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The fossil on the cover is *Vicarya yokoyamai* Takeyama, an Early Middle Miocene gastropod from the Kurosedani Formation at Kakehata, Yatsuo-cho, Nei-gun, Toyama Prefecture, central Japan (Collected by T. Kotaka and K. Ogasawara, IGPS No. 99075, photo by S. Ohtomo and Y. Kikuchi,  $\times 0.9$ ).

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**PALAEONTOLOGICAL SOCIETY OF JAPAN**

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## 856. LATE PALEOZOIC FORAMINIFERS OF THE OGAWADANI FORMATION, SOUTHERN KWANTO MOUNTAINS, JAPAN\*

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**Abstract.** Forty-seven species of Middle Carboniferous to Middle Permian foraminifers are discriminated from the limestone blocks of the Ogawadani Formation, distributed in the Southern Belt of the Chichibu Terrane in the Kwantō Mountains. Among them, nine fusulinacean species belonging to five genera are described with brief geologic note of the Ogawadani Formation.

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### Introduction

Huzimoto (1932) established a fault-bounded unit, the Shiromaru Paleozoic Belt, within Jurassic formations near Shiromaru in the southern part of the Kwantō Mountains. Four fusulinacean species, such as *Fusulina girtyi* (Dunbar and Condra), *Pseudofusulina ambigua* (Deprat)?, *Pseudofusulina krafftii* (Schellwien) and *Cancellina primigena* (Hayden), were described from Unazawa, Otakezawa and Komyosan within this belt (Huzimoto, 1936). He also introduced the Tamagawa Group for the unit containing Jurassic Torinosu-type fossiliferous limestones and Jurassic radiolarian cherts, which is distributed in the west of the Shiromaru Paleozoic Belt (Huzimoto, 1939). Subsequently, Kobayashi (1939) found *Neoschwagerina* (*Yabeina*?) sp. from Aterazawa, north of Okutama (Hikawa), and he doubted Huzimoto's view of the Tamagawa Group.

Recently, Hisada (1984) listed *Triticites*? sp., *Pseudoschwagerina* sp., *Acervoschwagerina* sp., *Pseudofusulina* sp. and *Schwagerina*? sp. from the limestone blocks exposed at Kawanoridani and Ogawadani. These blocks are included in the

Ogawadani Formation proposed by Ozawa and Kobayashi (1986).

Through a detailed field work in the southern part of Kwantō Mountains, I newly obtained many fusulinaceans and other foraminifers from the limestone blocks contained in the Ogawadani Formation. Total number of foraminiferal species attains to 47 referable to 32 genera. They came from 24 localities of my own collection and also of previous workers. Nine fusulinacean species of them are described herein. All materials described and cited are stored in Department of Geology, National Science Museum, Tokyo.

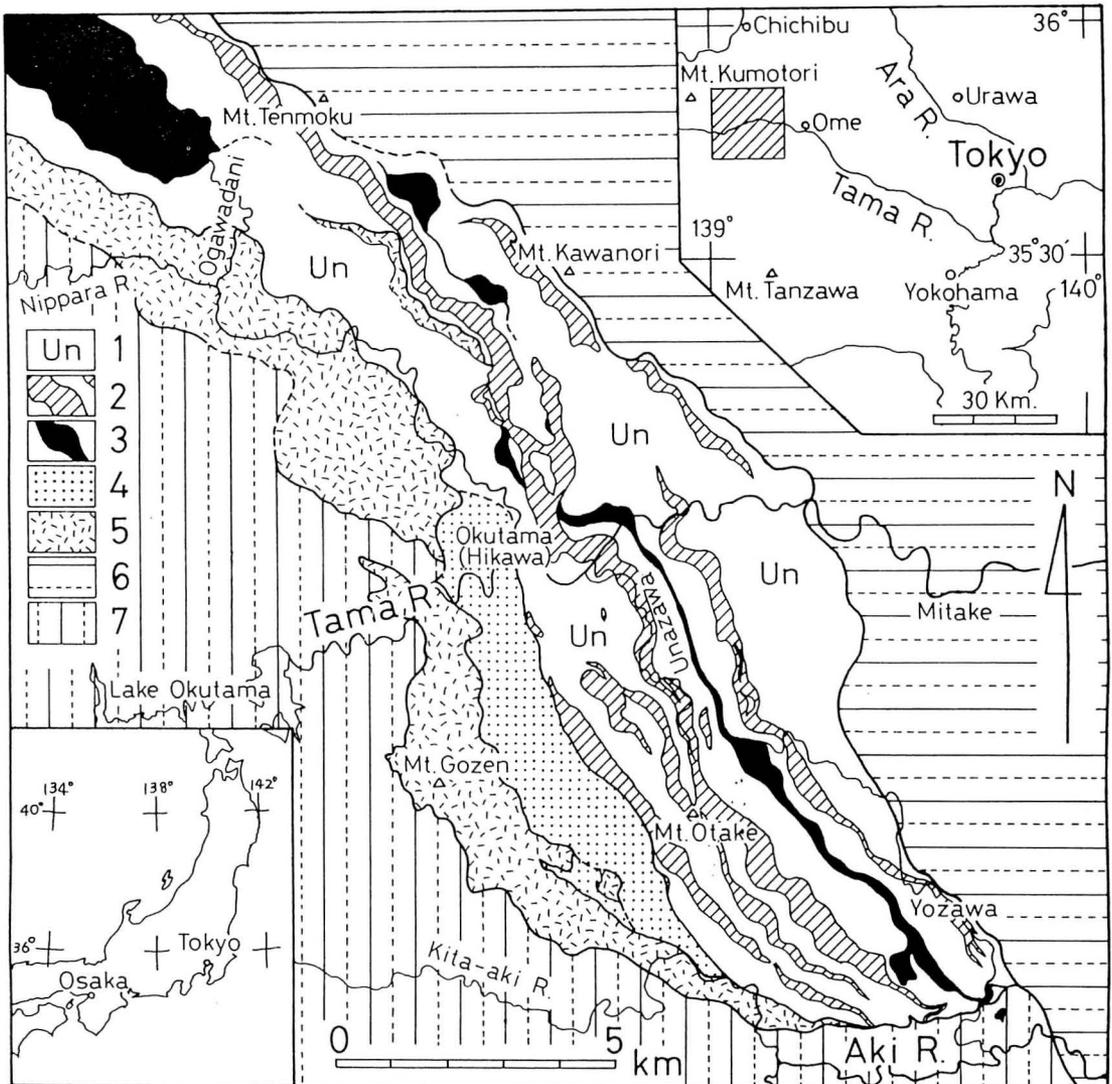
### Geologic setting

The Tamagawa Group is composed of four formations, such as the Unazawa, Ogawadani, Hikawa and Gozenyama Formations (Ozawa and Kobayashi, 1986). This group is complexly folded and faulted, but it generally strikes northwest to southeast and steeply dips northeast.

The Ogawadani Formation, typically crops out in the Ogawadani valley, a tributary of the Nippara River, is discontinuously distributed more than 14 km in length and about 2 km in

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**Figure 1.** Geological map of the Southern Belt of the Chichibu Terrane in the southern part of the Kwanto Mountains. 1–5: Southern Belt of the Chichibu Terrane composed of the Tamagawa Group; 1: sandstone and shale of the Unazawa Formation, 2: chert and siliceous shale of the Unazawa Formation, 3: Ogawadani Formation, 4: Hikawa Formation, 5: Gozenyama Formation, 6: Middle Belt of the Chichibu Terrane, 7: Shimanto Terrane.

the maximum width. This formation is in a fault contact with the Unazawa Formation (Figure 1). The Ogawadani is characterized by various sized and shaped blocks of basaltic rocks, limestones and cherts which are chaotically embedded within arenaceous and sheared pelitic rocks. Longer diameter of blocks attains more than 50 m. The age of limestones is Middle Carboniferous

to Middle Permian given by foraminifers, whereas the age of cherts mostly indicates Late Triassic by conodonts. These blocks are considered to be exotic and arenaceous and pelitic rocks are matrix of the Ogawadani Formation. The pelitic matrix is assigned to Jurassic on the basis of radiolarians from the Ogawadani valley (Hisada, 1984).

Limestones of this formation commonly occur in association with basaltic rocks and/or as small blocks within mafic hyaloclastite. Most of them are lithologically micritic limestone. Some of the micritic limestones contain siliceous

concretions or radiolarian remains replaced by calcite, and alternating beds of chert and micritic limestone. Encrinal, algal, oölitic and pisolitic limestones are also recognized.

Table 1 shows the Late Paleozoic foraminifers discriminated from the limestone blocks of the Ogawadani Formation. Fossil localities are shown in Figure 2.

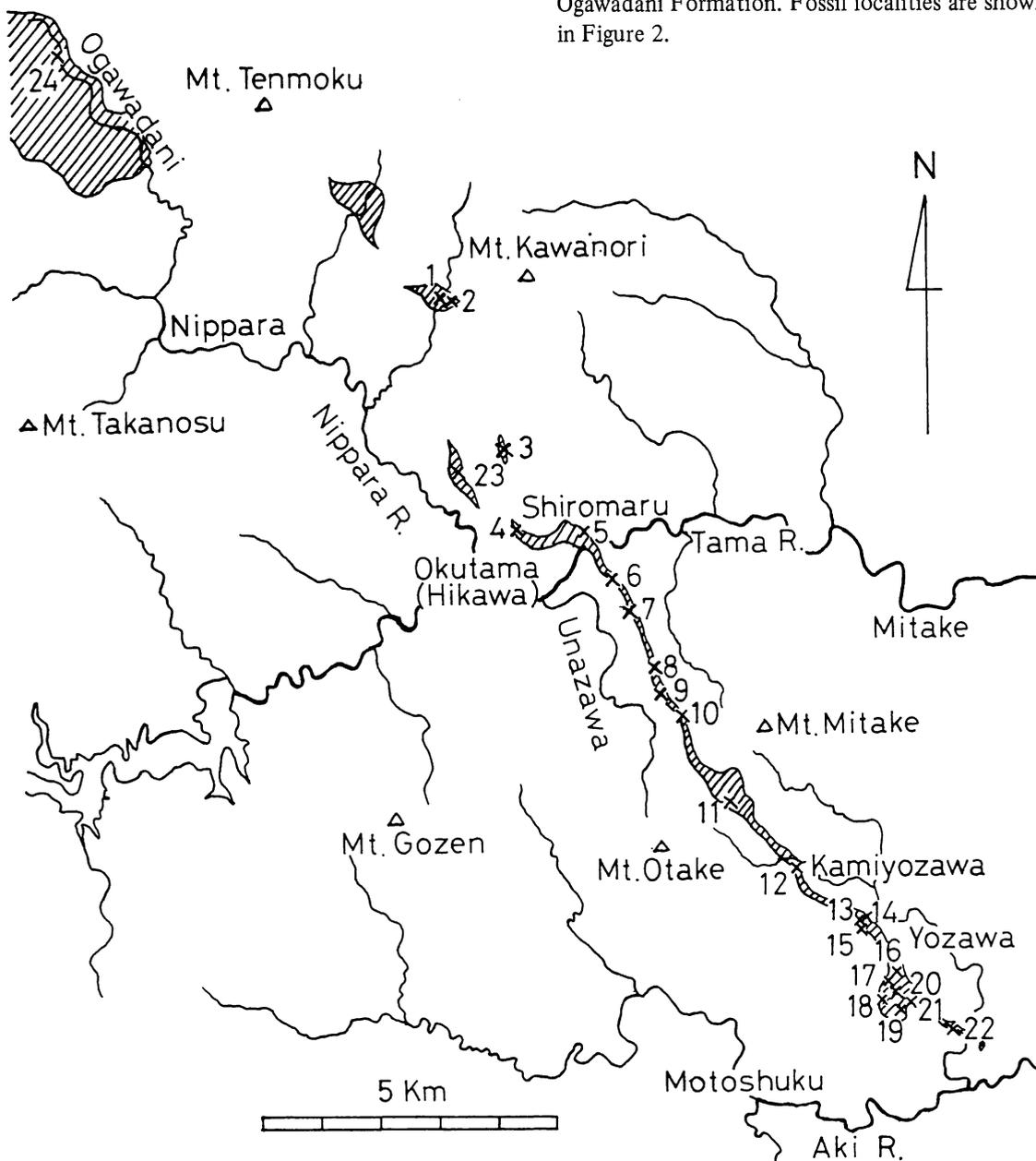


Figure 2. Localities of the Late Paleozoic foraminifers. Shaded area shows the distribution of the Ogawadani Formation.



### Systematic description

Family Fusulinidae von Möller, 1878

Genus *Beedeina* Galloway, 1933 emend. Ishii,  
1958

*Beedeina higoensis* (Kanmera)

Figures 4-7-17

*Fusulina higoensis* Kanmera, 1954, p. 133-136, pl. 14,  
figs. 1-11.

*Beedeina higoensis doii* Ishii, 1958, pl. 3, fig. 1 (not  
described).

*Beedeina higoensis* (Kanmera); Suyari, 1962, p. 8, pl. 4,  
figs. 6, 7; Ozawa, 1975, pl. 8, figs. 14, 15 (not  
described); Ishibashi, 1984, p. 204-206, pl. 23, figs.  
7-11, pl. 24, figs. 1-8, pl. 25, figs. 1-4.

**Description:**—Shell relatively large, inflated fusiform in shape with straight axis of coiling, arched to broadly arched periphery, almost straight lateral sides and bluntly pointed poles. Mature specimens of 9 volutions, more than 6 mm in axial length and more than 2.5 mm in median width, giving approximate form ratio of 2.5.

Proloculus spherical to subspherical and 160 to 210  $\mu\text{m}$  in longer diameter. Length and width gradually increase in inner three to four volutions, becoming nearly constant in succeeding ones, and decreasing in the outermost one. Inner and outer volutions nearly the same in their outlines, but with sharply pointed poles in the former.

Spirotheca thin, approximately 30  $\mu\text{m}$  in outer volutions, composed of tectum, diaphanotheca and inner and outer tectoria.

Septa narrowly spaced and intensely fluted throughout shell, especially in polar regions. In tunnel regions, they are unfluted and plane in inner two to three volutions, and weakly fluted and coated with dense calcareous materials in outer ones. Septal fluting rather regular, half to three fourth as high as chamber height, reaching top of chambers in polar regions and producing combination of adjacent septa. Septal count from the fourth to seventh volutions, 20(?), 22, 27 and 32, respectively.

Tunnel generally high and narrow, bordered

by massive chomata. Its path rather straight, and its angle less than 20 degrees.

**Remarks:**—Although generic validity of *Beedeina* was denied by Rozovskaya (1975) and Ross (1979), I am of an opinion that *Beedeina* is phylogenetically distinguishable from *Fusulina* as Ishii (1958) concluded.

The materials identified with *Fusulina girtyi* from Unazawa by Huzimoto (1936) are different from the original ones from the Middle Pennsylvanian Brereton Limestone, Illinois of Dunbar and Condra (1928) in shape of shell and weaker septal fluting. Although any additional materials have not been obtained from Unazawa, Huzimoto's ones would be belonged to either *Beedeina schellwieni* (Staff) or the present species.

**Occurrence:**—Rare in dark gray micritic limestone at Locs. 1 and 2 (Kawanoridani) and very rare in light gray algal sparitic limestone at Loc. 21 (450 m east of Mt. Komyosan).

Family Schwagerinidae Dunbar and  
Henbest, 1930

Genus *Parafusulina* Dunbar and  
Skinner, 1931

"*Parafusulina*" *gigantea* (Deprat)

Figure 4-18

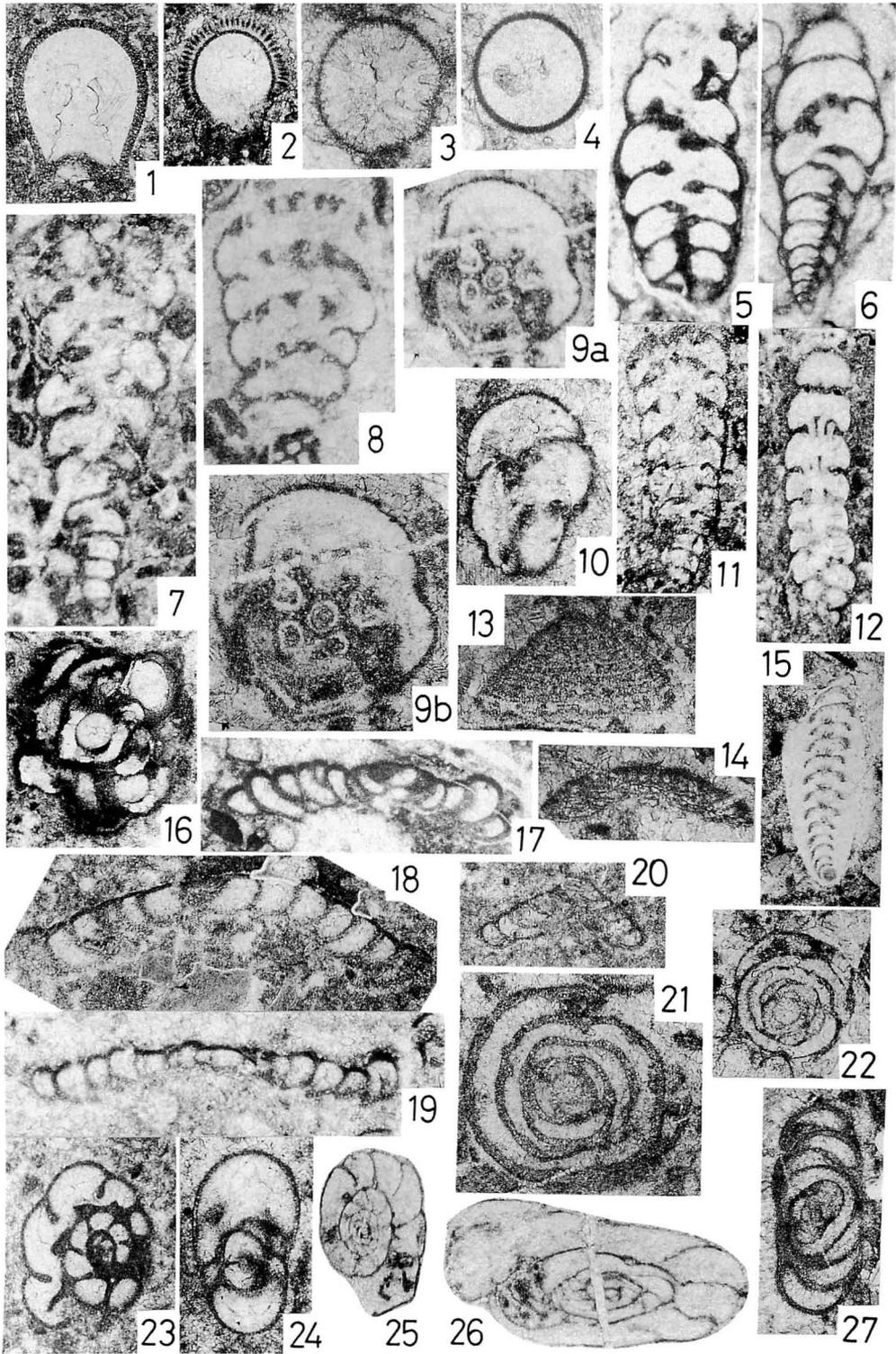
*Fusulina gigantea* Deprat, 1913, p. 29, 30, pl. 1, figs.  
1-6.

*Schellwienia gigantea* (Deprat); Ozawa, 1925, p. 32-33,  
pl. 4, fig. 9.

*Parafusulina gigantea* (Deprat); Toriyama, 1958, p.  
200-203, pl. 36, figs. 2-11; Toriyama and Sugi,  
1959, p. 19-21, pl. 1, figs. 1-5; Sheng, 1963, p. 73,  
201, pl. 20, figs. 1-5, 9, 11, pl. 21, figs. 3-5; Leven,  
1967, p. 171, pl. 24, figs. 2, 3, 5; Toriyama and  
Pitakpaivan, 1973, p. 48-51, pl. 5, figs. 13-20; Lin  
*et al.*, 1977, p. 70, pl. 19, fig. 4; Toriyama and  
Kanmera, 1979, p. 44-46, pl. 5, figs. 10-13, pl. 6,  
figs. 1-6.

*Pseudofusulina gigantea* (Deprat); Hasegawa *et al.*, 1979,  
pl. 81, fig. 1 (not described).

**Remarks:**—Morphologic variation of the present material is uncertain because of a small number of well-oriented sections. The illustrated specimen is characterized by a large subspherical



proloculus with more than 0.8 mm in its longer diameter, thick spirotheca with very coarse alveolar keriotheca, thick septa, somewhat regular and high septal fold. Thick septa are due to secondary coating of dark calcareous material.

Among the described species, the present material is the closest to "*Parafusulina*" *gigantea* (Deprat), widely distributed in Southeast Asia, South China and Pamir. In Japan, the present species has been exclusively found in the Akiyoshi Limestone. "*P.*" *gigantea* was originally described from the upper Middle Permian of Laos (Deprat, 1913), where it occurs in association with *Yabeina globosa* (Yabe) and others. Subsequent workers, above mentioned, showed that this species occurred throughout Middle Permian.

Morphologic characters, such as thick spirotheca and septa of this species are dissimilar to those of the type species of *Parafusulina*. Although this species would be referable to other genus, the conclusion is reserved. *Schwagerina ibukiensis* Kobayashi from the Ibukiyama Limestone (Kobayashi, 1957) is similar to the present species rather than *Schwagerina chiapasensis* Thompson and Miller. However, *S. ibukiensis* has more regular and intense septal fold and thinner spirotheca than those of the present species.

*Occurrence*:—Rare in conglomeratic limestone at Loc. 18 (Mt. Komyosan).

*Parafusulina hirayuensis* Igo

Figures 5-1,2

*Parafusulina hirayuensis* Igo, 1959, p. 250–252, pl. 4, figs. 1–3.

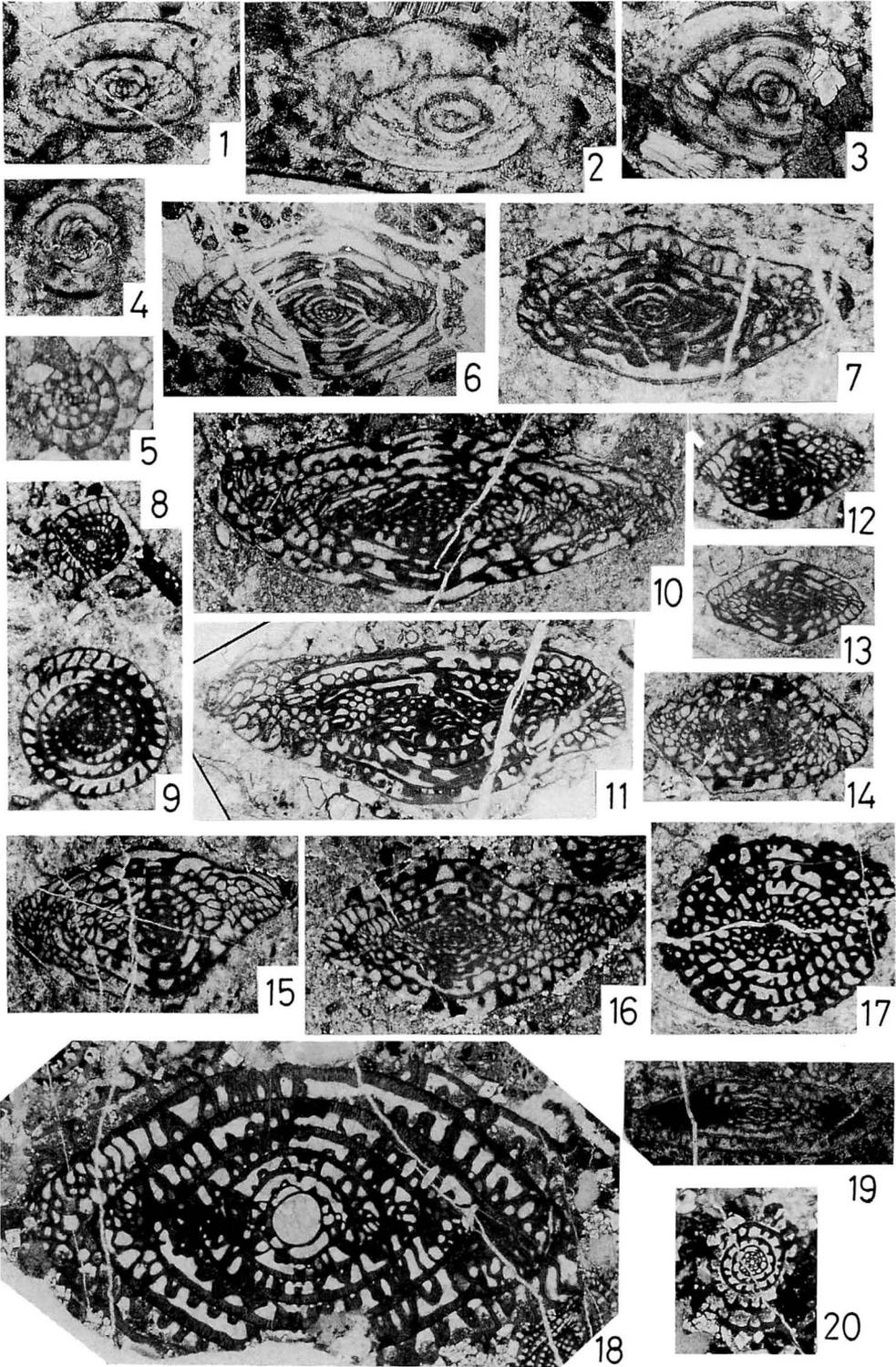
*Description*:—Shell large, elongate fusiform to subcylindrical in shape with nearly straight axis of coiling, broadly arched to straight periphery, almost straight lateral sides and rounded to bluntly pointed poles. Mature specimens of 8 to 9 volutions, 14.5 to 15 mm in axial length and 4 to 4.5 mm in median width, giving form ratio about 3.5.

