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

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Hyotissocameleo, a new Cretaceous oyster subgenus and its shell microstructure, from Wadi Tarfa, Eastern Desert of Egypt

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Abstract. On the basis of rib morphology and other characters, *Ostrea tissoti* Peron and Thomas found in Egyptian Campanian sediments is placed in the genus *Cameleolopha* Vyalov, 1936 and the subgenus *Hyotissocameleo* n. subgen. This new subgenus is distinguished from *Cameleolopha* s.s. in having dichotomous to trichotomous round-crested radial ribs, chomata, a long triangular resilifer and a reniform to comma-shaped adductor muscle scar. The main part of the shell shows regularly foliated and in part cross-foliated structure. Neither chalky deposits nor chambers are recorded. Silicification of the original calcitic structure is recognized. Recrystallization and dolomitization resulting from diagenetic processes are observed.

Key words: Cretaceous, Egypt, oyster, shell microstructure, systematics

Introduction

Intraspecific and interspecific variations in shell morphology are both very wide in oysters. This results in the occurrence of confusing homeomorphs at all taxonomic levels in the superfamily and enhances the difficulty of oyster taxonomy. It is essential to study populations rather than individuals for the reliable and accurate identification of oysters (Kassab and Zakhera, 1994, 2000). Dhondt (1985) noted that *Lopha* (*Actinostreon*) Bayle, 1878, *Cameleolopha* Vyalov, 1936, *Nicaisolopha* Vyalov, 1936 and *Acutostrea* Vyalov, 1936, all tend to have homeomorphic shells.

Specimens of *"Ostrea" tissoti* Peron and Thomas treated in this paper, were collected from Upper Cretaceous sediments in the northern part of the Eastern Desert of Egypt (Figure 1). This species has been attributed to the genus *Nicaisolopha* Vyalov, 1936 (Kuss and Malchus, 1989; Malchus, 1990). We analyzed its morphology and shell microstructure and reached the conclusion that it belongs to the genus *Cameleolopha* Vyalov, 1936 of the subfamily Lophinae Vyalov, 1936. A new subgenus *Hyotissocameleo* is proposed to accommodate the morphological differences of the species.

Sample preparation

To facilitate SEM observations of *"Ostrea" tissoti*, shells of this species were sectioned in radial, transverse and oblique directions, and parallel to the long axis of the shell. The sectioned surface of each specimen was polished and etched with 0.1 N hydrochloric acid for 20 seconds and then coated with gold for scanning electron microscopy (SEM). Silicified parts and their surroundings have been subjected to microprobe analysis for mineralogical determination.

Mode of occurrence and taphonomy

A large number of specimens of *"Ostrea" tissoti* were collected from yellowish brown, marly mudstone that appears at several Campanian horizons in the Duwi Formation. The oysters occur as articulated and disarticulated valves, arranged parallel to the bedding plane. No preferred orientation of the valves, convex up or down, was observed. The subequal size and thickness of valves may serve to exhibit the differential effect of storms. Several xenomorphs show the oysters lived on a shelly or hard bottom. Spatulate forms with a small attachment area represent a phenotype that lived on a relatively soft bottom.
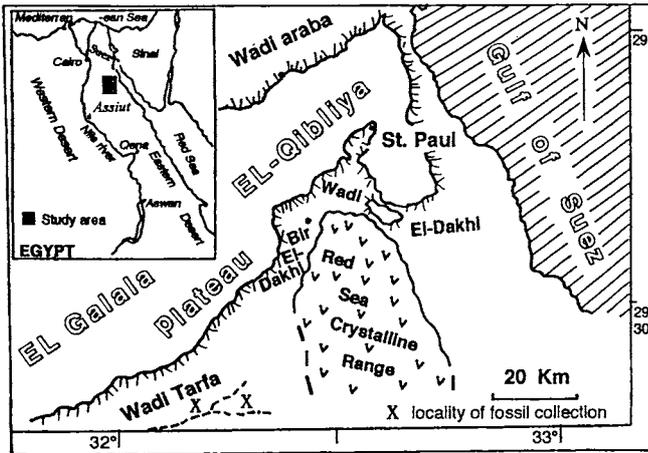
Figure 1. Index map of Wadi Tarfa area, Eastern Desert of Egypt, showing the sampling locality of the Cretaceous oyster.

The presence of few juvenile shells besides those of adults in the same assemblage is indicative of limited or short episodic storm events that caused the shells to form shell-banks. It is very rare to find other bivalves or macroscopic fossils. A low rate of accumulation of muddy clastics allowed the valves to be close to each other, sometimes with the right valves adhering to each other, due to later diagenetic processes.

Silicification and dolomitization during diagenesis are recognized. Silicification affected the calcium carbonate skeletal material, as will be mentioned later, as well as the matrix in which the shells were enclosed. Dolomitization affected only the matrix. The limited dolomitization is indicated by the presence of dolomitic rhombs in the cement between the valves or in sediments filling holes in the shell. The holes are thought to have been formed by dissolution of shell material during the animal's life or shortly after death, but before

consolidation of the enclosing sediments.

Biometrical remarks

A biometric analysis has been made for individuals of shell height more than 23 mm. Smaller specimens are rare in occurrence. This is probably related to low mortality of the juveniles or presence of some kind of post-mortem sorting and fragmentation of smaller shells. Overall morphology and measurements and the internal architecture of the shell of "*Ostrea*" *tissoti* are diagrammatically shown in Figures 2, 3 respectively.

Although the bivariate scatter diagrams (Figure 4) show weak correlation between pairs of height, length and width, it suggests a large constraint of environmental conditions on shell morphology.

For some individuals the dimensions of the adductor muscle of their right valve are sometimes larger than those of their left valve (Table 1). This is probably related to left valve convexity, which leads to contraction of the size of the muscle pad. When the difference between length of the adductor muscle pad (Al) and the maximum diameter of the adductor muscle pad (Ad) (Table 1) is small, the muscle (by its long diameter) becomes close to perpendicular to the shell long axis, while a greater difference is reflected in a steeper dip to the point that the muscle becomes obliquely vertical (maximum difference). This difference is proportional to the ratio of shell height and length.

Shell microstructure

Shell microstructure is important in bivalve systematics (Douvillé, 1936; Newell, 1965; Taylor *et al.* 1969; Stenzel, 1971; Waller, 1978; Torigoe, 1981; Freneix, 1982; Dhondt, 1985; Carter 1990; Malchus, 1990, Aqrabawi, 1993, Zakhera 1999). The terminology used here follows the descriptive nomenclature outlined by Carter (1990) and Malchus (1990). Stenzel (1971) erected the new genus *Hyotissa* and called it pycnodonteine on the basis of the presence of a vesicular
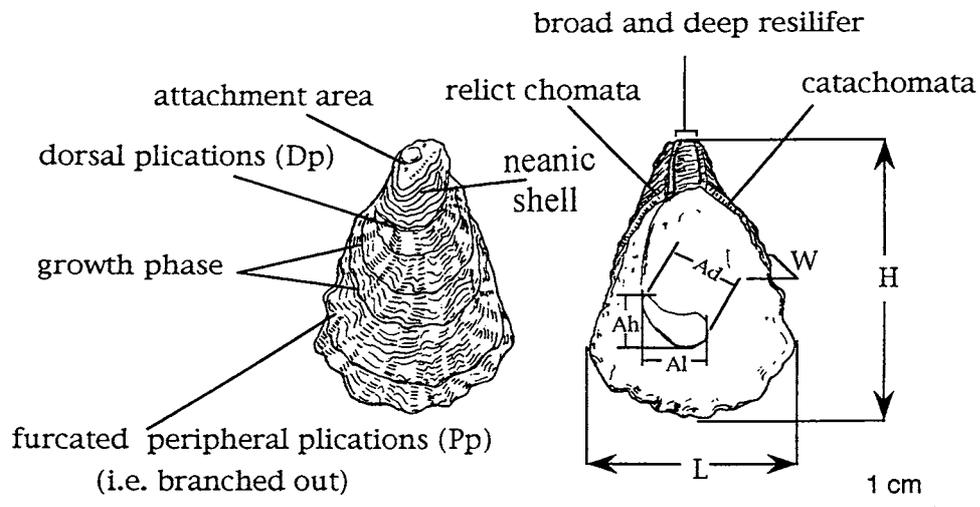
Figure 2. Measured characters and some morphologic features of *Cameleolopha* (*Hyotissocameleo*) *tissoti* (Peron and Thomas).
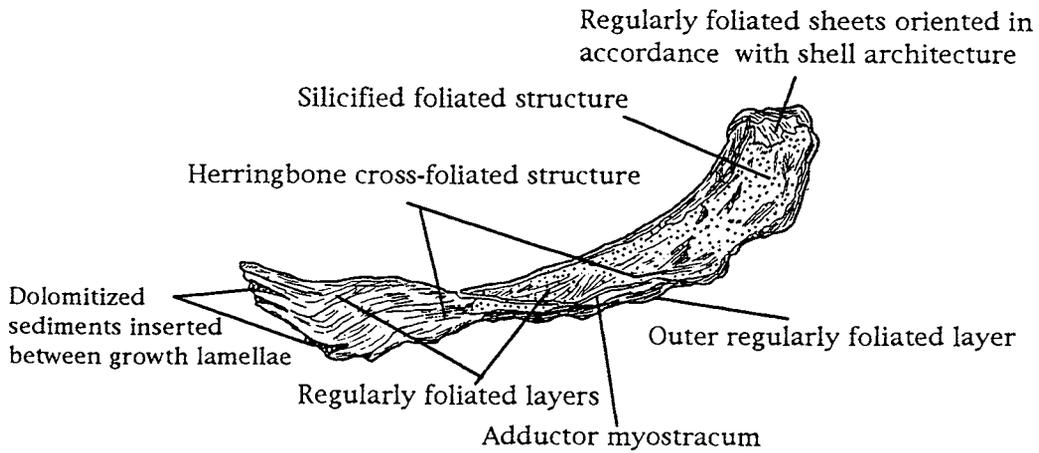
Figure 3. Microstructural framework and distribution of diagenetic effects (silicification and dolomitization) in *Cameleolopha (Hyotissocameleo) tissoti* (Peron and Thomas) as seen in radial section.
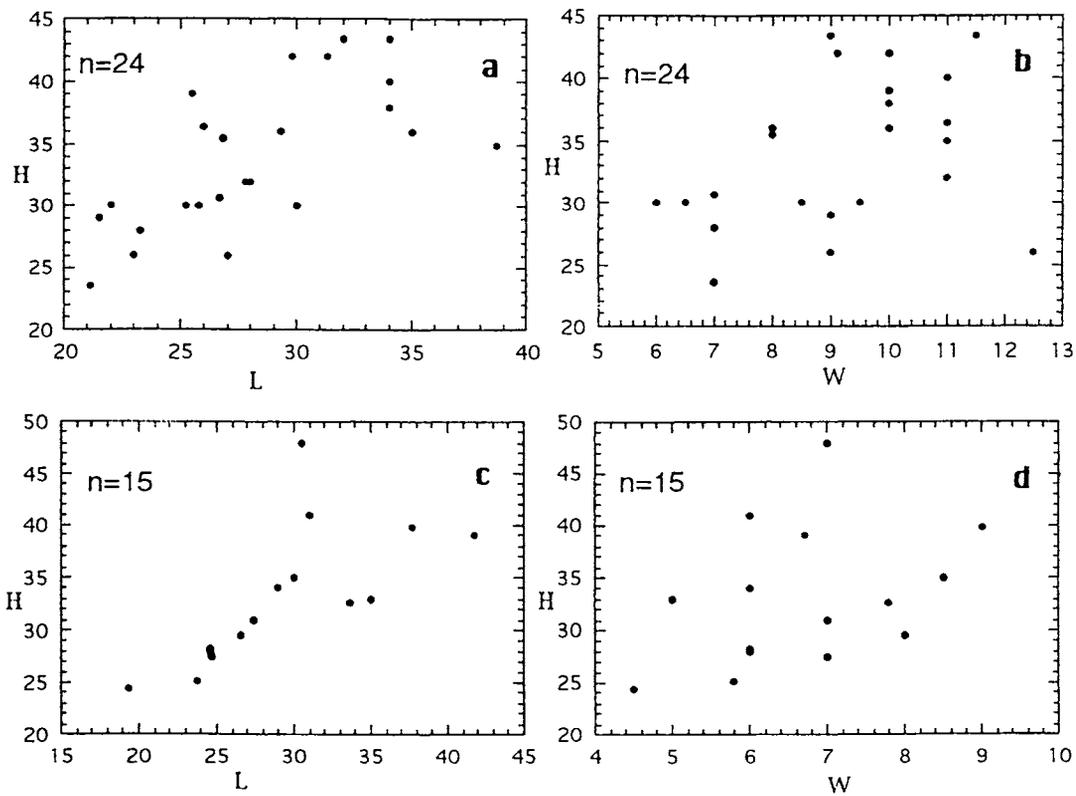
Figure 4. Bivariate scatter diagram of *Cameleolopha (H.) tissoti* (Peron and Thomas) for height (H) against length (L) and height against width (W). **a, b** for left valves; **c, d** for right valves. *n* = number of valves. H, L and W are in mm.

wall structure. Malchus (1990) proposed a new family Paleolophidae on the basis of the presence of a strongly lenticular, simply foliated microstructure. The carbonate skeleton of "*Ostrea*" *tissoti* in its current state of preservation is entirely made of calcite, as ascertained by Miegen's stain-

ing method. The shell wall is composed of the following layers with different microstructures.

Prismatic layer

This is the outermost layer of both valves (Figure 5A). It

Table 1. Measurements (in mm) of *Cameleolopha* (*Hyotissocameleo*) *tissoti* (Peron and Thomas). Abbreviations: H = Height. L = Length. W = Width (valve concavity). Ah = Height of the adductor muscle pad. Al = Length of the adductor muscle pad. Ad = Maximum diameter of the adductor muscle pad. Dp = No. of dorsal plications (ribs directly connected to the smoothly concentric neanic disc). Pp = No. of peripheral plications (ribs at the shell margin which originated as Dp and extended bifurcationally toward the shell margins). Nos. 1–15 on left and right valves are not of the same individuals.

Specimen number	H	L	W	Ah	Al	Ad	Dp	Pp	Specimen number	H	L	W	Ah	Al	Ad	Dp	Pp
Left valve									Right valve								
1	43.5	32.3	9	8	10	12	9	21	1	33	35	5	-	-	-	8	11
2	39	25.5	10	7	5	9	11	19	2	39	41.8	6.7	-	-	-	9	17
3	36.4	26	11	10	11	12	5	12	3	41	31	6	10	11.7	12.5	7	12
4	28	23.3	7	8	7	9	8	13	4	39.8	37.7	9	11	10	11.5	12	18
5	35.5	26.8	8	10	11	12	10	11	5	35	30	8.5	6.5	10	11	10	14
6	30.7	26	7	9.3	7	9	-	10	6	32.7	33.6	7.8	8	11	11.5	8	12
7	43.5	34	11.5	9.5	11	13	-	14	7	34	29	6	8.5	10	10	7	13
8	40	34	11	14	8	15	6	27	8	28	24.6	6	8.6	8.5	9.2	11	13
9	26	27	12.5	12	7	12	15	18	9	29.6	26.6	8	6	8	10	8	13
10	30	30	6.5	7	8	9	9	14	10	28.3	24.6	6	8	9	10	9	16
11	32	27.8	11	9	12	12	11	15	11	24.4	19.4	4.5	5	6	6.8	8	11
12	30	25.8	9.5	8	6.5	9	12	18	12	25.2	23.8	5.8	4	8	9	8	11
13	35	38.7	11	8	13.3	13.3	5	17	13	31	27.4	7	11	8	11	10	18
14	23.5	21.1	7	7	9	10	10	19	14	48	30.5	7	8.5	11	12	4	8
15	30	22	6	5	9	11	-	12	15	27.5	24.7	7	5	7	8	10	14
16	32	28	11	7.5	10.5	11	-	18									
17	42	31.3	10	11	10	12.5	9	16									
18	38	34	10	-	-	-	10	17									
19	36	35	10	-	-	-	11	14									
20	42	29.8	9.1	-	-	-	10	15									
21	29	21.5	9	8.5	6	10	6	11									
22	36	29.5	8	9	10	11	7	12									
23	26	23	9	6	7	8	6	11									
24	30	25.2	8.5	11	8	11	10	18									

is composed of prisms, about 9 μm long and up to 4.5 μm in diameter. The prisms are arranged slightly oblique to the outer surface of the valve. The prismatic layer has been encountered only in places where the valves are attached to each other and protected from erosion. The preservation of the prismatic layer in this species might be due to burial of the shell in the soft substrate and could not be referred to burial during life as observed in the dorsoventrally elongate oyster *Konbostrea* (Chinzei, 1986).

Foliated layers

There are two types of foliated structures. One is the regular type and the other is the crossed-foliated structure, in which the foliated sheets cross each other at a low angle.

Regularly foliated structure. — This structure is synonymous with the simply foliated structure of Malchus (1990). It is built up of long, thin calcitic laths with pointed ends, arranged parallel to one another to form a foliated sheet. The sheets are, in turn, arranged nearly parallel to one another. The orientation of sheets parallels the general trend of shell architecture (Figure 3). The shell architecture is influenced by shell morphology. The regularly foliated structure is predominant in this species, as it constitutes the structural framework of the shell, between the outer prismatic layer

➡ **Figure 5.** Microstructure of *Cameleolopha* (*Hyotissocameleo*) *tissoti* (Peron and Thomas). **A.** The outer prismatic layer (arrow) of the lower individual (a) below the dark groove (cementing zone of the upper oyster), radial section. **B.** Regularly foliated sheets in the umbonal area, radial section. **C.** Herringbone cross-foliated structure, radial section. **D.** Differential response of the calcitic structure (low relief, shown as c) and the more resistant secondary silica (high relief, shown as s) to the etching acid; the adductor myostracum is indicated by arrow. **E.** Spherical unit (s), as a secondary product of recrystallization, with its smooth rounded boundary embedded in a foliated layer (f), parallel section. **F.** Higher magnification of **E**, showing the fine homogeneous filling of the spheres. **G.** Silicified sheets (lower right) normal to the adjacent unit of foliated sheets (upper left) with corroded contact, the circled spots indicate the locations of the microprobe investigations, transverse section. **H.** Silicified foliated structure with cavities of various shapes, radial section.
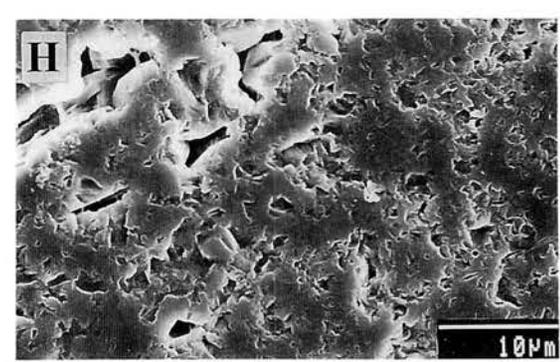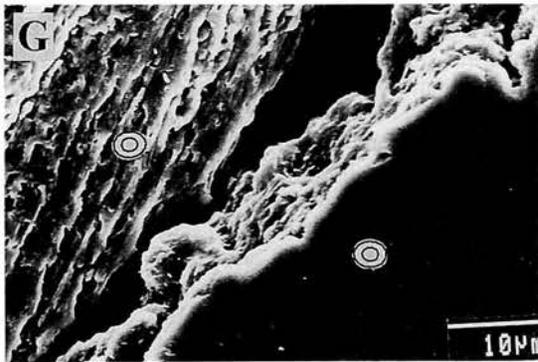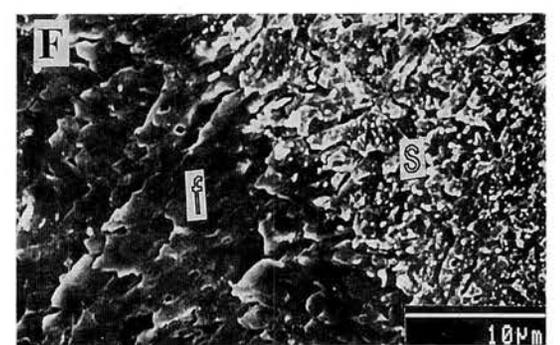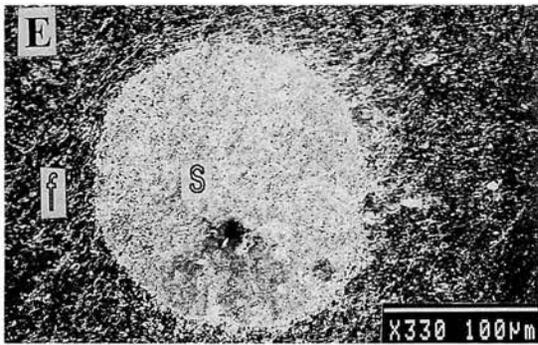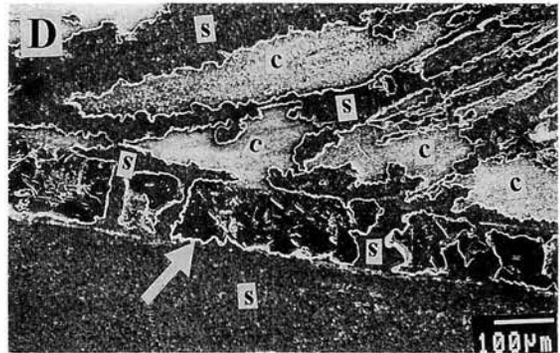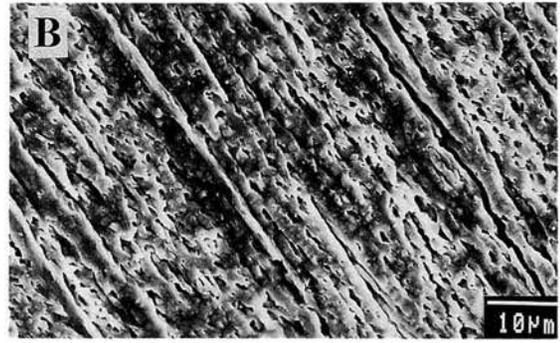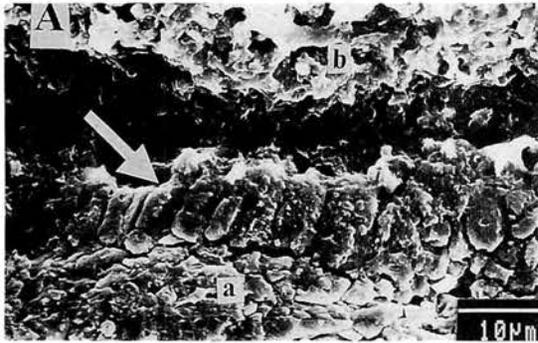
and the innermost regularly foliated layer (Figures 3 and 5B).

Herringbone cross-foliated structure.—At low magnification we observed some layers, each consisting of two sublayers, in the middle part of the shell cross-section (Figure 3). The second-order elements of each sublayer are parallel to one another, inclined at an acute angle to the opposite sublayer. As a result, the sublayers show a regular alternating pattern (Figure 5C). This arrangement of foliated sheets was called "herringbone cross-foliated structure" by Malchus (1990).

Adductor myostracum

The relict of adductor myostracum, ranging from 0.3 to 0.35 mm in thickness, is easily traceable in the specimens examined although it does not retain its original, probably aragonitic, microstructure (Figure 5D). It is composed of coarse-grained calcite. The calcite layer filling the space of the myostracum was fractured and partly replaced by silica mineral (Figures 3 and 5D). Preservation of relicts of original aragonitic crystallites have been reported, even in Paleozoic fossils (Rollins, 1966; Carter and Tevesz, 1978). In these cases, the aragonite is often preserved within the silicified part of the shell, but we could not find aragonite in this Cretaceous oyster. This suggests that silicification occurred after alteration of the myostracal aragonite to stable calcite.

The microstructure of this species does not show any sign of chalky deposits or chambers within its shell. The absence of chalky deposits in oyster of the Lophinae was mentioned by Torigoe (1981) as one of the characteristic differences between them and members of the Ostreinae, besides the obvious chomata and other characters of the soft parts. Chinzei and Seilacher (1993) reported accidental chambering in the shell of a Recent *Lopha*, the chambers being filled with dendritic calcite crystals characterized as a "Christmas tree". Aqrabawi (1993) has broadened the characteristic morphological range of *Nicaisolopha* Vyalov, 1936, to include the presence of some empty and chalky lenses within its simply foliated structure. So, the absence of empty lenses and chalky deposits in the species examined here is worth noting. This supports its affinity to the Lophinae as well as its exclusion from genus *Nicaisolopha*.

Diagenetic alteration in shell microstructure

Diagenetic alterations in the shell microstructure are expressed by silicified foliated structure and recrystallized spheroidal units.

Silicified foliated structure.—A quasihomogeneous structure occupies the inner part of the shell near the umbo. This area tapers toward the anterior, posterior and ventral margins (Figure 3). We can observe the original sheets of foliated structure only in some well-prepared sections (Figure 5H). The homogeneous material is made up of large crystals of a silica mineral detected by microprobe analysis (Figure 6) and SEM observations (Figures 5G, H). The silicification is seen mainly in the inner part of the shell. This is consistent with the view that silicification tends to start in the internal parts of the shell and spread outward (Suzuki *et al.*, 1993). Suzuki *et al.* (1993) observed that

Foliated part
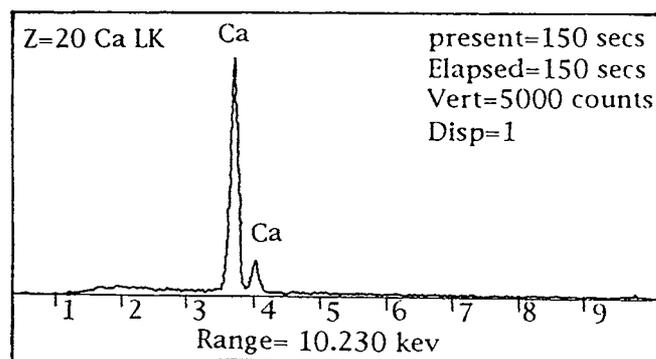
Altered part
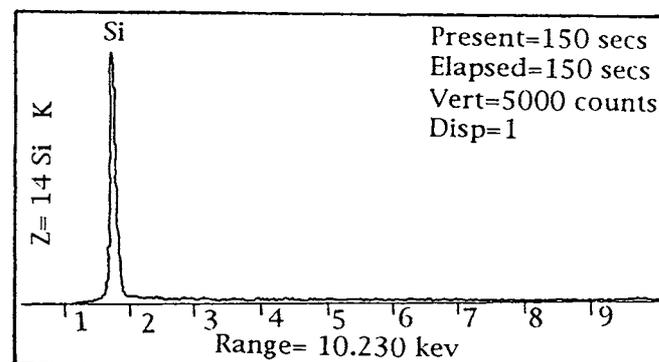
Figure 6. Microprobe chart for a spot of foliated structure, showing a predominance of **Ca** (above) and the altered part showing predominance of **Si** (below).

silicification has been recorded in such bivalves with originally aragonitic shells as glycymerids and venerids, and that it plays a significant role in preserving the original aragonitic structures. This study reveals that silicification can also occur in originally calcitic shells, leading to disordering of the original fabrics of shell microstructure.

Spheroidal units.—Many spheroidal units, each 150 to 200 μm diameter (Figure 5E), are observed as sporadic spheres in the mid-ventral part of the shell. These spheres are composed of fine (1.1 to 5.5 μm) aggregates of calcite that are irregularly shaped and have no preferred orientation. These aggregates have the appearance of a homogeneous structure (Figure 5F). Figure 5F also shows the sudden change in lath size and arrangement of the calcitic aggregates of this spherical units and its surrounding foliated structure. This arrangement with its false homogeneous appearance is considered to be a secondary product of recrystallization processes.

Systematic description
(by M. Zakhera)

Family Ostreidae Rafinesque, 1815
Subfamily Lophinae Vyalov, 1936

Discussion.—As the species seems to be a lophine oyster, relevant systematic views are briefly reviewed.

Vyalov (1936) established the subfamily Lophinae in the family Ostreidae for the oysters having radially sculptured valves and a plicated or undulating commissure. At the same time, he described the sculpture of *Nicaisolopha* as vague folds. According to Stenzel (1971), the subfamily Lophinae includes the genus *Lopha* Röding, 1798 with subgenera *Abruptolopha* Vyalov, 1936 and *Actinostreon* Bayle, 1878; the genera *Alectryonella* Sacco, 1897, *Cameleolopha* Vyalov, 1936, *Nicaisolopha* Vyalov, 1936 and *Rastellum* Faujas de Saint-Fond, 1799, with subgenus *Arctostrea* Pervinquière, 1910. Recently, *Arctostrea* has been treated as a discrete genus (Carter, 1968; Zakhera and Kassab, 1999). In light of Thomson's (1954) work, Stenzel (1971) considered *Alectryonia* Fischer de Waldheim, 1808, *Dendostrea* Swainson, 1835 and *Pretostrea* Iredale, 1939, as synonymous of *Lopha* Röding. Meanwhile Torigoe (1981) morphologically discriminated *Dendostrea* Swainson, 1835 as a separate genus not equivalent to *Lopha*. Malchus (1990) emphasized the importance of shell microstructure rather than shell morphology in his classification of Mesozoic oysters. Consequently, he referred the Cretaceous *Nicaisolopha*, which has a typical lophine form and was formerly assigned to the Lophinae, to his new ostreid subfamily Liostreinae Malchus, 1990. At the same time he erected, on the basis of a characteristic microstructure, another new family, Palaeolophidae, for some other Mesozoic lophine oysters, including *Rastellum* Faujas de Saint-Fond, 1799, *Palaeolopha* Malchus, 1990, and *Oscillopha* Malchus, 1990. He also pointed out that *Cameleolopha* Vyalov, 1936 could be synonymous with *Nicaisolopha* Vyalov, 1936.

A large sample of the present species, in a very good state of preservation, enables us to examine its morphological and microstructural characters precisely, to take the effects of homeomorphy into account and determine its proper systematic position. The species has recently been placed in the genus *Nicaisolopha* Vyalov, 1936. According to Stenzel (1971), *Nicaisolopha* Vyalov, 1936 is mainly characterized by 4–7 radial folds that are not dichotomous; the folds are undulatory, round-crested, and separated by equal, rounded interspaces, on both valves. The genus has no chomata; the adductor muscle imprint is reniform, deeply concave at its dorsal margin; the ligamental area is low and long; the left valve resilifer is shallowly excavated and slightly longer than the bourrelets; and the right valve resilifer is flat, with growth squamae slightly raised in the later growth stage.

On the other hand, *"Ostrea" tissoti* Peron and Thomas has 10–27 clearly dichotomous (sometimes trichotomous) radial ribs, rather than broad radial folds as in *Nicaisolopha*. This species is smaller in size and it has distinct chomata, which are absent in *Nicaisolopha* and *Cameleolopha* s.s. It has a reniform to comma-shaped adductor muscle imprint and a resilifer deeply excavated in the left valve that is about two times longer than the bourrelets. Compact, closely spaced growth lines, rather than growth squamae, tend to be promi-

nent at the end of growth phases. Based on these characteristics, I transferred this species from *Nicaisolopha* to *Cameleolopha*.

Genus *Cameloelopha* Vyalov, 1936

Type species.—Ostrea cameleo Coquand, 1869.

Subgenus *Hyotissocameleo* Zakhera subgen. nov.

Derivation of name.—From a combination of *Hyotisso,* in reference to its general hyotissinine form and *Cameleo,* in reference to the genus name *Cameleolopha* Vyalov, 1936.

Type species.—Ostrea tissoti Peron and Thomas, 1891.

Diagnosis.—Shell having numerous fine chomata and relict chomata. Resilifer long. Radial ribs narrow with rounded crests tending to start from the umbonal area, and branching dichotomously or trichotomously.

Comparison.—*Hyotissa* Stenzel, 1971 has only a superficial resemblance to *Hyotissocameleo* in its general shell form. They differ in shell microstructure, shape of adductor scar and the style of ornamentation. *Hyotissocameleo* differs from *Cameleolopha* s. s. in the following points:

1. Possession of distinct chomata and relict chomata (not mentioned in the designation of *Cameleolopha s.s.* in Stenzel, 1971, probably they were very weak and overlooked).

2. Existence of wider range in the number of radial ribs (10 to 27 as peripheral ones), while the number ranges from 12 to 20 in *Cameleolopha* s.s.

3. In *Hyotissocameleo,* the radial ribs are straight or weakly undulating in their crest direction, continuous from near the umbo to the commissure as a general trend, and dichotomously or trichotomously branching. In *Cameleolopha* s.s. the radial ribs are, by contrast, curved and diverge outward as the animal grows.

