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

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Middle Miocene deep-water molluscs from the Arakawa Formation in the Iwadono Hills area, Saitama Prefecture, central Japan

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Abstract. Twenty-five molluscan taxa were identified from three localities of the lower Middle Miocene Arakawa Formation in the Iwadono Hills area, Saitama Prefecture, central Japan. This fauna consists of two types of assemblage (protobranch-dominant and septibranch-dominant) and is inferred to represent a deep-water fauna (bathyal depths) on the basis of its taxonomic structure. Similarities in generic composition between the molluscan fauna of the Arakawa Formation and that of the bathyal zone in modern Sagami Bay suggest that the marine climate during the Arakawa deposition is comparable with that of the intermediate water of Sagami Bay. One new species, *Neilonella tsukigawaensis*, is described herein, and the stratigraphic relationship between the Arakawa and the overlying Goudo Formation is briefly mentioned.

Key words : Arakawa Formation, deep-water molluscan fauna, Iwadono Hills, Miocene, intermediate water

Introduction

Mollusc-bearing marine Miocene strata are exposed in the Iwadono Hills area, located in the eastern margin of the Kanto Mountains, Saitama Prefecture, central Japan (Figure 1-A). They are stratigraphically divided into the Arakawa, Goudo, Syougunzawa, Hatoyama, and Imazyuku Formations in ascending order (Majima, 1989). Molluscan fossils from the Goudo and Syougunzawa Formations have been listed and partly illustrated by Hatai and Masuda (1962) and Majima (1989), but there has not been any paleontological work on the molluscan fauna from the Arakawa Formation in the Iwadono Hills area.

During my field survey in the Iwadono Hills area from 1993 to 1994, approximately one hundred specimens of molluscan fossils were collected from the Arakawa Formation, in which two types of deep-water assemblages were recognized. The purpose of this paper is to report the molluscan fauna of the Arakawa Formation in the Iwadono Hills area and to discuss the inferred paleobathymetry and marine paleoclimate of the formation based on the molluscan faunal analysis.

Geologic setting and age

Miocene strata distributed in the Iwadono Hills area are separated by a fault from Pre-Tertiary metamorphic rocks in the western part and are overlain by the Plio-Pleistocene Monomiyama Formation in the southern part (Figure 1-B). Koike *et al.* (1985) and Majima (1989) recently studied the geology of the Iwadono area, but their stratigraphic divisions are slightly different from each other (Figure 2). In this paper, I follow Majima's (1989) division because he made it clear that the lowermost Miocene stratigraphic unit in the Iwadono area belongs to the Arakawa Formation (Watanabe *et al.*, 1950), which is widely distributed in the central part of Saitama Prefecture.

The Arakawa Formation in the northern study area is exposed narrowly and sporadically (Figure 1-C). It consists mainly of diatomaceous siltstone and sandy siltstone, both of which commonly contain sand-sized fragments of schist. In this lithological feature, the Arakawa Formation can be distinguished from the other Miocene siltstone-dominant formations in the Iwadono area. Although partial sections were measured at the place where the megafossils were collected, structural complexities and poor exposures make it difficult to correlate these sections. The Arakawa Formation is considered to be overlain by the Goudo Formation, which is composed mainly of sandstone and conglomerate, but their stratigraphic relationship is unclear, as will be mentioned.

The geologic age of the Arakawa Formation recently became better defined by means of diatom biostratigraphy. Kurihara (1994MS) obtained for the first time from the formation (Loc. 1 of Figure 1-C and Table 1) a diatom assemblage, which he assigned to the early Middle Miocene *Denticulopsis lauta* Zone (NPD 4A) of Akiba's (1986) Neogene North Pacific Diatom Zonation (Horiuchi and Yanagisawa, 1994).

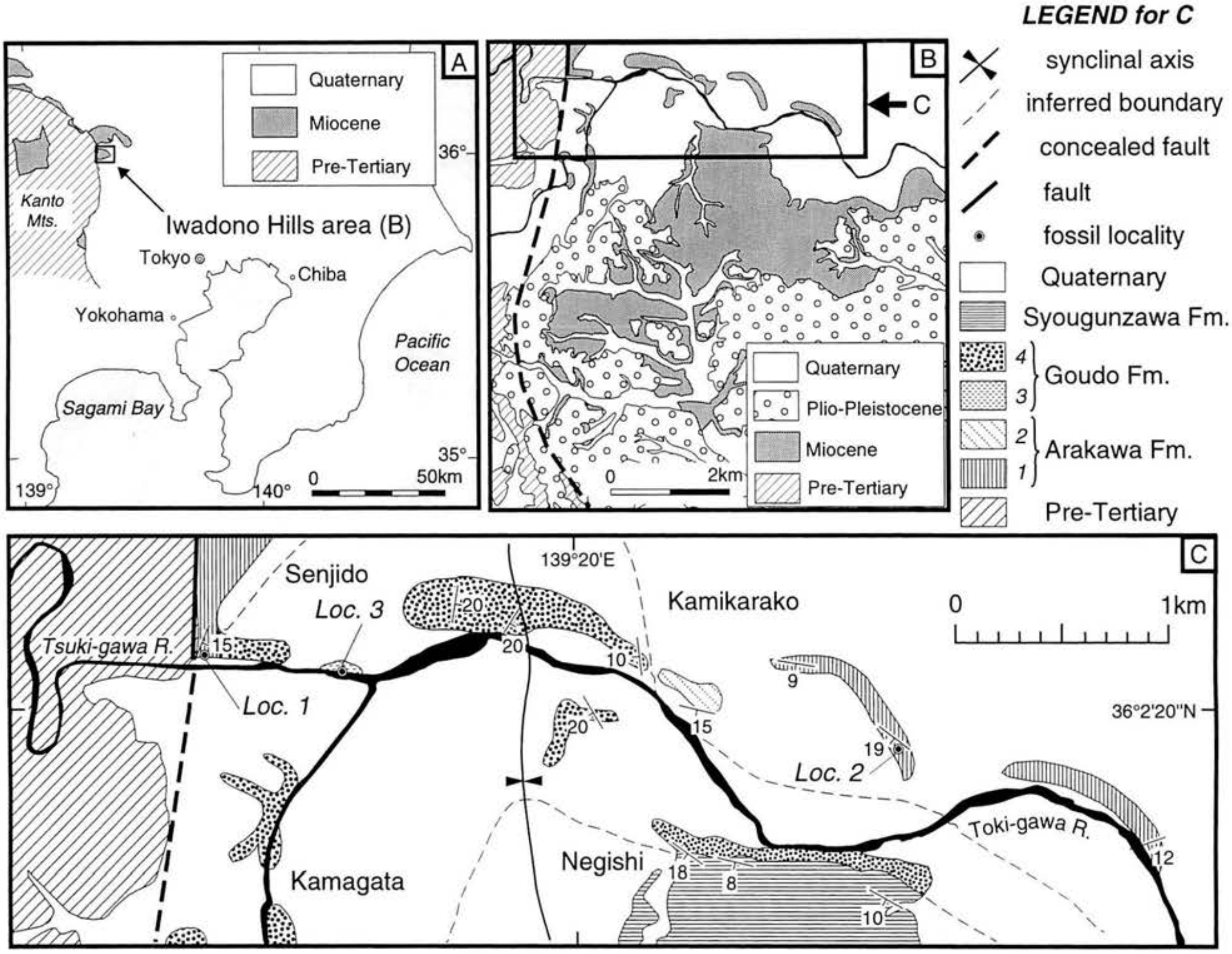

Figure 1. (A) Index map showing the Iwadono Hills area, and the geologic sketch map of eastern margin of the Kanto Mountains. (B) Geologic sketch map of the Iwadono area. (C) Geologic map of the northern part of the Iwadono area with the fossil localities. Legend: 1, diatomaceous siltstone; 2, sandy siltstone; 3, conglomerate consisting mainly of sandy siltstone boulders; 4, sandstone and conglomerate.

Koike *et al.* (1985)			Majima (1989)
Tokigawa Group	Ohashi Fm.	Imajuku Ss. Mm.	Imazyuku Fm.
		Hatoyama Ss. & Slt. Mm.	Hatoyama Fm.
	Iwadono Fm.	Shogunzawa Slt. Mm.	Syougunzawa Fm.
		Negishi Ss. Mm.	Goudo Fm.
		Godo Cgl. Mm.	
unconformity			*unconformity?*
Kamikarako Fm.			Arakawa Fm.

Figure 2. Comparison of stratigraphic divisions of the Miocene in the Iwadono Hills area by recent workers. Fm., Formation; Mm., Member; Cgl., Conglomerate; Ss., Sandstone; Slt., Siltstone.

According to Y. Yanagisawa (per. com.), the formation in the Iwadono area is assigned for the most part to NPD 4A, with the lowermost part extending to the latest Early Miocene *Crucidenticula kanayae* Zone (NPD 3A). Therefore, the Arakawa Formation in the Iwadono area ranges from the uppermost Lower to lower Middle Miocene in age. The molluscan fossils treated in this paper cooccurred with a diatom assemblage assigned to the middle part of NPD 4A, which is characterized by the occurrence of the very short-ranging species *Cavitatus lanceolatus*. According to the latest age estimation of diatom datum levels by Yanagisawa and Akiba (1998), NPD 4A with *C. lanceolatus* ranges from 15.6 to 15.2 Ma. The Goudo Formation yields larger foraminifers including *Lepidocyclina* sp., which also suggest a lower Middle Miocene (Blow's N. 8–9) age (Majima, 1989).

Table 1. List of the diatom fossils from the Arakawa Formation (Loc. 1) and from sandy siltstone boulders in the Goudo Formation (Loc. 3) (identified by Y. Yanagisawa). Numbers indicate those of individuals for species that occur from 100 individuals selected at random. + indicate recognizable species.

Sample locality	Loc. 1	Loc. 3
Sample number	Sg 3	Iwd 9
Diatom zone	4A	4A
Actinocyclus ingens f. *ingens* (Rattray) Whiting et Schrader	5	16
A. ingens f. *nodus* (Baldauf) Whiting et Schrader	+	1
A. ingens f. *planus* Whiting et Schrader	6	13
A. octonarius Ehrengerg	—	1
Actinoptychus senarius (Ehrenberg) Ehrenberg	+	3
Cavitatus exiguus Yanagisawa et Akiba	1	2
C. jouseanus (Sheshukova) Williams	+	2
C. lanceolatus Akiba et Hiramatsu	5	1
C. linearis (Sheshukova) Akiba et Yanagisawa	+	—
C. miocenicus (Schrader) Akiba et Yanagisawa	—	1
Cestodiscus sp. (concave)	+	—
Coscinodiscus lewicianus Greville	+	1
C. marginatus Ehrenberg	1	—
C. perforatus Ehrenberg	—	1
Crucidenticula kanayae var. *kanayae* Akiba et Yanagisawa	+	—
Delphineis miocenica (Schrader) Andrews	1	—
Denticulopsis ichikawae Yanagisawa et Akiba	8	3
D. lauta (Bailey) Simonsen	8	3
D. cf. *okunoi* Yanagisawa et Akiba	+	—
Girdle view of D. lauta group	7	+
Hemiaulus bipons (Ehrenberg) Grunow in Heurck	+	—
Ikebea tenuis (Trun) Akiba	+	—
Nitzschia challengeri Schrader	+	—
Paralia sulcata (Ehrenberg) Cleve	13	11
Planifolia tribranchiata Ernissee	—	1
Stellarima microtrias (Ehrenberg) Hasle et Sims	1	—
Stephanopyxis spp.	1	2
Thalassionema cf. *hirosakiensis* (Kanaya) Schrader	+	—
T. nitzschioides (Grunow) H. et M. Peragallo	44	38
Thalassosira leptopus (Grunow) Hasle et Fryxell	+	—
Thalassiothrix logissima Cleve et Grunow	+	+
Total number of valves counted	100	100
Resting spore of *Chaetoceros*	18	12

Remarks on the stratigraphic relationship between the Arakawa Formation and the overlying Goudo Formation

The stratigraphic relationship between the Arakawa and Goudo Formations is unclear because of the lack of a boundary outcrop, except for a fault contact.

Previous workers pointed out that the Arakawa Formation might be unconformably overlain by the Goudo Formation primarily on the basis of structural differences (Koike *et al.*, 1985) or the presence of pebbles presumably derived from the Arakawa Formation in the Goudo Formation (Majima, 1989).

Recently, I found new evidence by which to consider the stratigraphic relationships of the two formations.

A conglomerate facies including abundant sandy siltstone boulders (more than 2 m in maximum diameter) is observed in the very coarse-grained sandstone matrix of the Goudo Formation at Loc. 3 (Figures 1-C and 3-C). The boulders are considered to have been derived from the Arakawa Formation, because: (1) the sandy siltstone boulders commonly contain sand-sized fragments of schist; this lithofacies characterize the Arakawa Formation as mentioned before; (2) the sandy siltstone lithology of the boulders resembles that of the Arakawa Formation exposed at Kamikarako (see Figure 1-C); (3) the boulders are too large to have been transported from outside the Iwadono area, and (4) the diatom assemblage in the boulders is assigned in age to Akiba's NPD 4A, which is the same as the Arakawa Formation (Table 1). Although the exact boundary between the Arakawa and Goudo Formations could not be observed at Loc. 3, the facies including the boulders may represent a basal unit of the Goudo Formation which presumably covers the Arakawa Formation with an erosional contact. However, it is difficult to conclude that the relationship between these two formations is an unconformity, because of the lack of chronological data indicating the time gap between them.

Occurrence of molluscs

Molluscan fossils treated in this paper were collected from the diatomaceous siltstone of the Arakawa Formation (Locs. 1, 2) and from the sandy siltstone boulders in the Goudo Formation (Loc. 3) (Figure 1-C). The boulders are considered to have been derived from the Arakawa Formation as mentioned before, thus the molluscan fossils contained in the boulders are treated as derived from the Arakawa Formation. Columnar sections showing the sampling horizon of Locs. 1 and 2 are shown in Figures 3-A and B, respectively.

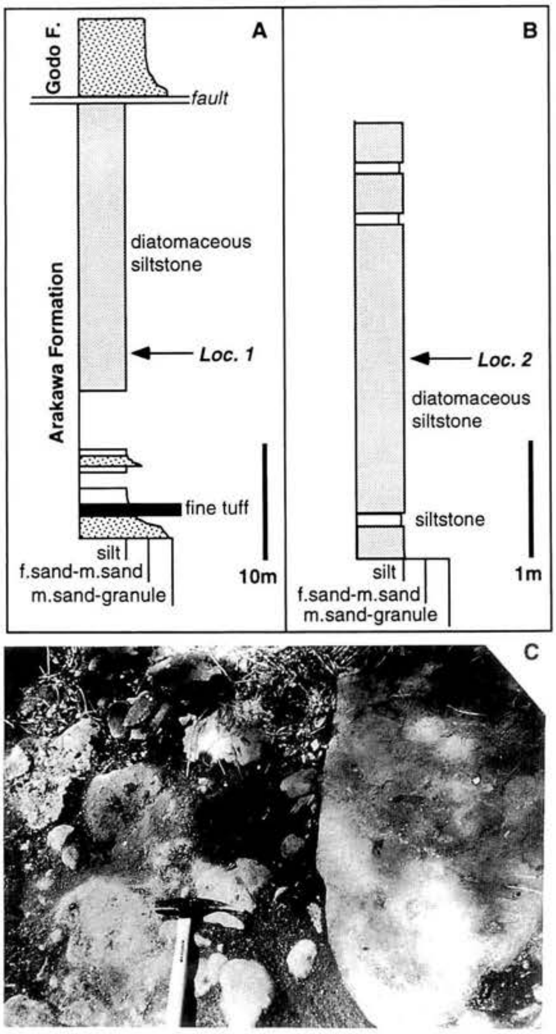

Figure 3. Columnar sections showing the sampling horizon of Locs. 1 (A) and 2 (B). Field photo showing mode of occurrence of sandy siltstone boulders at Loc. 3 (C).

Preservation of molluscs from the Arakawa Formation is generally poor and varies in relation to their enclosing lithology. Molluscan shells from the diatomaceous siltstone at Locs. 1 and 2 are completely dissolved and are preserved as molds, whereas those from the sandy siltstone at Loc. 3 often retain their shell material. Molluscan fossils from the diatomaceous siltstone have suffered more significant post-depositional deformation than those from the sandy siltstone.

The mode of fossil occurrence remains almost constant at the three localities. Molluscan fossils are sporadically distributed in random orientation within the intensively bioturbated massive silty matrix. The shells generally do not show signs of post-mortem wear or breakage. Most bivalve shells are disarticulated (Table 2). The intensively bioturbated sediments suggest that burrowing animals reworked the shells, in which case the empty bivalve shells may have been disarticulated by bioturbation and not retained their life position. The sporadic occurrences of the shells and their showing no sign of abrasion and breakage suggest that the molluscan assemblage is essentially parautochthonous.

Molluscan assemblages

Six gastropods, one scaphopod and 18 bivalves were identified from the Arakawa Formation in the Iwadono area (Table 2).

On the basis of occurrence of the characteristic species, two types of molluscan assemblages are recognized. The essentially parautochthonous nature of the molluscan fossils suggests that these assemblages may represent former benthic communities. Characteristics of specific compositions of each assemblage are described below.

Type I: *Myonera osawanoensis* assemblage

This assemblage is recognized in diatomaceous siltstone at Locs. 1 and 2. It is characterized by the dominance of *Myonera osawanoensis*, which accounts for nearly 50% of the total number of the specimens. Commonly associated species are *Portlandia* sp. and *Delectopecten* cf. *peckhami*.

Type II: *Neilonella tsukigawaensis* assemblage

This assemblage is recognized in massive sandy siltstone boulders at Loc. 3. It is characterized by the dominance of *Neilonella tsukigawaensis* sp. nov., which accounts for about 25% of the total number of the specimens. Subdominant species are *Portlandia* sp. and *Orectospira* sp.

Paleobathymetry

For the paleobathymetric interpretation of Cenozoic molluscan faunas, the taxonomic structure method is useful because it can discriminate between shallow- (less than 200 m) and deep-water (greater than 200 m) faunas. This method was developed by Hickman (1974, 1984) and is based on the observation that the percent composition of species representing major taxonomic division of the molluscan group changes with depth in modern major regional faunas.

Table 2. List of the molluscan fossils from the Arakawa Formation. Numbers represent those of individuals. For bivalves, the numbers naked and in the parenthesis represent those of disarticulated and articulated valves, respectively.

Assemblage type	I		II
Locality	Loc. 1	Loc. 2	Loc. 3
Puncturella sp.	1	–	–
Bathybembix ? sp.	1	–	–
Bolma ? sp.	–	–	1
Orectospira sp.	–	–	4
Epitonium sp.	–	–	1
Ancistrolepis sp.	–	–	2
Fissidentalium sp.	–	–	1
Acila sp.	–	–	1
Bathymalletia chitensis Shikawa and Kase	1	–	–
Neilonella isensis Shibata	–	–	2
Neilonella tsukigawaensis sp. nov.			(2) 8
Tindaria ? sp.	–	3	–
Nuculana (*Testyleda*) sp.	–	–	1
N. (*Crassoleda*) aff. *pennula* (Yokoyama)	–	2	2
Portlandia sp.	4	10	7
Acar sp.	–	–	1
Delectopecten cf. *peckhami* (Gabb)	1	2	–
Anomiidae gen. et sp. indet.	1	–	1
Lucinoma sp.	–	–	3
Conchocele sp.	–	–	1
Macoma ? sp.	–	–	1
Halicardia sp.	–	–	1
Cuspidaria sp.	1	–	–
Cardiomya mitsuganoensis Shibata	–	2	–
Myonera osawanoensis (Tsuda)	(6)11	(3)14	–

As Hickman (1984) has emphasized, the taxonomic structure method is a tool for analyzing not individual assemblages but entire faunas. I examined the taxonomic composition of the whole bivalve fauna of the Arakawa Formation in the Iwadono area. The composition of the gastropod fauna was not examined because of the very low species diversity of gastropods in the Arakawa Formation.

Figure 4 illustrates the taxonomic composition of the bivalve fauna of the Arakawa Formation and those from the modern shelf, bathyal, and abyssal zones for comparisons. As shown in this figure, the proportions of protobranchs and heterodonts in modern shallow- and deep-water faunas are remarkably reversed. Hickman (1984) used the predominance of protobranchs over heterodonts as an indicator of deep water for paleobathymetric interpretation of Paleogene molluscan faunas. The Arakawa bivalve fauna is clearly indicative of deep water in the remarkable predominance of protobranchs. Another distinct feature in the taxonomic composition of the Arakawa bivalve fauna is the subdominance of septibranchs, which is also characteristic of deep water in modern faunas. Proportionally, the structure of the Arakawa bivalve fauna is most similar to that of the modern abyssal fauna. However, this similarity is superficial because the taxonomic structure method is not able to discriminate between bathyal and abyssal faunas.

Next, I examined the compilations of modern bathymetric ranges of the constituent genera of the Arakawa fauna on the basis of the distribution data of Recent molluscs by Higo and Goto (1993). As a result, it became clear that both Type-I and -II assemblages contain genera restricted to bathyal depths such as *Myonera* and *Halicardia*, respectively and that the other genera have a wide range taking in the sublittoral to bathyal zones. Bathymetric ranges of *Myonera* and *Halicardia* in the modern northwestern Pacific are 400-900 m and 400-1,500 m, respectively (Higo and Goto, 1993). There is no genus restricted to the sublittoral zone. Therefore, both Type-I and -II assemblages can be considered to represent a fauna of bathyal depths. It is difficult to discuss in more detail the paleobathymetry of both assemblages and their bathymetric relationship with the present data.

Both Type-I and -II assemblages are dominated by protobranch bivalves in terms of species number and are comparable with the Protobranch Communities, one of the six Cenozoic deep-water molluscan community types of Hickman (1984). There is, however, a difference between Type-I and -II in terms of major taxonomic groups of dominant species. The type-II assemblage clearly belongs to the Protobranch Communities in the dominance of a protobranch bivalve, *Neilonella tsukigawaensis* sp. nov. On the other hand, the Type-I assemblage differs from the typical Proto-

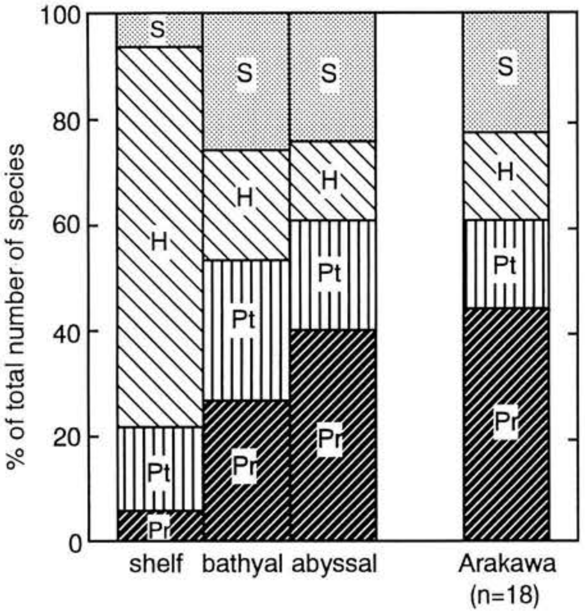

Figure 4. Taxonomic composition of the bivalve fauna of the Arakawa Formation and those from modern shelf (less than 200 m), bathyal (200-2,000 m) and abyssal (greater than 2,000 m) zones for comparisons (after Hickman, 1984). Pr, Protobranchs ; Pt, Pteriomorphs ; H, heterodonts ; S, septibranchs. Letter n represents the number of species.

branch Communities in the dominance of a septibranch bivalve, *Myonera osawanoensis*. Such an assemblage dominated by a septibranch bivalve may be distinguishable from Hickman's six Cenozoic deep-water molluscan community types and may represent a new one, the Septibranch Communities.

Marine paleoclimate

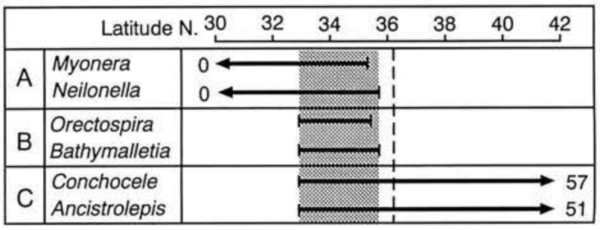

Figure 5. Latitudinal range of the selected genera of the Arakawa fauna in the modern northwestern Pacific. Overlapped area of A, B and C-type genera is indicated by shade. Dotted line represents the latitude of the Iwadono Hills area.

The marine paleoclimatic aspect of the Arakawa fauna is here inferred on the basis of the observed latitudinal ranges of the constituent genera in the modern northwestern Pacific by Kuroda and Habe (1952) and Higo and Goto (1993).

The Arakawa fauna contains several genera that show distinct latitudinal distributions and which can be grouped into three types on the basis of their distribution patterns ; namely, A, B, and C-types (Figure 5). The A-type genera are widely distributed to the south of Lat. 36°N, the B-type are restricted between 33° and 36°N, and the C-type are widely distributed to the north of 33°N. The A-type genera, *Myonera* and *Neilonella*, can be regarded as southern elements, and the B-type genera, *Orectospira* and *Bathymalletia*, are nearly equivalent to the Southwestern Japonic elements of Nobuhara (1993). The C-type genera, *Ancistrolepis* and *Conchocele*, are known as northern elements, because their main distribution is in northern sea areas (Okutani, 1968).

In the Pacific coast of Japan, the cooccurrence of the three types of genera is now restricted to deep water of Lat. 33° to 36°N. According to Okutani's (1968) study of the deep-water molluscan fauna in Sagami Bay (approximately Lat. 35.2°N ; see Figure 1-A), the cooccurrence of the three types of genera is typically recognized at depths of 400 to 1,000 m, where they would be bathed in the intermediate water at 6 to 8°C, and where most of the constituent genera (about 80%) of the Arakawa fauna occur. Such similarities

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→ **Figure 6.** (For bivalves, RV and LV are used for abbreviation of right valve and left valve, respectively.) **1a-b.** *Puncturella* sp., Loc. 1, rubber cast, ×4, (a) dorsal view, (b) lateral view, IGUT 11847. **2.** *Bathybembix* ? sp., Loc. 1, rubber cast, ×2.5, IGUT 11848. **3.** *Bolma* ? sp., Loc. 3, rubber cast, ×1.5, IGUT 11849. **4.** *Epitonium* sp., Loc. 3, rubber cast, ×2.5, IGUT 11851. **5, 6a-b.** *Orectospira* sp., Loc. 3, 5. rubber cast, ×2, IGUT 11850-2 ; 6. ×2.3, (a) ; lateral view, (b) basal view, IGUT 11850-1. **7a-b, 12.** *Neilonella isensis* Shibata, Loc. 3, ×3.5, 7. RV (a) dorsal view, (b) lateral view, IGUT 11833 ; 12. LV, IGUT 11832. **8a-b, 9a-b, 10a-b.** *Neilonella tsukigawaensis* sp. nov., Loc. 3, ×3.5, 8. LV, (a) dorsal view, (b) lateral view, IGUT 11834-1, holotype ; 9. LV (a) dorsal view, (b) lateral view, IGUT 11834-2, paratype ; 10. LV, (a) rubber cast, (b) internal mold, IGUT 11834-3, paratype. **11.** *Ancistrolepis* sp., Loc. 3, ×1.5, IGUT 11852. **13.** *Bathymalletia chitensis* Shikama and Kase, Loc. 1, rubber cast of RV, ×2.5, IGUT 11836. **14, 15.** *Nuculana* (*Crassoleda*) aff. *pennula* (Yokoyama), 14. Loc. 3, LV, ×3.5, IGUT 11839 ; 15. Loc. 2, rubber cast of RV, ×3, IGUT 11840. **16.** *Nuculana* (*Thestyleda*) sp., Loc. 3, LV, ×3, IGUT 11838. **17.** *Tindaria*? sp., Loc. 1, internal mold of LV, ×4, IGUT 11835. **18, 19.** *Portlandia* sp., 18. Loc. 2, internal mold of RV, ×1.5, IGUT 11841-1 ; 19. Loc. 1, internal mold of RV, ×1.5, IGUT 11841-2. **20.** *Delectopecten* cf. *peckhami* (Gabb), Loc. 1, internal mold of RV, ×2, IGUT 11837. **21.** *Lucinoma* sp., Loc. 3, RV, ×2, IGUT 11842. **22.** *Macoma*? sp., Loc. 3, internal mold of RV, ×1.5, IGUT 11843. **23a-b.** *Halicardia* sp., Loc. 3, RV, ×1.5, (ainal undulations and a depressed and triangle-shaped rostrum. The shell outline is somewhat variable in the examined specimens as illustrated. **24.** *Cuspidaria* sp., Loc. 1, rubber cast of RV, ×3, IGUT 11844. **25, 26, 27.** *Myonera osawanoensis* (Tsuda), 25. Loc. 2, internal mold of LV, ×3, IGUT 11845-3 ; 26. Loc. 1, internal mold of LV, ×3, IGUT 11845-2 ; 27. Loc. 1, internal mold of LV, ×3, IGUT 11845-1.

This species is closely related to *Myonera dautzenbergi* Prashad, 1932, which currentlyl mold of LV, ×3, IGUT 11845-2 ; 27. Loc. 1, internal mold of LV, ×3, IGUT 11845-1. **28, 29.** *Cardiomya mitsuganoensis* Shibata, Loc. 2, rubber cast of LV, ×5, 28. IGUT 11854-1 ; 29. IGUT 11854-2.


1a


1b


2


3


4


5


6a

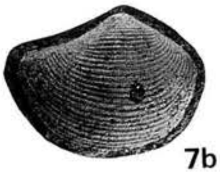

6b


7a


8a


9a


10a


7b


8b


9b


10b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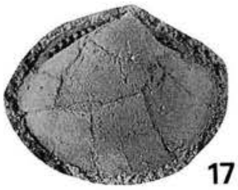
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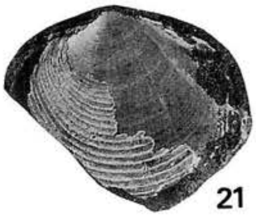
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23a


23b


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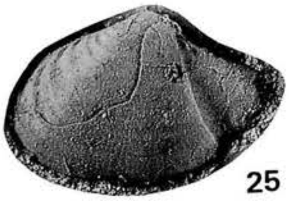
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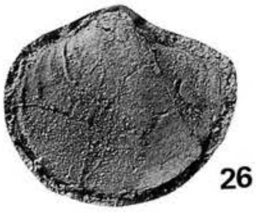
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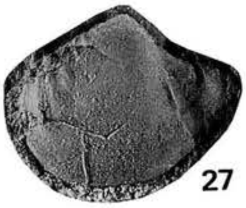
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28


29

in the generic composition between the molluscan fauna of the Arakawa Formation and of the bathyal zone in modern Sagami Bay suggests that the marine climate during the Arakawa deposition was similar to that of the intermediate water of modern Sagami Bay.

Systematic paleontoiogy

A new species and another species in a new combination are described in this section. All the illustrated specimens are deposited in the Institute of Geoscience, University of Tsukuba, under the IGUT collection catalogue numbers.

Family Malletiidae
Genus **Neilonella** Dall, 1881

Neilonella tsukigawaensis sp. nov.

Figures 6-8a, b, 9a, b, 10a, b

? *Neilonella* cf. *soyoae* Habe. Shibata *in* Itoigawa *et al.*, 1974, p. 47-48, pl. 1, fig. 18 ; Itoigawa *et al.*, 1981, pl. 1, fig. 7 ; Itoigawa *et al.*, 1982, p. 7.

Type.—The holotype is a left valve (IGUT 11834-1). The paratypes, IGUT 11834-2, 3. All from Loc. 3 : a riverside exposure along the Tsuki-gawa River, about 250 m downstream of the Tsuki-gawa Bridge, Senjido, Ranzan-machi, Hiki-gun, Saitama Prefecture.

Diagnosis.—Moderate-sized species of *Neilonella*, characterized by its elongate-ovate outline, broad umbo, and surface sculptured all over with densely spaced distinct commarginal ribs.

Description.—Shell moderate in size for the genus, rarely exceeding 10 mm in length, elongate-ovate, inequilateral, equivalve, moderately inflated ; umbo broad, not so prominent, located at about two fifths of the length ; antero-dorsal margin nearly straight, gradually bending down rounded anterior portion ; postero-dorsal margin long, broadly concave, abruptly turned to posterior margin at rostrated posterior end ; ventral margin smoothly convex ; lunule indistinct ; escutcheon broadly concave, circumscribed by a blunt ridge from beak to posterior end ; external surface sculpted all over with densely spaced distinct commarginal ribs ; anterior teeth about 11 in number, posterior teeth more than 10 ; muscle scar and pallial line unknown.

Comparison.—This new species is most similar to *Neilonella soyoae* Habe, 1958, a Japanese living species, in shell size and form. However, *N. soyoae* is distinguished from this new species by its smoother surface. *Neilonella isensis* Shibata, 1970 differs from this new species in its smaller shell size and higher shell outline with coarser commarginal ribs.

Judging from descriptions, this new species may be conspecific with *Neilonella* cf. *soyoae* of Shibata *in* Itoigawa *et al.* (1974) and Itoigawa *et al.* (1981, 1982) from the Oidawara Formation in Gifu Prefecture. It is, however, difficult to conclude that the two forms are conspecific because these authors illustrated only a poorly preserved internal mold.

Measurements.—Holotype, Length 7.9 mm, height 4.6 mm, width 2.4 mm [Figure 5-8 ; IGUT 1184-1]. Paratypes, length 9.2 mm, height 4.8 mm, width 2.2 mm [Figure 5-9 ; IGUT 11834-2] ; length 8.1 mm, height 4.6 mm, width 2.0 mm [Figure 5-10 ; IGUT 11834-3].

Family Cuspidariidae
Genus **Myonera** Dall, 1886

Myonera osawanoensis (Tsuda, 1959)

Figures 6-25, 26, 27

Cuspidaria osawanoensis Tsuda, 1959, p. 73, pl. 2, figs. 2a, b.
Cuspidaria sp. Shibata *in* Itoigawa *et al.*, 1974, p. 110, pl. 35, figs. 3, 4.
Cuspidaria (*Tergula*) sp. Itoigawa *et al.*, 1981, pl. 22, fig. 9 ; Itoigawa *et al.*, 1982, p. 119.

Remarks.—Many specimens referred to this species were obtained from Locs. 1 and 2, but most of them were damaged during the sampling. This species is characterized by having a well inflated disc with rough commarginal undulations and a depressed and triangle-shaped rostrum. The shell outline is somewhat variable in the examined specimens as illustrated.

This species is closely related to *Myonera dautzenbergi* Prashad, 1932, which currently inhabits bathyal depths in Sagami Bay and Indonesian waters (Higo and Goto, 1993), but differs in surface ornamentation. The external surface of the disc of *M. dautzenbergi* is not sculptured with rough undulations.

This species was originally described by Tsuda (1959) under the genus *Cuspidaria* from the Miocene Kurosedani Formation in Toyama Prefecture, but is treated herein as a *Myonera* by virtue of having an umbonal-ventral sharp step separating the rostrum from the disc, which is a diagnostic character of *Myonera*.

Judging from their description and illustration, *Cuspidaria* sp. (n. sp.) of Shibata *in* Itoigawa *et al.* (1974) and *Cuspidaria* (*Tergula*) sp. of Itoigawa *et al.* (1981, 1982) from the Oidawara Formation in Gifu Prefecture seem to be included within the variation of this species.

Measurements.—Length 11.0 mm, height 6.9 mm, width 2.4 mm [Figure 5-25 ; IGUT 11845-3] ; length 9.5 mm, height 7.1 mm [Figure 5-26 ; IGUT 11845-2] ; length 9.0 mm, height 7.0 mm, width 2.4 mm [Figure 5-27 ; IGUT 11845-1].

Acknowledgments

I would like to express my sincere appreciation to Hiroshi Noda (University of Tsukuba) for his invaluable suggestions and discussions on the present study. Thanks are due to Kenshiro Ogasawara (University of Tsukuba) and Carole S. Hickman (University of California, Berkeley) for reading the early draft of this paper and giving helpful comments. I am also indebted to Leopoldo De Silva, Jr. (University of Tsukuba) for his correcting my English, and to Yukio Yanagisawa (Geological Survey of Japan) for his identifications and valuable suggestions on diatom fossils.

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Paleontological Research, vol. 3, no. 4, pp. 234-248, 6 Figs., December 30, 1999

Apparatus of a Triassic conodont species *Cratognathodus multihamatus* (Huckriede)

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Abstract. A Triassic conodont *Cratognathodus multihamatus* (Huckriede) from the pelagic limestone of the Taho Formation in Ehime Prefecture, Southwest Japan is newly reconstructed as an octomembrate apparatus with segminate Pa, angulate Pb, breviform digyrate M, alate Sa, breviform digyrate Sb_1, extensiform digyrate Sb_2, bifurcate bipennate Sc_1, and bipennate Sc_2 elements. Among the elements, the Pb, M, and S series were regarded as those of a septimembrate or octomembrate species *Gladigondolella tethydis* (Huckriede) by previous authors. *Cr. multihamatus* may comprise a lineage of the Gondolellidae; it occurs in the Tethyan realm and ranges from late Spathian or early Anisian to late Carnian.

Key words: *Cratognathodus multihamatus* (Huckriede), Gondolellidae, octomembrate apparatus, Taho Formation, Triassic

Introduction

The form species of conodonts, *Cratognathodus kochi* (Huckriede, 1958), *Cratognathodus posterognathodus* Mosher 1968, *Cypridodella venusta* (Huckriede, 1958), *Diplododella lautissima* (Huckriede, 1958), *Enantiognathus stoppeli* (Bender, 1967), *Cypridodella spengleri* (Huckriede, 1958), *Hindeodella petrae-viridis* Huckriede 1958, and *Hindeodella multihamata* Huckriede 1958 were recovered from the Triassic in various areas of Tethyan realm. These eight form species also occur abundantly in the limestone strata of the Taho Formation outcropped at Tahokamigumi, Shirokawa-cho, Higashiuwa-gun, Ehime Prefecture in Shikoku. As a result of statistic analysis of conodont fauna with these form species from various levels of the upper Spathian or lower Anisian to middle Anisian and upper Carnian strata of the formation, it has been made clear that these form species are the elements of a conodont skeletal apparatus and *Cr. kochi*, *Cr. posterognathodus*, *Cy. venusta*, *D. lautissima*, *E. stoppeli*, *Cy. spengleri*, *H. petrae-viridis*, and *H. multihamata* are assigned to the Pa, Pb, M, Sa, Sb_1, Sb_2, Sc_1, and Sc_2 elements, respectively.

I propose *Cratognathodus multihamatus* (Huckriede) herein for this octomembrate apparatus and describe the elements of the apparatus. Furthermore, I scrutinize the phylogeny of this species and compare it with the previously reconstructed Triassic and some Paleozoic conodont apparatuses.

All of the described specimens are kept in the Department of Science Education, Faculty of Education and Human Sciences, Yokohama National University (YNU).

Biostratigraphic setting

The limestone strata of the Taho Formation attain approximately 75 m in thickness and correspond to Griesbachian to middle Anisian and upper Carnian to lower Norian. Upper Anisian to lower Carnian strata are missing due to a fault (Koike, 1996).

In the Taho Formation, *Cratognathodus multihamatus* ranges from the uppermost part of the *Neospathodus homeri* Zone in the upper Spathian or the basal part of the *Chiosella timorensis* Zone in the lower Anisian to the *Metapolygnathus nodosus* Zone in the upper Carnian. The elements of this species are particularly abundant in the lower Anisian where 930 specimens were recovered from approximately 5 kg of limestone from level 1197. On the other hand, they are very rare in number and poor in preservation in the upper Carnian (Table 1).

