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

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Orthoconic cephalopods from the Lower Permian Atahoc Formation in East Timor

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Abstract. Three species of orthoconic cephalopods, *Mooreoceras* sp. and *Atahococeras timorensis* gen. and sp. nov. of the Pseudorthoceratidae, and an indeterminate genus and species of the Bactritidae are described from the Lower Permian Atahoc Formation in the Cribas area, East Timor. Apparent changes in the surface ornamentation of *Atahococeras* are considered to be genus-level criteria that separate it from the most closely related genus, *Bitauinioceras*. This assemblage signifies a non-ammonoid cephalopod fauna in the northern margin of Gondwana near the Sakmarian/Artinskian boundary.

Key words: *Atahococeras* gen. nov., Bactritida, East Timor, Gondwana, Orthocerida, Sakmarian/Artinskian boundary

Introduction

Timor is the largest (maximum ca. 365 km long and 100 km wide) island in the Banda Arc of the Indonesian Archipelago, where corresponds to a collision zone between the Indo-Australian and Asian Plates. Thus, the geology of this island is structurally complex. Carter *et al.* (1976) stated that the older rocks on Timor consist of the autochthonous Australian facies and overthrusting units derived from the Asian island arc. The purpose of this study is to document and describe an Early Permian orthocerid and bactritid cephalopod fauna of the Atahoc Formation, which is part of the autochthonous facies. The materials were collected by one of us (K. N.) from the right bank of the River Sumasse, west of Cribas under cooperation with H. Suzuki and T. Takahashi during field work of 1961 in East Timor (Figure 1). Other than "Orthocéres" that were reported by Gageonnet and Lemoine (1958), this is the first description of non-ammonoid cephalopods from the Atahoc Formation.

The Lower Permian Atahoc Formation is made up of the oldest exposed sediments in East Timor, and forms the Cribas Anticline together with the Upper? Permian Cribas, the Triassic Aitutu and the Triassic to Jurassic Wai Luli Formations in the Cribas area (Audley-Charles, 1968; Figure 1). It consists of more than 600 m of sandstone and shale with thin intercalated beds of limestone and basaltic lava. The stratigraphic position of the present cephalopod-bearing

reddish shale is considered to correspond to the ammonoid horizon of Audley-Charles (1968, p. 6, fig. 2, columnar section of the Cribas Anticline), about 150 m below the top of the Atahoc Formation. Since Grunau (1953, 1956) first assigned this formation to the Sakmarian (Lower Permian) based on ammonoids, a number of subsequent workers have given support to this determination (e.g., Schouppé, 1957; Shimizu, 1966; Audley-Charles, 1968). More recent and detailed paleontological research by Nishida *et al.* (1997) revealed co-occurrence of ammonoids with the present orthocerids and bactritid, namely *Somoholites beluenis* (Haniel), *Agathiceras* cf. *sundaicum* Haniel, *Metapronorites timorensis* (Haniel) and *Atsabites weberi* Haniel. They concluded that the fossil horizon corresponds stratigraphically to the boundary between the Somohole and Bitauini Formations in West Timor, the age of which horizon is correlative with near the Sterlitamakian (latest Sakmarian)/Aktastinskian (earliest Artinskian) boundary.

Blendinger *et al.* (1992) stated, on the basis of ammonoids, that a conspecific middle Permian fauna flourished from Timor to the western Mediterranean along the northern margin of Gondwana. We shall not comment on the paleobiogeographic implications of the present result, because knowledge concerning Permian nautiloids and bactritoids in this province is still sparse. Besides a record of a Wordian (early Late Permian) fauna from Oman (Niko *et al.*, 1996), the present paper represents the only other documentation of non-ammonoid cephalopods with modern

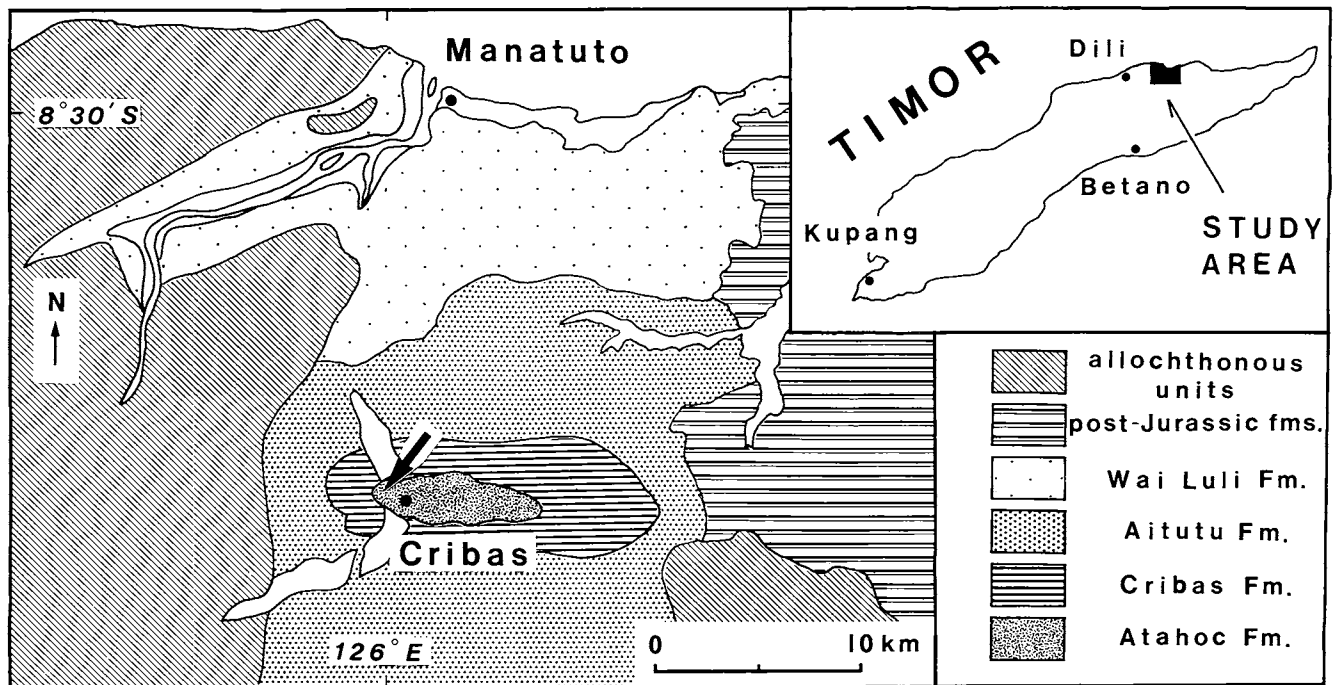


Figure 1. Map showing fossil locality (arrow), and geology of the Cribas area, East Timor (modified from Audley-Charles, 1968).

taxonomic treatment in the northern margin of Gondwana, and therefore provides the base data for paleobiogeography of nautiloids and bactritoids.

The specimens studied are deposited in the paleontological collections of the Department of Geology and Mineralogy, Faculty of Science, Kyoto University (KU).

Systematic paleontology

Subclass Nautiloidea Agassiz, 1847

Order Orthocerida Kuhn, 1940

Superfamily Pseudorthocerataceae Flower and Caster, 1935

Family Pseudorthoceratidae Flower and Caster, 1935

Subfamily Pseudorthoceratinae Flower and Caster, 1935

Genus *Mooreoceras* Miller, Dunbar and Condra, 1933

Type species.—*Mooreoceras normale* Miller, Dunbar and Condra, 1933.

Mooreoceras sp.

Figures 2.1–2.4; 3.9

Description.—Relatively large-sized orthocones with gradual shell expansion, and dorsoventrally depressed, oval cross section; apical end of a fragmentary specimen (KUTMP 20004; Figure 2.2–2.4) is 21.4 mm in dorsoventral diameter and 27.0 mm in lateral diameter, giving a form ratio of 1.26; shell surface lacks annulation, but details are not preserved. Sutures transverse, nearly straight in observable parts; camerae short, maximum dorsoventral

diameter/length ratio approximately 3.4; septal curvature shallow. Siphuncle subcentral, shifted dorsally from center, consists of cytochoanitic septal necks, 0.70–0.99 mm in length, and inflated connecting rings that are subcylindrical to fusiform in shape; adnation area narrow. Cameral deposits thin, episeptal-mural apically and mural adorally; endosiphuncular deposits weakly developed, form annuli that are unfused and restricted near septal foramina.

Discussion.—Although the surface ornamentation of the examined specimens is not observable, their oval shell cross sections, short camerae, inflated connecting rings with the narrow adnation area and unfused annuli of the endosiphuncular deposits are the characteristics of *Mooreoceras*.

This discovery is of particular interest as one of the relatively rare records of Permian *Mooreoceras*, which also occurs in Early Permian faunas of the Blaine and Dog Creek Formations in Texas (*Mooreoceras "normale"* and *M. gigantea* Clifton, 1942), the Gallytharra Limestone in West Australia (*Mooreoceras* sp., Teichert, 1951; Teichert and Glenister, 1952), and the Barfield Formation in East Australia (*Mooreoceras australis* Waterhouse, 1987).

Material.—KUTMP 20003, 40.2 mm in length, and KUTMP 20004, 47.2 mm in length; both are incomplete phragmocones.

Subfamily Spyroceratinae Shimizu and Obata, 1935
Genus *Atahoceras* gen. nov.

Type species.—*Atahoceras timorensis* sp. nov.

Diagnosis.—Like *Bitauioceras* but differs by apparent

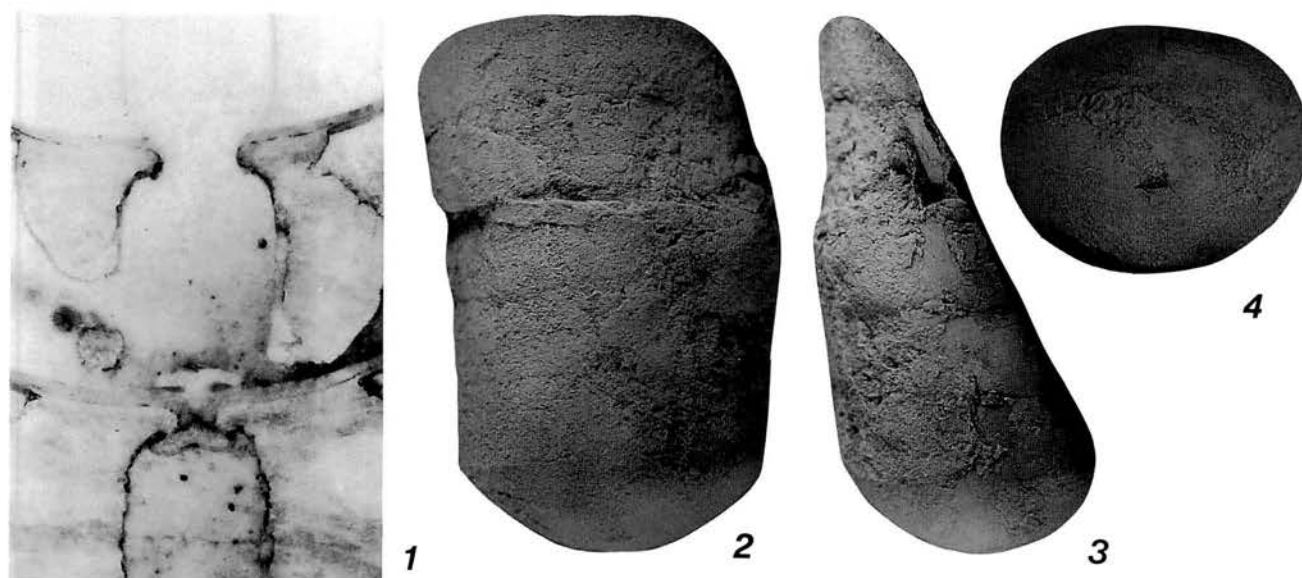


Figure 2. *Mooreoceras* sp. 1. KUTMP 20003, longitudinal polished section, showing details of siphuncle, $\times 7$. 2-4. KUTMP 20004; 2. ventral view, $\times 1.5$; 3. Lateral view, venter on left, $\times 1.5$; 4. Septal view of apical end, venter down, $\times 1.5$.

changes in surface ornamentation; i.e., only transverse lirae on juvenile shell, then strongly oblique ridges are added, and reticulated ridges with ribs on the most adoral shell; constriction absent.

Etymology.—The generic name is derived from the Atahoc Formation, in which the type specimens were found.

***Atahoceras timorensis* sp. nov.**

Figure 3.1-3.8

Diagnosis.—As for the genus.

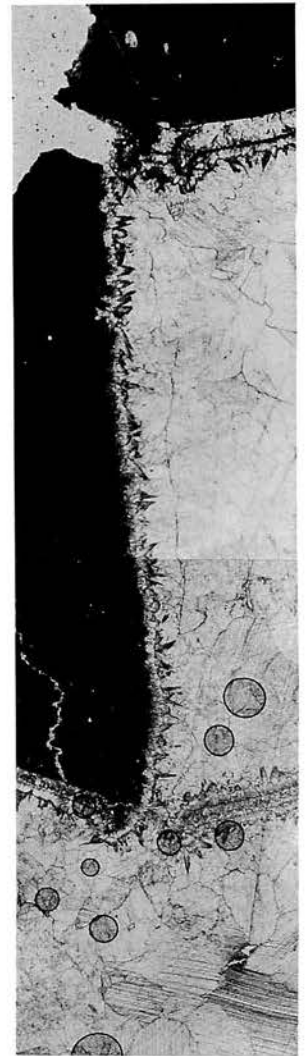
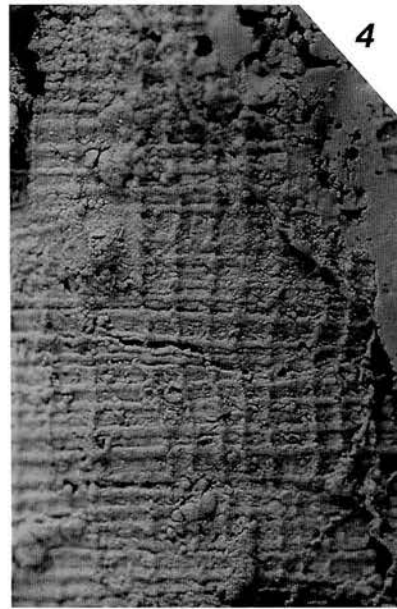
Description.—Orthoconic shells with circular cross section, gradual shell expansion; angle of shell expansion ranges from 4.8° to 5.5° ; largest specimen (holotype; Figure 3.2-3.4, 3.7, 3.8) of phragmocone reaches 17.5 mm in diameter. Surface ornamentation apparently changes with shell growth: 1) only transverse lirae of somewhat unequal size in juvenile shell (up to 3.9 mm in shell diameter), 2) apically strongly oblique and adorally longitudinal ridges that are absent for approximately 5 mm in shell length, but immediately are succeeded by similar ridges, in addition transverse and relatively strong lirae, 3) longitudinal ridges, broad transverse ridges, in addition very weak lirae are also present in interspaces of transverse ridges (beyond 4.5 mm in shell diameter), then 4) longitudinal ridges, and transverse ornamentation consists of ridges and broad, annulation-like but subdued ribs; these ridges form a reticulate pattern (at least up to 11.5 mm in shell diameter); strong sinuation in transverse ornamentation not recognized; transverse constrictions caused by shell thickening and surface constriction are absent. Sutures straight, directly transverse in apical shell; adoral sutures not observed, but weak obliquity of approximately 5° to rectangular direction of shell axis recognized in longitudinal section; strongly concave septa form

long camera, with maximum width/length ratio approximately 1.4 in most adoral camerae; mural part of septum relatively wide. Siphuncle central in position, narrow; septal necks suborthochoanitic, short, 0.9 mm in length in well-preserved septal necks of holotype; connecting ring not preserved; ratio of outside diameter of septal neck/corresponding shell diameter approximately 0.08. Cameral and endosiphuncular deposits not detected.

Discussion.—The surface ornamentation of the juvenile shell, the septal neck structure and the cameral form of *Atahoceras* gen. nov. are in common with *Bitaunioceras* (Shimizu and Obata, 1936), which is based on *Orthoceras bitauniense* Haniel (1915, pl. 56, figs. 5a-c) from the Bitau Formation in West Timor. The diagnostic features of *Atahoceras* appear in the adoral shell, where the changes in surface ornamentation and the absence of the constrictions separate the new genus from *Bitaunioceras*. Except for its possessing periodic surface constrictions and salients, *Bitaunioceras elegantulum* (Gemmellaro, 1890, pl. 11, figs. 12-17; Niko and Nishida, 1987) from the Lower Permian of Sicily is more similar to *Atahoceras timorensis* sp. nov. in having the longitudinal ornamentation than the other *Bitaunioceras* species. Ontogenetic changes in the surface ornamentation of this Sicilian species are unknown.

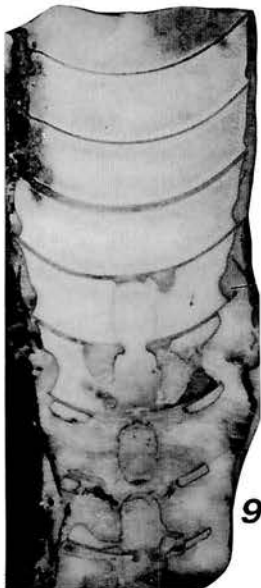
Haniel (1915, pl. 56, figs. 3a-c, 4) described "*Orthoceras*" *welteri*, which has the reticulate ornamentation, from the Bitau Formation. Owing to the lack of detailed information about its internal structure and juvenile shell morphology, the generic assignment of this species is uncertain in modern classification. However, sinuation of its transverse surface ornamentation distinguishes "*O.*" *welteri* from *A. timorensis* sp. nov. at the species level.

Reticulate ornamentation is recognized in some genera belonging to Pseudorthoceratidae, Orthoceratidae and



7

8



5

6



Geisonoceratidae. Among them, a Carboniferous pseudorthoceratid *Sueroceras* (Riccardi and Sabattini, 1975; type species, *S. irregulare* Riccardi and Sabattini, 1975, pl. 22, figs. 1–12, from Argentina), which has a relatively similar pattern to *Atahococeras*. However, its internal structure, such as partly cyrtocoanitic septal necks, shorter camerae, and thick lining deposits in the siphuncle, suggests that *Sueroceras* has a close phylogenetic relationship with *Dolorthoceras* (Miller, 1931) rather than with *Bitauinioceras* and *Atahococeras*.

Etymology.—The specific name refers to the island of Timor.

Material.—The holotype, KUTMP 20001, is an incomplete phragmocone 68.9 mm in length. In addition, a single paratype 26.2 mm in length, KUTMP 20002, that represents a more apical phragmocone than the holotype.

Subclass Bactritoidea Shimanskiy, 1951
Order Bactritida Shimanskiy, 1951
Family Bactritidae Hyatt, 1884

Genus and species indeterminate

Figure 3.10

Discussion.—This species is represented by a single specimen of a longitudinal thin section. Its diagnostic features are as follows: initial camera (protoconch) subcircular in section, 0.51 mm in diameter, 0.48 mm in length, in conjunction with probably cylindrical second to third developmental stages of phragmocone; adoral diameter of second camera smaller than that of initial camera, 0.37 mm; first three septa recognized, but they and their septal necks are not well preserved.

The general shape and size of the initial camera of the present species are characteristic to the family Bactritidae as shown by Clarke (1894), Erben (1964) and Mapes (1979). Haniel (1915) reported two orthoconic forms, "*Orthoceras*" sp. indet. Nr. 2 (fig. 38) and "*O.*" sp. indet. Nr. 3, which have marginal siphuncular positions, from the Bitauini Formation. Although they may be assignable to the family Bactritidae in modern terms, the materials are too incomplete to discuss relationships with this species.

Material.—KUTMP 20005, 1.0 mm in length, is an apical phragmocone with a complete initial camera.

Acknowledgments

The third author is indebted to Hiroyuki Suzuki and Toru Takahashi, former students of Kyoto University, for their assistance in the field.

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← **Figure 3.** 1–8. *Atahococeras timorense* gen. and sp. nov. 1, 5, 6. Paratype, KUTMP 20002; 1. Side view, silicone rubber cast, ×3; 5. Details of apical surface ornamentation, silicone rubber cast, ×10; 6. Details of adoral surface ornamentation, silicone rubber cast, ×10. 2–4, 7, 8. Holotype, KUTMP 20001; 2. Longitudinal thin section, ×2; 3. Transverse polished section at apical end, ×2; 4. Details of surface ornamentation, silicone rubber cast, note reticulated ridges and subdued ribs, ×10; 7. Longitudinal thin section, showing details of siphuncle, ×7; 8. Longitudinal polished section, showing details of septal neck, ×10; 9. *Mooreoceras* sp., KUTMP 20003, longitudinal polished section, ×2; 10. Bactritidae, genus and species indeterminate, KUTMP 20005, longitudinal thin section, ×40.

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A new species of *Ancistrolepis* (Gastropoda: Buccinidae) from the Iwaki Formation (lower Oligocene) of the Joban coal field, northern Japan

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Abstract. *Ancistrolepis* (*Ancistrolepis*) *iwakiensis* sp. nov. from the lower Oligocene of the Joban coal field, northern Japan closely resembles both *Ancistrolepis* (*A.*) *matchgarensis* (Makiyama) from the upper Eocene to Oligocene of Sakhalin and *Ancistrolepis* (*A.*) *rategiensis* Titova from the upper Eocene of northwestern Kamchatka. *A.* (s. s.) *iwakiensis* sp. nov. documents an early evolutionary history of *Ancistrolepis* (s. s.) that appeared in the northwestern Pacific during late Eocene time.

Key words: *Ancistrolepis*, early Oligocene, Gastropoda, northwestern Pacific

Introduction

The Ancistrolepidinae is one of the most common groups of the gastropod family Buccinidae: it occurs in shallow to deep waters in the boreal and arctic regions. Unlike some other buccinids, the fossil and living species of Ancistrolepidinae have a restricted distribution, being found only in the northern Pacific. The systematics of the subfamily is still not clearly understood (Amano *et al.*, 1996).

According to Egorov and Barsukov (1994), who studied the living species of Ancistrolepidinae, the subfamily contains six genera: *Ancistrolepis* (with three subgenera: *Ancistrolepis* (s.s.), *Bathyancistrolepis*, and *Clinopegma*), *Pseudoliomesus*, *Neancistrolepis*, *Sulcosinus*, *Japelson*, and *Parancistrolepis*. The species of *Ancistrolepis* (s.s.) live at present in lower sublittoral to bathyal waters (100 to 690 m) around Honshu, Hokkaido, Sakhalin, and Kamchatka (Higo and Goto, 1993). In addition, *Ancistrolepis* (*A.*) *vietnamensis* Sirenko and Goryachev has been recorded at depths from 400 to 700 m in the South China Sea (Egorov and Barsukov, 1994).

Titova (1993) discussed the evolution of the fossil Ancistrolepidinae in the northern Pacific, and adopted the systematics of Ancistrolepidinae as follows: *Ancistrolepis* (with *Ancistrolepis* (s.s.), *Bathyancistrolepis*, and *Clinopegma*), *Neancistrolepis*, and *Pseudoliomesus*. She suggested that *Ancistrolepis* (s.s.) appeared in the northwestern Pacific (northern Japan to Kamchatka) during the late Eocene. However, the Paleogene Ancistrolepidinae are rather scarce in the northern Pacific. Matsui (1958) described the earliest representatives of Ancistrolepidinae in Japan from the Urahoro and Ombetsu Groups (upper

Eocene to lower Oligocene) of the Kushiro coal field, eastern Hokkaido, placing the species in *Neptunea*. These species are here referred as *Ancistrolepis* (*A.*) *huruhatani* (Matsui), *A.* (*A.*) *subcarinatus* (Matsui), and *A.* (*Bathyancistrolepis*) *sitakaraensis* (Matsui). Honda (1989) also originally described *Ancistrolepis* (*A.*) *ogasawarai* as a *Neptunea* from the Charo Formation (lower Oligocene) of the Ombetsu Group. In addition, *Ancistrolepis* (*A.*) *modestoides* (Takeda) has been recorded from the Poronai Formation (upper Eocene to lowermost lower Oligocene) of the Ishikari coal field, central Hokkaido, and the Urahoro and Ombetsu Groups (Takeda, 1953; Matsui, 1958; Honda, 1989).

The southernmost area yielding Paleogene *Ancistrolepis* (s.s.) is located in the Joban coal field, northeastern Honshu, northern Japan (Figure 1). Only two poorly preserved specimens of *Ancistrolepis* (s.s.) have been recorded from the lower Oligocene of the Joban coal field. They are *Ancistrolepis* sp. cf. *A.* (*A.*) *subcarinatus* (as *Neptunea ezoana* Takeda; Kamada, 1962, p. 166, pl. 20, fig. 19) from the Iwaki Formation and *Ancistrolepis* (*A.*) sp. (as *A. yamanei* Kanehara, 1937, p. 13, pl. 4, fig. 8, in part) from the Asagai Formation (Titova, 1993).

Yanagisawa *et al.* (1989) studied the subsurface litho- and biostratigraphy of the Cenozoic strata in the Futaba area of the Joban coal field (Figure 1). Their drill core A-1 yielded numerous well-preserved molluscan fossils at seven horizons of the Iwaki (IW-1-3) and Asagai (AS-1-4) Formations (Figure 2). The mollusks include *Acila* (*Truncacila*) *oyamadensis* Hirayama, *Cyclocardia laxata* (Yokoyama), *Clinocardium asagaiense* (Makiyama), *Papyridea* (*Profulvia*) *harrimani* Dall, *Mya* sp., and *Turritella* sp. (Yanagisawa *et al.*, 1989). In this paper, I describe a new species of

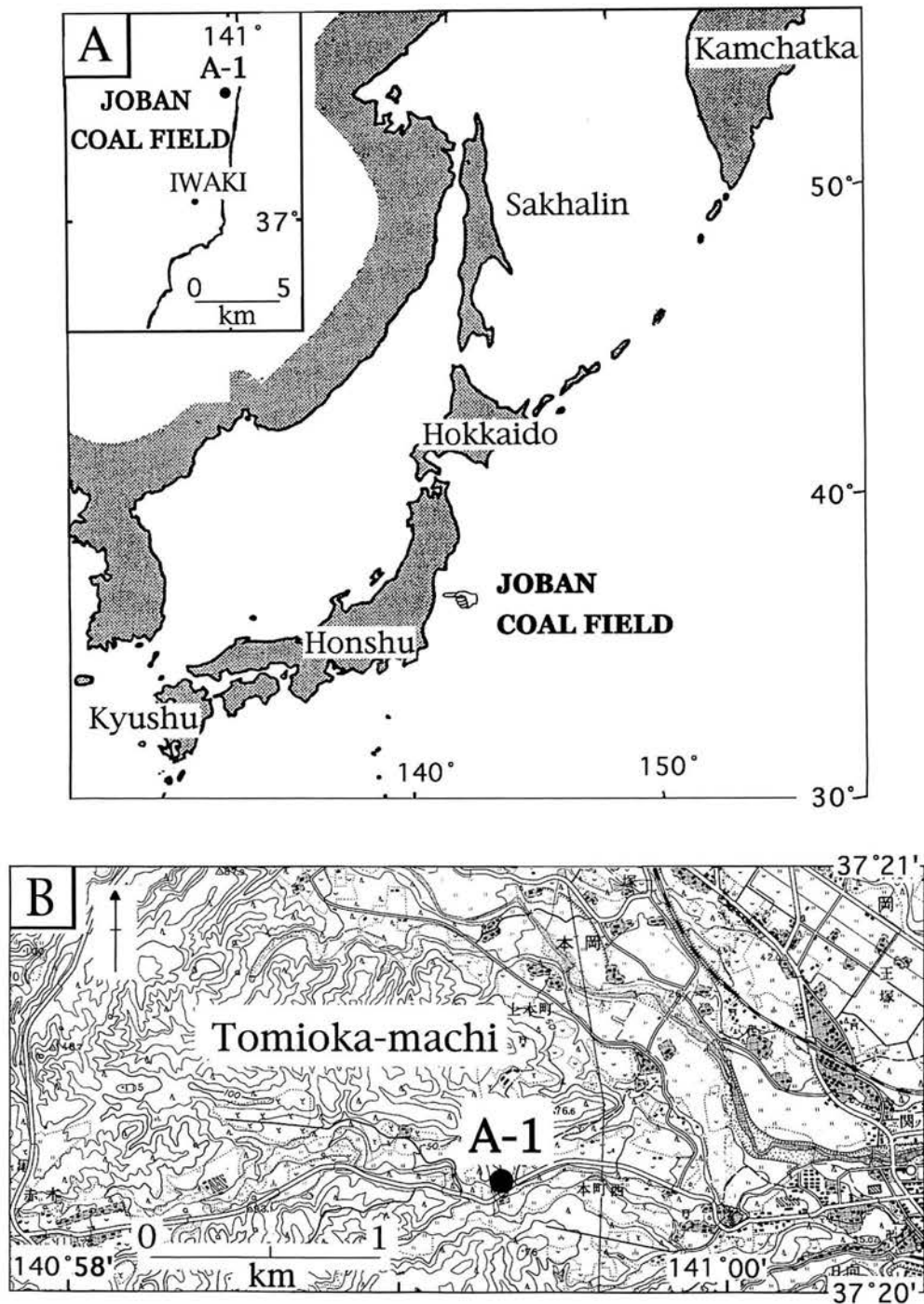


Figure 1. A. Map of the northwestern Pacific showing the location of the Joban coal field and place names referred to in the text. B. Map of the Joban coal field showing the location of drill core A-1 (parts of 1:25,000 scale maps, "Iwaki-Tomioka" and "Yonomori" published by the Geographical Survey of Japan).

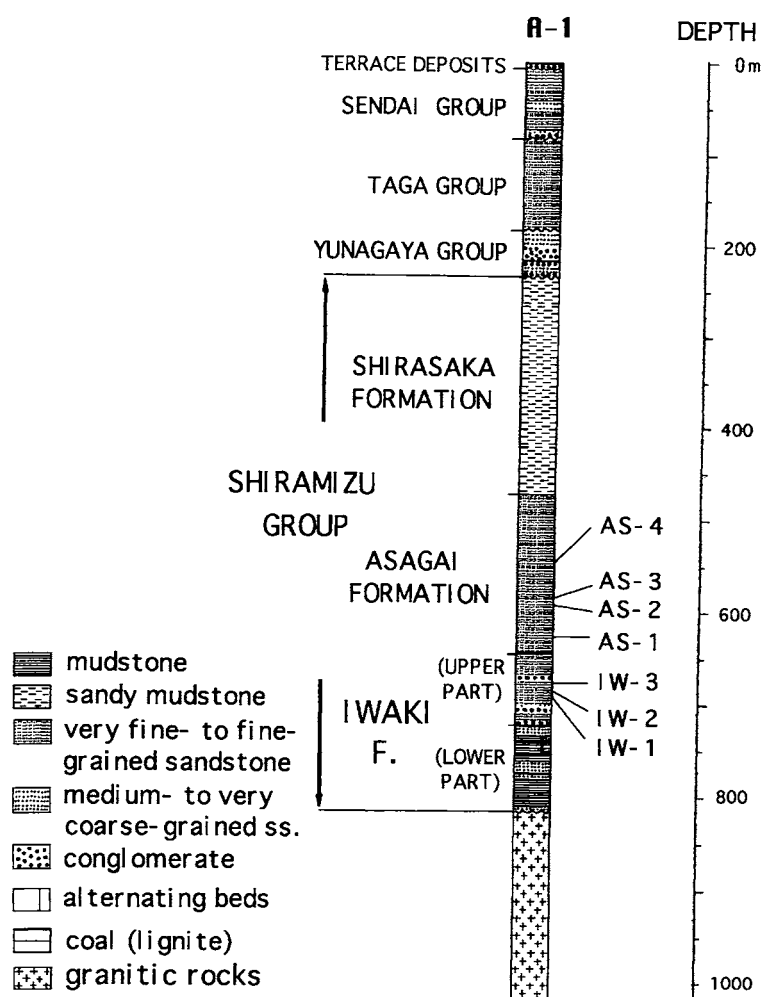


Figure 2. Columnar section of drill core A-1 (compiled from Yanagisawa *et al.*, 1989; Kubo *et al.*, 1994). IW-1-3, AS-1-4; fossil horizons.

Ancistrolepis (s.s.) obtained from the horizon IW-3 of the Iwaki Formation in drill core A-1.

Geological setting

Drill core A-1 of Yanagisawa *et al.* (1989) is lithologically divided into six units, which are, in ascending order, the basement granitic rocks (pre-Tertiary), the Shiramizu (lower Oligocene), Yunagaya (lower Miocene) and Taga (middle to upper Miocene) Groups, the upper part of the Sendai Group (upper Pliocene), and terrace deposits (Pleistocene) (Yanagisawa *et al.*, 1989; Kubo *et al.*, 1994; Figure 2).

The Shiramizu Group is further divided into the Iwaki, Asagai, and Shirasaka Formations, in ascending order (Figure 2). The lower part of the Iwaki Formation consists largely of mudstone with intercalating arkose, fine- to medium-grained sandstone, coal seams, and coaly mudstone. The upper part of the formation is composed of silty, very fine- to fine-grained sandstone with intercalated fine- to medium-grained sandstone and coal seams (Yanagisawa *et al.*,

1989). The Asagai Formation is made up of massive, very fine- to fine-grained sandstone with small carbonaceous fragments. The Shirasaka Formation consists of grey sandy mudstone (Yanagisawa *et al.*, 1989).

Tomida (1986) dated the Iwaki Formation as early Oligocene by the occurrence of the mammalian fossil *Entelodon*. Using fossil diatoms and silicoflagellates, Yanagisawa *et al.* (1989) also dated the Shirasaka Formation as early Oligocene. Consequently, the Shiramizu Group as a whole should be attributed to the lower Oligocene (Yanagisawa *et al.*, 1989).

Description of new species

Family Buccinidae Rafinesque, 1815
Subfamily Ancistrolepidinae Habe and Sato, 1972
Genus *Ancistrolepis* Dall, 1895
Subgenus *Ancistrolepis* s.s.

Type species.—*Chrysodomus eucosmius* Dall, 1891

***Ancistrolepis (Ancistrolepis) iwakiensis* sp. nov.**

Figure 3

Neptunea sp., indet. Yanagisawa *et al.*, 1989, pl. 12, fig. 6.

Type locality.—At a depth of 675.00 to 675.20 m in drill core A-1 (GSJ B326), along a tributary of the Tomioka-gawa, Honcho-nishi, Tomioka-machi, Futaba-gun, Fukushima Prefecture, Japan (Lat. 37°20'16"N, Long. 140°59'20"E; Figure 1B).

Holotype.—GSJF15135 (Figure 3) in the Geological Museum, Geological Survey of Japan, Tsukuba, Japan.

Etymology.—The name is derived from the formation name "Iwaki."

Material.—One specimen (holotype GSJF15135).

Diagnosis.—Shell moderate in size and fusiform. Spire high, with five whorls. Surface sculptured with three (four on penultimate whorls) subrounded spiral cords. Each interspace occupied by one fine cord.

Description.—Shell moderate in size, rather thin, and fusiform. Whorls five in number, and divided by moderately incised suture. Whorl profile moderately convex with rounded shoulder. Surface sculptured with spiral cords, which intersect feeble growth lines. Three spiral cords on upper whorls, four on fourth (penultimate) whorl, equally spaced, subrounded, and narrower than interspaces. Each interspace on third to fourth whorls occupied by one fine cord. Four spiral cords on upper part of body whorl, subrounded, and narrower than interspaces. More than six spiral cords on lower part, very low, subrounded, and much broader than interspaces. Each interspace on upper part of body whorl occupied by one fine cord.

Measurements.—Holotype, GSJF15135, height 56.5 mm+, diameter 34.7 mm, pleural angle 36°.

Horizon.—IW-3, upper part of the Iwaki Formation (Figure 2). Lower Oligocene.

Associated fauna.—The new species is associated with *Clinocardium asagaiense* (Yanagisawa *et al.*, 1989).

Remarks.—One rather well-preserved, nearly complete specimen, with pale brown shell material, was obtained from the greenish-grey, fine-grained sandstone of the upper part of the Iwaki Formation. The specimen largely lacks the siphonal area, because the core diameter is limited to approximately 60 mm. The features of the siphonal area are therefore not observable.

The new species resembles *Ancistrolepis* (*A.*) *matchgarensis* (Makiyama, 1934) from the Matchigar Formation (upper Eocene to Oligocene; Barinov and Gladenkov, 1998) of northern Sakhalin and the Arakai Formation (Oligocene) of southern Sakhalin (Titova, 1993). *Ancistrolepis matchgarensis* has only three primary cords, however, the new species has both three or four primary cords and one secondary cord. Titova (1993, p. 12, figs. 2A-D) described *Ancistrolepis* (*A.*) *rategiensis* from the Rategian Formation (upper Eocene) of northwestern Kamchatka. The present new species differs from *A. rategiensis* in having more broadly rounded spiral cords. *Ancistrolepis iwakiensis* sp. nov. also differs from *A.* (*A.*) sp. (= *Ancistrolepis yamanei* Kanehara, 1937, p. 13, pl. 4, fig. 8, in part; see Titova, 1993) from the Asagai Formation in

having a less convex whorl profile and a fine cord between the spiral cords.

Discussion

The genus *Ancistrolepis* (s.s.) is the earliest representative of the Ancistrolepidinae, which probably originated from a common ancestor with the *Neptunea altispirata* group (Titova, 1993). *N. altispirata* was originally described by Nagao (1928) from the Doshi Formation (upper Eocene to lowermost lower Oligocene Funazuan stage; Honda, 1994) of Kyushu, southern Japan. *N. altispirata* has also been recorded from the upper Eocene of western Kamchatka (Gladenkov *et al.*, 1991). The *N. altispirata* group includes *N. onbetsuensis* Matsui from the Omagari and Charo Formations (uppermost upper Eocene to lower Oligocene) of the Kushiro coal field, eastern Hokkaido, and *Neptunea vinjukovi* Krishtofovich from the Oligocene of northern Sakhalin (Titova, 1993). The new species is similar to species of the *N. altispirata* group in having a rather moderately elevated spire.

Honda (1991, 1994) noted that several cold-water genera such as *Neptunea*, *Clinocardium*, and *Mya* appeared from tropical or subtropical ones of Japan and Sakhalin from late middle Eocene to early Oligocene time. Titova (1993) also noted that *Ancistrolepis* (s.s.) appeared in the region of northern Japan to Kamchatka during late Eocene time. These four genera originated in the northwestern Pacific, probably concurrent with the Eocene-Oligocene transition to a global cooling trend.

Titova (1993) divided *Ancistrolepis* (s.s.) into the *Ancistrolepis eucosmius* and *A. grammatus* stocks. The *A. eucosmius* stock is characterized by having a smaller shell, less numerous and weaker radial cords than the *A. grammatus* stock. Accordingly, the new species belongs to the *A. grammatus* stock based on general features of the shell. Titova (1993) further subdivided the *A. eucosmius* stock from the late Eocene to early Miocene into three groups. These are: 1) the *Ancistrolepis huruhatai*-*A. subcarinatus* group from the upper Eocene and lower Oligocene of Hokkaido and northern Honshu; 2) the *Ancistrolepis rategiensis*-*A. matchgarensis* group from the upper Eocene and Oligocene of northern Honshu, Hokkaido, Sakhalin, and Kamchatka; and 3) the group of *Ancistrolepis clarki* Tegland and *A. rearensis* (Clark) from the Oligocene and lower Miocene of Northwest America, which probably evolved from *A. rategiensis*. The *A. huruhatai*-*A. subcarinatus* group is characterized by well-developed secondary spiral cords (Titova, 1993). The new species has only one secondary cord, so it belongs to the *A. rategiensis*-*A. matchgarensis* group of Titova (1993).

Acknowledgments

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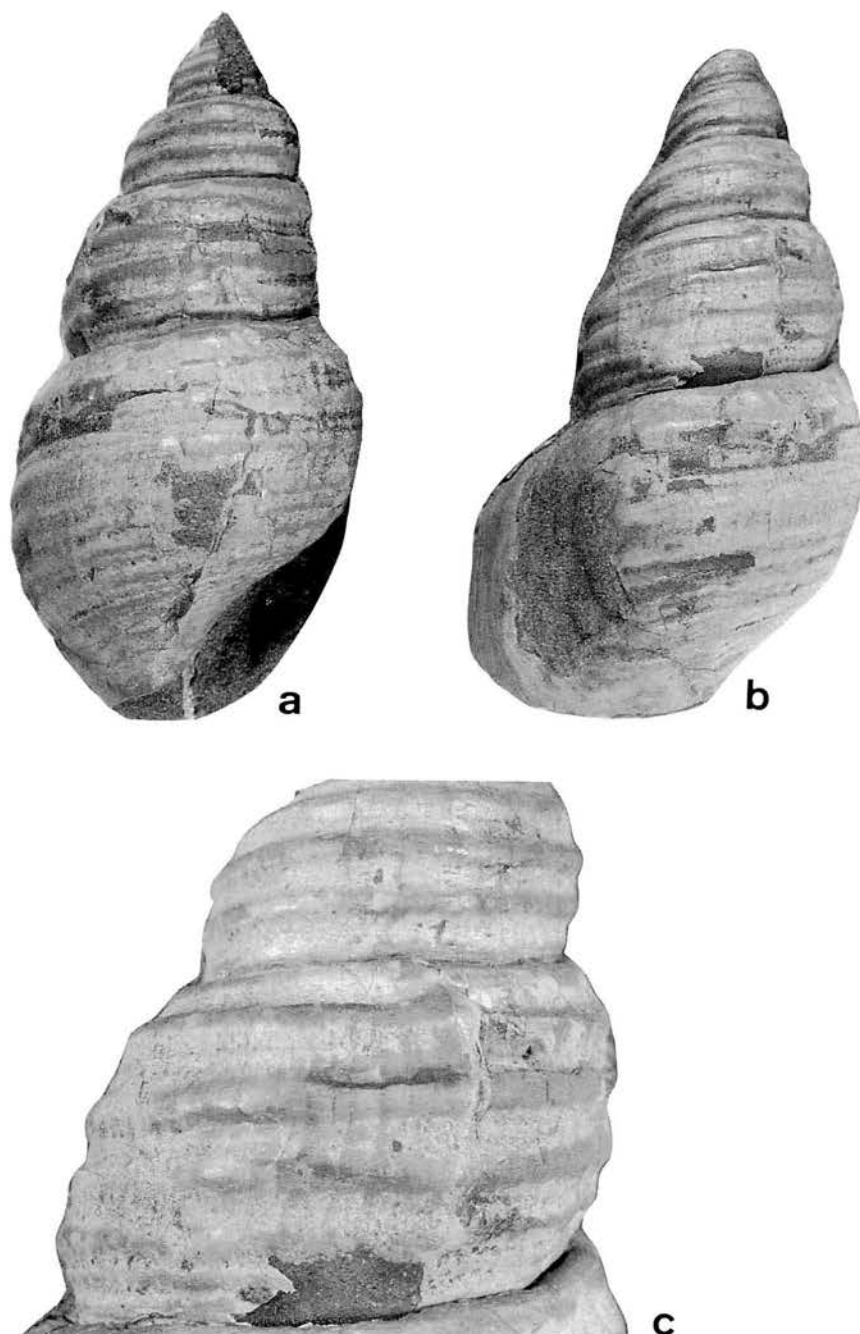


Figure 3. *Ancistrolepis (Ancistrolepis) iwakiensis* sp. nov., Horizon IW-3, Holotype, GSJF15135. **a.** Apertural-backside view, $\times 1.5$. **b.** Backside view, $\times 1.5$. **c.** Close-up of the third to fourth (penultimate) whorls, $\times 3.1$. GSJ; Geological Museum, Geological Survey of Japan, Tsukuba, Japan.

are expressed to Yukio Yanagisawa (Geological Survey of Japan), for providing the opportunity to study the specimen. Thanks are also expressed to Louie Marincovich, Jr. (California Academy of Sciences), for critical review of the manuscript, and to Paul Callomon (Elle Scientific Publications), for proofreading an early draft of the manu-

script.

