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The fossil on the cover is *Trilophodon sendaicus* Matsumoto, an extinct elephant, which was described from the Pliocene Tatsunokuchi Formation developed in the vicinity of Sendai, Northeast Honshu, Japan. (IGPS coll. cat no. 87759 (A), length about 18.5 cm)

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**932. MOLLUSCAN FAUNA FROM THE LATE MIOCENE HATSUSE
FORMATION IN THE MIURA PENINSULA,
KANAGAWA PREFECTURE, JAPAN***

KIYOSHI OKUMURA

Department of Natural Science, Naruto University of Education,
Naruto City, Tokushima Prefecture, 772

and

YUTAKA YAMAGISHI

Kurihama Junior High School, Yokosuka City, Kanagawa Prefecture, 238

Abstract. The Hatsuse Formation distributed in the southern part of the Miura Peninsula mainly consists of well-bedded marine tuff breccia, lappili tuff, and scoriaceous sandstone and siltstone of marine origin with intercalated thin layers of pumice and conglomeratic sandstone. The molluscan fossils occur from a rather coarse-grained sandstone associated with fragments of pyroclastic rocks. The Hatsuse Fauna named herein is composed of three species of Gastropoda, one species of Scaphopoda, and 15 species of Bivalvia.

The Hatsuse Fauna is characteristically an admixture of euneritic and subneritic forms, though all of them are warm-water dwellers. In consideration of species composition and their mode of occurrence, the shallow-water dwellers are interpreted to be the ones which were displaced into the outer neritic environment.

The geologic age of the Hatsuse Fauna indicates Late Miocene, and is correlated with the Zushi Fauna distributed in the northern part of the Miura Peninsula, Kanagawa Prefecture and the Senhata Fauna of the Boso Peninsula, Chiba Prefecture.

Key words. Hatsuse, Miura, Zushi, Senhata, Mollusca.

Introduction

The Hatsuse Formation was originally described by Suzuki (1932) for the marine strata distributed around Hatsuse-Machi in the northern part of Miura City, southernmost part of the Miura Peninsula, Kanagawa Prefecture. He also reported a large number of molluscan fossils from this formation, though these fossils were undoubtedly collected from part of the Pleistocene Miyata Formation.

Subsequently, the Tertiary strata distribut-

ed in the southern part of the Miura Peninsula have been lithologically divided into the Misaki, Aburatsubo and Hatsuse Formations in ascending order, and those formations have tentatively been correlated with Tertiary strata in the northern part of the Miura Peninsula (Akamine *et al.*, 1956; Mitsunashi and Yabe, 1968). The precise geological age of these strata has remained undetermined. One important reason for this is that, hitherto, no fossils have been found from the Hatsuse Formation.

Recently, numerous fossil molluscs were collected by the present authors from the Hatsuse Formation. This is probably the

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first fossil collection from this formation. This fauna includes some characteristic species as shown in Table 1. It can be considered that those fossil molluscs carry very important information for age determination and correlation of the Tertiary strata in this area.

The purpose of the present work is to discriminate the molluscan fossils from the Hatsuse Formation, to attempt to determine the geological age, and to correlate these strata with molluscan faunas in the northern part of the Miura and Boso Peninsulas.

Acknowledgments

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Brief note on the geology around the fossil localities

The Miocene strata, in which the present fossil localities are included, are overlain unconformably by the Pleistocene Miyata Formation. According to Akamine *et al.* (1956), the Miocene strata distributed in the southern part of the Miura Peninsula can be divided into three stratigraphic units: Misaki, Aburatsubo and Hatsuse Formations in ascending order. These formations are mainly characterized by pyroclastic rocks.

The Misaki Formation is overlain conformably by the Aburatsubo Formation, which is overlain partially by the Hatsuse Formation. The Hatsuse Formation consists mainly of brownish or yellowish andesitic tuff breccia and lapilli tuff which are partially interbedded with scoriaceous sandstone, pyroclastic siltstone and thin layers of pumic and conglomeratic sandstone. Cross-laminations are well developed in this formation and serve to distinguish it from the underlying Aburatsubo Formation. The overlying Miyata

Formation (Pleistocene) consists mainly of loose sandstone.

The Hatsuse Formation shows a strike trending generally from N 60°W to EW with the exception of the Nagahama and Arasaki areas where it trends from N 30°E to N60°E. Also, marked folds and faults which trend in a northwest-to-southeast direction are developed in this formation.

There are three major synclines in Mito, Nagahama and Kaneda and two anticlines in Kurosaki-no-Hana and Kami-Miyada. Their axes cross the line of strike of the Hatsuse Formation (Figure 1). The Minami-Shitaura and Hikihashi faults are reverse faults thrusting up from southwest to northeast and can be observed in several places. The Hikihashi Fault, one of the thrust faults, is the boundary between the Hatsuse and Aburatsubo Formations.

The maximum thickness of the Hatsuse Formation is estimated to be about 460 m by Akamine *et al.* (1956).

Fossil localities and fossil occurrences

Molluscan fossils were collected from two localities near the Wakamiya Shrine, Kanda, Hatsuse-machi, Miura City. One (Loc. A) is a small exposure on the east side of the Public Hall of Kanda region, Miura City and other one (Loc. B) is a small cutting exposed on the mountain foot about 250 m south of the shrine, and about 450 m northeast of Loc. A (Figure 1). Both fossil localities can be regarded as of equivalent stratigraphic position.

Loc. A: Molluscan fossils occurred from a massive, conglomeratic tuffaceous sandstone. Most of the molluscs are sporadically scattered, and are mostly inner or outer molds, except for the following species; *Glycymeris rotunda* (Dunker), *Chlamys miurensis* (Yokoyama), *Miyagipecten matsumoriensis* Masuda, and *Amussiopecten akiyamae* Masuda.

The dominant species at Loc. A include

Glycymeris rotunda, *Chlamys miurensis*, *Amusiopecten akiyamae*, *Miyagipecten matsumoriensis*, *Laevicardium* sp., and *Clinocardium* sp.

Loc. B: Molluscan fossils occurred from a pyroclastic, conglomeratic sandstone. Fossils are sporadically scattered as in Loc. A, but are more dense in this locality than in Loc. A. The dominant species from this locality are as follows; *Glycymeris rotunda*, *Indocrassatella* cf. *tenuilirata* (Shuto), *Laevicardium angustum* (Yokoyama), *Oxyperas bernardi* (Pilsbry), and *Anisocorbula* cf. *venusta* (Gould).

The molluscan fossils from both localities are poorly preserved; even such thick-shelled molluscs as *Cypraea*, *Clinocardium* and *Anisocorbula* are represented by water-worn fragments or incomplete specimens, though a few species are rather well preserved.

Characteristics of the Hatsuse Fauna

The molluscan fossils discriminated from the Hatsuse Formation include three species of Gastropoda, one species of Scaphopoda and 15 species of Bivalvia. Among them, two species of Gastropoda, one species of Scaphopoda, and 11 species of Bivalvia are identified specifically. One species of Bivalvia is discriminated as a new species (Table 1).

From a bathymetrical viewpoint, most of the fossil molluscan species from Loc. A are considered to be shallow-water dwellers in fine-grained sandy or silty bottoms because of the presence of such genera as *Cypraea* and *Azorinus* whose present-day distribution ranges from the intertidal zone to 50 m depth. However, other of the molluscs could possibly live in deeper waters down to about 300 m. The molluscan fossils from Loc. B are also represented by rather shallow-water inhabitants in fine-grained sandy or silty bottoms except for *Mikadotrochus* and *Crepidula*.

The former genus dwells on deep-water

rocky or gravelly bottoms at depths ranging from about 50 to 200 m (Habe and Kosuge, 1967), whereas the latter inhabits rocky or shelly bottom from littoral depths to 180 m (Keen, 1963). Another rather deep-water dweller is *Fissidentalium* found at Loc. B and this species presently lives from about 50 to 200 m depth (Habe and Kosuge, 1967).

In terms of faunal similarities between the A and B localities, only a few species are common to both, namely *Glycymeris rotunda*, *Chlamys miurensis*, *Amusiopecten akiyamae* and *Azorinus abbreviatus*. Other than these four, the two localities are characterized by different molluscs.

Judging from the foregoing, it is clear that the present molluscan association represents a mixture of shallow and rather deep-water dwellers, and of rocky- or shelly-bottom dwellers and sandy- or muddy-bottom dwellers. These species are considered to have been transported for some distance from the initial living site in shallow to deep waters.

Most of the species constituting the present molluscan association are shallow, warm-water dwellers with the exception of a few deep-water dwellers. The three extant species among the fauna, namely *Glycymeris rotunda*, *Oxyperas bernardi*, and *Azorinus abbreviatus*, are known to be distributed in the warm Kuroshio Current region and in temperate waters off the coast of southern to central Japan (south of latitude 35°N, namely south of the Boso Peninsula).

Geological age and correlation

Some species of the Hatsuse Fauna are restricted to strata of Miocene age. *Miyagipecten matsumoriensis* has been reported from middle to late Miocene strata distributed in areas north of the Kanto region. *Amusiopecten akiyamae* has been reported from late Miocene formations in Inagozawa and Zushi (Masuda, 1962) and also in Senhata (O'Hara and Ito, 1980; described as *A.*

Table 1. Geologic distributions of the molluscan fossils from the Hatsuse Formation.

Species	Geologic range and localities			Miocene			Plio.	Pleist.	Recent	Local.	
	E	M	L	A	B						
1 <i>Mikadotrochus</i> cf. <i>yoshiwarai</i>		h									+
2 <i>Crepidula</i> cf. <i>nidatoriensis</i>		h									+
3 <i>Cypraea</i> sp.		h								+	
4 <i>Fissidentalium</i> cf. <i>yokoyamai</i>		h									+
5 <i>Glycymeris</i> <i>rotunda</i>										+	+
6 <i>Chlamys</i> <i>miurensis</i>										+	+
7 <i>Amusiopecten</i> <i>akiyamae</i>										+	+
8 <i>Miyagipecten</i> <i>matsumoriensis</i>											+
9 <i>Indocrassatella</i> cf. <i>tenuilirata</i>		h									+
10 <i>Laevicardium</i> <i>angustum</i>											+
11 <i>L.</i> sp.		h								+	
12 <i>Clinocardium</i> cf. <i>hataii</i>		h								+	
13 <i>C. hatsusense</i> , n. sp.		h								+	
14 <i>C.</i> sp.		h									+
15 <i>Pitar</i> <i>kaniei</i>										+	
16 <i>Oxyperas</i> <i>bernardi</i>											+
17 <i>Azorinus</i> <i>abbreviatus</i>										+	+
18 <i>Anisocorbura</i> cf. <i>venusta</i>		h									+
19 <i>A.</i> sp.		h									+

Abbreviation Plio.: Pliocene, Pleist.: Pleistocene, E: Early, M: Middle, L: Late, Local.: Fossil localities, h: Known only from the Hatsuse Formation.

praesignis). To the best of the present authors' knowledge, this species seems to have a restricted stratigraphic range from the latest middle Miocene to late Miocene. *Chlamys miurensis* was originally described by Yokoyama (1920) from the basal part of the Zushi Formation in Zushi City. Subsequently, Shikama (1973) reported it from the basal part of the Zushi, O'Hara and Ito (1980) from the Late Miocene Senhata Formation of the Boso Peninsula, Ozaki (1954) from the basal conglomerate of the "Tyosi" Pliocene in Choshi City, and Kamada and Hayasaka (1959) from the Pliocene of Futaba-Tomioka area in Fukushima Prefecture. *Mikadotrochus yoshiwarai* was originally described from the "Tyosi" Pliocene by Ozaki (1954). It was also recorded from the late Miocene

Zushi Formation (Shikama, 1973) and the Senhata Formation (O'Hara and Ito, 1980).

From these data, the molluscan fauna from the Hatsuse is correlated with the Zushi Fauna (Shikama, 1973) in the Miura Peninsula and with the Senhata Fauna (O'Hara and Ito, 1980) in the Boso Peninsula.

This correlation is supported by the geologic ranges of the respective constituent species of the Hatsuse Fauna (Table 1). Moreover, this correlation agrees well with that proposed by Mitsunashi and Yazaki (1968) and Mitsunashi *et al.* (1979), who based their correlation on the tephra distribution in the southern Kanto region including the Boso and Miura Peninsulas. According to their result, the typical HK and OK key tephra beds are recognized in the Hatsuse and

Senhata Formations in the Miura and Boso Peninsulas (Omori *et al.*, 1986).

Systematic description

Family Pleurotomariidae

Genus *Mikadotrochus* Lindoholm, 1927

Mikadotrochus cf. *yoshiwarai* (Ozaki, 1954)

Figure 2-1a, b

Compared with.—

Pleurotomaria yoshiwarai Ozaki, 1954, p. 9-10, pls. 1-2.

Mikadotrochus yoshiwarai (Ozaki). Shikama, 1973, p. 92, pl. 16, figs. 3-4; O'Hara and Ito, 1980, p. 138-139, pl. 7, figs. 1a-c.

Remarks.—The specimen at hand is incomplete. The characteristic features of the present species are as follows; shell rather thin, depressed trochiform with more than six whorls; each whorl slightly convex; surface of whorls ornamented with many spiral threads bearing granules which are formed by their intersection of growth lines.

The original description of the species by Ozaki (1954) states "surface with fine, smooth, revolving striae crossed by growth lines." However, the Hatsuse specimen differs slightly from the type specimen in its whorl sculpture. The difference between these two specimens is possibly due to their state of preservation; actually, the type specimen appears to be an abraded shell. A narrow and obscure slit band revolves at a position somewhat anterior to the middle of the whorl. In other words, five spiral striae above (posterior of) the slit and three spirals beneath the slit are counted on the fifth whorl. Base and umbilical portions are missing.

The present species is closely related to *Mikadotrochus yoshiwarai* (Ozaki, 1954) described from the Neogene of the Choshi (Tyosi) district, Chiba Prefecture, but the incomplete, small, immature specimen under discussion does not permit more precise comparison with the species.

M. yoshiwarai has been reported from the

basal part of the Zushi Formation (late Miocene) of the Miura Peninsula (Shikama, 1973) and the Senhata Formation (late Miocene) of the Boso Peninsula (O'Hara and Ito, 1980), besides the type locality in Choshi City (probably from the basal part of the Naarai Formation, late Pliocene).

Registration number.—NUH [Naruto University palaeontological collections from the Hatsuse Formation] 87001.

Family Crepidulidae

Genus *Crepidula* Lamarck, 1799

Crepidula cf. *nidatoriensis* Otuka, 1934

Figure 2-5a, b, c

Compared with.—

Crepidula nidatoriensis Otuka, 1934, p. 626, pl. 48, figs. 63a-b.

Shell medium for the genus, semi-ovate in outline, with two whorls; apex strongly turned posteriorly and nearly touching body whorl; surface almost smooth except for fine radial lines running from central part of dorsal area to aperture. Length 21 mm, height 16 mm, width 20 mm, minimum diameter of aperture 16 mm.

Remarks.—The single specimen in hand is somewhat abraded. The present specimen is close to *C. nidatoriensis* Otuka, 1934, reported from the Kadonosawa Miocene, but the present species is distinct by having a more conspicuous apex, which more strongly curves posteriorly than that of the latter, and the fine radial lines running from the central part of the dorsal area to the aperture and crossing it at a right angle. *C. nidatoriensis sogai* Kamada, 1962, reported from the Numanouchi and Kokozura Miocene in the Joban district is similar to the present specimen, but the strongly curved apex and fine radial lines on the dorsal part in *Crepidula* cf. *nidatoriensis* serve to distinguish it from Kamada's subspecies. This specimen possibly represents a new form, but is insufficient to permit the establishment of a new species.

Registration number.—NUH 87002.

Family Cypraeidae
Genus *Cypraea* Linnaeus, 1758
Cypraea sp.

Figure 2-4a, b, c

Remarks.—More or less depressed incomplete specimens are at hand. These specimens are characterized by having no visible spire, body whorl covered completely by callus, and narrow aperture with denticulated outer lip. *Cypraea* is usually distributed in warm temperate to tropical regions.

Registration number.—NUH 87003.

Family Dentaliidae
Genus *Fissidentalium* Fischer, 1885
Subgenus *Fissidentalium* s.s.
Fissidentalium (*Fissidentalium*) cf. *yokoyamai* (Makiyama, 1931)

Figure 2-9

Compared with.—

Dentalium (*Fissidentalium*) *yokoyamai* Makiyama, 1931, p. 44, pl. 1, fig. 1.

Shell slender with elongate tube, gradually attenuating toward apex; slightly curved dorsally; shell very thin with large numbers of flat-topped, slightly elevated longitudinal riblets crossed by fine growth lines; longitudinal ribs bifurcated, separated by interspaces which are wider than the ribs. Longest specimen at hand; 40 mm in length, diameter of aperture 7 mm, and 3 mm at apex.

Remarks.—The present species is closely allied to Makiyama's species described from the Kakegawa Pliocene, Shizuoka Prefecture, and *D. (F.) watanabei* Kanno from the Chichibu Basin, Saitama Prefecture, but the present specimens differ from the latter two by having numerous and fine longitudinal riblets on the external surface. However, the few rather abraded specimens at hand do not permit the establishment of a new species.

Registration number.—NUH 87004.

Family Glycymeriidae
Genus *Glycymeris* da Costa, 1778
Subgenus *Glycymeris* s.s.
Glycymeris (*Glycymeris*) *rotunda*
(Dunker, 1882)

Figure 2-2a, b

Glycymeris rotunda (Dunker). Makiyama, 1927, p. 29, pl. 1, figs. 1-4; Makiyama, 1952, p. 131-138; Hayasaka, 1962, pl. 45, figs. 8a-9b; Habe and Kosuge, 1967, p. 126, pl. 46, fig. 15; Kuroda, Habe and Oyama, 1971, p. 532, pl. 71, fig. 6; Matsukura 1986, p. 89, pl. 6, figs. 14, 15; Okumura, 1988, p. 39, pl. 12, fig. 1.
Pectunculus yamakawai Yokoyama, 1922, p. 190, pl. 16, figs. 4, 5.

Remarks.—The present species is represented by the following characteristics: 1) thick and solid, obliquely suborbicular shell, medium in size, more or less inflated shell; 2) beak pointing slightly forwards; 3) ligamental area narrow, triangular with subequilateral chevron grooves; 4) about ten strong teeth arranged obliquely in anterior and posterior sides; 5) surface sculptured by numerous low radial ribs, and inner margin with about 40 crenations.

Several well preserved articulated as well as nonarticulated valves were collected. This species occurs rather frequently at both localities A and B.

Geographic distribution.—N. lat. 31° to 42° (Kuroda and Habe, 1952). This species lives in fine-grained sandy bottoms in a depth range of 30-300 m.

Geologic range.—Late Miocene to Recent.
Registration number.—NUH 87005.

Family Pectinidae
Subfamily Chlamydinæ
Genus *Chlamys* Röding, 1798
Chlamys miurensis (Yokoyama, 1920)

Figure 2-8, 10, 11

Pecten miurensis Yokoyama, 1920, p. 157-158, pl. 12, figs. 2-6.

Chlamys miurensis (Yokoyama). Ozaki, 1954, p. 15, pl. 9, figs. 1-2; Kamada and Hayasaka, 1959, p.

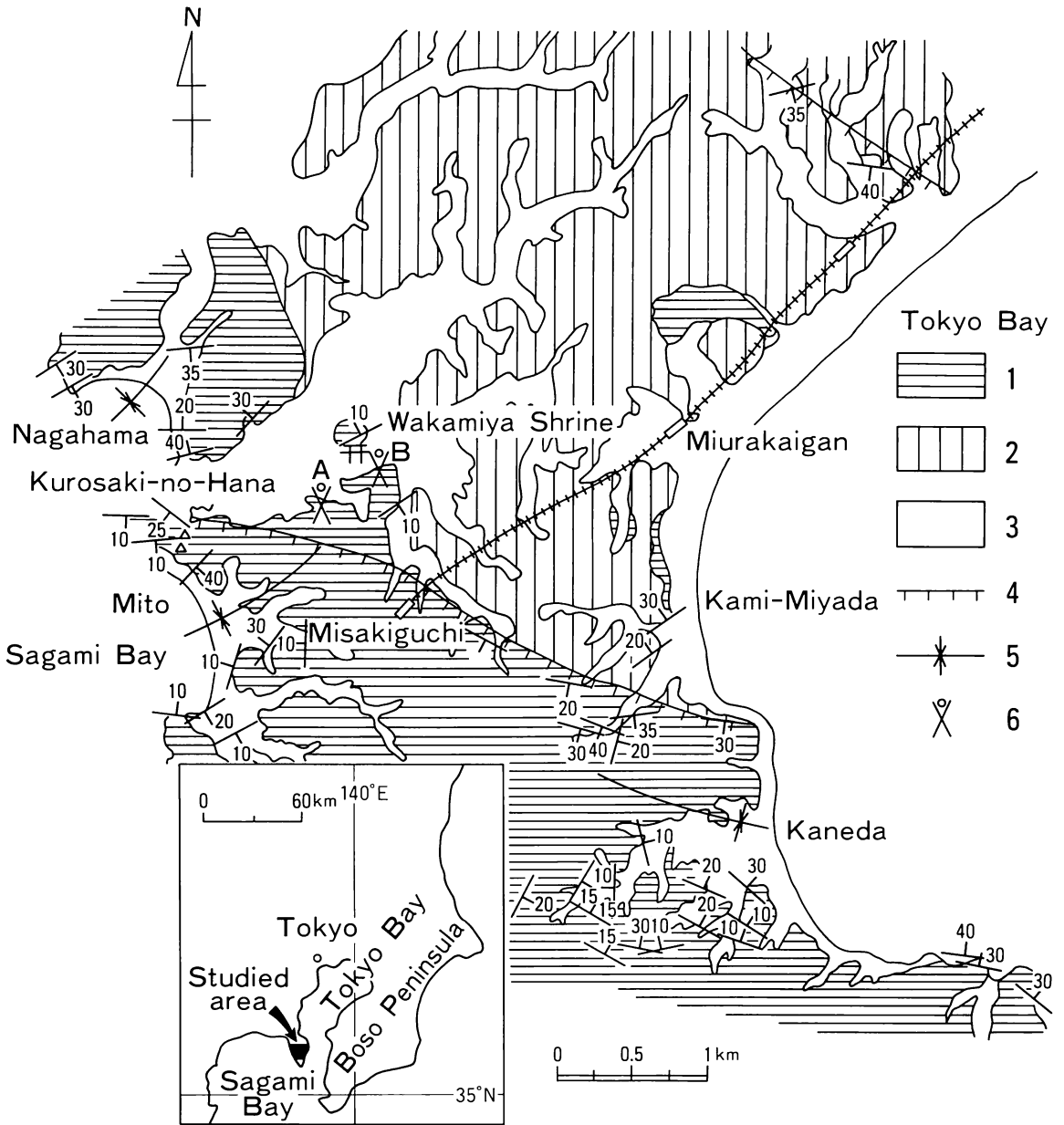
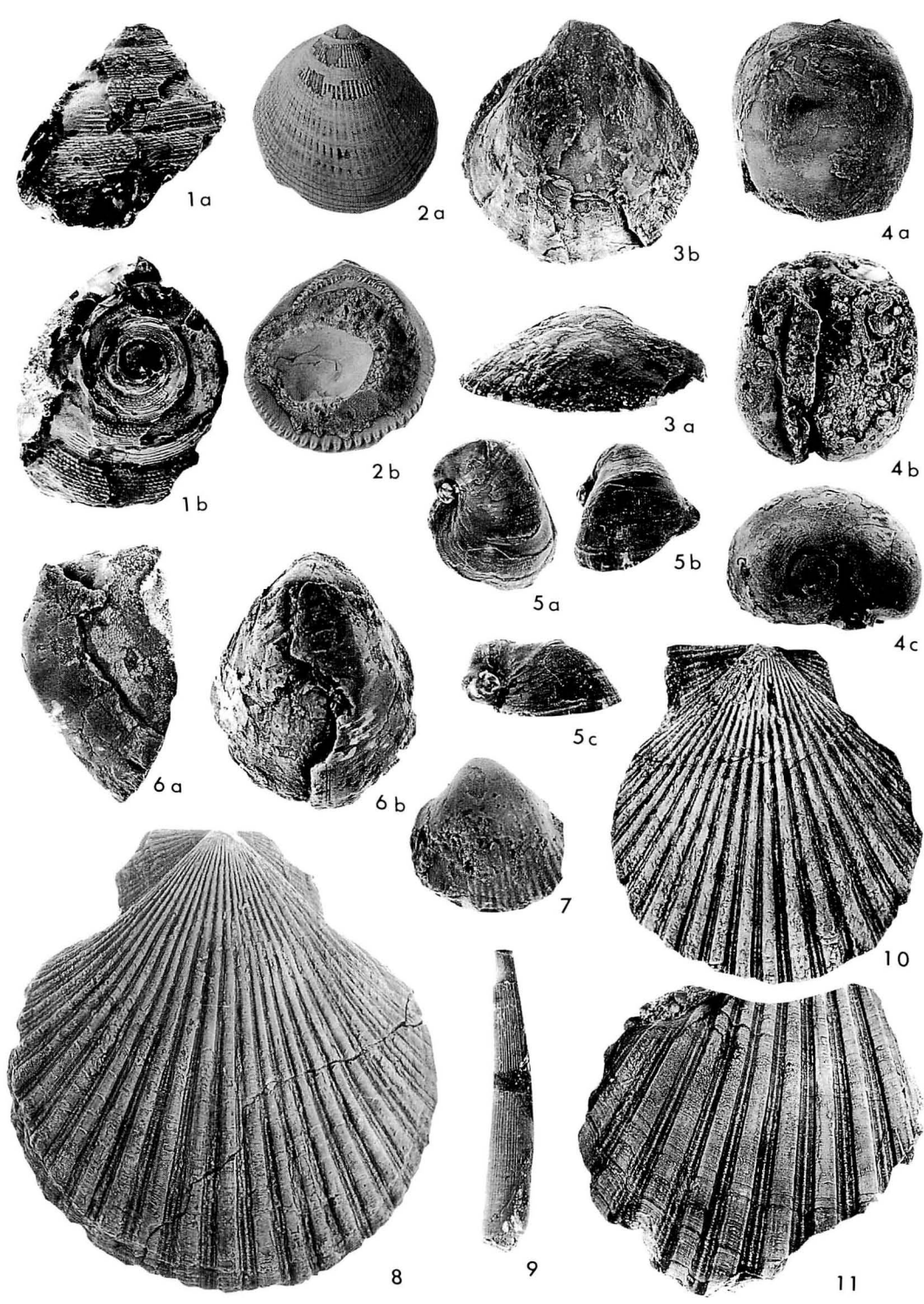


Figure 1. Fossil localities in the Miura Peninsula

1: Hatsuse Formation (Miocene) 2: Miyata Formation (Pleistocene) 3: Alluvium deposits 4: Fault
 5: Syncline 6: Fossil locality



21, pl. 2, fig. 2; Masuda, 1962, p. 177, pl. 23, fig. 1; Shikama, 1973, p. 166, pl. 17, fig. 4; O'Hara and Ito, 1980, pl. 16, fig. 2.

Remarks.—This species was originally described by Yokoyama (1920) from the Tagogegawa Conglomerate Member (the basal conglomerate of the Zushi Formation) distributed in the northern part of the Miura Peninsula. This species is characterized by having 22–25 rather compressed radial ribs on the surface which bear several riblets on the respective radials; the radial ribs appear to be flush with the surface owing to abrasion, but there are some scaly riblets as seen in the ventral margin illustrated in Figures 2–9, 10, 11.

Two or three intercalary riblets bearing distinct scales appear in the interspaces of the radial ribs. This species closely resembles *Chlamys kaneharai* which has a wide distribution essentially in middle Miocene strata in the Kanto region, but *C. miurensis* is distinguished by having several riblets on each radial ribs, whereas only three riblets are developed on each radial of *C. kaneharai*. Moreover, among the three radial riblets of *C. kaneharai*, the central one is most conspicuous. In addition, this species possesses two or three intercalary riblets in the interspaces of the radials, whereas *C. kaneharai* is provided with only one scaly riblet between adjacent radial ribs.

Geographic distribution.—Pacific coast, south of Fukushima Prefecture to Shizuoka Prefecture.

Geologic range.—Late Miocene to late Pliocene.

Registration number.—NUH 87006, 87007,

87008.

Subfamily Pectininae

Genus *Amussiopecten* Sacco, 1897

Amussiopecten akiyamae Masuda, 1962

Figure 3–4a, b

Amussiopecten planicostulatus (Nomura and Niino). Akiyama, 1957 (non Nomura and Niino, 1932), p. 32, pl. 7, figs. 2–4.

Amussiopecten akiyamae Masuda, 1962, p. 224, pl. 27, figs. 1–3; Masuda, 1986, pl. 2, fig. 4.

Amussiopecten iitomiensis (Otuka). Shikama, 1973, pl. 17, fig. 6.

Amussiopecten praesignis (Yokoyama). O'Hara and Ito, 1980, p. 131–132, pl. 14, figs. 5–7; pl. 15, figs. 1–5.

Remarks.—This species was originally described by Masuda (1962) based on specimens collected from the Inagozawa Formation in Chiba Prefecture. *Amussiopecten planicostulatus* described by Akiyama (1957) based on specimens collected from the Zushi Formation is also included in the present species. *A. iitomiensis* (Otuka) can be distinguished from the present species by having fewer but more prominent radial ribs than those of the present species and no intercalary threads between the radials. *A. praesignis* (Yokoyama) also differs from the present species by having squarish, rather high, flat-topped radial ribs on the right valve and rather broad and roof-shaped radials on the left valve.

Geographic distribution.—This species have been reported only from the southern Kanto region, the Boso and Miura Peninsulas.

Geologic range.—Late Miocene.

Registration number.—NUH 87009.

Genus *Miyagipecten* Masuda, 1952

← **Figure 2.** Molluscan fossils from the Hatsuse Formation (1). **1a–b.** *Mikadotrochus* cf. *yoshiwarai* Ozaki, ×1.2, Loc. B, Reg. No. NUH 87001. **2a–b.** *Glycymeris* (*Glycymeris*) *rotunda* (Dunker), ×1.1, Loc. A, Reg. No. NUH 87005. **3a–b.** *Clinocardium* cf. *hataii* Hayasaka, ×1.1, Loc. A, Reg. No. NUH 87015. **4a–c.** *Cypraea* sp., ×1.3, Loc. A, Reg. No. NUH 87003. **5a–c.** *Crepidula* cf. *nidatoriensis* Otuta, ×1.2, Loc. B, Reg. No. NUH 78002. **6a–b.** *Laevicardium* sp., ×0.8, Loc. A, Reg. No. NUH 87014. **7.** *Clinocardium* sp., ×1.1, Loc. A, Reg. No. NUH 87017. **8, 10, 11.** *Chlamys miurensis* (Yokoyama), ×0.6, 8: Loc. A, Reg. No. NUH 87006, 10: Loc. B, Reg. No. NUH 87007, 11: Loc. A, Reg. No. NUH 87006. **9.** *Fissidentalium* (s. s.) cf. *yokoyamai* Makiyama, ×1.1, Loc. B, Reg. No. NUH 87004.

Miyagipecten matsumoriensis Masuda, 1952

Figure 3-6

Miyagipecten matsumoriensis Masuda, 1952, p. 252, pl. 24, figs. 4a-7b; Masuda, 1957, p. 31, pl. 4, figs. 1a-4; Masuda, 1962, p. 226, pl. 27, fig. 13; Masuda, 1977, p. 5-6, pl. 1, figs. 1-4; Masuda, 1986A, pl. 2, fig. 1; Masuda, 1986B, pl. 8, fig. 9; Masuda and Noda, 1977, pl. 2, fig. 6; Masuda and Takegawa, 1965, pl. 1, fig. 11; O'Hara and Ito, 1980, pl. 16, figs. 1a-c.

Remarks.—Only one left valve is at hand. This species is characterized by having a large, circular outline and low convex thin shell. The shell surface is nearly smooth except for fine, concentric growth lines and radial striations on the umbonal area. The inner surface is smooth without inner riblets. The anterior auricle of left valve is rather small. *Miyagipecten matsumoriensis* is known from Middle and Upper Miocene strata in Northeast Honshu (Masuda, 1952, 1957, 1977; Masuda and Noda, 1977; Masuda and Takegawa, 1965; Iwasaki, 1970) and the Boso Peninsula (O'Hara and Ito, 1980).

The genus *Miyagipecten* has been reported from the lower part of the Yakataga Formation of southern Alaska by Kanno (1971).

Geographic distribution.—Northeast Honshu and Kanto region.

Geologic range.—Middle to Late Miocene.

Registration number.—NUH 87010.

Family Crassatellidae

Genus *Indocrassatella* Chavan, 1952*Indocrassatella* cf. *tenuilirata* (Shuto, 1957)

Figure 3-5, 12

Compared with.—

Crassatellites tenuiliratum Shuto, 1957, p. 72-73, pl. 22, figs. 6-8, 12; O'Hara and Ito, 1980, pl. 16, fig. 5.

Remarks.—Two abraded specimens are at hand. This species is characterized by having a subtrapezoidal, moderately inflated thin shell with regularly rounded concentric ribs.

The anterior shell margin is rounded and the posterior one truncated. The species somewhat resembles *Crassatella pauxilla* (Yokoyama, 1925; Kanno, 1960; Kanno and Chung, 1973), but it differs from the latter by having a more inflated large shell. However, a more precise comparison between these allied species is prevented due to the poor condition of the material.

Registration number.—NUH 87011, 87012.

Family Cardiidae

Genus *Laevicardium* Swainson, 1840*Laevicardium angustum* (Yokoyama, 1925)

Figure 3-3a, b

Cardium angustum Yokoyama, 1925, p. 12, pl. 4, figs. 2a-b.

Cardium (Laevicardium) angustum Yokoyama. Kuroda, 1931, p. 53, pl. 5, fig. 10.

Laevicardium angustum Yokoyama. Kanno, 1960, p. 259, pl. 39, figs. 14a-b.

Remarks.—An internal mold is in the collection. This species is characterized by having an extremely high shell compared with its length (1.5 times the length), a strongly convex and longitudinally ovate outline, subequilaterally concave anterodorsal margin, strongly convex posterodorsal margin, and prominent umbo.

Geographic distribution.—Shigarami Formation in Nagano Prefecture, Hatsuse Formation in Kanagawa Prefecture, and Chichibu Basin in Saitama Prefecture.

Geologic range.—Early Miocene to Early Pliocene.

Registration number.—NUH 87013.

Laevicardium sp.

