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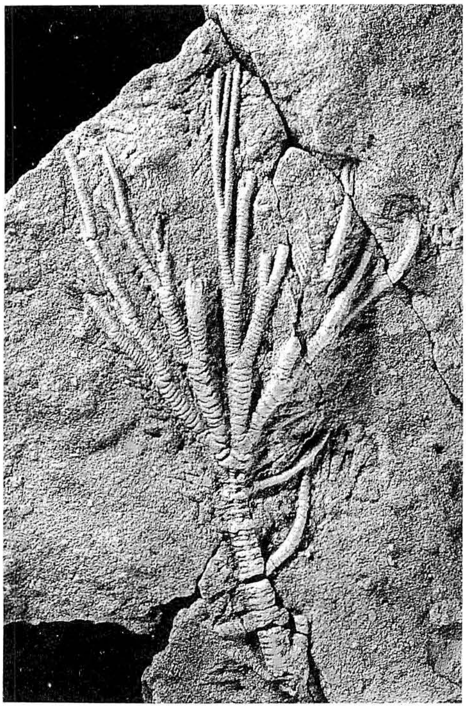

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The fossil on the cover is *Isocrinus* (*Chladocrinus*) *hanaii* Oji, an Early Cretaceous (Aptian) crinoid, which was described from the Hiraiga Formation exposed at Haipe, Tanohata-mura, Shimo-Hei County, Iwate Prefecture, Northeast Japan. (University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

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964. INITIAL VALVES OF THE MIOCENE EXTINCT DIATOM GENUS *DENTICULOPSIS* SIMONSEN*

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Abstract. Morphologic and stratigraphic study of the Miocene fossil diatom genera *Katahiraia* Komura and *Yoshidaia* Komura reveals that they are the initial valves of the genus *Denticulopsis* Simonsen. They have almost the same morphology and stratigraphic range as the corresponding vegetative valves of *Denticulopsis,* but differ in having a rounded valve shape in cross section and a central raphe. Probable vegetative *Denticulopsis* species are suggested for each of *Katahiraia* and *Yoshidaia* species on the basis of morphology and stratigraphic ranges.

Key words. Miocene marine diatom, *Denticulopsis, Katahiraia, Yoshidaia,* initial valve, auxospore.

Introduction

Denticulopsis is an extinct marine diatom genus which was erected by Simonsen (1979) and later emended by Akiba and Yanagisawa (1986). It is one of the most important diatom groups in the Miocene diatom biostratigraphy in the middle- to high-latitude North Pacific, because it includes a number of short-lived species which serve as remarkable biostratigraphic markers (e.g. Maruyama, 1984b; Koizumi, 1985; Barron, 1985; Akiba, 1986; Bodén, 1992).

Modern taxonomic study of the genus *Denticulopsis* began in 1961, when Simonsen and Kanaya (1961) made the first taxonomic synthesis of this species group, demonstrating its stratigraphic utility in the Neogene sediments of California and Japan. During the past three decades, systematic study of this genus has been greatly improved by many successive works (Schrader, 1973a, b, 1976; Simonsen, 1979; Maruyama, 1984a, Akiba and Yanagisawa, 1986; Tanimura, 1989, Harwood and Maruyama, 1992). Recently, a detailed taxonomic synthesis has been made on this genus by Yanagisawa and Akiba (1990), who presented its most probable evolutionary lineages based on both scanning electron microscopy (SEM) and biostratigraphic analysis.

However, there still remain some problems concerning the taxonomy of *Denticulopsis.* One of these is its taxonomic relationship with the genera *Katahiraia* and *Yoshidaia,* both of which were erected by Komura (1976) from Neogene sediments of Hokkaido, Japan. The two genera are very similar in morphology to *Denticulopsis* except that they have a rounded valve shape in cross section and a central raphe, in contrast to the flat valve face and a marginal raphe of *Denticulopsis.* Because of this morphologic similarity, Yanagisawa and Akiba (1990) suggested that *Katahiraia* and *Yoshidaia* species may be the initial valves of *Denticulopsis,* but they failed to present substantial evidence to support it.

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In the course of my continued study, diatom frustules consisting of a *Katahiraia*-type epivalve and a *Denticulopsis*-type hypovalve were occasionally found. This is an additional evidence to strongly suggest that *Katahiraia* is the initial valve of *Denticulopsis*. In this paper, the morphology of initial valves of some *Denticulopsis* species are described and the life cycle of this genus is suggested in relation to the initial valve formation.

Materials and methods

Samples used in this study are listed in Table 1. Sample JOB 557A was collected by the present author. Samples JDS 5801 and 6-9 were offered by Fumio Akiba and Itaru Koizumi, respectively. Samples of DSDP Hole 438A were those studied by Akiba *et al.* (1982), Maruyama (1984b), Akiba (1986) and Yanagisawa and Akiba (1990). In this study, I examined slides of some selected samples of DSDP Hole 71 which were studied by Barron (1983).

The samples were processed and prepared by a standard method. Light microscopy was carried out at a magnification of 1000X. The stratigraphic distribution of *Katahiraia* and *Yoshidaia* was examined in DSDP Hole 438A.

Results and observation

Selected specimens of *Katahiraia* and *Yoshidaia* species found in this study are illustrated in Figures 1 and 2, with their related *Denticulopsis* species. In this study the following six species are identified: *Katahiraia oblonga* Komura, *K. pauperata* Komura, *K. aspera* Komura, *Yoshidaia divergens* Komura, *Y. constricta* Komura and *Y. loculata* Komura.

The stratigraphic occurrences of the *Katahiraia* and *Yoshidaia* species in the DSDP Hole 438A are shown in Figure 3.

In the following, the results of observation on some *Katahiraia* and *Yoshidaia* species are described. Terminology generally follows Yanagisawa and Akiba (1990) who discussed the basic terminology of *Denticulopsis* using several schematic drawings.

According to the original description of Komura (1976), both of the genera *Katahiraia* and *Yoshidaia* are characterized by central canal raphe, but the two genera can be differentiated by perforation on valve surface; *Katahiraia* has double-layered perforation composed of outer finely and regularly perforated wall and inner coarse and irregular areolation, whereas *Yoshidaia* has single-layered fine perforation with regularly arranged puncta.

Table 1. Samples used in this study

Samples and cores	Area	Latitude and longitude	Formation
JOB 557A	Joban Coalfield	36°47.37′ N, 140°44.38′ E	Isohara Formation
JDS 5801	Kushiro Coalfield		Chokubetsu F.
Sample 6-9	Shimokita Peninsula	41°15.00′ N, 141°19.66′ E	Gamanosawa F.
DSDP Hole 438A	Northwest Pacific	40°37.79′ N, 143°14.15′ E	
DSDP Hole 71	Eastern equatorial Pacific	04°28.28′ N, 140°18.91′ W	

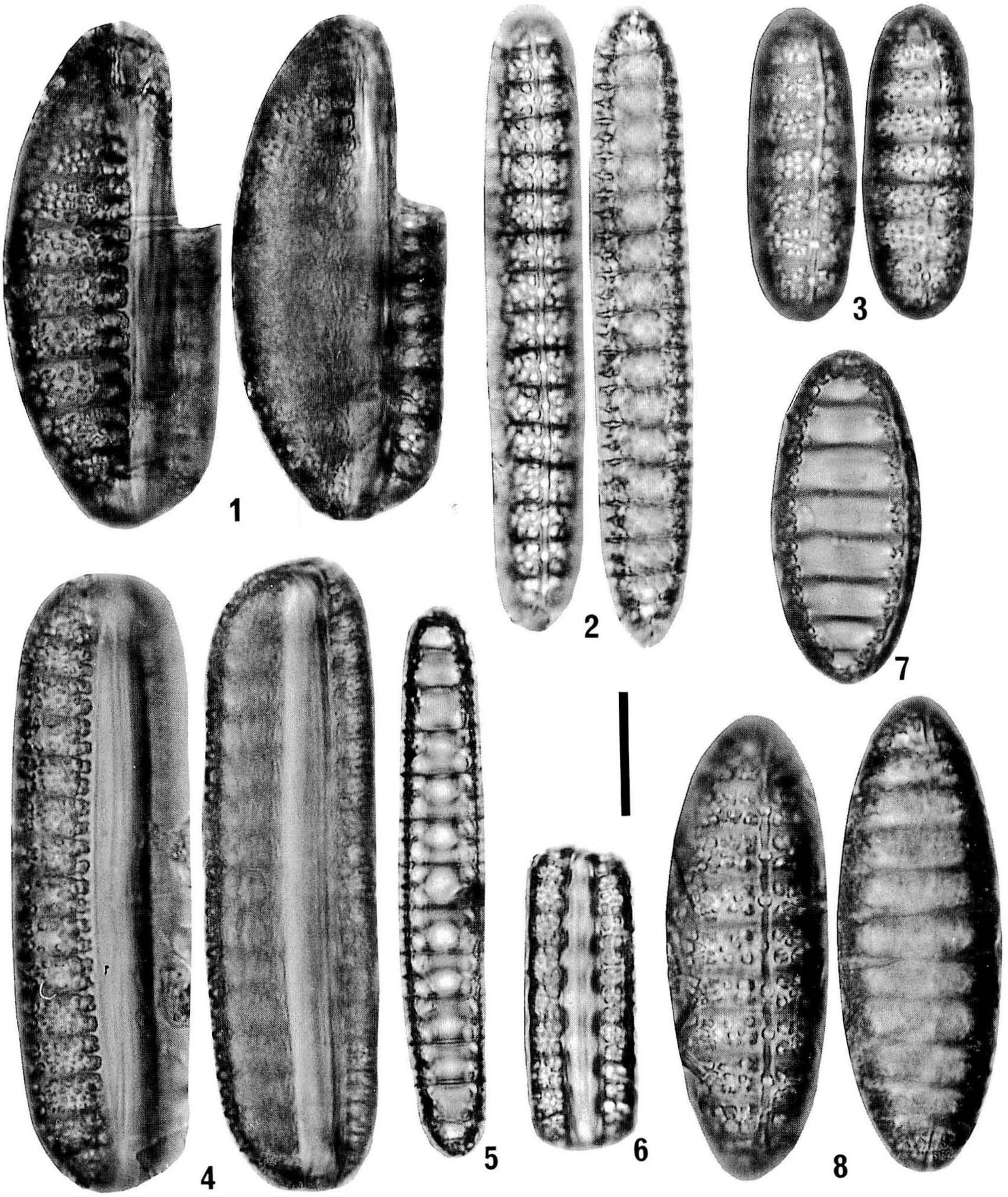


Figure 1. **1.** Frustule consisting of a *Katahiraia*-type epivalve (left) and a *Denticulopsis*-type hypovalve (right) (JOB 557A, Isohara Formation). **2.** *Katahiraia pauperata* Komura (DSDP Hole 438A, 67-1, 27-32 cm). **3.** *Katahiraia oblonga* Komura (DSDP Hole 438A, 67-1, 112-113 cm). **4.** Frustule consisting of a *Katahiraia*-type epivalve (left) and a *Denticulopsis*-type hypovalve (right) (DSDP Hole 438A, 67-1, 27-32 cm). **5.** *Denticulopsis hyalina* (Schrader) Simonsen (DSDP Hole 438A, 68-1, 30-34 cm). **6.** *Denticulopsis hyalina* (Schrader) Simonsen (DSDP Hole 438A, 68-1, 30-34 cm). **7.** *Denticulopsis miocenica* (Schrader) Simonsen (JDS 5801, Chokubetsu Formation). **8.** *Katahiraia aspera* Komura (JDS 5801, Chokubetsu Formation). Scale bar equals 10 μm.