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Carbon-isotope stratigraphy and its chronostratigraphic significance for the Cretaceous Yezo Group, Kotanbetsu area, Hokkaido, Japan

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Abstract. A positive carbon isotopic excursion across the Cenomanian/Turonian boundary in the Kotanbetsu area, Hokkaido, Japan provides accurate positioning of the boundary. A microscopic study based on organic petrology reveals that the organic matter included in mudstones of the Kotanbetsu River section is exclusively terrestrial. The results of stratigraphic time-series analysis of stable carbon isotopes from these mudstone samples can be translated as representing an average of a terrestrial plant community signal. The isotopic fluctuation through this time interval records information on the global ocean-atmosphere system. Two internationally recognized events characterize the uppermost Cenomanian through middle Turonian. On the basis of this study the Cenomanian/Turonian boundary can be recognized within a stratigraphic range of ~14 meters. This horizon of the boundary is concordant with that from biostratigraphy (ammonoids, inoceramids and planktonic foraminifers). Above the middle Turonian strata, the isotopic pattern supports the biochronology of planktonic foraminifers rather than that of inoceramids.

Key words: biostratigraphy, carbon isotope, Cenomanian/Turonian boundary, Coniacian, correlation, Cretaceous, Kotanbetsu, terrestrial organic matter, Yezo Group

Introduction

International chronostratigraphic correlation of the Cretaceous Yezo Group, especially the Cenomanian through Turonian has been extensively discussed in this decade mainly with reference to the Oyubari area and by the use of megafossils (e.g. Nishida *et al.*, 1993a; Hirano, 1995) and planktonic foraminifers (Motoyama *et al.*, 1991; Hasegawa, 1995, 1997; Takashima *et al.*, 1997). On the other hand, carbon-isotope stratigraphy through the Cretaceous was first shown by Sholle and Arthur (1980) to be a potential correlational tool in the Tethyan region. After this pioneering study, many carbon-isotopic studies using marine carbonate and marine organic matter across the Cenomanian/Turonian (C/T) boundary were performed for detailed correlation at the same resolution as biostratigraphy (e.g. Pratt, 1985; Gale *et al.*, 1993). In Japan, Hasegawa (1995, 1997) analyzed the stable carbon-isotope composition of terrestrial organic carbon from the Oyubari section and discussed its isotope stratigraphy against the control of the planktonic foraminiferal biostratigraphy. Hasegawa

(1995) identified the well-known positive isotopic event caused by an Oceanic Anoxic Event (Schlanger and Jenkyns, 1976) at the C/T boundary and supported the idea that it was a global signal (e.g. Gale *et al.*, 1993; Jenkyns *et al.*, 1994). This was subsequently compared with the carbon-isotope curve derived from marine carbonate carbon established in southern England (Jenkyns *et al.*, 1994) and Italy (Corfield, 1995; Jenkyns *et al.*, 1994). This led to the identification of three isotopic events as global markers for correlation (Hasegawa, 1997). Even though carbon-isotope stratigraphy can be a powerful tool for international correlation (Hasegawa, 1997; Beerling and Jolley, 1998; Gröcke *et al.*, 1999), it has not been employed for detailed stratigraphic positioning of the C/T boundary in other areas of Hokkaido Island except for a study in the Tappu area by Hasegawa and Saito (1993). Nishida *et al.* (1992, 1993b) performed detailed biostratigraphy of megafossils and foraminifers along the Kotanbetsu River in the Kotanbetsu area, Hokkaido focusing on the positioning of the C/T boundary. Hatsugai *et al.* (1999) also discussed detailed planktonic foraminiferal biostratigraphy using internationally

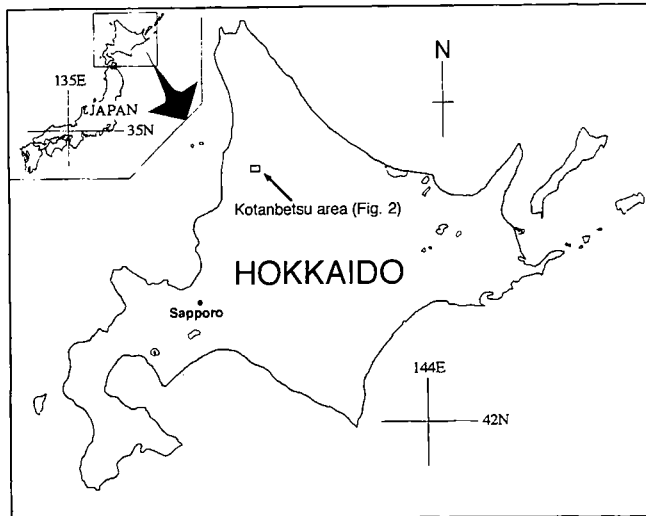


Figure 1. Index map showing the locality of the Kotanbetsu area.

recognized species along the same section.

The purpose of this study is to show how carbon-isotope stratigraphy is a powerful and important tool for correlation. The Kotanbetsu River section was selected as the best section to demonstrate the applicability of carbon-isotope stratigraphy not only for intra-regional but also for inter-regional correlation of the Yezo Group.

Geological setting

The Yezo Group exposed along the Kotanbetsu River in the Kotanbetsu area, Hokkaido, Japan (Figure 1) is interpreted as a forearc basin (Okada, 1979, 1983). The sequence of the Cenomanian through Turonian is represented, in ascending order, by six lithologic units, namely Mf-h, Mi,

Mj-o, Ua-b, Uc-e and Uf-g which were originally defined by Igi *et al.* (1958). These lithologic units strike meridionally and dip westward at an angle of $\sim 60^\circ$. They are nearly continuously exposed and are composed dominantly of dark gray mudstone with either occasional intercalations of sandstone layers of less than 30 cm in thickness or alternating layers of turbiditic sandstone and siltstone. Frequency of intercalating sandstone layers increases in the Units Mi and Ua-b.

The averaged rate of sedimentation for this succession is inferred as approximately 200 m/m.y. based on planktonic foraminiferal biostratigraphy (Hatsugai *et al.*, 1999) using the first occurrence of *Helvetoglobotruncana helvetica* and the first occurrence of the genus *Archaeoglobigerina* and time scale of Gradstein *et al.* (1995). This is more than ten times as fast as the English Chalk section (Jenkyns *et al.*, 1994).

Based on four K-Ar ages from four different bentonite layers encompassing the Unit Mi (Shibata and Miyata, 1978; Shibata *et al.*, 1997), Shibata *et al.* (1997) concluded that the K-Ar age of C/T boundary in the Tappu area was $93.1 \pm 1.2(1\sigma)$. Hirano *et al.* (1997) also obtained similar K-Ar ages from the Tappu and Oyubari sections.

Materials and methodology

Samples were collected along the Kotanbetsu River in the Kotanbetsu area (Figures 1, 2). All samples subjected to isotopic analysis were obtained from the pelagic mudstone unit, whereas turbidite units were ignored. The stratigraphic intervals for samples are between 20–100 m along the section (Figure 2). Powdered mudstones were treated with a 5N solution of HCl for 12 hours to remove carbonate minerals. Each acid-processed sample was then baked in an oven at 850°C for 8 hours in a tube under vacuum together with CuO to convert organic carbon into CO_2 gas. After purification of CO_2 gas on a cryogenic vacuum line, carbon-isotope analyses were performed with a Finnigan MAT

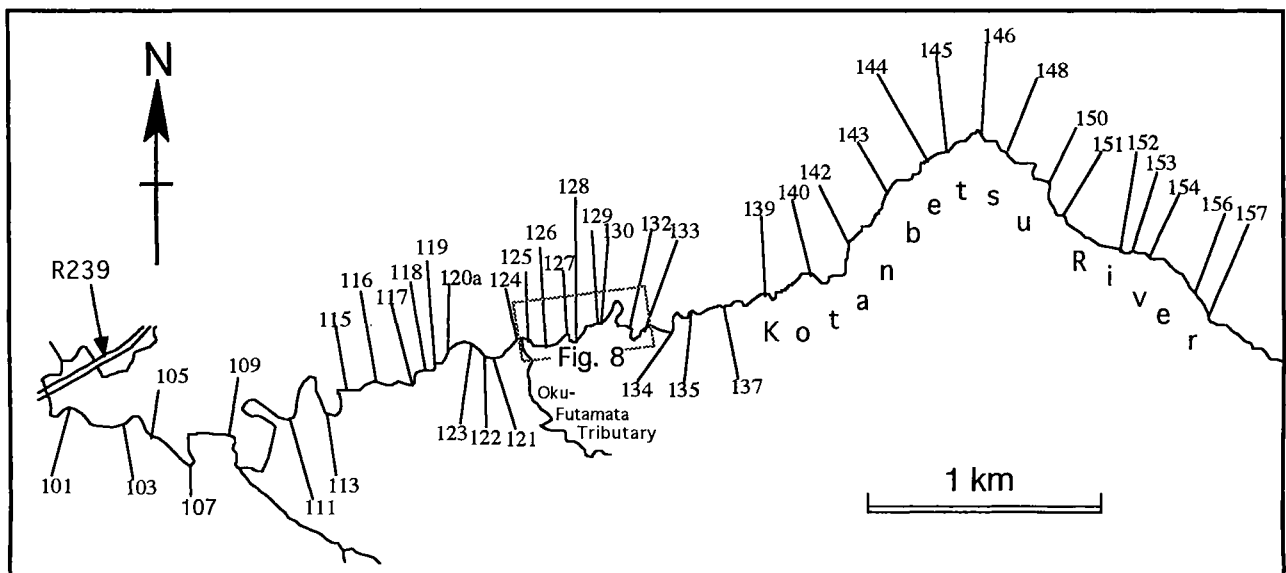


Figure 2. Map showing sampling localities in the Kotanbetsu area.

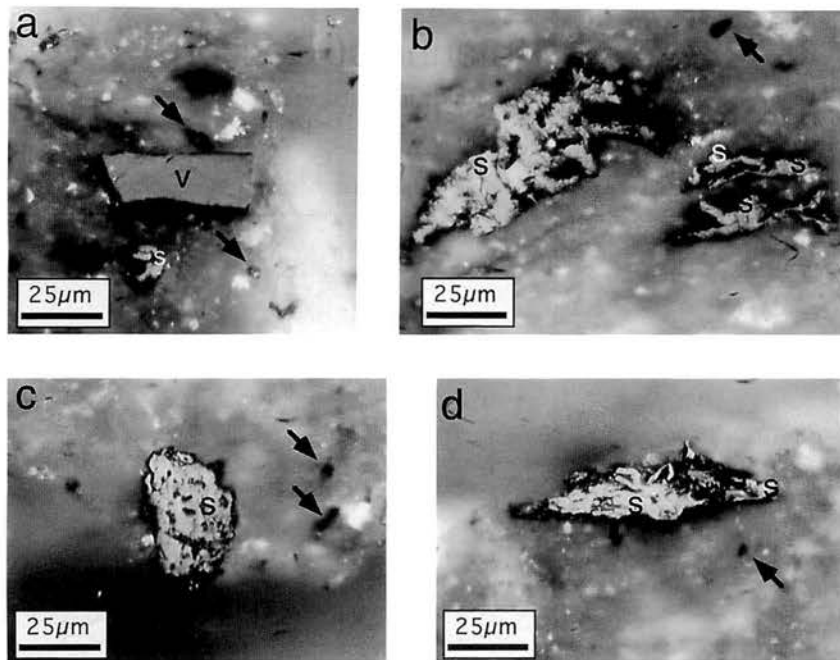


Figure 3. Kerogen observed under microscope with reflected light. Note that most structured particles are identified as semifusinite and vitrinite, which are terrestrial in origin (see text for details). Semifusinites which have obvious lignitic cellular structure in selected samples document vascular plants as their origin. Examples of indeterminate vitrodetrinites and inertodetrinites are also indicated by arrows. **a.** Vitrinite (v) with smaller particles of semifusinite (s) from KOT-148. **b.** Semifusinites (s) with obvious cellular structure from KOT-130. **c.** Semifusinites (s) with obvious cellular structure from KOT-129. **d.** Semifusinites (s) with obvious cellular structure from KOT-101.

delta-E mass spectrometer at Indiana University. The results reported herein are obtained using reference CO_2 as a working standard calibrated by NBS standards. Carbon-isotope results are expressed in the standard delta notation with respect to the PDB standard, where $\delta^{13}\text{C} = \left\{ \left(\frac{^{13}\text{C}/^{12}\text{C}}{\text{sample}} / \frac{^{13}\text{C}/^{12}\text{C}}{\text{standard}} - 1 \right) \times 1000 \right\}$, with a reproducibility of analyses of $\pm 0.1\text{‰}$. The isotopic values were checked by an isotopically known laboratory standard (triphenylamine). Total organic carbon (TOC) content of whole rock was estimated by CO_2 gas volume with a Baratron pressure transducer.

For visual observation of kerogen, crushed mudstone was made into polished blocks following the standard preparation procedure (Bustin *et al.*, 1983). Polished pellets were examined using a MPV-2 microscope to identify organic particles.

Results

Visual observation of kerogen

Kerogen was analyzed on selected samples optically under reflected light and in fluorescent mode. Microscopic observation was carried out on seven selected samples (KOT-101, 113, 126, 129, 130, 148 and 152) as representa-

tive horizons of stratigraphically-important isotopic events (see below) through the Kotanbetsu River section. Kerogen from all selected samples is dominated by semifusinite and vitrinite with a minor amount of particulate vitrodetrinite and inertodetrinite (Figure 3a-d) derived exclusively from cellular lignins of terrestrial vascular plants. Preservation of cell structure in semifusinite indicates its origin as woody plant matter. Organic matter of other than terrestrial woody plant origin (alginite and liptinite) was rarely ($\ll 1\%$) detected during microscopic examination. Sporinites, resinates and bitumens were the only fluorescent organic matters in the samples. This fluorescent property can be explained by the absence of marine organic matter. Some nonoxidized vitrinite might have incorporated marine organic molecules through the process of condensation during early stage of diagenesis. But in such a case, marine alginite and/or liptinite should have been more conspicuous components under microscope. The result from visual observation of kerogens strongly suggests no significant incorporation of marine organic materials in the kerogens.

Carbon isotopes and total organic carbon (TOC)

A stratigraphic profile with carbon isotope ratios ($\delta^{13}\text{C}$) for terrestrial organic matter from the Kotanbetsu area is shown

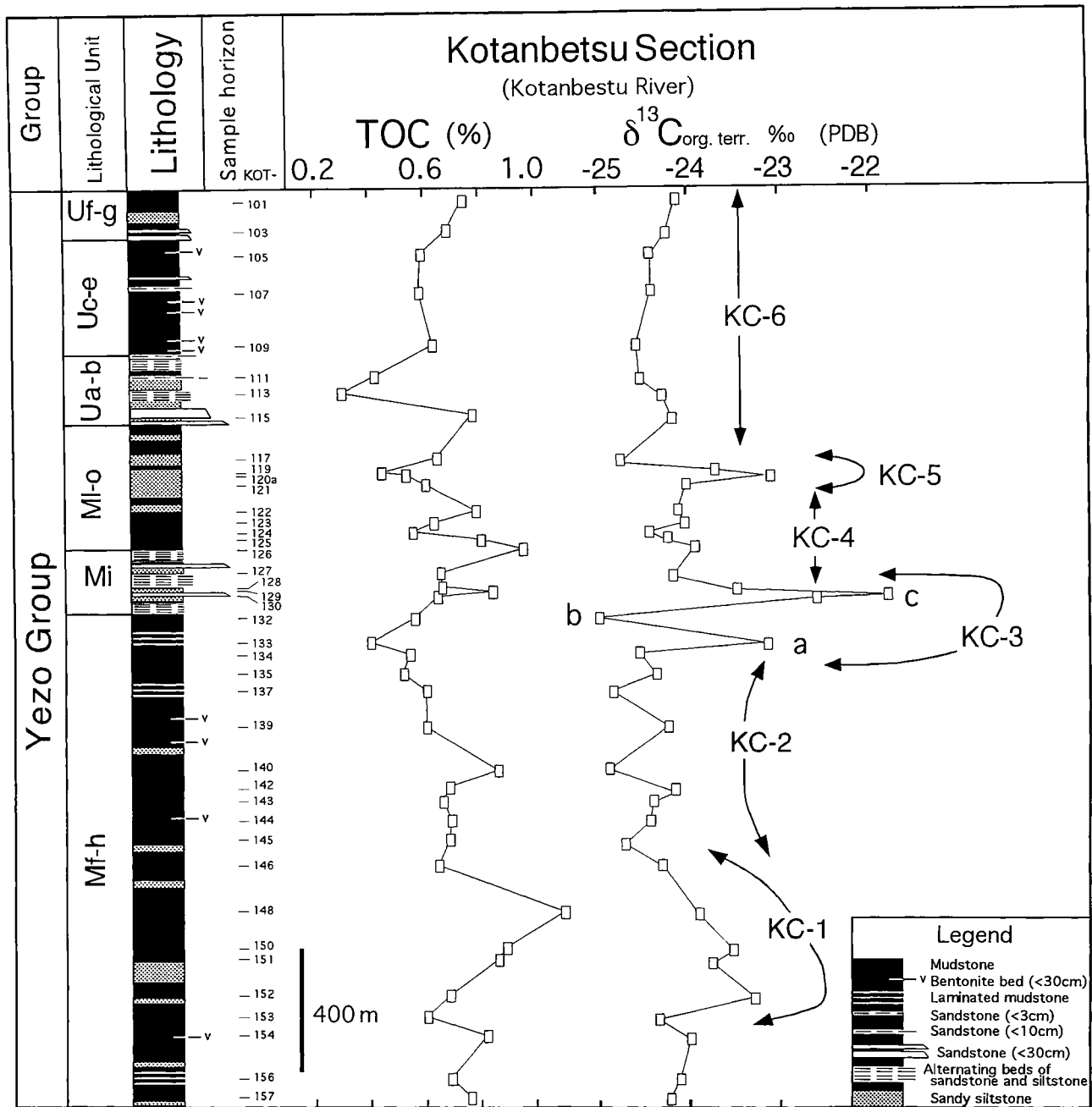


Figure 4. Carbon isotope profile of terrestrial organic matter in the Kotanbetsu River section, Hokkaido, Japan. Labels KC-1 to KC-6 indicate different events on the $\delta^{13}\text{C}$ curve discussed in the text. KC-3 is composed of three subevents namely KC-3a, KC-3b and KC-3c. Note a sharp peak of $\delta^{13}\text{C}$ values (KC-3c) at the middle of the section and a stepwise negative shift through KC-3c~KC-6.

in Figure 4. The profile is divided into six "events" by characteristics in the isotopic fluctuation and are expressed by a KC-numerical notation (designating Kotanbetsu carbon isotope event):

KC-1: Characterized by a positive isotopic event (-23.3‰) observed in the lower part of Unit Mf-h. Above the peak at KOT-152, $\delta^{13}\text{C}$ shows a gradual negative shift toward -24.7‰ at KOT-145.

KC-2: Segment of relatively negative values fluctuating

between -24.2 and -24.9‰ through the upper Unit Mf-h.

KC-3: Characterized by two positive excursions. At the top of Unit Mf-h, $\delta^{13}\text{C}$ reaches -23.1‰ at the horizon KOT-133 (KC-3a: designated as "a" in Figure 4). However, the value rebounds down to -25.0‰ at KOT-132 just above KOT-133 (KC-3b: designated as "b"). The most prominent feature is a sharp positive excursion of $\sim 2.5\text{--}3 \text{‰}$ which occurs in the middle Unit Mi at the horizon KOT-130 and 129 (KC-3c: designated as "c").

Table 1. Carbon isotopic ratio and TOC along the Kotanbetsu section. The Cenomanian/Turonian boundary is expected just above KOT-129 (see text for details).

Sample	$\delta^{13}\text{C}$ org. terr. ‰ (PDB)	TOC (%)
KOT-101	-24.1	0.74
KOT-103	-24.2	0.68
KOT-105	-24.4	0.59
KOT-107	-24.4	0.58
KOT-109	-24.6	0.63
KOT-111	-24.5	0.42
KOT-113	-24.3	0.30
KOT-115	-24.2	0.77
KOT-117	-24.8	0.64
KOT-119	-23.7	0.44
KOT-120a	-23.1	0.53
KOT-121	-24.0	0.60
KOT-122	-24.1	0.78
KOT-123	-24.1	0.63
KOT-124	-24.4	0.55
KOT-125	-24.2	0.80
KOT-126	-23.9	0.95
KOT-127	-24.2	0.65
KOT-128	-23.5	0.66
KOT-129	-21.8	0.84
KOT-130	-22.6	0.64
KOT-132	-25.0	0.56
KOT-133	-23.1	0.40
KOT-134	-24.6	0.54
KOT-135	-24.4	0.52
KOT-137	-24.9	0.60
KOT-139	-24.2	0.60
KOT-140	-24.9	0.86
KOT-142	-24.2	0.68
KOT-143	-24.4	0.66
KOT-144	-24.4	0.69
KOT-145	-24.7	0.68
KOT-146	-24.3	0.64
KOT-148	-23.9	1.10
KOT-150	-23.5	0.89
KOT-151	-23.7	0.86
KOT-152	-23.3	0.68
KOT-153	-24.4	0.60
KOT-154	-24.0	0.82
KOT-156	-24.1	0.69
KOT-157	-24.2	0.76

KC-4: Relatively stable isotopic ratios above KC-3c excursion. $\delta^{13}\text{C}$ drops rapidly above KOT-129 and stabilizes around -24.0‰ between the middle Unit Mi and the middle Unit MI-o.

KC-5: Characterized by a minor positive excursion of

$\sim 1\text{‰}$ at KOT-120 followed by a negative shift back to KC-6.

KC-6: Characterized by stable isotopic ratio between -24.8 and -24.1‰ . The most negative value is recorded in the lowest part of this interval (-24.8‰).

Values of total organic carbon content (TOC) range between 0.2 and 1.0% with no notable fluctuation in the Kotanbetsu River section.

Discussion

No organic-rich layer across the C/T boundary

In spite of fine parallel laminations in the Mi Unit indicating limited benthic activity and dysaerobia, no TOC spike (extraordinary accumulation of organic matter) at the C/T boundary (=peak horizon of $\delta^{13}\text{C}$; see following discussion) was observed (Figure 4) contrary to the case of many carbonate sections around the world (e.g. Schlanger *et al.*, 1987). This is caused by the depositional environment of the Kotanbetsu section, which was far different from that of those sections with an accumulation of organic matter at the boundary. The sedimentation rate of the Kotanbetsu section is about 200 m/m.y. and substantially all materials including organic matter are terrestrial in origin. Most of the organic matter in the mudstone samples are very residual lignitic material. Therefore, the concentration of organic matter across the section was controlled predominantly by the content of organic matter in terrigenous debris and never affected by oceanographic events.

Factors controlling carbon-isotope fluctuations

Kerogen from two samples representing the KC-3 event were optically examined and the results were compared with those from KC-4, KC-6 and KC-1. All visually checked samples are dominated by semifusinite and vitrinite. This means organic matter in the samples is derived from nothing but lignins of terrestrial woody C_3 plants which are exclusively resistant to oxidation. Rare occurrences of small amounts of alginite, sporinite, resinite, and bitumen should not affect the following discussion dealing with differences larger than 0.1‰ of carbon isotopic fluctuation. Since these samples were selected from the intervals of major isotopic events of stratigraphic importance, the isotopic fluctuation of terrestrial organic carbon obtained in this study cannot be ascribed to the composition of kerogens. That the lithological evidence shows no significant change of depositional environment also suggests that the composition of kerogens is a feature of the sedimentary rock through the Kotanbetsu River section.

In Figure 5, $\delta^{13}\text{C}$ values are plotted against TOC with no systematic relation revealed between them. This indicates that the $\delta^{13}\text{C}$ values are independent of mechanisms of supply and deposition of organic matter; organic matter derived from lignins of terrestrial woody C_3 plants has not been carbon-isotopically biased by these mechanisms and has essentially kept its original isotopic signature. As mentioned above, the isotopic fluctuation of organic carbon in the Kotanbetsu River section can be interpreted as representing the average biomass of woody plants in the provenance area. The isotopic fluctuation of global atmospheric CO_2 is

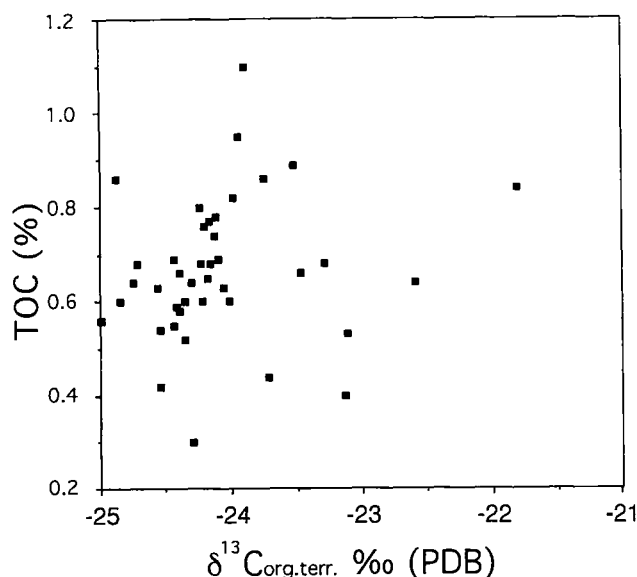


Figure 5. Carbon-isotope ratios of terrestrial organic carbon ($\delta^{13}\text{C}_{\text{org.terr.}}$) against total organic carbon content (TOC; dry weight %) along the Kotanbetsu River section.

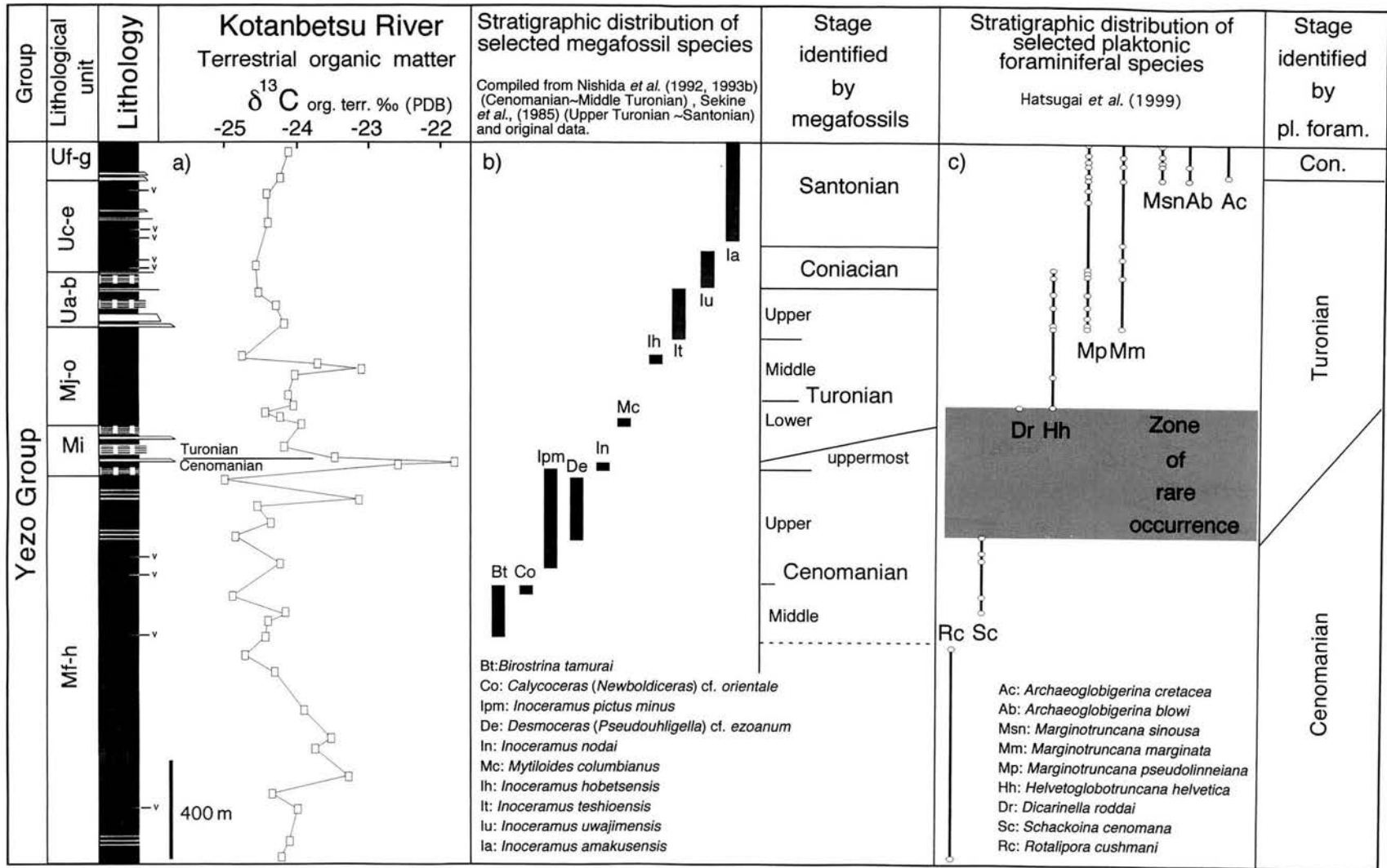
interpreted to be a primary factor responsible for $\delta^{13}\text{C}$ fluctuation of the terrestrial biomass as discussed in Hasegawa (1997), Beerling and Jolley (1998) and Gröcke *et al.* (1999). If this assumption is accepted and other environmental and/or ecological factors are negligible, $\delta^{13}\text{C}$ fluctuation of terrestrial organic matter is essentially parallel to that of carbonates. Arthur *et al.* (1988) ascribed a discrepancy of amplitude observed between marine carbonate and marine organic carbon across the C/T boundary to a marked decrease of partial pressure of CO_2 in the ocean-atmosphere system. Gröcke *et al.* (1999) discussed the possibility that the partial pressure of atmospheric CO_2 may have also affected carbon-isotopic fluctuation of fossil woods as a secondary factor in conjunction with the isotopic composition of CO_2 . If $\delta^{13}\text{C}$ of atmospheric CO_2 during the deposition of the studied sequence exclusively reflects proportion of fluxes of organic and inorganic carbons into/out of the ocean-atmospheric reservoir, changes of partial pressure of atmospheric CO_2 should lead to exaggeration of the $\delta^{13}\text{C}$ events in terrestrial and marine organic matter against marine carbonates (see also discussion of Popp, *et al.*, 1989; Gröcke *et al.*, 1999). Therefore, even if the $\delta^{13}\text{C}$ curve obtained in this study was affected by the partial pressure of atmospheric CO_2 , it is still plausible to correlate it with $\delta^{13}\text{C}$ curves derived from marine carbonates as well as those from terrestrial organic matter of other Hokkaido sections. Kuypers *et al.* (1999) discussed a turnover from a C_3 plant community to a C_4 -dominated community, which had been derived from a decrease of partial pressure of CO_2 , as a factor in an exaggerated $\delta^{13}\text{C}$ excursion of n-alkanes. This factor could only exaggerate a positive excursion of $\delta^{13}\text{C}$. The kerogens examined under the microscope show predominance of lignitic macerals in both samples from the C/T boundary excursion (KOT-129 and 130) and other horizons.

This indicates no turnover of C_3/C_4 plant communities was involved with the $\delta^{13}\text{C}$ excursion at the C/T boundary shown in the present study. Shift of atmospheric humidity and taxonomic turnover in the provenance of organic matter may have affected carbon isotopic fractionation during photosynthesis of the biomass (O'Leary, 1993). These factors could result in some local, regional or sometimes global isotopic disturbance and should be considered during carbon-isotope correlation. Nguyen Tu *et al.* (1999) proposed that environmental stress derived from salinity had affected significantly the carbon isotopic composition of fossil terrestrial plants from Cenomanian strata. However, the organic matter treated in this study is interpreted to have been transported from wide and distant provenance. It should be highly mixed enough to eliminate such a local salt stress discussed in Nguyen Tu *et al.* (1999).

Significance of carbon isotope stratigraphy as a tool for correlation

The Kotanbetsu River section has been subdivided into stages by biostratigraphic studies of megafossils (Nishida *et al.*, 1992, 1993b) and planktonic foraminifera (Nishida *et al.*, 1992; Hatsugai *et al.*, 1999) (Figure 6). No biochronological study of megafossils is available above the middle Turonian along the Kotanbetsu River section. However, Sekine *et al.* (1985) studied the Tappu area next to the Kotanbetsu area and that study was adopted to draw boundaries above the middle Turonian. Planktonic foraminiferal biostratigraphy (Hatsugai *et al.*, 1999) indicates no appreciable diachroneity in lithologies between the Tappu and Kotanbetsu areas.

As Hatsugai *et al.* (1999) noted, stages defined by both megafossils and planktonic foraminifera correspond well with each other below the upper part of Unit Mj-o (Figure 6). There are two conspicuous isotope events (KC-3 and KC-4) in the Kotanbetsu River section which can be correlated internationally (Figure 7). KC-1 is regionally correlated to H1 of the Oyubari section (Figure 7) by its shape and amplitude of isotopic fluctuations as well as by biostratigraphic position (within planktonic foraminiferal *Rotalipora cushmani* Zone). Though this event could be globally correlated, however, it is not conclusive because of low chronological resolution across this event in Japan. KC-2 is the common event of three Hokkaido sections (Oyubari, Tappu and Kotanbetsu; Figure 7) and equivalent to H2 in the Oyubari area (Hasegawa, 1997). This negative isotopic feature of KC-2/H2 cannot be observed in European sequences (Jenkyns *et al.*, 1994). Shift of atmospheric humidity and/or taxonomic turnover in the provenance of organic matter may explain this event, which is specific to terrestrial organic carbon (see O'Leary, 1993). KC-3 is the most prominent feature of the Kotanbetsu River section and is regarded to be the best worldwide stratigraphic marker across the C/T boundary in relation to the Oceanic Anoxic Event II (Schlanger and Jenkyns, 1976; Arthur *et al.*, 1988). KC-3 is composed of a double peak and a trough between (Figure 4). These subevents in KC-3, namely KC-3a, b and c ("a", "b" and "c" in Figure 4) can be correlated with isotopic subevents a, b and c, respectively at the C/T boundary of the Oyubari (Hasegawa, 1995) and Tappu areas (Hasegawa, 1994), al-



Carbon-isotope stratigraphy of the Yezo Group

Figure 6. Comparison of carbon isotope-stratigraphy and biostratigraphy along the Kotanbetsu River section. a) Carbon isotope stratigraphy. The Cenomanian/Turonian boundary expected from the isotope stratigraphy is drawn just above the isotopic "spike". b) Stratigraphic distribution of age indicative of macrofossil species. Data source: Nishida *et al.* (1992, 1993b) and original data of this study for the Cenomanian through Middle Turonian, Sekine *et al.* (1985) for strata above the Middle Turonian. c) Stratigraphic distribution of age indicative of planktonic foraminiferal species. Zone of rare occurrence is observed in the middle of this section encompassing the prominent isotopic event (KC-3). Cenomanian/Turonian boundary is limited between the last occurrence of *Schackoina cenomana* and the first occurrence of *Helvetoglobotruncana helvetica*. Coniacian is identified at the top of the section. See Figure 3 for legend.

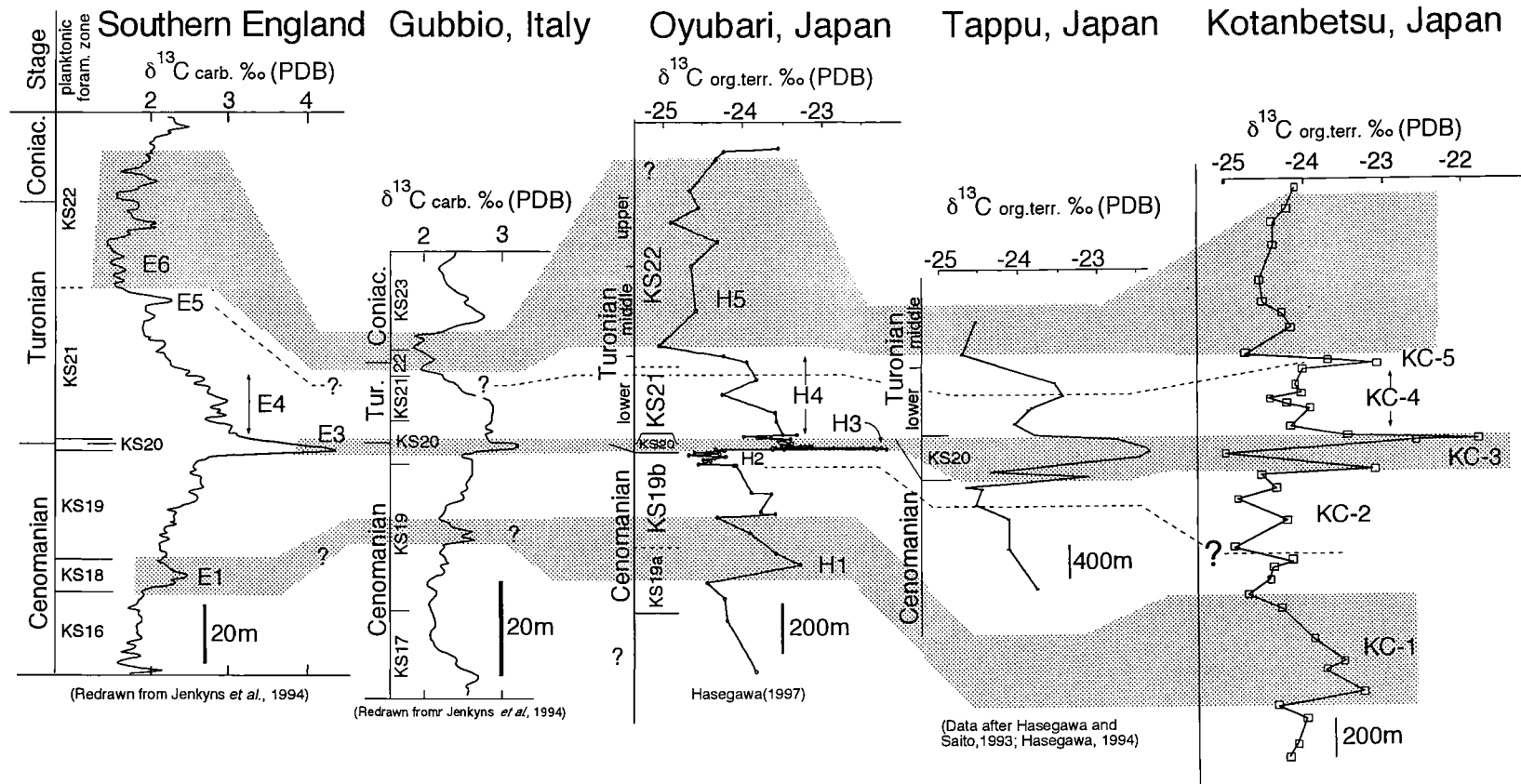


Figure 7. Comparison of carbon-isotope profiles for carbonate (southern England and Gubbio, Italy) and terrestrial organic matter (Oyubari, Tappu and Kotanbetsu sections, Japan). Event notations for southern England and Oyubari are given by Hasegawa (1997). Note the good correlation between the three carbon-isotope events (spike at the C/T boundary, shoulder at the lower Turonian and a minimum at middle or upper Turonian). Biochronology for planktonic foraminifera is based on Caron (1985), Robaszynski and Caron (1979) and Sliter (1989) and for megafossils is based on Toshimitsu *et al.* (1995). $\delta^{13}\text{C}_{\text{carb.}}$: carbon-isotope ratio of carbonate; $\delta^{13}\text{C}_{\text{org.terr.}}$: carbon-isotope ratio of terrestrial organic matter.

