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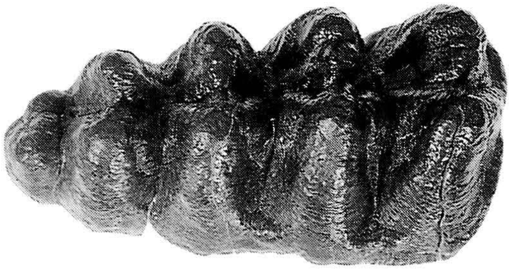

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The fossil on the cover is *Trilophodon sendaicus* Matsumoto, an extinct elephant, which was described from the Pliocene Tatsunokuchi Formation developed in the vicinity of Sendai, Northeast Honshu, Japan. (IGPS coll. cat no. 87759 (A), length about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

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926. ON THE EVOLUTIONARY CLASSIFICATION OF THE FAMILY LEPIDOCYCLINIDAE (FORAMINIFERIDA)*

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Abstract. The nepionic types of the microspheric juvenarium of almost all genera of the family Lepidocyclinidae are described, giving the framework of the evolution and classification of the family Lepidocyclinidae. From the viewpoint of the nepionic types, the development of periembryonic chambers of megalospheric forms, and the chronological occurrences of various taxa included in the family Lepidocyclinidae, all the lepidocyclinids are grouped into three lineages. As such, the family Lepidocyclinidae is thought to be heterogeneous in origin. The family Lepidocyclinidae comprises three subfamilies: Lepidocyclininae, Helicolepidininae, and Eulepidininae, the last one a new subfamily; these are briefly described.

Key words. Uniserial nepiont, reduced uniserial nepiont, asymmetric biserial nepiont, symmetric biserial nepiont, Lepidocyclinidae, Eulepidininae, n. subfamily.

Introduction

The origin and evolution of the family Lepidocyclinidae Scheffen, 1932 has been reported on by Barker and Grimsdale (1936), Tan (1936b), Rutten (1941), Hanzawa (1964, 1965), Matsumaru (1971a, b), Frost and Langenheim (1974), Sirotti (1982), Butterlin (1977, 1987), and others. The fundamental route of the evolution of lineages within the family Lepidocyclinidae has been described by Barker and Grimsdale (*op. cit.*). Their thesis has been developed by many authors as follows: Lower Eocene *Helicostegina gyralis* Barker and Grimsdale, which evolved from Upper Paleocene *Eoconuloides lopeztrigoi* (Palmer), equipped with counter septa, then evolved into Middle Eocene *Eulinderina guayabalensis* (Nuttall), which had only a single whorl of nepionic chambers followed by arcuate equatorial chambers in cyclical arrangement. *Eulinderina guayabalensis* intergraded with *E. semiradiata* Barker and Grimsdale, which had numerous equatorial chambers in cyclical arrangement. The latter gave rise to *Polylepidina chiapasensis* (Vaughan), with one or two principal auxiliary chambers. Moreover, *Helicostegina gyralis* Barker and Grimsdale was another ancestor to either Middle to Upper Eocene *Helicostegina polygyralis* (Barker), which had a longer and tightly coiled uniserial portion and a thickened spiral wall, or Upper Eocene to lowest Oligocene *Helicostegina paucispira* (Barker and Grimsdale), which had arcuate chambers in cyclical arrangement. According to Cole (1960), *Helicostegina polygyralis* (Barker) is a senior synonym of *Helicostegina soldadensis* Grimsdale, 1941 (= *Helicosteginoides* Caudri, 1975), but the present author does not accept Cole's views regarding the synonymy of *Helicostegina polygyralis*, and recognizes both *Helicostegina polygyralis* (Figure 8-1) and *H. soldadensis* (Figure 10-1—3). *Helicostegina polygyralis* (Barker), comprising various forms with different-

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length spiral chambers, evolved into *Helicolepidina spiralis* (Tobler), with one or two principal auxiliary chambers and radial stolons.

After the publication of Barker and Grimsdale (1936), Rutten (1941) thought that *Pseudolepidina* Barker and Grimsdale, 1937 could have arisen from *Helicostegina* Barker

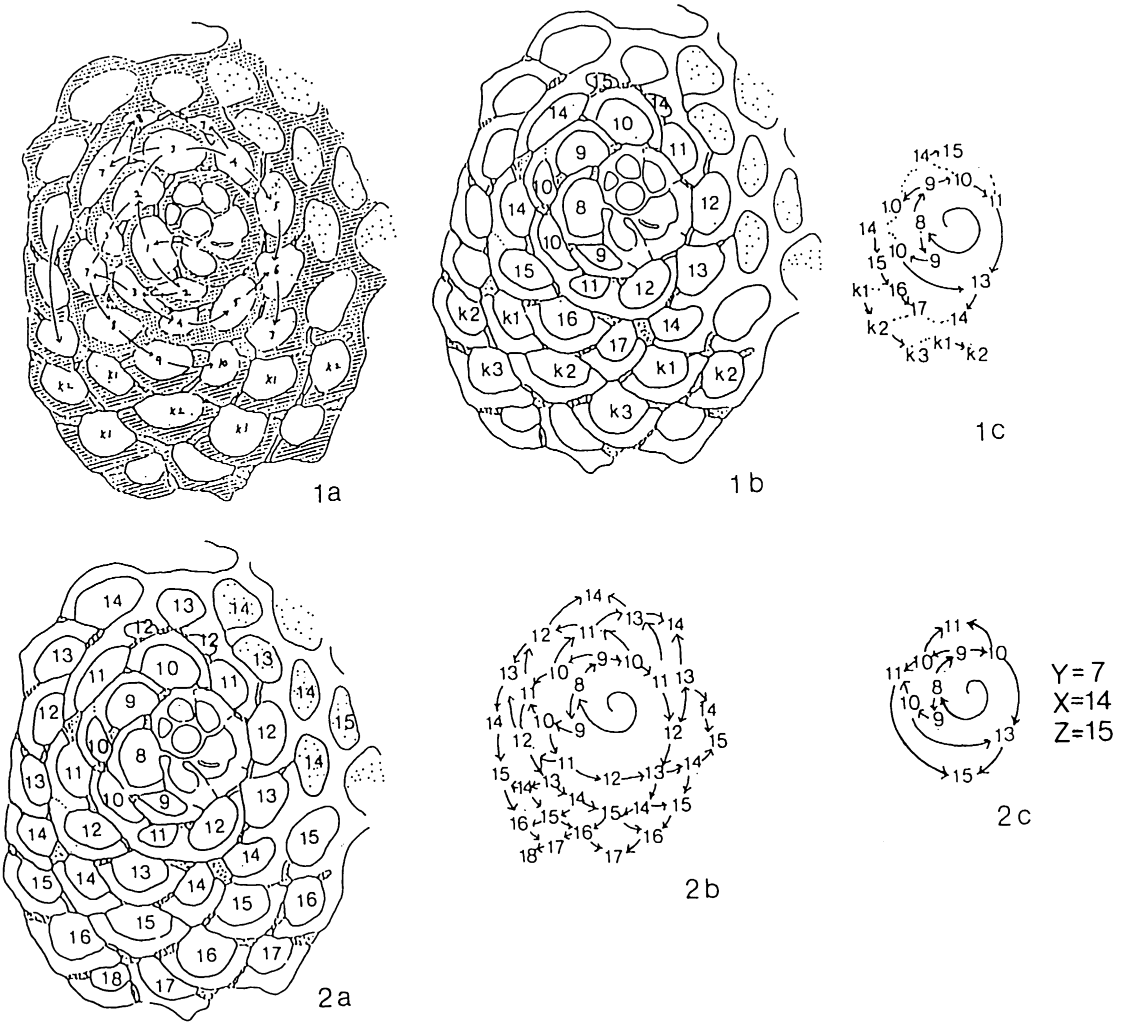

Figure 1. A drawing showing the ontogenetic change from spiral to concentric growth of microspheric *Lepidocyclina* (*Eulepidina*) *papulifera* Douvillé from Rembang, Java, Indonesia (Tan Sin Hok, 1934, fig. 4 ; 1a of Fig. 1). The numbering of spiral to concentric nepionic and postnepionic chambers, including the first chamber, proloculus (1b of Figure 1), and the schematic diagram of chamber budding formation of microspheric *L.* (*Eulepidina*) *papulifera* follows Tan's idea (1b-c of Figure 1). Chambers of the first spiral and several concentric cycles are easily shown by single lines. The lower three are an alternative interpretation by the author (2a-c of Figure 1). In 2b, the concentric growth is shown at the 14th budding stage. The fundamental chamber budding formation is relevantly shown at the lower right (2c of Figure 1). In order to explain the growth pattern, it is useful to distinguish some parameters. The number of spiral chambers with only one chamber forming the aperture is designated by Y (Y=7 in 2a-c of Figure 1). The total number of initial spirally coiled nepionic chambers, excluding the symmetric chamber, is designated by X (X=14 in 2a-c of Figure 1). There is the closing chamber or symmetrical chamber in the place where the initial spire meets the second spire. The position of the closing chamber is shown as Z (Z=15 in 2a-c of Figure 1).

and Grimsdale, 1936, while *Actinosiphon* Vaughan, 1929, *Triplalepidina* Vaughan and Cole, 1938, *Lepidocyclina* (*Lepidocyclina*) Gümbel, 1870, and *L.* (*Pliolepidina*) Douvillé, 1911 could have evolved from *L.* (*Polylepidina*) Vaughan, 1924. Frost and Langenheim (1974) considered that *Lepidocyclina* (*Polylepidina*) was an ancestor to *Pseudolepidina, Lepidocyclina* (*Lepidocyclina*), *L.* (*Nephrolepidina*) Douvillé, 1911, and *L.* (*Eulepidina*) Douvillé, 1911. According to Sirotti (1982), *Lepidocyclina mantelli* (Morton) and *Eulepidina ocalana* (Cushman), both of the subfamily Lepidocyclininae Scheffen, 1932, were considered to have derived from Upper Eocene *Lepidocyclina gubernacula* Cole, remarkably developing radial equatorial stolons lying on different planes. The latter evolved from *Lepidocyclina proteiformis* Vaughan. Also, it is noted that *Lepidocyclina proteiformis* derived from *Polylepidina chiapasensis* Vaughan, which evolved from *Eulinderina semiradiata* Barker and Grimsdale. Sirotti (*op. cit.*) also thought that *Nephrolepidina ecuadorensis* (Hofker) and *Helicolepidina spiralis* (Tobler), both of the subfamily Helicolepidininae Tan, 1936, evolved from *Helicostegina paucispira* Barker and Grimsdale, acquiring radial equatorial stolons lying on the same plane. This is based on Hofker's hypothesis (1968) of *Nephrolepidina* springing from *Helicostegina*.

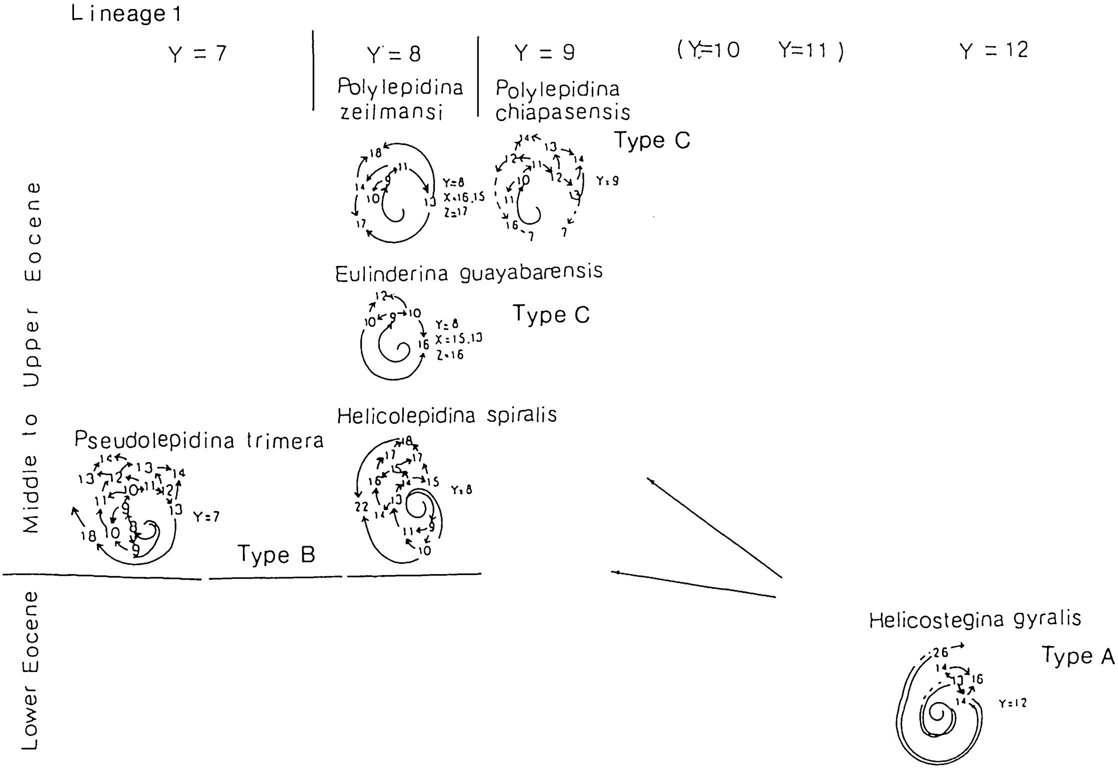

Figure 2. Schematic diagram of chamber budding formation of microspheric forms of *Helicostegina gyralis* Barker and Grimsdale (topotype, Sabaneta, Veracruz, Mexico, BM (NH) P39150), *Pseudolepidina trimera* Barker and Grimsdale (Adams, 1987, pl. 3, fig. 14), *Helicolepidina spiralis* (Tobler) (El Alto, NW Peru, BM (NH) P30248), *Eulinderina guayabalensis* (Nuttall) (Barker and Grimsdale, 1936, pl. 34, fig. 11), *Polylepidina zeilmansi* (Tan Sin Hok) (Tan Sin Hok, 1936a, pl. 1, fig. 8), and *Polylepidina chiapasensis* (Vaughan) (J. Butterlin's 1182 specimen, Corinto no. 1 well, 930-935(8), Mexico). These forms belong to lineage 1 of the Lepidocyclinidae.

Recently, Butterlin (1987) stated that *Lepidocyclina* (*Polylepidina*) was an ancestor to all the subgenera *Lepidocyclina, Eulepidina*, and *Nephrolepidina*. In the recent classification of the family Lepidocyclinidae, Adams (1987) removed the Paleocene genera *Actinosiphon* Vaughan, 1929 and *Orbitosiphon* Rao, 1940 from the family Lepidocyclinidae, placing the first genus in a new family, the Actinosiphonidae, while the other was included in the family Orbitoididae Schwager, 1876. The Middle Eocene *Pseudolepidina* was referred to the subfamily Helicolepidininae. However, in Loeblich and Tappan (1987), *Actinosiphon* and *Orbitosiphon*, as a synonym of the former, were referred to the subfamily Lepidorbitoidinae Vaughan, 1933, while *Pseudolepidina* was referred to the subfamily Lepidocyclininae.

Thus these differing opinions have caused considerable chaos around the question of the origin, evolution, and classification of the family Lepidocyclinidae. The author has had an alternative opinion on these problems and gives his considerations in this paper. Before proceeding to describe the family Lepidocyclinidae, some problems should be mentioned.

We should expect more abundant fossils of all the taxa of the family Lepidocyclinidae even though many authors have reported them. Unfortunately, we have never seen microspheric forms of *Actinosiphon* and *Orbitosiphon*, and no one has observed the upper Maastrichtian and Danian orbitoids that must straddle the Cretaceous/Tertiary boundary. Such gaps have to be bridged largely by speculation, and paleontological or biological interpretation is necessary. In particular, it is important to recognize the embryonic and nepionic (or periembryonic) types representing the megalospheric and microspheric forms of all the taxa of the family Lepidocyclinidae, and Cretaceous and Paleogene orbitoidal Foraminifera.

As far as we know to date, we have fortunately discovered the following Upper Cretaceous and Tertiary orbitoidal Foraminifera in the Indo-Pacific region (=Indo-Pacific of Figure 5): *Lepidorbitoides bisambergensis* (Jaeger), *L. minor* (Schlumberger), *L. socialis* (Leymerie), *Siderolites* ? sp., *Orbitocyclina* sp., *Orbitocyclinoides schencki* Brönnimann, *Pseudorbitoides* sp., *Sulcorbitoides* sp., *Sulcoperculina inaequalis* Ho, *S. cubensis* Palmer, *S. vermunti* Thiadens, *Actinosiphon tibetica* (Douvillé), *Orbitoclypeus suruaensis* (van der Vlerk), *O. mollucсana* (Henrici), *O. kimurai* Matsumaru, *Polylepidina zeilmansi* (Tan), *P. birmanica* Rao, *P. antillea* (Cushman), and *Helicostegina* cf. *paucispira* (Barker and Grimsdale) (Douvillé, 1916; Tan, 1936a; van der Vlerk, 1923; Davies and Pinfold, 1937; Henrici, 1934; Rao, 1942; Smout and Haque, 1956; Ho Yen *et al*., 1976; Hashimoto *et al*., 1978,

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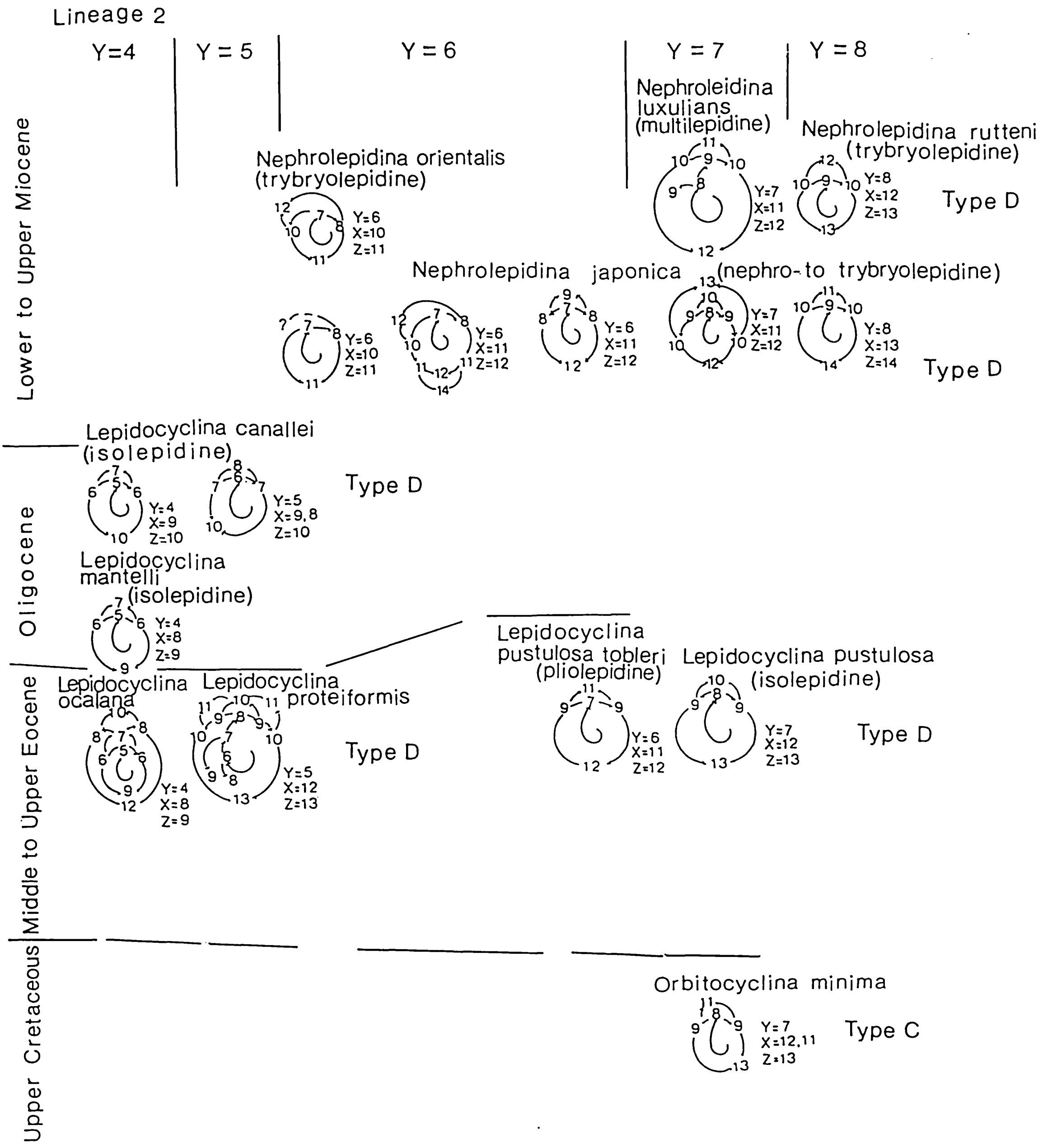
→ **Figure 3.** Schematic diagram of chamber budding formation of microspheric form of *Orbitocyclina minima* (Douvillé) (Gorsel, 1978, fig. 18), *Lepidocyclina ocalana* Cushman (Cole, 1941, pl. 13, fig. 6), *Lepidocyclina proteiformis* (Vaughan) (Tantoyuca, Veracruz, Mexico, BM (NH) P32-630), *Lepidocyclina tobleri* (Douvillé) (A. Sirotti's 63/3/8 specimen, Vistabella-Point, Trinidad), *Lepidocyclina pustulosa* Douvillé (Butterlin, 1971, pl. 2, fig. 8), *Lepidocyclina mantelli* (Morton) (Marianna Limestone, Little Stave Creek, Alabama, BM (NH) P47331), *Lepidocyclina canellei* Lemoine and Douvillé (left: A. Silvestri, ANFR 74-111 specimen, Cuba-Martinico; right: Cole, 1961, pl. 37, fig. 5), *Nephrolepidina japonica* (Yabe) (left to right: Topotype, Abuta Limestone (Matsumaru, 1969), Japan, slide 34-16; Ibid., slide 27; Kamiyokoze Formation, Une, Japan, slide 13; Saginosu Formation, Kuroya, Japan, slide 1; Saginosu Formation, Kimo, Japan, slide 32), *Nephrolepidina orientalis* (van der Vlerk) (Sarawak specimen, SK-2065), *Nephrolepidina luxulians* Tobler (Tabanio no. 1 well, 2,600-2,610 feet, Java sea) and *Nephrolepidina rutteni* (van der Vlerk) (Shimoshiroiwa Formation, Japan, SH-3, slide 5). The terms pliolepidine, isolepidine, nephrolepidine, trybliolepidine and multilepidine in parentheses have been properly understood as the important characters of the megalospheric nucleoconch of each species, and they have been of primary importance in generic or subgeneric classification. These forms belong to lineage 2 of the Lepidocyclinidae.

Premoli Silva and Brusa, 1981 ; Hashimoto and Matsumaru, 1984 ; Matsumaru and Kimura, 1989). Therefore, these foraminiferal genera or species from the Caribbean-Gulf coast of Mexico and Europe-Mediterranean regions (= America-Europe of Figure 5) existed in the Indo-Pacific region as endemic taxa, although no Eocene *Lepidocyclina, Pseudolepidina*, or *Helicolepidina* have as yet been discovered in this region.

Almost all of the forms referred to the family Lepidocyclinidae have an equatorial chamber layer and a lateral chamber layer superposing both above and below the for-



mer. The morphological characters of the embryonic apparatus and periembryonic spires accompanied by the development of a principal auxiliary chamber and adauxiliary chamber of the megalospheric form of this family have been regarded as being of main taxonomic importance. As such, the study of the microspheric form of the family Lepidocyclinidae has made little progress since Tan's research (1934-36, 1939).

The author studied the microspheric form of the family Lepidocyclinidae to obtain phylogenetic information about budding chamber formations; this information is drawn from the ontogenetic stages developed by the microspheric generation, because each form appears to recapitulate some of the important events in its phylogenetic history. Also, the author feels that the nepionic types give the framework of a natural classification. As a result of the present study, the origin of the family Lepidocyclinidae is thought to be heterogeneous, and all of the lepidocyclinids are grouped into three lineages according to the nepionic types of their microspheric form, although the morphological features of the embryonic and periembryonic chambers of the megalospheric form have to be added.

The present paper was read October 2, 1990 at the Fourth International Symposium on Benthic Foraminifera, BENTHOS '90, Sendai, Japan.

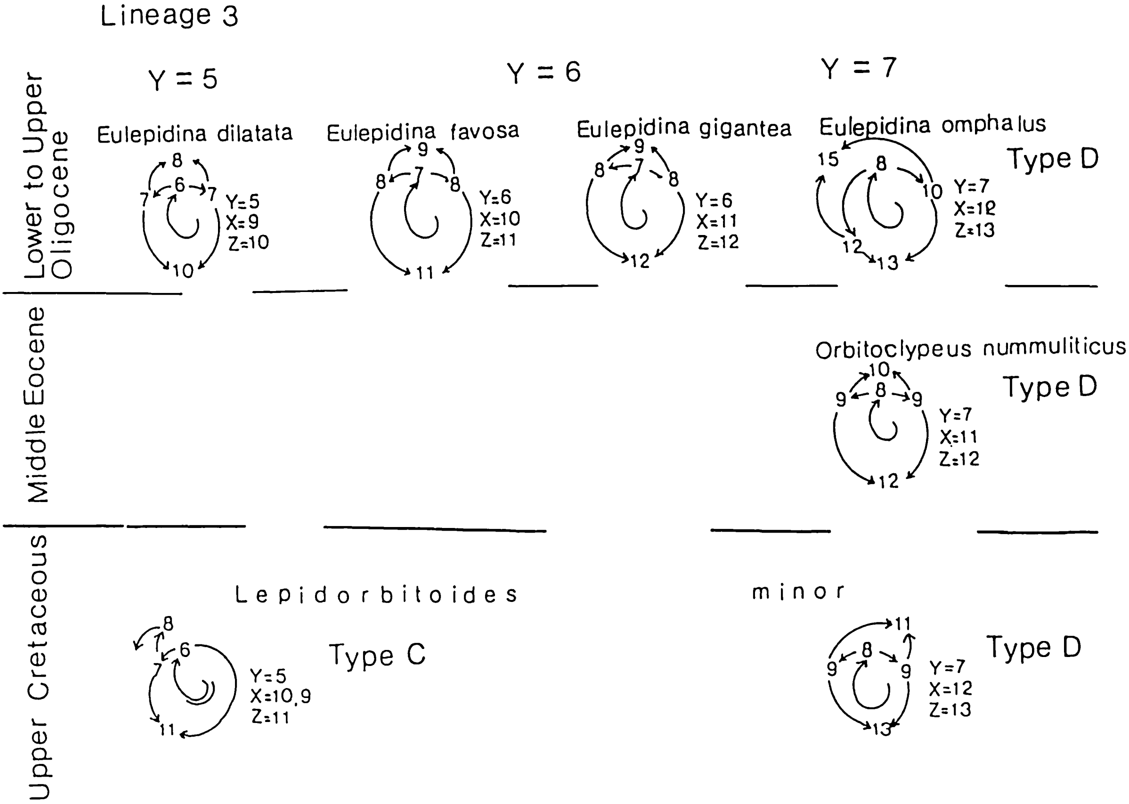


Figure 4. Schematic diagram of chamber budding formation of microspheric forms of *Lepidorbitoides minor* (Schlumberger) (left: MacGillavry, 1963, pl. 6, fig. 2; right: Gorsel, 1978, fig. 14 (c)), *Orbitoclypeus nummuliticus* (Gümbel) (Sirotti, 1987, pl. 2, fig. 3), *Eulepidina dilatata* (Michelotti) (A. Sirotti's specimen, Sciacca, Sicily), *Eulepidina favosa* (Cushman), 1919 (Huasteca Formation, Tamismolon, Veracruz, Mexico), *Eulepidina gigantea* (Martin) (Tan Sin Hok, 1935a, pl. 3, fig. 4) and *Eulepidina omphalus* (Tan Sin Hok) (*Ibid*, pl. 4, fig. 5). These forms belong to lineage 3 of the Lepidocyclinidae.

The nepionic types of each form of the family Lepidocyclinidae and three lineages

Tan (1934) interpreted the budding chamber formation of microspheric *Eulepidina papulifera* (Douvillé) as follows: as seen in the upper row (1a-c) of Figure 1, two nepionic spires, starting from a retrovert aperture recognized in the first chamber (1a of Figure 1 ; 8th chamber, including proloculus, recounted by the author, 1b-c), which developed from a single coil of periembryonic chamber, meet each other from opposite directions to make a symmetric chamber (6th chamber of Tan, 1a ; 13th chamber of the author's recounting, 1b-c). But Tan unfortunately presumed a wrong course for the successive budding spires that lead up to annularly disposed chambers (Figure 1, 1a-c). This made it difficult for later scientists to read and evaluate his study.

In contrast with Tan's interpretation, as seen in the lower row (2a-c) of Figure 1, the author found that the 14th chamber, counting from the proloculus, gave rise to annular growth. As a matter of fact, the 14th chamber is defined as the first annularly disposed chamber, and it is the frontal chamber of the first symmetrical chamber.

Generally speaking, the juvenarium or nepionic chambers of the microspheric form consist of a minute spherical proloculus and a number of succeeding chambers spirally disposed. The number of spirally disposed chamber is designated as Y. They are surrounded by a set of primary and secondary spires of nepionic chambers, and both spires join each other to make a symmetrical chamber. X is the number of chambers developed from a pair of primary and secondary spires, respectively. Z is designated for the first symmetrical chamber counting from the proloculus. Then these nepionic chambers are enclosed by the first annularly disposed chambers (14th chamber, 2a-c of Figure 1).

In all of the forms in the family Lepidocyclinidae and its relations, there are four different nepionic types:

A: uniserial nepiont (or nepionic chambers); as seen in Figure 2, the postnepiont buddings after the first whorl of nepionic chambers are observed at least in the 13th budding stage of *Helicostegina gyralis* Barker and Grimsdale. The uniserial nepiont group is found in *Helicostegina*. Spiral thickening of the primary coil can be seen.

B: reduced uniserial nepiont; the first whorl of nepionic spires became increasingly shortened. *Helicolepidina* and *Pseudolepidina* belong to this group (Figure 2). Thickening of the spiral wall can be seen.

C: asymmetric biserial nepiont; a pair of primary and secondary spires are introduced as a newly acquired character as shown by asymmetric spires of different length (Figures 2-4). *Orbitocyclina, Lepidorbitoides* (part), *Eulinderina, Polylepidina*, and *Lepidocyclina* (part) belong to this group.

D: symmetric biserial nepiont; both primary and secondary spires as shown by symmetric spires of equal length (Figures 3-4). *Lepidorbitoides, Lepidocyclina, Orbitoclypeus*, and *Eulepidina* belong to this group.

Lineage 1 has an ancestor, *Helicostegina gyralis* Barker and Grimsdale, possessing uniserial nepiont (type A). *Helicolepidina* (type B nepiont), *Pseudolepidina* (type B nepiont), *Eulinderina* (type C nepiont), and *Polylepidina* (type C nepiont) are known in lineage 1 (Figures 2, 5). The nepionic chambers of microspheric *Polylepidina chiapasensis* (Vaughan), the type species of *Polylepidina*, is unfortunately incompletely known, so that no exact determination is possible. Fortunately the author could regard the nepionic chambers of microspheric *Polylepidina zeilmansi* (Tan) as the type C nepiont. The four genera *Helicolepidina, Pseudolepidina, Eulinderina* and *Polylepidina* are supported by both the reduced number of uniserial nepionic chambers and the development of postnepionic spires (Figure 2). The microspheric form with an asymmetric biserial

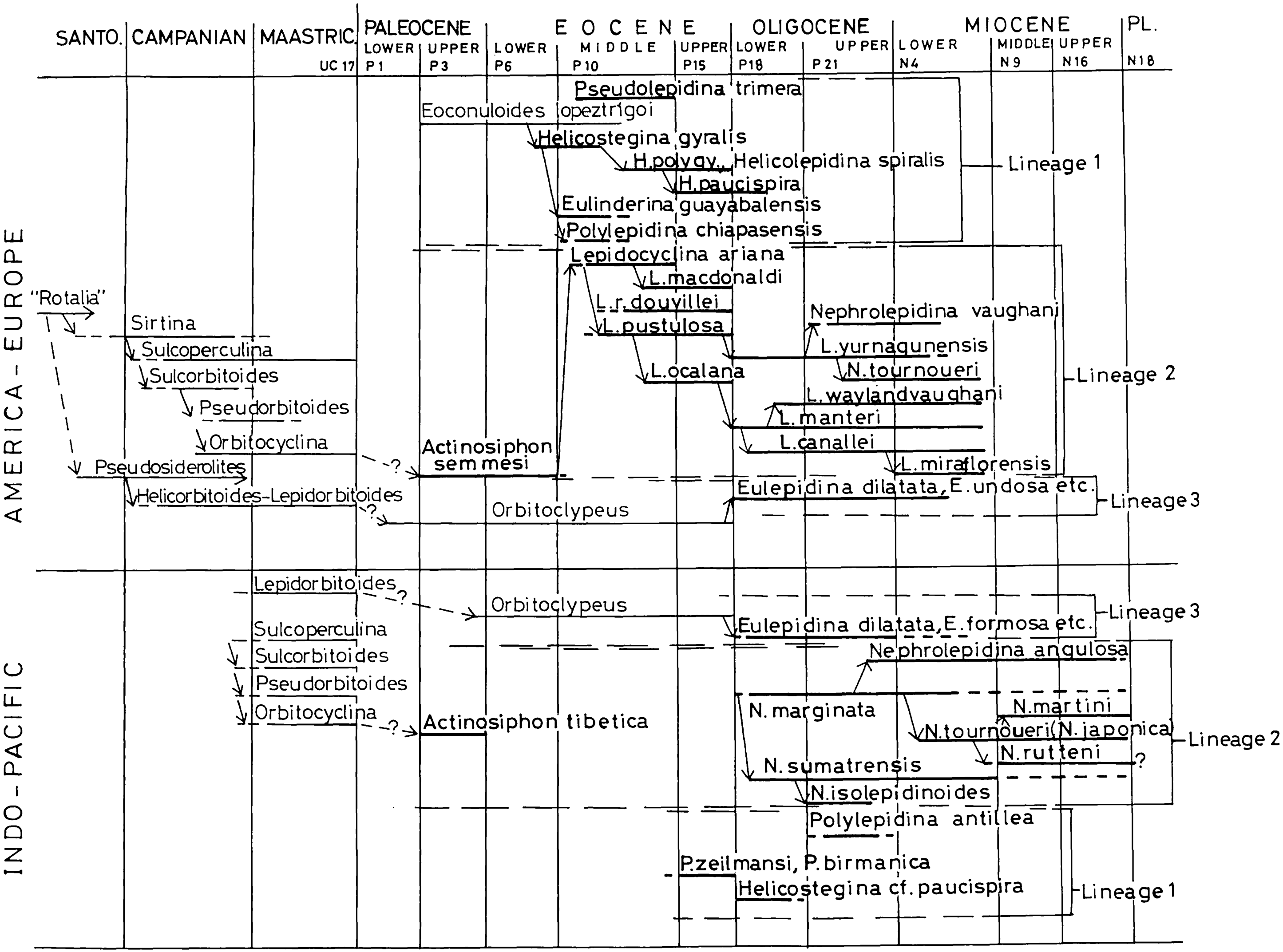


Figure 5. Pedigree chart showing the tentative evolution of the family Lepidocyclinidae (in bold), and Cretaceous and Paleogene orbitoidal foraminiferal genera and species (ordinary lettering) related to the Lepidocyclinidae.

nepiont (type C) originates from each form either with an uniserial nepiont (type A) or with a reduced uniserial nepiont (type B). According to Barker and Grimsdale (1936), *Eulinderina guayabalensis* (Nuttall) evolved from *Helicostegina gyralis* Barker and Grimsdale. As such, the form with type C nepiont originated from one with a type A nepiont.

Lineage 2 is most exhibited by the symmetric biserial nepiont (type D) of each microspheric form of both *Lepidocyclina* and *Nephrolepidina* (Figures 3, 5). The microspheric form of Upper Paleocene to upper Lower Eocene *Actinosiphon* is obscure, but that the microspheric *Actinosiphon* was a symmetric biserial nepiont can be inferred from the fact that the symmetric biserial nepiont, which was recognized in each form of Middle Eocene *Lepidocyclina pustulosa* Douvillé, *L. tobleri* (Douvillé), *L. ocalana* Cushman, and *L. proteiformis* Vaughan, could have evolved from the asymmetric biserial nepiont of Maastrichtian *Orbitocyclina minima* (Douvillé), on which Vaughan (1929a) established *Orbitocyclina* as a valid genus, and that *Actinosiphon* existed in the geologic time span between *Lepidocyclina*

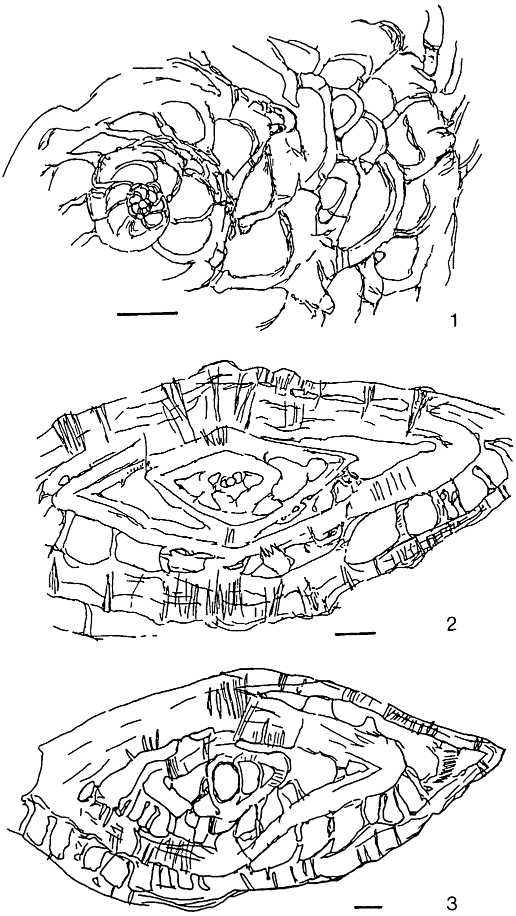


Figure 6. *Helicostegina gyralis* Barker and Grimsdale. **1**. Equatorial section of a microspheric form (BM (NH) P39150) equipped with counter septa, showing the uniserial nepiont, type A. **2-3**. Vertical sections of both microspheric and megalospheric forms (both of BM (NH) P33356). Scale bars = 100 microns.

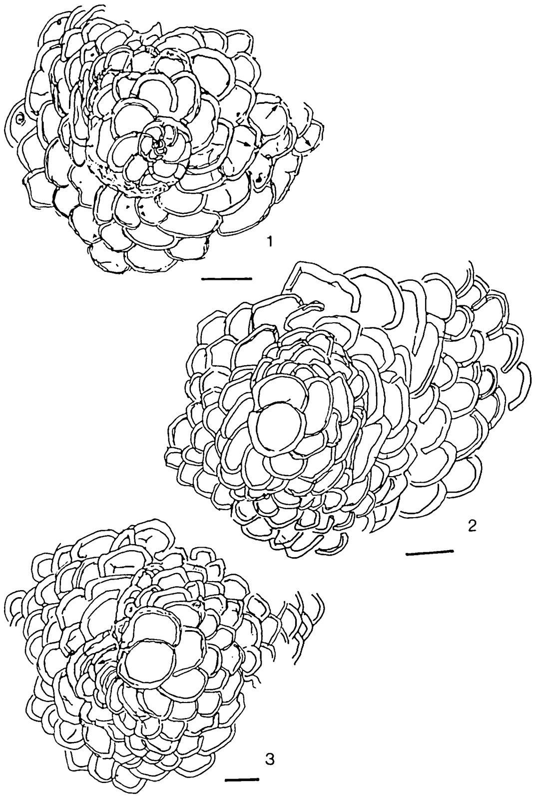
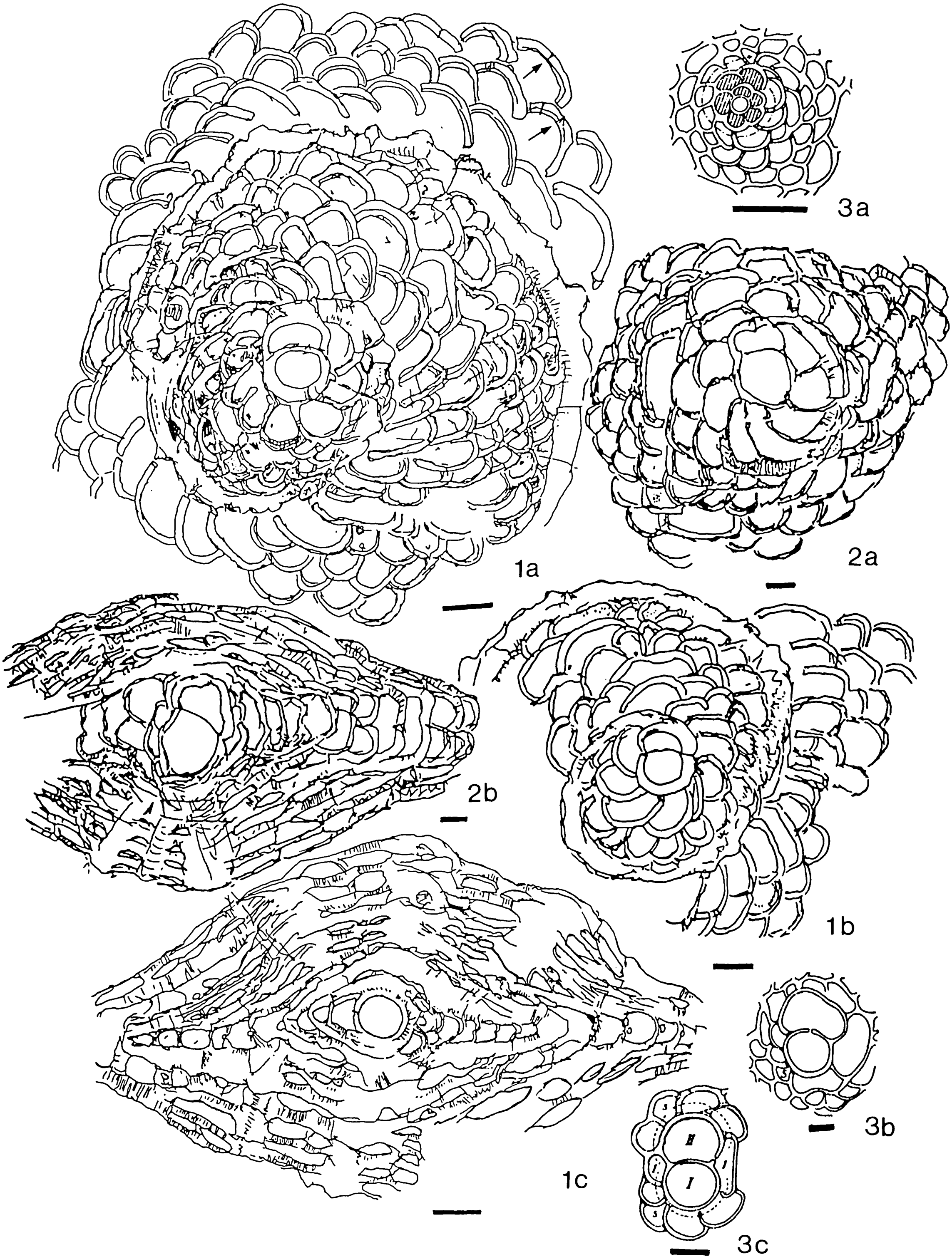


Figure 7. *Helicolepidina spiralis* (Tobler). **1-3**. Equatorial sections. **1**. A microspheric form (BM (NH) P302-48) with radial stolons, showing the reduced uniserial nepiont, type B. **2-3**. Megalospheric forms (**2**: BM (NH) P30247; **3**: BM (NH) P30249). Arrow showing a radial stolon. Scale bars = 100 microns.


3a
2a
1a
2b
1b
3b
II
I
5
3c
1c

and *Orbitocyclina*. Also, as stated later, the presence of radial stolons, recognized in equatorial chambers of *Orbitocyclina minima* (Douvillé), *Orbitocyclinoides schencki* Brönnimann, *Actinosiphon semmesi* Vaughan, *A. tibetica* (Douvillé), *Lepidocyclina ariana* Cole and Ponton, and *L. proteiformis* (Vaughan), can represent a bridge in the phylogenetic development from *Orbitocyclina*

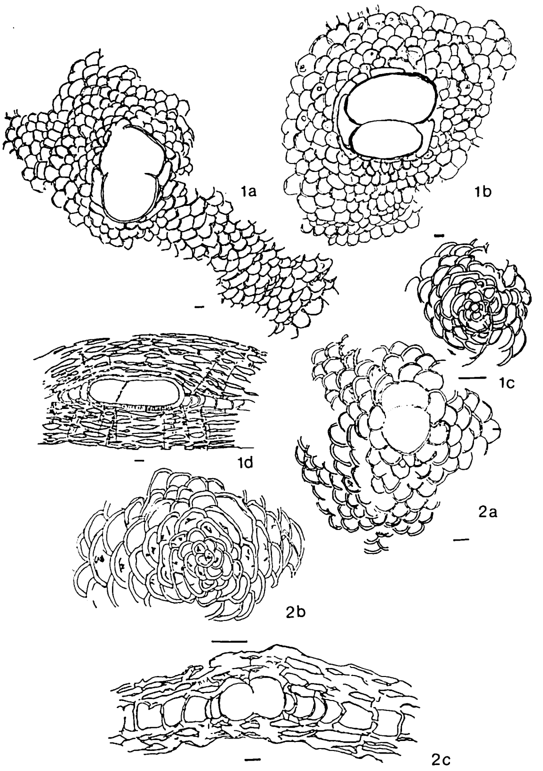


Figure 9. 1. *Lepidocyclina mantelli* (Morton). 1a-c. Equatorial sections of megalospheric and microspheric forms (**1a**: BM (NH) P47328; **1b**: BM (NH) P47326; **1c**: BM (NH) P47330). **1a-b.** Both megalospheric forms showing the development of adauxiliary chambers. **1c.** A microspheric form showing the symmetric biserial nepiont, type D. **1d.** Vertical section of a megalospheric form (BM (NH) P47324). **2.** *Lepidocyclina proteiformis* Vaughan. **2a-b.** Equatorial sections of both megalospheric and microspheric forms (BM (NH) Ex P32630). **2a.** A megalospheric form showing 4 nepionic spires of periembryonic chambers. **2b.** A microspheric form showing the symmetric biserial nepiont, type D. **2c.** Vertical section. BM (NH) Ex P32630. Scale bars = 100 microns.

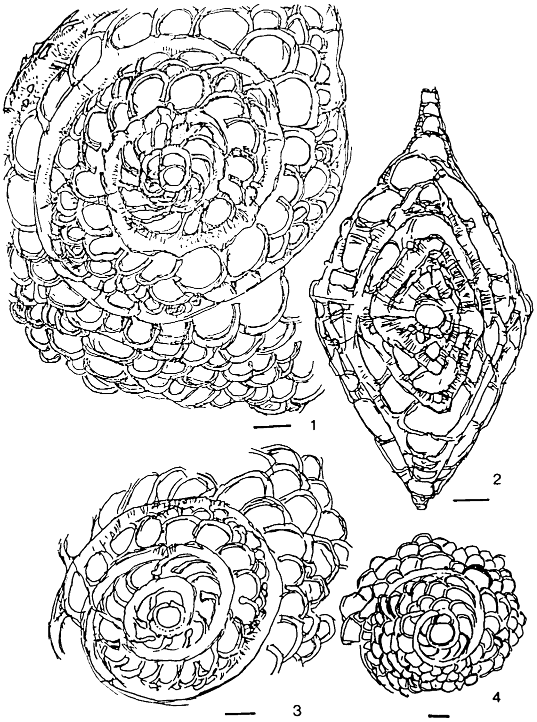


Figure 10. **1-3.** *Helicostegina soldadensis* Grimsdale. **1, 3.** Equatorial sections of megalospheric forms (**1**: BM (NH) P38379; **3**: BM (NH) P4915). **2.** Vertical section of a megalospheric form (BM (NH) P4916). **4.** *Helicostegina paucispira* (Barker and Grimsdale). Equatorial section of a megalospheric form (BM (NH) P47311). Scale bars = 100 microns.

← **Figure 8.** **1.** *Helicostegina polygyralis* (Barker). **1a-b**. Eqatorial section of megalospheric forms (both of BM (NH) Ex P32627) equipped with counter septa. Arrows showing radial stolons. **1c**. Vertical section of amegalospheric form (BM (NH) Ex P32627). **2**. *Eulinderina* sp. **2a**. Equatorial section of a megalospheric form (BM (NH) P33325) equipped with counter septa. **2b**. Vertical section of a megalospheric form (BM (NH) P33325), showing an equatorial chamber layer divided into some zones near periphery of test. **3**. *Polylepidina zeilmansi* (Tan). **3a-c**. Equatorial sections of microspheric and megalospheric forms (Tan, 1936, pl. 1, figs. **3b-c**, 8). **3a**. Asymmetric biserial nepiont, type C. **3b-c**. Megalospheric forms, showing 4 nepionic spires of periembryonic chambers. Scale bars = 100 microns.

through *Actinosiphon* to *Lepidocyclina*.

From Middle Eocene to Upper Miocene megalospheric lepidocyclinids in lineage 2, the embryonic apparatus evolved from isolepidine through nephrolepidine to trybliolepidine. The pliolepidine and multilepidine embryonic apparatus can be regarded as a peculiar structure in which some series of iso- to nephrolepidine and nephro- to trybliolepidine embryonic apparatus fuse into a cohesive whorl.

Cole (1963) observed *Lepidocyclina ocalana* Cushman, which posesses a wedge-like equatorial plate or wedge-shaped compact layers in the equatorial chamber layer. As such, this species is closely related to *Triplalepidina veracruziana* Vaughan and Cole, from the Upper Eocene beds of Mexico, the type species of *Triplalepidina* Vaughan and Cole, 1938. Recently, *Triplalepidina* was abandoned by Cole (1963) as a synonym of *Lepidocyclina* Gümbel, 1870, while the former was distinguished by Hanzawa (1964) from the latter based on the addition of a new structural constituent. Based on the present view of the nepionic chambers of the microspheric form of *Lepidocyclina ocalana*, this

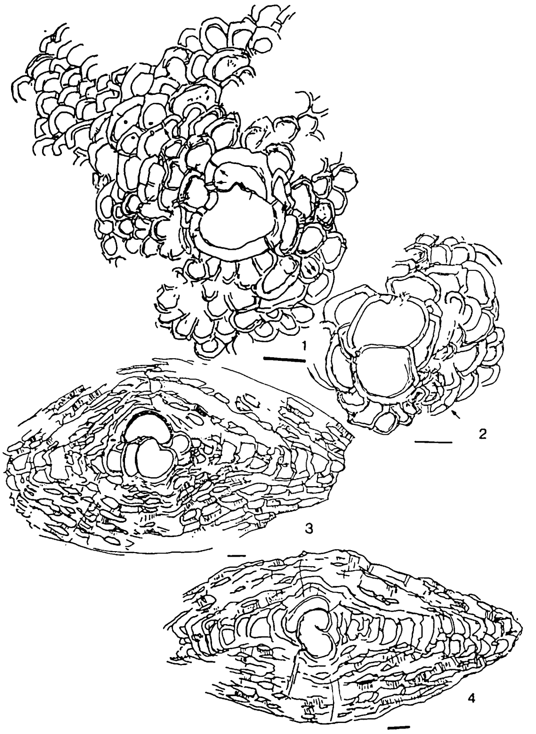


Figure 11. **1-4.** *Pseudolepidina trimera* Barker and Grimsdale. **1-2.** Equatorial sections of megalospheric forms (**1**: BM (NH) P33031 ; **2**: BM (NH) P33033) showing radial stolons or stoloniferous foramina (arrow). **3-4.** Vertical sections of megalospheric forms (**3**: BM (NH) P33037 ; **4**: BM (NH) P33032). Scale bars = 100 microns.

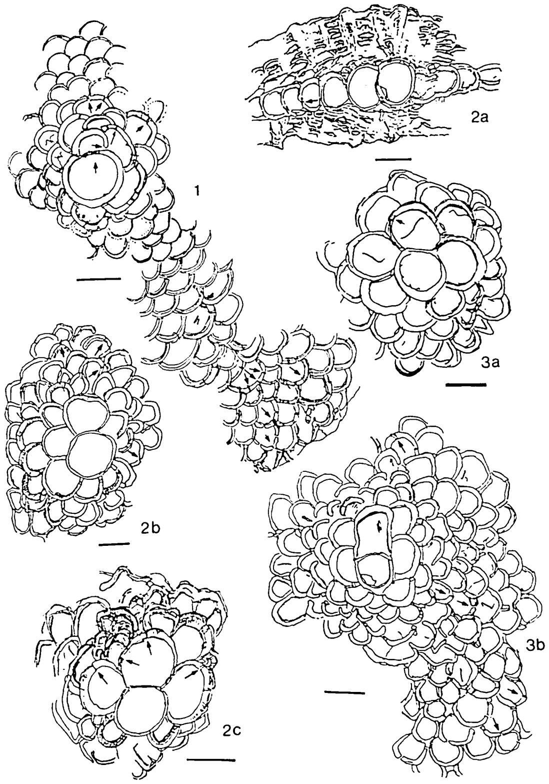


Figure 12. **1.** *Actinosiphon semmesi* Vaughan. Equatorial section of a megalospheric form (BM (NH) P32633). Arrows showing apertural foramina or radial stolons. **2-3.** *Actinosiphon tibetica* (Douvillé). **2a.** Vertical section of a megalospheric form (*Lepidorbitoides tibetica* Douvillé of BM (NH) F949). **2b-c.** Equatorial sections of megalospheric forms (*Lepidorbtoides tibetica* of BM (NH) F944 and F949). Arrows showing radial stolons or stoloniferous foramina. **3a-b.** Equatorial sections of megalospheric forms (*Lepidocyclina* (*Polylepidina*) *punjabensis* Davies of BM (NH) P34987). Arrows showing radial stolons or stoloniferous foramina. Scale bars = 100 microns.

species posesses the same symmetric biserial nepiont (type D) as *Lepidocyclina* species and is regarded as the genus *Lepidocyclina*.

The nepionic type of lineage 3 developed from both the asymmetric biserial nepiont with spiral thickening of the primary coil, and the symmetric biserial nepiont without spiral thickening recognized in the microspheric *Lepidorbitoides minor* (Schlumberger), to the symmetric biserial nepiont without spiral thickening of microspheric *Orbitoclypeus* Silvestri, 1907. The latter gave rise to the same nepiont as microspheric *Eulepidina* Douvillé, 1911 (Figures 3, 5). The common morphological features among *Lepidorbitoides* Silvestri, 1907, *Orbitoclypeus*, and *Eulepidina* are their general shape and the number and disposition of the lateral chambers. The main evolution of lineage 3 is not completely clear, but the evolution involves the development of adauxiliary chambers. We can see the development of adauxiliary chambers from *Lepidorbitoides minor* (Schlumberger) to *L. socialis* (Leymerie), whereas the adauxiliary chambers of *Orbitoclypeus* and *Eulepidina* are numerous in the equatorial plane.