Figure 2-6a, b

Remarks.—An incomplete left valve is at hand. This unnamed species has a strongly abraded shell from the central disk to the ventral border, and lacks shell material from the umbonal area as shown in Figure 2-6a. The characteristic features of this species are

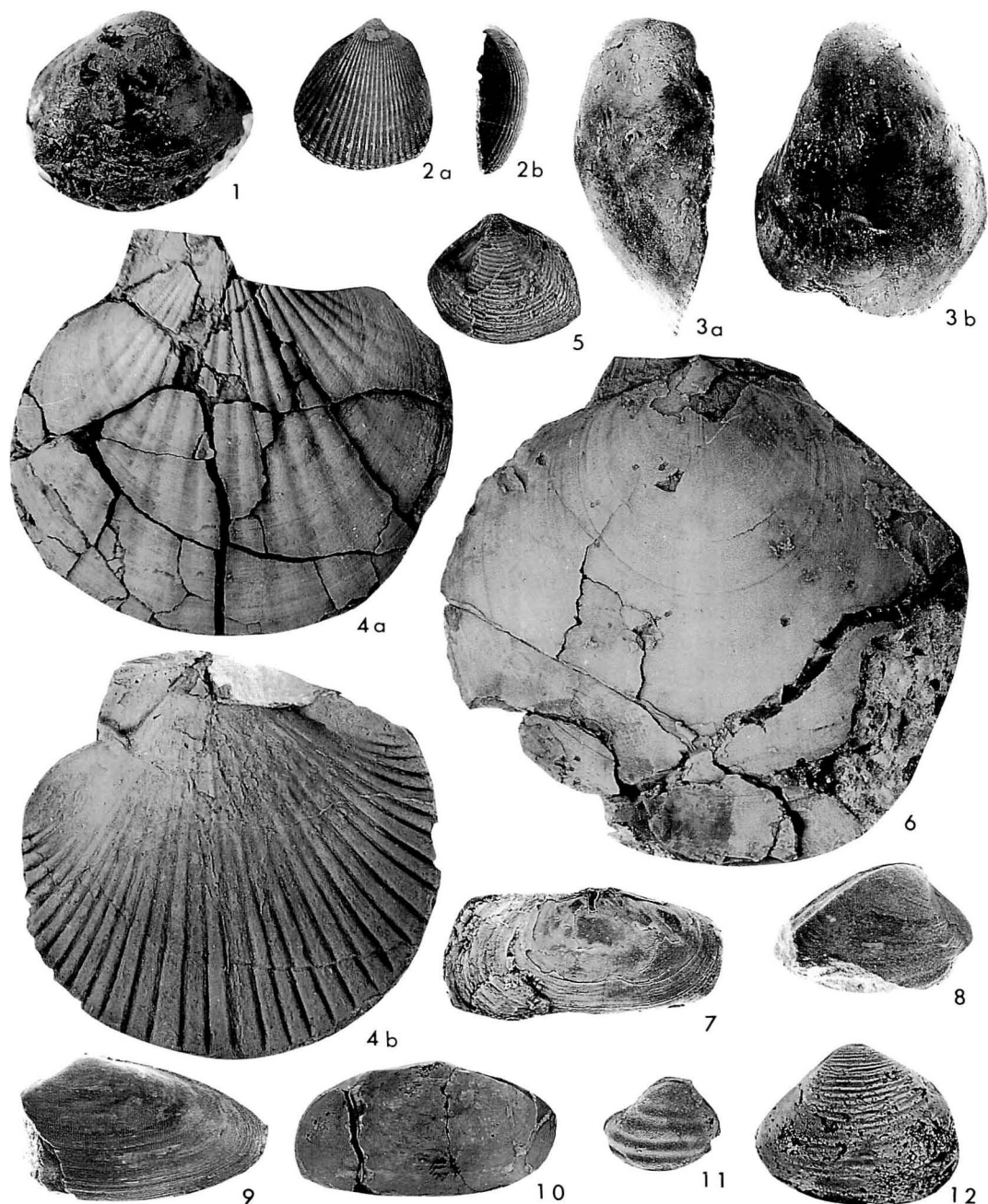


Figure 3. Molluscan fossils from the Hatsuse Formation (2). **1.** *Pitar kaniei* Shikama, $\times 1.1$, Loc. A, Reg. No. NUH 87019. **2.** *Clinocardium hatsusense* n. sp., $\times 1.5$, Loc. A, Reg. No. NUH 87016. **3a-b.** *Laevicardium angustum* (Yokoyama), $\times 1.1$, Loc. B, Reg. No. NUH 87013. **4a-b.** *Amusiopecten akiyamae* Masuda, $\times 0.5$, Loc. A, Reg. No. NUH 87009. **5, 12.** *Indocrassatella* cf. *tenuiliata* (Shuto), $\times 1.1$, 5: Loc. A, Reg. No. NUH 87012, 12: Loc. A, Reg. No. NUH 87011. **6.** *Miyagipecten matsumoriensis* Masuda, $\times 0.7$, Loc. B, Reg. No. NUH 87010. **7, 10.** *Azorinus abbreviatus* (Gould), $\times 1$, 7: Loc. B, Reg. No. NUH 87021, 10: Loc. A, Reg. No. NUH 87022. **8.** *Anisocorbula* cf. *venusta* (Gould), $\times 1.7$, Loc. B, Reg. No. NUH 87023. **9.** *Oxyperas bernardi* (Pilsbry), $\times 1$, Loc. A, Reg. No. NUH 87020. **11.** *Anisocorbula* sp., $\times 1.3$, Loc. B, Reg. No. NUH 87024.

its medium size and inflated-ovate and rather thick shell. Hinge apparatus is missing.

Registration number.—NUH 87014.

Genus *Clinocardium* Keen, 1936
Clinocardium cf. *hataii* Hayasaka, 1956

Figure 2-3a, b

Compared with.—

Clinocardium hataii Hayasaka, 1956, p. 18, pl. 2, figs. 3a-b.

Remarks.—The present species was originally described by Hayasaka (1956) from the Pliocene of the Futaba district, Fukushima Prefecture. The characteristic features of this species include: shell medium in size, equilateral, suborbicular and moderately inflated with conspicuous beak; anterodorsal margin rounded, merging with rounded ventral border; posterior and posterodorsal margins broadly rounded; surface sculptured with more than 20 strong radial ribs, but an accurate determination of the number of radials is difficult to obtain because of their poor state of preservation; hinge unknown.

This species somewhat resembles *L. shiobarense* described from the Kanomatazawa Miocene of Tochigi Prefecture, but the lesser number of strong radials in the present species serve to distinguish it from *L. shiobarense*.

Registration number.—NUH 87015.

Clinocardium hatsusense, n. sp.

Figure 3-2a, b

Description.—Shell small for the genus, rather flattened, thin, quadrilateral shape; posterodorsal margin nearly straight meeting with narrowly rounded posteroventral border; ventral margin broadly and regularly arched, ascending to anterior margin; anterodorsal margin short, making a rather distinct corner with anterior margin; umbo prominent; apical angle about 105°; surface ornamented with about 50 flat-topped and

squarish radial ribs, separated by interspaces which are narrower than breadth of radial ribs; hinge inaccessible; inner margin crenulated corresponding to external radial ribs.

Measurements (in mm.).—

Specimens	Length	Height	Thickness	Valve	Type
NUH 87016	14.0	10.5	3.7	right	Holotype
NUH 870171	13.0	10.0	3.0	right	Paratype
NUH 870172	11.0	8.0	2.5	right	"
NUH 870173	10.0	7.5	2.5	left	"

Remark.—This new species is characterized by its quadrilateral shape, which serves to distinguish it from other allied species.

Registration number.—NUH 87016 (Holotype); 870171, 870172, 870173 (Paratype).

Clinocardium sp.

Figure 2-7

Remarks.—An inner mold is at hand. This specimen is medium-sized, its width as long as high, moderately convex, and equilateral with prominent umbo. The surface is ornamented with many radial ribs, how many is uncertain owing to the inadequate state of preservation.

Registration number.—NUH 87018.

Family Veneridae

Genus *Pitar* Römer, 1857

Pitar kaniei Shikama, 1973

Figure 3-1

Pitar kaniei Shikama, 1973, p. 201, pl. 17, figs. 12-13.

Remarks.—The present species was originally described by Shikama (1973) from the late Miocene Zushi Formation of the Miura Peninsula. The following characters of the present species correspond well with Shikama's species; shell medium in size and moderately inflated; beak prominent and turned forward; ventral margin broadly arched; posteroventral corner slightly angulated, anterior margin narrowly rounded;

length about 28 mm., and thickness about 6.5–7.0 mm.

Geographic distribution.—Miura Peninsula, Kanagawa Prefecture.

Geologic range.—Late Miocene.

Registration number.—NUH 87019.

Family Mactridae

Genus *Oxyperas* Mörch, 1853

Oxyperas bernardi (Pilsbry, 1904)

Figure 3-9

Oxyperas bernardi (Pilsbry). Kuroda, Habe and Oyama, 1971, p. 670, pl. 95, figs. 1-2; Matsuura 1977 pl. 9, fig. 19; O'Hara and Ito, 1980, pl. 16, fig. 6.

Oxyperas aff. *bernardi* (Pilsbry). Hayasaka, 1973, pl. 6, fig. 4.

Remarks.—An incomplete, strongly abraded right valve missing the anterior quarter of the shell is at hand.

Geographic distribution of living species: South of the Boso Peninsula (about N. lat. 35°) to N. lat. 25° (Kuroda and Habe, 1952), and living from littoral depths to 100 m (Kuroda, Habe and Oyama).

Geologic range.—Late Miocene to Recent.

Registration number.—NUH 87020.

Family Solecurtidae

Genus *Azorinus* Récluz, 1869

Azorinus abbreviatus (Gould, 1861)

Figure 3-7, 10

Azorinus abbreviatus (Gould). Habe and Kosuge, 1967, p. 160, pl. 60, fig. 18; Hayasaka and Hashimoto, 1970, p. 20, pl. 1, figs. 10-11; Kuroda, Habe and Oyama, 1971, p. 681, pl. 99, fig. 5.

Remarks.—Two abraded specimens are at hand. The shell is thin, weakly swollen, and characterized by a slight depression running from the umbo to ventral margin. Living specimens of this species inhabit muddy bottoms in waters from 10 to 80 m deep, and are distributed south of the Boso Peninsula to the East China Sea, Southeast Asia and Indian Ocean.

Geologic range.—Late Miocene to Recent.

Registration number.—NUH 87021, 87022.

Family Corbulidae

Genus *Anisocorbula* Iredale, 1930

Anisocorbula cf. *venusta* (Gould, 1861)

Figure 3-8

Compared with.—

Anisocorbula venusta (Gould). Hayasaka, 1961, p. 63, pl. 5, figs. 7a-b; pl. 6, figs. 8a-b; Matsu-shima, 1969, pl. 11, fig. 14; Kuroda, Habe and Oyama, 1971, p. 707, pl. 102, fig. 15; Itoigawa (in Itoigawa, Shibata and Nishimoto, 1974), p. 103, pl. 32, figs. 7a-8b.

Remarks.—Two specimens are at hand. The present species is characterized by having a solid, slightly inflated, subtrigonal shell with a small, weakly pointed beak situated more or less anteriorly, and a blunt ridge running from the beak to posteroventral corner. The present species closely resembles *Anisocorbula venusta*, but these much abraded specimens do not permit definite identification with typical *A. venusta*.

Registration number.—NUH 87023.

Anisocorbula sp.

Figure 3-11

Remarks.—Two poorly preserved specimens are at hand. Shells are small in size, ovate-trigonal in shape with a blunt ridge running from beak to posteroventral corner. Concentric surface sculpture is slightly visible near the ventral margin. The hinge apparatus is inaccessible.

Various species of this genus are distributed in the west Pacific regions south of southern Hokkaido in littoral to inner neritic waters.

Registration number.—NUH 87022.

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三浦半島南部初声層産軟体動物化石群: 同層産軟体動物化石の19種を識別し, そのうち, 腹足綱3種, 掘足綱1種および斧綱15種(うち1新種を含む)の記載を行った。解析の結果, 構成種はすべて暖海生種であること, neritic 生息種と outer neritic 生息種の混合によってこの化石群が構成されていること, また, 特徴種からこの群集は中新世後期のものであることを明らかにした。

奥村 清・山岸 稔

933. INTRASPECIFIC VARIATION AND HETEROCHRONY
OF *PHANEROLEPIDA PSEUDOTRANSENSA* OZAKI
(GASTROPODA : TURBINIDAE) FROM THE
PLIOCENE NOBORI FORMATION, PACIFIC
SIDE OF SOUTHWESTERN JAPAN*

RYUICHI MAJIMA

Geological Institute, Yokohama National University, Yokohama, 240

and

AKIHIRO MURATA

Institute of Geosciences, Shizuoka University, Shizuoka, 422

Abstract. The recent discovery of 79 specimens of *Phanerolepida pseudotransenna* Ozaki from the Pliocene Nobori Formation indicates that the species shows a very wide range of individual variation in its surface ornamentation. This variation is interpreted to be caused by differences in timing of the onset of ornamental development among individuals in the population. An evolutionary lineage, *Nehalemia hieroglyphica* → *Phanerolepida oregonensis* → *P. pseudotransenna* → *P. transenna*, is established on the basis of their stratigraphic occurrences, and by comparison of ontogenetic developments of shell ornamentation. At least the first two speciation events are considered to be the results of heterochrony.

Phanerolepida rehderi MacNeil is designated as a junior synonym of *P. pseudotransenna*. Four opercula are reported and illustrated in association with their own shells, near to their life position.

Key words. *Phanerolepida*, intraspecific variation, heterochrony, Gastropoda, Pliocene, Nobori Formation, southwestern Japan.

Introduction

Phanerolepida is a very interesting genus from the malacological, conchological and paleontological viewpoints. Ecologically it is a homalopomatine, exceptionally living in the very deep sea, and morphologically it bears a peculiar rhombohedral network pattern of ornamentation. The evolution and migration of *Phanerolepida*, from its first appearance in the early Oligocene of western

North America (Hickman, 1972) to its later occurrences which have been restricted to the Japanese Neogene and Recent faunas, are of special interest.

In Japan, the following five species of *Phanerolepida* have previously been known :

Phanerolepida transenna (Watson, 1879), Pliocene (Otuka, 1949 ; Okutani, 1968)—Recent (Watson, 1879 and 1886 ; Dall, 1907 ; Okutani, 1964, 1966, 1968, 1969 ; Noda and Ogasawara, 1976) ;

P. expansilabrum Kuroda, 1931, Miocene (Kuroda, 1931 ; Watanabe *et al.*, 1950 ; Shibata, 1974 [as *P. cf. expansilabrum*] ;

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Noda and Kikuchi, 1980; Itoigawa *et al.*, 1981, 1982 [as *P. cf. expansilabrum*]);

P. pseudotransenna Ozaki, 1956, ? Miocene (Hatai and Masuda, 1962)—Pliocene (Ozaki, 1956; Noda and Ogasawara, 1976; Mimoto, 1986).

P. rehderi MacNeil, 1961, Pliocene (MacNeil, 1961; Noda and Ogasawara, 1976; Noda, 1980, 1988); and

P. okinawana Noda, 1988, Pliocene (Noda, 1988).

Their morphological comparison and taxonomic validity have not been well documented because some of them were proposed on the basis of poorly preserved material in which the type material of *P. pseudotransenna* is included. From summer of 1987 to April of 1990, we collected 79 specimens of *P. pseudotransenna*, including many that are well preserved. The aim of this study is to describe *P. pseudotransenna* in detail, to show the mode of individual ontogenetic variation, to explain the origin of this variation, and to evaluate the role of heterochrony in the evolution of the genus.

Abbreviations

The following abbreviations are used in this paper:

IGSU, Institute of Geosciences, Shizuoka University, Shizuoka, 422 Japan; and NSM, National Science Museum, Shinzuyuku, Tokyo, 169 Japan.

Collecting localities

Specimens of *Phanerolepida pseudotransenna* examined for this study were collected from the massive mudstone of the Pliocene Nobori Formation of the Tonohama Group, exposed in a quarry at Nobori, Hanemachi, Muroto City, Kochi Prefecture, on the Pacific side of southwestern Japan (Figure 1). Our three localities in the quarry from which the species was collected are as follows:

IGSU loc. no. 62-35-1: a cliff located in southern end of the quarry, consisting of massive, pale gray mudstone intercalated with lenticular molluscan shell beds about 10 cm in maximum thickness and over 6 m in maxi-

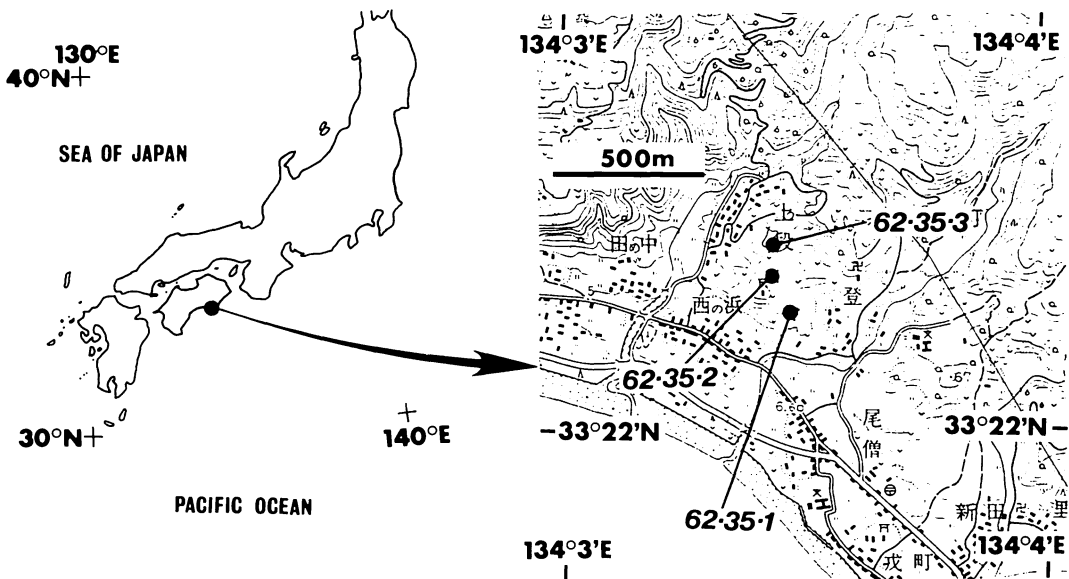


Figure 1. Index map showing the fossil localities of *Phanerolepida pseudotransenna* Ozaki from the upper Pliocene Nobori Formation. The fossil localities are plotted on a 1:25,000-scale topographic map of Japan, Quadrangle "Hane," Geographical Survey of Japan.

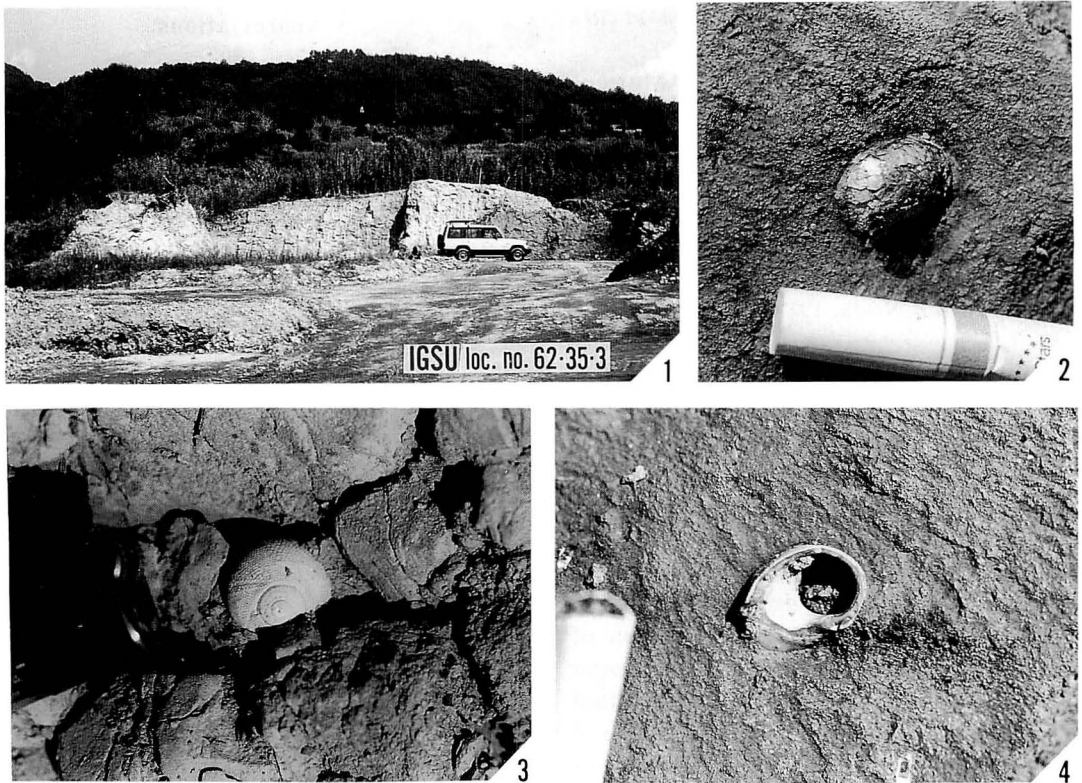


Figure 2. A view of the quarry cliff (1) and the mode of occurrence of *Phanerolepida pseudotransenna* Ozaki (2–4) at IGSU loc. no. 62-35-3.

mum width. The matrix of the lenticular shell beds is composed of mudstone.

IGSU loc. no. 62-35-2: a cliff, situated near the center of the quarry, consisting of massive, pale brownish gray, weakly weathered mudstone.

IGSU loc. no. 62-35-3: a large cliff (Figure 2-1) exposed in northern end of the quarry consisting of massive, pale gray mudstone.

Except for the lenticular shell beds at IGSU loc. no. 62-35-1, the molluscan fossils from these localities are considered to have been preserved *in situ*, because: (1) they occur sporadically in massive mudstone (Figure 2-2–4); (2) many bivalves are preserved in articulated condition; and (3) four specimens of *Phanerolepida pseudotransenna* bear opercula within their own apertures near to

their life position (Figure 8).

The massive mudstone of the three localities sporadically yields the following deep-water species: *Tenuileda ikebei* (Suzuki and Kanehara, 1936), *Portlandia* sp., *Limopsis tajimae* Sowerby, 1914, *L. chitanihana* Yokoyama, 1926, *Glycymeris nipponica* (Yokoyama, 1920), *Acesta goliath* (Sowerby, 1883), *Delectopecten peckhami* (Gabb, 1869), *Nemocardium* sp., *Cuspidaria hirasei* Kuroda, 1948, *Fissidentalium yokoyamai* (Makiyama, 1931), *Bathybembix aeola* (Watson, 1878), *Ginebis argenteonitens* (Lischke, 1872), *Phanerolepida pseudotransenna* Ozaki, 1956, *Aulacofusus cerulescens* Kuroda and Habe, 1966, *Neptunea noboriensis* Ozaki, 1956, *Turrancilla suavis* (Yokoyama, 1926), *Fulgoraria (Musashia) cancellata* Kuroda and Habe, 1950, *F. (Saotomea) delicata* (Fulton,

1940), and *Makiyamaia coreanica* (Adams and Reeve, 1849).

The lenticular shell beds at IGSU loc. no. 62-35-1 bear the species *Anadara* (*Tosarca*) *tosaensis* (Noda, 1965), *Glycymeris* cf. *yessoensis* (Sowerby, 1886), *Chlamys satoi* (Yokoyama, 1928), *Chlamys* sp., *Cryptopecten vesiculosus* (Dunker, 1877), *Amussiopecten praesignis* (Yokoyama, 1922), *Venericardia panda* (Yokoyama, 1926), *Dimya* sp., *Crasatellites* sp., *Paphia* sp., *Placamen tiara* (Dillwyn, 1817), *Dentalium* sp., *Umbonium* (*Suchium*) *suchiense* Yokoyama, 1923, *Phanerolepida pseudotransenna* Ozaki, 1956, *Turritella perterebra* Yokoyama, 1923, *Glossaulax*

hyugensis (Shuto, 1964), *G. hagenoshitensis* (Shuto, 1964), *Mammilla* sp., *Cryptonatica andoi* (Nomura, 1935), *C. adamsiana* (Dunker, 1859), *Babylonia elata* (Yokoyama, 1923), *Siphonalia tonohamaensis* Nomura, 1937, *S. yabei* Nomura, 1937, *Baryspira albocallosa* (Lischke, 1873), *Oliva mustellina* (Yokoyama, 1923), *Granulifusus dualis* (Yokoyama, 1928), *Conus* sp., *Orthosurcula pervirgo* (Yokoyama, 1928), *Spirotropis subdeclivis* (Yokoyama, 1926), and *Architectonica* sp. Because these molluscs are composed of both shallow and deep water species, they are considered to have been more or less reworked.

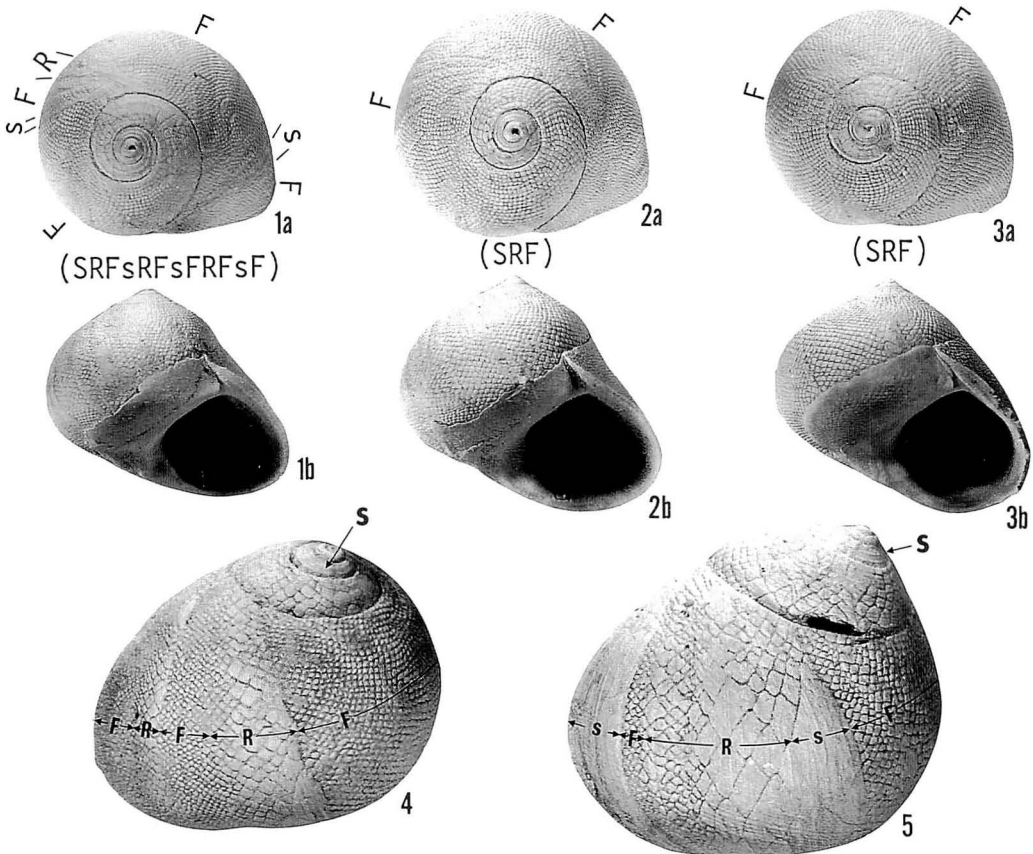


Figure 3. *Phanerolepida pseudotransenna* Ozaki. 1a–3b, IGSU loc. no. 62-35-1, $\times 1.7$: 1a–1b, IGSU M37; 2a–2b, IGSU M38; 3a–3b, IGSU M39. Letters around shell indicate successive ornament patterns on body whorl. 4, 5, IGSU loc. no. 62-35-3, $\times 2.6$: 4, IGSU M60; 5, IGSU M64. Arrows R, F, and S indicate the extent of the respective patterns on body whorl.

Table 1. Comparison for letter formula between Shinzato and Nobori specimens. See text for details.

SHINZATO FORMATION OKINAWA (NODA AND OGASAWARA, 1976) 43 SPECIMENS		NOBORI FORMATION (IGSU LOC. NO. 62-35-3) 25 SPECIMENS	
LETTER FORMULA	NUMBER OF SPECIMENS	LETTER FORMULA	NUMBER OF SPECIMENS
SRF	10	SRF	11
SRF _s F	5	SRF _s F	2
S _s F	1		
SRF _s	21	SRF _s	1
SR _s	2		
S _s F _s	1		
S _s	3	?S _s	1
		SR	1
		SRFRF	2
		SRF _s R _s	1
		SRFRFRF	1
		SRFRFRF _s	1
		SRFRFRFRF	1
		SRF _s RF _s RF	1
		SRF _s FRFRF	1
		SRFRFRF _s RF _s	1
(A)			
LETTER FORMULA		LETTER FORMULA	
SRF		SRF	
SRF(s)F→SRFRF		SRF(s)F→SRFRF	
S(s)F→SRF			
SRF(s)→SRFR		SRF(s)→SRFR	
SR(s)→SR			
S(s)F(s)→SRFR			
S(s)→SR		?S(s)→?SR	
		SR	
		SRFRF	
		SRF(s)R(s)→SRFR	
		SRFRFRF	
		SRFRFRF(s)→SRFRFRFR	
		SRFRFRFRF	
		SRF(s)RF(s)RF→SRFRFRF	
		SRF(s)FRFRF→SRFRFRFRF	
		SRFRFRF(s)RF(s)→SRFRFRFRFR	
(B)			
LETTER FORMULA	NUMBER OF SPECIMENS	LETTER FORMULA	NUMBERS OF SPECIMENS
SR	5	SR	(1+?1)
SRF	11	SRF	11
SRFR	22	SRFR	2
SRFRF	5	SRFRF	4
		SRFRFRF	2
		SRFRFRFR	1
		SRFRFRFRF	2
		SRFRFRFRFR	1
(C)			

Intraspecific variation of *Phanerolepida pseudotransenna* Ozaki

Ornamentation of the teleoconch of *Phanerolepida pseudotransenna* is divided into four patterns: three or four spiral cords on the smooth surface (**S** in abbreviation; Figure 3-4-5 [arrow S]), a roughly developed rhombohedral network (**R**; Figure 3-4-5 [arrow R]), a finely developed rhombohedral network (**F**; Figure 3-4-5 [arrow F]), and a smooth surface occasionally bearing very fine spiral striae (**s**; Figure 3-5 [arrow s]). The pattern boundaries are commonly sharply separated from each other, but the pattern **R**, when **R** immediately follows the pattern **S**, is sometimes superposed by weak spiral cords that continue from the spiral cords of the pattern **S** (Figure 3-1a) and the **R** is sometimes gradually changed into the **s** (see boundary between the **R** and **s** in Figure 3-5). In the following discussion, we use a letter formula for the description of the shell ornamentation for respective individuals. The above four abbreviations of the pattern are arranged ontogenetically. For example, when the teleoconch is sculptured from earlier to later with **S** → **R** → **F** → **s**, then we use the letter formula "SRFs."

Noda and Ogasawara (1976) showed the individual variety of the shell ornamentation of *Phanerolepida rehderi* MacNeil, 1961, here considered to be a junior synonym of *P. pseudotransenna* Ozaki, 1956, by using material from the upper Pliocene Shinzato Formation, Okinawa Prefecture, southern Japan. Noda and Ogasawara's (1976) work is summarized as follows.

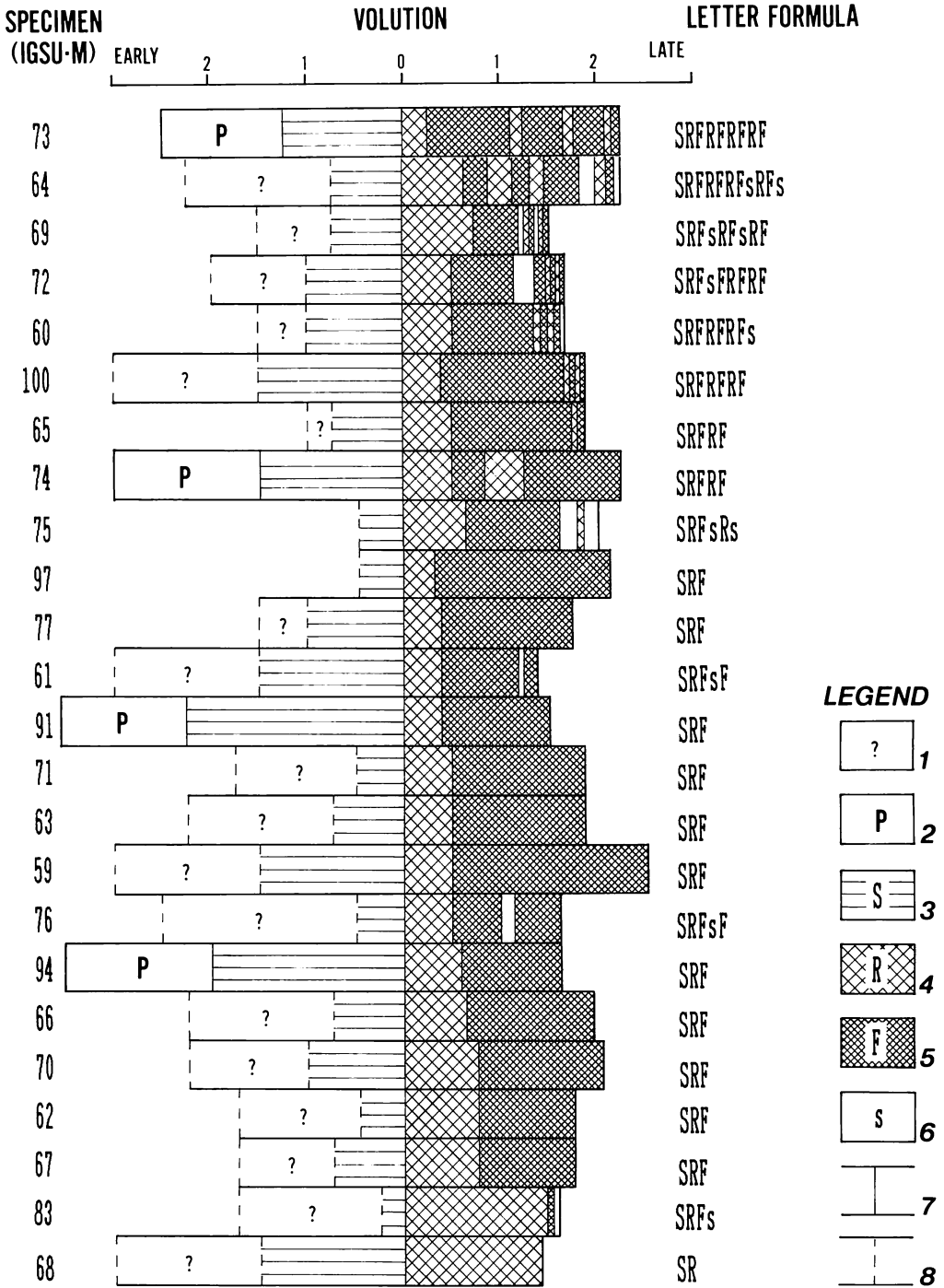
Surface ornamentation of teleoconch changes ontogenetically. The first, second, and rarely third teleoconchs have the pattern **S**, and its later teleoconchs are sculptured with **R**, **F**, and/or **s**. The degree of development of these four patterns (**S**, **R**, **F**, and **s**) is greatly variable in individuals. The 43 Shinzato specimens were classified into the following 7 different development types (Table 1-

A): **SRF** (10 specimens), **SRFsF** (5 specimens), **SsF** (1 specimen), **SRFs** (21 specimens), **SRs** (2 specimens), **SsFs** (1 specimen), and **Ss** (3 specimens).