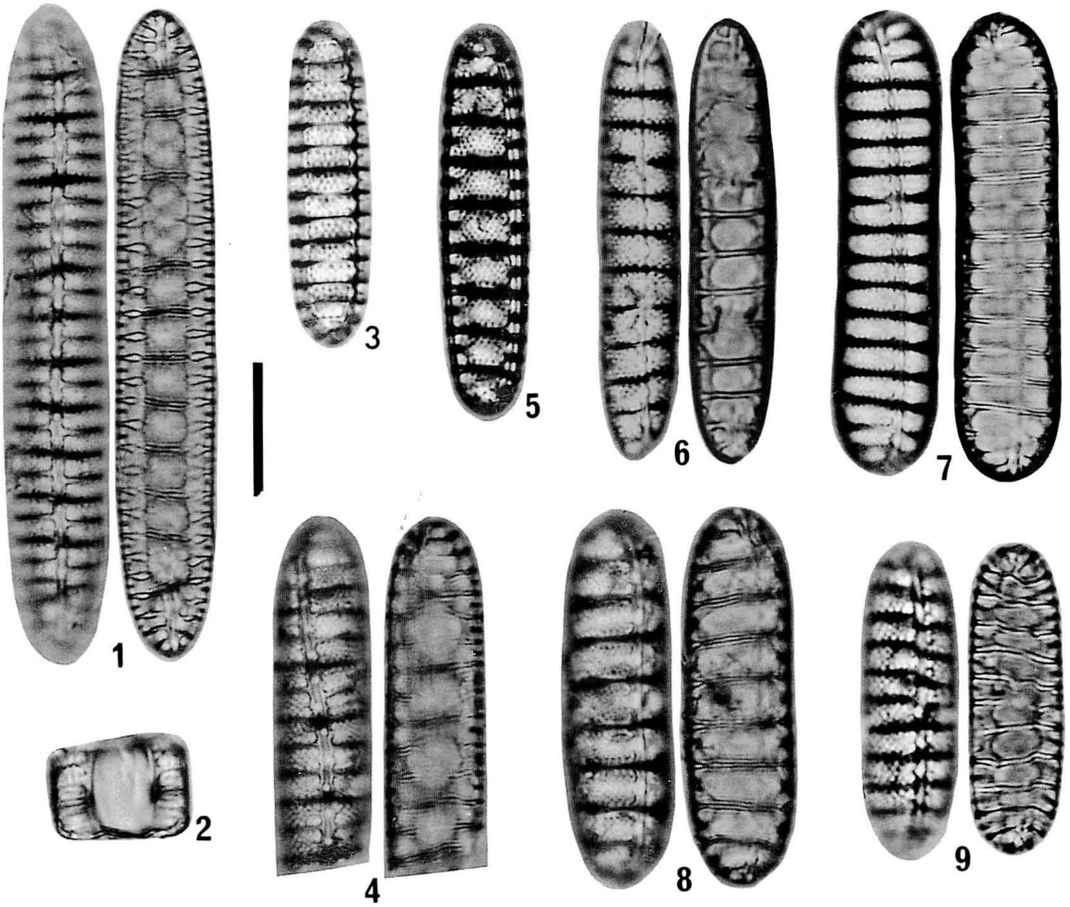


Figure 2. **1.** *Yoshidaia loculata* Komura (DSDP Hole 438A, 65-2, 18-21 cm). **2.** *Denticulopsis simonsenii* Yanagisawa et Akiba (DSDP Hole 438A, 64-3, 10-14 cm). **3.** *Denticulopsis simonsenii* Yanagisawa et Akiba (DSDP Hole 438A, 66-1, 121-123 cm). **4.** *Yoshidaia loculata* Komura (DSDP Hole 438A, 66-2, 34-36 cm). **5.** *Denticulopsis lauta* (Bailey) Simonsen (DSDP Hole 438A, 70-1, 16-20 cm). **6.** *Yoshidaia divergens* Komura (DSDP Hole 438A, 79-1, 51-54 cm). **7.** *Yoshidaia constricta* Komura (Sample 6-9, Gamanosawa Fomation). **8.** *Yoshidaia divergens* Komura (DSDP Hole 438A, 68-4, 68-72 cm). **9.** *Yoshidaia divergens* Komura (DSDP Hole 71, 21-4, 60-62 cm). Scale bar equals 10 μm.

***Katahiraia oblonga* Komura** (Figure 1-3), **and *Katahiraia pauperata* Komura** (Figure 1-2)

Katahiraia oblonga Komura (1976, p. 386-387, text-fig. 6, pl. 41, fig. 6) and *K. pauperata* Komura (1976, p. 387-388, text-fig. 7, pl. 41, fig. 7) have a thickly silicified linear valve with rounded apices (Figures 1-2, 1-3). Primary pseudosepta and marginal ribs are present, but secondary pseudosepta are absent. Valve shape in cross section is rounded so that the valve face and mantle can not be separated. The whole valve surface is perforated with double-layered punctation composed of outer fine perforation and inner coarse areolation. A raphe runs along the apical axis or somewhat subcentrally with each portula between each two primary pseudosepta.

These two species share a set of common morphological features mentioned above, and they are differentiated only by their slightly different valve outline; *K. oblonga* has a

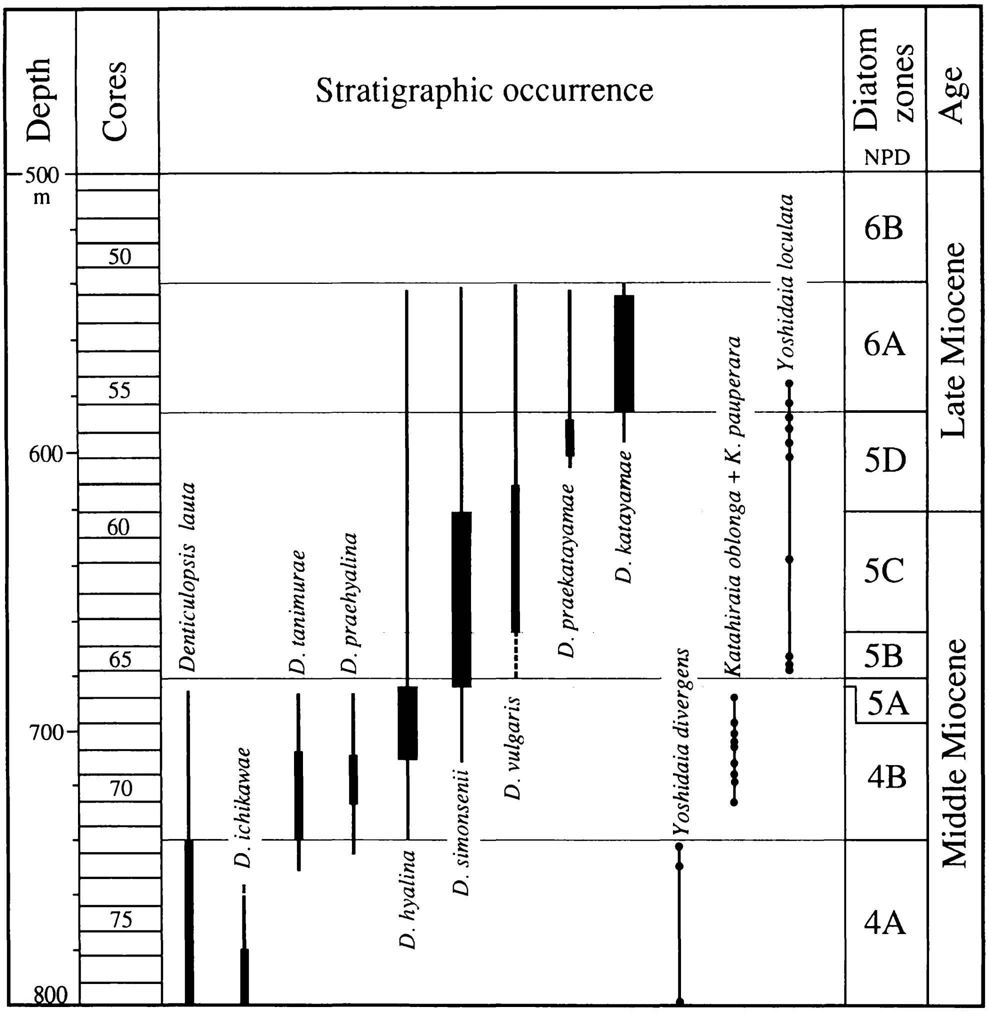


Figure 3. Stratigraphic occurrences of *Katahiraia, Yoshidaia* and *Denticulopsis* species in DSDP Hole 438A. Diatom zones are after Akiba (1986).

broader and shorter valve, and *K. pauperata* has a more slender and longer valve. However, this difference is not clear enough to separate the two species distinctly. Consequently, they might be treated as a single taxon of *Katahiraia. Katahiraia* sp. (Komura, 1976, p. 388, text-fig. 8, pl. 40, fig. 13) may also be included in this taxon because of its intimate similarity to *K. oblonga* and *K. pauperata.*

Except for the central raphe and rounded cross section of valve, a number of morphologic characteristics of *K. oblonga* and *K. pauperata,* including the linear valve outline, thickly silicified valve, absence of secondary pseudosepta and double-layered perforation, are common to *Denticulopsis hyalina* (Schrader) Simonsen (Figure 1-5, 1-6), and also to *D. praehyalina* Tanimura and *D. tanimurae* Yanagisawa et Akiba.

In samples JOB 557A from the Isohara Formation and DSDP Hole 438A, 68-1, 30-34 cm, I have found heterovalvate frustules consisting of a *Katahiraia*-type epivalve which has rounded valve face and apices, and a flat-faced *Denticulopsis*-type hypovalve (Figures 1-1, 1-4).

At the DSDP Hole 438A, both *K. oblonga* and *K. pauperata* are found, though extremely rare, in 9 samples, all of which fall within NPD 4B (the *Denticulopsis hyalina* Zone) of Akiba (1986) (Figure 3). Their stratigraphic range is seemingly coincident with the interval where *D. hyalina, D. praehyalina* and *D. tanimurae* occur abundantly (Figure 3).

