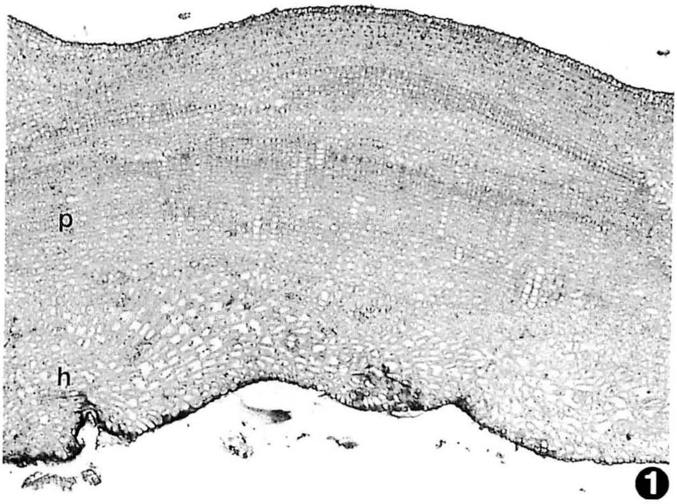
Neogoniolithon fosliei sensu Adey *et al.* (1982) has a multilayered hypothallium less than 250 μm thick (Figure 4-5). Its constituent filaments are, in longitudinal section, initially more or less parallel to the thallus surface and become curved upwards or merely slanted downwards. The filaments do not form recumbent arching tires of cells (noncoaxial) in most part, but an occasional coaxial cell arrangement is observed where the substratum is more or less depressed (Figure 4-6). Cell fusions are common. Cells are 12-42 μm long and 7-16 μm in diameter.

Hypothallium (Figures 3-3 and 4-7) of *N. fosliei sensu* Masuda (1989) is multilayered, noncoaxial, and much thinner (less than 120 μm thick) than those of *N. fosliei sensu* Gordon *et al.* (1976) and *N. fosliei sensu* Adey *et al.* (1982). Cell fusions are common. Cells are 9-40 μm long and 5-16 μm in diameter.

b-5. Reproductive tissue

Tetrasporangial conceptacles of *N. fosliei sensu* Gordon *et al.* (1976) are uniporate.

→ **Figure 3.** Vertical sections through thalli (1, 2, and 3) and the uppermost parts of perithallia (4, 5, 6, and 7). The letters "e", "i", "p" and "h" indicate epithallium, intercalary meristem, perithallium, and hypothallium, respectively. Note trichocytes in vertical columns (arrow) and trichochyte hair (7). **1** and **4**: *Neogoniolithon fosliei sensu* Gordon *et al.* (1976), IGPS Coll. Cat. No. 100958. **2** and **5**: *N. fosliei sensu* Adey *et al.* (1982), IGPS Coll. Cat. No. 99311. **3**, **6**, and **7**: *N. fosliei sensu* Matsuda (1989), IGPS Coll. Cat. No. 102470.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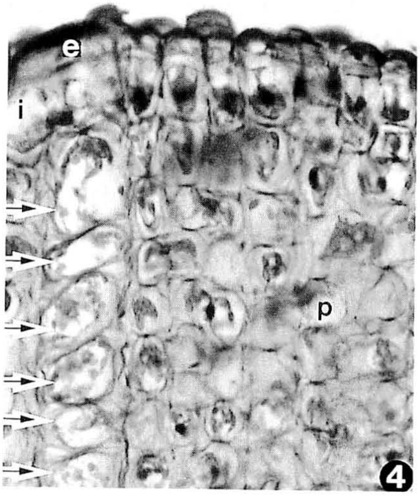
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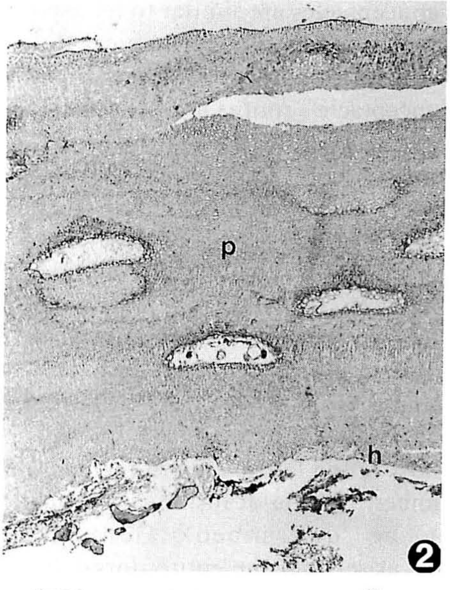
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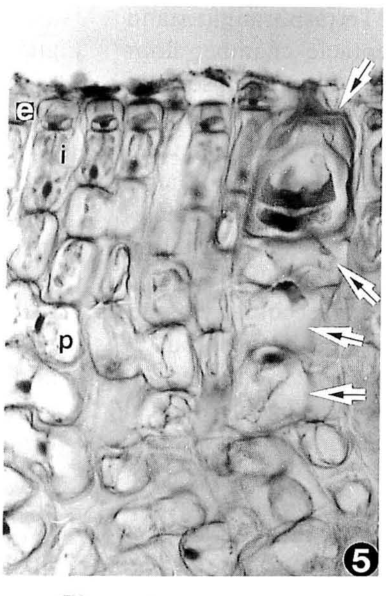
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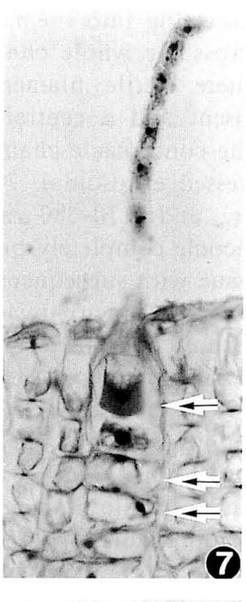
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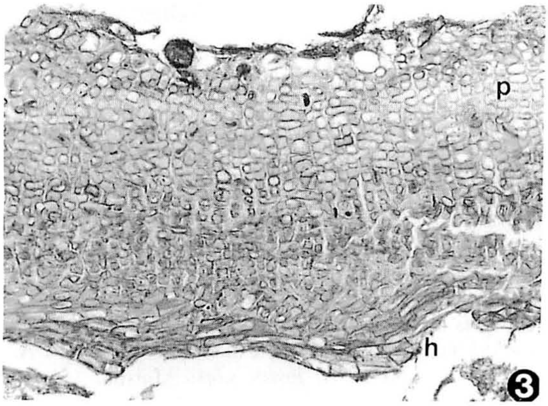
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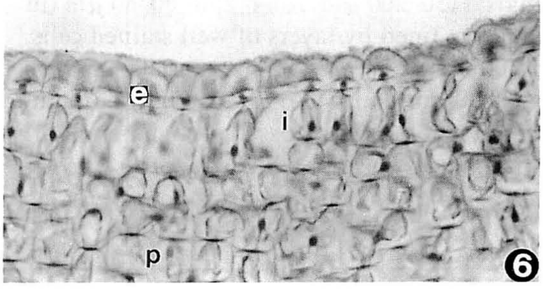
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1: 250 μm 3: 100 μm

2: 500 μm 4-7: 30 μm

Their roofs are raised conspicuously above the surrounding thallus surface, showing a conical outer appearance (Figure 5-1). Anatomically, conceptacle roofs consist of filaments which originate from an area surrounding the conceptacle floor (=fertile area) and terminate at pore canals. Cells forming the roofs are disposed concentrically in the lower part of the roofs adjacent to the upper conceptacle walls, which show a coaxial cell arrangement in the hypothallium. Mature conceptacles have roofs which are 25-38 cells thick. Pore canals (300-500 μm long and 70-200 μm in diameter) are lined by well stained cells which are orientated perpendicular to or at an acute angle with the canals and projecting into them. Tetrasporangia stand across the whole conceptacle chamber floor where sterile filaments or paraphyses are absent and a central columella is missing. The conceptacle chambers are laterally compressed ellipsoidal, 760-1,040 μm in diameter, and 170-380 μm high. Conceptacles become completely buried in the perithallial tissue with subsequent vegetative growth and some of them are invaded by secondary tissue. Sexual conceptacles have not been found.

Neogoniolithon fosliei sensu Adey *et al.* (1982) has asexual conceptacles, anatomical features of which are the same as those of *N. fosliei sensu* Gordon *et al.* (1976), except for having sterile filaments among the tetrasporangia (Figures 5-2 and 5-3). Mature conceptacles have roofs 12-15 cells thick, pore canals (150-200 μm long and 60-80 μm in diameter) lined by layers of well stained cells, and laterally compressed ellipsoidal chambers (550-890 μm and 140-170 μm high) containing tetrasporangia across the chamber floor. Conceptacles become buried and some of them are invaded by secondary tissue. Female conceptacle roofs are produced by circumconceptacular filaments which grow to form extremely laterally compressed conical chambers. The roofs are 12-17 cells thick at pore canals which are 40-160 μm long and up to 100 μm in diameter and lined by well stained cells orientated more or less perpendicular to the canals (Figure 6-1). Chambers are 440-710 μm in diameter and 100-190 μm high, and each of them contains several tens of supporting cells across the chamber floor. The supporting cell has one or two carpogonial filaments, each of which consists of a lower hypogynous cell and a terminal carpogonium. Some carpogonia were seen with trichogynes (Figure 6-2). Carposporangial conceptacles are similar to tetrasporangial conceptacles in such anatomical features as roof structure and pore structure (Figure 6-3). Conceptacle roofs are conspicuously raised above the surrounding thallus surface and consist of 11-15 layers of cells. Pore canals are 100-130 μm long and up to 80 μm in diameter. Chambers are 490-780 μm in diameter and 140-160 μm high, and contain carposporophytes. Mature carposporophytes consist of a fusion cell, several-celled gonimoblast filaments, and terminal carposporangia (Figure 6-4). A fusion cell is thin, continuous, and irregularly shaped, covering most of the fertile area in the conceptacle chamber. Mode of fusion cell formation cannot be determined. Gonimoblast filaments arise from the entire dorsal surface of the fusion cell. Male conceptacles have not been found.

Asexual conceptacles of *N. fosliei sensu* Matsuda (1989) show the same anatomical features as those of *N. fosliei sensu* Gordon *et al.* (1976) (Figures 5-4 and 5-5). The plants examined in this study contain bisporangia,

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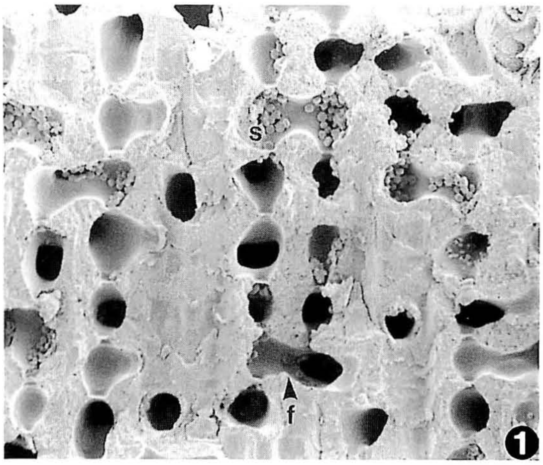
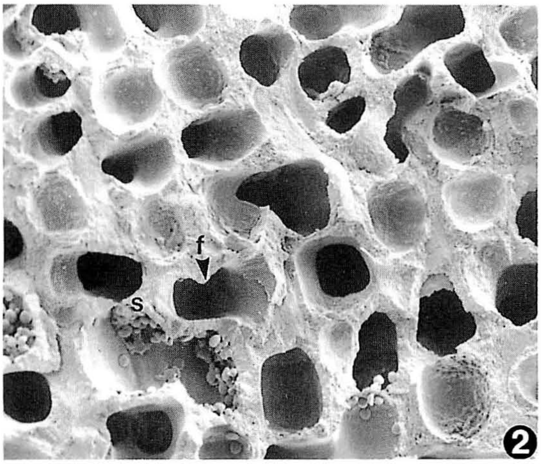
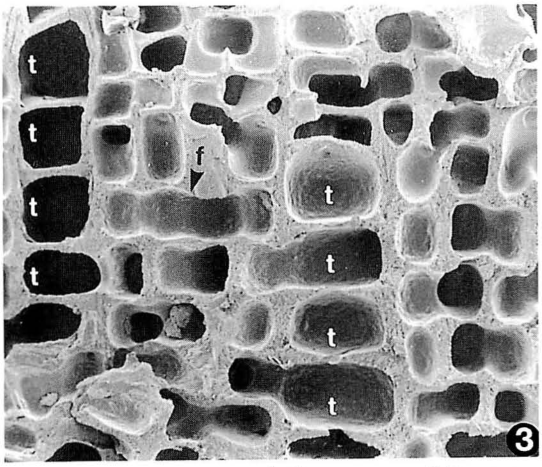
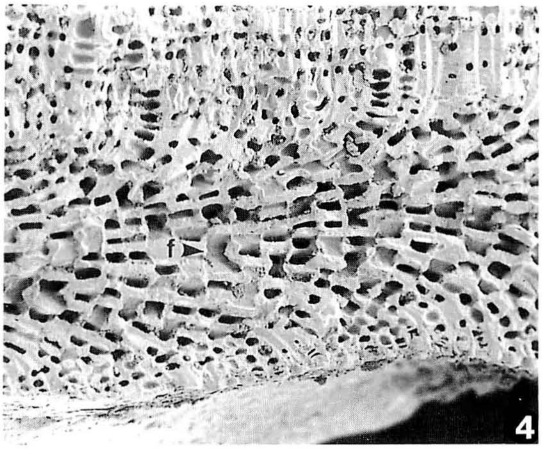
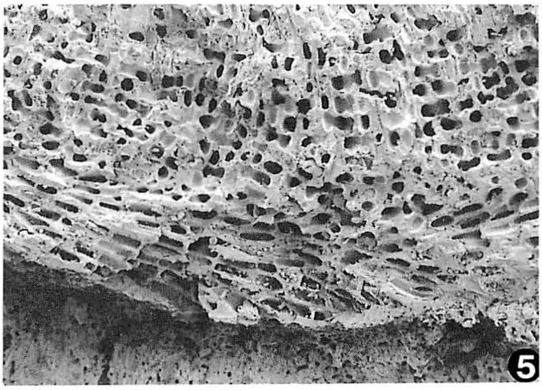
→ **Figure 4.** Scanning electron micrographs of epithallia (1, 2, and 3) and hypothallia (4, 5, 6, and 7). Note cell fusions (f), floridean starch gravels (s), and trichocytes (t) in vertical columns buried in perithallial tissues. **1** and **4**: *Neogoniolithon fosliei sensu* Gordon *et al.* (1976), IGPS Coll. Cat. No. 100959. **2**: *N. fosliei sensu* Adey *et al.* (1982), IGPS Coll. Cat. No. 100964. **3** and **7**: *N. fosliei sensu* Matsuda (1989), IGPS Coll. Cat. No. 100999. **5** and **6**: *N. fosliei sensu* Adey *et al.* (1982), IGPS Coll. Cat. No. 100965.

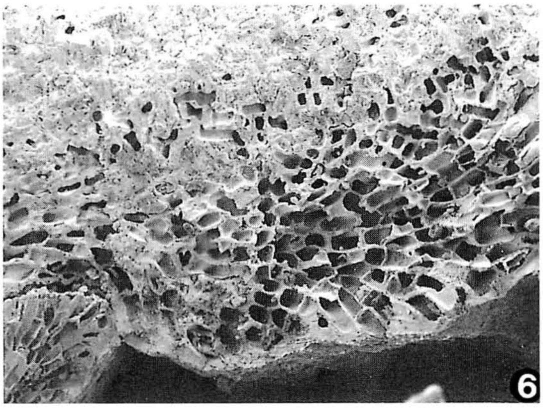




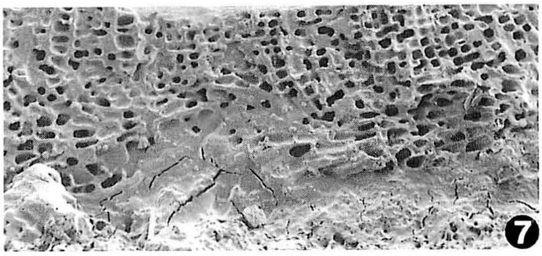








1-3: —— 20 μm
4-7: —— 100 μm



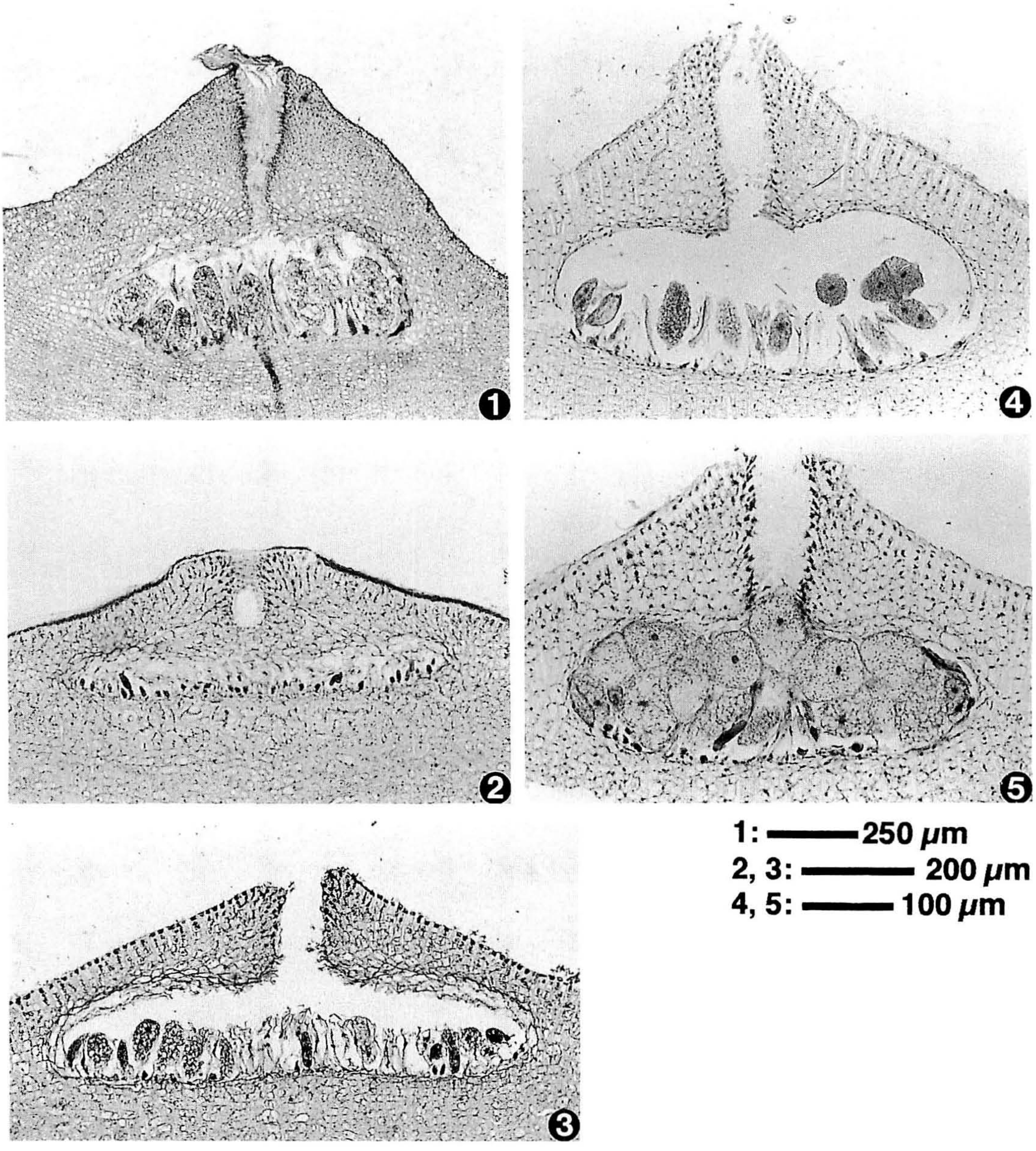


Figure 5. Asexual conceptacles (1–5). **1**: Mature tetrasporangial conceptacle of *N. fosliei sensu* Gordon *et al*. (1976), IGPS Coll. Cat. No. 100958. **2**: Stage in tetrasporangial conceptacle development of *N. fosliei sensu* Adey *et al*. (1982), IGPS Coll. Cat. No. 100998. **3**: Mature tetrasporangial conceptacle of *N. fosliei sensu* Adey *et al*. (1982), IGPS Coll. Cat. No. 100998. **4** and **5**: Mature bisporangial conceptacle of *N. fosliei sensu* Matsuda (1989), IGPS Coll. Cat. No. 102470 (4) and IGPS Coll. Cat. No. 102469 (5).

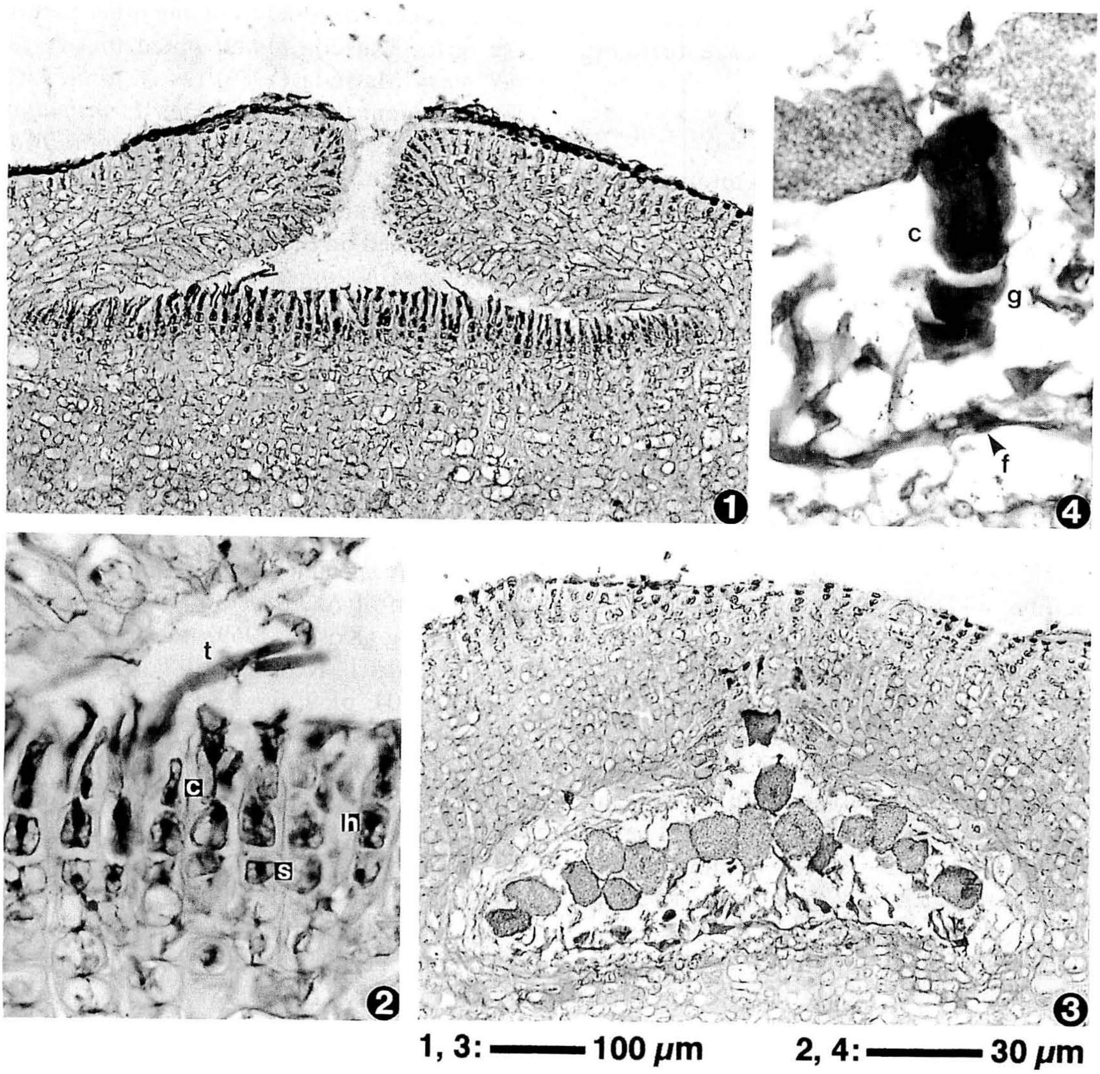


Figure 6. Female and carposporangial conceptacles of *N. fosliei sensu* Adey *et al*. (1982). **1**: Female conceptacle. **2**: Supporting cells and carpogonial filaments. Each supporting cell (s) has a carpogonial filaments, each of which is composed of a dorsal hypogynous cell (h) and a terminal carpogonium (c). Some carpogonia have trichogynes (t). **3**: Carposporangial conceptacle. **4**: Carposporophyte. Note that a fusion cell, a dorsal gonimoblast filament (g), and a terminal carposporangium (c). **1-4**: IGPS Coll. Cat. No. 100996.

but tetrasporangia have not been observed. Mature conceptacles have roofs which are 15-29 cells thick at pore canals (160-220 μm long and 50-65 μm in diameter). Conceptacle chambers are laterally compressed ellipsoidal, 450-480 μm in diameter and 110-150 μm high, and contain bisporangia across the entire chamber floor. Conceptacles become buried and invaded by secondary tissue. Sexual conceptacles have not been found.

All the three plants show almost the same anatomical features of tetrasporangial conceptacles. This implies that their tetrasporangial conceptacle development proceeds in the same manner. This mode is in agreement with that of *Neogoniolithon fosliei* reported by Penrose (1992b).

c. Ecological features

Neogoniolithon fosliei sensu Gordon *et al.* (1976) is distributed in forereef environment to a depth of 35 m, especially common at depths from 5 to 30 m. It covers more or less smooth hard substrates, and is found as large patches up to 20 cm in diameter. It is a rather minor species in the Ryukyu Islands (Iryu and Matsuda, 1987). Sloughing off the epithallium as observed in *N. fosliei sensu* Gordon *et al.* (1976) is known in some other nonarticulated corallines (Adey, 1965; Suneson, 1982; Masaki *et al*., 1984). It is explained that such strategies are to remove germlings of other algal spores and microorganisms from the thallus surface.

Assessed was standing crop (coverage, relative density, and frequency) of *N. fosliei sensu* Adey *et al.* (1982) (as *Spongites* sp. A) growing on a well illuminated, flat substrate in a forereef environment to a depth of 30 m by Iryu and Matsuda (1988). *N. fosliei sensu* Adey *et al.* (1982) is less dominant than *Porolithon onkodes, Lithophyllum insipidum*, and *Neogoniolithon conicum* at 1 m depth. This plant increases with depth to its peak at 15 m depth, where its standing crop is the highest of all the coralline-algal species examined. Below 15 m depth it decreases with water depth, and is absent at depths greater than 30 m. It has the greatest mean coverage of the coralline-algal species in the depth range studied (5.7%). The present species is distributed also in the moat, where it occurs approximately as commonly as in the shallowest forereef environment.