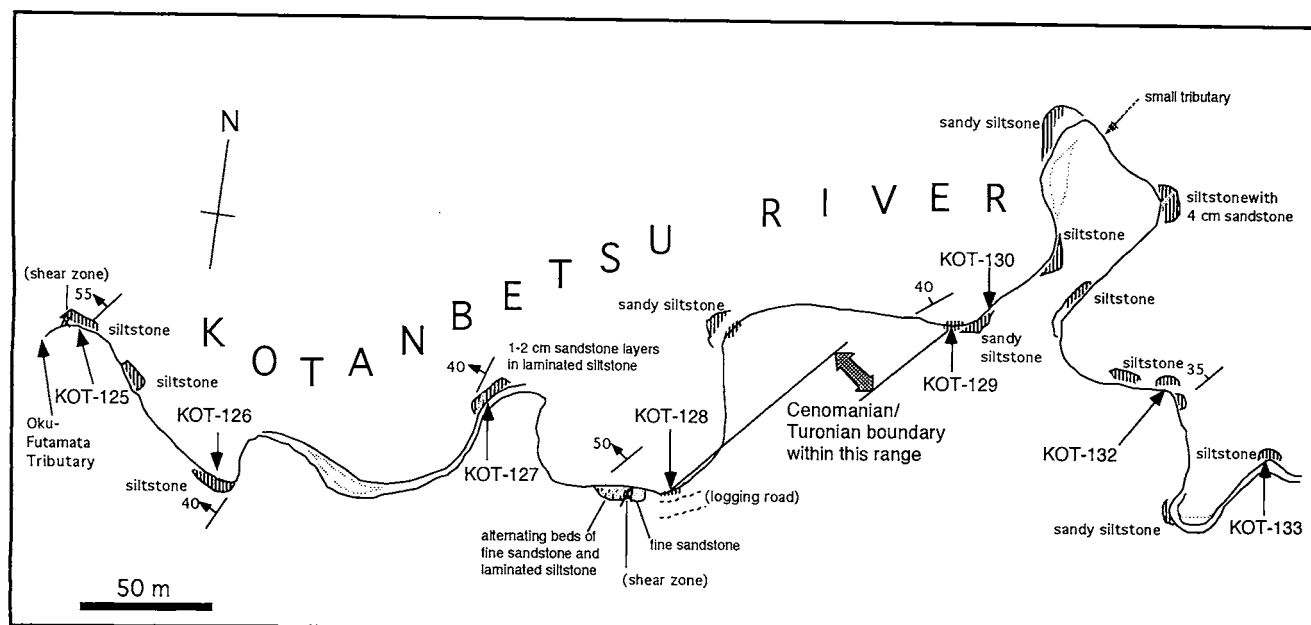


Figure 8. Plan map along the Kotanbetsu River showing detailed position of the Cenomanian/Turonian boundary expected from carbon isotope stratigraphy. The possible boundary is limited stratigraphically within ~ 14 m between KOT-129 and KOT-128.

though inconclusively, due to sparse sampling encompassing KC-3 and difference of amplitude of the subevent KC-3b. Hence it is still open to question whether the entire KC-3 or only KC-3c corresponds to the globally observed carbon isotope excursion at the C/T boundary (see Schlanger *et al.*, 1987). As discussed in detail by Hasegawa (1995), the C/T boundary can be drawn just above the positive $\delta^{13}\text{C}$ excursion; the C/T boundary in the Kotanbetsu River section is drawn just above the horizon of KOT-129 (Figures 6, 8). The horizon of the C/T boundary is stratigraphically limited to ~ 14 m between KOT-129 and KOT-128.

Nishida *et al.* (1993b) reported occurrences of *Inoceramus nodai* just below KOT-129. In the Oyubari area, *I. nodai* was reported from 10 m below the carbon-isotopic excursion identifying the C/T boundary (Hasegawa, 1995; Nishida *et al.*, 1993a; Hirano, 1995) suggesting *I. nodai* is an important boundary marker in Hokkaido. According to Hatsugai *et al.* (1999), KC-3 is stratigraphically included in a "zone of rare occurrence" of planktonic foraminifera. A similar planktonic foraminiferal event encompassing the carbon isotopic excursion at the C/T boundary is also reported from the Oyubari area (Hasegawa, 1999) and the Tappu area (Hasegawa, 1994) suggesting an environmental deterioration across the boundary. Controlling factors other than $\delta^{13}\text{C}$ fluctuation in the global CO_2 reservoir may have disturbed the stratigraphic position of KC-3 and might have spoilt the discussion above the C/T boundary. In such a case, additional "noise" should be superimposed on the global signal derived from isotopic change of the CO_2 reservoir. Even though such a possibility cannot completely be rejected, KC-3 event showing similar magnitude of $\delta^{13}\text{C}$ excursion to that of carbonate (e. g. Jenkyns *et al.*, 1994; Pratt *et al.*, 1985) and terrestrial organic matter (Hasegawa and

Saito, 1993; Hasegawa, 1997) should contain the least "noise" for correlation of the C/T boundary. Uličný *et al.* (1997) interpreted isotopic fluctuation of organic carbon encompassing parasequence boundary near the C/T boundary based on a steady isotopic ratio of terrestrial organic carbon through the sequence in Bohemia. The present study and Hasegawa (1997) clearly shows that this interpretation cannot be accepted because the major positive "spike" of terrestrial organic carbon exists across the C/T boundary. Based on 200 m/m.y. for sedimentation rate; duration of KC-3 (from KOT-133 to KOT-129) is estimated as 0.73 m.y.

Another international event is KC-4 just above the C/T boundary and is represented by a stable "plateau" of the isotopic curve (Figure 7). Both megafossil and planktonic foraminiferal chronology indicate KC-4 falls in the lower-middle Turonian (Figure 6). Both in the Oyubari and Tappu areas, a similar isotopic event is also recognized. On the isotopic curve of the Kotanbetsu River section, there is a minor positive event (KC-5) above KC-4. A similar feature also exists on the curve from the Tappu section but is diminished in magnitude on the curves from Oyubari (Figure 7). KC-5 could be correlated to E5 of southern England (Figure 7); however, this is not definite because of the insufficient age control and different magnitude of the positive excursion between these areas. Therefore, KC-5 can be either a global signal or a local/regional isotopic perturbation superimposed on the global KC-4 event caused by influx of less mixed (isotopically not averaged) plant debris derived from a narrower provenance.

Contrary to the chronostratigraphic concordance of megafossil and planktonic foraminifera below the middle Turonian, there are considerable discrepancies above it (Hatsugai *et al.*, 1999). Motoyama *et al.* (1991) also discussed a chronostratigraphic discrepancy on the

Turonian/Coniacian boundaries at the Oyubari area between megafossils and microfossils. Even though internationally it is recognized that the total range of *Helvetoglobotruncana helvetica* is limited to the middle Turonian (Robaszynski and Caron, 1979; Caron, 1985; Sliter, 1989), the stratigraphic distribution of *Inoceramus teshioensis* spans the Upper Turonian and *Inoceramus uwajimensis* the Coniacian (Toshimitsu *et al.*, 1995) which all overlap the range of *H. helvetica*. The first occurrence of *Inoceramus amakusensis* is positioned far below the first occurrence of *Margino-truncana sinuosa* (indicating the top of the Turonian; Caron, 1985) and genus *Archaeoglobigerina* (indicating the basal Coniacian; Caron, 1985). They show clear discrepancies with the stratigraphic relationship compiled by Toshimitsu *et al.* (1995) (Figure 6; see also Table 1 of Toshimitsu *et al.*, 1995). As a result, the stages identified by megafossils tend to give a younger age than that identified by planktonic foraminifers. These chronological inconsistencies occur above the top of the stratigraphic range of *I. hobetsensis*. This fact means that stratigraphic distributions of either/both inoceramids (*I. teshioensis*, *I. uwajimensis* and *I. amakusensis*) and/or planktonic foraminifers (*H. helvetica*, *M. sinuosa* and genus *Archaeoglobigerina*) show diachroneity.

Above isotopic profile KC-5, the carbon-isotope ratio reaches a minimum at KOT-117. This horizon can be correlated to the oldest part of the negative isotope event (H5 of the Oyubari section and E6 of the South England section; see Fig. 6 and 8 of Hasegawa, 1997). The steady isotopic ratios between -24.6 and -24.1‰ above horizon KOT-115 suggest that this section does not extend to the upper part of the Santonian. Hasegawa *et al.* (1997) reported a positive carbon-isotope event in the middle Santonian from an equivalent of the Yezo Group in Sakhalin. This Santonian event can be correlated to southern England (Jenkyns *et al.*, 1994) and Italy (Corfield, 1995; Jenkyns *et al.*, 1994). If the Kotanbetsu River section in this study reached the Santonian, the positive excursion should be observed near the top of the stratigraphic column in Figure 6. Comparing general carbon isotopic patterns from southern England and Italy (Corfield, 1995; Jenkyns *et al.*, 1994; Figure 7), the uppermost part of the Kotanbetsu River section studied herein can be interpreted to be the lower part of the Coniacian. This chronological assumption is close to the age assignment by planktonic foraminifera rather than that based on inoceramids.

Conclusion

In order to demonstrate the applicability of carbon-isotope stratigraphy of the Yezo Group for correlation, a stratigraphic time-series isotopic analysis of terrestrial organic carbon was studied from the Cenomanian to Coniacian along the Kotanbetsu River in Hokkaido, Japan. The carbon-isotope curve generated was compared with similar profiles of terrestrial organic carbon from Oyubari and Tappu in Hokkaido (Hasegawa, 1995, 1997) and marine carbonate from southern England and Italy (Jenkyns *et al.*, 1994). The salient conclusions are as follows:

1. The origin of organic carbon is interpreted to be exclusively terrestrial woody plants. Petrographic study on or-

ganic matter in mudstone samples reveals practically no marine organic matter in the seven examined samples. The carbon-isotope ratios of organic matter from the Kotanbetsu River section can be interpreted as that of an average lignitic material from woody plants. Global carbon-isotope events can be recognized in the isotopic curve from Kotanbetsu.

2. Event KC-3 records the isotopic event of the Cenomanian/Turonian boundary. It is still unclear which carbon-isotope event, namely all of KC-3 or only KC-3c, represents the C/T boundary. Notwithstanding this, the Cenomanian/Turonian boundary is drawn just above sample KOT-129, which has the most positive $\delta^{13}\text{C}$ ratio.

3. Event KC-4 is correlated to the event H4/E4 of both the Oyubari and southern England sections.

4. A negative event above KC-5 is correlated to the earliest part of event H5/E6 of Oyubari and southern England.

5. The most plausible chronologic interpretation for the younger part of KC-6 is middle Turonian to Coniacian and supports planktonic foraminiferal evidence rather than that derived from inoceramids. In spite of occurrences of *Inoceramus amakusensis*, the studied succession does not reach the Santonian because the general isotopic pattern differs from that of the Santonian from southern England (Jenkyns *et al.*, 1994) and Sakhalin (Hasegawa *et al.*, 1997).

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Taxonomic revision of *Pisulina* (Gastropoda: Neritopsina) from submarine caves in the tropical Indo-Pacific

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Abstract. Species of the tropical Indo-Pacific gastropod *Pisulina* (superorder Neritopsina), previously known only from empty shells and regarded as a genus of Smaragdiinae (Neritidae), are revised on conchological criteria. *Pisulina* dwells in gloomy to totally dark, tropical and subtropical, shallow-water submarine caves, where their empty shells are ubiquitous. Study of the previously described modern and fossil species and examination of newly collected material from more than 50 submarine caves on Pacific islands show that there are six species in the genus: *P. adamsiana* Nevill and Nevill, 1869 (Holocene), *P. subpacificica* Ladd, 1966 (late Miocene), *P. biplicata* Thiele, 1925 (Recent), *P. maxima* new species (Recent), *P. tenuis* new species (Recent), and *Pisulina* sp. (Pleistocene). An analysis of previously unstudied shell characters (shell form, shell microstructure, protoconch morphology, and opercular features) of *Pisulina* and other modern, representative genera of Neritopsina places the genus close to the freshwater and brackish-water genus *Neritilia*, based on three unique characters (inclined protoconch, spiral ridges on the protoconch surface, and perpendicularly arranged prisms in the outer shell layer), and both genera are herein included in the family Neritiliidae. This study shows that the protoconch and shell microstructure analysis is important for re-evaluating fossil species previously placed in Neritidae.

Key words: Neritiliidae, *Pisulina*, protoconch, shell microstructure, submarine cave

Introduction

Pisulina Nevill and Nevill, 1869 has been a gastropod genus of systematically uncertain placement. Aside from the type species, *Pisulina adamsiana* Nevill and Nevill, 1869, the genus has included one modern species, *Pisulina biplicata* Thiele, 1925, and one fossil species, *Pisulina subpacificica* Ladd, 1966. The species previously have been known only from empty shells, so knowledge of their anatomy, operculum, radula and habitat have been entirely lacking. Empty shells occasionally have been found in beach drift from the tropical western Pacific (Habe, 1963; Hinoide and Habe, 1991; Fukuda, 1993; Loch, 1994; Sasaki, 1998) and have been dredged from 70 m off southern Africa (Herbert and Kilburn, 1991).

Nevill and Nevill (1869) thought the genus was close to

Teinostoma (currently classified in Vitrinellidae of Caenogastropoda; e.g., Ponder and de Keyser, 1998) and *Calceolina* [junior synonym of *Teinostoma* (*Calceolata*); Thiele, 1929] based on overall similarity in shell morphologies. Thiele (1925) was the first author to place *Pisulina* in Neritidae, and this familial allocation was followed in his monograph (Thiele, 1929). Wenz (1938) included *Pisulina* in the subfamily Smaragdiinae Baker, 1923, of Neritidae, and was subsequently followed by Knight *et al.* (1960) and Komatsu (1986). However, Herbert and Kilburn (1991) found that *Pisulina* differs in protoconch morphology not only from *Teinostoma* but also from *Smaragdia*, the type genus of Smaragdiinae. They observed that the change of coiling axis occurs between the larval shell and teleoconch whorls in *P. adamsiana*, although they followed Robertson's (1971) view that this change occurs between the embryonic and

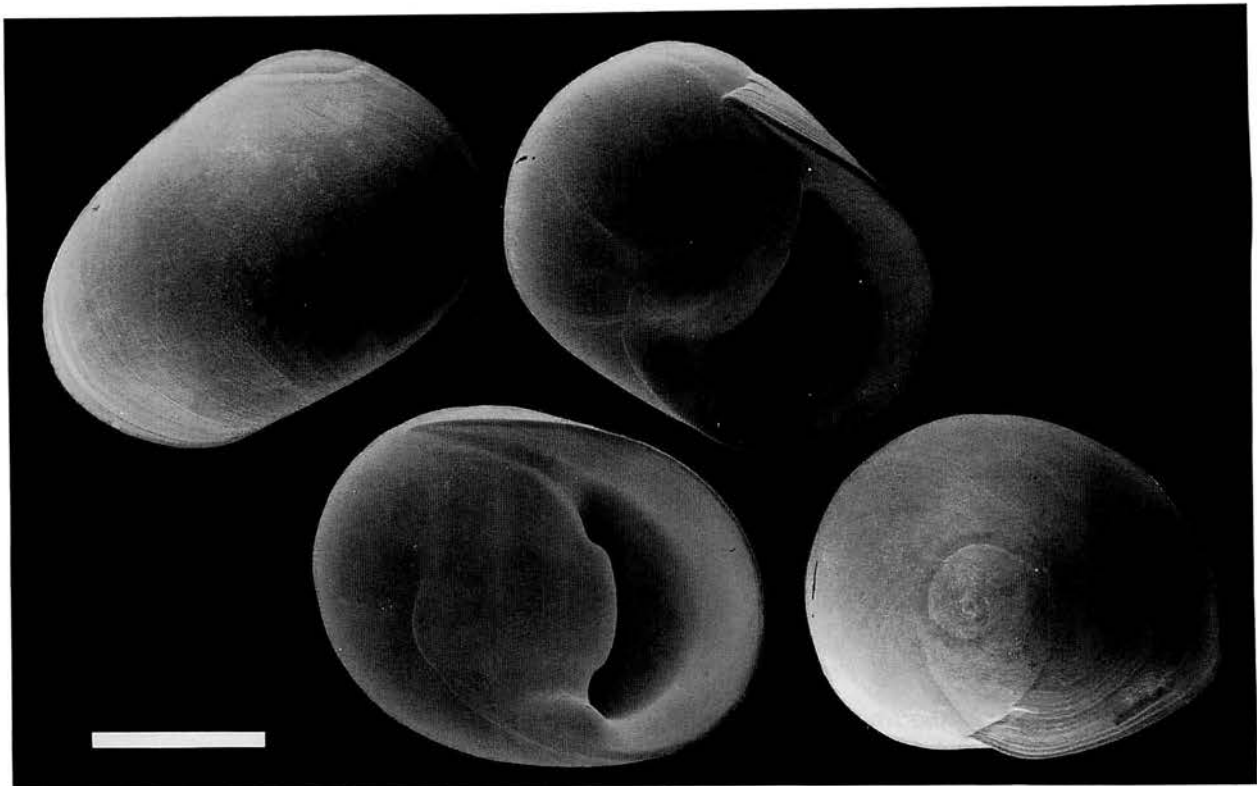


Figure 1. *Pisulina adamsiana* Nevill and Nevill, 1869 from Sipadan Island, Sabah, Malaysia (NSMT-Mo71619). Scale bar = 2 mm.

post-embryonic shells in *Smaragdia*. However, they did not elaborate on the systematic position of this enigmatic genus from their observations, and the systematic position of *Pisulina* has remained speculative.

Since 1989, the junior author and his co-workers have been conducting biological sampling in shallow-water submarine caves on tropical and subtropical Pacific islands with the help of skilled SCUBA divers. During the course of the sampling, they have found a molluscan community that is distinctive in species composition and reproductive biology (Kase and Hayami, 1992; Hayami and Kase, 1993, 1996). They also found that a huge number of empty shells of *Pisulina* species had accumulated in the bottom sediments in many caves, and that living animals were abundant on the walls and ceilings of several caves in Hawaii, Saipan, Palau, the Philippines and Malaysia.

The purpose of this paper is (1) to describe the conchological characteristics of *Pisulina* in detail, (2) to define the genus and discuss its systematic position based on conchological characteristics, (3) to review all previously known species of *Pisulina*, and (4) to describe new species.

Materials and methods

We examined more than 5000 empty shells of *Pisulina* species obtained from the bottom sediments of more than 50 submarine caves, tunnels, grottos or caverns (at depths

ranging from 1.3 to 55 m), on tropical and subtropical Pacific islands. We also examined shells in beach drift and dredged samples, and fossil shells from Henderson Island (the Pitcairn Group) and Niue Island (Cook Islands). In the descriptions given below, the "Material examined" headings refer to empty shells, unless otherwise stated. Living animals were obtained from walls inside caves and tunnels by hand, or by brushing the undersurface of coral rubble on the bottom sediments. Empty shells were obtained from the sediments (mainly calcareous mud) of the cave floors by hand sorting.

For comparison, we examined embryonic shells of *Neritilia rubida* (Pease, 1865) from Tahiti. In addition, live specimens of another *Neritilia* species [collected in a stream in Tabaru Valley, Yonaguni Island, Okinawa Prefecture, Japan; identified by Kubo and Koike (1992) as *N. rubida*] were kept in a freshwater aquarium, and embryonic shells were obtained after spontaneous oviposition and following development. In the aquarium, egg capsules which each retained only one embryo were laid in small pits on the undersurface of limestone cobbles taken from the original habitat. The veligers were hatched as embryonic shells after two weeks of oviposition.

We prepared specimens for SEM observation using standard techniques: shells were cleaned with an ultrasonic cleaner, dried, mounted on stages, coated with gold, and examined under a scanning electron microscope (JOEL T330A), or were examined in a low-vacuum mode without a

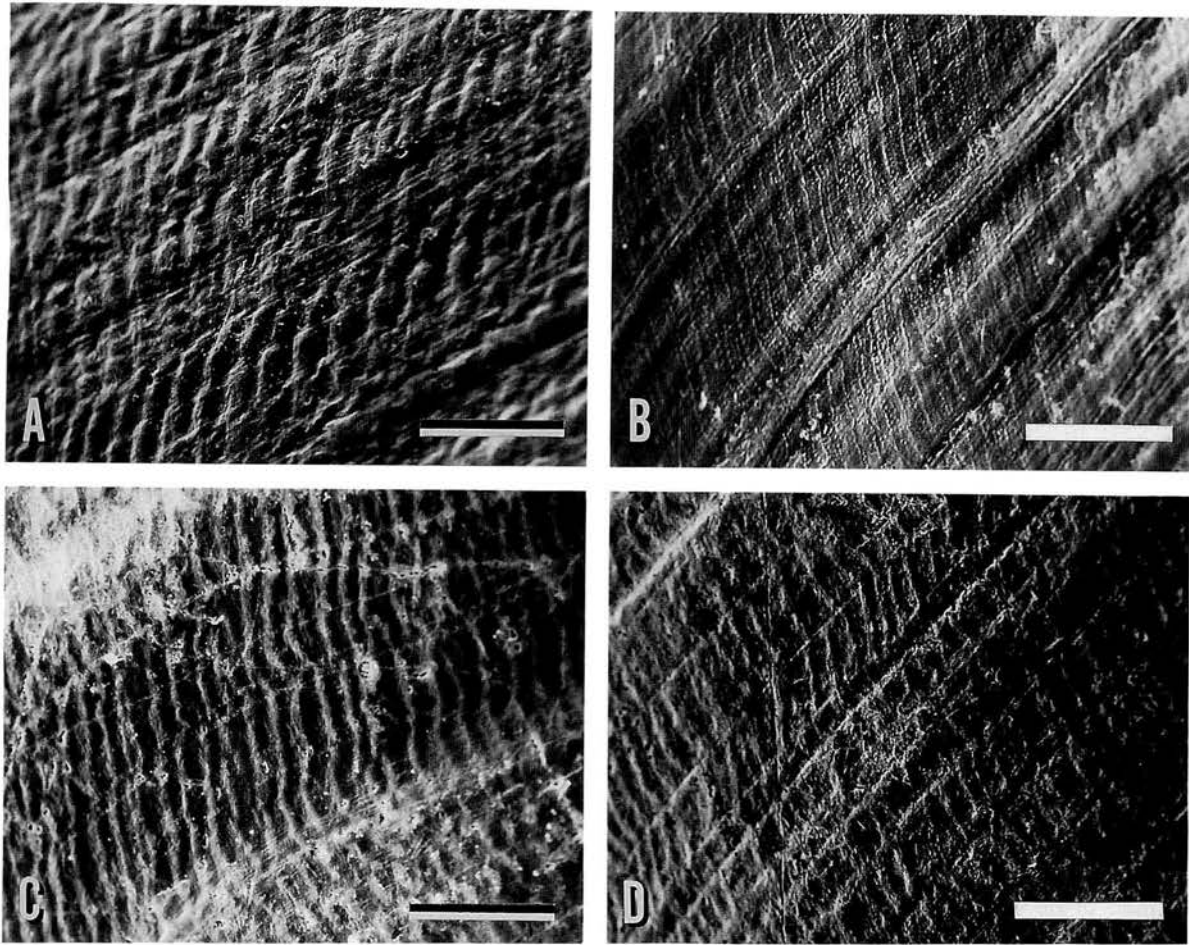


Figure 2. SEM micrographs of the subsutural surface of the last teleoconch whorls in four modern *Pisulina* species; all are oblique apical views. Scale bars = 50 μm . **A.** *Pisulina adamsiana* Nevill and Nevill from Sipadan Island, Malaysia. **B.** *Pisulina biplicata* Thiele from Shimoji Island, Okinawa, Japan. **C.** *Pisulina maxima* sp. nov. from Sipadan Island. **D.** *Pisulina tenuis* sp. nov. from Yonaguni Island, Okinawa.

metal coating in another SEM (JEOL 5200LV). Polished and etched sections were prepared for microstructural analysis of the shell wall in the following manner: blocks of shells were embedded in synthetic resin, polished, cleaned ultrasonically to remove polishing grit, etched in 0.3% acetic acid for 60 seconds, and cleaned again. The terminology and usage of shell ultrastructure follow Carter and Clark (1985).

Museum abbreviations. — AMS: Australian Museum, Sydney; MNHB: Museum für Naturkunde der Humboldt-Universität, Berlin; MNHN: Muséum National d'Histoire Naturelle, Paris; NSMT: National Science Museum, Tokyo; UMZC: University Museum of Zoology, Cambridge, England; USNM: National Museum of Natural History, Washington.

Systematic description

Superorder Neritopsina Cox and Knight, 1960
Family Neritiliidae Schepman, 1908

Genus *Pisulina* Nevill and Nevill, 1869

Pisulina Nevill and Nevill, 1869, p. 160.

Type species. — *Pisulina adamsiana* Nevill and Nevill, 1869, by monotypy.

Distribution and age. — Tropical and subtropical Indo-Pacific. Late Miocene to Recent.

Diagnosis. — Shell small to medium in size, globose neritiform, white, smooth, solid. Inner lip of aperture smooth, convex, covered with a thick and widespread callus, with a robust projection or 3 to 7 teeth on margin. Outer lip with a weak inner ridge inside and a sharp margin. Protoconch either multispiral or paucispiral; multispiral

protoconch with a larval shell inclined approximately 30° to teleoconch axis, sculptured with several spiral ridges, and embryonic shell partially covered by larval shell whorls and also by first teleoconch whorl due to protoconch inclination. Outer layer of shell wall very thin, simple prismatic structure; each prism almost perpendicularly arranged to the outer shell surface. Operculum semicircular, paucispiral, thin, concave externally; external surface smooth, corneous, reddish straw in color; inner surface calcified except for marginal area, with an apophysis near base of inner margin.

General conchological features

Teleoconch.—The shell is small to medium in size, globose to subglobose or sometimes hemispherical, solid, white, and translucent when it is fresh (Figure 1). The teleoconch coils number less than four, increase rapidly in size, and have a less convex upper whorl surface. The suture is shallowly impressed. The last whorl is well inflated and has a round periphery. The exterior surface bears microscopic spiral ridges and very fine growth lines (Figure 2A–D). The aperture is small to large and crescent-shaped to semicircular in outline. The outer lip is prosocline, angled 30° to 50° from the shell axis, sharp along its margin, and is thickened interiorly into an indistinct inner ridge. The inner lip is covered with a smooth, thick and convex callus that spreads widely onto the base of the previous whorl. The adaxial margin of the inner lip bears a robust projection in *P. adamsiana* and *P. subpacificana*, and three to seven teeth in all other species. The inner line of the callus surrounds the columellar area, then merges gradually with the basal lip. The inner walls of the whorls are resorbed, producing a hollow cavity inside (Figure 3), except for the last 1/3 whorl, where the cavity forms a relatively long, narrow, tube-like inner space and continues to the apertural opening. Inside the whorls is a funnel-like cavity which is separated from the main cavity by a steep wall and positioned just beneath the inner lip callus. This cavity, visible from the outside through the translucent inner lip callus, encases the distal end of an adapically projected digestive gland. Two muscle attachment scars are carved as shallow depressions; one corresponds to the left shell muscle of the animal, is spirally elongate and located beneath the convex part of the inner line of the aperture, while the other corresponds to the right shell muscle, is subcircular in shape and located close to the apex.

Protoconch.—The protoconch is deeply immersed in the first teleoconch whorl, separated from the teleoconch by a clear line of demarcation, and is either multispiral or paucispiral (Figures 4A–F; 5A–E). A multispiral protoconch,

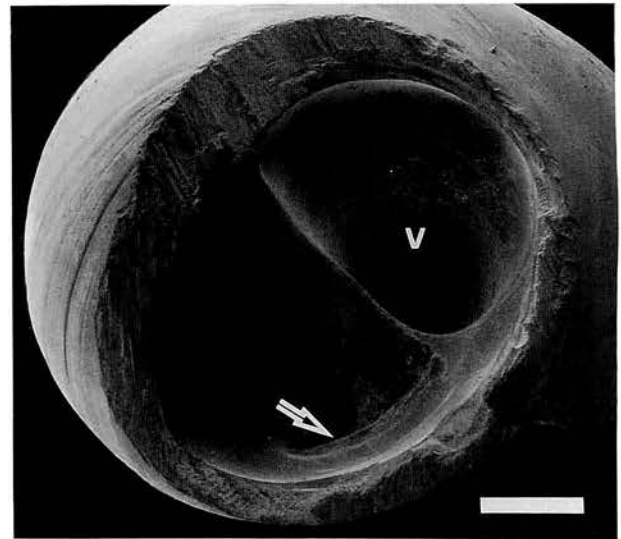
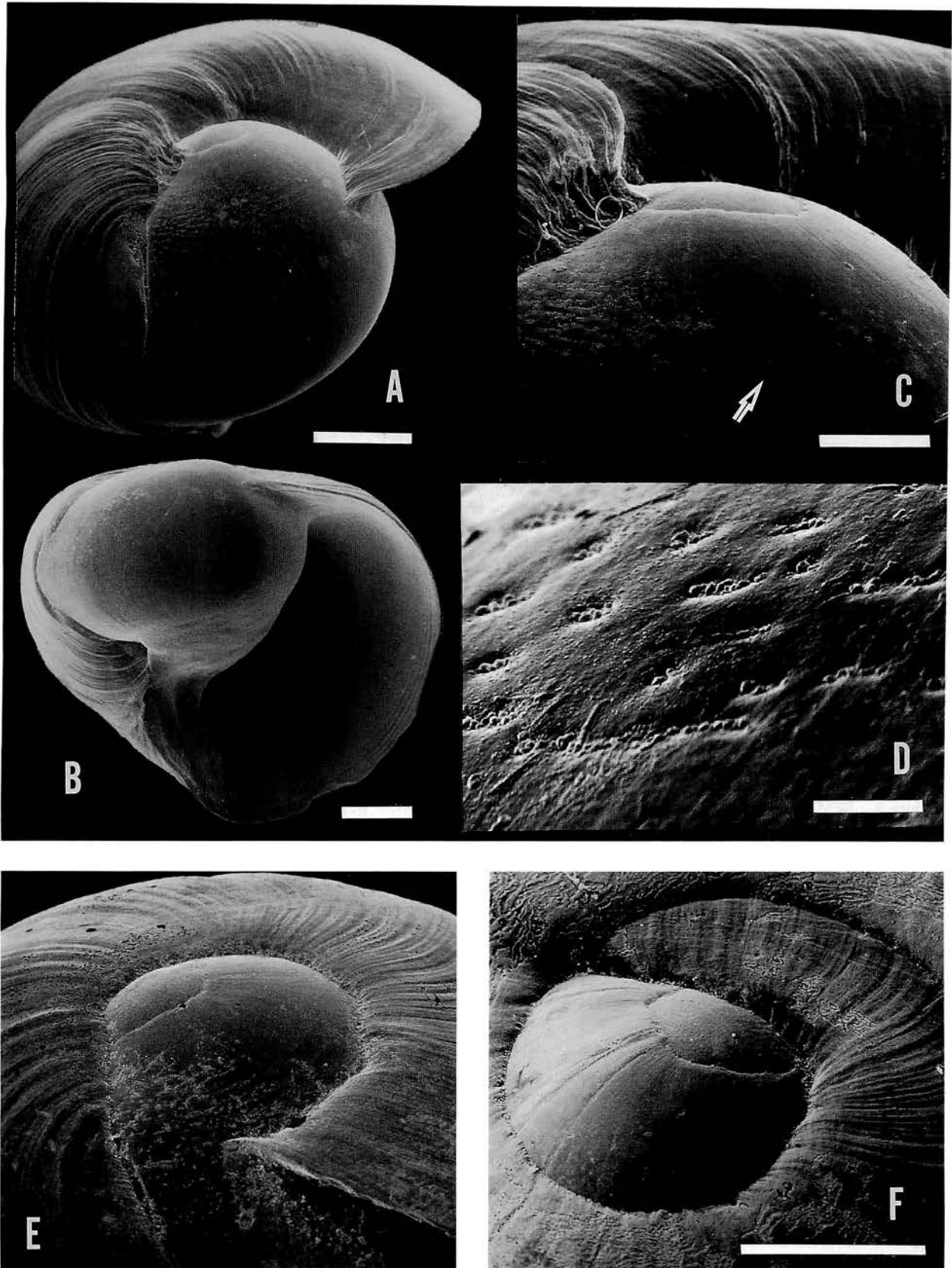


Figure 3. Shell (apical whorls removed) of *Pisulina adamsiana* Nevill and Nevill from South Kona, Hawai'i Island, showing the hollow internal space and the vertical cavity (v), the latter encasing the digestive gland of the animal; oblique apical view. Arrow indicates the elongate left muscle scar. Scale bar = 500 μ m.

seen in *P. adamsiana* and *P. subpacificana*, consists of an embryonic shell (protoconch-I) and larval shell (protoconch-II). The embryonic shell is generally smooth and largely involved with the larval shell that bears four or five spiral ridges and many minute pits. The axis of the multispiral protoconch is sharply inclined (approximately 30°) compared to the teleoconch whorls, so the embryonic shell is partly covered by the initial teleoconch whorl (Figure 4A, E, F). The inner walls of the protoconch are resorbed into the teleoconch. A paucispiral protoconch, seen in some species, consists only of a large and smooth embryonic shell. In this case, the coiling axis of the protoconch appears to be the same as that of the teleoconch.

Shell microstructure.—The shell consists of three layers, excluding the myostracum, and Figure 7 shows their occurrence in the shell. The outermost layer (OL) is very thin (less than 20 μ m thick in *P. adamsiana*), and is composed of simple, irregular prisms (Figure 6A, B). Each prism is less than 2 μ m long, 0.3 μ m thick, and oriented with its long axis less than 10° to the outer shell surface. The middle layer (ML) is of very thick, simple crossed-lamellar structure (Figure 6A–D). The inner shell layer (IL) consists of alter-

Figure 4. SEM micrographs of the multispiral protoconch in *Pisulina adamsiana* Nevill and Nevill. All specimens came from off South Kona, Hawai'i Island. **A–D.** Juvenile specimen with 0.6 of a teleoconch whorl. **A.** Abapertural view showing the biconvex and opisthocline larval shell aperture. Scale bar = 100 μ m. **B.** Apertural view. Scale bar = 100 μ m. **C.** Detail of the apical area of the protoconch, oblique lateral view. Embryonic shell partly exposed. Arrow indicates spiral ridges on the shoulder of the larval shell. Scale bar = 50 μ m. **D.** Close-up of the larval shell surface near the aperture, showing the presence of granules within pits. Scale bar = 5 μ m. **E.** Oblique apical view of a juvenile specimen with 0.9 of a teleoconch whorl, showing faint spiral ridges on the larval shell surface. Scale bar = 100 μ m. **F.** Oblique apical view of an immature shell with 1.7 teleoconch whorls, showing wavy ridges on the embryonic shell surface that are visible due to a lesser degree of overlapping by the teleoconch whorl. Scale bar = 100 μ m.



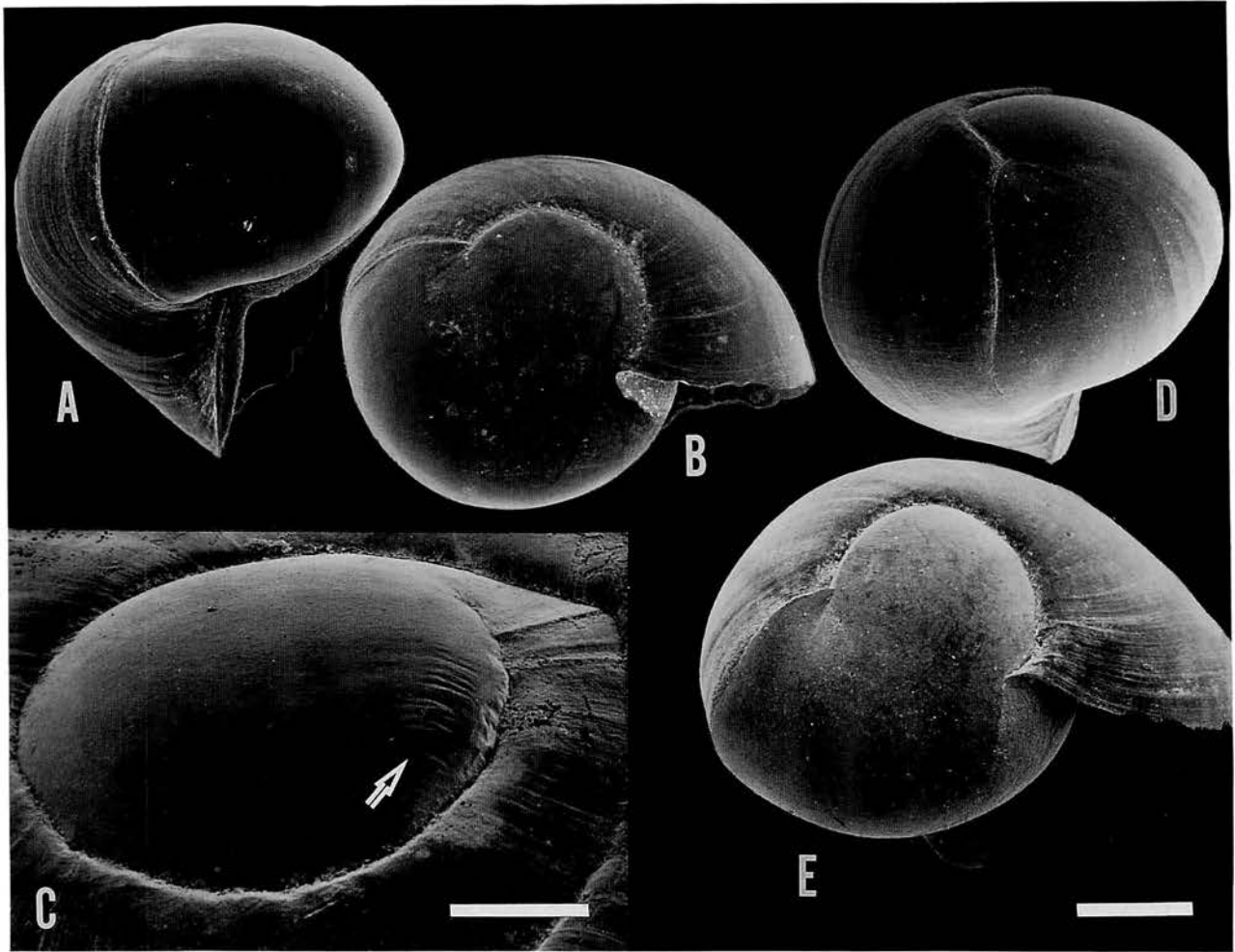
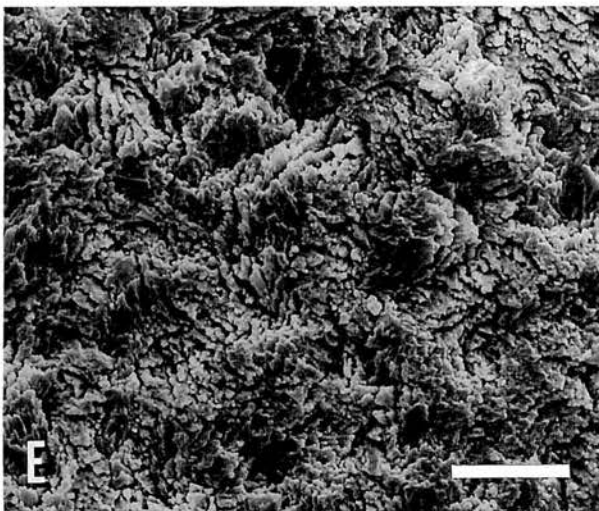
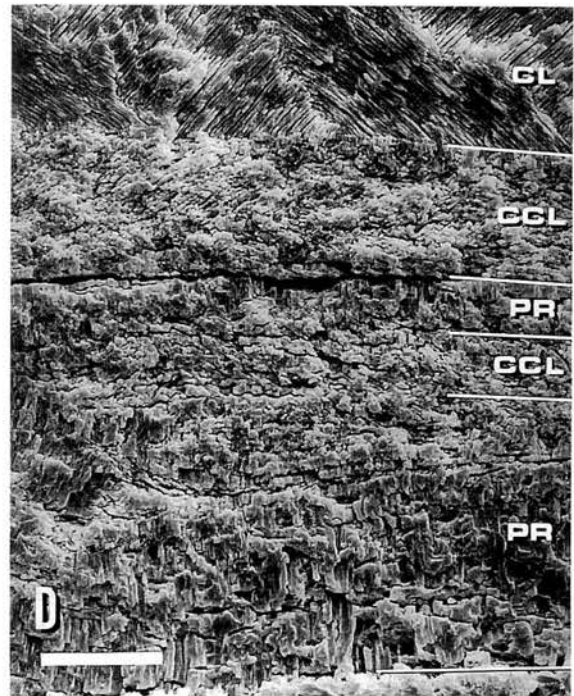
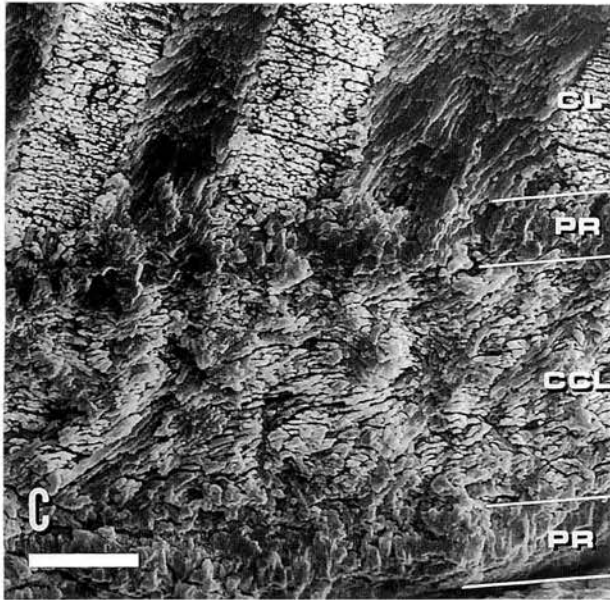
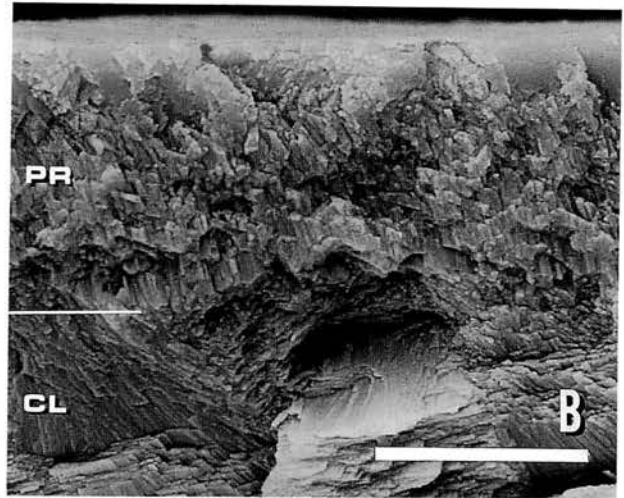


Figure 5. SEM micrographs of paucispiral protoconchs in *Pisulina* species. **A, B.** *Pisulina biplicata* Thiele, juvenile specimen with 0.5 of a whorl from off Kohama Island, Okinawa. Scale bar = 100 μm . **A.** Abapertural view. **B.** Slightly oblique apical view. **C.** *Pisulina maxima* sp. nov., oblique apical view of an immature specimen from off Aulong Island, Rock Islands, Palau. Arrow indicates longitudinal folds on the protoconch near the suture with the first teleoconch whorl. Scale bar = 50 μm . **D, E.** *Pisulina tenuis* sp. nov., juvenile specimens with 0.5 and 0.6 of a teleoconch whorl, respectively, from Yonaguni Island, Okinawa. Scale bar = 100 μm . **D.** Abapertural view showing transverse growth ridges near the protoconch aperture. **E.** Slightly oblique apical view.

