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**Cover** : A terminally resorbed maxillary tooth of iguanodontids (*Ornithischia* : *Ornithopoda*). The specimen is from the Kuwajima Formation, the Neocomian section of the Tetori Group, in Shiramine-mura, Ishikawa County, Ishikawa Prefecture, the west coast of Central Honshu, Japan (Shiramine-mura Board of Education, Coll. Cat. No. SBEI 001, 23 mm in dorsoventral length).

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## Some new species of freshwater bivalves from the Mio-Pliocene Churia Group, west-central Nepal

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**Abstract.** Systematic study of the Mio-Pliocene freshwater molluscan fossil fauna from the Churia Group of Nepal has revealed many new species. In this first publication of the study, the bivalves are described. The new species of bivalves are *Lamellidens arungensis*, *Lamellidens longiformis*, *Indonaia churia*, *Indonaia narayani*, *Indonaia jimuriensis*, *Indonaia tenella*, *Parreysia binaiensis*, *Parreysia zigzagcostata* and *Physunio chitwanensis*.

**Key words:** Siwaliks, Churia Group, freshwater molluscs, Mio-Pliocene, Nepal

### Introduction

The Middle Miocene to Pleistocene Churia Group (Tokuoka *et al.*, 1986) of Nepal, equivalent to the Siwaliks of India and Pakistan, is well exposed in the southernmost foothills of the Himalayas. Sediments of this Group contain abundant fossil flora and fauna, among which molluscs make up an important group. In spite of many reports about the abundance of molluscan fossils, there are no detailed studies, and their taxonomy, distribution and diversity are poorly understood.

Comparatively more work related to the taxonomy of molluscs from the Siwaliks has been carried out in India, Burma and Pakistan (Vredenburg and Prashad, 1921; Annandale, 1924; Prashad, 1927, 1930; Vokes, 1935, 1936; Bhatia and Mathur, 1973; Bhatia, 1974). Although several paleontological studies have been carried out in the Nepal Siwaliks, all have emphasized the vertebrate fauna (Munthe *et al.*, 1983; Corvinus, 1988; West *et al.*, 1991) with little work related to molluscs (West *et al.*, 1975; Takayasu, 1988, 1992). The present systematic study is being carried out for the first time in the Nepal Siwaliks in order to understand the distribution and paleoecology of the Late Tertiary freshwater fauna.

The Churia Group was deposited contemporaneously with uplift of the Himalayas. It is regarded as a fluvial deposit, up to 6,000 m thick, which was deposited without any major break. In these sediments most molluscan fossils are preserved *in situ*, contrary to terrestrial fossils, which are commonly preserved far from their habitat. Therefore, molluscs should be better indicators of aquatic ecological conditions prevailing at the time. Similarly, if

changes in the type and distribution of molluscs in time and space can be evaluated ecological variations due to changes in climate as well as topography during the rise of the Himalayas can also be gauged. Apart from controlling the climate of the Eurasian Continent, the Himalayas, at present, are a major biogeographic barrier. Its role as a paleobiogeographic barrier can also be determined by studying the presence or absence of different elements in the molluscan assemblage. In this context, a detailed study of molluscan fossils can play an important role.

In order to investigate these problems, a basic study of identifying and describing fossil molluscs is being carried out. Most molluscs are recognized to be new species. In this paper, new species of bivalves are described with an outline of geology and fossil localities. In the next paper, gastropods will be described with a discussion of molluscan distribution.

### Acknowledgments

We would like to thank Prof. K. Kizaki of Tribhuvan University (Professor Emeritus of The University of Ryukyus) and Prof. T. Tokuoka of Shimane University, who provided much needed field data and encouragement for this study. We also thank Dr. J. Itoigawa (Professor Emeritus of Nagoya University) and Prof. I. Kobayashi of Niigata University, for their guidance and advice. We are much obliged to the Central Department of Geology, Tribhuvan University, for their assistance and support.

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Peabody Museum of Natural History, Yale University, who loaned the museum specimens for study. We are very grateful to Dr. K. Ayyasami, Geological Survey of India, Indian Museum, Calcutta, who made available the museum specimens for comparative study.

### Geological Setting and Fossil Localities

Molluscs discussed in this study were collected from fossil localities (F11 to F23) reported by Tokuoka *et al.* (1986) and two additional localities (F24 and F25), from west-central Nepal (Figure 1). As the lithostratigraphy and magnetostratigraphy of the area (Figure 2) have been established by Tokuoka *et al.* (1986), their nomenclature is adopted here.

In the studied area (Figure 1), which covers the Arung Khola and Binai Khola valleys, the Churia Group is confined by the Main Boundary Thrust to the north and by the Frontal Churia Thrust to the south. The Central Churia Thrust within this group separates it into a North and a South Belt. The strata in the North Belt are steeply inclined toward the north, whereas in the South Belt the beds are less steeply inclined. All the beds have a general east-west strike. Lithostratigraphically the Churia Group is divided into the Arung Khola, Binai Khola, Chitwan and Deorali Formations, in ascending order. As a whole the Churia Group shows a coarsening-upward sequence, attaining a thickness of up to 6,000 m.

The Middle Miocene to early Late Miocene Arung Khola Formation is composed mainly of irregular alternating beds of fine-grained sandstone and siltstone with intercalations of variegated and coal black mudstone. It is subdivided into a lower (Al), middle (Am) and upper (Au) members. The Late Miocene to Early Pliocene Binai Khola Formation is dominated by thick-bedded sandstone and thin-bedded alternating beds of sandstone and siltstone with intercalations of pepper-and-salt sandstone. It is subdivided into a lower (Bl), middle (Bm) and upper (Bu) member. The Chitwan Formation, of Late Pliocene to Early Pleistocene age, is composed predominantly of gravel beds with subordinate sand and silt layers. The uppermost Deorali Formation, of Late Pleistocene age, consists of poorly sorted boulder-conglomerate beds.

The North Belt contains strata up to the middle member of the Binai Khola Formation, whereas in the South Belt strata from the upper member of the Arung Khola Formation onward are distributed.

Most fossil occurrences are concentrated between the upper member of the Arung Khola Formation and the middle member of the Binai Khola Formation. In the studied area molluscan fossils are distributed at 15 sites (from F-11 to F-25) and are grouped into five stratigraphic horizons, F (Au), F (Bl-1), F (Bl-2), F (Bm-1) and F (Bm-2) (Figure 2). From the data so far collected the molluscan fossils are found to occur around 9.0 Ma, at F (Au) horizon, about the middle part of the upper member of the Arung Khola Formation. Above the topmost horizon F (Bm-2) (upper part of the middle member of the Binai Khola Formation) freshwater molluscan fossils are uncommon.

Molluscan fossils are generally found in dark gray to black mudstone and silty sandstone. Some specimens are deformed but most of the bivalves have conjoined valves suggesting little or no transportation. Within a fining-upward sequence formed by a meandering river system, molluscan fossil horizons occur at two specific levels: at the transitional part from the lower coarse-grained unit to the upper fine-grained unit, and at the uppermost part of the upper fine-grained unit. Most of the fossil horizons lie at the latter level with only F-12 occurring at the former level (Takayasu, 1992). One fossil locality, F-21, consists of two layers of mud blocks intercalated in a thick-bedded sandstone. According to Tokuoka *et al.* (1986), these fossil-bearing blocks have been derived from the underlying fossil bed. Most of the fossil localities contain a rich fauna, with varying states of preservation. Molluscan fossils are found with fish pharyngeal teeth, fish scales, crocodile teeth, bone fragments and charophyte gyrogonites.

All the specimens described here are deposited at the Toyohashi Museum of Natural History, Toyohashi, 441-31 Japan.

### Systematic paleontology

Class Bivalvia

Family Unionidae Fleming, 1828

Genus *Lamellidens* Simpson, 1900

*Type species.*—*Unio marginalis* Lamarck, 1819. Recent, East India.

*Geologic range.*—Miocene to Recent.

*Remarks.*—The genus has elongated elliptical shell and pointed behind. Anterior end is narrow and posterior end broad with posterior dorsal wing. Umbonal part is covered with curved radiating ridges which may be slightly zigzag-shaped or almost concentric, fading out gradually. Dentition is composed of compressed, elongated pseudocardinal and long posterior lamellar teeth.

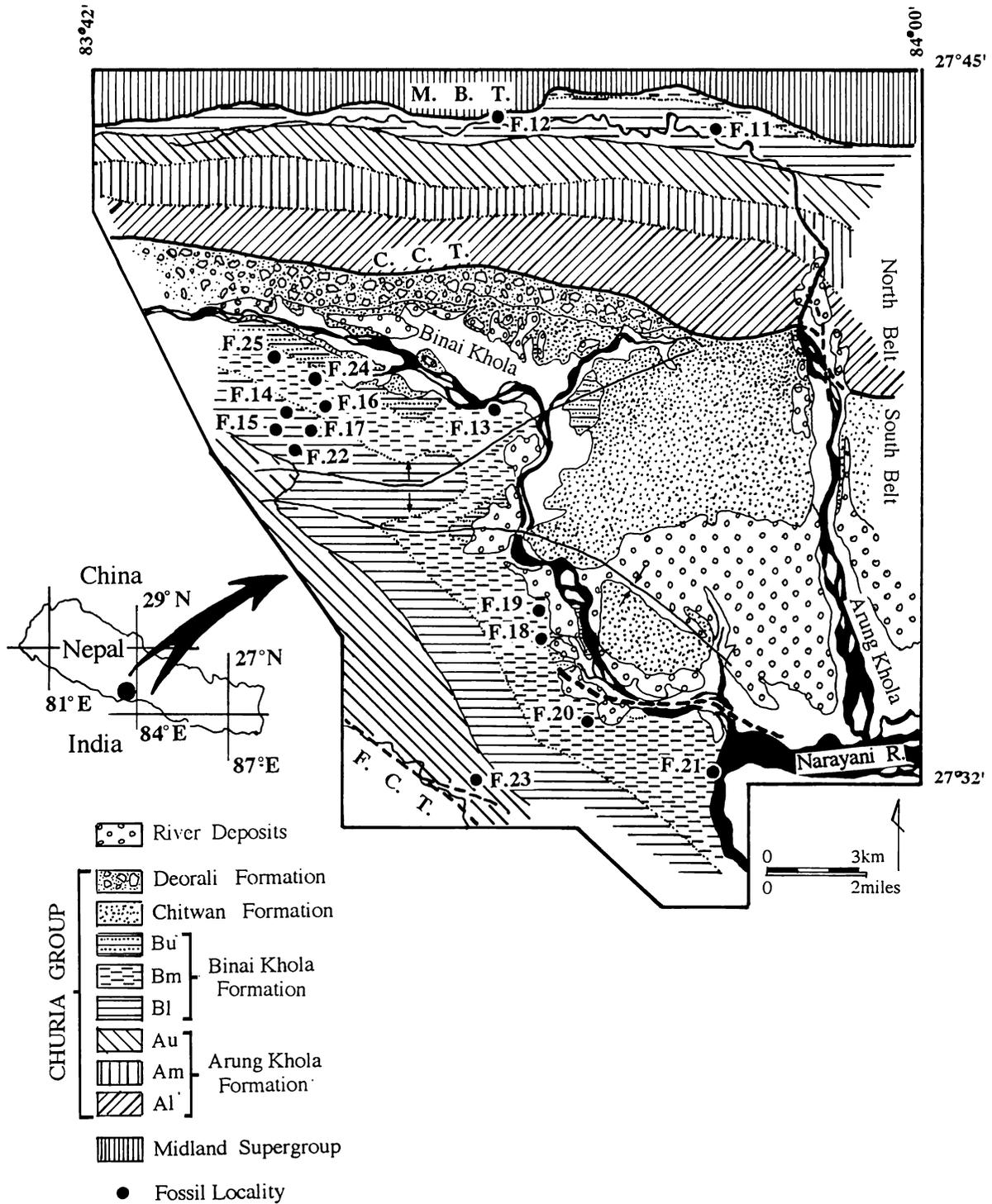
The genus *Lamellidens* was established for widely distributed species of Unionidae in India and Burma. Many representative species of this genus of the Indian subcontinent are well documented in Preston (1915). Fossil species of this genus have been reported from the Siwaliks of Pakistan (Vokes, 1935, 1936), India and Burma (Prashad, 1921, 1927, 1930; Annandale, 1924).

### *Lamellidens arungensis* n. sp.

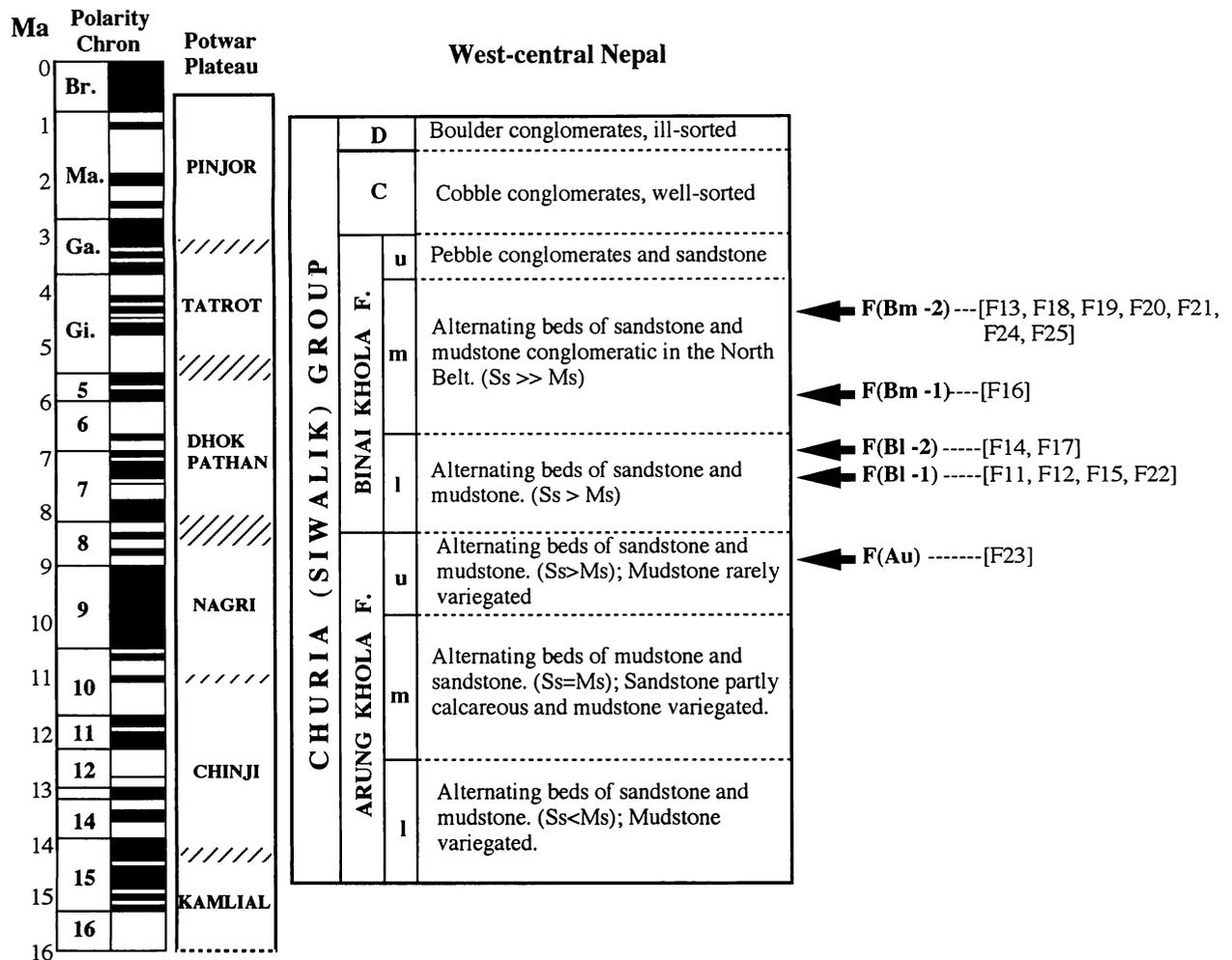
Figures 3-1-4

*Type locality.*—The left bank of the west to east flowing Arung Khola (F-11 in Figure 1), about 700 m west of the confluence with the Murali Khola. Lower member of the Binai Khola Formation.

*Description.*—Shell moderately large for the genus, subrhomboidal in outline and moderately elongated. Valves subinflated and a little thick. Umbo only slightly



**Figure 1.** Generalized geological map of the Arung-Binai Khola area, west-central Nepal (after Tokuoka *et al.*, 1986), with molluscan fossil localities.



**Figure 2.** Stratigraphic position of fossil horizons with magnetostratigraphy and chronology of the Arung-Binai Khola area correlated with the Potwar Plateau of Pakistan (after Takayasu, 1988).

raised, broadly rounded and situated at anterior third of the shell. Dorsal margin nearly straight and long. Anterior margin regularly and somewhat narrowly rounded. Ventral margin widely rounded and rather long. Posterior margin truncated above the medial line. Posterior ridge indistinct and not extending to the ventral margin. Posterior wing long and narrow. Ligament placed posterior to the beak, quite long and protruding. Shell surface with concentric growth lines. Hinge only partially observed in the paratype 2, a left valve, two long lamellar teeth, upper one more prominent.

**Measurements (in mm).—**

TMNH * coll. cat. no.	Length	Height	Depth	Valve
02027 (Holotype)	83.4	48.2	11.8/2	Both (slightly compressed)
02028 (Paratype 1)	70.0	40.8	—	Left (slightly compressed)
02029 (Paratype 2)	70.0	42.0	—	Left
02030 (Paratype 3)	67.6	33.3	—	Right (incomplete)

\* Abbreviation for Toyohashi Museum of Natural History, Toyohashi, Japan.

**Comparison.**—The present species differs from *Lamel-*

*lidens lewisi* Vokes (1936) from the Upper Siwalik of Pakistan in that the former is smaller in size and has more broadly rounded ventral margin. It can be distinguished from *Lamellidens jammuensis* Prasad (1921), Upper Siwalik Beds, Jammu, in having a less inflated shell, smaller posterior wing and more narrowly rounded anterior margin.

**Etymology.**—The name is taken from the river, Arung Khola, which flows by the type locality.

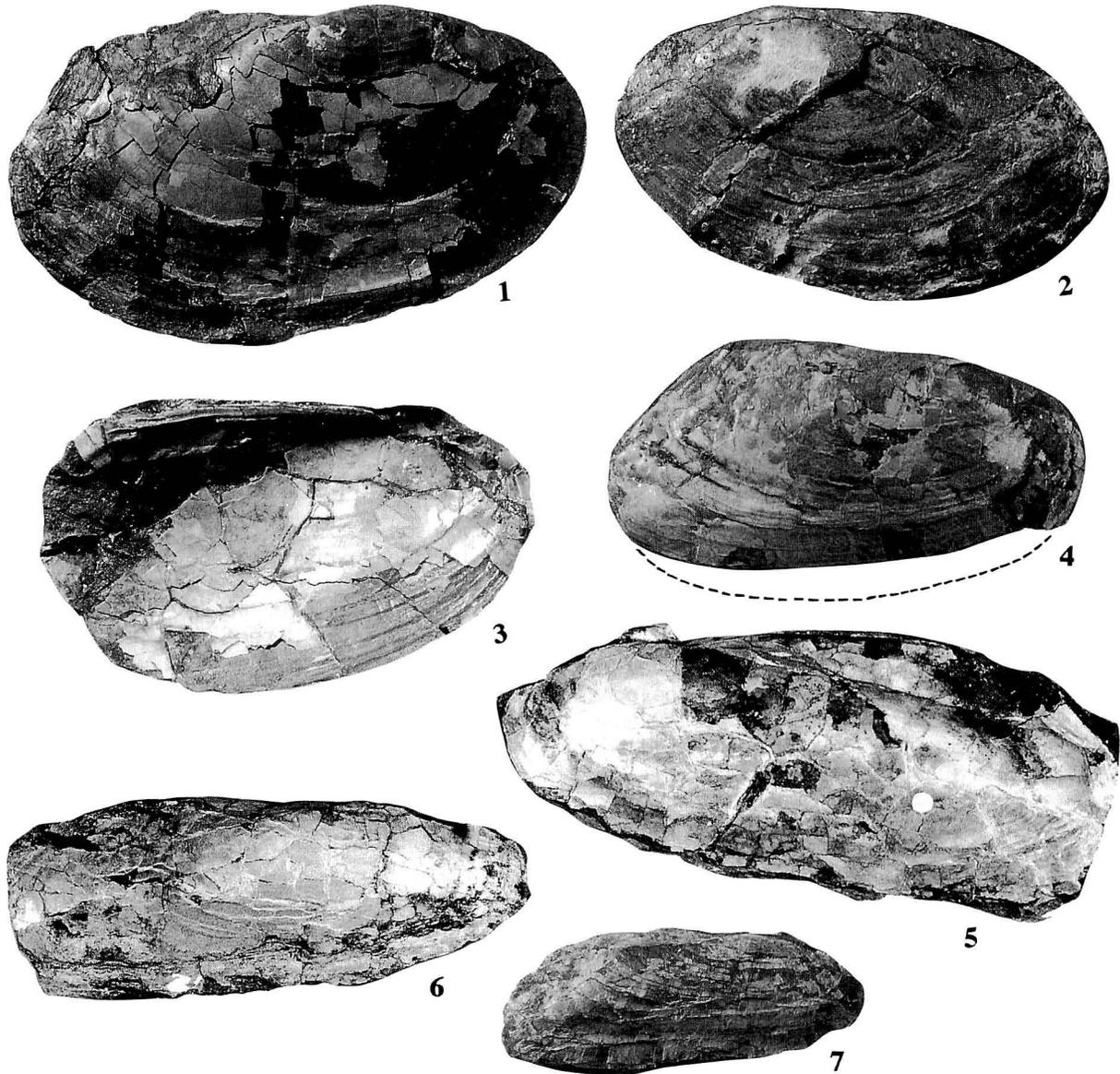
**Stratigraphic range.**—Lower to middle member of the Binai Khola Formation.