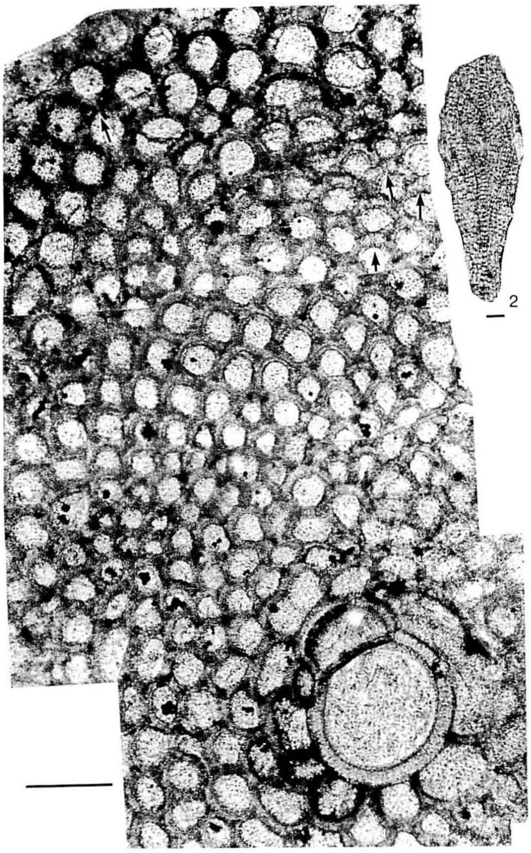


Figure 13. 1–2. *Actinosiphon semmesi* Vaughan. **1.** Equatorial section of holotype (USNM 321783). Arrows showing radial stolons. **2.** Vertical section of cotype (USNM321782). Scale bars = 100 microns.

The origin of lineage 1 starts from Upper Paleocene *Eoconuloides*, but that of lineage 2 and lineage 3 seems probably to be Upper Cretaceous "*Rotalia*", judging from the fossil records of *Siderolites* ?, *Sulcoperculina, Sulcorbitoides*, and *Pseudorbitoides* in the Indo-Pacific region. Gorsel (1978) has already inferred this from the fossil occurrences in the America-Europe region. Detailed consideration of this point is beyond the scope of this paper (Figure 5).

Discussion of some megalospheric forms of *Actinosiphon*, *Lepidocyclina*, *Nephrolepidina*, and *Eulepidina*

Actinosiphon Vaughan, 1929 was described with the type species *Actinosiphon semmesi* Vaughan from the Lower Eocene Chicontepec Formation, Mexico. Its arcuate- to ogival-shaped equatorial chamber walls carry radial stolons, which are characteristic of this genus. As stated earlier, Rutten (1941) supposed that *Actinosiphon* evolved from *Polylepidina* Vaughan, 1924 as it reduced the size of the nepionic chambers and developed radial stolons. De Cizancourt (1951) considered that *Lepidorbitoides* cf. *planasi* Rutten, described from the Paleocene San Juan Limestone, Venezuela, by Caudri (1944), and *Polylepidina barbadensis* (Vaughan), described from Paleocene blocks derived from Joes River mudflows, Barbados, by Vaughan (1945), are synonymous; she placed the species in *Actinosiphon*. Grimsdale, in van

Raadshooven (1951, p. 488), considered *"Lepidocyclina" barbadensis* Vaughan, described from the Paleocene Guasare Formation, Venezuela, by van Raadshooven, and *Actinosiphon semmesi* Vaughan as the same species. Also, Rutten, in van Raadshooven (*op. cit.*), suggested that if the genera *Lepidorbitoides* and *Orbitocyclina* were included as subgenera in the genus *Lepidocyclina*, there could not be much objection to also including the genus *Actinosiphon* as a subgenus. Rao (1940, 1944) treated *L.* (*Polylepidina*) *punjabensis* Davies, 1937 and *Lepidorbitoides tibetica* Douvillé, 1916, from Kampa Dzong, Tibet, as the same species, and he established the new generic name *Orbitosiphon* ; Smout and Haque (1956) also abandoned *L.* (*Polylepidina*) *punjabensis* as a synonym of *Lepidorbitoides tibetica*, but thought *tibetica* belonged in *Actinosiphon.*

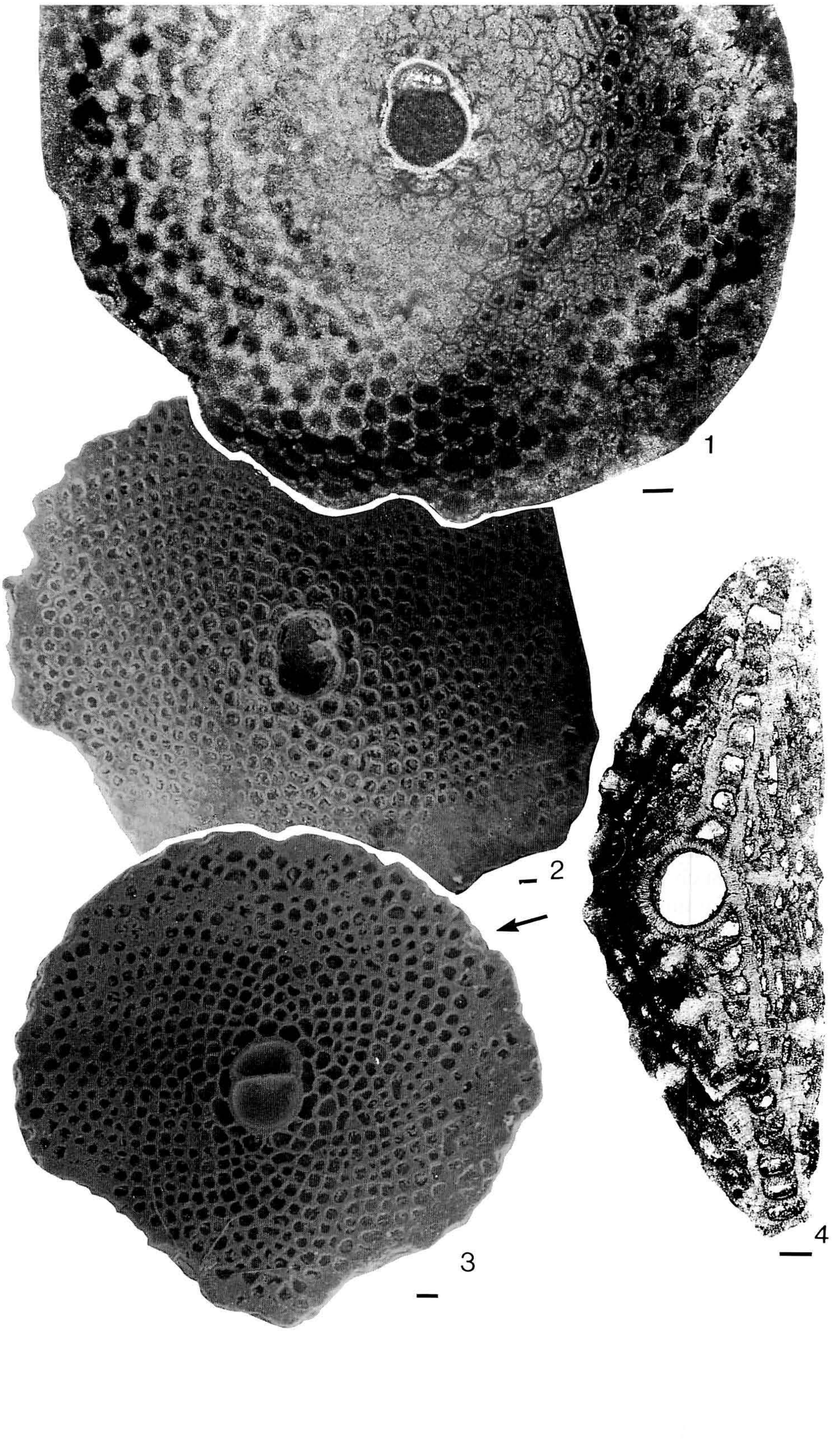
The author saw the holotype (USNM 321783) and topotype (BM (NH) P51967) of *Actinosiphon semmesi* Vaughan, and the topotype (BM (NH) P51969, P34987) and other specimens (BM (NH) P34987, F467) of *Lepidocyclina* (*Polylepidina*) *punjabensis* Davies, from the Paleocene Ranikot Beds of the Punjab Salt Range, Pakistan. Although Adams (1987) differentiated *Orbitosiphon praepunjabensis* from *L.* (*P.*) *punjabensis* (BM (NH) P51969), radial stolons were visible in the equatorial chambers in all of the forms listed above (Figures 12, 13). The author regards *L.* (*P.*) *punjabensis* Davies and *Orbitosiphon praepunjabensis* Adams, 1987 as *Actinosiphon tibetica* (Douvillé), because of the existence of radial stolons in the equatorial chambers.

Moreover, the author studied *Lepidocyclina ariana* Cole and Ponton, from the Middle Eocene Punta Mosquito Formation, Venezuela, in which radial stolons were found (Figures 15, 16). As such, the author considered that Upper Paleocene to Lower Eocene *Actinosiphon semmesi* Vaughan could have evolved into Middle Eocene *Lepidocyclina ariana* Cole and Ponton. Also, Vaughan (1936) has described upper Middle to Upper Eocene *Lepidocyclina proteiformis* Vaughan as having radial stolons.

Brönnimann (1944, p. 39) described Upper Cretaceous *Orbitocyclinoides schencki* Brönnimann, from Kerman, Iran, which possessed radial stolons and more nepionic spires than *Orbitocyclina*. As such, Brönnimann considered that there are close phylogenetic relationships between "*Lepidocyclina*" *punjabensis* (Davies) and *Orbitocyclinoides schencki* Brönnimann. As stated before, the former species is a junior synonym of *Actinosiphon tibetica* (Douvillé) (Figure 12-3a – b). In light of present knowledge, the author supposes that the phylogenetic relationships among *Orbitocyclina*, including *Orbitocyclinoides, Actinosiphon,* and *Lepidocyclina* are a recognition of an underlying community during different geologic stages.

The next problem concerns the phylogeny of *Eulepidina* Douvillé, 1911. Hanzawa (1964, p. 308) considered that *Eulepidina* might have derived from *Nephrolepidina* with the remarkable development of the deuteroconch, whereas Adams (1987, p. 312) thought that *Lepidocyclina* (*Eulepidina*) originated from *Lepidocyclina* s. str., which possessed equatorial chambers arranged in circles, and that it could not have arisen from any known species of *Lepidocyclina* (*Nephrolepidina*). Sirotti (1982) supposed that Upper Eocene *Eulepidina ocalana* (Cushman) derived from Upper Eocene *Lepidocyclina gubernacula* Cole, whereas Butterlin (1987) considered that Lower Oligocene *Lepidocyclina* (*Eulepidina*) *undosa* Cushman evolved from Lower Oligocene *Lepidocyclina chaperi* Lemoine and Douvillé.

⟶ **Figure 14.** *Lepidocyclina ariana* Cole and Ponton. **1.** Equatorial section. **2**-**3.** Equatorial views. **3.** Arrow showing the position of radial stolons (**Figure 15**-**1a** – **c**). **4.** Vertical section. Middle to Upper Eocene Punta Mosquito Formation, Venezuela. Scale bars = 100 microns.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The author wants to indicate that *Eulepidina*, possessing an increased number of adauxiliary chambers, is essentially different from both *Lepidocyclina* and *Nephrolepidina*, which possess from only a few to ten adauxiliary chambers, though some species have twelve or rarely fourteen. In order to observe the megalospheric nucleoconch, S.E.M. pictures were taken from specimens of *Lepidocyclina ariana* Cole and Ponton, from the Middle to Upper Eocene Punta Mosquito Formation, Venezuela, *L. ocalana* Cushman, from the Upper Eocene Ocala Limestone, Florida, U.S.A., *Nephrolepidina morgani* (Lemoine and Douvillé), from the upper Aquitanian to lower Burdigalian at Saint-Paul-les-Dax, SW France, and *Nephrolepidina japonica* (Yabe), from the Lower Miocene Kamiyokoze Formation, Japan (Figures 14, 17-19). The protoconch and deuteroconch of the megalospheric embryonic chambers of these *Lepidocyclina* and *Nephrolepidina* species are pierced by numerous very small perforations (1-3 microns) or several large stoloniferous foramina (10-12 microns) that connect the adauxiliary and lateral chambers (Figures 17-19).

In *Eulepidina dilatata* (Michelotti), from the Aquitanian at Escornebéou, SW France, the deuteroconch embracing the circumference of the protoconch is pierced by many large stoloniferous foramina (15-20 microns), which are arranged in a few rows in the equatorial plane and which connect the adauxiliary chambers (Figure 20). This morphogenetic pattern, present in megalospheric forms of *Eulepidina dilatata* (Michelotti), is the same as the one well investigated in *Orbitoclypeus nummuliticus* (Gümbel) by Sirotti (1987). Accordingly, the author considers that an evolutionary path from Paleocene-Eocene *Orbitoclypeus* to Oligocene-Lower Miocene *Eulepidina* exists (Figure 5).

The classification of the family Lepidocyclinidae

Both the nepionic types of the microspheric juvenarium and the peculiar embryonic and periembryonic chambers of megalospheric forms characterize the following classification of the family Lepidocyclinidae.

Generic distinction

Family Lepidocyclinidae Scheffen, 1932

Test discoidal to lenticular, with vacuolar and rarely developed or well-developed lateral chambers and distinct equatorial layer of chambers; chamber walls perforated by stolons and perforations. Paleocene to Upper Miocene.

Subfamily Lepidocyclininae Scheffen, 1932

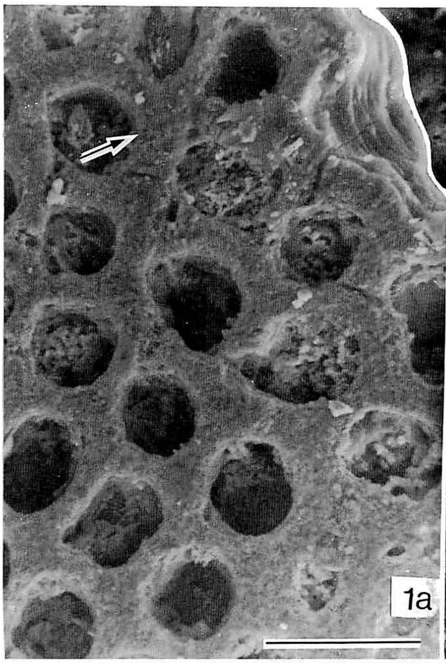
Test lenticular, with a distinct equatorial chamber layer equipped with lateral layers on each side. Paleocene to Upper Miocene.

Lepidocyclina Gümbel, 1870

Type species.—Nummulites mantelli Morton, 1833

Bilocular megalospheric apparatus subequal or equal in size; a multilocular nucleoconch is present. Periembryonic chambers have more than quadriserial nepionic spires, and arcuate, ogival, rhombic, spatulate, or hexagonal equatorial chambers are arranged cyclically. Microspheric generation is exhibited by symmetric to rarely asymmetric biserial nepionts. An equatorial

→ **Figure 15.** **1-2.** *Lepidocyclina ariana* Cole and Ponton. **1a-c.** Equatorial views of a megalospheric form (**Figure 14-3**) showing radial stolons (arrows) and diagonal stolons. **2.** Equatorial views of a megalospheric form (**Figure 14-2**) showing a radial stolon (arrow). Scale bars = 100 microns.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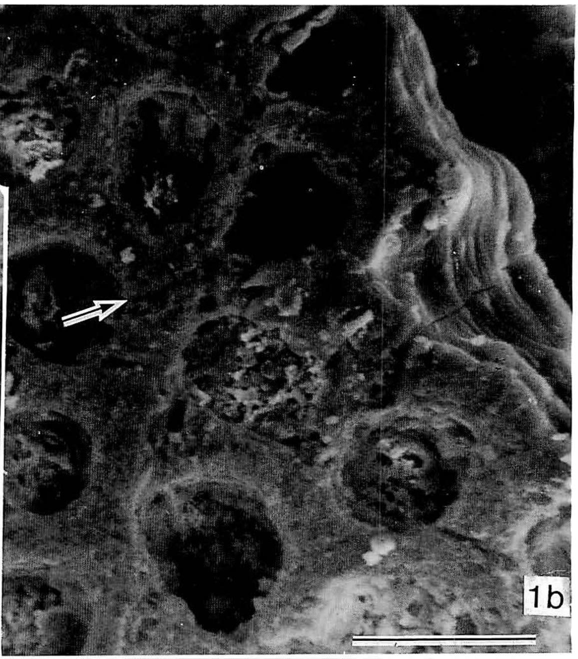
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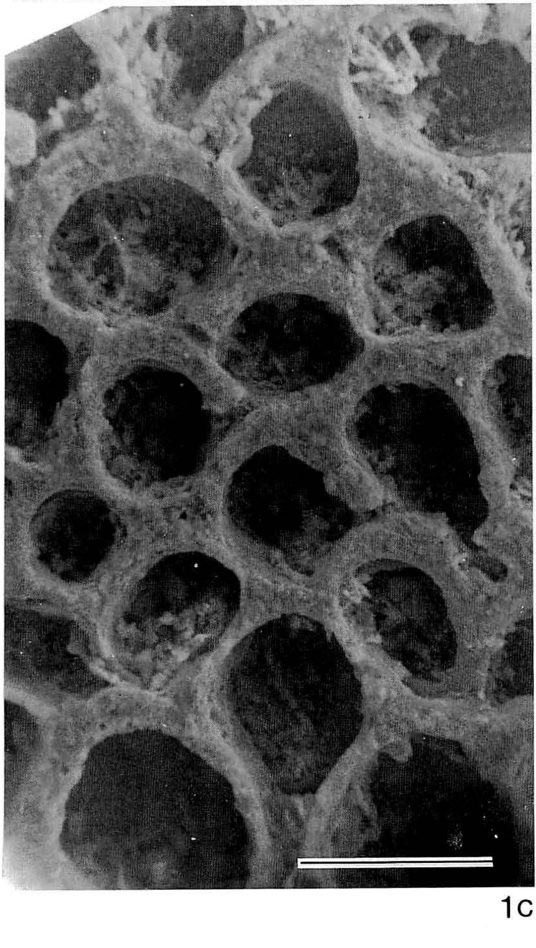
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chamber layer is rarely divided into some zones near the periphery of the test. Lateral chambers present.

Figure 3 (pars): Schematic diagram of chamber budding formation of microspheric forms of *Lepidocyclina ocalana* Cushman, *L. proteiformis* (Vaughan), *L. tobleri* (Douvillé), *L. pustulosa* Douvillé, *L. mantelli* (Morton), and *L. canallei* Lemoine and Douvillé. Figure 9: Equatorial and vertical sections of megalospheric and microspheric forms of *Lepidocyclina mantelli* (Morton) and *L. proteiformis* Vaughan. Figures 14-17: Equatorial and vertical sections, and equatorial views of megalospheric forms of *Lepidocyclina ariana* Cole and Ponton. Figure 18-1-2: Oblique views of megalospheric forms of *Lepidocyclina ocalana* Cushman.

Nephrolepidina H. Douvillé, 1911

Type species.—*Nummulites marginata* Michelotti, 1841

Bilocular embryo, deuteroconch distinctly larger than protoconch; a multilocular nucleoconch is present. Periembryonic chambers have 6 to 28 nepionic spires. Equatorial chambers are arcuate, ogival, rhombic, spatulate, or hexagonal, arranged cyclically to polygonally, with the exception of a stellate form. Microspheric juvenarium developed into a symmetric biserial nepiont is present. Lateral chambers present.

Figure 3 (pars): Schematic diagram of chamber budding formation of microspheric forms of *Nephrolepidina japonica* (Yabe), *N. orientalis* (van der Vlerk), *N. luxulians* Tobler and *N. rutteni* (van der Vlerk). Figure 18-3: Oblique view of a megalospheric form of *Nephrolepidina morgani* (Lemoine and Douvillé). Figure 19: Equatorial and oblique views of megalospheric forms of *Nephrolepidina japonica* (Yabe).

Actinosiphon Vaughan, 1929

Type species.—*Actinosiphon semmesi* Vaughan, 1929b

Bilocular embryo, unequal or rarely equal in size; periembryonic chambers have 2 to 4 nepionic spires. Equatorial chambers arcuate, ogival, spatulate, or hexagonal, somewhat circularly arranged. Radial stolons in equatorial chambers are present. Lateral chambers are well developed.

Figure 12: Equatorial and vertical sections of megalospheric forms of *Actinosiphon semmesi* Vaughan and *A. tibetica* (Douvillé). Figure 13: Equatorial and vertical sections of megalospheric forms of *Actinosiphon semmesi* Vaughan.

Subfamily Helicolepidininae Tan, 1936b

Test discoidal to lenticular, with bilocular embryo surrounded by thickened wall with vacuolar and rarely developed or well-developed lateral chambers, no or one adauxiliary chamber, one to four or six ? periembryonic spires are present. Thickening of the spiral wall is present or absent. Radial stolons are rarely present. Middle Eocene to Lower Oligocene.

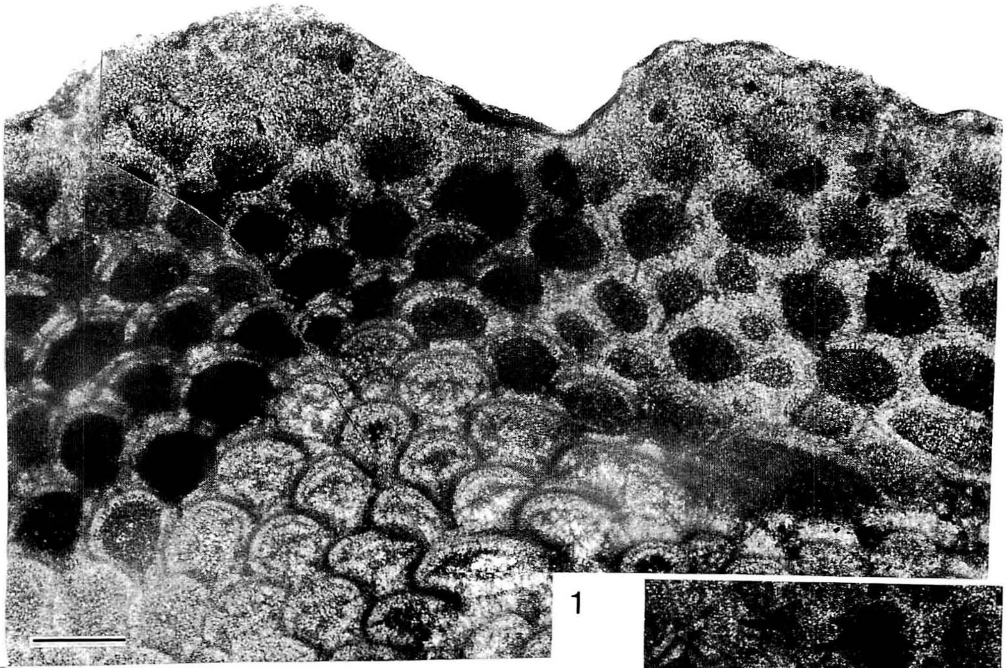
Helicostegina Barker and Grimsdale, 1936

Type species.—*Helicostegina dimorpha* Barker and Grimsdale, 1936

Early chambers in an involute trochospiral coil, later ones are subdivided ventrally or on both sides to form arcuate chamberlets. Adult stage consists of annularly disposed arcuate chamberlets. Microspheric uniserial nepiont is present.

Figure 2 (pars): Schematic diagram of chamber budding formation of a microspher-

→ **Figure 16.** *Lepidocyclina ariana* Cole and Ponton. **1, 3.** Equatorial sections of a megalospheric form (**Figure 14-1**) showing radial and diagonal stolons. **2.** Equatorial view of a megalospheric form (**Figure 14-2**) showing radial stolons (arrows). Scale bars = 100 microns.



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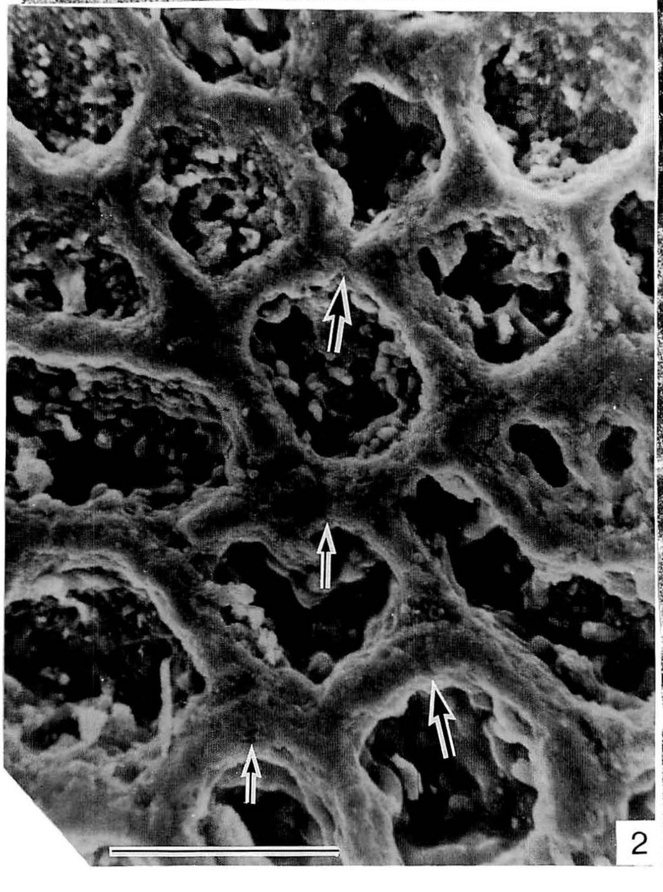

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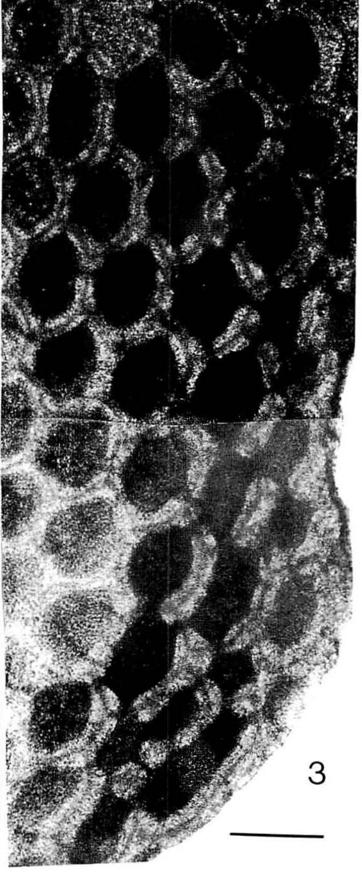

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ic form of *Helicostegina gyralis* Barker and Grimsdale. Figure 6: Equatorial and vertical sections of megalospheric and microspheric forms of *Helicostegina gyralis* Barker and Grimsdale. Figure 8-1a–c: Equatorial and vertical sections of megalospheric forms of *Helicostegina polygyralis* (Barker). Figure 10: Equatorial and vertical sections of megalospheric forms of *Helicostegina soldadensis* Grimsdale and *H. paucispira* (Barker and Grimsdale).

Helicolepidina Tobler, 1922

Type species.—*Lepidocyclina* (*Helicolepidina*) *spiralis* Tobler, 1922

Bilocular embryo followed by planispiral coil of one or two whorls, termed the helicolepidine string. Microspheric reduced uniserial nepiont is present. Lateral chambers are well developed.

Figure 2 (pars): Schematic diagram of chamber budding formation of a microspheric form of *Helicolepidina spiralis* (Tobler). Figure 7: Equatorial sections of megalospheric and microspheric forms of *Helicolepidina spiralis* (Tobler).

Eulinderina Barker and Grimsdale, 1936

Type species.—*Planorbulina* (*Planorbulinella*) *guayabalensis* Nuttall, 1930

Bilocular embryo followed by trochoid coil of one whorl, spire with thick outer wall followed by arcuate chambers arranged cyclically. An equatorial chamber layer is rarely divided into some zones near the periphery of the test. Microspheric asymmetric biserial nepiont is present. Lateral chambers vacuolar and rarely developed or well developed.

Figure 2 (pars): Schematic diagram of chamber budding formation of a microspheric form of *Eulinderina guayabalensis* (Nuttall). Figure 8-2a–b: Equatorial and vertical sections of megalospheric forms of *Eulinderina* sp.

Polylepidina Vaughan, 1924

Type species.—*Lepidocyclina* (*Polylepidina*) *chiapasensis* Vaughan, 1924

Bilocular embryo, subequal in size: periembryonic chambers have 2 to 4 unequal nepionic spires. Arcuate equatorial chambers are arranged cyclically. Microspheric asymmetric biserial nepiont is present. Lateral chambers present, but sometimes only a few layers.

Figure 2 (pars): Schematic diagram of chamber budding formation of microspheric forms of *Polylepidina zeilmansi* (Tan Sin Hok) and *P. chiapasensis* (Vaughan). Figure 8-3a–b: Equatorial sections of microspheric and megalospheric forms of *Polylepidina zeilmansi* (Tan Sin Hok).

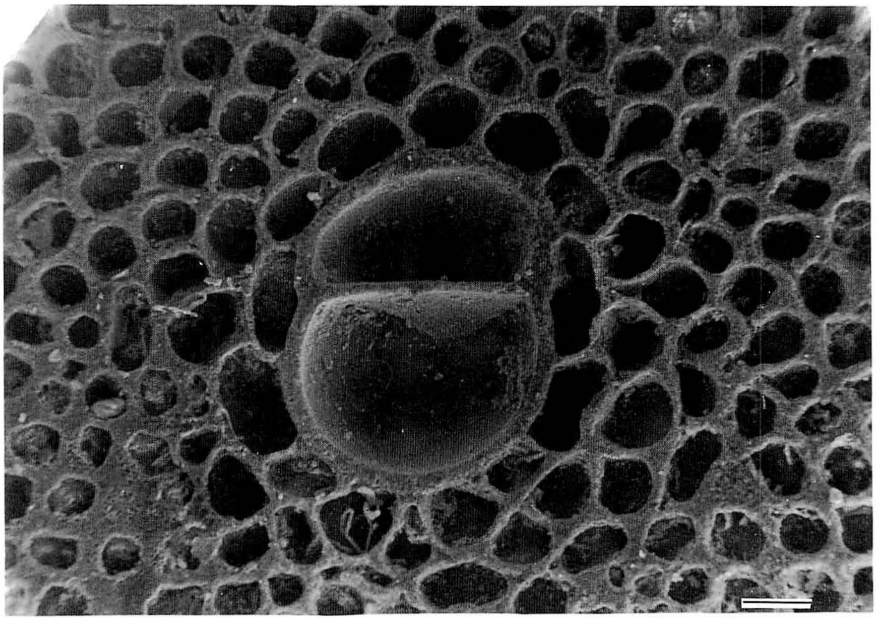
Pseudolepidina Barker and Grimsdale, 1937

Type species.—*Pseudolepidina trimera* Barker and Grimsdale, 1937

Bilocular embryo, subequal or equal in size; large third principal auxiliary chamber on the convex side of the equatorial plane is present. All periembryonic chambers have 4 unequal nepionic spires. Arcuate equatorial chambers are arranged cyclically. An equatorial chamber layer is divided into some zones near the periphery of test. Microspheric reduced uniserial nepiont is present.

Figure 2 (pars): Schematic diagram of chamber budding formation of a microspheric form of *Pseudolepidina trimera* Barker and Grimsdale. Figure 11: Equatorial and ver-

→ **Figure 17.** *Lepidocyclina ariana* Cole and Ponton. **1-2.** Equatorial views of megalospheric forms (**Figure 14-3**) showing the structure of embryonic chambers, development of periembryonic chambers (4 nepionic spires) and very small perforations (2-3 microns) of embryonic chambers. Scale bars = 100 microns.



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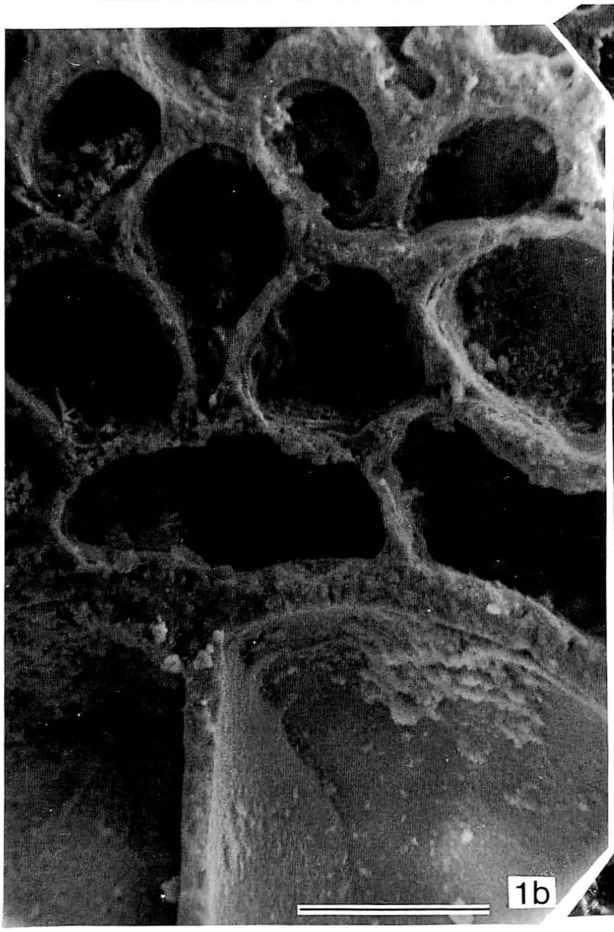

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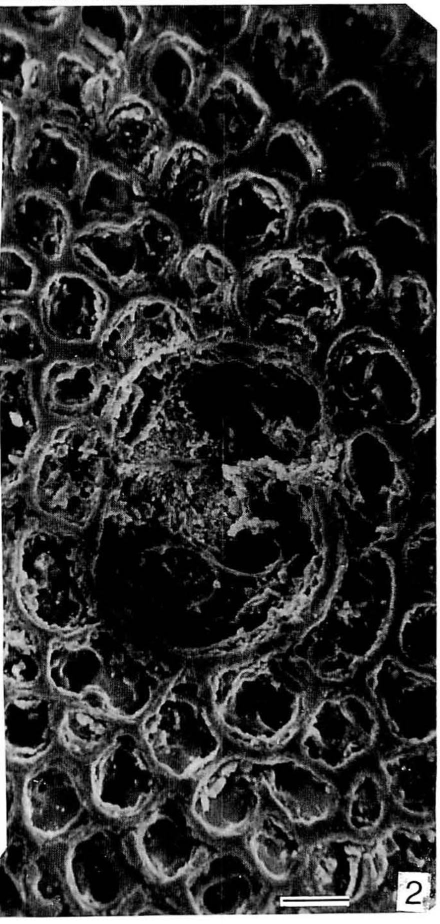

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tical sections of megalospheric forms of *Pseudolepidina trimera* Barker and Grimsdale.

Eulepidininae Matsumaru, new subfamily

This new subfamily of the family Lepidocyclinidae is established to accomodate only the group of *Eulepidina*, which possesses a lenticular test with a distinct equatorial chamber layer equipped with lateral chamber layers at each side. Lower Oligocene to Lower Miocene.

Eulepidina H. Douvillé, 1911

Type species.—Orbitoides dilatata Michelotti, 1861

Generic description : Large bilocular megalospheric nucleoconch from 300 to 1,850 microns in diameter with cuboidal protoconch surrounded nearly or completely by deuteroconch, both surrounded by a thick wall from 22 to 110 microns thick pierced by numerous stolons that lead to many adauxiliary chambers that have more than 30 nepionic spires. Microspheric juvenarium developed into a symmetric biserial nepiont is present. Equatorial chambers are arcuate, ogival, spatulate, or hexagonal, arranged cyclically to polygonally. Numerous lateral chambers are well differentiated from the equatorial layer. Lower Oligocene to Lower Miocene.

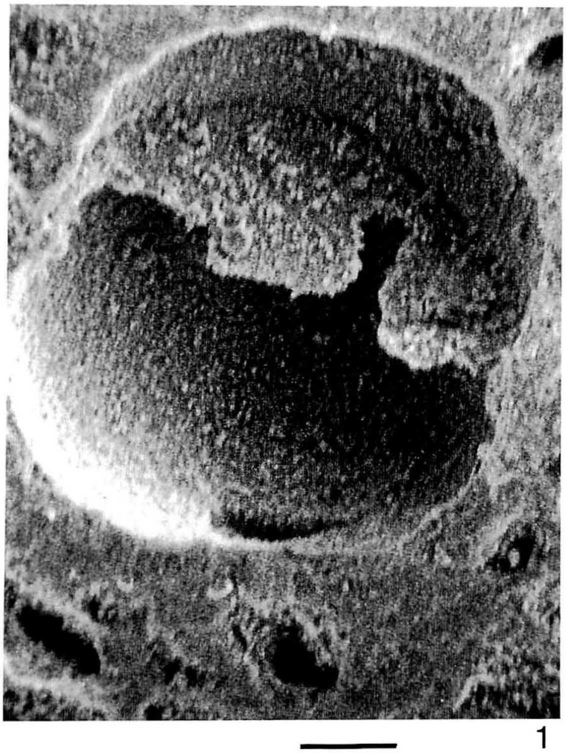
Remarks.—Eulepidina Douvillé, 1911 is distinguished from *Lepidocyclina* Gümbel, 1870 and *Nephrolepidina* Douvillé, 1911 by a large embryonic apparatus, a thick-walled megalospheric nucleoconch, and numerous nepionic spires. Also the former can be distinguished from *Actinosiphon* Vaughan, 1929 and all forms of the subfamily Helicolepidininae by numerous nepionic spires. A serious look should be taken at the phylogenetic relationship between *Orbitoclypeus* and *Eulepidina*, because they both possess the same periembryonic nepionic spires.

Figure 1 : Equatorial section of a microspheric form of *Eulepidina papulifera* (Douvillé) and a drawing of the same showing the ontogenetic change of growth of microspheric *Eulepidina papulifera*. Figure 4 (pars) : Schematic diagram of chamber budding formation of microspheric forms of *Eulepidina dilatata* (Michelotti), *E. favosa* (Cushman), *E. gigantea* (Martin) and *E. omphalus* (Tan Sin Hok). Figure 20 : Oblique view of a megalospheric form of *Eulepidina dilatata* (Michelotti).

Acknowledgments

During the author's Foraminifera study in Europe, through financial assistance from the Ministry of Education of Japan in 1985, and the courtesies of JAPEX (Japan Petroleum Exploration Co., Ltd.) and Modena University, Italy in 1989, the author gained much helpful information, examined papers and observed type and valuable specimens of the Upper Cretaceous and Tertiary orbitoidal Foraminifera, and conducted discussions of many problems with European scientists. The author was enabled to collect many fossil specimens through the courtesy of a number of scientists. As such, the author expresses his cordial thanks to these organizations and acknowledges the help of the following individuals: Professors M. Neumann, J. Butterlin, A. Blondeau, Dr. A. Poignant (Université Pierre et Marie Curie (Paris VI)) ; Dr. M.-T.

→ **Figure 18.** **1-2.** *Lepidocyclina ocalana* Cushman. Oblique views of embryonic and periembryonic chambers, very small perforations (2-3 microns) and stoloniferous foramina (10-12 microns) can be seen into the embryonic chambers. **3.** *Nephrolepidina morgani* (Lemoine and Douvillé). Oblique view of embryonic and periembryonic chambers of a megalospheric form (upper Aquitanian to lower Burdigalian beds at Saint-Paul-les-Dax, France) showing stoloniferous foramina scattered into the embryonic chambers. Scale bars = 100 microns.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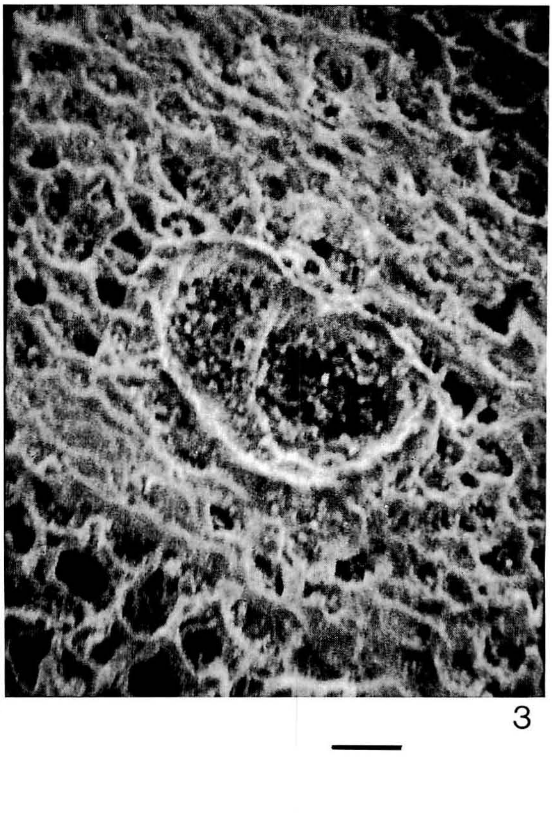
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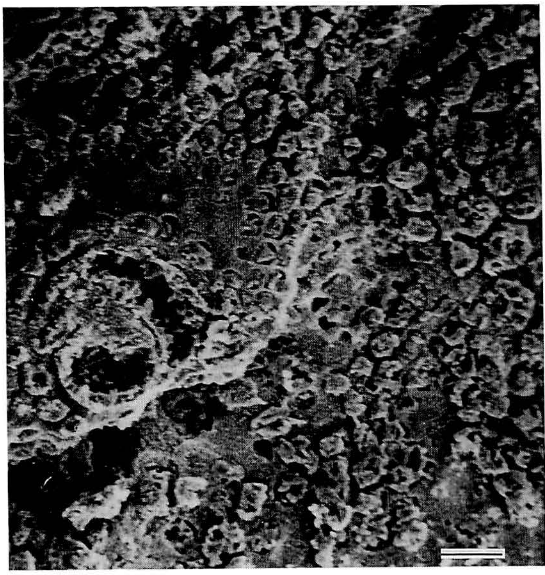
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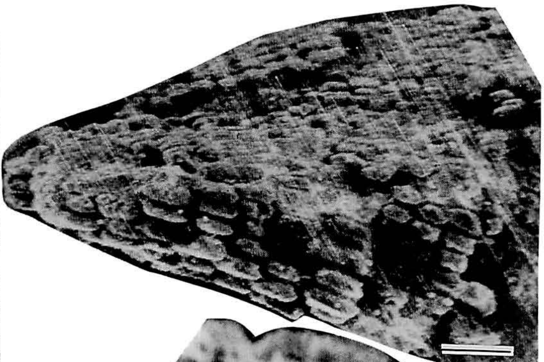
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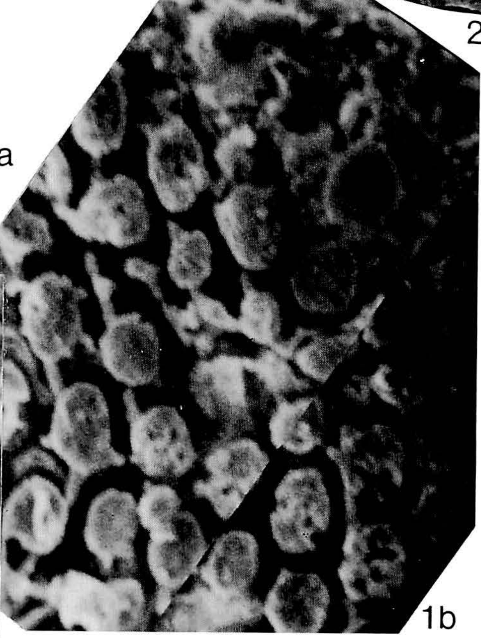
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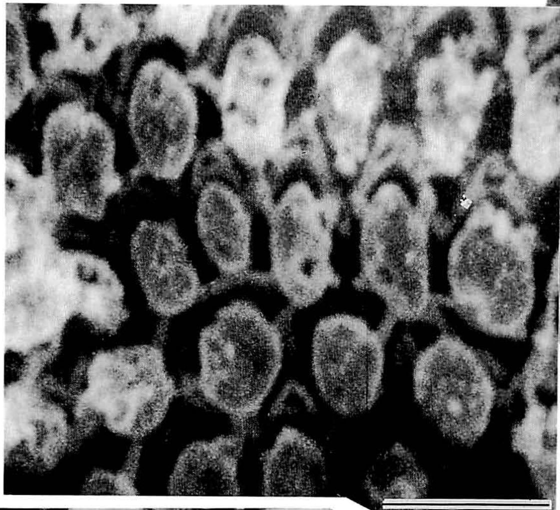
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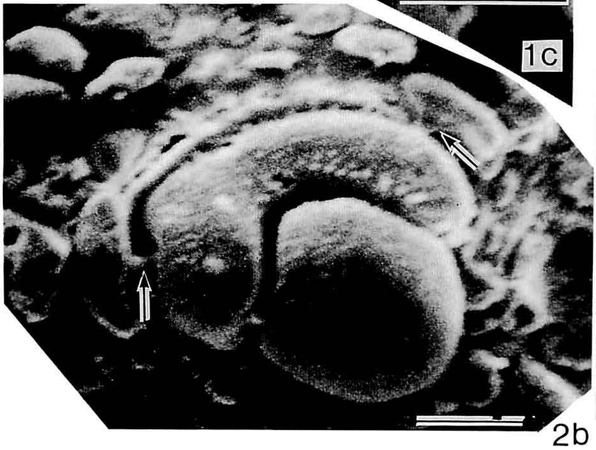
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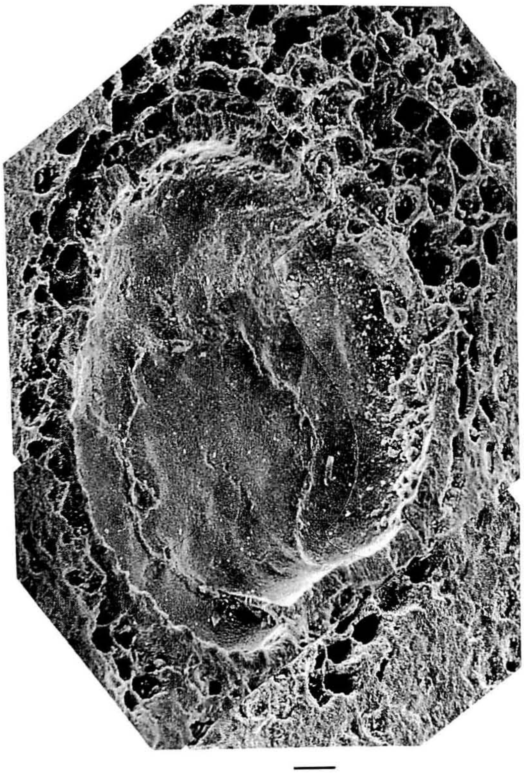

Figure 20. *Eulepidina dilatata* (Michelotti). Oblique view of a megalospheric form (Aquitanian at Escornebēou, France) showing the embryonic and periembryonic chambers and a few rows of many big stoloniferous foramina (15-20 microns). Scale bar = 100 microns.

Vēnec-Peyre (Musēum National d'Histoire Naturelle, Paris); Dr. D. Decrouez (Musēum d'Histoire Naturelle de Genēve); Prof. H. Hagn, Dr. K. Karl-Heinz (München University); Dr. F. Rögl (Natural History Museum, Vienna); Dr. C.G. Adams, Mr. R.L. Hodgkinson (British Museum (Natural History)); Prof. A. Sirotti (Modena University); Prof. F. Schiavinotto (Roma University); Prof. R. Röttger (Kiel University); Dr. K. Drobne (Paleontoloski Institut Ivana Rakovca ZRC, SAZU, Ljubliana).

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← **Figure 19.** *Nephrolepidina japonica* (Yabe). **1, 3.** Equatorial views of megalospheric forms showing the embryonic and periembryonic chambers, stoloniferous foramina (arrow), and diagonal and annular stolons of equatorial chambers. **2a-b.** Oblique views of megalospheric forms showing stoloniferous foramina (arrow) connecting between deuteroconch and adauxiliary chambers, and diagonal stolons between equatorial and lateral chambers. The Lower Miocene Kamiyokoze Formation, Japan. Scale bars = 100 microns.

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Lepidocyclinidae 科 (有孔虫目)の進化論的分類に関して；第三紀の Lepidocyclinidae 科とそれに近縁な白亜紀および古第三紀の“Orbitoids”有孔虫の微球型標本について，詳細な観察を行なった結果，彼等の周期芽室のタイプは，4 型 (uniserial nepiont, reduced uniserial nepiont, asymmetric biserial nepiont および symmetric biserial nepiont) からなることが明らかになった。著者は，これらの類別と顕球型標本の胚芽室や周胚芽室の発達および Lepidocyclinidae 科のあらゆる分類群とその年代的な産出記録を基に検討すると，いずれも，Lepidocyclinidae 科の種属は，3 分類系統 (Lepidocyclininae 亜科，Helicolepidininae 亜科，Eulepidininae 亜科，新称) に所属していることが明らかになった。また，著者は、3 亜科に所属する各属の分類を記載した。これまでに，Lepidocyclinidae 科は，古第三紀の *Eoconuloides* 属から発生し，進化したとされてきたが，本研究によって始めて 3 亜科は，*Eoconuloides* 属から，あるいは白亜紀の“*Rotalia*”属から Maastrichtian 世の *Orbitocyclina* 属を経て由来し，また同世の *Lepidorbitodies* 属，さらには古第三紀の *Orbitoclypeus* 属への進化を経て由来したものであって，それらは起源的には混成のものであることも明らかにされた。

松丸国照

Trans. Proc. Palaeont. Soc. Japan, N.S., No. 164, pp. 910-927, 8 Figs., December 30, 1991

927. ON SOME ACANTHOCERATID AMMONITES FROM THE TURONIAN OF HOKKAIDO

(STUDIES OF THE CRETACEOUS AMMONITES FROM HOKKAIDO—LXIX)

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Abstract. New or revised information is given on the taxonomy and stratigraphic occurrence of the following five species: (1) *Pseudaspidoceras flexuosum* Powell, 1963, which has recently been found at four localities in the lowest part of Member IIn, i.e. basal Turonian, in the Oyubari area. One of the examined specimens was the holotype of *Pseudaspidoceras* (*Ampakabites*) *kawashitai* Matsumoto and Obata, 1982, which now falls into synonymy with *Ps. flexuosum.* (2) *Neomphaloceras pseudomphalum* (Matsumoto, 1975), whose revised diagnosis is given. It occurs in the lower part of the Middle Turonian. (3) *Neomphaloceras costatum* (Matsumoto and Kawashita, 1978), which was erroneously assigned to *Mammites* or *Morrowites*. It occurs in the upper part of the Middle Turonian. (4) *Mammites* aff. *nodosoides* (Schlüter), which is more evolute than typical *M. nodosoides.* (5) *Mammites* n. sp. (?), which has peculiar bar-like ribs across the venter and spatulate ventrolateral horns on the body chamber.

Key words. *Pseudaspidoceras, Neomphaloceras, Cunningtoniceras, Mammites, Morrowites*, Turonian.

Introduction

While engaged in a biostratigraphic study aimed at establishing an integrated scheme of zonation by means of ammonites, inoceramids and foraminifera, I became aware of some erroneous points in the taxonomic and stratigraphic assignment of some ammonites from the Turonian of Hokkaido. There were also new finds of important species which are useful for zonation and correlation. In this paper I describe five selected Turonian species, giving the revised or new information and discussing their implications.

The investigated specimens came mostly from the localities indicated in the maps of the biostratigraphic papers (Tanabe *et al.*, 1975; Matsumoto *et al.*, 1991). They are stored in the following institutions, with abbreviations in parentheses:

- Department of Earth & Planetary Sciences [formerly Department of Geology], Kyushu University, Fukuoka (GK)
- Mikasa City Museum, Mikasa (MCM)
- University Museum, University of Tokyo (UMUT)
- Faculty of Education, Waseda University (WE)
- Yokosuka City Museum, Yokosuka (YCM)

The terminology used in the description of ammonites is the same as that in my recent papers (*e.g.* Matsumoto, 1988, p. 4), which followed essentially that in the *Treatise* (Arkell *et al.*, 1957) with some modifications.

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Palaeontological descriptions

Family Acanthoceratidae de Grossouvre, 1894

Genus *Pseudaspidoceras* Hyatt, 1903

Type species.—*Ammonites footeanus* Stoliczka, 1864.

Remarks.—See Kennedy *et al.* (1987, p. 34-41) for the generic characters and scope of variability. I now agree with them in regarding *Ampakabites* Collignon, 1965 as a synonym of *Pseudaspidoceras*. Cobban *et al.* (1989, p. 40) have also given the diagnosis.

Pseudaspidoceras flexuosum Powell

Figures 1-3

Pseudaspidooeras flexuosum Powell, 1963, p. 318, pl. 32, figs. 1, 9, 10 ; text-figs. 2a-c, f, g.

Pseudaspidoceras (*Ampakabites*) *kawashitai* Matsumoto and Obata, 1982, p. 75, pl. 3, fig. 1 ; text-fig. 2.

Pseudaspidoceras flexuosum Powell ; Kennedy *et al.*, 1987, p. 34, pl. 2, figs. 1-4, 8-13, 16-17 ; text-figs. 3A-C, 5, 6C, D, 7A, C (with full synonymy).

Pseudaspidoceras flexuosum Powell ; Cobban *et al.*, 1989, p. 41, fig. 91L.

Material.—(1) MCM. A83-1 (plaster cast GK. H9629) (Figure 1) collected by Y. Kawashita (May 30, 1978) at loc. Y5599 on the right branch in the upper reaches of the Kamimaki-zawa ; (2) WE. A110Y coll. by H. Hirano at his loc. Y070077d (89), i.e. T. M.'s loc. Y5232 (east end) on the right bank of the Hakkin-zawa ; (3) MCM. A193-1 (Figure 2) coll. by Y.K., T.M. & M. Noda (Aug. 24, 1983) at loc. Y5165b ; (4) GK. H8367 (Figure 3) coll. by H.H., K. Tanabe, M.N. & T.M. (Aug. 1, 1975) at loc. Y6015c, both on the right side of the Taki-no-sawa from the lowest part of Member IIn (Matsumoto, 1942), Middle Yezo Group of the Oyubari area.

Description.—The specimens (1) and (2) have the body chamber for about half a whorl and are fairly large, *viz.* about 250 mm in diameter at the preserved end. The specimens (3) and (4) are incomplete but, if restored, they would be very large, roughly twice as large as the former two.