We observed 79 specimens (see Appendix) from the Nobori Formation, of which we analyzed 25 well preserved specimens from the IGSU loc. no. 62-35-3, where *P. pseudotransenna* occurs autochthonously and most abundantly. Among the 25 specimens (Table 1-A, Figures 4, 5), 11 specimens are classifiable into Type **SRF** (Figure 5-9a-10b), 2 specimens into **SRFsF** (Figure 5-8a-8b), 1 specimen into **SRFs**, and 1 specimen into a questionable **Ss** (Figure 5-12a-12b). The remaining 10 specimens bear ornamentation that is not classifiable into any of the types of Noda and Ogasawara (1976) (Table 1-A). They consist of the Type **SR** (1 specimen; Figure 5-11a-11b), **SRFRF** (2 specimens; Figure 5-6a-6b), **SRFsRs** (1 specimen; Figure 5-7a-7b), **SRFRFRF** (1 specimen; Figure 5-5a-5b), **SRFRFRFs** (1 specimen; Figures 3-4, 5-4a-4b), **SRFRFRFRF** (1 specimen; Figure 5-1a-1b), **SRFsRFsRF** (1 specimen; Figure 5-3a-3b), and **SRFRFRFsRsFs** (1 specimen; Figures 3-5, 5-2a-2b). The ranges of individual variation of the shell-surface ornamentation of the Shinzato and Nobori specimens are quite different (Table 1-A).

We propose herein a sorting scheme for the surface ornamentation. As noted above, the pattern **R** sometimes becomes coarser and changes gradually into the pattern **s** (Figure 3-5). Thus, the pattern **s** is considered to be the coarsest part of the pattern **R**. In the following discussion of pattern arrangement the **s** is replaced by **R** (Table 1-B).

In this sorting scheme (Table 1-B), the three patterns **S**, **R**, and **F** are regularly arranged in both the Shinzato and Nobori specimens: that is, the teleoconch ornamentation always begins with the pattern **S**; the **S** is always followed by the pattern **R**; the **R** is always succeeded by the pattern **F**; and the **R**



and **F** appear repeatedly in some specimens (Table 1-C).

These differences among individual ornamental patterns are not considered to be controlled by age differences because there is no relationship between number of whorls and ornament type (Figure 4; Noda and Ogasawara, 1976, fig. 3).

We propose a model to explain the different ranges of individual variation between the Shinzato and Nobori specimens. This model maintains that the differences among these individual ornamental types are controlled by the differences in timing of the onset of ornamental development in individuals and that the onset timing of respective individuals differs successively (Figure 6-1). In Figure 6-1, if the onset timing is extremely accelerated, then an **SRFRFRFRF**-type ornamentation results, while if the onset timing is greatly delayed, then an **SR**-type ornamentation appears. In this model, the range of individual variation on shell ornamentation is primarily controlled by the range of variation in timing of the onset of the ornament development (Figure 6-1). The Nobori specimens are, therefore, considered to have a wider range in timing of the onset of ornament development than the Shinzato specimens. This mode of individual variation controlled by such a mechanism has been reported by Majima (1985, 1988), who studied the heterochronic evolution of three naticid gastropods.

The patterns **R** and **F** in the later adult stage of some specimens (IGSU M69, M72,

M60, M100 and M65 in Figure 4) are very closely arranged in comparison with the others. We consider these close arrangements to be caused by slow growth rate due either to the later adult stage, worse trophic conditions, or reproductive activity.

Evolution of *Phanerolepida*

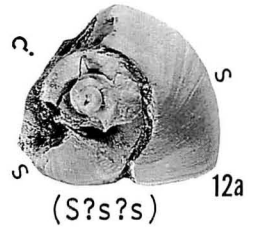
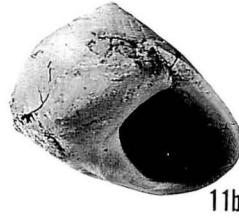
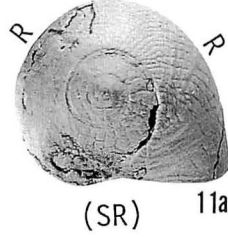
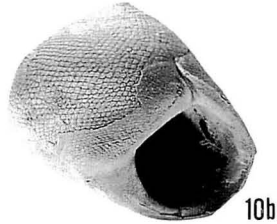
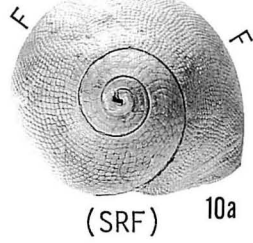
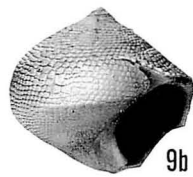
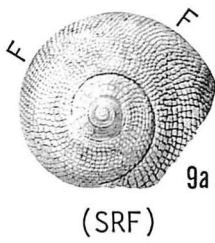
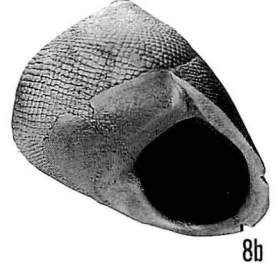
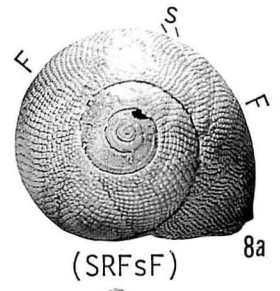
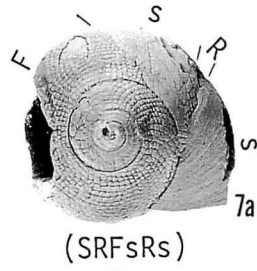
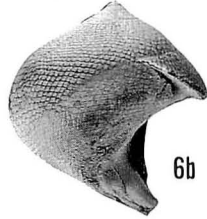
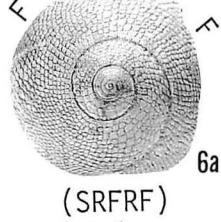
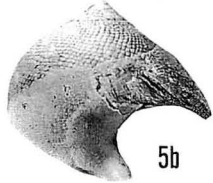
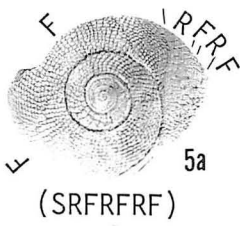
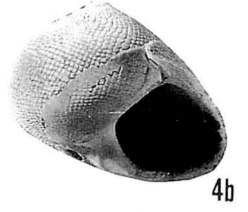
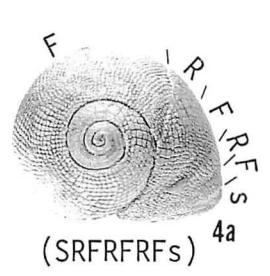
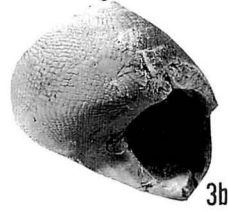
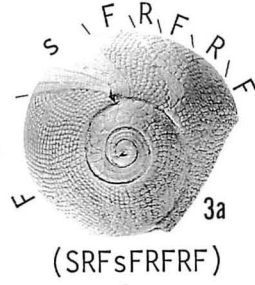
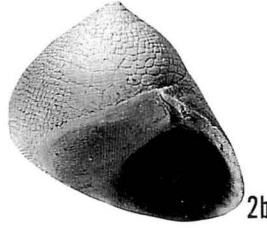
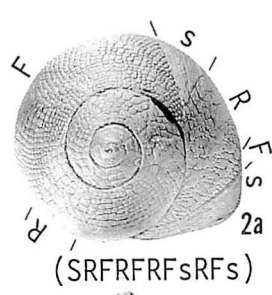
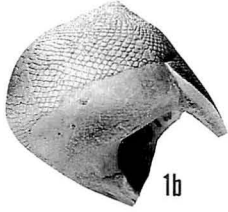
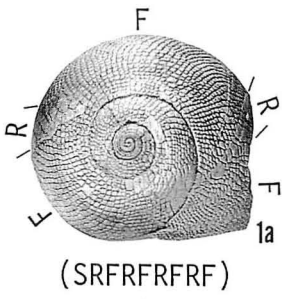
We hypothesize that the Recent *Phanerolepida transenna* evolved from Eocene *Nehalemia hieroglyphica* through Oligocene *P. oregonensis* and Pliocene *P. pseudotransenna*. In the speciation events represented, at least two events are considered to have been the results of heterochrony, as discussed below.

Phanerolepida is considered to have evolved from the western North American species *Nehalemia hieroglyphica* Hickman, 1974. *Nehalemia hieroglyphica* Hickman shares characteristics of both *Phanerolepida* and *Homalopoma* and occurs near the top of the Eocene Cowlitz Formation, approximately 450 m stratigraphically beneath the oldest occurrence of *Phanerolepida*, *P. oregonensis* Hickman, in the lower Oligocene Keasey Formation (Hickman, 1974). On the teleoconch surface, *N. hieroglyphica* is ornamented with strong spiral ribs separated by approximately equal interspaces (Hickman, 1974). This ornamentation is considered to be comparable to the pattern **S** of *P. pseudotransenna* (Figure 6-3).

Phanerolepida oregonensis is considered to have evolved from *N. hieroglyphica*, and has a net-like, coarse rhombohedral pattern of sur-

← **Figure 4.** Individual variation of ornamentation on shells of *Phanerolepida pseudotransenna* Ozaki at IGSU loc. no. 62-35-3. Respective lateral columns illustrate successive ornamental patterns. The "O" position of the volution coincides with the boundary between the patterns **R** and **S** but not with protoconch/teleoconch boundary. In many specimens, the protoconch/teleoconch boundary is indistinct due to weathering. Legend: 1, protoconch or pattern **S** (three or four spiral cords on the smooth surface) indeterminate due to weathering; 2, protoconch; 3, pattern of three or four spiral cords; 4, roughly developed rhombohedral network pattern; 5, finely developed rhombohedral network pattern; 6, smooth surface occasionally bearing very fine spiral striae; 7, sculptural boundary preserved; 8, sculptural boundary or early conchs indeterminate due to weathering.

IGSU M86 specimen (Figure 5-12a-b; Table 1-A, ?**Ss**) is not illustrated in this figure because of its imperfect preservation of ornamentation. So the total number of specimens in this figure is 24, but not 25 mentioned in the text.



face ornamentation, and its early teleoconchs have a faint spiral sculpture superposed on the rhombohedral network (Hickman, 1972) (Figure 6-2). The coarse rhombohedral network pattern is considered to be comparable to the pattern **R** of *P. pseudotransenna*, and the superposed faint spirals are probably comparable with the spiral ribs of *N. hieroglyphica*, and also with the pattern **S** of *P. pseudotransenna*.

Phanerolepida pseudotransenna is inferred to have evolved from *P. oregonensis* in a migration process from the eastern Pacific to the western Pacific during the late Oligocene or early Miocene. The former species shows a very wide range of individual variation in ornamentation and has a variant bearing **SR**-type ornamentation which is interpreted as a relic of *P. oregonensis*. In some specimens of *P. pseudotransenna*, the pattern **R** that immediately follows the pattern **S** is superposed by weak spiral cords that continue from the spiral cords of the pattern **S** (Figure 3-1a), just as with the early teleoconchs of *P. oregonensis*. This similarity supports the above interpretation for the lineage.

Phanerolepida transenna is considered to have evolved from *P. pseudotransenna*, and commonly shows an ontogenetic ornamental sequence on the teleoconch, i.e., faint spiral sculpture → coarse rhombohedral network pattern → fine rhombohedral network pattern, which are considered to be comparable with the patterns **S**, **R**, and **F** of *P. pseudotransenna*, respectively. The derivation of *P. transenna* from *P. pseudotransenna* is supported by evidence that *P. pseudotransenna* has a variant bearing **SRF**-type ornamentation that is considered to be a fore-runner of *P. transenna*. The precise individual variation of the ornamentation of *P. transenna* is not well known because of the lack of available specimens, but the following

can be stated. The faint spiral sculpture of *P. transenna* may be indistinct in some specimens, and the fine rhombohedral network pattern is commonly widely developed, finer in grain size than the pattern **F** of *P. pseudotransenna*, and may be interrupted by the coarse rhombohedral network pattern.

The evolutionary lineage *Nehalemia hieroglyphica* (ornament pattern: **S**) → *P. oregonensis* (**S**+**R** → **R**) → *P. pseudotransenna* (**S** → **R** ← variation → **S** → **R** → **F** → **R** → **F** → **R** → **F** → **R** → **F** → **R**) is considered to be an example of peramorphosis (Figure 6). Peramorphosis is the occurrence of the ancestral adult morphology in a descendant juvenile stage of development (McNamara, 1986). A highly variable onset timing of ornament development in individuals occurs in the evolutionary process from *P. oregonensis* to *P. pseudotransenna*. Although the wide range of individual ontogenetic variation in *P. pseudotransenna* makes interpretation of the heterochrony complicated, this evolution is evidently a peramorphosis because many specimens of *P. pseudotransenna* have the ancestral patterns **S** and **R** in their younger stages.

Systematic Paleontology

Class Gastropoda Cuvier, 1797
 Subclass Prosobranchia Milne-Edwards, 1848
 Order Archaeogastropoda Thiele, 1925
 Family Turbinidae Rafinesque, 1815
 Subfamily Homalopomatinae Keen, 1960

Genus *Phanerolepida* Dall, 1907
 Type species.—*Turbo transenna* Watson, 1879, by monotypy. Holocene, Pacific side of central and southwestern Japan (Noda and Ogasawara, 1976).

← **Figure 5.** *Phanerolepida pseudotransenna* Ozaki. IGSU loc. no. 62-35-3. ×1.7. 1a-1b, IGSU M73; 2a-2b, IGSU M64; 3a-3b, IGSU M72; 4a-4b, IGSU M60; 5a-5b, IGSU M100; 6a-6b, IGSU M74; 7a-7b, IGSU M75; 8a-8b, IGSU M61; 9a-9b, IGSU M94; 10a-10b, IGSU M67; 11a-11b, IGSU M68; 12a-12b, IGSU M86. Letters around the shell indicate the successive patterns on body whorl.

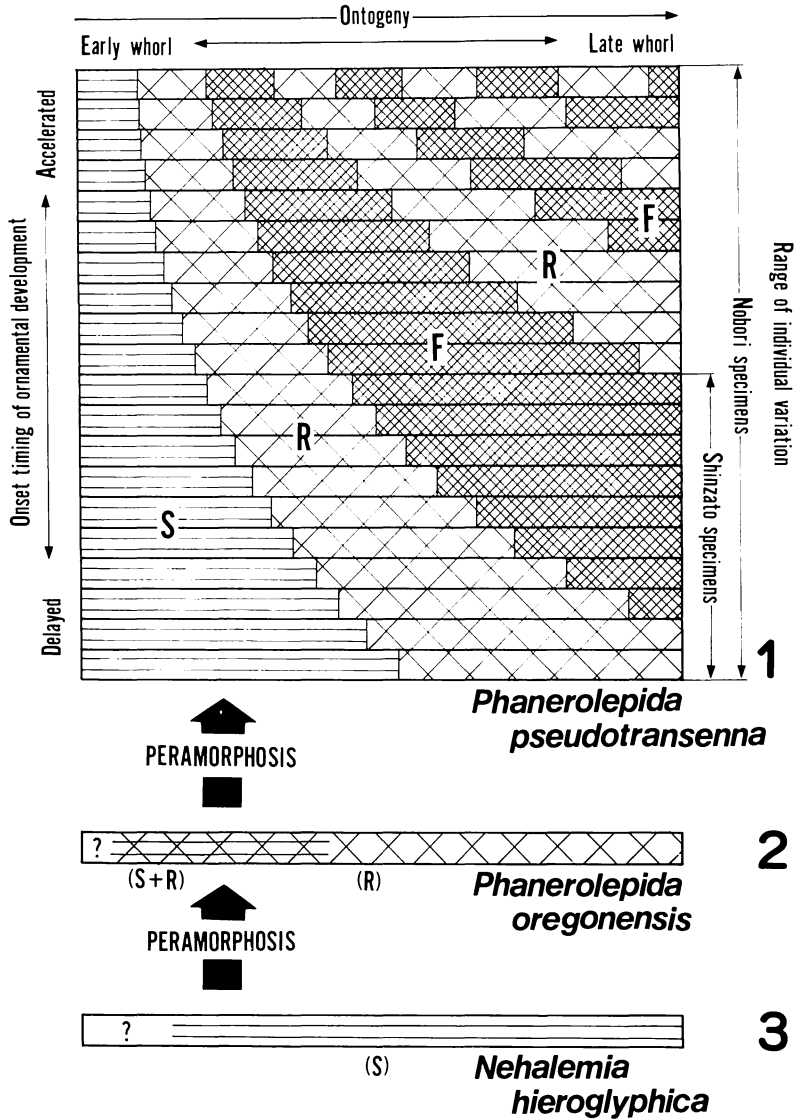


Figure 6. Schematic illustration of a model for the explanation of individual variation of *Phanerolepida pseudotransenna* Ozaki (1), and a heterochrony of *Nehalemia hieroglyphica* Hickman (3) → *Phanerolepida oregonensis* Hickman (2) → *P. pseudotransenna* Ozaki (1) lineage. Note that the difference of individual variation between Shinzato and Nobori specimens is interpreted to be caused by variation in the onset timing of ornament development for each individual.

Phanerolepida pseudotransenna
Ozaki, 1956

Figures 3, 5, 7, 8

Phanerolepida pseudotransenna Ozaki, 1956, p. 1-2, pl. 1, figs. 1-2; Noda and Ogasawara, 1976, pl. 1, fig. 13; Masuda and Noda, 1976, p. 246;

Mimoto, 1986, p. 36, pl. 15, figs. 5a-6b.

? *Phanerolepida pseudotransenna* Ozaki. Hatai and Masuda, 1962, pl. 40, figs. 26, 27.

Phanerolepida rehderi MacNeil, 1960, p. 30, pl. 7, figs. 6-8, 11-13; Hickman, 1972, figs. 3, 7, 11, 13; Noda and Ogasawara, 1976, pl. 1, figs. 1a-10b; Masuda and Noda, 1976, p. 246; Noda, 1980, p. 11, pl. 6, fig. 1; Noda and Kikuchi, 1980, pl. 1,

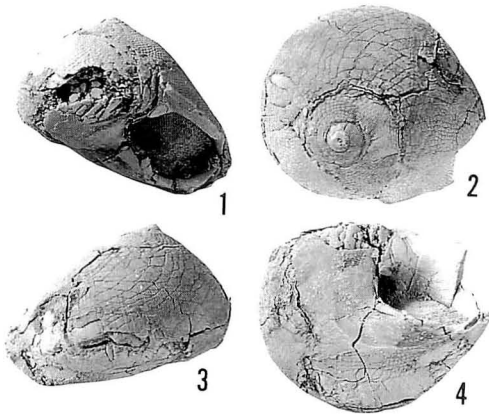


Figure 7. Four views of the holotype of *Phanerolepida pseudotransenna* Ozaki. NSM P1 4368. $\times 1.8$. Nisinotani, Nobori, Hane-machi, Muroto City, Kochi Prefecture, Pacific side of southwestern Japan. Upper Pliocene Nobori Formation.

figs. 2a, 2b, ?3, ?4 [figs. 3, 4, showing opercula isolated from the shell]; Noda, 1988, p. 34, pl. 5, figs. 1a-3c.

Phanerolepida transenna (Watson). Aoki and Baba, 1984, p. 73, figs. 1a, 1b [not *Phanerolepida transenna* (Watson, 1879)].

Type material.—NSM P1 4368 (holotype: Figure 7) from Nisinotani, Nobori, Hane-machi (Ozaki, 1956), Muroto City, Kochi Prefecture, Pacific side of southwestern Japan. Pliocene Nobori Formation of the Tonohama Group.

Stratigraphic occurrence.—? Miocene: Tokigawa Formation, Saitama Prefecture (Hatai and Masuda, 1962). Pliocene: Nobori Formation, Kochi Prefecture; Shinzato Formation, Okinawa Prefecture (MacNeil, 1960; Noda and Ogasawara, 1976; Noda, 1980, 1988).

Remarks.—We collected 5 opercula of *P. pseudotransenna* from IGSU loc. no. 62-35-3, of which 4 are preserved in their own apertures near to their life position (Figure 8-1, 8-3-5). These opercula are indistinguishable from those of the Recent species, *P. transenna*.

Phanerolepida rehderi MacNeil, 1960, a

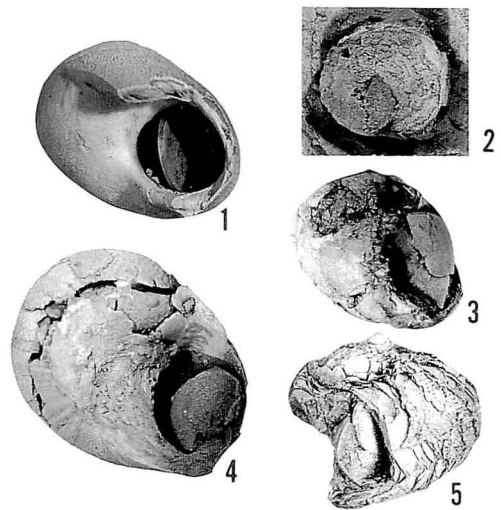


Figure 8. Opercula of *Phanerolepida pseudotransenna* Ozaki. IGSU loc. no. 62-35-3. $\times 1.7$. 1, 3-5, opercula preserved in the aperture near to their life position. 2, operculum occurring isolated from its own shell. 1, IGSU M73; 2, IGSU M117; 3, IGSU M112; 4, IGSU M69; 5, IGSU M111.

Pliocene species of Okinawa, southern Japan, is here designated as a junior synonym of the present species for the first time. The two species are identical to each other in shell form. Although the two species have different ranges of individual ornamental variations (Table 1-A), these differences are interpreted as intraspecific variation resulting from the variational range of onset timing of ornament development (Figure 6-1).

Phanerolepida expansilabrum Kuroda, 1931 from the Miocene of Japan is intermediate in age between *P. oregonensis* and *P. pseudotransenna*. Because *P. expansilabrum* has previously been known only by poorly preserved specimens, specific comparisons among the three species must await availability of numerous well preserved specimens of the Miocene species.

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Hane 羽根, Kochi 高地, Muroto 室戸, Nishinotani 西ノ谷, Nobori 登, Okinawa 沖縄, Saitama 埼玉, Shinzato 新里, Tokigawa 都幾川, Tonohama 唐浜,

高知県の鮮新統登層産 *Phanerolepida pseudotransenna* Ozaki (腹足綱: リュウテンサザエ科) の種内変異と異時性: *Phanerolepida pseudotransenna* Ozaki の最近発見された 75 標本は殻表面装飾に非常に大きな変異を示す。この変異は個体間の装飾発達の開始時期の差異に起因すると解釈される。層序的産出と殻の装飾の個体発生上の変異の比較から *Nehalemia hieroglyphica* → *Phanerolepida oregonensis* → *P. pseudotransenna* → *P. tansenna* という進化系列が推定された。そのうち、少なくとも初めの 2 つの種分化は異時性の結果であると考えられる。

Phanerolepida rehderi MacNeil を個体変異の比較に基づいて *P. pseudotransenna* の新参シノニムとした。殻と伴った 4 つの蓋が生息時の位置に近い状態で産出した。

間嶋隆一・村田昭浩

Appendix. Measurements, letter formula and remarks for all examined specimens of *Phanerolepida pseudotransenna* Ozaki from the Nobori Formation.

Specimen IGSU	Locality IGSU	Shell height	Shell width	Aperture height	Number of whorl	Letter formula of shell-surface ornamentation	Remarks
M37	62-35-1	17.0	20.0	12.4	4 1/2+	SRFsRFsFRFsF	Fig. 3-1
M38	62-35-1	17.8	20.3	13.1	4+	SRF	Fig. 3-2
M39	62-35-1	17.7	19.8	12.4	4 1/2+	SRF	Fig. 3-3
M40	62-35-1	16.9	20.2	12.3	4+	SRF	
M41	62-35-1	16.4	19.0+	10.8	3 1/2+	SRF	
M42	62-35-1	15.6	17.2+	11.4	4 1/2+	SsRF	
M43	62-35-1	17.8+	17.7+	12.5+	3 1/2+	SRF?F	
M44	62-35-1	10.9+	16.5+	—	3+	SRF	
M45	62-35-1	12.3+	16.9	11.8	1 1/2+	?F	Deformed
M46	62-35-1	11.3+	15.3+	9.8+	1 1/2+	?F	
M47	62-35-1	11.0+	18.5	13.5	1/2+	?F	
M48	62-35-2	14.0+	20.0+	9.5+	3+	?F	Deformed
M49	62-35-2	9.9	15.0	8.0	3 1/2+	?RF	Deformed
M50	62-35-2	14.7	17.1+	12.2	3+	?R?R	Deformed
M51	62-35-2	15.1	19.5+	10.1	4 1/2+	?F	Deformed
M52	62-35-2	15.8	18.4	11.9	4 1/4	SRF?F	Deformed
M53	62-35-2	12.7+	17.0	11.5	2+	?F	Deformed
M54	62-35-2	11.3+	15.8+	11.0+	2+	?F?F?	Deformed
M55	62-35-2	8.4+	15.2+	8.0+	2 1/2+	?FR	Deformed
M56	62-35-2	11.0+	19.1+	—	1+	?F?	Deformed
M57	62-35-2	8.8+	13.8+	—	1/2+	?F	Deformed
M58	62-35-2	8.8+	11.2+	—	3+	?F?	Deformed
M59	62-35-3	16.3	18.8	10.7	5+	SRF	Fig. 4
M60	62-35-3	13.5	16.7	9.8	4 1/2+	SRFRFRF	Figs. 3-4, 4, 5-4
M61	62-35-3	15.8	18.1	11.6	4 1/2+	SRFsF	Figs. 4, 5-8
M62	62-35-3	14.2	17.0	10.6	3 1/2+	SRF	Fig. 4
M63	62-35-3	15.9	17.4	11.7	4+	SRF	Fig. 4
M64	62-35-3	17.2	19.0	11.9	4 1/2+	SRFRFRFsRFs	Fig. 3-5, 4, 5-2
M65	62-35-3	14.8	18.2	10.5	3+	SRFRF	Fig. 4
M66	62-35-3	17.2	20.3	13.0	4+	SRF	Fig. 4
M67	62-35-3	17.0	19.5+	12.5	3 1/2+	SRF	Figs. 4, 5-10
M68	62-35-3	14.1	18.0	11.2	5+	SR	Figs. 4, 5-11
M69	62-35-3	16.3	17.8	10.9	3 1/2+	SRFsRFsRF	Figs. 4, 8-4, with operculum
M70	62-35-3	16.8	19.1+	12.4	4+	SRF	Fig. 4
M71	62-35-3	16.3	19.6+	12.4	4+	SRF	Fig. 4
M72	62-35-3	15.6+	16.7+	11.1+	3 1/2+	SRFsFRFRF	Figs. 4, 5-3
M73	62-35-3	15.0+	17.1+	12.0+	5	SRFRFRFRF	Figs. 4, 5-1, 8-1, with operculum
M74	62-35-3	16.3+	16.4+	12.1+	6 1/2	SRFRF	Figs. 4, 5-6
M75	62-35-3	15.0	17.6+	12.4	3 1/2+	SRFsRs	Figs. 4, 5-7
M76	62-35-3	14.0	19.5	9.3+	4+	SRFsF	Fig. 4

Specimen IGSU	Locality IGSU	Shell height	Shell width	Aperture height	Number of whorl	Letter formula of shell-surface ornamentation	Remarks
M77	62-35-3	15.4	17.3	11.7	3 1/2+	SRF	Fig. 4
M78	62-35-3	14.5	18.4	11.9	3+	?RF	
M79	62-35-3	16.2	19.3	12.8	3 1/2+	?FR?s	
M80	62-35-3	16.6	19.5	13.1	4 1/2+	?RF	Deformed
M81	62-35-3	14.9+	17.3+	11.6+	3+	?RFsR?F	Deformed
M82	62-35-3	14.3+	19.7+	10.8+	3+	?F	Deformed
M83	62-35-3	14.0	17.8	11.3	3 1/2+	SRFs	Fig. 4
M84	62-35-3	14.2	18.8+	10.2+	3+	SRF?F	Deformed
M85	62-35-3	14.7+	18.4+	13.0	2+	?FRF?F	
M86	62-35-3	14.5	16.5+	11.3	4+	S?s?s	Fig. 5-12
M87	62-35-3	16.4	18.6	13.0	3 1/2+	SRF?F?F	Deformed
M88	62-35-3	13.5	18.3+	12.8+	3 1/2+	?FR?F	Deformed
M89	62-35-3	16.7	18.1+	13.8	3 1/2+	SRF?F	
M90	62-35-3	13.3+	17.3+	10.6+	3+	?F	Deformed
M91	62-35-3	14.2+	15.1+	10.8+	5 1/2	SRF	Fig. 4
M92	62-35-3	12.2+	15.3+	10.0+	4+	SR?	
M93	62-35-3	13.1+	17.5+	10.9+	4+	S?F?	Deformed
M94	62-35-3	11.6+	14.1+	8.9+	6	SRF	Figs. 4, 5-9
M95	62-35-3	11.4+	13.4+	9.3+	4 1/2+	SR?	
M96	62-35-3	14.1+	14.8+	10.2+	5+	SRF?F	
M97	62-35-3	12.7+	18.4+	—	3+	SRF	Fig. 4
M98	62-35-3	12.7+	18.0+	11.0	—	?R?	Deformed
M99	62-35-3	—	21.4	12.6	—	?RF	
M100	62-35-3	13.3+	15.4+	—	5 1/2+	SRFRFRF	Figs. 4, 5-5
M101	62-35-3	13.6+	19.0+	11.0+	3+	?RF?F	
M102	62-35-3	—	12.7+	11.2+	—	?F	Deformed
M103	62-35-3	11.9+	15.3+	9.8+	2 1/2+	?F?F	Deformed
M104	62-35-3	9.3+	13.4+	8.3+	—	?F	Deformed
M105	62-35-3	—	14.8+	—	3+	?RF	
M106	62-35-3	15.0+	11.2+	10.3+	3 1/2+	SR?F	
M107	62-35-3	14.1+	11.4+	—	4+	SR?FRF?F	
M108	62-35-3	12.5+	15.0+	8.9+	4+	SRF?Fs	
M109	62-35-3	10.6+	14.5+	—	2 1/2+	SRF?FsRF?	
M110	62-35-3	13.9+	13.3+	—	2 1/2+	?F?	
M111	62-35-3	13.2+	14.9+	10.3+	4 1/2+	?F?F?	Fig. 8-5, with operculum
M112	62-35-3	—	13.3+	9.5+	—	?F?	Fig. 8-3, with operculum
M113	62-35-3	11.6+	11.9+	8.7+	3 1/2+	SRF?	Deformed
M114	62-35-3	—	19.2+	—	3+	S?F?F	
M115	62-35-3	12.6+	15.3+	9.5+	4+	SRF?F	
M116	62-35-3	7.1+	10.5+	7.0+	3+	?RF?	

934. VERBEEKINID AND NEOSCHWAGERINID FUSULINACEANS FROM
THE AKIYOSHI LIMESTONE GROUP ABOVE THE *PARAFUSULINA*
KAERIMIZENSIS ZONE, SOUTHWEST JAPAN*

KATSUMI UENO

Institute of Geoscience, University of Tsukuba, Ibaraki, 305

Abstract. The Akiyoshi Limestone Group above the *Parafusulina kaerimizensis* Zone in the Kaerimizu area can be divided into the *Parafusulina kaerimizensis*, *Afghanella ozawai*, *Neoschwagerina craticulifera robusta*, *Verbeekina verbeeki-Afghanella schencki*, *Neoschwagerina fusiformis*, *Verbeekina verbeeki* and *Colania douvillei* Zones in ascending order, mainly on the basis of the stratigraphic distribution of verbeekinid and neoschwagerinid fusulinaceans. In this paper, 10 species of verbeekinid and neoschwagerinid fusulinaceans including one new subspecies, *Neoschwagerina craticulifera robusta*, are described. Also, the fusulinacean biostratigraphy of the Akiyoshi Limestone Group above the *Parafusulina kaerimizensis* Zone in the Kaerimizu area is briefly noted.

Key words. Akiyoshi Limestone Group, fusulinacean biostratigraphy, Middle Permian, *Parafusulina kaerimizensis* Zone, Neoschwagerinidae, Verbeekinidae.

Introduction

The Akiyoshi Limestone Group, covering almost the whole area of the Akiyoshi Plateau situated in the central part of Yamaguchi Prefecture, southwest Japan, is considered to have formed as a large organic reef complex during Late Paleozoic time (Ota, 1968). This limestone contains rich shallow marine fossil remains such as foraminifers, algae, sponges, corals, brachiopods, mollusks and others. Since Ozawa's fundamental work in 1923, fusulinacean foraminifers have often been studied in connection with the biostratigraphic subdivision of the Akiyoshi Limestone Group, except for its lowermost part (e.g. Ozawa, 1925b; Toriyama, 1954, 1958; Hasegawa, 1958, 1963; Murata, 1961; Sakaguchi *et al.*, 1966; Yanagida *et al.*, 1971; Ota *et al.*, 1973; Ota, 1977; Matsusue, 1986; Ueno, 1989; Ozawa and Kobayashi, 1990).

Concerning the biostratigraphic zonation by fusulinaceans in the Permian sequence of the Akiyoshi Limestone Group, Ota (1977) subdivided it into 11 zones. Recently, Ozawa and Kobayashi (1990) established 17 fusulinacean zones in the same part.

The fusulinacean family Verbeekinidae arose from the family Ozawainellidae at the beginning of the Middle Permian and the family Neoschwagerinidae was derived from the former in the middle of that period. These two families flourished through Middle Permian time. It is known that they have significant value for biostratigraphic zonation in the Middle Permian of the Tethyan realm. About 30 species of the families Verbeekinidae and Neoschwagerinidae have been recorded from the Akiyoshi Limestone Group.