4. The radial ribs in *Hyotissocameleo* have rounded crests, while these are angular in *Cameleolopha* s.s.

The Cenomanian species *Ostrea cameleo* Coquand, 1869, the type species of the genus *Cameleolopha,* can be distinguished from *Ostrea tissoti* Peron and Thomas by the characters noted above. The material identified as *Hyotissa armata* (Goldfuss) by Pugaczewska (1977, p.194, pl. 12, figs. 4–5) from Poland, has bifurcated radial ribs, compact and closely spaced growth lines and a high ligamental area with deep resilifer. So it might be included in *Hyotissocameleo. Cameleolopha bellaplicata* (Conrad) could be attributed to the subgenus *Hyotissocameleo* as it has the same shell form and style of ornamentation.

Cameleolopha pauciplicata Kassab and Mohamed, 1996 has weak chomata and differs from *Cameleolopha (Hyotissocameleo) tissoti* in having a triangular shell form that is tapering dorsally, has fewer number of angular, curved dichotomous radials and no relict chomata.

On the basis of the presence of weak chomata in some species of *Cameleolopha* s.s., the shape and position of the adductor muscle and the ribbing ornamentation, *Cameleolopha* s.s. and *Hyotissocameleo* came from the same ancestor, which was probably *"Ostrea" loriolis* Coquand and/or *"Ostrea" cornuelis* Coquand in the

1a   1b   2a   2b

3   4   5   6

7   8a   8b   8c

9a   9b   10   11

12   13   14   15
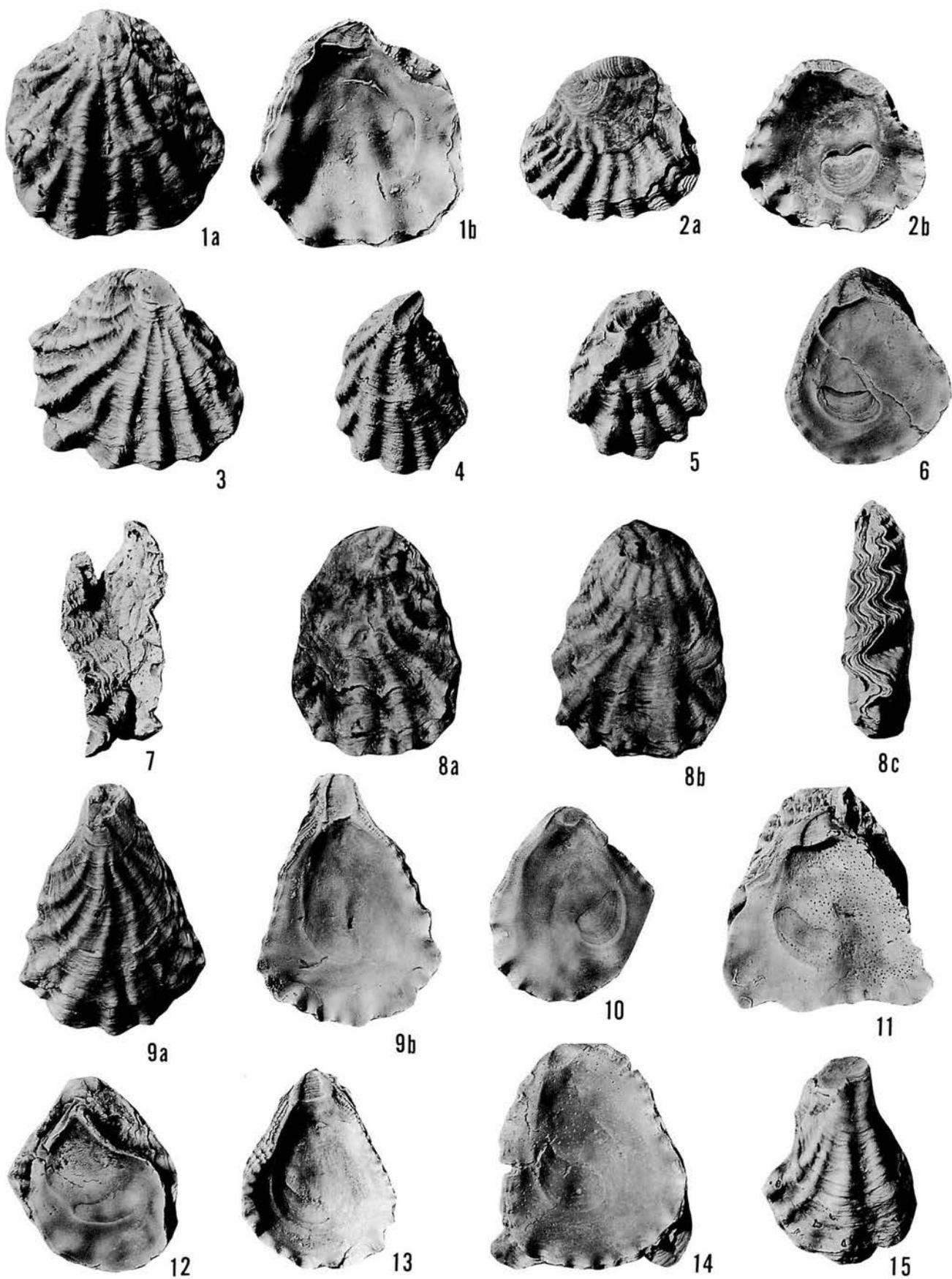
Neocomian passing by "*Ostrea*" *complicata* Mahmoud in the Albian and *Lopha syphax* Coquand in the Cenomanian.

Cameleolopha (Hyotissocameleo) tissoti
(Peron and Thomas, 1891)

Figure 7

Ostrea forgemolli Coquand. 1869, p. 25, pl. 2, figs. 9-11 (non figs. 1-8).

Ostrea tissoti Peron and Thomas. 1891, p. 196, pl. 24, figs. 1-7.

Alectryonia tissoti (Peron and Thomas). Dacqué, 1903, p. 365, pl. 34, figs. 11-12.

Lopha tissoti (Peron and Thomas). Fourtau, 1917, p. 54, pl. 5, figs. 1-5; Bandel *et al.*, 1987, pl. 2, figs. 5a, b.

Nicaisolopha tissoti (Peron and Thomas). Kuss and Malchus, 1989, p. 902; Malchus, 1990, p. 174, pl. 19, figs. 7-16, 18.

Material.—One hundred and twenty-seven specimens, as separated left and right valves, conjoined valves and a few fragments, have been collected from yellowish-brown, marly mudstone of Campanian sediments (Duwi Formation) in Wadi Tarfa of the northern part of Eastern Desert of Egypt. They are housed in the Geological Museum of Aswan University, bearing the prefix KZASW with serial numbers.

Measurements—Measurements on complete specimens are listed in Table 1.

Description—Shell small in size (up to 5 cm), not strongly inflated, subequivalve. Outline suborbicular to spatulate. No auricles. Left valve (LV) more capacious than right valve (RV). Maximum convexity of valve occurs ventrally, corresponding to position of adductor muscle. Umbo terminal, pointed. No umbonal cavities in most individuals while some left valves have a small and very shallow one beneath hinge plate. Chomata well developed both anterodorsally and posterodorsally in vicinity of hinge. Anachomata on right valve long (up to 2 mm), thin, closely arranged, straight and sometimes tilted in same valve. Corresponding catachomata on left valves less pronounced and easily overlooked in some valves. Relict chomata also present. Ligament triangular, high in left valve, low in right valve; straight or posteriorly or anteriorly curved. Ligament area tripartite with a resilifer twice as broad as both bourrelets, or slightly more. Anterior bourrelet longer than posterior one. Adductor muscle imprint comma-shaped in elongated individuals, kidney like in suborbicular ones, and situated posteroventrally. Quenstedt muscle insertions very small, located below resilifer. Attachment area small to medium on left valves with corresponding xenomorphic areas on right valves. Medium-sized attachment area might distort

shell shape and sculpture. Neanic part of shell smooth. Both valves have narrow round-crested radial ribs, always at least dichotomous, sometimes trichotomous, especially on shell periphery. They are usually 10-18 in number and may attain 27 in number along shell margin. These radials are crossed by tight nonappressed growth lamellae which are intermittently prominent. Commissure plicate, interlocking at valve margin. Plication impressed on internal valve surface only for thin-shelled valves.

Occurrence.—It seems likely that *Cameleolopha (Hyotissocameleo) tissoti* (Peron and Thomas) is a well represented Tethyan species in North Africa. The species was recorded from the same age interval from Tunisia by Peron and Thomas, 1891. It was also recorded from Tripoli by Krumbeck (1906) under the name of *Ostrea* cfr. *forgemoli* Coquand.

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← Figure 7. *Cameleolopha (Hyotissocameleo) tissoti* (Peron and Thomas). All figures in natural size. **1a, b.** KZASW 4/7-1. External and internal views of a typical rounded right valve, showing bifurcating radial ribs, dorsal catachomata and comma-shaped adductor pad. **2.** KZASW 4/7-2. **2a.** External view of a right valve showing xenomorphic area and prominent lamellae marking the growth phases. **2b.** Internal view of 2a. **3-5.** External views of left valves showing different shapes and sizes of the attachment area. **3.** KZASW 4/7-3. **4.** KZASW 4/7-4. **5.** KZASW 4/7-5. **6.** KZASW 4/9-1. Internal view of a right valve. **7, 11.** KZASW 4/11-1. Two cemented left valves. **8a, b.** KZASW 4/7-6. External views of right valves, showing "zigzag" commissure. **9a, b.** KZASW 4/7-7. External and internal views of a typical spatulate left valve, showing radial bifurcating, and deep, wide resilifer. **10.** KZASW 4/9-2. Internal view of a right valve. **12.** KZASW 4/7-8. Cemented right valve with another left valve. **13.** KZASW 4/11-2. Internal view of a right valve. **14.** KZASW 4/11-3. Internal view of a right valve, showing a different outline and different resilifer size and orientation. **15.** KZASW 4/7-9. Left valve with fewer radial ribs but still ventrally bifurcated.

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Molecular phylogeny and morphological evolution of laqueoid brachiopods

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Abstract. One of the virtues of molecular phylogeny for paleontology is that it can provide independent and often reliable sets of data from living relatives to test various evolutionary hypotheses inferred from fossil forms. In this study, we present results of a molecular phylogenetic analysis of 12 species of 7 genera belonging to the Laqueoidea, which is the most prolific of the brachiopod superfamilies in the seas around Japan. Onto a phylogenetic tree based on partial sequences (1218 bp) of the mitochondrial *cox1* gene, we superimposed various external and internal morphologic characters of both juveniles and adults for the taxa examined. The resulting patterns indicated that several lineages experienced paedomorphic evolution in terms of the brachidial (loop) morphology, and that, contrary to some traditional views, certain adult features, such as the bilateral loop, possession of a cardinal process, and a rectimarginate commissure, had homoplasious distributions. Examination of the character distributions also revealed, however, that anterior nonbifurcation of the septal pillar at the axial phase is a synapomorphy for a major clade recognized in the molecular analysis. Those results suggest that early loop ontogeny, information about which is still fragmentary, would be useful in assessing relationships among laqueoid brachiopods, including certain Mesozoic genera.

Key words: Brachiopoda, cytochrome c oxidase I (*cox1*) gene, Laqueoidea, loop ontogeny, mitochondrial DNA, molecular phylogeny, Recent

Introduction

The Laqueoidea is one of the larger terebratulide brachiopod superfamilies, being well represented in both present-day waters and Cenozoic strata of Japan. The members of this superfamily, as well as other superfamilies within the order Terebratulida, are characterized by the possession of calcareous internal skeleton known as the loop which continually undergoes considerable morphological change during growth before attaining the full adult stage. Due to its complexity and diversity, loop morphology has been the prime tool for the inference of phylogenetic relationships among laqueoid brachiopods and for the classification of long-looped brachiopods generally at various taxonomic levels (Hatai, 1936, 1940; Muir-Wood et al., 1965; MacKinnon, 1993). However, the assumption that loop morphology reflects phylogeny has not been fully tested, nor has it been possible to discuss loop evolution without the risk of circular arguments. Ideally phylogenies should be based on characters that are completely independent of the loop. One such would be molecular characteristics.

Although molecular trees are only working hypotheses of the true evolutionary relationships of living species, they are useful in providing a basis for discussion of the likely history of a character of interest. In studies of morphological character states, predictions can be made about the probable direction of morphological character state transformations and combinations of characters in basal versus derived species, and therefore we can reassess the morphological characters that support the relationships. Because only morphological characters can be used to establish the phylogenetic affinities of ancient fossil taxa, the success of a morphological approach for fossils can be increased greatly if patterns of character state evolution are considered in the light of an independently estimated phylogeny.

Previous brachiopod molecular systematics have been based on immunological comparisons of shell macromolecules (Collins et al., 1988; Curry et al., 1991; Endo et al., 1994) and on nucleotide sequence comparisons of nuclear 18S ribosomal ribonucleic acids (rRNA) and mitochondrial 12S rRNA (Cohen and Gawthrop, 1996, 1997; Cohen et al., 1998a, 1998b). The novel overall patterns of loop evolution

that the immunological data indicated were largely unsupported by the results of 18S rRNA sequence comparisons (Cohen and Gawthrop, 1997; Cohen *et al.*, 1998b). Besides, it was difficult using the immunological data to resolve relationships among closely related genera. Even with the 18S rRNA data, which offered direct measurements of molecular similarity and thus are more reliable, detailed relationships among the long-looped terebratulide brachiopods remained unclear because the tempo of the 18S rRNA sequence evolution was considered too slow to provide adequate variations among these forms (Cohen *et al.*, 1997).

Both the nucleotide and amino acid sequences of the mitochondrial cytochrome c oxidase subunit I (*cox1*) gene turned out to provide a potentially useful framework for shallower phylogenies, especially of the relationships among the long-looped laqueoid brachiopods (Saito *et al.*, 2000). In this paper, we report the phylogenetic relationships of laqueoid brachiopods inferred from the *cox1* sequences and discuss evolutionary processes of the loop and of other morphologic characters in laqueoid brachiopods, including some possibly basal Mesozoic fossils.

Material and methods

Brachiopod samples and molecular phylogenetic analysis.—Twenty-seven specimens representing a total of 16 species of terebratulide brachiopods including 11 laqueoid species were available for this study (Table 1).

Full details of DNA extraction, amplification and sequencing methods are described in Saito *et al.* (2000). In brief, *cox1* sequences (1218 bp or 406 amino acids in length) were obtained by the direct sequencing of DNA amplification products synthesized by PCR. Amino acid sequences were deduced by reference to the genetic code of brachiopod mitochondrial DNA (Saito *et al.*, 2000). Phylogenetic analysis by maximum-parsimony (MP) was performed with PAUP version 3.1 (Swofford, 1993), using the exhaustive search algorithm and equal weighting for all substitutions. To evaluate the robustness of the internal branches, 500 bootstrap replications were executed. Analysis by neighbor-joining (NJ; Saitou and Nei, 1997) and maximum-likelihood (ML) were performed with Molphy version 2.3 (Adachi and Hasegawa, 1996a) using the mtREV24-F model (Adachi and Hasegawa, 1996b) for amino acid data and HKY85 model for nucleotide data (Hasegawa *et al.*, 1985), using the "Local Rearrangement Search" option. For each internal branch, a local bootstrap probability (LBP) was estimated by the RELL method (Kishino *et al.*, 1990) with 1000 replications. TreeView version 1.4 (Page, 1996) was used to draw trees.

Because of the low intraspecific nucleotide sequence variations in the examined individuals (less than 2%), and the lack of any amino acid difference within each species, one individual was selected to represent the species in the phylogenetic analysis. These representative nucleotide sequences will appear in the DDBJ nucleotide sequence database with the Accession Numbers AB026501–AB026516 shown in Table 1.

For analysis of deeper relationships within the Laqueoidea, both the amino acid and the 1st and 2nd codon

Table 1. Specimens used in this study and their sampling localities. Accession numbers refer to the DDBJ nucleotide sequence database.

Species	Locality	Accession number
Ingroup (Laqueoidea)		
Laqueus rubellus 1	Sagami Bay	AB026501
L. rubellus 2	Sagami Bay	
L. rubellus 3	Sagami Bay	
L. blanfordi	Otsuchi, Tohoku	AB026502
L. quadratus 1	SW of Oshima	AB026505
L. quadratus 2	SW of Oshima	
L. californicus	Monterey Bay, California, USA	AB026503
L. c. vancouveriensis	Monterey Bay, California, USA	AB026504
Pictothyris picta 1	off Mishima	AB026506
Pictothyris picta 2	Sagami Bay	
Jolonica nipponica	Izu Islands, W of Takase	AB026509
Frenulina sanguinolenta 1	Vava'u, Tonga	AB026510
F. sanguinolenta 2	Vava'u, Tonga	
Shimodaia pterygiota 1	Off Shimoda	AB026511
S. pterygiota 2	Off Shimoda	
Terebratalia coreanica 1	Otsuchi, Tohoku	AB026508
T. coreanica 2	Wakkanai, Hokkaido	
Coptothyris grayi 1	Otsuchi, Tohoku	AB026507
C. grayi 2	Wakkanai, Hokkaido	
Outgroup (long-looped forms)		
Ecnomiosa sp. 1	Izu Islands	AB026512
Ecnomiosa sp. 2	Izu Islands	
Campages sp.	SW of Yonejima	AB026513
Outgroup (short-looped forms)		
Terebratulina crossei	Otsuchi, Tohoku	AB026514
Terebratulina pacifica	off Oshima	AB026515
Gryphus davidsoni	S of Oshima	AB026516

position nucleotide sequences were used as data sets. Because little variation was detected in the amino acid sequences and the 1st and 2nd codon positions of nucleotide sequences, analyses of five *Laqueus* species were performed separately with full lengths of the nucleotide data.

Morphological observations.—Observation of juvenile loop morphologies of two laqueoid species, *Jolonica nipponica* and *Terebratalia coreanica*, was carried out on a Hitachi S-2400S Scanning Electron Microscope using the methods described by Saito (1996).

Results

Laqueoid relationships

Of the terebratulides analyzed, *Ecnomiosa* sp. and *Campages* sp. clustered basal to the laqueoids and monophyly of laqueiods were strongly supported (100% LBP, Figure 1). Therefore, we used *Ecnomiosa* sp. and *Campages* sp. as the outgroups for the analyses of all laqueoids sampled and within the species of *Laqueus*. Analyses were also made for an ingroup comprising the 6 genera of Laqueoidea using *Laqueus rubellus* as outgroup.

Analyses based on different tree-building methods (NJ, ML, and MP) and different data sets converged to indicate four possible topologies for the relationships among laqueoid genera (Trees 1 to 4; Figure 2). The results of the molecular phylogenetic analysis are summarized in Figure 3.

All resulting trees clearly indicated the basal placement of *Laqueus* in the Laqueoidea. The local bootstrap support of this node is high in all analysis (99-100%). Among the remaining six genera (*Terebratalia, Coptothyris, Shimodaia, Frenulina, Pictothyris* and *Jolonica*), the close relationship between *Jolonica* and *Pictothyris* is consistently supported by high bootstrap values (82-99%). Three of the four trees (Trees 1 to 3) show very similar topologies: the close association of *Shimodaia-Frenulina-Pictothyris-Jolonica*, with *Terebratalia* and *Coptothyris* left outside. The positions of *Terebratalia* and *Coptothyris* differ slightly in each tree but

they are generally positioned close to one another in the four cladograms. Tree 4 shows early branching of *Shimodaia* within the 6 genera.

The NJ analysis consistently supported Tree 1 (Figure 2). The ML analysis supported Tree 1 or Tree 2, however, the log-likelihood differences among Trees 1 to 3 are very small when amino acid sequences are used. The LBP support for the branch including *Terebratalia* or *Coptothyris* is low (19-
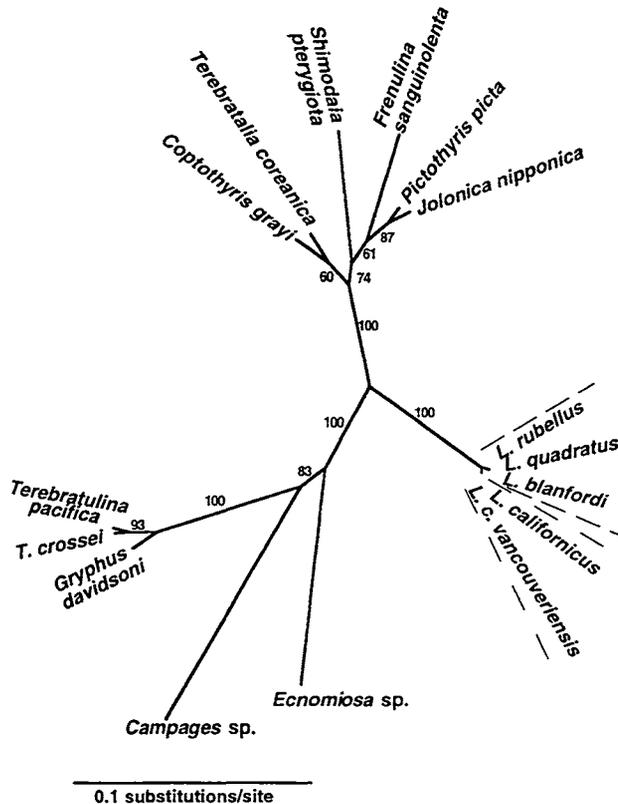

Figure 1. NJ tree based on amino acid sequences. The number at each internal node of the tree indicates the percentage of node occurrence in 500 bootstrap replicates.
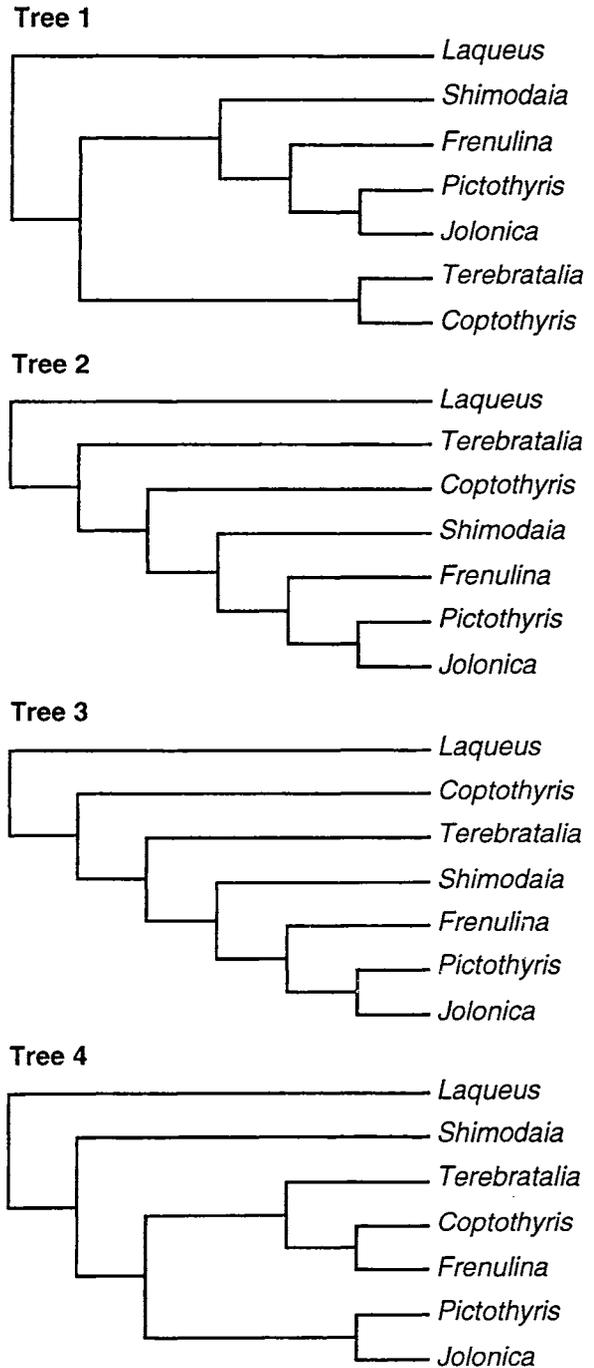

Figure 2. Four possible topologies for the relationships among laqueoid genera.

Tree ID.	Tree topology	MP		ML			
				aa		1st+2nd	
		aa	1st+2nd	lnL	BP	lnL	BP
Tree 1	((Laq,((((Pic,Jol),Fre),Shi),(Tra,Cop))),Ecn,Cam)	228	349	-2418.64±109.10(ML)	0.2887	-2855.96±101.53(ML)	0.4484
Tree 2	((Laq,(((((Pic,Jol),Fre),Shi),Cop),Tra)),Ecn,Cam)	230	351	-2419.42±108.87(-0.8)	0.2626	-2863.78±102.18(-7.8)	0.0369
Tree 3	((Laq,(((((Pic,Jol),Fre),Shi),Tra),Cop)),Ecn,Cam)	228	349	-2419.54±109.61(-0.9)	0.2410	-2859.35±101.83(-3.4)	0.2996
Tree 4	((Laq,((((Pic,Jol),Fre),(Tra,Cop)),Shi)),Ecn,Cam)	226(MP)	348(MP)	-2423.61±109.48(-5.0)	0.2077	-2860.59±101.85(-4.6)	0.2151

Tree ID.	Tree topology	MP		ML			
				aa		1st+2nd	
		aa	1st+2nd	lnL	BP	lnL	BP
Tree 1	(Laq,((((Pic,Jol),Fre),Shi),(Tra,Cop)))	125	206	-1852.65±77.85(-5.5)	0.0715	-2183.02±75.88(-3.9)	0.0891
Tree 2	(Laq,(((((Pic,Jol),Fre),Shi),Cop),Tra))	124	206	-1847.14±77.19(ML)	0.6903	-2179.14±75.71(ML)	0.4130
Tree 3	(Laq,(((((Pic,Jol),Fre),Shi),Tra),Cop))	124	206	-1852.30±78.06(-5.2)	0.1245	-2182.64±75.92(-3.5)	0.1915
Tree 4	(Laq,((((Pic,Jol),Fre),(Tra,Cop)),Shi))	123(MP)	205(MP)	-1861.79±79.67(-14.6)	0.1137	-2182.97±76.15(-3.8)	0.3064

Figure 3. Summary of phylogenetic analysis showing the total maximum parsimony tree length, the log-likelihood (± standard errors) and the bootstrap probabilities for each of the plausible trees. Species name abbreviations: Laq = *Laqueus rubellus*, Pic = *Pictothyris picta*, Jol = *Jolonica nipponica*, Fre = *Frenulina sanguinolenta*, Shi = *Shimodaia pterygiota*, Tra = *Terebratalia coreanica*, Cop = *Coptothyris grayi*, Ecn = *Ecnomiosa* sp., Cam = *Campages* sp. Upper Box: relationships of 7 laqueoid genera with *Ecnomiosa* sp. and *Campages* sp. as outgroup. Lower Box: relationships of 6 laqueoid genera (*Shimodaia, Frenulina, Jolonica, Pictothyris, Coptothyris, Terebratalia*) with *Laqueus rubellus* as outgroup. aa: amino acid data. 1st + 2nd: nucleotide data of 1st and 2nd codon positions.

66%) in all analyses. The node of the *Shimodaia-Frenulina-Pictothyris-Jolonica* clade is supported by moderate to high LBPs (70-100%).

The MP analysis consistently supported Tree 4 (Figure 2). However, the tree length differences amongst the four trees are only one or two steps (Figure 3). Besides, the Retention Index (RI) for all four topologies was also relatively low (RI = 0.446-0.663), indicating that support for Tree 4 in MP analysis is not strong. When 500 bootstrap replicates were performed, the resulting consensus trees showed either unresolved trichotomy or the clustering of *Shimodaia-Frenulina-Pictothyris-Jolonica* with a low BP value (51-56%). It is known that the MP analysis is more susceptible to 'unequal rate effects' than the NJ or ML analysis, and can lead to a wrong tree when the nucleotide substitution rates greatly vary among different branches (Saitou and Imanishi, 1989). The observed branch length variation among the ingroup taxa (Figure 1) suggests that the tree indicated by the MP analysis may not be reliable.

These results lead to the conclusion that any one of Tree 1, 2, or 3 represents the best estimate of the true phylogeny, but the available *cox1* data being inadequate to make a final determination from among them. More data are needed to resolve the positions of *Terebratalia* and *Coptothyris*. Thus, the strict consensus tree of Trees 1 to 3 is proposed as a basis for reconstruction of laqueoid evolution.

Figure 4 gives the ML tree of 5 species of the genus *Laqueus*. Two coherent groups were assessed; (1) the Japanese group (*L. rubellus, L. blanfordi, L. quadratus*) and (2) the North American group (*L. californicus, L. c. vancouveriensis*). Each cluster was supported by a high LBP value (100%). The NJ and MP analyses yielded the
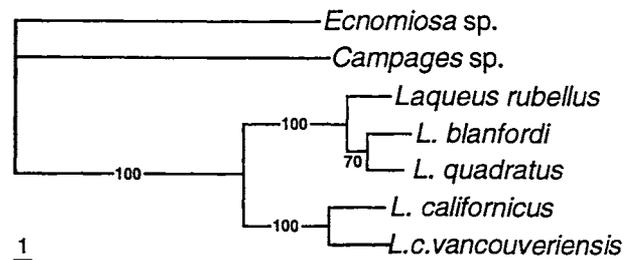
Figure 4. NJ tree of *cox1* nucleotide sequences for the relationships within the genus *Laqueus*. The same topology was obtained by other methods of analysis (MP and ML). The numbers in the tree represent LBP values.

same tree topology.

Character state distributions among laqueoid brachiopods

Molecular analyses of *cox1* sequences, as described above, provide a preliminary framework for the elucidation of phylogenetic relationships among some laqueoid brachiopods. Onto this molecular framework, we superimposed some morphological characters of those brachiopods, such as shell traits (outline, commissure shape and coloration), adult loop morphology, cardinalia at the annular phase of loop ontogeny, and type of the septal pillar at the axial phase (Figure 5). Details of the selected morphological characters for each species are summarized in Table 2. Loop ontogenetic series of laqueoid species are shown in Figure 6. Figure 7 illustrates hitherto undescribed early loop stages of *Terebratalia coreanica* and *Jolonica nipponica*.

Table 2.   Comparisons of selected morphological characters of 7 species of the Laqueoidea.

Species	maximum size (cm)	adult loop pattern	axial/annular septal pillar	cardinalia	cardinal process	deltidial plates in adult	ornament and coloration
Laqueus rubellus	3.5	bilateral	bifurcate	inner and outer hinge plates, inner resting on the median septum	absent	conjunct	yellowish red with stripes
Pictothyris picta	3.5	latero-vertical	nonbifurcate	no inner hinge plates, the cardinalia are divergent	present	conjunct	irregular divaricating stripes of white upon red background
Jolonica nipponica	2.5	bilacunar	nonbifurcate	divided hinge plates, with high crural-bases, hinge-sockets deep	present	conjunct	rose-red; some have intervening-bands of light yellow mottling.
Frenulina sanguinolenta	1.5	bilateral	nonbifurcate	the cardinalia bear disjunct, inner hinge-plates elevated well above the valve floor	present	disjunct in small conjunct in large	yellowish brown with short irregular red stripes marginally
Shimodaia pterygiota	0.7	incomplete annular	nonbifurcate	steeply dipping inner hinge plates which converge on a low median septum	absent	disjunct	red-mottled, with intervening bands of white mottling.
Terebratalia coreanica	5.9	trabecular	bifurcate	callus between the socket-ridges joined to septum	present	conjunct	red with layers of white, rather dull
Coptothyris grayi	5.0	teloform	bifurcate	callus deposit between the socket-ridges with which septum unites	present	disjunct	dull red with radial ribs

Shell shape and coloration.— Externally, laqueoid species exhibit great variability in shell size and shape. In this study, it became apparent that the only external shell character that supported phylogenetic relationships was the pattern of shell coloration (Figure 5; top and second row). All the species in the clade of *Shimodaia-Frenulina-Pictothyris-Jolonica* exhibit irregular red stripes or mottling patterns, while shells of others are radially striped (in *L. rubellus* and *T. coreanica*) or have uniform coloration (in *C. grayi*, *L. blanfordi*, *L. quadratus*, *L. californicus* and *L. c. vancouveriensis*). Other external characters, such as the type of the commissure and completeness of deltidial plates, did not show any systematic distribution on the molecular phylogenetic tree.

Adult loop morphology.—The adult loop pattern is often thought to represent phylogenetic affinity among laqueoid genera, and has been used as a key character to divide the superfamily into families and subfamilies. For example, *Laqueus* and *Frenulina* have often been included in the same subfamily (Kingeninae in Richardson, 1975; Laqueinae in Smirnova, 1984) based on their possession of a bilateral adult loop. A close relationship between *Pictothyris* and *Laqueus* has also been maintained based on similarity of external characters, as well as adult loop patterns; the adult laterovertical loop of *Pictothyris* has been considered to be at a stage one step more advanced than that of *Laqueus* (see Thomson, 1927; Hatai, 1940; Smirnova, 1984).

However, the results of the molecular study suggest that these interpretations, based on adult loop morphology, are not reliable. The three genera possessing a bilateral, or laterovertical, adult loop (Figure 5; third row; boxed) did not form a clade, supporting the conclusion that a bilateral loop appeared independently in the lineage leading to *Laqueus* and *Frenulina*.