Neogoniolithon fosliei sensu Matsuda (1989) is not a dominant plant, and has been found at very restiricted environments of the reef. It covers rather flat substrate originating from various kinds of corals located at the reef edge to forereef shallower than 5 m depth, where the water is very turbulent. No material has been collected from any other parts of the reef. Matsuda (1989) noted that *N. fosliei sensu* Matsuda (1989) (as *N. fosliei*) was less dominant than *P. onkodes, L. insipidum*, and *N. conicum* (as *Paragoniolithon conicum*), and covers less than 5% of the well lighted artifical substrates (polyvinyl chloride plates) placed on the ridge of a spur. But the coverage of *N. fosliei sensu* Matsuda (1989) is significantly higher on the plate set on a reef rock projecting into a narrow groove than the former. He estimated the lateral growth rate of the present plant as approximately 3 mm/month in case of no grazing.

2. Lectotype specimen of *Neogoniolithon fosliei*

Since the specimens studied in the original description of *N. fosliei* by Heydrich (1897a) are missing (Koster, 1969), the isotype specimen (Heydrich, Red Sea, El Tor, no. 50: see Foslie, 1904, pl. 9, fig. 1; 1929, pl. 46, fig. 1) deposited in the "Foslie Crustose Coralline Herbarium" of Det Kongelige Norske Videnskabers Selskab Museet, Trondheim, Norway (TRH) was chosen by Adey *et al.* (1982) as the holotype specimen. However this is apparently the lectotype specimen (Woelkerling, 1985). Anatomical micrographs of the lectotype specimen were provided by Woelkerling (1985, 1987, 1988) and Penrose (1992b).

The plant of the lectotype specimen consists of a part of the irregular crustose thallus which covers a coral branch. Anatomically the lectotype specimen has a dorsiventral organization. Epithallium is composed of a single layer of laterally compressed, rounded cells. Perithallium is multilayered. Trichocytes are present solitarily at the dorsal thallus surface or in vertical columns at the surface or within the perithallium. In the latter case, up to 16 cells are arranged in each column. Hypothallium is multilayered and coaxial. Cell fusions are recognized both in the hypothallium and perithallium.

Taxonomic Implications

It is obvious that the differences in morphology and anatomical features of vegetative and reproductive tissues described above are thought to be great enough for classifying the three plants into three different species. The comparative study of the three plants with nonarticulated coralline algal species hitherto known leads to the following conclusions.

(1) *Neogoniolithon fosliei sensu* Gordon *et al*. (1976) is conspecific with the type specimen of *N. fosliei* housed in TRH.

(2) The temporary name "*Neogoniolithon* sp. A" should be given to *N. fosliei sensu* Adey *et al*. (1982) in spite of similarities to *N. myriocarpum* (Foslie) Setchell and Mason in external morphology and some anatomical features.

(3) *Neogoniolithon fosliei sensu* Matsuda (1989) is not assisgnable to any coralline species, and thus herewith described as *N. tenuicrustaceum* sp. nov.

Neogoniolithon fosliei (Heydrich) Setchell et Mason

Neogoniolithon fosliei, 1943, Setchell and Mason, p. 90; Lemoine, 1965, p. 7; Lemoine, 1966, p. 13; Womersley and Bailey, 1970, p. 311; Gordon *et al*., 1976, p. 261, pl. 6, figs. 2-5, pl. 7, fig. 1; Zhang and Zhou, 1980, p. 352, pl. 2, figs. 1-4; Zhang, 1983, p. 80, pl. 43, fig. 3; Cribb, 1983, p. 51; Cribb and Cribb, 1985, p. 62; Woelkerling, 1985, p. 148, figs. 49-51; Woelkerling, 1987, p. 147, figs. 2, 5, 6; Woelkerling, 1988, p. 140, fig. 135; Penrose, 1992b, p. 339, figs. 1-29.

Basionym. — *Lithothamnion fosliei* Heydrich, 1897a, p. 58, text-fig. 1, pl. 3. figs. 9-11.

Synonymy. —

Lithophyllum fosliei (Heydrich) Heydrich, 1897b, p. 410; Lemoine, 1911, p. 142, text-fig. 71.

Archaeolithothamnion fosliei (Heydrich) Foslie, 1898, p. 4.

Goniolithon fosliei (Heydrich) Foslie, 1901, p. 8; Foslie, 1903, p. 470, pl. 25, fig. 3; Foslie, 1904, p. 46, text-fig. 19, pl. 9, figs. 1-5; Howe, 1918, p. 294; Foslie, 1929, p. 29, pl. 46, figs. 1-5; ?Johnson, 1961, p. 932, pl. 275, fig. 7 (fossil material); Johnson, 1964, p. 25, pl. 13, fig. 2 (as *Goniolithon* cf. *G. fosliei*).

Lectotype. — Heydrich, Red Sea, El Tor, no. 59, housed in TRH.

Japanese name. — Foslie-ishimo (Yoshida *et al*., 1990).

Description. — Thallus crustose, anchored to substratum full to localized, extensive, sometimes exceeding 20 cm in diameter, thick (up to 5 mm in thickness); surface smooth to lobed; abundant large raised conical conceptacles scattered; color pale red or grayish red. Epithallium single-layered; cells laterally elongated, 6-10 μm long and 7-15 μm in diameter. Perithallium multilayered, cells 6-16 μm long and 5-13 μm in diameter; fusions common. Trichocytes arranged in long vertical columns, up to 20 cells in each column; 6-27 μm long and 14-22 μm in diameter. Hypothallium coaxial, 200-400 μm thick; fusions common; cells 17-49 μm long and 11-20 μm in diameter. Secondary hypothallium formation often seen. Tetrasporangial conceptacles conical, 1,250-1,700 μm in outside diameter, 760-1,040 μm in inside diameter, and 170-380 μm high. Tetrasporangia across floor of conceptacle chamber.

Remarks. — Penrose (1992b) noted that the present species shows a wide range of variation in its morphology and habit: irregularly lobed crust epiphytic on seaweed; epilithic plant with flattened thallus surface or wart-like protuberances; and unattached branching mass (=rhodolith). In contrast, all the previous authors stated that this species has thick (up to a few millimeters), flattened to lobed, crustose thalli, not possessing any protuberances or branches, and is epilithic or growing on corals. In the Ryukyu Islands, the wide variation noted by Penrose (1992b) is not observed. It seems that Penrose (1992b) underestimated the taxonomic significance of growth form and habitat of nonarticulated coralline algae.

Based on their study of the original type collections of *Melobesia brassica-florida* Harvey and *M. notarsii* Dufour, Woelkerling *et al*. (1993) stated that these species and *N.*

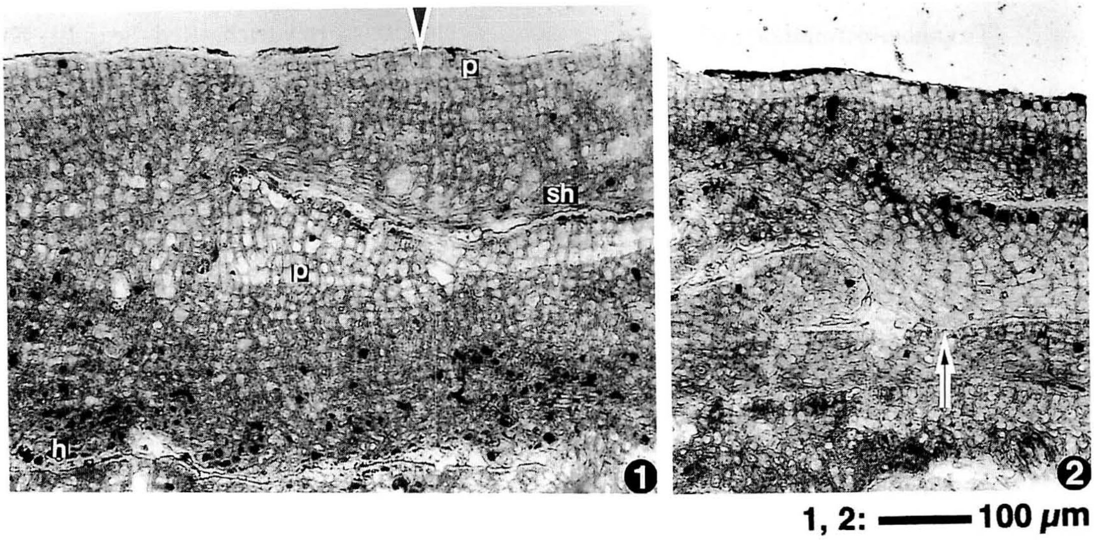


Figure 7. Ground section of the lectotype specimen of *Neogoniolithon myriocarpum* (Foslie) Setchell and Mason housed in TRH (Levander, Red Sea, Massanka, 1894-95, Mus. Zool., Helsingfors, slide 557). Note undulated perithallial filaments (arrow head) and secondary hypotallium disposing coaxial (arrow). The letters "h", "p", and "sh" indicate hypothallium, perithallium, and secondary hypothallium, respectively.

fosliei are conspecific and that the specific epithet *brassica-florida* (Harvey, 1849) has nomenclatural priority over the others. However, little can be known of the reproductive tissue from the lectotype specimens, because the male conceptacle with remains of spermatangia can be observed in the lectotype of *Melobesia brassica-florida* and the empty tetrasporangial (or carposporangial) conceptacle can be seen in that of *M. notarsii*. Moreover, growth forms of the lectotype specimens of *Melobesia brassica-florida* (warty appearance) and *M. notarsii* (crust-like to warty) are different from that of *N. fosliei*. Thus, it cannot be considered that these three species are conspecific.

Distribution. — Red Sea (Heydrich, 1897a ; Reinbold, 1903 ; Lemoine, 1911, 1965, 1966 ; Papenfuss, 1968), Indian Ocean (Foslie, 1903, 1904 ; 1929), Western Pacific (Foslie, 1904 ; Johnson, 1964 ; Gordon *et al*., 1976 ; Tsuda and Wray, 1977 ; Zhang and Zhou, 1980 ; Zhang, 1983 ; Iryu and Matsuda, 1987 ; Yoshida *et al*., 1990 ; Kawana *et al*., 1992), Mid-Pacific (Adey *et al*., 1982), South Pacific (Setchell, 1926 ; Lemoine, 1965 ; Womersley and Bailey, 1970), and Australia (Howe, 1918 ; Cribb, 1983 ; Cribb and Cribb, 1985 ; Penrose, 1992b).

Geologic range. — Pleistocene (Johnson, 1961 ; Iryu, 1992) to Recent.

Neogoniolithon sp. A

Description. — Thallus crustose, firmly adherent to substratum, less than 10 cm in diameter, thick (up to 3 mm in thickness) ; surface glossy and minutely rugulose ; abundant raised conical conceptacles scattered except for thallus margin ; color light pink to pale orange on vegetative surface but attaining yellowish spot on conceptacles. Epithallium usually a single cell layer ; cells rounded, laterally elongated, 4-10 μm long and 7-17 μm in diameter. Perithallium multilayered ; cells 9-20 μm long and 7-15 μm in diameter ; fusions common. Trichocytes in long vertical columns, up to 10 cell in each column, 4-34 μm long and 16-28 μm in diameter. Hypothallium multilayered, noncoaxial, 200-400 μm thick ; fusions common : cells 13-42 μm long and 7-16 μm in diameter. Tetrasporangial conceptacles conical, 800-1,500 μm in outside diameter, 550-890 μm in inside diameter, and 140-170 μm high. Tetrasporangia across floor of conceptacle chambers ; sterile filaments present among tetrasporangia. Female conceptacles slightly raised above thallus surface, 440-710 μm in inside diameter and 100-190 μm high ; several tens of supporting cells across chamber floor. Carposporangial conceptacles conical, 490-780 μm in inside diameter and 140-160 μm high. Gonimoblast filaments arising all over the dorsal surface of fusion cell ; fusion cell thin and continuous covering most of chamber floor.

Remarks. — With respect to the outer morphology and internal structure observed in ground section, this species is very similar to *Neogoniolithon myriocarpum* Foslie, whose lectotype specimen (Foslie, 1904, pl. 9, fig. 6 ; 1929, pl. 40, fig. 6) chosen by Adey and Lebednik (1967) was housed in TRH (Figures 7-1 and 7-2). At present, it cannot be determined whether the present species is conspecific with *N. myriocarpum*, because some important features, such as epithallium and reproductive tissue, cannot be observed in ground section. In order to clarify this problem, the lectotype specimen and material collected from the type locality (Red Sea) should be investigated for the important features mentioned above. This species is conspecific with *Neogoniolithon* sp. A of Iryu and Matsuda (1987) and *Spongites* sp. A of Iryu (1991a, 1991b), Iryu and Matsuda (1988), Kawana *et al.* (1992) and Iryu (1992).

This species has a fusion cell which is thin, continuous and irregularly shaped, covering most of the fertile area in the carposporangial conceptacle chamber (Figures 6-3 and 6-4). This contrasts with the occurrence of the discontinuous fusion cell of *N. fosliei* shown by Penrose (1992b).

Distribution. — Western Pacific (Iryu and Matsuda, 1987, 1988), Mid-Pacific (Adey *et al.*, 1982).

Geologic range. — Pleistocene (Iryu, 1992) to Recent.

Neogoniolithon tenuicrustaceum Iryu et Matsuda sp. nov.

Holotype. — I.G.P.S. Coll. Cat. No. 102459 (Figure 2-3).

Type Locality. — Kabira, Ishigaki-jima, Ryukyu Islands.

Etymology. — The specific epithet "tenuicrustaceum" refers to the thin crustose thallus of the present species.

Japanese name. — Usukawa-ishimo (new name).

Description. — *Crustae tenues, ad 500 μm crass., ad 10 cm diam., firme adhaerentes ad substratum ; superficies rugulosa ; color flavida ad sub-aurantiaca ; multa conceptacula parva tholiformia super superficiem sparsa. Epithallium ex unico strato cellularum tholiformium constans ; increassationes membranae dorsalis lateralis perspicuae ; cellulae 3-8 μm long. et 7-14 μm diam. Perithallium pluristratosum ; fusion cellulae saepe adest ; cellulae 8-15 μm long. et 5-13 μm diam. Trichocystae in linis verticalibus dispositae, vel in linea, vel cumulatae 2-10 cellularum, 7-29 μm long. et 12-29 μm diam. Hypothallium, pluristratosum tenue, minus quam 120 μm crass., non coaxiale ; fusion adest ; cellulae 9-40 μm long. et 5-16 μm diam. Conceptacula tetrasporangialia uniporata, 600-760 μm diam. exteriora, 450-480 μm diam. interiora atque 110-150 μm alt. Tetrasporangia trans totum pavimentum conceptaculi disposita.*

Crust thin, up to 500 μm thick, up to 10 cm in diameter, firmly adherent to substratum ; surface rugulose ; color pale yellow to orange yellow ; abundant small raised conceptacles scattered over surface. Epithallium a single layer of domed cells ; dorsal lateral wall thickenings marked; cells 3-8 μm long and 7-14 μm diameter. Perithallium multilayered; cell fusion frequent; cells 8-15 μm long. and 5-13 μm diameter. Trichocytes arranged in vertical columns, 2-10 cells in each column, 7-29 μm long and 12-29 μm in diameter. Hypothallium multilayered, thin (less than 120 μm thick), non coaxial; fusion present; cells 9-40 μm long and 5-16 μm in diameter. Tetrasporangial conceptacles uniporate, 600-760 μm in outside diameter, 450-480 μm in inside diameter, and 110-150 μm high. Tetrasporangia across entire conceptacle floor.

Distribution. — Ryukyu Islands (Iryu, 1991b; Kawana *et al*., 1992).

Geologic range: — No fossil material is known.

Discussion

1. Generic circumscription of *Neogoniolithon*

The genus *Neogoniolithon* was defined by Setchell and Mason (1943) as coralline algae which have all of the following features: (1) thallus nonarticulated; (2) hypothallium coaxial: (3) trichocytes arranged in vertical columns; (4) conceptacles (asexual, male, and female) uniporate; and (5) tetrasporangia (always ?) across the chamber floor of the conceptacle. Hamel and Lemoine (1953) modified and extended the generic concept to include two types of species with a coaxial and a noncoaxial hypothallium. Then, this extended concept had been accepted by most workers (Adey, 1970; Cabioch, 1972; Gordon *et al*., 1976; Johansen, 1976, 1981; Adey *et al*., 1982), with further modification, disregarding feature (5) of Setchell and Mason (1943). Woelkerling (1985), however, explicitly limited *Neogoniolithon* to include species with a coaxial hypothallium as defined in the original protolog, and reassessed the status of the genus *Spongites* to encompass species with a noncoaxial hypothallium. By this time, the classification scheme is completed in which those genera with multilayered perithallium throughout the vegetative tissue in the subfamily Mastophoroideae could be divided by means of differences in trichocyte occurrence and arrangements and in hypothallium organization into six genera: *Hydrolithon* Foslie (1909), *Porolithon* Foslie (1909), *Pseudolithophyllum* emend. Adey (1970), *Spongites* Kützing (1841), *Neogoniolithon* Setchell and Mason (1943), and *Paragoniolithon* Adey *et al*. (1982). On the other hand, Woelkerling (1985) noted the possibility that such characters are too variable to provide a reliable basis for delineating those genera. Penrose and Woelkerling (1988) confirmed Woelkerling's statement, and considered the genera *Porolithon, Hydrolithon*, and *Pseudolithophyllum* emend. Adey (1970) to be heterotypic synonyms of *Spongites*. Penrose (1991, 1992a, 1992b) proposed a new classification scheme in which *Neogoniolithon, Spongites*, and *Hydrolithon* are distinguishable from one another on differences in reproductive tissues, *i.e*., tetrasporangial conceptacle development and anatomy, spermatangial arrangement, and carposporophyte morphology. *Neogoniolithon* was considered to be distinguished from the other species by possessing all of the following features: (1) tetrasporangial conceptacle roof formed by filaments surrounding the fertile area; (2) spermatangia simple and borne on both the floor and roof of male conceptacle chambers; and (3) gonimoblast filaments arising from the entire dorsal surface of fusion cells.

The above historical review attests the important fact that the occurrence of tetrasporangia across the entire conceptacle chamber floor (= feature (5) given by Setchell and Mason (1943)) has been completely neglected since the 1970's, although Hamel and Lemoine (1953) and Masaki (1968) used it as one of the characters to circumscribe *Neogoniolithon*. Our study of the *Neogoniolithon-Spongites* complex in the Ryukyus reveals that plants belonging to the

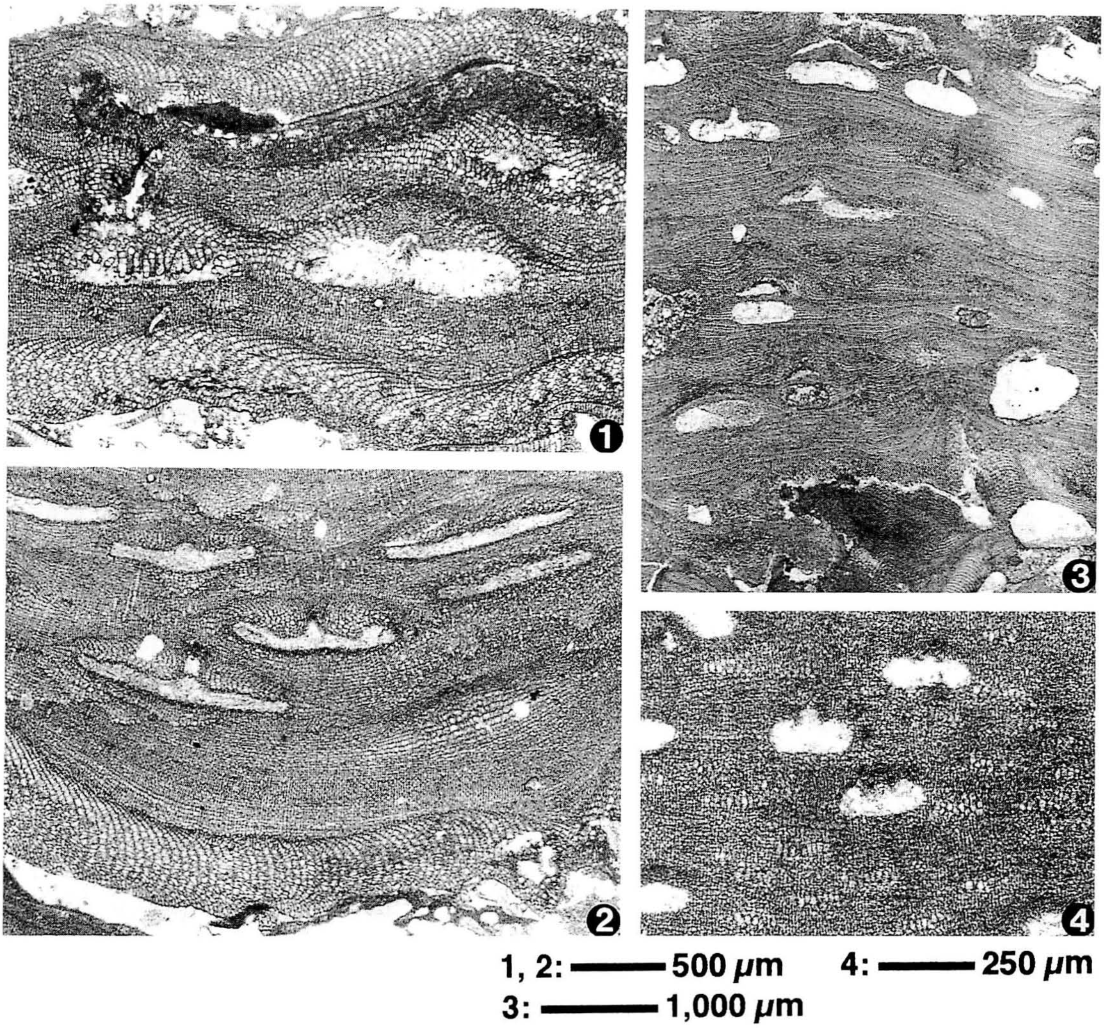


Figure 8. Fossil *N. fosliei* (1 and 2), *Neogoniolithon* sp. A (3), and *Hydrolithon onkodes* (4). 1 : IGPS Coll. Cat. No. 99304. 2 : IGPS Coll. Cat. No. 99305. 3 : IGPS Coll. Cat. No. 99313. 4 : IGPS Coll. Cat. No. 99334.

complex either have bi-/tetrasporangia across the whole conceptacle chamber floor without a central columella, spermatangia occurring on both the floor and roof of the male conceptacle chambers, and gonimoblast filaments arising dorsally from the entire surface of a fusion cell, or have bi-/tetrasporangial conceptacles formed peripherally in the conceptacle chamber floor with a central columella, spermatangia confined to the floor of male conceptacle and gonimoblast filaments arising only from the margin of a fusion cell. Other combinations of these three features are not observed. Judging from previous taxonomic works with a complete set of asexual, male and female conceptacles, the same is true of plants of the *Neogoniolithon-Spongites* complex. Masaki (1968) reported that *Neogoniolithon accretum* (Foslie et Howe) Setchell et Mason possesses the former combination, while he showed that the following 9 species, which should be referred to *Spongites* in the current sense, have the latter one: *Lithophyllum absimile* Foslie et Howe; *L. caribaeum* Foslie; *L. decipience* (Foslie) Foslie; *L. samoense* Foslie; *L. shioense* Foslie; *L. yendoi* Foslie; *Porolithon boergesenii* (Foslie); *P. colliculosum* Masaki; and *P. orbiculatum* Masaki. Moreover, Chamberlain (1993) showed that *Spongites yendoi* (Foslie) Chamberlain and *S. decipiens* (Foslie) Chamberlain have the latter combination of reproductive features. These observations imply the possibility that the position of bi-/tetrasporangia within the conceptacle chamber or the presence or absence of a central columella may be of potential significance to delineate *Neogoniolithon* and *Spongites*, as well as gametangial and carposporophyte features. The use of the position of bi-/tetrasporangia within the conceptacle chamber leads phycologists to much easier identification of plants of the *Neogoniolithon-Spongites* complex than the use of the latter characters, because sexual plants are much less abundant than asexual ones and it is not easy to observe the reproductive features of sexual plants.

2. Paleontological implications

a. Generic delineation of *Neogoniolithon, Spongites,* and *Hydrolithon* in fossils

The introduction of the new classification scheme for the *Neogoniolithon-Spongites-Hydrolithon* complex requires revision of the generic delineation of the fossil corallines assigned to the complex. Thus, we, paleoalgologists, must deal with the problem of whether the three genera can be distinguished from one another in fossils.

It is impossible to distinguish *Neogoniolithon* from *Spongites* because the criteria used for delineating the two genera are not preserved in fossils. Whereas *Hydrolithon* must, theoretically, be differentiated from the other genera because it has tetrasporangial conceptacles, the development and morphology of which are quite different from those of the others: the tetrasporangial conceptacle pore canals of *Hydrolithon* are lined by a ring of vertically elongated cells arranged nearly parallel to the canals and never projecting into the canals, reflecting that the conceptacle roofs are formed by filaments among the tetrasporangia, while in *Neogoniolithon* and *Spongites*, the roof formation is due to the growth of filaments surrounding the tetrasporangia and the pore canals are lined by several layers of cells perpendicular to or at an acute angle with the canals and projected into them. This difference is recognized in the coralline algal skeletons, and thus it may be observable in fossils if the skeletons are completely preserved. However, according to our observation on fossil corallines of the Pleistocene Ryukyu Group, it is not always determinable, except for some cases, whether the fossil corallines have the former type of asexual conceptacle pore canals or the latter, because the cells lining the pores are not preserved in fossils due to post-mortem destruction (Figure 8-4). Consequently, in fossils, *Hydrolithon* cannot be strictly distinguished from *Neogoniolithon* and *Spongites*.