Very recently, I have discussed the origin and early evolution of verbeekinid and neoschwagerinid fusulinaceans, based on biostratigraphic evidence obtained from the

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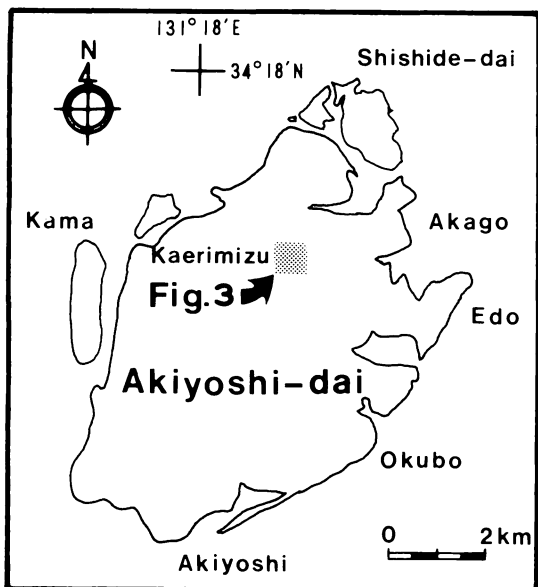


Figure 1. Map showing the Kaerimizu area in the Akiyoshi Plateau.

Akiyoshi Limestone Group below the *Misellina (M.) claudiae* Zone in the Kaerimizu area (Ueno, 1991a, 1991b).

This paper deals with the biostratigraphy of verbeekinid and neoschwagerinid fusulinaceans from the Akiyoshi Limestone Group above the *Parafusulina kaerimizensis* Zone in the Kaerimizu area, and 10 species of them including one new subspecies, *Neoschwagerina craticulifera robusta*, are described. In addition, the fusulinacean biostratigraphy of the Akiyoshi Limestone Group above the *Parafusulina kaerimizensis* Zone is briefly noted.

Fusulinacean biostratigraphy

The Kaerimizu area is a large doline located in the northeastern part of the Akiyoshi Plateau (Figure 1). Ota (1977) divided the Akiyoshi Limestone Group in this area into the following 10 fusulinacean zones in ascending order: the *Fusulinella biconica*, *Triticites simplex*, *Pseudofusulina vulgaris*, *Pseudofusulina ambigua*, *Misellina claudiae*,

Parafusulina kaerimizensis, *Afghanella schencki*, *Neoschwagerina craticulifera*, *Verbeekina verbeeki* and *Colania douvillei* Zones.

I recognized seven fusulinacean biohorizons characterized by the first and last occurrence of some marker species in the stratigraphic interval between Ota's *Parafusulina kaerimizensis* and *Colania douvillei* Zones (Figure 2). Each biohorizon is well recognized in the examined sections of the Kaerimizu area and defines the base of each fusulinacean zone established herein.

The fusulinacean zones are distributed almost concentrically in the Kaerimizu Doline, being younger toward the bottom of the doline, except for the southern part of the surveyed area where the *Afghanella ozawai* and *Neoschwagerina craticulifera robusta* Zones are shown as the inlier in the *Parafusulina kaerimizensis* Zone (Figure 3). Consequently, the Akiyoshi Limestone Group in this area lies almost horizontally and is in reverse order.

A total of 11 species of verbeekinid and neoschwagerinid fusulinaceans were identified from the Akiyoshi Limestone Group above the *Parafusulina kaerimizensis* Zone in the Kaerimizu area. Their stratigraphic distribution is shown in Figure 4. The fusulinacean biostratigraphy of the *Parafusulina kaerimizensis* Zone through the *Colania douvillei* Zone is summarized as follows.

Parafusulina kaerimizensis Zone: This zone is defined as the stratigraphic interval between the first occurrence of *Parafusulina kaerimizensis* and that of *Afghanella ozawai*, and is about 15 m in thickness. Stratigraphic relationship with the underlying *Misellina (M.) claudiae* Zone is conformable. Well sorted foraminiferal sparitic limestone and algal foraminiferal sparitic limestone are predominant. The following fusulinaceans are discriminated: *Rauserella* aff. *breviscula* Sosnina, *Rauserella* sp., *Minojapanella (Rus-siella) pulchra* Miklukho-Maklay, *Neo-*

Z O N E	FUSULINACEAN BIOHORIZON
<i>Colania douvillei</i>	◀ F. <i>Colania douvillei</i>
<i>Verbeekina verbeeki</i>	◀ L. <i>Neoschwagerina fusiformis</i> & <i>Pseudodoliolina pseudolepida</i>
<i>Neoschwag. fusiformis</i>	◀ F. <i>Neoschwagerina fusiformis</i>
<i>Verbeekina verbeeki</i> - <i>Afghanella schencki</i>	◀ F. <i>Verbeekina verbeeki</i> & <i>Afghanella schencki</i>
<i>Neoschwagerina</i> <i>craticulifera robusta</i>	◀ F. <i>Neoschwagerina craticulifera robusta</i>
<i>Afghanella ozawai</i>	◀ F. <i>Afghanella ozawai</i>
<i>Paraf. kaerimizensis</i>	◀ F. <i>Parafusulina kaerimizensis</i>
<i>Misellina (M.) claudiae</i> (PART)	◀ F. <i>Neoschwagerina simplex</i> ◀ F. <i>Maklaya pamirica</i>

F.: First occurrence

L.: Last occurrence

Figure 2. Fusulinacean zones and biohorizons above the *Parafusulina kaerimizensis* Zone.

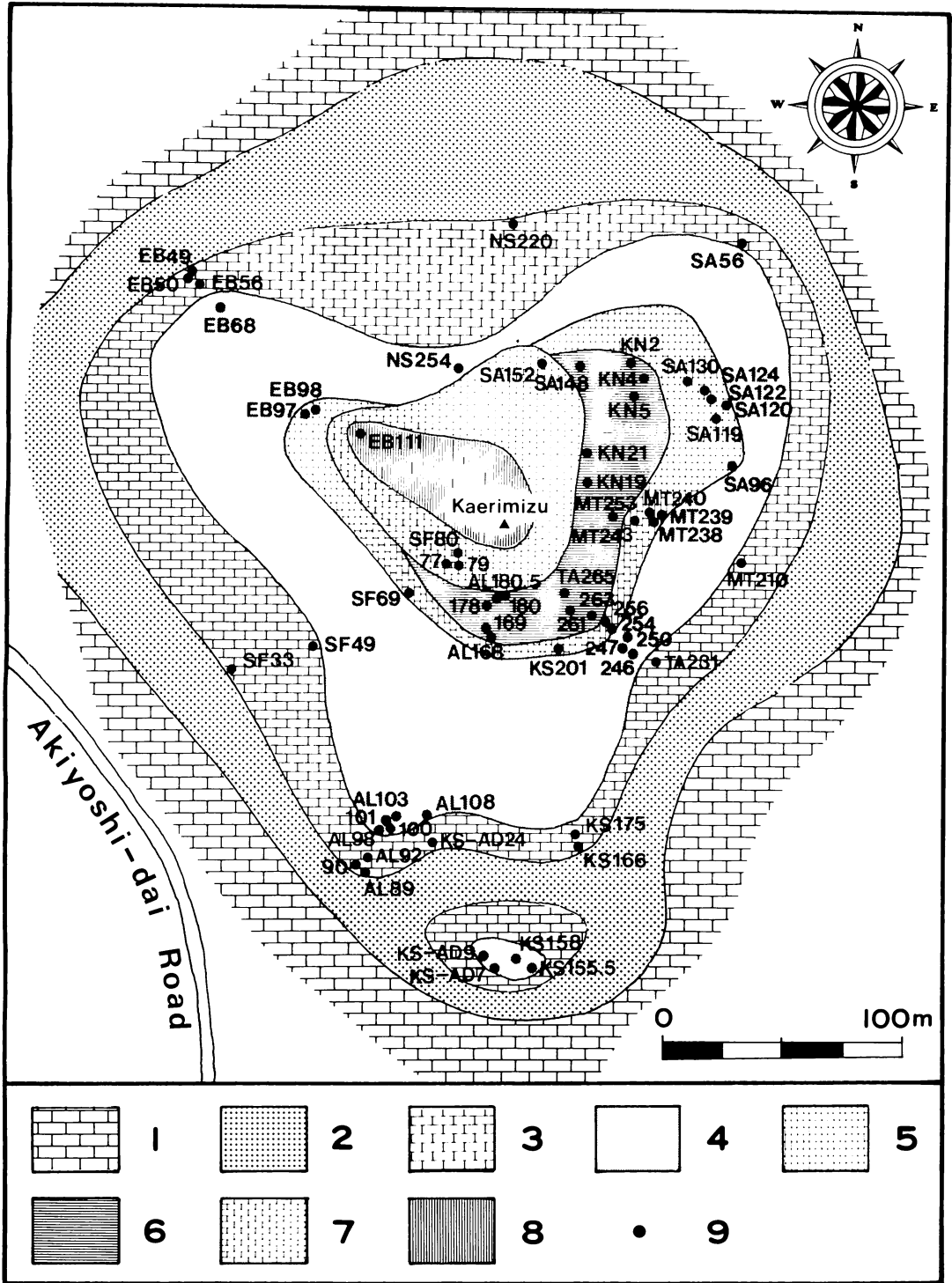
fusulinella giraudi Deprat, *N. pseudogiraudi* (Sheng), *Neofusulinella* sp., *Pseudoreichelina* sp., *Pseudoendothyra* spp., *Parafusulina kaerimizensis* (Ozawa), *P. lutugini* (Schellwien) and *Chusenella alpina* (Kochansky-Devidé and Ramovš).

Afghanella ozawai Zone: *Afghanella ozawai* Zone, about 10 m thick, conformably overlies the *Parafusulina kaerimizensis* Zone. Limestone facies of the present zone is similar to that of the *Parafusulina kaerimizensis* Zone. The fusulinacean fauna includes *Rauserella* aff. *breviscula* Sosnina, *Rauserella* sp., *Schubertella rara* Sheng, *Neofusulinella*

giraudi Deprat, *N. pseudogiraudi* (Sheng), *Pseudoendothyra* spp., *Parafusulina kaerimizensis* (Ozawa), *Pseudodoliolina* cf. *ozawai* Yabe and Hanzawa, *Afghanella ozawai* Hanzawa and *Afghanella* sp.

Neoschwagerina craticulifera robusta Zone: This zone is in conformable contact with the subjacent *Afghanella ozawai* Zone and is about 20 m in thickness. The lower limit of the present zone is defined by the first occurrence of *Neoschwagerina craticulifera robusta*, subsp. nov. Algal foraminiferal sparitic limestone and foraminiferal micritic limestone are predominant. The identified

→ **Figure 3.** Distribution of fusulinacean zones and fossil localities in the Kaerimizu area. 1: *Misellina (M.) claudiae* Zone (Mc), 2: *Parafusulina kaerimizensis* Zone (Pk), 3: *Afghanella ozawai* Zone (Ao), 4: *Neoschwagerina craticulifera robusta* Zone (Nc), 5: *Verbeekina verbeeki-Afghanella schencki* Zone (V-A), 6: *Neoschwagerina fusiformis* Zone (Nf), 7: *Verbeekina verbeeki* Zone (Vv), 8: *Colania douvillei* Zone (Cd), 9: fossil locality studied herein.



fusulinaceans are as follows: *Rauserella* aff. *breviscula* Sosnina, *Rauserella* spp., *Dunbarula schubertellaeformis* Sheng, *Neofusulinella pseudogiraudi* (Sheng), *Pseudoreichelina* sp., *Pseudoendothyra* spp., *Parafusulina kaerimizensis* (Ozawa), *Chusenella referta* Skinner and Wilde, *C. alpina* (Kochansky-Devidé and Ramovš), *C. schwagerinaeformis* Sheng, *Pseudodoliolina* cf. *ozawai* Yabe and Hanzawa, and *Neoschwagerina craticulifera robusta*, subsp. nov.

Verbeekina verbeeki-*Afghanella schencki* Zone: This zone, about 10 m in maximum thickness, is defined as the stratigraphic interval between the first occurrence of both *Verbeekina verbeeki* and *Afghanella schencki* and that of *Neoschwagerina fusiformis*, and conformably overlies the *Neoschwagerina craticulifera robusta* Zone. Foraminiferal sparitic limestone is dominant

with a subordinate amount of algal micritic limestone and muddy limestone. The fusulinacean fauna includes *Rauserella* cf. *sphaeroidea* Sosnina, *Rauserella* sp., *Dunbarula schubertellaeformis* Sheng, *Dunbarula* spp., *Schubertella* sp., *Neofusulinella* sp., *Staffella* sp., *Pseudoendothyra* spp., *Parafusulina edoensis* (Ozawa), *P. gigantea* (Deprat), *Parafusulina* spp., *Chusenella?* cf. *pindingensis* (Sheng), *Chusenella* sp., *Verbeekina verbeeki* (Geinitz), *Pseudodoliolina pseudolepida* (Deprat), *Afghanella schencki* Thompson and *A. cf. sumatrinaeformis* (Gubler).

Neoschwagerina fusiformis Zone: *Neoschwagerina fusiformis* Zone, about 10 m in maximum thickness, is in conformable contact with the underlying *Verbeekina verbeeki*-*Afghanella schencki* Zone. In this zone, foraminiferal sparitic limestone is pre-

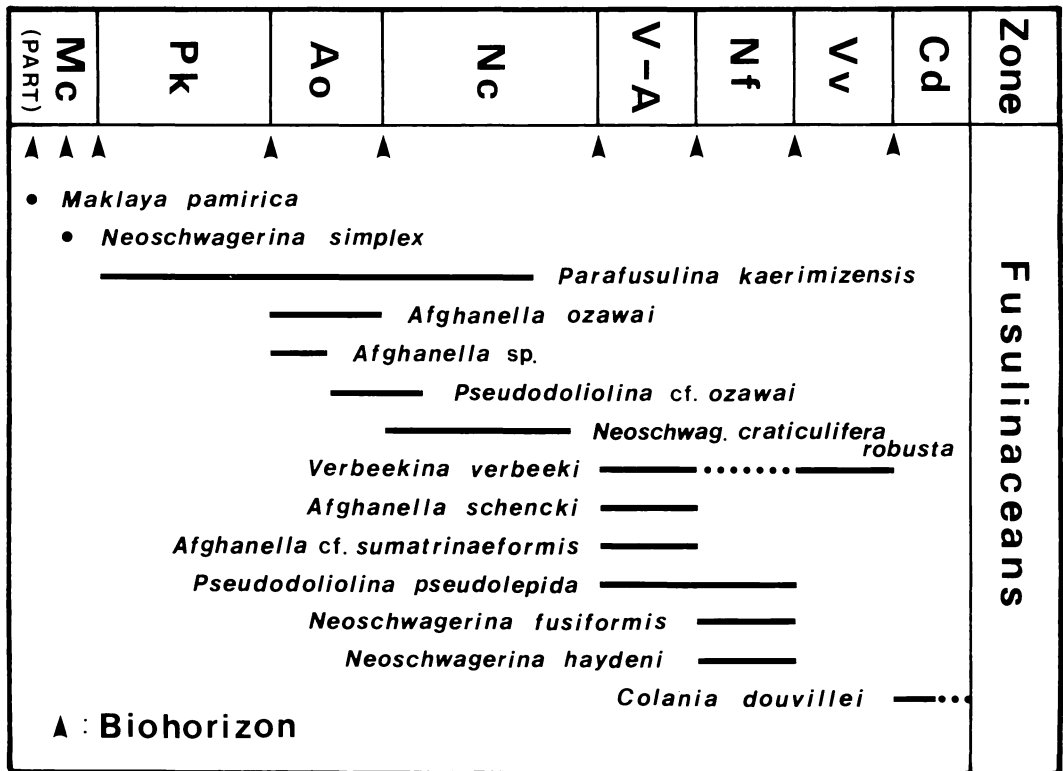


Figure 4. Stratigraphic distribution of verbeekinid, neoschwagerinid and some related fusulinaceans. (abbreviations of zone names: see legend of Figure 3)

dominant with a subordinate amount of foraminiferal micritic limestone and muddy limestone. The following fusulinaceans are identified: *Rausarella* sp., *Dunbarula schubertellaeformis* Sheng, *Dunbarula* spp., *Schubertella* sp., *Neofusulinella* sp., *Pseudoendothyra* spp., *Parafusulina* sp., *Schwagerina* sp., *Pseudodoliolina pseudolepida* (Deprat), *Neoschwagerina fusiformis* Skinner and Wilde, and *N. haydeni* Dutkevich and Khabakov.

Verbeekina verbeeki Zone: The lower limit of the *Verbeekina verbeeki* Zone is defined by the last occurrence of *Neoschwagerina fusiformis* and *Pseudodoliolina pseudolepida*. In the same horizon, *Verbeekina verbeeki* appears again, which is diagnostic in the *Verbeekina verbeeki-Afghanella schencki* Zone but barren in the *Neoschwagerina fusiformis* Zone. The thickness of the present zone is about 10 m. A stratigraphic hiatus may exist between the *Verbeekina verbeeki* Zone and subjacent ones, judging from the distribution of fusulinacean zones. The following fusulinaceans are discriminated: *Rausarella* sp., *Dunbarula schubertellaeformis* Sheng, *Dunbarula* spp., *Neofusulinella* sp., *Pseudoreichelina* sp., *Pseudoendothyra* spp., *Chusenella referta* Skinner and Wilde, and *Verbeekina verbeeki* (Geinitz).

Colania douvillei Zone: The *Colania douvillei* Zone occupies the highest stratigraphic position in the Kaerimizu area and only crops out at the bottom of the doline. It is at least 5 m in thickness and in conformable contact with the *Verbeekina verbeeki* Zone. The lower limit of the present zone is defined by the first occurrence of *Colania douvillei*. The upper limit, however, can not be confirmed in the Kaerimizu area. Algal sparitic limestone and muddy limestone are dominant. The present zone is rather poor in foraminifers and only two species of fusulinaceans, *Pseudoendothyra* sp. and *Colania douvillei* (Ozawa), are identified.

The geologic age of the *Parafusulina kaer-*

imizensis Zone through the *Colania douvillei* Zone is considered to be the Murgabian of the standard stratigraphic scheme in the Tethyan province proposed by Leven (1980).

Systematic paleontology

All specimens identified in this paper are deposited in the paleontological collections of the Akiyoshi-dai Museum of Natural History. The abbreviation ASM is the prefix of the specimen repository number.

Order Foraminiferida Eichwald, 1830

Suborder Fusulinina Wedekind, 1937

Superfamily Fusulinacea von Möller, 1878

Family Verbeekinidae Staff and Wedekind, 1910

Subfamily Verbeekininae Staff and Wedekind, 1910

Genus *Verbeekina* Staff, 1909

Type species.—*Fusulina verbeeki* Geinitz, 1876.

Verbeekina verbeeki (Geinitz, 1876)

Figures 5-1–6, 6-1–5

Fusulina verbeeki Geinitz, 1876, p. 399–400.

Schwagerina verbeeki (Geinitz). Staff, 1909, p. 506, pl. 7, figs. 5, 7; Deprat, 1912, p. 40–41, pl. 1, figs. 7–11; Colani, 1924, p. 108–113, pl. 15, fig. 14, pl. 18, figs. 2, 5, 16–21, 25–27, pl. 19, figs. 1–7, 11, 13.

Verbeekina verbeeki (Geinitz). Ozawa, 1925b, p. 48–51, pl. 10, figs. 6–7; Lange, 1925, p. 260–261, pl. 3, fig. 66a, pl. 5, fig. 66b; Ozawa and Tobler, 1929, p. 48, pl. 5, fig. 5; Chen, 1934, p. 101–102, pl. 16, fig. 1; Gubler, 1935, pl. 1, figs. 10–16; Thompson, 1936, p. 197–200, pl. 24, figs. 1–8; Huzimoto, 1936, p. 101–104, pl. 9, fig. 8, pl. 21, figs. 1–3; Thompson, 1948, pl. 16, figs. 7–12 (same as pl. 24, figs. 1–2, 4, 6–8 of Thompson, 1936, p. 197–200); Kochansky-Devidé and Ramovš, 1955, p. 389, 416, pl. 4, figs. 1–3; Chen, 1956, p. 9, 47–48, pl. 9, figs. 5–6, pl. 13, figs. 1–2; Miklukho-Maklay, 1957, p. 113–114, pl. 3, fig. 2; Kobayashi, 1957, p. 301–302, pl. 9, figs. 5–7; Toriyama, 1958, p. 205–208, pl. 37, figs. 1–6, pl. 38, figs. 1–6; Rauscher-Chernousova and Fursen-

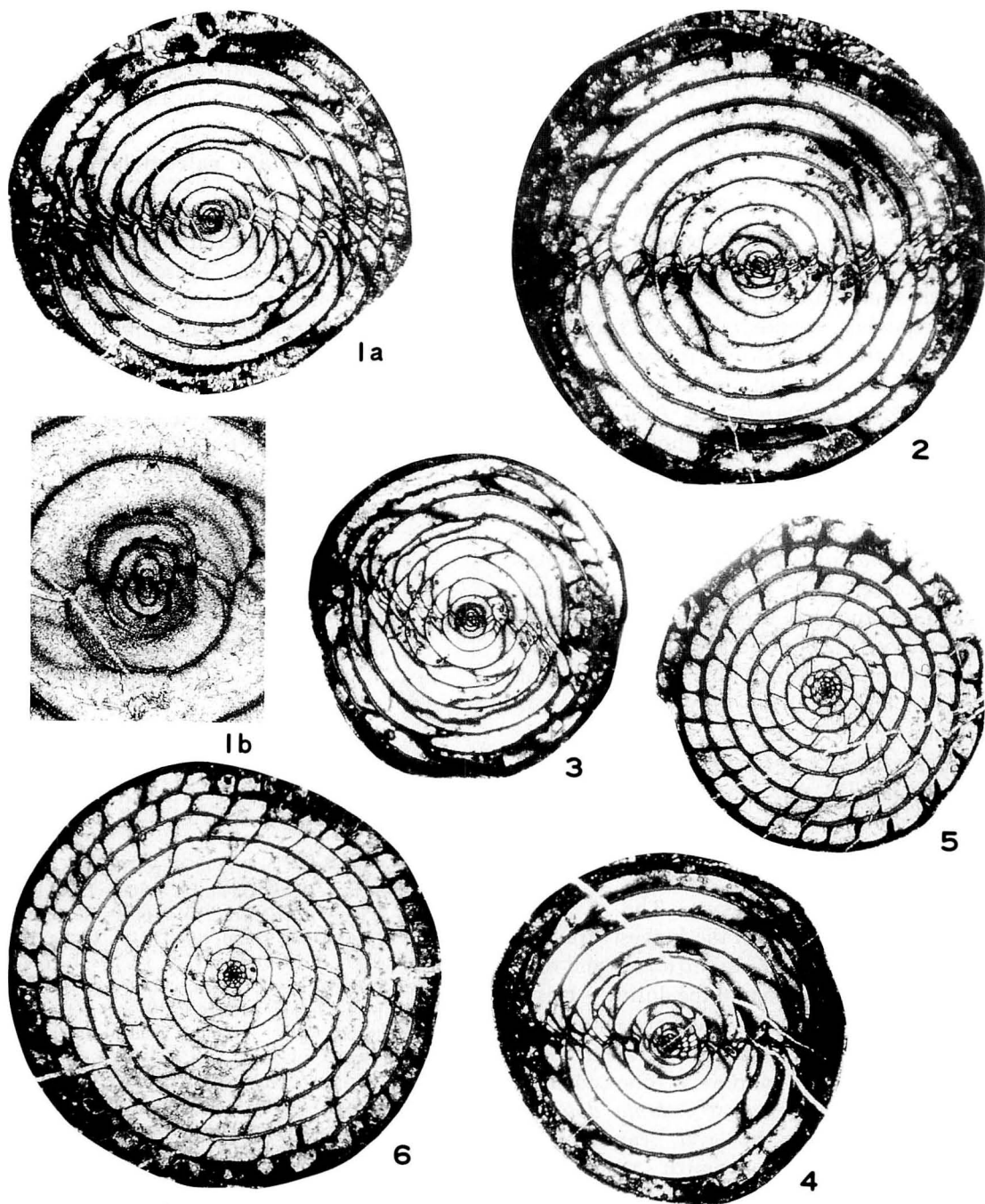


Figure 5. 1-6. *Verbeekina verbeeki* (Geinitz), 1a, 2-4: axial sections, ASM25156, ASM25162, ASM25161, ASM25155, 5, 6: sagittal sections, ASM25164, ASM25165, $\times 10$, 1b: enlarged part of 1a, $\times 40$.

ko, 1959, pl. 10, fig. 5; Nogami, 1961, p. 167-169, pl. 2, figs. 1-4; Sheng, 1963, p. 85-86, 215-216, pl. 26, figs. 1-5; Hanzawa and Murata, 1963, pl. 4, fig. 8; Igo, 1964, p. 62-63, pl. 2, fig. 1; Ishii and Nogami, 1964, p. 24, pl. 8, figs. 4-6; Pasini, 1965, pl. 16, fig. 1; Leven, 1965, p. 140, pl. 4, fig. 1; Ishii, 1966, pl. 6, fig. 9; Sheng, 1966, p. 138-139, pl. 23, fig. 1 (same as pl. 13, fig. 1 of Chen, 1956, p. 9, 47-48); Skinner and Wilde, 1966, pl. 17, fig. 6; Igo, 1967, pl. 6, figs. 1-2; Leven, 1967, p. 205, pl. 38, fig. 1; Choi, 1970, p. 348-349, pl. 15, figs. 1-3; Ozawa, 1970a, pl. 2, fig. 1; Tien, 1970, p. 35-37, pl. 6, figs. 1-10; Toriyama and Pitakpaivan, 1973, p. 50-53, pl. 6, figs. 1-5; Zhang and Wang, 1974, p. 293, pl. 152, fig. 3; Toriyama, 1975, p. 66-68, pl. 14, fig. 12; Rozovskaya, 1975, pl. 27, figs. 6-7; Sheng and Sun, 1975, p. 47, pl. 2, fig. 13; Ozawa, 1975, pl. 10, figs. 10-11; Toriyama and Kanmera, 1977, p. 8-9, pl. 1, figs. 8-10; Lin *et al.*, 1977, p. 83-84, pl. 25, fig. 9; Ota, 1977, pl. 1, figs. 5-6; Liu *et al.*, 1978, p. 81, pl. 18, fig. 17; Ding, 1978, p. 288, pl. 100, fig. 2; Chen and Yang, 1978, p. 105, pl. 27, fig. 3; Kobayashi, 1979, pl. 4, figs. 9-10; Hasegawa *et al.*, 1979, pl. 85, figs. 1-5, 7; Tien, 1979, p. 130-132, pl. 21, figs. 3-9, pl. 22, fig. 1B, pl. 23, fig. 3B; Kahler and Kahler, 1979, p. 215-217, pl. 2, fig. 4, pl. 10, figs. 1-2, 4-5; Wang *et al.*, 1981, p. 58-59, pl. 19, fig. 6; Wang *et al.*, 1982, p. 99, pl. 27, figs. 1-2; Xie, 1982, p. 66, pl. 32, fig. 3 (same as pl. 25, fig. 9 of Lin *et al.*, 1977, p. 83-84); Sun *et al.*, 1983, p. 33, pl. 9, fig. 5; Chen, 1984, p. 64, pl. 17, figs. 1-2; Yang, 1985, pl. 2, fig. 34; Tien, 1986a, pl. 7, fig. 13; Tien, 1986b, pl. 12, fig. 11; Ishibashi, 1986, p. 105-107, pl. 15, figs. 2-8, pl. 16, figs. 1-3; Wang and Tang, 1986, pl. 2, fig. 16; Kobayashi, 1986, p. 145, pl. 4, fig. 8, pl. 9, fig. 6; Wang and Zhou, 1986, pl. 2, figs. 1-2; Han *et al.*, 1987, pl. 2, figs. 1-2, 6; Loeblich and Tappan, 1988, pl. 298, figs. 1-5 (same as pl. 24, figs. 1-2, 6-8 of Thompson, 1936, p. 197-200); Kobayashi, 1988a, p. 8, pl. 11, figs. 10-14; Kobayashi, 1988b, p. 443, figs. 5-3-4; Tien, 1989, pl. 33, figs. 7-8; Ozawa and Kobayashi, 1990, pl. 10, fig. 11.

Verbeekina verbeeki forma A, Pitakpaivan, 1965, p. 53-54, pl. 6, fig. 5.

Material.—Axial sections; ASM25157 from Loc. SF77, ASM25158 from Loc. SF79, ASM25155, ASM25156 from Loc. SF80, ASM25160 from Loc. SA120, ASM25161, ASM25162, ASM25163 from Loc. SA152. Sagittal sections; ASM25164 from Loc. SA96, ASM25165 from Loc. SA152. Axial

section of polyvalent individual; ASM25159 from Loc. TA256.

Description.—Shell large and almost spherical with very shallow umbilicus. Mature specimens having 13 to 15 volutions, 5.40 to 7.20 mm in length and 5.15 to 7.00 mm in width, with a form ratio of about 1.00.

Inner 3 to 5 volutions eostaffelloid and tightly coiled with rotated axis of coiling in some case. Beyond the fifth volution, shell becomes spherical and loose rather rapidly. Chamber height almost constant throughout length of shell. Radius vectors of the first to twentieth volutions of well oriented axial section (Figure 5-1) 0.05, 0.08, 0.12, 0.20, 0.34, 0.60, 0.88, 1.19, 1.56, 1.91, 2.23 and 2.51 mm, and form ratios 0.50, 0.53, 0.67, 0.92, 0.97, 1.05, 1.06, 1.09, 1.05, 1.03, 1.03 and 1.04, respectively.

Proloculus spherical and exceedingly minute for shell size. Its outside diameter varies from 0.030 to 0.060 mm, averaging 0.045 mm for 8 specimens.

Spirotheca thin and composed of a single structureless layer in inner 3 volutions, but of a tectum and lower fibrous alveolar keriotheca beyond the fourth volution. Alveolar keriotheca finer than that observed in neoschwagerinids. Thickness of spirotheca of the first to thirteenth volutions of above-mentioned specimen 0.010, 0.010, 0.010, 0.020, 0.015, 0.025, 0.030, 0.040, 0.055, 0.065, 0.090, 0.065 and 0.050 mm.

Septa thin, unfluted throughout shell length and bending anteriorly. They are composed of the same elements as the spirotheca. Average septal counts of the first to thirteenth volutions for 3 specimens 6, 9, 11, 11, 8, 8, 10, 12, 18, 19, 25, 30 and 36, respectively.

Parachomata numerous, small and low, and semicircular in transverse section. They are well developed in inner juvenile volutions, but sporadically and inconstantly observed in some outer ones, because they develop only on both sides adjacent to septa and decrease in height rather rapidly toward

the center of the chambers.

Remarks.—*Verbeekina verbeeki* (Geinitz) is one of the most familiar verbeekinids in the Middle Permian of the Tethyan province.

The Akiyoshi specimens are quite similar to the topotypes restudied and redescribed by Thompson (1936).

In the Kaerimizu area, the distribution of

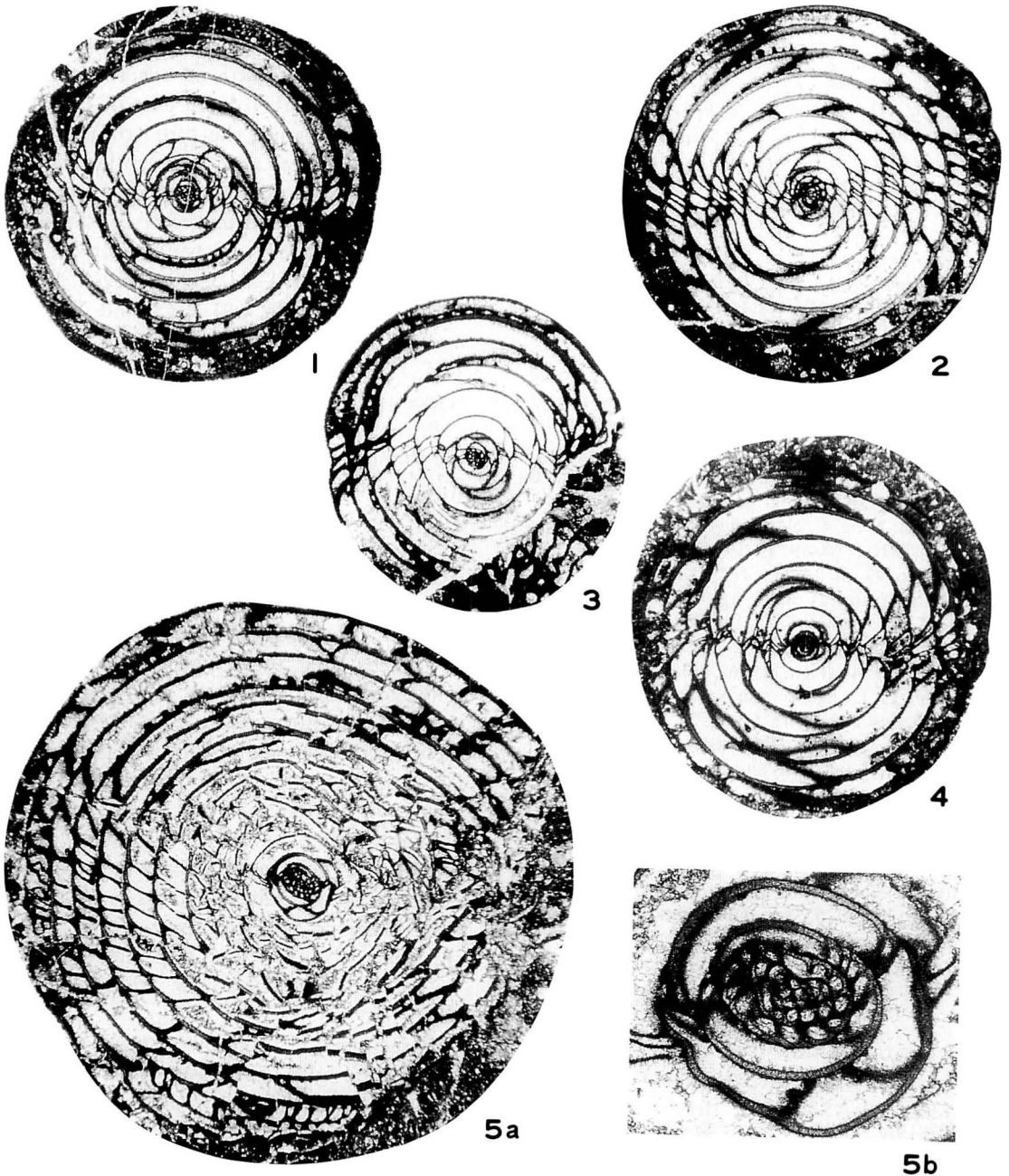


Figure 6. 1-5. *Verbeekina verbeeki* (Geinitz), 1-4: axial sections, ASM25157, ASM25158, ASM25160, ASM25163, ASM25159, 5a: axial section of polyvalent individual, $\times 10$, 5b: enlarged part of 5a, $\times 40$.

