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The fossil on the cover is *Isocrinus* (*Chladocrinus*) *hanaii* Oji, an Early Cretaceous (Aptian) crinoid, which was described from the Hiraiga Formation exposed at Haipe, Tanohata-mura, Shimo-Hei County, Iwate Prefecture, Northeast Japan. (University Museum of the University of Tokyo coll. cat. no. ME6950, paratype specimen, length about 11 cm)

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948. EARLY MIOCENE (AQUITANIAN) LARGER FORAMINIFERA FROM THE SHIMIZU FORMATION, ASHIZURI CAPE, KOCHI PREFECTURE, SHIKOKU, JAPAN*

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Abstract. Early Miocene (Aquitanian) larger Foraminifera are first described from the calcareous matrix of volcanic conglomerate and sandstone of the Shimizu Formation in the Shimanto Belt, Tosa Shimizu City, Ashizuri Cape, Kochi Prefecture, Shikoku. The joint occurrence of *Miogypsinoides dehaartii* (van der Vlerk), *Spiroclypeus margaritata* (Schlumberger) and *Victoriella conoidea* (Rutten) enables the age of the calcareous matrix of volcanic conglomerate and sandstone of the Shimizu Formation to be assigned to the Early Miocene (Aquitanian). Detailed stratigraphic studies, which were carried out in Ashizuri Cape, Tosa Shimizu City, Shikoku, show that the mudstone yielding the Late Eocene (Priabonian) larger Foraminifera described by Matsumaru and Kimura (1989) is not in the Shimizu Formation, but in the Kurusuno Formation (Myint Thein *et al.*, 1991; Myint Thein, 1992). As such, the newly described larger Foraminifera from the Shimizu Formation indicate an age for the formation of Early Miocene (Aquitanian).

Key words. Miogypsinoides, Miogypsina, Nephrolepidina, Spiroclypeus, Aquitanian, Shimizu Formation.

Introduction

The Shimanto Belt in Kochi Prefecture, Shikoku, which is known as a tectonic belt along the outermost zone of Southwest Japan, consists of highly deformed flysch deposits and melange complex with some exotic blocks (*e.g.* basalt, red pelagic shale, etc.). In Ashizuri Cape, Kochi Prefecture, the Shimizu Formation, which occupies the southernmost part of the Shimanto Belt, exhibits syndepositionally deformed flysch and debris flow deposits, and rarely yields fossils.

Recently, Matsumaru and Kimura (1989) found Late Eocene (Priabonian) larger Foraminifera from a gray tuffaceous mudstone of the Shimizu Formation at Takahata Village, Tosa Shimizu City, Kochi Prefecture, but

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Myint Thein et al. (1991) and Myint Thein (1992) consider it as belonging to the Kurusuno Formation from the viewpoint of lithologic characteristics. Therefore, the Kurusuno Formation contains Asterocyclina stella (Gümbel), Orbitoclypeus kimurai Matsumaru, O. sp., Discocyclina sella (d'Archiac), and the age of the formation is Late Eocene (Priabonian) (Matsumaru and Kimura, 1989). On the other hand, the age of the Shimizu Formation had to be reexamined. Myint Thein et al. (1991) fortunately found Upper Cretaceous radiolarians such as Protoxiphotractus perplexus Pessagno, etc. from deformed mudstone of the Shimizu Formation exposed along the coastal bench at Tsuro Village, Tosa Shimizu City in Ashizuri Cape, Kochi Prefecture. However, these fossils are considered to be allochthonous. Yuiiro Ogawa, one of the Myint Thein et al. research group, sent nine thin sections from the calcareous matrix of volcanic conglomerate and sandstone of the Shimizu Formation, Tosa Shimizu City, Ashizuri Cape, to Kuniteru Matsumaru for study of the larger Foraminifera. The fossil locality for the present study is along the sea coast on the southern part of Ohki Beach, Tosa Shimizu City in Ashizuri Cape, Kochi Prefecture (Lat. 37°47′15.4″N., Long. 132°57′34.6″E.) (Figure 1).

The purpose of this paper is primarily to make the first description and discussion of 5 genera and 5 species of larger Foraminifera, and 1 genus and 1 species of smaller Foraminifera from the Shimizu Formation, and secondarily to propose a geological age based on the presence of age-diagnostic species. All specimens described herein have been deposited in the collections of the Department of Geology, Faculty of Education, Saitama University.

Geological age

The larger and smaller Foraminifera found from the calcareous matrix of volcanic con-

glomerate and sandstone of the Shimizu Formation, Tosa Shimizu City, Ashizuri Cape, Kochi Prefecture were determined as follows: Miogypsinoides dehaartii (van der Vlerk), Miogypsina sp., Nephrolepidina praejaponica Matsumaru, Spiroclypeus margaritata (Schlumberger) and Victoriella conoidea (Rutten), which belong to the larger Foraminifera, and Pararotalia sp. belonging to the smaller Foraminifera. *Miogypsinoides* dehaartii and Spiroclypeus margaritata are diagnostic larger Foraminifera indicative of the Tertiary e5 of the East Indian Letter Classification (Matsumaru, 1974). The present fauna in the calcareous matrix of the Shimizu Formation at this location is especially characterized by the joint occurrence of Miogypsinoides dehaartii (van der Vlerk), Spiroclypeus margaritata (Schlumberger) and Victoriella conoidea (Rutten).

Miogypsinoides dehaartii was first described by van der Vlerk (1924) from Dr. F. Weber's sample from the Orbitoiden-Mergelkalk and Foraminiferenkalk, Larat Island, Tanimbar Islands, Indonesia. In 42 years later, van der Vlerk was led to the conclusion that the stratum of type locality of Miogypsinoides dehaartii is of Aquitanian age, based on biometrical investigations on Miogypsinoides dehaartii, Lepidocyclina sp. and Cycloclypeus sp. This judgement is especially based on statistical comparison of the value Factor A showing the degree of development of embryonic chambers between Larat Lepidocyclina from Indonesia and Lepidocyclina of Aquitanian age in sample FR475 from Grand Nid-Sausset, Marseille, France (van der Vlerk, 1964).

Spiroclypeus margaritata (Schlumberger, 1902) was described from the "Oligocene" limestone of Teweh, Barito Basin, Borneo, Indonesia. Schlumberger stated that this species resembles *Heterostegina* sp. of Prof. K. Martin, University of Leiden, from the "Oligocene" beds near Dax, Aquitaine Basin, France. Recently, Butt (1966) described *Spiroclypeus blankenhorni* Henson var. or-



Figure 1. Map showing the fossil locality (arrow) at the southern part of Ohki Beach, Tosa Shimizu City, Ashizuri Cape, Kochi Prefecture, and geological map of the study area.



nata Henson from Escornébeou near Dax, where the Aquitanian stratotype is located, and Martin's *Heterostegina* sp. from near Dax can be assigned to this species.

Spirocypeus blankenhorni and S. blankenhorni var. ornata were originally described from the Lower Miocene of Aintab, Turkish Syria (Henson, 1937). Adams et al. (1983) state that Spiroclypeus blankenhorni var. ornata is known from the Chattian Stage in the Mediterranean region, while Spiroclypeus blankenhorni and S. margaritata are common in the Aquitanian Stage in both the Mediterranean and Indo-Pacific regions. They do not, however, give any evidence or criticism of the species concepts among Spiroclypeus blankenhorni, S. blankenhorni var. ornata and S. margaritata. The present authors consider that the former two may be a junior synonym of the latter, judging from Henson's description and illustration. In Kita-Daito-Zima (North Borodino Island), Japan, Hanzawa (1940, p. 764, p. 790) once noted that Spiroclypeus margaritata occurs in Zone 4 (302.31 m-394.98 m) of drill cores of the Daito Limestone as an Aquitanian form, its geological horizon being assigned to that stage based on Spiroclypeus attaining its climax of development in the Aquitanian.

Debourle and Delmas (1955) described Victoriella aquitanica from the Oligocene (probably Aquitanian) of Mimizan, Landes, France. They differentiated Victoriella aquitanica from Victoriella 'plecte'' (Chapman), which is a junior synonym of Victoriella conoidea (Rutten), by its regularly trochospiral form through ontogeny. Glaessner and Wada (1959, p. 199) were of the opinion that Victoriella aquitanica would prove to be a synonym of Victoriella conoidea, and also state that Victoriella conoidea is rare in the late Eocene and widespread in the Oligocene to Aquitanian. Recently, Chaproniere (1984) described Victoriella conoidea from sample 70614 of the Puketi Formation, Waitakere Group from Kaipara Harbour of Huketere Peninsula, New Zealand. He expressed the age of the Puketi Formation as Zone N. 5 in terms of the planktonic foraminiferal zonal scheme of Blow (1969). The Puketi Formation is then correlated with the Aquitanian based on the same zonal scheme (Blow, op. cit.).

Therefere, the conspicuous presence of such age-diagnostic species as *Miogypsinoides dehaartii, Spiroclypeus margaritata* and *Victoriella conoidea* enables the occurrence of the present larger foraminiferal assemblage in the Shimizu Formation to be set as Aquitanian. As such, an Early Miocene (Aquitanian) age, Tertiary e5, is assigned to the calcareous matrix of volcanic conglomerate and sandstone of the Shimizu Formation forming the Shimanto Belt, in the southern part of Ohki Beach, Tosa Shimizu City, Ashizuri Cape, Kochi Prefecture.

Description of species

Family Miogypsinidae Vaughan, 1928 Genus *Miogypsinoides* Yabe and Hanzawa, 1928 *Miogypsinoides dehaartii* (van der Vlerk, 1924)

Figures 2-1, 3-2 left, 3-3-5

- Miogypsina dehaartii van der Vlerk, 1924, p. 429-431, text-figs. 1-3.
- Miogypsina abunensis Tobler, 1927, p. 323-330, textfigs, 3, 5.
- Miogypsinoides dehaartii (van der Vlerk) var. pustulosa Hanzawa, 1940, p. 780-782, pl. 39, figs. 20-21, pl. 40, figs. 2-29, pl. 42, fig. 13, text-fig. 5.
- Miogypsinoides lateralis Hanzawa, 1940, p. 783, pl. 39, figs. 10-14.

Miogypsinoides sp. aff. dehaartii (van der Vlerk). Brönnimann, 1940, p. 80-81. pl. 8, fig. 19.

Miogypsina (Miogypsinoides) dehaartii van der Vlerk.

[←] Figure 2. 1. Miogypsinoides dehaartii (van der Vlerk). Oblique section. 2. Spiroclypeus margaritata (Schlumberger). Vertical section. 3. Victoriella conoidea (Rutten). Tangential section near axial plane. 4. Nephrolepidina praejaponica Matsumaru. Vertical section. 5, 6. Pararotalia sp; 5, Oblique section, 6. Vertical section. 1, 5, 6, ×100; 2, 3, 4, ×40.

Drooger, 1953, p. 110-114, pl. 1, figs. 15-26; Raju, 1974, p. 80-81, pl. 1, figs. 19-25, pl. 3, fig. 8, pl. 4, figs. 2-4; Adams and Belford, 1974, p. 497, pl. 73, figs. 12-14; Matsumaru and Barcelona, 1982, p. 84-89, pl. 14, fig. 6 (left); Hashimoto, Matsumaru and Alcantara, 1982, p. 33-37, pl. 10, fig. 8, pl. 11, fig. 22; Chaproniere, 1984, p. 46-47, pl. 7, figs. 7a-b, pl. 8, figs. 1-3, pl. 17, figs. 15-17, text-fig. 17.

- Miogypsinoides dehaartii (van der Vlerk). Cole, 1954, p. 602, pl. 220, figs. 1-8; Cole, 1957a, p. 339-340, pl. 111, figs. 5-7, 9-16 (non fig. 8); Cole, 1957b, p. 769, pl. 243, figs. 1-2 (non fig. 3), pl. 244, fig. 3; Hanzawa, 1957, p. 92, pl. 15, figs. 3, 7, 9, 12, 19, 22, pl. 19, fig. 3, pl. 21, fig. 4; Coleman, 1963, p. 13, pl. 2, figs. 13-20; van der Vlerk, 1966, p. 422-423, pl. 1, figs. 1-4 (non fig. 5), 7-10, pl. 2, fig. 1 (non fig. 3); Bielle and Caralp, 1967, p. 36-42, pl. 4, figs. 1-2; Cole, 1969, p. C10-12, pl. 1, figs. 2-12, 15, 20 (non figs. 1, 13-14, 16-19); Matsumaru, 1974, p. 107-109, pl. 17, figs. 2-5, 10-12, 14-15, 18-19, 21, 24-25; Matsumaru, 1976, p. 196-198, 204, pl. 4, figs. 7, 14, 17 (non figs. 3, 23).
- Miogypsinoides sp., Coleman, 1963, p. 13-14, pl. 3, figs. 1-6.
- Miogypsinoides sp. cf. dehaartii (van der Vlerk). Bielle and Caralp, 1967, p. 36-42, pl. 4, figs. 3-6.
- Miogypsinoides abunensis (Tobler). Matsumaru, 1974, p. 107-109, pl. 17, fig. 22; Matsumaru, 1976, p. 196-198, pl. 4, figs. 8, 11.

Miogypsinoides formosensis Yabe and Hanzawa. Matsumaru, 1976, p. 196-198, pl. 4, figs. 6, 12, 19.

Miogypsinoides bantamensis Tan. Matsumaru, 1976, p. 196-198, pl. 4, figs. 15, 18.

Description.—Test is of moderate size, 1.0 to 1.4 mm long, more than 0.6 mm wide and 0.4 to 0.5 mm thick, fan-shaped in outline and biconvex. The surface of the test is smooth or covered with pustules of 40 to $80 \,\mu$ m in diameter.

The embryonic chambers consist of spherical protoconch, $117 \,\mu m$ in diameter, and kidney-shaped deuteroconch, more than 88 μm in diameter, which are at the begining of a single whorl of subquadrate-shaped nepionic chambers. The protoconch is separated from the apical border of test by intervention of the deuteroconch, and γ parameter (Drooger, 1952) shows a negative value of about 30 degrees.

The number of nepionic chambers is more than 8. Eight rows of ogival to rhombic equatorial chambers are developed, 94 to 104 μ m in radial length and 80 to 88 μ m in tangential length on the frontal side of nepionic stage, gradually enlarging toward frontal margin of the test. Internal height of the equatorial chambers is 120 to 208 μ m in vertical sections.

The lateral layers are compact and laminated, with vertical canals of 6 to 8 μ m in diameter penetrating lateral layers from septa of equatorial chambers. The rudimentary lateral chambers of 80 to 112 μ m width and 24 to 32 μ m height occur sometimes over the nucleoconch near the surface of the test.

Remarks.—Although there are no equatorial sections of specimens for study, the present form is easily identified as *Miogypsinoides* dehaartii (van der Vlerk) in every respect: apical position of embryonic chambers, negative γ parameter, single whorl of nepionic chambers, equatorial chamber rows and compact laminated structure of lateral layers. van der Vlerk (1924, 1966) confirmed the presence of rudimentary lateral chambers in his *Miogypsina dehaartii* from the type locality. This species is, however, classified as a *Miogypsinoides* by many authors and also was placed in the subgenus *Miogypsinoides* of *Miogypsina* by van der Vlerk (1966).

Tan Sin Hok (1936, p. 51-52) established a new subgenus *Conomiogypsinoides* based on *Miogypsina abunensis* Tobler, but Hanzawa (1940, p. 768-769) regarded *Conomiogypsinoides* to be nothing but a synonym of *Miogypsinoides*, whose type species is *Miogypsina dehaartii* van der Vlerk. van der Vlerk (1966) investigated again an assemblage of *Miogypsinoides dehaartii* from the type local-

 $[\]rightarrow$ Figure 3. 1. Spiroclypeus margaritata (Schlumberger). Vertical section. 2 (left), 3-5. Miogypsinoides dehaartii (van der Vlerk). All figures of vertical sections, except for oblique section of Figure 3-4. 2 (right). Miogypsina sp. Oblique section. 6, 7, 8. Nephrolepidina praejaponica Matsumaru; 6, 7. Oblique sections, 8, Vertical section. All figures $\times 40$.



ity and regarded *Conomiogypsinoides* to be a synonym of *Miogypsinoides*. The present authors synonymize *Miogypsinoides abunen*sis (Tobler) with *Miogypsinoides dehaartii*, because both species have in common the development of compact laminated structure of lateral layers.

Genus Miogypsina Sacco, 1893 Miogypsina sp.

Figure 3-2 right

Description.—Several random thin sections assigned to the genus *Miogypsina* are in the present collection, but none of them adequately exhibits the equatorial and vertical planes. The oblique sections indicate a small test with a diameter of 1.0 to 1.5 mm and there are 4 to 5 regular layers of lateral chambers on each side of the equatorial layer. Some pillars with diameters of as much as 40 μ m are scattered throughout the inflated portion of the test.

Remarks.—Due to the lack of equatorial sections the present form is not identified, but may be used as *Miogypsina borneensis* Tan, because this species is in association with Miogypsinoides dehaartii in the type locality. Also, in the fauna of Zones 3 and 4 of Kita-Daito-Zima, Miogypsina borneensis is associated with Miogypsinoides dehaartii var. pustulosa Hanzawa, M. bantamensis Tan, M. lateralis Hanzawa, Miogypsina polymorpha (Rutten), Lepidocyclina (Nephrolepidina) tournoueri Lemoine and R. Douvillé, L. (N.) plicomargo Hanzawa, Spiroclypeus margaritata (Schlumberger), Cycloclypeus communis Martin, Operculina gaimardi d'Orbigny, Heterostegina depressa d'Orbigny, Rotalia gaimardi d'Orbigny, Planorbulinella larvata (Parker and Jones), Austrotrillina howchini (Schlumberger), Borodinia septentrionalis Hanzawa, and others (Hanzawa, 1940). The present larger foraminiferal fauna with Miogypsina sp. from the Shimizu Formation in Ashizuri Cape can therefore be correlated in this manner with a partial fauna

from Zones 3 and 4 of Kita-Daito-Zima.

Family Lepidocyclinidae Scheffem, 1932 Genus Nephrolepidina H. Douvillé, 1911 Nephrolepidina praejaponica Matsumaru, 1989

Figures 2-4; 3-6-8.

Nephrolepidina praejaponica Matsumaru. Matsumaru and Kimura, 1989, p. 265, 267, figs. 6-1-13.

Description.—Test small, lenticular, with diameter of 1.6 to 2.3 mm and thickness of 0.7 mm. Conical pillars are from 42 to 83 μ m in diameter, and distributed on the central part of the test surface.

The embryonic chambers exposed in oblique sections are nephrolepidine, and the protoconch is subcircular with a diameter of more than $136 \,\mu$ m. The second chamber or deuteroconch, which embraces the protoconch, has an internal diameters of more than 176 μ m. The ratio (=DII/DI) of the inner diameter of deuteroconch (II) to that of protoconch (I) is 1.3. The distance across both the protoconch and deuteroconch is 232 μ m. The outer wall of the embryonic chambers is about 20 μ m thick.

The equatorial chambers of arcuate form near the periembryonic chambers change from ogival to short hexagonal near the periphery. Those near the periphery have a radial diameter from 56 to 70 μ m and a transverse diameter from 52 to 80 μ m. Height increases gradually towards periphery, about 40 μ m near the center and about 65 μ m near the periphery.

The lateral chambers are arranged in a tier of 6 to 10 layers over the center. Chambers over the center and at the periphery have a length of 77 to $120 \,\mu$ m, a height of 20 to 30 μ m, and floors and roofs 15 to $20 \,\mu$ m thick.

Remarks.—Though a sufficient number of thin sections was not available for study, the present specimen has the same features of small embryonic chambers and short hexagonal equatorial chambers as *Nephrolepidina*



Figure 4. Spiroclypeus margaritata (Schlumberger). 1, 4, 5, 7, 8, 9, vertical sections. 2, 3, 6, oblique sections. All figures $\times 40$.

praejaponica Matsumaru from the Lower Member of the Misaki Formation, Tosa Shimizu City, Kochi Prefecture, Shikoku (Matsumaru and Kimura, 1989). The present form is thus assigned to Nephrolepidina praejaponica.

Nephrolepidina praejaponica is considered to exhibit more primitive features than Nephrolepidina japonica (Yabe) as already indicated by Matsumaru and Kimura (op. cit.). According to Matsumaru (1971, p. 164), Nephrolepidina japonica is considered to have derived from Nephrolepidina tournoueri, but the former may be a junior synonym of the latter. In Europe, Early Miocene (Burdigalian) Nephrolepidina tournoueri evolved from Late Oligocene (Chattian) to Early Miocene (Aquitanian) Nephrolepidina morgani (Lemoine and R. Douvillé) (de Mulder, 1975). Nephrolepidina praejaponica may then be assigned to Nephrolepidina morgani. As the nepionic spiral of Nephrolepidina praejaponica is obscure, the name prae*japonica* is used in the present instance.

Nephrolepidina praejaponica was found in the Late Early Miocene (Burdigalian) Misaki Formation (Matsumaru and Kimura, 1989) and the Early Miocene (Aquitanian) Shimizu Formation in this paper, both in Tosa Shimizu City. As both formations are bounded by faults, the stratigraphical relationship between them cannot be demonstrated (Figure 1). It is, however, inferred that both the Misaki and Shimizu Formations, which are characterized by Nephrolepidina praejaponica, are in close stratigraphical relationship.

Family Nummulitidae de Blainville, 1827 Genus Spiroclypeus H. Douvillé, 1905 Spiroclypeus margaritata (Schlumberger, 1902)

Figures 2-1-9; 3-1.

- Heterostegina margaritata Schlumberger, 1902, p. 252-253. pl. 7, fig. 4.
- Spiroclypeus orbitoideus H. Douvillé, 1905, p. 460-

462, pl. 14, figs. 1-6; Tan, 1937, p. 183-184, pl. 1, figs. 2-4, pl. 2, figs. 1-13, pl. 3, figs. 1-7 (non figs. 8, 24), pl. 4, fig. 1; Cole, 1957a, p. 332-333, pl. 95, figs. 6-12; Matsumaru, 1976, p. 200, pl. 1, figs. 1, 8, 10; Hashimoto, Matsumaru and Sugaya, 1981, p. 59, pl. 13, fig. 8.

- Spiroclypeus leupoldi van der Vlerk, 1925, p. 14-15, pl. 2, fig. 16; pl. 5, figs. 41, 48; Yabe and Hanzawa, 1929, p. 188, pl. 24, fig. 9; Cole, 1954, p. 577-578, pl. 208, figs. 1-19; Hanzawa, 1957, p. 45-46, pl. 5, figs. 7-13; Matsumaru, 1974, p. 108, pl. 15, figs. 2-4, 10, 13-15, 21-23, 28; Matsumaru, 1976, p. 199-200, pl. 1, figs. 4-7, 14-15, 21, 23-24; Hashimoto, Matsumaru and Alcantara, 1982, p. 34-36, pl. 10, figs. 18-20, pl. 11, figs. 1-7, 9.
- *Spiroclypeus wolfgangi* van der Vlerk, 1925, p. 15-16, pl. 2, fig. 15, pl. 5, figs. 39, 49; Tan, 1937, p. 183, pl. 1, fig. 1.
- *Spiroclypeus yabei* van der Vlerk, 1925, p. 16, pl. 2, fig. 19, pl. 5, figs. 40, 50; Tan, 1937, p. 183, pl. 1, figs. 5-6, pl. 3, figs. 10-11, pl. 4, figs. 8-10, text-fig. 1; Cole, 1954, p. 580-581, pl. 207, figs. 1-14, pl. 208, figs. 20-26; Cole, 1957b, p. 764, pl. 239, figs. 9-10.
- Spiroclypeus tidoenganensis van der Vlerk, 1925, p. 16-17, pl. 1, fig. 12, pl. 5, figs. 42, 47; Tan, 1937, p. 183, pl. 1, fig. 10, pl. 2, figs. 4-5, pl. 3, fig. 12, pl. 4, figs. 2-5, 19-21; Hanzawa, 1957, p. 46-47, pl. 3, figs. 1-6, pl. 4, figs. 1, 8-10; Cole, 1957a, p. 332, pl. 95, figs. 13-15; Matsumaru, 1976, p. 200, pl. 1, figs. 3, 9, 12, 18-20, 22, pl. 6, fig. 15; Hashimoto and Matsumaru, 1978, p. 85-86, pl. 11, fig. 2; Hashimoto, Matsumaru and Sugaya, 1981, p. 60-61, pl. 13, figs. 9, 12.
- Spiroclypeus margaritata (Schlumberger). Yabe and Hanzawa, 1925, p. 627-630, pl. 2, figs. 10, pl. 3, figs. 8-9, pl. 4, figs. 3-8, text-figs. 1-4; Yabe and Hanzawa, 1929, p. 187, pl. 23, figs. 1, 3-4, pl. 24, figs. 1-5; Krijnen, 1931, p. 89, pl. 1, figs. 1-3; Tan, 1937, p. 182-183, pl. 2, fig. 12, pl. 3, fig. 9, pl. 4, figs. 6-7; Hanzawa, 1940, p. 789-790, pl. 42, figs. 3-9; Cole, 1954, p. 578-580, pl. 206, figs. 10-25, pl. 207, figs. 15-16; Matsumaru, 1974, p. 108, pl. 15, figs. 16, 24, 26; Hashimoto and Matsumaru, 1975, p. 122, pl. 13, figs. 11-12; Hashimoto, Matsumaru and Sugaya, 1981, p. 59-60, pl. 13, fig. 3; Hashimoto, Matsumaru and Alcantara, 1982, p. 34-36, pl. 11, fig. 8.
- Spiroclypeus margaritata (Schlumberger) var. umbonata Yabe and Hanzawa, 1929, p. 187-188, pl. 124, figs. 5-8.
- Spiroclypeus higginsi Cole, 1939, p. 185, pl. 23, figs. 10-15, pl. 23, fig. 13; Hanzawa, 1957, p. 45, pl. 5, figs. 1-6, 14; Cole, 1957a, p. 332, pl. 95, figs. 1-5, pl. 109, fig. 16; Cole, 1957b, p. 763-764, pl. 239, figs. 11-12, 14; Matsumaru, 1974, p. 108, pl. 15,

figs. 1, 5, 8, 12, 18-19; Matsumaru, 1976, p. 199, pl. 1, figs. 2, 11, 16-17.

Description.—Test small, biconvex, bordered by a rather thin flange, central area 1.8 to 3.3 mm in diameter and 0.70 to 0.95 mm in thickness. The central portion has rather evenly distributed small pillars having a diameter of about 40 μ m. In some specimens the umbonal pustule becomes larger and has a diameter of 270 to 350 μ m.

The embryonic chambers consist of a spherical protoconch followed by a reniform deuteroconch; protoconch has diameter of 114 to 250 μ m, deuteroconch of 220 to 225 μ m. The height of the embryonic chambers in vertical section is 125 to 170 μ m. The embryonic chambers are followed by an undivided operculine chamber and the following chambers are divided into heterostegine chamberlets. The chamberlets near the periphery of the test are rectangular with radial length of 96 to 166 μ m and with tangential length of 64 to 104 μ m.

The lateral chambers are low to rather high, appressed between thick and thin floors and roofs. There are 6 lateral chambers on each side of the equatorial plane at the central part of the test. Lateral chambers have a length of 73 to 208 μ m and a height of 6 to 27 μ m. The floors and roofs have thickness of 20 to 94 μ m.

Remarks.—There is a confusion in the definition of the species of *Spiroclypeus*. Although there is no equatorial section of the studied specimen, the present form should be identified as *Spiroclypeus margaritata* (Schlumberger, 1902) for the following reasons.

Tan (1937, p. 182) divided the species of *Spiroclypeus* into the pustulate group, which is characterized by features of prominent pillars of the central portion of the test, and the reticulate group, which is characterized by the development of an externally reticulate appearance of the septa of the lateral chambers on the central part of the test. He regar-

ded Spiroclypeus margaritata and S. tidoenganensis van der Vlerk, 1925, as belonging to the pustulate group, while S. leupoldi van der Vlerk, 1925, and S. orbitoideus H. Douvillé, 1905, belong to the reticulate group. Spiroclypeus margaritata from Kita-Daito-Zima has, however, been revised as a member of the reticulate group by Hanzawa (1940, p. 789-790).

On the other hand, van der Vlerk (1925) identified a fragile form of Spiroclypeus from the Naintoepo Beds, Tidoengsche Landen, East Borneo as Spiroclypeus yabei, but Cole (1969, p. 8) assigned S. yabei as a synonym of S. margaritata. Though Hanzawa (1957, p. 46) distinguished S. tidoenganensis from S. margaritata from the Tagpochou Limestone, Saipan by the development of pustules and pillars traversing lateral chambers, Cole (1969, p. 8-10) regarded the former as a synonym of the latter. Also, Krijnen (1931, p. 94) described S. leupoldi, S. margaritata and S. tidoenganensis from Loc. 633L of the upper Naintoepo Beds, East Borneo, but Tan (1937, pl. 2, fig. 12; pl. 4, figs. 6-7) identified them as S. margaritata. Spiroclypeus higginsi Cole found from Guam by Cole (1939), was later a synonym of S. leupoldi in Cole (1969, p. 9), but the former was regarded as a primitive species of the latter by Matsumaru (1974), based on the specimens from the Mangagoy and Bislig Formations, Mindanao Island, Philippines.

From the above, it is inferred that the *Spiroclypeus* in the west Pacific region should be identified as *Spiroclypeus margaritata*.

Family Victoriellidae Chapman and Crespin, 1930 Genus Victoriella Chapman and Crespin, 1930 Victoriella conoidea (Rutten, 1914)

Figure 2-3

Carpenteria conoidea Rutten, 1914, p. 47, pl. 7, figs. 6-9.

Carpenteria proteiformis Goës var. plecte Chapman,

1921, p. 320, pl. 51, fig. 3.

- Carpenteria proteiformis Goës. Cushman, 1921, p. 361-362, pl. 73, figs. 2-3; Yabe and Hanzawa, 1929, p. 178, pl. 15, fig. 15.
- Victoriella conoidea (Rutten). Glaessner and Wade, 1959, p. 199, pl. 1, figs. 1-5, pl. 2, figs. 1-5, 7-10, pl. 3, fig. 3, text-figs. 1-4; Hornibrook, 1968, p. 64, fig. 11; Chaproniere, 1984, p. 50, pl. 13, figs. 5a-b.

Description.—Test conical, with a small attachment area near the apex; juvenile stage free, a low trochospiral coil, the coiling being high-spired, with three or four subspherical chambers per whorl in the adult stage, then erect conical in growth, 1.50 mm in length and 0.84 mm in width. Aperture umbilical, surrounded by a thick lip. Wall coarsely perforate, except for the imperforate region around the aperture, with pillars which displace the pores; wall structure calcareous, bilamellid, consisting of an inner lining and an outer lamella.

Remarks.—The present form is referred to *Victoriella conoidea* (Rutten) by peculiar features of its trochospirally coil, which differs in the direction of the axis of coiling from the nepionic stage, bilamellid walls and remarkable regular chamber shape and arrangement. Glaessner and Wade (1959) described *Carpenteria proteiformis* Goës and var. *plecte* Chapman, 1921 as junior synonyms of *Victoriella conoidea* (Rutten). The authors follow their opinion.

Family Rotaliidae Ehrenberg, 1839 Subfamily Pararotaliinae Reiss, 1963 Genus Pararotalia Y. Le Calvez, 1949 Pararotalia sp.

Figures 2-5-6

Description.—Test in a trochospiral coil, biconvex, periphery subacute, serrated, the dorsal side less vaulted than the ventral side, 0.7 to 0.8 mm in diameter and 0.5 to 0.6 mm in thickness; chambers flat to elevated on the spiral side, with an umbilical shoulder surrounding a large solid umbilical plug, smooth knob surrounded by a groove. The plug is 200 to $320 \,\mu$ m in diameter. The wall is thick, calcareous and perforate.

Remarks.—The illustrations of the present specimen show an oblique section of the ventral side of the test and a vertical section. They do not reveal the detailed structure, but the present form is similar to *Rotalia mecatepecensis* Nuttall, which was described from the Tagpochau Limestone, Saipan by Hanzawa (1957, p. 59-60), or *Rotalia floscula* Todd and Post from Bikini Drill Holes (Todd and Post, 1954). Judging from the description and illustration of *Rotalia mecatepecensis* and *R. floscula*, both species are within the genus *Pararotalia* by Le Calvez (1949). As such, the present form is identified as *Pararotalia* sp.

References cited

- Adams, C.G. and Belford, D.J., 1974 : Foraminiferal biostratigraphy of the Oligocene-Miocene limestones of Christmas Island (Indian Ocean). *Palaeontology*, vol. 17, part 3, p. 475-506.
- —, Gentry, A.W. and Whybrow, P.J., 1983: Dating the terminal Tethyan event. In, Meulenkamp, J.E. ed., Reconstruction of marine paleoenvironments, Utrecht Micropal. Bull. 30, p. 273-298.
- Bielle, M. and Caralp, M., 1967: Les Miogypsinidae de deux coupes profondes des Landes. *Bull. Soc. Geol. France, ser.* 7, vol.9, p.36-42.
- Blow, W.H., 1969: Late Middle Eocene to Recent planktonic foraminiferal biostratigraphy. In, Brönnimann, P. and Renz, H.H., eds., Proceedings of the First International Conference on Planktonic Microfossils, Geneva, 1967, vol. 1, p. 199-421. E.J. Brill, Leiden.
- Brönnimann, P., 1940: Über die tertiären Orbitoididen und die Miogypsiniden von Nordwest Marokko. Schweiz. Pal. Ges., Abh., vol. 63, art. 1, p. 1-113.
- Butt, A.A., 1966 : Late Oligocene Foraminifera from Escornebeou, S.W. France. Schotanus and Jens, Utrecht. p. 1-123.
- Chapman, F., 1921: Report of an examination of material obtained from a bore at Torquay. *Geol. Surv. Victoria, Record*, no. 4, p. 315-324.
- —, and Crespin, I., 1930: Rare Foraminifera from deep borings in the Victorian Tertiaries-Victoriella gen. nov., Cycloclypeus communis Martin, and Lepidocyclina borneensis Provale.

Proc. Royal Soc. Victoria, new ser. 42, p. 110-115.

- Chaproniere, G.C.H., 1984 : Oligocene and Miocene larger Foraminiferida from Australia and New Zealand. *BMR Jour. Australian Geology and Geophysics*, 188, p. 1-98.
- Cole, W.S., 1939: Larger Foraminifera from Guam. Jour. Paleont., vol. 13, no. 2, p. 183-189.
- —, 1954: Larger Foraminifera and smaller diagnostic foraminifera from Bikini drill holes. U.S. Geol. Surv., Prof. Paper 260-0, p. 569-608.
- —, 1957a: Larger Foraminifera of Saipan. *Ibid.*, 280-I, p. 321-360.
- —, 1957b: Larger Foraminifera from Eniwetok Atoll drill holes. *Ibid.*, 260-V, p. 743-784.
- —, 1969: Larger Foraminifera from deep drill holes on Midway Atoll. *Ibid.*, 680-C, p. 1-15.
- Coleman, P.J., 1963: Tertiary larger Foraminifera of the British Solomon Islands, southwest Pacific. *Micropaleontology*, vol. 9, no. 1, p. 1-38.
- Cushman, J.A., 1921 : Foraminifera of the Philippine and adjacent seas. U.S. Nat. Mus., Bull. 100, vol. 4, p. 1-608.
- de Blainville, H.M.D., 1827 : Manuel de malacologie et de conchyliologie (1825). Paris : F.G. Levrault.
- Debourle, A. and Delman, M., 1955: Victoriella aquitanica, nouveau foraminifère de l'oligocène d'Aquitaine. Bull. Soc. Geol. France, ser. 6, vol. 5, p. 47-49.
- de Mulder, E.F.J., 1975 : Microfauna and sedimentary tectonic history of the Ionian islands and western Epirus (Greece). Utrecht Micropal. Bull. 13, p. 1-139.
- Douvillé, H., 1905: Les foraminifères dans le Tertiaire de Borneo. *Bull. Soc. Geol. France, ser.* 4, vol. 5, p. 435-464.
- —, 1911: Les foraminifères dans le Tertiaire des Philippines. *Philippine Jour. Sci.*, vol. 6, no. 2, p. 53-80.
- Drooger, C.W., 1952: Study of American Miogypsinidae. Thesis Univ. Utrecht, Vonk and Co., Zeist., p. 1-80.
 - —, 1953: Some Indonesian Miogypsinidae. Proc. Koninkl. Ned. Akad. Wetensch., ser. B, 56, p. 104-123
- Ehrenberg, C.G., 1839: Über die Bildung der Kreidefelsen und des Kreidemergels durch unsichtbare Organismen. Phys. Abhandl. Konig. Akad. Wissensch. Berlin, 1838, p. 59-147.
- Glaessner, M.F. and Wade, M., 1959: Revision of the foraminiferal family Victoriellidae. *Mi*cropaleontology, vol. 5, no. 2, p. 193-212.
- Hanzawa, S., 1940: Micropaleontological studies of drill cores from a deep well in the Kita-Daito-Zima (North Borodino Island). Jubilee Pub. Comm. Prof. H. Yabe's 60th Birthday, vol. 2.

Tohoku Imp. Univ., Sendai, p. 755-802.

- —, 1957: Cenozoic Foraminifera of Micronesia. Geol. Soc. America, Mem. 66, p. 1-163.
- Hashimto, W. and Matsumaru, K., 1975: Larger Foraminifera from the Philippines. Part 3. Limestones from Eastern Coastal Ranges of North and Central Luzon. Geol. Palaeont. Southeast Asia, vol. 16, p. 117-125.
- and —, 1978: Larger foraminifera from the Philippines. Part 8. Larger foraminifera from Central Samar. *Ibid.*, vol. 19, p. 81-88.
- —, —, and Alcantara, P.M., 1982: Larger Foraminifera from the Philippines. Part 13. Larger Foraminifera from the Trankalan Limestone and the Escalante (Toboso) Formation, West of Lanao River Valley, Northeastern Occidental Negrons. *Ibid.*, vol. 24, p. 31-38.
- —, —, and Sugaya, M., 1981: Larger Foraminifera from the Philippines. Part 11. On the Coal Harbor Limestone, Cagraray Island, Batan Island Group, Albay province. *Ibid.*, vol. 22, p. 55-62.
- Henson, F.R.S., 1937: Larger Foraminifera from Aintab, Turkish Syria. *Eclog. Geol. Helv.*, vol. 30, no. 1, p. 45-57.
- Hornibrook, N. de B., 1968 : A handbook of New Zealand Microfossils (Foraminifera and Ostracoda). New Zealand Geol. Surv., Handbook, ser. 62, p. 1-136.
- Krijnen, W.F., 1931: Het genus Spiroclypeus in het Indo-Pacifische gebied. Geol.-Mijnb. Genoot. Ned. Kolonien, Verc., Geol. ser., vol. 9, p. 77-111.
- Le Calvez, Y., 1949: Revision des foraminifères Lutetiens du Bassin de Paris. II. Rotaliidae et familles affines. Mém. Serv. Carte Geol. Detaillée, France, p. 1-54.
- Matsumaru, K., 1971: Studies on the genus Nephrolepidina in Japan. Sci. Rep., Tohoku Univ., 2nd. ser. (Geol.), vol. 42, no. 2, p. 97-185.
- —, 1974: Larger Foraminifera from East Mindanao, the Philippines. Geol. Palaeont. Southeast Asia, vol.. 14, p. 101-115.
- —, 1976: Larger Foraminifera from the islands of Saipan and Guam, Micronesia. In, Takayanagi and Saito, T. eds., Progress in Micropaleontology. Micropaleontology Press Spec. Publ., New York., p. 190-213.
- and Barcelona, B.M., 1982: Tertiary stratigraphy of the Tayabas Isthmus and Central Part of Bondoc Peninsula, Luzon, the Philippines and larger Foraminifera. *Geol. Palaeont. Southeast Asia*, vol. 23, p. 77-90.
- and Kimura, K., 1989: Larger Foraminifera from the Eocene Shimizu and Misaki Formations in Tosa Shimizu City, Kochi Prefecture, Shikoku, Japan. *Trans. Proc. Palaeont. Soc. Japan*, *N.S.*, no. 156, p. 255-269.

- Myint Thein, Ogawa, Y. and Akiyama, T., 1991: Finding of Cretaceous radiolarians from the block of sheared olistostrome in the southern part of the Shimanto Belt near the Ashizuri Cape, Kochi Prefecture. *Jour. Geol. Soc. Japan*, vol. 97, no. 8, p. 667-669.
- Myint Thein, 1992: Analysis of sedimentary facies and paleogeographic reconstruction of the coherent and chaotic rock bodies in the Shimanto Supergroup, SW Shikoku, Japan. Mem. Fac. Sci., Kyushu Univ., ser. D, Earth and Planetary Sciences, vol. 27, no. 2, p. 75-99.
- Raju, D.S.N., 1974 : Study of Indian Miogypsinidae. Utrecht Micropal. Bull. 9, p. 1-148.
- Reiss, Z., 1963: Reclassification of perforate Foraminifera. Bull. Geol. Surv. Israel, vol. 35, p. 1-111.
- Rutten, L.M., 1914 : Foraminiferen führende Gesteine von Niederlandisch Neu-guinea. Uitkomsten Nederlandsch Nieuw-Guinea Expeditie in 1903, Geol., vol. 6, p. 21-51.
- Sacco, F., 1893: Sur quelques Tinoporinae du Miocene de Turin. Bull. Soc. Belge Geol. Paleont. Hydr. (1893-1894), vol. 7, p. 204-207.
- Scheffen, W., 1932: Zur Morphologie und Morphogenese der "Lepidocyclinen". Paläont. Zeitschrift, vol. 14, p. 233-256.
- Schlumberger, C., 1902: Note sur un Lepidocyclina nouveau de Borneo. Samml. Geol. Reichsmus. Leiden, ser. 1, vol. 6, p. 250-253.
- Tan Sin Hok, 1936: Zur Kenntniss der Miogypsiniden. Ing. Neder.-Ind., 4, Mijnb. Beol., Vol. 3, no. 3, p. 45-61.
- —, 1937: On the genus Spiroclypeus H. Douvillé with a description of the Eocene Spiroclypeus

vermicularis nov. sp. from Koetai in east Borneo. Ibid., vol. 4, no. 10, p. 177-193.

- Tobler, A., 1927: Verkalkung der Lateralkammern bei *Miogypsina. Eclog. Geol. Helv.*, vol. 20, p. 323-330.
- Todd, R. and Post, R., 1954: Smaller Foraminifera from Bikini drill holes. U.S. Geol. Surv., Prof. Paper 260-N, p. 547-568.
- van der Vlerk, I.M., 1924 : Miogypsina dehaartii nov. spec., de Larat (Moluques). Eclog. Geol. Helv., vol. 18, p. 429-431.
- —, 1925: A study of Tertiary Foraminifera from the "Tidoengsche Landen" (E. Borneo). Dutch East Indies, Dienst Mijnb., Wetensch. Meded., no. 3, p. 13-32.
- —, 1964: Biometric research on European Lepidocyclines. Proc. Kon. Ned. Akad. Wetensch., Amsterdam, ser. B, vol. 67, no. 5, p. 1-10.
- —, 1966: Miogypsinoides, Miogypsina, Lepidocyclina et Cycloclypeus de Larat (Moluques). Eclog. Geol. Helv., vol. 59, no. 1, p. 421-429.
- Vaughan, T.W., 1928: Subfamily Miogypsininae Vaughan. In, Cushman, J.A., Foraminifera: their classification and economic use. Spec. Publ. Cushman Lab. Foram. Res., vol. 1, p. 354.
- Yabe, H. and Hanzawa, S., 1925 : A Lepidocyclinalimestone from Klias Peninsula, B.N. Borneo. Geol. Mijnb. Genoot. Nederl. Kolonjen, Verh., Geol. ser., vol. 8, p. 617-632.
- and —, 1928: Tertiary foraminiferous rocks of Taiwan (Formosa). *Proc. Imp. Acad. Tokyo.*, vol. 4, no. 9, p. 533-536.
- and —, 1929: Tertiary foraminiferous rocks of the Philippines. Sci. Rep., Tohoku Imp. Univ., 2nd ser. (Geol.), vol. 11, no. 3, p. 137-190.

Ashizuri Cape 足摺岬, Misaki Formation 三崎累層, Ohki Beach 大岐海岸, Shimanto Belt 四万十帯, Shimizu Formation 清水累層, Takahata 高畑, Tosa Shimizu City 土佐清水市.

高知県足摺岬の清水累層から産する初期中新世(アキタニアン期)大型有孔虫:清水累層の火山起源のれき岩,砂岩中の石灰質充填物から産した大型有孔虫5属5種と小型有孔虫1属1種を記載した.大型有孔虫Miogypsinoides dehaartii, Spiroclypeus margaritata, Victoriella conoidea 動物群は,初期中新世(アキタニアン期)を示し、日本列島からは初めて報告された.同群中のNephrolepidina praejaponica は初期中新世(ブルディガリアン 期)の三崎累層から知られているため、清水累層と三崎累層の層位関係は、極めて近接した関係にあることが推定された.