Cratognathodus multihamatus is a Tethyan species and the elements of the species were reported as form species from various parts of the Tethyan realm by many authors. In the biostratigraphic study of conodonts in Austria, Huckriede (1958) proposed and described the form species *Prioniodina kochi, Lonchodina venusta, Roundya lautissima, Lonchodina spengleri, Hindeodella petrae-viridis*, and *Hindeodella multihamata*. These species are assigned to the Pa, M, Sa, Sb_2, Sc_1, and Sc_2 elements of the *Cr. multihamatus* apparatus, respectively. The form species *Ozarkodina saginata* de-

Table 1. Occurrence of Pa, Pb, M, Sa, Sb_1, Sb_2, Sc_1, and Sc_2 elements of *Cratognathodus multihamatus* (Huckriede) obtained from 3 to 5 kg of limestone of the Taho Formation.

Stratigraphic level	Elements								
	Pa	Pb	M	Sa	Sb_1	Sb_2	Sc_1	Sc_2	Sc_1?+Sc_2?
Carnian									
1133	13	10	3	2	1	2	5	1	3
Anisian									
1202	31	50	49	9	27	13	11	20	51
1199	14	9	9	2	9	8	2	2	4
1198	29	20	8	5	3	4	4	9	8
1197	242	126	150	18	82	51	19	164	79
1196	20	6	9	3	6	14	3	12	12
1195	38	18	28	6	8	9	6	29	13
1324	23	5	6	3	4	4	1	4	7
1132	18	5	14	2	10	11	10	10	8
1194	52	13	26	5	10	12	8	18	11
1323	63	31	35	3	17	29	7	30	15
016	29	28	21	8	9	31	8	50	19
1193	143	45	38	12	33	36	17	54	39
1130	74	40	17	5	21	27	10	29	30
1322	70	32	25	6	18	25	8	17	36
1129	95	32	45	17	34	49	13	27	38
1321	155	67	68	15	43	65	19	55	29
015	45	14	7	3	12	13	2	29	13
1192	12	9	11	2	6	3	4	9	7
1128	34	16	16	3	7	9	4	10	16
014	37	19	14	2	3	12	3	14	9
1191	59	48	50	16	29	37	11	18	19
1127	265	113	135	39	72	113	48	63	86
1316	66	35	32	7	23	19	9	22	17
Spathian ?									
013	42	26	26	9	7	11	3	19	12
1183	18	3	6	1	2	8	2	6	2
total	1687	821	845	203	615	495	237	721	583
ratio	8.3	4.0	4.2	1	3.0	2.4	1.2+	3.6+	

scribed by Huckriede (1958) was distinguished from the form species *Cratognathodus posterognathus* Mosher (Pb element of *Cr. multihamatus* apparatus) by its shorter posterior process (Mosher, 1968). The form species *Ozarkodina saginata* illustrated by Huckriede (1958) is, however, probably based on incomplete specimens of *Cr. posterognathus* lacking a part of the posterior process. The specimen of the form species *Apatognathus* sp. illustrated by Huckriede (1958) is poorly preserved but the features of the processes and denticulation agree well with those of the Sb_1 element of *Cr. multihamatus*. According to Huckriede (1958), most of the form species occur commonly in the upper Anisian to Carnian.

Bender (1967) reported Spathian and early Anisian conodonts from Chios and other Greek islands in the Mediterranean Sea and described the Pa, Pb, M, Sb_2, Sc_1, and Sc_2 elements of *Cr. multihamatus* as the form species proposed by Huckriede (1958). The specimens of the form species *Hindeodella stoppeli* illustrated by Bender (1967) are incomplete but the features of the lateral processes agree with the Sb_1 element of *Cr. multihamatus*. The Pa and Pb elements occur first in the upper part of the middle *Neospathodus homeri* Zone (late Spathian or early Anisian) and other elements occur first in the lower or middle part of the lower *N. homeri* Zone (late Spathian).

Mosher (1968) studied Triassic conodonts of Austria, North America, and Germany, and described the form species assignable to the Pa, Pb, M, Sa, Sb_2, Sc_1, and Sc_2 elements of *Cr. multihamatus* from the Middle and Upper Triassic limestones in Austria. In part the specimens illustrated as the form species *Prioniodina petrae-viridis* by Mosher (1968, Pl. 116, Figs. 30, 31) are referable to the Sb_1 element. Furthermore, Mosher (1968) reported the occurrence of the Pb, Sb_1, and Sc_2 ? elements in the Middle and Upper Triassic of North America, but did not report any occurrences of the elements of *Cr. multihamatus* in the Muschelkalk of Germany. According to Mosher (1968), all of the elements appear first in the late Anisian and the Pb, M, Sa, and Sc_1 elements range to early Ladinian, but the Pa, Sb_1, Sb_2, and Sc_2 elements range to Carnian or Norian in Austria.

In their biostratigraphic study of the Lower to Upper Triassic conodonts in some areas of Europe in the Tethyan realm, Kozur and Mostler (1972) described the form species referable to the Pb, M, Sa, and Sb$_2$ elements of *Cr. multihamatus*. One of the specimens of the form species *Hindeodella spengleri* (Huckriede) illustrated by Kozur and Mostler (1972, pl. 7, fig. 11) is referable to the Sc$_1$ element of *Cr. multihamatus*. Most of the specimens of the form species *Enantiognathus petraeviridis* (Huckriede) illustrated by Kozur and Mostler (1972, pl. 10, figs. 1, 2 ; pl. 14, figs. 4, 5, 8, 12) are the Sb$_1$ element of *Cr. multihamatus*. The form species *Cratognathodus kochi*, the Pa element of *Cr. multihamatus*, is regarded as the immature form of the "gladigondolelliform" (Pa) element of *Gladigondolella tethydis* (Huckriede) by Kozur and Mostler (1972). According to them, the biostratigraphic ranges of the elements are within the Ladinian to early Carnian.

In the report on Triassic conodonts from Turkey, Gedik (1975) described the form species referable to the Pa, Pb, M, Sb$_2$, and Sc$_2$ elements of *Cr. multihamatus*. The specimens illustrated by Gedik (1975) as the form species *Hibbardella magnidentata* (Tatge) (pl. 4, figs. 8-10), *Enantiognathus ziegleri* (Diebel) (pl. 5, fig. 3), and *Prioniodina* (*Frabellignathus*) *latidentata* (Tatge) (pl. 8, figs. 13-15) are probably referable to the Sa, Sb$_1$, and Sc$_1$ elements of *Cr. multihamatus*, respectively. According to Gedik (1975), all of the elements appear first in the Zone A of the early Anisian just above the *Chiosella timorensis* Zone and range to the late Carnian.

Summarizing the above-mentioned reports, *Cr. multihamatus* is a diagnostic species in the Tethyan realm and ranges from late Spathian or early Anisian to late Carnian as recognized in the Taho Formation.

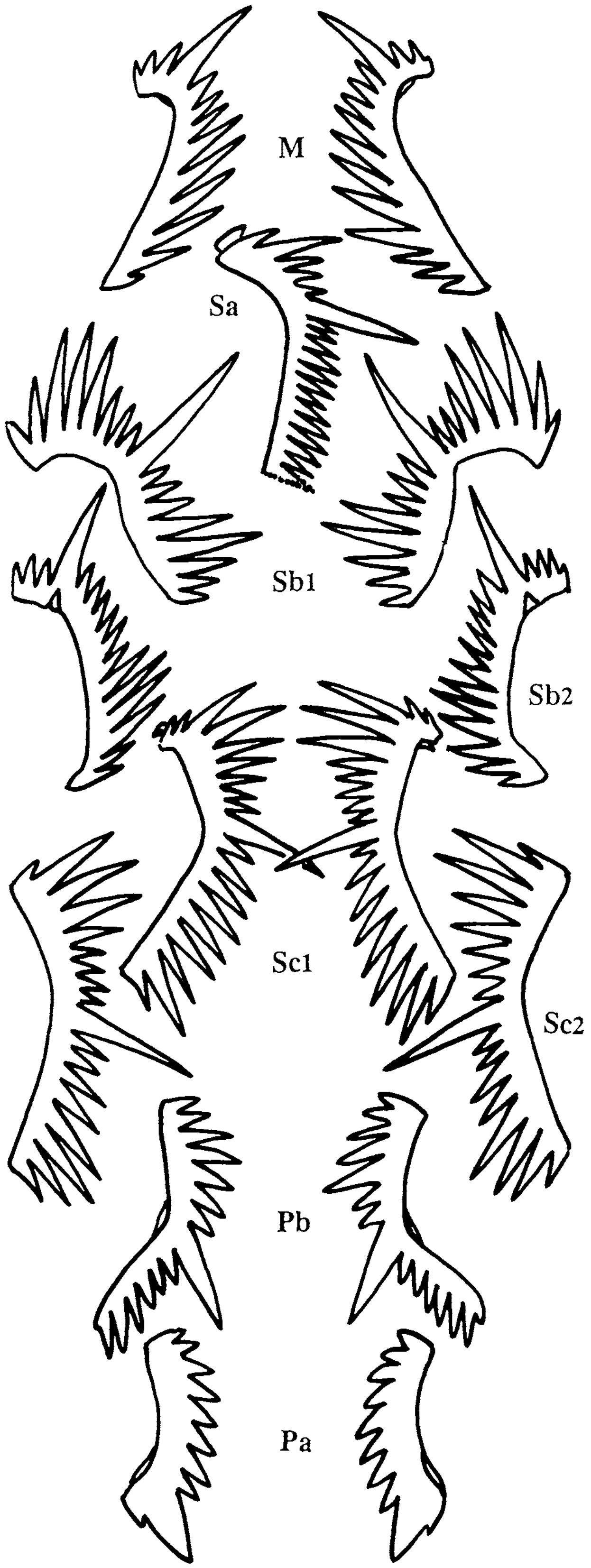
Appartus of *Cratognathodus multihamatus* (Huckriede)

Cratognathodus multihamatus is reconstructed as an octomebrate skeletal apparatus in this study (Figure 1). The elements are Pa, Pb, M, Sa, Sb$_1$, Sb$_2$, Sc$_1$, and Sc$_2$.

The Pa element is a segminate (neospathodiform) type having an arched anterior process with 3 to 10 relatively short and broad, discrete denticles, a large broad cusp, and an expanded basal cavity. One or two small denticles may be present behind the cusp. It is identical with the form species *Cratognathodus kochi* (Huckriede, 1958).

The Pb element is an angulate (ozarkodiniform) type possessing a strongly and laterally bending unit, an anterior process with 3 to 6 relatively large, discrete denticles, a posterior process with 4 to 6 short, slender, discrete denticles, a large cusp, and a slightly expanded basal cavity. It is identical with the form species *Cratognathodus saginatus* (Huckriede, 1958) and *Cratognthodus posterognathus* Mosher, 1968.

The M element is a breviform digyrate (cypridodelliform) type having a short lateral process with 1 to 3 short denticles, a long lateral process with 8 to 10 short to long denticles, a large cusp, and an expanded basal cavity. It is identical



→ **Figure 1.** A hypothetically reconstructed apparatus of *Cratognathodus multihamatus* (Huckriede) from the Taho Formation.

with the form species *Cypridodella venusta* (Huckriede, 1958).

The Sa element is an alate (diplododelliform) type possessing 2 long lateral processes with 3 to 5 short to long, discrete denticles, a long posterior process with more than 10 short, indiscrete denticles, a large cusp, and a slightly expanded basal cavity. It is identical with the form species *Diplododella lautissima* (Huckriede, 1958).

The Sb_1 element is a breviform digyrate (enantiognathiform) type possessing subequal-sized slender lateral processes with 7 to 10 short to long, discrete denticles, a slender long cusp, and a slitlike basal cavity. It is probably identical with the form species *Enantiognathus stoppeli* (Bender, 1967).

The Sb_2 element is an extensiform digyrate (prioniodiniform) type having a short lateral process with 2 to 5 short denticles, a long lateral process with 10 to 13 short to long, indiscrete denticles, a slender long cusp, and a triangular basal cavity. It is identical with the form species *Cypridodella spengleri* (Huckriede, 1958)

The Sc_1 element is a bipennate (hindeodelliform) type posessing a bifurcate long anterior process with 5 to 8 short to long, discrete denticles, a long posterior process with more than 5 short to long, discrete denticles, a slender long cusp, and a slitlike basal cavity. It is identical with the form species *Hindeodella petrae-viridis* Huckriede, 1958.

The Sc_2 element is a bipennate (hindeodelliform) type having slender long anterior and posterior processes carrying 5 to 12 short to long, discrete denticles, a slender long cusp, and a slitlike basal cavity. It is identical with *Hindeodella multihamata* Huckriede, 1958.

The number of elements of *Cr. multihamatus* occurring in each level is shown in Table 1. The frequencies of the Pa, Pb, M, Sa, Sb_1, Sb_2, Sc_1, and Sc_2 elements from the samples of the Spathian or Anisian to Carnian are 1687, 812, 845, 203, 615, 495, 237+, and 721+, and an approximate ratio of the elements is 8.3 : 4.0 : 4.2 : 1 : 3.0 : 2.4 : 1.2+ : 3.6+, respectively.

The natural assemblage of *Neogondolella* sp. recovered by Rieber (1980) from the Middle Triassic of Switzerland and *Gondolella pohli* reconstructed by von Bitter and Merrill (1998) based on many natural assemblages from Illinois are composed of a single unpaired alate Sa, single pairs of segminiplanate Pa, angulate Pb, breviform digyrate M, breviform digyrate Sb_1, and extensiform digyrate Sb_2, and two pairs of bipennate Sc elements. Orchard (1998) regarded, however, the Sc elements in *Neogondolella* as being composed of Sc_1 and Sc_2, and the *Neogondolella* apparatus as an octomembrate type.

As mentioned further on, *Cr. multihamatus* represents a close phylogenetic relationship with neogondolellids and is referable to the Gondolellidae. Therefore, *Cr. multihamatus* probably has as many elements as *Neogondolella* sp. (Rieber, 1980) and *G. pohli*. In that case, the abundance of segminate Pa elements is very high compared with other elements in *Cr. multihamatus*. The reason is probably due to robustness of Pa elements. On the other hand, alate Sa elements are considerably low in abundance. This is presumably due to their fragility. The same tendency in abundance of Pa and Sa elements is observed in apparatuses of *G. pohli* (von Bitter and Merrill, 1998, table 1).

Cratognathodus multihamatus and previously reconstructed apparatuses

Kozur and Mostler (1971) reconstructed a multielement species *Gladigondolella tethydis* (Huckriede) with 11 or 12 elements. The elements are identical with the form species *Cr. posterognathus*, *Cy. venusta*, *D. lautissima*, *Cy. spengleri*, *H. petrae-viridis*, *H. multihamata*, *Cr. saginatus*, *Didymodella alternata* (Mosher), *Lonchodina hungarica* Kozur and Mostler, *H. pectiniformis* (Huckriede), and *G. tethydis*. Among these form species, the first six correspond with the Pb, M, Sa, Sb_2, Sc_1, and Sc_2 elements of the *Cr. multihamatus* apparatus, respectively. Furthermore, one of the specimens demonstrated as *Enantiognathus petraeviridis* by Kozur and Mostler (1971, pl. 1, fig. 14) is referable to the Sb_2 element of *Cr. multihamatus*.

Hirsch (1981, 1994) also reported a multielement species *G. tethydis* composed of eight elements. Judging from the simple illustration by Hirsch (1994), the eight elements are identical with the form species, *Cr. posterognathus*, *Cy. venusta*, *D. lautissima*, *H. petrae-viridis*, *H. multihamata*, *Cr. saginatus*, *H. pectiniformis*, and *G. tethydis*. As mentioned above, the first five form species correspond with the Pb, M, Sa, Sc_1, and Sc_2 elements of *Cr. multihamatus*, respectively.

The correlation coefficient of occurrence is very low between the *Cr. multihamatus* apparatus and the Pa element of *G. tethydis* in the Taho Formation: *Cr. multihamatus* appears first at the upper part of the *Neospathodus homeri* Zone in the late Spathian or the basal part of the *Cr. timorensis* Zone in the early Anisian but the Pa element of *G. tethydis* appears later, at the base of the *Paragondolella bulgarica* Zone (Figure 2). Among the studied samples yielding *Cr. multihamatus* (Table 1), the occurrence of the Pa elements of *G. tethydis* is restricted within the levels 1197, 1198, and 1202 in the *P. bulgarica* Zone and the number of the elements found in about 3 to 5 kg of limestone is only 2, 2, and 25, respectively.

According to Muttoni *et al.* (1998), the Pa elements of *G. tethydis* appear first near the base of the *Paragondolella bifurcata-Neospathodus kockeli* Zone in Pelsonian of Anisian of Italy. The first appearance of the Pa elements of *G. tethydis* in Italy is nearly the same in age as their first appearance in Japan. As mentioned previously, *Cr. multihamatus* appears first in the late Spathian or earliest Anisian in Tethyan realm. Therefore, the first appearances of *Cr. multihamatus* and the Pa element of *G. tethydis* are obviously different in the Tethyan realm.

Kozur and Mostler (1972) regarded the form species *Cr. kochi* (= Pa elements of *Cr. multihamatus*) as immature forms of the "gladigondolelliform" (Pa) elements of *G. tethydis*. As mentioned above, mature forms of the Pa elements of *G. tethydis*, however, never occur in the *N. homeri* and *Cr. timorensis* Zones which yield the abundant form species *Cr. kochi*. Furthermore, Pa elements of *Cr. multihamatus* and immature forms of Pa elements of *G. tethydis* are easily distinguished from each other by the feature of lateral expansion of process, denticulation, and the shape of the basal cavity.

As far as observed conodont faunas in Japan are con-

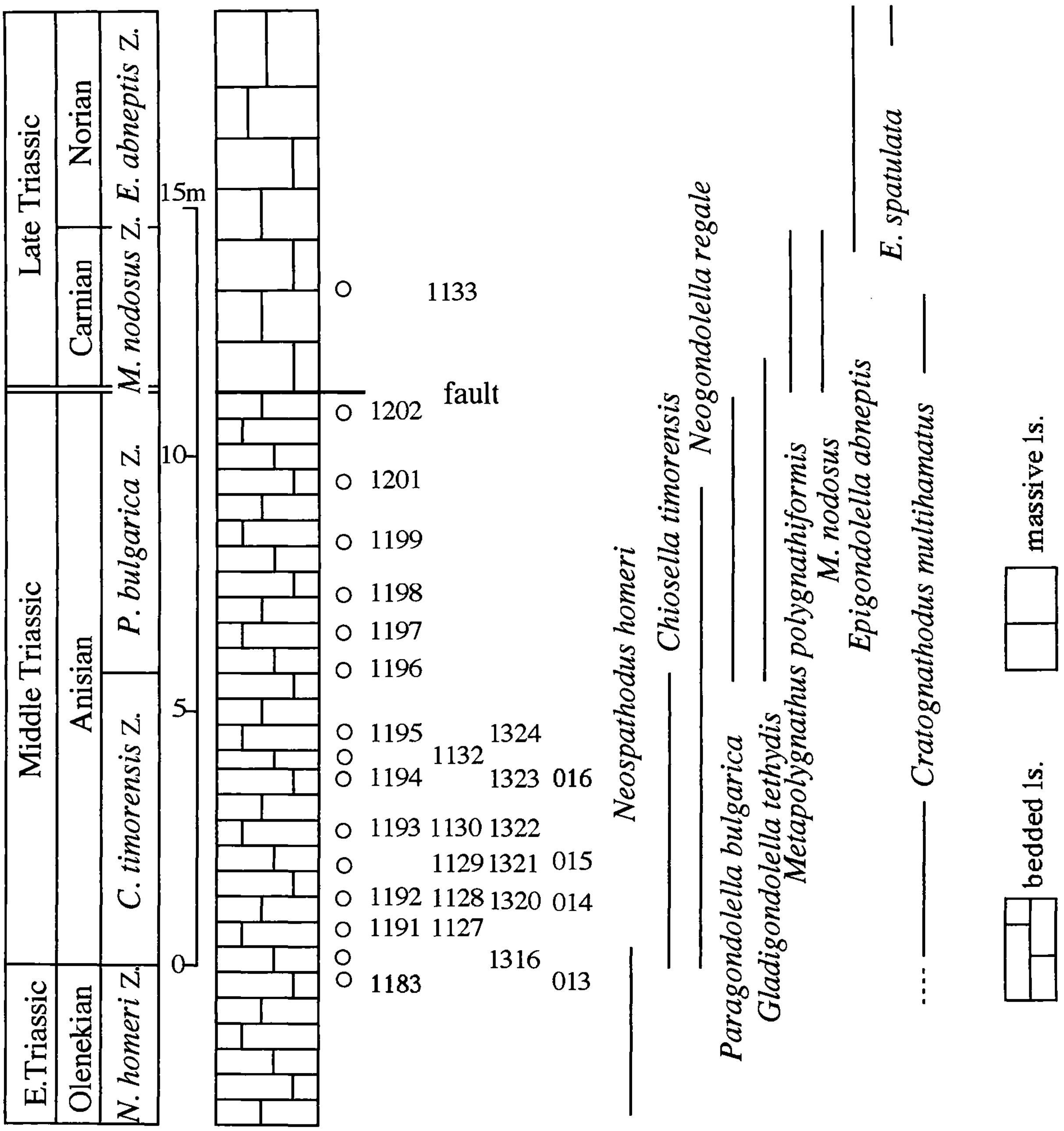


Figure 2. Stratigraphic section and vertical distribution of *Cratognathodus multihamatus* (Huckriede) and important pectiniform conodonts in the Taho Formation.

cerned, the correlation coefficient of occurrence is very low among the Pa element of *G. tethydis* and other pectiniform and ramiform elements. For example, a late Anisian or early Ladinian limestone sample collected from Izuriha near Kyoto yields about 550 specimens of *G. tethydis* Pa elements, but other elements associated with them are mainly of the *Cr. multihamatus* apparatus with some "ozarkodiniform" Pb and a few "enantiognathiform" Sb_1 of unidentified apparatuses. The abundances of the Pa, Pb, M, Sa, Sb_1, Sb_2, Sc_1, and Sc_2 elements of *Cr. multihamatus* in the sample are 19, 56, 36, 17, 30, 59, 72+, and 33+, respectively. Thus, the *G. tethydis* apparatus reconstructed by Kozur and Mostler (1971) and Hirsch (1981, 1994) is problematical. Furthermore, it is difficult to reconstruct *G. tethydis* as a multielement apparatus with Pa and any other elements at present.

Phylogeny of *Cratognathodus multihamatus*

As mentioned above, *Cr. multihamatus* is characterized by possessing segminate Pa, angulate Pb, breviform digyrate M, alate Sa, breviform digyrate Sb_1, extensiform digyrate Sb_2, bifurcate bipennate Sc_1, and bipennate Sc_2 elements.

Among these elements, Pa is one of the most important components for scrutinizing the phylogeny of *Cr. multihamatus*.

The Pa element of *Cr. multihamatus* with a relatively large cusp and large discrete denticles is morphologically very different from not only the typical Spathian neospathodid species: *Neospathodus homeri* (Bender) and *N. triangularis* (Bender) but also from the immature forms of the typical Anisian neogondolellid, paragondolellid, and chiosellid species: *Neogondolella regale* Mosher, *Paragondolella bulgarica* (Budurov and Stefanov), and *Chiosella timorensis* (Nogami), all of which exhibit a small cusp and subequal indiscrete denticles. The Pa element of *Cr. multihamatus*, however, represents some morphologic similarities to the immature forms of the Pa elements of *Gladigondolella tethydis*, which appeared later than *Cr. multihamatus* in Anisian time, and *Paragondolella navicula* (Huckriede) and *P. hallstattensis* Mosher, which appeared in Norian time. Furthermore, the Pa element closely resembles the "ozarkodiniform" element of *Celsigondolella watznaueri watznaueri* (Kozur) and the form species *Pollognathus sequens* (Kozur), which are regarded as the endemic Ladinian conodont species of the German Basin (Kozur and Mostler, 1972; Kozur, 1989).

The presence of "enantiognathiform" Sb_1 element in *Cr. multihamatus* is also considerably important in establishing its phylogenetic relationship with the previously reconstructed conodonts. The natural assemblage of *Neogondolella* sp. recovered by Rieber (1980) from the Middle Triassic of Switzerland is composed of as many as 15 elements belonging to Pa, Pb, M, Sa, Sb_1, Sb_2, and Sc (von Bitter and Merrill, 1998). The Sb_2 element of *Neogondolella* sp. is of the typical "enantiognathiform" type (von Bitter and Merrill, 1998) and morphologically quite similar to the Sb_1 of *Cr. multihamatus*. The Pennsylvanian *Gondolella pohli* reconstructed by von Bitter and Merrill (1998) based on natural assemblages from Illinois also includes a single pair of "enantionathiform" Sb_2 elements accompanied by a single unpaired Sa, single pairs of Pa, Pb, M, and Sb_1, and two pairs of Sc elements.

Orchard (1998) reviewed all gondolellids and pointed out that *Neogondolella* is an octomembrate apparatus with an "enantiognathiform" type occupying the Sb_1 position adjacent to the Sa element and a single pair of Sc elements always having a bifurcate anterior process. Orchard (1998) regarded the Sc element with a bifurcate anterior process as the Sc_2 but now is of the opinion that it is the Sc_1 (personal communication).

In addition to the "enantiognathiform" element, the presence of the Sc element with a bifurcate anterior process in *Cr. multihamatus* represents a phylogenetic relationship with *Neogondolella*. Furthermore, the Pb, M, Sa, and Sb_1 elements of *Cr. multihamatus* also basically have the same morphology as those of *Neogondolella* sp. and *Gondolella pohli*.

The skeletal apparatus of *Pseudofurnishius murcianus* reconstructed by Ramovš (1977, 1978) based on many clusters in the upper Ladinian of Slovenia is setpimembrate with "enantiognathiform" elements. The "pollognathiform" element of *P. murcianus* shows some similarities to the Pa elements of *Cr. multihamatus*. The "pollognathiform" elements were identified with *Pollognathus sequence* by Ramovš (1977). All elements except for the "pseudofurnishiform" Pa and "chirodelliform" Sb_1? elements in *P. murcianus* are basically similar to their counterparts in *Cr. multihamatus*.

The Ladinian *Budurovignathus mungoensis* (Diebel) apparatus reconstructed by Mietto (1982) based on clusters from Italy also includes "enantiognathiform" elements with the Pa, M, Sa, and Sc elements.

The *Xaniognathus* and *Cypridodella* apparatuses statistically reconstructed by Sweet (1981, 1988) are composed of six elements such as the Pa, Pb, M, Sa, Sb, and Sc, among which the Pb is regarded as the "enantiognathiform" digyrate type. The Pb element is closely similar to the Sb_2 element of *Neogondolella* sp. of Rieber (1980). Sweet (1988) regarded *Neogondolella, Gondolella, Xaniognathus*, and *Cypridodella* as belonging to the family Gondolellidae based on the common occurrence of "enantiognathiform" elements among their apparatuses, and as having a close phylogenetic relationship with *Ellisonia* of the family Ellisoniidae, which also bears "enantiognathiform" elements. *Pseudofurnishius* and *Budurovignathus* are as well included in the Gondolellidae by many authors (Sweet, 1988; Kozur, 1989, and others).

Although Dzik (1991) recognized that *Gondolella* is characterized by the presence of lo (enantiognathiform) elements, he claimed the presence of enantiognathiform-like elements in some undescribed apparatuses of the Devonian Hibbardellidae which are unlikely to have any relationships to *Gondolella*.

Sweet (1988) assumed the origin of both of the Gondolellidae and Ellisonidae to be *Idioprioniodus* or a closely related genus with "enantiognathiform" elements in the Mississippian. Von Bitter and Merrill (1998) also considered that the Mississippian *Idioprioniodus* is a likely ancestor of the Pennsylvanian *Gondolella* based on their recognition of an evolutionary trend of reduction of the posterior process in the anguliplanate Pa elements.

Dzik (1991) pointed out that reduced posterior processes in the platform (p) elements are characteristic of *Gondolella* and a similar feature occurs in some Devonian *Ozarkodina*. On the basis of morphologic similarities in both platform and ramiform elements. Dzik (1991) regarded the Devonian *Pinacognathus* (?) sp. as the probable ancestor of the Gondolellidae.

In summary, I conclude that *Cr. multihamatus* should be included in the Gondolellidae because *Cr. multihamatus* has segminate Pa elements similar to immature forms of some neogondolellid Pa elements and bears "enantiognathiform" Sb_1 elements which are common in the Gondolellidae, and Sc_1 and other elements which are basically similar in morphology to those of neogondolellid and gondolellid apparatuses.

The segminate Pa elements in *Cr. multihamatus* represent close morphologic similarity with the anterior process of the angulate (ozarkodiniform) Pb elements, which are basically the same in morphology as those of *Neogondolella* sp. of Rieber (1980) and *Gondolella pohli*. This feature suggests that both elements in the P position have a mutual relationship in feeding mechanism, but while the Pa elements acquired broad variation in morphology (anguliplanate *Gladigondolella*, segminate *Neospathodus*, and segminiplanate *Gondolella* and *Neogondolella*), the Pb element remained angulate during the evolution of the Gondolellidae. The ancestral form of the Pa elements of the Gondolellidae may be referable to an angulate (ozarkodiniform) element like the Pb elements.

In that case the ancestor of the Gondolellidae should be searched for in conodonts with "ozarkodiniform"-like Pa and "ozarkodiniform" Pb elements. The conodonts possessing such Pa and Pb elements were not included in the Ordovician family-group of the order Prioniodinida Sweet, 1988 in which the family Gondolellidae was included by Sweet (1988). On the other hand, Ordovician conodonts *Bryantodina*? *staufferi* Bergström and Sweet and *Plectodina* of Sweet (1988) in the Spathognathodontidae of the order Ozarkodinida Dzik, 1976 possess "ozarkodiniform"-like Pa and "ozarkodiniform" Pb elements (Sweet, 1988).

Dzik (1991) included the order Prioniodinida erected by Sweet (1988) within the order Ozarkodinida and regarded the Gondolellidae as having a phylogenetic relationship with the Spathognathodontidae.

On the basis of morphologic similarity between the Pa and Pb elements in *Cr. multihamatus* and those of the species in the Spathognathodontidae, I would like to support the opinion of Dzik (1991) that the Gondolellidae is phylogenetically related to the Spathognathodontidae of the order Ozarkodinida.

Systematic Paleontology

Phylum Conodonta
Order Ozarkodina
Superfamily Gondolellacea
Family Gondolellidae
Genus ***Cratognathodus***

Type species.—Hindeodella multihamata Huckriede, 1958, p. 148-149.

Revised diagnosis.—Cratognathodus newly proposed herein contains species with octomembrate apparatus of as many as 15 elements: single pairs of segminate Pa, angulate Pb, breviform digyrate Sb$_1$, extensiform digyrate Sb$_2$, bipennate Sc$_1$ and Sc$_2$ elements, and a single unpaired alate Sa element. Pa elements characterized by relatively broad cusp with expanded basal cavity and large discrete denticles.

Remarks.—Mosher (1968) enacted the genus *Cratognathodus* and included the following four form species in the genus, *Prioniodina kochi* Huckriede, *Cr. posterognathus* newly proposed, and two unidentified species, which are both characterized by the presence of a strong broad cusp with a widely expanded basal cavity, and relatively small number of discrete denticles. As mentioned previously, *Cratoganthodus kochi* and *Cr. posterognathus* are respectively identical with the Pa and Pb elements of the *Cr. multihamatus* apparatus. Among the three specimens illustrated as *Cr. kochi* by Mosher (1968), one specimen (pl. 113, fig. 7) is misidentified and another specimen (pl. 113, fig. 4) is not a typical Pa element of the *Cr. multihamatus* apparatus. Mosher (1968), however, regarded the form species *Prioniodina kochi* Huckriede as the type species of his *Cratognathodus*.

Later, Kozur and Mostler (1972) claimed that the genus *Cratognathodus* created by Mosher (1968) is not a valid taxon because the holotype and all other specimens previously described as the form species *Cr. kochi* are immature forms of the "gladigondolelliform" (Pa) elements of *Gladigondolella tethydis* (Huckriede).

Based on my observation on Pa elements of *G. tethydis* from the Taho Formation and other limestone formations in Japan, the immature forms of the element are characterized by a narrow platform-like anterior process and gradually increasing denticles in length toward the anterior as observed in the mature forms. The immature forms of the Pa elements of *G. tethydis* can be, therefore, easily distinguished from the form species *Cr. kochi* (= Pa element of *Cr. multihamatus*).

The Pa element of *Cr. multihamatus* represents various features in the shape and size of the cusp and denticulation on the anterior process (Figure 3). The holotype of the form species *Cr. kochi* (Huckriede, 1958, pl. 12, fig. 11) possessing a short broad cusp and subequal denticles is safely assigned within the range of morphologic variation of the Pa element of *Cr. multihamatus* and agrees well with the specimens illustrated in Figure 3-16, 26.

Cratognathodus multihamatus (Huckriede)

Figures 3-5

Pa element

Prioniodina kochi Huckriede, 1958, p. 159, pl. 11, fig. ?37, pl. 12, figs. 11, 12, pl. 14, fig. 4; Spasov and Ganev, 1960, p. 89, pl. 1, fig. 23, pl. 2, fig. 12; Čatalov and Stefanov, 1966, pl. 1, fig. 3; Bender, 1967, p. 527, non pl. 5, fig. 12; Hirsch, 1969, pl. 1, fig. ?7.

Neoprioniodus cf. *kochi* (Huckriede), Ishii and Nogami, 1966, non

→ **Figure 3.** **1-31**, Pa elements of *Cratognathodus multihamatus* (Huckriede) from the Taho Formation. all ×60. 1: YNUC15881 from Lev. 1316. 2: YNUC15882 from Lev. 1195. 3: YNUC15883 from Lev. 1197. 4: YNUC15884 from Lev. 1324. 5: YNUC15885 from Lev. 1196. 6: YNUC15886 from Lev. 1321. 7: YNUC15887 from Lev. 1316. 8: YNUC15888 from Lev. 1127. 9: YNUC15889 from Lev. 1197. 10: YNUC15890 from Lev. 1197. 11: YNUC15891 from Lev. 1191. 12: YNUC15892 from Lev. 1130. 13: YNUC15893 from Lev. 1323. 14: YNUC15894 from Lev. 1183. 15-16: YNUC15895-15896 from Lev. 1321. 17: YNUC15897 from Lev. 1323. 18: YNUC15898 from Lev. 1127. 19: YNUC15899 from Lev. 1321. 20: YNUC15900 from Lev. 1195. 21-24: YNUC15901-15904 from Lev. 1193. 25: YNUC15905 from Lev. 1128. 26: NUC15906 from Lev. 1321. 27: YNUC15907 from Lev. 1193. 28: YNUC15908 from Lev. 1195. 29: YNUC15909 from Lev. 1193. 30: YNUC15910 from Lev. 1127. 31: YNUC 15911 from Lev. 1320.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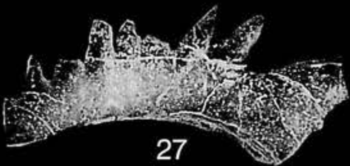
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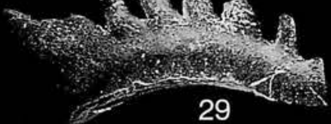
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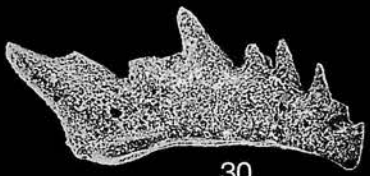
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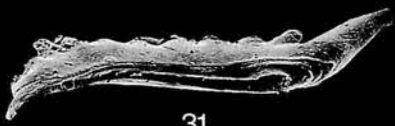
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pl. 1, fig. 12.

Cratognathodus kochi (Huckriede), Mosher, 1968, p. 919, pl. 113, figs. 3, ?4, non fig. 7 ; Jenkins and Jenkins, 1971, non fig. 5, no. 29 ; Sahni and Chhabra, 1974, p. 263, 265, pl. 3, figs. D, ? E, F, non fig. I ; Gedik, 1975, p. 111-112, pl. 5, fig. 23 ; Budurov, 1976, pl. 4, fig. 29 ; Sudar, 1977, pl. 5, fig. 4 ; Čatalov and Budurov, 1978, pl. 1, fig. 8 ; Koike, 1981, pl. 1, fig. 21 ; Koike, 1982, p. 20, pl. 9, fig. 15, non fig. 16 ; Önder, 1984, p. 76, pl. 22, figs. ?7, ?8.

non *Prioniodina? kochi germanica* Kozur, 1968a, p. 139-140, pl. 1, figs. 24, 25 ; Kozur, 1968b, pl. 3, figs. 15, 19, 21 ; Kozur, 1968c, p. 1081.

Cratognathodus cuspidatus Koike, 1982, p. 20-21, pl. 9, figs. ?17, 18.

Pb element

Ozarkodina saginata Huckriede, 1958, p. 153-154, pl. 13, figs. 16, 17, 20 ; Mosher, 1968, p. 932, pl. 115, fig. ?14, non fig. 15.

Pseudoozarkodina saginata (Huckriede), Vrielynck, 1987, p. 229-230, pl. 14, figs. 9-11.

Cratognathodus posterognathus Mosher, 1968, p. 919, pl. 113, figs, 10, 14 ; Koike, 1973, p. 98, pl. 17, figs. 30, 31 ; Budurov and Stefanov, 1975, pl. 1, fig. ?35 ; Koike, 1981, pl. 1, fig. 30 ; Koike, 1982, p. 20, pl. 9, figs. 20, 21 ; Önder, 1984, p. 77, pl. 22, figs. 9-11.

Lonchodina? posterognathus (Mosher), Kozur and Mostler, 1971, pl. 1, fig. 10 ; Mock, 1971, pl. 1, fig. 9 ; Kozur and Mostler, 1972, p. 19, pl. 10, figs. 6, 7, 11.

Lonchodina angulata Budurov, 1971, p. 28, pl. 1, figs. 5-9, 12 ; Čatalov and Budurov, 1975, p. 1248, pl. 1, fig. 8.

Cratognathodus posterognathus posterognathus Mosher, Gedik, 1975, p. 112, pl. 5, figs. 19, 20, 22.

Cratognathodus posterognathus angulatus (Budurov), Gedik, 1975, p. 113, pl. 8, figs. 25, 26.

Cratognathodus angulatus (Budurov), Budurov, 1976, pl. 4, figs. 17, 18 ; Čatalov and Budurov, 1978, pl. 1, fig. 2.

M element

Lonchodina venusta Huckriede, 1958, p. 152-153, pl. 11, fig. 25 ; Spasov and Ganev, 1960, p. 82, pl. 1, figs. 15-17 ; Hirsch, 1969, pl. 1, fig. 5.

Cypridodella venusta (Huckriede), Mosher, 1968, p. 922-923, pl. 114, figs. 1, 7, ?13 ; Gedik, 1975, p. 115-116, pl. 7, figs. 16-18 ; Koike, 1982, p. 23, pl. 7, fig. 47 ; Önder, 1984, p. 78-79, pl. 22, figs. 5, 6.

Prioniodina (*Cypridodella*) *venusta* (Huckriede), Kozur and Mostler, 1971, pl. 1, figs. 3, 4 ; Mock, 1971, pl. 2, figs. 5, 10, 11 ; Kozur and Mostler, 1972, p. 32, pl. 11, figs. 16, 24, pl. 12, fig. 11, pl. 15, fig. 3.

Prioniodina venusta (Huckriede), Čatalov and Budurov, 1975, p. 1248, pl. 1, fig. 12 ; Budurov, 1976, pl. 4, figs. 23-26 ; Sudar, 1977, pl. 5, fig. 9 ; Čatalov and Budurov, 1978, pl. 1, fig. 1 ; Vrielynck, 1987, p. 226-228, pl. 10, fig. 15, pl. 11, figs. 1, 2.

? *Cypridodella pronoides* (Budurov), Koike, 1982, p. 22, pl. 7, figs. 48, 49.

Sa element

Roundya lautissima Huckriede, 1958, p. 160, pl. 11, fig. 41, pl. 13, figs. 13, 15 ; Spasov and Ganev, 1960, p. 90, pl. 2, figs. 15, 22.

Diplododella lautissima (Huckriede), Ishii and Nogami, 1966, pl. 1, fig. 15 ; Mosher, 1968, p. 924, pl. 114, fig. 20 ; Koike, 1973, p. 101, pl. 17, fig. 32 ; Sahni and Chhabra, 1974, p. 270, pl. 3, fig. ?S ; Budurov, 1976, pl. 4, fig. 36 ; Sudar, 1977, pl. 5, fig. 2.