Cardinalia.— The cardinal process is prominent in most laqueoids; however, species belonging to the genera *Laqueus* and *Shimodaia* lack it. The molecular phylogenetic tree indicates that the cardinal process may have been lost at least twice independently (Figure 5; fourth row). *S. pterygiota* possesses steeply dipping inner hinge plates

which converge on a low median septum to form a sessile septalium, comparable to that occurring in young *L. rubellus* and *Laqueus* sp. (Saito, 1996; MacKinnon *et al.*, 1997). This resemblance may also have resulted from parallel evolution.

Juvenile loop morphology.—At the axial phase of early loop development, when the median septum has a pair of flanges on its posterior part, the anterior part of the median septum bifurcates only in the basal species in the molecular phylogenetic tree, namely, *L. rubellus*, *C. grayi* and *T. coreanica* (Figure 5; fifth row). In all other species that form a clade, i.e., *F. sanguinolenta*, *P. picta*, *J. nipponica* and *S. pterygiota*, the septal pillar remain nonbifurcate until the annular phase (Figure 5; fifth row; boxed; Saito, 1996; MacKinnon *et al.*, 1997). Although the adult loop patterns may be misleading, early bifurcation of the septal pillar may be a useful character in assessing relationships among laqueoid genera.

Discussion

Laqueoid classification

Taxonomic assignments of the seven laqueoid genera investigated in this paper (*Laqueus*, *Terebratalia*, *Coptothyris*, *Shimodaia*, *Frenulina*, *Jolonica* and *Pictothyris*) have been controversial for a long time. Opinions as to which genera should be included in the family Laqueidae varied depending on the features that each author conjectured important. For example, Richardson (1973, 1975) considered the families Kingenidae, Macandreviidae and Laqueidae as synonymous, and proposed uniting them in the family Laqueidae, based on resorption patterns in loop development and the presence of dental plates. In this view, the seven ingroup genera compared in our molecular study are included in the family Laqueidae. Smirnova (1984) defined the Laqueidae as those with a loop of the late frenuliniform stage (i.e. bilacunar loop) or of more advanced stages, in which the connections between the ascending and descending branches remain joined to the septum at all stage. In so doing, she included a number of lower Cretaceous genera in the Laqueidae (*Zittellina*, *Zeuschneria*, *Tulipina*, *Waconella*),
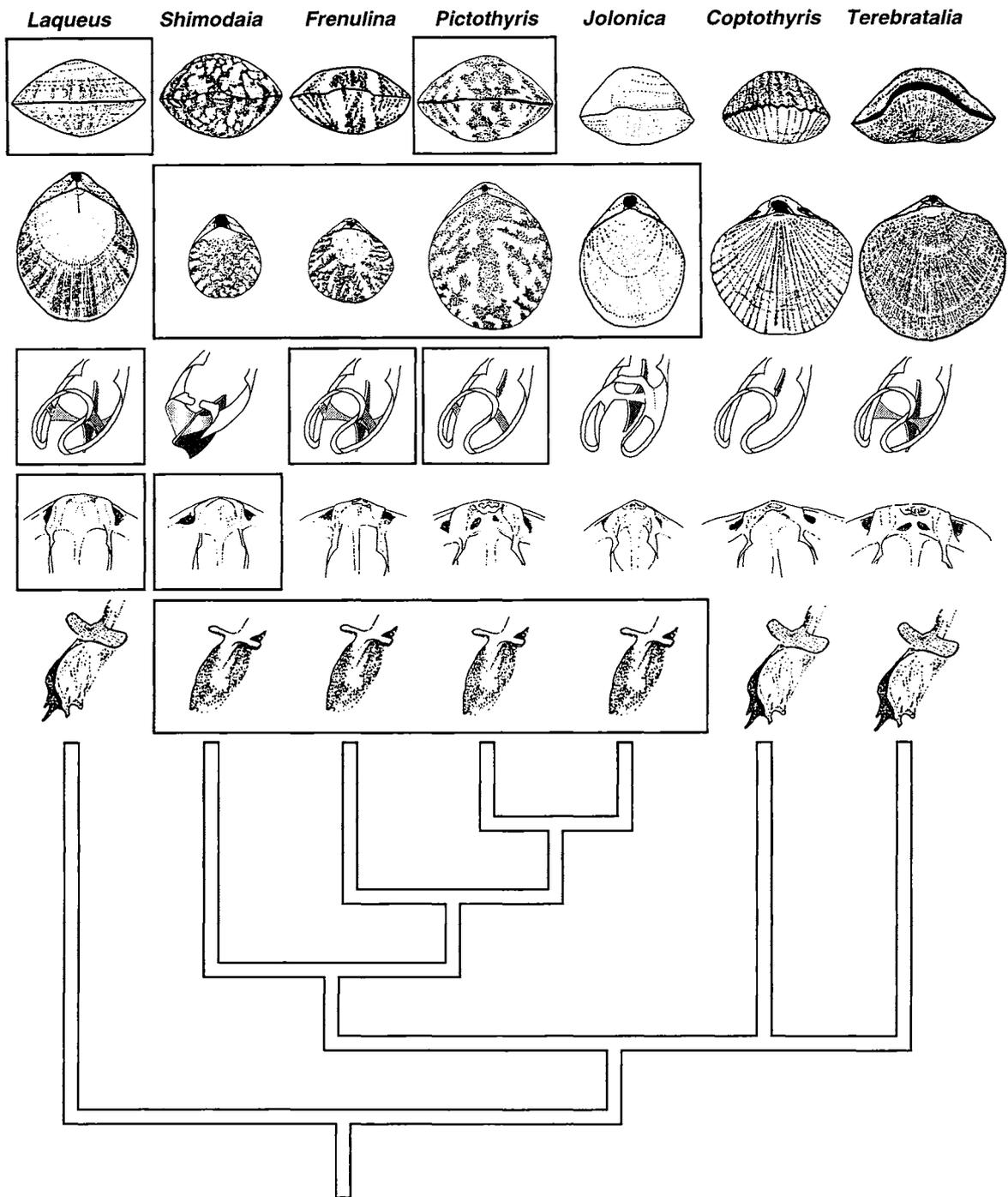
Laqueus   Shimodaia   Frenulina   Pictothyris   Jolonica   Coptothyris   Terebratalia

Figure 5. Morphological characters of laqueoid species superimposed on the molecular phylogenetic tree. The tree topology represents the consensus of the Trees 1, 2, and 3 (cf. Figure 3). Vertical lengths of the branches are arbitrary. Morphological characters (from top to bottom): anterior view of the shells; dorsal view of the shells; adult loop pattern; cardinalia in the annular phase; septal pillar at the axial phase. The drawings are not strictly to scale. The rectimarginate commisure of Laqueus and Pictothyris (top row; boxed) which was previously considered to be evidence uniting these genera, appeared separately in the molecular phylogenetic tree. In the shell external features, the red-white dot coloration (second row; boxed) supports a close relationship between Shimodaia, Frenulina, Pictothyris and Jolonica. Characters such as the adult bilateral or latero-vertical loop pattern (third row; boxed), and the absence of cardinal process (fourth row; boxed), do not reflect phylogeny. The non-bifurcation of the septal pillar in the axial phase (bottom row; boxed) supports the Shimodaia-Frenulina-Jolonica-Pictothyris clade.

but excluded certain genera such as *Terebratalia* and *Coptothyris*, which exhibited a trabecular or teloform adult loop pattern. Zezina (1984) elevated the subfamily Terebrataliinae (Richardson, 1975) to family status, and distinguished it from the Laqueidae that accommodated such genera as *Laqueus, Frenulina, Aldingia, Jolonica, Pictothyris, Compsoria* and *Ecnomiosa*. More recently, in summarizing the biogeography of articulated brachiopods, Richardson (1997) included 13 living genera in the family Laqueidae (*Coptothyris, Jolonica, Pictothyris, Terebratalia, Laqueus, Tythothyris, Simplicithyris, Frenulina, Ecnomiosa, Compsoria, Aldingia*, and two other undiscussed genera), but she did not provide explicit criteria for this classification.

Concerning the familial groupings of the seven Recent genera, the following two points can be drawn from the results of our *cox1* study. Firstly, in the rooted monophyletic cluster of laqueoids that included *Terebratalia* and *Coptothyris, Laqueus* branched off first, followed by a trichotomous cluster comprised of *Terebratalia , Coptothyris* and the subcluster of *Shimodaia, Frenulina, Jolonica*, and *Pictothyris* (Figure 5). Therefore, if *Terebratalia* and *Copthothyris* are excluded from the Laqueidae and included in the Terebrataliidae, then *Laqueus* and the remaining four genera (*Shimodaia, Frenulina, Jolonica*, and *Pictothyris*) should be accommodated in at least two separate families. A grouping including *Laqueus, Shimodaia, Frenulina, Jolonica*, and *Pictothyris* to the exclusion of *Terebratalia* and *Copthothyris* would be paraphyletic at best.

Secondly, in analyses of all the available terebratulide forms including other than laqueoids, *Ecnomiosa* branched off outside not only of the laqueoids, but also of the terebratelloids of the Southern Hemisphere (Saito et al., in press). Thus, on molecular grounds, the view of including *Ecnomiosa* in the family Laqueidae (Richardson, 1997) is not supported. MacKinnon and Gaspard (1996) reported that the descending branches of *Ecnomiosa* grow only from the crura unlike other long-looped brachiopods, justifying our conclusion based on loop ontogeny.

Inclusion of *Terebratalia* and *Coptothyris* and exclusion of *Ecnomiosa* imply that the adult loop morphology alone cannot be used as the prime character to define the Laqueoidea. Instead, presence of a pair of flanges on the septal pillar at the axial stage of loop ontogeny (Figure 8; Saito, 1996) and also the presence of dental plates in the ventral valve appear to be more explicit and better-suited character states to define this superfamily, and are to be incorporated as such in the diagnosis of the Laqueoidea in the forthcoming revised Treatise (MacKinnon, pers. comm., 2000).

Processes of loop evolution

Paedomorphosis.— It is evident from comparison of the ontogenetic sequences of the loop morphology (Figure 6) with phylogenetic relationships (Figure 5), that paedomorphic loop evolution occurred at least twice among laqueoids, in the lineages that produced *Shimodaia* and *Jolonica*. As discussed in MacKinnon *et al.* (1997), adult individuals of *Shimodaia* have an incomplete annular loop, the brachidial ring being incomplete due to resorption of the very narrow transverse band. Adult individuals of *Jolonica* dis-

play a bilacunar loop, a loop with two pairs of connecting bands (lateral and mediovertical), although the width of the bands are different from that in the bilateral loop such as that found in *Laqueus*. The adult loop phases of both *Shimodaia* and *Jolonica* are comparable with juvenile loop phases in other laqueid members, and based on the molecular cladograms (Figure 5), it is more parsimonious to consider the abbreviated ontogenies of *Shimodaia* and *Jolonica* as independent synapomorphies.

Williams and Hurst (1977) pointed out that the most significant trend within the post-Paleozoic long-looped terebratulides is the neotenous elimination of later stages of loop ontogeny and a simultaneous simplification of the lophophore. Our results indicate that such complex evolutionary processes have indeed been at work in laqueoids.

Bifurcation.— As reported by Richardson (1975) and Saito (1996), the loop ontogenies of laqueoid species appear to be roughly the same until the bilacunar phase. However, at the earlier axial phase, characterized by the development of septal flanges, two types of septal pillar can be recognized; in one form of septal pillar the anterior edge becomes bifurcate whereas in the other form of septal pillar the anterior edge is nonbifurcate (Saito, 1996; Figure 6). In *Laqueus* sp. (Figures. 8.1, 8.2), *T. coreanica* (Figure 8.3) and *C. grayi* (Figure 8.4), the septal pillar is anteriorly bifurcate. On the other hand, *Pictothyris* sp. (Figure 8.5), *Jolonica nipponica* (Figure 8.6), *F. sanguinolenta* (Figure 8.7) and *Shimodaia pterygiota* (Figure 8.8) all exhibit a nonbifurcate septal pillar and retain remains of projections until the annular phase (Figure. 9.5-9.8).

The results of molecular phylogeny indicate paraphyly for those with the bifurcate septal pillar (Figure 5). Thus, bifurcation is considered as the ancestral state and nonbifurcation a synapomorphy. Two Mesozoic laqueoid genera (*Gemmarcula* and *Trigonosemus*) show the anterior bifurcation of the septal pillar at the annular phase (Elliott 1947; Cooper 1955; Steinich 1965). This observation accords well with our contention that anterior bifurcation of the septal pillar is an ancestral character (Figure 5).

Evolution of Bilateral Loop.— As discussed earlier, the *cox1* results indicated that species with a bilateral adult loop did not form a monophyletic cluster (Figure 5). Two interpretations are possible for the evolution of the bilateral loop; one is that parallel evolution occurred, i.e., the bilateral loop evolved twice independently, and the other is that the bilateral loop is a plesiomorphic character.

The former interpretation tends to be supported by the fact that the two Cretaceous laqueoid genera, *Gemmarcula* and *Trigonosemus*, possess a trabecular loop. But the latter interpretation becomes equally possible if another genus such as *Waconella* from the Lower Cretaceous that has a bilateral loop in the adult phase is taken into consideration. *Waconella* has been considered as one of the members of the ancestral group from which *Laqueus* is derived, because of the possession of the same type of adult loop, cardinalia and shell shape, as well as the close geographical distribution with other laqueoid genera (Owen, 1970; Smirnova, 1984). Since a deep diversification between *Laqueus* and other laqueoid genera is inferred from the *cox1* analysis, this connection between *Waconella* and *Laqueus* seems quite

anterior
bifurcation
of the septum

fl

fl

Coptothyris

teloform

bilacunar

Shimodaia

"annular"

Jolonica

bilacunar

Terebratalia

trabecular

Laqueus *Frenulina*

bilateral

Pictothyris

latero-vertical

Figure 6.

Figure 7.

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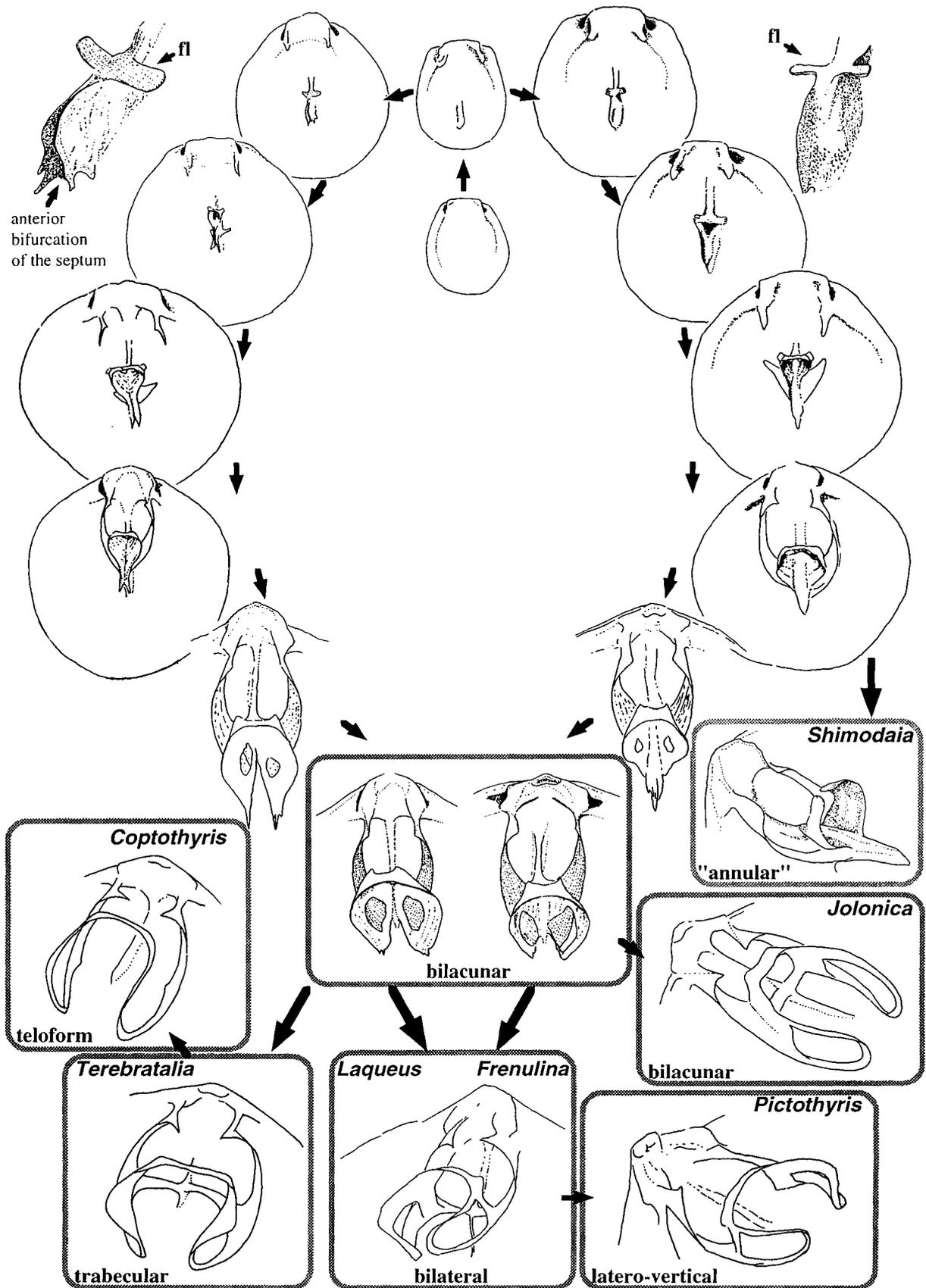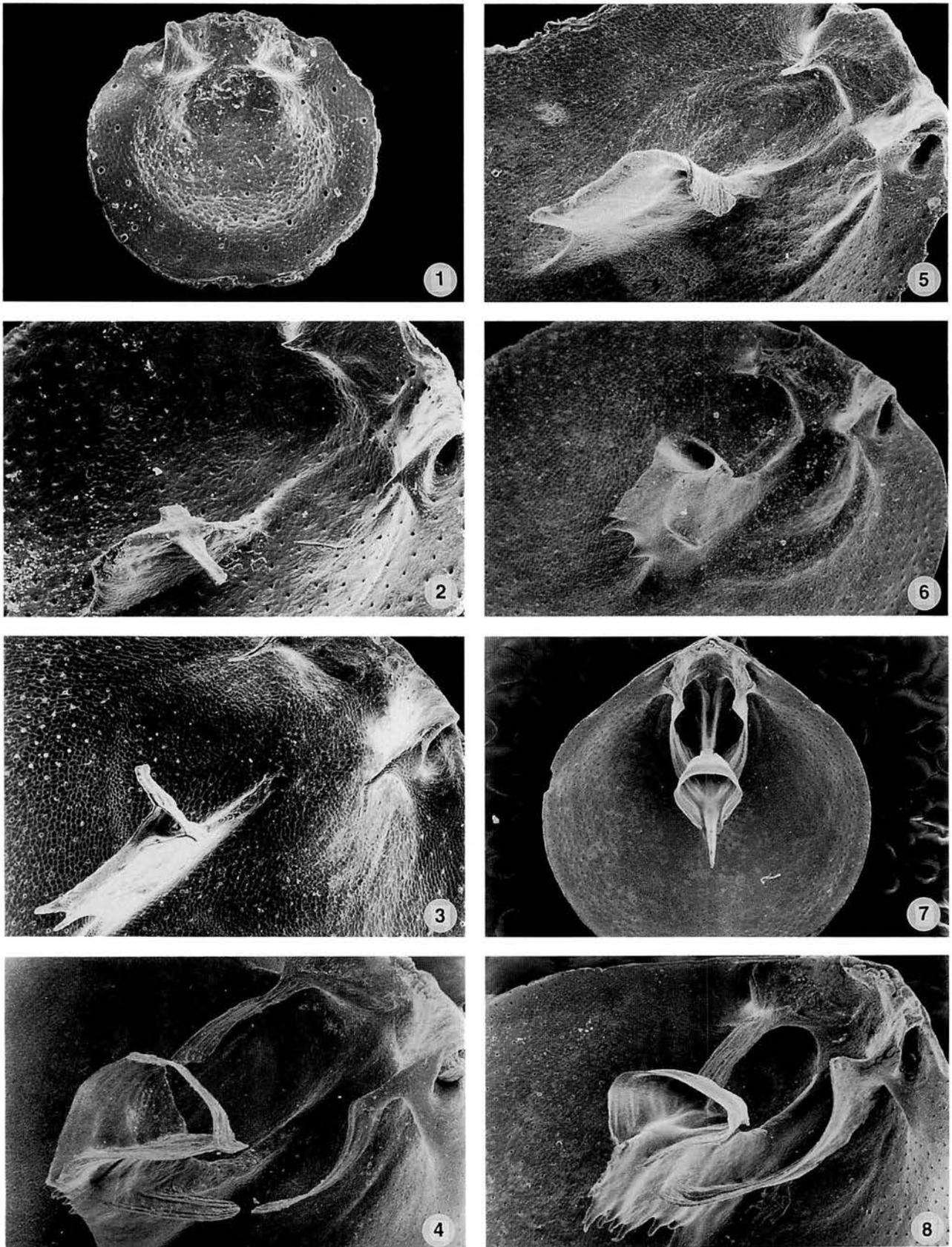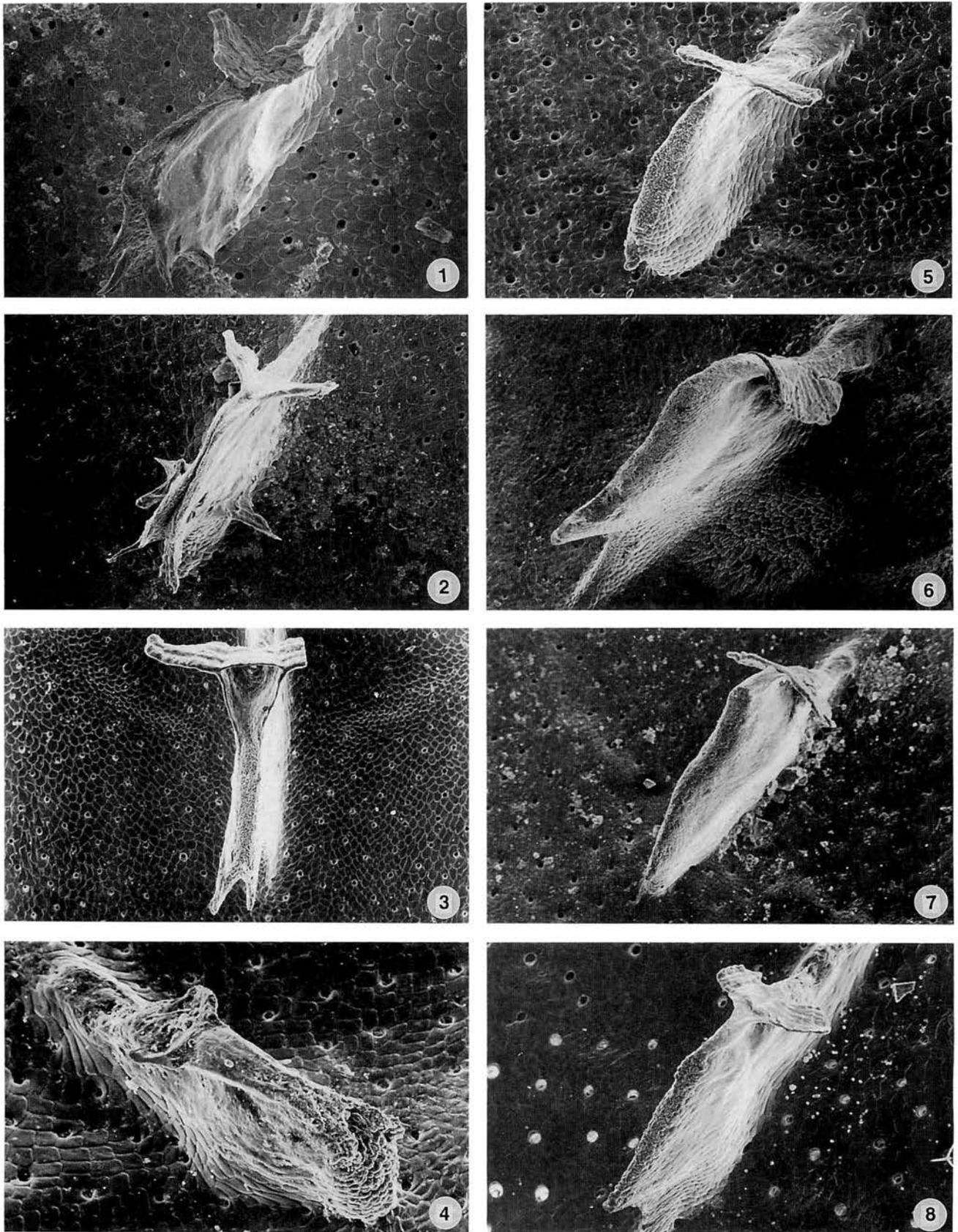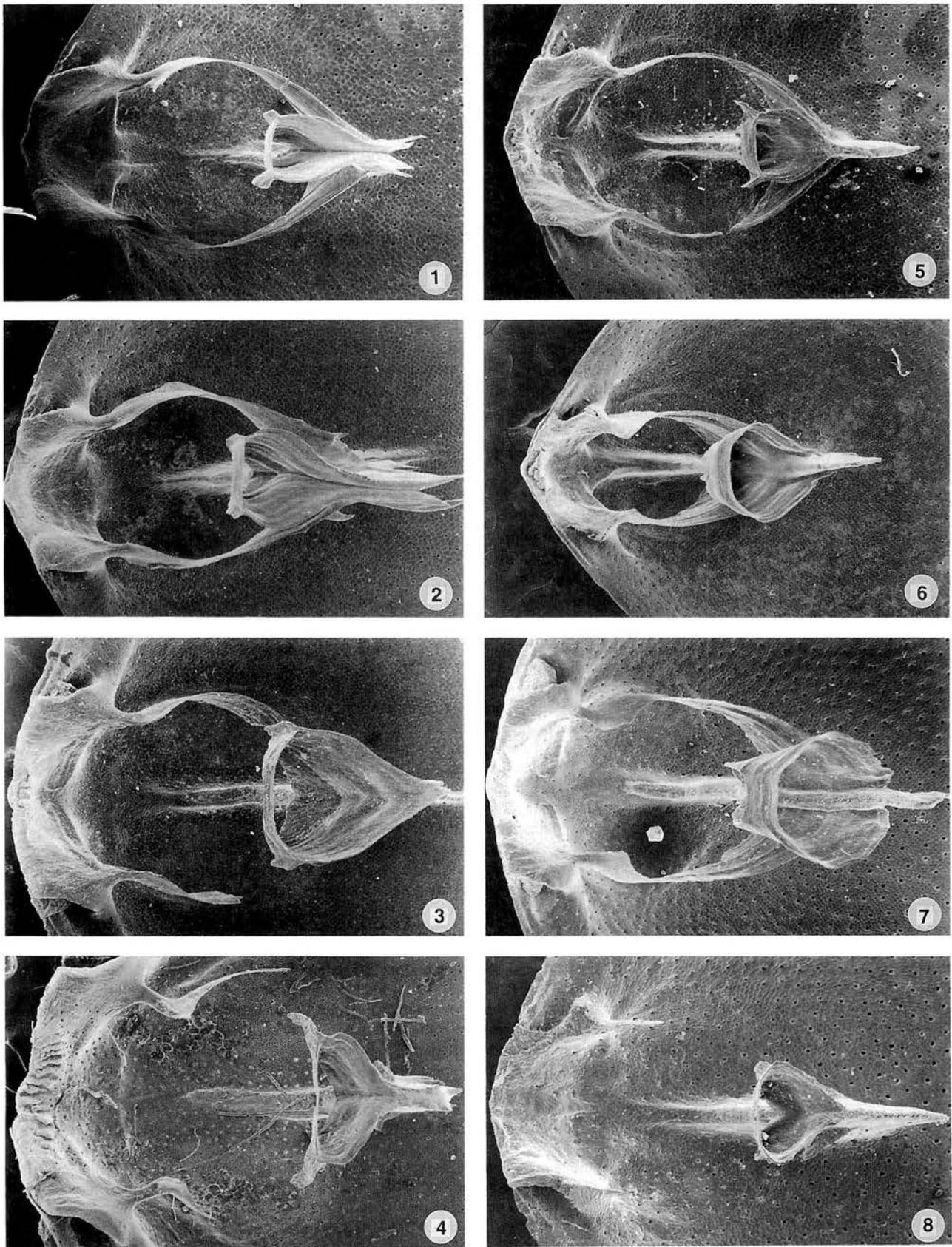

Figure 8.

Figure 9.

probable, although the oldest fossil record of *Laqueus* is middle Miocene (Hatai, 1938). However, the early loop ontogeny of this genus is not reported, and it is not known whether *Waconella* has the laqueoid character of the flanges at the axial phase. The ancestral state of the laqueoid loop, therefore, cannot be established at present based on the morphology of fossil forms. The relationships of Mesozoic genera to the Cenozoic ones should become clearer when the early loop ontogenies, especially at the axial and annular phases of Mesozoic genera, are further examined.

Conclusions

Molecular phylogenetic analysis using the *cox1* gene suggests that only a few morphological characters, such as coloration of the shell and bifurcation of the septal pillar, may be of use in deciphering the phylogenetic relationships of laqueoids. Other characters like cardinalia, external morphologies of the shell, notably, adult loop patterns, all of which have previously been considered as taxonomically important, are likely to have undergone a complex evolutionary history, and thus have to be treated with caution when used in taxonomic studies.

Reconstruction of the relationships of fossil and Recent terebratulide brachiopods is reliant mainly on the morphology of hard parts such as the shell, the loop and occasionally spicules, i.e., characters that can relatively easily be preserved in fossils. In addition, careful observations of early loop development, especially of the fossil taxa, would be useful in filling existing gaps in the fossil record of the Laqueoidea and other superfamilies, and in resolving evolutionary relationships among fossil and Recent species. In any event, it appears important to evaluate the taxonomic value of each character, by means of molecular phylogeny of living species, to help clarify the phylogenetic history of terebratulide brachiopods and of other organisms in general.

Figure 6. Loop ontogeny of the living laqueoid genera studied. Drawings are not to scale. The Laqueoidea is characterized by the presence of a pair of flanges (fl) on the septal pillar at the axial phase, and the patterns of ring resorption to produce the bilacunar loop pattern. The route to the bilacunar phase is two-fold; one with (left) and one without (right) anterior bifurcation of the median septum. The common bilacunar pattern for two types and adult patterns are boxed. Note that ontogenetic sequences to the adult patterns do not necessarily correspond with the phylogenetic relationships revealed by the molecular data.

Figure 7. Scanning electron microscopic images of early loop morphologies for *Terebratalia* and *Jolonica*. 1-4. *Terebratalia coreanica*. **1.** Dorsal view, specimen UMUT RB28050 (L = 0.6 mm: L is the length of the dorsal valve), displays no loop-supporting structure (Prebrachidial phase), x77. **2.** A specimen 1.5 mm in length shows septal flanges (Axial phase; oblique view), specimen UMUT RB28051, x63. The anterior part of the septal pillar is bifurcate. Cardinal process begins to develop during this stage. **3.** Specimen UMUT RB28052 (L = 2.2 mm) displays a small hood with rudiments of the flanges, x48. Crura extend from areas at the base of the inner socket ridges. **4.** Oblique view of the specimen UMUT RB28053 (L = 4.0 mm), showing the ring which retains the rudiments of the flanges (Annular phase), x32. The anterior part of the median septum is bifurcate. The descending branches extend further toward one another, albeit still unconnected. Further development of *Terebratalia coreanica* as those figured in Saito (1996). 5-8. *Jolonica nipponica*. **5.** Lateral view of the smallest specimen UMUT RB28054 (L = 2.7 mm) displaying flanges (Axial phase), x37. Note that the ventral edge of the septal pillar is non-bifurcate. Crura project out from near the base of each inner socket ridge. **6.** Posterodorsal view of the second smallest specimen UMUT RB28055 (L = 3.2 mm), showing a small hood, and small plates (future descending branches) on the septal pillar (Cucullate phase), x30. The crura and the descending branches extend further toward one another. 7-8. Annular phase. **7.** Dorsal view of a larger specimen UMUT RB28056, (L = 3.8 mm) showing the annular phase loop and well developed cardinal process, x15. **8.** Oblique view of the annular phase loop of the same specimen as in Fig. 8.6, showing the anteriorly spinose septal pillar and the ring with rudiments of the flanges. The septal pillar is spinous, but remains non-bifurcate, x31.