Proloculus subspherical and 275 to 383  $\mu\text{m}$  in their longer diameter. The first volution oval to inflated fusiform with rounded poles. Succeeding three to four volutions elongate fusiform with sharply pointed poles. Radius vector 0.28, 0.42, 0.60, 0.86, 1.14, 1.45, 1.81 and 2.11 mm from the first to eighth volutions in the specimen illustrated in Figure 5-1; 0.20, 0.32, 0.47, 0.69, 1.02, 1.29, 1.57, 1.91 and 2.27 mm from the first to ninth ones in Figure 5-2, respectively.

Spirotheca composed of thin tectum and fine alveolar keriotheca. Spirothecal thickness 29, 46, 64, 77, 95, 126, 110 and 91  $\mu\text{m}$  from the first to eighth volutions in Figure 5-1; 28, 39, 49, 75, 97, 101, 98, 110 and 72  $\mu\text{m}$  from the first to ninth ones in Figure 5-2, respectively.

Septa intensely fluted throughout shell, and coated by dark calcareous materials. Septal folding somewhat regular and about half as high as chambers in median part of shell, but becomes irregular and higher toward poles and highly

← **Figure 3.** 1, 3, 4. *Tubertinina* spp. lateral sections, 1: Loc. 10, MPC 3775,  $\times 60$ ; 3, 4: Loc. 21, MPC 3692,  $\times 80$ . 2. *Radiosphaera* sp., lateral section, Loc. 18, MPC 3764,  $\times 60$ . 5, 6. *Palaeotextularia* sp. A, Loc. 21, 5: MPC 3693; 6: MPC 3695,  $\times 30$ . 7, 10, 12. *Palaeotextularia* sp. C, lateral sections, 7, 10: Loc. 13, MPC 3716, MPC 3669,  $\times 30$ ;  $\times 40$ ; 12: Loc. 14, MPC 3652,  $\times 20$ . 8, 9. *Cribrogenerina*? sp. 8: lateral section; 9: transverse section, both Loc. 13, MPC 3667, 8, 9a:  $\times 30$ ; 9b:  $\times 40$ . 11. *Palaeotextularia* sp. B, lateral section, Loc. 2, MPC 3807,  $\times 20$ . 13, 14. *Abadehella coniformis* Okimura and Ishii, lateral sections, Loc. 13, 13: MPC 3670; 14: MPC 3669,  $\times 35$ . 15. *Pachyphloia ovata* Lange, lateral section, Loc. 13, MPC 3732,  $\times 40$ . 16. Fisherinidae gen. et sp. indet., lateral section, Loc. 10, MPC 3781,  $\times 30$ . 17, 19. *Tetrataxis* sp. A, lateral sections, Loc. 21, 17, 19: MPC 3692,  $\times 25$ . 18. *Tetrataxis* sp. B, lateral section, Loc. 14, MPC 3653,  $\times 40$ . 20. *Tetrataxis conica* Ehrenberg, lateral section, Loc. 14, MPC 3653,  $\times 40$ . 21. *Baisalina* sp. cf. *B. globosa* Wang, lateral section, Loc. 13, MPC 3731,  $\times 40$ . 22. *Agathammina* sp., lateral section, Loc. 12, MPC 3681,  $\times 40$ . 23, 24. *Endothyra* sp., 23: parallel section, Loc. 10, MPC 3782,  $\times 40$ ; 24: tangential section, Loc. 21, MPC 3693,  $\times 60$ . 25, 26. *Rauserella* sp., oblique sections, Loc. 15, 25: MPC 3708; 26: MPC 3707,  $\times 25$ . 27. *Hemigordius*? sp., lateral section, Loc. 13, MPC 3730,  $\times 40$ .



complicated in polar regions.

Tunnel low, narrow in inner volutions, but broad in outer ones. Rudimentary chomata present and restricted in inner two volutions. Lateral sides toward polar regions of inner five volutions filled with dense deposits.

*Remarks*:—The present materials show considerably wide morphologic variation in size of proloculus, radius vector, septal fluting and others. Among the described materials, the present ones are the closest to *Parafusulina hirayuensis* Igo, originally described from the Hirayu Pass, east of Takeyama, northernmost part of the Mino Terrane. The original and the present specimens are common in large subcylindrical shell, development of septal fluting, axial filling, and broad and low tunnel in outer volutions.

*P. hirayuensis* is similar to such forms of *Parafusulina* as *P. subextensa* Chen, *P. iisakai* Igo and Ogawa and *P. hayashii* Igo. From the Akasaka Limestone, Morikawa (1958) proposed many new species referable to *Parafusulina*, some of which are allied to *hirayuensis*. However, most of them are insufficient to compare their morphologic characters in specific level.

*Occurrence*:—Rare in gray micritic limestone at Loc. 15 (430 m northwest of Mt. Komyosan).

Family Verbeekinidae Staff and Wedekind, 1910

Subfamily Verbeekininae Staff and Wedekind, 1910

Genus *Verbeekina* Staff, 1909

*Verbeekina verbeeki* (Geinitz)

Figures 5-3,4

*Remarks*:—This species is one of the most well-known fusulinacean species in the Tethyan

Province. The following synonym list of this species is presented after Toriyama and Kanmera (1977);

Lin *et al.*, 1977, p. 83, pl. 25, fig. 9; Liu *et al.*, 1978, p. 81, pl. 18, fig. 17; Ding, 1978, pl. 100, fig. 2 (not described); Kobayashi, 1979, pl. 4, figs. 9, 10 (not described); Hasegawa *et al.*, 1979, pl. 85, figs. 1–5, 7 (not described); Tien, 1979, p. 130–132, pl. 21, figs. 3–9; Wang *et al.*, 1981, p. 58, 59, pl. 19, fig. 6; Wang *et al.*, 1982, p. 99, pl. 27, figs. 1, 2; Xie, 1982, pl. 32, fig. 3 (not described); Sun *et al.*, 1983, p. 33, pl. 9, fig. 5; Ishibashi, 1986, p. 105–107, pl. 15, figs. 2–8, pl. 16, figs. 1–3; Kobayashi, 1986, p. 145, pl. 4, fig. 8, pl. 9, fig. 6.

*Occurrence*:—Rare in gray sparitic limestone at Loc. 13 (Mitsugo Limestone Cave) and conglomeratic limestone at Loc. 18 (Mt. Komyosan).

Subfamily Misellininae

Miklukho-Maklay, 1958

Genus *Pseudodoliolina* Yabe and Hanzawa, 1932

*Pseudodoliolina pseudolepida* (Deprat)

Figures 6-1a–8

*Remarks*:—The present materials are identical with the original ones by Deprat (1912) except for higher and narrower parachomata of the former. Small and narrow calcareous deposits occasionally present at the top of chamber in outer volutions.

*Pseudodoliolina pseudolepida* is widespread, especially in Japan, South China and Southeast Asia. After the description of this species by Toriyama and Kanmera (1977), the synonym list of this species is as follows:

Liu *et al.*, 1978, p. 83, pl. 20, fig. 5; Ding, 1978, p. 288, pl. 98, fig. 6; Toriyama and Kanmera, 1979, p.

← **Figure 4.** 1, 2. *Dunbarula schubertellaeformis* Sheng, 1: axial section, Loc. 12, MPC 3681; 2: tangential section, Loc. 13, MPC 3668, both  $\times 40$ . 3, 5. *Neofusulinella* sp., 3: tangential section, MPC 3635,  $\times 40$ ; 5: parallel section, MPC 3765,  $\times 30$  both Loc. 18. 4. *Dunbarula*? sp., tangential section, Loc. 14, MPC 3653,  $\times 40$ . 6. *Yangchienia compressa* (Ozawa), axial section, Loc. 18, MPC 3632,  $\times 15$ . 7–17. *Beedeina higoensis* (Kanmera) 7, 10, 11, 16: tangential sections; 8, 12–15, 17: oblique sections; 9: sagittal section, 7: Loc. 1; 8–10, 12–16; Loc. 2; 11, 17: Loc. 21, 7–17: MPC 3822; 3828; 3828; 2823; 3691; 3826; 3828; 3825; 3824; 3827; 3693, 7:  $\times 15$ ; 8–10, 12, 14–16:  $\times 11$ ; 11, 13, 17:  $\times 10$ . 18. "*Parafusulina*" *gigantea* (Deprat), axial section, Loc. 18, MPC 3630,  $\times 10$ . 19, 20. *Chusenella* spp., 19: tangential section, Loc. 13; MPC 3728; 20: sagittal section, Loc. 18, MPC 3765, both  $\times 10$ .

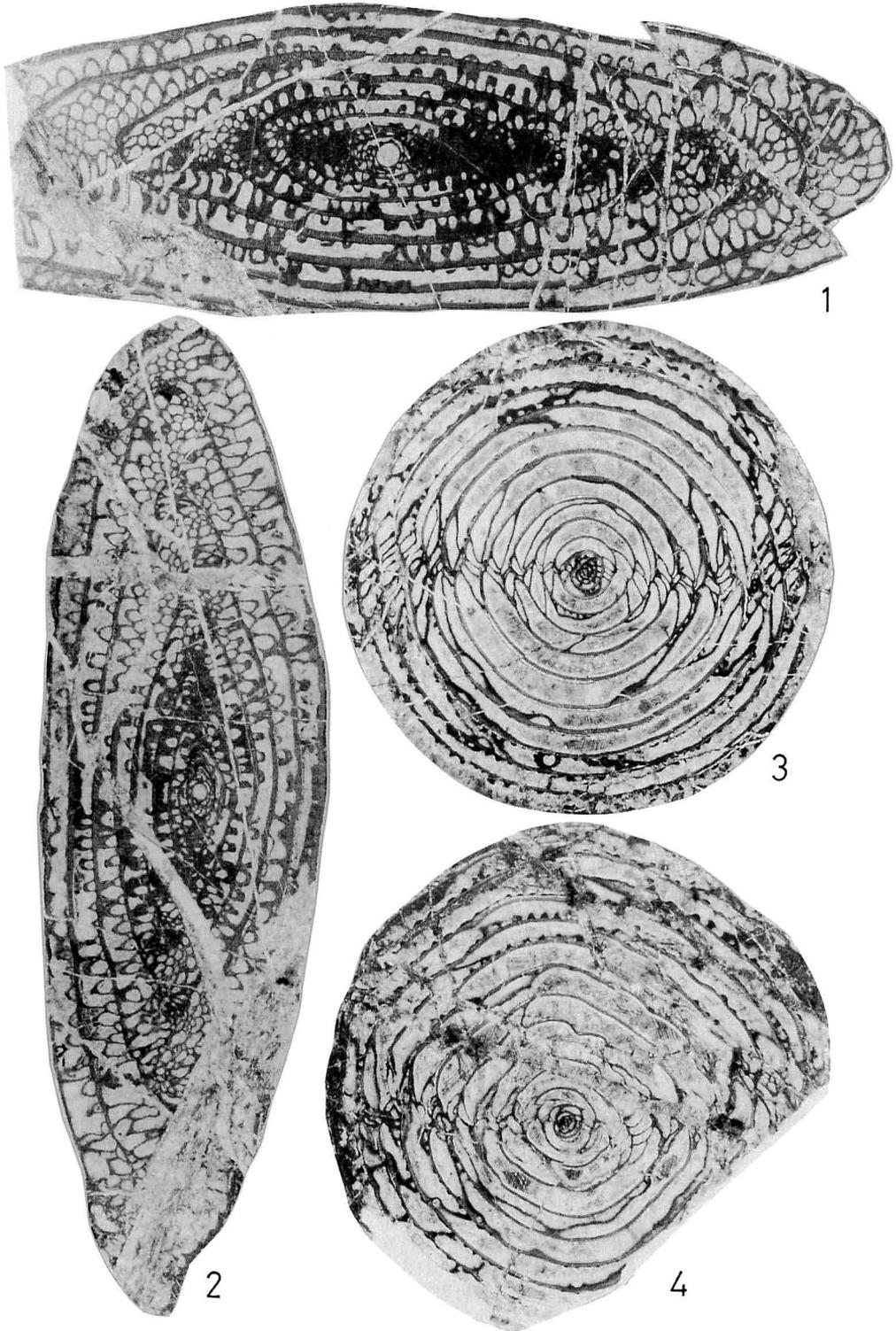


Figure 5. 1, 2. *Parafusulina hirayuensis* Igo, axial sections, Loc. 15, 1: MPC 3707; 2: MPC 3708, x 10. 3, 4. *Verbeekina verbeeki* (Geinitz), 3: tangential section, MPC 3715; 4: axial section, MPC 3716, both Loc. 13, x 10.

54–56, pl. 8, figs. 7–13; Hasegawa *et al.*, 1979, pl. 83, figs. 1, 2, 4 (not described); Tien, 1979, p. 132–134, pl. 20, figs. 4–6; Li *et al.*, 1979, pl. 2, fig. 5 (not described, the same as Pl. 2, fig. 2 of Han, 1985); Sun *et al.*, 1983, p. 37, pl. 9, fig. 3; Han, 1985, p. 684, pl. 2, figs. 2–4.

*Occurrence*:—Common in gray sparitic limestone at Loc. 13 (Mitsugo Limestone Cave) and rare in conglomeratic limestone at Loc. 18 (Mt. Komyosan).

Family Neoschwagerinidae Dunbar and Condra, 1928

Subfamily Neoschwagerininae Dunbar and Condra, 1928

Genus *Neoschwagerina* Yabe, 1903

*Neoschwagerina craticulifera* (Schwager)

Figures 6-13–16, 18, 19; 7-1

*Remarks*:—The present specimens resemble most of those described from the various localities within the Tethyan Province. However, those described from Jilin, Northeast China (Han, 1980) and from Xizang (Tibet) (Chu, 1982) are excluded from this species. Two illustrations (Pl. 33, figs. 9, 10) among the three (Pl. 33, figs. 9–11) from Jilin are referable to the genus *Lepidolina*, and the other would be assignable to other species of *Neoschwagerina*. The Xizang material is also referable to the genus *Lepidolina*. The following synonym list of this species is followed by Toriyama and Kanmera (1977):

Lin *et al.*, 1977, p. 90, pl. 28, fig. 13; Liu *et al.*, 1978, p. 89, pl. 21, fig. 11; Toriyama and Kanmera, 1979, p. 74–77, pl. 12, figs. 11–18; Kobayashi, 1979, pl. 4, figs. 6–8 (not described); Hasegawa *et al.*, 1979, pl. 84, figs. 9–17 (not described); Wang *et al.*, 1982, p. 105, pl. 29, fig. 7; Xie, 1982, p. 69, pl. 33, fig. 12; Sun *et al.*, 1983, p. 38, pl. 10, figs. 2, 12; Ishibashi, 1983, pl. 13, figs. 10–12 (not described); Ishibashi, 1986, p. 108, 109, pl. 17, figs. 1–12.

*Occurrence*:—Common in gray micritic limestone at Loc. 7 (280 m SSW of Mt. Shiroyama), very rare in gray oölitic limestone at Loc. 9 (1.8 km WNW of Mt. Mitake) and common in conglomeratic limestone at Loc. 18 (Mt.

Komyosan).

*Neoschwagerina haydeni* Dutkevich and Khabakov

Figures 7-2a–b–11

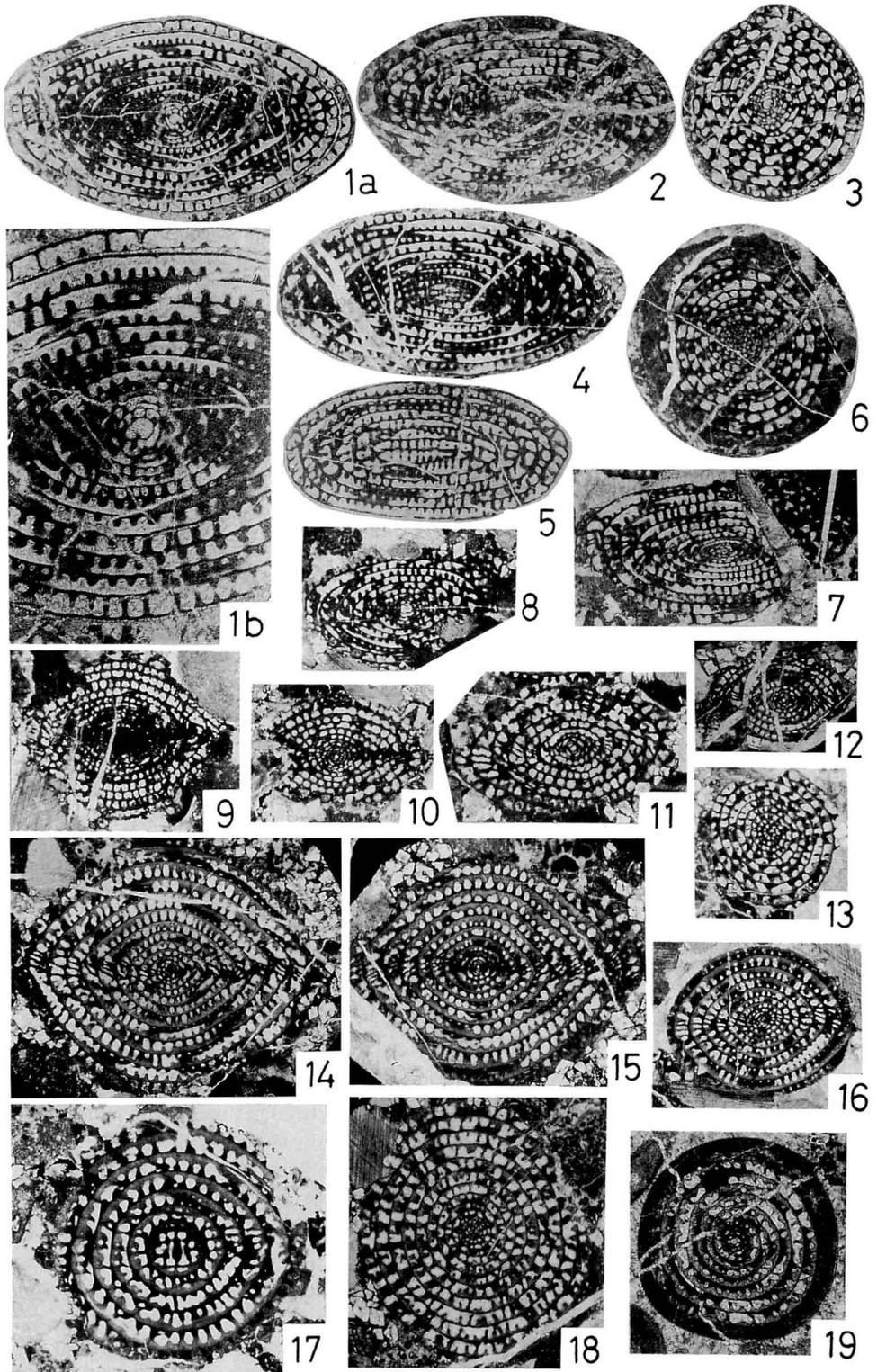
*Neoschwagerina craticulifera haydeni* Dutkevich and Khabakov; Thompson, 1946, p. 155, 156, pl. 23, figs. 12, 13; Kanmera, 1957, pl. 19, fig. 24 (not described; the same as Thompson, 1946, pl. 23, fig. 12); Toriyama, 1958, p. 220–223, pl. 41, figs. 6–8; Suyari, 1962, p. 35, 36, pl. 11, fig. 5; Ishizaki 1962, p. 173–175, pl. 12, figs. 4–6.

*Neoschwagerina haydeni* Dutkevich and Khabakov; Honjo, 1959, p. 147–149, pl. 3, fig. 10; Minato and Honjo, 1959, pl. 3, fig. 2 (not described); Sheng, 1963, p. 103, 104, 236, 237, pl. 32, figs. 1–8; Zhang and Wang, 1974, p. 292, pl. 151, fig. 7; Liu *et al.*, 1978, p. 89, pl. 21, fig. 6; Toriyama and Kanmera, 1979, p. 77–80, pl. 12, figs. 19–22, pl. 13, figs. 1–8; Hasegawa *et al.*, 1979, pl. 84, figs. 1–8 (not described); Wang *et al.*, 1981, p. 63, pl. 15, figs. 1, 2, 5, 7; Wang *et al.*, 1982, p. 106, pl. 30, fig. 7; Sun *et al.*, 1983, p. 39, pl. 10, fig. 13.

*Neoschwagerina cf. haydeni* Dutkevich and Khabakov; Ding, 1978, pl. 101, fig. 2 (not described).

*Description*:—Shell inflated fusiform with nearly straight axis of coiling, broadly arched periphery, straight lateral sides and rounded poles. Mature shell of 14 to 15 volutions, approximately 6 to 8 mm in axial length and 4.4 to 5.5 mm in median width, giving form ratio about 1.4.

Proloculus spherical, minute and about 40 to 90  $\mu\text{m}$  in diameter. The first one to one and a half volutions ellipsoidal with short axis of coiling. The second to seventh volutions fusiform to inflated fusiform with pointed to bluntly pointed poles, gradually increasing their height and width. Beyond the eighth volution, height of volution becomes nearly the same. From the first to eleventh volutions of the specimen illustrated in Figure 7-2a–b, axial length 0.03, ?, 0.15, 0.26, 0.41, 0.64, 0.90, 1.20, 1.56, 1.81 and 2.07 mm; radius vector 0.07, 0.09, 0.15, 0.22, 0.31, 0.45, 0.63, 0.81, 1.01, 1.23 and 1.44 mm, respectively. From the first to twelfth volutions of the specimen illustrated in Figure 7-3, axial length 0.05, 0.14, 0.23, 0.43, 0.59, 0.80, 0.98, 1.17, 1.47, 1.77, 2.06 and 2.29 mm; radius vector



0.08, 0.12, 0.20, 0.29, 0.41, 0.55, 0.68, 0.84, 1.04, 1.25, 1.47 and 1.68 mm, respectively.

Spirotheca composed of tectum and thick finely alveolar keriotheca except for juvenile volutions. Spirothecal thickness from the third to eleventh volutions 22, 26, 35, 48, 74, 62, 111, 51 and 65  $\mu\text{m}$  in the specimen illustrated in Figure 7-2a–b. Septal count attains 30 to 34 in the tenth volution. Between the adjacent septa, axial septula well developed. Axial septula first appear in the fifty volution. Their number gradually increases ontogenetically. Two, rarely one, axial septula regularly arranged between adjacent septa in the thirteenth and later ones.

Primary transverse septula well developed throughout shell except for juvenile volutions. They are broad and triangular or fan-shaped in cross section. Combination of well-developed primary transverse septula and axial septula subdivides each chamber into ellipsoidal to rectangular chamberlets. Secondary transverse septula first appeared in peripheral parts of the thirteenth volution, but absent in median part of shell.

Parachomata massive and high, more than half as high as chambers in places. In such cases, parachomata are connected with lower end of primary transverse septula. Foramina elliptical to circular, open at basal part of septa in cross sections.

*Remarks:*—Among the described materials, the Chinese ones from the Maokou Limestone of Guizhou (Sheng, 1963) most closely resembles the present ones in shape and size of shell, development of septula and parachomata.

*N. haydeni* is closely related to *N. craticulifera*, but the former can be distinguished from the latter in having larger shell, more number of volutions and well-developed septula. *N. haydeni* is allied to *N. margaritae* Deprat in development

of both axial and transverse septula. The two occur nearly the same stratigraphic level. The former is easily distinguished from the latter in straight lateral sides and more pointed poles of each volution.

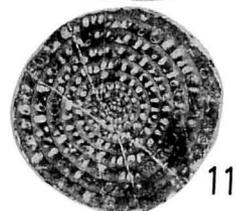
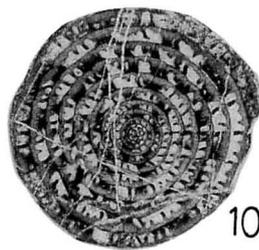
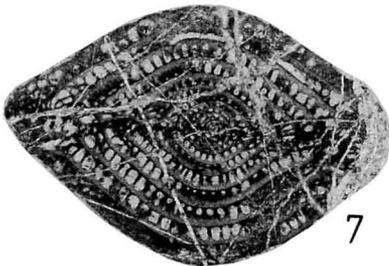
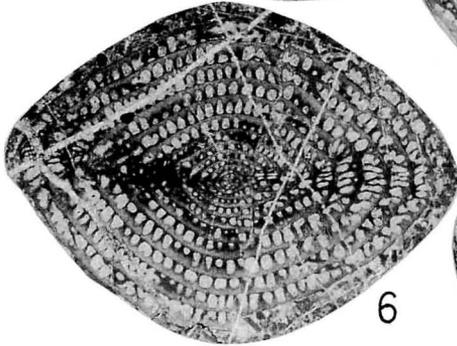
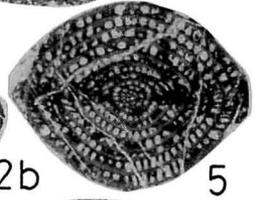
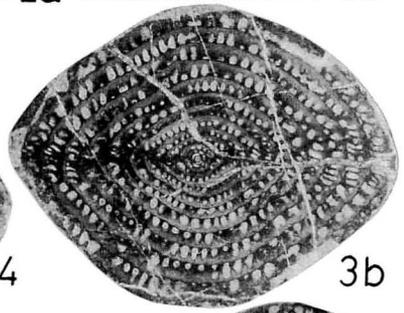
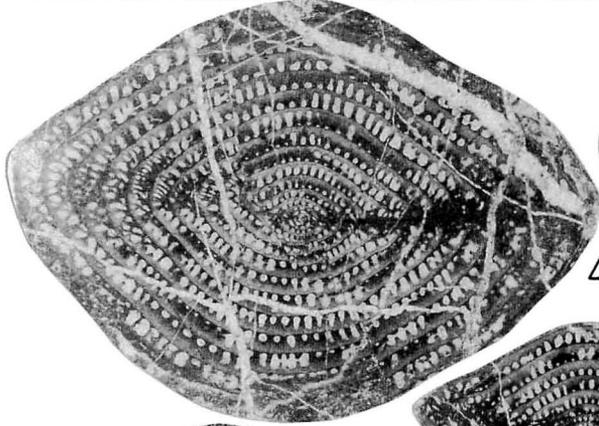
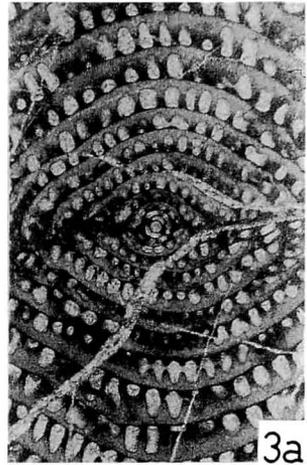
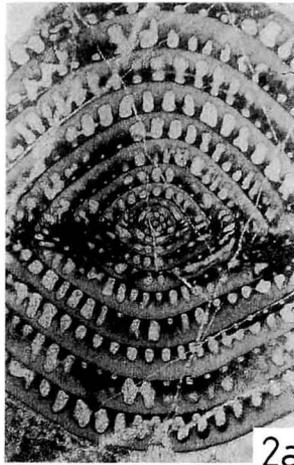
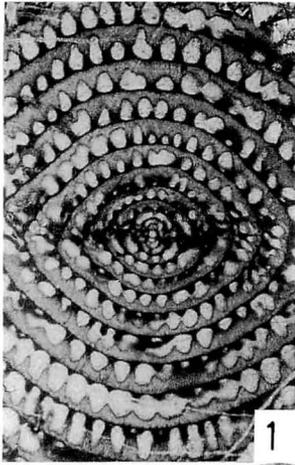
*Occurrence:*—Common to rare in gray micritic, partly dolomitic, limestone at Loc. 12 (Otakezawa Limestone Cave) and abundant to common in gray micritic and sparitic limestones at Loc. 13 (Mitsugo Limestone Cave).