It is concluded that *Neogoniolithon, Spongites*, and *Hydrolithon* are not distinguishable from one another in fossils based on current taxonomic concepts which are applicable to living coralline algae. How then should paleoalgologists classify the algae coming under this complex? Two ways appear to be possible. One would be to lump the three genera together as a single "genus". In this case, the "genus" reveals a much broader spectrum of the subfamily Mastophoroideae and becomes a mere unit without any phylogenetic, paleobiogeographic, or paleoecologic significance. The other would be to adopt the older classification scheme which Adey and Macintyre (1973) set up with some modification, if needed. The "genera" in this case are of little phylogenetic value, but are units of paleobiogeographic and paleoecologic significance, because each "genus" shows a characteristic geographic distribution and has a peculiar ecologic niche in the present-day marine environment (Adey, 1970). These pieces of knowledge enable us to utilize fossil nonarticulated coralline algae as excellent paleoenvironmental indicators. A comparison of the utility of these two alternatives shows that the latter is much better for paleoalgology, and thus is adopted here.

b. Fossil counterparts

Neogoniolithon fosliei (Figures 8-1 and 8-2) and *Neogoniolithon* sp. A (Figure 8-3) abundantly occur in the Pleistocene Ryukyu Group consisting of reef and its related sediments. They can be used as indicators of the water depth at which the group accumulated, because of their abundant occurrence and their specific depth range on the present-day reefs of the Ryukyu Islands (Iryu and Matsuda, 1988). Iryu (1992) discriminated four fossil nonarticulated coralline algal species assemblages from the group, each of which was thought to represent a peculiar depth range. His Assemblage B is characterized by the presence of *N. fosliei* or *Neogoniolithon* sp. A and the absence of *Porolithon onkodes*. The assemblage is considered to have existed at depths from 20 to 35 m. Outcrops where Assemblage B is recognized have many pile up thalli of *N. fosliei* and *Neogoniolithon* sp. A, which, together with other nonarticulated corallines and corals, form a more or less convex mound called the "sediment binding structure" (Iryu, 1992, Fig. 9). Fossil *N. tenuicrustaceum* is unknown.

It is expected that fossil *N. fosliei* and *Neogoniolithon* sp. A occur in reef limestones of the Indo-Pacific regions as well as the Ryukyu Islands. Their known occurrence is however very limited (*N. fosliei* from the Pleistocene (?) of Funafuti, Johnson, 1961). This does not indicate their actual occurrence, because fossil corallines have not been fully studied in such regions. Further research is needed to know their geologic range and paleogeographic distribution.

Conclusions

(1) *Neogoniolithon fosliei sensu* Gordon *et al.* (1976) is conspecific with the lectotype specimen of *N. fosliei*.

(2) *Neogoniolithon fosliei sensu* Adey *et al.* (1982) is described as *Neogoniolithon* sp. A, although it is very similar to *N. myriocarpum* in some outer and skeletal features.

(3) *Neogoniolithon fosliei sensu* Matsuda (1989) is not referable to any of the nonarticulated coralline algae hitherto known, and thus is described as a new species, *N. tenuicrustaceum.*

(4) The arrangement of bi-/tetrasporangia in bi-/tetrasporangial conceptacle chambers may be used to differentiate *Neogoniolithon* from *Spongites*.

(5) *Neogoniolithon, Spongites*, and *Hydrolithon* cannot be strictly distinguished from one another as fossils.

Acknowledgment

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フォーズリーイシモ (紅藻，サンゴモ科) およびその関連種の分類学的研究：フォズリーイシモはイシノミモドキ属の模式種とされている．近年グアム，ハワイ，琉球列島から本種が報告されてきたが，それらの外形，内部構造には相違点がみいだされる．われわれは琉球列島石垣島でこれらに同定される無節サンゴモを採取し，形態学的，解剖学的研究を行った．その結果，これらは異なる3種，フォズリーイシモ，イシノミモドキ属の一種，ウスカワイシモ (新種) に分類されることが明らかとなった．また，イシノミモドキ属の識別に際して，二分/四分胞子嚢巣内における二分/四分胞子嚢の配置を用いることができる可能性のあることが明らかとなった．

井龍康文・松田伸也

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970. ORDOVICIAN (LLANVIRNIAN) STROMATOPOROIDS FROM THE YOUNGWOL AREA, SOUTHERN KOREA*

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Abstract. The Ordovician stromatoporoid *Labechiella regularis* (Yabe and Sugiyama) has been recovered from the shallow ramp facies of the Yeongheung Formation (Llanvirnian) of the Ogcheon Fold Belt in southern Korea. The skeletal characteristics of this species have been altered by diagenesis. It represents the first discovery of a stromatoporoid from the southern part of the Korean peninsula. This Middle Ordovician stromatoporoid occurrence extends the geographical range of the species, previously reported from other parts of Asia.

Key words. Llanvirnian, Ordovician, stromatoporoids, Ogcheon Belt, southern Korea.

Introduction

Ordovician stromatoporoids of the North China-Korea Platform, inclusive of North China, Manchuria and the Korean peninsula, are poorly documented. The first study of stromatoporoids from the North China-Korea Platform was by Yabe and Sugiyama (1930a, b), followed by Endo (1932), Ozaki (1938), Yang and Dong (1962), Dong (1982), Dong and Wang (1984) and Lin and Webby (1988, 1989). However, these publications have mostly focused on the North China region, except that of Yabe and Sugiyama (1930a, b), which included two northern Korean localities. Stromatoporoids have not previously been recognized from southern Korea.

This study describes stromatoporoids from the Yeongheung Formation of southern Korea, to which is assigned a Middle Ordovician (Llanvirnian) age.

During recent sampling, 45 specimens were collected from the Yeongheung Formation in Youngwol County, Kangwon Province of southern Korea. All the well preserved specimens proved to represent the labechiid stromatoporoid *Labechiella regularis* (Yabe and Sugiyama, 1930a). This species, as well

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as most other labechiid stromatoporoids of the same age reported previously from other areas of the North China-Korea Platform, is older than, or contemporaneous with those from the Chazy Group of North America that, prior to the 1980s, were mainly regarded as the oldest stromatoporoids (Stock, 1983).

Geologic and stratigraphic settings

The Cambro-Ordovician sedimentary rocks distributed both in the southern and northern parts of the Korean peninsula constitute the Joseon Supergroup. In southern Korea it is extensively exposed as widely scattered localities within the Ogcheon Fold Belt (Figure 1a), presumably a continental margin depression trending northeast to southwest, but most sections are in the Taebaeksan Limestone Plateau of Kangwon Province, southern Korea.

The Yeongheung Formation represents the uppermost part of the Joseon Supergroup occurring in Youngwol County and its vicinity. The formation consists of dark grey dolomitic limestone and grey to bluish grey limestone intercalated in places with several thin beds of shale and argillite, and was probably deposited in the axial zone of the extended Ogcheon Basin (Chang, 1985).

Yoo (1991) recognized four repetitions of a shallowing-upward cycle, each composed of a shallow ramp facies migrating upward into peritidal facies. Thickening upward of the peritidal facies in each grand cycle indicates that the Yeongheung Formation was deposited during the four regressive phases.

The detailed stratigraphic correlation and age determination of the formation have been hampered by scattered exposures, lack of distinctive marker horizons and lack of age-diagnostic megafossils. Based on the trilobite genus *Basiliella* and some poorly preserved cephalopods, Kobayashi (1966) previously correlated the Yeongheung Formation with the Middle Ordovician Toufangian Series in Liaoning and Shandong Provinces of North China.

In recent attempts to provide a more refined biostratigraphy based on conodonts, Lee (1989) has dated the middle part of the Yeongheung Formation as late Llanvirnian (Middle Ordovician) in age. He reported some conodont species including *Plectodina onychodonta* from the middle part of the Yeongheung Formation, from which the stromatoporoids described herein were collected, and correlated this part of the sequence with the Upper Majiagou Formation of North China. *Plectodina ony-*

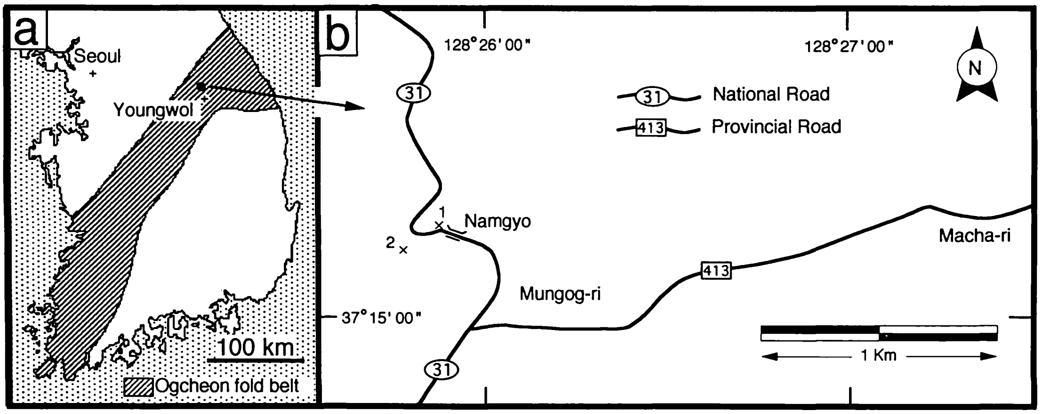

Figure 1. Localities of stromatoporoids of the middle part of Yeongheung Formation (b), Youngwol County, southern Korea (a). Crosses point to stromatoporoid localities 1 and 2 dealt with herein.

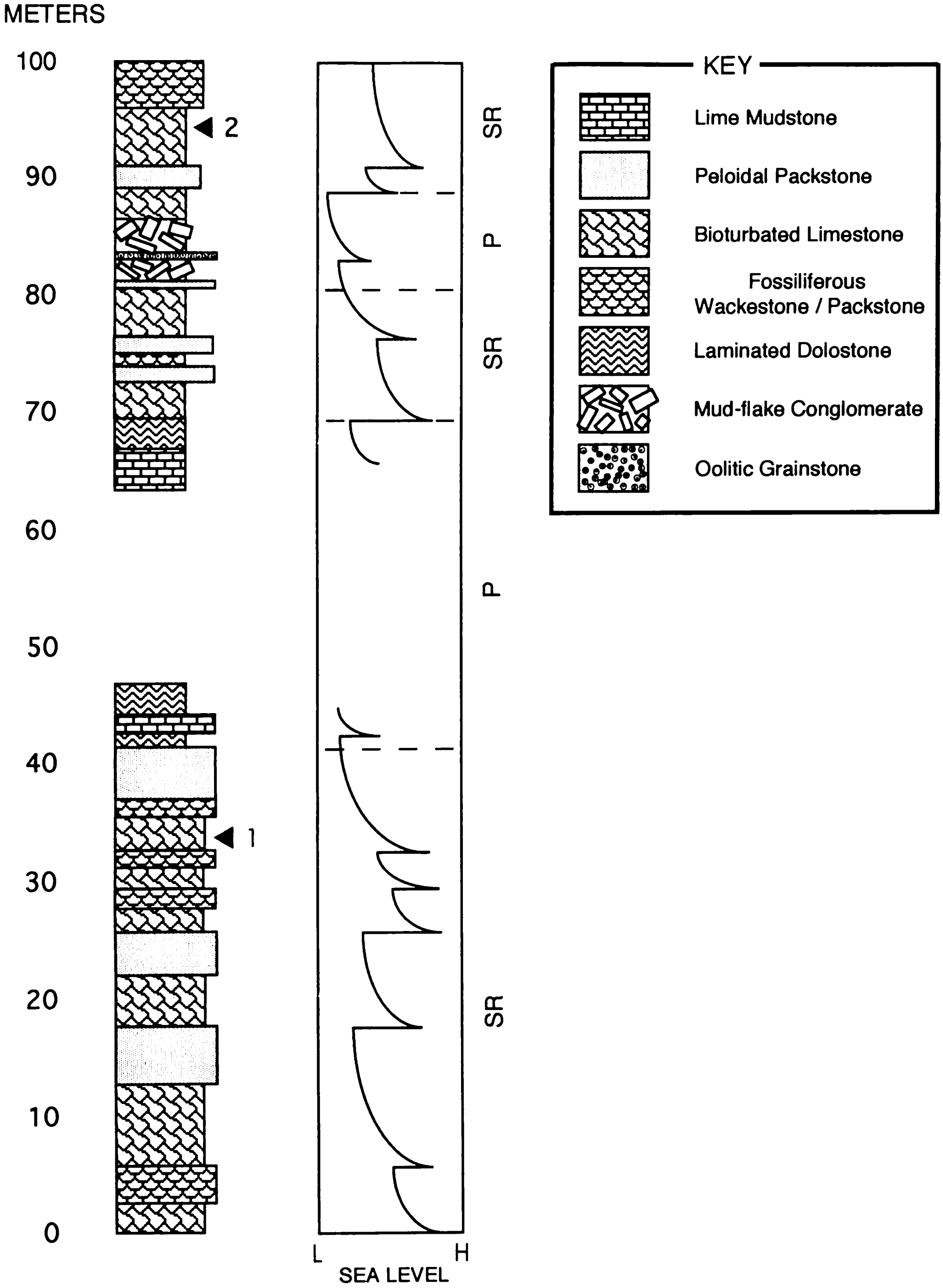

Figure 2. Measured section at Namgyo near Mungog-ri (Figure 1b), showing stratigraphic positions of localities of *Labechiella regularis* with relationship of relative sea level fluctuations inferred from the vertical changes in sedimentary facies. Vertical lithologic changes represent a threefold repetition of a shallowing-upward cycle. Arrow 1 indicates lower stromatoporoid bed at locality 1, Arrow 2 indicates upper stromatoporoid bed at locality 2, respectively. SR : Shallow Ramp Facies ; P : Peritidal Facies (modified from Yoo, 1991).

chodonta is a biostratigraphic indicator of the late Llanvirnian, e.g., the Upper Majiagou Formation in North China (An, 1981), a unit which also contains some of the earliest stromatoporoids in the North China-Korea Platform (Yabe and Sugiyama, 1930a, b; Dong, 1982).

The fossil localities and occurrences

Megafossils are rare and in general very poorly preserved in the Yeongheung Formation. The stromatoporoid specimens were collected from a measured section in the middle part of the formation near the village of Mungog-ri, about 13 km NNE from Youngwol (Figure 1b). In this section two stromatoporoid-bearing horizons were recognized: each from a lithofacies of prominent burrow-mottling, suggesting deposition during deeper subtidal intervals (Figure 2). The fact that scattered crinoid ossicles and orthid cephalopod fragments are occasionally found in these horizons also suggests as open shelf with of comparatively high energy environment (shallow ramp facies of Yoo, 1991).

Some stromatoporoid skeletons found in upper horizons were in growth position with a laminar to domed shape (Figure 3), and in larger skeletons well developed mamelons were observed. Latilaminae are in many cases clearly observed in outcrops, showing that earlier generations of skeletons expanded outwards on the muddy bottom. According to Kano's (1990) definition of the ecomorphotypes of the laminar-domed stromatoporoids, such a growth habit indicates that the species is ambitopic.

Some specimens, however, were not analyzed due to their poor preservation. Although the external form of the skeletons is preserved, dolomitization and silicification often obscure the internal structures of the skeletons. However, a number of better preserved specimens were available to allow the description, diagnosis and an estimate of variation in the species.

Systematic description

Taxonomic procedures.—The problem of the present species is the diagenetic alteration (dolomitization and/or silicification). Skeletal microstructures of most specimens are poorly preserved and the original structure of some important elements (e.g., wall microstructure, thickness of original walls and pillars) is difficult to recognize. For this reason certain measurements (thickness of laminae and pillars) should be given limited

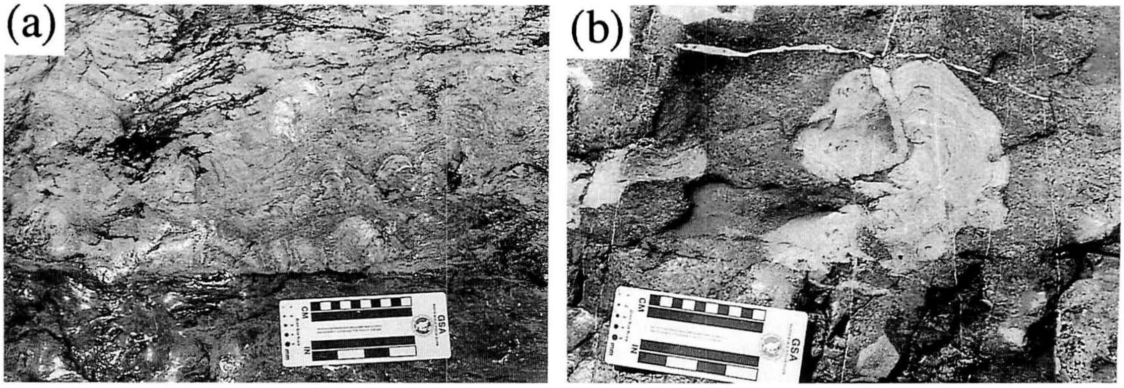

Figure 3. External growth modes of *Labechiella regularis*. (a) A laminar specimen resting on a muddy substrate in growth position (Locality 2). (b) A toppled domed specimen (Locality 1). Scale in centimeters and inches.

emphasis in taxonomic subdivision. The silicification seriously destroys the skeletal structures, and some silicified specimens do not even preserve their gross structure (Figure 4f). The dolomitization is a less serious problem. Therefore, the description is restricted to specimens which are not silicified.

Classification of the extinct group of the Palaeozoic stromatoporoids at the higher taxonomic level has been in debate. Affinity to the Phylum Porifera is the opinion of the majority (e.g., Stearn, 1972, 1975, 1982; Webby, 1986) because some of the stromatoporoids exhibits an internal structure which is similar to that of the recent calcareous demosponges. However, because no spicules have been found to confirm their affinities within the sponges, other possible affinities (Mori, 1982; Kazmierczak, 1976; Kazmierczak and Kempe, 1990) cannot be refuted.

In this study suprageneric assignments were used following Webby (1979, 1993). Terminology of external forms refers to Kershaw and Riding (1978).

Class Stromatoporoidea Nicholson and Murie, 1878
Order Labechiida Kühn, 1927
Family Labechiidae Nicholson, 1879
Genus *Labechiella* Yabe and Sugiyama, 1930a

Type species: *Labechiella serotina* (Nicholson, 1886)

Labechiella regularis (Yabe and Sugiyama)

Figures 3 and 4a-e

Labechia regularis Yabe and Sugiyama, 1930a, p. 56, pl. 18, figs. 5-6, pl. 21, fig. 8; Ozaki, 1938, p. 210, pl. 26, figs. 2a-d; Yavorsky, 1955, p. 56, pl. 24, figs. 4-5, Webby, 1969, p. 649, pl. 120, fig. 1, pl. 121, figs. 3-6, pl. 124, figs. 1-2.

Labechia regularis var. *tenuis* Yabe and Sugiyama, 1930a, p. 57, pl. 21, figs. 9-10, Yabe and Sugiyama, 1930b, p. 9, pl. 3, fig. 1, pl. 4, figs. 1-2.

Labechia tuvensis Yavorsky, 1968, p. 48, pl. 1, figs. 3-4.

Tuvaechia regularis (Yabe and Sugiyama). Bogoyavlenskaya, 1971, p. 309, pl. 2, fig. 1.

Labechiella regularis (Yabe and Sugiyama). Webby, 1979, p. 92, figs. 3a-b, Webby, 1991, p. 200, fig. 39.

Material.—Eleven specimens from Locality 1 and one from Locality 2 (Figures 1 and 2). All specimens are in the collection of the Department of Geology, Andong National University, Andong, Korea.

Description.—The species exhibits a low domed to laminar form and commonly shows ragged margins with sediment layers within the skeletons (Figure 4c). Skeletons are small, mostly less than 10 cm in width and 5 cm in height, although the largest specimen reaches 60 cm in width and 25 cm in height (Figure 3a). Mamelons are recognized on the upper surfaces of some specimens and are spaced from 2 to 5 cm apart. Latilaminae are commonly found from 8 to 15 mm in width.

Skeletons consist of thin laminae intersected by thick recrystallized pillars in vertical section (Figure 4a). Laminae are parallel, flat, or slightly concave, and continuous between pillars over a few centimeters. Spacing of laminae is regular and the distance between two laminae mostly ranges from 0.20-0.60 mm (Figure 4e). Pillars seem to be thick (0.2-0.4 mm), persistent, and often extending through more than five laminae, however the pillars are selectively altered by diagenesis. The dolomitized pillars commonly consist of large blocky dolomite crystals with fringes of smaller crystals (Figure 4e). The pillars may have been once dissolved and later filled by dolomite. In tangential section, the pillars are spaced from 0.7-0.12 mm apart (Figures 4b and d).

Remarks.—Gross skeletal structures, such as spacing of laminae and pillars, indicate that the present specimens resemble *Labechiella regularis.* Pillars of the present specimens display lighter center and darker mar-

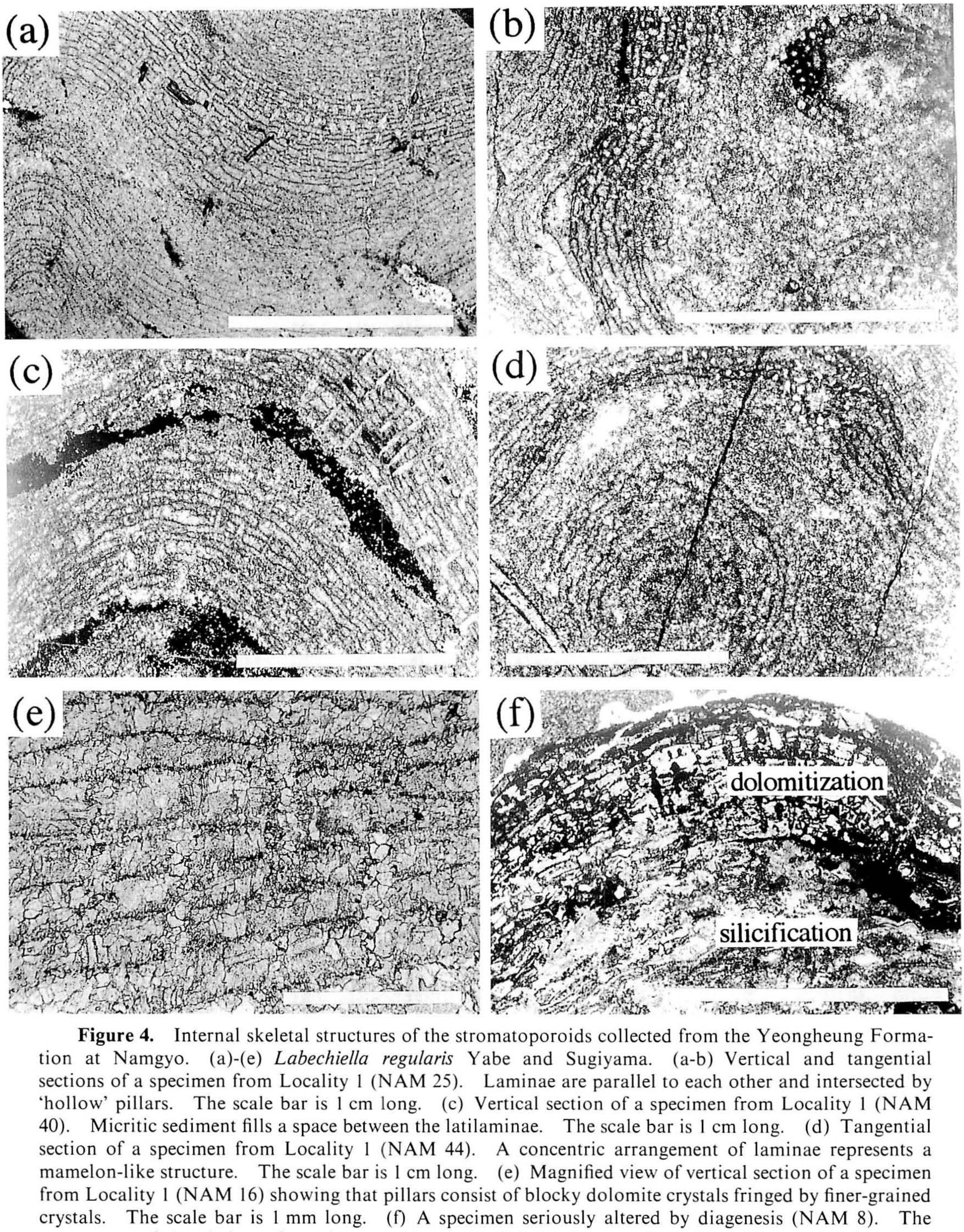

Figure 4. Internal skeletal structures of the stromatoporoids collected from the Yeongheung Formation at Namgyo. (a)-(e) *Labechiella regularis* Yabe and Sugiyama. (a-b) Vertical and tangential sections of a specimen from Locality 1 (NAM 25). Laminae are parallel to each other and intersected by 'hollow' pillars. The scale bar is 1 cm long. (c) Vertical section of a specimen from Locality 1 (NAM 40). Micritic sediment fills a space between the latilaminae. The scale bar is 1 cm long. (d) Tangential section of a specimen from Locality 1 (NAM 44). A concentric arrangement of laminae represents a mamelon-like structure. The scale bar is 1 cm long. (e) Magnified view of vertical section of a specimen from Locality 1 (NAM 16) showing that pillars consist of blocky dolomite crystals fringed by finer-grained crystals. The scale bar is 1 mm long. (f) A specimen seriously altered by diagenesis (NAM 8). The upper part of the skeleton is replaced by fine-grained dolomite crystals and exhibits a micritic microstructure. The lower part of the skeleton is silicified, thus obliterating the gross structure. The scale bar is 1 cm long.

gins which look like the 'hollow' pillars that may characterize the genus *Stromatocerium* (Nestor, 1976). However, the 'hollow' structure of the present specimens is diagenetic. Furthermore, Webby (1969, 1979) described *Labechiella regularis* with the pillars exhibiting light colored centers, and he also considered them to be secondary structures.

Labechiella mingshankouensis (Ozaki) from the Ordovician of the Northern China also exhibits regular laminae, however they are more widely spaced. *L. variabilis* (Yabe and Sugiyama) is also similar to *L. regularis*, however it exhibits wider and less regular spacing of laminae.

L. regularis was first reported as a species of *Labechia* by Yabe and Sugiyama (1930a), although it has the parallel and regular horizontal skeletal elements of typical members of *Labechiella*. Bogoyavlenskaya (1971) proposed a new genus *Tuvaechia* with *L. regularis* as the type species. According to Bogoyavlenskaya (1971), *Tuvaechia* was differentiated from the forms of *Labechiella serotina* type by having an isolated distribution of pillars in tangential sections. At the time of proposal of *Tuvaechia*, Bogoyavlenskaya (1971) had only investigated the plates of Yabe and Sugiyama (1930a) using additional drawings to repair poorly preserved skeletal parts. Furthermore, there is another problem in the proposal. Mori (1971) had already showed that both isolated and fused distributions of pillars can be seen in single specimens of some labechiid stromatoporoids (e.g., *Labechia conferta*) and that they cannot have a taxonomic importance, such as differentiating characteristics between *Tuvaechia* and *Labechiella*.