Figure 6. SEM micrographs showing microstructures of the shell and operculum in *Pisulina adamsiana* Nevill and Nevill. **A.** Fractured shell surface of the outer lip of the aperture, cut perpendicular to the apertural margin, showing very thin outer prismatic layer and thick simple crossed-lamellar middle layer. The shell margin is to the right and the shell surface toward the top. Scale bar = 100 μm . **B.** Close-up of the fractured shell surface near the outer shell surface in A, showing details of the outer prismatic layer (PR) and the middle crossed-lamellar layer (CL). Scale bar = 10 μm . **C-E.** Etched surfaces of the section shown in Figure 7. **C.** The etched surface of an abapertural shell area, showing simple crossed-lamellar middle layer (CL) and inner layer. The inner shell surface faces toward the bottom. The inner layer consists of two irregular prismatic sublayers (PR) and an intervening complex crossed-lamellar layer (CCL). Scale bar = 10 μm . **D.** An etched shell surface near the back of the inner line of the inner lip shows the simple crossed-lamellar middle layer (CL) and the inner layer. The inner layer consists of alternating irregular prismatic sublayers (PR) and complex crossed-lamellar sublayers (CCL). Scale bar = 20 μm . **E.** Complex crossed-lamellar structure of the reconstructed inner shell wall. Scale bar = 10 μm . **F.** Fractured surface of an operculum, showing spherulitic prismatic structure. Scale bar = 10 μm .



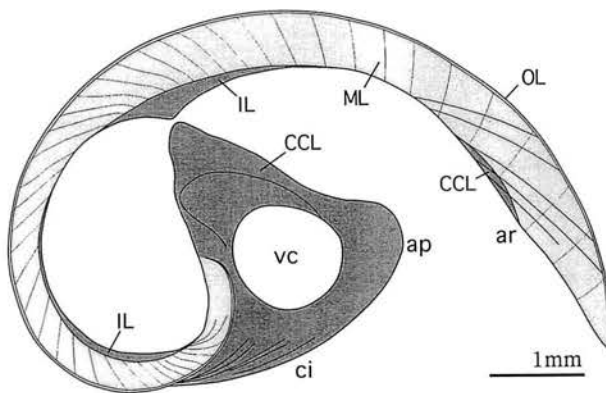


Figure 7. Arrangement of shell layers in *Pisulina adamsiana* Nevill and Nevill. The section is roughly perpendicular to the shell axis. Abbreviations: OL: very thin outer layer with prismatic structure; ML (light gray): thick middle layer with simple crossed-lamellar structure; IL (dark gray): inner layer made up of alternating sublayer(s) of complex crossed-lamellar and simple prismatic structures; CCL (dark gray): complex crossed-lamellar structure; ap: apertural projection; ar: apertural ridge; ci: callused inner lip of aperture; vc: vertical cavity.

nating sublayer(s) of complex crossed-lamellar and simple prismatic structure (Figure 6C, D). The prismatic sublayers consist of irregular prisms that are arranged vertically. The first-order lamellae of the complex crossed-lamellar structure are indistinct, variable in shape, and composed of a small number of thin, lath-like second-order lamellae (Figure 6E). The same shell structure is present in the robust inner lip area and in a small area just posterior to the inner ridge of the aperture, which are areas constructed secondarily after absorption of the original layers (CCL in Figure 7).

Operculum.—The operculum is semicircular in shape, with a minimum length/maximum length ratio of ca. 0.7, paucispiral, rather thin, and has a concave exterior surface (Figures 8A, B; 9A–C). The exterior surface fits well into the convex surface of the shell's inner lip when the animal fully extends its head-foot mass. The number of volutions may be up to 1.7, apart from the nucleus. The operculum consists of an outer corneous layer (up to 5 μm thick) and inner calcareous layers. The surface of the outer corneous layer is smooth (except for faint growth lines), reddish straw in color, and the color gradually becomes paler from the margin to nucleus. The nucleus appears only on the outer surface, is semicircular, located more or less abaxially and adapically from the center, paucispiral in *P. adamsiana* (Figure 8B) and concentric in the other modern species (Figure 9C). The inner surface of the operculum is calcified, except for the marginal area. The calcified area is covered with fine growth lines and bears a long apophysis near the base of the inner margin. The apophysis appears first as a weak ridge along the opercular suture, then becomes a curved calcified rod, and finally projects beyond the margin while remaining attached along its whole length to the basal margin of the operculum by a thin septum-like base. The muscle attachment scar can be divided into three areas: two are shallow, elongate depressions that are positioned at the

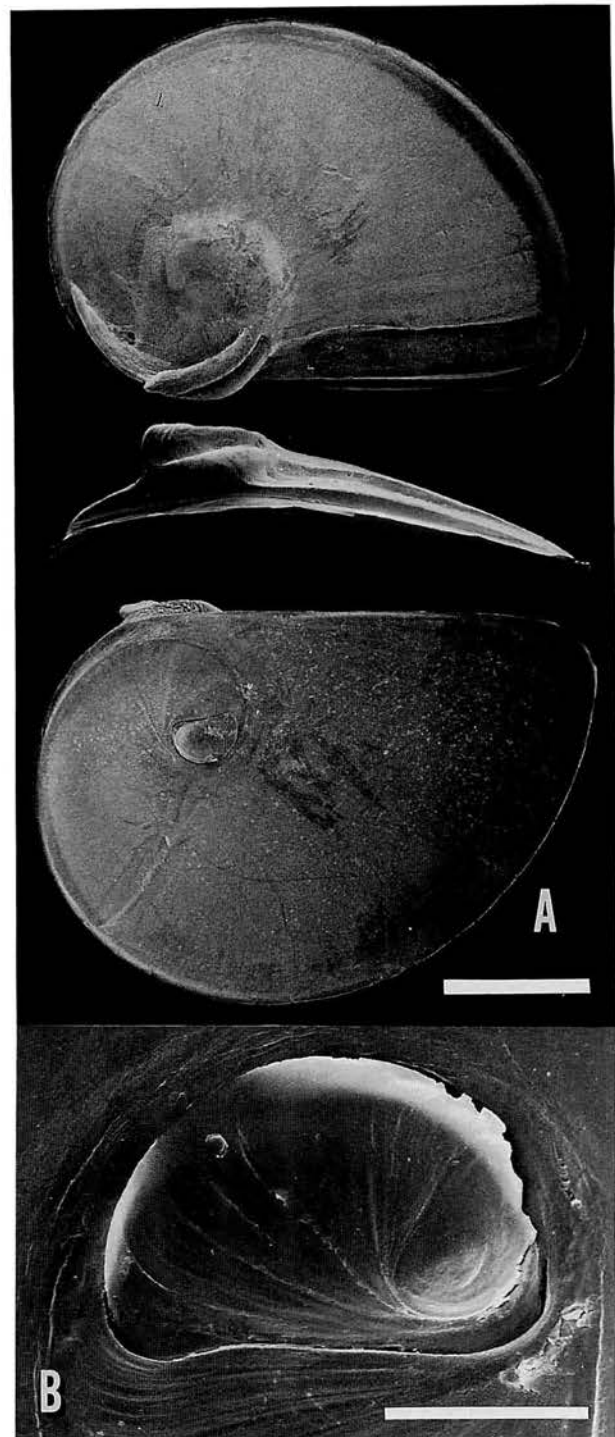


Figure 8. Operculum of *Pisulina adamsiana* Nevill and Nevill from Sipadan Island, Malaysia. **A.** Internal, lateral and external views (arranged from top to bottom). Scale bar = 500 μm . **B.** Oblique lateral view of the paucispiral nucleus on the external surface, showing 0.3 of a volution. Scale bar = 100 μm .

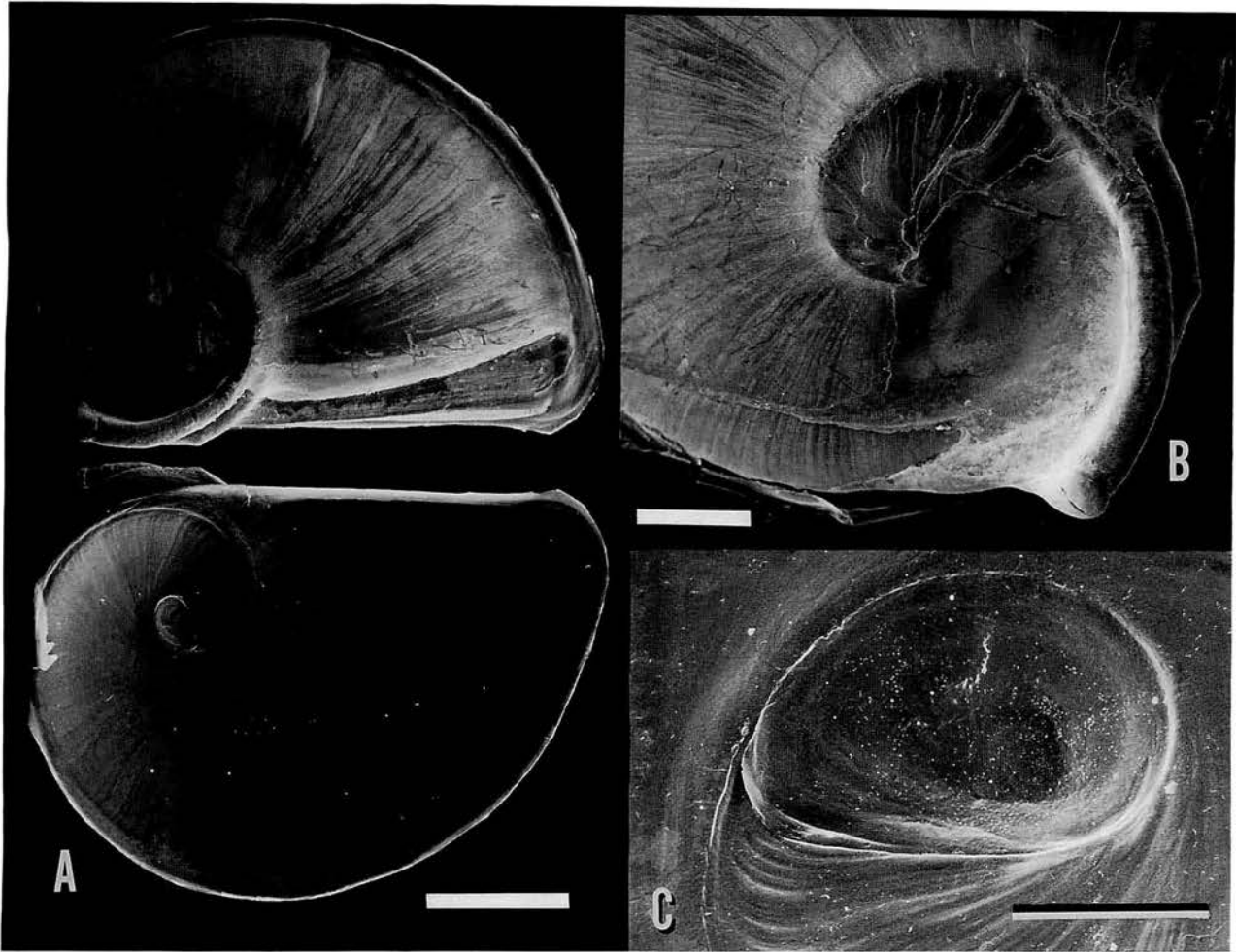


Figure 9. Operculum of *Pisulina maxima* sp. nov. from Sipadan Island, Malaysia. **A.** Internal (top) and external (bottom) views. Scale bar = 500 µm. **B.** Detail of apophysis and muscle attachments on the internal surface. Scale bar = 200 µm. **C.** Oblique view of the concentrically growing nucleus on the external surface of operculum. Scale bar = 100 µm.

inner and basal margins, and the other is between the apophysis and nucleus and is thicker than the other calcified areas due to having additional calcitic layers (Figure 9B). The calcareous part of the operculum is composed of spherulitic prisms (Figure 6F).

Systematic position of *Pisulina*

The protoconch morphology and shell microstructure of *Pisulina* are unique and almost identical to those of the freshwater genus of Neritopsina, *Neritilia* Martens, 1879; these are the only conchological characters useful for systematic placement.

Apart from species with non-planktotrophic development (see below), protoconchs of extant aquatic members of Neritopsina are quite uniform in shape and differ from those of all other gastropods (Bandel, 1982; Sasaki, 1998). The protoconchs of the following genera have been figured previ-

ously as SEM images: *Nerita* (Bandel, 1982; Sasaki, 1998), *Smaragdina* (Robertson, 1971; Bandel, 1982; Herbert and Kilburn, 1991), *Clithon*, *Neritina*, *Septaria* (Bandel and Riedel, 1998) [Neritidae]; *Phenacolepas* (Bandel, 1982; Sasaki, 1998), *Shinkailepas*, *Olgasolaris* (Beck, 1992) [Phenacolepadidae] and *Neritopsis* (Bandel and Frýda, 1999) [Neritopsidae]. These genera all share the same protoconch features: the embryonic shell is globular in shape, and the larval shell is oval to globular naticiform and has less than 3.5 volutions. As Bandel (1982) has noted, the larval shell is smooth except for fine growth lines, coils almost planispirally, and the suture line abuts the surface more adapical to the previous suture, so that the number of coils cannot be counted from the outside. Moreover, the inner walls of the larval shell are absorbed internally (*Neritopsis* is a possible exception; Bandel, 1992).

The protoconch of *Pisulina adamsiana* is fundamentally the same as in the Neritopsina mentioned above. However,

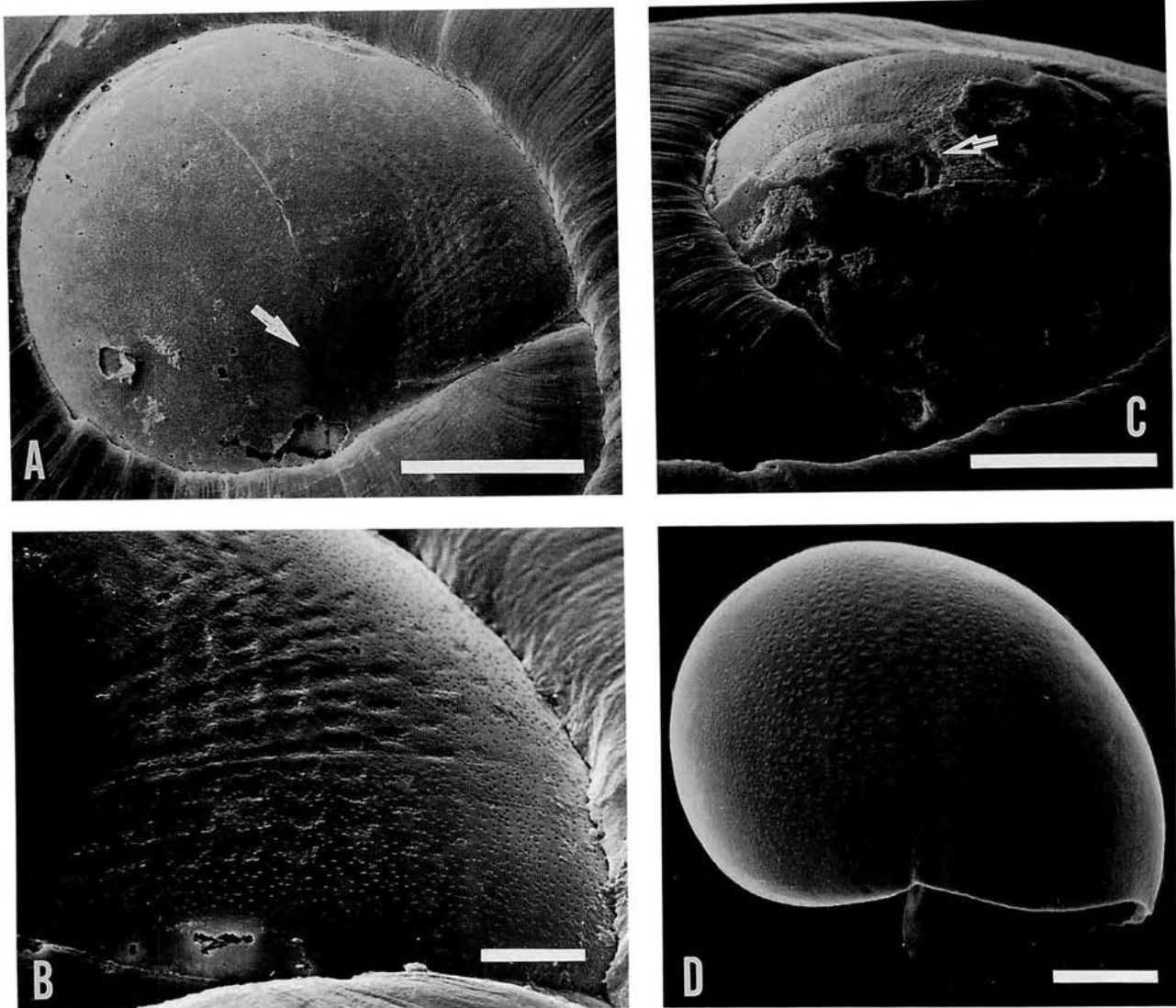


Figure 10. Multispiral protoconch and embryonic shell of *Neritilia*. **A-C.** Immature shells of *Neritilia rubida* (Pease) from Tahiti. **A.** Apical view of a juvenile shell with 1.2 teleoconch whorls. The surface is mostly intact. Arrow indicates the apex of the larval shell. Scale bar = 100 μm . **B.** Oblique close-up of the larval shell surface in A, showing the presence of spiral and axial ridges and minute pits entirely covering the protoconch surface. Scale bar = 20 μm . **C.** Oblique apertural view of juvenile shell with 1.2 teleoconch whorls. Outermost layer of the protoconch is partially eroded, so that the suture and growth lines of the larval shell are visible. Arrow indicates suture line. Scale bar = 100 μm . **D.** Apical view showing an embryonic shell of *Neritilia* sp. that was extracted from an egg capsule shortly before hatching. Part of the operculum protrudes from the aperture. Scale bar = 20 μm .

as already pointed out by Herbert and Kilburn (1991), the larval shell of *P. adamsiana* is distinctly tilted with respect to the teleoconch (Figure 4A-F). This tilting resulted from the change in direction of the growth lines from the larval shell (opisthocline) and the teleoconch whorls (prosocline). In addition, *P. adamsiana* has characteristic ridges (Figure 4A, C, E) and microscopic pits (Figure 4C, D) on the larval shell surface near the aperture (see description of *P. adamsiana*, below), which are sculptural features unknown in the other aquatic groups of Neritopsina.

We have found that members of the freshwater and brackish-water genus *Neritilia* have a protoconch almost identical to that of *P. adamsiana*, suggesting a close affinity between the two genera. Bandel and Riedel (1998) have already noted the unique protoconch morphology of *Neritilia* within the superfamily Neritoidea. The protoconch surface of the type species, *Neritilia rubida*, is smooth and has no suture line, so it appears to be a simple globular protoconch (Figure 10A, B). However, this is due to the subsequent laying down of a very thin calcareous layer over the surface of a



Figure 11. Oblique lateral view of a paucispiral nucleus with 0.3 of a volution on the operculum of *Neritilia* sp. from Yonaguni Island, Okinawa. Scale bar = 50 μ m.



Figure 12. Radula of *Pisulina maxima* sp. nov. from Sipadan Island, Malaysia. The radula is characterized by a large, strongly oblique outer lateral tooth and the absence of a central tooth, the features almost identical to that of *Neritilia* (see Baker, 1923). Scale bar = 50 μ m.

multispiral protoconch. In specimens whose protoconch surfaces are slightly eroded, the suture line and distinct growth lines are visible (Figure 10C), the once-hidden embryonic shell emerges close to the suture of the teleoconch, and a discontinuity in coiling is noticeable between the larval shell and teleoconch. The number of larval shell coils cannot be precisely counted, but appears to be about one, as seen in *P. adamsiana* (the paucispiral nucleus of the operculum, which is formed during the larval phase, is also similar to that of *P. adamsiana* in number of volutions; Figure 11). The calcareous layer over the protoconch appears to have been secreted after the last whorl of the larval shell was formed. In addition to the presence of this calcareous layer, *N. rubida* shows additional minor differences in its protoconch: the inclination of the coiling axis appears to be somewhat smaller, the larval shell has more numerous spiral ridges (five or six; Figure 10B) than *P. adamsiana*, and the microscopic pits are scattered all over the surface of both embryonic and larval shells without an evident pattern (Figure 10B, D). Bandel and Riedel (1998, fig. 6A, B) figured the protoconch of *Neritilia* sp. cf. *N. rubida*, from the Matutinao River, Cebu, the Philippines. The spirally arranged pits on the larval shell of this species differ from those described here for *N. rubida*. The spiral rows of pits in the Philippine *Neritilia* species evidently are a homologous character shared with *P. adamsiana*.

Shell microstructure is a second clue to the close relationship between *Pisulina* and *Neritilia*. Previous descriptions of shell microstructure of Neritopsina have been mostly restricted to Neritidae (e.g., Bøggild, 1930; Gainey and Wise, 1980; Bandel, 1990). The presence of a calcitic outer layer (with a homogeneous or prismatic structure) and aragonitic middle and inner layers (crossed-lamellar structure) are features shared among Neritopsina (e.g., Ponder and Lindberg, 1997:103). *Pisulina* has shell microstructure features that are basically the same as seen in Neritidae (Figures 6A-E;

7). However, *Pisulina* differs markedly from Neritidae in the inclination of prisms in the outer layer. The prisms are arranged almost perpendicularly in *Pisulina* (Figure 6B), while they are almost horizontal or very oblique relative to the exterior shell surface in neritids (Bøggild, 1930; Knight *et al.*, 1960:123; Bandel, 1990; personal observation). Although the outer prismatic layer is brown in color and much thicker than in *Pisulina*, *Neritilia rubida* shares characteristic features regarding the inclination and size of prisms with *Pisulina*.

The monogeneric family Neritiliidae was erected for the genus *Neritilia* by Schepman (1908) based upon its unique radular morphology. However, the genus has been assigned to the subfamily Neritiliinae of Neritidae (e.g., Baker, 1923; Thiele, 1929; Wenz, 1938; Knight *et al.*, 1960). Holthuis (1995) has recently shown the paraphyly of "Neritidae" and concluded that *Neritilia* is the sister group of Neritidae and Phenacolepadidae. Thus, *Neritilia* should be classified as an independent family of the superorder Neritopsina, namely Neritiliidae Schepman, 1908, rather than being placed in Neritidae.

Although the detailed systematic position of *Pisulina* must ultimately be determined by phylogenetic analysis based on conchological, anatomical, and molecular criteria, it is reasonable to conclude at present that *Pisulina* is not a member of Neritidae, but should be allocated along with *Neritilia* to Neritiliidae. The close relationship between the two genera is also confirmed by radular and anatomical characters (Figure 12; Kano and Kase, in preparation). We believe that the protoconch with the whorl inclination and spiral ridges, and the almost perpendicular prisms in the outer shell layer, are synapomorphies of *Pisulina* and *Neritilia*.

These synapomorphies are important criteria for re-

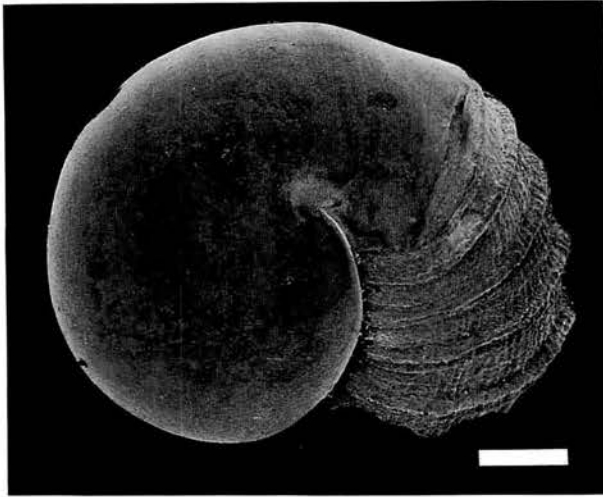


Figure 13. Paucispiral protoconch of *Neritopsis radula* (Linnaeus), juvenile specimen with 0.2 of a teleoconch whorl, from Yonaguni Island, Okinawa, in apical view. Bandel and Frýda (1999) illustrated a multispiral protoconch of *N. radula* from Mauritius. Further research is needed to resolve whether *N. radula* from the western Indian Ocean and Pacific are different species or an example of poecilogony (different early ontogenies within a single species; Bandel and Riedel, 1998), unknown among the Gastropoda. Scale bar = 100 μ m.

evaluating fossil species previously placed in Neritidae, which ranges in age from Triassic to Recent. Knight *et al.* (1960) recognized 19 fossil genera (4 are still living) in the family and diagnosed most genera solely on the basis of teleoconch characters. The apical whorls of fossil neritids tend to be lost by abrasion and/or dissolution, but in rare instances they are preserved intact in sediments deposited in low-energy, soft-bottom environments. By examining fossil species, we have found that two species, *Pisulinella miocenica* Kano and Kase, 2000, and "*Neritilia*" *tracyi* Ladd, 1965, both from the Miocene of the Marshall Islands, are undoubtedly members of Neritiliidae. As in *Neritilia* and *Pisulina*, these two species possess an inclined protoconch bearing spiral ridges, but differ from *Neritilia* and *Pisulina* in important ways (Kano and Kase, 2000; unpublished data).

Implications of paucispiral protoconch

Pisulina species have either a paucispiral or multispiral protoconch. Nevertheless, the species are undoubtedly closely related to one another, because of the many close similarities in other shell characters. We suggest that the paucispiral protoconch originated from the multispiral protoconch of an ancestral *Pisulina* species, as described below.

Most aquatic species of Neritopsina have a long planktotrophic duration after hatching from their egg capsule, and feeding veligers secrete a multispiral larval shell. However, species of some freshwater genera (e.g., *Theodoxus*) have a very large (ca. 0.9 mm) paucispiral protoconch and their development is quite different from that

of other members of Neritopsina. They undergo benthic development, and metamorphosis occurs within the egg capsule by means of nurse-egg feeding (Bandel, 1982). The juveniles crawl out from the capsule with their foot. According to Holthuis (1995), free-swimming veligers (ancestral for the group) were lost at least four times in the evolutionary history of Neritidae, and in *Nerita* and *Vitta* the loss occurred within the genus (or subgenus). The non-planktotrophic (benthic or lecithotrophic) development of *Pisulina* seems to have originated from a planktotrophic ancestor, after the origin of the genus, by exploiting an adaptive modification different from freshwater neritids. Benthic development is much more prevalent in freshwater invertebrates than in their marine relatives, because the downstream loss of freshwater larvae in moving water is the primary determinant for benthic development (Holthuis, 1995). Meanwhile, the non-planktotrophic development of *Pisulina* may be an adaptation to the unique cryptic environments in marine caves. Kase and Hayami (1992) and Hayami and Kase (1996) have shown that the predominance of non-planktotrophic development and the dominance of brooding species among submarine cave bivalves primarily resulted from an adaptation to food-limited conditions. Although no examples of this have been found in gastropods so far, it may be that *Pisulina* underwent non-planktotrophic development and acquired a paucispiral protoconch by adapting to a cryptic habitat. *Neritopsis radula* (Linnaeus, 1758), another cave-dwelling species of Neritopsina, developed a similar paucispiral protoconch (Figure 13).

It is worth noting that paucispiral and concentric opercular nuclei are connected with multispiral and paucispiral protoconchs. The paucispiral nucleus (the operculum of a veliger) grows during the planktotrophic period, while the concentric nucleus is formed in the egg capsule, providing an additional criterion for inferring the mode of development in gastropods.

Pisulina adamsiana Nevill and Nevill, 1869

Figures 1; 2A; 3-4; 6-8

Pisulina adamsiana Nevill and Nevill, 1869, p. 160, pl. 17, fig. 4; Thiele, 1925, p. 32, pl. 3, fig. 16; Thiele, 1929, p. 111, fig. 54; Wenz, 1938, p. 431, fig. 1060; Knight *et al.*, 1960, p. 285, fig. 185-3; Habe, 1963, p. 231, 232, fig. 1; Ladd, 1977, p. 14, 15, pl. 1, figs 1, 2; Herbert and Kilburn, 1991, p. 320-322, figs. 1-3; Hinoide and Habe, 1991, p. 49 (in part), fig. 1.

Material examined.—INDIA: "Calcutta"; 1 specimen, coll. Paetel, MNHB.—"Ganges River delta" (21°40'N, 88°00'E); pre 1913, 3 specimens, AMS C-034497.—MALDIVES: Ari Atoll; 25 m depth; January 1996; 1 specimen, coll. S. Gori.—JAPAN: "Shodokutsu (= small cave)", Ie Island, Okinawa (26°42.9'N, 127°50.1'E); 20 m depth, totally dark submarine cave; 1988; 12 specimens.—"Umagai" diving site, north of Hatohama, east of Kume Island (26°21.1'N, 126°53.1'E); 24-28 m depth, submarine caves, totally dark inside; July 1996, 2 specimens.—"Witch's House (= Majono-yakata)" diving site, northwest of Shimoji Island, Miyako Islands, Okinawa (24°49.3'N, 125°08.3'E); 35 m depth, submarine

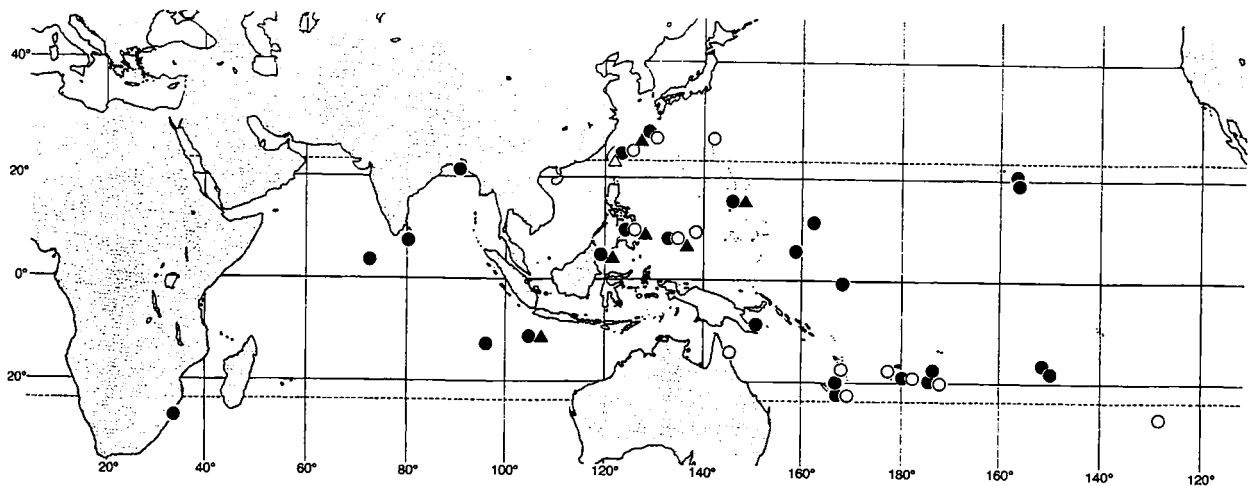


Figure 14. The geographic distribution of Recent *Pisulina* species. *Pisulina adamsiana* Nevill and Nevill (solid circles), *Pisulina bisplicata* Thiele (open circles), *Pisulina maxima* sp. nov. (solid triangles) and *Pisulina tenuis* sp. nov. (open triangle). The type locality of *P. bisplicata* is not plotted, because it was designated only as "Indian Ocean."

cave, totally dark inside; 54 specimens (10 specimens NSMT-Mo71618). — "Toriike" diving site, northwest of Shimoji Island (24°49.1'N, 125°08.3'E); 12–40 m depth, several caves branching from a huge tunnel, gloomy to totally dark inside; 1992–1996, 2 specimens. — "Black Hole" diving site, northwest of Shimoji Island (24°49.1'N, 125°08.3'E); 35 m depth, submarine cave, totally dark inside; 1 specimen. — "Sabachi Cave", southeast of Yonaguni Island, Yaeyama Islands, Okinawa (24°26.1'N, 122°57.5'E); 25–30 m depth, submarine cave, totally dark inside; September 1994, 2 specimens. — MALAYSIA: "Turtle Cavern", Sipadan Island, west Celebes Sea, Sabah (5°04.8'N, 118°36.5'E); 9–17 m depth, totally dark inside; May 1997, 10 specimens (including 9 live individuals; 1 empty shell NSMT-Mo71619). — PHILIPPINES: "Marigondon Cave" diving site, Mactan Island, Cebu (10°15.8'N, 123°59.2'E); 27 m depth, large submarine cave, totally dark inside; May 1994, more than 1000 specimens; November 1998, 3 live specimens. — Balicasag Island, Panglao, Bohol (9°32.7'N, 123°40.7'E); 14–40 m depth; submarine caverns, gloomy inside; May 1994, 162 specimens (10 specimens NSMT-Mo71620). — "Mapatin Cave" diving site, southwest of Maricaban Island, Batangas, Luzon (13°40.0'N, 120°49.0'E); 46 m depth, lava tube, totally dark inside; November 1998, 1 live specimen. — PALAU: "Virgin Hole", west of Ngemelis Island, Rock Islands (7°07.3'N, 134°14.1'E); 17 m depth, submarine cave, totally dark inside; April 1995, 4 specimens. — "Siaes Tunnel" diving site, southwest of Siaes drop off, ca. 6 km west-northwest of Aulong Island, Rock Islands (7°18.7'N, 134°13.6'E); 24–53.5 m depth, huge submarine tunnel; April 1995, 141 specimens; December 1997, 19 specimens. — NORTHERN MARIANAS: near "Grotto" diving site, north of Saipan Island (15°15.3'N, 145°49.5'N); 12–30 m depth, huge cave, gloomy to totally dark inside; November 1997, 31 specimens (including 3 live individuals). — near "Tinian Grotto" diving site, west of Tinian Island; 50–51 m depth, huge cave, gloomy to totally dark; November 1997, 6 specimens. — POHNPEI: "Plang Point" diving site, west of Pohnpei Island (6°51.4'N, 158°

06.6'E); 55m depth, cavern, gloomy inside; November 1999, 2 specimens. — HAWAII: "Worm Cave", off Ahihi-Kinaiu, Makena, Maui Island (20°35.3'N, 156°25.8'W); 26–31 m depth, submarine cave, gloomy to totally dark inside; October 1997, 54 specimens (including 5 live individuals). — "Lost Crater Caves" diving site, off Ahihi-Kinaiu (20°35.3'N, 156°25.7'W); 25 m depth, submarine lava cave, gloomy inside; October 1997, 1 live individual. — "Long Lava Tube", off Pali Kaholo, South Kona, Hawai'i Island (19°21.8'N, 155°56.8'W); 11 m depth, long lava tunnel, gloomy; November 1997, 16 specimens. — "Gustav Cave", off Ka'u Loa Point, South Kona (19°19.1'N, 155°53.2'W); 6–8 m depth, submarine cave, gloomy to totally dark inside; November 1997, 19 live individuals. — PAPUA NEW GUINEA: between Magulata and Kabuluna Points, Kiriwina Island, Trobriand Group (8°27'S, 150°59'E); 73 m depth, coral sand bottom, outside outer reef; June 1970, 1 specimen, coll. W. F. Ponder and P. H. Colman, AMS C-345150. — NAURU: Aiwo (0°32.6'S, 166°54.5'E); 15–25.5 m depth, cavern, open to gloomy inside; November 1999, 43 specimens. — AUSTRALIA: "Hangover Cave" diving site, west of Direction Island, Cocos (Keeling) Islands (12°06.3'S, 96°52.5'E); 51–52.3 m depth, cavern, gloomy inside; December 1999, 4 specimens. — "Boat Cave" diving site, Christmas Island; 2.4 m depth; totally dark inside; November 1999, 1 specimen. — "Thunder Dome" diving site, Christmas Island; 7.7–10.2 m depth, long cave, totally dark inside; December 1999, 12 specimens. — NEW CALEDONIA: east of Nuu Poa islet, Iles des Pins, New Caledonia (22°31.6'S, 169°25.8'E); 17–19.5 m depth, meandering submarine cave, gloomy inside; October 1996, 3 specimens, MNHN. — FIJI: north of Ono Island, Great Astrolabe reef (18°51.8'S, 178°27.0'W); 7–16 m depth; submarine tunnel, gloomy inside; December 1996, 2 specimens. — northwest of Dravuni Island, Great Astrolabe reef (18°45.3'S, 178°28.0'W); 23–24 m depth; December 1996, 18 specimens. — TONGA: north of Haano Island, Ha'apai Group (19°38.2'S, 174°18.0'W); 44 m depth, cavern; December 1996, 6 specimens. — west of Mo'ung'one Island, Ha'apai

Table 1. Comparison of shell characters in five species of *Pisulina*. Some of the character states in *Pisulina subpacific* Ladd (those shown in parentheses) may not represent general features of the species, owing to the immature condition of the holotype.

Species	Shell diameter of largest specimen	Shell thickness	Width of ridges on teleoconch surface	Apertural width	Number of inner lip teeth
<i>Pisulina adamsiana</i>	6.7 mm	thick	ca. 7 μm	small	1
<i>Pisulina subpacific</i>	(1.2 mm)	thick	?	small	1
<i>Pisulina biplicata</i>	4.8 mm	thick	ca. 1 μm	small	3-5
<i>Pisulina maxima</i> sp. nov.	13.7 mm	very thick	ca. 4 μm	very large	3-7
<i>Pisulina tenuis</i> sp. nov.	4.0 mm	thin	ca. 4 μm	large	4-5

Species	Situation of inner line near base	Tubercle on basal lip	Protoconch coiling	Max. dimension of protoconch exposed above teleoconch
<i>Pisulina adamsiana</i>	absent	present	multispiral	155-215 μm
<i>Pisulina subpacific</i>	absent	(absent)	multispiral	275 μm
<i>Pisulina biplicata</i>	present	absent	paucispiral	155-220 μm
<i>Pisulina maxima</i> sp. nov.	present	absent	paucispiral	180-275 μm
<i>Pisulina tenuis</i> sp. nov.	present	absent	paucispiral	210-300 μm

Group (19°23.2'S, 174°28.6'W); 20.5-37.5 m depth, submarine cave, totally dark inside; December 1996, 1 specimen.—"Sea Fans Cave" diving site, east of Taungiskika Island, Vava'u Group (18°39.7'S, 174°04.2'W); 7 m depth, submarine cave, gloomy inside; December 1996, 9 specimens.—SOCIETY ISLANDS: Tetuatiare Passage, north of Raiatea (16°49.5'S, 151°29.6'W); 10 m depth; submarine caves, gloomy inside; December 1996, 1 specimen, MNHN.—"Cave Arue" diving site, west of Tahiti Island (17°30.9'S, 149°32.1'W); 22-30 m depth; submarine caves, gloomy inside; December 1996, 12 specimens, MNHN.—"Banc des Daulphins" diving site, west of Tahiti Island (17°29.9'S, 149°38.3'W); 20 m depth; submarine cavern, gloomy inside; December 1996, 103 specimens (50 specimens registered; MNHN).

Distribution and age.—Tropical and subtropical Indo-Pacific (Figure 14). Holocene.

Diagnosis.—Medium-sized *Pisulina* characterized by a thick, globose to obliquely ovate shell, a robust projection on inner lip, and ca. 7 μm-wide wavy spiral ridges over teleoconch surface; protoconch multispiral, with exposed portion drop-shaped and 155 to 215 μm in maximum dimension; larval shell with 3 or 4 spiral ridges and many microscopic pits; inner line of inner lip callus continuous with basal lip without a sinus; basal lip with a weak tubercle.

Description.—Shell small, up to 6.7 mm wide and 7.0 mm high, thick, globose to obliquely ovate, with a low spire and a blunt apex (Figure 1). Protoconch multispiral. Embryonic shell covered by larval shell whorls and by first teleoconch whorl to varying degrees based on protoconch inclination, smooth, sometimes with faint wavy ridges near teleoconch suture (Figure 4F); exposed portion of embryonic shell 70 to 90 μm in maximum dimension. Larval shell coils about 1 volution, surrounded largely by first teleoconch whorl, obliquely ovate, about 360 μm wide and 250 μm high,

inclined about 30° to teleoconch (Figure 4A, B, E, F); exposed drop-shaped area 155-215 μm in maximum dimension, almost smooth except for unevenly spaced growth lines; surface near apertural lip sculptured with 3 or 4 indistinct, ca. 3 μm-wide, 80 to 140 μm-long spiral ridges (Figure 4C), and also with many pits more or less irregularly arranged in a spiral direction and sometimes giving rise to short grooves (bearing granules up to 0.5 μm in diameter) by being connected with one another (Figure 4D). Apertural lip of larval shell biconvex, opisthocline and very discordant with first teleoconch whorl (Figure 4A). Teleoconch coils less than 3.3 in number, smooth to somewhat polished, first whorl coils almost planispirally; teleoconch surface with dense, ca. 7 μm-wide spiral ridges, subdivided by growth lines (Figure 2A). Aperture narrow and semilunar; outer lip prosocline, angled 35° to 40° to shell axis, beveled and not reflected; inner lip thickened by callus, with a broad, strong, quadrangular projection at its middle and a weak tubercle on the base; inner line of inner lip callus is an inverse-S shape, without sinuation at base. Operculum (Figure 8A) with a paucispiral nucleus 215 to 230 μm in maximum dimension (Figure 8B); apophysis moderately long and weakly curved spirally.