### *Neoschwagerina simplex* Ozawa

Figure 6-17

- Neoschwagerina simplex* Ozawa, 1927, p. 153, 154, pl. 34, figs. 7–11, 22, 23, pl. 37, figs. 3a, 6a; Chen, 1956, p. 55, 56, pl. 12, figs. 13–16; Honjo, 1959, p. 139–142, pl. 3, figs. 1, 4, 5, pl. 4; Minato and Honjo, 1959, pl. 1, fig. 2 (not described); Suyari, 1962, p. 36, pl. 11, fig. 1; Kanmera, 1963, p. 112, 113, pl. 13, figs. 1–6, pl. 14, figs. 1–6, pl. 19, fig. 15; Leven, 1967, p. 189, 190, pl. 32, figs. 8–10; Ozawa, 1970, pl. 4, figs. 9 (the same as pl. 10, fig. 16 of Ozawa, 1975), 10 (not described); Lin *et al.*, 1977, p. 91, pl. 28, fig. 3; Liu *et al.*, 1978, p. 90, pl. 21, fig. 8; Sashida, 1980, p. 305, 306, pl. 35, figs. 8–10.
- Neoschwagerina cf. simplex* Ozawa; Kanmera, 1957, pl. 20, fig. 1 (not described); Kanuma, 1960, p. 67, 68, pl. 11, figs. 1, 10, 11.
- Neoschwagerina sphaerica* (Maklay); Honjo, 1959, p. 159, pl. 3, fig. 3.
- Neoschwagerina simplex simplex* Ozawa; Toriyama, 1975, p. 99–101, pl. 19, figs. 25–28, pl. 20, figs. 1–21.
- Neoschwagerina simplex tenuis* Toriyama and Kanmera; Toriyama, 1975, p. 97–99, pl. 19, figs. 14–24.
- Neoschwagerina cf. simplex tenuis* Toriyama and Kanmera; Toriyama and Kanmera, 1979, p. 74, pl. 12, fig. 10.
- ? *Neoschwagerina simplex simplex* Ozawa; Li *et al.*, 1979, pl. 2, fig. 8 (not described, the same as Pl. 2, fig. 11 of Han, 1985, p. 685).
- non. *Neoschwagerina simplex* Ozawa; Han, 1980, p. 90, pl. 33, figs. 7, 8.

← **Figure 6.** 1a–8. *Pseudodoliolina pseudolepida* (Deprat), 1, 2, 7: axial sections; 3: sagittal section; 4, 5: tangential sections; 6: parallel section; 8: oblique section, 1–6: Loc. 13; 7, 8: Loc. 18, 1–8: MPC 3666; 3722; 3665; 3668; 3723; 3724; 3729; 3633, all  $\times 10$  except for 1b:  $\times 20$ . 9–12. *Neoschwagerina* sp. A, axial sections, Loc. 18, 9–12: MPC 3761; 3764; 3762; 3631,  $\times 10$ . 13–16, 18, 19. *Neoschwagerina craticulifera* (Schwager), 13, 16: oblique sections; 14, 15: axial sections; 18, 19: sagittal sections, all from Loc. 18 except for 19: Loc. 9, 13–16: MPC 3634; 3629; 3628; 3763; 18: MPC 3627; 19: MPC 3801,  $\times 10$ . 17. *Neoschwagerina simplex* Ozawa, tangential section, Loc. 18, MPC 3760,  $\times 10$ .



*Remarks:*—Honjo (1959) described the topotype materials of this species. He designated the lectotype for the specimen illustrated as fig. 8 of Pl. 34 (incomplete axial section) of Ozawa (1927), and also noticed the absence of secondary transverse septula of this species. Whereas, the terms of “septa”, “axial septula” and “secondary axial septula” of Honjo (1959) were in confusion in his description. His “secondary axial septula” should be restrictedly defined as axial septula according to his not fully-grown sagittal section (Honjo, 1959, Pl. 3, fig. 5). This is also comprehensible from Ozawa’s original description, in which mentioned is “auxiliary meridional septa rarely found in later whorls”.

Simple framework of septula, rather thick spirotheca and prominent parachomata of the Ogawadani materials are similar to *Neoschwagerina simplex* rather than *N. craticulifera*. However, the present materials have larger shell than original ones. Specific as well as generic assignment is doubtful of the specimen identified with *Cancellina primigena* (Hayden) by Huzimoto (1936) from Mt. Komyosan. The illustrated specimen has stout and short primary transverse septula, massive parachomata and rather thick spirotheca. These characters are diagnostic to *Maklaya* or primitive species of *Neoschwagerina* rather than *Cancellina*. More number of specimens are required for further comparisons.

*N. spherica* (Maklay) described from the Akasaka Limestone (Honjo, 1959) and *N. simplex tenuis* Toriyama and Kanmera from the Rat Buri Limestone of Thailand (Toriyama, 1975) are considered to be junior synonym of the present species based on their stratigraphic occurrences and morphologic characters. Two illustrated specimens described from Northeast China by Han (1980) are slightly deformed and abraded in their outer volutions. Han’s materials are not referable to *N. simplex* on the

basis of their well-developed transverse septula.

*Occurrence:*—Rare in conglomeratic limestone at Loc. 18 (Mt. Komyosan).

#### *Neoschwagerina* sp. A

Figures 6-9-12

*Remarks:*—Development and shape of septula and parachomata and thin spirotheca of the present materials resemble those of such species of *Cancellina* as *C. tenuitesta* Kanmera and *C. akasakensis* (Morikawa and Suzuki). The former species was described from the Kozaki Formation in association with *Neoschwagerina simplex* Ozawa (Kanmera, 1963). The latter species was proposed by Morikawa and Suzuki (1961) as *Neoschwagerina akasakensis* from the sixth zone (*Neoschwagerina rotunda* Zone) of the Akasaka Limestone which was subdivided into fifteen fusulinacean zones by Morikawa (1958).

On the contrary, endothyroid coiling in initial stage of the present materials is diagnostic to *Neoschwagerininae*. Endothyroid coiling is lack in genera referable to *Lepidolininae* including *Cancellina* except for their microspheric forms. This unnamed species is, accordingly, not assignable to *Cancellina* but *Neoschwagerina*. The present materials may be representative of inner volutions of *N. craticulifera*. However, it is less possible on the basis that they are not co-existed with *N. craticulifera* in the same limestone block. Spirothecal thickness, shape of septula and parachomata are different between the two.

*Occurrence:*—Common to rare in conglomeratic limestone at Loc. 18 (Mt. Komyosan).

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← **Figure 7.** 1. *Neoschwagerina craticulifera* (Schwager), enlarged photograph of Fig. 6-15, × 20. 2a-11. *Neoschwagerina haydeni* Dutkevich and Khabakov, 2-7: axial sections; 8, 10, 11: sagittal sections; 9: parallel section, Loc. 13, 2-11: MPC 3720; 3721; 3717; 3714; 3664; 3725; 3727; 3712; 3719; 3663, all × 10 except for 2a and 3a: × 20.

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関東山地南部小川谷層産の古生代後期有孔虫化石：関東山地の秩父帯南帯を構成する小川谷層の石灰岩ブロックから、32属47種の石炭紀中期～ペルム紀中期の有孔虫化石が識別された。これらをリストするとともにフズリナ超科に含まれる5属9種：*Beedeina higoensis* (Kanmera), "*Parafusulina*" *gigantea* (Deprat), *P. hirayuensis* Igo, *Verbeekina verbeeki* (Geinitz), *Pseudodoliolina pseudolepida* (Deprat), *Neoschwagerina craticulifera* (Schwager), *N. haydeni* Dutkevich and Khabakov, *N. simplex* Ozawa, *N. sp. A* を記載した。小林文夫

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857. PERMIAN SPHINCTOZOAN SPONGES FROM THE  
ICHINOTANI FORMATION, HIDA MASSIF,  
CENTRAL JAPAN

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**Abstract.** Two new Permian sphinctozoan sponges, *Cystauletes kingi* and *Amblysi-phonella hidensis* are described from the uppermost part of the Ichinotani Formation which crops out in the Mizuyagadani valley, Fukuji, Hida Massif, central Japan. The genus *Cystauletes* was first introduced by King from the Desmoinesian of Oklahoma, U.S.A. and *Cystauletes mammosus* King was described as a monotypic species of this genus. The present new species is characterized by larger size than the American species. *Amblysiphonella hidensis* is characterized by high chambers with rather thin exowalls as compared with other species of this genus.

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### Introduction

Upper Paleozoic sponges were introduced by the classical works of Zittel (1877, 1878), Steinmann (1882), Waagen and Wentzel (1887), and Hinde (1888). Subsequently, Girty (1908) described Permian sponges from the Guadalupe Mountains of Texas and he proposed several new genera. Mansuy (1913, 1914) described some Permian sponges from Indochina. Gerth (1929) introduced a rich Permian sponge fauna from Timor including several new genera and species. In the 1930's to 1940's Carboniferous and Permian sponges were described from various

additional regions, such as Sicily, Italy (Parona, 1933); Karawanken, Austria (Peltzmann, 1930); Kwangsi, China (Yü, 1935); Texas and other states of U.S.A. (King, 1933, 1943, *etc.*).

After World War II, Termier and Termier (1955, 1977), Termier, Termier and Vachard (1977) contributed to the study of Upper Paleozoic sponges on the basis of rich collections from Tunisia. Finks (1960) also published a comprehensive monographic study of Upper Paleozoic siliceous sponges from the Texas region, and he (Finks, 1970) also discussed some interesting problems concerning evolution and history of Paleozoic sponges. Seilacher (1962) proposed a new major classification of calcareous

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sponges.

Recently, Permian sponges have been described from China (Deng, 1981, 1982) and Venezuela (Rigby, 1984). Rigby and Potter (1986) reported an interesting Ordovician sponge fauna from northern California and they described many new forms and discussed phylogeny of the Lower and Middle Paleozoic genera. Their report is also very informative in discussions of phylogeny of Upper Paleozoic forms. Aleotti, Dieci and Russo (1986) restudied Permian sphinctozoan sponges from Sicily that were previously reported by Parona (1933). These current studies, mentioned above, contributed to our understanding of many paleontological problems of the Upper Paleozoic sphinctozoan sponge faunas. However, our knowledge concerning sponge faunas, in general, is still limited when compared with most of other Upper Paleozoic invertebrate fossil groups.

Common occurrences of fossil sponges have been known from Japanese Upper Paleozoic limestones and coherent sedimentary rocks, however, these fossils were largely ignored by most Japanese paleontologists. Yabe (1902) first pointed out the occurrence of Permian calcareous sponges from Japan. Subsequently, Hayasaka (1918, 1923) studied some Upper Paleozoic calcareous sponges collected from China and Japan. Yabe and Sugiyama (1934) described two new species of *Amblysiphonella* and proposed a new genus, *Rhabdactinia*, from Permian rocks of Shikoku. The same authors described several species of what they termed stromatoporoids from Permian of Japan (Yabe and Sugiyama, 1930, 1933). Some of these are now known not to be stromatoporoids (Mori, 1980), and some of them seem to be calcareous sponges. Inai (1936) proposed a new Carboniferous genus, *Discosiphonella*, from northeast China. Akagi (1958) described a new Permian species from west Japan. Most of the described Upper Paleozoic sponges in Japan are species of *Amblysiphonella*.

As will be mentioned later, our material was collected from the Lower Permian of the uppermost Ichinotani Formation exposed in the

Fukuji area, Hida Massif, central Japan. It includes a new species of *Cystauletes*, which until now has been known only from the Pennsylvanian of Oklahoma, U.S.A. This paper is, thus, the second report of the occurrence of this genus, which seems to be noteworthy. The other sphinctozoan sponge associated with this new species is a new species of *Amblysiphonella*, which is the most commonly reported genus in Permian rocks of Japan and the Tethyan faunal realm.

### Acknowledgment

We thank Professor J. Keith Rigby, Department of Geology, Brigham Young University, Provo, Utah, who read the manuscript and offered many helpful comments. We acknowledge the support of this research by the Grant-in-Aid for Scientific Research from the Ministry of Education, Science and Culture, Japanese Government (No. 62540597).

### Geologic setting

The Ichinotani Formation crops out along the Ichinotani, Mizuyagadani and Mizuboradani valleys, in the Fukuji area, Hida Massif, central Japan. This formation consists mainly of limestone and subordinate shale and tuff. Most of the limestones are fossiliferous, well bedded and dark gray to black, with interbeds of pale gray, massive to thickly bedded limestones. Stratigraphic and paleontologic investigations have previously concerned fusulinaceans, smaller foraminifers, corals, cephalopods, calcareous algae and other minor groups. They have been studied by several specialists, such as Igo (1957), Kato (1959), Niikawa (1978), Adachi (1985), Niko (1986), Niko and Hamada (1987) and many others. These studies proved that the geologic age of the Ichinotani Formation ranges from the latest Viséan through the Early Permian Asselian.

The present sponges came from the uppermost part of the Ichinotani Formation which crops out along the lower reaches of the Mizuyagadani valley (Figure 1). Limestone beds

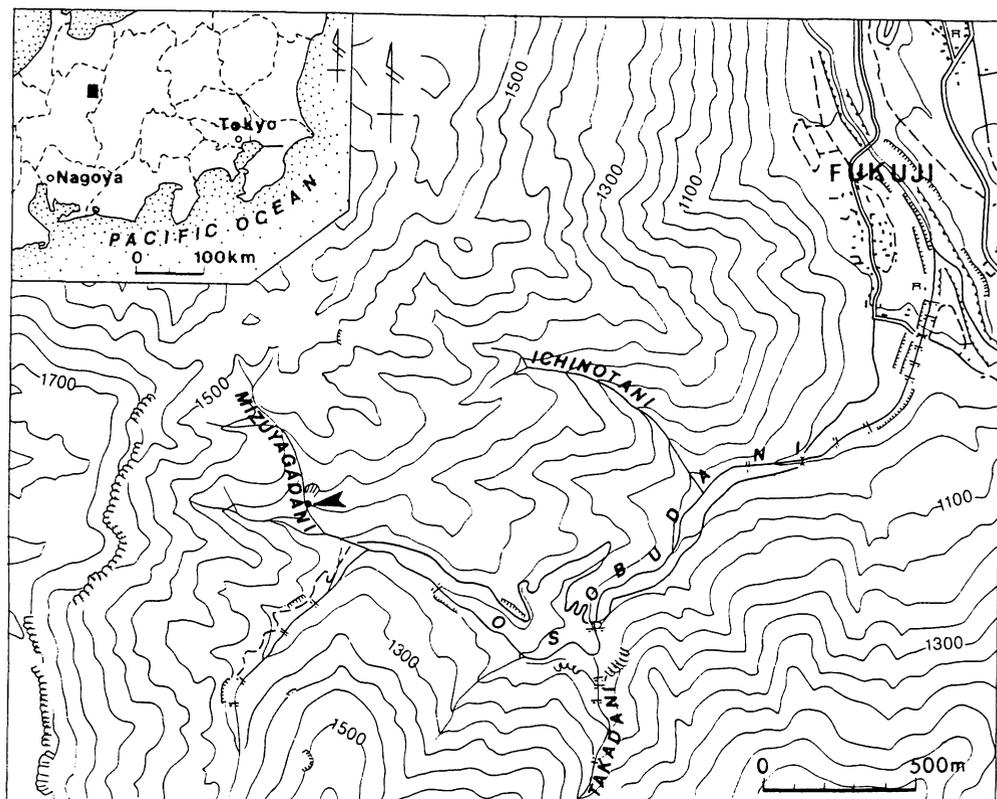
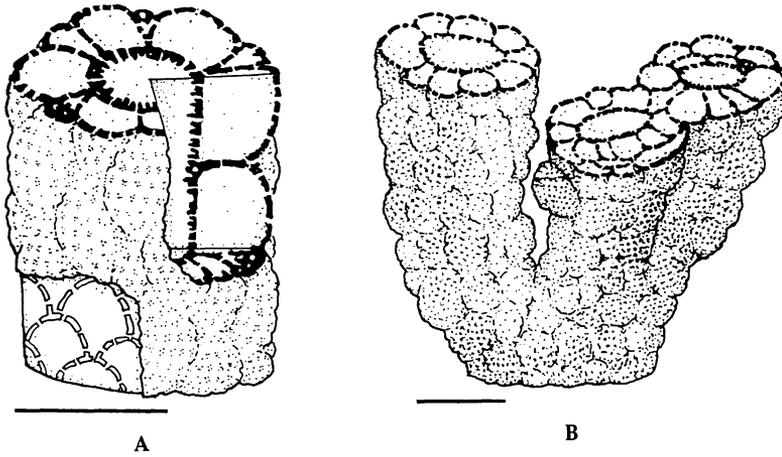


Figure 1. Locality map.

at this outcrop are abundantly fossiliferous, thickly bedded to massive and mostly pale gray, but frequently include pale red and pale green muddy material, and are approximately 5m-thick. They yield abundant calcareous algae, fusulinaceans, smaller foraminifers, sponges, bryozoans and crinoid stems, with subordinate associations of pelecypods, gastropods, nautiloids, and brachiopods. The geologic age of these limestone beds is thought to be Asselian on the basis of the occurrence of *Quasifusulina longissima ultima* Kanmera. Furthermore, these beds immediately overlie limestones containing *Pseudoschwagerina morikawai* Igo, which is the most characteristic species of the basal Permian of the Ichinotani Formation. The beds also are conformably overlain by the Mizuyagadani Formation which consists of calcareous tuff, and alternating sandstone, shale and siliceous tuff. The Mizuyagadani Formation yields corals,

brachiopods, orthoceratids and radiolarians which indicate a Sakmarian age (Igo, 1959, Niko et al., 1987, Niko, 1987).

Sphinctozoan sponges are particularly abundant approximately in the middle of the 5 meters limestone beds, but they are very difficult to separate from limestone. Most specimens on the weathered surface show pale red because they are owing coated by oxidized muddy material. Sponge bodies are filled with calcareous mud, including fragments of various fossils. Central tubes of some specimens were partly filled with sparry calcite and lime mud, showing geopetal structures. Sessile foraminifers, *Tuberitina*, and calcareous algae are attached to endwall surfaces of some specimens. The sedimentary environments of this limestone are thought to be very shallow back reef lagoonal sea on the basis of limestone lithology and paleontologic evidence.



Figures 2A, B. *Cystauletes kingi* Igo, Igo and Adachi, n. sp. A, a part of the body restored from the serial sections of paratype; B, branched bodies restored from the holotype; scale bar is 1 cm.

### Description of species

Class Calcarea Bowerbank, 1884

Order Sphinctozoa Steinmann, 1882

Suborder Porata Seilacher, 1962

Family Cystothalamiidae Girty, 1908

Genus *Cystauletes* King, 1943

*Cystauletes kingi* Igo, Igo and Adachi, n. sp.

Figures 2A–B; 4-1a–2c; 5-1a–3; 6-1a–3b

**Diagnosis.**—*Cystauletes* having a large bifurcated cylindrical body, about 3 cm in diameter. Entire body dendroid and may be about 10 cm long. Central tube also large, about 1.5 cm in diameter. Spherical to subspherical and glomerated chambers diagonally arranged and partly overlapping, and about 1.0 cm in diameter. Wall perforated by numerous pores of about 0.4 mm in diameter.

**Description.**—Sponges consist of almost straight or slightly sinuous and distally branching

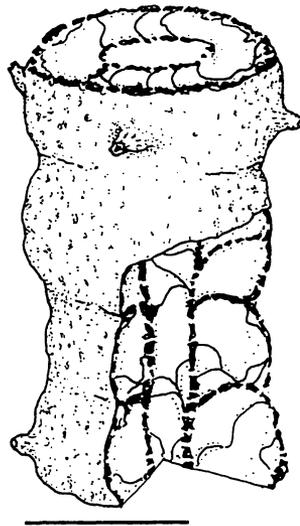
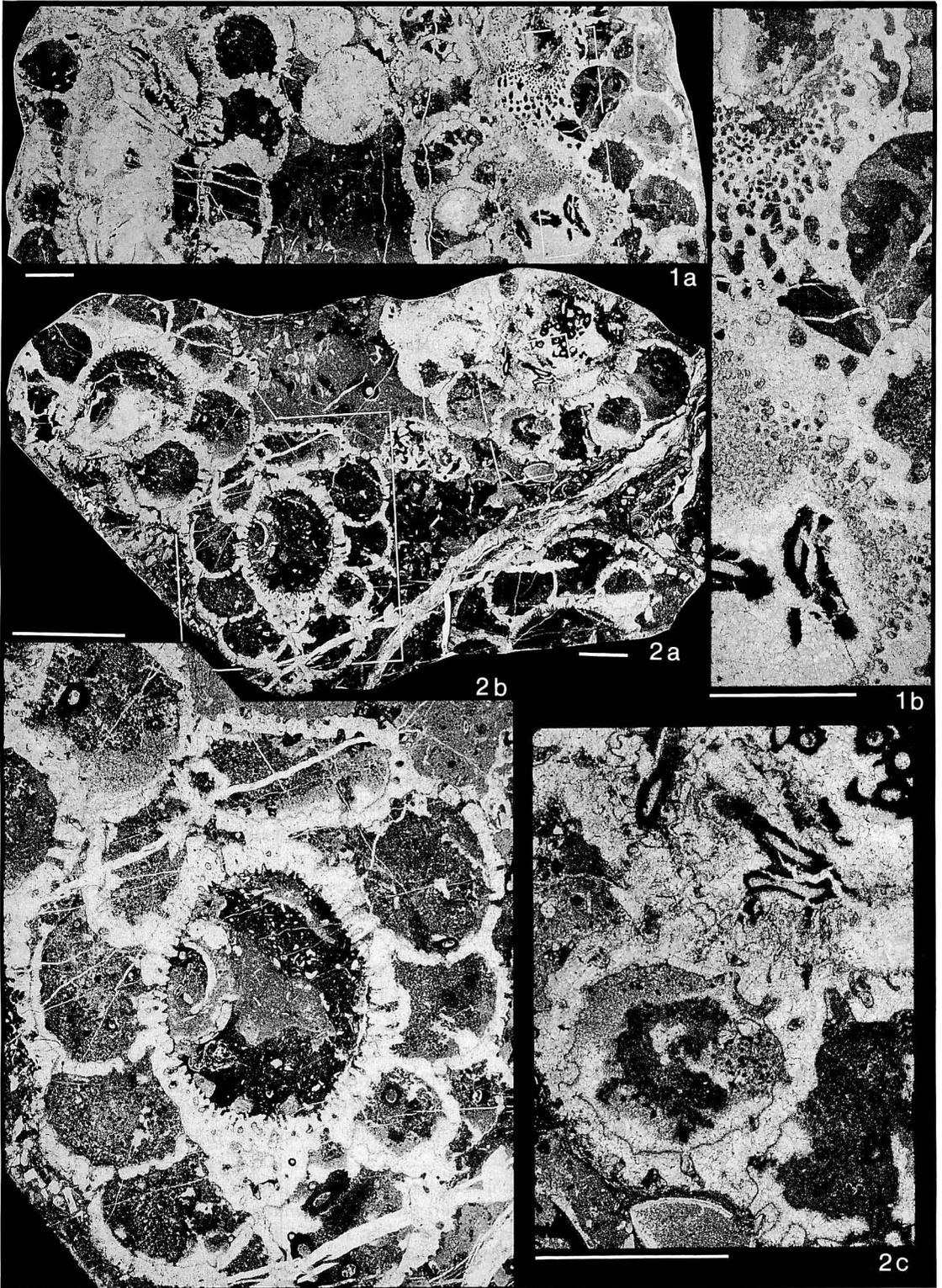


Figure 3. *Amblysiphonella hidensis*, Igo, Igo and Adachi, n. sp. A part of the body restored from the holotype; scale bar is 1 cm.

cylindrical bodies 2.5 to 3.5 cm in diameter. Proximal portion of sponge is more or less tapered and its diameter increases slightly with

→ **Figure 4.** *Cystauletes kingi* Igo, Igo and Adachi, n. sp. 1a–2c, holotype, Reg. no. IGUT 5380; 1a, longitudinal section of bifurcated bodies; 1b, enlarged from a part of right body of 1a showing meshwork and vermiform patterns of endopores; 2a, horizontal section of bifurcated bodies; 2b, enlarged from a part of middle body showing detailed feature of pores of wall; 2c, enlarged from a part of upper right body of 2a showing structure of exowall and endowall; white lines enclosed in 1a and 2a indicate enlarged portion; all scale bars are 5.0 mm.



growth. Branching is bifurcate at about 10 degrees. Thrice-bifurcate branching is observed in the holotype, but the last bifurcation is represented by a small incipient bud. Complete sponges are unknown in our collection, but total lengths may attain about 10 cm.

