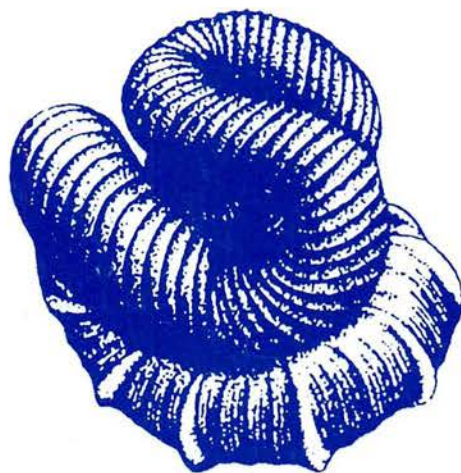


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Cover: Idealized sketch of *Nipponites mirabilis* Yabe, a Late Cretaceous (Turonian) nosteratid ammonite. Various reconstructions of the mode of life of this species have been proposed, because of its curiously meandering shell form (after T. Okamoto,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

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Recognition of breeding populations in foraminifera: an example using the genus *Glabratella*

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Abstract. Four morphospecies of foraminifera, *Glabratella opercularis*, *G. subopercularis*, *G. nakamurai*, and *G. patelliformis*, all of which have similar test morphologies, were reclassified by the use of both morphological characters and interbreeding experiments. Because specimens of *Glabratella* have been shown to reproduce sexually, it should be possible to determine breeding populational boundaries within *Glabratella* and to compare these with morphologically based taxonomic boundaries.

Using stable characters, three morphogroups were reclassified from the four morphospecies. Laboratory interbreeding experiments revealed that individuals belonging to the same morphogroup formed gamontogamous pairs and then reproduced. However, individuals belonging to different morphogroups did not produce any gamontogamous pairs. This indicates that each of the reclassified morphogroups represents a distinct breeding population.

Within the same morphogroup, individuals collected from two different localities closer than 100 km apart could interbreed with each other. However, individuals from more than 500 km apart could not breed with each other, even though the morphological characters of the individuals were very similar. This suggests that the population structure of the *P. opercularis* morphogroup is very similar to those of ring species.

Key words: benthic foraminifera, breeding populations, interbreeding experiments, morphospecies, ring species

Introduction

Conventionally, the species-level systematics of foraminifera have been carried out only with morphological characters of the test. Recently, biogeographic data, indicating areal and depth distributions in the sea, have also been used for defining foraminiferal species in addition to morphological data (e. g., Matoba, 1970). Fifty or sixty thousand foraminiferal morphospecies, both modern and extinct ones, have been described (Bock *et al.*, 1985; Loeblich and Tappan, 1988; Culver, 1993). However, doubt remains whether or not foraminiferal species defined by test morphologies are equivalent to breeding populations that can interbreed within a morphologically defined population (Boltovskoy and Wright, 1976).

According to the definition of Mayr (1969), a species is the array of populations that are actually or potentially able to interbreed and that are reproductively isolated from other such arrays under natural conditions. This definition is mainly appropriate for metazoan taxa with two sexes, and it is problematic to adopt this concept to protistan taxa, which have both sexual and asexual reproduction during their life cycles.

How should we define species among protistan taxa?

Sonneborn (1957) discussed the species concept in Protista. He carried out breeding experiments within a *Paramecium* species complex that enabled him to recognize breeding populations that could form conjugation pairs. He called this "breeding population" a "syngen". A "syngen" may be comparable to a "species". However, there still exists much controversy about the nature of species in protistan taxa, in particular foraminifera (Boltovskoy, 1954; Grell, 1959; Nyholm, 1961; Schnitker, 1974; Tendal, 1990).

In this study, as a first step toward solving the species problem in foraminifera, we have examined whether morphologically based species have the same boundaries as breeding populations for foraminifera. Breeding populations of *Glabratella* can be recognized rather easily, because specimens of this genus have been observed participating in sexual reproduction through formation of gamontogamous pairs (Myers, 1943). Observation of sexual reproduction is a positive method for determining the degree to which populations interbreed in foraminifera.

Sixteen morphospecies of *Glabratella* are known from the sea adjacent to the Japanese Islands (Matoba, 1970;

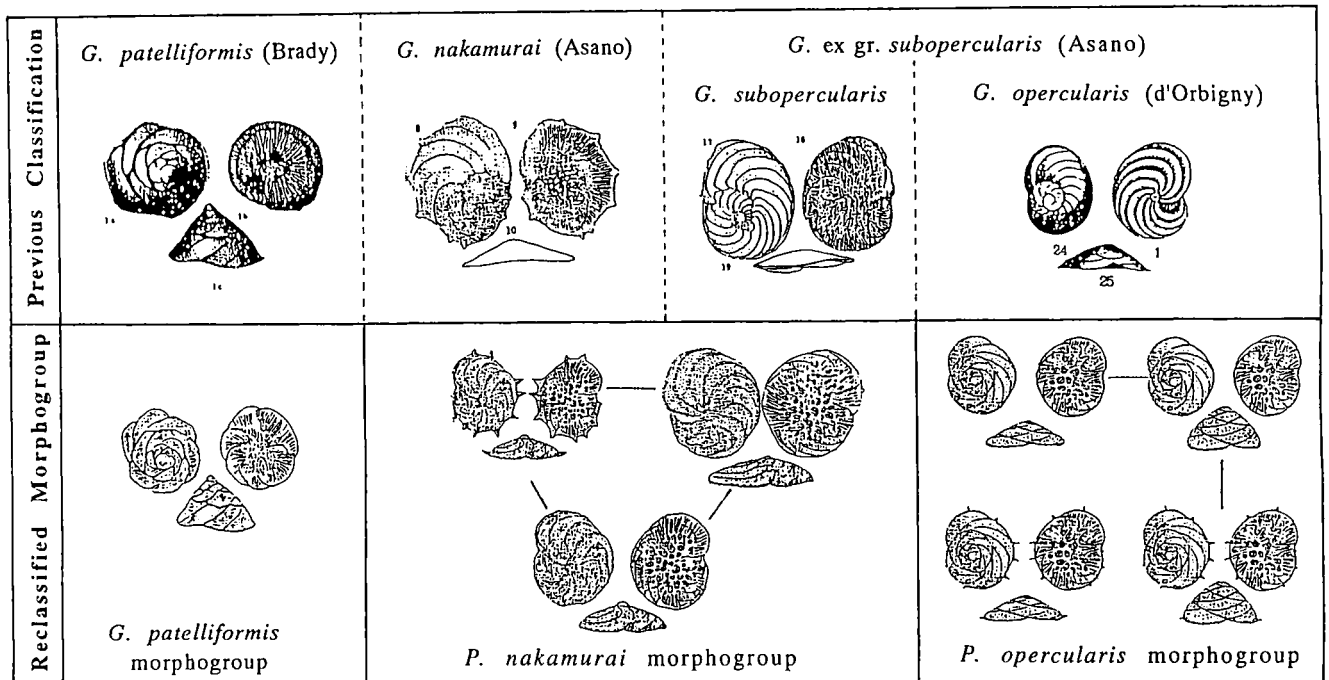


Figure 1. Four selected morphospecies of *Glabratella* that exhibit similar test morphologies. Original illustrations are shown in the upper panel. Reclassified morphogroups are shown in the lower panel. Not to the scale.

Kanesaki, 1987MS). Most of them live in the intertidal zone of rocky shores. They crawl on leaves or thalli of seaweeds and graze microalgae or organic detritus on the surface of seaweeds (Kitazato, 1984, 1988, 1994). Among these *Glabratella* species, *G. nakamurai* (Asano), *G. opercularis* (d'Orbigny), *G. patelliformis* (Brady), and *G. subopercularis* (Asano) have similar test morphologies (Figure 1). Some specimens have mixed morphological characters of two species. Thus, it is sometimes difficult to identify specimens at the species level. In this study, we tried to reclassify these four morphospecies by making use of both morphological characters and the results of interbreeding experiments in the laboratory.

Methods of study

Samples for the study were collected from the intertidal zone of rocky shores adjacent to the Japanese Islands (Kanesaki, 1987MS). Living individuals were collected at tide pools in Omaezaki Cape (34°36'N, 138°14'E) and Shimoda Bay (34°39'N, 138°57'E), both in Shizuoka Prefecture, central Japan. Additional samples were collected at tide pools in Oshika Peninsula, Miyagi Prefecture (36°15.0'N, 136°08.4'E) and Echizen-Matsushima Coast, Fukui Prefecture (38°23.9'N, 141°24.7'E) for interbreeding experiments among different localities. Sampling localities are shown in Figure 2.

Two approaches were used during the course of this study. Firstly, we carefully observed the ontogeny of test morphologies of *Glabratella* morphospecies, both of agamont and gamont specimens, using a scanning electron

microscope.

Secondly, culture experiments were carried out to examine the breeding ability of reclassified morphogroups. Seaweed with attached living foraminifera was collected from tide pools and placed in large culture tanks filled with well oxygenated sea water (Kitazato, 1984, 1988). Living foraminifers were transferred from the culture tank into a small petri dish for observation under a binocular microscope.

Individuals were cultured in petri dishes. A diatom species, *Navicula* sp., was isolated from the tide pool of the Omaezaki Cape, cultured, and used as a food source. *Glabratella* spp. ate little of other single-celled algae such as *Chlorella* and *Dunaliella* (Chlorophyceae), *Amphiprora* (Diatomophyceae) and *Cryptomonas* (Cryptophyceae) species.

Both intraspecific and interpopulational breeding experiments were carried out using a small petri dish. Two individuals, each collected from a different locality or different morphogroup, were placed on a small petri dish (28mm inner diameter) with fresh seawater. The formation of a gamontogamous pair was observed in the petri dish using a phase-contrast apparatus attached to an inverted microscope (Nikon-TMD Cultivation Microscope System and Olympus IMT-2 Inverted Microscope System). An automatic microphotographic system (Nikon-HFM) attached to the inverted microscope was used to record the process of gamontogamy. Interspecific breeding experiments by three morphospecies were carried out using a large petri dish (87mm inner diameter). Twenty gamont individuals of the three morphogroups were mixed in a petri dish and ob-

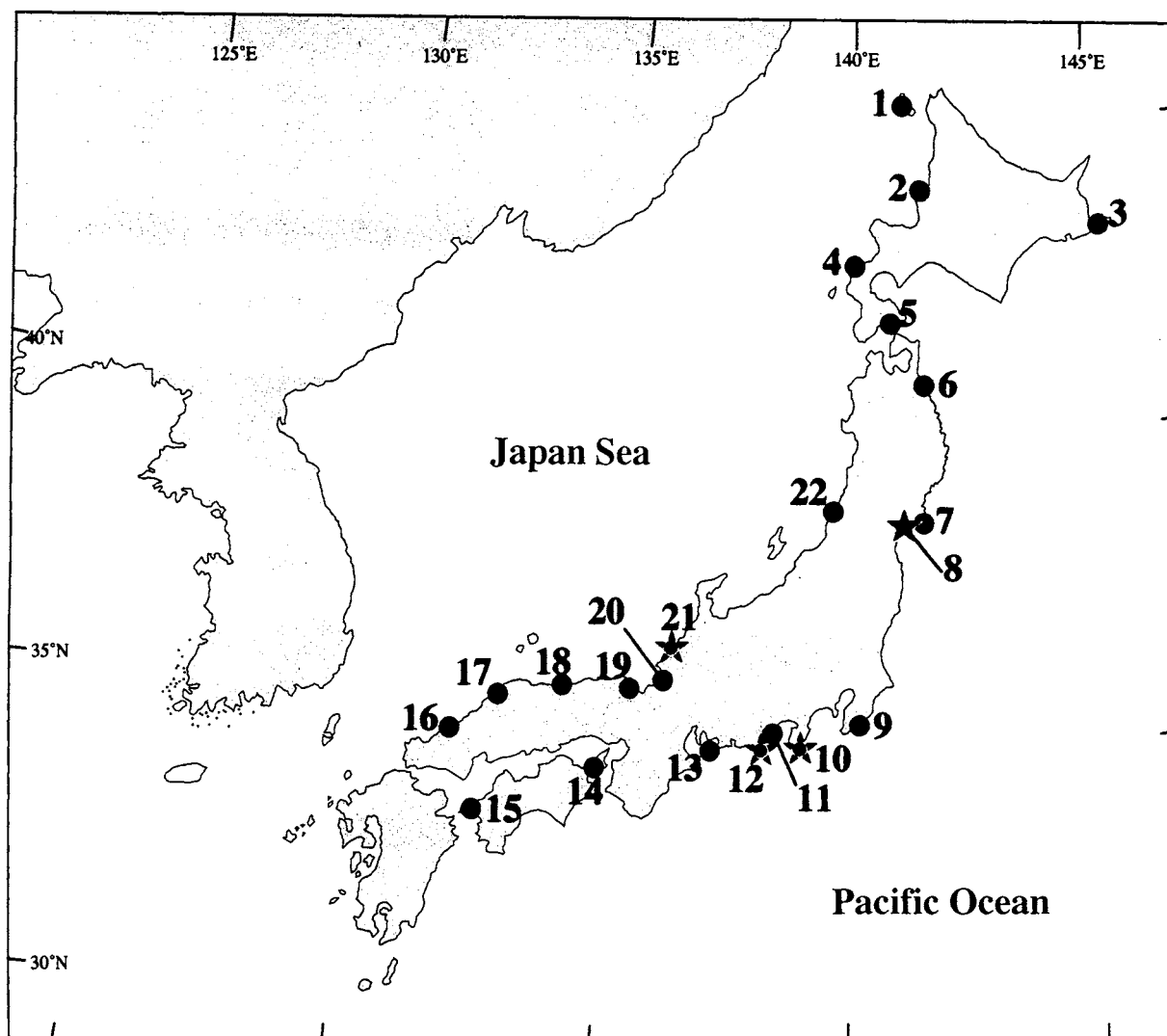


Figure 2. Map showing sampling localities. Closed circles indicate localities for measuring height/diameter ratio of *Planoglabratella opercularis* morphogroup. Asterisks are localities where interpopulational breeding experiments were carried out. 1. Rebuntou. 2. Rumoi. 3. Nokamappu. 4. Biya. 5. Kattoshimisaki. 6. Hachinohe. 7. Hamagurihama. 8. Oshika Peninsula (Sendai Bay). 9. Kamogawa-Bentenjima. 10. Shimoda (Ooura). 11. Obama. 12. Omaezaki. 13. Irakomisaki. 14. Yoroizaki. 15. Takaura. 16. Tsuchida. 17. Futamata. 18. Nagawase. 19. Momojima-Nishi. 20. Hayase. 21. Echizen-Matsushima. 22. Kobato.

served almost continually until individuals formed gamont-gamogamous pairs. It is easy to distinguish specific morphogroups under a binocular microscope.

Results and discussion

Morphological observations

Glabratella species have trochospiral, spiroconvex, and conical tests. The umbilical side is flattened with a slightly depressed umbilicus. The surface of the spiral side is rugose. The umbilical side is ornamented with rows of pustules that form radially aligned striae. Sutures are flush with the surface on the spiral side in general, but depressed on the umbilical side. The aperture opens at the interiomarginal part of the ventral side of the ultimate chamber of the

test. The aperture is an arched slit that is bordered by a weakly developed rim. Radial striae, which form groove and ridge systems, are developed on the ventral face. Radial striae probably have a function related to rhizopodial activity during movement or feeding (Kitazato, 1992).

These morphological characters are common to all four morphospecies. They are also common to both agamont and gamont individuals, although the test size of the agamont is about twice as large as that of the gamont.

Several kinds of sculpture on the ventral side of the test, such as tubercules, radial granules, and crenulation of the suture line between chambers, together with surface relief and basic chamber shapes, are stable during ontogeny in each morphogroup (Figure 3). We tried to reclassify *Glabratella* morphospecies into several morphotypes using

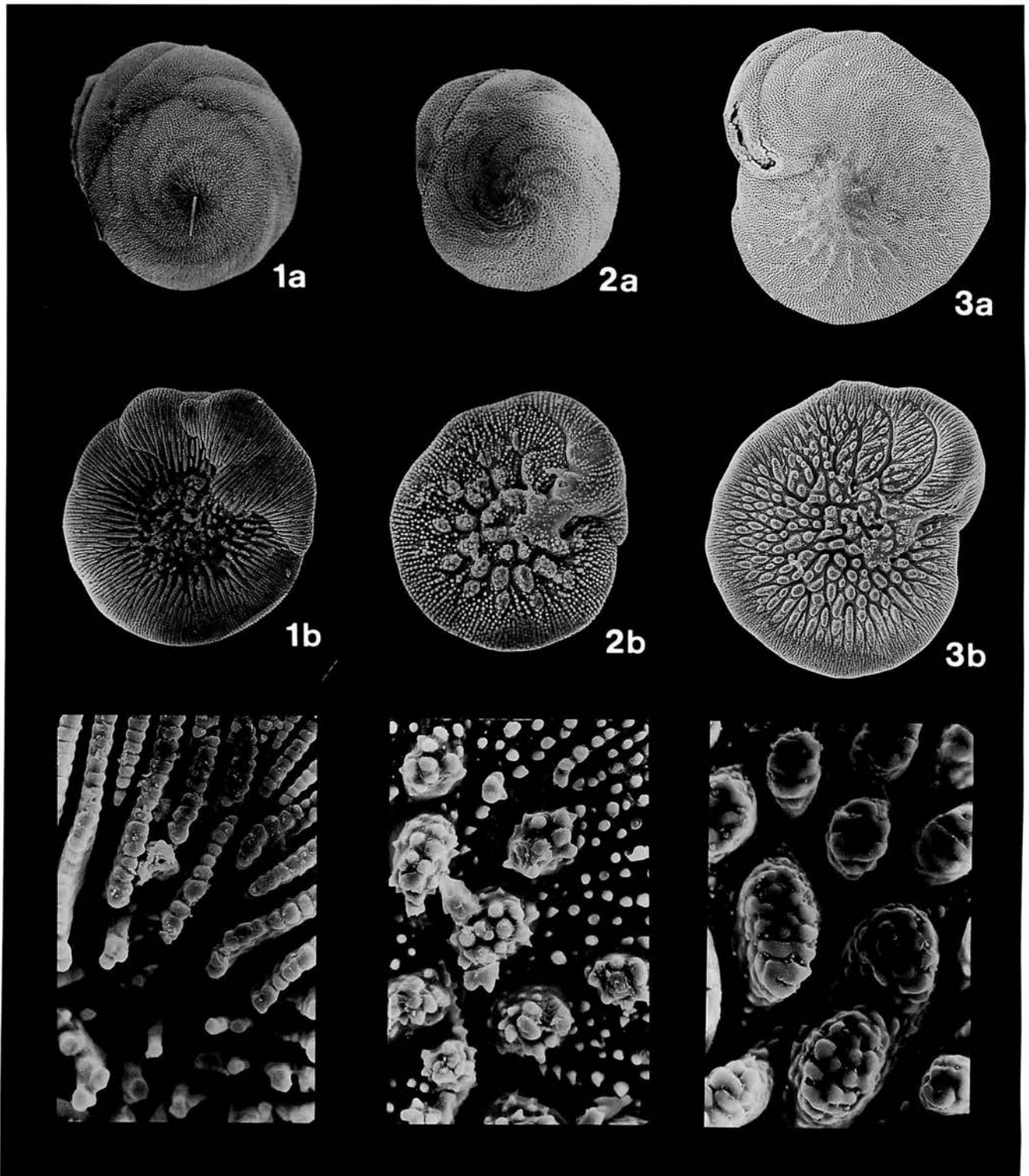


Figure 3. Overview of test morphologies of three morphogroups of the genus *Glabratella*. Dorsal (a) and ventral (b) views and enlargement of ventral surface (c) are shown for 1–4. **1a–c.** *Glabratella patelliformis* morphogroup. **1a.** $\times 94$. **1b.** $\times 94$. **1c.** $\times 540$. **2a–c.** *Planoglabratella opercularis* morphogroup. **2a.** $\times 94$. **2b.** $\times 94$. **2c.** $\times 540$. **3a–c.** *Planoglabratella nakamurai* morphogroup. **3a.** $\times 86$. **3b.** $\times 78$. **3c.** $\times 600$.

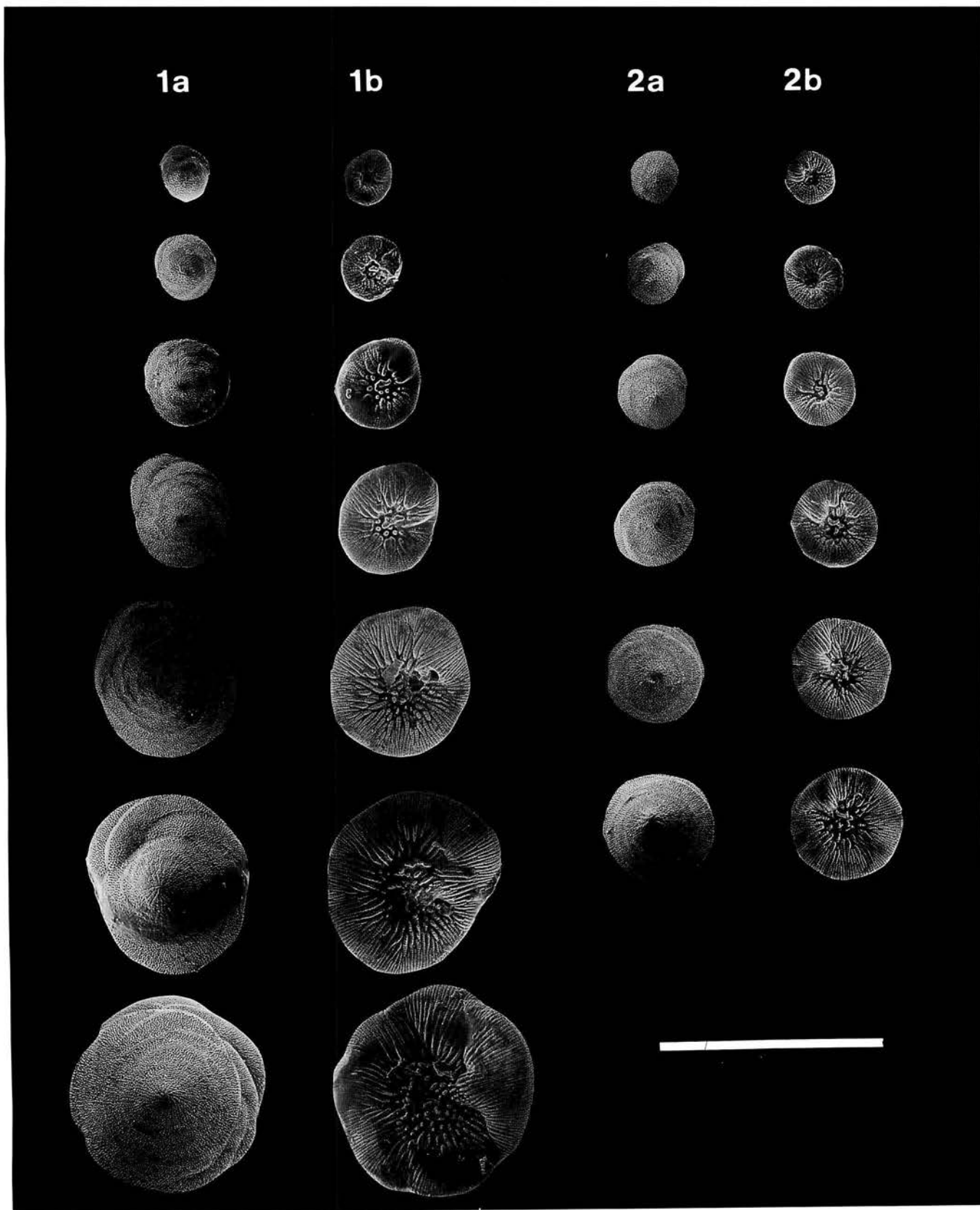


Figure 4.

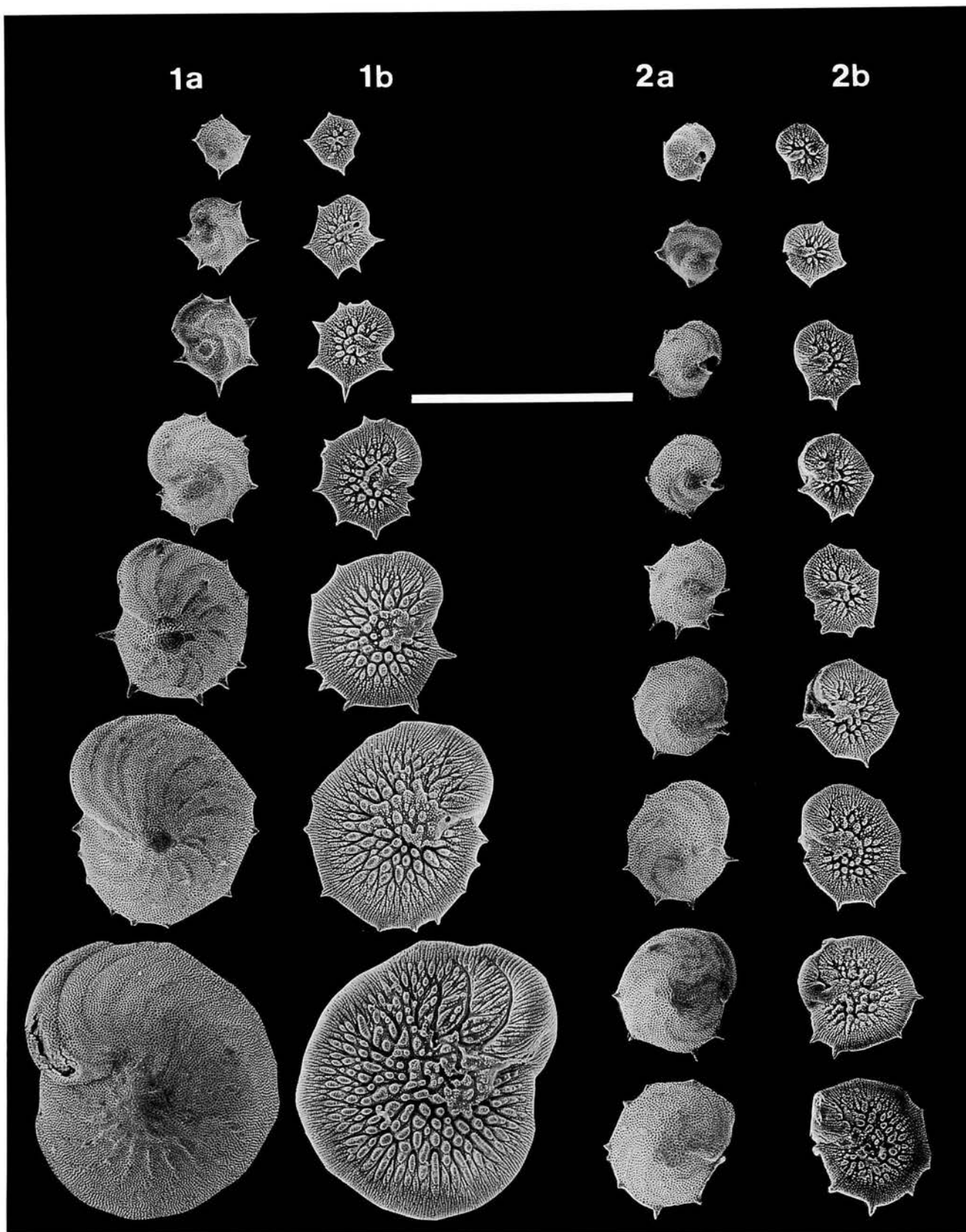


Figure 5.

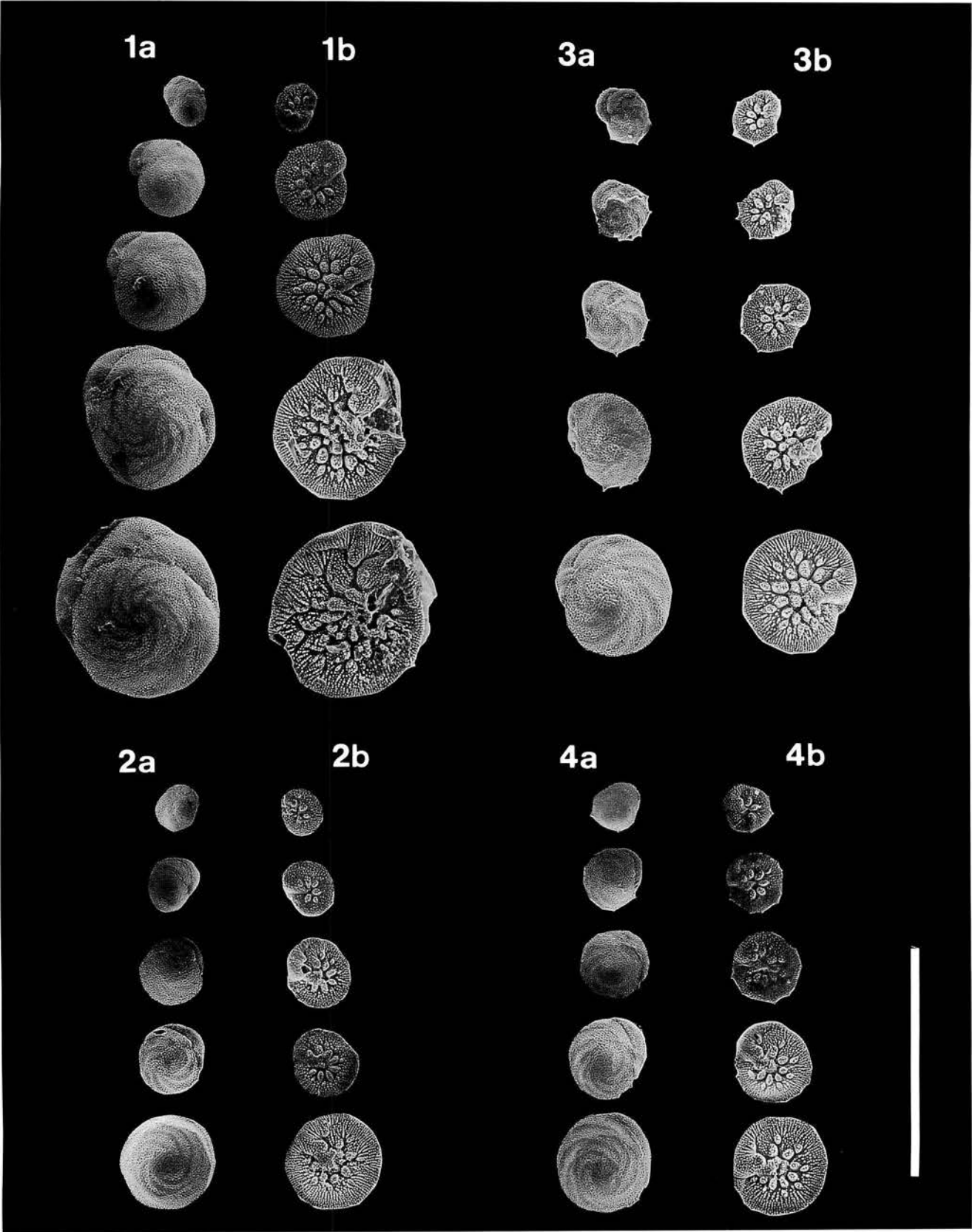


Figure 6.

only these stable morphological characters.

The four morphospecies were reclassified into three morphogroups (Figure 1). The characters of each reclassified morphogroup are as follows.

i) *Glabratella patelliformis* morphogroup (= *Discorbina patelliformis* Brady, 1884): This morphogroup is characterized by a strongly crenulated suture line between chambers, radial ridges made from a straight arrangement of needles, and needlelike tubercles at the center of the ventral side (Figure 3.1a–c).

ii) *Planoglabratella opercularis* morphogroup (= *Discorbina opercularis* d'Orbigny, 1839): This one is characterized by having rather smooth suture lines in comparison to *G. patelliformis*, sparsely arranged radial ridges, and spiny tubercles on the central area of the ventral side (Figure 3.2 a–c). Recently, Loeblich and Tappan (1988) separated flat *Glabratella* species from genus *Glabratella*, and established *Planograbratella* as a new generic name. Here, we apply the new generic name to *G. nakamurai* and *G. opercularis*, following Loeblich and Tappan (1988).

iii) *Planoglabratella nakamurai* morphogroup (= *Discorbina nakamurai* Asano, 1951): This morphogroup is characterized by simple bowl-like sutures, radial ridges only at the peripheral part of the ventral side, and tough flamboidal tubercles that cover most of the ventral surface (Figure 3.3a–c).

These morphological characters are present continuously through all growth-stages within the same morphogroup (Figures 4–6). These characters are also continuously present in both gamont and agamont tests, even though gamont and agamont test sizes are different.

Several morphological characters such as peripheral spines, height/diameter (=H/D) ratio and others vary with growth and also with the ambient environment. Peripheral spines of *P. nakamurai* disappeared in later growth stages, becoming covered by nonspiny chambers (Figure 5). The involutely coiled whorl in *P. nakamurai* sometimes becomes evolute at maturity. The mature stage of *P. nakamurai* is quite similar to the holotype of *G. subopercularis* (Asano). Thus, we regard *G. subopercularis* as a junior synonym of *P. nakamurai*.

The height/diameter ratio of the test of *P. opercularis* varies from locality to locality. The H/D ratio of populations in the Japan Sea was higher than in the Pacific (Figure 7). The H/D ratio at each locality was calculated from the slope of linear regression of height against diameter from one population. One hundred specimens were measured at

each locality. Along the Pacific, a population from Omaezaki Cape showed a higher mean H/D ratio than one from Ooura in Shimoda Bay (Figure 7). The H/D ratio also varied seasonally (Figure 8). The difference in H/D ratios of allopatric populations was larger than the seasonal fluctuations at one locality.

Like *P. nakamurai*, there are both spinose and nonspinose individuals of *P. opercularis* (Figure 6). However, peripheral spines of this morphogroup appeared at all ontogenetic stages (Figure 6.3, 6.4). This phenomenon was not observed in *P. nakamurai*. This morphological variation in *P. opercularis* also appeared in all localities around the Japanese Islands. Geographic variation in the proportion of spinose and nonspinose individuals in individual populations has not yet been analyzed.

Interbreeding experiments

Interbreeding experiments were carried out among three morphogroups that were reclassified based on morphological characters to examine whether or not these morphogroups represented interbreeding populations. Interbreeding experiments were also made among populations of *P. opercularis*, which are distributed in remote localities along the Japanese Islands.

Formation of a gamontogamous pair progressed as follows (Figure 9):

- 1) When two individuals came near enough to reach each other by rhizopodia, they immediately extruded a bundle of rhizopodia between them (Figure 9.1).
- 2) They maintained contact via these bundles for a few minutes, but the tests remained at some distance from each other (Figure 9.1).
- 3) After a few minutes they pulled each other until their tests touched (Figure 9.2, 9.3).
- 4) Still connected by the bundles, they lifted their tests and stuck themselves together along their ventral sides (Figure 9.4–9.8). Subsequently, most of the rhizopodia were withdrawn into the paired tests. To form a gamontogamous pair took approximately one hour on average. The exchange of gametes took place directly between the pair. We could not directly observe exchange of gametes between a pair through the tests, because *Glabratella* tests are too thick-walled and thus not transparent enough. Two-chambered agamontic juveniles appeared outside the pair one or two days after pair formation.

The processes of constructing a gamontogamous pair in

Figure 4. 1–2. Ontogeny of both agamont and gamont of *Glabratella patelliformis* (Brady). Collected at Omaezaki Cape, Shizuoka Prefecture. Scale bar indicates 500 μm . **1a.** Dorsal view of agamont. **1b.** Ventral view of agamont. **2a.** Dorsal view of gamont. **2b.** Ventral view of gamont.

Figure 5. 1–2. Ontogeny of both agamont and gamont of *Planoglabratella nakamurai* (Asano). Collected at Hayama, Kanagawa Prefecture. Scale bar indicates 500 μm . **1a.** Dorsal view of agamont. **1b.** Ventral view of agamont. **2a.** Dorsal view of gamont. **2b.** Ventral view of gamont.

Figure 6. 1–4. Ontogeny of *Planoglabratella opercularis* (d'Orbigny) both with and without peripheral spines. From Omaezaki Cape, Shizuoka Prefecture. Scale bar indicates 500 μm . Dorsal (a) and ventral (b) views are shown for 1–4. **1a.** Agamont individuals without peripheral spines. **1b.** Agamont individuals without peripheral spines. **2a.** Gamont individuals without peripheral spines. **2b.** Gamont individuals without peripheral spines. **3a.** Agamont individuals with peripheral spines. **3b.** Agamont individuals with peripheral spines. **4a.** Gamont individuals with peripheral spines. **4b.** Gamont individuals with peripheral spines.