949. LOWER PERMIAN FUSULINACEANS FROM BAN PHIA, CHANGWAT LOEI, NORTHEASTERN THAILAND*

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Abstract. Dark gray, thin-bedded limestones intercalated with calcareous sandstone and shale are exposed at about 3 km southwest of Ban Phia, Changwat Loei, northeastern Thailand. These limestones yield well-preserved fusulinaceans which indicate a late Early Permian (late Yakhtashian) age and represent a new additional Permian fusulinacean fauna in Thailand. The following species are new to science; *Darvasites ingavati, Pseudofusulina siamensis, Staffella? ovalis, Nankinella? loeiensis,* and *Pseudoendothyra? constricta.*

Key words. Fusulinacean, Loei, Lower Permian, Saraburi Limestone, Thailand, Yakhtashian.

Introduction

Fusulinaceans are one of the most intensively studied fossil groups in the Upper Paleozoic of Thailand (*e.g.*, Pitakpaivan, 1965; Igo, 1972; Toriyama, 1975; Toriyama and Kanmera, 1979; Ingavat and Douglass, 1981). Toriyama (1984) summarized these previous works and established 20 almost successive fusulinacean zones of late Early Carboniferous to Late Permian age. Although three or four faunal breaks were recognized, these zones were regarded as the standard biostratigraphy of the Upper Paleozoic in Southeastern Asia.

In November and December of 1990, Hisayoshi Igo, Katsuo Sashida, and Kenichiro Hisada of the University of Tsukuba, and Nikorn Nakornsri and Apsorn Ampornmaha of the Geological Survey Division, Department of Mineral Resources, Thailand made a field survey in the Changwat Loei area, northeastern Thailand; they collected limestones exposed along a roadside gutter, about 3 km southeast of Ban Phia, northeast of Loei (Figure 1).

We found an interesting fusulinacean fauna in these limestone beds, which indicate a Yakhtashian age of the Tethyan standard (late Early Permian). This fauna represents a newly recognized Permian fusulinacean zone in Thailand. We describe these materials in this paper.

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

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Figure 1. Map showing the fossil locality near Ban Phia, northeast of Loei, northeastern Thailand.

assistance with field work. The present manuscript was linguistically benefitted by Ms. Jean Thyfault.

Geologic setting

The Loei area is geologically called the "Loei Folded Belt" and is underlain by Middle to Upper Paleozoic rocks and widely overlain by thick Mesozoic non-marine strata called the "Khorat Series." Recently, the Upper Paleozoic rocks exposed in this area were divided into the Carboniferous Wang Saphung Formation and Permian Saraburi Group. The latter was further subdivided into the Dan Sai Shale, Saraburi Limestone, and Khao Luak Formation by Bunapas (1983) in descending order. According to the geologic map "Changwat Loei," scale 1: 250,000 (Charoenpravat *et al.*, 1976), the Permian rocks in this area are grouped as the Ratburi Group and subdivided into the Pha Dua, E-Lert, and Nam Mahoran Formations in descending order. The Ratburi Group has long been used as the Permian lithologic unit in Thailand, but it is now restricted to the limestone exposed in Peninsular Thailand, and the Saraburi Group (or Limestone) is commonly accepted to be in the Loei Folded Belt (Bunapas, 1983).

The Nam Mahoran Formation (or Saraburi Limestone) consists mainly of pale gray to white, massive to thickly bedded, and fossiliferous limestone, and it overlies the Wang Saphung Formation. Although actual stratigraphic contact between both formations has never been reported, their relation is regarded as conformable. The Nam Mahoran Formation constitutes high hills surrounded by steep cliffs, and the Wang Saphung Formation topographically occupies the low land. Furthermore, the Nam Mahoran yields Early Permian fusulinaceans (Igo, 1972), brachiopods (Yanagida, 1967), and other fossils, but the Wang Saphung vields Upper Carboniferous fossils (e.g., Igo, 1972; Yanagida, 1974, 1975; Toriyama et al., 1975). Subsequently, Fontaine et al. (1981) pointed out the occurrence of Devonian and Carboniferous fossils in the north of the Loei area and subdivided the Paleozoic rocks into the Ban Sa Ngao and Ban Khok Phai Formations in ascending order. These two formations are apparently equivalent with the Nong Dok Bua and Wang Saphung Formations in the present area.

Fusulinacean limestones exposed along a roadside gutter near Ban Phia are alternated



Figure 2. Columnar section with indication of sampling levels. 1: muddy limestone, 2: calcareous sandstone, 3: covered.

with calcareous sandstone and shale; the exposed area is about 30 m thick (Figure 2). On the basis of lithologic character, this sequence belongs to a part of the Wang Saphung Formation, and newly obtained paleontological data show that it apparently represents a much higher sequence than that exposed in Ban Sup, Ban Na Nam Man, along the Huai Nam Kai River, north of Ban Phia (Igo, 1972).

The present paleontological collections were made at five different levels (Loe-34, 35, 36, 37, and 38). Limestone beds are thinbedded (30-50 cm), black to dark brown, mostly muddy fusulinacean and algal wackestone with thin intercalations of shale, but a limestone bed in the middle part (Loe-36) is coarse-grained, muddy, and fusulinaceancrinoidal grainstone. As is discussed below, the geologic age of the fusulinacean fauna discriminated in the present study is Yakhtashian (late Early Permian), and this age is much younger than previous dating of the Nam Mahoran Formation by means of fusulinaceans and brachiopods (Asselian, early Early Permian). Recently we have found a Gzhelian (latest Carboniferous) fusulinacean fauna in a limestone of the Nam Mahoran Formation exposed near Ban Na Din Dam, east of Loei. These new paleontological data show that the stratigraphic relationship between the Wang Saphung and Nam Mahoran Formations is not simple superposition, but rather their upper and lower parts interfinger each other.

Appraisal of fusulinacean fauna

Fusulinaceans are rather rare in the lower levels (Loe-37, -38) but are abundant in the upper levels (Loe-34, -35, -36) of the section studied in this paper (Table 1). The present fusulinacean fauna is characterized by the abundant occurrence of the species belonging to the genera *Staffella*?, *Nankinella*?, *Pamirina, Darvasites*, and *Pseudofusulina*. The genera *Pamirina* and *Darvasites* have been known extensively in various areas of the Tethyan realm. The present fauna is similar to the Pamirina (Pamirina) darvasica-Darvasites contractus fauna reported from the upper Yakhtashian of Darvas (e.g., Kalmykova, 1967; Leven, 1970a, 1980) in the joint occurrence of the two zonal species. Pseudoreichelina darvasica Leven and species of Schubertella and Toriyamaia are also common in the Darvas fauna. A similar fauna characterized by Pamirina and Darvasites was reported from the Carnic Alps (Kahler and Kahler, 1980), Qinghai (Sheng and Sun, 1975), and Xiaodushan and Guangnan, eastern Yunnan (Zhou et al., 1987), both of South China. In these districts, however, the

fauna is characterized mainly by the occurrence of well-known species of schwagerinids such as *Chalaroschwagerina vulgaris* (Schellwien), *Pseudofusulina kraffti* (Schellwien), and *P. fusiformis* (Schellwien). The schwagerinids in the present fauna are represented mostly by *Pseudofusulina siamensis*, sp. nov., which is characterized by a small-sized shell. *Staffella*? *ovalis*, sp. nov. and other staffellids are rather common in the present fauna, but they are rare in the faunas reported from the above-mentioned districts.

Toriyama (1984) summarized the fusulinacean biostratigraphy in Thailand and established 20 almost continuous

Sample	Loe 38	Loe 37	Loe 36	Loe 35	Loe 34
Species					
Pamirina (Pamirina) darvasica Leven			++	+++	+++
Pamirina (Levenia) sp.					+
Schubertella melonica Dunbar and Skinner			++		++
S. sp. A			+		
S. sp. B		+	+		++
<i>Toriyamaia</i> sp.			+		+
Minojapanella (Minojapanella) sp.			+		
Darvasites contractus (Schellwien)			++		++
D. ingavati, sp. nov.			++		
Pseudofusulina siamensis, sp. nov.	+		+++		
P. sp. A					+
P. sp. B					+
P. sp. C					++
P. sp. D			+		+
Pseudoreichelina darvasica Leven	+			+	+
Staffella? ovalis, sp. nov.					++
<i>S.</i> sp. A		+			
S.? sp. B			+		
Nankinella ? loiensis, sp. nov.	+		+++		+
Sphaerulina cf. croatica Kochansky-Devidé			+		++
Pseudoendothyra? constricta, sp. nov.				++	
<i>P</i> .? sp.				+	

Table 1. List of fusulinaceans from Ban Phia, Changwat Loei.

+++: abundant ++: common +: rate

fusulinacean zones by his own and collaborators' studies. Among them, 14 zones are regarded to be Permian, and he pointed out three or four major faunal breaks in the Sakmarian-Yakhtashian, Dzhulfian, and probably in the uppermost Dorashamian. The Sakmarian-Yakhtashian interval is represented in between the Asselian Triticites ozawai-Paraschwagerina yanagidai Zone (Igo, 1972) and the upper Yakhtashian Misellina otai-M. cfr. termieri Zone (Toriyama, 1975). According to a recent study by Watanabe (1991), however, the Triticites ozawai-Paraschwagerina yanagidai Zone should be correlated with the latest Carboniferous (Gzhelian) rather than the earliest Permian (Asselian). Ingavat and Douglass (1981) reported the occurrence of Monodiexodina sutschanica (Dutkevitch) and M. shiptoni (Dunbar) from northwest Thailand, and they correlated this fauna with those of the post-Artinskian beds of the Salt Range, Pamirs, and others. The occurrence of the genus Monodiexodina is restricted mostly to calcareous sandstone or coarse-grained, siliceous limestone interbedded with arenaceous rocks. It is entirely absent from or very rarely occurring in ordinary limestone facies; therefore, the biostratigraphic relationship between the Monodiexodina Zone and other fusulinacean zones established in limestone is not clear. Torivama (1984) placed the Monodiexodina shiptoni Zone of northwest Thailand in the upper Yakhtashian, but this zone may represent an age younger than Yakhtashian. The Misellina otai-M. cfr. termieri Zone also represents a younger age than Toriyama's proposed one and can be correlated with the lower Bolorian based on the first appearance of Misellina (s.s.) in other Tethyan regions (e.g., Ueno, 1991b).

As mentioned above, the fusulinacean zones apparently indicating the Asselian to Yakhtashian are absent in Thailand according to previous reports. The present upper Yakhtashian fauna, however, is a new addition to the fusulinacean biostratigraphic units of Thailand and fills in a part of the Early Permian interval.

Systematic paleontology

Order Foraminiferida Eichwald, 1830 Suborder Fusulinina Wedekind, 1937 Superfamily Fusulinacea von Möller, 1878 Family Ozawainellidae Thompson and Foster, 1937 Subfamily Ozawainellinae Thompson and Foster, 1937 Genus *Pamirina* Leven, 1970 emend. Kobayashi, 1977

Discussion. —There are two diverse opinions on the taxonomic position of the genus *Pamirina*. One is that *Pamirina* belongs to the family Ozawainellidae (*e.g.*, Leven, 1970a) and the other that it belongs to the family Staffellidae (*e.g.*, Rozovskaya, 1975). This problem is worth discussing as it also concerns the classification and phylogeny of the higher multiapertural fusulinaceans, the families Verbeekinidae and Neoschwagerinidae.

The genus Pamirina was established by Leven (1970a) with the occurrence of the type species of Pamirina darvasica Leven in the upper Yakhtashian (Artinskian) Safetdaron Suite of southwestern Darvas. Based on the shell shape and spirothecal composition, Leven classified this genus in the family Ozawainellidae and excluded staffellied genera as the ancestor of Pamirina because their spirothecal structure is quite different from that of the latter. He considered an ozawainellid genus such as Eostaffella or Pseudostaffella a possible ancestor of the genus Pamirina, although their occurrence is rare in the Upper Carboniferous and Lower Permian.

In the interpretation of Rozovskaya (1975), *Pamirina* is morphologically intermediate between the genera *Pseudoendothyra* and *Misellina*, although the spirothecal structure of *Pseudoendothyra* is different from those of the other two genera. She regarded *Pamirina* as belonging to the family Staffellidae.

Kobayashi (1977) first pointed out the existence of two distinct groups in Pamirina. One has a thickly lenticular shell, and the other has a subspherical shell. The spirotheca of the former consists of a single structureless layer in the inner volutions, and a tectum and lower, less dense layer (protheca) in the outer ones. The other subspherical type has a spirotheca consisting of a single structureless layer in the inner volutions; a tectum and lower, less dense layer in the middle ones; and a tectum and fine alveolar keriotheca in the outer volutions. He interpreted the former type to be more primitive than the latter, but their stratigraphic occurrence was not definitely confirmed. Kobayashi (op. cit.) assigned the genus Pamirina to the family Ozawainellidae and insisted that the family Verbeekinidae is the direct descendant of the family Ozawainellidae.

Recently, Rauser-Chernoussova (1988) described some "pamirinids" from the Artinskian of the Caspian Basin in Central Asia and emphasized that the genus Pamirina is surely referable to the family Staffellidae rather than to the Ozawainellidae, because its spirothecal composition is identical with that of staffellids. The Caspian "pamirinids", however, have a spirotheca completely replaced by secondary mineralization, which is quite different in composition compared with that of original Pamirina described by Leven (1970a). Accordingly, all of the Caspian "pamirinids" of Rauser-Chernoussova (1988) should be referred to such staffellid genera as Staffella, Sphaerulina, or Pseudoendothyra.

Very recently, Ueno (1991a) studied materials collected from the Akiyoshi Limestone Group of western Japan and split a new subgenus *Levenia* from *Pamirina*. This new subgenus does not have any fine alveolar layer in the spirotheca. He explained that *Levenia* is an ancestor of *Pamirina* (s.s.) based on the previously mentioned spirothecal structure and stratigraphic occurrence. According to Ueno (1991a), both *Pamirina* (s.s.) and *Levenia* have a microgranular spirotheca similar to that of the ozawainellids. No evidence of secondary mineralization has been observed in their spirotheca.

All specimens referable to the genus Pamirina (s.l.) studied herein have a microgranular spirotheca (see Figures 3-3b, 3-9b, and 3-10b), whereas staffellids (e.g., Staffella? ovalis, sp. nov. and others), even in the same thin section, have a light-brownish spirotheca which has been completely replaced by secondary mineralization. This suggests that the spirothecal compositions of *Pamirina* (s.l.) and staffellids fundamentally differ. Consequently, it is invalid to include the genus Pamirina in the family Staffellidae. Judging from the spirothecal composition and general shell shape, it seems most suitable, as Leven (1970a) originally considered, that the genus Pamirina should be referred to the family Ozawainellidae.

Huang and Zeng (1984) proposed the subgenus Nanpanella for the genus Pamirina, with the type of Pamirina (Nanpanella) laxa Huang and Zeng from the Lower Permian Longlinian of Longlin, Guangxi of South China. Nanpanella, however, has a spirotheca replaced by secondary mineralization and is apparently assignable to the family Staffellidae (Sheng *et al.*, 1988).

Subgenus Pamirina Leven, 1970 Pamirina (Pamirina) darvasica Leven, 1970

Figures 3-1-9, 4-1-33

Pamirina darvasica Leven, 1970a, p. 23-24, pl. 1, figs. 1-9, 23-24 (not pl. 1, figs. 10-11); Rozovskaya, 1975, pl. 35, figs. 4-5 (same as pl. 1, figs 1-2 of Leven, 1970a); Kobayashi, 1977, p. 14-15, pl. 2, figs. 1a-b, 2-3; Liu et al., 1978, p. 80, pl. 18, figs. 8, 12; Kahler and Kahler, 1980, p. 187-188, pl. 3, fig. 8 (not pl. 3, fig. 7); Loeblich and Tappan, 1988, pl. 295, fig. 11 (not pl. 295, fig. 12, same as pl. 1, fig. 1 of Leven, 1970a); Xia, in Ding et al., 1991, pl. 10, fig. 22.



Figure 3. 1-9. Pamirina (Pamirina) darvasica Leven, 1-3a, 4-7: axial sections, IGUT-KU0231, KU0232, KU0233, KU0234, KU0235, KU0236, KU0237, 8, 9a: sagittal sections, IGUT-KU0263, KU0264, \times 40, 3b, 9b: enlarged parts of 3a and 9a, \times 100. 10. Pamirina (Levenia) sp., 10a: axial section, IGUT-KU0273, \times 40, 10b: enlargement of 10a, \times 100. 11-13. Toriyamaia sp., 11: tangential section, IGUT-KU0274, 12: sagittal section, IGUT-KU0275, 13: axial section, IGUT-KU0276, \times 30. 14: Minojapanella (Minojapanella) sp., diagonal section, IGUT-KU0277, \times 40. 15-19: Schubertella sp. B, axial sections, IGUT-KU0278, KU0279, KU0280, KU0281, KU0282, \times 40. 20-25: Schubertella melonica Dunbar and Skinner, axial sections IGUT-KU0283, KU0284, KU0285, KU0286, KU0287, KU0288, \times 40. 26, 27. Schubertella sp. A, 26: tangential section, IGUT-KU0289, 27: axial section, IGUT-KU0290, \times 40.



- Chinlingella chinlingensis Wang and Sun, 1973, p. 152-153, 172, pl. 1, figs. 12, 17-32, pl. 3, figs. 1, 5, 10.
- Chinlingella nobilis Wang and Sun, 1973, p. 153-154, 173, pl. 1, figs. 1-5, 9-11.
- Staffella aff. mölleri Ozawa. Sakagami and Iwai, 1974, p. 54-55, pl. 4, figs. 1-13.
- Pamirina orbiculoidea Sheng and Sun, 1975, p. 45-46, pl. 1, figs. 11-14; Zhou et al., 1987, pl. 2, figs. 5-6; Ding et al., 1989, pl. 2, figs. 27-28.
- Pamirina nobilis (Wang and Sun). Lin et al., 1977, p. 20, pl. 3, figs. 21-22; Sun et al., 1983, p. 9, pl. 2, fig. 15 (same as pl. 1, fig. 1 of Wang and Sun, 1973); Xia et al., 1986, pl. 9, figs. 6, 8; Zhou et al., 1987, pl. 2, figs. 3-4; Ding et al., 1989, pl. 2, fig. 21.
- Pamirina chinlingensis (Wang and Sun). Sun et al., 1983, p. 9, pl. 2, fig. 17 (same as pl. 1, fig. 19 of Wang and Sun, 1973); Nie and Song, 1983, pl. 1, figs. 23-24; Xia et al., 1986, pl. 10, fig. 9; Zhou et al., 1987, pl. 2, figs. 1-2; Ding et al., 1987, pl. 1, figs. 4-5; Loeblich and Tappan, 1988, pl. 295, figs. 8-10 (same as pl. 1, figs. 19-20, 31 of Wang and Sun, 1973); Sun and Zhang, 1988, pl. 3, figs. 7, 15; Ding et al., 1989, pl. 2, figs. 23-26.
- Pamirina (Pamirina) chinlingensis (Wang and Sun). Huang and Zeng, 1984, pl. 4, fig. 7.
- Pamirina (Pamirina) darvasica Leven. Huang and Zeng, 1984, pl. 4, fig. 14; Ueno, 1991a, p. 744– 745, figs. 3–1–7.
- Pamirina angulata Xia, in Ding et al., 1991, p. 128, pl. 9, figs. 8-9.
- Pamirina adulta Xia, in Ding et al., 1991, p. 127-128, pl. 9, figs. 10-11, 14.

Description.—Shell small and almost spherical with slightly umbilicated axial regions and broadly rounded periphery. Mature specimens having 5 to 6 volutions, 0.47 to 0.81 mm in length and 0.48 to 0.87 mm in width. Form ratio ranges from 0.81 to 1.06, averaging 0.92 for 39 specimens.

Inner few volutions lenticular in shape and almost planispirally to skew coiled. Shell becomes expanded and spherical beyond the third or the fourth volution. Radius vectors of the first to the fifth, and the fifth and a half volution of well oriented axial section (Figure 4-2) 0.03, 0.05, 0.12, 0.19, 0.30, and 0.36 mm, and form ratios 0.56, 0.63, 0.92, 0.91, 0.89, and 0.95, respectively.

Proloculus small and spherical. Its outside diameter ranges from 0.030 to 0.055 mm, averaging 0.043 mm for 55 specimens.

Spirotheca thin and composed of a single structureless layer in inner volutions, of a tectum and lower, less dense layer (protheca) in middle ones, and of a tectum and clearly defined fine alveolar keriotheca in outer volutions. Thickness of spirotheca of the first to the fifth and the fifth and a half volution of the above-mentioned specimen 0.005, 0.010, 0.015, 0.025, 0.030, and 0.025 mm, respectively.

Septa straight and plane. Tips of septa in sagittal section slightly swollen. Septal sutures commonly depressed. Septal counts of the first to the fifth volution of typical sagittal section (Figure 4-31) 8, 9, 12, 13, and 15, respectively. Chomata low, broad, commonly asymmetrical, and developed in outer volutions. Tunnel angles of the third to the fifth volution of the above-mentioned axial section 24, 37, and 49 degrees, respectively.

Remarks.—Broad morphological variations, especially in the coiling nature of the juvenarium, are observed in the Loei specimens. Form having a straight axis of coiling (e.g., Figure 4-6) is identical with Pamirina (P.) darvasica originally described by Leven (1970a) from the Yakhtashian of Darvas, whereas that having a rotated axis of coiling in the juvenile volutions (e.g., Figure 4-1) is quite similar to Pamirina (P.) orbiculoidea proposed by Sheng and Sun (1975) from the Qinghai district of South China. The Loei specimens seem to comprise a single population, hence the former species, darvasica, is considered to be a senior synonym with the latter one, orbiculoidea.

[←] Figure 4. 1-33. Pamirina (Pamirina) darvasica Leven, 1-25: axial sections, IGUT-KU0238, KU0239, KU0240, KU0241, KU0242, KU0243, KU0244, KU0245, KU0246, KU0247, KU0248, KU0249, KU0250, KU0251, KU0252, KU0253, KU0254, KU0255, KU0256, KU0257, KU0258, KU0259, KU0260, KU0261, KU0262, 26-33: sagittal sections, IGUT-KU0265, KU0266, KU0267, KU0268, KU0269, KU0270, KU0271, KU0272, ×40.

Pamirina (P.) adulta and P. (P.) augusta described by Xia (in Ding et al., 1991) from the Lower Permian Nagatoella-Darvasites (Nd) and Pamirina globosa (Pv) Subzones of the Pamirina Zone (upper part of the Beiyangshan Limestone) in Zhen'an, Shaanxi are identical with P. (P.) darvasica Leven.

Materials.—Axial sections: IGUT-KU0231—KU0234, KU0236—KU0245, KU0247—KU0250, KU0252, KU0253, KU0255—KU0262 from Loe-34; KU0254 from Loe-35; KU0235, KU0246, KU0251 from Loe-36. Sagittal sections: IGUT-KU0263, KU0265, KU0267—KU0271 from Loe-35, KU0266 from Loe-36.

Subgenus Levenia Ueno, 1991 Pamirina (Levenia) sp.

Figure 3-10

Description .- Shell minute and thickly lenticular with slightly depressed axial regions and broadly rounded periphery. Specimen having 5 volutions, 0.34 mm in length and 0.49 mm in width, giving a form ratio of 0.70. Axis of coiling slightly rotated in inner volutions. Radius vectors of the first to the fifth volution 0.02, 0.04, 0.07, 0.12, and 0.19 mm, and form ratios 0.57, 0.73, 0.70, 0.72, and 0.73, respectively. Proloculus minute and spherical, being 0.035 mm in outside diameter. Spirotheca very thin and composed of a single structureless layer in inner volutions, but of a tectum and lower, less dense layer (protheca) in outer ones. Thickness of spirotheca of the first to the fifth volution 0.005, 0.005, 0.010, 0.015, and 0.020 mm, respectively. Very small chomata discernible in outer volutions.

Remarks.—The present species somewhat resembles *Pamirina* (*Levenia*) *tethydis* originally described by Kobayashi (1977) from the Hanagiri Limestone of the Kwanto Mountains, central Japan. The former can be distinguished from the latter in having a slightly rotated axis of coiling in the inner volutions. The specific identification, however, is postponed because only one specimen was obtained in this study.

Material.—Axial section : IGUT-KU0273 from Loe-34.

Family Schubertellidae Skinner, 1931 Subfamily Schubertellinae Skinner, 1931 Genus Schubertella Staff and Wedekind, 1910 Schubertella melonica Dunbar and Skinner, 1937

Figures 3-20-25

Schubertella melonica Dunbar and Skinner, 1937, p. 611-613, pl. 57, figs. 10-14; Chang, 1963, p. 44, pl. 1, figs. 9-10, 13; Chen and Wang, 1983, p. 38-39, pl. 2, figs. 16-17; Nie and Song, 1983, pl. 2, fig. 11; Da and Sun, 1983, p. 16, pl. 25, fig. 13. *Schubertella* ex gr. *melonica* Dunbar and Skinner.

Leven and Scherbovich, 1978, p. 85, pl. 1, fig. 6.

Description.—Shell small and fusiform with bluntly pointed polar ends and straight or slightly convex lateral slopes. Mature shell of $4\frac{1}{2}$ to 5 volutions 0.70 to 1.10 mm in length and 0.45 to 0.61 mm in width. Form ratio varies from 1.57 to 1.80, averaging 1.68 for 8 specimens.

Inner $1\frac{1}{2}$ to 2 volutions skew coiled with a short axis of coiling. Shell expands gradually beyond the third volution. Radius vectors of the first to the fifth volution of illustrated axial section (Figure 3-24) 0.05, 0.08, 0.14, 0.22, and 0.34 mm, and form ratios 0.89, 0.88, 1.56, 1.74, and 1.49, respectively.

Proloculus small and spherical, measuring 0.035 to 0.050 mm in outside diameter.

Spirotheca thin and composed of a tectum and lower, less dense layer. Thickness of spirotheca of the first to the fifth volution of the above-mentioned specimen 0.010, 0.015, 0.025, 0.030, and 0.035 mm, respectively.

Septa unfluted and almost plane. Massive chomata developed in outer volutions. Tunnel path straight. Tunnel angles of the third to the fifth volution of axial section mentioned above 29, 38, and 23 degrees, respectively.

Remarks.—The Loei specimens are almost

identical with the original ones described by Dunbar and Skinner (1937) from the Lower Permian of Texas, except for a slightly smaller shell in the former.

Materials.—Axial sections : IGUT-KU0286 from Loe-34; KU0283—KU0285, KU0287, KU0288 from Loe-36.

Schubertella sp. A

Figures 3-26-27

Descriptive remarks.-Shell small and elongate fusiform with bluntly pointed poles. Axial section of $4\frac{1}{2}$ volutions (Figure 3-27) 1.21 mm in length and 0.49 mm in width, giving a form ratio of 2.50. Inner 2 volutions skew coiled. Radius vectors of the first to the fourth and the fourth and a half volution 0.05, 0.07, 0.13, 0.21, and 0.27 mm, and form ratios 0.67, 1.00, 1.46, 2.05, and 2.32, respectively. Proloculus small and spherical, being 0.045 mm in outside diameter. Spirotheca thin and composed of a tectum and lower, less dense layer. Thickness of spirotheca of the first to the fourth volution 0.010, 0.010, 0.020, and 0.025 mm, respectively. Chomata asymmetrical and developed in outer volutions. Tunnel angles of the second to the fourth volution 19, 29 and 42 degrees, respectively.

This species resembles *Schubertella kingi* Dunbar and Skinner, but differs from the latter in having a slightly larger shell.

Materials.—Axial section : IGUT-KU0290. Tangential section : IGUT-KU0289. Both from Loe-36.

Schubertella sp. B

Figures 3-15-19

Remarks.—Schubertella sp. B can be easily distinguished from *S. melonica* Dunbar and Skinner in having a smaller shell and form ratio.

Materials.—Axial sections : IGUT-KU0278, KU0280—KU0282 from Loe-34; KU0279 from Loe-36. Genus Toriyamaia Kanmera, 1956 Toriyamaia sp.

Figures 3-11-13

Remarks.—Several poorly oriented specimens were obtained and identified with *Toriyamaia* sp. The specific identification is postponed until better materials are available.

Materials.—Sagittal section : IGUT-KU0275 from Loe-34. Tangential section : IGUT-KU0274 from Loe-34. Oblique section : IGUT-KU0276 from Loe-36.

Family Boultoniidae Skinner and Wilde, 1954 Genus *Minojapanella* Fujimoto and Kanuma, 1953 Subgenus *Minojapanella* Fujimoto and Kanuma, 1953 *Minojapanella (Minojapanella)* sp.

Figure 3-14

Remarks.—Although the present material is poorly preserved, the spirothecal composition and intensely fluted septa of the specimen indicate it to be referable to the genus *Minojapanella*.

Material.—Diagonal section : IGUT-KU0277 from Loe-36.

Family Schwagerinidae Dunbar and Henbest, 1930 Subfamily Schwagerininae Dunbar and Henbest, 1930 Genus Darvasites Miklukho-Maklay, 1959

Darvasites contractus (Schellwien, 1909)

Figures 5-1-13

- *Fusulina contracta* Schellwien (MS). Staff, 1909, pl. 7, fig. 8.
- *Fusulina contracta* Schellwien, 1909, p. 159-163, pl. 13, figs. 9-12.
- *Triticites contractus* (Schellwien). Chen, 1934a, p. 34-35, pl. 5, fig. 13, pl. 7, figs. 1-4; Chen, 1934b, p. 41-42, pl. 7, figs. 2-3.
- Triticites sinensis Chen, 1934a, p. 36-38, pl. 7, figs. 8, 12.
- Hemifusulina contracta (Schellwien). Chang, 1963, p. 49-50, pl. 3, figs. 1-3, 10; Sheng, 1966, p. 73,



Figure 5. 1-13. Darvasites contractus (Schellwien), 1, 5, 7, 8, 10: axial sections of megalospheric form, IGUT-KU0291, KU0295, KU0297, KU0298, KU0300, 2, 6, 12: slightly oblique axial sections of megalospheric form, IGUT-KU0292, KU0296, KU0302, 3, 4: sagittal sections of megalospheric form, IGUT-KU0293, KU0294, 9, 11: tangential sections of megalospheric form, IGUT-KU0299, KU0301, $\times 15$, 13: axial section of microspheric form, IGUT-KU0303, $\times 30$. 14-20. Darvasites ingavati Igo, Ueno and Sashida, sp. nov., 14: axial section of the holotype, IGUT-KU0304, 15: sagittal section of paratype, IGUT-KU0305, 16-20: axial sections of paratypes, IGUT-KU0306, KU0307, KU0308, KU0309, KU0310, $\times 15$. 21, 22: Pseudofusulina sp. A, axial sections IGUT-KU0311, KU0312, 21: $\times 15$, 22: $\times 10$.

pl. 10, fig. 4 (same as pl. 7, fig. 1 of Chen, 1934a).

- Triticites (Darvasites) cf. contractus (Schellwien), Kochansky-Devidé, 1964, pl. 18, fig. 5.
- Darvasites ex gr. contractus (Schellwien). Ramovš and Kochansky-Devidé, 1965, p. 331-332, pl. 4, fig. 1 (same as pl. 18, fig. 5 of Kochansky-Devidé, 1964).
- Hemifusulina sinensis (Chen). Sheng, 1966, p. 75, pl. 7, fig. 7 (same as pl. 7, fig. 8 of Chen, 1934a).
- Darvasites contractus (Schellwien). Leven, 1967, p. 136, pl. 4, figs. 5-6; Kochansky-Devidé, 1970, p. 196, 231-232, pl. 5, figs. 9-11; Ramovš and Kochansky-Devidé, 1979, pl. 3, fig. 12; Kahler and Kahler, 1980, p. 195, pl. 5, fig. 2; Kahler, 1983, p. 59, pl. 7, fig. 7; Kahler, 1985, p. 49-51, pl. 3, figs. 2-4
- Triticites (Darvasites) contractus (Shellwien). Kalmykova, 1967, p. 166-168, pl. 2, figs. 9-13.
- *Eoparafusulina contracta* (Schellwien). Sheng and Sun, 1975, p. 38-39, pl. 5, fig. 11; Lin *et al.*, 1977, p. 45, pl. 9, fig. 15 (same as pl. 7, fig. 1 of Chen, 1934a); Da and Sun, 1983, p. 98, pl. 8, fig. 16; Xia and Zhang, 1985, p. 130-131, pl. 28, fig. 11.
- *Eoparafusulina bellula* Skinner and Wilde. Sheng and Sun, 1975, p. 38, pl. 5, figs. 1-3.
- *Eoparafusulina sinensis* (Chen). Wang *et al.*, 1982, p. 81-82, pl. 19, figs. 3, 5 (3 : same as pl. 7, fig. 8 of Chen, 1934a).
- ? Eoparafusulina contracta (Schellwien). Liu et al., 1978, p. 67, pl. 15, fig. 12; Wang et al., 1982, p. 81, pl. 19, fig. 1; Chen and Wang, 1983, p. 83, pl. 14, figs. 13, 17; Wang, 1987, pl. 7, fig. 14; Luo et al., 1989, pl. 2, fig. 7.
- not Triticites (Rauserites) contractus (Schellwien). Rozovskaya, 1958, p. 101, pl. 9, figs. 10-12.

Description.—Shell of megalospheric form small for the genus and ellipsoidal with rounded polar ends and almost straight ventral part. Microspheric form smaller than megalospheric one. Mature specimens of megalospheric form having 7 to 8 volutions, 2.25 to 3.95 mm in length and 1.30 to 1.80 mm in width. Form ratio varies from 1.73 to 2.51, averaging 1.94 for 7 specimens. Microspheric form of 7 $\frac{1}{2}$ volutions (Figure 5-13) 1.38 mm in length and 0.83 mm in width, giving a form ratio of 1.67.

In megalospheric form, axis of coiling straight throughout growth and inner 3 or 4 volutions rather tightly coiled. In microspheric form, inner few volutions tightly and skew coiled. Radius vectors of the first to the eighth volution of typical axial section of megalospheric form (Figure 5-1) 0.09, 0.13, 0.19, 0.26, 0.37, 0.49, 0.68, and 0.82 mm, and form ratios 1.44, 1.85, 1.90, 2.11, 2.08, 2.27, 2.04, and 2.02, respectively. Radius vectors of the first to the seventh volution of illustrated axial section of microspheric form 0.04, 0.07, 0.10, 0.14, 0.20, 0.27, and 0.38 mm, and form ratios 1.00, 1.00, 1.20, 1.50, 1.80, 1.89, and 1.71, respectively.

Proloculus of megalospheric form small and spherical. Its outside diameter ranges from 0.100 to 0.140 mm, averaging 0.115 mm for 19 specimens. Proloculus of microspheric form spherical and minute, being 0.030 mm in outside diameter.

Spirotheca composed of a tectum and lower structureless layer in inner few volutions, but of a tectum and coarse keriotheca in outer ones in both forms. Thickness of spirotheca of the first to the eighth volution of the above-mentioned megalospheric specimen 0.010, 0.010, 0.025, 0.030, 0.030, 0.065, 0.075, and 0.055 mm, respectively.

Septa moderately and regularly fluted throughout length of shell except for central part. Septal counts of the first to the eighth volution of one illustrated sagittal section (Figure 5-4) 5, 9, 13?, 15, 19, 18, 16, and 18, respectively.

Chomata massive and well developed in all volutions except for the last one in some specimens. Tunnel path straight. Tunnel angles of the first to the seventh volution of the above-mentioned megalospheric specimen 29, 44, 34, 32, 38, 40, and 32 degrees, respectively. Axial fillings absent.

Remarks.—Darvasites contractus was originally described by Schellwien (1909) from the Lower Permian of Darvas. Subsequently, Kalmykova (1967) also described and illustrated this species from Darvas. The Loei specimens are identical with Schellwien's original and Kalmykova's topotype specimens, and a further discussion is unnecessary. Darvasites sinensis proposed by Chen (1934a) from the lower part of the Chuanshan Limestone of southern Jiangsu (Kiangsu) has an ellipsoidal shell, massive chomata throughout growth, and moderately and regularly fluted septa; it is considered to be a junior synonym of Darvasites contractus (Schellwien).

Dimorphism is recognized in the Loei specimens. The microspheric individual is characterized by a skew-coiled juvenarium and has a smaller shell and much smaller proloculus than do the megalospheric individuals.

Materials.—Axial sections of megalospheric form: IGUT-KU0291, KU0297 from Loe-34; KU0295, KU0298, KU0300 from Loe-36. Slightly oblique axial sections of megalospheric form: IGUT-KU0292, KU0296 from Loe-34; KU0302 from Loe-36. Sagittal sections of megalospheric form: IGUT-KU0294 from Loe-34; KU0293 from Loe-36. Tan-

Table 2. Measurements of Darvasites ingavati Igo, Ueno and Sashida, sp. nov (in mm)

Reg. no.		Elaura	Lanath	Width	n F.R.		Radius vector						
		Figure	Length	width		D.1 .	1	2	3	4	5	6	
1	IGUT-KU0304	5-14	2.88	1.55	1.85	0.110	0.09	0.13	0.21	0.34	0.52	0.69	
2	IGUT-KU0306	5-16	2.90	1.45	2.00	0.115	0.09	0.14	0.22	0.35	0.55	0.77	
3	IGUT-KU0307	5-17	2.45	1.38	1.78	0.115	0.08	0.14	0.19	0.31	0.50	0.71	
4	IGUT-KU0308	5-18	2.58	1.35	1.91	0.110	0.09	0.16	0.27	0.47	0.70		
5	IGUT-KU0309	5-19	2.80	1.35	2.07	0.125	0.12	0.19	0.33	0.53	0.73		
6	IGUT-KU0310	5-20	2.00	1.00	2.00	0.120	0.09	0.15	0.23	0.37	0.53		

			Form	ratio			Thickness of spirotheca								
	1	2	3	4	5	6	1	2	3	4	5	6			
1	1.11	1.61	2.09	2.03	1.98	1.99	0.010	0.015	0.030	0.065	0.070	0.080			
2	1.55	1.79	2.00	2.00	1.98	1.96	0.015	0.025	0.045	0.060	0.070	_			
3	1.13	1.14	1.50	1.66	1.56	1.68	0.015	0.020	0.030	0.055	0.070				
4	1.56	1.81	1.68	1.48	1.81		0.015	0.025	0.040	0.070	0.080				
5	1.33	1.50	1.65	1.64	1.87		—	0.030	0.045	0.065	0.060				
6	1.56	1.67	1.96	2.00	1.96		0.010	0.030	0.030	0.055	0.070				

		Tun	nel ang	le (deg	rees)	
	1	2	3	4	5	6
1	32	25	32	44	39	23
2	44	32	40	36	36	—
3	—	_	42	48	45	—
4	—	44	51	42	44	
5		—	38	25	_	
6		30	33	48	—	

F.R.: Form ratio D.P.: Diameter of proloculus gential sections of megalospheric form: IGUT-KU0299 from Loe-34; KU0301 from Loe-36. Axial section of microspheric form: IGUT-KU0303 from Loe-34.

Darvasites ingavati Igo, Ueno and Sashida, sp. nov.

Figures 5-14-20

Diagnosis.—Small *Darvasites* with oval shell, broadly rounded median portion, small rudimentary chomata, and regularly fluted septa.

Description.—Shell small for the genus and oval in shape with bluntly pointed axial regions and broadly rounded median portion. Mature specimens of 5 to 6, rarely 6 $\frac{1}{2}$ volutions 2.00 to 2.90 mm in length and 1.00 to 1.55 mm in width. Form ratio ranges from 1.78 to 2.07, averaging 1.94 for 6 specimens. The holotype of 6 $\frac{1}{2}$ volutions 2.88 mm in length and 1.55 mm in width with a form ratio of 1.85.

The first volution rather tightly coiled. Axis of coiling straight throughout growth. Radius vectors of the first to the sixth volution of the holotype 0.09, 0.13, 0.21, 0.34, 0.52, and 0.69 mm, and form ratios 1.11, 1.61, 2.09, 2.03, 1.98, and 1.99, respectively.

Proloculus small and spherical. Its outside diameter ranges from 0.100 to 0.125 mm, averaging 0.114 mm for 7 specimens.

Spirotheca composed of a tectum and lower structureless layer in inner few volutions, but of a tectum and coarse keriotheca in outer ones. Thickness of spirotheca of the first to the sixth volution of the holotype 0.010, 0.015, 0.030, 0.065, 0.070, and 0.080 mm, respectively.

Septa moderately and regularly fluted throughout length of shell except for central part. Intensity of septal fluting increases toward polar ends. Septal counts of the first to the sixth volution of sagittal section of paratype (Figure 5-15) 6, 11, 10, 14, 18, and 24?, respectively.

Chomata small but developed in all volu-

tions except for the last one in some specimens. Tunnel path straight. Tunnel angles of the first to the sixth volution of the holotype 32, 25, 32, 44, 39, and 33 degrees, respectively. Axial fillings absent.

Remarks.—The present new species is characterized by an oval shell and rather small chomata. It can be distinguished easily from *Darvasites contractus* (Schellwien) by its shell shape and development of chomata.

Darvasites ingavati, sp. nov. somewhat resembles D. citrus originally described by Ramovš and Kochansky-Devidé (1965) from the Permian of Croatia. The former, however, differs from the latter in having a larger shell.

Etymology.—This specific name is dedicated to Mrs. Rucha Ingavat, former paleontologist of the Geological Survey Division, Department of Mineral Resources, Thailand, for her contribution to the study of fusulinaceans in Thailand.

Materials.—Axial section of the holotype: IGUT-KU0304. Axial sections of paratypes: IGUT-KU0306—KU0310. Sagittal section of paratype: IGUT-KU0305. All specimens from Loe-36.

Measurements.—See Table 2.

Genus Pseudofusulina Dunbar and Skinner, 1931 Pseudofusulina siamensis Igo, Ueno and Sashida, sp. nov.

Figures 6-1-15

Diagnosis.—Pseudofusulina having a small elongate fusiform shell with tightly coiled juvenarium and small chomata in all volutions except for the last one. Septa moderately and regularly fluted.

Description.—Shell small for the genus and elongate fusiform with bluntly pointed polar ends and almost straight lateral slopes. Mature shell having 7 to 8 volutions, 4.88 to 6.70 mm in length and 2.10 to 2.73 mm in width. Form ratio ranges from 2.18 to 2.73, averaging 2.35 for 7 specimens. The



Figure 6. 1-15. *Pseudofusulina siamensis* Igo, Ueno and Sashida, sp. nov., 1: axial section of the holotype, IGUT-KU0313, 2, 5-7, 13: axial sections of paratypes, IGUT-KU0314, KU0317, KU0318, KU0319, KU0325, 3, 4, 9, 10, 15: sagittal sections of paratypes, IGUT-KU0315, KU0316, KU0321, KU0322, KU0327, 8, 11: slightly oblique axial sections of paratypes, IGUT-KU0320, KU0323, 12, 14: tangential sections of paratypes, IGUT-KU0324, KU0326. 16, 17. *Pseudofusulina* sp. B, 16: tangential section, IGUT-KU0338, 17: axial section, IGUT-KU0329. 18: *Pseudofusulina* sp. D, slightly oblique axial section, IGUT-KU0330. 19-23. *Pseudofusulina* sp. C, 19: tangential section IGUT-KU0331, 20-22: axial sections, IGUT-KU0332, KU0333, KU0334, 23: sagittal section, IGUT-KU0335. All × 10.