Chambers are numerous, spherical to sub-spherical, glomerated and diagonally arranged. They partly overlap each other, therefore, chambers appear in two rows in the horizontal section and in three rows in most tangential sections. Diameters of chambers are 0.8 to 1.1 cm, measured at right angles to the long axis.

Exowalls and interwalls of chambers are perforated by numerous exopores and interpores, 0.35 to 0.50 mm in diameter. Exopores are densely disposed and are mostly circular pits surrounded by low rims on weathered surfaces of chambers. Exopores and interpores are not simple pores, but some of them bifurcate within walls or others irregularly penetrate into walls.

The retrosiphonate central tube is almost straight or slightly sinuous. It ranges 1.0 to 1.3 cm in diameter and does not have any partitions. The endowall is 1.0 to 1.8 mm thick and perforated by numerous endopores. Endopores are almost the same size as the exopores and interpores, but are more densely and irregularly disposed. Endopores appear as vermiform and meshwork patterns in sections of the walls.

Exowalls and endowalls consist of mosaics of sparry calcite and their surfaces are coated by very thin dark layers.

*Remarks.*—All the specimens could not be separated from the enclosing matrix, therefore, we prepared thin and polished sections, including several serial sections. The present new species is similar to *Cystauletes mammosus* King, which was described from the Pawnee Limestone, Marmaton Group, Desmoinesian Series, Pennsylvanian of Oklahoma, U.S.A. However, this American species was not well illustrated and

detailed comparison of the internal structures and branching of the body is difficult. However, the present new species has a much larger body, chamber and central tube than in the American species. Also the chambers of our Japanese species are more spherical than those in *C. mammosus*.

The species is named in honor of Ralph H. King who established this genus in 1943.

*Material.*—The holotype, Reg. no. IGUT 5380, and 5 paratypes, Reg. nos. IGUT 5381–5385, are all stored at the Institute of Geoscience, University of Tsukuba. All specimens were collected from the uppermost part of the Ichinotani Formation, the Mizuyagadani valley, Fukuji, Gifu Prefecture.

Family Sebergasiidae Steinmann, 1882  
Genus *Amblysiphonella* Steinmann, 1882

*Amblysiphonella hidensis* Igo, Igo and Adachi, n. sp.

Figures 3; 7-1a–3b

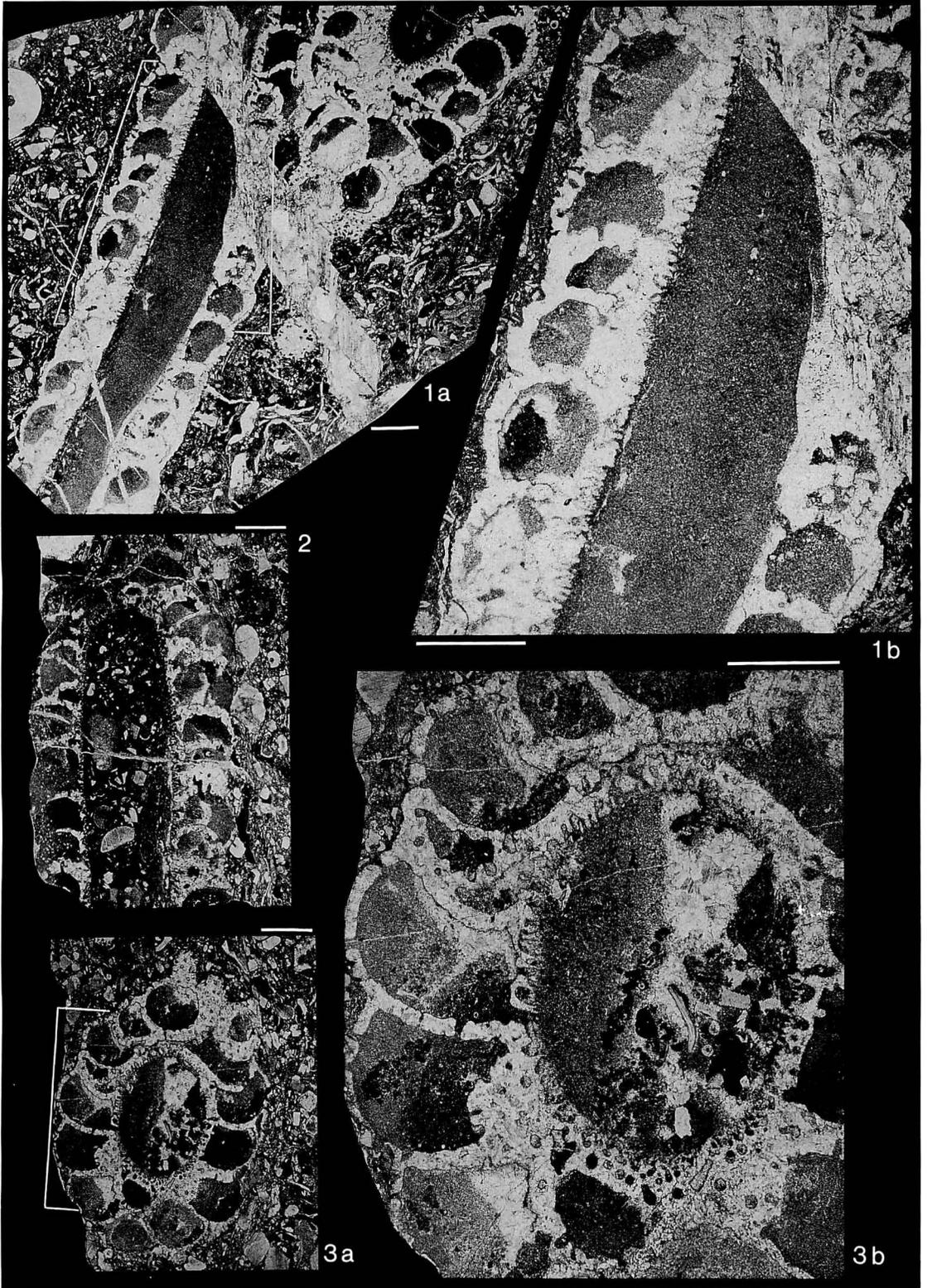
*Diagnosis.*—*Amblysiphonella* having a weakly annulated, large cylindrical and branching body, 1.6 to 2.0 cm in diameter and may be up to 10.0 cm in long. Retrosiphonate central tube 4.0 to 7.0 mm in diameter and surrounded by annular large chambers. Rather large hemispherical vesiculae developed in both chambers and central tube. Perforated walls rather thin, less than 1.0 mm thick.

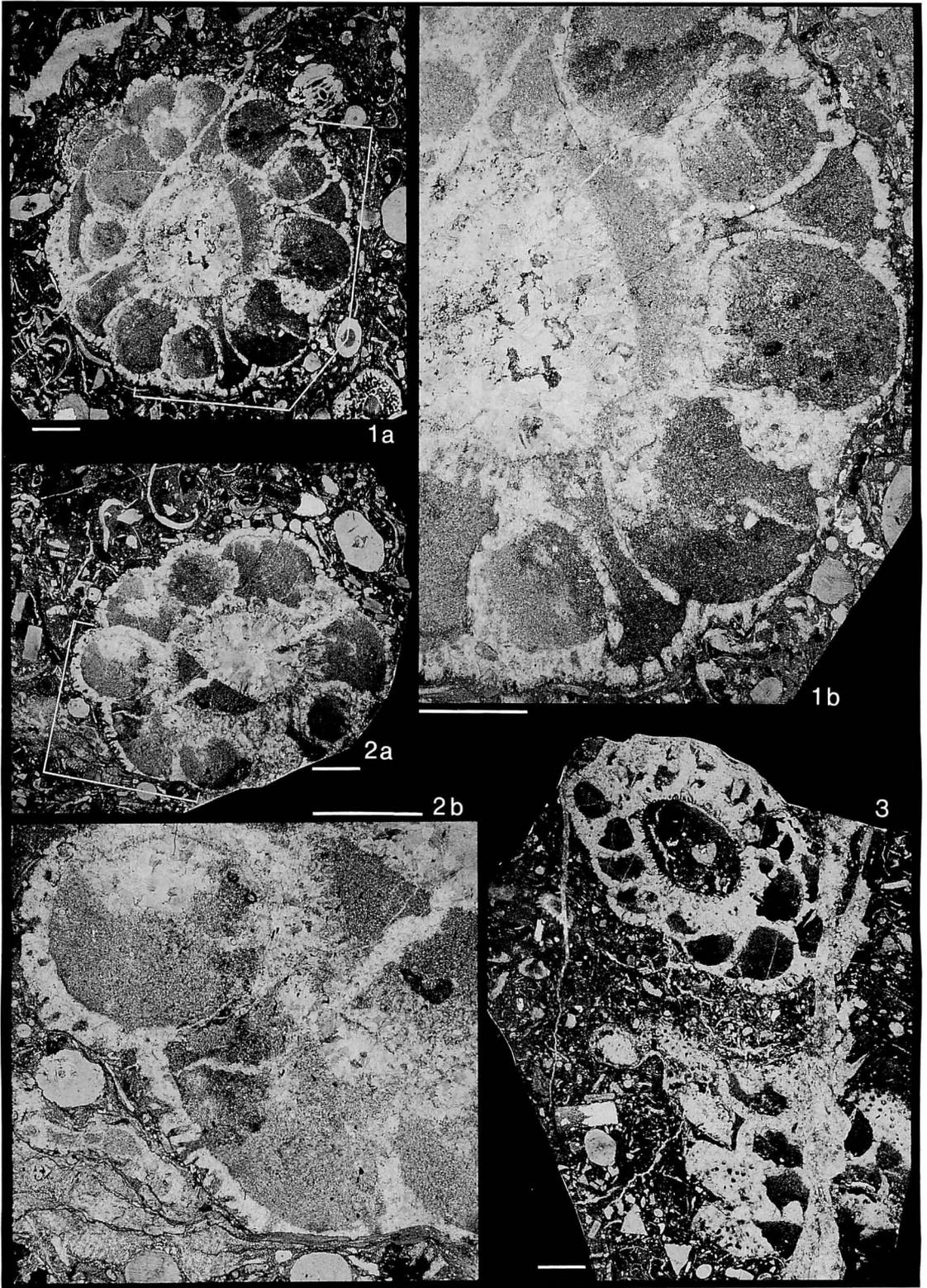
*Description.*—Sponges having cylindrical, slightly annulated and almost straight body and distally branching. Entire body is not preserved, but tapers slightly proximally and ranges from 1.6 to 2.4 cm in diameter and may be more than 8.0 cm long. Branching is bifurcate at rather narrow angles of about 10 degrees. Our specimens branch only once.

A retrosiphonate central tube extends throughout the sponge and is almost straight or

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→ **Figure 5.** *Cystauletes kingi* Igo, Igo and Adachi, n. sp. 1a–2b, paratype, Reg. no. IGUT 5381; 1a, 2a, two horizontal sections of the same individual showing geopetal texture; 1b, 2b, enlarged from a part of body of 1a and 2b showing detailed feature of pores of wall; 3, paratype, Reg. no. IGUT 5382; oblique horizontal and longitudinal sections of the same individual; white lines enclosed in 1a and 2a indicate enlarged portion; all scale bars are 5.0 mm.





slightly sinuous, with a diameter of 5.3 to 7.7 mm. The endowall is more or less variable in thickness and is 0.30 to 0.60 mm thick.

Chambers around the central tube are weakly annulated. They are high and subquadrate in cross section with a slightly arched top and base in longitudinal section. They are 5.0 to 7.0 mm wide and 7.6 to 9.2 mm high. Rather large hemispherical vesicles are developed in chambers and have a thin dark inner layer. Rather stout exaules are developed on the surface of exowall. Basal diameters of exaules are about 1.0 mm and are covered with a cribribulla, but its length is uncertain.

Exowalls and interwalls are rather thin compared with the size of sponge body, for they are only 0.63 to 1.00 mm thick. They are perforated by numerous pores, 0.20 to 0.26 mm in diameter. These pores are circular to subcircular and some exopores have a low rim. Endopores are almost the same size and shape as the exopores.

*Remarks.*—The present new species is similar to *Amblysiphonella dichotoma* (Yabe) described from Kobama and Yakejima of Okatsu, southern Kitakami Mountains (Yabe, 1902; Hayasaka, 1918), but the former has a larger body, thinner walls and higher chambers. Furthermore, *A. dichotoma* has well developed diaphragms in the central tube and chambers. *Amblysiphonella sikokuensis* Yabe and Sugiyama, reported from Mimikiri, Sakawa of Kochi Prefecture (Yabe and Sugiyama, 1934), also resembles the present new species, but the former has well developed diaphragms and smaller chambers and central tube. Walls of the two previously known species have a median dark line, but the present new species has a dark thin inner layer.

*Amblysiphonella asiatica* Yü, described from En-young-hsien, Kwangsi Province, southern China, is similar to the present Japanese species, but the former has a larger body and traces of

horizontal diaphragms in the central tube. *A. vesiculosa* Waagen and Wentzel, described from the Salt Range (Waagen and Wentzel, 1887) and Guangxi, China (Deng, 1981), resembles the present new species. However, the former has a larger body and thicker walls and more well-developed vesiculae. *A. jiaojaensis* Deng (1982), reported from southwest China, is similar to our present species in dimensions, however, the former has a slightly larger body and lower chambers than in our species. The diameter of central tube of *A. jiaojaensis* is characteristically small in comparison to the diameter of body. *A. markamensis* Deng, introduced from the same locality, is also similar to our species, however, the latter has a more slender central tube and higher chambers.

*Material.*—The holotype, IGUT 5386, and one paratype IGUT 5387, stored at the Institute of Geoscience, University of Tsukuba. All specimens were collected from the uppermost part of the Ichinotani Formation, the Mizuyagadani valley, Fukuji, Gifu Prefecture.

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← **Figure 6.** *Cystauletes kingi* Igo, Igo and Adachi, n. sp. **1a–1b**, paratype, Reg. no. IGUT 5382; **1a**, longitudinal section; **1b**, enlarged from a part of the body of **1a** showing detailed feature of pores of wall; **2**, paratype, Reg. no. IGUT 5384; longitudinal section; **3a–3b**, paratype, Reg. no. IGUT 5383; **3a**, horizontal section; **3b**, enlarged from a part of the body of **3a** showing detailed feature of pores of wall; white lines enclosed in **1a** and **3a** indicate enlarged portion; all scale bars are 5.0 mm.



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← **Figure 7.** *Amblysiphonella hidensis* Igo, Igo and Adachi, n. sp. 1a–3b, Holotype, Reg. no. IGUT 5386; 1a, horizontal section; 1b, enlarged from a part of the body of 1a; 3a, longitudinal section; 3b, enlarged from a part of the body of 3a showing detailed structure of chambers, central tube and vesiculae; 2a–2b, paratype, Reg. no. IGUT 5387; 2a, horizontal section of bifurcated bodies; 2b, enlarged from a part of right body; white lines enclosed indicate enlarged portion; all scale bars are 5.0 mm.

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Fukuji 福地, Ichinotani 一の谷, Hida 飛驒, Kitakami 北上, Kobama 小浜, Mizuboradani 水洞谷, Mizuyagadani 水屋ガ谷, Okatsu (Ogatsu) 雄勝, Sakawa 佐川, Yakejima 八景島.

飛驒山地一の谷層産のペルム紀カイメン化石：岐阜県吉城郡上宝村福地の水屋ガ谷に露出する一の谷層最上部の石灰岩からは保存良好なカイメン化石が産出する。多くの連続薄片や研磨標本を作成した結果、*Cystauletes kingi*, *Amblysiphonella hidensis* の2新種が識別された。*Cystauletes* 属は1943年 King によって、アメリカ合衆国オクラホマ州の中部ペンシルバニア系から monotypic で提唱されたものである。今回の新種はこの属の産出報告としては世界で2度目で、模式種の *mammilosus* よりも全体に大きい骨格をもつ。*Amblysiphonella hidensis* は従来知られているものより chamber が高く、壁が薄いことで区別される。

猪郷久義・猪郷久治・安達修子

## 858. A SPHENODISCID AMMONITE ACQUIRED RARELY FROM THE CRETACEOUS OF JAPAN\*

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**Abstract.** This paper is the first record of a sphenodiscid ammonite from Japan. While ammonite faunas from the Upper Campanian and Maastrichtian strata of Japan have recently been under intensive investigation, Mr. Masahiko Takada fortunately found a sphenodiscid ammonite from the Zone of *Pachydiscus awajiensis* in the Izumi Group of Awaji Island and has kindly provided it through Mr. Masahiro Sato for our study. It is fairly large and characterized by the mediolateral and ventrolateral nodes, low fastigiate to nearly tabulate venter of the middle-aged whorl and a nearly smooth, adult body-chamber with the spirally extended mediolateral zone of inflation, shallowly concave spiral zone outside the inflation and broadly rounded venter. Although sutures are not well exposed, it represents a new species, which is allied to *Libyoceras afikpoense* Reymont but distinguished by its more numerous nodes and less acute venter of the phragmocone than those of that Reymont's species.

Morozumi's tentative correlation of the Zone of *P. awajiensis* to the upper Upper Campanian is approved on the ground of this ammonite and restudied *P. awajiensis* itself.

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### Introduction

In spite of the fairly intensive investigations of ammonite faunas from the Upper Campanian and Maastrichtian of Japan, no species of the Sphenodiscidae has been described. This may be due to the general scarcity of pseudoceratitic ammonites in the Upper Cretaceous of Japan and may be interesting from the viewpoint of palaeobiogeography or palaeoecology. For the biostratigraphic purpose, however, it is desirable to get members of the superfamilies Hoplitaceae and Acanthocerataceae at successive stratigraphic levels.

The Izumi Group of the Izumi Mountains and

the westerly contiguous hills of Awaji Island has been proved to be of late Campanian to Maastrichtian age on the evidence of ammonite faunas (Matsumoto and Morozumi, 1980; Morozumi, 1985). It is one of the major stratigraphic units from which a discovery of sphenodiscids could be expected, although ammonite species recorded so far from the Izumi and Awaji areas are mainly those of the Pachydiscidae, Phylloceratidae, Tetragonitidae, Gaudryceratidae, Nostoceratidae, Baculitidae and a rare species of the Scaphitidae.

Meanwhile, Mr. Masahiko Takada fortunately found an ammonite from Awaji which was unfamiliar to him and provided it through Mr. Masahiro Sato for our study. This is the first record of a sphenodiscid ammonite from Japan.

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\* Received March 15, 1988; accepted May 30, 1988.

Although it is a single specimen, we describe it in this paper to stimulate people for further hunting.

### Palaeontological descriptions

#### Family Sphenodiscidae Hyatt, 1900

*Remarks*:—Succeeding to Wright (1957, p. L437), Howarth (1965) reviewed comprehensively the family Sphenodiscidae, giving diagnosis of the included genera and their geological ages. More recently Zaborski (1982) has proposed the family Libycoceratidae for the two genera *Libycoceras* Hyatt, 1900 and *Indoceras* Noetling, 1897. Zaborski says that the origin of these two genera is different from that of *Sphenodiscus* etc., although he does not indicate what it is. Furthermore, he suggests, though with a query, that the origin of *Sphenodiscus* may lie either in Lenticeratinae or in *Placenticeras*. In the latter case the Sphenodiscidae should be transferred to the Hoplitaceae. Anyhow, the Sphenodiscidae in this paper is treated provisionally in a broad sense as in Howarth (1965).

#### Genus *Libycoceras* Hyatt, 1900

*Type species*:—*Sphenodiscus ismaelis* Zittel, 1884.

#### *Libycoceras awajiense* sp. nov.

Figures 1,2

*Holotype*:—A specimen found by Masahiko Takada from the Zone of *Pachydiscus awajiensis* at loc. Aw 7 (Nagata) of Morozumi (1985),

Awaji Island. This was in a calcareous nodule in dark grey sandy siltstone; altered test is preserved for the major parts, except for a peculiarly damaged part on the right side. The specimen is cross-cut to two pieces in a natural state through the point close to the umbilicus. A cross-section of the inner whorls is visible obscurely on the cutting plane.

*Description*:—The shell is fairly large. The actually measured dimensions are shown in Table 1. The specimen is probably adult. The last septum is at about  $d=145$  mm. The body-chamber can be assumed as long as  $180^\circ$ ; then the entire shell diameter would be about 220 mm.

The shell is discoidal and involute, with a very narrow, almost closed umbilicus. The whorl is much higher than long, with its height increasing at a moderate ratio. There is a spiral zone of elevation at the level about the middle of flanks slightly closer to the umbilicus; that is the zone of the maximum whorl-breadth. From this zone the inner part of flank slopes down toward the umbilicus and the outer flanks converge toward the venter.

In the observable part of the phragmocone nodes are aligned on this elevated zone at wide intervals, numbering 7 per half whorl. Also there are nodes on the ventrolateral shoulder, normally two ventrolateral nodes corresponding to one mediolateral node. The venter is narrow, almost tabulate or low fastigate, with a reduced keel on the siphonal line. The venter of the next inner

Table 1.

Position	Diameter	Umbilicus	Height (H)	Breadth (B)	B/H	H/h
M	180 (1)	—	109 (.61)	46 (.26)	.42	1.56
M-90°	148 (1)	—	90 (.61)	39 (.26)	.43	
M-180°		—	70	32 (ic)	.46	
				35 (c)	.50	

Height = Whorl-height; Breadth = Whorl-breadth; M = Measured position indicated in Fig. 1; h = whorl-height at  $180^\circ$  adapically from M; c = costal; ic = intercostal.

→ **Figure 1.** *Libycoceras awajiense* sp. nov.

Holotype from loc. Aw 7 (Nagata), Awaji Island (M. Takada Coll.). Left lateral (A), ventral (B) and frontal (C) views,  $\times 0.8$ . Scale bar = 20 mm. M: measured position, Arrow: position of the last septum.

Photos by courtesy of Dr. M. Noda.



whorl is similarly low fastigate and never so acute as to be called lanceolate. The ventrolateral nodes are somewhat clavate, whereas the mediolateral ones are subrounded but low. Both nodes are rather blunt on the visible outer whorl and disappear on the main part of the body-chamber.

The low fastigate shape of the venter is obscured in the last part of the septate whorl and the venter of the body-chamber is broadly rounded, without angulation at the ventrolateral shoulders. A very faint trace of the reduced keel may be discernible along the median line of the gently arched venter in some favourable light, but speaking generally there is no keel on the venter of body-chamber. The spiral zone of elevation at about the middle of flank broadens and the body-chamber is gently inflated there, whereas there appears a zone of shallow depression outside the inflated zone.

The external surface of the body-chamber is nearly smooth and fine and dense lirae (growth-lines?) or striae are discernible where the preservation is favourable. The lirae are gently sigmoidal on the flank, showing a gentle convexity on the middle part of flank and a moderate projection on the ventrolateral part, passing across the venter vertically. Similar radial lines or striae are also discernible on the surface of the phragmocone, whereas the ribs are scarcely developed.

*Comparison:*—This specimen resembles in gross morphology and ornamentation the holotype and other examples of *Libycoceras afikpoense* Reyment (1955, p. 89) (see also Zaborski) (1982, p. 308), *L. crossense* Zaborski (1982, p. 309) and *L. dandense* (Howarth) (1965, p. 396 under *Nenambolites*) (see Zaborski, 1982, p. 313), from the Upper Campanian of West Africa (Angola or Nigeria, or both), but is not identical with any of them. It is larger than the largest examples of them.

With respect to the shell-form with the maximum breadth of whorl at the level of the mediolateral tubercles, *L. afikpoense* is the closest one among the three mentioned above to the present species, but its mediolateral tubercles

are disposed at much wider intervals and accordingly less numerous (4 per half whorl) than those of our species. This is applied also to the ventrolateral tubercles. Moreover, these tubercles, particularly the ventrolateral ones, are prominent and persist well to the adult outer whorl in that Nigerian species, whereas the tubercles are blunt and disappear on the main part of the adult body-chamber in our species. The existence of a spiral zone of shallow depression outside the mediolateral zone of gentle inflation on the body-chamber seems to be characteristic of our species. According to Zaborski (1982, p. 309), *L. afikpoense* shows little variation. Therefore we regard the above differences of our form to be sufficient for specific separation.

Lewy (1977, p. 247) observed a certain extent of variation in what he regarded as *L. afikpoense* with respect to the stage at which the venter is flattening or broadening and also to the ratio of the distance between the mediolateral tubercle and the umbilical seam and that between the ventrolateral and the mediolateral tubercles. Zaborski (1982) calls the forms from the Middle East *L. afikpoense*-like. The specimens illustrated by Lewy (1977, pl. 1, figs. 1–6 under *L. afikpoense* and figs. 9–12 under *L. ismaele*) have mediolateral tubercles nearly as numerous as those in our form but less numerous and much more distant ventrolateral tubercles than those in our form. There is, thus, a possibility that subspecific distinctions could exist between populations of separate provinces. This idea should be examined on the basis of sufficient material. At this moment we describe the specimen from Awaji under a new specific name.

In *L. crossense* the tubercles are subdued and finally disappear on the said adult whorl, which is much smaller than that of ours. Also the interspaces between the tubercles in that species are as wide as those of *L. afikpoense*. The rib-like structures extend inward from the tubercles in the middle aged shell of *L. crossense*, but such structures are scarcely seen in our form.

With respect to the low fastigate venter in the middle aged whorl and the broadly rounded



**Figure 2.** *Libycoceras awajiense* sp. nov.

Right side of the holotype, showing an injury and peculiar trace marks,  $\times 0.94$ .

Photos by courtesy of Dr. M. Noda.

venter in later whorl, *L. crossense* is similar to our form, but its whorl is more compressed than that of ours.

The outer whorl of *L. dandense* has low ribs on the outer flanks and ventrolateral clavi at the

end of the ribs, but the mediolateral tubercles are lost or remain as slight elevations on the ribs. This ornamentation is different from that of our form. An example of *L. dandense* illustrated by Zaborski (1982, fig. 17) is fairly large, about 140

mm in diameter at the end of the phragmocone, and may be nearly comparable in size with our form, but the former is evidently more compressed than the latter.