Figure 8. Comparison of the median septum morphology at the axial phase among laqueoid species. **1.** *Laqueus* sp. (L = 1.9 mm), specimen UMUT RB28057, x155. **2.** *Laqueus* sp. (L = 1.9 mm), specimen UMUT RB19819, x114. **3:** *Terebratalia coreanica* (L = 2.2 mm), specimen UMUT RB28052, x73. **4.** *Coptothyris grayi* (L = 1.3 mm), specimen 28498 in the collection of Tohoku University, x228. **5.** *Pictothyris* sp. (L = 1.5 mm), specimen UMUT RB19830, x113. **6.** *Jolonica nipponica* (L = 2.7 mm), specimen UMUT RB28054, x63. **7.** *Frenulina sanguinolenta* (L = 2.0 mm), specimen UMUT RB28058, x77. **8.** *Shimodaia pterygiota* (L = 1.54 mm), specimen UMUT RB28059, x120.

Figure 9. Comparative views of cardinalia at the annular phase in eight laqueoid species. **1.** *Laqueus* sp. (L = 2.7 mm), specimen UMUT RB19821, x39. **2.** *Laqueus blanfordi* (L = 3.7 mm), specimen UMUT RB28060, x30. **3.** *Terebratalia coreanica* (L = 4.0 mm), specimen UMUT RB28053, x30. **4.** *Coptothyris grayi* (L = 2.3 mm), specimen UMUT RB28061, x31. **5.** *Pictothyris* sp. (L = 2.5 mm), specimen UMUT RB19836, x37. **6.** *Jolonica nipponica* (3.8 mm), specimen UMUT RB28056, x24. **7.** *Frenulina sanguinolenta* (L = 3.9 mm), specimen UMUT RB28062, x30. **8.** *Shimodaia pterygiota* (L = 2.2 mm), specimen UMUT RB28063, x48.

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The genus *Hourcquia* (Ammonoidea, Pseudotissotiidae) from the Upper Cretaceous of Hokkaido, Japan: biostratigraphic and biogeographic implications

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Abstract. Stratigraphic and ontogenetic descriptions of three species of *Hourcquia* from the Cretaceous Yezo Supergroup of Hokkaido, Japan are given for the first time. *H. ingens, H. hataii* and *H. kawashitai* occur in the *Inoceramus teshioensis* Zone of the upper Turonian. *Hourcquia* evolved and radiated in not only the Tethyan and adjacent areas but also the Northwest Pacific region for a short period in the late Turonian.

Key words: Ammonoid, Hokkaido, *Hourcquia*, late Turonian, Yezo Supergroup

Introduction

The genus *Hourcquia* Collignon, 1965 of the family Pseudotissotiidae is characterized by having trapezoidal whorl sections with a rounded keel, coarse ribs, and umbilical and ventrolateral tubercles. Species of the genus are known to occur from the upper Turonian of Madagascar (Collignon, 1965), Venezuela (Renz, 1982), New Mexico, and Texas (Anonymous, 1981). These areas belong to the Tethyan and surrounding realms.

Distribution of the present genus extends also to the northwest Pacific region. Five species of *Hourcquia* are known from the Cretaceous Yezo Supergroup of Hokkaido, Japan (Hashimoto, 1973; Matsumoto and Obata, 1982; Matsumoto and Toshimitsu, 1984; Toshimitsu and Maiya, 1986) and Sakhalin, Russia (Matsumoto, 1970). However, no detailed analysis has been undertaken of their exact stratigraphic occurrences and variations of shell growth. Further work based on better material is desirable for elucidating the ontogeny, biostratigraphy and biogeography of the genus.

Recently, we collected several well-preserved specimens referable to *Hourcquia* from the Cretaceous Yezo Supergroup in the Ikushumbetsu, Miruto and Haboro areas, Hokkaido (Figure 1). In this paper, we describe three species of the genus and discuss their biostratigraphic and biogeographic implications.

Note on stratigraphy

The Cretaceous Yezo Supergroup consists of clastic deposits in a forearc basin. The supergroup is widely distributed in the median zone of Hokkaido (Figure 1) and is divided into four groups, the Lower Yezo, Middle Yezo, Upper Yezo and Hakobuchi groups in ascending order (Okada, 1983).

Ikushumbetsu and Miruto areas

The Middle and Upper Yezo groups, ranging from the Albian to Santonian stages, are exposed along the Ikushumbetsu and Horomui rivers and their tributaries. The Middle Yezo Group is subdivided into the lower-lying 'Main Part' (Matsuno et al., 1964) and the Mikasa Formation (Matsumoto, 1951). The former consists of well-bedded sandstone or laminated mudstone with sandstone intercalations. The latter consists mainly of sandstone exhibiting hummocky cross-stratification; it is subdivided into four units, Ta of sandstone, Tb of sandstone to muddy sandstone, Tc of mudstone, and Td of sandstone to muddy sandstone, in ascending order (Matsuno et al., 1964). The Upper Yezo Group consists mainly of sandy mudstone in the lower part and homogenous fine-grained mudstone in the
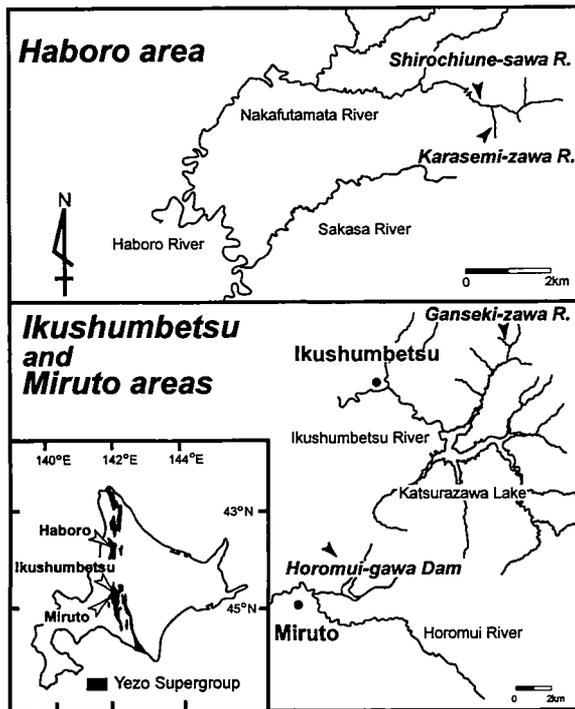
Figure 1. Maps of the Haboro and Ikushumbetsu-Miruto areas showing the localities of the *Hourcquia* species examined.

upper part. The group conformably overlies the Mikasa Formation, although the lithologic boundaries are diachronous (Ando, 1990).

The specimen assigned to *Hourcquia ingens* was obtained from the lower part of the Upper Yezo Group along the Ganseki-zawa, a stream of the Ikushumbetsu River (Figure 1). This part consists mainly of intensively bioturbated sandy mudstone with intercalations of discontinuous sandstone beds, interpreted as distal storm-sheets on the outer shelf. That specimen is associated with *Subprionocyclus minimus* and *Inoceramus teshioensis* (Figure 2), which are diagnostic fossils of the upper part of the upper Turonian (see Toshimitsu *et al.*, 1995).

The specimen assigned to *Hourcquia kawashitai* was found in the unit Td of the Mikasa Formation, composed of muddy bioturbated sandstone of inner-shelf type, near the Horomui-gawa Dam of the Miruto area. Ando (1990) refers the stratigraphic level of the locality to the upper Turonian.

Haboro area

The Middle and Upper Yezo groups, ranging from the middle Turonian to lower Campanian stages, are exposed in the upper reaches of the Haboro River. The Shirochi Formation of the Middle Yezo Group consists of mudstone with intercalations of thin turbidite-sandstone beds (Toshimitsu, 1985). The Upper Yezo Group conformably overlies the Shirochi Formation and consists mainly of mudstone in the lower part and mudstone with intercalations of thin sandstone in the middle part, while the upper part coarsens upward, beginning with mudstone and ending with cross-bedded sandstone (Toshimitsu, 1985).

The specimens determined as *Hourcquia hataii* were extracted from calcareous concretions in float along the Shirochiune-sawa and Karasemi-zawa valleys. The Shirochi Formation of offshore mudstone is distributed in this area and correlated with the *Inoceramus teshioensis* Zone of the upper Turonian (Toshimitsu and Maiya, 1986). Those specimens were found associated with *Subprionocyclus neptuni* and *Inoceramus teshioensis* in the concretions.

Repository of specimens.—The specimens described and figured herein are reposited in the National Science Museum, Tokyo with prefix of NSM PM and in the Institute of Geoscience, University of Tsukuba (formerly the Institute of Geology and Mineralogy, Tokyo University of Education) with prefix of TKU.

Abbreviations.—D = shell diameter; NSM PCL = National Science Museum, Paleontological Collection Locality.

Systematic descriptions

Superfamily Acanthoceratoidea Grossouvre, 1894
Family Pseudotissotiidae Hyatt, 1903
Subfamily Hourcquiinae Renz, 1982
Genus *Hourcquia* Collignon, 1965

Type species.— *Hourcquia mirabilis* Collignon, 1965.

Hourcquia ingens Collignon, 1965

Figures 3a–d, 4, 5

Hourcquia ingens Collignon, 1965, p. 80, pl. 412, figs. 1704–1706, pl. 413, fig. 1708; Matsumoto and Obata, 1982, p. 79, pl. 4, fig. 2a–c.
Hourcquia ingens var. *antsakoazatensis* Collignon, 1965, p. 82, pl. 413, figs. 1707, 1710.

Type.—Holotype is the original of Collignon (1965, p. 80, pl. 412, fig. 1704), from the Masiaposa area, Madagascar.

Material.—One specimen, NSM PM16159. Shell moderately large, 110 mm in D at preserved last septum, and consists of only phragmocone.

Locality. —NSM PCL 4–15–3 [= Loc. 319 in Futakami (1986)]: a cliff along Ganseki-zawa, a tributary of the Kami-ichino-sawa River in the Ikushumbetsu area, Hokkaido (Figure 1).

Description.—Coiling moderately involute, with fairly narrow and deep umbilicus, rounded umbilical shoulder, and gently convex to nearly vertical umbilical wall. Shell surface ornamented, more distinctively on inner whorls, with prorsiradiate ribs tuberculated at umbilical and ventrolateral shoulders, springing in pairs from umbilical tubercles and intercalated shorter ones. Whorl cross-section subtrapezoidal on inner whorls and subtriangular on outer preserved whorl, with maximum breadth at umbilical tubercles; rounded keel on fastigate venter, obtuse ventrolateral shoulder. Lateral lobe of suture line asymmetrically divided and deeply incised (Figure 5).

Comparison. — The immature shell described as *Hourcquia ingens* by Matsumoto and Obata (1982, pl. 4, fig. 2a–c) from Hokkaido is more involute than our specimen
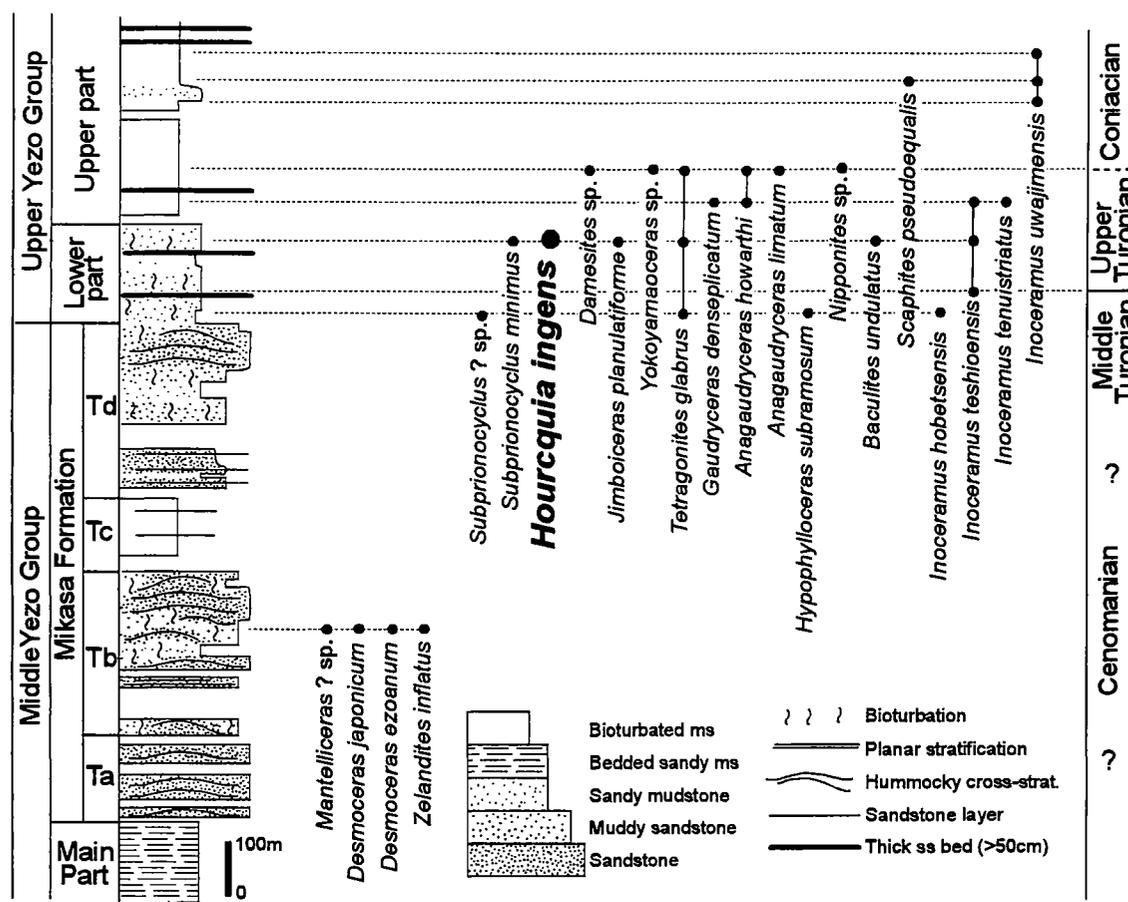
Figure 2.　Columnar section and stratigraphic distribution of ammonoids and inoceramids along the Ganseki-zawa Valley, Ikushumbetsu.　*Hourcquia ingens* Collignon occurs from the lower part of the Upper Yezo Group, in association with *Subprionocyclus minimus* (Hayasaka and Fukada), an index ammonite of the uppermost part of the upper Turonian in Japan.

NSM PM16159.　The specimens from Madagascar display wide variation in the width of the umbilicus during the immature growth-stage (Collignon, 1965, figs. 1705, 1706, 1708, 1710).　Both specimens from Japan are included in the range of variation for the species.

Hourcqia ingens closely resembles *Hourcquia moralesi* Renz (1982, p. 104, pl. 34, fig. 2) from the upper Turonian of Venezuela in having a subtriangular whorl section and bifurcated, intercalated and projected ribs.　The latter is, however, distinguished from the former in retaining the ornamentation until a late growth-stage.

Occurrence. — Upper Turonian, *Coilopoceras requieni-Romaniceras deveriai* Zone in Madagascar.　Upper part of the upper Turonian, *Subprionocyclus minimus* Subzone of *Inoceramus teshioensis* Zone in Hokkaido, Japan.

Hourcquia hataii Hashimoto, 1973

Figure 6a-j, 7, 8

Hourquia hataii Hashimoto, 1973, p. 316, pl. 35, text-fig. 2.

Type.—Holotype (TKU30492), by monotypy, is the specimen figured by Hashimoto (1973, pl. 35) from the

Nigorikawa River (Loc. 6373114p) in the Teshio area, northern Hokkaido.

Material.—Two specimens extracted from calcareous concretions in float along the Shirochiune-sawa Valley and its small tributary, the Karasemi-zawa Valley, in the Haboro area, Hokkaido are used in the following description: NSM PM16161, from the same place as Loc.　RH2096 in Toshimitsu (1985), consists mainly of phragmocone of 70 mm in D at depressed apertual part; NSM PM16162, from the lower course of the Karasemi-zawa Valley, 30 mm in D at compressed apertual part.

Description. — Shell displays large ontogenetic variation (Figures 6a-j).　In initial growth-stage (D < 5 mm), shells involute with depressed whorl section.　Immature (5 < D < 50 mm), shells evolute with, firstly, compressed whorl section and less ornamentation on shell surface, and, later, subtrapezoidal whorl section, rounded keel, bifurcated and intercalated ribs, and ventral and umbilical bullae.　At later growth-stage (D > 50 mm), shell involute with steep umbilical wall; whorl cross-section then subtrapezoidal with strong ventrolateral and umbilical tubercles and rounded broad keel.

Initial chamber elliptical in median section (Figure 7),
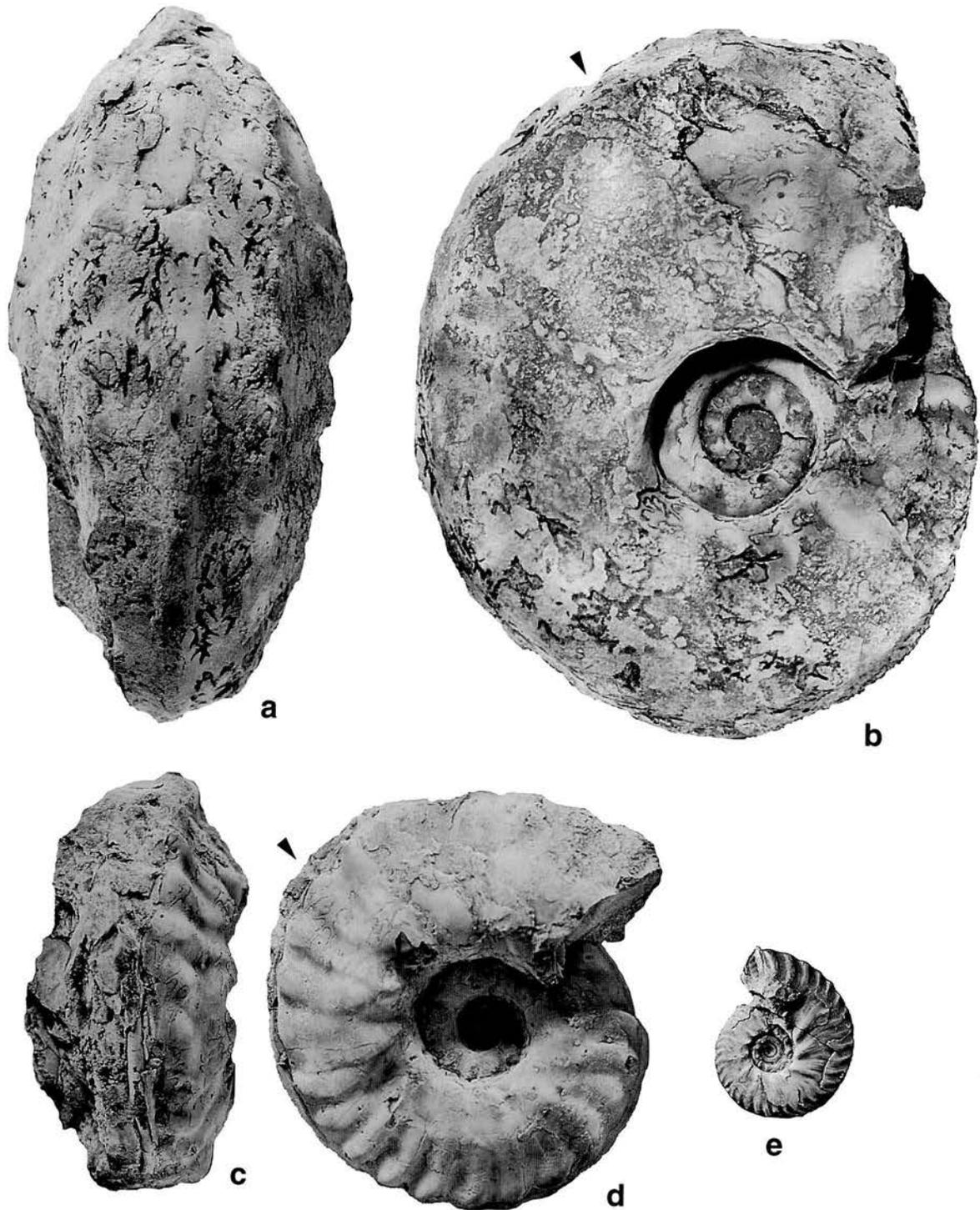
Figure 3. **a–d.** *Hourcquia ingens* Collignon, NSM PM16159, from NSM PCL 4–15–3 [= the locality 319 in Futakami (1986)], Ikushumbetsu, ×1.0. **c, d.** Inner whorls of a and b. Note the change of shell shape and ornamentation through growth. Dimensions for each growth-stage observed at the solid arrows. b; D (shell-diameter) = 104.0 mm, U (umbilical-diameter) = 25.1 mm, B (whorl-breadth) = 53.6 mm, H (whorl-height) = 47.5 mm; d; D = 65.5mm, U = 16.8 mm, H = 27.0 mm. **e.** *Subprinocyclus minimus* (Hayasaka and Fukada), NSM PM16163, from NSM PCL 4–15–3, Ikushumbetsu, ×1.2.

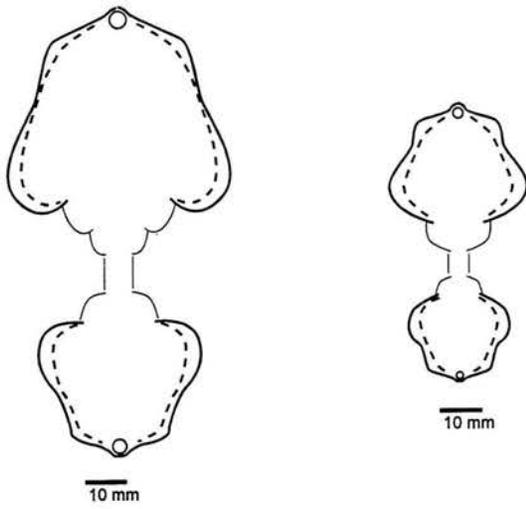**Figure 4.** Median cross sections of *Hourcquia ingens* Collignon, NSM PM16159 showing the ontogenetic change of whorl-shape (right to left). The dashed line shows the inter-costal whorl cross-section.
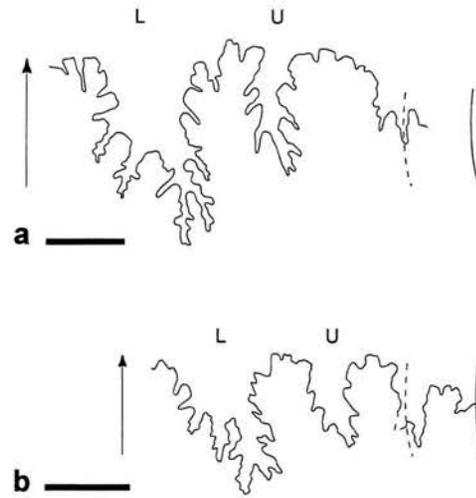

Figure 5. Suture line of *Hourcquia ingens* Collignon, NSM PM16159. **a**. Whorl-height = 24.4 mm. **b**. Whorl-height = 21.3 mm. Scale bars = 5.0 mm. L; lateral lobe, U; umbilical lobe.
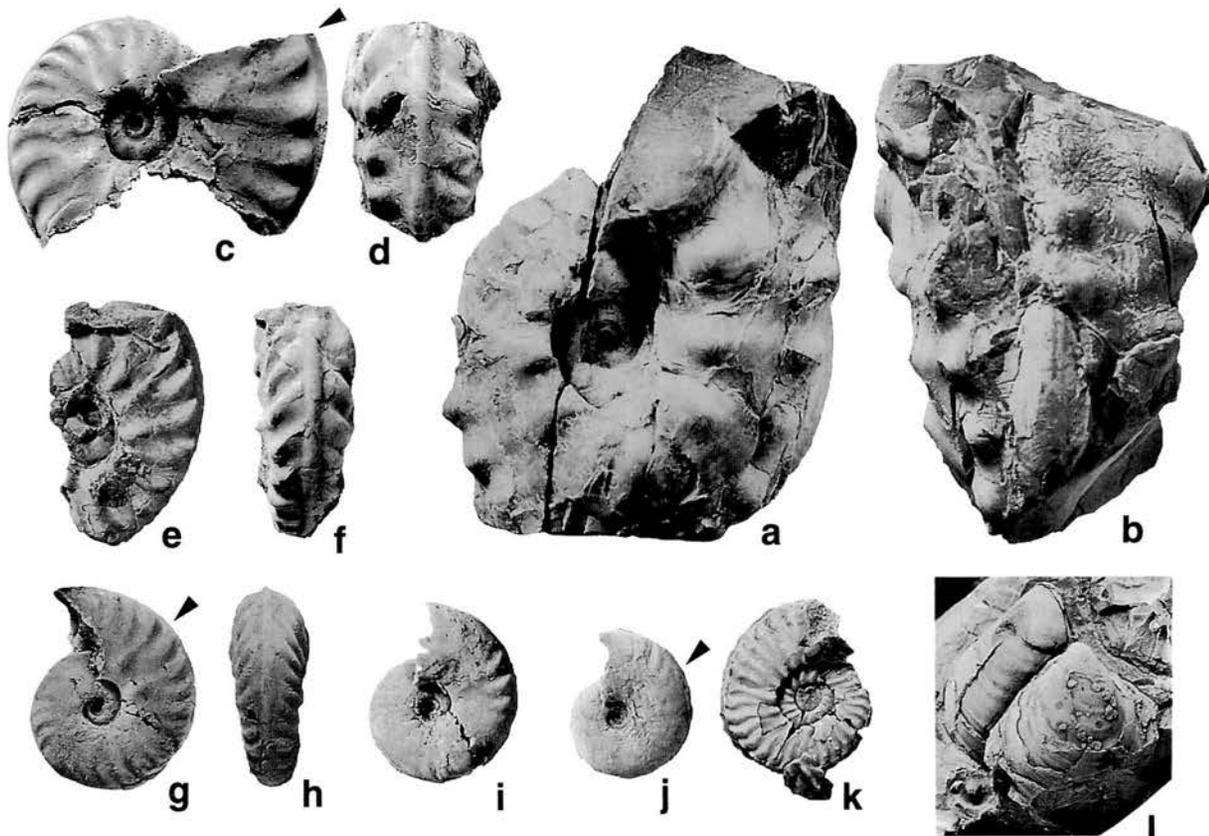
Figure 6. a–j. *Hourcquia hataii* Hashimoto. **a, b**. NSM PM16161, from the Shirochiune-sawa River, ×1.0. **c, d**. Inner whorls of a and b [NSM PM16161], ×1.0. **e, f**. NSM PM16162, from the Karasemi-zawa River, ×1.0. **g, h**. Inner whorls of a and b [NSM PM16161], ×1.0. **i, j**. Inner whorls of a and b [NSM PM16161], ×1.2. Note the change of shell-shape and ornamentation throughout growth. Dimensions for each growth-stage observed at the solid arrows. c; D = 43.0 mm, U = 8.5 mm, B = 20.2 mm, H = 20.2 mm: g; D = 23.4 mm, U = 5.7 mm, B = 9.2 mm, H = 10.6 mm: j; D = 12.7 mm, U = 2.7 mm, B = 5.8 mm, H = 6.0 mm. **k**. *Subprionocyclus neptuni* (Geinitz), NSM PM16164, associated with NSM PM16162, ×1.2. **l**. *Inoceramus teshioensis* Nagao and Matsumoto, NSM PM16165, associated with NSM PM16161, ×1.2.

Figure 7. a. Median cross sections of *Hourcquia hataii* Hashimoto, NSM PM16161 showing the ontogenetic change in whorl-shape (right to left). The dashed line shows the inter-costal whorl cross-se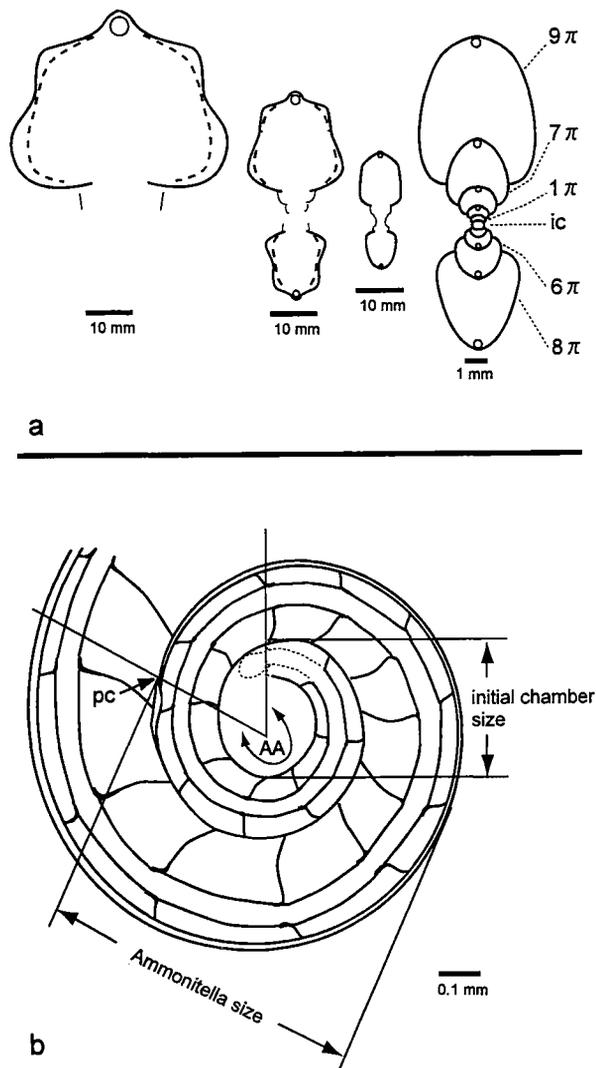ction. Angles for whorl-diameter are measured from the base of the caecum (see b). ic; initial chamber. b. Early internal shell structure of *Hourcquia hataii*, NSM PM16161 showing measurements of initial chamber size, ammonitella size, and ammnonitella angle (AA). The ammonitella angle is defined as the angle from the base of the caecum to the primary constriction (pc).
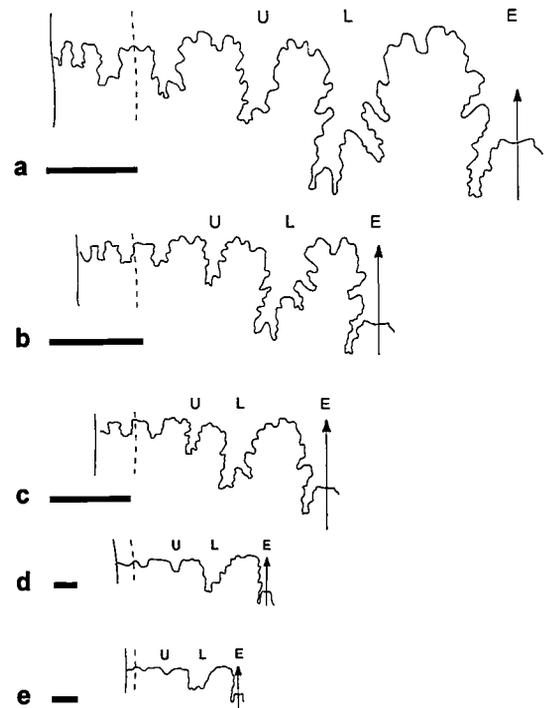

Figure 8. Suture line of *Hourcquia hataii* Hashimoto, NSM PM16161. a. Whorl-height = 20.5 mm. b. Whorl-height = 14.1 mm. c. Whorl-height = 10.3 mm. d. Whorl-height = 5.7 mm. e. Whorl-height = 4.0 mm. Scale bars for a–c = 5.0 mm, for d, e = 1.0 mm. E; external lobe, L; lateral lobe, U; umbilical lobe.

measuring 0.46 mm in diameter. Siphuncular tube occupying subcentral position in first whorl and subsequently moving towards ventral side in second whorl. Ammonitella size and angle in median section 0.78 mm and 303° respectively. Lateral lobe of suture line asymmetrically divided and deeply incised (Figure 8).

Comparison. — *Hourcquia hataii* closely resembles *Hourcquia mirabilis* from Madagascar (Collignon 1965, p. 77, fig. 1703) and *H. krausei*, monotypic, from Venezuela (Renz 1982, p. 104, pl. 34, fig. 1) in respect of the strong

ventrolateral and umbilical tubercles on the subtrapezoidal whorl in the later growth-stage. The latter two are distinguished from the former in having a concavely impressed spiral band on the flank.

Discussion. —The monotypic holotype of *Hourcquia hataii* was extracted from a calcareous concretion in float without any age-diagnostic information; Hashimoto (1973) interpreted the horizon as being Coniacian. We found two specimens referable to *H. hataii* together with *Inoceramus teshioensis* and *Subprionocyclus neptuni* (Figure 6k, l) in the same concretions. Since the latter is diagnostic of the Upper Turonian, we revise the stratigraphic occurrence of the present species to within the Upper Turonian.

Occurrence. — Upper Turonian, *Inoceramus teshioensis* Zone, Hokkaido, Japan.

Hourcquia kawashitai Matsumoto and Toshimitsu, 1984

Figures 9–12

Hourquia kawashitai Matsumoto and Toshimitsu, 1984, p. 233, pl. 32, figs. 1, 2; pl. 33, figs. 1–3; pl. 34, fig. 2, text-figs. 2, 3.