Reg. no.		Figure	Length	Width	F.R.	DP	Radius vector							
		liguic				D.F.	1	2	3	4	5	6	7	8
1	IGUT-KU0313	6-1	5.18	2.28	2.27	0.120	0.11	0.15	0.21	0.34	0.51	0.77	1.06	
2	IGUT-KU0314	6-2	5.70	2.48	2.30	0.115	0.10	0.16	0.20	0.30	0.53	0.81	1.15	1.39
3	IGUT-KU0317	6-5	4.88	2.15	2.27	0.125	0.10	0.15	0.23	0.36	0.59	0.86	—	
4	IGUT-KU0318	6-6	4.90	2.25	2.18	0.120	0.11	0.16	0.25	0.40	0.59	0.87	1.24	
5	IGUT-KU0319	6-7	5.05	2.10	2.40	0.110	0.08	0.14	0.21	0.34	0.55	0.80	1.13	
6	IGUT-KU0325	6-13	5.25	2.28	2.30	0.150	0.10	0.16	0.24	0.34	0.54	0.79	1.03	

Table 3. Measurements of Pseudofusulina siamensis Igo, Ueno and Sashida, sp. nov. (in mm)

	Form ratio								Thickness of spirotheca							
	1	2	3	4	5	6	7	8	1	2	3	4	5	6	7	8
1	1.00	1.60	2.41	2.46	2.45	2.47	2.43		0.010	0.015	0.025	0.040	0.080	0.090	0.110	
2	1.10	1.25	1.76	2.29	2.13	1.99	1.91	1.99	0.010	0.025	0.035	0.050	0.050	0.100	0.120	0.120
3	1.30	1.67	1.76	2.11	1.88	2.08	—		0.020	0.020	0.035	0.050	0.095	0.095	—	
4	1.00	1.24	1.50	1.66	1.80	2.06	1.96		0.015	0.025	0.030	0.045	0.090	0.110	—	
5	1.75	2.07	2.41	2.43	2.58	2.54	2.41		0.010	0.020	0.035	0.035	0.060	0.130	0.120	
6	1.10	1.44	1.92	2.37	2.48	2.28	—		0.015	0.020	0.025	0.050	0.080	0.110	0.100	

		Tunnel angle (degrees)													
	1	2	3	4	5	6	7	8							
1		46	44	50	53	47	30?								
2	—		35	38	41	46	—	—							
3	30	40	55	43	43	37									
4	_	—	25	27	35	42	—								
5	29	41	45	51	49	45	_								
6		34	37	46	52	50									

Reg. no.		Figure	Septal counts									
		rigure	1	2	3	4	5	6	7			
1	IGUT-KU0315	6-3	8	12	15	15	18	21	_			
2	IGUT-KU0316	6-4	7	11	11	14	15	19				
3	IGUT-KU0321	6-9	8	11	13	14	18	21				
4	IGUT-KU0322	6-10	8	12	18	17	21					
5	IGUT-KU0327	6-15	7	11	12	17	18	21				

holotype of 7 volutions 5.18 mm in length and 2.28 mm in width, giving a form ratio of 2.27.

The first 1 or 2 volutions rather tightly coiled. Beyond the second or the third volution, shell expands uniformly and becomes fusiform to elongate fusiform. Axis of coiling straight throughout growth. Radius vectors of the first to the seventh volution of the holotype 0.11, 0.15, 0.21, 0.34, 0.51, 0.77, and 1.06 mm, and form ratios 1.00, 1.60, 2.41, 2.46, 2.45, 2.47, and 2.43, respectively.

Proloculus small and spherical. Its outside diameter varies from 0.100 to 0.150 mm, averaging 0.119 mm for 22 specimens.

Spirotheca thin and consists of a tectum and keriotheca. Thickness of spirotheca of the first to the seventh volution of the holotype 0.010, 0.015, 0.025, 0.040, 0.080, 0.090, and 0.110 mm, respectively.

Septa thin and regularly fluted throughout length of shell except for central part. Septal counts of the first to the sixth volution of sagittal section of one of the paratypes (Figure 6-4) 7, 11, 11, 14, 15, and 19, respectively.

Chomata small and observed in the first to penultimate volution. Tunnel path almost straight. Tunnel angles of the first to the sixth volution of axial section of one paratype (Figure 6-7) 29, 41, 45, 51, 59, and 45 degrees, respectively. No axial fillings present.

Remarks.—Pseudofusulina siamensis, sp. nov. is a species of this genus having a characteristic small shell, whose size is more or less similar to that of the genus *Triticites*. The former, however, has more fluted septa than



Figure 7. 1-4. Pseudoreichelina darvasica Leven, 1, 2: axial sections, IGUT-KU0336, KU0337, 3: tangential section, IGUT-KU0338, 4: parallel section, IGUT-KU0339. 5-13. Pseudoendothyra? constricta Igo, Ueno and Sashida, sp. nov., 5: axial section of the holotype, IGUT-KU0340, 6-9, 11-13: axial sections of paratypes, IGUT-KU0341, KU0342, KU0343, KU0344, KU0346, KU0347, KU0348, 10: parallel section of paratype, IGUT-KU0345. 14: Pseudoendothyra? sp., axial section, IGUT-KU0349. All ×40.

does the latter. It is also allied to the genus *Daixina* in some respects but differs from the latter in having a smaller and more compactly coiled shell. The stratigraphic position of the present species and *Daixina* is different.

Etymology.—The specific name comes from Siam, the ancient name of Thailand.

Materials.—Axial section of the holotype : IGUT-KU0313. Axial sections of paratypes : IGUT-KU0314, KU0317—KU0319, KU0325. Sagittal sections of paratypes : IGUT-KU0315, KU0316, KU0321, KU0322, KU0327. Slightly oblique axial sections of paratypes : IGUT-KU0320, KU0323. Tangential sections of paratypes : IGUT-KU0324, KU0326. All specimens from Loe-36.

Measurements.—See Table 3.

Pseudofusulina sp. A

Figures 5-21-22

Remarks.—The present species somewhat resembles *Pseudofusulina krotowi* (Schellwien) but differs from the latter by its smaller shell and less fluted septa.

Materials.—Axial sections : IGUT-KU0311, KU0312 from Loe-34.

Pseudofusulina sp. B

Figures 6-16-17

Remarks.—Pseudofusulina sp. B is similar to *P. kraffti* (Schellwien) to some extent but differs from the latter in having a smaller shell.

Materials.—Axial section : IGUT-KU0329. Tangential section : IGUT-KU0328. Both from Loe-34.

Pseudofusulina sp. C

Figures 6-19-23

Remarks.—Pseudofusulina sp. C differs from *P. siamensis*, sp. nov. in having a slightly larger proloculus and less fluted septa.

Materials.—Axial sections : IGUT-

KU0332-KU0334. Sagittal section : IGUT-KU0335. Tangential section : IGUT-KU0331. All specimens from Loe-34.

Pseudofusulina sp. D

Figure 6-18

Remarks.—The present species can be distinguished from *Pseudofusulina siamensis*, sp. nov. and *Pseudofusulina* sp. C in having a larger proloculus.

Material.—Slightly oblique axial section : IGUT-KU0330 from Loe-34.

Family Staffellidae Miklukho-Maklay, 1949 Genus Pseudoreichelina Leven, 1970 Pseudoreichelina darvasica Leven, 1970

Figures 7-1-4

Pseudoreichelina darvasica Leven, 1970b, p. 19-20, pl. 1, figs. 6-13; Lipina and Rozanov, 1973, pl. 6, figs. 8-10 (same as pl. 1, figs. 7-8, 11 of Leven, 1970b); Rozovskaya, 1975, pl. 35, fig. 6 (same as pl. 1, fig. 8 of Leven, 1970b); Loeblich and Tappan, 1988, pl. 254, figs. 17-18 (same as pl. 1, figs. 8, 13 of Leven, 1970b); Ueno, 1992, p. 8-10, figs. 5-1-16.

Descriptive remarks.—Shell consists of 2 parts. Early part of 4 volutions, lenticular and coiled planispirally with shallowly umbilicated axial regions and angular periphery. Later one uniserial and rectilinear, consisting of 6 to 9 chambers. Total length of shell 1.28 to 1.40 mm. Spirotheca light-brownish colored and replaced by secondary mineralization. Aperture basal in coiled part, but median in rectilinear one.

Pseudoreichelina darvasica Leven is known from the upper Yakhtashian (Artinskian) Safetdaron Suite of southwestern Darvas (Leven, 1970b) and the upper Yakhtashian of the Akiyoshi Limestone Group, southwest Japan (Ueno, 1992). The Loei specimens are identical with both of the Darvas and Akiyoshi ones.

Materials.—Axial sections : IGUT-KU0336, KU0337 from Loe-34. Tangential



Figure 8. 1-4. Staffella? sp. B, 1, 2, 4: axial sections, IGUT-KU0350, KU0351, KU0353, 3: sagittal section, IGUT-KU0352. 5-14. Nankinella? loeiensis Igo, Ueno and Sashida, sp. nov., 5: axial section of the holotype, IGUT-KU0354, 6: sagittal section of paratype, IGUT-KU0355, 7-14: axial sections of paratypes, IGUT-KU0356, KU0357, KU0358, KU0359, KU0360, KU0361, KU0362, KU0363. 15: Staffella sp. A, tangential section, IGUT-KU0364. All × 30.
section : IGUT-KU0338 from Loe-34. Parallel section : IGUT-KU0339 from Loe-38.

> Genus Staffella Ozawa, 1925 Staffella? ovalis Igo, Ueno and Sashida, sp. nov.

Figures 9-9-15

Diagnosis.—Small Permian *Staffella* having a thickly lenticular or oval shell with broadly rounded periphery and slightly umbilicated polar regions. Coiling planispiral throughout growth. Spirotheca with fine alveolar structure. Chomata distinct.

Description.—Shell small for Permian representatives of this genus and thickly lenticular or oval with broadly rounded periphery and shallowly depressed polar regions. Mature specimens having $7\frac{1}{2}$ to 8 $\frac{1}{2}$ volutions, 1.20 to 1.45 mm in length and 1. 33 to 1.75 mm in width. Form ratio varies from 0.79 to 0.91, averaging 0.83 for 7 specimens. Holotype specimen of 8 volutions 1.20 mm in length and 1.53 mm in width, giving a form ratio of 0.79.

Shell expands uniformly throughout growth. Axis of coiling straight. Radius vectors of the first to the eighth volution of the holotype 0.08, 0.13, 0.19, 0.26, 0.35, 0.48, 0.63, and 0.76? mm, and form ratios 0.88, 0.77, 0.79, 0.77, 0.83, 0.83, 0.79, and 0.78, respectively.

Proloculus spherical or somewhat irregular in shape, being 0.050 to 0.080 mm in outside diameter.

Spirotheca light-brownish colored and rather thin, replaced by secondary mineralization. Fine alveolar structure visible in spirotheca of outer volutions. Thickness of spirotheca of the first to the eighth volution of the holotype 0.010, 0.015, 0.020 ?, 0.020, 0.020, 0.030, 0.040, and 0.040 mm, respectively.

Septa thin and planar. Septal counts of the fourth to the seventh volution of sagittal section of one paratype (Figure 9-10) 9, 11, 12, and 14, respectively.

Chomata small, asymmetrical, and developed in all volutions. Tunnel path straight and narrow. Tunnel angles of the second to the seventh volution of axial section of one paratype (Figure 9-13) 24, 21, 21, 21, 23, and 28 degrees, respectively. Axial fillings present in some specimens.

Remarks.—Staffella ? transiens originally described by Kochansky-Devidé (1965) from the Pv_1 (Lower Permian) of Croatia, is the

Reg. no.		Figure	Length	Width	F.R.	ПР	Radius vector									
		I iguit				D .1 .	1	2	3	4	5	6	7	8		
1	IGUT-KU0376	9-12	1.23	1.43	0.86	_	0.09	0.14	0.19	0.27	0.34	0.44	0.58	0.76		
2	IGUT-KU0377	9-13	1.23	1.50	0.82	0.080?	0.08	0.13	0.19	0.26	0.36	0.49	0.63			
3	IGUT-KU0378	9-14	1.25	1.50	0.83	0.090	0.10	0.16	0.20	0.28	0.36	0.49	0.60	0.75		
4	IGUT-KU0379	9-15	1.20	1.53	0.79	0.050	0.08	0.13	0.18	0.25	0.34	0.47	0.61	0.74		

Table 4. Measurements of Staffella ? ovalis Igo, Ueno and Sashida, sp. nov. (in mm)

	Form ratio								Thickness of spirotheca								
	1	2	3	4	5	6	7	8	1	2	3	4	5	6	7	8	
1	0.78	0.64	0.65	0.64	0.74	0.84	0.90	0.85	0.010	0.015	0.020	0.030	0.025	0.025	0.040	0.030	
2	0.50	0.54	0.65	0.85	0.81	0.82	0.82		0.015	0.020	0.020	0.020	0.025	0.030	0.035		
3	0.60	0.56	0.71	0.79	0.81	0.80	0.84	0.82	0.015	0.015	—	0.020	0.030?	0.030	0.050	0.060	
4	0.88	0.77	0.79	0.77	0.83	0.83	0.79	0.78	0.010	0.015	0.020?	0.020	0.020	0.030	0.040	0.040	



Figure 9. 1-8. Sphaerulina cf. croatica Kochansky-Devidé, 1, 2, 4-8: axial sections, IGUT-KU0365, KU0366, KU0368, KU0369, KU0370, KU0371, KU0372, 3: tangential section, IGUT-KU0367. 9-15. Staffella? ovalis Igo, Ueno and Sashida, sp. nov., 15: axial section of the holotype, IGUT-KU0379, 9, 12-14: axial sections of paratypes, IGUT-KU0373, KU0376, KU0377, KU0378, 10, 11: sagittal sections of paratypes, IGUT-KU0375. All \times 30.

closest to the present new species. The former, however, has a larger shell, more volutions, and slightly smaller form ratio than the latter.

Staffella ? ovalis, sp. nov. somewhat resembles S. yaziensis originally described by Wang and Sun (1973) from the Yazi Formation of the Qinling (Chinling) Range, South China. However, the former has a larger shell and more volutions than does the latter.

Presence of fine alveolar structure in the spirotheca of the present form is inconsistent with the original diagnosis of the genus *Staffella*. The present new species is, therefore, tentatively assigned to the genus *Staffella*.

Etymology.—This specific name is derived from the Latin *ovalis*, meaning oval.

Materials.—Axial section of the holotype : IGUT-KU0379. Axial sections of paratypes : IGUT-KU0373, KU0376—KU0378. Sagittal sections of paratypes : IGUT-KU0374, KU0375. All specimens from Loe-34.

Measurements.-See Table 4.

Staffella sp. A

Figure 8-15

Remarks.—Staffella sp. A differs from *Staffella*? *ovalis*, sp. nov. in having a larger form ratio and absence of fine alveolar structure in the spirotheca.

Material.—Tangential section : IGUT-KU0364 from Loe-37.

Staffella ? sp. B

Figures 8-1-4

Remarks.—This species is characterized by having a *Staffella*-like rounded periphery in the inner volutions and *Nankinella*-like angular periphery in the last one, and a replaced spirotheca composed of a tectum and fine alveolar keriotheca. Therefore, it is tentatively assigned to the genus *Staffella*.

Materials.—Axial sections: IGUT-KU0350, KU0351, KU0353. Sagittal section: IGUT-KU0352. All specimens from Loe-36.

Reg. no.		Figure	Length	Width	F.R.	D.P.	Radius vector								
		I iguie					1	2	3	4	5	6	7		
1	IGUT-KU0354	8-5	0.90	1.65	0.55	0.060	0.08	0.15	0.26	0.43	0.66	0.87			
2	IGUT-KU0356	8-7	0.83	1.58	0.52	0.070	0.08	0.15	0.24	0.40	0.61	0.79			
3	IGUT-KU0357	8-8	0.88	1.53	0.57	0.065	0.09	0.16	0.24	0.35	0.49	0.67	0.86		
4	IGUT-KU0358	8-9	0.95	1.70	0.56	0.085	0.09	0.15	0.21	0.32	0.48	0.61	0.81		
5	IGUT-KU0361	8-12	0.80	1.40	0.57	0.070	0.06	0.12	0.19	0.29	0.45	0.64			

Table 5. Measurements of Nankinella ? loeiensis Igo, Ueno and Sashida, sp. nov. (in mm)

	·····		Fo	orm rat	io			Thickness of spirotheca								
	1	2	3	4	5	6	7	1	2	3	4	• 5	6	7		
1	0.50	0.50	0.50	0.50	0.49	0.46			0.015	0.020	0.025	0.035	0.020?			
2	0.75	0.67	0.56	0.56	0.54	0.53		0.010	0.020	0.020	0.035	0.035	0.040			
3	0.44	0.50	0.45	0.53	0.58	0.57	0.53		0.010	0.015	—	0.040	0.050	0.025		
4	0.56	0.53	0.55	0.58	0.51	0.62	0.55	0.010	0.010	0.020	—	0.025	0.030	0.040		
5	0.50	0.50	0.50	0.57	0.48	0.47		0.005	0.015	0.030	0.035	0.040	0.040			

Genus Nankinella Lee, 1934 Nankinella ? loeiensis Igo, Ueno and Sashida, sp. nov.

Figures 8-5-14

Diagnosis.—Permian Nankinella having a small lenticular shell with angular periphery and almost straight lateral slopes. Axis of coiling straight throughout growth. Spirotheca with fine alveolar structure. Chomata distinct.

Description.—Shell small for Permian representatives of the genus and lenticular with angular periphery and almost straight lateral slopes. Axial regions slightly depressed. Mature specimens of 6 to 7, rarely $7\frac{1}{2}$ volutions 0.73 to 1.05 mm in length and 1.48 to 1.75 mm in width. Form ratio ranges from 0.49 to 0.63, averaging 0.55 for 11 specimens. Holotype specimen of 6 volutions 0.90 mm in length and 1.65 mm in width with a form ratio of 0.55.

Shell involute throughout except for inner few volutions and expands gradually. Axis of coiling straight throughout growth. Radius vectors of the first to the sixth volution of the holotype 0.08, 0.15, 0.26, 0.43, 0.66, and 0.87 mm, and form ratios 0.50, 0.50, 0.50, 0.50, 0.49, and 0.46, respectively.

Proloculus small and spherical. Its outside diameter varies from 0.060 to 0.085 mm, averaging 0.067 mm for 9 specimens.

Spirotheca light brown and replaced by secondary mineralization. Fine alveolar structure discernible in spirotheca. Thickness of spirotheca of the second to the sixth volution of the holotype 0.015, 0.020, 0.025, 0.035, and 0.020? mm, respectively.

Septa not fluted and slightly bending anteriorly. Septal counts of the first to the sixth volution of illustrated sagittal section of paratype (Figure 8-6) 9?, 11, 13, 12, 16, and 19, respectively.

Small but rather prominent chomata present in all volutions. Tunnel path narrow and almost straight. Tunnel angles of the second to the seventh volution of axial section of one paratype (Figure 8-8) 12, 12, 15, 15, 12, and 14 degrees, respectively.

Remarks.—*Nankinella*? *loeiensis*, sp. nov. somewhat resembles *N. quasihunanensis* described by Sheng (1963) from the Wujiaping (Wuchaping) Limestone of the Guizhou (Kueichow) district. The former, however, can be distinguished from the latter in having a smaller shell. Moreover, the present new species occupies a much lower stratigraphic position than that of Sheng's species.

The present new species also differs from *Nankinella inflata* (Colani) in having a smaller shell.

In this study, *loeiensis* is questionably assigned to the genus *Nankinella*, because it has a fine alveolar structure in the spirotheca, which is inconsistent with the original diagnosis of the genus.

Etymology.—This species is named for the local geographical name Loei, from where the specimens were collected.

Materials.—Axial section of the holotype: IGUT-KU0354. Axial sections of paratypes: IGUT-KU0356—KU0363. Sagittal section of paratype: IGUT-KU0355. All specimens from Loe-36.

Measurements.—See Table 5.

Genus Sphaerulina Lee, 1933 Sphaerulina cf. croatica Kochansky-Devidé, 1965

Figures 9-1-8

Compare. -

Sphaerulina croatica Kochansky-Devide, 1965, p. 123-125, 143-144, pl. 5, fig. 9, pl. 6, figs. 1-14, pl. 7, figs. 1-8, pl. 8, fig. 1; Rui, 1979, pl. 1, figs. 20-21.

Description.—Shell small and almost spherical with slightly umbilicated axial regions and broadly expanded periphery. Mature specimens having 5 to 6 volutions, 1.03 to 1.50 mm in length and 1.13 to 1.40 mm in width. Form ratio ranges from 0.91 to 1.11, averaging 1.02 for 7 specimens.

Axis of coiling straight throughout growth.

Outer volutions expanded rather rapidly and become loose compared with inner ones. Radius vectors of the first to the sixth volution of typical axial section (Figure 9-8) 0.08, 0.14, 0.21, 0.36, 0.54, and 0.72 mm, and form ratios 0.88, 0.86, 1.05, 0.97, 1.06, and 1.09, respectively.

Proloculus small and almost spherical, being 0.060 to 0.080 mm in outside diameter.

Spirotheca light brown, rather thick and recrystallized by secondary mineralization. Fine alveolar structure discernible in spirotheca. Thickness of spirotheca of the first to the sixth volution of the above-mentioned specimen 0.010, 0.020, 0.025, 0.070, 0.090, and 0.070 mm, respectively.

Septa rather thick, plane, and slightly bending anteriorly. Low and small chomata observed in outer volutions.

Remarks.—Sphaerulina croatica was originally described by Kochansky-Devide (1965) from the Pv_1 and Pds (Lower and Middle Permian) of Croatia. The Loei specimens have a slightly smaller shell and fewer volutions than the latter.

This species can be easily distinguished from *Sphaerulina crassispira* Lee, the type species of the genus, in having a more loosely coiled shell.

Materials.—Axial sections : IGUT-KU0365, KU0366, KU0368—KU0370, KU0372 from Loe-34; KU0371 from Loe-36. Tangential section : IGUT-KU0367 from Loe-34.

Genus Pseudoendothyra Mikhailov, 1939 Pseudoendothyra? constricta Igo, Ueno and Sashida, sp. nov.

Figures 7-5-13

Diagnosis—Small Permian Pseudoendothyra having a lenticular shell with bluntly

Reg. no. 1 IGUT-KU0340 2 IGUT-KU0341 3 IGUT-KU0342 4 IGUT-KU0343 5 IGUT-KU0344	Figure	Length	Width	FR	ΠP	Radius vector					
		Tiguie	Length	width	1.1.	D.I.	1	2	3	4	5
1	IGUT-KU0340	7-5	0.36	1.03	0.35	0.060	0.07	0.13	0.19	0.35	0.55
2	IGUT-KU0341	7-6	0.34	0.90	0.38	0.060	0.06	0.12	0.18	0.32	0.49
3	IGUT-KU0342	7-7	0.30	0.97	0.31	0.050	0.08	0.14	0.24	0.40	
4	IGUT-KU0343	7-8	0.27	0.76	0.36	0.050	0.05	0.10	0.16	0.28	0.46
5	IGUT-KU0344	7-9	0.34	0.74	0.41	0.045	0.07	0.14	0.23	0.38	
6	IGUT-KU0347	7-12	0.41	0.87	0.47	0.055	0.06	0.11	0.16	0.27	0.49
7	IGUT-KU0348	7-13	0.37	1.16	0.32	0.060	0.07	0.12	0.19	0.35	0.52

Table 6. Measurements of Pseudoendothyra? constricta Igo, Ueno and Sashida, sp. nov. (in mm)

		F	orm ra	tio		Thickness of spirotheca								
	1	2	3	4	5	1	2	3	4	5				
1	0.86	0.69	0.60	0.56	0.46	0.010	0.015	0.025	0.025	0.025				
2	0.67	0.67	0.58	0.48	0.44	0.010	0.010	0.010	0.015	0.025				
3	0.75	0.64	0.56	0.49		0.015	0.010	0.030	0.020					
4	0.60	0.60	0.59	0.55	0.47	0.005	0.010	0.020	0.020	0.020				
5	0.57	0.50	0.54	0.46		0.010	0.020	0.020	0.015					
6	0.67	0.55	0.53	0.50	0.42	0.010	0.015	0.025	0.030	0.010				
7	0.57	0.50	0.50	0.44	0.39	0.010	0.015	0.020	0.020	0.020				

pointed periphery and shallow umbilicus. Outermost volution commonly evolute. Spirotheca with fine alveolar structure. Chomata present.

Description.—Shell small for Permian representatives of the genus and lenticular with bluntly pointed periphery and slightly umbilicated axial regions. Mature specimens having $4\frac{1}{2}$ to $5\frac{1}{2}$ volutions, 0.27 to 0.41 mm in length and 0.76 to 1.16 mm in width. Form ratio ranges from 0.32 to 0.47, averaging 0.37 for 7 specimens. The holotype of 5 volutions 0.36 mm in length and 1.03 mm in width with a form ratio of 0.35.

Axis of coiling almost straight. Shell involute except for the last volution and expands uniformly. Radius vectors of the first to the fifth volution of the holotype (Figure 7-5) 0.07, 0.13, 0.19, 0.35, and 0.55 mm, and form ratios 0.86, 0.69, 0.60, 0.56, and 0.46, respectively.

Proloculus small and spherical, being 0.045 to 0.060 mm in outside diameter.

Spirotheca light brown and slightly recrystallized. Fine alveolar structure observed in spirotheca. Thickness of spirotheca of the first to the fifth volution of the holotype 0.010, 0.015, 0.025, 0.025, and 0.025 mm, respectively.

Septa unfluted. Chomata small and asymmetrical, developed in all volutions except for the first one in some specimens. Tunnel path straight. Tunnel angles of the first to the fifth volution of axial section of one paratype (Figure 7-8) 17, 17, 15, 17, and 25 degrees, respectively.

Remarks.—Fine alveolar structure is observed in the spirotheca of the present new species. This seems inconsistent with the original diagnosis of the genus *Pseudoendothyra*. Accordingly, the present new species is tentatively assigned to *Pseudoendothyra*.

Pseudoendothyra? *constricta*, sp. nov. somewhat resembles *P. obiniouensis* which was originally described by Leven (1970b) from the Yakhtashian of Darvas. However, the former differs from the latter in having a slightly larger shell with more volutions, smaller form ratio and more rounded periphery, and fine alveolar structure in the spirotheca.

Etymology. — The specific name is derived from the Latin *constrictus*, meaning constricted.

Materials.—Axial section of the holotype: IGUT-KU0340. Axial sections of paratypes: IGUT-KU0341—KU0344, KU0346 —KU0348. Parallel section of paratype: IGUT-KU0345. All specimens from Loe-35. Measurements.—See Table 6.

Pseudoendothyra ? sp.

Figure 7-14

Remarks.—Fine alveolar structure is discernible in the spirotheca of the present species. This species is closely allied to *Pseudoendothyra*? constricta, sp. nov., but differs from the latter in having a slightly longer axis of coiling and larger form ratio.

Material.—Axial section : IGUT-KU0349 from Loe-35.

References cited

- Bunapas, S., 1983: Paleozoic succession in Thailand. Proceedings of the Workshop on Stratigraphic Correlation of Thailand and Malaysia, vol. 1, Technical Paper, p. 29-76.
- Charoenpravat, A., Wongwanich, T., Tantiwanit, W. and Theetiparivatra, U., 1976: Geological Map of Changwat Loei, Sheet NE47-12, ser. 1: 250, 000. Geol. Surv. Div., Dept. Min. Res. Thailand.
- Chang, L.H. (Zhang, L.X.), 1963: Upper Carboniferous fusulinids from Keping and its adjacent regions, southwestern Sinkiang (I). Acta Palaeont. Sinica, vol. 11, no. 1, p. 36-70, pls. 1-3. (in Chinese and Russian)
- Chen, S (Chen, X), 1934a: Fusulinidae of South China, Part 1. *Palaeont. Sinica*, ser. B, vol. 4, fasc. 2, p. 1-185, pls. 1-16.
- —, 1934b: Fusulinidae of the Huanglung and Maping limestones, Kwangsi. Mem. Nat. Res. Inst. Geol., no. 14, p. 33-54, pls. 6-8.
- and Wang, J.H., 1983: The fusulinids of the Maping Limestone of the Upper Carboniferous from Yishan, Guangxi. *Palaeont. Sinica, N.S. B*, no. 19, p. 1-139, pls. 1-25. (in Chinese with

English abstract)

- Da, Y.T. and Sun, Q.L., 1983: Fusulinida. In, Regional Geology Surveying Team of Xinjiang et al, chiefly eds., Paleontological Atlas of Northwest China, Xinjiang Weiwuer Aut. Region Vol., no. 2 (Late Paleozoic), p. 7-113, pls. 1-30. Geol. Publ. House, Beijing. (in Chinese)
- Ding, P.Z., Jin, T.G. and Sun, Y.F., 1987: An excursion guide to Permian geology of Xikou area, Zhen'an County, Shaanxi. Bull. Xi'an Inst. Geol. Mineral Resour., Chinese Acad. Geol. Sci., no. 15, p. 113-138, pls. 1-5. (in Chinese with English abstract)
- —, —— and ——, 1989: Carboniferous-Permian boundary of Xikou area of Zhen'an, south Shaanxi, east Qinling Range. 11^e Congr. Internat. Strat. et Géol. Carbon., Beijing, 1987, Compte Rendu, Tome 2, p. 199-206, pls. 1-4.
- Ding, Y.J., Xia, G.Y., Li, L., Yu, X.G., Zhao, S.Y. and Zhao, Z., 1991: The Carboniferous-Permian boundary and faunas from Xikou area, Zhen'an, Shaanxi in eastern Qinling Range. Bull. Tianjin Inst. Geol. Mineral Resour., Chinese Acad. Geol. Sci., no. 24, p. 1-202, pls. 1-31. (in Chinese with English abstract and description of new genera and family)
- Dunbar, C.O. and Skinner, J.W., 1937: The Geology of Texas, Volume III, Part 2. Permian Fusulinidae of Texas. Univ. Texas Bull., no. 3701, p. 517-825, pls. 42-81.
- Fontaine, H., Poumot, C. and Songsirikul, B., 1981: New Upper Paleozoic formations in Northeast Thailand in Devonian and Lower Carboniferous. *CCOP Newsletter*, vol. 8, no. 4, p. 1-7.
- Huang, Z.X. and Zeng, X.L., 1984: The early Early Permian (Longlinian Stage) fusulinid fauna from Longlin, Guangxi. Earth Sci.-Jour., Wuhan Coll. Geol., vol. 26, no. 3, p. 11-24, pls. 3-4. (in Chinese with English abstract and description of new genera and subgenus)
- Igo, H., 1972: Fusulinacean fossils from Thailand. Part 6, Fusulinacean fossils from North Thailand. Geol. Palaeont. Southeast Asia, vol. 10, p. 63-116, pls. 9-19. Univ. Tokyo Press.
- Ingavat, R. and Douglass, R.C., 1981: Fusuline fossils from Thailand, Part 14, The fusulinid genus *Monodiexodina* from Northwest Thailand. *Ibid.*, vol. 22, p. 23-34, pls. 6-10.
- Kahler, F., 1983 : Fusuliniden aus Karbon und Perm der Karnischen Alpen und der Karawanken. *Sonderhefte der Carinthia II*, vol. 41, p. 1-107, pls. 1-11.
- —, 1985: Oberkarbon und Unterperm der Karnischen Alpen, Ihre Biostratigraphie mit Hilfe der Fusuliniden. *Ibid.*, vol. 42, p. 1-93, pls. 1-11.
- ----- and Kahler, G., 1980: Fusuliniden aus den

Kalken der Trogkofel-Schichten der Karnischen Alpen. In, Flügel, E. ed., Die Trogkofel-Stufe im Unterperm der Karnischen Alpen, Ibid., vol. 36, p. 183-254, pls. 1-9.

- Kalmykova, M.A., 1967: Permskie fuzulinidy Darvaza. Trudy Vses. Nauchno-Issled. Geol. Inst. (VSEGEI), nov. ser., vol. 116, Biostratigraficheskiy sbornik, no. 2, p. 116-287, pls. 1-32. (in Russian)
- Kobayashi, F., 1977: Some considerations on the ancestor of the family Verbeekinidae (Fusulinacea). Trans. Proc. Palaeont. Soc. Japan, N.S., no. 105, p. 1-16, pls. 1-2.
- Kochansky-Devidé, V., 1964 : Die Mikrofossilien des jugoslawischen Perms. *Paläont. Zeitschr.*, Bd. 38, 3/4, p. 180-188, pl. 18-19.
- —, 1965: Karbonske i permske fuzulinidne foraminifere Velebita i Like.-Srednji i gornji perm. Acta geol. Jugosl. akad., vol. 5, p. 101-150, pls. 1-13.
- —, 1970: Permski mikrofosili zahodnih Karavank. Geologija-Razprave in Porocila, vol. 13, p. 175-256, pls. 1-26.
- Leven, E.Ya., 1967 : Stratigrafiya i fuzulinidy permskikh otlozheniy Pamira. Akad. Nauk SSSR, Trudy Geol. Inst., vol. 167, p. 1-224, pls. 1-39. (in Russian)
- —, 1970a: O proiskhozhdenii vysshikh fuzulinid. Paleont. Zhurnal, 1970, no. 3, p. 18-25, pl. 1. (in Russian)
- —, 1970b: Novyi rod permskikh aberrantnykh fuzulinidy. *Ibid.*, 1970, no. 4, p. 16-20, pl. 1. (*in Russian*)
- —, 1980: Ob'yasniiel'naya zapiska k stratigraficheskoy shkale permskikh otlozheniy oblasti Tetis. 51p., Minist. Geol. SSR. Vses. Ordena Lenina Nauchno-Issled. Geol. Inst. (VSEGEI), Leningrad. (in Russian)
- and Scherbovich, S.F., 1978: Fuzulinidy i Stratigrafiya asselyskogo yarusa Darvaza. 162 p., 21 pls. Izdatel. (Nauka), Moskva. (in Russian)
- Lin, J.X., Li. J.X., Chen, G.X., Zhou, Z.R. and Zhang, B.F., 1977: Fusulinida. In, Hubei Inst. Geol. Sci. et al. eds., Paleontological Atlas of Central South China, no. 2 (Late Paleozoic), p. 4-96, pls. 1-30. Geol. Publ. House, Beijing. (in Chinese)
- Lipina, O.A. and Rozanov, A.Y., 1973: O gomologicheskoi izmenchivosti foraminifer i arkheotsiat. Akad. Nauk SSSR, Sibirskoe Otdel., Trudy Inst. Geol. i Geofiz., vol. 49, p. 13-31, pls. 3-6. (in Russian)
- Liu, Z.A., Xiao, X.M. and Dong, W.L., 1978: Protozoa. In, Working Group of Stratigraphy and Paleontology of Guizhou ed., Paleontological Atlas of Southwest China, Guizhou Vol., no. 2

(Carboniferous to Quaternary), p. 12-98, pls. 1-24. Geol. Publ. House, Beijing. (in Chinese)

- Loeblich, A.R., Jr. and Tappan, H., 1988: Foraminiferal genera and their classification. 970 p., 847 pls. Van Nostrand Reinhold Co., New York.
- Luo, J.D., Hong, Z.Y., Xu, H.Q., Lin, X.S., Yi, W.J., Li, Y.L. and Wu, F.B., 1989: On the Carboniferous-Permian boundary in Fujian. 11^e Congr. Internat. Strat. et Géol. Carbon., Beijing, 1987, Compte Rendu, Tome 2, p. 216-228, pls. 1-4.
- Nie, Z.T. and Song, Z.M., 1983: Fusulinids of Lower Permian Qudi Formation from Rutog of Xizang (Tibet), China. *Earth Sci.-Jour., Wuhan Coll. Geol.*, vol. 19, no. 1, p. 29-42, pls. 1-2. (in Chinese with English abstract)
- Pitakpaivan, K., 1965: Fusulinacean fossils from Thailand, Part 1. Fusulines of the Rat Buri Limestone of Thailand. Mem. Fac. Sci., Kyushu Univ., ser. D, Geol., vol. 17, no. 1, p. 1-69, pls. 1-6.
- Ramovš, A. and Kochansky-Devidé, V., 1965: Razvoj mlajsega Paleozoika v okolici Ortneka na Dolenjskem. Slovenska Akad. Znanosti Umetnosti (Ljubljana), Cl. 4, Historia Nat. Medicina, Razprave, Dissert. 8, p. 323-416, pls. 1-18.
- and , 1979: Karbonske in permske plasti v severnih Julijskih Alpah. Geologija-Razprave in Porocila, vol. 22, no. 1, p. 21-54, pls. 1-6.
- Rauser-Chernoussova, D.M., 1988: O polozhenii roda *Pamirina* v sisteme fuzulinid. *Paleont. Zhurnal*, 1988, no. 4, p. 13-19, pls. 1-2. (*in Russian*)
- Rozovskaya, S.E., 1958: Fuzulinidy i biostratigraficheskoe raschlenenie verkhnekamennougol' nykh otolozheniy Samarskoy Luki. Akad. Nauk SSSR, Trudy Geol. Inst., vol. 13, p. 57-120, pls. 1-15, (in Russian)
- —, 1975: Sostav, sistema i filogeniya otryada fuzulinida. Akad. Nauk SSSR, Trudy Paleont. Inst., vol. 149, p. 1-227, pls. 1-35. (in Russian)
- Rui, L., 1979: Upper Permian fusulinids from western Guizhou. Acta Palaeont. Sinica, vol. 18, no. 3, p. 271-297, pls. 1-4. (in Chinese with English abstract)
- Sakagami, S. and Iwai, J., 1974 : Fusulinacean fossils from Thailand, Part 8. Permian fusulinaceans from the Pha Duk Chik Limestone and in the limestone conglomerate in its environs, North Thailand. Geol. Palaeont. Southeast Asia, vol. 14, p. 49-81, pls. 4-9, Univ. Tokyo Press.
- Schellwien, E., 1909: Monographie der Fusulinen, Teil II, Die asiatischen Fusulinen. A. Die Fusulinen von Darwas. *Palaeontogr.*, Bd. 56, p. 137-176, pls. 13-16.
- Sheng, J.Z. (Sheng, J.C.), 1963: Permian fusulinids of

Kwangsi, Kueichow and Szechuan. Palaeont. Sinica, N.S. B, no. 10, p. 1-247, pls. 1-36.

- ----, 1966 : Fusulinids of China. 177 p., 27 pls., Sci. Publ. House, Beijing. (in Chinese)
- and Sun, D.D., 1975: Fusulinids of Qinghai.
- 97 p., 14 pls., Ibid. (in Chinese)
- —, Zhang, L.X. and Wang, J.H., 1988 : Fusulinida. 240 p., Ibid. (in Chinese)
- Staff, H. von, 1909: Beiträge zur Kenntnis der Fusuliniden. Neues Jahrb. Min., Geol., Paläont., Beil., Bd. 27, p. 461-508, pls. 7-8.
- Sun, Q.L. and Zhang, L.X., 1988: Early Permian fusulinids from the Kongkashan pass of Xinjiang. Acta Micropalaeont. Sinica, vol. 5, no. 4, p. 367-378, pls. 1-4. (in Chinese with English abstract)
- Sun, X.F., Gao, C.X. and Zhang, X.L., 1983: Fusulinida. In, Xi'an Inst. Geol. Mineral Resour. ed., Paleontological Atlas of Northwest China, Shaanxi, Gansu and Ningxia Vol., no. 2 (Upper Paleozoic), p. 3-40, pls. 1-10. Geol. Publ. House, Beijing. (in Chinese)
- Toriyama, R., 1975: Fusuline fossils from Thailand, Part 9. Permian fusulines from the Rat Buri Limestone in the Khao Phlong Phrab area, Sara Buri, central Thailand. *Mem, Fac. Sci., Kyushu* Univ., ser. D, Geol., vol. 23, no. 1, p. 1-116, pls. 1-21.
- —, 1984: Summary of the fusuline faunas in Thailand and Malaysia. Geol. Palaeont. Southeast Asia, vol. 25, p. 137-146. Univ. Tokyo Press.
- —, Hamada, T., Igo, H., Ingavat, R., Kanmera, K., Kobayashi, T., Koike, T., Ozawa, T., Pitakpaivan, K., Piyasin, S., Sakagami, S., Yanagida, J., and Yin, E.H., 1975 : The Carboniferous and Permian Systems in Thailand and Malaysia. *Ibid.*, vol. 15, p. 39-76.
- and Kanmera, K., 1979: Fusuline fossils from Thailand, Part 12. Permian fusulines from the Ratburi Limestone in the Khao Khao area, Saraburi, central Thailand. *Ibid.*, vol. 20, p. 23-93, pls. 4-14.
- Ueno, K., 1991a: Pamirina (Permian Fusulinacea) from the Akiyoshi Limestone Group, southwest Japan. Trans. Proc. Palaeont. Soc. Japan, N.S., no. 161, p. 739-750.
- —, 1991b: Early evolution of the families Verbeekinidae and Neoschwagerinidae (Permian Fusulinacea) in the Akiyoshi Limestone Group, southwest Japan. *Ibid.*, no. 164, p. 973-1002.
- —, 1992: Permian aberrant fusulinaceans from the Akiyoshi Limestone Group, southwest Japan. Sci, Repts., Inst. Geosci., Univ. Tsukuba, Sec. B, vol. 13, p. 1-13.
- Wang, K.L. and Sun, X.F., 1973 : Carboniferous and Permian foraminifera of the Chinling Range and

its geologic significance. Acta Geol. Sinica, 1973, no. 2, p. 137-178, pls. 1-7. (in Chinese with English abstract and description of new species)

- Wang, Y.H., 1987: Late Carboniferous fusulinids in middle and lower Yangtze valley. Bull. Nanjing Inst. Geol. Mineral Resour., Chinese Acad. Geol. Sci., vol. 8, no. 2, p. 85-91, pls. 1-2. (in Chinese with English abstract)
- Wang, L.L., Wang. J.H., Zhu, Z.G., Lin, G.W., Zhang, L.X. and Quian, Q., 1982: Fusulinida. In, Nanjing Inst. Geol. Mineral Resour. chiefly ed., Paleontological Atlas of East China, no. 2 (Late Paleozoic), p. 5-108, pls. 1-30. Geol. Publ. House, Beijing. (in Chinese)
- Watanabe, K., 1991: Fusuline biostratigraphy of the Upper Carboniferous and Lower Permian of Japan, with special reference to the Carboniferous-Permian boundary. *Palaeont.* Soc. Japan, Spec. Papers, no. 32, p. 1-150.
- Xia, G.Y., Li, J.X., Wang, Y.H. and Dong, W.L., 1986: The fusulinid zones and the boundary of Carboniferous-Permian in Longlin region, Guangxi. Bull. Yichang Inst. Geol. Mineral Resour.,

Chinese Acad. Geol. Sci., no. 11, p. 67-104, pls. 1-11. (in Chinese with English abstract)

- and Zhang, Z.C., 1985: Protozoa. In, Tianjin Inst. Geol. Mineral Resour. ed., Paleontological Atlas of North China, no. 1 (Paleozoic vol.), p. 32-150, pls. 1-35. Geol. Publ. House, Beijing. (in Chinese)
- Yanagida, J., 1967: Early Permian brachiopods from central Thailand. *Geol. Palaeont. Southeast Asia*, vol. 3, p. 46-97, pls. 11-23. Univ. Tokyo Press.
- —, 1974: Middle Carboniferous brachiopods from Loei, North Thailand. *Ibid.*, vol. 14, p. 7-23, pls. 2-3.
- —, 1975: Upper Carboniferous brachiopods from Wang Saphaung, North Thailand. *Ibid.*, vol. 16, p. 1-31, pls. 1-3.
- Zhou, T.M., Sheng. J.Z. and Wang, Y.J., 1987: Carboniferous-Permian boundary beds and fusulinid zones at Xiaodushan, eastern Yunnan. *Acta Micropalaeont. Sinica*, vol. 4, no. 2, p. 123-160, pls. 1-6.

Akiyoshi 秋吉, Beiyangshan 北羊山, Chuanshan 船山, Guangnan 広南, Guangxi 広西, Guizhou (Kueichow) 貴州, Hanagiri 花桐, Jiangsu (Kiangsu) 江蘇, Kwanto 関東, Longlin 隆林, Qinghai 青海, Qinling (Chinling) 秦嶺, Shaanxi 陝西, Wujiaping (Wuchaping) 呉 家坪, Xiaodushan 小独山, Yazi 址子, Yunnan 雲南, Zhen'an 鎮安.

タイ北東部ロエイ県ヒア村産下部ペルム系紡錘虫:タイ国北東部ロエイ県のヒア村に小 規模に露出する石灰岩層は石灰質砂岩と互層し、岩相上石炭系のワンサプーン層の一部と 見られる。今回この石灰岩からこれまでダルバスや中国南部の下部ペルム系のYakhtashian (Artinskian)上部から報告されている紡錘虫化石群に類似するものを識別した。この 時代を示す紡錘虫化石群はタイ国では初めてその存在が確認された。また今回の発見に よって石炭系に限られると見られていたワンサプーン層とペルム系ナムマホラン層は指交 関係にある可能性が強くなった。新たに提唱した新種はDarvasites ingavati, Pseudofusulina siamensis, Staffella? ovalis, Nankinella? loeiensis, Pseudoendothyra? constricta の 5種である。 猪郷久義・上野勝美・指田勝男

950. SKELETAL STRUCTURES OF LOWER AND MIDDLE MIOCENE LOPHOPHAENIDS (RADIOLARIA) FROM CENTRAL JAPAN*

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Abstract. Nine species of five lophophaenid genera are described from the Lower Miocene Toyohama Formation, Morozaki Group, Aichi Prefecture and the lowest Middle Miocene Oidawara Formation, Mizunami Group, Gifu Prefecture, central Japan. A special attention is given to describing and illustrating the details of their skeletal structures which possess one or two horizontal rings, since it is believed that these details are important in establishing the taxonomy and clarifying the phylogenetic relationships. The examination discriminates seven types of skeletal structure. Four species are newly described, and two new genera, *Steganocubus* and *Cryptogyrus*, are also erected herein.