Hibbardella lautissima (Huckriede), Mosher and Clark, 1965, p. 561, pl. 65, figs. ?1, ?3, ?4 ; Kozur and Mostler, 1971, pl. 1, fig. 13 ; Mock, 1971, pl. 3, figs. 7, 13 ; Kozur and Mostler, 1972, p. 12, pl. 9, fig. 10, pl. 12, figs. 10, 13 ; Vrielynck, 1987, p. 195-196, pl. 11, figs. 3-7.

pars *Hibbardella magnidentata* (Tatge), Gedik, 1975, p. 122-123, pl. 4, figs. 8-10 (only).

Sb_1 element

Apatognathus sp. Huckriede, 1958, p. 147, pl. 11, fig. 29.

? *Hindeodella stoppeli* Bender, 1967, p. 510, pl. 2, figs. 6, 15-17.

pars *Prioniodina petrae-viridis* (Huckriede), Mosher, 1968, p. 934-935, pl. 116, figs. 30, 31 (only).

pars *Enantiognathus petraeviridis* (Huckriede), Kozur and Mostler, 1972, p. 9, pl. 10, figs. 1, 2, pl. 14, figs. 4, 5, 8, 12 (only).

Sb_2 element

Lonchodina spengleri Huckriede, 1958, p. 152, pl. 10, figs. 54, ? 55, ?56, pl. 11, fig. 6, pl. 12, fig. 9, pl. 13, figs. 1, 6, 10, pl. 14, fig. 11 ; Budurov, 1962, p. 119, pl. 1, figs. ?5-8 ; Mosher and Clark, 1965, p. 562, pl. 66, fig. ?5 ; Bender, 1967, p. 513-514, pl. 3, figs. 12, ?13-15, non fig. 17.

Prioniodina spengleri (Huckriede), Čatalov and Budurov, 1975, p. 1248, pl. 1, fig. ?13, non fig. 14 ; Sudar, 1977, pl. 5, fig. ?11 ; Čatalov and Budurov, 1978, pl. 1, fig. 5, non figs. 4, 6, pl. 2, fig. 20, non figs. 19, 21.

Prioniodina spengleri (Huckriede), "*dimitrovi*" element, Budurov, 1976, pl. 3, figs. 8, 18.

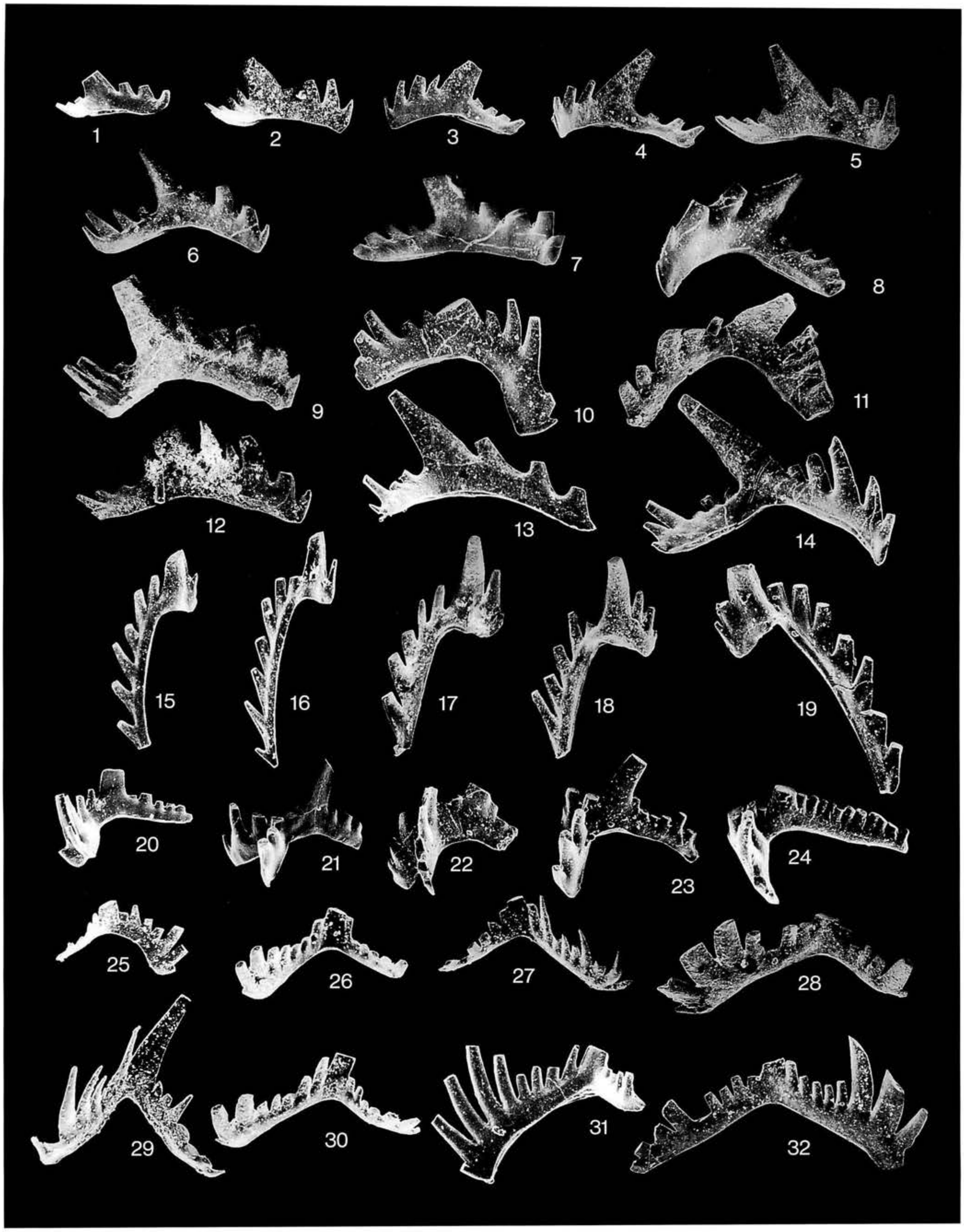
Prioniodina spengleri (Huckriede), "*spengleri*" element, Budurov, 1976, pl. 3, figs. ?9, ?11-15, 16-18, non figs. 20-25, non pl. 4, figs. 37-39.

Prioniodina (*Flabellignathus*) *spengleri sapanlii* Gedik, 1975, p. 146-147, pl. 7, figs. 22, 26, 27, 30.

Cypridodella spengleri (Huckriede), Mosher, 1968, p. 922, pl. 113, figs. 19, 20, 25, non fig. 18 ; Koike, 1973, p. 100, pl. 16, fig. 31 ; Sahni and Chhabra, 1974, p. 269, fig. 3-?O ; Önder, 1984, p. 78, non pl. 22, figs. 3, 4.

Hindeodella (*Metaprioniodus*) *spengleri* (Huckriede), Kozur and Mostler, 1971, pl. 1, fig. 12 ; Mock, 1971, pl. 2, fig. ?13, non fig. 14 ; Kozur and Mostler, 1972, p. 16-17, non pl. 7, fig. 11, pl. 10, fig. 4, pl. 15, figs. 1, 5.

→ **Figure 4.** Pb, M, Sa, and Sb_1 elements of *Cratognathodus multihamatus* (Huckriede) from the Taho Formation, all ×60. **1-14**, Pb elements, 1 : YNUC15912 from Lev. 1191. 2 : YNUC15913 from Lev. 1321. 3-5 : YNUC15914-15916 from Lev. 1130. 6 : YNUC15917 from Lev. 1321. 7 : YNUC15918 from Lev. 1316. 8 : YNUC15919 from Lev. 1321. 9 : YNUC15920 from Lev. 1322. 10 : YNUC15921 from Lev. 1193. 11 : YNUC from Lev. 1130. 12 : YNUC 15923 from Lev. 1316. 13 : YNUC15924 from Lev. 1197. 14 : YNUC15925 from Lev. 1192. **15-19**, M elements, 15 : YNUC15926 from Lev. 1321. 16 : YNUC15927 from Lev. 1197. 17 : YNUC15928 from Lev. 1323. 18 : YNUC15929 from Lev. 1193. 19 : YNUC15930 from Lev. 014. **20-24**, Sa elements, 20 : YNUC15931 from Lev. 016. 21 : YNUC15932 from Lev. 1127. 22 : YNUC15933 from Lev. 1129. 23 : YNUC15934 from Lev. 1193. 24 : YNUC15935 from Lev. 1195. **25-32**, Sb_1 elements, 25 : YNUC15936 from Lev.1197. 26-27 : YNUC15937-15938 from Lev. 1196. 28-29 : YNUC15939-15940 from Lev. 1197. 30 : YNUC15941 from Lev. 1196. 31-32 : YNUC15942-15943 from Lev. 1197.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Sc_1 element

Hindeodella petrae-viridis Huckriede, 1958, p. 149-150, pl. 11, fig. ? 46, pl. 13, figs. ?7, ?8, 9, 11, 12, 14, pl. 14, fig. 6, non fig. 7; Spasov and Ganev, 1960, p. 81, pl. 1, figs. 3, 4; Budurov, 1962, p. 116, pl. 1, figs. ?19, ?20; Mosher and Clark, 1965, p. 562, pl. 65, fig. ?9; Ishii and Nogami, 1966, pl. 1, fig. ?14; Čatalov and Stefanov, 1966, pl. 1, figs. 4, 7, ?16; Hirsch, 1969, pl. 1, fig. 4.

Prioniodina petrae-viridis (Huckriede), Mosher, 1968, p. 934-935, pl. 116, figs. 28, 29, non figs. 30, 31; Sahni and Chhabra, 1974, p. 284-285, fig. 5, ?A, C, ?D, ?E; Sudar, 1977, pl. 5, figs. ?7, ?12; Önder, 1984, p. 86-87, pl. 23, figs. 16-21.

Prioniodina (*Flabellignathus*) *petraeviridis* (Huckriede), Gedik, 1975, p. 145-146, pl. 8, figs. 11, 27.

Prioniodina spengleri (Huckriede), "*petraeviridis*" element, Budurov, 1976, pl. 4, figs. 38, 39, non fig. 37.

Parachirognathus petrae-viridis (Huckriede), Bender, 1967, p. 524, pl. 5, figs. ?1, 2, 3, ?4, ?5, 6, non figs. 8, 9.

Enantiognathus petraeviridis (Huckriede), Mock, 1971, pl. 1, fig. 3, non figs. 4, 10, pl. 2, fig. 17; Kozur and Mostler, 1972, p. 9, pl. 10, fig. ?3, non figs. 1, 2, pl. 12, fig. ?16, non pl. 14, figs. 4, 5, 8, 12; Kemper *et al.*, 1976, pl. 6, fig. ?8; Vrielynck, 1987, p. 188, pl. 9, fig. ?10, non figs. 11, 12.

Diplododella petraeviridis (Huckriede), Koike, 1981, pl. 1, fig. 26; Koike, 1982, p. 26-27, pl. 7, fig. 25.

Prioniodina (*Flabellignathus*) *latidentata* (Tatge), Gedik, 1975, p. 143-144, pl. 8, figs. 13-15, ?16-18, ?20, ?21, ?23, ?24.

pars *Hindeodella* (*Metaprioniodus*) *spengleri* (Huckriede), Kozur and Mostler, 1972, p. 16-17, pl. 1, fig. 11 (only).

Sc_2 element

Hindeodella multihamata Huckriede, 1958, p. 148-149, pl, 10, figs. 52, 53, pl. 12, fig. 23; Čatalov and Stefanov, 1966, pl. ?1, fig. 15; Bender, 1967, p. 508-509, pl. 2, figs. ?18, 20; Mosher, 1968, p. 925, pl. 114, fig. 19; Kozur and Mostler, 1971, pl. 1, fig. 9; Koike, 1973, p. 104, pl. 17, figs. 26-29, non fig. 25; Sahni and Chhabra, 1974, p. 274-275, fig. 4, A, D; Budurov, 1976, pl. 4, fig. 40; Chhabra, 1981, pl. 1, figs. 14, 17; Koike, 1982, p. 30, pl. 9, figs. 23, 25, non fig. 24; Vrielynck, 1987, p. 201-202, pl. 14, fig. ?6, non figs. 4, 5.

Neohindeodella multihamata (Huckriede), Koike, 1981, pl. 1, fig. 17.

Hindeodella (*Metaprioniodus*) *pectiniformis* (Huckriede), Kozur and Mostler, 1972, p. 15-16, pl. 5, figs. 1, 2, pl. 14, figs. 19, ?23, 24.

Prioniodina (*Flabellignathus*) *pectiniformis* (Huckriede), Gedik, 1975, p. 144-145, pl. 8, fig. 22.

Prioniodina libita Mosher, 1968, p. 934, pl. 115, figs. 17, 26, 29; Önder, 1984, p. 86. pl. 23, figs. 13, 14.

Description.—Pa and Pb elements have common morphologic characteristics such as stout unit, broad cusp, and discrete denticles. M, Sa, Sb_1, Sb_2, Sc_1, and Sc_2 elements possess long cusp, and thin process with long denticles. All elements possess distinct basal cavity.

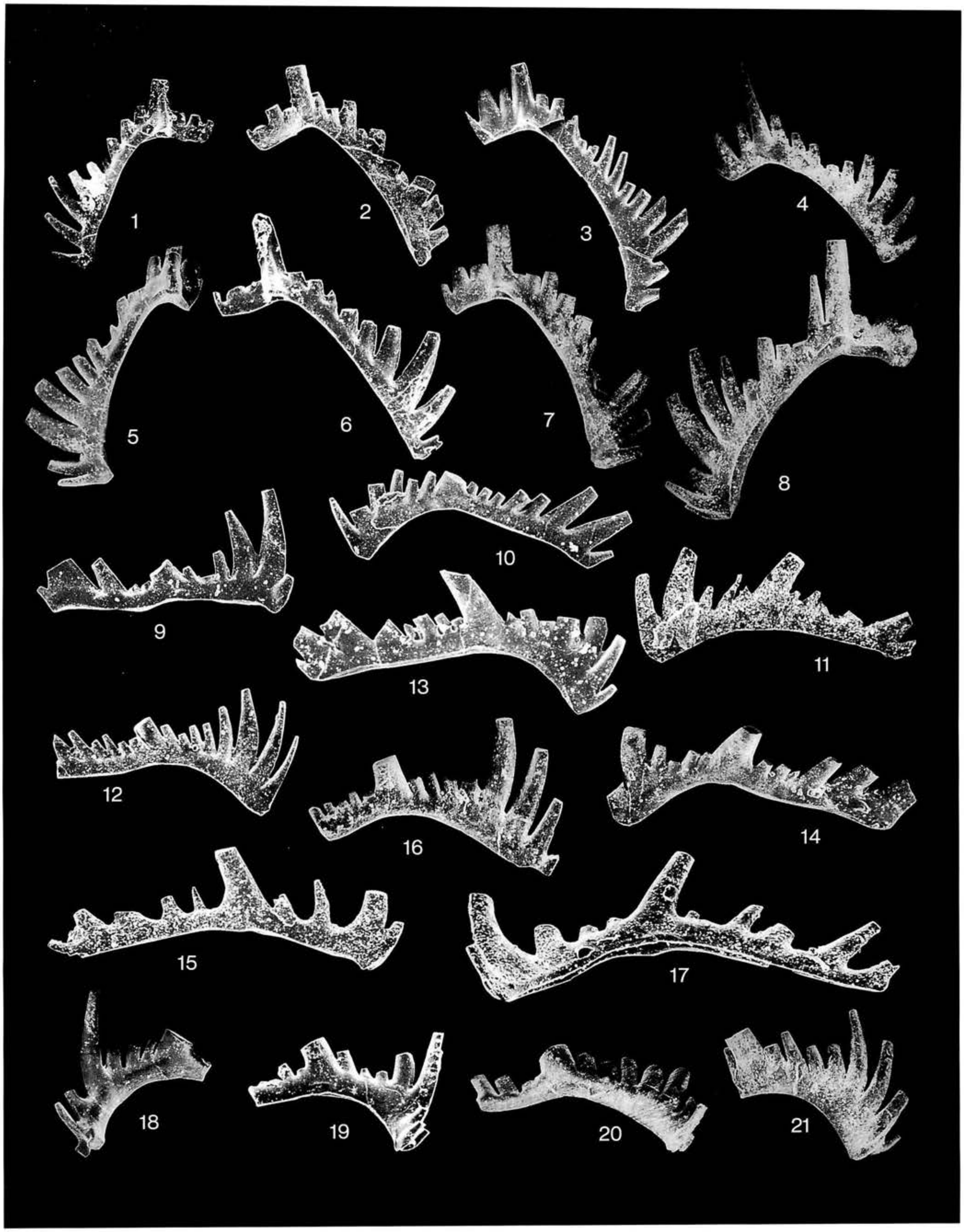
Pa element: Paired segminate elements with arched and laterally curved process. Length of anterior process ranges from 250 to 720 μm. Anterior process relatively low to high and carries 3 to 10 denticles. Denticles represent broad variation in denticulation and size: narrowly to broadly discrete and subequal to highly unequal in size. In the case of consisting of highly unequal denticles, they tend to become larger in central portion on anterior process in some specimens and become larger toward anterior in others. One or two denticles may be present behind cusp. Cusp shows a morphologic variation in relative size, shape, and degree of inclination: narrow to broad, short to long, and medium-angled to subparallel with anterior process. Basal cavity shallow, narrowly to widely expanded laterally. Basal cavity margin thin in immature form and tends to be thick in mature form. Basal groove narrow and extends from basal cavity to anterior end.

Pb element: paired angulate element with subequal anterior and posterior processes in length. Both processes meet at an angle of about 120 to 160 degrees in both upper and lateral views. Posterior process may be convex inward. Length of anterior and posterior processes ranges from 160 to 400 μm, respectively. Denticles on anterior process 3 to 6 in number, short, discrete, and tend to increase in length and inclination posteriorly. Denticles on posterior process 3 to 6 in number, short, slender, discrete, and tend to increase in length and inclination posteriorly. Cusp large and stands commonly on anterior process and uncommonly on posterior process. Basal cavity a laterally compressed lenticular shape flaring outward in lower view. Basal groove extends anteriorly and posteriorly from basal cavity to beneath processes.

M element: Paired breviform digyrate elements with short and long lateral processes ranging from 60 to 140 μm and from 530 to more than 670 μm in length, respectively. Both processes meet at an angle of about 80 to 100 degrees in antero-posterior views. Short lateral process may be convex inward and carries 1 to 3 short denticles or none in some specimens. Long lateral process projects strongly downward and slightly convex outward. Denticles on long lateral process 8 to 10 in number, curve inward, and tend to increase in size and inclination downward. Cusp large and curves posteriorly. Basal cavity expanded posteriorly and slightly depressed on anterior side. Small lip of basal cavity present on posterior side and rounded keel extends from basal margin of lip to halfway up cusp. Narrow basal groove beneath both processes extends into basal cavity.

Sa element: Alate elements with two long lateral processes and long posterior process. Length of each lateral process ranges from 160 to 250 μm. Length of posterior process unknown due to its incompleteness and more than 330 μm in moderately large specimens. Lateral processes form an angle of 60 to 90 degrees with each other in anterior

→ **Figure 5.** Sb_2, Sc_1 and Sc_2 elements of *Cratognathodus multihamatus* (Huckriede) from the Taho Formation. all ×60. **1-8**, Sb_2 elements, 1-2: YNUC15944-15945 from Lev. 1316. 3: YNUC15946 from Lev. 1321. 4: YNUC15947 from Lev. 1323. 5: YNUC15948 from Lev. 1321. 6: YNUC15949 from Lev. 1191. 7: YNUC15950 from Lev. 1321. 8: YNUC15951 from Lev. 1183. **9-17**, Sc_2 elements, 9-15: YNUC15952-15958 from Lev. 1197. 16: YNUC15959 from Lev. 1193. 17: YNUC15960 from Lev. 1197. **18-21**, Sc_1 elements, 18: YNUC15961 from Lev. 1127. 19: YNUC15962 from Lev. 1191. 20: YNUC15963 from Lev. 1322. 21: YNUC15964 from Lev. 1127.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view and 90 to 120 degrees with posterior process in lateral view. Denticles on each lateral process 3 to 5 in number, discrete, tend to be large in central portion. Inclination of denticles tends to increase toward cusp. Denticles on posterior process more than 11 in number, short, indiscrete and standing perpendicular. Cusp as long as largest denticle on lateral processes and slightly curves posteriorly. Basal cavity moderately expanded and narrow basal groove extends beneath lateral and posterior processes.

Sb_1 element: Paired breviform digyrata elements with subequal, long, slender lateral processes. Length of each lateral process ranges from 170 to 450 μm. Both processes meet at an angle of about 90 to 120 degrees in upper view and are convex anteriorly. Denticles on each lateral process 7 to 10 in number, indiscrete, slightly inclined posteriorly, and tend to increase in length distally, the largest being the distalmost 2nd or 3rd. Cusp slender and as large as largest denticle on lateral processes. Basal cavity slitlike, narrow basal groove extends from basal cavity toward lateral processes.

Sb_2 element: Paired extensiform digyrate elements with short and long lateral processes. Length of short and long processes ranges from 130 to 200 μm and from 460 to 640 μm, respectively. Both processes meet at an angle of 100 to 130 degrees in antero-posterior views. Denticles on short lateral process 2 to 5 in number and tend to increase in length and inclination toward cusp. Denticles on long lateral process 10 to 13 in number, weakly curve posteriorly, and tend to increase in length distally, the largest being the distalmost 3rd or 4th. Inclination of denticles tends to increase toward cusp. Cusp slender, as large as large denticles on long lateral process, and slightly curves posteriorly. Basal cavity forms triangular shape in lower view. Small lip of basal cavity present on posterior side and narrow keel extends from basal margin of lip to approximately halfway up cusp. Narrow basal groove extends from basal cavity to beneath both lateral processes.

Sc_1 element: Paired bipennate elements with bifurcate long anterior process and long posterior processes. Length of anterior process ranges from 230 to 370 μm. Length of posterior process cannot be measured because of its incompleteness. Anterior process bends at an angle of 30 to 80 degrees downward and 10 to 20 degrees inward. Denticles on anterior process 5 to 8 in number, tend to increase abruptly in size, being largest in anterior to middle portion, and then decreasing in size posteriorly. Bifurcation projects anterolaterally and forms an angle of about 160 degrees in both upper and lateral views and carries 1 to 3 small, discrete denticles. Posterior process may carry almost the same number of denticles as on anterior process. Cusp as long as longest denticle on anterior process. Basal cavity slitlike, narrow basal groove extends toward anterior and posterior processes.

Sc_2 element: Paired bipennate elements with long, slender anterior and posterior processes with long, discrete denticles. Length of anterior and posterior processes ranges from 300 to 470 μm and 380 to 750 μm, respectively. Anterior process bends at an angle of 30 to 80 degrees downward and 10 to 30 degrees inward. Denticles on anterior process 5 to 9 in number and tend to be largest in anterior to middle portion and increase in inclination posteriorly. Denticles on posterior process 5 to 12 in number and tend to increase in size and inclination posteriorly. Basal cavity slitlike, very small lip of basal cavity turned upward on inner side. Narrow groove extends from basal cavity toward anterior and posterior processes.

Remarks.—The "ozarkodiniform" element of *Celsigondolella watznaueri watznaueri* (Kozur) is somewhat similar to the Pa element of *Cr. multihamata*. The former has, however, a conspicuously long cusp whose feature is out of the range of morphologic variation of the latter. The form species *Pollognathus sequence* (Kozur) and *P. germanicus* (Kozur) fairly resemble the Pa element of *Cr. multihamatus* but the former have a relatively long and slender cusp.

The holotype and other specimens of the form species *Ozarkodina saginata* illustrated by Huckriede (1958) are all incomplete and lack most of their posterior processes, which has caused some confusion in determination among angulate elements. The stout unit with relatively long discrete denticles of *O. saginata* shares characteristics with the Pb element of *Cr. multihamatus*. The holotype and another specimen of the form species *Cratognathodus posterognathus* (=the Pb element of *Cr. multihamatus*) shown by Mosher (1968) are of young forms of the form species *Or. saginata*.

One specimen figured as the form species *Lonchodina venusta* (=the M element of *Cr. multihamatus*) by Huckriede (1958) is incomplete and lacks the distal half of the longer lateral process but well represents such characteristic morphology as long denticles on the lateral process and broadly expanded basal cavity.

All specimens previously figured as the form species *Diplododella lautissima* and specimens determined by me as the Sa element of *Cr. multihamatus* lack most of their posterior processes. The Sa element can be distinguished, however, from the form species *D. magnidentata* (Tatge) by the anteriorly projecting lateral processes with long discrete denticles.

The specimens illustrated as the form species *Hindeodella stoppeli* by Bender (1967) are all incomplete but they appear to correspond to the Sb_1 element of *Cr. multihamatus* because of their "enantiognathiform" digyrate type with a broad angled junction of the lateral processes.

All specimens including the holotype of the form species *Lonchodina spengleri* (the Sb_2 element of *Cr. multihamatus*) are incomplete and lack most of the longer lateral process. The identification of this element is, however, not so difficult because of its extensiform digyrate type and the presence of a triangular basal cavity.

The holotype of the form species *Hindeodella petraeviridis* (=the Sc_1 element of *Cr. multihamatus*) illustrated by Huckriede (1958) is of a part of the anterior process and lacks the bifurcation on the anterior processes. Therefore, some workers regarded this form species as bipennate type without the bifurcate anterior process or breviform digyrate types. The holotype possesses, however, a faint trace of the bifurcation on the basal part of the anteriormost denticle. Huckriede (1958) claimed that the form species *H. petraeviridis* is characterized by the presence of the bifurcation on the anterior process and four specimens figured by Huckriede (1958) carry distinct bifurcation. It is very difficult to distinguish Sc_2 from Sc_1 elements of *Cr. multihamatus* if the Sc_2 elements are incomplete and lack the anterior portion of their anterior processes.

The form species *Prioniodella pectiniformis* erected by Huckriede (1958) is based on the specimens of a part of the posterior process with long discrete denticles. The features agree well with those of Sc_2 elements of *Cr. multihamatus*.

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Evolutionary history of the Cenozoic bivalve genus *Kaneharaia* (Veneridae)

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Abstract. **The evolutionary history of the bivalve genus *Kaneharaia* (Dosiniinae) is discussed. The genus *Kaneharaia* is restricted to the North Pacific region and contains four species: *K. kaneharai* (Yokoyama), *K. kannoi* (Masuda), *K. ausiensis* (Ilyina) and *K.* sp. *K. ausiensis* survived until the mid-Pliocene while the other three species became extinct at the end of the Miocene. In addition to these species, *Dosinia mathewsonii* from the upper Oligocene San Ramon Formation of California and *D. whytneyi* from the early middle Miocene Astoria Formation of Oregon most probably belong to the genus *Kaneharaia*. *Kaneharaia* evolved from the common ancestor with *Dosinia* because both genera share many common characteristics such as the subumbonal pit, the brown-coloured surface, and the finely crossed lamellar structure in the outer layer. Based on the fossil record, *Kaneharaia* first appeared in the northeastern Pacific during the late Oligocene and migrated westward during the early middle Miocene Climatic Optimum in the North Pacific.**

Key words: Bivalvia, evolution, *Kaneharaia*, *Dosinia*, Dosiniinae

Introduction

Kaneharaia is an extinct genus of Dosiniinae (Bivalvia: Veneridae) which was first proposed as a subgenus of *Dosinia* Scopoli, 1777 by Makiyama (1936), based on *Dosinia kaneharai* Yokoyama, 1926 from the Miocene Kanomatazawa Formation in Tochigi Prefecture as its type species. Species of *Kaneharaia* have been found in the Miocene deposits of Honshu and Hokkaido, Japan, Sakhalin and Kamchatka, Russia and northern Korea, and also in the lower Pliocene of Honshu (Masuda, 1967; Amano, 1983; Gladenkov *et al.*, 1987; Amano and Sato, 1995). Other than *K. kaneharai*, the following species and subspecies of *Kaneharaia* have been described: *K. kaneharai* (Yokoyama, 1926), *K. ausiensis* (Ilyina, 1954), *K. kaneharai ouchiensis* (Kanno, 1955), *K. kannoi* (Masuda, 1963), *K. kaneharai fujinensis* (Masuda, 1967), *K. kaneharai rumoiensis* (Amano,1983), *K. kaneharai uandiensis* (Sinelnikova, 1987 *in* Gladenkov *et al.*, 1987).

Makiyama (1936) and Masuda (1967) pointed out that *Kaneharaia* is similar to *Dosinidia* Dall, 1902 (=*Dosinia* Scopoli, 1777) in the absence of escutcheon and lamellated concentric sculpture which are common characters in other Japanese dosiniine genera such as Phacosoma Jukes-Brown, 1912, *Dosinella* Dall, 1902 and Dosinorbis Dall, 1902. However, no detailed comparison of hinge structure between *Kaneharaia* and *Dosinia* has been made.

When they examined the shell microstructure of *Kaneharaia kaneharai* and *Phacosoma* spp., Kobayashi *et al.* (1968) and Hikida (1996) showed that the shell microstructure is a useful character for diagnosing some genera within Dosiniinae and separated *Kaneharaia* from *Phacosoma* as a distinct genus based on the difference of microstructure of the outer layer: spherulitic structure in *Kaneharaia* and composite prismatic structure in *Phacosoma*. However, these authors did not examine the shell microstructure of dosiniine species from the Cenozoic of the North Pacific, including *K. ausiensis*.

Thus, the lack of enough information on hinge structure and shell microstructure prevents us from understanding the detailed relationship among the *Kaneharaia* and other dosiniines from the Cenozoic of the North Pacific.

Recently, it has become clear that some molluscan genera originated in the northeastern Pacific and then migrated to the northwestern Pacific during the early middle Miocene (Vermeij, 1991; Amano *et al.*, 1993; Matsubara, 1994; Reid, 1996; Amano and Vermeij, 1998; Amano, 1998). If we can make clear the close phylogenetic relationship between *Kaneharaia* and the American *Dosinia* species, it should be possible to judge whether *Kaneharaia* is another example of a westward spreading genus or not.

Fortunately, we were able to collect some well preserved specimens of *Kaneharaia ausiensis* (Ilyina) from the Miocene of Sakhalin and also examined previously undocumented specimens of *K. ausiensis* from the Pliocene of Hokkaido and of *K.* sp. from the Miocene of Kodiak Island. Here we examine the morphology of this material in detail and the shell microstructure of *K. ausiensis* and the Recent *Dosinia* species as well in order to clarify the evolutionary history of *Kaneharaia*.

Materials

A number of fossil specimens identified as *Kaneharaia ausiensis* were collected from the following four localities (Figure 1) : Loc. 1, river bank about 2 km upstream of Lesnaya River in southeastern Sakhalin ; early middle Miocene Ausinskaya Formation : Loc. 2, roadside cliff about 2.5 km north of Baykovo in southwestern Sakhalin (the type locality of *Dosinia ausiensis* Ilyina, 1954) ; early middle Miocene Ausinskaya Formation : Loc. 3, roadside cliff about 500 m northwest of Kotobuki Bridge in Kamitokushibetsu, Hokkaido ; middle Miocene Shibiutan Formation : Loc. 4, bank of the Horonitachibetsu River near Numata dai-go in Hokkaido ; early Pliocene Horokaoshirarika Formation yielding the Pliocene index fossil, *Fortipecten takahashii* (Yokoyama). These specimens are housed at Joetsu University of Education (JUE).

Five fossil specimens identified as *Kaneharaia* sp. were provided by Emeritus Professor Saburo Kanno of the University of Tsukuba. These specimens are from the middle Miocene Ejoviy Horizon of Korf Bay in eastern Kamchatka and from the early middle Miocene Narrow Cape Formation on Kodiak Island, Alaska. Detailed information on these localities are unfortunately unknown. These are also stored in Joetsu University of Education (JUE). Besides these specimens, we examined the type specimens of *Kaneharaia kannoi* and *K. kaneharai fujinensis* stored in the Museum of Natural History of Tohoku Univeristy (IGPS).

We examined the shell microstructure of two fossil and four Recent species (Table 1).

Systematic notes on northern Pacific species

Family Veneridae Rafinesque, 1815
Subfamily Dosiniinae Deshayes, 1853
Genus **Kaneharaia** Makiyama, 1936

Comparison.—As pointed out by Makiyama (1936), Hatai (1938) and Masuda (1967), *Kaneharaia* and *Dosinia* share many features such as absence of the escutcheon and lamellated concentric ribs, and presence of a wide triangular

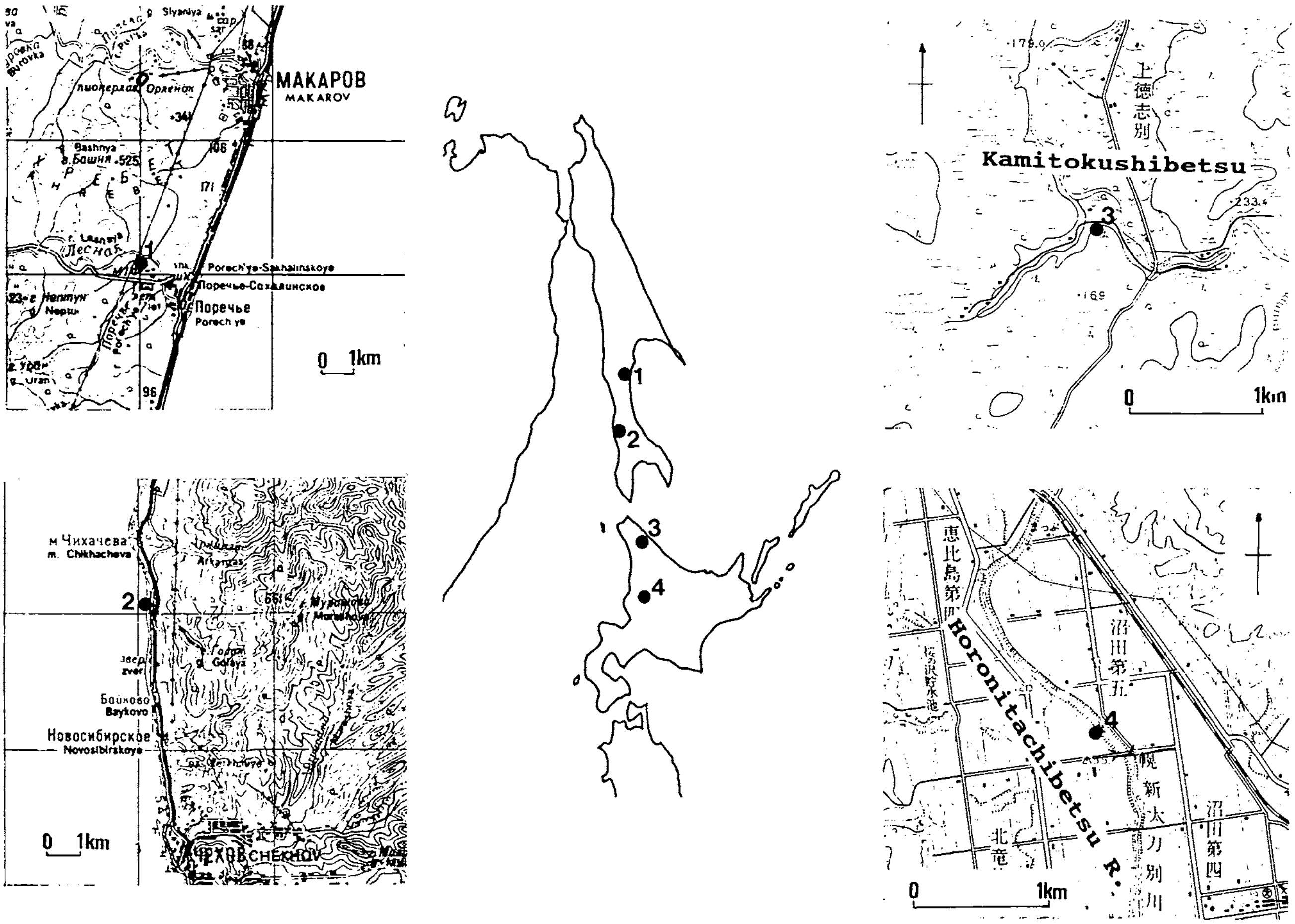


Figure 1. Collecting localities of *Kaneharaia* (using the topopgraphical maps "Occhube" and "Moseushi", scale 1 : 50,000, published by Geographical Survey of Japan).

Table 1. Shell structure of outer layer of Dosiniinae

Species	SSO**	Age	Localities and formations
**Kaneharaia ausiensis* (Ilyina)	sph+fcl	Miocene	Ausinskaya F., Sakhalin (Loc. 1)
K. kaneharai (Yokoyama)	sph+fcl	Miocene	Kubota F., Fukushima Pref.
**Dosinia discus* (Reeve)	fcl	Recent	Florida in USA
**D. dunkeri* (Philippi)	fcl	Recent	Panama
**D. ponderosa* (Gray)	fcl	Recent	California in USA
Phacosoma japonicum (Reeve)	cpr	Recent	Ohita Pref.
P. japonicum (Reeve)	cpr	Pleistocene	Omma F., Ishikawa Pref.
P. japonicum (Reeve)	cpr	Pliocene	Tatsunokuchi F., Miyagi Pref.
P. troscheli (Lishcke)	cpr	Recent	Fukuoka Pref.
P. tomikawensis (Takagi)	cpr	Pleistocene	Omma F., Ishikawa Pref.
P. tatunokutiensis (Nomura)	cpr	Pliocene	Tatsunokuchi F., Miyagi Pref.
P. hataii (Masuda)	cpr	Miocene	Kubota F., Fukushima Pref.
**P. akaisiana* (Nomura)	cpr	Miocene	Yatsuo G., Toyama Pref.
P. kawagensis (Araki)	cpr	Miocene	Mizunami G., Gifu Pref.
P. nomurai (Otuka)	cpr	Miocene	Mizunami G., Gifu Pref.
Austrodosinia anus (Philippi)	cpr	Recent	New Zealand
**Pectunculus exoleta* (Linnaeus)	cpr	Recent	Galcia in Spain

* Species treated in this study. The data of other species are based on Hikida (1996).

** Shell structure of outer layer (sph ; spherulitic structure, fcl ; finely crossed lamellar structure, cpr ; composite prismatic structure, *see also* Hikida, 1996)

pallial sinus. In addition to these characters, we found that both genera have a subumbonal pit on the hinge plate (Figures 2 1-5, 13b, 3 1, 3, 6b, 11a) and sometimes have a brown-coloured shell surface.

The above features are not observed in *Phacosoma* Jukes-Brown, 1912, *Dosinella* Dall, 1902, *Dosinorbis* Dall, 1902 and *Austrodosinia* Dall, 1902 (Figures 3-2, 4, 5, 10 ; *see also* Fischer-Piette and Delmas, 1967). *Pectunculus* Da Costa, 1778 lacks not only the escutcheon, but also the subumbonal pit (Figure 3-8).

Morphologically, *Kaneharaia* differs from *Dosinia* by having a narrower thin plate above the nymph, a thick middle cardinal tooth of both valves, and a long anterior cardinal tooth in the left valve extending to the basal line of hinge plate.

As already pointed out by Kobayashi *et al.* (1968), Shimamoto (1986) and Hikida (1996), the inner layer throughout the Dosiniinae has the same microstructure (homogeneous structure). According to Hikida (1996), the outer layer of *Kaneharaia* is spherulitic in structure while in *Phacosoma, Austrodosinia, Pectunculus* and *Dosinella* the outer layer has a composite prismatic structure (Table 1).

We have found that the outer layer of *K. ausiensis* from Sakhalin (Loc. 1) has a spherulitic structure like *K. kaneharai*, but also was a finely crossed lamellar structure near the beak and ventral margin. On the other hand, the outer layers of *Dosinia discus* and *D. ponderosa* are composed totally of the finely crossed lamellar structure (Figure 4). On *D. ponderosa*, our observation supports the results by Carter and Lutz (1990), not by Taylor *et al.* (1973). Adding *D. dunkeri* to these two species, it has become clear that all the species of *Dosinia* here examined have the same finely crossed lamellar structure (Table 1). Thus, the outer shell microstructure of *Kaneharaia* has the features partly in common with *Dosinia*, but not with other dosiniines.