Type. — Holotype, YKC.57 – 6 – 20 – E, Y. Kawashita's Collection, is the original of Matsumoto and Toshimitsu (1984, pl. 32, fig. 1), from the Karasemi-zawa Valley in the Haboro area, northwestern Hokkaido (Figure 1).

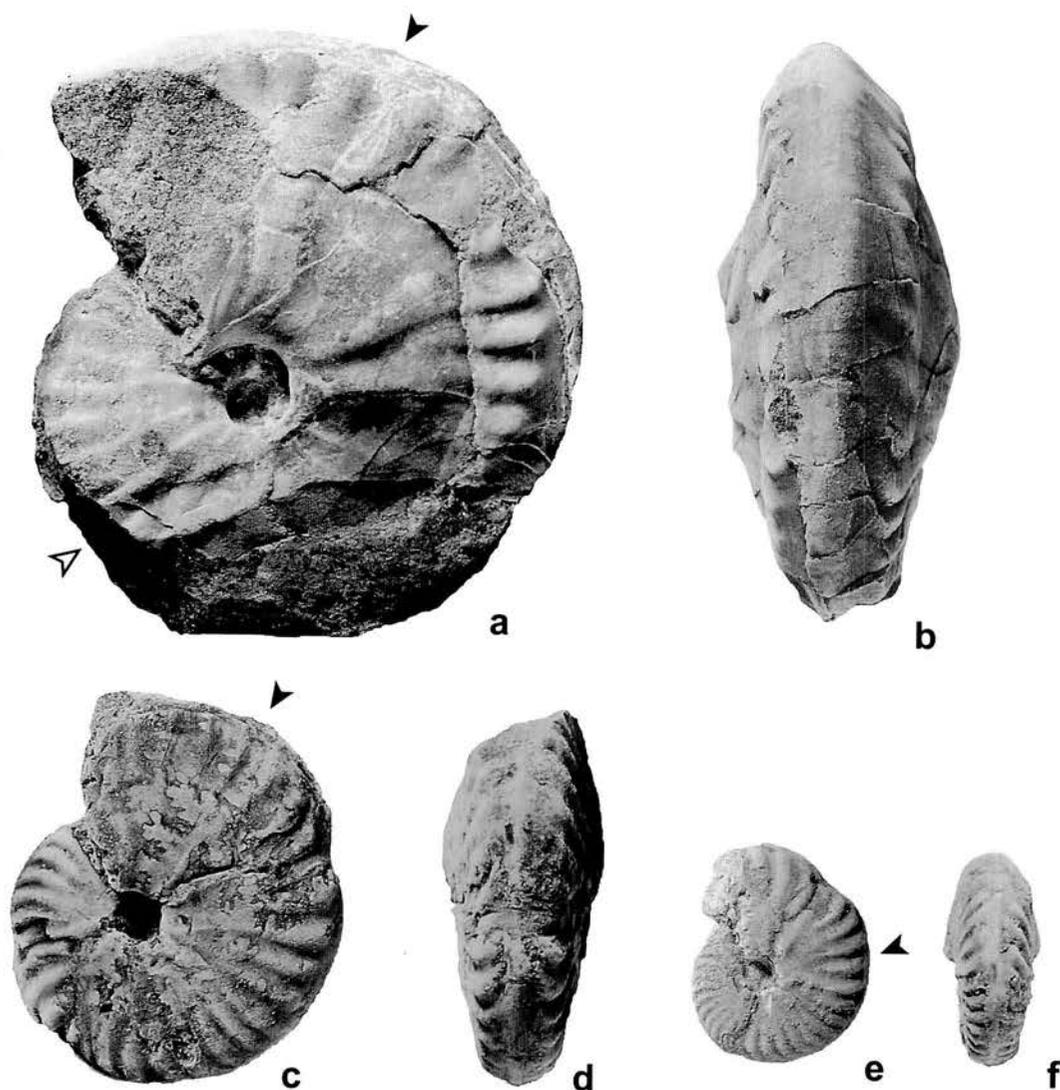*Material.* —One specimen, NSM PM16160. Immature

Figure 9. *Hourcquia kawashitai* Matsumoto and Toshimitsu, NSM PM16160, from NSM PCL 4–14–15, Miruto, ×1.0. **c–f.** Inner whorls of a and b. Dimensions for each growth stage observed at the solid arrows. a; D = 81.3 mm, U = 9.2 mm, B = 28.5 mm, H = 40.5 mm: c; D = 49.7 mm, U = 4.9 mm, B = 19.0 mm, H = 25.0 mm: e; D = 25.1 mm, U = 2.9 mm, B = 9.8 mm, H = 13.1 mm. The white arrow shows the location of the last suture-line.

shell, 82 mm in D, and consists of phragmocone and long body chamber occupying about 270° in spiral length, without complete aperture.

Locality.—NSM PCL 4–14–15: a cliff about 2 km north of the Horomui-gawa Dam in the Miruto area, Hokkaido (Figure 1).

Description.—Coiling very involute, with narrow and deep umbilicus, rounded umbilical shoulder and nearly vertical umbilical wall. Shell surface ornamented with prorsiradiate ribs tuberculated at umbilical and ventrolateral shoulders, springing in pairs from umbilical tubercles and with intercalated shorter ones. Ribs weaker on flank. Whorl cross-section high subtrigonal with maximum breadth at umbilical tubercles, rounded keel on roof-shaped venter, obtuse ventrolateral shoulder.

Initial chamber elliptical in median section, measuring 0.42 mm in diameter. Caecum subelliptical in lateral view (Figure 11). Prosiphon not preserved. Siphuncular tube occupies subcentral position in first whorl and gradually moves toward ventral side in second whorl. Ammonitella size and angle in median section, 0.89 mm and 310°, respectively. Lateral lobe of suture line asymmetrically divided and deeply incised (Figure 12).

Comparison.—Although the specimen NSM PM16159 is an immature shell, the shape and ornament are essentially the same as those of the inner whorl of *Hourcquia kawashitai* (Matsumoto and Toshimitsu, 1984; pl.32, fig.2).

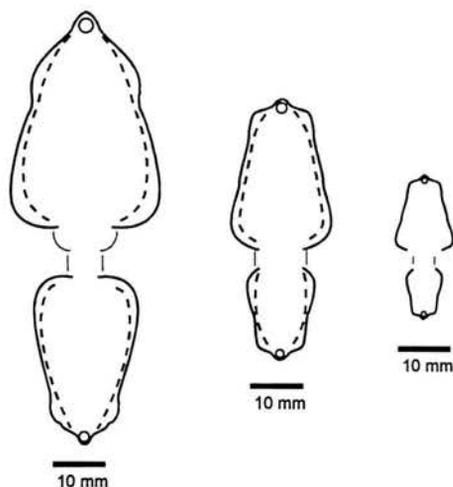*Occurrence.*—Upper Turonian, *Inoceramus teshioensis*

Figure 10. Median cross sections of *Hourcquia kawashitai* Matsumoto and Toshimitsu, NSM PM16160 showing the ontogenetic change in whorl-shape (right to left). The dashed line shows the intercostal whorl cross-section.
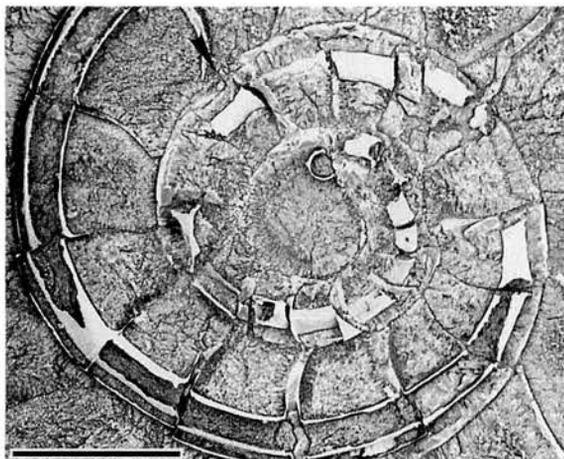

Figure 12. Suture line of *Hourcquia kawashitai* Matsumoto and Toshimitsu, NSM PM16160. **a**. Whorl height = 28.6 mm. **b**. Whorl height = 14.0 mm. **c**. Whorl height = 9.3 mm. Scale bars for a, b = 5.0 mm, for c = 1.0 mm. E; external lobe, L; lateral lobe, U; umbilical lobe.

Figure 11. SEM micrograph of the early internal shell structure of *Hourcquia kawashitai* Matsumoto and Toshimitsu, NSM PM16160, in median section. The arrow shows the primary constriction. Scale bar = 0.5 mm. See Figure 7-B for measurements of initial chamber size, ammonitella size, and ammnonitella angle.

Zone in Hokkaido, Japan.

Discussion

Five species of *Hourcuia*, *H. mirabilis*, *H. ingens*, *H. pacifica*, *H. hatai* and *H. kawashitai*, have been described up to now from the Cretaceous of Hokkaido and Sakhalin. Almost all species were not collected *in situ* but from calcareous concretions in float without specific stratigraphic evidence. Previous authors thought that the biostratigraphic horizon of *H. hataii* was the Coniacian, that of *H. pacifica* was the upper Turonian to Coniacian, and that of the other
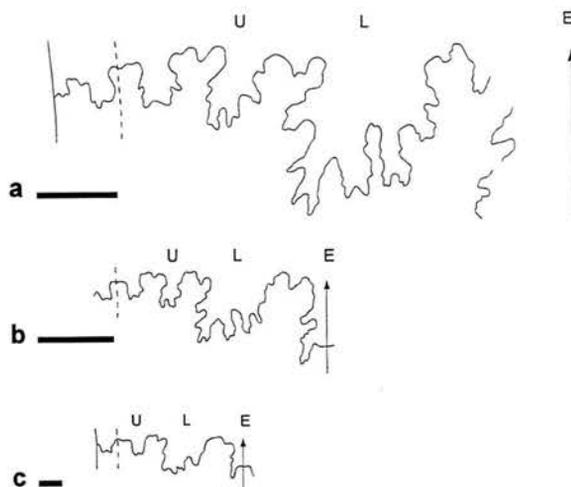
three species was the upper Turonian. In this paper, we have determined the precise biostratigraphic horizons of the following three species. *H. ingens* occurred in the upper part of the upper Turonian associated with *Subprionocyclus minimus*, *H. hataii* occurred in the Upper Turonian with *S. neptuni*, and *H. kawashitai* was also obtained from the upper Turonian. In the Tethyan and adjacent regions, *Hourcquia* radiated only during the late Turonian; *H. mirabilis* and *H. ingens* in Madagascar (Collignon, 1965), *H. krausi* and *H. moralesi* in Venezuela (Renz, 1982), *H.* cf. *mirabilis* in New Mexico and Trans-Pecos Texas (Anonymous, 1981). In consequence the genus *Hourcquia* seems to be useful for inter-regional biostratigraphic correlation.

In Hokkaido and Sakhalin, it is generally considered that the ammonoid fauna is characteristic of the North Pacific bio-province, different from both the Tethyan and Boreal provinces, during the post-Albian. However, the occurrence of *Hourcquia* species in the Yezo Supergroup, including two pandemic ones, *H. mirabilis* and *H. ingens* and three endemic ones, *H. pacifica*, *H. hataii*, and *H. kawashitai*, demonstrates that this genus evolved and radiated in not only the Tethyan and adjacent regions but also possibly in the northwest Pacific region for a short period in the late Turonian. In a similar manner, the Tethyan vascoceratids entered into the Yezo forearc basin for a short period in the early Turonian (Matsumoto, 1973; Matsumoto, 1978; Matsumoto and Muramoto, 1978). The oxygen isotope evidence suggests two cycles of rapid warming during earliest Turonian and middle to late Turonian time (Jenkyns *et al.*, 1994; Clarke and Jenkyns, 1999). The extended distributions of *Hourcquia* and vascoceratids seem to have been influenced by episodic global climatic optimums.

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Some additional Wuchiapingian (Late Permian) ammonoids from the Southern Kitakami Massif, Northeast Japan

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Abstract. Permian ammonoids, *Dzhulfoceras* cf. *furnishi, D.* sp. and *Stacheoceras?* sp., are described from the Southern Kitakami Massif, Northeast Japan. The first two and the last were collected from the Lower and Middle Toyoman Series, respectively. The occurrence of *Dzhulfoceras* supports the previous correlation of the Lower Toyoman Series with the Wuchiapingian (Dzhulfian). This occurrence of *Dzhulfoceras* is the first record of the genus outside the Middle East and supports the conclusion that a close paleobiogeographic relationship existed between the Middle East and the Southern Kitakami in Late Permian time.

Key words: *Dzhulfoceras*, Equatorial Tethyan Province, Southern Kitakami Massif, *Stacheoceras*, Upper Permian, Wuchiapingian

Introduction

Fossils including ammonoids are rare in the black shale of the Upper Permian Toyoman Series in the Southern Kitakami Massif, Northeast Japan. However, the few ammonoids that have been recovered are useful biostratigraphic tools for dating the Toyoman formations and for estimating the paleobiogeographic situation of the massif. To date, sixteen species belonging to 11 genera of ammonoids have been described from the Toyoman Series (Bando, 1975; Ehiro, 1996; Ehiro and Bando, 1985; Ehiro et al., 1986; Murata and Bando, 1975). The genera are *Pseudogastrioceras, Stacheoceras, Timorites, Cyclolobus, Eumedlicottia, Neogeoceras, Araxoceras, Vescotoceras, Eusanyangites, Xenodiscus* and *Paratirolites*. Based on these ammonoids, especially those belonging to the Cyclolobidae, Araxoceratidae, Xenodiscidae and Dzhulfitidae, the Lower to Middle and Upper Toyoman Series have been correlated with the Wuchiapingian (Dzhulfian) and Changhsingian (Dorashamian), respectively (Ehiro and Bando, 1985; Ehiro et al., 1986; Ehiro, 1996). This ammonoid fauna is typical of the Equatorial Tethyan Province (Ehiro, 1997) and closely related to the Late Permian ammonoid faunas of South China and the Middle East.

In this paper two new occurrences of Late Permian ammonoids are described. Two specimens were collected from the Suenosaki Formation in the Utatsu area, and one specimen came from the Toyoma Formation in the Motoyoshi area (Figure 1). Both occurrences indicate the Wuchiapingian horizon.

Late Permian ammonoids from Utatsu and Motoyoshi

In the Utatsu area, the uppermost Kanokuran (Middle Permian) to Middle Toyoman Suenosaki and Upper Toyoman Tanoura Formations are widely distributed (Ehiro and Bando, 1985). Two specimens of ammonoids described here as *Dzhulfoceras* cf. *furnishi* Ruzhencev and *D.* sp. were found in a calcareous nodule collected from a shale bed exposed along the Ishihama coast (see locality 3 of Ehiro and Bando, 1985). The fossil horizon belongs to the lower part of the Suenosaki Formation, which is correlated with the lower part of the Lower Toyoman Series. From this locality Ehiro and Bando (1985) and Ehiro et al. (1986) described some Wuchiapingian ammonoids, such as *Pseudogastrioceras* sp., *Stacheoceras iwaizakiense* Mabuti, *Timorites intermedius* (Wanner), *Araxoceras* cf. *rotoides* Ruzhencev, *A.* sp., *Vescotoceras japonicum* (Bando and Ehiro) and *V.* sp., and correlated the lower part of the Suenosaki Formation with the Wuchiapingian (Dzhulfian).

Dzhulfoceras belongs to the family Araxoceratidae and is indicative of Wuchiapingian age, although the genus ranges up to the Changhsingian. To date, three species of *Dzhulfoceras* have been described from the Upper Dzhulfian (*Vedioceras* bed) in Transcaucasia (*D. furnishi* Ruzhencev,
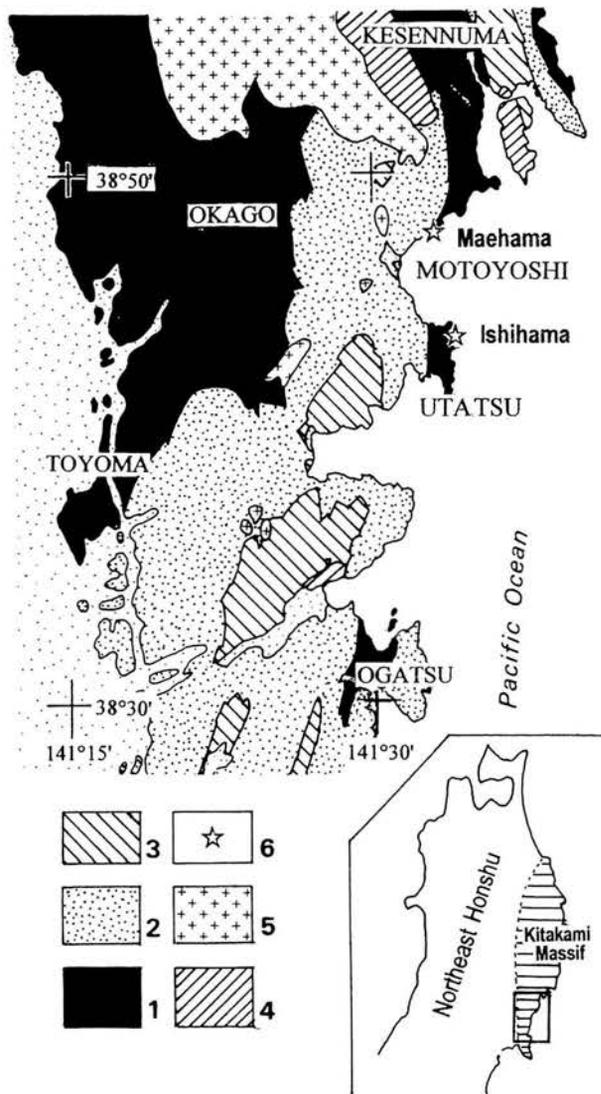
Figure 1. Map showing the fossil localities and geology of the southern part of the Southern Kitakami Massif. 1. Permian, 2. Triassic, 3. Jurassic, 4. Lower Cretaceous, 5. Early Cretaceous granitic rocks, 6. ammonoid localities.

D. inflatum Ruzhencev and *D. paulum* Ruzhencev; Ruzhencev, 1962, 1963) and from the Dorashamian (Unit 7 of the Hambast Formation) in Abadeh, Central Iran (*D. furnishi*; Bando, 1979). The Ishihama specimens of *Dzhulfoceras* described herein are the first recovery of the genus outside the Middle East. The *Dzhulfoceras* specimens show a close faunal relationship, in association with the previously reported ammonoids, to those of the Dzhulfian. The presence of *Dzhulfoceras* in South Kitakami supports the conclusion that the lower Suenosaki Formation is correlatable with the Wuchiapingian (Dzhulfian) (Ehiro and Bando, 1985), and that the South Kitakami region belonged to the Equatorial Tethyan ammonoid province during Permian time (Ehiro, 1997).

At the Maehama coast of the Motoyoshi area the Toyoma Formation consists mainly of massive black shale with a subordinate amount of lenticular thin sandstone beds. It is overlain unconformably by the Lower Triassic Hiraiso Formation. Murata and Bando (1975) reported an araxoceratid ammonoid, *Araxoceras* cf. *kiangsiense* Chao, from the black shale about 15 m below the boundary between the Toyoma and Hiraiso Formations. They correlated this part of the stratigraphic succession, which belongs to the Middle Toyoman Series based on the associated molluscan fossils, with the Dzhulfian. Later Zakharov (1986) compared this species to *Eusanyangites bandoi* Zakharov and Pavlov, which was recovered from the Wuchiapingian bed of Primorye, Far East Russia (Zakharov and Pavlov, 1986).

The present ammonoid specimen described here as *Stacheoceras*? sp. was collected from black shale exposed on the Maehama coast, at the same locality as Murata and Bando (1975). *Stacheoceras* is a long-ranging Permian genus and provides less precision in stratigraphic correlations.

Systematic descriptions

Superfamily Cycloboidea Zittel, 1895
Family Vidrioceratidae Plummer and Scot, 1937
Genus *Stacheoceras* Gemmellaro, 1887

Type species.—*Stacheoceras mediterraneum* Gemmellaro, 1887.

Stacheoceras? sp.

Figure 2.3a–d

Material.—A relatively small incomplete specimen, IGPS coll. cat. no. 108551, collected from the Toyoma Formation exposed on the Maehama coast, Motoyoshi-cho, Motoyoshi-gun, Miyagi Prefecture.

Remarks.—The specimen consists of about one half volution of the body chamber and fragments of phragmocone with an estimated diameter of 21 mm. The involute conch with a narrow umbilicus is subglobular (Figure 2.3a–c). At the maximum estimated diameter the height, width and umbilical diameter are about 12.0, 15.5 and 5.0 mm, respectively. The surface of the body chamber bears fine but prominent transverse ribs with intercalary ones, which start at 1/3 height of the whorl. The body chamber is also marked by rather prominent transverse constrictions, which are nearly straight. The suture lines, only partly preserved and displaying parts of the lateral suture, consist of more than three pairs of rounded saddles and trifid lobes (Figure 2.3d). Their exact positions with respect to the venter are unknown, because they are on a fragmental phragmocone.

Involute subglobular shells with transverse ribs are characteristic for some genera which belong to the families including and not limited to the Marathonitidae, Perrinitidae, Vidrioceratidae and Cyclolobidae. Judging from the shape of the trifid lateral lobe of the suture, it could belong to *Waagenia* or more likely *Stacheoceras*. The present speci-
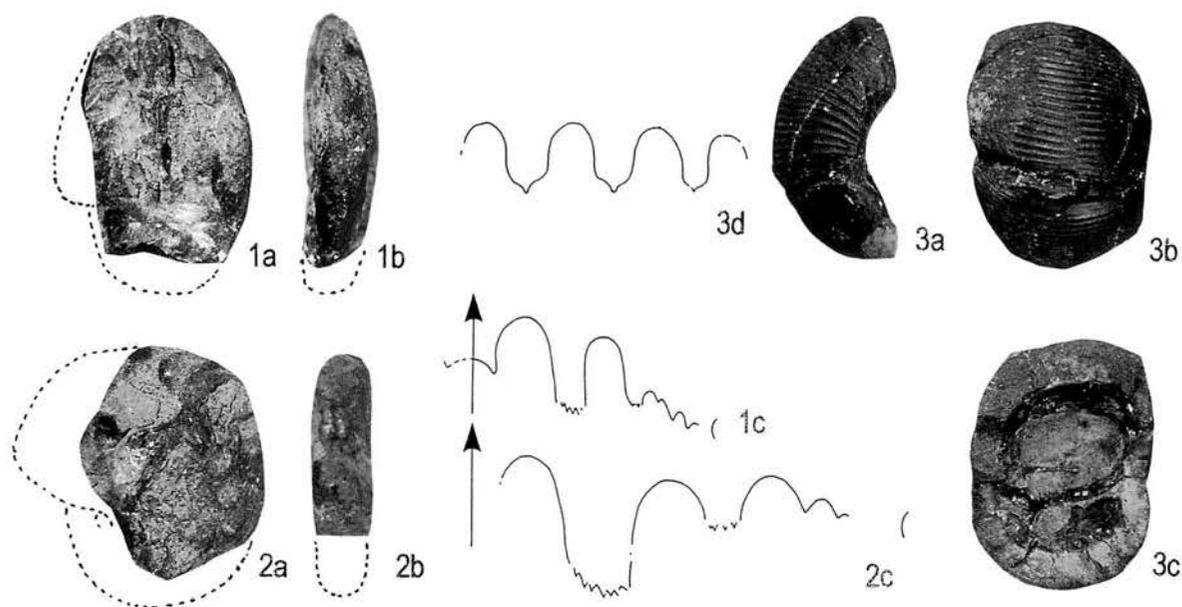
Figure 2. **1.** *Dzhulfoceras* cf. *furnishi* Ruzhencev, IGPS coll. cat. no. 108552, lateral (1a) and ventral (1b) views, ×2.5, and suture line (1c), ×7. **2.** *Dzhulfoceras* sp., IGPS coll cat. no. 108553, lateral (2a) and ventral (2b) views, ×2.5, and suture line (2c), ×7. **3.** *Stacheoceras*? sp., IGPS coll. cat. no. 108551, lateral (3a), ventral (3b) and dorsal (3c) views, ×1.6, and a part of the lateral suture line, ×8. Dotted lines show estimated conch outlines.

men is, however, too poorly preserved to identify it with confidence at the generic level and therefore the specimen is placed in *Stacheoceras* with strong reservations.

Superfamily Otoceratoidea Hyatt, 1900
Family Araxoceratidae Ruzhencev, 1959
Genus **Dzhulfoceras** Ruzhencev, 1962

Type species.—*Dzhulfoceras furnishi* Ruzhencev, 1962.

Dzhulfoceras cf. **furnishi** Ruzhencev, 1962

Figure 2.1a–c

Compare.—
Dzhulfoceras furnishi Ruzhencev, 1962, p. 99, pl. 5, figs. 1a, b, text-fig. 8a; Bando, 1979, p. 128, pl. 6, figs. 8a–c, 9a, b, text-fig. 6A.

Material.—A partly complete phragmocone, IGPS coll. cat. no. 108552, collected from the lower part of the Suenosaki Formation exposed along the Ishihama coast, Utatsu-cho, Motoyoshi-gun, Miyagi Prefecture.

Descriptive remarks. — The specimen is a deformed phragmocone with an estimated diameter of 14 mm. The conch is involute and thinly discoidal, with a pinpoint umbilicus (Figure 2.1a, b). The compressed shell has nearly parallel, but slightly convex flanks. The venter and ventrolateral shoulders are rounded. No ornamentation is observed on the shell surface. The ceratitic suture consists of a moderately wide ventral lobe, large and high rounded ventrolateral saddle, large and deep first lateral lobe, moderately high second lateral saddle, relatively small and shallow

second lateral lobe and four pairs of small rounded saddles and pointed lobes (Figure 2.1c). Only the first and second lateral lobes are denticulate.

Based on the shell form, especially on the rounded shape of its ventrolateral part, and the form of the suture, the present specimen can be assigned with confidence to *Dzhulfoceras*. Among the species of the genus *Dzhulfoceras* it most closely resembles *D. furnishi* Ruzhencev in having nearly parallel sides of the shell. The present specimen is not sufficiently well preserved to allow a confident species assignment.

Dzhulfoceras sp.

Figure 2.2a–c

Material.—An incomplete phragmocone, IGPS coll. cat. no. 108553, collected from the lower part of the Suenosaki Formation exposed on the Ishihama coast, Utatsu-cho, Motoyoshi-gun, Miyagi Prefecture.

Remarks. — The specimen is a small fragment of phragmocone of about one half volution with an estimated diameter of 14 mm. The conch is compressed, involute and thinly discoidal. The slightly convex sides are subparallel, and the venter and the ventral shoulders are rounded (Figure 2.2a, b). No ornamentation is observed on the shell surface. The suture line is partly preserved on the lateral part of the conch. It consists of a large and high rounded ventrolateral saddle, large and deep serrated first lateral lobe, moderately high rounded second lateral saddle, relatively small and shallow serrated second lateral lobe and more than two pairs of small rounded saddles and pointed

lobes (Figure 2.2c).   The ventral suture is not preserved.

This specimen is assigned to *Dzhulfoceras*, judging from the shell shape and sutural outline.   It is, however, impossible to assign the specimen to a species with confidence because of the poor state of preservation.

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Middle Carboniferous orthoconic cephalopods from the Omi Limestone Group, Central Japan

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Abstract. A Middle Carboniferous (probable late Bashkirian) fauna of orthoconic cephalopods was collected from bioclastic rudstone/grainstone in the Omi Limestone Group, Central Japan. This fauna belongs to the Taishaku-Akiyoshi-South China Faunal Province. Recognized herein are the orthocerid nautiloid *Bogoslovskya omiensis* sp. nov., the bactritids *Bactrites nagatoensis* Niko, Nishida and Kyuma, 1991 and *Bactrites* sp., and an indeterminate body chamber. This is the first reliable documentation of orthoconic cephalopods from the Omi Limestone Group.

Key words: Bactritida, Middle Carboniferous, Omi Limestone Group, Orthocerida

Introduction

Since the beginning of the Twentieth Century, some Carboniferous cephalopods have been occasionally reported by non-specialists of this group from the Omi Limestone Group, an accreted reefal buildup in Niigata Prefecture, Central Japan. The taxa cited include *Gastrioceras* sp. by Yabe (1904), *Eoasianites* cf. *orientale* (Yin) by Kato and Nakamura (1962), *Eoasianites* sp., *Gastrioceras* aff. *reticulatus* Yin, *Paralegoceras* sp. and *Reticuloceras*? sp. by Igo and Koike (1963, 1964), *Pseudorthoceras* sp. by Koizumi (1975), and *Pseudoparalegoceras*? sp. and *Stroboceras* sp. by Oyagi (2000). Unfortunately, these taxa were presented without detailed descriptions and/or illustrations, so an evaluation of their significance can not be made at this time. As the first attempt to give a reliable documentation of the Omi cephalopod fauna, the present report sheds light on the orthoconic nautiloids and bactritoids for taxonomic, biostratigraphic and paleobiogeographic purposes.

The collecting site that yielded these cephalopods is situated at the southern corner of Higashiyama Quarry, Latitude 36°59′27″N and Longitude 137°47′8″E, where light gray, massive bioclastic rudstone/grainstone limestone is exposed. This cephalopod-bearing limestone is Middle Carboniferous (probable late Bashkirian) in age and may be part of the reef front facies (Niko and Hasegawa, 2000). The geologic setting of the Omi Limestone Group has been described in Hasegawa *et al.* (1969, 1982), Hasegawa and Goto (1990), and Nakazawa (1997), thus it will not be repeated herein. During field work in 1997 to 1999, nearly thirty specimens identified as *Bogoslovskya omiensis* sp.

nov., *Bactrites nagatoensis* Niko, Nishida and Kyuma, *Bactrites* sp., along with an indeterminate body chamber were collected in cooperation with Mr. Toshiaki Kamiya. This association of genera is characteristic of the Taishaku-Akiyoshi-South China Province (Niko, 2000).

All specimens studied are reposited in the University Museum of the University of Tokyo (UMUT).

Systematic paleontology

Subclass Nautiloidea Agassiz, 1847
Order Orthocerida Kuhn, 1940
Superfamily Orthoceratoidea M'Coy, 1844
Family Orthoceratidae M'Coy, 1844
Subfamily Michelinoceratinae Flower, 1945
Genus *Bogoslovskya* Zhuravleva, 1978

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

Bogoslovskya omiensis sp. nov.

Figure 1.1–1.3, 1.5–1.9

Diagnosis.—Species of *Bogoslovskya* with 6°–7° angle of shell expansion, approximately 0.9 in form ratio of shell, transverse surface lirae; form ratio of camera 1.8–3.1; siphuncle strongly eccentric, its position ratio 0.13.