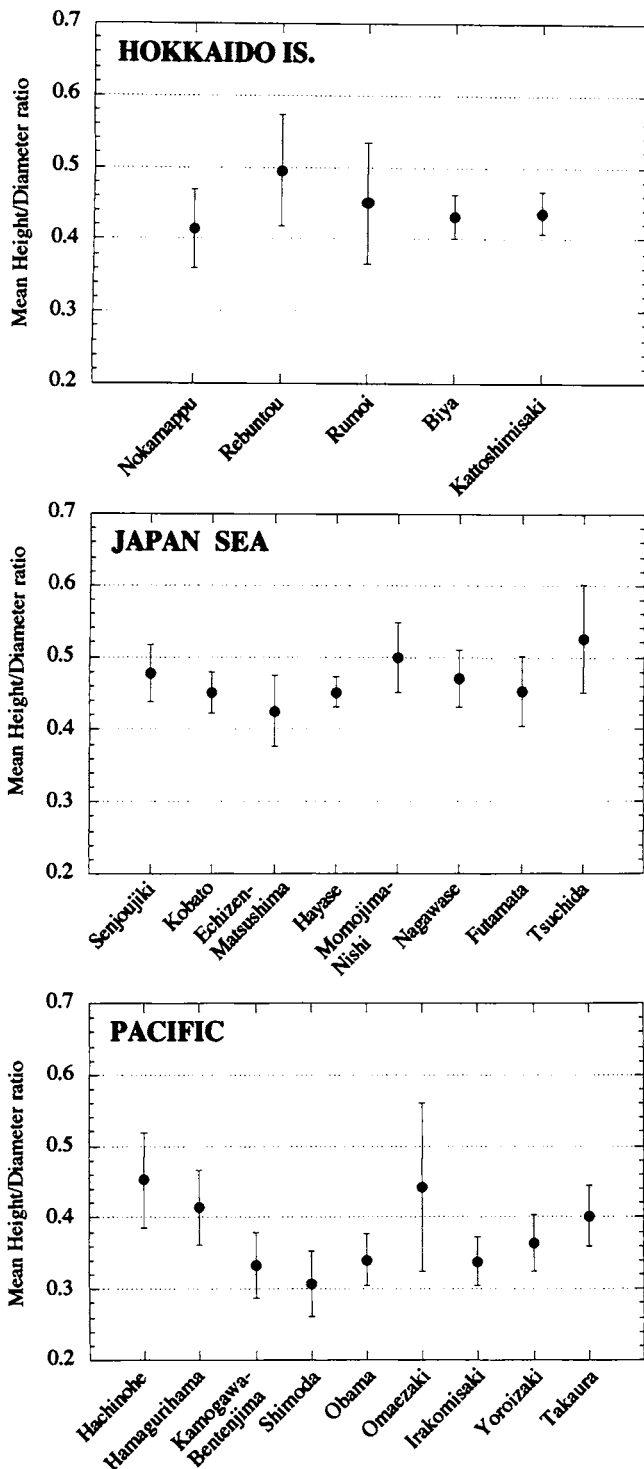


Figure 7. Geographic distributions of height/diameter ratio of *Planoglabratella opercularis* morphogroup around the Japanese Islands from various samples taken during different seasons. Black circles mask average height/diameter ratio at different localities. Bars straddling circles indicate the range of one standard deviation of data at each locality.

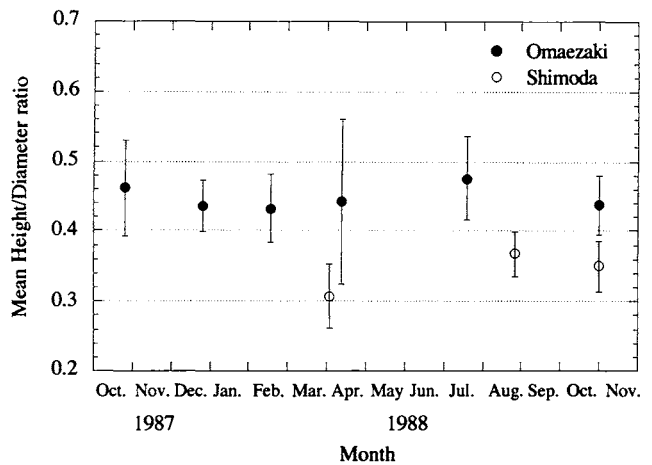


Figure 8. Seasonal differences of average height/diameter ratios of *Planoglabratella opercularis* both at Omaezaki Cape and Shimoda Bay, in Shizuoka Prefecture. Black circles show the data from Omaezaki Cape. Open circles show the data from Shimoda Bay. Bars indicate the range of one standard deviation of data at each locality.

Glabratella are mostly the same as those described by Le Calvez (1950) for *Discorbis mediterraneensis*.

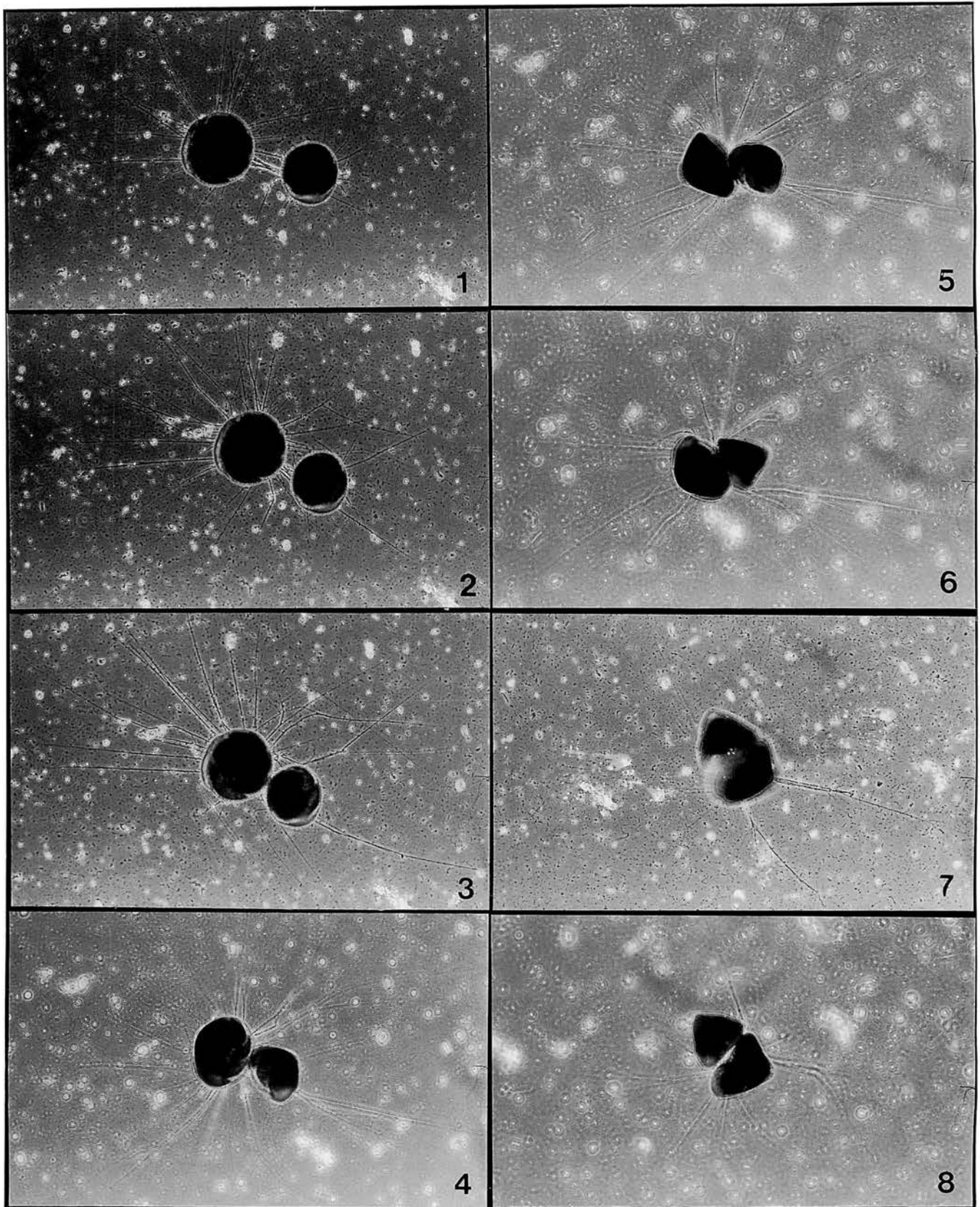
The results of the interbreeding experiments are summarized in Figure 10. Individuals that belonged to the same morphogroup mated, but those that belonged to separate morphogroups did not (Figure 10A). These results suggest that the species reclassified by morphology can probably be considered to be breeding populations.

However, there are individuals within the same population of a morphogroup that did not mate. Although they touched each other, they did not go further in forming a pair; instead, the rhizopods were disconnected and the individuals moved independently. The results indicate that some kinds of sexual differentiation may exist in *Glabratella*, as suggested by Le Calvez (1950), Grell (1957, 1958a, b, 1959), Weber (1965) and Berthold (1971) for several species that formed gamontogamous aggregates during fertilization.

Gamont individuals from the same parental agamont sometimes formed pairs; however, there was no exchange of gametes. This could mean that autogamy may not occur in *Glabratella*, even though autogamy has been found among species of the genus *Rotaliella* as described in Grell (1973).

Individuals from different morphogroups never reacted to each other, even if their rhizopodia were close enough to touch.

As described above, two morphological variations occur in *P. opercularis*, i. e., presence/absence of peripheral spines and height/diameter ratio. Both individuals with and without peripheral spines were able to form gamontogamous pairs and reproduced during culture experiments (Figure 10B). SEM photographs of a gamontogamous pair formed by a spinose and a nonspinose individual are shown in Figure 11. Both high and low trochospiral individuals also formed gamontogamous pairs (Figures 10B, 12.1, 12.2) and also re-



A INTERSPECIFIC BREEDING EXPERIMENTS

	<i>P. nakamurai</i>	<i>P. opercularis</i>	<i>G. patelliformis</i>
<i>P. nakamurai</i>	7/18	0/48	0/22
<i>P. opercularis</i>		11/30	0/33
<i>G. patelliformis</i>			1/4

B INTRASPECIFIC BREEDING EXPERIMENTS*Planoglabratella opercularis* (d'Orbigny)

	spinose	non-spinose	high H/D ratio	low H/D ratio
spinose	2/3	7/9	***	***
non-spinose		35/58	***	***
high H/D ratio			11/30	9/14
low H/D ratio				47/73

C INTERPOPULATIONAL BREEDING EXPERIMENTS*Planoglabratella opercularis* (d'Orbigny)

	Echizen-Matsushima	Oshika Peninsula	Shimoda	Omaezaki
Echizen-Matsushima	1/3	***	***	0/3
Oshika Peninsula		2/6	***	0/6
Shimoda			47/73	10/61
Omaezaki				16/41

Figure 10. Results of interbreeding experiments with both inter- and intraspecific populations. Results of interpopulational breeding experiments are also shown. Numerals to the left of the slash show combinations that actually formed a gamontogamous pair. Numerals to the right of the slash indicate the number of experiments for each combination. ***: no experimental data. A. Interspecific breeding experiments, B. Intraspecific breeding experiments, C. Interpopulational breeding experiments.

produced (Figure 12.3, 12.4). These results clearly show that all variants belong to the same population and can interbreed. Both spines and H/D ratio were formerly used as key morphological characters for defining *Glabratella* species. We have not yet examined how these morphological characters appear in daughter or granddaughter cells.

Interbreeding experiments among *P. opercularis* populations from different localities indicate that geographically remote populations do not make gamontogamous pairs (Figures 10C, 13). Gamont specimens between Omaezaki

Cape and Shimoda Bay made gamontogamous pairs and reproduced. However, individuals between Omaezaki Cape and Oshika Peninsula, Miyagi Prefecture and between Omaezaki and Echizen-Matsushima Coast, Fukui Prefecture did not make gamontogamous pairs with each other, even though morphological characteristics of *P. opercularis* populations at the three localities are very similar. These interbreeding experiments of individuals of remotely separated populations show that the interbreeding abilities of populations are closely related to geographic distances between

Figure 9. Series of photographs showing the process of forming a gamontogamous pair of *Glabratella patelliformis* (Brady) on September 1, 1987. Photographed in 1. 1548 hours, 2. 1549 hours, 3. 1550 hours, 4. 1554 hours, 5. 1555 hours, 6. 1556 hours, 7. 1557 hours, 8. 1600 hours. Collected at Shimoda Bay, Shizuoka Prefecture.

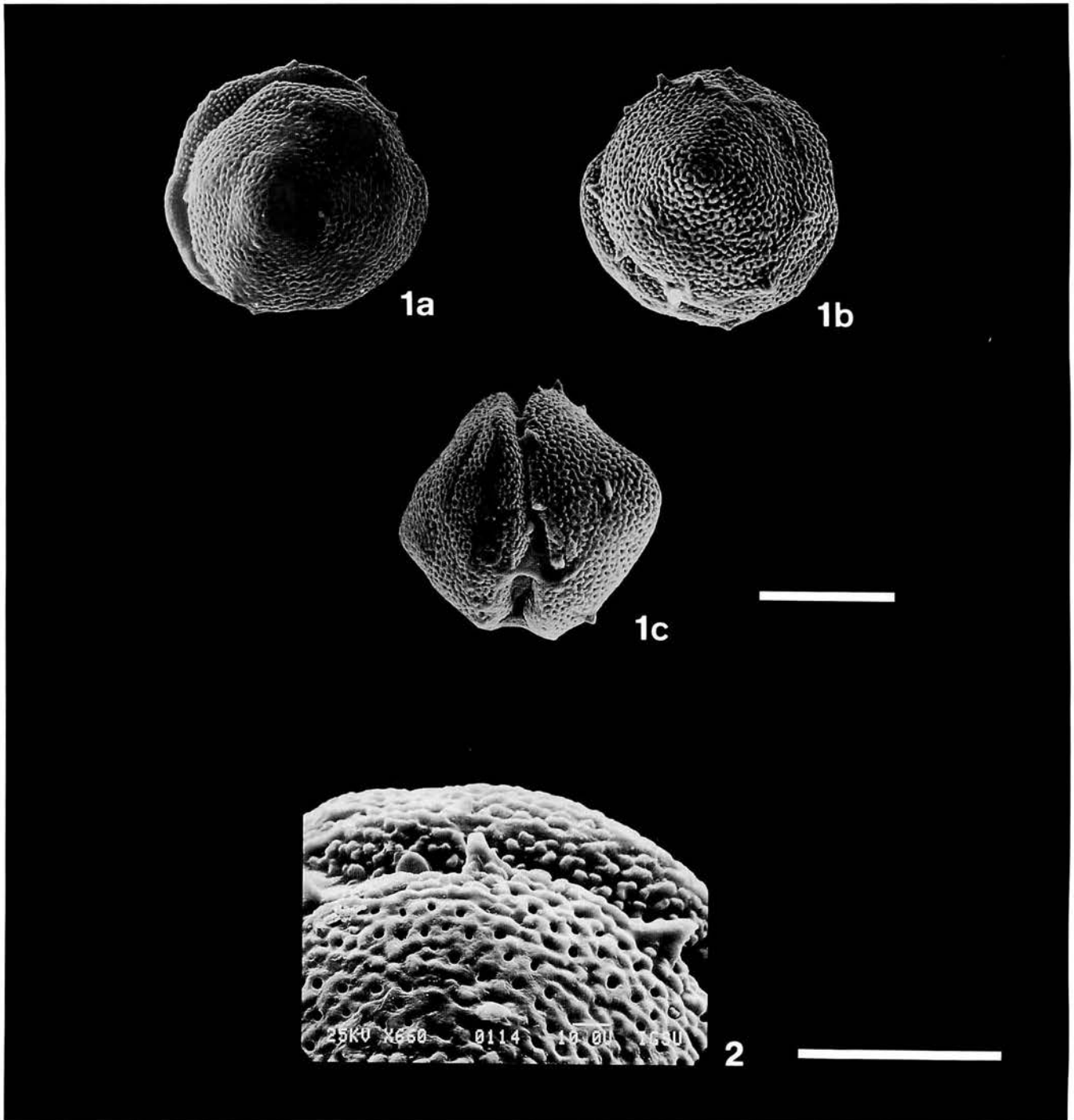


Figure 11. Gamontogamous pair between individuals with peripheral spines and without spines of *Planoglabratella opercularis* (d'Orbigny). Scale bars for **1 a, b, c** and for **2** indicate 100 μ m and 50 μ m respectively. **1a.** Specimen without peripheral spines, **1b.** Specimens with peripheral spines, **1c.** Side view of gamontogamous pair. **2.** Enlargement of peripheral spines.

Figure 12. Photographs showing the reproductive process of *Planoglabratella opercularis* (d'Orbigny) from a gamontogamous pair during culture experiments. **1.** Gamontogamous pair between individual showing high height/diameter ratio of Omaezaki population and individual showing low height/diameter ratio of Shimoda population. Agamont juveniles are visible within one pair. Photographed at 2130 hours, November 4, 1988. **2.** Side view of gamontogamous pair. Upper right individual shows higher height/diameter ratio than that of lower left individual. Photographed on November 4, 1988, 2140 hours. **3.** Spreading of agamont offspring from the parental pair. Photographed on November 5, 1988. Juvenile agamonts have two chambers when they leave. **4.** Juvenile agamont individuals with three chambers. Photographed on November 7, 1988.

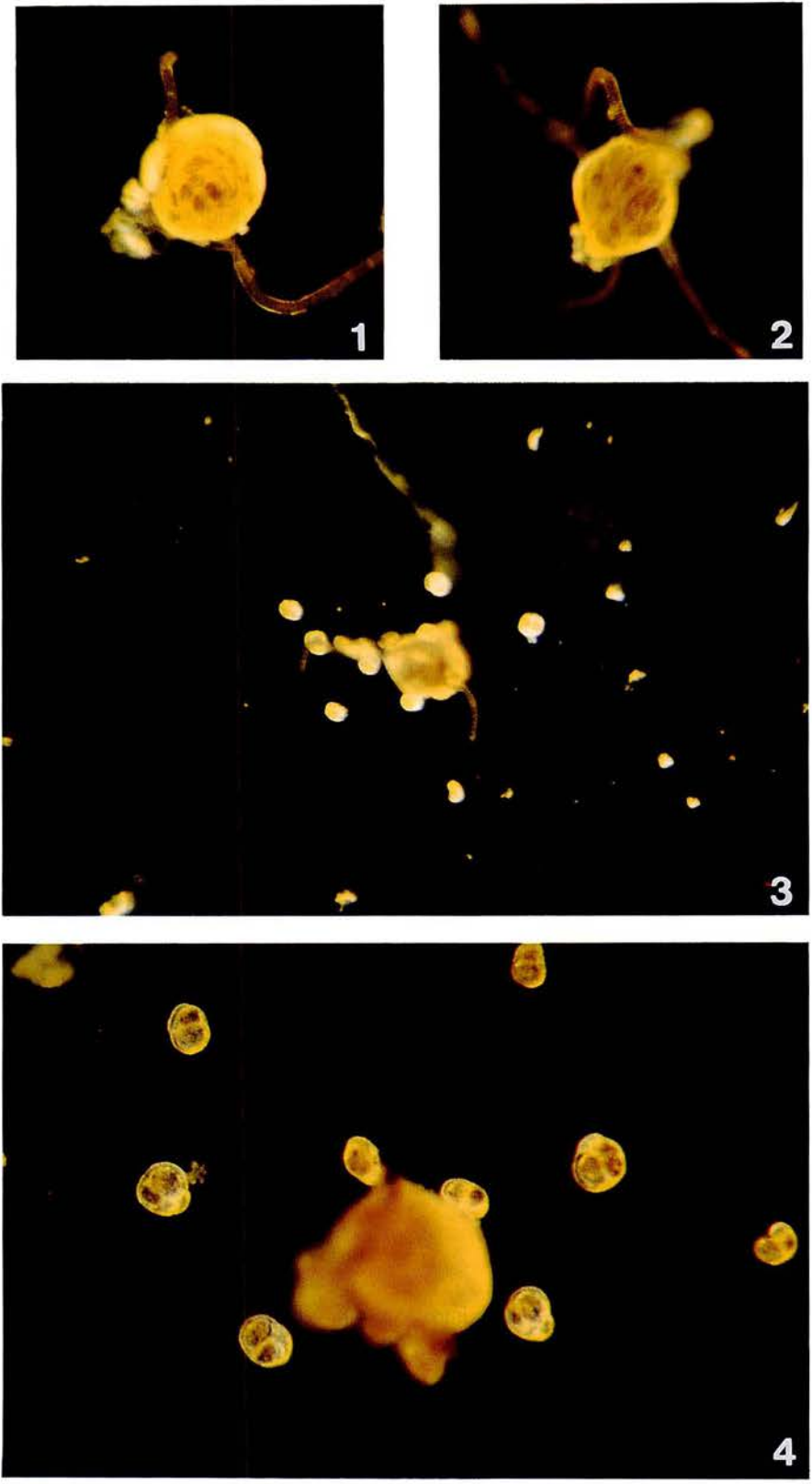


Figure 12.

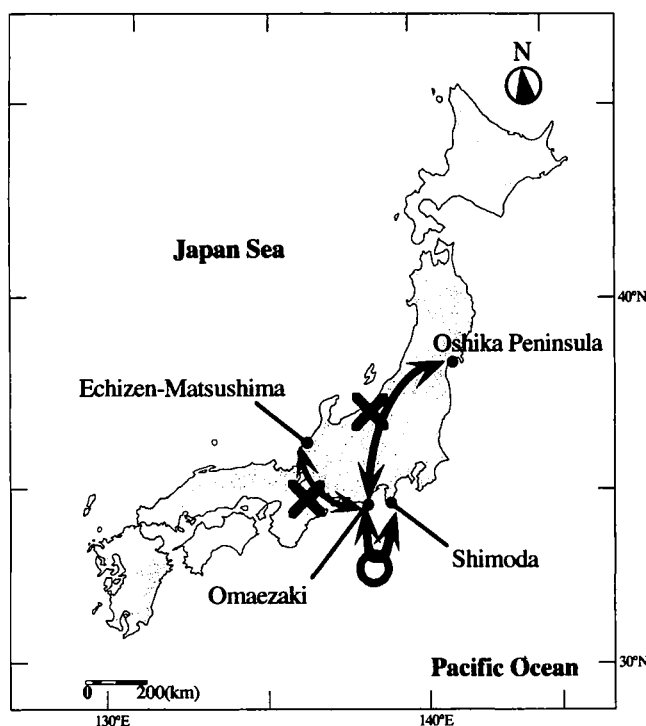


Figure 13. Results of interbreeding experiments of individuals among geographically remote populations. Map shows localities from which individuals actually tried to interbreed. Circle and cross marks in the figure refer the populations that can and cannot interbreed, respectively. The results show that individuals from proximate localities can interbreed.

them. Individuals that succeeded in interbreeding belong to proximate populations. For instance, Omaezaki Cape is only 100 km from Shimoda Bay at the closest distance along the shoreline. In contrast, individuals from distant localities failed to interbreed. Oshika Peninsula is about 500 km from Omaezaki Cape. The Echizen-Matsushima Coast is more than 1000 km from Omaezaki Cape. Thus geographic distance is critical in determining interbreeding abilities among populations of a single morphospecies in *Glabratella*. This phenomenon suggests that populations of this glabratellan morphospecies have characteristics of ring species, with chains of local populations that can interbreed between neighboring populations.

Summary

Four *Glubratella* morphospecies were reclassified into three morphogroups, according to stable morphological characters. There are several key morphological characters that are stable with ontogenetic stages, life cycle, and/or geographic distance. Certain morphological characters changed during ontogeny. Interbreeding experiments show that reclassified morphospecies can breed within one morphogroup. Several morphological characters are not stable during ontogeny. This shows that we cannot use every morphological feature to define *Glubratella* species.

Interbreeding experiments using individuals collected from geographically remote populations demonstrate that individuals of closely located populations can breed with each other, whereas individuals from distant populations cannot interbreed. These results suggest that glabratellan populations are chains of small, reproductively isolated populations.

Interbreeding experiments are a powerful tool to elucidate populational structure of morphologically defined species in foraminifera.

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Foraminal structures of some Japanese species of the genera *Ammonia* and *Pararotalia*, family Rotaliidae (Foraminifera)

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Abstract. Rotaliid foraminifera have a complicated foraminal structure that has been recognized as the so-called toothplate. As to the interpretation of this toothplate, however, there has been confusion among foraminiferologists as to whether it is the same as the buliminid toothplate or not. In order to elucidate the apertural and foraminal structure, we examined some Japanese species of the genera *Ammonia* and *Pararotalia*.

The apertures of *Ammonia* and *Pararotalia* show fundamentally the same style of construction, but the resultant structures are different among species. We recognized two main components instead of the indefinite toothplate in the aperture: foraminal plate and umbilical coverplate. The foraminal plate constructed out of a foramen is a free structure of the bilamellar wall. This plate is originally formed in the final chamber where it delimits the posterior side of the final aperture. The umbilical coverplate closes the umbilical side of the preceding foramen. This coverplate is originally bilamellar and is continuous from the foraminal plate. Both the foraminal plate and umbilical coverplate are formed when the final chamber is constructed. The umbilical coverplate interconnects the new and preceding foraminal plate, which may lead to the original concept of toothplate. However, the umbilical coverplate is not associated with the final chamber wall, but assists in closing the umbilical side of the preceding chamber wall. Such a chamber construction is restricted to rotaliids, thus we reject the term toothplate as only indicating modified structures that pass through the aperture.

Descriptions of the rotaliid aperture are of value when we note the foraminal plate and umbilical coverplate. Thus two types of foramen, *Ammonia*-type and *Pararotalia*-type, were developed in the rotaliids.

Key words: aperture, foraminal plate, rotaliid foraminifera, taxonomy, toothplate.

Introduction

The toothplate is a characteristic structure developed in some taxa of benthic foraminifera (originally called “tooth plate”, recently “toothplate”; e. g., Loeblich and Tappan, 1964, 1987). It has a varied morphology, usually manifested as a protruded free structure passing through the aperture. Before Hofker (1950, 1951a, b) recognized this structure as a useful systematic criterion of hyaline calcareous foraminifera, various distinctive parts of the aperture were called lip, tongue, tooth, partition and flap. Hofker’s toothplate was regarded as a homologous structure with these variously named structures. Many forms having these apertural decorations have been classified into a number of families based on their apertural morphologies. Thus most hyaline calcareous foraminifera were included in Hofker’s order

Dentata (Hofker, 1951a). However, morphologically, some of these structures should be grouped together in the same category and some should be clearly differentiated from it. The toothplate concept includes so many forms of apertural complexity that rigid application of this term leads to ambiguous comparisons in systematics. In particular, the apertural complex of Hofker’s Protoforaminata, the group having protoforamen, is different from that of his Deuteroforaminata, the group having both protoforamen and deuteroforamen.

In addition to such a confused recognition of the toothplate and related structures, development of the scanning electron microscopes (SEM) permitted the lamellar structure of the toothplate to be examined. The toothplate has been recognized as a bilamellar structure consisting of an inner lining and an outer lamella (Hansen and Reiss, 1971). However, the lamellarity is not consistent, since Revets (1993)

suggested that the buliminid toothplate is made from the inner lining. Thus, the concept of toothplate is still confused among foraminiferal researchers in its structural and morphological aspects. The rotaliid toothplate is the best example of this, it being unclear whether it should be recognized as homologous with the buliminid toothplate or not on the basis of morphology and structure.

We describe the apertural and foraminal structures based on artificially dissected specimens and suggest the necessity of recognizing the morphological variation of the aperture.

Methods

Internal structure of foraminiferal test was examined by a scanning electron microscope using a hardened canada balsam (Nomura, 1983c). Some authors stress the importance of lamellar structure, particularly to the understanding of toothplate structure (e. g., Revets, 1989, 1993). In reconstructing the lamellar structure for the sectioned and etched specimens that have been embedded in epoxy resin we encountered difficulties, particularly for thinner walls. Alternatively, we etched the sectioned specimens with 0.5% phosphoric acid to observe the internal structure before removing the canada balsam. This method gives better results in interpreting the three-dimensional lamellar structures within walls.

Previous observations on the aperture of *Ammonia*

Earlier workers examined thin sections of foraminifera or examined the test with naturally broken walls to observe the toothplate. In this way, the toothplate of *Ammonia beccarii* (Linné), type species of the genus *Ammonia*, has been recognized as a free structure asymmetrically folded longitudinally and convex towards the umbilical side of the chamber (Hofker, 1950, 1951a, b; Reiss and Merling, 1958). Reiss and Merling (1958) showed various figures of the toothplate and related structures, and introduced several terms for its specific structures. They described the toothplate to "run always from the intercameral foramen towards the umbilical side for part of the way, turning through torsion towards the dorsal side at their distal ends." Thus the toothplate is convex towards the umbilical center. The rotaliid septal flap, originally proposed by Smout (1954), is also regarded by those authors as an extension of the toothplate, although they retain the term septal flap. Cifelli (1962) suggested the toothplate of *A. beccarii* was not homologous with the original toothplate and he separately called it an axial plate and a lip. He observed that the axial plate is imperforate and the umbilical extension of the plate passes into a chamber flap, without any openings into the umbilical area. The lip, in the different sense of Reiss and Merling (1958), is formed by the axial plate anteriorly projecting through the aperture at the bottom of the septum, except for the final one. Before the recognition of these apertural modifications by these workers, Ishizaki (1943) first noted the morphological difference between the aperture (as the final opening) and the foramen (as the preceding opening). However, he did not refer to any specific anatomical observations.

Based on SEM examination, Seibold (1971) recognized the axial wall as forming a different part of the toothplate in *Ammonia*. Seibold's axial wall and lip correspond to Cifelli's axial plate and chamber flap. Hansen and Reiss (1971) first introduced the concept of a foraminal plate and an umbilical coverplate instead of the toothplate for the rotaliid foraminifera, suggesting the presence of this plate in all chambers, including the final one. They interpreted the septal flap which forms not only the foraminal plate on an axial chamber wall (=previous coil), but also the umbilical coverplate, as showing a continuous lamellar structure. Their observations corroborate Reiss and Merling's explanation. The septal flap consists of an inner lining, which covers the preceding bilamellar septal wall. This lamellar model has been adopted in Lykke-Andersen (1976). Thus the foraminal plate and the coverplate are bilamellar in the original construction. They suggested that the so-called fissure and intraseptal passage are formed as an imperfect adhesion of the septal flap to the preceding chamber. They referred to this fissure as an interocular space. Müller-Merz (1980) supplied detailed anatomical information on rotaliids and she discussed the apertural structure based on the foraminal plate and cover plate (same sense of umbilical coverplate) model.

Lévy *et al.* (1986) suggested the suprageneric similarities of some rotaliids, including *Ammonia*, to discorbids. They pointed out a similarity in internal structure for which they used the term paries proximus instead of the toothplate. They describe "It (=paries proximus=toothplate) is a thin plate which divides from the septum towards the umbilical face and which constitutes an oblique groove-like fold, instead the chamber, joining the preceding coil. This plate also spreads backwards, that is, in a proximal direction, closing the edge of the folium of the preceding chamber. In equatorial section we give the name 'retroparies' to the back part of the paries proximus." Their paries proximus and the retroparies correspond to the foraminal plate and umbilical coverplate respectively. Although their proposal to subsume the rotaliids within the discorbids at the family level is rejected by Haynes and Whittaker (1990), based on ontogenetic analyses of umbilical modifications, including canals and fissures, there is a similarity in the structure of paries proximus in both taxonomic groups.

The complexity of the internal structure of *Ammonia* is reflected in these different terms. On the other hand, differing recognition of the internal structure among researchers makes for uneasy interpretations. Hottinger *et al.* (1991) redefined the toothplate, particularly in relation to that of *Pararotalia* (see below). They stressed the presence of their toothplate (s.s.) in *Pararotalia* and its absence in *Ammonia*, indicating a difference in suprageneric classification. Revets (1993) questioned whether the rotaliid toothplate was homologous to the buliminid toothplate. He mentioned "The internal structures in rotaliids are not equivalent to toothplates, rather they all seem to conform to the foraminal plate coverplate concept." His argument originated from the difference between the bilamellar structure of rotaliid walls and the single-layer inner lining origin of the buliminid toothplate. Simple usage of the toothplate thus leads to confusion among researchers. The situation is

similar in cassidulinids. Nomura (1983a, b) showed that simply the presence or absence of a toothplate is of little taxonomic value. We should describe the apertural decoration with careful attention to the various parts.

Previous observations on the aperture of *Pararotalia*

The detailed apertural structure of *Pararotalia* has been discussed by Loeblich and Tappan (1957, 1964) and Reiss and Merling (1958), based on its type species *Pararotalia inermis* (Terquem) from the Eocene of Paris Basin. Loeblich and Tappan (1987) described the aperture as interiomarginal and extraumbilical-umbilical, and the foramen as areal with the attachment of the toothplate at the proximal margin of the penultimate chamber. Loeblich and Tappan's toothplate is seemingly used in a broad sense, but they distinguished an umbilical plate (=umbilical coverplate here) and an internal septum from the chamber wall (Loeblich and Tappan, 1957). The umbilical coverplate and the internal septum were recognized as secondary structures which can be broken away in the final chamber. Reiss and Merling (1958) stressed that the toothplate (internal septum and umbilical plate of Loeblich and Tappan) is a primary formed structure, but they regarded the umbilical plate as chamber wall.

As to the toothplate of the Japanese *Pararotalia*, Ujiie (1966) described *P. nipponica* as follows: "tooth plate imper-

forate, extending from proximal margin of last intercameral foramen to distal (peripheral) margin of aperture, adhering its basal (umbilical) margin on proximal margin of spirothecal wall of last chamber throughout whole chamber-length, developing its upper (dorsal) free part broadly but very thinly in form of spatula with concave face turned to axial side and its upper anterior margin bent inwardly." Interestingly, the spatula-shaped portion of the upper toothplate has been interpreted as dissolved in the penultimate chamber based on a secondary wall which closes up an umbilical slit. His observation is similar to Loeblich and Tappan's umbilical plate formation model. However, a real image of the umbilical slit has not been clearly indicated. It may correspond to the interiomarginal slit of the aperture.

Hansen and Reiss (1971) indicated that the original wall structure of *Pararotalia* is identical to that of *Ammonia*. The umbilical coverplate (umbilical plate of Loeblich and Tappan, 1957) extends back from the foraminal plate to the preceding foraminal plate.

Hottinger *et al.* (1991) showed SEM micrographs of their defined toothplate of *P. inermis*. They describe the toothplate as "originating from the septal flap and connected to the inner ventral chamber wall, an imperforate toothplate extends to the distal chamber wall, attached to the dorsal corner of the primarily interiomarginal, extraumbilical aperture, and protruding with a free, serrated edge into the latter." Their toothplate is associated with a canal, which

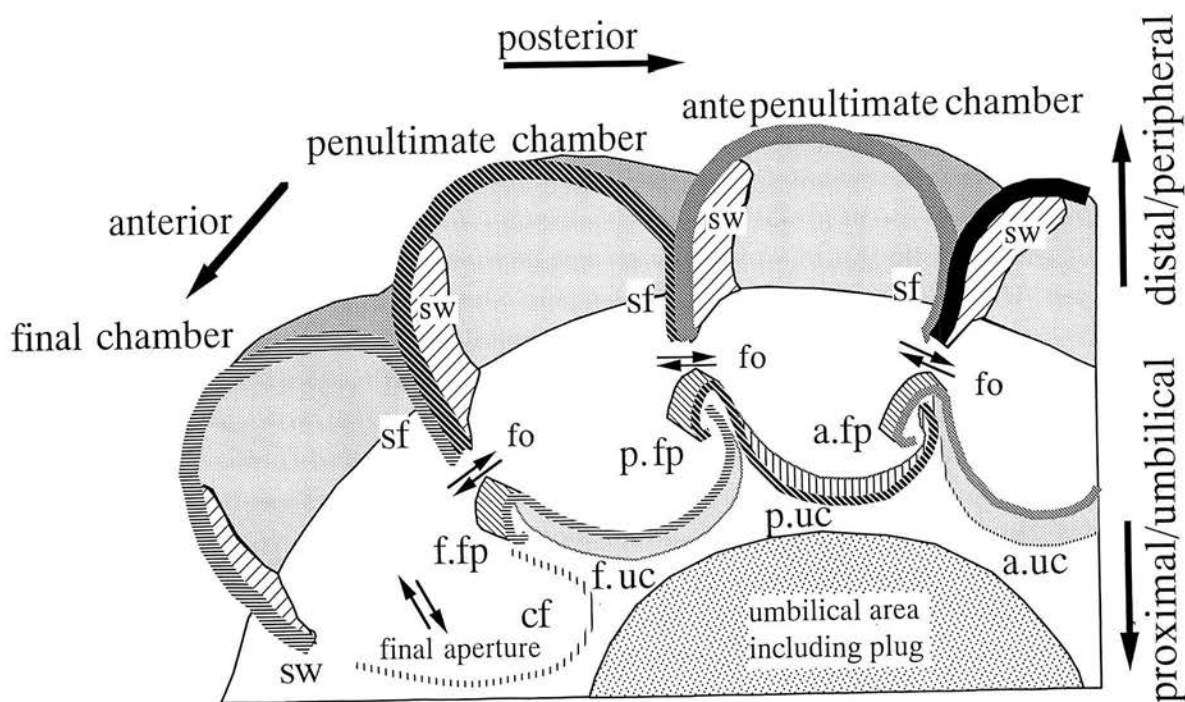


Figure 1. Schematic illustration of internal structure in the genus *Ammonia*. The aperture is an interiomarginal long slit extending from the peripheral side to the umbilicus. The final chamber continues to the foraminal plate and the umbilical coverplate of the penultimate chamber on the umbilical side. Thus, the coverplates around the umbilicus are delayed for one chamber lumen. The so-called toothplate corresponds to the ensemble of foraminal plate and umbilical coverplate. Abbreviations: a.fp=antepenultimate foraminal plate; a.uc=antepenultimate umbilical coverplate; cf=chamber flap; f.fp=final foraminal plate; f.uc=final umbilical coverplate; fo=foramen; p.fp=penultimate foraminal plate; p.uc=penultimate umbilical coverplate; sf=septal flap; sw=septal wall.

communicates with the chamber and with the furrow around an umbilical plug.