**Localities.**—F-11, F-12, F-16 and F-17.

***Lamellidens longiformis* n. sp.**

Figures 3-5—7

**Type locality.**—The right bank of the Narayani River, 500 m south of the confluence with the Binai Khola (F-21 in Figure 1). Middle member of the Binai Khola Forma-



**Figure 3.** 1-4. *Lamellidens arungensis* n. sp. 1: holotype, TMNH02027, 2: paratype 1, TMNH02028, 3: paratype 2, TMNH02029, 4: paratype 3, TMNH02030. 5-7. *Lamellidens longiformis* n. sp. 5: holotype, TMNH02031, 6: paratype 1, TMNH02032, 7: paratype 2, TMNH02033. All figures are natural size.

tion.

*Description.*—Shell moderately large, much elongated in outline and very inequilateral. Anterior end narrower than posterior end. Valves thick and quite inflated, more so along the medial part. Umbo small, low, inconspicuous and very anteriorly placed, at anterior fifth of the valve. Dorsal margin straight and very long. Anterior margin narrowly rounded and short. Ventral margin very long and gently curved to nearly straight. Posterior margin incompletely preserved in the holotype, but as observed in the paratype 2, narrowly rounded at the medial part, almost straight above it and forming a broad

angle with the straight dorsal margin. Posterior ridge well developed, high, long and round-topped, separated from the posterior wing by a distinct groove. Posterior wing long and narrow. Shell surface covered with concentric growth lines as observed in the paratype 2. Internal structure and hinge not observed.

*Measurements (in mm).*—

TMNH coll. cat no.	Length	Height	Depth	Valve
02031 (Holotype)	90.0+	40.2+	22.2+ /2	Both
02032 (Paratype 1)	91.0+	37.0	21.0+ /2	Both
02033 (Paratype 2)	52.0	20.0	16.9/2	Both

*Comparison*.—Owing to its rather elongated shape, *Lamellidens longiformis* is quite distinct from most of the other *Lamellidens* species except *L. subparallelus*. Vokes (1935) from the Lower Siwalik of Pakistan. The present species possesses a longer posterior wing, more anteriorly placed umbo, and narrower anterior end and is smaller in size than *L. subparallelus*.

*Etymology*.—It is named for its characteristic long shell shape.

*Stratigraphic range*.—Middle member of the Binai Khola Formation.

*Localities*.—F-16 and F-21.

#### Genus *Indonaia* Prashad, 1918

*Type species*.—*Unio caeruleus* Lea, 1831. Recent, West Bengal, India.

*Geologic range*.—Miocene to Recent.

*Remarks*.—The genus is characterized by ovate and slightly elongated shell with thin but relatively solid valves. The umbonal area and a part or all of the shell is marked by narrow and fine zigzag sculpture. Pseudocardinals are short and stout, and posterior lateral teeth are lamelliform.

The genus *Indonaia* was established by Prashad (1918) for Indian species previously grouped with the genus *Nodularia* Conrad (1853) after examining the soft parts and the glochidium structure. In the *Treatise on Invertebrate Paleontology*, Haas (1969) treated the genus *Indonaia* as a synonym of *Radiatula* Simpson (1900), a subgenus of *Parreysia* Conrad (1853). Further, Subba Rao (1989) has also followed Haas (1969) mentioning the main differences between *Parreysia* s.s. and *Radiatula*, the former having a swollen ventral margin and the latter an almost straight one. However, the type species of *Radiatula*, *Unio crispisulcatus*, has a rather swollen ventral margin like that of *Parreysia* s.s. On the other hand, the type species of *Indonaia*, *U. caerulea*, has a longer and nearly straight ventral margin, which more resembles the present new species. Therefore, *Indonaia* is kept as an independent genus in the present report. It is also used in the same manner by Brandt (1974) for Thai species. Fossil species of this genus are recorded from Pakistan (Vokes, 1935, 1936), India (Prashad, 1927; Bhatia and Mathur, 1973) and Burma (Vredenburg and Prashad, 1921; Annandale, 1924).

#### *Indonaia churia* n. sp.

Figures 4-1—3

*Type locality*.—The right bank of the Narayani River about 500 m south of the confluence with the Binai Khola (F-21 in Figure 1). Middle member of the Binai Khola Formation.

*Description*.—Shell moderately large, elongated oval in shape with subtruncated posterior end. Valves moderately thick and rather inflated. Umbo prominent, rounded, anteriorly directed and situated at one third the distance from anterior end. Dorsal margin slightly

curved. Anterior margin short and regularly rounded. Ventral margin long and gently curved. Posterior margin narrowly rounded and somewhat truncated. Posterior ridge bluntly rounded. Posterior slope narrow and a little convexed. Shell surface marked only with concentric growth lines. Hinge partially exposed (in holotype, a right valve) but slightly eroded; hinge slender with a small, short pseudocardinal and a long, gently curved lamellar tooth. Adductor muscle scars are observed in the core of the paratypes. Anterior one oval in outline, deeply impressed and posterior one similar in outline but larger and shallower. Pallial line fairly impressed and without sinus. Inner ventral margin smooth.

#### *Measurements (in mm)*.—

TMNH coll. cat. no.	Length	Height	Depth	Valve
02034 (Holotype)	40.6+	25.4+	8.1+	Right
02035 (Paratype 1)	41.0	29.0	14.0/2	Both (incomplete)
02036 (Paratype 2)	44.7+	30.5+	14.0/2	Both (incomplete)

*Comparison*.—*Indonaia churia* has a more anteriorly placed and less prominent umbo than *Indonaia prashadi* Vokes (1936) from the Lower Siwalik of Pakistan. The present species can be distinguished from *Indonaia mittali* Prashad (1927) of the Upper Siwalik, Jammu, Kashmir as the former possesses a less prominent umbo and shorter anterior end. It also differs from *Indonaia glyptica* Vredenburg and Prashad (1921) from the Miocene Irrawaddy Series, Burma, in having a less rounded ventral margin and smaller umbo.

*Etymology*.—It is named after the low mountain range, the Churia.

*Stratigraphic range*.—Middle member of the Binai Khola Formation.

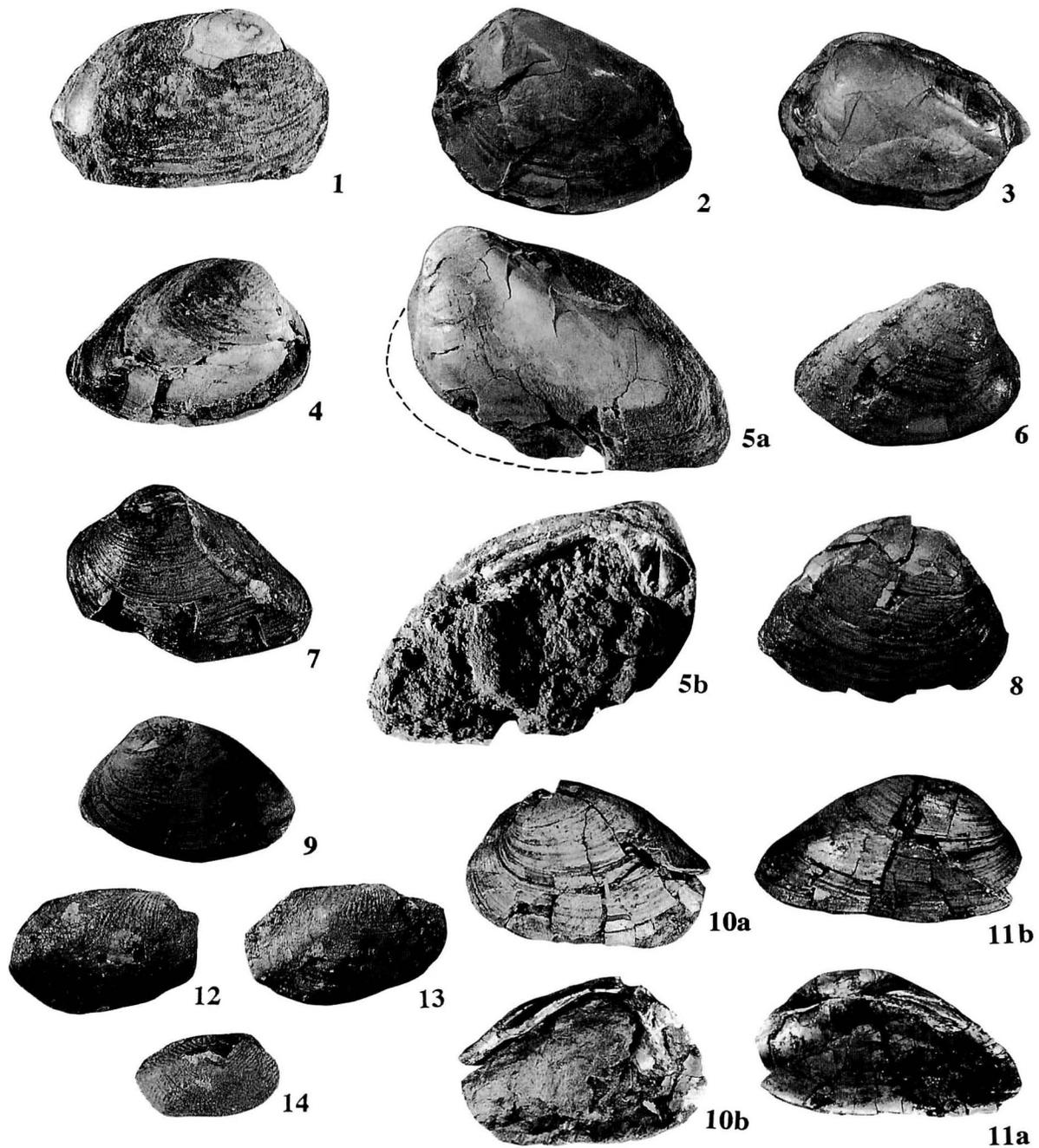
*Localities*.—F-21 and F-24.

#### *Indonaia narayani* n. sp.

Figures 4-4—7

*Type Locality*.—Right bank of the Narayani River, about 500 m south of the confluence with the Binai Khola (F-21 in Figure 1). Middle member of the Binai Khola Formation.

*Description*.—Shell moderately large and ovate trigonal in outline. Valves fairly thick and inflated. Umbo prominent, anteriorly directed, rounded and placed very anteriorly, at one fourth of the shell length. Dorsal margin rather arched with maximum curvature just behind the umbo. Anterior margin short and regularly rounded. Ventral margin long and very gently arched. Posterior margin sharply curved. Posterior ridge distinct and nearly straight. Posterior slope narrow and convexed. Ligament small, lenticular in shape and placed just behind the umbo. Surface of the shell bearing fine concentric growth lines with zigzag sculpture limited on the umbonal area. The dentition can not be observed in the holotype but is well exposed in the paratype 1 (left valve). Hinge plate slender and long with short interdentum. Anterior pseudocardinal consists of two short and sharp ridges;



**Figure 4.** 1-3. *Indonaia churia* n. sp. 1: holotype, TMNH02034, 2: paratype 1, TMNH02035, 3: paratype 2, TMNH02036. 4-7. *Indonaia narayani* n. sp. 4: holotype, TMNH02037, 5: paratype 1, TMNH02038; 5a, outer surface of left valve, 5b, inner view of left valve, 6: paratype 2, TMNH02039, 7: paratype 3, TMNH02040. 8-11. *Indonaia jimuriensis* n. sp. 8: holotype, TMNH02041, 9: paratype 3, TMNH02044, 10: paratype 1, TMNH02042; 10a, outer view of left valve, 10b, inner view of left valve, 11: paratype 2, TMNH02043; 11a, outer view of right valve, 11b, inner view of right valve. 12-14. *Indonaia tenella* n. sp. 12: holotype, TMNH02047, 13: paratype 1, TMNH02048, 14: paratype 2, TMNH02049. All figures are natural size.

anterior one larger and posterior placed just below the beak. Posterior lamellar laterals two, long, bladelike (lower one is more prominent). Anterior adductor scar deeply impressed and oval in shape whereas posterior one larger and shallower. Pallial line faintly impressed and entire.

*Measurements (in mm).—*

TMNH coll. cat. no.	Length	Height	Depth	Valve
02037 (Holotype)	33.3	32.9	12.0/2	Both
02038 (Paratype 1)	52.3+	32.0+	12.7+	Left (incomplete)
02039 (Paratype 2)	31.6	24.9	8.0	Right
02040 (Paratype 3)	36.0	26.0+	—	Left (incomplete)

*Comparison.*—The present species has a more protruding posterior end and more anteriorly placed umbo than the preceding species, *Indonaia churia*. In shape and size *Indonaia narayani* is somewhat similar to *Indonaia glyptica* Vredenburg and Prasad (1921) from the Miocene Irrawaddy Series, Burma, but the former has a less prominent umbo and less rounded ventral margin. It has a smaller umbo situated more anteriorly with a much arched dorsal margin compared to *Indonaia mittali* Prasad (1927) from the Upper Siwalik, Jammu, Kashmir.

*Etymology.*—The new species is named after the major river of Nepal, the Narayani, as its type locality lies along its bank.

*Stratigraphic range.*—Middle member of the Binai Khola Formation.

*Localities.*—F-18, F-21 and F-24.

*Indonaia jimuriensis* n. sp.

Figures 4-8—11

*Type locality.*—About 1.3 km northwest of Dumkibas, at the left bank of the Jimuri Khola (F-19 in Figure 1). Middle member of the Binai Khola Formation.

*Description.*—Shell moderately large, about 38.0 mm in size, elongated oval in outline. Valves moderately thick, not very solid and slightly inflated. Umbo rounded, small situated anteriorly at one third of the shell length. Dorsal margin broadly arched. Anterior margin rounded and a little high. Ventral margin long and gently curved. Posterior margin short and narrowly rounded. Posterior ridge not prominent but rounded and extending to the posterior end. Posterior slope narrow and slightly convex. Surface of the shell smooth with fine concentric growth lines only. Umbonal cavity shallow. Dentition exposed in paratype 1 and paratype 2. Hinge plate slender. Pseudocardinals short and compact; one in the right valve and two in the left valve. Posterior lamellar laterals are long and smooth; one in the right valve and two in the left valve (lower one more prominent). Anterior adductor muscle scar deeply impressed and oval in shape; posterior one shallower, larger and round in shape. Pallial line faintly impressed and entire. Inner ventral margin smooth.

*Measurements (in mm).—*

TMNH coll. cat. no.	Length	Height	Depth	Valve
02041 (Holotype)	38.2+	27.5+	11.7/2	Both (slightly compressed)
02042 (Paratype 1)	35.9+	23.7	8.3	Left (slightly deformed)
02043 (Paratype 2)	37.8+	21.0+	8.0	Right (slightly deformed)
02044 (Paratype 3)	26.9+	22.8	—	Left
02045	38.4+	25.7+	—	Both (crushed)
02046	37.2	25.8	6.6	Left

*Comparison.*—Due to its less prominent and broadly rounded umbo, *Indonaia jimuriensis* can be distinguished from most of the other species of *Indonaia*. The present species, however, is slightly similar in outline to *Parreysia latouchei* Vredenburg and Prasad (1921) from the Miocene Irrawaddy Series of Burma but the former has no zigzag sculpture and the umbo is more rounded.

*Etymology.*—It is named after the River Jimuri Khola, flowing near its type locality.

*Stratigraphic range.*—Middle member of the Binai Khola Formation.

*Locality.*—F-19.

*Indonaia tenella* n. sp.

Figures 4-12—14

*Type locality.*—South of Dumkibas (F20 in Figure 1), along the Kedi Khola, about 800 m upstream from the confluence with the Binai Khola. Middle member of the Binai Khola Formation.

*Description.*—Shell small in size, rounded trapezoidal in shape. Valves rather thin and a little inflated. Umbo slightly raised, inconspicuous, rounded and situated at anterior third of the shell. Dorsal margin long and nearly straight. Anterior margin short and narrowly rounded. Ventral margin long and broadly rounded. Posterior margin truncated. Posterior ridge moderately prominent, rounded and terminates at posterior margin forming an angulation just below the medial line. Posterior wing wide and flat. The umbonal area as well as half the disk area sculptured with fine zigzag lines and rest of the shell surface covered with irregular concentric growth lines. The internal structures as well as the dentition can not be observed.

*Measurements (in mm).—*

TMNH coll. cat. no.	Length	Height	Depth	Valve
02047 (Holotype)	30.8+	19.3+	5.0+	Right
02048 (Paratype 1)	30.4+	19.0	5.0+	Right
02049 (Paratype 2)	21.6	12.2	—	Right

*Comparison.*—*Indonaia tenella* is somewhat similar to *Indonaia hasnotensis* Vokes (1935) from the Middle Siwalik of Pakistan in shell outline and surface sculpture but the former is much smaller in size and has a thinner shell with a more straight dorsal margin. The present new species is also similar to *Parreysia (Radiatula) lima* (Subba Rao, 1989, p.190, figures 528-531), a Recent species of northeast India, in size and surface sculpture, but the former has a less rounded posterior end, narrower anterior margin and more rounded ventral margin.

*Etymology.*—It is named so as it means 'quite delicate'

in Latin.

*Stratigraphic range*.—Middle member of the Binai Khola Formation.

*Localities*.—F-20 and F-25.

### Genus *Parreysia* Conrad, 1853

*Type species*.—*Unio multidentatus* Philippi. Recent, India.

*Geologic range*.—Miocene to Recent.

*Remarks*.—The genus is characterized by a heavy, inflated and rounded subrhomboidal shell with radial zigzag sculpture on the umbo or on the whole of the disk. Pseudocardinals are irregular, heavy and striated. Lateral teeth are lamelliform, short and two in each valve.

In the *Treatise on Invertebrate Paleontology* Haas (1969) subdivided this genus into two subgenera, *Parreysia* s.s. and *Radiatula* Simpson (1900) for the South Asian species. As already mentioned the type species of the subgenus *Radiatula* is much similar to *Parreysia* s.s. and therefore the genus *Parreysia* is not further subdivided in this paper. Many fossil species of this genus have been reported from the Siwaliks of Pakistan (Vokes, 1935, 1936), India (Prashad, 1927) and Burma (Vredenburg and Prashad, 1921).

### *Parreysia binaiensis* n. sp.

Figures 5-1—5

*Type locality*.—About 700 m west of the confluence of the west-east flowing Arung Khola and the north-south flowing Murali Khola (F-11 in Figure 1). Lower member of the Binai Khola Formation (B1).

*Description*.—Shell moderately large for the genus, subtrigonal in shape with rather thick and inflated valves. Umbo large, inflated and situated subcentrally toward anterior side. Dorsal margin arched. Anterior margin regularly rounded. Ventral margin short and moderately curved. Posterior margin short, nearly straight and subtruncated. Posterior ridge prominent, sharply rounded and diagonally extends from umbo to posteroventral angulation. Posterior slope a little wide and flat. Ligamental groove shallow and extends from beak to small angulation in the posterodorsal margin. Umbonal area with zigzag sculpture and remaining area covered with irregular concentric growth lines. Umbonal cavity moderately deep. Hinge plate thick; anterior and posterior teeth set nearly at right angle with flat, short interdentum. Dentition moderately heavy; pseudocardinals irregularly serrated, strong, two in the left valve (anterior one is parallel to the dorsal margin and larger) and one in the right; laterals relatively short, straight and two in both valves (upper one larger and lower one composed of few short, inclined ridges). Anterior adductor muscle scar deeply impressed and oval in shape with small and shallow pedal protractor muscle scar just below it. Posterior adductor muscle scar oval in shape, shallower and larger with pit-like pedal retractor muscle scar above. Pallial line faintly impressed without sinus. Inner ventral

margin smooth without crenulation.

### *Measurements (in mm)*.—

TMNH coll. cat. no.	Length	Height	Depth	Valve
02050 (Holotype)	39.85	33.9	11.7	Left
02051 (Paratype 1)	35.1	32.5	12.2	Right
02052 (Paratype 2)	38.0	32.9	19.5/2	Both
02053 (Paratype 3)	24.2+	21.6	12.5/2	Both (incomplete)
02054 (Paratype 4)	20.7+	19.0	6.8+	Left
02055	41.4+	38.5	12.8	Left
02056	28.6+	28+	9.2	Left
02057	26.6+	20.5	11.8	Left

*Comparison*.—The present species shows some similarity in surface sculpture and umbo position to *Parreysia detterai* Vokes (1936) from the Upper Siwalik Series, Pakistan, but the latter is more triangular in shape with a very arched hinge plate and almost vertical posterior ridge. It differs from *Parreysia tatrotensis* Vokes (1935), also from the Upper Siwalik Series, in having a less elongated shape and no posterior wing. The new species is distinct in its trigonal outline, inflated umbo and strong hinge plate from all the species of the Recent *Parreysia* group from India and Burma illustrated by Subba Rao (1989).

*Etymology*.—The new fossil species is named after the River Binai Khola after which the formation containing the above described fossil is also named.

*Stratigraphic range*.—Lower member of the Binai Khola Formation.

*Localities*.—F-11 and F-12.

### *Parreysia zigzagicostata* n. sp.

Figures 5-6—10

*Type locality*.—About 700 m west of the confluence of the Arung Khola and the Murali Khola (F-12 in Figure 1). Lower member of the Binai Khola Formation.

*Description*.—Shell moderately large in size and rounded trigonal in shape. Valves inflated and moderately thick. Umbo subcentral, toward anterior half, prominent and narrowly rounded. Dorsal margin broadly rounded. Anterior margin regularly rounded. Ventral margin short and gently rounded. Posterior margin subtruncated. Posterior ridge prominent with wide and slightly concave posterior slope. Ligamental groove narrow and faintly impressed, extending from the beak to the angulation in the posterodorsal margin. Shell surface strongly sculptured with radial zigzag ridges from umbonal area to more than half of the disk area and the lower part covered with concentric growth lines. Umbonal cavity shallow and broadly rounded. Dentition well developed with strong hinge plate separated by a little long interdentum. Pseudocardinals irregularly serrated, moderately strong, two in the left valve (upper-anterior one most developed and ridgelike) and one in the right; laterals short but strong, curved, two in both valves (upper one more prominent and bladeliike; lower one weakly developed diagonal ridges). Anterior adductor muscle scar oval in shape, deeply impressed with shallow pedal

protractor muscle scar just below it. Posterior one larger but shallower with pit-like pedal retractor muscle scar just above. Pallial line faintly impressed and entire. Inner margin smooth without crenulation.