Occurrence.—L. regularis has been reported from the Middle to Late Ordovician of China (Yabe and Sugiyama, 1930a; Ozaki, 1938), northern Korea (Yabe and Sugiyama, 1930b), Siberia (Yavorsky, 1955, 1968; Bogoyavlenskaya, 1971) and Australia (Webby, 1969, 1991).

It is widely accepted that the stromatoporoids originated in the Llanvirnian (Webby, 1969, 1980, 1984, 1987; Stock, 1983) with the globally distributed stromatoporoid assemblage dominated by labechiids (Webby, 1993). Stromatoporoid faunas of the Llanvirnian have a low diversity but a wide distribution, suggesting their rapid dispersal. They became more diverse in the Caradocian and replaced the algal-sponge associations in the reef environment (Webby, 1984; Copper, 1988).

Acknowledgments

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Macha-ri 磨嵯里，Mungog-ri 文谷里，Namkyo 南橋，Youngwol 寧越．

韓国 Youngwol からのオルドビス紀 (Llanvirnian) 層孔虫：韓国北東部の Youngwol 付近に分布する Llanvirnian (中部オルドビス系) の浅海性石灰岩層から層孔虫化石 *Labechiella regularis* (Yabe and Sugiyama) を報告した．試料はドロマイト化や珪化作用を受け, 骨格の微細構造の保存は必ずしも良好ではないが, laminae と pillars の特徴から上記の種と同定が可能である．本試料は韓国からの最初の層孔虫化石の報告であるとともに，世界的に見ても最も古い層孔虫化石の 1 つであると言える．中部オルドビス系の層孔虫化石群集の多様性は低いが，本種を含めて，多くの種が広い地理的分布を示しており，層孔虫は進化の初期段階で急速に拡散していったと考えられる．

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971. PLAGIACANTHIDAE (RADIOLARIA) FROM THE UPPER MIOCENE OF EASTERN HOKKAIDO, JAPAN*

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Abstract. Well-preserved radiolarians are abundant in diatomaceous siltstones of the Taiki Formation (Upper Miocene) in the Toyokoro Hills region, and the Chokubetsu, Atsunai and Shiranuka Formations (Middle Miocene to Lower Pliocene) in the Atsunai Coast region, eastern Hokkaido, Japan. Fifteen samples are studied from five routes; Oikamanai River, Yudou River, Noyaushi River, Ishii-zawa River and Atsunai Coast routes. Plagiacanthidae species are a principle component of these assemblages.

Seven genera of Lophophaeninae (including two new genera and six new species), two of Clathromitrinae and one of Sethoperinae are described. Three groups of Plagiacanthidae having characteristic internal skeletal structures are recognized.

- Group 1 : The first segment is distinguished from the second segment by only **AL**.
- Group 2 : The first segment is distinguished from the second segment by **AL** and **VL** (instead of **AL** and **LL** when **V** is lacking).
- Group 3 : The first segment is distinguished from the second segment by **DL** and **VL**, or **AL-AL**, **AL and VL**, or **DL** and **LL**.

All genera of groups 1 and 2 are included in Lophophaeninae, while two genera of group 3 are in Clathromitrinae, one is in Sethoperinae and one is in Lophophaeninae.

Key words. Radiolaria, Plagiacanthidae, internal skeletal structure, Upper Miocene, Hokkaido.

Introduction

The suprageneric classification of Nassellaria has been approached in two ways, namely based on the internal skeletal structure and the other based on the external skeletel structure. Riedel (1967, 1971) classified mainly Cenozoic Nassellaria based on the whole skeletal structure including the internal skeletal structure. Petrushevskaya (1971a, 1971b, 1975, 1981) introduced a classification scheme based on the internal skeletal structure. Takemura (1986) also classified Jurassic Nassellaria based on the internal skeletal structure. Empson-Morin (1981) suggested the possibility that the internal skeletal structure was formed during late ontogeny and recommended a classification of Nassellaria based only on the external skeletal structure. Swanberg and Bjørklund (1987) studied living nassellarians to clear up the question of the skeletal growth and revealed that arches connecting two internal spicules are formed during a "precephalic stage". Recently, Nishimura (1990) studied the growth line structure of the nassellarian skeleton, and insisted that the internal skeletal structure of nassellarians was formed during early ontogeny and was an effective element in higher taxonomic classification such as the family level. The studies of Swanberg and Bjørklund (1987) and Nishimura (1990) suggest that it is suitable to classify Nassellaria at the suprageneric

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level based on the internal skeletal structure rather than the external one. Although suprageneric classifications based on the internal skeletal structure were introduced by some authors, the specific and generic constancy of each internal skeletal element is indistinct. Petrushevskaya (1971a, 1971b) used **AL** for the suprageneric level and did not use **V** and **AD** for any taxonomic levels. Nishimura (1990) used **V** for specific level and **AL** and **AD** for the suprageneric level. It is necessary to ascertain the taxonomic levels (specific, generic or suprageneric) at which each internal skeletal element is constantly present.

Plagiacanthidae are an important group in the radiolarian assemblages of the present study. The family Plagiacanthidae was defined by Hertwig (1879), and emended by Petrushevskaya (1971a). Petrushevskaya (1971b) divided it into two families and four subfamilies. Nishimura (1990) broke up this group into five families.

The present study clears up the correlation between internal and external skeletal structures, and confirms which internal skeletal elements are constant at the specific, generic or suprageneric level. In addition, this study introduces one monogeneric and two polygeneric groups of Plagiacanthidae based on the internal skeletal structure that is constant at the generic level.

Materials and method of study

The study area is in eastern Hokkaido at about Lat. 42°50′N to 43°00′N, Long. 143°50′E to 144°00′E (Figure 1). The routes

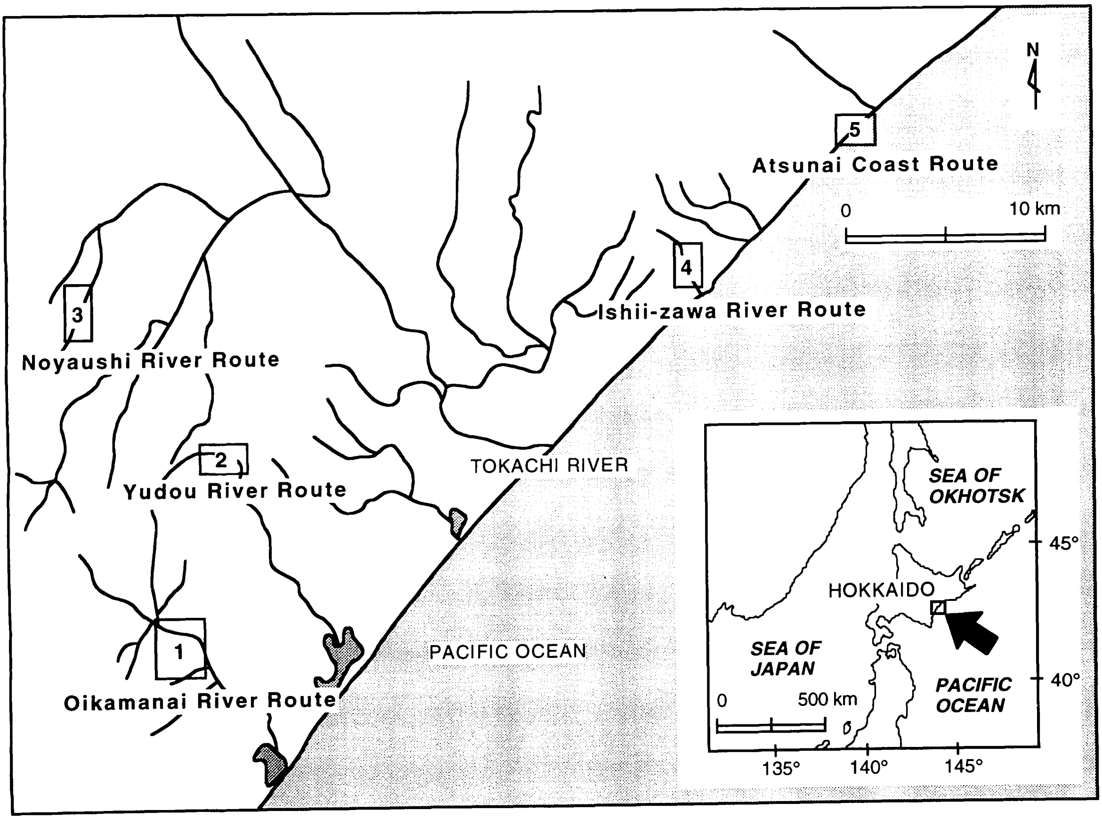


Figure 1. Index map showing localities of study routes.

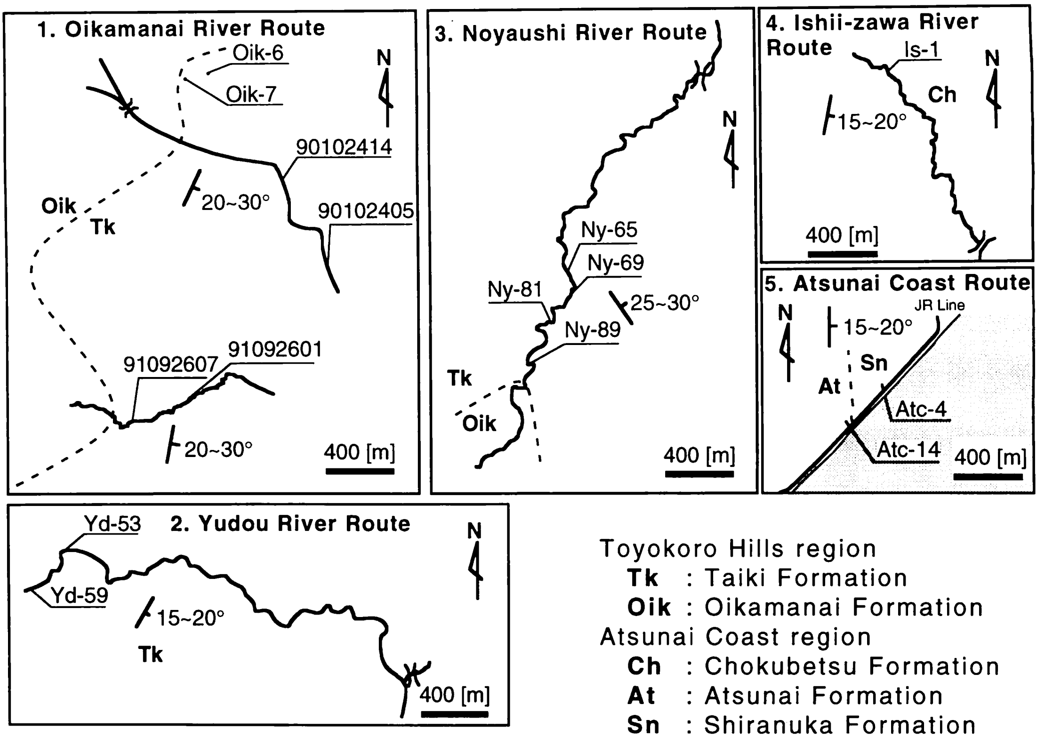


Figure 2. Map showing localities of study samples.

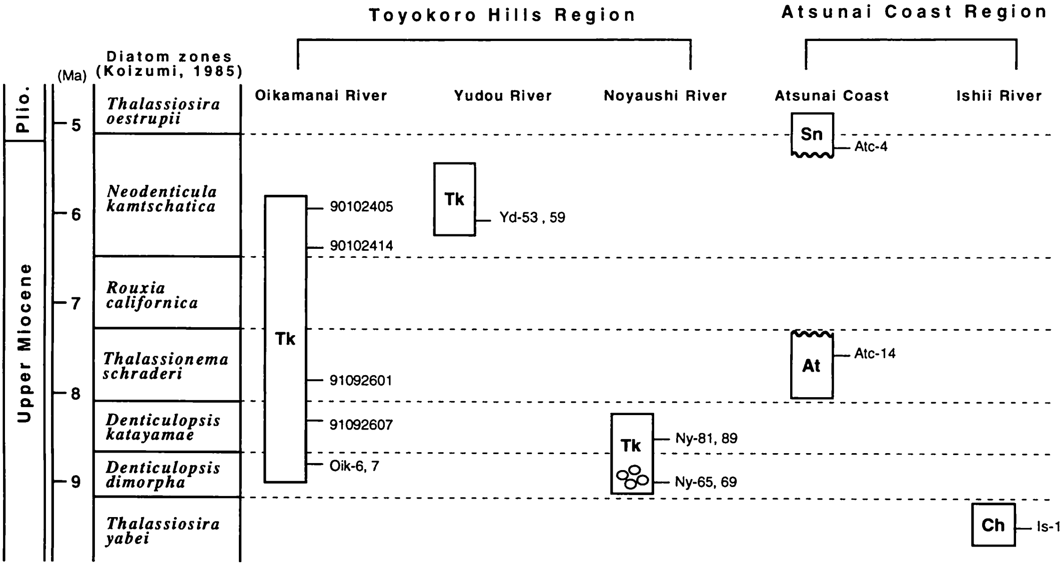


Figure 3. Ages of study samples. Diatom zones are from Koizumi (1985) and their ages are from Oda (1986). Abbreviations of formation names are the same as those in Figure 2.

examined are mainly the Upper Miocene strata, including the Taiki Formation (Yamaguchi and Satoh, 1989; Yamagishi *et al.*, 1990) distributed in Toyokoro Hills region, and the Chokubetsu, Atsunai and Shiranuka Formations (Tada and Iijima, 1986) distributed in the Atsunai Coast region (Figure 2). Well-preserved radiolarian fossils are abundant in diatomaceous siltstones from these formations. The present study is based on 15 samples from 5 routes; Oikamanai River, Yudou River, Noyaushi River, Ishii-zawa River and Atsunai Coast routes. Each sample, sampling route, formation name and correlation with diatom zones (from Koizumi, 1985) are shown in Figure 3. In the Noyaushi River route, although horizons of Ny-65 and -69 are situated higher than Ny-81 and -89 which indicate the *Denticulopsis katayamae* Zone, they indicate the *Denticulopsis dimorpha* Zone. This points out that Ny-65 and -69 are allochthonous blocks derived from lower horizons, possibly by slumping of sea floor deposits.

The radiolarian assemblages are composed of species that belong to the Actinommidae, Spongodiscidae, Theoperidae and Plagiacanthidae (Fig. 4). Plagiacanthidae species are one of the main groups of these radiolarian assemblages.

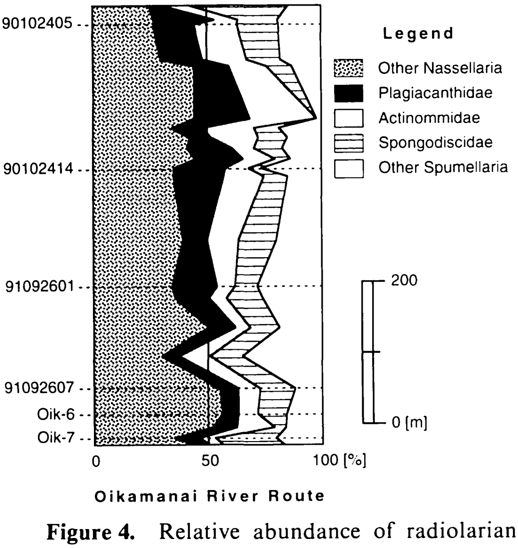


Figure 4. Relative abundance of radiolarians at the family level in the Oikamanai River route. This chart shows that Plagiacanthidae are one of the main groups in the yielded radiolarian assemblages.

To extract radiolarian specimens, crushed rock samples are immersed in a solution of hydrofluoric acid. To restrain the dissolution of radiolarian skeletons by hydrofluoric acid, crushed rock samples are left in a mixed solution of hydrofluoric acid, hydrochloric acid and hydrogen peroxide for no longer than six to eight hours. This mixed solution consists of:

$HF\ (0.5\sim1.0\%)+HCl\ (10\sim15\%)+H_2O_2\ (15\sim20\%)$, in a ratio of 1 : 1 : 1.

After extraction of specimens, they are sieved through a 75 μ mesh screen, the residue on the screen is cleaned by boiling in the solution of hydrogen peroxide (5 to 8 %) for about 10 to 30 minutes and then adding a little hydrochloric acid and boiling until the reaction is ended (about 5 to 10 minutes). Finally, the residue is sieved through a 75 μ mesh screen again, washed by distilled water, and dried. Radiolarian specimens are picked from the dried residue, mounted on an SEM stub, coated with gold and observed under the SEM.

Stratigraphic ranges (applying the diatom zones from Koizumi, 1985) of described species are defined by the observations for the smear slides studied by Funakawa (1993).

Terminology of internal and external skeletal structures

The terminology of the internal skeletal structure follows Dumitrica (1991). The internal skeletal elements of Nassellarians are divided into internal spicules and connecting arches. In this study, the confirmed internal spicules of Plagiacanthidae are median-bar (**MB**), apical spine (**A**), dorsal spine (**D**), ventral spine (**V**), right and left lateral spines (**L**) and right and left secondary lateral spines (**l**) (Figure 5). The basic scheme of connecting arch follows Petrushevskaya (1968), "skel-

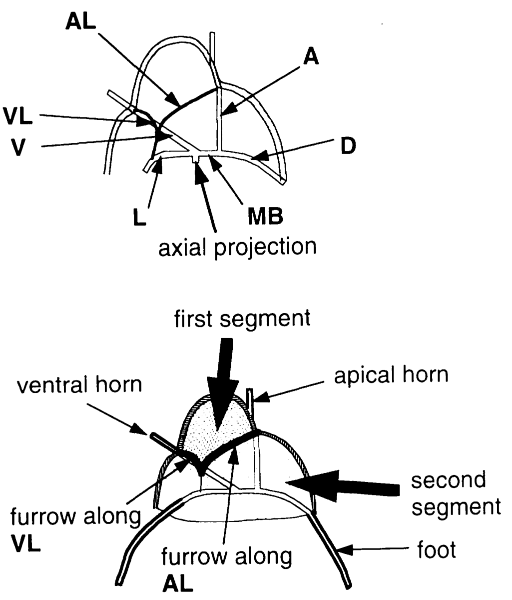


Figure 5. Terminology of the internal and external skeletal structures of Plagiacanthidae (these figures are for *Pseudodictyophimus gracilipes*). Secondary lateral spines (**l**) are not designated in this figure.

eton connecting two basic spicules". Additionally, the present study proposes a definition that the loci of these arches are not disturbed by pore arrangement. Because they are formed during a "precephalic stage" (Swanberg and Bjørklund, 1987), later skeletal growth is controlled by their position. In Plagiacanthidae, two **AL** (connecting **A** and **L**), two **VL** (connecting **V** and **L**), two **DL** (connecting **D** and **L**), **AD** (connecting **A** and **D**, **LL** (connecting both **L**), **AL-AL** (connecting both **AL** at the dorsal side), two **Al** (connecting **A** and **l**), two **Ll** (connecting **L** and **l** at the right and left sides), two **Dl** (connecting **D** and **l**) and **VL-VL** (connecting right and left **VL** at the ventral side) are confirmed in the present study. Where these connecting arches are in the shell, distinct or indistinct furrows are formed along them. By the combination of furrows along **VL, LL, DL, AL-AL, Ll** and **Dl**, the first segment is distinguished from the second segment.

To observe Plagiacanthidae externally, the following structures are recognized: an apical rib on the first segment extended from **A**, an apical horn extended from the apical rib or directly from **A**, a ventral horn extended directly from **V**, dorsal and lateral ribs on the second segment extended from **D** and **L**, and three feet extended from dorsal and lateral ribs or dircetly from **D** and **L**.

Taxonomic descriptions

Suborder Nassellaria Ehrenberg, 1875
Superfamily Plagiacanthoidea Hertwig, 1879,
emend. Petrushevskaya, 1971a
Family Plagiacanthidae Hertwig, 1879,
emend. Petrushevskaya, 1971a
Subfamily Lophophaeninae Haeckel, 1881,
emend. Petrushevskaya, 1971b

Genus *Amphiplecta* Haeckel, 1881, emend. Petrushevskaya, 1971b

Type species: *Amphiplecta acrostoma* Haeckel, 1887.

Remarks.—The skeleton is composed of two segments. Internal skeletal structure is composed of **MB, A, D, L, V, AL** and **VL**. The junction of **A** and **AL** is on the shell. The first segment is cylindrical and distinguished from the second segment by **AL** and **VL** or the furrows along them. The apical rib is well-developed. A skeleton-like **AD** is present and located outside the shell. The second segment is widely expanded but poorly developed, with indistinct dorsal and lateral ribs.

Amphiplecta acrostoma Haeckel

Figure 6, 1a-1b

Amphiplecta acrostoma Haeckel, 1887, p. 1223-1224, pl. 97, fig. 10.
Amphiplecta acrostoma Haeckel; Petrushevskaya, 1971b, p. 103, pl. 54, figs. 2-7.

Remarks.—The first segment is cylindrical and its apex is not closed. The shell of the

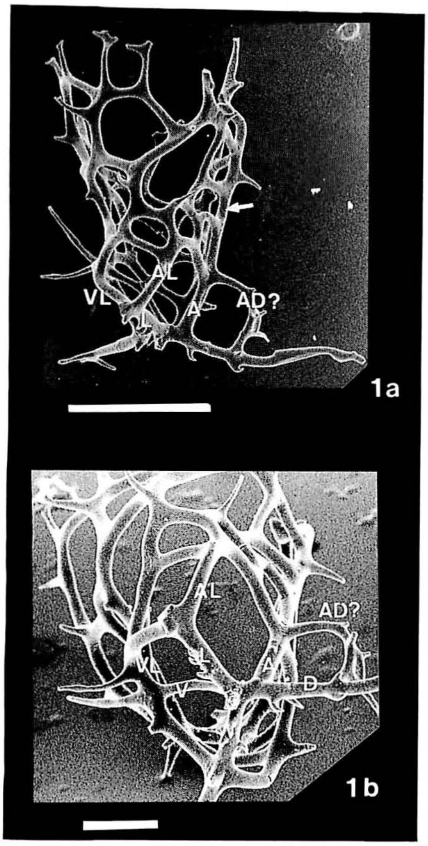


Figure 6. 1a, 1b : *Amphiplecta acrostoma* Haeckel, Atc-14. 1a : left lateral) view ; 2a : oblique basal (left lateral view. Arrow of 1a points to the apical rib. Scale bars : 1a=50 μm ; 1b=20 μm.

first segment is a rough meshwork formed by thin pore bars without fine spines. The apical horn extends at the apex of the first segment but is poorly developed. Pores are irregularly shaped and randomly arranged. Axial projection is distinct. The second segment is very poorly developed below **AL** and **VL** as divergent spines extending from **D** and **L**. A skeleton-like **AD** tends to be broken because it is not within the shell.

Dimensions.—Measurements are based on nine specimens. Diameter at the apex of the first segment is 54-90 (average is 67) μm, the maximum of the first segment is 58-119 (92) μm, total height of the shell (almost equal to that of the first segment) is 70-143 (112) μm.

Occurrences—90102414, 91092607, Oik-6, Yd-59 and Atc-14. Few to very rare in abundance.

Stratigraphic range—The lower limit is in the *Denticulopsis dimorpha* Zone, the upper limit is not confirmed.

Genus *Ceratocyrtis* Bütschli, 1882, emend. Petrushevskaya, 1971b

Type species : *Cornutella cucullaris* Ehrenberg, 1873 (designated by Petrushevskaya, 1971b).

Remarks.—The skeleton is composed of two segments. Internal skeletal structure is composed of **MB, A, D, L, V, AL** and **VL**. Some specimens lack **V**, and **LL** is present instead of **VL**. The junction of **A** and **AL** is on the shell. The first segment is distinguished from the second segment by the furrows along **AL** and **VL** (or **LL**). The first segment is hemispherical with a short apical rib. The second segment is bell-shaped without distal feet. Dorsal and lateral ribs are absent.

In this genus, the apical horn and ventral horn are poorly developed. It is distinguished from *Pseudodictyophimus* and *Corythomelissa* by the absence of the dorsal and lateral ribs and distal feet, and from *Lophophaena* by its small first segment.

Ceratocyrtis histricosus (Jørgensen)

Figure 7, 1a-1b

Helotholus histricosus Jørgensen, 1905, p. 137, pl. 16, figs. 86-88.

Ceratocyrtis histricosus (Jørgensen) : Bjørklund, 1976, pl. 8, figs. 19-24, pl. 11, figs. 4, 5.

Remarks.—Surface of the shell is smooth without spines. The first segment is hemispherical and with a poorly developed apical horn. Pores in the first segment are circular and randomly arranged. Axial projection is as long as a spine. The distal end of the second segment is open with teeth around it. Pores in the second segment are circular to subcircular and larger than in the first segment.

This species is similar to *Ceratocyrtis histricosus* in Sugiyama (1993) although having the smooth-surfaced second segment.

Dimensions.—Measurements are based on 20 specimens. The maximum diameter of the first segment is 24-36 (29) μm, of the second segment 69-148 (101) μm, total height of the shell (not including apical horn) is 64-138 (86) μm.

Occurrences.—All samples. Few to rare in abundance.

Stratigraphic range.—All zones. The upper and lower limits are not confirmed.

Ceratocyrtis multicornus Funakawa, sp. nov.

Figure 7, 2a-2b

Arachnocorys sp. B group; Funakawa, 1993, pl. 2, figs. 1a-3b.

Holotype.—OCU CR-0002 (90102405)

Description.—Surface of the shell is somewhat spiny. The first segment is hemispherical with one to five stout horns that do not extend from **A** but are simple projections of the shell. The apical horn and ventral horn are poorly developed. Pores in the first segment are circular to subcircular and randomly arranged. Axial projection is present. The furrows subdividing the first and second segments are distinct. The second segment is conical to bell-shaped. The distal end of the second segment is fully open with teeth around it. Pores in the second segment are subcircular and irregularly arranged, larger than those in the first segment. Pore bars are thin and narrow.

Dimensions.—Measurements are based on 14 specimens. The maximum diameter of the first segment is 29-36 (32) μm, of the second segment 69-104 (81) μm, total height of the shell (not including apical horn and distal teeth) is 53-94 (73) μm.

Remarks.—This species is distinguished from other species of *Ceratocyrtis* by having one to five or more horns on the shell that are unrelated to the internal spicules.

Etymology.—The specific name means "many horns" in Latin

Occurrences.—90102405, 90102414, Yd-53 and 59. Common in abundance.

Stratigraphic range—the species is restricted to the *Neodenticula kamtschatica* Zone and dies out in the middle to upper part of the zone. In the Yudou River route, its disappearance process is characteristic. In the middle part of the same zone, the relative abundance of this species is 3% to 15% just above a horizon where it occurs abundantly, it disappears abruptly. Refer to Funakawa (1993), Fig. 6.