***Katahiraia aspera* Komura** (Figure 1-8)

Katahiraia aspera Komura (1976, p. 385, text-fig. 5, pl. 41, figs. 1-4) is typified by its broad and oval valve outline (Figure 1-8). Other morphological features are almost the same as those of *K. oblonga* and *K. pauperata* described above. Detailed SEM observation of this species was carried out by Yanagisawa and Akiba (1990, pl. 10, figs. 3-3). This form exhibits close affinity to *Denticulopsis miocenica* (Schrader) Simonsen (Figure 1-7) in having an oval valve shape and a thickly silicified valve, but it differs by the possession of a central raphe, rounded valve face and double-layered perforation on the whole valve surface. *Katahiraia aspera* is generally larger than *D. miocenica* (Yanagisawa and Akiba, 1990, fig. 19).

Komura (1976) presented several girdle views of *K. aspera* (Komura, 1976, text-fig. 5, figs. 7, 8 ; pl. 41, fig. 5), but these specimens might probably be large forms of *Denticulopsis hyalina* bacause they have flat valve faces.

Although it does not occur in DSDP Hole 438A, rare specimens of *K. aspera* are rarely found in the upper part of NPD 4B (the *D. hyalina* Zone) in several onland sections of Japan. The sample JDS 5801 collected from the Chokubetsu Formation of Kushiro Coalfield in eastern Hokkaido is one of these samples which contain abundant *K. aspera* as well as *D. miocenica.*

***Yoshidaia divergens* Komura** (Figures 2-6, 2-8, 2-9), **and *Y. constricta* Komura** (Figure 2-7)

Yoshidaia divergens Komura (1976, p. 389-390, text-fig. 9, pl. 40, figs. 6-8) and *Y. constricta* Komura (1976, p. 390-391, text-fig. 10, pl. 40, figs. 9, 10, pl. 41, fig. 8) are linear in valve outline with rounded apices and a central or subcentral raphe (Figure 2-6, 2-7). They have primary pseudosepta and marginal ribs, but lack secondary pseudosepta. The valve surface is rounded in cross section and therefore the valve face and mantle can not be distinguished (Yanagisawa and Akiba, 1990, pl. 9, figs. 10, 11). The valve surface is covered with fine perforation without reduction of puncta. The frustule of *Y. divergens* possesses some girdle bands quite similar to those of *Denticulopsis* (Yanagisawa and Akiba, 1990, pl. 9, fig. 10).

According to Komura (1976), *Y. divergens* and *Y. constricta* are separated mainly by their valve outline, but this difference is not significant enough and they may be safely interpreted as intraspecific variations. The valve of *Y. divergens* or *Y. constricta* is most similar to *Denticulopsis lauta* (Bailey) Simonsen (Figure 2-5) and *D. ichikawae* Yanagisawa et Akiba in all aspects except that it has the central raphe and convex valve face.

In DSDP Hole 438A, *Yoshidaia divergens* was detected in three samples within NPD 4A (the *Denticulopsis lauta* Zone), where *D. lauta* and *D. ichikawae* occur abundantly (Figure 3). *Yoshidaia constricta* was found in sample 6-9 from the Gamanosawa Formation in Shimokita Peninsula (Figure 2-7), a sample containing a diatom assemblage correlative with NPD 4A.

***Yoshidaia loculata* Komura** (Figures 2-1, 2-4)

Yoshidaia loculata Komura (1976, p. 391, text-fig. 11, pl. 40, fig. 11, pl. 41, fig. 9) is linear in outline with rounded apices. The raphe is located in the valve center (Figure 2-1), almost straight but slightly curved near the apex (Figure 2-4). Primary pseudosepta, secondary pseudosepta and marginal ribs are present. The valve shape in cross section is strongly convex without distinction between the valve face and mantle. The whole valve surface is perforated with fine puncta without reduction of puncta.

Yoshidaia? densicostata Komura (Komura, 1976, p. 392-393, text-fig. 12, pl. 40, fig. 12) is very similar in morphology to *Y. loculata,* and the two species may constitute the same taxonomic unit.

Yoshidaia loculata resembles *Y. divergens* in having linear valve outline and fine perforation but is distinguished by the presence of secondary pseudosepta. It also exhibits obvious affinities to *Denticulopsis simonsenii* Yanagisawa et Akiba (Figures 2-2, 2-3) and *D. vulgaris* (Okuno) Yanagisawa et Akiba with its linear outline, fine perforation and the presence of secondary pseudosepta. The *Yoshidaia loculata* valve is usually larger than those of *D. simonsenii* and *D. vulgaris* (Yanagisawa and Akiba, 1990, fig. 20).

In DSDP Hole 438A, *Y. loculata* is recognized in 10 samples ranging from the base of NPD 5A (the *Crucidenticula nicobarica* Zone) to lower part of NPD 6A (the *Denticulopsis katayamae* Zone) (Figure 3). This interval approximates the stratigraphic interval where *D. simonsenii* and *D. vulgaris* occur most abundantly.

Discussion

The genera *Katahiraia, Yoshidaia* and *Denticulopsis* are morphologically very similar to each other, sharing a set of common morphological features including linear or linear-elliptical valve outline, rounded apices, valve interior chambered by a number of transapical pseudosepta, the presence of marginal ribs, the structure of the basal ridge, two types of perforation pattern on the valve surface, the presence of a canal raphe system and so on. Morphologic differences among *Katahiraia, Yoshidaia* and *Denticulopsis* include only the convexity of the valve surface and the location of the raphe ; the valves of *Katahiraia* and *Yoshidaia* have a convex valve surface and a central raphe, while *Denticulopsis* possesses a flat valve face and a marginal raphe (Figure 4). No other distinct differences exist between the two.

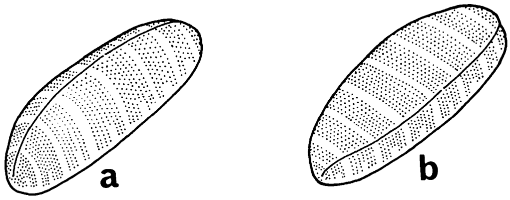


Figure 4. Schematic drawings of the valves of *Katahiraia* and *Yoshidaia* (a), and the valve of *Denticulopsis* (b).

The morphologic and stratigraphic features of *Katahiraia* and *Yoshidaia* are summarized as follows : (1) The valve surface is rounded in cross section so that the valve face and mantle can not be differentiated. (2) The raphe runs along the valve center in contrast to the marginal raphe of *Denticulopsis.* (3) Each species of *Katahiraia* and *Yoshidaia* has its corresponding *Denticulopsis* species which have almost the same morphologic features except for the rounded valve surface and the central raphe. (4) The valve surface is covered with the same type of perforation as that of the mantle of the corresponding *Denticulopsis* species. (5) *Katahiraia* and *Yoshidaia* species are relatively larger in size than the corresponding *Denticulopsis* species. (6) The occurrence of *Katahiraia-Yoshidaia* species is always extremely scarce. (7) The stratigraphic ranges of these forms are roughly coincident with the ranges of the corresponding *Denticulopsis* species.

These morphologic resemblances and stratigraphic coincidences between *Katahiraia-Yoshidaia* and *Denticulopsis* species clearly indicate that they are different products of the same genotypes. This is also confirmed by the presence of "Janus cells", i.e. the frustules with an epivalve of *Katahiraia*-type and a hypovalve of *Denticulopsis*-type.

There may be three cases where a single

diatom genotype produces different morphotypes in its life cycle: (1) resting spores, (2) environmental modification, and (3) auxospore and initial valves. Among the three cases, the resting spores may be excluded, because most of the raphid diatoms such as *Denticulopsis* do not form resting spores (Round *et al*., 1990).

The second possibility, environmental modification, occurs where morphology is modified in response to change in various environmental factors such as temperature, salinity and silicate availability. For example, Fryxell (1991) reported that *Eucampia antarctica* produces two different seasonal morphotypes; winter and summer forms, in response to seasonal changes in oceanographic factors. If *Katahiraia* and *Yoshidaia* are such a case, they might be found fairly commonly in conjunction with the occurrence of *Denticulopsis* species. However, they are always extremely rare and hence it seems very unlikely that *Katahiraia* and *Yoshidaia* species are the environmental morphotypes of *Denticulopsis.*

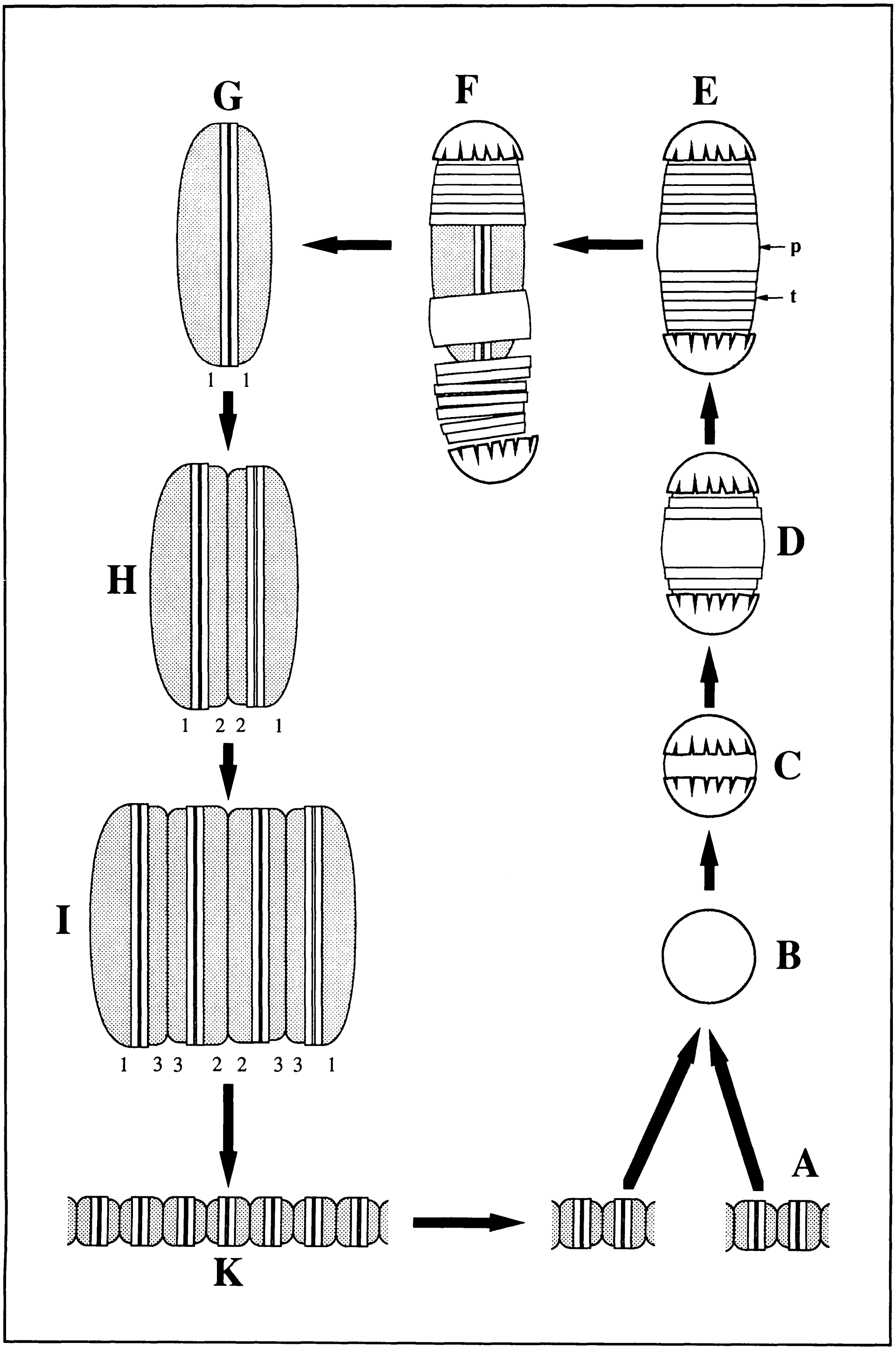
The remaining third possibility, auxospores and initial valves, seems to best agree with *Katahiraia* and *Yoshidaia,* as will be discussed in detail in the following section.