*Measurements (in mm).—*

TMNH coll. cat. no.	Length	Height	Depth	Valve
02058 (Holotype)	30.6+	25.9+	8.3	Right
02059 (Paratype 1)	29.0+	22.1+	9.2	Left
02060 (Paratype 2)	23.5	17.4	10.0/2	Both
02061 (Paratype 3)	21.3	17.0	11.4/2	Both
02062 (Paratype 4)	27.7+	20+	10.1	Right

*Comparison.*—*Parreysia zigzagcostata* is characterized by its broadly rounded hinge plate, less prominent umbo and strong zigzag sculpture. The preceding species *Parreysia binaiensis* is distinguished from the present species in having a more arched hinge plate, much rounded, raised umbo and zigzag sculpture limited to the umbonal area. The new species is also more elongated than *Parreysia detterai* Vokes (1936) from the Upper Siwalik of Pakistan and the dorsal margin in the latter is very arched. *Unio edwini* described by Gupta (1930) from the Miocene Irrawaddy Beds of Burma, has a shell sculpture like *Parreysia zigzagcostata* but in the former the ribs are coarser and persistent down to several shell layers. In shell outline the present species is similar to the Recent Burmese species *Parreysia bhamoensis* (Subba Rao, 1989, p. 177, figures 446–447) but the latter has faintly marked zigzag sculpture and lamellar pseudocardinals and is larger in size.

*Etymology.*—It is named after its characteristic shell surface sculpture.

*Stratigraphic range.*—Lower member of the Binai Khola Formation.

*Localities.*—F-11 and F-12.

Genus *Physunio* Simpson, 1900

*Type species.*—*Unio gravidus* Lea, 1856 = *Unio superbus* Lea, 1843. Recent, South East Asia.

*Geologic range.*—Pliocene to Recent.

*Remarks.*—The genus is characterized by thin, rhomboidal or obovate shell with more or less high posterior wing and produced posterior base. Umbo is anteriorly placed and sculptured with zigzag folds. Hinge consists of elongated pseudocardinal and short lamellar laterals.

This genus is divided into three subgenera, *Physunio* s.s., *Lens* and *Velunio* in the *Treatise on Invertebrate Paleontology*. From its ovate-rhomboidal outline and high wing, the present fossil species doubtlessly belongs

to the genus *Physunio*, but due to poor preservation of the specimens a more exact assignment cannot be made at present. This is the first report of fossil *Physunio* from South Asia. The genus is considered an Indo-Chinese element; its westernmost extension is up to Assam, northeast India at present but it is mainly distributed in Cambodia, Vietnam and Thailand (Annandale, 1918). Therefore, the present finding indicates a much wider western extension during Pliocene time.

*Physunio chitwanensis* n. sp.

Figures 5–11–14

*Type Locality.*—Right bank of the Narayani River, 500 m south of the confluence with the Binai Khola (F-21 in Figure 1). Middle member of the Binai Khola Formation.

*Description.*—Shell moderately large in size. Rounded rhomboidal in outline with anterior end narrower than posterior. Valves moderately thick and not much inflated. Umbo, low, inconspicuous, anteriorly directed, situated at about one fourth the distance from anterior end. Dorsal margin nearly straight and slightly long. Anterior margin short and regularly rounded. Ventral margin anteriorly short and arched, posteriorly long and nearly straight. Posterior margin long and truncated with bluntly produced basal part. Posterior ridge faintly developed, posterior slope wide and slightly concave. Posterior wing well developed, high and subtrigonal in outline. Surface of the shell marked with concentric growth lines as observed in paratype 1. Hinge and the internal structures of the shell not observed but in paratype 2 (right valve), one long well developed posterior lateral parallel to the dorsal margin observed.

*Measurements (in mm).—*

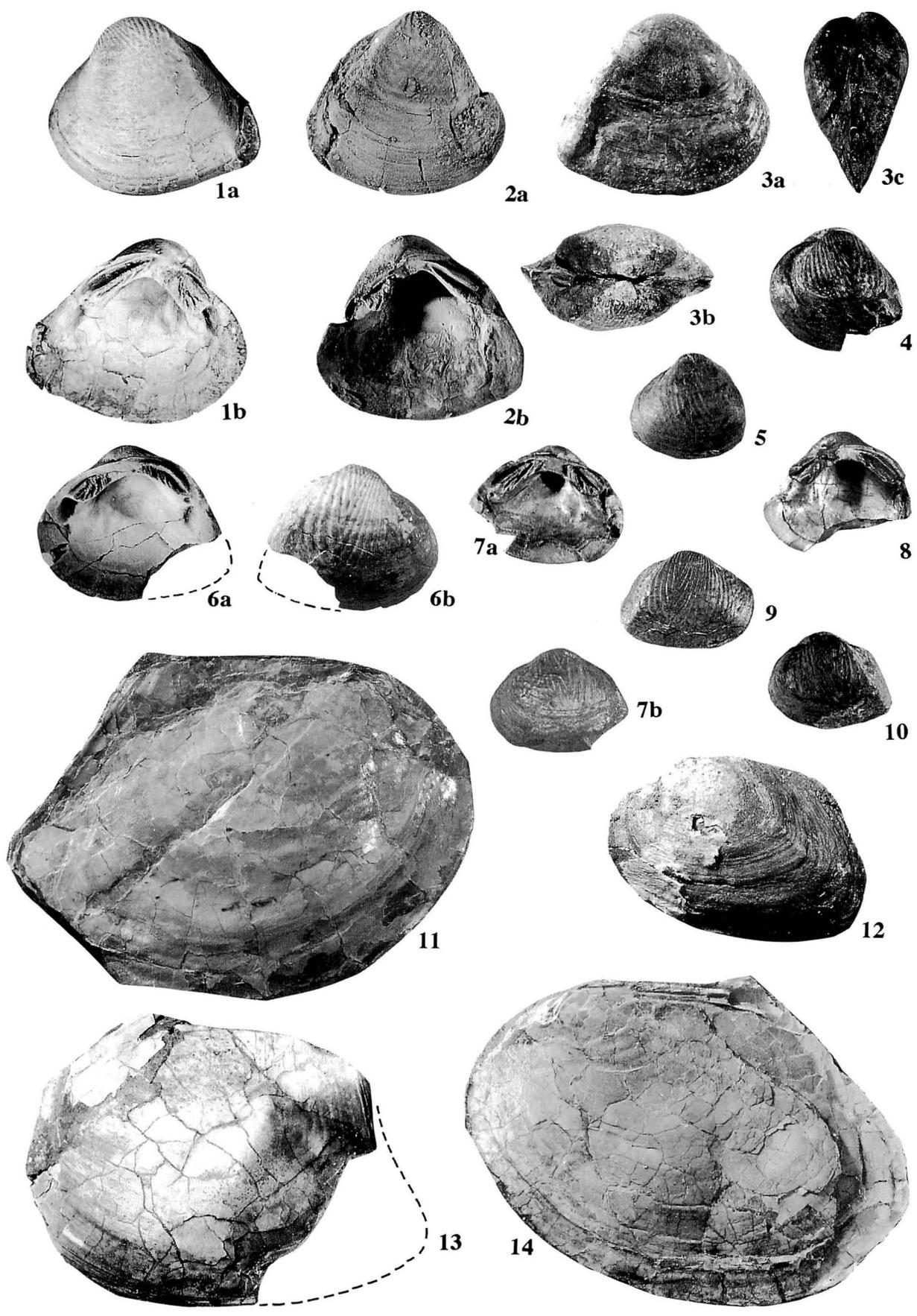
TMNH coll. cat. no.	Length	Height	Depth	Valve
02063 (Holotype)	82.9+	62.8	—	Right
02064 (Paratype 1)	46.8	31.8	6.0	Left
02065 (Paratype 2)	80.8	57.5+	16.0/2	Both (little compressed)
02066 (Paratype 3)	65.0+	52.3+	20.7/2	Both (incomplete)

*Comparison.*—Owing to its distinctive shell outline with high posterior wing it is placed in the genus *Physunio*. The present species is somewhat similar to the Recent Burmese species *Physunio micropteroides* Annandale (1918) in having a low umbo and a subtrigonal wing, but the former is larger in size and less elongated.

*Etymology.*—It is named after the valley of Chitwan, part of which is the study area.

*Stratigraphic range.*—Middle member of the Binai Khola Formation.

**Figure 5.** 1–5. *Parreysia binaiensis* n. sp. 1: holotype, TMNH02050; 1a, outer view, 1b, inner view, 2: paratype 1, TMNH02051; 2a, outer view, 2b, inner view, 3: paratype 2, TMNH02052; 3a, outer view of the right valve, 3b, dorsal view, 3c, posterior view, 4: paratype 3, TMNH02053, 5: paratype 4, TMNH02054. 6–10. *Parreysia zigzagcostata* n. sp. 6: holotype, TMNH02058; 6a, inner view of right valve, 6b, outer view of right valve, 7: paratype 1, TMNH02059; 7a, inner view of left valve, 7b, outer view of left valve, 8: paratype 4, TMNH02062, 9: paratype 2, TMNH02060, 10: paratype 3, TMNH02061. 11–14. *Physunio chitwanensis* n. sp. 11: holotype, TMNH02063, 12: paratype 1, TMNH02064, 13: paratype 3, TMNH02066, 14: paratype 2, TMNH02065. All figures are natural size.



Localities.—F-20 and F-21.

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## Organic components in enameloid of extant and fossil shark teeth

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**Abstract.** Structure and texture of a Pliocene shark tooth have been investigated using histochemical methods and scanning electron microscopy and compared with an extant related species. As a result it was revealed that the fossil shark tooth contained organic components comparable to those of the living species, and that collagens and non-collagen proteinaceous molecules in the fossil enameloid had a characteristic distribution pattern virtually identical to the living counterparts. This evidence suggests that fossil shark teeth contain useful information by which to investigate the evolution of developmental regimes of various vertebrate teeth.

**Key words :** Fossil shark, enameloid, organic components

### Introduction

The sequential processes of dental development have been revealed by biochemical approaches, and recently studies on the genetic basis of odontogenesis have been initiated using molecular biological techniques. Detailed mechanisms of odontogenesis have been histologically researched since Hertwig (1874). Observations with TEM of elasmobranch tooth germ have been performed (Sasagawa, 1989 ; Probst and Skobe, 1988 ; Goto, 1978a), and developmental processes of odontogenesis have been elucidated increasingly at the gene level in mammalian tooth (Gilbert, 1991). As the dental developmental system is obviously a product of evolution, investigations from the viewpoint of evolutionary biology, including those on extinct organisms, should help in the understanding of the mechanisms of odontogenesis.

Hard tissues, for example, shells, bones, and teeth, are the common constituents of fossil records. To know the relationships between the genetic mechanisms and the resulting structures of mineralized tissues would greatly help the understanding of extinct fossil organisms.

Previous works on fossil hard tissues focused on the morphological and mineralogical properties of hard tissues, while biochemical and molecular biological approaches on biomineralization have been performed a little on molluscan shell (de Jong *et al.*, 1974 ; Weiner *et al.*, 1976 ; Weiner *et al.*, 1979) and vertebrate teeth (Glimcher *et al.*, 1990). Vertebrates are suitable for this kind of research because of a great accumulation of biochemical and molecular biological data on extant species.

Among the vertebrates, elasmobranchs are thought to occupy an important position in the evolution of vertebrate

hard tissues, because of the characteristic structures of chondrichthyan hard tissues (Probst and Skobe, 1988). Body surfaces of an Ordovician heterostracan, *Astraspis*, were covered with dermal armor which had a tooth-like structure, consisting of an enameloid layer, a dentin-like layer, and a bone-like basement (Halstead, 1974). Goto (1988) pointed out that the structure constructed with these three layers is the basic structure in vertebrate hard tissues, which is recognized in selachian scales and teeth. The outer layer of fish tooth is referred to as enameloid (Poole, 1967), since involvement of mesenchymal participation is suggested in amelogenesis in fishes. This unusual phenomenon of the mesenchymal participation in amelogenesis also makes selachians intriguing for the study of dental development and evolution.

In this study, both extant and fossil shark teeth were investigated using histochemical methods. Collagen, non-collagenous proteins, and carbohydrates were stained *in situ* in thin sections of enameloid to compare the structures observed in living and fossil samples. Observations were also made under scanning electron microscopy.

### Materials and Methods

*Extant and fossil shark samples :* A specimen of *Lamna ditropis* (Family Lamnidae : 1.5 m in total body length) was obtained in a commercial landing at Kesenuma port, northeastern Japan. The upper and lower jaws were detached and immediately thereafter frozen at the port and stored at  $-20^{\circ}\text{C}$ . An isolated tooth identified as *Carcharocles megalodon* belonging to the same family (9

cm in crown height) was collected from the Pliocene deposits (about 3 m.y.a.) at Iwaibukuro, Chiba, central Japan, and has been preserved dry in the University Museum of the University of Tokyo. The dentin and dental base are lacking in this specimen; the space of dentin is filled with tuffaceous sandy sediments instead. The enameloid, on the other hand, is well preserved, with a smooth outer surface comparable to that of living sharks. The specimen has a grayish appearance due to secondary pyrite, which occurs as cubic particles in cracks. However, EPMA element analysis showed that the fossil material preserved fluorapatite (content of F was about 4%) as in living shark teeth. The thickness of the enameloid measured about 1 mm for the fossil specimen and 200  $\mu\text{m}$  for the living ones.

**Scanning electron microscopy:** Teeth of the living shark and a resin-embedded tooth portion of the fossil shark were cut in longitudinal and labio-lingual directions, and the sectioned surfaces were polished using graded powders (No. 6000 carborundum powder, Iwamoto Mineral Co., Tokyo). After removal of powders with an ultrasonic cleanser, the polished surfaces were etched with 0.1 N HCl for one minute, washed with distilled water, air dried for a few days to dehydrate, and then coated with Pt-Pd alloy prior to scanning electron microscopy (S-2400S; Hitachi).

**Histochemical preparations:** Teeth of the living shark were cut tangentially and thin-sectioned (100  $\mu\text{m}$  ground sections). All specimens of both living and fossil teeth enameloid were embedded in Bond E (epoxy resin, produced by Konishi Co., Osaka, Japan) and sectioned (100  $\mu\text{m}$  ground sections) almost parallel to the outer surface for observation of non-collagenous material in a wide view. As a negative control one of the sections of the fossil tooth was soaked in a solution of sodium hypochlorite (10%, v/v) for several days before the following fixation procedures to destroy organic components. All thin sections of both the living and fossil samples were incubated in a neutralized formalin solution (10%, v/v) at room temperature overnight to fix the organic components. They were washed with distilled water, etched with an aqueous solution of EDTA (0.5 M, pH 8.0) for 6 hours, and then fixed with neutralized formalin (10%, v/v) once more and washed with distilled water.

Independent from the preparations for thin sectioning, enameloid tissues were physically isolated from a jaw of the extant shark, and separation from dentin was performed with mechanical and chemical procedures under an optical microscope. The isolated enameloid tissues were placed in neutralized formalin (10%, v/v) and completely demineralized by decalcification in 1 N HCl for one week. After washing with distilled water, they were fixed with neutralized formalin (10%, v/v), followed by washing with distilled water. Complete demineralization of a portion of the fossil tooth left only powder residues, and did not permit any histochemical analyses.

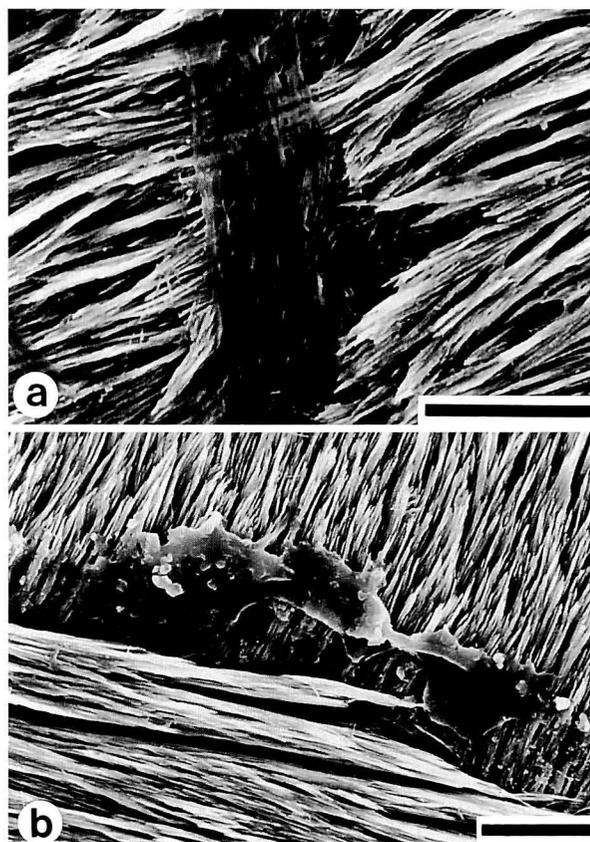
Collagens and other proteins in the thin sections of both extant and fossil specimens were stained with Collagen Stain Kit solution A (Collagen Kenkyu Kai, Kiyose, Tokyo)

that includes Sirius red F3BA for collagen staining and Fast green FCE for non-collagenous protein (Lopez de León and Rojkind, 1985), and carbohydrates stained with the PAS method using Schiff's reagent. The HCl demineralized enameloid of living samples was also stained with Collagen Stain Kit solution A. After staining the collagen for one hour, samples were incubated in distilled water at room temperature overnight to thoroughly remove excess reagents.

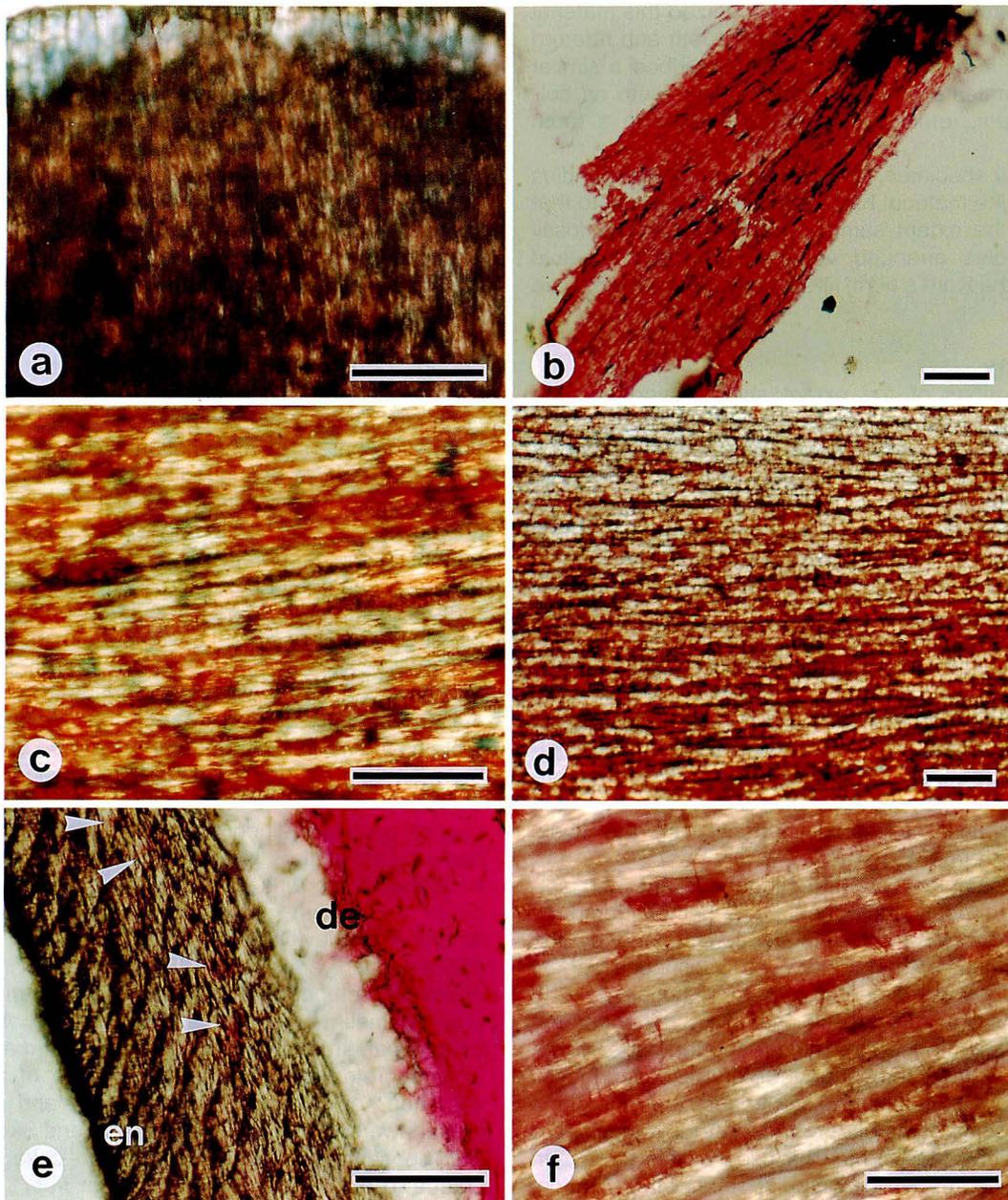
## Results

### Scanning electron microscopy

Bundles of needle-like material (apatite minerals) are distributed in the enameloid of the extant shark, and they are arranged longitudinally and parallel to the enameloid surface (Figure 1a). Sawada (1960) and Kitamura (1960) referred to this structure as filament-like. Sheet-like amorphous material arranged vertical to the enameloid surface and covering the bundles was recognized under the SEM. The amorphous material obviously was resis-



**Figure 1.** Scanning electron micrographs of living and fossil shark tooth enameloid. The etched surface of enameloid from living shark (*L. ditropis*) (a) and fossil shark (*C. megalodon*) (b). Bottom to top in each micrograph corresponds to the direction toward the tooth surface. Scale bars = 10  $\mu\text{m}$ .