Descriptive terms for aperture and its related structure

In order to avoid confusion with respect to the aperture and foramen and their related structures, we use the following terms (Figure 1).

Chamber flap.—Original extension of chamber wall, covering umbilical sutural fissure, decorated with small spines.

Pararotalia forms an umbilical shoulder associated with nodes on this portion (Loeblich and Tappan, 1957), instead of forming a free chamber flap. [*chamber flap*: Cifelli, 1962] [*chamber lobe*: Parvati, 1971; Haynes and Whittaker, 1990] [*folium*: Hottinger *et al.*, 1991] [*lip*: Hofker, 1950, 1951a, b; Reiss and Merling, 1958; Seibold, 1971; Müller-Merz, 1980] [*umbilical lip*: Ujiié, 1965].

Foramen.—Opening connecting chamber lumina through septa, having a rounded, oval shape. Its shape is different from the final aperture. There are two types of foramen: the *Ammonia*-type and *Pararotalia*-type, based on the position and inclination of the foraminal plate to the walls of previous whorl (Figures 2, 3). [*intercameral foramen*: Smout, 1954] [*areal intercameral foramen*: Parvati, 1971] [*septal foramen*: Hofker, 1950, 1951a, b].

Foraminal plate.—Anterior plate extended from an umbilical coverplate (Figures 1, 2). It is formed on the proximal side of the aperture, leaving a foramen rounded or oval in shape. The foraminal plate is curled to the posterior out of the foramen, forming a hook-like structure in horizontal section (Figure 2), sometimes it is completely bent, resulting in

a columnar shape. This plate usually appears as an isolated plate adjoining the foramen of each chamber, including the final chamber, thereby some authors regarded it as a free structure of the toothplate. Our understanding of this plate agrees with the description of Hansen and Reiss (1971). They suggested that the chamber wall, septal flap, foraminal plate and umbilical coverplate are formed as one continuous structure. The foraminal plate of *Pararotalia* obliquely leans onto the chamber wall of the previous whorl and changes it to a protruded lip (lower lip) (Figure 3) [*anterior projection of umbilical plate*: Parvati, 1971] [(apertural) *lip*: Cifelli, 1962] [*foraminal plate*: Hansen and Reiss, 1971; Müller-Merz, 1980; Revets, 1993] [*internal septum*: Loeblich and Tappan, 1957] [*paries proximus*: Lévy *et al.*, 1986] [*toothplate*: Reiss and Merling, 1958; Ujiié, 1965, 1966] [*part of toothplate*: Hottinger *et al.*, 1991].

Hinge.—Junction of the foraminal plate and the umbilical coverplate. It delimits the proximal border or basal border of the foramen. In the *Ammonia*-type foramen, the hinge adheres to the umbilical/proximal side of the apertural opening on the previous whorl (Figure 2), and in the *Pararotalia*-type it adheres to the distal side of the aperture (Figure 3).

Labial aperture.—Opening usually formed on the posterior side of the chamber, except for the final one. Originally this foramen was denoted a protoforamen to distinguish it from a deutoforamen (Hofker, 1950, 1951a, b). Reiss and Merling (1958) recognized three parts of this aperture, namely, anterior, umbilical, and posterior. However, we recognized it as a single opening in the umbilical coverplate into the upper side of deeply incised sutures or sometimes into the umbilicus. The labial aperture is usually devoid of small spines around its opening. [*protoforamina*: Hofker,

Ammonia-type foramen

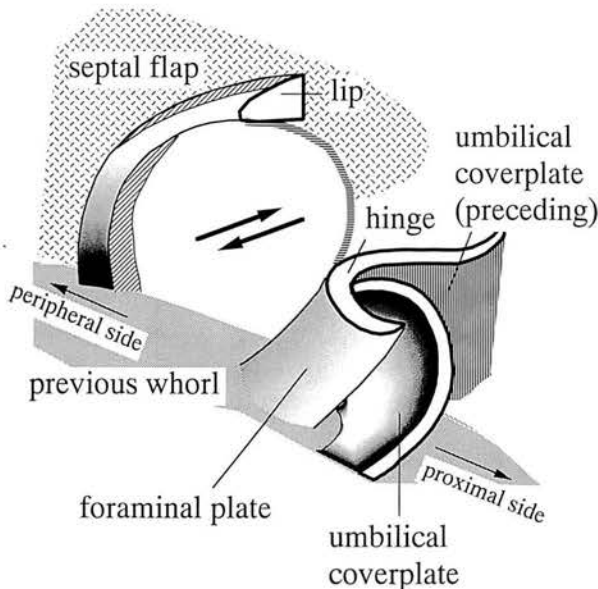


Figure 2. Schematic illustration of *Ammonia*-type foramen. The hinge, junction of the umbilical coverplate and the foraminal plate, butts against the previous whorl. The umbilical coverplate adheres to the preceding foraminal plate or the preceding umbilical coverplate.

Pararotalia-type foramen

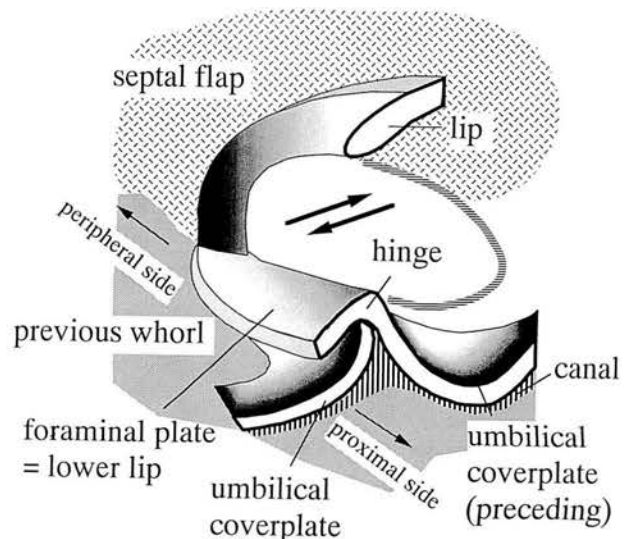


Figure 3. Schematic illustration of *Pararotalia*-type foramen. The hinge, junction of the umbilical coverplate and the foraminal plate, is much inclined toward the peripheral side of the aperture. Thus the foraminal plate appears as a protruded lip on the lower side.

1950, 1951a, b]

Lip.—Plate-like or tube-like structure formed in aperture and foramen. It is distinguished from the lower lip of *Pararotalia*. Sometimes the lip is referred to as the apertural rim.

Lower lip.—Lip usually associated with the foramen of *Pararotalia* and never seen in final aperture. It is formed by an adhesion of the basal part of the foraminal plate to the other, distal side of the final aperture, thereby the foramen of *Pararotalia* is areal. The lower lip is intrinsically the same as the foraminal plate, but structurally different. A tooth-

plate in the sense of Hottinger *et al.* (1991, 1993), which is a different concept from the so-called toothplate, corresponds to our lower lip. To avoid the confused usage of "toothplate," we do not use their toothplate.

Septal attachment.—Attachment of final septal wall to previous whorl, dividing the final aperture into two openings.

Umbilical coverplate.—Wall formed on the umbilical side of each chamber except for the final one, covered with chamber flap, usually forming a labial aperture in *A. japonica* and *A. tepida*, but usually without a labial aperture in *A. beccarii* and *P. nipponica*. This coverplate constitutes the

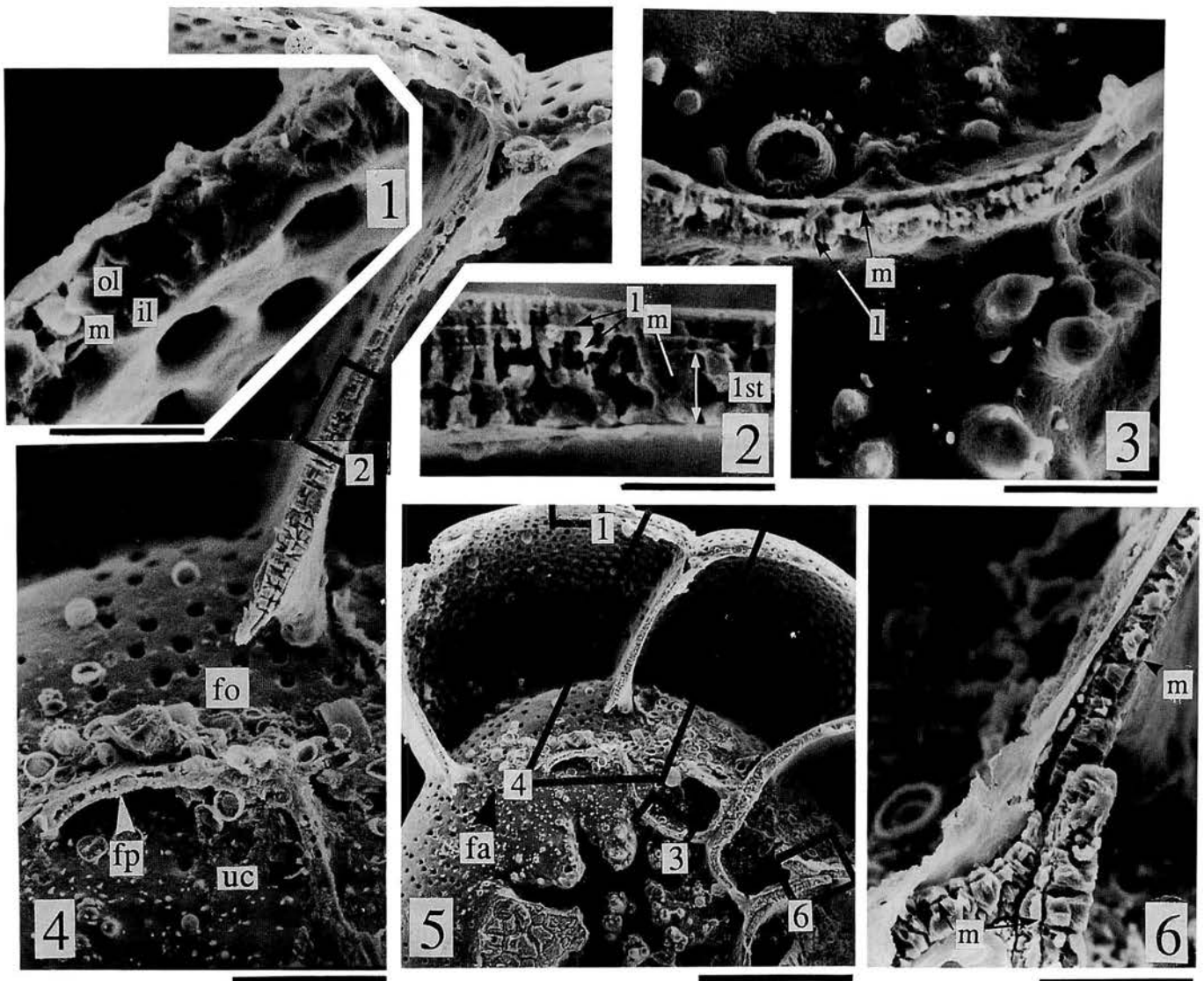


Figure 4. Walls of *Ammonia* sp. etched with 0.5 % phosphoric acid solution showing lamellar structures. 1. Detail of the final chamber showing the outer layer (ol) and inner lining (il) divided by the incised median layer (m). Scale bar: 5 μ m. 2. Detail of the penultimate septal wall (closeup of no. 4) showing the multiple layers (l) developed on the main bilamellar structure (1st) with the median layer (m). Scale bar: 5 μ m. 3. Detail of the penultimate umbilical coverplate showing a trilamellar structure consisting of the primary bilamellar with median layer (m) and secondary layer (l) (closeup of no. 5). Scale bar: 5 μ m. 4. Detail of the penultimate septal wall, the penultimate foramen (fo), the final foraminal plate (fp), and the final umbilical coverplate (uc). Scale bar: 23.1 μ m. 5. Opened umbilical side of the final and the preceding chamber walls. fa=final aperture. Scale bar: 75 μ m. 6. Detail of the junction of the ante-penultimate septal wall, the foraminal plate, and the umbilical cover plate (closeup of no. 5). m=median layer. Scale bar: 7 μ m

main part of the umbilical side of the chamber lumen and encloses the preceding foraminal plate. The foraminal plate should be an anterior projection of this coverplate. The foraminal plate lies within every chamber lumen, but the umbilical coverplate is located in the umbilical side of the preceding chamber. The umbilical coverplate is inclined to the previous whorl of the test, making a canal between the plate and the previous whorl in *Pararotalia*. [axial plate: Cifelli, 1962] [cover plate: Müller-Merz, 1980] [umbilical coverplate: Hansen and Reiss, 1971; Revets, 1993] [part of umbilical plate: Parvati, 1971] [retroparies: Lévy *et al.*, 1986] [umbilical plate: Loeblich and Tappan, 1957]

Lamellar structure

The final chamber wall of *Ammonia* sp. etched with phosphoric acid solution is typically bilamellar, consisting of inner and outer calcareous lamellae, and a middle incised lamella (in the sense of a primary organic membrane where calcification takes place; Hemleben *et al.*, 1977) (Figure 4.1, 4.5). Both the inner and outer calcareous lamellae extend back to cover the penultimate wall, but only the inner lining of the bilamellar structure is superimposed on the outer lamella of the penultimate septal wall, forming a septal flap (Smout, 1954). Such a lamellar structure has been illustrated by Hansen and Lykke-Andersen (1976). In addition to this model, we found multiple lamellae (originally bilamellar with an additional two calcareous lamellae) in the penultimate

septal wall near foramen (Figure 4.2, 4.4, 4.5), indicating that the preceding septal wall is not always three calcareous lamellae consisting of original bilamellar plus secondary lamella (= inner lining). This feature is not in agreement with the statements of Hansen and Lykke-Andersen (1976) and Hottinger *et al.* (1991), who noted a trilamellar structure for the preceding septal wall. Their demonstrations follow a typical model of layering. However, the secondary lamellae of the preceding septal walls are variable in different portions. Thus, it matters whether the section looked at was from the umbilicus or spiral side of the test. Our demonstration of multiple lamellae is based on a section from umbilical side of the test (Figure 4.5).

The final foraminal plate is very thin but clearly shows the bilamellar structure. The additional layering does not occur on the final and preceding foraminal plate, which keeps the wall in thin condition. The umbilical coverplate is originally bilamellar, connecting to the foraminal plate in the hinge, but this coverplate has additional layering. Figure 4.3 shows the trilamellar wall of the rudimentary umbilical coverplate consisting of the original bilamellar wall covered with a new secondary lamella. Although we morphologically defined the two apertural types in *Ammonia* and *Pararotalia*, the lamellar structure of the foraminal plate and umbilical coverplate of the *Pararotalia nipponica* is the same as observed in *Ammonia*.

The lamellar structure at the junction of the foraminal plate, umbilical coverplate and preceding septal wall is very

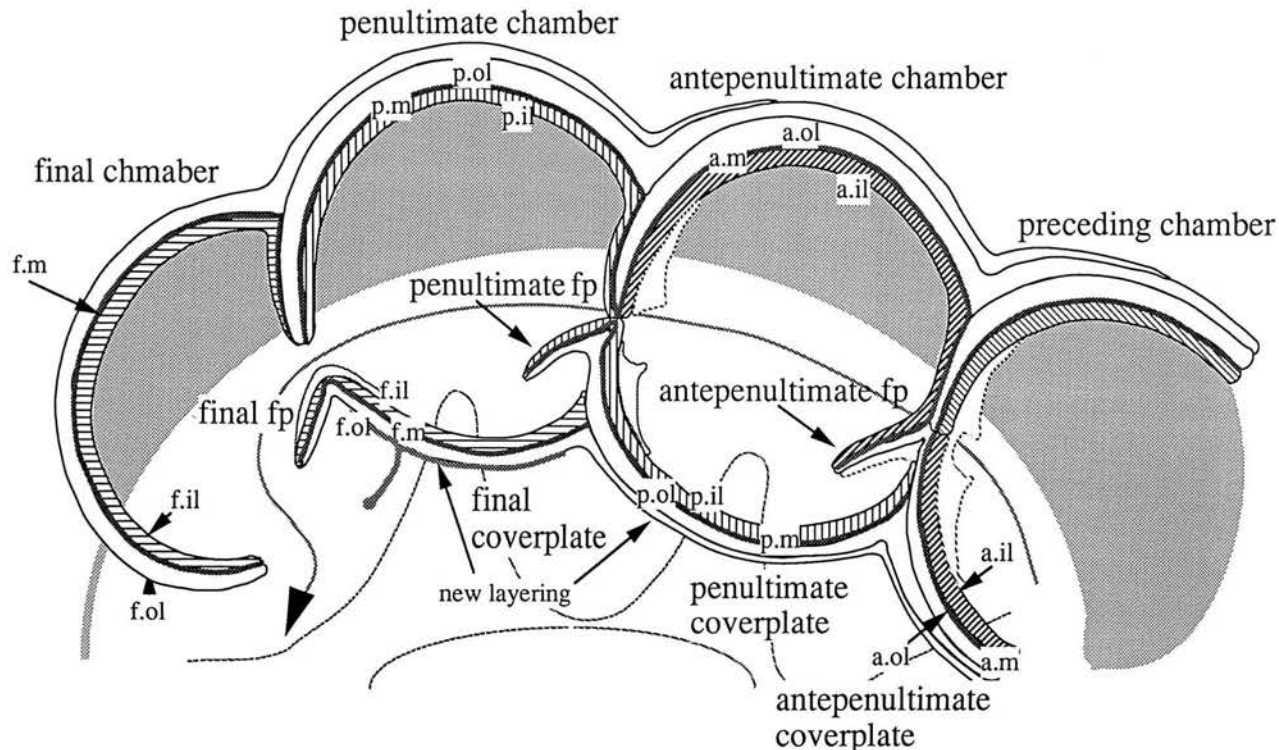


Figure 5. Schematically illustrated lamellar structure in the various parts of the last four chamber walls. Abbreviations: a.il=antepenultimate inner lining; a.m=antepenultimate median layer; a.ol=antepenultimate outer lamella; f.il=final inner lining; f.m=final median layer; f.ol=final outer lamella; p.il=penultimate inner lining; p.m=penultimate median layer; p.ol=penultimate outer lamella; fp=foraminal plate.

complicated (Figure 4.5, 4.6). The inner lining of the foraminal plate connects to the septal flap and the inner lining of the umbilical coverplate connects to the preceding inner lining of the septal wall. In Figure 5, the continuity and discontinuity of each lamella in various portions of the last four chambers are schematically illustrated. This lamellar model is similar to that of Hansen and Lykke-Andersen (1976), except for the median layer of the septal wall illustrated as a discontinuous layer at the junction area.

Description of apertural structures

Ammonia sp.

Figures 2, 4.1–4.6, 6.1–6.8, 7.1

Materials.—Over 10 specimens of *Ammonia* sp. from Recent sediment of brackish Lakes Shinjiko and Nakaumi, Japan. This form has been recognized as a major form of *Ammonia* in Japan, and is identical to *A. beccarii* forma A (Takayanagi, 1955, p. 44, text-figs. 31a–c, in part) and to *A. beccarii* forma 1 (Matoba, 1970).

Diagnosis of test.—The specimens are characterized by having nine to ten chambers in the final whorl, with an open umbilicus without a distinct plug, but with numerous spines in and around the umbilicus. Umbilical side of the test is flat or somewhat concave; spiral side is gently inflated. Periphery rounded, very slightly lobulate. Sutures are limbate and slightly inflated on the spiral side, but limbate and incised on the umbilical side. Imperforate chamber flap, associated with spines for each chamber, is developed and each flap is imbricated, covering the incised suture near the umbilicus. Chambers are transparent with numerous fine pores.

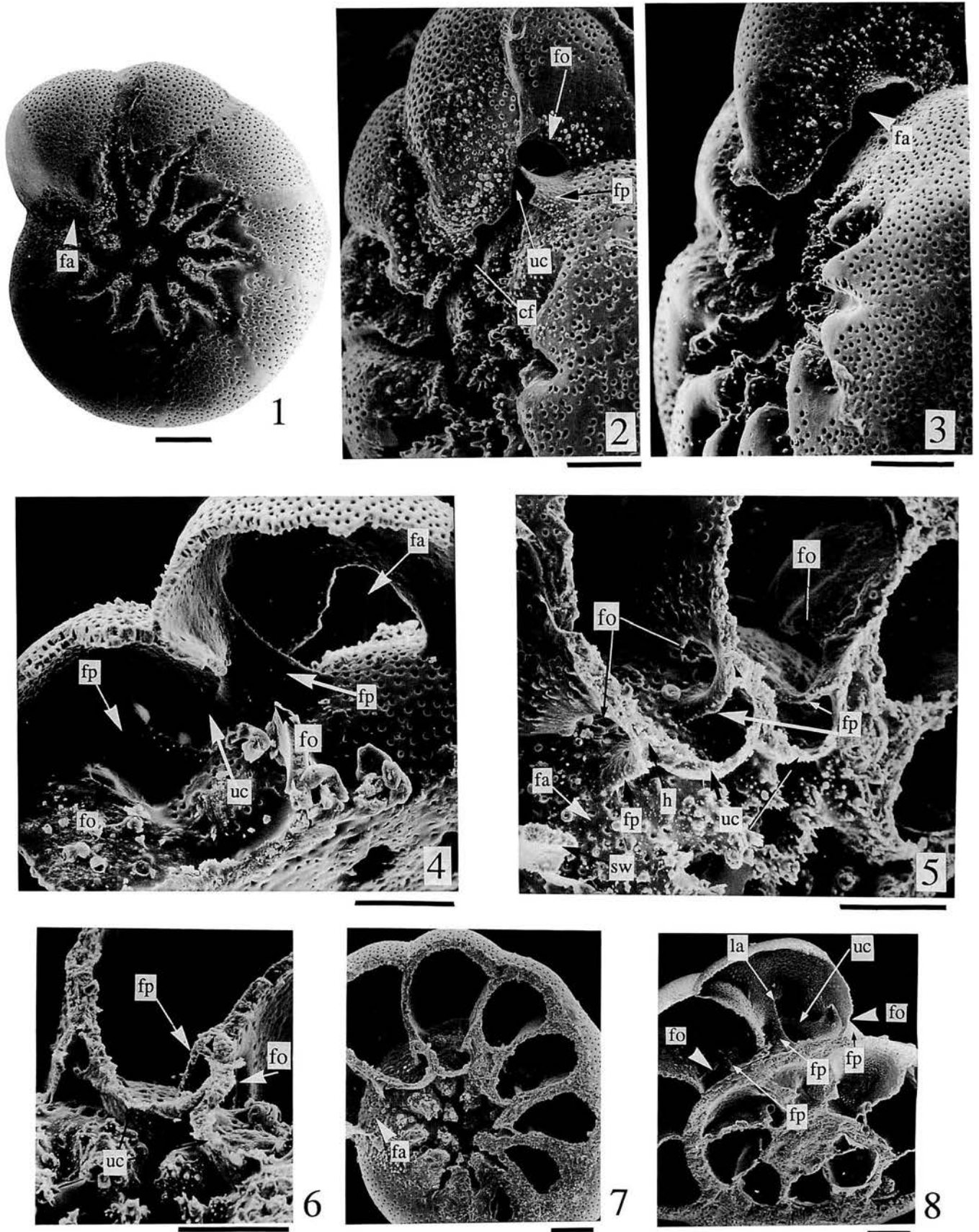
Apertural structures.—The final interiomarginal apertural opening is large without any free structure outside the aperture (Figure 6.1, 6.3). Thus the new foraminal plate is only formed between the foramen and proximal side of the finally formed chamber (Figure 6.2–6.4). When the new chamber is formed, the foraminal plate is usually covered with a new umbilical coverplate, which also covers the apertural opening (Figures 6.4–6.7, 7.1). Both the foraminal plate and umbilical coverplate are formed in a series of proximal side walls of the preceding chamber (Figure 6.5, 6.6). The foraminal plate is left, without further development in the chamber lumen, which shows a hook-like structure when observed in horizontal section (Figure 6.5). The umbilical coverplate is less perforate (Figure 6.4), sometimes forms a very small labial aperture (Figure 6.8). However, this is not significant for this species. Chamber flaps are decorated with small spines, imbricated around the depressed umbilical center, and they are not fused with each other (Figure 7.1). Sutures are always incised, having a fissure shape, but they do not form canals.

Remarks.—The examined species has been previously identified as *Ammonia beccarii* (Linné) by Japanese micropaleontologists. We doubt the taxonomic status of this species. *Ammonia beccarii* was originally collected from beach sands of the Adriatic Sea at Rimini, Italy. The type description given by Linné (1758) is not very helpful. In many subsequent works, *A. beccarii* has been broadly in-

terpreted as possessing wide variations in the test morphology. Cushman (1928) recognized three forms in *Ammonia beccarii*, which represent the different generations of this species. Thereafter Japanese micropaleontologists have used this taxonomic name for widely varied forms of *A. beccarii*. However, we cannot accept such forms in the Japanese *beccarii*. Typical *Ammonia beccarii* is characterized by a large test with well developed sutural knobs and fluted sutures on both dorsal and ventral sides. The number of chambers in the final whorl is about 13 chambers in *A. beccarii*, while the Japanese form has a smooth test surface without sutural knobs and usually less than 10 chambers in the final whorl. Thus the Japanese form is quite different from the typical form of *A. beccarii*. With respect to such morphological variation, Walton and Sloan (1990) recognized three different morphotypes in *Ammonia beccarii*. The Japanese form without the umbilical plug falls within the morphological range of their forma *tepida* and the form with the umbilical plug falls within the range of forma *parkinsoniana*. Schnitker (1974) based on the culturing of *Ammonia* and Walton and Sloan (1990) based on geographic distribution suggested a possible morphologic gradation between forma *tepida* and forma *parkinsoniana*, but no such clear gradation has been found between forma *beccarii* and the morphotypes *tepida* and *parkinsoniana*. Ecological observations show that *A. beccarii* (s.s.) and *A. tepida* have different morphofunctional adaptations to their habitats and environments (Debenay *et al.*, 1998). According to Debenay *et al.* (1998), *A. beccarii* (s.s.) lives on some algae as epiphytic life, whereas *A. tepida* lives in brackish sediments as endopelic life. The Japanese *A. beccarii* is similar to their *A. tepida*. Poag (1978) and Walton and Sloan (1990) mentioned that the geographic distribution of the typical form of *A. beccarii* (s.s.) appears to be limited to the Mediterranean, the eastern Atlantic coast and the western Atlantic coast from Florida to Nova Scotia. Whittaker (personal comm.) suggested that true *A. beccarii* lives only in the Mediterranean Sea and does not occur outside of it. These views are biogeographically supported, as no similarities exist between the Mediterranean fauna and the Indo-Pacific fauna (Rögl and Steiniger, 1984). Thus, no typical live or fossil *A. beccarii* occurs in and around Japan. This means the Japanese form does not represent *Ammonia beccarii* (s.s.).

Another problem in the systematics of *Ammonia beccarii* is introduced from DNA analysis. Pawlowski *et al.* (1995) showed a high similarity of the ribosomal DNA sequences between *A. beccarii* (s.s.) and the Japanese "*A. beccarii*." The Japanese form they examined in their DNA study is the same as we morphologically examined. Our morphologic comparison, however, indicates a taxonomic difference between the two entities. The different results arrived at by morphological comparison and molecular analysis cannot be reconciled at this time.

For these reasons, we hesitate to identify the Japanese form as *A. beccarii*, despite its being a well known species in brackish and shallow waters.



Ammonia japonica (Hada)

Figure 7.2-7.5

Type reference.—*Rotalia japonica* Hada, 1931, p. 137, text-figs. 93a-c.

Materials.—*A. japonica* (Hada) from Recent sediment of the Sakai Suido Strait near Miho Bay, the Sea of Japan.

Diagnosis of test.—Examined specimens are characterized by an inflated test with nine to ten chambers. Chambers are wedge-shaped toward the umbilicus. An umbilical plug is not usually developed in this species. The chamber flaps are less developed than in *Ammonia* sp. Radiate sutures on both the umbilical and spiral sides are straight. Umbilical sutures are incised and decorated with fine spines.

Apertural structures.—The final aperture is divided into two openings by the septal attachment (Figure 7.2-7.5). The anterior aperture is interiomarginal, with an arch-shaped opening and the posterior one is not easily seen, as it is covered by the chamber flap, but its shape is arched (Figure 7.4). The lip is somewhat protruded. The foraminal plates are curled and protrude out of the foramen when observed in horizontal section (Figure 7.3, 7.5). The foraminal plate without a free structure extends to form the ventral chamber wall in the final chamber (Figure 7.4). The umbilical coverplate is formed under the chamber flap when a new chamber is formed, but remains open in the upper part of the final aperture, forming a rounded labial aperture for each chamber but the final one (Figure 7.5). The chamber flap is triangular and points to the umbilicus and becomes larger as a new chamber is added, covering the labial aperture. Ventral sutures with small spines are deeply incised toward the umbilicus, like a fissure.

Remarks.—*Ammonia japonica* is morphologically distinguished from *Ammonia* sp. by having straight, radiate sutures on the dorsal side and a more inflated test. Development of the septal attachment is another characteristic feature of this species which distinguishes it from allied species. *Ammonia inflata* should be allied to *A. japonica* in having straight radiate sutures.

Ammonia sp.cf. **A. parkinsoniana** (d'Orbigny)

Figure 7.6-7.8

Type reference.—Cf. *Rosalina parkinsoniana* d'Orbigny, 1839, p. 99, pl. 4, figs. 25-27.

Materials.—Several specimens of *Ammonia* sp. cf. *parkinsoniana* from Recent sediment of brackish Lake Nakaumi.

Diagnosis of test.—Examined specimens are characterized by a thick lenticular test, having a distinct umbilical plug (Figure 7.6). The size is smaller than the examined form of *Ammonia* sp. The umbilical area is less decorated by spines and compact. The umbilical and spiral sides are inflated and the nonlobulate periphery is subacute. Chambers are eight to nine on the umbilical side and less inflated. Sutures on umbilical side are less incised and the ones on the spiral side are distinctly limbate for the test size. Walls are transparent with numerous fine pores and the test walls are brown in color.

Apertural structures.—The test morphology of *Ammonia* sp. cf. *A. parkinsoniana* differs from that of *Ammonia* sp. in having an umbilical plug and a small and more compact test. However, the apertural structure is very similar to that of *Ammonia* sp. (Figure 7.7, 7.8). The major difference is found in the less developed chamber flap (Figure 7.7). The final aperture is interiomarginal, mostly covered with a small chamber flap (Figure 7.7). The base of the foraminal plate adheres to the previous whorl and extends rearward to contact the umbilical coverplate. The umbilical coverplate covers the final apertural opening, leaving a rounded foramen (Figure 7.7). No labial aperture is formed in this species. Thus the foraminal plate is concealed by the umbilical coverplate, and remains in a plate-like structure in the preceding chamber lumen.

Remarks.—This form is identical to the form having the umbilical plug in *A. beccarii* forma 2 (Matoba, 1970, p. 48, pl. 5, figs. 11a-c, in part). Despite having the umbilical plug, this form is different from *Ammonia beccarii* (s.s.) on account of its small test and smooth test walls. According to Walton and Sloan (1990), this form falls within the range of morphotypic variation of *Ammonia beccarii* forma *parkinsoniana*. We tentatively identified this examined form with *Ammonia* sp. cf. *A. parkinsoniana*, pending further comparison with the type species.

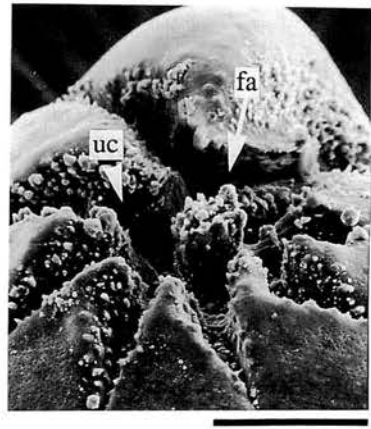
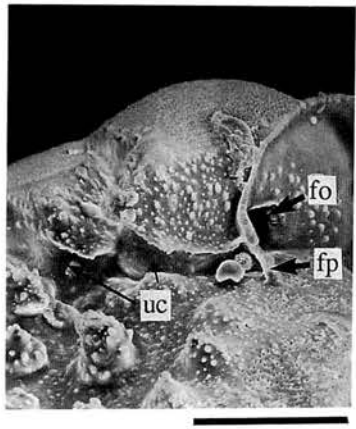
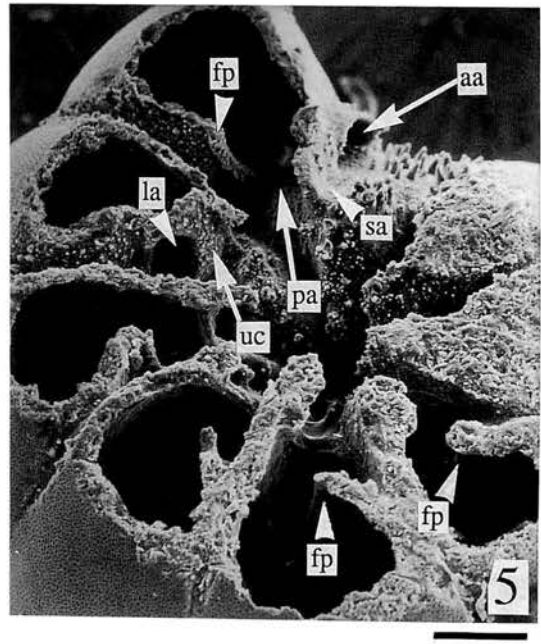
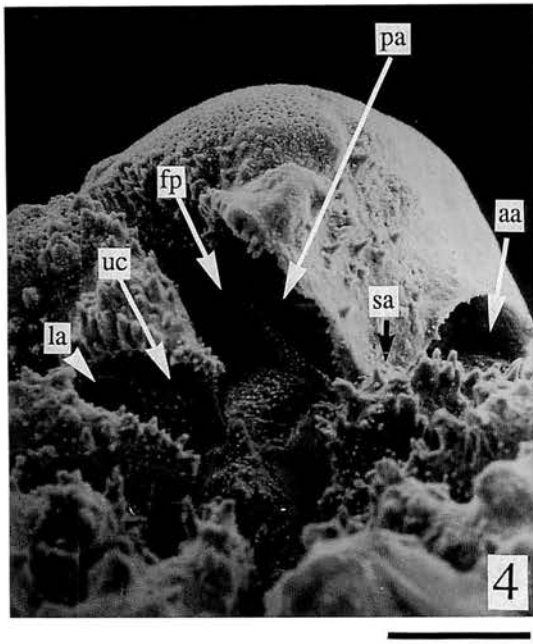
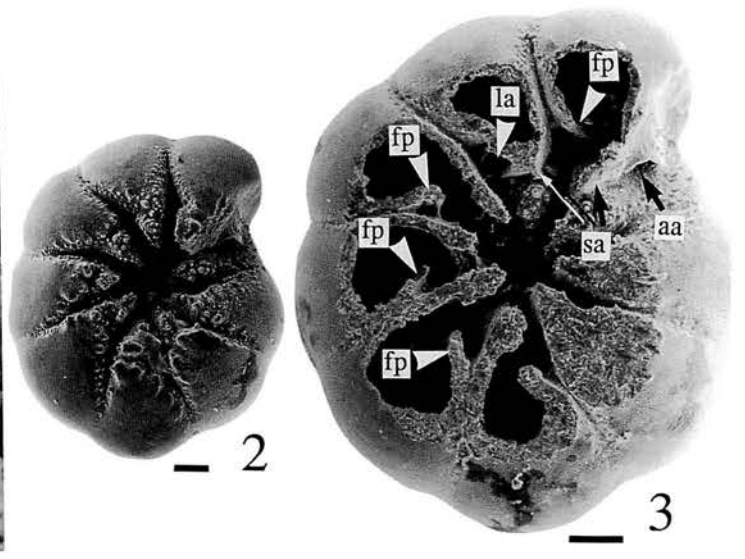
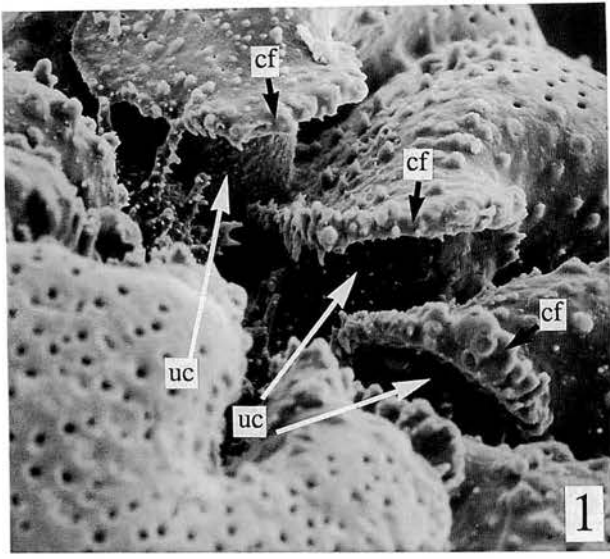
Ammonia tepida (Cushman)

Figure 8.1-8.3

Type reference.—*Rotalia beccarii* (Linné) var. *tepida* Cushman, 1931, p. 61, pl. 13, figs. 3a-c.