Remarks.—According to Herbert and Kilburn (1991), the holotype from Southern Province of Sri Lanka (Ceylon) is thought to be in the Indian Museum, Calcutta. We have not examined the type specimen, but there is little possibility of mistaking the shells at hand with any but this remarkable species.

Pisulina adamsiana is a quite distinctive species because it has a single robust quadrangular projection on the inner lip, whereas other modern species have multiple teeth. Moreover, this is the only modern species with a multispiral protoconch (Figure 4) and a paucispiral opercular nucleus (Figure 8B), which strongly suggest a relatively long



Figure 15. *Pisulina subpacificica* Ladd, 1966. Holotype (USNM 648341). Scale bar = 1 mm.

planktotrophic period for this species (see below). Furthermore, *P. adamsiana* differs from other *Pisulina* species by the inner line of its inner lip callus being inversely S-shaped, by the lack of a sinuation between the basal lip and the inner line of the inner lip callus, and by the presence of a weak tubercle on its basal lip (see Table 1).

Intraspecific variation of shell characters is small in this species, perhaps because of genetic homogeneity related to its well-developed dispersion ability. Scheltema (1971) estimated the duration of pelagic stage less than 55 days for *Smaragdia viridis* (Linnaeus, 1758). Taking the smaller size and fewer number of the larval shell whorls into consideration, the planktotrophic period of *P. adamsiana* is assumed to be shorter than that of *S. viridis*.

Koike (1985) described the spermatozoon ultrastructure of "*P. adamsiana* (?)" and stated that the spermatozoon is similar to that in *Clithon retropictus* (Martens, 1879), *Neritina plumbea* Sowerby, 1855, *Neritina variegata* Lesson, 1830, and *Septaria porcellana* (Linnaeus, 1758). However, the sperm of *P. adamsiana* from Sipadan Island is similar to the sperm of *Waldemaria* in Helicinidae rather than to the sperm of neritids (J. Healy, personal communication). It is likely that Koike's (1985) identification of *P. adamsiana* is incorrect.

Pisulina subpacificica Ladd, 1966

Figure 15

Pisulina subpacificica Ladd, 1966, p. 59, pl. 11, fig. 10.

Material examined.—Holotype from Bikini Island, Bikini Atoll, Marshall Islands; horizon in drill hole, at a depth of 789–799 feet (240–244m), late Miocene, USNM 648341.

Distribution.—Marshall Islands, known only from the type locality. Late Miocene.

Diagnosis.—Small *Pisulina* characterized by a globose and thick shell, a semilunar aperture and a strong quadrangular projection on inner lip; exposed portion of protoconch drop-shaped, ca. 275 μ m in maximum dimension.

Description.—Shell minute, 1.2 mm wide, 1.4 mm high, globose, thick, eroded, creamy in color, opaque, with a very low spire (Figure 15). Protoconch surrounded by first teleoconch whorl, drop-shaped in apical view, and visible portion is ca. 275 μ m in maximum dimension. Teleoconch of 1.5 whorls, with first whorl coiled almost planispirally; exterior surface lacking visible sculpture. Aperture small and semilunar in shape; outer lip prosocline, angled 35° to shell axis; inner lip thick and blunt at margin due to erosion, bearing a large, robust, adaxially convex quadrangular projection ca. 310 μ m wide and ca. 120 μ m high at its midpoint; inner line of inner lip callus inversely S-shaped, strongly concave in parietal area, and continues to basal lip without sinuation.

Remarks.—This Miocene species is known only from the holotype. *Pisulina subpacificica* is very similar to *P. adamsiana* in having a large, broad and quadrangular projection on its inner lip. Moreover, the present species seems to possess a multispiral protoconch as seen in *P. adamsiana*, judging from the drop-shaped protoconch that is exposed above the first teleoconch. Ladd (1966) separated this species from *P. adamsiana* based on its smaller shell size and lower spire, but the holotype of *Pisulina subpacificica* is unequivocally an immature specimen so these differences cannot be used to separate the two species. Fortunately, there are two characteristics that convincingly separate these two species. In *P. subpacificica*, the maximum dimension of the exposed portion of the protoconch is much larger (Table 1), and the inner lip projection is much stronger and twice as large as in *P. adamsiana*.

Pisulina biplicata Thiele, 1925

Figures 2B; 5A, B; 16; 17A

Pisulina biplicata Thiele, 1925, p. 32, pl. 3, fig. 15.

Pisulina adamsiana Nevill and Nevill. Komatsu, 1986, p. 42, 43, pl. 8, fig. 9; Hinoide and Habe, 1991, p. 49 (in part), fig. 2; Fukuda, 1993, p. 31, fig. 120; Sasaki, 1998, p. 117, figs. 78g, h.

Material examined.—Holotype from Indian Ocean ("East India?"), coll. von Finsch, MNHB. —JAPAN: Tsuchihama, Amami-Oshima Island, Kagoshima (28°24.4'N, 129°21.1'E); beach drift; July 1991, 14 specimens.—March 1993, 18 specimens.—Sankakubama, Naze-shi, Amami-Oshima Island (28°23.1'N, 129°30.3'E); beach drift; July 1991, 36 specimens.—Ankyaba, Kakeroma Island, Amami Islands

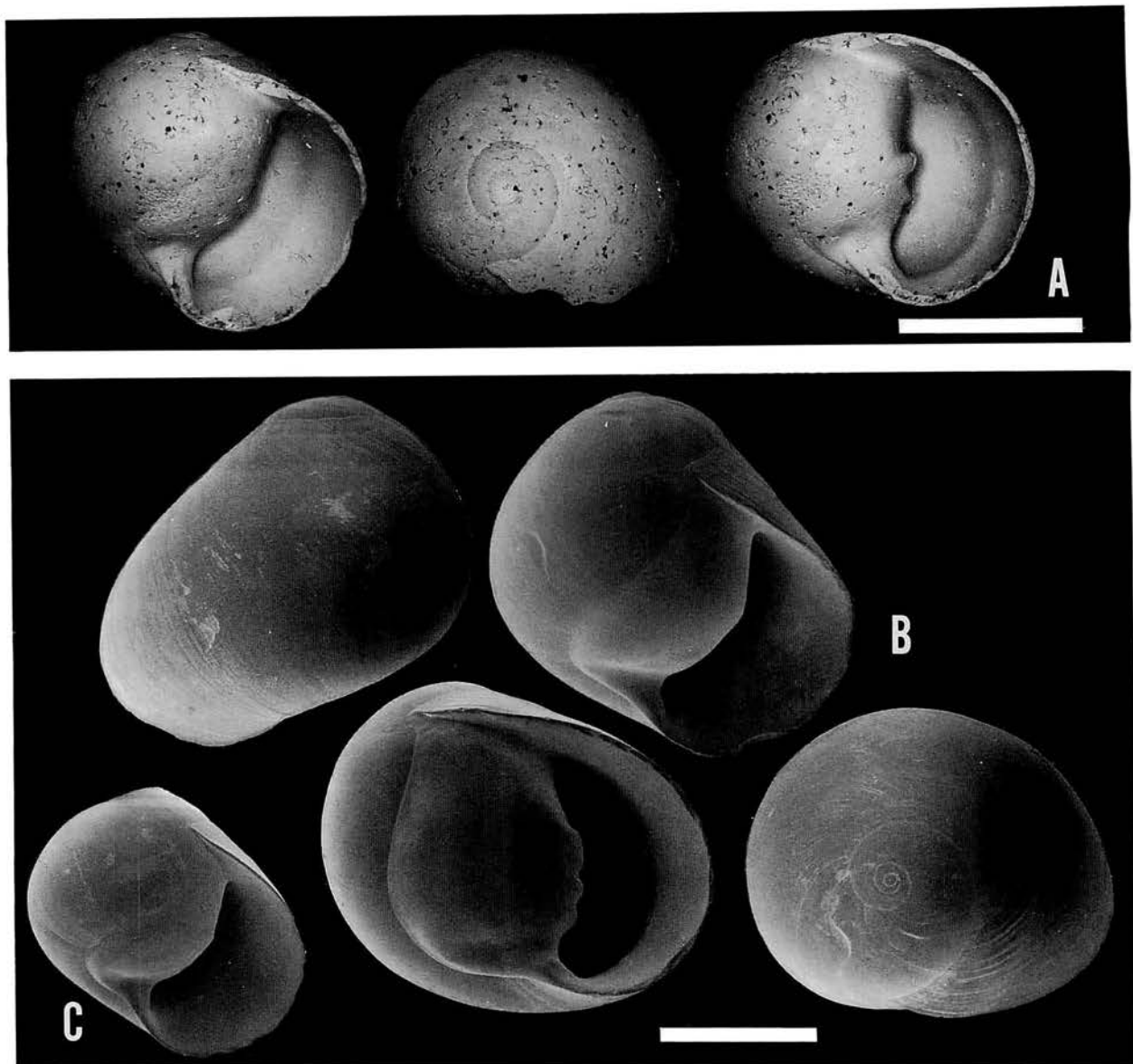


Figure 16. *Pisulina biplicata* Thiele, 1925. **A.** Holotype (MNHB), juvenile shell. Scale bar = 1 mm. **B.** Mature shell (four views) from Shimoji Island, Okinawa (NSMT-Mo71621). **C.** Mature shell (lower left specimen only) from Yap Island (NSMT-Mo71623). Scale bar = 2 mm for B and C.

(28°06.2'N, 129°21.1'E); beach drift; August 1993, 18 specimens.—Kunigami, Okinoerabu Island, Amami Islands (27°25.9'N, 128°42.8'E); beach drift; August 1992, 3 specimens.—"Devil's Palace (= Mao-no-kyuden)" diving site, Shimoji Island, Miyako Islands, Okinawa (24°49.7'N, 125°08.2'E); 25 m depth, submarine tunnels, gloomy inside; 1992, 93 specimens (10 specimens NSMT-Mo71621).—"Cross Hole" diving site, northwest of Irabu Island, Miyako Islands (24°51.6'N, 125°09.5'E); 15 m depth, submarine cave gloomy inside; 4 specimens, coll. M. Taniguchi.—north of Kohama Island, Yaeyama Islands (24°21.5'N, 123°58.9'E); 15–20 m depth, crevices; March 1996, more than 1000

specimens (20 specimens NSMT-Mo71622).—off Nishinohama, Kuroshima Island, Yaeyama Islands (24°14.6'N, 123°59.0'E); 10 m depth, sandy bottom; March 1996, 1 specimen.—PHILIPPINES: Balicasag Island, Panglao, Bohol (9°32.7'N, 123°40.7'E); 14–40 m depth; submarine caverns, gloomy inside; May 1994, 56 specimens.—PALAU: "Siaes Tunnel" diving site, southwest of Siaes dropoff, ca. 6 km west-northwest of Aulong Island, Rock Islands (7°18.7'N, 134°13.6'E); 24–53.5 m depth, huge submarine tunnel; April 1995, 3 specimens.—YAP: "Spanish Wall" diving site, west of Gilman, Yap Island (9°27.2'N, 138°02.5'E); 20–24 m depth, caverns and a small tunnel; November 1997, 18

specimens (6 specimens NSMT-Mo71623).—"Big Bend" diving site, west of Kanifay, Yap Island (9°28.1'N, 138°02.8'E); 8 m depth, a small cave, gloomy inside; November 1997, 4 specimens.—AUSTRALIA: Michaelmas Cay, Great Barrier Reef, Queensland (16°36'S, 145°59'E); May to June 1926, 1 specimen, coll. T. Iredale and G. P. Whitley (G. B. R. Boring Expedition), AMS C-345143.—Green Island, Great Barrier Reef (16°46'S, 145°58'E); May 1926, 1 specimen, coll. T. Iredale (G. B. R. Expedition), AMS C-345144.—East Face, Lizard Island, Great Barrier Reef (14°40'S, 145°29'E); 20 m depth; December 1974, 1 specimen, coll. W. F. Ponder, P. H. Colman and I. Loch, AMS C-345145.—NEW CALEDONIA: east of Nuu Powa islet, Iles des Pins, New Caledonia (22°31.6'S, 169°25.8'E); 17–19.5 m depth, meandering submarine cave, totally gloomy inside; October 1996, 2 specimens, MNHN.—Noumea (22°16'S, 166°27'E); pre-1950, 1 specimen, coll. T. Iredale, AMS C-345147.—VANUATU: White Sands, ca. 40 km from Port Vila, southeast of Efate Island (17°47'S, 168°33'E); March 1975, 2 specimens, coll. P. H. Colman, AMS C-345148.—west of Efate Island (17°39.1'S, 168°11.3'E); cavern; October 1996, 1 specimen.—"Taj Mahal" diving site, west of Efate Island (17°38.4'S, 168°08.7'E); 18 m depth, submarine cave, gloomy to totally dark inside; October 1996, 7 specimens.—FIJI: Nadi Bay (Tomba Ko Nandi), Viti Levu Island (17°44'S, 177°25'E); 9–35 m depth; 1962, 2 specimens, coll. J. Laseron, AMS C-345149.—northwest of Dravuni Island, Great Astrolabe reef (18°42.5'S, 178°29.8'W); 8 m depth, submarine cave, totally dark inside; December 1996, 1 specimen.—northwest of Dravuni Island, Great Astrolabe reef (18°45.3'S, 178°28.0'W); 23–24 m depth, cavern, gloomy to totally dark inside; December 1996, 5 specimens.—north of Ono Island, Great Astrolabe reef (18°51.8'S, 178°27.0'W); depth 7–16 m, submarine tunnel, gloomy inside; December 1996, 13 specimens.—TONGA: east of Fao Island, Ha'apai Group (19°46.5'S, 174°22.6'W); 6–7.5 m depth, submarine tunnel, gloomy inside; December 1996, 2 specimens.—southwest of Mo'ung'one Island, Ha'apai Group (19°38.3'S, 174°29.6'W); 11–28 m depth, cavern; December 1996, 3 specimens.—PITCAIRN GROUP: North Beach, Henderson Island; middle or late Pleistocene sediments in an uplifted cave; 1 specimen, coll. R. C. Preece (Pitcairn Islands Scientific Expedition 1991–2), UMZC.

Distribution and age.—Tropical and subtropical areas of the Indo-Pacific (Figure 14). Middle or late Pleistocene to Recent.

Diagnosis.—Medium-size *Pisulina* characterized by a glossy, thick, globose to pear-shaped shell, a high conical spire, a paucispiral protoconch, a semilunar aperture, and 3 to 5 blunt, somewhat squarish teeth along inner lip; teleoconch surface with microscopic spiral rows of granules.

Description.—Shell small, up to 4.8 mm wide and 5.5 mm high (1.7 mm wide and 1.6 mm high in holotype; Figure 16A), thick, globose to pear-shaped, with a moderately low to rather high conical spire (Figure 16B, C). Protoconch paucispiral, coiling almost planispirally with a slightly angulate periphery, ca. 310 μ m wide and ca. 250 μ m high, not inclined with respect to teleoconch (Figure 5A, B); outer lip of protoconch with faint and fine growth lines, remainder of protoconch smooth except for 15 to 25 indistinct longitudi-

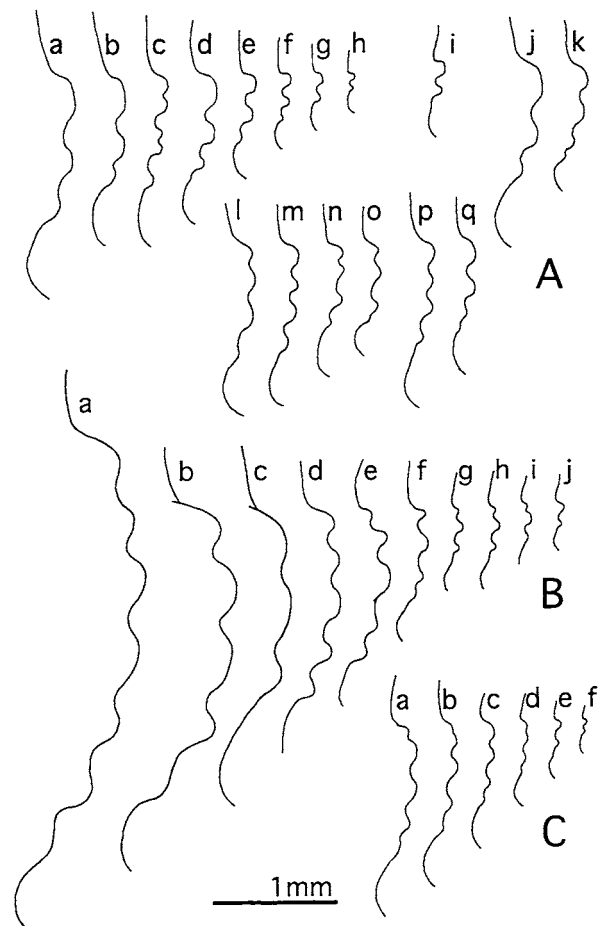


Figure 17. Ontogenetic changes in the apertural teeth of individuals of three *Pisulina* species from different geographic regions, seen in oblique apertural view. **A.** *Pisulina biplicata* Thiele, a–h: from Okinawa, i: Indian Ocean (Holotype), j: the Philippines, k: Palau, l–o: Yap, p–q: Fiji. **B.** *Pisulina maxima* sp. nov., a: Saipan Island (Holotype), b: the Philippines, c–j: Palau. **C.** *Pisulina tenuis* sp. nov., a–f: Okinawa.

nal folds; protoconch aperture longitudinally straight and clearly demarcated from teleoconch; visible portion of protoconch 155 to 220 μ m in maximum dimension (ca. 170 μ m in holotype). Teleoconch of up to 3.3 whorls (2.2 in holotype); last whorl inflated and with a small, somewhat concave area below suture; exterior surface smooth and glossy, but weakly sculptured with faint growth lines and microscopic spiral ridges (ca. 1 μ m wide; Figure 2B), consisting of rows of minute granules. Aperture semilunar, small; outer lip prosocline, angled 40° to 50° to shell axis and beveled; inner lip heavily callused with 3 to 5 rather blunt and somewhat squarish teeth at margin (Figure 17A); inner line of inner lip callus convex on columellar area, and continues toward the basal lip with a shallow sinus.

Remarks.—The shell of *P. biplicata* is frequently found as beach drift in southern Japan, but live specimens have not been found. Several opercula most probably from *P. biplicata* have been found together with more than 1000

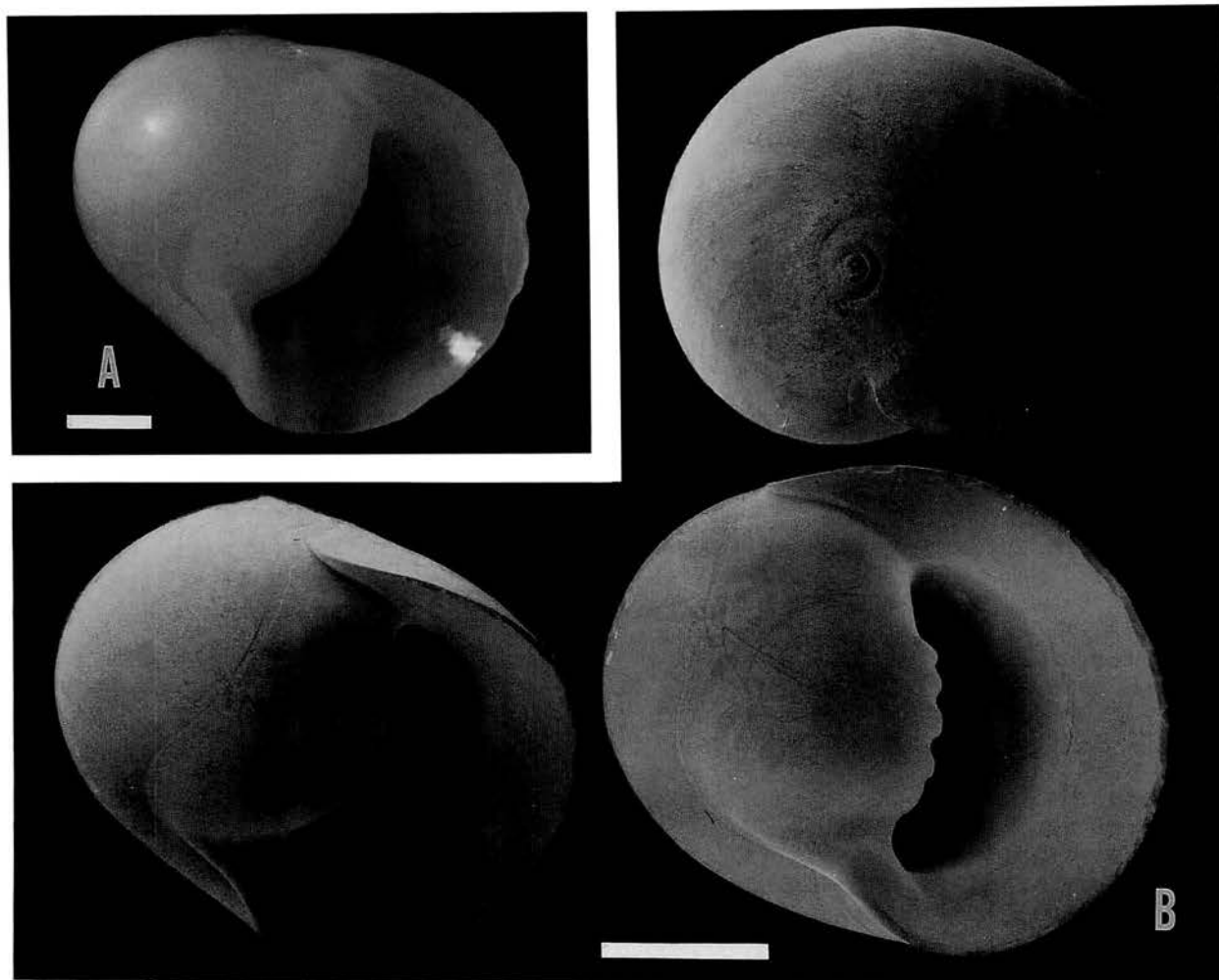


Figure 18. *Pisulina maxima* sp. nov. **A.** Holotype (NSMT-Mo71624) from Saipan. **B.** Paratype (NSMT-Mo71625) from Balicasag Island, Philippine Islands. Scale bars = 2 mm.

empty shells of this species in sediments from crevices north of Kohama Island in Okinawa Prefecture. The operculum of *P. biplicata* is almost identical to that of *P. adamsiana*.

Variation in shell characters is primarily manifested by the number and shape of teeth along the inner lip (Figure 17A). Specimens from Japan and the Philippines generally bear three squarish teeth, while those from Micronesian and southern Pacific islands commonly have more than three round teeth.

Japanese authors have long overlooked *P. biplicata* and misidentified it as *P. adamsiana* (Komatsu, 1986; Hinoide and Habe, 1991; Fukuda, 1993; Sasaki, 1998). Thiele (1925) established *P. biplicata* based on a single specimen and distinguished it from *P. adamsiana* by its supposed lower spire and the presence of two teeth on its inner lip. Unfortunately, these characters cannot be used to separate the two species, because the holotype of *P. biplicata* clearly is an immature specimen. The degree of spire elevation is highly dependent on growth stage, and mature *P. biplicata*

possess the highest spire in this genus. Also, the presence of only two teeth along the inner lip (Figures 16A; 17A-i) is attributed to the immature state of the holotype.

Examination of thousands of specimens from a number of localities clearly reveals that this species can easily be distinguished from *P. adamsiana* by the presence of a paucispiral protoconch, multiple teeth along the inner lip and a sinus in the inner line of the inner lip callus (Table 1). In addition, the shell surface of *P. biplicata* is covered with rows of microscopic granules, while that of *P. adamsiana* is covered with dense microscopic ridges (Figure 2A, B).

***Pisulina maxima* sp. nov.**

Figures 2C; 5C; 9; 17B; 18

Holotype.— NSMT-Mo71624, A huge cave near the "Grotto" diving site, on the northern side of Saipan Island, northern Mariana Islands (15°15.3'N, 145°49.5'N); 20–23.6 m depth.

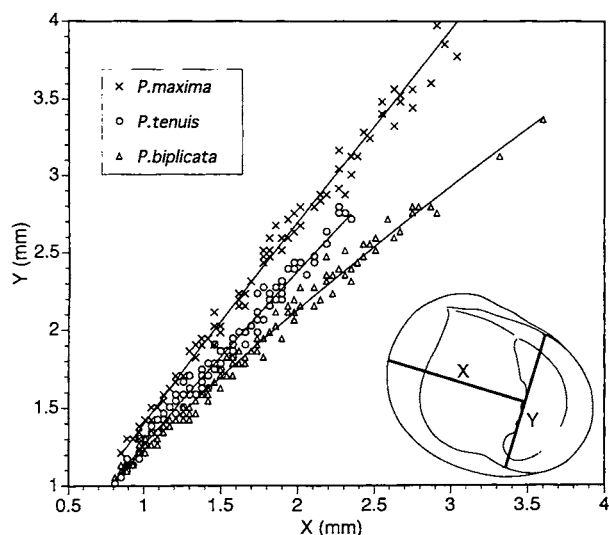


Figure 19. Relationship between the shape of the last whorl and the aperture in three *Pisulina* species: *Pisulina maxima* sp. nov. ($Y=1.668X^{0.945}$, $R^2=0.995$, $n=100$), *Pisulina tenuis* sp. nov. ($Y=1.650X^{0.914}$, $R^2=0.985$, $n=100$) and *Pisulina biplicata* Thiele ($Y=2.417X^{0.789}$, $R^2=0.989$, $n=100$). Specimens were measured in the following way under a microscope with a drawing attachment: X = apertural length from the abapertural margin of whorl to apertural teeth along the axis of the maximum dimension; Y = apertural height along an axis that is perpendicular to X and in contact with the apertural teeth. Shells used for measurements were selected arbitrarily to include all the ontogenetic stages greater than $Y = 1$ mm. Probabilities that the observed differences in the slopes of the growth lines arose by chance were calculated using a formula shown in Imbrie (1956). This figure shows that *P. biplicata* and *P. tenuis* are significantly different in having distinct slopes ($P < 0.01$); *P. maxima* and *P. tenuis* are meaningfully different ($0.01 < P < 0.05$). Nineteen specimens of *P. maxima* greater than 4 mm in the Y dimension are not plotted in this graph (the largest such specimen attains $Y = 7.53$ mm).

Paratypes.—JAPAN: Serakaki, Onna, Okinawa Island; 25 m depth, submarine cave; August 1998, 3 specimens, coll. H. Kinjo.—MALAYSIA: "Turtle Cavern", Sipadan Island, west Celebes Sea, Sabah ($5^{\circ}04.8'N$, $118^{\circ}36.5'E$); 9–17 m depth, totally dark inside; May 1997, 17 live individuals.—PHILIPPINES: "Marigondon Cave" diving site, Mactan Island, Cebu ($10^{\circ}15.8'N$, $123^{\circ}59.2'E$); 27 m depth, large submarine cave, totally dark inside; May 1994, 1 specimen.—Balicasag Island, Panglao, Bohol ($9^{\circ}32.7'N$, $123^{\circ}40.7'E$); 14–40 m depth, submarine caverns, gloomy inside; May 1994, 2 specimens (NSMT-Mo71625).—PALAU: "Siaes Tunnel" diving site, southwest of Siaes dropoff, ca. 6 km west-northwest of Aulong Island, Rock Islands ($7^{\circ}18.7'N$, $134^{\circ}13.6'E$); 24–53.5 m depth, huge submarine tunnel; April 1995, 65 specimens; December 1997, 148 specimens (30 specimens NSMT-Mo71626).—"Blue Hole" diving site, northwest of Ngemelis Island, Rock Islands ($7^{\circ}08.3'N$, $134^{\circ}13.3'E$); 36–38 m depth, submarine cave, totally dark inside; December 1997, 2 live individuals.—NORTHERN

MARIANAS: (the type locality); 12–30 m depth, huge cave, gloomy to totally dark inside; November 1997, 24 specimens (10 specimens NSMT-Mo71627); October 1999, 11 specimens.—near "Tinian Grotto" diving site, west of Tinian Island; 50–51 m depth, huge cave, gloomy to totally dark; November 1997, 3 specimens.—AUSTRALIA: "Thundercliff Cave" diving site, Christmas Island ($10^{\circ}28.4'S$, $105^{\circ}36.4'E$); 1.3–6 m depth, totally dark inside; November 1999, 4 specimens.

Distribution and age.—Southeast Asia (Figure 14). Recent.

Diagnosis.—Large *Pisulina* characterized by a subglobose to hemispherical and very thick shell, a paucispiral protoconch with an almost smooth surface, a large semicircular aperture and 3 to 7 teeth along inner lip; microscopic spiral ridges on shell surface are ca. $4 \mu\text{m}$ wide.

Description.—Shell medium in size, up to 13.7 mm wide and 12.1 mm high (10.9 mm wide and 9.8 mm high in holotype), very thick, somewhat swollen hemispherical in shape (Figure 18); spire very low and apex pointed. Protoconch paucispiral, a simple low dome-shape in apical view, glossy, smooth, without inclination to teleoconch; visible portion surrounded by teleoconch 180 to 275 μm in maximum dimension, ornamented by 15 to 25 indistinct longitudinal folds, with faint growth lines on outer lip (Figure 5C); protoconch aperture clearly demarcated from teleoconch by a sharp line. Teleoconch whorls less than 4 in number (3.8 in holotype), striated by microscopic growth lines and spiral ridges ca. $4 \mu\text{m}$ wide (Figure 2C), the last whorl coiling nearly planispirally. Aperture semicircular, largely open, prosocline with an angle of 30° to 35° to shell axis; outer lip thick, widely beveled and slightly dilated outward; inner lip covered with a moderately thick callus, convex adaxially at middle, with 3 to 7 dull teeth (Figure 17B); inner line of inner lip callus convex at columellar area and continues to basal lip with shallow concavity. Operculum with a concentric nucleus ca. 220 μm in maximum dimension (Figure 9C), and bears a long and spirally curved apophysis (Figure 9A, B).

Remarks.—This new species is similar in protoconch morphology to *P. biplicata*, but is primarily distinguished from the latter by its much larger shell size and less glossy teleoconch surface. In addition, the whorls of *P. maxima* expand more rapidly than in *P. biplicata*, so that the former species has a lower spire and a larger aperture than the latter species (Figure 19). This species further differs from *P. biplicata* in the number and shape of the inner lip teeth: *P. maxima* has up to seven rounded teeth, with the largest one located centrally, whereas *P. biplicata* has less than five squarish teeth, with the largest tooth located adapically. In addition, the third tooth ontogenetically appears above the first and second ones in the new species, while it appears below them in *P. biplicata* (Figure 17).

***Pisulina tenuis* sp. nov.**

Figures 2D; 5D, E; 17C; 20

Holotype.—NSMT-Mo71628, "Sabachi Cave," southeast of Yonaguni Island, Yaeyama Islands, Okinawa, Japan ($24^{\circ}26.1'N$, $122^{\circ}57.5'E$); 25–30 m depth, submarine cave,

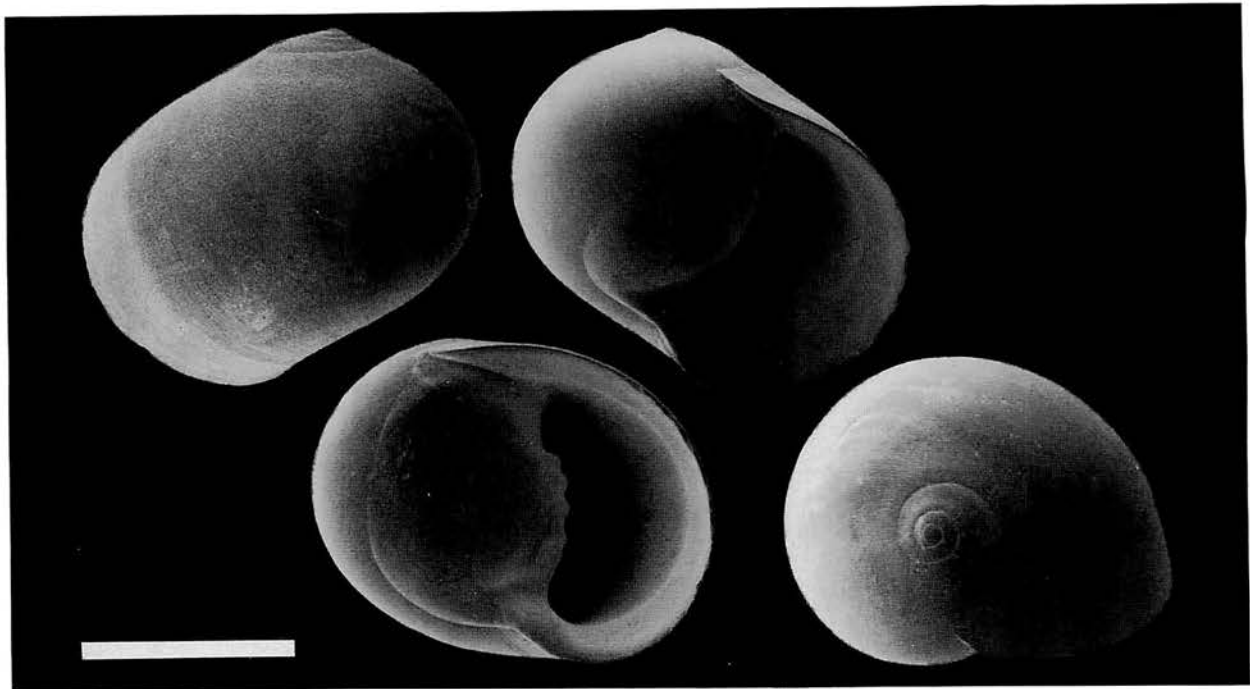


Figure 20. *Pisulina tenuis* sp. nov. Holotype (NSMT-Mo71628) from Yonaguni Island, Okinawa. Scale bar = 2 mm.

totally dark inside.

Paratypes.—More than 1000 specimens from the type locality; September 1994 (100 specimens registered; NSMT-Mo71629).

Distribution and age.—Known only from Yonaguni Island, Japan (Figure 14). Recent.

Diagnosis.—Small *Pisulina* characterized by a thin shell, subglobose to swollen hemispherical shape, a moderately large semicircular aperture, and 4 or 5 teeth along inner lip. Protoconch paucispiral, ovate and smooth. Teleoconch surface with spiral ridges ca. 4 μ m wide.

Description.—Shell small, 4.0 mm wide and 3.6 mm high in largest specimen (3.9 mm wide and 3.5 mm high in holotype), obliquely ovate to hemispherical in shape, and thin but solid. Spire low, with a pointed apex (Figure 20). Protoconch paucispiral, smooth except for 15 to 25 indistinct longitudinal folds near suture, glossy, ca. 330 μ m wide and ca. 270 μ m high, coils almost planispirally, and not inclined to teleoconch (Figure 5D, E); visible portion surrounded by teleoconch 210 to 300 μ m in maximum dimension (ca. 210 μ m in holotype); outer lip sculptured with indistinct growth lines and ridges (Figure 5D); protoconch aperture demarcated clearly from teleoconch and weakly sinuous in its middle part. Teleoconch coils up to 2.9 in number (2.8 in holotype), slightly concave below suture; exterior surface smooth except for faint growth lines and microscopic spiral ridges ca. 4 μ m wide (Figure 2D). Aperture semicircular in shape and widely open; outer lip prosocline, angled 35° to 40° from shell axis, weakly beveled and somewhat thickened on interior; inner lip moderately thick, bearing a convex

adaxial margin and 4 or 5 dull teeth of almost equal strength (Figure 17C); inner line of inner lip callus convex in columellar area and continues to basal lip with a shallow sinus.

Remarks.—*Pisulina tenuis* sp. nov. most closely resembles *P. maxima*, since both species share the same protoconch morphology, shell form and surface microsculpture. The two species are also similar in the number and shape of the inner lip teeth. However, *P. tenuis* clearly differs from *P. maxima* by its thinner shell and smaller shell size (see Table 1). A morphometric analysis shows that *P. tenuis* differs from *P. maxima* in having a smaller Y/X ratio (Figure 19).

Pisulina tenuis has not yet been found alive. Opercula thought to belong to this species were found among a vast number of empty shells at the type locality. The opercular features of *P. tenuis* are the same as seen in *P. adamsiana* and *P. maxima*.

Pisulina sp.

Figure 21

Material examined.—North Beach, Henderson Island, Pitcairn Group; middle or late Pleistocene sediments in an uplifted cave; 2 specimens, coll. R. C. Preece (Pitcairn Islands Scientific Expedition 1991–2), UMZC.

Distribution and age.—Known only from Henderson Island. Middle or late Pleistocene.

Description.—Shell small, thick, up to 4.2 mm wide and 3.8 mm high, hemispherical in outline (Figure 21A). Spire

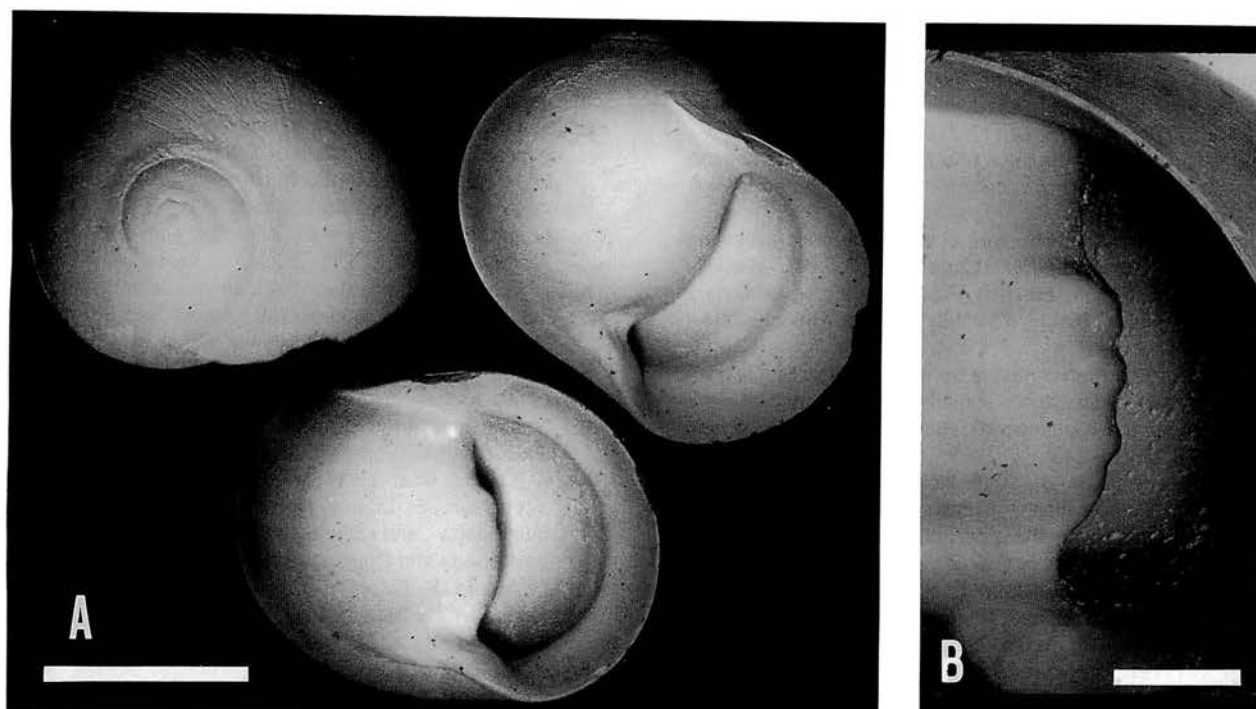


Figure 21. *Pisulina* sp. from Henderson Island, Pitcairn Group (UMZC). **A.** Scale bar = 2 mm. **B.** Oblique apertural view showing details of apertural teeth. Scale bar = 500 μ m.

relatively high, with a protruding apex. Protoconch poorly preserved, smooth, a simple dome-shape, 205 to 240 μ m in maximum dimension and sunken into teleoconch. Teleoconch of up to 3.1 volutions, concave below suture; exterior surface eroded to some extent, but seemingly smooth except for indistinct growth lines. Aperture semicircular and large; outer lip prosocline, angled about 35° to shell axis, beveled and slightly expanded outward; inner lip covered with a moderately thick callus, roundly convex with 4 dull teeth at margin (Figure 21B); inner line of inner lip callus merges into basal lip with a shallow sinus.

Remarks.—This unnamed Pleistocene species is similar to *P. tenuis* in shell size, the shape of its teleoconch whorls, and the number and shape of the teeth on the inner lip (Figure 21B). Moreover, both species have almost the same dimensions for the portion of the protoconch exposed above the teleoconch whorls. This fossil species seems to be distinct from *P. tenuis* by its thicker shell and higher spire, but it is left unnamed until better preserved material is available.

Several fossil specimens similar to this unnamed fossil species have been collected from early to middle Pleistocene sediments on Niue, Cook Islands, by G. Paulay. They differ slightly from *Pisulina* sp. by having a lower spire and fewer teeth on the inner lip, and by the absence of a concavity below the suture of the teleoconch whorls. However, the specimens from Niue cannot be compared in detail, owing to their poor state of preservation.