Key words. Radiolaria, lophophaenids, skeletal structures, Lower and Middle Miocene, central Japan

Introduction

I recently reported the occurrence of well preserved radiolarians in the Lower Miocene Toyohama Formation, Morozaki Group, Aichi Prefecture (Sugiyama, 1992), and illustrated one characteristic species identified as Helotholus vema Hays, 1965. This species, having a unique basal ring (Hays, 1965) in the skeleton, was originally described from Antarctic sediments, and is one of the most characteristic species of the Pliocene radiolarian fauna of the Antarctic region (e.g. Hays, 1965; Chen, 1975). Moreover, Kellogg (1975) and Weaver (1983) mentioned that H. vema was derived from an ancestral elongated form (H. praevema Weaver, 1983) by increases of thoracic width during the Late Miocene to Pliocene interval. My previous identification is, therefore, stratigraphically problematic and a taxonomic reexamination should be necessary.

However, it seems that the taxonomic position of *H. vema* is essentially problematic. The problems can be summarized in the following two points: One concerns whether the genus Helotholus Jørgensen, 1905, is a junior synonym of the genus Ceratocyrtis Bütschli, 1882, or not, and the other is whether H. vema really belongs to this genus or not. Concerning the former problem, Petrushevskaya (1971b) was the first who formally synonymized these two genera, and her action seems to be reasonable. Thus the problem is out of interest for this paper. However, the latter problem remains unsettled although over the past two decades many papers have discussed the taxonomy of H. vema, although Weaver (1983), Chen (1975), Lazarus (1990), and others kept the original generic assignment for this problematic species. On the contrary, Petrushevskaya (1971b), Dumitrica (1973), Sanfilippo (1988), and others referred H. vema to the genus

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Pseudocubus Haeckel, 1887, based on the similarity of their skeletal structures.

Moreover, one can point out that the taxonomic problem of H. vema concerns not only Pseudocubus but also other genera. For example, some species of the genus Antarctissa Petrushevskaya, 1967, seem to have a skeletal structure similar to H. vema and Pseudocubus, although their precise skeletal structure has not been fully described yet (e.g., Antarctissa ewingi Chen, 1974, pl. 3, fig. 6; A. whitei Bjørklund, 1976, pl. 13, fig. 13). In addition, a certain external similarity is present between the genera Antarctissa. Botryopera and Ceratocyrtis (=Helotholus)as discussed by Petrushevskaya (1986). Consequently, we cannot determine the generic assignment of H. vema without establishing a consistent taxonomy for all the genera mentioned above. There is no need to stress that perfect understanding of their skeletal structures is necessary before everything for that purpose. Our present state of knowledge about their skeletal structures is, however, too poor to consider their precise taxonomy, much less their phylogeny.

During the subsequent investigations on radiolarian assemblages from the Toyohama Formation and the lowest Middle Miocene Oidawara Formation, Mizunami Group, Gifu Prefecture, I have fortunately obtained well preserved materials whose speletal structure is the same or similar to the above mentioned problematic taxa, and, as a result of the examination, I realized that to stress ring structure in the skeleton is very useful for their taxonomy. In the present study, therefore, I focus on describing the structures in detail using a scanning electron microscope (SEM) in order to present fundamental taxonomic information. The results should contribute to our better grasp of taxonomy of all nassellarians in future.

Geologic setting and age

The Morozaki Group is widely distributed

in the southern part of the Chita Peninsula. Aichi Prefecture, and is divided into the Himaga, Toyohama, Yamami and Utsumi Formations in ascending order (Shibata, 1977). It abundantly yields a deep sea fossil fauna composed chiefly of Echinodermata, Crustacea, Mollusca and Pisces which characterizes a bathyal and mesopelagic oceanic environment (Shibata, 1977; Hachiya et al., 1988). The Toyohama Formation, the second lowest one of this group, is composed mainly of thick, tuffaceous mudstone accompanied by a subordinate amount of sandstone and tuff layers. The tuffaceous mudstone sometimes intercalates with calcareous nodules which are approximately 10 cm in major diameter and usually contain chelipeds of the thalassinidean decapod Callianassa titaensis Nagao. Radiolarians are very well preserved in the nodules, and a preliminary report by Sugiyama (1992) revealed that they are relatively rich in cool-temperate indicators. Four rock samples treated in this study named TH-1, 2, 3 and 4, the first three samples were already used in Sugiyama (1992), are also decapod-bearing calcareous nodules embedded in a tuffaceous mudstone of the Toyohama Formation (Figure 1). They were obtained approximately from the middle part of the Toyohama Formation. More than 150 radiolarian species have been recovered from these samples.

The precise geologic age of the Toyohama Formation is not known yet. However, I obtained the following radiolarian species in my subsequent investigations: one individual of Lychnocanoma elongata (Vinassa de Regny) from TH-2, one individual of Stichocorys sp. aff S. delmontensis (Campbell and Clark) from TH-4 and four individuals of S. armata (Haeckel) from TH-2, 3 and 4. They indicate that part of the Toyohama Formation corresponds to an interval from the Lower Miocene Stichocorys delmontensis Zone to the Middle Miocene Dorcadospyris alata Zone of Riedel and Sanfilippo (1978), according to Sakai (1980). My preliminary



Figure 1. Map showing localities of the samples TH-1, 2, 3 and 4 from the Toyohama Formation, Morozaki Group.

investigation on the co-existing diatoms has revealed that the flora is dominated by *Kisseleviella carina* Sheshukova-Poretzkaya and lacks *Denticulopsis* species. The Toyohama Formation is, therefore, correlative with the Early Miocene *Kisseleviella carina* Zone to *Actinocyclus ingens* Zone (Koizumi, 1985). Although further detailed investigations should be necessary for precise age determination, I tentatively consider that the age of the studied samples is of late Early Miocene in this study.

The Lower to Middle Miocene Mizunami Group distributed in the Mizunami basin, Gifu Prefecture, is considered as a contemporaneous heterotopic facies of the Morozaki Group. According to Itoigawa (1974), the Mizunami Group is divided into four formations of which the Oidawara Formation, composed mainly of tuffaceous and diatomaceous mudstone, disconformably overlies the other three formations. Itoigawa *et al.* (1974) recognized the *Nelionella —Phanerolepida* molluscan assemblage from this formation, and inferred a lower sublittoral depositional environment. Mori (1974) examined diatoms from this formation, and estimated an inshore to coastal depositional environment affected by oceanic water.

The studied route covers approximately the whole section of the Oidawara Formation from the lowest disconformity to the uppermost unconformity (Figure 2). The Oidawara Formation in this route is composed of two lithologic units divided by a sharp boundary: lower unit consisting of pumiceous sandstone to sandy siltstone, with or without underlying basal conglomerate, and intercalating several tuff layers; and upper unit composed of monotonous diatomaceous siltstone. The lower unit may represent a shallower depositional environment than that of the upper unit judging from its coarser lithology. The occurrence of radiolarians in the lower unit is very rare, whereas the upper unit yields a large quantity of siliceous microfossils such as diatoms, silicoflagellates and radiolarians. This study



Figure 2. Route map and geologic column of the Oidawara Formation, Mizunami Group in the studied area, showing the locality and horizon of samples OD-17, 18, 21, 26, 27 and 28.

deals with six rock samples OD-17, 18, 21, 26, 27 and 28 from the upper unit. More than 120 species of radiolarians have been recovered from these samples.

Sugano (1976) already reported the occurrence of 34 species of radiolarians in the Oidawara Formation, and correlated it to the *Melittosphaera magnaporulosa* Zone (Nakaseko and Sugano, 1973) which ranges in age from Early to early Middle Miocene. In this study, I obtained the following index species throughout the upper unit : *Calocycletta costata* (Riedel), *C. virginis* (Haeckel), *Stichocorys delmontensis* (Campbell and Clark), *Dorcadospyris forcipata* (Haeckel) and *Ceratocyrtis stoermeri* Goll and Bjørklund. It is, therefore, concluded that this formation is correlative with the *Calocycletta costata* Zone of Riedel and Sanfilippo (1978) and the *Ceratocyrtis broeggeri* Zone of Goll and Bjørklund (1989). The six studied samples are thus of an Early to Middle Miocene age, according to Riedel and Sanfilippo (1978), Sakai (1984), Goll and Bjørklund (1989) and so on.

Descriptive terminology

As mentioned in the introduction, the main purpose of the present study is to understand the skeletal structures of some lophophaenids from the Lower to Middle Miocene of central



Figure 3. Characteristic index species from the Toyohama and Oidawara Formations. 1: Lychnocanoma elongata (Vinassa de Regny), ESN 146431, TH-2. 2: Stichocorys sp. aff. S. delmontensis (Campbell and Clark), ESN 146432, TH-4. 3: Dorcadospyris forcipata (Haeckel), ESN 146451, OD-26. 4: Stichocorys delmontensis (Campbell and Clark), ESN 146452, OD-28. 5: Calocycletta costata (Riedel), ESN 146453, OD-26. All scale bars = $50 \,\mu$ m.

Japan. They are, however, so complicated geometrically that some special terms are necessary to formulate them. In the first place, descriptive terms used in this study, adding traditional ones, are listed and briefly explained below. Schematic illustrations are also shown in Figure 4.

Arch: Skeleton connecting two basic rays. The expression follows Petrushevskaya (1968).



Figure 4. Schematic illustrations of idealized skeletal structure.

Sagittal plane : A meridional plane passing through MB.

MB: Median bar.

A: Apical ray (spine).

 \mathbf{A}' : Lateral branch of \mathbf{A} from the junction of

PR. It always lies in the sagittal plane.

D: Dorsal ray (spine).

D': Lateral branch of D from the junction of **MB** and **A**. The angle between **D** and **D'** is commonly 30°-45°. Two **D'**, one at each side of **D**, may be present in a specimen. Well-developed **D'** is undiscerned from proper secondary lateral ray (1).

L: Primary lateral ray (spine). The orientation is shown as Lr, meaning right primary lateral ray, in due place. This follows not Petrushevskaya (1968, fig. 1) but De Wever (1981, fig. 1) and Dumitrica (1991, fig. 1).

 \mathbf{L}' : Long lateral branch of \mathbf{L} . The angle between \mathbf{L} and \mathbf{L}' is commonly less than 45°. One \mathbf{L} usually has one \mathbf{L}' on the dorsal side. \mathbf{I}' : Stout, laterally directed bar arising from **PR**. It lies between \mathbf{D} and \mathbf{L} in basal view. \mathbf{I}'' : Longitudinal bar extending from the junction of \mathbf{I}' and **PR**. In basal view, two \mathbf{I}'' usually make a larger angle than two \mathbf{I}' do, and commonly lie in a plane perpendicular to the sagittal plane.

V: Vertical ray (spine).

V': Stout, laterally directed bar arising from **PR**. It is nearly in the sagittal plane.

V'': Longitudinal bar extending from **PR**. It commonly arises from the same position as **V** and **V'**, but rarely has a different position. **Ax**: Axial spine.

L-R: Longitudinal bar typically connecting the middle part of **L** and **PR** situating at the junction of **L** and **L'**. The length is variable, so it is in some cases hardly recognized. The position is also more or less unstable, especially when **L'** is strongly developed. Then it connects **PR** not with **L** but with **L'**. This skeleton possibly corresponds to *bb'* and *cc'* of Swanberg and Bjørklund (1987).

PR: Proximal ring which can be connected with **A**, **A'**, two **l'**, two **l''**, two **L-R**, **V**, **V'** and **V''**. It is situated on a horizontal plane near the stricture between the first and second segments. According to Petrushevskaya (1968), **PR**+two **L-R** are homologous with arches two ap + two pj when **V** is present, whereas they correspond to two ap + ppwhen **V** is absent. They are also homologous with arcs b'x'c' + b'dec' of Swanberg and Bjørklund (1987). Further comments are given in the next section along with comments on **DR**.

DR: Distal ring which connects the distal parts of A, two l'' and V''.

X: Distance between **PR** and **DR**.

 \mathbf{Y} : Distance between \mathbf{DR} and the top of the eucephalis.

Notes on skeletal ring and taxonomy

It is well known that nassellarians have an internal skeleton, consisting of MB and basic rays (A, D, L, l, V and Ax) with or without arches, and that many radiolarian taxonomists consider the skeletal structure as the most important criterion for classification. For example, the main purpose of studies by Riedel (1967, 1971), Petrushevskaya (1971a, 1971b, 1981), Takemura (1986), Nishimura (1990), and others is to establish the natural system of nassellarians based on their skeletal structure. Their common conception is that the morphology occurring in earlier ontogenetic stages may be a more conservative for phylogeny than features formed in latter stages. That is to say, their conception conforms to that of heterochrony (McNamara, 1986).

Besides the arrangement of the basic rays of the internal skeleton, Petrushevskaya (1968) was the first who recognized the significance of arches for all nassellarian classification. Her comprehensive studies (Petrushevskaya, 1971a, 1971b, 1981, *etc.*) appear to have influenced many subsequent investigators. Among them a special mention must be paid for the result of Swanberg and Bjørklund (1987), who examined the incipient ontogeny of the living cannobotryid *Amphimelissa* setosa (Cleve) in detail, and revealed that most arches (corresponding to the term "arcs" in their paper) occur prior to the development of **D**, **l**, **V** and **Ax**. From this, one can immediately suppose that the arch structure of nassellarian skeleton is a more conservative feature than the final pattern of arrangement of the basic rays.

Among the arches, those developed nearly horizontally at or near the collar region are easy to observe even if the shell wall is thickly developed on specimens, since it normally has a rather thin or incomplete wall and the arches are easily recognizable as ridges or swells on the wall in most cases. Those arches look as if to form a "ring" and to have a distinctive character as an independent skeletal element in basal view. However, except for Nishimura (1990) who used the term "basal ring" for this structure of all nassellarians, most investigators have paid attention to it as a characteristic of the skeleton mainly for two taxa: acanthodesmiids those nassellarians and with the Pseudocubus-type skeletal structure whose "rings" are not directly attached to the shell wall but connected with it through intervening connector bars. They are tentatively called Pseudocubus group, which does not correspond to any present nomenclatures. For acanthodesmiids, the relevant authors are Haeckel (1887) and Goll (1958) who used the term "basal ring", whereas Haeckel (1887), Popofsky (1908, 1913), and Dumitrica (1973) used the term "ring" for the Pseudocubus group. Moreover, Hays (1965) and Lazarus (1990) used similar terms including the word "ring", which are "basal horizontal ring" and "internal ring", respectively. They are apparently for the Pseudocubus group.

It is obvious that **PR** used in this paper is applicable only to the *Pseudocubus* group, as defined in the way explained in the third section. Of the nine species described in this paper, it has revealed that seven, excluding two *Ceratocyrtis* species, have such **PR** in their skeleton (Table 1). Then one can

Table 1. Correlation of seven typical skeletal structures discriminated in the present study.

species characteristic morphology	PR	DR	Α'	ľ	۷	v	Y/X	shell		
Pseudocubus obeliscus	0	0		0	0	-	s	1		
Steganocubus subtilis S. lipus	0	0	0	0	1	0	s	0		
Botryopera (?) leptostraca	0	0	0	0	0	-	L	0		
Botryopera (?) whitei	0	0	0	0	0	0	L	0		
Botryopera (?) sp. A	0	0	0	0	0	?	L	0		
Cryptogyrus trachylobus	0	0	-	_	0	-	L	0		
Ceratocyrtis stoermeri C. sp. aff. C. histricosus	0	-	-	-	0	_	—	0		

notice that the skeletal structure of the group is commonly characterized by possessing another, horizontal or nearly horizontal connection of arches above **PR**, which may be parts of eucephalic lattice bars. This cannot be formulated by Petrushevskaya's (1968) method, but seems to be a significant skeleton closely related to **PR**. Because of the similarity of the general shape to **PR** and the position in the skeletal structure, I call it **DR** in this paper.

The subfamily or family assignment of the Pseudocubus group has been unsettled. For example, Petrushevskaya (1971b, 1981) assigned Pseudocubus to the subfamily Plagiacanthinae Hertwig, 1879, emend. Petrushevskaya, 1971a, whereas Sanfilippo (1988) put it in the family Cannobotryidae Haeckel, 1881, emend. Riedel, 1967. However, my investigations proved that it has a close phylogenetic relationship to the subfamily Lophophaeninae Haeckel, 1881, emend. Petrushevskaya, 1971b, although the typical lophophaenin "ring" is not free from the shell wall and is actually not horizontal : Their arches ap and pj or ap and pp when V is absent have a certain common part just above L, in spite of its various lengths. This is notable because the part is considered to be homologous with L-R of the Pseudocubus group (Figure 5). Moreover, a lopho-



Figure 5. Schematic illustration showing correspondence between Petrushevskaya's (1968) arches and **PR** and **L-R** of this study.

phaenin skeletal structure is generally characterized by possessing prominent L' and often also A' and D' (e.g. the genera Lophophaena Ehrenberg, 1847, and Pseudodictyophimus Petrushevskaya, 1971b, Fig. 23–2a-3b). These features are undoubtedly in common with the Pseudocubus group, and two species of the genus Ceratocyrtis Butschli, 1882, described in this paper have this type of skeletal structure. Consequently, I consider that the Pseudocubus group is a member of Lophophaeninae and that it would be better to raise the subfamily to family rank.

Systematic description

All specimens treated in this study are deposited in the Department of Earth and Planetary Sciences, School of Science, Nagoya University (ESN).

> Class Radiolaria Order Nassellaria

Family Lophophaenidae Haeckel, 1881, emend. Petrushevskaya, 1971b

Remarks.—The diagnosis used in this study follows Petrushevskaya (1971b), although she subdivided this taxon in her later studies. For example, the family Lampromotridae Haeckel, 1881, emend. Petrushevskaya in Petrushevskaya and Kozlova, 1972, and the subfamily Ceratocyrtinae Petrushevskaya, 1981, are obviously junior synonyms of Lophophaenidae, based on their skeletal structures. The precise subdivision requires further detailed investigations in future.

> Genus *Pseudocubus* Haeckel, 1887, emend. Petrushevskaya, 1971b

Pseudocubus Haeckel, 1887, p. 1010.—Petrushevskaya, 1971b, p. 149.Obeliscus Popofsky, 1913, p. 279.

Talariscus Loeblich and Tappan, 1961, p. 227.

Type species: *P. obeliscus* Haeckel, 1887 (designated by Campbell, 1954).

Pseudocubus obeliscus Haeckel

Figures 7-1a-3b; 8-1a-1b

Pseudocubus obeliscus Haeckel, 1887, p. 1010, pl. 94, fig. 11.—Petrushevskaya, 1971b, p. 150, figs. 76 —1-6.

Plectophora triacantha Popofsky, 1908, p. 262, pl. 29, fig. 1, pl. 30, fig. 1

Obeliscus peudocuboides Popofsky, 1913, p. 280, pl. 29, figs. 4, 5.

Description.—Test pyramidal in shape, having stout three-bladed scaffolds above **PR**,



Figure 6. Schematic illustrations of typical skeletal structure of *Pseudocubus obeliscus* Haeckel. (a): Dorsal view, (b): Right lateral view. (c): Basal view. (d): Right lateral view of gerontic form (?).



Figure 7. 1a-3b: *Pseudocubus obeliscus* Haeckel. 1a-1b: ESN 146501, TH-3. 2a, 2b: ESN 146502, TH-4. Arrow of 2a points to secondary arch. 3a, 3b: ESN 146503, TH-3. This specimen has six longitudinal scaffolds, indicated by arrows, owing to the irregular bifurcation of primary skeleton, which may also contribute to the incompletion of DR. Scale bars: 1a, 2a and $3a=50 \ \mu m$; others=20 μm .



Figure 8. 1a-1d: *Pseudocubus obeliscus* Haeckel, ESN 146541, TH-4, 1a; ventral view, 1b; enlargement of oblique basal view, 1c; enlargement of apical view, 1d; enlargement of left lateral view. Scale bars: $1a = 50 \ \mu m$; others = $20 \ \mu m$.

usually lacking shell completely. Longitudinal scaffolds usually four in number, composed of A, two l'' and V'', tied by both PR and **DR**, and tapering beyond **DR**. The scaffolds sometimes bifurcate at the middle part (Figure 7-3a). **PR** is either circular or three-bladed in cross section and usually oval in entirety. The minor diameter always lies in the sagittal plane. **DR** is three-bladed in cross section. It has a circular outline when one views it from the basal or apical side. A side of **DR** is, however, always convex upward in lateral view, and has one verticil of one or two conical spines on the top. In adult specimens (?), the scaffolds have spinules above **DR**, and secondary arches may be developed from the tips of them (Figure 7-2a). The secondary arches finally form

another horizontal connection, a side of which is also convex upward in lateral view and has a conical spine on the top. In such cases the eucephalic wall is loosely definable on the upper half of the test and some thick arches are vertically or obliquely developed outside the eucephalic part (Figures 8-1a -1d). Basic spicules located at the base of the test, consisting of MB, A, D two L, V, with or without Ax. A directed upward, circular in cross section in the proximal part, straight or slightly bent to dorsal side at the junction of **PR**, and prolonged into a stout three-bladed spine beyond it. One or two apophyses usually present on the proximal exterior side of A. In most specimens, D and two L extending either laterally or slightly downward, circular in cross section, more or

less tapering distally, and having several small apophyses on the basal side. In gerontic specimens (?), however, two L become longer and three-bladed, and have a verticil of a few or several spinules radiating in all directions. Then D' is well developed, but Dremains rodlike. L' always missing. Two l' stout, commonly conical and proximally bladed, becoming longer and distally pronged like two L in gerontic specimens (?). Two I" extend upward from the corresponding points to two l'. V rodlike, thin, directed obliquely upward, extending to PR. V of some specimens not extending into V'' and, in such cases, two V" may be present in the specimens. Ax wartlike, sometimes undiscerned from the basal apophyses on the **D** and two **L**. Two L-R long or short, sometimes unequal. A' and V' missing. Each junction of DRand \mathbf{A}, \mathbf{V}'' and two \mathbf{l}'' bears one spine on the exterior side.

Remarks.—Variation of the skeletal structure is in rare cases observed with respect to the intersecting position of V and PR, number of V'' and length of L-R. Although



Figure 9. Schematic illustrations of typical skeletal structure of *Steganocubus subtilis* gen. et sp. nov. (a): Dorsal view. (b): Right lateral view. (c): Basal view.

Petrushevskaya (1971b) mentioned that the development of V is capable of intensely varying, all the examined specimens have V. On the other hand, none have A' and V'. Judging from the descriptions of previous studies (Haeckel, 1887; Popofsky, 1908, 1913; Petrushevskaya, 1971b), however, it is certain that this species is morphologically



Figure 11. 1a, 1b: Steganocubus subtilis Sugiyama, gen. et sp. nov., ESN 146507, TH-2, paratype. Scale bars = $50 \mu m$. This specimen has a quite irregular skeletal structure, so that the elements cannot be named.

[→] Figure 10. 1a-4b: Steganocubus subtilis Sugiyama, gen. et sp. nov. 1a-1d: ESN 146504, TH-4, holotype. Arrow of 1d points to vestigial D'. 2a, 2b: ESN 146505, TH-4, paratype. 3a, 3b: ESN 146403, same specimen as Sugiyama (1991, pl. 1, fig. 3), TH-1, paratype. 4a, 4b: ESN 146506, TH-2, paratype. This specimen has reduced D and lacks V'. Scale bars: 1a, 2a, 3a and $4a = 50 \ \mu m$; others = 20 μm .



much more variable than the result confirmed in this study.

Dimensions (in μ m).—Based on measurement of 22 completely preserved specimens examined by SEM. Height of test; 50-93. Maximum width of test; 60-98. Maximum diameter of **PR**; 18-30.

Occurrence.—TH-1, 2, 3, 4 and OD-17, 18 (very rare in abundance).

Genus Steganocubus Sugiyama, gen. nov.

Etymology.—From the Greek *steganos*, covered, and *kybos*, a cube; masculine gender.

Included species.—S. subtilis Sygiyama sp. nov. (type species) and S. lipus Sugiyama sp. nov.

Diagnosis.—Large cephalis enclosing internal skeleton. A, two l", V" relatively long. A', D, two L, two l' and V" commonly extending to the shell wall. They are, however, sometimes reduced or absent irregularly (Figures 10-4b; 11-1b). I" usually lies in a bisectional position between D and L. D' and L' vestigial (Figure 10-1d) or completely absent. V missing. L-R and Ax variable in length. A few, short connector bars irregularly developed especially on the ventral side. They connect PR and the shell wall or DR. DR lies in a high position in the cephalis. Y/X is less than 1. Thorax may be present.

Remarks.—This genus is distinguished from Pseudocubus externally by the presence of the shell wall, and internally by having stout and long A', D and V', and by lacking V completely. This genus was undoubtedly derived from Pseudocubus by direct acquisition of the shell wall on the skeleton, accompanied by a certain modification of the skeletal structure. It is, therefore, clear that the segment above **DR** corresponds not to the whole cephalis but to the upper part of the eucephalic lobe.

Helotholus vema Hays, 1965, seems to nearly satisfy the generic diagnosis of this genus, and one can be fairly certain that H. vema is more or less related to the present new genus. However, it often has V in the skeleton (e.g. Petrushevskaya, 1971b, figs. 24-2, 3 and 4; Chen, 1975, pl. 16, fig. 4 : Weaver, 1976, pl. 1, fig. 11). Moreover, a personal preliminary investigation, the results of which will be published in the near future, revealed that the typical form of H. vema has six longitudinal scaffolds as illustrated by Petrushevskaya (1971b, fig. 17-5) and another well known form having bladed scaffolds including four longitudinal ones and lacking V as illustrated by Lazarus (1990, figs. 1-5) is possibly conspecific with Pseudocubus warreni Goll, 1980. Furthermore, as mentioned in the introductory section, Kellogg (1975) and Weaver (1983) concluded that the typical form of H. vema was derived from a more elongated ancestor H. praevema Weaver, 1983, by the sinking of the cephalis into the thorax and simultaneous increase of thoracic width during a short interval. The latter species may lack **PR** free from the shell wall judging from Weaver's (1983) original description. If their observations and conclusion are right, H. vema and two species of Steganocubus gen. nov. are regarded as convergent forms having phylogenetically independent **PR** free from the shell wall. Although such a situation is practically suspected, I cannot reject it completely at present. The assignment of H. vema to this new genus is reserved at this time based on the above mentioned facts.

Steganocubus subtilis Sugiyama, sp. nov.

[→] Figure 12. 1a-4b: Steganocubus lipus Sugiyama, gen. et sp. nov. 1a, 1b: ESN 146508, OD-27, holotype. 2a, 2b: ESN 146509, OD-28, paratype. 3a, 3b: ESN 146510, OD-27, paratype. This specimen has an irregular skeletal structure. 4a, 4b: ESN 146511, OD-28, paratype. Arrows of 1b, 2b and 4b point to 1". Scale bars: 1a, 2a, 3a and $4a = 50 \,\mu$ m; others = $20 \,\mu$ m.



Figures 10-1a-4b; 11-1a, 1b

Helotholus vema Hays-Sugiyama, 1992, pl. 1, fig. 3.

Description.—Cephalis hemispherical to dome-shaped, porous, with or without short external spines. It is composed of three lobes of which the eucephalic one is usually discernible externally by a certain stricture corresponding to the place of **DR**. Ante- and postcephalic lobes are equal in size. Thorax may be developed, but is short with an obscure collar stricture. Wall thin, bearing numerous, short by-spines on the upper half. Pores are circular to oval, variable in size, without regular arrangement. Skeletal construction as with genus: **Ax** wartlike or absent. All of the elements of the skeleton are circular in cross section.

Remarks.—This species is similar to *Helotholus vema* Hays but is distinguished from the latter species by its smaller test dimensions, common development of \mathbf{D} , shorter \mathbf{Ax} , and complete lack of \mathbf{V} .

Dimensions (in µm).-Based on measure-



Figure 13. Schematic illustration of typical skeletal structure of *Botryopera* (?) *leptostraca* sp. nov. (a): Dorsal view. (b): Right lateral View. (c): Basal view.

ment of 42 specimens examined by SEM. Height of test; 50–93. Maximum width of test; 55–85. Maximum diameter of **PR**: 15–30.

Holotype.—ESN 146504 (Figs. 10-1a—1d) from TH-4.

Occurrence.—TH-1, 2, 3 and 4 (common in abundance).

Etymology.-From the Latin subtilis, minute.

Steganocubus lipus Sugiyama, sp. nov.

Figures 12-1a-4b

Description.-Cephalis is composed internally of three lobes of ante-, eu- and postcephalis. They are, however, hardly recognized externally owing to the secondary development of the microgranular covering on the upper part of the cephalic wall. Thorax relatively long, not closed distally, having a more or less distorted shape in cross section. Collar stricture may be distinct. Pores are circular to oval, deeply set in pore frames. They are without regular arrangement on the upper part of the cephalic wall, but show more or less longitudinal arrangement on the lower part of the cephalic and the whole thoracic wall. Numerous short by-spines extending from the pore frames. Skeletal structure is identical to that of S. subtilis sp. nov. but the development of Ax is more prominent.

Remarks.—This species is morphologically distinguished from *S. subtilis* by having a more elongated and thicker shell wall, more or less regularly arranged pores, and distinct **Ax**. However, the true phylogenetic relationship between the two species is at present uncertain, and they possibly represent only morphologic variants of one and the same species.

Dimensions (in μm).—Based on measure-

[→] Figure 14. 1a-4b: Botryopera (?) leptostraca Sugiyama sp. nov. 1a, 1b: ESN 146512, OD-27, holotype. 2a, 2b: ESN 146513, OD-17, paratype. 3a, 3b: ESN 146514, OD-17, paratype. 4a, 4b: ESN 146515, OD-21, paratype. Arrows of 1a, 2a and 3a point to delicate meshwork between by-spines. Arrows of 1b and 2b point to short 1". 5a, 5b: Botryopera (?) whitei (Bjørklund), ESN 146516, OD-18. Scale bars: 1a, 2a, 3a, 4a and $5a = 50 \mu m$; others = $20 \mu m$.





Figure 15. Schematic illustrations of typical skeletal structure of *Botryopera* (?) *whitei* (Bjør-klund). (a): Dorsal view. (b): Right lateral view. (c): Basal view.

ment of 18 specimens examined by SEM. Height of test; 65-123. Maximum diameter of test; 65-100. Maximum diameter of **PR**; 10-25.

Holotype.—ESN 146508 (Figures 12-1a, 1b) from OD-27.

Occurrence.—OD-17, 18, 26, 27 and 28 (very rare in abundance).

Etymology.-From the Greek lipos, fat.

Genus Botryopera Haeckel, 1887

Botryopera Haeckel, 1887, p. 1108.

Trisulcus Popofsky, 1913, sensu Petrushevskaya, 1971b, p. 140 (partim).

Type species.—*B. cyrtoloba* Haeckel, 1887 (designated by Petrushevskaya, 1975).

Remarks.—The generic concept used in this study mainly follows that of Petrushevskaya (1975, 1981, 1986). This genus is easily distinguished from *Pseudocubus* and *Steganocubus* gen. nov. by its large eucephalic lobe sitting on **DR**. This seems to be closely related to the value of Y/X, which is much larger than 1 in this genus. One can remark that the detailed skeletal structure is at the present time not well understood with respect to every species in the genus. Therefore, the generic assignment of the following three species remains tentative. In order to solve this problem it is necessary to redescribe the type species in detail, including its skeletal structure.

> Botryopera (?) leptostraca Sugiyama, sp. nov.

Figures 14-1a-4b

Description.-Eucephalic wall pierced by numerous circular to oval pores of relatively small size, possessing a large number of byspines on the surface, rimmed by **DR** on the lower margin. Perforate, delicate shell wall develops downward from DR or slightly higher level than **DR**. It is cylindrical or truncated conical in the lateral view, and corresponds to ante- and postcephalic wall. Delicate meshwork may also develop between by-spines (Figs. 14-1a, 2a and 3a). **DR** and **PR** are always connected by a part of **A**, two I'', V and two pillars developed near the junctions of two L-R and PR. Further connector bars may be present between both rings. A' well-developed. D and two L have one verticil of one to three spinules of which D' and L' are moderately developed and sometimes extend to the shell wall. Two I' are proximally amalgamated with two short 1". V situated in the sagittal plane and may penetrate the shell wall outside beyond the junction of **DR**. V' and V'' are completely absent. All of the skeletal elements are circular in cross section.

Remarks.—This species is similar to Botryopera (?) pseudoantarctissa Petrushevskaya in Petrushevskaya and Kozlova (1979), but differs from the latter species in having Vin the sagittal plane, and rather delicate shell wall.

Dimensions (in μm).—Based on measurement of 24 specimens examined by SEM. Height of test; 65-95. Meximum width of test; 65-73. Maximum diameter of **PR**: 15-25.

Holotype.-ESN 146512 (Figures 14-1a



Figure 16. 1a-6b: *Botryopera* (?) *whitei* (Bjørklund). 1a, 1b: ESN 146517, OD-18. 2a, 2b: ESN 146518, OD-18. 3a, 3b: ESN 146519, OD-17. 4a, 4b: ESN 146520, OD-17. 5: ESN 146521, OD-18. 6a, 6b: ESN 146522, OD-17. Scale bars: 1a, 2a, 3a, 4a, 5 and $6a = 50 \ \mu m$; others = $20 \ \mu m$.



-1b) from OD-27.

Occurrence.—TH-4, OD-17, 18, 21, 26, 27 and 28 (very rate in abundance).

Etymology.—From the Greek, *leptos*, delicate, and *ostracon*, shell.

Botryopera (?) whitei (Bjørklund)

Figures 14-5a-5b; 16-1a-6b; 17-1a-3

Antarctissa whitei Bjørklund, 1976, p. 1125, pl. 13, figs. 9-14, pl. 15, fig. 4.

Botryopera oceanica whitei (Bjørklund)-Petrushevskaya and Kozlova, 1979, p. 122, figs. 325-328.

Description.—Shell dome- to bullet-shaped, entirely spongy due to the development of secondary meshwork all around. Thick bristles may develop on the shell surface. Primary lattice work of eucephalis is, however, relatively rough, and the size of pores is thus similar to Cryptogyrus trachylobus sp. nov. rather than to B. (?) leptostraca sp. nov. (Figure 16-6a). Shallow stricture rarely expressed on the shell wall. Fundamental skeletal structure is common with that of B. (?) leptostraca sp. nov. It is, however, much more complicated by the development of additional connector bars between PR, DR and the shell wall. **PR** is quite irregular in outline. **DR** is usually embedded in the shell wall, so that the position is not clear from the basal view. D' and L' well developed, sometimes extending outside the shell wall. V usually swerves from the sagittal plane and makes an acute angle with Lr, rarely with Ll. It is sometimes free from DR and directly penetrates the shell wall beyond the junction of **PR**. V' and V'' may be present but are hardly distinguished from other connector bars.

Remarks.—Although Petrushevskaya and Kozlova (1979) treated this species as a subspecies of *B. oceanica* (Ehrenberg, 1872), such spongy externality may be diagnostic for this

species group alone. Bjørklund (1976) mentioned that the occurrence of this species in the Norwegian Sea is restricted to the Upper Miocene to Pliocene, but the Oidawara Formation is undoubtedly lowest Middle Miocene judging from all available geological and paleontological data. The age difference suggests the immigration of it from the western Pacific to North Atlantic or that the occurrence was strongly affected by paleooceanographic conditions. Further examination is necessary to clarify the problem. B. (?) whitei differs from B. (?) leptostraca sp. nov. in its much spongier shell wall and swerved V. Even if V lies near the sagittal plane (Figs. 16-3a, 3b), the former species can be distinguished from the latter by the development of D', L', V', and spongy network on the shell wall. It is very difficult to distinguish this species from Steganocubus *lipus* sp. nov. when the specimens are laterally set on a strewn slide.

Dimension (in μm).—Based on measurement of 47 specimens examined by SEM. Height of test; 58-100. Maximum width of



Figure 18. Schematic illustrations of typical skeletal structure of *Cryptogyrus trachylobus* gen. et sp. nov. (a): Dorsal view. (b): Right lateral view. (c): basal view.

[←] Figure 17. 1a-3: Botryopera (?) whitei (Bjørklund). 1a, 1b: ESN 146523, OD-18. 2a, 2b: ESN 146524, OD-18. 3: ESN 146525, OD-17, transmitted light micrograph. Arrow points to swerved V. 4a-4d: Botryopera (?) sp. A, ESN 146526, TH-4. Arrows of 4b point to two 1". Scale bars: 1a, 2a, 3 and $4a = 50 \ \mu m$; others = 20 μm .



test; 50-75. Maximum diameter of **PR**; 15-30.

Occurrence.—OD-17, 18, 21, 26, 27 and 28 (rare in abundance).

Botryopera (?) sp. A

Figures 17-4a-4d

Description.-Eucephalic wall rugged, pierced by numerous circular to oval pores of relatively small size, having many rodlike by-spines on the upper half, edged by DR on the bottom. Additional shell wall developed from slightly higher level than DR (Figure 17-4c). It is cylindrical in shape, quite delicate, and incomplete in the proximal part. The skeletal structure is nearly identical to that of B. (?) leptostraca sp. nov., but differs from the latter in having questionable V' which is proximally amalgamated with V and distally bends downward (Figures 17-4b-4d). V extends beyond the junction of **PR**, and penetrates the shell wall. D'vestigial. L' missing.

Remarks.—This species is distinguished from B. (?) leptostraca and B. (?) whitei in having numerous by-spines on the upper part of the eucephalis and much thinner additional shell wall. The existence of questionable V' is also diagnostic of this species. The proposal of a new name is postponed because of the small number of available individuals.

Dimensions (in μ m).—Based on two specimens examined by SEM. Height of test; 85-90. Maximum width of test; 60-63. Maximum diameter of **PR**; 15-18.

Occurrence.—TH-4 (very rare in abundance).

Genus Cryptogyrus Sugiyama, gen. nov.

Etymology.—From the Greek *cryptos*, hidden, and *gyros*, circle; masculine gender.

Type species.—*C. trachylobus* Sugiyama sp. nov. (by monotypy).

Diagnosis.- Test consisting of exclusively large eucephalis, with or without loosely defined ante- and postcephalic lattice shell, and having a distinct ring structure in the skeleton. **PR** is thick, circular in cross section. **DR** is composed of four arches which are convex upward and forms the lower margin of a large eucephalic chamber. Y/Xis much larger than 1. A is short, usually not forming external prolongation. \mathbf{A}' absent. **D** and two **L** relatively thin. **D'** and **L'** may be distinct. \mathbf{l}' and \mathbf{V}' missing. Two \mathbf{l}'' and V'' are short. When one views from the basal side, two l" always lie in a plane perpendicular to the sagittal plane. V is commonly present, but rarely absent as an intraspecific variation. In the latter cases, **PR** and **DR** are connected by five bars consisting of \mathbf{A} , two \mathbf{I}'' and two pillars developed on the ventral side (Figure 19-4b). There are no additional connector bars between PR and additional lattice wall.

Remarks.—This genus differs from *Botryopera* in lacking \mathbf{A}' , two \mathbf{I}' and \mathbf{V}' , and having only four connector bars between \mathbf{PR} and \mathbf{DR} in typical specimens. Further remarks are given in the discussion of the type species.

Cryptogyrus trachylobus Sugiyama, sp. nov.

Figures 19-1a-5; 20-1a-2b

Description.—Skeletal structure as with genus: **D** and two **L** variable in length. They are sometimes markedly long, and irregularly curved and bifurcated distally (Fig. 19 -1d), and often have a few conical spinules

[←] Figure 19. 1a-5: Cryptogyrus trachylobus Sugiyama, gen. et sp. nov. 1a-1e: ESN 146527, OD-27, holotype. Arrows of 1b point to the distal part of V and thick arch connecting L with by-spine, respectively. Arrow of 1c also points to the distal part of V. Arrow of 1d points to the bifurcation of L. 2a, 2b: ESN 146528, OD-17, paratype. D of this specimen is broken off. 3: ESN 146529, OD-18, paratype. 4a-4b: ESN 146530, OD-18, paratype. Arrows of 4b point to two irregularly developed pillars between PR and DR. 5: ESN 146531, OD-17, paratype. Scale bars: 1a, 1b, 2a, 3, 4a and $5=50 \mu m$; others=20 μm .



near the junctions of A and L-R. D' and L' may be recognizable among the spinules. Big eucephalis supported by the skeleton, pierced by large, oval to circular pores, having numerous by-spines on the surface. Among the by-spines, those extending from the lower margin of the eucephalic lattice shell, which are directed obliquely downward, are commonly much longer and thick-Additional thick arches often grow er. between the tips of them and distal parts of **D** and two L (Figures 19-1b, 20-2a). The development of secondary network between neighboring by-spines is also present in some specimens (Figure 20-1a). Adult specimens (?) (Figures 19-2a, 3a) have coarse lattice wall which corresponds to ante- and postce-



Figure 21. Schematic illustrations of typical skeletal structure of *Ceratocyrtis* sp. aff. *C. histricosa* (Jørgensen). (a): Dorsal view. (b): Right lateral view. (c): Basal view.



Figure 22. Schematic illustrations of skeletal variation of the genus *Ceratocyrtis*. (a) and (b); right lateral view, (c) and (d); basal view. (a) and (c); extreme structure with L-R connecting L and PR, (b) and (d); another extreme structure with L-R connecting L' and PR.

← Figure 20. 1a-2b.: Cryptogyrus trachylobus Sugiyama, gen. et sp. nov. 1a, 1b: ESN 146532, OD-18, paratype. Arrow of 1a points to secondary arch between by-spines. 2a, 2b: ESN 146533, OD-18, paratype. Arrows of 2a point to well developed arches connecting two L with by-spines. 3a, 3b: Ceratocyrtis sp. aff. C. histricosa (Jørgensen), ESN 146534, TH-4. Arrow of 3b points to short L-R. 4a-6: Ceratocyrtis stoermeri Goll and Bjørklund. 4a, 4b: ESN 146535, OD-28. Arrow of 4b points to the tip of Ax. 5a, 5b: ESN 146536, OD-26. Arrow of 5b points to short L-R. 6: ESN 146537, OD-26. Scale bars: 1a, 2a, 3a, 4a, 4b, 5a and $6=50 \,\mu\text{m}$; others=20 μm .



Figure 23. 1a, 1b: Ceratocyrtis sp. aff. C. histricosa (Jørgensen), ESN 146538, TH-4. Arrows of 1b point to L-R. 2a, 2b: Lophophaena sp., ESN 146842. White arrows of 2b point D', black one does L-R. This specimen is from the Pliocene Nobori Formation, Shikoku, Southwest Japan (corresponding to the Spongaster pentas Zone of Riedel and Sanfilippo, 1978). Further information is given in Sugiyama et al. (1992). 3a, 3b: Pseudodictyophimus lectari Caulet, ESN 146843. Black arrows of 3b point to D', white ones to L-R. Locality same as for the preceding species. Scale bars: 1a, 2a and $3a = 50 \,\mu m$; others = 20 μm .

phalic wall and is formed by further development of secondary network below the eucephalic chamber. The wall roughly encloses the basic internal skeleton.

Remarks.—The development of additional lattice wall below the eucephalis has quite a wide variational range in the population. It is, however, continuous between individuals, and may represent either ontogenetic stages or phenotypic variation of the adult stage. When the additional wall is indefinable, this species is similar to the species of the genera *Peridium* Haeckel, 1881, *Phormacantha* Jørgensen, 1905, and *Plectacantha* Jørgensen, 1905. The former species is, however, distin-

guished from them by having two thick I'' arranged in a plane perpendicular to the sagittal plane, lacking a long external prolongation of **A**, and having ante- and postcephalis in adult specimens (?). This species resembles *Botryopera* (?) *leptostraca* sp. nov., from which it differs in having larger pores on the eucephalis and the features mentioned in the generic remarks.

Dimension (in μ m).—Based on measurement of 22 specimens examined by SEM. Height of test; 60–93. Maximum width of test; 55–85. Maximum diameter of **PR**; 10–25.

Holotype.—ESN 146527 (Figures 19-1a

-1e) from OD-27.

Occurrence.—TH-4, OD-17, 18, 21, 26, 27 and 28 (very rare in abundance).

Etymology.—From the Greek *trachys*, rough, and *lobos*, lobe.

Genus Ceratocyrtis Bütschli, 1882, emend. Petrushevskaya, 1971b

Ceratocyrtis Bütschli, 1882, p. 536.—Petrushevskaya, 1971b, p. 98.

Helotholus Jørgensen, 1905, p. 137.

Bathlocalpis Clark and Campbell, 1942, p. 64.

Type species.—Cornutella? *cucullaris* Ehrenberg, 1873 (designated by Petrushevskaya, 1971b).