Verbeekina verbeeki (Geinitz) is stratigraphically separated into two intervals, namely the *Verbeekina verbeeki-Afghanella schencki* Zone and the *Verbeekina verbeeki* Zone. Most of the individuals found in the former zone are generally smaller in size and have fewer volutions than those in the latter one, although other important morphological characters are in close agreement.

Occurrence.—Abundant in the *Verbeekina verbeeki-Afghanella schencki* and *Verbeekina verbeeki* Zones.

Subfamily Pseudodoliolininae Leven, 1963

Genus *Pseudodoliolina* Yabe and Hanzawa, 1932

Type species.—*Pseudodoliolina ozawai* Yabe and Hanzawa, 1932.

Pseudodoliolina pseudolepida (Deprat, 1912)

Figures 7-1–10

Doliolina pseudolepida Deprat, 1912, p. 46, pl. 5, figs. 6-9, pl. 6, fig. 4.

Doliolina lepida mut. *pseudolepida* Deprat, Deprat, 1913, p. 50.

Doliolina lepida (Schwager). Ozawa, 1927, p. 152-153, pl. 45, figs. 1-2 (not pl. 37, figs. 1c, 7b, 8b, 9b); Gubler, 1935, p. 95-99, pl. 4, figs. 3-10, 11?, 12?, pl. 5, figs. 14-15; Ciry, 1941, pl. 1, fig. 2.

Pseudodoliolina pseudolepida (Deprat). Thompson and Foster, 1937, p. 141-142, pl. 25, figs. 2-4; Thompson, 1948, pl. 17, figs. 3-4 (same as pl. 25, figs. 2, 4 of Thompson and Foster, 1937, p. 141-142); Kochansky-Devidé and Ramovš, 1955, p. 416-417, pl. 4, figs. 7-10, pl. 8, fig. 6; Toriyama, 1958, p. 211-212, pl. 39, figs. 20-25; Nogami, 1961, p. 163-165, pl. 1, figs. 7-11; Ishii and Nogami, 1961, pl. 25, fig. 7 (same as pl. 1, fig. 7 of Nogami, 1961, p. 163-165); Suyari, 1962, p. 32, pl. 12, fig. 10; Hanzawa and Murata, 1963, p. 23, pl. 20, figs. 1-5; Sheng, 1963, p. 97-98, 229-230, pl. 29, figs. 1-9; Sheng, 1966, p. 143, pl. 26, fig. 4; Ozawa, 1970a, pl. 3, figs. 7-8; Tien, 1970, p. 39-40, pl. 7, figs. 6-9, pl. 8, figs. 1-4; Toriyama and Pitakpaivan, 1973, p. 53-57, pl. 6, figs. 6-13; Zhang and Wang, 1974, p. 294, pl. 152, fig. 8; Sheng and Sun, 1975, p. 50, pl. 14, figs. 1-2; Ozawa, 1975, pl. 10, fig. 13; Toriyama and Kan-

mera, 1977, p. 12-14, pl. 1, figs. 13-18, pl. 2, figs. 1-6; Lin *et al.*, 1977, p. 89, pl. 27, fig. 11; Liu *et al.*, 1978, p. 83, pl. 20, fig. 5; Ding, 1978, p. 288, pl. 98, fig. 6; Toriyama and Kanmera, 1979, p. 54-56, pl. 8, figs. 7-13; Hasegawa *et al.*, 1979, pl. 83, figs. 1, 2, 4; Tien, 1979, p. 132-134, pl. 20, figs. 4-6; Kahler and Kahler, 1979, p. 224-225, pl. 3, fig. 3; Sun *et al.*, 1983, p. 37, pl. 9, fig. 3; Chen, 1984, p. 68, pl. 19, fig. 4; Yang, 1985, pl. 2, fig. 28; Tien, 1986a, pl. 7, fig. 11 (same as pl. 20, fig. 5 of Tien, 1979, p. 132-134); Tien, 1986b, pl. 11, fig. 10, pl. 12, figs. 1-3, 5D, 11B; Han *et al.*, 1987, pl. 2, fig. 4; Kobayashi, 1988a, p. 10, pl. 5, figs. 18-21, pl. 6, fig. 18; Kobayashi, 1988b, p. 443-445, figs. 6-1-8; Tien, 1989, pl. 32, figs. 6-7; Ozawa and Kobayashi, 1990, pl. 10, fig. 8.

Pseudodoliolina cf. *pseudolepida* (Deprat). Kawano, 1961, p. 105-107, pl. 10, figs. 8-10.

Pseudodoliolina aff. *pseudolepida pseudolepida* (Deprat). Kanmera, 1963, p. 108-109, pl. 14, figs. 15-18.

Pseudodoliolina ozawai Yabe and Hanzawa. Chen and Yang, 1978, p. 112, pl. 30, figs. 4-5.

Pseudodoliolina sp., Hasegawa *et al.*, 1979, pl. 83, figs. 3, 5-7; Tien, 1989, pl. 32, figs. 8-10 (9: same as pl. 11, fig. 1 of Tien, 1986b).

Material.—Axial sections; ASM25167 from Loc. AL169, ASM25166 from Loc. AL180.5, ASM25168 from Loc. KN4, ASM25169 from Loc. TA261, ASM25170 from Loc. SA119, ASM25171 from Loc. EB98, ASM25172 from Loc. MT253. Sagittal sections; ASM25173, ASM25174 from Loc. TA263. Tangential section; ASM25175 from Loc. KS201.

Description.—Shell medium to large for genus, cylindrical with broadly rounded polar regions and convex lateral slopes. Mature specimens of 11 to 14 volutions, 4.55 to 6.23 mm in length and 1.90 to 3.10 mm in width. Form ratio ranges from 1.97 to 2.51, averaging 2.20 for 16 specimens.

Shell expands gradually through growth with an almost straight axis of coiling. The first volution spherical, but later ones become cylindrical rather rapidly. Radius vectors of the first to thirteenth volutions of illustrated axial section (Figure 7-1) 0.11, 0.17, 0.21, 0.27, 0.32, 0.41, 0.49, 0.59, 0.71, 0.85, 1.06, 1.25 and 1.41 mm, and form ratios 1.00, 1.97, 2.10, 2.30, 2.63, 2.71, 2.80, 2.83, 2.83, 2.74, 2.50, 2.31 and 2.17, respectively.

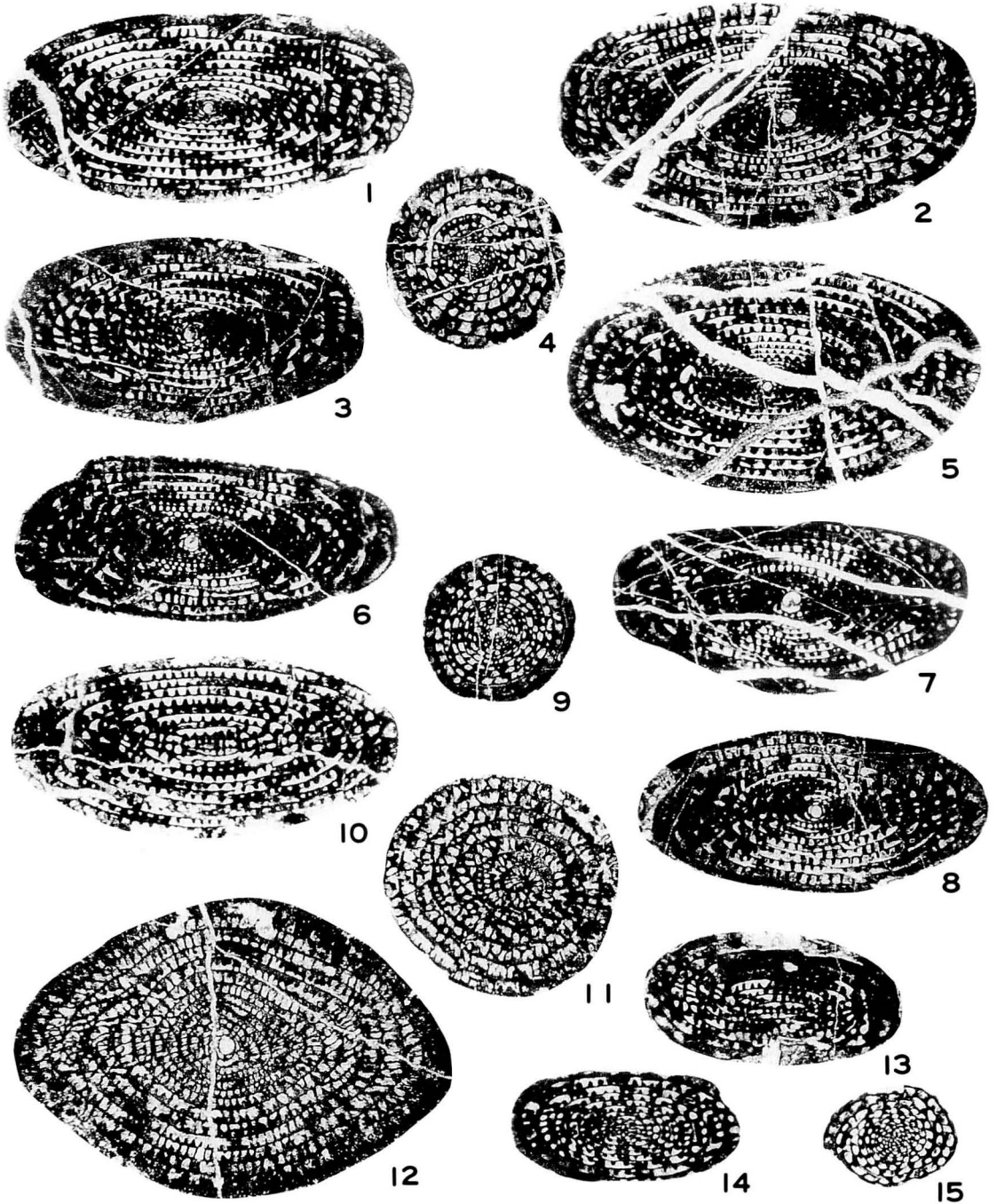


Figure 7. 1-10. *Pseudodoliolina pseudolepida* (Deprat), 1-3, 5-8: axial sections, ASM25170, ASM25169, ASM25167, ASM25171, ASM25166, ASM25168, ASM25172, 4, 9: sagittal sections, ASM25173, ASM25174, 10: tangential section, ASM25175. 11, 12. *Colania douvillei* (Ozawa), 11: diagonal section, ASM25213, 12: axial section, ASM25212. 13-15. *Pseudodoliolina cf. ozawai* Yabe and Hanzawa, 13: tangential section, ASM25177, 14: oblique section, ASM25178, 15: sagittal section, ASM25176. All $\times 10$.

Proloculus commonly spherical but rarely irregular. Its outside diameter varies from 0.150 to 0.300 mm, averaging 0.211 mm for 22 specimens.

Spirotheca thin and composed of a single structureless layer in inner few volutions, but consists of a tectum and a lower, less dense layer in outer ones. Alveolar structure not observable even in outermost volution. Thickness of spirotheca of the first to thirteenth volutions of above-mentioned specimen 0.010, 0.005, 0.010, 0.010, 0.010, 0.015, 0.015, 0.015, 0.010, 0.020, 0.020, 0.020 and 0.025 mm.

Septa numerous and slightly bending anteriorly. They consist of the same elements as the spirotheca.

Parachomata narrow and high, well developed in all volutions, and attain about $\frac{1}{2}$ to $\frac{2}{3}$ of chamber height.

Remarks.—*Pseudodoliolina pseudolepida* (Deprat) is one of the most common species of the genus and widespread in the Middle Permian of the Tethyan province. The Akiyoshi specimens are quite identical with Deprat's original ones.

This species is easily distinguished from *Pseudodoliolina ozawai* Yabe and Hanzawa by a larger shell and greater number of volutions.

Hasegawa *et al.* (1979) reported *Pseudodoliolina* sp. from the *Verbeekina heimi* Subzone (equivalent to the *Verbeekina verbeeki-Afghanella schencki* Zone in this study) in the Kaerimizu area. Judging from their illustrations, *Pseudodoliolina* sp. has a slightly smaller proloculus than *P. pseudolepida* (Deprat). However, this difference is hardly sufficient to warrant the specific separation of these forms.

Occurrence.—Abundant in the *Verbeekina verbeeki-Afghanella schencki* and *Neoschwagerina fusiformis* Zones.

Subfamily Neoschwagerininae Dunbar and Condra, 1927

Genus *Neoschwagerina* Yabe, 1903

Type species.—*Schwagerina craticulifera* Schwager, 1883.

Neoschwagerina craticulifera robusta
Ueno, subsp. nov.

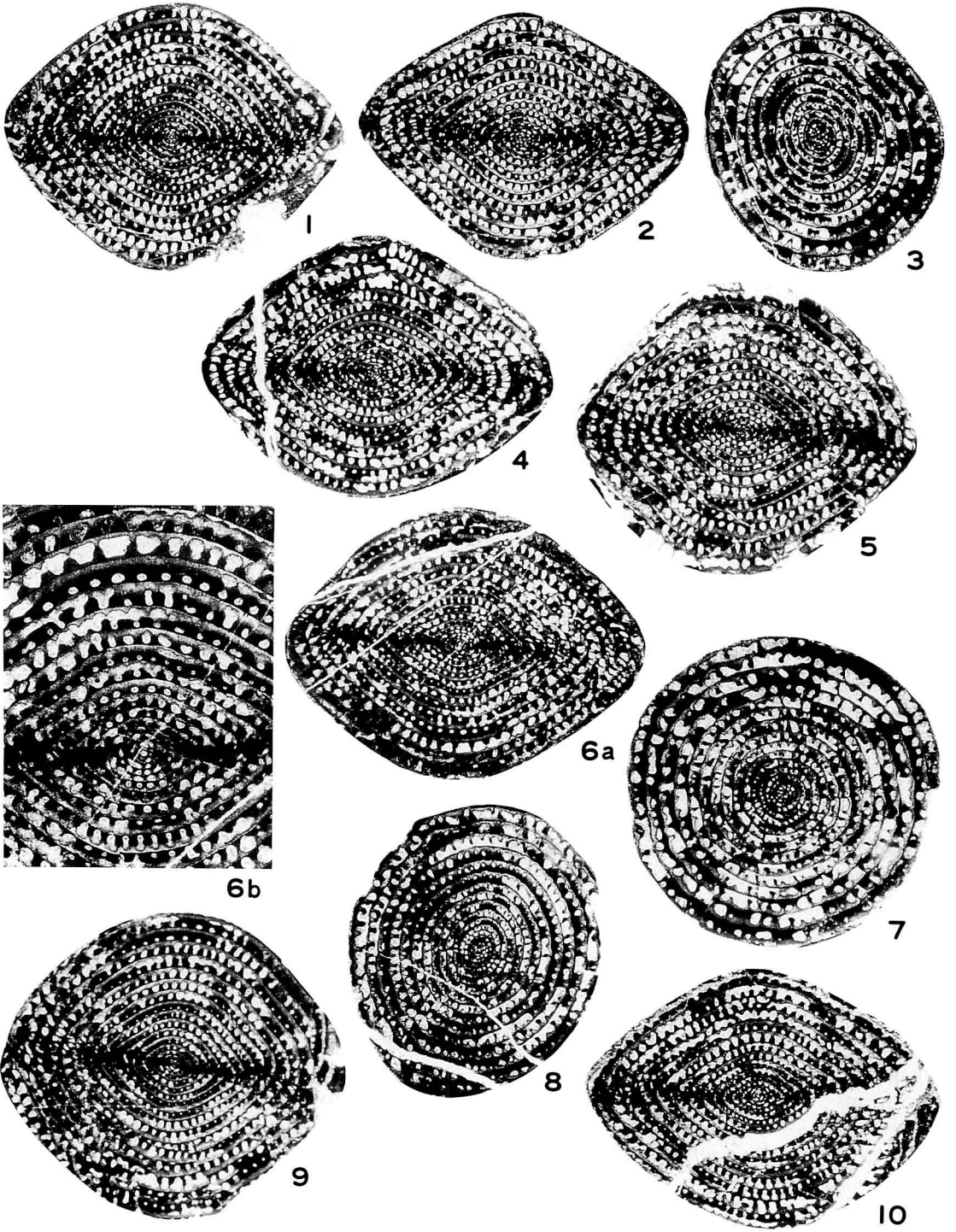
Figures 8-1–10, 10-6–11

Material.—Axial section of the holotype; ASM25179 from Loc. TA246. Axial sections of paratypes; ASM25180 from Loc. TA246, ASM25181 from Loc. AL98, ASM25182 from Loc. AL100, ASM25183 from Loc. AL101, ASM25184 from Loc. AL108, ASM25185 from Loc. KS-AD7, ASM25186 from Loc. KS-AD9, ASM25187 from Loc. KS158, ASM25188 from Loc. NS254. Sagittal sections of paratypes; ASM25189 from Loc. TA246, ASM25190 from Loc. TA247, ASM25191 from Loc. TA250, ASM25192 from Loc. EB68, ASM25193 from Loc. KS155.5. Slightly oblique axial section of paratype; ASM25194 from Loc. AL103.

Diagnosis.—Large *Neoschwagerina* having an inflated fusiform shell with bluntly pointed polar ends, almost straight or slightly convex lateral slopes, very small proloculus, and low, broad and fan-shaped primary transverse septula. Inner few volutions skew-coiled, outer ones planispiral. Parachomata narrow and high.

Description.—Shell large for genus and inflated fusiform with bluntly pointed polar ends. Lateral slopes almost straight or slightly convex. Mature specimens having 16 to 19 volutions, 4.50 to 5.95 mm in length and 3.55 to 4.85 mm in width. Form ratio ranges from 1.06 to 1.44, averaging 1.27 for 15 specimens.

Inner 2 or 3 volutions tightly and skew-coiled. Beyond the third or fourth volution, shell expands gradually with a straight axis of coiling. Radius vectors of the first to seventeenth volutions of the holotype 0.05, 0.08,



0.12, 0.17, 0.22, 0.29, 0.39, 0.51, 0.67, 0.77, 0.91, 1.05, 1.25, 1.43, 1.64, 1.83 and 1.97 mm, and form ratios 0.90, 1.03, 1.25, 1.24, 1.45, 1.62, 1.62, 1.57, 1.51, 1.58, 1.52, 1.49, 1.43, 1.43, 1.38, 1.36 and 1.38, respectively.

Proloculus very small and spherical. Its outside diameter ranges from 0.040 to 0.090 mm, averaging 0.054 mm for 17 specimens.

Spirotheca thin to medium, composed of a tectum and alveolar keriotheca. Thickness of spirotheca of the first to seventeenth volutions of the holotype 0.010, 0.010, 0.015, 0.015, 0.015, 0.030, 0.040, 0.065, 0.055, 0.030, 0.020, 0.030, 0.050, 0.020, 0.030, 0.020 and 0.025 mm. Primary transverse septula low, broad and fan-shaped, and well developed beyond the fourth volution. They are observed immediately above each parachomata and abut tops of parachomata adjacent to septa. No secondary transverse septula developed even in outermost volution.

Septa composed of downward deflections of tectum and alveolar keriotheca. Septal counts of the second to seventeenth volutions of typical sagittal section of paratype (Figure 8-8) 3?, 9, 14, 17, 20, 19, 22, 21, 26, 26, 25, 26, 29, 30, 34 and 33, respectively. Axial septula present beyond the sixth volution. Two axial septula occasionally inserted between 2 adjacent septa in outer volutions.

Parachomata high, rather narrow, and begin to occur in the third volution. They attain a height about $\frac{2}{3}$ that of chambers.

Remarks.—*Neoschwagerina craticulifera robusta*, subsp. nov. is closely similar to *N. craticulifera* (s.s.), especially in the nature of the primary transverse septula and parachomata, but differs from the latter in having a larger shell, more volutions and a smaller form ratio. The present new subspecies also resembles *Neoschwagerina margaritae* Deprat, but differs from the latter in having a smaller shell and a different shell shape. The

morphological characters of *Neoschwagerina craticulifera robusta*, subsp. nov. suggest that the present new subspecies is phylogenetically intermediate between *N. craticulifera* (s.s.) and *N. margaritae* Deprat.

Measurements.—See Table 1.

Occurrence.—Abundant in the *Neoschwagerina craticulifera robusta* Zone.

Neoschwagerina fusiformis

Skinner and Wilde, 1967

Figures 9-1-14

Neoschwagerina fusiformis Skinner and Wilde, 1967, p. 16-17, pl. 19, figs. 1-8; Ding, 1978, p. 288-289, pl. 98, fig. 3; Wang *et al.*, 1981, p. 64-65, pl. 18, figs. 1-2, 11; Chen, 1984, p. 69, pl. 19, fig. 3 (same as pl. 98, fig. 3 of Ding, 1978, p. 288-289).

Material.—Axial sections; ASM25195, ASM25196, ASM25197 from Loc. KN2, ASM25198, ASM25199A,B from Loc. KN4, ASM25200 from Loc. KN21, ASM25201, ASM25202 from Loc. TA265, ASM25203A,B from Loc. AL168. Sagittal sections; ASM25204 from Loc. KN2, ASM25205 from Loc. KN5, ASM25206 from Loc. AL180.

Description.—Shell medium to large for genus and fusiform to elongate fusiform with bluntly pointed poles and almost straight to slightly convex lateral slopes. Mature specimens of 14 to 18 volutions 4.65 to 7.90 mm in length and 2.70 to 4.70 mm in width. Form ratio ranges from 1.43 to 1.90, averaging 1.65 for 17 specimens.

Axis of coiling straight through growth except for inner few volutions of some specimens. Radius vectors of the first to fifteenth volutions of typical axial section (Figure 9-12) 0.08, 0.11, 0.13, 0.18, 0.24, 0.29, 0.35, 0.42, 0.51, 0.69, 0.79, 0.97, 1.13, 1.29 and 1.46 mm, and form ratios 0.53, 0.76, 1.15, 1.66, 1.49, 1.69, 1.89, 2.02, 1.98, 1.71, 1.99, 1.84, 1.77, 1.78 and 1.75, respectively.

← **Figure 8.** 1-10. *Neoschwagerina craticulifera robusta*, subsp. nov., **6a**: axial section of the holotype, ASM25179, **1, 2, 4, 5, 9, 10**: axial sections of paratypes, ASM25184, ASM25180, ASM25181, ASM25188, ASM25186, ASM25182, **3, 7, 8**: sagittal sections of paratypes, ASM25189, ASM25191, ASM25190, ×10, **6b**: enlarged part of **6a**, ×40.

Table 1. Measurements of *Neoschwagerina craticulifera robusta*, subsp. nov. F.R. : From ratio, D.P. : Diameter of proloculus (in mm).

Reg. no.	Figure	Length	Width	F.R.	D.P.	Radius vector																			
						1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	
1	ASM25179	8-6	5.69	4.20	1.35	0.060	0.05	0.08	0.12	0.17	0.22	0.29	0.39	0.51	0.67	0.77	0.91	1.05	1.25	1.43	1.64	1.83	1.97	—	
2	ASM25180	8-2	5.53	3.85	1.44	0.065	0.06	0.09	0.12	0.16	0.21	0.28	0.37	0.49	0.61	0.77	0.92	1.10	1.29	1.47	1.65	1.86	—		
3	ASM25181	8-4	5.50	4.05	1.36	—	0.05	0.07	0.12	0.17	0.22	0.31	0.40	0.52	0.65	0.81	0.95	1.11	1.27	1.49	1.68	1.88	—		
4	ASM25183	10-9	5.60	4.35	1.29	0.050	0.04	0.07	0.10	0.13	0.19	0.25	0.34	0.44	0.57	0.72	0.89	1.04	1.22	1.40	1.55	1.78	1.99	2.19	
5	ASM25184	8-1	5.10	4.05	1.26	0.050	0.05	0.08	0.11	0.15	0.21	0.30	0.40	0.52	0.64	0.75	0.88	1.08	1.27	1.46	1.64	1.82	2.03		
6	ASM25187	10-10	5.18	4.00	1.30	0.045	0.05	0.06	0.10	0.13	0.17	0.25	0.34	0.46	0.57	0.70	0.83	1.00	1.15	1.31	1.46	1.71	1.92	—	
7	ASM25186	8-9	5.15	4.85	1.06	0.045	0.05	0.08	0.11	0.15	0.20	0.29	0.42	0.53	0.67	0.81	0.95	1.12	1.29	1.46	1.67	1.86	2.18	2.39	2.52

	From ratio																			
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	
1	0.90	1.13	1.25	1.24	1.45	1.62	1.62	1.57	1.51	1.58	1.52	1.49	1.43	1.43	1.38	1.36	1.38	—	—	
2	0.73	0.56	0.71	0.94	1.09	1.28	1.45	1.43	1.44	1.42	1.48	1.44	1.41	1.38	1.39	1.40	—	—	—	
3	—	1.28	1.25	1.47	1.52	1.56	1.63	1.52	1.57	1.60	1.56	1.58	1.52	1.47	1.48	1.44	—	—	—	
4	0.60	0.64	0.85	1.15	1.33	1.58	1.66	1.78	1.66	1.58	1.46	1.40	1.34	1.36	1.40	1.36	1.21	—	—	
5	0.70	0.76	0.87	1.00	1.27	1.16	1.37	1.36	1.32	1.44	1.42	1.37	1.39	1.30	1.29	1.26	—	—	—	
6	0.60	0.77	0.75	1.00	1.28	1.31	1.31	1.28	1.34	1.33	1.30	1.28	1.25	1.24	1.27	1.24	1.23	—	—	
7	0.70	0.75	0.87	1.13	1.28	1.50	1.35	1.40	1.37	1.32	1.31	1.23	1.21	1.20	1.18	1.17	1.10	1.09	—	—

	Thickness of spirotheca																			
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	
1	0.010	0.010	0.015	0.015	0.015	0.030	0.040	0.065	0.055	0.030	0.020	0.030	0.050	0.020	0.030	0.020	0.025	—	—	
2	0.005	0.005	0.010	0.010	0.015	0.020	0.025	0.020	0.055	0.045	0.060	0.030	0.045	0.040	0.040	—	—	—	—	
3	0.005	0.005	0.010	0.015	0.015	0.020	0.020	0.030	0.030	0.030	0.080	0.040	0.030	0.070	0.045	0.040	—	—	—	
4	0.005	0.005	0.010	0.010	0.015	0.015	0.025	0.040	0.050	0.040	0.040	0.040	0.040	0.030	0.030	0.075	0.035	0.035	—	
5	0.005	0.005	0.010	0.010	0.020	0.025	0.030	0.025	0.060	0.055	0.060	0.025	0.030	0.025	0.030	0.020	0.025	—	—	
6	0.005	0.010	0.010	0.015	0.015	0.020	0.020	0.025	0.050	0.030	0.030	0.025	0.030	0.025	0.040	0.040	0.030	—	—	
7	0.010	0.010	0.015	0.020	0.020	0.045	0.030	0.035	0.040	0.035	0.025	0.030	0.035	0.040	0.030	0.050	0.030	0.040	—	—

Proloculus small and spherical. Its outside diameter varies from 0.030 to 0.130 mm, averaging 0.081 mm for 21 specimens.

Spirotheca rather thin for genus and composed of a tectum and alveolar keriotheca. Thickness of spirotheca of the first to fifteenth volutions of specimen mentioned above 0.005, 0.005, 0.005, 0.010, 0.025, 0.030, 0.030, 0.025, 0.030, 0.030, 0.025, 0.025, 0.025, 0.035 and 0.040 mm. Primary transverse septula thin and well developed beyond the third volution. They occur immediately above each parachomata and abut tops of parachomata adjacent to septa. One secondary transverse septulum rarely and rather inconstantly inserted between 2 adjacent primary transverse septula.

Septa thin, bending anteriorly and composed of downward deflections of spirothecal element. Septal counts of the third to sixteenth volutions of typical sagittal section (Figure 9-2) 12, 14, 15, 15, 16, 17, 24, 23, 27, 27, 30, 28, 30? and 28?. Axial septula begin to occur in the fifth volution. One axial septulum inserted between 2 adjacent septa in inner volutions, but usually 2, rarely 3 in outer ones.

Parachomata narrow and high, reaching about $\frac{2}{3}$ the height of chambers.

Remarks.—*Neoschwagerina fusiformis* was originally described by Skinner and Wilde (1967) from the Permian of Tunisia. The holotype specimen (Skinner and Wilde, 1967, pl. 19, fig. 1) has a minute proloculus and skew-coiled inner volutions, and is considered to be a microspheric form of the species. Most of the Akiyoshi specimens are quite similar to one of the paratypes (Skinner and Wilde, 1967, pl. 19, fig. 2).

This species somewhat resembles *Neoschwagerina haydeni* Dutkevich and Khabakov in its essential morphological characters, especially in the nature of septula and parachomata. However, the former can be distinguished from the latter in having a more elongate shell and larger form ratio.

Occurrence.—Abundant in the *Neo-*

schwagerina fusiformis Zone.

Neoschwagerina haydeni Dutkevich
and Khabakov, 1934

Figures 10-1-5

Neoschwagerina craticulifera (Schwager). Hayden, 1909, p. 248-249, pl. 21, figs. 1-7.

Neoschwagerina craticulifera haydeni Dutkevich and Khabakov, 1934, p. 94-99, pl. 2, figs. 6-8, pl. 3, figs. 1-2; Thompson, 1946, p. 155-156, pl. 23, figs. 12-13; Thompson, 1948, pl. 20, figs. 3-4 (same as pl. 23, figs. 12-13 of Thompson, 1946); Kanmera, 1957, pl. 19, fig. 24 (same as pl. 23, fig. 12 of Thompson, 1946); Toriyama, 1958, p. 220-223, pl. 41, figs. 7-8 (not pl. 41, fig. 6); Suyari, 1962, p. 35-36, pl. 11, fig. 5; Ishizaki, 1962, p. 173-175, pl. 12, figs. 4-6.

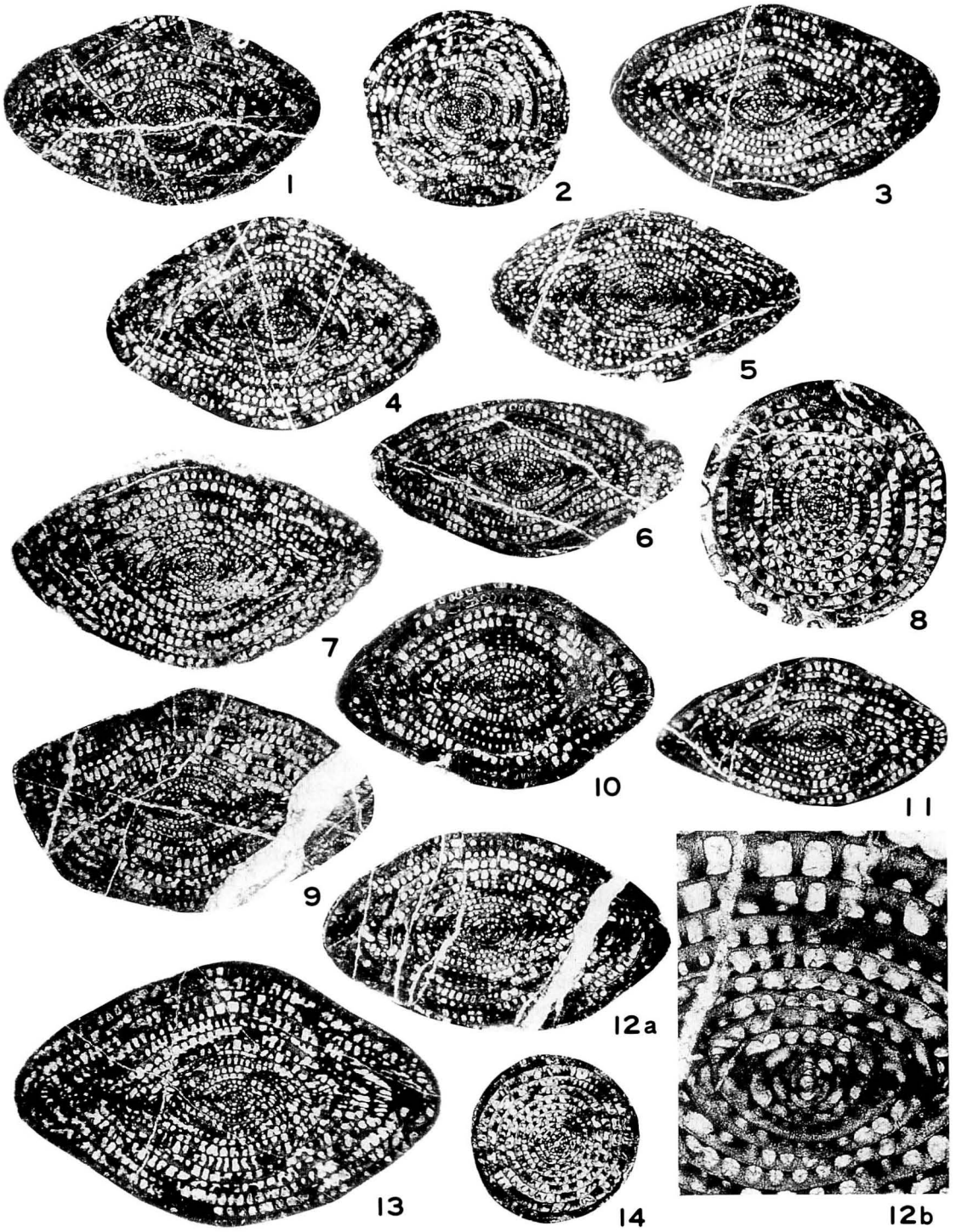
Neoschwagerina haydeni Dutkevich and Khabakov. Honjo, 1959, p. 147-149, pl. 3, fig. 10; Minato and Honjo, 1959, pl. 3, fig. 2; Sheng, 1963, p. 103-104, 236-237, pl. 32, figs. 1-8; Zhang and Wang, 1974, p. 292, pl. 151, fig. 7; Chen and Yang, 1978, p. 116, pl. 32, figs. 3-5; Liu *et al.*, 1978, p. 89, 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; 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; Lin, 1984, p. 171-172, pl. 14, fig. 12; Chen, 1984, p. 69, pl. 21, fig. 2; Yang, 1985, pl. 2, fig. 12; Kobayashi, 1988b, p. 445-447, figs. 7 - 2-11; Ozawa and Kobayashi, 1990, pl. 10, figs. 12-14.

Neoschwagerina cf. haydeni Dutkevich and Khabakov. Ding, 1978, p. 289, pl. 101, fig. 2.

Material.—Axial sections; ASM25207 from Loc. AL178, ASM25208 from Loc. AL180, ASM25209 from Loc. KN21, ASM25210 from Loc. SA148. Sagittal section; ASM25211 from Loc. KN19.