Acknowledgments

The materials in this paper were collected during the submarine cave expeditions in the tropical Pacific islands for the last 10 years directed by the second author. Special thanks are due to S. Ohashi and S. Kinjo who joined all the expeditions as members and dove many deep caves. Without doubt, our expeditions would have failed had it been without their self-sacrificing cooperation. Other members of the expedition include I. Hayami (Kanagawa University) and G. Paulay (University of Guam), to whom we are acknowledged. We thank the following persons who helped us in various ways: M. Cathrein (Christmas), K. Ekawa (Kagoshima), A. Fielding (Hawaii), R. Gibson (Vanuatu), S. Gori (Italy), B. Holthuis (Guam), H. Kinjo (Okinawa), H. Kubo (Okinawa), C. Meyer (Guam), K. Mochizuki (Palau), K. Ogura (Okinawa), H. Saito (NSMT), M. Severns (Hawaii), J. Starmer (Palau), M. Taniguchi (Okinawa) and Y. Yamazaki (Palau). ORSTOM (Noumea) and the University of the South Pacific gave facilities and logistic support for our expeditions in New Caledonia and Fiji, respectively. We also thank the following for the loan of materials: M. Glaubrecht (MNHB), I. Loch (AMS) and J. Thompson (USNM). This study was supported by grants to T. K. from the Ministry of Education, Science and Culture, Japan (nos. 06454003, 08041162, 11691196 and 11833018), the Fujiwara Natural History Foundation, and the Research Institute of Marine Invertebrates.

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A new potamolepid freshwater sponge (Demospongiae) from the Miocene Nakamura Formation, central Japan

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Abstract. The freshwater sponge *Oncosclera kaniensis* sp. nov. of the demospongian family Potamolepidae is described from the Early Miocene Nakamura Formation (Mizunami Group) in Gifu Prefecture, central Japan. This is the first fossil record of the Potamolepidae in the world and also is the first documentation of fossil sponges from the Nakamura Formation. Paleocology of *Oncosclera kaniensis* sp. nov. is briefly discussed.

Key words: freshwater sponge, Potamolepidae, *Oncosclera*, Early Miocene, Nakamura Formation

Introduction

A number of well preserved sponges assignable to a new species of the genus *Oncosclera* Volkmer-Ribeiro, 1970 of the family Potamolepidae (Demospongiae) were recovered from the Early Miocene Nakamura Formation, Mizunami Group in Gifu Prefecture, central Japan. This is the first fossil record of the genus *Oncosclera* as well as of the family Potamolepidae. The discovery dramatically extends the fossil record of the family Potamolepidae back to the Early Miocene. Recent species of potamolepid sponges are distributed in South America, Africa, and Asia, and have been considered as Gondwanian elements (Volkmer-Ribeiro and De Rosa-Barbosa, 1978). The discovery of a fossil potamolepid sponge from Japan is very important for future paleogeography and phylogenetic analysis. The purpose of this paper is to describe a new species and discuss its paleoecology.

Geologic setting

The fossil sponges were collected from tuffaceous sandstone exposed on a riverbed of the Kiso River, Dota area of the Minokamo basin, Kani City, Gifu Prefecture, central Japan (Figure 1). Distributed in this riverbed is the Mizunami Group, a stratotype of the Lower to Middle Miocene in Japan, that is composed of nonmarine sediments, while the group is composed of marine sediments in the neighboring Mizunami and Iwamura basins.

A recent detailed lithostratigraphical study of the Mizunami Group along the Kiso River in the Minokamo basin by Shikano (1995) has shown that the group can be divided into three formations in ascending orders: the Hachiya Formation, Nakamura Formation, and Hiramaki Formation.

The Nakamura Formation, from which the fossil sponges were recovered, is 130 m thick, of fluvial and lacustrine origin, and subdivided into the Lower Member, Middle Member, and Upper Member. The potamolepid sponges described here were recovered from a sandstone layer of the Upper Member, about 2 m below the contact with the Hiramaki Formation (Figure 2). The Upper Member is estimated to be 30 m thick and consists of tuffaceous mudstone, sandstone, conglomerate, and lignite. The basal layer of the Upper Member consists of massive tuff, and was dated as 21.7 ± 1.5 Ma by the fission track method (Shikano, 1995).

The sponge-bearing sandstone layer is ill-sorted and contains much granular material and organic debris. Other fossils associated in this sandstone layer are diatoms, macroplants, molluscs, fishes, and mammals. The fossil molluscs in this sandstone include an undescribed viviparid gastropod, *Bellamyia* sp. and undetermined unionid bivalves such as *Anodonta* sp. and "*Unio*" sp. The fossil fishes were identified as *Cypris* sp., Cyprininae gen. et sp. indet., and Cultrinae gen. et sp. indet. (Yasuno, 1982; 1983). The fossil molluscs and cyprinids are all permanent freshwater dwellers. The fossil mammals from the sandstone layer are *Plesiosorex* sp., *Amphilagus* sp., *Youngofiber sinensis*, *Anchitheriomys* sp., *Pseudotheridomys* sp., and *Apeomys* (?) sp. (Tomida and Setoguchi, 1994; Tomida and Goda, 1995; Tomida *et al.*, 1995).

Systematic description

Class Demospongiae Sollas, 1885
Order Hadromerida Topsent, 1894
Family Potamolepidae Brien, 1967
Genus *Oncosclera* Volkmer-Ribeiro, 1970

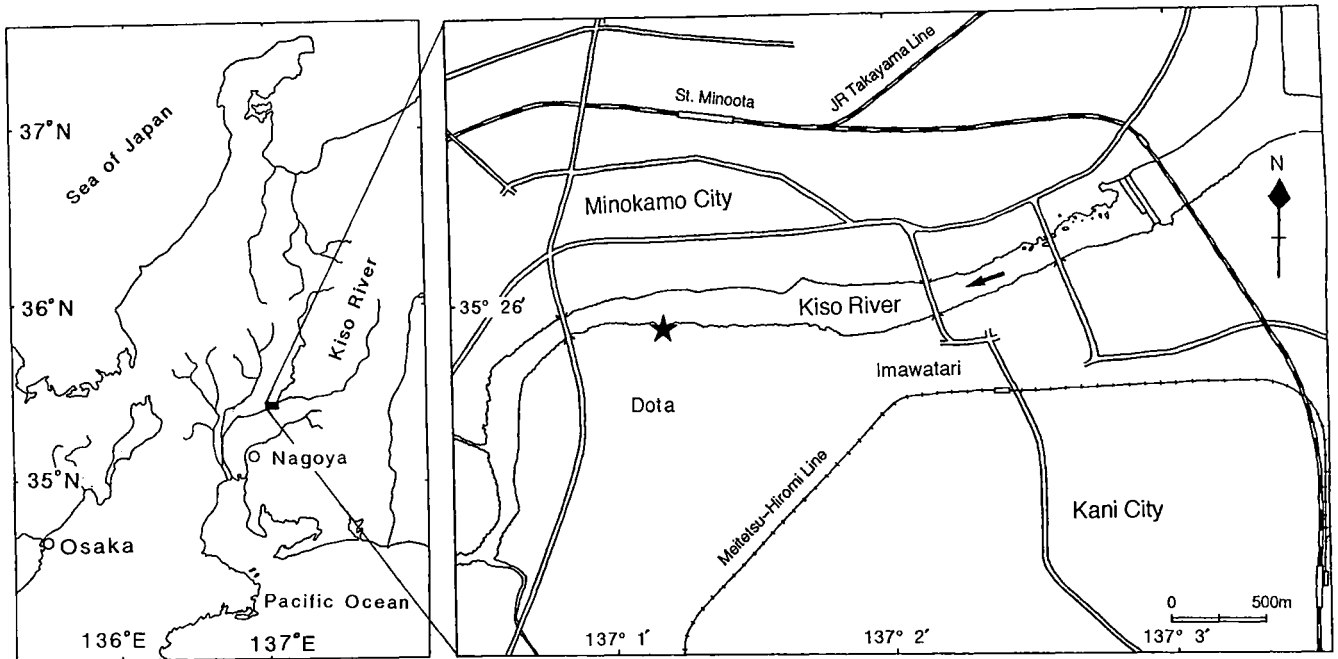


Figure 1. Map showing the sponge locality of the Nakamura Formation, Dota, Kani City.

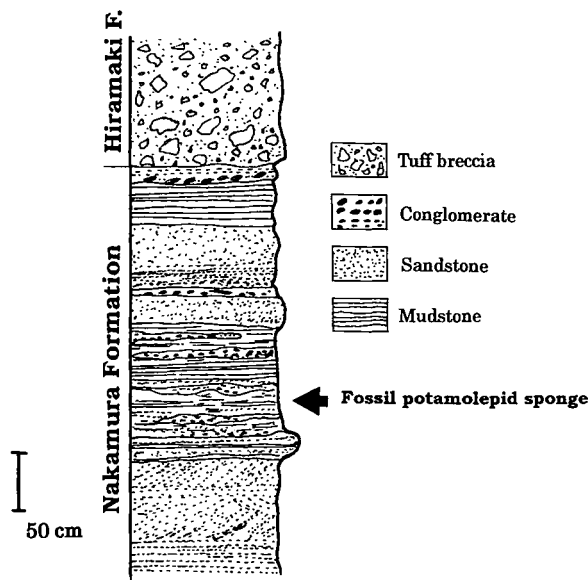


Figure 2. Columnar section showing the sponge-bearing horizon in the Nakamura Formation.

Type species: Spongilla jewelli Volkmer, by original designation.

Diagnosis.—Megascleres slightly curved, stout, occasionally microspined, amphioxea to amphistrongyla. Microscleres absent. Gemmoscleres short, stout, feebly curved, extremely variable, amphistrongyla or amphioxea, swollen at central portion, usually spined; spines more numerous at both ends.

Discussion.—Brien (1967) proposed the new family Potamolepidae for the Ethiopian genera *Potamolepis* and *Potamophloios*. The family consists of six genera: *Oncosclera*, *Uruguayia*, *Sterrastrolepis*, *Potamolepis*, *Potamophloios*, and *Stratospongilla*, and the family is considered to have been derived from a certain marine group of the order Hadromerida (Volkmer-Ribeiro and De Rosa-Barbosa, 1978). Of the six genera above, *Oncosclera*, *Uruguayia* and *Sterrastrolepis* from South America have been thought in part to be relicts of the Gondwanian fauna (Volkmer-Ribeiro, 1981).

Oncosclera was originally introduced as a genus of the family Spongillidae by Volkmer-Ribeiro (1970), which included two living species in Brazil, *O. jewelli* (Volkmer, 1963) and *O. navicella* (Carter, 1881). This genus is very close to the genus *Stratospongilla*, but differs from the latter in the absence of microscleres. The genus *Oncosclera* from South America consists of ten species: *Oncosclera petricola* (Bonetto and Ezcurra, 1967), *O. stolonifera* (Bonetto and Ezcurra, 1967), *O. schubarti* (Bonetto and Ezcurra, 1967), *O. ponsi* (Bonetto and Ezcurra, 1968), *O. tonollii* (Bonetto and Ezcurra, 1968), *O. atrata* (Bonetto and Ezcurra, 1970), *O. spinifera* (Bonetto and Ezcurra, 1973), and *O. intermedia* (Bonetto and Ezcurra, 1973) by Volkmer-Ribeiro (1981), who suggested that the number will be reduced by synonymies in future studies. *Spongilla* (*Stratospongilla*) *diahoti* Rützler, 1968 from northern New Caledonia was transferred to the genus *Oncosclera* by Volkmer-Ribeiro and Rützler (1997). According to Volkmer-Ribeiro (1970, 1981), *Spongilla rousseletti* Kirkpatrick, 1906 and *S. (Stratospongilla) shulbotzi* Weltner, 1913 from central Africa, *S. (Stratospongilla) gilsoni* Topsent, 1912 from the Fiji Islands, and *S. clementis* Annandale, 1909 from the Philippines belong to the genus *Oncosclera*.

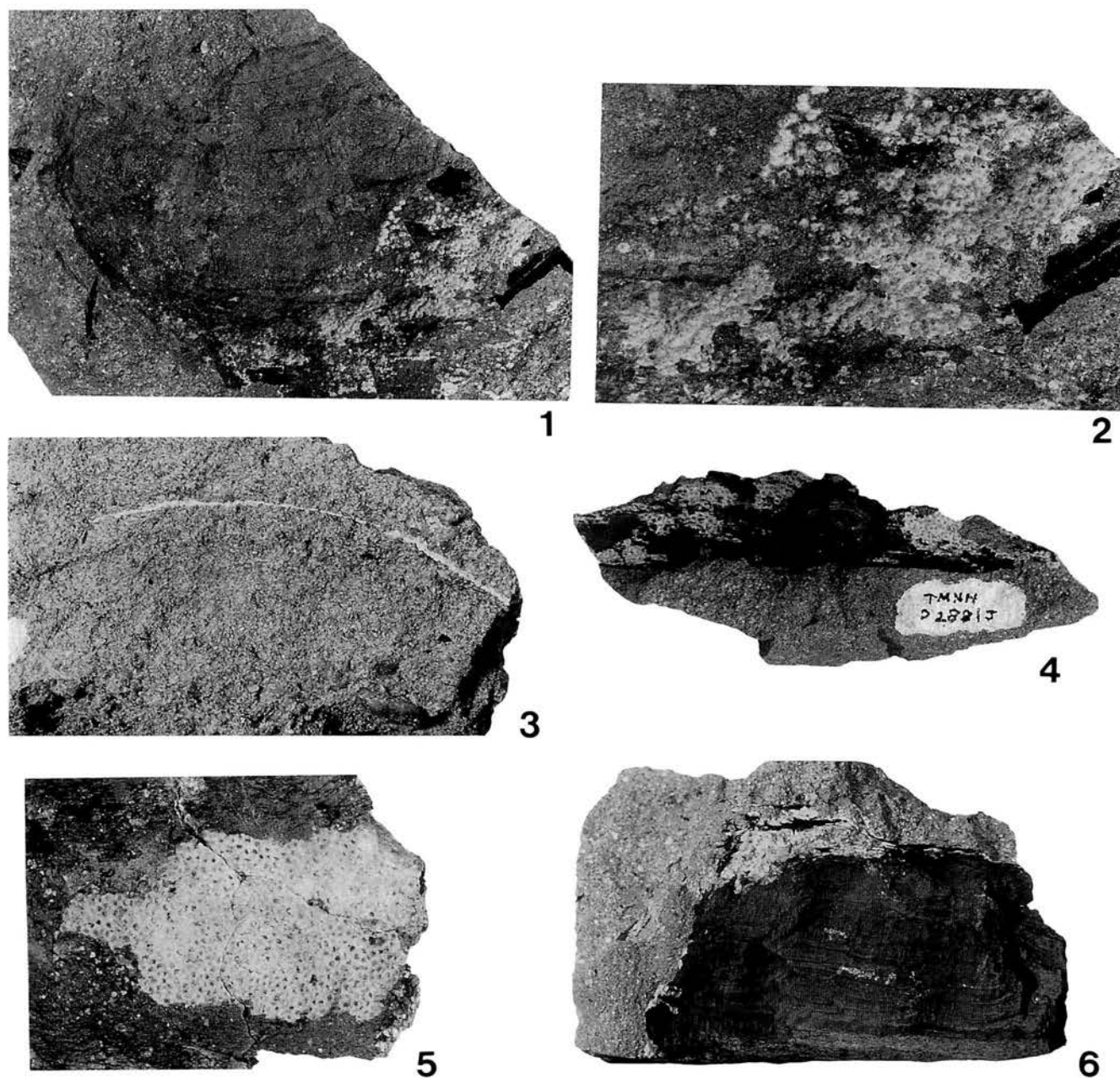


Figure 3. *Oncosclera kaniensis* sp. nov. 1. Sponge bodies encrust the postero-ventral area of the left valve of *Anodonta* sp., TMNH-02882 (paratype), $\times 1$. 2. Enlargement of the sponge bodies of TMNH-02882, $\times 2.1$. 3. Sponge bodies encrust the surface of *Anodonta* sp., vertical section, TMNH-02889a (paratype), $\times 1.2$. 4. Sponge bodies encrust the surface of a cortex fragment (black color), TMNH-02881j (holotype), $\times 1.2$. 5. Attached surface of sponge bodies, TMNH-02886 (paratype), showing the outline of the gemmules represented by ring spots, $\times 2.0$. 6. Sponge bodies encrust the surface of a wood fragment, TMNH-02887, $\times 1.2$.

***Oncosclera kaniensis* sp. nov.**

Figures 3-5

Type locality.—Riverbed on the Kiso River, Dota, Kani City, Gifu Prefecture, Japan (Figure 1).

Etymology.—The species name is after Kani City, the mu-

nicipality of the type locality.

Material studied.—Twenty-two specimens. Holotype: TMNH-02881 a-m, on 13 isolated blocks. Paratypes: TMNH-02885, 2883a, b, 02882, 02884 a, b, 02886. All deposited in the Toyohashi Museum of Natural History.

Diagnosis.—A species of *Oncosclera* characterized by

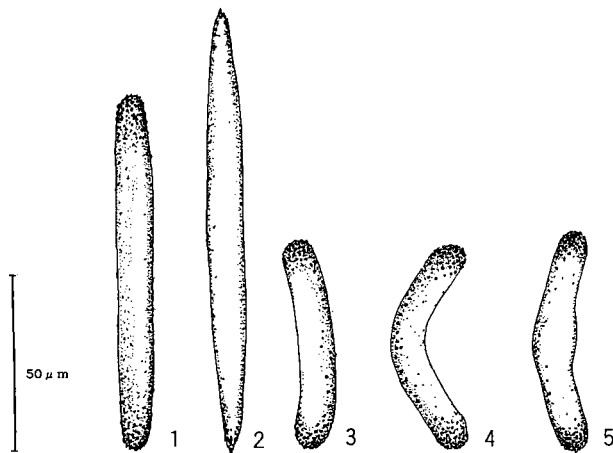


Figure 4. Spicular components of *Oncosclera kaniensis* sp. nov. 1. Amphistrongylous megasclere. 2. Amphioxeous megasclere. 3-5. Three forms of gemmoscleres. Scale bar=50 μ m.

domination of amphistrongylous megascleres, small amount of amphioxeous megascleres, amphistrongylous gemmoscleres, and dense covering of spines at both ends.

Description.—Sponge encrusting shell surfaces of bivalve and wood fragments. Sponge surface even and generally less than 1 mm in thickness. Skeletal components consisting of megascleres and gemmoscleres. Gemmules with round spots, firmly adhering to basal part of sponge body, about 500 μ m in diameter, but compressed subspherically. Megascleres moderately small, almost straight, solid, amphistrongyla to amphioxea, covered with distinct spines at both ends, 100 to 179 μ m in length and 7 to 15 μ m in thickness. Majority of megascleres stout and cylindrical amphistrongyla (Figure 4.1), occasionally with a few intermixed true amphioxea (Figure 4.2). Microscleres absent. Gemmoscleres stout, variably curved, inflated at middle (Figure 4.3-4.5); amphistrongyla densely covered with distinct spines that are numerous at both ends; some of spines polyfurcate, and inner curved area smooth, 23 to 100 μ m in length, 4 to 7 μ m in thickness.

Comparison.—The present new species is assigned to the genus *Oncosclera* in its shape and surface ornamentation of megasclere and gemmosclere. The new species is similar to the following Recent species from Argentina: *Oncosclera ponsi* (Bonetto and Ezcurra, 1968), *Oncosclera atrata* (Bonetto and Ezcurra, 1970), and *Oncosclera tonollii* (Bonetto and Ezcurra, 1968). Of the three species *O. kaniensis* sp. nov. is most similar to *Oncosclera ponsi* in spicular components, but it differs in having spinose amphioxeous megascleres. The present new species differs from *Oncosclera atrata* from the Parana River, Argentina in having amphistrongyla densely covered with distinct spines at both ends of the gemmoscleres. It also differs from *Oncosclera tonollii* from the Uruguay River, Argentina (Bonetto and Ezcurra, 1967) in having a less spinose surface of gemmoscleres and megascleres. This new species has gemmoscleres similar to the Recent species *Oncosclera*

jewelli (Volkmer, 1963) known only from the Tainhas River of Brazil (Volkmer-Ribeiro, 1970) and *O. schubarti* (Bonetto and Ezcurra, 1967) from the Uruguay River, Argentina, but differs distinctly from the latter species in its spinose amphistrongylous and amphioxeous megascleres.

Paleoecology.—Potamolepids commonly have highly silicified skeletons and lack spongin fibers. Many species of the genus *Oncosclera* encrust stable bottom surfaces in streams. *Oncosclera atrata* inhabits a curved bank of a tributary of the Parana River in the Misiones Province, Argentina, where it encrusts surfaces of partly submerged rocks (Bonetto and Ezcurra, 1970). *Oncosclera ponsi* and *O. tonollii* encrust rocky bottoms in rapid and turbulent waters in the Uruguay River (Bonetto and Ezcurra, 1968). Both species grow in the upper and lower surfaces of the rocks, and the sponges encrusting the lower surfaces are disposed to grow exuberantly. *Oncosclera jewelli* in the Tainhas River of Brazil also encrusts exclusively stable bottom surfaces in fast streams close to rapids and/or falls. *Oncosclera navicella* in the Amazon River of Brazil and Iguazu Fall of Argentina, on the other hand, encrusts ligaments and valves of the living freshwater bivalve *Anodontites trapesialis forbesianus* and *Paxyodon symmatophorus* (Volkmer-Ribeiro, 1970; Tavares and Volkmer-Ribeiro, 1997).

Oncosclera kaniensis sp. nov. is represented entirely by fossilized sponge bodies and encrusts two types of substrates: shell surface of the unionid bivalve *Anodonta* sp. (Figure 3.1-3.3) and surface of wood fragments (Figure 3.4-3.6). The sponge bodies on the unionid bivalve encrust the ventral and posterior parts of almost horizontally embedded articulated valves that are preserved as composite moulds (Figure 6.1). They also encrust the outer surfaces of isolated valves that are diagenetically compacted and embedded with the convex side up (Figure 6.2). The sponge bodies also encrust strongly compacted woods almost entirely (Figure 6.3) and encrust partly the wood fragments that remain in possession of annual rings (Figure 6.4). The shells and wood fragments may have provided hard substrates for colonization of the fossil sponges in the soft bottom environment. The gemmules of *O. kaniensis* sp. nov. can be seen by naked eye as ring spots. The gemmules of the fossils are located at the basal portion of the sponge as in *O. jewelli* and *O. navicella* (Figure 3.5). These facts strongly suggest that *O. kaniensis* sp. nov. dwelled in a river like the Recent *Oncosclera* species and had a habitat preference to the upper and lower surfaces of hard substrates (Figure 6.5-6.8). The unusual preservation of the megascleres and gemmoscleres of *O. kaniensis* sp. nov. may have resulted from its comparatively stout skeleton, strong attachment to the substrates and rapid burial after death.

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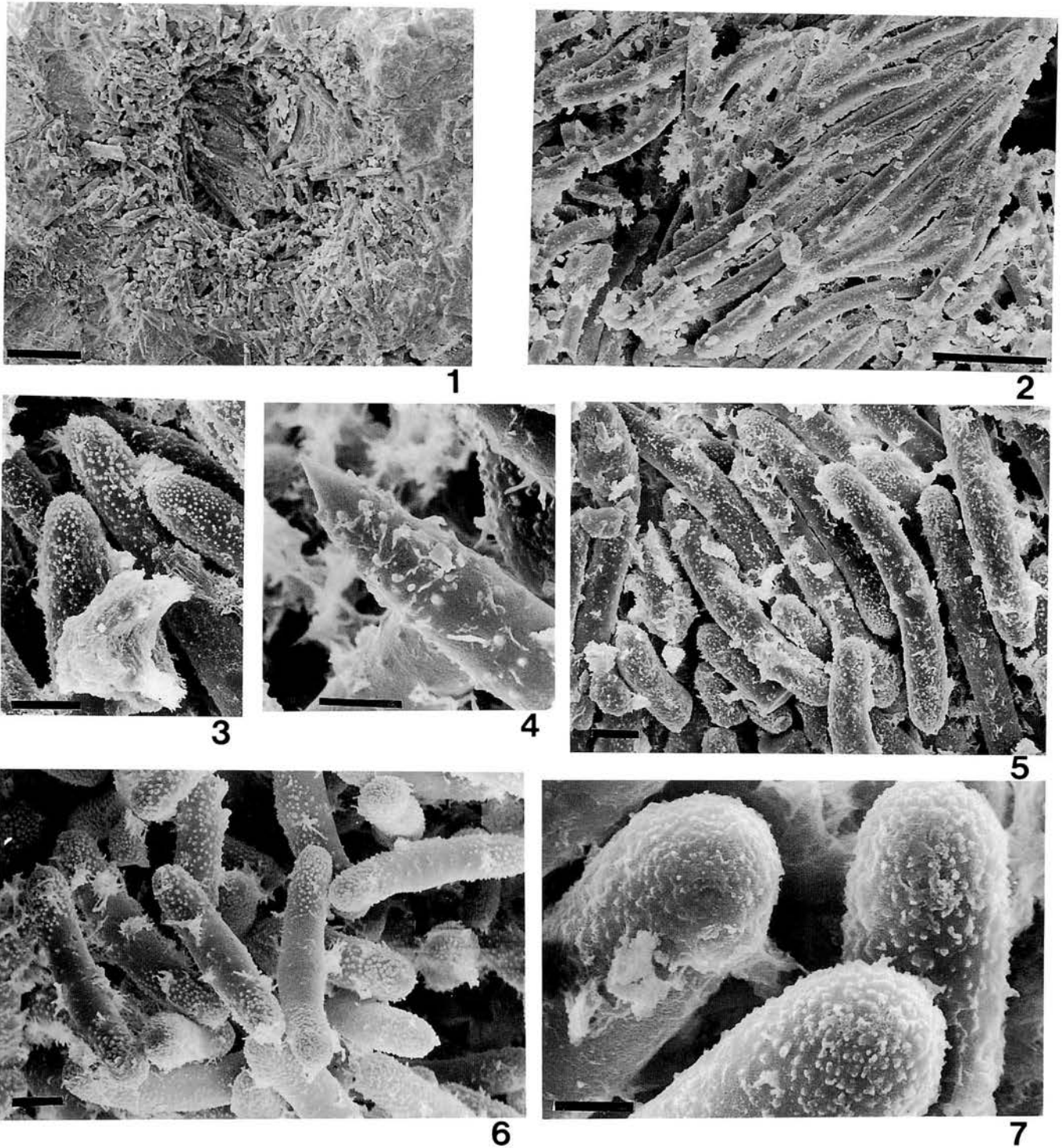


Figure 5. SEM micrographs of *Oncosclera kaniensis* sp. nov. 1. Gemmule, vertical section, scale bar=100 μm. 2. Amphistrongyloous megascleres, scale bar=50 μm. 3. End parts of amphistrongyloous megascleres, scale bar=10 μm. 4. End parts of amphioxeous megascleres, scale bar=5 μm. 5. Gemmoscleres, scale bar=10 μm. 6. Gemmoscleres, scale bar=10 μm. 7. End parts of gemmoscleres. scale bar=5 μm.

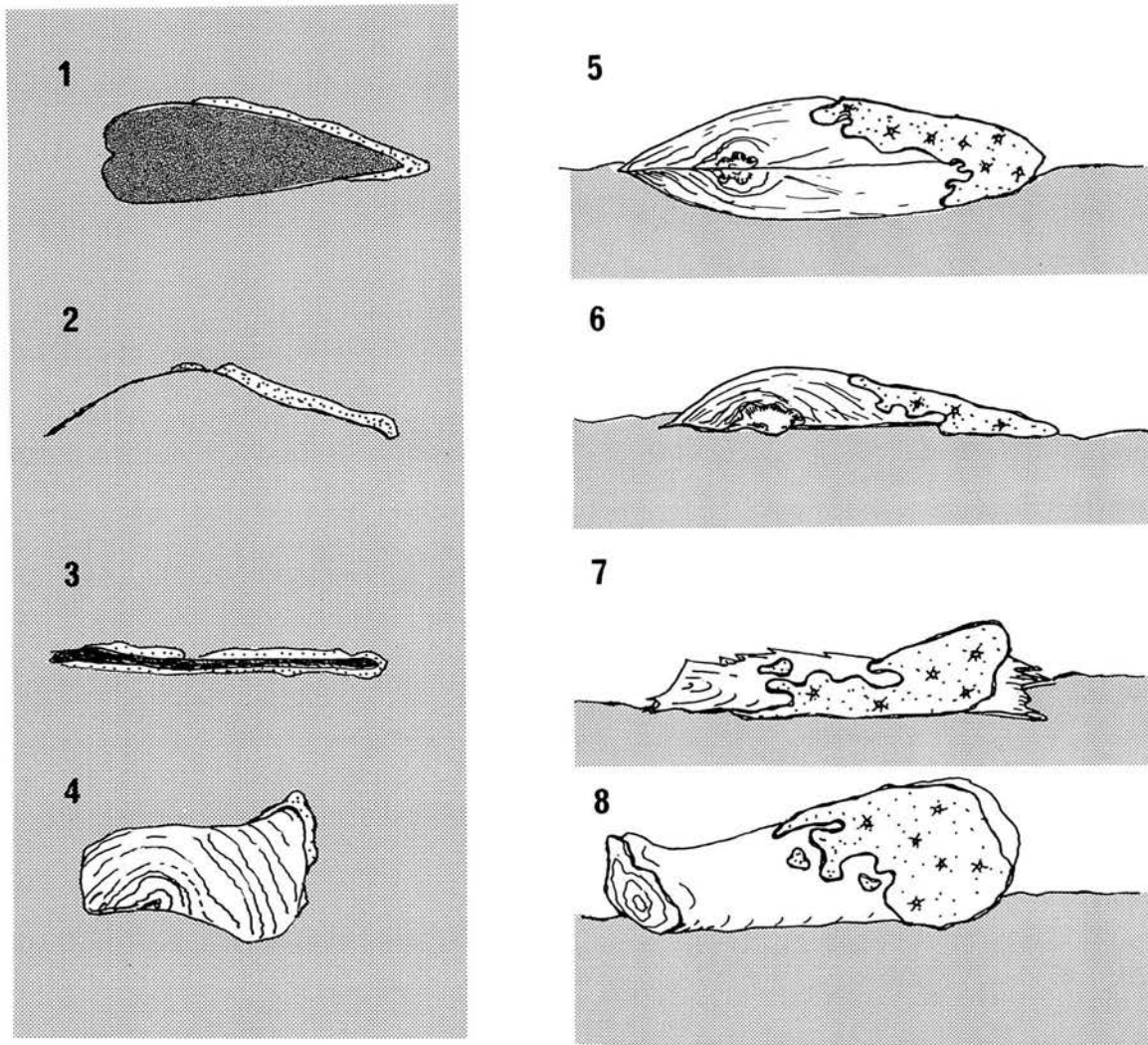


Figure 6. Mode of occurrences of *Oncosclera kaniensis* sp. nov. 1-4. Four types of encrustation. 1. Sponge bodies encrust an articulated valve of the unionid bivalve *Anodonta* sp. The bivalve is embedded with its commissure plane almost horizontal and is preserved as a composite mould. 2. Sponge bodies encrust the outer surface of an isolated valve of the unionid bivalve *Anodonta* sp. The valve is compacted diagenetically. 3. Sponge bodies encrust a strongly compacted wood fragment almost entirely. 4. Sponge bodies encrust a wood fragment that retains its annual rings. 5-8. Reconstruction of the four types of encrustation for 1 to 4, respectively.

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Additions to Cretaceous decapod crustaceans from Hokkaido, Japan—Part 1. Nephropidae, Micheleidae and Galatheidae

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Abstract. Four new species of decapod crustaceans are described from the Upper Cretaceous Upper Yezo Group in Hokkaido, Japan. The monotypic genus *Paki* (Thalassinidea, Micheleidae) is erected with *P. rurkonsimpu* sp. nov. *Hoploparia kamuy* sp. nov. (Astacidea, Nephropidae) represents the first record of the genus *Hoploparia* from the Turonian-Santonian of Japan. *Luisogalthea* gen. nov. (Anomala, Galatheidae), erected with the type species *L. tomitai* sp. nov., contains two North American Cretaceous species, *Galathea cretacea* Stenzel and *Eomunidopsis cobbani* Bishop. *Eomunidopsis kojimai* sp. nov. (Anomala, Galatheidae) represents the first record of the genus from the North Pacific realm.

Key words: Crustacea, Decapoda, Hokkaido, Japan, Upper Cretaceous, Upper Yezo Group

Introduction

The Upper Cretaceous decapod Crustacea from Hokkaido comprises nine species, *Linuparus japonicus* Nagao, 1931 (Palinura, Palinuridae), *Callianassa ezoensis* Nagao, 1941 (Thalassinidea, Callianassidae), and seven brachyurans (Collins, Kanie and Karasawa, 1993). In the present paper we describe four additional new species, one astacidean, one thalassinidean and two anomalans, from the Upper Yezo Group of Hokkaido.

The described specimens are deposited in the Mikasa City Museum (MCM) and the Mizunami Fossil Museum (MFM).

Systematic paleontology

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

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

Hoploparia kamuy sp. nov.

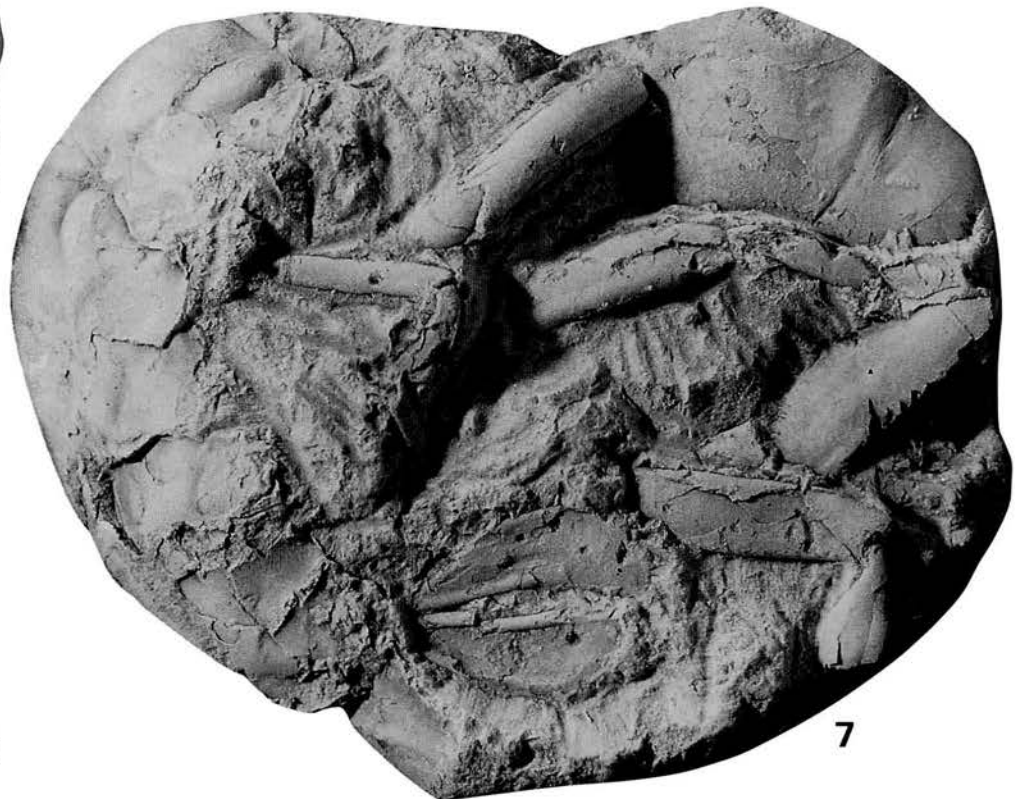
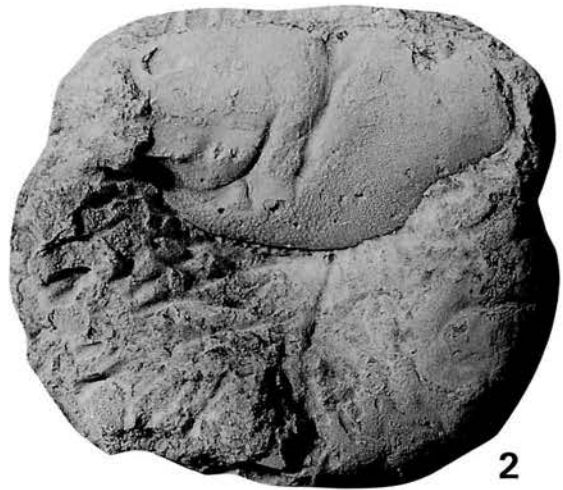
Figure 1.1, 1.2, 1.5, 1.6

Diagnosis.—Moderate-sized *Hoploparia*. Carapace with well developed grooves on anterior half. Antennal region bearing antennal ridge and one postantennal spine.

Abdominal somites simple without tubercles and spines.

Description.—*Hoploparia* with moderate-sized body. Carapace laterally compressed. Rostrum and posterior part of carapace lacking. Surface finely granulated. Orbit small, rounded, bordered by narrow, rounded ridge. Postcervical groove well defined, deep, broad, obliquely extending ventrally, becoming shallower at junction with hepatic groove. Branchiocardiac groove weak. Intercervical groove shallow, extending anteroventrally to, but not joining cervical groove. Second intercervical groove broad, shallow, extending to cervical groove. Hepatic groove shallow, curving to join antennal and cervical grooves. Cervical groove well defined, deep, slightly arcuate, parallel to postcervical groove, extending ventrally to join antennal groove. Antennal groove weakly arcuate, well defined over prominence omega. Prominence omega well defined, triangular. Gastro-orbital groove shallow, extending to near upper part of cervical groove. Antennal region with antennal ridge and with small, forwardly directed postantennal spine. Metorbital spine present, small. Supraorbital and postorbital spines wanting.

Terga of abdominal somites 1–5 smooth, but tergum of somite 6 finely pitted; tergum of somite 1 short; somite 2 largest of all terga. All pleura of somites finely punctuate. Pleuron of somite 1 reduced. Pleuron of somite 2 subrectangular; margins gently convex; anteroventral and posteroventral corners smoothly rounded; surface with marginal furrows joining transverse furrow on anterior part of tergum. Pleura of somites 3–5 triangular, transversely convex with sharp, posteroventral corners with shallow, broad marginal furrow along posterior margin. Pleuron of somite 6 reduced. Telson broken, but dorsal surface finely pitted.



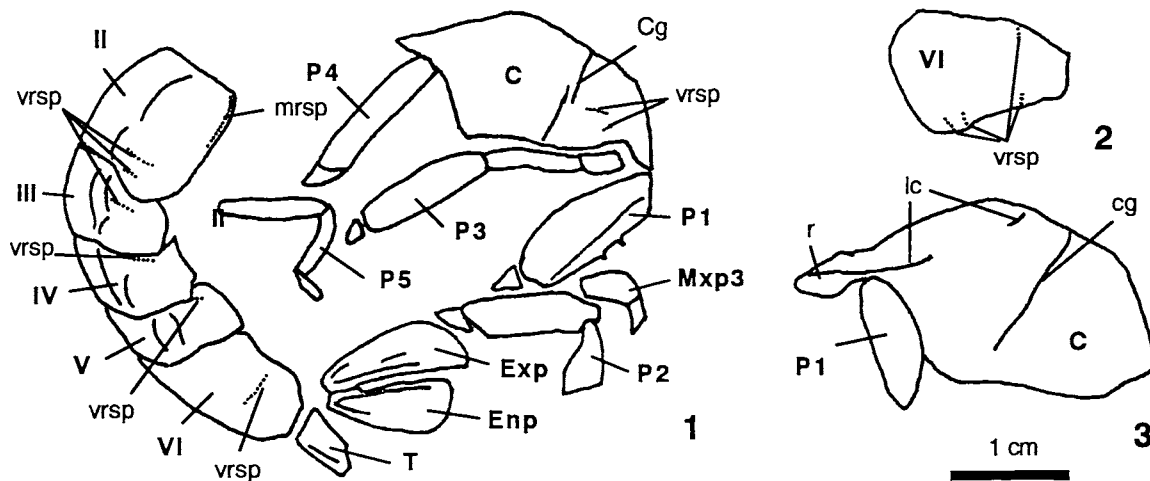


Figure 2. *Paki rurkonsimpu* gen. et sp. nov., MCM.A539 (holotype). 1. Carapace, abdominal somites, telson, uropod and pereopods, right lateral view. 2. Abdominal somite 6, dorsal view. 3. Carapace and pereopod 1, left lateral view. **Abbreviations:** C, carapace; cg, cervical groove; **Enp**, uropodal endopod; **Exp**, uropodal exopod; lc, lateral carina; mrsp, marginal row of setal pits; **Mxp3**, maxilliped 3; **P1**, pereopod 1; **P2**, pereopod 2; **P3**, pereopod 3; **P4**, pereopod 4; **P5**, pereopod 5; r, rostrum; **T**, telson; vrsp, vertical row of setal pits; **II**, abdominal somite 2; **III**, abdominal somite 3; **IV**, abdominal somite 4; **V**, abdominal somite 5; **VI**, abdominal somite 6.

Uropodal exopod triangular in outline, finely pitted dorsally, with weakly convex lateral margin and with diaeresis.

Chelae of pereopod 1 unknown. Some pereopods preserved, slender.

Discussion.—The species differs from *Hoploparia miyamotoi* Karasawa, 1998, the only known Japanese species from the Maastrichtian Izumi Group, by having the carapace with an antennal ridge and with well developed cervical and postcervical grooves. *H. kamuy* sp. nov. lacks well developed ridges between terga and pleura of abdominal somites, and marginal spines of pleura of abdominal somites 3–5.

Hoploparia kamuy sp. nov. is most similar to *Hoploparia pusilla* Secretan, 1964, from the Campanian of Madagascar, but differs in that the carapace bears a weak hepatic groove, a straight gastro-orbital groove, and a well defined prominence omega. *H. kamuy* sp. nov. resembles *Hoploparia arbei* Aguirre-Urreta, 1989 from the Puesto El Almo Formation (Turonian-Coniacian) of Argentina, but differs by absence of two tubercles on pleura of abdominal somites and of a granulated ridge on the branchial region.

Hoploparia kamuy represents the first record of the genus from the Turonian-Santonian of Japan.

Etymology.—The specific name is formed from 'kamuy', the name of a god in the Ainu language of Hokkaido.

Material examined.—MCM.A609 (holotype), Loc. YEZ-16, Oyubari, Yubari City; Upper Yezo Group (Lower Santonian;

Inoceramus amakusensis Zone by Ando and Kodama (1998)); collected by N. Nikkawa. MCM.A536 (paratype), Loc. YEZ-17, Ponbetsuzawa, Mikasa City; the basal part of the Upper Yezo Group (Upper Turonian; *Inoceramus teshioensis* Zone by Ando and Kodama (1998)); collected by S. Matsuda.