In these four specimens the whorl is more or less higher than broad and subrectangular or subtrapezoid in section, with nearly flat, subparallel flanks, abruptly bent umbilical edge and vertical umbilical wall. The venter looks more or less arched, but this may be due partly to secondary compression and partly to the original variability.

The ornament on the body chamber and the preceding last part of the phragmocone is well shown by the 1st and 2nd specimens. They have primary ribs at wide intervals, numbering 5 or 6 per half whorl. Each primary rib arises from the umbilical bulla, which is prominent on the late part of the body chamber. Often the rib is indistinctly doubled on the flank, consisting of a stronger, rectiradiate or gently flexuous major rib and a weaker, somewhat flexuous branched minor one, both of which are looped at the outer ventrolateral, more or less clavate tubercle, whereas the inner ventrolateral node or bullate swelling is on the major one.

On the interspace between the primary ribs there are a few weaker ribs, some of which arise from weak umbilical bullae singly or doubled and looped at the small and weak inner or outer ventrolateral nodes, depending on the presence or absence of either of the latter two. Some other weak ribs have no umbilical node. These weak ribs or subcostae are rather irregular in curvature, but are often gently convex on the flank and somewhat rursiradiate on the ventrolateral part. Also faint, inner or outer ventrolateral nodes or swellings may or may not exist on these subcostae. The arched, weak ribs, sometimes doubled, seem to occur on the venter but are obscured in these specimens by erosion.

The major ribs on the next inner whorl are weaker and less distant than those on the outer whorl.

The third specimen shows a part of the body chamber and the fourth one consists of

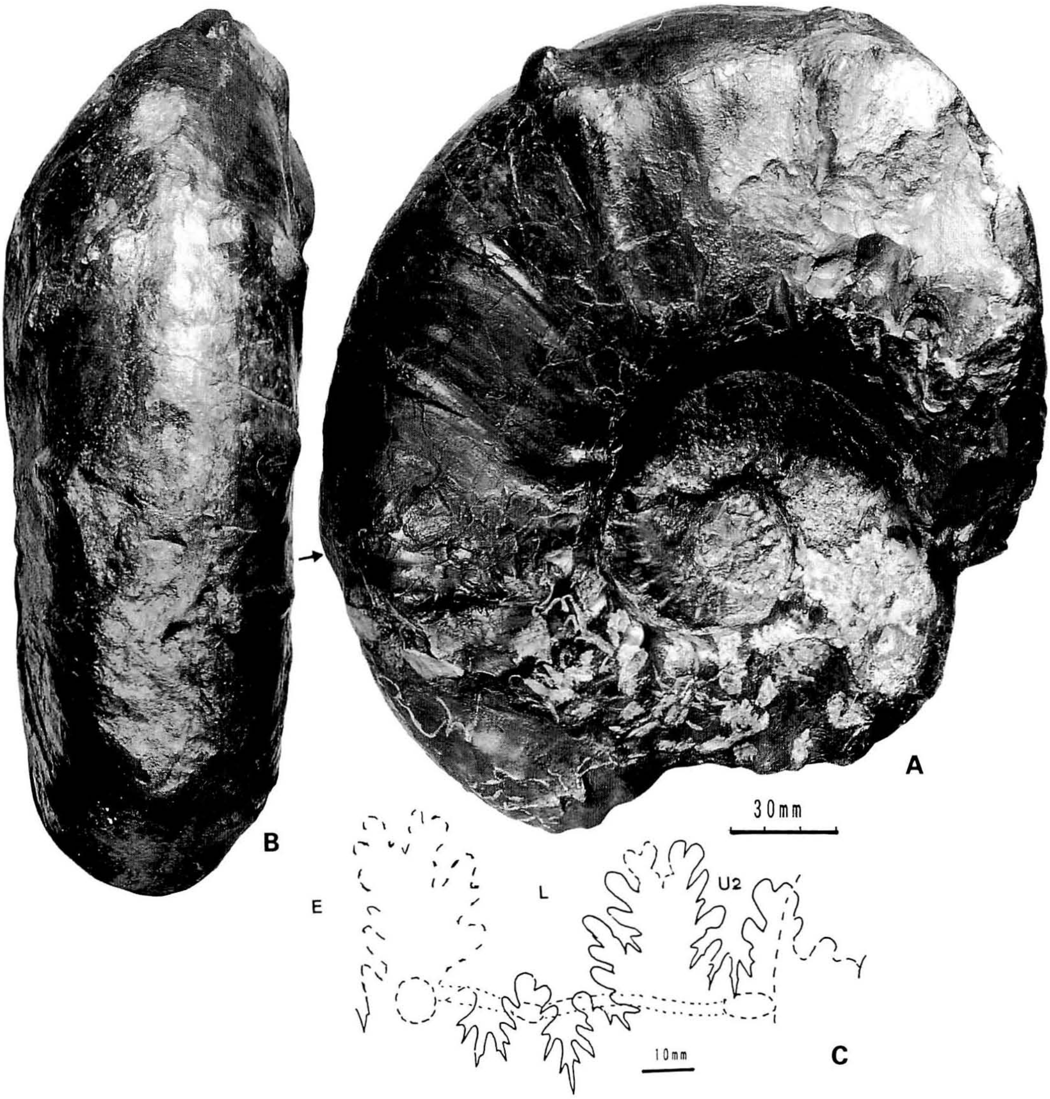

Figure 1. *Pseudaspidoceras flexuosum* Powell. The first specimen MCM. A83-1 from Y5599, Kamimaki-zawa of Oyubari area. **A, B** : lateral and ventral views ; **C** : the last suture of GK. H9629, which is a plaster cast of the holotype of *Ps.* (*Ampakabites*) *kawashitai* Matsumoto and Obata, 1982. Arrow indicates the position of the last suture, of which E and E/L saddle are not well exposed. (Photos by M. Noda ; T.M. *delin.*)

fragmentary pieces of a late septate whorl. They show similar mode of ribbing to that in the outer whorl of the foregoing two specimens. An apparent difference in the ornament is that both the outer and inner ventrolateral tubercles are distinct in the 1st and 2nd specimens but only one of them is well developed in the 3rd and 4th. Actually, in the 3rd specimen the clavate outer ventrolateral tubercles are well developed but the inner ones are obscure, whereas in the 4th specimen the inner ventrolateral nodes are larger. Faint ribs run across the venter with a gentle forward convexity, showing some-

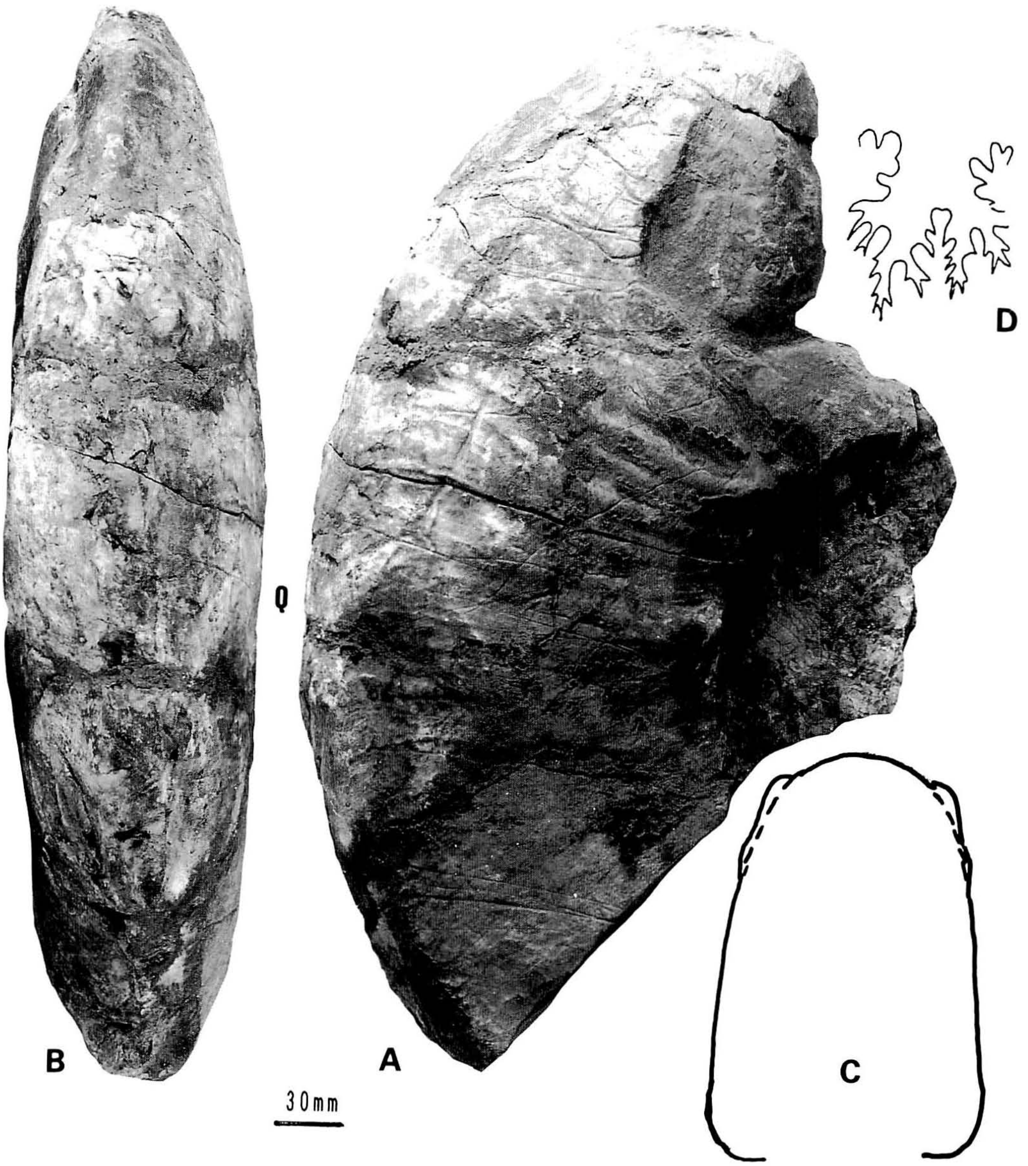

Figure 2. *Pseudaspidoceras flexuosum* Powell. The third specimen MCM. A193-1 from Y5165b, Taki-no-sawa of Oyubari area. **A, B**: lateral and ventral views; **C**: whorl section at Q; **D**: the first lateral lobe L on the inner whorl. (Photos by M. Noda; T.M. *delin.*)

times a doubled feature. An obscure zone of elevation is discernible on the mid-venter in a part of the 4th specimen.

Sutures of the late growth-stage are observable on the specimens (1), (3) and (4). They are similar to those illustrated finely by Collignon (1965, pl. 389, fig. 1664) in showing tall and rather narrowed stems of E/L and L/U2 saddles, fairly deep lobules and somewhat phylloid terminals of folioles. The breadth of L, however, seems to be variable in this species, ranging from very broad as in Powell's (1963) text-fig. 2f to fairly narrow as in Collignon's (*loc. cit.*). In this respect our

Table 1. Measurements (in mm) of *Pseudaspidoceras flexuosum*.

Specimen, remarks	D	U	H	B	B/H
(1) E	~200(1)	76(.32)	103(.43)	~78(.33)	0.76
〃 E-90° (LS+25°)	205(1)	60(.29)	92(.35)	72(.35)	0.77
(2) LS+150°	~250(1)	81(.32)	95(.38)	~70(.28)	0.74
(3) restored	~525(1)	185(.35)	205(.39)	—	—
〃 Q in Fig. 2	—	—	188	~108	066*
(4) E-90°	—	—	108	85	0.79
Holotype (Powell, 1963)	~230(1)	94(.41)	99(.43)	83(.36)	0.84
Paratype (〃 〃)	145(1)	49(.34)	57(.39)	49(.34)	0.87
Collignon, 1965, f. 1662	132(1)	34(.26)	62(.47)	46(.35)	0.74
Cobban & Scott, 1972	165(1)	48(.29)	73(.44)	48(.29)	0.66*

D=diameter, U=width of umbilicus, H=whorl-height, B=whorl-breadth ; E=at the preserved end, E-90°=at the point 90° adapically from E, LS=at the last septum, LS+150°=at the point 150° adorally from LS,*=secondarily compressed ; ~=approximate or inferred. Hokkaido specimens (1)-(4) as indicated in *Material*. For comparison, measurements on selected foreign specimens are shown below the line (cited from literature).

examples (Figures 1C, 2D and 3E) and another in Kennedy *et al*. (1987, fig. 3C) are intermediate. Also the subdivision of L varies from bipartite to asymmetrically tripartite.

Dimensions.—See Table 1.

Remarks.—When Matsumoto and Obata (1982, p. 75) established *P.* (*Ampakabites*) *kawashitai* on specimen (1), they depended on Collignon (1965) and Cobban and Scott (1972) in evaluating *Ampakabites* as a distinct taxon of generic rank.

Now, I however follow Kennedy *et al*. (1987, p. 34-41), who have shown a great extent of variation in *P. flexuosum* Powell, 1963, with which *Kamerunoceras* (*Ampakabites*) *auriculatum* Collignon, 1965 and *Ampakabites collignoni* Cobban and Scott, 1972 have been synonymized. Similarly, *P.* (*A.*) *kawashitai* Matsumoto and Obata, 1982 should be also regarded as a synonym (see above description and comparison below).

Comparison.—The fairly large specimens (1) and (2) from Hokkaido have well separated inner and outer ventrolateral tubercles on the primary ribs on the outer whorl. They closely resembles the holotype of *P. flexuosum* designated by Powell (1963, pl. 32, figs. 1, 9 and text-fig. 2c) in shell size (D=230 mm estimated by Powell ; "medium-size" by Kennedy *et al*., 1987, p. 38 is inadequate, because the photograph in Powell, 1963 is reduced to ×0.5), whorl shape and ornament, although the latter is only a fragmentary body chamber. With respect to the distinctness of inner and outer ventrolateral tubercles, our specimens (1) and (2) are comparable with *Ampakabites collignoi* Cobban & Scott (1972, p. 81, pl. 29, figs. 1-3 ; text-figs. 39, 40), from the Bridge Creek Limestone Member of the Greenhorn Limestone of Colorado, although the latter is smaller and seems to be secondarily compressed.

A fragmentary septate whorl, UMUT. MM6890, from the Obirashibe area, which was called *Mammites* sp. by Yabe (1909, p. 411) and described by Matsumoto *et al*. (1978, p. 14, pl. 6, fig. 2 ; text-fig. 6) under *Ampakabites* (?) sp., is similar to the form mentioned above in the outline of whorl section, major ornament and sutural pattern, but I hesitate to make the specific identification until more specimens are obtained from the correlatable stratigraphic level in the

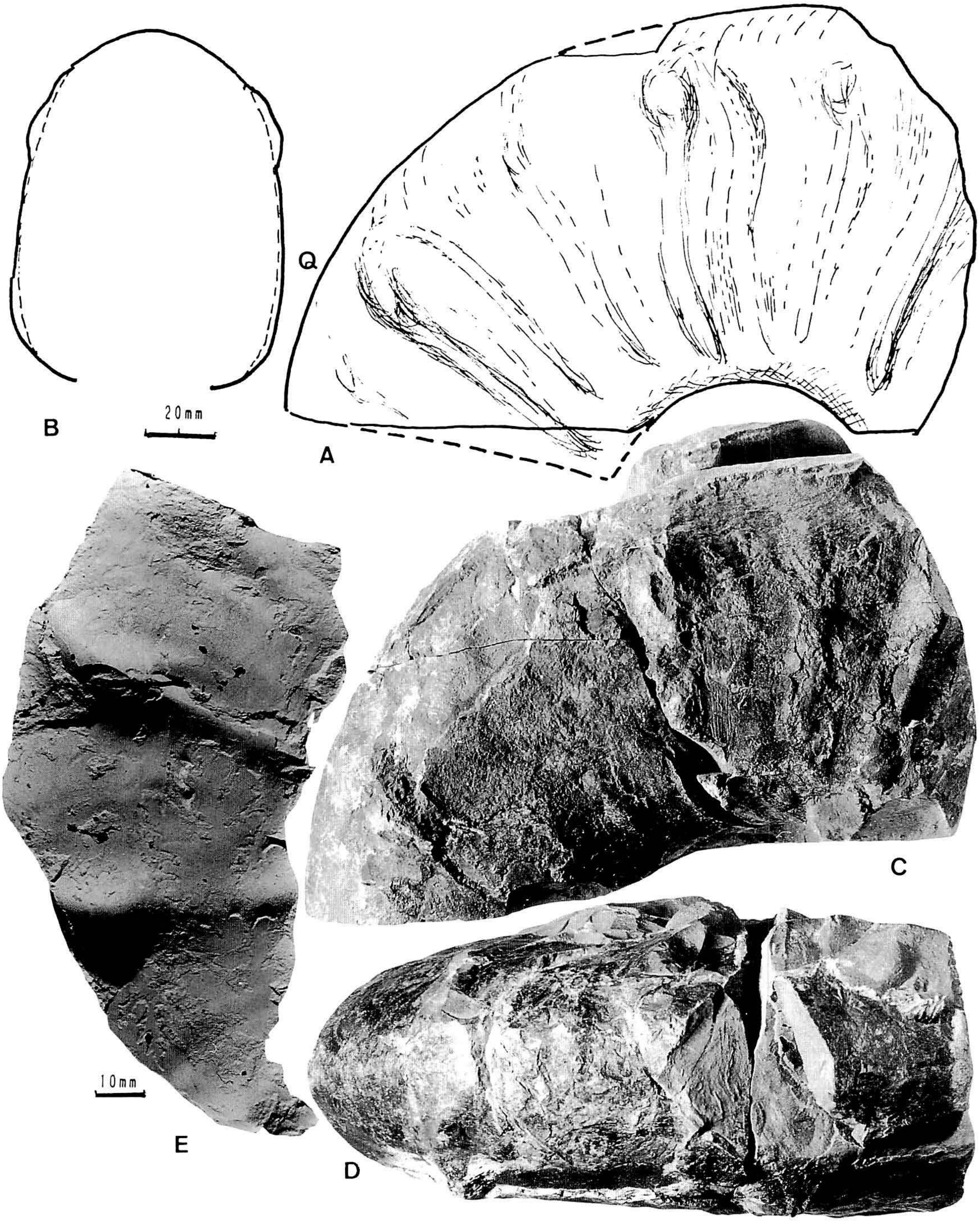

Figure 3. *Pseudaspidoceras flexuosum* Powell. Fragmentary pieces of the fourth specimen GK. H8367 from Y6015c, Taki-no-sawa of the Oyubari area. **A**-**D** : late part of the septate whorl in lateral view (**A, C**), whorl-section at Q (**B**) and ventral view (**D**). **E** : rubber model taken from the composite external mould of a middle-aged part of the same individual, showing impressed sutures. (T.M. *delin* ; photos by M. Noda)

Obirashibe area.

In the 3rd specimen from the Oyubari area, the inner ventrolateral (i.e., outer flank) tubercles are weakened or obsolete and the outer ventrolateral clavi are distinct. In this respect this form resembles the Madagascar specimens described by Collignon (1965, p. 29, pl. 388, fig. 1662; p. 31, pl. 389, fig. 1664) and some examples from western Texas (Kennedy *et al*., 1987, text-figs. 7A-C). The large but still septate 4th specimen shows distinctly the inner ventrolateral (or rather outer flank) tubercles but the outer ventrolateral clavi are obscure.

Despite a large number of specimens from western Texas, no example of complete preservation has been illustrated by Kennedy *et al.* (1987). An example from Hokkaido, shown in Figure 1, may therefore represent one of the best preserved specimens of *P. flexuosum*. In that specimen the last two sutures are approximated and situated at about 175 to 185 mm in diameter. Its body chamber occupies at least half a whorl, although its final ventral and outer lateral portions were destroyed.

Discussion.—On the basis of the two morphotypes from Hokkaido, I would suggest as a working hypothesis that they might represent the dimorphs, *viz.* a microconch which shows distinctly both the inner and outer ventrolateral tubercles even in the adult stage and a macroconch in which either of the inner and outer ventrolateral tubercles are reduced in more or less late growth-stages. The diameter of the latter in the adult stage is very large, being roughly twice as large as the former. Whether this interpretation could be maintained in a large number of specimens from the type locality in western Texas and contiguous areas or the feature is merely a variation should be decided by further investigation.

Occurrence.—Summarizing the locality records in the item *Material*, the described four specimens occur in the lower part of Member IIn, which is assigned certainly to the basal Turonian. Integrated data of biostratigraphy in this area are described in another paper by Matsumoto *et al.* (1991).

P. flexuosum is one of the most diagnostic species in the basal Turonian of western Texas (Kennedy *et al.* 1987) and has been reported to occur in New Mexico, Arizona, Colorado, Germany, Nigeria and Madagascar. This is the first record of *P. flexuosum* from Japan. The fact that four individuals were found within a limited area seems to suggest that this species is not rare in Japan. We should search for more examples in this and other areas in Hokkaido.

Genus *Neomphaloceras* Matsumoto and Obata, 1982

Type species.—*Yubariceras pseudomphalum* Matsumoto, 1975.

Diagnosis.—Very similar to *Cunningtoniceras* Collignon, 1937 in the shell-form, ornament and suture, but distinguished in having an additional row of lateral tubercles.

Discussion.—*Cunningtoniceras* Collignon, 1937 has been revived by Cobban (1987, p. 9), who noticed a peculiar sutural pattern in *Euomphaloceras* of the correct sense, which shows narrow E/L saddle and very broad, roughly bipartite L.

Cunningtoniceras has the normal acanthoceratid sutures and is regarded as a direct derivative of *Acanthoceras* (see Wright and Kennedy, 1987). It is characterized by multiple ribbing and tuberculation on the outer part of the whorl at least in part and also development of ventrolateral horns on the adult whorl. Cobban *et al.* (1989) have described three species of *Cunningtoniceras* recently found from the late Cenomanian *Metoicoceras mosbyense* Zone of New Mexico, whereas a rare example of *Cunningtoniceras* has been recorded from the Middle Turonian of Japan (Matsumoto and Suekane, 1989).

In my view, *Neomphaloceras* can possibly be regarded as a descendant of *Cunningtoniceras* acquiring an additional row of lateral tubercles. It retains ancestral characters in showing extra ribs and tubercles on the ventral part of immature whorls and horned ventrolateral tubercles in the adult. Its suture is also quite similar to that of *Cunningtoniceras*. A weak point in this interpretation is the apparent missing link in the latest Cenomanian and earliest Turonian (see discussion below). Possibly some marine biota may have been affected by frequent unfavourable conditions, such as anoxic events, during this time interval. One may recall here the almost absence of fossil nautiloids in Pliocene and Pleistocene strata until the rejuvenated appearance of the Recent species of *Nautilus* (Teichert and Matsumoto, 1988).

Neomphaloceras pseudomphalum
(Matsumoto)

Figures 4 and 5

Yubariceras pseudomphalum Matsumoto, 1975, p. 146, pl. 22, fig. 1.

Neomphaloceras pseudomphalum (Matsumoto): Matsumoto and Obata, 1982, p. 73, pl. 2, fig. 1; pl. 5, fig. 1.

Neomphaloceras pseudomphalum (Matsumoto): Matsumoto *et al*., 1985, p. 162, pl. 5, fig. 1.

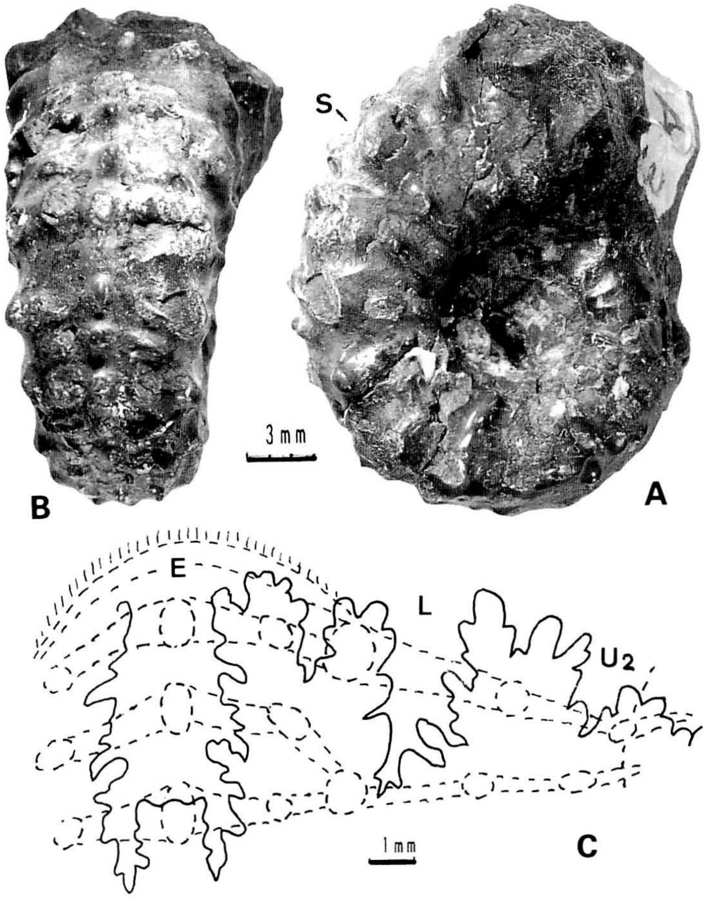

Figure 4. *Neomphaloceras pseudomphalum* (Matsumoto). An immature specimen, YCM. GP716. **A, B**: lateral and ventral views; **C**: external suture at S; ribs and tubercles are drawn by dotted lines; constriction-like groove hatched. (reproduced from Matsumoto and Suekane, 1987, pl. 4, figs. 1, 2 and text-fig. 3 of Sci. Rept. Yokosuka City Museum, no. 35 by permission).

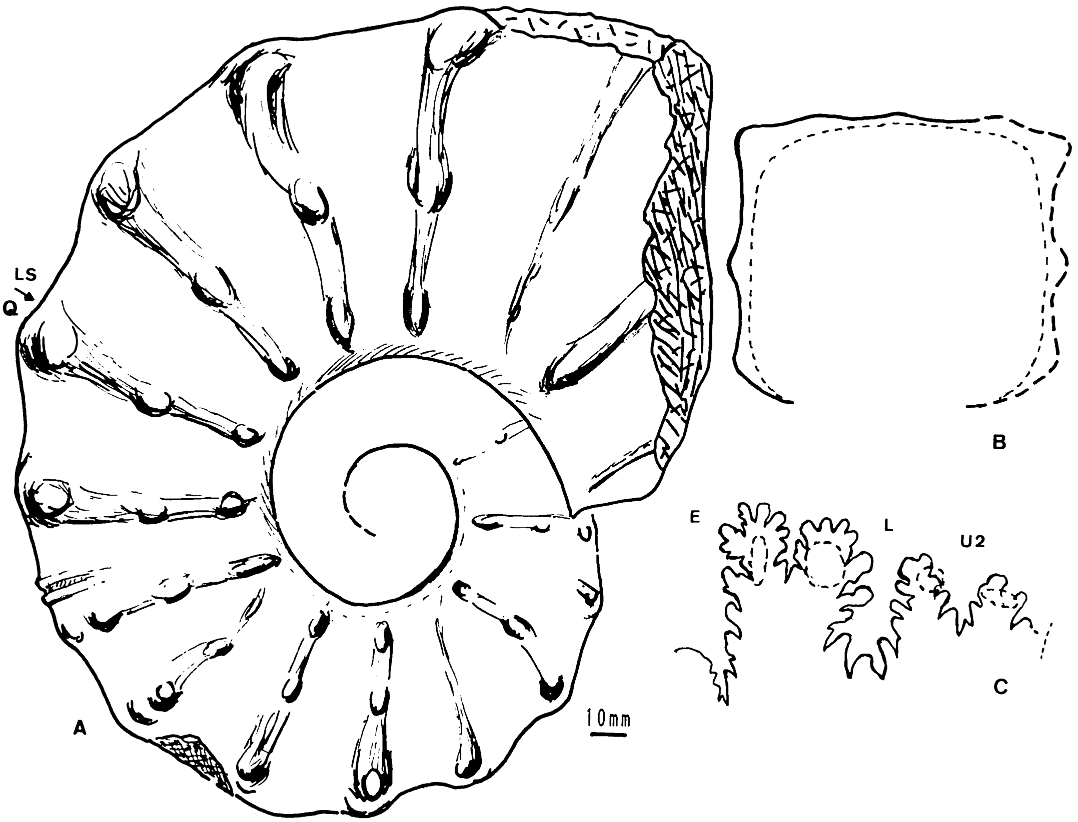

Figure 5. *Neomphaloceras pseudomphalum* (Matsumoto). An example of an adult shell, MCM. A175-1, from the Kaneobetsu-zawa of the Oyubari area. **A** : lateral view ; **B** : whorl-section at Q ; **C** : the second last suture. (T.M. *delin.*)

Neomphaloceras pseudomphalum (Matsumoto) ; Matsumoto and Suekane, 1987, p. 10, pl. 4, figs. 1-2, 4-7, 10-11 ; text-fig. 8.

Material.—In addition to the eight specimens described in the above-listed papers, here is a fine specimen, MCM. A175-1 (Figure 5) collected by Koji Hasegawa from an outcrop of the Kaneobetsu-zawa, Oyubari area.

Remarks.—The medium-sized holotype and YCM. 717, one of Suekane's specimens, represent the shell at middle growth-stage. The smaller paratype and the three specimens described by Matsumoto and Suekane (1987) show the characters of younger stages. The two larger specimens described by Matsumoto and Obata (1982) and Matsumoto *et al.* (1984) are adult but their body chambers are incomplete. K. Hasegawa's specimen represents a nearly complete adult shell. I have seen more specimens in Y. Kera's private collection from the Oyubari area. On the basis of these specimens the specific diagnosis may be given as follows :

Diagnosis.—The shell is fairly large in the adult and rather evolute, showing a moderate rate of whorl expansion, a little (i.e. about 1/4) involution and a moderately wide umbilicus. The whorl is somewhat broader than high (*e.g.*, $B/H = 1.24$ in measured examples) and widely subrectangular or subquadrate in cross section, with a broadly arched or nearly flat venter, subparallel flanks, abruptly bent umbilical shoulders and vertical umbilical wall.

At first the shell looks nearly smooth, only with constrictions and associated flares ; soon ribs appear on which tubercles are developed in nine rows. The young and middle-aged whorls have moderately strong primary ribs and also occasionally intercalated or branched, weaker or somewhat shorter ribs. These ribs are nearly rectiradiate on the main part of the flank and curved forward to form a ventral projection. There are furthermore branched or intercalated extra riblets normally with tubercles in three rows on the venter, some of which may be projected considerably and accompanied by a constriction-like groove. The tubercles are in nine rows, of which the three rows (i.e. umbilical, lateral and inner ventrolateral) on each flank are nearly equidistant (see Matsumoto, 1975, pl. 22, fig. 1 and Figure 4 of this paper).

The outer whorl of an adult shell, of which the body chamber occupies slightly more than half (i.e. about 200°), has distant major ribs with occasionally intercalated weaker and somewhat shorter ribs. The tubercles on the major ribs are prominent on the flank but much weakened or almost obsolete on the venter. The inner ventrolateral tubercles on the body chamber are especially strengthened into horn-like protuberances, amalgamating the weakened outer ventrolateral tubercles into their thickened basal part. A riblet associated with a narrow and shallow constriction may remain persistently on the ventral part of the last septate whorl. On the last portion of the body chamber a few nodeless ribs may occur probably as flanges on the apertural margin.

The suture is of typical *Acanthoceras* pattern, showing massive, bipartite E/L saddle and fairly narrow L.

Dimensions.—See Table 2.

Comparison and discussion.—The young to middle-aged form of this species resembles "*Acanthoceras*" *carvertense* Powell (1963, p. 315, pl. 33, figs. 8-9 ; pl. 34, figs. 6, 9 ; text-fig. 2e), from the Lower Turonian of west Texas-north Mexico, in shell form and ornamentation, but for the presence of an additional row of lateral tubercles in the former. As to the latter species Powell (1963, p. 136) suggested its affinity with *Kanabiceras*, i.e. *Euomphaloceras* redefined by Cobban (1987), whereas Kennedy *et al.* (1987, p. 33) referred it to *Kamerunoceras.*

Matsumoto *et al.* (1989, p. 30) have noted that there are two types of sutural pattern in the species of *Kamerunoceras* defined by Kennedy and Wright (1979) ; one is the normal type like that of *Acanthoceras*, as seen in *K. eschii* (Solger), the type species, and *K. turoniense* (d'Orbigny) and the other is the peculiar type like that of *Euomphaloceras* (in the sense of Cobban, 1987) as seen in the revived *Schindewolfites*. As I have not examined the specimens of '*Ac.*' *carvertense*, I can hardly decide which type of sutural pattern is shown by this species. The too brief description of the suture without illustration by Kennedy *et al.* (1987, p. 34) does not enlighten me. If its suture has narrow E/L

Table 2. Measurements (in mm) of *Neomphaloceras pseudomphalum*.

Specimen, remarks	D	U	H	B	B/H	MR : VR
Holotype, E(c)	93.0(1)	30.0(.32)	—	—	—	7 : 15
〃 E-45°(ic)	—	—	35.0	42.0	1.20	—
Paratype (c)	19.3(1)	6.6(.34)	7.5(.39)	10.2(.55)	1.24	—
Fig. 5 LS+70°(c)	206.0(1)	62.0(.30)	88.0(.43)	—	—	7 : 8
〃 LS(c)	167.0(1)	49.0(.29)	71.0(.43)	~88 (.53)	1.24	6 : 9

MR : VR = number of major ribs *versus* that of all ribs on venter per half whorl, (c) = costal, (ic) = intercostal. See Table 1 for others.

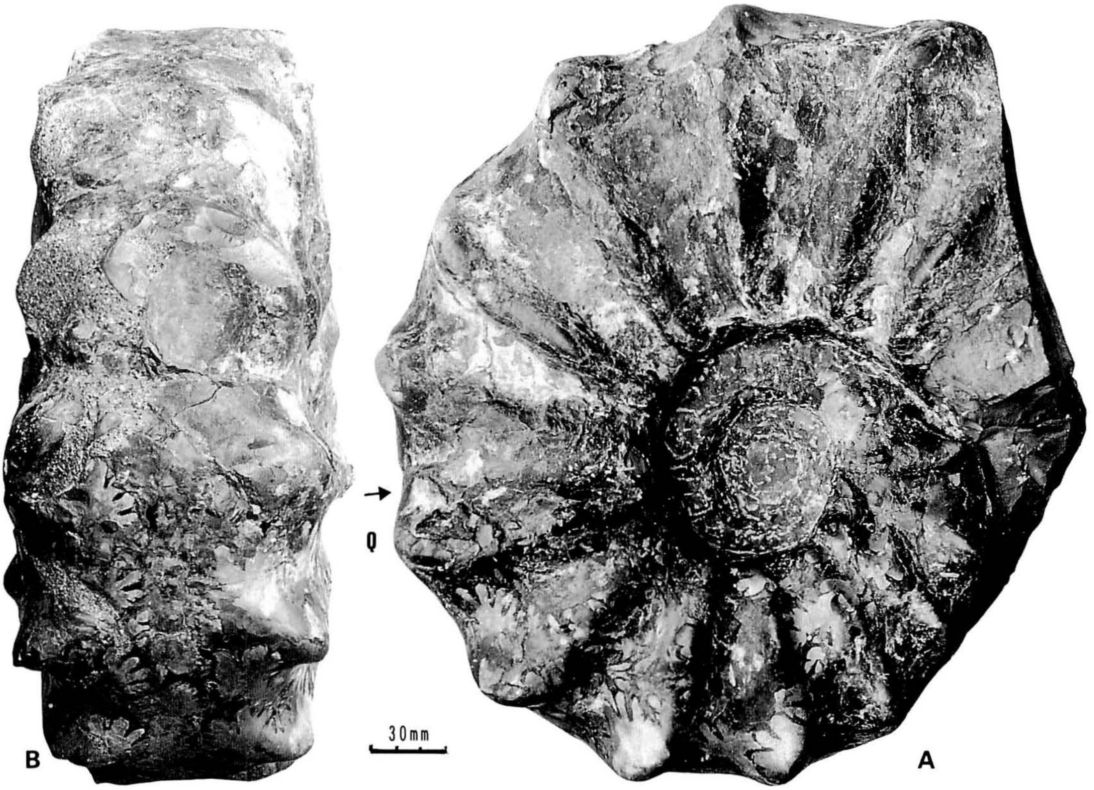

Figure 6. *Neomphaloceras costatum* (Matsumoto and Kawashita).
Lateral (**A**) and ventral (**B**) views of the holotype, MCM. A45-4. (Photos by M. Noda)

saddle and very broad L like that of *Euomphaloceras*, it should be assigned to *Schindewolfites* or rather to *Paraburroceras* Cobban, Hook and Kennedy, 1989. If it is normal *Acanthoceras* type, that species could be either *Kamerunoceras* or possibly immature *Cunningtoniceras*. In the latter case that species could be ancestral for *N. pseudomphalum*, being a candidate which could fill a part of the missing link mentioned in the foregoing page.

Occurrence.—So far as reliable locality records are concerned, this species occurs in the unnamed zone immediately below the zone where the typical form of *Inoceramus hobetsensis* Nagao and Matsumoto is characteristic in the Obirashibe, Ashibetsu and Oyubari areas. The known age is early Middle Turonian, although the true vertical range should be determined by further investigation.

Neomphaloceras costatum (Matsumoto and Kawashita)

Figures 6 and 7

Mammites costatus Matsumoto and Kawashita *in* Matsumoto *et al*., 1978, p. 5, pl. 1, figs. 1, 2; pl. 2, figs. 1, 2; text-figs. 1, 2.
Mammites wingi wingi Morrow; Wright and Kennedy, 1981, p. 80-81 (pars.).
Neomphaloceras cf. *pseudomphalum* (Matsumoto); Matsumoto *et al*., 1985, p. 163, pl. 6, fig. 1

Material.—The following specimens are reexamined, in which the temporary numbering in previous papers is indicated in brackets; holotype, MCM. A45-4 [Y. Kawashita's Coll. 51-8-20] (Figures 6, 7) in a nodule fallen loose in a small stream called the Shogakko-no-sawa, Kashima ; paratype, MCM. A45-5 [Kawashita's Coll. 51-11-14] (plaster cast GK. H9630) (Matsumoto *et al.*, 1978, pl. 1, fig. 2 ; pl. 2, fig. 2) from the outcrop of mudstone with interbeds of sandstone at loc. Y5201 on the right side of the Hakkinzawa ; another illustrated specimen under *Neomphaloceras* cf. *pseudomphalum* by Matsumoto *et al.* (1985, pl. 6, fig. 1), from the outcrop of mudstone at loc. Y5240 on the right bank of the Kaneobetsu-zawa, close to the confluence with the Shuparo River.

Diagnosis.—The whorl is rather evolute, expanding at a moderate rate, and encircles an umbilicus of moderate width. The adult shell is large, with diameter well over 300 mm in the holotype. The whorl is slightly broader than high and subquadrate in section, with a roughly flat venter, subparallel flanks ; abruptly bent umbilical edge and nearly vertical umbilical wall.

The ribs are distant on the outer whorl, as a rule alternately long and short on the septate part and almost all long on the adult body chamber, with occasional exceptions. The tubercles are in nine rows, *viz.* those at the umbilical edge on the long ribs, more or less bullate ; those somewhat inside the midflank, conical earlier but bullate later and which may weaken or become obsolete especially on some shorter ribs ; those at the inner ventrolateral shoulder are strong and thick, enlarging with growth, and horn-like on the adult body chamber ; the outer ventrolateral ones weakening and finally amalgamated by the basal part of the horns ; those on the siphonal line which may remain as traces (indistinct elevations) on the broadened but lowered ribs on the venter.

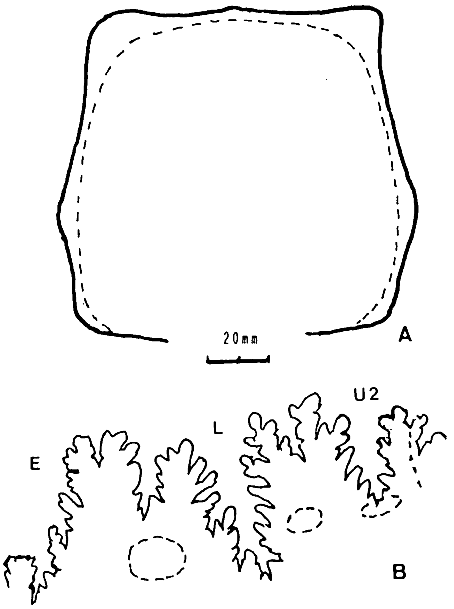

Figure 7. *Neomphaloceras costatum* (Matsumoto and Kawashita). **A** : whorl-section at Q of Fig. 6 ; **B** : the second last suture of the holotype. (T.M. *delin.*)

The ribs are nearly rectiradiate on the main part of the flank, gently curved forward on the outer flank toward the large ventrolateral nodes, and lowered and broadened on the venter, showing a broad convexity. A few extra riblets may remain faintly even on the venter of the adult stage. Near the apertural margin of the body chamber there are a few ribs which are not so widely separated as the ribs on the main part and the tubercles on them are blunted. They may have worked as flanges along the peristome at the final growth-stage.

The suture is of normal acanthoceratid pattern, showing deep E, massive, broad and bipartite E/L saddle, relatively narrow and fairly deep L, rather obscurely bipartite L/U2 saddle of moderate breadth and smaller U2 and auxiliaries.

Dimensions.—See Table 3.

Discussion.—*Mammites costatus* Matsumoto and Kawashita, 1978 was regarded by Wright and Kennedy (1981, p. 80) as a synonym of *Mammites wingi* Morrow, 1935 because of the good similarity in size, whorl section, ribbing and tuberculation. There is, however, an unmistakable difference in the suture. *M. wingi* has narrow (taller than wide) E/L saddle and peculiarly broad, bifid L. For this and other reasons Cobban and

Table 3. Measurements of *Neomphaloceras costatum*

Specimen, remarks	D	U	H	B	B/H	MR : VR
Holotype, E-30°(c)	324.0(1)	95.0(.29)	132.0(.41)	—	—	5 : 7
〃 Q in Fig. 7(c)	—	—	108.0	119.0	1.10	5 : 7
〃 2nd LS (ic))	—	—	105.0	112.0	1.07	5 : 7

Hook (1983, p. 9) have proposed the genus *Morrowites*, with *M. wingi* Morrow as its type species. I agree with them. Another point is that this species has a row of flank tubercles, which are added to and not displaced from the umbilical tubercles. Moreover, it has a siphonal row of tubercles, even if they weaken in the late growth-stage.

In short the said similarity is a homeomorphy and this species cannot be referred to *Morrowites wingi* nor to any species of *Mammites*. The development of *Mammites*-like horned ventrolateral tubercles on its subquadrate outer whorl is another homeomorphy. I was sorry to have carelessly assigned it to *Mammites*, but now I should refer it to *Neomphaloceras*.

Comparison.—N. costatum resembles *N. pseudomphalum* but they can be discriminated ; *viz. N. pseudomphalum* has broader whorls with larger ratios of B/H, narrower, less predominent ribs, more prominent tubercles, of which the laterals are more separated from the umbilical ones and the ventrolateral horns are more pronounced, as compared with *N. costatum*. They seem to be stratigraphically separated.

This species looks somewhat similar to *Mammites daviesi* Spath (1935, p. 415, fig. 1 ; pl. 32), from Ramri island (Southeast Asia), and to *M. mocamedensis* Howarth (1966, p. 6, pl. 3), from Angola, in the coarse ribbing, but the latter two species should be referred to *Morrowites* because of their pecliar sutures. They show no lateral tubercles or united ventrolateral horns.

Occurrences.—The age of this species was incorrectly inferred as early Turonian. Through the stratigraphic reinvestigation (Matsumoto *et al.*, 1991) it should be revised to Middle Turonian. The localities of the examined specimens are all in the *Inoceramus hobetsensis* zone of the Oyubari area and some of them (*e.g.*, Y5240) are rather in a higher part of this zone. I should, however, investigate further to know the true stratigraphic range of this species and its phylogenic relationship with *N. pseudomphalum*.

Genus *Mammites* Laube
and Bruder, 1887

Type species.—Ammonites nodosoides Schlüter, 1871.

Diagnosis.—The adult shell is fairly to very large in the type and related species but medium-sized in some others. The whorl is subquadrate to subrectangular or subtrapezoidal in section. The ribs are coarse and more or less distant but may be more crowded with branched or intercalated ones. The umbilical tubercle is conical and/or bullate ; the inner and outer ventrolateral tubercles normally more or less clavate, of which the inner one is prominent, enlarging on the outer whorl to a strongly protruded horn and absorbs the outer one. The suture is similar to that of *Acanthoceras*, showing fairly deep E, massive or broad, bipartite E/L saddle and rather narrow L.

Discussion.—Wright and Kennedy (1981, p. 75) stated that the relative width of E/L and L varies considerably in *Mammites*. I do not think the said variation is gradational, and recognize two different types. I agree with Cobban and Hook (1983, p. 9), who have established *Morrowites* for the *Mammites*-like ammonites in the shell-form and ornament but have an "unusually broad, bifid lateral lobe (L)" and rather narrow and tall E/L saddle. The difference is clearly shown by their illustrations (*op. cit.*, text-figs. 4, 5, 7 in comparison with text-fig. 2). How the unusual pattern was formed seems to be suggested by their text-fig. 6A, B. This is quite similar to what I stated (*in* Matsumoto *et al.*, 1989, p. 30) about the sutures of *Cunningtoniceras, Lotzeites* and *Euomphaloceras*.

Cobban and Hook (1983) described, besides the type species, *Morrowites wingi* (Morrow), *Morrowites depressus* (Powell), *Morrowites subdepressus* Cobban and Hook and *Morrowites* cf. *dixeyi* (Reyment). I have pointed out above that *Mammites daviesi* Spath and *M. mocamedensis* Howarth should be also referred to *Morrowites*.

Remarks.—Examples of *Mammites* do occur in the Cretaceous of Japan, but they are still few or poorly preserved. I should, however, provide here some information so that more material can be added in the future.

Mammites aff. *nodosoides* (Schlüter)

Mammites aff. *nodosoides* (Schlotheim); Matsumoto, 1981, p. 58, fig. 2.

Descriptive remarks.—I examined in the Mikasa City Museum a specimen collected by H. Oyobikawa from the Nakakinembetsu, a tributary of the Obirashibe River. Although its right side is dissolved in the rock matrix for a taphonomical reason, its left half is fairly well preserved. The dimensions (in mm) at the preserved end (intercostal) are as follows:

D=257 (1) U=98 (.38) H=91 (.35)
B (restored)=61 (.24) B/H=0.67

The body chamber is preserved for about half a whorl and is nearly complete. This ammonite is thus similar in size to some adult shells of *Mammites nodosoides* (Schlüter) (see Wright and Kennedy, 1981), but its whorl is more evolute and has a wider umbilicus than any illustrated or measured examples of *M. nodosoides*.

The ribs on the outer whorl of this specimen are distant and especially widely separated on the last part of the septate whorl and the early half of the body chamber. Intercalated shorter ribs occur only on the inner whorl. The umbilical tubercles are bullate and strengthen in the late stage. On the body chamber the ventrolateral horns are well developed, stretching upward and somewhat laterally.

The suture is of normal *Acanthoceras* type.

To sum up, this specimen generally resembles some examples of *M. nodosoides* in the ornament and suture, but there is some difference in the frequency of shorter ribs and degree of involution. Although there are a few more but poorly preserved specimens of *Mammites* from loc. R2307 (Nakakinembetsu) of the Obirashibe area and loc. Y6017 (Taki-no-sawa) of the Oyubari area, they are insufficient to know the extent of variation in our form. I should call the described specimen provisionally *Mammites* aff. *nodosoides* (Schlüter).

Occurrence.—Although the Lower Turonian Member Mj of the Middle Yezo Group is exposed fairly extensively along the River Naka-kinembetsu of the Obirashibe area, the exact point of the locality is not recorded for the described specimen. Loc. R2307 where a comparable specimen was obtained is certainly assigned to Member Mj and *Mytiloides goppelnensis* Badilet and Sornay occurs in the same member at a nearby locality. Another specimen at loc. Y6017 came from the Lower Turonian Member IIn in the Taki-no-sawa section of the Oyubari area.

Mammites sp. nov. (?)

Figure 8

Material.—A single incompletely preserved specimen, GK. H8371 (Fig. 8) collected by M. Koshizaka (August 10, 1972) from a transported nodule in the lower course of the Taki-no-sawa (640 m upstream from its mouth), Oyubari area.

Description.—Although the specimen is incomplete, it shows a part of the body chamber and some part of the septate whorl as shown in the photograph. For a taphonomical reason the left half is obscured but can be restored from the right half. Thus, its approximate intercostal dimensions (in mm) are as follows:

D=133 (1) U=48 (.36) H=49 (.37)
B=56 (.42) B/H=1.14

The whorl was originally somewhat broader than high. broadest at about the mid-height and subrounded in the intercostal section, with a broadly rounded to nearly flat venter and gently convex flank, which passes to a steeply inclined umbilical wall, without forming subangular edge. The whorl is

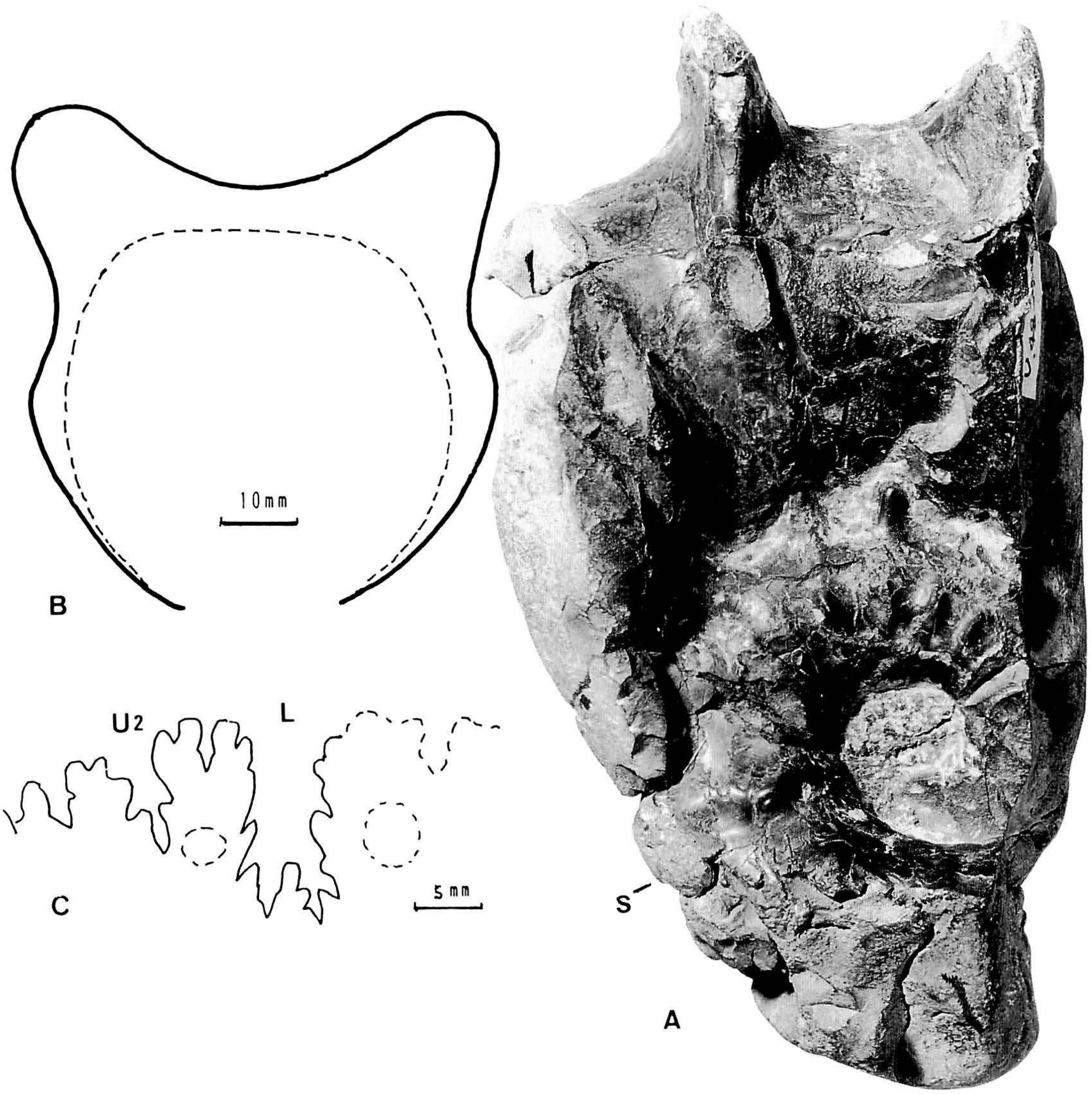

Figure 8. *Mammites* sp. nov. (?). GK. H8371 from the Taki-no-sawa, collected and donated by M. Koshizaka. **A**: lateral view; **B**: restored whorl-section; **C**: suture at S of **A**. (Photo by M. Noda; T. M. *delin.*)

rather evolute and the umbilicus is of moderate width.

The shell is ornamented with simple, rectiradiate, long and rather narrow ribs, which are widely separated on the outer whorl and their interspaces are somewhat wider than the ribs even on the next inner whorl. The ribs have bullate tubercles on the inner flank of the septate whorl and considerably high, bullate ones at the mid-flank of the body chamber. The inner ventrolateral tubercles are spinose on the septate whorl, stretching along the umbilical wall of the outer wall. The outer ventrolateral tubercles, which should exist at this stage, are not observable owing to the unfavourable state of preservation. On the body chamber the inner and outer ventrolateral tubercles are united into a high but rather narrow spatulate protuberance, which is not clavate but extends to a bar-like rib, running straight across the venter, though with decreasing height toward the mid-venter.

The suture is like that of normal *Mammites*; *viz.* E/L saddle is broad, L deeper than wide; L/U2 saddle situated on the row of inner lateral tubercles.

Comparison.—This specimen is distinct from the lectotype and other specimens of *Mammites nodosoides* in its subrounded intercostal whorl section, narrower major ribs without branched or intercalated minor ribs, narrowly bullate tubercles on the inner to middle part of the flank instead of rather conical umbilical nodes and the spatulate ventrolateral protuberances extending to the barlike ribs on the venter, instead of rather clavate ventrolateral horns, on the body chamber. Therefore, this specimen probably represents a new species, but I choose to postpone proposition of a new name until better preserved specimens can be obtained in situ from a well-defined stratigraphic position.

Discussion.—*Pseudaspidoceras cornucostale* Morrow (1935, p. 469, pl. 51, fig. 1; text-fig. 5), from the Greenhorn Formation of Kansas, seems to have somewhat spatulate ventrolateral horns on the outer whorl, but its ribs are thicker and have nodes at the umbilical edge. Its suture is quite dissimilar to that of normal *Mammites*, showing narrow and asymmetric E/L saddle and very broad L.

Occurrence.—As for *Material*. The place where Koshizaka collected this ammonite as a boulder is occupied by Middle Turonian strata. As the specimen is much eroded, it may have transported from a fairly upstream part where Lower Turonian strata are well exposed.