The venter of our form in the middle aged shell, with diameters from about 50 mm to 100 mm, is low fastigiate, but its summit is not so acute as that of *L. afikpoense* or *L. dandense* at the corresponding growth stages. In this respect our form seems to approach to *Indoceras balchistanense* Noetling (1897, p. 74), in which the siphonal keel disappears at the diameter about 70 mm in the middle-aged shell. That species differs from ours in the absence of the mediolateral tubercles and the presence of very faint ribs on the outer flank in the major part of the phragmocone.

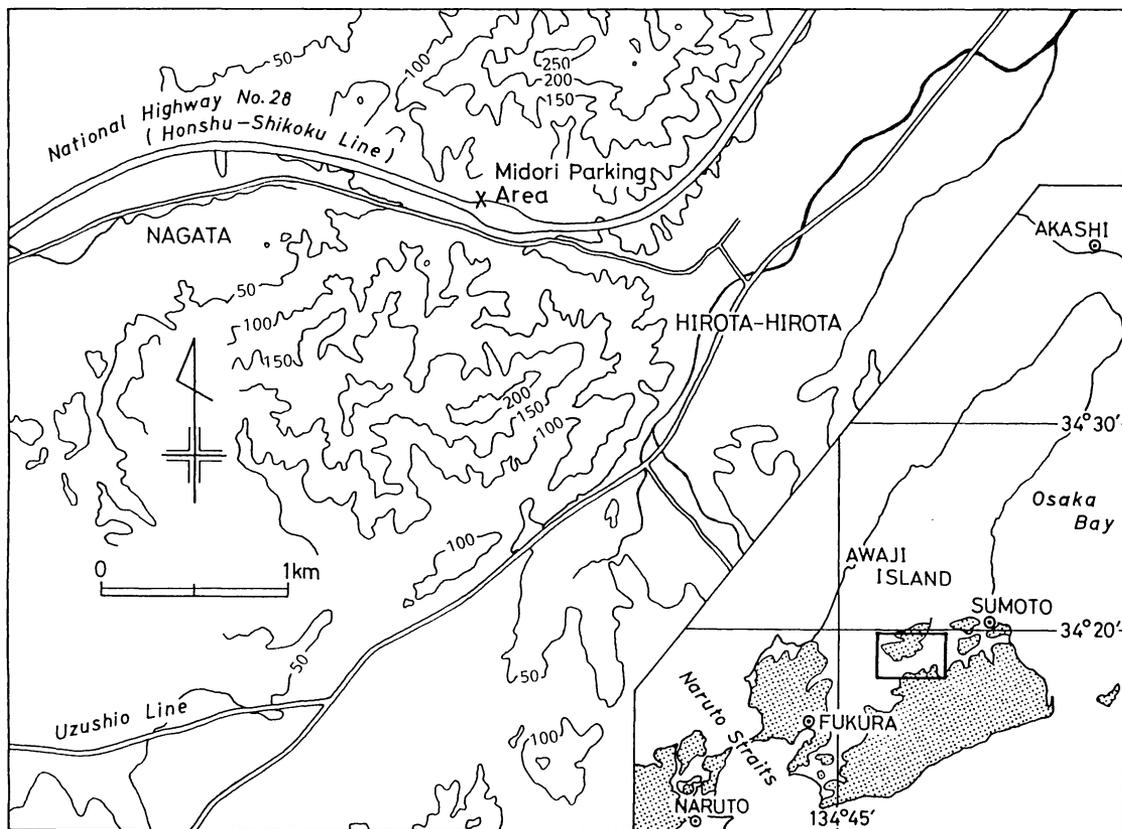
On the ground of the above comparisons, we

are inclined to conclude that the specimen from Awaji represents a new species of *Libyoceras*, although a single specimen is available so far.

For more precise comparison and discussion, the ontogenic change of every character should be investigated. It is indeed too bad that we are not successful to expose the full pattern of the suture. However, we dare to describe it as a new species for the moment to stimulate people to hunt for additional, more favourably preserved specimens.

**Occurrence:**—Loc. Aw 7 (Nagata) of Morozumi (1985), exactly 1.5 km east of Nagata, Midori-cho, Mihara-gun, Hyogo Prefecture. The specimen occurs in fine-sandy siltstone of the Seidan Formation.

National Highway No. 28 was under construction in the year 1985–1987, passing through



**Figure 3.** Map showing the details around the fossil locality, marked by x. Inset is the index map of Awaji Island, with dotted pattern outlining the distributional area of Cretaceous strata. (Y. Morozumi delin.)

Aw 7. The outcrop of Aw 7 was enlarged and numerous (more than 100) fossil specimens were collected there (Fig. 3). The great majority of them belongs to *Pachydiscus awajiensis* Morozumi and the rest consists of a single sphenodiscid ammonite described above, an example of *Neophylloceras* aff. *mikobokense* (Collignon) (see Morozumi, 1985), several specimens of *Baculites inornatus* Meek (Obata and Matsumoto, 1963), "*Anisomyon*" *problematicus* (Nagao et Otatume) and *Yaadia obsoleta* (Kobayashi et Amano). This fossiliferous exposure is the stratotype of the Zone of *Pachydiscus awajiensis* proposed by Morozumi (1985, p. 13). It is stratigraphically about 200 m above the base of the Izumi Group in this area.

### Biostratigraphic correlation

On account of the palaeogeographic separation, marine faunas of the Campanian and Maastrichtian ages in the Japanese province are considerably different from those in West Europe where stratotypes of the stages exist. Species which are common between the two provinces are very few. For this reason it is difficult to draw precisely the Campanian-Maastrichtian boundary in the stratigraphic sections in the Japanese province.

The late Cretaceous Izumi Group, which extends from east to west for about 300 km in Southwest Japan, consists of thick piles of the turbidite facies for the major part (see Tanaka, 1965). There is, however, in the basal part of the group, a unit of muddy sediments which contain fossiliferous nodules. It probably represents a neritic shelf facies. This unit is diachronous, becoming gradually younger from west to east, as evidenced by the tracing of key tuff beds or tuffite in geological mapping (e.g., Suyari, 1973) and also by guide species occurring in several places (see Matsumoto, 1980; Morozumi, 1985, figs. 12, 13).

At a locality (numbered here 1) in the city of Matsuyama near the western end of the outcropping belt of the basal unit of the Izumi Group, *Sphenoceras schmidtii* (Michael), *S.*

*sachalinensis* (Sokolow), *Gaudryceras striatum* (Jimbo) etc. form a characteristic assemblage. In the coastal area (2) facing the Seto Inland Sea, about 40 km to the east from Matsuyama, *Bevahites* aff. *B. lapparenti* Collignon (Matsumoto and Obata, 1963) and *Delawarella* sp. (Inami and Ochi, 1986) were obtained together with *Inoceramus (Endocostea)* sp. These species from the two places (1, 2) in the northwestern part (Ehime Prefecture) of Shikoku indicate the upper part of the Lower Campanian in a bipartite scheme.

At several localities (3), about 70 to 80 km east of (2) in the Sanuki (or Asan by some people) Mountains, northeastern part (Kagawa Prefecture) of Shikoku, *Metaplacentoceras subtilistriatum* (Jimbo) occurs characteristically (Bando and Hashimoto, 1984). This species is associated with *Hoplitoplacentoceras monju* Matsumoto, *H. fugen* Matsumoto and many other ammonites in the type locality and adjacent area of northern Hokkaido, indicating the lower Upper Campanian (Matsumoto and Miyauchi, 1984). The ammonite faunule from the basal siltstone in the eastern part (4) of the Sanuki Mountains, easterly contiguous to (3), has yet to be worked out, for only *Baculites kotanii* was described clearly (Matsumoto *et al.*, 1980) among others, which occur at several levels higher than the Zone of *M. subtilistriatum*.

Further to the east in the Island of Awaji, Morozumi (1985, p. 4–13, especially tables 1, 2 and figs. 1–3) has shown that the siltstone in the basal unit (which he called the Seidan Formation) becomes younger eastwards and distinguished the following zones in the Awaji section of the Izumi Group in ascending order (with numbered type locality in parentheses):

Zone of *Didymoceras awajiense* (5, Anaga)

Zone of *Pravitoceras sigmoidale* (6, Minato)

Zone of *Pachydiscus awajiensis* (7, Nagata)

Zone of *Nostoceras hetonaiense* (8, Mitsu-gawa)

Zone of *Pachydiscus* aff. *subcompressus* (9, Yamamoto)

(Numbers follow those in Shikoku as explained above. See Fig. 4).

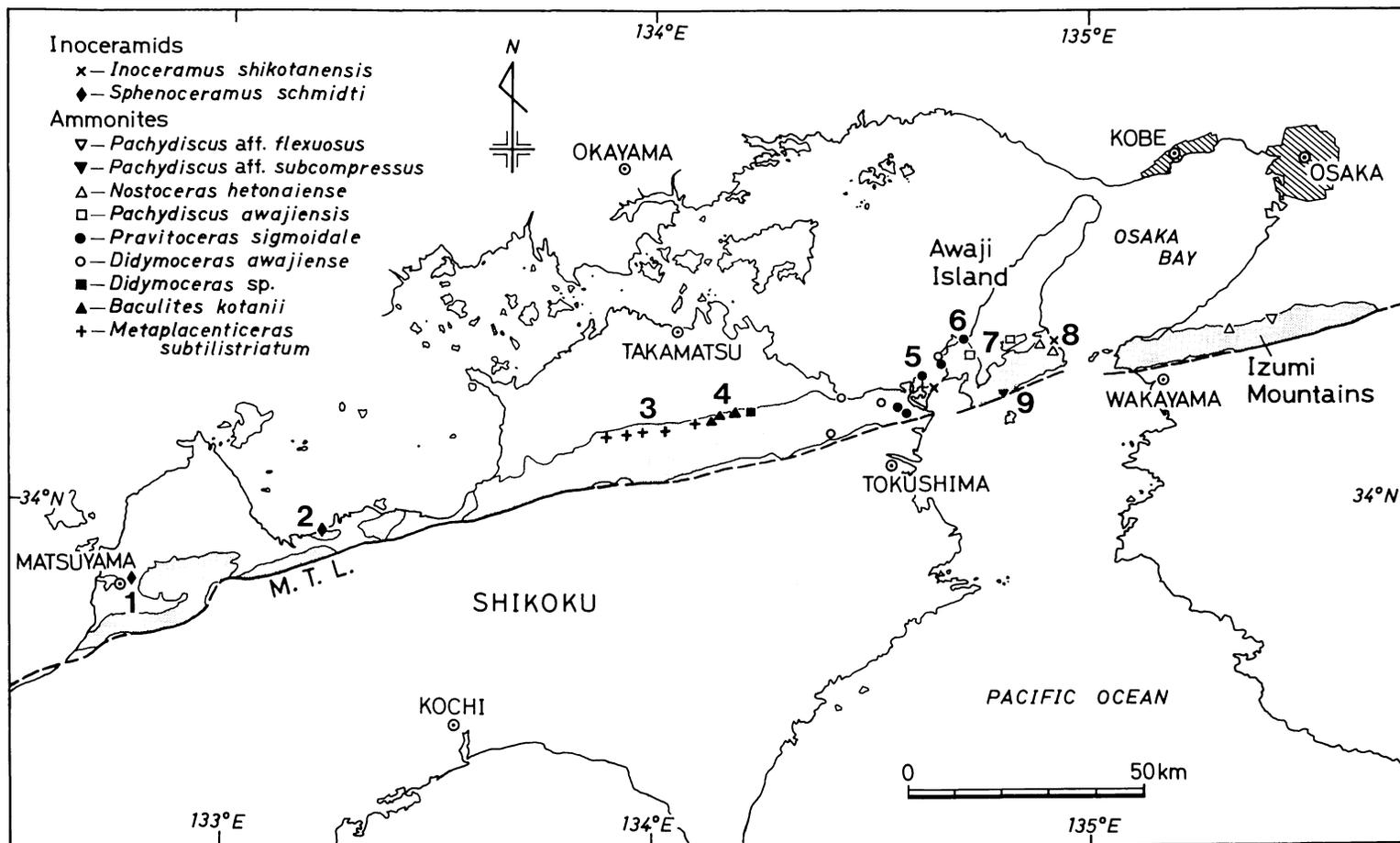


Figure 4. Map showing selected fossil localities of the Izumi Group with zonal indices. Dotted area indicates the distribution of the Izumi Group. M. T. L.: Median Tectonic Line. (Adopted from Morozumi, 1985, fig. 12)

In addition to the domestic correlation, Morozumi (1985, p. 46–53) tentatively attempted at international correlation, with the lower three zones (5, 6, 7) being correlated to the Upper Campanian and the upper two (8, 9) to the Maastrichtian. To draw the stage boundary between the Zone of *Pachydiscus awajiensis* and the Zone of *Nostoceras hetonaiense* is quite tentative as the author himself repeatedly remarked.

It should be noted that *P. awajiensis* Morozumi, 1985 is fairly similar to *P. koeneni* de Grossouvre, 1894, which occurs commonly in Germany, Switzerland, Austria, Poland, Donbas, Kopet Dag etc. In the former, represented by the holotype (Morozumi, 1985, text-fig. 4 and pl. 2, fig. 1) and the paratype (Ditto, pl. 2, fig. 2), the ribs are narrow and separated by broader interspaces, the longer ribs are gently flexuous, showing a concave curve at about the umbilical shoulder and another concavity on the outer flank. Such a biconcave flexuosity may occasionally appear on some of the longer ribs in the latter species but normally the long ribs are almost rectiradiate on the inner flank, starting from the umbilical bullae, as seen in the lectotype designated by Kennedy and Summesberger (1984, pl. 14, fig. 2 = *Ammonites galicianus* of Schlüter, 1872, pl. 19, fig. 3) and many other examples (e.g. illustrated by Moberg, 1885 under *Amm. oldhami*; Błaszkiwicz, 1980; Kennedy and Summesberger, 1984). Also the ribs look somewhat coarser and are separated by narrower interspaces in *P. koeneni* than in *P. awajiensis*, but this may be due to the state of preservation in that many examples from Europe are internal moulds, whereas the shell is preserved in the specimens from Awaji.

The above mentioned differences seem to occur constantly but are by no means great. Therefore, someone may consider *P. awajiensis* as a geographical subspecies of *P. koeneni* of the Boreal region.

Incidentally, Kennedy and Summesberger (1984, p. 158) regarded *P. koeneni* as macroconchs and the bituberculate *Amm. heldensis* Schlüter, 1867 (p. 19, pl. 3, fig. 1) as

microconchs of one and the same species. They are so confident that they put *P. koeneni* de Grossouvre, 1894 as a junior synonym of *P. heldensis* (Schlüter, 1867). This could be so, but may give a difficulty. From the Zone of *P. awajiensis* no example of the small, bituberculate counterpart has been obtained. Without getting an adequate microconch, we hesitate to state either that *P. awajiensis* is closely allied to *P. heldensis* or that it may be a subspecies of *P. heldensis*. Apart from the nomenclatorial difficulty, the close resemblance between *P. awajiensis* and *P. koeneni* would support the tentative conclusion of Morozumi (1985) to refer the Zone of *P. awajiensis* to the Upper Campanian instead of the Lower Maastrichtian.

The sphenodiscid ammonite obtained from the type locality of *P. awajiensis* is a new species and cannot work as a direct indicator of age. It is, however, allied to *Libycoceras afikpoense*, as we have described above. That species occurs abundantly in the basal part of the Nkporo Shale of Nigeria. Reyment (1955) ascribed the age of this formation to the Maastrichtian, but now Zaborski (1982, 1985) has shown with sufficient evidence that the lower part of the Nkporo Shale, which contains *L. afikpoense*, *Sphenodiscus lobatus lobatus* (Tuomey, 1856) (see Zaborski, 1982, p. 316) and certain other ammonites, is referred to the Upper Campanian (Zaborski, 1982, fig. 36; 1985, p. 61). Therefore, we can state that *Libycoceras awajiense* approves indirectly Morozumi's assignment of the Zone of *Pachydiscus awajiensis* to the upper Upper Campanian.

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日本の白亜系から稀に得られたスフェノディスク科アンモナイト：本邦の白亜系の最上部またはそれに近い部分から Sphenodiscidae に属するアンモナイトをかねてから探求していた。このほど淡路島長田の高速道路工事で拡大された崖から高田雅彦氏採集の唯一個を、佐藤政裕氏をへて研究に提供して下さった。両側面とも保存され、住房の主要部もあり、直径18cm、欠損部を復元すれば約22cmで比較的大型といえる。へそはほとんど開かずぎわめて小さい。見えている範囲の気房部の外面はほぼ平坦かごく低い屋根型で中央に細くて弱いキールの名残りがあつた。外面の両肩に鈍い突起が間を置いて配列し、さらに側面の中ほどにその半数の鈍くて丸い突起が広い間隔で（半巻きに7個）配列する。住房の主要部ではこれらの突起は消失するが、側面中ほどの隆起帯は存続し、そこで殻はやや膨らみ、その外側は浅く凹む、外面は広くなり、肩のかどがとれてゆるいアーチ状を呈する。殻表面の放射状成長線は緩い2凹波曲を示すが、外面を垂直に横断している。残念なことに縫合線の詳しい型がわからない。

概形と装飾から本種は *Libycoceras* に属するとみなされ、ナイジェリアに多産する *L. afikpoense* Reymont に類似するが、後者では突起がもっと広い間隔で数少ないが長く存続し、また幼～中年期の外面が鋭く尖っている。その他の種とも異なるので新種 *L. awajiense* とする。

この標本は和泉層群西淡層の *Pachydiscus awajiensis* 帯に産した。同帯はカンパニアン・マストリヒチアの境に近く、Morozumi (1985) は暫定的にカンパニアン最上部に対比した。*L*属はマ階上部にまで存続するが、*L. afikpoense* はカンパニアン上部に産し、日本のと近似のものがイスラエルの同階上部からも報告されている。また *P. awajiensis* は西欧その他の同階上部産の *P. koeneni* de Giossouvre に近似である。これらの事実はさきの対比論を支持するといえる。

松本達郎・両角芳郎

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## 859. FUNCTIONAL AND TAXONOMIC IMPLICATIONS OF INTERNAL RIBS OF *PROPEAMUSSIUM*\*

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**Abstract.** The macroscopic and microscopic features of internal ribs in several living and fossil pectinaceans from the western Pacific were observed, and their functional and taxonomic significances were considered. *Propeamussium* shares internal ribs with *Amusium* and some other genera of the Pectinidae, but the resemblance must be superficial because their fundamental structure is quite different. The commonly paired internal ribs of pectinids are formed by the thick secretion of outer foliated layer near the ventral margin and primarily serve the tight interlocking of valve margins. On the other hand, each of the internal ribs of propeamussiids is represented by a lecticular core of fibrous prismatic (or foliated) calcite almost imbedded in the inner layer of crossed lamellar aragonite. Genetically, the cores seem to have originated from the “middle layer” (a thin layer beneath the prismatic layer) in the right valve and from the outer layer in the left valve and to be produced by some patchy isolation of shell-secreting mantle tissue. The distal ends of internal ribs are just apposed to those of the counter valve so as to contact each other when the valves are tightly closed. The internal ribs of propeamussiids may be functionally analogous to the auricular crura of free-living pectinids; the distal ends probably serve as buttresses to counteract not only external compressive stress but also powerful contracting force of quick adductor muscle for swimming.

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### Introduction

Previous suprageneric classification of post-Paleozoic pectinaceans seems to have attached too much importance to the presence or absence of internal ribs without considering their developmental background. *Propeamussium* and some other related deep-sea genera, which apparently share internal ribs with *Amusium*, were commonly referred to the Amusiinae (Thiele 1935, Orlov 1960, *etc.*) or to the *Amusium* group of the Pectinidae (Hertlein *in* Cox *et al.* 1969, Vokes 1980). Since Waller (1971) pointed out the primitive shell features of *Propeamussium*, however, it has been recognized that this genus is fundamentally different from *Amusium* and other pectinids in many essential

characters and is rather similar to the Pernopectinidae from the Upper Paleozoic (Waller 1972, 1978; Newell and Boyd 1985). A distinct family, Propeamussiidae Abbott, 1954, was redefined and became widely accepted, whereas *Amusium* remained in the Pectinidae because the shell microstructure and anatomical features are typical of the family. Both the Pectinidae and the Propeamussiidae may or may not possess internal ribs, and therefore homologous relationship of internal ribs between the two families may be strongly doubted.

During the course of my extensive survey of the shell morphology and microstructure of Japanese deep-sea pectinaceans, it was noticed that the arrangement, developmental origin and function of internal ribs are considerably different between the Pectinidae and the

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Propeamussiidae. This paper is mainly concerned with functional and taxonomic evaluations of this character on the basis of several Cenozoic-Recent species of the two families.

### Internal ribs of the Pectinidae

In the Pectinidae conspicuous internal ribs occur not only in *Amusium* but also in a number of warm-water genera (e.g. *Pecten*, *Aequipecten*, *Annachlamys*, *Equichlamys* and *Amusiopecten*). In many cases the internal ribs are regularly paired and occur along the margins of each internal elevation corresponding with an interval between two external radial costae. As recognized well in articulated specimens of *Pecten* (especially in the full-grown stage), the outer sides of the paired internal ribs are in contact with those of the counter valve near the ventral margin so as to ensure the tight interlocking of disk margins (Fig. 1-5a).

The internal ribs of *Amusium* are not necessarily stronger than those of *Equichlamys* and *Amusiopecten*, but have been noticed by previous taxonomists because the external surface is nearly smooth. Contrary to expectation, their arrangement is discrepant between the right valve (RV) and the left valve (LV). In every articulated specimen of *Amusium japonicum* and *Amusium pleuronectes*, so far examined, RV (yellowish valve) has more numerous and more regularly paired internal ribs than LV (reddish valve) of the same individual (Fig. 1-4a). The internal ribs must reinforce the relatively thin valves to a certain extent, but it is unknown whether this structure bears other functional meaning or represents only a vestigial structure. From the geographic and stratigraphic distributions I presume that *Amusium* was phylogenetically derived from *Amusiopecten*-like weakly costate warm-water species (not from *Lentipecten* as considered by some previous authors), and that the paired regularity of internal ribs as well as the interlocking function was almost lost in accordance with the disappearance of radial costae. The thin shells and smooth external surface of *Amusium* are no doubt advantageous

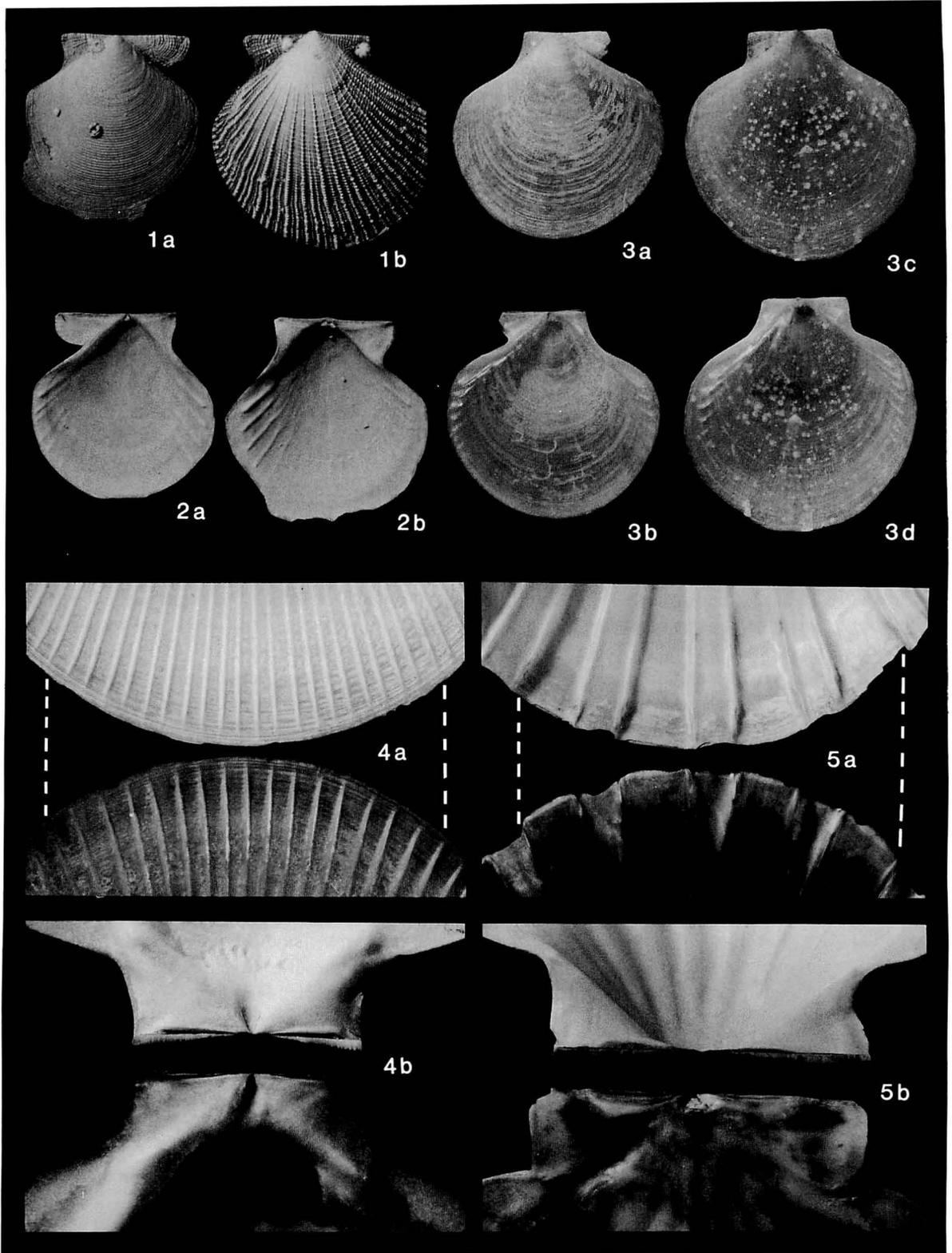
for swimming habit, because they can minimize the gravity and drag force.