Infraorder Thalassinidea Latreille, 1831
Superfamily Axiioidea Huxley, 1879
Family Micheleidae Sakai, 1992
Genus *Paki* gen. nov.

Type species.—*Paki rurkonsimpu* sp. nov. by monotypy.

Diagnosis.—Large-sized micheleid. Rostrum of carapace with rounded tip; lateral carina well developed; cervical groove distinct; *linea thalassinica* absent; anterolateral region with two vertical rows of setal pits anterior to cervical groove. Terga and pleura of abdominal somites 2–5 bounded by weak ridge; pleuron of somite 2 with two vertical rows of setal pits posteriorly and with marginal row of setal pits anteriorly; pleura of somites 3–6 with single vertical row of setal pits anteriorly; pleuron of somite 6 with two vertical rows of setal pits anteriorly and single vertical row of setal pits posteriorly. Telson rectangular with two longitudinal carinae. Uropodal exopod and endopod with median dorsal ridge and with convex margins.

Figure 1. 1, 2, 5, 6. *Hoploparia kamuy* sp. nov. 1. MCM.A536 (paratype), carapace, abdominal somites, telson and uropod, $\times 2.0$, right lateral view. 2. MCM.A609 (holotype), carapace and abdominal somites, $\times 2.0$, left lateral view. 5. MCM.A536 (paratype), abdominal somites and uropod, $\times 2.0$, left lateral view. 6. MCM.A609 (holotype), abdominal somites, $\times 2.0$, right lateral view. 3, 4, 7. *Paki rurkonsimpu* gen. et sp. nov. 3. MCM.A539 (holotype), carapace and eye stalks, $\times 3.0$, dorsal view. 4. MCM.A539 (holotype), carapace and left pereopod 1, $\times 3.0$, left lateral view. 7. MCM.A539 (holotype), carapace, abdominal somites, telson, uropod and pereopods, $\times 3.0$, right lateral view.

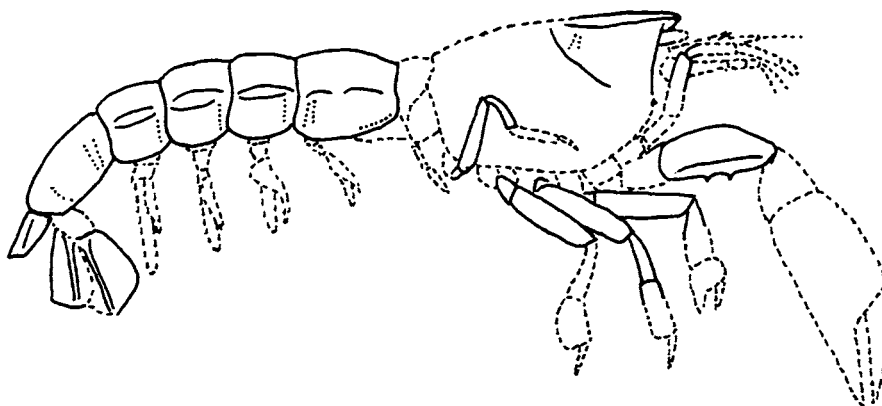


Figure 3. Reconstruction of *Paki rurkonsimpu* gen. et sp. nov.

Discussion.—The present new genus and species is assigned to the family Micheleidae Sakai, 1992 in the superfamily Axioidea Huxley, 1879 by lacking *linea thalassinica* on the carapace and by having rows of setal pits on the carapace and pleura of abdominal somites. According to Poore (1997) Micheleidae contains four Recent genera, *Michelea* Kensley and Heard, 1991, *Tethisa* Poore, 1994, *Meticonaxius* De Man, 1905 and *Marcusiarius* Rodrigues and de Carvalho, 1972. The pattern of rows of setal pits on the anterior part of the carapace and the characters of propodi of pereopods 1–5 are not observed, but in the character of the remaining carapace and abdominal somites, the genus is most similar to *Meticonaxius* and *Marcusiarius*. Two rows of pits anterior to the cervical groove on the carapace, two vertical rows of pits on the pleuron of abdominal somite 2, and rounded margins of the uropodal exopod and endopod readily distinguish the new genus from *Meticonaxius* and *Marcusiarius*. *Paki* differs from *Tethisa* by having rows of setal pits on abdominal somites 3–5 and having an ovate uropodal exopod. The new genus also differs from *Michelea* in that the carapace bears a lateral carina and rows of pits in front of the cervical groove.

In the pattern of rows of setal pits on the abdominal somites *Upogebia rhacheochir* Stenzel, 1945 from the Turonian Britton Formation of Texas belongs to the family Micheleidae and may be assigned to *Meticonaxius* or *Marcusiarius*. However, a well preserved carapace of Stenzel's species is needed to more precisely define the systematic position. Poore (1997: 364) described *Marcusiarius* sp. from the Albian of Gault, Folkestone of England. Therefore, these occurrences extend the geologic range for the family Micheleidae back to the Cretaceous.

Etymology.—The generic name is derived from the word, 'paki', meaning shrimp in the Ainu language of Hokkaido; masculine gender.

***Paki rurkonsimpu* sp. nov.**

Figures 1.3, 1.4, 1.7; 2.1–2.3; 3

Description.—Large micheleid. Carapace laterally compressed. Anterior half of carapace poorly preserved. Rostrum extended anteriorly into rounded tip; dorsal surface missing. Eye stalks visible in dorsal view. Lateral carina well developed. Cervical groove distinct. *Linea thalassinica* absent. Anterolateral region with two vertical rows of setal pits anterior to cervical groove.

Abdominal somites 2–6 preserved. Somite 2 about 1.5 times as long as 3. Terga and pleura of somites 2–5 bounded by weak ridges. Pleuron of somite 2 with two vertical rows of setal pits posteriorly and with marginal row of setal pits anteriorly; pleura of somites 3–6 with single vertical row of setal pits anteriorly; pleuron of somite 6 reduced with two vertical rows of setal pits anteriorly and single vertical row of setal pits posteriorly. Surfaces of pleura of somites 2–5 finely punctuate. Telson rectangular, slightly wider than long, about 1/3 times as long as somite 6; lateral margin divergent posteriorly; dorsal surface with two longitudinal carinae and with two pits anteriorly. Uropodal exopod, lacking posterior half, with median dorsal ridge, convex anterolateral margin and finely serrated lateral margin. Uropodal endopod lacking anterior half, bearing median dorsal ridge and convex posterior margin.

Merus of pereopod 1 bearing convex lateral margin with longitudinal ridge and with two spines on ventral margin. Carpus and merus of pereopod 2 flattened. Propodus of pereopod 3 flattened; merus about 1.5 times as long as carpus. Merus of pereopod 4 ovate in cross section. Pereopod 5 short; merus about 1.5 times as long as carpus. Merus and carpus of maxilliped 3, slender, flattened laterally.

Discussion.—The species is similar to *Upogebia rhacheochir*, but differs by possessing two vertical and one marginal rows of setal pits on the pleuron of the abdominal somite 2.

Etymology.—The specific name is derived from the word 'rurkonsimpu', meaning a fairy living in seas in the Ainu language of Hokkaido.

Material examined.—MCM.A539 (holotype), Loc. YEZ-18, Kotanbetsu, Tomamae-cho, Tomamae-gun; Upper Yezo Group (Lower Campanian; *Sphenoceramus orientalis* Zone);

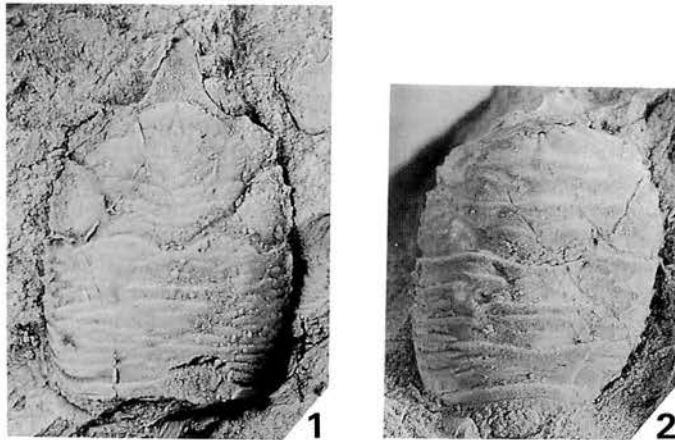


Figure 4. 1. *Luisogalatea tomitai* gen. et sp. nov., MFM247.010 (holotype), carapace, $\times 3.0$, dorsal view. 2. *Eomunidopsis kojimai* sp. nov., MFM247.011 (holotype), carapace, $\times 3.0$, dorsal view.

collected by H. Hayakawa.

Infraorder Anomala Boas, 1880
 Superfamily Galatheoidea Samouelle, 1819
 Family Galatheidae Samouelle, 1819
 Genus *Luisogalatea* gen. nov.

Type species.—*Luisogalatea tomitai* sp. nov.

Diagnosis.—Moderate-sized galatheid. Carapace excluding rostrum, longer than wide, dorsally longitudinally gently convex. Rostrum triangular, simple, lacking lateral spines, concave dorsally; lateral margins smooth but bearing a small lateral projection on distal fifth. Lateral margin gently convex with small spines. Dorsal surface rugose without spines. Cervical and postcervical grooves well defined.

Discussion.—There may be, in the general outline of the carapace, similarity between *Luisogalatea* and the Tithonian-Maastrichtian genus, *Eomunidopsis* Via Boada, 1981, but absence of a median dorsal ridge on the rostrum and presence of spines on the lateral margin of the carapace readily distinguish *Luisogalatea* from *Eomunidopsis*. In *Eomunidopsis* supplementary dorsal furrows of the carapace are more or less developed.

Stenzel (1945) described two new galatheids, *Galathea cretacea* and *Galathea? limonitica* from the Pawpaw Shale (Albian-Cenomanian) of Texas. Bishop (1985) described *Eomunidopsis cobbani* Bishop, 1985 from the Campanian Larimer Sandstone of Colorado and assigned both of Stenzel's species to *Eomunidopsis*. Fraaye and Collins (1996: 323) suggested that these American species, *G. cretacea* and *E. cobbani*, having the rostrum without a median ridge, possibly belonged to *Paragalathea* Patruilius, 1959. *G. cretacea* differs from members of *Galathea* Fabricius, 1793 by having a triangular rostrum with smooth lateral margins. *Paragalathea* is characterised by having a large, broadly triangular rostrum and by having the dorsal surface of the carapace more or less tuberculate and with smooth lateral margins that diverge anteriorly. Both *G.*

cretacea and *E. cobbani* are transferred from *Eomunidopsis* to the present genus in that their carapaces have the genus characteristics of an acutely triangular rostrum with smooth lateral margins and without a median rostral ridge, a rugose dorsal surface, and gently convex lateral margins bearing spines. Only *Galathea? limonitica* belongs to the genus *Eomunidopsis* by exhibiting well defined carapace furrows.

Etymology.—The generic name is dedicated to the late Spanish paleocarcinologist, Dr. Luis Via Boada; feminine gender.

Species included.—*Luisogalatea tomitai* sp. nov., *Luisogalatea cobbani* (Bishop, 1985) comb. nov. from the Campanian-Maastrichtian of U.S.A., *Luisogalatea cretacea* (Stenzel, 1985) comb. nov. from the Cenomanian of U.S.A.

***Luisogalatea tomitai* sp. nov.**

Figure 4.1

Diagnosis.—Carapace excluding rostrum, subquadrate, dorsally longitudinally gently convex, width about 3/4 the length. Rostrum triangular, smooth dorsally with median depression; lateral margins bearing a small lateral projection on distal fifth. Orbital margin concave. Outer orbital angle weakly produced. Anterolateral angle with small spine. Lateral margin with 6 small spines. Orbitofrontal region depressed. Gastric, cardiac and branchial regions with transverse ridges and without spines. Cervical and epibranchial grooves well defined.

Description.—Carapace excluding rostrum, subquadrate in outline, dorsally longitudinally gently convex, width about 3/4 the length, greatest width about midlength. Rostrum triangular, gently downturned, about 1/4 as long as carapace width at the base, about 1/4 times as long as carapace length; dorsal surface smooth, with median depression; lateral margins smooth but bearing a small lateral projection on distal fifth. Orbital margin concave. Outer orbital angle weakly produced. Anterolateral angle with small spine. Lateral margin gently convex, bearing 6 small, forwardly di-

rected spines; 2 between cervical and epibranchial notches, and 4 posterior to epibranchial notch.

Orbitofrontal region depressed. Gastric region inflated; gently arched, raised edge between orbitofrontal and gastric regions; epigastric region ornamented with interrupted, transverse ridges, lacking spines, with shallow, median depression; proto- and mesogastric regions with 6 broadly rounded V-shaped ridges. Hepatic regions flattened. Cervical groove well defined, broad, deep. Cardiac region weakly marked, gently convex with 8 transverse ridges. Epibranchial regions inflated, separated from mesobranchial regions by deep postcervical grooves, ornamented with weak, transverse ridges. Other branchial regions densely decorated with interrupted transverse ridges.

Discussion.—*Luisogalthea tomitai* sp. nov. resembles *L. cretacea* (Stenzel) from the Pawpaw Shale (upper Albian) of Texas, but differs in having the rostrum with a smooth dorsal surface, the outer orbital angle with a weak projection, and the gastric, cardiac and branchial regions with fine ridges.

Etymology.—From A. Tomita who collected the type specimen.

Material examined.—MFM247.010 (holotype), Loc. YEZ-19, Nakafutamatagawa, Haboro-cho, Tomamae-gun; Upper Yezo Group (Santonian; *Inoceramus amakusensis* Zone by Ueda *et al.* (1961)).

Genus *Eomunidopsis* Via Boada, 1981

Type species.—*Galathea navarrensis* Van Straelen, 1940 by original designation.

Diagnosis.—Céphalothrax allongé, portant des crêtes transversales saillantes. Régions délimitées par des sillons bien visibles. Rostre caractérisé par sa pointe tridentée, dépourvu de dentelure sur ses bords latéraux et orné d'une carène médiane (from Via Boada, 1982).

Eomunidopsis kojimai sp. nov.

Figure 4.2

Diagnosis.—Carapace excluding rostrum, subquadrate, slightly longer than wide, dorsal surface moderately convex longitudinally. Orbital margin slightly concave. Outer orbital angle not produced. Anterolateral angle with small spine. Lateral margin gently convex with 8 small spines. Gastric, cardiac, hepatic and branchial regions ornamented with transverse and/or oblique ridges. Cervical and postcervical grooves well defined.

Description.—Carapace excluding rostrum, subquadrate in outline, about 4/5 times as wide as long. Rostrum not preserved about 1/4 as long as carapace width at the base. Orbital margin slightly concave. Outer orbital angle not produced. Anterolateral angle with very small spine. Lateral margin gently convex, armed with 8 small, forwardly directed spines; 1 anterior to cervical notch, 4 between cervical and epibranchial notches, 3 behind epibranchial notch.

Dorsal surface moderately convex longitudinally. Orbital regions flattened. Gastric region inflated; epigastric region vaulted, broadly triangular with oblique anterior ridge, interrupted, transverse ridge and median ridge behind it; proto- and mesogastric regions with 2 transverse ridges, anterior

one extending to hepatic region, gently curved ridge behind anterior one; mesogastric region with 3 gently curved ridges behind posterior transverse ridge, anterior and posterior ones shorter than middle; protogastric region with a pair of oblique ridges behind anterior transverse ridge. Hepatic regions ornamented with short, oblique ridges anteriorly. Cervical groove deep, broad. Cardiac region poorly defined with 3 transverse ridges diminishing in length posteriorly. Epibranchial region with 5 irregular, oblique ridges. Postcervical groove distinct. Other branchial regions with interrupted transverse ridges.

Discussion.—*Eomunidopsis kojimai* sp. nov. has close affinity with *Eomunidopsis navarrensis* (Van Straelen, 1940) from the Cenomanian of Spain, but differs by the presence of spines on the lateral margins of the carapace, and by absence of granules and tubercles on ridges of the dorsal regions. Ridges of the dorsal regions in *E. kojimai* are coarser than those in *E. navarrensis*. The new species resembles *Eomunidopsis meerssensensis* Collins, Fraaye and Jagt, 1995 from the Maastrichtian Maastricht Formation of the Netherlands. In *E. kojimai* ridges are transversely and obliquely arranged on the dorsal surface while in *E. meerssensensis* transverse ridges cover the dorsal surface.

Eomunidopsis, earliest known from the Oxfordian (Fraaye and Collins, 1996), is recorded from the Tithonian of Austria and Bulgaria (Via Boada, 1982), from the Cenomanian of Spain (Via Boada, 1982), from the Albian-Cenomanian of U.S.A. (Bishop, 1985) and the Maastrichtian of the Netherlands (Collins, Fraaye and Jagt, 1995). The occurrence of *E. kojimai* indicates that the genus reached Japan by the Santonian.

Etymology.—From Mr. T. Kojima who collected the type specimen.

Material examined.—MFM247.011 (holotype), Loc. YEZ-20, Wakkauenbetsugawa, Nakagawa-cho, Teshio-gun; Nigorikawa Formation (Santonian), Upper Yezo Group (Osana *et al.*, 1960).

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Early Silurian (Llandoveryan) radiolarians from the Ise area of the Hida "Gaien" Belt, central Japan

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Abstract. A moderately well-preserved Llandoveryan (early Early Silurian) radiolarian fauna has been discovered from the Ise area of the Hida "Gaien" Belt, in Izumi Village, Fukui Prefecture, central Japan. This is the oldest known radiolarian fauna in Japan, and was recovered from calcareous nodules in the siliceous shale portion of a sedimentary sequence consisting of siliceous shale, alternating tuffaceous sandstone and shale, and tuffaceous sandstone. The fauna contains *Haplotaeniatum tegimentum*, *Syntagactinia afflicta*, *S. excelsa*, *Oriundogutta* sp., *Inanihella* sp., *Auliela* sp., *Palaeoephippium?* sp., and *Orbiculopylorum* sp. This fauna is characterized by an abundance of species in the genera *Haplotaeniatum*, *Syntagactinia* and *Oriundogutta*, and is comparable with the early to middle Llandoveryan *Haplotaeniatum tegimentum* Assemblage and its equivalents in the southern Urals, Germany, and Nevada. Seventeen species of radiolarians belonging to 12 genera were systematically investigated.

Key words: Hida "Gaien" Belt, Ise area, Llandoveryan, Radiolaria, Silurian

Introduction

An understanding of the biostratigraphy and taxonomy of Silurian and Devonian radiolarians has progressed remarkably in the past decade (e.g., Nazarov and Ormiston, 1993; Noble and Aitchison, 1995). Numerous late Early Silurian to Middle Devonian radiolarian studies have been published for Japan (e.g., Wakamatsu *et al.*, 1990; Furutani, 1990; Aitchison *et al.*, 1996; Umeda, 1998), Australia (e.g., Stratford and Aitchison, 1997; Aitchison *et al.*, 1999), the United States (Noble, 1994), the southern Urals (Amon *et al.*, 1995), westernmost China (Li, 1994), and Germany (Kießling and Tragelehn, 1994). Based on these radiolarian biostratigraphic studies, we can estimate the age of radiolarian-bearing rocks of this interval.

Ordovician to early Early Silurian radiolarian biostratigraphy has been outlined by Nazarov and Popov (1980), Nazarov (1988), and Nazarov and Ormiston (1993). In addition to these studies, conducted in Kazakhstan and the southern Urals by Nazarov and his collaborators, a large number of Ordovician radiolarians have been reported from Spitsbergen (Fortey and Holdsworth, 1971), Newfoundland (Bergström, 1979; Renz, 1990a), the United States (Dunham and Murphy, 1976; Renz, 1990a, b; Kozur *et al.*, 1996), Australia (Webby and Blom, 1986; Goto *et al.*, 1992; Umeda *et al.*, 1992; Iwata *et al.*, 1995), Estonia (Nazarov and Nylvak, 1983), the Baltic region (erratic boulders) (Eisenack, 1971; Górka, 1994), China (Wang, 1993; Li,

1995), and Scotland (Aitchison, 1998; Danelian and Clarkson, 1998). In contrast, besides Nazarov's works (Nazarov, 1998; Nazarov and Ormiston, 1993), only a few papers describing early Early Silurian (Llandoveryan) radiolarians were published before the mid-1990s (Rüst, 1892; Stürmer, 1951, 1952, 1966; Goodbody, 1986). More recently, Llandoveryan faunas have been described from the Cherry Spring Chert in Nevada (Noble *et al.*, 1997; Noble *et al.*, 1998), Dalarna, Sweden (Maletz and Reich, 1997), Cornwallis Island, Arctic Canada (MacDonald, 1998), and Germany (Noble *et al.*, 1998). These studies demonstrate that Llandoveryan radiolarians have a high biostratigraphic potential. Early Silurian radiolarians, however, are still insufficiently known. Additional collecting is needed to establish a biostratigraphy and provide information on the faunal composition for this time period.

We are now studying the lithostratigraphy and radiolarian biostratigraphy of the Hida "Gaien" (=marginal) Belt in order to understand its tectonic and paleobiogeographic history (Kurihara and Sashida, 1998). We fortuitously discovered Llandoveryan radiolarians in calcareous nodules from the siliceous shale part of the clastic and volcanoclastic sequence exposed in the Ise area of the westernmost part of the Hida "Gaien" Belt, in Izumi Village, Ohno County, Fukui Prefecture. This early Early Silurian radiolarian fauna is the oldest one known in Japan. In this paper, we discuss the age assignment of the radiolarian fauna and systematically describe 17 species which belong to 12 genera including

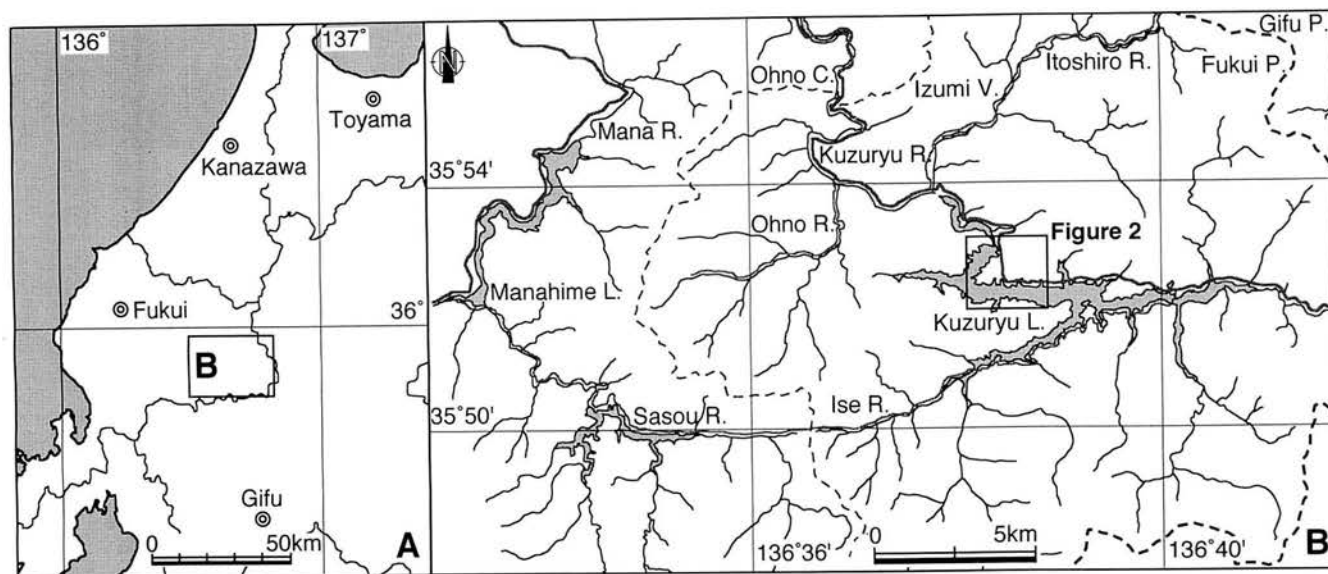


Figure 1. Index map showing the study area.

four undetermined genera.

Geologic setting

The Hida "Gaien" Belt, one of the most structurally complex areas in the Japanese geologic framework, occurs in a narrow area between the Hida and Mino Terranes. This belt is composed of weakly metamorphosed or unmetamorphosed Paleozoic and Mesozoic strata, including Ordovician to Devonian sediments, crystalline schists, and basic to ultrabasic rocks. Outcrops of these rocks can be found in the Omi-Renge, Fukuiji, Moribu (Arakigawa), Naradani and Ise areas (e.g., Komatsu, 1990; Igo, 1990). The latter four of these five areas are covered by Middle Paleozoic strata and have been investigated by many workers (e.g., Tazawa *et al.*, 1997). Recent micropaleontological investigations of Ordovician strata show them to be fairly widely distributed in the Hitoegane district of the Fukuiji area (Tsukada and Koike, 1996; Tsukada, 1997).

The Ise area, which extends from Izumi Village to Ohno City, Fukui Prefecture, is situated in the westernmost part of the Hida "Gaien" Belt. Its constituent rocks are exposed around Kuzuryu Lake and in the upper reaches of the Ise River to the Sasou-Mana River (Figure 1). The geology of this area has been studied by Kawai (1956), Kawai *et al.* (1957), Yamada (1967), and the Metal Agency of Japan (1980). Miyakawa and Yamada (1988) summarized the stratigraphy of the sedimentary rocks cropping out around Kuzuryu Lake, based on the studies of Yamada (1967) and Ohno *et al.* (1977). They subdivided these rocks into the following eight lithostratigraphic units, in ascending order: an unnamed Silurian unit, the Lower to Middle Devonian Kamianama Group, Middle Carboniferous Nagano Formation, Lower Permian Oboradani Formation, Middle Permian Nojiri Group and Magatoji Formation, post-Permian? Ohtani and Motodo Formations, and the Ashidani Group of unknown age. Among these litho-

stratigraphic units, the Nojiri Group, which is subdivided into the Oguradani Formation and overlying Konogidani Formation, crops out widely around Kuzuryu Lake. The other units, especially the Silurian and Devonian strata, complexly occur in narrow zones on the north side of Kuzuryu Lake and along the upper reaches of the Ise River.

Strata in this area contain rich Carboniferous and Permian fossils, including fusulinacians and corals in the Oboradani and Ohtani Formations, and brachiopods in the Oguradani Formation (e.g., Niko and Watanabe, 1987; Niko *et al.*, 1997; Tazawa and Matsumoto, 1998). The Devonian limestone of the Kamianama Group yields various kind of fossils (e.g., Hamada, 1959; Okazaki *et al.*, 1974; Kamiya and Niko, 1997) but no detailed paleontological study of them has been published. Recently, micropaleontological investigation by the present authors revealed the occurrence of Late Silurian to Middle Devonian radiolarians in the Kamianama Group (Kurihara and Sashida, 1998).

Lithology of the radiolarian-bearing rocks

The Early Silurian radiolarian-bearing calcareous nodules were collected from the siliceous shale portion of a sequence that consists of thin alternations of tuffaceous sandstone and shale, tuffaceous sandstone, and siliceous shale. The sequence crops out along a stream near the Kagero Tunnel, west of Nojiri, Izumi Village (Figure 2). Similar rocks are exposed in a roadcut east of the Anama Temple. These strata were previously assigned to the Konogidani Schalstein Formation (Ozaki *et al.*, 1954), the Tomedoro Schalstein "Member" [=Formation] (Kawai, 1956; Kawai *et al.*, 1957; Metal Agency of Japan, 1980), and the Permian Konogidani Formation (Yamada, 1967; Miyakawa and Yamada, 1988). Revision of the litho- and biostratigraphy in this area is needed (Kurihara, 1999).

In this stratigraphic section, the beds generally strike N25° to 35°W and dip 70° to 80°S (and sometimes almost verti-

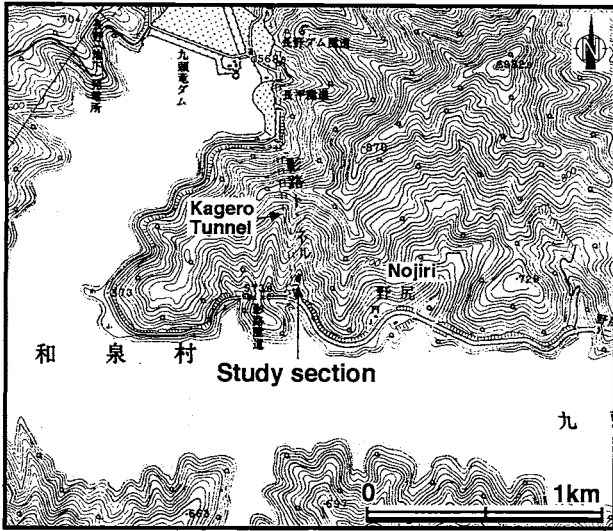


Figure 2. Locality map showing the location of the study section. Base map is after 1:25,000-scale topographic map of Japan, Quadrangle "Echizen-Asahi", Geographical Survey Institute of Japan.

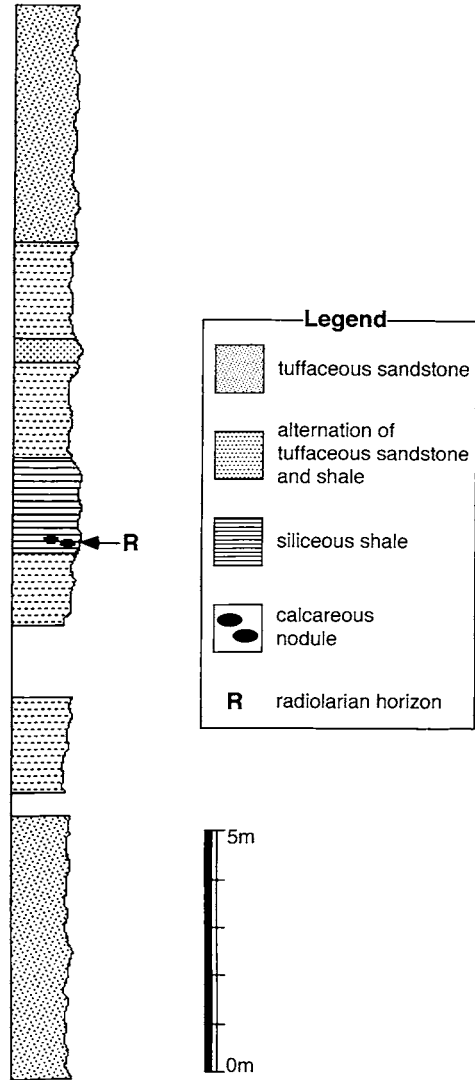


Figure 4. Column along the study section.

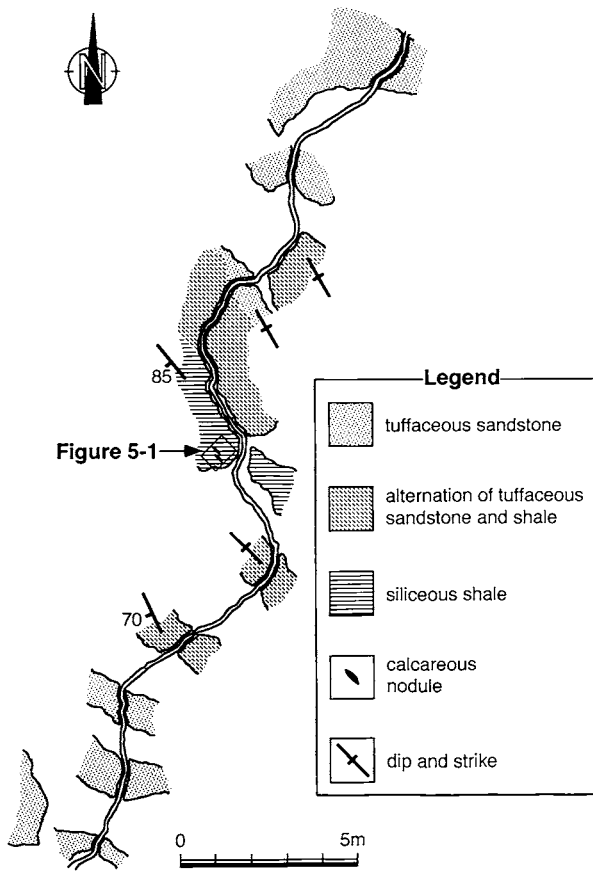


Figure 3. Route map along the study section.

cally) (Figure 3). Although the stratigraphically highest structures were inaccessible in this section, we tentatively regard these rocks as a north-upward sequence, because sedimentary structures such as graded beddings indicating a north-upward orientation are observable at an outcrop east of the Anama Temple. The rock sequence of this section is as follows, in ascending order: tuffaceous sandstone (about 5.5 m); alternating tuffaceous sandstone and shale (about 4.5 m); siliceous shale (2 m); alternating tuffaceous sandstone and shale (4.5 m); and tuffaceous sandstone (5 m) (Figure 4). The tuffaceous sandstone is medium- to coarse-grained, massive and dark green to dark gray in color. The alternating tuffaceous sandstone and shale is thinly bedded and dark gray, gray, dark green, and black in color. Microscopic observation reveals that the sandstone layers are composed mainly of angular quartz fragments with a small amount of plagioclase and opaque minerals. The shale layers are partly similar to chert and contain very fine quartz grains in a muddy matrix with frequent thin lamina-

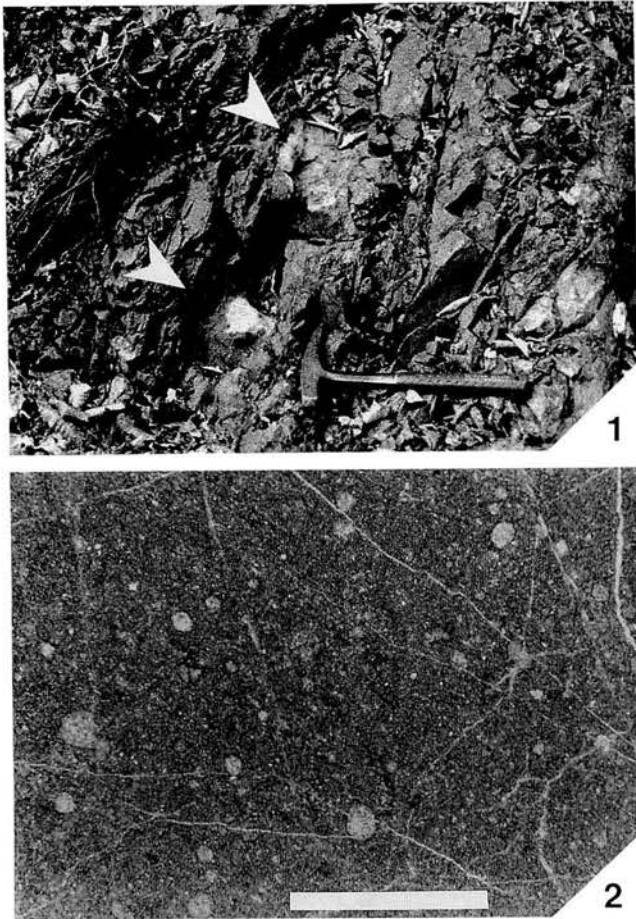


Figure 5. 1. Photograph showing the occurrence of radiolarian-bearing calcareous nodules (white arrows) in the study section (see Figure 3 for locality). 2. Photomicrograph of radiolarian-bearing calcareous nodule. Scale bar=1 mm.

tions of coarse quartz grains. The siliceous shale is dark gray and pale green in color and the thickness of each bed is 2 to 5 cm. In this exposure, the shale contains two calcareous nodules which are lenticular in shape and measure 15 cm and 6 cm in the major and minor axes, respectively (Figure 5.1). These nodules are hard, compact, dark gray in color and contain many radiolarian spheres. Radiolarian skeletons are scattered in a calcareous and muddy matrix, most are altered to calcite, and only their outlines formed of fine-grained quartz are preserved (Figure 5.2).

Method of extracting radiolarians

We collected calcareous nodules, siliceous shale, and the shaly part of the alternating tuffaceous sandstone and shale for radiolarian analysis. In order to extract radiolarians from the calcareous nodules, we soaked crushed rocks, each several centimeters in diameter, in a dilute acetic acid solution (5%) for 10 to 12 hours. For the siliceous rock samples, crushed rocks were soaked in a dilute hydrofluoric acid

Table 1. List of Llandoveryan radiolarians from the calcareous nodule.

HAPLENTACTINIIDAE

- Haplotaeniatum tegimentum* Nazarov & Ormiston
- Haplotaeniatum* sp. A
- Syntagentactinia afflicta* Nazarov & Ormiston
- Syntagentactinia excelsa* Nazarov & Ormiston
- Syntagentactinia* ? sp.

INANIGUTTIDAE

- Oriundogutta* sp.
- Oriundogutta* ? sp.
- Inanihella* sp.
- Inanihella* ? sp.
- Inaniguttidae gen. et sp. indet. sp. A

ANAKRUSIDAE

- Auliela* sp.

PALAEOSCENIDIIDAE

- Palaeoephippium* ? sp.

SPONGURIDAE

- Sponguridae gen. et sp. indet. sp. A

PYLENTONEMIDAE

- Cessipylorum* ? sp.

INCERTAE SEDIS

- Orbiculopylorum* sp.
- Spumellaria gen. et sp. indet. sp. A
- Spumellaria gen. et sp. indet. sp. B
- Spumellaria gen. et sp. indet.

(HF) solution (5 to 10%) for about 24 hours. The samples were washed and sieved through 270# nylon mesh. Radiolarians picked from the dried residues were coated with gold in a vacuum evaporator and observed with a scanning electron microscope. Other specimens were sealed on a slide glass and observed with a transmitted light microscope.

Radiolarian fauna and age

Radiolarians were recovered only from the calcareous nodules, and were absent in the siliceous shale and the shaly part of the alternating tuffaceous sandstone and shale. The identified radiolarians consist of 18 species belonging to 13 genera (Table 1). Radiolarians extracted from the calcareous nodules are generally poorly preserved, and unidentified spumellarian fragments are also numerous. This fauna is characterized by abundant species of the families Haplentactiniidae and Inaniguttidae, in association with Anakrusidae, Palaeoscenidiidae, Sponguridae, and Pylentonemidae. *Haplotaeniatum* and *Syntagentactinia*, in the family Haplentactiniidae, are common and are characterized by large, spherical, spongy, or concentric-layered shells. The following Haplentactiniidae species are present:

Haplotaeniatum tegimentum Nazarov and Ormiston, *Haplotaeniatum* sp. A, *Syntagentactinia afflicta* Nazarov and Ormiston, *Syntagentactinia excelsa* Nazarov and Ormiston, and *Syntagentactinia?* sp. Radiolarians of the family Inaniguttidae comprise the next most-dominant faunal component, including the following species: *Oriundogutta* sp., *Inanihella* sp., *Inanihella?* sp., and Inaniguttidae gen. et sp. indet. sp. A. Species in the families Palaeoscenediidae and Sponguridae are less common, although *Palaeoephippium?* sp. and Sponguridae gen. et sp. indet. sp. A are present. The following species were allocated to the families Anakrusidae, Pylentonemidae, and to incertae sedis; *Auliela* sp., *Cessipylorum?* sp., and *Orbiculopylorum* sp.

Silurian radiolarian biostratigraphy was first rationalized by Nazarov (1988) and Nazarov and Ormiston (1993), who proposed two radiolarian assemblages: the Early Silurian *Haplotaeniatum tegimentum* Assemblage and the Late Silurian *Inanihella tarangulica-Secuicollacta cassa* Assemblage. The *H. tegimentum* Assemblage, described from a middle Llandoveryan to Wenlockian siliceous rock sequence in the Sakmarsky Suite of the southern Urals, is characterized by *Haplotaeniatum labyrinthum* Nazarov and Ormiston, *H. cathenatum* Nazarov and Ormiston, *H. tegimentum* Nazarov and Ormiston, *Haplentactinia silurica* Nazarov and Ormiston, *Syntagentactinia excelsa* Nazarov and Ormiston, and *S. afflicta* Nazarov and Ormiston. As noted above, the present radiolarian fauna is characterized by species of *Haplotaeniatum* and *Syntagentactinia*, and therefore is referable to the *H. tegimentum* Assemblage of Nazarov (1988) and Nazarov and Ormiston (1993).

Noble *et al.* (1997) made a preliminary study of an early Llandoveryan radiolarian fauna in the Cherry Spring Chert of Nevada. They extracted from sulfide nodules a well-preserved radiolarian fauna consisting of abundant, large pylomate sphaerellarians identified as *Cessipylorum* (?) sp. A and *Cessipylorum* (?) sp. B, some rotasphaerids such as *Rotasphaera* sp. and *Secuicollacta* spp., and *Oriundogutta* sp. In addition, Noble *et al.* (1998) noted that the Nevada fauna described by Noble *et al.* (1997) contains abundant species of *Haplotaeniatum*. From the Frankenwald and Thuringia, Germany, Noble *et al.* (1998) also reported *Secuicollacta* spp. from black, organic-rich chert, the age of which is constrained by co-occurring graptolites as early Rhuddanian to early Telychian (early to late Llandoveryan). In the Main Valley, Germany, black chert gravel in Pleistocene river deposits contains well-preserved radiolarians, and was probably derived from the Frankenwald (Stürmer, 1951, 1952, 1966). Richter (1951) cited the age of this gravel as middle Rhuddanian to Aeronian (early to middle Llandoveryan), and Noble *et al.* (1998) identified the following species in it: *Syntagentactinia?* sp., *Orbiculopylorum adobensis* Noble, Braun and McClellan, *Orbiculopylorum* sp., and *Haplotaeniatum* sp.

Noble *et al.* (1997) pointed out the following characters of the Nevada fauna: (1) the species belonging to the family Inaniguttidae of the Wenlockian to Ludlowian, which have long and robust spines, are different from inaniguttids of the Nevada fauna. (2) Wenlockian to Ludlowian rotasphaerids commonly have six rods per spine unit and highly diversified spines such as grooved or bladed ones. In contrast,

rotasphaerid species in the Nevada fauna have five rods per spine unit and rod-shaped spines. (3) The Nevada fauna does not contain species in the families Palaeoscenediidae and Ceratoikiscidae, which are notable taxa in Wenlockian faunas (Goodbody, 1986; Renz, 1988). Rotasphaerids have never been found in the present fauna, although their absence may be due in part to preservational bias, as these taxa are small and delicate. The morphological characters of the inaniguttids and the absence of ceratoikiscids are consistent with the work of Noble *et al.* (1997). The Nevada fauna also contains species of *Syntagentactinia* and *Haplotaeniatum*. In addition, large spherical radiolarians with the concentric and loosely spongy layers of the German fauna (Stürmer, 1951, 1952, 1966; Noble *et al.*, 1998) are very similar to the species of *Syntagentactinia* and *Haplotaeniatum* in the present fauna. Although *Orbiculopylorum* is rare, the present fauna is similar in its taxonomic composition to those in Nevada and Germany.