Acknowledgements

Director Mamoru Kera and Mr. Kikuo Muramoto of the Mikasa City Museum kindly afforded me facilities to study there, especially for the study of the valuable specimens which Messrs. Yoshitaro Kawashita, Koji Hasegawa and Hiroshi Oyobikawa collected. Mr. Masatada Koshizaka generously presented an interesting ammonite from his collection to Kyushu University for this study and Professor Hiromichi Hirano and Mr. Yasuharu Kera kindly showed me other interesting specimens with necessary information. I am grateful to Dr. W.A. Cobban and Dr. M.K. Howarth for their instructive suggestions. Dr. Masayuki Noda kindly helped me in the field work and also in taking photographs. Miss Akiko Murakami and Miss Kazuko Hara assisted me in preparing the typescript.

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北海道の白亜系チュロニアン産アカントケラス科アンモナイトについて：北海道の上部白亜系チュロニアン (以下 Tu と略記) の地層から産した次の5種のアンモナイトについて，その分類ならびに層序的産出の知見を更新して記述した。(1) *Pseudaspidoceras flexuosum* Powell。Tu 最下部の示準種である本種が複数地点の同じ層準 (大夕張の部層 IIn 最下部) から産出した。実は *P.* (*Ampakabites*) *kawashitai* Matsumoto & Obata は本種のシノニムである。(2) *Neomphaloceras pseudomphalum* (Matsumoto)。幼・中・成各期の標本に基づき特徴を明記した。中部 Tu の下部に産する。本属の系統は *Cunningtoniceras* 起源であろうと示唆した。(3) *Neomphaloceras costatum* (Matsumoto & Kawashita)。本種は当初 *Mammites* の新種, 後には *Morrowites wingi* (Morrow) のシノニムとされていたが, 再検討の結果 *Neomphaloceras* に入れるべきで，層準も中部 Tu の比較的上部である。(4) *Mammites* aff. *nodosoides* (Schlüter)。本当の *Mammites* は日本にもいた。*M. nodosoides* に似るが巻きが緩く臍が広い。稀だが下部 Tu (推定も含む) に産する。(5) *Mammites* sp. nov. (?) 越坂正直が大夕張滝の沢で採集・提供の標本で代表される。外側の肩の角状突起がへら状で巻きの方向に直交, その他特異な形質を示すが, 転石で保存も不完全なので, 新種の設立を差し控え，図示・記載して今後の追加資料を期する。 松本達郎

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928. LATE PERMIAN FUSULINACEAN FAUNA OF DOI PHA PHLUNG, NORTH THAILAND*

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Abstract. Eight species and seven genera of fusulinaceans are identified from two localities in the lower member of the Huai Thak Formation in the Doi Pha Phlung area, northeast of Lampang, north Thailand. They include *Reichelina* cf. *changhsingensis* Sheng and Chang, *Gallowayinella guidingensis* Liu, Xiao and Dong, *Palaeofusulina sinensis* Sheng, *P.* cf. *laxa* Sheng and *Codonofusiella* aff. *kwangsiana fusiformis* Sheng. This fusulinacean fauna is characterized by abundant *Gallowayinellà guidingensis* Liu, Xiao and Dong, is similar to that in the Changxing Limestone and its equivalents in South China, and indicates an early Changxingian or early Dorashamian age.

Key words. Changxingian, Doi Pha Phlung, Dorashamian, *Gallowayinella,* Huai Thak Formation, Upper Permian.

Introduction

The Upper Permian formations in Thailand are very restricted and paleontological information about them is limited in comparison to those of the Lower and Middle Permian. To date, Upper Permian foraminifers have been reported only from seven localities (Baum *et al.,* 1970 ; Brönnimann *et al.,* 1978 ; Sakagami and Hatta, 1982 ; Hahn and Siebenhüner, 1982 ; Ingavat, 1984).

In the summer of 1988, we visited the Doi Pha Phlung area and collected many rock samples containing abundant Upper Permian fossil remains from the Huai Thak Formation. This area is situated about 10 km southwest of Ngao in the Lampang district of north Thailand (Figure 1), and Sakagami and Hatta (1982) reported the Late Permian *Palaeofusulina-Colaniella* Fauna from limestone blocks collected at the eastern foot of Khao Doi Pha Phlung.

In this paper, a unique fusulinacean fauna found at two localities in the lower member of the Huai Thak Formation, in which *Gallowayinella guidingensis* Liu, Xiao and Dong is abundant, is described. The faunal affinity and correlation are also discussed with special reference to the stratigraphic distribution of the genus *Gallowayinella.*

All specimens identified in this paper are deposited in the Collection of the Department of Earth and Planetary Sciences, Faculty of Science, Kyushu University. The abbreviation GK.D is the prefix for the specimens' repository numbers.

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Previous works and geologic setting

In the Lampang district, the Permian formations, generally called the Ratburi Group in Thailand, are widely distributed. Piyasin (1972) divided the Ratburi Group in this area into the following three formations in ascending order, namely, the Kiu Lom, Pha Huat and Huai Thak. The first two yield *Pseudoschwagerina* sp. and *Neoschwagerina* sp., and are correlated with the Lower and Middle Permian, respectively.

The Huai Thak Formation in the Doi Pha Phlung area may be divided into lower and upper members. In the lower member, black shale is predominant with a subordinate amount of calcareous shale, sandstone and lenticular limestone. The upper member consists mainly of massive to weakly stratified limestone (the "Doi Pha Phlung Limestone") with black shale. The general strike of the Huai Thak Formation is almost north to south and its dips gently to the east.

Sakagami and Hatta (1982) identified the *Palaeofusulina-Colaniella* Fauna from four limestone blocks collected at the eastern foot of Khao Doi Pha Phlung, which may have come from the "Doi Pha Phlung Limestone". They compared this fauna to the late Late Permian *Palaeofusulina-Colaniella* Fauna and most probably to the *Palaeofusulina sinensis-Colaniella parva* Fauna of Ishii, Okimura and Nakazawa (1975).

Later, Waterhouse (1983) reported a rich brachiopod fauna from three localities included in two horizons in the lower part of the Huai Thak Formation. This brachiopod fauna is characterized by abundant *Oldhamina squamosa* Huang, and is closely similar to that in the early Changxingian of South China, which is assigned to the early Dorashamian.

Recently, Ishibashi and Chonglakmani (1990) reported a small ammonoid fauna comprising *Pseudogastrioceras* aff. *szechuanense* Chao and Liang, *Paratirolites nakornsrii* Ishibashi and Chonglakmoni and *Xenodiscus ?* sp. from the shale bed in the uppermost part of the Huai Thak Formation. They concluded that the geologic age of this fauna is late Dorashamian.

The fusulinacean fauna characterized by abundant *Gallowayinella guidingensis* Liu, Xiao and Dong was found at two localities in the lower part of the Huai Thak Formation (Figure 1). One locality (Loc. HT 1) is at the left bank of the Huai Mae Phlung river, about 1.5 km north of the summit of Khao Doi Pha Phlung, and is one of Waterhouse's brachiopod localities. At this locality, a black shale member of about 3 m in thickness crops out, and abundant brachiopods and foraminifers, and sparse trilobites, bryozoans, bivalves and corals were found. Fusulinaceans were found in the lower part of this outcrop.

Another locality (Loc. HT 2) is situated at about 750 m southwest of Loc. HT 1. It is a thin lenticular conglomeratic limestone exposed on the northern ridge of Khao Doi Pha Phlung. This limestone is mainly composed of coarse crinoidal and algal remains with micritic matrix.

The stratigraphic relationship between these two localities is not confirmed directly because of the poor exposure. Judging from the general dip and strike, however, the former horizon may be slightly lower than the latter. The latter one is succeeded by the "Doi Pha Phlung Limestone" with a considerable stratigraphic interval.

Faunal affinity and correlation

As shown in Table 1, eight species among seven genera of fusulinaceans were identified from Locs. HT 1 and HT 2.

In the fusulinacean fauna, *Gallowayinella*

Table 1 List of fusulinaceans from the lower member of the Huai Thak Formation.

Species	HT1	HT2
Reichelina cf. *changhsingensis*	+++	++
Primoriina sp.		+
Gallowayinella guidingensis	+++	+++
Palaeofusulina sinensis	++	+
P. cf. *laxa*	+	
Codonofusiella aff. *kwangsiana fusiformis*	+	
Sphaerulina sp.	+	
Kahlerina? sp.	+	

+++ : abundant, ++ : common, + : rare

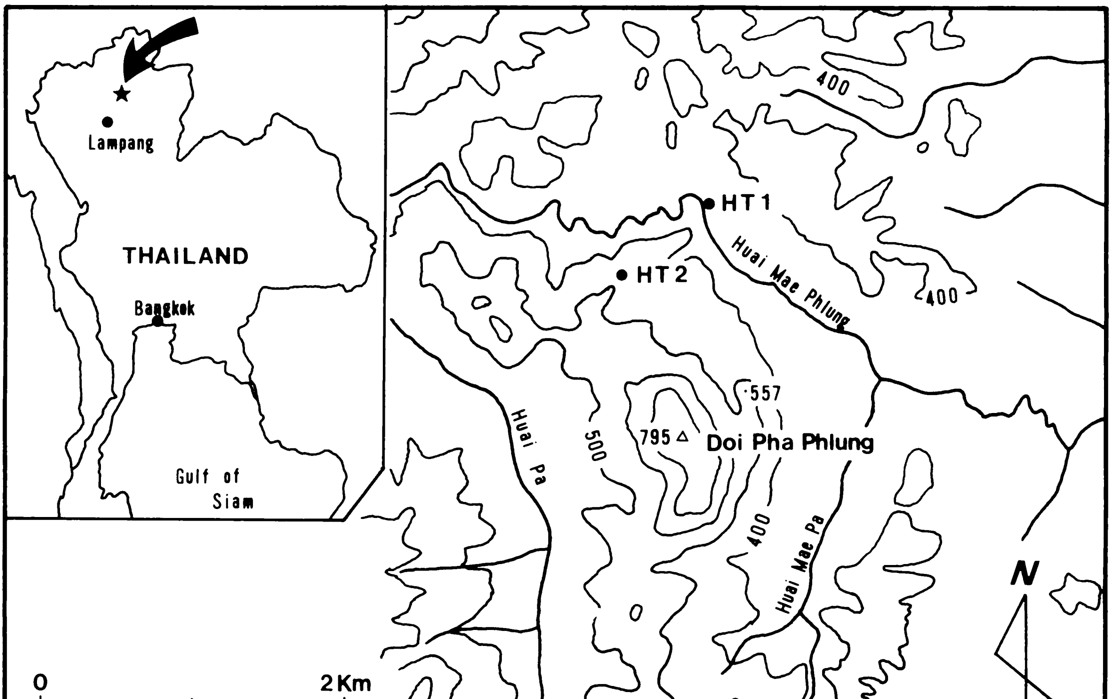

Figure 1. Map showing the fossil localities.

guidingensis Liu, Xiao and Dong is abundant at both localities. *Reichelina* cf. *changhsingensis* Sheng and Chang is abundant at Loc. HT 1, and common at Loc. HT 2. *Palaeofusulina sinensis* Sheng is common at Loc. HT 1, but very rare at Loc. HT 2. *Codonofusiella* aff. *kwangsiana fusiformis* Sheng is identified from only one specimen from Loc. HT 1. Smaller foraminifers are very rich at both localities and these assemblages are similar.

Fusulinacean foraminifers are one of the most important and reliable fossils for examining the geologic age of Permian strata. *Palaeofusulina sinensis* was originally described by Sheng (1955) from the Changxing (Changhsing) Limestone of Guizhou (Kueichow), Sichuan (Szechuan) and Jiangxi (Kiangsi) districts in South China. This species has hitherto been reported from many localities of the Changxing Limestone or its equivalents in the eastern part of the Tethyan region, and its biostratigraphic distribution is restricted to the Changxingian or Dorashamian of the Upper Permian. *Palaeofusulina laxa* was originally described by Sheng (1963) also from the Changxing Limestone.

The genus *Reichelina* flourished in the Late Permian in the Tethyan region, although its first appearance is in the late Artinskian (Toriyama, 1971). *Reichelina changhsingensis* Sheng and Chang, one of the most common species of the genus in the eastern Tethys, has been reported from the Wujiaping (Wuchiaping) Limestone and Changxing Limestone in South China (Sheng and Chang, 1958 and others).

The biostratigraphic distribution and geologic age of the genus *Gallowayinella* have been discussed by many fusulinacean students since the middle of this century. Sheng (1955) reported fusulinacean faunas from the Upper Permian Changxing Limestone in Jiangxi, southern Sichuan and central Guizhou districts, and he stated that the *Gallowayinella* Horizon is possibly correlated with that of the *Palaeofusulina* Horizon, although the stratigraphic relationship between *Gallowayinella* and *Palaeofusulina* is not known exactly.

Sheng and Lee (1974) showed that the genus *Gallowayinella* is one of the main constituents of the *Codonofusiella* Zone in South China, which is equivalent to the Wujiapingian of the Upper Permian.

Sheng and Rui (1980) biostratigraphically reexamined 22 *Gallowayinella* localities in seven areas in South China. They concluded that the *Gallowayinella meitienensis* Subzone can be established in the lower part of the *Palaeofusulina* Zone, and the genus *Gallowayinella* is one of the marker fossils which characterize the beginning of the Changxingian.

Lin (1980) discussed the age and stratigraphic significance of the genus *Gallowayinella* in South China. He established the following three fusulinacean zones in the Lopingian Stage: *Codonofusiella lui, Gallowayinella meitienensis* and *Palaeofusulina sinensis* Zones in ascending order. According to him, the first zone corresponds to the Wujiapingian, while the other two correspond to the Changxingian. He concluded that the stratigraphic distribution of the genus *Gallowayinella* is restricted to the lower part of the Changxing Limestone, and the boundary between the Changxing Limestone and the Wujiaping Limestone can be drawn at the base of the *Gallowayinella meitienensis* Zone.

Luo and Zhang (1987), on the other hand, emphasized the biostratigraphic importance of the genus *Gallowayinella* not only in the lower part of the *Palaeofusulina* Zone but also in the upper part of the *Codonofusiella* Zone in South China, based on a stratigraphic evidence observed in Shanggao, the Jiangxi district.

As mentioned above, the genus *Gallowayinella* has been reported from the upper Wujiapingian and lower Changxingian of South China, although it is common in the lower Changxingian.


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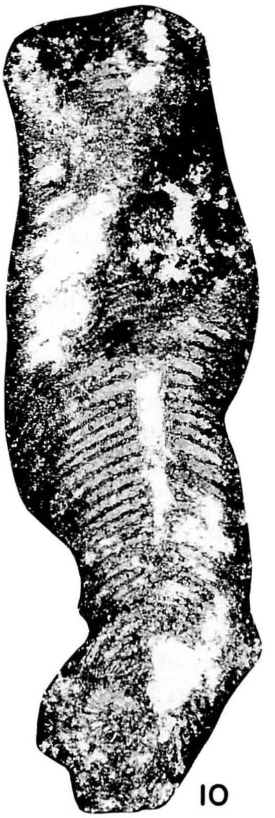
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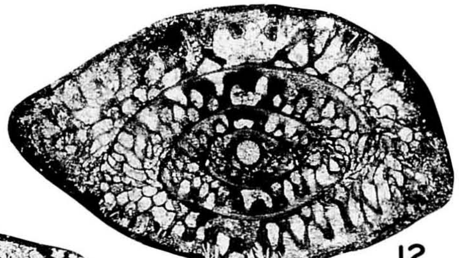
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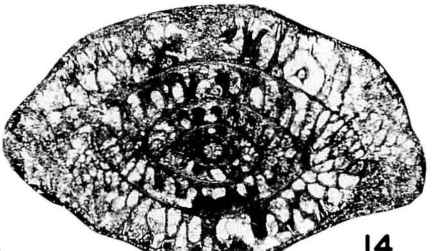
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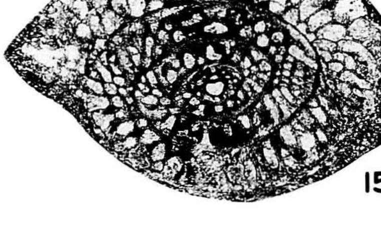
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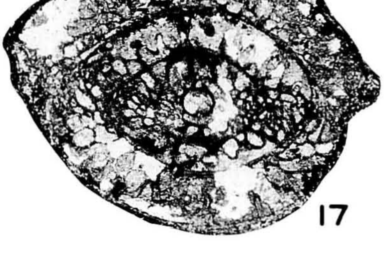
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In the Doi Pha Phlung area, *Gallowayinella guidingensis* Liu, Xiao and Dong occurs in association with *Reichelina* cf. *changhsingensis* Sheng and Chang, *Palaeofusulina sinensis* Sheng and *P.* cf. *laxa* Sheng. This fusulinacean fauna is quite similar to that in the lower Changxingian reported from many areas in South China and is considered to be of early Changxingian or early Dorashamian age. Consequently, the lower part of the Huai Thak Formation is correlated with the lower Dorashamian. This conclusion is consistent with that obtained from the brachiopod fauna by Waterhouse (1983).

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 *Reichelina* Erk, 1942

Reichelina cf. *changhsingensis*
Sheng and Chang, 1958

Figures 2-1 – 11, 4-3

Compare. –

Reichelina changhsingensis Sheng and Chang, 1958, p. 207, 211-212, pl. 1, figs. 1-11 ; Sheng, 1963, p. 27-28, 150-151, pl. 1, figs. 23-29 ; Sheng, 1966, p. 18, pl. 1, fig. 11 (same as pl. 1, fig. 1 of Sheng and Chang, 1958, p. 207, 211-212) ; Lin *et al.*, 1977, p. 13, pl. 2, fig. 7 ; Igo and Igo, 1977, p. 93, pl. 13, figs. 21-24 ; Liu *et al.*, 1978, p. 14, pl. 1, figs. 6-8 (6-7 : same as pl. 1, figs. 30, 39 of Sheng, 1963, p. 27-28, 150-151) ; Chen and Yang, 1978, p. 22, pl. 3, figs. 26-27 ; Sun, 1979, pl. 1, figs. 8-9, 14 ; Rui, 1979, pl. 1, fig. 5 ; Sakagami, 1980, figs. 2-1-2, 5-6, 10 ; Zhao *et al.*, 1981, pl. 4, figs. 1-6 ; Wang *et al.*, 1981, p. 15-16, pl. 21, figs. 3-8 ; Wang *et al.*, 1982, p. 11, pl. 1, figs. 31-32 ; Sun *et al.*, 1983, p. 7, pl. 1, figs. 12-13 ; Igo, 1983, p. 104, pl. 1, figs. 7-8 ; Sheng and Rui, 1984, p. 33, pl. 1, figs. 1-2 ; Chen, 1984, p. 17, pl. 1, fig. 18 ; Yang, 1985, pl. 1, figs. 19-20 ; Yamagiwa and Hisada, 1986, p. 181-182, pl. 1, figs. 1-15 ; Kobayashi, 1986, p. 141, pl. 3, figs. 20-25, 28 ; Gu, 1987, pl. 5, figs. 1-3 ; Zhu, 1989, pl. 5, figs. 7-8 ; Zhu, 1990, p. 40, pl. 1, fig. 1.

Reichelina aff. *changhsingensis* Sheng and Chang, Sakagami and Hatta, 1982, p. 5, pl. 1, figs. 1-3.

Material studied. – Axial sections ; GK.D 14727b, GK.D 14727c from Loc. HT 1 and GK.D 14743 from Loc. HT 2. Tangential sections ; GK.D 14731c, GK.D 14718, GK.D 14725 from Loc. HT 1 and GK.D 14735 from Loc. HT 2. Parallel sections ; GK. D 14728b and GK.D 14721 from Loc. HT 1. Diagonal sections ; GK.D 14715, GK.D 14728a from Loc. HT 1 and GK.D 14734 from Loc. HT 2. Additional specimens were also available from both localities.

Description. – Shell minute, discoidal with angular periphery and straight axis of coiling. Mature specimens having 4 to 4 ½ volutions, 0.19 to 0.22 mm in length and 0.61 to 1.55 mm in width, giving form ratios of 0.13 to 0.36.

Inner 3 ½ to 4 volutions uniformly coiled, but the last half one becomes expanded rapidly and forms a cockscomb-like uncoiling part. It attains a size 2 or 3 times larger than inner coiling part. Radius vectors of the first to fourth volution of illustrated typical axial section (Figure 2-4) 0.06, 0.14, 0.21 and 1.30 mm, and form ratios 0.33, 0.36, 0.38 and 0.08, respectively.

Proloculus spherical and minute, being 0.03 to 0.04 mm in outside diameter.

Spirotheca thin, composed of a tectum and

← **Figure 2. 1-11.** *Reichelina* cf. *changhsingensis* Sheng and Chang, **3a, 4, 5** : axial sections, GK.D 14727b, GK.D 14727c, GK.D 14743, **6, 8, 9** : tangential sections, GK.D 14735, GK.D 14731c, GK.D 14718, **7, 10** : parallel sections, GK.D 14728b, GK.D 14721, **1, 2, 11** : diagonal sections, GK.D 14715, GK.D 14728a, GK.D 14734, ×40, **3b** : enlargement of **3a**, ×75. **12-16.** *Palaeofusulina sinensis* Sheng, **12, 14, 15** : axial sections, GK.D 14729a, GK.D 14722, GK.D 14729c, **16** : sagittal section, GK.D 14714, **13** : tangential section, GK. D 14729b, ×30. **17** : *Palaeofusulina* cf. *laxa* Sheng, axial section, GK.D 14720, ×30.

Table 2. Measurements of *Reichelina* cf. *changhsingensis* Sheng and Chang. F.R. : Form ratio, D.P. : Diameter of proloculus (in mm).

	Reg. no.	Fig.	Length	Width	F.R.	D.P.	Radius vector				
							1	2	3	4	4 ½
1	GK. D 14727b	2-3	0.20	0.75	0.27	0.04	0.06	0.09	0.15	0.22	0.53
2	GK. D 14727c	2-4	0.19	1.55	0.13	0.04	0.06	0.14	0.21	1.30	
3	GK. D 14743	2-5	0.22	0.61	0.36	0.03	0.07	0.11	0.19	0.39	

	Form ratio				
	1	2	3	4	4 ½
1	0.36	0.39	0.40	0.41	0.09
2	0.33	0.36	0.38	0.08	
3	0.46	0.51	0.46	0.27	

probably diaphanotheca. Septa also thin and not fluted. Chomata low and broad, extending to axial regions. Tunnel path straight.

Remarks.—The present form closely resembles *Reichelina changhsingensis* which was originally described by Sheng and Chang (1958) from the Changxing Limestone on the southern slopes of Dameishan (Tameishan) and Daoduishan (Taotuishan) of South China, except for having a more expanded last volution.

Sakagami and Hatta (1982) described *Reichelina* aff. *changhsingensis* Sheng and Chang from the limestone blocks at the eastern foot of Khao Doi Pha Phlung. They stated that *Reichelina* aff. *changhsingensis* Sheng and Chang is seemingly very close to *R. changhsingensis* Sheng and Chang in its general features, except for a more expanded last volution. The present form is probably conspecific with *Reichelina* aff. *changhsingensis* Sheng and Chang described by Sakagami and Hatta (1982).

Measurements.—See Table 2.

Occurrence.—Abundant in Loc. HT 1 and common in Loc. HT 2.

Genus *Primoriina* Sosnina, 1981

Primoriina sp.

Figures 4-6–7

Material studied.—Axial sections; GK.D 14740 and GK.D 14742 from Loc. HT 2.

Descriptive remarks.—Shell minute and thick lenticular with angular periphery. Specimen of 4 volutions (Figure 4-6) 0.26 mm in length and 0.37 mm in width, giving a form ratio of 0.70.

The present form is similar to *Primoriina rotunda* described by Sosnina (1981) from the *Metadoliolina lepida* Zone of Sikhote-Alin in USSR. However, the specific identification is postponed owing to the insufficiency of Doi Pha Plung materials.

Occurrence.—Rare in Loc. HT 2.

Family Boultoniidae Skinner and Wilde, 1954

Genus *Gallowayinella* Chen, 1934

Gallowayinella Chen, Thompson, 1964, p. C406; Lin *et al.*, 1977, p. 43; Wang *et al.*, 1982, p. 30; Sheng *et al.*, 1988, p. 74-75.

Gallowaiina Chen, 1934, p. 237; Rozovskaya, 1975, p. 62; Loeblich and Tappan, 1988, p. 261.

Gallowaiinella Chen, Dunbar and Skinner, 1937, p. 571-572; Dunbar and Henbest, 1942, p. 85; Thompson, 1948, p. 45; Sheng, 1955, p. 292; Chen, 1956, p. 2, 21; Rauser-Chernoussova and Fursenko, 1959, p. 211-212; Sheng, 1966, p. 69; Leven, 1967, p. 131; Liu *et al.*, 1978, p. 25;

Chen and Yang, 1978, p. 41.
Gallowayina Chen, Thompson, 1964, p. C406 (not *Gallowayina* Ellis, 1932).

Type species.—*Gallowaiina meitienensis* Chen, 1934.

Remarks.—The generic name *Gallowaiina* dedicated to J.J. Galloway was originally proposed by Chen (1934). Dunbar and Skinner (1937) proposed the new name *Gallowaiinella* for *Gallowaiina,* since the name *Gallowaiina* may be construed as an inadvertent error in spelling this surname as a base for the generic name and is automatically correctable to *Gallowayina* which has been preoccupied by Ellis (1932). After that, Thompson (1964) noted that the generic name *Gallowaiinella* is also defective in the same way as *Gallowaiina* (ICZN Arts. 32(d) and 52(f)) and should be emended to *Gallowayinella.* He also stated that this seemed to be the most acceptable nomenclatural solution, although he commented that it would be necessary to recognize the validity of *Gallowaiina,* since it differs by a single letter from *Gallowayina* Ellis (ICZN Art. 56(b)). Recently, Loeblich and Tappan (1988) restored the generic name to *Gallowaiina,* which Chen was originally proposed in 1934.

In the case of *Gallowaiina* Chen, 1934, ICZN Art. 52(f) would be more effective because it is named in honor of J.J. Galloway, although both ICZN Arts. 52(f) and 56(b) come into existence. Consequently, the generic name *Gallowayinella* seems to be suitable instead of *Gallowaiina.*

Up to the present, the following 16 species and one variety from the Lopingian of South China have been proposed by the Chinese students. Among them, nine species are valid as follows.

Gallowayinella meitienensis Chen, 1934
G. meitienensis var. *evoluta* Chen, 1934 (= *Palaeofusulina evoluta)*
G. wutuensis Kuo, 1948 (= *Wutuella wutuensis*; type species of *Wutuella* Sheng, 1963)
G. minima Chen. 1956 (= *Lantschichites minima)*
G. decora Lin, 1977
G. cylindrica Deng, 1977
G. fusiformis Zhou, 1977
G. megalocula Yang, 1978 (= *G. meitienensis* Chen)
G. cervicalis Yang, 1978 (= *G. meitienensis* Chen)
G. angulata Yang, 1978
G. guidingensis Liu, Xiao and Dong, 1978
G. quasicylindrica Ding, 1978 (= *Ziguiella quasicylindrica*; type species of *Ziguiella* Lin, 1980)
G. laxa Lin, 1980 (= *G. guidingensis* Liu, Xiao and Dong)
G. jiaogensis Zhang, 1981
G. ellipsoidalis Wang, 1982 (= *G. meitienensis* Chen)
G. histoformis Xie, 1982
G. lepingensis Sheng and Rui, 1984

Geologic age.—Late Wujiapingian to early Changxingian or late Dzhulfian to early Dorashamian (Late Permian).

Geographic distribution.—Pamir, USSR (Leven, 1967), North Thailand (this study), South China (Chen, 1934 and others).

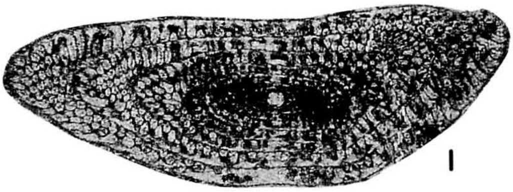
Gallowayinella guidingensis Liu, Xiao and Dong, 1978

Figures 3-1–15, 4-8–10

Gallowayinella guidingensis Liu, Xiao and Dong, 1978, p. 25-26, pl. 3, figs. 8-9; Lin, 1980, pl. 1, fig. 2.
Gallowayinella cylindrica Deng, Lin, 1980, pl. 1, fig. 3.
Gallowayinella laxa Lin, 1980, p. 41, pl. 1, figs. 4-5.

Material studied.—Axial sections; GK.D 14731a, GK.D 14724a, GK.D 14730, GK.D 14723, GK.D 14716, GK.D 14731b, GK.D 14726, GK.D 14711, GK.D 14713 from Loc. HT 1 and GK.D 14738, GK.D 14737, GK.D 14741, GK.D 14733 from Loc. HT 2. Sagittal sections; GK.D 14719, GK.D 14717 from Loc. HT 1 and GK.D 14739 from Loc. HT 2. Slightly oblique axial section; GK.D 14736 from Loc. HT 2. Axial section of immature specimen; GK.D 14727a from Loc. HT 1. In addition, some other specimens from Locs. HT 1 and HT 2 were studied.

Description.-Shell large for genus, subcylindrical to elongately fusiform with almost straight to gently arched median portion and bluntly pointed polar ends. Mature specimens having 6 to 7 volutions, 4.33 to 5.60 mm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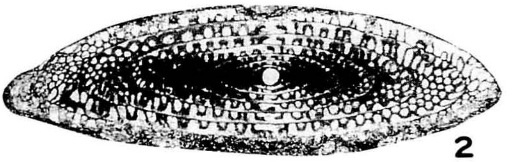
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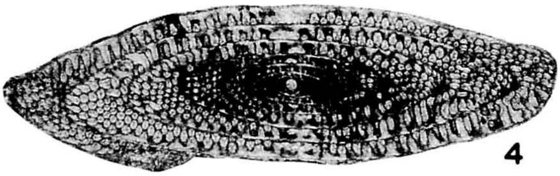
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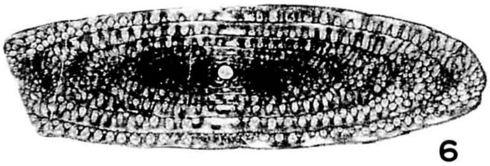
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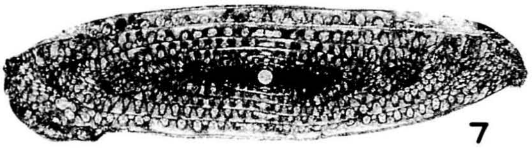
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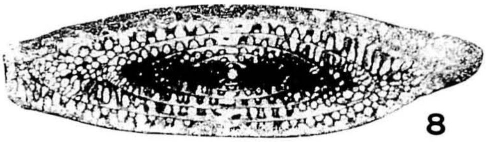
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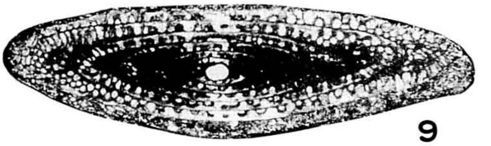
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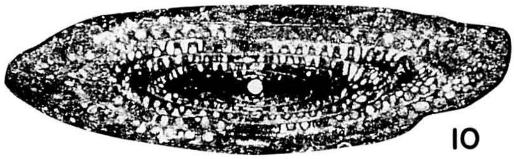
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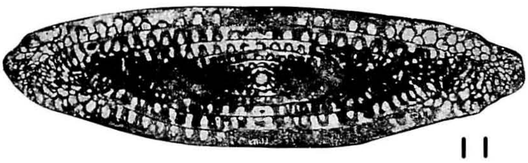
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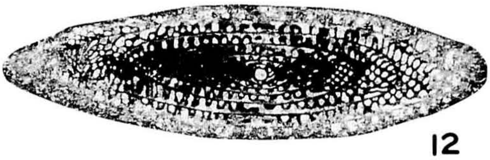
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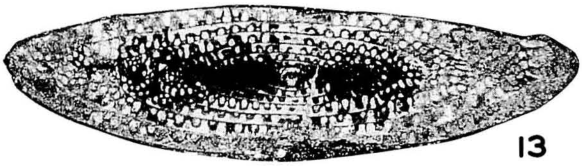
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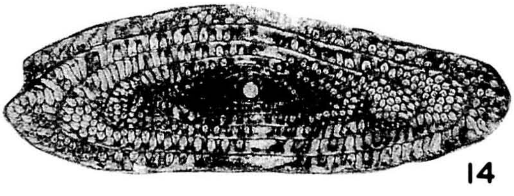
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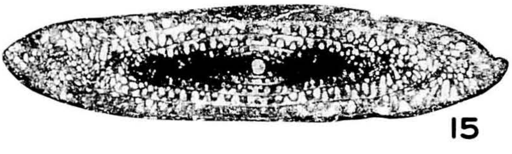
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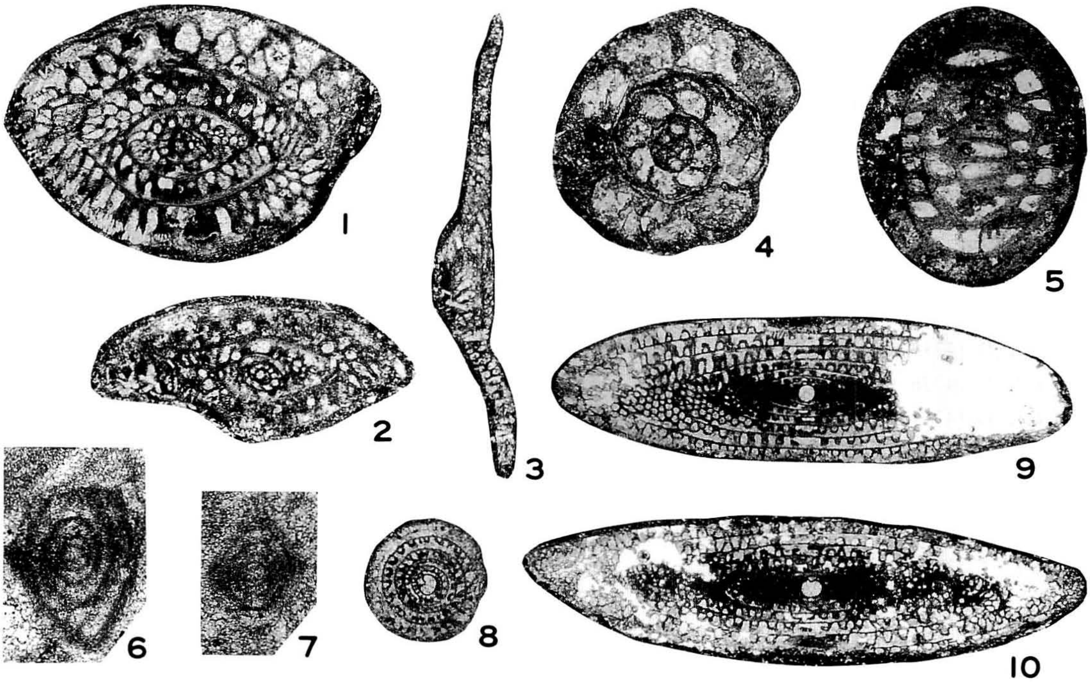

Figure 4. **1**: *Palaeofusulina sinensis* Sheng, tangential section, GK.D 14732, ×30. **2**: *Codonofusiella* aff. *kwangsiana fusiformis* Sheng, axial section, GK.D 14724b, ×40. **3**: *Reichelina* cf. *changhsingensis* Sheng and Chang, tangential section, GK.D 14725, ×40. **4**: *Kahlerina ?* sp., sagittal section, GK.D 14712, ×40. **5**: *Sphaerulina* sp., tangential section, GK.D 14728c, ×20. **6, 7**: *Primoriina* sp., axial sections, GK.D 14740, GK.D 14742, ×75. **8-10.** *Gallowayinella guidingensis* Liu, Xiao and Dong, **8**: sagittal section, GK.D 14717, **9, 10**: axial sections, GK.D 14711, GK.D 14713, ×15.

in length and 1.10 to 1.50 mm in width. Form ratio ranges from 3.41 to 4.36, averaging 3.80 for 26 specimens.

Inner 1 to 2 volutions tightly coiled, but outer ones expanded uniformly. Axis of coiling straight throughout. Average radius vectors of the first to seventh volutions, for 10 specimens 0.12, 0.17, 0.25, 0.34, 0.46, 0.57 and 0.69 mm, and form ratios 2.28, 3.10, 3.53, 3.96, 4.08, 4.02 and 3.62, respectively.

Proloculus commonly spherical, but slightly compressed in some specimens. Outside diameter of proloculus ranges from 0.11 to 0.24 mm, averaging 0.16 mm for 54 specimens.

Spirotheca thin, composed of an upper thin tectum and lower hyaline layer (diaphanotheca). Average thickness of spirotheca of the first to seventh volution for 10 specimens 0.014, 0.014, 0.016, 0.020, 0.021, 0.021 and 0.018 mm, respectively.

Septa intensely and regularly fluted throughout length of shell exept for central part of it, attaining to more than 2/3 of chamber height. Septal counts of the first to fifth volution of illustrated sagittal section (Figure 3-5) 13, 27, 33, 39 and 41.

Rudimentary chomata observed only in the first volution of some specimens. Tunnel

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← **Figure 3.** **1-15.** *Gallowayinella guidingensis* Liu, Xiao and Dong, **1, 2, 4, 6-13**: axial sections, GK.D 14738, GK.D 14731a, GK.D 14737, GK.D 14741, GK.D 14733, GK.D 14724a, GK.D 14730, GK.D 14723, GK.D 14716, GK.D 14731b, GK.D 14726, **3, 5**: sagittal sections, GK.D 14739, GK.D 14719, **14**: slightly oblique axial section, GK.D 14736, **15**: axial section of immature specimen, GK.D 14727a. All ×15.

Table 3 Measurements of *Gallowayinella guidingensis* Liu, Xiao and Dong. F.R. : Form ratio, D.P. : Diameter of proloculus (in mm).

	Reg. no.	Fig.	Length	Width	F.R.	D.P.	Radius vector						
							1	2	3	4	5	6	7
1	GK. D 14731a	3-2	4.50	1.13	3.98	0.18	0.13	0.17	0.25	0.34	0.44	0.56	—
2	GK. D 14737	3-4	5.20	1.40	3.71	0.13	0.08	0.12	0.20	0.29	0.41	0.54	0.71
3	GK. D 14733	3-7	4.90	1.23	3.98	0.15	0.11	0.14	0.21	0.28	0.37	0.49	0.65
4	GK. D 14724a	3-8	4.60	1.20	3.83	0.12	0.12	0.20	0.27	0.38	0.51	0.63	
5	GK. D 14730	3-9	4.45	1.18	3.77	0.18	0.13	0.20	0.27	0.35	0.45	0.57	
6	GK. D 14716	3-11	4.95	1.28	3.87	0.13	0.12	0.18	0.27	0.37	0.50	0.65	
7	GK. D 14726	3-13	5.60	1.40	4.00	0.16	0.11	0.16	0.23	0.32	0.43	0.55	0.70
8	GK. D 14711	4-9	4.80	1.35	3.56	0.17	0.12	0.18	0.24	0.33	0.45	0.57	0.71
9	GK. D 14713	4-10	5.20	1.35	3.85	0.21	0.12	0.17	0.24	0.31	0.44	0.56	—

	Form ratio							Thickness of spirotheca						
	1	2	3	4	5	6	7	1	2	3	4	5	6	7
1	2.24	2.88	3.98	4.03	4.00	3.93	—	0.010	0.010	0.015	0.020	0.020	0.025	—
2	2.25	3.17	3.10	3.62	3.85	3.89	3.66	0.010	0.010	0.015	0.015	0.020	0.020	0.020
3	1.45	3.07	3.67	4.79	4.84	4.80	—	0.010	0.010	0.010	0.020	0.020	0.015	0.020
4	2.75	3.03	3.48	3.49	3.63	3.68		0.015	0.015	0.020	0.020	0.025	—	
5	2.00	2.75	3.37	3.86	4.40	4.23		0.015	0.015	0.010	0.015	0.015	—	
6	2.26	2.74	3.22	3.70	4.00	3.85		0.015	0.010	0.020	0.020	0.025	0.020	
7	2.91	3.88	3.60	3.98	3.90	4.00	3.86	0.020	0.020	0.020	0.020	0.025	0.025	—
8	2.50	2.89	3.23	3.76	3.97	3.73	3.33	0.015	0.015	0.020	0.025	0.020	0.025	0.015
9	1.78	2.76	3.11	4.03	3.91	4.11	—	0.010	0.015	0.015	0.020	0.015	0.015	—

path narrow and almost straight. Axial fillings present in the first to fourth or fifth volution.

Remarks.—The present form is quite identical with *Gallowayinella guidingensis* described by Liu *et al.* (1978) from the Changxing Limestone in the Guizhou district of South China. In its original description, Liu *et al.* (1978) have illustrated only two specimens. In the Doi Pha Phlung specimens, there are some variations in the shell shape, size, form ratio, diameter of proloculus and density of axial fillings. They all can be included in the intraspecific variations.

Gallowayinella guidingensis Liu, Xiao and Dong somewhat resembles *G. meitienensis* Chen, the type species of this genus from the Meitian (Meitien) Limestone of Hunan, South China. However, the former can be distinguished from the latter in having a more elongately fusiform shell and larger form ratio.

The present species resembles *Gallowayinella cylindrica* originally described by Deng (in Lin *et al.*, 1977) from the Longtan Formation of Guangdong. However, the former has a smaller form ratio than the latter.

Gallowayinella laxa described by Lin (1980) is considered to be the immature stage of *G. guidingensis* Liu, Xiao and Dong.

Measurements.—See Table 3.

Occurrence.—Abundant in Locs. HT 1 and HT 2.

Genus *Palaeofusulina* Deprat, 1912

Palaeofusulina sinensis Sheng, 1955

Figures 2-12—16, 4-1

Palaeofusulina sinensis Sheng, 1955, p. 295-296, 305-306, pl. 1, figs. 13, 16, pl. 4, figs. 1-15 ; Sheng, 1963, p. 50-51, 175, pl. 9, figs. 1-9 ; Sheng, 1966, p. 67, pl. 9, fig. 3 (same as pl. 4, fig. 2 of Sheng, 1955, p. 295-296, 305-306) ; Zhang and Wang, 1974, p. 295, pl. 153, fig. 8 ; Lin *et al.*, 1977, p. 43, pl. 9, fig. 4 ; Liu *et al.*, 1978, p. 22, pl. 2, fig. 15 ; Chen and Yang, 1978, p. 40, pl. 8, figs. 1-2 ; Sun, 1979, pl. 1, figs. 22-23 ; Rui, 1979, pl. 3, figs. 20-21 ; Wang *et al.*, 1981, p. 20-21, pl. 21, figs. 15, 17-18, 20 ; Sakagami and Hatta, 1982, p. 5-7, pl. 1, figs. 8-22 ; Wang *et al.*, 1982, p. 28, pl. 4, fig. 22 ; Sun *et al.*, 1983, p. 20-21, pl. 4, fig. 17 ; Lin, 1984, p. 158, pl. 9, fig. 30, pl. 10, fig. 7 ; Sheng and Rui, 1984, p. 37, pl. 2, figs. 17-19 ; Chen, 1984, p. 26, pl. 3, fig. 4 ; Yang, 1985, pl. 1, figs. 23-25 ; Gu, 1987, pl. 6, figs. 1-2 ; Zhu, 1989, pl. 8, figs. 12-13 ; Fan *et al.*, 1990, pl. 6, figs. 14-16.

Palaeofusulina cf. *sinensis* Sheng, Sheng and Chang, 1958, p. 207-208, 212, pl. 1, figs. 21-25 ; Zhao *et al.*, 1981, pl. 4, figs. 30-31 ; Gu, 1987, pl. 6, fig. 3.

?*Palaeofusulina sinensis* Sheng, Xie, 1982, p. 17, pl. 7, fig. 1.

Material studied.—Axial sections ; GK.D 14729a, GK.D 14722 and GK.D 14729c. Sagittal section ; GK.D 14714. Tangential sections ; GK.D 14729b and GK.D 14732. All of the illustrated specimens were obtained from Loc. HT 1. Additional specimens were also available from both localities.

Description.—Shell small, bulged fusiform with almost straight axis of coiling and bluntly pointed polar ends. Mature specimens having 4 to 4 ½ volutions, 1.85 to 2.10 mm in length and 1.20 to 1.48 mm in width. Form ratio ranges from 1.54 to 1.74, averaging 1.61 for 4 specimens.

The first volution tightly coiled. Beyond the second volution, shell expands rather rapidly and becomes loose with growth. Average radius vectors of the first to fourth and fourth and a half volutions for 3 specimens 0.09, 0.18, 0.36, 0.57 and 0.69 mm, and form ratios 1.70, 1.91, 1.73, 1.70 and 1.39, respectively.

Proloculus almost spherical, being 0.08 to 0.14 mm in outside diameter, averaging 0.11 mm for 4 specimens.

Spirotheca thin and two-layered, composed of a tectum and diaphanotheca. Very minute fibrous structure observable in a diaphanotheca of some specimens. Average thickness of spirotheca of the first to fourth, and fourth and a half volutions for 3 specimens 0.018, 0.020, 0.022, 0.015 and 0.020 mm, respectively.

Septa intensely and narrowly fluted. Septal counts of the first to third volutions of

Table 4. Measurements of *Palaeofusulina sinensis* Sheng. F.R. : Form ratio, D.P. : Diameter of proloculus (in mm).

	Reg. no.	Fig.	Length	Width	F.R.	D.P.	Radius vector				
							1	2	3	4	4 ½
1	GK. D 14729a	2-12	2.10	1.21	1.74	0.14	0.12	0.22	0.41	0.67	
2	GK. D 14722	2-14	1.96	1.23	1.59	0.10	0.08	0.17	0.34	0.52	0.69
3	GK. D 14729c	2-15	1.85	1.20	1.54	0.08	0.08	0.16	0.34	0.52	0.69

	Form ratio					Thickness of spirotheca				
	1	2	3	4	4 ½	1	2	3	4	4 ½
1	1.83	1.91	1.71	1.68		0.020	0.020	0.020	—	
2	1.38	1.94	1.84	1.83	1.43	0.015	0.020	0.025	0.015	0.020
3	1.88	1.88	1.65	1.60	1.35	0.020	0.020	0.020	0.015	0,020

illustrated sagittal section (Figure 2-16) 10, 20 and 31. Chomata present but inconspicuous. Tunnel path narrow and almost straight. Axial fillings absent.

Remarks.—The Doi Pha Phlung specimens can be fairly assigned to *Palaeofusulina sinensis* Sheng, which has been reported from many localities in the Changxing Limestone and its equivalents of South China, based on the important morphological characters.

Measurements.—See Table 4.

Occurrence.—Common in Loc. HT 1 and rare in Loc. HT 2.

Palaeofusulina cf. *laxa* Sheng, 1963

Figure 2-17

Compare.—

Palaeofusulina laxa Sheng, 1963, p. 54, 179, pl. 11, figs. 1-9; Lin *et al.*, 1977, p. 42, pl. 8, fig. 23; Liu *et al.*, 1978, p. 24, pl. 2, fig. 21 (same as pl. 11, fig. 2 of Sheng, 1963, p. 54, 179); Chen and Yang, 1978, p. 38, pl. 7, figs. 8-9; Wang *et al.*, 1982, p. 28, pl. 4, fig. 23; Sun *et al.*, 1983, p. 21, pl. 4, fig. 19; Zhu, 1989, pl. 8, figs. 9-10.

Material studied.—Axial section; GK.D 14720 from Loc. HT 1.

Description.—Shell small, subspherical with bluntly pointed polar ends. Length and width of shell having 4 volutions, 1.73 mm and 1.31 mm, with a form ratio of 1.32. Shell expands rather rapidly. Outer 2 volutions loosely coiled as compared with inner ones. Radius vectors of the first to fourth volution 0.12, 0.25, 0.44 and 0.71 mm, and form ratios 1.67, 1.56, 1.43 and 1.30, respectively. Proloculus spherical, being 0.13 mm in outside diameter. Spirotheca thin, composed of a tectum and rather thick diaphanotheca. Thickness of spirotheca of the first to fourth volutions 0.020, 0.025, 0.030 and 0.025 mm, respectively. Chomata not observed. Axial fillings absent.

Remarks.—The present species closely resembles *Palaeofusulina laxa* originally described by Sheng (1963) from the Changxing Limestone of Guizhou, in the shell shape and rate of expansion. However, the exact identification is postponed until the sufficient materials are accumulated.

Rui and Sheng (1981) included *Palaeofusulina laxa* Sheng into the genus *Parananlingella* which they newly established at that time. Howevere, the expansion of the outermost volution in *Palaeofusulina laxa* Sheng is not so distinct as compared with *Parananlingella acervula* Lui and Sheng, the type species of the genus *Parananlingella.* The former species, *laxa*, should be left in the genus *Palaeofusulina*, to which it was originally referred.

Occurrence.—Rare in Loc. HT 1.

Genus *Codonofusiella* Dunbar and Skinner, 1937

Codonofusiella aff. *kwangsiana fusiformis* Sheng, 1963

Figure 4-2

Compare.—

Codonofusiella kwangsiana fusiformis Sheng, 1963, p. 45, 170, pl. 6, figs. 10-15; Lin *et al.*, 1977, p. 40, pl. 8, figs. 9-10 (same as pl. 6, figs. 11, 15 of Sheng, 1963, p. 45, 170); Liu *et al.*, 1978, p. 27, pl. 3, fig. 7.

Material studied.—Axial section; GK.D 14724b from Loc. HT 1.

Description.—Shell small, fusiform with bluntly pointed poles with 4 volutions. Length and width of shell 1.03 mm and 0.49 mm, respectively, and giving a form ratio of 2.10. The first volution coiled almost perpendicularly to outer ones. Proloculus small, being 0.45 mm in outside diameter. Radius vectors of the first to fourth volutions 0.05, 0.08, 0.14 and 0.27 mm, and form ratios 1.11, 1.40, 2.14 and 1.89, respectively. Spirotheca thin, composed of a tectum and diaphanotheca. Septa strongly and regularly fluted. Chomata distinct.

Remarks.—The present form is similar to *Codonofusiella kwangsiana fusiformis* Sheng in the shell shape, but differs from the latter in having more fluted septa.

Occurrence.—Rare in Loc. HT 1.

Family Staffellidae Miklukho-Maklay, 1949

Genus *Sphaerulina* Lee, 1934

Sphaerulina sp.

Figure 4-5

Material studied.—Tangential section; GK.D 14728c from Loc. HT 1.

Remarks.—Greneral shell shape, the spirothecal composition and presence of very fine alveolar structure in the present specimen indicates that it is included in the genus *Sphaerulina*, although it is not properly oriented.

Occurrence.—Rare in Loc. HT 1.

? Family Verbeekinidae Staff and Wedekind, 1910

Subfamily Kahlerininae Leven, 1963

Genus *Kahlerina* Kochansky-Devidē and Ramovš, 1955

Kahlerina ? sp.

Figure 4-4

Material studied.—Sagittal section; GK.D 14712 from Loc. HT 1.

Remarks.—The generic assignment of the present specimen is tentative, because only one sagittal section is insufficient for study.

Occurrence.—Rare in Loc. HT 1.

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Changxing (Changhsing) 長興, Dameishan (Tameishan) 大煤山, Daoduishan (Taotuishan) 稲堆山, Guangdong 広東, Guizhou (Kueichow) 貴州, Jiangxi (Kiangxi) 江西, Hunan 湖南, Longtan 龙潭, Meitian (Meitien) 梅田, Shanggao 上高, Sichuan (Szechuan) 四川, Wujiaping (Wuchiaping) 呉家坪.

タイ国北部 Doi Pha Phlung 地域の後期二畳紀紡錘虫群集：タイ国北部，Lampang 北東の Doi Pha Phlung 地域に分布する Huai Thak 層下部層から 7 属 8 種から成る紡錘虫群集を検出した。そのうち種の同定ができたものは *Reichelina* cf. *changhsingensis* Sheng and Chang, *Gallowayinella guidingensis* Liu, Xiao and Dong, *Palaeofusulina sinensis* Sheng, *P.* cf. *laxa* Sheng, *Codonofusiella* aff. *kwangsiana fusiformis* Sheng の 5 種である。この紡錘虫群集は *Gallowayinella guidingensis* Liu, Xiao and Dong を特徴種とし，中国南部の長興石灰岩およびその同時代層に見られる紡錘虫群集に類似する。その時代は前期 Changxingian あるいは前期 Dorashamian と考えられる。 上野勝美・坂上澄夫

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929. PERMINERALIZED *OTOZAMITES* LEAVES (BENNETTITALES) FROM THE UPPER CRETACEOUS OF HOKKAIDO, JAPAN*

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Abstract. The present paper deals with the description of external and internal features of two types of permineralized *Otozamites* leaves. We establish *Otozamites kerae*, sp. nov. and *O. takahashii*, sp. nov. to accommodate the present leaves. The former is characterized by small-sized leaf and pinnae with denser veins, and by the presence of roofing cells over the stomata and the absence of papillae and trichomes on both sides of cuticles. The latter is characterized also by small-sized leaf and pinnae with less dense veins, and by the presence of roofing cells over the stomata and of ramentum-like trichomes on the lower cuticle. Well-preserved leaf cuticles of both species and histological features of the former species are described in detail. The occurrence of both species is one of the youngest records of *Otozamites* in the Mesozoic.

Key words. Permineralized *Otozamites*, Upper Cretaceous, Hokkaido (Japan)

Introduction

The Upper Yezo Group of marine origin (mostly Coniacian-Santonian in age) is distributed widely in the median part of Hokkaido and yields various fossil plants in the calcareous (often ammonite-bearing) nodules it contains. Although they are represented mostly by tiny fragments, most of them are permineralized by calcium carbonate and therefore their internal details are rather well preserved.

This paper gives the description of two new species of permineralized *Otozamites* leaves collected by Messrs. Yasuji Kera, Masatoshi Kera, Ken'ichi Saiki and Hiroshi Takahashi from the Upper Yezo Group exposed at the Kumaoizawa and Kamimakizawa Valleys and Nakakinenbetsu (Obira) Valley (Figure 1). They are all fragmental, but show unique external and internal features. *Otozamites* species are abundant and varied in the Triassic, Jurassic and Early Cretaceous plant sites, but are rare in the Late Cretaceous plant sites. The occurrence of both species is one of the youngest records of the genus *Otozamites* in the Mesozoic.

In order to make a histological study of the Kumaoizawa and Kamimakizawa specimens, they were sliced along various surfaces with a diamond saw with a 0.4 mm thick blade. Then cellulose acetate peels were made. Cuticular preparations were made from all specimens at hand.

The examined specimens and slides (peels and cuticular preparations) for *Otozamites kerae* and cuticular preparations for *O. takahashii* are kept in the Institute of Natural History, Tokyo.