The formation of the auxospore and initial cells takes place during the life cycle of diatoms (e.g. Round *et al.,* 1990). The presumed life cycle of pennate diatoms is summarized in Figure 5. After a phase of vegetative multiplication, during which the cell size has greatly decreased, pennate diatoms undergo a meitosis and sexual reproduction to form a zygote (Figure 5, A). This is followed by auxospore formation (B) and bipolar expansion of the auxospore (C-D). As the auxospore expands, a number of transverse perizonial silica bands are deposited around the surface of the auxospore (D-E). After the expansion is completed, the cell size is restored and the first theca of new generation, namely the initial epi- and hypovalves are laid down immediately under the perizonial bands (E). As the shape of the auxospore is circular in cross section, the initial cell, which is moulded directly by the auxospore, has also a rounded cross section without distinction between the valve face and valve mantle. The perizonial bands gradually break open to reveal the initial cell (F-G). After that, the first cell division of the initial cell takes place to form two new normal vegetative hypovalves which contact each other back to back so that they have flat valve faces (H). The vegetative multiplication continues to make a long colony chain of cells (I-K).

If the auxospore and the initial cells of the fossil diatom *Denticulopsis* were formed, then they may be present in the fossil record. The perizonial bands of auxospore, however, are too delicate to remain as fossils, because they might be easily dissolved. In contrast, the initial valves, silicified as thickly as the normal vegetative valves, may be found in the fossil record although they will be very rare.

Williams (1990) pointed out that fossil initial valves will be readily recognized by their distinctive morphological modifications, in combination with their large size and shape, and he has succeeded in identifying fossil initial valve of *Tetracyclus* from nonmarine diatomaceous deposits. Mayama and Kobayashi (1991) have also recognized a fossil initial valve which is presumed to be produced by *Eunotia arcus,* applying the

⟶ **Figure 5.** Inferred life cycle of *Denticulopsis.* **A.** Sexual reproduction. **B.** Auxospore formation. **C-E.** Bipolar expansion and formation of perizonium (p: primary transverse perizonial band, t; transverse perizonial band). **F.** Detachment of perizonial bands after the initial cell formation under the auxospore casing. **G.** Initial cell composed of an initial epivalve (left) and an initial hypovalve (right). The two initial valves are noted as 1. **H.** First cell division of initial cell to form two new normal vegetative (noted as 2). **I.** Second cell division. New valves formed in this cell division are noted as 3. **K.** Chain of relatively small frustules after multiple cell divisions.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criteria used for identifying initial valves in living populations.

According to Round *et al.* (1990) and other basic studies (e.g. Geitler, 1932, 1969, 1970; Ehrlich *et al.,* 1982; Mann, 1982, 1984a, 1984b; Mann and Stickle, 1989; Mayama and Kobayashi, 1991), the initial valves are structured with a slightly modified morphology compared with the normal vegetative valves because, as they are produced beneath the auxospore wall, they are not subjected to the same constraints as the normal vegetative valves.

The modified morphologic features of the initial valves are as follows: (a) The initial valves form much more rounded morphologies than the valve shape of vegetative cells because they are moulded directly by the auxospore casing which originally has a strongly arched section. This rounded morphology is the most diagnostic feature of the initial valves in pennate diatoms (e.g. Mann, 1984b, Mayama and Kobayashi, 1991) and also in centric diatoms (e.g. Round, 1982). (b) In some raphid diatoms, the raphe of the initial valves is slightly different in location and morphology from that of the normal valves. Mann (1984b) reported that the initial epivalve of *Rhoicosphenia curvata* has much shorter and unequal raphe slits compared with vegetative valves. Mayama and Kobayashi (1991) noted a slightly shifted raphe slit of the initial valve in *Eunotia arcus.* (c) The perforation pattern of the initial valves is somewhat modified from that of the vegetative valves. Mayama and Kobayashi (1991) described slight modification of the perforation pattern on the initial valves of *Eunotia arcus.* (d) The initial valves often have a rather simple structure. (e) The initial valves are larger than any other vegetative valves because the size reduction by cell division starts from the initial cells.

These morphologic characteristics can be used as good criteria to distinguish the initial valves from the vegetative valves in both living and fossil assemblages, and they are in excellent agreement with the features of the *Katahiraia* and *Yoshidaia* species.

The rounded valve surface of *Katahiraia* and *Yoshidaia* agrees well with the most general feature of the initial valves. The central raphe of *Katahiraia* and *Yoshidaia* can be explained as one of the structural modifications of the initial valves. The raphe on normal vegetative valve of *Denticulopsis* is located along the boundary between the valve face and the valve mantle. In the case of an initial valve, however, there is no constraint on the location of the raphe because the initial valve is rounded in cross section so that the valve face and mantle can not be distinguished. This may explain partly the reasons why the raphe of the initial valve is located in the valve center.

The perforation pattern on the valve surface of *Katahiraia* and *Yoshidaia* can be also interpreted as one of modified morphology of the initial valves. Furthermore, the relatively large size of *Katahiraia* and *Yoshidaia* species well coincides with the general morphologic nature of the initial valves. The extremely rare findings of *Katahiraia* and *Yoshidaia* species are reasonably understood if these species are the initial valves.

The frustule composed of a *Katahiraia*-type epivalve and a *Denticulopsis*-type hypovalve (Figures 1-1, 1-4) can be considered to be a terminal cell of a colony chain, a heterovalvate cell consisting of an initial valve and a vegetative normal valve (Figures 5-H, 5-I)

In summary, the forms described as *Katahiraia* and *Yoshidaia* species by Komura (1976) seem best considered as the initial valves of *Denticulopsis* species on the basis of morphology and stratigraphic data. However, other possibilities can not completely be precluded, because it is impossible, as *Denticulopsis* species are all extinct, to culture them and make them produce auxospores and initial cells.

Probable normal vegetative *Denticulopsis*

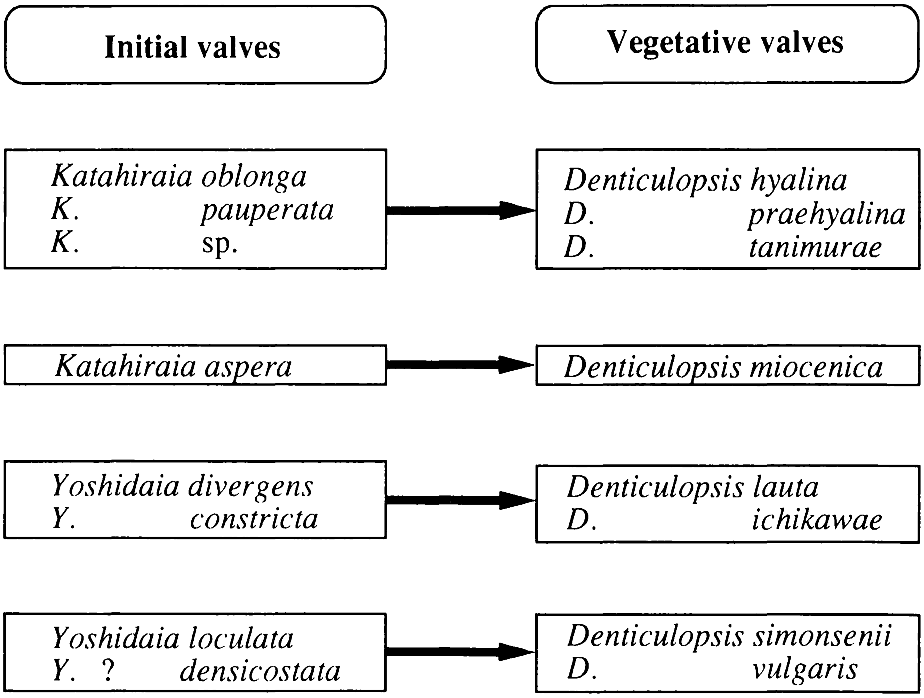

Figure 6. Relationship between the species of *Katahiraia, Yoshidaia* and *Denticulopsis.*

species corresponding to *Katahiraia* and *Yoshidaia* species are listed in Figure 6.

Katahiraia oblonga, K. pauperata or *Katahiraia* sp. may be the initial valve of *Denticulopsis hyalina, D. praehyalina* or *D. tanimurae,* because all of them share the same morphologic features as well as nearly the same stratigraphic ranges. Similarly, *K. aspera* must be the initial valve of *D. miocenica. Yoshidaia divergens* or *Y. constricta* may be the initial valve of *Denticulopsis lauta* or *D. ichikawae.* They are all characterized by linear valve outline, single-layered perforation and the absence of secondary pseudosepta. *Yoshidaia loculata* or probably *Y.* ? *densicostata* may be the initial valve of *Denticulopsis simonsenii* or *D. vulgaris.*

In this study, I determined the initial valves corresponding to the eight *Denticulopsis* species listed in Figure 6, but those of the other *Denticulopsis* species including *D. praedimorpha, D. dimorpha, D. ovata, D. praekatayamae* and *D. katayamae* have not been encountered. This is probably due to extremely rare occurrence of the initial valves, and if so, they will be found through further thorough examination.

Since it is strongly suggested that the genera *Katahiraia* and *Yoshidaia* are the initial valves of *Denticulopsis,* the three genera should be taxonomically united to a single genus. The generic erection of the genus *Katahiraia* Komura (1976) predates *Yoshidaia* by Komura (1976) and *Denticulopsis* by Simonsen (1979), and therefore the epithet *Katahiraia* has priority under ICBN (Greuter *et al*., 1988). Thus, all *Denticulopsis* species should be transferred to the genus *Katahiraia,* but it is impossible to do this at present, because a one-to-one correspondence between *Denticulopsis* and *Katahiraia-Yoshidaia* species is unknown at the present except for the relationship between *K. aspera* and *D. miocenica* (Figure 6). For example, we are now aware that *K. oblonga* is probably the initial valve of either *D. hyalina, D. praehyalina* or *D. tanimurae.* However, we cannot determine which species is the vegetative valve of *K. oblonga* because the initial valves of the three *Denticulopsis* species are presumed to have the same morphology. Detailed investigation of the type materials of *Katahiraia* and *Yoshidaia* species is required for the establishment of a one-to-one correspondence between these species, but I have not yet examined these materials. In this paper, therefore, the generic name *Denticulopsis* Simonsen is tentatively retained.