**Figure 2.** Optical micrographs of thin sections and HCl-demineralized sample of shark teeth enameloid stained with Collagen Stain Kit except for (e) and (f), which were stained by PAS method. (a) Thin section of living shark tooth enameloid. (b) HCl-demineralized enameloid of living shark tooth, this section is parallel to the plane of enameloid-dentin junction. (c) Thin section of fossil shark tooth enameloid. (d) Thin section of fossil shark tooth enameloid with bleach treatment. Collagen and non-collagen proteins are stained red and green, respectively. (e) living shark and (f) fossil shark tooth enameloid stained by PAS method. Polysaccharides are stained red. Right to left direction in the left panel (e) corresponds to the direction toward the tooth surface. The fossil shark enameloid (f) was cut parallel to the tooth surface. The left side of photographs of (c), (d), and (f) is to the top of tooth. en : enameloid, de : dentin. Scale bars = 100  $\mu\text{m}$ .

tant to acid etching. Reif (1973) recognized this material in SEM observation of a *Heterodontus* tooth and referred to it as organic fibrils. Goto (1978a) described a similar amorphous material observed within shark teeth as collagenous fibers, referred to as Korff's fibrils in a tooth germ.

In the fossil specimen, the arrangement of the bundles of a needle-like material had a similar appearance to that observed in the extant sample (Figure 1b). In the fossil sample, bundles arranged vertically to the enameloid surface and the Korff's fibril-like amorphous material were observed.

### Histochemistry

In thin sections of the extant shark stained by the collagen staining method (Lopez de León and Rojkind, 1985), non-collagen proteinaceous parts and collagenous parts are stained green and red, respectively (Figure 2a). As mentioned above, living shark enameloid contains collagenous material known as Korff's fibrils, but the collagens in the thin section did not exhibit a clear shape, showing instead a continuously spread pattern in the enameloid tissue (Figure 2a). Non-collagen proteinaceous material displayed a heterogeneous appearance and showed an irregular distribution pattern in thin section (Figure 2a).

Extant shark enameloid, which was completely demineralized in 1 N HCl and stained by the same collagen staining method, was indicated by regularly arranged green spots (Figure 2b). In this sample, collagen fibers also showed a regular pattern, with the fibers crossing each other (Figure 2b).

The fossil sample contains collagenous and non-collagen proteinaceous components, as demonstrated by optical microscopy of the thin section stained by the collagen staining method (Figure 2c). Collagens appear in a heterogeneous distribution pattern (Figure 2c). In thin sections of the fossil sample, non-collagen proteinaceous components exhibit a spotted pattern, with the green spots irregularly arranged. In the case of fossil materials, it is sometimes experienced that inorganic materials, possibly minerals produced by diagenesis, are stained green by the staining kit used in this study. In the negative control which was bleached before fixation, the green spots were not observed (Figure 2d). The green spots shown in Figure 2c, therefore, are not inorganic but proteinaceous in nature.

Carbohydrate staining of the thin sections using the PAS method demonstrated that carbohydrates, possibly polysaccharides, occur in both living and fossil shark enameloid (Figures 2e, 2f). The carbohydrates in the fossil tooth had a somewhat different distribution pattern from that of the living sample. In the former, carbohydrates were often recognized at the boundary of the mineral bundles, while in the latter, they showed a patched distribution pattern regardless of the mineral bundles.

### Discussion

Recently, it has been revealed that non-collagenous proteins play an important role in amelogenesis. Termine *et al.* (1980) clarified, using biochemical analyses, that non-collagenous proteins, proline-rich amelogenin and acidic enamelin exist in bovine enamel. Subsequently, cDNA sequences of the amelogenin precursor genes of various mammals were determined (Snead *et al.*, 1987; Shimokawa *et al.*, 1988). Fincham *et al.* (1991) argued, on the basis of the determined amelogenin sequences that post-secretory processing cleaves amelogenin precursors in several steps to control the rates of mineralization during odontogenesis. Compared to amelogenin, enamelin is poorly characterized by molecular biological methods. This may partly be due to the fact that the enamelin content in mammalian enamel is considerably lower than that of amelogenin (Termine *et al.*, 1980).

Selachians may provide an advantage in the study of enamelin, because it is suggested that enamelin-like protein is the predominant component of the non-collagenous enameloid proteins (Herold *et al.*, 1988; Kemp, 1985; Slavkin *et al.*, 1983a). But non-collagenous matrix proteins of fish enameloid have not been characterized on the level of DNA sequence yet and are confusing for the following reasons. Antibodies prepared against mammalian enamelin and amelogenin have detected enamel proteins *in situ* in shark teeth, cyclostome horny cap, and bony fish teeth (Herold *et al.*, 1980). Slavkin *et al.* (1983a) demonstrated using electrophoresis that shark teeth and hagfish caps contained a proteinaceous component that had a molecular weight comparable to enamelin. Amelogenin too was detected in amelogenesis of selachian tooth with polyclonal antibody against murine amelogenin (Slavkin *et al.*, 1983b). However, Herold *et al.* (1988) and Ishiyama *et al.* (1994) claimed by immunohistochemical methods that there existed not amelogenin but only enamelin in fish enameloid matrix. According to anatomical study with TEM enameloid matrix proteins were secreted by odontoblasts in spite of ameloblastic secretion of mammalian enamelin and amelogenin (Sasagawa and Akai, 1992). Prostack and Skobe (1988) by TEM observation recognized a non-collagenous fiber unique to elasmobranch tooth, "Giant fiber", secreted by odontoblasts in the developing enameloid matrix. It is also supposed that the giant fiber is a product of ameloblastic secretion as enamelin (Kemp, 1985).

Non-collagenous proteins had a heterogeneous patched distribution in living shark enameloid (Figure 2a), while the completely demineralized enameloid (Figure 2b) had a pattern of regularly arranged green spots. This result poses a problem in differently prepared samples. The difference of the observed structures between the sample completely demineralized with HCl and the thin sections etched with EDTA is also the case for collagens. Figure 2b shows a regularly knitted structure of collagen fibers, but the thin section of the same living material indicates an irregular structure of collagens. These differences are attributed to differences in the degree of

demineralization and in cutting directions.

It is likely that the green stained non-collagenous proteins in the living shark enameloid represent enamelin-like protein, because the enamelin-like protein is known as the predominant component of the non-collagenous enamel proteins in selachians (Herold *et al.*, 1988; Kemp, 1985; Slavkin *et al.*, 1983a). Optical micrography of the fossil sample in thin section also reveals a spotted distribution of the non-collagenous proteins (Figure 2c). It is suggested that this proteinaceous material is homologous to the 'enamelin-like' protein observed in the living sample, because they have the same distribution pattern.

From SEM observations, it was revealed that the enameloid of fossil shark does not differ from that of living shark in the arrangement of the amorphous materials. Amorphous material in the living sample can be identified as Korff's fibers (Figure 1a) in a tooth germ. Garant (1970) recognized collagen fibers between palisade aggregations of apatite mineral in a developing enameloid on the basis of TEM observation. It is supposed that this amorphous material is identified as the interpalisade collagen fiber. The amorphous materials in the fossil sample, therefore, have the texture of the collagenous Korff's fibers. They were recognized at the boundaries of bundles (Figure 1b). The distribution pattern of these materials is clearly distinguished from that of the non-collagen proteinaceous materials observed in Figure 2. Thin sections stained by PAS method indicate that polysaccharides exist at the boundaries of bundles (Figure 2f). It is, therefore, likely that the amorphous materials in the fossil sample represent polysaccharides, although it may also be possible that they represent collagens, since collagens were detected histochemically in the fossil thin section (Figure 2c).

According to previous researches on both fossil and extant materials with biochemical and histochemical techniques Samata (1988) and Glimcher *et al.* (1990) reported non-collagenous enamel proteins preserved in tooth of a Pliocene (3 m. y. a.) elephant and a Cretaceous (105 m. y. a.) crocodile and analyzed their amino acid composition. Concerning lower vertebrates, on the basis of staining results Isaacs *et al.* (1963) postulated that Paleozoic primitive vertebrate fossils preserve collagen and polysaccharides in dentin. Iwata and Uozumi (1970) showed TEM photographs of morphologically degraded collagen in Pliocene lamnid shark teeth. Goto (1978b) detected non-collagenous protein on the basis of amino acid composition of the extract from Miocene shark enameloid. This study provided new data that showed preservation of collagen, non-collagenous proteins, and polysaccharides *in situ* in fossil teeth.

As the non-collagen proteins are suspected to be enamelin-like proteins, *in situ* immunohistochemical research with antibodies may be the logical next step to confirm the results obtained in this study. Based on histochemical observations, together with further biochemical characterizations of constituent proteins, the studies on fossil enameloid may provide important information in clarifying mechanisms of odontogenesis and

evolution of animal hard tissues.

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## Early to Middle Miocene molluscan fossils from the Megami and Ebie limestones in Shizuoka Prefecture and their implications for the formation of a Miocene coral–algal reef within the Japanese faunal realm

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**Abstract.** Eight fossil molluscan species, including *Cryptopecten yanagawaensis* (Nomura and Zinbo) and *Turbo (Marmarostoma) mekamiensis* Nishiwada, are described on the basis of material obtained from the late Early to early Middle Miocene Megami and Ebie limestones in the Sagara district, Shizuoka Prefecture, Japan. *Cryptopecten yanagawaensis* has been recorded from late Early to early Middle Miocene formations in Japan. The occurrence of this species indicates that the reef limestones in the Megami Formation were formed within the Japanese faunal realm in Miocene time.

In this paper some comments are made on the origin and sedimentary environments of the limestones in the Megami Formation.

**Key words:** Molluscan fossils, Miocene, coral–algal reef, Megami and Ebie Limestones, Japan

### Introduction

A number of allochthonous reef limestone blocks, ranging in diameter from a centimeter to more than a hundred meters, occur in the abyssal turbidite sequence of the Early/Middle Miocene Megami Formation in the Sagara district, Shizuoka Prefecture, central Japan. The Megami and Ogami limestones are among the larger of these blocks. They have long been of special interest to paleontologists, because they yield abundant and well-preserved Miocene shallow marine fossils such as crustose coralline algae (Nishiwada, 1894; Ishijima, 1933; Iryu and Sasazawa, 1989), larger foraminifers (Hanzawa, 1943; Matsumaru, 1971), hermatypic corals (Eguchi and Mori, 1976), molluscs (Nishiwada, 1894) and decapod crustaceans (Karasawa, 1993).

The origin of the limestones has also been debated among geologists and paleontologists, who have made different interpretations of the sedimentary setting of the limestones and different scenarios for the formation process of these allochthonous limestone blocks.

Konishi *et al.* (1988) and Sugiyama (1992) suggested that the Megami and other limestone bodies were originally formed on a seamount in an ocean realm and are now found as allochthonous blocks in the Miocene ac-

cretionary complex.

On the contrary, Nakamori *et al.* (1991) reported that the limestones had formed initially on a shallow shelf of the island arc, and were then transported to a deeper sedimentary basin, such as a trough on the continental slope or a trench floor.

During field survey of the Sagara district, the senior author found well-preserved pectinid fossils from a small limestone named the Ebie Limestone and also from the Megami Limestone. As a result of our taxonomic investigation, the fossils are identified as *Cryptopecten yanagawaensis* (Nomura and Zinbo), *Chlamys* sp. A and *Chlamys* sp. B. In this paper, the molluscan fossils from the Megami and Ebie limestones are described systematically. In addition, some comments are made on the origin and sedimentary environments of the limestone lithology and the zoogeographical and ecological information provided by the molluscan species.

### Geologic notes on the fossil localities

Neogene marine sediments are extensively distributed in the Sagara district, Shizuoka Prefecture, central Japan. They are classified into the Megami Formation, the Sagara Group and the Kakegawa Group, in upward sequence.

The Megami Formation is narrowly distributed as an inlier in the Sagara Group, forming the core of a southwesterly plunging anticline called the Megami Anticline. It consists mainly of mudstone and fine-grained sandstone in which a number of allochthonous reef-limestone blocks are contained. Benthonic foraminifers indicating an abyssal environment occur in the mudstone (Nakamori *et al.*, 1991). The formation is assigned to a late Early to early Middle Miocene age (Blow's N8 to N9 Zones) based on the index planktonic foraminifers found in the mudstone (Saito, 1963; Oda, 1971; Ujiie, 1975). The age of

the limestone blocks is also determined as 17–16 Ma by means of calcareous nannoplankton and larger foraminifers (Nakamori *et al.*, 1991).

The molluscan fossils described in this paper were obtained from the limestones at two localities as described below.

*Ebie Limestone*: A small limestone block approximately 10 m in diameter crops out in the valley to the north of Ebie, Sagara-cho, Shizuoka Prefecture (Loc. 1 in Figure 1). Light brown calcarenite yielded commonly *Cryptopecten yanagawaensis* (Nomura and Zinbo) and

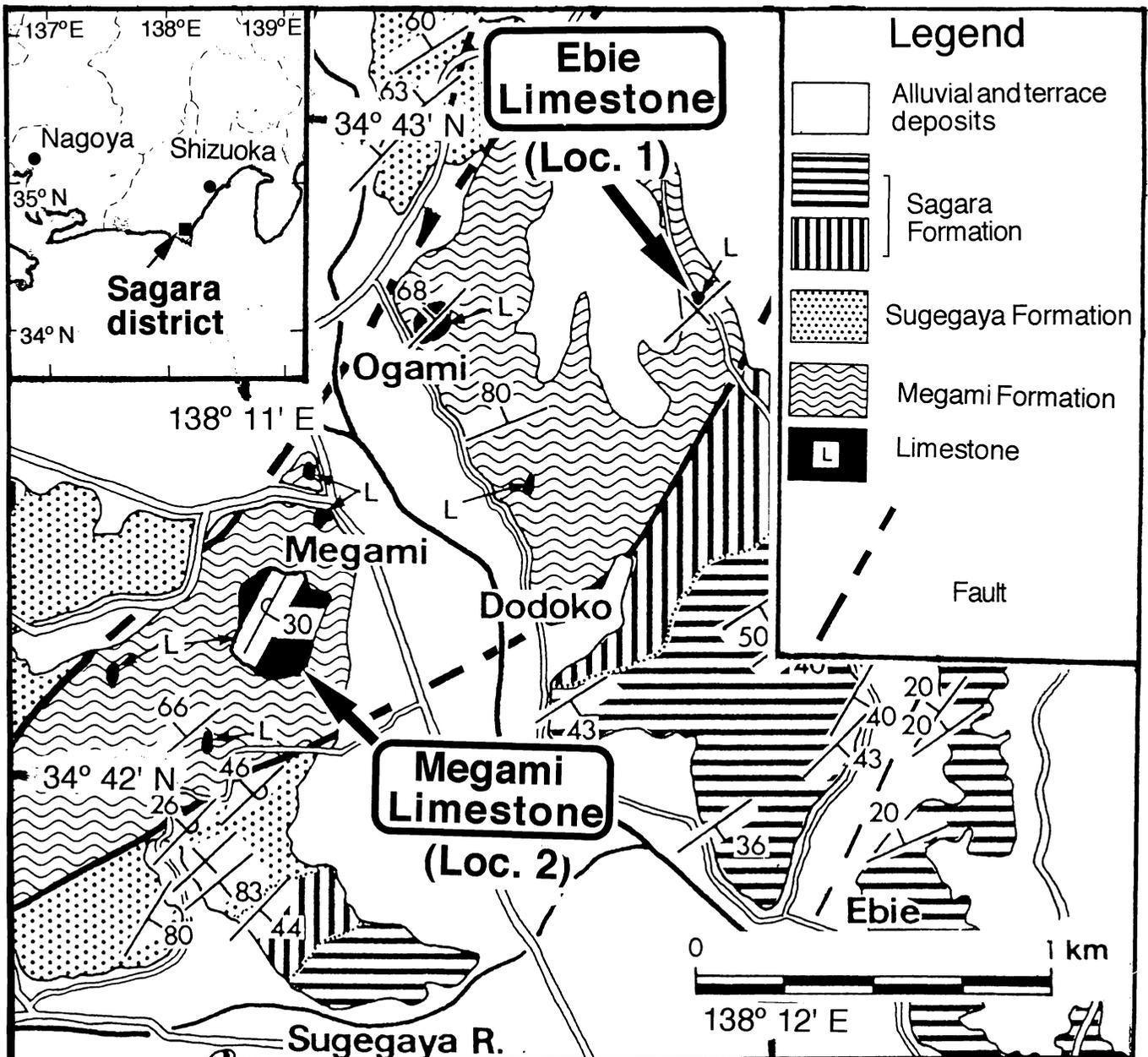


Figure 1. Index map showing fossil localities in the Megami Formation. The fossil localities are plotted on the geologic map of Nakamori *et al.* (1991).

*Chlamys* sp. A together with abundant larger foraminifers such as *Nephrolepidina nipponica* (Hanzawa), *Miogypsina kotoi* Hanzawa, and *Homotrema rubrum* (Lamarck).

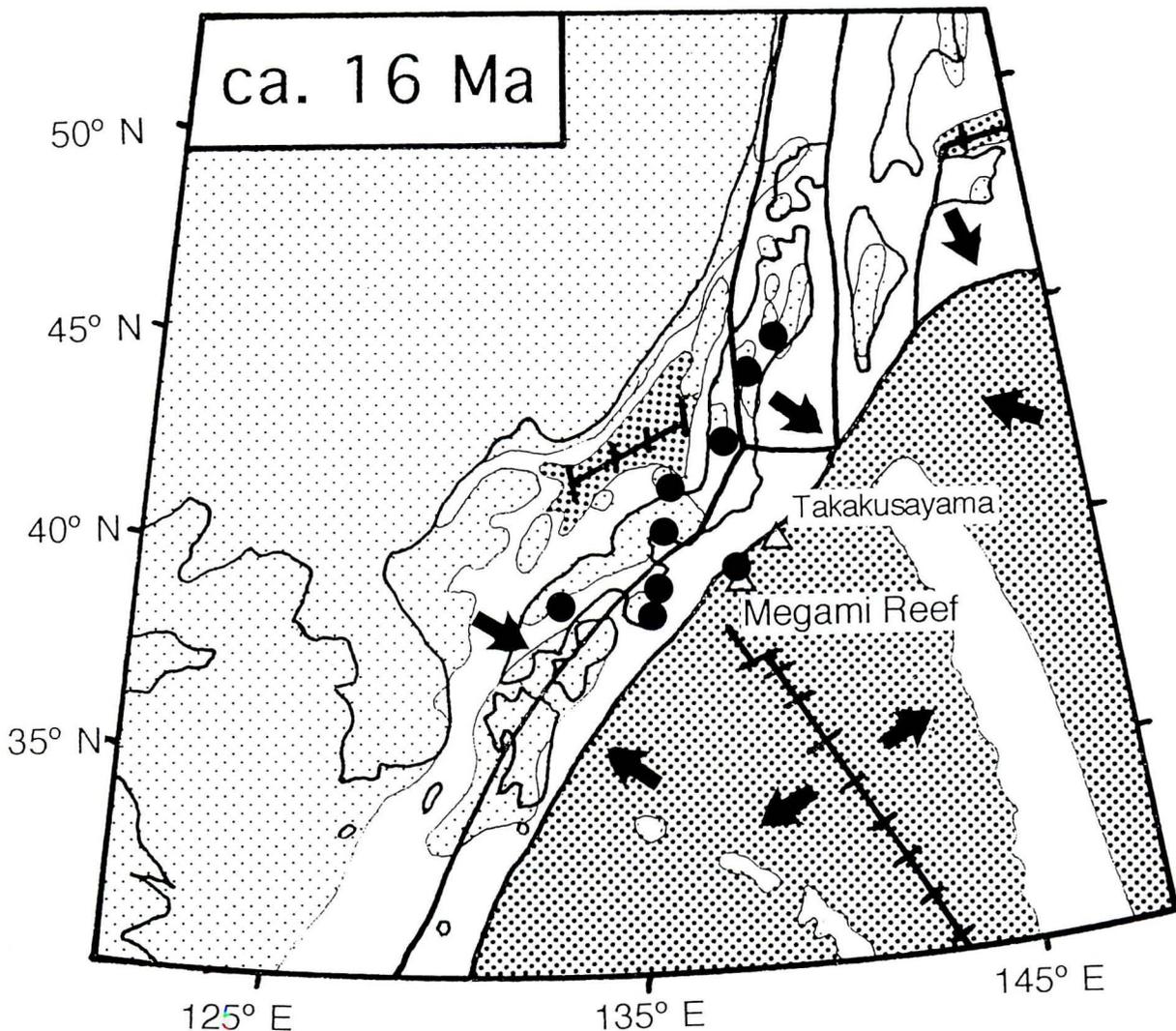
**Megami Limestone:** The fossil locality is a cliff in the limestone quarry of the Megami Limestone at Taisyakuyama, Megami, Sagara-cho (Loc. 2 in Figure 1). Light, buff-colored coralline algal limestone yielded the following molluscs: *Turbo mekamiensis* Nishiwada, "*Cypraea*" sp., *Conus* sp., *Chlamys* sp. A, *Chlamys* sp. B, *Spondylus* sp. and *Periglypta* sp. cf. *P. reticulata* (Linneaus).

#### Origin and sedimentary setting of the limestones

The Megami and Ogami limestones are considered to be coral-algal reef limestones which formed in a warm shallow marine environment during the Miocene (Eguchi and Mori, 1976; Konishi *et al.*, 1988; Iryu and Sasazawa, 1989). They consist mainly of hermatypic coral-coraline

algal boundstone with fine-grained sediments as interstitial fillings. Among the reef-building organisms, crustose coralline algae including such species as *Lithothamnium ramosissimum*, *Mesophyllum erubescens* and *Archaeolithothamnium megamiensis* are major framework contributors to the Megami coral-algal reef, together with hermatypic corals of the order Scleroderma including such genera as *Favia*, *Echinophyllia*, *Cyphastrea*, *Acropora*, *Polites*, *Goniopora* and *Stylophora* (Ishijima, 1960; Eguchi and Mori, 1976; Iryu and Sasazawa, 1989). Irregularly shaped coralline frameworks are often filled with fine-grained packstones and wackestone which yield such molluscan fossils as *Turbo (Marmarostoma) mekamiensis*, "*Cypraea*" sp., *Conus* spp., *Chlamys* spp., *Spondylus* sp. and *Periglypta* cf. *reticulata*. A decapod assemblage characteristic of reef and lagoonal environments occurs together with these molluscs (Karasawa, 1993).

In contrast to the litho- and bio-facies of the Megami



**Figure 2.** Paleogeographic map around the Japanese Islands at ca. 16 Ma, showing the occurrence of *Cryptoptecten yanagawaensis* (black circles). Modified from Pickering, Underwood and Taira (1993).