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Description

Class Cycadopsida
Order Bennettitales
Genus *Otozamites* Braun
in Münster, 1842
Otozamites kerae Ohana et Kimura,
sp. nov.

Figures 2-7

Material.—Holotype; INH-1A (collected by Y. Kera from the Kamimakizawa at talus). Other specimens examined; INH-1B (counterpart of INH-1A), INH-2 (collected by M. Kera from the Kamimakizawa at talus) and INH-3 (by K. Saiki from the Kumaoizawa from rolling rock). *Stratum typicum*: Upper Yezo Group (mostly Coniacian-Santonian in age). *Locus typicus*: Middle course of the Kamimakizawa (roughly 142°08′05″E, 43°07′43″N; an eastern branch of the Shuparo River), Kashima, Yubari City. *Derivatio nominis*: After Yasuji Kera, who collected the holotype. *Occurrence*: Rather rare.

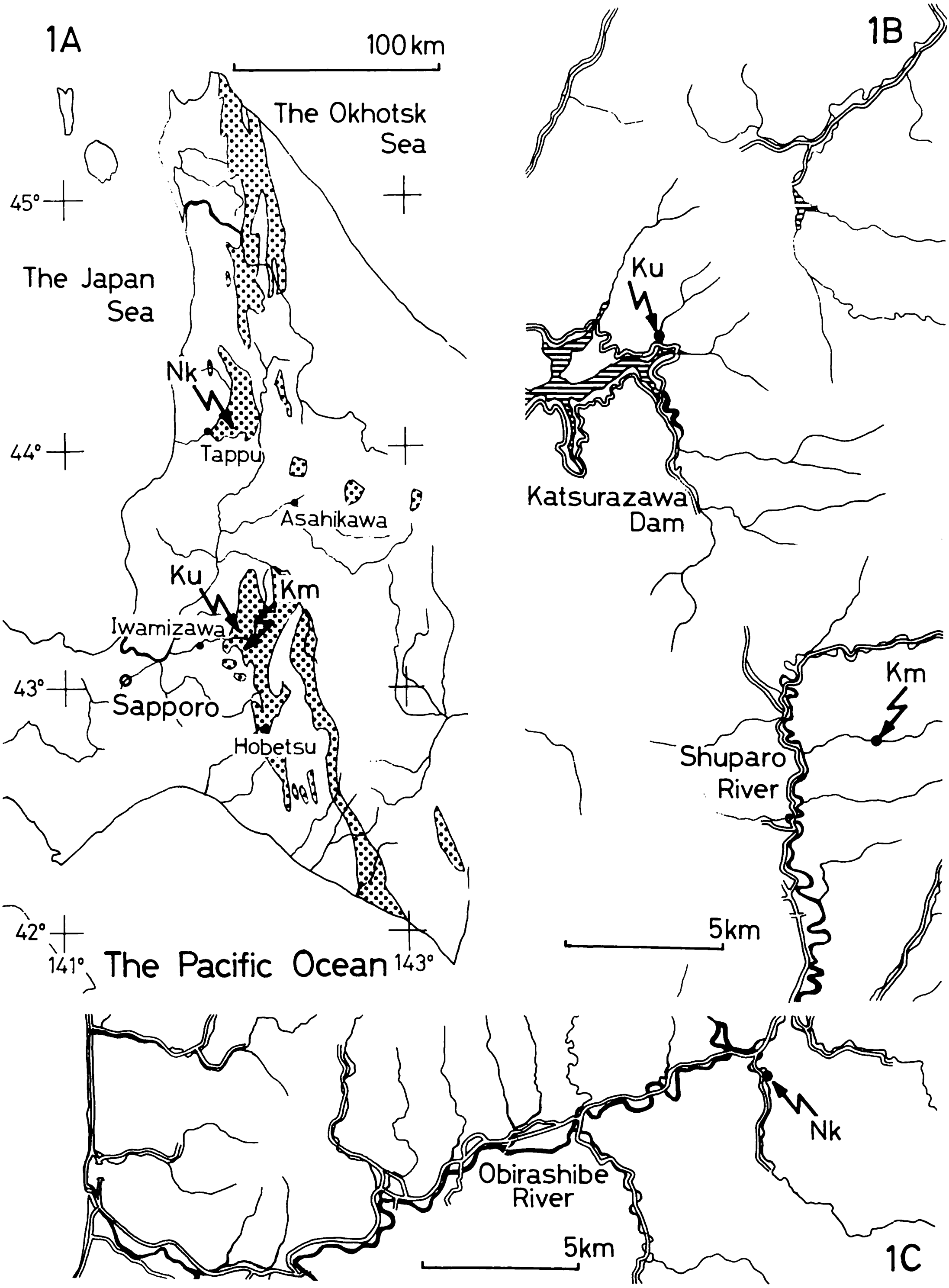
Description.—1. *External features* (Figures 2A-E): The piece of leaf is pinnate with thick rachis. Its petiole is not preserved. Judging from the leaf fragments obtained, the leaf is small, long and narrow, with nearly parallel margins for the most part. It is up to 2.2 cm across in its widest part, narrowing gradually towards both ends. The pinnae are alternate, set closely, attached to upper surface of rachis at an angle of 40 degrees. They are oblong or nearly rectangular in form, typically 1.2 cm long and 4.5 mm wide at middle; acroscopic basal part is markedly expanded to form a rounded angle (auricle), but the basiscopic basal margin is usually concealed by the rounded part of the pinna of the opposite side. Margins are entire with broadly rounded apex. The veins are densely crowded, radiated from the basiscopic basal part and are dichotomously forked repeatedly at all levels; the density is 40-42 per cm at the middle of pinna. Reproductive organs are not known.

2. *Internal features*: 1) Rachis (Figures 3A-J, 5A-H, 6A-D): In cross section, the rachis is obpentagonal in form (Figures 3A-J), 2.6 mm × 2.4 mm thick. It shows epidermal and hypodermal layers, ground tissue and vascular bundles. Epidermal layer (Figures 5C, H) is one cell thick. The cells are rectangular in cross section, 8-10 μm thick adaxially and 15 μm thick abaxially. Cuticle is obscure in cross section.

Hypodermal layer (Figures 5C, E, F, H) is 6-8 cells thick (120-140 μm thick) in cross section. Hypodermal cells are thick-walled and sclerenchymatous, but those of adaxial side are rather thin-walled (Figure 5H).

Ground tissue consists mostly of large, thin-walled parenchymatous cells. They are round or oval in form (Figures 5B-H, 6B) in cross section, (20)-50-(90) μm in diameter, and with small intercellular spaces in between. A few rather thick-walled cells with cellular contents, isolated or grouped [Cc in Figure 5C; secretary cells or idioblast; cf. Rao and Achuthan, 1968, text-fig. 9], 40-50 μm in diameter, are scattered in the ground tissue (Figures 5B-H, 6B).

Vascular bundles are arranged in a double series in the form of a 'U' (Figures 3A-J, 5A, 6A); the concavity of the 'U' faces upward and the bundles vary from 12 to 13 in number separating from each other laterally. Some of the bundles are in a state of incomplete division. The bundles are collateral, endarch, with poorly preserved phloem (Figures 5B-H) and well-preserved xylem with spiral and scalariform tracheids (Figures 6C-D).


1A
100 km
The Okhotsk Sea
45°
The Japan Sea
Nk
Tappu
44°
Asahikawa
Ku
Km
Iwamizawa
43°
Sapporo
Hobetsu
42°
141°
The Pacific Ocean
143°
1B
Ku
Katsurazawa Dam
Km
Shuparo River
5km
Nk
Obirashibe River
5km
1C

The xylem in the outer and inner sides of the 'U' faces in opposite direction.

Thick-walled sclerenchymatous cells (mechanical tissue or fibres ?) are present outside and inside the phloem (Figures 5B–H). They do not extend to the space between the adjacent bundles. These sclerenchymatous cells are less developed in the inner bundles of the 'U' (Figure 5D).

2) Pinnae (Figures 4, 7A–L): Structurally the pinna consists of a single cell layer of upper epidermis with well-preserved cuticle, a single cell layer of upper hypodermis consisting of thick-walled cells followed by one or two layers of vertically elongated thin-walled palisade cells, spongy tissue with large intercellular spaces in between, a single cell layer of lower hypodermis and a single cell layer of lower epidermis with well-preserved cuticle. Vascular bundles (veins) are located in a row in the spongy tissue.

The pinna is 0.3–0.36 mm in vertical thickness (Figures 4, 7A–C, G) and is somewhat thicker along the margins. The pinna margin is usually broadly rounded in sectional view.

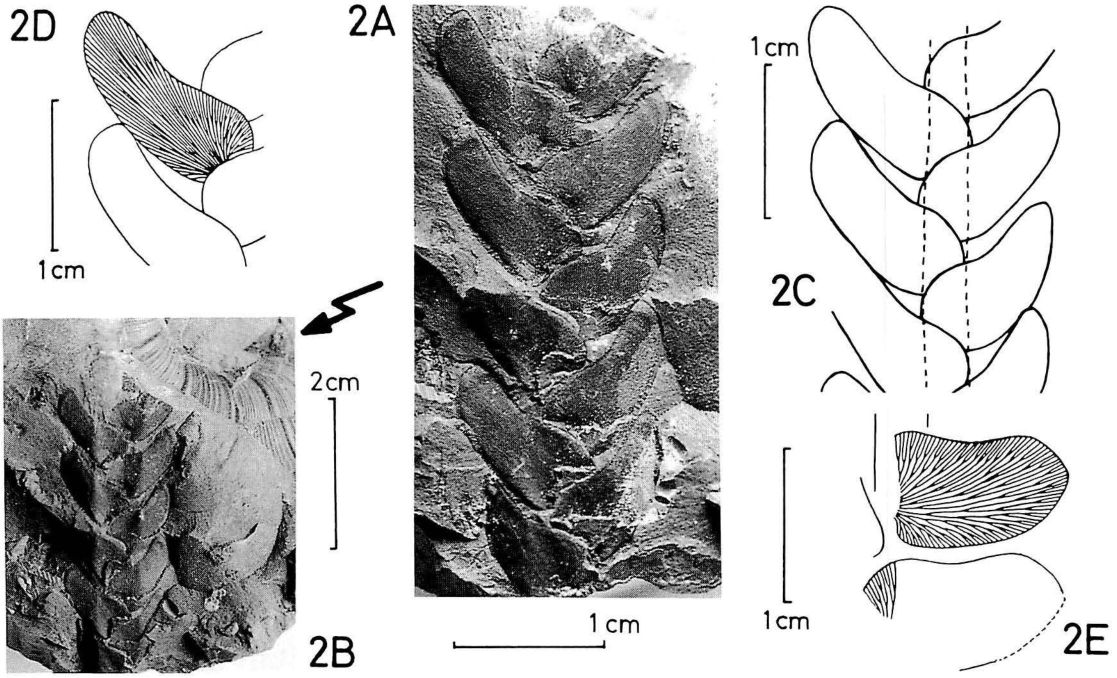
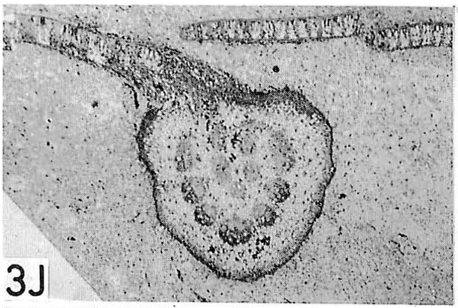
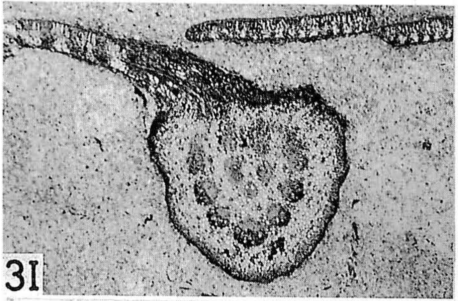


Figure 2. *Otozamites kerae*, sp. nov. **2A.** A leaf fragment (holotype ; enlarged twice). Its upper part is buried in the rock matrix. INH-1A (collected by Y. Kera from the Kamimakizawa). **2B.** Counterpart of the holotype. The arrow indicates an associated ammonite. Two median ridges in this figure cover the lateral ridges of the concealed rachis. **2C.** Imbricated pinnae with marked acroscopic basal angles (auricles) drawn partly from the holotype. Both dotted lines indicate real position of the lateral edges of a concealed rachis. **2D.** Venation of a pinna drawn from the holotype. **2E.** Venation of small pinnae from INH-3 (collected by K. Saiki from the Kumaoizawa).

← **Figure 1.** Localities of *Otozamites* leaves described in this paper. **1A.** A median region of Hokkaido Island, showing the exposed areas of Upper Cretaceous sediments (dotted areas) and three localities of *Otozamites* leaves. Nk ; Nakakinenbetsu Valley (Tappu, Obira-cho), Ku ; Kumaoizawa Valley, Km ; Kamimakizawa Valley. **1B.** Detailed plant sites of Kumaoizawa (Ku, roughly at long. 142°03′00″E, lat. 43° 14′27″N) and Kamimakizawa (Km). **1C.** Detailed plant site of Nakakinenbetsu (Tappu, Obira-cho) (Nk).


3J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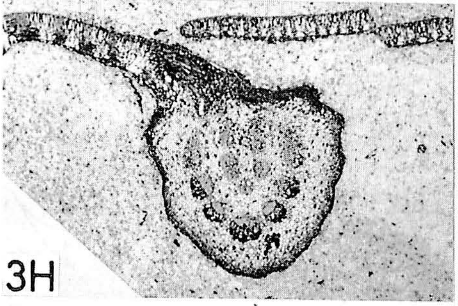
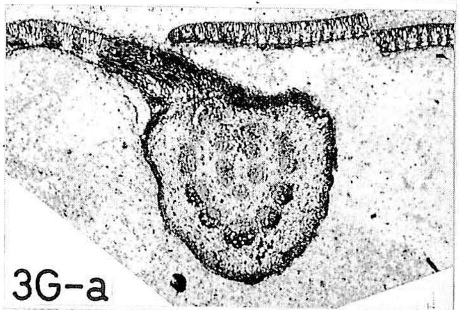
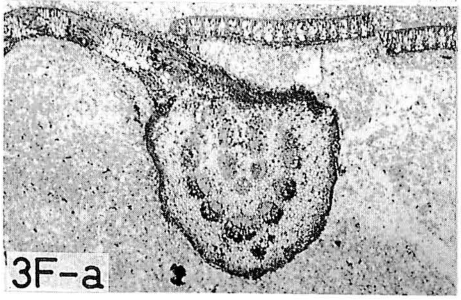
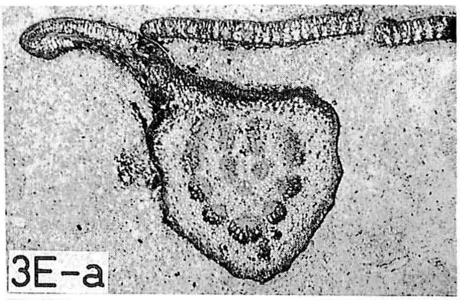

3H


3G-a
5mm


3F-a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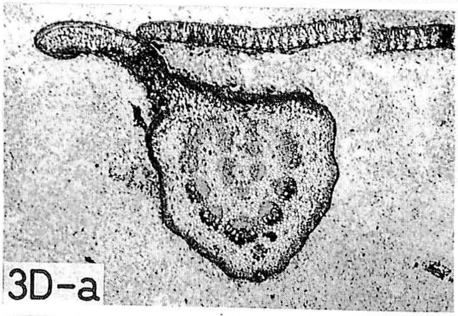
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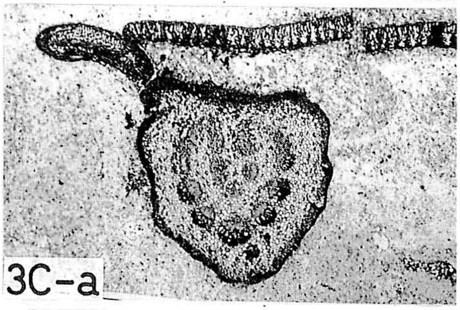
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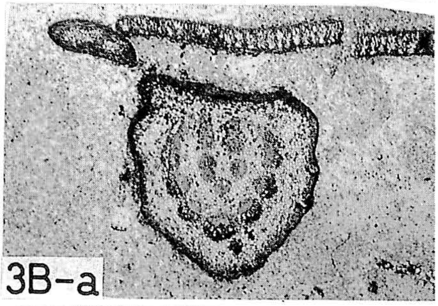
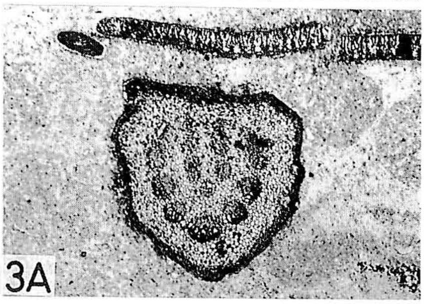
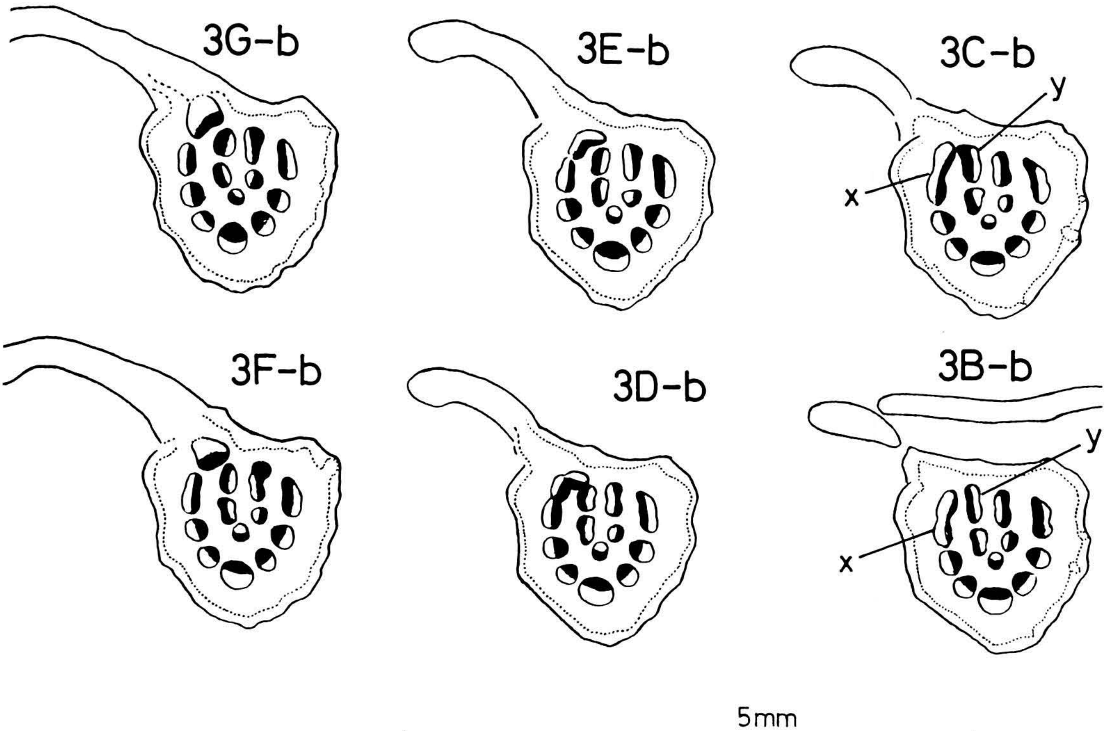

3B-a


3A



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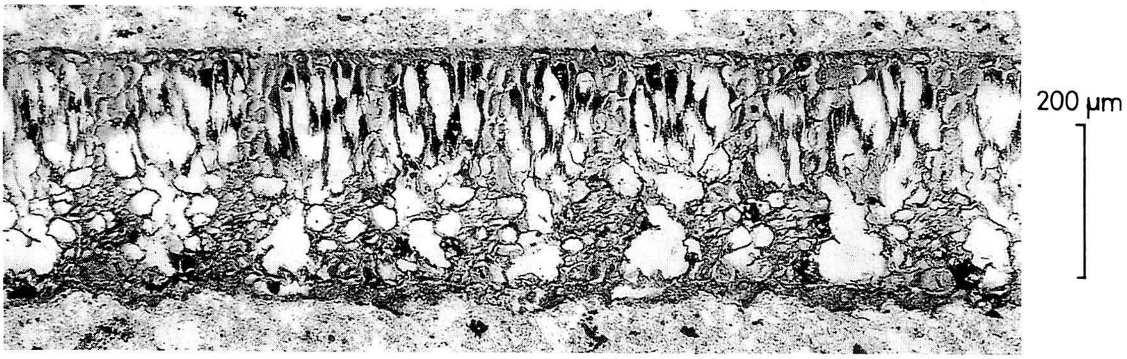


Figure 3 (left and top) and **Figure 4.** *Otozamites kerae,* sp. nov. **3A–J.** Serial cross sections of the buried rachis with pinnae (holotype) cut and photographed successively, 0.1 mm apart, in ascending order from Figure 3A to Figure 3J. They show the arrangement of vascular bundles (double series in the form of a 'U') and the mode of vascular supply to a pinna (details, see text). Figures 3B–b, 3C–b, 3D–b, 3E–b, 3F–b and 3G–b are drawn from Figures 3B–a, 3C–a, 3D–a, 3E–a, 3F–a and 3G–a, respectively. **Figure 4.** A cross section of a pinna (holotype) enlarged.

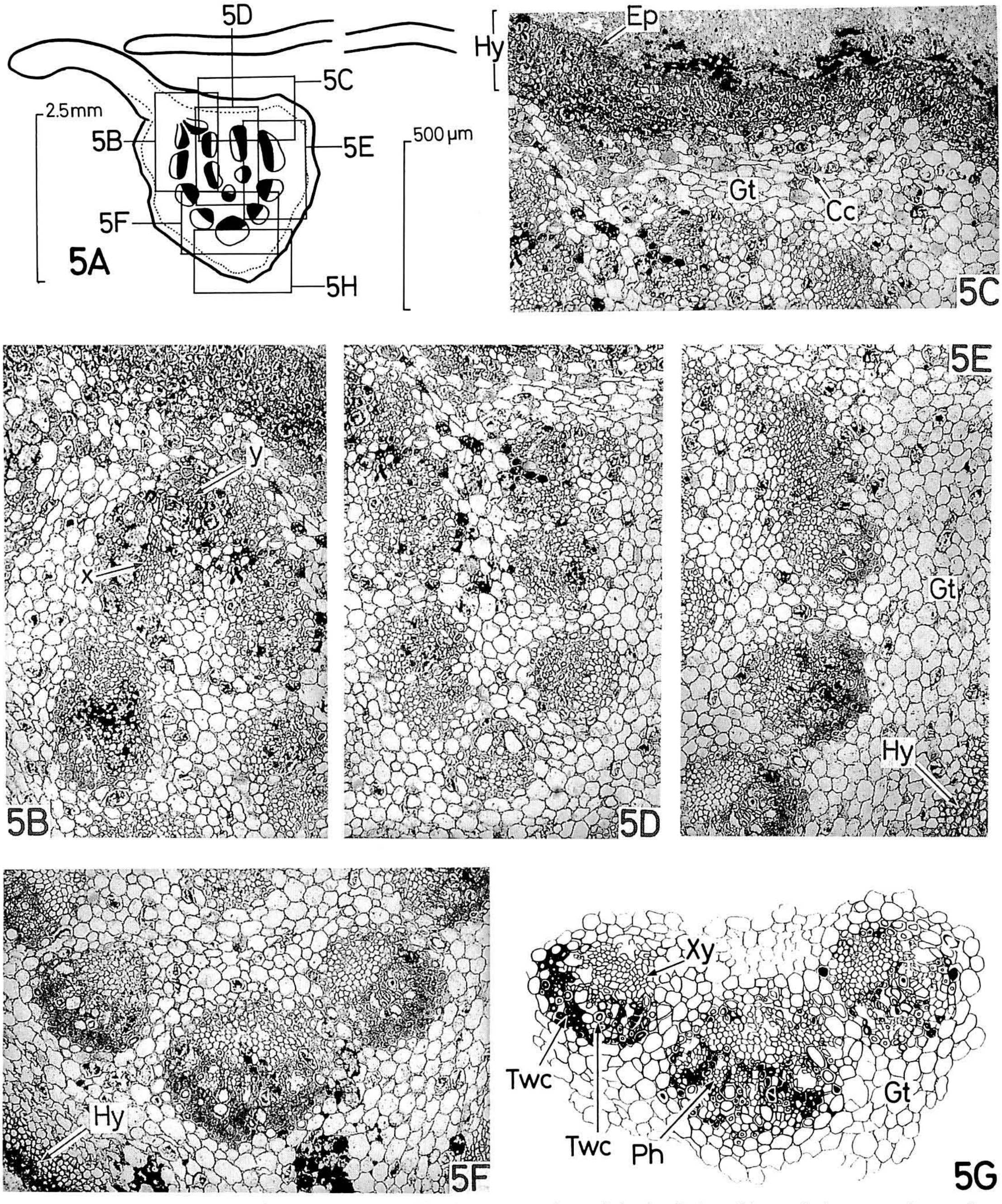
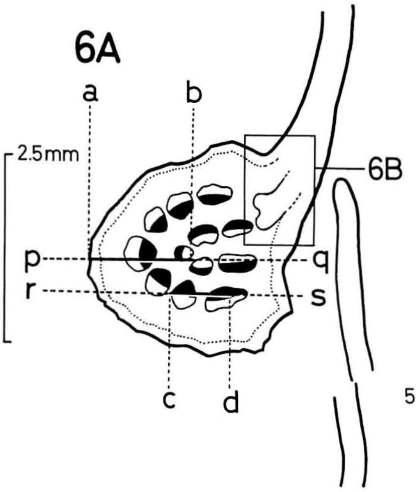
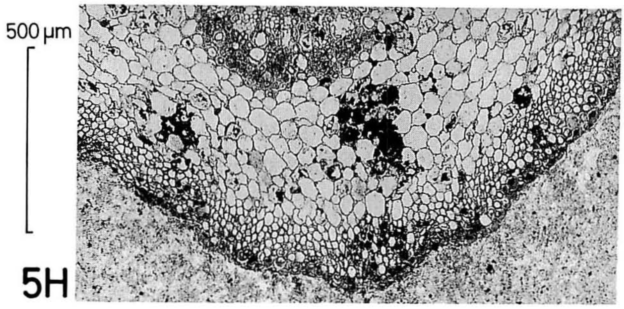


Figure 5. *Otozamitas kerae,* sp. nov. **5A.** A cross section of the buried rachis made between those of **Figure 3D** and **Figure 3E,** indicating the areas of the corresponding detailed micrographs (**Figures 5B–F, H**). In each vascular bundle, black part shows xylem and the other part shows phloem with thick-walled sclerenchymatous cells (mechanical tissue or fibres ?). **5B.** Adaxial vascular bundles in the left side of the double 'U'-shape series. Two terminal bundles (x and y) are about to unite with each other. **5C.** Adaxial side of the rachis. It shows poorly preserved epidermal cell layer (Ep), thick hypodermal layer (Hy), ground tissue (Gt) and cells with cellular contents (secretary cells or idioblast ; Cc). **5D.** Vascular bundles on the inside of the 'U'. In each phloem part, thick-walled sclerenchymatous cells (mechanical tissue or fibres ?) are less developed than in each phloem part of the outer bundles of the 'U'. **5E.** Vascular bundles on the outside of the 'U'. **5F.** Vascular bundles on the abaxial side of the outside of the 'U'. **5G.** Drawn partly from **Figure 5F.** Xy ; xylem, Ph ; phloem, Twc ; thick-walled sclerenchymatous cell (mechanical tissue or fibres ?). **5H.** Abaxial side of the rachis. The cells of hypodermal layer are rather thin-walled.

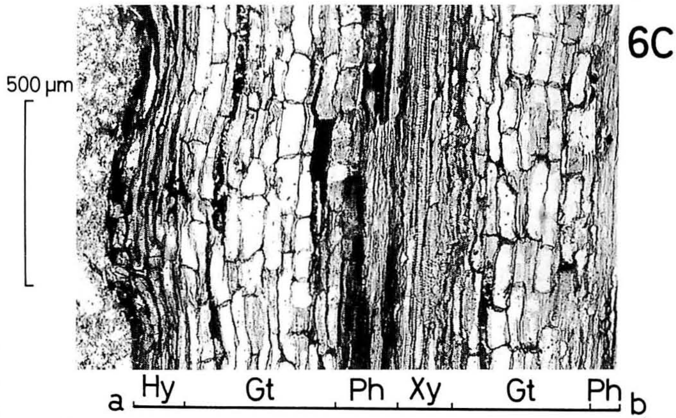
6A



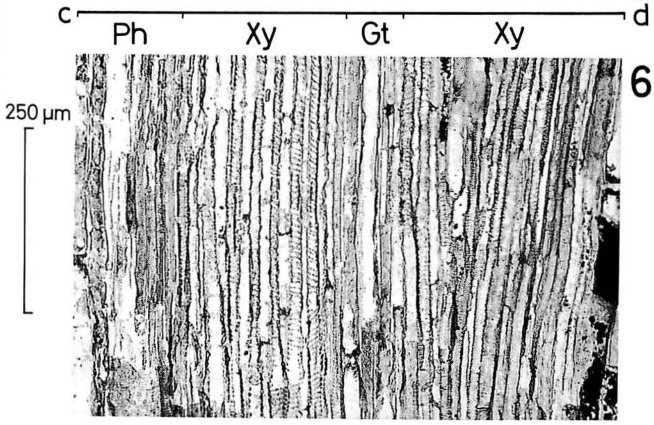
5H



6C



6D



6B

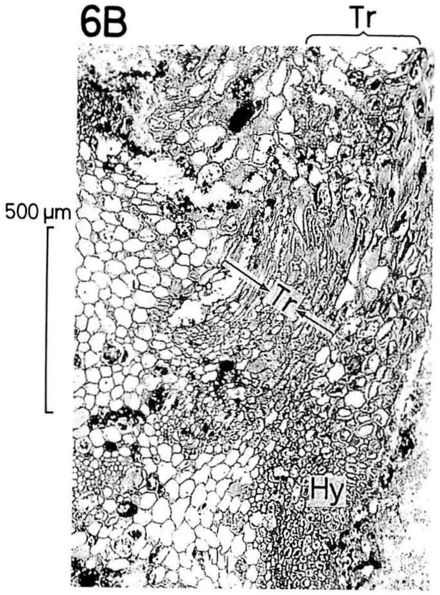


Figure 6. *Otozamites kerae,* sp. nov. **6A.** Cross section of the buried rachis with pinnae, enlarged from **Figure 3G.** Showing the area of the detailed micrograph (**Figure 6B**) and the vertically cut lines (p–q and r–s). **6B.** Pinna-trace (Tr) originated from a united bundle at the terminal position of the left side of the 'U' (see **Figures 3F-b** and **3G-b**) (in both **Figures 6A** and **6B**, the right side is really the upper side). **6C.** A vertical section of the rachis cut along the p–q line in **Figure 6A** between a and b. Hy ; hypodermis, Gt ; ground tissue, Ph ; phloem, Xy ; xylem. **6D.** A vertical section of the rachis cut along the r–s line in **Figure 6A** between c and d. In this micrograph, the left-side xylem is made up of spiral tracheids (primary xylem part ?) and the right-side xylem of scalariform tracheids (secondary xylem part ?).

Cells of the upper epidermis are rectangular in cross section, 25 μm long and 7.5 μm high, but they are larger and squarish around the marginal region. In surface view, they are rectangular, 50-85 μm long and 30 μm wide, with marked sinuous anticlinal walls; the sinuosity is 15 μm long (wave-length) and 20 μm wide (amplitude) in anticlinal walls, and is 10 μm long and 10 μm wide in end walls (Figure 7F).

In our observation of upper cuticle, it consists only of ordinary cells, and no stoma, trichome or papilla have been found on the outer periclinal walls.

Cells in the upper and lower layers of hypodermis are polygonal and thick-walled; their lumina are often markedly reduced in volume. The lower layer of hypodermis is interrupted at the stomatal region (Figures 7A-C, E).

The palisade cells are well developed, 95-125 μm long and 20-25 μm wide in cross section, but the area above a vascular bundle is devoid of palisade cells (Figures 7A-D).

The spongy cells are irregular in form and larger, 30-50 μm in diameter, but the area below the vascular bundle is usually devoid of spongy cells (Figures 7A-E).

In our observation of cross section of pinnae and their lower cuticle, stomata are distributed between vein courses by a single or sometimes 2-3 rows. Cells on the vein courses are elongate-rectangular, with less sinuous walls, and those between the stomatal rows are isodiametric with less sinuous walls. The marginal zone of pinna, ca. 250 μm wide, is devoid of stoma (Figure 7I).

Stomata are syndetocheiric. Guard cells are sunken and each cell is 50 μm long and 12 μm wide, and strongly cutinized; aperture is typically 17 μm long and transversely oriented to the veins (Figure 7H). Subsidiary cell is 20 μm wide and its walls are not sinuous but straight (Figures 7J-K).

Stomatal apparatus is also sunken in the bottom of a large oval pit formed by surrounding 8-10 epidermal cells. In addition, these epidermal cells form a dome-shaped roof, 80-100 μm long, 70-90 μm wide and up to 35 μm high from the surface of guard cell, and with a rounded or stellate mouth. Roof cells are somewhat thickened toward the mouth which does not lie just above the stoma, but at the end toward the rachis, while the stoma is at distal end to the rachis (Figures 7H-K). No papilla has been found on the ordinary cells except for the roof cells, and no trichome or trichome base has been found on the epidermal cells (Figures 7H-I).

In cross section, there is a large chamber inside each stoma (Figures 7A-C, E). In longitudinal cross section of a pinna, the vascular bundles are 31-35 in number (the same as the number of veins), each of which is located at the lower part of spongy tissue and consists of small masses of adaxial xylem and poorly preserved abaxial phloem. They are irregularly surrounded by a parenchymatous sheeth consisting of large cells (Figures 7A-E).

Between the adaxial hypodermis and vascular bundle (vein), there develops a wedge-shaped mechanical tissue consisting of large sclerenchymatous cells in 2-4 horizontal rows (Figures 7A-D); the uppermost row consists of 4-5 cells and the lowermost row of 1-2 cells. These mechanical tissue cells are not seen in cuticular preparations. Figure 7L shows inside view of a stomatal apparatus (SEM micrograph).

3) *Probable course of vascular supply to the pinna*: Figures 3A-H and 5B show serial cross section of the rachis and obliquely cut three pinnae buried in the rock matrix (the lower extension of Figure 2A) for 1 mm in length of the rachis. In Figures 3B (a-b) and 3C (a-b), at first two bundles (x and y) from the left adaxial corner come to be elongated vertically and are constricted in the middle. Then upper portions of both bundles come in contact and unite with each other [Figures 3D (a-b), 5B] to form a single bundle which is separate from lower parts of the constriction [Figures 3E (a-b), 3F (a-b)]. A pinna

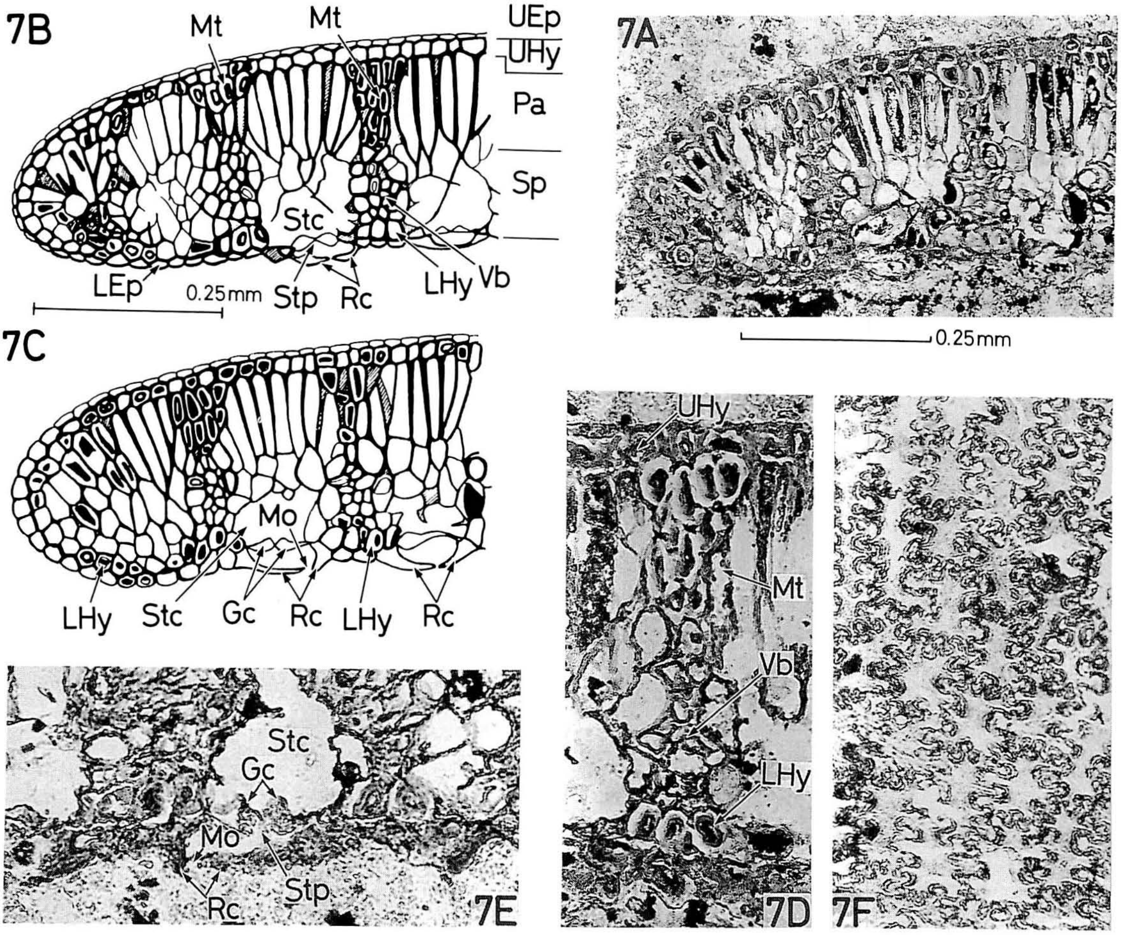
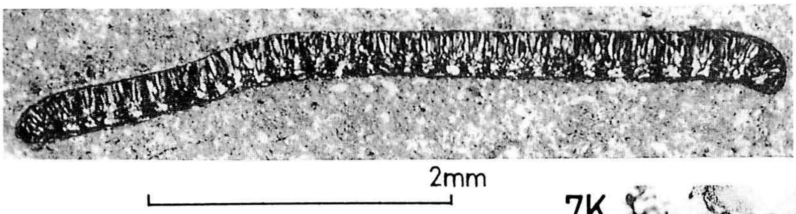


Figure 7. *Otozamites kerae,* sp. nov. **7A.** A longitudinal section of a buried pinna (holotype) cut nearly along its median portion (enlarged). **7B.** Drawn from **Figure 7A.** It shows upper and lower epidermal layers (UEp and LEp), upper and lower hypodermal layers (UHy and LHy), palisade and spongy tissues (Pa and Sp), vascular bundle (vein ; Vb), wedge-shaped mechanical tissue (Mt), stomatal chamber (Stc), guard cells (Gc), stomatal pit (Stp) and dome formed by roof cells (Rc) with mouth. In **Figures 7B** and **7C,** shaded areas show the cell walls. **7C.** A longitudinal section of a buried pinna (holotype). The marginal region is rather thickened compared to **Figure 7A. 7D.** Wedge-shaped mechanical tissue (Mt) made up of thick-walled and large cells extending upward from the vascular bundle (vein ; Vb). **7E.** Abaxial part of a pinna (longitudinal section) enlarged partly from **Figure 4.** It shows two large-spaced stomatal chambers (Stc), guard cells (Gc), stomatal pit (Stp) and a dome formed by roof cells (Rc) with a mouth (Mo). **7F.** Enlarged upper cuticle made up only of ordinary cells. Their long axis is in parallel to the veins. The anticlinal and end walls are markedly sinuous and thickened and with rounded loops (often mushroom-shaped) reaching nearly to the middle of the cell. Cells on the vein courses are not specialized.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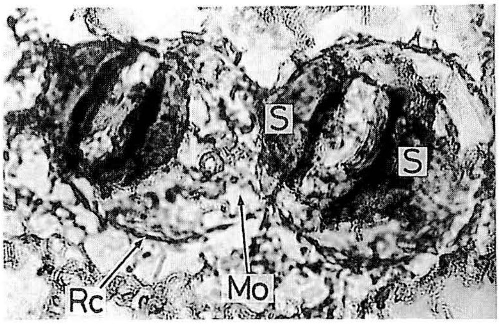
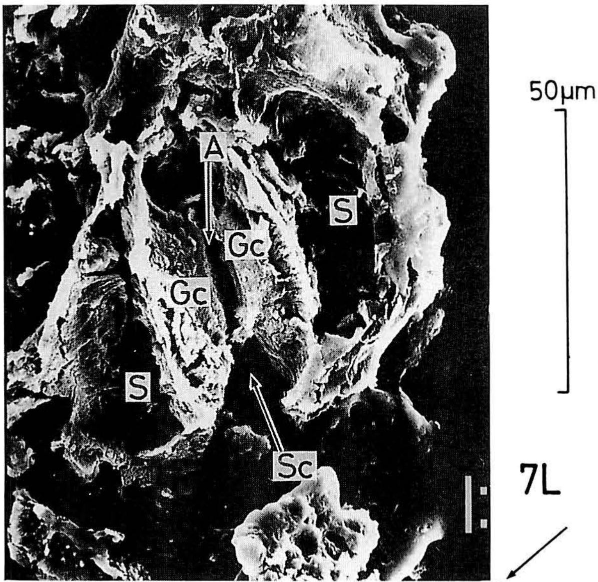
7G


100µm
S
S
Rc
Mo

7K


50µm
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Gc
Gc
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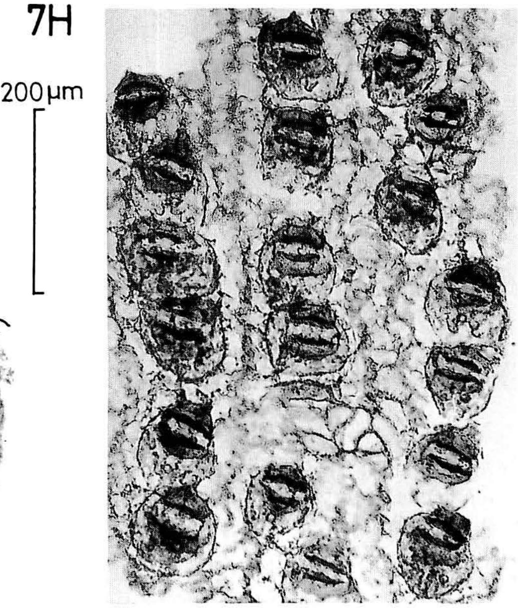
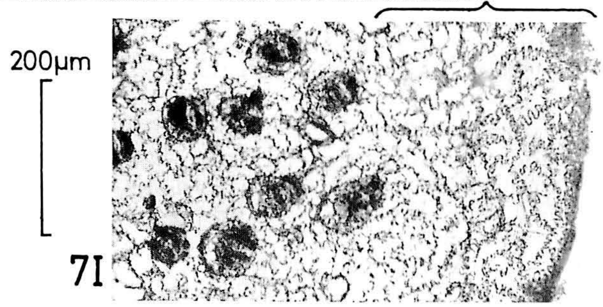
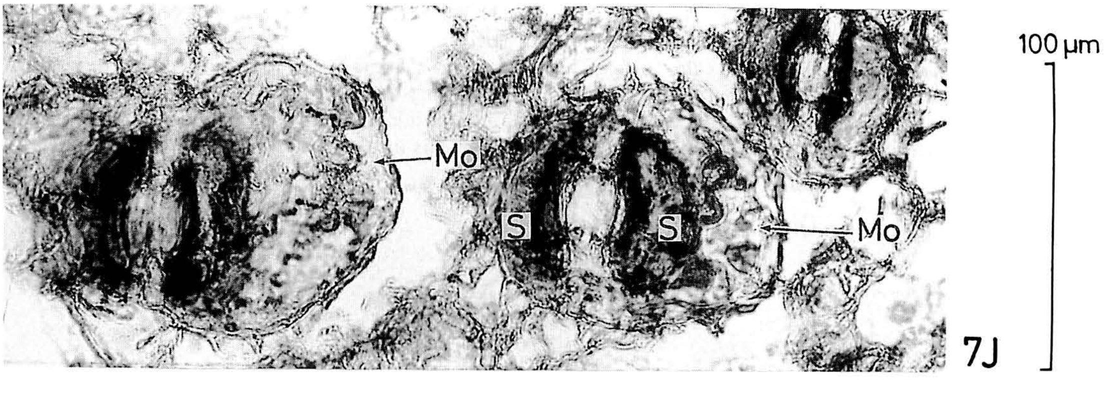
S
Sc


200µm

7H


200µm
7L

7I


Mo
S
S
Mo
100µm

7J

receives this single bundle [Figures 3F (a–b), 3G (a–b), 6B] at the pinna base, but unfortunately, details of the mode of branching of this single bundle at the very base of pinna are not visible.

Discussion and comparison.—Externally, the present *Otozamites* leaves are small, long and narrow having comparatively thick rachis and falcate, closely set, imbricate and oblong or nearly rectangular pinnae with broadly rounded apex and densely crowded and radiated veins.

A number of *Otozamites* species have been described from Mesozoic plant beds. Among them, we could not find the leaves externally similar in habit to the present ones. Therefore, even on the basis of external form of the present leaves, it would be reasonable to create *Otozamites kerae*, sp. nov. to accommodate the present leaves.

Apart from the present specimens, internal features of the bennettitalean leaf-rachises or petioles have been described for the following taxa :

Ptilophyllum amarjolense Bose : Bose, 1953 ; Bose and Kasat, 1972a.
P. cutchense Morris : Bancroft, 1913 ; Rao and Achuthan, 1967.
P. guptai Sharma : Sharma, 1967.
P. sahnii Gupta et Sharma : Bose and Kasat, 1972a.
Dictyozamites falcatus (Morris) Medlicott et Blanford : Bancroft, 1913 ; Bose and Zeba-Bano, 1978.
D. indicus Feistmantel : Bose and Zeba-Bano, 1978.
Dictyozamites sp. : Bose and Kasat, 1972b.
Williamsonian-type stems : Bancroft, 1913.

The arrangenent of vascular bundles in *Ptilophyllum* rachises is a double series of 'U'-shape (Rao and Achuthan, 1967 ; Bose and Kasat, 1972a), but the number of bundles is larger (20–32 in *Ptilophyllum amarjolense,* 23–32 in *P. sahnii,* 25–32 in *P. cutchense*) than that of the present *Otozamites kerae.*

In *Ptilophyllum guptai*, pinna trace-bundles are two in number at their origin (Sharma, 1967), instead of a united one as in the present *Otozamites kerae.* While, in *Ptilophyllum cutchense* the number of trace-bundle is single at its origin (Rao and Achuthan, 1967).

According to Bose (1953) and Bose and Kasat (1972a), in the petiole of *Ptilophyllum amarjolense*, the vascular bundles are 11 in number (5 abaxial, 2 lateral and 4 adaxial) and arranged in a reniform manner. Unfortunately the petiole of *Otozamites kerae* is not known.

In the rachis of *Dictyozamites falcatus*, the vascular bundles are 25–30 in number and are also arranged in a double 'U'-shaped series, surrounded by an incomplete layer of thick-walled mechanical tissue (Bose and Zeba-Bano, 1978).

As mentioned above, the arrangement of vascular bundles in the rachises of the bennettitalean genera, *Ptilophyllum, Dictyozamites* and the present *Otozamites* is similar, but the latter differs from the anatomically known rachises of *Ptilophyllum* and *Dictyozamites* in having small number of vascular bundles and less developed mechanical tissue surrounding them.

The mechanical tissue of pinna in association with vascular bundle (vein) is unique in *Otozamites kerae,* and is considered to be good for reinforcement of the weakness of the

←— **Figure 7.** *Otozamites kerae,* sp. nov. **7G.** An oblique longitudinal section of a pinna (holotype). The rachis is located under the left edge. **7H.** Stomatal rows between adjacent veins (lower cuticle ; holotype). Each stoma is covered with a dome formed by roof cells of which the mouth is situated at the lower side of this micrograph (toward the rachis-side). Apertures are directed transversely or sometimes somewhat obliquely. Guard cells are invisible, because they are sunken. A pair of dark parts shows heavily cutinized subsidiary cells. Anticlinal and end walls of the ordinary cells are less sinuous than those of upper ordinary cells. **7I.** Lower cuticle (holotype). The arrow shows non stomatal marginal zone where the sinuosity of ordinary cells is nearly the same as that of upper ordinary cells. **7J.** Three stomata with their own domes formed by roof cells of which mouths are stellate. S ; subsidiary cell, Rc ; roof-cell, Mo ; mouth of a dome. **7K.** Two stomata with the same dome as shown in **Figure 7J.** **7L.** Inner view of a stoma (SEM-micrograph). A ; aperture, Gc ; guard cell, Sc ; stomatal chamber.

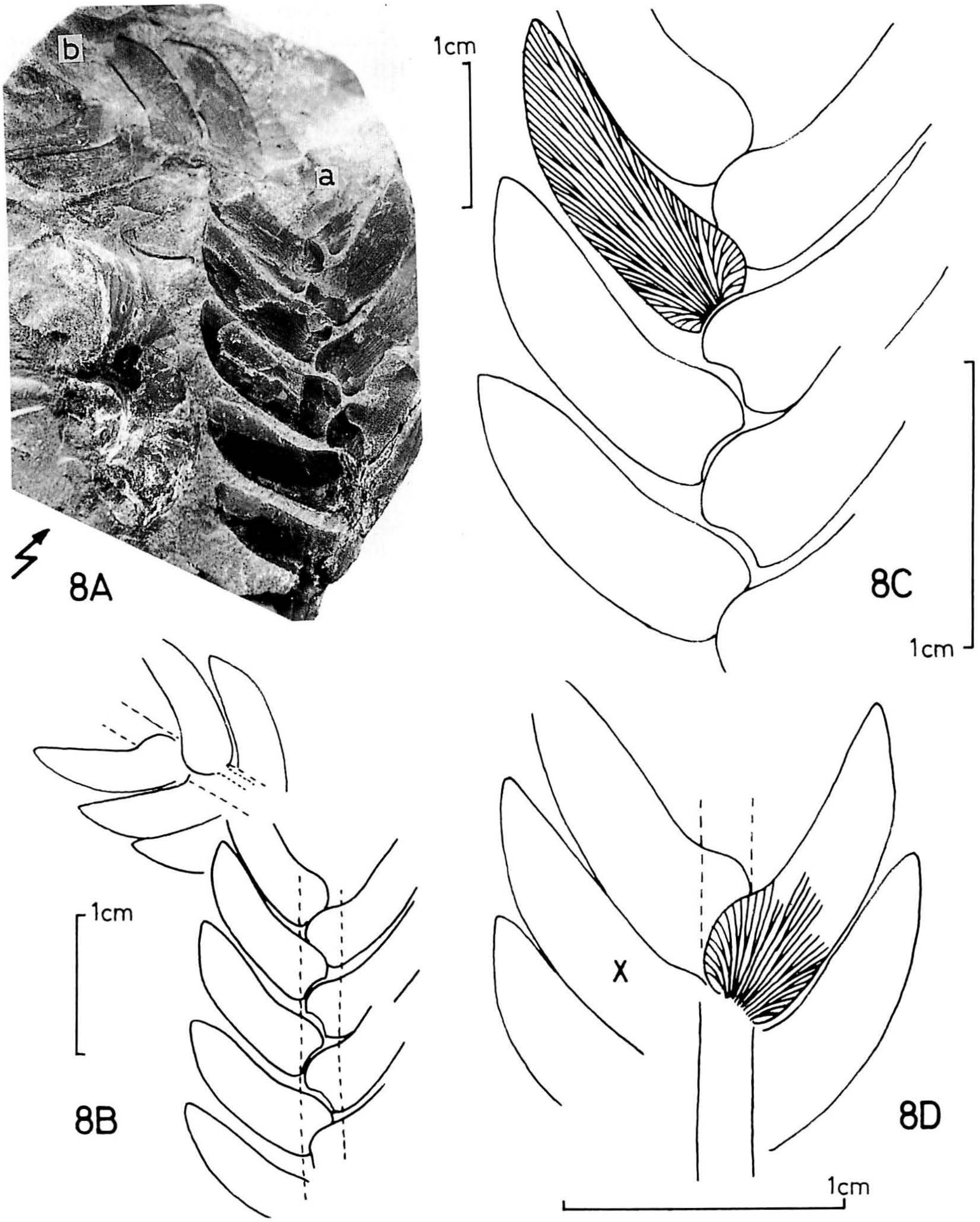


Figure 8. *Otozamites takahashii,* sp. nov. **8A.** A broken leaf (holotype, INH-4A indicated by 'a' (surface view)] collected by Hiroshi Takahashi at the Nakakinenbetsu (Obira) locality (**Figure 1C**) in association with an ammonite indicated by the arrow. **8B.** A sketch of the holotype, showing well-developed auricles concealing the rachis entirely. Dotted lines indicate position of rachis. **8C.** A part of a leaf enlarged from the holotype, showing the venation. **8D.** The auricle of a pinna (indicated by 'X') stripped away to show the origin of radiated veins [INH-4B indicated by 'b' in **Figure 8A** (wrong-side view)].