Conclusion

A combination of morphologic observation and stratigraphic study of the Miocene fossil diatom genera *Katahiraia* Komura and *Yoshidaia* Komura strongly suggests that they are the initial valves of the genus *Denticulopsis* Simonsen. These forms possess nearly the same morphology and stratigraphic ranges as the corresponding normal vegetative valves of *Denticulopsis,* but they differ in having the rounded valve face and the central raphe.

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Joban 常磐, Kushiro 釧路, Shimokita 下北, Isohara 磯原, Chokubetsu 直別, Gamanosawa 蒲野沢.

中新世絶滅珪藻 *Denticulopsis* 属の初生蓋殻: *Katahiraia* 属および *Yoshidaia* 属として記載された中新世の珪藻化石について，形態学的及び層序学的な研究を行った．その結果，これらは，*Denticulopsis* 属の初生蓋殻である可能性が高いことがわかった．この2つの属は，*Denticulopsis* 属に形態が非常によく似ているが，蓋殻表面が丸みを帯びていること，縦溝が蓋殻の中央にあることによって，*Denticulopsis* 属とは区別される．こうした特徴は，珪藻類の初生蓋殻に見られる一般的な特徴によく合致する．また，*Katahiraia* 属および *Yoshidaia* 属の種の層序学的産出範囲は，対応する *Denticulopsis* 属の種のそれとよく一致する．

柳沢幸夫

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965. LOBED OAK LEAVES FROM THE TERTIARY OF EAST ASIA WITH REFERENCE TO THE OAK PHYTOGEOGRAPHY OF THE NORTHERN HEMISPHERE*

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Abstract. The reinvestigation of floristic components together with recent radiometric dating of the fossil-bearing deposits reveals that the "Miocene" floras including lobed oaks in East Asia (Japan, North Korea and Primorye) are Oligocene in age. These Oligocene floras consist mainly of temperate deciduous broad-leaved trees and conifers; they are characterized by commonly containing lobed and serrate/dentate oak leaves. Four fossil species of lobed oaks are confirmed from the Oligocene of East Asia: *Quercus kobatakei* Tanai and Yokoyama, *Q. kodairae* Huzioka, *Q. sichotensis* Ablaev and Gorovoi and *Q. ussuriensis* Kryshtofovich, all of which belong to the subgenus *Quercus*. *Quercus ussuriensis* belongs to the section Cerris, and is more closely similar to extant European or West Asian species than to those of East Asia. The remaining three species belong to the sections Prinus or Quercus, and they are similar to some extant species of North American Prinus or European/West Asian Quercus. A brief survey of the fossil lobed oak record in the Northern Hemisphere suggests that the phylad of Cerris originated in East Asia and eastern Kazakhstan during the Oligocene, and that it dispersed to West Asia and Europe, but never to the New World. Tertiary phytogeographic history of the sections Prinus and Quercus is conjectural, because these two sections are now difficult to distinguish only by leaf characters.

Key words. *Quercus*, Fagaceae, Tertiary, phytogeography, evolution, East Asia.

Introduction

Fossil oaks have been commonly known from the Tertiary of East Asia; they are especially abundant from the Neogene as well as in other regions of the Northern Hemisphere. Most Neogene oaks, including both the deciduous and evergreen, show close resemblance to the extant species of East Asia even in gross leaf characters, although some species hitherto described need to be reinvestigated in their modern relationships. On the one hand, Paleogene oaks, especially of pre-Oligocene time, are the most difficult to relegate confidently to particular species group of extant oaks.

The deeply lobed oak leaves from the "Miocene" formations of both Japan (Tanai and Yokoyama, 1975) and southern Primorye (Ablaev and Gorovoi, 1974; Ablaev *et al.*, 1976) provided new evidence of the Tertiary history of the deciduous broad-leaved forests of East Asia, because oaks having deeply

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lobed leaves are not native today to East Asia. Prior to these discoveries, several lobed oak species, although not as deeply incised, have been reported from the "Miocene" formations of southern Primorye (Kryshtofovich, 1937) and northeastern Korea (Huzioka, 1954, 1972). These species have remained uncertain in their modern relationships.

Many species of well-preserved oak leaves were found from the Oligocene Wakamatsuzawa flora of northeastern Hokkaido, Japan (Uemura and Tanai, 1981 ; Tanai and Uemura, 1983). Among these oaks is a most common species that has a peculiar foliar shape with dentate trigonal lobe ; it is referable to a species, *Quercus ussuriensis*, of North Korea and southern Primorye. Thus, lobed oak species are characteristic of Oligocene or "Miocene" floras of Northeast Asia.

It is the principal purpose of this paper to reinvestigate all the fossil lobed oak species of East Asia and the ages of the fossil-bearing formations, and further to discuss the phytogeographic significance of these oaks.

Fossil record of lobed oak leaves in East Asia

Lobed oak leaves have been described or only illustrated from the Tertiary of Japan, North Korea and Primorye by many authors, whereas no fossil record is yet known from Sakhalin and China (Fig. 1). These fossils are represented by various foliar shapes, and they have been sometimes confused in taxonomy as in the case of modern oak leaves.

Primorye

The brown-coal-bearing formations, called the Usty-Davydovkaya series of Middle Miocene time (Nalivkin, 1973), are widely distributed in southern Primorye and yield many temperate conifers and broad-leaved fossils including lobed oaks. *Quercus ussuriensis* represented by a peculiar leaf with trigonal lobes was first described from Kraskino (old name : Novokievsk) along the Posiet Inlet (Kryshtofovich, 1937), and was later known from the "Oligocene" deposits in Rechnol near Vladivostok (Klimova, 1971). From Kraskino were further added two species of lobed oaks, *Q. sichotensis* and *Q. kodairae* by Ablaev (1978) and Ablaev *et al.* (1993).

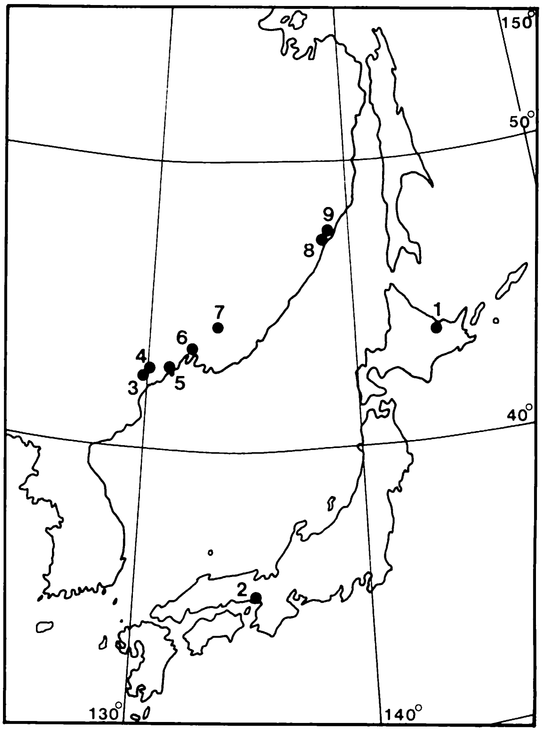

Figure 1. Fossil localities of lobed oak leaves in East Asia. 1. Wakamatsuzawa and Minamigaoka, Kitami City, Hokkaido, 2. Kobe City, Hyogo Prefecture, 3. Kungshim, Hamg'yeong-bukudo, 4. Kogeonweon, Hamg'yeong-bukudo, 5. Kraskino, South Primorye, 6. Rechnoi, South Primorye, 7. Rettikhovka, South Primorye, 8. Sonbe, Sikhote-Alin, 9. Dembi, Sikhote-Alin.

The Miocene or Oligocene plant-bearing deposits that include *Engelhardia* fruits are distributed in several small basins in the coastal region east of the Sikhote-Alin range. Some of these floras contain some lobed oak leaves ; for instance, *Quercus ussuriensis* or *Q. kodairae* are known from Dembi and

Sonbe, situated on the opposite coast of South Sakhalin (Akhmetyev and Bratzeva, 1973; Akhmetyev in Takhtajan, *ed*., 1982).

Lobed oak leaves are known from the brown-coal-bearing deposits, called the "Late Miocene" Khasanskaya Formation (Ablaev, 1978), in the Rettikhovka depression southwest of the Sikhote-Alin range; two species, *Q. sichotensis* and *Quescus* sp., were first described from here (Ablaev and Gorovoi, 1974). Furthermore, to them were added several species: *Q. arsenjevii* and *Q. kodairae* (Ablaev, 1978), *Q. pseudolyrata* (Klimova, 1976) and *Quercus* sp. (Alekseenko and Krassilov, 1980).

All these floras containing lobed oak leaves are similar in floristic composition and components: they are composed mainly of temperate trees such as Pinaceae, Taxodiaceae, Juglandaceae, Betulaceae, Fagaceae and Aceraceae. However, these floras have been controversial in geological age: some authors (Ablaev and Gorovoi, 1974; Ablaev, 1978) considered the floras to be of middle to Late Miocene age, while other authors (Klimova, 1971; Akhmetyev and Bratzeva, 1973) asserted the floras to be of Oligocene age.

North Korea

Tertiary coal-bearing deposits that include abundant plant fossils are well developed in the Kyeongweon district of the northeastern end of North Korea; especially, the Kogeonweon flora from the Upper coal-bearing formation (the so-called *Engelhardia* bed) is composed commonly of temperate plants such as Pinaceae, Taxodiaceae, Betulaceae, Fagaceae and Aceraceae (Huzioka, 1972). Of the Fagaceae, *Quercus endoana* and *Q. kodairae* having shallowly or deeply lobed leaves were described (Huzioka, 1954, 1972). Recently, Ablaev *et al*. (1993) reported three lobed oaks, *Q. endoana*, *Q. kodairae* and *Q. sichotensis* from the *Engelhardia* beds of Kyeongweon.

The Kungshim flora, which includes *Q. kodairae*, is known in the Heoryeong coal field south of Kyeongweon district; it is quite similar to the Kogeonweon flora in composition and components (Huzioka, 1972). These two floras, the Kogeonweon and Kungshim, have been generally accepted to be early Middle Miocene in age by most authors (Endo, 1938; Huzioka, 1952, 1972; Tanai, 1961), although suggested to be of Oligocene age by Oishi (1936).

Kamchatka

A single fragmentary leaf was described as *Quercus* sp. cf. *pseudolyrata* from a Miocene flora in the middle course of the River Levaya Pirozhnokovaya, western Kamchatka (Chelebaeva, 1968). It is, however, too fragmentary to determine definitely whether or not this fossil represents a lobed oak leaf.