In *Amusium* and some other free living pectinids auricular crura, which are the distally extended loci of auricular denticles, are well developed (Figs. 1-4b, 5b). As was interpreted by Waller (1969), they are apposed rather than interlocking and seem to serve as buttresses against compressive stresses, because the antero-dorsal and postero-dorsal disk margins of such pectinids are widely open even in tightly closed condition. The internal ribs of the Pectinidae are always formed by the thickening of outer foliated calcite layer near the ventral margin and then covered by the inner layer of crossed lamellar aragonite. The auricular crura are probably of different origin from the internal ribs, because they are produced by the thick secretion of the inner layer.

### Shell structure of the Propeamussiidae

Although it is not the principal aim of this paper to describe the shell microstructure, appropriate knowledge of the characteristic layering of propeamussiid valves seems to be indispensable for the consideration of the functional and evolutionary significances of internal ribs. Here, previous studies on this matter are briefly reviewed, and some results of my SEM observations are presented. About the terminology I follow Carter and Clark II (1985) who presented a comprehensive classification scheme of molluscan shell microstructure.

*Previous studies.* In spite of many outstanding comprehensive studies on the shell microstructure of bivalves (e.g. Bøggild 1930, Taylor, Kennedy and Hall 1969, 1971), the peculiar features of *Propeamussium* had been unnoticed until Waller (1971) pointed out its primitiveness and similarity to some Paleozoic pectinoids. As successively studied by Waller (1972, 1978, 1984), the extant species of *Propeamussium* are clearly distinguishable from the Pectinidae by many important characteristics. Among others, the development of a simple prismatic calcite layer on the greater part of the external surface



of RV until the latest growth stage, the distribution of inner layer (crossed lamellar aragonite) on the internal surface beyond the pallial myostracum, and the absence of true ttenolium even in the early growth stage are enough to be regarded as family-level diagnostic characters (Fig. 3).

In living specimens of *Propeamussium*, as previously noticed by Kuroda (1931), the ventral area of RV, called flexible prismatic apron by Newell and Boyd (1985) and marginal apron here, easily becomes concave when the valves are closed. The flexibility is of course due to the structure of this area consisting of a single layer of simple prismatic calcite (Fig. 4). Discrepant shell microstructure between RV and LV in some living and fossil species of *Propeamussium* was, independently of Waller's works, pointed out by Okubo and Inoue (1975), who showed some SEM photographs of the natural, fracture and sectional surface for the first time. More recently Newell and Boyd (1985) also observed some living species of *Propeamussium* and compared the microstructure with that of *Pernopecten* and other Late Paleozoic pectinoid genera.

The descriptions of shell microstructure by these authors are not necessarily coincident with one another. For example, the outer layer of LV and the "middle layer" (a thin layer beneath the prismatic outer layer) of RV were described by Waller (1972) as composed of foliated calcite but

assigned by Newell and Boyd (1985) to fibrous prismatic structure. The apparent discrepancy, I think, may have arisen from the variable crystal elongation of calcite laths among species (or observed portions). Carter and Clark II (1985) described the outer layer of LV of *Propeamussium dalli* as lath-type fibrous prismatic but noted that regularly foliated structure (Gamma 135 blades) also occur in this species. Okubo and Inoue (1975) considered that the outer foliated layer of LV of "*Luteamussium sibogae*" [= *Propeamussium sibogai*] is thinly covered with a porcellaneous layer and that there is a thin fibrous layer on the internal surface of both valves. I presume that these thin surface layers are not of original structure but products of weathering, because their material was said to be dead shells.

*Results of observations.* I have carried out, though still preliminarily, SEM observations of shell microstructure on the basis of the following nine propeamussiids:

- Propeamussium caducum* (Smith, 1885)
- Propeamussium cmadoritinctum* (Kuroda, 1931) [Figs. 2-1,2]
- Propeamussium jeffreysi* (Smith, 1885) [Fig. 2-3]
- Propeamussium sibogai* (Dautzenberg and Bavay, 1904) [Fig. 2-4]
- Propeamussium watsoni* (Smith, 1885) [Figs. 2-5,6]
- Polynemamussium alaskense* (Dall, 1872) [Fig. 1-3]
- Polynemamussium intuscostatum* (Yokoyama, 1920) [Figs. 1-1,2]

← **Figure 1.**

*Polynemamussium intuscostatum* (Yokoyama, 1920)

1. Articulated valves (UMUT RM18274) × 4, from Sagami Bay (off Jogashima islet, 100m). 1a: RV with incomplete marginal apron, 1b: LV.
2. Articulated valves (UMUT RM18275) × 4, from the same locality. 2a: interior of RV without marginal apron, 2b: LV.

*Polynemamussium alaskense* (Dall, 1872)

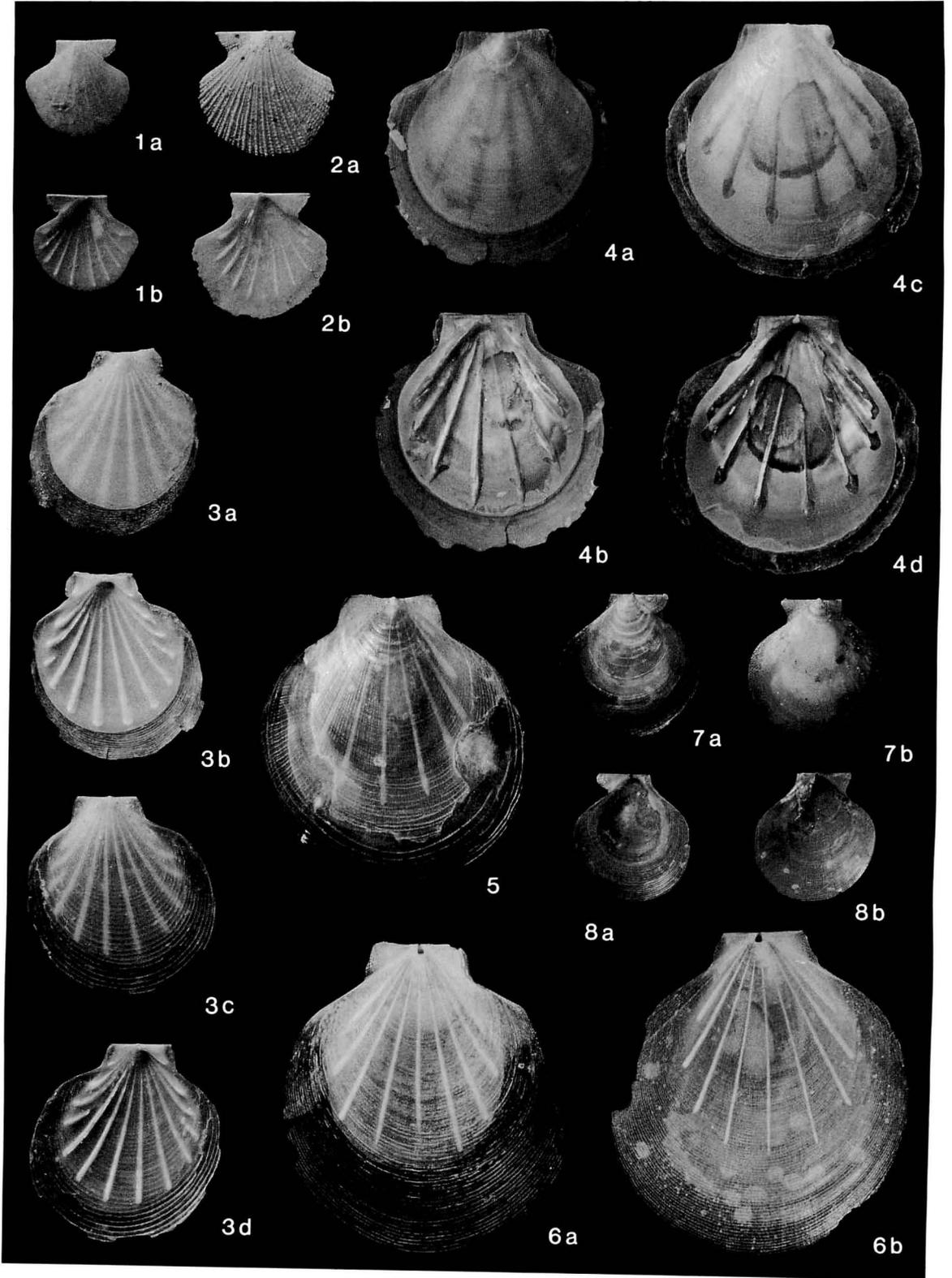
3. Articulated valves (UMUT RM18276) × 1.5, from Japan Sea (off Otaru City of Hokkaido, 150m). 3a: RV without marginal apron, 3b: interior of the same valve, 3c: LV, 3d: interior of the same valve.

*Amusium japonicum* (Gmelin, 1791)

4. Young articulated valves (UMUT RM18277) × 1.2, from Hyuga-nada (off Touriyama of east Kyushu). 4a: discrepant internal ribs between RV (upper) and LV (lower), 4b: hinge areas showing apposed auricular crura.

*Pecten albicans* (Schröter, 1802)

5. Full-grown articulated valves (UMUT RM18278) × 0.8, from Tosa Bay (off Kochi City of Shikoku). 5a: interlocking internal ribs between RV (upper) and LV (lower), 5b: hinge areas showing apposed auricular crura.



*Cyclopecten bistriatus* (Dall, 1916)

*Cyclopecten nakaii* Okutani, 1962 [Figs. 2-7,8]

Besides, the shell structure of *Delectopecten* species was examined, because this deep-water genus is also characterized by thin translucent shells and was regarded by some Japanese authors (e.g. Oyama 1944, Habe 1977) as related to *Propeamussium* and *Cyclopecten*.

All of these examined species of *Propeamussium*, *Polynemamussium* and *Cyclopecten* share the diagnostic characters of the Propeamussiidae defined by Waller (1972, 1978). On the contrary, *Delectopecten* obviously belongs to the Pectinidae, because of the presence of true ctenolium and because the outer layer of RV and LV are similarly composed of regularly foliated calcite except for the narrowly distributed simple prismatic layer on the earliest dissoconch of RV [SEM photographs were already shown by Hayami and Okamoto (1986)]. According to Runnegar's (1984) crystallographic study of foliated calcite, the calcite laths of the outer layer of *Delectopecten* are referable to a rhombohedral form (10 $\bar{1}$ 2) [or Gamma 135 blades of Carter and Clark II (1985)].

The shell microstructures of these nine extant propeamussiids are essentially similar, but there are some minor variations. The crystal habit of calcite laths in the outer layer of LV and the

"middle layer" of RV varies considerably not only among species but also within the same layer of an individual. In *Propeamussium watsoni*, for example, the inner part of the outer layer of LV reveals lath-type fibrous prismatic structure (Fig. 5-3A), whereas its outer part is clearly composed of regularly foliated calcite (Gamma 135 blades) (Fig. 5-3B). Though crystallographic relation between fibrous prismatic calcite and foliated calcite should be further studied, the apparent difference between the two microstructures, at least in this case, is merely attributable to the variation in the elongation of laths. Lath-type fibrous prismatic calcite often seems to change by gradation into foliated calcite also in other species of the *Propeamussium*. The growth direction of laths is invariably almost radial (more precisely, orthogonal to growth increments) in fibrous prismatic shell but often much fluctuated in foliated shell. In *Polynemamussium* and *Cyclopecten* the outer layer of LV and the "middle layer" of RV are almost invariably composed of regularly foliated calcite.

In most propeamussiids the shell microstructure is similar between the outer layer of LV and the "middle layer" of RV. *Propeamussium jeffreysi*, however, represents an exception, in which the outer layer of LV, unlike the regularly foliated (or prismatic fibrous) "middle layer" of

← **Figure 2.**

*Propeamussium cmadoritinctum* (Kuroda, 1931)

1. Right valve without marginal apron (UMUT CM18279) × 2, from the Upper Pleistocene Wan Formation at the north of Kamikatetsu, Kikai Island. 1a: exterior, 1b: interior.
2. Left valve (UMUT CM18280) × 2, from the same locality. 2a: exterior, 2b: interior.

*Propeamussium jeffreysi* (Smith, 1885)

3. Articulated valves (UMUT RM18281) × 1.5, from Enshu-nada (ca. 300m). 3a: RV with incomplete marginal apron, 3b: interior of the same valve, 3c: LV, 3d: interior of the same valve.

*Propeamussium sibogai* (Dautzenberg and Bavay, 1904)

4. Articulated valves (UMUT RM18282) × 1.5, from Kumanonada (off Owase City of Kii Peninsula, 150m). 4a: RV with incomplete marginal apron, 4b: interior of the same valve, 4c: LV, 4d: interior of the same valve.

*Propeamussium watsoni* (Smith, 1885)

5. Living specimen with injured-and-repaired valves (UMUT RM18283) × 1.5, from Hyuga Sea Basin (KT-86-16, St.D2, 1650m). Left view.
6. Articulated valves (UMUT RM18284) × 1.2, from the same locality, 6a: interior of RV, 6b: interior of LV.

*Cyclopecten nakaii* Okutani, 1962

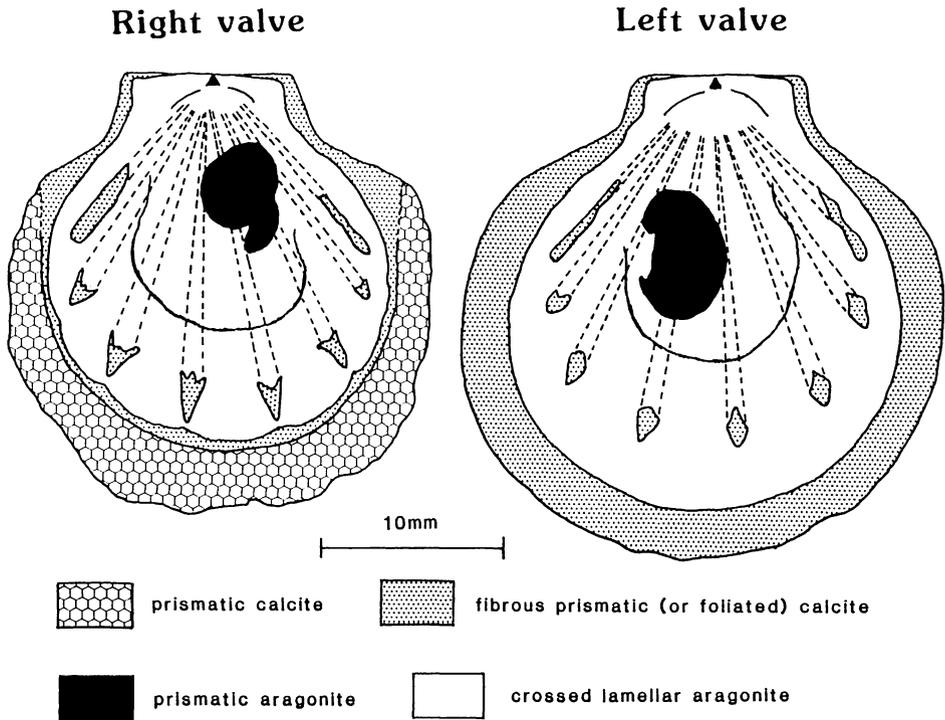
7. Living specimen (UMUT RM18285) × 2, from Izu Sea (KT-87-19, St.TW7, 1182-1215m). 7a: right view, 7b: left view.
8. Articulated valves (UMUT RM18286) × 2, from the same locality. 8a: interior of RV, 8b: interior of LV.

RV (Fig. 5-5A), reveals semifoliated microstructure in Carter and Clark II's (1985) classification (Fig. 5-6).

In the Propeamussiidae the greater part of the disk of RV is invariably covered with a prismatic outer layer. Radial and other conspicuous external sculptures never appear on the surface of this microstructure (Waller 1972). The prisms are commonly polygonal and nearly perpendicular (or only slightly oblique) to the surface (Figs. 5-1,2B,4), but fine commarginal costellae on the external surface of RV, if present, are constructed by commarginal rows of radially [orthogonally] elongated prisms, as were described by Carter and Clark II (1985) in *Propeamussium dalli*. Therefore, the prismatic layer is often represented by a zonal alternation of simple prisms and orthogonally elongated prisms. In some species of *Propeamussium* and *Cyclopecten* faint intermittent orthogonal striae

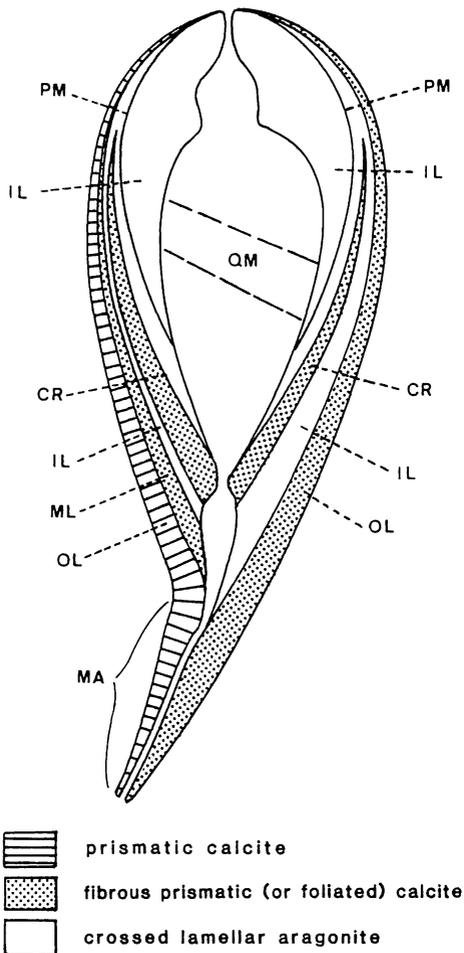
are observed on the top of commarginal costellae of RV. The orientation of the intermittent striae is apparently similar to that of the "*Camp-tonectes striae*" of the Pectinidae, but the crystallographic background must be different (see also Hayami and Okamoto, 1986).

Waller (1976) mentioned, though briefly, that foliation actually occurs within the simple prisms themselves in RV of the Propeamussiidae and some other pteriomorph families. On this ground he regarded the foliated structure in advanced pteriomorphs as having evolved from simple prismatic structure. Such foliated simple prisms are clearly observable on the internal surface of RV (only near the ventral periphery of marginal apron) in *Propeamussium watsoni* and *Cyclopecten nakaii*, and can be expected in other species of this family as well (Fig. 5-2A). However, the foliation in the prisms is undoubtedly of Gamma 120 blades, which



**Figure 3.** Internal shell features of *Propeamussium sibogai*, drawn on the basis of an articulated specimen (UMUT RM18282). RV looks somewhat smaller than LV, because of the incomplete marginal apron. [adapted from Hayami 1988]

## Right valve      Left valve



**Figure 4.** Schematic vertical section of *Propeamussium* (along the top of an internal rib). When the valves are closed, the marginal apron of RV becomes concave, and the distal end of each internal rib is in contact with that of the counter valve. The convexity and thickness of valves are much exaggerated. OL: outer layer, ML: "middle layer", IL: inner layer, PM: pallial myostracum, CR: core of internal rib, MA: marginal apron, QM: quick adductor muscle.

represent the basal pinacoid (0001) of calcite (see Runnegar 1984). Therefore, the foliation in the outer prismatic layer of RV is crystallographically different from that of other layers. I presume that foliated structure is easily derived from lath-type fibrous prismatic structure, but it is doubtful whether such foliated prisms directly

suggest the origin of foliated structure.

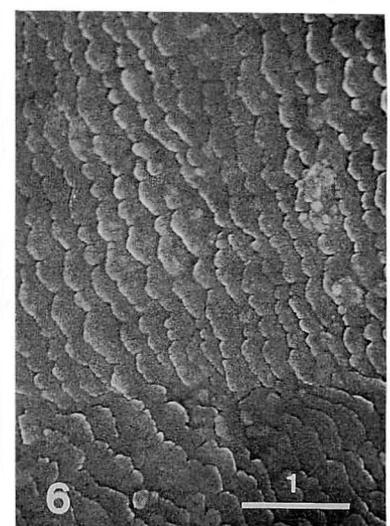
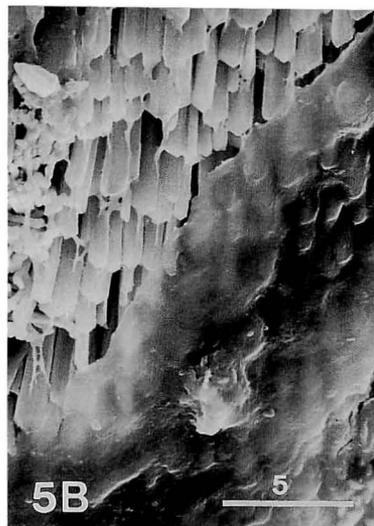
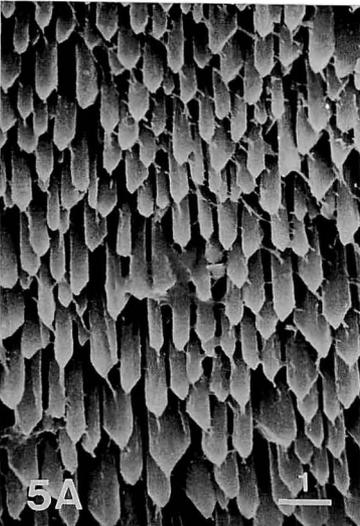
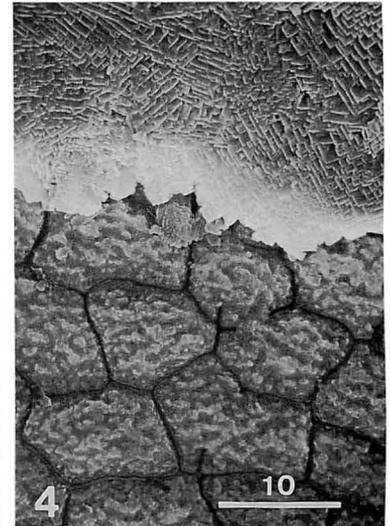
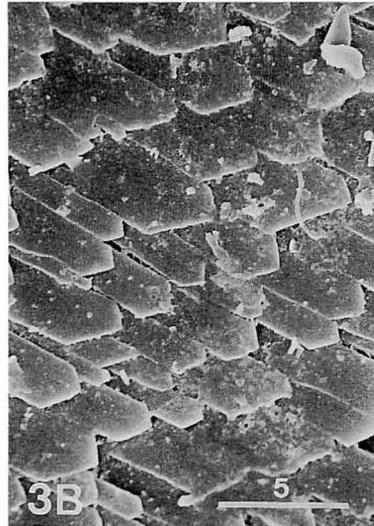
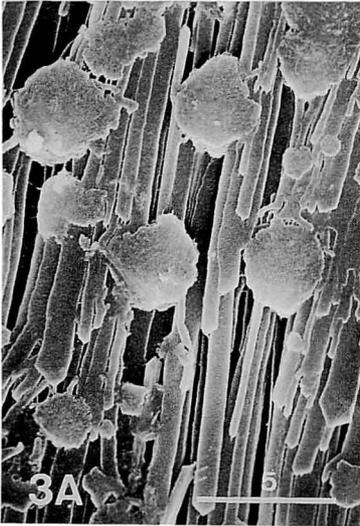
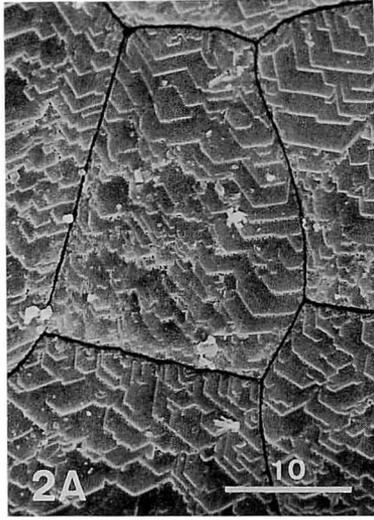
*Taphonomic evaluation of marginal apron.* Some taxonomists (especially paleontologists) regarded the relative length of internal ribs and size discrepancy between the two valves as useful criteria for subdivision of the Propeamussiidae. *Parvamussium*, for instance, was often discriminated from *Propeamussium* by the distal ends of internal ribs approaching the "valve margin". Many species of this family were described as "RV smaller than LV", or "internal ribs reaching the valve margin in RV but not in LV". Such descriptions, as pointed out by Newell and Boyd (1985), seem to have arisen from observations of incomplete specimens.

I have collected many living specimens of *Propeamussium*, *Polynemamussium* and *Cyclopecten* from the Japanese deep-waters by dredging and trawling, but size discrepancy between RV and LV has not been observed in any species. When the valves are closed, the marginal apron of RV, which is invariably composed of a single layer of prismatic calcite, is always reflex along the internal surface of LV (Fig. 4). The marginal apron is enough flexible in wet condition owing to the conchiolin filling the interspace of prisms, but, if dried, it becomes very fragile and is apt to be broken into pieces. Since the marginal apron of RV is rarely preserved in fossils (e.g. Figs. 2-1a,b) and dried museum specimens, taxonomists must be careful.