Ceratocyrtis sp.

Figure 7, 3a-3b

Description.—Surface of the shell is spiny. Some specimens identified as this species have poorly developed **V** and **VL**. When **V** is poorly developed, it is only recognized as an upwardly directed projection at the intersection of **MB** and **L**. The apical horn and ventral horn are poorly developed. The apical rib is indistinct because of the complicated meshwork structure of the shell. Pores in the first segment are circular and irregularly arranged. Axial projection is present but small. The distal end of the second segment is fully open with teeth around it. In some specimens, the lower part of the second segment is distinguished from the upper part by pore shape and arrangement. In the lower part, pores are quadrangular but in the upper part they are circular to subcircular.

Dimensions.—Measurements are based on 10 specimens. The maximum diameter of the first segment is 23-30 (27) μm, of the second segment 53-85 (72) μm, total height of the shell (not including apical horn and distal teeth) is 64-86 (74) μm.

Remarks.—This species is distinguished from *Ceratocyrtis histricosus* by fine and complicated skeleton of the second segment and a smaller shell than that of *C. histricosus.* It is

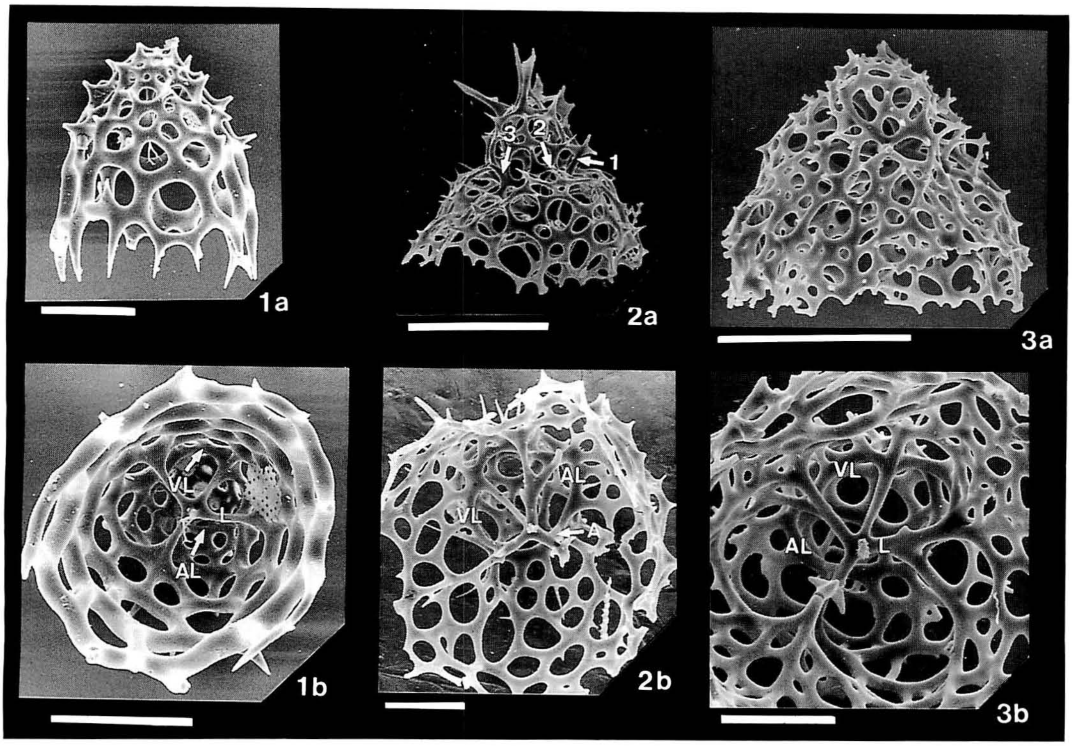


Figure 7. **1a, 1b** : *Ceratocyrtis histricosus* (Jørgensen), Ny-89. 1a : ventral to left lateral view ; 1b : basal view. **2a, 2b** : *Ceratocyrtis multicornus* Funakawa, sp. nov., OCU CR-0002, 90102405, holotype. 2a : left lateral view ; 2b : basal view. Arrow 1 of 2a points to the apical rib, 2 to the furrow along **AL** and 3 to the furrow along **VL**. **3a, 3b** : *Ceratocyrtis* sp., 91092601. 3a : ventral view ; 3b : basal view. Scale bars : 2b and 3b$=20\ \mu$m ; others$=50\ \mu$m.

distinguished from *C. multicornus* sp. nov. by its fine and complicated skeleton and the absence of some horns on the first segment.

Occurrences.—90102414 and 91092601. Common to very rare in abundance.

Stratigraphic range.—This species occurs commonly in the *Thalassionema schraderi* Zone, rarely in *Neodenticula kamtschatica* Zone. The upper and lower limits are not confirmed.

Genus *Lophophaena* Ehrenberg, 1847, emend. Petrushevskaya, 1971b

Type species : *Lophophaena galeaorci* Ehrenberg, 1854=*Lophophaena apiculata* Ehrenberg, 1873.

Remarks.—The skeleton is composed of two segments. Internal skeletal structure consists of **MB, A, V, D, L, AL** and **VL**. The junction of **A** and **AL** is on the shell. The first segment is distinguished from the second segment by the furrows along **AL** and **VL**. The first segment is almost spherical to ellipsoidal with a short apical rib. The second segment is bell-shaped to subcylindrical. Development of feet, dorsal and lateral ribs is variable.

Lophophaena simplex Funakawa, sp. nov.

Figure 8, 1a-2c

Holotype.—OCU CR-0003 (Ny-89)

Description.—The first segment is subspherical to ellipsoidal. One to four (occasionally more) robust horns that are unrelated to the apical rib are on the shell. These horns are shorter than the half-height of the first segment. The apical horn and ventral horn are unbladed and poorly developed. Pores in the first segment are circular to subcircular and randomly arranged. Axial projection is present and in some specimens it is well-developed like a spine. The second segment is bell-shaped with indistinct dorsal and lateral ribs, without feet extended from them. In most specimens, there are many external unrelated to internal spicules on the lower part of the second segment. Pores in the second segment are circular to subcircular and randomly arranged but in the lower part are arranged weakly along longitudinal ribs. The distal end of the second segment is open with teeth, but in some specimens, tends to be closed by a porous plate. Surface of the second segment is without spines.

Dimensions.—Measurements are based on 12 specimens. The maximum diameter of the first segment is 47-69 (54) μm, of the second segment 78-102 (91) μm, total height of the shell (not including apical horn) is 98-133 (111) μm.

Remarks.—This species is distinguished from other species of *Lophophaena* by its stout horns, and from *Ceratocyrtis multicornus* sp. nov. by its larger subspherical to ellipsoidal first segment.

Etymology.—The specific name means "simple" in Latin.

Occurrences.—Oik-6, 7, Ny-65, 69, 81, 89 and Is-1. Few to very rare in abundance.

Stratigraphic range.—The upper limit is in the *Denticulopsis katayamae* Zone. The lower limit is not confirmed.

Lophophaena triangula Funakawa, sp. nov.

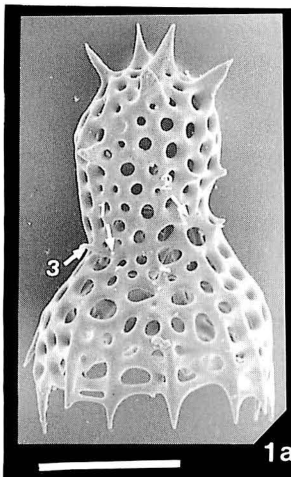
Figure 8, 3a-4b

(?) *Lophophaena* sp.; Petrushevskaya, 1971b, pl. 57, fig. 7.

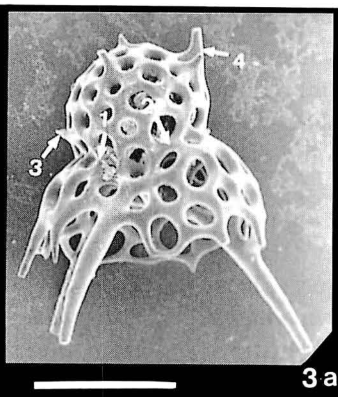
Holotype.—OCU CR-0004 (Ny-81)

Description.—Surface of the shell, especially that of the first segment, has numerous fine spines. The first segment is spherical to subspherical. **AL** and **VL** form a distinct internal ring. Bacause the junction of **AL** and **VL** is situated on a similar horizon to the junction of **A** and **AL**, the furrows and internal ring lie nearly in the same horizon. The apical horn and ventral horn are unbladed and poorly developed. Pores in the first segment are circular to subcircular and randomly arranged, almost equal in size. Axial projection is present. The second segment is bell-shaped with three distinct dorsal and lateral ribs that are indistinct externally. Pores in the second segment are circular to subcircular and randomly arranged, vary in size, with almost all of them being larger than those of the first segment. Generally, the distal end of the second segment is fully open, but in some specimens it tends to be closed by a porous plate. The development of the porous plate is variable. Feet extending from distal end of the second segment are unbladed and longer than the height of the second segment. Some specimens have feet that do not extend from the internal spicules (Figures 8-4a, 4b)

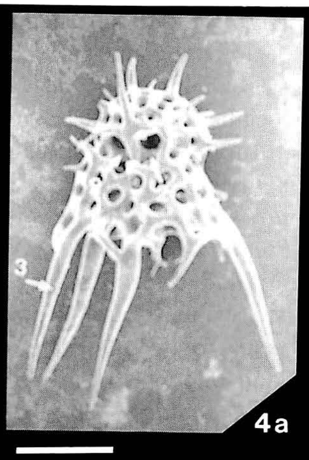
→ **Figure 8.** **1a-2c**: *Lophophaena simplex* Funakawa, sp. nov. **1a, 1b**: OCU CR-0003, NY-89, holotype. 1a: left lateral view; 1b: basal view. Arrow 1 of 1a points to the furrow along **VL**, 2 to the furrow along **AL** and 3 to the ventral horn. **2a, 2b**: NY-89. 2a: right lateral view; 2b: enlargement of oblique basal (right lateral) view; 2c: enlargement of dorsal view. Arrow of 2a points to the ventral horn and 2c to the apical horn. **3a-4b**: *Lophophaena triangula* Funakawa, sp. nov. **3a, 3b**: OCU CR-0004, NY-81, holotype. 3a: left lateral view; 3b: basal view. Arrow 1 of 3a points to the furrow along **VL**, 2 to the furrow along **AL**, 3 to the ventral horn and 4 to the apical horn. **4a, 4b**: NY-81. 4a: dorsal view; 4b: enlargement of basal view. Arrow 1 of 4a points to the apical rib, 2 to the **AL**, 3 to a foot unrelated to the internal spicule and 4b to the ventral horn. Scale bars: 1a, 2a, 3a, 4a = 50 μm; others = 20 μm.



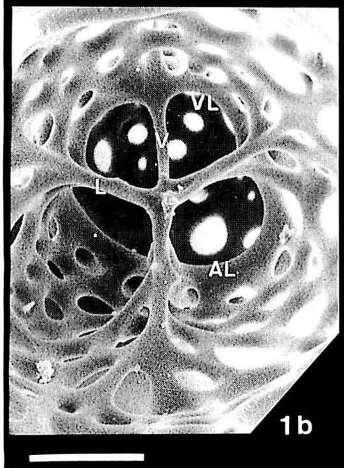
1a



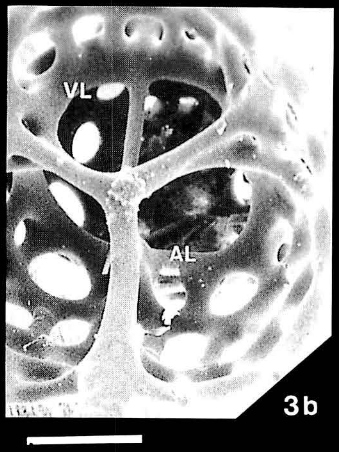
3a



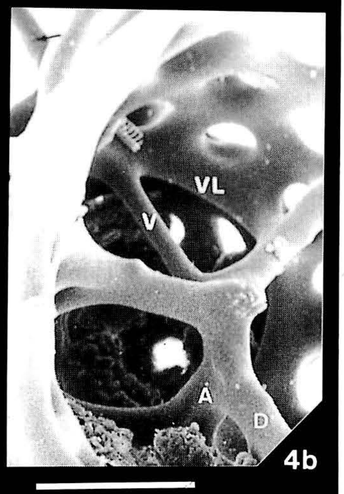
4a



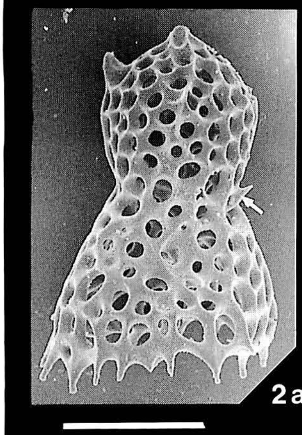
1b



3b

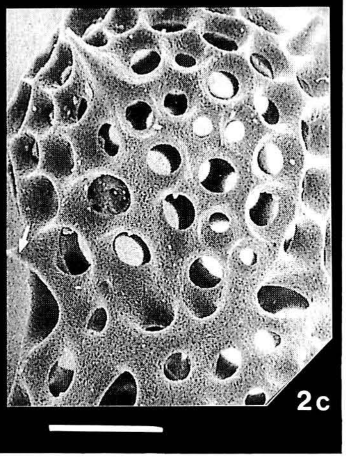


4b



2a

2b



2c

Dimensions.—Measurements are based on nine specimens. The maximum diameter of the first segment is 41-58 (49) μm, of the second segment 72-92 (82) μm, total height of the shell (not including apical horn and distal foot) is 74-96 (83) μm.

Remarks.—This species is distinguished from *Pseudodictyophimus gracilipes* (Bailey) by the unbladed feet and large, almost spherical first segment, and from *Lophophaena simplex* sp. nov. by its three feet and distinct dorsal and lateral ribs. This species is similar to *Lophophaena* sp. of Petrushevskaya (1971b), but pores are larger and fewer than Petrushevskaya's (1971b) species.

Etymology.—The specific name means "triangle" in Latin.

Occurrences.—Ny-65, 69, 81, 89 and Is-1 Few to rare in abundance.

Stratigraphic range.—The upper limit is in the *Denticulopsis katayamae* Zone. The lower limit is not confirmed.

Genus *Marimoum* Funakawa, gen. nov.

Diagnosis.—The skeleton is composed of two segments. Internal skeletal structure is composed of **MB, A, D, L, V, DL, VL** and **AL.** In some specimens, right or left (or both) **1, Al, Dl, Ll** and one **VL-VL** are present. The first segment is bell-shaped to hemispherical and distinguished from the second segment by **DL** and **VL** and the furrows along them in most specimens. When **1, Al, Dl** and **VL-VL** exist, the boundary dividing the two segments consists of **VL, Ll** and **Dl**. At the dorsal side of the first segment, the shell tends to be double-layered. The inner layer includes the apical rib, and the outer one is a cobweb-like meshwork.

Type species.—*Marimoum robustum* Funakawa, sp. nov. (by monotypy).

Remarks—This genus is distinguished from *Amphiplecta* by having **DL** and well-developed outer layer on the dorsal side of the shell. It has a skeleton externally similar to that of *Cryptogyrus* Sugiyama, 1993, but is distinguished from the latter by its distinct **DL**.

Etymology.—The generic name is derived from the Japanese word for spherical algal growths unique to Lake Akan, eastern Hokkaido, Japan (neuter gender).

Marimoum robustum Funakawa, sp. nov.

Figure 9, 1a-4d

Holotype.—OCU CR-0006 (Yd-59)

Description.—Many specimens do not have **1** but one (right or left) or two **1** exist in some specimens. When **1** are present, also present are **Ll** and **Dl** instead of **DL**. The combination of these arches and the angles between **MB** and **1** are variable. The arch composition of the boundary dividing the two segments is **DL** and **VL** in most specimens, **Ll** and **VL**, or **Dl, Ll** and **VL** or **Dl, Ll, VL** and **VL-VL** in a few specimens (Figure 10). The furrows along these arches are indistinct because of the spiny surface of the shell. Indistinct apical horn extends from the apical rib. Surface of the inner layer is spiny, pores there are circular and very small. The outer layer is a cobweb-like meshwork on the dorsal side of the shell. Axial projection. The second segment is less than 1/3 of the height of the first segment and lacks distinct feet. Similar to the first segment, the surface of the second segment is spiny and cobwebby. Internal skeletal elements are characteristi-

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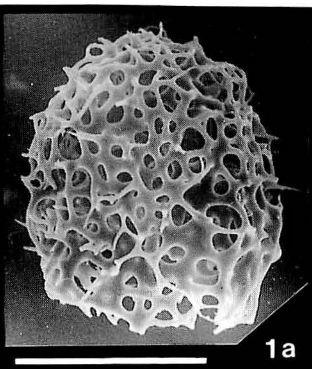
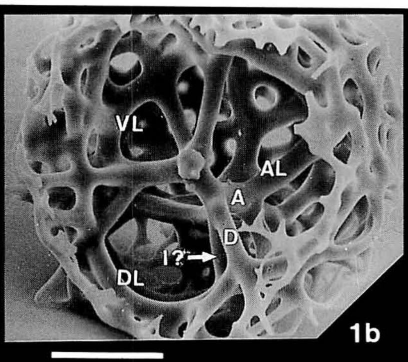
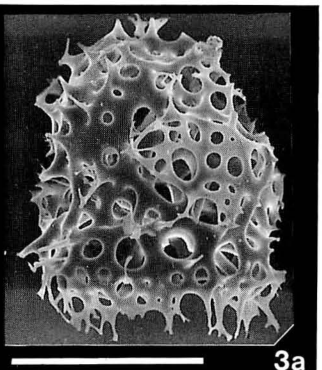
→ **Figure 9. 1a-4d**: *Marimoum robustum* Funakawa, gen. et sp. nov. **1a, 1b**: OCU CR-0006, 91092601, holotype. 1a : ventral to left lateral view ; 1b : basal view. **2a, 2b** : Atc-4. 2a : dorsal to right lateral view; 2b : basal view. Arrow of 2a points to the apical rib. **3a, 3b** : Yd-59. 3a : right lateral view ; 3b : basal view. **4a-4d** : Atc-4. 4a : dorsal to right lateral view ; 4b : basal view ; 4c : enlargement of basal view ; 4d : enlargement of dorsal view. Arrow 1 of 4a points to **1**, 2 to **Al**, 3 to **Dl**, 1 of 4b to **VL-VL**, 2 to **VL**, white arrow of 4c to **Al**, black arrow to **VL-VL** and black arrow of 4d to the apical horn. Scale bars : 1a, 2a, 3a, 4a and 4b = 50 μm, others = 20 μm.



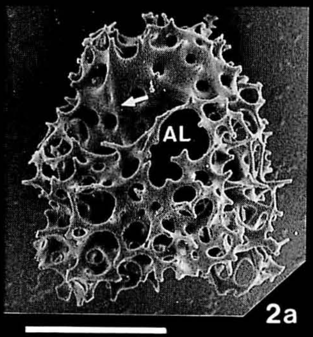
1a



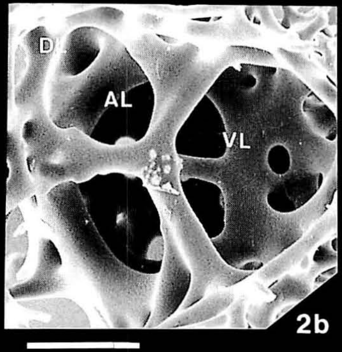
1b



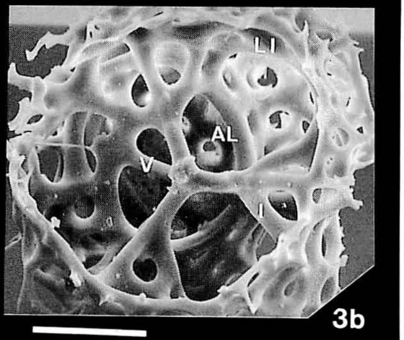
3a



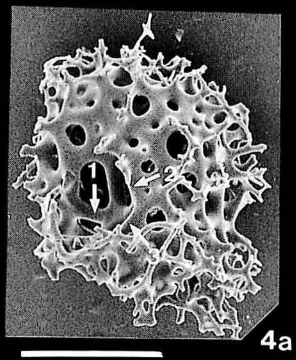
2a



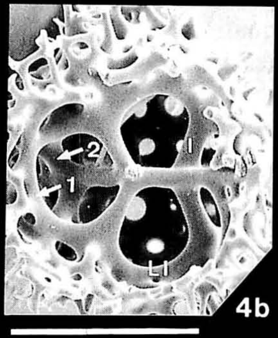
2b



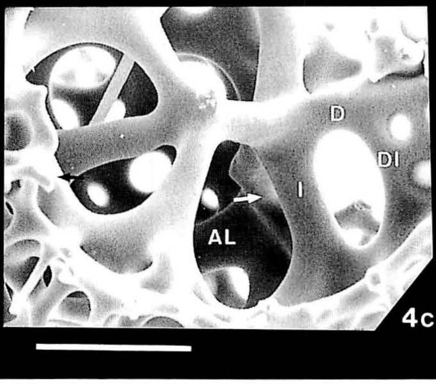
3b



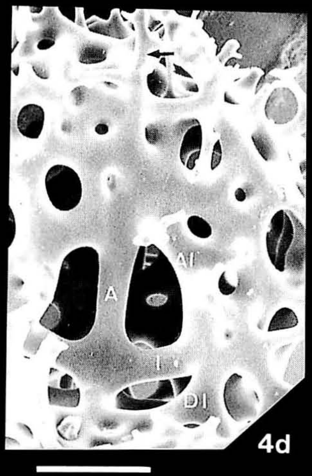
4a



4b



4c



4d

cally robust.

Dimensions.—Measurements are based on 12 specimens. The maximum diameter of the first segment is 39-50 (45) μm, of the second segment 60-81 (69) μm. Total height of the shell is 71-88 (82) μm.

Remarks.—The internal skeletal structures of this species have much variation (Figure 10). One or two **1** are regarded as intraspecific variation because their development and direction are unstable when they exist. In the same way, the elements, **Al, Dl** and **VL-VL** are subject to intraspecific variation, because most specimens lack them and the combination of them varies when they do exist. This species is distinguished from *Cryptogyrus trachylobus* Sugiyama, 1993, by its doublelayered shell on the dorsal side of the shell and its smaller pores in the inner layer of the first segment. It resembles *Botryopera* (?) *leptostraca* Sugiyama, 1993, externally but is distinguished by the internal skeletal structure. This species has shorter skeleton between the junction of **L** and **AL** and the junction of **AL** and **VL** (equal to "L-R" in Sugiyama, 1993) than is the case in *B.* (?) *leptostraca.*

Etymology.—The specific name means "stout" in Latin.

Occurrences.—90102405, 90102414, Yd-53, 59, Atc-4 and 14. Common to few in abundance.

Stratigraphic range.—This species occurs commonly in the *Neodenticula kamtschatica* Zone. The lower limit is in the *Thalassionema schraderi* Zone. In the Atsunai Coast route, this species occurs in the *Thalassionema oestrupii* Zone and its upper limit is not confirmed.

Genus *Peridium* Haeckel, 1881

Type species : *Peridium spinipes* Haeckel, 1887.

Remarks.—The skeleton is composed of two segments. Internal skeletal structure consists of **MB, A, D, L, V, AL** and **VL.** When **V** is not present **LL** is present instead of **VL.** The first segment is large and inverted drop-shaped with a long distinct apical rib and its apex is closed. The shell has circular to subcirular pores. The junction of **A** and **AL** is on the shell. The second segment is poorly developed.

This genus is distinguished from *Amphiplecta* by the inverted-dropshape of the first segment. *Peromelissa* Haeckel, emend. Petrushevskaya, 1971b, and *Arachnocorallium* Haeckel, emend. Petrushevskaya, 1971b, have a similarly shaped first segment but are distinguished from *Amphiplecta* by their well-developed second segment. This genus also resembles *Cryptogyrus* but is distinguished by its shorter skeleton between the junction of **L** and **AL** and the junction of **AL** and **VL** (or **LL**), that is equal to "L-R" in Sugiyama (1993), than in the latter genus.

Peridium sp. aff. *P. spinipes* Haeckel

Figure 11, 1a-1c

aff. *Peridium spinipes* Haeckel, 1887, p. 1154, pl. 53, fig. 9.

Description.—The first segment is large, inverted-drop-shaped. Pores in first segment are circular to subcircular. Surface of the first segment is somewhat spiny. The apex of the first segment is closed. Axial projection is distinct. The second segment is poorly developed and truncated conical-shaped. Pores in the second segment are larger than those in the first segment.

Dimensions.—Measurements are based on only two specimens. The maximum diameter of the first segment is 76-80 μm, total height of the shell (almost equal to that of the first segment) is 96-100 μm.

Remarks.—This species has a skeleton similar to that of *P. spinipes* but differs from the latter species by broader pore bars and the spiny surface of the shell. Skeletal structures of this species resemble the inner layer of *Marimoum robustum* gen. et sp. nov., but it is

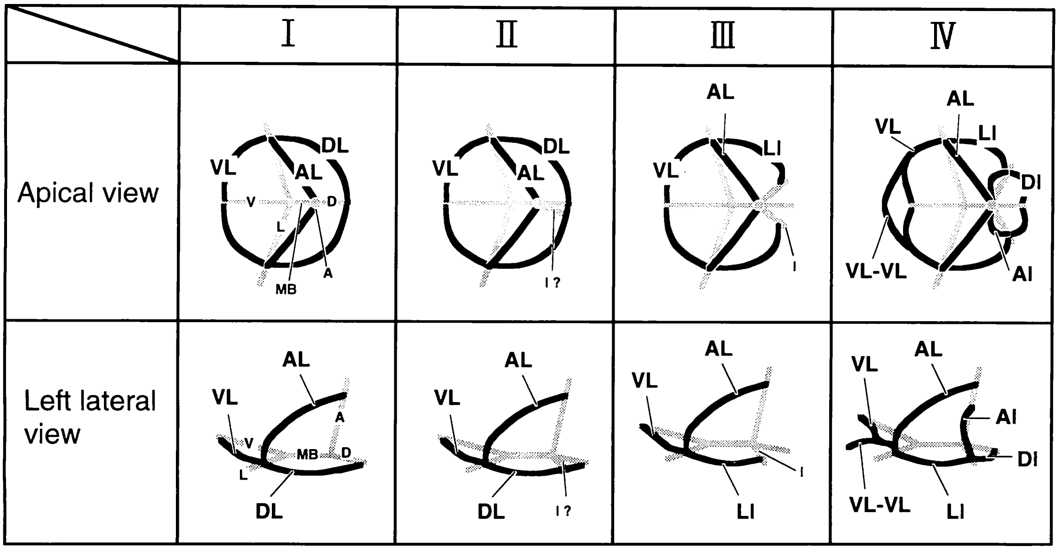


Figure 10. The simplified figures of the internal skeletal structures of *Marimoum robustum*. These figures show the high variability of the internal skeletal structure. Figures in column I are for the specimen of Fig. 9-2; II are for Fig. 9-1, that is the holotype; III are for Fig. 9-3; IV are for Fig. 9-4. In these figures, gray indicates connecting arches and black internal spicules.

distinguished from the latter species by its fine skeleton and the absence of **DL**, and from *Cryptogyrus trachylobus* by its thinner pore bars and its shorter skeletons between the junction of **L** and **AL** and the junction of **AL** and **VL**.