Description.—Shell medium to large for genus and thickly fusiform with rounded polar ends and almost straight lateral slopes. Mature specimens having 15 to 17 volutions, 5.10 to 6.00 mm in length and 3.80 to 4.15 mm in width, giving form ratios of 1.31 to 1.54.

Axis of coiling straight except for inner few volutions of some specimens. Shell expands gradually through growth. Radius vectors of the first to sixteenth volutions of illustrated



axial section (Figure 10-1) 0.06, 0.10, 0.14, 0.20, 0.26, 0.35, 0.43, 0.52, 0.63, 0.76, 0.88, 1.03, 1.16, 1.31, 1.46 and 1.66 mm, and form ratios 0.58, 0.74, 0.81, 1.10, 1.29, 1.31, 1.53, 1.63, 1.66, 1.61, 1.59, 1.53, 1.54, 1.58, 1.53 and 1.50, respectively.

Proloculus small and spherical, being 0.060 to 0.070 mm in outside diameter averaging 0.063 mm for 3 specimens.

Spirotheca thin for genus and composed of a tectum and alveolar keriotheca. Thickness of spirotheca of the first to sixteenth volutions of above-mentioned specimen 0.005, 0.005, 0.010, 0.015, 0.015, 0.020, 0.015, 0.020, 0.020, 0.035, 0.035, 0.030, 0.025, 0.025, 0.025 and 0.030 mm. Thin primary transverse septula first appear in the third or fourth volution. They develop immediately above each parachomata and abut tops of parachomata adjacent to septa. One secondary transverse septulum sometimes inserted between 2 adjacent primary ones.

Septa thin, bending anteriorly and composed of downward deflections of tectum and alveolar keriotheca. Axial septula begin to occur in the fifth volution. Beyond the seventh volution, 2 axial septula commonly observed. Three axial septula rarely inserted between 2 adjacent septa in outer few volutions.

Parachomata narrow and high adjacent to septa, but low and semicircular in central part of chamber.

Remarks.—*Neoschwagerina haydeni* Dutkevich and Khabakov somewhat resembles *N. craticulifera robusta*, subsp. nov., described above, in shell shape. However, the former can be easily distinguished from the latter in having a thinner spirotheca, more slender transverse septula and parachomata.

Occurrence.—Common in the *Neoschwagerina fusiformis* Zone.

Subfamily Lepidolininae
Miklukho-Maklay, 1958

Genus *Colania* Lee, 1934 emend.
Ozawa, 1970

Type species.—*Colania kwangiana* Lee, 1934.

Colania douvillei (Ozawa, 1925)

Figures 7-11-12

Neoschwagerina globosa (Yabe). Douvillé, 1906, p. 182, pl. 17, fig. 18, figs. 1-2; Deprat, 1912, p. 51, pl. 4, figs. 1-2 (not pl. 4, figs. 3-4); Deprat, 1913, p. 55; Deprat, 1914, p. 29-30; Ozawa, 1922, p. 368-372; Colani, 1924, p. 152-153, pl. 23, figs. 1-2, 4-14, 22-34, 36-38, pl. 25, figs. 9, 13, pl. 26, figs. 3-5.

Neoschwagerina douvillei Ozawa, 1925a, pl. 3, fig. 6, pl. 4, fig. 5; Ozawa, 1925b, p. 55-57, pl. 11, figs. 5-7; Huzimoto, 1936, p. 114-115, pl. 23, figs. 1-5; Toriyama, 1947, p. 78-79, pl. 17, fig. 8; Chen, 1956, p. 12, 58-59, pl. 13, figs. 3-4, 6-7 (not pl. 13, fig. 5, pl. 14, fig. 7); Toriyama, 1958, p. 223-227, pl. 41, figs. 9-13, pl. 42, figs. 1-6; Sakagami, 1958, p. 92-93, pl. 14, figs. 7-10; Kanuma, 1960, p. 70-71, pl. 13, figs. 5-7; Nogami, 1961, p. 180-183, pl. 5, figs. 1-5; Sada, 1961, p. 123-125, pl. 12, figs. 1-8; Sheng, 1963, p. 102-103, 235-236, pl. 33, figs. 1-7; Hanzawa and Murata, 1963, pl. 4, figs. 3-4, pl. 17, figs. 1-10; Sheng, 1966, p. 146, pl. 25, fig. 1; Sheng and Sun, 1975, p. 51-52, pl. 13, figs. 11-14; Lin *et al.*, 1977, p. 92, pl. 28, fig. 12; Liu *et al.*, 1978, p. 89, pl. 24, fig. 1; Han, 1980, p. 90, pl. 34, figs. 13-15; Xie, 1982, p. 69, pl. 34, fig. 1; Wang *et al.*, 1982, p. 106, pl. 30, fig. 5.

Neoschwagerina cf. douvillei Ozawa. Kawano, 1960, pl. 25, figs. 12-13; Kawano, 1961, p. 107-108, pl. 11, figs. 2-5; Yoshimura, 1961, pl. 3, fig. 4; Suyari, 1962, p. 36, pl. 10, fig. 14.

Colania douvillei (Ozawa). Ozawa, 1970a, pl. 7, figs. 8-10; Choi, 1972, p. 371-372, pl. 46, figs. 1-6; Toriyama, 1975, p. 103, pl. 20, figs. 22-26; Toriyama and Kanmera, 1977, p. 17-24, pl. 2, figs. 7-17, pl. 3, figs. 1-16; Ota, 1977, pl. 1, figs. 3-4; Sakagami and Miyama, 1988, fig. 1-15; Kobayashi, 1988a, p. 13, pl. 7, figs. 7-9, pl. 8, figs. 1-8; Ozawa and Kobayashi, 1990, pl. 11, figs. 1-2.

Gifuella douvillei (Ozawa). Hasegawa *et al.*, 1979,

← **Figure 9.** 1-14. *Neoschwagerina fusiformis* Skinner and Wilde, **1, 3-7, 9-11, 12a, 13**: axial sections, ASM25203A, ASM25198, ASM25196, ASM25195, ASM25197, ASM25200, ASM25203B, ASM25201, ASM25199A, ASM25199B, ASM25202, **2, 8, 14**: sagittal sections, ASM25204, ASM25205, ASM25206, ×10, **12b**: enlarged part of **12a**, ×40.

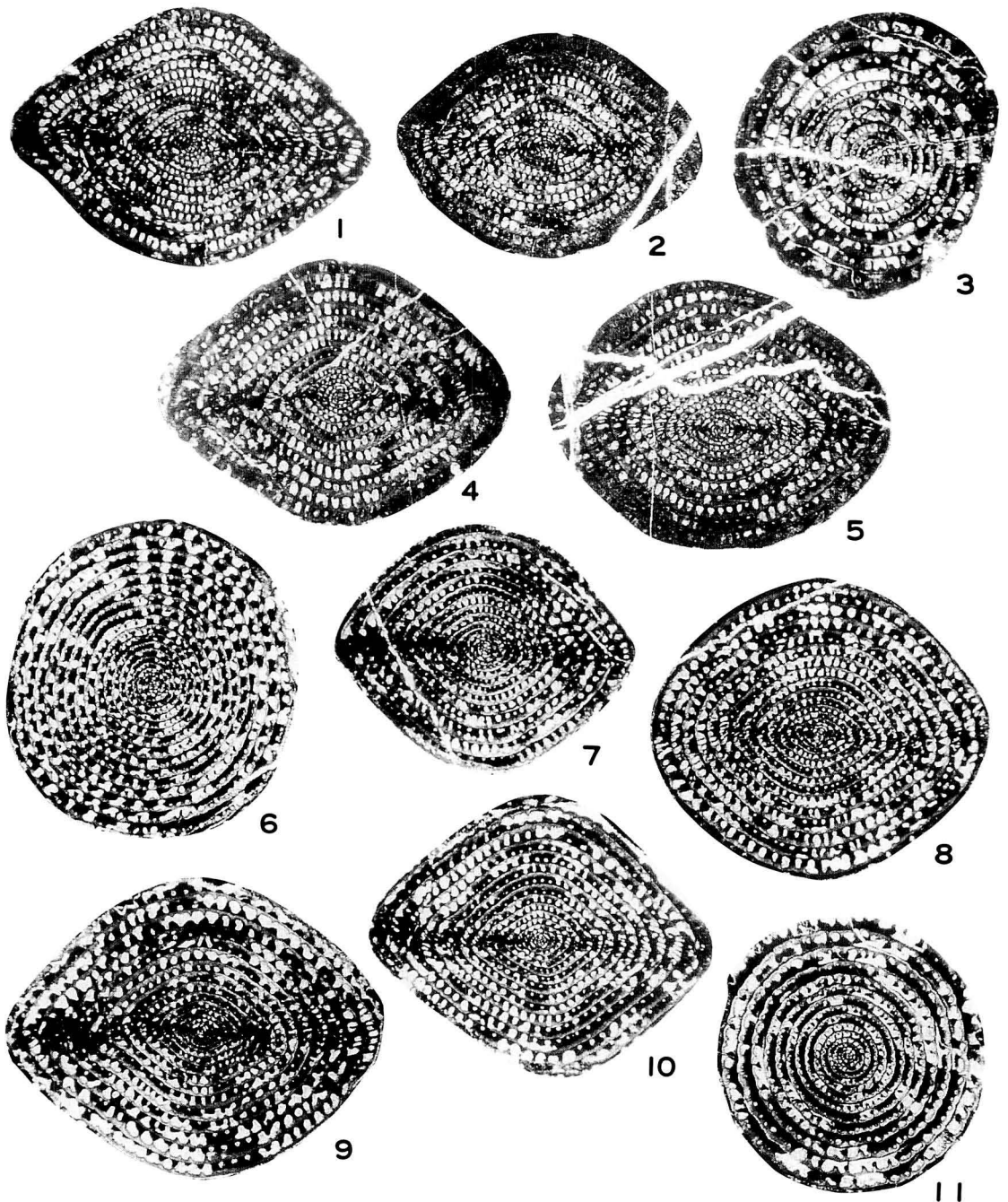


Figure 10. 1-5. *Neoschwagerina haydeni* Dutkevich and Khabakov, 1, 2, 4, 5: axial sections, ASM25209, ASM25208, ASM25210, ASM25207, 3: sagittal section, ASM25211. 6-11. *Neoschwagerina craticulifera robusta*, subsp. nov., 7, 9, 10: axial sections of paratypes, ASM25185, ASM25183, ASM25187, 6, 11: sagittal sections of paratypes, ASM25193, ASM25192, 8: slightly oblique axial section of paratype, ASM25194. All $\times 10$.

- pl. 86, figs. 1-6.
 not *Neoschwagerina douvillei* Ozawa. Gubler, 1935, p. 111-113, pl. 6, fig. 2, pl. 7, figs. 7-8, 10-11, pl. 8, fig. 6; Ishii, 1966, pl. 5, fig. 4; Igo, 1967, pl. 7, figs. 6-8, pl. 8, fig. 7; Tien, 1970, p. 48-49, pl. 11, figs. 1-15, pl. 12, figs. 1-13; Wang *et al.*, 1981, p. 62-63, pl. 18, fig. 5; Yang, 1985, pl. 2, fig. 14.
 not *Colania douvillei* (Ozawa). Ozawa, 1970b, p. 35-38, pl. 3, figs. 1-10, pl. 4, figs. 1-10, pl. 5, figs. 1-5, pl. 6, figs. 1-9; Tien, 1979, p. 137-139, pl. 22, figs. 1-10, pl. 23, figs. 1-2; Tien, 1986a, pl. 8, fig. 2 (same as pl. 22, fig. 2 of Tien, 1979); Tien, 1986b, pl. 11, figs. 1-6, 9A; Tien, 1989, pl. 33, figs. 1-6(2-3: same as pl. 11, figs. 5, 1 of Tien, 1986b).
 not? *Neoschwagerina douvillei* Ozawa. Chen and Yang, 1978, p. 117, pl. 32, figs. 7-9.

Material.—Axial section; ASM25212. Diagonal section; ASM25213. Both from Loc. EB111.

Description.—The following description is based on one axial section (Figure 7-12).

Shell large and inflated fusiform with broadly rounded polar ends and straight axis of coiling. Length and width of shell having 13 volutions, 6.80 mm and 4.55 mm, respectively. Form ratio about 1.50. Shell expands gradually through growth. Radius vectors of the first to twelfth volutions 0.22, 0.33, 0.44, 0.54, 0.67, 0.79, 0.96, 1.16, 1.36, 1.56, 1.74 and 1.95 mm, and form ratios 0.91, 1.15, 1.22, 1.28, 1.37, 1.48, 1.52, 1.48, 1.57, 1.49, 1.53 and 1.51, respectively. Proloculus somewhat irregular, being 0.210 mm in outside diameter. Spirotheca thin and composed of a tectum and alveolar keriotheca. Thickness of spirotheca of the first to twelfth volutions 0.015, 0.030, 0.020, 0.025, 0.020, 0.025, 0.040, 0.030, 0.025, 0.035, 0.035 and 0.040 mm. Primary transverse septula thin and begin to appear in the second volution. No secondary transverse septula present. Parachomata narrow and high, meeting the tops of primary transverse septula adjacent to septa.

Remarks.—*Colania douvillei* (Ozawa) is widespread in the Middle Permian rocks in the eastern part of the Tethyan province, and also in the huge limestone masses in the Inner Zone of southwest Japan, such as Akiyoshi,

Taishaku, Atetsu and Omi. The present specimens agree closely with ones reported from these limestone plateaus.

Occurrence.—Rare in the *Colania douvillei* Zone.

Subfamily Sumatrininae Silvestri, 1933

Genus *Afghanella* Thompson, 1946

Type species.—*Afghanella schencki* Thompson, 1946.

Afghanella ozawai Hanzawa, 1954

Figures 11-1-17

Neoschwagerina (Yabeina) schellwieni (Deprat). Ozawa, 1925a, pl. 2, figs. 8-10.

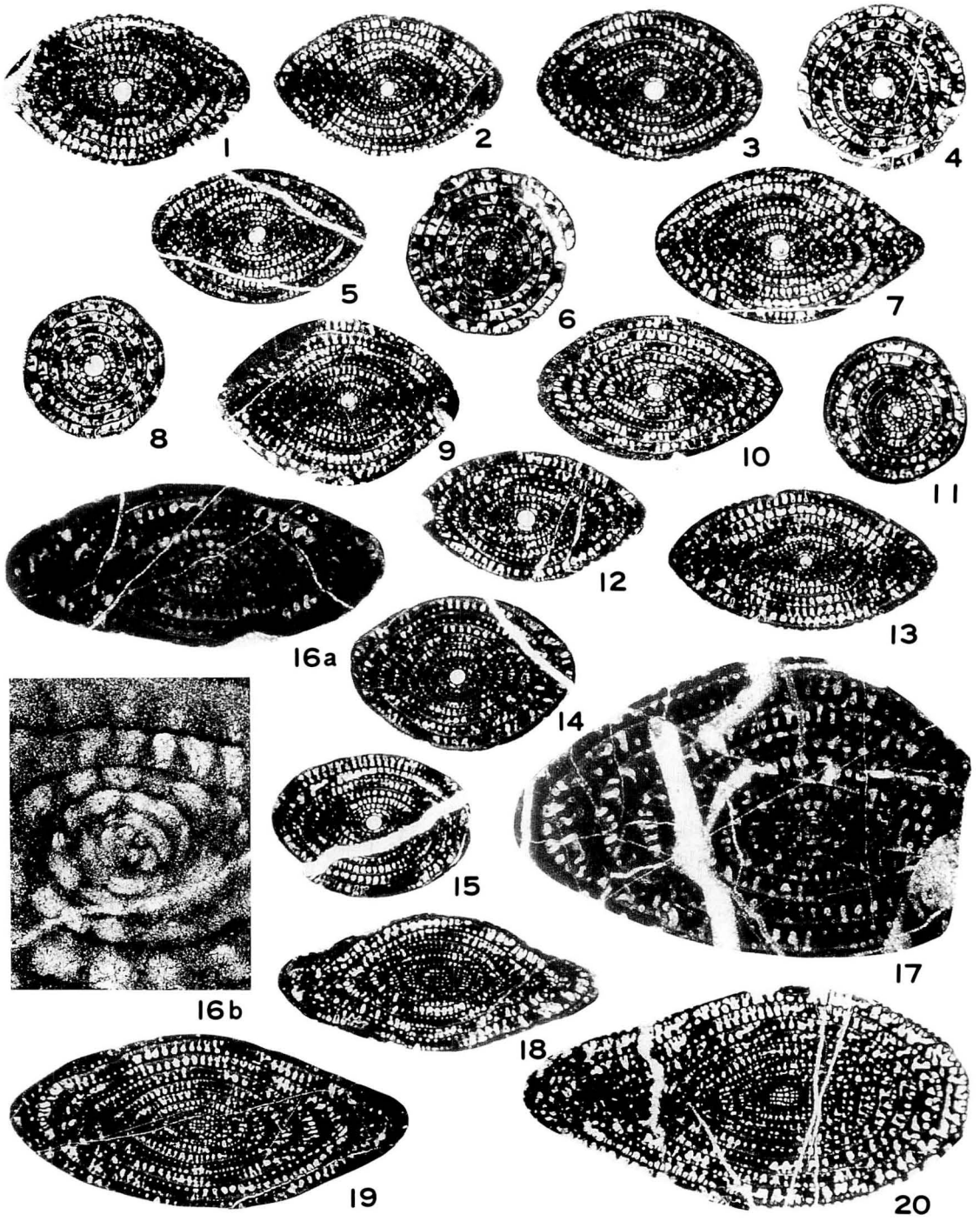
Yabeina schellwieni (Deprat). Ozawa, 1925b, p. 60-61, pl. 10, figs. 3a, 4 (4: same as pl. 2, fig. 9 of Ozawa, 1925a).

Cancellina schellwieni (Deprat). Ozawa, 1927, p. 161, pl. 34, fig. 18 (same as pl. 2, fig. 9 of Ozawa, 1925a), pl. 44, fig. 1b, pl. 45, fig. 3.

Afghanella ozawai Hanzawa, 1954, p. 3-7, pl. 1, figs. 1-6, pl. 2, figs. 1-4; Kanmera, 1957, pl. 19, figs. 12-13; Toriyama, 1958, p. 252-254, pl. 48, figs. 11, 13-14 (not pl. 48, figs. 12, 15-17), Kawano, 1961, p. 117-119, pl. 15, figs. 3-11; Hanzawa and Murata, 1963, pl. 2, figs. 1-2; Ozawa, 1970a, pl. 6, figs. 6-7 (same as pl. 19, figs. 12-13 of Kanmera, 1957); Lin *et al.*, 1977, p. 95, pl. 30, fig. 3; Hasegawa *et al.*, 1979, pl. 82, figs. 11-16; Xie, 1982, p. 72, pl. 35, fig. 6 (same as pl. 30, fig. 3 of Lin *et al.*, 1977, p. 95); Kobayashi, 1988a, p. 14, pl. 5, figs. 22-25; Ozawa and Kobayashi, 1990, pl. 10, figs. 1-2.

Afghanella schencki Thompson. Toriyama, 1958, p. 250-251, pl. 1?, 2, 4-5, 10 (not pl. 48, figs. 3, 6-9); Ota, 1977, pl. 2, figs. 1-2.

Material.—Axial sections of megalospheric form; ASM25214 from Loc. EB49, ASM25215, ASM25216 from Loc. EB50, ASM25217, ASM25218 from Loc. EB56, ASM25219, ASM25220 from Loc. TA231, ASM25221 from Loc. MT210, ASM25222 from Loc. NS220, ASM25223 from Loc. SF49, ASM25224A from Loc. KS-AD24. Sagittal sections of megalospheric form; ASM25224B from Loc. KS-AD24, ASM25225 from Loc. SF33, ASM25226 from Loc. AL92,



ASM25227 from Loc. EB49. Axial sections of microspheric form; ASM25228 from Loc. SA56, ASM25229 from Loc. AL90.

Description.—Shell small to medium for genus and inflated fusiform to fusiform with bluntly pointed poles. Dimorphism well observed. Megalospheric specimens having 7 to 9 volutions, 2.55 to 4.20 mm in length and 1.53 to 2.53 mm in width. Form ratio ranges from 1.38 to 1.99, averaging 1.67 for 20 specimens. Microspheric form of 9 to 10 volutions 2.95 to 4.55 mm in length and 1.40 to 2.30 mm in width, giving form ratios of 1.98 to 2.11.

Axis of coiling straight throughout in megalospheric form. Inner 2 or 3 volutions tightly and skew coiled in microspheric form. Radius vectors of the first to seventh volutions of well oriented axial section of megalospheric form (Figure 11-2) 0.15, 0.22, 0.32, 0.44, 0.58, 0.73 and 0.92 mm, and form ratios 1.40, 1.64, 1.62, 1.66, 1.72, 1.67 and 1.65, respectively.

Proloculus of megalospheric form large for shell size, spherical to somewhat irregular, being 0.165 to 0.320 mm in outside diameter, averaging 0.239 mm for 49 specimens. Proloculus of microspheric form minute and spherical, being 0.030 to 0.040 mm in outside diameter, averaging 0.036 mm for 5 specimens.

Spirotheca thin to medium, composed of a tectum and alveolar keriotheca. Thickness of spirotheca of the first to seventh volutions of above-mentioned specimen 0.010, 0.025, 0.040, 0.025, 0.070?, 0.050 and 0.030 mm.

Primary transverse septula developed in all volutions. Their tips slightly swollen. Lower edges of primary transverse septula in contact with tops of parachomata adjacent to

septa. One secondary transverse septulum inserted between 2 adjacent primary transverse septula in outer volutions.

Septa consist of downward deflections of tectum and anterior and posterior extensions of keriotheca. Lower half of septa usually solidified and pendant-shaped in cross section. Septal counts of the first to eighth volutions of one illustrated sagittal section (Figure 11-4) 8, 18, 23, 23, 24, 26, 28? and 31?. Axial septula begin to appear in the second or third volution. Two axial septula usually inserted between 2 adjacent septa. Parachomata massive and triangular in transverse section, rarely narrow and high, and well developed in all volutions.

Remarks.—Small shell size and the nature of axial and transverse septula in *Afghanella ozawai* Hanzawa indicate that it is one of the most primitive species in this genus. The stratigraphic position of the present species also supports this conclusion.

Afghanella ozawai Hanzawa somewhat resembles *A. robbinsae* and *A. africana*, both described by Skinner and Wilde (1967) from the Permian of Tunisia. However, the former differs from the latter two in having a thicker spirotheca and fewer axial septula between 2 adjacent septa.

Occurrence.—Abundant in the *Afghanella ozawai* Zone.

Afghanella schencki Thompson, 1946

Figures 12-1-11

Afghanella schencki Thompson, 1946, p. 153-155, pl. 25, figs. 1-12; Thompson, 1948, pl. 18, figs. 1-5 (same as pl. 25, figs. 1-3, 7, 10 of Thompson, 1946, p. 153-155); Chen, 1956, p. 14, 67-68, pl. 12, figs. 4-9; Toriyama, 1958, p. 250-251, pl. 48, figs. 3, 6-9 (not 1?, 2, 4-5, 10); Sheng, 1958, p.

← **Figure 11.** 1-17. *Afghanella ozawai* Hanzawa, 1-3, 5, 7, 9, 10, 12-15: axial sections of megalospheric form, ASM25217, ASM25215, ASM25224A, ASM25218, ASM25220, ASM25214, ASM25219, ASM25216, ASM25221, ASM25222, ASM25223, 4, 6, 8, 11: sagittal sections of megalospheric form, ASM25226, ASM25225, ASM25227, ASM25224B, ×10, 16a, 17: axial sections of microspheric form, ASM25229, ASM25228, ×20, 16b: enlarged part of 16a showing minute proloculus and skew coiled juvenile volutions, ×100. 18-20: *Afghanella* sp., tangential sections, ASM25230, ASM25231, ASM25232, ×10.

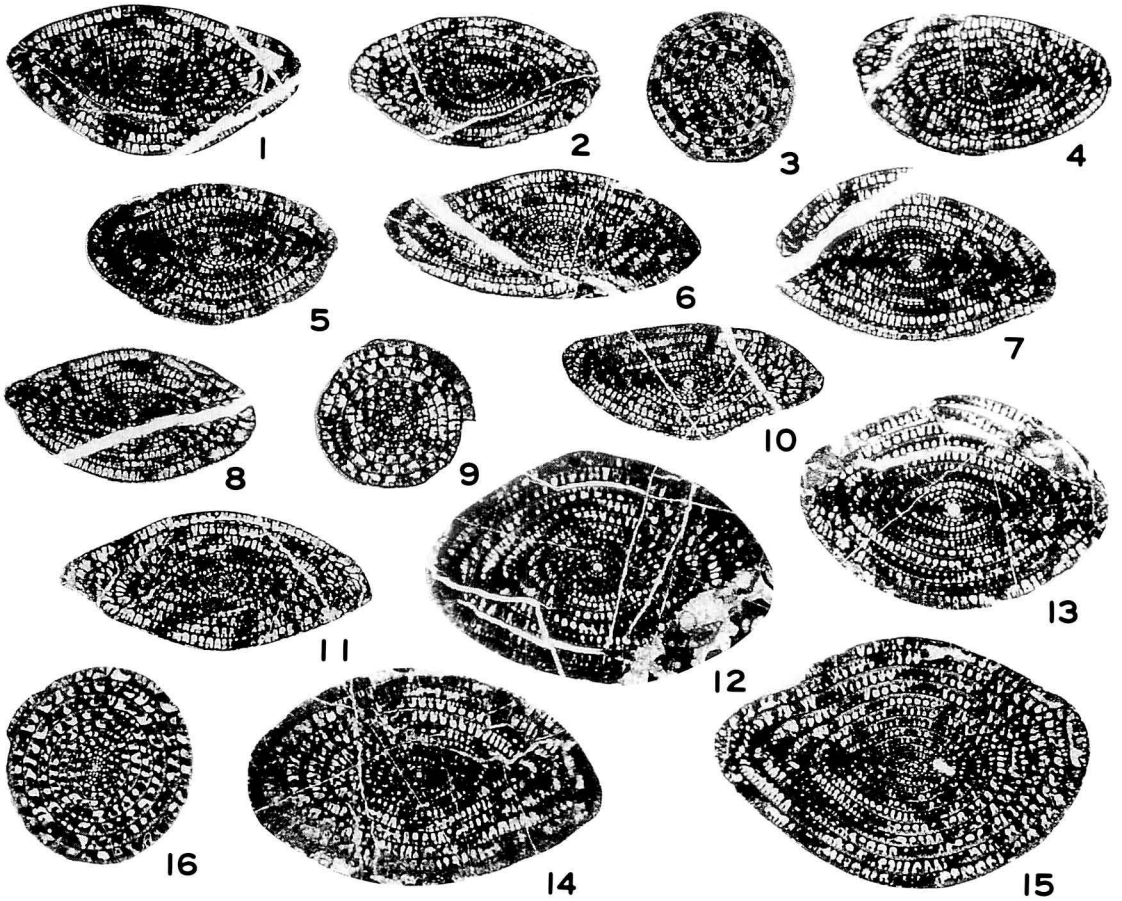


Figure 12. 1-11. *Afghanella schencki* Thompson, 1, 2, 4-8, 10, 11: axial sections, ASM25238, ASM25235A, ASM25235B, ASM25234, ASM25240, ASM25236, ASM25237, ASM25239, ASM25233, 3, 9: sagittal sections, ASM25242, ASM25241. 12-16. *Afghanella* cf. *sumatrinaeformis* (Gubler), 12-15: axial sections, ASM25244, ASM25245, ASM25246, ASM25243, 16: sagittal section, ASM25247. All $\times 10$.

277, 289-290, pl. 4, figs. 9-10; Sheng, 1963, p. 109-110, 244-245, pl. 36, fig. 20; Pasini, 1965, pl. 17, fig. 1a, 1b (same as pl. 25, fig. 12, 7, of Thompson, 1946, p. 153-155); Sheng, 1966, p. 151, pl. 26, fig. 6; Leven, 1967, p. 198, pl. 36, figs. 4, 7-8, pl. 37, fig. 3; Zhang and Wang, 1974, p. 291, pl. 151, fig. 1; Rozovskaya, 1975, pl. 33, figs. 5-7 (same as pl. 25, figs. 2-3, 7 of Thompson, 1946, p. 153-155); Lin *et al.*, 1977, p. 95, pl. 30, fig. 4; Chen and Yang, 1978, p. 121, pl. 34, figs. 3-4; Liu *et al.*, 1978, p. 96, pl. 23, fig. 4; Kahler and Kahler, 1979, p. 251-252, pl. 8, fig. 5, pl. 9, fig. 2; Hasegawa *et al.*, 1979, pl. 82, figs. 5-10; Da and Sun, 1983, p. 113, pl. 30, fig. 3; Sun *et al.*, 1983, p. 39-40, pl. 10, fig. 5; Chen, 1984, p. 71-72, pl. 22, fig. 1; Sun and Zhang, 1985, p. 506, pl. 1, figs.

7, 9-10; Yang, 1985, pl. 3, fig. 21; Loeblich and Tappan, 1988, pl. 306, figs. 3-6 (same as pl. 25, figs. 2-3, 6-7 of Thompson, 1946, p. 153-155); Ozawa and Kobayashi, 1990, pl. 10, figs. 5-7.

Afghanella ozawai Hanzawa. Toriyama, 1958, p. 252-254, pl. 48, figs. 12, 15-17 (not pl. 48, figs. 11, 13-14).

Afghanella schencki schencki Thompson. Toriyama and Kanmera, 1979, p. 58-61, pl. 9, figs. 8-24.

Material.—Axial sections; ASM25233 from Loc. MT240, ASM25234 from Loc. MT243, ASM25235A,B from Loc. SA119, ASM25236 from Loc. SA120, ASM25237

from Loc. SA130, ASM25238 from Loc. SF69, ASM25239 from Loc. TA254, ASM25240 from Loc. EB97. Sagittal sections; ASM25241 from Loc. SA130, ASM25242 from Loc. MT239.

Description.—Shell small to medium for genus and elongate fusiform with bluntly pointed polar regions and almost straight to slightly convex lateral slopes. Mature shell of 9 to 11 volutions 3.33 to 4.55 mm in length and 1.50 to 2.35 mm in width. Form ratio ranges from 1.74 to 2.37, averaging 1.96 for 18 specimens.

Shell expands gradually through growth. Axis of coiling straight throughout. Radius vectors of the first to ninth volutions of typical axial section (Figure 12-1) 0.12, 0.16, 0.25, 0.33, 0.43, 0.55, 0.68, 0.83 and 0.99 mm, and form ratios 1.48, 1.81, 1.80, 1.85, 2.00, 1.96, 1.96, 1.94 and 1.86, respectively.

Proloculus small and spherical. Its outside diameter varies from 0.070 to 0.195 mm, averaging 0.121 mm for 19 specimens.

Spirotheca thin and consists of a tectum and probably very thin alveolar keriotheca. Thickness of spirotheca of the first to ninth volutions of specimen mentioned above 0.015, 0.025, 0.020, 0.015, 0.025, 0.015, 0.020, 0.025 and 0.025 mm.

Primary transverse septula very thin and developed in all volutions. Tips of primary transverse septula slightly swollen and in contact with tops of parachomata adjacent to septa. One secondary transverse septulum inserted between 2 adjacent primary transverse septula in outer 3 or 4 volutions.

Septa thin and bending anteriorly. Tips of septa solidified and pendant-shaped. Septal counts of the first to tenth volutions of illustrated sagittal section (Figure 12-3) 9, 14, 16, 18, 16, 18, 21, 19, 21 and 26, respectively. Axial septula first appear in the fifth volution. Two, rarely 3 axial septula observed in outer 3 or 4 volutions. Parachomata narrow and high.

Remarks.—*Afghanella schencki* was originally described by Thompson (1946) from

the Bamian Limestone of Afghanistan. The proloculus in the Akiyoshi specimens is slightly smaller than that in the original ones.

Afghanella schencki Thompson can be easily distinguished from *A. ozawai* Hanzawa in having a more elongate shell, more volutions, smaller proloculus, thinner spirotheca and more developed primary transverse and axial septula. The stratigraphic distribution of these two species is also different.

Occurrence.—Abundant in the *Verbeekina verbeeki-Afghanella schencki* Zone.

Afghanella cf. *sumatrinaeformis*
(Gubler, 1935)

Figures 12-12-16

Compare—

Neoschwagerina annae (Volz). Hayden, 1909, p. 250-251, pl. 22, figs. 8-14.

Neoschwagerina sumatrinaeformis Gubler, 1935, p. 123-127, pl. 5, figs. 3-4, 10, 17, pl. 7, fig. 2.

Sumatrina sumatrinaeformis (Gubler). Ciry, 1941, pl. 1, figs. 8-9.

Afghanella sumatrinaeformis (Gubler). Kochansky-Devidé and Ramovš, 1955, p. 391-392, 417, pl. 5, figs. 1-10; Chen, 1956, p. 14, 68-69, pl. 7, figs. 9-11; Kanmera, 1957, pl. 19, figs. 16-17 (same as pl. 5, figs. 3-4 of Gubler, 1935, p. 123-127); Sheng, 1966, p. 152, pl. 22, fig. 11 (same as pl. 7, fig. 9 of Chen, 1956, p. 14, 68-69); Leven, 1967, p. 198-199, pl. 37, figs. 1-2; Ozawa, 1970a, pl. 6, figs. 10-11 (same as pl. 5, figs. 3-4 of Gubler, 1935, p. 123-127); Tien, 1970, p. 55, pl. 13, figs. 9-10, pl. 14, figs. 5-9; Rozovskaya, 1975, pl. 33, figs. 8-9 (same as pl. 5, figs. 3-4 of Gubler, 1935, p. 123-127); Toriyama and Kanmera, 1979, p. 63-68, pl. 10, figs. 14-24; Yang, 1985, pl. 3, fig. 22; Loeblich and Tappan, 1988, pl. 306, figs. 7-9 (same as pl. 5, figs. 3-4, 10 of Gubler, 1935, p. 123-127).

Afghanella cf. *schencki* Thompson. Kanmera, 1957, pl. 19, figs. 14-15.

Material.—Axial sections; ASM25243 from Loc. TA256, ASM25244 from Loc. SA122, ASM25245 from Loc. SA124, ASM25246 from Loc. MT238. Sagittal section; ASM25247 from Loc. MT239.

Description.—Shell medium to large for genus and thickly fusiform with bluntly

pointed to rounded axial regions and slightly convex lateral slopes. Mature specimens having 11 to 13 volutions, 4.05 to 4.98 mm in length and 2.58 to 3.50 mm in width, giving form ratios of 1.26 to 1.53. Shell expands gradually through growth. Proloculus small to medium, being 0.090 to 0.175 mm in outside diameter, averaging 0.124 mm for 4 specimens. Spirotheca thin and composed of a tectum and thin alveolar keriotheca. Primary transverse septula observed in all volutions. Tips of primary transverse septula solidified and pendant-shaped, joining with tops of parachomata. One, rarely 2 secondary transverse septula inserted between 2 adjacent primary transverse septula. Septa thin but usually coated with dense calcareous material. Tips of septa slightly swollen. One axial septulum usually occurs between 2 adjacent septa beyond the fifth volution, but 2 axial septula rarely inserted in outer ones. Parachomata prominent and well developed in all volutions.