Japan

A fossil oak with a deeply lobed leaf in Japan was first reported from the "Miocene" Kobe Group of western Honshu by Shikama (1938) and later by Kobatake (1961), although these fossils were only illustrated with no valid description. These "Miocene" lobed oak leaves were described as *Quercus kobatakei* by Tanai and Yokoyama (1975), based on many specimens which were collected in Kobe City. This oak species is one of the common members of the Kobe flora, and two further species of lobed oaks, *Q. kodairae* and *Q. endoana*, were recently added in the flora (Hori, 1987). The Kobe flora has been accepted to be early Middle Miocene in age by many authors (e.g., Shikama, 1938; Kobatake, 1961; Tanai, 1961), because most of the components were referred to those of the Daijima-type flora which is late Early to early Middle Miocene in age. However, the radiometric dating of the Kobe Group was recently done by some authors, although the measured values were somewhat scattered: the upper part of the Group was dated as 31.4±1.9 Ma (Matsuo, 1988) or as 32.8±2.1 to 36.9±0.8 (Ozaki and Matsuura, 1987), while the lower part of the Group was dated as 33.3±2.6 Ma (Ozaki and Matsuura, 1988).

The Oligocene Wakamatsuzawa flora including *Engelhardia* (*Palaeocarya*) fruits was reported from Kitami, northeastern Hokkaido (Uemura and Tanai, 1981). It is composed principally of temperate plants such as Pinaceae, Taxodiaceae, Juglandaceae, Betulaceae and Fagaceae; of the Fagaceae species, a peculiar oak, *Quercus ussuriensis*, is most abundant in number of specimens and allows a discussion of the variation of leaf characters. A fragmentary leaf probably referable to *Q. sichotensis* is also included in this flora.

Age discussion

All the floras of Primorye, North Korea and northeastern Hokkaido including the above-noted lobed oak species, are closely similar in composition and components. The characteristic trees are temperate plants such as Pinaceae (*Abies, Keteleeria, Picea, Pseudolarix*), Taxodiaceae (*Metasequoia, Sciadopitys*), Juglandaceae (*Cyclocarya, Pterocarya*), Betulaceae (*Alnus, Betula, Carpinus*), Fagaceae (*Castanea, Fagus, Quercus*), Hamamelidaceae (*Hamamelis*) and Aceraceae (*Acer*), although including some warmer plants such as *Glyptostrobus*, *Engelhardia* and *Liquidambar*. Most of these temperate trees, especially dicots, are closely related to Early Miocene species and were typically referred to Miocene species hitherto by some authors (e.g., Huzioka, 1972; Ablaev, 1978). A cautious taxonomic investigation of North Korean fossils revealed that some species of the Betulaceae and Fagaceae are distinguishable from those of Early Miocene floras (Huzioka, 1954, 1972). For instance, distinguished from *Fagus antipofi*, which is common in Early Miocene floras of East Asia, are two beech species, *F. protolongipetiolata* and *F. koraica*, which were described from the Kogeonweon and Kungshim floras (Huzioka, 1972). *Fagus protolongipetiolata* was also described from Rettikhovka (Ablaev, 1987). Beech leaves closely similar to the two above-noted Korean species are found in the Oligocene Wakamatsuzawa flora of Hokkaido.

The floristic resemblance to Miocene floras led the floras of Primorye and North Korea that include lobed oaks to be dated as Middle Miocene (Huzioka, 1972) or as even Late Miocene in age (Ablaev, 1978). In fact, these floras from Primorye, North Korea and northeastern Hokkaido are generally similar in composition to the Early Miocene (the Aniai-type) and the late Early Miocene (the Daijima-type) floras of Japan. They are, however, different from the Aniai-type flora in having many species of oaks and some evergreen trees such as *Quercus* (*Cyclobalanopsis*) and *Ilex*, and also from the Daijima-type flora in having no species of Lauraceae and Theaceae. Furthermore, a marked difference is that they contain *Engelhardia*, *Platanus* and *Craigia* (Tiliaceae), which are unknown in Miocene floras of East Asia with one exception. *Platanus* is commonly found in the Paleogene of East Asia, but some Neogene records (Suzuki, K., 1958; Tanai and Suzuki, N., 1963) are invalid. Fruits of *Craigia*, which was recently transferred from *Pteleaecarpum* (Kvaček *et al.*, 1991), is usually found in the Eocene of North China, Hokkaido and Kamchatka (Bůžek *et al.*, 1989; Tanai, MS), with an exception of the Late Miocene occurrence at Botchi, Sikhote-Alin (Bůžek *et al.*, 1989). As discussed in the case of *Engelhardia*-bearing floras of East Asia (Tanai and Uemura, 1983), the Kraskino, Rettikhovka, Kogeonweon, Kungshim and Wakamatsuzawa floras represent the Oligocene vegetation of East Asia.

The Futamata andesite lava coeval to the Wakamatsuzawa Formation was dated as 31.44±1.0 Ma (K/Ar dating) (Shibata and Tanai, 1982). Dacite just above the plant-bearing beds of Dembi, Sikhote-Alin is 34 Ma in radiometric age (Akhmetyev and Bratzeva, 1973). The Dembi flora is closely similar to the Kraskino and Rettikhovka floras of southern Primorye in composition and components; these three floras are considered to be coeval. *Quercus ussuriensis*, though unillustrated, is also known in the Dembi flora (Akhmetyev and Bratzeva, 1973). Taking account of the floristic characteristics together with radiometric dating, the lobed oak leaf-bearing floras of southern Primorye (Rettikhovka and Kraskino), North Korea (Kogeonweon and Kungshim) and Hokkaido (Wakamatsuzawa) are Early Oligocene in age.

Differing from the above-noted five floras that are composed mostly of temperate plants, the Kobe flora of western Honshu indicates typically a warmer aspect; it comprises a mixture of temperate and warm-temperate trees such as Pinaceae, Taxodiaceae, Juglandaceae, Betulaceae, Fagaceae, Ulmaceae, Hamamelidaceae, Lauraceae, Menispermaceae, Rosaceae, Leguminosae, Aceraceae, Sapindaceae, Theaceae, Rhamnaceae, Cornaceae, Nyssaceae and Oleaceae, associated with palms (Kobatake, 1961; Hori, 1976, 1987). Most of these plants, hitherto referred mostly to Miocene species, are more similar to those of Early Miocene floras than to those of Late Eocene floras of North Kyushu and Hokkaido. Accordingly, the Kobe flora is younger than Late Eocene in age, although Ozaki (1992) asserted it to be of Late Eocene age only on the basis of radiometric dating of the plant-bearing formations. The Kobe flora is generally similar to the late Early Miocene Daijima-type flora in composition and components, but it contains many exotic plants which have been unknown in the Daijima-type floras. A further detailed taxonomic investigation may separate the temperate taxa of the Kobe flora from Miocene species; for instance, of many beech leaves referred to *Fagus stuxbergi* (Hori, 1987), some are distinct from this Late Miocene species in having a long petiole and long stalked cupula, and the species seems to be close to *F. protolongipetiolata* of North Korea. Furthermore, noteworthy for the Kobe flora is common *MacClintockia*; this extinct genus has been reported from the Paleocene to the Lower Oligocene of East Asia, Greenland and western North America. Thus, considering the floristic components together with radiometric dating, the Kobe flora may be early Early Oligocene in age (Tanai, 1992).

From the above discussion it is concluded that some fossil lobed oak leaves in East Asia are characteristic of Oligocene floras: several oak species with deeply lobed leaves are common in the Oligocene floras of Primorye, North Korea and Japan. The Rettikhovka and Kraskino floras of Primorye, the Kogeonweon and Kungshim floras of North Korea and the Wakamatsuzawa flora of Hokkaido are probably contemporaneous in age, and may represent the temperate vegetation during Early Oligocene time. On the one hand, the Kobe flora of western Honshu shows a warmer phase of Early Oligocene vegetation, and it may be somewhat older than the above-noted five floras in age.

Systematic discussion

Leaves of the extant oaks range from entire to toothed or lobed in margin, craspedodromous to camptodromous, or sometimes mixed craspedodromous in secondary vein termination, and coriaceous to chartaceous in texture. We cannot avoid confronting the following difficulties when fossil oak leaves are discussed in their modern relationships.

First, the leaf shape and marginal features, especially in lobed form, are frequently variable within a species. Such foliar variation and intergradation of leaf shape are further accentuated by natural interspecific hybridization (e.g., Muller, 1952; Palmer, 1948; Jensen and Eshbaugh, 1976), although natural hybridization between different subgenera has not been authenticated (Tucker, 1974). Second, there are many examples of parallel and convergent evolution of leaf forms between the species of different subgenera or sections (e.g., Tucker, 1974). To avoid misinterpretation of modern relationships, it is necessary to compare the fossil materials with the extant leaves at the level of detailed leaf architecture including fine venation. The cleared leaves of about 250 extant oak species from the world are now being investigated by the senior author (T.T.); the set of gross features (especially margin), fimbrial vein, areolation and ultimate veinlets may provide a useful key to dscriminate the subgenera or sections (Tanai, 1986, 1988).

Furthermore, we have another problem in that infrageneric taxonomy of *Quercus* has not yet been fully established as applicable in its entirety, including Central American oaks. Comprehensive work was done for all world species by Camus (1936-1954) and for all American species by Trelease (1924), but their classification systems are now controversial. They divided the genus into too many subsections (more than 100 by Camus) or series (about 100 by Trelease); however, these subdivisions are uncertain to represent natural groups in the subgenera or sections proposed (Elias, 1971).

Our infrageneric treatment here discussed for fossil oaks followed those of Rehder (1940), Elias (1971) and Krüssmann (1986): three subgenera, *Cyclobalanopsis*, *Erythrobalanus* and *Quercus* (*Lepidobalanus*) are recognized. The subgenus *Erythrobalanus* is subdivided into four sections of Phellos, Nigrae, Rubrae and Stenocarpae, and the subgenus *Quercus* into six sections of Cerris, Suber, Ilex, Gallifera, Quercus and Prinus. If the intermediate characters between *Erythrobalanus* and *Quercus* are emphasized, some species of Stenocarpae are treated as the subgenus *Protobalanus* (Trelease, 1924).

Cyclobalanopsis is easily separable from other subgenera in cupules with the scales connated into concentric rings, while the other subgenera are characterized by having cupules with imbricate scales (appressed or spreading). All the extant leaves of the subgenera *Erythrobalanus*, *Quercus* and *Protobalanus* have usually a thick fimbrial vein on the margin, which is lacking in *Cyclobalanopsis* (Tanai, 1986, 1988).

Class Magnoliopsida
Order Fagales
Family Fagaceae
Genus *Quercus* L.

Quercus kobatakei Tanai and Yokoyama

Figures 2-1, 4-1, 2

Quercus kobatakei Tanai and Yokoyama, 1975, p. 131, pl. 1, figs. 1, 3, pl. 2, fig. 2; Hori, 1987 (part), pl. 60, figs, 1-3, 5, pl. 61, figs. 1-6, 8.

Quercus japonoalba Kobatake, nom, nud., 1961, p. 85, pl. 3, fig. 21; Hori, 1976, p. 103, pl. 14, fig. 56, Ph-pl, 7, fig. 2.

Quercus pseudolyrata auct. non Lesq., Klimova, 1976, fig. 1-a.

? *Quercus sichotensis* auct. non Ablaev and Gorovoi, Ablaev *et al.*, 1993. p. 71, pl. 4, figs, 1, 7, pl. 14, fig. 3.