Limestone, the Ebie Limestone is entirely composed of detrital limestone (calcirudite and calcarenite), which is considered to have been formed on the fore-reef slope of the Megami reef. In the limestone, two pectinids, *Cryptopecten yanagawaensis* and *Chlamys* sp. A, occur in large numbers together with abundant larger foraminifers, including *Nephrolepidina nipponica* and *Miogypsina kotoi*. Nakamori *et al.* (1991) reported the occurrence of granules and pebbles of shale, siliceous sandstone and chert in the Ebie Limestone, and also the occurrence of granule- to pebble-sized gravels of sandstone and shale from the Oumagadani Limestone. However, careful petrographic examination of these rocks revealed that they are weathered dacitic volcanic rocks and not sedimentary rocks. Consequently, no terrigenous materials have been confirmed in the Megami, Ebie and Oumagadani limestones. This fact strongly suggests that the limestones were formed in an open-sea environment. Makiyama (1963) reported the occurrence of a mass of basalt close to the Ogami Limestone. We also confirmed the occurrence of an allochthonous block of basalt in the siltstone of the Megami Formation. The lithologic association of reef-limestone and basalt strongly implies that the limestones were originally formed on a basaltic seamount in an open-sea environment.

Recent geotectonic studies have elucidated the plate tectonic evolution of the Philippine Sea (Hill *et al.*, 1993). During the Oligocene to Miocene (ca. 27–14 Ma), backarc rifting occurred behind the Izu-Bonin Arc to produce the Shikoku Basin and Kyushu-Palau Ridge (Pickering, Underwood and Taira, 1993). The Megami coralline reef was formed most likely on a basaltic seamount in the northeastern part of the Shikoku Basin standing close to the proto-Japanese Islands during a period of remarkable warming of the marine climate about 16 Ma (Sugiyama, 1992).

Present knowledge suggests that the distribution of *Cryptopecten yanagawaensis* is confined to the late Early to early Middle Miocene of Honshu, Japan. The occurrence of this species is significant for the origin and sedimentary setting of the Megami and other limestones, because it provides the evidence that the coral-limestone was formed within the Miocene Japanese faunal realm (Figure 2).

In a phase of rapid sea-floor spreading in the Sea of Japan, central and southern Honshu rotated clockwise during 16–15 Ma. This clockwise rotation resulted in the collision of the sea mounts with the Honshu Arc. Reef limestones like the Megami Limestone and pillow basalts like the Takakusayama Basalt which formed the upper surface of the seamounts were scraped off to form an accretionary complex in a trench area.

Summarizing the above short discussion, it may be inferred that the Megami and other limestones were originally formed on a seamount in the northeastern part of the Philippine Sea close to Central Japan and accreted to the Honshu Arc during the opening of the Sea of Japan.

### Systematic descriptions

Class Bivalvia Linnaeus, 1758  
Order Ostreoida Ferussac, 1822  
Family Pectinidae Rafinesque, 1815  
Subfamily Chlamydinæ Korobkov, 1960  
Genus *Cryptopecten* Dall, Bartsch  
and Rehder, 1938

*Type-species*.—*Cryptopecten alli* Dall, Bartsch and Rehder, 1938 [= *Pecten (Chlamys) bullatus* Dautzenberg and Bavay, 1912]. Hawaii, Philippines and Japan, Late Pliocene to Recent.

*Generic diagnosis*.—see Hayami (1984, p. 90–91).

#### *Cryptopecten yanagawaensis* (Nomura and Zinbo)

Figures 3–1–4

*Pecten (Aequipecten ?) yanagawaensis* Nomura and Zinbo, 1936, p. 337, pl. 20, figs. 2a, b.

*Pecten (Aequipecten) yanagawaensis* Nomura and Zinbo, Nomura, 1940, p. 19, pl. 1, figs. 10–13.

*Cryptopecten yanagawaensis* (Nomura and Zinbo). Masuda, 1958, p. 189, pl. 27b, figs. 1–8; Itoigawa, Shibata and Nishimoto, 1974, p. 67, pl. 11, figs. 6–9; Taguchi, Ono and Okamoto, 1979, pl. 4, figs. 1, 2; Hayami, 1982, p. 235; Hayami, 1984, p. 113–115, pl. 8, figs. 6–9; Sato, 1984, p. 257, pls. 36, 37; Chijiwa and Tomita, 1985, pl. 41, fig. 7; Masuda, 1986, pl. 1, fig. 5; Sato, 1991, p. 70–78, pls. 12, 13.

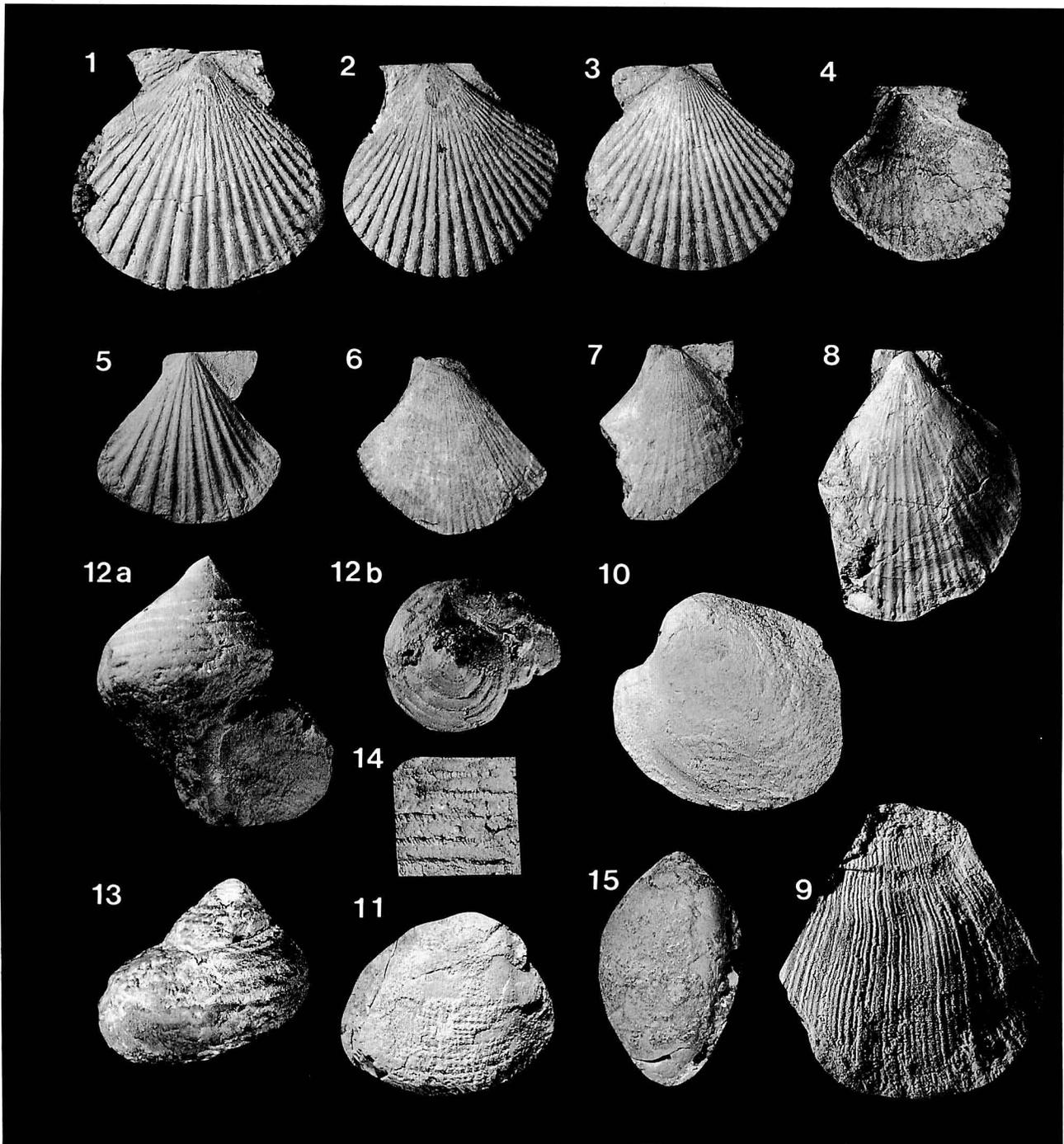
*Aequipecten yanagawaensis* (Nomura and Zinbo). Masuda, 1962, p. 192, pl. 26, fig. 8; Masuda and Takegawa, 1965, pl. 1, figs. 12, 13; Masuda, 1973, pl. N-54, figs. 14–16; Ogasawara, 1976, p. 44, pl. 3, figs. 3, 6; Katto and Masuda, 1978, pl. 5, figs. 4, 5; Itoigawa, Shibata, Nishimoto and Okumura, 1981, pl. 7, figs. 2, 3; Itoigawa, Shibata, Nishimoto and Okumura, 1982, p. 46; ? Shikama, 1973, p. 190, 194.

*Type and type locality*.—The holotype (Saito Ho-on Kai Museum, Sendai, Reg. No. SM8553; Nomura and Zinbo, 1936, p. 337, pl. 20, figs. 2a, 2b) from the early Middle Miocene Yanagawa Formation at a river cliff of the Abukuma-gawa, southwest end of Yanagawa Park, Yanagawa town, Fukushima Prefecture, north Japan (37°51.1'N, 140°36.1'E). length, 21.5 mm; height, 20 mm high; depth, 5 mm.

*Species diagnosis*.—see Hayami (1984, p. 113).

*Materials*.—Four illustrated specimens (Earth Sciences, Nagoya Univ. Reg. No. ESN2536–2539) and more than ten poorly preserved specimens from the Lower to Middle Miocene Ebie Limestone at Sagara town, Shizuoka Prefecture, central Japan.

*Description*.—Shell moderate in size, slightly inflated, nearly equiconvex, height subequal to length; equilateral or somewhat inequilateral, radiately ribbed, apical angle of disk approximately 100°; ears moderate in size, anterior one slightly larger than posterior; anterodorsal and posterodorsal margins of disk straight or slightly concave, byssal notch moderate in depth. Outer surface of disk ornamented with 21–24 elevated and rounded radial ribs,



**Figure 3.** All figures in natural size unless otherwise stated. **1-4.** *Cryptopecten yanagawaensis* (Nomura and Zinbo) Loc. 2 (Ebie Limestone). 1: left valve, ESN 2536, 2: left valve, ESN 2537, 3: left valve, ESN 2538, 4: left valve, ESN 2539. **5.** *Chlamys* sp. A, right valve, ESN 2540, Loc. 1 (Megami Limestone)  $\times 2$ . **6-8.** *Chlamys* sp. B. 6: right valve, ESN 2541, Loc. 2 (Ebie Limestone), 7: right valve, ESN 2542, Loc. 2 (Ebie Limestone), 8: left valve, ESN 2543, Loc. 1 (Megami Limestone). **9.** *Spondylus* sp., left valve, ESN 2544, Loc. 1 (Megami Limestone),  $\times 0.75$ . **10-11.** *Periglypta* sp. cf. *P. reticulata* (Linnaeus). 10: inner mold of left valve, Loc. 1 (Megami Limestone), 11: right valve, Loc. 1 (Megami Limestone). **12-14.** *Turbo (Marmarostoma) mekamiensis* Nishiwada. 12: Loc. 1 (Megami Limestone); 12a: apertural view, 12b: upper side view, 13: adapertural view, ESN 2545, Loc. 1 (Megami Limestone), 14: a part of last whorl showing spiral cords and interstitial threads, ESN 2546, Loc. 1 (Megami Limestone). **15.** "*Cypraea*" sp., adapertural view, Loc. 1 (Megami Limestone).

each of which consists of a comparatively narrow central ridge and a pair of relatively narrow hollow parts; rib interspace marked with a number of fine radial threads. Radial ribs are weakly impressed on the inner surface of the shell, and a relatively large semi-circular adductor muscle scar is observed.

*Dimensions (in mm) and number of radial ribs.* —

Specimen	ESN 2536	ESN 2537	ESN 2538	ESN 2539
Valve	left	left	left	left
Height	24.7	24.8	21.6	18.8
Length	26.2	26.1	22.0	19.6
Depth	3.6	3.9	3.5	—
Radial ribs	22	24	20	—

*Remarks.*—The specimens from the Ebie Limestone, here assigned to *Cryptopecten yanagawaensis*, are well comparable in size, number of radial ribs, and other shell characteristics with the type and other specimens of *C. yanagawaensis* from late Early to early Middle Miocene formations in central and northern Honshu. The present species is very akin to *Cryptopecten hsintienensis* Masuda and Huang, 1993, described from the Middle Miocene Kuanyinshan Sandstone, northern Taiwan, but differs in having a larger and less inflated equiconvex shell. The stratigraphic occurrences of *C. yanagawaensis* seem to be restricted to the upper Lower to lower Middle Miocene in north and central Honshu. Specimens from the Uematsu Formation in the Kushimoto district, Kii Peninsula, are also undoubtedly referable to this species.

*Occurrence.*—Abundant in the Ebie Limestone.

*Known distribution.*—This species is known from the Yanagawa Formation at Yanagawa, Fukushima Prefecture (type locality), the Moniwa Formation at Moniwa and Junishin (Masuda, 1958; Sato, 1991), Taira Member of the Kanagase Formation of Ogawara (Masuda and Takegawa, 1965) near Sendai, Miyagi Prefecture, the Nagaoka Formation, Tochigi Prefecture (Sato, 1991), the Tsugawa Formation, Niigata Prefecture (Tsuda, 1965), the Kurosedani Formation, Toyama Prefecture (Tsuda, 1965), the Sunakozaka Formation at Higashi-ichise near Kanazawa, Ishikawa Prefecture, (Ogasawara, 1976), the Akeyo (Shukunohora Sandstone) and Oidawara Formations at Mizunami, Gifu Prefecture (Itoigawa, Shibata and Nishimoto, 1974), the Onuma Formation, Mie Prefecture (Chijiwa and Tomita, 1985), the Uematsu Formation at Kushimoto, Wakayama Prefecture, and the Bihoku Group in Okayama Prefecture (Taguchi, Ono and Okamoto, 1979).

The present report from the late Early to early Middle Miocene Ebie Limestone provides additional occurrence data on this species.

*Geologic age.*—Late Early Miocene to early Middle Miocene (Blow's N8 and N9 Zones).

Genus *Chlamys* Röding, 1798  
*Chlamys* sp. A

Figure 3-5

*Descriptive remarks.*—A small right valve was obtained from the Megami Limestone. Shell is small and moderately convex with 13 main ribs and additional secondary ribbing. Ears are very unequal. Considering only important shell characters, this species is similar to *Chlamys (Chlamys) zeelandona* (Hertlein) from North Island, New Zealand.

*Occurrence.*—Rare in the Megami Limestone.

*Chlamys* sp. B

Figures 3-6-8

*Descriptive remarks.*—More than five specimens were obtained from the Ebie Limestone (Loc. 1) and three specimens were collected from the Megami Limestone. Shell is small to medium, depressed, slender, and slightly oblique. Ears are unequal. Surface of disk is sculptured by numerous radial riblets with no scale in interspaces.

*Occurrence.*—Common in the Megami and Ebie limestones.

Family Spondylidae Gray, 1826  
Genus *Spondylus* Linnaeus, 1758  
*Spondylus* sp.

Figure 3-9

*Descriptive remarks.*—An incomplete left valve was obtained from the Megami Limestone. The valve is rather large and elliptical. The surface is sculptured by numerous radiating striae which are nearly smooth. In the surface sculpture of the shell, this species is similar to *Spondylus sanguineus* Dunker but differs in having a much larger shell. It is also allied to *Spondylus anacanthus* Mawe but is distinguished from that species in lacking spines.

*Occurrence.*—Rare in the Megami Limestone.

Family Veneridae Rafinesque, 1815  
Genus *Periglypta* Jukes-Browne, 1914  
*Periglypta* sp. cf. *P. reticulata* (Linnaeus)

Figures 3-10, 11

*Descriptive remarks.*—Four poorly preserved specimens comparable to *Periglypta reticulata* came from the Megami Limestone. The shells of these specimens are rather thick, solid and heavy, inflated and roundly quadrate in shape. The posterodorsal margin is quadrately angled. The umbo is situated anteriorly. Strong radial ribs are crossed by concentric cords forming a coarse reticulation on the surface.

*Occurrence.*—Frequent in the Megami Limestone.

Class Gastropoda Cuvier, 1797  
Order Archaeogastropoda Thiele, 1925  
Family Turbinidae Rafinesque, 1815  
Genus *Turbo* Linnaeus, 1758  
Subgenus *Marmarostoma* Swainson, 1829

***Turbo (Marmarostoma) mekamiensis*** Nishiwada, 1894

Figures 3-12-14

*Type-specimen.*—*Turbo (Marmarostoma) mekamiensis* Nishiwada, 1894, p. 139, pl. 5, figs. 5a, 5b (Holotype, Univ. Mus. Univ. Tokyo, Reg. No. CM15259); Nishiwada, 1895, p. 240, pl. 29, figs. 5a, 5b (see also Nishiwada, 1894).

*Materials.*—Eleven topotype specimens including one registered specimen (ESN 2545) were considered in the following description.

*Description.*—Shell is medium-sized, heavy, globular and turbiniform, and is composed of four rounded whorls that are separated by shallow sutures with channels. Shoulder is not angled. Whorls are spirally sculptured with prominent, raised and rounded spiral cords, which number 12 on the last whorl, and narrow interstitial threads which are finely scaled (Figure 3-13). Subsutural spiral cords are a little wider than others. The basal lip near the columella is rather thick and slightly ridged. Aperture is nearly circular. Umbilicus is closed.

*Remarks.*—The present specimens are morphologically identical with *Turbo (Marmarostoma) mekamiensis* Nishiwada, 1894, also described from the Megami Limestone. It closely resembles *T. (M.) setosus* Gmelin, which lives in the central Pacific south of the Bonin and Okinawa Islands, but differs from that species in having a smaller number of spiral cords that are more flat-topped. It resembles *Turbo (Marmarostoma) argyrostoma* Linnaeus, but is distinguished from that species in having a smaller shell, a more rounded shoulder and shallower suture.

*Measurements (in mm).*—

Specimen	Hagima coll.	ESN 2545
Height of shell	44.0	38.0
Width	42.0	38.3
Height of body whorl	28.7	22.0
Height of aperture	26.0	—
Apical angles	85°	90°

*Occurrence.*—Common in the Megami Limestone (type locality). Late Early to early Middle Miocene.

Order Mesogastropoda Thiele, 1925  
Family Cypraeidae Rafinesque, 1815  
Genus ***Cypraea*** Linnaeus, 1758

**"*Cypraea*"** sp.

Figure 3-15

*Descriptive remarks.*—This species is mostly found as casts in the Megami Limestone. The illustrated specimen is a medium-sized, pyriform-ovate shell reaching 37 mm in length. It certainly belongs to *Cypraea* (s.l.) but the species identification is difficult owing to the poor preservation.

*Occurrence.*—Rare in the Megami Limestone.

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Sagara 相良, Kakegawa 掛川, Shizuoka 静岡, Takakusayama 高草山

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## Cephalopod fauna of the Nakadaira Formation (Lower Permian) in the Southern Kitakami Massif, Northeast Japan

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**Abstract.** Eight species referable to six genera of nautiloids and two species belonging to two genera of ammonoids are described from the Lower Permian Nakadaira Formation in the Southern Kitakami Massif, Northeast Japan. These nautiloids are *Tainoceras*, *Foordiceras*, *Pleuronautilus*, *Aphelaeceras*, *Parastenopoceras* and *Stearoceras*. *Pleuronautilus yahagiensis* is a newly proposed species. Ammonoids are *Agathiceras* and *Artinskia*. *Agathiceras* dominates the fauna.

**Key words:** Cephalopoda, Lower Permian, Nakadaira Formation, Southern Kitakami

### Introduction

In the Kitakami Massif, unlike the Middle and Upper Permian, cephalopod fossils are very rare in the Lower Permian. Only four species of nautiloid and one species of ammonoid have hitherto been reported. They are *Tainoceras kitakamiense* Hayasaka from the uppermost part of the Sakamotozawa Formation (Motoiwazawa Sandstone Member; Murata, 1971), *Metacoceras* sp. from the Rodai Formation (Yabe and Mabuti, 1935), *Tainoceras abukumaense* Hayasaka from the Nakadaira Formation (Ehiro, 1977), *Tylonautilus* cf. *permicus* Hayasaka from the Nishikori Formation (Ueda, 1963) and *Agathiceras* cf. *brouweri* Smith from the Sakamotozawa Formation (Kozumi, 1975). The last three species were only listed and no description was given.

Recently, the present author paleontologically reexamined the above-listed *T. abukumaense* (= *Pleuronautilus yahagiensis* sp. nov. of this paper) and reinvestigated the Nakadaira Formation at the fossil localities. In the course of this study, some additional cephalopod fossils were collected from the locality from which *T. abukumaense* was first reported, 500 m northwest of Nakadaira (Loc. A, Figure 1), and also from a new locality on a peak (482 m above sea level), about 500 m to the northeast of Natsugayoi (Loc. B, Figure 1) and 2 km north of Nakadaira, both in Yahagi-town, Rikuzen-Takata City, Iwate Prefecture.

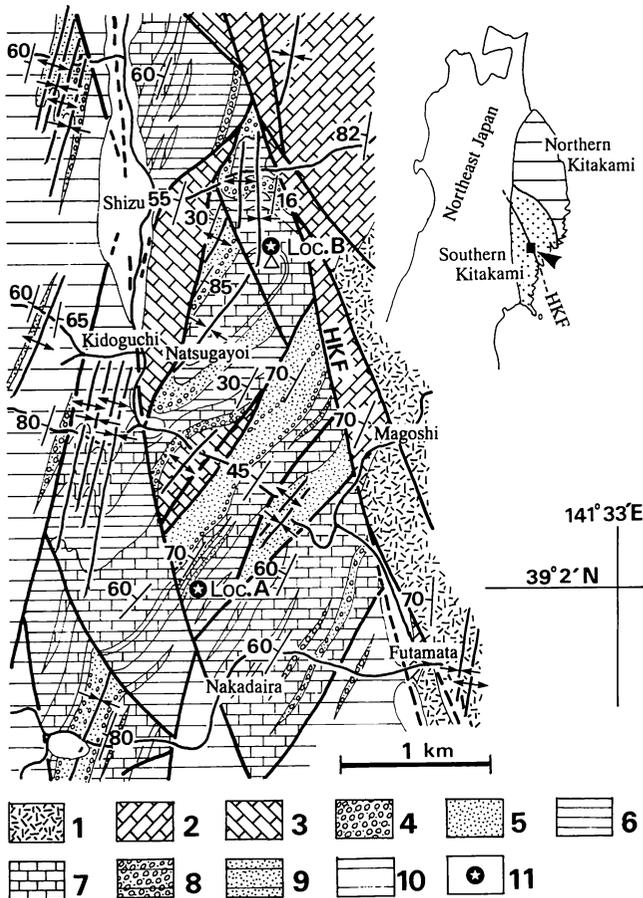
The purpose of this paper is to describe cephalopods from the Nakadaira Formation and to discuss a cephalopod biostratigraphy of Permian strata in the Southern Kitakami Massif.