Materials.—*Ammonia tepida* (Cushman) from Recent sediment of the Sakai Suido Strait near Miho Bay, the Sea

Figure 6. External and internal apertural structure of *Ammonia* sp. Scale: 50 μ m. 1. Umbilical side view. This form mostly has an open umbilicus. Fine umbilical plug is shown, but it is usually indistinct in optical observation. 2. Oblique view of the umbilical side. The final chamber is removed, thus the penultimate foramen and the foraminal plate can be seen. The umbilical coverplates cannot be seen because they are concealed by the chamber flaps. 3. Oblique view of the umbilical side. The final aperture is an interiomarginal slit from the peripheral side to the umbilicus. Note long slit of the apertural opening is different from rounded intercameral opening. 4. Internal features of the final and penultimate chambers. Spiral side of walls is removed. Walls of the foraminal plate and the umbilical coverplate are smooth. 5. Opened umbilical side showing the foraminal plates and the umbilical coverplates convex towards the umbilicus. The umbilical coverplate adheres to the hinge of the preceding foraminal plate and umbilical coverplate. 6. The umbilical coverplate convex toward the umbilicus. The umbilical coverplate is curled and butts against the previous chamber whorl. 7. External view of the opened umbilicus. 8. Spiral side walls removed. Foraminal plate and umbilical coverplate shown in the penultimate chamber. Very small labial aperture may be seen in this specimen, but it is usually rare. Abbreviations: cf=chamber flap; fa=final aperture; fp=foraminal plate; h=hinge; fo=foramen; la=labial aperture; sw=septal wall; uc=umbilical coverplate.



7

8

of Japan.

Diagnosis of test.—This species has a small test for this genus and has six to seven chambers in the final whorl. The umbilicus is depressed, without a plug. Sutures incised and decorated with small spines on the umbilical side and flush with surface on the spiral side. Ventral chambers are broad and oval. Chamber flaps are developed, imbricated, and cover the sutures near the umbilicus.

Apertural structures.—The final aperture is interiomarginal and consists of a single opening extending to the umbilicus, with the developed chamber flap (Figure 8.1). The foraminal plate is formed on the proximal side of the foramen (Figure 8.2), and the hinge is much inclined and curled to connect to the posterior part of the chamber flap. Thus the posterior part of the chamber flap is concave where the labial aperture is formed except for the final chamber (Figure 8.1). The labial aperture is rather large and rounded in shape, which can be seen from a posterior oblique view (Figure 8.3). The umbilical coverplate is completely covered with the chamber flap, but always developed except in the final chamber (Figure 8.2).

Remarks.—Seibold (1971) put *A. tepida* in the genus *Discorbis*, based on differences of the internal structure such as the relationships between the toothplate (=foraminal plate), axial wall (=umbilical coverplate here), and septal lamellarity (that is, single or double). That idea is invalid, because these internal structures are not characteristic of *Discorbis*, but of *Ammonia*.

Lévy *et al.* (1986) pointed out no critical differences in the internal structure between *A. beccarii* and *A. tepida*. However, the development of the large labial aperture of *A. tepida* is not only significant in distinguishing this species from *A. beccarii*, but also from our examined *Ammonia* sp. herein. All examined specimens are in accordance with Cushman's original concept of *Ammonia beccarii* var. *tepada* (s.s.) and represent the typical *Ammonia beccarii* forma *tepada* of Walton and Sloan (1990). Although there are externally gradational morphologies in Walton and Sloan's forma *tepada*, our *tepada* is different from the other end member form (e. g., *Ammonia* sp. herein) in the presence of the labial aperture. *Ammonia tepida* may represent a definite species as suggested by Pawlowski *et al.* (1995). We are of the opinion that forma *tepada* of Walton and Sloan (1990) needs further consideration based on observations of the internal structure.

Ammonia tochiensis (Uchio)

Figure 8.8, 8.9

Type reference.—*Rotalia tochiensis* Uchio, 1951, p. 374, pl. 5, figs. 1a–c.

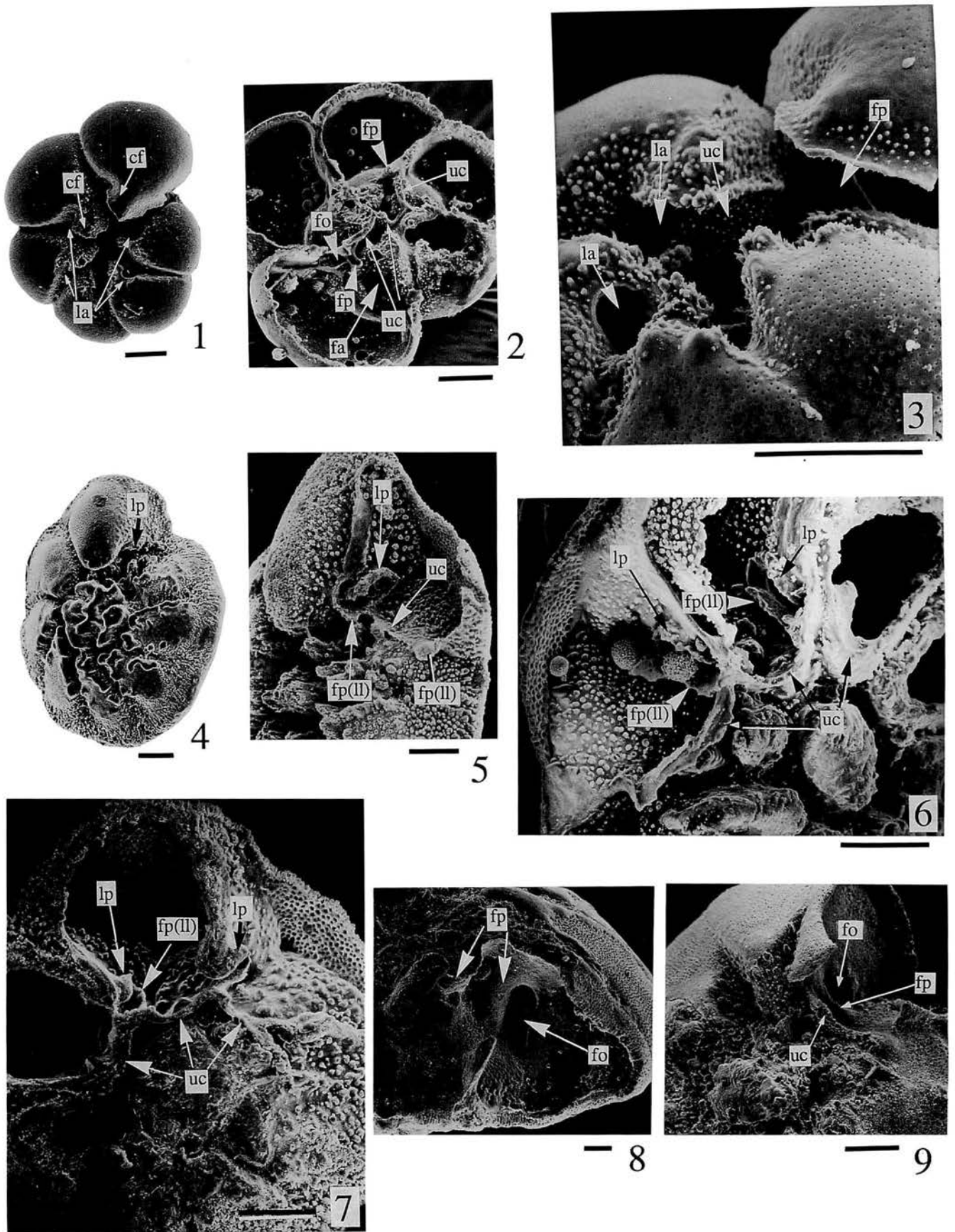
Materials.—One examined specimen from the type locality of this species, the Momiyama Formation, Tochigi Prefecture; five specimens from the Miocene Bihoku Group, Southwest Honshu, Japan. This species is very common in early middle Miocene shallow deposits of Japan.

Diagnosis of test.—Most examined specimens are naturally broken, without the final chamber, but well preserved specimens show the interiomarginal aperture. An umbilical plug is distinctly developed. Chamber flaps are less developed, thus chambers around the umbilical plug are serrated. 13–15 chambers in the final whorl. Sutures distinct and limbate on both sides of test and less incised on umbilical side. Sutures on spiral side are raised.

Apertural structures.—The final aperture is interiomarginal, mainly open on the umbilical side, but covered with a less developed chamber flap. The hinge is columnar in shape, formed at a high angle to the preceding whorl near the umbilicus, with a less developed free margin of the foraminal plate (Figure 8.8). The base of the foraminal plate on the previous whorl is strongly bent toward the posterior. The umbilical coverplate adheres to the edge of the preceding foraminal plate, leaving a concave space between the umbilical coverplate and the foraminal plate (Figure 8.9). Labial apertures are found in an incised suture near the umbilicus.

Remarks.—The internal structure with emphasis on the aperture has been discussed by Ujiié (1965). He described exactly the final aperture as showing an interiomarginal-basal narrow slit, but the description with respect to the foramen is unclear. We did not observe such a structure indicating "interiomarginal foramen converted from aperture, probably by partial resorption of apertural face slightly before addition of new chamber." His toothplate structure is not clearly distinguished from the chamber wall or the umbilical coverplate. His description says the free structure (foraminal plate?) is added after the formation of the new chamber. In our view the umbilical coverplate positioned in the penultimate chamber is formed simultaneously with the foraminal plate as well as the final chamber wall.

Figure 7. External and internal apertural structure of *Ammonia* sp., *Ammonia japonica* (Hada, 1931), and *Ammonia* sp. cf. *A. parkinsoniana* (d'Orbigny, 1836). Scale: 50 μ m. 1. Closeup figure of the chamber flaps and the umbilical coverplates in *Ammonia* sp. 2. Umbilical side view of *A. japonica*. 3. *A. japonica* with artificially removed chamber walls of the umbilical side. 4. Oblique view of the umbilical side of *A. japonica*. Proximal part of the septal wall adheres to the previous whorl in its final chamber (septal attachment in here), thus the anterior and posterior apertures are shown. The foraminal plate with its thickened rim represents the posterior end of the final chamber. 5. Oblique view of the umbilical side of dissected *A. japonica*. The posterior aperture changes into the labial aperture with development of the umbilical coverplate. 6. Umbilical side view of *A. sp. cf. A. parkinsoniana*. 7. Oblique view of the umbilical side of *A. sp. cf. A. parkinsoniana* without the final chamber. The umbilical coverplates seal the previous interiomarginal apertures. 8. Oblique view of the umbilical side of *A. sp. cf. A. parkinsoniana* showing opening of final aperture. No labial apertures are shown. Abbreviations: aa=anterior part of aperture; cf=chamber flap; fa=final aperture; fp=foraminal plate; fo=foramen; la=labial aperture; pa=posterior part of aperture; sa=septal attachment; uc=umbilical coverplate.



***Pararotalia nipponica* (Asano)**

Figures 3, 8.4–8.7

Type reference.—*Rotalia nipponica* Asano, 1936, p. 614, pl. 31, figs. 2a–c.

Materials.—*Pararotalia nipponica* (Asano) from Recent sediment of the Sakai Suido Strait near Miho Bay, the Sea of Japan.

Diagnosis of test.—The specimens examined are characterized by a well developed umbilical plug. Eight chambers on the umbilical side, inflated without a chamber flap, and having a rounded triangular shape around the umbilical plug. Sutures on the umbilical side are mostly radiate, deeply incised, but those on the spiral side are tangential. Umbilical spiral suture is covered with overhanging chambers (=umbilical shoulder), but it is never sealed up by the umbilical shoulders.

Apertural structures.—The final aperture is an interior-marginal slit, extending from the midbase of the apertural face to the umbilicus (Figure 8.4). The lip is thick and protruded. The chamber flap is undeveloped, thus the umbilical canal and sutural grooves are well shown as deep fissures on the umbilical side. The foraminal plate is only associated with the foramen and the base of its hinge adheres to the distal end of the preceding apertural opening, thereby forming the protruded lip (Figure 8.5–8.7), which is here called the lower lip (Figure 3). Thus the foramen is areal in position (Figure 8.5). The umbilical coverplate is developed around the umbilical plug except in the final chamber and connects to the foraminal plate (Figure 8.6, 8.7). No openings corresponding to a labial aperture are found in the umbilical coverplate, indicating the foramen is the main passage between the chambers.

Remarks.—The previously described toothplate of this species is morphologically very ambiguous and confused. The toothplate of Ujiie (1966) may correspond to the umbilical coverplate, according to his description and sketched figures (see above). He noted the umbilical slit (=aperture in original form) is closed with secondary calcification, and then the free toothplate disappears. Because of the absence of such a free structure in the penultimate and preceding chamber, he considered this to indicate partial dissolution of the toothplate. However, such an ingenious explanation is

unnecessary. Originally, there are no free structures comparable to his suggested structure in *P. nipponica*.

External test shape of *Pararotalia nipponica* is similar to that of *P. inermis*. We can observe the protruded structure demonstrated by Hottinger *et al.* (1991) on the umbilical side of *nipponica*'s foramen. This free part of the walls, which is called a toothplate by them, is structurally the same as the lower lip. We find also this type of foramen in *Neorotalia*, as can be seen in the detailed figures of Hottinger *et al.* (1991, 1993).

Discussion

Our observations suggest that the foraminal plate and umbilical coverplate complexes are variable at species level. Moreover, the interrelationships of these plates with neighboring structures are too complicated to easily understand without detailed anatomical observations. Thus, the simple application of the presence or absence of the so-called toothplate to taxonomic decisions is not a reliable criterion.

The foraminal plate and umbilical coverplate are a specified part of the chamber wall formed simultaneously in association with the preceding foramen. On this point, the final aperture is connected with the preceding foramen via the foraminal plate, which may be apparently correlated with the original toothplate concept of Hofker (1950, 1951a, b). Nevertheless, the critical point is that the foraminal plate involves both the final aperture and the preceding foramen. The umbilical coverplate serves only to seal the preceding apertural opening and is not associated with the formation of the final chamber wall. Such foraminal plate and umbilical coverplate structures are characteristic of the rotaliids, not of other taxa with a toothplate. The buliminid toothplate extends within the chamber lumen and no parts of it are concerned with the preceding chamber (e. g., Hofker, 1950, 1951a, b; Revets, 1989). We regard this difference of the toothplate as of primary importance in distinguishing the rotaliid aperture from others. Thus we follow the foraminal plate and umbilical coverplate concept of Hansen and Reiss (1971) and Revets (1993), who stressed the significance of applying only the terms foraminal plate and coverplate to rotaliid taxonomy rather than accepting the general toothplate concept.

Figures 8. External and internal apertural structure of *Ammonia tepida* (Cushman, 1931), *Ammonia tochiensis* (Uchio, 1951), and *Pararotalia nipponica* (Asano, 1936). Scale: 50 μ m. 1. Umbilical side view of *Ammonia tepida*. Note well developed chamber flaps. 2. Oblique view of the umbilical side of dissected *A. tepida*. The umbilical coverplates adhere to the preceding umbilical coverplate, apart from the hinge in this species. 3. Umbilical side view of *A. tepida* indicating the foraminal plate, umbilical coverplate, and labial aperture. 4. Umbilical side view of *P. nipponica*. The final aperture is an interior-marginal slit extending from the peripheral side to the umbilicus. 5. Oblique view of the umbilical side of dissected *P. nipponica*. The antepenultimate aperture is an oval surrounded by the lip and the lower lip (=foraminal plate). The remnant of the dissected penultimate chamber wall shows the lower lip linking to the umbilical coverplate. 6. *P. nipponica* with removed chamber walls of the umbilical side showing the lower lips and the umbilical coverplates. The lower lips represent the foraminal plates as a continuation to the umbilical coverplates. 7. Umbilical side view of *P. nipponica* with the final three chambers removed. The continuous structure of the lower lip (=foraminal plate) and the umbilical coverplate is clearly shown. The umbilical coverplates adhere to the previous whorl at a low angle. 8. Peripheral view of dissected *A. tochiensis*. Columnar-shaped foraminal plate is due to a posterior bend of the plate. The umbilical coverplate adheres to the bent edge of the preceding plate. 9. Oblique view of the umbilical side of dissected *A. tochiensis*. The complex of foramen, foraminal plate and umbilical coverplate is shown in the antepenultimate chamber. Abbreviations: cf=chamber flap; fa=final aperture; fp (l)=foraminal plate (lower lip); fp=foraminal plate; fo=foramen; la=labial aperture; uc=umbilical coverplate; l=lip.

On the other hand, different opinions appeared in the discussion and description of the rotaliids by Hottinger *et al.* (1991, 1993). They are consistent in using the term toothplate by revising its concept. In addition to the original concept, their toothplate includes a new point of view such as an association with a canal. They defined the toothplate as "A toothplate separates partly or entirely the main chamber lumen from an axial space....Interconnected toothplates produce a primary canal." According to their definition, *Pararotalia* is associated with a toothplate as it has an umbilical canal, while *Ammonia* is not associated with a toothplate as it has no umbilical canal. The presence or absence of their toothplate is due to whether the canal is formed or not. Their toothplate concept in relation to structures such as foraminal plate, umbilical coverplate and umbilical plate is subordinate in significance. As we observed in the aperture of *Pararotalia*, the umbilical coverplate obliquely leans to the walls of the previous whorl. The inclination of the foraminal plate is much the same as the umbilical coverplate and changes to a lip in this type of foramen (Figure 3). Thus we usually observe the canal between the umbilical plate/foraminal plate and the previous whorl of the test. This structural reconstruction is similar to that of *Neorotalia* demonstrated by Hottinger *et al.* (1991, p. 29, figure 7) and *Pararotalia* (Hottinger *et al.*, 1993, p. 141, pl. 200, figs. 10, 11). This means that their toothplate is nothing but our foraminal plate, which is here called the lower lip in order to emphasize the structural difference from the *Ammonia*-type foramen. The same view can be seen in Revets (1993), who stated "The internal structures delimiting the canals are the perfect homologues of the foraminal- and coverplate of *Ammonia*."

In addition to different interpretations for the toothplate among these authors, there are also discrepancies with respect to the lamellar structure. Hansen and Reiss (1971) observed that the foraminal plate is bilamellar. Later, Revets (1993) confirmed the bilamellar structure of the rotaliid genus *Neorotalia*, along with the taxonomic significance of the buliminid toothplate consisting only of a modification of the inner lining. Hottinger *et al.* (1991) state that the septal flap, consisting of the inner lamella (=inner lining), may extend into the foraminal plate, coverplate, and toothplate. Thus an additional inner lamella is imposed on the original bilamellar walls, producing trilamellar walls. A similar view of lamellar structure was suggested by Revets (1993) when he stated "As the coverplate butts into the foraminal plate of the prepenultimate chamber, it covers its outside by a secondary lamella, so that this foraminal plate cum coverplate is trilamellar." Our observations of *Ammonia* sp. indicate, however, that the foraminal plate is always bilamellar and the preceding umbilical coverplate is covered with an outer lamella of newly formed coverplate (Figure 5). The foraminal plates never receive additional lamella from the new umbilical coverplate. We need further comparisons to ascertain the variation in the lamellar structure.

Conclusions

We studied the internal structure of some Japanese species of the genera *Ammonia* and *Pararotalia* to validate

Hofker's original concept of the toothplate (Hofker, 1950; 1951a, b). Two major structures, the foraminal plate and the umbilical coverplate (Hansen and Reiss, 1971), are distinguished instead of the general term toothplate. The lamellar structure of the foraminal plate and umbilical coverplate is originally bilamellar. Two types of aperture except for the final one, *Ammonia*-type and *Pararotalia*-type foramen, are recognized, according to the position of the foraminal plate constructed in the aperture. The description of the foraminal plate/umbilical coverplate structure is significant to rotaliid taxonomy in understanding intraspecific morphological variation. However, the structural complex should not be treated as a unit in order to make generic-level distinctions.

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The turrilitid ammonoid *Mariella* from Hokkaido—Part 3 (Studies of the Cretaceous ammonites from Hokkaido and Sakhalin—LXXXVII)

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Abstract. *Mariella (Mariella) lewesiensis* (Spath, 1926) from the Cretaceous of the Hobetsu district, south-central Hokkaido, is described. It is represented by a large specimen, from which a question may arise about the previous view of dimorphism. This species is not directly related to *M. (M.) dorsetensis* (Spath, 1926). It has some affinities with *M. (M.) cenomanensis* (Schlüter, 1876).

Key words: Cretaceous, dimorphism, Hokkaido, *Mariella (Mariella) lewesiensis*, Turrilitidae

Introduction

Altogether eight species of the genus *Mariella* from Hokkaido have been described successively in Part 1 (Matsumoto *et al.*, 1999) and Part 2 (Matsumoto and Kawashita, 1999) under the same title as this paper. They are based primarily on a number of specimens from the mid-Cretaceous members of the Middle Yezo Subgroup in the Soeushinai area [=Shumarinai–Soeushinai area by some authors] of northwestern Hokkaido and on supplementary material from the correlative part in the Yubari Mountains of central Hokkaido.

An additional species of *Mariella* described here is represented by a large specimen which was found by T. K. from the Hobetsu district of south-central Hokkaido. At the request of the Mikasa City Museum [MCM] the specimen was temporarily put on public display there without, however, its being assigned specific name. With the consent of MCM we have recently investigated it to settle its systematic allocation. The described specimen is now officially registered at the National Science Museum [NSM] in Tokyo as a donation by T. K.

Paleontological description (continued)

Mariella (Mariella) lewesiensis (Spath, 1926)

Figures 2–4

Turrilites bergeri Sharpe, 1857, p. 65 (*pars*), pl. 26, fig. 10 only.

Turrilites lewesiensis Spath, 1926, p. 429.

Mariella lewesiensis (Spath). Spath, 1937, p. 512.

Mariella (Mariella) dorsetensis (Spath, 1926). Renz *in*, Renz *et al.*, 1963, p. 1095, pl. 1, fig. 3; Klinger and Kennedy, 1978, p. 31, pl. 9, fig. F, text-figs. 3A, 8A; Kennedy *et al.*, 1979, p. 18, pl. 1, fig.

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Mariella (Mariella) lewesiensis (Spath, 1926). Kennedy, 1971, p. 27, pl. 8, figs. 1, 4, 5, 8; Juignet and Kennedy, 1976, p. 62, pl. 3, fig. 17; Atabekian, 1985, p. 37, pl. 7, fig. 1; pl. 8, fig. 1; Wright and Kennedy, 1996, p. 339, pl. 100, figs. 4, 13, 23, 27; pl. 101, figs. 2, 3; pl. 103, figs. 6–8.

Type.—Holotype, by monotypy, is BMNH 3355B, the original of Sharpe, 1857, pl. 26, fig. 10 (reillustrated by Wright and Kennedy, 1996, pl. 101, fig. 3). It was studied by T. M. at the British Natural History Museum (BMNH) in 1979.

Material.—NSM PM16123. This specimen was collected by T. K. on 19 September 1973 at his locality no. 21 from the mudstone outcrop on the right side of a stream called the Matsukashimapu, about 600m NW of Sanushi Bridge, Inasato area in the Hobetsu district, south-central Hokkaido (Figure 1). The geologic structure is complicated in the Inasato area, where strata seem to be much disordered by folding and thrusting.

Description.—The specimen (Figures 2, 3) is in the state of half-ammonoid preservation (see Maeda, 1987 for this technical term). It is, however, magnificent in its large size, nearly 270mm in total height consisting of 7 preserved whorls and roughly 120mm in diameter at the last whorl (i.e., part of the body chamber). It would be nearly 400mm in tower height, if the missing younger whorls were added. The estimated apical angle is 21°. The late part (at the fifth whorl from the preserved top in Figure 2) is secondarily displaced from the main part, whereas the middle whorl (the third whorl from the preserved top) is almost undeformed.

The septal suture is partly exposed on this whorl (Figure 4).

The upper part of the exposed whorl face is broadly convex and smooth. It slopes down to the gently convex or nearly vertical main flank, which in turn slopes down

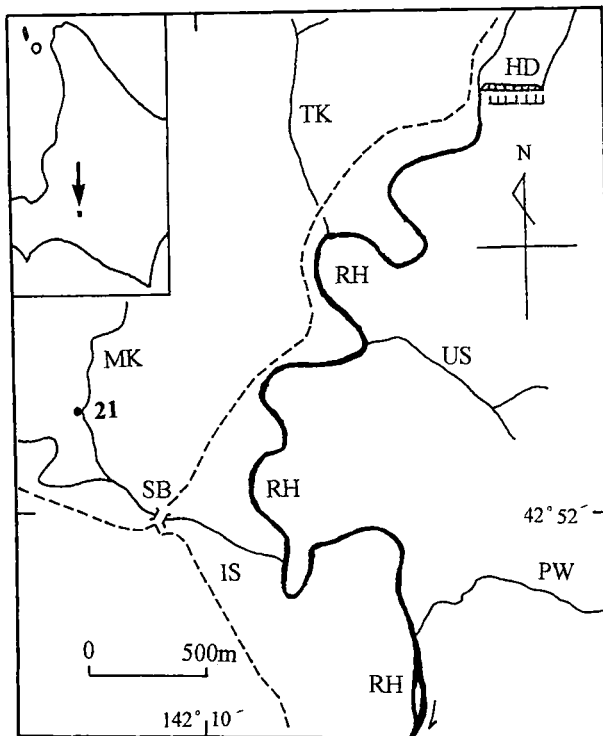


Figure 1. Map showing the location of T. Kijima's Loc. 21 where *Mariella (Mariella) lewesiensis* (Hobetsu specimen) was obtained. HD=Hobetsu Dam; IS=Inasato; MK=Matsukashimapu-zawa; PW=Penke-wakka-tannenai-zawa; RH=River Hobetsu; SB=Sanushi Bridge across the River Sanushibe; TK=Takikawa-no-sawa; US=Uesugi-zawa. The term sawa or zawa means a rivulet. Broken line: highway.

considerably inward. Thus the interwhorl junction is deeply impressed.

Each whorl is ornamented by tubercles in four rows. The tubercles of the upper two rows are coarse and fairly strong, although those of the second row are slightly smaller than those of the first row. On the whorls of the early to middle growth stages the tubercles are somewhat transversely and obliquely elongated. In later growth stages the tubercles of the upper two rows are very coarse, showing a subelliptical base, a domelike shape and a spinose peak. The tubercles of the third row are somewhat smaller than those of the second row in the early to middle growth stages. In the later growth stages they become much smaller, weaker and obliquely clavate (i.e., spirally elongated) in contrast to the enlarged tubercles of the upper two rows. The three rows on the exposed whorl face are disposed at subequal but slightly decreasing intervals downward (Figures 2, 3).

The tubercles of the fourth row are close to those of the third and run along the lower whorl seam, giving crenulation to the interwhorl junction. They are scarcely visible in earlier growth stages, but become more obvious on the lower whorl face in later stages. The tubercles of the first to fourth rows are aligned in an obliquely adoral orientation, but they do not form clear ribbing. Although the basal surface is not fully exposed, distinct ribs do not seem to run from the tuber-

cles of the fourth row. A series of shallow dimplelike depressions is discernible between the upper two rows of tubercles, but it does not form a wide and deep furrow like that of *Mariella (Wintonia)*.

Comparison.—The middle part of this specimen is comparable with the septate holotype and some other example of *M. (M.) lewesiensis* (e.g., Wright and Kennedy, 1996, pl. 101, figs. 3, 2; Atabekian, 1985, pl. 8, fig. 1). In its less deformed whorl, i.e., the third whorl from the top, the height [H] is 32mm at diameter [D] 72mm, hence, H/D is 0.47. These proportions conform with those of the holotype at a corresponding stage, where H=30.5mm, D=67.0mm and H/D=0.47. Similarity is also observable in the ornament. There are 21 tubercles in each row per whorl in the holotype. The Hobetsu specimen shows eleven tubercles in the exposed half of the whorl at the middle growth stage, although the number seems to decrease to 7 or 8 at the last stage. The smooth surface in the upper part of the exposed whorl face immediately below the upper seam is a diagnostic character of this species. This feature is clearly observed in the Hobetsu specimen. The faint ribbing on the basal surface in this species also occurs in our specimen. To sum up, the described specimen is certainly identified with *M. (M.) lewesiensis*.

Discussion.—The Hobetsu specimen attains enormous size for *Mariella (M.) lewesiensis*. This raises the problem of dimorphism. Wright and Kennedy (1996, p. 340) have pointed out a dimorphic pair in this species, namely they regarded SMC B35910 (Wright and Kennedy, 1996, pl. 103, fig. 7) as an adult macroconch and SMC B35905 (Wright and Kennedy, 1996, pl. 100, fig. 27) as an adult microconch. The former is about 200mm in estimated original tower height with an inferred apical angle of 22°, whereas the latter is about 150mm in tower height with an apical angle of 21°.

The specimen from Hobetsu is almost twice as large as the so-called macroconch example (SMC B35910) from England in regard to the total whorl height (400mm) and also to the diameter (120mm) of the last whorl. This fact throws doubt on the previous evidence of dimorphism in *M. (M.) lewesiensis*. Further investigation, including the statistical examination on a sufficient number of specimens, is required for a definite conclusion.

Mariella (M.) lewesiensis has been often confused with *M. (M.) dorsetensis* (Spath). This is shown by the synonymy given in the description of the latter in Part 1 (Matsumoto *et al.*, 1999, p. 107) and that of the former in Part 3. Here we would like to comment that the two specimens illustrated by Benavides-Cáceres (1956, p. 108, pl. 40, figs. 8, 9) under "*Paraturrilites lewesiensis* (Spath)" should both be revised to *M. (M.) dorsetensis* (Spath), although one of them (Benavides-Cáceres, 1956, pl. 40, fig. 8 only) was considered so by many authors. Likewise, what was called *M. (M.) lewesiensis* (Spath) by Marcinowski (1974, pl. 32, fig. 13 without description), from the Lower Cenomanian of the Polish Jura Chain, is probably *M. (M.) dorsetensis*, because of the distinct ribs on the upper whorl face and the rows of granular tubercles on the convex flank at subequal intervals.

The morphological distinction between the two species has been already discussed in Part 1 (Matsumoto *et al.*, 1999). We offer here remarks on their affinities. *M. (M.)*



Figure 2. *Mariella* (*Mariella*) *lewesiensis* (Spath). Lateral view of NSM PM16123, $\times 2/3$. (Photo courtesy of Katsumi Shinohara, without whitening)



Figure 3. *Mariella* (*Mariella*) *lewesiensis* (Spath). NSM PM16123. Specimen turned about 60° clockwise from the position in Figure 2, $\times 2/3$. (Photo courtesy of Katsumi Shinohara, without whitening)



Figure 4. *Mariella (Mariella) lewesiensis* (Spath). External suture partly exposed on the preserved third whorl of NSM PM16123. E: external lobe; L: lateral lobe. Bar scale: 5 mm.

dorsetensis is closely allied to *M. (M.) bergeri* (Brongniart) of latest Albian age. The affinities of *M. (M.) lewesiensis* have not been much discussed, but recently Wright and Kennedy (1996, p. 344) have pointed out a close relationship between *M. (M.) lewesiensis* and *M. (M.) cenomanensis* (Schlüter, 1867). We would agree with them, although well preserved examples of *M. (M.) cenomanensis* have not been described from Hokkaido. Based on the description and plentiful illustrations by Wright and Kennedy (1996, p. 342, with a full synonymy, and pl. 100, figs. 3, 24, 26; pl. 101, figs. 1, 4; pl. 102, fig. 14; pl. 103, fig. 9; pl. 110, fig. 3; pl. 111, figs. 1, 3; text-figs. 136A and 141B; also Wright and Kennedy, 1995, text-fig. 129E for the suture), the following points are evident. In *M. (M.) cenomanensis* the upper part of the exposed whorl face is convex and smooth as in *M. (M.) lewesiensis*. The tubercles of the upper two rows are coarse in both species, but in the former the tubercles of the second row are clavate (i.e., spirally elongated) and disposed in the lower part of the flank, being separated from the first row by a broad, smooth zone. Some examples of *M. (M.) cenomanensis* (e.g., Wright and Kennedy, 1996, pl. 101, figs. 1, 2) are nearly as large as the Hobetsu specimen of *M. (M.) lewesiensis*.

Incidentally, "*Mariella (Mariella)* n. sp. aff. *lewesiensis* (Spath)," was mentioned by Kanie *et al.* (1977, p. 113, pl. 1, fig. 8) in their Madagascar paper. Actually it is one of the specimens (TKD 30080A from Loc. 71204 in the Shumarinai area) of *M. (M.) dorsetensis*, as has been recently described by Matsumoto *et al.* (1999, p. 108).

Distribution.—*Mariella (M.) lewesiensis* has been reported to occur in the Lower Cenomanian of southern England, France, Germany, Switzerland, Poland, Turkmenistan, Iran, Zululand (South Africa) and Madagascar (see synonymy for the references). Now its distribution is extended to Japan in the northwestern Pacific region.

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Dicotyledonous leaf macrofossils from the latest Albian-earliest Cenomanian of the Eromanga Basin, Queensland, Australia.

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Abstract. Ten types of dicotyledonous angiosperm cuticle are described from bore core samples from the Early Cretaceous (latest Albian-earliest Cenomanian) of the Eromanga Basin, central Queensland. To date, these are the oldest organically preserved angiosperm macrofossils in Australia. Most of this material is found as small dispersed fragments, but two more intact lobed leaves were found. The affinities of some specimens are suggested to lie with the Chloranthaceae and Illiciaceae, and possibly the Platanaceae, but the rest are unknown. None of the cuticles show the paracytic stomatal arrangement which is common in extant plant families often regarded as 'primitive'. However, one of the cuticle forms exhibits a 'plastic,' variable form of subsidiary cell arrangement, which has previously been suggested as the most primitive condition. These angiosperms were a small component of an overwhelmingly gymnosperm (mostly conifer) dominated flora. They grew in clastic swamps, but may also have occurred in coal swamps or sandy levees. The notably thin cuticle of some forms is consistent with an understory or deciduous habit.

Key words: angiosperm, Australia, Cretaceous, cuticle, stomate

Introduction

The first angiosperms appeared in Australia during the Barremian-early Aptian, and by the end of the Albian over 20 angiosperm(id) pollen types are known (Burger, 1990). Based on pollen records the angiosperms had originated somewhere distal to Australia by the Valanginian (Brenner and Bickoff, 1992; Brenner, 1996). The oldest angiosperm macrofossils in Australia are impressions from the Aptian of the Otway Basin in Victoria (Douglas, 1994). These impressions include a dicot identified as *Hydrocotylophyllum lusitanicum* Teixeira (Douglas, 1965). A further specimen, previously interpreted by Drinnan and Chambers (1986) as a possible fern, was later claimed as the world's oldest flower (Taylor and Hickey, 1990; although this distinction is now claimed by Late Jurassic material from China, Sun *et al.* 1998). The Australian Late Cretaceous angiosperm macrofossil record is very poor, probably due to a lack of outcrop. Scattered impressions and some cuticular debris are known from drill core material from the later part of the Victorian Cretaceous but have not been formally documented. McLoughlin *et al.* (1995) illustrated several dicotyledonous leaf impressions of probable Cenomanian age from the Eromanga Basin of central Queensland. Their material came from surface outcrop of the Winton Formation (Vine and Day, 1965; Exon and Senior, 1976) which has

undergone considerable weathering. Below this zone, in samples obtained from bore cores for this study, weathering and lithification have been minimal and anatomical details (including cuticle) of fossil plants are preserved (Pole, 1999; Pole and Douglas, 1999). This material has been dated palynologically as close to the Albian-Cenomanian boundary (Dettmann and Playford, 1969; Helby *et al.*, 1987; Dettmann *et al.*, 1992). The purpose of this paper is to document the dicotyledonous macrofossils from bore core samples of the Eromanga Basin.