Type.—Holotype HUMP no. 25969, paratype no. 25970; Ochiai, Suma-ku, Kobe City, Japan; Shirakawa Formation (Early Oligocene).

Discussion.—This species is characterized by the following features: the deeply lobed leaves with 3 to 6 pairs of lanceolate to triangular lobes; the upper pairs of lobes are the larger and more divergent; each lobe is mostly entire on the margin, but is rarely undulate on the basal side; lobe apex is acute, having sometimes a projecting tip (but not aristate) in which the secondary vein ends; the sinus is usually broadly opened with rounded bottom; thick fimbrial vein is of third order in thickness. The ultimate veinlets were mistaken as more than twice branching because of ill-preserved specimens (Tanai and Yokoyama, 1975), but the additional well-preserved specimens from Kobe indicate that the veinlets are mostly single to once branching, and rarely lacking in large areoles (about 0.8 to 1 mm across) (Fig. 2-1).

Quercus kobatakei resembles *Q. sichotensis* of Primorye in general appearance, as includ-

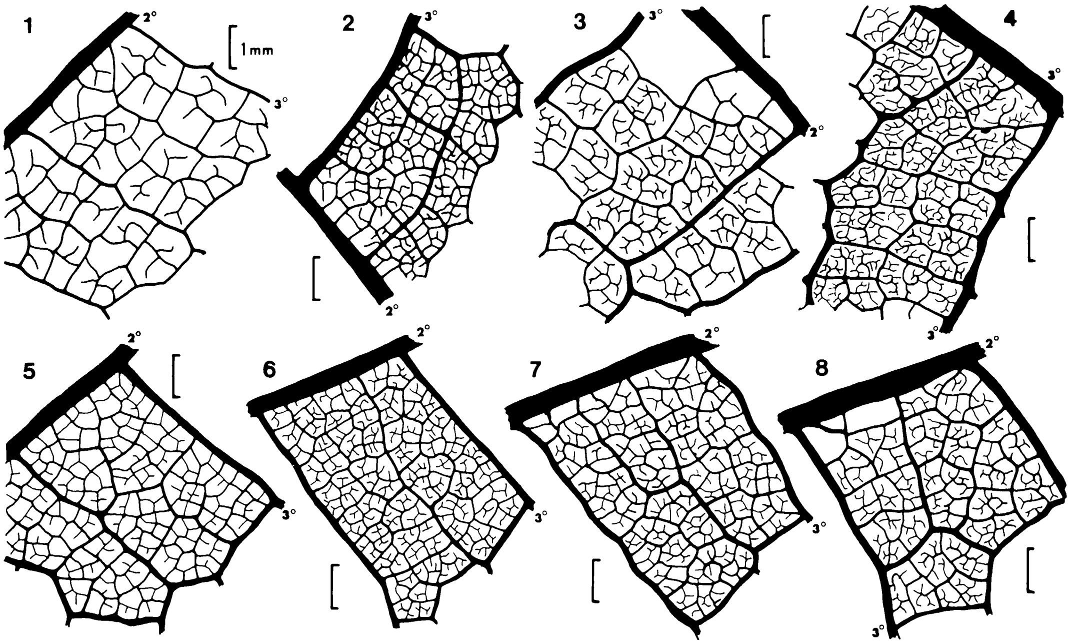

Figure 2. The detailed venation features of some lobed oak fossils and the related extant oaks. Except as otherwise indicated, line for scale in each figure represents 0.5 mm. 2° and 3° in each figure indicate the secondary and tertiary veins, respectively. 1. *Quercus kobatakei* Tanai and Yokoyama (Fig. 4-1), 2. *Quercus kodairae* Huzioka (Fig. 4-5), 3. *Quercus ussuriensis* Kryshtofovich (Fig. 5-4), 4. *Quercus macrolepis* Kotschy (NSM Paleobot. Ref. Coll. no. T-2399), 5. *Quercus lyrata* Walt. (NSM Paleobot. Ref. Coll. no. T-114), 6. *Quercus alba* L. (NSM Paleobot. Ref. Coll. no. T-113), 7. *Quercus petraea* (Mattus.) Liebm. (NSM Paleobot. Ref. Coll. no. T-1872), 8. *Quercus macranthera* Fisch. and Mey. (NSM Paleobot. Ref. Coll. no. T-1873)

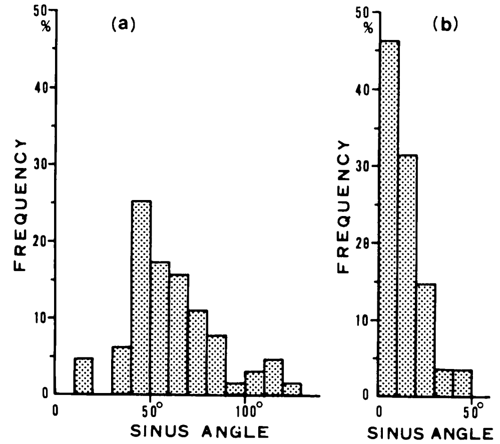

Figure 3. The frequency of the opening angles of lobe sinus in leaves of (a) *Quercus kobatakei* (63 sinuses of 14 specimens and (b) *Quercus sichotensis* (54 sinuses of 9 specimens).

ed in the latter by Ablaev (in Takhtajan, *ed*., 1982). However, *Q. kobatakei* is distinguished from the Primorye species in having a more broadly opened sinus with rounded bottom ; for instance, the opening angles of the sinus are largely between 30° and 80° in *Q. kobatakei* (Fig. 3a), while they are mostly less than 30° in *Q. sichotensis* (Fig. 3b). Two incomplete specimens of *Q. sichotensis* described from Kraskino and Kogeonweon (Ablaev *et al*., 1993) are probably referred to *Q. kobatakei* in having wider angles of sinus. A single leaf, illustrated as *Q. pseudolyrata* from Rettikhovka (Klimova, 1976), does not belong to the black oak group because of the lack of a bristle-tip in the lobe apex, and is included in *Q. kobatakei*.

As discussed by Tanai and Yokoyama (1975), *Q. kobatakei* is closely similar to some extant species of the section Prinus such as *Q. alba* L. and *Q. lyrata* Walt. of eastern North America in having deep lobation with lanceolate lobes, especially close to the latter in widely opening angles of sinus. On the one hand, *Q. kobatakei*, is rather similar in the veinlet feature to *Q. alba* than to *Q. lyrata*: the veinlets of *Q. alba* are single to once (rarely twice) branching, while those of *Q. lyrata* are single or lacking. The fossil leaves are, however, different from the North American species in having a usually pointed lobe-tip and more than thrice larger areoles. Leaves of the extant *Q. garryana* Dougl. and *Q. gambelii* Nutt. of the western United States and adjacent northern Mexico also resemble *Q. kobatakei* in general shape, but these extant species are distinguishable from the fossil in having more than twice branching veinlets with a dendroid pattern.

Quercus kobatakei is also similar to some extant species of the section Quercus such as *Q. pyrenaica* Willd. and *Q. frainetto* Tenn. of southern Europe in having many lanceolate and deeply dissected lobes, although these European species are different in having a rounded apex and usually no or a single veinlet. Most extant species of the East Asian and eastern North American Prinus are typically lacking or single (rarely once branching) in veinlets, and the lobed species of the section Prinus are indistinguishable from those of the section Quercus only by foliar characters. Accordingly, it is now difficult to determine that *Q. kobatakei* belongs to either section.

Occurrence.—Kobe, western Honshu; Rettikhovka, Primorye.

Collection.—Holotype HUMP no. 25969, paratype no. 25970; Mus. PTGU no. 5.

Quercus kodairae Huzioka

Figures 2-2, 4-3—5

Quercus kodairae Huzioka, 1954 (part), p. 196, pl. 25, figs. 8-10, not fig. 7, 11; Huzioka, 1972, p. 53, pl. 5, fig. 5; Ablaev, 1978, pl. 15, fig. 4, pl. 17, fig. 5; Akhmetyev (in Takhtajan, *ed.*), 1982, p. 107, pl. 71, figs. 1-7; Ablaev *et al.*, 1993 (part), p. 74, pl. 4, pl. 16, fig. 2.

Type.—Lectotype AKMG 6674-(8); Kogeonweon, Yongpukudong, North Korea; the "coal-bearing *Engelhardia* beds" (Early Oligocene).

Supplementary Description.—Leaves wide oblong to wide elliptic in general outline, 4.3 to 15.5 (estimated) cm long and 3.2 to 10.0 cm wide, length/width ratio varying from 1.34 to 1.92; apex acute to slightly acuminate; base acute, rarely obtuse; margin dentate with large lobe-like teeth; teeth one per secondary vein, lanceolate to narrow ovate with acute tip (A1), separated by trigonal sinus; petiole thick, 5 mm long in small leaf, but mostly incomplete. Venation pinnate; midvein thick basally, but becoming markedly thinner apically, sometimes flexuous on apical part; secondary veins 6 to 9 pairs, opposite to subopposite, regularly spaced, diverging at angles of 40° to 50°, but at smaller angles on apical part, nearly straight but sometimes curving basally near margin, entering teeth centrally; intercostal tertiary veins thin, convex percurrent, 5 or 6 per 1 cm; marginal tertiary veins forming loops within lobed teeth; quaternary veins forming four-sided and irregularly sized mesh; the higher order venation thin, indistinct; fimbrial vein distinctly present.

Discussion.—This species was first established by Huzioka (1954) on the basis of 4 leaves from Kogeonweon, North Korea, in-

→ **Figure 4.** (All figures in natural size). **1, 2.** *Quercus kobatakei* Tanai and Yokoyama, 1: Y. Matsuo's collection (Kobe Educ. Center), loc. Husehata, Kobe City, 2: Holotype HUMP 25969, loc. Ochiai, Kobe City. **3-5.** *Quercus kodairae* Huzioka, 3: Holotype AKMG 6674-(8), loc. Kogeonweon, North Korea, 4: IGPS 92333, loc. Kogeonweon, North Korea. 5: Y. Matsuo's collection (Kobe Educ. Center), loc. Kizu, Kobe City. **6.** *Quercus sichotensis* Ablaev and Gorovoi, NSM-PP 16356, loc. Okuhata, Kobe City (collected by H. Matsuo).