From the above morphological and shell microstructure data, we conclude that *Kaneharaia* is close to *Dosinia* than any other genus within the Dosiniinae.

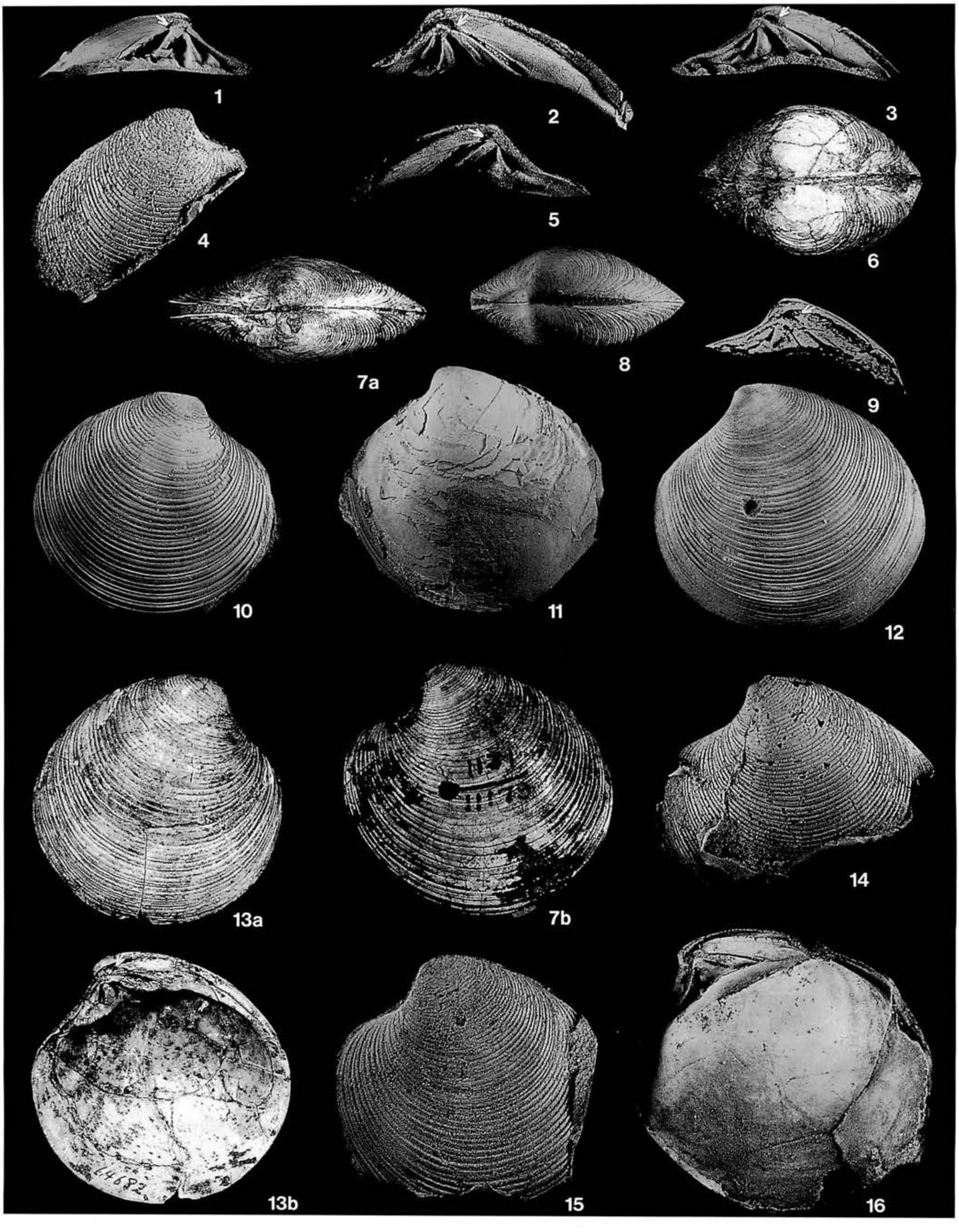
Remarks on American species.—*Dosinia* mathewsonii Gabb, 1869 was described from the upper Oligocene San Ramon Formation of California (Figure 2-7a, b). This species is characterized by the absence of the escutcheon, and presence of many wide concentric ribs, a subumbonal pit (Figure 2-9) on the hinge plate, and a brown-coloured shell surface. It is especially allied to *K. ausiensis* in having an almost identical shell shape and number of concentric ribs (15 between 10 mm and 20 mm from beak). Although no information on the pallial sinus shape of "*D.*" *mathewsonii* could be obtained, it is most probably included in the genus *Kaneharaia*.

When she examined the dosiniines from the early middle Miocene Astoria Formation in Oregon, Moore (1963) synonymized *Dosinia* mathewsonii with *Dosinia whitneyi* (Gabb, 1869). However, *D. whitneyi* is based on a single fragment. It is too difficult to obtain any information on the inner structure of *D. whitneyi*. For the above reasons, we do not use the species name *D. whitneyi*. The Astoria specimens would be better included in *Kaneharaia* rather than *Dosinia*, because the anterior cardinal tooth in the left valve extends to the basal line of the hinge plate and the plate above the nymph is narrow. However, there is also no information on pallial sinus shape in the Astoria specimens. Therefore, it is difficult to conclude whether the Astoria species can be accurately included in the genus *Kaneharaia*.

Kaneharaia ausiensis (Ilyina, 1954)

Figures 2—1-5, 8, 10-12, 14-16 ; 3—14

Dosinia ausiensis Ilyina, 1954, p. 228, 229, pl. 18, figs. 7, 8 ; Zhidkova *et al.*, 1968, p. 107, 108, pl. 5, fig. 2, pl. 18, figs. 7, 8.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Dosinia mirabilis Uozumi (MS). Fujie *et al*., 1964, pl. 6, fig. 4.

Dosinia (*Kaneharaia*) *kaneharai kannoi* Masuda. Masuda, 1967, pl. 2, fig. 9; Noda, 1992, p. 83, 84, pl. 4, fig. 1.

Dosinia (*Kaneharaia*) *kaneharai rumoiensis* Amano, 1983, p. 50, 51, pl. 4, fig. 12, pl. 5, figs. 1, 5, 10.

Dosinia (*Kaneharaia*) *kaneharai uandiensis* Sinelnikova *in* Gladenkov *et al*., 1987, p. 35, pl. 7, figs. 4, 6.

Dosinia (*Kaneharaia*) *ausiensis* Ilyina. Gladenkov *et al*., 1987, p. 35, fig. 3; Amano and Sato, 1995, p. 7, figs. 4-3, 6, 12; Amano *et al*., 1996, p. 637, figs. 4-3, 8.

Dosinia (*Kaneharaia*) *kaneharai* Yokoyama. Shimizu and Fujii, 1995, fig. 6.

Type Locality.—Klyuch Bezimyaniy (Japanese name, Ausi) in Chekhov district, southwestern Sakhalin (Loc. 2); early middle Miocene Ausinskaya Formation. Holotype, VNIGRI no. 7/6819.

Description of Sakhalin specimens.—Shell medium in size (47.4 mm in maxmum length), suborbicular in outline, moderately inflated. Anterodorsal margin slightly concave, passing into well rounded ventral margin; posterodorsal margin broadly arcuate. Beak protruding, weakly prosogyrate, anteriorly situated. Surface sculptured by dense concentric ribs; concentric ribs 15-17 in number between 10 mm and 20 mm from beak, flattened near beak but becoming rounded and elevated near ventral margin. Lunule long, narrow, shallow, and not depressed by any distinct groove. Escutcheon lacking. Hinge plate consisting of one anterior lateral tooth and three cardinal teeth; middle cardinal tooth of right valve thick and simple; anterior lateral tooth of left valve rather large. Subumbonal pit small, situated at uppermost part of nymph plate. Pallial sinus rather shallow and triangular in shape.

Remarks.—The Sakhalin specimens have the same shell characters as the Hokkaido specimens other than shell size: the Pliocene Horokaoshirarika specimen attains 60.6 mm in maximum length while that of the type specimen is 55 mm.

When they examined the fossil fauna from the Ausinskaya Formation in Novoselovo of southwestern Sakhalin, Amano *et al*. (1996) considered the following two subspecies to be junior synonyms of *D*.(*K*.) *ausiensis*: *D*.(*K*.) *kaneharai rumoiensis* Amano, 1983 and *D*. (*Kaneharaia*) *kaneharai uandiensis* Sinelnikova, 1987. They also considered that the specimens illustrated by Masuda (1967, pl. 2, fig. 9) and Noda (1992, pl. 4, fig. 1) as *D*.(*K*.) *kannoi* can be assigned to *D*.(*K*.) *ausiensis*.

Fujie *et al*. (1964) illustrated a specimen referred to *Dosinia mirabilis* Uozumi (MS) from the Miocene Tokushibetsu Formation in Hokkaido. Judging from its subcircular shell, fine concentric ribs and dentition with a subumbonal pit, this specimen should be referred to *K. ausiensis*.

Shimizu and Fujii (1995) illustrated a specimen of *D*.(*K*.) *kaneharai* Yokoyama from the "Otogawa fauna (type II)" of Toyama Prefecture. This specimen obviously has concentric ribs much more than the typical form of *K. kaneharai* and many elevated ribs near the ventral margin. Therefore, the Otogawa specimen should be referred to *K. ausiensis* rather than to *K. kaneharai*.

Comparison.—*Kaneharaia ausiensis* resembles *Kaneharaia kannoi* Masuda, 1963 from the lower middle Miocene Heiroku Formation of North Korea in having fine concentric ribs. However, *K. ausiensis* differs from *K. kannoi* (Figure 2-6) in its less inflated shell and more numerous concentric ribs (usually 12-13 between 10 mm and 20 mm from the beak in *K. kannoi*).

K. ausiensis differs from *K. kaneharai* Yokoyama in its orbicular rather than ovate shell and has much more numerous concentric ribs (15-17 between 10 mm and 20 mm from the beak instead of 8-12 in *K. kaneharai*)

Distribution.—Early middle Miocene Ausinskaya and Uandinskaya Formations in Sakhalin, and Chikubetsu Formation in Hokkaido; middle Miocene Togeshita, Tachikaraushinai and Shibiutan Formations in Hokkaido; late Miocene (?) "Otogawa Formation"; early Pliocene Horokaoshirarika Formation in Hokkaido and Joshita Formation in Honshu.

Kaneharaia sp.

Figures 3—9, 11-13

Dosinia cfr. *mathewsoni* Gabb, Khomenko, 1933, p. 17, pl. 2, fig. 10, pl. 3, fig. 4.

Dosinia margaritana Wiedy, Slodkewitsch, 1938, pl. 88, figs. 3, 4.

? *Dosinia* (*Dosinia*) *whitneyi* Gabb, Moore, 1963, p. 73-74, pl. 24, figs. 3-10.

Dosinia (*Kaneharaia*) *rumoensis* Amano [sic], Gladenkov *et al*., 1987, p. 34-35, pl. 8, figs. 1, 2, 4, 7-11.

Remarks.—Five specimens from eastern Kamchatka, Russia and Kodiak Island, Alaska resemble *K. ausiensis* in the absence of an escutcheon and lamellated concentric ribs and the presence of a wide pallial sinus and a narrow subumbonal pit. However, these specimens have more numerous (18-22) and more flattened concentric ribs than in *K. ausiensis*, and therefore they can easily be separated from the latter at the species level.

Khomenko (1933) recorded *Dosinia* cfr. *mathewsoni* Gabb, 1869 from Korf Bay of eastern Kamchatka, with which our specimens discussed here are identical. Thereafter, Slodkewitsch (1938) reasigned Komenko's specimens to *Dosinia margaritana* Wiedey, 1928. When they described the fauna from Korf Bay, Gladenkov *et al*. (1987) identified their speci-

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← **Figure 2. 1-5, 8, 10-12, 14-16**: *Kaneharaia ausiensis* (Ilyina). 1; ×1.1, JUE no. 15670-1: 3; ×1.2, JUE no. 15670-2; Loc. 1, Ausinskaya F.; white arrow indicating a subumbonal pit. 2; ×1.05, JUE no. 15666-3: 15; ×1.1, JUE no. 15666-2; Loc. 3, Shibiutan F. 4; ×1.2, JUE no. 15667-2: 5; ×1.15, JUE no. 15667-3: 14; ×1, JUE no 15667-4: 16; ×1, JUE no. 15667-5; Loc. 4, Horokaoshirarika F. 8; ×1, JUE no. 15664-5: 10; ×1, JUE no. 15664-1: 12; ×1, JUE no. 15664-3; Loc. 1, Ausinskaya F. 11; ×1, JUE no. 15665-1, topotype, Loc. 2, Ausinskaya F. **6, 13**: *Kaneharaia kannoi* (Masuda). 6; ×0.9, IGPS no. 73203: 13a-b; ×0.8, IGPS no. 64682, holotype, Heiroku F. **7a-b, 9**: "*Dosinia*" mathewsoni Gabb. 7a-b; ×1, UCMP no. 11173, San Ramon F.: 9; ×1, UCMP no. 11149, reproduced from pl. 7, fig. 5 of Clark (1918), San Ramon F. White arrows in 1, 2, 3, 5, 9, 13b shows the subumbonal pit.


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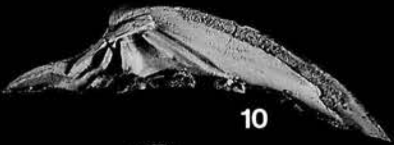
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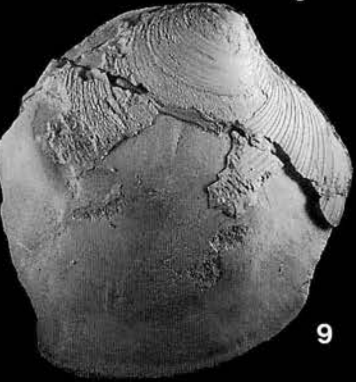
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13a


11b


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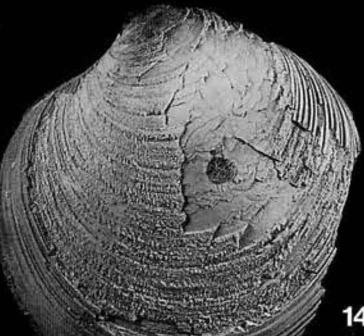
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6b


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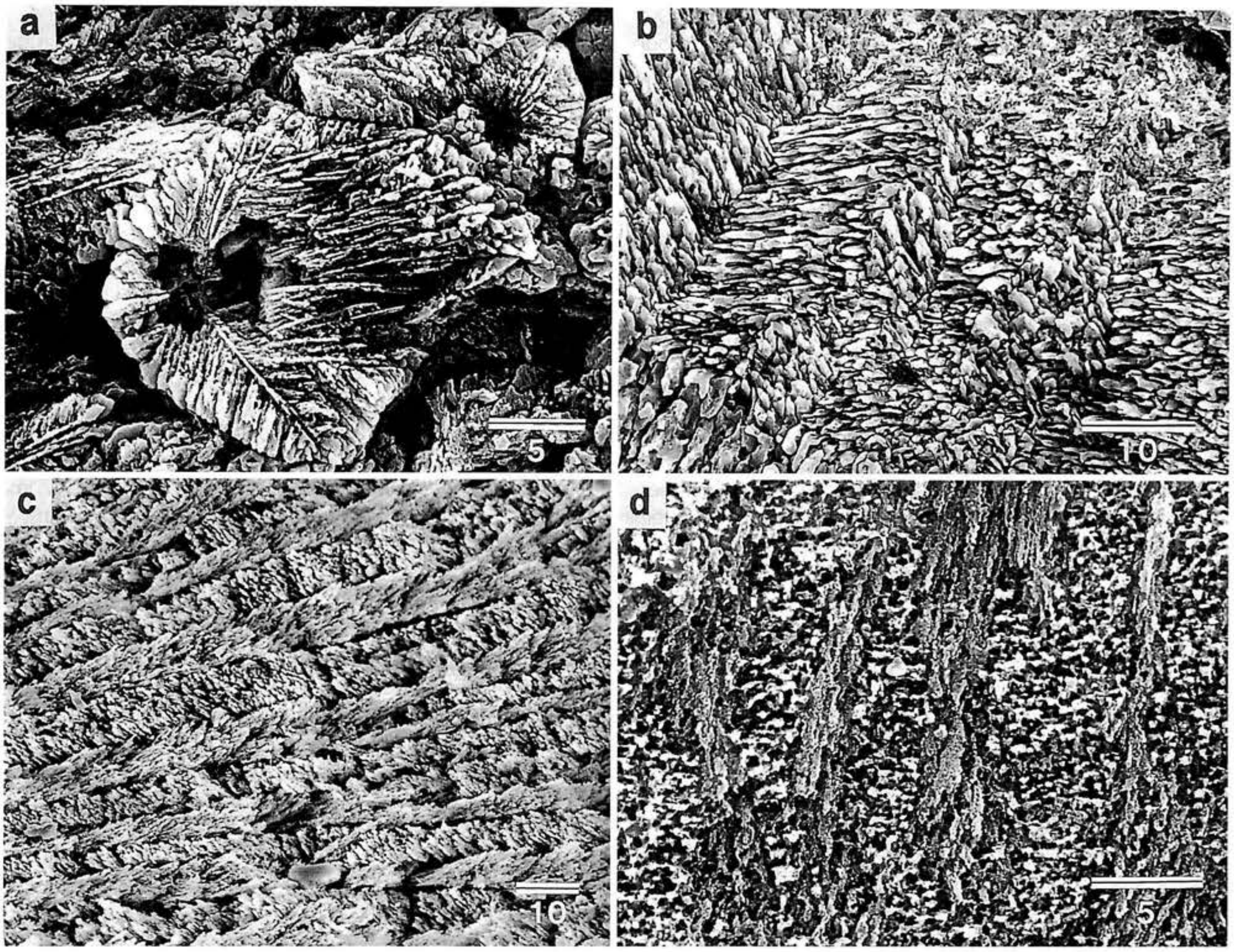

Figure 4. SEM photographs of shell microstructures of *Kaneharaia* and *Dosinia* ; scale in μm ; polished and etched (with 0.6% (v/v) HCl ; 10 sec.) section. **a** : Spherulitic structure of the outer layer of *Kaneharaia ausiensis* showing spherical to subspherical configuration of 3-12 μm in diameter. The elongated structural subunits grow radially in all directions from central parts of the spherulite. The central parts appear to be etched more quickly than the surroundings. **b** : Finely crossed lamellar structure recognized near the beak of *K. ausiensis*. Acicular crystals aggregate to form a higher structural unit (first order lamella), and they are inclined in opposite directions in the adjacent first order lamellae. Long axes of the first order lamellae are arranged perpendicularly to the outer shell surface (upper right). **c** : Finely crossed lamellar structure of the outer layer of *Dosinia ponderosa*. The first order lamellae are arranged in a feathery, radial manner toward the ventral margin (shell surface). **d** : Finely crossed lamellar structure recognized near the beak of *Dosinia discus*. Individual first order lamellae are sometimes branched, their long axes being arranged perpendicularly to the outer shell surface.

← **Figure 3.** **1, 7** : *Kaneharaia kaneharai* (Yokoyama). 1 ; ×1, JUE no. 15671-2 : 7 ; ×0.8, IGPS no. 90511 ; Loc. Tanagura, Kubota F. **2** : *Phacosoma japonicum* (Reeve), ×1, JUE no. 15672, Loc. Tomikawa, Recent. **3** : *Dosinia ponderosa* (Gray), ×0.8, UC Davis, Loc. Puerto Penasco, Sonora, Mexico, Recent. **4** : *Dosinella penicillata* (Reeve), ×1, JUE no. 15673, Loc. Okayama, Recent. **5** : *Phacosoma tatunokutiensis* (Nomura), ×1, JUE no. 15674, Loc. Tatsunokuchi, Tatsunokuchi F. **6a-c** : *Dosinia discus* (Reeve), ×1, JUE no. 15675, Loc. Virginia Beach, USA, Norfork F. 8 : *Pectunculus exoleta* (Linnaeus), ×1, JUE no. 15676, Loc. Galicia, Spain, Recent. **9, 11-13** : *Kaneharaia* sp. 9 ; ×1, JUE no. 15668-2 : 13a-b, ×1, JUE no. 15668-1 ; Loc. Kodiak Is., USA, Narrow Cape F. 11a ; ×1.2 ; 11b ; ×1, JUE no. 15669-1 : 12a-b ; ×1, JUE no. 15669-2 ; Loc. Korf Bay, Russia, Ejobyi Horizon. **14** : *Kaneharaia ausiensis* (Ilyina), ×1, JUE no. 15665-2, topotype, Loc. 2, Ausinskaya F. **10** : *Phacosoma tomikawensis* (Takagi), ×1, JUE no. 15679, Loc. Kakuma, Omma Formation. White arrows in 1, 3, 6b, 11a show the subumbonal pit.

mens as *Dosinia* (*Kaneharaia*) *rumoensis* Amano [sic]. Our specimens seem to constitute a new species, but poor preservation of the Kamchakta and Kodiak specimens prevents us from establishing a new species.

Allison (1978) and Marincovich and Moriya (1990) only listed *Dosinia* and *D. whitneyi* respectively from the Narrow Cape Formation in Kodiak Island. Judging from the location, we suspect that their specimens are identical with the present species.

Distribution.—Early middle Miocene Ejoviy Horizon, Korf Bay, eastern Kamchatka, Russia; early middle Miocene Narrow Cape Formation, Kodiak Island, Alaska.

Revision of *Kaneharaia*

Dosinia (*Kaneharaia*) *kaneharai ouchiensis* was described by Kanno (1955) from the Miocene Yoshigasawa Formation in Miyagi Prefecture. Acccording to him, this subspecies can be dicriminated from *K. kaneharai* (s.s.) by its higher shell. However, the holotype and topotype specimens of *D.*(*K.*) *kaneharai ouchiensis* were slightly compressed laterally, judging from Kanno's (1955) figures and topotype specimens stored at IGPS. As mentioned by Masuda (1967), it is sometimes hard to distinguish *D.*(*K.*) *kaneharai ouchiensis* from *K. kaneharai* (s.s.). Therefore, there is no reason to follow this separation.

D.(*K.*) *kaneharai fujinensis* was established by Masuda (1967) from the Miocene Fujina Formation in Shimane Prefecture. This subspecies was separated from *K. kaneharai* (s.s.) based on an elongated shell. However, the shell outline of *K. kaneharai* (s.s.) in our specimens from the Kanomatazawa Formation shows a wide range of variation from subcircular to elongate ovate shell. The surface of the holotype of *D.* (*K.*) *kanaharaia fujinensis* is sculpted by 11 concentric ribs between 10 mm and 20 mm from the beak just the same as in *K. kaneharai* (s.s.). For the above reasons, we also do not accept the separation of *D.*(*K.*) *kanaharaia fujinensis* from *K. kaneharai kaneharai* (s.s.).

Evolutionary history of *Kaneharaia*

To sum up the discussion above, the genus Kaneharaia consists of four species in the North Pacific region,: *K. kaneharai* (Yokoyama)(middle-late Miocene), *K. kannoi* (Masuda) (early middle Miocene), *K. ausiensis* (Ilyina) (early middle Miocene-early Pliocene) and *K.* sp (early middle Miocene). Moreover, as described above, the Astoria species of "*Dosinia*" and "*D.*" *mathewsonii* most probably belong to the genus *Kaneharaia*.

There is no Oligocene record of *Kaneharaia* in the northwestern Pacific region. On the other hand, one species most probably included in *Kaneharaia* and two species of *Dosinia* have been reported from the upper Oligocene of northwest and central America. "*Dosinia*" *mathewsoni* from the upper Oligocene of California is most probably a *Kaneharaia* as discussed above. Woodring (1982) recorded *D.* aff. *delicatissima* Brown and Pilsbry, 1913 from the upper Oligocene Bohio Formation of Panama. On the Atlantic coast, Palmer (1927) illustrated *D. chipolana* Dall, 1903 from the Oligocene Silex beds of Florida.

Taking the phylogenetic relationship and fossil records into consideration, *Kaneharaia* first appeared in the northeastern Pacific during the late Oligocene.

Among the northwestern Pacific species, *K. kannoi* is confined to the early middle Miocene in northeastern Honshu and North Korea while *K. kaneharai* might be directly derived from *K. kannoi* and occurs from the middle to late Miocene in Honshu (Figure 5). *K. ausiensis* is related to *K. kannoi* and first appeared in the early middle Miocene in Sakhalin and Hokkaido. This species also occurs in the early Pliocene of Hokkaido and central Honshu. *K.* sp. is locally restricted to eastern Kamchatka and Kodiak Island in the early middle Miocene. From the early middle Miocene Astoria Formation in Oregon, *Kaneharaia*-like species have been reported.

Judging from the above distribution, *Kaneharaia* migrated to the northwestern Pacific region during the early middle Miocene time, corresponding to the Neogene Climatic Optimum. Thus, *Kaneharaia* represents another example of a mollusc that shows westward spreading in the North Pacific and is an exceptional in being an extinct genus among this group.

When she discussed the evolution of *Mercenaria* Schumacher, 1817, Harte (1998) pointed out that all Japanese "*Mercenaria*" should be placed in *Securella* Parker, 1949 because

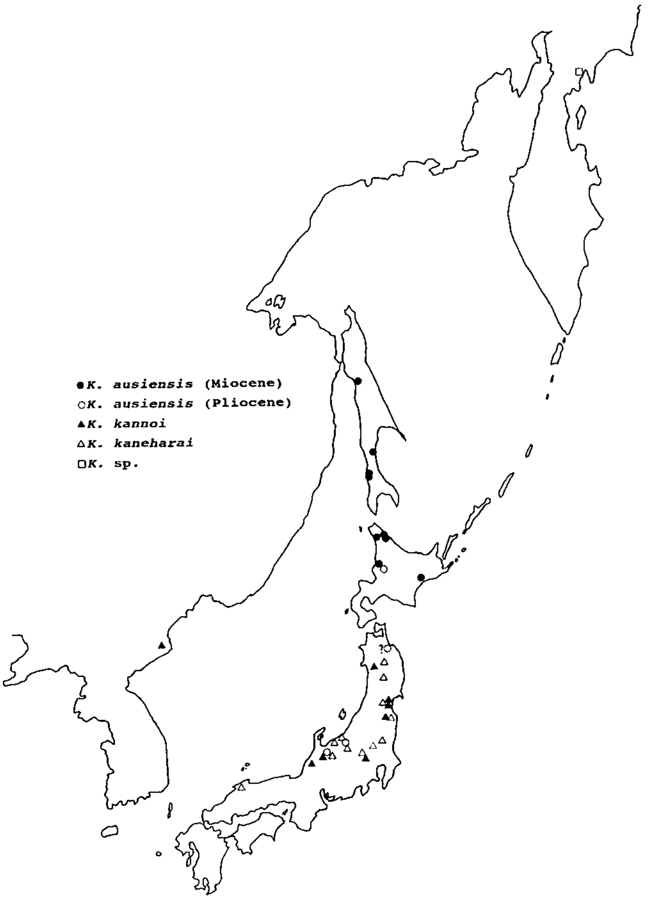

Figure 5. Distribution of *Kaneharaia*.

they lack a rugose nymph. According to her, *Mercenaria* arose from the early Oligocene *S. mississippiensis* during the late Oligocene. *Securella* first appeared in the northeastern Pacific in the late Oligocene while the oldest record of *Securella* in the northwestern Pacific date from the Miocene (Harte, 1998). Such an evolutionary pattern is very similar to that of *Kaneharaia* and *Dosinia*. It is reasonable to conclude that both genera have a common ancestor. Then, after the late Oligocene, *Kaneharaia* fluorished in the North Pacific region like *Securella*. On the other hand, *Dosinia* radiated in the Atlantic coast region like *Mercenaria*.

Besides *Kaneharaia* and *Securella*, Amano (1998) listed *Compsomyax* (Veneridae) as another example of a westward-spreading group. More examples of this type of migration will no doubt be found in other venerids.

Acknowledgements

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A new Foraminifera from the upper Middle Eocene of the Ebro Basin, Spain

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Abstract. ***Serraia cataloniensis*** **gen. et sp. nov. is differentiated from other pellatispiracean Foraminifera by the presence of one or more intercalary whorls of median chambers winding in the same direction as the primary whorl, and by frequent protoconchal and deureroconchal diverticula and a short spire of chambers around the deuteroconch.** ***S. cataloniensis*** **is described from the La Tossa Formation of the Bartonian regressive cycle of sedimentation in the Ebro Basin, Barcelona region, Spain.**

Key words : Bartonian regressive cycle, Ebro Bassin, La Tossa Formation, Late Bartonian, ***Serraia cataloniensis*****, Spain**

Introduction

At the second meeting of the IGCP 393, "Neritic Events at the Middle-Upper Eocene Boundary", in Vic, Spain, 2-6 September 1997, the field trip guided by Serra-Kiel *et al.* (1997) took us to different outcrops of Lutetian and Bartonian sediments in the Ebro Basin, southeastern Pyrenean Foreland Basin, Catalonia, Spain. The Puig Aguilera outcrop lies at 41°35′N. Lat. 1°39′E. Long., on the Puig Aguilera, a mountain 5 km northeast of the town of Igualada, 50 km northwest of Barcelona (Figure 1). The geologic section in the Puig Aguilera outcrop (Serra-Kiel *et al.*, 1997, p. 43, fig. 38 ; Figure 1) begins with marls alternating with sandstone beds in the lower sequence. Above this sequence, there is an interval of marls and sandstones alternating with limestone beds. Serra-Kiel *et al.* (1997) interpret the former as belonging to the upper part of the Bartonian transgressive facies of the La Tossa Formation (Ferrer, 1971), while the latter belongs to the Bartonian regressive facies of the same formation. Sample 4 at the Puig Aguilera outcrop is from the marls corresponding to the Bartonian regressive facies and is rich in larger foraminifers. Especially common are *Asterocyclina stellaris* (Brunner, 1848 MS., in Rütimeyer, 1850), *Discocyclina pratti* (Michelin, 1946), *D. sella* (d'Archiac, 1850), *Heterostegina reticulata* Rütimeyer, 1850, *Operculina schwageri* Silvestri, 1928, *Pellatispira madaraszi* (Hantken, 1875), *Orbitocliypeus* sp., and *Nummulites* sp.

The regressive facies of the Bartonian cycle occurs in the Igualada and Vic areas, eastern Ebro Basin, Barcelona region, and changes laterally. The facies of the La Tossa Formation in the Igualada area is correlated to the Saint Marti Xic Limestone Formation (Reguant, 1967) represented by deltaic and reef sediments in the Vic area. On top of the deltaic-reef complex of the Bartonian regressive cycle and below the evaporitic sediments of the Cardona Formation (Riba, 1975) in the Igualada and Vic areas, there is a Terminal Complex, named by Trave (1992), which reflects the change from marine to continental sedimentation. The Terminal Complex corresponds to the magnetostratigraphic scale from 17.2 to 17.1, and to planktonic foraminiferal Zone P. 15 of Berggren *et al.* (1995). Thus the age of the Bartonian regressive facies of the Bartonian marine sediments in the Igualada and Vic areas is regarded as Late Bartonian.

One of the major achievements of project IGCP 393 was the identification of additional larger foraminifers. *Serraia cataloniensis* gen. et sp. nov. occurs in marls in sample 4, which Dr. Serra-Kiel kindly sent to the author for study, and is found there in association with *Biplanispira mirabilis* (Umbgrove, 1937) and the foraminifers listed above.

Systematic paleontology

Order Foraminiferida
Suborder Rotaliina
Superfamily Nummulitacea
Family Pellatispiridae Hanzawa, 1937

Remarks.—In addition to the type genus, Matsumaru (1996a, p. 110-118) assigned the genus *Biplanispira* Umbgrove, 1937 to the family Pellatispiridae Hanzawa, 1937, because of its characteristic planispiral to low trochospiral coiling, subsutural and intraseptal radial canals, vertical canals or fissures, and no marginal cord, following Loeblich and Tappan's (1987) classification. Also Matsumaru (1996a) emended the diagnosis of the family such that the secondary and surface chambers are differentiated from the spiral and umbilical sides of the test. Moreover Matsumaru (1996b) transferred the genus *Bolkarina* Sirel, 1981 to the family

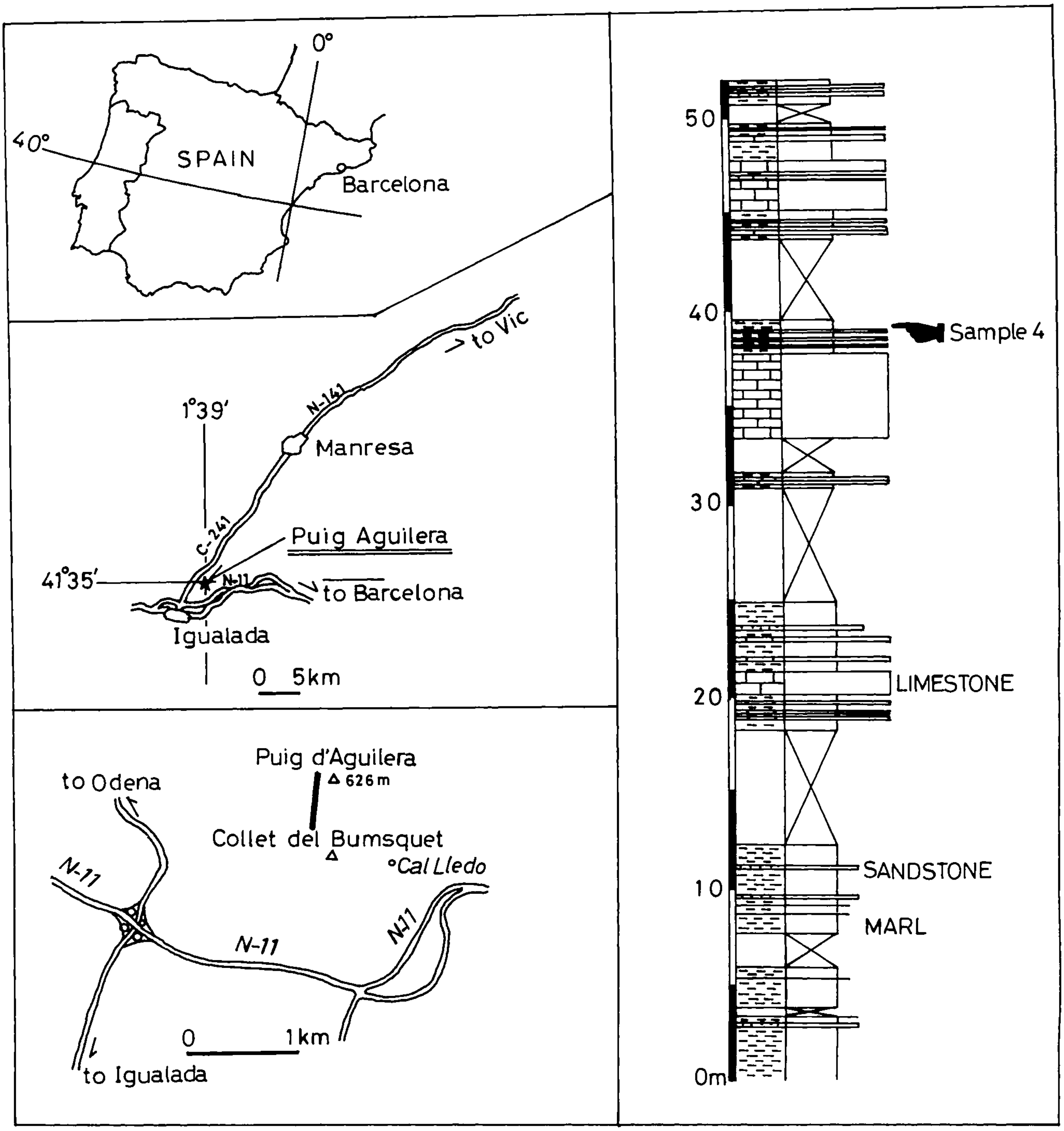

Figure 1. Geographic and stratigraphic position of sample locality (sample 4) from Puig Aguilera outcrop, Igualada City, northwest of Barcelona, Spain.

Discocyclinidae Galloway, 1928 from the family Pellatispiridae.

Genus *Serraia* gen. nov.

Type species.—*Serraia cataloniensis* sp. nov.

Diagnosis.—A pellatispiriid genus characterized by remarkable development of secondary and tertiary spiral chambers of intercalary whorls in early growth stage of planispiral to low trochospiral whorl of primary spiral chambers, and by frequent presence of protochoncal and deuteroconchal diverticula and short spiral chambers around deuteroconch.

Description.—Test lenticula, bilaterally symmetrical in outline with granules extending to pillars distributed rather spirally over surface of test; bilocular embryo of protoconch and deuteroconch frequently containing protoconchal and deuteroconchal diverticula, and a short spire of small chambers around deuteroconch, followed by a primary coil of loosely evolute, later becoming involute whorls of large spiral chambers (i. e. primary spiral chambers), together with secondary and tertiary intercalary whorls of small spiral chambers (i. e. secondary and tertiary spiral chambers) added between whorls of primary coil; all chambers connected by a basal foramen with intraseptal, subsutural and rather canals, winding in same direction as primary whorls towards periphery of test; later primary spiral chambers subdivided into irregularly arranged spiral chambers at peripheral part of test as seen in *Biplanispira*. Lateral layers thickest at center and gradually attenuated towards periphery of test, pierced by numerous vertical pores opening between numerous pillars embeded in lateral layers, and by numerous vertical and radial canals; vertical pores opening covered by thin and finely cribrate roofs of small surface chambers. Test wall calcareous, thick, fibrous and lamellar with two layers of fibrous structure, inner one thin and compact, and outer one thick and coarsely perforate.

Etymology.—The genus name is after Dr. Josep Serra-Kiel, who provided the pellatispiracean-bearing sample in this study.

Stratigraphic horizon.—Upper part of the La Tossa Formation.

Comparison.—The present genus resembles the genus *Biplanispira* Umbgrove by the presence of a single median layer of primary spiral chambers, and later bifurcating layers of spirally disposed chambers. However, *Serraia* is distinguished from *Biplanispira* in having the second and third median layers of chambers developed from the third and fourth chambers of the primary spiral chambers, respectively, which wind in the same direction as the primary whorl, and also in having frequent protoconchal and deuteroconchal diverticula and a short single layer of chambers around the deuteroconch. *Serraia* resembles *Dictyoconoides* Nuttall, 1925 and *Dictyokathina* Smout, 1954 in having median chambers formed by repeated doubling (originated from bilocular embryonic and median chambers) and in having a test wall with fibrous, lamellar structure that is pierced by vertical canals. However, this new genus is distinguished from them in having double median chambers originated from the primary spiral chambers in an early nepionic stage, in having median layers of fibrous structure, and in lacking an umbilical mass of numerous pillars. Moreover, *Serraia* is distinguished from the genus *Boninella* Matsumaru, 1996a in having chamber layers with fibrous and lamellar structure.

Serraia cataloniensis sp. nov.