Occurrences.—Only Atc-4. Very rare in abundance.

Stratigraphic range.—Neodenticula kamtschatica Zone.

Peridium sp.

Figure 11, 2a-2b

Description.—**V** and **VL** are absent and **LL** is present instead of **VL, AL** and **LL** form the furrows between two segments. The first segment is cylindrical and its gradual diameter gradient is weak and increases upwardly. Its apex tends to be closed. In the first segment, pores are few, circular to subcircular and randomly arranged. Pore bars are very broad. The apical rib is long and distinct. The apical horn is poorly developed and recognized only as a small projection at the apex of the shell. Axial projection is distinct. The second segment is very poorly developed and recognized only as downwardly directed short spines diverging from **D** and **L**.

Dimensions.—Measurements are based on five specimens. The maximum diameter of the first segment is 64-72 (68) μm, total height of the shell (almost equal to that of the first segment) is 80-100 (94) μm.

Remarks. —The internal skeletal structure of this species is characterized by the absence of **V** and presence of **LL** instead of **VL**. It is unclear whether these characters are particular to this species or a matter of intraspecific variation. This species is distinguished from *Peridium* sp. aff. *P. spinipes* by broader pore bars and fewer pores in the first segment than in the latter species. This species is distinguished from *Amphiplecta acrostoma* by large and few pores.

Occurrences.—Atc-4 and Is-1. Very rare in abundance.

Stratigraphic range.—The upper and lower limits are not confirmed.

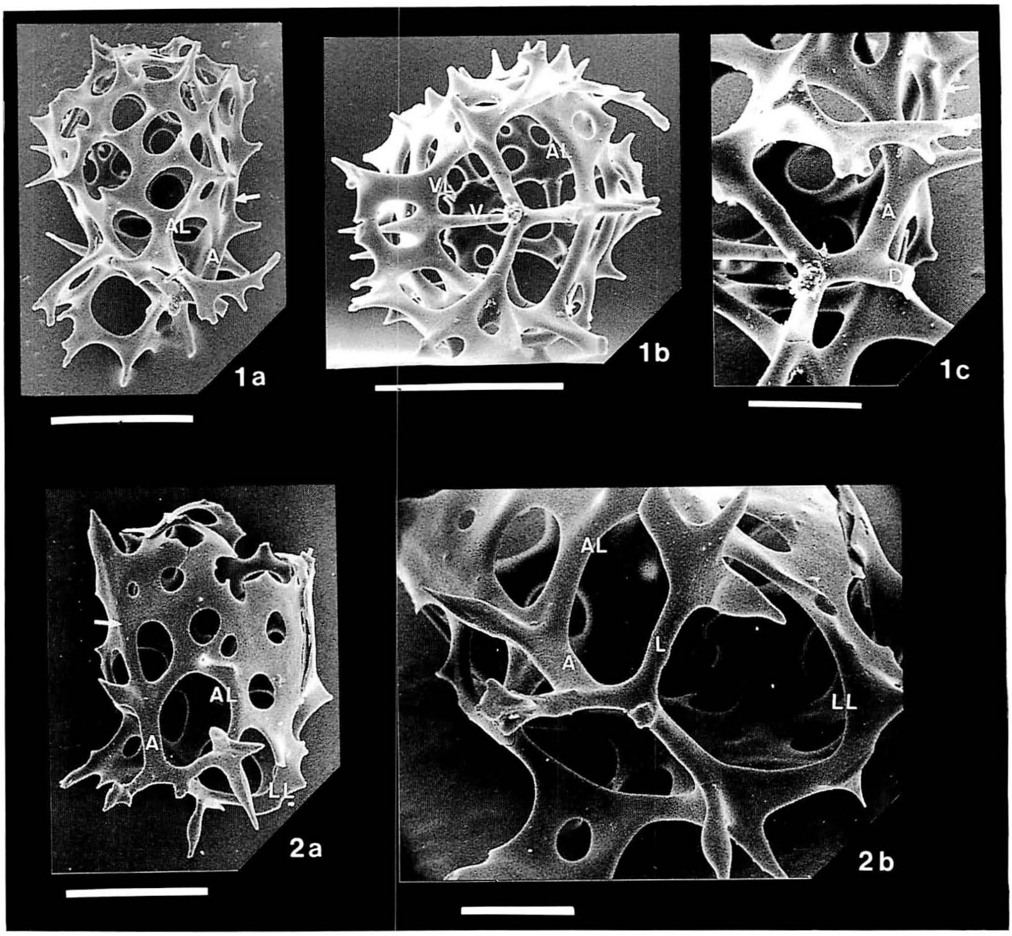


Figure 11. **1a-1c** : *Peridium* sp. aff. *P. spinipes* Haeckel, Atc-4. 1a : left lateral view ; 1b : basal view ; 1c : enlargement oblique basal (left lateral) view. Arrows of 1a and 1c point to the apical rib. **2a, 2b** : *Peridium* sp., 91092607. 2a : dorsal to right lateral view ; 2b : oblique basal (right lateral) view. Arrow of 2a points to the apical rib. Scale bars : 1b, 1c=20 μm ; others=50 μm.

Genus Pseudodictyophimus
Petrushevskaya, 1971b

Type species.—*Dictyophimus gracilipes* Bailey, 1856.

Remarks.—The skeleton is composed of two segments. Internal skeletal structure consists of **MB, A, D, L, V, AL** and **VL**. The junction of **A** and **AL** is on the shell. The first segment is hemispherical with short apical rib. The second segment is bell-shaped with three distinct dorsal and lateral ribs.

Pseudodictyophimus gracilipes (Bailey)

Figure 12, 1a-1b

Dictyophimus gracilipes Bailey, 1856, p. 4, pl. 1, fig. 8.
Pseudodictyophimus gracilipes (Bailey) ; Petrushevskaya, 1971b, pl. 48, figs 1, 3-6, pl. 49, figs. 6-7.
Pseudodictyophimus sp. ; Nishimura, 1990, p. 96, pl. 18, figs. 5a-b (not pl. 16, figs. 9-10b).

Remarks.—Surface of the shell is smooth without spines. The apical horn is fine and unbladed. The ventral horn extends obliquely upward and is almost as long as the apical horn. Pores in the first segment are circular to subcircular and randomly arranged. Axial projection is distinct. The second segment is bell-shaped and its horizontal section is weakly trigonal because of distinct dorsal and lateral ribs. Pores in the second segment are circular to subcircular and randomly arranged, larger than those of the first segment. Distal end of the second segment is fully open. Three-bladed distal feet extend outside from near the end of the second segment, and their length is equal to or greater than the diameter of the second segment.

Pseudodictyophimus sp. in Nishimura (1990) has skeletal structures almost the same as in this species except for the presence of **AD**. Nishimura's (1990) species may be included in this species because the present study confirms that the development of the skeleton-like **AD** in this species is a matter of intraspecific variation.

Dimensions.—Measurements are based on 25 specimens. The maximum diameter of the first segment is 21-35 (30) μm, of the second segment 50-88 (72) μm, total height of the shell (not including apical horn and distal feet) is 42-76 (62) μm.

Occurrences.—All samples. Common to rare in abundance.

Stratigraphic range.—All zones. The upper and lower limits are not confirmed.

Pseudodictyophimus tanythorax
Funakawa, sp. nov.

Figure 12, 2a-3b

Holotype.—OCU CR-0005 (Oik-7)

Description.—Surface of the shell is smooth, without spines. The first segment is hemispherical. The apical horn is unbladed or three-bladed. The ventral horn is shorter than the apical horn. Pores in the first segment are circular to subcircular and randomly arranged. Axial projection is distinct. Development of the second segment is variable but in most specimens it is well-developed. Pores in the second segment are circular to subcircular and randomly arranged, vary in size, being generally larger than those of the first segment. The distal end of the second segment is fully open and surrounded by teeth. Three-bladed feet extend outside at the lower part of the second segment.

Dimensions.—Measurements are based on 24 specimens. The maximum diameter of the first segment is 28-40 (33) μm, the second segment is 63-85 (70) μm, total height of the shell (not include apical horn and distal teeth) is 58-100 (79) μm.

Remarks.—This species has a highly variable skeleton due to the development of the second segment and feet. This species is distinguished from *P. gracilipes* by its long and stout apical horn and straightly prolonged feet. It is distinguished from *Lophophaena triangula* sp. nov. by its long and stout apical horn and a smaller first segment than in the latter species.

Etymology.—The specific name means "long thorax" in Greek.

Occurrences.—All samples. Common to very rare in abundance.

Stratigraphic range.—All zones. The upper and lower limits are not confirmed.

Genus *Tripodocyrtis* Funakawa, gen. nov.

Type species—*Tripodocyrtis elegans* Funakawa, sp. nov. (by monotypy).

Diagnosis.—The skeleton is composed of two segments. Internal skeletal structure consists of **MB, A, D, L** and **AL**. The junction of **A** and **AL** is on the shell. Connecting arches in this genus comprise only **AL**, without **VL** or **LL**. The first segment is distinguished from the second segment at the apical to lateral side by the furrows along **AL**, but at the ventral side the boundary between the two segments is not recognizable because **VL** and **LL** are absent. The first segment is hemispherical with a short apical rib. The second segment is widely expanded bell-shaped with three distinct dorsal and lateral

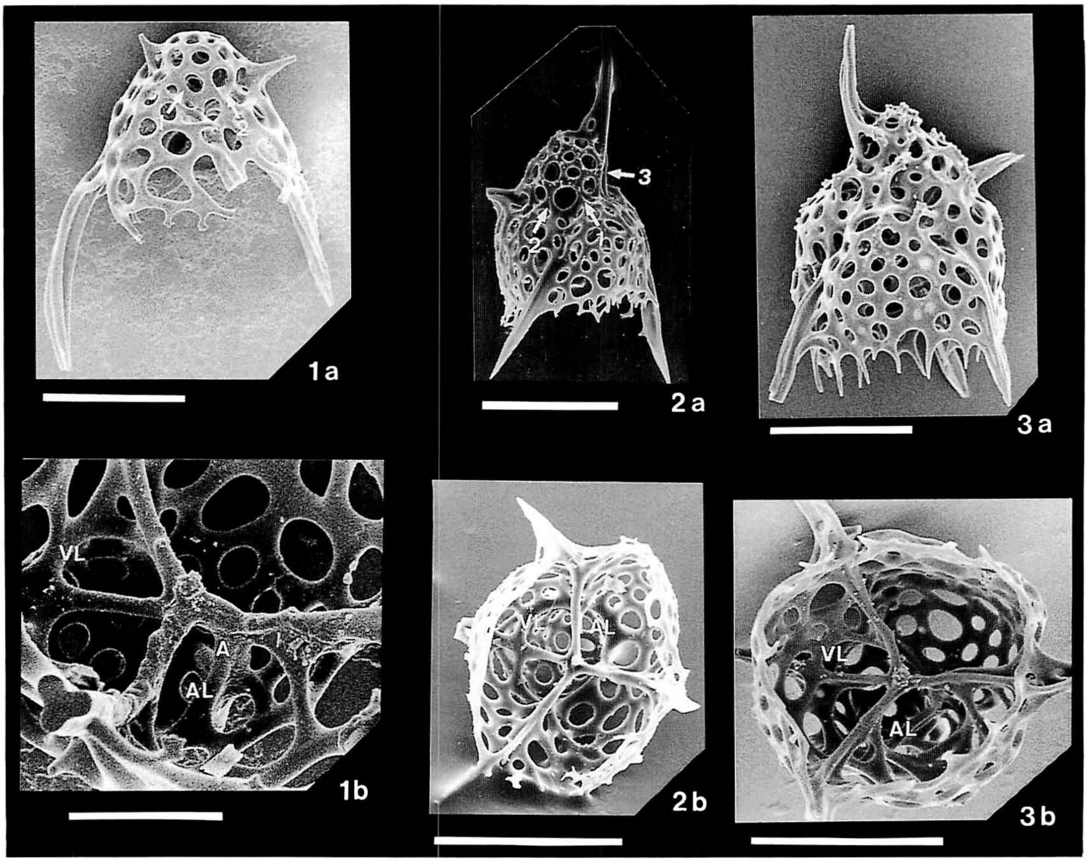


Figure 12. **1a, 1b** : *Pseudodictyophimus gracilipes* (Bailey), Ny-81. 1a : right lateral view ; 1b : oblique basal (right lateral) view. Arrow 1 of 1a points to the furrow along **AL**, 2 to the furrow along **VL**. **2a-3b** : *Pseudodictyophimus tanythorax* Funakawa, sp. nov. **2a, 2b** : OCU CR-0005, Ny-69, holotype. 2a : left lateral view ; 2b : basal view. Arrow 1 of 2a points to the furrow along **AL**, 2 to the furrow along **VL** and 3 to the apical rib. **3a, 3b** : Is-1. 3a : right lateral view ; 3b : basal view. Scale bars : 1b=20 μm ; others=50 μm.

ribs extending to distal feet.

Remarks.—This genus is distinguished from *Pseudodictyophimus, Ceratocyrtis* and *Lophophaena* by the absence of **V, VL** and **LL**.

Etymology.—The generic name means "three feet basket" in Greek (masculine gender).

Tripodocyrtis elegans Funakawa, sp. nov.

Figure 13, 1a-2b

Dictyophimus sp. cf. *D. platycephalus* Haeckel ; Nishimura, 1990, p. 17, fig. 7.

Holotype.—OCU CR-0001 (Ny-89)

Description.—The shell is somewhat spiny. The apical horn is unbladed, very weak and shorter than the cephalic height. Pores in the first segment are circular to subcircular and randomly arranged. Axial projection is distinct. The horizontal section of the second segment is somewhat triangular because of three distinct dorsal and lateral ribs. Pores in the second segment are circular to subcircular and randomly arranged, generally they are larger than those of the first segment. Three feet extend downward at the distal end of the second segment. Feet are long, unbladed and almost equal to the diameter of the second segment. The distal end of the second segment is fully open.

Dimensions.—Measurements are based on 18 specimens. The maximum diameter of the first segment is 30–47 (36) μm, of the second segment 60–102 (77) μm, total height of the shell (not including apical horn and feet) is 36–65 (53) μm.

Remarks.—This species is distinguished from *Pseudodictyophimus gracilipes* by the absence of the furrows at the ventral side. This species is distinguished from *Pseudodictyophimus gracilipes tetracanthus* (Popofsky) in Petrushevskaya (1971b) by the unbladed feet. It differs from *Dictyophimus platycephalus* Haeckel by its weak apical horn and incomplete furrows between the first and second segments. *Dictyophimus* sp. cf. *D. platycephalus* Haeckel in Nishimura (1990) has been described as having **AD**. In this study, although some specimens placed into this species have an indistinct skeleton-like **AD**, most specimens lack it. Therefore the skeleton-like **AD** is not stable at the specific level and its existence is regarded as a matter of intraspecific variation within this species.

Etymology.—The specific name means "elegance" in Latin.

Occurrences.—90102405, 90102414,

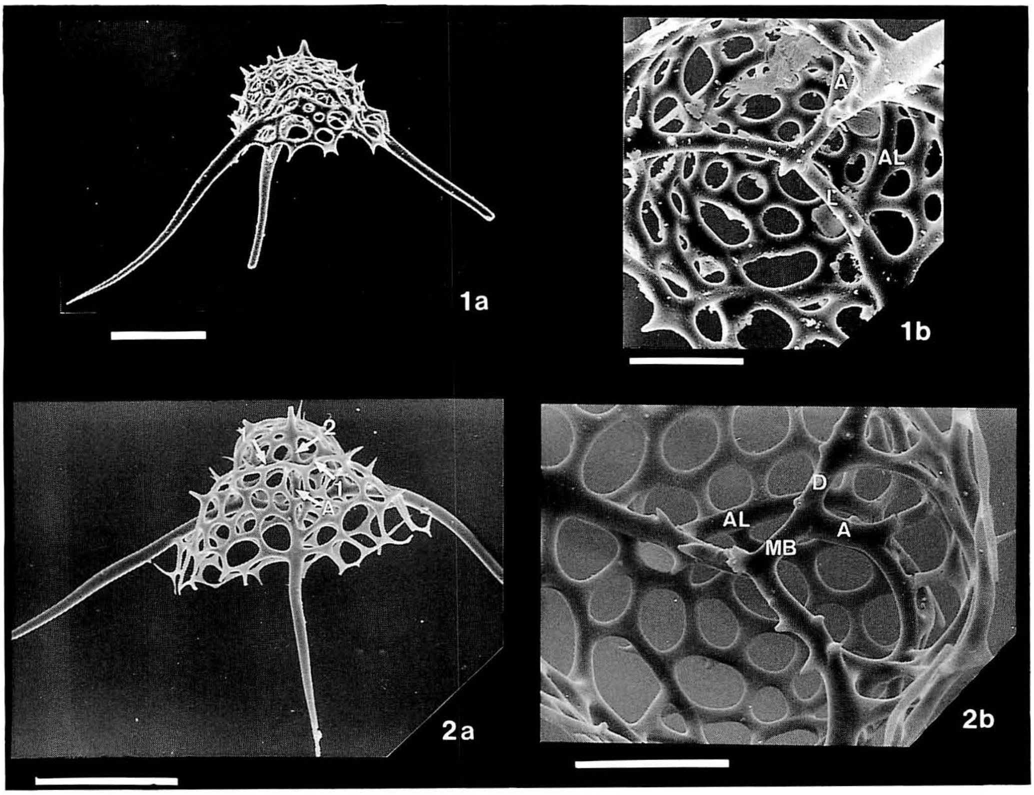


Figure 13. **1a-2b**: *Tripodocyrtis elegans* Funakawa, gen. et sp. nov. **1a, 1b**: OCU CR-0001, Ny-89, holotype. **1a**: ventral view; **1b**: basal view. **2a, 2b**: Oik-6. **2a**: dorsal view; **2b**: basal view. Arrow 1 of **2a** point to the furrows along **AL**, 2 to the apical rib. Scale bars: **1a** and **2a** = 50 μm; **1b**, **2b** = 20 μm.

91092601, 91092607, Oik-6, 7, Ny-81, 89, Atc-4, 14 and Is-1. Few to very rare in abundance.

Stratigraphic range.—All zones. The upper and lower limits are not confirmed.

Subfamily Clathromitrinae Petrushevskaya, 1971b

Genus *Corythomelissa* Campbell, 1951

Type species : *Lithomelissa corythium* Ehrenberg, 1873.

Remarks.—The skeleton is composed of two segments. Internal skeletal structure consists of **MB, A, D, V, L, AL, VL** and **AL-AL**. The junction of **A** and **AL** is inside the shell, so the furrows along **AL** are incomplete. **AL-AL** is at the dorsal side of the shell and forms a weak furrow. The first segment is distinguished from the second segment by the furrows along **AL-AL, AL** and **VL**. The first segment is hemispherical to cup-shaped without the apical rib. The apical horn extends from **A** directly at or near the apex of the first segment. The second segment is bell-shaped with distinct dorsal and lateral ribs that extend downward as distal feet.

Corythomelissa horrida Petrushevskaya

Figure 14, 1a-1b

Corythomelissa horrida Petrushevskaya, 1975, p. 589-590, pl, 11, figs. 14-15, pl. 21, fig. 9.

Remarks.—The skeleton is composed of two segments. The shell is very robust and its surface is spiny. The furrows subdividing the first and second segments are indistinct because of the many spines on the shell. The first segment is hemispherical or cup-shaped. The apical horn is robust and three-bladed. The ventral horn is three-bladed, shorter and narrower than the apical horn. Pores in the first segment are subcircular and randomly arranged. Axial projection is distinct. Feet are three-bladed and their length is generally less than the diameter of the second segment. In most specimens, the distal end of the second segment is fully open but, in some specimens, it tends to be closed by a porous plate. The development of the porous plate is variable. Pores in the second segment are circular to subcircular and randomly arranged. This species is identified as *C. horrida* although it is somewhat larger than Petru-

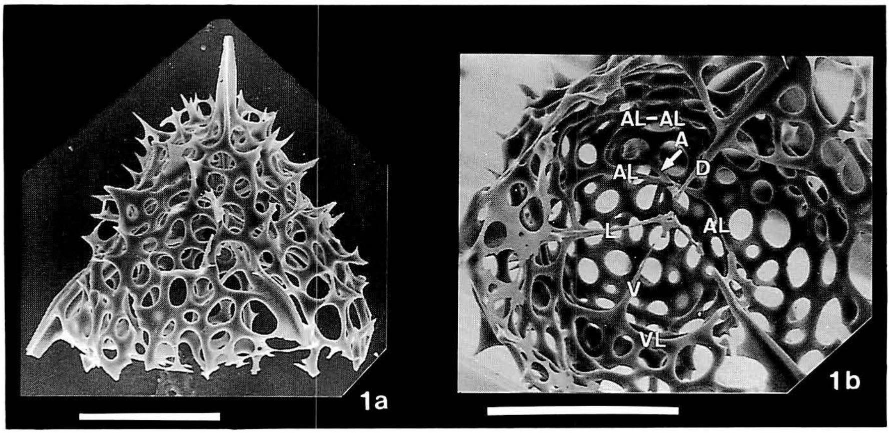


Figure 14. **1a, 1b** : *Corythomelissa horrida* Petrushevskaya, Oik-7. 1a : dorsal view ; 1b : basal view. Scale bars : =50 μm.

shevskaya's (1975) specimens.

Dimensions.—Measurements are based on 11 specimens. The maximum diameter of the first segment is 56–68 (63) μm, of the second segment 106–144 (120) μm. Total height of the shell (not including apical horn and distal feet) is 74–126 (96) μm.

Occurrences.—91092607, Oik-6, 7, Ny-81, 89, Atc-4, 14 and Is-1. Very rare in abundance.

Stratigraphic range.—All zones. The upper and lower limits are not confirmed.

Genus *Euscenarium* Haeckel, 1887, sensu. Petrushevskaya, 1981

Type species: *Euscenium tricolpium* Haeckel, 1887.

Remarks.—The skeleton is composed of two segments. Internal skeletal structure consists of **MB, A, V, D, L, DL, VL, AL** and **AD**. The first segment is hemispherical to bell-shaped, large and well-developed with an apical horn. The apical horn extends directly from **A** near the apex of the first segment. The first segment is distinguished from the second segment by **DL** and **VL** and furrows along them. The second segment is poorly developed with distinct dorsal and lateral ribs that extend downward as distal feet.

Euscenarium sp. aff. *E. tricolpium* (Haeckel)

Figure 15, 1a-1b

aff. *Euscenium tricolpium* Haeckel, 1887, p. 1147, pl. 53, fig. 12.

aff. *Archiscenium tricolpium* (Haeckel); Petrushevskaya, 1971b, p. 75, pl. 36, fig. 2. = *Euscenarium tricolpium* (Haeckel); Petrushevskaya, 1981, fig. 28.

(?) *Cladoscenium tricolpium* (Haeckel); Jørgensen, 1905, p. 134, pl. 15, figs. 71–73.

Description.—In the first segment, the shell is constricted by three longitudinal furrows along **AL** and **AD** where they are in the shell. The first segment is bell-shaped and its surface is smooth without spines, pores are absent in most specimens. When pores are present, they are circular and very small. Three-bladed apical horn is very stout. The ventral horn extends horizontally, shorter and narrower than the apical horn. In some specimens, **A** has a pair of distinct trigonal or spiny lateral projections on its middle part. **D** has a pair of trigonal lateral projections. Axial projection is distinct. The second segment is composed of a porous wall with teeth around its distal end. Dorsal and lateral ribs are distinct. Three feet, which extend from dorsal and lateral ribs, are three- or four-bladed and well-developed. They almost equal in length the height of the first segment.

Dimensions.—Measurements are based on nine specimens. The maximum diameter of the first segment is 50–78 (64) μm, of the second segment 56–88 (77) μm. Total height of the shell (not including apical horn and distal feet) is 57–82 (71) μm.

Remarks.—This species resembles *Euscenium tricolpium* Haeckel, 1887, and *Euscenarium tricolpium* (Haeckel) in Petrushevskaya (1971b) but differs from them by the dorsal side of the first segment. In *Euscenium tricolpium* and *Euscenarium tricolpium,* the dorsal side of the first segment is composed of little, narrow bars interconnected but in this species that part is composed of a robust wall with a few small pores.

Occurrences.—90102405, 90102414, 91092601, Yd-53, 59, Atc-4 and 14. Rare to very rare in abundance.

Stratigraphic range.—In the Atsunai Coast route, this species occurs in the *Thalassiosira oestrupii* Zone and the upper limit is not confirmed. The lower limit is in the *Thalassionema schraderi* Zone.

Euscenarium (?) sp.

Figure 15, 2a-2b

Description.—The first segment is hemispherical, and its shell is robust. Pores in the first segment are circular to subcircular, randomly arranged and variable in size. The apical horn is three-bladed and smaller in length than the height of the first segment. **V** extends horizontally to a ventral horn that is unbladed and generally poorly developed, and which is shorter than the apical horn. **D** has a pair of lateral projections and **A** has a pair of trigonal or spiny lateral projections and a dorsal projection. **AD** is recognized distinctly only near the junction from **A.** Axial projection is distinct. The second segment is poorly developed, truncated conical to subcylindrical with dorsal and lateral ribs. Pores in the second segment are circular to subcircular, randomly arranged and equal in size to those in the first segment. Three long feet are three-bladed and generally their length is larger than the diameter of the second segment. The height of the second segment is less than that of the first segment, and its diameter is 1.5 times that of the first segment.

Dimensions.—Measurements are based on only two specimens. The maximum diameter of the first segment is 75-77 μm, of the second segment 54-62 μm. Total height of the shell (not including apical horn and distal feet) is 107-135 μm.

Remarks.—This species is distinguished from *Pseudodictyophimus gracilipes* and *Tripodocyrtis elegans* by the furrows along **DL** and **VL** and an internal ring formed by **DL** and **VL.** It is distinguished from *Euscenarium* sp. aff. *E. tricolpium* by its porous first segment. The generic assignment of this species is questionable because three furrows along **AL** and **AD** on the first segment are absent (see the description of *Euscenarium* in Haeckel, 1887, p. 1146). In this study, this species is included in *Euscenarium* because of the similarity of the internal skeletal structure between this species and *Euscenarium* sp. aff. *E. tricolpium.* Further study is needed to confirm the generic assignment of this species.