Dicotyledon leaf fragments were recognised by having net venation comprising more than one order, or thickness of veins, and confirmed with epidermal characters. Angiosperm cuticle was recognised partly by its robustness, i. e. it is strong enough to survive processing and handling. This eliminates from consideration the ferns, which in any case, are generally distinct on morphological characters (van Cotthem, 1970a). The Early Cretaceous fern *Weichselia*, which does have relatively thick cuticle, is singularly unique in morphology. *Weichselia* is more similar to *Equisetum* and some gymnosperms (Alvin, 1974), having relatively large, randomly oriented guard cells, which are not sunken or over arched by subsidiary cells, but have an outer stomatal ledge. On these criteria there is little else in the Early Cretaceous which could be confused as dicotyledonous, with the possible exception of the Caytoniales. Harris

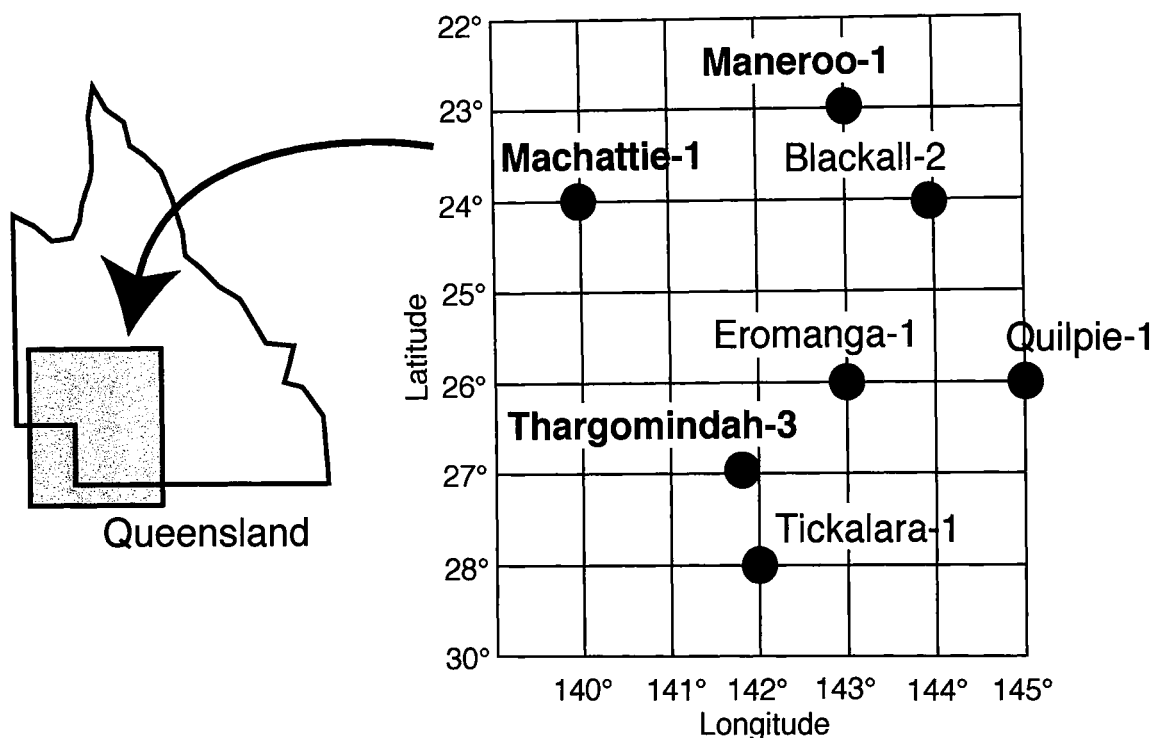


Figure 1. Locality map. The position of the study area within Queensland, Australia, is shown at left, and the position of all drill cores sampled within the study area is shown at right. Names of drill cores which provided dicotyledonous cuticle are in bold.

(1940) described *Sagenopteris* cuticle which had guard cells, apparently (according to his sketch) without outer stomatal ledges, no distinct subsidiary cells, and trichomes with basal cells. A cuticle type from the Winton Formation with possible affinities to the Caytoniales is described in Pole and Douglas (1999). Monocotyledon cuticle is generally distinct and is discussed in Pole (1999).

My separation of fossil cuticles into morphological groups is based on my experience with the cuticle of extant plants. In my opinion the forms described below represent individual species.

Materials and methods

Seven bore cores were selected from the Eromanga Basin in central Queensland (Figure 1); GSQ Blackall-1, GSQ Eromanga-1, GSQ Quilpie-1, GSQ Machattie-1, GSQ Maneroo-1, GSQ Thargomindah-3, and GSQ Tickalara-1 (these cores are stored in a Geological Survey of Queensland (GSQ) warehouse at Zillmere, Brisbane). Each core penetrates fluvial sediment of the Winton Formation and the underlying marine sediment of the Allaru and Mackunda Formations. Samples of approximately 5 cm³ each were selected for macrofossil preparation, based on a visual appraisal of the sediment. Each sample was numbered consecutively and prefixed with the first three letters of the bore core name. Stratigraphic details of samples which contained dicotyledonous macrofossils are given as

Table 1. Stratigraphic details of samples with dicotyledonous macrofossils.

SAMPLE	DEPTH/M	FORMATION
MAC-3	155.44	Winton
MAC-7	193.49	Winton
MAC-11	319.7	Mackunda
MAN-6	28.8	Winton
MAN-7	29.4	Winton
MAN-8	29.7	Winton
MAN-9	29.8	Winton
MAN-11	29.95	Winton
MAN-12	30.0	Winton
MAN-20	39.4	Winton
MAN-22	42.0	Winton
MAN-23	42.3	Winton
MAN-28	80.4	Winton
MAN-30	86.8	Winton
MAN-34	161.6	Mackunda
MAN-42	326.4	Mackunda
THA-24	218.0	Winton
THA-32	240.3	Winton
THA-41	292.3	Winton
THA-47	313.3	Winton

Table 1 (details of all samples are given in Pole and Douglas, 1999). Carbonaceous muds were preferred, sands were avoided unless they contained prominent carbonaceous horizons, and lignites were also generally avoided (previous experience and some tests indicated these usually do not preserve cuticle). Carbonaceous material was sparse in the marine sediment. Only two nearly intact leaves were recognised in hand specimen, the rest were small fragments of leaf lamina exhibiting some net venation or cuticle. In total, 235 samples were taken. Samples were numbered consecutively from the top of the core and given a prefix of the first three letters of the core name.

Most of the sample was processed for cuticle, leaving a small amount as a voucher specimen. Samples usually broke down into a sludge with the addition of warm water, but sometimes addition of a little hydrogen peroxide was needed. Sludge was washed through 500 and 125 μm mesh sieves, with most workable cuticle being retained on the 500 μm . Further clearing of cuticle involved increasing concentrations of warm peroxide. This treatment was controlled so that fragments retained veins or resin glands. Further clearing so that only cuticle remained used aqueous chromium trioxide. Any adhering silicates were removed

with hydrofluoric acid.

Samples were scanned under a binocular microscope, the dominant floristic components were estimated, and specimens were removed with tweezers for transmitted light microscopy (TLM) or (when sufficient extra material was available) scanning electron microscopy (SEM). Crystal Violet was used to stain when necessary.

There are insufficient data for the dicotyledonous cuticles to formally diagnose new taxa and an informal system of nomenclature is used. Macrofossils and slides are catalogued with the prefix 'SL' and are stored in the Department of Botany, University of Queensland. Specimens mounted on Electron Microscope stubs are catalogued with the prefix 'S'. Specimens for TLM viewing were mounted on microscope slides with glycerine jelly, and those for SEM viewing on stubs with double-sided tape and coated with gold.

Results

Dicotyledon sp. A

Figures 2, 3

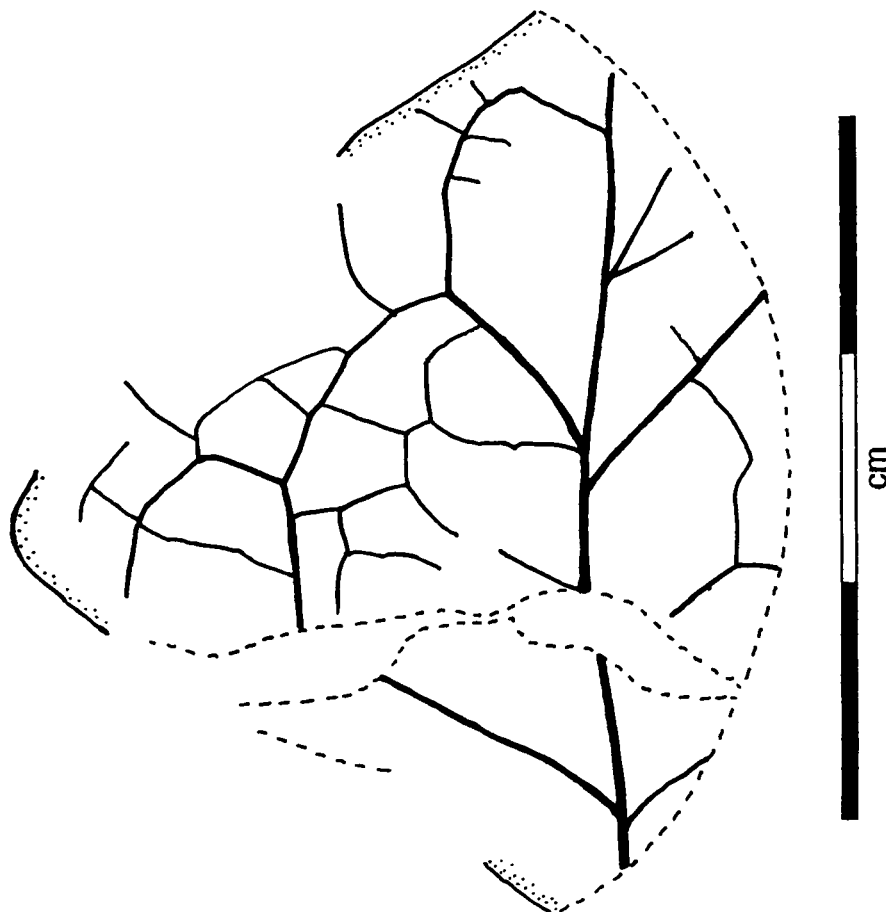


Figure 2. *Dicotyledon* sp. A, SL797. Line drawing of the only near-intact dicotyledon fossil found. Stipple = margin, dashes = broken lamina. See Fig. 3 for photographs.

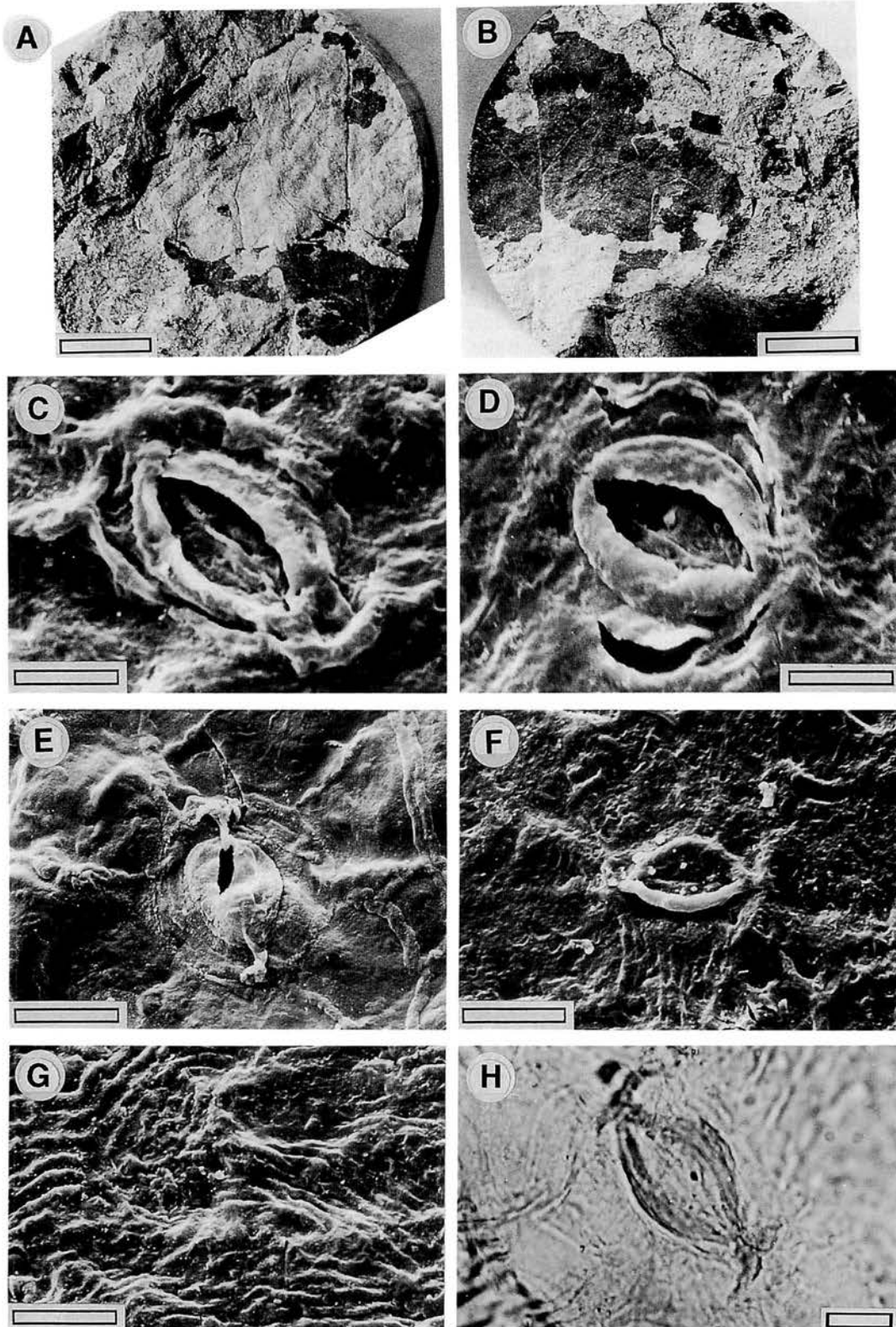


Figure 3. Dicotyledon sp. A. **A.** Intact leaf on bedding surface of drill core sample, SL797, scale: 1 cm. **B.** Counterpart of SL797, scale: 1 mm. **C.** SEM of outer surface of stomate, S761, scale: 10 μ m. **D.** SEM of outer surface of stomate, S763, scale: 10 μ m. **E.** SEM of inner surface of stomate, S763, scale: 20 μ m. **F.** SEM of outer surface of stoma showing ridges extending from lateral margin, S761, scale: 20 μ m. **G.** SEM of outer upper leaf surface showing ridges, S773, scale: 20 μ m. **H.** TLM of stomate, SL678, scale: 10 μ m.

Reference specimen.—SL797 (almost intact leaf on bedding surface, MAN-11).

Referred specimen and occurrence.—SL996; MAC-3 (dispersed cuticle).

Description.—Leaf lobed, length about 40 mm, width about 50 mm (midrib-margin 24 mm), hypostomatic; on abaxial surface stomatal orientation random; outline of guard cell pair ovate, outer stomatal ledge broad, T-piece thickenings at poles prominent; subsidiary cells not visible under

TLM, under SEM typically 6 isodiametric contact cells visible; cuticle very thin, epidermal cell flanges not visible under TLM; on surface ridges of cuticle sometimes present over outer walls of guard cells, also bands of fine ridges prominent, extending laterally from guard cells; glabrous; adaxial surface epidermal cell flanges visible under TLM, isodiametric, polygonal, straight-walled; finely and evenly ridged on surface; glabrous.

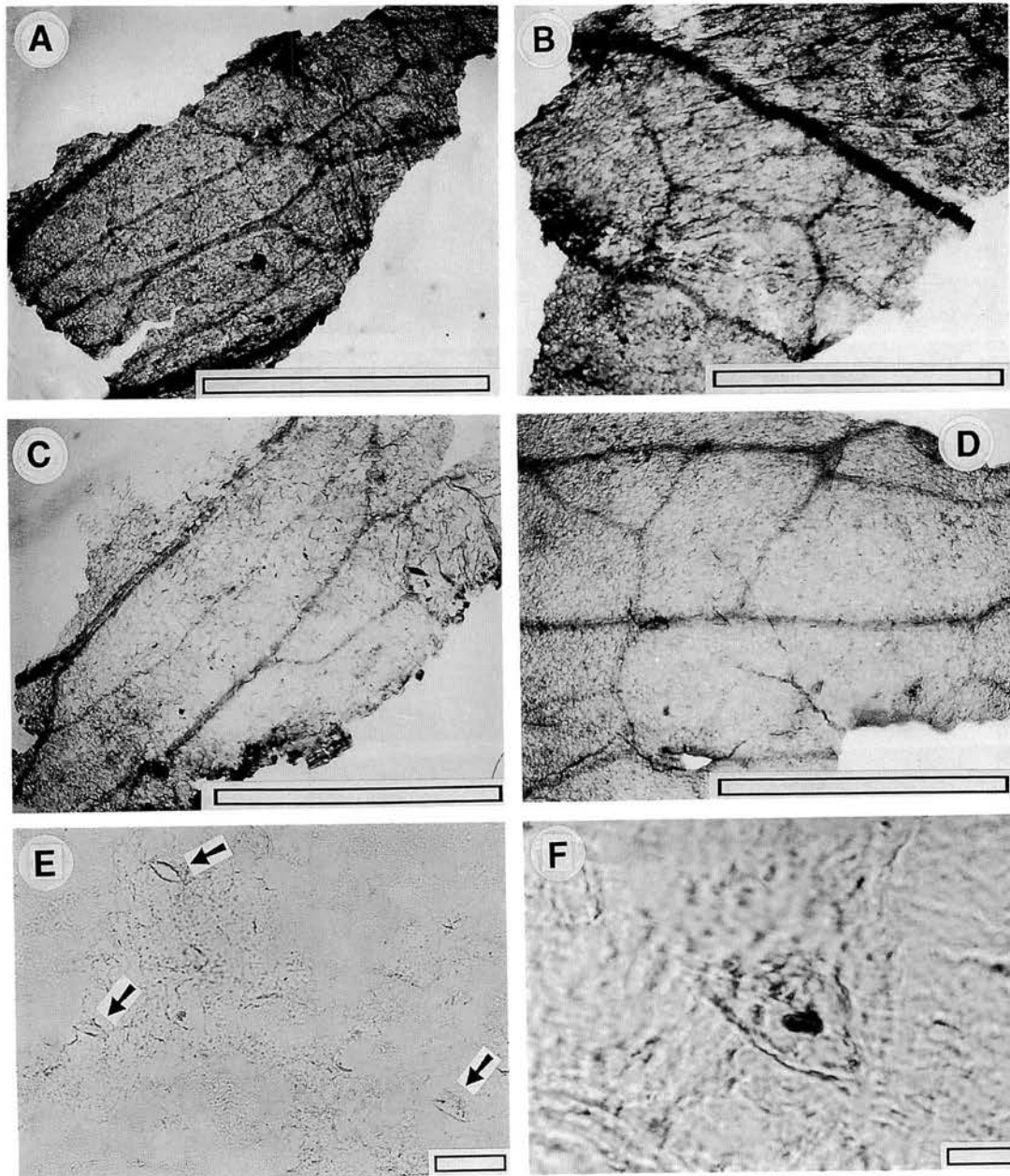


Figure 4. Dicotyledon sp. B. **A–D.** TLMs of leaf fragments with net-venation, scale: 1 mm. **A.** SL776. **B.** SL777. **C.** SL774. **D.** SL773. **E.** TLM of cuticle showing widely separated, aligned stomata (arrowed), SL787, scale: 50 µm. **F.** TLM detail of single stomate, note narrow, elliptical rim, SL787, scale: 10 µm.

Dicotyledon sp. B

Figure 4

Reference specimen.—SL787 (dispersed cuticle, MAN-23).

Referred specimens and occurrence.—SL997, MAN-9; SL774, MAN-11; SL773, MAN-20; SL771, MAN-22; SL776,

SL777, MAN-23; SL788, MAN-34.

Description.—Leaf shape unknown, small fragments of lamina exhibit net-venation; stomata scattered, infrequent, visible under TLM as very thin, aligned (at least over small areas), elliptical, outer stomatal ledges; cuticle otherwise very thin, no clearly distinguished subsidiary cells, epidermal cell flanges generally not visible, isodiametric, smooth,

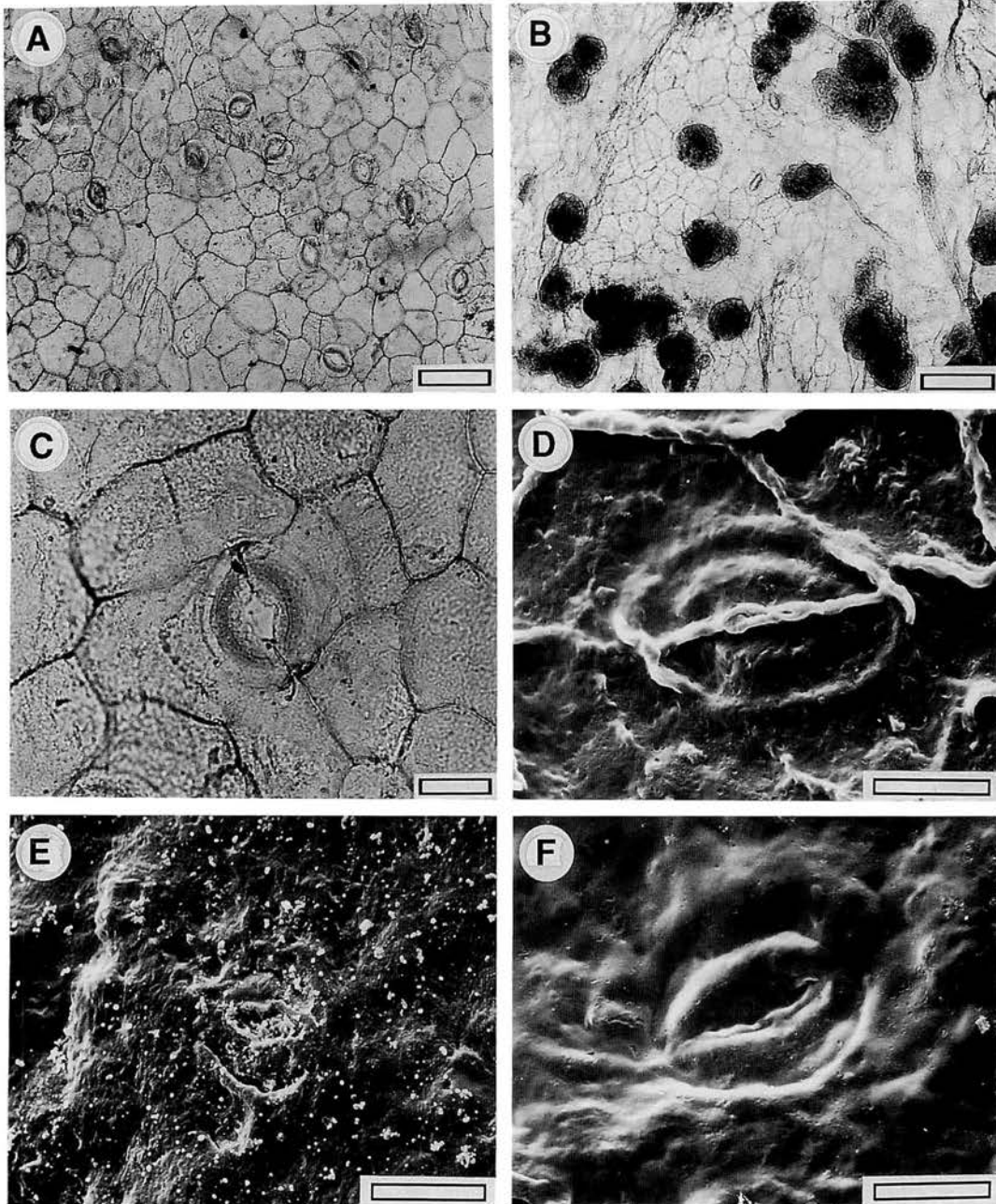


Figure 5. Dicotyledon sp. C. **A.** TLM, SL738, scale: 100 μ m. **B.** TLM with numerous dark resin bodies still attached, SL735, scale: 100 μ m. **C.** TLM of single stomate, SL738, scale: 25 μ m. **D.** SEM of inner surface of single stomate, note T-piece thickening, S765, scale: 20 μ m. **E.** SEM of outer surface of single stomate, S759, scale: 20 μ m. **F.** SEM of outer surface of single stomate, S765, scale: 20 μ m.

slightly thicker over veins; glabrous.

Dicotyledon sp. C

Figure 5

Reference specimen.—SL738 (dispersed cuticle, MAN-30).

Referred specimens and occurrence.—SL731, MAN-6; S760, MAN-7; SL733, MAN-8; S765, MAN-9; S759, MAN-11; SL735, MAN-12; SL739, MAN-42; SL676, THA-32.

Description.—Stomatal orientation random, outer stomatal ledges broad; distinct, thin T-piece thickenings at guard cell poles; peristomatal thickening sometimes present; no clear or consistent subsidiary cell arrangement but lateral contact cells often divided tangentially to give irregular-shaped subsidiary cells; normal epidermal cells polygonal, smooth; major veins (midrib?) visible as more elongate, rectangular epidermal cells; outer cuticular surface smooth; typically glabrous but sparse poral trichome bases sometimes present; resin bodies from within leaf lamina often adhering to

cuticle (e. g. SL735).

Note.—The resin bodies are similar to those widespread throughout the extant magnoliids (Metcalf, 1987; pers. obs.).

Dicotyledon sp. D

Figure 6

Reference specimen.—SL676 (dispersed cuticle, THA-32)

Referred specimens and occurrence.—SL895, MAC-7; SL677, THA-41

Description.—Stomatal distribution over leaf unknown; stomata randomly oriented; guard cell pair outline ovate, central portion covered by broad outer stomatal ledge; T-piece thickenings present at guard cell poles; subsidiary cell pattern variable, polar and lateral subsidiary cells typically recognisable, but sometimes not; lateral subsidiary cells present in up to three layers (including the hexacytic arrangement of van Cotthem, 1970b), apparently formed by

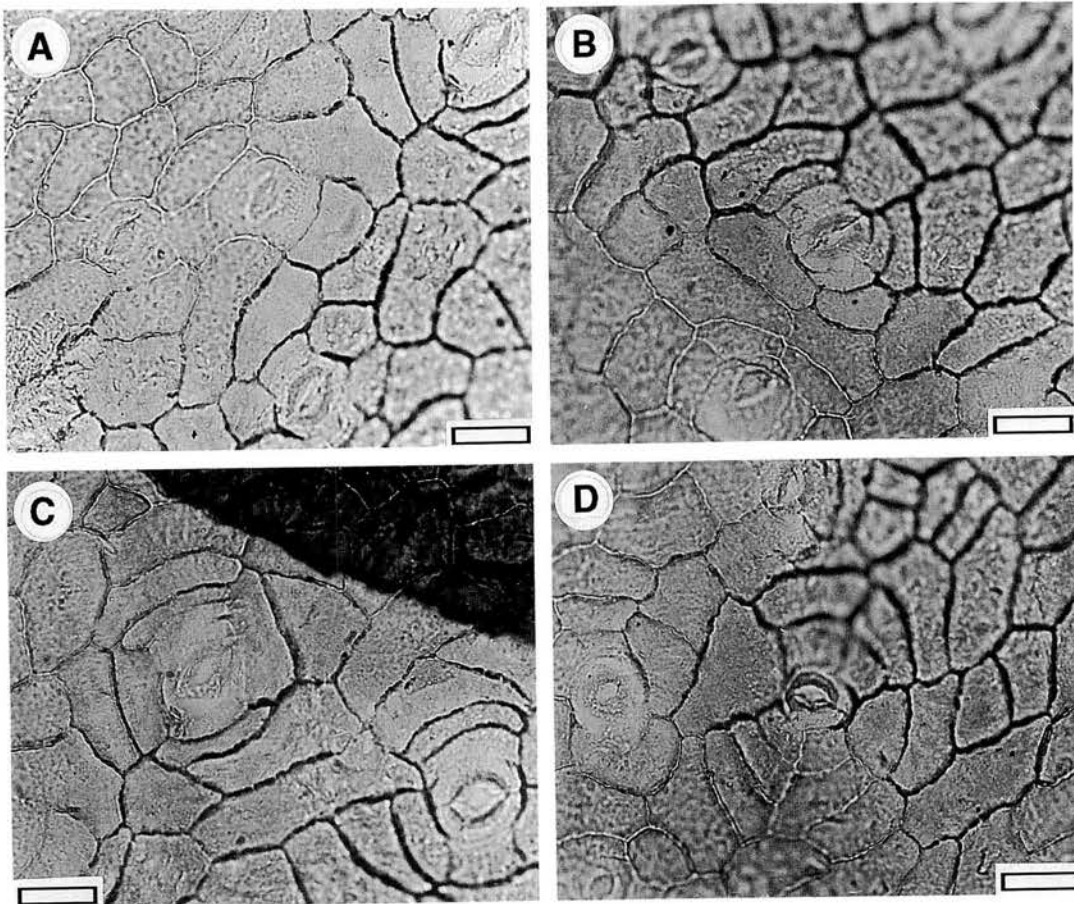


Figure 6. Dicotyledon sp. D, all SL676, TLMs of stomata of varying type, scale: 25 μ m. **A.** Stomata with single lateral subsidiary cells on either side, some have divided radially. **B.** Stoma with 3 lateral subsidiary cells on one side, and two on the other which have both divided radially. **C.** Stomata with two lateral subsidiary cells. **D.** Stoma with six lateral subsidiary cells on one side.

elongate, tangential divisions of contact cells, sometimes also radially divided (i. e. giving six lateral subsidiary cells on one side of stoma); polar subsidiary cells irregular (probably just unmodified contact cells) or sometimes elongate, forming from tangential division of contact cell; veins not reflected in epidermal cells; glabrous.

Dicotyledon sp. E

Figure 7

Reference specimen.—SL772 (only specimen, small leaf with apex and base missing, two teeth present, MAN-34).

Description.—Leaf toothed or lobed, preserved lamina length 6 mm, up to 4 mm wide, teeth/lobes 0.8 mm wide and high; first order venation externodromous; tooth vascularisation central; stomata visible only as thin, elliptical outer stomatal ledges; aligned with midrib when close, or aligned with lateral venation further away; resin bodies numerous within lamina.

Dicotyledon sp. F

Figure 8

Reference specimen.—SL678 (dispersed cuticle, only

specimen, THA-24).

Description.—Stomatal distribution over leaf unknown; stomata randomly oriented; outer stomatal ledges prominent, elliptical, sometimes narrowing abruptly before poles; prominent T-piece thickenings at stomatal poles; subsidiary cells not visible; cuticle very thin, epidermal cell flanges not visible in TLM, faint under SEM; outer epidermal surface ornamented by swirling bands of fine ridges sometimes starting at right angles from lateral subsidiary cells, but also with no consistent orientation to stomates; sometimes peristomal ridges present along edges of guard cells.

Note.—The general appearance of the cuticle, particularly the surface ornamentation, appearance of the outer stomatal ledge, and the prominent T-piece thickenings are comparable with two extant genera of the Illiciaceae, *Kadsura* (Schisandraceae; cf. fig. 24F Metcalfe, 1987) and *Illicium* (Illiciaceae; cf. fig. 22B Metcalfe, 1987), suggesting a relationship with this order. The same features are comparable with *Eucalyptophyllum oblongifolium* Fontaine from the Potomac Group, which was suggested by Upchurch (1984, p. 544 and cf. his figure 7) to represent “an extinct group of at least ordinal rank... that is related in some way to Chloranthaceae and Illiciaceae.”

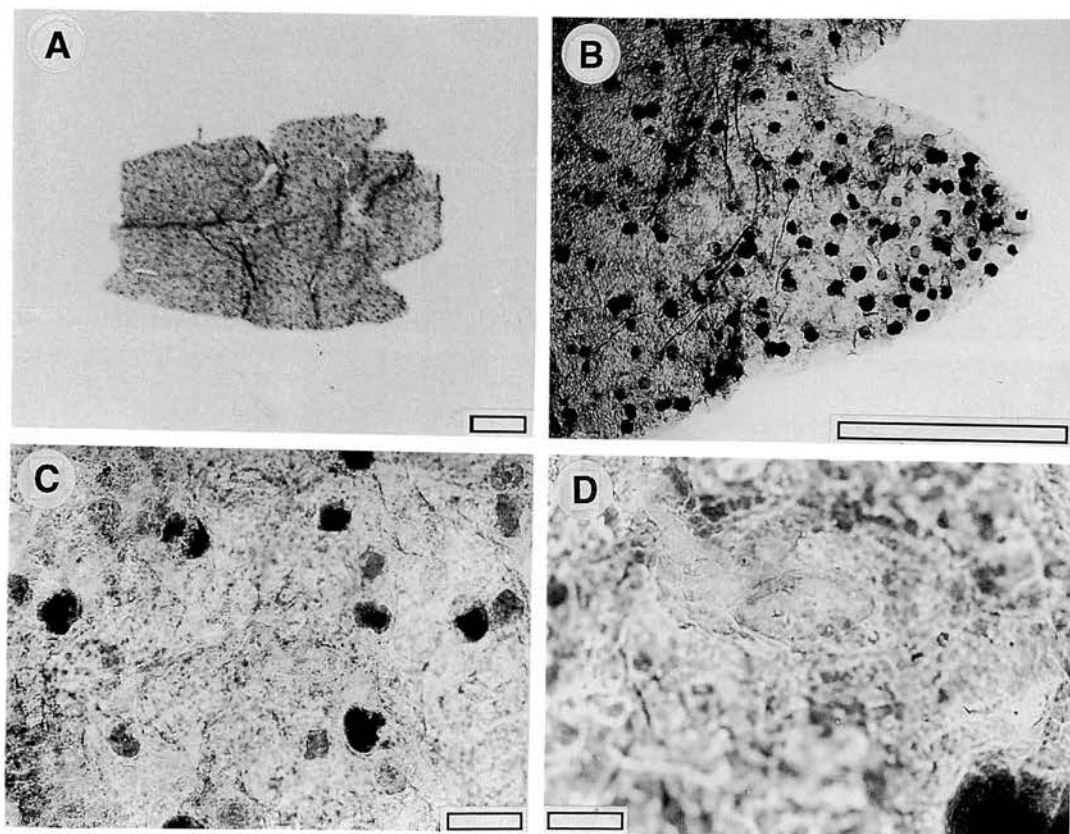


Figure 7. Dicotyledon sp. E, all SL772. **A.** TLM of complete specimen, note teeth and broken apex, scale: 1 mm. **B.** TLM detail of tooth showing numerous resin bodies, scale: 1 mm. **C.** TLM detail showing stoma (arrowed) and resin bodies, scale: 100 μ m. **D.** TLM detail of single stoma, scale: 25 μ m.

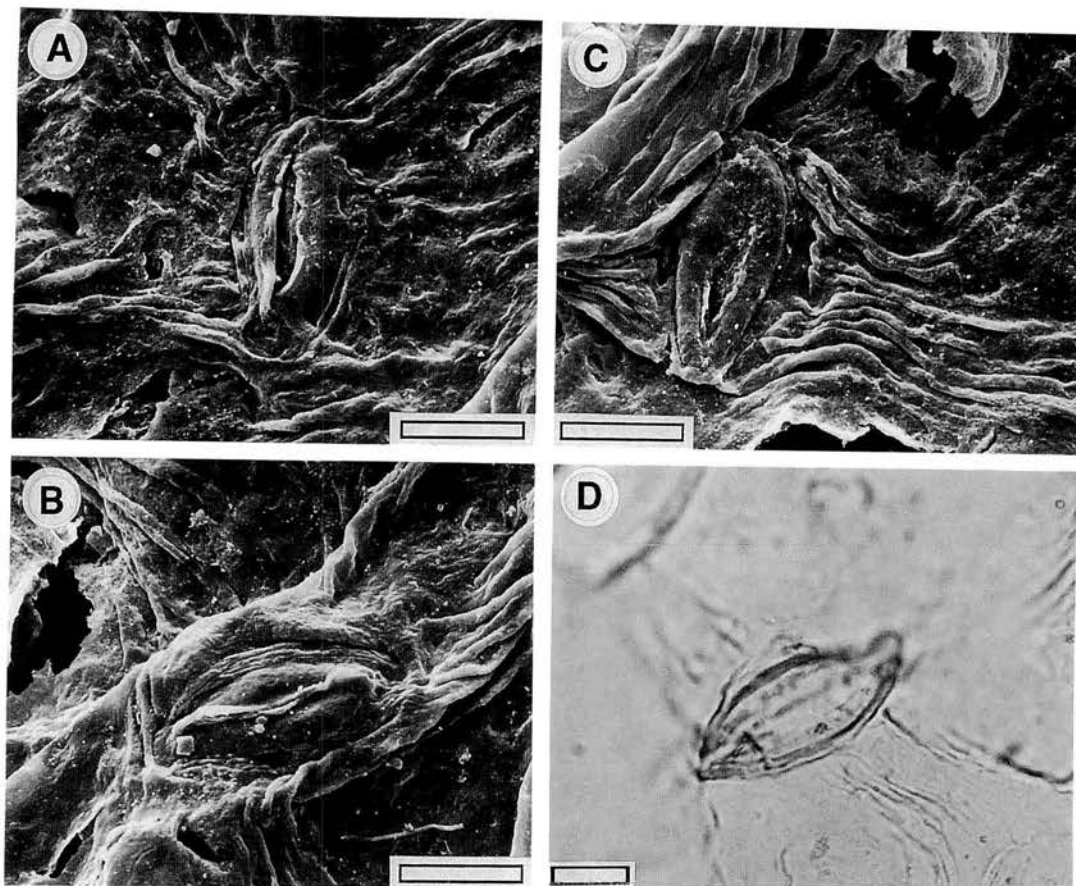


Figure 8. *Dicotyledon* sp. F. **A–C.** SEMs of outer surface of single stomate, all S764, scale: 20 μ m. **D.** TLM of outer surface of single stomate, SL768, scale: 10 μ m.

Dicotyledon sp. G

Figure 9

Reference specimen.—SL894 (dispersed cuticle, only specimen, MAC-11).

Description.—Stomatal distribution over leaf unknown; stomata randomly oriented; normal stomata sunken under and occluded by frilled, radiating rim of cuticle; giant stomata common, exposed, with thin, elliptical, outer stomatal ledge, surrounded by low tangentially oriented ridges; major veins only reflected in epidermal cells; glabrous.

Dicotyledon sp. H

Figure 10A, B

Reference specimen.—SL987 (dispersed cuticle, only specimen, MAC-3).

Description.—Stomatal distribution over leaf unknown; stomata randomly oriented; normal stomata dense; outer stomatal ledge broad, narrowing at poles, not extending full length of guard cells; moderate T-piece thickenings at stomatal poles; peristomal thickenings sometimes present; giant stomata present; no distinct subsidiary cells; contact

cells of separate stomata often abut, sometimes shared; outer stomatal ledge wide; normal epidermal cell shape irregular, rounded, generally slightly elongate; fine ridges on outer surface of cuticle oriented parallel to stomatal pore; major veins reflected in more rectangular, slightly papillate epidermal cells; glabrous.