Figures 2-1—3; 3-1—5; 4-1—3; 5-1—3

Material.—Holotype: a megalospheric specimen in a half test, Saitama University coll. no. 8841 (Figures 2-1; 3-1); Paratype: equatorial sections of megalospheric specimens, Saitama University coll. no. 8842 (Figures 2-2; 3-5), Saitama

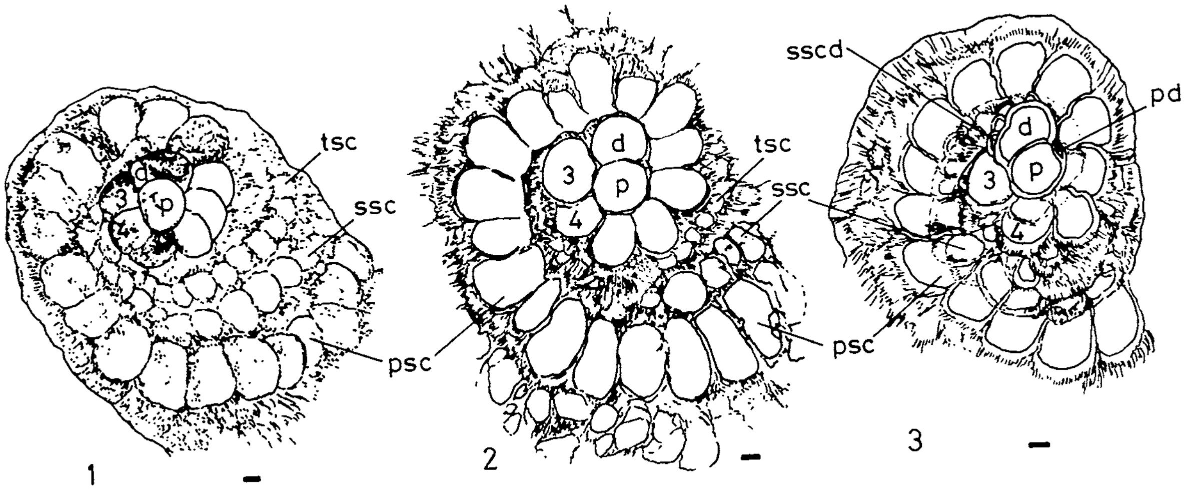

Figure 2. *Serraia cataloniensis* gen. et sp. nov. Drawings of megalospheric specimens. **1.** Holotype, Saitama University coll. no. 8841 (see also Figure 3-1). **2.** Paratype (see also Figure 3-5), Saitama University coll. no. 8842. **3.** Paratype (see also Figure 5-2), Saitama University coll. no. 8843. Abbreviations: p=protoconch; pd=protoconchal diverticulum; d=deuteroconch; 3, 4=third and fourth primary spiral chambers; psc=primary spiral chambers; ssc=secondary spiral chambers; tsc=tertiary spiral chambers; sscd=short spiral chambers around deuteroconch. Scale bars=100 μm.

1a

1b

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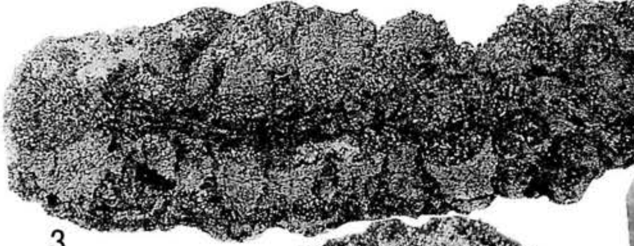

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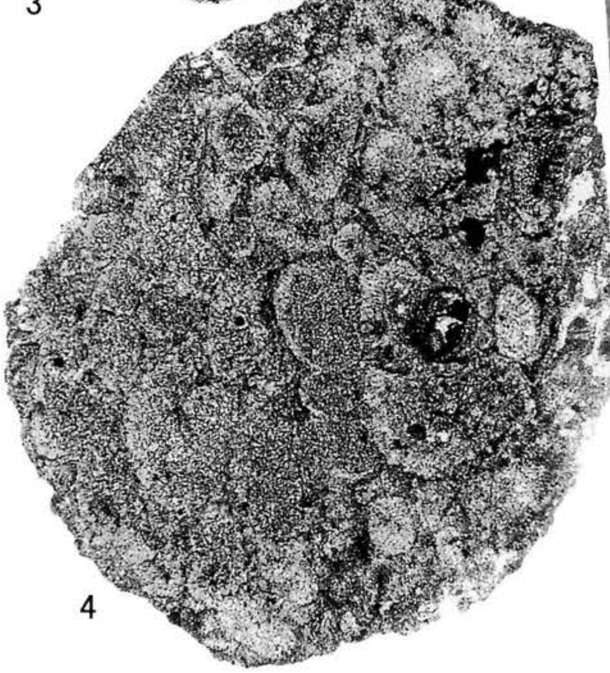

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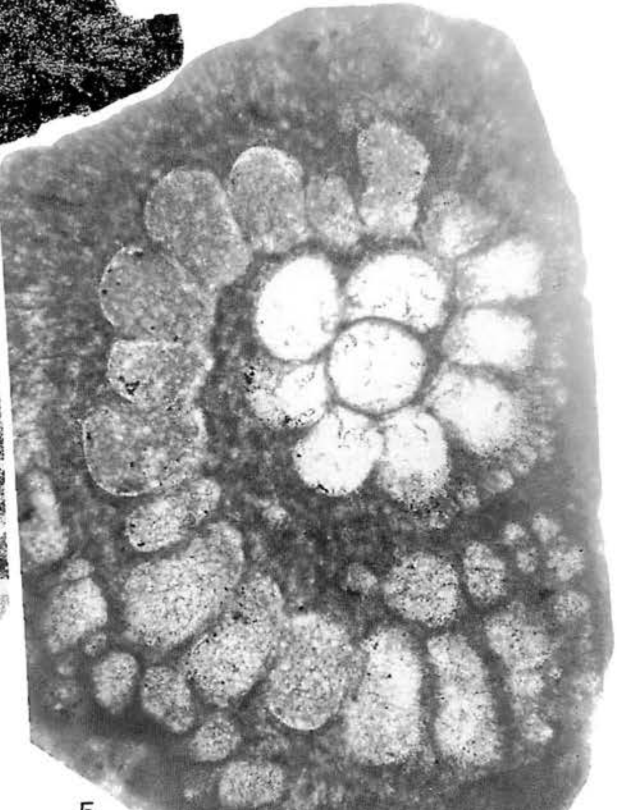

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University coll. no. 8843 (Figures 2-3 ; 5-2), Saitama University coll. no. 8846 (Figure 5-1), Saitama University coll. no. 8847 (Figures 5-3a-b), and Saitama University coll. no. 8850 (Figure 3-4) ; Paratype : test surface and/or equatorial views of megalospheric or microspheric specimens, Saitama University coll. no. 8844 (Figures 4-1a-c), Saitama University coll. no. 8845 (Figures 4-2a-b), Saitama University coll. no. 8848 (Figure 3-2) and Saitama University coll. no. 8851 (Figures 4-3a-b) ; Paratype : vertical sections of megalospheric specimen, Saitama University coll. no. 8849 (Figure 3-3).

Description.—Test thin (0.6 to 0.9 mm in thickness), lenticular (2.0 to 4.0 mm in diameter) with rather thick marginal periphery ; form ratio (diameter/thickness) 4.0 to 7.7 in megalospheric form ; and 9.0 in single microspheric form observed which is 4.5 mm in diameter. Megalospheric embryonic chambers biloculine ; subspherical to spherical protoconch ranging from 160×140 to 370×370 μm in diameter in seven specimens, and reniform deuteroconch 200×160 to 430×370 μm in diameter in seven specimens ; whole embryonic chambers 320 to 600 μm in diameter across both protoconch and deuteroconch in seven specimens ; outer wall of embryonic chambers 20 to 30 μm thick in seven specimens ; third primary spiral chamber 100×120 to 265×350 μm in radial and tangential diameters in seven specimens ; and fourth primary spiral chamber 60×120 to 240×215 μm in radial and tangential diameters in seven specimens. Other primary spiral chambers developed into a planispirally to low trochospirally evolute whorl in mature stage and into involute whorl in gerontic stage ; first whorl divided by septa into 7 to 10 chambers, first whorl and a half with 15 to 20 chambers, and second whorl with 25 ? to 33 ? chambers in seven specimens. Secondary spiral chambers of second median layer in planispiral to low trochospiral whorl 60×100 to 220×240 μm in maximum radial and tangential diameters in seven specimens. Tertiary spiral chambers of third median layer in planispiral to low trochospiral whorl 100×200 to 200×130 μm in maximum radial and tangential diameters in five specimens ; both secondary and tertiary spiral chambers wind in same direction as primary spiral chambers. Median layer of primary spiral chambers subdivided into irregularly arranged, spiral chamber layers towards periphery. Protoconchal diverticula arcuate, 28×42 to 30×62 μm in radial and tangential diameters in three specimens, and deuteroconchal diverticula arcuate 80 ?×140 ? μm and 83×145 μm in radial and tangential diameters in two specimens. Short spiral chambers around deuteroconch frequently present and arcuate, 25×62 to 40×93 μm in maximum radial and tangential diameters in two specimens. Lateral layers thickest at center and attenuated towards periphery of test, and pierced by numerous open pores or vertical canals of 8 to 20 μm diameter. Pore openings covered by thin roofs of small surface chambers with 135×38 to 145×40 μm in maximum tangential diameter and height in three specimens. Test wall thick, fibrous, and perforate ; canal system showing radial, simple and marginal, and intraseptal canal present. Dorsal and umbilical pillars present over lateral walls ; smaller ones 85 to 100 μm in diameter, and larger ones 135 to 185 μm in diameter. Aperture with longitudinal grooves on base of apertural face ; in present material, measurements of seven megalospheric forms given in Table 1.

Etymology.—The species name is derived from the province of Catalonia, Spain.

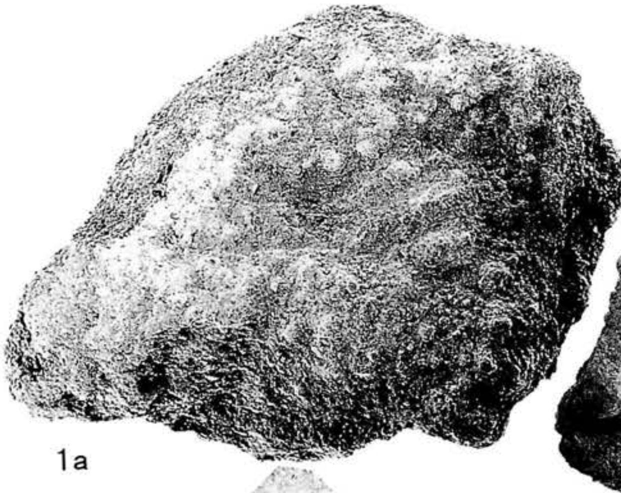
Type locality.—Sample locality (Sample 4) of Puig Aguilera outcrop, Igualada, 50 km northwest of Barcelona, Spain (Figure 1).

Remarks.—*Serraia cataloniensis* sp. nov. resembles *Biplanispira mirabilis* (Umbgrove, 1936), but is easily distinguished from the latter in having the secondary and tertiary spiral chambers developed in the same direction as the primary spiral chambers, and in posessing frequent protoconchal and deuteroconchal diverticula and short spiral chambers around the deuteroconch. The author considers that this new species may have evolved from *Biplanispira mirabilis* (Umbgrove) by developing secondary and tertiary spiral chambers directly from the spiral chambers.

Acknowledgments

The author thanks Josep Serra-Kiel, Universitat de Barcelona, for his kindness in sending sample materials for study. He also thanks Edward Robinson, Department of Geography and Geology, the University of the West Indies, Jamaica, Alphonse Blondeau, Maître de Conférence honoraire, Université Pierre et Marie Curie (Paris VI), and Earl E. Brabb, Geologist Emeritus, U. S. Geological Survey, Menlopark, California, for their kind reading of the manuscript, and Ministry of Education, Japan, for financial assistance toward presenting results at the 2nd Meeting of IGCP 393.

← **Figure 3.** *Serraia cataloniensis* gen. et sp. nov. **1a.** External view (spiral side) of megalospheric specimen (holotype), showing large- and small-sized granules, and rather thick marginal periphery of test. **1b.** Equatorial and internal view of holotype showing embryonic chambers with half-broken deuteroconch ; primary spiral chambers with 5th, 9th and 12th broken chambers, and secondary and tertiary spiral chambers, all coiling in same direction except for peripheral chambers. ×26. **2.** External view of spiral side of test in microspheric specimen, paratype, Saitama University coll. no. 8848, ×22. **3.** Vertical section of megalospheric specimen, paratype, Saitama University coll. no. 8849, showing spiral and surface chambers, lateral layers thickest at center and attenuated towards periphery, large and small pillars, pore openings, and canals, ×43. **4.** Eqautorial section of broken specimen, paratype, Saitama University coll. no. 8850, showing irregularly-arranged primary spiral chambers towards periphery of test, coiling opposite direction to primary whorl as seen in *Biplanispira*, and also coiling in same direction as primary whorl, ×43. **5.** Equatorial section of megalospheric specimen, paratype, Saitama University coll. no. 8842, showing embryonic chambers, primary spiral chambers, and secondary and tertiary spiral chambers, all coiling in same direction, ×40.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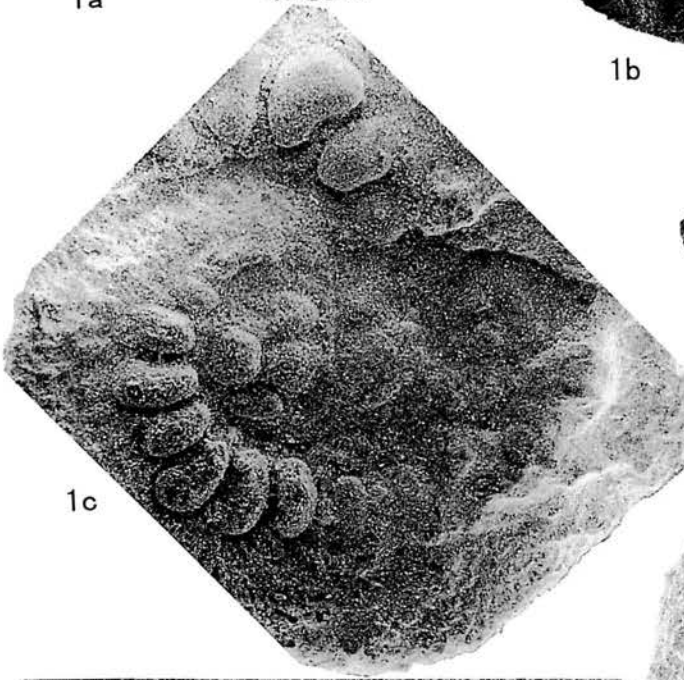
1b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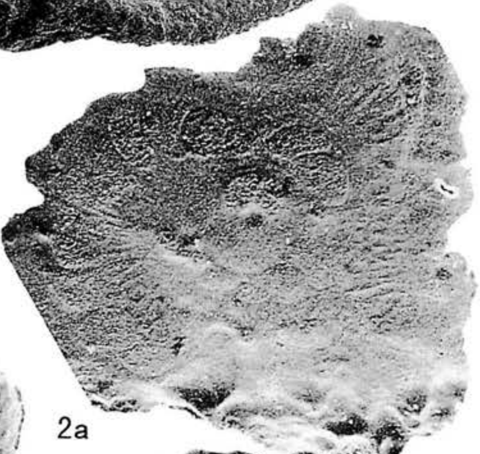
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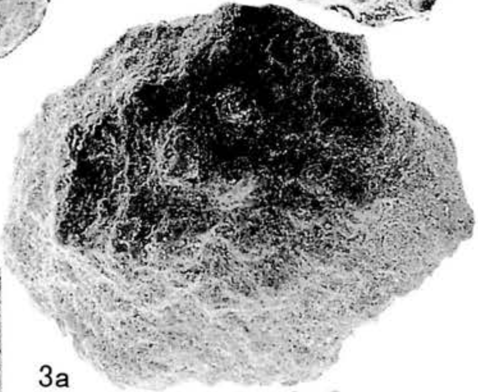
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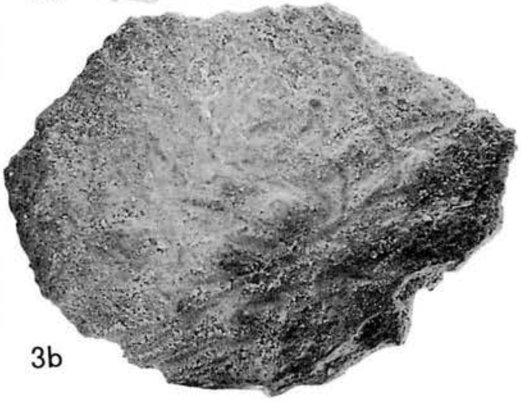
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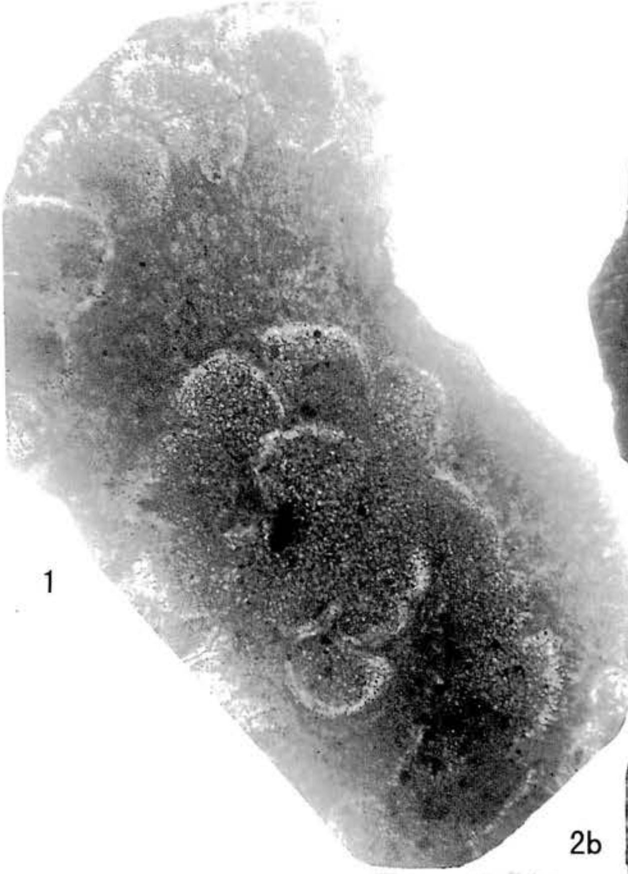
Table 1. Measurements of internal equatorial view and equatorial sections of *Serraia cataloniensis* sp. nov.

Specimen	Holotype no. 8841 (Fig. 3-1)	Paratype no. 8842 (Fig. 3-5)	Paratype no. 8843 (Fig. 5-2)	Paratype no. 8846 (Fig. 5-1)	Paratype no. 8847 (Fjg. 5-3)	Paratype no. 8844 (Fig. 4-1)	Paratype no. 8845 (Fig. 4-2)
Diameter (mm)	3.6	3.1	2.3	3.0	3.0	4.0	2.0
Thickness (mm)	0.9	0.6	0.3	0.4	0.5	0.9	0.3
Form ratio (diameter/thickness)	4.0	5.2	7.7	7.5	6.0	4.4	6.7
Embryonic chambers							
protoconch diameter (μm)	370×370	350×290	302×272	235×265	360×250	220×140	160×140
deuteroconch diameter (μm)	374×212	320×208	350×230	235×170	430×340	220×160	200×160
distance across both chambers (μm)	600	498	502	435	600	320	320
wall thickness (μm)	30	30	20	28	30	28	22
Protoconchal diverticula							
radial diameter (μm)			30	30	28		
tangential diameter (μm)			62	42	42		
Deuteroconchal diverticula							
radial diameter (μm)				80 ?	83		
tangential diameter (μm)				140 ?	145		
Spiral chambers around deuteroconch							
radial diameter (μm)			33 40 40		25 33		
tangential diameter (μm)			72 52 93		62 40		
Primary spiral chambers							
Third chamber							
radial diameter (μm)	145	265	208	100	220	135	100
tangential diameter (μm)	280	350	290	140	290	165	120
Fourth chamber							
radial diameter (μm)	200	165	240	140	180	60	80
tangential diameter (μm)	160	145	215	140	220	120	110
number in 1st whorl	8	8	7	9	10	7	9
number in 1+1/2 whorl	16	18	15	17	18	15	18
number in 2nd whorl	30?	33?	28?	29	29?	29	25?
Secondary spiral chambers							
radial diameter (μm)	230	220	230	190	140	60	60
tangential diameter (μm)	160	240	230	200	186	100	100
Tertiary spiral chambers							
radial diameter (μm)	200	120	100	100		100	
tangential diameter (μm)	130	95	200	200		200	

← **Figure 4.** *Serraia cataloniensis* gen. et sp. nov. **1a.** External view of megalospheric specimen, paratype, Saitama University coll. no. 8844, in umbilical side of test, showing dextral distribution of large- and small-sized granules. **1b.** Equatorial and internal view of same specimen of Figure 4-1a, showing embryonic chambers, and primary, secondary and tertiary spiral chambers, all coiling in sinistral direction, ×26. **1c.** Central part of internal view of Figure 4-1b, showing embryonic and primary spiral chambers, and secondary and tertiary spiral chambers, ×43. **2a.** Equatorial and internal view of megalospheric specimen, paratype, Saitama University coll. no. 8845, ×43. **2b.** Central part of internal view in Figure 4-2a, showing embryonic and primary spiral chambers, and secondary spiral chambers connected by intraseptal, subsutural and radial canals from third chamber and 7 th chamber of primary spiral chambers, ×107. **3a.** External view of megalospheric specimen, paratype, saitama University coll. no. 8851, showing spiral side of test. **3b.** External view of same specimen as Figure 4-3a showing umbilical side of test, ×26.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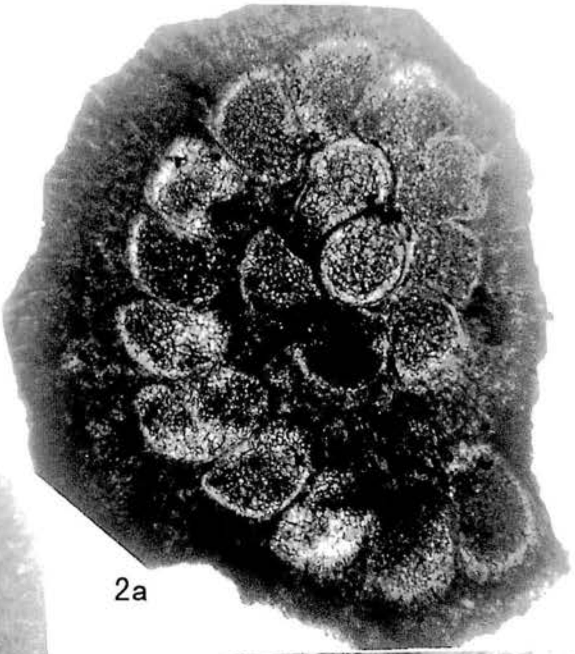
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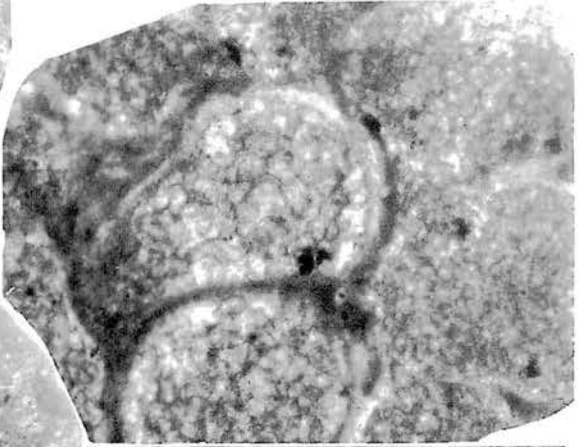
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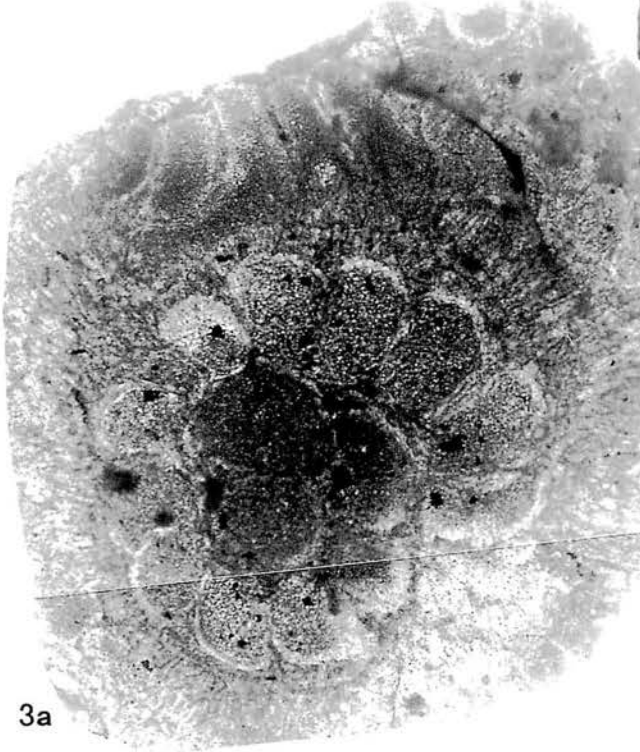
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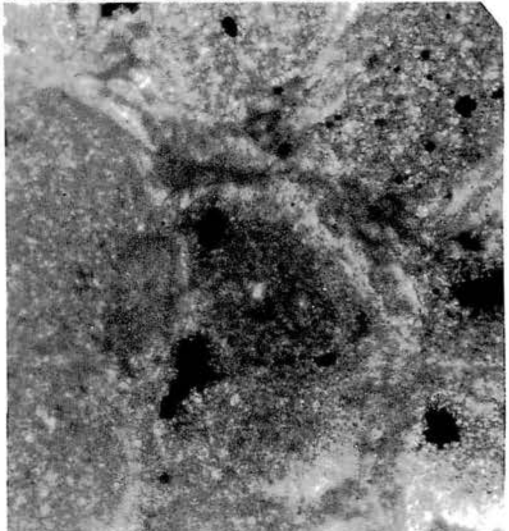
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← **Figure 5.** *Serraia cataloniensis* gen. et sp. nov. **1.** Equatorial section of megalospheric specimen, paratype, Saitama University coll. no. 8846, showing embryonic chambers, primary spiral chambers, and secondary and tertiary spiral chambers, all coiling in same direction, ×43. **2a.** Equatorial section of megalospheric specimen, paratype, Saitama University coll. no. 8843, showing embryonic and primary spiral chambers, secondary spiral chambers, protoconchal diverticulum, and short spiral chambers arranged deuteroconch, ×43. **2b.** Central part of equatorial section in Figure 5-2a, showing protoconchal diverticulum and short spiral chambers around deuteroconch connected by deuteroconchal stolons and probably intraseptal, subsutural and radial canals from third chamber, ×107. **3a.** Equatorial section of megalospheric specimen, paratype, Saitama University coll. no. 8847, showing embryonic, primary and secondary spiral chambers, deuteroconchal diverticulum, and short spiral chambers around deuteroconch, ×43. **3b.** Central part of equatorial section in Figure 5-3a, showing deuteroconchal diverticulum, and short spiral chambers connected by deuteroconchal stolons and intraseptal, subsutural and radial canals or stolons? ×95.

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The Late Bathonian gastropod fauna of Kutch, western India-a new assemblage

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Abstract. The Middle Jurassic sediments of Kutch have been known all over the world as a veritable storehouse of diverse fauna, particularly ammonites. The present investigation has brought to light a rich haul of gastropods hitherto unknown in Kutch. The present assemblage includes eleven new species belonging to nine genera. They are: *Colpomphalus jumarense* sp. nov.; *Emarginula karuna* sp. nov.; *Helicacanthus chanda* sp. nov.; *Riselloidea tagorei* sp. nov.; *R. elongata* sp. nov.; *Onkospira kutchensis* sp. nov.; *Proconulus jadavpuriensis* sp. nov.; *Neritopsis* (*Neritopsis*) *patchamensis* sp. nov.; *N.* (*Hayamiella*) *sankhamala* sp. nov.; *Hayamia mitra* sp. nov. and *Globularia spathi* sp. nov.

The assemblage shows strong Tethyan affinity at generic level, but species display marked endemism since Kutch belongs to a distinct Indo-Madagascan Faunal Province. The present finding refines and widens the spatiotemporal distribution of these genera.

Key words: Gastropoda, Kutch, Middle Jurassic, systematics, western India

Introduction

The marine Jurassic sediments of Kutch were deposited in a newly emerging basin that developed as an extension of the Tethys during separation of Africa and India consequent to the rifting of the Gondwana Superplate (Biswas, 1982, 1991). The Jurassic rocks yield many diverse shallow marine taxa. The fossils are numerous and remarkably well preserved. Amongst them the ammonites attract the most attention of palaeontologists. Among the ammonites many are time-diagnostic forms that provide finer time resolution and help in establishing regional standard biozonations and intercontinental correlation with Europe and other areas. The faunal horizons that yield gastropods, may be assigned to an age ranging from the Late Bathonian to Tithonian.

Many classic studies on this biota, e.g., Cephalopoda (Waagen, 1873-75; Spath, 1927-33), Bivalvia (Kitchin, 1900; Cox, 1940, 1952), Brachiopoda (Kitchin, 1900) and corals (Gregory, 1893, 1900) were made by great masters of the last and this centuries. It is rather surprising that the vast gastropod fauna from the different sections of the mainland and 'islands' of Kutch escaped their notice, notwithstanding the scanty reports of a few gastropod species (Maithani, 1967; Mitra and Ghosh, 1979).

In this present endeavour, we describe 11 new species of the Bathonian, some of which continue to the base of the Middle Callovian. The present study covers a large number of specimens systematically collected in the field with a precise stratigraphic background by us and other members of the Palaeontological Laboratory, Department of Geological Sciences, Jadavpur University.

These species belong to nine genera of seven families. They are *Colpomphalus jumarense* sp. nov.; *Emarginula karuna* sp. nov.; *Helicacanthus chanda* sp. nov.; *Riselloidea tagorei* sp. nov.; *R. elongata* sp. nov.; *Onkospira kutchensis* sp. nov.; *Proconulus jadavpuriensis* sp. nov.; *Neritopsis* (*Neritopsis*) *patchamensis* sp. nov.; *N.* (*Hayamiella*) *sankhamala* sp. nov.; *Hayamia mitra* sp. nov.; and *Globularia spathi* sp. nov. They show strong Tethyan affinity at generic level, especially with Europe (see Knight *et al.*, 1960). Biogeographic distributions of the other Kutch biota suggest prevalence of faunal migrational pathways across the Tethys particularly with Europe (Hallam, 1982; Krishna and Cariou, 1990; Kayal and Bardhan, 1998). The faunas are, however, marked by strong provincialism at species level. The sediments developed due to repeated marine transgression-regression cycles in a basin that emerged from the breakup of Gondwana Superland and was surrounded by East Africa, Madagascar and western India (see also Fürsich *et al.*, 1991). This newly formed basin acted as the Eden of evolution for many immigrant faunas that invaded it (Dutta *et al.*, 1996). Rapid diversification of various taxa marks a strong endemism of fauna which constitutes what is called the Indo-Madagascan or Ethiopian Faunal Province. This record of new taxa widens our knowledge about spatiotemporal distribution of the Jurassic gastropod fauna, which are less comprehensively known and poorly documented in the existing literature.

It should be noted here that recent advances in the studies of suprageneric classification of gastropods have drawn attention to some lacunae in the earlier traditional classifications (e.g. Wenz, 1938—44; Knight *et al.*, 1960). Many higher taxonomic categories are now considered to be paraphyletic, e.g., the Archaeogastropoda (e.g. Hickman and McLean, 1990), and poorly delineated. Major revisionary works are now available for many important groups including their extinct taxa, e.g., on Naticidae and Trochidae (see Kabat, 1991; Hickman and McLean, 1990). Some new schemes have deployed cladistic methodology emphasising the role of derived (apomorphic) conditions and included large character sets. But excessive weight has been given to the characters related to soft parts. The systematic position of many extinct lineages remain still problematic since shell characters may be convergent (Hickman and McLean, 1990). Thus a large amount of uncertainty still prevails in respect of the classification of fossil gastropods. Under such circumstances our endeavour has been to largely retain the general framework (subordinal level and above) of classification given in the Treatise on Invertebrate Paleontology (Knight *et al.*, 1960) while effecting some family or subfamily level changes with regard to certain Kutch taxa in the light of modern classification. In this context the following brief discussion would clarify the taxonomic hierarchies followed in the present study. Particular attention should be drawn to our categorisation of the genera *Riselloidea* and *Onkospira* under the family Trochidae instead of Amberleyidae of the earlier classification and the genus *Helicacanthus* under Turbinidae instead of Nododelphinulidae following Hickman and McLean (1990). Dealing in detail with the shell characters of Amberleyidae, Hickman and McLean (1990) have been very explicit in pointing to the trochid innovations in its shell morphology that are shared with the living species. Of the many trochid subfamilies recognised by them the subfamily Eucyclinae is of particular interest; it covers erstwhile Amberleyidae (Family) and Amberleyinae (Subfamily) and has been divided into three tribes among which the Tribe Eucyclini comprises only the fossil trochids of Middle Triassic to Oligocene age. While discussing this subfamily they have also dealt with those shell characters of the three tribes that separate them from other trochid subfamilies. The historical treatment presented by them clearly demonstrates the weak foundation on which the Amberleyidae of Wenz (1938) and Cox's (*in* Knight *et al.*, 1960) eucycline taxa and superfamily Amberleyacea stand. Similar detailed character analyses that include hard part features have resulted in the placement of erstwhile Nododelphinulidae in the subfamily Angariinae (family Turbinidae) and Proconulinae tentatively under Calliostomatinae (Trochidae) taking into account the assignments which have also been followed here. The scheme used here is logical under rather conflicting positions presently prevailing in fossil gastropod taxonomy and leaves room for more detailed work on an improved, widely acceptable classification.

Stratigraphy

The Mesozoic rocks occupy nearly half of the area in Kutch, covering the mainland as well as three Rann 'islands', and lie nonconformably on the Pre-Cambrian basement (Biswas and Deshpande, 1968). On the mainland the Mesozoic rocks are represented by: Patcham Formation, Chari Formation, Katrol Formation, Bhuj Formation and Deccan Trap in ascending order (for details see Mitra *et al.*, 1979). The thick pile of sediments exceeds more than 3,000 m (Biswas, 1991) and has been regionally folded into three parallel anticlines running northwest-southeast. The Jurassic rocks are best developed in the central anticline (Wynne, 1872; Rajnath, 1932; Poddar, 1959). A set of zones of culmination is observed along the anticlines. These zones of culmination crop out as topographical domes at Jara, Jumara, Nara, Keera etc. (Figure 1) where the inliers of older rocks belonging to the Patcham and Chari Formations mainly occur at the core.

The present gastropod faunas come mainly from the different levels of the Patcham Formation which is partially exposed at Jumara, the locality for the stratotype of the Chari Formation. The Middle Jurassic sediments of the 'islands' belts are included in the formations equivalent to the Patcham Formation and even older ones (Biswas, 1977; Fürsich *et al.*, 1994). Here gastropods occur sporadically, becoming locally abundant at Kuar Bet near Patcham 'island'. The gastropod assemblage of this area appears to be quite distinct from that of Jumara and is dominated mainly by *Katosira* Koken. This level, judged by the associated fauna and stratigraphic position, may represent the Bajocian (see also Fürsich *et al.*, 1994) and these gastropods are therefore not included in the present study.

The exposed sequence of the Patcham Formation at Jumara, which is about 47 m thick, consists of alternations of two distinct lithofacies (Beds 24-26 of Rajnath, 1932; Beds 1-2 of Bardhan *et al.*, 1994) (Figure 2). The lower facies is an alternation between coralline rudstone and cream-coloured

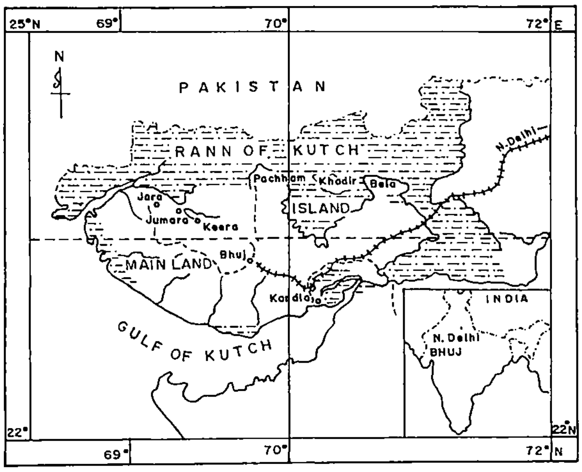


Figure 1. Geographic location of Kutch with Keera and Jumara, the type area of the Chari Formation. The patterned area is the Rann of Kutch.

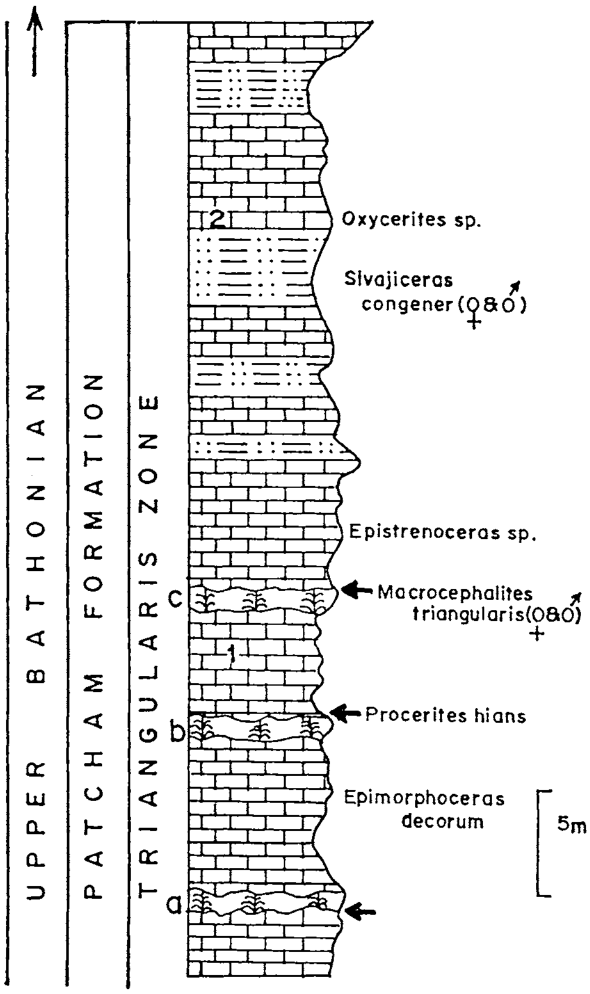


Figure 2. Stratigraphic distribution of key ammonite taxa within the Patcham Formation of Jumara. Key : 1, Coralline limestone (rudstone) alternating with white to brown-coloured limestone(wackestone). Arrows indicate occurrences of different gastropod species. 2, Repeated alternations between white and cream-coloured limestone (wackestone and marl).

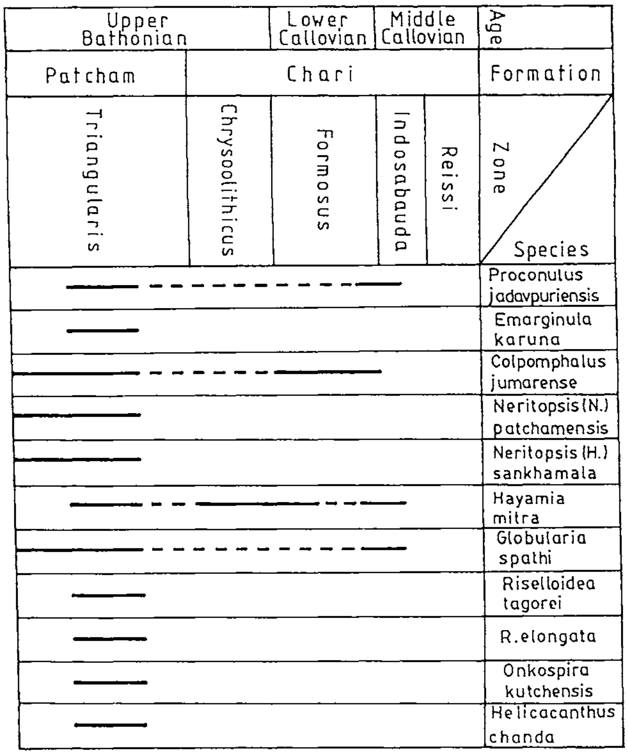


Figure 3. Range chart of different species of gastropods in Kutch. Zones are modified after Dutta (1992).

wackestone. Biostromes of diverse corals appear at several levels where gastropods are most abundant. The coral biostromes occur in the form of parallel-sided, thin tabular beds. They dominantly consist of largely intact fossils with or without interstitial mud (Dutta *et al.*, 1996). There are large varieties of corals (Gregory, 1900 ; Pandey and Fürsich, 1993), most of them being in life attitude. Besides corals and gastropods, many other taxa including ammonites also characterise this horizon. The facies is marked by the first appearance of *Macrocephalites* Zittel in Kutch. Judging by its faunal content and a recently found excellent time-diagnostic ammonite, *Epistrenoceras* Bentz (Kayal and Bardhan, 1998), this lower part of the Patcham Formation can safely be assigned to the late Bathonian. The upper facies is, on the other hand, an alternation between cream-coloured wackestone and mud. It supports sparse fauna including gastropods. Only some fragmentary perisphinctid ammonites belonging to *Procerites* Siemiradzki have been reported from it. This also suggests a late Bathonian age (see also Callomon, 1993 ; Dutta *et al.*, 1996). Recently, Dutta (1992) made a substantial revision of the standard zonations within the Bathonian-Callovian Stages of Kutch. We follow here the biostratigraphic scheme of Dutta (1992) with modification, and stratigraphic distribution of the present gastropod species is shown in Figure 3 (after Bardhan *et al.*, 1994 with modification).