Description.—Orthocones with 6°–7° angle of shell expansion and laterally compressed cross section yielding lateral/dorsoventral diameter ratio (form ratio of shell) of approximately 0.9; largest specimen (paratype, UMUT PM 27892) of phragmocone reaches 16.5 mm in dorsoventral di-
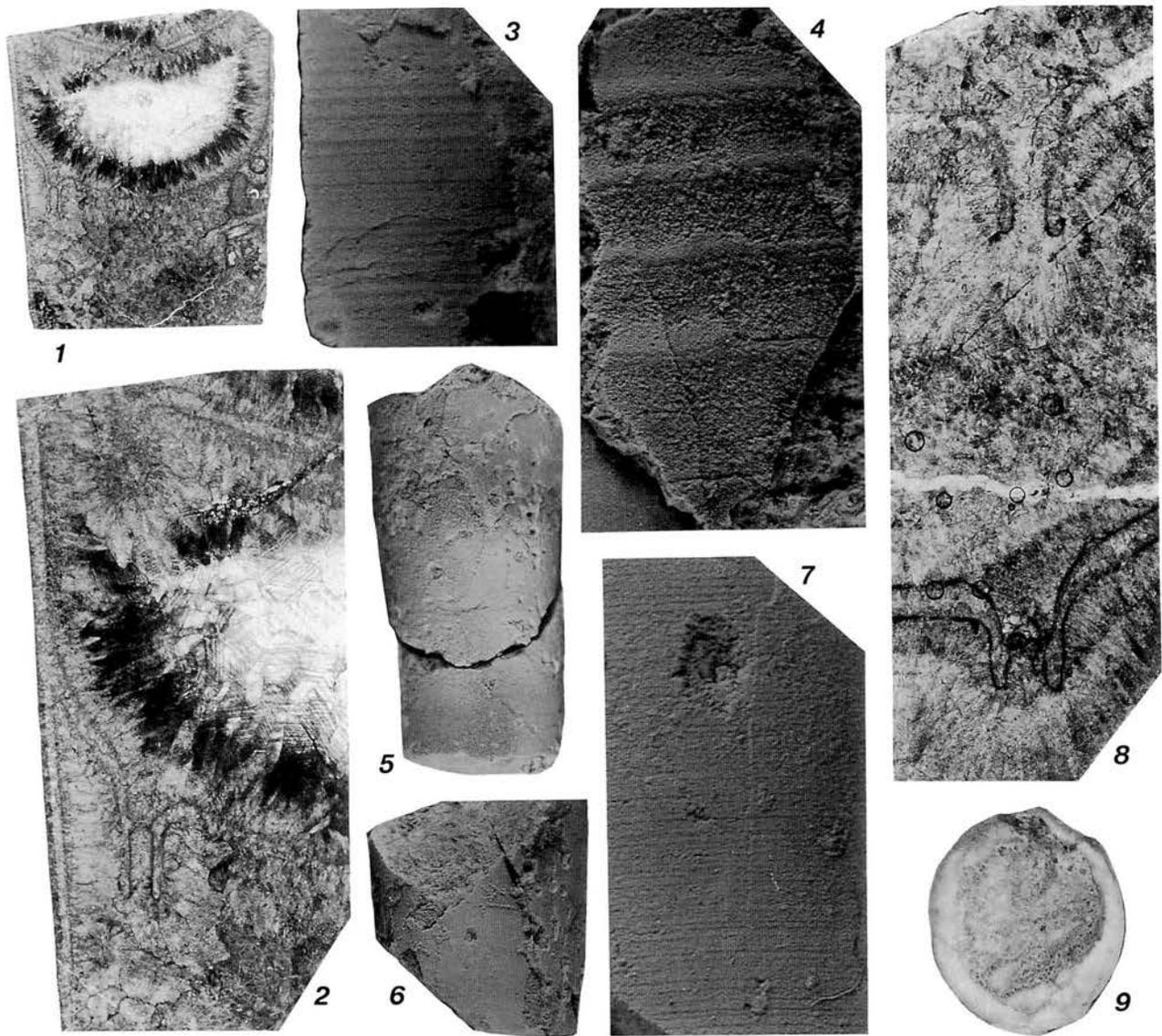
Figure 1. 1-3, 5-9. *Bogoslovskya omiensis* sp. nov. 1-3. Holotype, UMUT PM 27890; **1**, dorsoventral thin section, ×5; **2**, details of apical siphuncle, ×14; **3**, details of surface ornamentation of apical shell, ×10. **5, 8.** Paratype, UMUT PM 27891; **5**, side view of anti-siphuncular side, ×2; **8**, details of adoral siphuncle, thin longitudinal (but not dorsoventral) section, × 14. **6, 7, 9.** Paratype, UMUT PM 27892; **6**, side view, siphuncular side on right(?),× 2; **7**, details of surface ornamentation of adoral shell, ×10; **9**, polished section near adoral end, siphuncular side down(?), slightly deformed, × 2. **4.** Indeterminate body chamber, UMUT PM 27918, details of surface ornamentation, ×5.

ameter. Surface ornamentation of apical shell (represented by holotype, up to 7.9 mm in dorsoventral diameter) consists of subdued transverse lirae with somewhat unequal size and intervals, then it shifts to closely spaced, fine, transverse

lirae on adoral shell (ditto paratypes). Sutures not observed, but obvious obliquity not observed in dorsoventral section. Septa moderately deep; cameral length relatively short for genus, 4.1 mm in length, with maximum dorsoventral diame-

➡ **Figure 2.** 1-5. *Bactrites nagatoensis* Niko, Nishida and Kyuma, 1991. **1.** UMUT PM 27897, dorsal view, ×3. **2-4.** UMUT PM 27895; **2**, ventral view, ×3; **3**, dorsal view, ×3; **4**, apical view, venter down, ×3. **5.** UMUT PM 27896, dorsal view, ×1.5. **6-12.** *Bactrites* sp. **6-8, 10, 11.** UMUT PM 27916; **6**, apical view, venter down, ×3; **7**, dorsoventral thin section, venter on left, ×14; **8**, details of apical septal neck, venter on left, ×14; **10**, ventral view, ×3; **11**, dorsal view, ×3. **9, 12.** UMUT PM 27917; **9**, longitudinal (near dorsoventral) polished section, venter on right, ×2; **12**, details of adoral septal neck, longitudinal (near dorsoventral) thin section, venter on right, ×14. **13.** Indeterminate body chamber, UMUT PM 27918, side view, ×1.5.
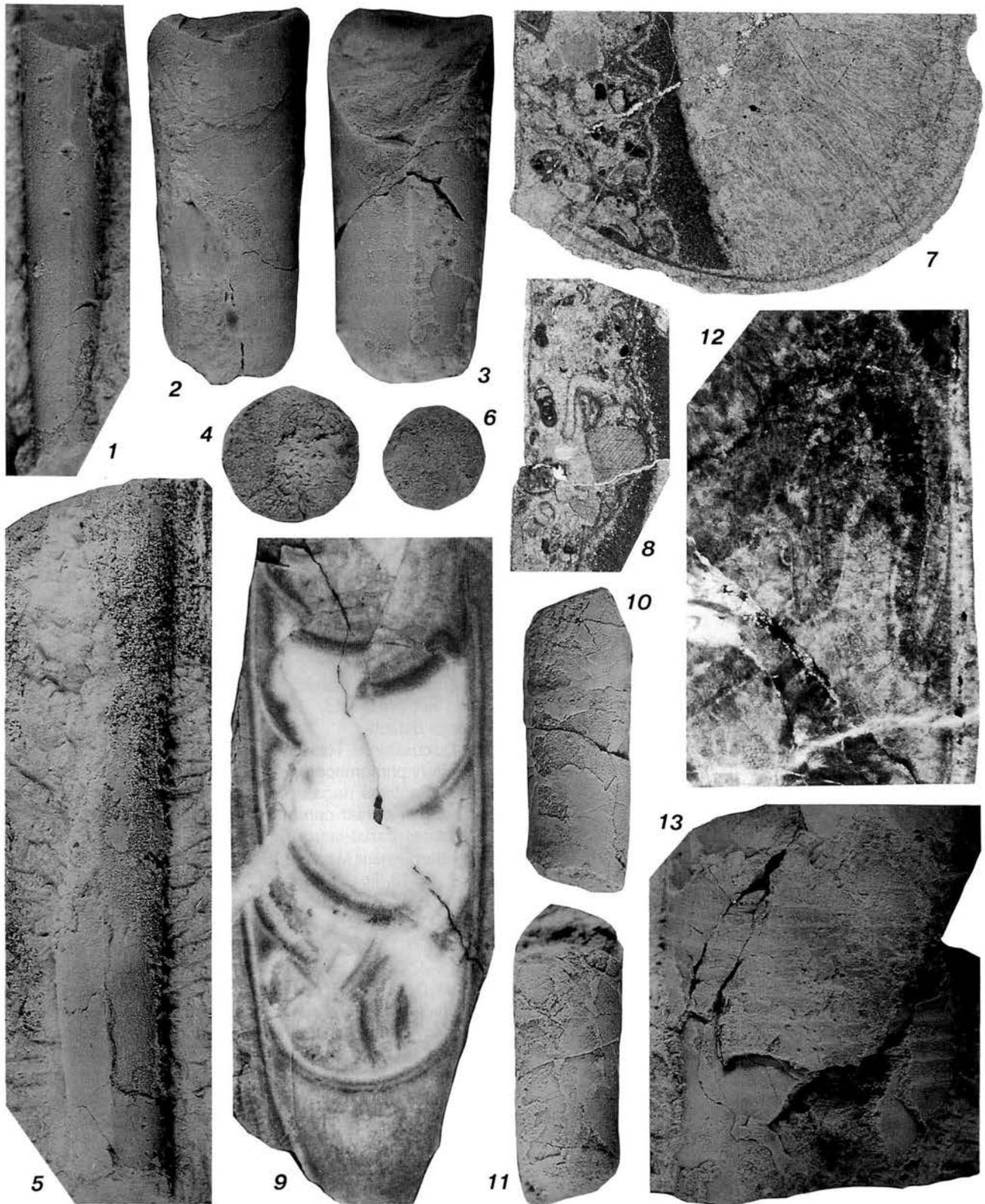
ter/length ratio (form ratio of camera) 1.8 in apical shell; this ratio increases to 2.5-3.1 in adoral shell. Siphuncular position strongly eccentric and submarginal, minimum distance of central axis of siphuncle from shell surface per corresponding dorsoventral shell diameter (siphuncular position ratio) is 0.13 in holotype. Septal necks long for family; they are orthochoanitic and cylindrical in apical shell, then shifts gently tapering and funnel-shaped orthochoanitic forms in adoral shell; length of septal necks on anti-siphuncular (dorsal?) side ranges from 1.03 mm to 1.28 mm; siphuncular diameters 0.42-0.70 mm at tips of septal neck, where septal foramen is 0.23-0.42 mm in diameter, giving a diameter of septal neck/corresponding dorsoventral shell diameter ratio of approximately 0.06. Annulus of weak auxiliary deposits recognized in septal foramina. Connecting ring not preserved; no cameral deposits detected.

Discussion.—Among the three previously known Upper Paleozoic species of this genus (see Niko *et al.*, 1995, 1997, Niko and Ozawa, 1997), *Bogoslovskya omiensis* sp. nov. bears the greatest similarity to *B. akiyoshiensis* Niko, Nishida and Kyuma (1995, figs. 1.1-1.14) from the Middle Carboniferous (Moscovian) in the Akiyoshi Limestone, Southwest Japan. Although the gross shell shape and the surface ornamentation suggest the close phylogenetic relationship of the both species, the main character of *Bogoslovskya omiensis* that separates it from *B. akiyoshiensis* is the more eccentric siphuncular position, with a siphuncular position ratio of 0.13 versus 0.19 for the corresponding shell diameter in *B. akiyoshiensis.*

Etymology.—The specific name is derived from the Omi Limestone Group, in which this species occurs.

Material examined.—The holotype, UMUT PM 27890, is an incomplete phragmocone 9.3 mm in length. The following two paratypes of the incomplete phragmocones are assigned: UMUT PM 27891, 27.0 mm in length, and UMUT PM 27892, 12.8 mm in length. They represent more adoral shells than the holotype. In addition, two fragmentary specimens, UMUT PM 27893, 27895 are referred to this species with reservation.

Subclass Bactritoidea Shimanskiy, 1951
Order Bactritida Shimanskiy, 1951
Family Bactritidae Hyatt, 1884
Genus *Bactrites* Sandberger, 1843

Type species.—*Bactrites subconicus* Sandberger, 1843.

Bactrites nagatoensis Niko, Nishida and Kyuma, 1991

Figure 2.1-2.5

Bactrites nagatoensis Niko, Nishida and Kyuma, 1991, p. 715, figs. 2.1-2.10, 3.1-3.5.
Bactrites cf. *nagatoensis* Niko, Nishida and Kyuma. Niko *et al.*, 1997, p. 106, figs. 3.9, 4.8.

Discussion. — Twenty-one bactritid specimens of the orthoconic phragmocones with an angle of adoral shell expansion of approximately 5° - 6° were collected from Higashiyama Quarry. The shell diameters range from 2.3 mm (UMUT PM 27907) to 25.1 mm (UMUT PM 27915).

They have the shell morphology typical of the holotype, which is from the Moscovian (Middle Carboniferous) of the Akiyoshi Limestone, with rapid shell expansion for *Bactrites* and a single dorsal carina throughout the known phragmocone. A form possibly conspecific with this species also occurs in the Moscovian limestone of the Dala (Huanglong) Formation, Guizhou Province, South China (Niko *et al.*, 1997). Comparisons of *Bactrites nagatoensis* to three Laurentian species (*B. finisensis* Mapes, 1979, pl. 23, figs. 4-6, *B. mexicanus* Miller, 1944, pl. 20, figs. 8, 9, pl. 21, figs. 4-6, and *B. peytonensis* Mapes, 1979, pl. 8, figs. 4-14, pl. 9, figs. 2, 3, 6-8, 12, 13, 15, 17-19, pl. 14, figs. 7, 8, 10) having a dorsal carina are referable in Niko *et al.* (1991, p. 715).

Material examined.—UMUT PM 27895-27915.

Bactrites sp.

Figure 2.6-2.12

Description.—Orthocones with gradual shell expansion indicating near 2° in angle; cross section of shell circular; largest specimen (UMUT PM 27917) attains approximately 19 mm (slightly deformed) in diameter at adoral phragmocone. Surface ornamentation and carina absent, wrinkled layer not observed. Except for ventral lobe, sutures are nearly straight and slightly oblique at 6°-15° to rectangular direction of shell axis, toward aperture on dorsum. Septal curvature moderate; cameral length moderate with approximately 1.6 in diameter/length ratio. Siphuncular position ventral margin; ventral septa attached to shell wall; septal necks orthochoanitic, relatively long for genus; dorsal septal necks 0.82-1.26 mm in length; diameter of septal foramen/corresponding shell diameter is approximately 0.07; connecting ring not preserved. No cameral and endosiphuncular deposits detected.

Discussion.—This species is known from the two fragmentary phragmocones, but is easily separable from associated *Bactrites nagatoensis* by the slenderer shell and the lacking a dorsal carina. The features approach those of *Bactrites carbonarius* Smith (1903, pl. 6, figs. 9-11), *B. fayettevillensis* Mapes (1979, pl. 9, figs. 9-11, pl. 10, figs. 6-8, pl. 13, figs. 1, 7, 8, 11, 12, 14-16, pl. 14, fig. 9, pl. 15, figs. 1, 2, 6, 7, 12-14), *B. longocameratus* Shimanskiy (1949, fig. 1), *B. milleri* Mapes (1979, pl. 10, fig. 10, pl. 12, figs. 4, 8-12), *B. quadrilineatus* Girty (1909, pl. 6, figs. 1, 1a, 1b, 2-4, 4a), *B. smithianus* Girty (1909, pl. 6, fig. 5, 6?), and *B.* sp. (Niko *et al.*, 1991, figs. 3.6-3.9). Due to the poor preservation of the Omi specimens and the relatively simple morphology of this group for *Bactrites*, specific comparisons cannot be made at this time.

Material examined.—UMUT PM 27916, 27917.

Subclass, Order, Superfamily, Family, Genus, and Species uncertain

body chamber

Figures 1.4, 2.13

Discussion. — A fragmentary body chamber of an orthoconic shell, 67.5 mm in length and 39 mm+ (deformed)

in diameter, is available for this study. Although its surface ornamentation consisting of weak annulations and lirae shows an affinity to the mature modification of some bactritids including *Bactrites peytonensis* Mapes and *Bactrites*? sp. morphotype 13 (Mapes, 1979, pl. 2, figs. 14–16), lack of knowledge of the siphuncular structure and position precludes a positive identification even to be subclass level. Similar ornamentation is also known to occur in the Carboniferous orthocerids, such as *Brachycycloceras* (Miller *et al.*, 1933), *Cryptocycloceras* (Shimansky, 1968), *Cycloceras* (M'Coy, 1844), and *Reticycloceras* (Gordon, 1960).
Material examined.—UMUT PM 27918.

Acknowledgments

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Mode of occurrence and composition of bivalves of the Middle Jurassic Mitarai Formation, Tetori Group, Japan

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Abstract. The Middle Jurassic Mitarai Formation distributed in Shokawa Village, Gifu Prefecture, central Japan, is interpreted as deposits of wave-dominated shelf environments. The muddy shelf deposits yield abundant molluscs showing various modes of occurrence that can be divided into three fossil assemblages: (1) the autochthonous *Modiolus maedae-Tetorimya carinata* assemblage with commonly *in-situ* preserved semi-infauna and deep burrowers; (2) the *Entolium inequivalve* assemblage characterized by mixed autochthonous infauna and parautochthonous free-living elements; and (3) the allochthonous *Inoceramus maedae* assemblage. The *Entolium inequivalve* assemblage contains the chemosymbiotic bivalve *Solemya* and is associated with a low-diversity ichnofauna suggestive of low oxygen conditions.

Key words: bivalves, fossil assemblage, ichnofauna, Jurassic, low oxygen condition, Mitarai Formation, taphonomy

Introduction

The Middle Jurassic Mitarai Formation, Tetori Group, is exposed in the vicinity of Shokawa Village, Gifu Prefecture, central Japan (Figure 1) and is composed of shallow marine deposits. The formation yields abundant benthic macrofossils and has been well studied by geologists and palaeontologists (Maeda, 1952, 1961; Hayami, 1959a, b, 1960; Masuda *et al.*, 1991; Matsukawa and Nakada, 1999). Maeda (1952) and Matsukawa and Nakada (1999) provided the geologic map and described the stratigraphy of the formation in this area. Masuda *et al.* (1991) broadly discussed the depositional environments and tectonic nature of the Tetori basin situated along the East Asian continental margin. The benthic fauna of the Mitarai Formation mainly consists of bivalves. It has been described from a taxonomic point of view by Hayami (1959a, b, 1960). However, no palaeoecological or taphonomic studies of this fauna exist, although the bivalves show variable modes of occurrence ranging from an apparently allochthonous type to an autochthonous type preserving the life orientation. Moreover, the relationship between depositional environments and benthic assemblages, faunal compositions and ichnofauna are hardly known in the Jurassic of East Asia.

In this paper, the depositional environments of the Mitarai Formation are reconstructed based on facies analysis. The bivalves are grouped into three fossil assemblages, and their habitats and the nature of the assemblages are discussed. Particular emphasis has been placed on the composition of the benthic fauna and the modes of fossil occurrences which are described in detail.

Geological framework

The Jurassic to Cretaceous Tetori Group is composed of nonmarine and shallow-marine deposits, and is widely distributed in the north-central part of Japan (Figure 1). The group is divided into three subgroups, the Kuzuryu, Itoshiro and Akaiwa in ascending order (Maeda, 1952, 1961). The Kuzuryu Subgroup is subdivided into the Ushimaru and Mitarai formations (Matsukawa and Nakada, 1999). These formations typically crop out in the study area of the Shokawa Village, Gifu Prefecture.

The lower part of the Ushimaru Formation unconformably overlies basal granitic rocks, and consists of fluvial, coarse clastic deposits and estuarine (in a broad sense) deposits containing abundant brackish-water molluscs such as *Crassostrea* sp., *Myrene tetoriensis* and *Tetoria yokoyamai*.
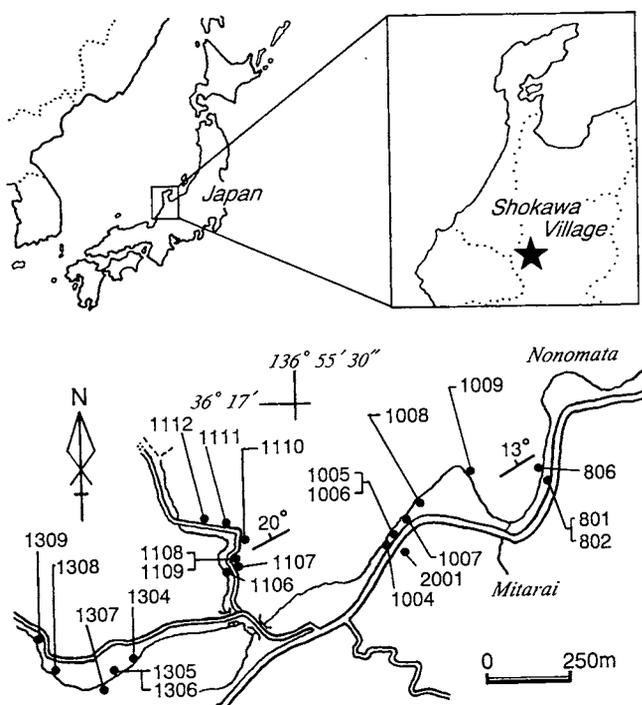
Figure 1. Map of Shokawa Village, showing the localities of molluscan fossil samples from the Mitarai Formation.

The upper Ushimaru Formation is composed of alternating beds of sandstone and mudstone commonly yielding brackish-water and marine molluscs, and is interpreted as estuarine and shallow marine deposits, which are conformably overlain by the marine Mitarai Formation (Kumon and Kano, 1991; Matsukawa and Nakada, 1999). The Mitarai Formation is about 45 m thick and consists of a basal conglomerate, sandstone and dark grey mudstone with abundant marine fossils such as ammonites, crinoids, gastropods and bivalves (Figure 2). The ammonite, *Lilloetia* sp., suggests a Callovian (Middle Jurassic) age (Sato and Kanie, 1963). This formation is overlain by shallow marine sandstone of the Otaniyama Formation, Itoshiro Subgroup (Maeda, 1952; Kumon and Kano, 1991; Matsukawa and Nakada, 1999).

Lithostratigraphy and depositional environments of the Mitarai Formation

Lithostratigraphy

The succession ranging from the uppermost Ushimaru Formation to the Mitarai Formation yields abundant marine molluscan fossils and is characterized by a transgressive sequence followed by regression (Matsukawa and Nakada, 1999). The uppermost Ushimaru Formation is composed of conglomerate and sandstone (Figure 2). The Mitarai Formation is mainly dominated by mudstone. The uppermost Ushimaru Formation of this paper is almost equivalent to the M1 member of the Mitarai Formation (Hayami, 1959).

The uppermost part of the Ushimaru Formation is composed of about 16 m of thick fine-grained sandstone with an about 40-cm-thick basal conglomerate bed. This conglomerate bed contains well rounded pebbles and cobbles, and exhibits a sharp erosional contact with the underlying sandstone. The sandstone is characterized by hummocky cross-stratification and bioturbation. Maeda (1952) and Hayami (1960) reported the marine bivalve *Inoceramus maedae* from this sandstone. The HCS sandstone is capped locally by a thin conglomerate, which marks the base of the Mitarai Formation. The lower part of the Mitarai Formation consists of mudstone interbedded with trough and hummocky cross-stratified and parallel-laminated sandstone beds. The alternating beds of mudstone and sandstone gradually change upward into bioturbated massive mudstone. The upper part of this mudstone is intercalated with thin, parallel-laminated sandstone beds (1-4 cm thick) and a thick, very fine-grained sandstone bed (Loc.1112). It is finally overlain by fine- to medium-grained sandstone of the Otaniyama Formation. The sandstone of the basal Otaniyama Formation yields rare disarticulated valves and fragments of *Inoceramus maedae*. The upper Mitarai Formation and the basal Otaniyama Formation form a coarsening-upward succession.

Depositional environments

The HCS sandstone of the upper Ushimaru Formation containing typical shallow marine bivalves is interpreted as wave-dominated nearshore sediments deposited above fair-weather wave base. HCS is a diagnostic sedimentary structure formed under waning storm and wave or combined-flow conditions (e.g. Duke *et al.*, 1991; Cheel and Leckie, 1993). HCS sandstones without associating muddy sediments imply deposition shallower than fair-weather wave base (Walker and Plint, 1992). The conglomerate bed at the base of the HCS sandstone (Figure 3.1) is in erosional contact with estuarine deposits of the Ushimaru Formation. This erosional surface, probably a result of strong shoreface erosion during transgression, marks an increase in water depth. Thus, the conglomerate can be interpreted as a transgressive lag deposit.

The Mitarai Formation is composed mainly of mudstone yielding marine fossils, which is interpreted to represent inner and outer shelf deposits below fair-weather wave base. In the lower part, the alternating beds of HCS sandstone and bioturbated mudstone probably indicate deposition during repetition of storm and fair-weather conditions in inner shelf environments. Parallel-laminated sandstone beds possibly represent tempestites generated by storm-induced flow (Walker and Plint, 1992). Bioturbated thick mudstone without sandstone intercalation overlying these alternating units may reflect an increase in water depth during transgression, and is interpreted as outer shelf deposits.

The thick sandstone beds of the upper Mitarai Formation (Locs. 1308, 1112) and the basal sandstone of the Otaniyama Formation (Loc. 1309) contain *Inoceramus maedae*, and probably represent nearshore environments. The coarsening- and shallowing-upward successions of the upper Mitarai and basal Otaniyama formations are interpreted to indicate deltaic systems (Kumon and Kano, 1991; Matsukawa and Ito, 1995), suggesting a regressional phase, that is, relative sea-level fall.
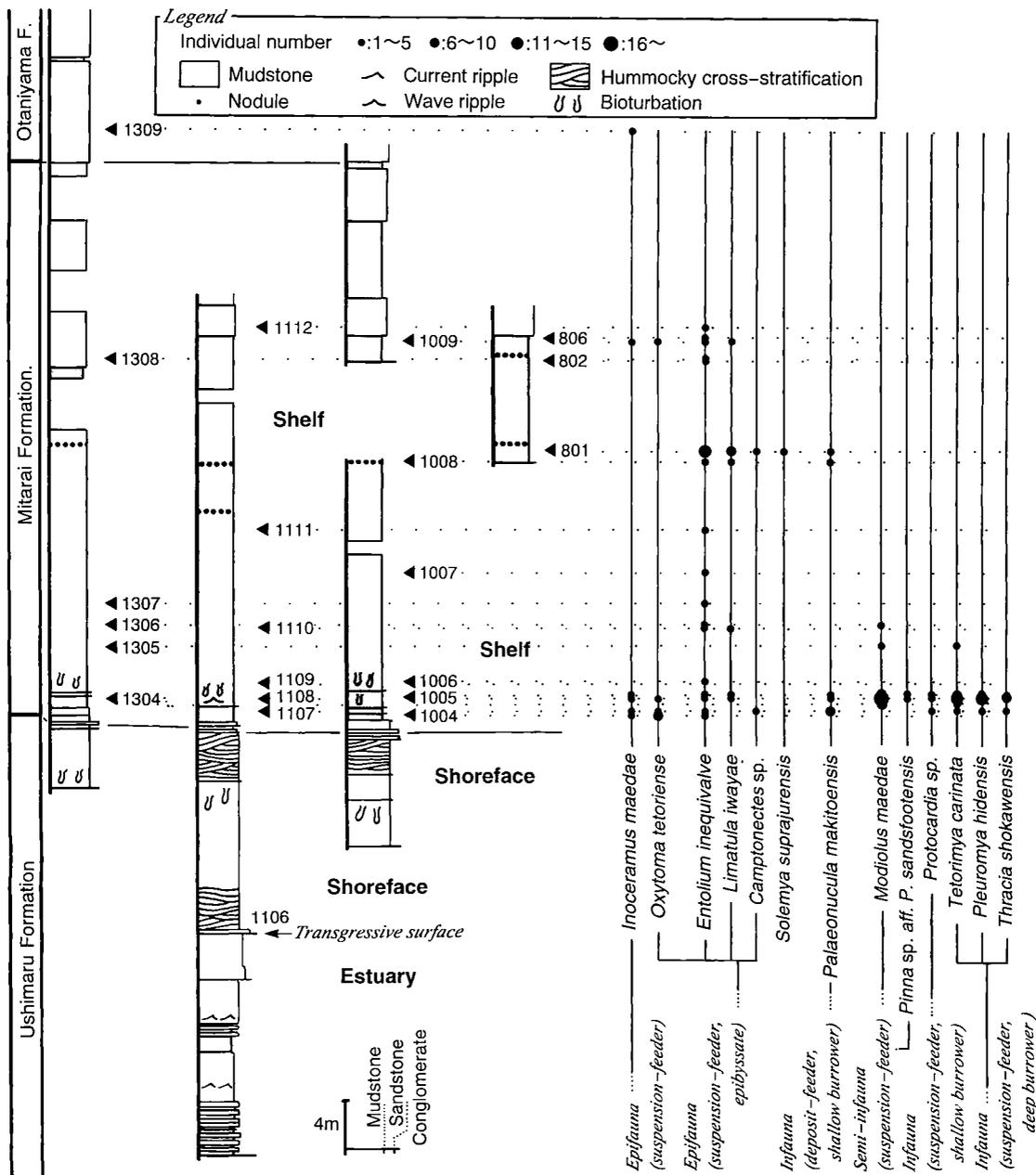
Figure 2. Columnar sections of Mitarai and Otaniyama Formations, showing the horizons of the samples examined and stratigraphic occurrences of bivalve species.

Mode of occurrence and composition of bivalves

Methods

Bivalve fossils are found very sporadically in muddy deposits of the Mitarai Formation. These shells do not form shell beds, except for minor shell lenses in several horizons. Bivalves were counted on outcrop surfaces, and were collected bed by bed. Due to the limited material and marked differences in fossil preservation between samples, we did not carry out quantitative analysis of the fossil assemblages.

Based on the faunal composition and modes of fossil occurrences the samples from various localities were grouped in three assemblages, the *Modiolus maedae-Tetorimya carinata*, the *Entolium inequivalve*, and the *Inoceramus maedae* assemblage. The *Inoceramus maedae* assemblage, which exceptionally forms minor shell lenses, was distinguished from the others by its mode of occurrence.

Life habits of the bivalves were reconstructed based on analogy with closely related living taxa, and also by referring to previous studies (Scott, 1974; Wright 1974; Fürsich, 1977,
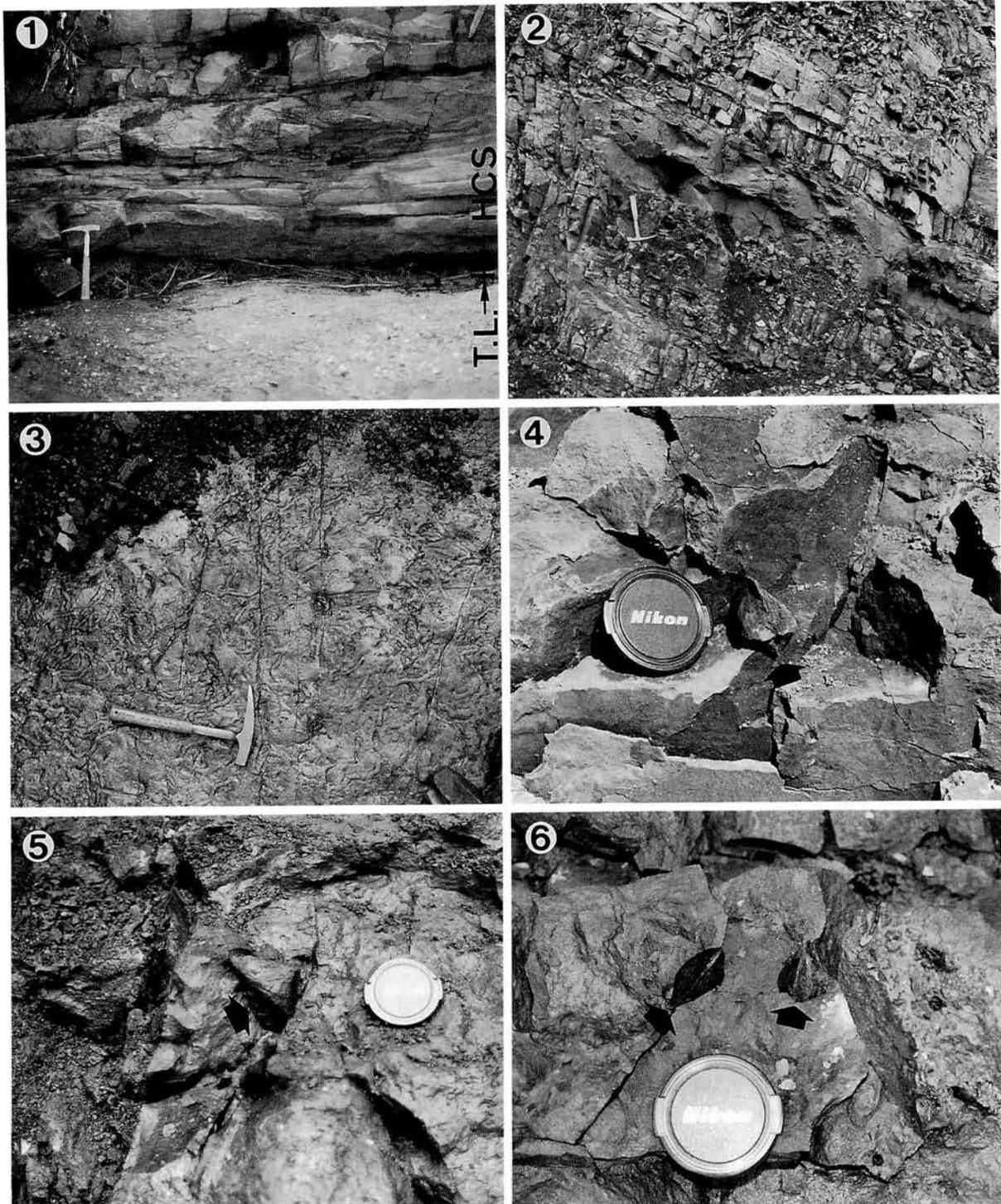
Figure 3. Photos showing sedimentary structures, trace fossils and modes of fossil occurrences. **1.** Conglomerate and overlying hummocky cross-stratified sandstone (HCS) (Ushimaru Formation, loc. 1106). The conglomerate is interpreted to represent a transgressive lag deposit (T.L.). The hammer is 28 cm long. **2.** Exposure of alternating beds of sandstone and mudstone (lower Mitarai Formation, loc. 2001). **3.** Bedding plane of intensely bioturbated mudstone with large two-dimensional burrows (lower Mitarai Formation, loc. 1108). **4.** Vertical section of mudstone containing articulated *Tetorimya carinata* Hayami (arrowed) (lower Mitarai Formation, loc. 1108). **5.** Vertical section of mudstone containing articulated *Modiolus maedae* Hayami (arrowed) (lower Mitarai Formation, loc. 1108). **6.** Plan view of mudstone containing articulated *Modiolus maedae* Hayami (arrowed) (lower Mitarai Formation, loc. 1005). Posterior parts of *M. maedae* are found.