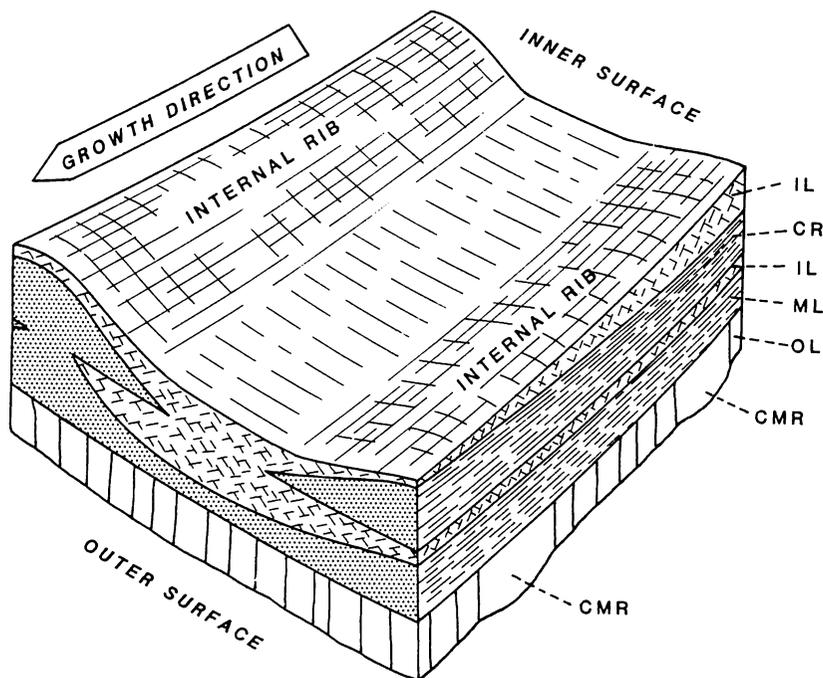
### Internal ribs of the Propeamussiidae

*Structure of internal ribs.* Internal ribs occur in many species of the Propeamussiidae, though undeveloped in *Cyclopecten* (Figs. 2-8a,b) and young valves of *Polynemamussium* (Figs. 1-2a,b, 3b,d). Unlike the Pectinidae, they are never paired and have no relation to the external sculpturing. For example, if a left valve of *Propeamussium jeffreysi* is seen through, it is readily recognized that the internal ribs slightly curve outwards and are often more or less oblique to the external radial costae in LV (Figs. 2-3c,d).

As diagrammatically shown by Waller (1972),



## Structure of internal ribs (right valve)



**Figure 6.** Block diagram showing the structure of internal ribs in RV of *Propeamussium*. The lenticular core of internal rib is sometimes not completely separated from the "middle layer". The interval of internal ribs is not to scale. OL: outer layer of prismatic calcite, ML: "middle layer" of fibrous prismatic (or foliated) calcite, CR: core of internal rib (fibrous prismatic or foliated calcite), IL: inner layer of crossed lamellar aragonite, CMR: commarginal rib ("radially" elongate prismatic calcite).

← **Figure 5.** Shell microstructure of propeamussiids. All are SEM photographs and show internal surface of shell with growth direction downward, except for Fig. 5-1, which is an oblique view of fractured surface. Scale unit in microns.

**1–3.** *Propeamussium watsoni* (Smith), from the same locality as Fig. 2-5. **1:** Middle part of disk (RV) (UMUT RM18287). Slightly weathered outer surface, prismatic outer layer, fibrous prismatic "middle layer" and crossed lamellar inner layer are observed from the upper to the lower. **2A:** Foliated prisms near the periphery of marginal apron (RV) (UMUT RM18288). The foliation seems to be Gamma 120 blades. **2B:** "Middle layer" of fibrous prismatic calcite covering the eroded surface of prismatic outer layer (the same valve). **3A:** Outer layer of fibrous prismatic calcite partly covered with patches of crossed lamellar inner layer (LV) (UMUT RM18289). **3B:** Outer layer of regularly foliated calcite (Gamma 135 blades) changed gradually from fibrous prismatic calcite (the same valve).

**4.** *Polynemamussium intuscostatum* (Yokoyama, 1920) from the same locality as Fig. 1-1. "Middle layer" of foliated calcite (Gamma 135 blades) covering the eroded surface of prismatic outer layer (RV) (UMUT RM18290).

**5–6.** *Propeamussium jeffreysi* (Smith, 1885) from the same locality as Fig. 2-3. **5A:** "Middle layer" of fibrous prismatic calcite showing accretional growth (RV) (UMUT RM18291). **5B:** Distal end of an internal rib showing accretional growth of the core (the same valve). **6:** Outer layer of semifoliated calcite (LV) (UMUT RM18292).

Okubo and Inoue (1975) and also in this paper (Fig. 6), each internal rib bears a core of fibrous prismatic (or narrowly foliated) calcite, which is almost imbedded in the inner layer of crossed lamellar aragonite. The core is exposed on the internal surface only at the distal end where its accretional growth occurs (Figs. 3,5-5B). It must, therefore, grow like the outer layer in spite of its situation in the inner layer. In transverse sections of the middle part of the disk, each internal rib is represented by a lenticular core enclosed with the inner layer. In ordinary bivalves (including the Pectinidae) pallial myostracum is formed along the boundary between the outer and inner layers, but in propeamussiids, curiously enough, it lies within the inner layer. In *Propeamussium* pallial myostracum is formed between the cores of internal ribs and the internal shell surface, broadly waving in accordance with the lenticular cores (Figs. 7-1B,2B).

In *Propeamussium dalli* from the Caribbean Sea the internal ribs of LV commonly disappear in the later growth stage, but such a tendency is rarely observed in western Pacific species. Moreover, the arrangement of internal ribs, in every Japanese species of *Propeamussium* and *Polynemamussium* so far examined, is perfectly coincident between RV and LV. Insertion of short internal ribs occur simultaneously in the two valves. Though the internal ribs (and their cores) are generally thicker in RV than in LV, their distribution pattern of one valve seen through from the exterior agrees well with that on the interior of the counter valve (e.g. Figs. 2-3a,b,c,d, 4a,b,c,d). The internal ribs never

extend beyond the margin of the distribution of crossed lamellar aragonite.

*Function of internal ribs.* Owing to the flexibility of the marginal apron of RV, the distal end of each internal rib can be directly in contact with that of the counter valve, when the valves are closed (Fig. 4). In *Propeamussium sibogai* and some other species of this genus, the crossed lamellar layer is more extensively distributed in LV than in RV (Figs. 2-4b,d). Nevertheless, the contact relation is maintained, because the distal ends of internal ribs of RV almost reach the margin of the inflexible inner layer. This fact strongly suggests that the internal ribs serve not only as a frame to support the thin and fragile shell but also as solid buttresses to counteract external and internal forces. In this respect this structure may be functionally (not genetically) analogous to the auricular crura of free living pectinids. In *Propeamussium* the outermost internal ribs (instead of auricular crura) commonly occur near the boundaries between the disk and two auricles. They seem to be serially homologous with other internal ribs, even though two or more cores may be piled up therein.

Most of extant propeamussiids dwell on deep-sea and low-energy muddy bottoms. It is generally supposed that predation pressure is much weaker in comparison with shallow level bottoms. Nevertheless, I occasionally meet with injured-and-repaired shells of *Propeamussium* that indicate non-lethal attacks by some biting predators (e.g. Fig. 2-5). Though the life mode of propeamussiids is still poorly known, relatively large species with internal ribs, except for the

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→ **Figure 7.** Transverse sections of the valves of *Propeamussium watsoni* (Smith, 1885) from the same locality as Fig. 2-5. All are SEM photographs taken after one minute's etching by 10% acetic acid. Scale unit in microns.

**1A:** Lenticular core of an internal rib in the dorsal part of disk near the demarcation line (RV) (UMUT RM18293).

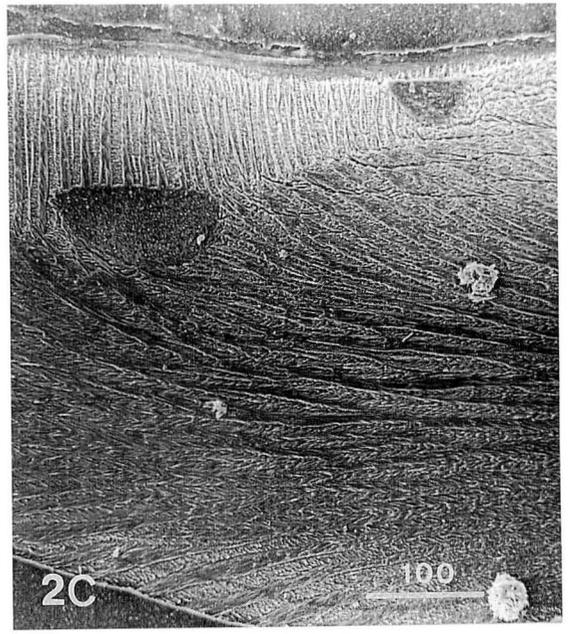
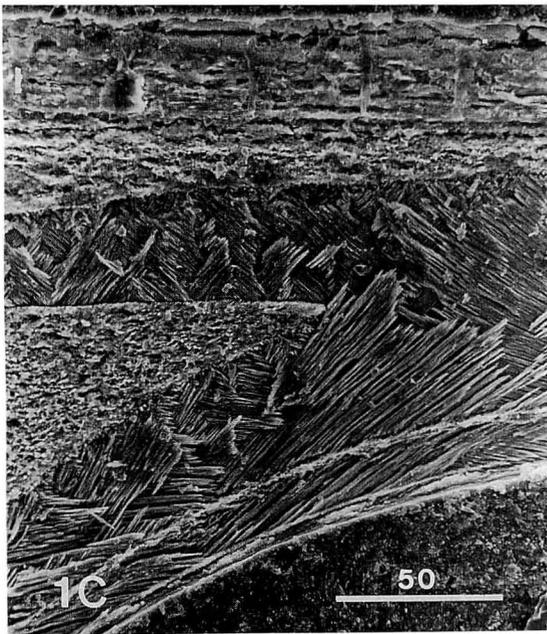
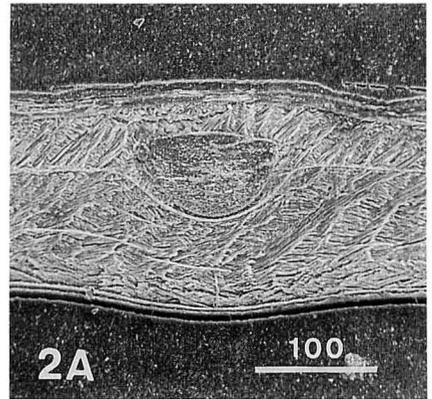
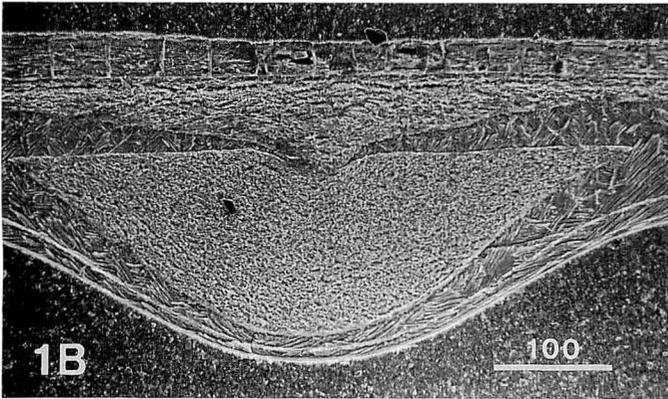
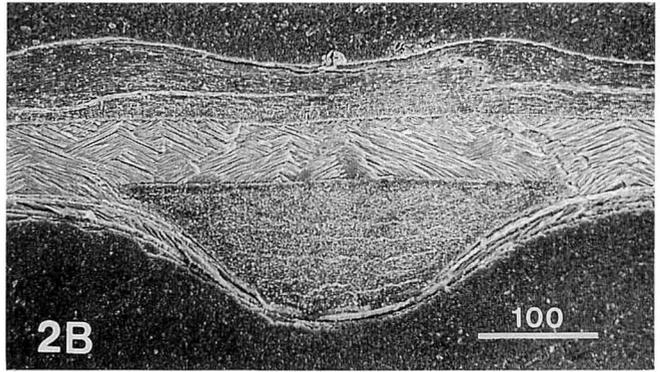
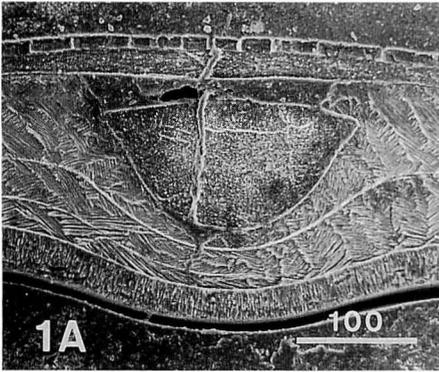
**1B:** Lenticular core of the same internal rib in the middle part of disk, not completely separated from the "middle layer".

**1C:** Close-up of the same section. Pallial myostracum observed within the crossed lamellar inner layer between the core and the inner surface.

**2A:** Lenticular core of an internal rib in the dorsal part of disk near the demarcation line (LV) (UMUT RM18294).

**2B:** Lenticular core of the same internal rib in the middle part of disk.

**2C:** Two lenticular cores in the anterodorsal part of the same valve immediately after their origination.



early byssate stages, probably have swimming ability to escape from predators.

Thayer (1972) examined the obliquity of quick (striated) adductor muscle in various monomyarian bivalves, and tested successfully the hypothesis that oblique quick muscle is advantageous for swimming habit because it enables quicker clapping motion. The quick muscle of *Propeamussium* is generally remarkably oblique as exemplified by *P. dalli* (Thayer 1972, fig. 4A) and *P. sibogai* (in this paper); the obliquity is comparable with or surpass the values in *Placopecten magellanicus* and *Amusium japonicum* which are known as active swimmers. The reduction of byssal notch with growth and the widely gaped antero- and postero-dorsal disk margins also suggest swimming habit.

Reinforcement of valves by internal ribs may be effective in *Propeamussium*, because powerful contraction of quick adductor muscle for swimming must give considerable strain to the fragile valves. The thicker internal ribs in RV appear to compensate the relative weakness of shell strength of RV due to the prismatic calcite and the absence of external radial sculpturing.

*Origin of internal ribs.* The internal ribs of the Pectinidae may have developed as an auxiliary structure for interlocking of valve margin (Fig. 1-5a). They must have occurred, at least primarily, in relation to the external radial sculpturing. Although internal shell features of many fossil pectinids remain undescribed, conspicuous internal ribs are scarcely known in pre-Oligocene species. On the other hand, undoubted species of the Propeamussiidae with distinct internal ribs already appeared in the Middle Triassic (Nakazawa 1961) and commonly occur in Jurassic and later and Cenozoic off-shore muddy sediments. The genus-level classification of fossil and extant propeamussiids should be reexamined with considering the taphonomy and differential preservation, but the basic features appear to be quite conservative. Internal ribs must have developed independently in the Pectinidae and the Propeamussiidae, because, as noted before, they are clearly different in many essential characters.

As discussed by Waller (1971, 1972, 1978), the Propeamussiidae may have been derived from the Late Paleozoic family Pernopectinidae. The discrepant shell microstructure between RV and LV was previously described by Newell (1937–1938) in some species of *Pernopecten*; the outer layer is prismatic in RV and fibrous in LV, and the inner layer of both valves is crossed lamellar. Recently Newell and Boyd (1985) also described the shell structure of *Pernopecten* sp. on the basis of some well preserved silicified specimens. A marginal apron was probably present also in *Pernopecten*, judging from the “discrepant” size and shape between the two valves (e.g. Newell 1937, fig. 42). Internal ribs are absent, and an ostracum corresponding to the “middle layer” of RV is still undescribed in Pernopectinidae. This state, however, may not be much different from that of some extant species of *Cyclopecten*, in which the “middle layer” is thin in comparison with other layers. In these respects, *Cyclopecten* seems to exhibit more primitive features than *Propeamussium*. I presume that *Propeamussium* (and some related genera with internal ribs) originated from *Pernopecten* through some undescribed *Cyclopecten*-like species. The development of internal ribs is probably related to the swimming strategy, because they are scarcely coexistent with byssal notch and pseudoctenolium.

In RV of *Propeamussium* the lenticular cores of internal ribs share common shell microstructure with the “middle layer” (Figs. 5-5A, 5B). Both of them grow accretionally only on the extra-pallial internal surface and are similarly composed of lath-type fibrous prismatic (or regularly foliated) calcite. The “middle layer” is sometimes more or less thickened just along the internal ribs, as recognized in the transverse sections. Moreover, in serial transverse sections of RV of *Propeamussium watsoni* and *P. sibogai*, it is actually observed that the cores are sometimes not completely separated from the “middle layer” (Fig. 7-1B). Little has been known about the mechanism producing such a composite shell layering. Yet, the observed facts seem to indicate that the internal ribs are produced by some

patchy cells which were inwardly isolated from the mantle tissue secreting the "middle layer".

In LV of *Propeamussium* similar developmental relation may exist between the cores of internal ribs and the outer layer of fibrous prismatic (or foliated) calcite. Though the resemblance of shell microstructure is not so decisive as that in RV, the lenticular core originates at first from a point adjacent to the outer layer, as exemplified in the transverse section of early disk of *Propeamussium watsoni* (Fig. 7-2C).

### Conclusion

As the result of this comparative study, the following conclusions were obtained about the structure, function and development of the internal ribs of *Propeamussium*.

1. Each internal rib bears a lenticular core of lath-type fibrous prismatic (or narrowly foliated) calcite, which grows accretionally only at the distal end in spite of its situation in the inner layer of crossed lamellar aragonite.

2. Owing to the flexible marginal apron of RV, the distal ends of internal ribs are just in contact with those of the counter valve when the valves are closed. They serve solid buttresses to counteract the destructive force produced by the powerful contraction of quick adductor muscle for swimming.

3. The cores of internal ribs share similar fibrous prismatic (or foliated) microstructure with the "middle layer" in RV and with the outer layer in LV. Developmentally, they were most certainly differentiated from these layers by some patchy isolation of shell-secreting mantle tissue.

Homeomorphic relation between *Amusium* and *Propeamussium* can be realized by the different developmental background and primary function of internal ribs as well as many other basic features. The Propeamussiidae, which include *Polynemamussium* and *Cyclopecten* in addition to *Propeamussium*, are commonly characterized by the striking inequivalveness not only in the shape and sculpturing but also in the

shell microstructure. This family should be regarded as a significant example of "living fossils", because such strikingly discrepant valves are common in Paleozoic pectinoids but unknown in other living pteriomorph families.

The suprageneric classification of the Pectinacea is still in great confusion. It is largely due to insufficient evaluation of taxonomic characters. As were clarified by Waller (1972, 1984) and also in this paper, the limit and diagnostic characters of the Propeamussiidae are very clear regardless of the presence or absence of internal ribs, even though their discrimination from the Pernopectinidae depends on further studies. Although there are a few fossil genera of dubious familial position, they are probably not intermediate between the Pectinidae and the Propeamussiidae. Further studies of the shell crystallography, anatomy, development and ecology of propeamussiids would lead us to better understanding of the evolution of the suborder Pectinina.

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I am very grateful to Dr. Thomas R. Waller (Smithsonian Institution) and Dr. Norman D. Newell (American Museum of Natural History) for various stimulation, to Mr. Shoichiro Hayashi (Isshiki Town), Mr. Eiji Tsuchida (Oceanogr. Inst., University of Tokyo) and Dr. Kenji Mochizuki (Univ. Mus., University of Tokyo) for their kind supply of materials, and also to Miss Tomoko Yamashita and Mr. Akira Tsukagoshi for their assistance in scanning electron microscopy.

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*Propeamussium* の内肋の機能のおよび分類学的意味：三疊紀以降半深海の泥相に多いワタゾコツキヒガイ属 (*Propeamussium*) は、ツキヒガイ属 (*Amusium*) と見かけの上で内肋を共有するが、系統的には全く異なり、古生代後期に栄えた Pernopectinidae の特徴をとどめる「生きた化石」として注目される分類群である。*Propeamussium* のほか *Polynemamussium*, *Cyclopecten* が *Propeamussiidae* の特徴を共有する。今回、西太平洋地域の現生および化石イタヤガイ上科の数種について、内肋の巨視的・微視的特徴を観察し、その機能的・分類学的意味を考察した。*Amusium* を含むイタヤガイ科の内肋は、腹縁近くの外層で外表の放射肋に応じて形成され、本来は腹縁の噛み合わせを確実にする補助的役割を果たしている。これに対して、*Propeamussium* の内肋は、交差板構造の内層の中に繊維状構造を示すレンズ状のコアを伴って形成され、その末端部で付加成長する。このコアは発生的には、右殻では稜柱層直下の“中層”から、左殻では外層から分化したと考えられる。内肋の末端は両殻の間で対置し、殻を閉じた時に互いに接するようにできている。おそらく、遊泳のための強力な閉殻筋の緊縮が薄質の殻に与える破壊力を和らげるバットレスの役割を果たしていると考えられる。速水 格

## 860. LARVAL PALEOECOLOGY OF FIVE BIVALVE SPECIES FROM THE UPPER PLIOCENE OF SOUTHWEST JAPAN\*

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**Abstract.** Juvenile shells of five bivalve species, *Glycymeris rotunda*, *Limopsis tajimae*, *Oblimopa japonica*, *Crenulilimopsis oblonga* and *Venericardia panda* from the Upper Pliocene deposits of Kakegawa, Miyazaki and Okinawajima regions, southwest Japan retain the prodissoconch in their initial shell portion. Based on comparison of their prodissoconch morphology and morphometry with those of modern species hitherto investigated, developmental types of the five species were presumed: direct development for *V. panda* having a relatively large (185–259  $\mu\text{m}$  in length) prodissoconch, and lecithotrophic with a short non-feeding pelagic stage for other four species characterized by relatively large (ca. 150–200  $\mu\text{m}$  in length) prodissoconch I and well-marked prodissoconch II. *C. oblonga* and *L. tajimae* both show remarkable intraspecific variation in prodissoconch II size, and the specimens from the northern region generally possess larger prodissoconch II than those from the southern region.

Judging from the knowledge on larval history of some Recent bivalves in relation to water temperature and the paleoceanographic setting of the study areas in late Pliocene age, the latitude dependent variation of prodissoconch size observed in the two species may reflect the difference in durations of larval stage depending on the changes in temperature of marine environments.

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### Introduction

Bivalves secrete a peculiar calcified shell, named prodissoconch in the early growth stage prior to metamorphosis (Thorson, 1950; Ockelmann, 1965; Jablonski and Lutz, 1980, 1983). The relationships of prodissoconch morphology, developmental types, egg and hatching sizes and durations of embryonic and larval stages in Recent bivalves have been investigated by a number of researchers (e.g. Loosanoff *et al.*, 1951; Yoshida, 1953; Loosanoff and Davis, 1963; Ockelmann, 1965; Sastry, 1965, 1979;

Chanley, 1965, 1966, 1969; Chanley and Chanley, 1970; Turner and Johnson, 1971). These works make it possible to infer the developmental type of a given species from larval shell morphology with some confidence.

Prodissoconch and early dissoconch morphology can be readily observed in many well-preserved bivalves with an aid of the scanning electron microscope (SEM). Comparative analysis of early developmental stages of living and fossil bivalves will, therefore, provide reliable information to understand the evolutionary history, paleobiogeography and paleoecology of the organism (Jablonski and Lutz, 1983). In spite of

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this, studies on fossil material are rare (LaBarbera, 1974; Lutz and Jablonski, 1978; Jablonski and Lutz, 1978). This probably because of the difficulty in determining the exact taxonomic positions of fossil larval shells.

This paper describes prodissoconch morphology of five bivalve species from the Upper Pliocene deposits of the Pacific coastal regions of southwest Japan, and discusses its larval paleoecological implications.

### Material and methods

**Material:**—Pliocene marine fossiliferous deposits are sporadically distributed along the Pacific coastal regions of southwest Japan. They crop out extensively in the Kakegawa (central Japan), Miyazaki (eastern Kyushu) and southern Okinawa-jima regions and the sediments in these regions are called the Kakegawa, Miyazaki and Shimajiri Groups respectively.

Well-preserved juvenile shells of the following five bivalve species from these groups are treated in this paper: *Glycymeris rotunda* (Dunker), *Limopsis tajimae* Sowerby, *Oblimopa japonica* (A. Adams), *Crenulilimopsis oblonga* (A. Adams) and *Venericardia panda* (Yokoyama) (Table 1). These species occur commonly in the study areas, but specimens retaining the prodissoconch stage are extremely rare. The juvenile shells utilized were collected from several localities of the Kakegawa, Miyazaki and Okinawa-jima areas (Fig. 1). According to the previous planktonic foraminiferal biostratigraphic works (Tsuchi and Ibaraki, 1979; Natori, 1979; Tanaka and Ujiie, 1984), the fossil localities are all included in the zones of N.19 to N.21 of the Upper Pliocene age (2–3 Ma). The molluscan assemblages from the Kakegawa, Miyazaki and Shimajiri Groups are characterized by upper sublittoral to the upper bathyal associations, and are summarized as the Kakegawa Fauna (Chinzei,

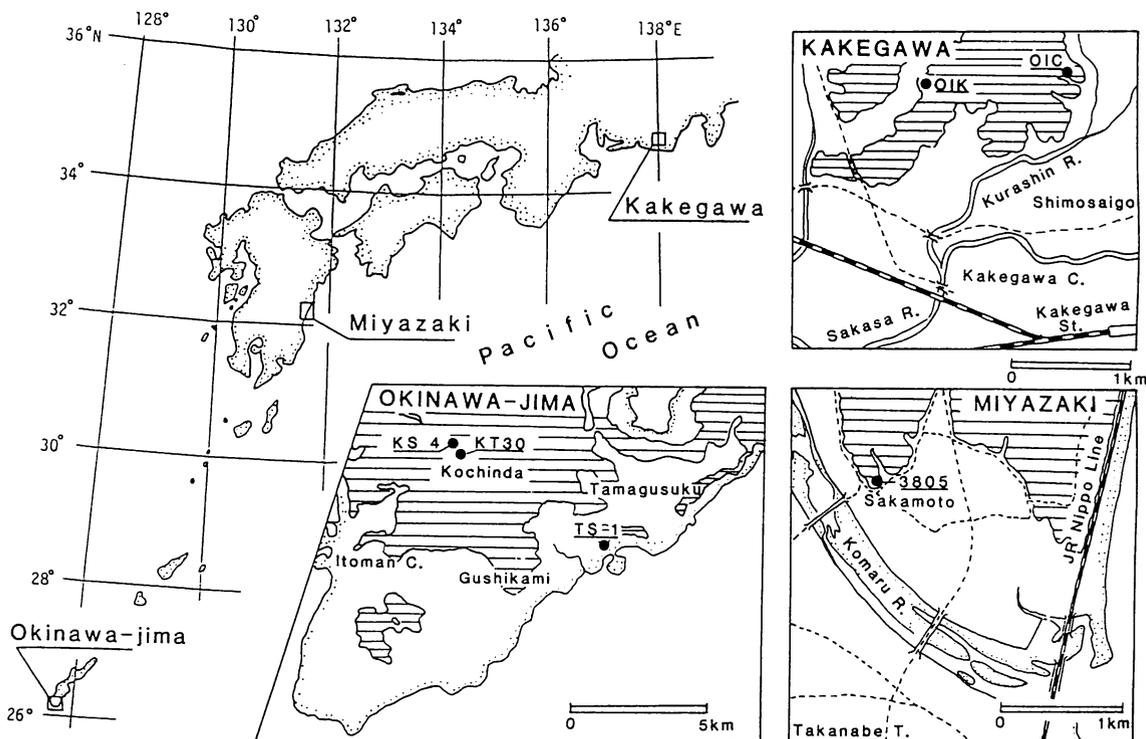


Figure 1. Map of southwest Japan, showing the fossil localities of the bivalve samples studied. Pliocene outcrops are horizontally lined (adapted from Tanaka and Ujiie (1984) for Okinawa-jima Island).