Systematic Paleontology

All the materials studied are deposited in the Department of Geological Sciences, Jadavpur University, Calcutta, India (JU). Measurements are not provided since specimens are plentiful for most of the species, over three hundred in the case of *Riselloidea tagorei*. These can be provided upon request.

Subclass Prosobranchia
Order Archaeogastropoda
Suborder Macluritina
Superfamily Euomphalacea
Family Helicotomidae
Genus **Colpomphalus** Cossmann, 1916

Type species.—*Straparollus altus* d'Orbigny, 1853 ; original designation.

Colpomphalus jumarense sp. nov.

Figure 4-1, 2

Material.—Seven specimens. JUM/g 19-22, 594-596. Specimen JUM/g 19 is designated holotype; the rests are paratypes. JUM/g 19-22 were collected from Bed 1, Jumara and JUM/g 594-596 from Bed 2, Keera (see Bardhan *et al.*, 1994).

Diagnosis.—Average-sized *Colpomphalus* (6 to 10 mm high); whorls 4 to 5 in number, gradate with wide sloping concave ramp; ornamentation of three strong spiral carinae, irregularly spaced and middle one relatively weaker, close to first one; prominent collabral ridges prosoclinal on ramp.

Description.—Shell small in size, maximum height about 10 mm; thick, phaneromphalous; highly depressed and turbiniform with height about half of shell diameter. Apical angle ranges between 120° and 130°. Whorls 4 to 5 in number including protoconch and separated in early stage by weakly grooved suture which becomes conspicuous in later ontogeny. Protoconch poorly preserved, seemingly consists of one and a half smooth, planispiral whorls. Spire very low, conical, obtusely pointed owing to near-planispiral coiling of early whorls. Spire occupies one-fourth of shell height. Body whorl very large, width slightly greater than twice of height; shell rapidly increases in diameter. Whorls gradate with wide sloping ramp, which is concave at upper whorl surface. Outer whorl surface inclined abapically. Body whorl consists of three revolving carinae, which are irregularly spaced. First one situated in ramp margin while third carina at base of whorl forms umbilical border, second carina is close to first. First and third are stronger than second. Umbilical wall steep. Transverse, prosoclinal ridges fine to sharp, intersect carinae and form pointed tubercles at junctions. Tubercles are variable in number, 20 to 25 on body whorl. Aperture subquadrangular, width of aperture is greater than height. Columellar and basal lips form an angulation at their junction.

Discussion.—Relatively low spire, concave upper whorl surface, tuberculate periphery and angular peristome place the present species securely within the genus *Colpomphalus*. It however, differs from *Colpomphalus exsertus* (Hudleston, 1893) (Knight *et al.*, 1960, fig. 106, 7) from the Bajocian of England mainly in shell ornamentation. *C. exsertus* is ornamented with two revolving carinae and fine collabral threads; conversely, the present species has three strong revolving carinae and strong collabral ridges which are prosocline on ramp. Besides, the present species has fewer whorls and a relatively more protruded spire.

The general shell outline, apertural shape, little raised spire and number of whorls of the present species are comparable with those of the Lower Jurassic (Middle Aalenian) *Colpomphalus baugieri* (d'Orbigny) (1853, p. 307, pl. 321, figs. 13-16) (see also Fischer, 1997, p. 121, pl. 24, figs. 1a-c) of Niort, France. But the European form is stratigraphically older and relatively smaller in size. It is less coarsely ornate and is characterised by numerous fine spiral striae, which are lacking in the present species.

Colpomphalus altus (d'Orbigny) (1853, p. 314, pl. 332, figs. 5-8) (also see Fischer, 1997, p. 124, pl. 22, figs. 5a-c), the type species, is a contemporaneous species from France and is based on a monotypic holotype which is broken and immature and hence comparison is very difficult. Its restored diameter is about 8 mm and thus appears to be smaller. It appears similarly but less strongly ornate, basal ornamentation consisting of numerous striae which are conspicuous by their absence in the Kutch species.

Etymology.—After Jumara area of Kutch, Gujarat, where the species occurs.

Suborder Pleurotomariina
Superfamily Fissurellacea
Family Fissurellidae
Subfamily Emarginulinae
Genus **Emarginula** Lamarck, 1801

Type species.—*Emarginula conica* Lamarck, 1801; original designation.

Emarginula karuna sp. nov.

Figure 4-3—5

Material.—Five specimens. JUM/g 71-75. Specimen JUM/g 71 is designated holotype; the rest are paratypes. Specimens are mostly broken, but their original shells are preserved. All were collected from Bed 1 of Jumara.

Diagnosis.—Averaged-sized *Emarginula* (8 to 13 mm high); shell short; apex slightly curved; narrow, raised selenizone extending more than three-fourths of shell height from base; in transverse section, shell nearly flattened along selenizone. Shell ornamented with strong, closely spaced axial ribs intersected by relatively weaker spiral cords; weaker axial rib intercalates between two stronger ribs; very fine, dense, transverse and crescent-shaped ribs with concavity towards aperture subdivide selenizone.

Description.—Shell short, maximum height achieved 13 mm; cap-shaped. Apex curved pointing to rear, protoconch missing. Shell convex, slightly flattened along selenizone. Narrow, slightly raised selenizone between two ridges extending more than three-fourths of shell height from base.

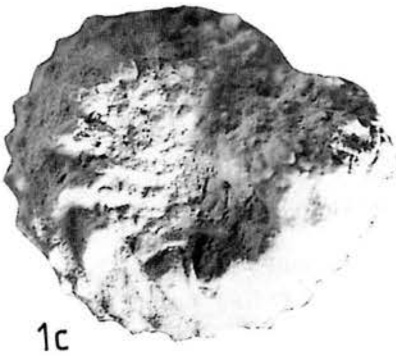
Shell ornamented with strong axial ribs intersected by relatively weaker spiral cords resulting in reticulation. Weaker axial rib intercalates between two stronger ribs. This secondary axial rib is similar in strength or may be sometimes weaker than spiral cords. Very fine, dense and transverse ribs subdivide selenizone to form lunula. They are crescentic in shape with a concavity towards the aperture. All collabral and longitudinal elements are weak in early ontogeny. Peristome ovate.

Discussion.—*Emarginula karuna* sp. nov. is similarly ovate and elevated as *Emarginula* (*Emarginula*) *conica* Lamarck (Knight *et al.*, 1960, figs. 140, 1a-c), the type species, which is a Recent form. But it differs mainly in ornamentation being characterised by axial ribs of variable strength. Moreover, selenizone is not depressed.

Emarginula (*Tauschia*) *orthogonia* Tausch, 1890 (Knight *et al.*, 1960, figs. 140, 11a-b), resembles the present form in


1a


1b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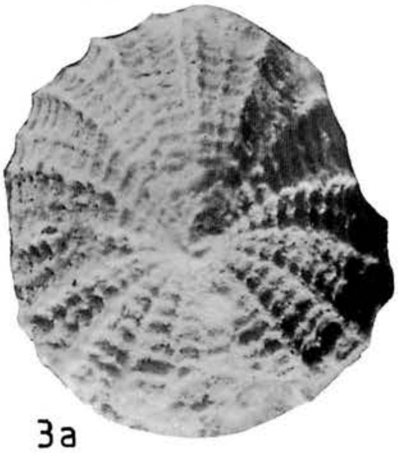
2b

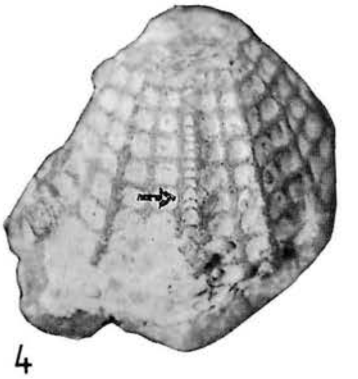

2a


2c


3a


3b


3c


4


6a


5


7a


6b


7b

having similarly raised selenizone, but can be distinguished by stronger collabral ribs and absence of fine axial threads between the two stronger ones. Apex of the *E.* (*T*). *orthogonia* is also more strongly curved.

Emarginula (*Altomarginula*) *desnoyersi* Eudes-Deslongchamps, 1842 (Knight *et al.*, 1960, figs. 140, 7a-b), is a Bathonian form that differs in shell size and ornamentation. The present species is larger in size, less elevated with raised selenizone and bears spiral elements, which the European form lacks.

The present species differs from *Emarginula* (*Emarginula*) *vadanaei* Toni, 1912 (Szabo, 1980, pl. 4, figs. 10-11; Conti and Monari, 1991, pl. 7, figs. 7-14), in shell size, ornamentation and curvature of the apex. The Bakony and Turkey specimens are smaller in size. Although they have similar slightly elevated selenizone, it extends for only about one-third of the shell height while in the present form it extends more than three-fourths of the shell height from the base. Furthermore, the present species is ornamented with strong longitudinal ribs and its apex is less curved.

Emarginula lepsuisi Gemmellaro, 1878 is another comparable Jurassic form. It can, however, be differentiated from the Kutch form by its convex shell along the selenizone and fewer ribs (see also Szabo, 1980).

Etymology.—The species is named in honour of late Karun Chandra Mitra, a renowned palaeontologist of the Department of Geological Sciences of Jadavpur University.

Suborder Trochina
Superfamily Trochacea
Family Turbinidae
Subfamily Angariinae
Genus ***Helicacanthus*** Dacqu in Wenz, 1938

Type species.—*Turbo thurmanni* Pictet and Campiche, 1863; original designation.

Helicacanthus chanda sp. nov.

Figures 4-6, 7; 5-1, 2

Material.—Ten specimens, JUM/g 35-44. JUM/g 35 is designated holotype; the rest are paratypes. All specimens have their original shell preserved. Only two specimens are intact and the rest are lacking mostly their apical parts. All were collected from Bed 1, Jumara.

Diagnosis.—Average-sized *Helicacanthus* (about 18 mm high); height greater than diameter; a broad nearly flat ramp on upper surface, outer whorl concave; dense, fine prosoclinal striae on whorls and within umbilicus; both carinae and cords may be granulated.

Description.—Shell of medium size, maximum height about 18 mm; thick, phaneromphalous turbiniform with height slightly greater than diameter. Apical angle ranges between 47° and 54°. Whorl at least 4 in number including protoconch and separated by strongly grooved suture. Protoconch dome-shaped, consisting of one and a half smooth whorls. Spire low, conical occupying about one-third of shell height. Body whorl large, rapidly increases in diameter, width slightly greater than height. A broad, nearly flat ramp on upper surface of whorls. Outer face of whorls narrow, slightly concave, bordered by two strong spiral carinae, first one being stronger. Prominent spiral cords 3 to 4 in number appear after second angulation and are restricted at base. Cords and occasionally carinae show regular granulation. Dense prosoclinal striae present on whorls and also within umbilicus. Aperture orbicular in outline, both outer and inner lips thick and base rounded.

Discussion.— The characteristic shell outline, presence of two strong carinae on outer whorls and apertural shape assure its generic position. The present species is distinguishable from the type species *Helicacanthus thurmanni* (Pictet and Campiche, 1863), (Knight *et al.*, 1960, fig. 204, 2) from the Aptian of Switzerland by its slender form and in ornamental features. The type species is ornamented with numerous spiral cords, which are present between the carinae and also within the umbilicus, whereas in the present species spiral cords are restricted only at the base and umbilicus is ornamented with dense axial threads.

Cox and Arkell (1948-50) mentioned but did not describe one species of this genus, *Helicacanthus tegulatus* (Lycett) (1863, p. 102, pl. XLV, figs. 17, 18), from the Bathonian Forest Marble of England. Besides this, the present form is the second oldest species of the genus which otherwise ranges from the Upper Jurassic to Lower Cretaceous (see Knight *et al.*, 1960).

Etymology.—The species is named in honour of late S.K. Chanda, a famous sedimentologist of the Department of Geological Sciences, Jadavpur University

Family Trochidae
Subfamily Eucyclinae
Genus ***Riselloidea*** Cossmann, 1909

Type species.—*Risellopsis subdisjuncta* Cossmann, 1908; original designation.

← **Figure 4.** **1, 2.** *Colpomphalus jumarense* sp. nov. ×3. **1a-c.** Holotype, from Bed 1, Jumara, JUM/g 19, apical, abapertural and basal views. Note strong collabral ridges and presence of three spiral carinae on body whorl (1b). **2a-c.** Paratype, from Bed 2, Keera, JUM/g 595, apical, apertural and basal views. **3-5.** *Emarginula karuna* sp. nov. Bed 1, Jumara, ×4. **3a-c.** Holotype, JUM/g 71, protoconch missing; apical and two lateral views. **4.** Paratype, apical part damaged, JUM/g 72, oblique lateral view showing selenizone (see arrow). **5.** Paratype, both apical part and peristome damaged, JUM/g 73, oblique lateral view. **6, 7.** *Helicacanthus chanda* sp. nov. from Bed 1, Jumara ×3. **6a, b.** Holotype, complete shell, JUM/g 35, apertural and abapertural views. **7a, b.** Paratype, complete shell, umbilicus showing axial ornamentation (7a), JUM/g 36, apertural and abapertural views.

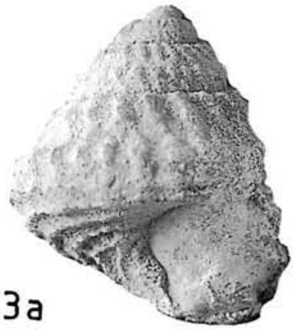

2a


2b


1a


1b


3c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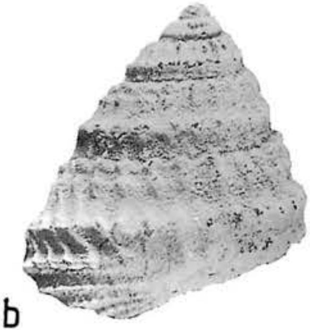
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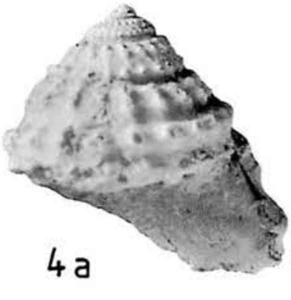
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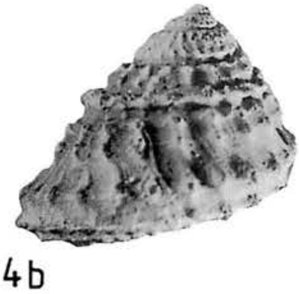
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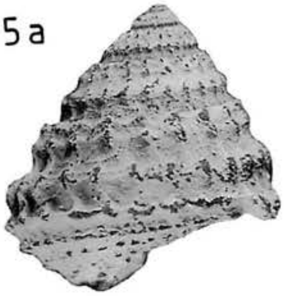
5b

5a




6b


6a

Riselloidea tagorei sp. nov.

Figure 5-3—6

Material.—Over 300 specimens. JUM/g 148 is designated holotype; JUM/g 145-147 and JUM/g 149-166 are paratypes. Most of the specimens have their original shell preserved. All were collected from Bed 1, Jumara.

Diagnosis.—Medium to large-sized *Riselloidea* (10 to 15 mm high). Species shows wide intraspecific variation in shell profile with height greater than diameter changing to diameter greater than height; whorls cyrtoconoid to straight; axial elements stronger than spiral ones; three spiral tuberculate carinae of variable strength and 3 to 4 basal cords with granulation.

Description.—Shell medium to large in size, maximum height being achieved 15 mm; weakly cyrtoconoid to straight; trochiform and anomphalous. Apical angle ranges between 55° to 95°. Shell diameter may be greater or smaller than height. Whorls 4 to 5 in number including protoconch, which consists of two smooth, rounded whorls. Spire conical, low to moderately high, occupying one-fourth to one-third of shell height. Whorls regularly expanded, may be separated by relatively deep-channelled suture. Shell ornamented with three revolving carinae, third one is stronger than other two. First inter area forming a ramp, larger than that of second one which may sometimes be depressed. Relatively weak, prosoclinal riblets intersect carinae and produce pointed tubercles at crossing points. Axial elements running suture to suture, 20 in number on body whorl. Base weakly convex with 3 to 4 strong spiral cords with regular granulation resulting from interception of fine axial growth lines. Peristome is prosocline with thickened columellar lip. Aperture quadrangular to subquadrangular with angulations at middle carina and suture; outer lip thin.

Discussion.—Cossmann (1909) proposed the genus *Riselloidea* and designated his *Risellopsis subdisjuncta* Cossmann, as the type species. The present species resembles the type species in ornamentation and other general features but is relatively larger and has a rounded base.

The present species is very close to *Riselloidea biarmata* (Münster, 1844) (Cox and Arkell, 1948-50, p. 58; Knight *et al.*, 1960, fig. 203, 8) from the Great Oolite Series, England and the Middle Jurassic of Germany. However, it has a wide range of variation particularly in shell outline and larger shell size, quadrangular apertural outline, prosoclinal peristome and convex base. Moreover, it is ornamented with three tuberculate carinae whereas *R. biarmata* bears only two rows of tubercles.

Conti and Fischer (1982) described two new *Riselloidea* species from the Middle Jurassic sequence of Italy. These species are very small in size and differ in some morphological aspects from the present species. *Riselloidea martariensis* Conti and Fischer (1982, pl. 3, figs. 11a-d, 12) differs, besides being small, in having a convex whorl outline and more depressed suture and in variation in number of axial elements.

Riselloidea subreticularis Conti and Fischer (1982, pl. 3, figs. 13a-d, 14), a smaller species than *R. martariensis*, resembles the present form in shell outline, but has a larger aperture, less dense axial ribs and convex whorl outline. In *R. subreticularis*, spiral cords appear only in the last whorl, while they are present right from the early whorls except for the protoconch, in the present species.

R. reticularis (Cossmann *in* Piette, 1864—91) (also see Conti and Fischer, 1982), a Bathonian species, has a close correspondence with the present species. It has comparable radial elements but differs mainly in having 4 spiral carinae instead of three and 5 to 7 basal cords instead of 3 to 4 in the present species. Further, we are not aware of any kind of intraspecific variation within *R. reticularis*.

Riselloidea multistriata (Böckh) (1874, p. 110, pl. VI, fig. 5) (also see Szabo, 1982, pl. 3, figs. 3-6) has a comparable size, but its convex whorls and dense, fine collabral cords distinguishes it from the Kutch form. Moreover, in *R. multistriata* basal cords are fine and more numerous, about 8 against 3 to 4 in the present population

Etymology.—After the great Indian poet, R.N. Tagore.

Riselloidea elongata sp. nov.

Figure 6-1—3

Material.—Seven specimens, JUM/g 138-144. Specimen JUM/g 138 is designated holotype; the rest are paratypes. The specimens have their original shell preserved. The present collection has been made from Bed 1, Jumara.

Diagnosis.—Large-sized *Riselloidea* (about 15 mm high); shell slender, height being twice shell diameter; whorls straight conical and numerous; base flat to weakly convex; two spiral, tuberculate carinae of equal strength, 3 to 4 basal cords with no granulation.

Description.—Shell slender, large, maximum height achieved 15 mm; anomphalous, trochiform; straight conical in outline, with height about twice the shell diameter. Apical angle ranges from 20° to 25°. Whorls numerous, seven in number including protoconch, which consists of two smooth and rounded whorls. Spire moderately long, occupying about half of shell height. Shell ornamented with two spiral carinae, more or less of equal strength, each bordering suture. Axial elements are weakly prosocline, running suture to suture. They are 20 in number on body whorl. Feeble tubercles are formed at intersecting points of trans-

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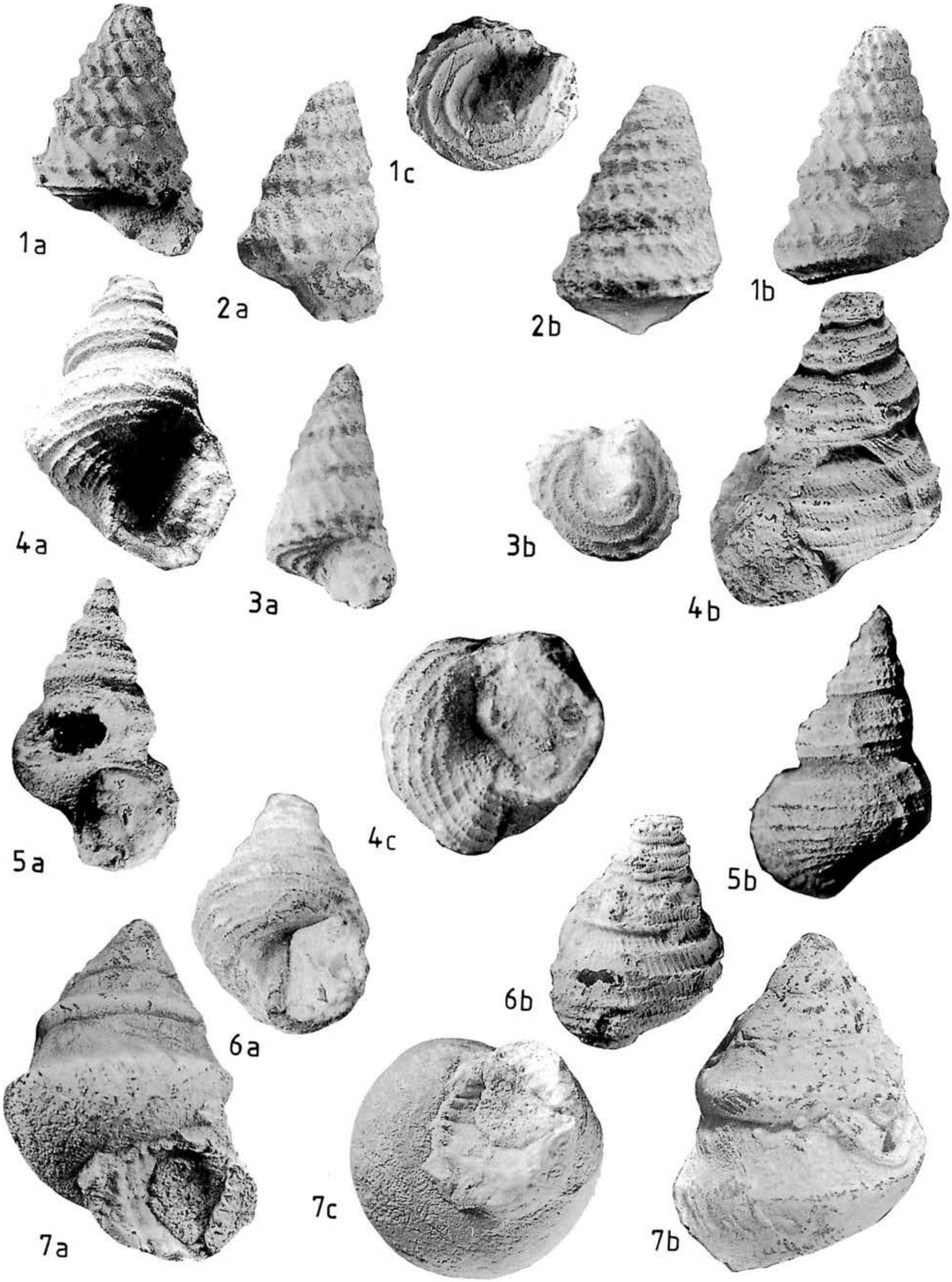
← **Figure 5. 1, 2.** *Helicacanthus chanda* sp. nov from Bed 1, Jamara, ×3. **1a, b.** Paratype, JUM/g 38, apertural and abapertural view; abapertural view (1b) showing dense axial striae. **2a, b.** Paratype, almost complete, JUM/g 39, apertural and abapertural views. Note granulated basal cords in apertural view (2a). **3-6.** *Riselloidea tagorei* sp. nov. from Bed 1, Jumara, ×3. **3a-c.** Holotype, complete shell, JUM/g 148, apertural, abapertural and basal views. **4a-c.** Paratype, complete shell, JUM/g 157, apertural, abapertural and basal views. **5a, b.** Paratype, complete shell, JUM/g 147, abapertural and basal views. **6a, b.** Paratype, complete shell, JUM/g 159, abapertural and apical views.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7a
7b
7c

verse and longitudinal elements. Base flat to weakly convex with 3 to 4 faint spiral cords. No granulation on cords at crossing points when intersected by very feeble axial growth lines. Aperture almost circular to subquadrangular; columellar lip thickened by callus; base narrow and slightly rounded.

Discussion.—*Riselloidea elongata* sp. nov. comes from the same stratigraphic level and geographic locality as *Riselloidea tagorei* sp. nov. These two species are comparable in having more or less similar size, conical and straight-walled shell outline, and nearly flattened base. *R. elongata* however, differs from *R. tagorei* in being more slender and high-spired. It has also more whorls and less shell rugosity, with only two rows of tubercles instead of three in *R. tagorei*. Besides, basal cords of *R. elongata* lack granulations, which are typical of *R. tagorei*.

The Kutch species has a close resemblance with *Riselloidea biarmata* (Münster, 1844), described from the Great Oolite Series, England and the Middle Jurassic, Germany (Cox and Arkell, 1948-50, p. 58, Knight *et al.*, 1960, fig. 203, 8). The present species, however, can be distinguished by its larger size, slender shape and absence of granulation on the basal cords.

The present species resembles *Riselloidea periniana* (d'Orbigny) (1853, p. 266, pl. 310, figs. 12, 13) (also see Fischer, 1997, p. 103, pl. 21, fig. 24) from the Plansbachian of France. Both species have a similar higher shell outline, high spire and surface ornamentation with two rows of tuberculate carinae. However, the older European form is smaller in height, having deeply grooved suture and more oblique axial riblets. Moreover, it has granulation at the basal cords, a feature which is absent in the present species.

Etymology.—After its elongated shape.

Genus **Onkospira** Zittel, 1873

Type species.—*Turbo ranellatus* Quenstedt, 1858; Original designation.

Onkospira kutchensis sp. nov.

Figure 6-4—6

Material.—Twenty-six specimens. JUM/g 45-70. JUM/g 45 is designated holotype; the rest are paratypes. All the specimens have their original shell preserved. Only two specimens are intact with the rest lacking their apical part. All were collected from Bed 1, Jumara.

Diagnosis.—Average-sized *Onkospira* (13 to 25 mm high); whorls 5 in number including protoconch; spire short; strong spiral cords, 3 to 4 in number throughout ontogeny, basal cords 7 to 8; axial threads very fine, may be absent in some variants; two strong prosoclinal varices on each whorl, showing slight offset in successive whorls.

Description.—Shell medium in size, maximum height achieved about 25 mm; thick, anomphalous and turbiniform with shell diameter about half of shell height. Apical angle ranges between 25° and 32°. Whorls 5 in number including protoconch. Protoconch consists of two smooth and rounded whorls. Spire highly elevated and about half of shell height. Whorls regularly expanding, strongly to slightly convex with sloping ramp. Suture impressed. Surface ornamented with 3 to 4 strong spiral cords throughout ontogeny and fine prosoclinal threads. Both are cancellate at their junction. Second and third cords from suture relatively stronger. Two strong prosoclinal varices located on each whorl and show slight offset on successive whorls. Last varix situated just behind outer lip. Basal cords are relatively fine and closely spaced, 7 to 8 in number. Aperture oval with its height slightly greater than width. Outer lip rounded and inner lip arcuate and reflected. Both lips are thick.

Discussion.—The turbiniform shell outline, convex whorl sides, predominance of spiral ornamentation and presence of varices are the characteristic features of *Onkospira*. From the above morphological description the generic position of the present species seems secure. So far, species of *Onkospira* have been reported from Europe and Japan ranging in age from the Upper Jurassic to Lower Cretaceous. The discovery of the present species brings down the lower limit of stratigraphic range of *Onkospira* as far as the Upper Bathonian.

The present form resembles *Onkospira gracilis* Zittel, 1873 (Knight *et al.*, 1960, fig. 203, 1) reported from the Tithonian of the Czech Republic. But *O. gracilis* is characterised by strongly convex, more numerous whorls, prominent collabral riblets and varices showing alignment on successive whorls.

The present species differs from *Onkospira haipensis* described by Kase (Kase, 1984, pl. 11, figs. 9-12) mainly in shell ornamentation. In some variants of *O. haipensis*, spiral cords are strong and tubercles are present at the intersection.

Etymology.—After Kutch, western India, from where the specimens have been collected.

? Subfamily Calliostomatinae
Genus **Proconulus** Cossmann, 1918

← **Figure 6.** 1-3. *Riselloidea elongata* sp. nov. from Bed 1, Jumara, ×3. **1a-c.** Holotype, JUM/g 138, apical part damaged; apertural, abapertural and basal views; note two rows of spiral carinae and basal cords lacking granulation. **2a, b.** Paratype, apical part damaged, JUM/g 139; apertural and abapertural views. **3a, b.** Paratype, complete shell, JUM/g 141, apertural and basal views. **4-6.** *Onkospira kutchensis* sp. nov. from Bed 1, Jumara, ×3. **4a-c.** Holotype, apical part damaged, original shell preserved, JUM/g 45, apertural, abapertural and basal views; note slight offset of varices in last two whorls (4b). **5a, b.** Paratype, complete shell, JUM/g 46, apertural and adapertural views. **6a, b.** Paratype, apical part damaged, original shell preserved, JUM/g 47, apertural and abapertural views. **7a-c.** *Proconulus jadavpuriensis* sp. nov. from Bed 1, Jumara, ×3, Holotype, complete shell, JUM/g 76, apertural, abapertural and basal views; note abapertural view showing very fine opisthocline threads near aperture.

Type species.—Trochus guillieri Cossmann, 1885; original designation.

Proconulus jadavpuriensis sp. nov.

Figures 6-7; 7-1, 2

Material.—Sixty-two specimens. JUM/g 76-137. Specimen JUM/g 76 is designated holotype; the rest are paratypes. Most of the specimens are intact and have the original shell preserved. JUM/g 81-86 were collected from Bed 7 and the rest are from Bed 1 of Jumara.

Diagnosis.—Average-sized *Proconulus* (15 to 20 mm high); smooth shell; whorls less numerous; flat in early stage, feebly concave later, periphery marked by angular keel; base feebly convex.

Description.—Shell small, maximum height 20 mm; anomphalous, thick, conical; acute juvenile whorls; trochiform with height slightly greater than diameter. Apical angle ranges between 50° and 60°; whorls less numerous, five in number including protoconch, separated by impressed suture. Protoconch conical, consists of two smooth, rounded whorls. Spire moderately high, occupying about one-third of shell height. Whorls flat or feebly concave in early stage, concavity increases during ontogeny. Periphery is sharply angulate like a carina, which occurs just above suture. Body whorl large with diameter slightly greater than height. Shell smooth except for some fine prosocline threads, especially prominent near aperture of adult specimens; base rounded. Aperture circular to subquadrangular, width of aperture slightly greater than height, base of aperture rounded. Both outer and inner lips thick, collumellar part has a thick callus.

Discussion.—The shell shape of the present species has a close correspondence with some species of *Epulotrochus* Cossmann, especially *E. epulus* (d'Orbigny, 1850). Szabo (1981), while describing the Hungarian Lower to Middle Jurassic gastropods, also observed the same similarites. Some smooth variants of his *Proconulus epuliformis* Szabo (1981, pl. 1, figs. 6-8) shows a striking resemblance to *E. epulus*. Szabo (1981) and Kase (pers. comm., 1992) acknowledged the need for a revision of these genera. The present species has thick callus and from the nature of the nucleus whorl and ornaments it is retained within *Proconulus*.

Present study includes numerous specimens, which enable us to examine both ontogenetic and intraspecific variations. The population shows low intraspecific variability.

The present species shows a resemblance in shell shape to *Proconulus rimosus* Szabo (1981, pl. 1, figs. 9-13), though the latter species has a wide range of variation in this respect. However, *P. rimosus* is an ornamental form with prominent spiral elements, which are even tuberculated in the early stage. The present species has a smooth shell except for some fine, faded axial threads which appear only at the adult stage in some variants. It is further characterised by slightly concave whorl and marked angular keel just above the suture.

Proconulus jadavpuriensis sp. nov. closely resembles *Proconulus brutus* (d'Orbigny) (1853, p. 283, pl. ccxv, figs. 13-16) (Cossmann, 1885, p. 285, pl. vii, figs. 23, 24; Cox and Arkell, 1948-50, p. 59; also see Fischer, 1997, p. 112, pl. 19, figs. 6, 7) described from the Great Oolite of England. The latter species has a similar shell and apertural shape with a convex base, but differs in shell ornamentation, being characterised by five strongly tuberculate spiral bands and a very obscure suture while the present species has a smooth shell and very impressed suture. Besides, the present species has a concave whorl outline.

Proconulus epuliformis has a more or less similar whorl outline and smooth or feebly ornamented shell but differs in having a high conical shell, more numerous whorls and flattened base. Moreover, the present species is characterised by a well marked angular keel and impressed suture.

P. jadavpuriensis sp. nov. exhibits some degree of resemblance to the upper Bajocian species *Proconulus acanthus* (d'Orbigny) (1853, p. 273, pl. 312, figs. 9-12) (also see Fischer, 1997, p. 107, pl. 19, figs. 4a, b, 5) described from Port-en-Bessin (Calvados) in overall shell outline with angular periphery, size and apical angle. However, the present species differs from the latter in having a distinctly concave whorl outline, impressed suture and smooth shell except for some prosocline threads near the aperture, while the latter is distinguished by straight whorl outline and finely granular spiral cords.

Etymology.—After Jadavpur University.

Suborder Neritopsina
Superfamily Neritacea
Family Neritopsidae
Subfamily Neritopsinae
Genus **Neritopsis** Grateloup, 1832
Subgenus **Neritopsis** s. str.

Type species.—Neritopsis moniliformis Grateloup, 1832; original designation.

Neritopsis (Neritopsis) patchamensis sp. nov.

Figure 7-3—5

Material.—Eight specimens. JUM/g 1-3, 5, 8-11. Holotype, JUM/g 1; the rest are paratypes. The specimens have their original shell preserved and were collected from Bed 1 of Jumara.

Diagnosis.—Small *Neritopsis* (8 to 11 mm high); whorls rounded with wide, gently sloping ramp; spire slightly protruding; whorls cancellated, both axial and spiral cords of equal strength, axial cords numerous (12 to 16) on body whorl; aperture very large, axially ovate with slight angulation near suture.

Description.—Shell small in size, maximum height about 11 mm, moderately thick, subglobose; height of shell about three-fourths of shell diameter. Apical angle ranges between 110° and 120°. Whorls rounded with wide gently sloping ramp, slightly angulate at suture. Protoconch not well discernible, but appears to be smooth and consisting of about two whorls. Spire short, body whorl very large and increases rapidly in diameter. Suture impressed, running along a furrow. Whorls cancellated throughout later ontogeny, resulting from intersection of axial and spiral cords of equal strength. Axial cords 12 to 16 in number on body whorl, prosocline in beginning but becoming gentler during ontogeny. Spiral cords 10 to 14 in number on body whorl and irregularly spaced. Aperture very large, axially ovate and slightly angulate near suture ; inner lip slightly thickened by callus accompanied by a shallow furrow running parallel to it and resulting in a pseudoumbilicus.

Discussion.—*Neritopsis* (*Neritopsis*) *patchamensis* sp. nov. shows some degree of resemblance to the Lower and Middle Jurassic forms from Europe (Szabo, 1982 ; Conti and Szabo, 1989). It differs from *Neritopsis* (*Neritopsis*) *papodensis* Szabo (1982 pl. 1, figs. 6-9) in having a less protruded spire and less convex whorl surface with relatively broader ramp. It is coarsely ornate with stronger axial elements than in *N.* (*N*). *papodensis*.

The present species, although it resembles strongly *Neritopsis abbas* Huddleston (1894, p. 341, pl. XXVII, figs. 11a-c) (also see Conti and Szabo, 1989, pl. 1, figs. 10-11) in shell shape, is much smaller in size with a less protruded spire. In *N. abbas*, spiral cords dominate with very faint axial growth lines near the aperture, but in the present species, axial elements are equally prominent and cut across the spiral cords resulting in a conspicuous cancellate ornamentation.

Neritopsis (*Neritopsis*) *spinigera* Szabo (1982, pl. 1, figs. 10-18) has been described on the basis of mostly damaged specimens. It, however, can be distinguished by its bicarinate ornamentation, long spine and fewer and stronger axial elements.

The Middle Jurassic (Bajocian—Bathonian) form *Neritopsis* (*Neritopsis*) *bajocensis* d'Orbigny (1852, p. 223, pl. 300, figs. 8—10 ; Fischer, 1997, p. 86, pl. 17, figs. 14a—c, 15a—c) can be compared with the present form in general globose shape and apertural outline. Close examination reveals that in the present species the height is less than the diameter while in the European form it is just the reverse. Further, the Kutch species has strongly cancellated ornamentation in the later ontogeny resulting from intersection of equally strong axial and spiral cords, but the European form has dominant spiral cords with very feeble axial elements. Besides, the Kutch species is less than half the size of *N.* (*N.*) *bajocensis*.

Etymology.—Refers to the Patcham Formation in which the species is exclusively confined.

Subgenus **Hayamiella** Kase, 1984

Type species.—*Neritopsis* (*Hayamiella*) *japonica* Kase, 1984 ; original designation.

Neritopsis (Hayamiella) sankhamala sp. nov.

Figure 7-6, 7

Material.—Ten specimens, JUM/g 4, 6, 7, 12-18. JUM/g 6 is designated holotype ; the rest are paratypes. The specimens have their original shell preserved. The present collection has been made from Bed 1 of Jumara.

Diagnosis.—Small size for genus (6 to 8 mm high) ; narrow ramp, whorls bordered by subcarinate angulation ; spire slightly protruding, suture impressed with a subsutural channel ; cancellate ornamentation, axial element developed into varices, irregularly spaced, 6 to 9 ; spiral cords 9 to 13 ; prominent tubercles at intersection of spiral and axial elements ; aperture circular to slightly axially ovate.

Description.—Shell small in size, maximum height achieved 8 mm ; low-spired and naticiform. Shell diameter greater than height. Apical angle ranges between 105° and 122°. Narrow ramp, whorls bordered by subcarinate angulation. Protoconch seemingly smooth but number of whorls not discernible, may consist of more than one whorl, spire slightly protruding. Body whorl large, rapidly widening. Suture impressed with a prominent subsutural channel. Cancellate ornamentation with much stronger axial elements. Varices become stronger and interspace increases ontogenetically. Varices 6 to 9 in number on body whorl and orthocline. Spiral cords 9 to 13, strength varies, stronger ones irregularly intercalate with finer cords. Fine but prominent tubercles appear at intersection of spiral cords and varices. Aperture very large, near circular to slightly ovate axially ; inner lip with narrow callus. Furrow running parallel to inner lip, resulting in a pseudoumbilicus.