1984; Aberhan, 1994).

Modiolus maedae-Tetorimya carinata assemblage

This assemblage contains the following bivalves: the deep-infaunal *Tetorimya carinata*, *Thracia shokawensis*, *Pleuromya hidensis*, and *Goniomya* sp.; the endobyssate *Modiolus maedae* and *Pinna* sp. aff. *P. sandsfootensis*; the shallow infaunal *Palaeonucula makitoensis*, "*Palaeoneilo*"

sp., and *Protocardia* sp.; and the epibyssate or free-living *Entolium inequivalve*, *Limatula iwayae*, *Oxytoma tetoriense*, *Chlamys mitaraiensis* and *Camptonectes* sp. (Figure 4).

M. maedae and *T. carinata* are characteristic species of this assemblage. The *M. maedae-T. carinata* assemblage consists of abundant deep-burrowers, two semi-infaunal taxa, and several shallow infaunal and epifaunal elements. The deep-burrowing, semi-infaunal and shallow infaunal bi-
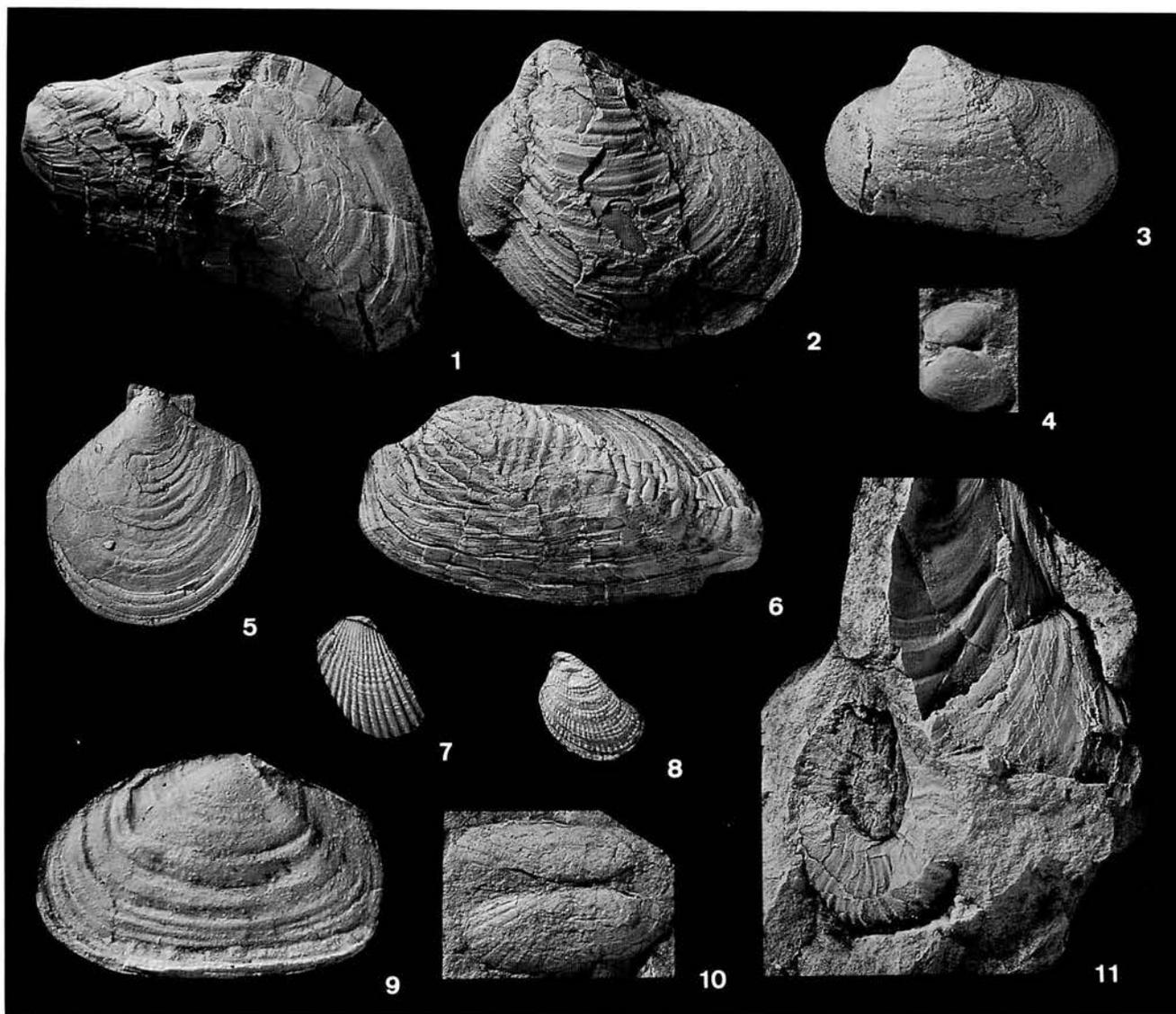

Figure 4. Bivalves from the Mitarai Formation. All specimens ×1.0. **1.** *Modiolus maedae* Hayami. Left external cast, lower Mitarai Formation, loc. 1108. **2.** *Tetorimya carinata* Hayami. Left valve, lower Mitarai Formation, loc. 2001. **3.** *Pleuromya hidensis* Hayami. Left external cast, lower Mitarai Formation, loc. 1108. **4.** *Protocardia* sp. with gaping articulated valves (butterfly position), lower Mitarai Formation, loc. 1108. **5.** *Entolium inequivalve* Hayami. Right valve, upper Mitarai Formation, loc. 801. **6.** *Goniomya* sp. Left external cast, lower Mitarai Formation, loc. 1108. **7.** *Limatula iwayae* Hayami. Right external cast, upper Mitarai Formation, loc. 1008. **8.** *Oxytoma tetoriense* Hayami. Left external cast, lower Mitarai Formation, loc. 1108. **9.** *Thracia shokawensis* Hayami. Left external cast, lower Mitarai Formation, loc. 1108. **10.** *Solemya suprajurensis* Hayami with gaping articulated valves (butterfly position), upper Mitarai Formation, loc. 801. **11.** Fragment of *Inoceramus maedae* Hayami (external mould) and ammonite from shell lens, lower Mitarai Formation, loc. 1005.

valves occur usually dispersed and are almost invariably preserved as articulated valves. *M. maedae*, *T. carinata* and *P. hidensis* are arranged with their sagittal plane perpendicular to the bedding plane with their posterodorsal or posterior margin pointing upward (Figures 3.4-6, 5) which is interpreted as keeping their life orientation. Especially all 50 individuals of *M. maedae* collected during the study are articulated and preserved *in situ*. Shells of *Pinna* sp. also preserve their life position with the umbones directed downward. Some of the shallow infaunal bivalves such as *Palaeonucula makitoensis* and *Protocardia* sp. are found articulated in butterfly position. Epifauna is usually disarticulated, only rarely articulated. Occasionally, disarticulated epifaunal bivalves, fine shell debris and crinoid fragments form small shell lenticles (about 1cm thick and 10 -30 cm wide) with plant fragments. This assemblage occurs in bioturbated mudstone with intercalated thin sandstone beds in the lower part of the Mitarai Formation, which represents inner shelf deposits within the transgressive phase of the formation.

Entolium inequivalve assemblage

The assemblage consists of the shallow-burrowing *Palaeonucula makitoensis* and "*Palaeoneilo*" sp., the epifaunal *Entolium inequivalve* and *Limatula iwayae*, and the deep-infaunal *Solemya suprajurensis*.

The *E. inequivalve* assemblage is characterized by a mixture of epifaunal and shallow infaunal bivalves. *E. inequivalve* and *L. iwayae* are common and occasionally preserved parallel to the bedding plane. Although the epifauna is usually disarticulated, the right and left valve of the same individual occasionally overlap. Shallow infaunal burrowers consist of the deposit-feeding bivalves *P. makitoensis* and "*Palaeoneilo*" sp., and are usually preserved in articulated condition. The very rare *S. suprajurensis* is also preserved with their valves articulated. This assemblage is found in bioturbated mudstone of the upper Mitarai Formation, except in its lower part (Locs. 801, 806, 1008).

Inoceramus maedae assemblage

The assemblage is characterized by the co-occurrence of the epifaunal bivalves *Inoceramus maedae*, *Entolium inequivalve*, *Limatula iwayae*, and *Oxytoma tetoriense*, and the shallow-burrowing *Palaeonucula makitoensis* and *Protocardia* sp.

Epifauna dominates, in particular disarticulated and fragmented valves of *I. maedae*. *E. inequivalve*, *L. iwayae*, *O. tetoriense*, *P. makitoensis* and *Protocardia* sp. rarely occur in disarticulated and fragmented condition. These bivalves usually form small shell lenses (20-100 cm wide) associated with ammonites, crinoids, and abundant plant fragments. Some of the ammonites are fragmented and show selective dissolution of inner whorls. The shell lenses commonly overlie HCS and parallel-laminated sandstone beds. This assemblage is found throughout the Mitarai Formation (Locs. 1004, 1009).

Trace fossils

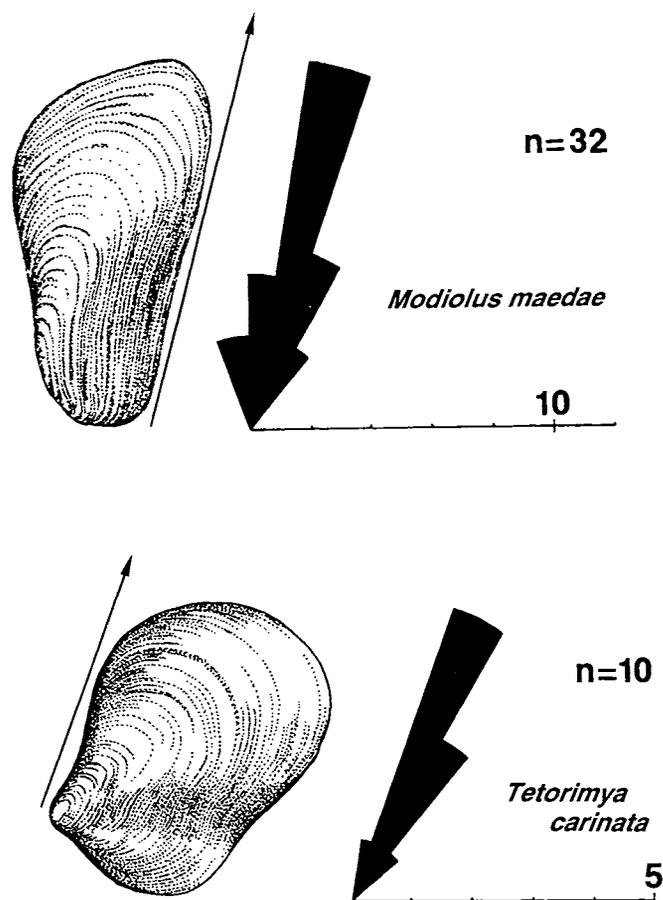The lower part of Mitarai Formation (inner shelf deposits)

Figure 5. Modes of fossil occurrences of *Modiolus maedae* Hayami and *Tetorimya carinata* Hayami. Almost all specimens are arranged with their sagittal plane perpendicular to the bedding plane with the posterodorsal or posterior margin pointing upward.

contains several kinds of trace fossils; *Spirophycus* isp., *Phycosiphon* isp., *Skolithos* isp., *Palaeophycus* isp., *Teredolites* isp., and a large two-dimensional burrow (*Beaconites*?; Figures 3.3, 6.1). *Skolithos* isp., *Palaeophycus* isp., the large two-dimensional burrows and intense obscure mottling are restricted to this horizon, whereas *Spirophycus* isp. and *Phycosiphon* isp. are very abundant throughout the Mitarai Formation.

The upper part of the Mitarai Formation, which can be interpreted to represent an outer shelf environment, is characterized by low diversity of trace fossils consisting solely of *Spirophycus* isp. and *Phycosiphon* isp. (Figure 6.2). Beds full of *Spirophycus* (15-70 cm thick) are common in this part.

Teredolites isp. is a boring in drift wood produced by wood-boring bivalves (Teredinidae). These wood pieces are commonly found within small shell lenses including *Inoceramus maedae* and ammonite fragments.
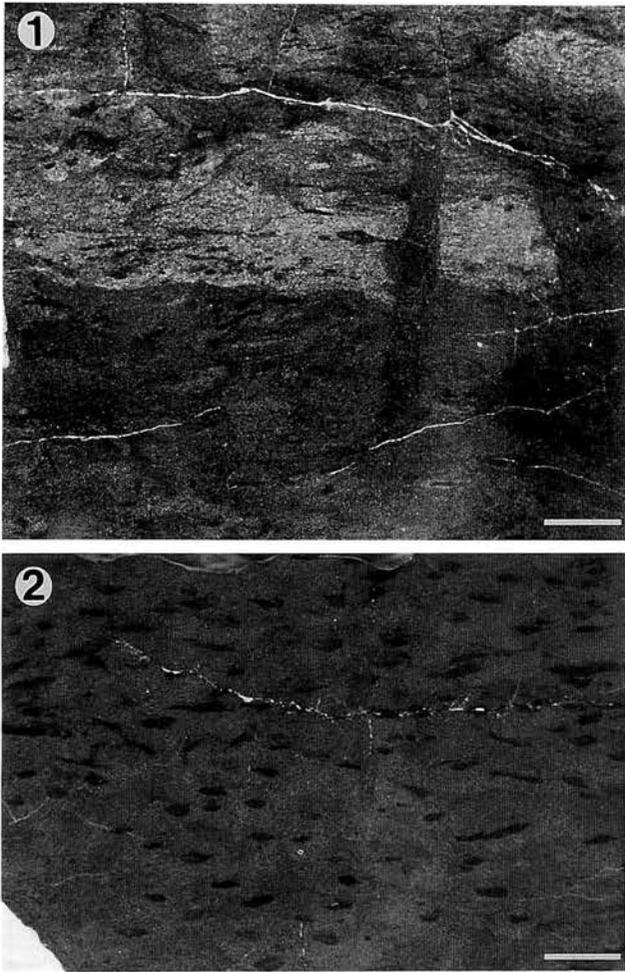
Figure 6. Vertical section of bioturbated mudstones of the lower Mitarai Formation: (1), loc. 1108, and the upper Mitarai Formation: (2), loc. 801. Scale bars are 1cm. **1.** *Spirophycus* isp., *Skolithos* isp. and obscure mottling are found. **2.** *Spirophycus* isp. Note low diversity of trace fossils.

Discussion

Autochthonous and allochthonous occurrence of bivalves

The *Modiolus maedae-Tetorimya carinata* assemblage is composed mainly of autochthonous bivalves. Almost all deep infaunal and semi-infaunal bivalves are preserved with their sagittal plane perpendicular to the bedding, which is indicative of their life orientation (Figures 3.3–6, 5, 7). In particular, the modes of occurrence of *Modiolus* and *Pinna* are very similar to that of present-day ones. Shallow infaunal bivalves, such as *Palaeonucula* and *Protocardia*, are articulated and do not retain their life position, indicating that these taxa were easily exhumed after death. The members of this assemblage probably occur more or less *in situ*, and are interpreted as the autochthonous fauna of inner shelf deposits.

By contrast, the *Entolium inequivalve* assemblage is dominated by the epifaunal recliners *E. inequivalve* and *Limatula iwayae* and occurs in outer shelf deposits. Most examples of the two taxa are preserved with their valves disarticulated; rarely, disarticulated valves of the same individual overlap each other. Therefore, most epifaunal species are interpreted to represent parautochthonous occurrences. Articulated *Palaeonucula makitoensis* and *Solemya suprajurensis* probably indicate autochthonous occurrences.

Epifaunal elements of the *Inoceramus maedae* assemblage are considered to be typically allochthonous. *I. maedae* from muddy shelf deposits invariably is fragmented and disarticulated and occurs in shell lenses overlying storm sand sheets. *I. maedae* occurs in coastal sandstones of the basal Otaniyama Formation (Loc. 1309), as well as in the HCS sandstones of the Ushimaru Formation (Maeda,1952; Hayami, 1960). Probably *I. maedae* underwent transport from nearshore areas during storm events.

Influence of low oxygen conditions on the infauna of the *Entolium inequivalve* assemblage

The *Entolium inequivalve* assemblage, occurring in open shelf environments, is composed of an autochthonous infauna and a parautochthonous free-living epifauna. The infauna was probably influenced by low oxygen conditions. The assemblage is characterized by a low-diversity fauna and consists of autochthonous *Palaeonucula makitoensis* and *Solemya suprajurensis* in association with reworked individuals of free-living *Entolium inequivalve* and byssate *Limatula iwayae*. These genera are typical of Jurassic mid- to outer-shelf and oxygen-controlled environments (Aberhan, 1994). Moreover, Recent representatives of *Solemya* live in muddy bays of stagnant water conditions and in deep-sea areas characterized by low oxygen levels, and are components of the chemosynthetic community (Reid and Bernard, 1980; Felbeck *et al.*, 1981). Therefore, the low diversity of this assemblage probably is a result of lowered oxygen levels within the sediment.

Furthermore, this assemblage is associated with the grazing traces (pascichnia) *Spirophycus* and *Phycosiphon*, whereas dwelling traces (domichnia) such as *Skolithos* and *Palaeophycus* are absent. These pascichnia exhibit a low-diversity, moderately high density and small size, suggestive of opportunistic producers (Bromley, 1996). Ekdale and Mason (1988) proposed that pascichnia-dominated trace fossil assemblages are formed under less oxygenated conditions than domichnia-dominated ones. Hence, the character of the ichnofauna supports our interpretation of relatively low oxygen-conditions.

Conclusions

1. Three bivalve assemblages are distinguished in the Jurassic Mitarai Formation, Tetori Group. The *Modiolus maedae-Tetorimya carinata* assemblage contains abundant semi-infaunal and deep-burrowing taxa in preserved life orientation and represents the undisturbed, autochthonous fauna of inner shelf environments. The *Entolium inequivalve* assemblage occurs in outer shelf deposits and is characterized by a mixture of autochthonous infaunal ele-
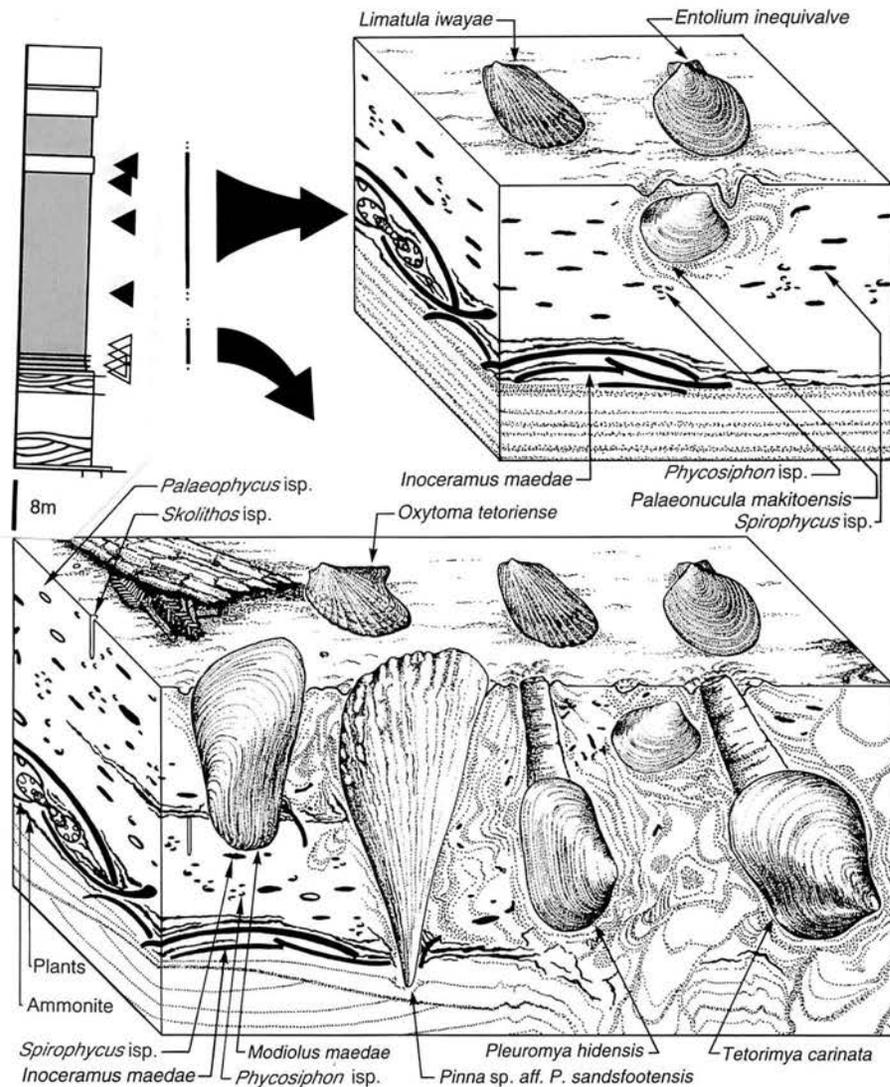
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Figure 7. Ecological reconstruction of the bivalve fauna in shelf deposits of the Mitarai Formation.

ments and parautochthonous byssate or free-living epifauna. The *Inoceramus maedae* assemblage consists of fragments and disarticulated valves and represents typical allochthonous occurrences. In particular *Inoceramus maedae* underwent transport from sandy nearshore areas.

2. The *Entolium inequivalve* assemblage contains the chemosymbiotic bivalve *Solemya*, and is associated with a low-diversity ichnofauna, which suggests lowered oxygen conditions.

3. Palaeoecological and taphonomic data allow a more refined reconstruction of palaeoenvironments and their changes through time than sedimentary features alone.

Acknowledgments

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Regular axopodial activity of *Diplosphaera hexagonalis* Haeckel (spheroidal spumellarian, Radiolaria)

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Abstract. The physiological ecology of a spherical polycystine species, *Diplosphaera hexagonalis* collected from the surface water of the Kuroshio Current in the East China Sea off Sesoko Island, Okinawa, was observed in a culture dish for three days. The observed specimen demonstrated cyclic extension and contraction of axopodia by a regular interval of ca. 630 seconds. Each cycle was divided intro four phases based on the state of the axopodia and movement of axopodial vacuoles. Vertical migration in response to axopodial motility was also observed. The specimen began to rise accompanied with the axopodial extension, floated in the seawater and often moved horizontally when its axopodia were radiated symmetrically, and began to sink in correspondence with the axopodial contraction. The effect of thermal currents on this behavior is easily neglected on the ground of the definite coincidence with the rhythmic extension and contraction of axopodia. The rhythm appears to play important roles in the physiological ecology of this species, including food capture and possibly buoyancy. The taxonomic section presents a nearly complete synonym list of *D. hexagonalis* and summarizes that the genus *Diplosphaera* is a senior synonym of *Astrosphaera*, *Drymosphaera* and *Leptosphaera*. Thus, *Diplosphaera hexagonalis* is the only valid name for this species, according to ICZN Article 55.3. *Diplosphaera* is considered herein to belong not to the family Actinommidae but to the Astrosphaeridae, unlike in most previous paleontological and biological studies. The family Macrosphaeridae Hollande and Enjumet, 1960, to which the genus *Diplosphaera* was assigned, is treated as an invalid name because the type genus *Macrosphaera* has not been established yet.

Key words: axopodia, *Diplosphaera hexagonalis*, East China Sea, living radiolaria, Okinawa, physiological ecology

Introduction

Radiolaria is an informal taxonomic group of planktonic unicellular Protoctista generally possessing a plane, line or point skeletal symmetry of the test. This group includes the classes Polycystina possessing a siliceous test, Acantharia with a strontium sulfate test, and Phaeodaria having a siliceous test with incorporated organic substances (Margulis and Schwartz, 1988; The Committee on Systematics and Evolution of the Society of Protozoologists, 1980). Of these radiolarians, solitary spheroidal Polycystina ranges in age from the middle Cambrian to the present (Nazarov, 1988). Since the polycystine group is widely distributed in the open oceans, information on its physiological ecology will provide new insights both in analysis of paleoceanographic analyses and the establishment of a natural classification.

Although previous studies have revealed detailed information on physiological and ecological information (living features, longevity, prey, and skeletal growth under culture conditions and some fine structures) of some discoidal spumellarians such as *Dictyocoryne truncatum* (Ehrenberg) and *Spongaster tetras* (Haeckel) (e.g. Anderson *et al.*, 1989a, 1989b; Anderson and Matsuoka, 1992; Matsuoka, 1992; Matsuoka and Anderson, 1992; Sugiyama and Anderson, 1997), we know little about the physiological ecology of spheroidal spumellarians. Examination of the cytological structures of solitary spherical polycystines has provided some groundwork for these analyses (Anderson, 1976, 1981, 1983; Anderson *et al.*, 1998; Cachon and Cachon, 1972a, 1972b, 1976, 1985; Haeckel, 1862; Haecker, 1907; Hertwig, 1879, 1932; Hollande and Enjumet, 1954, 1960; Hollande *et al.*, 1965; Swanberg *et al.*, 1990),
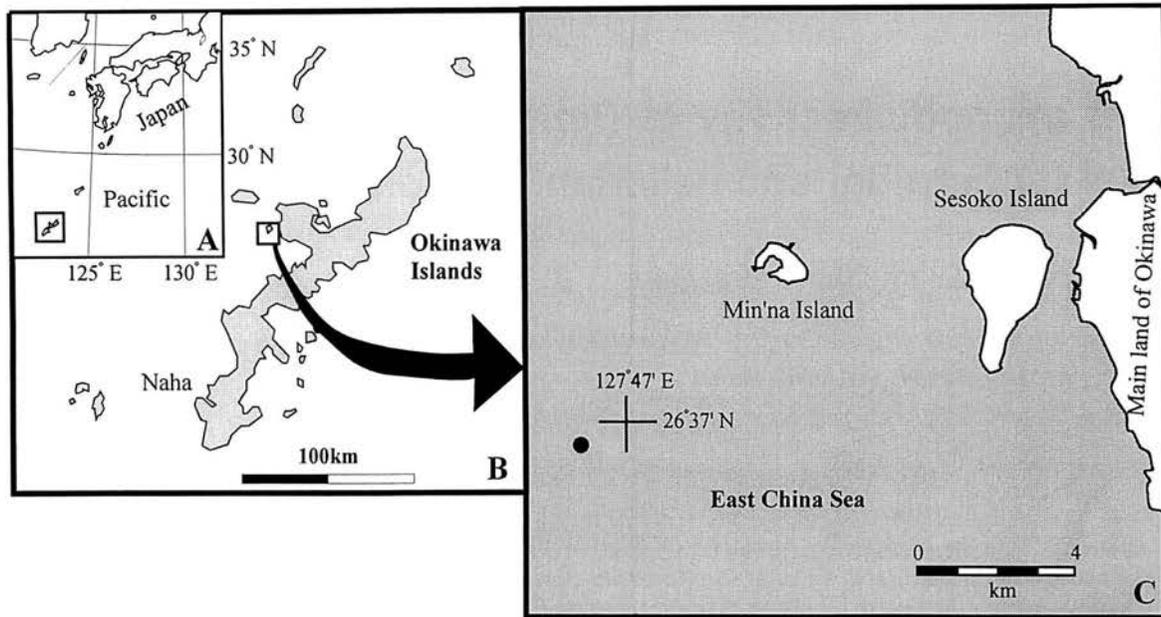
Figure 1. Sampling location. **A.** A map showing the position of Okinawa Islands (open square). **B.** The Okinawa Islands and its adjacent islands. **C.** The sampling location (solid circle).

but there have been only limited investigations of the nutritional role of symbionts (Anderson *et al.*, 1983, 1985) and the possible reproductive role of swarm cells released by mature specimens during laboratory culture (Anderson, 1978, 1984 and others).

In order to observe living features of radiolarians in the surface seawater of the Kuroshio Current, some Japanese radiolarian paleontologists have collaborated on observation tours of living organisms at the Sesoko Tropical Biosphere Research Center (STBRC), University of the Ryukyus, Sesoko Island, Okinawa Prefecture, Southwest Japan, since 1997 (Figure 1). During the 2nd tour held on October 5th to 14th, 1998, we made three samplings on October 7th, 8th and 12th, 1998, and encountered approximately 40 species in laboratory examinations. As a result, we obtained extensive information about their pseudopodial behavior using normal still and video photography.

Among the observed radiolarians, we particularly traced continuous axopodial activity of one specimen of *Diplosphaera hexagonalis* Haeckel, a solitary spheroidal spumellarian representative of the observed radiolarian fauna, during four days from October 7th to 10th, 1998. Our interest was especially aroused since it systematically repeated axopodial extension and contraction cycles at regular intervals. In this report, we present a detailed description of the features of the extension and contraction cycles and possible implication for the physiological ecology of *D. hexagonalis* in relation to this cyclical axopodial activity. A probable physiological function and an explanation of a mechanism of the cycles are also discussed. This paper also describes the taxonomic classification of *D. hexagonalis* in order to resolve the confusion surrounding its generic and family positions.

Materials and methods

Plankton samples containing the observed *Diplosphaera hexagonalis* were collected on October 7th, 1998, at a locality (Station 1; Figure 1) approximately 12 km west of Sesoko Island and more or less affected by the warm-water Kuroshio Current. Ambient seawater temperature and salinity at the sampling location were 28.5 °C and 34.0 ‰, respectively. The sample was collected by 3 min. tow using a 36 μm mesh net. On return to the laboratory at STBRC, small portions of the sample were placed into sorting dishes, examined with binocular microscopes, and each individual radiolarian was separated from other matter using a Pasteur pipette into a glass vial (ca. 25 mm diam. ×50 mm tall), a glass culture dish (50 mm or 90 mm diam.) or a single well of a multiwell tissue culture plate (23 mm diam. ×20 mm tall) (FALCON® 3043, Becton Dickinson Labware, Lincoln Park, N. J.) previously filled with ambient seawater from the sampling location. These culture containers with radiolarians were placed either in a temperature-controlled bath with fluorescent light units or in temperature-uncontrolled baths without fluorescent light units. The temperature of the former bath was kept at 28 °C by a heater-chiller balance, whereas that of the latter was about 27 °C, the room temperature of the laboratory, throughout the culture work. Both types of baths were covered by metal foil during the night to produce a day/night cycle. The radiolarians were cultured without exchange of the seawater, no supply of food, nor removal of any filth.

Continuous axopodial activity of one *D. hexagonalis* individual was observed from October 7th to 10th October, 1998, using Nikon Diaphot and Olympus CK2 inverted microscopes, mainly following previously established protocols

(Anderson *et al.*, 1989a). We used a video camera (SONY HANDYCAM DCR-TRV9), with a resolution of 0.76 million pixels, attached to the Nikon Diaphot microscope through a TV adapter and digital camera (FUJIFIX HC–300) in order to record vivid images of radiolarian activity. The observations were recorded on five 60–minute videotapes and more than 10 pictures. Only for one individual was the continuous axopodial activity described in this paper ascertained. Although six to ten other individuals were observed with two inverted microscopes for snapshots using normal cameras as well, we did not confirm whether other specimens show continuous axopodial behavior or not.

Observational results of living *Diplosphaera hexagonalis*

The skeleton of *Diplosphaera hexagonalis* (Figure 2.1) consists of one spherical primus exosphere, one polyhedral secondus exosphere with triangular frameworks, and a dozen triradiate auxiliary spines radiating from the primus exosphere (for skeletal terms see Suzuki, 1998). This species was assigned to the family Astrosphaeridae based on criteria published by Hollande and Enjumet (1960).