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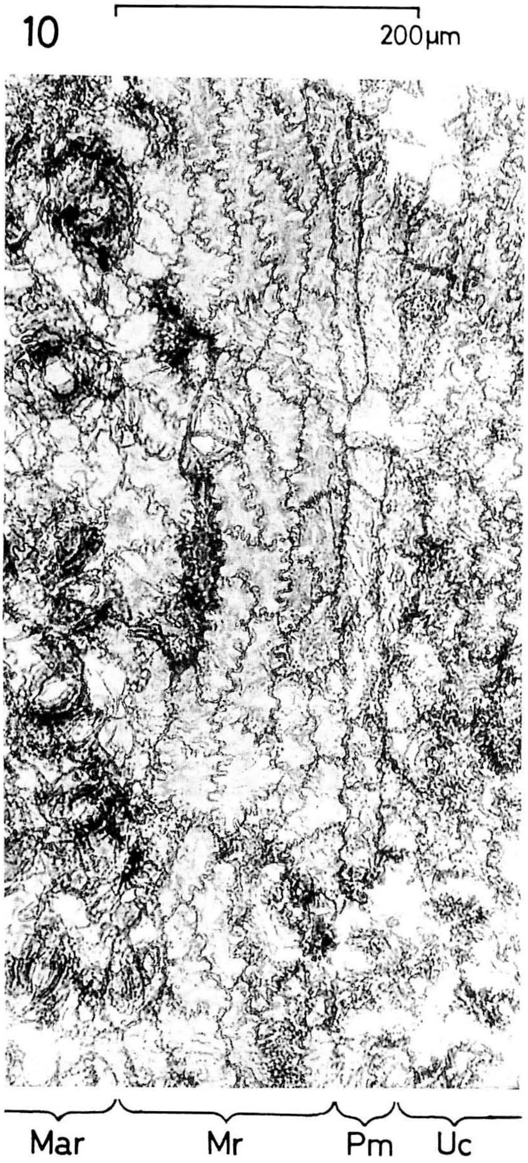


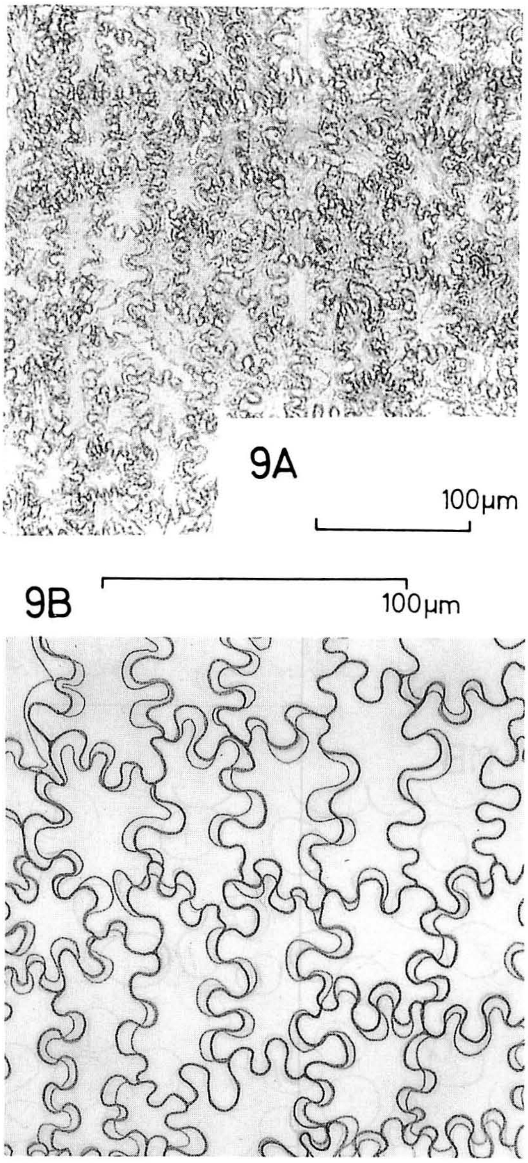
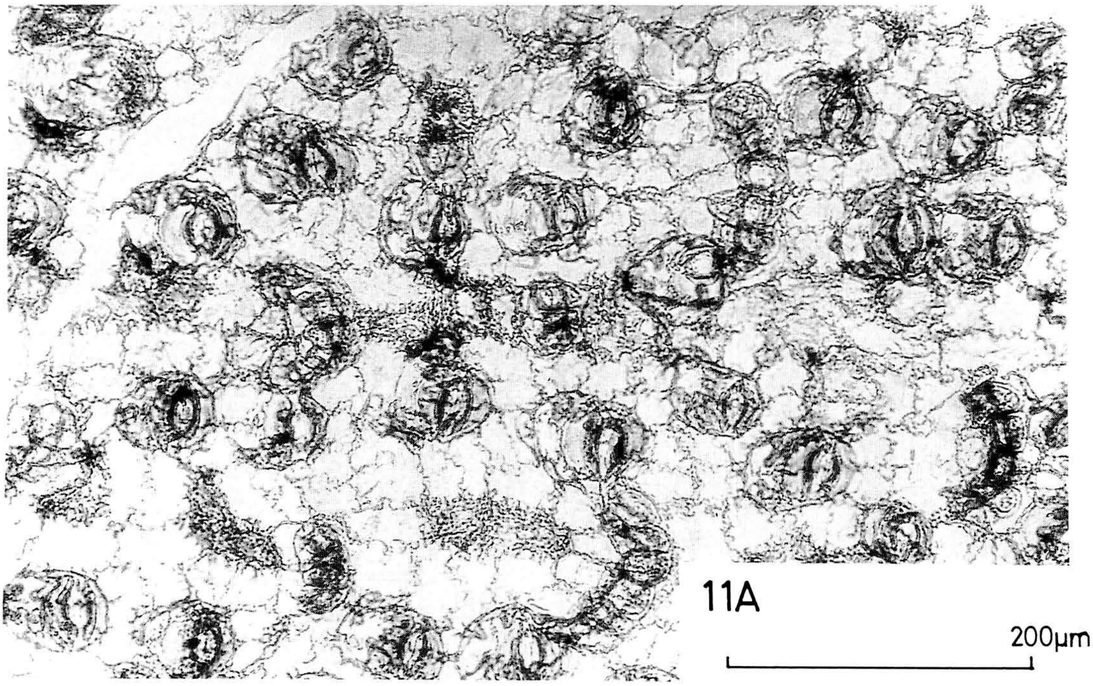
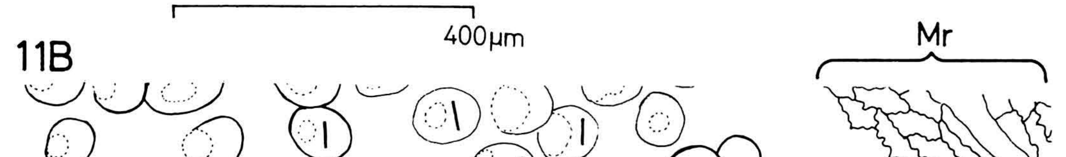


Figure 9 and **Figure 10.** *Otozamites takahashii,* sp. nov. **9A.** Upper cuticle consisting only of the ordinary cells with sinuous anticlinal and end walls (holotype). **9B.** Sinuous walls of upper ordinary cells enlarged partly from **Figure 9A.** Periclinal walls are all smooth in surface view. **Figure 10.** Marginal part of a pinna. Upper and lower cuticles were unfolded on the same plane (Mar ; main region of the lower cuticle with stomata, Mr ; marginal region of the lower cuticle consisting only of ordinary cells, Pm ; part of pinna margin, Uc ; upper cuticle) (holotype).



11A



11B

pinna architecture due to the existence of a large space (stomatal chamber) inside each stoma (Figures 4, 7A-C, E).

Stomatal roofing cells (or roof cells) similar in structure to those of *Otozamites kerae* were described by Harris (1969) for *O. beani* (Lindley et Hutton), *O. graphicus* (Leckenby) and *O. leckenbyi* Harris, and by Barale (1987) for *O. pterophylloides* Schimper. Such roofing cells are thought to be unique to some of the *Otozamites* species hitherto described, and have not been recorded in the leaves of other bennettitalean genera.

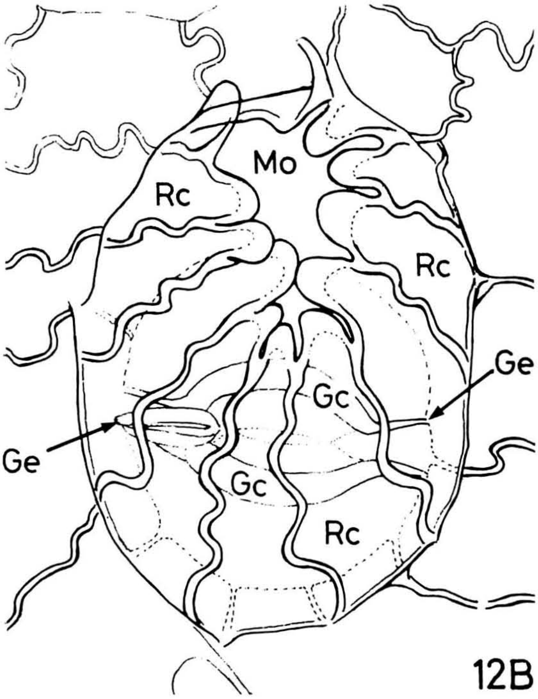
A stellate or oval-shaped mouth of a stomatal pit formed by 8 or more outer monocyclic or dicyclic encircling cells has been recorded in other gymnospermous genera, like *Ticoa, Ruflorinia* and *Mesosingeria* (Archangelsky, 1963) and *Otozamites parviauriculata* Menēndez (Menēndez, 1966) and other cycadalean genera (*e.g.* Harris, 1964). But each mouth in those cases unexceptionally opens just above a stomatal aperture.

Diagnosis.—Leaf small, long and narrow, nearly parallel-sided for the most part, up to 2.2 cm wide. Pinnae alternate, closely set, imbricate, oval or rectangular in form, typically 1.2 cm long and 4.5 mm wide, with markedly auriculated acroscopic base and broadly rounded apex, and attached to upper surface of rather thick rachis. Veins densely crowded, 40-42 per cm in density, and radiated.

Rachis obpentagonal in cross section, 2.6 mm wide and 2.4 mm high, being made up of an epidermal layer of one cell thick, a hypodermal layer 6-8 thick-walled cells thick (120-140 μm thick), parenchymatous ground tissue, vascular bundles, 12-13 in number, arranged in a double 'U'-shaped series. Vascular bundle made up of spiral and scalariform tracheids and phloem with thick-walled sclerenchymatous cells (mechanical tissue or fibre ?). Xylem in the outer and inner sides of the 'U' facing in opposite directions. Thin-walled cells with dark contents are scattered in the ground tissue (secretary cells or idioblast). (Cuticle of the rachis poorly preserved.) Pinnae 0.3-0.36 mm thick, upper and lower epidermal layers one cell thick, upper and lower hypodermal layers one cell thick, palisade and spongy tissues present, vascular bundles (veins) and wedge-shaped mechanical tissues, each extending above each bundle upward. Epidermis (cuticle) hypostomatic. Upper epidermis rectangular, consisting of uniform ordinary cells with markedly sinuous walls. Lower epidermis consisting of main part and nonstomatal marginal zone. In the main part, stomata distributed between adjacent veins in 1-3 rows. Stomata syndetocheiric. Guard cells sunken, stomatal pit covered by roof cells originated from encircling cells. The mouth of a dome formed by roof cells oval or stellate, located on the rachis side. Stomatal aperture transverse or sometimes oblique to the vein course. Trichomes and papillae absent on both epidermis. (Petiole, stem and reproductive organs not known.) *Registered slides* (All from the holotype): INH-1-C-13 (Figure 3A), C-14 (Figure 3B), C-16 (Figure 3C), C-18 (Figure 3D), C-20 (Figure 3E), C-25 (Figures 5B-F, H), C-28 (Figures 3F, 7A, C), C-30 (Figure 3G), C-32 (Figure 3H), C-33 (Figure 3I), C-34 (Figures 3J, 4, 6B, 7E), C-35 (Figures 7B, D), R-6 (Figure 6C), R-11 (Figure 6D), L-4 (Figure 7G), Cu-1 (Figure 7I), Cu-2 (Figures 7H, J, K), Cu-3 (Figure 7F), Cu-4 (Figure 7L).

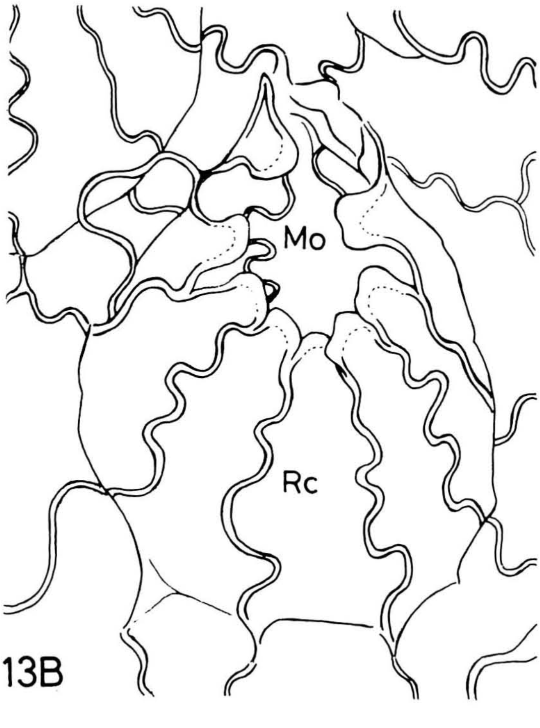
← **Figure 11.** *Otozamites takahashii,* sp. nov. **11A.** Main region of the lower cuticle (holotype), showing irregularly disposed stomata with covering dome (or sac)-shaped roof cells and ramentum-like trichomes. The rachis is located at the left hand of this figure. **11B.** A sketch of the lower cuticle (holotype), showing most of main region with stomata and trichomes (Tr) and a part of marginal rim (or zone) (Mr). Open circle indicates the roof with a mouth (dotted open circle) located unexceptionally at its left hand corner. Solid dash line shows position and direction of stomatal aperture. In this figure, general direction of veins is in parallel to the x-y line and the rachis is located on the left.

12A



12B

13A



13B

Otozamites takahashii Ohana et Kimura, sp. nov.

Figures 8-13

Materials.—Holotype; INH-4, with counterparts (collected by H. Takahashi at talus) *Stratum typicum*: Upper Yezo Group (mostly Coniacian-Santonian in age). *Locus typicus*: Lower course of the Nakakinenbetsu Valley (a tributary of the Obirashibe River) (roughly 141°55′51″E, 44°03′30″N), Tappu, Obira-cho, Rumoē-gun, Hokkaido.

Derivatio nominis.—After Hiroshi Takahashi, who collected the holotype.

Occurrence.—Rare (at present).

Description.—Two tiny leaf fragments were obtained. They are preserved on the same rock slab with an ammonite as shown in Figure 8A.

1. *External features* (Figure 8A-D): Leaves are nearly parallel-sided, 2 cm wide but whole length is unknown. Pinnae are closely set, alternate, imbricate and attached to upper surface of rachis at an angle of 55 degrees. Pinnae are generally rectangular in form, typically 1.25 cm long and nearly parallel-sided for the most part, 3.5 mm wide and slightly falcate; acroscopic margin is nearly straight throughout and apical basiscopic margin is rounded; apex is obtusely pointed or rounded. Acroscopic angle is remarkably expanded to form an auricle which conceals the rachis entirely. Veins are delicate, densely crowded, originate from middle of base (Figure 8C), then radiated and forked dichotomously at all levels, and end with the margins; the density is 40 per cm at the middle of pinna.

2. *Cuticular features*: Cuticle is hypostomatic, fairly sturdy and hard to fold in preparation; therefore, it is difficult to know its thickness.

Upper cuticle consists only of ordinary cells (Figures 9A, B) which are typically rectangular, 25-65 μm long and 20-30 μm wide with sinuous anticlinal (lateral) and end walls. The sinuosity of anticlinal walls is typically 15 μm long (wave-length) and 10 μm wide (amplitude), and that of end wall is less marked. Peripheral walls are smooth and no papillae and trichomes are recognized.

Lower cuticle is divided into a marginal rim (Figure 10) and main region (Figures 11A, B). Both vein course and interveinal region are less marked. The marginal rim consists of ordinary cells which are different in size and sinuosity from those of upper cuticle. They are irregular in size, 40-150 μm long and 15-30 μm wide, and their sinuosity is also irregular and less developed. The main region consists of ordinary cells and stomata (Figures 10, 11A, B). The ordinary cells are irregular, 20-80 μm long and 20-50 μm wide, rectangular, square to nearly triangular in form; their sinuosity is less developed than that of upper ordinary cells. The stomatal complex is syndetocheiric. The stomata are densely crowded, but do not appear to form stomatal files and bands; their density is 70-90 per square mm. In a stoma, guard cells and subsidiary cells are sunken in a stomatal pit with surrounding ordinary cells. Guard cells are 40-50 μm long and thickly cutinized on the inside and subsidiary cells are rather small, each 50-60 μm long and 15 μm wide, and less cutinized.

← **Figure 12** and **Figure 13.** *Otozamites takahashii*, sp. nov. **12A.** A roof (or sac) consisting of roof cells originated from encircling cells surrounding a stoma. The mouth (Mo) is stellate in form. The roof cells near the mouth are generally much cutinized (holotype). **12B.** A sketch of a roof and a sunken stoma. As a matter of fact, the roof and sunken stomatal apparatus cannot be seen in one focus. In this sketch, roof cells (Rc) and a stomatal apparatus are drawn with the same clearness. Guard cell ends (Ge) on the left-hand side adhere closely to one another, but those at the right-hand side are much separated possibly in the course of preservation. Subsidiary cell outlines are shown by the dotted lines. Guard cells (Gc) are heavily cutinized along their lateral margins. **13A.** A typical roof with stellate mouth (holotype). The stomatal apparatus is out of focus. **13B.** A sketch of a roof shown in **Figure 13A.** In both figures (**Figures 13A** and **13B**), the rachis is located upward.

The stomatal aperture is transverse to the veins (Figures 12A, B, 13A, B). The stomatal pit is covered by a dome-shaped or sac-shaped roof consisting of 10-12 ordinary cell extensions surrounding a stoma. The mouth of each roof is stellate and more or less cutinized and is not located above the stomatal pit (or aperture) but unexceptionally at or near the rachis-side edge of a roof (Figures 10, 11A, B, 12A).

The ramentum-like trichomes are present randomly on the lower cuticle. Their preserved part consists of 5 cells in a row. They are club-shaped and nearly parallel-sided, 100-150 μm long ahd 20 μm wide; most of them are at right angles to the vein course and are 13 per square mm in density (Figures 11A, B). No papilla is recognized on the ordinary and subsidiary cells. Petiole, stem and reproductive organs are not known.

Discussion and *comparison.*—Two leaf specimens from Obira are small, elongated with slender pinnae having marked auricles and crowded delicate veins. Therefore, the Obira leaves are different in external form of pinnae from those of *Otozamites kerae* described in this paper. Unfortunately we failed to get sectional peels of pinnae and rachis of the Obira leaves.

In the Obira leaves, upper ordinary cells are irregular in form and size, and their anticlinal and end walls are rather thin and their sinuosity less marked than *Otozamites kerae.*

The Obira leaves have stomatal files and bands undeveloped, but in *Otozamites kerae,* stomatal bands are well marked in the interveinal region. Ramentum-like trichomes are present on the lower cuticle in Obira leaves, but trichome is not observed in *Otozamites kerae*. Thus, both leaves are specifically distinct. The presence of the so-called roof (or sac cells, or roofing cells) covering the stomatal pit is a characteristic feature of many *Otozamites* species (*e.g.* Harris, 1969; Barnard and Miller, 1976). Figures 12 and 13 show well-preserved roofs, but the stomatal apparatus is sunken, and so it is impossible to make microscopic observation of both organs together.

In some species, such as *Otozamites pulcher* Barnard et Miller, the mouth is open at its edge on the rachis-side. Such a roof is not known in the leaves of other bennettitalean genera.

The internal structure of many *Otozamites* species from Mesozoic plant sites has been described (*e.g.* Harris, 1969; Archangelsky and Baldoni, 1972; Barnard and Miller, 1976). However, both the species, *Otozamites kerae* and *O. takahashii*, described herein are different in their cuticles being without papillae and trichomes (except for the ramentum-like trichomes in *O. takahashii*).

The present ramentum-like trichomes are similar in form to the imprinted ramenta on the peduncle of *Williamsonia hildae* (Harris, 1969, fig. 58D).

Diagnosis.—Leaf small in size. Pinnae set closely, alternate, imbricate, attached to upper surface of rachis, rectangular with obtusely pointed apex and well-marked auricle concealing the rachis entirely. Veins delicate, crowded and radiated.

Cuticle hypostomatic. Upper cuticle consisting only of ordinary cells with less marked sinuous walls. Lower cuticle with marginal rim devoid of stomata, main region consisting of ordinary cells with syndetocheiric stomata not in files or bands. Roof formed by the extension of 10-12 encircling cells with its stellate mouth open at rachis side. Ramentum-like trichomes present on the lower cuticle. Other trichomes and papillae absent on both cuticles.

Registered slides (All from the holotype).—INH-4-01 (Figures 9B, 10, 11B, 13A), 4-02 (Figures 11A, 12A), 4-03 (Figure 9A).

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Hokkaido 北海道, Kashima 鹿島, Kamimakizawa 上巻沢, Kumaoizawa 熊追沢, Nakakinenbetsu 中紀念別, Obira 小平, Obirasibe 小平蘂, Rumoé (or Rumoi) 留萌, Tappu 達布, Yezo Group 蝦夷層群.

北海道上部白亜系産鉱化 *Otozamites* 葉化石：北海道の中軸帯西側に分布する上部蝦夷層群の石灰質ノジュル中には，断片ではあるが，細胞組織がよく保存されている植物化石を産する。本論文は，夕張市上巻沢，三笠市熊追沢および小平町中紀念別川から採集された *Otozamites* 葉標本の外形および内部の細胞組織を詳細に観察し，*O. kerae* および *O. takahashii* の2新種を識別した。*Otozamites kerae* では葉の三次元的形質がよく保存され，葉軸には double-'U' 型に配列する維管束とその経路も一部追跡することができた。また葉の裏面には気孔を被うドーム型の細胞を識別した。*Otozamites takahashii* では，葉の三次元的形質を明らかにすることはできなかったが，気孔を被うドーム型の細胞を識別するとともに，きわめて特徴ある鱗毛の存在が識別できた。*Otozamites kerae* に認められた葉の三次元的形質は，*Otozamites* 属では最初の観察であり，ベネチテス目の葉に関する知識を増進させることに貢献した。

大花民子・木村達明

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930. *STENOPTERIS CYCLOSTOMA* SAIKI, KIMURA ET HORIUCHI SP. NOV. (POSSIBLE PTERIDOSPERM), FROM THE LOWER CRETACEOUS CHOSHI GROUP, IN THE OUTER ZONE OF JAPAN*

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Abstract. *Stenopteris cyclostoma* Saiki, Kimura et Horiuchi, sp. nov. is based on leaf fragments obtained from the Choshi Group of marine origin. This species is characterized by its fern-like pinnate leaves with wedge-shaped pinnae divided into narrow segments directed forward, each with a single vein, and cycad-like leaf cuticle bearing thick-walled cells. Such a leaf form has not been recorded in any extant or fossil cycads. We regard the present plant as a possible pteridosperm. *Stenopteris cyclostoma* is the first reliable record of a pteridospermous plant in the Ryoseki-type flora in the Outer Zone of Japan except for the record of *Sagenopteris*. This paper deals with the detailed macro- and microscopical description of *Stenopteris cyclostoma*.

Key words. Pteridosperm, *Stenopteris*, Lower Cretaceous, Choshi Group.

Introduction

A single broken pinnate leaf was obtained from the Barremian Ashikajima Formation of the Choshi Group, which is mostly of marine origin. In addition, two specimens kept at the National Science Museum, Tokyo were examined. They were collected by Nihei Takagi from the sandy shale bed at Hatoyama, Choshi Peninsula (possibly belonging to the Ashikajima Formation ; localities are shown in Figure 1) and were described by Nishida (1960) as *Czekanowskia rigida* Heer.

Fortunately, in the three specimens mentioned above the cuticle is well preserved. According to our observation, their cuticle is rather cycad-like, but in external forms they are far apart from known extant and fossil cycads and are rather fern-like. Hence we regard the present leaf fragments as a possible

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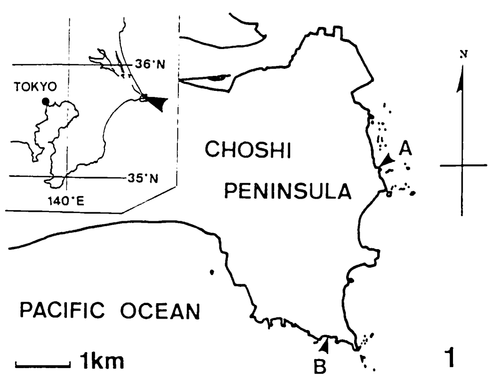


Figure 1. Localities of *Stenopteris cyclostoma* Saiki, Kimura et Horiuchi, sp. nov., in the Ashikajima Formation, Choshi Group. A ; Ashikajima locality. B ; Hatoyama locality.

pteridosperm and refer them to *Stenopteris* Saporta em. Harris (1964), and propose the name *S. cyclostoma*, sp. nov. This paper deals with its detailed macro- and microscopical description.

In fact, it is quite difficult to determine the taxonomic position for such leaf fragments, depending only on their external morphology. In many cases, such leaf fragments would unavoidably be placed in form-genera such as *Sphenopteris* or *Acrostichopteris* for convenience's sake. The Yorkshire *Stenopteris* had also been assigned to *Sphenopteris, Hymenophyllites* and even to *Ruffordia* (Harris, 1964).

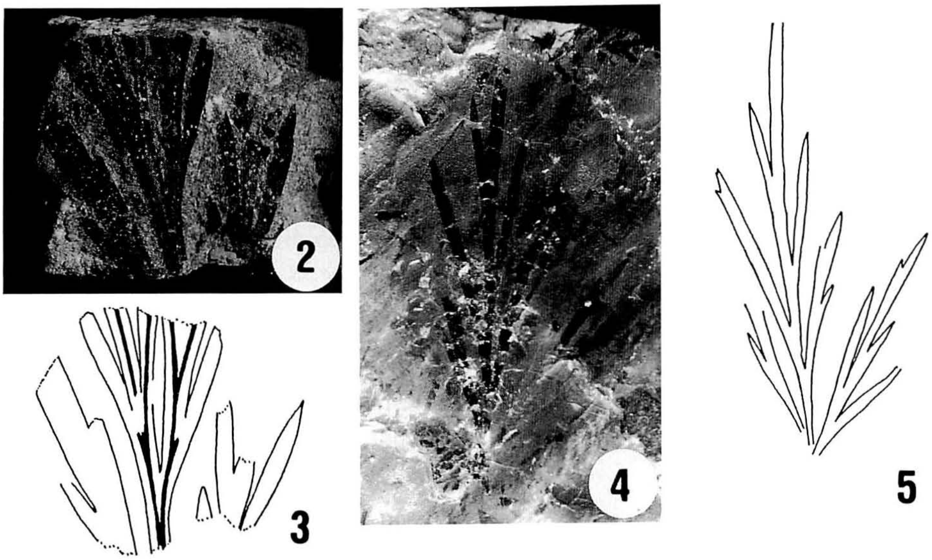
As repeatedly mentioned by one of us (Kimura), there were two distinct floras during Late Jurassic and Early Cretaceous time in Japan and its adjacent regions: the Tetori-type flora distributed in the Inner Zone of Japan and its extension, which flourished under a warm-temperate environment, and the Ryoseki-type flora distributed typically in the Outer Zone of Japan and its extension, which flourished under a subtropical-tropical and rather arid environment (*e.g.*, Kimura, 1987a, b).

The Ryoseki-type flora is characterized by the abundance of matoniaceous (including *Weichselia*, restricted in occurrence to the Early Cretaceous plant sites) and schizaeaceous ferns, of varied bennettitaleans such as *Zamites* and *Ptilophyllum* (including *Nipponoptilophyllum* with leaves of bipinnate habit), of varied cycadaleans such as *Nilssonia* with coriaceous leaves (including *N. schaumburgensis*-type leaves) and of varied cheirolepidiaceous and other conifers, such as *Frenelopsis, Brachyphyllum, Cupressinocladus* and *Parasequoia*. The above genera and groups have not been recorded in the Tetori-type flora except for schizaeaceous ferns. It is worth mentioning that so far to our knowledge, ginkgoaleans, czekanowskialeans and *Podozamites* leafy shoots have not been recognized in the Ryoseki-type flora.

The Lower Cretaceous Choshi Group is mostly of marine origin and yields abundant fossil plants of the Ryoseki type in association with various fossil animals. Although most fossil plants are fragmental, most gymnospermous plants fortunately have well-preserved cuticles.

The Ryoseki-type flora is known from Upper Jurassic-Lower Cretaceous plant sites mainly along the Pacific Coast of Japan for about 1,500 km (roughly from 131°E to 142°E and from 33°N to 40°N), but unfortunately fossil ferns or fern-like plants have lost details of their reproductive organs and leaf cuticles, of the gymnosperms, except for the Choshi plant sites. Therefore, fairly a large number of plants in the Ryoseki-type flora have been left undetermined taxonomically or they have been unavoidably placed in form-genera for convenience. In fact, no fossil plants assignable to pteridosperms had been recorded in the Ryoseki-type flora except for *Sagenopteris* leaves or leaflets and *Pachypteris* ? sp. (Kim and Kimura, 1987 ; Oishi, 1940, p. 422).

Under the circumstances, the presence of the present pteridospermous *Stenopteris cyclostoma* with cycadalean cuticle would be significant for the taxonomy of the Mesozoic fern-like plants in the Ryoseki-type flora in Japan. It is highly probable that we can obtain additional specimens in future from



Figures 2–5. *Stenopteris cyclostoma* Saiki, Kimura et Horiuchi, sp. nov.: **2.** External form of the holotype (NSM PP-9009). ×1.5. **3.** Drawn from the holotype, showing veins dichotomously forked. **4.** External form of one of paratypes (NSM PP-7516). Reinserted from Nishida (1960, pl. 2, fig. 12). ×1. **5.** Drawn from Figure 4, showing alternately lobed lamina. ×1.

the Choshi Group which would be taxonomically useful for the plants at present remaining unclassified or undetermined in the Ryoseki-type flora.

Acknowledgements

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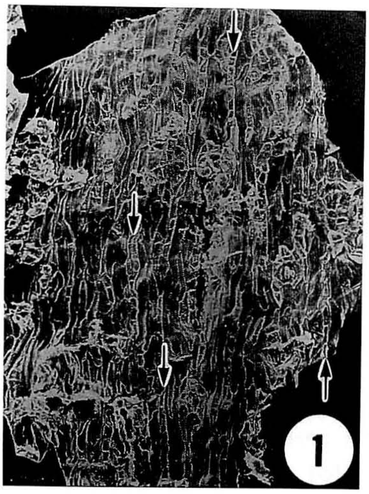
This study was supported in part by the Grant-in-Aid for Scientific Research from the Ministry of Education, Science and Culture (no. 02640615 given to Kimura).

Material and methods

Three leaf-fragments investigated were obtained from the Ashikajima Formation

→ **Figure 6.** Cuticles of *Stenopteris cyclostoma* Saiki, Kimura et Horiuchi, sp. nov. 1, 2, 8 and 9 are SEM-photographs prepared from the holotype (NSM PP-9009). **1.** Internal view of the upper (adaxial) cuticle. Rows of the thick-walled cells are indicated by arrows. ×65. **2.** Internal view of the lower (abaxial) cuticle. Note that the thick-walled cells are absent. ×65. **3.** Distribution and orientation of stomata, drawn from **Figure 1.** Orientation of stomatal aperture is ignored in the stoma figured by 'open circle'. **4.** Distribution and orientation of stomata, drawn from Figure 2. **5.** A stoma prepared from NSM PP-7516. ×500. **6.** A stoma photographed by phase contrast microscope (NSM PP-7516). ×400. **7.** Stomata photographed by light microscope, showing thickly cutinized subsidiary cells (NSM PP-7516). × 200. **8.** Internal surface of thin-walled cell of the upper cuticle, showing granules. ×20,000. **9.** Inside view of upper cuticle, showing thick- and thin-walled cells. ×550. K; thick-walled cell, N; thin-walled cell.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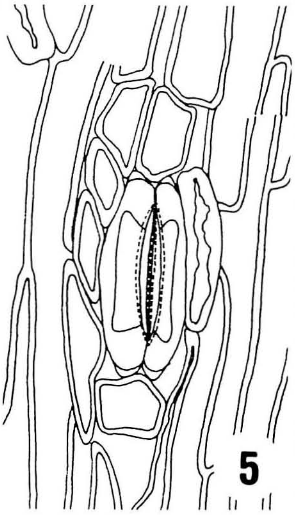
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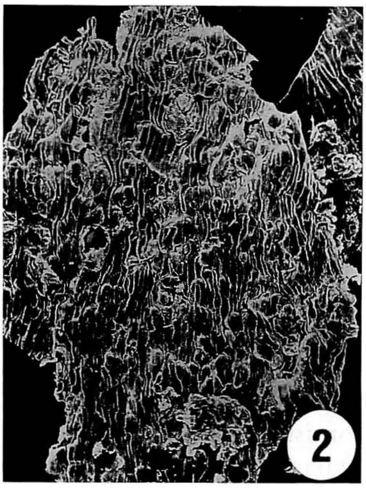
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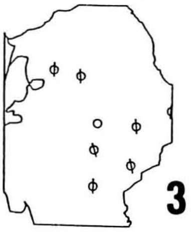
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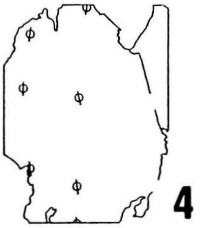
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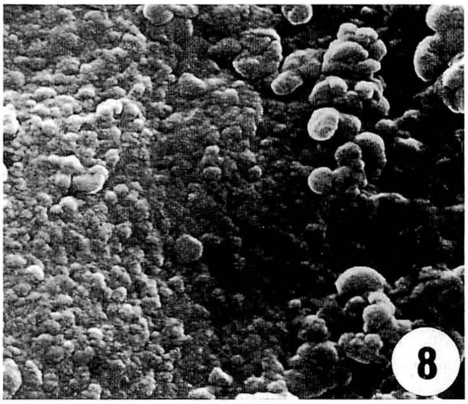
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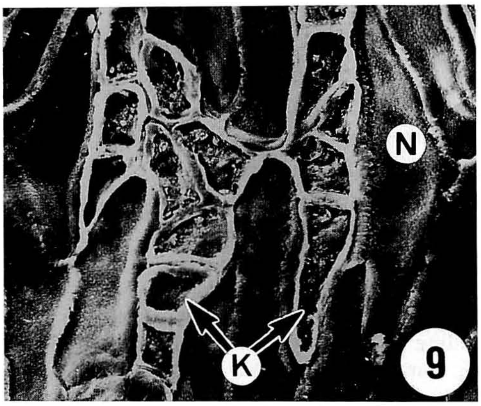
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(Barremian in age) of the Choshi Group (Obata *et al*., 1982). The holotype (NSM PP-9009; Figures 2-3) was collected from Ashikajima, Choshi City, Chiba Prefecture (Figure 1A). Other specimens (paratypes) (NSM PP-7513 and 7516) were collected from Hatoyama (Figure 1B) and were kept in the National Science Museum, Tokyo (Figures 4-5). The holotype, its SEM-stages and cuticular preparations are also kept in the National Science Museum, Tokyo.

Fossil leaves were treated by Schulze's solution followed by diluted NaOH and mounted in Canada balsam. Eight genera of extant cycads (*Bowenia, Ceratozamia, Cycas, Dioon, Encephalartos, Macrozamia, Stangeria* and *Zamia*) used for cuticular comparison were treated in 10% chromic oxide for 24 hours at room temperature.

For the SEM observation, cuticles were coated by gold with a JEOL FC-1100 apparatus and photographed by JEOL J-15.

Description of specimens

Three leaf-fragments were examined (Figures 2-5). The largest specimen (NSM PP-7516) is 5.5 cm long. Pinnae are wedge-shaped and are dissected alternately up to three times or more to form slender segments. The segment is linear, up to 30 mm long and about 2 mm wide, narrowing gradually toward the acute apex. Each segment bears a single median vein, approximately 0.5 mm wide. Veins are dichotomously forked at an angle of 15-30 degrees and the angle tends to get reduced upward. Basal portion of segments is narrowed slightly. Lateral vein is absent.

Scanning electron micrographs (Figures 6-1, 2) show upper and lower cuticles of the same part of the holotype. Cuticle is amphistomatic. Stomata are distributed approximately 20 per square mm on both sides. Stomatal bands are rather well defined, separated by nonstomatal bands 5-13 cells wide (110-200 μm in width) (Figures 6-1, 2, 3, 4). Papilla or trichome base is absent.

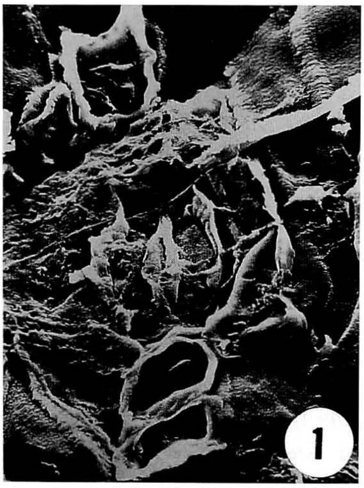
Upper (adaxial) cuticle consists of stomata and two types of ordinary cells; one with cutinized periclinal walls, about 8 μm thick (thin-walled cells) and the other with periclinal walls consisting of two cuticular layers (thick-walled cells) (Figures 6-1, 9). Inner surface of periclinal walls is disorganized.

Thin-walled cells are elongate-rectangular or short-rectangular or sometimes triangular in shape, 60-160 μm long and 10-35 μm wide. Anticlinal walls of the thin-walled cells are straight, rather broad, ca. 2 μm high and ca. 5 μm wide. Inner surface of periclinal walls is granulated; the granules are ca. 0.2 μm in diameter (Figure 6-8).

Thick-walled cells are 15-50 μm long and 6-25 μm wide, rectangular or triangular in shape, consisting of both external and internal cuticular layers. The external layer is about 8 μm thick, corresponding to that of thin-walled cells, and the internal layer is less than 1 μm thick. The thick-walled cells form longitudinal rows, 2-14 cells long (60-400 μm) and typically a single cell (sometimes up to 4 cells) wide. The rows are scattered between thin-walled cells. The

⟶ **Figure 7.** *Stenopteris cyclostoma* Saiki, Kimura et Horiuchi, sp. nov., the holotype (NSM PP-9009). **1.** Internal view of a stoma, showing sunken aperture. ×650. **2.** External view of a stoma. Groove surrounding the stomatal aperture is indicated by an arrow. ×650. **5.** Cross section of a thick-walled cell, showing external and internal layers. ×5,500. **6.** A figure drawn from Figure 5. e.l.; external layer of thick-walled cell, i.l.; internal layer of thick-walled cell. ×5,500. **8.** Light microscope photograph of cells. Note well stained thick-walled cells. ×500. **Figures 7-3, 4.** *Stangeria eriopus* Nash, for comparison. **3.** Internal view of a stoma for comparison. ×650. **4.** External view of a stoma. ×650. **Figures 7-7, 9.** *Dioon spinulosum* Dyer, for comparison. **7.** Cross section of cuticle, showing external and internal layers of thick-walled cell. ×1,700. **9.** Thick-walled cells stained by alcoholic safranin, for comparison. ×500. **Figures 7-1, 2, 3, 4, 5, 7** are SEM-photographs.

930. *Stenopteris cyclostoma* sp. nov.



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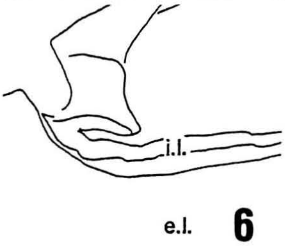

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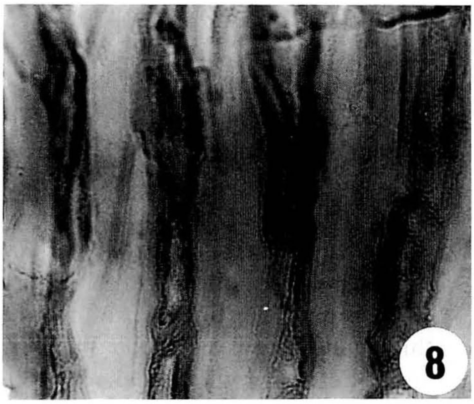

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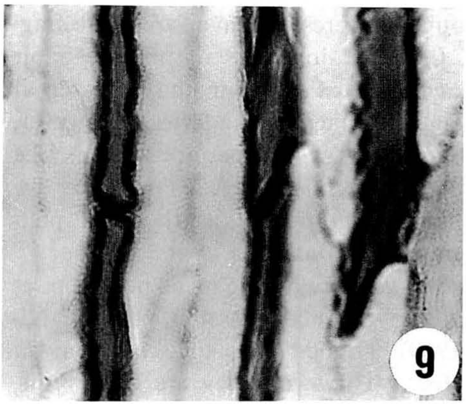

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morphology of the present thick-walled cells is similar to those of some extant cycads in two-layered construction (Figure 7-7). The thick-walled cells are well stained by alcoholic safranin as seen in some extant cycads (Figures 7-8, 9).

Lower (abaxial) cuticle is thinner than the upper. It consists of thin-walled cells and stomatal apparatuses. Thin-walled cells of upper and lower cuticles are similar to each other.

Stomatal apparatus is haplocheiric, 50-80 μm in diameter (Figures 6-5, 6, 7 ; Figure 7-1). Subsidiary cells are thickly cutinized, consisting of polar and 4-6 lateral cells. Polar cells are rectangular or polygonal in shape, 27-46 μm long. Lateral subsidiary cells are bean-shaped, about 20-45 μm long. Guard cells are slightly sunken, each cell 35-50 μm long and 5-7 μm wide. Stomatal aperture is fusiform, about 12 μm long. Outer stomatal ridge (rim) is thickened, forming a fusiform opening, about 10 μm long. Papilla is absent around the stomatal aperture (Figure 7-2). Morphology of the present stomatal apparatus is similar to those of some extant cycads, especially of *Stangeria eriopus* Nash (Figures 7-3, 4).

Discussion and comparison

Although the present leaves are quite fragmental, they are doubtless of pinnate habit and what we regard as a pinna has an external resemblance to that of some ferns. However, the leaf cuticle is gymnospermous and is like those of some extant cycads. Hence we regard the present leaves as those of pteridospermous *Stenopteris*.

On the basis of two specimens now kept at the National Science Museum, Tokyo, Nishida (1960) assigned them to *Czekanowskia rigida* Heer. However, they are clearly distinguishable from the leaves of *Czekanowskia* by the presence of the thick-walled cells. In addition, Nishida (1960) mentioned the presence of dwarf (or short) shoots covered by scale-leaves at the base of a wedge-shaped leaf-bundle. But we found neither such dwarf shoots nor scale-leaves in his specimens.

Among the Mesozoic pteridosperms known from the present Northern Hemisphere, several leaves assigned to genera such as *Pachypteris* Brongniart, *Stenopteris* Saporta and *Thinnfeldia* Ettingshausen have a rather close external resemblance to the present leaves. Of these, the leaves of *Pachypteris* and *Thinnfeldia* are clearly distinguished from the present leaves by having pinnate venation. Externally the present leaves are most close to those of *Stenopteris* and their external and cuticular features agree generally with Harris' emended diagnosis of *Stenopteris* (Harris, 1964). Harris (1932, 1937) described two species of *Stenopteris* from Scoresby Sound, East Greenland and three species of this genus from the Yorkshire Jurassic (Harris, 1964). However, the present leaves are different from those of Harris' five species because of the presence of thick-walled cells and lack of trichomes.

From the Choshi Group, we collected many Ryoseki-type gymnosperms with preserved cuticles. Generally, they are characterized by the absence of trichomes or less developed trichomes, if present. It seems that these plants might have flourished under an oceanic environment during Early Cretaceous time.

Thomas and Bancroft (1913) recognized thick-walled cells in the cycads. According to Pant and Nautiyal (1963), the thick-walled cells are present in extant cycads excluding *Cycas* and some fossil cycads, and they have thickened anticlinal walls and are easily stained by alcoholic safranin (Figure 7-9).

According to our SEM-observation, the thick-walled cells in *Dioon spinulosum* Dyer are not caused by a thickened cuticle, but by two cuticular layers (Figure 7-7). Such a two-layered structure is also recognized in *Bowenia, Ceratozamia, Encephalartos, Macrozamia* and *Zamia*, but it has not been recognized in *Stangeria* and *Cycas*. The thick-walled cells of the present fossil leaves have similar structure to the above and are also easily stained by alcoholic safranin (Figures 7-5, 6, 8). Therefore, we could not differentiate between the thick-walled cells of the present fossil leaves and those of extant cycads.

The present cuticle is very close to that of *Almargemia incressata* originally described by Archangelsky (1966) from the Baquero Formation, Argentina in the presence of thick-walled cells and cycad-like stomata, respectively. *Almargemia* was supposed by Archangelsky (1966) as a cycadalean, because both thick- and thin-walled cells were present on the same epidermal plane. But the ultimate segments of *Almargemia* are distinguished from those of the present leaves by having 3-4 veins.

So far as we know, the present leaves differ in external form from those of extant and fossil cycads hitherto known, but they resemble in their external form those of some ferns or pteridosperms. On the other hand, the cuticle in the present specimen bears characteristic thick-walled cells which have been said to be a characteristic feature of most extant cycads. The present leaves are not those of fern, because in ferns a cuticle is generally absent or less developed.

Under the circumstances, it seems to be appropriate to give the present plant a new generic name. But at present we refrain from doing it and regard the present plant as a new species of pteridospermous *Stenopteris*, because the present specimens are all fragmental and the plant is most close to *Stenopteris* in external morphology. In fact, as stated by Harris (1964, p. 31), the taxonomic division of the non-bennettitalean cycadophyte leaves into Cycadales and Pteridospermales is difficult when depending only on their leaf-form and leaf-cuticle, since we have no single character to mark the two classes from one another.

Taxonomy

Pteridospermales (?)
Genus *Stenopteris* Saporta,
1873 em. Harris, 1964

Stenopteris cyclostoma
Saiki, Kimura et Horiuchi, sp. nov.

Figures 2-6, 7-1, 2, 5, 6, 8

Czekanowskia rigida Heer: Nishida, 1960, p. 191, pl. 2, figs. 12, 13.

Holotype: NSM PP-9009. *Paratypes*: NSM PP-7513, 7516. *Stratum typicum*: Ashikajima Formation (Barremian in age), Choshi Group. *Locus typicus*: Ashikajima, Choshi City, Chiba Prefecture. *Derivatio nominis*: After circular stomatal complex.

Occurrence. — Rather rare at present.

Diagnosis. — (Whole leaf unknown). Pinnae wedge-shaped, dissected alternately up to three times or more to form slender segments. A segment linear in shape, narrowing gradually toward the acutely pointed apex. Each segment bearing a single median vein. Veins dichotomously forked at an angle of 15-30 degrees, the angle tending to reduce upward. Basal portion of segments slightly narrowed. Lateral vein absent.

Cuticle amphistomatic. Stomata approximately 20 per square mm on both sides, forming well-defined rows. Papilla or trichome base absent. Upper (adaxial) cuticle consisting of stomata, and two types of ordinary cells: One with cutinized periclinal walls (thin-walled cells) and the other with periclinal walls consisting of two cuticular layers (thick-walled cells). Lower (abaxial) cuticle thinner than the upper, consisting of thin-walled cells and stomata. Thin-walled cells similar to those of the upper cuticle. Stomatal apparatus haplocheiric. Subsidiary cells thickly cutinized, consisting of 2 polar cells and 4-6 lateral cells. Guard cells slightly sunken. Stomatal aperture longitudinally orientated and sunken. External surface of stoma surrounded by well-defined groove. Outer stomatal ridge (rim) thickened, forming fusiform opening. (Reproductive organs not known.)

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Ashikajima 海鹿島，Choshi 銚子，Hatoyama 波止山，Ryoseki 領石，Tetori 手取.

下部白亜系銚子層群産 *Stenopteris* 属新種：得られた化石はすべて，シダ型葉の断片であるが，その上面の通常細胞は，大部分の現生ソテツ葉および一部の化石ソテツ葉に認められる2層からなる cuticle 層が存在する。本化石葉は，外形はシダ型である点に特徴があり，その外形は従来知られている化石葉の中でシダ種子類と考えられている *Stenopteris* に最も近いので，ここに *Stenopteris cyclostoma* を新種として提唱する。

斎木健一・木村達明・堀内順治

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931. EARLY EVOLUTION OF THE FAMILIES VERBEEKINIDAE AND NEOSCHWAGERINIDAE (PERMIAN FUSULINACEA) IN THE AKIYOSHI LIMESTONE GROUP, SOUTHWEST JAPAN*

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Abstract. Fifteen species of verbeekinid and neoschwagerinid fusulinaceans are discriminated from the Akiyoshi Limestone Group below the *Misellina* (*M.*) *claudiae* Zone in the Kaerimizu area. Among them, *Misellina* (*Brevaxina*) *nipponica*, sp. nov., *M.* (*M.*) *postclaudiae*, sp. nov. and *M.* (*M.*) ? *ventricosa*, sp. nov. are new to science. Stratigraphic distribution of the early representatives of verbeekinid and neoschwagerinid fusulinaceans, besides their ancestral forms, makes it possible to establish 10 fusulinacean biohorizons in the stratigraphic interval between the first occurrence of *Pamirina* (*Levenia*) *leveni* and that of *Parafusulina kaerimizensis*. Of them, three biohorizons, which are well recognized in the surveyed area, define the base of the *Pamirina* (*Levenia*) *leveni*, *Misellina* (*Brevaxina*) *dyhrenfurthi otai* and *Misellina* (*M.*) *claudiae* Zones established herein. Biostratigraphic evidence observed in the Akiyoshi Limestone Group provides many important data concerning the origin and early evolution of the families Verbeekinidae and Neoschwagerinidae.

Key words. Akiyoshi Limestone Group, Kaerimizu, Middle Permian, Neoschwagerinidae, Verbeekinidae.

Introduction

The families Verbeekinidae and Neoschwagerinidae flourished and diversified in the Middle Permian of the Tethyan realm, and are considered to be the most important fusulinacean groups in determining biostratigraphic zonation and geologic age in that period. Since the beginning of this century, dozens of works have been devoted to the phylogeny and classification of the Verbeekinidae and Neoschwagerinidae (*e.g.* Deprat, 1913; Ozawa, 1925a, 1927; Lee, 1933; Gubler, 1935; Thompson, 1948; Kanmera, 1957; Miklukho-Maklay *et al.*, 1958; Minato and Honjo, 1959; Morikawa and Suzuki, 1961; Hanzawa and Murata, 1963; Ozawa, 1970; Leven, 1982; Yang, 1985). Ozawa (1970) rethought the phylogenetic relationship of the neoschwagerinid species and confirmed that three distinct lineages are present in the family Neoschwagerinidae. He also gave diagnoses of all genera referred to the Verbeekinidae and Neoschwagerinidae. Up to the present, about 300 species have been proposed belonging to these families.

In the Akiyoshi Limestone Group below the *Misellina* (*M.*) *claudiae* Zone, the following six species of verbeekinid and neoschwagerinid fusulinaceans, *Misellina* (*M.*) *claudiae* (Deprat), *M.* (*M.*) *ovalis* (Deprat), *M.* (*M.*) *parvicostata* (Deprat), *M.* (*Brevaxina*) *dyhrenfurthi otai* Sakaguchi and Sugano, *Maklaya pamirica* (Leven) and *M. akiyoshiensis* Ota (MS), occur, although totally about 30 species of them are recorded in the whole extent of the Akiyoshi Lime-

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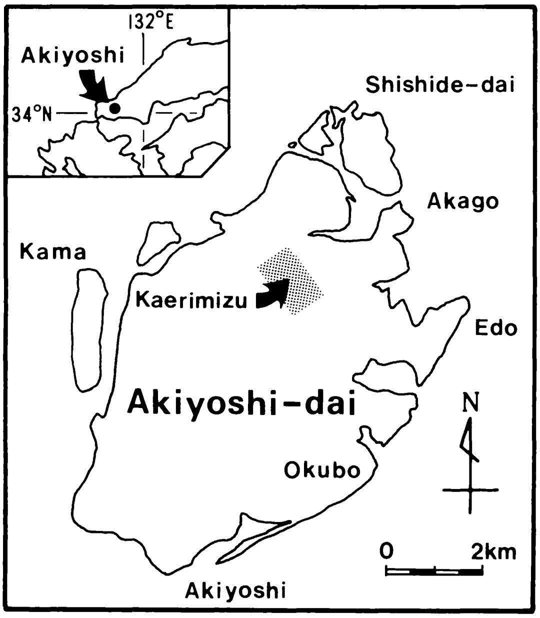


Figure 1. Map showing the Kaerimizu area in the Akiyoshi Plateau.

stone Group (Toriyama, 1958; Ota, 1977; Ozawa and Kobayashi, 1990 and others).

Recently, I reported three species referable to the genus *Pamirina* and one species tentatively assigned to the subgenus *Brevaxina* of the genus *Misellina* from the *Pamirina* (*Levenia*) *leveni* Zone in the Akiyoshi Limestone Group of the Kaerimizu area, and discussed the evolution of the genus *Pamirina*, which is considered to be an ancestral phylogenetic stock of the family Verbeekinidae (Ueno, 1991). In that paper, I proposed the subgenus *Levenia* for primitive *Pamirina* without alveolar structure in the spirotheca.

In the present paper, I discuss the early evolution and phylogeny of verbeekinid and neoschwagerinid fusulinaceans in the Akiyoshi Limestone Group below the *Misellina* (*M.*) *claudiae* Zone in the Kaerimizu area. Moreover, 14 species of verbeekinid and neoschwagerinid fusulinaceans including three new ones; *Misellina* (*Brevaxina*) *nipponica, M.* (*M.*) *postclaudiae* and *M.* (*M.*)? *ventricosa,* are also described.

Geologic setting

The Kaerimizu area is situated in the northeastern part of the Akiyoshi Plateau (Figure 1). Since the discovery of large-scale overturned structure by Ozawa (1923), more than a dozen geological and paleontological studies have been carried out (Ozawa, 1925b; Hanzawa, 1954; Toriyama, 1954, 1958; Hasegawa, 1958, 1963; Sakaguchi *et al.*, 1966; Sakaguchi and Sugano, 1966; Kawano, 1967; Ota, 1968, 1977; Ota *et al.*, 1973; Hasegawa *et al.*, 1979; Ozawa and Kobayashi, 1990; Ueno, 1991). Ota (1977) divided the Akiyoshi Limestone Group in this area into the following 10 zones: the *Fusulinella biconica, Triticites simplex, Pseudofusulina vulgaris, Pseudofusulina ambigua, Misellina claudiae, Parafusulina kaerimizensis, Afghanella schencki, Neoschwagerina craticulifera, Verbeekina verbeeki* and *Colania douvillei* Zones in ascending order.

According to my recent investigation, Ota's *Pseudofusulina ambigua* Zone can be subdivided into the lower *Pseudofusulina* ex gr. *kraffti* and the upper *Pamirina* (*Levenia*) *leveni* Zones, and *Misellina claudiae* Zone into the lower *Misellina* (*Brevaxina*) *dyhrenfurthi otai* and the upper *Misellina* (*M.*) *claudiae* Zones, respectively,

Figure 2 shows the distribution of fusulinacean zones in the Kaerimizu area. The zones are distributed concentrically and get younger downward. Consequently, the Akiyoshi Limestone Group in this area lies almost horizontally and is in reverse order.

In the stratigraphic interval between the first occurrence of *Pamirina* (*Levenia*) *leveni* and that of *Parafusulina kaerimizensis,* 10 fusulinacean biohorizons, which are defined by the first occurrence of the characteristic species of verbeekinid, neoschwagerinid and their ancestral fusulinaceans, are recognized. They are shown in Figure 3. Of these, three biohorizons characterized by the first occurrence of *Pamirina* (*Levenia*) *leveni, Misellina* (*Brevaxina*) *dyhrenfurthi otai* and *Misellina*

(*M.*) *claudiae*, are well recognized in the examined sections and define the base of three fusulinacean zones, respectively. Others are observed only in some sections.