Table 1. List of material studied. Number of specimens used for measurements is shown in parentheses.

Family	Species	Kakegawa G.		Miyazaki G.		Shimajiri Group		Recent St. A
		OIC	OIK	3805	KT30	KS1	TS1	
Glycymerididae	<i>Glycymeris rotunda</i> (Dunker)	9 (2)		16 (3)				
Limopsidae	<i>Limopsis tajimae</i> Sowerby		16(11)	9 (4)	7 (7)			
	<i>Oblimopa japonica</i> (A. Adams)	20(16)						
	<i>Crenulilimopsis oblonga</i> (A. Adams)		1 (1)	44(36)		4 (4)	3 (3)	3 (3)
Cardiidae	<i>Venericardia panda</i> (Yokoyama)	13 (7)		13 (5)		3 (3)		

1978, 1986).

In addition to these fossil samples, juvenile shells of *C. oblonga* collected from off Osezaki, northeastern Suruga Bay (Station A, 200–300 m deep: lat. 35°05'N, long. 138°45'E) were used for comparison of prodissoconch size. Among the five species examined, *V. panda* is an extinct species, while others are still living in the relatively deeper environments off southwest Japan (Habe, 1977). All specimens studied are stored in the University Museum of the University of Tokyo.

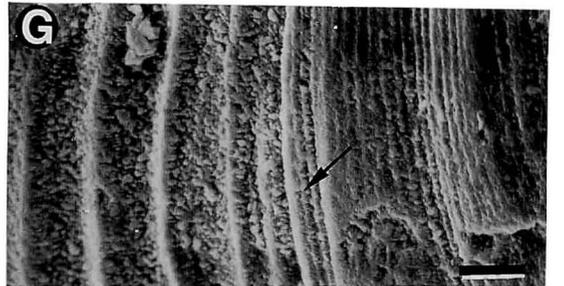
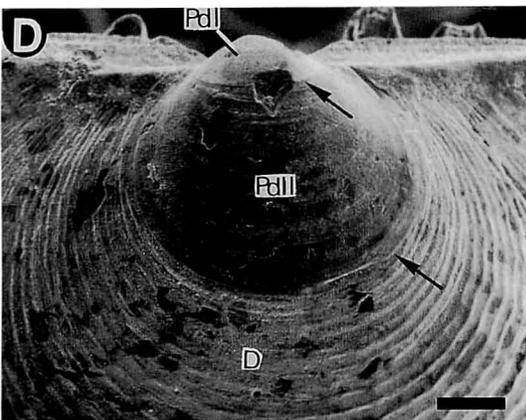
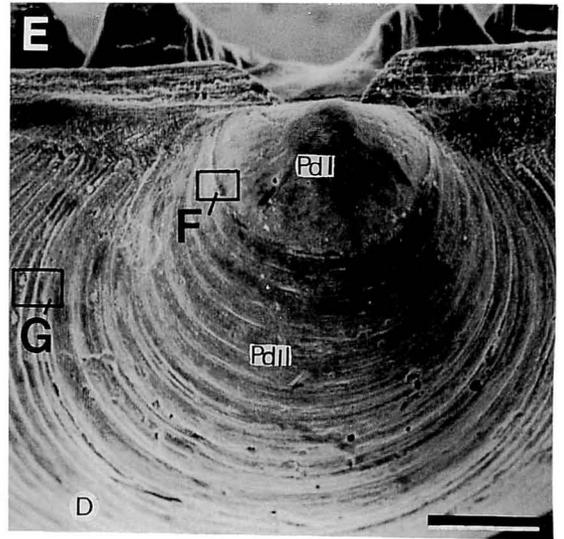
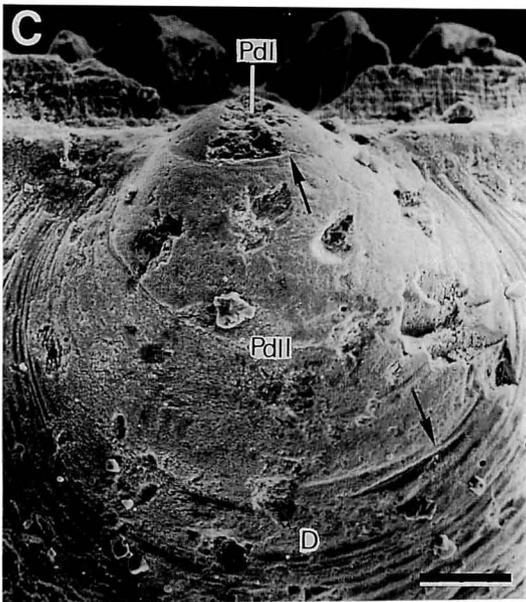
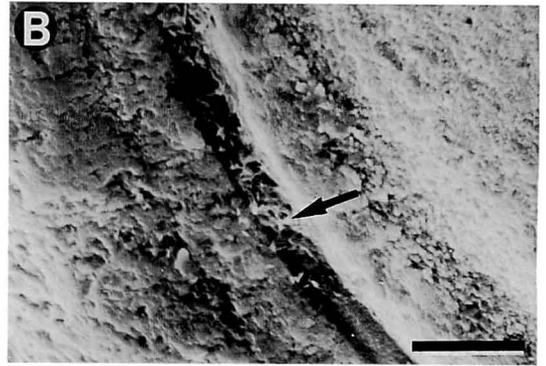
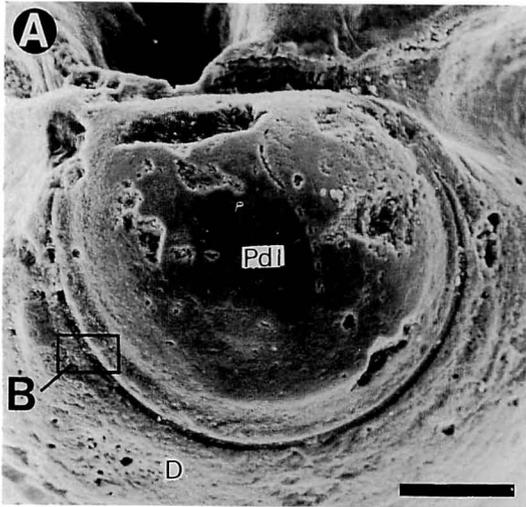
**Methods:**—Fossil-bearing, silty to fine sandy sediments were sieved using a 1mm mesh screen, and juvenile shells were extracted from residues under a binocular microscope. Taxonomic positions of the juvenile specimens were determined from comparison of surface ornament and hinge structure with the medium to large specimens from the same fossil localities. Observations of early shell morphology were made with scanning electron microscopy (Hitachi, S-430), and the dimensions of the larval stages were measured using a digital micrometer (accuracy  $\pm 1 \mu\text{m}$ ; calibrated by a standard sample for IC measurement) of the image processor (Hitachi, EP 1050) attached to the SEM. We followed Werner (1939) and Rees (1950) for the terminology of bivalve larval shells.

### Prodissoconch morphology

As in other bivalve larvae described previously

(Werner, 1939; Rees, 1950; Ockelmann, 1965; Chanley and Andrews, 1971; Jablonski and Lutz, 1980; among others), the prodissoconch in the five species examined is divided into two ecologically and morphologically well defined stages, prodissoconch I (Pd I) and prodissoconch II (Pd II) (Figs. 2–3). Prodissoconch I is an initial shell secreted by the shell gland and mantle epithelium during the stage developing from the non-shelled trochophore (Carriker and Palmer, 1979). It is fairly similar among the species examined in having a D-shaped outline with a straight hinge line and a coarse and irregularly punctate surface under the SEM (Figs. 2–3). The only difference is that the prodissoconch I in *Venericardia panda* is less inflated and more broadly rounded than those of other four species.

Prodissoconch II is deposited by the mantle edge along the shell margin and inside the prodissoconch I during the veliger stage (Ockelmann, 1965; Carriker and Palmer, 1979). This stage is well developed in *Limopsis tajimae*, *Oblimopa japonica*, *Crenulilimopsis oblonga* and *Glycymeris rotunda*, but it is absent in *V. panda* (Figs. 2A–B). In the former four species the Pd I – Pd II boundary is clearly marked because concentric growth lines first appear in the Pd II stage (Figs. 2–3). The growth lines are dense, fine and regular-spaced in *L. tajimae* (Figs. 3A–D), *C. oblonga* (Figs. 3E–I) and *G. rotunda* (Fig. 2C), while those in *O. japonica* are combination of major undulations and minor striations (Fig. 2G).



Dissoconch corresponds to the shell secreted after metamorphosis. Morphological change at the prodissoconch-dissoconch boundary differs among the five species examined. In *V. panda* a conspicuous constriction occurs at the boundary (Fig. 2B), followed by broad-spaced concentric growth bands in the early dissoconch stage. Radial ribs first appear at the stage of about 500  $\mu\text{m}$  in shell height. In other four species abrupt expansion of growth line spacing is commonly observable at the prodissoconch II-dissoconch boundary under the SEM (Figs. 2C, G; 3D, I), forming a sharp transitional line of demarcation, named the metamorphic line (Carriker and Palmer, 1979).

#### Variation of prodissoconch size

Statistical data of the lengths of prodissoconchs I and II for the species examined are summarized in Table 2. Every species has a relatively large Pd I, ranging from 150  $\mu\text{m}$  to 200  $\mu\text{m}$  in length.

Intra- and interspecific variation of prodissoconch II length is much larger than that of prodissoconch I. The length is largest (365–490  $\mu\text{m}$ ) in *G. rotunda* and *O. japonica*, intermediate (244–415  $\mu\text{m}$ ) in *L. tajimae*, and smallest (213–328  $\mu\text{m}$ ) in *C. oblonga*. Concerning *C. oblonga* and *L. tajimae*, the specimens from the southern region generally possess a larger prodissoconch II than those from the northern region (Table 2).

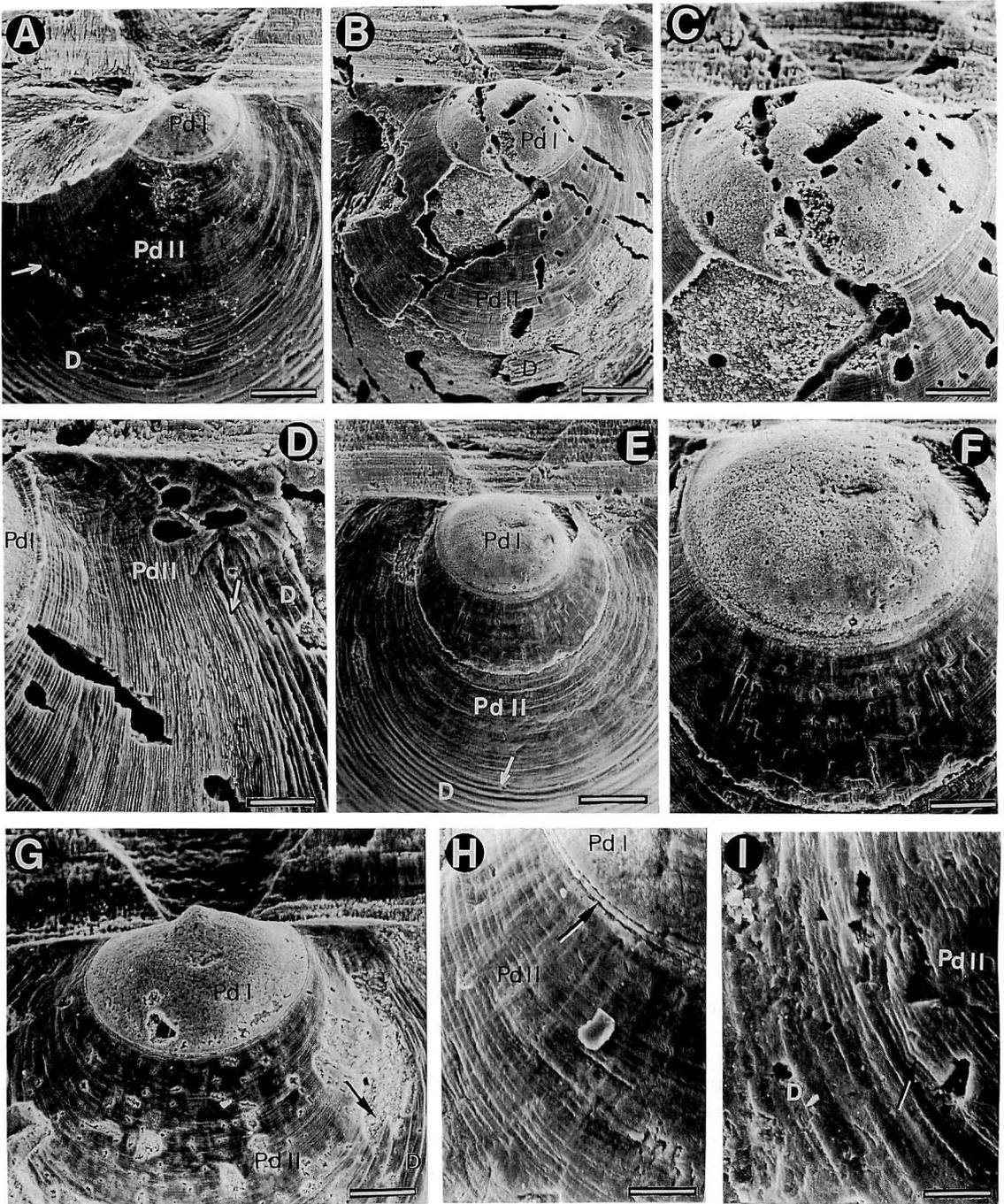
#### Discussion

Developmental types in the marine benthic invertebrates including bivalves are summarized into three main categories: pelagic development, direct development and ovoviviparity (Thorson, 1946, 1950; Ockelmann, 1965). Pelagic develop-

ment is further classified into planktotrophic (= larvae feeding on phytoplankton during the veliger stage) and lecithotrophic (= larvae feeding on their own yolk content during a relatively short pelagic stage) (Thorson, 1950).

With the development of culture methods, early life history and larval shell morphology in the Bivalvia have been investigated for a number of species by rearing veliger larvae in the laboratory (e.g. Thorson, 1936, 1950; Yoshida, 1953; Loosanoff and Davis, 1963; Ockelmann, 1965; Chanley and Andrews, 1971; Allen and Sanders, 1973; Sastry, 1979; Waller, 1981). Especially Ockelmann's (1965) work on larval ecology of more than 200 species mainly from north Atlantic provided adequate criteria to recognize developmental types from larval shell morphology and morphometry. According to his work and Thorson (1936), in planktotrophic larvae, prodissoconch I is small (70–150  $\mu\text{m}$  in length), reflecting the low yolk supply, and prodissoconch II is relatively large (200–600  $\mu\text{m}$  in length), suggesting a long duration of the veliger stage. In the species having a lecithotrophic larval development, prodissoconch I is large (135–230  $\mu\text{m}$  in length) reflecting the large yolky eggs, and prodissoconch II stage is absent or poorly developed. Species of direct development type have unusually large (230–500  $\mu\text{m}$  in length) prodissoconchs, which are often inflated and broadly rounded with a straight hinge line. Recently, several authors documented detailed methods to recognize developmental types in modern and fossil larval shells under the SEM (Turner and Boyle, 1975; Lutz, 1977; Jablonski and Lutz, 1980, 1983). Larval ecology of the five species treated in this paper is not yet well understood. Comparison of the results of this study with the criteria mentioned above may provide a reliable basis to determine their developmental types. Among the

← **Figure 2.** SEM photographs of the early shell growth stage of three bivalve species from the Upper Pliocene of southwest Japan. Pd I: prodissoconch I, Pd II: prodissoconch II, D: dissoconch. Arrows in B, C, F and G indicate Pd I – Pd II boundary and/or prodissoconch-dissoconch boundary. A–B. *Venericardia panda* (Yokoyama). UMUT CM 18273-1 (loc. 3805, Miyazaki Group). C. *Glycymeris rotunda* (Dunker). UMUT CM 18263-1 (loc. 3805). D–G. *Oblimopa japonica* (A. Adams). D. UMUT CM 18267-1, E–G. UMUT CM 18267-2 (loc. OIC, Kakegawa Group). Scale bars: 50  $\mu\text{m}$  (A), 100  $\mu\text{m}$  (B–E), 150  $\mu\text{m}$  (F–G).



**Figure 3.** SEM photographs of the early shell growth stage of two bivalve species from the Upper Pliocene of southwest Japan. Pd I: prodissoconch I, Pd II: prodissoconch II, D: dissoconch. Arrows in A–B, D–E, G, and I indicate Pd I – Pd II boundary and/or prodissoconch-dissoconch boundary. A–D. *Limopsis tajimae* Sowerby. A. UMUT CM 18266-1 (loc. KT 30, Shimajiri Group). B–D. UMUT CM 18265-1 (loc. 3805, Miyazaki Group). E–I. *Crenulilimopsis oblonga* (A. Adams). E–F. UMUT CM 18271 (loc. TS01, Shimajiri Group). G. UMUT CM 18269-1 (loc. 3805, Miyazaki Group). H–I. UMUT CM 18269-2 (loc. 3805). Scale bars: 100  $\mu\text{m}$  (A–B, E), 50  $\mu\text{m}$  (C, F, G) and 140  $\mu\text{m}$  (H, I).

Table 2. Statistical data of the prodissococonch length (in microns) in the five species examined. N: number of individuals,  $\bar{X}$ : sample mean, s: standard deviation, V: coefficients of variation, O.R.: observed range.

Species	Sample	Prodissococonch I					Prodissococonch II				
		N	$\bar{X}$	s	V	O. R.	N	$\bar{X}$	s	V	O. R.
<i>Grycymeris rotunda</i>	3805	3	180.6	14.0	7.8	165-199	2	462.5	27.5	6.0	435-490
	OIC	2	189.0	11.0	5.8	189-200	2	413.0	48.0	11.6	365-461
<i>Limopsis tajimae</i>	KT30	7	188.1	8.5	4.5	169-198	7	253.1	5.4	2.1	244-260
	3805	4	181.3	10.9	6.0	163-191	4	312.8	25.4	8.1	291-355
	OIK	10	176.2	10.3	5.8	156-191	11	373.4	31.1	8.3	306-415
<i>O. japonica</i>	OIC	16	190.1	7.2	3.8	175-200	15	416.7	29.1	7.0	375-475
<i>Crenulilimopsis oblonga</i>	KS4	4	167.0	6.7	4.0	160-178	4	240.0	11.2	4.7	225-255
	TS1	3	174.7	8.0	4.6	169-186	3	238.3	18.2	7.6	213-255
	3805	36	177.6	9.8	5.5	153-193	35	298.6	16.8	5.6	265-328
	OIK	1	165				1	300			
	St. A	3	186.3	1.7	0.9	184-188	1	385			
<i>V. panda</i>	KS4	3	198.7	11.9	6.0	185-214					
	3805	5	224.6	9.9	4.4	213-240					
	OIC	7	244.6	10.8	4.4	230-259					

five species, only *V. panda* lacks prodissococonch II stage, suggesting the absence of a planktonic larval stage. The prodissococonch I size of this species is rather small to be direct development (ca. 185–259  $\mu\text{m}$ ), but we infer this mode of development on the basis of the absence of prodissococonch II. The four arcoids, *Glycymeris rotunda*, *Oblimopa japonica*, *Limopsis tajimae* and *Crenulilimopsis oblonga* are characterized by a relatively large prodissococonch I (ca. 150–200  $\mu\text{m}$  in length) and a well-marked prodissococonch II. Not many arcoids have been studied, but the most familiar planktotrophic ones (e.g. *Anadara transversa*, *A. broughtonii*, *Noetia ponderosa*) have a small prodissococonch I of 90  $\mu\text{m}$  or less (Loosanoff and Davis, 1963; Chanley, 1966). We therefore judge the development type of the four species as lecithotrophic with a short pelagic stage.

As stated briefly, the three limopsids studied are now distributed in the lower sublittoral to upper bathyal zones (50–2,000 m in depth) of southwest Japan (Habe, 1977). Of these, *L. tajimae* was studied ecologically by Horikoshi and Tanaka (1980), who recognized yearly development of relatively large eggs in the medium to large individuals (20–35 mm in shell length) from the upper bathyal zone (250–450

m depth) off Suruga Bay, central Japan. Oliver and Allen (1980) distinguished two types of egg and prodissococonch size in seven deep sea species of *Limopsis* from the Atlantic: species from slope depths having medium-sized eggs and prodissococonchs and species with an abyssal distribution having relatively large eggs and prodissococonchs. These authors presumed the developmental type of the seven species as lecithotrophic, although they did not show direct data. Most species studied by Oliver and Allen (1980) apparently inhabit deeper environments than the three species studied by us. The results of this work and Oliver and Allen (1980) may suggest a variety of developmental types in *Limopsis*, possibly lecithotrophic for species in the sublittoral to upper bathyal zones and direct for species in the lower bathyal to abyssal zones.

Among the five species examined, three species, *C. oblonga*, *L. tajimae* and *V. panda* show large intraspecific variation of prodissococonch II size. Furthermore, the size in the northern individuals is generally larger than that in the southern ones. Pliocene to early Pleistocene sediments in the Kakegawa, Miyazaki and Okinawa-jima areas are now considered to have deposited in the same paleogeographic realm, and the fauna is comparable to the living

fauna in the waters off southwestern Japan associated with the warm Kuroshio current (Chinzei, 1978). In the northwestern Pacific along the Kuroshio, there is a difference in surface temperature of 5–6°C between Okinawa and central Japan regions throughout a year (Japan Meteorological Agency, 1987). Such a temperature gradient might have been present in the Pacific coastal region of southwest Japan in the late Pliocene age. In connection with this problem, an inverse relationship between temperature and maximum size of larval shells has been reported in Recent species such as *Mytilus edulis* (Bayne, 1965) and *Mya arenaria* (Lutz and Jablonski, 1978). In laboratory studies, duration of larval stage and the rate of growth of larvae both become shorter and more rapid at high than at low temperatures in *Ostrea virginica* (Nelson, 1908), *O. edulis* (Korringa, 1941) and *Venus* (= *Mercenaria*) *mercenaria* (Loosanoff *et al.*, 1951). These observations indicate that at high temperatures, the high rate of growth is insufficient to compensate for the short time available for feeding, and this results in a smaller prodissoconch size at higher temperatures (Bayne, 1965; Lutz and Jablonski, 1978).

These lines of evidence seem to suggest that geographic variation of prodissoconch II size recognized in the two species reflect the difference in durations of larval stage, which was possibly related to the latitudinal gradient in ambient marine temperature.

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Kakegawa 掛川, Miyazaki 宮崎, Shimajiri 島尻, Takanabe 高鍋, Sakamoto 坂本, Kochinnda 東風平, Tamagusuku 玉城, Osezaki 大瀬崎, Suruga Bay 駿河湾.

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西南日本上部鮮新統産二枚貝5種の幼生古生態: 二枚貝類は、発生の初期に原殻 (prodissoconch) と呼ばれる特徴的な殻をつくる。原殻はさらに、無装飾の原殻 I (prodissoconch I) と細かな同心円肋装飾からなる原殻 II (prodissoconch II) に区別され、それぞれふ化以前、ふ化後の幼生期に形成される。今回、西南日本太平洋岸に分布する掛川層群、宮崎層群、島尻層群のほぼ同層位 (2-3 Ma) から産した二枚貝5種 (*Glycymeris rotunda*, *Limopsis tajimae*, *Oblimopa japonica*, *Crenulilimopsis oblonga*, *Venericardia panda*) の原殻を観察し、現生種の資料との比較からそれらの幼生古生態を考察した。検討した5種のうち *V. panda* は、大型の原殻 I を有するものの、原殻 II を欠くことから、直接発生型に属すると考えられる。その他の4種は、やや大型の原殻 I と、明瞭な原殻 II を持つことから、卵栄養型に属し比較的短い浮遊幼生期を持っていたと推定される。さらに *C. oblonga* と *L. tajimae* については、より北の地域の標本ほど、原殻 II のサイズが大きかったことがわかった。現生種における水温と関係した幼生生活史のデータや、後期鮮新世当時における古海洋学的背景からみて、おそらく両種にみられた原殻 II のサイズの地理的変異は、水温に規制された浮遊幼生期の長さの違いから生じたものと推察される。

棚部一成・図子良樹

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## 行 事 予 定

	開 催 地	開 催 日	講演申込締切日
1989年年会・総会	京 都 大 学	1989年 2 月 3 日～5 日	1988年11月20日
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1989年年会・総会では「機能形態に関するシンポジウム」  
 世話人・鎮西清高・亀井節夫が予定されています。

### Errata

No. 149, 855. MATSUOKA, Keiji:  
 Pliocene Freshwater Bivalves (*Lamprotula* and *Cuneopsis*: Unionidae) from the  
 Iga Formation, Mie Prefecture, Central Japan.

P. 419, 421, 423, 425, 427, 429 running title read 855 for 856.

Proceeding:

P. 431 (正) 仲谷英夫 (誤) 仲谷秀夫

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