Remarks.—The generic concept including the synonymy follows Petrushevskaya (1971b).

Ceratocyrtis stoermeri Goll and Bjørklund

Figures 20-4a-6

Ceratocyrtis stoermeri Goll and Bjørklund, 1989, p. 731, pl. 5, figs. 5-9.

Description.—Test large, two-segmented form with ambiguous external stricture. The first segment very small, pierced by small, circular to subcircular pores set in thick frames from which arise small by-spines. The second segment large, campanulate, more or less tapering distally, pierced by large, subcircular to circular pores surrounded by circular to polygonal-shaped thick frames: the upper part is spinous; the middle part, where the thorax is widest and the ridges of the pore frames are sharpest, has the largest diameter of the pores; and the lower part is rather smooth in outline. The termination of the second segment is in line in lateral view, often accompanied by a delicate sieve plate at the base. Two segments internally partitioned by **PR** which is composed of distinct arches but nearly horizontal. MB relatively short. A makes a nearly right angle from the horizontal, and merges into **PR**. **D** extends downward with a large angle from the horizontal, and may have one, rarely a few branches in the distal part. Two **L** extending slightly downward, having distinct **L-R** in the middle part, and may branch off in the distal part like **D**. **L'** rarely present. **V** connects with **PR**. **Ax** thick, long, usually bifurcated in the distal part.

Remarks.—Morphology of this species is quite stable except for the development of the basal sieve plate.

Dimensions (in μ m).—Based on 11 specimens examined by SEM. Height of test; 120-150. Maximum width of test; 105-140. Maximum diameter of **PR**; 20-30.

Occurrence.—OD-17, 18 (very rare in abundance) and OD-26, 27 and 28 (rare in abundance).

Ceratocyrtis sp. aff. C. histricosa (Jørgensen)

Figures 20-3a, 3b; 23-1a, 1b

aff. Helotholus histricosa Jørgensen, 1905, p. 137, pl. 16, figs. 86-88.

Ceratocyrtis sp. aff. C. histricosus (Jørgensen) -Sugiyama, 1991, pl. 1, fig. 9.

Description.—Test large, two-segmented by a distinct external stricture which corresponds to the place of **PR**. The first segment hemispherical, small, pierced by circular to subcircular pores of small size, ornamented by numerous, long by-spines arising from the pore frames, corresponding to upper part of eucephalis. The second segment campanulate, large, pierced by circular to subcircular pores of large size, having long by-spines on the upper half. Skeletal structure as with C. stoermeri. A and V usually penetrate the shell wall to form conical to rodlike spines which are longer and thicker than by-spines. L' is commonly well developed, then L-R may connect the proximal part of \mathbf{L}' and \mathbf{PR} (Fig. 22).

Remarks.—This species differs from C. stoermeri in having distinct stricture between

the first and second segments, longer byspines on the shell surface, external prolongations of \mathbf{A} and \mathbf{V} , and the lack of prominent ridges on the pore frames. It also differs from *C. histricosa* (Jørgensen) in having a more spinous shell wall and longer second segment.

Dimensions (in μ m).—Based on ten specimens examined by SEM. Height of test; 90-160. Maximum width of test; 80-160. Maximum diameter of **PR**; 20-35.

Occurrence.—TH-1, 2, 3 and 4 (rare in abundance).

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References

- Bjørklund, K.R., 1976: Radiolaria from the Norwegian Sea, Leg 38 of the Deep Sea Drilling Project. In, Talwani, M., Udintsev, G., et al., Init. Rep. DSDP, vol. 38, p. 1101-1168, pls. 1-24. U.S. Govt. Printing Office, Washington. D.C.
- Bütschli, O., 1882: Beiträge zur Kenntnis der Radiolarien skelette, insbesondere der Cyrtida. Zeitschr. Wiss. Zool., vol. 36, p. 485-540, pls. 31-33.

- Campbell, A.S., 1954: Radiolaria. In, Moore, R.C. and Campbell, A.S., eds., Treatise on Invertebrate Paleontology, D, Protista 3, p. 11-163.
- Chen, P. -H., 1974: Some new Tertiary Radiolaria from Antarctic deep-sea sediments. *Micropaleontology.*, vol. 20, no. 4, p. 480-492, pls. 1-4.
- —, 1975 : Antarctic Radiolaria. In, Hayes, D.E., Frakes, L.A., et al., Init. Rep. DSDP, vol. 28, p. 437-513. U.S. Govt. Printing Office, Washington, D.C.
- Clark, B.L. and Campbell, A.S., 1942: Eocene radiolarian faunas from the Mt. Diablo area, California. *Geol. Soc. Amer., Spec. Paper*, no. 39, p. 1-112, pls. 1-9.
- De Wever, P., 1981: Une nouvelle sous-famille, les Poulpinae, et quatre nouvelles espèces de Saitoum Radiolaires mésozoiques téthysiens. *Géobios*, no. 14 (1), p. 5-15.
- Dumitrica, P., 1973: Cretaceous and Quaternary Radiolaria in deep sea sediments from the northeast Atlantic Ocean and Mediterranean Sea. In, Ryan, W.B.F., Hsü, K.J., et al., Init. Rep. DSDP, vol. 13, p. 829-901, pls. 1-28. U.S. Govt. Printing Office, Washington, D.C.
- , 1991: Middle Triassic Tripedurnulidae, n. fam.
 (Radiolaria) from the Eastern Carpathians
 (Romania) and Vicentinian Alps (Italy). *Rev. Micropaleont.*, vol. 34, no. 4, pp. 261-278, pls. 1, 2.
- Ehrenberg, C.G., 1847: Über die mikroskopischen kieselschaligen Polycystinen als mächtige Gebirgsmasse von Barbados und über das Verhältniss der aus mehr als 300 neuen Arten bestehenden ganz eigenthümlichen Formengruppe jener Felsmasse zu den jetzt lebenden Thieren und zur Kreidebildung. Eine neue Anregung zur Erforschung des Erdlebens. Kgl. Acad. Wiss. Berlin. Ber., Jahre 1847, p. 40-60, pl. 1.
- —, 1872: Mikrogeologischen Studien über das kleinste Leben der Meeres-Tiefgründe aller Zonen und dessen geologischen Einfluss. Kgl. Akad. Wiss. Berlin, Abhandl., Jahre 1872, p. 131-399, pls. 1-12.
- —, 1873: Grössere Felsproben des Polycystinen-Mergels von Bardados mit weiteren Erläuterungen. *Ibid.*, Jahre 1873, p. 213-263.
- Goll, R.M., 1958 : Classification and phylogeny of Cenozoic Trissocyclidae (Radiolaria) in the Pacific and Caribbean Basins. *Jour. Paleont.*, vol. 42, no. 6, p. 1409-1432, pls. 173-176.
- —, 1980: Pliocene-Pleistocene radiolarians from the east Pacific Rise and the Galapagos spreading center, Deep Sea Drilling Project Leg 54. In, Rosendahl, B.R., Hekinian, R., et al., Init. Rep. DSDP, vol. 54, p. 425-453, pls. 1-7. U.S. Govt. Printing Office, Washington, D.C.
- and Bjørklund, K.R., 1989: A new radiolarian biostratigraphy for the Neogene of the Norwegian Sea: ODP Leg 104. In, Eldholm, O., Thiede, J., Taylor, E. et al., Proc. ODP Sci. Results, vol. 104, p. 697-737, pls. 1-5. Ocean Drilling Program, College Station, Texas.
- Hachiya, K., Yamaoka, M. and Mizuno, Y., 1988: Deep sea fauna from the Middle Miocene Morozaki Group in the Chita Peninsula, Aichi Prefecture, Central Japan. Jour. Growth, vol. 27, no. 4, p. 119-139. (in Japanese with English abstract).
- Haeckel, E., 1881: Entwurf eines Radiolarien-Systems auf Grund von Studien der Challenger-Radiolarien. Jenaische Zeitschr. Naturwiss., vol. 15 (n. ser., vol. 8, no. 3), p. 418-472.
- —, 1887: Report on the Radiolaria collected by H.M.S. Challenger during the years 1873-76. *Rept. Voy. Challenger, 1873-1876, Zool.*, vol. 18, pts. 1-2. p. i-clxxxviii, 1-1803, pls. 1-140, 1 map.
- Hays, J.D., 1965: Radiolaria and late Tertiary and Quaternary history of Antarctic seas. *Biol. Antarctic Seas, II, Antarctic Res. Ser.*, vol. 5, p. 125-184, pls. 1-3.
- Hertwig, R., 1879 : Der Organismus der Radiolarien, p. I-IV, 1-149, pls. 1-10, Jena, G. Fischer.
- Itoigawa, J., 1974: Geology and paleontology of Mizunami City. XVII. Paleoenvironment, paleogeography and geological history of the Mizunami group. Bull. Mizunami Fossil Mus., no. 1, p. 365-367. (in Japanese)
- ____, Shibata, H. and Nishimoto, H., 1974 : *Ibid*. IV.
 Mollusca. *Ibid*., p. 43-204, pls. 1-63. (*in Japanese*)
- Jørgensen, E., 1905: The protist plankton and the diatoms in bottom samples. Bergens Mus. Skr., 1905, p. 49-151, 195-225, pls. 1-18.
- Kellogg, D.E., 1975: The role of phyletic change in the evolution of *Pseudocubus vema* (Radiolaria). *Paleobiology*, vol. 1, p. 359-370.
- Koizumi, I., 1985 : Diatom biochronology for late Cenozoic northwest Pacific. Jour. Geol. Soc. Japan, vol. 91, no. 3, p. 195-211.
- Lazarus, D., 1990: Middle Miocene to Recent radiolarians from the Weddell Sea, Antarctica, ODP Leg 113. *In*, Barker, P.F., Kennett, J.P., *et al.*, *Proc. ODP Sci. Results*, vol. 113, p. 709-727, pls. 1-7. Ocean Drilling Program, College Station, Texas.
- Loeblich, A.R., Jr., and Tappan, H., 1961: Remarks on the systematics of the Sarcodina (Protozoa), renamed homonyms and new and validated genera. *Proc. Biol. Soc. Washington*, vol. 74, p. 213-234.
- McNamara, K.J., 1986 : A guide to the nomenclature of heterochrony. *Jour. Paleont.*, vol. 60, no. 1, p. 4-13.

- Mori, S., 1974: Geology and paleontology of Mizunami City. XIV. Diatom. Bull. Mizunami Fossil Mus., no. 1, p. 293-303, pls. 98-100. (in Japanese)
- Nakaseko, K. and Sugano, K., 1973: Neogene radiolarian zonation in Japan. *Mem. Geol. Soc. Japan*, no. 8, p. 23-33, pls. 1-4. (*in Japanese with English abstract*)
- Nishimura, H., 1990 : Taxonomic study on Cenozoic Nassellaria (Radiolaria). Sci. Rep., Inst. Geosci., Univ. Tsukuba, sec. B, vol. 11, p. 69-172.
- Petrushevskaya, M.G., 1967: Radiolarii otryadov Spumellaria i Nassellaria Antarkticheskoi oblasti (po materialam Sovetskoi, Antarkticheskoi Ekspeditsii). *Issled. Fauny Morei*, vol. 4 (12), Resultaty biol. issled. Sov. Antarkticheskoi Ekspeditsii (1950-1958), no. 3, p. 5-186.
- —, 1968: Gomologii v skeletakh radiolyarii Nassellaria.
 1. Osnovnye dugi v semeistve Cyrtoidea. Zool. Zhurnal, vol. 47, no. 9, p. 1296-1310.
- —, 1971a: On the natural system of polycystine Radiolaria (Class Sarcodina). In, Farinacci, A. ed., Proc. II Planktonic Conference, p. 981-992. Technoscienza, Rome.
- —, 1971b: Radiolarii Nassellaria v planktone Mirovogo Okeana. *Issled. Fauny Morey*, Leningrad, Nauka, vol. 9 (17), Radiolarii mirovogo okeana po materialam sovetskikh ekspeditsii, p. 5-287.
- —, 1975: Cenozoic radiolarians of the Antarctic, Leg 29, DSDP. In, Kennett, J.P., Houtz, R.E., et al., Init. Rep. DSDP, vol. 29, p. 541-675, pls. 1-44. U.S. Govt. Printing Office, Washington, D. C.
- —, 1981: Radiolyarii otryada Nassellaria Mirovogo Okeana. Opredeliteli po Faune SSSR. *Izdav. Zool. Inst. Akad. Nauk. SSSR*, no. 128, p. 1-406.
- —, 1986: Evolution of the Antarctissa group. Marine Micropaleont., vol. 11, p. 185-195.
- , and Kozlova, G.E., 1979: The history of the microplankton of the Norwegian Sea. Chapter 5. Description of the radiolarian genera and species. *Issled. Fauny Morei*, vol. 23 (31), p. 86-157. (*in Russian*).
- Popofsky, A., 1908: Die Radiolarien der Antarktis (mit Ausnahme der Tripyleen). Deutsche Südpolar-Exped. 1901-1903, vol. 10 (Zool, vol. 2), p. 185-305, pls. 20-36.
- ____, 1913: Die Nassellarien des Warmwassergebietes. *Ibid.*, vol. 14 (Zool, vol. 6), p. 217-416, pls. 28-38.
- Riedel, W.R., 1967: Protozoa (Subclass Radiolaria). In, Harland, W.B. et al., The Fossil Record, p. 291-298. Geol. Soc. London.
- ----, 1971 : Systematic classification of Polycystine

Radiolaria. *In*, Funnel, B.M. and Riedel, W.R., *eds.*, *Micropalaeontology of oceans*, p. 649-661. Cambridge Univ. Press

- and Sanfilippo, A., 1978: Stratigraphy and evolution of tropical Cenozoic radiolarians. *Micropaleontology*, vol. 23, no. 1, p. 61–96, pls. 1– 10.
- Sakai, T., 1980: Radiolarians from Sites 434, 435, and 436, northwest Pacific, Leg 56, Deep Sea Drilling Project. *In*, Scientific Party, *Init. Rep. DSDP*, vol. 56, 57, p. 695-733, pls. 1-10. U.S. Govt. Printing Office, Washington, D.C.
- —, 1984: Neogene radiolarian datum planes of the equatorial and northern Pacific. In, Ikebe, N. and Tsuchi, R. eds., Pacific Neogene Datum Planes, p. 35-39. Univ. Tokyo Press.
- Sanfilippo, A., 1988 : Pliocene Radiolaria from Bianco, Calabria, Italy. *Micropaleontology*, vol. 34, no. 2, p. 159-180, pls. 1-2.
- Shibata, H, 1977: Miocene mollusks from the southern part of Chita Peninsula, central Honshu. Bull. Mizunami Fossil Mus., no. 4, p. 45-53.
- Sugano, K., 1976: Miocene radiolarian fossils from the Oidawara Formation, Mizunami Group, central Japan. *Ibid.*, no. 3, p. 17-24, pls. 4-7. (*in Japanese with English abstract*)

Sugiyama, K., 1992: Early Miocene radiolarians

from the Toyohama Formation, Morozaki Group, Aichi Prefecture. Jour. Geol. Soc. Japan, vol. 98, no. 1, p. 65-67, pl. 1. (in Japanese)

- —, Nobuhara, T. and Inoue, K., 1992: Preliminary report on Pliocene radiolarians from the Nobori Formation, Tonohama Group, Shikoku, Southwest Japan. *Jour. Earth and Planet. Sci.*, *Nagoya Univ.*, vol. 39, p. 1-30, pls. 1-30.
- Swanberg, N.R. and Bjørklund, K.R., 1987: The pre-cephalic development of the skeleton of *Amphimelissa setosa* (Actinopoda: Nassellarida). *Marine Micropaleont.*, vol. 11, p. 333-341.
- Takemura, A., 1986: Classification of Jurassic nassellarians (Radiolaria). *Palaeontographica*, *Abt.* A, vol. 195, p. 29-74, pls. 1-12.
- Weaver, F.M., 1976: Antarctic Radiolaria from the southeast Pacific Basin, Deep Sea Drilling Project, Leg 35. In, Hollister, C.D., Craddock, C., et al., Init. Rep. DSDP, vol. 35, p. 569-603, pls. 1-9. U.S. Govt. Printing Office, Washington, D. C.
- —, 1983: Cenozoic radiolarians from the Southwest Atlantic, Falkland Plateau region, Deep Sea Drilling Project Leg 71. In, Ludwig, W.J., Krasheninnikov, V.A., et al., Ibid., vol. 71, p. 667-686, pls. 1-6.

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中部日本下部~中部中新統産 Lophophaenidae 科放散虫の骨格構造について:愛知県師 崎層群豊浜累層(下部中新統)および岐阜県瑞浪層群生俵累層(中部中新統)より得られ た5属9種の Lophophaenidae 科放散虫類の骨格構造を検討した。それらは7種類のタイ プに細分され、すべてのタイプに分類基準として重要と思われる環状構造が認められる。2 新属4新種を提唱した。

72

951. A FOSSIL POPULATION OF *GINKGO* LEAVES FROM THE XINGYUAN FORMATION, INNER MONGOLIA*

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Abstract. Fossil Ginkgo is one of the index genera characterizing the Late Jurassic-Early Cretaceous Tetori-type and Siberian-type floras in Eastern Eurasia. Fossil Ginkgo leaves are sometimes crowded in occurrence, thickly massed and appressed on the same bedding plane, so representing a fossil population. One of us (Zhao) and his Chinese coworkers collected a number of detached fossil Ginkgo leaves from such an occurrence from the Xingyuan Formation (=Jiufotang Formation) at the Xilutian Open Coal-Mine, near Chifeng area, Zhaowudameng District, Inner Mongolia. These Ginkgo leaves are varied in size, form and mode of lamina-division. Nevertheless, they form a single fossil population, and thus belong to the same species, because their morphological features are similar and are thought to be within the range of variation and their cuticular features except for minor points are the same. This paper deals with the description of these leaves, with geographical and stratigraphical distributions of fossil Ginkgo leaves in the western part of Northeast China, and with generic and specific revision of some previous works and makes a brief comparison of the present population with those hitherto known. The present population of fossil Ginkgo leaves is at least the same as those of Fuxin, Shahezi, Damoguaihe and Dabao Formations in Northeast China. In the case of a small number of fossil Ginkgo leaves, it is difficult to identify them down to species so far as they do not show their unique morphological or cuticular features. The present study shows that it is difficult to assess any distinction between the genera Ginkgo and Baiera. The Ginkgo leaves comprising the present population is named by us as Ginkgo manchurica (Yabe et Oishi) Meng et Chen.

Key words. Fossil Ginkgo leaves, fossil Ginkgo population, younger Mesozoic, Northeast China.

Introduction

Fossiliferous younger Mesozoic sediments of nonmarine origin bearing rich coal-seams are developed in the Chifeng area, Zhaowudameng District (roughly 41°17′-45°24′N and 116°21′-120°59′E), Inner Mongolia, China. As to the geology of this area, no formal paper has been published except for a brief note by Shang and Zheng (1991). According to them, the Mesozoic sediments in this area are divided into Xingyuan (ca. 380 m thick), Yuanbaoshan (ca. 186 m thick) and Shuiquan (ca. 245 m thick) Formations in upward sequence. The Xingyuan Formation is equivalent to the Jiufotang Formation

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wihch is extensively distributed in West Liaoning Province (Figure 1 and Table 2).

They listed the following plant taxa from the Xilutian Open Coal-Mine of the Pingzhuan Coal-Field (Figure 1) (*; nomen nudum):

From the Xingyuan Formation (=Jiufotang Formation): Acanthopteris alata (Fontaine) Zhang, Coniopteris saportana Heer, Nilssoniopteris chifengensis sp. nov.*, Nilssonia sinensis Yabe et Oishi, Ginkgo manchurica (Yabe et Oishi) Meng et Chen, tapkensis Doludenko et Rasskazova, *G*. Sphenobaiera longifolia (Pomel) Florin, S. nantianmenensis Wang, Czecanowskia rigida Heer, Ixostrobus heeri Prynada, Pityolepis piceaoides sp. nov.*, P. pseudotsugaoides sp. nov.*, Tsuga taxoides Tan et Zhu, T. zhouiana sp. nov.*, Sphenolepis kurriana (Dunker) Schenk, Elatides curvifolia (Dunker) Nathorst, E. harrisii Zhou, Cephalotaxopsis asiatica HBDYS**, Sabinites neimongolica Tan et Zhu, Pagiophyllum cf. triangulare Prynada, Elatocladus smittiana (Heer) Seward, E. yuanbaoshanensis sp. nov.*, E. manchurica Yabe et Oishi, E. sp., Lindleycladus eichwaldii (Schimper), Scarburgia triangularis Meng, Conites sp. (**; not the author's or authors' name but the name of the institution: HBDYS being after Huabei Dizhi Yanjin Sou in Chinese=North China Institute of Geosciences)

From the Yuanbaoshan Formation: Acanthopteris onychioides (Vassilevskaja et Kara-Mursa) Zhang, Arctopteris kolymensis Samylina, Cladophlebis sp., Doratophyllum nilssoniopteroides sp. nov.*, Ginkgo concinna Heer, G. manchurica (Yabe et Oishi) Meng et Chen, G. sibirica Heer, G. tapkensis Doludenko et Rasskazova, G. truncata Li, Sphenobaiera biloba Prynada, Phoenicopsis angustifolia Heer, Pityophyllum sp., Pityolepis sp.

The fossil plant taxa listed above should be critically reexamined; for instance, the generic name *Lindleycladus* established by Harris (1979) would at present be valid only for the former *Podozamites lanceolatus* (Lindley et Hutton) leafy shoots with longitudinally oriented stomata from the Yorkshire Jurassic. However, at a glance from the above list, the fossil plant assemblages of both formations look to be of the Tetori type (*e.g.* Kimura, 1987a, b), though the list shows many coniferous taxa which are questionable in identification.

Recently, one of us (Zhao) and his Chinese coworkers collected a number of fossil plants from the Xingyuan Formation at the Xilutian Open Coal-Mine (Figure 1) for the purpose of making detailed palaeobotanical studies on the Xingyuan plant assemblage (Xingyuan flora). Previous to our studies, Zhao and Tao (1991) described a new *Ginkgo* species and illustrated several fossil plants collected from the Xingyuan Formation.

In this paper, we describe *Ginkgo* leaves from the Xingyuan Formation. These leaves are crowded in occurrence, sometimes thickly massed and appressed on the same bedding plane. In addition, we revise and briefly review the *Ginkgo* leaves hitherto described or recorded from the younger Mesozoic plant sites in the western part of Northeast China, and make a brief comparison of the present population of *Ginkgo* leaves with those hitherto known.

As to the geological age of the Xingyuan (or Jiufotang) Formation, there are two different opinions among Chinese geologists and palaeontologists; one regards it as latest Jurassic and the other as earliest Cretaceous. We are of the opinion that at present it is difficult to make a precise age determination of the Jiufotang Formation and its equivalent, because this formation is wholly of non-marine origin and has not yielded any fossils indicating its precise age.

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Figure 1. Location of the fossil plant site in the present work. A : Xilutian Open Coal-Mine. B : Fossil plant site belonging to the Xingyuan Formation (=Jiufotang Formation), corresponding to Locality no. 22 in Figure 7 and Table 2. C : Pingzhuang Station. According to the informal communication from K. Zhao, the Xingyuan (=Jiufotang) and Yuanbaoshan (=Shahai+Fuxin) Formations are distributed in this area (see Table 2).

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Material and methods

Fossil *Ginkgo* leaves were collected from the Xingyuan (Jiufotang) Formation at the Xilutian Open Coal-Mine (roughly Lat. 42° 00'N; long. 119°12'E) near Pingzhuang, Chifeng, Zhaowudameng, Inner Mongolia (Figure 1; indicated by '22' in Figure 7). These leaves for cuticular study were peeled off from tuffaceous shale and treated in Schulze's solution followed by diluted potassium hydroxide (ca. 10%), stained with safranin, and then washed in alcohol and xylene before mounting in canada balsam. For the SEM observations cuticles were sputter coated with gold and photographed with a Hitachi S-800, 20 kv.

The specimens, cuticular preparations and SEM stages examined and described in this paper are kept in the Institute of Botany, Academia Sinica, Xiangshan, Beijing.

Description

Ginkgoales Genus Ginkgo Linnaeus Ginkgo manchurica (Yabe et Oishi) Meng et Chen

Figures 2-6

1991. Ginkgoites pingzhuangensis Zhao et Tao : Zhao and Tao, p. 965, pl. 2, figs. 14-16.

Specimens examined : NCP 8259-8273, 8277-8278, 8283, 8288-8291, 8332, 8343, 8345, 8348-8351, 8353-8354, 8367, 8369.

Locality and horizon: Xilutian Open Coal-Mine: Xingyuan (Jiufotang) Formation (possibly uppermost Jurassic or lowest Cretaceous).

Occurrence : Very abundant.

Description of specimens : Obtained speci-

mens were all detached leaves; some with preserved petiole. Cuticle is well preserved.

1) External morphology (Figures 2-3): Laminae are generally fan-shaped or semicircular in form, but remarkably varied in size, 1.5-13 cm in radius (or high). Petioles are long and slender, 1-2 mm thick; the longest one is 3.8 cm long, but their abscission part is missing in general. The lamina is fundamentally divided into two parts by a deep median sinus reaching almost to the tip of the petiole to form the most simple lamina. Each part is generally further dichotomously divided once to three or more times into broader to fairly slender segments or lobes by deeper or shallower sinuses. The final number of ultimate segments or lobes is 24 in each part (Figures 21, 31, 2m, 3m,).



Figure 2. Ginkgo manchurica (Yabe et Oishi) Meng et Chen. Photographs; all in natural size. Detached leaves of varied sizes, forms and modes of the lamina-division. A-type of leaves : 2a (NCP-8350), 2b (NCP-8348). B-type of leaves : 2c (NCP-8345), 2d (NCP-8332). C-type of leaves : 2e (NCP-8347), 2f (NCP-8353), 2g (NCP-8290), 2h (NCP-8277), 2i (NCP-8343). D-type of leaves : 2j (NCP-8260), 2k (NCP-8359), 21 (NCP-8266). E-type of leaf : 2m (NCP-8265).

We provisionally classified our leaves (laminae) into the following five types (A-E types):

(1) A-type of lamina (Figures 2a, 3a, 2b, 3b, 3n, 3o): smaller in size (typically 1.5 cm in radius), divided totally into 4-6 segments.

(2) B-type of lamina (Figures 2c, 3c, 2d, 3d, 3p): Rather larger in size (typically 2.5 cm in radius), divided totally into 4-6 segments.

(3) C-type of lamina (Figures 2e, 3e, 2f, 3f, 2g, 3g, 2h, 3h, 2i, 3i): Medium-sized (typi-



cally 3 cm in radius), divided totally into 8-14 segments or lobes.

(4) D-type of lamina (Figures 2j, 3j, 2k, 3k, 21, 31): Rather much larger in size (typically 5 cm in radius), divided totally into 12-20 segments including lobes.

(5) E-type of lamina (Figures 2m, 3m): Extremely large in size (10 cm in radius), divided into at least 18 segments in this specimen.

The above classification is for the sake of

convenience and there are no strict morphological boundaries among the present laminae; as a matter of fact, morphological variation between A- and B-types, B- and C-types, C- and D-types and D- and E-types are gradual and continuous.

So far as our specimens are concerned, the frequency of these types breaks down as follows: A-type (6%), B-type (14%), C-type (27%), D-type (40%) and E-type (3%). As mentioned below, if these specimens belong



Figure 3. Ginkgo manchurica (Yabe et Oishi) Meng et Chen. Line-drawings; all in natural size. Figures 3a-m were drawn from Figures 2a-m respectively. 3n-p, additional drawings; 3n-o, A-type of leaves (NCP-8350). 3p, B-type of leaf (NCP-8369).

to the same species, then the C- and D-types of the leaves can be regarded as representative of the species.

Both the right and left halves of a laminia are normally almost bilaterally symmetrical in size, form and number of segments or lobes. The segments of lobes usually bear rounded or obtuse apex. In general, the more the number of segments or lobes, the higher the lamina.

The vascular bundle appears to be single (?) in the petiole. It is then repeatedly divided dichotomously into the lamina, ending at the distal margins of the ultimate segment or lobe, not converging at the apex, but sometimes coming close together there. No thick veins along the margins of lamina are present as seen in extant or some fossil *Ginkgo* leaves. The number of veins is 6-8 (14-24 per cm in density) near the apex of the ultimate segment or lobe.

2) Cuticular features (Figures 4-6): We could observe cuticle in all the specimens obtained. Cuticle is hypostomatic, but a few occasional stomata are recognized on the marginal regions of segments or lobes on the adaxial side. The upper (adaxial) cuticle is mostly 1-1.5 μ m thick and slightly thicker

than that of the lower (abaxial) one. The upper cuticle consists mainly of vein-course cells, 4-8 rows of elongated cells and interveinal ordinary cells, isodiametric and polygonal in outline and irregularly arranged (Figurers 4d-e, 5a-A, 5b-d). Anticlinal and end walls of ordinary and vein-course cells are mostly slightly sinuous. The sinuousity is much clearer in the interveinal ordinary cells than the vein-course cells. Each periclinal wall is markedly papillate at its centre (Figures 4d, 5a-A, 5b-c).

The lower (Abaxial) cuticle consists of ordinary cells and stomatal complexes. On the vein course, cells are 5-10 rows of elongated cells. Their anticlinal walls are unevenly thickened, but periclinal walls are smooth or slightly papillate (Figures 4a-b, 5e, 6b). The outline of interveinal ordinary cells is usually indistinct under the light microscope but much clearer under the phase-contrast and SEM microscopes (Figures 6d-e). On some ordinary cells, a papilla 6-10 μ m in diameter is present on each periclinal wall (Figures 4b-c).

Stomatal complexes are scattered along the interveinal areas, forming 2-3 rows. They are irregularly orientated, but often longitudinal. Stomatal complex is haplocheilic and monocyclic or occasionally amphicyclic. Guard cells are sunken (Figures 4b, 4f, 4g, 5f). Subsidiary cells are 5-8 in number, markedly thickened near the aperture, and each with a large-sized papilla overarched above the guard cells (Figures 4f, 4g, 5f). Figures 6d-f show the inner view of stomata (SEM micrographs). Papilla is present on most of the ordinary cells (Figure 6a) and Figure 6b shows inner view of the papillae on the ordinary cells (SEM micrograph). Trichome is not seen on both surfaces. Resin body is also not observed between veins. Stem, twig and reproductive organs are not known.

Discussion: In extant Ginkgo biloba Linnaeus, it is well known that the leaves are quite varied in size, form and mode of lamina division, according to those on the long shoots, on the occasional off-shoots (outgrowths) and on the short shoots (*e.g.* Seward, 1919, fig. 630; Sakisaka, 1958; Harris *et al.*, 1974).

One of us (Kimura) cultivated several seedlings of Ginkgo biloba in the field garden belonging to his institute under artificially worst conditions with regard to water supply and amount of natural light for three years. We found that the leaves sprouted every May, but did not grow in size. They remained miniatures (about 2 cm in radius) until every fall season. However, their cuticular features did not differ from those of normally growing leaves. If the detached leaves of extant Ginkgo biloba were fossilized as impressions, then the above-mentioned miniatures of Ginkgo biloba leaves or those with multidivided laminae on the occasional outgrowths would have been separated as different species from the normal leaves.

The diagnostic features of fossil Ginkgo and Baiera leaves depended only on their

[→] Figure 4. Ginkgo manchurica (Yabe et Oishi) Meng et Chen. Cuticular features (I). 4a, Lower (abaxial) cuticle, showing the vein (v) and interveinal (iv) areas. Surface view prepared from an E-type of leaf (Figures 2m, 3m). The dark dots are stomata and small light dots are papillae in the interveinal area (slide no. NCP-MI8265a). 4b, Lower (abaxial) cuticle, showing stomata (s) and papillae (p) in the interveinal area. Surface view. Enlarged partly from Figure 4a. 4c, Lower (abaxial) cuticle. Phase contrast micrograph, showing vein (v) and interveinal areas. Surface view, prepared from one of the D-type leaves (NCP-8267) (slide no. NCP-MI8267a). 4d-e, Upper (adaxial) cuticle, showing vein (to the left in Figure 4d and to the right in Figure 4e) and interveinal areas. Surface view. Figure 4d; phase contrast micrograph. Figure 4e; normal light micrograph. Dark dots show the papillae prepared from a D-type leaf (shown in Figures 2k, 3k; NCP-8359) (slide no. NCP-MI8359a). 4f-g, Stomatal complexes on the lower (abaxial) cuticle, showing thickly cutinized and papillate subsidiary cells, seven (1-7) in Figure 4f and six (1-6) in Figure 4g. Inner view prepared from a B-type leaf (shown in Figures 2c, 3c; NCP-8345) (slide no. NCP-MI8345a).





mode of lamina division and number of veins in the ultimate segment or lobe. We feel that this much used distinction between the two genera *Ginkgo* and *Baiera* is negligible.

The present Ginkgo leaves are all detached and thickly massed and appressed on the same bedding plane of the tuffaceous shale The leaves themselves can be peeled off bed. easily and their cuticle is seen to be well preserved. They differ from each other in size, form and mode of lamina division. However, these features vary gradually and continuously and no morphological boundaries can be drawn amongst them. Also their cuticular features are almost the same, except for such minor points as sinuosity of anticlinal walls of ordinary cells and developmental degree of papillae on the epidermal cells. However, these features can vary from lamina to lamina according to position. Under the circumstances, we regard our fossil Ginkgo leaves as belonging to the same fossil population and showing only the variation in a single *Ginkgo* species.

About 70 Ginkgo (including Ginkgoites and Baiera) 'species' or 'forms' (except Sphenobaiera and Pseudotorellia) were reported from various localities and stratigraphical horizons of younger Mesozoic age in North and Northeast China under the generic names of Baiera, Ginkgo and Ginkgoites (Figure 7; Tables 1-2). It is very doubtful whether such a large number of 'species' (or 'forms' really existed.

Since the early 1900's pioneer studies of the fossil plants were made in western and northern Liaoning and southeast Songliao regions mainly by Yokoyama (1906), Yabe (1908, 1922), Yabe and Oishi (1933) and Oishi (1933). Table 2 shows the Jurassic-Lower Cretaceous stratigraphical units bearing fossil Ginkgo (including Baiera and Ginkgoites) leaves (with asterisk) and Figure 7 shows the localities of fossil Ginkgo (including Baiera and Ginkgoites) leaves in Northeast China, compiled by us.

1) In western Liaoning, fossil Ginkgo (including Baiera and Ginkgoites) leaves are abundant in the Beipiao, Haifanggou, Shahai and Fuxin Formations. The fossil population of these leaves from the Fuxin Formation is similar to ours.

2) In north Lianing and southeast Songliao, fossil *Ginkgo* (including *Baiera* and *Ginkgoites*) leaves are abundant in the Shahezi Formation. This fossil population is also similar to ours.

3) In Daxinganling region (Inner Mongolia), fossil *Ginkgo* (including *Baiera* and *Ginkgoites*) leaves are abundant in the Xingyuan Formation (=Jiufotang Formation; the present one) and are rather abundant in the Hongqi, Damoguaihe, Yuanbaoshan and Yimin Formations. Of these, the fossil population of leaves from the Damoguaihe, Yuanbaoshan and Yimin Formations is similar to ours.

4) The fossil population of *Ginkgo* (including *Baiera* and *Ginkgoites*) leaves in the Dabao Formation (eastern Liaoning) is quite similar to ours.

5) In eastern Jilin and eastern Heilongjiang, there are Jurassic and Lower Cretaceous sediments mostly of non-marine origin. But the occurrence of fossil *Ginkgo* (including *Baiera* and *Ginkgoites*) leaves is so sporadic that we are still ignorant about their specific identification and the range of varia-

 $[\]leftarrow$ Figure 5. Ginkgo manchurica (Yabe et Oishi) Meng et Chen. Cuticular features (II). 5a, Wellpreserved upper (adaxial; A) and lower (abaxial; B) cuticles. Surface view. SEM-micrograph prepared from a lobe of the D-type leaf (shown in Figures 2k, 3k; NCP-8359) (stage no. NCP-8359SEM-2). 5b, Upper (adaxial) cuticle, showing the vein (left side) and interveinal (right side) areas. Inner view. SEM-micrograph prepared from the same lobe as Figure 5a-A (stage no. NCP-8359SEM-2). 5c, Vein area (vein course) of the upper (adaxial) cuticle, enlarged partly from the same lobe as Figure 5a-A. 5d, Interveinal area of the upper (adaxial) cuticle, enlarged from the same lobe as Figure 5a-A. 5d, Surface view, showing an aperture (ap) and papillate subsidiary cells (1-5).



tion.

Under the circumstances, it is highly probable that the same population of *Ginkgo* leaves was distributed at least in eastern Inner Mongolia and eastern, western and northern Liaoning in Jurassic and Early Cretaceous time. The details are shown below.

Yabe and Oishi (1933) described 13 'species' or 'forms' of *Ginkgo* (including *Baiera* and *Ginkgoites*) from the following localities (their current spellings are shown in parentheses):

Southwestern Jilin: Tao-chia-tun (Taojiatun) and Huo-shih-ling (Huoshiling).

Northeastern Liaoning: Pa-tao-ho (Badaohao; near Fuxin), Ta-tai-shan (Dataishan = Changtu; near Siping) and Sha-ho-tze (Shahezi = Changtu).

The above-mentioned localities belong to the Shahai and Shahezi Formations (Table 2).

Central Liaoning: Wei-chia-pu-tzu (Weijiapuzi=Tianshifu; near Benxi), Nien-tzukou (Nianzigou) and Eru-tao-kou (Erdaogou).

The former two localities belong to the Dabao Formation and the latter to the Sangeling Formation (Table 2).

The taxa described by Yabe and Oishi (1933) are: Ginkgoites ? crassinervis Yabe (Taojiatun), G. digitata (Brongniart) var. huttoni Seward (after Kryshtofovich, 1924; without illustration) (Badaohao), G. cf. sibirica (Heer) [Shahezi, Taojiatun, Huoshiling, Weijiapuzi, Nianzikou and Dataishan (after Yokoyama, 1906)], Baiera cf. asadai Yabe et Oishi (Erdaogou), Cf. B. concinna (Heer) (Shahezi), B. cf. gracilis Bunbury [Huoshiling, Nianzigou (after Yokoyama, 1906), Taojiatun (after Yabe, 1908), Shahezi], B. kidoi Yabe et Oishi, 1933 (= B. cf. angustiloba Yabe, 1908) (Taojiatun; after Yabe, 1908 Huoshiling), B. manchurica Yabe et Oishi, 1933 [Shahezi, Dataishan (after Yokoyama, 1906), Taojiatun (after Yabe, 1908) and Huoshiling], B. minima Yabe et Oishi, 1933 (Shahezi), B. orientalis Yabe et Oishi, 1933 (Huoshiling), B. cf. phillipsi Nathorst (Huoshiling), B. sp. a (Huoshiling) and B. sp. b (Shahezi).

We are of the opinion that so far as the external morphology of these *Ginkgo* (including *Baiera* and *Ginkgoites*) leaves illustrated by Yabe and Oishi (1933) is concerned, most of them are indistinguishable specifically from the present *Ginkgo* leaves as shown below:

 Ginkgoites cf. sibirica (Heer); pl. 31, fig. 8 (Shahezi)=our A-type, pl. 32, figs. 4-5, 8B (Taojiatun), fig. 6 (Huoshiling) and fig. 7 (Weijiapuzi)=our B- and C-types.

(2) Cf. *Baiera concinna* (Heer); pl. 32, fig. 6 (Shahezi) = our B-type.

(3) *B*. cf. *gracilis* Bunbury; pl. 32, fig. 13B (Shahezi; indeterminable), fig. 14 (Shahezi), fig. 15 (Huoshiling) and pl. 33, fig. 5 (Shahezi)=our C-type.

(4) *B. kidoi* Yabe et Oishi, 1933; pl. 33, fig. 3 (Huoshiling) = our D-type.

(5) *B. manchurica* Yabe et Oishi, 1933; pl. 32, figs. 12, 13A and pl. 33, fig. 1 (Shahezi)=our C-type.

(6) B. minima Yabe et Oishi, 1933; pl.32, fig. 11 (Shahezi)=our C-type.

(7) B. orientalis Yabe et Oishi, 1933; pl.
33, fig. 4 (Huoshiling)=our C-type.

(8) *B*. cf. *phillipsi* Nathorst; pl. 33, fig. 2 (Huoshiling)=our C-type.

(9) B. sp. a (Yabe and Oishi, 1933); pl.32, fig. 17 (Huoshiling)=our A-type, pl. 33,

 $[\]leftarrow$ Figure 6. Ginkgo manchurica (Yabe et Oishi) Meng et Chen. Cuticular features (III). 6a, Lower (abaxial) cuticle treated by KOH with much more time, showing the vein and interveinal areas. Inner view. In the interveinal areas, many stomata (light ones) and papillae (small oval) are scattered. But it is difficult to distinguish the stomatal complexes in such a low magnification. SEM-micrograph prepared from a D-type leaf (shown in Figures 21, 31; NCP-8266) (stage no. NCP-8266SEM-4). 6b, Papillae, enlarged from Figure 6a. Inner view. 6c-f, Stomatal complexes, prepared from an E-type leaf (shown in Figures 2m, 3m; NCP-8265). Inner view. SEM-micrographs (stage no. NCP-8265SEM-1).



2 (compiled by us).

- Baiera, Ginkgo and Ginkgoites 'species' or 'forms' hitherto described or recorded by previous Table 1. authors from Jurassic-Early Cretaceous plant sites in Northeast China. *; with description of external feature.

 - **; with description of external and cuticular features.
 - ***; without description and illustration (list only).
 - F.; formation, G.; group.