Occurrences.—Only Ny-81. Very rare in abundance.

Stratigraphic range.—*Denticulopsis katayamae* Zone.

Subfamily Sethoperinae Haeckel, emend. Petrushevskaya, 1971a

Genus *Clathrocorys* Haeckel, 1881

Type species: *Clathrocorys* Haeckel, 1887.

Clathrocorys (?) sp.

Figure 15, 3a-3b

Clathocorys sp.; Nakaseko and Nishimura, 1982, pl. 49, fig. 4.

Description.—The skeleton is composed of two segments. Internal skeletal structure consists of **MB, A, D, L, V, AL, AD, DL** and **LL. V** extends obliquely upward and protrudes outside as the ventral horn at the lower part of the first segment. **VL** is absent. The first segment is large, hemispherical and distinguished from the second segment by distinct furrows along **DL** and **LL**, and by a well-developed internal ring formed by these arches. The shell of the first segment is robust with fine spines. Three-bladed apical horn is stout and extends directly from **A** at the apex of the first segment. The ventral horn is very poorly developed and recognized only as a fine spine. Parts of **AD** and **AL** are almost in the shell. Three ribs located on the outside of the first segment along **AL** and **AD** connect the apical horn and the three feet. In the first segment, pores are very small or absent. The second segment is composed of a latticed wall, pyramidal and triangular in horizontal section with three distinct dorsal and lateral ribs. Pores in the second segment are subcircular to irregular in shape and randomly arranged.

Dimensions.—Measurements are based on seven specimens. The maximum diameter of the first segment is 57-72 (63) μm, of the second segment 80-240 (143) μm. The maximum height of the first segment is 41-52 (47) μm, total height of the shell 60-224 (122) μm.

Remarks.—The generic assignment is questionable because the species differs in external

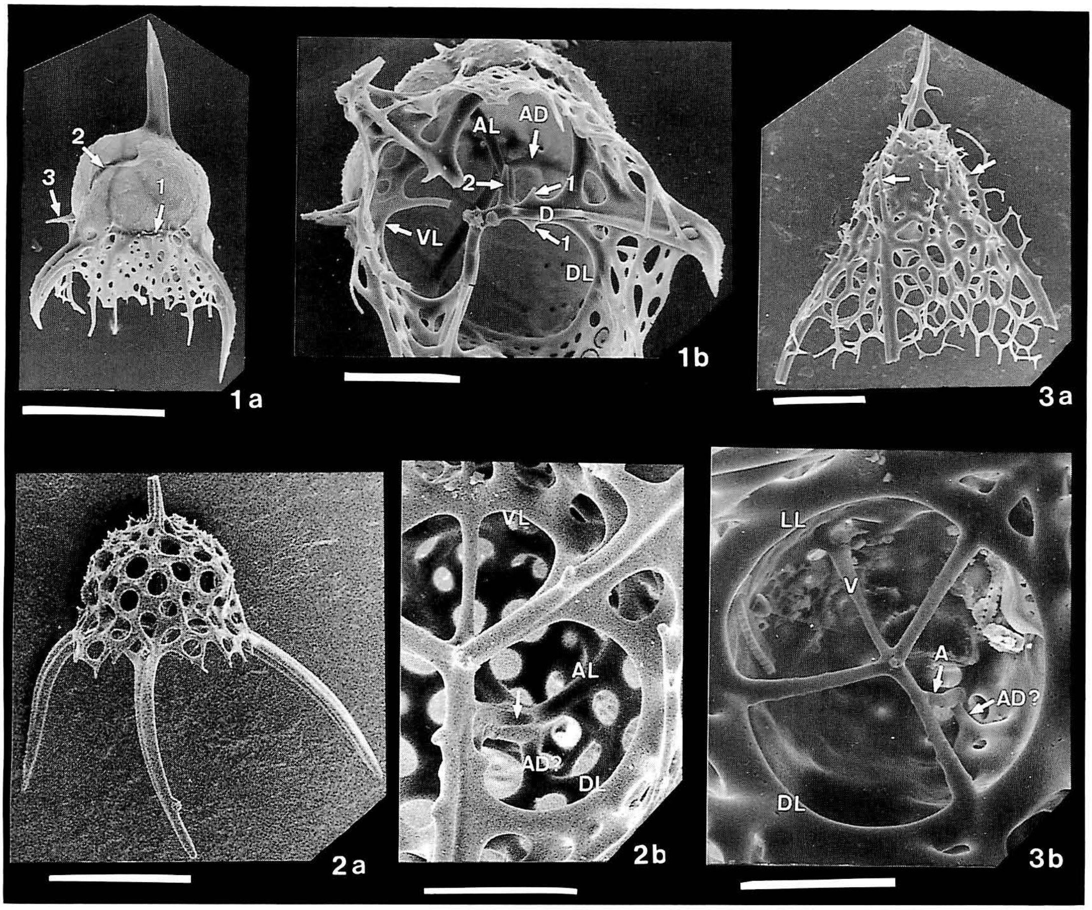


Figure 15. **1a, 1b**: *Euscenarium* sp. aff. *E. tricolpium* (Haeckel), 91092601. 1a: left lateral view; 1b: basal view. Arrow 1 of 1a points to the furrow along **DL**, 2 to the furrow along **AL**, 3 to the ventral horn, 1 of 1b to the projections of **D** and 2 to the projection of **A**. **2a, 2b**: *Euscenarium* (?) sp., Ny-81. 2a: dorsal view; 2b: enlargement of basal view. Arrow of 2a points to the projection of **A**. **3a, 3b**: *Clathrocorys* (?) sp., 90102414. 3a: ventral to right lateral view; 3b: enlargement of basal view. Arrows of 3a point to ribs along **AL**. Scale bars: 1a, 2a and 3a = 50 μm; others = 20 μm.

form from the type species, *C. murrayi*, the internal skeletal struture of which is unknown. In this paper, the generic name, *Clathrocorys*, is used for this species following Haeckel (1887). The second segment of this species tends to be broken, so the diameter and height of the second segment are very unreliable. This species is distinguished from *Euscenarium* (?) sp. by the three distinct external ribs on the first segment .

Occurrences.—90102405, 90102414, Yd-53 and Atc-4. Rare to very rare in abundance.

Stratigraphic range.—In the Atsunai Coast route, this species occurs in the *Thalassiosira oestrupii* Zone and the upper limit is not confirmed. The lower limit is in the *Neodenticula kamtschatica* Zone

Discussion

The constant internal skeletal elements at the generic level are **MB, A, L, D, AL, VL,** (LL), **DL** and **AL-AL**. Detailed observation of the internal skeletal structures of Plagiacanthidae makes the following clear. Development of **V** is variable in some species. *Clathocorys* (?) sp. has **LL** constantly but **VL** are absent. When **V** is lacking, **LL** is constant in Lophophaeninae except for *Tripodocyrtis.* Development of **AD** is also variable in some genera. Only two species, *Euscenarium* sp. aff. *E. tricolpium* and *Clathrocorys* (?) sp. have **AD** consistently, other species have poorly developed **AD** recognized only as an indistinct skeletal element. In some specimens included in *Marimoum robustum,* **l, AL, Ll, Dl** and **VL-VL** are present but they fall within the intraspecific variation of this species as mentioned in the remarks on this species. **V, AD, l, Al, Ll, Dl** and **VL-VL** are therefore apparently not of value for the suprageneric classification of Plagiacanthidae.

The correlation between the internal and external skeletal structures is clarified. Connecting arches that are constant at the generic level control completely the boundary between the first and second segments. This indicates that the boundary between the two segments is the most important criterion for suprageneric taxonomy within the Plagiacanthidae.

In this study, the following three groups are recognized in Plagiacanthidae (Figure 16), characterized by the composition of connecting arches that form the boundary between the two segments. The generic composition of each group is also shown in Figure 16.

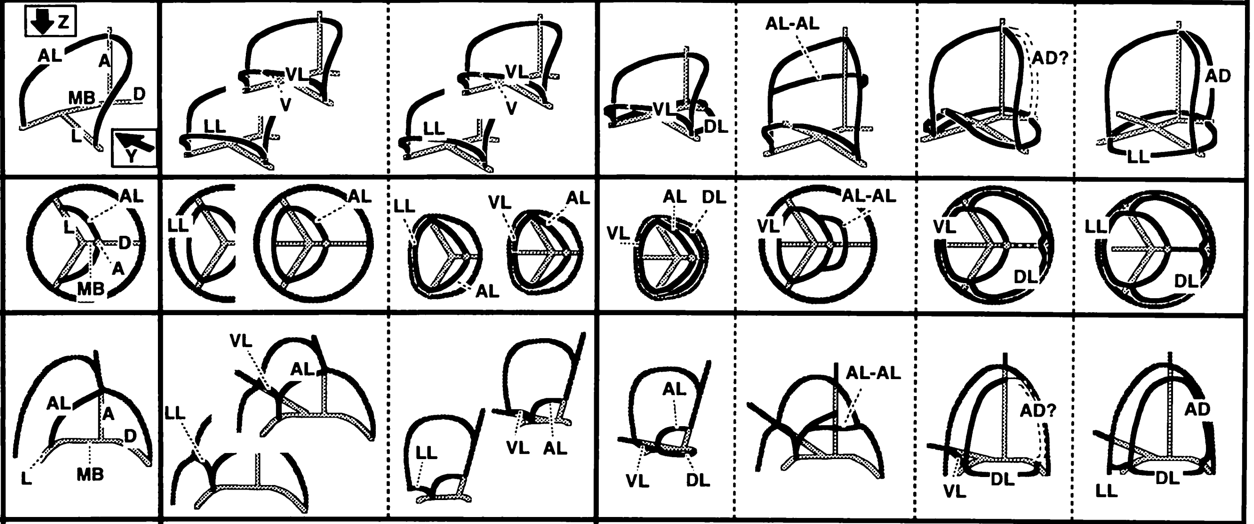
- Group 1 : Internal spicules are composed of **MB, A, D** and **L.** Connecting arches are composed only of **AL.** The boundary between the two segments is restricted to the apical to lateral side of the shell, the furrows are formed along **AL. MB** is situated inside the second segment. This group is monogeneric.
- Group 2 : Internal spicules are composed of **MB, A, D, L,** and **V.** Connecting arches are composed of **AL** and **VL.** The boundary between the two segments completely encircles the shell, the furrows are formed along **VL** or **LL** on the ventral side and along **AL** on the apical to lateral side. **MB** is situated inside the second segment. This group is polygeneric.
- Group 3 : Internal spicules are composed of **MB, A, D, L,** and **V.** Connecting arches are composed of **AL, LV (LL)** and **DL.** The boundary between the two segments completely encircles the shell. The furrows are formed along **VL** or **LL** at the ventral side and along **DL** or **AL** and **AL-AL** at the dorsal side. **MB** is situated near the boundary of the first and second segments. This group is polygeneric.

The correlation between these groups and subfamilies of Petrushevskaya (1971b) is that all genera of groups 1 and 2 are included in Lophophaeninae, while two genera of group 3 are in Clathromitrinae, one is in Sethoperinae and the other in Lophophaeninae (Figure 16).

These three groups in the present study are effective to establish a phylogenetic classification at the suprageneric (family and subfamily) level. In this study, the following two phylogenetic problems are pointed out.

Corythomelissa horrida has some skeletal similarties with *Euscenarium* and *Clathrocorys,* such as the absence of the apical rib and the presence of the arches on the dorsal side of the shell. In the present study, although differences exist in the internal skeletal structure, in that *C. horrida* has **AL-AL** and the latter two have **DL,** this species is included in group 3 based on the skeletal similarities among these three taxa. To explicate the group to which this species belongs, study of the internal skeletal structures of its ancestral forms is needed.

Another problem concerns the taxonomic complex formed by groups 2 and 3. The inner layer of the first segment of *Marimoum* gen. nov., which has **DL,** is similar to the first segment of *Peridium,* which does not have **DL.** Although they are included in different



	GROUP 1	GROUP 2		GROUP 3			
Arches subdividing two segments	only **AL**	**AL** and **VL** or **AL** and **LL**		**DL** and **VL**	**AL**, **AL-AL** and **VL**	**DL** and **VL**	**DL** and **LL**
Z Apical view							
Y Left lateral view							
Composition of internal skeletal elements	**MB**, **A**, **D**, **L**; **AL**	**MB**, **A**, **D**, **V**, **L**; **AL** and **VL** (**LL** instead of **VL** when **V** lacks)		**MB**, **A**, **D**, **V**, **L**; **AL** and **VL** **DL**	**AL-AL**	**DL** and **AD?**	**DL**, **LL** and **AD**
Generic composition	*Tripodocyrtis*	*Amphiplecta* *Ceratocyrtis* *Lophophaena* *Pseuedodictyophimus*	*Peridium*	*Marimoum*	*Corythomelissa*	*Euscenarium*	*Clathrocorys*
Subfamilies of Petrushevskaya (1971b)	Lophophaeninae				Clathromitrinae		Sethoperinae

Figure 16. Three groups of the Plagiacanthidae based on the composition of connecting arches that form the boundary between the first and second segments. Figures of *Marimoum* are for the holotype specimen of *Marimoum robustum*. In these figures, black indicates connecting arches, light gray internal spicules, and dark gray the shell wall. Composition of the internal skeletal elements, generic compositions and correlation between these groups and the subfamilies of Petrushevskaya (1971b) are shown.

groups in this study, it is possible that they are somewhat phylogenetically correlated based on the skeletal similarity mentioned above. On the other hand, two genera of group 2, *Ceratocyrtis* and *Pseudodictyophimus,* have different skeletal characters from *Peridium,* for example, their small hemispherical first gegment and well-developed second segment. These skeletal differences indicate that the former two genera may differ in phylogeny from the latter one, although their internal skeletal stuctures are similar. These taxonomic complexes indicate that group 2 is polyphyletic, with one of its memebers phylogenetically correlated with a member of group 3.

The skeletal structures of Plagiacanthidae treated in this study are limited during the late Miocene age. In order to elucidate the above phylogenetic problems, it is necessary to study them phylogenetically for a longer time interval, for example, Paleogene to Recent.

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北海道東部，上部中新統から産出するPlagiacanthidae科：北海道東部に分布する上部中新統の珪藻質シルト岩からは，保存の良好な放散虫化石が多産する。Plagiacanthidae科は放散虫化石群集の主要構成種群であり，2新属6新種を含む10属16種を識別した。得られた個体の内部骨格の詳細な観察から，種内で変化する内部骨格形質，種レベルおよび属レベルで安定となる内部骨格形質を識別した。属レベルで安定となる内部骨格形質は，属より高次の分類を行う上で非常に有効である。このうち，個体のfirst segmentとsecond segmentを区別するconnecting archの構成は，Plagiacanthidae科の形態を規制する最も重要な要素である。本研究では，このconnecting archの構成に基づいてPlagiacanthidae科を3分類群に識別した。また，これらの分類群における系統学的な問題点を明らかにした。

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972. DISCOVERY OF MIDDLE PENNSYLVANIAN FUSULINACEANS AND CONODONTS FROM THE COPACABANA GROUP IN THE LAKE TITICACA REGION, BOLIVIA*

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Abstract. Fusulinaceans and conodonts indicating the Atokan (early Middle Pennsylvanian) of North America are now discovered for the first time from the lower part of the Copacabana Group which was previously considered Virgilian (latest Pennsylvanian) to Leonardian (early Middle Permian) in age. The fusulinaceans, *Profusulinella* sp. indet. and *Profusulinella munda* Thompson, and conodonts, *Diplognathodus orphanus* (Merrill), *Idiognathodus delicatus* Gunnell and *Neognathodus medadultimus* Merrill are described and illustrated. These faunules may be included in the Midcontinent-Andean Province.

Key words. *Profusulinella*, Conodonts, Lake Titicaca region, Copacabana Group, Middle Pennsylvanian.

Introduction

Since 1980, Sakagami and his collaborators have been working on a biostratigraphic study of the Upper Paleozoic Copacabana Group in Central Andes. Three succeeding fusulinacean zones, the *Triticites* Zone, *Pseudoschwagerina* Zone and *Eoparafusulina* Zone, have been established in the Copacabana Group around Lake Titicaca (Sakagami, ed., 1984, 1986). Furthermore, after reviewing, revising and correlating the stratigraphic sections, Sakagami *et al*. (1991) placed the boundary between the Carboniferous and Permian at the base of the *Pseudoschwagerina* Zone in the Copacabana Group. At the same time, they also noted that the "*Triticites* Zone" of the Copacabana Group in the Cuyavi and Yampupata routes was abnormally thicker than in the Yaurichambi, Ancoraimes, and Matilde routes. During our laboratory work, we discovered some fusulinaceans and conodonts indicating an Atokan (Pennsylvanian) age for the "*Triticites* Zone" in the Cuyavi and Yampupata routes.

Map of the study area around Lake Titicaca is shown in Figure 1.

Acknowledgements

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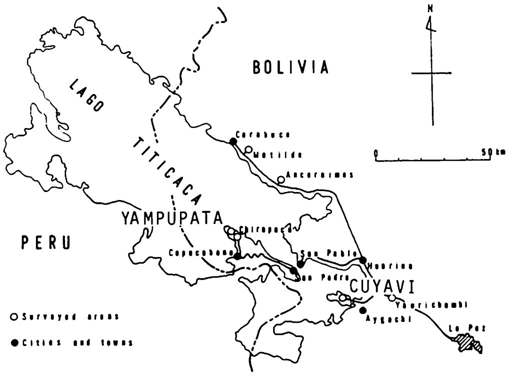

Figure 1. Location map showing Cuyavi and Yampupata.

Professor Juichi Yanagida of Kyushu University, Mr. Tetsuya Kawabe of Chiba University, Kiyoshi Okamoto, former member of JICA, and Mr. Raul Garcia D. of the Servicio Geologico de Bolivia for their kind cooperation in the field and discussions.

Geological setting and age determination

In the Cuyavi route, the Copacabana Group overlies the Carboniferous Gondwana Series with a slight angular-unconformity. The Copacabana Group along this route consists mainly of limestone, marl, dolomite and mudstone-shale associated with sandstone and cherty rock. The thickness is measured as more than 380 m although the upper limit is not confirmed. The Carboniferous Atokan faunules described here are found from the lower part of the group (Cu04 to Cu46b), which was previously considered to be Virgilian (lower part of the *Triticites* Zone) (see Figure 2).

The fusulinacean faunules are known from the Cu46a and Cu46b horizons. *Profusulinella* sp. indet. from the lower horizon (Cu46a) is similar to some species described from midcontinental North America as mentioned in the description. *Profusulinella* sp. indet. is also found in a float collected around the Yp10 horizon in the Yampupata

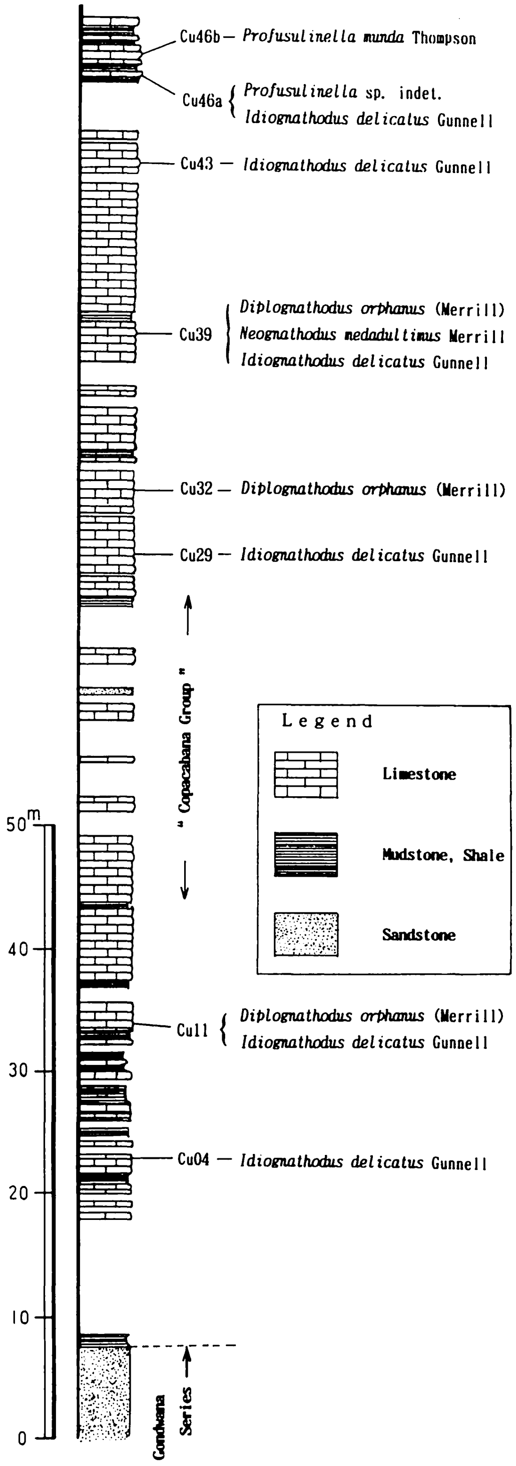

Figure 2. Columnar Section of the lower part of the Copacabana Group at Cuyavi route (Revised from Sakagami, *ed*., 1986).

route. *Profusulinella munda* from the upper horizon (Cu46b) was originally reported from the Middle Pennsylvanian of Texas (U.S.A.) by Thompson (1948). Accordingly, these fusulinacean faunules may be included in the Midcontinent-Andean Province.

The conodonts are known from the Cu04, Cu11, Cu29, Cu32, Cu39, Cu43, and Cu46a horizons in the Cuyavi route. *Idiognathodus delicatus* Gunnell is found from the Cu04, Cu11, Cu29, Cu39, Cu43, and Cu46a horizons, *Diplognathodus orphanus* (Merrill) from the Cu11, Cu32, and Cu39 horizons, and *Neognathodus medadultimus* Merrill from the Cu39 horizon (see Figure 2).

Idiognathodus delicatus has been reported from the late Morrowan to early Virgilian Series of the U.S.A. (Gunnell, 1931 ; Ellison, 1941 ; Webster, 1969 ; von Bitter, 1972 ; Baesemann, 1973 ; Manger and Sutherland, 1984), the Lower Pennsylvanian of Colombia (Stibane, 1967), and the Middle Carboniferous of Japan (Koike, 1967 ; Igo, 1974) and Europe (Boogaard and Bless, 1985).

Diplognathodus orphanus was reported from the early to late Atokan Series in the U.S.A. (Merrill, 1973 ; Grayson, 1984 ; Grubbs, 1984 ; Manger and Sutherland, 1984), and from the Middle Carboniferous of Japan (Igo, 1974) and Europe (Boogaard and Bless, 1985).

Neognathodus medadultimus was reported from the early Atokan to middle Desmoinesian Series in the U.S.A. (Murray and Chronic, 1965 ; Merrill, 1972 ; Grubbs, 1984 ; Manger and Sutherland, 1984) and from the Lower Pennsylvanian of Colombia (Stibane, 1967).

Manger and Sutherland (1984) reported Morrowan-Atokan conodont faunas from the Marble Falls Limestone in the eastern Llano region of Texas (U.S.A.). They stated that *Idiognathodus delicatus, Diplognathodus orphanus* and *Neognathodus medadultimus* were found in association from a horizon slightly below the *Profusulinella* horizon of middle Atokan age.

In view of the above facts and data, it is undoubtedly certain that the middle Atokan of the Pennsylvanian System is present in the lower part of the Copacabana Group distributed in the Lake Titicaca region, although the boundary between the *Profusulinella*-bearing Zone (Atokan) and the upper *Triticites*-bearing Zone (Virgilian) is still obscure.

Repository : All specimens treated in the present study will be registered in the Collections of the Department of Earth Sciences, Faculty of Science, Chiba University, Japan.

Descriptions of fusulinaceans and conodonts

1. Fusulinaceans

Genus *Profusulinella* Rauzer-Chernousova & Belyaev, 1936

Profusulinella sp. indet.

Figures 3-1—7

Shell minute, rather loosely coiled and ellipsoidal with straight axis of coiling. Mature shell attains 5 volutions, the length and width are 1.1 to 1.5 mm and 0.6 to 0.9 mm, respectively, giving form ratios 1.6 to 2.0. Proloculus spherical, its average diameter is 0.085 mm. Average radius vectors of the first to fifth volutions of 7 specimens 0.079, 0.132, 0.201, 0.311 and 0.421 mm, respectively. Average ratios of the half-length to radius vector of the first to fifth volutions in 5 specimens 1.1, 1.3, 1.5, 1.7, and 1.7, respectively. Spirotheca is composed of a tectum and upper and lower tectoria, gradually thickened from inner to outer volutions except for the last volution. Average thickness of spirotheca of the first to fifth volutions of 6 specimens 0.011, 0.013, 0.018, 0.020 and 0.019, respectively. In most parts of the shell, septa

⟶ **Figure 3.** **1-7.** *Profusulinella* sp. indet., ×20 except for **5b** (×30) which is the enlarged photograph of **5a**. **8-26.** *Profusulinella munda* Thompson, ×20 except for **22b** (×100) which is the enlarged part of **22a**. The specimen numbers are indicated in Tables 1 and 2.