Discussion.—Kase (1984) erected a subgenus *Hayamiella* within the genus *Neritopsis* and described *N.* (*H.*) *japonica* Kase (p. 84, pl. 8, figs. 6a-c, 17) from the Upper Aptian of Japan as type species. He distinguished *Neritopsis* s. str. from *Hayamiella* on the basis of the presence of spiral cords, larger shell size and wider shell outline. He also admitted that distinction may not be very clear as there exist some intermediate forms (see also Hayami, 1960). The present species is characterised by small shell size, globose shape and coarsely cacellated ornamentation with much stronger axial elements, but it has a wider shell outline. Because of the similarities in many diagnostic characters we place the present species within the subgenus *Hayamiella*.

The present species has similarities with the type species *N.* (*H.*) *japonica* in many important morphological characters like small shell size, globose shape and cancellated ornamentation, so that their inclusion within the same subgenus is justified. However, *N.* (*H.*) *sankhamala* is still smaller in size, wider in outline and having fewer but stronger axial elements than *N.* (*H.*) *japonica*. Moreover, the type species comes from a higher stratigraphic horizon (Aptian).

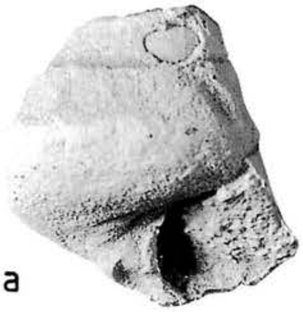
The present species is closer to *Neritopsis* (*Neritopsis*) *patchamensis* sp. nov., but is relatively smaller in diameter with a narrower ramp area. Its axial elements are stronger and fewer on body whorl. Besides, it differs in having subcarinate angulation, tubercles, a circular aperture and a subsutural channel.

Neritopsis (*Hayamiella*) *sankhamala* sp. nov. is comparable to some European forms. It is close in size to *Neritopsis dumortieri* Conti and Szabo (1989, pl. 1, figs. 12-13) from the Southern Alps. This European species is based on the monotypic holotype, which is a damaged specimen. *N. dumortieri* bears three rows of spiral carinae and transverse elements of equal strength. Long hollow spines are present at the intersection point. The present species, on the other


2a


1b


2b


1a


3 a

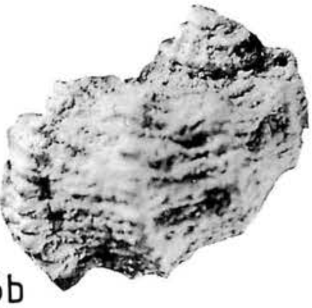

3 b


3 c


5


6 a


4


6 b


7a


7c


7b

hand, possesses strong varices and small tubercles.

Neritopsis (*Neritopsis*) *spinigera* Szabo (1982, pl. 1, figs. 10-18) differs mainly in having a more closely ornate form with long spines and more protruded spire.

The present species shows a remarkable correspondence in size, shape and ornamentation to *Neritopsis* (*Neritopsis*) *elegantissima* Hörnes (1853, p. 763) (Szabo, 1982, pl. 1, figs. 1-3), but closer examination reveals that the Kutch form has a circular aperture, varices 6 to 9 in number, subcarinate angulation and tubercles. Moreover, *N.* (*N*). *elegantissima* comes from a much older horizon of the Lower Jurassic (U. Sinemurian).

Neritopsis (*Hayamiella*) *sankhamala* sp. nov. has a close resemblance to *Neritopsis guerrei* Hébert and Deslongchamps (1860, p. 185, pl. I, figs. 4a-d) described from the Great Oolite of England (see also Cox and Arkell, 1948-50, p. 64). One variant even appears to be more close in having similar distant and unevenly placed axial elements. The present species, however, can be distinguished by its relatively distant spiral cords, stronger varices and presence of prominent tubercles.

Etymology.—Refers to an Indian ornament—a chain of small and globular gastropod shells

Genus **Hayamia** Kase, 1980

Type species.—*Hayamia rex* Kase, 1980 (in Kase and Maeda, 1980); original designation.

Hayamia mitra sp. nov.

Figure 8-1—3

Material.—Five specimens, JUM/g 31-34, 597. JUM/g 31 is designated holotype, the rest are paratypes. JUM/g 32, 33 are internal moulds, the holotype and one of the paratypes (JUM/g 597) represent composite state of preservation. JUM/g 34 with shell remains. JUM/g 31, 33 were collected from Bed 1, JUM/g 597, from Bed 6, JUM/g 32, from Bed 7 of Jumara; JUM/g 34 from Bed 2, Keera (see Bardhan *et al*., 1994).

Diagnosis.—Medium-sized *Hayamia* (about 24 mm high); height less than diameter, spire slightly protruding, suture impressed with prominent subsutural channel, aperture large; prominent, numerous spiral cords with finer subordinate ones in between.

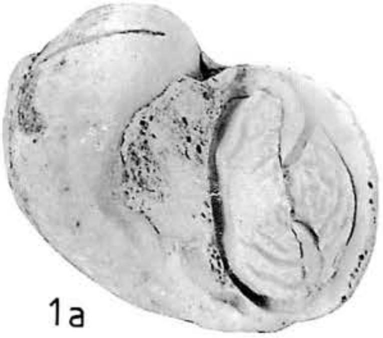
Description.—Shell medium-sized, maximum height achieved 24 mm; phaneromphalous; moderately thick, ovate and naticiform in outline with height of shell is about three-fourth of shell diameter. Apical angle ranges between 120° and 160°. Whorls rapidly expanding, convex in outline; whorls make two and a half volutions. Protoconch is not well discernible. Spire slightly protruding, about one-eighth of shell height. Body whorl very large, increases rapidly in diameter with a wide and weakly convex sutural ramp. Suture impressed with subsutural channel. Shell is ornamented with prominent and widely spaced spiral cords and several subordinate ones in interspaces; spiral elements are intercepted by very faint axial growth lines observed particularly near peristome; internal mould smooth. Aperture very large, elliptical in outline and expanded in direction oblique to axis. Height of aperture slightly greater than width. Both outer and inner lips thin and entire. Thin and somewhat obscure callus covers inner lip. Operculum thick, solid and elliptical in outline, its outer surface ornamented with both radial and concentric elements, abaxial part broken, but its adaxial margin has a curvaceous chevron shaped-outline.

Discussion.—Kase (1980) introduced the genus *Hayamia* (Kase and Maeda, 1980, pl. 35, figs. 3—10) in the family Neritopsidae from the Lower Cretaceous of central Japan to distinguish it from *Neritopsis*. The genus also includes some previously described Jurassic and Cretaceous species of *Neritopsis*. The main features which characterise *Hayamia* are spiral striae with or without costellae, absence of parietal tubercles and an elliptical operculum lacking any quadrangular process at the adaxial edge; although there is a certain amount of similarity with *Neritopsis*, these features probably confer an independent status to the genus. While *Hayamia* is included in the subfamily Neritopsinae, it has opercular feature resembling that of *Naticopsis* belonging to the subfamily Naticopsinae. Thus, it appears that *Hayamia* occupies an intermediate position between *Neritopsis* and *Naticopsis*. The actual phylogenetic relationship among the three genera is not yet clear (Kase. pers. comm., 1999) and has to be worked out by detailed study of properly weighted characters linking and separating them. In consonance with its genus the Kutch species *Hayamia mitra* sp. nov. has also a similar status and presently we place the species provisionally under the subfamily Neritopsinae.

The Kutch species displays some resemblance to the type species *Hayamia rex* Kase (in Kase and Maeda, 1980, pl. 35, figs. 5—10) in size and surface ornamentation. But it differs from the latter in its overall shape with shell diameter measuring more than height, less protruded spire and slightly asymmetric elliptical operculum. *Hayamia chosiensis* Kase (in Kase and Maeda, 1980, pl. 35, figs. 3—4) also bears some similarity with the present species, but differs in having more dense spiral striae, more protruded spire and circular aperture with curved angulation at the adapical part.

Etymology.—The species is named in honour of late K.C. Mitra, a renowned palaeontologist in the Department of

← **Figure 7.** **1, 2.** *Proconulus jadavpuriensis* sp. nov. from Bed 1, Jumara, ×3. **1a, b.** Paratype, broken at apical part, JUM/g 77, apertural and basal views. **2a, b.** Paratype, peristome slightly damaged, JUM/g 79, apertural and abapertural views. **3-5.** *Neritopsis* (*Neritopsis*) *patchamensis* sp. nov. from Bed 1, Jumara, ×3. **3a-c.** Holotype, JUM/g 1, apertural, abapertural and apical views; apical view showing closely spaced axial cords. **4.** Paratype, JUM/g 3, apical view. **5.** Paratype, body whorl broken, JUM/g 9, abapertural view. **6, 7.** *Neritopsis* (*Hayamiella*) *sankhamala* sp. nov. from Bed 1, Jumara, X4. **6a, b.** Holotype, JUM/g 6, apical and abapertural views showing distant and strong axial cords. **7a-c.** Paratype, young shell, JUM/g 16, apertural, abapertural and apical views.


1a

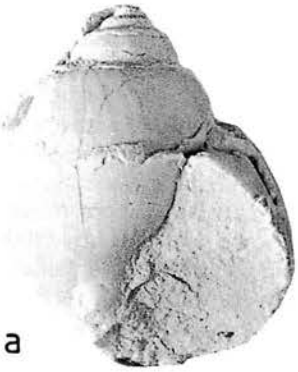

1b

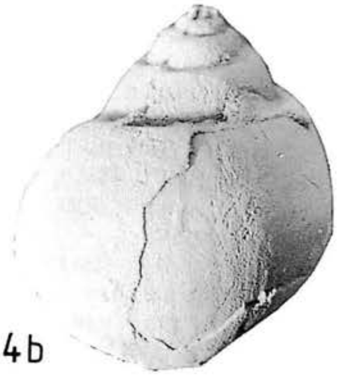

1c


2a


2b


3


4a


4b


5


6a


6b

Geological Sciences of Jadavpur University.

Order Caenogastropoda
Superfamily Naticacea
Family Naticidae
Subfamily Globulariinae
Genus **Globularia** Swainson, 1840

Type species.—*Ampullaria sigaretina* Lamarck, 1804; original designation.

Globularia spathi sp. nov.

Figure 8-4—6

Material.—Eight specimens. JUM/g 23-30. Holotype, JUM/g 23; the rest are paratypes. Three specimens are intact and rest are broken. Mostly internal moulds, in three specimens (JUM/g 23, 24, 25) part of the original shell is preserved. JUM/g 23 was collected from Bed 1, JUM/g 24, 26-30 from Bed 7 of Jumara and JUM/g 25 from Keera.

Diagnosis.—Medium-sized *Globularia* (about 30 mm high); spire relatively high; suture impressed throughout; umbilicus narrowly open, sheath narrow; aperture subelliptical; ornamented with fine prosoclinal growth lines conspicuous near aperture.

Description.—Shell of medium size, maximum height about 30 mm; globose, moderately thick, phaneromphalous and naticiform in outline with height slightly smaller than diameter. Apical angle ranges from 95° to 106°. Whorls at least five in number, separeted by deeply channelled suture bordered by sharp periphery. Protoconch not discernible. Spire relatively high, obtusely conical, occupying about one-fourth to one-sixth of shell height. Body whorl with height slightly higher than diameter. Whorls convex, angulation present near suture. Whorl surface ornamented with fine prosoclinal growth lines conspicuous near aperture. Aperture wide, subelliptical in outline, with height nearly twice width, acute above and broadly rounded below. Parietal area covered by thick callus. Umbilicus narrowly opens; sheath narrow.

Discussion.—In a recent major taxonomic revision of the family Naticidae, Kabat (1991) has stabilised many family and genus level names. He removed *Natica fluctuata* G.B. Sowerby, 1825 from *Globularia* and designated it as the type species of *Cernina* Gray, 1847.

This is the largest naticiform species collected from Kutch. *Globularia* (*Nanggulania*) *puruensis* (Martin, 1914) (Wenz, 1941, fig. 2933) has a very short spire, both axial and spiral threads and a large aperture. In the present species, the spire is comparatively long, only prosoclinal growth lines are present as surface ornamentation and the aperture is smaller than that of *G.* (*N.*) *puruensis*.

The present species can be compared with *Globularia* (*Globularia*) *izumiensis* Kase (1990, figs. 2.16-22, 2.25). Kase's species has a shell diameter greater than the height, low spire, and weakly impressed suture in early whorls. Further, it has a flattened upper whorl surface and subovate aperture. In contrast, the present species has a shell diameter smaller than its height, a more protruding spire, and a strongly impressed suture all through during growth. Aperture is subelliptical and whorls have a convex upper surface with angulation near the suture.

The present species resembles *Globularia rupellensis* (d'Orbigny) (1852, p. 203, pl. 293, figs. 1-3) (see Fischer, 1997, p. 77, pl. 16, figs. 1a, b, 2) from the Oxfordian—Kimmeridgian of Europe in general shell outline, apical angle, apertural shape etc. But the European form is much larger, the largest being about three times that of the present species. However, the obvious difference lies in the nature of the ornamentation. *G. rupellensis* is characterised by spiral striae with punctuation along their alignment, whereas the Indian species is ornamented with fine prosoclinal growth lines. Moreover, the suture of the present species remains deeply impressed all through ontogeny.

The present species is comparable with *Globularia zangis* (d'Orbigny) (1852, p. 198, pl. 291, figs. 10-11) (also see Fischer, 1997, p. 74, pl. 15, fig. 9) from the Callovian of France but differs in having a smaller shell size, higher apical angle and flatter outer whorl surface in early ontogeny. The ornamental aspects, however, cannot be compared since the holotype of the European form is an internal mould.

A close correspondence can be observed between the present species and *Globularia*? sp. described by Sohl (1965, pl. 4, figs. 10-15) from the Middle Jurassic Carmel Formation of Utah, North America. Sohl's specimens are undoubtedly *Globularia* with the diagnostic narrow sheath. Sohl compared them with some British Jurassic gastropods (Cox and Arkell, 1948-50, p. 83). His form is similarly high-spired like the present species, but is smaller and less globose. The smoothness of the American specimens, however, may be attributed to complete silicification, which might have destroyed the finer details of ornamentation.

Etymology.—Named in honour of L.F. Spath, a famous palaeontologist.

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← **Figure 8. 1-3.** *Hayamia mitra* sp. nov. ×2. **1a-c.** Holotype, JUM/g 31, from Bed 1, Jumara, apertural, abapertural and apical views; mostly internal mould, part of shell remains near aperture, apical part damaged, well preserved operculum. **2a, b.** Paratype, internal mould, from Bed 1, Jumara, JUM/g 33, abapertural and apical views. **3.** Paratype, from Bed 2, Keera, JUM/g 34, with shell remains, showing spiral ornaments of variable strength, abapertural view. **4-6.** *Globularia spathi* sp. nov. ×2. **4a, b.** Holotype, from Bed 1, Jumara, JUM/g 23, mostly shell remains, showing axial ornamentation; apertural and abapertural views. **5.** Paratype, from Bed 7, Jumara, JUM/g 24, abapertural view. **6a, b.** Paratype, young shell, internal mould, from Bed 7, Jumara, JUM/g 26, apertural and abapertural views.

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Hilgendorf's planorbid tree–the first introduction of Darwin's Theory of Transmutation into palaeontology

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Abstract. **Franz Hilgendorf (1839-1904)'s palaeontological studies on the Miocene planorbid snails of the Steinheim basin (Germany) frame his scientific work from his dissertation in 1863 to his last publication on this subject in 1901. Hilgendorf discovered that the different planorbids are not mixed in each layer, and noticed gradual transitions between different morphs of successive layers. These findings led to his hypothesis of species transmutation illustrated by his planorbid tree. This was the first phylogenetic tree reconstructed on the basis of real fossil evidence, and therewith it was the first palaeontological example of Darwin's Theory of Transmutation. Although Hilgendorf did not refer to Darwin emphatically, he can be called the first one who introduced Darwin's Theory of Transmutation into palaeontology.**

Key words: Hilgendorf, phylogenetic tree, planorbids, Steinheim, theory of transmutation

Introduction

Franz Hilgendorf is famous mainly for his zoological work, of which the Hilgendorf Exhibition (Yajima, 1997, 1998) focused on his merits for ichthyology and fishery sciences in Japan. However, his palaeontological work is no less important. Hilgendorf started his scientific career with a palaeontological study on the Miocene planorbid snails of the Steinheim basin. This was the subject of his dissertation (Hilgendorf, 1863) and of his first publication (Hilgendorf, 1866), and although he was later on mainly concerned with zoological subjects, the Steinheim snails remained on his mind for the rest of his life. His last paper on the Steinheim snails was published three years before his death (Hilgendorf, 1901). Thus, the planorbid studies frame his scientific work.

Already in his first study Hilgendorf recognised gradual transitions between the snails of successive layers. He documented and interpreted these findings in his first publication with a phylogenetic tree, which is the first palaeontological documentation of species transmutation. His hypothesis, heavily disputed at that time, was largely confirmed over the last two decades (Mensink, 1984; Gorthner, 1992; Povel, 1993; Nützel and Bandel, 1993; Finger, 1998).

Although Hilgendorf's findings were most important for the discussion of Darwin's Theory, which was published only few years before (Darwin, 1859), Hilgendorf did not refer emphatically to Darwin in his papers. On the other hand, Darwin himself mentioned Hilgendorf in his sixth edition of the 'On the origin of species..', published in 1872, within Chapter 10 (On the imperfection of the geological record), subchapter 'On the absence of numerous intermediate varieties in any single formation', as follows: "... Hilgendorf has described a most curious case of ten graduated forms of *Planorbis multiformis* in the successive beds of a fresh-water formation in Switzerland" [wrong geographic information by Darwin]. Hilgendorf's historical role has been already recognised by Abel (1929), and the significance of Hilgendorf's studies from a Neo-Darwinian point of view is discussed in detail by Reif (1983a, 1983b, 1985, 1986).

To assess whether Hilgendorf was familiar with Darwin's Theory, the present paper gives a brief chronological survey of Hilgendorf's planorbid studies, paying special attention to remarks on Darwin and Darwinism. Finally, a brief account of the research on the Steinheim snails after Hilgendorf's death with emphasis on the connection between Hilgendorf's contribution and the latest work at Steinheim is added. Before that, some information about the Steinheim basin, and also the state of knowledge of the Steinheim snails before Hilgendorf are given.

The Steinheim basin–a meteorite crater

The Steinheim basin is situated on the Swabian Alb in southern Germany (Figure 1). Today it is known that the basin was formed by a meteorite impact, about 15 million years ago, which is, expressed in geological time, the Middle Miocene of the Tertiary. The Steinheim basin is a complex impact crater structure with an almost circular outline, and a central uplift, called the central hill. The basin has a diameter of about 3.5 km, and is 120 m deep today. Soon after the impact the crater filled with water and became a lake. It is supposed that the water supply came mainly from the subterranean karst system and from precipitation. How

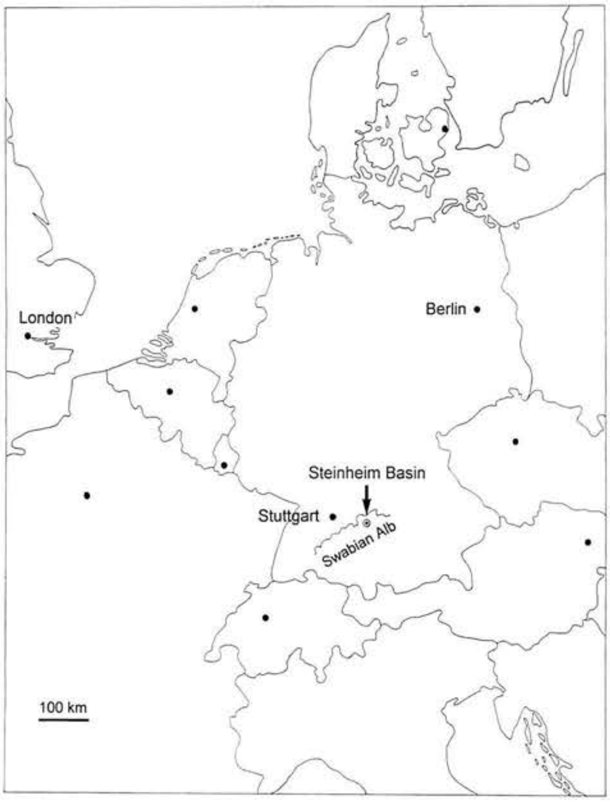

Figure 1. Location of the Steinheim basin.

long the lake actually existed is not exactly known. Between some hundreds of thousands to two million years are suggested. This is what we today call a long-lived lake (Gorthner, 1994). At the end of the lake period the basin was completely filled with lake sediments. The fact that we can recognise the basin again today is due to partial erosion during the Quaternary, the last two million years. However, the lake sediments preserved reach a thickness of 30 to 40 meters, and are very rich in well preserved fossils. About 100 species of fossil plants and more than 250 species of fossil animals have been found so far. The snails comprise about 100 species, of which the planorbids are the most abundant group.

The knowledge of the Steinheim snails before Hilgendorf

In 1862 when Hilgendorf started his studies not much was known about the Steinheim basin, neither about its origin nor its palaeontology. However, the occurrence of amazing quantities of calcareous shells within the Steinheim sands was documented for the first time already about 150 years before, by the physician Lentilius (1711). Lentilius was fascinated by the amount and multiformity of these shells, and it seemed to him enigmatic for what reason God had created such a variety of tiny shells (Figure 2). At that time it was not yet known that these shells are remains of once living animals, what we call today fossils, but it was believed that all species were created by God and remained unchanged since their creation. This dogma of the fixity of species was still universal when the study of von Klein (1847) was publi-

Figure 2. Ensemble of Steinheim snails within the sediment (photo : H. Lumpe, Staatliches Museum für Naturkunde Stuttgart). The width of the shells is about 4 to 5 mm.

shed. Von Klein's study is one of the first scientific studies of the Steinheim snails and reflects the latest knowledge about this subject at the time when Hilgendorf started with his studies. Von Klein distinguished five planorbid species, four of which he allocated to the genus *Planorbis*, and one to the genus *Valvata*. From the latter species, called *Valvata multiformis*, he distinguished five varieties. According to von Klein all of these species and varieties occurred always mixed within each layer of the Steinheim deposits.

Hilgendorf's dissertation and first publication

Before Hilgendorf went to Tübingen he had studied in Berlin for two years. He came to Tübingen in 1862, attracted by Friedrich August Quenstedt, in order to study palaeontology. Quenstedt was a professor of geology and palaeontology at the University of Tübingen, and became famous by his comprehensive stratigraphical investigations of the Jurassic Swabian Alb by means of ammonites. In the autumn of 1862, Hilgendorf accompanied Quenstedt on an excursion to Steinheim, during which he first became acquainted with the Steinheim basin and its snails.

By collecting snails in Pharion's sand pit on this excursion, as well as during the following weeks, Hilgendorf discovered that the different varieties of *Valvata multiformis* are never mixed, but that they occur separately in the different layers. From the lowermost beds onwards he noticed a sequence of flat or planispiral shells to trochispiral shells and again to planispiral ones in the upper parts of the section. Moreover, the different morphs were connected by transitional morphs. Most surprising was the discovery that transitions were not only found between the different varieties of *Valvata multiformis* but also between species of *Planorbis* and some of the varieties of *Valvata* - in other words: he found gradual transitions between two different genera. These findings, of course, were not compatible with the dogma of the fixity of species.

Hilgendorf stated these findings in his dissertation which was submitted in spring, 1863. His dissertation comprises 42 pages, and does not include any figures. In the 1980s Prof. Wolf-Ernst Reif from the Palaeontological Institute of the University of Tübingen discovered a collection of 25 cards of thick paper with Steinheim snails glued onto it which could be clearly identified as Hilgendorf's, because of hand-written captions on the cards (Reif, 1983a).

While each of the cards from no. 1 to no. 17 contains snails of different beds, the cards no. 18 to no. 25 illustrate transitions from one taxon to another, and card no. 24 gives a complete phylogenetic diagram of Hilgendorf's results. Reif (1983a) reconstructed a phylogenetic diagram according to card no. 24 (Figure 3). It corresponds fairly well with Hilgendorf's interpretation given in his dissertation, and shows three modes of species transformation in course of time: 1. gradual transformation, 2. splitting into two daughter species, and 3. fusion of two species.

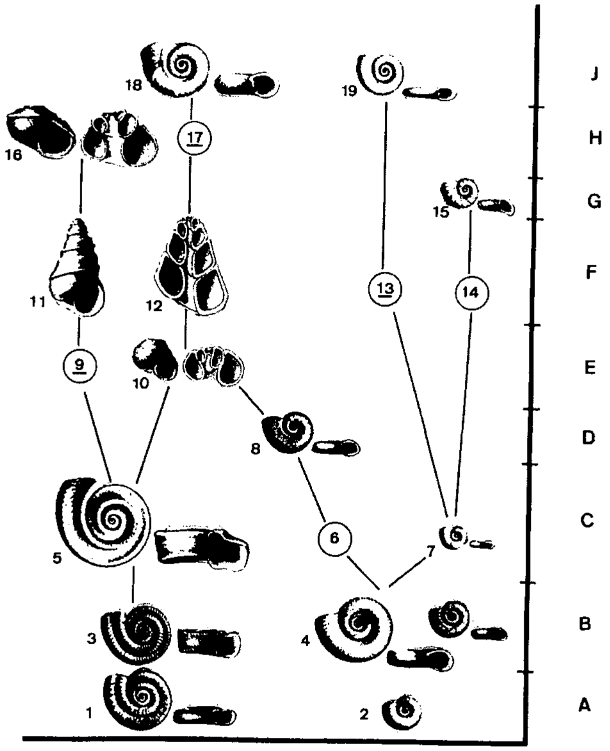

Figure 3. Reconstructed phylogenetic diagram of Hilgendorf's dissertation according to card no. 24. Circled numbers: either not identifiable (underlined) or missing. Examples for species transformation are: 1. gradual transformation: sequence from no. 1 to no. 5; 2. splitting into two daughter species: no. 5 splits into no. 9 and no. 10; 3. fusion of two species: no. 8 and no. 10. Reproduced from Reif (1983a, fig. 3) with permission of Paläontologische Gesellschaft.

Actually, Hilgendorf never seriously suggested fusion of lineages, but merely raised it as a doubtful possibility. Considering the planorbid varieties of the third layer (see Figure 3, layer D), he raises the question of whether fusion of two varieties could have led to this situation (Hilgendorf, 1863, p. 26). However, on the last page of his dissertation, there is an additional note to this subject (Hilgendorf, 1863, p. 42): "Darauf würde das schöne Bild, das Darwin uns vom Zusammenhange der Spezies in einem Zweige-reichen Baume vorführt, nicht passen, die Zweige eines Baumes wachsen nicht wieder zusammen." [This does not fit the nice picture of a tree with many branches which Darwin presented to illustrate the descent of the species - the branches of a tree never fuse again]. This note also exemplifies that Hilgendorf was already acquainted with Darwin's Theory during his first study.

Already after one year at Tübingen Hilgendorf went back to Berlin and continued his studies of natural sciences, especially organic chemistry, but subsequently he concentrated more and more on zoology. He got a position at the Humboldt Museum, and in 1865 he again started an investigation of the Steinheim snails, which was supported by the Royal Prussian Academy of Sciences. This new field work at Steinheim took two months and led to his first publication (Hilgendorf, 1866), which is still today the crucial publication on the Steinheim snails.

This paper is based on a study of a large amount of material collected thoroughly bed by bed from three sand pits around the central hill, as well as from the western margin of the basin. Already the title of this paper: "*Planorbis multiformis* im Steinheimer Süsswasserkalk" [*Planorbis multiformis* within the calcareous freshwater deposits of Steinheim], reveals Hilgendorf's solution of the taxonomic problems, which confronted him through his findings. He considered all planorbid snails found to belong to one species, *P. multiformis*. And the subtitle: "Ein Beispiel von Gestaltveränderung im Laufe der Zeit" [An example of morphological change during time], so to say, gives an explanation for his solution. Moreover, this is also a clear confession of belief in Darwin's Theory of Transmutation.

However, Hilgendorf did not refer to Darwin in this paper. The first part of the publication comprises a detailed stratigraphical description of the sections, and a morphological characterisation of the 19 varieties or subspecies of *P. multiformis* which he distinguished. Using the biostratigraphical distribution of these subspecies, Hilgendorf subdivided the Steinheim deposits into ten zones or beds. In the second part of the paper he discussed the transitions between subspecies of successive beds. By arranging the subspecies in a stratigraphical scheme and marking transitions between two subspecies by a connecting line, Hilgendorf's phylogenetic tree became graphical. The planorbid tree is illustrated in the middle of the lithographic plate at the end of the paper, surrounded with illustrations of all subspecies, including also cross-sections of the snails.

Figure 4 shows a reconstructed and magnified version of this tree. The whole tree arises from a small and planispiral planorbid, called *aequeumbilicatus*, which is considered the founder population. The branch at the right hand comprises ten bigger morphs. Today, this branch is called the 'main branch', and is the most studied and discussed part of the tree so far. Especially the transition between the trochispiral form *trochiformis* and the planispiral form *oxystommus* later became a subject of controversial discussions. While the second branch, in the middle of the tree, splits from the *steinheimensis* form, and comprises only two forms, the third branch, at the left hand, splits from the founder population, and comprises seven forms. Today, these two branches are called the 'side branches'.

In contrast to the diagram reconstructed by Reif (1983a), according to Hilgendorf's cards and dissertation, this new tree involves only two modes of speciation: gradual transformation and splitting, but no fusion. Additionally, the whole tree arises from one founder species. This interpretation was compatible with Darwin's Theory.

The controversy with Sandberger

There was no critical reaction to Hilgendorf's publication for the first few years, but during the time Hilgendorf was in Japan, Fridolin von Sandberger started to controvert Hilgendorf. Sandberger was a professor of geology at Würzburg, and he was reputed to be an authority on fossil snails. By three very short articles (Sandberger, 1873, 1874a, 1874b), he totally rejected Hilgendorf's interpretation. Sandberger neither accepted the allocation of all Steinheim planorbids to one species, nor the occurrence of the different varieties of *Valvata* in a stratigraphically orderly fashion, nor the transitions, but sustained von Klein's concept, and thus the fixity of species.

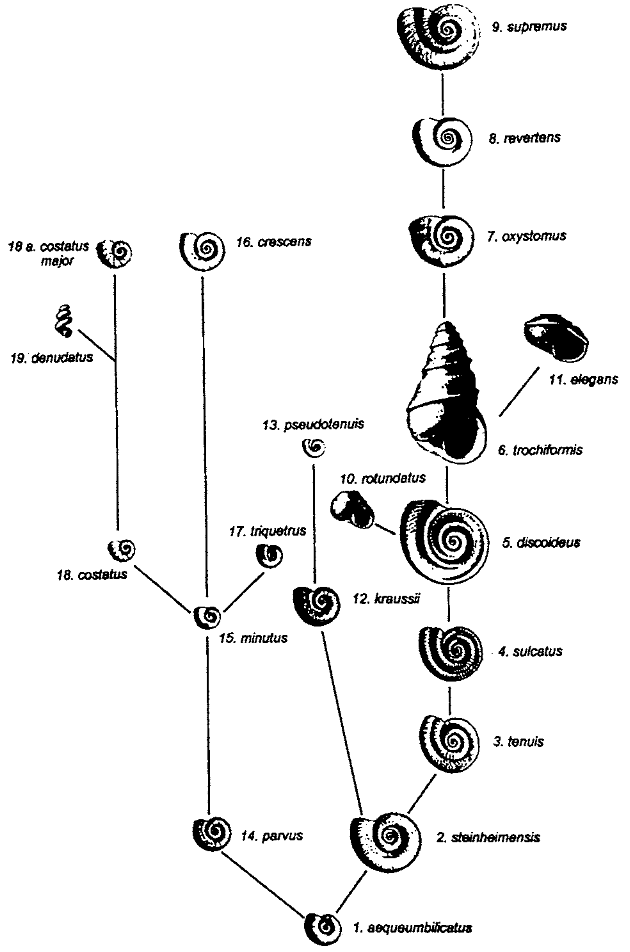

Figure 4. Reconstructed version of Hilgendorf's 1866 planorbid tree.

Hilgendorf got wind of Sandberger's criticism in Tokyo, and commented on it in November 1874, with a letter to his friend Eduard von Martens, which was published in the "Zeitschrift der Deutschen Geologischen Gesellschaft" (Hilgendorf, 1875). The controversy lasted till 1877 and reached its summit at the 'Meeting of Natural Scientists and Physicians' in Munich. Although the dispute exemplifies Hilgendorf's excellent attitude of being always obliged to the facts, I do not want to discuss it in detail (see Hilgendorf 1877a, 1877b, 1877c, 1877d). Summarising, the following assessment can be given:

1. The background of Sandberger's attacks had been only to a minor extent a dispute against the validity of Darwin's Theory. Unfortunately, the dominant motivation for his rigid attitude apparently was his antipathy toward the Prussians (see Hilgendorf, 1879, p. 90).

2. However, responding to Sandberger's accusation, Hilgendorf had checked his findings again and again by field

investigations, and had found more evidence of his hypothesis.

3. Despite the trouble that Hilgendorf had to suffer from this controversy, another positive effect was that his findings became well known in professional circles, and finally most of the experts accepted his hypothesis.

In order to demonstrate the stratification, as well as the transitions, at the Munich Meeting, Hilgendorf had collected new material and had taken photographs during his third season of field activities in Steinheim, which took nine weeks. One of these photos, actually assembled from two photos, is a panoramic view of the western side of the central hill. At that time, the sand pit had still a large expanse. Another photo taken by Hilgendorf himself shows a detail of Pharion's sand pit, obviously taken to demonstrate the stratification, because it shows the same part of Pharion's sand pit as a sketch drawn by Hilgendorf.

Hilgendorf's planorbid papers after 1877

Concerning Hilgendorf's familiarity with Darwin's Theory, his publication of 1879 (Hilgendorf, 1879) provides most clear evidence. This paper was published in the journal "Kosmos" which was founded only two years before, in 1877, for the purpose of promoting the concept of natural evolution. On the editorial board appear the names of Charles Darwin and Ernst Haeckel. Haeckel was the most prominent exponent of Darwinism in Germany, and had coined the term "Phylogenie" in 1866.

Hilgendorf (1879) gives a full account of his data and his theoretical concepts. The paper contains a newly drawn phylogenetic tree, showing most of the snails in cross-sections (Figure 5). The tree is almost identical with that of 1866, except that the founder population is missing. Already in 1866 Hilgendorf was in doubt whether there was only one planorbid form in the lowermost beds from which all the other forms had been developed. Now he withdrew this hypothesis, because it seemed to him that too little was known about the deposits on the western margin of the basin where this form occurs. In this paper Hilgendorf also formulated a concept for the recognition of evolutionary lineages in palaeontology including the practical method of bed-by-bed investigation. Finally, he summarised his data and his interpretations in 27 theorems. These theorems also contain problems and hypotheses, which became a subject of discussion only later, for example the law of irreversibility of evolutionary changes. Nevertheless, Hilgendorf did not speculate on the reasons for the species transmutation in the Steinheim basin. This seemed to him still too early, but he gave some hints for further investigations, for example to check the embryonic part of the gastropod shells, which should provide evidence for speciation, and to check other groups of Steinheim fossils for transmutation (Hilgendorf, 1879, p. 94 and 98). Hilgendorf mentioned in his paper of 1879 also the findings of Neumayr and Paul (1875) who had also found gradual transformations in Tertiary gastropods of Slovenia. In a footnote of their paper they credited Hilgendorf as the first one who had provided evidence for gradual transformation by a detailed palaeontological study.

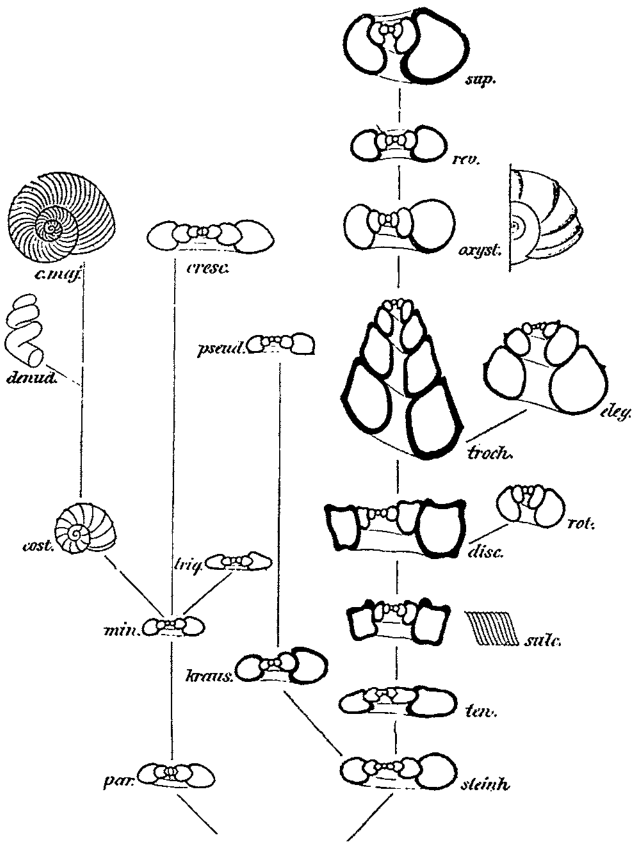

Figure 5. Planorbid tree of Hilgendorf (1879). Reproduced with permission of *Kosmos*.

After 1879, two additional papers of Hilgendorf (1881, 1901) on the Steinheim snails were published. In 1881 he commented on the paper of Hyatt (1880). Hyatt was an American scientist, who had been studying the Steinheim snails since 1872. Then, Sandberger had claimed that Hyatt's view would support his statements and would disprove Hilgendorf's interpretation. But in fact, Hyatt was a Darwinian, and was attracted to this study by Hilgendorf's first publication. Generally speaking, Hyatt's findings support Hilgendorf's interpretation, except for some differences in the question of the stem species and the transition between the trochispiral and the planispiral form. Moreover, Hyatt promoted Hilgendorf's subspecies to species rank.

In his last paper Hilgendorf (1901) once again took care of the most disputed transition between the trochispiral and the planispiral form, and illustrated the transitions by a series of photographs.

The planorbid tree after Hilgendorf's death

From 1901 to the present day more than 30 papers on the Steinheim planorbids have been published. Till the beginning of the last decade the most important steps confirming Hilgendorf's findings were made by Gottschick (1920) and Wenz (1922), as well as Mensink (1984). Gottschick and Wenz have been the first who examined again the Steinheim snails of all beds in detail. Although, in contrast to Hilgendorf, they regarded the morphological changes of the planorbids as ecophenotypic, they fully confirmed the occurrence of the different morphs within the different beds. Mensink also studied the planorbids of all beds, and additionally he checked the occurrence of Hilgendorf's main branch planorbids at a large number of sites spread over the whole Steinheim basin. Moreover, Mensink demonstrated the gradual transitions of the main branch planorbids by means of biometrical investigations. The significance of Gottschick's and Mensink's results are discussed in detail by Reif (1985), and recently, Mensink's data set was reconsidered by means of multivariate methods (Povel, 1993).

In connection with Hilgendorf's (1879) hints for further investigations mentioned above, *i.e.*, to study the embryonic part of the shells and to check other groups of Steinheim fossils, both approaches were carried out only during the last decade, more than 100 years after Hilgendorf's publication. With respect to the embryonic part of the gastropod shells (protoconch), Gorthner (1992) and Nützel and Bandel (1993) were able to show by means of SEM analyses of the protoconch structures that both Hilgendorf's main branch and side branch planorbids are valid species. Moreover, the most recent study shows by such protoconch analyses that Hilgendorf's *aequeumbilicatus*, which is called *Gyraulus kleini* today, did not consist of three different species giving rise to three lineages as Gottschick (1920) suggested, but that *Gyraulus kleini* was the only founder species of the whole planorbid lineage (Finger, 1998).