Baiera cf. angustiloba Heer : Yabe, 1908, Shahezi F.*

- Baiera asadai Yabe et Oishi, 1928 : Zhang et al., 1980, Guojiadian (Haifanggou) F.* and Dabao F.*** : Zhang and Zheng, 1987, Haifanggou F.*** : Wang et al., 1989, Haifanggou F.***
- Baiera cf. asadai Yabe et Oishi, 1928 : Yabe and Oishi, 1933, Sangeling F.* and Dabao F.***
- Baiera balejensis (Prynada) Zheng, 1980 : Zhang et al., 1980, Zhuanshanzi F.*
- Baiera concinna (Heer) Kawasaki, 1925, Zhang <u>et al</u>., 1980, Guojiadian (Haifanggou) F.* : Zhang and Zheng, 1987, Haifanggou F.*** : Wang <u>et al</u>., 1989, Haifanggou F.***
- Cf. Baiera concinna (Heer) Kawasaki, 1925 : Yabe and Oishi, 1933, Shahezi F.* : Oishi, 1933, Shahezi F.** : Sze et al., 1963, Shahezi F.** (Yabe and Oishi's and Oishi's specimens, 1933) : Zhang and Zheng, 1987, Haifanggou F.***
- Baiera czekanowskiana Heer, 1976 : Zhang and Zheng, 1987, Haifanggou, F.** : Wang et al., 1989, Haifanggou F.***
- Baiera furcata (Lindley et Hutton) Braun, 1843 : Zhang <u>et al</u>., 1980, Damoguaihe F.* and Beipiao F.* : Wang <u>et al</u>., 1985, Jubao F.*** and Jiufengshan F.*** : Zhang and Zheng, 1987, Beipiao F.*** and Haifanggou F.*** : Wang <u>et al</u>., 1989, Beipiao F.***
- Baiera cf. furcata (Lindley et Hutton) Braun, 1843 : Wang et al., 1985, Jubao F.***
- <u>Baiera gracilis</u> (Bean MS) Bunbury, 1851 : Yokoyama, 1906, Dabao F.* : Yabe, 1922, Shahezi F.* : Sze <u>et al</u>., 1963, Fuxin F.***, Shahezi F.*** and Sangeling F.* (Yabe and Oishi's specimen, 1933) : Zhang <u>et al</u>., 1980, Guojiadian (Haifanggou) F.* and Dabao F.*** : Wang <u>et al</u>., 1985, Dabao F.***, Beipiao F.***, Haifanggou F.***, Wanbao F.*** and Manketouebo F.*** : Zhang and Zheng, 1987, Beipiao F.*** and Haifanggou F.*** : Wang <u>et al</u>., 1989, Haifanggou F.***
- Baiera cf. gracilis (Bean MS) Bunbury, 1851 : Yabe, 1908, Shahezi F.* : Yabe and Oishi, 1933, Shahezi F.* and Dabao F.*** : Oishi, 1933, Shahezi F.** : Sze <u>et al.</u>, 1963, Shahezi F.** (Yabe and Oishi's and Oishi's specimens, 1933) and Dabao F.* (Yokoyama's specimen, 1906) : Yang and Sun, 1982, Shahezi F.* and Yingcheng F.*** : Wang <u>et al</u>., 1985, Hongqi F.*** and Beipiao F.*** : Zhang, 1987, Fuxin F.*** : Wang <u>et al</u>., 1989, Fuxin F.*** and Beipiao F.***
- Baiera cf. guilhaumati Zeiller, 1903 : Sze, 1931, Fuxin F.***
- Baiera <u>kidoi</u> Yabe et Oishi, 1933 : Yabe and Oishi, 1933, Shahezi F.* : Oishi, 1933, Shahezi F.** : Sze <u>et al.</u>, 1963, Shahezi F.** (Yabe and Oishi's and Oishi's specimens, 1933) : Zhang et al., 1980, Shahezi F.*
- <u>Baiera manchurica</u> Yabe et Oishi, 1933 : Yabe and Oishi, 1933, Shahezi F.* : Oishi, 1933, Shahezi F.** : Sze <u>et al.</u>, 1963, Shahezi F.** (Yabe and Oishi's and Oishi's specimens, 1933) : Zhang <u>et al</u>., 1980, Shahezi F.* (Yabe and Oishi's specimen, 1933) : Wang <u>et al</u>., 1985, Shahezi F.*** : Hao <u>et al</u>., 1986, Shahezi F.***
- Baiera minima Yabe et Oishi, 1933 : Yabe and Oishi, 1933, Shahezi F.* : Oishi, 193 Shahezi F.** : Sze <u>et al</u>., 1963, Shahezi F.** (Yabe and Oishi's and Oishi's specimen, 1933) : Zhang <u>et al</u>., 1980, Shahezi F.* (Yabe and Oishi's specimen, 1933) and Anmin F.* : Hao <u>et al</u>., 1986, Fuxin F.*** 1933,

Baiera orientalis Yabe et Oishi, 1933 : Yabe and Oishi, 1933, Shahezi F.*

Baiera cf. phillipsi Nathorst, 1880 : Yabe and Oishi, 1933, Shahezi F.* : Oishi, 1933, Shahezi F.**

Baiera pulchella Heer, 1876 : Toyoma and Oishi, 1935, Damoguaihe F.* Baiera sp. a (Yabe et Oishi, 1933) : Yabe and Oishi, 1933, Shahezi F.* : Oishi, 1933, Shahezi F.** Baiera sp. b (Yabe et Oishi, 1933) : Yabe and Oishi, 1933, Shahezi F.* : Oishi, 1933, Shahezi F.** Baiera ? sp. 3 (Sze et al., 1963) : Sze et al., 1963, Fuxin F.* Baiera sp. (Wang et al., 1985) : Wang et al., 1985, Wanbao F.*** and Changliangzi Ŧ.*** Ginkgo adiantoides (Unger) Heer, 1878 : Zhang et al., 1980, Yimin F.* <u>Ginkgo chilinensis</u> (Lee) Zhang <u>et al</u>., 1980 : Zhang <u>et al</u>., 1980, Shahezi F.* and Damoguaihe F.*** <u>Ginkgo</u> ? <u>crassinervis</u> (Yabe et Oishi) Zhang <u>et al</u>., 1980 : Zhang <u>et al</u>., 1980, Shahezi F.* (Yabe and Oishi's specimen, 1933) Ginkgo curvata Chen et Meng, 1988 : Chen et al., 1988, Fuxin F.* Ginkgo dayanensis Chang, 1980 : Zhang et al., 1980, Damoguaihe F.* Ginkgo digitata (Brongniart) Heer, 1876 : Kryshtofovich, 1924, ? Fuxin F.*** : Sze et al., 1963, Damoguaihe F.* (Toyama and Oishi's specimens, 1935) and Fuxin F.*** : Zhang et al., 1980, Damoguaihe F.*, Yimin F.*, Anmin F.***, Huolinhe F.***, Dabao F.***, Beipiao F.*** and Shahezi F.*** : Wang et al., 1985, Didao F.***, Anmin F.***, Jiufotang F.*** and Jiufengshan F.*** : Hao et al., 1986, Changcai F.*** : Zhang and Zheng, 1987, Beipiao F.*** : Wang et al., 1989, Boipiao F.*** Beipiao F.*** Ginkgo cf. digitata (Brongniart) Heer, 1876 : Wang et al., 1989, Sunjiawan F.*** Ginkgo cf. hermelini (Nathorst) Hartz, 1896 : Sze, 1931, Beipiao F.* <u>Ginkgo huttoni</u> (Sternberg) Heer, 1876 : Sze <u>et al.</u>, 1963, Beipiao F.*** and Fuxin F.*** : Zhang <u>et al.</u>, 1980, Beipiao F.* and Shahezi F.* : Wang <u>et al</u>., 1985, Xiaodonggou F.***, Anmin F.*** and Zhushan (Muling) F.*** : Hao <u>et al</u>., 1986, Fuxin F.*** : Zhang and Zheng, 1987, Lanqi F.*** and Beipiao F.*** : Wang <u>et al</u>., 1989, Fuxin F.***, Lanqi F.*** and Beipiao F.*** Ginkgo cf. huttoni (Sternberg) Heer, 1876 : Zhang, 1987, Fuxin F.*** and Shahai F.*** Ginkgo ingentiphylla Meng et Chen, 1988 : Chen et al., 1988, Fuxin F.** Ginkgo lepida Heer, 1876 : Krasser, 1905, Shahezi F.* : Yokoyama, 1906, Dabao F.* : Wabe, 1908, Shahezi F.*: Zhang et al., 1980, Jiufotang F.* and Naizishan F.*: Wang et al., 1985, Dongshencun F.*** and Hongqi F.*** : Zhang and Zheng, 1987, Haifanggou F.*** and Lanqi F.*** : Wang et al., 1989, Haifanggou F.*** and Lanqi F.*** Ginkgo cf. lepida Heer, 1876 : Wang et al., 1989, Haifanggou F.*** <u>Ginkgo manchurica</u> (Yabe et Oishi) Meng et Chen, 1988 : Chen <u>et al</u>., 1988, Fuxin F.** and Xiaominganbei (Fuxin and Shahai) F.* <u>Ginkgo obrutschewi</u> Seward, 1911 : Zhang and Zheng, 1987, Haifanggou F.*** : Wang <u>et al.</u>, 1989, Haifanggou F.*** Ginkgo cf. obrutschewi Seward, 1911 : Zhang et al., 1980, Beipiao F.***, Haifanggou F.*, Xiaoyingzi F.* and Houjiatun F.* : Zhang and Zheng, 1987, Haifanggou F.*** : Wang et al., 1989, Haifanggou F.*** Ginkgo orientalis (Yabe et Oishi) Florin, 1936 : Zhang et al., Shahezi F.* (Yabe and Oishi's specimen, 1933) Ginkgo paradiantoides Samylina, 1967 : Chen et al., 1988, Shahai F.* Ginkgo pluripartita (Schimper) Heer, 1881 : Chen et al., 1988, Xiaominganbei (Fuxin and Shahai) F.* ? Ginkgo pusilla Heer, 1876 : Wang et al., 1985, Peide F.*** Ginkgo schmidtiana Heer, 1876 : Krasser, 1905, Shahezi F.* Ginkgo sibirica Heer, 1876 : Zhang et al., 1980, Damoguaihe F.*, Yimin F.*, Shahezi

F.*, Yingcheng F.*** and Fuxin F.*** : Wang <u>et al.</u>, 1985, Longzhaogou G.***, Jubao F.*** and Anmin F.*** : Zhang and Zheng, 1987, Lanqi F.***, Haifanggou F.*** and Beipiao F.*** : Chen <u>et al.</u>, 1988, Fuxin F.* : Wang <u>et al.</u>, 1989, Fuxin F.***, Shahai F.***, Haifanggou F.*** and Lanqi F.*** to truncata (Li) Chen et Meng, 1988 : Chen <u>et</u> al., 1988, Fuxin F.** and Xiaominganbei (Fuxin) F.* <u>Ginkgo</u> Ginkgo sp. (Yokoyama, 1906) : Yokoyama, 1906, Shahezi F.* <u>Ginkgo</u> sp. (Wang <u>et al</u>., 1985) : Wang <u>et al</u>., 1985, Ganhe F.***, Jiufengshan F.***, Hongqi F.*** and Manketouebo F.*** <u>Ginkgo</u> sp. 1 (Chen <u>et al.</u>, 1988) : Chen <u>et al</u>., 1988, Fuxin F.* <u>Ginkgo</u> sp. 2 (Chen <u>et al.</u>, 1988) : Chen <u>et al.</u>, 1988, Fuxin F.** Ginkgoites chilinensis Lee, 1963 : Sze et al., 1963, Shahezi F.** (Yabe and Oishi's specimen, 1933) <u>Ginkgoites</u> ? <u>crassinervis</u> Yabe et Oishi, 1933 : Yabe and Oishi, 1933, Shahezi F.* : Sze <u>et al.</u>, 1963, Shahezi F.* (Yabe and Oishi's specimen, 1933) : Yang and Sun, 1982, Shahezi F.* Ginkgoites digitata (Brongniart) Seward, 1919 : Toyama and Oishi, 1935, Damoguaihe <u>Ginkgoites digitata</u> (Brongniart) var. <u>huttoni</u> Seward : Yabe and Oishi, 1933, ? Fuxin F.*** <u>Ginkgoites ferganensis</u> (Brick in Sixtel) Wang <u>et al</u>., 1985 : Wang <u>et al</u>., 1985, Hongqi F.*** Ginkgoites fuxinensis Li, 1981 : Li, 1981, Haizhou (Fuxin) F.** <u>Ginkgoites</u> cf. <u>lepidus</u> (Heer) Florin, 1936 : Sze <u>et al</u>., 1963, Beipiao F.*** and Dabao F.* (Yokoyama's specimen, 1906) : Wang <u>et al</u>., 1985, Beipiao F.*** Ginkgoites marginatus (Nathorst) Florin, 1936 : Wang et al., 1985, Hongqi F.*** : Wang et al., 1989, Beipiao F.*** Ginkgoites obrutschewi Seward, 1919 : Wang et al., 1985, Xiaodonggou F.*** : Hao <u>et</u> <u>al.</u>, 1986, Huolinhe F.*** <u>Ginkgoites</u> <u>orientalis</u> (Yabe et Oishi) Florin, 1936 : Sze <u>et al</u>., 1963, Shahezi F.* (Yabe and Oishi's specimen, 1933) : Wang <u>et al</u>., 1985, Shahezi F.*** : Hao <u>et al</u>., 1986, Shahezi F.*** and Fuxin F.*** : Wang <u>et al</u>., 1989, Shahai F.*** <u>Ginkgoites sibirica</u> (Heer) Seward, 1919 or <u>Ginkgoites sibiricus</u> (Heer) Seward, 1919 : Toyama and Oishi, 1935, Damoguaihe F.* : Sze <u>et al.</u>, 1963, Damoguaihe F.* (Toyama and Oishi's specimens, 1935), Shahezi F.*** and Dabao F.*** : Wang <u>et al.</u>, 1985, Hongqi F.***, Beipiao F.***, Anmin F.***, Jiufotang F.*** and Kuntouboluo F.*** : Hao <u>et al</u>., 1986, Fuxin F.*** : Zhang, 1987, Shahai F.*** and Fuxin F.*** <u>Ginkgoites</u> cf. <u>sibirica</u> (Heer) Seward, 1919 or <u>Ginkgoites</u> cf. <u>sibiricus</u> (Heer) Seward : Yabe and Oishi, 1933, Shahezi F.* and Dabao F.* : Oishi, 1933, Shahezi F.** : Sze <u>et al</u>., 1963, Shahezi F.** (Yabe and Oishi's and Oishi's specimens, 1933) and Dabao F.*** : Wang <u>et al</u>., 1985, Jiufotang F.***, Beipiao F.*** and and Taivangling F.*** Ginkgoites cf. taeniatus (Braun) Harris, 1935 : Wang et al., 1985, Hongqi F.*** Ginkgoites truncatus Li, 1981 : Li, 1981, Haizhou (Fuxin) F.** Ginkgoites wulungensis Li, 1981 : Li, 1981, Haizhou (Fuxin) F.** Ginkgoites sp. 1 (Sze et al., 1963) : Sze et al., 1963, Shahezi F.** (Yabe and Oishi's and Oishi's specimens, 1933) Ginkgoites sp. 4 (Sze et al., 1963) : Sze et al., 1963, Shahezi F.** (Yabe and Oishi's and Oishi's specimens, 1933) Ginkgoites sp. (Li, 1981) : Li, 1981, Haizhou (Fuxin) F.** <u>Ginkgoites</u> spp. : Wang <u>et al</u>., 1985, Huoshiling F.***, Taiyangling F.***, Changliangzi F.***, Xiaoling F.***, Houjiatun F.***, Jiuda F.*** and Changantun (Taiyangling) F.*** : Hao <u>et al</u>., 1986, Sunjiawan F.***

Table 2.Main Jurassic-Lower Cretaceous stratigraphical units in Northeast China (compiled by us).*: Occurrence of Ginkgo (including Baiera and Ginkgoites) leaves is known.F.; formation,
Gr.; group.

(1) The numbers correspond to those in Figure 7.

(2) The boundary between Upper Jurassic and Lower Cretaceous strata in this figure is still controversial.

Region				North					
Strati- graphic Units		West Liaoning		Liaoning & SE- Songliao	Xipo (W)	Dongpo (E)	Zhelimu- meng	Zhaowu- dameng	East Liaoning
Cretaceous	Lower	Sunjiawan F. 10·27 *		Quantou F.					
		Banlashan F. 10·27 *		Denglouku F. 21·24·34? *					Dayu F.
				Yingcheng F. 21:23:24:25:26	Vincin E *	Vinsin Est			Nieerku E
		Fuxin F. * 4.5.6.10.28		*		YIMIN F.*	Huolinhe F.	Yuanbao- shan F. * 13·22	
		Shahai F.* 4·5·6·10·27		Shahezi F.* 21·23·24·25·26	Damoguai- he F. * 29:30:31	he F. * 14·15·16	7.8.9.28 *		Lishugou F.
Jurassic	Upper	Jiufotang F. 4·5·6·10 *					?	Xingyuan F. 13·22 *	?
		Yixian	2nd	Huoshiling F.	Yiliekede F.	Ganhe F. 14·15 *	Baoshi F.	Baiyingaolao F	
		F. ∗ 5∙6∙10		21 * ?	Shangkuli F.	Jiufeng- shan F.* 14:15:16			Xiaoling F.*
			ISt					Manitu F. 13 *	2.3
					Murui F.	Longjiang F.	Fujiawazi F.	Manketoue- bo F. <u>13</u> *	Xiaodonggou F. * *
	Middle	Tuchengzi F.		Baicheng F.		Juba	ao F. *		Sangeling F. *
		Lanqi F. * 4·5·6				7·8·9 Wanbao F. * 7·8·9			Dabao F.* 2·3
		Haifanggou F. 4·5·6·10 *							Zhuanshanzi F. * 2·3
	Lower	Beipiao F.* 4·5·6				Hongqi F. * 7·8·9			Changliangzi
		Xinglonggou F.							F. * 2·3
		Kuntouboluo F. *							

Table 2. (continued)

East lilin E-Heilongijan								
Jilin	region	Hu	niiang reg	aion		1	Jixi, Boli, Shuanyashan & Wandashan region	
Jilin	Jiaohe	Shiren Sanyuan- pu	Liu	uhe	Helong- xishan	Yanji		
Quantou F.	Liyan F.	Heiweizi F.				Longjing F.	Houshigou F.	
Denglouku F. * 11	Baojiatun F	Sankeyushu F.				Dalazi F.	Decreha 5	
Jinjiatun F.	Moshilazi F				Quanshui- cun F.	Quanshui- cun F.		ngsnan r.
Naizi-Cha- shan ng-	Naizi- Wulin shan F.	Henaton	ashan F	Shiren F.	Changcai F. 33 *	Changcai F.		Muling F. * 12·17·18·20
F. * an F. 11	F. * 32		gonar .			Xishanping F.	Chengzihe F. * 12·17·18·20	
		Xiahuap	idianzi F.	?		?	SI	hihebei F.
Anmin F. 11·23 *		Linzitou F.	Baodaqiao F.	Sidaogou F			Didao 12·17·18	o F. * 19·20
Jiuda F. 11 *		Yingzuilazi F.	Dashatan F.	· JIUAOGOU F.				
Deren F. 11 *		Guosong F.	Lamenzi F.	Changbai F.			ſ	Chaoyan- tun F.
Taiyangling F. * 11			Houjiatun F. *				lou Gr.(Lower)	Peide F.
							Longzhaog	Dongshengcun F. * 12
Banshiding- zi F.			Xiaoyingzi F. * 1					

fig. 6 (Huoshiling)=our C-type, pl. 33, fig. 10 (Huoshiling)=indeterminable.

(10) B. sp. b (Yabe and Oishi, 1933); pl.
35, fig. 3A (Shahezi) = our C-type.

In addition to the above, identification of the following forms seem to be doubtful.

(11) Ginkgoites ? crassinervis Yabe et Oishi, 1933; pl. 32, fig. 8A (Taojiatun).

(12) G. digitata (Brongniart) var. huttoni Seward; Kryshtofovich, 1924 (Badaohao; without illustration).

(13) Baiera cf. asadai Yabe et Oishi, 1928; pl. 32, figs. 9-10 (Erdaogou).

In the same year, Oishi (1933) described the cuticles of the following Ginkgoites and Baiera 'species' from Northeast China, of which the external forms of laminae were described by Yabe and Oishi (1933): Ginkgoites cf. sibirica (Heer), Cf. Baiera concinna (Heer), B. cf. gracilis Bunbury, B. kidoi Yabe et Oishi, B. manchurica (Heer), B. cf. gracilis Bunbury, B. kidoi Yabe et Oishi, B. manchurica Yabe et Oishi, B. minima Yabe et Oishi, B. cf. phillipsi Nathorst, B. sp. a and B. sp. b. So far our careful reexamination of Oishi's published work does not reveal any specifically diagnostic features amongst the preceding. Their cuticles are quite similar to ours.

Subsequently, many studies were made by Chinese workers on the fossil *Ginkgo* (including *Baiera* and *Ginkgoites*) leaves from Northeast China.

In the monograph made by Sze et al. (1963), they established Ginkgoites chilinensis Lee (from Huoshiling) as a new species and included Baiera cf. phillipsi Nathorst (described by Yabe and Oishi, 1933 and Oishi, 1933) in their G. chilinensis. As mentioned above, Baiera cf. phillipsi corresponds to our C-type of leaf. The works of Yabe and Oishi (1933) and Oishi (1933) were followed by other workers without any critical reexamination.

Zhang et al. (1980) listed 21 Ginkgo (including Baiera and Ginkgoites) 'species' with brief descriptions and illustrations known from the Mesozoic plant sites in Northeast China. They were collected from different localities and horizons, but all of them were illustrated only for their external forms. In their monograph, they established *Ginkgo dayanensis* Chang from the Damoguaihe Formation (Table 2) together with *G. sibirica* Heer and *G. digitata* (Brongniart) Heer. We are of the opinion that the former two are similar to our C-type and the latter to our A-type leaves.

Li (1981) originally described Ginkgoites truncatus, G. wulungensis, G. fuxinensis and G. sp. on the basis of Ginkgo leaves with preserved cuticles from the Haizhou Formation (=Fuxin Formation; Table 2), western Liaoning. His Ginkgoites truncatus and G. fuxinensis are like our B-type and C-type, respectively. It is easy to find out that there is no difference in the cuticular features between Ginkgoites fuxinensis and the present leaves. We feel that Li's Ginkgoites species might be included in the same fossil population as ours.

From the Fuxin and Tiefa Sedimentary Basins (Figure 7), western Liaoning, Chen et al. (1988) described 9 Ginkgo species including their two new species, G. curvata and G. ingentiphylla, and such species as G. paradiantoides Samylina, G. pluripartita (Schimper) Heer, G. sibirica Heer, G. truncata Li, G. sp. 1 and G. sp. 2. We observe that the leaves regarded by them as Ginkgo curvata appear to be deformed in preservation and correspond to our B- and C- types. The leaves regarded by them as Ginkgo ingentiphylla are much bigger than the others and are just like our E-type. Their Ginkgo *pluripartita* is very close in form to our B-type and their G. truncata and G. paradiantoides are our A-type. So far as the published features of their leaves (including their Ginkgo manchurica) are concerned, we are inclined to regard all their leaves as belonging to the same population as ours.

If the above observations are correct, then there would be far fewer *Ginkgo* 'species' than hitherto presumed during Jurassic and Early Cretaceous time in Northeast China and adjacent regions. In addition, the generic difference between *Ginkgo* (or *Ginkgoites*) and *Baiera* becomes obscure.

Other Ginkgo populations: Heer (1876) originally described Ginkgo sibirica, G. lepida, G. schmidtiana, G. flabellata and G. pusilla from the Jurassic of Ust Balej, Irkutsk Basin. Doludenko and Rasskazova (1972) used the generic name Ginkgoites after Seward (1919) and regarded the species of Heer mentioned above as conspecific and included them in Ginkgoites sibirica. Heer (1876) also established Ginkgo concinna from the Jurassic of Ust Balej. According to Doludenko and Rasskazova (1972), Heer's Ginkgo concinna is distinct together with their Ginkgoites tapkensis and G. heeri known from the Irkutsk Basin.

On the other hand, Doludenko and Lebedev (1972) also regarded Heer's Ginkgo lepida, G. schmidtiana, G. flabellata and G. pusilla as synonyms of Heer's G. sibirica and regarded Heer's Ginkgo concinna and their Ginkgoites tylensis Lebedev from southern Priokhotie, and Ginkgoites vachrameevi Doludenko et Lebedev and Ginkgoites sp. known from the Bureja Basin as distinct.

It is highly probable that there is another population of *Ginkgo* leaves (*Ginkgo sibirica* population) in the Irkutsk Basin, although as far as we know, the detailed limit of morphological and cuticular variations for Heer's species has not been shown beyond the works of Doludenko and Rasskazova (1972) and Doludenko and Lebedev (1972).

In fact, *Ginkgo* leaves corresponding to our A-type and E-type have not been found from the Irkutsk Basin. In addition, we are ignorant as to the occurrence of *Ginkgo* leaves in the Irkutsk Basin.

We suggest that the identification of fossil Ginkgo (including Baiera and Ginkgoites) leaves should be made not only from their external morphology and cuticular features, but also from their occurrence. It is quite difficult to make a precise identification in the cases of sparse occurrence or when preserved cuticles are lacking, though cuticular features of *Ginkgo* (or *Baiera*) leaves, if present, are not so effective and in some cases cannot help in specific or even generic identification.

In the case of crowded occurrences of fossil Ginkgo (or Baiera) leaves, we can treat them as a single population as in the present study. The same results were arrived at as follows: (1) Kimura et al. (1983) on the basis of impressions of various types of Ginkgo (or Baiera) leaves from the Carnian Momonoki Formation, Southwest Japan; they were thickly massed and appressed in occurrence. The Ginkgo (or Baiera) populations known from the Norian Nariwa Group, Southwest Japan (Kimura et al., 1983) and from the Upper Triassic Daedong Supergroup, Korea (Kimura and Kim, 1985) are the same or nearly the same as the Momonoki population. (2) Ohana and Kimura (1986) described diminutive Ginkgo leaves with preserved cuticle from the uppermost Cretaceous (Maastrichtian) Omichidani Formation in the Inner Zone of Central Japan, as a single Ginkgo population. (3) Horiuchi and Kimura (1986) described Ginkgo leaves with nearly entire or shallowly lobed margins and with preserved cuticle from the Palaeogene Noda Group, as a single Ginkgo population. (4) Zhou and Zhang (1989) described a Ginkgo population consisting of various Ginkgo leaves with preserved cuticle from the Middle Jurassic Yima Formation, Henan, China.

These populations are different from each other, according to their geographical and stratigraphical positions. As a matter of course, difference of populations corresponds to difference of species.

Nomenclature : We here adopt the generic name Ginkgo according to Harris et al. (1974), instead of Ginkgoites (Seward, 1919).

In external morphology, our C- and Dtypes of leaves are clearly representative of the present population, and are close to *Ginkgoites* cf. *sibirica, Baiera* cf. *gracilis, B. kidoi,* B. manchurica, B. minima, B. orientalis, B. cf. phillipsi, B. sp. a and B. sp. b described by Yabe and Oishi (1933). As mentioned before in this paper, we feel that they are conspecific.

Chen et al. (1988) revised Baiera manchurica Yabe et Oishi as Ginkgo manchurica (Yabe et Oishi) Meng et Chen (comb. nov.) and included Baiera minima Yabe et Oishi, B. orientalis Yabe et Oishi, Ginkgoites fuxinensis Li and G. wulungensis Li in Ginkgo manchurica as being synonymous. Under the circumstances, we give the leaves of the present population the name Ginkgo manchurica (Yabe et Oishi) Meng et Chen.

Ginkgoites pingzhuangensis described by Zhao and Tao (1991) as a new species on the basis of the specimen (NCP-8265) which is the same specimen as that shown in the present Figures 2m, 3m, should rightly be withdrawn.

References

- Chen, F., Meng, X.Y., Ren. S.Q. and Wu, C.L., 1988: The Early Cretaceous flora of Fuxin Basin and Tiefa Basin, Liaoning Province. 180 p., 69 pls. Geol. Publ. House, Beijing. (in Chinese with English summary and description of new species)
- Doludenko, M.P. and Lebedev, E.L., 1972: Ginkgoites sibirica and 'G. huttonii' of East Siberia. Trans. Geol. Inst., Acad. Sci. USSR, vol. 230, p. 82-102, pls. 1-3. (in Russian)
- Doludenko, M.P. and Rasskazova, E.S., 1972: Ginkgoales and Czekanowskiales of the Irkutsk Basin.
 In 'Mesozoic plants (Ginkgoales and Czekanowskiales) of East Siberia'. *Ibid.*, p. 7-43, pls. 1-49. (*in Russian*)
- Hao, Y.C., Su, D.Y., Yu, J.X., Li, P.X., Li, Y.G., Wang, N.W., Qi, H., Guan, S.Z., Hu, H.G., Liu, X., Yang, W.D., Ye, L.S., Shou, Z.X. and Zhang, Q.B., 1986: Stratigraphy of China (no. 12): The Cretaceous System of China. 301 p., 16 pls. Geol. Publ. House, Beijing. (in Chinese)
- Harris, T.M., Millington, W. and Miller, J., 1974: *The Yorkshire Jurassic flora.* IV, 1 Ginkgoales and 2 Czekanowskiales. viii+150 p., 8 pls. British Mus. (Nat. Hist.).
- Heer, O., 1876 : Beiträge zur Jura Flora Ostsibiriens und des Amurlandes (in Flora fossilis arctica, Bd,

4, H. 2). Acad. imp. sci. St.-Pétersb., Mém., vol. 22, p. 1-122, pls. 1-31.

- Horiuchi, J. and Kimura, T., 1986: Ginkgo tzagajanica Samylina from the Palaeogene Noda Group, Northeast Japan, with special reference to its external morphology and cuticular features. Trans. Proc. Palaeont. Soc. Japan, N.S., no. 142, p. 341-353, pls. 65-68.
- Kimura, T., 1987a: Recent knowledge of Jurassic and Early Cretaceous floras in Japan and phytogeography of this time in East Asia. Bull. Tokyo Gakugei Univ., ser. IV, vol. 39, p. 87-115.
- Kimura, T., 1987b: Geographical distribution of Palaeozoic and Mesozoic plants in East and Southeast Asia. In, Taira, A. and Tashiro, M. eds., Historical biogeography and plate tectonic evolution of Japan and Eastern Asia. p. 135-200. Terrapub., Tokyo.
- Kimura, T. and Kim, B.K., 1985 : Outline of the Late Triassic Daedong flora in the Korean Peninsula.
 III Congreso Latinoamericano de Paleontologia.
 Mexico. Simposio sobre floras del Triásico Tardio, su Fitogeografía y Paleoecología, Mem., p. 1-4.
- Kimura, T., Naito, G. and Ohana, T., 1983: Baiera cf. furcata (Lindley et Hutton) Braun from the Carnic Momonoki Formation, Japan. Bull. Natn. Sci. Mus., Tokyo, ser. C, vol. 9, p. 91-114.
- Krasser, F., 1905 : Fossil Pflanzen aus Transbaikalien der Mongolei und Mandschurei. *Akad. Wiss Wien Denkschr.*, Bd. 78, p. 589-634, pls. 1-4.
- Kryshtofovich, A.N., 1924: Remains of Jurassic plants from Pataoho, Manchuria. Bull. Geol. Soc. China, vol. 3, p. 6-8.
- Li, B.X., 1989: On the cuticular structures of Ginkgoites from the Haizhou Formation (Upper Jurassic) in Fuxin (Fushin), Western Liaoning. Acta Palaeont. Sinica, vol. 20, p. 208-215, pls. 1-4. (in Chinese with English abstract and description of new species)
- Ohara, T. and Kimura, T., 1986: Ginkgo diminuta, sp. nov., from the Upper Cretaceous Omichidani Formation in the Inner Zone of Japan. Proc. Japan Acad., vol. 62B, p. 345-348.
- Oishi, S., 1933: A study on the cuticles of some Mesozoic gymnospermous plants from China and Manchuria. Sci. Rep., Tohoku Imp. Univ., 2nd ser., vol. 12, p. 239-252, pls. 36-39.
- Sakisaka, M. (1958): Study on *Ginkgo*. 144 p. Kazamashobo, Tokyo. (*in Japanese*)
- Seward, A.C., 1919: Fossil plants, vol. 4. 543 p. Cambridge.
- Shang, P. and Zheng, X.L., 1991: Studies on the Early Cretaceous plants from the Pingzhuang Coal-Field, Inner Mongolia. *Kexue-Tongbao* (Chinese version), vol. 36, p. 639-640. (*in*

Chinese)

- Sze, H.C., 1931: Beiträge zur liasischen Flora von China. Mem. Nat. Res. Inst. Geol., Acad. Sinica, no. 12, p. 1-85, pls. 1-10.
- Sze, H.C., Li, X.X., Li, P.J.. Zhou, Z.Y., Wu, S.Q., Ye, M.N. and Shen, G.L., 1963: Mesozoic plants from China (Fossil plants of China, vol. 2). 429 p., 118 pls. Sci. Press, Beijing. (in Chinese)
- Toyama, S. and Oishi, S., 1935: Notes on some Jurassic plants from Chalai Nor Prov., North Hsingan, Manchoukuo. Journ. Fac. Sci., Hokkaido Imp. Univ., ser. 4, vol. 3, p. 61-77, pls. 3-5.
- Wang, S.E., Bai, Y.H., Chen, P.J., Chen, T.E., Chen, Z.W., Deng, K.L., Dong, G.Y., Gu, Z.W., He, G.X., Hong, Y.C., Li, Y.G., Liao, W.H., Liu, S.W., Liu, X.T., Shou, Z.X., Sun, D.L., Wang, N.W., Wang, S.T., Wang, Y.G., Wang, Y.X., Xu, Y.K., Yang, W.D., Yao, J.X., Yu, J.S., Zhang, Q.B., Zhang, R.J., Zhang, W.P., Zhang, Z.C. and Zhao, X.Y., 1985: *The Jurassic System of China* (Stratigraphy of China, no. 11). 350 p., 16 pls. Geol. Publ. House, Beijing. (*in Chinese*)
- Wang, W.L., Zheng, S.L., Zhang, L.J., Pu, R.G., Zhang, W., Wu, H.Z., Ju, R.H., Dong, G.Y. and Yuan, H., 1989: Mesozoic stratigraphy and palaeontology of western Liaoning, I. 168 p. Geol. Publ. House, Beijing. (in Chinese with English abstract)
- Yabe, H., 1908 : Jurassic plants from Tao-chia-t'un, China. Bull. Imp. Geol. Surv. Japan, vol. 21, p. 5-12, pls. 1-2.
- Yabe, H., 1922: Notes on some Mesozoic plants from Japan, Korea and China, in the collection of the Institute of Geology and Palaeontology of the Tohoku Imperial University. Sci. Rep.,

Tohoku Imp. Univ., 2nd ser., vol. 7, p. 1–28, pls. 1–6.

- Yabe, H. and Oishi, S., 1933 : Mesozoic plants from Manchuria. *Ibid.*, vol. 12, p. 195-238, pls. 30-35.
- Yang, X.L. and Sun, L.W., 1982: Fossil plants from the Shahezi and Yingcheng Formations in southern part of the Songhuajiang-Liaohe Basin, NE-China. Acta Palaeont. Sinica, vol. 21, p. 558-596, pls. 1-3. (in Chinese)
- Yokoyama, M., 1906 : Mesozoic plants from China. Jour. Coll. Sci., Imp. Univ. Tokyo, vol. 21, p. 1-39, pls. 1-12.
- Zhang, W., Zhang, Z.C. and Zheng, S.L., 1980: Division of plants. In 'Palaeontological atlas of Northeast China. (2) Mesozoic and Cenozoic volume.' p. 221-339, pls. 103-210. Geol. Publ. House, Beijing. (in Chinese)
- Zhang, W. and Zheng, S.L., 1987: Early Mesozoic plant fossils from West Liaoning. In 'Mesozoic stratigraphy and palaeontology of Western Liaoning, 3.' p. 239-338, pls. 1-30. Geol. Publ. House, Beijing. (in Chinese)
- Zhang, Z.C., 1987: Study on the plant fossils from Fuxin Formation, Fuxin region, Liaoning. Ditto, p. 369-386, pls. 1-7. Geol. Publ. House, Beijing. (in Chinese)
- Zhao, L.M. and Tao, J.R., 1991: Fossil plants from Xingyuan Formation, Pingzhuang, Chifeng, Nei Mongol. Acta Bot. Sinica, vol. 33, no. 12, p. 963-967, pls. 1-2. (in Chinese with English abstract)
- Zhou, Z.Y. and Zhang, B.L., 1989: A Middle Jurassic Ginkgo with ovule bearing organs from Henan, China. Palaeontographica, Abt. B, Bd. 221, p. 113-133, pls. 1-8.

Geographical and stratigraphical names: Japan: Momonoki 桃ノ木, Nariwa 成羽, Noda 野田, Omichidani 大道谷, Tetori 手取

Korea: Daedong 大同

China: Anmin 安民, Badaohao 八道檺, Baicheng 白城, Baiyingaolao 白音高老, Banlashan 半拉山, Banshidingzi 板石頂子, Baodaqiao 包大橋, Baojiatun 保家屯, Baoshi 宝 石, Beijing 北京, Beipiao 北票, Benxi 本溪, Binxian 賓縣, Boli 勃利, Changan 長安, Changantun 長安屯, Changbai 長白, Changcai 長財, Changchun 長春, Changliangzi 長 梁子, Changtu 昌図, Chaoyang 朝陽, Chanyangtun 朝陽屯, Chengzihe 城子河, Chifeng 赤峰, Dabao 大堡, Dalazi 大拉子, Damoguaihe 大磨拐河, Dashatan 大沙灘, Dataishan 大台山, Daxinganling 大興安嶺, Dayu 大峪, Donglouku 登婁庫, Deren 徳仁, Didao 滴 道, Dongpo 東坡, Dongshan 東山, Dongshengcun 東勝村, Erdaogou 二 道溝, Fujiawazi 傅家窪子, Fuxin 阜新, Ganhe 甘河, Gannan 甘南, Guojiadian 郭家店, Guosong 果松, Haifanggou 海房溝, Haizhou 海州, Hegang 鶴崗, Heihe 黒河, Heilongjian 黒龍 江, Helong 和龍, Henan 河南, Hengtongshan 亨通山, Hongqi 紅旗, Houjiatun 候家屯, Houshigou 候石溝, Hulun Nur 呼倫湖, Hunjiang 渾江, Huolinhe 霍林河, Huoshiling 火 石 嶺, Jiaohe 蛟 河, Jilin 吉林, Jinjiatun 金 家 屯, Jiuda 久 大, Jiufengshan 九 峰 山, Jiufotang 九佛堂, Jixi 鶏西, Jubao 巨宝, Xingkai (Khanka)興凱, Kuntouboluo 坤頭波 羅, Lamenzi 拉門子, Lanqi 藍旗, Liaoning 遼寧, Liaoyuan 遼源, Lingyuan 凌源, Lingyuan

zitou 林子頭, Lishugou 梨樹溝, Liuhe 柳河, Liyan 礫岩, Longjing 龍井, Longzhaogou 龍爪溝, Manitu 瑪尼吐, Manketouebo 満克頭鄂博, Moshilazi 磨石砬子, Muling 穆稜, Murui 木 瑞, Naizishan 奶子山, Nenjiang 嫩江, Nianzigou 碾子溝, Nieerku 聶 耳庫, Peide 裴徳, Pingzhuang 平庄, Quanshuicun 泉水村, Quantou 泉頭, Sangeling 三個嶺, Sankeyushu 三棵榆樹, Shahai 沙海, Shahezi 沙河子, Shangkuli 上庫力, Shenyang 瀋陽, Shihebei 石河北, Shiren 石人, Shuanyashan 双鴨山, Shuiquan 水泉, Sidaogou 四道溝, Siping 四平, Songhuajiang 松花江, Songliao 松遼, Sunjiawan 孫家湾, Taiyangling 太陽 嶺, Taoan 洮安, Taojiatun 陶家屯, Tianshifu 田師傳, Tiefa 鉄法, Tongliao 通遼, Tuchengzi 土城子, Ulanhot 烏蘭浩特, Wanbao 萬宝, Wandashan 完達山, Weijiapuzi 魏家 鋪子, Wulin 烏林, Xiahuapidianzi 下樺皮甸子, Xiangshan 香山, Xiaodonggou 小東溝, Xiaoling 小嶺, Xiaominganbei 小明 安碑, Xiaoyingzi 小營子, Xilutian 西 露 天, Xingyuan 杏園, Xipo 西坡, Xishanping 西山坪, Yanji 延吉, Yiliekedc 伊列克得, Yima 義 馬, Yimin 伊敏, Yingcheng 營城, Yingzuilazi 鷹嘴砬子, Yixian 義縣, Yuanbaoshan 元 宝山, Zalainor 扎賚諾爾, Zhaowudameng 昭烏達盟, Zhelimumeng 哲里木盟, Zhuanshanzi 轉山子, Zhushan 珠山

内蒙古の上部ジュラ~下部白亜系杏園(Xingyuan)層産イチョウ葉個体群:ジュラ紀後 期から白亜紀前期にかけて,化石イチョウ葉は,ユーラシア東部のシベリア型および手取 型植物群の特徴的な構成要素であり,ときに,同一地層面上に密集して産出する。このた び内蒙古の杏園層から,以上のような産状を示す化石イチョウ葉が発見され,また例外な くそれらの cuticle がよく保存されている。これらのイチョウ葉は大きさ,形,葉身の分裂 の状態などきわめて変化に富むが,その産状,および各葉の cuticle の示す特徴が同一であ ることから,これらのイチョウ葉は,同一個体群に属し,かつ同一種に属するものと判断 される。

私どもは、便宜的にこれらのイチョウ葉を A~Eの5つの型にわけ、かつて中国東北部、 とくに遼寧省および古蒙古から記載された約70種類のイチョウ葉との比較を試みた結果、 当時のイチョウ葉の「種」の数は、きわめて少数であること、またこれらの種は、地域的 また時代的に、それぞれ、固有の個体群を形成していたことが明らかとなった。また Ginkgo 属と Baiera 属との間の差異は存在しないものと考えられる。

私どもは、内蒙古東部および遼寧省西部地域の上部ジュラ系~下部白亜系から知られて いるイチョウ葉個体群の構成種として, Ginkgo manchurica (Yabe et Oishi) Meng et Chen を選定した。 趙立明・大花民子・木村達明

952. DIMORPHISM OF LATE CRETACEOUS FALSE-PUZOSIINE AMMONITES, *YOKOYAMAOCERAS* WRIGHT AND MATSUMOTO, 1954 AND *NEOPUZOSIA* MATSUMOTO, 1954*

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Abstract. Yokoyamaoceras jimboi Matsumoto, previously assigned to the Kossmaticeratidae, and Neopuzosia ishikawai (Jimbo), N. japonica (Spath), and N. haboroensis Matsumoto and Inoma, previously assigned to the Puzosiinae, all co-occurring in Santonian to lower Campanian deposits of the Upper Cretaceous Yezo Group in Hokkaido, Japan, and Sakhalin, Russia, are reinvestigated on the basis of many well-preserved specimens. Observations on the stratigraphic occurrence, morphological variation, and shell ontogeny show these four nominal species to be dimorphs of but a single biospecies. The first two morphospecies represent the macroconch $\langle M \rangle$, and the latter two microconch $\langle m \rangle$ for which the earlier available name is Yokoyamaoceras ishikawai (Jimbo, 1894), which is referred to the Kossmaticeratidae. This is suggested by the mode of ontogenetic shell growth, particularly of the umbilicus.

A dimorphic lineage can be traced back to certain upper Turonian-Coniacian Kossmaticeras $\langle M \rangle$ and Yokoyamaoceras $\langle m \rangle$ species. The superficial morphological resemblance between the species and Mesopuzosia spp. is mere homeomorphy.

Key words. Dimorphism, Cretaceous ammonites, Yokoyamaoceras, Neopuzosia, Kossmaticeratidae, Puzosiinae

Introduction

Two desmoceratacean genera, Yokoyamaoceras Wright and Matsumoto, 1954, previously assigned to Kossmaticeratidae, and Neopuzosia Matsumoto, 1954, previously assigned to Puzosiinae, are very similar in external shell morphology and surface ornament, differing chiefly in the presence of tubercles in the latter. Both genera are indigenous to the late Cretaceous Pacific Realm, and they are reliably known only from Hokkaido, Sakhalin, Koryak-Kamchatka, France (Kennedy, 1986), California, and British Columbia (Haggart and Ward, 1989), Argentine (Nullo *et al.*, 1980), and Antarctica (Olivero, 1984). Species of the two genera were described from Hokkaido and Sakhalin chiefly by Matsumoto (1954b, 1955, 1956). Their generic and specific diagnoses were, however, based on a limited number of specimens rather than population samples, and the extent of intraspecific variation could not be confidently determined from previous studies.

I recently obtained many well-preserved specimens of Yokoyamaoceras and Neopuzosia from the Upper Cretaceous Yezo Group in Hokkaido and Sakhalin (Figure 1). They suggest that the two genera, and particularly four coexisting nominal species: Yokoyamaoceras jimboi Matsumoto, 1955, Neopuzosia ishikawai (Jimbo, 1894), N.

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Figure 1. Index map of Hokkaido and South Sakhalin showing distribution of the Cretaceous Yezo Group (compiled from Matsumoto, 1954a; Tanaka, 1963; Geological Survey of Hokkaido, 1980; Zakharov et al., 1984). Locality names are abbreviated as follows. NB: Naiba (=Naibuchi: 47°21'N, 142°32'E); TS: Teshio (44°47'N, 142°02' E); AB: Abeshinai (=Saku: $44^{\circ}42'N$, $142^{\circ}02'E$); EM: Embetsu (44°38'N, 141°59'E); HB: Haboro (44°16'N, 141°54'E); KT: Kotambetsu (44°11'N, 141°59'E); TP: Tappu (=Obira: 44°05'N, 141°56' E); BI: Bibai (43°22'N, 142°02'E); IK: Ikushumbetsu (= Mikasa : $43^{\circ}15'N$, $142^{\circ}04'E$); MJ : Manji (141°57'E, 43°07'N); YU: Yubari (43°04'N, 141°57' E); OY: Oyubari (=Shuparo: 43°08'N, 142°05' E); HO: Hobetsu (42°52'N, 142°08'E); UK: Urakawa (42°11'N, 142°45'E).

japonica (Spath, 1922), and *N. haboroensis* Matsumoto and Inoma, 1972, ranging from Santonian to lower Campanian, are synonyms. This is based on the following observation, which suggests a wide range of morphologic variation, as well as dimorphism :

1) Nominal species show coincident distribution both in time and space.

2) Several morphological characters, previously regarded as criteria for discrimination of species, show continuous variation in large samples.

3) Extreme similarity of immature stages.

4) A pair of large and small forms can be recognized (Figures 2, 3).

Following the works of Callomon (1955) and Makowski (1963), numerous examples of dimorphism in ammonoids have been reported; in the Paleozoic (e.g., Davis et al., 1969), and in Mesozoic ammonites, particularly from Jurassic ones (Callomon, 1963, 1985; Westermann, 1964; Lehmann, 1966 ; Pal-1966, 1967, etc.). These works framan. contributed greatly to systematic and phylogenetic reconsideration of ammonite relationships. Dimorphism is also recognized among Cretaceous ammonites (Kennedy and Wright, 1985), and several taxa have been studied from this viewpoint, e.g., scaphitid heteromorphs (Cobban, 1969; Tanabe, 1977a, 1977b, etc.), acanthoceratids (Wright and Kennedy, 1984; Kennedy and Wright, 1985), placenticeratids (Kennedy and Wright, 1983), and hoplitoidines (Reyment, 1988). However, many Cretaceous taxa remain to be investigated more precisely.