The *Pamirina* (*Levenia*) *leveni* Zone, about 25 m thick, conformably overlies the *Pseudofusulina* ex gr. *kraffti* Zone. This zone is defined as the stratigraphic interval between the first occurrence of *Pamirina* (*Levenia*) *leveni* and that of *Misellina* (*Brevaxina*) *dyhrenfurthi otai*. Algal oncoidal limestone is predominant with a subordinate amount of algal sparitic limestone and muddy limestone. I have previously listed the identified fusulinaceans from the *Pamirina* (*Levenia*) *leveni* Zone (Ueno, 1991).

The *Misellina* (*Brevaxina*) *dyhrenfurthi otai* Zone is about 15 m in thickness, and conformably overlies the *Pamirina* (*Levenia*) *leveni* Zone. The limestone facies of this zone is similar to that of the *Pamirina* (*Levenia*) *leveni* Zone. The following fusulinaceans are discriminated : *Toriyamaia laxiseptata* Kanmera, *Schubertella* sp., *Mesoschubertella* sp., *Neofusulinella* sp., *Pseudofusulina postkraffti* (Leven), *Pseudoreichelina* spp., *Pseudoendothyra yobarensis* (Ozawa), *Pseudoendothyra* spp., *Misellina* (*Brevaxina*) *dyhrenfurthi otai* Sakaguchi and Sugano, and *Misellina* (*M.*) sp. A.

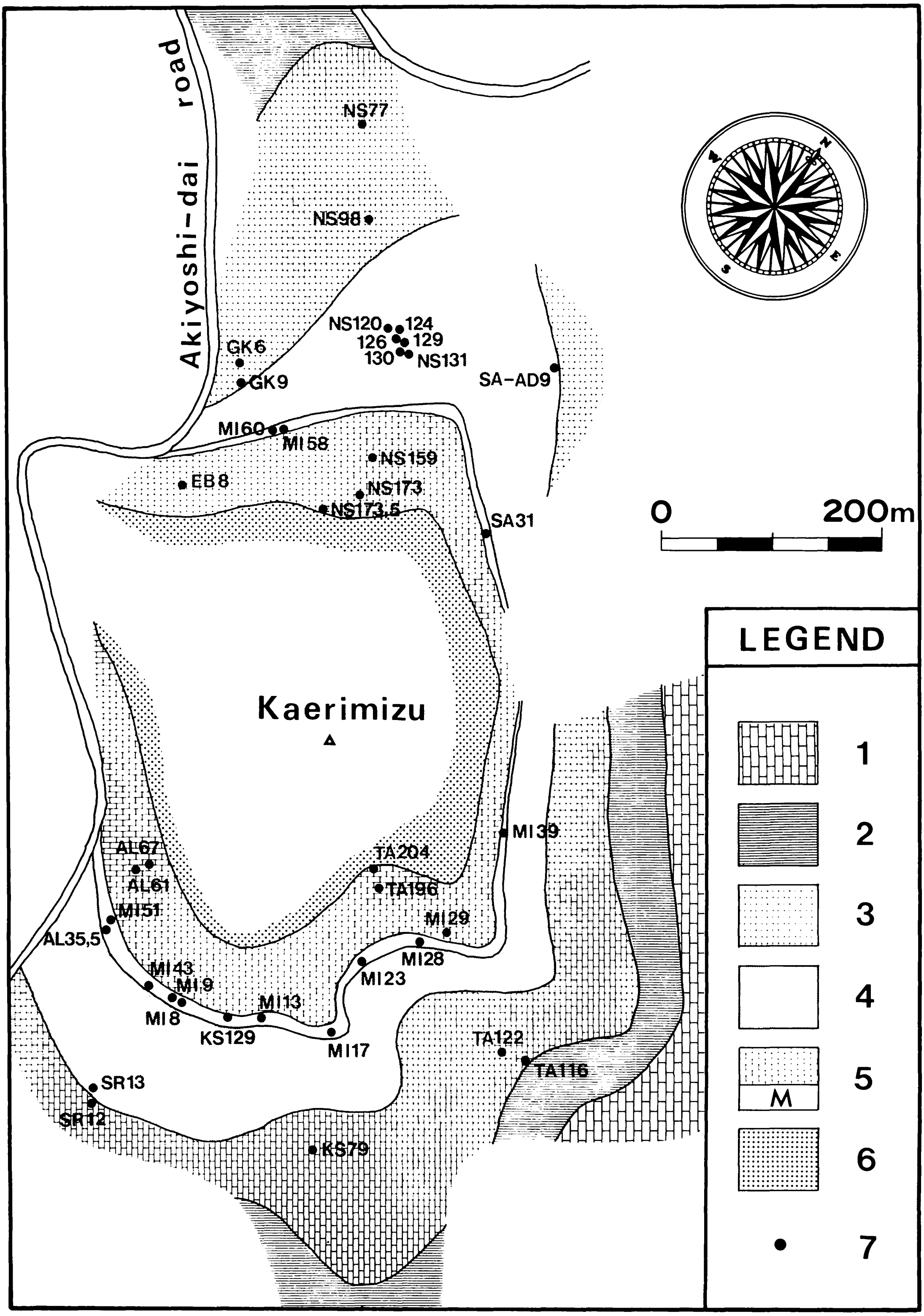
The *Misellina* (*M.*) *claudiae* Zone, about 30 m thick, is defined as the stratigraphic interval from the first occurrence of *Misellina* (*M.*) *claudiae* to that of *Parafusulina kaerimizensis*. The stratigraphic relationship between the present zone and the subjacent *Misellina* (*Brevaxina*) *dyhrenfurthi otai* Zone is conformable. Foraminiferal algal sparitic limestone is dominant in the lower part, algal micritic limestone and muddy limestone are predominant with a subordinate amount of algal sparitic limestone in the middle and upper parts. The identified fusulinaceans are : *Mesoschubertella* sp., *Neofusulinella giraudi* Deprat, *N. pseudogiraudi* (Sheng), *Neofusulinella* sp., *Minojapanella* (*Russiella*) *pulchra* Miklukho-Maklay, *Pseudofusulina* cf. *quasifusuliniformis* Leven, *Nagatoella orientis* (Ozawa), *Nagatoella* sp., *Chusenella tingi* Chen, *Pseudoendothyra* spp., *Misellina* (*M.*) *claudiae* (Deprat), *M.* (*M.*) *postclaudiae,* sp. nov., *M.* (*M.*) *spinosa* Han, *M.* (*M.*)? *ventricosa,* sp. nov., *Misellina* (*M.*) sp. B, *Armenina salgirica* Miklukho-Maklay, *A.* cf. *asiatica* Leven, *Maklaya saraburiensis* Kanmera and Toriyama, *M. pamirica* (Leven), *Maklaya* sp. and *Neoschwagerina simplex* Ozawa.

The geologic age of these three zones is considered as follows : the *Pamirina* (*Levenia*) *leveni* Zone is almost late Yakhtashian, the *Misellina (Brevaxina) dyhrenfurthi otai* Zone is early Bolorian, and the *Miselliana* (*M.*) *claudiae* Zone is late Bolorian to Kubergandian of the standard stratigraphic scheme for the Tethyan province proposed by Leven (1980).

Some considerations on the early evolution and phylogeny of the families Verbeekinidae and Neoschwagerinidae

A total of 15 species of verbeekinid and neoschwagerinid fusulinaceans are identified in the *Pamirina* (*Levenia*) *leveni, Misellina* (*Brevaxina*) *dyhrenfurthi otai* and *Misellina* (*M.*) *claudiae* Zones. The stratigraphic distribution of the verbeekinid and neoschwagerinid fusulinaceans are shown in Figure 4.

Concerning the early evolution and phylogeny of the families Verbeekinidae and Neoschwagerinidae, the occurrences of *Misellina* (*Brevaxina*)? sp., *Misellina* (*M.*) sp. A, *M.* (*M.*)? *ventricosa,* sp. nov. and *Misellina* (*M.*) sp. B in the Akiyoshi Limestone Group are significant and interesting. They suggest an intimate phylogenetic relationship between *Pamirina* (s.s.) and *Brevaxina, Brevaxina* and *Misellina* (s.s.), *Misellina* (s.s.) and *Armenina,* and *Misellina* (s.s.) and *Maklaya,* respectively (Figure 5).


Akiyoshi-dai road
NS77
NS98
NS120
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NS131
SA-AD9
GK6
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MI60
MI58
NS159
EB8
NS173
NS173.5
SA31
0
200m
Kaerimizu
LEGEND
1
2
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M
6
7
MI39
TA204
TA196
AL67
AL61
MI51
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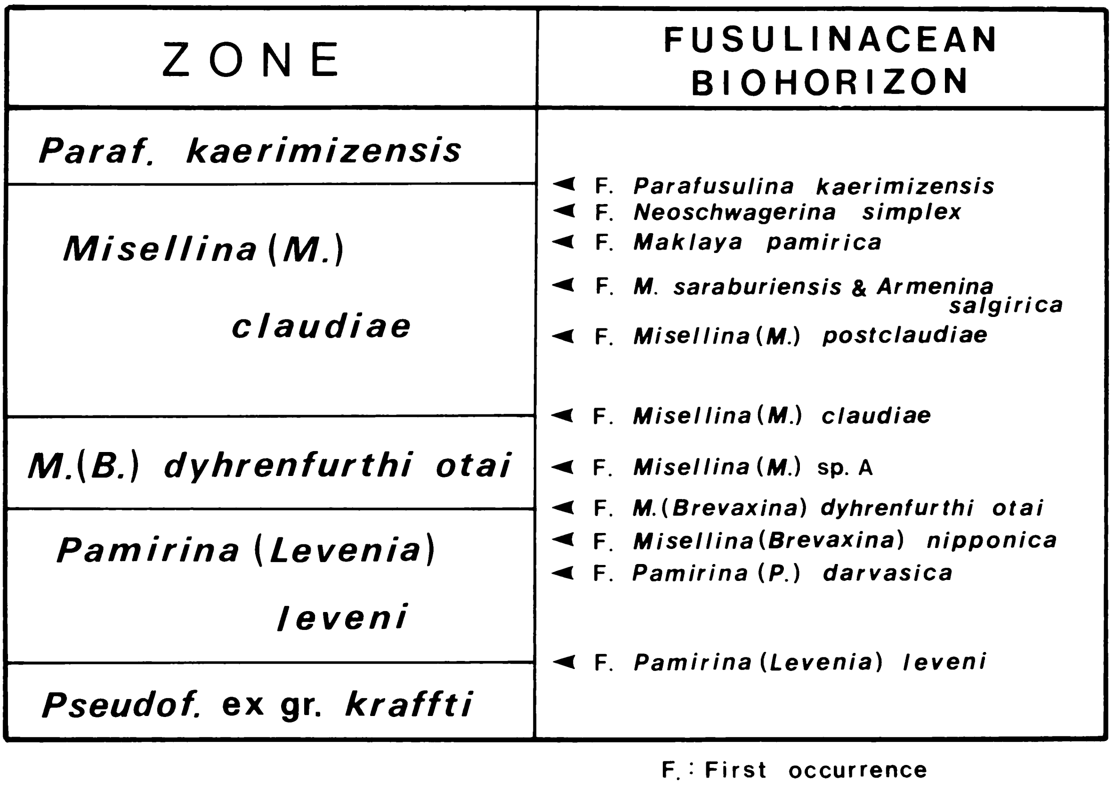

Figure 3. Fusulinacean biohorizons in the *Pamirina* (*Levenia*) *leveni*, *Misellina* (*Brevaxina*) *dyhrenfurthi otai* and *Misellina* (*M.*) *claudiae* Zones.

Based on biostratigraphical and morphological observations, it has been considered that certain species of *Levenia*, *Pamirina* (s.s.), *Brevaxina* and *Misellina* (s.s.) comprise a single evolutionary series, and that *Misellina* (s.s.) is the ancestral stock of later verbeekinid and neoschwagerinid genera (Ozawa, 1970; Kobayashi, 1977 and others). The occurrences of some transitional forms or closely related species between two distinct genera together with the biostratigrapic evidence in the Akiyoshi Limestone Group prove the above-mentioned considerations. Evidently, the Akiyoshi Limestone Group has an almost continuous record in relation to the origin and early evolution of the families Verbeekinidae and Neoschwagerinidae.

Systematic paleontology

Among the illustrated fusulinaceans, four species; *Pamirina* (*P.*) *darvasica* Leven, *Pamirina* (*Levenia*) *leveni* Kobayashi, *P.* (*L.*) *evoluta* Sheng and Sun, and *Misellina* (*Brevaxina*) ? sp. have already been described (Ueno, 1991). All specimens identified in this paper are deposited in the paleontological collections of the Akiyoshi-dai Museum of Natural History. The abbreviation ASM is the prefix of the specimen repository number.

← **Figure 2.** Distribution of foraminiferal zones and fossil localities in the Kaerimizu area. 1: *Chalaroschwagerina vulgaris* Zone, 2: *Pseudofusulina* ex gr. *kraffti* Zone, 3: *Pamirina* (*Levenia*) *leveni* Zone, 4: *Misellina* (*Brevaxina*) *dyhrenfurthi otai* Zone, 5: *Misellina* (*M.*) *claudiae* Zone (M: *Misellina* (*M.*) *claudiae* swarmed layer), 6: *Parafusulina kaerimizensis* Zone, 7: fossil locality studied herein.

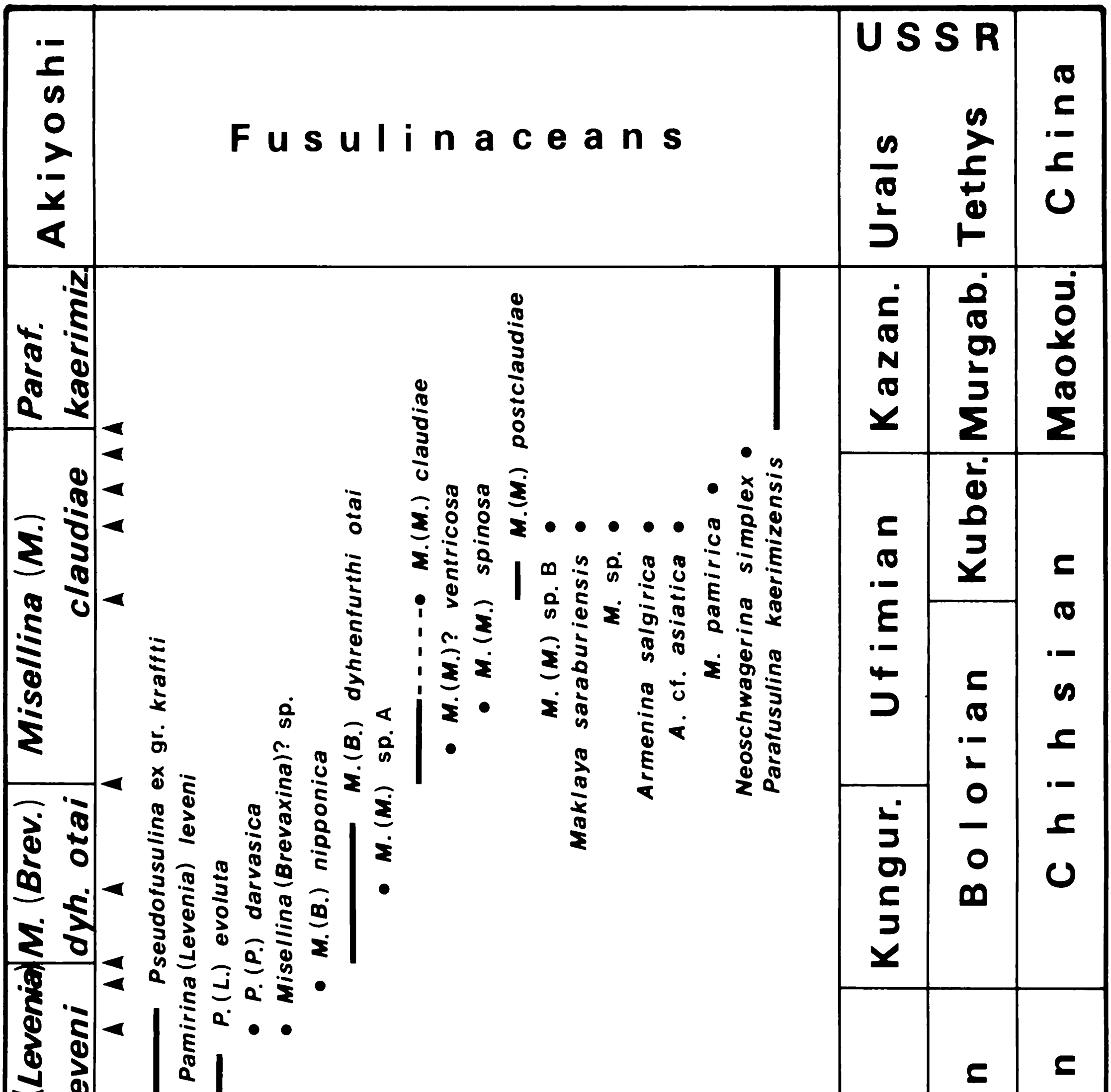

Figure 4. Stratigraphic distribution of early representatives of verbeekinid and neoschwagerinid fusulinaceans in the Akiyoshi Limestone Group.

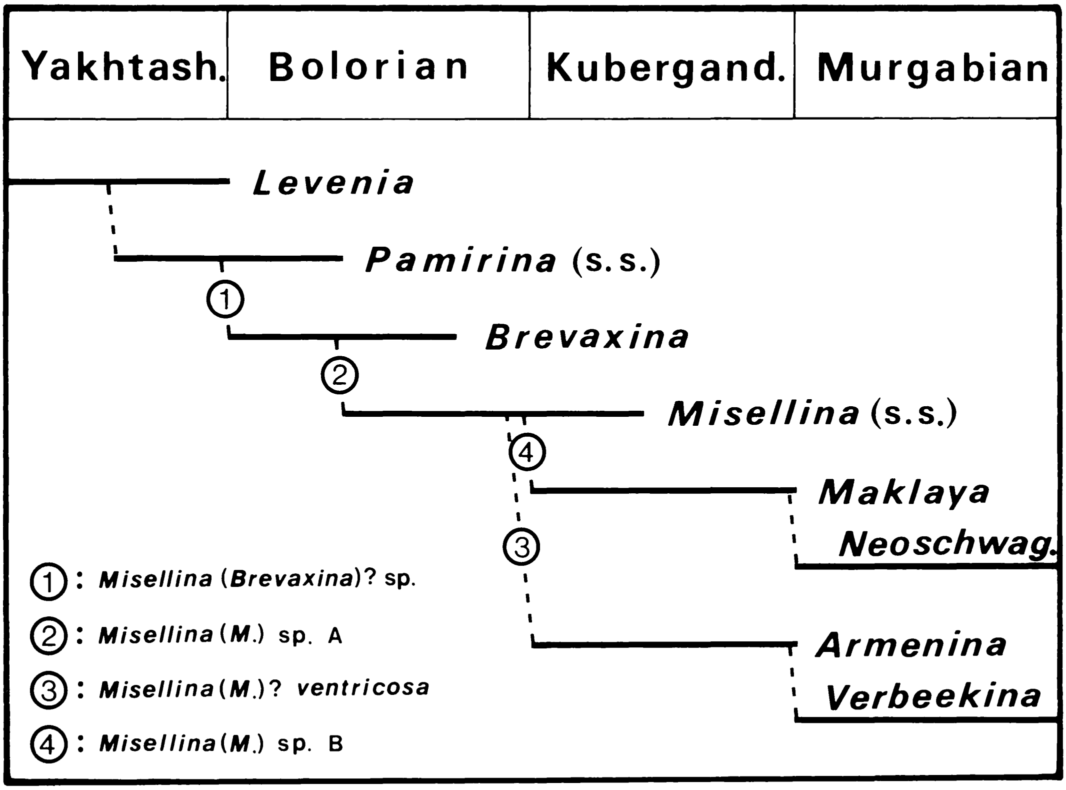

Figure 5. Reconstruction of early phylogeny of some verbeekinid, neoschwagerinid and their ancestral fusulinacean genera.

Order Foraminiferida Eichwald, 1830
Suborder Fusulinina Wedekind, 1937
Superfamily Fusulinacea
von Möller, 1878
Family Verbeekinidae Staff
and Wedekind, 1910
Subfamily Misellininae
Miklukho-Maklay, 1958

Genus *Misellina* Schenck
and Thompson, 1940
Subgenus *Brevaxina* Schenck
and Thompson, 1940

Type species.—*Doliolina compressa* Deprat, 1915.

Misellina (Brevaxina) nipponica
Ueno, sp. nov.

Figures 7-1–12

Brevaxina ibukiensis Kobayashi, Zhou *et al*., 1987, pl. 6, fig. 13.

Misellina (*Brevaxina*) aff. *otakiensis* (Huzimoto), Ueno, 1991, p. 742 (listed).

Material.—Axial section of the holotype; ASM25082. Axial sections of paratypes; ASM25083A, B, ASM25084, ASM25085, ASM25086, ASM25088B. Slightly oblique axial sections of paratypes; ASM25087, ASM25088A, ASM25089A. Sagittal sections of paratypes; ASM25089B, ASM25090. All specimens from Loc. GK9. Some other specimens from Loc. GK9 were studied.

Diagnosis.—Small *Brevaxina* having a spherical shell with shallow umbilicus, and tightly and skew-coiled inner volutions. Spirotheca relatively thin. Septa short and straight. Parachomata small and incipient.

Description.—Shell small for genus and

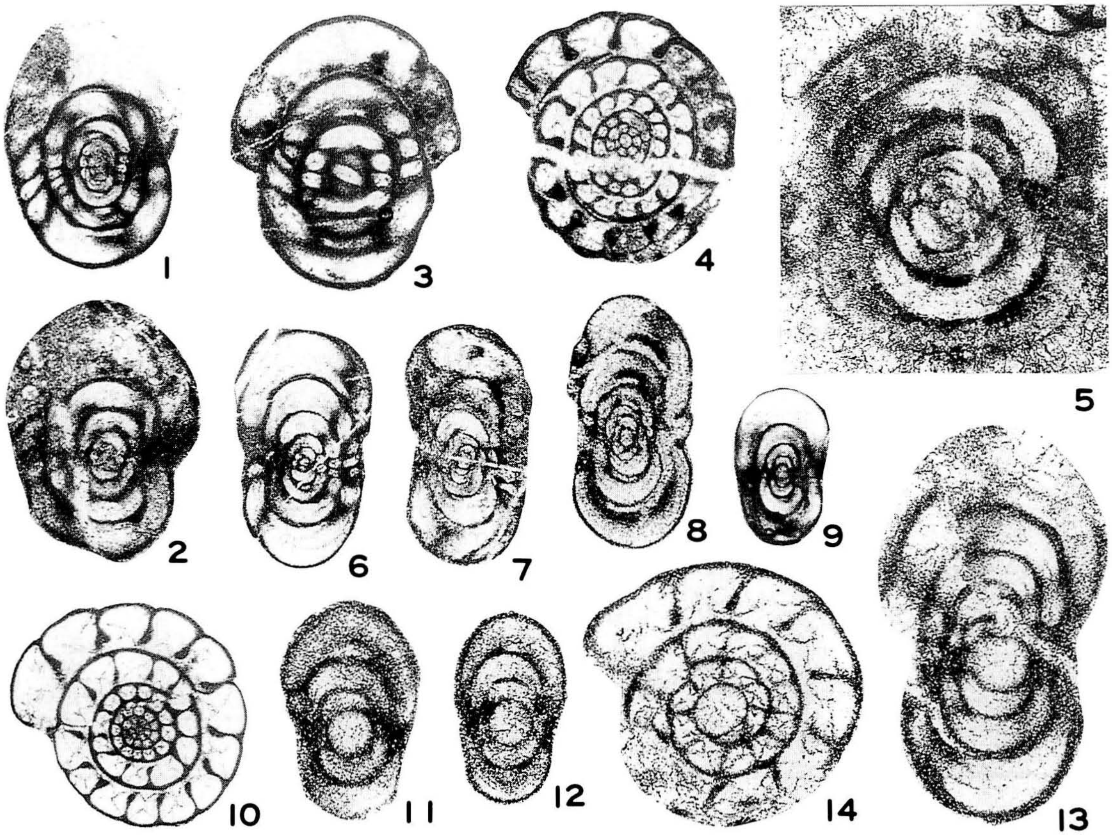

Figure 6. **1–4.** *Pamirina* (*Pamirina*) *darvasica* Leven, **1, 2**: axial sections, ASM25007, ASM25005, **3**: tangential section, ASM25008, **4**: sagittal section, ASM25002, ×40. **5**: *Misellina* (*Brevaxina*) ? sp., axial section, ASM25004, ×75. **6–10.** *Pamirina* (*Levenia*) *leveni* Kobayashi, **6–9**: axial sections, ASM 25019, ASM25018A, ASM25021, ASM25025, **10**: sagittal section, ASM25028, ×40. **11–14.** *Pamirina* (*Levenia*) *evoluta* Sheng and Sun, **11–13**: axial sections, ASM25014, ASM25013A, ASM25016, **14**: sagittal section, ASM25010, ×100. (after Ueno, 1991).

almost spherical with slightly umbilicated axial regions. Mature specimens having 5 to 6 volutions, 0.82 to 0.97 mm in length and 0.78 to 1.07 mm in width. Form ratio ranges from 0.91 to 1.10, averaging 1.02 for 9 specimens. Holotype specimen of 6 volutions 0.92 mm in length and 0.96 mm in width, giving a form ratio of 0.96.

Inner 2 volutions tightly and skew-coiled, outer ones planispirally coiled. Shell expands gradually through growth. Radius vectors of the first to sixth volutions of the holotype 0.06, 0.10, 0.15, 0.24, 0.36 and 0.50 mm, and form ratios 0.83, 0.75, 1.00, 1.00, 1.03 and 0.94, respectively.

Proloculus small and spherical. Its outside diameter varies from 0.045 to 0.065 mm, averaging 0.054 mm for 9 specimens.

Spirotheca thin and composed of a single structureless layer in inner few volutions, but of a tectum and fine alveolar keriotheca in outer ones. Thickness of spirotheca of the first to sixth volutions of the holotype 0.005, 0.010, 0.015, 0.020, 0.030 and 0.035 mm.

Septa short, straight and composed of downward deflections of spirothecal elements. Tips of septa slightly solidified. Septal counts of the second to fifth volutions

Table 1. Measurements of *Misellina (Brevaxina) nipponica,* sp. nov.

Specimen		Figure	Length	Width	F.R.	D.P.	Radius vector					
							1	2	3	4	5	6
1	ASM25082	7-1	0.92	0.96	0.96	0.050	0.06	0.10	0.15	0.24	0.36	0.50
2	ASM25083A	7-2	0.89	0.95	0.94	0.060	0.05	0.07	0.14	0.26	0.41	0.49*
3	ASM25084	7-3	0.93	0.86	1.08	0.045	0.06	0.10	0.16	0.24	0.32	0.46
4	ASM25088B	7-4	0.84	0.80	1.05	0.055	0.06	0.10	0.17	0.28	0.44	
5	ASM25085	7-5	0.97	1.07	0.91	0.045	0.07	0.11	0.17	0.27	0.41	0.58
6	ASM25083B	7-6	0.89	0.89	1.00	—	0.06	0.11	0.20	0.32	0.45	

	Form ratio						Thickness of spirotheca					
	1	2	3	4	5	6	1	2	3	4	5	6
1	0.83	0.75	1.00	1.00	1.03	0.94	0.005	0.010	0.015	0.020	0.030	0.035
2	0.80	0.86	0.93	0.89	0.95	1.10*	0.005	0.010	0.015	0.025	0.040	0.040*
3	0.83	0.90	0.88	1.00	1.06	0.98	0.010	0.015	0.025	0.030	0.040	0.040
4	0.91	0.85	1.06	1.00	0.93		0.010	0.010	0.020	0.030	0.040	
5	0.69	0.86	0.91	0.82	0.90	0.87	0.005	0.010	0.015	0.030	0.040	0.050
6	0.67	1.00	0.91	0.89	0.92		0.010	0.020	0.020	0.025	0.030	

F.R.: Form ratio, D.P.: Diameter of proloculus (in mm). *: 5 ½ volution

of one sagittal section of paratype (Figure 7-11) 6, 9, 12 and 15.

Parachomata small, semicircular and incipient. They developed beyond the third volution, being about ¼ to ⅓ as high as chambers.

Remarks.—Small shell size, rudimentary parachomata and the stratigraphic distribution of the present new species indicate it to be one of the most primitive species in the subgenus *Brevaxina.*

Misellina (*Brevaxina*) *nipponica,* sp. nov. somewhat resembles *M.* (*B.*) *otakiensis* originally described by Huzimoto (1936) from the Otaki district of the Kwanto Mountains. However, the former has a smaller form ratio and less developed parachomata than the latter.

Misellina (*Brevaxina*) *ibukiensis* illustrated by Zhou *et al.* (1987) has a more spherical shell, smaller number of volutions and weaker parachomata than the original specimens of Kobayashi (1957) from the Ibukiyama Limestone, and is quite identical with the present new species.

Misellina (*Brevaxina*) *nipponica,* sp. nov. somewhat resembles *M.* (*B.*) *minima* described by Lin (in Lin *et al.*, 1977) from the Lower Permian Chihsia Formation of Guangxi, but differs from the latter in having a larger form ratio.

The present new species can be easily distinguished from *Misellina* (*Brevaxina*) *dyhrenfurthi* (Dutkevich) in having a smaller shell and more rudimentary parachomata.

Measurements.—See Table 1.

Occurrence.—Rare in the uppermost part of the *Pamirina* (*Levenia*) *leveni* Zone.

Misellina (*Brevaxina*)
dyhrenfurthi otai
Sakaguchi and Sugano, 1966

Figures 7-13—25

Misellina otai Sakaguchi and Sugano, 1966, p. 145-147, pl. 1, figs. 1-12.


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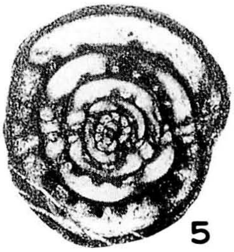
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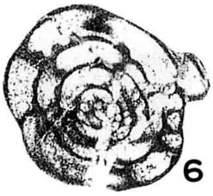
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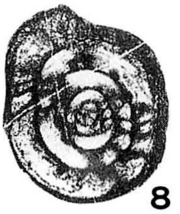
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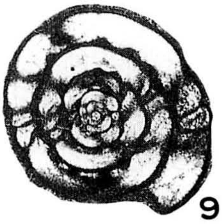
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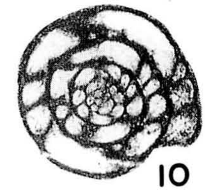
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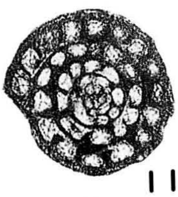
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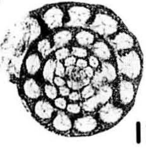
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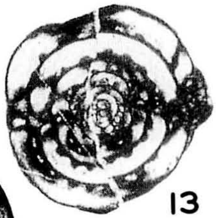
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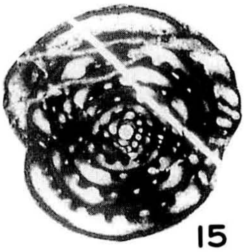
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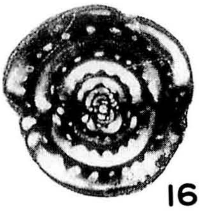
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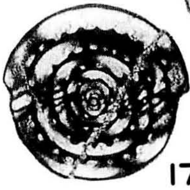
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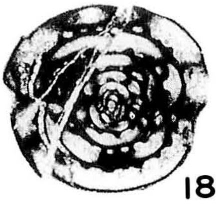
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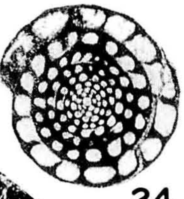
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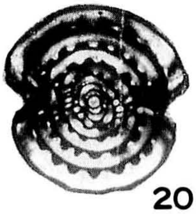
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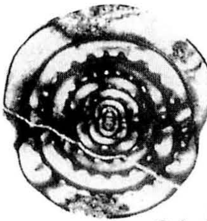
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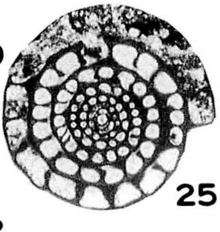
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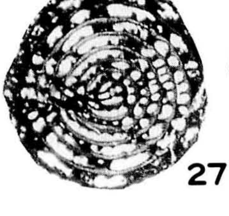
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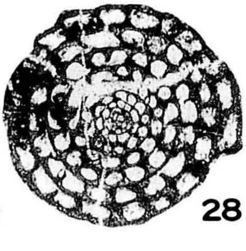
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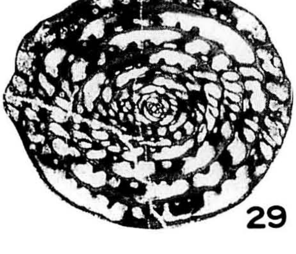
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Misellina (*Brevaxina*) sp. nov., Ozawa, 1970, pl. 2, figs. 12-14.

Brevaxina parva Wang and Sun, 1973, p. 155, 174, pl. 2, figs. 1-3; Sun *et al*., 1983, p. 35, pl. 8, fig. 9 (same as pl. 2, fig. 1 of Wang and Sun, 1973, p. 155, 174).

Misellina cf. *dyhrenfurthi* (Dutkevich), Ozawa, 1975, pl. 10, figs. 4-5 (same as pl. 2, figs. 12-13 of Ozawa, 1970).

Brevaxina dyhrenfurthi (Dutkevich), Lin *et al*., 1977, p. 86, pl. 26, figs. 12-13.

Misellina dyhrenfurthi (Dutkevich), Ozawa and Kobayashi, 1990, pl. 9, figs. 1-2.

Material.—Axial sections; ASM25091 from Loc. NS122, ASM25092, ASM25096, ASM25101 from Loc. SR13, ASM25093, ASM25094 from Loc. NS126, ASM25095 from Loc. SA-AD9, ASM25097 from Loc. EB8 (float block), ASM25098 from Loc. NS130, ASM25099 from Loc. NS124, ASM 25100A from Loc. NS129. Sagittal sections; ASM25100B from Loc. NS129, ASM 25102 from Loc. NS131. Additional specimens were abundantly obtained from the *Misellina* (*Brevaxina*) *dyhrenfurthi otai* Zone.

Description.—Shell almost spherical or slightly quadrate with shallowly depressed axial regions and convex lateral slopes. Mature specimens of 6 ½ to 8 volutions 1.03 to 1.58 mm in length and 1.04 to 1.53 mm in width. Form ratio ranges from 0.97 to 1.15, averaging 1.04 for 25 specimens.

Axis of coiling straight through growth except for inner 1 or 2 volutions of some specimens. Chamber height almost constant throughout length of shell. Radius vectors of the first to seventh volutions of typical axial section (Figure 7-18) 0.07, 0.10, 0.15, 0.23, 0.34, 0.50 and 0.67 mm, and form ratios 0.71, 0.80, 0.90, 1.39, 1.32, 1.18 and 1.12, respectively.

Proloculus small and spherical. Its outside diameter ranges from 0.045 to 0.110 mm, averaging 0.070 mm for 36 specimens.

Spirotheca thin and composed of a single structureless layer in inner 2 or 3 volutions, but consists of a tectum and lower alveolar keriotheca in outer ones. Thickness of spirotheca of the first to seventh volutions of above-mentioned specimen 0.008, 0.010, 0.005, 0.010, 0.020, 0.025 and 0.020 mm.

Septa unfluted and slightly inclined anteriorly. They are composed of downward deflections of the tectum and extensions of the alveolar keriotheca on either sides of the tectum. Septal counts of the first to eighth volutions of one illustrated sagittal section (Figure 7-24) 5, 10, 12, 14, 14, 18, 18 and 15, respectively.

Parachomata small, semicircular to triangular in shape with obtuse apex, and well developed beyond the third volution. They attain about ⅓ to ½ of chamber height.

Remarks.—This subspecies was originally described by Sakaguchi and Sugano(1966) as a distinct species of the genus *Misellina* from the upper part of the *Pseudofusulina vulgaris* Zone in the Kaerimizu area. They stated that the present species resembles *Misellina* (*Brevaxina*) *compressa* (Deprat), the type species of the subgenus *Brevaxina,* in having an almost spherical shell and well-developed umbilical depressions even in the outer volutions of some specimens, but differs from the latter in having a smaller and more spherical shell.

Sakaguchi and Sugano (1966) did not refer in the original description to the fact that the present species closely resembles *Misellina*

← **Figure 7. 1-12.** *Misellina* (*Brevaxina*) *nipponica,* sp. nov., **1**: axial section of the holotype, ASM25082, **2-7**: axial sections of paratypes, ASM25083A, ASM25084, ASM25088B, ASM25085, ASM25083B, ASM25086, **8-10**: slightly oblique axial sections of paratypes, ASM25088A, ASM25089A, ASM25087, **11, 12**: sagittal sections of paratypes, ASM25089B, ASM25090, ×30. **13-25.** *Misellina* (*Brevaxina*) *dyhrenfurthi otai* Sakaguchi and Sugano, **13-23**: axial sections, ASM25097, ASM25098, ASM25092, ASM25096, ASM25099, ASM25093, ASM25100A, ASM25101, ASM25095, ASM25094, ASM25091, **24, 25**: sagittal sections, ASM25100B, ASM25102, ×20. **26-29.** *Armenina salgirica* Miklukho-Maklay, **26**: slightly oblique axial section, ASM25127, **27**: tangential section, ASM25128, **28**: sagittal section, ASM25129, **29**: axial section, ASM25130; **26, 28, 29**: ×15, **27**: ×10.

(*Brevaxina*) *dyhrenfurthi* (s.s.), which was originally described by Dutkevich (in Likharev *et al*., 1939) from the Darvas region of the USSR. In most of the important characters, such as the shell shape, form ratio and development of parachomata they are quite similar to each other. However, the Akiyoshi specimens differ from the Darvas ones in having a larger shell and more volutions. Hence the Akiyoshi form, *otai,* is treated as a subspecies of *Misellina* (*Brevaxina*) *dyhrenfurthi* (s.l.). It is considered that *Misellina* (*Brevaxina*) *dyhrenfurthi otai* Sakaguchi and Sugano is more advanced than *M.* (*B.*) *dyhrenfurthi dyhrenfurthi* (Dutkevich), and the former is a descendant of the latter.

Misellina (*Brevaxina*) sp. nov. illustrated by Ozawa (1970) and *M.* cf. *dyhrenfurthi* (Dutkevich) of Ozawa (1975) have 8 volutions in the mature stage and a slightly larger shell than that of *M.* (*B.*) *dyhrenfurthi* (s.s.). Ozawa's specimens are almost identical with *Misellina* (*Brevaxina*) *dyhrenfurthi otai* Sakaguchi and Sugano.

Brevaxina parva originally described by Sun and Wang (1973) from the Lower Permian Yazi Formation of the Chinling Range in South China quite resembles *M.* (*B.*) *dyhrenfurthi otai* Sakaguchi and Sugano in essential morphological characters. The former is considered to be a junior synonym of the latter.

Occurrence.—Abundant in the *Misellina* (*Brevaxina*) *dyhrenfurthi otai* Zone.

Subgenus *Misellina* Schenck and Thompson, 1940

Type *species.*—*Doliolina ovalis* Deprat, 1915.

Misellina (*Misellina*) *claudiae* (Deprat, 1912)

Figures 8-1—13

Doliolina claudiae Deprat, 1912, p. 44-45, pl. 4, figs. 5-9 ; Lee, 1933, pl. 2, fig. 5, 5a ; Chen, 1934, p. 99-100, pl. 16, figs. 13-20 ; Huzimoto, 1936, p. 104-105, pl. 21, figs. 4-9.

Verbeekina claudiae (Deprat), Ozawa, 1925a, pl. 2, figs. 1-2 ; Ozawa, 1925b, p. 52-53, pl. 11, figs. 9-11.

Misellina aff. *claudiae* (Deprat), Kanmera, 1956, pl. 36, fig. 15 ; Nogami, 1961, p. 169-171, pl. 7, figs. 7-9.

Misellina cf. *claudiae* (Deprat), Kobayashi, 1957, p. 296-297, pl. 1, fig. 19.

Misellina claudiae (Deprat), Toriyama, 1958, p. 208-211, pl. 39, figs. 1-19 ; Sakagami, 1958, p. 89-90, pl. 4, figs. 1-2 ; Kanuma, 1960, p. 64-65, pl. 11, figs. 2-9 ; Ishizaki, 1962, p. 166-167, pl. 10, figs. 11-17 ; Kanmera, 1963, p. 110-112, pl. 14, figs. 7-14 ; Sheng, 1963, p. 91, 222-223, pl. 28, fig. 15, pl. 30, figs. 12-19 ; Sheng, 1966, p. 140-141, pl. 22, fig. 8 (same as pl. 4, fig. 5 of Deprat, 1912, p. 44-45) ; Takaoka, 1966, p. 62-63, pl. 9, fig. 16 ; Leven, 1967, p. 181-182, pl. 30, figs. 7-8 ; Igo, 1967, p. 13-14, pl. 7, fig. 9, pl. 8, fig. 7 ; Douglass, 1967, pl. 6, figs. 17-20 ; Koike *et al.* 1968, p. 206-207, pl. 32, figs. 3-4 ; Ozawa, 1970, pl. 3, figs. 16-18 (18 : same as pl. 2, fig. 5 of Lee, 1933) ; Choi, 1972, p. 637-639, pl. 1, figs. 1, 2? ; Wang and Sun, 1973, pl. 2, figs. 4-5, 13, 15 ; Ozawa, 1975, pl. 10, fig. 9 (same as pl. 3, fig. 16 of Ozawa, 1970) ; Ota, 1977, pl. 2, figs. 3-4 ; Lin *et al.*, 1977, p. 85, pl. 26, fig. 5 ; Kobayashi, 1977, pl. 2, figs. 15-16 ; Liu *et al.*, 1978, p. 84, pl. 19, fig. 6 ; Minato *et al.*, 1979, pl. 41, fig. 2(same as pl. 1, fig. 2 of Choi, 1972, p. 637-639) ; Hasegawa *et al.*, 1979, pl. 77, figs. 4-5, 8-10, 12-14, 16-22 ; Lin *et al.*, 1979, pl. 4, figs. 8-12 ; Xie, 1982, p. 66, pl. 32, figs. 4-5 ; Leven, 1982, pl. 2, figs. 4, 7 (7 : same as pl. 30, fig. 7 of Leven, 1967, p. 181-182) ; Wang *et al.*, 1982, p. 101, pl. 28, figs. 6-7 ; Sun *et al.*, 1983, p. 34, pl. 9, fig. 6 ; Zhou, 1984, p. 118-119, pl. 1, figs. 14-15 ; Zhou and Zhang, 1984, pl. 2, figs. 8-11 ; Chen, 1984, p. 65, pl. 18, figs. 5-7 ; Xia and Zhang, 1985, p. 150, pl. 29, fig. 7 ; Sun and Zhang, 1985, p. 505, pl. 1, figs. 2-5 ; Han, 1985, p. 683, pl. 1, fig. 18 ; Yang, 1985, pl. 2, figs. 1-2 ; Wang and Tang, 1986, pl. 2, fig. 18 ; Zhang and Li, 1987, p. 405-406, pl. 3, figs. 10, 20, 24 ; Sun and Zhang, 1988, pl. 4, figs. 4-6, 8-10 ; Ozawa and Kobayashi, 1990, pl. 9, figs. 5-6 ; Tong *et al.*, 1990, pl. 4, fig. 5.

Misellina (*Misellina*) *claudiae* (Deprat), Toriyama, 1975, p. 55-57, pl. 13, figs. 1-2 ; Ishibashi, 1984, p. 221-222, pl. 31, figs. 6-15.

Misellina minor (Deprat), Chen and Yang, 1978, p. 107, pl. 26, fig. 10.

? *Misellina claudiae* (Deprat), Kalmykova, 1967, p. 215, pl. 30, figs. 13-14 ; Chen and Yang, 1978, p. 107, pl. 26, figs. 8-9.

non *Misellina claudiae* (Deprat), Hanzawa and Murata, 1963, pl. 6, figs. 7-8 ; Han, 1976, p. 62, pl.

15, figs. 10-13.

Material.—Axial sections of megalospheric form; ASM25103 from Loc. MI51, ASM 25104 from Loc. MI9, ASM25105 from Loc. MI39, ASM25106 from Loc. AL35.5, ASM 25107A,B from Loc. MI23, ASM25108 from Loc. SA31, ASM25109 from Loc. MI43. Sagittal sections of megalospheric form; ASM 25110 from Loc. MI8, ASM25111 from Loc. MI58, ASM25112A from Loc. MI60. Axial sections of microspheric form; ASM 25113 from Loc. MI13, ASM25114 from Loc. MI28. In addition, many specimens from the *Misellina* (*M.*) *claudiae* Zone were studied.

Description.—Megalospheric shell small and short ellipsoidal with broadly rounded to somewhat umbilicated axial regions and convex lateral slopes. Microspheric shell slightly larger than megalospheric one, and subglobular to fusiform with broadly rounded to bluntly pointed poles. Mature shell consists of 8 to 9 volutions in megalospheric form, but 10 to 11 volutions in microspheric one. Length and width of megalospheric form 1.68 to 2.73 mm and 1.38 to 2.23 mm, respectively. Form ratio ranges from 1.18 to 1.38, averaging 1.27 for 23 specimens. Microspheric specimens 2.05 to 2.29 mm in length and 1.73 to 2.48 mm in width. Form ratio varies from 1.16 to 1.43, averaging 1.28 for 7 specimens.

Axis of coiling straight throughout in megalospheric form. Inner few volutions tightly and skew coiled in microspheric form. Height of chamber almost constant in both forms. Radius vectors of the first to eighth volutions of typical megalospheric form (Figure 8-6) 0.11, 0.16, 0.24, 0.34, 0.46, 0.60, 0.77 and 0.93 mm, and form ratios 0.82, 1.00, 1.08, 1.12, 1.20, 1.16, 1.10 and 1.24, respectively.

Proloculus of megalospheric form large for genus and spherical to somewhat irregular. Its outside diameter ranges from 0.105 to 0.220 mm, averaging 0.135 mm for 30 specimens. Proloculus of microspheric form minute and measuring 0.030 to 0.070 mm in outside diameter, averaging 0.048 mm for 8 specimens.

Spirotheca thin and composed of a single structureless layer in inner 2 volutions, but moderate in thickness and composed of a tectum and alveolar keriotheca beyond the third volution. Lower surface of spirotheca uneven in some forms. Thickness of spirotheca of the first to eighth volutions of above-mentioned megalospheric specimen 0.010, 0.020, 0.030, 0.040, 0.045, 0.075, 0.075 and 0.040 mm.

Septa numerous, bending anteriorly and composed of downward deflections of tectum and anterior and posterior extensions of keriotheca. Septal counts of the first to eighth volutions of one illustrated sagittal section of a megalospheric form (Figure 8-10) 7, 10, 11, 16, 15, 18, 21 and 26, respectively.

Low and broad parachomata well developed in all volutions except for the first one in megalospheric form and inner 2 or 3 volutions in microspheric one. Height of parachomata about ⅓ to ½ that of chambers.

Remarks.—Dimorphism is well observed in the Akiyoshi specimens prepared for this study. The microspheric form is characterized by a larger shell, more volutions and smaller proloculus than the megalospheric form. Moreover, the inner volutions of the microspheric form are compactly and skew coiled.

The Akiyoshi specimens quite agree with the original ones of Deprat (1912) from Yunnan, and no further comparison is necessary.

Occurrence.—Abundant in the lower part of the *Misellina* (*M.*) *claudiae* Zone and rare in the middle part of the same zone.

Misellina (*Misellina*) *postclaudiae* Ueno, sp. nov.

Figures 8-15—18

Material.—Axial section of the holotype; ASM25120 from Loc. MI29. Axial sections of paratypes; ASM25119 from Loc. AL61, ASM25121 from Loc. AL67. Sagittal sec-


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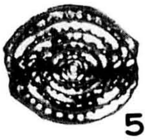
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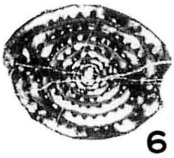
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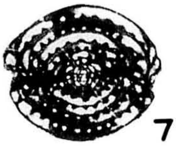
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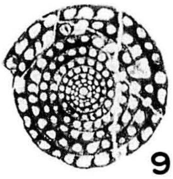
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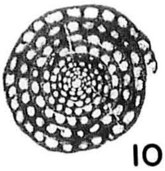
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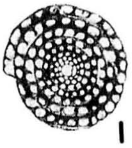
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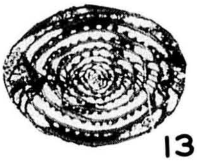
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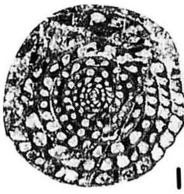
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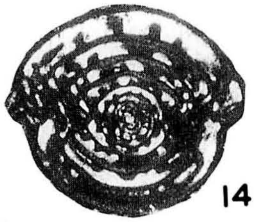
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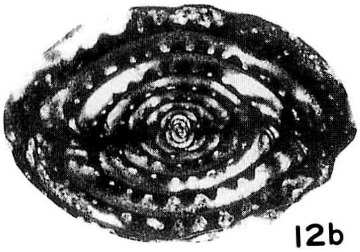
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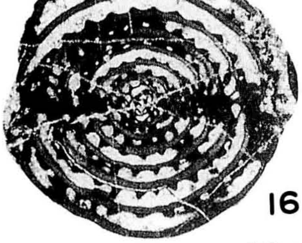
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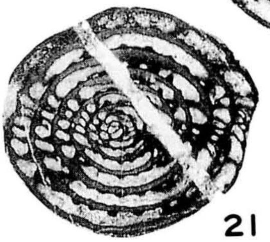
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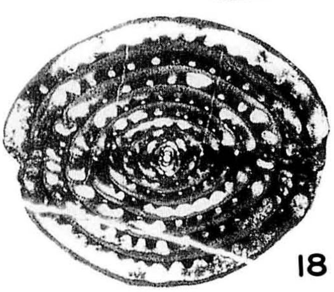
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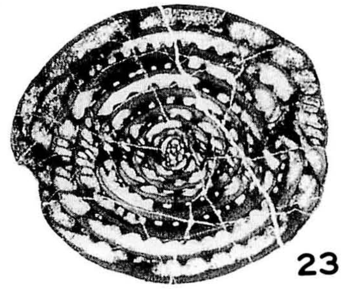
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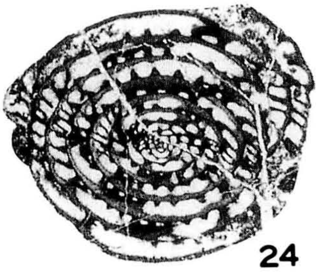
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tion of paratype; ASM25122 from Loc. AL 67. Some additional specimens from Loc. AL67 were studied.

Diagnosis.—Large *Misellina* having a subglobular to short ellipsoidal shell with rounded polar ends, almost straight axis of coiling and numerous volutions. Inner few volutions rather tightly coiled. Spirotheca thin, with slightly undulated lower surface in some case. Septa slightly bending anteriorly. Well-developed parachomata beyond the third volution.

Description.—Shell large for genus and subglobular to short ellipsoidal with rounded axial regions and broadly convex lateral slopes. Mature specimens having 10 to 11 volutions, 2.63 to 2.96 mm in length and 2.13 to 2.65 mm in width, giving form ratios of 1.09 to 1.24. Holotype specimen of 10 ½ volutions 2.96 mm in length and 2.38 mm in width, giving a form ratio of 1.24.

Axis of coiling almost straight throughout growth. Inner few volutions tightly coiled, but later ones expanding gradually. Radius vectors of the first to tenth volutions of the holotype 0.07, 0.12, 0.16, 0.23, 0.31, 0.42, 0.56, 0.71, 0.93 and 1.14 mm, and form ratios 0.71, 0.87, 0.94, 1.22, 1.39, 1.50, 1.38, 1.44, 1.29 and 1.25, respectively.

Proloculus small and spherical. Its outside diameter ranges from 0.050 to 0.080 mm, averaging 0.065 mm for 5 specimens.

Spirotheca thin to medium, and composed of a single structureless layer in inner 3 volutions, but of a thin tectum and rather thick alveolar keriotheca in outer ones. Lower surface of spirotheca slightly undulated in middle volutions of some specimens. Thickness of spirotheca of the first to tenth volutions of the holotype 0.010, 0.010, 0.015, 0.020, 0.020, 0.050, 0.045, 0.040, 0.065 and 0.040 mm.

Septa slightly bending anteriorly and composed of downward deflections of spirothecal elements. Septal counts of the third to seventh volutions of illustrated sagittal section of paratype 11, 13, 16, 17 and 19, respectively.

Parachomata well developed in all volutions except for inner 2, and semicircular to triangular in transverse section. Height of parachomata about ⅓ to ½ as that of chambers.

Remarks.—*Misellina* (*M.*) *postclaudiae,* sp. nov. is somewhat similar to the microspheric form of *M.* (*M.*) claudiae (Deprat). However, the former can be distinguished from the latter in having a slightly larger shell and an almost straight axis of coiling even in the compactly coiled inner volutions.

The present new species also resembles *Maklaya cutalensis* (Leven) from the Kubergandian of the Pamir in general shell morphology. However, the former can be easily distinguished from the latter in having no primary transverse septula.

In the present new species, low and broad protrusions of the lower surface of the spirotheca are observed in the middle volutions of some specimens. However, these are too poorly shown to recognize as the primary transverse septula.

Measurements.—See Table 2.

Occurrence.—Rare in the middle part of the *Misellina* (*M.*) *claudiae* Zone.

← **Figure 8.** **1-13.** *Misellina* (*Misellina*) *claudiae* (Deprat), **1-8**: axial sections of megalospheric form, ASM25103, ASM25104, ASM25105, ASM25106, ASM25107A, ASM25108, ASM25107B, ASM25109, **9-11**: sagittal sections of megalospheric form, ASM25110, ASM25111, ASM25112A, **12a, 13**: axial sections of microspheric form, ASM25113, ASM25114, **12b**: enlargement of **12a**; **1-11, 12a, 13**: ×10, **12b**: ×20. **14**: *Misellina* (*Misellina*) sp. A, axial section, ASM25123, ×20. **15-18.** *Misellina* (*Misellina*) *postclaudiae,* sp. nov., **18**: axial section of the holotype, ASM25120, **15**: sagittal section of paratype, ASM25122, **16, 17**: axial sections of paratypes, ASM25119, ASM25121; **15**: ×10, **16-18**: ×15. **19-24.** *Misellina* (*Misellina*)? *ventricosa,* sp. nov., **23**: axial section of the holotype, ASM25115A, **19, 22**: axial sections of paratypes, ASM25115B, ASM25116A, **20, 21, 24**: slightly tangential sections of paratypes, ASM25117, ASM25116B, ASM25118, ×15.