Remarks.—The present species quite agrees with *Afghanella sumatrinaeformis* (Gubler) in the essential shell characters except for having a smaller proloculus.

Afghanella cf. *sumatrinaeformis* (Gubler) differs from *A. schencki* Thompson in having a more thickly fusiform shell, smaller form ratio and more volutions.

Occurrence.—Common in the *Verbeekina verbeeki*-*Afghanella schencki* Zone.

Afghanella sp.

Figures 11-18-20

Material.—Tangential sections; ASM25230 from Loc. KS175, ASM25231 from Loc. AL89, ASM25232 from Loc. EB56.

Remarks.—Three tangential sections are referable to *Afghanella* sp. This unidentified species resembles *Afghanella ozawai* Hanzawa, which coexists with it, in the nature of the transverse septula. However, the former has a larger and more elongate shell than those of the latter. At any rate, the exact

specific identification is postponed until better material is accumulated.

Occurrence.—Rare in the lower part of the *Afghanella ozawai* Zone.

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Akiyoshi 秋吉, Akiyoshi-dai 秋吉台, Atetsu 阿哲, Kaerimizu 帰り水, Omi 青海, Taishaku 帝釈, Yamaguchi 山口.

秋吉石灰岩層群, *Parafusulina kaerimizensis* 帯以降の Verbeekinidae 科および Neoschwagerinidae 科紡錘虫類: 秋吉台北東部の帰り水地域に分布する *Parafusulina kaerimizensis* 帯より上位の秋吉石灰岩層群から 11 種の Verbeekinidae 科および Neoschwagerinidae 科紡錘虫類を識別した。さらにこれら紡錘虫類の層序分布に基づいて, *Parafusulina kaerimizensis* 帯以降の秋吉石灰岩層群を下位から *Parafusulina kaerimizensis* 帯, *Afghanella ozawai* 帯, *Neoschwagerina craticulifera robusta* 帯, *Verbeekina verbeeki-Afghanella schencki* 帯, *Neoschwagerina fusiformis* 帯, *Verbeekina verbeeki* 帯, *Colania douvillei* 帯の 7 化石帯に分帯した。本論では 1 新亜種 (*Neoschwagerina craticulifera robusta*, subsp. nov.) を含むこのうちの 10 種を記載するとともに, *Parafusulina kaerimizensis* 帯以降の紡錘虫生層序についても簡単に述べる。

上野勝美

935. A NEW CRYPTIC SPECIES OF *PYCNODONTE* FROM RYUKYU ISLANDS: A LIVING FOSSIL OYSTER*

ITARU HAYAMI

Geological Institute, University of Tokyo,
Hongo 7-3-1, Bunkyo-ku, Tokyo, 113

and

TOMOKI KASE

National Science Museum, Hyakunin-cho
3-23-1, Shinjuku-ku, Tokyo, 169

Abstract. A new enigmatic oyster was found alive from several poorly lighted submarine caves of Miyako and Okinawa Islands, southern Japan. It belongs to the genus *Pycnodonte*, which occurs commonly in the Cretaceous-Miocene of the Tethyan realm but had been believed extinct. Its shell shape is variable, but the right valve is paper thin and has an extremely wide depositional surface of flexible outer prismatic layer. Nevertheless, every diagnostic character of *Pycnodonte* (s.s.) is well recognized (e.g. long dorsal margin, dorsally located and subcircular adductor muscle insertion, wide commissural shelf, vermicular chomata, vesicular shell structure and remarkable radial gashes on the right valve). It is suggested that this oyster is a significant example of a living fossil, and that *Pycnodonte* has survived for many millions of years by transforming itself into a cryptic organism.

Key words. cryptic, *Pycnodonte*, submarine cave, living fossil.

Introduction

The technical development and popularization of scuba diving in recent years enabled us to examine the diversity and ecology of various organisms indigenous to sublittoral sheltered environments. Submarine cave faunas, in particular, have emerged as an interesting subject of study because they seem to offer substantial evidence to test various theories of systematics, evolutionary ecology and marine biogeography. Cryptic faunas also may contain paleontologically interesting species because such sheltered places serve as suitable refuges to archaic and anachronistic organisms.

High levels of endemism in cryptic organisms have attracted the attention of many biologists. Riedl (1966) made a comprehensive review on the biota of coastal caves and illustrated the spectral distribution of various organisms (including some bivalves) in some wave-excavated intertidal grottoes of the Mediterranean region. Since Hartman and Goreau (1970) discovered sclerosponges resembling stromatoporoids (problematic Paleozoic and Mesozoic fossil organisms) in some sublittoral crevices of Caribbean coral reefs, several species of articulate brachiopods, bryozoans, polychaetes and decapod crustaceans have been recognized also as unique constituents of cryptic communities, and their origin and evolutionary significance have been discussed by many

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investigators (Jackson, Goreau and Hartman, 1971; Jackson and Winston, 1982; Iliffe, Hart and Manning, 1983; Kobluk, 1988; etc.). However, the unique features of molluscs in such sheltered environments have been little studied.

On the fore-reef slopes of Shimoji-shima and Ie-jima of the Ryukyu Islands, southern Japan, there are numerous limestone caves which seem to have been formed by underground water during some low sea-level stages of the Pleistocene and drowned during the post-glacial sea-level rise. Since a few years ago, we have been studying the cryptic faunas (especially molluscs) in these caves with the vigorous assistance of several skilled divers. As reported preliminarily (Hayami and Kase, 1991; Kase and Hayami, in press.), several characteristic molluscs including *Neritopsis radula* (a living fossil snail) have been found alive in some of these caves, and the calcareous muddy sediments therefrom bear numerous dead shells of bivalves and gastropods which are different from the shallow-water faunas of ordinary exposed environments. The diversity, ecology, origin and evolutionary significance of these cryptic faunas may be an interesting subject to study.

In spite of the apparent great species diversity, most of these molluscs are very small in size (commonly less than 5 mm in maximum length). Some sclerosponges, corals, soft sponges, articulate brachiopods, bryozoans, ostracods and decapod crustaceans were also found alive in some of these caves, but the biomass per unit space is generally much smaller than that of the exposed environment around the caves.

The new oyster described here is an exceptionally large-sized species among the cave bivalves. It was first discovered by M. Taniguchi, a skilled diver of Miyako Island, at the poorly lighted walls and ceilings of several caves (about 20 meters below sea level) along the western coast of Shimoji-shima of Miyako Islands (Figure 1). The same species has been found also from simi-

larly sheltered environments of Okinawa (Ie-jima and Seragaki beach). In spite of its enigmatic shell morphology, many essential characters indicate that this oyster belongs to the genus *Pycnodonte*, which flourished in Cretaceous and Paleogene periods in the Tethyan realm and had been believed to be an extinct taxon. Its cryptic habitat is also meaningful, because such a sheltered place may offer a refuge for archaic organisms. In this article we describe its morphology and life habit and discuss its evolutionary significance as a "living fossil".

On the genus *Pycnodonte*

Before going into the description, previous systematic studies of pycnodonteine oysters are briefly reviewed because the newly discovered cryptic species seems to belong to *Pycnodonte*.

In spite of great intraspecific morphologic variability and frequent convergence, natural classification of fossil and extant oysters has been attempted by many investigators. Among others, Stenzel's (1959, 1971) scheme may be the most elaborate and influential. He classified oysters into two families, Gryphaeidae and Ostreidae, and further subdivided the former into three subfamilies, Gryphaeinae, Pycnodonteinae and Exogyriinae. Stenzel's scheme has been substantially followed by many subsequent authors, though Torigoe (1981) raised the Pycnodonteinae as a distinct family, Harry (1985) subdivided the Pycnodonteinae into three tribes (Pycnodontini, Neopycnodontini and Hyotissini), and Carter (1991) regarded the Gryphaeidae and the Ostreidae as constituting distinct superfamilies.

Important criteria for these family- or subfamily-level classifications are 1) shell characters (particularly, presence or absence of chalky deposit and vesicular shell structure, commissural shelf, chomata, and shape of muscle scar) and 2) anatomical characters of soft parts (particularly, the status of the

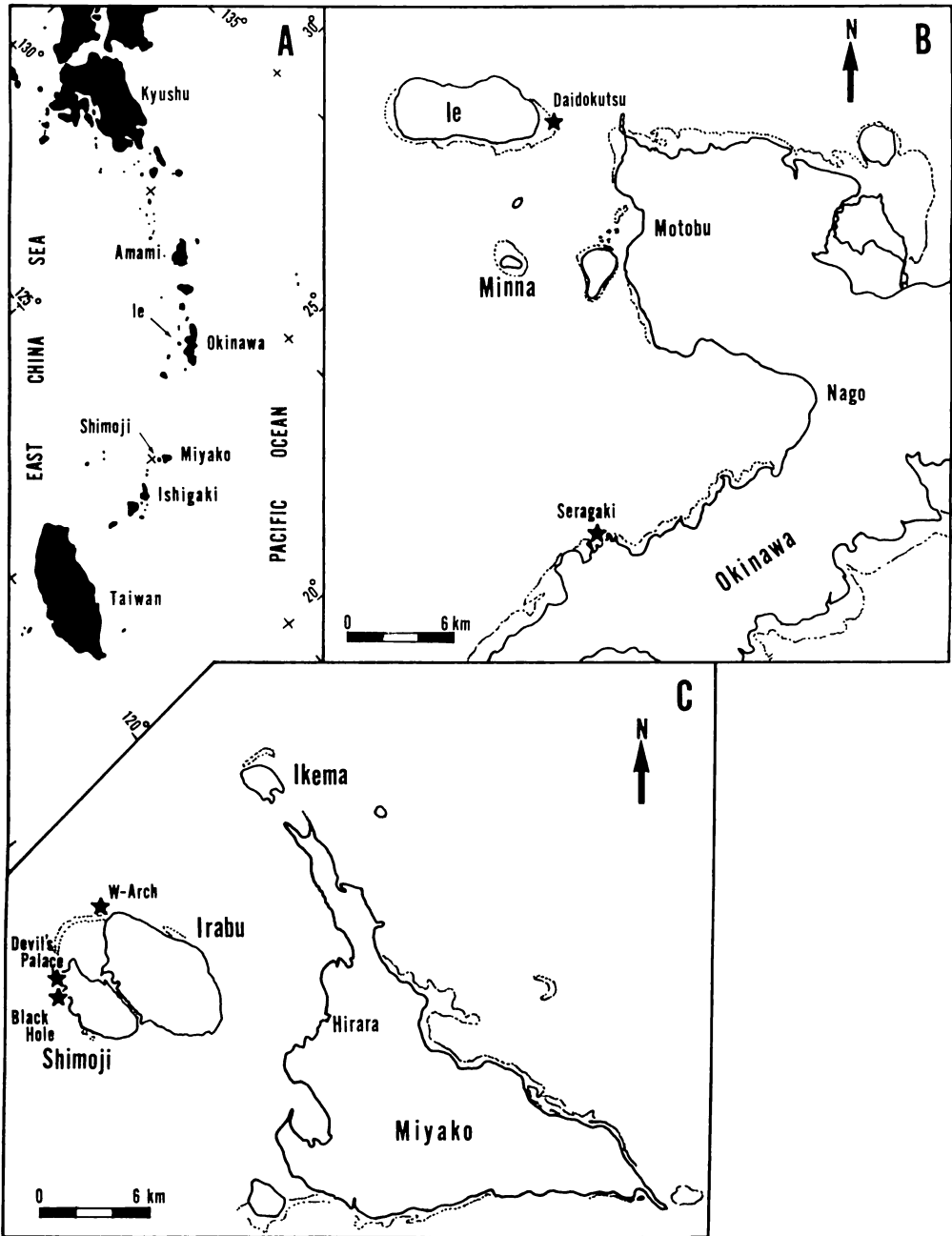


Figure 1. Map showing the localities (indicated by asterisks) of *Pycnodonte (Pycnodonte) taniguchii* n. sp. in Ryukyu Islands of Japan. A: Index map, B: Central part of Okinawa Island, C: Miyako Islands.

promyal passage, heart-kidney-rectum complex, digestive tract, labial palp fusion and anal appendage) and 3) reproductive strategy (incubatory or non-incubatory). In

accordance with Stenzel's system (with some modifications), Torigoe (1981) described the shell and soft parts of all the extant oysters in Japanese waters, and Harry (1985) gave a

synopsis of all the supraspecific taxa of extant oysters in the world.

Stenzel (1971) distinguished the Pycnodontinae from the Gryphaeinae by the presence of a well defined commissural shelf, vermiculate chomata and vesicular shell structure, but treated the former as derived from the latter, regarding *Gryphaea (Bilobissa)* from the Middle-Upper Jurassic as transitional between the two subfamilies. Subsequent studies of shell microstructure, however, do not necessarily support Stenzel's scheme. According to Siewert (1972) and Hudson and Palmer (1976), *Pycnodonte* and *Hyotissa* considerably differ from the Gryphaeinae but resemble the Ostreidae in the structural chambering and in lacking well defined crossed foliated structure. Siewert (1972) supposed that *Pycnodonte* together with many ostreid genera was derived from *Lopha* which constituted a stock independent from *Gryphaea* throughout the Jurassic.

Carter (1991) critically reviewed all the available data about the shell microstructure of fossil and extant oysters, and admitted the structural resemblance between the Pycnodontinae and the Ostreidae, although he did not change Stenzel's (1971) system in which the Pycnodontinae is regarded as a subfamily of the Gryphaeidae. Contrary to Stenzel's description, "No prismatic shell layer except in *Neopycnodonte*"; an outer layer of calcitic simple prisms is commonly observed in RV of many fossil and extant pycnodontine species. Vesicular shell structure, which was regarded by Stenzel (1971) as diagnostic of the Pycnodontinae, exists also in a lophine oyster, *Dendostrea folium*. Therefore, the origin and the familial position of the Pycnodontinae is still controversial. If much weight is given to the shell structure and structural chambering, the Pycnodontinae may be considered to be more closely related to the Ostreidae (especially the Lophinae) than to the Gryphaeinae. Nevertheless, as to the content and limit of the Pycnodontinae, most recent investigators

seem to support Stenzel's (1971) scheme.

Discrimination of the Pycnodontinae from the Ostreidae is justified also by comparative anatomy of extant species. As illustrated by Torigoe (1981), the Pycnodontinae shares a Z-shaped digestive tract with the Lophinae, but the rectum penetrates (or comes into contact with) the pericardium of the heart in *Neopycnodonte* and *Hyotissa*, while it passes the dorsum of the heart in all the genera of the Ostreidae (including the Lophinae). Adductor muscle insertion is subcircular in the Pycnodontinae (like the Gryphaeinae) but reniform in the Ostreidae. The status of the promyal passage and labial palp fusion may be also important to discriminate the Pycnodontinae from the Ostreidae. Habe (1977) regarded *Pretostrea* as a pycnodontine genus and referred several Japanese species to it, but Torigoe (1981) clarified on the basis of anatomy that some of them belong to *Hyotissa* and other species to *Dendostrea* (of the Lophinae). These anatomical characters are useful to see through shell convergence.

Pycnodonte Fischer de Waldheim, 1835, as defined by Stenzel (1971) and many recent workers, had been regarded as an extinct genus, though its descendant(?) genus *Neopycnodonte* Stenzel, 1971, is represented by a single extant circumglobal species, *N. cochlear* (Poli). *Hyotissa* Stenzel, 1971, which comprises several tropical-subtropical species and corresponds to the tribe Hyotissini Harry, 1985, is another extant pycnodontine genus, but the Lopha-like plicate valves, subequivalve shell, internal surface with a moiré luster and huge adductor muscle insertion are dissimilar from those of *Pycnodonte* and *Neopycnodonte*.

A large number of fossil species of *Pycnodonte* (including *Gigantostrea*, *Phygraea* and *Costeina* as subgenera) have been known mainly in the Tethyan realm from late Early Cretaceous to early Miocene. Probably owing to biased fossil preservation, only left valves were described in many fossil

species. Though the intraspecific variation and detailed shell characters of the type species are poorly known, the genus *Pycnodonte*, as defined by Stenzel (1971: p. N1106), seems to be characterized by strongly convex LV, irregular but generally subcircular to semicircular outline, wide commissural shelf, vermicular chomata, gently undulated LV rarely with well defined radial costae and flat to concave RV. Radial gashes of RV is a very conspicuous feature of *Pycnodonte*, though they sometimes occur also in other genera of the Pycnodontinae (e. g. Harry, 1985: p. 136, fig. 16) and some species of the Gryphaeinae (e. g. Duff, 1978: pl. 8, fig 7b).

Subgeneric division of *Pycnodonte* is controversial and somewhat confusing. *Pycnodonte* (s.s.) [type species: *Pycnodonte radiata* from the Upper Cretaceous of the Crimea] is generally defined by the improminent umbo, long dorsal margin, developed auricular parts and absence of radial ribs on LV. *Gigantostrea* Sacco, 1897 [type species: *Ostrea gigantea* Solander in Brander, 1766, from the Eocene of England], was regarded as synonymous with *Pycnodonte* (s.s.) by Stenzel (1971: p. N1107), but Palmer and Brann (1965: p. 149) and Wilson (1987: p. 13) applied this subgeneric name to several species from the Eocene-Miocene of the Atlantic Coastal Plain of USA, and Fleming (1966: p. 23) also to two species from the Paleogene of New Zealand. *Gigantostrea* seems to differ from *Pycnodonte* (s.s.) in the planoconvex to biconvex outline, less inequivalve shell and undeveloped auricles.

Phygraea Vyalov, 1936 [type species: *Phygraea frauscheri* Vyalov, 1936 (= *Gryphaea pseudovesicularis* Gümbel, 1861), from the Paleocene of eastern Europe] shows planoconvex to concavoconvex outline and

conspicuous radial gashes of RV like *Pycnodonte* (s.s.), but its subgeneric distinction can be based on the *Gryphaea*-like outline (though the resemblance is due to convergence), much thicker LV, prominent umbo of LV, short dorsal margin, and undeveloped auricles. This subgenus possibly includes *Pycnodonte vesicularis* (Lamarck, 1806) from the Upper Cretaceous of western Europe, west and north Africa, south India and New Caledonia. Woods (1913) and Freneix (1960, 1972) described the wide morphologic variation of *P. vesicularis*, and many European authors regarded *P. radiata*, the type species of *Pycnodonte*, as synonymous with *P. vesicularis*. This view was rejected and *P. vesicularis* was referred to *Phygraea* by Stenzel (1971) and some subsequent authors, chiefly because its subcircular shell form looks different from the figured original specimen of *P. radiata*. The shape difference between *Pycnodonte* (s.s.) and *Phygraea*, as discussed later, may be related to different modes of life.

In addition, *Costeina* Vyalov, 1965 [type species: *Pycnodonte (Costeina) costei* Coquand, 1869, from the Upper Cretaceous of north Africa] may be characterized by the presence of dichotomous radial ribs on the surface of LV, and *Crenostrea* Marwick, 1931 [type species: *Ostrea (Crenostrea) wuellerstorfi* Zittel, 1864, from the Oligocene of New Zealand] seems to be subgenerically distinguished by the pointed umbo of LV and very strong chomata, though RV of their type species are insufficiently known. Squires and Demetron (1990) proposed *Pegma* [type species: *Pycnodonte (Pegma) bajaensis* Squires and Demetron, 1990, from the Eocene of Baja California] as a subgenus of *Pycnodonte*, but we think that it is, if not synonymous with, closely related to *Hytissa*.

→ **Figure 2.** *Pycnodonte (Pycnodonte) taniguchii* n. sp., Holotype (UMUT RM18908), brownish individual. **1a**: Exterior of LV with many dead shells of juvenile individuals, **1b**: Interior of LV, the depositional surface of middle layer showing pepper-and-salt appearance, **1c**: Exterior of RV, showing remarkable radial gashes. **1d**: Interior of RV, showing wide depositional surface of prismatic outer layer. All figures $\times 0.7$.



1a



1b



1c



1d

Table 1. Observed specimens of *Pycnodonte (Pycnodonte) taniguchii*, n. sp.

No.	Reg. no.	Length	Height	Thickness	Phenotype	Locality	Type	Remarks
1	RM18908	103 mm	138 mm	71 mm	brownish	W-Arch	Holotype	dried
2	RM18909	87 mm	124 mm	71 mm	whity	Black Hole	Paratype	dried
3	RM18910	109 mm	105 mm	68 mm	whity	Devil's Palace	Paratype	in alcohol
4	RM18911	96 mm	84 mm	45 mm	brownish	W-Arch	Paratype	in alcohol
5	RM18912	97 mm	76 mm	39 mm	brownish	Seragaki Beach	Paratype	in alcohol
6	RM18913	97 mm	101 mm	53 mm	brownish	W-Arch	Paratype	sectioned
7		123 mm	125 mm	66 mm	brownish	W-Arch		anatomized
8		81 mm	84 mm	28 mm	brownish	W-Arch		anatomized

Registered specimens are in the University Museum, University of Tokyo (UMUT).

Speciment Nos. 7 and 8 were anatomized by Dr. Torigoe of the Hiroshima University.

The geographic distribution of *Pycnodonte* was said to be worldwide (Stenzel, 1971: p. N1107), but this genus has been known almost exclusively from low-middle latitudinal regions. Cretaceous species are common in western Europe, Crimea, north and west Africa, south India and Gulf Coast regions. Paleogene species show almost the same geographic distribution as Cretaceous ones. In Japan large species of *Pycnodonte* seems to be rare, but Tashiro (1978) described a small species from the Santonian of west Kyushu, and Hanai and Oji (1981) noticed numerous individuals (mostly LV) of an undescribed species adhering to an Aptian fossil beachrock in north Honshu. As revised by Oyama, Mizuno and Sakamoto (1960: p. 129), *Ostrea crassis* Nagao, 1928, from the Oligocene of west Kyushu seems to belong to *Pycnodonte*, although Nagao (1928) wrongly described the right and left valves in reverse. All the extant representatives of the Pycnodontinae (*Neopycnodonte* and *Hyotissa*) are also tropical to warm-temperate inhabitants (Harry, 1985, 1986; Nicol, 1991).

Systematic description

? Family Gryphaeidae Vyalov, 1936
 Subfamily Pycnodontinae Stenzel, 1959
 Genus *Pycnodonte* Fischer
 de Waldheim, 1835
 Subgenus *Pycnodonte* s.s.

Pycnodonte (Pycnodonte) taniguchii Hayami and Kase, n. sp.

Figures 2-7

Material.—Several living specimens from the submarine caves on the western coast of Shimoji-shima, Miyako Islands, Ryukyu (Table 1). The holotype (UMUT RM18908) from one of the caves, a diving point called "W-Arch" (Lat. 24°51'43"N, Long. 125°09'41"E, ca. 20 m below sea level).

Diagnosis.—A large and concavo-convex extant species of *Pycnodonte* (s.s.), the adult shell of which is characterized by an unusually wide commissural shelf, an attachment area extending over the long geniculated dorsal margin of LV, distinct vermicular chomata, dorsally situated subcircular adductor insertion, variably developed vesicular structure, moderately thick LV, and more or less hollowed RV with a paper-thin and flexible distal area and remarkable radial gashes on the external surface.

General shell features.—Shell large for the genus, often exceeding 100 mm in length and height, very inequivalve, more or less prosocline, nonplicated, presumably dimorphic in coloration (commonly purplish brown but sometimes ivory white). Outline variable, usually flat and subcircular in young stage but becoming linguiform or fan-shaped in adult. LV strongly convex, solid, relatively thin except for middle-ventral area in adult stage, characterized by improminent umbo, broadly undulated and puckery surface and

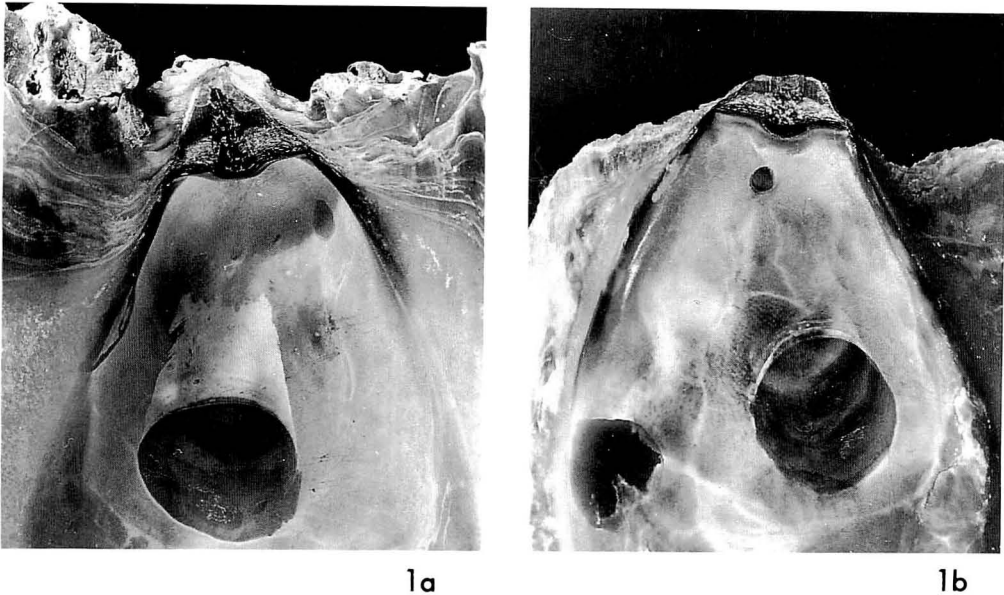


Figure 3. *Pycnodonte (Pycnodonte) taniguchii* n. sp., Holotype (UMUT RM18908). **1a**: Umbonal area of LV, showing the ligament area and muscle insertions, **1b**: Umbonal area of RV, showing the ligament area and muscle insertions. All figures $\times 1.5$.

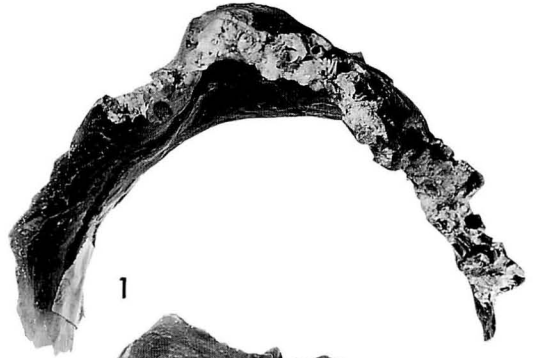
generally well developed auricular parts, sometimes having a posterior radial sulcus but lacking any well-defined radial sculpture and hyote spines. Attachment area, which occupies the whole external surface of LV in early stage (up to 20–30 mm in height), extends along the entire dorsal margin in adult, geniculated at the umbonal area in dorsal view. RV broadly and deeply concave except flattened or feebly convex umbonal area, sticking to the inner surface of LV with flexible distal area, extremely thin and light (in the holotype, LV is 221 gram and RV is 26 gram in weight), characterized by remarkable radial gashes on the external surface. Ligament area relatively narrow, subtriangular with an apical angle of about 60° in LV, though its apical part was commonly corroded in RV; resilifer small, subcentral, slightly opisthoclinal. Subumbonal cavity of LV moderately deep. Inner surface of both valves shiny but does not show a moiré luster. Adductor muscle insertion comparatively small (with a diameter about

1/10 of shell height), subcircular, without elevated rim, slightly longer than high in LV but nearly as long as high in RV, with its center placed at one-fifth to one-fourth of shell height from the dorsal margin in adult (unusually dorsally situated). Gill protractor muscle scar (Quenstedt muscle insertion by Stenzel, 1971) distinct in both valves, situated anteriorly in LV but subcentrally nearly below the resilifer in RV. Chomata relatively weak but distinct, moderate in length, vermicular, situated on the outer slopes of a pair of small ridges. Commissural shelf unusually broad, occupying almost the distal half of shell; its proximal margin markedly angulated on the internal surface of RV.

Shell microstructure.—The outer layer of LV often ragged but consists of accumulated regularly foliated calcite which dips slightly relative to depositional surface. The middle layer of LV composed of thick accumulation of composite crossed foliated calcite. In purplish-brown individuals this layer catches



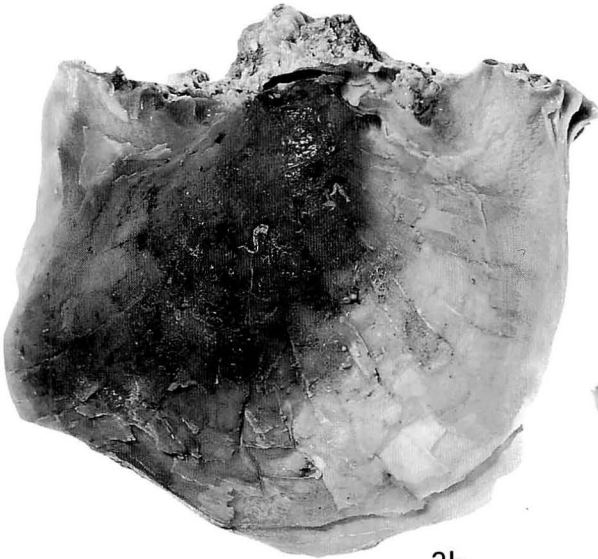
2a



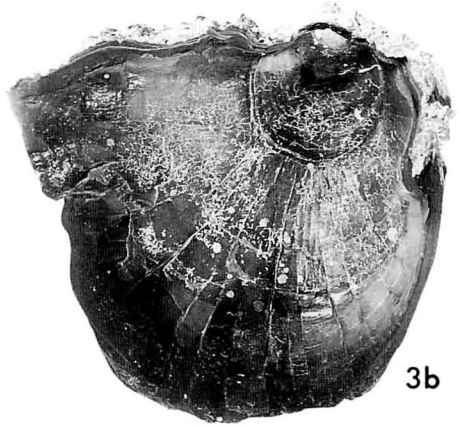
1



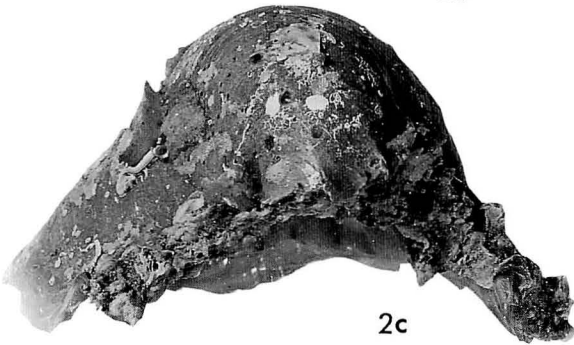
3a



2b



3b



2c



3c

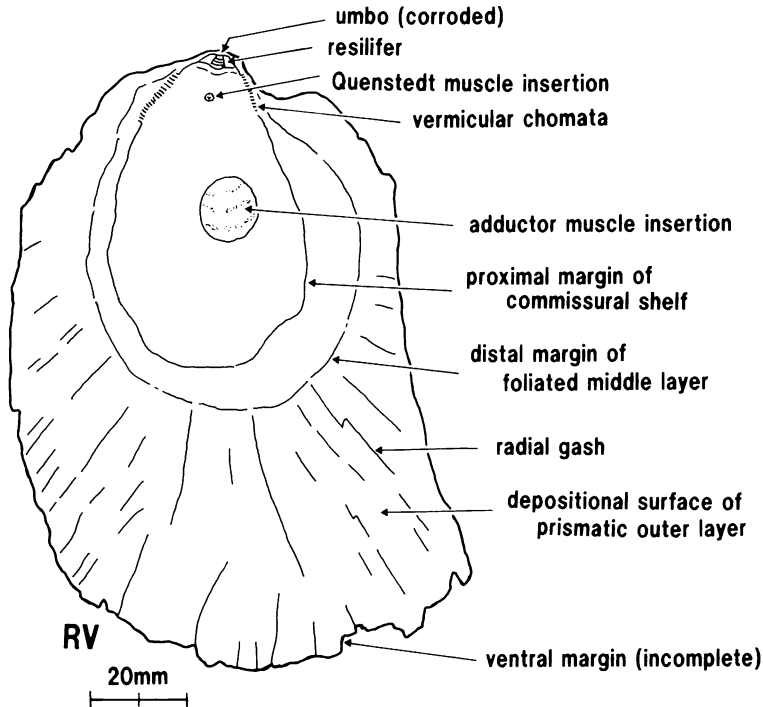


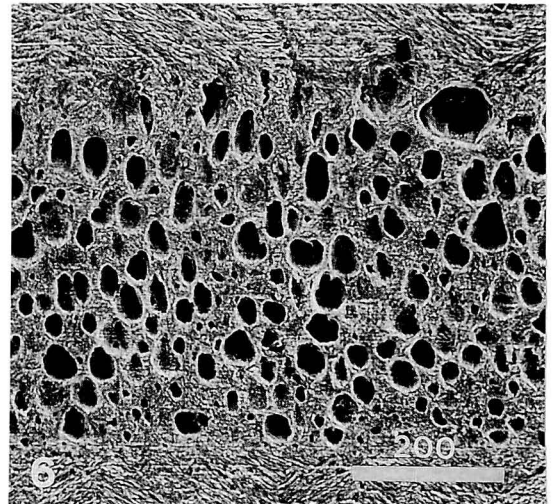
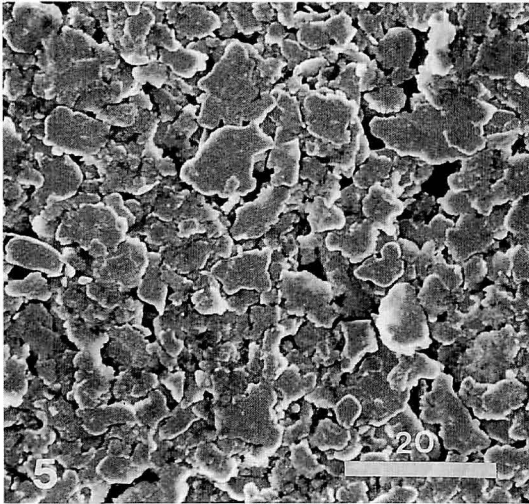
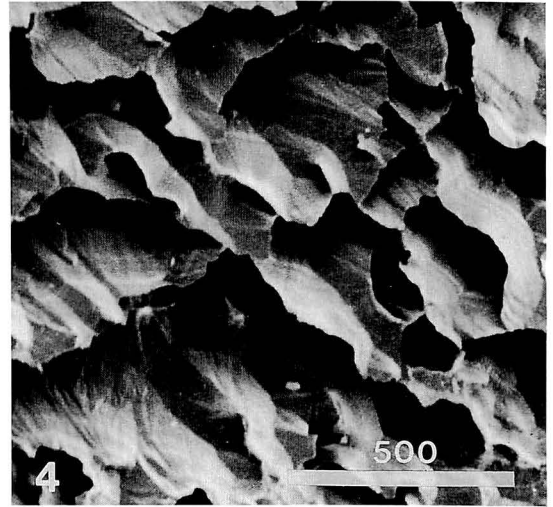
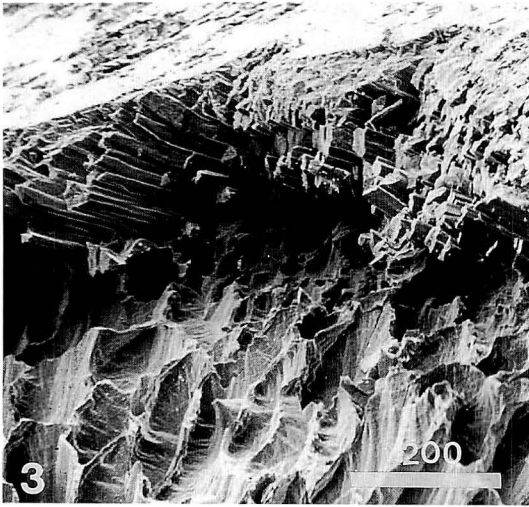
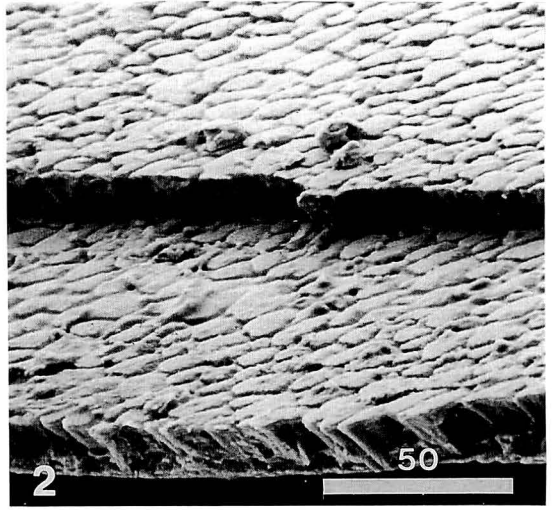
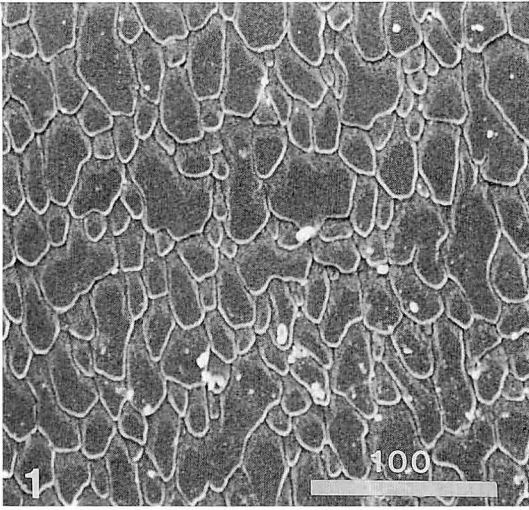
Figure 5. Sketch of the internal surface of RV (based on the holotype).

many yellowish lenses which bear numerous ellipsoidal vacuoles of about $40\ \mu\text{m}$ in maximum diameter (Figure 6-6). The brownish and yellowish parts irregularly intermingled, so that the depositional surface shows a pepper-and-salt appearance (Figure 2-1b). Development of vesicular structure quite variable in LV; in some individuals there are large cavities with very coarse vesicular structure between the outer and middle layers, but in many other individuals this structure is not observed at all. The outer layer of RV comparatively thick in the middle-ventral area (attaining almost 1 mm in total), composed of several sublayers of simple prismatic calcite which are interrupted by thin conchiolin seats or cavities (Figure 6-2). Calcite prisms variable in size, but commonly $20\text{--}50\ \mu\text{m}$ in diameter and reclined about 50° to the sur-

face. Its depositional surface extremely wide, occupying almost the entire distal half of shell. Owing to this structure, the distal part of RV without backing of middle layer very flexible when alive. Radial gashes occur only in this outer layer. A number of flat cavities exist in and below the prismatic outer layer, in which vesicular structure is commonly developed (Figure 6-3, 4). Middle layer of RV cross foliated, solid and rarely vacuolated, easily separable from outer layer. The inner layer of both valves composed of complex crossed foliated calcite but generally very thin.