In this paper, I first attempt to reconstruct the dimorphism of the kossmaticeratid *Yokoyamaoceras* and puzosiine *Neopuzosia*. Second, I discuss their taxonomic position at the family level, based on the mode of early shell ontogeny compared with that of other desmocerataceans.

Repository of specimens.—The following abbreviations are used to indicate the repository of specimens mentioned in this paper, UMUT: University Museum, University of Tokyo, Tokyo 113; GK: Geological Department, Kyushu University, Fukuoka 812. Material utilized here is shown in Table 1.

Diagnoses of Yokoyamaoceras and Neopuzosia

Yokoyamaoceras.—The genus Yokoyamaoceras was first established by Wright and Matsumoto (1954), with Holcodiscus kotoi Jimbo, 1894, from the Coniacian of the Tappu area, Hokkaido, Japan, as type species. They defined Yokoyamaoceras as



(Macroconch)

(Microconch)

Figure 2. Schematic illustration of macro- and microconchs recognized in *Neopuzosia* and *Yo-koyamaoceras*. The macroconchs $\langle M \rangle$ consist of two morphospecies: "*ishikawai*" and "*japonica*." "*haboroensis*" and "*jimboi*" comprise the microconchs $\langle m \rangle$. The macroconchs are usually three times larger than the microconchs. Scale bars: 10 mm long.

one of the tuberculate dwarf groups in the family Kossmaticeratidae, and regarded it as an offshoot of *Kossmaticeras* in subsequent publications (Matsumoto, 1955, 1981). Kennedy (1986) recently placed this genus in the subfamily Puzosiinae.

Species of this genus generally have small, moderate coiling to evolute, somewhat compressed shells with dense, fine, flexuous prorsiradiate ribs that are truncated somewhat obliquely by periodic constrictions, as *Kossmaticeras* and some puzossines. Alternate or opposite tubercles appear on ribs at each ventrolateral shoulder in the adult or near adult stage. These tubercles may disappear in the last 60° -150° volution of body chamber. Tuberculation is variable, both in strength and density, but was said to be the most distinct character by which the genus can be discriminated from puzosiines. Umbilical tubercles are not prominent even though they appear in some doubtful forms. The suture line is of kossmaticeratid type, simple, with a symmetrically tripartite lateral lobe (L) and more weakly retracted umbilical elements than in puzosiines (Wright and Matsumoto, 1954; Matsumoto, 1955, 1956, 1981, 1991). Six species of Yokoyamaoceras have been described from the middle Turonian to Santonian. In this paper, I treat them as morphospecies, with double quotation marks. The morphospecies are as follows with brief diagnoses and stratigraphic ranges as revised by Obata et al. (1978) and my recent observa-



Morphosecies	No. of specimens	Localities
"Yokoyamaoceras kotoi"	5	ТР КТ НВ
"Y. jimboi"	25	NB. HB. KT. TP. IK. HB.
"Y. ornatum"	4	AB. HB
"Y. (?) mysticum"	1	UK
"Y. minimum"	5	TP. IK. MJ
"Neopuzosia japonica"	24	NB. TS. EM. AB. KT. TP. LIK
"N. ishikawai"	30	NB. TS. AB. HB. KT. TP. IK. UK
"N. haboroensis"	8	NB. TS. AB. HB. KT. TP
Desmoceras (Pseudouhligella) japonicum	20	AB, TP, IK
Mesopuzosia pacifica	20	KT, TP, MJ, OY, HB
M. yubarensis	5	YU. OY. IK
Jimboiceras planulatiforme	10	ТР
Hauericeras (Gardeniceras) angustum	5	NB, TS, IK, UK
Kossmaticeras theobaldianum paucicostatum	8	TP, IK
Anapachydiscus sp.	5	AB

 Table 1.
 Material utilized in this paper including UMUT. and GK. type specimens.
 Abbreviations of locality names are as same as in Figure 1.

tions.

"Yokoyamaoceras kotoi (Jimbo, 1894)"

Holotype.—UMUT. MM7517 (Figures 4-15, 4-16), from the Obirashibe (=Obirashibets) River, Tappu (TP in Figure 1).

Diagnosis.—Morphospecies showing many distinct ribs and dense, extensive tuberculation over one whorl. The holotype has about 25 ribs per half a whorl, and 23 of them develop tubercles at the ventrolateral shoulder. Tuberculation appears at a shell diameter of 15 mm or less, and continues for more than a whorl. The shell attains at least 35 mm diameter. The apertural features of the fully grown adult stage are unknown.

Occurrence.-Coniacian.

"Yokoyamaoceras jimboi Matsumoto, 1955"

Holotype.—UMUT. MM7625 (Figures 4-9, 4-10), from the Saushi-sanushibe Valley, Hobetsu (HO).

Diagnosis.—Morphospecies possessing fine, weak ribbing and with a brief, irregular tuberculate stage. Ribs finer (numbering about 30-40 per half a whorl) and weaker than those of "Y. kotoi." The ventrolateral tubercles alternate, distributed with an incidence of one tubercle per 3-4 ribs. Tubercles appear at diameter of 20 mm or less, and extend for about one-third to half a volution of the adult body chamber. Adult shells range from 25 to 35 mm diameter. Lateral lappets are present in every specimen with a complete aper-

Figure 3. Adult macroconchs (1-4, ×0.67) and adult microconchs (5-8, ×1.5). All the specimens are here assigned to Yokoyamaoceras ishikawai (Jimbo, 1894). 1, 3, "Neopuzosia ishikawai (Jimbo)" ⟨M⟩, UMUT. MM18341, from the lower Santonian of the Kotambetsu River (Loc. KT-5040). 2, 4, "N. japonica (Spath)" ⟨M⟩, UMUT. MM18337, from the Santonian of the Naiba River, South Sakhalin. 5, 6, an intermediate form between "N. haboroensis Matsumoto and Inoma" and "Yokoyamaoceras jimboi Matsumoto, 1955" ⟨m⟩, UMUT. MM18385, from the uppermost lower Santonian of the Kotambetsu River (Loc. KT-5302). 7, 8, "Yokoyamaoceras jimboi Matsumoto" ⟨m⟩, UMUT. MM18357, from the lower Santonian of the Obirashibe River (Loc. TP-022).



102

ture (Figure 5).

Occurrence.-Lower Santonian except for the uppermost part.

"Yokoyamaoceras ornatum Matsumoto, 1956"

Holotype.-GK. H5210, from the Abeshinai River (AB).

Diagnosis.—Morphospecies characterized by much influated shell with subquadrate cross section, and very coarse, flexuous distinct ribbing of about 20 ribs per half a whorl.

Occurrence.—Coniacian. Except for difference in cross section, general features of "Y. ornatum" are quite similar to those of contemporaneous Y. kotoi, and there are some intermediate forms between the two morphospecies.

"Yokoyamaoceras (?) mysticum Matsumoto, 1955"

Holotype.—GK. H3379, from Loc. U-147p, Urakawa (UK).

Diagnosis.—Morphospecies with tubercles at both ventrolateral shoulder and umbilical margin.

Occurrence.—Only the holotype is known from the Santonian (Matsumoto, 1955, p. 156-157), and the identity of this species is still uncertain.

"Yokoyamaoceras minimum Matsumoto, 1956"

Holotype.—GK. H4204, found in a pebble in the Ikushumbetsu River (IK).

Diagnosis.—Morphospecies characterized by very small shell size and irregular but prominent tuberculation. The adult is 20 mm or less in shell diameter, with a pair of lappets. Occurrence.—Upper Turonian to Coniacian.

"Yokoyamaoceras yokoii Matsumoto, 1991"

Holotype.—TMNH (=Toyohashi Museum of Natural History) 501, from Mj-k Member, Satonosawa Valley, Tappu (TP).

Diagnosis.—Morphospecies characterized by small shell with subtrigonally shouldered venter, in which asymmetrically approximated two rows of tubercles appear.

Occurrence.-Middle Turonian.

Neopuzosia.-Neopuzosia is characterized by a moderate-sized, compressed (B/H: about 0.6-0.7 in adult), somewhat widely umbilicate Puzosia-like shell with slightly convex sides, perpendicular umbilical wall. 6-8 periodic constrictions per whorl, and fine, flexuous prorsiradiate ribs. The constrictions, associated with double collar ribs, are projected forwards on periphery, and can be observed in almost all ontogenetic stages. Α constriction usally truncates 2-4 ribs just behind it. Distant, rather straight ribs may appear suddenly on the living chamber of some adult shells, but flexuous ribbing still remains in others. In contrast to other true puzosiines in Hokkaido and Sakhalin, the shell never attains a large size, and the maximum diameter is usually less than 150 mm.

The type-species of *Neopuzosia* is based on a type specimen from the Urakawa area, Hokkaido. It was first described as *Desmoceras gaudama* Forbes, 1846 by Yokoyama (1890). Subsequently, Spath (1922) established the genus *Kitchinites*, based on

[←] Figure 4. Microconchs × 1.2. All the specimens, except 15, 16, are here assigned to Yokoyamaoceras ishikawai (Jimbo, 1894). Arrows show successive change of forms. 1, 2, an intermediate form between "Yokoyamaoceras jimboi Matsumoto" and "Neopuzosia haboroensis Matsumoto and Inoma," UMUT. MM18351, from the uppermost lower Santonian of the Kotambetsu River (Loc. KT-5302). 3, 4, "N. haboroensis Matsumoto and Inoma," holotype, GK. H5654, from the upper lower Santonian of the Miginosawa Valley (Loc. IA-1564), Haboro. 5-12, "Yokoyamaoceras jimboi Matsumoto." 5, 6, GK. H5201, exact locality uncertain, Ikushumbetsu. 7, 8, a depressed form, UMUT. MM7623a, Kikumenzawa Valley, Ikushumbetsu. The specimen was originally described as Yokoyamaoceras kotoi by Matsumoto (1955). 9, 10, holotype, UMUT. MM7625a, from the Santonian of the Saushi-sanushibe Valley, Hobetsu. 11, 12, UMUT. MM18359, from the lower Santonian of the Kumaoizawa Valley (Loc. IK-300), Ikushumbetsu. 13, 14, an intermediate form between "Y. jimboi" and "Y. kotoi," UMUT. MM18350, from the lower Santonian of the Kotambetsu Valley (Loc. KT-5606). 15, 16, Yokoyamaoceras kotoi (Jimbo), holotype, UMUT. MM7517, from the Coniacian of the Obirashibe River, Tappu.



Figure 5. Schematic diagram showing the diagnostic features and size in the adult stage for the four morphospecies discussed plus "*Yokoyamaoceras kotoi* (Jimbo, 1894)." The latter species can be considered as an ancestral form of the microconchs.

Holcodiscus pondicherryanus Kossmat, 1897 from India. He placed Yokoyama's specimen within his genus, and gave it a new specific name: Kitchinites japonicus. Matsumoto (1954b) proposed Neopuzosia as an independent puzosiid genus in which flexuous ribbing still remains even in the adult stage compared with Kitchinites (Kitchinites), and this division has been followed by several studies (Matsumoto, 1988, etc.). On the other hand, Wright (1957) ranked Neopuzosia as a subgenus of Kitchinites in the subfamily Puzosiinae. Neopuzosia is currently regarded as transient from Mesopuzosia of the Turonian-Coniacian to Kitchinites (Kitchinites) of the Campanian-Maastrichtian (Matsumoto, 1954b, 1981, 1988; Matsumoto et al., 1972). Matsumoto (1954b, p. 95) interpreted "N. ishikawai" as a descendant of Mesopuzosia yubarensis (Jimbo), and "N. japonica" as derived from M. pacifica Matsumoto. Three Neopuzosia species have been described from Hokkaido and Sakhalin, but I treat them provisionally as morphospecies with double quotation marks in this paper. Details are as follows.

"Neopuzosia japonica (Spath, 1922)"

Lectotype.—Yokoyama (1890, pl. 19, figs. 5a, b) from the Urakawa area (UK; exact locality unknown).

Diagnosis.—Morphospecies showing coarser and stronger ribbing than "*N. ishikawai.*" The rib density is 25-30 per half a whorl at 100 mm shell diameter. Some adult shells may exhibit straight and somewhat stronger prorsiradiate ribbing, but others still possess flexuous ribbing as in the juvenile.

Occurrence.—Santonian to lower Campanian.

"Neopuzosia ishikawai (Jimbo, 1894)"

Lectotype.—UMUT. MM7507 (Figures 6-5, 6-6), from the Santonian of the Obirashibe River, Tappu (TP).

Diagnosis.—Morphospecies possessing fine, dense sigmoid ribbing (numbering about 30-40 per half a whorl at 100 mm shell diameter). The ribs are prorsiradiate, strongly projected forwards on periphery even in adult shells.

Occurrence.—Santonian to lower Campanian.

"Neopuzosia haboroensis Matsumoto and Inoma, 1972"

Holotype.—GK. H5654 (Figures 4-3, 4-4) from the Miginosawa Valley, Haboro (HB).

Diagnosis.—Morphospecies characterized by a small, lappeted shell. The adult shell ranges from 25 to 40 mm diameter.

Occurrence.—Uppermost lower Santonian to lower Campanian.

I will concentrate my discussion mainly on the four Santonian to lower Campanian morphospecies: "N. ishikawai," "N. japonica," "N. haboroensis," and "Yokoyamaoceras jimboi" for they are abundant compared with other morphospecies from different horizons. For convenience, I adopt their specific epithets for the expression of these morphospecies, e.g., "ishikawai" for "Neopuzosia ishikawai (Jimbo, 1894)" etc.

Mode of occurrence

The species of "Yokoyamaoceras" and "Neopuzosia" discussed here are found in the central slope basin facies and the western shelf facies of the Yezo Group in Hokkaido (Matsumoto, 1942, 1954a; Okada, 1979, 1983). Figure 7 shows stratigraphic occurrence of Yokoyamaoceras and Neopuzosia in the Turonian- Santonian sequence along the Kotambetsu River, northwest Hokkaido. Strict facies-dependent distributions are not seen.

The species of "Yokoyamaoceras" and "Neopuzosia" frequently co-occur in the same place (Table 2). Well-preserved examples are usually obtained sporadically from calcareous concretions embedded in the muddy deposits, in association with other ammonites, inoceramids, other benthic fossils, and numerous plant remains. Most are found in a good state of preservation, except for the partial collapse of the living chamber during diagenesis (Maeda, 1987). Inner whorls with


protoconchs are usually well preserved, and amenable to ontogenetic study. A few specimens, larger than 100 mm in diameter, show the slight dissolution of their inner whorls. They are never concentrated into shell beds.

Adult features and variation

If we take no account of the barrier of traditional classification, the coexisting four morphospecies can be easily grouped into two categories: "macroconch" $\langle M \rangle$ and "microconch" $\langle m \rangle$ proposed by Callomon (1955, 1963) for dimorphic ammonites, in which juvenile shell morphologies closely resemble each other. The prerequisites for recognizing dimorphism (e.g., Callomon, 1963, 1969, 1981; Makowski, 1963 etc.) are discussed below; Figure 2 illustrates the two forms schematically. The macroconch consists of "ishikawai" (Figures 3-1, 3-3) and "japonica" (Figures 3-2, 3-4). "Haboroensis" (Figures 4-3, 4-4) and "*jimboi*" (Figures 3-7, 3-8) represent the microconchs. Both forms are nearly identical in the immature stage, but exhibit remarkable dimorphic features in the adult; there are no intermediates. Macroconchs are three times (or maximum four times) larger than the microconchs (Figure 5).

Macroconchs.—"Ishikawai" was distinguished from contemporaneous "*japonica*"by previous authors (*e.g.*, Matsumoto, 1954b) by its weaker and finer ribbing. Plots of rib density against shell diameter (Figure 8) show that the ribs tend to coarsen as the shell reaches maturity. Rib density converges finally to around 30 per half a whorl in both macroconchs. Both macroconchs show a wide continuous variation (Figure 6), and the ranges of variation of the two "species" overlap. Besides ribbing, they share many common morphologic characteristics. The differences between the type specimen of "ishikawai" $\langle M \rangle$ and "japonica" $\langle M \rangle$ are, therefore, considered as within the range of intraspecific variation, and I summarize both macroconchs together as "ishikawai" after this.

Fully grown shells comprise 8-9 whorls, and generally reach 90-140 mm diameter. The body chamber extends for 240° to 280°. The general coiling pattern is slightly modified towards the aperture of the adult, as a result of decrease of whorl expansion rate (Figures 3-1, 3-2). At the same time, the whorl becomes slightly compressed, and ornament may strengthen somewhat particularly on the periphery. These features indicate maturity, though approximation of the last few septa and simplification of the last suture (Kennedy and Cobban, 1976) are not clearly observed. The aperture never develops peristomal modifications. The aperture line is a simple prorsiradiate or concave pattern, which gently projects forwards on the periphery (Figure 2).

Microconchs.—"Jimboi" and "haboroensis" are nearly identical to macroconchs up to 15 or 20 mm shell diameter (Figure 9). Rib density of microconchs is the same as that of macroconchs (Figure 8). Fully grown shells possess 12-14 septa per whorl, and the body chamber length ranges from 240° to 280°, as in macroconchs. However, microconchs show quite different adult features from the macroconchs in shell size, mode of tuberculation, and peristomal modifications.

Fully grown shells, comprising 6-7 whorls, are no more than 25-40 mm diameter. In later growth stages, alternate ventrolateral tubercles appear in "*jimboi*." They appear on the first half of adult body chamber, and

[←] Figure 6. Macroconchs ×1.0. 1-3, "Neopuzosia japonica (Spath)," UMUT. MM18331, from the upper Santonian of the Omoshirubeshibetsu Valley (Loc. EM-404), Embetsu. 4, "N. japonica (Spath)," UMUT. MM6638, from the uppermost Santonian or lowermost Campanian of the Tannosawa Valley (Loc. T-472), Abeshinai. 5, 6, "N. ishikawai (Jimbo)," lectotype, UMUT. MM7507, from the Santonian of the Obirashibe River, Tappu. 7, UMUT. MM18336; 8, UMUT. MM18386, "N. ishikawai (Jimbo)," from the lower Santonian of the Kaminosawa Valley (Loc. KT-5200), Kotambetsu.



Figure 7. Historical changes of macroconch "*ishikawai*" and "*japonica*," and microconch "*jimboi*" and "*haboroensis*" lineage in the Turonian-Santonian sequence along the Kotambetsu River (KT). Solid circle : occurrence of microconchs $\langle m \rangle$; Open circle : occurrence of macroconchs $\langle M \rangle$. SS. : sandstone. MS. : mudstone.

Table 2.Fossil assemblages showing coexistence of macro- and microconchs at the same places. 1, an
example housed in a calcareous nodule of 300 mm diameter, Ikushumbetsu (IK). 2, another
example housed in a calcareous nodule of 200 mm diameter, Teshio (TS). VA: very
abundant; A: abundant.

(1) Locality: IK-300 (Lower Santonian)	
Species	Individuals
<pre></pre>	
Neophylloceras ramosum (Meek)	1
Gaudryceras tenuiliratum Yabe	1
Tetragonites glabrus (Jimbo)	2+
Damesites damesi (Jimbo)	12+
" <i>Neopuzosia ishikawai</i> (Jimbo)" 〈M〉	3
" <i>Yokoyamaoceras jimboi</i> Matsumoto" 〈m〉	4
Hauericeras (Gardeniceras) angustum Yabe	3
Polyptychoceras pseudogaultinum (Yokoyama)	5+
<pre></pre>	
Inoceramus (Inoceramus) amakusensis Nagao and Matsumoto	3
Inoceramus (Sphenoceramus) naumanni Yokoyama	60+
<pre> (GASTROPOD)</pre>	
Serrifusus sachalinensis (Nagao)	1
(PLANT REMAINS)	VA

(2) Locality : TS-8007 (Upper Santonian)	
Species	Individuals
(AMMONITES)	
Gaudryceras tenuiliratum Yabe	3
Damesites sugata (Forbes)	2
"Neopuzosia ishikawai (Jimbo)" $\langle M \rangle$ and "N. japonica (Spath)" $\langle M \rangle$	2
" <i>Neopuzosia haboroensis</i> Matsumoto and Inoma" 〈M〉	2
immature shells of "Neopuzosia sp." $\langle M \rangle$ or $\langle m \rangle$	9+
Hauericeras (Gardeniceras) angustum Yabe	1
Polyptychoceras sp.	1+
(BIVALVES)	
Inoceramus (Sphenoceramus) naumanni Yokoyama	60+
immature bivalves gen. indet.	3
⟨GASTROPODS⟩	
"Avellana" problematica Nagao	1
Tibia japonica (Nagao)	1
(PLANT REMAINS)	Α



Figure 8. Plots of rib density in relation to shell diameter (D) for medium-to-large specimens of four morphospecies. The mode of ribbing shows a wide extent of variation even at the same shell size. It varies continuously, and discrimination of "*ishikawai*" from "*japonica*" is impossible. Such variation in ribbing is regarded as intraspecific.

extend over $120^{\circ}-240^{\circ}$ of whorl. The tuberculation is absent in "*haboroensis*," however, it is unsuitable for taxonomic discrimination as stated below.

The tuberculation of the microconchs clearly changes chronologically both in density and extent of appearance. Though there is a certain degree of variation even in the coexisting specimens, microconchs tend to lose their tuberculation at progressively higher stratigraphic levels. Typical examples of microconchs from different stratigraphic levels are shown in Figures 4 and 7. The lowermost Santonian forms (*e.g.*, Figures 4-13, 4 -14) are characterized by dense tuberculation on the adult body chamber. The specimen illustrated possesses 18 ventrolateral tubercles, appearing over about half a volution (170°) of the body chamber. It shows somewhat intermediate features between Coniacian "kotoi" (Figures 4-15, 4-16) and "jimboi." Irregularly tuberculate specimens, typical "jimboi," are dominant in the main part of the lower Santonian. The holotype (Figures 4-9, 4-10) has 8 tubercles extending over one-third of a volution of the body chamber. In the upper Santonian and lower Campanian, microconchs are represented by nontuberculate "haboroensis" (Figures 4-3, 4-4), and tuberculate forms are unknown at this level.

Recently, I collected several specimens



Figure 9. Immature shells of macro- and microconchs $\times 1.0$. All the specimens are here assigned to *Yokoyamaoceras ishikawai* (Jimbo, 1894). 1-3, "*Y. jimboi* Matsumoto" $\langle m \rangle$, in a calcareous concretion from the lower Santonian of the Kotambetsu Valley (Loc. KT-5056). 1, UMUT. MM18346; 2, 3, UMUT. MM18344. 4-12, coexistent "*Neopuzosia* species" in a calcareous concretion from the upper Santonian of the Kokuneppu Valley (Loc. TS-8007), Teshio. 4, UMUT. MM18380; 5, UMUT. MM18381, immature shells of "*N. ishikawai* (Jimbo)" $\langle M \rangle$ or "*N. haboroensis* Matsumoto and Inoma" $\langle m \rangle$. 6, 7, "*N. ishikawai* (Jimbo)" $\langle M \rangle$, UMUT. MM18382. 8-12, ontogenetic development of "*N. haboroensis* Matsumoto and Inoma" $\langle m \rangle$, UMUT. MM18387.

intermediate between tuberculate and successive nontuberculate forms (*e.g.*, Figures 4-11, 4-12 via Figures 4-5, 4-6 to Figures 4-1, 4-2). One of them, from the uppermost lower Santonian (Figures 4-1, 4-2), is faintly tuberculate, with only 6 indistinct ventrolateral tubercles on a limited portion (ca. 70° in whorl volution) of the adult living chamber. It exhibits features clearly transient between those "*jimboi*" (Figures 4-5, 4-6) and "*haboroensis*" (Figures 4-3, 4-4). The two

microconch morphospecies are thus linked together into a single lineage by such intermediate forms.

In the full-grown mature stage of "*jimboi*" $\langle m \rangle$ and "*haboroensis*" $\langle m \rangle$, a characteristic biconcave constriction develops at the end of the body chamber, from which a pair of lateral lappets and a rostrum project adorally (Figures 2, 3-5-3-8, 4). The biconcave constriction is adjacent to the last periodic constriction. It never appears at any other

growth stage, and is easily differentiated from the normal periodic constrictions by the difference in curvature. The lappets are 2-5 mm long, and have a simple tapering shape. The distinctive apertural modifications are regarded as diagnostic of maturity in microconchs (Kennedy and Cobban, 1976; Callomon, 1981). "Jimboi" $\langle m \rangle$ and "haboroensis" $\langle m \rangle$ closely resemble each other in size and apertural features at maturity (Figures 4, 5).

Besides these features, parabolic lines (="demarcation lines" by Matsumoto *et al.*, 1972; Matsumoto, 1991; Figure 2) appear repeatedly just in front of the periodic constriction in several specimens of microconch. However, the appearance of parabolic lines should be excluded from the criteria for recognition of microconchs, because they are not peculiar to microconchs but are also fairly common in macroconchs (Figure 3-1), and even in huge puzosiines.

Ontogenetic shell growth

To confirm the dimorphic relationship among the four morphospecies discussed above, I have paid much attention to the early shell morphology, which may possibly reflect phylogeny as well as other diagnostic features. For the analysis of ontogenetic shell growth, I prepared cross sections of more than 30 specimens of the four morphospecies and other desmocerataceans (Table 1) by polishing the shells along the center of the protoconch. The following parameters (abbreviations used in the text, figures, and tables are shown in parentheses) were measured at intervals of half a whorl (180°) on each sectioned specimen using a digital micrometer (accuracy $\pm 1 \ \mu$ m) attached to an overhead profile projector (V-16D, Nikon); whorl radius (R), whorl breadth (B) and umbilical radius (C). The whorl volution is expressed by π (=180°) scale from the center of protoconch.

Figure 10 shows the median cross sections

of early growth stage of "ishikawai" $\langle M \rangle$, "haboroensis" $\langle m \rangle$, and "jimboi" $\langle m \rangle$ compared with three other desmocerataceans. The macroconchs are treated as "ishikawai." The protoconchs of dimorphs are nearly identical, having an ellipsoid shape, 0.5 mm wide and 0.3 mm diameter. They are enclosed by the extremely depressed first whorl. In all morphospecies, the siphuncular tube lies at first in the center of the camera just as in Nautilus. Thereafter, it moves towards the venter, and finally closes to the ventral shell wall at the 3-4 π stage. The whorl is depressed at first, but whorl height grows more rapidly than breadth as the shell grows. The umbilical shoulder appears at the 4-5 π stage.

The profiles of "*haboroensis*" $\langle m \rangle$ (Figures 10-1), "ishikawai" $\langle M \rangle$ (Figures 10-2), and "jimboi" (m) (Figures 10-3) are almost identical. They share abrupt narrowing of umbilicus once at the second to fourth whorl (see also Tanabe and Shigeta, 1987, fig. 4). It is most conspicuous at 5-6 π stage where umbilical shoulders project into the umbilical void and form a remarkable "umbilical break." On the succeeding third to fourth whorl the umbilicus widens gradually, and finally the shell shows a somewhat evolute Puzosia-like morphology. Kossmaticeras theobaldianum paucicostatum (Figure 10-4) also shows a quite similar profile of juvenile shell shape. In contrast, Mesopuzosia pacifica, which was considered as the ancestor of "*japonica*" $\langle M \rangle$, never exhibits such umbilical narrowing in the early stage (Figure 10-6).

Early ontogenetic growth patterns of whorl radius, breadth, and umbilical radius are essentially similar among the three morphospecies (Figure 11). The growth of the whorl radius (R) exhibits monophasic allometry at least for the early stage (2-12 π stage; D \cong 0.7-18 mm). That of whorl breadth (B) of the three morphospecies shows diphasic allometry, and the growth ratio increases markedly at the 2-3 π stage, which may result from rapid whorl growth after the



Figure 10. Median cross sections of early growth stage showing the ontogenetic change of whorl shape and siphuncular position. 1, "Neopuzosia haboroensis Matsumoto and Inoma" $\langle m \rangle$, UMUT. MM18376, upper Santonian. 2, "N. ishikawai (Jimbo)" $\langle M \rangle$, UMUT. MM18369, lower Santonian. 3, "Yokoyamaoceras jimboi Matsumoto" $\langle m \rangle$, UMUT. MM18372, lower Santonian. 4, Kossmaticeras theobaldianum paucicostatum Matsumoto, UMUT. MM18374, Coniacian. 5, Desmoceras (Pseudo-uhligella) japonicum Yabe, UMUT. MM18379, middle Cenomanian. 6, Mesopuzosia pacifica Matsumoto, UMUT. MM18362, middle Turonian.



Figure 11. Ontogenetic allometry of radius vector (R), whorl breadth (B), and umbilical radius (C) in relation to whorl volution for three morphospecies in the early stage. Whorl volution of 2-12 π corresponds approximately to shell diameter of 0.7-18 mm.

formation of the primary constriction (=hatching).

Double logarithmic plots of umbilicus versus shell diameter for selected specimens of four morphospecies show a similar growth pattern throughout their ontogeny (Figure 12). Remarkable reduction of umbilical growth is present between 1-4 mm diameter, and thereafter the umbilicus shows an isometric growth pattern. The first flection point at a diameter of 1.5 mm obviously corresponds to the stage of abrupt umbilical narrowing in the second whorl. The second flection point at a diameter of 3 mm reflects



Figure 12. Allometric relationship between shell diameter (D) and umbilicus (U) for the four morphospecies and *Mesopuzosia pacifica*. Ontogenetic change of measurements in each specimen is linked by a line (same as in Figure 13).

its maximum decrease and formation of the "umbilical break" around the third whorl stage (see also Figures 10, 11C). The umbilical growth patterns of the four morphospecies markedly differ from that of *Mesopuzosia pacifica* in the presence of growth reduction at 1-4 or 5 mm diameter.

The ontogenetic changes of whorl shape expressed by breadth-height ratio (B/H) versus shell diameter (D) of the four morphospecies are also essentially similar up to 15-20 mm diameter, and show a gradual decrease of this parameter with growth (Figure 13). At the stage less than 1 mm diameter, whorls are twice as wide as high, and the B/H ratio then decreases rapidly. Rate of decrease reduces abruptly at a diameter of 4 mm. In macroconchs, this ratio decreases gradually after 15-20 mm diameter, and at maturity it attains 0.6-0.7, which is somewhat larger than that of *Kitchinites* (s.s.) species from the Campanian to Maastrichtian (*e.g.*, Howarth, 1965; Henderson, 1970). In full-grown microconchs, the ratio is quite variable as compared with macroconchs, and tuber-culation appears coincidentally in "*Y. jimboi.*"

Contrarily, Mesopuzosia pacifica exhibits a



Figure 13. Ontogenetic changes of the breadth-height ratio (B/H) in relation to shell diameter (D) for four morphospecies plus *Mesopuzosia pacifica*.

somewhat different pattern of decreasing B/H ratio from those of the four morphospecies (Figure 13), particularly in the early growth stage in the presence of a sudden fall at 1.2 mm diameter and in the absence of the flection point at 4 mm diameter.

Dimorphism of four morphospecies

The following observations strongly suggest the presence of dimorphism among the four morphospecies :

1) They frequently co-occur in the Santonian to lower Campanian in Hokkaido.

2) All morphospecies share similar shell morphology in the immature stage.

3) Their adult shell sizes are discretely bimodal: the macroconch $\langle M \rangle$ ("*ishikawai*" and "*japonica*") has a simple aperture, and the microconch $\langle m \rangle$ ("*jimboi*" and "*haboroensis*") has lappets.

4) Macroconchs may show slight numerical dominance, but great disparity in the relative frequency of the two froms is not observed.

5) Some diagnostic features, such as rib density and mode of tuberculation are unsuitable for taxonomic discrimination, because of their wide range of variation.

However, the taxonomic barrier between the Puzosiinae and Kossmaticeratidae has prevented us from recognizing the dimorphism, and gave rise to somewhat complicated problems. Matsumoto et al. (1972) already commented on dimorphism in "Neopuzosia." They hypothesized that "ishik*awai*" $\langle M \rangle$ and lappeted "*haboroensis*" $\langle m \rangle$ were a dimorphic pair. On the other hand, Matsumoto (1981, 1991) also commented on possible dimorphism between species of Yokoyamaoceras $\langle m \rangle$ and Kossmaticeras $\langle M \rangle$. These hypotheses were, however, not confirmed by these authors because of the marked disparity both in stratigraphic occurrence and frequency of presumed dimorphs. For example, Y. *jimboi* $\langle m \rangle$ is quite common in the lower Santonian of Hokkaido and

Sakhalin, but Kossmaticeras spp., presumed $\langle M \rangle$, almost disappear in the upper Coniacian.

Recently, Matsumoto (1988) described dimorphism independently in every "Neopuzosia species." This is, however, quite inconsistent with the situation in "N. haboroensis" which is represented only by lappeted microconchs. Similarly, Alabushev and Alabusheva (1988) assumed sexual dimorphism within "Y. jimboi" by differences of septation, shell ornament, and constrictions. However, this interpretation should be rejected because both of their "dimorphs" are undoubtedly lappeted. Although the function of lappets is still obscure, this feature is peculiar to the microconchs (Kennedy and Cobban, 1976, etc.). The two forms in "jimboi" by Alabushev and Alabusheva (1988) and "haboroensis" are, therefore, included in the wide morphologic variation of microconch $\langle m \rangle$.

If we take no account of the taxonomic artifice, but take "*Neopuzosia*" into consideration together with "*Yokoyamaoceras*" and *Kossmaticeras*, differences in the range and the occurrence of dimorphs disappear completely (Figure 7). Consequently, one "kossmaticeratid" and three "puzosiines" can be classified as a single, dimorphic biospecies.

Higher taxonomic considerations

If one "kossmaticeratid" and three "puzosiines" can be lumped together under a biospecies, a problem naturally arises as to its suprageneric position. Kennedy (1986) presumed a dimorphic relationship between *Yokoyamaoceras* and *Neopuzosia*, and placed both genera together in Puzosiinae. On the other hand, morphological resemblance between *Kossmaticeras* and *Kitchinites* (s.l.) including *Neopuzosia* was already pointed out by previous authors (*e.g.*, Kossmat, 1897; Yabe, 1927; Matsumoto, 1954b). Besides the four morphospecies discussed here, there are many puzzling examples as to whether tuberculate and nontuberculate forms should be placed in Puzosiinae or Kossmaticeratidae (Kennedy *et al.*, 1979, *etc.*). The ambiguity of diagnostic criteria between the two suprageneric groups is responsible for such doubts as to their classification (*e.g.*, truncated ribbing by periodic constriction, and tuberculation).

As already admitted to some extent by Matsumoto (1955, p. 155), the sutural difference between "Yokoyamaoceras" and "Neopuzosia" is also ambiguous. "Ishikawai" $\langle M \rangle$, "haboroensis" $\langle m \rangle$, and "jimboi" $\langle m \rangle$ are not distinguishable from one another by their sutures at the same shell size, about 20 mm diameter. The sutures of kossmaticeratid "jimboi" $\langle m \rangle$ also show "puzosiine features," such as an asymmetrically tripartite L and a retracted umbilical element (Matsumoto, 1954b, 1988; Figure 14).

In contrast, information on phylogeny is to be found in early ontogeny, because ecological constraints may not so strongly influence the juvenile shell morphology. Ontogenetic changes of umbilicus/diameter ratio (U/D) in "jimboi" $\langle m \rangle$, "haboroensis" $\langle m \rangle$, and *"ishikawai"* (including "*japonica*") (M) are shown in Figure 15 compared with those of other desmocerataceans. The three morphospecies and Kossmaticeras theobaldianum paucicostatum (Kossmaticeratidae, Coniacian) show a quite similar ontogenetic pattern for this parameter with respect to a remarkable umbilical reduction in the 4-8 or 9π stage (about 1.3-7 mm shell diameter). The minimum point in the graph corresponds to the temporal formation of a sharp umbilical break at the 5-6 π stage (about 2-3 mm shell diameter) on their profiles (Figure 10). The temporal abrupt reduction of the umbilicus at an early stage seems to be a characteristic feature of the Kossmaticeras group. Both Desmoceras (Pseudouhligella) japonicum (Desmoceratidae, middle Cenomanian; Figure 10-5) and Anapachydiscus sp. (Pachydiscidae, upper Santonian) also possess similar patterns for

ontogenetic change of U/D (Figure 15).

In contrast to this, true puzosiines such as *Mesopuzosia pacifica* (Turonian; the direct descendant of *Puzosia*), *M. yubarensis* (Coniacian), and *Jimboiceras planulatiforme* (Turonian) never show the narrowing of the umbilicus in the early growth stage. Their umbilicus is still wide during the 4-9 π stage (U/D \cong 40%), and thereafter its umbilicus/ diameter ratio gradually decreases (U/D \cong 35%). *Hauericeras* (*Gardeniceras*) angustum (Hauericeratinae, Santonian) also shares a similar ontogenetic change of U/D ratio with *Mesopuzosia*. There are no intermediates between the *Kossmaticeras* and *Mesopuzosia* groups in this parameter. *Neopuzosia*



Figure 14. Suture lines of macro- and microconchs. 1, adult suture of "Neopuzosia ishikawai" $\langle M \rangle$ at about 140 mm diameter, UMUT. MM6640, Santonian. 2-4, immature stures at about shell diameter of 20 mm; 2, "N. ishikawai" $\langle M \rangle$, UMUT. MM18380, upper Santonian; 3, "N. haboroensis" $\langle m \rangle$, UMUT. MM18383, upper Santonian; 4, "Yokoyamaoceras jimboi" $\langle m \rangle$, UMUT. MM18344, lower Santonian.



Figure 15. Ontogenetic changes of the umbilicus/diameter ratio (U/D) in relation to whorl volution for three morphospecies of "*Yokoyamaoceras*" and "*Neopuzosia*," and selected species of *Kossmaticeras*, *Desmoceras*, *Anapachydiscus, Mesopuzosia*, and *Hauericeras*. This figure shows that the three morphospecies are clearly distinguished from the true puzosiines in the abrupt narrowing of umbilicus in the limited stage of $4-9 \pi$ stage ($\cong 1.3-7$ mm shell diameter).

and Yokoyamaoceras obviously belong in the Kossmaticeras group in terms of early shell shape. Thus the four morphospecies in question should be placed in the family Kossmaticeratidae.

Besides this, several morphological features cast doubts on puzosiine origin of the four morphospecies. "Neopuzosia ishikawai" and "N. japonica" never exceed 150 mm diameter, but true puzosiines, e.g., Mesopuzosia, commonly attain gigantic shell-size (500 mm or larger). In addition, the adult shells of Kossmaticeras (Collignon, 1955; Kennedy and Klinger, 1985; Matsumoto, 1991), Yokoyamaoceras, Neopuzosia (Figures 2, 3-1, 16-1, 16-3), and Kitchinites (Kitchinites) (Henderson, 1970; Macellari, 1986) similarly have a characteristic double collar rib, interspaced with a sharp, deep furrow, on the shell surface at the position of the periodic constriction on the internal mold. In contrast, the collar feature of puzosiines is quite different. The shells of true puzosiines have adapical collars only, and the furrow at the constriction on the shell surface is obscure (Figure 16-2, 16-4). These may also suppose the kossmaticeratid origin of "Neopuzosia" and Kitchinites. Comparable geographic distribution of Kitchinites (Kitchinites) and diverse kossmaticeratids in the southern hemisphere during the late Campanian to Maastrichtian (Henderson, 1970; Macellari, 1986; Bando et al., 1987 etc.) should also be noted.

The superficial resemblance of external shell morphology of *Mesopuzosia* and *Neopuzosia* in the middle to late growth stages is a homeomorphy, a phenomenon that is widespread among ammonites (Kennedy and Cobban, 1976).

The acceptance of kossmaticeratid affinities of the four morphospecies brings further results. I agree with Matsumoto's presumption (Matsumoto, 1981, 1991) that the origin of lineages with such dimorphs can be traced back to the Coniacian, or further, to the Turonian (Figure 7) though examples from



Figure 16. Comparison on collar rib of Yokoyamaoceras ishikawai (Jimbo) $\langle M \rangle$ with that of a true puzosiine at the same shell size (D=approximately 100 mm). 3 and 4 are schematic profiles of collar ribs. 1, 3, Y. ishikawai (Jimbo) $\langle M \rangle$. 2, 4, Mesopuzosia pacifica Matsumoto. A sharp, deep furrow between the collars on the shell surface is one of the characteristic features of kossamaticeratids. It does not develop in shells of true puzosiines.

lower stratigraphic horizons are rare. "Neopuzosia haboroensis" $\langle m \rangle$ and "Yokoyamaoceras jimboi" $\langle m \rangle$ possibly originated in Yokoyamaoceras yokoii $\langle m \rangle$, Y. minimum $\langle m \rangle$ or Y. kotoi $\langle m \rangle$ (Figures 4-15, 4-16) of Turonian-Coniacian age via some intermediate forms (Figures 4-13, 4-14).

On the other hand, the macroconch "Neopuzosia ishikawai" of Santonian-early Campanian age can be traced likewise to the species of Turonian-Coniacian Kossmaticeras $\langle M \rangle$, which is contemporaneous with the above Yokoyamaoceras species $\langle m \rangle$. The shell ornament may weaken simultaneously, in parallel, in both macroconchs and microconchs (Figure 7). Such simultaneous change provides powerful arguments in support of dimorphism (Callomon, 1981), though the morphologic change of the macroconch during the Santonian to lower Campanian is slight.

Handling of such dimorphic "species" involves several complicated nomenclatorial

problems debated by some paleontologists (e.g., Westermann, 1969; Callomon, 1981). I lump the four nominal species in a single evolutionary biospecies belonging to the family Kossmaticeratidae. Thus the microconch genus Yokoyamaoceras Wright and Matsumoto, 1954, and specific epithet of the macroconch: ishikawai of "Desmoceras ishikawai Jimbo, 1894," are adopted in the revised nomenclature of the species.

Conclusion

Three supposed puzosiines, Neopuzosia ishikawai (Jimbo, 1894), N. japonica (Spath, 1922), and N. haboroensis Matsumoto and Inoma, 1972, and a kossmaticeratid Yokoyamaoceras jimboi Matsumoto, 1955, occurring from the Santonian to the lower Campanian sequence of the Yezo Group in Hokkaido, Sakhalin and Korvak-Kamchatka, are not independent biospecies but dimorphs of a single species of Kossmaticeratidae, Yokovamaoceras ishikawai (Jimbo, 1894) revised here (Figure 7). The mode of ontogenetic shell growth, particularly the umbilicus, reveals a kossmaticeratid origin for Y. ishikawai. Thus the dimorphic lineage can be traced back to Kossmaticeras $\langle M \rangle$ and Yokoyamaoceras $\langle m \rangle$ of Coniacian-Turonian age.

Though little has been investigated about dimorphism, there are several contemporaneous pairs of nontuberculate and tuberculate genera in the family Kossmaticeratidae, *e.g.*, *Marshallites* and *Eomadrasites* in the Cenomanian, and *Maorites* and *Jacobites* of the Campanian. The ancetral *Kossmaticeras* and the descendent *Kitchinites* should, therefore, be more closely investigated to determine the nature of their dimorphism.

Yokoyamaoceras ishikawai is a peculiar "false puzosiine" showing homeomorphy with Mesopuzosia. On the other hand, true puzosiines such as Puzosia and descendant Mesopuzosia attain large shell size, and are fairly abundant through the Albian to Coniacian of the Yezo Group in Hokkaido and Sakhalin (Matsumoto, 1988; Maeda, 1991). However, they almost disappear in the upper Coniacian. Y. ishikawai might possibly have adapted to the vacated niche of such true puzosiines during the Santonian and early Campanian, and succeeded in surviving in the Far East region of the northern hemisphere where Late Cretaceous kossmaticeratids are otherwise unknown.

In addition, the umbilical ontogeny of *Mesopuzosia* and *Hauericeras* is quite different from that of other desmocerataceans (Figure 15). This casts doubt on the puzosiine origin of *Kitchinites*, and may also indicate a need for further phylogenetic re-examination of the Puzosiinae and Hauericeratinae in the large superfamily Desmocerataceae (Wright, 1981).

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Systematic paleontology

Superfamily Desmocerataceae Zittel, 1895 Family Kossmaticeratidae Spath, 1922 Subfamily Kossmaticeratinae Spath, 1922

Genus Yokoyamaoceras Wright and Matsumoto, 1954

Type species.—*Holcodiscus kotoi* Jimbo, 1894, p. 33, pl. 5, figs. 2, 2a, b, by original designation of Wright and Matsumoto (1954).

Synonym.—Neopuzosia Matsumoto, 1954 [type species: Kitchinites japonicus Spath, 1922]. Yokoyamaoceras and Neopuzosia were proposed in the same year, but the date of publication for the former is July 31, while that of the latter is October 30.