Dicotyledon sp. I

Figure 10C, D

Reference specimen.—SL737 (only specimen, poorly preserved leaf fragment near apex, bases of teeth present, MAN-28).

Description.—Leaf margin with small teeth; stomatal distribution over leaf hypostomatic; stomata randomly oriented; guard cell pair outline ovate; outer stomatal ledge narrow, not extending full length of guard cells; no obvious subsidiary cells; epidermal cell flanges prominent; normal outline polygonal, isodiametric; midrib reflected in epidermal cells.

Dicotyledon sp. J

Figure 10E, F

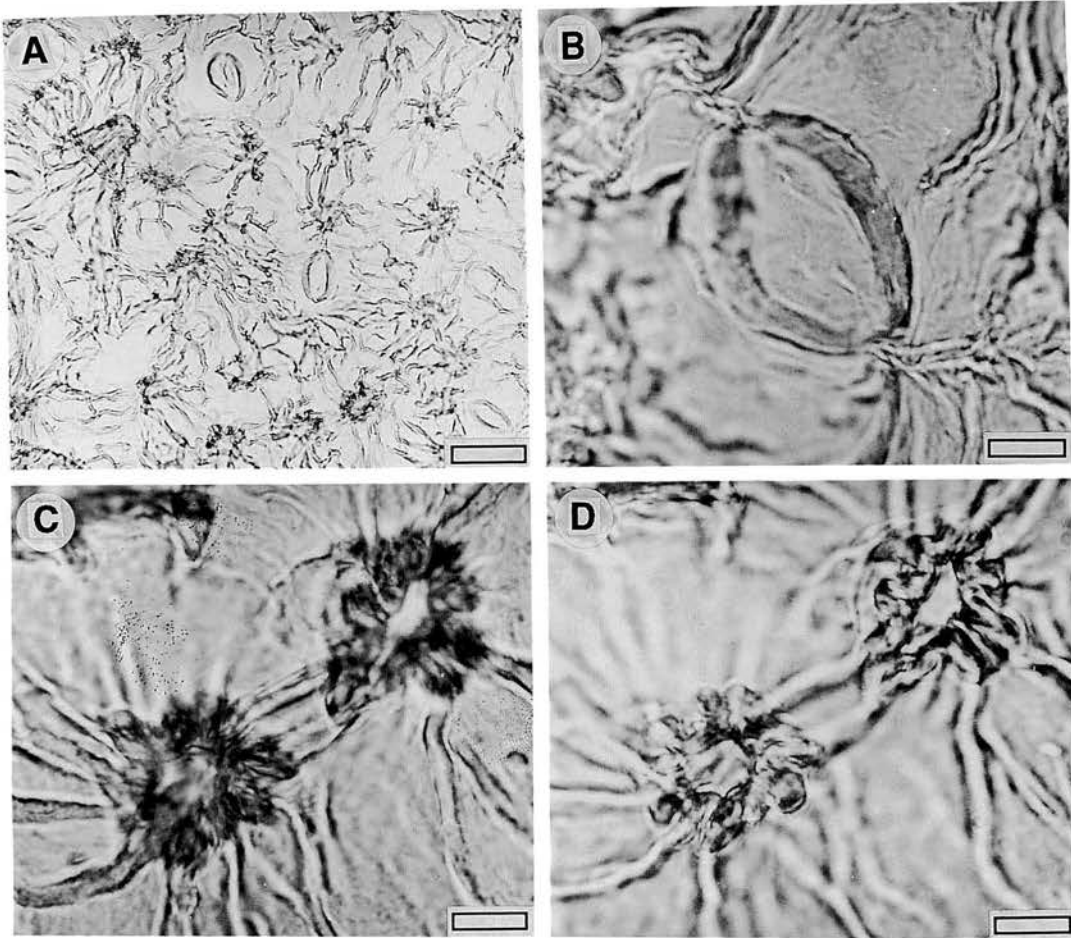


Figure 9. Dicotyledon sp. G, all SL894. **A.** TLM showing exposed giant stomata and normal stomata obscured by cuticle ridges, scale: 50 μ m. **B.** TLM detail of giant stomate, scale: 10 μ m. **C, D.** TLM of two normal stomates. **C.** Lower focus. **D.** Higher focus, scale: 10 μ m.

Reference specimen.—SL679 (dispersed cuticle, only specimen, THA-47).

Description.—Stomatal distribution over leaf hypostomatic; on abaxial surface stomata generally aligned but some oblique, striations aligned with stomates, elliptical, thickened outer stomatal ledge, epidermal cell flanges not visible under TLM; glabrous; adaxial surface also with parallel striations, glabrous.

Identification

Worldwide, most described angiosperm leaf fossils of Albian-Cenomanian age are impressions only, lacking cuticle. However, in this study, although cuticular preservation is good, most material is found as small, dispersed fragments in amongst a large amount of coniferous material (the chances of a bore core sampling a complete leaf are slim). This situation is frustrating, as a combination of gross leaf morphology and venation combined with anatomical detail would be a great help in identification. Nevertheless, these

are the best preserved angiosperms from the Australian Cretaceous to date, and the cuticle is amongst the oldest from angiosperms in the world. The few Cenomanian records of cuticle include Upchurch (1984, 1995) and Kvacek (1983, 1992), and for the Albian that of Crane *et al.* (1993).

The current knowledge of mid-Cretaceous angiosperms is based on pollen, flowers, and leaves, and includes several identifications of extant taxa. For instance, the Upper Albian Potomac Group of North America has yielded reproductive material regarded as of probable chloranthoid, hamamelididean, magnoliidean, platanoid, and rosidae affinities (Friis *et al.*, 1986; Crane *et al.*, 1986). The Cenomanian, or possibly late Albian Dakota Formation has yielded possible Magnoliales (Dilcher and Crane, 1984). These inferred affinities are at high taxonomic levels (but have still raised dispute, e. g. Hughes, 1994), nevertheless they may form a starting point for comparing fossil cuticle. Upchurch and Wolfe (1993) summarised the data from Cretaceous leaf fossils, including the latest Albian to middle Cenomanian period. Similar to the reproductive material

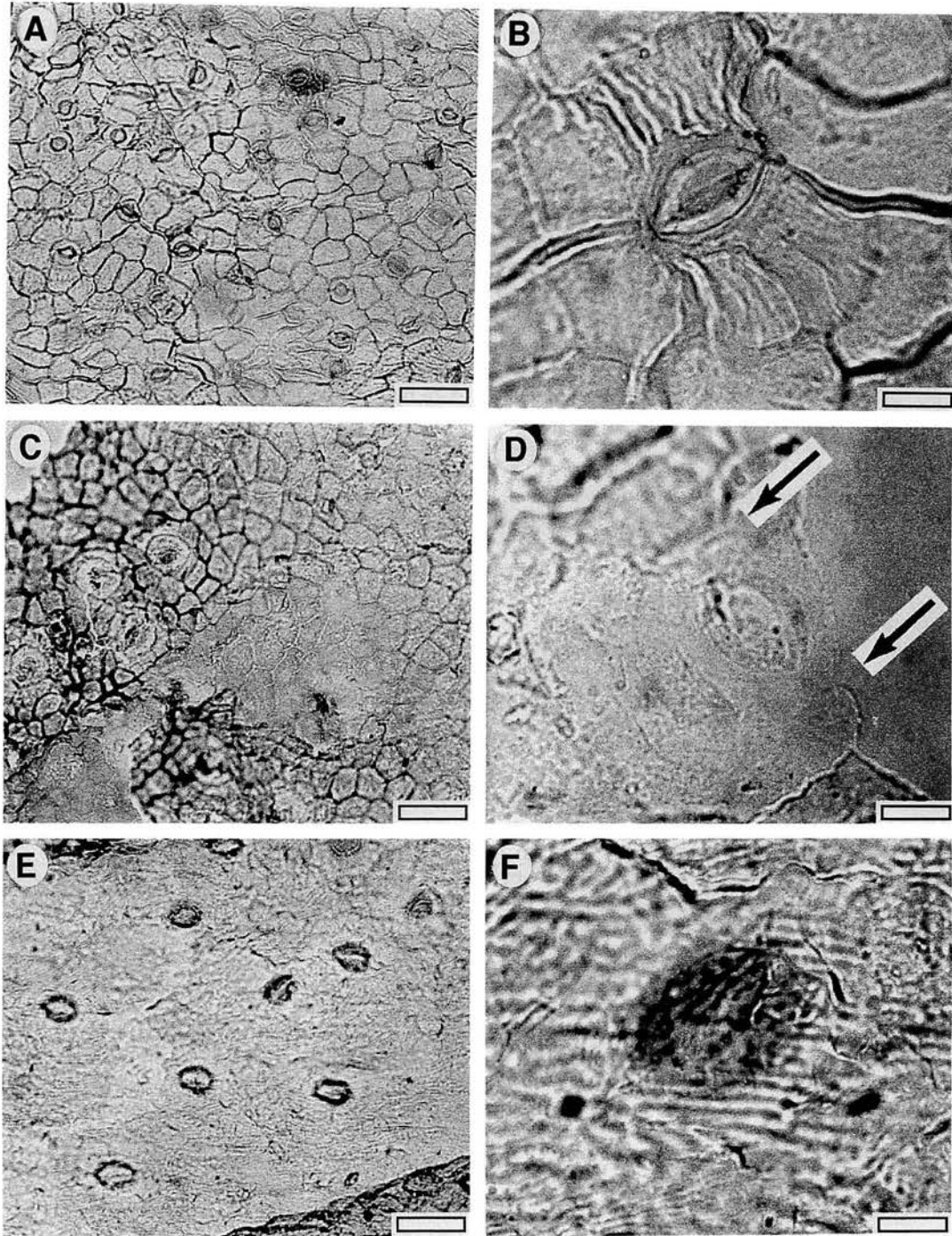


Figure 10. A, B. *Dicotyledon* sp. H, both SL987. A. Scale: 50 μ m. B. Scale: 10 μ m. C, D. *Dicotyledon* sp. I, both SL737. C. scale: 50 μ m. D. Arrows point to opposite poles of a single stomate, scale: 10 μ m. E, F. *Angiosperm* sp. J, both SL679. E. Scale: 50 μ m. F. Scale: 10 μ m.

the affinities included the Magnoliales, Laurales, Hamamelidales (aff. to Platanaceae) and the Rosidae. Thus, even at this relatively early stage, several of the major clades of angiosperms recognised by Chase *et al.* (1993), were present.

Despite having some indication of 'where to look' for the affinities of the Eromanga material, taxonomic placement is far from obvious. For one taxon (Dicotyledon sp. F) an affinity with the Chloranthaceae and Illiciales has been suggested, but for the others their identity remains completely unknown. This situation may result from a combination of inadequate material for comparison with extant plants as well as the likelihood that plants of this age had combinations of cuticle characters unknown today (e. g. Upchurch, 1984). Certainly none of the cuticle has any of the characteristic features of extant Australian families such as Lauraceae, Myrtaceae, or Proteaceae which are well known in the Tertiary record (and which would not be expected for this time). *Platanus* or extinct relatives were widespread in the mid-Cretaceous, including New Zealand (Pole, 1992), but none of the fossil cuticle is comparable to extant *Platanus* (documented by Brett, 1979). However, cuticle of Albian *Sapindopsis*, regarded as Platanaceae by Crane *et al.* (1993), compares favourably with Dicotyledon spp. A, F, and H in the presence of surface striations and form of the outer stomatal ledge. Curiously, where subsidiary cells can be seen, none of the Eromanga cuticle shows the paracytic subsidiary cell arrangement which is common in extant plant families often regarded as 'primitive', i. e. the 'paleoherbs' of Donoghue and Doyle (1989). However, Upchurch (1984) reported a plastic, variable condition of the subsidiary cell arrangement for Lower Cretaceous Potomac Group cuticles and suggested it to be an even more primitive style, although Baranova (1992) remarked that several extant taxa also show such plasticity. This plasticity is shown by Dicotyledon sp. D from the Eromanga. As for whole leaf form, the single larger leaf fragment of Dicotyledon sp. A is not comparable with any of the material illustrated by McLoughlin *et al.* (1995) from younger Winton Formation deposits, although its lobed form would not be out of place in their assemblage.

Distribution

All samples containing dicotyledonous fossils come from the Winton Formation, except three (MAC-11; MAN-34, 42), which came from the underlying Mackunda Formation.

Angiosperm cuticle was not found in sandy samples. This could be a result of its not surviving in that environment (i. e. fluvial abrasion destroyed the cuticle), or because physical distortion by sand grains during compaction may have rendered the cuticle unrecognisable. It may also be a real absence, suggesting angiosperms were typically absent along relatively high-energy sedimentary environments such as river margins or levees. However, the three Mackunda Formation samples come from marine sediments to where the fossils contained must have been transported by fluvial activity. Out of the 144 fossiliferous samples which were fine-grained or muddy, only 20 of them contained dicotyledonous remains and these were restricted to three of the

seven cores; GSQ Machattie-1, GSQ Maneroo-1, and GSQ Thargominda-3 (Appendix 1). This suggests that, at least in the lower-energy floodplain environments, dicotyledons were either patchy in their distribution, or were relatively small plants, producing little biomass. They were evidently a small component of what was, on a regional scale, an overwhelmingly gymnosperm (mostly conifer) dominated flora (Pole, in prep.). Burger (1990), on the basis of palynological data, also concluded the angiosperms were patchily distributed. One sample (MAC-11) comes from a thin unit of Winton Formation bounded above and below by marine sediments which probably accumulated very close to sea level, perhaps as a delta lobe. The other samples are interpreted as accumulating essentially in an overbank/floodplain environment (see facies analysis of the Eromanga core by Fielding, 1992).

Although no dicotyledon fossils were recovered from coal, some samples were stratigraphically close. Sample THA-47 comes from a mud immediately below the prominent coal seam of Thargomindah-3. Samples MAN 6, 8, 9, 11, 12 (closely spaced, all coming from a 4.5 m-thick muddy unit) are close to the prominent coal seam of Maneroo-1 but separated from it by a 3.5 m-thick sandy bed. The most reasonable assumption is that the angiosperms grew in clastic swamps, but growth on sandy levees or in coal swamps cannot be discounted. The plants were probably woody rather than herbaceous, as herbs are unlikely to become fossilised and their very delicate cuticle would not be expected to be preserved, or to survive the preparation process. Even so, some of the fossil cuticle is notably thin, consistent with understory plants or deciduousness.

Summary

Latest Albian-earliest Cenomanian assemblages from the Eromanga Basin, Australia include sporadic fragments of dicotyledonous leaf cuticle, and rare semi-intact leaves. Ten types can be distinguished with the affinities of at least one possibly being with the Chloranthaceae and Illiciales.

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A new pseudorthoceratid cephalopod from the Kazanian (middle Late Permian) of Japan

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Abstract. A new cephalopod species, *Dolorthoceras nakazawai* (Orthocerida: Pseudorthoceratidae), is described from the Permian Mizuyagadani Formation, Central Japan. Its Kazanian age, based on a fusulinid species, makes this the youngest record of *Dolorthoceras*. This is the first undoubted occurrence of the genus in Japan.

Key words: *Dolorthoceras nakazawai* sp. nov., Orthocerida, Mizuyagadani Formation, Permian, Kazanian

Introduction and geologic setting

A new pseudorthoceratid cephalopod species, *Dolorthoceras nakazawai*, is described from a float block of limestone in the upper reaches of Ichinotani Valley in the Fukuji area, Gifu Prefecture, Central Japan. The vicinity of the collecting site is underlain by the Mizuyagadani Formation (Igo, 1956), which consists mostly of clastic sediments and has a “lenticular” limestone in its upper part (see fig. 2 in Niko *et al.*, 1987). The cephalopod-bearing limestone consists of bioclastic wackestone and has a characteristic appearance that is dark gray micrite, with sporadic crinoid fragments as the main allochemical constituent, and is identical in lithology with the “lenticular” limestone noted above. With the exception of apparently reworked fossils, the age of this formation has been discussed on the basis of foraminifers (Okimura *et al.*, 1984), radiolarians (Niko *et al.*, 1987; Umeda and Ezaki, 1997), corals (Kamei, 1957; Igo, 1959), brachiopods (Kamei, 1957) and cephalopods (Niko and Nishida, 1987; Nishida and Niko, 1989). Among them, radiolarians in tuffaceous mudstone and acidic tuff range from Sakmarian (middle Early Permian) to Midian (middle Late Permian), and ammonoids reported by Nishida and Niko (1989) are the only fossils known from the “lenticular” limestone excepting crinoid fragments. Although the precise age of the limestone is a pending question, we found the index fusulinid *Parafusulina* cf. *kaerimizensis* (Figure 1), associated with the pseudorthoceratid cephalopod *Dolorthoceras nakazawai* sp. nov., from the same locality and in limestone of similar lithology (but from another float block). It is possible that this limestone is a redeposited olistolith or has been introduced by faulting, but its age can be

determined by the presence of *Parafusulina* cf. *kaerimizensis*. Based on the assembled evidence, we conclude that the specimen of *D. nakazawai* was derived from the “lenticular” limestone in the Mizuyagadani Formation, and that its age is Kazanian (middle Late Permian).

The abbreviation UMUT for the repository stands for the University Museum of the University of Tokyo.

Systematic paleontology

Order Orthocerida Kuhn, 1940
Superfamily Pseudorthocerataceae Flower
and Caster, 1935

Family Pseudorthoceratidae Flower and Caster, 1935
Subfamily Spyroceratinae Shimizu and Obata, 1935

Genus *Dolorthoceras* Miller, 1931

Type species.—*Dolorthoceras circulare* Miller, 1931.

Dolorthoceras nakazawai sp. nov.

Figure 2

Diagnosis.—Species of *Dolorthoceras* with circular shell cross section; sutures oblique, attaining 16° to rectangular direction of shell axis; siphuncular position nearly central with asymmetrical septal necks; cameral deposits form circumsiphuncular ridge and mamiform growth; endosiphuncular deposits form thick lining on ventral siphuncular wall.

Description.—Orthoconic shell with circular cross section, reaches 7.4 mm in diameter near adoral end; shell expansion moderate with approximately 5° angle; shell surface

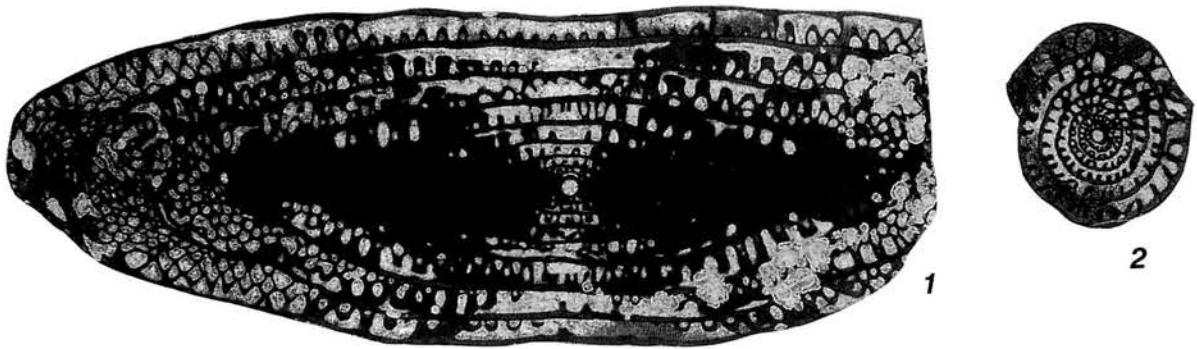
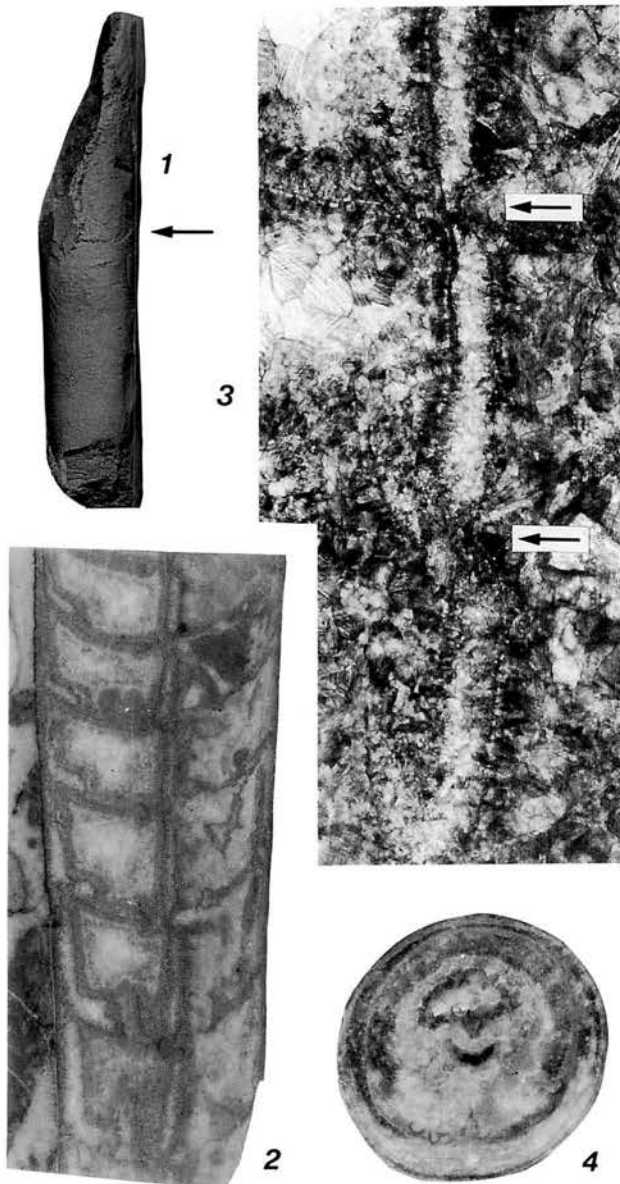


Figure 1. *Parafusulina* cf. *kaerimizensis* (Ozawa) from the Fukuji area, thin sections. 1. Axial section, $\times 10$. 2. Sagittal section, $\times 10$.



smooth, obvious ornamentation not recognized. Sutures not observed, but with relatively strong obliquity, ranging from 12° to 16° to rectangular direction of shell axis, as recognized in dorsoventral section, toward aperture on venter; septal curvature moderate to relatively deep, steeper in venter than dorsum; camerae relatively long for genus in apical phragmocone, with maximum width/length ratio 1.7 at shell diameter approximately 5.4 mm, being increased to 3.3 near adoral end. Siphuncle nearly central in position; septal necks asymmetrical in form, suborthochoanitic to rarely cyrtochoanitic in ventral siphuncular wall, and strongly curved cyrtochoanitic in dorsal siphuncular wall; length of septal necks short, ranging from 0.31 mm to 0.56 mm; brims short with length nearly equal to septal necks in adoral and ventral siphuncular wall, but in other portions they are shorter than septal necks; adnation area very narrow; connecting rings weakly inflated, subcylindrical with constrictions at septal foramina; ratio of maximum external diameter of connecting ring/corresponding shell diameter is approximately 0.2. Ventral cameral deposits well developed, episeptal-mural or episeptal and mural on rare occasions, always form circumsiphuncular ridge and mamiform growth; dorsal cameral deposits episeptal-mural indicating L-shaped longitudinal profile, relatively thin. Endosiphuncular deposits restricted to ventral siphuncular wall, where they form a thick lining with crescentic transverse profile.

Discussion.—With the exception of *Dolorthoceras*, the relatively simple shell morphology of the present species has much in common with Late Paleozoic Spyroceratinae such as *Adnatoceras* (Flower, 1939), *Euloxoceras* (Miller *et al.*, 1933), *Mitorthoceras* (Gordon, 1960) and *Shikhanoceras* (Shimanskiy, 1954). However, the combination of an uncompressed shell with a smooth surface, the very narrow adnation area and the short brims confirms the assignment

Figure 2. *Dolorthoceras nakazawai* sp. nov., holotype, UMUT PM 27826, from the Fukuji area. 1. Ventral view, $\times 2$. 2. Dorsoventral thin section, venter on right, $\times 5$. 3. Dorsoventral thin section, showing the details of the siphuncular structure. Arrows indicate septal necks, $\times 14$. 4. Transverse polished section at position indicated by arrow in Figure 2.1, venter down, $\times 5$.

of the species to *Dolorthoceras*, which was proposed by Miller (1931) from the Upper Carboniferous in the Aghil-Depsang (Central Range) of Central Asia. Its previously known range was Early Devonian to Early Permian, with an upper limit represented by two Artinskian species from the Urals, namely *Dolorthoceras siphocentrale* (Krotov, 1885, pl. 1, fig. 3; Shimanskiy, 1954, pl. 1, figs. 11, 12a, b) and *D. stiliforme* Shimanskiy (1948, figs. 1a, b; Shimanskiy, 1954, pl. 1, figs. 1–10, pl. 2, figs. 1–6). Thus, the present discovery of *Dolorthoceras* in the Mizuyagadani Formation extends the stratigraphic range of this genus upwards to the Kazanian.

The somewhat similar *Dolorthoceras stiliforme* is distinguished from *D. nakazawai* sp. nov. in having a subcentral siphuncular position, the usually simple mural cameral deposits and the unfused endosiphuncular deposits. Niko and Nishida (1987, fig. 3.3–3.5) assigned a specimen from the same formation to an indeterminate genus and species of the Pseudorthoceratidae having the surface annulation clearly separate from *D. nakazawai* at the generic level.

A poorly preserved specimen of *Dolorthoceras?* sp. from the Early Carboniferous Hikoroichi Formation in the southern Kitakami Mountains (Niko, 1990) was the only record of this genus in Japan until the present report.

Material.—Holotype and only known specimen, UMUT PM 27826, is an incomplete phragmocone 37.2 mm in length.

Etymology.—The specific name honors Dr. Keiji Nakazawa, in recognition of his contributions to the study of Permian mollusks.

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Early Carboniferous miospores from the southern Kitakami Mountains, northeast Japan

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Abstract. The first authenticated Early Carboniferous miospores in Japan are described from the upper part of the lower Hikoroichi Formation (HK2 Member) in the Hikoroichi area, southern Kitakami Mountains, northeast Japan. The stratigraphically significant miospores are *Auroraspora* sp. cf. *A. macra*, *Crassispora trychera*, *Schopfites* sp., *Spelaeotriletes crustatus*, and *S.* sp. cf. *S. pretiosus*, which suggest a late Tournaisian to early Viséan age and the "Vallatisporites Microflora" provincialism.

Key words: Hikoroichi Formation, late Tournaisian to early Viséan, miospores, southern Kitakami Mountains

Introduction

Because of their poor preservation and scarcity late Paleozoic plant fossils in Japan have aroused little interest among Japanese paleontologists. Microfloral research in the Upper Paleozoic of Japan is even more limited as it was commonly believed that spores and pollen are only preserved in terrestrial environments. However, there are many cases from around the world of Upper Paleozoic terrestrial microflora preserved in marine sediments, where they are significant to both stratigraphy and phytogeography (Sullivan, 1965; Yang, 1999). Prior to this paper there have been no reports of late Paleozoic miospores from Japan, although Takahashi and Yao (1969) reported the occurrence of problematic Permian plant microfossils from a sandstone block of the Jurassic melange in the Harayama area, Mino Belt, southwest Japan.

The Hikoroichi Formation is a Lower Carboniferous (Tournaisian and Viséan) formation, distributed in the Hikoroichi area, western part of the southern Kitakami Mountains (Figure 1). The Hikoroichi Formation overlies, with angular unconformity, the Middle Devonian Nakazato Formation (Okubo, 1951; Minato *et al.*, 1979), and is in turn overlain conformably by the Lower Carboniferous (Upper Viséan) Onimaru Formation (Mori and Tazawa, 1980; Tazawa, 1981, 1984b; Kawamura, 1983). According to Tazawa (1984b), the Hikoroichi Formation consists mostly of sandstone, with a basal conglomerate and intercalations of shales, acidic to intermediate tuffs and limestones, 560 m in total thickness, and is subdivided into the following four members in ascending order: (1) HK1 Member, sandstone

dominant, 164 m thick, (2) HK2 Member, shale dominant, 102 m thick, (3) HK3 Member, basic to intermediate tuff dominant, 114 m thick, (4) HK4 Member, sandstone dominant, 180 m thick (Figure 2).

The miospores, described below, are from samples collected from the middle horizon of the HK2 Member at the Onimaru Quarry in the Hikoroichi area (Figures 1, 2). All the specimens are housed in the Department of Geology, Faculty of Science, Niigata University with the registered number (NU-P1-NU-P5). The other fossils, corals (Kato *et al.*, 1989), bryozoans (Sakagami, 1989), brachiopods (Tazawa, 1984a, 1985, 1989), gastropods (Kase, 1988), cephalopods (Niko, 1990) and trilobites (Kaneko, 1989) were collected from almost the same horizon in the same quarry. However, the plants alone were collected from the lowermost part of the HK3 Member in the same locality (Asama *et al.*, 1985, 1989). These fossils from the HK2 and HK3 Members of the Hikoroichi Formation in the Onimaru Quarry are summarized in Table 1.

Miospore preservation and processing technique

The extraction of palynomorphs from Japanese Paleozoic rocks is difficult. Lithologies suitable for the preservation of palynomorphs make up only about 10% of the Hikoroichi Formation (see Figure 2). Further, the miospores preserved in the shales of the Hikoroichi Formation are rather dark and thermally mature and need strong oxidation after conventional palynological processing (Wood *et al.*, 1996). Processing of samples from the Hikoroichi Formation involved crushing the samples to pea size or even finer and

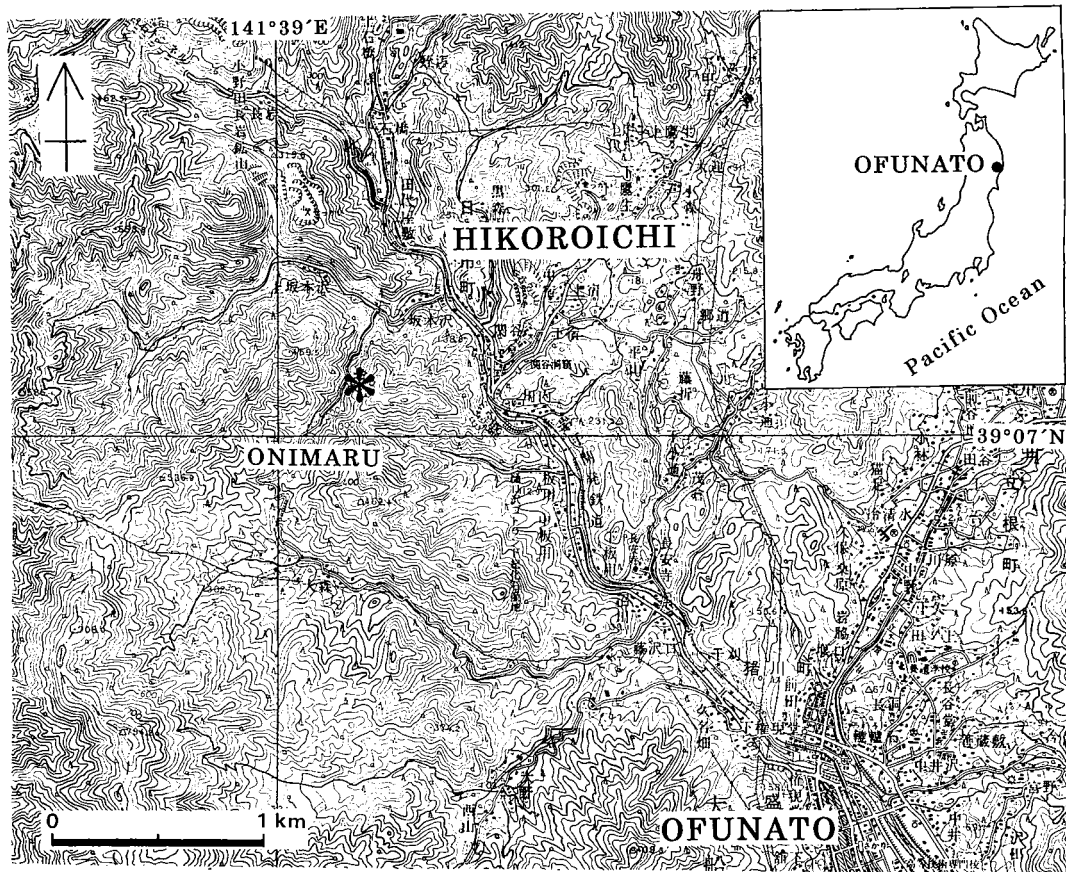
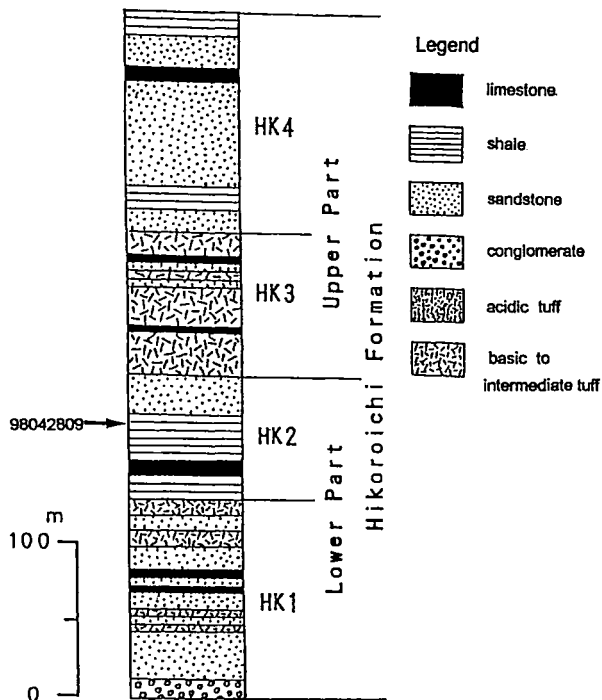


Figure 1. Index map showing the fossil locality (using the topographical map of “Sakari” scale 1:25,000 published by the Geographical Survey of Japan).



then demineralisation in dilute 35% HCL and 40% HF. Standard oxidation reagents did not react at all with the carbonized organic residues from the Hikoroichi Formation samples and so a very strong oxidation agent—fuming HN O_3 plus KCL (“fuming Schulze’s solution”) was used. The times required for oxidation using “fuming Schulze’s solution” vary from sample to sample (as in Western Yunnan, Yang, 1993). In general, suitable oxidation will be achieved after seconds of oxidation. However, oxidation times for the Hikoroichi samples varied from one to several minutes even when heating the oxidation tube in a beaker of boiling water. Using this technique brown or light-brown coloured miospores were produced. Permanent slides were made with the rapid mounting medium Entellan.

Figure 2. Columnar section of the Hikoroichi Formation in the Hikoroichi area; arrow showing the stratigraphical horizon of the miospore fossils collected (adopted from Tazawa, 1984b).

Table 1. The paleontological data from the HK2 and HK3 Members of the Hikoroichi Formation in the Onimaru Quarry, Hikoroichi area, southern Kitakami Mountains, northeast Japan

Taxonomic group	Literature source	Species
Lowermost part of the HK3 Member of the Hikoroichi Formation		
Plant	Asama <i>et al.</i> (1989)	<i>Psedusporochnus</i> n. sp., <i>Rhodeopteridium</i> sp. ?, <i>Sublepidodendron? wusihense</i> , <i>Lepidodendron</i> sp., <i>Archaeocalamites scrobiculatus</i>
HK2 Member of the Hikoroichi Formation		
Coral	Kato <i>et al.</i> (1989)	<i>Amygdalophyllum</i> sp., <i>Bifossularia</i> sp., <i>Lophophyllidium</i> sp., <i>Multithecopora</i> sp., <i>Syringopora</i> sp.
Bryozoa	Sakagami (1989)	<i>Acanthocladia?</i> sp. cf. <i>A. peculiaris</i> , <i>Hemitrypa?</i> sp.
Cephalopoda	Niko (1990)	<i>Adnatoceras onimarensis</i> , <i>Dolorthoceras</i> (?) sp., <i>Mooreoceras kinnoi</i> , <i>Neocycloceras</i> (?) sp., <i>Sueroceras nishimurai</i> .
Trilobite	Kaneko (1989)	<i>Linquaphillipsia choanjiensis</i> , <i>L. subconica</i> , <i>Liobole</i> (?) sp.
Gastropoda	Kase (1988)	<i>Baylea yvanii</i> , <i>Kawanamia onimarensis</i> , <i>Littorinides</i> sp., <i>Pseudozygopleura (Stephanozyga) nishimurai</i> , <i>Straparollus</i> (<i>Euomphalus</i>) <i>asanoi</i> , <i>S. (E.)</i> sp.
Brachiopoda	Tazawa (1989)	<i>Buxtonia</i> sp., <i>Lamellosathyris lamellosa</i> , <i>Linoprotonia</i> sp., <i>Marginatia</i> sp., <i>Unispirifer</i> sp.
Miospores	This paper	<i>Auroraspora</i> sp. cf. <i>A. macra</i> , <i>Calamospora</i> sp., <i>Crassispora</i> <i>trychera</i> , <i>Cyclogranisporites</i> sp., <i>Densosporites</i> sp., <i>Grandispora</i> sp. cf. <i>G. echinata</i> , <i>Leiotriletes</i> sp. cf. <i>L. incomptus</i> , <i>Microreticulatisporites araneum</i> , <i>Punctatisporites irrasus</i> , <i>P. minus</i> , <i>P. planus</i> , <i>Spelaeotriletes</i> sp. cf. <i>S. pretiosus</i> , <i>S. crustatus</i> , <i>Schophites</i> sp., <i>Verrucosisporites</i> sp.