Table 2. Measurements of *Misellina* (*M.*) *postclaudiae*, sp. nov.

Specimen		Figure	Length	Width	F.R.	D.P.
1	ASM25119	8-16	2.63	2.42	1.09	0.050 ?
2	ASM25121	8-17	2.63	2.13	1.23	0.075
3	ASM25120	8-18	2.96	2.34	1.24	0.075

	Radius vector									
	1	2	3	4	5	6	7	8	9	10
1	0.08	0.12	0.17	0.26	0.39	0.51	0.67	0.82	1.03	1.25
2	0.08	0.13	0.18	0.26	0.36	0.47	0.63	0.81	1.00	—
3	0.07	0.12	0.16	0.23	0.31	0.42	0.56	0.71	0.93	1.14

	Form ratio									
	1	2	3	4	5	6	7	8	9	10
1	0.56	0.71	0.89	1.13	1.00	1.04	1.07	1.18	1.06	—
2	0.60	0.69	0.79	1.04	1.32	1.50	1.35	1.27	1.27	—
3	0.71	0.87	0.94	1.22	1.39	1.50	1.38	1.44	1.29	1.25

	Thickness of spirotheca									
	1	2	3	4	5	6	7	8	9	10
1	0.010	0.020	0.025	0.040	0.050	0.050	0.075 ?	0.070	0.080	0.065
2	0.010	0.015	0.020	0.030	0.045	0.060	0.070	0.075	0.060	—
3	0.010	0.010	0.015	0.020	0.020	0.050	0.045	0.040	0.065	0.040

F.R. : Form ratio, D.P. : Diameter of proloculus (in mm).

Misellina (*Misellina*) *spinosa* Han, 1976

Figure 9-15

Misellina spinosa Han, 1976, p. 61-62, pl. 11, figs. 9-11 ; Yang, 1985, pl. 3, fig. 1.

Material. — Axial section ; ASM25112B from Loc. MI60.

Description. — Shell small, short ellipsoidal with rounded axial regions, and consisting of 6 volutions. Length 0.86 mm and width 0.70 mm, giving a form ratio of 1.23. Inner 2 volutions skew coiled, but outer ones planispirally coiled. Radius vectors of the first to sixth volutions 0.04, 0.09, 0.12, 0.20, 0.28 and 0.39 mm, and form ratios 0.75, 0.94, 1.13, 1.08, 1.18 and 1.19, respectively. Spirotheca thin and composed of a single structureless layer in inner 3 volutions, but of a tectum and fine alveolar keriotheca in outer ones. Thickness of spirotheca of the first to sixth volutions 0.005, 0.005, 0.010, 0.015, 0.020 and 0.025 mm. Parachomata small and rudimental, developed merely in outer 3 volutions.

Remarks. — *Misellina* (*M.*) *spinosa* was originally described by Han (1976) from the Lower Permian Sanmianjing Formation of Neimenggu (Inner Mongolia). It has a thinner spirotheca and less developed parachomata than any other known species of the

Table 3. Measurements of *Misellina* (*M.*) ? *ventricosa*, sp. nov.

Specimen		Figure	Length	Width	F.R.	D.P.
1	ASM25115B	8-19	2.08	1.89	1.10	0.050
2	ASM25116A	8-22	2.55	2.15	1.19	0.075
3	ASM25115A	8-23	2.87	2.48	1.16	0.065

	Radius vector										
	1	2	3	4	5	6	7	8	9	10	11
1	0.05	0.10	0.16	0.24	0.37	0.53	0.71	0.89			
2	0.08	0.13	0.18	0.25	0.38	0.51	0.67	0.85	1.06		
3	0.06	0.11	0.14	0.20	0.29	0.41	0.55	0.73	0.92	1.10	1.29

	Form ratio										
	1	2	3	4	5	6	7	8	9	10	11
1	0.80	0.60	0.81	0.92	1.08	1.07	1.10	1.12			
2	1.30	1.00	1.05	1.27	1.28	1.28	1.29	1.33	—		
3	0.50	0.52	0.57	1.15	1.17	1.26	1.25	1.23	1.21	1.20	1.14

	Thickness of spirotheca										
	1	2	3	4	5	6	7	8	9	10	11
1	0.005	0.010	0.020	0.040	0.050	0.060	0.060	0.060			
2	0.010	0.010	0.010	0.025	0.040	0.030	0.060	0.050	0.040		
3	0.005	0.010	0.010	0.020	0.030	0.050	0.075	0.065	0.080	0.055	0.055

F.R.: Form ratio, D.P.: Diameter of proloculus (in mm).

subgenus *Misellina*.

Occurrence.—Rare in the lower part of the *Misellina* (*M.*) *claudiae* Zone.

Misellina (*Misellina*) ?
ventricosa Ueno, sp. nov.

Figures 8-19—24

Material.—Axial section of the holotype; ASM25115A from Loc. MI17. Axial sections of paratypes; ASM25115B, ASM 25116A from Loc. MI17. Slightly tangential sections of paratypes; ASM25116B, ASM 25117 from Loc. MI17, ASM25118 from Loc. KS127. Some additional specimens from Loc. MI17 were studied.

Diagnosis.—Small verbeekinid having intermediate shell characters between the genera *Misellina* and *Armenina*. Shell short ellipsoidal with broadly rounded polar ends. Inner volutions tightly and skew coiled, outer ones rather loosely coiled. Spirotheca moderately thick, with fine alveolar keriotheca. Parachomata prominent and rather high.

Description.—Shell small, short ellipsoidal with broadly rounded axial regions and convex lateral slopes. Mature specimens having 8 ½ to 11 volutions, 2.08 to 2.87 mm in length and 1.89 to 2.48 mm in width. Form ratio ranges from 1.10 to 1.27, averaging 1.19 for 6 specimens. Holotype specimen of 11 volutions 2.87 mm in length and 2.48 mm in width with a form ratio of 1.16.

Inner 2 or 3 volutions tightly and skew coiled with a short axis of coiling. Outer volutions expanding gradually and becoming loose. Radius vectors of the first to eleventh volutions of the holotype 0.06, 0.11, 0.14, 0.20, 0.29, 0.41, 0.55, 0.73, 0.92, 1.10 and 1.29 mm, and form ratios 0.50, 0.52, 0.57, 1.15, 1.17, 1.26, 1.25, 1.23, 1.21, 1.20 and 1.14, respectively.

Proloculus small and spherical with outside diameters of 0.045 to 0.075 mm, averaging 0.059 mm for 4 specimens.

Spirotheca moderately thick and composed of a single structureless layer in inner 3 volutions, but of a tectum and fine alveolar keriotheca in outer ones. Thickness of spirotheca of the first to eleventh volutions of the holotype 0.005, 0.010, 0.010, 0.020, 0.030, 0.050, 0.075, 0.065, 0.080, 0.055 and 0.055 mm.

Parachomata prominent and rather high, and first appear in the third volution. Parachomata attain nearly ½ to ⅔ of chamber height.

Remarks. — The present new species is characterized by tightly and skew-coiled inner volutions, rather loosely coiled outer ones, and high and prominent parachomata. These biocharacters are somewhat heretical in the genus *Misellina,* and rather common in the genus *Armenina,* although its shell shape is slightly different from that of typical *Armenina.* From the morphological point of view, the present new species is considered to be transitional between the genera *Misellina* and *Armenina,* and here assigned tentatively to the genus *Misellina.*

Misellina (*M.*) ? *ventricosa,* sp. nov. can be distinguished easily from *M.* (*M.*) *postclaudiae,* sp. nov. in having more tightly coiled inner volutions, thicker spirotheca for corresponding volutions and finer alveolar keriotheca.

This new species somewhat resembles *Armenina salgirica* Miklukho-Maklay. However, the latter has a thinner spirotheca, more spherical shell, more tightly coiled inner volutions and more prominent parachomata than in the former.

Measurements. — See Table 3.

Occurrence. — Rare in the lower part of the *Misellina* (*M.*) *claudiae* Zone.

Misellina (*Misellina*) sp. A

Figure 8-14

Material. — Axial section ; ASM25123 from Loc. NS120.

Description. — Shell small, short ellipsoidal with rounded axial regions and inflated ventral sides, and having 9 volutions. Length 1.80 mm and width 1.55 mm with a form ratio of 1.16. Inner 2 volutions tightly coiled with a slightly rotated axis of coiling. Radius vectors of the first to ninth volutions 0.08, 0.11, 0.14, 0.20, 0.26, 0.32, 0.48, 0.63 and 0.81 ? mm, and form ratios 0.63, 0.71, 0.93, 1.00, 1.15, 1.25, 1.08, 1.03 and 1.05, respectively. Proloculus small and spherical, being 0.075 mm in outside diameter. Spirotheca composed of a single structureless layer in inner 2 volutions, but of a tectum and alveolar keriotheca beyond the third one. Thickness of spirotheca of the first to ninth volutions 0.005, 0.005, 0.010, 0.020, 0.020, 0.020, 0.025, 0.040 and 0.030 mm. Parachomata prominent and rather high, attaining about ⅔ the height of chambers. They are observed beyond the second volution.

Remarks. — *Misellina* (*M.*) sp. A is considered to be one of the most primitive forms in the subgenus *Misellina.* This species is somewhat similar to *Misellina* (*M.*) *parvicostata* and *M.* (*M.*) *minor,* both originally described by Deprat (1915). The specific identification, however, is postponed until additional materials become available.

Occurrence. — Rare in the middle part of the *Misellina* (*Brevaxina*) *dyhrenfurthi otai* Zone.

Misellina (*Misellina*) sp. B

Figures 9-11 – 13

Material.—Axial sections; ASM25124, ASM25125 from Loc. TA196, ASM25126 from Loc. NS159. Some other specimens from Loc. TA196 were studied.

Description.—Shell small and short ellipsoidal with rounded polar regions. Mature specimens of 9 to 10 ½ volutions 2.08 to 2.88 mm in length and 1.66 to 2.45 mm in width. Form ratio varies from 1.17 to 1.25, averaging 1.22 for 4 specimens. Shell expands gradually throughout growth. Axis of coiling straight. Radius vectors of the first to ninth volutions of typical axial section (Figure 9-12) 0.05, 0.11, 0.15, 0.22, 0.28, 0.40, 0.51, 0.64 and 0.78, and form ratios 1.11, 1.00, 1.07, 1.12, 1.25, 1.27, 1.23, 1.25 and 1.37, respectively. Proloculus small and spherical, being 0.060 to 0.095 mm in outside diameter, averaging 0.078 mm for 5 specimens. Spirotheca thin and composed of a single structureless layer in inner 3 volutions, but of a tectum and alveolar keriotheca in outer ones. In some specimens, lower surface of spirotheca slightly undulated and forms low and broad downward protrusions roughly corresponding to parachomata. Thickness of spirotheca of the first to ninth volution of above-mentioned specimen 0.010, 0.010, 0.010, 0.020, 0.015, 0.020, 0.040, 0.040 and 0.040 mm. Parachomata massive, broad and semicircular in transverse section, and developed beyond the second volution.

Remarks.—The present species somewhat resembles *Maklaya saraburiensis* Kanmera and Toriyama, which accompanies the former. However, *Misellina* (*M.*) sp. B has no primary transverse septula like that observed in the latter, although incipient downward protrusions are developed in some specimens of *M.* (*M.*) sp. B.

Occurrence.—Rare in the middle part of the *Misellina* (*M.*) *claudiae* Zone.

Subfamily Verbeekininae Staff and Wedekind, 1910

Genus *Armenina* Miklukho-Maklay, 1955

Type species.—*Armenina karinae* Miklukho-Maklay, 1955.

Armenina salgirica
Miklukho-Maklay, 1955

Figures 7-26–29

Armenina salgirica Miklukho-Maklay, 1955, fig. 1; Miklukho-Maklay, 1957, p. 120, pl. 4, fig. 3 (same as fig. 1 of Miklukho-Maklay, 1955); Leven, 1965, p. 141, pl. 4, fig. 3, pl. 6, figs. 1-3; Leven, 1967, p. 203, pl. 35, figs. 2-3, pl. 38, figs. 2, 6, pl. 39, fig. 4; Ozawa, 1970, pl. 2, fig. 6 (same as pl. 38, fig. 2 of Leven, 1967, p. 203); Yang, 1985, pl. 2, fig. 29.

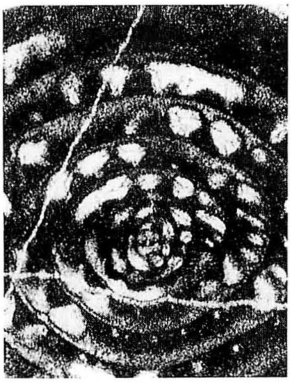
Material.—Axial section; ASM25130 from Loc. TA196. Slightly oblique axial section; ASM25127 from Loc. NS159. Sagittal section; ASM25129 from Loc. TA196. Tangential section; ASM25128 from Loc. NS 159. Some additional specimens from Loc. NS159 were studied.

Description.—Shell small for genus and subspherical with broadly rounded polar regions. Mature specimens having 9 to 11 volutions, 2.58 to 3.00 mm in length and 2.09 to 2.93 mm in width. Form ratio of well-oriented axial section (Figure 7-29) 1.16.

Inner 2 or 3 volutions tightly and skew coiled with a short axis of coiling. Beyond the third or fourth volution, coiling becomes loose as compared with inner ones. Radius vectors of the first to tenth volutions of above-mentioned axial section 0.07, 0.09, 0.12, 0.17, 0.26, 0.35, 0.47, 0.64, 0.85 and 1.07 mm, and form ratios 0.53, 0.72, 0.92, 1.18, 1.29, 1.29, 1.28, 1.24, 1.15 and 1.14, respectively.

Proloculus small and 0.060 to 0.080 mm in outside diameter, averaging 0.070 mm for 5 specimens.

Spirotheca thin and composed of a single structureless layer in inner 3 volutions, but of a tectum and fine alveolar keriotheca in outer ones. Lower surface of spirotheca slightly undulated in middle volutions of some specimens. Thickness of spirotheca of the first to tenth volutions of typical axial section



1b

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3

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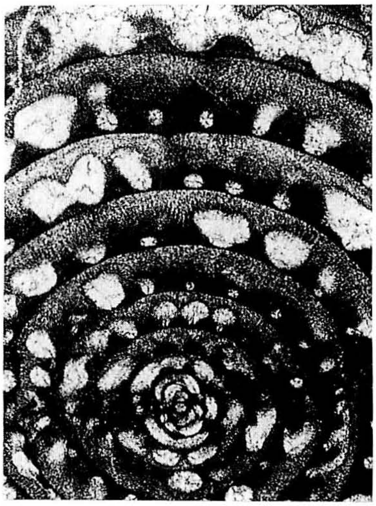
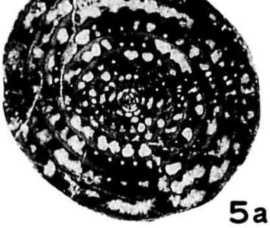


5b



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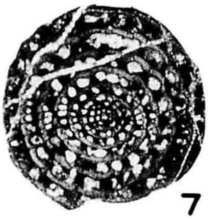

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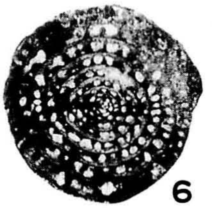

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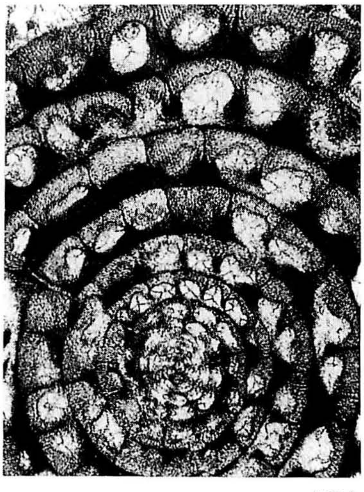

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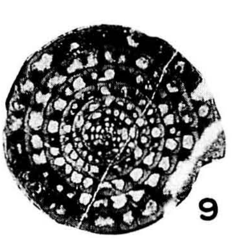
11



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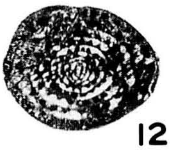
14a



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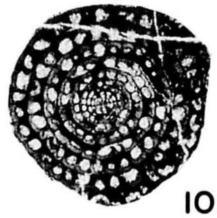
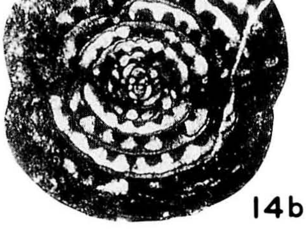
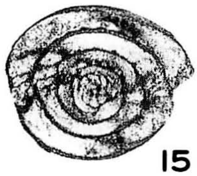


10a



14b

13



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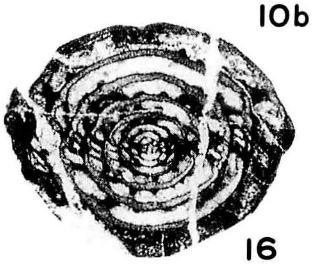

16

mentioned above 0.005, 0.005, 0.010, 0.015, 0.020, 0.020, 0.025, 0.035, 0.035 and 0.040 mm.

Septa slightly bending anteriorly and consist of downward deflections of tectum and anterior and posterior extensions of keriotheca. Septal counts of the third to ninth volutions of illustrated sagittal section (Figure 7-28) 9, 11, 14, 14, 17, 18 and 20 ?.

Parachomata rather narrow and high, reaching about ⅔ the height of chambers, and begin to occur in the third volution.

Remarks.—*Armenina salgirica* was introduced by Miklukho-Maklay (1955), based on a specimen from the Crimea, USSR. The Akiyoshi specimens are quite identical with the original one.

Leven (1967) also reported *Armenina salgirica* Miklukho-Maklay from the Kubergandian and lower Murgabian of the Pamir. His specimens have a larger shell and more volutions than those of the Crimean and Akiyoshi ones.

Occurrence.—Rare in the middle part of the *Misellina* (*M.*) *claudiae* Zone.

Armenina cf. *asiatica* Leven, 1967

Figure 9-16

Compare—

Armenina asiatica Leven, 1967, p. 204, pl. 38, fig. 3, pl. 39, figs. 2-3; Ozawa, 1970, pl. 2, fig. 9 (same as pl. 39, fig. 3 of Leven, 1967, p. 204); Tien, 1989, pl. 20, figs. 1-2.

Material.—Axial section; ASM25131 from Loc. TA196.

Description.—Shell small for genus and subspherical with a slightly longer axis of coiling. Specimen having 8 volutions, 1.93 mm in length and 1.55 mm in width with a form ratio of 1.25. Inner 2 volutions tightly and skew coiled, remaining volutions planispirally and rather loosely coiled. Radius vectors of the first to eighth volutions 0.09, 0.13, 0.19, 0.25, 0.37, 0.52, 0.67 and 0.81 mm, and form ratios 0.72, 0.88, 1.03, 1.04, 1.07, 1.06, 1.04 and 1.15, respectively. Proloculus small, being 0.045 mm in outside diameter. Spirotheca composed of a single structureless layer in the first volution, but of a tectum and fibrous alveolar keriotheca beyond the second one. Lower surface of spirotheca uneven. Parachomata low, semicircular and well developed beyond the third volution.

Remarks.—*Armenina asiatica* was originally described by Leven (1967) from the Kubergandian of the Pamir. The Akiyoshi specimen is very similar to the Pamir ones except for having a smaller shell and fewer volutions, and is considered to be an immature individual of *Armenina asiatica* Leven. The specific name, however, has been left tentative until sufficient materials are available.

Occurrence.—Rare in the middle part of the *Misellina* (*M.*) *claudiae* Zone.

Family Neoschwagerinidae Dunbar and Condra, 1927

Subfamily Neoschwagerininae Dunbar and Condra, 1927

Genus *Maklaya* Kanmera and Toriyama, 1968

Type *species.*—*Cancellina pamirica* Leven, 1967.

Maklaya saraburiensis Kanmera and Toriyama, 1968

Figures 9-1—4

← **Figure 9. 1-4.** *Maklaya saraburiensis* Kanmera and Toriyama, **1a, 2, 3**: axial sections, ASM25132, ASM25134, ASM25133, **4**: sagittal section, ASM25135, **1b**: enlarged part of **1a**; **1a, 2-4**: ×10, **1b**: ×40. **5-10.** *Maklaya pamirica* (Leven), **5a, 6**: axial sections, ASM25136, ASM25137, **7, 8**: tangential sections, ASM25139, ASM25138, **9, 10a**: sagittal sections, ASM25140, ASM25141, **5b, 10b**: enlarged parts of **5a** and **10a**; **5a, 6-9, 10a**: ×10, **5b, 10b**: ×40. **11-13**: *Misellina* (*Misellina*) sp. B, axial sections, ASM25125, ASM25124, ASM25126, ×10. **14**: *Maklaya* sp., axial section, ASM25142, **14a**: ×10, **14b**: enlargement of **14a**, ×20. **15**: *Misellina* (*Misellina*) *spinosa* Han, axial section, ASM25112B, ×30. **16**: *Armenina* cf. *asiatica* Leven, axial section, ASM25131, ×20.

Maklaya saraburiensis Kanmera and Toriyama, 1968, p. 41-43, pl. 4, figs. 17-20; Ozawa, 1970, pl. 4, figs. 14-15 (15: same as pl. 4, fig. 17 of Kanmera and Toriyama, 1968, p. 41-43); Toriyama, 1975, pl. 18, figs. 21-24(same as pl. 4, figs. 17-20 of Kanmera and Toriyama, 1968, p. 41-43).

Neoschwagerina saraburiensis (Kanmera and Toriyama), Han, 1985, p. 685, pl. 2, figs. 14-15.

Material.—Axial sections; ASM25132 from Loc. NS159, ASM25133, ASM25134 from Loc. TA196. Sagittal section; ASM 25135 from Loc. NS159. Some additional specimens from Locs. NS159 and TA196 were studied.

Description.—Shell small for genus, subspherical with rounded polar ends and convex lateral slopes. Mature specimens having 8 to 9 volutions, 1.90 to 2.20 mm in length and 1.68 to 2.05 mm in width. Form ratio ranges from 1.13 to 1.29, averaging 1.18 for 4 specimens.

Shell expands gradually throughout growth. Inner few volutions tightly coiled with a short and slightly rotated axis of coiling. Radius vectors of the first to eighth volutions of typical axial section (Figure 9-2) 0.09, 0.14, 0.22, 0.33, 0.43, 0.57, 0.77 and 0.88 mm, and form ratios 0.78, 0.93, 0.95, 1.02, 1.09, 1.11, 1.06 and 1.17, respectively.

Proloculus small and spherical. Its outside diameter ranges from 0.060 to 0.110 mm, averaging 0.088 mm for 6 specimens.

Spirotheca composed of a tectum and alveolar keriotheca. Lower surface of spirotheca undulatory with short but broad downward protrusions of keriothecal element, forming rudimentary primary transverse septula. They are observed beyond the third volution, and occur immediately above each parachomata joining with tops of parachomata adjacent to septa. Thickness of spirotheca of the first to eighth volutions of above-mentioned specimen 0.010, 0.020, 0.020, 0.035, 0.030, 0.035, 0.080 and 0.030 mm.

Septa consist of downward deflections of tectum and anterior and posterior extensions of keriotheca. Septal counts of the second to eighth volutions of illustrated sagittal section (Figure 9-4) 6, 9, 12, 13, 15, 18 and 21. No axial septula developed.

Parachomata observed beyond the third volution, being nearly ½ as high as chambers in inner volutions, but a little more than ½ to about ⅔ as high in outer ones.

Remarks.—*Maklaya saraburiensis* was originally described by Kanmera and Toriyama (1968) from the Rat Buri Limestone in the Khao Phlong Phrab area, central Thailand, and is considered to be the most primitive species of the genus. The Akiyoshi specimens quite agree with the Thailand ones.

Occurrence.—Rare in the middle part of the *Misellina* (*M.*) *claudiae* Zone.

Maklaya pamirica (Leven, 1967)

Figures 9-5—10

Neoschwagerina sp. (n. sp.), Sakaguchi, 1963, p. 115-116, pl. 8, figs. 7-10.

Cancellina pamirica Leven, 1967, p. 186-187, pl. 32, figs. 1, 3; Rozovskaya, 1975, pl. 29, fig. 6 (same as pl. 32, fig. 1 of Leven, 1967, p. 186-187); Leven, 1982, pl. 3, fig. 3 (same as pl. 32, fig. 1 of Leven, 1967, p. 186-187); Sun and Zhang, 1988, pl. 4, fig. 21.

Maklaya pamirica (Leven), Kanmera and Toriyama, 1968, p. 34-37, pl. 4, figs. 1-16; Ozawa, 1970, pl. 4, figs. 12-13 (same as pl. 4, figs. 1, 7 of Kanmera and Toriyama, 1968, p. 34-37); Toriyama, 1975, pl. 18, figs. 16-20(same as pl. 4, figs. 1-2, 11 of Kanmera and Toriyama, 1968, p. 34-37); Kahler and Kahler, 1979, p. 249-250, pl. 8, fig. 6; Ishibashi, 1984, p. 222-223, pl. 31, fig. 16; Yang, 1985, pl. 2, fig. 3; Loeblich and Tappan, 1988, pl. 300, figs. 8-11 (8-9: same as pl. 4, figs. 1, 11 of Kanmera and Toriyama, 1968, p. 34-37; 10-11: same as pl. 32, figs. 1, 3 of Leven, 1967, p. 186-187); Ozawa and Kobayashi, 1990, pl. 9, figs. 10-11; Fan *et al.*, 1990, pl. 7, figs. 19, 27.

Material.—Axial sections; ASM25136 and ASM25137. Sagittal sections; ASM25140 and ASM25141. Tangential sections; ASM 25138 and ASM25139. All specimens from Loc. NS173.

Description.—Shell medium to large for genus and almost spherical with rounded periphery. Mature specimens having 10 to

13 volutions, 2.75 to 3.60 mm in length and 2.60 to 3.25 mm in width, giving form ratios of 1.06 to 1.11.

Shell expands gradually throughout growth. Inner few volutions tightly coiled with a short and slightly rotated axis of coiling. Radius vectors of the first to thirteenth volutions of illustrated axial section (Figure 9-5) 0.04, 0.05, 0.09, 0.13, 0.18, 0.27, 0.39, 0.54, 0.73, 0.92, 1.19, 1.42 and 1.69 mm, and form ratios 0.71, 0.60, 0.53, 0.65, 0.94, 1.08, 1.08, 1.07, 1.04, 1.05, 1.02, 1.01 and 1.01, respectively.

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

Spirotheca rather thick and composed of a tectum and alveolar keriotheca. Short but broad, fan-shaped rudimentary primary transverse septula well developed beyond the fourth or fifth volution. They occur immediately above each parachomata joining with tops of parachomata adjacent to septa. Thickness of spirotheca of the first to thirteenth volutions of above-mentioned specimen 0.005, 0.005, 0.005, 0.010, 0.015, 0.040, 0.040, 0.070, 0.065, 0.070, 0.115, 0.060 and 0.060 mm.

Septa composed of downward deflections of spirothecal elements. Septal counts of the third to tenth volutions of one illustrated sagittal section (Figure 9-9) 7 ?, 9 ?, 12, 16, 19, 22, 25 and 25. No axial septula present.

Parachomata semicircular or triangular in transverse section, and first appear in the third volution. They attain about ½ as high as chambers.

Remarks.—*Maklaya pamirica* (Leven) differs from *M. saraburiensis* Kanmera and Toriyama in having a larger shell, more volutions and more developed primary transverse septula.

Neoschwagerina sp. (n. sp.) of Sakaguchi (1963) from the Tamba district has a spherical shell, relatively thick spirotheca, short and broad primary transverse septula and no axial septula. Judging from these shell characters, the Tamba specimens should be assigned to *Maklaya pamirica* (Leven).

Occurrence.—Rare in the upper part of the *Misellina* (*M.*) *claudiae* Zone.

Maklaya sp.

Figure 9-14

Material.—Axial section ; ASM25142 from Loc. NS159.

Description.—Shell small for genus and spherical with convex lateral slopes. Specimen consisting of 10 volutions, 2.10 mm in length and 2.00 mm in width, giving a form ratio of 1.05. Inner few volutions tightly coiled with a short and slightly rotated axis of coiling. Radius vectors of the first to ninth volutions 0.06, 0.09, 0.14, 0.20, 0.27, 0.37, 0.49, 0.64 and 0.81 mm, and form ratios 0.42, 0.56, 0.74, 0.82, 0.93, 1.07, 1.00, 1.00 and 1.06, respectively. Proloculus small and spherical, being 0.050 mm in outside diameter. Spirotheca rather thin and composed of a tectum and keriotheca. Thickness of spirotheca of the first to ninth volutions 0.005, 0.010, 0.015, 0.035, 0.020, 0.020, 0.035, 0.040 and 0.040 mm. Short but broad, fan-shaped incipient primary transverse septula occur facing each parachomata beyond the fourth volution. They become inconspicuous in outer few volutions. Parachomata massive and attain about ⅔ the height of chambers.

Remarks.—The present species somewhat resembles *Maklaya saraburiensis* Kanmera and Toriyama, but differs from the latter in having a smaller form ratio and more massive parachomata.

Occurrence.—Rare in the middle part of the *Misellina* (*M.*) *claudiae* Zone.

Genus *Neoschwagerina* Yabe, 1903

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

Neoschwagerina simplex Ozawa, 1927

Figures 10-1—12

Neoschwagerina simplex Ozawa, 1927, p. 153-154, pl.

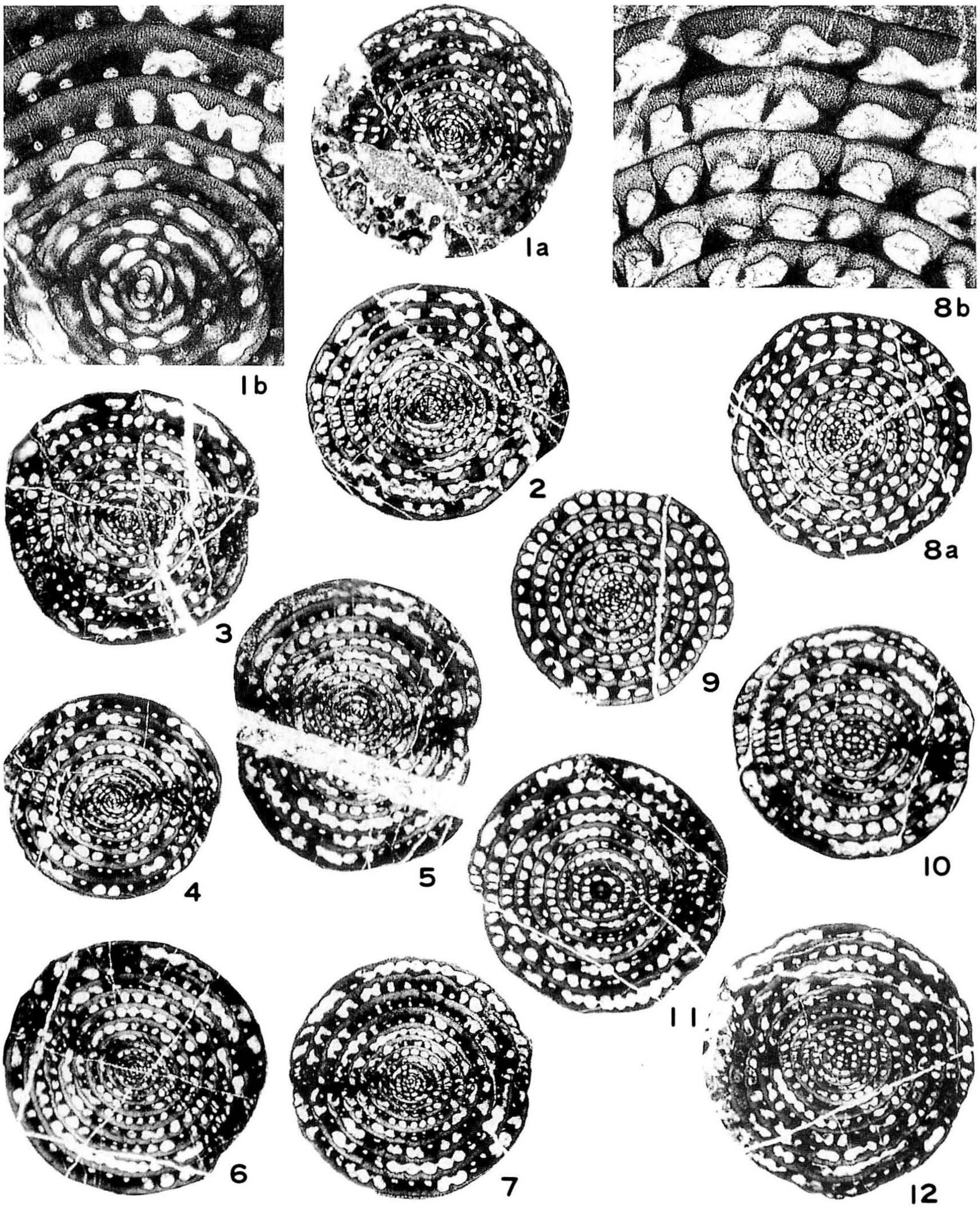

Figure 10. **1-12.** *Neoschwagerina simplex* Ozawa, **1a, 2-7**: axial sections, ASM25143, ASM25144, ASM25147, ASM25146, ASM25149, ASM25148, ASM25145, **8a, 9**: sagittal sections, ASM25150, ASM 25151, **10-12**: tangential sections, ASM25153, ASM25154, ASM25152, **1b, 8b**: enlarged parts of **1a** and **8a**; **1a, 2-7, 8a, 9-12**: ×10, **1b, 8b**: ×40.

34, figs. 7-11, 22-23, pl. 37, figs. 3a, 6a ; Chen, 1956, p. 11, 55-56, pl. 12, figs. 13-16 ; Kanmera, 1957, pl. 19, figs. 22-23 (same as pl. 34, figs. 7-8 of Ozawa, 1927, p. 153-154) ; Honjo, 1959, p. 139-142, pl. 3, figs. 1, 4-5, pl. 4 ; Minato and Honjo, 1959, pl. 1, fig. 2 ; Suyari, 1962, p. 36, pl. 11, fig. 1 ; Ishizaki, 1962, p. 175-177, pl. 12, figs. 7-8 ; Kanmera, 1963, p. 112-113, pl. 13, figs. 1-6, pl. 14, figs. 1-6, pl. 19, fig. 15 ; Leven, 1965, p. 143, pl. 4, fig. 4 ; Sheng, 1966, p. 145, pl. 25, fig. 8 (same as pl. 12, fig. 13 of Chen, 1956, p. 11, 55-56) ; Leven, 1967, p. 189-190, pl. 32, figs. 8-10 ; Igo, 1967, p. 14-15, pl. 5, figs. 10-11 ; Otuka and Kaneda, 1967, p. 26, pl. 3, figs. 3-5 ; Ozawa, 1970, pl. 4, figs. 9-11 (11 : same as pl. 34, fig. 7 of Ozawa, 1927, p. 153-154) ; Choi and Fujita, 1970, p. 376-377, pl. 1, figs. 10-12 ; Ozawa, 1975, pl. 10, fig. 16 (same as pl. 4, fig. 9 of Ozawa, 1970) ; Lin *et al.*, 1977, p. 91, pl. 28, fig. 3 ; Liu *et al.*, 1978, p. 90, pl. 21, fig. 8 ; Sashida, 1980, p. 305-306, pl. 35, figs. 8-10 ; Leven, 1982, pl. 2, fig. 9 (same as pl. 32, fig. 10 of Leven, 1967, p. 189-190) ; Yang, 1985, pl. 2, fig. 5 ; Kobayashi, 1988a, p. 11, pl. 6, figs. 1-17 ; Kobayashi, 1988b, p. 447-449, fig. 6-17.

Cancellina cf. simplex (Ozawa), Dutkevich and Khabakov, 1934, p. 91-94, pl. 2, figs. 4-5.

Cancellina primigena (Hayden), Miklukho-Maklay, 1957, p. 121-122, pl. 5, figs. 2-3.

Cancellina sphaerica Miklukho-Maklay, 1957, p. 122-125, pl. 5, fig. 1.

Neoschwagerina cf. *simplex* Ozawa, Kanmera, 1957, pl. 20, fig. 1 ; Kanuma, 1960, p. 67-68, pl. 11, figs. 1, 10-11 ; Sakaguchi and Yamagiwa, 1973, p. 75-76, pl. 1, figs. 1a-b ; Sakagami and Miyama, 1988, fig. 1-14 ; Tien, 1989, pl. 20, figs. 4-5.

Neoschwagerina sphaerica (Miklukho-Maklay), Honjo, 1959, p. 159, pl. 3, fig. 3 ; Chen and Yang, 1978, p. 115, pl. 31, figs. 7-8.

Neoschwagerina simplex simplex Ozawa, Toriyama, 1975, p. 99-101, pl. 19, figs. 25-28, pl. 20, figs. 1-21.

Neoschwagerina simplex tenuis Toriyama and Kanmera, Toriyama, 1975, p. 97-99, pl. 19, figs. 14-24 ; Leven, 1982, pl. 2, fig. 6.

Neoschwagerina cf. *simplex tenuis* Toriyama and Kanmera, Toriyama and Kanmera, 1979, p. 74, pl. 12, fig. 10.

? *Maklaya* sp., Li, 1986, p. 89, pl. 2, fig. 13.

? *Neoschwagerina simplex* Ozawa, Sun and Zhang, 1988, pl. 4, fig. 20 ; Ozawa and Kobayashi, 1990, pl. 9, fig. 12.

non *Neoschwagerina simplex* Ozawa, Sheng, 1963, p. 101-102, 234-235, pl. 34, figs. 14-15 ; Han, 1980, p. 90, pl. 33, figs. 7-8 ; Chen, 1984, p. 70, pl. 21, fig. 9.

non *Neoschwagerina* cf. *simplex* Ozawa, Koike *et al.*, 1968, p. 207-208, pl. 32, figs. 6-10.

non *Neoschwagerina simplex simplex* Ozawa, Han, 1985, p. 685, pl. 2, fig. 11.

non *Neoschwagerina simplex tenuis* Toriyama and Kanmera, Han, 1985, p. 685, pl. 2, figs. 12, 16.

Material.—Axial sections ; ASM25143, ASM25146 from Loc. TA204, ASM25144, ASM25145, ASM25147, ASM25148, ASM 25149 from Loc. NS173.5. Sagittal sections ; ASM25150 from Loc. NS173.5, ASM 25151 from Loc. TA204. Tangential sections ; ASM 25152, ASM25154 from Loc. TA204, ASM 25153 from Loc. NS173.5. Additional specimens from Locs. TA204 and NS173.5 were also studied.

Description.—Shell small to medium for genus and almost spherical. Mature specimens having 13 to 15 volutions, 3.48 to 4.18 mm in length and 3.28 to 4.15 mm in width. Form ratio ranges from 0.99 to 1.13, averaging 1.05 for 12 specimens.

Inner 3 or 4 volutions tightly coiled with a short and slightly rotated axis of coiling. Outer volutions expanding gradually. Radius vectors of the first to fifteenth volution of well oriented axial section illustrated by Figure 10-5 ; 0.05, 0.09, 0.11, 0.15, 0.20, 0.29, 0.38, 0.49, 0.64, 0.82, 1.05, 1.26, 1.50, 1.97 and 2.20 mm, and form ratios 0.67, 0.53, 0.57, 0.76, 0.90, 1.02, 1.11, 1.18, 1.11, 1.08, 0.98, 0.97, 0.94, 0.87 and 0.86, respectively.

Proloculus small and spherical. Its outside diameter ranges from 0.050 to 0.080 mm, averaging 0.058 mm for 11 specimens.

Spirotheca rather thick and consists of a tectum and alveolar keriotheca. Thickness of spirotheca of the first to fifteenth volution of above-mentioned specimen 0.005, 0.005, 0.005, 0.010, 0.025, 0.030, 0.060, 0.030, 0.040, 0.060, 0.120, 0.110, 0.070, 0.100 and 0.045 mm.

Septa composed of downward deflections of tectum and anterior and posterior extensions of keriotheca. Septal counts of the second to fourteenth volution of typical sagittal section (Figure 10-8) 6, 8, 9, 10, 13, 15, 18, 17, 21, 25, 29, 33 and 36, respectively. Low but broad, fan-shaped primary transverse septula well developed beyond the fifth volution. They are observed immediately above each parachomata joining with tops of parachomata adjacent to septa. Rudimentary axial septula sporadically and inconstantly occur in middle and outer volutions.

Parachomata semicircular or triangular in transverse section and well developed beyond the fifth volution.

Remarks.—This species is considered to be the most primitive representative of the genus *Neoschwagerina,* and the direct descendant of *Maklaya pamirica* (Leven). The former differs from the latter in having a larger shell, more volutions and incipient axial septula.

Toriyama (1975) illustrated rich materials of *Neoschwagerina simplex* Ozawa (*N. simplex simplex* Ozawa and *N. simplex tenuis* Toriyama and Kanmera) from the Rat Buri Limestone in the Khao Phlong Phrab area, central Thailand. The Thailand specimens have much larger proloculus than the Akiyoshi ones, although the other biocharacters are closely allied.

Occurrence.—Rare in the uppermost part of the *Misellina* (*M.*) *claudiae* Zone.

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Akiyoshi 秋吉, Akiyoshi-dai 秋吉台, Chihsia 栖霞, Chinling 秦嶺, Guangxi 広西, Ibukiyama 伊吹山, Kaerimizu 帰り水, Kwanto 関東, Neimenggu 内蒙古, Otaki 大滝, Sanmianjing 三面井, Tamba 丹波, Yazi 埡子, Yunnan 雲南.

秋吉石灰岩層群にみられる Verbeekinidae 科および Neoschwagerinidae 科紡錘虫類の初期変遷：秋吉台北東部の帰り水地域に分布する *Misellina* (*M.*) *claudiae* 帯以下の秋吉石灰岩層群から3新種；*Misellina* (*Brevaxina*) *nipponica*, sp. nov., *M.* (*M.*) *postclaudiae*, sp. nov., *M.* (*M.*)? *ventricosa*, sp. nov. を含む15種の Verbeekinidae 科および Neoschwagerinidae 科紡錘虫類を識別し，その中の14種を記載した。さらに，この15種と，両科の祖先型である *Pamirina* 属の紡錘虫類によって *Pamirina* (*Levenia*) *leveni* Kobayashi の出現から *Parafusulina kaerimizensis* (Ozawa) の出現までに10の時間面 (Biohorizon) を認定した。このうち，3つの時間面はそれぞれ *Pamirina* (*Levenia*) *leveni* 帯，*Misellina* (*Brevaxina*) *dyhrenfurthi otai* 帯，*Misellina* (*M.*) *claudiae* 帯の基底を定義している。秋吉石灰岩層群に見られるこれら Verbeekinidae 科，Neoschwagerinidae 科，そして *Pamirina* 属紡錘虫類の層序分布，および特定の2属間の系統関係を暗示する中間的形質を持つ種の産出は，Verbeekinidae 科および Neoschwagerinidae 科紡錘虫類の起源と初期の系統をうまく説明している。

上野勝美

Trans. Proc. Palaeont. Soc. Japan, N.S., No. 164, p. 1003, December 30, 1991

SHORT NOTES

27. *MELONIS UCHIOI*, A NEW NAME FOR A HOMONYM IN THE FORAMINIFERAL GENUS *MELONIS* FROM THE PACIFIC*

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In the course of a study of benthic foraminifera in the Pacific Ocean, I have recognized a homonym among species of the genus *Melonis*. *Nonion parkerae* was proposed by Uchio in 1960 for a Recent species inhabiting waters off the coast of California (Uchio, 1960, p. 60, pl. 4, figs. 9, 10). Matoba (1967) transferred Uchio's species to the genus *Melonis* and this combination was used by many authors. However, Uchio's species name was preoccupied by *Nonion parkerae* Le Calvez, established in 1959 for a species recovered from the Bay of Biscay (Berthois and Le Calvez, 1959, p. 362, pl. 1, figs. 13, 14). Because Uchio's species name was a junior primary homonym of Le Calvez's, it was invalid and should be replaced by another name (International Code of Zoological Nomenclature, 1985, 3rd ed., Articles 52b, 57b and 60). I therefore propose *Melonis uchioi*, new name, for this species.

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SHORT NOTES

28. A PECULIAR FUSULINACEAN FAUNA FROM THE YASUBA CONGLOMERATE, KOCHI PREFECTURE, SHIKOKU*

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A peculiar fusulinacean fauna is found in a small limestone pebble contained in the Yasuba Conglomerate, which has long been regarded as an Upper Permian limestone conglomerate (Toriyama, 1942 and others). It crops out typically north of Shingai, Tosa-yamada Town, Kochi Prefecture, Shikoku (Figure 1). Recently, Isozaki (1985) intensively restudied this conglomerate embedded in his Shingai Formation and insisted that the conglomerate can be subdivided into three types, Type I to Type III, which are all exotic in origin.

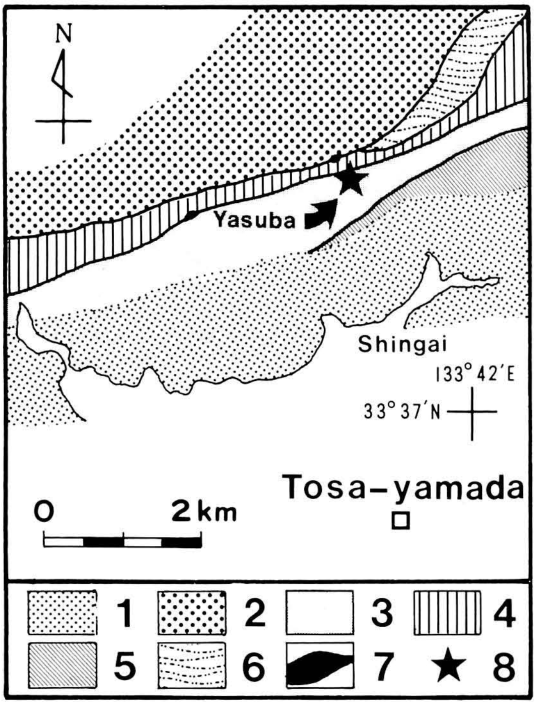

Figure 1. Geological map around the fossil locality. 1 : Cretaceous, 2 : Kamiyakawa Formation, 3 : Shingai Formation, 4 : "Shirakidani Group", 5 : Gonyu Formation, 6 : Agekura Formation, 7 : serpentinite, 8 : fossil locality. (Geological map after Isozaki, 1985)

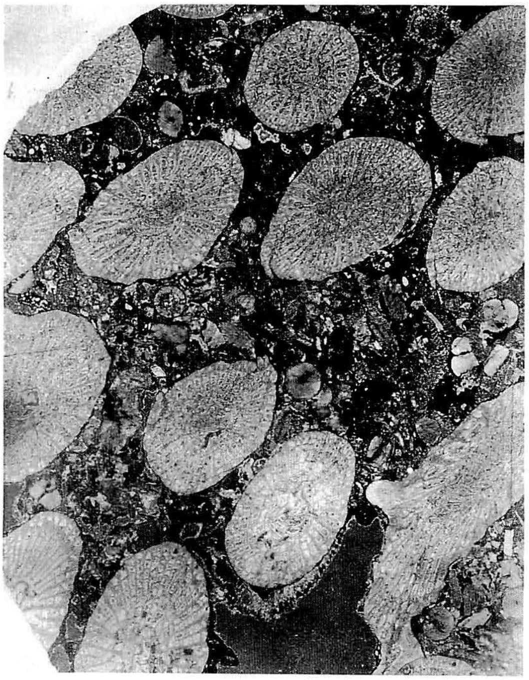

Figure 2. Thin section of *Waagenophyllum* biolithite containing the fusulinaceans studied herein, ×3.

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I disclosed the present fusulinacean fauna from a pebble contained in Isozaki's Type II conglomerate. This fauna is characterized by the abundant occurrence of *Lantschichites elegans* Sosnina, which was reported from the Middle Permian of southern Primor'e (Sikhote-Alin). Isozaki (*op. cit.*) considered that the Type II conglomerate was deposited in some area adjacent to the ancient Kurosegawa land (arc or microcontinent).

The limestone pebble containing this fusulinacean fauna is a *Waagenophyllum* biolithite with an algal bioclastic micritic matrix (Figure 2). Fusulinaceans and smaller foraminifers abundantly occur in the intercorallite sediments of this fasciculate coral biolithite, such as *Rauserella* sp., *Lantschichites elegans* Sosnina, *Nankinella* sp., *Chusenella* sp., *Tetrataxis* sp., *Climacammina* sp., *Neoendothyra* sp., *Pachyphloia* sp., *Nodosaria* sp. and *Frondina* sp. Among the fusulinaceans, *Lantschichites elegans* Sosnina is most characteristic and abundant. This species was originally described from the *Metadoliolina lepida* Zone of southern Sikhote-Alin, which is correlated with the late Midian of the Middle Permian (Kotlyar *et al.*, 1989). *Lantschichites* was introduced by Tumanskaya (1953) as a subgenus of the genus *Codonofusiella*, with *Codonofusiella* (*Lantschichites*) *maslennikovi* Tumanskaya as the type species. It has been reported mainly from the latest Middle Permian of Sikhote-Alin (Tumanskaya, 1953; Sosnina, 1968), South China (Chen, 1956; Sheng, 1963; Wang *et al.*, 1981) and Texas (Skinner and Wilde, 1954). Two species of *Lantschichites* have been reported in Japan; one is *Lantschichites inuboensis* (Chisaka) from the Takagami Conglomerate of the Choshi Peninsula (Chisaka, 1960) and the Iwaizaki Limestone of the southern Kitakami Mountains (Choi, 1970), and the other is *Lantschichites* sp. from the Mt. Nabekoshi area in the southern Kitakami Mountains (Tazawa, 1975). The present fusulinacean fauna found in a limestone pebble of the Yasuba Conglomerate is considered to be latest Middle Permian (late Midian) in age and has close similarity with that of Sikhote-Alin.

Acknowledgments: I would like to express my appreciation to Prof. Hisayoshi Igo of the University of Tsukuba for reviewing this manuscript. Thanks are also extended to Mr. Yutaka Tanaka for his kind cooperation in the field.

Systematic description

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

Family Boultoniidae Skinner and Wilde, 1954

Genus *Lantschichites* Tumanskaya, 1953

Lantschichites elegans Sosnina, 1968

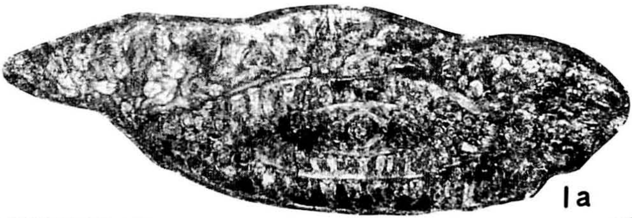
Figures 3-1–16

Lantschichites elegans Sosnina, 1968, p. 126–127, pl. 31, figs. 1-3.

Description.—Shell small, elongate fusiform with bluntly pointed polar ends. Mature specimens having 4 ½ to 5 ½ volutions, 2.18 to 2.78 mm in length and 1.28 to 1.95 mm in width. Shell of regularly coiled part 0.65 to 0.89 mm in width, giving form ratios of 3.12 to 3.87.

The first 1 or 1 ½ volutions tightly coiled at large angles to outer ones. Beyond the third volution, shell becomes elongate rather rapidly. Last half volution abruptly expanded, forming an uncoiled flaring lip about twice as large as earlier regularly coiled part. Radius vectors of the first to fifth, and fifth and a half volutions of well-oriented axial section (Figure 3-1a) 0.05, 0.08, 0.12, 0.20, 0.35 and 0.52 mm. Form ratios of the second to fifth, and fifth and a half volution of the same specimen 1.25, 2.67, 3.10, 3.33 and 2.87.

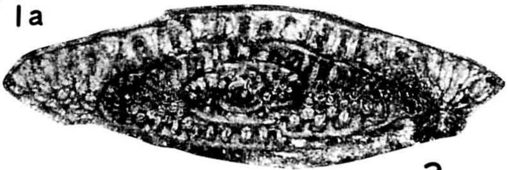
Proloculus small and spherical. Its out-


1a


2


1b


5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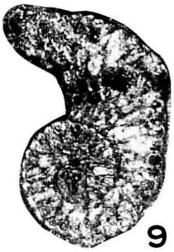
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side diameter ranges from 0.045 to 0.070 mm, averaging 0.057 mm for 7 specimens.

Spirotheca thin, slightly recrystallized and composed of a tectum and lower transparent layer (diaphanotheca). Thickness of spirotheca of the first to fifth volutions of above-mentioned axial section 0.005, 0.005, 0.015, 0.020 and 0.030 mm, respectively.

Septa intensely and regularly fluted throughout length of shell, forming high and narrow, omega-shaped septal loops. Cuniculi well developed in outer volutions. Chomata not observed. Weak axial fillings developed in inner 2 or 3 volutions.

Remarks.—This species can be distinguished from *Lantschichites maslennikovi* (Tumanskaya) in having a larger shell and form ratio, and from *L. inuboensis* (Chisaka) in having a larger shell.

The inner regularly coiled part of *Lantschichites elegans* is somewhat similar to that of *L. splendens* (Skinner and Wilde) from the uppermost Guadalupian of Texas. However, the former has a larger and more developed uncoiled flaring part than the latter.

Lantschichites minima (Chen) described and illustrated by Sheng (1963) from the upper part of the Maokou Limestone of Guangxi (Kwangsi) also resembles this species. However, the former differs from the latter in having a more slenderly cylindrical shell and larger form ratio.

Material.—Axial sections; IGUT-KU 0001, IGUT-KU0002, IGUT-KU0003, IGUT-KU0004. Axial section of immature specimen; IGUT-KU0005. Sagittal sections; IGUT-KU0006, IGUT-KU0007. Parallel sections; IGUT-KU0008, IGUT-KU0009, IGUT-KU0010, IGUT-KU0011, IGUT-KU0012, IGUT-KU0013, IGUT-KU0014, IGUT-KU0015. Tangential section; IGUT-KU0016.

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← **Figure 3.** **1-16.** *Lantschichites elegans* Sosnina, **1a**, **2-4**: axial sections, IGUT-KU0001, IGUT-KU0002, IGUT-KU0003, GUT-KU0004, **5**: axial section of immature specimen, IGUT-KU0005, **6-7**: sagittal sections, IGUT-KU0006, IGUT-KU0007, **8-15**: parallel sections, IGUT-KU0008, IGUT-KU0009, IGUT-KU0010, IGUT-KU0011, IGUT-KU0012, IGUT-KU0013, IGUT-KU0014, IGUT-KU0015, **16**: tangential section, IGUT-KU0016, ×30, **1b**: enlarged part of **1a**, ×75. **17**: *Rauserella* sp., axial section, IGUT-KU0017, ×30. **18**: *Nankinella* sp., tangential section, IGUT-KU0018, ×30. **19**: *Chusenella* sp., tangential section, IGUT-KU0019, ×10.

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