Diagnosis.—A dimorphic genus of moderately involute or evolute, somewhat compressed shells with prorsiradiate ribs truncated somewhat obliquely by well-marked periodic constrictions, which are associated with a double collar rib. The cross section exhibits temporal umbilical reduction, forming an umbilical break at the second to fourth whorl stage. Macroconch three or four times larger than lappeted microconch, but never attains a large size. Alternate or opposite ventrolateral tubercles appear in some adult microconchs.

Occurrence.—Middle Turonian to lower Campanian of Hokkaido, Sakhalin, Koryak-Kamchatka, France, California, British Columbia, Argentine, and Antarctica.

Yokoyamaoceras ishikawai (Jimbo, 1894)

Figures 3, 4-1-4-14, 6, 9, 10-1-10-3

Macroconch.-

- Desmoceras gaudama (Forbes). Yokoyama, 1890, p. 184, pl. 19. figs. 5a, b.
- Desmoceras ishikawai Jimbo, 1894, p. 28, pl. 17, figs. 5a, b.
- Kitchinites japonicus Spath, 1922, p. 127.

Kitchinites ishikawai (Jimbo). Spath, 1922, p. 127.

- Neopuzosia japonica (Spath). Matsumoto, 1954b, p. 91, pl. 17, figs. 1, 2; pl. 18, figs. 1-4; pl. 23, fig. 1; Matsumoto, 1963, p. 29, pl. 45, figs. 5a, b; Matsumoto, 1988, p. 11; p. 82, figs. 31A-F, 32A, 33A-C.
- Neopuzosia ishikawai (Jimbo). Matsumoto, 1954b, p. 94, pl. 19, figs. 1-4; pl. 23, figs. 2a-d (see for complete synonymy); Matsumoto, 1963, p. 43, pl. 60, fig. 5; Vereshchagin, Kinasov, Paraketsov, and Terekhova, 1965, p. 50, pl. 53, figs. 1a, b; pl. 54, fig. 1; Matsumoto, 1988, p. 11, figs. 32B-H, 33I-K.
- Kitchinites (Neopuzosia) japonicus Spath. Wright, 1957, p. 367; Haggart and Ward, 1989, p. 220, figs. 3•6, 5•9-5•12, 6.
- Kitchinites (Neopuzosia) ishikawai (Jimbo). Wright, 1957, p. 367.

Microconch.-

- Yokoyamaoceras kotoi Matsumoto, 1955, p. 152, text-fig. 12.
- Yokoyamaoceras jimboi Matsumoto, 1955, p. 152-153, fig. 13; pl. 9, figs. 4a, b, 5a, b (see for complete synonymy); Matsumoto, 1956, pl. 16, figs. 5a, b; Alabushev and Alabusheva, 1988, figs. 5, 6; Matsumoto, 1991, p. 100, pl. 22, fig. 7; pl. 23, figs. 1, 2.
- Kitchinites (Neopuzosia) haboroensis Matsumoto and Inoma, 1972, p. 384, pl. 47, figs. 5, 6.
- Kitchinites (Neopuzosia) aff. haboroensis (Matsumoto and Inoma). Obata, Futakami, Kawashita, and Takahashi, 1978, p. 144, fig. 6, pl. 1, figs. 4a-c.
- Kitchinites (Neopuzosia) cf. japonicus (Spath). Obata, Futakami, Kawashita, and Takahashi, 1978, p. 143, pl. 2, figs. 2a-c.
- Yokoyamaoceras aff. jimboi Matsumoto. Kennedy, 1986, p. 25, fig. 8-E; pl. 1, figs. 6-8.

Diagnosis.— Yokoyamaoceras of compressed (B/H=0.6-0.7 in adult $\langle M \rangle$), Puzosia-like shell with very fine, weak, flexuous ribs numbering 30-50 per half a whorl, and periodic constrictions numbering 6-8 per whorl. A biconcave constriction and a pair of lappets appear at the aperture of adult microconch. The lower Santonian microconch has impersistent, alternate ventrolateral tubercles, numbering 6-18 per 70°-240° of a volution.

Lectotype.—UMUT. MM7507 (=lectotype of Desmoceras ishikawai Jimbo, 1894, a macroconch of middle growth stage), designated by Matsumoto (1954, p. 94, as

Table 3. Dimensions (in mm) and ratios of *Yokoyamaoceras ishikawai* (Jimbo, 1984). 1, measurements of middle- to full-grown shells. 2, measurements of ontogenetic growth of UMUT. MM18365 $\langle M \rangle$, from the upper Santonian of the Kotambetsu River (Loc. KT-5031). -: calculated value; D: shell diameter; H: whorl height; B: whorl breadth; U: diameter of umbilicus; Rib/HW: number of ribs per half a whorl; Tbc/WV: number of ventrolateral tubercles per whorl volution; WV (π): whorl volution in π (=180°) scale; R: whorl radius; C: umbilical radius; $\langle L \rangle$: lectotype; (PC): protoconch.

(1)							
$\langle Macroconch \rangle$	D	Н	В	B/H	U	U/D%	Rib/HW
MM6642	26.8	9.8	8.8	0.90	8.6	32	_
MM7507 $\langle L \rangle$	37.7	15.5	13.3	0.86	12.2	32	54
MM6637	54.0	23.0	18.0	0.78	17.1	32	45
MM18340	80.2	30.2	23.2	0.77	28.0	35	41
MM18337	94.7	37.1	25.1	0.68	31.0	33	26
MM18341	-134	- 50	30.7	-0.61	50.3	- 38	32
<microconch></microconch>	D	Н	В	B/H	U	U/D%	Tbc/WV
MM18359	27.1	10.9	9.1	0.84	9.6	35	11/130°
MM18357	32.1	13.2	10.9	0.83	10.8	34	10/140°
MM18351	37.2	15.5	11.3	0.73	11.9	32	6/ 70°
GK. H. 5654	30.2	10.8	7.8	0.72	11.1	37	

(2)								
WV (π)	R	В	С	D	Н	B/H	U	U/D%
(PC)		0.585		0.328				
1	0.313	0.588	0.011	0.477	0.302	1.947	_	0.0
2	0.428	0.648	0.112	0.741	0.316	2.165	0.123	16.6
3	0.572	0.681	0.203	1.000	0.369	1.846	0.315	31.5
4	0.776	0.913	0.221	1.348	0.555	1.645	0.424	31.5
5	1.111	1.238	0.271	1.887	0.840	1.474	0.492	26.1
6	1.541	1.541	0.293	2.652	1.248	1.235	0.564	21.3
7	2.081	1.954	0.392	3.622	1.689	1.157	0.685	18.9
8	2.827	2.315	0.702	4.908	2.125	1.089	1.094	22.3
9	3.989	3.302	1.107	6.816	2.882	1.146	1.809	26.5
10	5.629	4.305	1.658	9.618	3.981	1.081	2.755	28.6
11	8.278	5.877	2.596	13.907	5.682	1.034	4.244	30.5
12	12.119	7.838	3.776	20.397	8.343	0.940	6.372	31.2
13	18.105	10.369	5.629	30.224	12.476	0.831	9.405	31.1

"*Neopuzosia ishikawai*"), from the Santonian of the Obirashibe River, northwest Hokkaido, Japan.

Material.—More than eighty specimens from the upper part of the Yezo Group at various points in Hokkaido and Sakhalin. UMUT. MM6624-6639, 6640-6644, 6675, 6883, 7507, 7623a, b, 7624a, b, 7625a, b, 7626, 7697, 7698, 7700, 9137, 18330-18353, 18365-18370, 18376, 18380-18387 ; GK. H3366, 5143, 5201, 5654-5656.

Dimensions.-Shown in Table 3.

Description.—Protoconch ellipsoidal, 0.5 mm wide and 0.3 mm diameter. Whorl globular at first. The umbilicus narrows temporally in the second to early fifth whorl stage (1.3-7 mm shell diameter). In the third whorl stage (D=2-3 mm; U/D=20%), a sharp umbilical break appears in the cross section.

After the fifth whorl stage ($D \ge 9 \text{ mm}$), the coiling becomes moderately evolute, with 40% of the previous whorl being covered. The rather shallow umbilicus comprises 30-35% of the diameter. The whorl section becomes compressed with growth, with the maximum breadth towards the inner flank. Slightly convex flanks converge to the rounded ventrolateral shoulders.

Very fine, flexuous prorsiradiate ribs are distinct from a diameter of 15 mm. The ribs arise at the umbilical margin, being gently flexed on the inner flank, and bend forwards across the outer flank and ventrolateral shoulder to project over the venter in a fairly strong convexity. These primary ribs bifurcate once or twice on the mid-flank, and loop across the venter, while shorter ribs are also intercalated.

Narrow, deep, prorsiradiate periodic constrictions numbering 6-8 per a whorl, appear at less than 5 mm diameter. They are straight on the inner flank, but sweep forwards over the venter in a deep convexity. Double collar ribs, interspaced with a deep furrow, flank the constrictions and become obvious in adults. The prominent adapical collar subdivides across the ventrolateral shoulder to give rise to two or four riblets arranged in a virgatotome pattern. Parabolic lines commonly appear in front of the periodic constrictions.

Phragmocones have 12-14 septa per whorl. Body chamber length ranges from 240° to 280° of a volution. Sutures with a large tripartite L and retracted umbilical elements, are variable. Macro- and microconchs are identical in overall shell morphology up to 15-20 mm diameter, and thereafter become dimorphic.

Macroconch $\langle M \rangle$.—Fully grown shell comprises 8-9 whorls (90-140 mm diameter). The expansion rate decreases slightly in the adult body chamber, and the aperture becomes narrower. The ribbing coarsens somewhat and numbers 25-30 per half a whorl, strengthening particularly on the periphery. Aperture simple. Tubercles never develop.

Microconch $\langle m \rangle$.—Fully grown shell, comprising 6-7 whorls, is 25-40 mm in diameter. Santonian forms, alternate In lower ventrolateral tubercles appear at 15-20 mm diameter, and extend to the early half of the adult body chamber. They sometimes give rise to two or three fine ribs which loop across the flank and converge at the umbilical margin. The upper Santonian to lower Campanian forms have no tubercles. The adapical collars are bullate on the venter in some microconchs. Finally, a biconcave constriction, which is in close proximity to the last normal constriction, paired lappets, and a rostrum appear at the aperture. The lappets are simple, tapering, and 2-5 mm long.

Discussion.—UMUT. MM7623a (Figures 4-7, 4-8) and MM7623b, which have a depressed body chamber (=larger B/H ratio; Figure 13), were previously assigned to Y. kotoi by Matsumoto (1955, p. 152, figs. 12, 13). However, these can be discriminated from Y. kotoi by irregular, less extensive tuberculation (about 160° in a volution), and there are many intermediates between depressed forms and typical "jimboi."

Therefore, these can be included in the variation of the present species $\langle m \rangle$.

Y. ishikawai is very closely related to Coniacian Kossmaticeras theobaldianum paucicostatum Matsumoto, 1955 $\langle M \rangle$ and Yokoyamaoceras kotoi (Jimbo, 1894) or Y. minimum Matsumoto, 1956 $\langle m \rangle$ in many respects. The species is, however, discriminated from such Coniacian forms by a more compressed shell form, finer, weaker ribbing $\langle M, m \rangle$, and more irregular tuberculation $\langle m \rangle$. The macroconch of this species also resembles the possible descendent Kitchinites (Kitchinites), particularly K. (K.) brevicostatus (Marshall) from the upper Campanian to Maastrichtian of the Mata Series, New Zealand in possessing fine, flexuous prorsiradiate ribbing (Henderson, 1970, p. 32, pl. 13, fig. 4). The latter is, however, much more compressed than the present species.

In addition, "Neopuzosia matsumotoi Collignon, 1961" from the Coniacian of Madagascar (Collignon, 1961, p. 54, pl. 23, fig. 1) should be rather regarded as a true puzosiine, Mesopuzosia as already stated by Howarth (1965) and Matsumoto (1988), because it never has double collar ribs.

Occurrence.—From the lower Santonian to lower Campanian in Hokkaido, Sakhalin, Koryak-Kamchatka, and British Columbia, California, and France. In Hokkaido and Sakhalin, tuberculate microconchs (="Y. *jimboi*") are stratigraphically confined to the main part of the *Inoceramus* (*Inoceramus*) *amakusensis* Zone in the lower Santonian. Nontuberculate microconchs (="N. haboroensis") are succeeded stratigraphically by tuberculate ones in the uppermost lower Santonian to lower Campanian (= uppermost part of I. (I.) amakusensis Zone, and I. (*Platyceramus*) japonicus and I. (Sphenoceramus) schmidti Zones).

Macroconch $\langle M \rangle$ (="*N. japonica*") also occurs from the Santonian to lower Campanian in British Columbia and Washington (Haggart and Ward, 1989). Tuberculate microconch $\langle m \rangle$ (="Y. *jimboi*") is only known from the lower Campanian in France (Kennedy, 1986).

References

- Alabushev, A.I., and Alabusheva, A.B., 1988: Dimorphism in the Late Cretaceous ammonite Yokoyamaoceras jimboi Matsumoto. Akademiya Nauk USSR, SVKNII, Far East Department, p. 1-17. (in Russian)
- Bando, Y., Sato, T., and Matsumoto T., 1987: Palaeobiogeography of the Mesozoic Ammonoidea, with special reference to Asia and the Pacific. In, Taira, A. and Tashiro, M. eds., Historical Biogeography and Plate Tectonic Evolution of Japan and Eastern Asia. p. 65-95. Terrapub, Tokyo.
- Callomon, J.H., 1955: The ammonite succession in the Lower Oxford Clay and Kellaways Beds at Kidlington, Oxfordshire, and the zones of the Callovian Stage. *Phil. Trans., Roy. Soc. London, Ser. B,* vol. 239, p. 215-264.
- —, 1963: Sexual dimorphism in Jurassic ammonites. Trans. Leicester Lit. Phil. Soc., vol. 57, p. 21-56, pl. 1.
- —, 1969: Dimorphism in Jurassic amonites: Some reflections. In, Westermann, G.E.G. ed., Sexual dimorphism in fossil Metazoa and taxonomic implications, p. 111-125., International Union of Geological Sciences, Ser. A, no. 1. E. Schweizerbart'sche Verlagsbuchhandlung, Stuttgart.
- —, 1981: Dimorphism in ammonoids. In, Senior, J.R. and House, M.R. eds., The Ammonoidea, p. 257-273. Systematic Association Special Vol. 18, Academic Press, London.
- —, 1985: The evolution of the Jurassic ammonite family Cardioceratidae. Spec. Pap. Palaeont., vol. 33, p. 49-90, pls. 1-4.
- Cobban, W.A., 1969: The late Cretaceous ammonites *Scaphites leei* Reeside and *Scaphites hippocrepis* (DeKay) in the Western Interior of the United States. U.S. Geol. Surv., Prof. Paper 619, p. 1-29, 5 pls.
- Collignon, M., 1955: Ammonites néocrétacées du Menabe (Madagascar), 3.-Les Kossmaticeratidae. Annls. géol. Serv. Mines, Madagascar, vol. 22, p. 1-54, 12 pls.
- —, 1961: Ammonites néocrétacées du Menabe (Madagascar), 7.-Les Desmoceratidae. Annls. géol. Madagascar, vol. 31, p. 1-115, 32 pls.
- Davis, R.A., Furnish, W.M., and Glenister, B.F., 1969: Mature modification and dimorphism in Late Paleozoic ammonoids. In, Westermann,

G.E.G. ed., Sexual dimorphism in fossil Metazoa and taxonomic implications, p. 101-110, pls. 2-5. International Union of Geological Sciences, Ser. A, no. 1. E. Schweizerbart'sche Verlagsbuchhandlung, Stuttgart.

- Forbes, E., 1846: Report on the fossil Invertebrata from Southern India, collected by Mr. Kaye and Mr. Cunliffe. *Trans. Geol. Soc. London, Ser. 2*, vol. 7, p. 97-174, pls. 7-19.
- Geological Survey of Hokkaido, 1980: Explanatory text of geological map of Hokkaido (1/ 600,000). 113 pp., 1 map. (in Japanese)
- Haggart, J.W., and Ward, P.D., 1989: New Nanaimo Group ammonites (Cretaceous, Sanotonian-Campanian) from British Columbia and Washington State. Jour. Paleont., vol. 63, p. 218-227.
- Henderson, R.A., 1970: Ammonoidea from the Mata Series (Santonian-Maastrichtian) of New Zealand. Spec. Pap. Palaeont., vol. 6, p. 1-82, 15 pls.
- Howarth, M.K., 1965: Cretaceous ammonites and nautiloids from Angola. *Bull. British Mus. Nat. Hist., Geol.*, vol. 10, p. 337-412, pls. 1-13.
- Jimbo, K., 1894: Beiträge zur Kenntniss der Fauna der Kreideformation von Hokkaido. Paläont. Abhandl., N. F., Ser. 2, no. 3, p. 1-48, 9 pls.
- Kennedy, W.J. 1986 : Campanian and Maastrichtian ammonites from northern Aquitaine, France. *Spec. Pap. Palaeont.*, vol. 36, p. 1–145, 23 pls.
- and Cobban, W.A., 1976: Aspects of ammonite biology, biogeography, and biostratigraphy. *Ibid.*, vol. 17, p. 1-94, 11 pls.
- and Klinger, H.C., 1985: Cretaceous faunas from Zululand and Natal, South Africa: the ammonite family Kossmaticeratidae Spath, 1922. Annls. S. Afr. Mus., vol. 95, no. 5, p. 165-231.
- and Wright, C.W., 1983: Ammonites polyopsis Dujardin, 1837 and the Cretaceous ammonite family Placenticeratidae Hyatt, 1900. Palaeontology, vol. 26, p. 855-873, pls. 85-87.
- and —, 1985: Evolutionary patterns in Late Cretaceous ammonites. Spec. Pap. Palaeont., vol. 33, p. 131-143.
- —, —, and Klinger, H.C., 1979: Cretaceous faunas from Zululand and Natal, South Africa: a new genus and species of tuberculate desmoceratacean ammonite from the Mzinene Formation (Albian). Annls. S. Afr. Mus., vol. 78, p. 29-38.
- (Albian). Annls. S. Afr. Mus., vol. 78, p. 29-38.
 Kossmat, F., 1897: Untersuchungen über die Südindische Kreideformation. Beitr. Paläont. Geol. Öst.-Ung., vol. 1, p. 1-46, 8 pls.
- Lehmann, U., 1966: Dimorphismus bei Ammoniten der Ahrensburger Lias-Geschiebe. *Paläont. Zeitschr.*, vol. 40, p. 26-55.
- Macellari, C.E., 1986.: Late Campanian-Maastrichtian ammonite fauna from Seymour Island (Antarctic Peninsula). *Paleont. Soc.*

Mem., vol. 18, p. 1-55.

- Maeda, H., 1987: Taphonomy of ammonites from the Cretaceous Yezo Group in the Tappu area, northwestern Hokkaido, Japan. Trans. Proc. Palaeont. Soc. Japan, N.S., no. 148, p. 285-305.
- —, 1991: Sheltered preservation: a peculiar mode of ammonite occurrence in the Cretaceous Yezo Group, Hokkaido, north Japan. *Lethaia*, vol. 24, p. 69-82.
- Makowski, H., 1963 : Problem of sexual dimorphism in ammonites. *Palaeont. Pol.*, vol. 12., p. 1–92, 20 pls.
- Matsumoto, T., 1942: Fundamentals in the Cretaceous stratigraphy of Japan, Part 1. Mem. Fac. Sci., Kyushu Imp. Univ., Ser. D, vol. 1, p. 129-280, pls. 5-20.
- ---- eds., 1954a: The Cretaceous System in the Japanese Islands. 324 pp., 20 pls. Japan Society for the Promotion of Science.
- —, 1954b: Family Puzosiidae from Hokkaido and Saghalien. Mem. Fac. Sci., Kyushu Univ., Ser. D, vol. 5, p. 69-118, pls. 9-23.
- —, 1955: Family Kossmaticeratidae from Hokkaido and Saghalien. Japan. Jour. Geol. Geogr., vol. 26, p. 115-164, pls. 8-10.
- —, 1956: Further notes on the Kossmaticeratids from Hokkaido. *Ibid.*, vol. 27, p. 173-187, pls. 14-16.
- —, ed., 1963: A survey of the fossils from Japan illustrated in classical monographs (Primarily a nomenclatorial revision). Palaeont. Soc. Japan, 25 th Anniv. Vol., 1963, 57 pp., 68 pls. Tokyo.
- ----, 1981: Ammonoids from Japan 9. Atlas of Japanese Fossils, no. 5, 6 pls. (in Japanese)
- (compilation), 1988 : A monograph of the Puzosiidae (Ammonoidea) from the Cretaceous of Hokkaido. *Palaeont. Soc. Japan, Spec. Papers*, no. 30, 179 p.
- (compilation), 1991: The Mid-Cretaceous ammonites of the Family Kossmaticeratidae from Japan. *Ibid.*, no. 33, 143 p., 31 pls.
- —, Muramoto, T., and Inoma, A., 1972: Two small desmoceratid ammonites from Hokkaido. *Trans. Proc. Palaeont. Soc. Japan, N.S.*, no. 87, p. 377-394, pl. 47.
- Nullo, G.B., De Nullo, F., and Proserpio, C., 1980: Santoniano-Campaniano estatigrafia y contenido ammontifero Cuena austral. Assoc. Geol. Argentina, Revista, vol. 35, p. 467-493, pls. 1-5.
- Obata, I., Futakami, M., Kawashita, Y., and Takahashi, T., 1978: Apertural features in some Cretaceous ammonites form Hokkaido. Bull. Natn. Sci. Mus., Tokyo, Ser. C, vol. 4, p. 139-155, pls. 1-3.
- Okada, H., 1979: The geology of Hokkaido and its plate tectonics. *Earth Monthly*, vol. 1, p. 869-877. (*in Japanese*)

- —, 1983: Collision orogenesis and sedimentation in Hokkaido, Japan. In, Hashimoto, M. and Uyeda, S. eds., Accretion tectonics in the Circum-Pacific Regions, p. 91-105. Terrapub, Tokyo.
- Olivero, E.B., 1984 : Nuevos ammonites campanianos de la Isla James Ross, Antartica. *Ameghiniana*, vol. 21, p. 53-84, pls. 1-6.
- Palframan, D.F., 1966: Variation and ontogeny of some Oxford Clay ammonites: *Taramelliceras richei* (de Loriol) and *Creniceras renggeri* (Oppel), from Woodham, Buckinghamshire. *Palaenotology*, vol. 9, p. 290-311, pls. 48-52.
- —, 1967: Variation and ontogeny of some Oxford Clay ammonites: Distichoceras bicostatum (Stahl) and Horioceras baugieri (d'Orbigny), from England. Ibid., vol. 10, p. 60-94, pls. 9-13.
- Reyment, R.A., 1988: Does sexual dimorphism occur in Upper Cretaceous ammonites? Senckenbergiana Lethaea, vol. 69, p. 109-119, pl. 1.
- Spath, L.F., 1922 : On the Senonian ammonite fauna of Pondoland. Trans. Roy. Soc. S. Africa, vol. 10, p. 113-147, pls. 5-9.
- Tanabe, K., 1977a: Functional evolution of Otoscaphites puerculus (Jimbo) and Scaphites planus (Yabe), Upper Cretaceous ammonites. Mem. Fac. Sci., Kyushu Univ., Ser. D, vol. 23, p. 367-407, pls. 62-64.
- —, 1977b: Mid-Cretaceous scaphitid ammonites from Hokkaido. Palaeont. Soc. Japan, Spec. Papers, no. 21, p. 11-22, pl. 1.
- and Shigeta, Y., 1987: Ontogenetic shell variation and streamlining of some Cretaceous ammonites. *Trans. Proc. Palaeont. Soc. Japan, N.S.*, no. 147, p. 165-179.
- Tanaka, K., 1963: A study on the Cretaceous sedimentation in Hokkaido, Japan. Geol. Surv. Japan, Rep., no. 197, 119 p., 3 pls.
- Vereshchagin, V.N., Kinasov, V.P., Paraketsov, K.V., and Terekhova, G.P., 1965: Field atlas of the Cretaceous fauna from northeast USSR. 66 p., 74 pls. National Industrial Geologic Commission, Magadan. (in Russian)

- Westermann, G.E.G., 1964: Sexual-Dimorphismus bei Ammonoideen und seine Bedeutung für die Taxionomie der Otoitidae (einschliesslich Sphaeroceratinae; Ammonitina, M-Jura). Palaeontographica, Ser. A, vol. 124, p. 33-73.
- ed., 1969: Sexual dimorphism in fossil Metazoa and taxonomic implications. 251 p., International Union of Geological Sciences, Ser. A, no. 1, E. Schweizerbart'sche Verlagsbuchhandlung, Stuttgart.
- Wright, C.W., 1957: Mesozoic Ammonoidea, L80-437. In, Moore, R.C. ed., Treatise on Invertebrate Paleontology, Part L, Mollusca 4, Cephalopoda-Ammonoidea. Univ. Kansas Press and Geol. Soc. America, Colorado.
- —, 1981: Cretaceous Ammonoidea. p. 157-174. In, Senior, J.R. and House, M.R. eds., The Ammonoidea. Systematic Association Special Vol. 18, Academic Press, London.
- and Kennedy, W.J., 1984: A monograph of the Ammonoidea of the Lower Chalk. *Palaeontogr. Soc. Monograph*, 126 p., 40 pls.
- and Matsumoto, T., 1954: Some doubtful Cretaceous ammonite genera from Japan and Saghalien. *Mem. Fac. Sci., Kyushu Univ., Ser. D*, vol. 4, p. 107-134, pls. 7, 8.
- Yabe, H., 1927: Cretaceous stratigraphy of the Japanese Islands. Sci. Rep., Tohoku Imp. Univ., Ser. 2, vol. 11, p. 27-100, pls. 3-9.
- Yokoyama, M., 1890: Versteinerungen aus der japanischen Kreide. *Palaeontographica*, vol. 36, p. 159-202, pls. 18-25.
- Zakharov, Y.D., Grabovskaya, V.S., and Kakishevich, T.G., 1984: Succession of the Late Cretaceous marine assemblages in south Sakhalin and its climatic characteristics in the northwestern Pacific. In "Systematics and evolution of invertebrates in the Far East," p. 41-90, pls. 9-15. Institute of Biology and Pedology, Far East Science Center, Akademiya Nauka, Vladivostok. (in Russian)
- Zittel, K.A., 1895: Grundzüge der Paläontologie (Paläozoologie). 972 p., München und Leipzig.

Abeshinai 安平志内, Bibai 美唄, Embetsu 遠別, Haboro 羽幌, Hobetsu 穂別, Hokkaido 北海道, Ikushumbetsu 幾春別, Kaminosawa 上の沢, Kikume(n)zawa 菊面沢, Kotambetsu 古丹別, Kumaoizawa 熊追沢, Manji 万字, Miginosawa 右の沢, Mikasa 三笠, Naibuchi 内 淵, Obira 小平, Obirashibe オビラシベ, Oyubari 大夕張, Satonosawa 佐藤の沢, Tannosawa 炭の沢, Tappu 達布, Teshio 天塩, Urakawa 浦河, Yezo 蝦夷, Yubari 夕張.

白亜紀後期の偽プゾシア類アンモナイト, Yokoyamaoceras Wright and Matsumoto, 1954 および Neopuzosia Matsumoto, 1954 の二型現象:北海道やサハリンのサントニアン ~カンパニアン階下部から同所的に産する "Neopuzosia ishikawai," "N. japonica," "N. haboroensis" (プゾシア亜科) と, "Yokoyamaoceras jimboi" (コスマティセラス科) の 4 形態種について,集団標本に基づき分類を再検討した.その結果, "4種"は形態変異の幅 が広く、今まで重視されてきた肋強度やイボの発現等の形質が分類基準に使えないこと; さらに、1)同所的な産出、2) 胚殻からの殻成長の酷似、3) 成熟の特徴などから"4種"は 同一種内の二型である可能性が高いことがわかった。すなわち前2者がマクロコンク、後 2者がミクロコンクで、すべて単一の生物種 Yokoyamaoceras ishikawai (Jimbo) として修 正定義される。また個体成長、特にヘソの成長様式は、Y. ishikawai がプゾシア起源ではな く、コスマティセラス科に属することを強く示唆する。したがって、二型の系列はチュー ロニアン~コニアシアン階の Kossmaticeras と Yokoyamaoceras に遡ると考えられる。本 種と Mesopuzosia との外見的な類似は収斂である。

PROCEEDINGS OF THE PALAEONTOLOGICAL SOCIETY OF JAPAN

日本古生物学会 1993 年年会・総会

日本古生物学会 1993 年年会・総会が,1月 29-31 日に 筑波大学で開催された (参加者 229 名).

シンポジウム

「実験古生物学 ― 現代によみがえる化石 ―」
世話人:北里 洋・大野照文・松岡數充
シンポジウム開催の趣旨
放散虫の飼育実験から何がわかるのか — 殻の役割につ
いての考察 ―
松岡 篤
コメント・・・・・北里 洋
Morphogenetic programming, a useful tool for under-
standing nature of organisms, exemplified by recent
and fossil foraminiferaJohann Hohenegger
原始地球環境下での有機物生成と生命の起源
化石生物の運動東 昭
コメント濱田隆士・舘野聡子・鈴木直極
コケムシの平面群体パターンに関する数理的解析
中島久男
コメント郡司幸夫・中村隆志
古生物学的,形態学的,および分子系統学的情報の統合
による進化生物学の新展開
小澤智生・林 誠司・岡本健児
パネル討論 (実験古生物学の展望と将来像)
特別講演

海底洞窟と古生物学・・・・・・・・・・・・・・・・・・・・・・・・・・・・・・・・・・・加速	頁友	富
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会長講演

カキの軽量構造・	- その形成様式と適応的意義
	••••••••••••••••••••••••••••••••••••••

個人講演

北海道東部網走市能取	半島付近の新第三系珪藻層序
南中国の貴州・広西地	域からの後期古生代放散虫化石
······八尾 昭·	于 浩・桑原希世子・安 泰庠

Some Cretaceous Radiolaria from Palawan, Philippines
······Fe P. Tumanda • Yolanda Maac-Aguilar
Cycladophora davisiana (放散虫) の起源について
本山 功
タイ国東南部から産する中・古生代放散虫の産出とその
意義指田勝男・安達修子・Nikorn Nakornsri・
Apsorn Amponmaha
新潟県青海石火岩石炭系下一上部境界付近の徴化石層
· 序···································
帝釈石火岩層群の中 — 上部石炭糸紡錘虫生層序
・・・・・・・・・・・上野勝美・水野嘉宏
秋吉石灰岩層群 (岩永台南部地域) のコノドント群集に
ついて谷川拓也・猪郷久治
スピッツベルゲン産上部石尿糸及ひベルム糸コノドント
猪雞久治・中村耕二・沖村雄二
備地層 (テポン糸) から産出した奇妙な装飾をもったコ
ノドントの新属について猪郷久義・安達修子
上原市中新世備北層群からの貝化石群集の垂直変化 ローム
長野県信州新町周辺の鮮新世貝化石群集
長野県北部の柵層産 Chlamys 禹(二枚貝)について
中新世 Mytuus の時空分布 一 予祭と今後の課題 一
・・・・・・・・・・・・・・・・・・・・・・・・・・・・・・・・・・・・・
省川県土圧層研より産出した貝化石研集 佐茹四美 専士 法
和歌山県田辺唐研の只化石研集十河 宗・奥村 宿 山口県口墨屋郡芸波三里屋にいたてあたたたルズ
山口県口直眉研與波戸糸眉における軟体動物化石
吊客灰田南部の下部中新統们平唐の動植物化石群の変遷
本邦利生11.北刀琴市米只類11.石矸の成立週程に関する ^一
考祭小型尿意四即 四生の「脚只な豆玉只の別をくたこの後畑様な」ズェル
現生の十脚日超尾亜日の外クチクラの飯細構造と石灰化
についし四村はるみ・呂阿仔一・女達修士 田美かりてたよこーギンロの日本ト株佐(たのの) デ
回有かりみにアミマガンソの足术と構造 (その2) 一 石 広気日火の SEM 細索
ー (以只) () () () () () () () () ()
风

現生および化石におけるヤドカリの宿貝内部に共生する
マガキ・・・・田中利雄
穿孔性二枚貝カモメガイ類の形態の変異と岩石の硬さと
の関係伊藤泰弘
現生及び化石硬組織における DNA の解析とその古生物
学的応用更科 功
二枚貝マルスダレガイ科 (Veneridae, Bivalvia) の殻体
構造とコンキオリンのアミノ酸組成について
小笠原諸島のカタマイマイ類における変異の起源 — 異
種間交雑とモザイク進化千葉 聡
介形虫類の背甲にみられる異時性〜Leptocythere 亜科を
例として~「「」」の「」」の「」の「」の「」の「」の「」の「」の「」の「」の「」の「」の「
人工孵化個体の殻の酸素同位比から推定されるオウムガ
イ類の産卵場所と初期生活史
······Neil H. Landman • 棚部一成 • J. Kirk Cochran •
John M. Arnold
熊野灘の表層堆積物中の底生有孔虫大串健一
霞ヶ浦ボーリングの有孔虫からみた古鬼怒湾の環境変化
······西村 昭·斉藤文紀·井内美郎
東赤道太平洋 (ODP Site 852) における珪藻化石の集積
速度岩井雅夫 · ODP Leg 138 乗船研究員
石油公団貯留岩形成過程解析技術研究試料 — 宮古島沖
底質サンプル ― のコケムシによる堆積環境の解析
·····································
中期中新世シロウリガイコロニー産底生有孔虫群集
······秋元和實
タイ北部 Ban Sangao の下部石炭系から産出した Hetero-
phyllia (Anthozoa, Dividocorallia)
杦山哲男・長井孝一・Nikorn Nakornsri
青海石灰岩石炭系の堆積相と reef builder の変遷につい
て中澤 努
中期ペルム紀サンゴ礁における solenoporacean algaeの
産状 — 南部北上帯岩井崎石灰岩の例 —
町山栄章・川村寿郎
日中の上部石炭系より産出するアラトコンキド様二枚貝
について西田民雄・久間裕子
中国南部でのペルム紀四射サンゴ類の消滅様式
飛驒外縁帯のペルム系森部層より Monodiexodina の発
見田沢純一・対馬勝吉・長谷川美行
秋吉石灰岩,石灰~ペルム系境界における小型有孔虫類
の消長
蝦夷層群中の Cenomanian/Turonian 堺界付近の岩相お
よび浮遊性有孔虫生層序 — Oceanic Anoxic Event と
の関係・・・・・長谷川卓
Benthic Foraminifera from the type locality of the Jam-

buro Group, southern Balochistan, Pakistan.

Imdad Ali Brohi • Ritsuo Nomura
中部太平洋の沈水した海山上の白亜紀石灰岩一ODF
Leg 143 の成果
非能唐文•ODP Leg 143 垂船科学去一厅
非能尿文 ODI Log 145 米加科子名 内
東京都四部の上総信件人大部化石信がら進山した家化石 はまたず
について
トウョウゾウ (Stegodon orientalis) の頭蓋とその糸紙
的位置について三枝春生
瀬戸内海産イノシシ属 (Sus) 化石について
大島光春・大塚裕之
御船哺乳類(熊本県御船町産:上部セノマニアン)は食
虫類か有袋類か?瀬戸口烈司
中国甘粛省霊台県雷家河層の発掘 — ユーラシアおよひ
北アメリカの新生代後期哺乳類動物群と古環境の変遷
史に関する調査報告(予報)
计在天大一页一万级一加双字印。
武藤武可・二仅存主・彼叩兵八・ 一 一 一 一 一 一 一 一 一 一 一 一 一 一 一 一 一 一 一
示 示
中新統野島層群から齧歯類化石の産出(予報)
加藤敬史
千葉県富津市の上総層群長波層から産出した雌の大型シ
カ科頭蓋骨化石・・・・・高桑祐司
First discovery of amphylagine ochotonid from the Early
Holocene of Japan
Yukimitsu Tomita • Takahisa Goda
長野県松本市近郊の中新統別所累層から産出したトゲウ
オ科 (Gasterosteidae) 魚類大江文雄・小池伯-
横浜市の中部更新統長沼層産バンドウイルカ属化石
《《《····》中部史》和《《····》(》《《···························
「水の旧
ブジガの祖尤は本当にグマなのが
次城県金砂畑村の鮮新世久木層産海牛類化石について
······二階堂草信• 匊池方又
放散虫と共生生物の観察 — 平板状の Spumellarida 目に
ついて松岡 篤
放射虫の飼育実験 — Dictyocoryne truncatum の温度お
よび塩分濃度耐性松岡 篤・O. Roger Andersor
底生有孔虫はなぜ高いところに上がりたがるのか?
······北里 洋•武藤朝子
日本で最もよく知られている介形虫, ウミホタル — その
研究史と発光の准化生能学的音義
市町街口・山床 豆・ノョン グノーエ
用四本十日からの毎四番日の熟小ノンソホの個体先生
現生カカミガイ (二枚貝類) における体成長と性成熟の
関係の解析とその進化古生物学的広用佐藤慎-
光共生二枚貝におけるソフトボトム内生型からハードボ

トム毒生刑への生能シストのシナリオ
白亜紀後期の大型アンモナイト: Canadoceras koss-
<i>mati</i> のタフォノミー前田晴良・山崎洋介
異常券アンモナイトにみられるリトロバーサルフックの
形成機構と適応的音味
ウミュリ・ウミシダ類の対捕食考適応・腕の白切と腕の
分岐パターンの准化
自己言及システム:パラドクスとしての時間発展
連珠に見る自律的学習中村降志・郡司幸夫
局所規則と大域規則の矛盾が牛み出す臨界状態
山本督文
タコの迷路学習における慣れの問題森山 徹
テッポウエビと共生するハゼの行動にみられる可塑性
本邦中新統産 Terebralia について高橋宏和
与那国島の八重山層群に見られる牛痕化石群集
·····································
火山灰層に記録される古生態学的情報 — 与那国島八重
山層群の例・・・・・・・・・・・・・・・・・・・・・・・・・・・・・・・・・・・・
生痕化石 Schaubcylindrichnus の三次元構造および形成
者の摂食様式
堆積物中に潜む見えないウニの生痕化石金沢謙一
掛川層群大日層の貝殼集積層 ― その内部構造と起源 ―
·······間嶋隆一 • 本目貴史
急速な埋没に対する二枚貝の反応とタフォノミー:アサ
リの埋没実験から近藤康夫・伊与田律子
産状と殻形態からみた白亜紀二枚貝 Nanonavis 類の古
生態 — 特に Nanonavis brevis を中心として —
加納 学
北海道穂別地域の深牛砂岩層産イノセラムス種
Sphenoceramus hetonaianus について
松本達郎・利光誠一・野田雅之
北海道三笠市の中部蝦夷層群から発見されたスエモノガ
イ科二枚貝のコロニィ
蟹江康光・坂井民江・吉川幸観・高橋武美
三方湖の湖底堆積物における珪藻遺骸群集
内陸湖沼における珪藻の塩分耐性に関する新知見
パリノモルフ群集と堆積相からみた西九州における完新

世後半の古環境・・・・・・・・・・・・・・・・・・・・・・・・松岡數充	
松島湾における現生底生有孔虫群集 — 1960 年代の群集	
との比較を中心として ―	
底生有孔虫群集からみた東インド洋北部の海洋構造の変	
化	
······野村律夫	
日本海溝における浮遊性有孔虫殻の溶解実験…大塚忠道	
前期更新統大桑層中部に記録されたミランコビッチサイ	
クル北村晃寿・神谷隆宏・酒井英男・堀井雅恵	
塩原層群 (湖成層) の珪藻群集とラミナの縞状パターン	
高見沢志郎・中森 亨	
群集の力学系と古環境 ― 環境変化と群集変化が整合し	
ない解析結果の成因は何か ―山崎和仁	
大量絶滅と多様性パターンの数理解析千葉 聡	
兵庫県淡路島の和泉層群より発見された原始的オサガメ	
科 (ウミガメ上科; カメ目)平山 廉	
仙台市南縁,名取川沿いの網木層産貝形虫化石	
石崎国熙・藤原 治・入月俊明	
中部日本, 瑞浪地域の初期中新世介形虫矢島道子	
八代海の介形虫 <i>Sinocythere</i> sp湯本道明	
常磐地域の中新統九面層の模式地における有孔虫群集	
長谷川四郎・根本直樹・亀丸文秀	
Plagoniidae 科 (Nassellaria 亜目) の分類について	
舟川 哲	
筒型珪藻にみられる新しいタイプの殻壁細胞器官とその	
機能	
Rosiella 属 (珪藻) の系統と進化柳沢幸夫	
珪藻 Stephanopyxis 属の被殻の微細構造と分類	
·······芳賀正和	
日本および中国東北部産 Neozamites (Bennettitales) 2	
種孫 革・仲澤 隆・大花民子・木村達明	

ポスターセッション

大法郎,利米冠一。昭田毗马	海底洞察のこれ目籍、「オナー故」加超大喜
本 建即 • 利 元 誠一 • 野田 雅 之	一世は 一世に 一世 に 、 し 、 、 、 、 、 、 、 、 、 、 、 、 、 、 、 、 、
群から発見されたスエモノガ	上部白亜系姫浦層群から産出した "らせん状 coprolite"
	は腸の化石か?加納 学
井民江・吉川幸観・高橋武美	石灰質ナノプランクトン Gephyrocapsa 属の大西洋にお
る珪藻遺骸群集	ける現世と最終氷期の形態変化
鹿島 薫・松原 久	松岡裕美・B. Molfino・A. McIntyre
分耐性に関する新知見	Polyptychoceras vancouverensis (Whiteaves), 1879 \ltimes \sim
鹿島 薫・松原 久	いて — 北海道上部蝦夷層群産の Polyptychoceras 類
からみた西九州における完新	との比較 —早川浩司

Palaeontological Society of Japan (PSJ) Council Actions

During its meeting on January 28, 1993, the PSJ Council enacted the following changes to its membership.

New members elected :		
Naoko Egi,	Kiyofumi Hasegawa,	Masashi Hirano,
Takeo Ichimura,	Naoki Ikegami,	Yasuhiro Itoh,
Kazuya Kinoshita,	Katsuhiko Kishi,	Naoki Kitamura,
Takahisa Makiguchi,	Katsutomo Mano,	Tsuneo Nakajima,
Eiichi Nishimura,	Hiroshi Oguri,	Hirokazu Ozawa,
Robert M. Ross,	Kazuhisa Sasaki,	Shinichi Sato,
Manabu Sugisawa,	Kenshu Shimada,	Kazuo Tomita,
Kazuhito Yamasaki,	Keiji Yamasaki,	Tetsuji Yamasaki,
Katsuhiko Yoshida,	Atsushi Yoshino,	Ryuichiro Watanabe,
Jie Yu.		
New Fellows approved :		
Masao Futakami,	Yukio Gunji,	Hiroshi Hayakawa,
Yasufumi Iryu,	Akihiro Kano,	Yasuo Kondo,
Yoshikazu Noda,	Kenichi Saiki,	Takeshi Setoguchi,
Seiichi Suzuki,	Hitoshi Tanaka,	Yukio Yanagisawa.
Resigned members:		
(Ordinary members):		
Kunio Kanamori,	Hiroaki Kobayashi,	Mika Shigei,
Toshiaki Suyama,	Shuichi Yanai.	
Deceased members :		
(Fellows)		
Yoshihisa Ohta,	Susumu Matsushita.	

New Honarary members approved by the 1993 Annual Meeting of the Society held on 29, January, 1993.

Keiji Nakazawa, Katsura Oyama.

◎1993 年例会(第 142 回例会)は,大阪教育大学で 6 月 26 日, 27 日に開催されます。 ◎1994 年年会・総会は,1994 年 1 月 27~29 日に,国立科学博物館分館で開催の予定です。
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CONTENTS

TRANSACTIONS

948.	Kuniteru Matsumaru, Myint Thein and Yujiro Ogawa: Early Miocene	
	(Aquitanian) larger Foraminifera from the Shimizu Formation, Ashizuri	
	Cape, Kochi Prefecture, Shikoku, Japan	1
949.	Hisayoshi Igo, Katsumi Ueno and Katsuo Sashida: Lower Permian	
	fusulinaceans from Ban Phia, Changwat Loei, northeastern Thailand	15
950.	Kazuhiro Sugiyama: Skeletal structures of Lower and Middle Miocene	
	lophophaenids (Radiolaria) from central Japan.	44
951.	Li-Ming Zhao, Tamiko Ohana and Tatsuaki Kimura : A fossil population of	
	Ginkgo leaves from the Xingyuan Formation, Inner Mongolia.	73
952.	Haruyoshi Maeda: Dimorphism of Late Cretaceous false-puzosiine ammo-	
	nites, Yokoyamaoceras Wright and Matsumoto, 1954 and Neopuzosia Mat-	
	sumoto, 1954.	97
PROC	EEDINGS	129