Hilgendorf's second hint, to check other Steinheim fossils for morphological changes, was taken up in a detailed bed-by-bed study of the Steinheim ostracods (Janz, 1992, 1997). Ostracod shells are the most abundant fossils among the Steinheim deposits, and there are also some species which show morphological changes through the profile. In the genus *Leucocythere*, speciation by a splitting event was detected (Janz, 1992), and the splitting hypothesis could be supported by a detailed study of the microfeatures of *Leucocythere* shells by Viehofen (1997). Moreover, the ostracod assemblage shows a pattern of shell alteration through the profile similar to that of the planorbids (Janz, 1993, Janz, in press). As to the reasons for these alterations, on which Hilgendorf did not speculate, there are two major factors possibly provoking evolutionary changes in both snails and ostracods: long-term ecological changes, as well as the longevity of the lake. While the long-term ecological changes were mainly due to lake level fluctuations, the longevity of the former Lake Steinheim was postulated by Gorthner and Meier-Brook (1985) because of the similarity of the heavily sculptured planorbids with endemic species of extant ancient lakes.

Conclusions

Summing up this brief chronological survey of Hilgendorf's studies on the Steinheim snails, it can be concluded:

1. By looking at Hilgendorf's palaeontological work more closely, it becomes evident that Hilgendorf was already a convinced Darwinian from the beginning of his studies.
2. Hilgendorf set a high value on demonstrating the objectivity of his methods of working based on an inductive approach, and perhaps for this reason did not refer to Darwin in his papers.
3. Nevertheless, he applied Darwin's Theory of Transmutation by his interpretation of the Steinheim snails, and therefore he can be called the first one to introduce Darwin's Theory into palaeontology.
4. Hilgendorf's interpretation has been generally confirmed by further studies, and hints he had given have led to findings supporting his hypothesis. However, there are still many questions to be answered, in order to fully understand the Steinheim planorbid tree.

Acknowledgements

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Keraocarpon gen. nov., magnolialean fruits from the Upper Cretaceous of Hokkaido, Japan

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Abstract. Two new permineralized magnolialean fruits derived from the Coniacian-Santonian strata of the Upper Yezo Group are described in this paper. Each fruit consists of floral head, convex receptacle and woody peduncle. Floral head consists of many conduplicate follicles with adaxial opening. Follicle is long stalked, unilocular and many seeded. Since the fruits differ from the already known ones of Magnoliales, a new genus *Keraocarpon* is proposed to include two new species, *K. yasujii* and *K. masatoshii*. A brief comparison of *Keraocarpon* to other magnolialean taxa is made. These two new species are distinguished from each other by the differences in size of various elements, number of follicles in the aggregate fruits, number of seeds per follicle, and other minor characters. The genus is characterized by aggregate fruits of many-seeded apocarpous stalked follicles on a slightly convex receptacle.

Key words : Aggregate fruits, follicle, Hokkaido, Japan, *Keraocarpon*, Magnoliales, Upper Cretaceous

Introduction

In 1980, Yasuji Kera collected a permineralized specimen of a magnolialean fruit from an ammonite-bearing floated nodule in the Kumaoizawa (brief map, see Ohana and Kimura, 1993, fig. 1), Mikasa City, Hokkaido. Around this locality, the fossiliferous Yezo Group of marine origin is exposed, and the coexisting ammonites indicate a Coniacian-Santonian age (Ohana and Kimura, 1991).

This specimen was briefly described by Ohana and Kimura (1987) as an unnamed magnolialean flower. Masatoshi Kera collected later a smaller specimen of the same kind along the bank in the upper course of the Ikushunbetsu River, which might be derived from the Upper Yezo Group.

After an extensive study of these specimens, this paper now describes them in detail as new fruits under a new name *Keraocarpon* gen. nov. Ohana, Kimura and Chitaley, with description of two new species *K. yasujii* and *K. masatoshii*. The genus and species described here have seeds inside the follicles and thus a new generic name *Keraocarpon* is better suited, instead of *Keranthus*.

Materials and methods

Both the fruits are permineralized. Their cells and minor structures are partly disintegrated by the subsequent crystallization of calcite. Two permineralized specimens are cut as indicated by arrows in Figure 2-2 and Figure 5-2.

Cutting surfaces were polished with carborundum abrasive and then etched with diluted HCl for half a minute. Peels on cellulose-acetate film were taken from the etched surfaces after washing off the acid with water. Cellulose-acetate film 0.034 mm thick ('Bioden, R. F. A.', Oken Co., Tokyo) was used to make the peel sections.

The specimens and their peel sections are kept at the Institute of Natural History, Tokyo (INH).

Systematic description

Class Magnoliopsida
Order Magnoliales (Family unknown)
Keraocarpon Ohana, Kimura and Chitaley gen. nov.

Etymology.—After Y. Kera who collected the type specimen of *Keraocarpon yasujii*.

Type species.—*Keraocarpon yasujii* Ohana, Kimura and Chitaley sp. nov.

Generic diagnosis.—*Keraocarpon* is a member of the woody polycarpous aggregated group of magnolialean fruit. Follicles stalked, many-seeded and spirally arranged on the receptacle.

Keraocarpon is unique in external form but vegetative parts and male organs are unknown. In transverse section, stalks have a large central pith, collateral bundles, and thin inner and thick outer cortices. The bundles consist of vascular elements with scalariform thicknings. Seeds : The follicle unilocular with many seeds alternately arranged in two rows. Seed coat thick with micropyle facing the adaxial suture of the follicle.

Remarks.—The new magnolialean genus *Keraocarpon* is distinguishable from other magnolialean fossil genera with apocarpous and conduplicate follicles (e. g. *Archaeanthus*; Dilcher and Crane, 1984) in having a long receptacle. *Lesqueria* (Crane and Dilcher, 1984) has an ovoid receptacle and bifid distal end of the follicle. *Protomonimia* has a concave receptacle and sessile follicles (Nishida and Nishida, 1988).

Recently, a magnolialean fructification was reported by Nishida *et al.* (1996) from the Upper Cretaceous of Hokkaido. According to them, it has more than 170 short-stalked apocarpous and adaxially sutured follicles on the slightly concave receptacle. Follicle has a single dorsal and a pair of ventral strands. The authors created a new genus *Hidakanthus* on the basis of their single specimen. Externally *Keraocarpon* differs from *Hidakanthus* with longitudinally compressed floral head and with short, strongly falcate follicles in the latter.

In addition we could not make a detailed comparison of *Keraocarpon* with *Hidakanthus*, because in the latter no seeds are preserved in the follicle, and printed scales were omitted in all photographic figures (see Nishida *et al.*, 1996, Figures 2-13).

Keraocarpon yasujii Ohana, Kimura and Chitaley, sp. nov.

Figures 1A, 2, 3, 4

Unnamed magnolialean flower with apocarpous follicles in Ohana and Kimura, 1987 p. 175, figures 1A-J.

Specimen.—INH-020 (holotype).

Locality.—Kumaoizawa (roughly 142°27′E, 42°42′N), Mikasa City, Hokkaido.

Horizon.—Coniacian-Santonian, Upper Yezo Group.

Etymology.—After Yasuji Kera, collector of the holotype.

Specific diagnosis.—Aggregate fruits large-sized. Receptacle slightly convex, disk-like. Follicles around 470, helically arranged; each follicle 2.4 cm long and 2.0 mm wide. Seeds numerous, 21-24 in each follicle.

Description.—Peduncle: The preserved part is 2.2 cm long and 1.2 cm or more in diameter (Figure 2-2A) consisting of a parenchymatous central pith, 5.0 mm in diameter, surrounded by collateral vascular bundles, 1.7 mm each, and cortex, about 1.7 mm wide. The vascular bundles are arranged concentrically, and include secondary xylem with scalariform vessels, and annular or pitted tracheids. The outer cortex consists mainly of sclerenchymatous cells which are in vertical ribs about 10 rows deep (Figure 2-3, arrows; Figure 4-7). Large cells (possibly resin cells) elliptical in cross section, 0.5 mm in major diameter, are scattered in the cortex; lining cells are not observed (Figure 4-7).

Receptacle: The receptacle is disk-like, slightly convex centrally, 2.7 cm in diameter and more than 6.5 mm thick, consisting mainly of parenchymatous cells and a number of slender fibrous bundles running vertically and horizontally (Figure 2-2B; Figure 4-8, 9).

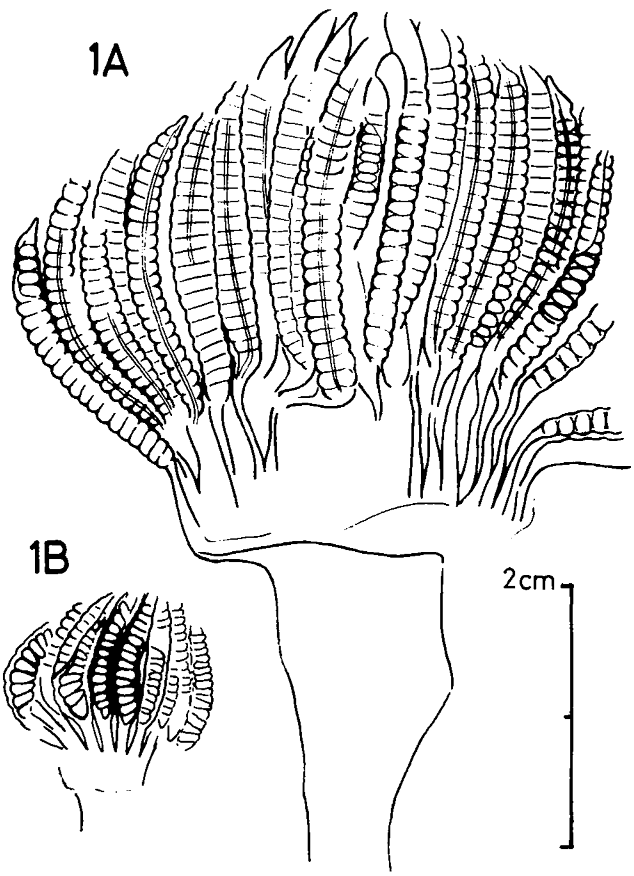

Figure 1. Longitudinally broken fruits. **1A**: *Keraocarpon yasujii* Ohana, Kimura and Chitaley, gen. et sp. nov. Drawn from Figure 2-1 (holotype). **1B**: *Keraocarpon masatoshii* Ohana, Kimura and Chitaley, sp. nov. Drawn from Figure 5-1 (holotype).

Follicles: The follicles are numerous and helically arranged (Figure 2-2D; Figure 2-5, 6). Parastichy is uncertain, because nearly half of aggregate fruits is missing. The estimated number of follicles is 470 or fewer. The follicles are apocarpous and conduplicate, typically 2.4 cm long and 2.0 mm wide (Figure 2-2), and circular or oblong, 1.5-2.0 mm in diameter, in transverse section (Figures 2-5, 6; Figure 3-5). Terminal of follicle with obtuse end is polygonal in transverse section (Figure 3-4). Wall of follicle consists of outer and inner layers and has a distinct adaxial median suture which is flanked on either side by a ridge, 150 μm high, forming an adaxial crest pair with minor projections (Figure 3-5). Each follicle has a single abaxial vascular bundle (Figure 2-5, 6; Figure 3-5). A pair of bundles is present in the adaxial crest. In addition, subordinate lateral bundles are present on the outer layer of the follicle wall (Figure 3-5). Spine-like projections are observed on the outer surface of inner follicles where walls are thinner (Figure 2-6).

Stalks: Each follicle has a stalk, 6.0-8.0 mm long and 0.6 mm in diameter (Figure 2-2C; penetrates inside). In longitudinal section, this stalk is inserted into the receptacle (Figure 3-1). In transverse section, it has a large central pith, collateral bundles, and thin inner and thick outer cortices (Figures 3-3, 4). The bundles consist of vascular elements with scalariform thickenings (Figures 4-4, 5, 6).

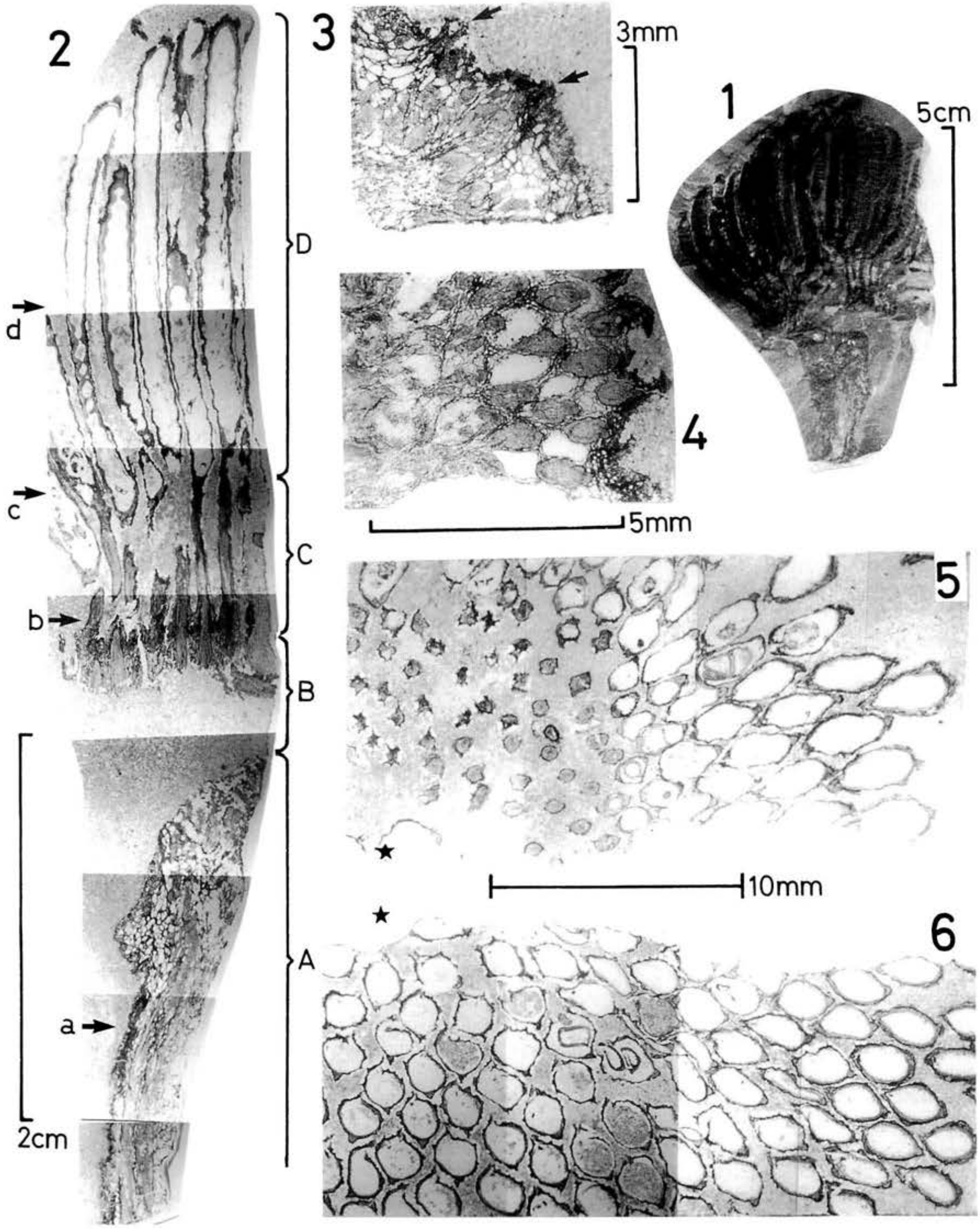

Figure 2. *Keraocarpon yasujii* Ohana, Kimura and Chitaley, gen. et sp. nov. **1.** A permineralized fruit (holotype). Its counter part is missing. **2.** A nearly radial longitudinal section of peduncle (A), poorly preserved receptacle (B), stalk of follicles (C) and apocarpous follicles (D). Surface of receptacle is slightly convex (composite photographs). **3.** A part of a transverse section of the peduncle, cut at 'a'-level in Figure 2-2 showing two sclerenchymatous ribs (arrows). **4.** Transverse section cut slightly above the receptacle (at 'b'-level in Figure 2-2). Vacant areas show the spaces among the proximal parts of stalks. **5.** Transverse section cut at 'c'-level in Figure 2-2, showing proximal parts of follicles (right side) and stalks (left side). In this section, stalks (C) correspond to the convex centre of receptacle. Centre of this fruit in this section is marked by the star. **6.** Transverse section of follicles each with adaxial suture, cut at 'd'-level in Figure 2-2. The centre of this fruit in this section is also indicated by a star.

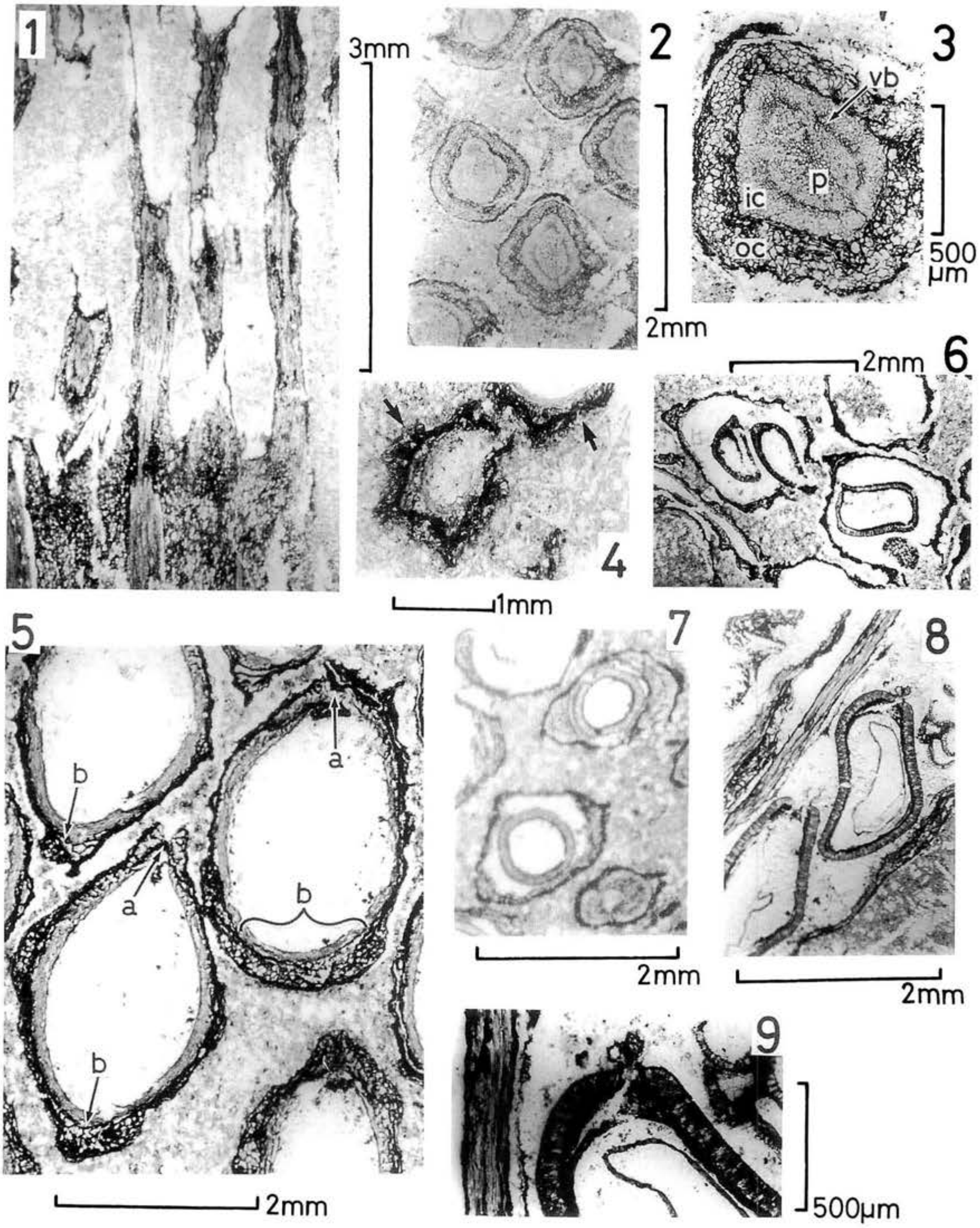

Figure 3. *Keraocarpon yasujii*, Ohana, Kimura and Chitaley, gen. et sp. nov. **1.** Longitudinal section of stalks. **2.** Tranverse section of stalks. **3.** Enlarged from Figure 3-2. Each stalk consists of thick outer cortex (oc) with large cells and oil-glands, inner cortex (ic) with small cells, vascular bundle (vb) and pith (p). Pith cells are similar to those of inner cortex. Cells of outer cortex are similar to those of receptacle. **4.** Transverse section of apical parts of two follicles (arrows). Seeds are absent. **5.** Transverse section of middle part of follicles with adaxial sutures facing upper side (arrow a), and abaxial thick bundles (arrow b). Two thin layers are seen in the transverse section of follicle walls. **6.** Transverse section of middle part of follicles with remains of seed coats inside. **7.** Transverse section of proximal part of follicles, showing the follicle walls and seed coats. **8.** Longitudinal section of a follicle with two thick seed coats. **9.** A thick seed coat, enlarged from Figure 3-8.

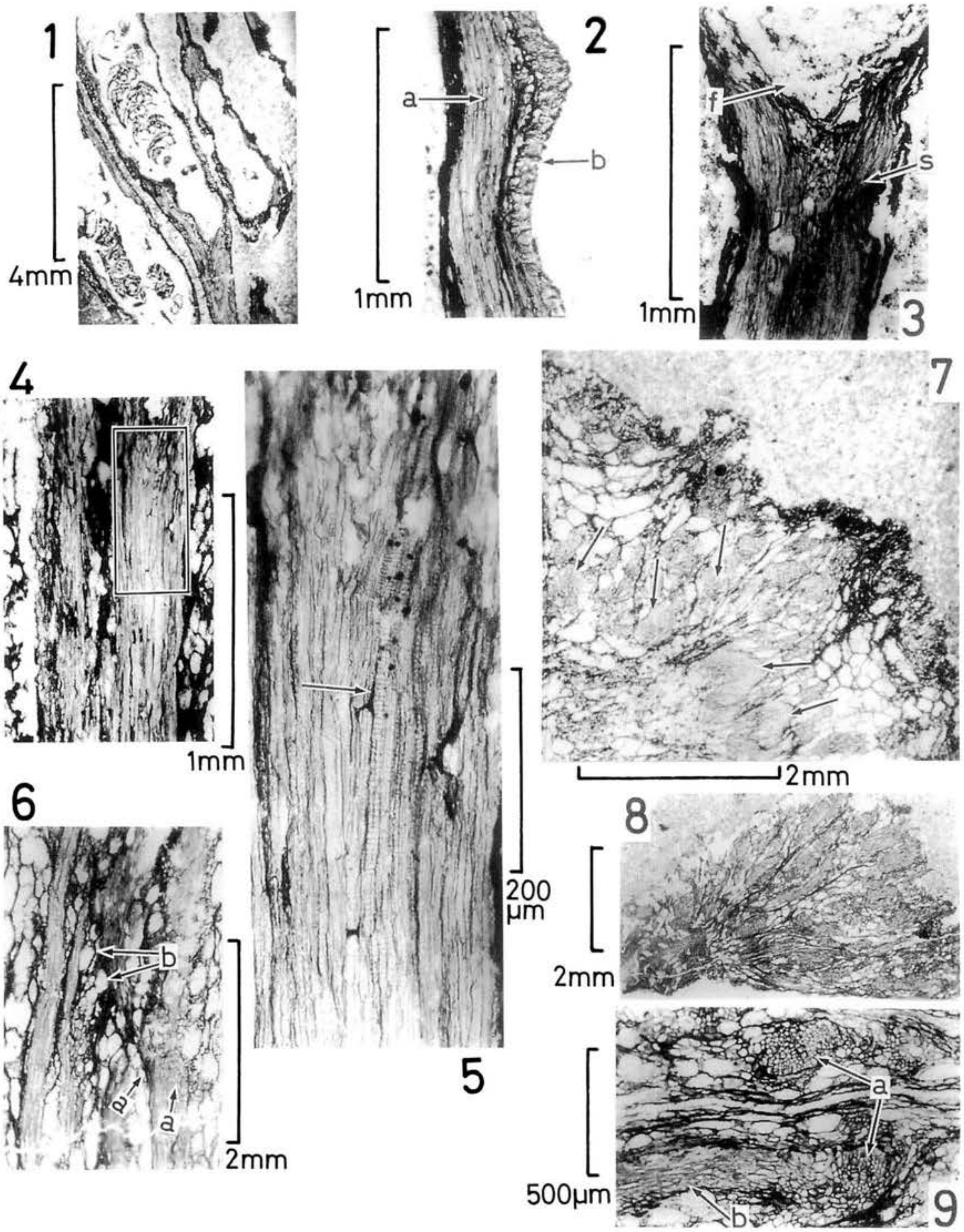

Figure 4. *Keraocarpon yasujii* Ohana, Kimura and Chitaley, gen. et sp. nov. **1.** Longitudinal section of proximal part of follicles, each with disintegrated seeds. **2.** Longitudinal section of the follicle wall (outer layer ; arrow a, inner layer ; arrow b). **3.** Longitudinal section of a stalk (arrow s) and the base of follicle chamber (arrow f). **4.** Longitudinal section of an enlarged stalk, showing scalariform bundles. **5.** Enlarged from the boxed area of Figure 4-4. Scalariform bundles are clearly seen (arrow). **6.** Tangential section of basal part of peduncle with eustele bundles (arrow a), showing the alternation of bundles and parenchymatous tissues (including oil glands) (arrow b). Pith is located to the right side. Phloem is not preserved. **7.** Transverse section of the basal part of peduncle, enlarged from Figure 2-3. Arrows indicate the eustele bundles. **8.** Transverse section of a part of receptacle, showing fibrous and crowded bundles. **9.** Enlarged from a part of Figure 4-8, showing vertically (arrow a) and horizontally oriented (arrow b) bundles.

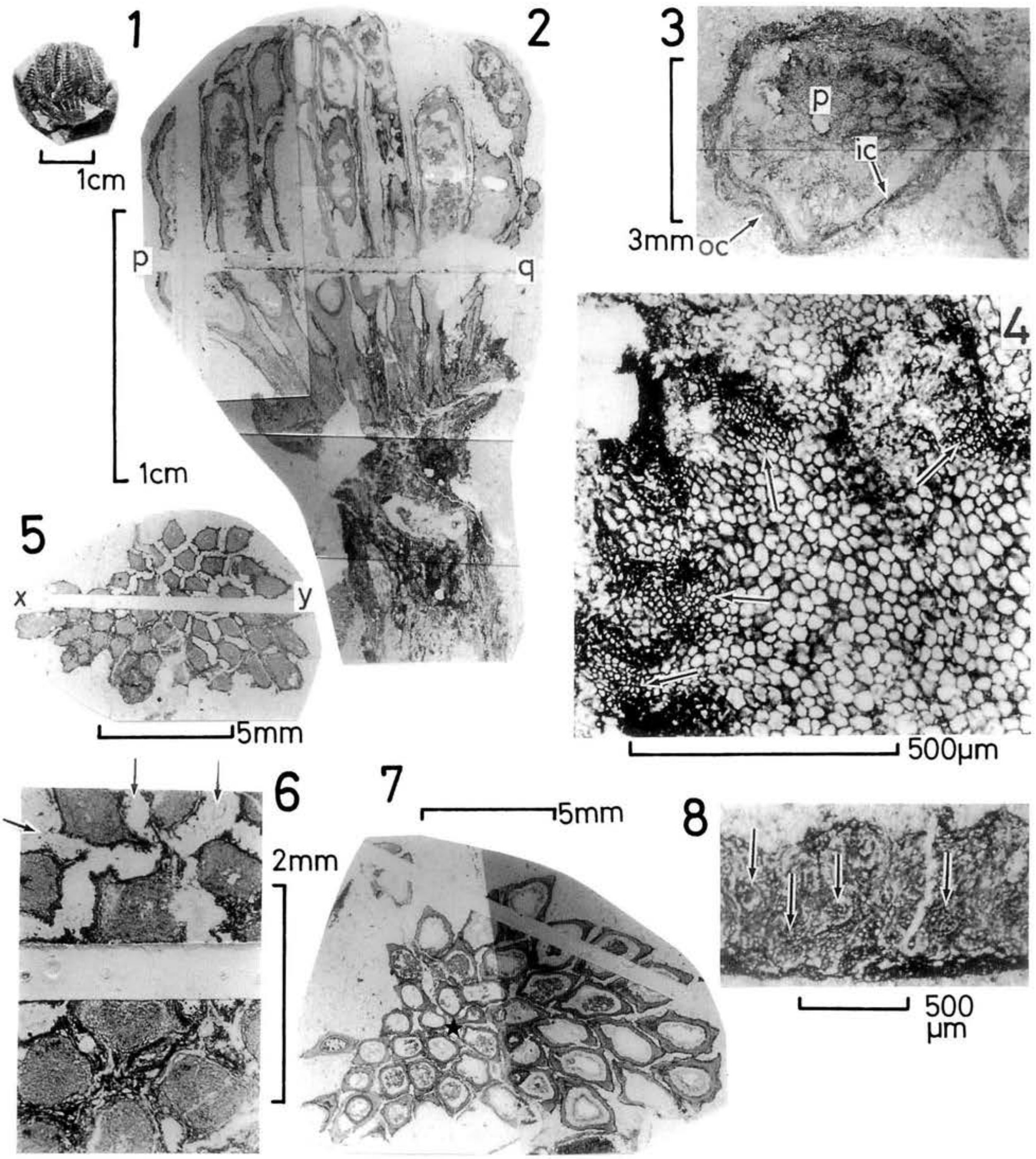

Figure 5. *Keraocarpon masatoshii*, Ohana, Kimura and Chitaley, sp. nov. **1.** Preserved parts of small aggregate fruit (holotype ; compare with *Keraocarpon yasujii* shown in Figure 2-1). **2.** Radial longitudinal section of an aggregate fruit, consisting of poorly preserved peduncle, receptacle and apocarpous follicles each with distinct stalk. **3.** Transverse section of peduncle, showing large pith (p), collateral vascular bundles, inner cortex (ic) and thick outer cortex (oc). **4.** Enlarged from Figure 5-3, showing pith and collateral vascular bundles (arrows). **5.** Transverse section of stalks. x-y ; zone lost by cutting (using a 0.4-mm-thick saw). **6.** Enlarged from Figure 5-5, showing polygonal or irregular outline of stalks. Arrows indicate openings filled with rock matrix. **7.** Transverse section of apocarpous follicles. Wall thickness varies according to the cutting plane. The adaxial suture faces the supposed centre of the fruit (star). **8.** Tangential section of edge of receptacle, showing horizontal vascular bundles (arrows).


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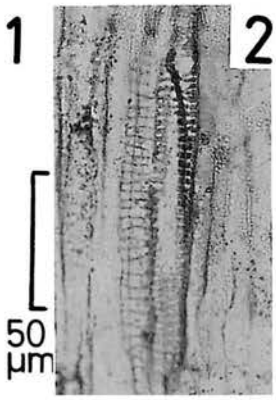
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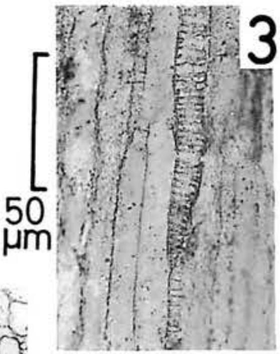
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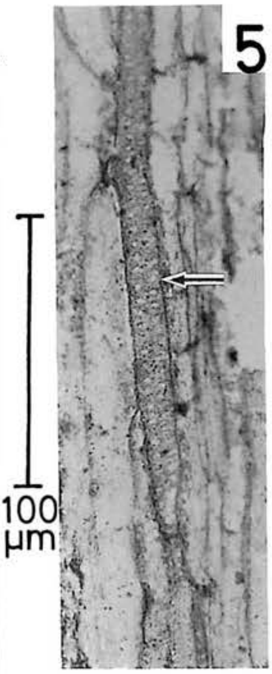
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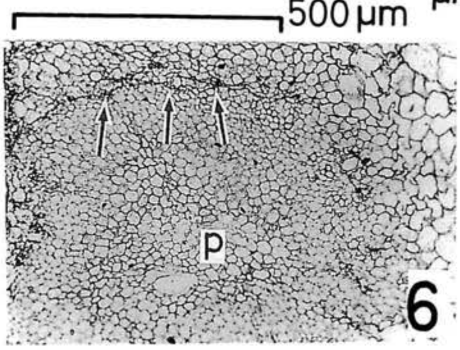
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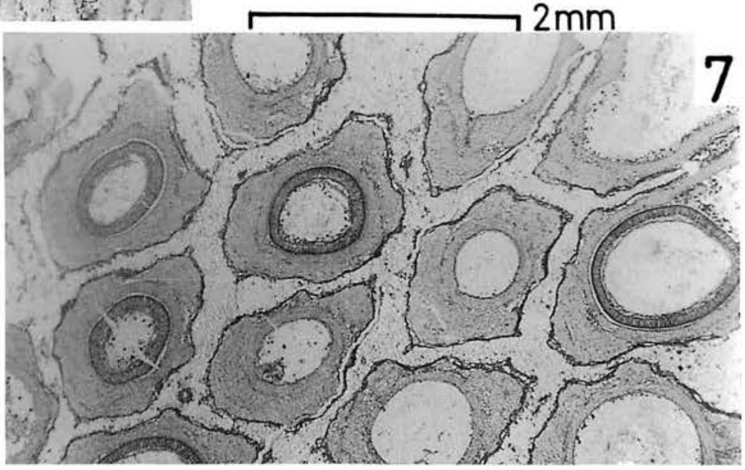
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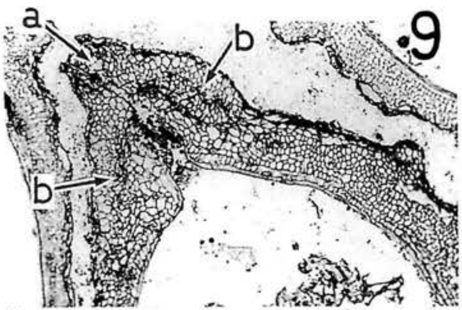
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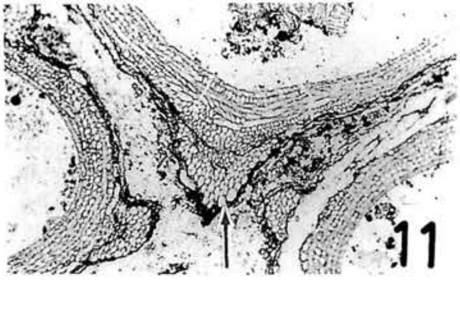
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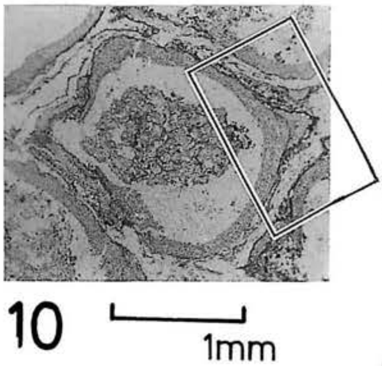
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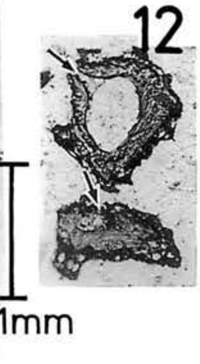
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Seeds: The follicle is unilocular with seeds alternately arranged in two rows, 21-24 in number in each follicle (Figure 3-6—9). Seed coat is thick with micropyle facing the adaxial suture of the follicle (Figure 3-6—9).

Keraocarpon masatoshii Ohana, Kimura and Chitaley, sp. nov.

Figures 1B, 5, 6

Specimen.—INH-021 (Holotype).

Locality.—Upper course of the Ikushunbetsu River bank, Mikasa City (4 km south of the Kumaoizawa locality where *Keraocarpon yasujii* was collected.)

Horizon.—Same as *K. yasujii.*

Etymology.—After Masatoshi Kera, collector of the holotype.

Specific diagnosis.—An aggregate fruit of follicles, small. Receptacle slightly convex. Number of follicles around 70. Stalk and wall of follicle thick. Seeds in each follicle, 15-18.

Description.—Preserved parts of this fruit are a permineralized peduncle, receptacle and apocarpous conduplicate follicles (Figures 1B, 5-1).

Peduncle: Peduncle is 5.5 mm in diameter, consisting of pith, collateral vascular bundles and cortex (Figure 5-2—4).

Receptacle: Receptacle is slightly convex disk-like, 1.0 cm in diameter and 3.5 mm thick.

Follicles: The follicles are helically arranged; their estimated number is 70. Since half of them are missing, the parastichy is uncertain. The follicles are apocarpous and conduplicate, 1.1 cm long, with transverse section circular or sometimes polygonal, 1.5-2.0 mm in diameter (Figure 5-7).

Stalk: 1.0-1.5 mm long and 0.8-1 mm thick, and is inserted into the receptacle to a depth of about 1.8 mm (Figure 5-2). It is circular to polygonal in transverse section, having a pith, vascular bundles and cortex (Figure 5-5, 6). The bundles consist of scalariform vessels and pitted tracheids (Figure 6-1—5). The follicles are adaxially sutured (Figure 5-7; Figure 6-7—10). The follicle wall consists of two layers of cells, the outer thick and the inner thin. In each follicle, a thick vascular bundle is on the abaxial side, and a pair of adaxial bundles are on either side of the suture. No suture is observed at the proximal part of the follicle (Figure 6-7). Most of the sutures are not fully open, suggesting that its seeds are not fully matured.

Seeds: Seeds are 15-18 in number in each follicle. The seed coat is of two layers (Figure 6-1, 7). There is almost no space between the seed and the inner wall of the follicle.

Remarks.—This species is distinguished from *K. yasujii*, the type species of *Keraocarpon*, by the smaller sizes of peduncle, receptacle, and follicle and the smaller numbers of follicles, and seeds in each follicle. The transverse section of follicle is not rhomboidal as illustrated by Nishida *et al.* (1996) in their *Hidakanthus*, but elliptical or polygonal (in this work). In both fruits no male organs or other vegetative parts have been found in organic connection.

The Upper Yezo Group of marine origin contains many varied type of fossil plants. It is, however, difficult to get entire or nearly entire plant specimens, because these terrestrial plants were disaggregated in the course of taphonomy.

Acknowledgements

We thank Yasuji Kera and Masatoshi Kera who offered their specimens for our study. This study was financially supported by the Grant-in-Aid for Scientific Research from the Ministry of Education, Science, Sports and Culture of Japan to Kimura and Ohana, 07640629 and from the Fujiwara Natural History Foundation to Ohana. We also thank the Cleveland Museum of Natural History, Cleveland, Ohio, U. S. A. for making available the services of S. Chitaley.

← **Figure 6.** *Keraocarpon masatoshii* Ohana, Kimura and Chitaley, sp. nov. **1.** Longitudinal section of a thick stalk. Its upward extension forms follicle wall to wrap a proximal seed. No adaxial suture is present below the position of the proximal seed. **2.** Scalariform vessels in the stalk enlarged from Figure 6-1. Some perforation plate of vessels are scalariform. **3.** Same, enlarged from Figure 6-1. **4.** An annular tracheid (arrow a) and scalariform vessels (arrow b) in stalk enlarged from Figure 6-1. **5.** Pitted tracheid. Pits are in two rows (arrow) enlarged from Figure 6-1. **6.** Transverse section of proximal part of a stalk, showing pith (p) and small collateral bundles (arrows). **7.** Transverse section of follicles, cut along the p-q line in Figure 5-2, showing thick and irregularly formed follicle walls. **8.** Transverse section cut along the middle part of a marginal follicle. Follicle is transversely rhomboidal and the seed is disintegrated. The position of the adaxial suture is indicated by an arrow. **9.** Transverse section of a follicle cut slightly above the section as in Figure 6-8, showing adaxial suture (arrow a). The vascular bundles are seen at each crest (arrow b). **10.** Transverse section of a central follicle, cut at the same level as in Figure 6-8, showing the wall. **11.** Enlarged from the boxed area of Figure 6-10, showing the abaxial bundle (arrow) and thick-layered follicle wall. **12.** Transverse section of apical part of two follicles with distinct adaxial sutures (arrows). The walls are irregular in form.

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