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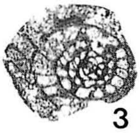
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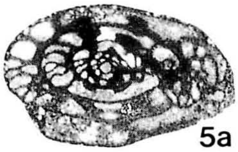
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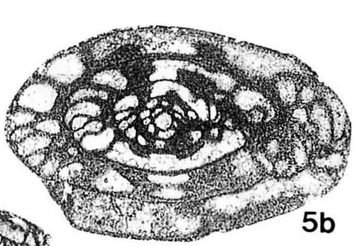
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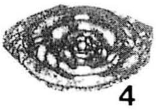
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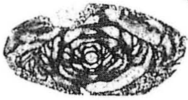
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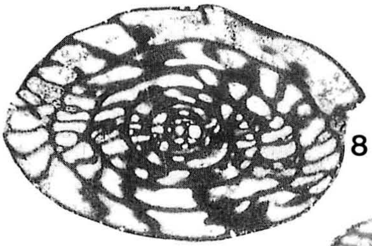
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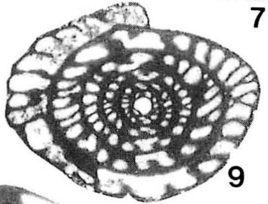
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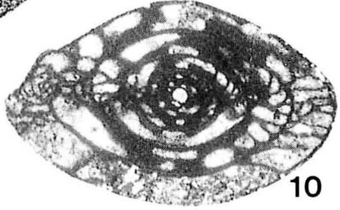
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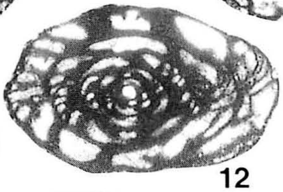
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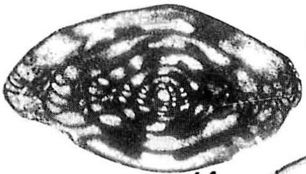
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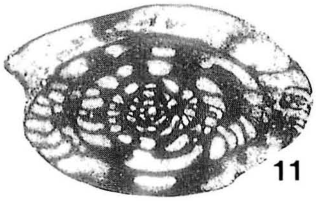
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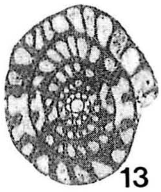
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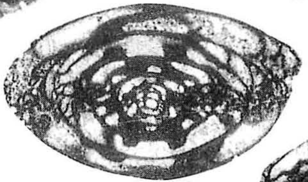
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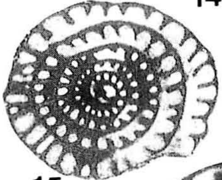
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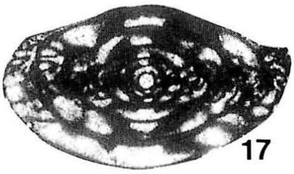
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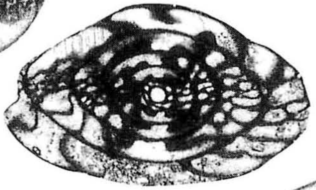
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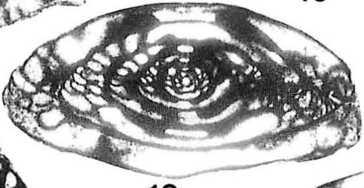
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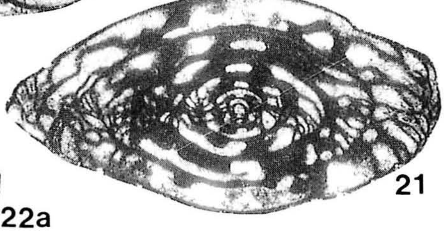
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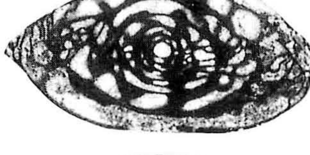
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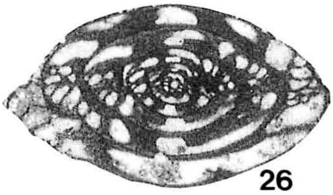
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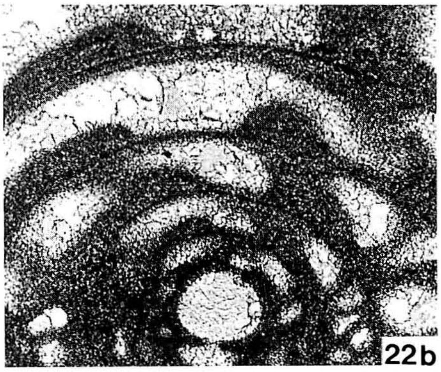
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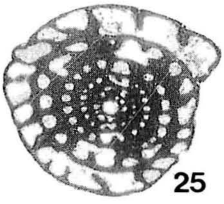
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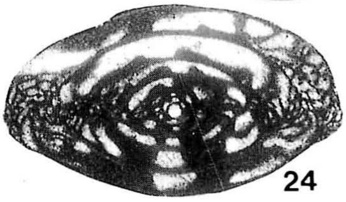
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are more or less the same thickness as spirotheca. They are almost plane in the median portion but become fluted only in axial regions. Average septal counts of the first to fourth volutions of 2 specimens 10, 13, 16 and 19, respectively. Chomata about half as high as the chambers, asymmetrical, tunnel sides are steep but polewards slopes are low. Average tunnel angles of second to fourth volutions of 5 specimens 21, 33, 36 and 43 degrees, respectively.

Remarks : —The present form resembles *Profusulinella marblensis* Thompson (1947), which was originally described from the upper part of the Marble Falls Limestone on the east side of the Llano Uplift of Texas (U.S.A.) in essential characters except for the shell form ; the form ratio in the latter is 1.3 instead of 1.6 to 2.0 in the former. The present form is also not unlike *Profusulinella copiosa* Thompson (1948), which was originally described from the lower Middle Pennsylvanian rocks in Powwow Canyon of Texas, in essential characters but the latter has a more rounded shell form and larger proloculus. The present form is most similar to *Profusulinella fittsi* (Thompson), described from the lower part of the Atoka Formation of Oklahoma by Thompson (1935), in size and general shape except for the somewhat smaller proloculus and much wider chomata of the latter species.

Occurrence : —Rare in Cu46a horizon of the Copacabana Group in the Cuyavi route, and also in a float collected from Yp10 horizon in the Yampupata route.

Specimen nos : —DESC-94001a, 94001b, 94001c, 94002a from Cuyavi ; DESC-94003a, 94003b, 94004a from Yampupata.

Profusulinella munda Thompson 1948

Figures 3-8—26

Profusulinella munda Thompson, 1948, p. 82, 83, pl. 27, fig. 4 ; pl. 30, figs. 1-7.

Shell small and inflated fusiform with straight axis of coiling. Mature shell attains 6 volutions, the length and width are 1.8 to 2.4 mm and 1.0 to 1.5 mm, respectively, giving form ratios 1.6 to 2.0. First to second volutions ellipsoidal to discoidal, but the outer volutions become inflated fusiform. Proloculus spherical and minute, its outside diameter is 0.09 to 0.13 mm, averaging 0.11 mm, that is rather large for the shell size. Shell rather loosely coiled. Average radius vectors of the first to sixth volutions of 19 specimens 0.098, 0.166, 0.258, 0.388, 0.481 and 0.712 mm, respectively. Average ratios of the half-length to radius vector of the first to sixth volutions in 14 specimens are 1.1, 1.3, 1.3, 1.6, 1.7 and 1.8, respectively.

Spirotheca composed of a tectum and upper and lower tectoria, gradually thickened from inner to outer volutions except for the last volution. Average thickness of spirotheca of the first to sixth volutions of 19 specimens are 0.014, 0.018, 0.023, 0.032, 0.031 and 0.027 mm, respectively. Septa in most parts of the shell have the same thickness as the spirotheca. They are almost plane in the median portion but become fluted only in axial regions. Average septal counts of the first to fifth volutions of 4 specimens 8, 16, 19, 22 and 28, respectively. Chomata about one-third to half as high as the chambers, tunnel sides steep but polewards slopes are low. Average tunnel angles of second to sixth volutions of 13 specimens 21, 23, 28, 35 and 38 degrees, respectively.

Remarks : —The present form quite agrees with *Profusulinella munda* Thompson, which was originally described from the upper part of the Green Canyon Group (lower Middle Pennsylvanian) in Texas (U.S.A.) by Thompson (1948), in essential characters. The present form can be easily distinguished from *Profusulinella manuensis* Roberts (in Newell *et al.*, 1953), which was described from the Alto Rio Manu of Peru, by its shell size and other characteristics. The present form can also be distinguished from the above-described *Profusulinella* sp. indet. by larger

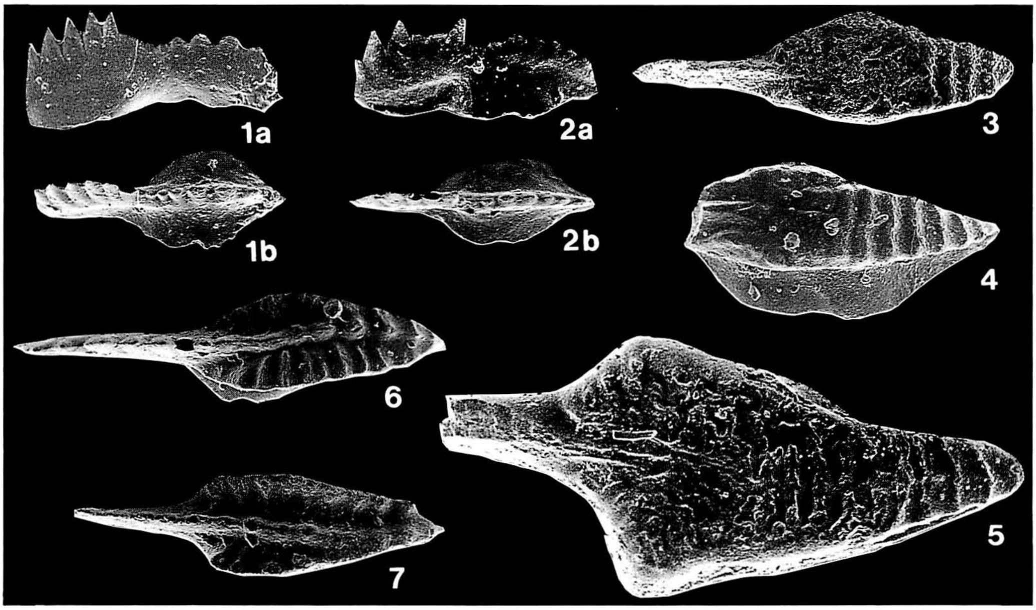

Figure 4. **1, 2.** *Diplognathodus orphanus* (Merrill), **1a, 1b**: lateral and upper views, respectively, Reg. no. DESC-94016, **2a, 2b**: lateral and upper views, respectively, Reg. no. DESC-94020. **3-5.** *Idiognathodus delicatus* Gunnell, upper views, Reg. nos. DESC-94023, 94026, 94022, respectively. **6, 7.** *Neognathodus medadultimus* Merrill, upper views, Reg. nos. DESC-94029, 94030, respectively. All figures are in ×60.

shell size.

Occurrence: —Abundant from Cu46b horizon in the Copacabana Group, Cuyavi route.

Specimen nos: —DESC-94005a, 94005b, 94006a, 94006b, 94006c, 94006d, 94007a, 94007b, 94008a, 94009a, 94009b, 94010a, 94010b, 94011a, 94011b, 94012a, 94013a, 94014a, 94015a.

2. Conodonts

Genus *Diplognathodus* Kozur & Merrill, 1975

Diplognathodus orphanus (Merrill, 1973)

Figures 4-1, 2

Spathognathodus orphanus Merrill, 1973, p. 309, pl. 3, figs. 45-56; Igo, 1974, p. 235, pl. 2, figs. 10-13.
Diplognathodus coloradoensis (Murray & Chronic); Landing and Wardlaw, (part), 1981, pl. 1, figs. 1, 6, 7, 9, 10, [not figs. 4, 5, 8 = *Diplognathodus coloradoensis* (Murray & Chronic)]; Savage and Barkeley, 1985, p. 1473, figs. 12 (9-16).
Diplognathodus orphanus (Merrill); Grayson, 1984, p. 48, pl. 1, fig. 6, pl. 2, figs. 24, 25; Grubbs, 1984, p. 69, pl. 1, figs. 3, 4; Manger and Sutherland, 1984, pl. 1, fig. 4; Boogaad and Bless, 1985, p. 145, fig. 6 (1-4).

Platform narrow and smooth. Blade-like carina passes through the center of the platform, 5 or 6 nodes present on it. Free blade thin, possesses 6 denticles. Anterior denticle is shorter than the others. Two low nodes present between free blade and carina. Free blade almost twice as high as carina in lateral view.

Remarks: —*Diplognathodus orphanus* resembles *Diplognathodus coloradoensis* (Murray & Chronic), but can be easily distinguished by the character of the carina; it is denticulate in the former but relatively nondenticulate with a smooth ridge in the latter.

Table 1. Measurements of *Profusulinella* sp. indet. (in mm)

	Reg. no.	Figure	Lenght	Width	F.R.	D.P.	Half Length				
							1	2	3	4	5
1	DESC-94001a	3-1	1.4	0.8	1.8	?	?	0.128	0.218	0.550	0.768
2	DESC-94001b	3-2	1.2	0.6	2.0	0.08	0.077	0.192	0.320	0.576	
3	DESC-94001c	3-3		0.6		?					
4	DESC-94002a	3-4	1.1	0.7	1.6	0.07	0.064	0.179	0.269	0.397	0.525
5	DESC-94003a	3-5a, b	1.5	0.9	1.7	0.09	0.102	0.205	0.384	0.666	0.900
6	DESC-94003b	3-6		0.7		0.09					
7	DESC-94004a	3-7	1.4	0.7	2.0	0.09	0.090	0.167	0.282	0.431	0.704

	Radius Vector					Ratio of Hl/Rv				
	1	2	3	4	5	1	2	3	4	5
1	0.064	0.115	0.179	0.269	0.431	?	1.1	1.2	2.0	1.8
2	0.090	0.154	0.230	0.333		0.9	1.3	1.4	1.7	
3	0.077	0.141	0.218	0.385						
4	0.064	0.102	0.179	0.256	0.385	1.0	1.8	1.5	1.6	1.4
5	0.090	0.154	0.243	0.371	0.525	1.1	1.3	1.6	1.8	1.7
6	0.090	0.141	0.192	0.307	0.481					
7	0.077	0.115	0.167	0.256	0.333	1.2	1.5	1.7	1.7	2.1

	Thickness of Spirotheca					Tunnel Angle (degrees)				Septal Count (degrees)				
	1	2	3	4	5	2	3	4	5	1	2	3	4	5
1	?	0.013	0.016	0.016	0.022	25	30	32						
2	0.010	0.013	0.016	0.016		19	41	46						
3	?	?	?	0.026						?	12	15	17	
4	0.016	0.013	0.016	0.016	0.016	21	30	41						
5	0.010	0.016	0.022	0.022	0.019	?	30	35	40					
6	0.013	0.013	0.019	0.022	0.019					10	14	17	21	?
7	0.010	0.010	0.016	0.019		?	?	24	45					

F.R.: Form ratio. D.P.: Diamater of proloculus.

On the basis of paleontological study of the upper Marble Falls Limestone of Texas (U.S.A.), Manger and Sutherland (1984) reported that the first appearance of *Diplognathodus orphanus* was earlier than that of *Diplognathodus coloradoensis*.

Occurrence: —One specimen from Cu11, three specimens from Cu32, and two specimens from Cu39 horizons, in the Copacabana Group, Cuyavi route.

Specimen nos: —DESC-94016 from Cu11; DESC-94017, 94018, 94019 from Cu32; DESC-94020, 94021 from Cu39.

Genus *Idiognathodus* Gunnell, 1931

Idiognathodus delicatus Gunnell, 1931

Figures 4-3—5

Idiognathodus delicatus Gunnell, 1931, p. 250, pl. 29, figs. 23-25; Ellison, 1941, p. 134, 135, pl. 22, figs. 31-36; Ellison and Graves, 1941, pl. 3, figs. 20, 23; Koike, 1967, p. 304, 305, pl. 2, figs. 18-23; Webster, 1969, p. 35-37, pl. 6, figs. 6-12; Thompson, 1970, p. 1046, pl. 139, figs. 24, 29; Merrill and King, 1971, pl. 76, figs. 13-22; von Bitter, 1972, p. 58, pl. 3, fig. 4; Baesemann, 1973, p. 699-700, pl. 1, figs. 18, 19, 23, 24; Igo, 1974, p. 234, pl. 1, figs. 1-9; Landing and Wardlaw, 1981, p. 1260, pl. 2, figs. 1-5; Grayson, 1984, p. 49, pl. 1, figs. 1, 2, 12, pl. 3, figs. 2, 3, 5, 6, 21, 23, 25, pl. 4, figs. 1, 6-8, 17, 24; Grubbs, 1984, p. 69, pl. 1, figs. 5-7; Manger and Sutherland, 1984, pl. 1, figs. 16, 17,; Boogaad and Bless, 1985, p. 146, figs. 7(1-9), 9(8); Savage and Barkeley, 1985, p. 1464-1466, figs. 8.1-8.4; Wang, Lane, and Manger, 1987, p. 128-129, pl. 4, figs. 4-8.

Platform in upper view long, lanceolate, tapers posteriorly and ornamented by 6 to 10 parallel transverse ridges.

Accessory lobes containing 3 or more node-like ridges which are parallel with carina are present on both sides of anterior portion of platform. In larger specimens, accessory lobes on both sides of carina are developed into many smaller nodes.

Remarks: —Boogaad and Bless (1985) documented the ontogenetic development of *Idiognathodus delicatus*. The present specimens agree with their growth stage forms in every respect.

Occurrence: —Two specimens from Cu04 and one specimen from Cu11, Cu29, Cu39, Cu43 and Cu46a in the Copacabana Group, Cuyavi route.

Specimen nos: —DESC-94022, 94023 from Cu04; DESC-94024, 94025, 94026, 94027 and 94028 from Cu11, Cu29, Cu39, Cu43 and Cu46a, respectively,

Genus *Neognathodus* Dunn, 1970

Neognathodus medadultimus Merrill, 1972

Figures 4-6, 7

Gnathodus roundyi Gunnell; Murray & Chronic (part), 1965, p. 598, pl. 1, figs. 1, 2 only.

Streptognathodus colombiensis Stibane, 1967, (part), p. 335-336, pl. 36, figs. 3-5 only.

Neognathodus medadultimus Merrill, 1972, p. 824-825, pl. 1, figs. 2-7; pl. 2, fig. 19; Grubbs, 1984, p. 71, pl. 3, fig. 3, 4, 10-13; Manger and Sutherland, 1984, pl. 1, figs. 13, 14.

Platform in upper view long, roughly lanceolate, and pointed posteriorly. A long and straight blade develops from carina at the anterior portion of the platform. Carina gradually bends toward the posterior and fuses on the outer parapet at two-thirds length of the platform. Inner parapet, ornamented with 9 or more node-like transverse ridges, well developed and parallel with carina.

Remarks: —The degree of fusion of the carina with the outer parapet is variable in the present species. The present species resembles *Neognathodus medexultimus* described originally by Merrill (1972) from the Pottsville and Allegheny Groups (Atokan to Desmoinesian) in eastern Ohio (U.S.A), but can be distinguished from the latter by position of the fusion of outer parapet and carina. The fusion in the present form occurs more posteriorly. The present specimen is also similar to *Gnathodus kanumai* (= *Gnathodus* cf. *roundyi* Koike, 1967, pl. 1, figs. 27, 28), which was described by Igo (1974) from the *Fusulinella biconica* Zone of the Akiyoshi

Table 2. Measurements of *Profusulinella munda* Thompson. (in mm)

	Reg. no.	Figure	Length	Width	F.R.	D.P.	Half Length					
							1	2	3	4	5	6
1	DESC-94005a	3- 8	2.4	1.5	1.6	0.09	0.154	0.269	0.410	0.653	0.896	1.203
2	DESC-94005b	3- 9		1.3		0.13						
3	DESC-94006a	3-10	2.2	1.4	1.6	0.12	0.128	0.243	0.410	0.602	1.088	1.280
4	DESC-94006b	3-11	2.1	1.3	1.6	?	0.102	0.192	0.320	0.512	0.845	1.090
5	DESC-94006c	3-12	1.9	1.2	1.6	0.12	0.128	0.269	0.448	0.742	0.998	
6	DESC-94006d	3-13		1.0		0.10						
7	DESC-94007a	3-14	2.0	1.1	1.8	0.10	0.102	0.205	0.320	0.525	0.794	1.075
8	DESC-94007b	3-15		1.3		0.13						
9	DESC-94008a	3-16	2.1	1.2	1.8	0.09	0.077	0.141	0.267	0.512	0.768	1.088
10	DESC-94009a	3-17	1.9	1.1	1.7	0.12	0.128	0.256	0.448	0.704	0.960	
11	DESC-94009b	3-18	2.2	1.3	1.7	0.13	0.128	0.307	0.538	0.896	1.115	
12	DESC-94010a	3-19	2.4	1.2	2.0	0.09	0.090	0.192	0.384	0.550	0.845	1.216
13	DESC-94010b	3-20		1.0		0.10						
14	DESC-94011a	3-21	2.9	1.5	1.9	0.10	0.064	0.192	0.384	0.666	1.088	1.600
15	DESC-94011b	3-22a, b	2.1	1.1	1.9	0.13	0.128	0.230	0.320	0.512	0.832	1.024
16	DESC-94012a	3-23	1.8	1.0	1.8	0.10	0.090	0.192	0.422	0.678	0.934	
17	DESC-94013a	3-24	2.3	1.3	1.8	0.12	0.090	0.166	0.333	0.576	0.845	1.216
18	DESC-94014a	3-25		1.4		0.13						
19	DESC-94015a	3-26	2.2	1.2	1.8	0.08	0.090	0.179	0.320	0.576	0.883	1.152

	Radius Vector						Ratio of Hl/Rv					
	1	2	3	4	5	6	1	2	3	4	5	6
1	0.090	0.192	0.295	0.431	0.527	0.806	1.7	1.4	1.3	1.5	1.7	1.5
2	0.102	0.154	0.256	0.384	0.525	0.704						
3	0.102	0.179	0.282	0.448	0.627		1.3	1.4	1.5	1.3	1.7	
4	0.090	0.154	0.240	0.358	0.512	0.717	1.1	1.2	1.3	1.4	1.6	
5	0.102	0.179	0.269	0.410	0.563		1.3	1.5	1.6	1.8	1.7	
6	0.102	0.167	0.256	0.384	0.563							
7	0.090	0.141	0.230	0.320	0.431	0.614	1.1	1.5	1.4	1.6	1.8	1.8
8	0.128	0.218	0.320	0.461	0.589	?						
9	0.090	0.141	0.205	0.320	0.486	0.666	0.9	1.0	1.3	1.6	1.5	1.6
10	0.115	0.192	0.282	0.431	0.602		1.1	1.3	1.6	1.6	1.6	

11	0.115	0.205	0.307	0.448	0.640		1.1	1.5	1.8	2.0	1.7	
12	0.077	0.128	0.192	0.320	0.448	0.640	1.2	1.5	2.0	1.7	1.9	1.9
13	0.102	0.167	0.294	0.461	0.538							
14	0.077	0.154	0.256	0.397	0.550	0.781	0.8	1.2	1.5	1.7	2.0	2.0
15	0.115	0.166	0.243	0.358	0.499		1.1	1.4	1.3	1.4	1.7	
16	0.077	0.141	0.230	0.346	0.499		1.2	1.4	1.8	2.0	1.9	
17	0.102	0.166	0.243	0.358	0.525	0.704	0.9	1.0	1.4	1.6	1.6	1.7
18	0.102	0.166	0.282	0.397	0.576	0.806						
19	0.090	0.141	0.218	0.346	0.499	0.678	1.0	1.3	1.5	1.7	1.7	1.7

	Thickness of Spirotheca						Tunnel Angle (degrees)					Septal Count (degrees)				
	1	2	3	4	5	6	2	3	4	5	6	1	2	3	4	5
1	0.024	0.024	0.026	0.029	0.032	0.032	?	?	?	?	?					
2	0.013	0.019	0.026	0.032	0.029	0.029						?	?	?	?	?
3	0.019	0.019	0.022	0.035	0.026		19	19	22	37	42					
4	?	0.019	0.022	0.029	0.032	0.029	20	20	28	23	28					
5	0.016	0.022	0.029	0.042	0.042		20	20	28	31	32					
6	0.013	0.016	0.016	0.026	0.029							9	14	15	19	?
7	0.013	0.016	0.016	0.029	0.032	0.029	20	25	28	39	40					
8	?	0.019	0.022	0.032	0.032	0.019						8	20	22	25	29
9	0.016	0.016	0.022	0.032	0.035	0.028	18	20	23	37	45					
10	0.010	0.016	0.035	0.051	0.026		24	29	34	38						
11	0.013	0.022	0.026	0.029	0.026		28	13	22	47						
12	0.016	0.016	0.022	0.042	0.029	0.026	23	24	32	37	47					
13	0.013	0.016	0.022	0.032	0.029							8	16	17	19	?
14	0.013	0.016	0.022	0.029	0.026	0.026	20	23	30	28	49					
15	0.010	0.013	0.013	0.026	0.032		22	26	29	32	32					
16	0.010	0.016	0.026	0.035	0.022		?	30	32	37						
17	0.016	0.026	0.032	0.022	0.032	0.032	14	20	24	28	30					
18	0.016	0.019	0.026	0.026	0.038	0.022						8	15	20	24	27
19	0.016	0.016	0.016	0.038	0.038	0.026	22	31	27	36	?					

F.R.: Form ratio. D.P.: Diameter of proloculus.

Limestone in Japan, but can be distinguished from the latter by having a bent carina instead of a straight one as in *Gnathodus kanumai*, and by the less developed outer parapet.

Occurrence: —Three specimens from Cu39 horizon in the Copacabana Group, in the Cuyavi route.

Specimen nos: —DESC-94029, 94030, 94031.

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ボリヴィア国チチカカ湖周縁のコパカバーナ層群からペンシルヴァニア紀中期の紡錘虫とコノドントの発見：これまでVirgilian（ペンシルヴァニア紀最後期）からLeonardian（ペルム紀中期前半）までの地層と考えられていたコパカバーナ層群の下部層から新たにAtokan（ペンシルヴァニア紀中期）を指示する紡錘虫とコノドントを発見した。これらの紡錘虫：*Profusulinella* sp. indet., *Profusulinella munda* Thompson；コノドント：*Diplognathodus orphanus* (Merrill), *Idiognathodus delicatus* Gunnell, *Neognathodus medadultimus* Merrillを記載，図示する。この化石動物群集はMidcontinent-Andean Provinceに含まれるであろう。

坂上澄夫・水野嘉宏

ANNOUNCEMENT

New Journal Format

As one of the prime activities commemorating the 60th anniversary of the foundation of the Palaeontological Society of Japan, the Council of the Society has voted to change the format of the society's non-Japanese language publication, the *Transactions and Proceedings of the Palaeontological Society of Japan*, to a page size of 215×280 mm, beginning with the April 1995 issue. Coincident with this size change, the journal will have a new look, be given a new title and new cover design, and it will adopt a volume and number system with annual volume consisting of quarterly issues. The new journal title is being carefully considered, so that it will reflect the Society's desire to make it a truly international journal dedicated to the dissemination of fundamental knowledge on all aspects of palaeontological research.

The new cover design should make this journal more eye-catching amongst rows of scientific journals on the library book shelves, thereby attracting the attention of prospective readers. The new format should enable the publication of more papers each year and allow for more variety in presentation of the contents.

The most important change caused by the new journal format concerns the illustrations. Figures will be published at a page size of 172×230 mm, double column width of 170 mm, or single column width of 85 mm. As of this date, all figures in submitted manuscripts must conform to the new journal format. Although the change may inconvenience some authors who are in the process of preparing manuscripts for this jounal, the Editor will make every effort to make this transition as smooth as possible.

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