### Geologic setting

#### A. General aspect of the Nakadaira Formation

The Nakadaira Formation is distributed in the Nakadaira district on the western side of the Hizume-Kesennuma Fault, which traverses the Southern Kitakami Massif with a NNW-SSE trend (Figure 1). The formation is composed of a thick (about 1,000 m) series of alternating beds of conglomerate, sandstone, shale and limestone, which has been complicated owing to folding and faulting (Ehiro, 1977). It unconformably overlies the Lower-Middle Carboniferous Kidoguchi Formation (Ehiro and Mori, 1993) and is in fault contact with the Lower Carboniferous Magoshi Formation and Lower-Middle Carboniferous Senbakaya Formation, both distributed on the eastern side of the Hizume-Kesennuma Fault. The Nakadaira Formation is conformably overlain by the Middle-Upper Permian Ochiai Formation, which is composed mainly of shales with subordinate amounts of sandstone, conglomerate and limestone. The Nakadaira Formation yields fusulinids such as *Robustoschwagerina schellwieni* Hanzawa and *Chalartoschwagerina vulgaris* (Schellwien and Dyhrenfurth) from the lower-middle part and *Pseudofusulina ambigua* (Deprat) and *P. fusiformis* (Schellwien and Dyhrenfurth) from the upper part (Ehiro, 1977). These fusulinids indicate that the formation is roughly correlatable with the type section of the Sakamotozawan Series in the Hikorochi district of the Southern Kitakami Massif.

The standard of reference sequence of the Sakamotozawa Formation has been divided biostratigraphically into five zones based on fusulinids (Kanmera and Mikami, 1965). They are in ascending order the *Zellia nunosei*, *Monodioxodina langsonensis*, *Pseudofusulina vulgaris*



**Figure 1.** Geologic map of the Nakadaira-Natsugayoi area (slightly modified from Ehro, 1977) with cephalopod localities (Loc. A and B). 1: Magoshi Formation, 2: Senbakaya Formation, 3: Kidoguchi Formation, 4-7: Nakadaira Formation (4: conglomerate, 5: sandstone, 6: shale, 7: limestone), 8-10: Ochiai Formation (8: conglomerate, 9: sandstone, 10: shale), 11: cephalopod locality. HKF: Hizume-Kesenuma Fault.

(= *Chalartoschwagerina vulgaris*), *Pseudofusulina fusiformis* and *Pseudofusulina ambigua* Zones.

**B. Cephalopod horizon and associated fauna at Nakadaira**

Near the fossil locality of the northwest of Nakadaira, the Nakadaira Formation is composed in ascending order of shale beds (more than 20 m in thickness), impure limestones (25-30 m), limestones (about 15 m), sandstones (10-12 m) and limestones (more than 15 m) (Figure 2a). The uppermost part of the shale bed sequence is somewhat calcareous and is intercalated with some thin (1 to 5 cm), irregularly lenticular limestones. The shale yields some fossils of solitary corals, bryozoans, brachiopods, gastropods, pelecypods, cephalopods and crinoid stems. The cephalopod fauna at Nakadaira consists of the following species:

Nautiloids.—*Tainoceras* sp., *Foordiceras* ? sp., *Pleuro-*

*nautilus yahagiensis* sp. nov., *P.* sp., *Aphelaeceras* cf. *falciferum* Yin, *Parastenopoceras* sp. and *Stearoceras* sp. Ammonoid.—*Agathiceras* sp.

The impure limestone occurring just above the shale yields such fusulinids as *Rugosofusulina alpina* (Schellwien) and *Pseudofusulina bona* ? Rosovskaya. *R. alpina* is very abundant. A limestone bed, about 40 m above the shale, contains *Chalartoschwagerina vulgaris* (Schellwien and Dyhrenfurth), *Pseudofusulina* ? sp., *Parafusulina* cf. *multiseptata* (Schellwien) and *Rugosofusulina* aff. *complicata* (Schellwien). The horizon of cephalopod fossils at Nakadaira is therefore correlated with the upper part of the Lower Sakamotozawa Formation, because *Rugosofusulina alpina*, found just above the cephalopod horizon, is restricted to the upper part of the *Monodioxodina langsonensis* Zone in the type Sakamotozawa Formation (Kanmera and Mikami, 1965).

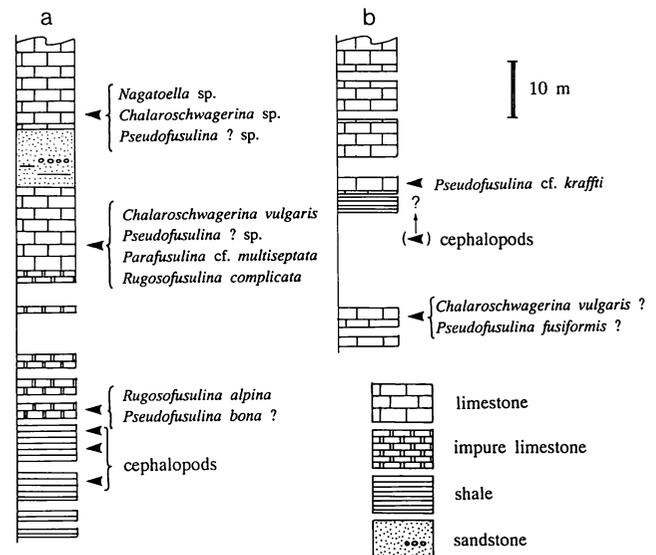
**C. Cephalopod horizon and associated fauna at Natsugayoi**

The Nakadaira Formation developed around the 482-m high peak, located northeast of Natsugayoi, is composed mainly of limestones and is interbedded with some shales (Figure 2b). Cephalopods, together with bryozoans, brachiopods and crinoid stems, were collected from loose impure limestone blocks on the north slope just below the peak. The cephalopod fauna collected at Natsugayoi comprises the following species:

Nautiloids.—*Foordiceras* sp., *F.* ? sp., *Pleuro-nautilus* sp. and *Stearoceras* sp.

Ammonoids.—*Agathiceras* sp. and *Artinskia* sp.

From the limestone which crops out on the 482-m high peak, Ehro (1977) reported a fusulinid species,



**Figure 2.** Columnar sections of the Nakadaira Formation near the cephalopod localities. a: northwest of Nakadaira (Loc. A in Figure 1), b: northeast of Natsugayoi (Loc. B in Figure 1).

*Pseudofusulina* cf. *kraffti* (Schellwien and Dyhrenfurth). A limestone bed lying about 50 m below the peak and below the cephalopod horizon yields such fusulinids as *Chalartoschwagerina vulgaris*? and *Pseudofusulina fusiformis*?

These fusulinids possibly indicate that the cephalopod horizon at Natsugayoi belongs to the Upper Sakamotozawan Series.

### Cephalopod fauna of the Nakadaira Formation

Most cephalopod genera present in the Nakadaira Formation have relatively long stratigraphic ranges. Those species belonging to the genus *Foordiceras* are known from Middle (Lower?) to Upper Permian strata and those of *Pleuronautilus* from Lower Permian to Middle Triassic beds (Kummel, 1953). *Aphelaeceras* species are abundant in Lower Carboniferous strata, but some species are also known from the Lower Permian of North China (Yin, 1933) and from the Upper Permian of South China (Zheng, 1984). The genus *Parastenopoceras*, which is so far represented by only one species (type species: *P. khvorovae* Ruzhentsev and Shimansky, 1954), is restricted to the Artinskian of the Urals. *Artinskia* ranges from the uppermost Carboniferous to Lower Permian (Artinskian) (Ruzhentsev, 1962). From these stratigraphic ranges, the geologic age of the middle to the upper part of the Nakadaira Formation is considered to be Early Permian, most probably Artinskian. This conclusion is in general accordance with previous correlations based on fusulinids: the Sakamotozawan Series was correlated with the Upper Wolfcampian to Middle Leonardian (Kanmera and Mikami, 1965) or with the Upper Chuanshanian (Mapingian) to Lower Chihhsian interval (Minato *et al.*, 1978).

The ammonoid fauna of the Nakadaira Formation is rather monotonous, largely represented by *Agathiceras*. For the Permian of the Southern Kitakami Massif, the present author proposed three ammonoid zones (Ehro, 1987): the *Timorites* Zone recognized in the middle and upper parts of the Kanokuran Series (Middle Permian), the *Araxoceras* Zone in the lower and middle parts of the Upper Permian Toyoman Series and the *Medlicottia kitakamiensis* Zone in the upper part of the Toyoman. Based on the new data presented in this study, I propose to add the *Agathiceras* Zone below the *Timorites* Zone (Ehro, 1995). The *Agathiceras* Zone extends from the upper part of the Lower Sakamotozawan to the lower part of the Kanokuran.

### Systematic descriptions

All the specimens described in this paper are deposited in the collections of Institute of Geology and Paleontology, Tohoku University (IGPS) and in the Rikuzen-Takata City Museum (RCM). They were collected by the author in the year 1991-1993 unless otherwise stated.

Subclass Nautiloidea Agassiz, 1847  
Order Nautilida Agassiz, 1847  
Superfamily Tainocerataceae Hyatt, 1883  
Family Tainoceratidae Hyatt, 1883  
Subfamily Tainoceratinae Hyatt, 1883  
Genus ***Tainoceras*** Hyatt, 1883  
[Type species: *Nautilus quadrangulus*  
McChesney, 1868]

#### ***Tainoceras* sp.**

Figures 3-1; 4-1a-c

*Material*.—One fragmental specimen, IGPS coll. cat. no. 102680, represented by outer and inner moulds, collected from Nakadaira.

*Descriptive remarks*.—The specimen is deformed and only one side of it is preserved. The conch is fairly large, thickly discoidal and evolute in outline, bearing a wide and deep umbilicus. The whorl is estimated to be slightly depressed dorsoventrally and the whorl section is sub-rectangular. The umbilical wall is steep and the umbilical shoulder acutely rounded. The flat lateral side bears prominent ribs which extend from the umbilical to ventral shoulder. The ribs are slightly concave and nodose at the ventral end. The venter is broadly rounded, but the center of it is narrowly sulcate. The presence of a pair of rows of nodes suggest they border a median sulcus.

The suture is only partly preserved. It consists of a low and rounded ventrolateral saddle, and a broad, shallow and slightly sinuous lateral lobe.

The paired ventral nodes are characteristic of the genus *Tainoceras*. Two species of *Tainoceras*, *T. abukumaense* Hayasaka and *T. kitakamiense* Hayasaka, previously reported from the Southern Kitakami (Hayasaka, 1962; Murata, 1971), differ from the present species in not having lateral ribs. Some species of *Tainoceras* having remarkable lateral ribs were described from the Middle Permian Maokouan formations of South China, and from the Middle and Upper Permian of the Salt Range, Pakistan. Among these species, the present species somewhat resembles *T. comptum* Reed (Reed, 1944, p. 353, pl. 60, fig. 1, pl. 62, fig. 2) described from the Upper? *Productus* Limestone of the Salt Range in being large in size, but it is distinguished from the latter by its narrower and sharp ribs. The present species may be a new species, because there are no other large species comparable to it. However, the specimen is clearly too incomplete to be treated as the type of a new species.

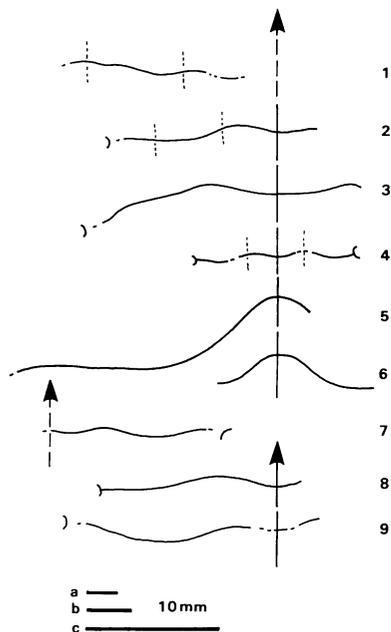
Genus ***Foordiceras*** Hyatt, 1883

[Type species: *Nautilus goliatus* Waagen, 1879]

#### ***Foordiceras* sp.**

Figures 3-2; 4-2a, b

*Material*.—A fragmented specimen, IGPS coll. cat. no. 102681, about a half volution of inner mould, collected from Natsugayoi.



**Figure 3.** Suture lines of nautiloids from the Nakadaira Formation. **1.** *Tainoceras* sp., IGPS coll. cat. no.102680. **2.** *Foordiceras* sp., IGPS coll. cat. no.102681. **3.** *Foordiceras*? sp., IGPS coll. cat. no.102682. **4.** *Pleuronautilus yahagiensis* sp. nov., IGPS coll. cat. no.102686. **5-6.** *Parastenopoceras* sp., 5: IGPS coll. cat. no.102689, 6: IGPS coll. cat. no.102690. **7-9.** *Stearoceras* sp., 7: IGPS coll. cat. no.102692, 8: IGPS coll. cat. no.102691, 9: IGPS coll. cat. no.102694. Scale bars: a for 5-6, b for 1 and 7, c for 2-4 and 8-9.

**Description.**—The conch is small, about 30 mm in diameter, and has a thickly discoidal outline, with a moderately large umbilicus. The shell form is slightly compressed with broadly arched venter and slightly convex sides that converge dorsally. The whorl section is subtrapezoidal. The ventral and umbilical shoulders are rounded. Transverse ribs, almost straight, extend from the umbilical to ventral shoulder.

The suture has a shallow and wide ventral lobe, a low saddle on the ventrolateral shoulder and a shallow lateral lobe which occupies nearly all the flank.

#### *Foordiceras*? sp.

Figures 3-3; 4-3, 4

**Materials.**—Fragmented inner and outer moulds, IGPS coll. cat. no.102682, collected from Nakadaira; another fragmental outer mould, IGPS coll. cat. no.102683, collected from Natsugayoi.

**Description.**—The Nakadaira specimen is strongly deformed ventrolaterally. The venter is broadly arched with rounded ventral shoulders. The sides, having straight radial ribs, may have been convex. The suture has a shallow ventral lobe, a low and rounded saddle on

the ventral shoulder, and a shallow lateral lobe.

The Natsugayoi specimen is represented by a fragmented, broadly convex flank inclining toward the umbilicus, with an acutely rounded ventral shoulder and broadly rounded umbilical shoulder. The umbilicus is rather large. The side is ornamented with radial ribs which extend from the umbilical to ventral shoulder. The ribs increase in height and width towards the ventral margin. The suture is unknown.

Judging from the general shell form and the shape of suture, these two specimens probably belong to the genus *Foordiceras*. This identification is, however, somewhat questionable, because of their very poor state of preservation.

Subfamily Pleuronautilinae Hyatt, 1890  
Genus *Pleuronautilus* Mojsisovics, 1882  
[Type species: *Pleuronautilus trinodosus*  
Mojsisovics, 1882]

#### *Pleuronautilus yahagiensis* sp. nov.

Figures 3-4; 4-5a-7

*Tainoceras abukumaense* Hayasaka. Ehro, 1977, p. 13.

**Materials.**—Holotype: An outer mould of a large specimen, IGPS coll. cat. no.102684, collected by M. Ehro in 1969. Paratypes: A fragmentary outer mould of a moderately large specimen, IGPS coll. cat. no.102685; Outer and inner moulds of a fragmented, small specimen, IGPS coll. cat. no.102686. All collected from Nakadaira.

**Diagnosis.**—*Pleuronautilus* having a semicoronate conch section and strong radial ribs with nodes on the ventral margin.

**Description.**—Three specimens are all elliptically deformed. The conch of the holotype, two and a half? volutions of which are exposed, is evolute and discoidal in outline, with a large, moderately deep umbilicus. The outer mould of the moderately large specimen (Figure 4-6), though the central region of its shell is not well preserved, seems to possess a small umbilical perforation, about 8 mm in the longest diameter. The umbilical shoulder is rounded and the umbilical wall is steep. The broadly rounded flanks converge toward the venter, but diverge near the acutely rounded ventral shoulder. The venter is slightly arched or flat, but becomes slightly concave in the mature stage. Therefore, the cross section of the conch is semioval to semicoronate in shape, with its greatest width near the umbilical shoulder. The diameter of the adoral end of the large specimen is 95 mm in the deformed state and its corresponding height, width and umbilical diameter measure about 33, 24 and 42 mm, respectively.

The flanks have strong radial ribs, which are straight throughout their entire length. They extend from the umbilical to ventral shoulder and have conspicuous elongated nodes on the ventral margin. The nodes coalesce to form almost continuous carinate ridges along the ventral shoulder. There are 19 ribs on the last whorl.

The interspaces between the ribs are somewhat wider than the ribs themselves, but are nearly equal in width to the ribs near the adoral end of the large specimen.

The suture lines are only poorly preserved on a fragmental and partly squashed inner mould of a small specimen (Figure 4-7). The suture (Figure 3-4) consists of a broadly rounded, shallow ventral lobe, a rounded saddle on the ventral shoulder, and a broadly rounded, shallow lateral lobe.

*Comparison.*—In having strong and straight ribs with nodes at the ventral margin, the present new species somewhat resembles *Pleuromutilus linchengense* (Yin) (described originally as *Huanghoceras*; Yin, 1933, p. 21, pl. 3, figs. 1-3) from the Lower Permian Taiyuan Series of North China, *Pleuromutilus tubercularis* (originally described as *Nautilus*; Abich, 1878, p. 22, pl. 3, figs. 5, 5a; Shimansky in Ruzhentsev and Sarycheva, 1965, p. 160, pl. 15, figs. 1a, 1b) and *Pleuromutilus* sp. 1 (Teichert and Kummel, 1973), the latter two having been described from the Upper Permian Dzhulfian bed of Dzhulfa. The new species is, however, clearly distinguishable from the other three forms by a semicoronate cross section.

*Etymology.*—From the local geographical name Yahagi, from which the specimens were collected.

#### *Pleuromutilus* sp.

Figures 4-8a-9

*Materials.*—Two specimens were examined: Outer and inner moulds, both fragmented, IGPS coll. cat. no. 102687, collected from Nakadaira. A fragmental outer mould, IGPS coll. cat. no. 102688, collected from Natsugayoi.

*Description.*—The conch is evolute and thickly discoidal in outline. The Nakadaira specimen (Figure 4-8) attains a diameter of at least 75 mm. The Natsugayoi specimen (Figure 4-9) is fragmented, but its size is estimated nearly equal to that of the Nakadaira one. The umbilicus is moderately large and rather deep. The central region of the shell is not well preserved. The umbilical shoulder is rounded and the umbilical wall is steep. The slightly convex flanks converge toward the venter. The venter is nearly flat and the ventral shoulders are acutely rounded to edged. The cross section of the conch is subtrapezoidal and the greatest whorl width is just over the umbilical shoulder.

The lateral sides are ornamented with strong radial ribs. They extend from the umbilical to ventral shoulder and become wider and lower toward the venter. From the

preserved last whorl, which is a little less than a half revolution, the specimen is estimated to have about 11 ribs in the last half whorl. The interspaces between the ribs and the ribs themselves are nearly equally wide in the last whorl.

The suture line is not observed.

Superfamily Trigonocerataceae Hyatt, 1884

Family Trigonoceratidae Hyatt, 1884

Genus *Aphelaeceras* Hyatt, 1884

[Type species: *Nautilus (Discites) disciformis* Meek and Worthen, 1873]

#### *Aphelaeceras* cf. *falciferum* Yin

Figures 4-10a, b

*Compare.*—*Aphelaeceras falciferum* Yin, 1933, p. 8, text-fig. 2, pl. 1, figs. 2-4.

*Material.*—An outer mould, RCM F762, collected by M. Sato in 1991 from Nakadaira.

*Description.*—The conch is evolute and thinly discoidal in outline, with a moderately large and shallow umbilicus. The conch diameter attains more than 110 mm in a deformed state. The umbilical shoulder is acutely rounded and the umbilical wall steep. The side is convex near the umbilical margin but flat or slightly concave from the central part to the ventral margin. The venter is nearly flat and the ventral shoulders are edged. The conch section is semioval to modified hexagonal, with its greatest width near the umbilical shoulder. The surface of the conch appears to be smooth.

*Comparison.*—The present specimen is comparable with *Aphelaeceras falciferum* Yin in shape of the conch section. However, whether or not it is conspecific with the latter is somewhat questionable, because the conch is rather poorly preserved and the suture is not known.