Palynostratigraphy

The miospore assemblages from the upper part of the lower Hikoroichi Formation (HK2 Member) in the Onimaru Quarry are relatively abundant compared with the Middle Permian ones from the Kanokura Formation in the Kamiyasse area, southern Kitakami Mountains, northeast Japan (Yang and Tazawa, 2000). Stratigraphically significant species include *Auroraspora* sp. cf. *A. macra*, *Crassispora trychera*, *Schopfites* sp., *Spelaeotriletes crustatus* and *S. sp. cf. S. pretiosus*. Common species are *Auroraspora* sp., *Calamospora* sp., *Crassispora* sp., *Cyclogranisporites* sp., *Densosporites* sp., *Grandispora* sp. cf. *G. echinata*, *Leiotriletes* sp. cf. *L. incomptus*, *Microreticulatisporites araneum*, *Punctatisporites minus*, *P. irrasus*, *P. planus* and *Verrucosisporites* sp.

Auroraspora macra is a common species in Lower Carboniferous (mainly Tournaisian) assemblages around the world (Van der Zwan and Walton, 1981). This species ranges from the latest Devonian (Famennian) to the earliest Viséan in Western Europe (Clayton *et al.*, 1977) and Australia (Playford, 1990). In Canada it ranges from the Tournaisian to early Viséan (Utting, 1987a, b). *Spelaeotriletes pretiosus* is mainly distributed from the Tournaisian to early Viséan in Poland (Turnau, 1978, 1979). Since it first appears in the late Tournaisian strata in Ireland, it was selected as an index

fossil for the PC (*Spelaeotriletes pretiosus*-*Raistrickia clavata*) Biozone by Higgs *et al.* (1988). However, it has occasionally been reported from the latest Devonian in Morocco (Rahmanin-Antari, 1990) and Eastern Alaska (Scott and Doher, 1967). *Spelaeotriletes crustatus* is commonly distributed from the late Famennian to late Tournaisian in SE Ireland (Higgs, 1975). *Crassispora trychera* is a characteristic species of the late Tournaisian to early Viséan in Western Europe (Clayton *et al.*, 1977), Poland (Turnau, 1978) and Canada (Utting, 1980; Utting *et al.*, 1989). It was once reported by Utting (1991) from the Lower Namurian in northern Yukon. *Schopfites* sp. is usually one of the common elements of the late Tournaisian and possible the early Viséan strata (Higgs *et al.*, 1988). The other species recorded include *Grandispora* sp. cf. *G. echinata*, *Leiotriletes* sp. cf. *L. incomptus*, *Densosporites* sp. and *Verrucosisporites* sp., which are also common members of the Early Carboniferous (mainly Tournaisian and Viséan) miospore assemblages from around the world.

Early Carboniferous (Tournaisian) miospore assemblages from Gengma, West Yunnan, China are correlated with the Western European BP and PC Biozones based on the occurrence of *Auroraspora macra*, *Kraeuselisporites hibernicus*, *Rugospora polyptycha*, *Spelaeotriletes balteatus* and *S. pretiosus* in the Longba Formation (Yang *et al.*, 1997).

All of the miospore taxa recorded from the Onimaru

		Western Europe Higgs <i>et al.</i> (1988)	Lower Yangtze Gao (1991)	S. Kitakami, Japan This paper	Nova Scotia Utting <i>et al.</i> (1989)
Carboniferous	Viséan	Pu: <i>Lycospora pusilla</i>	Pu: <i>L. pusilla</i>	?	No palynomorphs
	Tn3	<i>Schopfites claviger</i> CM: <i>Auroraspora macra</i>	<i>S. claviger</i> CM: <i>A. macra</i>	<i>Schopfites</i> sp. <i>Crassispora trychera</i> <i>Auroraspora macra</i>	<i>C. decorus</i> - <i>S. claviger</i> <i>S. pretiosus</i> var. <i>pretiosus</i>
		PC: <i>Spelaeotriletes pretiosus</i> <i>Schopfites claviger</i>	PB: <i>S. pretiosus</i> <i>Cingulizonates bialatus</i>	<i>Spelaeotriletes pretiosus</i>	<i>V. vallatus</i>
	Tn2	BP <i>Spelaeotriletes balteatus</i> <i>Rugospora polyptycha</i>	?		Section faulted possibly incomplete
		HD: <i>Kraeuselisporites hibernicus</i> <i>Umbonatisporites distinctus</i>	?		<i>E. rotatus</i> <i>H. explanatus</i>
		VI: <i>Vallatisporites verrucosus</i> <i>Retusotriletes incohatus</i>	VI: <i>V. verrucosus</i> <i>R. incohatus</i>		not studied
	Devonian	Tn1	LN: <i>Retispora lepidophyta</i> <i>Verrucosisporites nitidus</i>	LN: <i>R. lepidophyta</i> <i>V. nitidus</i>	

Figure 3. Suggested correlation of miospore assemblages from the southern Kitakami Mountains with late Devonian to early Carboniferous miospore biozones of Western Europe, Lower Yangtze and Nova Scotia.

Quarry are typical members of the latest Tournaisian (Tn3) in Western Europe (PB and CM Biozones), China (PC and CM equivalent Biozones), Nova Scotia and eastern Canada (*Spelaeotriletes pretiosus* var. *pretiosus* Biozone and *Crassispora trychera-Colatisporites decorus* Biozone). But most of them can extend to the early Viséan. A correlation chart of these biozones is provided in Figure 3.

The brachiopods (Tazawa, 1984a, 1985, 1989), gastropods (Kase, 1988) and cephalopods (Niko, 1990) from the HK2 Member of the Hikoroi Formation at the Onimaru Quarry indicate an early Viséan age (see Table 1). However, the palynomorph assemblages from that member have a strong late Tournaisian character and are without the typical Viséan genus *Lycospora*. Furthermore, some plant fossils (*Archaeocalamites scrobiculatus*, *Knorria* sp. and *Sublepidodendron? wushiense*) were described by Asama *et al.* (1985, 1989) from the lowermost part of the H3 Member of Kawamura (1983), which is supposed to be equal to the HK3 Member of Tazawa (1985) at the same locality (see Table 1). *Archaeocalamites scrobiculatus* is one of the dominant representatives of Viséan plant assemblages in both South China and North China (Wu, 1995), and has also been reported by Wu (1995) from the Tournaisian of South China together with *Eolepidodendron wushiense* Sze or *Sublepidodendron? wushiense* Sze. It seems likely that the plant-bearing bed of the lowermost part of the HK3 Member is early Viséan. The Viséan *Lycospora pusilla* Biozone can be informally divided into a lower division containing rare *Lycospora pusilla* and an upper division with abundant representatives of that species (Higgs, 1996). This suggests that the miospore-containing strata of Onimaru Quarry can be dated as late Tournaisian to early Viséan rather than solely early Viséan as suggested by the brachiopods, gas-

tropods and cephalopods.

Sullivan (1965, 1967) first defined the differences between the various Early Carboniferous microfloral assemblages around the world and demonstrated a clear relationship between their distribution and their probable paleolatitude. He described five distinct assemblage suites in the Early Carboniferous, two (*Vallatisporites* Suite and *Lophozonotriletes* Suite) in the Tournaisian and three (*Grandispora* Suite, *Monilospora* Suite and Kazakhstan Suite) in the Upper Mississippian (late Viséan-early Namurian). In 1981, Van der Zwan supported Sullivan's conclusion through his statistically based correlation of late Tournaisian and early Viséan assemblages from 14 selected areas using both Jaccard and Simpson correlation coefficients. Clayton (1985) made some progress on microflora provinces proposing seven microfloras instead of Sullivan's five suites. In general, five microfloras can be distinguished in the Early Carboniferous (Clayton, 1985, figs. 2, 3) around the world: the *Granulatisporites frustulentus* Microflora in Australia, the *Spelaeotriletes balteatus* Microflora in North Africa, the Kazakhstan Microflora in Kazakhstan, and the *Vallatisporites* Microflora (middle Tournaisian to early Viséan) and the *Grandispora* Microflora (middle-late Viséan), which extended from the eastern United States and eastern Canada through Western Europe to China. The *Lophozonotriletes* Microflora (middle Tournaisian to early Viséan) and the *Monilospora* Microflora (middle-late Viséan) were mainly distributed in Western Canada, Spitsbergen and the north-western part of Russia. Assemblages from Eastern Europe are more or less transitional in nature between the *Vallatisporites* Microflora and the *Lophozonotriletes* Microflora.

The microflora in the southern Kitakami Mountains can be

circumscribed within the *Vallatisporites* Microflora in the sense of Clayton's division (Clayton, 1985) based on the presence of *Auroraspora* sp. cf. *A. macra*, *Crassispora trychera*, *Spelaeotriletes crustatus*, *S.* sp. cf. *S. pretiosus* and *Schopfites* sp.

Systematic palynology

The suprageneric classification used is mainly based upon the schemes by Potonié and Kremp (1954), Potonié (1956, 1975), Dettmann (1963) and Smith and Butterworth (1967).

Anteturma Sporites H. Potonié, 1893

Turma Triletes Reinsch emend. Dettmann, 1963

Suprasubturma Acavatrilletes Dettmann, 1963

Subturma Azonotriletes Luber emend. Dettmann, 1963

Infraturma Laevigati (Bennie and Kidston) R. Potonié, 1956

Genus *Leiotriletes* (Naumova) Potonié and Kremp, 1954

Type species.—*Leiotriletes sphaerotriangulus* (Loose) Potonié and Kremp, 1954.

Leiotriletes sp. cf. *L. incomptus* (Felix and Burbridge)
Higgs, Clayton and Keegan, 1988

Figure 4.9

Compare.—

Punctatisporites incomptus Felix and Burbridge, 1967, p. 357, pl. 53, fig. 12.

Leiotriletes incomptus (Felix and Burbridge). Higgs *et al.*, 1988, p. 50, pl. 1, fig. 9.

Material.—Seven specimens logged from NU-P1 to NU-P4, Figure 4.9 from NU-P2.

Description.—Trilete acamerate miospores. Amb rounded triangular, sides convex. Suturæ simple and distinct, extending approximately to the equator. Laesurae bordered by flexuous labra. Exine laevigate, approximately 1.5–2 µm thick.

Diameter.—38–45 µm.

Remarks.—The Kitakami specimens are similar to those recorded by Felix and Burbridge (1967) as *Punctatisporites incomptus* and Higgs *et al.* (1988) as *Leiotriletes incomptus*, but are significantly smaller than the type (60–90 µm) and lack the prominent labra.

Genus *Punctatisporites* Ibrahim emend. Potonié
and Kremp, 1954

Type species.—*Punctatisporites punctatus* (Ibrahim) Ibrahim, 1933.

Punctatisporites irrasus Hacquebard, 1957

Figure 4.7

Punctatisporites irrasus Hacquebard, 1957, p. 308, pl. 1, figs. 7, 8; Sullivan, 1964, p. 372, pl. 2, figs. 3.4; Higgs *et al.* 1988, p. 51, pl. 1, fig. 17.

Punctatisporites cf. *irrasus* Hacquebard. Dolby and Neves, 1970, p. 365, pl. 1, fig. 1.

Material.—Six specimens logged from NU-P2 to NU-P5, Figure 4.7 from NU-P2.

Description.—Acamerate trilete miospores. Amb subcircular. Suturæ distinct to obscure with a narrow labra. Suturæ extend 1/2 to 3/4 of the spore radius, usually darkening along its length. Exine 1–2 µm thick, often laevigate or finely infragranulate accompanying large compression folds.

Diameter.—45–54 µm.

Remarks.—The Kitakami specimens conform very closely to those described by Sullivan (1964), Dolby and Neves (1970), and Higgs *et al.* (1988), who reported size ranges of 59–98 µm, 42–65 µm and 50–92 µm, respectively.

Infraturma Apiculati Bennie and Kidston
emend. R. Potonié, 1956

Genus *Schopfites* Kosanke, 1950

Type species.—*Schopfites dimorphus* Kosanke, 1950.

Schopfites sp.

Figure 4.12

Material.—One specimen logged from NU-P4, distal view.

Description.—Miospore trilete, acamerate. Amb oval to circular. Suturæ distinct to indistinct, straight, extend almost to equator of miospores. Intexine thin, indistinct to distinct, approximately conformable with the amb, about 3/4 of the diameter. Distal surface and equator ornamented with pilae, rounded baculae, and rare verrucae. The size of the elements ranges from 0.5–3 µm in height and 0.5–2.5 µm in width. Sculptural elements are normally discrete and closely spaced. Proximal surface laevigate.

Diameter.—35 µm.

Remarks.—This specimen is attributed to the genus *Schopfites* on the basis of the type and distribution of the ornamentation, patchy distal ornament predominantly of verrucae, bacula or pila suggested by Higgs *et al.* (1988).

Genus *Verrucosisporites* Ibrahim emend. Smith, 1971

Type species.—*Verrucosisporites verrucosus* (Ibrahim) Ibrahim, 1933.

Verrucosisporites sp.

Figure 4.8

Material.—One specimen from NU-P2.

Description.—Trilete acamerate miospore. Amb rounded triangular. Suturæ distinct, simple, length 2/3 to 3/4 the spore radius. Exine 2–3 µm thick. Distal surface and equatorial region of proximal surface ornamented with verrucae. Verrucae 1.5–2.5 µm in basal diameter, 1.5–2 µm in height with predominantly rounded tops. Elements evenly spaced 3–5 µm apart.

Diameter.—40 µm.

Remarks.—This sole specimen from the southern Kitakami Mountains is unlike the previously described species of the genus *Verrucosisporites*.

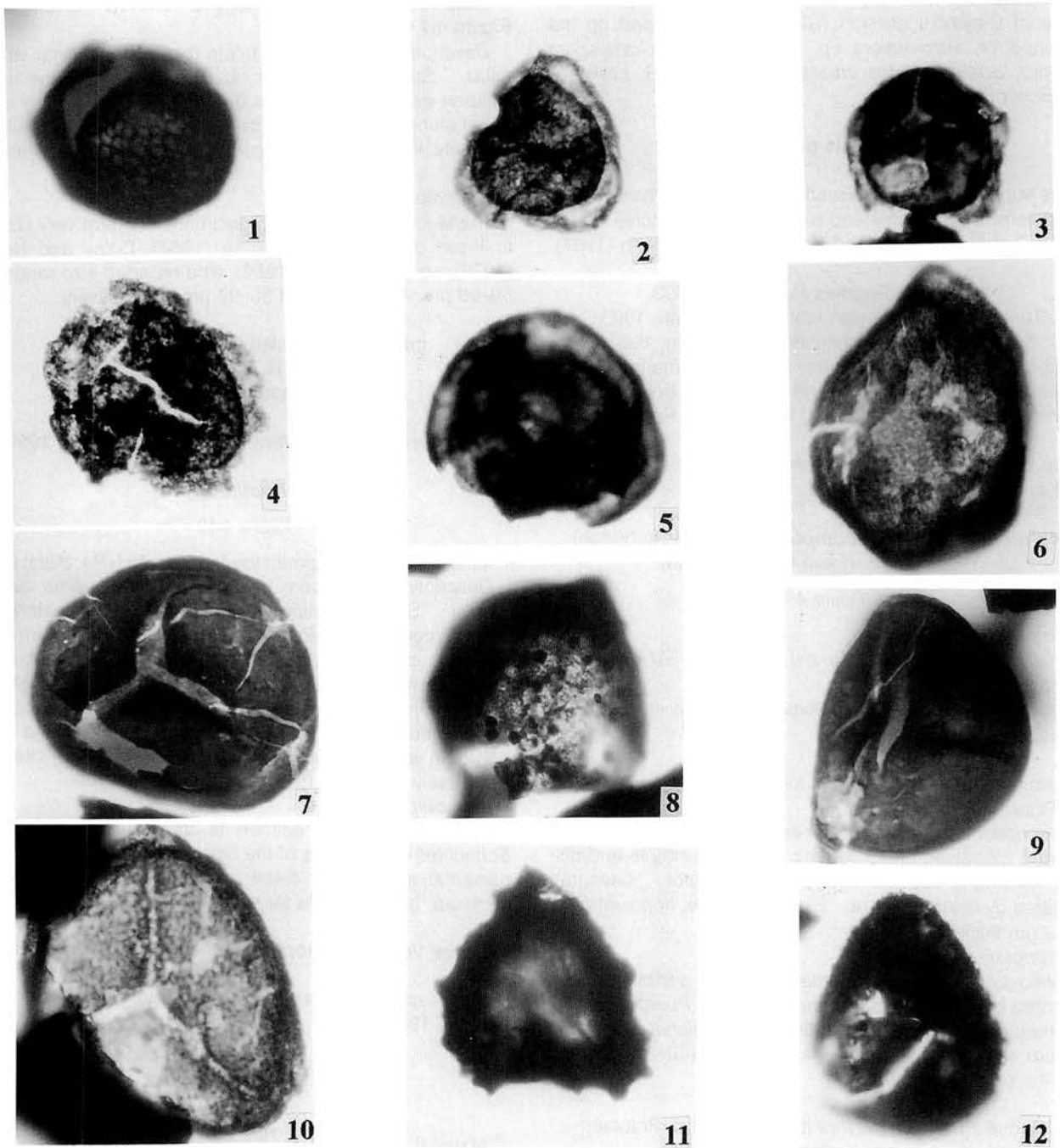


Figure 4. Early Carboniferous (late Tournaisian to early Viséan) miospores from the HK2 Member of the Hikoroichi Formation in the Onimaru Quarry, southern Kitakami Mountains, northeast Japan. The miospores are illustrated at the magnification of $\times 700$. 1. *Microreticulatisporites araneum* Higgs, Clayton and Keegan, proximal view, high focus, NU-P5. 2, 3. *Auroraspora* sp. cf. *A. macra* Sullivan. 2. Proximal view, median focus, NU-P4. 3. Proximal view, high focus, NU-P3. 4. *Spelaeotriletes* sp. cf. *S. pretiosus* (Playford) Neves and Belt, proximal view, median focus, NU-P4. 5, 6. *Spelaeotriletes crustatus* Higgs. 5. Proximal view, high focus, NU-P5. 6. Proximal view, median focus, NU-P3. 7. *Punctatisporites irrasus* Hacquebard, proximal view, high focus, NU-P2. 8. *Verrucosisporites* sp., distal view, median focus, NU-P2. 9. *Leiotriletes* sp. cf. *L. incomptus* (Felix and Burbridge) Higgs, Clayton and Keegan, proximal view, median focus, NU-P2. 10. *Crassispora trychera* Neves and Ioannides, proximal view, high focus, NU-P2. 11. *Densosporites* sp., distal view, median focus, NU-P2. 12. *Schopfites* sp., proximal view, median focus, NU-P4.

Infraturma Murornati Potonié and Kremp, 1954
Genus *Microreticulatisporites* Knox emend. Potonié
and Kremp, 1954

Type species.—*Microreticulatisporites lacunosus* (Ibrahim) Knox, 1950.

Microreticulatisporites araneum Higgs, Clayton
and Keegan, 1988

Figure 4.1

Dictyotriletes sp. Keegan, 1977, p. 552, pl. 2, figs. 13–14.
Dictyotriletes sp. B, Playford, 1978, p. 128, pl. 8, figs. 8–10.
Microreticulatisporites araneum Higgs, Clayton and Keegan, 1988,
p. 65, pl. 7, figs. 6, 9–10.

Material.—Six specimens logged from NU-P2, NU-P3,
NU-P5, Figure 4.1 from NU-P5.

Description.—Trilete acamerate miospores. Amb sub-
circular to convexly triangular. Suturæ distinct to indistinct,
straight to slightly sinuous and extending to the spore margin.
Exine 1.5–2 µm thick, ornamented with close reticulum
of tiny muri. Muri 0.5–1 µm in thickness, enclosing lumina
2–3 µm in width. Lumina usually polygonal to subcircular
in shape. Reticulation normally comprehensive but occa-
sionally less evident near equator and on the proximal sur-
face.

Diameter.—30–35 µm.

Remarks.—These specimens, recorded from the southern
Kitakami Mountains, are definitely attributed into *M.*
araneum because of their particular reticulation and the size
range.

Suprasubturma Laminatitriletes Smith and Butterworth, 1967
Subturma Zonolaminatitriletes Smith and Butterworth, 1967
Infraturma Crassiti

Genus *Crassispora* Bharadwaj emend. Sullivan, 1964

Type species.—*Crassispora kosankei* Potonié and Kremp
emend. Bharadwaj, 1957.

Crassispora trychera Neves and Ioannides, 1974

Figure 4.10

Crassispora trychera Neves and Ioannides, 1974, p. 78, pl. 7, figs.
6–8; Higgs *et al.*, 1988, p. 55, pl. 3, fig. 24.

Material.—Four specimens logged from NU-P2 and
NU-P3, Figure 4.10 from NU-P2.

Description.—Miospores trilete, variably camerate. Amb
subcircular to rounded triangular. Suturæ straight, simple,
extend almost to the margin of spores. The subparallel pe-
ripheral folding is often seen around the equator surface.
Distal surface ornamented by the combination of coni, pila
and grana (up to 1–1.5 µm in height).

Diameter.—53–68 µm.

Remarks.—These specimens are attributed to *C. trychera*
by the presence of variable camerate and distal ornament of
coni, pila and grana.

Suprasubturma Pseudosaccitriletes Richardson, 1965
Infraturma Monopseudosacciti Smith and Butterworth, 1967
Genus *Auroraspora* Hoffmeister, Staplin
and Malloy emend. Richardson, 1960

Type species.—*Auroraspora solisortus* Hoffmeister, Stap-
lin and Malloy, 1955.

Auroraspora sp. cf. *A. macra* Sullivan, 1968

Figure 4.2, 4.3

Compare.—
Auroraspora macra Sullivan, 1968, p. 124, pl. 27, figs. 6–10; Higgs
et al., 1988, p. 69, pl. 9, figs. 17–19.

Material.—Ten specimens logged from NU-P1 to NU-P4,
Figure 4.2 from NU-P4 and Figure 4.3 from NU-P3.

Diagnosis.—Size 48–68 µm, mean 58 µm (65 specimens);
amb subcircular to irregular; exoexine laevigate, intexine
laevigate to scabrate; trilete mark exceeds two-thirds radius
of spore body

Description.—Trilete camerate miospores. Amb fre-
quently irregular due to folding. Trilete straight, simple.
Suturæ distinct with labra extend up to 2/3 or more of the
spore radius. Exoexine thin, thickness not determinable,
often finely folded in an irregular pattern, usually pitted and
torn with fine grana. The equatorial darkened zone de-
scribed by Higgs *et al.* (1988) is occasionally observed,
Intexine 1.5 µm thick.

Diameter.—30–35 µm.

Remarks.—The specimens from the Hikoroichi Formation
are similar to those described by Sullivan (1968) and Higgs
et al. (1988) but are significantly smaller. Higgs *et al.*
(1988) extend the size range of *A. macra* to 35–65 µm. The
present specimens fall beyond this range and so are not at-
tributed to *A. macra sensu stricto*.

Genus *Spelaeotriletes* Neves and Owens, 1966

Type species.—*Spelaeotriletes triangulus* Neves and
Owens, 1966.

Spelaeotriletes crustatus Higgs, 1975

Figure 4.5, 4.6

Spelaeotriletes crustatus Higgs, 1975, pl. 6, figs. 7–9; non pl. 6, figs.
4–6.

Spelaeotriletes exiguus Keegan, 1977, p. 556, pl. 4, figs. 7–10.

Spelaeotriletes resolutus Higgs. Van der Zwan and Van Veen,
1978, pl. 2, fig. 1; Van der Zwan, 1980, pl. 18, fig. 5; Higgs
et al., 1988, pl. 13, figs. 8–9.

Material.—Seven specimens logged from NU-P3 to NU-
P5, Figure 4.5 from NU-P5 and Figure 4.6 from NU-P3.

Description.—Trilete camerate miospores. Amb convexly
triangular with rounded apices. Suturæ distinct, straight to
slightly sinuous. Suturæ extend up to 3/4 of the spore ra-
dius, terminating in curvaturæ perfectæ. Exoexine 1–2 µm
in thickness, distal surface and equator densely ornamented
with fine to coarse grana and less commonly coni and small

spinae. Sculptural elements 1–1.5 μm in width, up to 1 μm in height, discrete but often fused to give short irregular-shaped rugulae. Intexine distinct to obscure, laevigate, almost conformable with amb, comprising 3/4 or more of the total spore diameter and attached to the exoexine on the proximal surface only.

Diameter.—50–60 μm .

Remarks.—These specimens recorded from the southern Kitakami Mountains are similar to *S. crustatus* with ornament mainly of fine to coarse grana instead of conic or small spinae usually distributed on the distal surface and equator.

***Spelaeotriletes* sp. cf. *S. pretiosus* (Playford) Neves and Belt, 1971**

Figure 4.4

Compare.—

Pustulatisporites pretiosus Playford, 1964, p. 19, pl. 4, figs. 9–7; pl. 5, fig. 1; text-fig. 1a.

Spelaeotriletes pretiosus (Playford). Neves and Belt, 1971, p. 1241; Higgs et al., 1988, pl. 13, figs. 16–18.

Material.—Six specimens logged from NU-P2, NU-P4, Figure 4.4 from NU-P4.

Description.—Trilete camerate miospores. Amb rounded to convexly triangular. Trilete distinct to indistinct, sinuous, suturae extend almost to the equator, terminating in curvaturae imperfectae. Exine infragranulate, 2 μm thick at the equator. Exoexine ornamented with low, simple verrucae, mammillate verrucae and wide-based spinae. Ornament evenly to irregular distributed, usually concentrated at the distal polar region and often discernible at the equator. Verrucae subcircular in basal outline, 2–3 μm in width, 1–2 μm in height, with rounded flattened or more commonly mammillate tops. Bases of verrucae discrete, or fused to form very large irregular-shaped verrucae.

Diameter.—35–38 μm .

Remarks.—The present specimens are assigned to *Spelaeotriletes* cf. *pretiosus* on the basis of the type of ornament. Playford (1964) indicated a size of 98 to 195 μm for the type material of *S. pretiosus*. Higgs et al. (1988) recorded specimens between 68 and 110 μm . The present specimens are considerably smaller.

Infraturma Cingulicamerati Neves and Owens, 1966
Genus ***Densosporites*** Berry emend. Butterworth,
Jansonius, Smith and Staplin, 1964

Type species.—*Densosporites convensis* Berry in Butterworth, Jansonius, Smith and Staplin, 1963.

***Densosporites* sp.**

Figure 4.11

Densosporites sp. A, Higgs, Clayton and Keegan, 1988, p. 79, pl. 15, figs 10, 11.

Material.—Seven specimens logged from NU-P1 to NU-P4, Figure 4.11 from NU-P2.

Description.—Trilete cinguli-camerate miospores. Amb convexly triangular to subtriangular. Suturae obscure, simple, often gaping. Intexine often obscure. Exine 1–1.5 μm thick. Equatorial margin and distal surface ornamented with wide-based spinae, 1.5–2.5 μm in basal diameter and 1.5–3 μm in height. Spinae discrete but more commonly fused at their bases to form low sinuous and irregular cristae.

Diameter.—33–45 μm .

Remarks.—The Kitakami specimens are similar to those described by Higgs et al. (1988) in Ireland but just slightly smaller in size and with more dense ornament on the distal surface.

Conclusion

1. These records represent the first authenticated occurrence of Early Carboniferous miospores in Japan.

2. This significant miospore data might extend the geological age of the HK2 Member of the Hikoroichi Formation into late Tournaisian to early Viséan.

3. This miospore assemblage from the Hikoroichi area is more likely included in the *Vallatisporites* Microflora, which is to some degree similar to the Euramerican Realm in terms of megafloreal phytogeography.

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***Pisulinella miocenica*, a new genus and species of Miocene Neritiliidae (Gastropoda: Neritopsina) from Eniwetok Atoll, Marshall Islands**

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Abstract. *Pisulinella* is proposed as a new monotypic genus in the neritopsine family Neritiliidae, with the single species *Pisulinella miocenica* sp. nov. This new taxon occurs in subsurface Miocene sediments from Eniwetok Atoll, Marshall Islands, western Pacific. Nine specimens of *P. miocenica* were previously regarded as close to *Nerita* (*Amphinerita*) *polita* Linnaeus of the Neritidae. Reallocation of this species from Neritidae to Neritiliidae is based mainly on the shape of the protoconch, which is conspicuously tilted relative to the teleoconch whorls and has several spiral ridges. The discovery of this neritiliid species, previously allocated to the Neritidae, suggests that detailed examination of protoconchs is necessary for defining the systematic position of fossil neritopsines. *Pisulinella miocenica* sp. nov. may have lived in a cryptic habitat.

Key words: Eniwetok, Neritiliidae, *Pisulinella miocenica*, protoconch, submarine cave

Introduction

The gastropod superorder Neritopsina has a fossil record from Silurian to Recent (Tracey *et al.*, 1993). This group underwent major adaptive radiation in the geological past, which has resulted in fairly diverse shell morphology and soft-part anatomy. The early history of neritopsine evolution is unknown, although some suprageneric phylogenies have been proposed for extant groups (e. g. Holthuis, 1995). Bandel (1992) documented the supposed earliest neritopsine from the Ordovician, although it differs greatly in teleoconch morphology from modern relatives. Unconventional species of neritopsines occur even in Recent faunas, such as the bizarre gastropod *Pluviostilla palauensis*, possibly belonging to a new neritopsine group, from a submarine cave in Palau (Kase and Kano, 1999). Additional discoveries such as these may eventually lead to a better understanding of neritopsine evolution.

Neritopsines are usually "neritiform" and tightly coiled, but may also have a limpet-like shape or, rarely, be shell-less (Cox and Knight, 1960; Ponder, 1998). Frequent convergence and parallelism, however, prevent reliable classification of the fossil forms and hinder an understanding of neritopsine evolution. Cox and Knight (1960) recognized

19 fossil genera of Neritidae and diagnosed most genera solely on the basis of general teleoconch shape. These fossil neritopsines must be reexamined to document their more conservative characters, such as shell microstructure, shell muscle scars, and protoconchs, in order to clarify their systematic positions. We describe a new genus and species in the family Neritiliidae from Miocene sediments at Eniwetok Atoll in the Marshall Islands, with special attention being given to protoconch morphology. This new species was once thought to be a modern species of the family Neritidae.

Materials

The nine specimens described here were recovered from three deep subsurface cores drilled by the U. S. Geological Survey in 1951–1952 on Eniwetok Atoll in the Marshall Islands. The drill holes penetrated Recent to upper Eocene sediments, and the cores and cuttings of the drill holes yielded gastropods of remarkably high diversity, which were described by Ladd (1966, 1972, 1977) in his series of monographs on Cenozoic polyplacophorans and gastropods of tropical western Pacific islands. Specimens of the present new species were recovered from cores at depths ranging

from 253 to 298 meters (830 to 978 feet) below the surface and dated as early to late Miocene. See Ladd and Schlanger (1960) and Schlanger (1963) for details of the drilling operations and stratigraphic information.

All specimens used in this study are in the National Museum of Natural History, Washington, D. C. (USNM). SEM examinations were made in a low vacuum mode without a metal coating.

Systematic paleontology

Superorder Neritopsina Cox and Knight, 1960

Family Neritiliidae Schepman, 1908

Genus *Pisulinella* gen. nov.

Type species.—*Pisulinella miocenica* sp. nov.

Diagnosis.—Genus similar to *Pisulina*. Inner lip of aperture smooth, convex, bearing three or four inconspicuous teeth at margin; a shallow groove on inner lip callus extends

along inner line. Outer lip thick, with a blunt, rounded margin and with weak tubercles along the interior. Protoconch multispiral, inclined; larval shell sculptured with six or seven spiral ridges.

Etymology.—Combination of the neritiliid genus *Pisulina* and *ellus* (Latin: diminutive), referring to the smaller shell similar to *Pisulina*.

Discussion.—Neritiliidae Schepman, 1908 is a distinct family in Neritopsina, but until quite recently it had been thought to be a subfamilial taxon (Neritiliinae) of Neritidae (e. g. Cox and Knight, 1960; Ponder, 1998). Based upon her extensive anatomical study, Holthuis (1995) has clarified the paraphyly of Neritidae, and shown that *Neritilia* (the type genus of Neritiliidae) is the first offshoot in the clade "Neritidae" + Phenacolepadidae. Recently, Kano and Kase (in press) have reallocated the submarine-cave genus *Pisulina* from Smaragdiinae in Neritidae to Neritiliidae, based on finding 11 synapomorphies of *Pisulina* and *Neritilia* in the anatomical and shell characters.

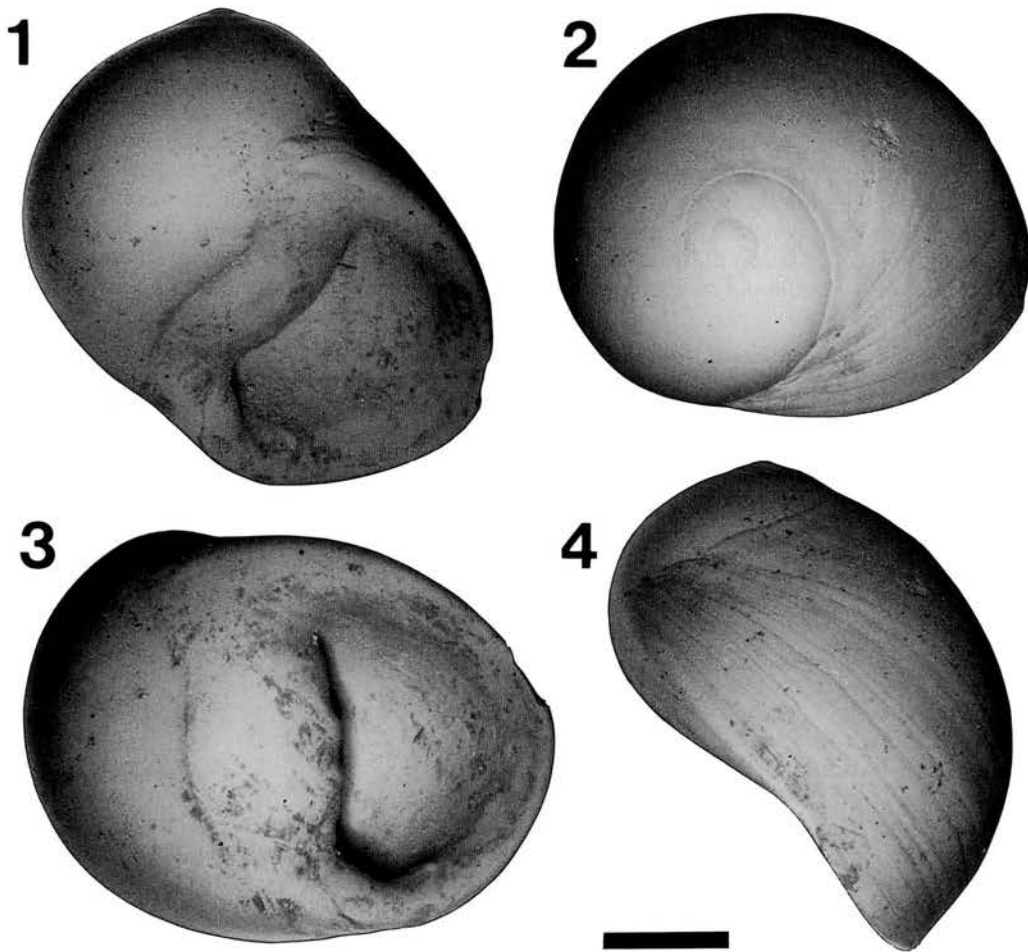


Figure 1. *Pisulinella miocenica* gen. et sp. nov. 1–4. Front, apical, apertural and lateral views of the holotype (USNM 648333). Scale bar = 1 mm.

The most important shell character for defining the taxonomic position of *Pisulinella* is protoconch morphology. The protoconchs of neritopsine species with planktotrophic development are unique and quite uniform in shape (e. g. Bandel, 1982). The larval shell is oval to globular-naticiform, smooth except for fine growth lines, and coils almost planispirally. Kano and Kase (in press) distinguish Neritiliidae from the other families in the superorder based on the fact that its coiling axis is remarkably tilted compared to that of the teleoconch, and because the protoconch surface bears several spiral ridges near the aperture. *Pisulinella* shares protoconch features with *Pisulina* and *Neritilia*, as described in the systematic part of this report. Although the soft anatomy of *P. miocenica* sp. nov. is not known, the new genus unequivocally belongs to Neritiliidae.