Nazarov and Ormiston (1993) inferred the age of the *H. tegimentum* Assemblage to be middle Llandoveryan to Wenlockian by showing that this assemblage occurs in a siliceous shale sequence that contains *Monograptus triangulatus* to *M. testis* zone graptolites. Noble *et al.* (1998) noted that the age of the *H. tegimentum* Assemblage is Rhuddanian (early Llandoveryan) to early Homeric (late Wenlockian) and that the lower range of this assemblage is consistent with the age of the Nevada and German faunas. However, they questioned the upper range of this assemblage, because the early to middle Llandoveryan radiolarian fauna is markedly different from the late Llandoveryan fauna. The late Llandoveryan faunas reported by Maletz and Reich (1997) and MacDonald (1998) lack large spongy spumellarians such as *Haplotaeniatum* and are characterized by the abundance of various taxa of rotasphaerids and entactiniids. According to Noble *et al.* (1998), the fauna from the middle Telychian (upper Llandoveryan) of Dalarna, Sweden contains *Haplotaeniatum* species but otherwise differs from the Nevada fauna in faunal composition. Therefore, as pointed out by Noble *et al.* (1998), the upper range of the *H. tegimentum* Assemblage does not extend above the Telychian, and possibly not above the Rhuddanian to Aeronian (early to middle Llandoveryan).

We cannot determine the precise age of the present fauna, but we assign it to the early to middle Llandoveryan, based on its similarity to the *H. tegimentum* Assemblage and to the Nevada and German faunas, as mentioned above.

Systematic paleontology

All specimens described in this paper are deposited in the Institute of Geoscience, University of Tsukuba (IGUT).

- Order Polycystina Ehrenberg, 1838, emend. Riedel, 1967b
- Suborder Spumellaria Ehrenberg, 1875
- Family Haplentactiniidae Nazarov in Nazarov and Popov, 1980
- Subfamily Haplentactiniinae Nazarov in Nazarov and Popov, 1980
- Genus *Haplotaeniatum* Nazarov and Ormiston, 1993

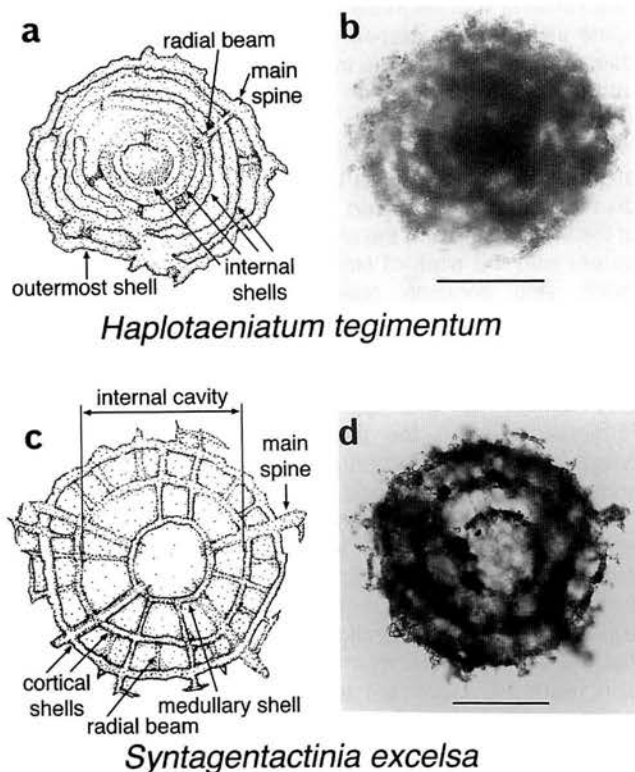


Figure 6. Schematic diagrams of skeletal structures and light transmission microphotographs of *Haplotaeniatum tegimentum* Nazarov and Ormiston (a, b) and *Syntagentactinia excelsa* Nazarov and Ormiston (c, d). Scale bars=100 μ m.

Type species.—*Haplotaeniatum labyrinthum* Nazarov and Ormiston, 1993.

Remarks.—Nazarov and Ormiston (1993) stated that the internal shells of this genus are interpreted as having formed by apophyses developed on the main spines. They also illustrated the schematic internal structure of this genus (Nazarov and Ormiston, 1993, text-figure 8b) and emphasized an important role of the main spines on skeletal structure as the characteristic of the family Haplentactiniidae. However, no specimen has the entactiniid-like internal structure formed by the main spines and extremely eccentrically positioned innermost shell among the photos presented by Nazarov and Ormiston (1993, pl. 3, figs. 9–16). Therefore, the generic diagnosis concerning the main spine by Nazarov and Ormiston (1993) is unconvincing, and the suprageneric classification of the genus *Haplotaeniatum* is problematic. We are not able to make an emendation for this genus owing to our poorly preserved material. However, the generic diagnosis and suprageneric classification of this genus will need to be revised on the basis of well-preserved material. In this paper, we follow the diagnosis presented by Nazarov and Ormiston (1993).

Haplotaeniatum tegimentum Nazarov
and Ormiston, 1993

Figure 7.1–7.13

Haplotaeniatum tegimentum Nazarov, 1988, p. 188, pl. 11, fig. 7 (nomen nudum); Nazarov and Ormiston, 1993, p.42, pl.3, figs. 14–16.

Description.—The external appearance of the shell is spherical, irregular spherical, or slightly elliptical. The outermost shell has many oval to irregularly rounded pores. In some specimens, a pylome-like oversized pore is present on the outermost shell surface (Figure 7.9–7.13). The inside of the outermost shell has an irregular spongy meshwork. The internal shells are spherical to subspherical, three to four in number, and concentrically arranged (Figure 6a, b). The innermost shell is often eccentrically positioned. Pores of the internal shells are circular to oval and differ in size. A small number of short, conical spines arise from the surface of the outermost shell. Under a transmitted light microscope, a radial beam (probably the main spine) penetrating the concentric internal shells and extending to the outermost shell is present (Figure 6a, b), but its detailed morphology is unclear owing to poor preservation. Short radial beams randomly arise from the outer surface of the internal shell. These beams connect the internal and outermost shells.

Measurements.—Based on 13 specimens, in μ m. Diameter of the outermost shell, 230–270, average, 250.

Remarks.—More than twenty specimens of this species were examined. According to the generic diagnosis of Nazarov and Ormiston (1993), this genus is characterized by having several concentric or spiral forms for the internal shells. A distinct spiral form was not observed in the present specimens, because the complex connections of the radial beams prevented us from appraising the inner structure of the shell. As shown in Figure 6a and 6b, several concentric internal shells are present. This species is distinguished from *Haplotaeniatum labyrinthum* Nazarov and Ormiston by having short, conical spines. *Haplotaeniatum cathenatum* Nazarov and Ormiston, which is characterized by having a large pylome, is similar to this species, especially to the above-described pylomate form. However, it is difficult to compare this species with *H. cathenatum*, because only one broken specimen of the latter species was illustrated by Nazarov (1988) and Nazarov and Ormiston (1993). *Haplotaeniatum? aperturatum* Noble, Braun and McClellan differs from the present species by having an irregular, spongy ball-like external shape and lacking a distinct internal shell.

Range and occurrence.—Middle to late Llandoveryan, southern Urals, southern Bashkiria and Northwestern Mugodzhari; Silurian, Cabriere, France; Llandoveryan, Ise area in the Hida "Gaigen" Belt.

***Haplotaeniatum* sp. A**

Figure 7.14–7.16

Description.—The shell is subspherical or slightly elliptical. The outermost shell has more than ten large circular to oval pores per hemisphere. The outermost shell bears no spines, but has small conical protuberances at the junction of intervening bars. The internal shell consisting of a loose lattice is subspherical, with large oval pores on its surface. Radial beams arise from the surface of the internal shell and connect the internal and cortical shells. These beams are

usually unbranched, but rarely bifurcate.

Measurements.—Based on three specimens, in μm . Diameter of the outermost shell, 230–270, average, 260.

Remarks.—This form is easily distinguished from other species of *Haplotaeniatum* by having large circular to oval pores and the loose lattice to its internal shell. This species is similar to specimens of *Haplotaeniatum primordialis?* (Rüst, 1892) described by Nazarov and Ormiston (1993). According to Nazarov and Ormiston (1993), the latter species is characterized by its smaller dimensions (194 to 208 μm) and a smaller number of internal shells. The present species differs from *H. primordialis?* (Rüst, 1892) by having a large diameter to the outermost shell.

Range and occurrence.—Llandoveryan, Ise area in the Hida "Gaien" Belt.

Genus ***Syntagactinia*** Nazarov in Nazarov and Popov, 1980

Type species.—*Syntagactinia biocculosa* Nazarov in Nazarov and Popov, 1980.

Syntagactinia afflicta Nazarov and Ormiston, 1993

Figure 7.17, 7.18

Syntagactinia afflicta Nazarov, 1988, pl. 11 fig. 6 (nomen nudum); Nazarov and Ormiston, 1993, p. 40, pl. 5, figs. 12, 13; Noble, Braun and McClellan, 1998, p. 723, fig. 5-2.

Description.—The shell of this species is composed of concentric cortical shells and a small medullary shell situated in the internal cavity. The cortical shells are spherical and two or three in number with long, robust, rod-shaped main spines. The main spines are commonly four in number and continuous into the medullary shell. In the interior of the medullary shell, however, the structure and emanation of the main spines are unclear. The diameter of the inner cortical shell is about two-thirds that of the outermost cortical shell. The surfaces of the outermost and inner cortical shells are irregularly perforated with oval to subangular pores. Many thin, radial beams connecting the outermost and inner cortical shells arise from the surface of the inner cortical shells. Due to being connected by many radial beams, the outermost and inner cortical shells form very complex sponge-like layers. Since only the broken medullary shell is preserved in our specimens, the detailed structure of the medullary shell is unclear. Based on observation with a transmitted light microscope, the diameter of the medullary shell is about one-third to one-fifth that of the outermost cortical shell.

Measurements.—Based on two specimens, in μm . Diameter of the outermost cortical shell, 280–300, average, 290; diameter of the inner cortical shell, 160–200, average, 180.

Remarks.—This species is easily distinguished from *Syntagactinia excelsa* Nazarov and Ormiston by having long, robust main spines. Nazarov in Nazarov and Popov (1980) described *Syntagactinia biocculosa* Nazarov and *Syntagactinia pauca* Nazarov from the Middle Ordovician strata of eastern Kazakhstan. Nazarov's figures in Nazarov

and Popov (1980) of these Ordovician species are transmitted light photomicrographs, so it is difficult to compare Silurian species with Ordovician species in detail. Nazarov and Ormiston (1993), however, mentioned that *S. afflicta* is distinguished from Ordovician species by the clearly expressed internal half-closed shells and the development in the majority of specimens of two to four rather than six main spines.

Range and occurrence.—Early Llandoveryan, northern Adobe Range, Nevada; middle to late Llandoveryan, southern Urals, southern Bashkiria and Northern Mugodzhzar; Llandoveryan, Ise area in the Hida "Gaien" Belt.

Syntagactinia excelsa Nazarov and Ormiston, 1993

Figures 7.19, 7.20; 8.1–8.7

Syntagactinia excelsa Nazarov and Ormiston, 1993, p. 40, pl. 6, figs. 13, 14.

Description.—The external appearance of the cortical shell is spherical, subspherical, or elliptical, with thin rod-like main spines. The main spines are directly continuous into the internal portion of the shell (Figure 6c, d). The cortical shell is composed of two or three layers with irregular, three-dimensional meshwork. The surface of the cortical shell is irregularly porous and has small spines. The medullary shell, consisting of a spherical to irregularly shaped loose lattice, is placed in the internal cavity and has a diameter about 30% that of the cortical shell diameter. The medullary and cortical shells are connected by short radial beams arising randomly from the surface of the medullary shell.

Measurements.—Based on five specimens, in μm . Diameter of the cortical shell, 200–270, average, 250; diameter of the medullary shell, 40–90, average, 70.

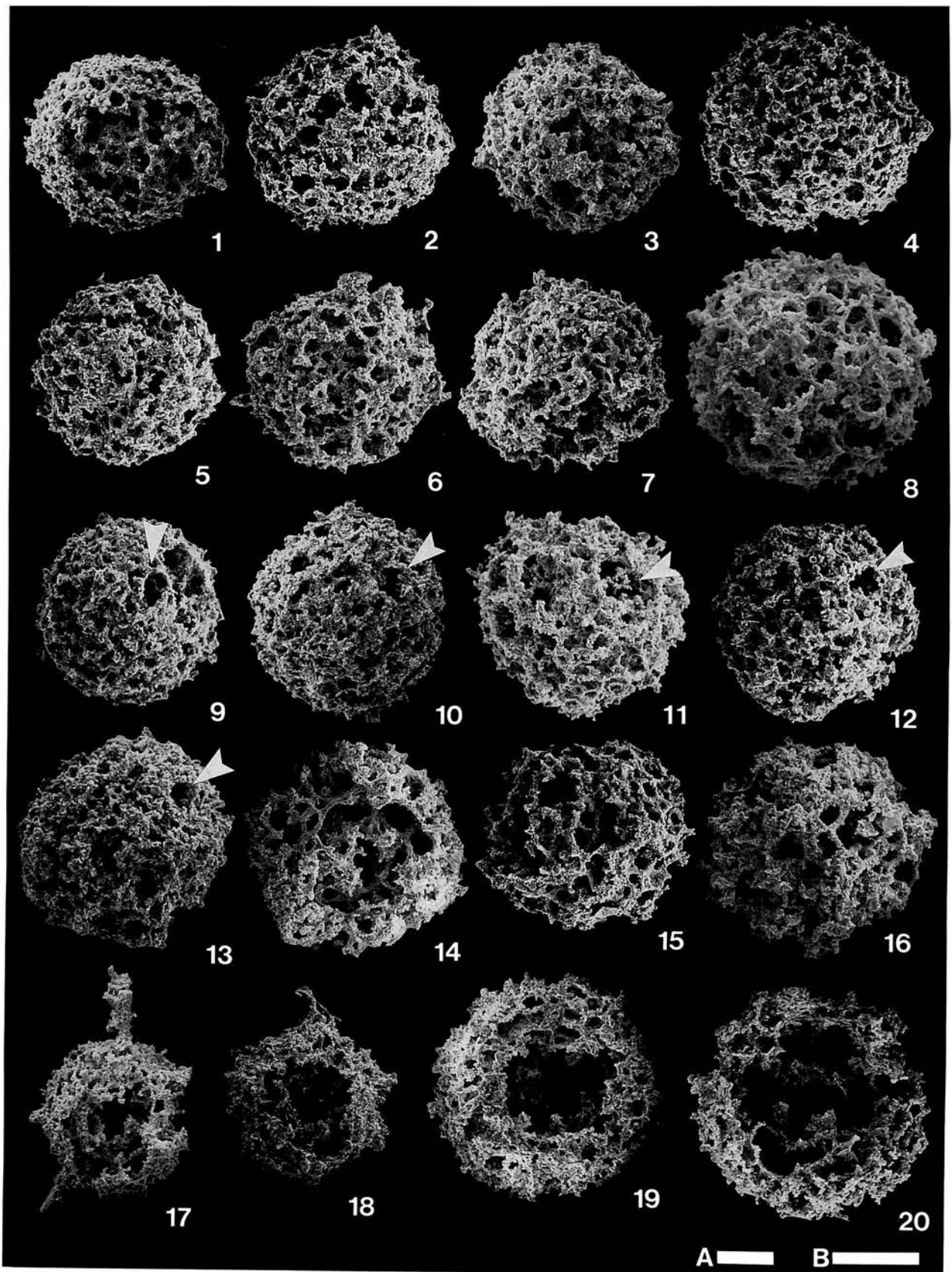
Remarks.—This species is distinguished from other species of this genus by having thin, weakly developed main spines. Some specimens of this species have a smaller cortical shell than that of *Syntagactinia afflicta* described above. Although Nazarov and Ormiston (1993) suggested that this species has a peculiar eccentric position of the medullary shell, this characteristic is not clearly shown in their illustrated specimen (Nazarov and Ormiston, 1993, pl. 4, fig. 13). The shell constitution of this species is similar to that of *Syntagactinia?* sp. illustrated by Noble *et al.* (1998) from chert gravel of the Main Valley, Germany. However, *Syntagactinia?* sp. of Noble *et al.* (1998) has a large diameter of the cortical shell, up to 700 μm . *Syntagactinia* sp. A of Noble *et al.* (1998) is similar to the present species, but differs from *S. excelsa* by having a distinctly latticed medullary shell.

Range and occurrence.—Middle to late Llandoveryan, southern Urals, southern Bashkiria and Northwestern Mugodzhzar; Llandoveryan, Ise area in the Hida "Gaien" Belt.

Syntagactinia? sp.

Figure 8.8

Remarks.—Only one poorly preserved specimen was obtained. The shell of this species is composed of an irregu-



larly fine spongy layer having three thick main spines. This spongy layer may be a product of the state of preservation. This species is similar to *Syntagactinia?* sp. of Noble *et al.* (1998), except that it has a rather small shell diameter. Although its detailed shell structure has not yet been examined, we tentatively include this form in *Syntagactinia*.

Range and occurrence.—Llandoveryan, Ise area in the Hida "Gaien" Belt.

Family Inaniguttidae Nazarov and Ormiston, 1984,
emend. Noble, 1994

Genus *Oriundogutta* Nazarov, 1988

Type species.—*Astroentactinia ramificans* Nazarov, 1975.

***Oriundogutta* sp.**

Figure 8.9–8.15

?*Oriundogutta* sp. Noble, Ketner and McClellan, 1997, pl. 1, figs. 7, 8.

Description.—The thick, spherical cortical shell is single and latticed with 10 to 15 external spines per hemisphere. The external spines are short, conical to rod-like and taper distally. Five to six main spines arising from the surface of the medullary shell in each hemisphere are long and have one or two short by-spines. The pores of the latticed shell are circular, and oval to irregularly circular in shape. Thick and broad pore frames are pentagonal or hexagonal in shape. The medullary shell is small, latticed and polyhedral to spherical in shape. The pores of the medullary shell are circular to oval and larger than those of the cortical shell. The pore frames of the medullary shell are thinner than those of the cortical shell. SEM and transmitted light microscopic observations show the absence of an internal spicule in the interior of the medullary shell.

Measurements.—Based on five specimens, in μm . Diameter of the cortical shell, 150–300, average, 210; diameter of the medullary shell, 60–110, average, 90.

Remarks.—More than twenty specimens of this species were examined and they bear diagnostic characters of the *Oriundogutta*: one porous, thick cortical shell, a polyhedral to spherical medullary shell, and more than eight external spines. It is distinguished from other species of this genus by having short, conical to rod-like external spines and a smaller number of these spines. ?*Oriundogutta* sp., reported by Noble *et al.* (1997) from the lower Llandoveryan of Nevada, is exceedingly similar to this species in external shape.

Range and occurrence.—Early Llandoveryan, northern Adobe Range, Nevada; Llandoveryan, Ise area in the Hida "Gaien" Belt.

***Oriundogutta?* sp.**

Figure 8.16–8.20

Remarks.—The cortical shell of this species is spherical and has three to four sturdy, rod-like main spines per hemisphere. Some of the examined specimens have several thin, needle-like spines. The external shell features of *Oriundogutta?* sp. are similar to those of *Oriundogutta ramificans* (Nazarov), except that the former's main spines are smaller in number. This species is distinguished from *Oriundogutta* sp. by having a finely perforated cortical shell and thin pore frames. The internal shell structure cannot be observed, so the generic position of this species is tentative.

Range and occurrence.—Llandoveryan, Ise area in the Hida "Gaien" Belt.

Genus *Inanihella* Nazarov and Ormiston, 1984,
emend. Noble, 1994

Type species.—*Helioentactinia bakanasensis* Nazarov, 1975.

***Inanihella* sp.**

Figure 9.1–9.4

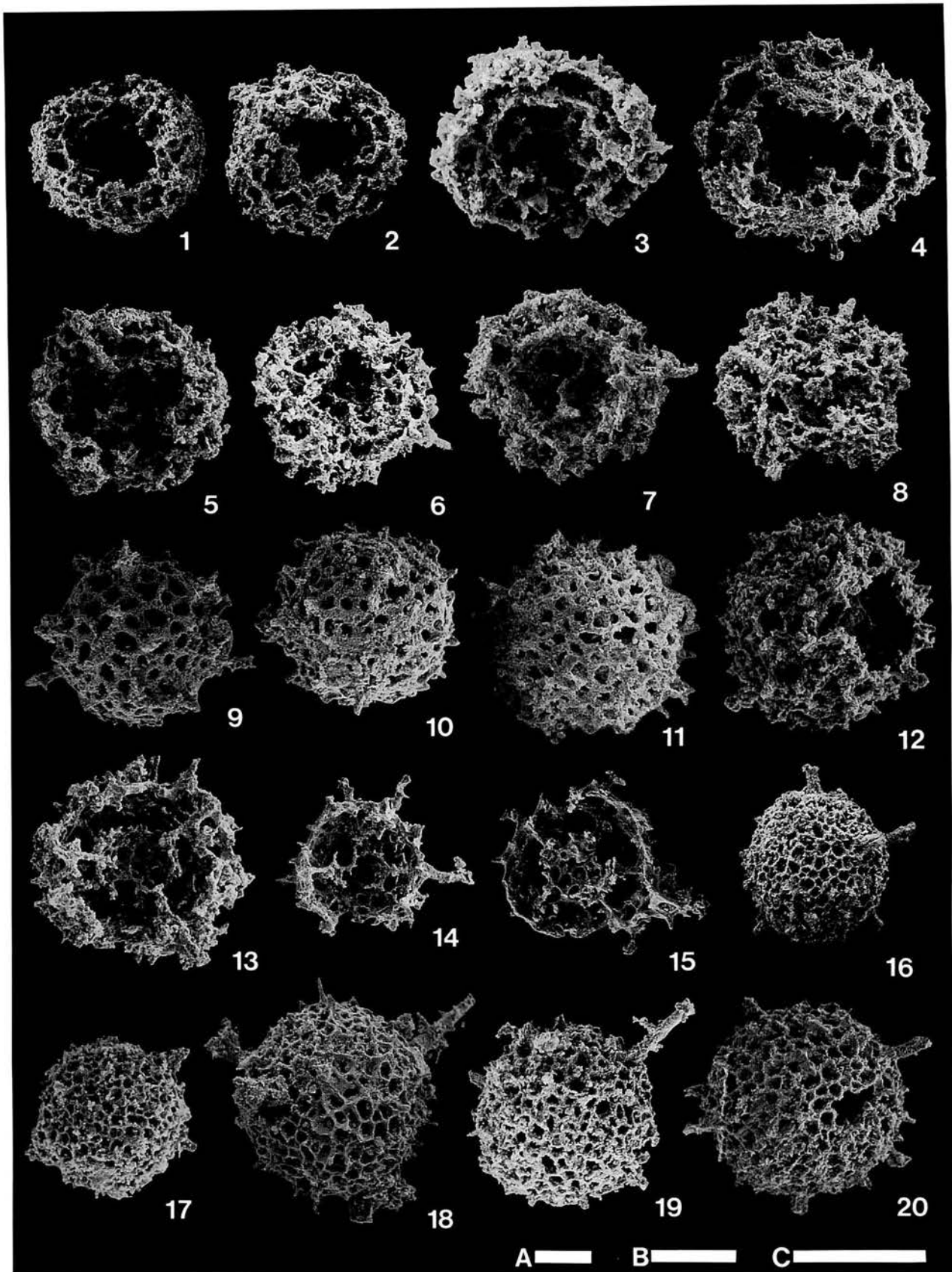
Description.—The shell of this species is composed of two latticed cortical shells with more than four main spines per hemisphere. The inner cortical shell is spherical and has circular to oval pores with pentagonal to hexagonal pore frames. The outer cortical shell is delicate and irregularly perforated. Several short, needle-like spines arise from the surface of the outer cortical shell. The inner and outer cortical shells are connected by many thin radial beams. Based on observations with a transmitted light microscope, the internal shell is single, and probably latticed, but its detailed structure has not been observed. The main spines are thin, rod-like and taper gently toward the distal end.

Measurements.—Based on four specimens, in μm . Diameter of inner cortical shell, 190–220, average, 200; diameter of outer cortical shell, 260–300, average, 280; maximum length of spine, 70.

Remarks.—This species is characterized by the presence of two cortical shells, yet no specimens were found that perfectly preserve the delicate outer cortical shell. The present form has a spine morphology similar to *Inanihella bakanasensis* (Nazarov) reported from the Middle Ordovician of Kazakhstan by Nazarov (1975).

Range and occurrence.—Llandoveryan, Ise area in the Hida "Gaien" Belt.

Figure 7. 1–13. *Haploaeniatum tegimentum* Nazarov and Ormiston, 1: IGUT-TK 863, 2: IGUT-TK 816, 3: IGUT-TK 874, 4: IGUT-TK 894, 5: IGUT-TK 782, 6: IGUT-TK 858, 7: IGUT-TK 875, 8: IGUT-TK 958, 9: IGUT-TK 860, 10: IGUT-TK 783, 11: IGUT-TK 794, 12: IGUT-TK 884, 13: IGUT-TK 776. White arrows of 9 to 13 indicate a pylome-like oversized pore. 14–16. *Haploaeniatum* sp. A, 14: IGUT-TK 866, 15: IGUT-TK 873, 16: IGUT-TK 801. 17, 18. *Syntagactinia afflicta* Nazarov and Ormiston, 17: IGUT-TK 897, 18: IGUT-TK 824. 19, 20. *Syntagactinia excelsa* Nazarov and Ormiston, 19: IGUT-TK 817, 20: IGUT-TK 747. Scale bars A and B each equal 100 μm ; A applies to 15, 17, 18, B to 1–14, 16, 19, 20.



Inanihella? sp.

Figure 9.5–9.7

Remarks.—The basic skeleton of this species is composed of a porous inner cortical shell with traces of delicate outer cortical shell. The internal shell structure has not yet been observed. Three or four rod-like main spines are present on the inner cortical shell per hemisphere. Many short conical spines arise from the junction of the pore frame of the inner cortical shell. The inner cortical shell and main spines of this species are very similar to those of the *Inanihella* sp. described above. Although only traces of the delicate outer cortical shell are present, we tentatively include this form in *Inanihella*.

Range and occurrence.—Llandoveryan, Ise area in the Hida "Gaien" Belt.

Inaniguttidae gen. et sp. indet. sp. A

Figure 9.8, 9.9

Remarks.—Several poorly preserved specimens were examined. This species is characterized by a large, spherical cortical shell with an oversized pore. This pylome-like pore is circular in shape and has no lip on its surrounding pore frame. The external shell morphology is somewhat similar to the *Oriundogutta* sp. herein. We tentatively include this species in the family Inaniguttidae. A larger sample of this species is needed in order to determine its generic position.

Range and occurrence.—Llandoveryan, Ise area in the Hida "Gaien" Belt.

Family Anakrusidae Nazarov, 1977

Genus *Auliela* Nazarov, 1977*Type species.*—*Auliela aspersa* Nazarov, 1977.*Auliela* sp.

Figure 9.10

Description.—The shell is spherical, with more than one hundred spines arising from the hemisphere. The spines are straight, cylindrical and taper gently toward the distal end. Most of these spines are short or broken, owing to poor preservation, but some attain 60 µm in length. There are no pores on the shell surface. The internal structure is unknown.

Measurements.—Based on one specimen, in µm. Diameter of shell, 300; maximum length of spine, 60.

Remarks.—Only one specimen of this species was examined. Our specimen has a spherical shell with numerous cylindrical spines. This character and the external shape indicate assignment to the genus *Auliela*. *Auliela aspersa* Nazarov, the type species of this genus, described from the

Middle Ordovician of eastern Kazakhstan by Nazarov (1977), is similar to the present species. The spines of *A. aspersa* Nazarov are described as being hollow, but the present specimen has mostly solid spines. This difference may be attributed to the development of secondary deposits of silica and poor preservation. This species, however, differs from *A. aspersa* Nazarov in having a rather smaller shell and shorter spines. *Auliela taplowensis* Webby and Blom, described from the Upper Ordovician of eastern Australia by Webby and Blom (1986), differs from this species by having longer spines and a smaller shell diameter.

Range and occurrence.—Llandoveryan, Ise area in the Hida "Gaien" Belt.

Family Palaeoscenidiidae Riedel, 1967a, emend.

Holdsworth, 1977; Goodbody, 1982;

Furutani, 1983; Goodbody, 1986

Genus *Palaeoephippium* Goodbody, 1986*Type species.*—*Palaeoephippium bifurcum* Goodbody, 1986.*Palaeoephippium?* sp.

Figure 9.11–9.13

Remarks.—Completely preserved specimens of this species have not yet been obtained. The basic skeleton of this species probably consists of a six-rayed form. The spines arising from each ends of a short medium bar are rod-like, gently tapered toward the distal end. Among these spines, three (probably four) spines have two or three rather thin secondary spines at the midpoint of their length, and the other spines lack the branched spines. *Palaeoephippium tricornis* Goodbody, described from the Cape Phillips Formation of the Canadian Arctic Archipelago by Goodbody (1986), has indistinguishable apical and basal spines and is similar to this species. Furthermore, this species has a resemblance to *Haplentactinia arrhinia* Foreman, 1963 in having a six-rayed basic spicule. However, the former species differs from the latter by having branches arising at one level along some spines and lacking an irregularly latticed shell. In this paper, we tentatively assign this species to the genus *Palaeoephippium*, considering its similarity to *P. tricornis*.

Range and occurrence.—Llandoveryan, Ise area in the Hida "Gaien" Belt.

Family Sponguridae Haeckel, 1887, emend.

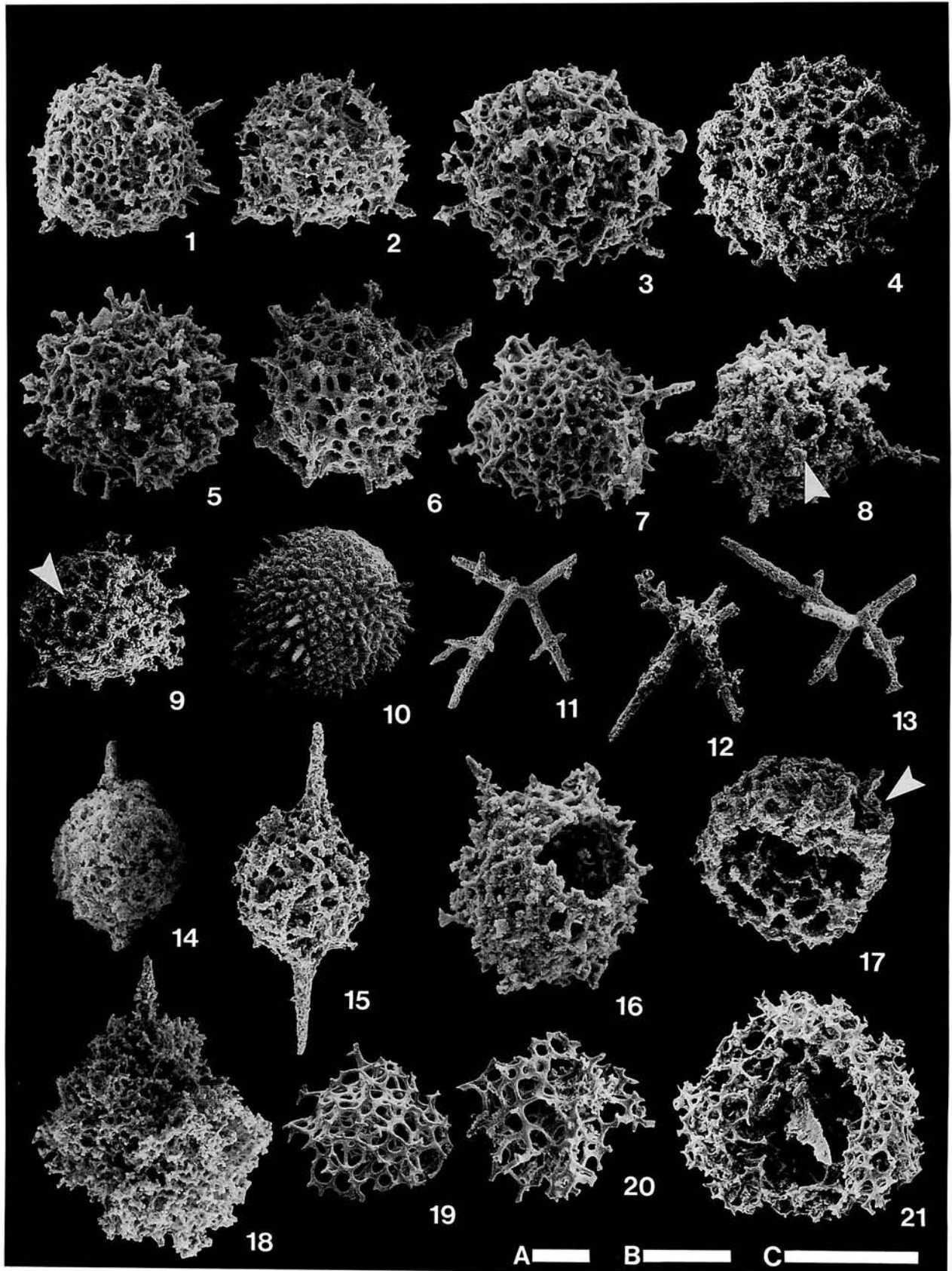
Pessagno, 1973

Sponguridae gen. et sp. indet. sp. A

Figure 9.14, 9.15

Description.—The shell is elliptical, with two polar main

Figure 8. 1–7. *Syntagactinia excelsa* Nazarov and Ormiston, 1: IGUT-TK 723, 2: IGUT-TK 836, 3: IGUT-TK 961, 4: IGUT-TK 864, 5: IGUT-TK 724, 6: IGUT-TK 822, 7: IGUT-TK 766. 8. *Syntagactinia?* sp., IGUT-TK 899. 9–15. *Oriundogutta* sp., 9: IGUT-TK 859, 10: IGUT-TK 895, 11: IGUT-TK 819, 12: IGUT-TK 879, 13: IGUT-TK 901, 14: IGUT-TK 761, 15: IGUT-TK 850. 16–20. *Oriundogutta?* sp., 16: IGUT-TK 892, 17: IGUT-TK 931, 18: IGUT-TK 845, 19: IGUT-TK 865, 20: IGUT-TK 919. Scale bars A, B and C each equal 100µm; A applies to 1, 8, 16, 17, B to 2–7, 9–11, 13–15, 18–20, C to 12.



spines. These spines are rod-like, strongly tapered, and identical in length and thickness. The proximal portions of the spines are weakly bladed. The surface of the outer shell has many circular to polygonal pores of irregular size. The interior of the shell consists of a loose, irregular spongy meshwork. The distinctly layered internal structure was not observed.

Measurements.—Based on one specimen, in μm . Length of major axis of shell, 190; length of minor axis of shell, 150; length of spines, 100.

Remarks.—Several poorly preserved specimens of this species were examined. Although the internal structure of the multiple concentric spongy layers is unknown, this form is characterized by an elliptical spongy shell and polar main spines, and is included in the family Sponguridae. Noble (1994) has recognized Late Silurian genera (*Pseudospongoprimum* Wakamatsu, Sugiyama and Furutani, 1990, and *Devoniglansus* Wakamatsu, Sugiyama and Furutani, 1990) of the family Sponguridae. The species assigned to *Pseudospongoprimum* by Noble (1994) are especially characterized by a subspherical to elliptical spongy shell with polar main spines, and they are similar to the present species. This unidentified species, however, differs from all species of *Pseudospongoprimum* by having a loose spongy meshwork and equal lengths to the polar main spines. The exact identification of this species is postponed until sufficient specimens have been examined.

Range and occurrence.—Llandoveryan, Ise area in the Hida "Gaien" Belt.

Family Pylentonemidae? Deflandre, 1963

Genus *Cessipylorum* Nazarov in Afanas'eva, 1986

Type species.—*Pylentonema insueta* Nazarov in Nazarov, Popov and Apollonov, 1975.

Remarks.—Nazarov and Ormiston (1993) tentatively placed the genera *Cessipylorum* and *Aciferopylorum* Nazarov and Ormiston, 1993 in the family Pylentonemidae Deflandre. We tentatively follow that placement.

Cessipylorum? sp.

Figure 9.16

Remarks.—Only one specimen was examined. The cortical shell is subspherical and irregularly porous, and bears a large circular aperture. The pore frame around the aperture is slightly turned up and has small conical spines. The presence of a medullary shell and an inner structure is unclear. The other species in *Cessipylorum*, such as *Cessipylorum apertum* (Nazarov), have long, robust main spines, but this species has only a few thin and short spines. The

generic placement of this species is tentative.

Range and occurrence.—Llandoveryan, Ise area in the Hida "Gaien" Belt.

Family Incertae sedis

Genus *Orbiculopylorum* Noble, Braun and McClellan, 1998

Type species.—*Orbiculopylorum marginatum* Noble, Braun and McClellan, 1998.

Orbiculopylorum sp.

Figure 9.17

Remarks.—The illustrated specimen is distinguished by a prominent pylome on the cortical shell. The cortical shell is thick and probably perforated. However, the detailed structure of the cortical shell cannot be observed, owing to poor preservation. The pylome is circular and flanged. The medullary shell consists of a loose lattice and is irregularly spherical and centrally located. This species is similar to *Orbiculopylorum adobensis* Noble, Braun and McClellan, described from the Cherry Spring Chert of Nevada by Noble *et al.* (1998). However, the former species differs from the latter by having a less compact medullary shell.

Range and occurrence.—Llandoveryan, Ise area in the Hida "Gaien" Belt.

Spumellaria gen. et sp. indet. sp. A

Figure 9.19, 9.20

Labyrinthine spumellarian Noble, Ketner and McClellan, 1997, pl. 1, fig. 14.

Description.—The shell consists of a spongy, three-dimensional meshwork and is irregularly spherical. The spongy meshwork is loose, delicate and has no regular structure or layering. The exterior meshwork seems to be looser than that in the interior. The pores framed by the looped, loose, spongy meshwork are circular to elliptical and vary in size. On the external surface of the shell, short subconical to cylindrical spines arise from the pore frame and usually bifurcate, or rarely trifurcate, at their distal end.

Measurements.—Based on two specimens, in μm . Diameter of shell, 120-170, average, 145.

Remarks.—This species is characterized by an irregular spongy shell without layering. A form referable to this species has been reported by Noble *et al.* (1997) as Labyrinthine spumellarian. *Haplotaeniolum fenestratum* Goto, Umeda and Ishiga, described from the Upper

Figure 9. 1-4. *Inanihella* sp., 1: IGUT-TK 973, 2: IGUT-TK 976, 3: IGUT-TK 986, 4: IGUT-TK 893. 5-7. *Inanihella?* sp., 5: IGUT-TK 975, 6: IGUT-TK 855, 7: IGUT-TK 937. 8, 9. *Inaniguttidae* gen. et sp. indet. sp. A, 8: IGUT-TK 956, 9: IGUT-TK 808. White arrows of 8 and 9 indicate an oversized pore. 10. *Auliela* sp., IGUT-TK 732. 11-13. *Palaeoehippium?* sp., 11: IGUT-TK 843, 12: IGUT-TK 737, 13: IGUT-TK 842. 14, 15. Sponguridae gen. et sp. indet. sp. A, 14: IGUT-TK 940, 15: IGUT-TK 827. 16. *Cessipylorum?* sp., IGUT-TK 922. 17. *Orbiculopylorum* sp., IGUT-TK 743. White arrow of 17 indicates a pylome. 18. Spumellaria gen. et sp. indet., IGUT-TK 972. 19, 20. Spumellaria gen. et sp. indet. sp. A, 19: IGUT-TK 725, 20: IGUT-TK 851. 21. Spumellaria gen. et sp. indet. sp. B, IGUT-TK 868. Scale bars A, B and C each equal 100 μm ; A applies to 1, 2, 8, 10, 14, 18, B to 3-7, 9, 11-13, 15-17, 19, 21, C to 20.

Ordovician of eastern Australia by Goto *et al.* (1992), is similar to this species in the basic construction of its spongy shell. However, *H. fenestratum* lacks certain diagnostic characteristics of *Haplotaeniatum*, such as concentric layers or a spiral form. The taxonomic placement of this species will depend on finding additional specimens.

Range and occurrence.—Early Llandoveryan, northern Adobe Range, Nevada; Llandoveryan, Ise area in the Hida "Gaien" Belt.

Spumellaria gen. et sp. indet. sp. B

Figure 9.21

Remarks.—Several broken specimens were obtained. The illustrated specimen has a spherical shell consisting of a spongy, three-dimensional meshwork. The spongy meshwork structure of this species is similar to that of *Spumellaria* gen. et sp. indet. sp. A, described above, but differs from the latter by having an internal cavity.

Range and occurrence.—Llandoveryan, Ise area in the Hida "Gaien" Belt.

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- ◎第150回例会は、2001年1月27日(土)と28日(日)に「茨城県自然博物館」で開催されます。シンポジウム案の申し込み締切日は2000年4月末日、個人講演の申し込み締切日は2000年12月1日(金)です。
- ◎2001年年会・総会は、21世紀最初の年会ですので、「21世紀の古生物学」を統一テーマとし、東京地区でシンポジウムを中心とした形式で、将来計画委員会を中心となって開催を企画することが決定しております。開催の案内や形式については「化石」67号、83-84頁をご覧ください。
- ◎第151回例会(2002年1月下旬開催予定)の開催申し込みは、今のところありません。
- ◎2002年年会・総会(2002年6月下旬開催予定)には福井県立博物館から開催申し込みがありました。
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