Living *D. hexagonalis* possesses a dark, grayish red, spherical cell body within the secondus exosphere, and fine, transparent axopodia radiating from the surface of the cell body (Figure 2.2, 2.3). The spherical cell is composed of
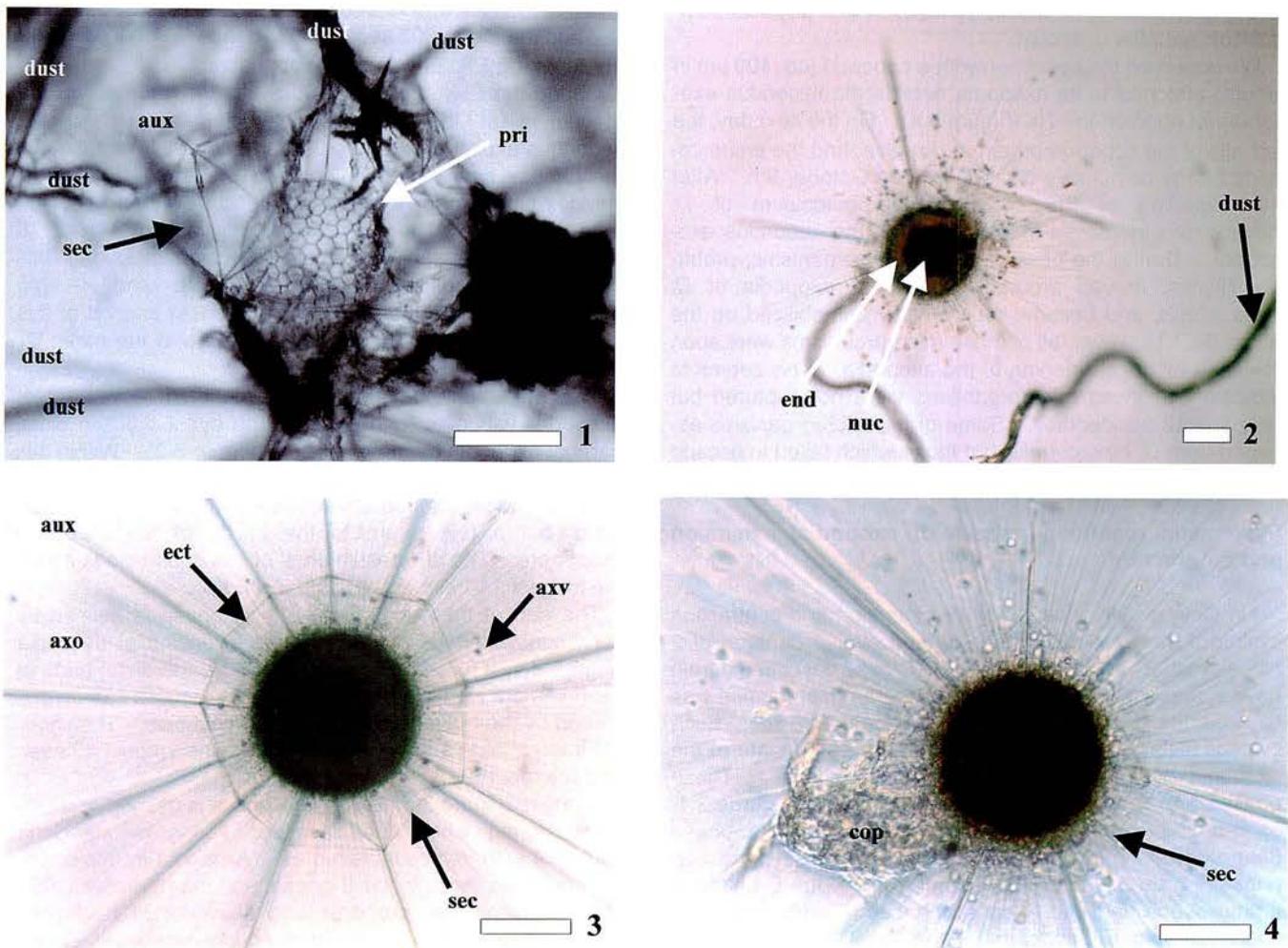

Figure 2. General view of *Diplosphaera hexagonalis* Haeckel. 1. Light transmitted microscopic photograph. 2–4. Inverted microscopic photographs, showing a bottom view. Scale bars are equal to 100 μm. 1. Skeleton structure of *D. hexagonalis* possessing a spherical primus exosphere (pri) and a polygonal frame of the secondus exosphere (sec). These two shells are connected with numerous auxiliary spines (aux). 2. Numerous yellow–brown axopodial vacuoles surround the endoplasm. Axopodia may begin to extend (EII–subphase). 3. This specimen has a small amount of axopodial vacuoles. Both the fine axopodia and axopodial vacuoles near the endoplasm indicate that this specimen is in the EI–subphase. 4. A copepod attached to *D. hexagonalis* is partially digested by the specimen. Abbreviations: nuc, nucleus; end, endoplasm; cop, copepod; ect, ectoplasm; axo, axopodia; aux, auxiliary spine; axv, axopodium vacuole; pri, primus exosphere.

two parts: (1) a more transparent light-colored, bubble-like outer part between the primus and secondus exospheres, corresponding to ectoplasm, and (2) a more opaque, spherical inner part within the primus exosphere. The latter is further subdivided into a deeper-colored central part, and the surrounding endoplasm which is slightly lighter-colored. The inner part is referred to as a nucleus according to Hollande and Enjumet (1960).

The length of the axopodia changes periodically from a minimum of 0.12 – 0.13 mm to longer than 2.0 mm. Vacuoles, dark amber or reddish gray in color, globular in shape and of a few to ten μm in diameter are displayed on each axopodium. The total number of vacuoles varies among specimens but it typically is about 200. The distribution of the vacuoles on the axopodia changes with the length of the axopodia. The biological function and physical composition remains unknown.

We observed the specimen with a copepod (ca. 400 μm in length) attached to its axopodia outside the secondus exosphere at noon on the 7th (Figure 2.4). On the next day, the entrails of the copepod began to dissolve, and the entire copepod body completely disappeared on October 9th. After the digestion of the copepod, the ectoplasm of *D. hexagonalis* increased in volume to fill the secondus exosphere. During the observations, other organisms, probably ciliates, moved around the halo of axopodia of *D. hexagonalis*, and became momentarily immobilized on the axopodia. However, all of these microorganisms were soon released by the shortening of the axopodia. This seems to indicate that these microorganisms were not captured but only snared accidentally. Some of the microorganisms escaped from *D. hexagonalis*, but those which failed to escape from the specimen were again snared by the axopodia.

Systematic repetition pattern of axopodial extension and contraction

On October 9th, a series of 17 extension and contraction cycles of the axopodia was observed over a duration of 2 hrs. 44 min. 21 sec. (Figure 4). The cycles described herein have a reasonably regular interval; the longest interval was 677 sec, the shortest 550 sec and the mean 633 sec. Each cycle is divisible into four phases based on the state of the axopodia and movement of axopodial vacuoles. These phases are as follows: S-phase (short phase, Figures 3.1, 5), E-phase (extension phase, Figures 3.2-3.5, 5), L-phase (long phase, Figures 3.6-3.7, 5) and C-phase (contraction phase, Figres 3.8-3.12, 5). Among them, the E-phase is further subdivided into three subphases (EI-subphase, EII-subphase and EIII-subphase), and the C-phase into two subphases (CI-subphase and CII-subphase). Although each cycle has almost the same interval, as mentioned above, phase and subphase intervals in each cycle differ considerably as shown in Figure 4. We tried to interrupt the axopodial movement by vibrations produced by tapping the dish with sticks but the cyclicity was uninterrupted, and what is more, the regularity was maintained in spite of contact by ciliates and other small organisms.

S-phase (Figure 3.1).—This phase is defined as an interval after C-phase, during which axopodial length is at a mini-

mum. Axopodia in this phase are composed of two kinds; one is named H-index type and the other is L-index type. The former type of axopodia has relatively high refractive index against seawater under the microscope, whereas the refractive index of the latter type is lower. Usually, H-index type axopodia are shorter than the L-index type in this phase. The length of the H-index type axopodia is about half of the primus exosphere diameter, while that of the L-index type axopodia is approximately double that of the H-index type. In this phase, most vacuoles on both types of axopodia are rarely moved outside the ectoplasm. The shortest interval of this phase is 4 sec, the longest 18 sec and the mean 12 sec.

E-phase.— This phase is defined as an interval after S-phase, during which most axopodia are extending. The shortest interval of this phase is 160 sec, the longest 474 sec and the mean 302 sec. The E-phase is subdivided into the following EI-, EII- and EIII-subphases.

During the EI-subphase, we still cannot see the outward movement of the axopodial vacuoles situated in the secondus exosphere (Figure 3.2). In contrast, vacuoles on the L-index type axopodia begin to move slowly inwards. H-index type axopodia begin to extend slowly and become more slender. The refractive index of both types of axopodia decreases with their extension. During this subphase, the difference between the L- and H- type axopodia becomes indistinct. The shortest interval of this subphase is 14 sec, the longest 86 sec and the mean 31 sec.

The EII-subphase starts by the outward movement of axopodial vacuoles, and ends by the event that the distal parts of axopodia become invisible (Figure 3.3). Within this subphase the axopodia maintain a continuous and slow extension. Most axopodial vacuoles continue to move outward, but a few return to the inside of the secondus exosphere. The shortest interval of this subphase is 2 sec, the longest 140 sec and the mean 85 sec.

The end of the subsequent EIII-subphase is defined by unrecognizableness of the outward extension of axopodia (Figure 3.4, 3.5). During this subphase, the distal parts of axopodia are invisible but the outward extension can be discerned by the movement of axopodial vacuoles. The shortest interval of this subphase is 46 sec, the longest 433 sec and the mean 217 sec.

L-phase (Figure 3.6, 3.7).—This phase is defined as an interval during which the specimen keeps radiate, long axopodia with immobile vacuoles. Axopodia in this phase are finer than those in the S-phase, and the refractive difference between the axopodia and seawater is negligible. Axopodial vacuoles are heterogeneously distributed around the halo of axopodia. The shortest interval of this phase is 29 sec, the longest 205 sec and the mean 100 sec.

C-phase. —This phase subsequent to the L-phase is marked by an abrupt contraction of axopodia towards the endoplasm, and ends when most axopodia finish shrinking. The shortest interval of this phase is 59 sec, the longest 282 sec and the mean 168 sec. This phase is subdivided into CI- and CII-subphases as follows.

In the CI-subphase, axopodial vacuoles begin to be moved back to the ectoplasm although the axopodia are not
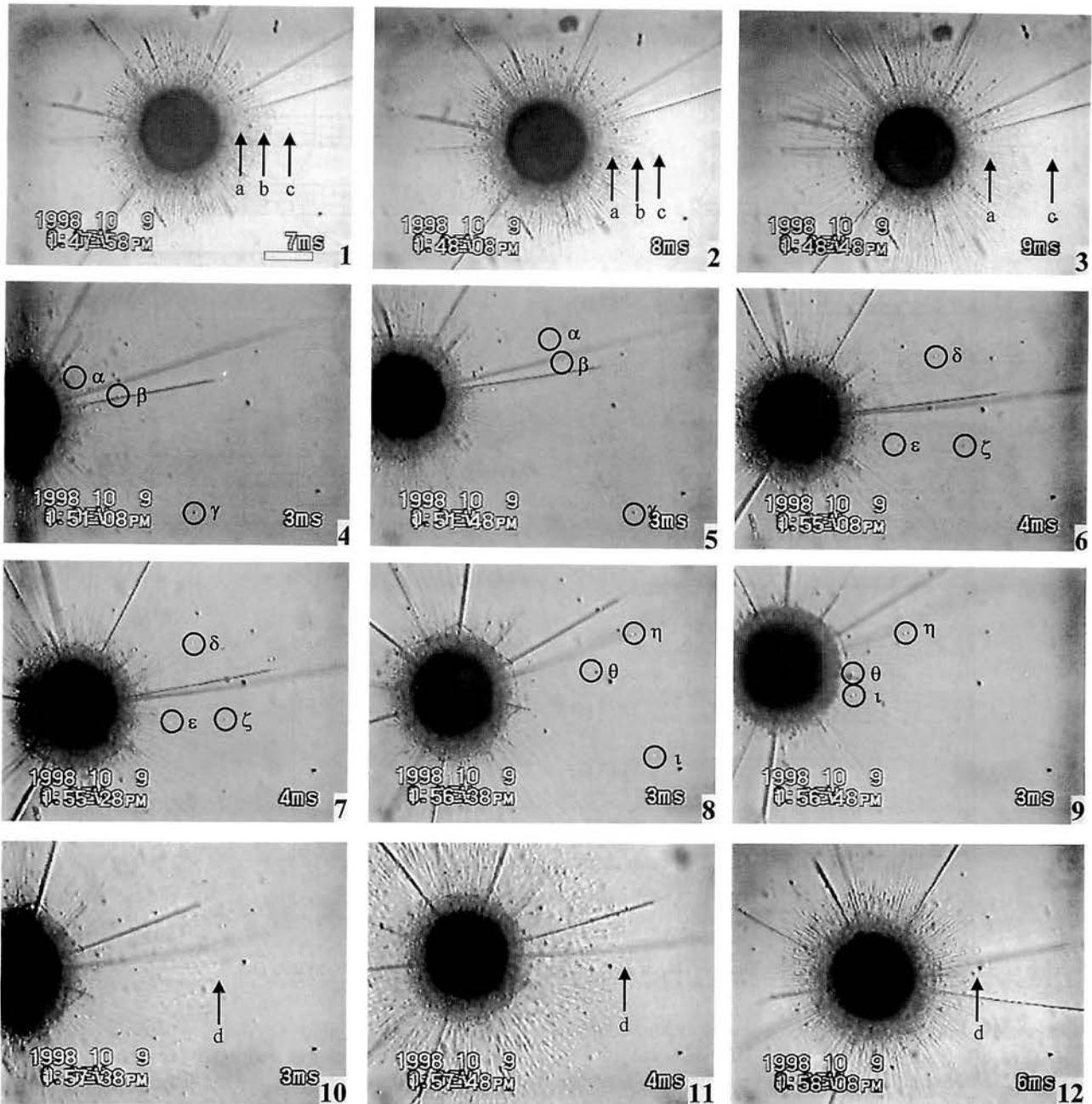
Figure 3. Four phases of extension and contraction of the axopodia. Scale bar is equal to 100 μm. **1.** S-phase. **2.** EI-subphase. **3.** EII-subphase. **4, 5.** EIII-subphase. **6, 7.** L-phase. **8, 9.** CI-subphase. **10-12.** CII-subphase. Arrows: a, the periphery of the dominant axopodial vacuoles; b, the distal part of H-index type axopodia; c, the distal part of L-index type axopodia; and d, the distal part of the contractile axopodia. Open circles with Greek symbols in Figure 3.4-3.9 represent axopodial vacuoles. The same Greek symbols in different figures imply the same axopodial vacuole.

yet contracted (Figure 3.8, 3.9). During this subphase the refractive index of the axopodia increases gradually accompanied by thickening of the axopodial diameter at the proximal point where it attaches to the cell body. A few axopodial vacuoles are moved inward relatively quickly. These vacuoles pass the secondus exosphere and reach near the surface of endoplasm. The shortest interval of this subphase is 34 sec, the longest 227 sec and the mean 133 sec.

The CII-subphase is characterized by an abrupt contraction of axopodia and followed by the S-phase after complete cessation of axopodial shrinking. At the beginning of this
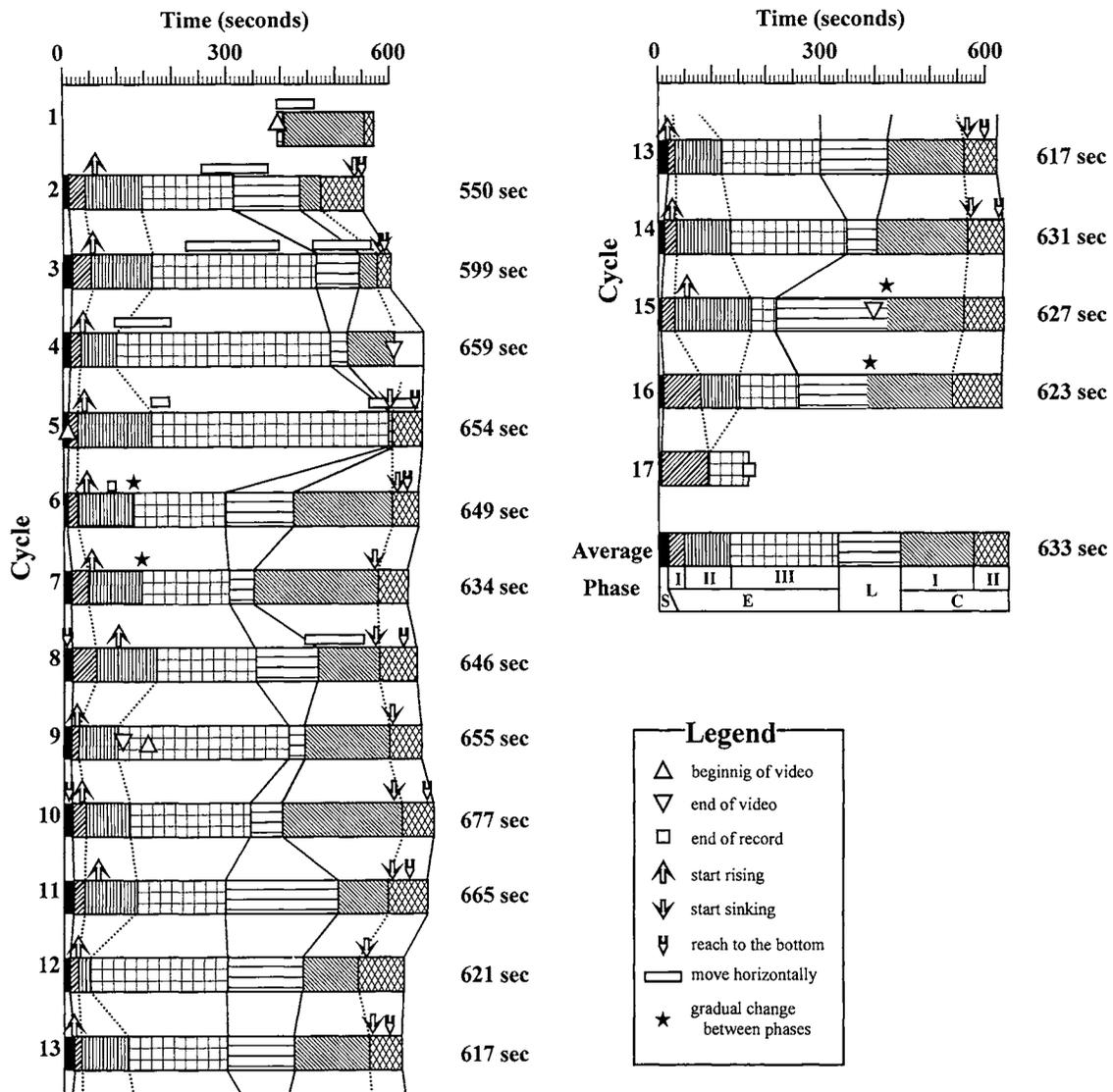
Figure 4. Diagram illustrating the four phases of the axopodia on 9th, Oct, 1998.

subphase, the periphery of the axopodia shrinks suddenly (arrow d in the Figure 3.10-3.12). The vacuoles on the distal part of the axopodia are moved inwards by this action, and the refractive index of the axopodia increases immediately (Figure 3.10). Subsequently, the axopodia shorten in a stepwise fashion with a concomitant increase of the refractive index at each step. The axopodial vacuoles are also moved inwards in the same stepwise fashion. The halo of axopodia in this subphase has a gelatinous spherical envelope with numerous pigmented dots (Figure 3.11). The shortest portion of this subphase is 25 sec, the longest 90 sec and the mean 64 sec.

Vertical migration in connection to axopodial motility

During the observation of *Diplosphaera hexagonalis*, we found that rising, floating and sinking motions in the culture vessel are always related to axopodial extension and contraction. Vertical migration was confirmed with video re-

cords and was counted 14 times at each expansion and contraction rhythm of the axopodia except for the last two rhythmic cycles which were not recorded on the video tape (Figure 4). It would be doubtful if this behavior depended on the effect of thermal currents in the observed dish, but the possibility of this effect is easily discarded: the relation of floating and sinking correlated with the changes in axopodial rhythm is so strict, and the radiolarian specimen did not show any other irregular rising and sinking movement in spite of particular careful observation as shown in Figure 4.

The specimen begins to rise from the bottom of the vessel during the interval from the middle EI-subphase to early EII-subphase accompanied with the axopodial extension (the up-arrows in Figure 4). Cessation of this movement is quite gradual. The specimen floats in the seawater and often moves horizontally during the EII-subphase through the middle CII subphase (the open rectangles in Figure 4). When the specimen is floating, its axopodia are radiated symmetri-
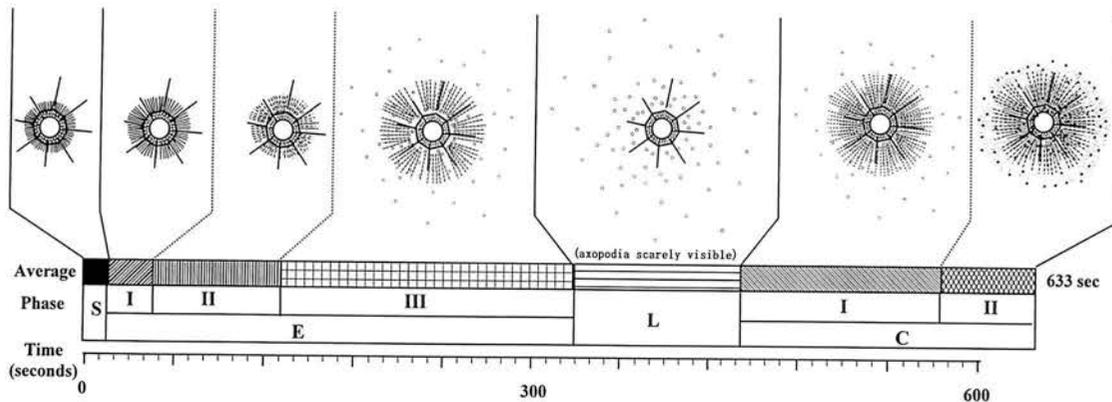
Figure 5. Schematic illustration of the cycle of extension and contraction of the axopodia. Solid thick line: siliceous skeleton. Solid fine line: H–index type axopodia. Dark gray small dot: axopodium vacuole. Dark to light gray fine lines: L–index type axopodia. The darkness of lines indicates a refractive index between the axopodia and the seawater.

cally from the cell body, which drifts in all directions very slowly. Around the late CI-subphase to the early CII-subphase, the specimen begins to sink in correspondence with the axopodial contraction (the down-arrows in Figure 4). After a few to 60 seconds, the body of the specimen reaches the bottom of the culture vessel.

Discussion

Although a rhythmic extension and contraction of radiolarian axopodia has been reported by Anderson (1983), the observation herein is the first evidence showing a regular rhythm of axopodial movement at approximately ten and a half-minute intervals. Our observation demonstrated that videotape recording is a fairly useful and advanced method by which to document the continuous activities of radiolarian axopodia. We accumulated a continuous record of *D. hexagonalis* with cyclic axopodial motions only from one specimen using videotapes, but other collected specimens (more than ten specimens) also appeared to have the same kind of rhythmical activity, judging from a series of still photograph images. Consequently, we can conclude that the above described cyclical motions are a common physical behavior of *D. hexagonalis*.

Spherical symmetry is probably not a major predictive factor in the occurrence of the regular, cyclical axopodial contractions observed in *D. hexagonalis*. Several spherical spumellarian species of genera with a double shell (e.g. *Hexacontium* spp. and *Spongodrymus* sp. indet.) also were observed during this experiment, but they never exhibited a similar rhythmic motion of the axopodial array. Likewise, other protista, including Acantharia and Heliozoa, have a symmetric distribution of axopodia around the cell body, but we have no information if they possess possible cyclical patterns as observed in *D. hexagonalis*. Currently, therefore, we can infer that the observed regular rhythm is peculiar to *D. hexagonalis* and its related taxa, and that a particular cytological apparatus of *D. hexagonalis* likely produces this rhythm.

The cytology of *D. hexagonalis* is unusual. There is no axoplast and the nucleus is surrounded by large vacuoles

(Hollande and Enjumet, 1960). However, as with other axopodial-bearing species, the axopodium contains an array of axially oriented internal microtubules (axoneme). An axoplast is absent also in other spherical polycystine genera including *Rhizoplegma*, *Centrocubus*, *Octodendron* and *Haplosphaera* (Cachon and Cachon, 1985). It is not known presently whether the absence of an axoplast is related to the regular rhythmic cycles of extension and contraction of the axopodia in *D. hexagonalis*. When the axoplast is present in other species, it is rich in tubulin monomers that polymerize to form microtubules and is usually located centrally where the microtubules of the axonemes converge. Hence, the axoplast may provide an organizing center for the axonemes. In the absence of an axoplast, the regular array of large vacuoles in *D. hexagonalis* could serve to support the axonemes and in addition may contribute to the cytoplasmic volume as the periphery array of axopodia expands. If the expansion of the axopodial array indeed contributes to enhanced buoyancy, then there must be a source of additional cytoplasmic volume to supply the added low-density mass produced by the expansion of the peripheral corona of axopodia. If the expanding axopodia were simply constructed at the expanse of existing cytoplasmic mass in the main cell body, without further expansion of internal volume, there would be no net gain in buoyancy. If, however, the vacuoles increase in size as the axopodia expand, this could result in less mass per unit volume, and produce an increased buoyancy. Likewise, according to this model, as the axopodia contract, the vacuoles may decrease in volume, thus accommodating the inward flow of cytoplasm toward the central body and producing a concomitant decrease in buoyancy. A dynamic adjustment in volume by the central vacuoles may provide a necessary mechanism for maintaining appropriate mass balance required to control buoyancy as the peripheral axopodial array expands and contracts. The rhythmic extension and contraction of the axopodia appear to play important roles in the physiological ecology and physical functioning of *D. hexagonalis*, including food capture and possibly the regulation of buoyancy as reported here.

The extension of protozoan axopodia usually occurs by

elongation of the microtubules when additional tubulin is polymerized at one end and they are shortened by disassembly of the tubulin, all in response to biochemically regulated cycles (e.g., Tilney and Byers, 1969). To understand the mechanism of the observed rhythmic extension and contraction of axopodia, it is essential to investigate more thoroughly changes in cytological structures and correlated biochemical processes with the aim of creating a more complete model of the rhythmic activity of axopodia in *D. hexagonalis*.

Systematic description

Family Astrosphaeridae Haeckel 1882,
sensu Hollande and Enjumet 1960
Genus *Diplosphaera* Haeckel 1860, emend.
Hollande and Enjumet, 1960

Type species.—*Astrosphaera gracilis* Haeckel 1862, designated by Campbell (1954).

Diplosphaera Haeckel, 1860, p. 804; Haeckel 1887, p. 246; Campbell, 1954, D.62; Hollande and Enjumet, 1960, p. 116; Kozur and Mostler, 1979, p. 12.
Astrosphaera Haeckel 1887, p. 250; Campbell, 1954, D61.
Drymosphaera Haeckel 1882, p. 452; Haeckel 1887, p. 248; Campbell, 1954, D.62.
Leptosphaera Haeckel, 1887, p. 243-244; Campbell, 1954, D.62.

Remarks.—*Diplosphaera* is regarded as the senior synonym of three other genera, *Astrosphaera, Drymosphaera* and *Leptosphaera*, based on the ontogenetic growth change of their skeletal structures and similarity of their cytological structures (Hollande and Enjumet, 1960). According to them, the *Leptosphaera*-form, the youngest, possesses two exospheres without by-spines. *Diplosphaera*- and *Drymosphaera*- forms appear in the next ontogenetic growth stage through the development of by-spines on one of these. When both exospheres have by-spines, this form is referred as an *Astrosphaera*-form.

Diplosphaera has been assigned to three different families: classical studies described it as a member of the Astrosphaeridae Haeckel 1882 (e.g. Haeckel, 1882, 1887; Campbell, 1954; Mast, 1910). Recent paleontologists and paleoceanographers prefer to assign it to the Actinommidae Haeckel 1862 (e.g. Kozur and Mostler, 1979; Takahashi, 1991). Finally, cytological researchers have regarded it as a member of "Macrosphaeridae" Hollande and Enjumet 1960 (e.g. Anderson, 1983; Cachon and Cachon, 1985; Hollande and Enjumet, 1960). However, since *Macrosphaera* had not been proposed as a genus name, the family name "Macrosphaeridae" violates Art 29.1 of ICZN (1999), which states that a family-group name is formed by adding the termination -idae to the stem of the name of the type genus, or to the entire name of the type genus. *Diplosphaera* is cytologically closely similar to the genus *Haplosphaera* Hollande and Enjumet 1960, the type genus of the "Macrosphaeridae" (Hollande and Enjumet, 1960). The phylogenetically close relationship between *Diplosphaera* and *Haplosphaera* suggests that the family

"Macrosphaeridae" is included in the Astrosphaeridae.

Hollande and Enjumet (1960) revealed that the genus *Actinomma* Haeckel 1862, the type genus of the Actinommidae, is one of the centroaxoplastid spumellarians with the axoplast enclosed by the nuclear membranous envelope, whereas the genus *Diplosphaera* of the Astrosphaeridae belongs to the anaxoplastid spumellarians without axoplast. This cytological difference between the Actinommidae and Astrosphaeridae suggests that *Diplosphaera* does not belong to the Actinommidae.

Almost all species assigned to *Diplosphaera* have been recovered from surface sediment or plankton samples due to their fragile skeletons. Only one species, *Drymosphaera ? pseudosagenoscena* Sugiyama 1992, is known from the lower Miocene (Sugiyama, 1992). All assigned species other than *D.? pseudosagenoscena* lack a microsphere, so that the lower Miocene species appears to belong to another genus.

Range.—Recent as far as known.
Known occurrence.—Equatorial and North Pacific, equatorial Atlantic and Mediterranean.

Diplosphaera hexagonalis Haeckel, 1887

Diplosphaera hexagonalis Haeckel 1887, p. 246, pl. 19, fig. 3; Hollande and Enjumet, 1960, p. 116, pl. 12, fig. 6, pl. 15, fig. 11, pl. 23, fig. 2, pl. 26, fig. 2: Cachon and Cachon, 1972a, pl. 35, figs. b, c; Anderson, 1983, p. 66-67; Fujioka, 1990, p. 136, pl. 39, fig. 7.
Astrosphaera hexagonalis Haeckel 1887, p. 250, pl. 19, fig. 4; Mast, 1910, p. 52; Popofsky, 1912, p. 105-106, text-fig. 16, pl. 8, fig. 2; Sugano, 1937, p. 64, figs. 21; Renz, 1976, p. 100-101, pl. 2, fig. 12; Tan and Tchang, 1976, p. 229, figs. 4a, b; Takahashi and Honjo, 1981, p. 147, pl. 2, fig. 12; Nishimura and Yamauchi, 1984, p. 24, pl. 14, figs. 1, 2; Boltovskoy and Jankilevich, 1985, pl. 1, fig. 17; Yamauchi, 1986, pl. 2, fig. 3; Fujioka, 1990, p. 136, pl. 38, fig. 7; Yeh and Cheng, 1990, pl. 3, fig. 2; Takahashi, 1991, p. 69, pl. 11, figs. 1-3; Boltovskoy, Alder and Abelmann, 1993, p. 1891; Tan, 1998, p. 164, figs. 152a, b (= the same figures of Tan and Tchang, 1976); Boltovskoy, 1998, p. 41, figs. 15-40.
Leptosphaera hexagonalis Haeckel 1887, p. 244, pl. 19, fig. 2. [nomen oblitum]

Remarks. — Most previous authors have identified *D. hexagonalis* as a species of *Astrosphaera*. As mentioned in the generic remarks, *Astrosphaera* is a junior synonym of the genus *Diplosphaera* (Hollande and Enjumet, 1960; Kozur and Mostler, 1979), which means that *Astrosphaera hexagonalis* is an unavailable name (Article 53.3 of ICZN, 1999). Thus, *Diplosphaera hexagonalis* is the valid name of this species.

Skeletal residues are obtained from surface sediment in the eastern Pacific Ocean, China Sea, and the Mediterranean (Tan and Tchang, 1976; Nishimura and Yamauchi, 1984), whereas they are not found in the sediment from the center of the equatorial Pacific (Renz, 1976; Takahashi, 1991). The skeleton of this species appears to dissolve easily at greater water depth as discussed by Takahashi (1991).

Known Range.—Recent.

Occurrences.—Equatorial Pacific, equatorial Atlantic, East China Sea, South China Sea, east off Okinawa, Shikoku and Taiwan, Mediterranean and west Patagonia.

Habitat.—Warm seawater. Surface to 300 m depth (Hollande and Enjumet, 1960; Renz, 1976).

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Return of published figures. The manuscripts of the papers published will not be returned to the authors. However, figures will be returned upon request by the authors after the paper has been published.

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行 事 予 定

◎第151回例会は，2002年1月26日（土），1月27日（日）に鹿児島大学理学部で開催されます．1月27日（日）午後に公開講演として「21世紀は自然史の時代 ―古生物学・フィールド科学からの提言―：世話人，森 啓・矢島道子」を実施致します．一般講演の申し込み締切は11月30日（金）です．

◎2002年年会・総会（2002年7月上旬開催予定）には福井県立恐竜博物館から開催申し込みがありました．また，第152回例会（2003年1月下旬開催予定）には横浜国立大学教育人間科学部から開催申し込みがありました．

◎古生物学会では，小人数で実施されるワークショップやショートコースを主催しております．学会から金銭を含む援助を行なうことができますので，企画をお持ちの方は行事係までお問い合せ下さい．

個人講演・シンポジウム案の申し込み方法
　個人講演の申し込みは予稿集原稿を直接行事係へお送り下さい．e-mail やファックスでの申し込みは，原則として受け付けておりません．
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