The family Neritiliidae heretofore included the two modern genera *Neritilia* Martens and *Pisulina* Nevill and Nevill (Kano and Kase, in press). *Pisulinella* is related to *Pisulina* rather than to *Neritilia*. *Neritilia rubida*, the type species of the genus, has a thin calcareous layer that covers the embryonic shell (Kano and Kase, in press). Bandel and Riedel (1998, fig. 6A, B) showed another example in a species of the genus from Cebu, Philippines, but the calcareous layer appears to be thinner than that of *N. rubida*. However, this layer is absent in *Pisulina* and *Pisulinella* (this condition in *Pisulina* is typically developed in *P. adamsiana*; see Herbert and Kilburn, 1991, fig. 3). Teleoconch morphology also indicates that *Pisulinella* is close to *Pisulina* rather than to *Neritilia*. In *Pisulinella* and *Pisulina* (particularly *P. adamsiana*), the inner line of the apertural inner lip callus has a reversed S-shape, and the basal lip bears a weak protuberance (Figures 1, 2). On the other hand, *Pisulinella*

possesses more numerous spiral ridges on the larval shell, and the exposed area of the embryonic shell is much smaller than in *Pisulina adamsiana*. The apertural morphology is also characteristic of *P. miocenica*. When the shell is fully grown, the outer lip is thickened along its interior with many obscure tubercles, and is blunt and rounded along its margin (Figure 2.1). Furthermore, the inner lip callus of *Pisulinella* has a shallow groove that extends along the inner line (Figure 2.2). None of the species of *Pisulina* and *Neritilia* have such features. We therefore conclude that *Pisulinella* is a distinct genus in Neritiliidae.

***Pisulinella miocenica* sp. nov.**

Figures 1–3

Nerita (*Amphinerita*) aff. *N. polita* Linnaeus: Ladd, 1966, p. 56, pl. 10, figs. 17, 18.

Diagnosis.—As for the genus.

Description.—Shell small, up to 4.0 mm in diameter, 3.7 mm in height (Table 1), thick, solid, obliquely ovate with a low spire, brownish cream in color without color markings (Figure 1). Inner walls of whorls resorbed, producing a hollow cavity inside. Protoconch multispiral, consisting of embryonic and larval shells, deeply immersed in first teleoconch whorl, separated from teleoconch by a clearly demarcated line; protoconch axis inclined significantly relative to teleoconch (Figure 3.1). Embryonic shell largely covered by larval shell and also sometimes by first teleoconch whorl, depending on protoconch inclination, and sculptured with faint, reticulate grooves (Figure 3.2); exposed portion of embryonic shell ca. 60 μ m in maximum dimension; larval

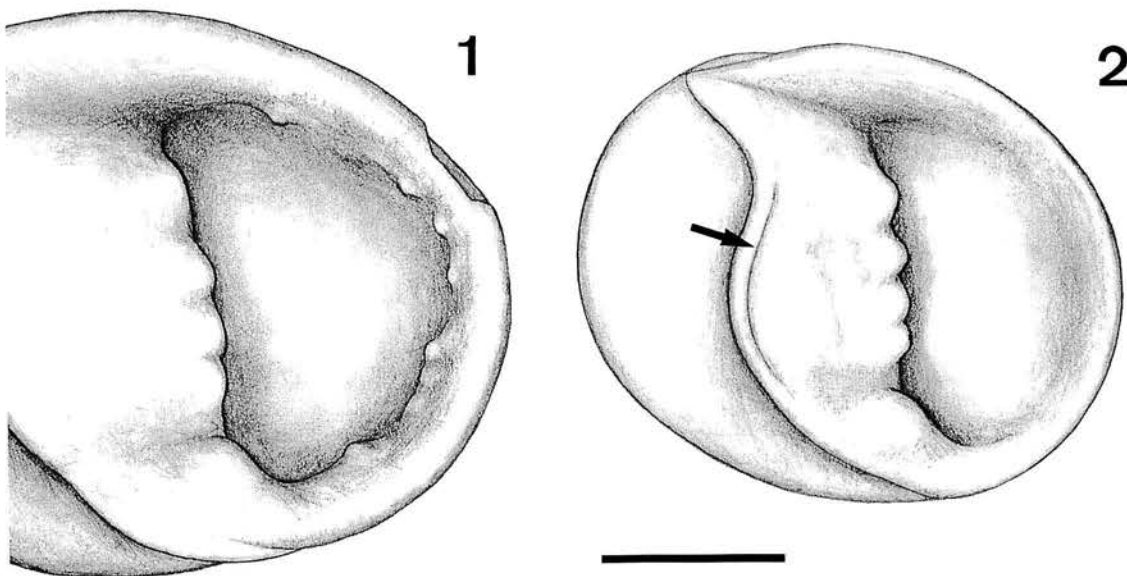


Figure 2. Drawings showing the detail of apertural characteristics in *Pisulinella miocenica* gen. et sp. nov. Scale bar = 1 mm. **1.** Holotype with four teeth along the inner lip, a weak protuberance in the basal lip, and many obscure tubercles on the outer lip. **2.** Paratype 6 (USNM), juvenile shell, with an unornamented outer lip that has a sharp margin. Arrow indicates a shallow groove in the inner lip callus along the inner line.

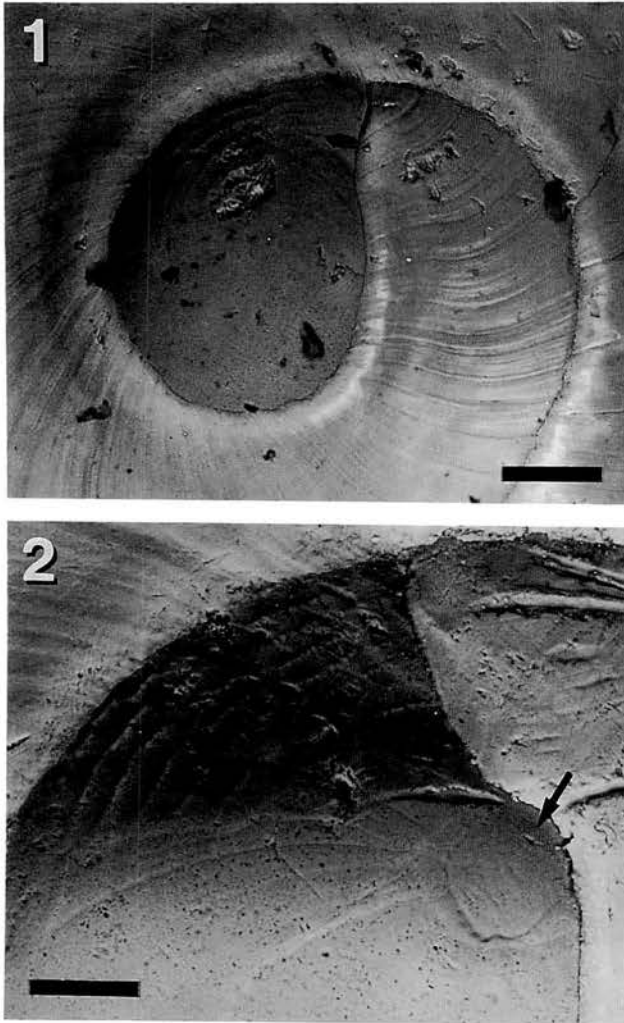


Figure 3. SEM micrographs of the protoconch of *Pisulinella miocenica* gen. et sp. nov. **1.** Apical area of paratype 8 (USNM). Scale bar = 100 μ m. **2.** Protoconch of the holotype, showing an exposed embryonic shell (arrow) and seven spiral ridges on the larval shell. Scale bar = 50 μ m.

shell surrounded by suture of first teleoconch whorl, and exposed drop-shaped area 295–375 μ m in maximum dimensions, sculptured with microscopic pits scattered all over surface, and also with six or seven, ca. 3- μ m-wide, up to 200- μ m-long spiral ridges near apertural lip. Teleoconch whorls less than 2.3 in number, increase rapidly in size, inflated with a round periphery, slightly concave below sutures; last whorl more or less descending abapically in final growth stage. Suture shallowly impressed. Shell surface smooth, polished, and ornamented with fine growth lines and microscopic, sparse spiral grooves. Aperture widely open and semicircular in outline. Outer lip prosocline, blunt at margin, angled 30° to 40° to shell axis, and thickened along interior with many weak tubercles (Figure 2.1). Inner lip covered with a white, smooth, thick and convex callus; adaxial margin bears 3 or 4 slightly protruding teeth, inner line of callus with a deep and distinct, reverse-S shaped groove surrounding columellar area and continuing to basal lip without situation; a shallow groove carved on inner lip callus extends along inner line (Figure 2.2). Basal lip usually bears a weak protuberance. Operculum unknown.

Etymology.—The species name is derived from the word Miocene, the age of the specimens.

Types.—Holotype: USNM 648333, drill hole F-1 at depth of 930–940 feet (283–287 m), Elugelab Island, Eniwetok Atoll, Marshall Islands, lower Miocene (Tertiary *f*). Eight paratypes, USNM, from three drill holes F-1, K-1B, E-1 (on Elugelab Island, Engebi Island, and Parry Island, respectively), Eniwetok Atoll, at a depth of 830–978 feet (253–298 m), lower to upper Miocene (Tertiary *f-g*). See Table 1 for details.

Occurrence.—This species is known only from drill-holes on Eniwetok Atoll, early to late Miocene.

Discussion.—Ladd (1966) assigned this species to *Nerita* (*Amphinerita*) in Neritidae and suggested an affinity to *N. (A.) polita* Linnaeus, a modern species widely inhabiting the tropical Indo-West Pacific, including the Marshall Islands. However, the present fossil species differs markedly from *N. (A.) polita* and also from other species of the subgenus in several important ways. The fully grown adult shell of *P. miocenica* is less than 4 mm in maximum diameter (Table

Table 1. Locality and shell measurements of *Pisulinella miocenica* gen. et sp. nov. Paratypes 6–8 are immature specimens and have a sharp margin along their outer lips. The outer lips of paratypes 4 and 5 are largely broken so that the diameters and heights (in parentheses) are not representative of the species.

Specimen	Hole number and depth (feet)	Number of teleoconch whorls	Diameter (mm)	Height	Maximum diameter of protoconch exposed (mm)
Holotype USNM 648333	F-1 (930–940)	2.3	3.8	3.7	375
Paratype 1 USNM	F-1 (920–930)	2.3	4.0	3.4	325
Paratype 2 USNM	F-1 or E-1 (940–950)	2.2	3.7	3.3	335
Paratype 3 USNM	F-1 (900–910)	2.2	3.6	3.3	360
Paratype 4 USNM	E-1 (830–840)	2.2	(2.7)	(2.9)	365
Paratype 5 USNM	F-1 (900–910)	2.1	(2.7)	(3.1)	295
Paratype 6 USNM	K-1B (968–978)	2.0	3.0	2.7	385
Paratype 7 USNM	K-1B (936–946)	1.8	2.8	2.5	340
Paratype 8 USNM	E-1 (900–910)	1.6	2.0	1.9	365

1), while the largest specimen of *N. (A.) polita* at hand, from Okinawa, Japan, is over 35 mm in maximum diameter. Even the smallest adult of *Nerita (Amphinerita)* species at hand is over 15 mm in maximum diameter. Moreover, the shells of *P. miocenica* are plain cream in color and lack the color pattern that is characteristic of *Nerita (Amphinerita)*. Ladd (1966, p. 11) stated that the fossil shells in the drill-hole section from which this species was recovered apparently never were raised above sea level to be leached and recrystallized. The shells of this new species are almost intact, and many mollusk shells from the same section retain original color patterns (e. g. *Smaragdia* species; see Ladd, 1966, pl. 11, figs. 5–9). These facts strongly suggest that shells of *P. miocenica* were originally plain white, but were subsequently stained brownish cream during fossilization. The presence of a distinct inner line in the callused apertural inner lip, also noted by Ladd (1966), is another character separating *P. miocenica* from *Nerita (Amphinerita)* species.

Schlanger (1963) stated that the reef-associated sediments in the drill-hole section from which the shells of *P. miocenica* were recovered were deposited in lagoonal and shore-bank environments. The basis for this belief was the very high content of delicate branching corals and the abundance of large mollusks. Gastropod species associated with *P. miocenica* in the drill holes include a number of microscopic and macroscopic species that also are suggestive of lagoonal and shore-bank environments within a coral reef. Interestingly, however, the plain creamy color of *P. miocenica* suggests a cryptic habitat for this species. Loss of shell color and reduction of shell size are adaptations to gloomy to totally dark cave habitats for mollusks (Kase and Hayami, 1992; Hayami and Kase, 1993, 1996). Four *Pisulina* species found in marine caves are plain white in color and lack color markings (Kano and Kase, in press). Seven species of undescribed neritiliid genera recently found in submarine caves of tropical Pacific islands, and a species of *Neritilia* recently found in anchialine caves (subterranean caves with haline water which have no surface connection to the sea; see Stock *et al.*, 1986), are entirely white (unpublished data). We suggest that *P. miocenica* was a cryptic species that inhabited submarine caves and/or crevices in a coral reef, and that the shells were secondarily transported to an open reef-associated environment by water currents and/or by subsequent destruction of the reef bodies.

Acknowledgements

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A new fossil bonito (Sardini, Teleostei) from the Eocene of England and the Caucasus, and evolution of tail region characters of its Recent relatives

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Abstract. A new species of a fossil bonito, *Gymnosarda prisca* (Scombridae, Perciformes) from the Early Tertiary shows an interesting combination of characters not seen in other, Recent, bonitos. The new species is based on hypural bones from the caudal region. Although a bonito, the fossil hypural plates possess a caudal notch, a character not known in Recent bonitos. The discovery of this new taxon causes a redefinition of the synapomorphies of the caudal region that define bonitos and their relatives, the tunas and Spanish mackerels. The fossil species has previously been described as part of *Scomberomorus saevus*.

Key words: bonitos, evolution, fossil, new species, synapomorphies, tunas

Introduction

The discovery of a new fossil fish has changed concepts of the characters that define tunas, bonitos and the evolution of their characters. Tunas and bonitos (tribes Thunnini and Sardini, Scombridae) have been stably defined for sometime according to characteristics described in Collette and Chao (1975), Collette (1978) and Collette *et al.* (1984). A new fossil scombrid, described here, shows a remarkable combination of characters which changes current concepts. This fossil species has been studied in the context of a phylogenetic study of the suborder Scombroidei. The main hypotheses (Collette *et al.*, 1984; Johnson, 1986; Finnerty and Block, 1995) on phylogenetic relationships of scombroid fishes, based on data of Recent taxa, present highly conflicting results. In an attempt to solve this problem, I carry out a phylogenetic analysis, containing Recent as well as fossil taxa. Here I present part of my results.

Scomberomorus saevus Bannikov was described from the Eocene of Turkmenistan and Kazakhstan (Bannikov, 1982, 1985). This paper concerns amongst others a specimen of a hypural plate, originally assigned to *S. saevus*. Hypural elements are bones that provide the principal support for the lepidotrichia of the tail in fishes, and are normally separate from one another. In the Scombridae the hypural elements are fused to such a degree that they form one single hypural plate. This plate articulates directly with the vertebral column. Bannikov (1982) did not describe hypural plates in the original description of *S. saevus*, although the type material did include these plates (Bannikov pers. comm., 1998).

They are described in a later account (Bannikov, 1985). These hypural elements are part of a series of paratypes. The holotype of *S. saevus* is a premaxilla. Bannikov's (1982, 1985) material of *S. saevus* includes one specimen which I have identified as Sardini. One fossil specimen from England has been identified as identical to the aforementioned Sardini.

Materials

Except for RAN PIN 1878–8 (premaxilla), the fossil material consists of hypural plates.

BMNH: the Natural History Museum, London:

New species: P6485, Isle of Sheppey, England, Ypresian (London Clay Formation).

Gymnosarda unicolor (Rüppell): 1934.3.31, Red Sea (Recent).

Scomberomorus nipponius (Cuvier): 1874.1.16.9, no data; 1890.2.26.90, inland sea, Japan (Recent).

Sarda orientalis (Temminck and Schlegel): 1920.7.23.59, Durban, South Africa (Recent).

RAN PIN: Russian Academy of Sciences, Paleontological Institute, Moscow:

New species: 1878–2 Western extremities of Ustyurt, Kazakhstan, Upper Eocene (Shorym Svita); 1878–4, Turkmenistan, Upper Eocene (Shorym Svita); 1878–8 (holotype of *S. saevus*), Mangyshlak Peninsula, Karagiye basin, Kazakhstan, Upper Eocene (Shorym Svita).

USNM: Natural History Museum, Smithsonian Institution, Washington DC:

Scomberomorus plurilineatus (Fourmanoir): 64809 and 269760, Durban, South Africa (Recent).

Sarda sarda (Bloch): USNM 26953, 26954, no data (Recent); 270730, New Jersey, U.S.A. (Recent); 270731, Ponte Delgada Fish Market, San Miguel, Azores (Recent).

Systematic palaeontology

Order Perciformes sensu Johnson and Patterson, 1993
Suborder Scombroidei sensu Carpenter *et al.*, 1995

Family Scombridae Rafinesque, 1815
Genus *Gymnosarda* Gill, 1862

Gymnosarda prisca sp. nov.

Figure 1A, B

Scomberomorus saevus Bannikov, 1982, p. 135 (in part); Bannikov 1985, p. 37 (in part).

Holotype.—BMNH P6485, (previously labelled "unidenti-

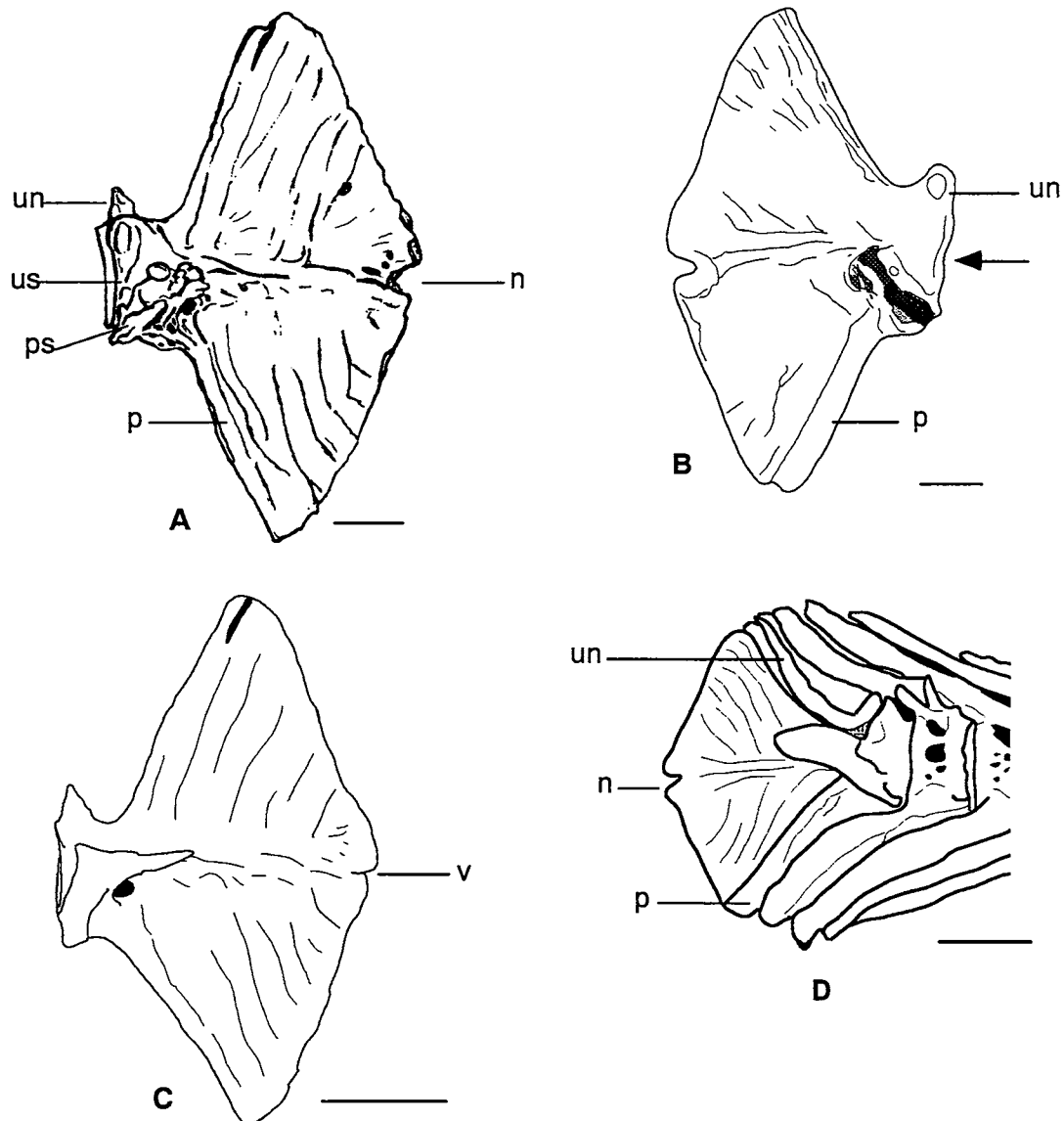


Figure 1. Hypural plates, lateral view. *Gymnosarda prisca* sp. nov. **A.** Holotype, BMNH P6485 (left view). **B.** RAN PIN 1878-4 (right view). Arrow indicates perspective of Figure 2A. **C.** *Gymnosarda unicolor* (Rüppell) (left view), after Collette and Russo (1984) and BMNH 1934.3.31. **D.** *Scomberomorus regalis* (Bloch): USNM 270053, (right view). Abbreviations: hyp5: fifth hypural, n: caudal notch, p: parhypural, ps: parhypurapophysis, un: uroneural, us: urostyle, v: remnant of caudal notch. Scale bars indicate 10 mm.

fied teleost") (Figure 1A).

Material.—Holotype, and RAN PIN 1878-4, (Figure 1B).

Etymology.—Priscus is Latin for "old", indicating it is an extinct ancient species of *Gymnosarda*. The only other species is the Recent *Gymnosarda unicolor*.

Diagnosis.—Species of a Sardini: uroneural and fifth hypural fused to hypural plate and urostyle cross-section with long axis horizontal. Differs from other Sardini by having parhypural fused to hypural plate and possession of caudal notch. Recent bonitos lack a conspicuous notch, and of Recent bonitos only *Gymnosarda unicolor* has a fused parhypural (see Figure 1).

Description.—Hypural plate, made up of fusion of urostyle, uroneural, hypurals 1-5 (hypural 5 not completely fused to plate) and parhypural. Plate diamond-shaped; sides equal in length. Height 75 mm (holotype, Figure 1A) or 79 mm (RAN PIN 1878-4, Figure 1B), which is twice the length without uroneural in both specimens (length: along axis of fish, height: along line perpendicular to axis). Posterior outline of diamond slightly swollen outwardly (more on dorsal side). Posteriorly, a clearly discernible notch. Markings made by fin rays crossing plate visible as shallow grooves, running parallel to rostral sides of diamond. Parhypurapophysis (damaged) making angle of about 41° with horizontal axis. Uroneural large, fused to urostyle [urostyle, according to definition of Potthoff (1975): fusion of preural centrum 1 and ural centrum]. Cross-section of urostyle round or slightly ovoid with the long axis vertical (as Thunnini, Figure 2).

Remarks.—The hypural plate-based taxon *G. prisca* is referable to the Sardini based on the diamond-shaped plate and the large anterior upturned end of the uroneural which is fused to the plate. With its proportions the hypural plate of *G. prisca* is almost identical to that of the Recent *G. unicolor* (Figure 1C). In *Gymnosarda*, the hypural plate is about twice as deep as long. In the other bonitos *Sarda*, *Orcynopsis* and *Cybiosarda* the hypural plate is less deep. *Allothunnus* was previously recognised as a bonito (Collette and Chao, 1975; Johnson, 1986). Collette *et al.* (1984) suggest that *Allothunnus* is better regarded as a primitive Thunnini, for which later convincing evidence has been found (Graham and Dickson, in press). *Gymnosarda unicolor* is unique among Recent bonitos in having a fused parhypural, just like *G. prisca*, and has a small vestige where *G. prisca* has a caudal notch (BMNH 1934.3.31 and Collette and Chao, 1975, p. 578 and fig. 56). No bonito with a caudal notch is known (Collette and Chao, 1975). I have not seen such notches in specimens of *Sarda* (BMNH 1920.7.23.59; USNM 26953, 26954, 270730 and 270731). Still, the *G. prisca* hypural plate possesses all other characteristics of a Sardini.

The specimen figured in Figure 2B (RAN PIN 1878-2) is an unknown scombrid, described and figured as *S. saevus* by Bannikov (1985, p. 37, figures 17 g, d) and is part of the *S. saevus* type series. The parhypural is fused to the plate and hence it is not a *Scomberomorus* (Table 1; see also Discussion), but no name as yet is assigned to that specimen. The systematic position of the taxon this plate represents is still under consideration.

Discussion

Previously, *G. prisca* was believed to belong to *Scomberomorus* because of apparent similarities with the latter (Figure 1D). It now seems that it is not a *Scomberomorus*. The most conspicuous character to identify a Sardini from a *Scomberomorini* is the cross-section of their urostyles (see their descriptions and Figure 2). *Gymnosarda prisca* has a hypural plate in which the cross-section of the urostyle is ovoid with the long axis vertical (Figure 2A), whereas in *Scomberomorini* the long axis is horizontal (Figure 2B). In *G. prisca* the parhypural is fused with the hypural plate, whereas in Recent *Scomberomorus* it is not. Collette and Russo (1984) mention that *Scomberomorus nipponius* and *Scomberomorus plurilineatus* have parhypurals partially fused to the hypural plate. In specimens of *S. plurilineatus* (USNM 264809 and 269760) and *Scomberomorus nipponius* (BMNH 1874.1.16.9 and 1890.2.26.90) the parhypural is not fused to the hypural plate. Possibly there is a light degree of fusion in specimens that I have not seen. Bannikov (1982) noted that the parhypural of *S. saevus* is separated from the hypural plate by a fissure. Although the parhypural can be clearly identified in the hypural plate of *G. prisca*, the division between the plate and the parhypural is not sharp enough to represent an autogenous parhypural.

The assignment of the name *S. saevus* to its whole type series is partially incorrect. Bannikov's (1982, 1985) holotype is RAN PIN 1878-8, which is a premaxilla that is identical to one of *Scomberomorus*. A *Scomberomorus* premax-

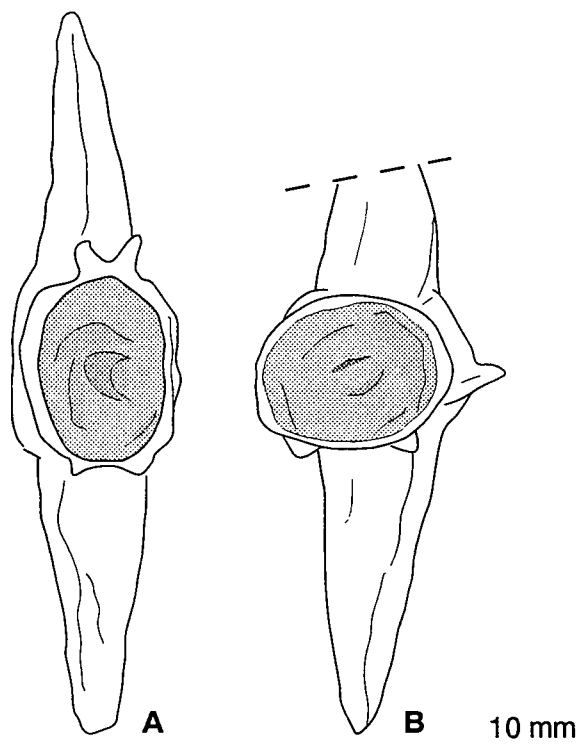


Figure 2. Hypural plates viewed to show the diameters of urostyles. **A.** *Gymnosarda prisca* sp. nov., RAN PIN 1878-4. **B.** *Scomberomorini* indet., RAN PIN 1878-2.

illa is recognised by a relatively long ascending process: 31–48% of the total premaxilla (Collette and Russo, 1984), and makes a sharp angle with the shank: 32°–61° (Collette and Russo, 1984). The holotype of *S. saevus* fits this description well. Being recognised as a *Scomberomorus* and being the holotype of the epithet *saevus*, the name *Scomberomorus saevus* is retained for this specimen.

Gymnosarda prisca shows a peculiar mix of characters. A noticeable caudal notch in the hypural plate is a primitive character, found in amongst others the Scomberomorini, where it can be large. I do not think that *G. prisca* can be anything but a Sardini and indeed, a *Gymnosarda*. According to Collette and Chao (1975) and Collette *et al.* (1984)

one of the synapomorphies of the scombrids above the Spanish mackerels (Scomberomorini) is the absence of the caudal notch (see Table 1). *Gymnosarda prisca* clearly possesses a large caudal notch. *Gymnosarda unicolor* is in fact not devoid of a caudal notch, it has a small, hard to spot vestigial one. It seems thus, that Sardini are not characterised by the absence of a caudal notch, but rather by a tendency of this notch to close down, and ultimately disappear in their evolution. Thunnini are characterised by a complete absence of the notch. The caudal notch in *G. prisca* is evidence that it is not a sharp divider above species level: the Scomberomorini have a notch; so do primitive Sardini and in advanced ones this notch has disappeared. Therefore, be-

Table 1. Overview of hypural plate characters of *Scomberomorus* and Sardini.

	Parhypural	Caudal notch	Uroneural	Hypural fusion pattern	Cross-section of urostyle
<i>Scomberomorus</i>	not fused	yes	not fused	1–4, 5	long axis vertical
<i>Gymnosarda prisca</i> sp. nov.	fused	yes	fused	1–5	long axis horizontal
<i>Gymnosarda unicolor</i> (Rüppell)	fused	remnant	fused	1–5	long axis horizontal
other Sardini	not fused	no	fused	1–5	long axis horizontal

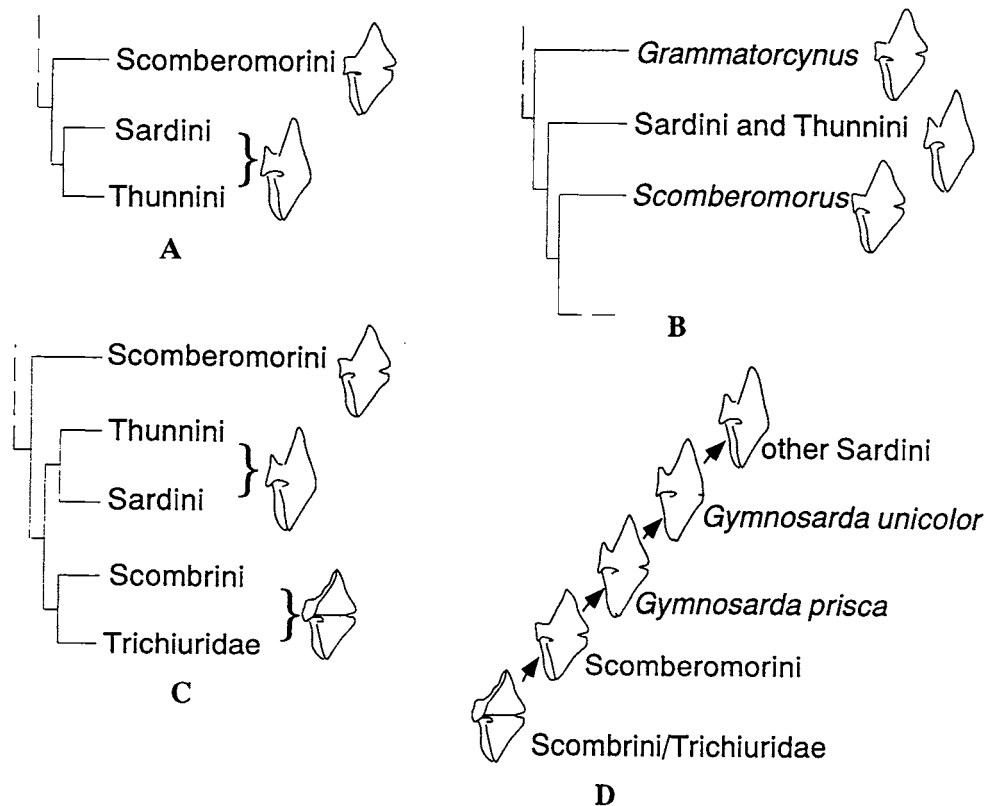


Figure 3. Phylogenetic relationships of Sardini, Thunnini and their closest relatives. **A.** After Collette *et al.* (1984). **B.** After Johnson (1986). **C.** After Finnerty and Block (1995). **D.** Proposed evolutionary sequence.

cause of the great similarities with *G. unicolor*, I describe this fossil taxon as a new species within this genus.

The small vestigial notch of *G. unicolor* suggests that more primitive bonitos have once had a large caudal notch. This is confirmed by *G. prisca*. This notch is a primitive feature, which thus suggests that the ancestor of the bonitos came from within the Scomberomorini (see Table 1).

Collette *et al.* (1984) and Johnson (1986) published phylogenies of Scombroidei based on morphological data (Figs. 3A and B). Finnerty and Block (1995) published a phylogeny based on DNA analyses (Figure 3C). In Collette *et al.* (1984), Sardini and Thunnini are the most advanced scombroids, with Scomberomorini as the sistergroup. According to Johnson (1986), Sardini+Thunnini are a specialised offshoot of a paraphyletic Scomberomorini. Finnerty and Block (1995) present a phylogenetic relationship in which the Sardini+Thunnini clade is sister-group to a Scombrini (mackerels)+Trichiuridae (cutlassfishes) clade. The clade containing these four taxa is in turn the advanced sistergroup to Scomberomorini. Keeping in mind the proposed evolutionary sequence (Figure 3D), all three hypotheses of relationships in Fig. 3A–C seem to be possible. Finnerty and Block's hypothesis is less parsimonious than the morphological ones, because it requires reversals. The caudal region of Scombrini and Trichiuridae is plesiomorphic compared to that of other Scombridae. Johnson's (1986) Scomberomorini are paraphyletic, caused by the offshoot of Sardini and Thunnini, but his phylogenetic hypothesis remains possible. However, this hypothesis is less parsimonious than that of Collette *et al.* (1984). If you map tail-region morphology on Johnson's (1986) phylogeny, there are character reversals (Figure 3B). Further research on the phylogeny of scombroids will hopefully contribute more to the solution of the controversy of these relationships.

Although based on a hypural plate only, I do think that phylogenetic hypotheses can be made using *G. prisca*. Hypural plates provide strong characters, which are well indicative of genera (see Uyeno and Fujii, 1975).

Conclusions

While studying the type series of *Scomberomorus saevus*, a new species has been found: *Gymnosarda prisca*. Sardini are to be characterised by a tendency of the hypural notch to close and disappear in their evolution. Thunnini are characterised by a complete absence of the notch. *Gymnosarda prisca* fits in with every one of the different scombroid cladograms, with respect to Recent Sardini-Scomberomorini relationships. Finnerty and Block's (1985) phylogeny seems to be less parsimonious than the morphological phylogenies. In Johnson's (1986) hypothesis, Scomberomorini are paraphyletic and the tail region evolution requires reversals.

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行事予定

◎第149回例会は、2000年6月24日(土)と25日(日)に「群馬県立自然史博物館」で開催されます。個人講演の申し込み締切日は2000年5月2日(火)です。6月24日(土)にシンポジウムとして「1500万年前頃の群馬の海—そのおいたちと生物たち—世話人 長谷川善和・高桑祐司・間嶋隆一」が開催されます。なお、このシンポジウムは富岡市民向けの公開講座もかねております。

お詫び：Paleontological Research vol.3, no. 4の行事予定では、第149回例会の開催日を「6月23日(土)から24日(日)」とし、個人講演の申し込み締切日を「5月4日」としておりましたが、開催日はカレンダーと一致せず、また締切日は祝日でしたので、上記のように訂正致します。申し訳ありませんでした。

◎第150回例会は、2001年1月27日(土)と28日(日)に「茨城県自然博物館」で開催されます。シンポジウム案の申し込み締切日は2000年4月末日、個人講演の申し込み締切日は2000年12月1日(金)です。

◎2001年年会・総会は、21世紀最初の年会ですので、「21世紀の古生物学」を統一テーマとし、東京地区でシンポジウムを中心とした形式で、将来計画委員会が中心となって開催を企画することが決定しております。開催の案内や形式については別にご案内致します。

◎第151回例会(2002年1月下旬開催予定)の開催申し込みは、今のところありません。

◎2002年年会・総会(2002年6月下旬開催予定)には福井県立博物館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わせ下さい。

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CONTENTS

Hiroshi Kitazato, Masashi Tsuchiya and Kenji Takahara: Recognition of breeding populations in foraminifera: an example using the genus <i>Glabratella</i>	1
Ritsuo Nomura and Yokichi Takayanagi: Foraminal structures of some Japanese species of the genera <i>Ammonia</i> and <i>Pararotalia</i> , family Rotaliidae (Foraminifera)	17
Tatsuro Matsumoto and Toshio Kijima: The turrilitid ammonoid <i>Mariella</i> from Hokkaido-Part 3 (Studies of the Cretaceous ammonites from Hokkaido and Sakhalin-LXXXVII)	33
Mike Pole: Dicotyledonous leaf macrofossils from the latest Albian-earliest Cenomanian of the Eromanga Basin, Queensland, Australia	39
Shuji Niko and Tamio Nishida: A new pseudorthoceratid cephalopod from the Kazanian (middle Late Permian) of Japan	53
Wei-Ping Yang and Jun-ich Tazawa: Early Carboniferous miospores from the southern Kitakami Mountains, northeast Japan	57
Yasunori Kano and Tomoki Kase: <i>Pisulinella miocenica</i> , a new genus and species of Miocene Neritiliidae (Gastropoda: Neritopsina) from Eniwetok Atoll, Marshall Islands	69
Kenneth A. Monsch: A new fossil bonito (Sardini, Teleostei) from the Eocene of England and the Caucasus, and evolution of tail region characters of its Recent relatives	75