Soft part.—The soft part relatively small, as recognized from the unusually wide commissural shelf. Promyal passage extends between RV and visceral mass, reaching the umbonal part. Visceral mass relatively

← **Figure 4.** *Pycnodonte (Pycnodonte) taniguchii* n. sp. **1**: Holotype (UMUT RM18908), dorsal view of articulated valves, **2a-c**: Paratype (UMUT RM18910), left, right and dorsal views of a whitish articulated individual. **3a-c**: Paratype (UMUT RM18911), left, right and dorsal views of a brownish articulated individual. All figures $\times 0.7$.



small, orange in color. Labial palp broadly fused, resembling that of *Neopycnodonte cochlear*. Digestive tract relatively thick, Z-shaped, never looped; rectum does not penetrate the pericardium of the heart but comes in contact with its posterodorsal part; anal papilla very long. In summary, every anatomical character resembles that of *Neopycnodonte* and *Hytissa* and differs significantly from that of the Ostreidae. (The description of anatomical characters is mainly based on Torigoe's personal communication.)

Comparisons.—The present new oyster shows every essential character of the Pycnodontinae called for by Stenzel (1971), Torigoe (1980), Harry (1985) and Carter (1991). In the shell morphology as well as the cryptic habitat, however, the present species is so unique that its distinction from other extant oysters can be based on various characters. The extreme inequivalveness, broad commissural shelf, dorsally situated adductor muscle, and thin and deeply concave RV with broad and flexible distal area (owing to the shell consisting of simple prismatic outer layer) in the adult stage are the most striking diagnostic characters of this species.

Among extant pycnodontine oysters, *Neopycnodonte cochlear* (Poli, 1795) may be most closely related to the present species because the two species share very dorsally situated adductor muscle, vermicular chomata, radial gashes and limitedly distributed vesicular structure in RV. According to Torigoe (pers. comm.), who anatomized an individual at our request, many anatomical characters are not much different

from those of *N. cochlear*, although the rectum does not pierce the pericardium in the present species. *N. cochlear* is regarded as a circumglobal species, having been recorded from various regions of the Indo-West Pacific, eastern and western Atlantic, and Mediterranean realms. It extends to greater depths (27 to 2,100 m) than any other extant oyster (Stenzel, 1971; Harry, 1985). In Japan, though it often was treated under the name of *Ostrea musashiana* Yokoyama, 1920, the species occurs commonly on the lower sublittoral to upper bathyal gravelly bottom (Kuroda, 1931; Habe, 1977; etc.). Although the soft parts are relatively small, the present species grows much larger than *N. cochlear* in shell size. The shape of the adult shell is also quite different because the attachment area of the present species extends entirely over the long dorsal margin of LV. Moreover, unlike *N. cochlear*, the simple prismatic outer layer of RV is well developed, and its depositional surface is much wider. The shell of *N. cochlear* is fragile, while the LV and the middle-inner layer of RV are generally solid in the present species.

The present species resembles the type species of *Pycnodonte* (s.s.) more closely than that of *Neopycnodonte* in various shell characters, e.g. concavo-convex valves, long dorsal margin and linguiform to fan-shaped outline in the adult stage and well developed radial gashes on the external surface of RV. Some specimens of the present species are surprisingly similar in shell shape to the figured original specimen of its type species, *P. radiata* Fischer de Waldheim, 1835 (reproduced by Stenzel, 1971: fig. J80), from the

← **Figure 6.** SEM photomicrographs showing shell microstructure of *Pycnodonte* (*Pycnodonte*) *taniguchii*, n. sp. Unit of scale in microns. **1:** Depositional surface of simple prismatic outer layer near the ventral margin of RV (UMUT RM18913); the venter is toward the lower, $\times 250$. **2:** Oblique internal view of fractured edge of multilayered simple prismatic outer layer near the ventral margin of RV (the same individual); the venter is toward the right upper, $\times 500$. **3:** Fractured external surface of middle part of RV (UMUT RM18909); vesiculate cavity below simple prismatic outer layer, $\times 100$. **4:** Vesiculate structure in a cavity between outer and middle layers of RV (the same individual), $\times 60$. **5:** Depositional surface of crossed foliated middle layer of LV (UMUT RM18913), $\times 1,000$. **6:** Slightly etched surface of subvertical section of LV (the same individual), vacuolated lenticular part embedded in crossed foliated middle layer; the venter is toward the right and the external surface toward the lower, $\times 100$.

Upper Cretaceous of the Crimea. In a number of fossil species of *Pycnodonte* RV looks much smaller than LV, as described and figured by many authors. Judging from the concordant ventral margins of two valves in all the living specimens of the present species, the "size discordance" in those fossil species may be only superficial, because the marginal part of RV was physically weak and may have been selectively lost before fossilization. Even in living specimens of the present species, this portion, if dried and not strengthened, is apt to be broken into pieces, just like the marginal apron of RV in living propeamussiids (see Hayami, 1988). Flexible distal area of RV, therefore, may be a ubiquitous feature in the genus *Pycnodonte*.

The apparently wide range of variation of shell form of the present species is partly attributable to ontogenetic change. Some immature specimens of the present species (e.g. UMUT RM18911) show shorter and arcuate dorsal margin and subcircular outline, resembling some species of the subgenus *Phygraea*, especially *Pycnodonte* (*Phygraea*) *mutabilis* (Morton, 1828) from the Campanian-Maastrichtian of the Gulf and Atlantic Coastal Plain, which was described by Gardner (1916) and Wade (1926) as *Gryphaea vesicularis* and by Stephenson (1941) as *Gryphaea mutabilis*. In this respect, some specimens of *Pycnodonte* (*Phygraea*) *vesicularis* (Lamarck, 1806), a widely distributed Late Cretaceous species in Europe, north and west Africa, India and New Caledonia (Stoliczka, 1870-1871; Woods, 1913; Darteville and Freneix, 1957; Freneix, 1960, 1972), also exhibit a similar outline. Those Cretaceous species of *Phygraea*, however, have much thicker shells, and, as interpreted by Jablonski and Bottjer (1983), probably were cup-shaped recliners on soft substrata.

On the other hand, fossil species of *Pycnodonte* (s.s.) were mostly lifelong sessile animals, because the shell is not very thick and because the attachment area seems to

extend over the long dorsal margin as seen in the present species. All fossil *Pycnodonte* (s.s. and *Phygraea*) share with the present species conspicuous radial gashes on RV, which indicate the presence of a well developed simple prismatic outer layer.

Vesicular shell structure is widespread in the fossil and extant species of the Pycnodontinae and has been regarded by Stenzel (1971) as diagnostic of this subfamily. This structure is actually observed in the present species (Figure 6-3, 4). In RV it is commonly seen in small cavities beneath the outer layer, although in LV its development is quite variable among individuals. As Carter (1991: p. 355, fig. 2E) ascertained the presence of locally developed vesicular structure in the middle layer of a lophine oyster, *Dendostrea folium*, taxonomic evaluation of this structure should be reconsidered. Chel'tsova (1969) mentioned the presence of vacuolated and "pinnate" structure in *Pycnodonte radiata*. The type species is possibly similar to the present species in this feature, though a more detailed comparison of shell microstructure has yet to be worked out.

Distribution.—In addition to the type locality, the present species was found alive in submarine caves on fore-reef slope ("Black Hole" and "Devil's Palace" as called by divers) along the western coast of Shimojishima of Miyako Islands, and similarly sheltered places at "Daidokutsu" of Ie-jima and at Seragaki near Manza Beach of Okinawa Island (all 20–30 m in depth) (Figure 1).

Observations and discussions

Cryptic habitat.—The habitat of the present oyster is hardly accessible to us, but its life habit can be recognized through divers' talk and underwater videotapes. Various cave organisms seem to show spectral distribution from the entrance to the innermost part in accordance with the change of physical and biological factors. Individuals of this oyster

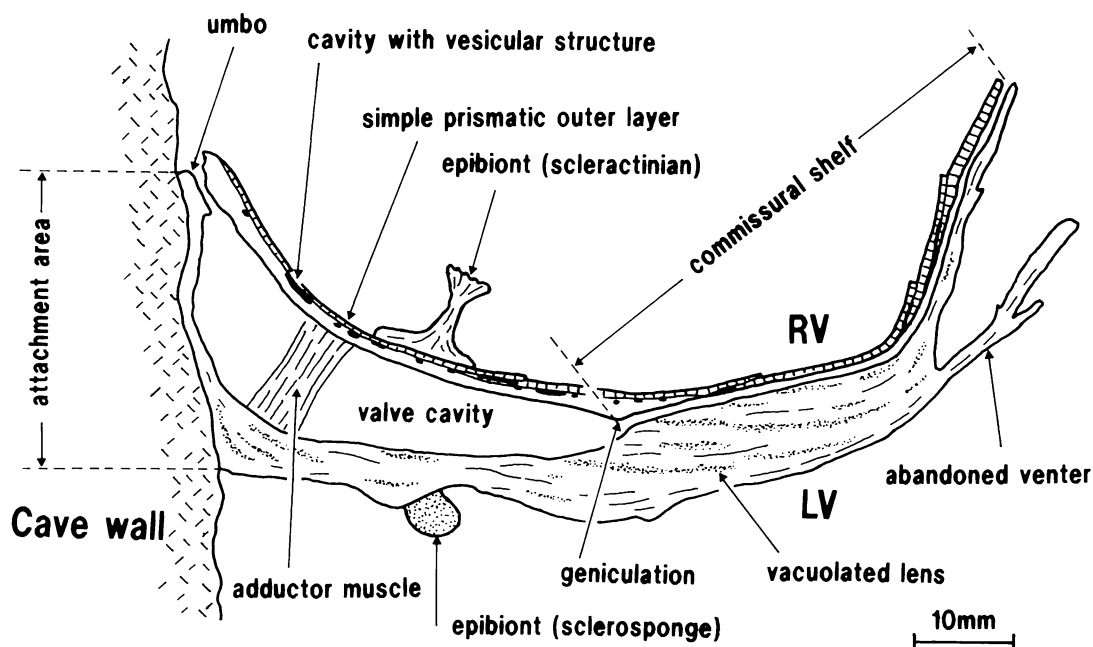


Figure 7. Subvertical section of *Pycnodonte (Pycnodonte) taniguchii*, n. sp. in living position (based on a sectioned articulated individual, UMUT RM18913).

always grow on gloomy walls or ceilings of submarine caves and other sheltered places open to fore-reef slopes under normal salinity and temperature. Such a large-sized suspension feeder as this oyster probably cannot live unless a considerable amount of phytoplankton is supplied from the exposed environment. It does not live in the totally dark innermost part of such caves, where *Neritopsis radula* and several characteristic minute molluscs are still found alive.

The present oyster, on the other hand, does not dwell in the ordinary exposed environment. This is probably the main reason why such a large-sized conspicuous bivalve had not been discovered by scientists and collectors until quite recently. Moreover, owing to the wide attachment area the LV seems to adhere to the cave wall for a long time after death, and the paper-thin RV, if disarticulated, is easily broken. Dead shells of *N. radula* are found on exposed bottoms and beaches, but they were certainly transported from sheltered environments by hermit crabs.

Various epibionts are observed on the surface of both valves of this oyster. Bryozoans and serpulids are most common, and certain species of scleractinian coral, barnacle and sclerosponge are occasionally found (Figure 7). A characteristic community consisting of sclerosponges, articulated brachiopods, bryozoans, annelids and scleractinian corals (commonly noncolonial) are found at or near the habitat of the present oyster. Such sclerosponge-bearing communities have been discovered at similarly sheltered places (mainly crevices and caves) in a number of Caribbean and Indo-West Pacific coral reefs, and their ecological and paleontological significance as well as their origin have been discussed by many authors (Hartman and Goreau, 1970; Jackson, Goreau and Hartman, 1971; Jackson, 1977, 1979; Kobluk, 1988; etc.). The present oyster is possibly also a constituent of such a cryptic community at least in this region.

Color dimorphism.—Of eight large specimens examined, two are ivory white and six

are purplish brown in shell coloration (Table 1). There is no intermediate individual, and the color type of infant individuals is difficult to determine. The two phenotypes are not different in various characters other than shell coloration. This fact suggests the presence of dimorphism, but the sample size at each locality is too small to ascertain their strictly sympatric relation and to clarify the relative frequency. Because the habitat of this oyster is very dark, selection can scarcely act on the variation of shell coloration.

Shell growth.—The shell shape of the present oyster changes significantly with growth. In the initial stage (up to 20–30 mm in shell height) every individual attaches itself to the cave wall or some other hard object (including the shell surface of larger individuals) with the whole surface of LV. In this stage both valves are nearly flat or only feebly convex, the commissural shelf is still narrow, and the test thickness is almost the same between the two valves. Although the attachment area extends along the entire dorsal margin of LV until the latest stage, the main part of the generated shell margin of LV sits up suddenly apart from the wall surface, and then the shell becomes very inequivalve and concavoconvex, as shown in Figure 7. In some cases numerous infant shells of the same oyster species adhere to the shell surface (Figure 2-1a, c), but such individuals probably cannot grow larger because we have never seen any cluster of large individuals.

Functional morphology.—As seen in the dorsal view of many specimens, the attachment area is commonly geniculated at the umbonal area (Figure 4-1). The chevron-like attachment area seems to strengthen the adherence. Divers could not collect any specimen without using a hammer. In many grown individuals of this oyster the ventral surface of LV is strongly puckered, so that this portion often looks branched in cross section (Figure 7). This feature indicates that a preexisting ventral margin was abandoned, and that a new margin grew from the

inside of the shell. The formation and function of the strongly puckered venter are probably similar to those of hyote spines in *Hyotissa* (Stenzel, 1971 : p. N1026). Repeated reconstruction of ventral margins result in the stronger convexity of LV and shell thickening of the middle-ventral portion. Judging from the occasionally imbricated simple prismatic outer layer, reconstruction of venter may occur also in RV, though the abandoned venter must be readily broken.

The RV of this oyster is extremely thin and has almost no physical strength, but its flexible distal part sticks so closely to the inner surface of LV that we can hardly examine the soft parts without breaking the shell. The strongly puckered venter of LV and unusually broad commissural shelf may be advantageous, because, as interpreted by Stenzel (1971 : p. N1025), they make it more difficult for shell-breaking predators to reach the soft part. In fact, individuals with injured-and-repaired shell are often met with in this species.

Radial gashes of RV, which were called “tuck grooves” by Harry (1985), are a very characteristic feature in many pycnodonteine oysters. As observed in the present oyster, they occur exclusively in the simple prismatic outer layer (Figure 2-1c, d, 5). Because this layer is commonly multilayered, the gashes rarely penetrate the shell except near the ventral margin. They may also contribute to the increase of flexibility of the distal part. In many fossil species of *Pycnodonte*, RV looks much smaller than LV. The presence of radial gashes, however, strongly suggests that those species had originally the flexible distal part of RV and concordant valve margins like the present species.

Evolutionary ecology.—In view of the very conservative morphology, the present oyster can be regarded as directly descended from some Cretaceous and Paleogene species of *Pycnodonte* (s.s.). This, however, does not necessarily mean that fossil species of

Pycnodonte were also cryptic animals. In fact, many small individuals of a pycnodonteine oyster, as recognized by Hanai and Oji (1981), attach themselves to the upper surface of a fossil beachrock in the Aptian of north Japan. Bottjer, Roberts and Hattin (1978) illustrated many individuals of *Pycnodonte kansasense* [sic] encrusting the surface of an inoceramid valve in the Turonian Greenhorn Limestone of Kansas. Kauffman (1967) and Tashiro (1978) also recorded similar occurrences respectively for *Pycnodonte? conjesta* from the Colorado Group in the Western Interior and *Pycnodonte amakusaensis* from the Santonian muddy sediments of west Japan. Kauffman and Sohl (1973) mentioned that small individuals of *Pycnodonte* often attached themselves to the surface of lower valves of rudists in the latest Cretaceous rudist reefs of the West Indies. Jablonski and Bottjer (1983), on the other hand, regarded *Pycnodonte (Phygraea) mutabilis* from the Late Cretaceous offshore chalky sediments of the Gulf and Atlantic Coastal region as an iceberg strategist (cup-shaped recliner by Seilacher, 1984). This is probably true about many species of the subgenus *Phygraea*, because of their gryphaeate morphology. These Cretaceous species of *Pycnodonte*, both sedentary and recliners, are thus not considered to have been cryptic organisms.

Typical Cretaceous and Paleogene species of *Pycnodonte* (s.s.) are generally characterized by a longer dorsal margin, better developed auricular part and commonly thinner shell than those of *Phygraea*. If the attachment area extends over the entire dorsal margin with growth, those fossil species should be regarded as lifelong sessile organisms like the present species. Cryptic life of these fossil species is still unlikely, because they occur abundantly together with many other epifaunal and infaunal bivalves.

Palmer and Fürsich (1974) examined the microgeographic distribution of various en-

crusting organisms on hardground and in small crevices at the base of the Bradford Clay (Bathonian) in England. As mentioned by Boucot (1981), this seems to represent an exceptional preservation of ancient sheltered biota. Palmer and Fürsich recorded that the upper (exposed) surface and the lower (sheltered) surface of the crevices were inhabited by more or less different organisms. An unnamed species of *Plicatula*, a brachiopod, some serpulids and bryozoans could be cryptic organisms because they predominantly occur on the lower surface of crevices. Some oysters belonging to *Liostrea*, *Exogyra*, ?*Nanogyra* and *Lopha* are occasionally found adhering to the lower surface, but they occur more abundantly on the exposed surface of the hardground. These crevices are only about 25 cm deep and measure up to 5 cm from roof to floor; their scale must be by far smaller than that of the submarine caves in which the present oyster dwells.

Why is the present oyster found only in sheltered places? If Cretaceous-Paleogene species of *Pycnodonte* were noncryptic, what drove the descendant to such a cryptic environment? There are two possible answers. One is an explanation regarding the change of habitat as a result of overgrowth competition among reef-building organisms; that is, in modern coral reefs, as Jackson (1977) interpreted for the restricted distribution of sclerosponge-fauna, rapidly encrusting colonial organisms predominantly occupy the surface of exposed hard bottom, excluding therefrom slowly growing sessile organisms. The other explanation is based on the assumption that the predation pressure on bivalves is relatively low in such a sheltered environment.

Many sedentary bivalves of similar size are known in and around Indo-West Pacific coral reefs. *Spondylus varius*, *Hyotissa hyotis* and *Chama lazarus* are often found alive on the exposed fore-reef bottom around the caves. Although little is known about the growth rates of these bivalves, it is unlikely that these

noncryptic bivalves grow much more rapidly than the present oyster. On the other hand, they are characterized by much thicker shells and more strongly armoured upper valves. The strongly puckered venter and broad commissural shelf may be effective to some extent against predation, but the shell of this oyster appears to be more delicate and defenseless in comparison with such massive sedentary bivalves in the exposed environment. Though nothing is known about the actual predators of this oyster, these lines of evidence seem to suggest that the second explanation is more plausible in this case.

Submarine cave faunas often contain deeper-water elements. Kobluk (1988) attributed the cause of resemblance between cryptic and deeper-water faunas mainly to analogous physical factors, especially to similarly low illumination level. Some submarine caves of Ryukyu Islands yield many incredibly extraneous bivalve genera and families, the bathymetric distributions of which extend to or are restricted to lower neritic, bathyal and even abyssal bottoms (Hayami and Kase, 1991; Kase and Hayami, in press). Deep-sea origin of the present oyster, however, is rather unlikely, because there is no evidence for *Pycnodonte* to have migrated to deep seas after the Paleogene. It may have survived for a long geologic period by wandering sublittoral cryptic environments.

Conclusion : significance as a living fossil

Although there are several extant representatives of the Pycnodontinae (*Neopycnodonte* and *Hyotissa*), this subfamily seems to have attained its acme in Late Cretaceous and Paleogene times. The genus *Pycnodonte* (including several subgenera) was a leading group of this subfamily during these periods, but there is no fossil record after the Middle Miocene. As described above, the newly discovered archaic oyster is considered to be a direct descendant of *Pycnodonte* (s.s.). Its shell morphology may look enigmatic at a

glance, but many important characters of this subgenus are well retained. In addition to the archaic morphology and evolutionary stasis, its cryptic habitat strongly suggests that the present species is a significant example of "living fossils". Its morphology, physiology and ecology must be informative for understanding the paleobiology of fossil *Pycnodonte* and related oysters.

Many Cretaceous and Paleogene species of *Pycnodonte*, however, were probably non-cryptic organisms, because they occur very abundantly together with other bivalves in various kinds of sediments. Two different life habits are assumed for fossil species of *Pycnodonte*. One is iceberg strategists (secondary cup-shaped recliners), and the other is lifetime sedentarists like the present species. Iceberg strategy is assumed in various families of Mesozoic bivalves (Jablonski and Bottjer, 1983; Seilacher, 1984), but is believed to have become much rarer in the Cenozoic, probably as the result of the increase of powerful predators (Hayami and Hosoda, 1988).

As advocated by Vermeij (1977, 1987) and others, the increase of predation pressure after the Mesozoic seems to have had a serious impact on the evolution of adaptive strategy of molluscs. Bivalve evolution seems to have followed several trends not only in morphology but also in behavior and habitat. In many free-living bivalves escaping ability from predators (e.g., by burrowing and by swimming) has increased. Some sedentary groups seem to have developed armored sculptures against the attack of durophagous predators. Another effective way of surviving must be to change habitat to a place of lower predation pressure. *Neopycnodonte*, which is probably also a descendant of *Pycnodonte*, now survives in deeper water than other oysters. It is generally supposed that submarine caves and other cavities as well as exposed deep-sea bottoms often provide suitable refuges for archaic and relatively defenseless organisms.

The inferred habitat change of *Pycnodonte* is noticeably similar in many respects to that of *Neritopsis*, which is a famous "living fossil" gastropod (Batten, 1984). *Neritopsis radula*, which is often found alive together with the present oyster in the same caves, shows very conservative morphology. Fossil records of *Neritopsis* are common in the Mesozoic and Paleogene (especially in the Tethyan realm), but *N. radula* from the Indo-West Pacific and a closely related Caribbean extant species are the only known representatives after the Miocene. To conclude, it is strongly suggested that *Pycnodonte* and *Neritopsis* have been surviving in shallow and warm seas for many millions of years by transforming themselves into cryptic animals. We may be able to have a glimpse of Mesozoic-type biota in such a cryptic environment. Further studies of organisms in submarine caves would provide concrete and significant evidence to test various theories in evolutionary biology.

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We thank sincerely Dr. Kenji Torigoe of Hiroshima University for his kind information about the anatomical characters of the present oyster. Our cordial thanks are also due to skillful divers, Messrs. Mitsutoshi Taniguchi (Miyako-jima), Shuichi Ohashi, Shigemitsu Kinjo and Hiroyuki Kinjo (Okinawa), and Miss Miyoko Uchima (Okinawa) for their self-devoting cooperation in collecting the material.

POSTSCRIPT. At the preparation of this manuscript we overlooked an important work (Dhondt, 1984: The unusual Cenomanian oyster *Pycnodonte biauriculatum*. *Geobios, Mém. spécial*, no. 8, p. 53-61), in which the morphology, distribution and paleoecology of a Cenomanian oyster *Pycnodonte* (*Pycnodonte*) *biauriculatum* (Lamarck, 1819) were described and discussed in detail. It was said that the species distributes widely (though episodically) along the northern margin of the Tethys from the Iberian Peninsula to Central Asia, sometimes forming crowded fossil banks as a monospecific community. The shell shape and long dorsal margin of *P. (P.) biauriculatum*

resembles those of the present species, but its LV is very thick like *Phygraea*. It is unlikely that the Cenomanian oyster was a cryptic organism, as Dhondt regarded the species as having been an iceberg strategist on a soft substrate. She treated the gender of the generic name *Pycnodonte* as neuter, though we are ignorant about the reason.

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Ie-jima 伊江島, Miyako Islands 宮古列島, Okinawa Island 沖縄島, Ryukyu Islands 琉球諸島, Seragaki Beach 瀬良垣ビーチ, Shimoji-shima 下地島.

琉球諸島から発見されたピクノドンテ属の隠生種(生きている化石カキ): 宮古列島の下地島および沖縄島西岸の海底洞窟(深度約20m)の薄暗い壁面にかなり大型の見馴れないカキが発見された。殻形態・微細構造・軟体部を検討した結果、この種はベッコウガキに最も近いが、現生の既知種に該当するものではなく、白亜紀-古第三紀にテチス海域で繁栄し、中新世に絶滅したと考えられてきた *Pycnodonte* 属の遺存種であることが明らかになった。*Pycnodonte (Pycnodonte) taniguchii* [和名: オオベッコウガキ (新称)] と名付けて記載し、その進化古生物学的意義を考察する。その形状・殻色は変異に富むが、稜柱構造の外層だけからなる右殻の腹縁部は紙のように薄く、生時には柔軟で、著しく広い形成面を示す。しかし *Pycnodonte* (s.s.) のすべての特徴(例えば、長い背縁に沿って広がる固着面、背側に位置する円形の閉殻筋痕、広い commissural shelf、蟲状の chomata、蜂の巣状の構造をもつ殻内の空洞、右殻表面の著しい放射状の割れ目)はよく保持されている。このカキは、ほぼ同所に生息するアマガイモドキと同様に、隠生化することによって長い地質時代を生き延びてきた「生きている化石」であることが強く示唆される。競合者や捕食者の少ない海底洞窟のような環境には、古い時代の生物相の一面が残されていると考えられる。
 速水 格・加瀬友喜

PROCEEDINGS OF THE PALAEONTOLOGICAL
SOCIETY OF JAPAN

日本古生物学会 1992 年年会・総会

日本古生物学会 1992 年年会・総会が 1 月 25 日—27 日に九州大学で開催された (参加者 198 名).

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国際学術会議報告

第 6 回化石刺胞類国際シンポジウム

……………加藤誠・森啓・新川公・江崎洋一
狩野彰宏・吉田靖・杉山哲男・長井孝一

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……………北里洋

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Palaeontological Society of Japan (PSJ) Council Actions

During its meeting on January 24, 1992, the PSJ Council enacted the following changes to its membership.

New members elected :

Yuuji Abe,	Toshiaki Futagawa,	Kouzi Hasegawa,
Tomoteru Hiyoriyama,	Yoshiyuki Hayashi,	Yoshinori Hikida,
Haruki Horikawa,	Masumi Ichikawa,	Shigeru Inaba,
Seiji Kakuta,	Takafumi Katoh,	Sanao Kashikura,
Hakuichi Koike,	Minoru Koitabashi,	Ken-ichi Kouko,
Katsue Koya,	Yukihide Matsumoto,	Hiroshi Matsuo,
Takehiro Morishige,	Masafumi Murayama,	Takehiro Nakamura,

Takashi Nakashima,
 Itsuro Oshiro,
 Takeshi Saito,
 Takehiro Sato,
 Harumi Sugawara,
 Isamu Terui,
 Hideo Yabe,

Ricardo Franco-Nieto,
 Johann G. Rigor,
 Takeyoshi Saito,
 Chieko Shimada,
 Ken Takagi,
 Yutaka Tsubaki,
 Koichi Yoshiba

Hiroyuki Oishi,
 Kazuyoshi Ryuzaki,
 Takuji Sasaki,
 Hiroko Suzuki,
 Michio Takahashi,
 Shigeeki Togashi,

New Fellows elected ;

Kazumi Akimoto,
 Tomoko Matsuda,
 Tomio Nakagawa,
 Hiroshi Nokariya,
 Osamu Sakamoto,
 Susumu Tomida,

Ren Hirayama,
 Atsushi Matsuoka,
 Hideo Nakaya,
 Masayuki Oishi,
 Tokiyuki Sato,
 Akifumi Tomizawa,

Ryuichi Majima,
 Keiji Matsuoka,
 Harufumi Nishida,
 Kiyoshi Okumura,
 Toshio Takagi,
 Yoshitaka Yabumoto

Resigned members ;

(Fellow)

Kazumi Suyari

(Ordinary members)

Tsutomu Kinoshita,

Hidekazu Yoshida

Deceased members ;

(Fellow)

Toru Makino

(Foreign members)

Li-Sho Chang

Bibliography 1986-1990 の刊行について

日本古生物学会では、1986-1990年の5年間に公表された論文（原著論文およびオリジナリティの高い総説論文等）を恒例により刊行することになりました。このBibliographyには従来通り日本古生物学会会員の論文を中心に収録致しますが、日本の資料を扱った国内・国外の非会員が公表した論文も含めることにします。

文献の収録は各会員の申告を基礎として行ないたいと思いますので、上記5年分の論文リストを下の例に従って作成し、1992年7月31日迄にお送り下さい。

文献リスト作成に際しては下記の注意事項を参照して下さい。なお、不明なことが有りましたら、委員会宛てご連絡下さい。

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[例]

WATANABE Kozo (1973): *Profusulinella* assemblage in the Omi Limestone, Niigata Prefecture, central Japan (Studies of Carboniferous fusulinacean of Omi, part 1). Transactions and Proceedings of the Palaeontological Society of Japan, New Series, no. 95, pp. 371-394, Plates 51-53, Figure 1, Tables 1-11.
Carboniferous Fusuline
[雑誌中の英文論文の例]

BANDO Yuji and KATTO Jiro (1980): On the Upper Triassic ammonoids from the Sampoan Group at Hitsuzan, Kochi City in Shikoku. In A. Taira and M. Tashiro (eds.): Selected papers in honor of Prof. Jiro Katto. Geology and Paleontology of the Shimanto Belt. Rinyakosaikai Press, Kochi, pp. 95-100. (高知市筆山の三宝山層群より産出した三疊紀後期のアンモナイトについて) (J.E.)
Triassic Ammonoidea
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Cretaceous to Tertiary Larger Foraminifera

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Miocene Mammalia

[論文集中の英文表題のない和文論文の例]

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PLIOCENE

PLIOCENE TO PLEISTOCENE

NEOGENE TO QUATERNARY

QUATERNARY

PLEISTOCENE

PLEISTOCENE TO HOLOCENE

HOLOCENE

Erratum**MATSUMOTO, TATSURO**

On some acanthoceratid ammonites from the Turonian of Hokkaido.

Trans. Proc. Palaeont. Soc. Japan, N.S., no. 164, p. 910-927, December, 1991.Figure 6 caption, printed on a gummed-label and inserted in this number, should be substituted for the erroneous figure caption appearing on page 920 of No. 164.

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◎1992年例会（第141回例会）は、6月20日（土）、21日（日）に岩手県立博物館（☎0196(61)2831）で開催されます。

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No. 164, p. 920: Fig. 6であるはずの図に、誤ってFig. 5の説明がくり返されています。訂正印刷した図の説明を本誌に挿入しましたので、お取り替え下さい。

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