Family Grypoceratidae Hyatt in Tittel, 1900

Genus *Parastenopoceras*

Ruzhentsev and Shimansky, 1954

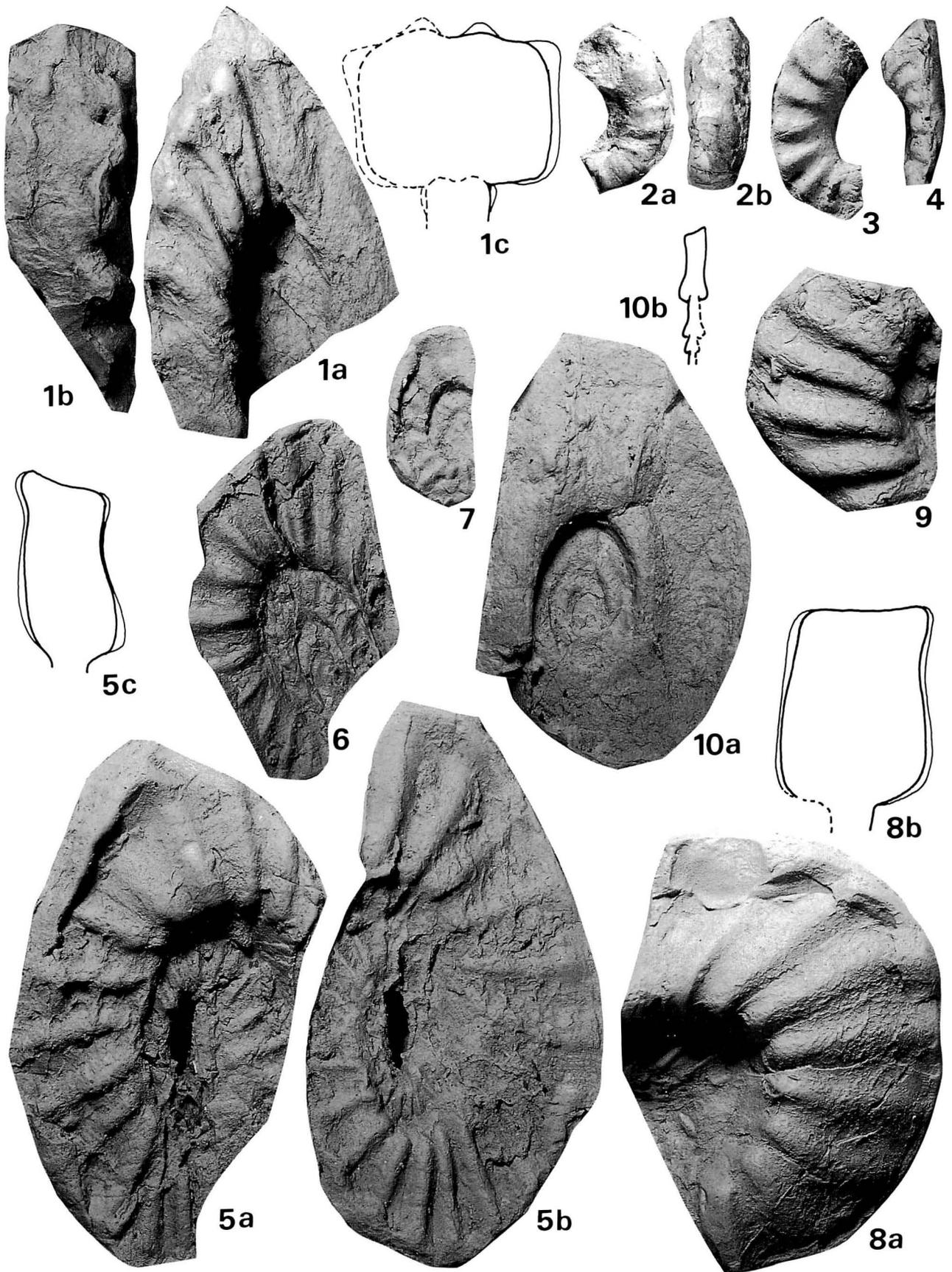
[Type species: *Parastenopoceras khvorovae* Ruzhentsev and Shimansky, 1954]

#### *Parastenopoceras* sp.

Figures 3-5, 6; 6-1a-2

*Materials.*—Two fragmental specimens, IGPS coll. cat. nos. 102689 and 102690, collected from Nakadaira.

**Figure 4.** 1. *Tainoceras* sp., IGPS coll. cat. no. 102680, lateral (a) and ventral (b) views, and cross section (c),  $\times 0.7$ . 2. *Foordiceras* sp., IGPS coll. cat. no. 102681, lateral (a) and ventral (b) views of the inner mould. 3, 4. *Foordiceras* ? sp., 3: IGPS coll. cat. no. 102683, 4: IGPS coll. cat. no. 102682, lateral views. 5-7. *Pleuromutilus yahagiensis* sp. nov., 5: IGPS coll. cat. no. 102684 (Holotype), 6: IGPS coll. cat. no. 102685, 7: IGPS coll. cat. no. 102686, lateral views (5a, 5b, 6, 7) and cross section (5c). 8, 9. *Pleuromutilus* sp., 8: IGPS coll. cat. no. 102687, 9: IGPS coll. cat. no. 102688, lateral views (8a, 9) and cross section (8b). 10. *Aphelaeceras* cf. *falciferum* (Yin), RCM F762, lateral view (a) and cross section (b),  $\times 0.75$ . All figures are approximately in natural size unless otherwise stated. Figures 1, 3-10 are rubber casts from outer moulds. Thin lines of cross sections show cross sections through rib and nodes.



*Descriptive remarks.*—The two specimens are large, fragmented phragmocones, more than 150 mm in diameter. Although the umbilical part is not preserved, the conch section appears to be semielliptical with convex to flat sides and a strongly convex venter. The shell surface is smooth. The suture lines are partly preserved: a high rounded ventral saddle and a broad lateral lobe are recognizable.

Although the present specimens are rather poorly preserved and their generic assignment is somewhat questionable, the suture and the conch section are diagnostic of the genus *Parastenopoceras*. Compared with *P. khvorovae* (Ruzhentsev and Shimansky, 1954, p. 99, pl. 9, figs. 4-5), the type species of the genus, which has a diameter of 34 mm, the present species is quite large.

Genus *Stearoceras* Hyatt, 1893

[Type species: *Endolobus gibbosus* Hyatt, 1891]

*Stearoceras* sp.

Figures 3-7-9; 6-3-6

*Materials.*—Three specimens, IGPS coll. cat. nos. 102691-102693, collected from Nakadaira; another specimen, IGPS coll. cat. no. 102694, from Natsugayoi.

*Description.*—The specimens are all fragmented and deformed, in part strongly obliquely deformed. They are small to moderate, ranging from about 30 mm to more than 60 mm in diameter. The conch is thickly discoidal and may be involute, with a small umbilicus. Its cross section is subtrapezoidal and depressed dorsoventrally. It possesses a broadly arched venter, somewhat convex sides which slightly converge ventrally, and a steep umbilical wall. The ventral shoulders are broadly rounded and the umbilical shoulders acutely rounded. The shell surface is smooth. The sutures form a broad and shallow ventral lobe, a low ventrolateral saddle, and a broad and shallow lateral lobe.

Subclass Ammonoidea Agassiz, 1847  
Order Goniatitida Hyatt, 1884  
Suborder Goniatitina Hyatt, 1884  
Superfamily Agathicerataceae Arthaber, 1911  
Family Agathiceratidae Arthaber, 1911  
Genus *Agathiceras* Gemmellaro, 1887  
[Type species: *Agathiceras suessi* Gemmellaro, 1887]

*Agathiceras* sp.

Figures 5-1, 2; 6-7-12

*Materials.*—Six specimens, IGPS coll. cat. nos. 102695-102700, collected from Nakadaira; another specimen, IGPS coll. cat. no. 102701, from Natsugayoi.

*Description.*—The specimens are small to moderate-sized, with a conch diameter of 27 to 52 mm in a deformed state. The conch is involute and thinly discoidal in outline, with an almost closed umbilicus. The conch section is semielliptical. The slightly convex sides converge toward the umbilicus and the umbilical shoulders are rounded. The venter is convex with rounded ventrolateral shoulders. The flanks are ornamented by more than 30 fine spiral lirae. The inner mould is marked by sinuous transverse constrictions numbering about four per volution.

The suture is poorly preserved. There are one bifid ventral lobe and three or four simple rounded lobes on the lateral sides.

Owing to the poor state of preservation and lateral deformation, identification is difficult at the level of species.

Order Prolecanitida Miller and Furnish, 1954  
Superfamily Medicottiaceae Karpinsky, 1889  
Family Medicottidae Karpinsky, 1889  
Subfamily Medicottinae Karpinsky, 1889  
Genus *Artinskia* Karpinsky, 1926

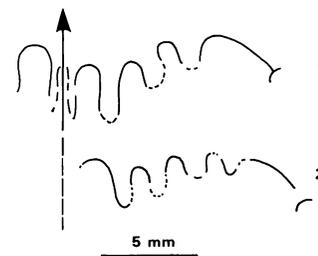
[Type species: *Goniatites flax* Eichwald, 1857]

*Artinskia* sp.

Figures 6-13a, b

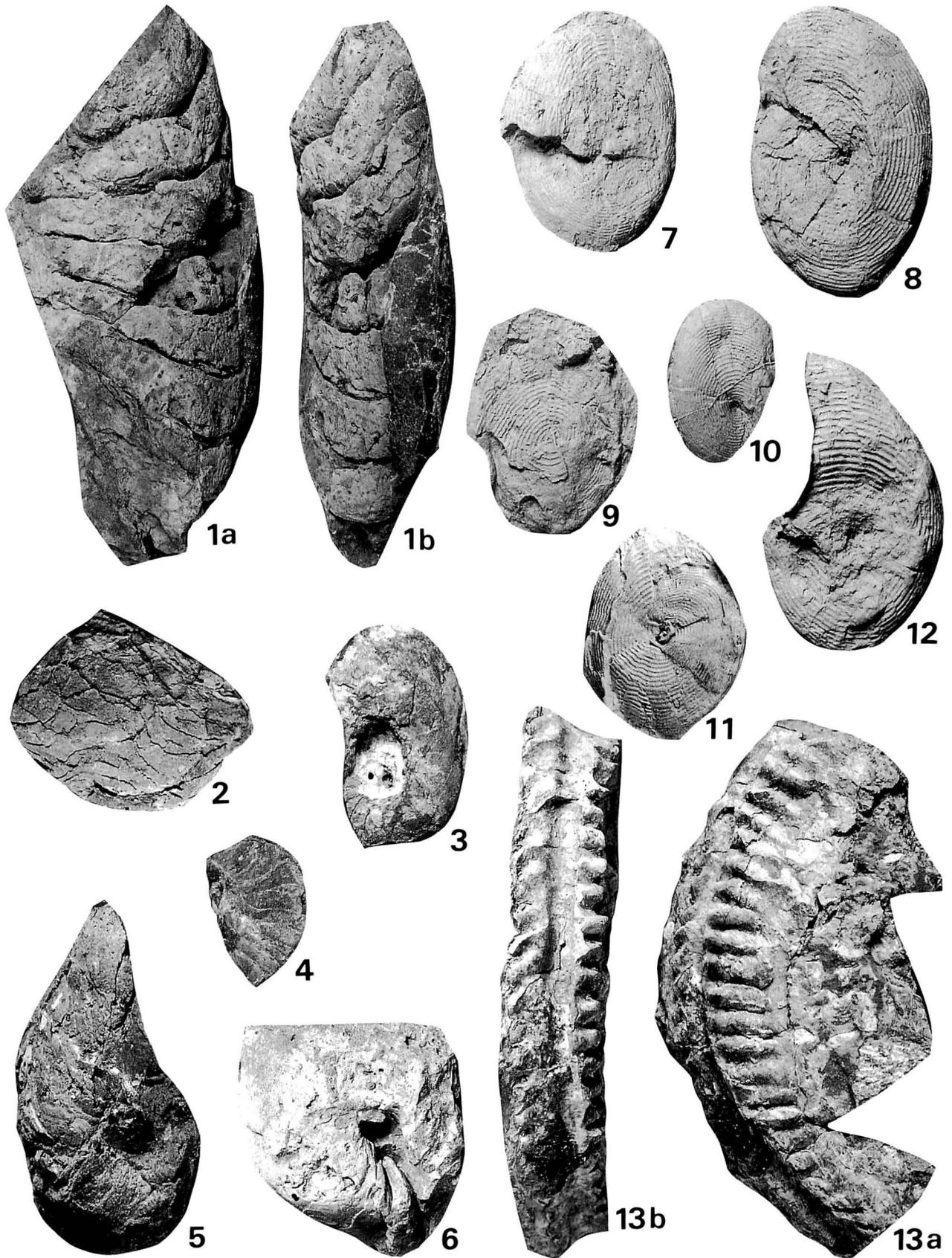
*Material.*—One fragmentary specimen, IGPS coll. cat. no. 102702, collected from Natsugayoi.

*Description.*—Only the ventral side and a portion of the lateral part of the living chamber? are preserved. The



**Figure 5.** Suture lines of *Agathiceras* sp. from the Nakadaira Formation. 1: IGPS coll. cat. no. 102697, 2: IGPS coll. cat. no. 102698.

**Figure 6.** 1, 2. *Parastenopoceras* sp., 1: IGPS coll. cat. no. 102689, 2: IGPS coll. cat. no. 102690, lateral (1a) and ventral (1b, 2) views. 1a-b =  $\times 0.6$ , 2 =  $\times 0.8$ . 3-6. *Stearoceras* sp., 3: IGPS coll. cat. no. 102691, 4: IGPS coll. cat. no. 102692, 5: IGPS coll. cat. no. 102693, 6: IGPS coll. cat. no. 102694, all lateral views. 3-5 =  $\times 1$ , 6 =  $\times 0.65$ . 7-12. *Agathiceras* sp., 7: IGPS coll. cat. no. 102695, 8: IGPS coll. cat. no. 102696, 9: IGPS coll. cat. no. 102697, 10: IGPS coll. cat. no. 102701, 11: IGPS coll. cat. no. 102698, 12: IGPS coll. cat. no. 102699, all lateral views,  $\times 1$ . 13. *Artinskia* sp., IGPS coll. cat. no. 102702, lateral view (a) and ventral view (b),  $\times 0.8$ . Figures 1-6, 13 are inner moulds, 7-12 are rubber casts from outer moulds.



fairly large conch, the diameter of which reaches more than 120 mm, appears to be flattened laterally. The venter is nearly flat, but bears a prominent median groove. The ventrolateral shoulders are narrowly rounded. On each side of the ventral groove is a row of prominent rounded nodes, which are transversely elongate and extend on to the lateral zones. On the fragmental outer mould of the flank near the ventral shoulder, there remains sinuous growth lines. The suture is unknown.

#### Acknowledgments

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SHORT NOTES

32

## A new Carboniferous cephalopod *Bogoslovskya akiyoshiensis* from Southwest Japan

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The Akiyoshi Limestone comprises an organic reef complex that was deposited on a seamount during Early Carboniferous to Middle Permian time. It is found as a large (8×16 km across) allochthonous body in the accretionary Akiyoshi Terrane with synchronous siliceous and Permian terrigenous clastic sediments in Southwest Japan (Kanmera *et al.*, 1990). The limestone is abundantly fossiliferous and provides knowledge of reef paleocommunities in a low-latitude oceanic sea environment. Taxonomic studies concerning the Akiyoshi cephalopod fauna began with Nishida (1971) and were followed by a series of works with his collaborators, including Nishida and Kyuma (1982, 1984), Kyuma and Nishida (1987, 1992), Niko *et al.* (1987, 1991). In the course of successive collecting efforts, twenty-nine specimens of a rare orthocerid cephalopod *Bogoslovskya* were recovered by Nishida and Kyuma from the Middle Carboniferous part of the Akiyoshi Limestone in the Isa area, Yamaguchi Prefecture. A new species *Bogoslovskya akiyoshiensis* is defined herein on the basis of these specimens. ASM stands for the Akiyoshi-dai Museum of Natural History.

### Systematic paleontology

Superfamily Orthocerataceae M'Coy, 1844

Family Orthoceratidae M'Coy, 1844

Subfamily Michelinoceratinae Flower, 1945

Genus *Bogoslovskya* Zhuravleva, 1978

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

*Diagnosis.*—Shell orthoconic with circular to laterally compressed cross section; surface smooth to finely liriate; sutures transverse, juvenile sutures with lateral lobes, but becoming straight adorally; siphuncle submarginal to subcentral, narrow; septal neck long, orthochoanitic; connecting rings cylindrical; auxiliary deposits occur in septal foramen of juvenile shell; lacking cameral deposits.

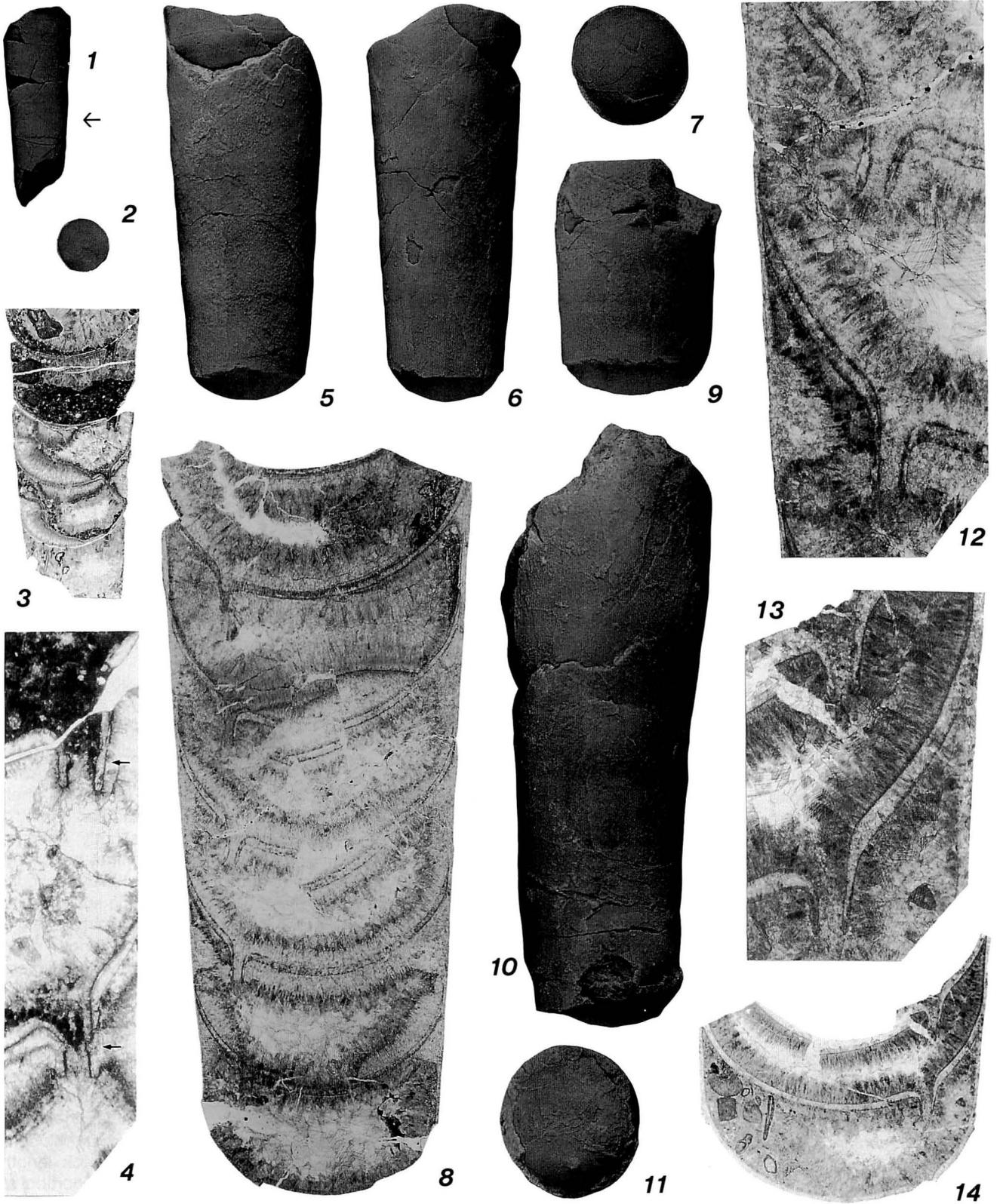
*Remarks.*—The juvenile shell morphology based on

*Bogoslovskya akiyoshiensis* Niko, Nishida and Kyuma sp. nov. has been added to the generic diagnosis.

*Bogoslovskya akiyoshiensis* Niko, Nishida and Kyuma sp. nov.

*Diagnosis.*—Species of *Bogoslovskya* with approximately 7 degrees angle of expansion; circular then compressed cross section; ornamentation of fine transverse lirae; width (maximum inner diameter of each camera in dorsoventral plane)/length ratio of camerae approximately 2.5-3.9 in adoral shell.

*Description.*—Orthocones with relatively rapid shell expansion for genus, angle ranges from 7.0 to 7.2 degrees; cross section of shell circular in juvenile shell, then becoming laterally compressed, breadth/height ratio of shell approximately 0.92; largest specimen (ASM 50220) of phragmocone reaches 18.5 mm in height; shell surface marked by fine lirae on anti-siphuncular (dorsal?) side of adoral shell, transverse and slightly oblique, toward aperture on anti-siphuncular side, lirae becoming finer toward siphuncular side; sutures slightly oblique, toward aperture on siphuncular side, juvenile sutures with weak but broad lateral lobes becoming nearly straight adorally; septa moderately deep; cameral length short for genus, width (maximum inner diameter of each camera in dorsoventral plane)/length ratio in apical shell 1.95-2.05, increasing to 2.48-3.93 adorally; siphuncle narrow, maximum diameter of septal neck/shell height approximately 0.06-0.08, submarginal position, minimum distance of central axis of siphuncle from shell surface per shell height in dorsoventral section ranges from 0.19 to 0.23; septal necks gently tapering orthochoanitic, in adoral siphuncle slightly directed toward central axis of siphuncle, thus septal necks form funnel shape; neck length moderate for genus, 1.3 mm of orthochoanitic portion at shell height 13.0 mm; annulus of weak auxiliary deposits occurs in apical septal foramen, connecting rings not preserved; no cameral deposits detected.



*Discussion.*—This species shares considerable adult shell morphology with the Late Devonian (Famennian) species *Bogoslovskya perspicua* Zhuravleva (1978, p. 57, pl. 3, figs. 4a, b; the type species of the genus) in essential features such as laterally compressed shell, siphuncular size and position, septal neck shape and lack of cameral deposits. Thus, the assignment of the species within the genus *Bogoslovskya* appears certain. *Bogoslovskya perspicua* is distinguished from *B. akiyoshiensis* sp. nov. only by its slightly narrower shell (angle of expansion 5–6 degrees versus approximately 7 degrees), longer camerae (width/length ratio approximately 1.7–1.8 versus 2.5–3.9 in *B. akiyoshiensis* sp. nov. in corresponding shell diameter) and lack of surface ornamentation. The juvenile shell morphology of *Bogoslovskya perspicua* is not known. Previously, *Bogoslovskya* has been reported only from the Middle to Upper Devonian of the Urals. Thus, this is the first record of *Bogoslovskya* outside the Urals, and the discovery extends the range of the genus into the Middle Carboniferous (Moscovian). The present new specimens reveal the possession of auxiliary deposits in the juvenile siphuncle, which may be comparable to the adhesive area of the genitio-intestinal ligament in living *Nautilus* (Blind, 1988).

*Etymology.*—The specific name is derived from the Akiyoshi Limestone, where this species occurs.

*Types.*—The holotype, ASM 50202, is an incomplete phragmocone, 36.2 mm in length. The following eight paratypes, all incomplete phragmocones, are assigned: ASM 50151, 50152, 50209, 50210, 50219, 50220, 50239, and 51260.

*Occurrence.*—This species occurs in a bioclastic grainstone to coquinoid limestone of Middle Carboniferous (Moscovian) age as indicated by the associated foraminifer *Fusulinella biconica* (Hayasaka). The collecting site is identical with locality IM 60 in Niko *et al.* (1991, fig. 1).

#### Acknowledgments

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Akiyoshi 秋吉, Isa 伊佐.

**Figure 1.** *Bogoslovskya akiyoshiensis* Niko, Nishida and Kyuma sp. nov. from the Akiyoshi Limestone Group. **1–4.** paratype, ASM 50152, juvenile shell, 1: lateral view, siphuncular side on left, arrow shows position of septal view given in 2,  $\times 2$ , 2: septal view, siphuncular side down,  $\times 2$ , 3: dorsoventral thin section,  $\times 4$ , 4: details of siphuncular structure, arrows indicate auxiliary deposits,  $\times 20$ . **5–8, 12.** holotype, ASM 50202, 5: view of siphuncular side,  $\times 2$ , 6: lateral view, siphuncular side on right,  $\times 2$ , 7: septal view of apical end, siphuncular side down,  $\times 2$ , 8: dorsoventral thin section,  $\times 4$ , 12: details of siphuncular structure,  $\times 10$ . **9.** paratype, ASM 50219, lateral view, siphuncular side on right,  $\times 2$ . **10, 11.** paratype, ASM 50220, 10: lateral view, siphuncular side on right,  $\times 2$ , 11: septal view of apical end, siphuncular side down,  $\times 2$ . **13, 14.** paratype, ASM 50209, 13: details of siphuncular structure,  $\times 10$ , 14: dorsoventral thin section,  $\times 4$ .

SHORT NOTES

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## Reexamination of the age of the *Canoptum* assemblage (Radiolaria) from acidic tuff in the Hiuchiwan Unit of the Tanba Group, Southwest Japan

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### Introduction

Species of the radiolarian genus *Canoptum* Pessagno, 1979 have often been found from Upper Triassic and Lower Jurassic strata in the Mesozoic accretionary complexes of Southwest Japan (e.g., Yao *et al.*, 1980; Ishiga, 1983; Fukudomi, 1990; Suzuki and Itaya, 1994; Iijima *et al.*, 1994). In general, *Canoptum* species occur in association with various other species of nassellarians, but occasionally they constitute a particular type of radiolarian assemblage, in which species of *Canoptum* make up 70–90% of the nassellarian individuals (Yao, 1990; Suzuki, 1993, 1995). The geologic age of all these *Canoptum*-dominant assemblages found in Southwest Japan has hitherto been considered as latest Triassic (Fukudomi, 1990; Musashino *et al.*, 1992; Takashiroyama Research Group, 1993; Itasaka *et al.*, 1994), because their species composition resembles that of the *Canoptum triassicum* assemblage (Yao, 1982) described from the uppermost Triassic chert of the Inuyama area. Furthermore, it has been taken as supporting evidence for this age assignment that typical Jurassic genera such as *Parahsuum*, *Droitus*, *Bagotum*, etc. are not found in these *Canoptum*-dominant assemblages.

The present author has reported the *Canoptum*-dominant assemblages in the Umenoki Unit of eastern Shikoku and the Kanoashi Complex of Shimane Prefecture, and named them the *Canoptum* assemblage (Suzuki, 1993, 1995). These *Canoptum* assemblages are concluded to be of Early Jurassic age, because the assemblages contain Early Jurassic species and occur from strata that also yield a typical Early Jurassic assemblage containing *Parahsuum*.

The present study deals with the third finding of the *Canoptum* assemblage in Lower Jurassic strata. The assemblage was found from acidic tuff in the Hiuchiwan Unit of the Tanba Group. Radiolarian assemblages from this acidic tuff were first reported by Musashino *et al.* (1992). They showed two types of radiolarian assemblage, i.e. the *Canoptum triassicum* and the *Parahsuum simplicum* assemblage, and referred their age to latest

Triassic and Early Jurassic, respectively. Reexamination of the species composition of the *Canoptum triassicum* assemblage of Musashino *et al.* (1992) leads to the conclusion that the assemblage should be attributed to the Early Jurassic rather than latest Triassic.

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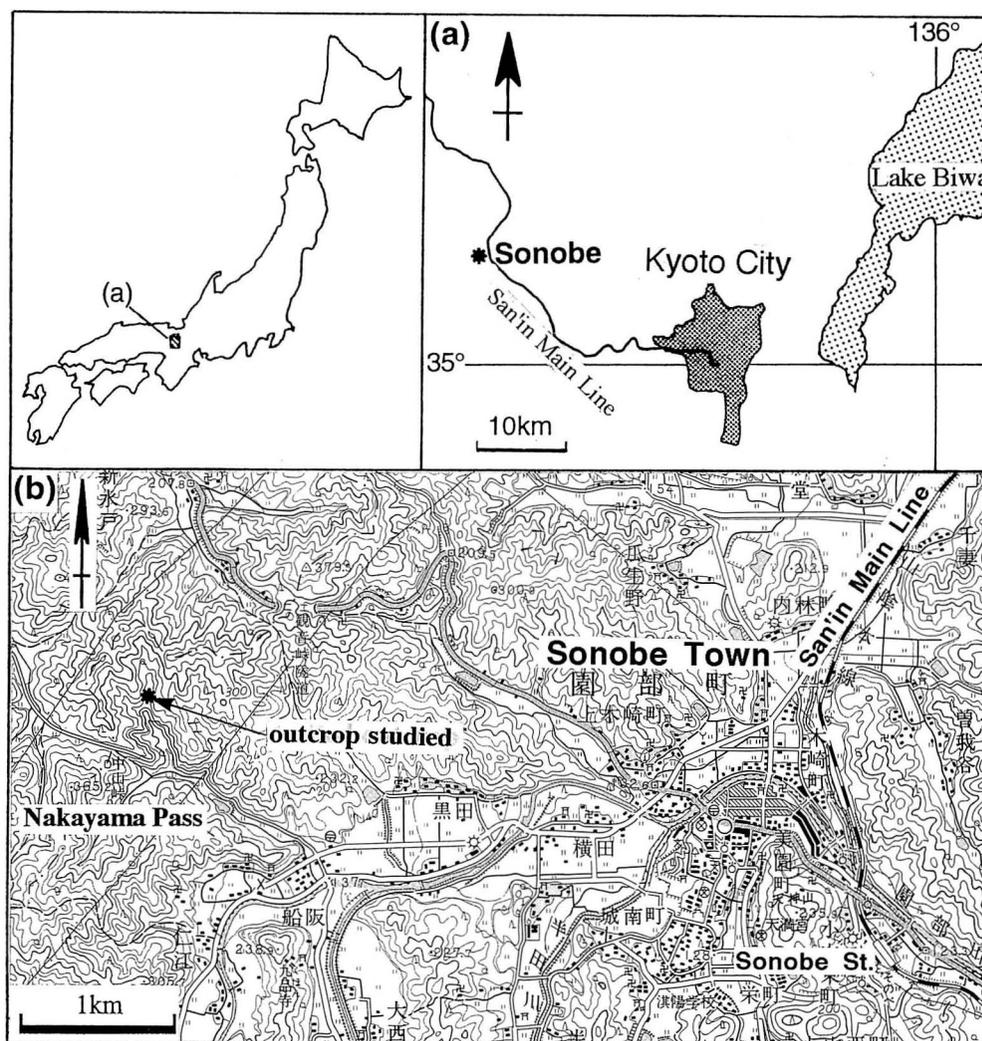
### Material

Acidic tuff containing radiolarian fossils at Nakayama Pass in Sonobe town, Kyoto Prefecture (Figure 1) belongs to the Hiuchiwan Unit of the Tanba Group (Imoto *et al.*, 1991). The Hiuchiwan Unit is an olistostromal complex composed of greenstone, limestone, chert, acidic tuff, mudstone and sandstone (Imoto *et al.*, 1991). The acidic tuff at Nakayama Pass is fine-grained and light green, stratified with intercalations of black mudstone. These strata strike N75–80°E, and dip 35–45° southwards. Sketch of the outcrop studied and columnar section are shown in Figure 2. The strata are continuous and there is no fault in the outcrop. The outcrop is a part of the section described by Musashino *et al.* (1992).

Seven rock samples were collected from the outcrop. These samples were processed with about 3% hydrofluoric acid for 24 hours and were sorted with a sieve between opening 180  $\mu\text{m}$  and 63  $\mu\text{m}$ . Obtained residues were confined between object glass and cover glass with mounting medium "Entellan New" to make the preparations. Radiolarian genera and species were identified under an optical microscope.

### Radiolarian assemblages and their age

Abundant radiolarian individuals were detected from five rock samples among the seven samples collected. The radiolarian species are listed in Table 1, and representative species are shown in Figure 3. While the samples 103a, 103d and 103e yield the *Canoptum*-dominant assemblage, the samples 103b and 103c yield the



**Figure 1.** Location of the outcrop studied. (b). Based on the topographic map "Sonobe", 1: 50,000 scale, Geographical Survey Institute.

assemblage containing abundant *Parahsuum* individuals. The two assemblages occur alternatively in a section 3.4 m thick (Figure 2).

The *Canoptum*-dominant assemblage from samples 103a, 103d and 103e is considered to be an equivalent of the *Canoptum* assemblage from the Kanoashi Complex reported by Suzuki (1995), because (1) *Canoptum* content reaches more than 70% of the nassellarian individuals, (2) there is a nassellarian species (gen. et sp. indet., Figure 3-4) that is closely similar to *Nassellaria* gen. et sp. indet. A, one of the characteristic species of the *Canoptum* assemblage of the Kanoashi Complex, and (3) typical Early Jurassic genera such as *Parahsuum*, *Droltus* and *Bagotum* are scarcely found in this assemblage.

In the assemblage containing *Parahsuum*, the following species were recognised as leading fossils: *Parahsuum ovale* Hori and Yao, *Droltus hecatensis* Pessagno and Whalen, and *Bagotum* sp. The occurrence of these

species indicates an Early Jurassic age. *Parahsuum ovale* is an index fossil of the *Parahsuum simplum* zone of the Inuyama area (Hori, 1990), suggesting an age from Hettangian to early Toarcian. The stratigraphic range of *Droltus hecatensis* and of the genus *Bagotum* makes further detailed age assignment possible. According to Pessagno and Whalen (1982), *Droltus hecatensis* ranges in age from Rhaetian (?)/Hettangian to early Pliensbachian, and the genus *Bagotum* Pessagno and Whalen occurs from strata younger than Sinemurian. Consequently, the assemblage containing *Parahsuum* suggests a Sinemurian or early Pliensbachian age, based on the occurrence of these taxa.

Although typical Early Jurassic genera common in Southwest Japan could scarcely be found in the *Canoptum* assemblage of Nakayama Pass, *Canoptum* species and *Natoba minuta* Pessagno and Poisson in this assemblage may suggest an Early Jurassic age. There

Table 1. List of radiolarians from the acidic tuff of Nakayama Pass.

species/sample No.	103a	103b	103c	103d	103e	103f
<i>Liosphaeridae</i> gen. et sp. indet.	*	*	*	*	*	*
<i>Praeconocaryomma</i> sp.						*
<i>Sphaerostylus</i> sp.		*			*	
<i>Pseudostylosphaera</i> sp.			*			
<i>Gorgansium</i> sp.		*	*	*	*	
<i>Triactoma</i> (?) sp.			*	*		
<i>Staurosphaera</i> (?) sp.			*			
<i>Stypolarcus</i> sp.					*	*
Hagiastrinae gen. et sp. indet.		*	*	*	*	
<i>Orbiculiforma</i> sp.					*	
<i>Palaeosaturnalis</i> sp.		*				
<i>Canoptum</i> sp.	*	*	*	*	*	*
<i>C. rugosum</i> PESSAGNO and POISSON					*	
<i>Tricolocampe</i> sp.	*			*	*	
<i>Natoba minuta</i> PESSAGNO and POISSON	*	*	*	*	*	*
<i>Cornutella</i> (?) sp.					*	
<i>Saitoum</i> sp.			*	*	*	
<i>Archicapsa</i> sp.	*	*	*			
<i>Parahsuum</i> sp.		*	*			
<i>P. ovale</i> HORI and YAO			*			
<i>Droltus</i> sp.		*	*		*	*
<i>D. hecatensis</i> PESSAGNO and WHALEN		*	*			
<i>Bagotum</i> sp.		*				
<i>Dictyocephalus</i> sp.				*		
<i>Stylocapsa</i> (?) sp.				*		
<i>Tricolocapsa</i> sp.					*	
<i>Stichocapsa</i> sp.		*				
<i>Laxtorum</i> (?) sp.					*	
<i>Nassellaria</i> gen. et sp. indet.	*			*	*	

are many individuals of *Canoptum* species in the assemblage which have H-type structure around circumferential ridges (Figure 3-1). Pessagno and Poisson (1981) mentioned that the H-type structure of *Canoptum* had been observed exclusively within Early Jurassic species. *Natoba minuta* was first described from the lower Pliensbachian of Turkey (Pessagno and Poisson, 1981). Unfortunately, there is no further report of its occurrence outside the locus typicus except for the Umenoki Unit of eastern Shikoku, in which Suzuki (in press) depicted *Natoba minuta* from lower Pliensbachian chert. The stratigraphic range of *Natoba minuta* is not yet clear, but it could probably be limited within the Lower Jurassic, because *Natoba minuta* has thus far been reported from neither the Upper Triassic nor Middle Jurassic. Based on the occurrence of these forms, the age suggested by the *Canoptum* assemblage of Nakayama Pass is Early Juras-

sic, so that there is no great difference between ages of the assemblage containing *Parahsuum* and the *Canoptum* assemblage.

Musashino *et al.* (1992) illustrated some species, which have been thought to suggest a Late Triassic age, from the same acidic tuffs at Nakayama Pass: *Triassocampe* sp., *Squinabolella* sp., *Sarla* (?) sp. and *Veghicyclia* sp. (Musashino's *Orbiculiforma multifora*). However, taking the occurrence of Early Jurassic species into consideration, these Late Triassic taxa could be fossils derived from Late Triassic strata, or their ranges may extend into the Early Jurassic. This study ascertained no radiolarian species indicative of a Late Triassic age, with the exception of isolated spiral spines of supumellarians.

Consequently, the section of acidic tuff studied at Nakayama Pass can be assigned to the Early Jurassic. It is certain that the *Canoptum*-dominant assemblage which

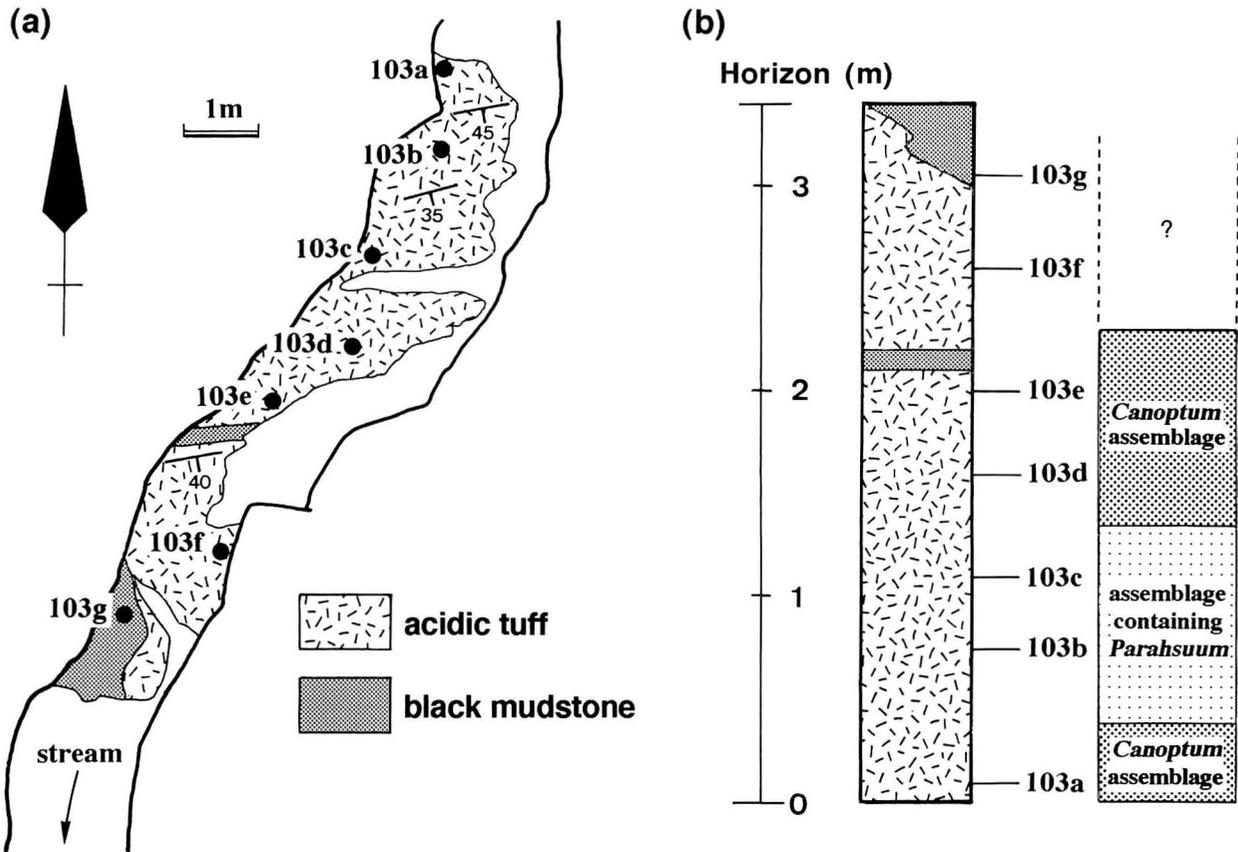


Figure 2. (a). Sketch of the outcrop studied. (b). Columnar section. Solid circles in Figure (a) represent sampling points.

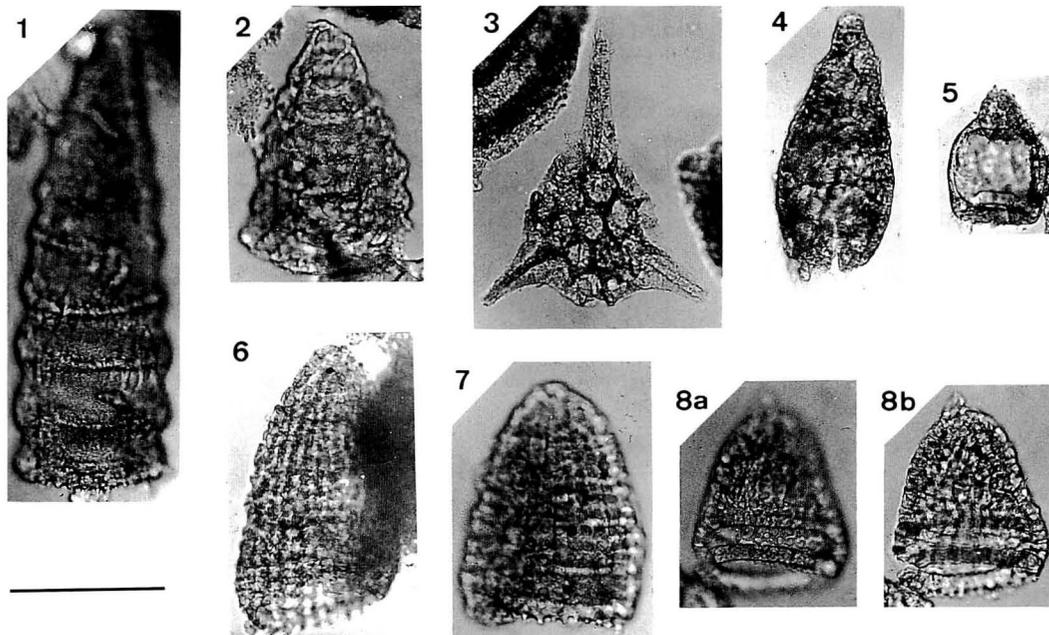


Figure 3. Radiolarians of the *Canoptum* assemblage (1 to 5) and the assemblage containing *Parahsuum* (6 to 8) at Nakayama Pass. 1: *Canoptum* sp., which possesses H-type structure around circumferential ridges, 2: *Canoptum rugosum* Pessagno and Poisson, 3: *Gorgansium* sp., 4: *Nassellaria* gen. et sp. indet., 5: *Notoba minuta* Pessagno and Poisson, 6: *Parahsuum ovale* Hori and Yao, 7: *Parahsuum* sp., 8a-b: *Droltus hecatensis* Pessagno and Whalen. Scale bar equals 100  $\mu$ m.

has hitherto been considered as latest Triassic occurs also from Lower Jurassic strata of Southwest Japan.

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### Palaeontological Society of Japan (JSP) Council Actions

During its meeting on June 23, 1995, the Council enacted the following changes to its membership.

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Shigeru Hiramatsu,	Kazuhiro Ishii,	Shunsuke Kawakami,
Sinji Kikuchi,	Masahiro Kishigami,	Takeshi Kon,
Hiroto Matsuki,	Nachio Minoura,	Taro Mito,
Jun Mitsuhashi,	Shigeo Miyazaki,	Rei Nakashima,
Kousuke Naruse,	Kumiko Nishiyama,	Harushige Noda,
Motoo Okada,	Masaaki Okuda,	Takuji Shibasaki,
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Yasuo Maeda

(Ordinary member)

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Harumi Sugawara		

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◎ 1996 年年会・総会は、1996 年 1 月 26～28 日に、大阪市立大学理学部で開催予定です。講演（含ポスターセッション）申込みは **12 月 5 日（必着）** 締切です。講演申込みの方法や予稿集原稿の書き方については、「化石」48 号または 54 号をご覧ください。なお、講演区分の中には、ポスターセッションも含まれます。

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