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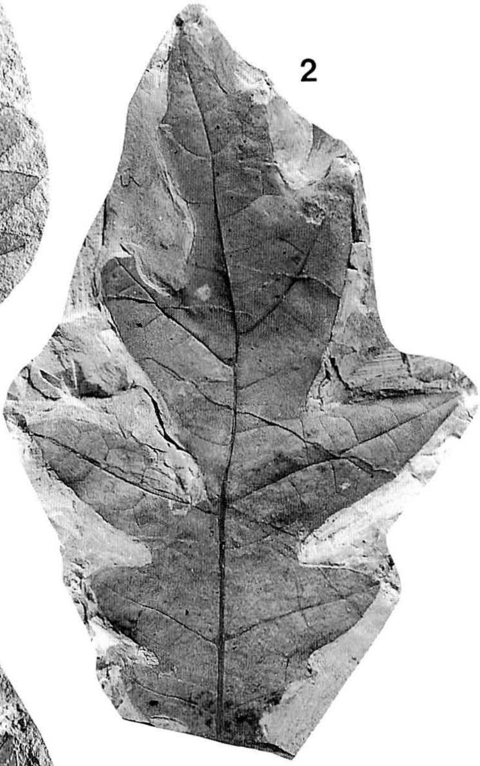

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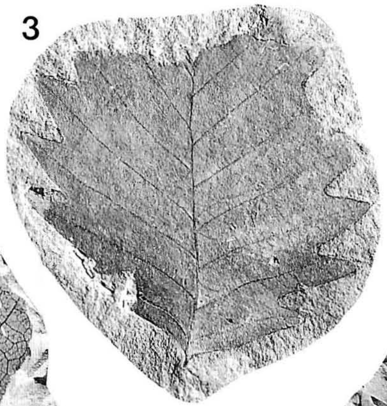

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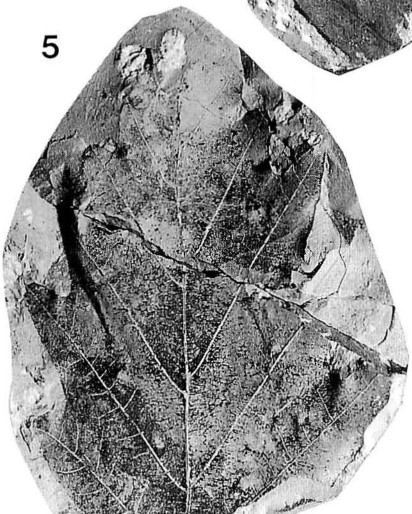

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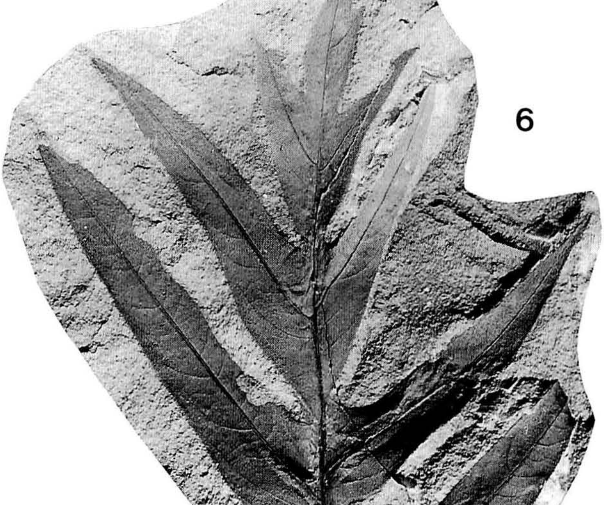

cluding a leaf of a different type that was later transferred to another species, *Q. endoana* Huzioka (Huzioka, 1972). *Quercus kodairae* is known from several localities of Primorye (Ablaev, 1978; Akhmetyev in Takhtajan, *ed*., 1982). Several leaves referable to *Q. kodairae* are also comfirmed in H. Matsuo's collection from Kobe, although a specimen illustrated as this species by Hori (1987) seems not to be *Quercus*. Thus, *Q. kodairae* is one of the characteristic plants in the Oligocene of East Asia.

The dentate margin with large, lobe-like teeth that are acutely tipped and one per secondary vein, marginal tertiary veins forming a series of brochidodromous loops within the teeth and a distinct fimbrial vein indicate that *Q. kodairae* is related to some extant species of the section Prinus and Quercus. The higher-order venation is not preserved in North Korean specimens described by Huzioka (1972), but a specimen from Kobe indicates that the ultimate veinlets are mostly none to single, sometimes once branching in small areoles (0.18 to 0.25 mm across) (Fig. 2-2). Such veinlet features are characteristic of most extant species of the sections Quercus and Prinus.

Among the extant species *Q. petraea* (Mattus.) Liebm. of the section Quercus closely resembles *Q. kodairae* in having regularly spaced secondary veins of less than 9 pairs, narrow ovate lobe-like teeth and convex-percurrent tertiary veins, but this West Asian species is different in the rounded tip of the lobe. The extant *Q. macranthera* Fisch. and Mey. of the section Quercus, living in Caucasas and Armenia, is also similar superficially to *Q. kodairae*, but leaves of this extant species have usually more secondary veins and single to once branching veinlets.

The acutely pointed tip of the lobes in *Q. kodairae* is rather unusual in leaves of the section Quercus and Prinus as in the above-described *Q. kobatakei*. No extant species of the section Prinus is comparable to *Q. kodairae* in leaf shape, marginal lobation and venation features, but it may be noteworthy that some species such as *Q. serrata* Thunb. of Japan and *Q. muehlenbergi* Englem. of eastern North America are acutely pointed in the lobe apex. The comparison of superficial features suggests that *Q. kodairae* may be more related to the section Quercus than to the section Prinus, although the taxonomic relationship should be considered tentative until these two sections can be divided by leaf characters.

Occurrence.—Kogeonweon and Kungshim, Hamg'yeong-Bukudo, North Korea; Sonbe, Dembi, Rettikhovka and Shakterski, Primorye; Kobe, western Honshu.

Collection.—Lectotype AKMG 6674-(8); AKMG 6674-(9), -(10); IGPS 92332, 92333 (not 92334); GIN 318, 3807; DVGI 655.

Quercus sichotensis Ablaev and Gorovoi

Figures 4-6, 5-5

Quercus sichotensis Ablaev and Gorovoi, 1974, p. 167, fig. 2; Ablaev, Vassiliev and Gorovoi, 1976, pl. 1, figs. 1-6; Ablaev, 1978, pl. 20, fig. 1; Ablaev in Takhtajan, 1982, p. 100, pl. 65, figs. 2-7.
Quercus kobatakei auct. non Tanai and Yokoyama, Hori, 1987 (part), pl. 60, figs. 4, 6-8.
Quercus sp., Alekseenko and Krassilov, 1980, p. 120, fig. 1a, b.
Quercus sp. (A), Hori, 1987, pl. 62, fig. 3; pl. 68, fig. 3.

Type.—Holotype DVGI 650/36; Rettikhovka, Primorye; the "coal-bearing Formation" (Oligocene).

Discussion.—The oblong lobes of 4 to 6 pairs, deeply indented sinus with narrow opening angles (Fig. 3b) whose bottom fre-

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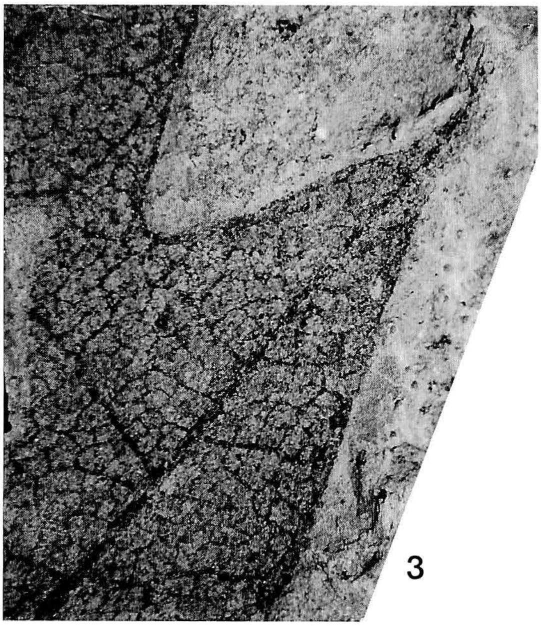
→ **Figure 5.** (All figures in natural size unless otherwise stated). **1-4.** *Quercus ussuriensis* Kryshtofovich, 1: NSM-PP 16336, loc. Wakamatsuzawa, Kitami City, 2: NSM-PP 16355, loc. Minamigaoka, Kitami City, 3: Enlargement of Fig. 5-2, showing attenuate tooth, ×14, 4: NSM-PP 16345, showing basal part of blade, loc. Minamigaoka, Kitami City. **5.** *Quercus sichotensis* Ablaev and Gorovoi, NSM-PP 16357, loc. Okuhata, Kobe City (collected by H. Matsuo).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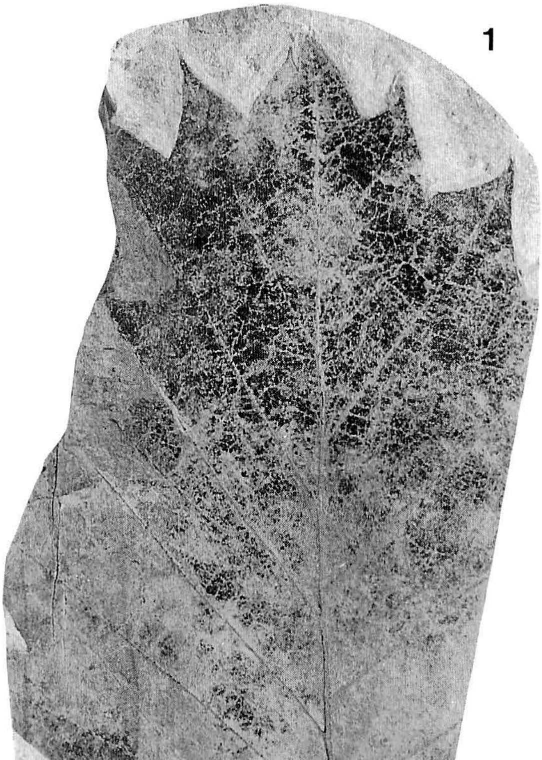
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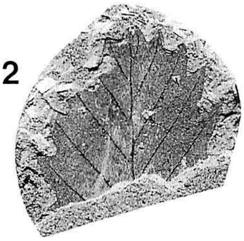
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quently reaches near the midvein, and subsidiary teeth existing on both apical and basal sides of lobe are characteristic features of *Q. sichotensis.* The intersecondary veins parallel to the secondary vein run along the lobe margin or bifurcate near the sinus bottom to embrace the sinus. The leaf base is mostly acute to obtuse, and is sometimes cordate with a pair of basally spreading lobes. These features distinguish *Q. sichotensis* from *Q. kobatakei*, although these two oaks are generally similar to each other, especially in number of lobes.

Four specimens illustrated as *Q. kobatakei* and a specimen as *Quescus* sp. from the Kobe Group (Hori, 1987) are included in *Q. sichotensis* ; they have deep and narrow sinus and well-developed intersecondary veins, although the lobes are entire at the margin. We also have several specimens from Kobe, which are referable to *Q. sichotensis* ; they show characteristic venation features of this species. A single fragmentary leaf from Kitami, although represented by only two lobes, is probably referable to *Q. sichotensis*, because one or two subsidiary teeth are on both the apical and basal sides of lobe.

Quercus sichotensis doubtlessly belongs to the white oak group, but its modern relationship has been uncertain. Ablaev (in Takhtajan, ed., 1982) compared this fossil species with the extant *Q. alba* L. and *Q. lyrata* Walt. of the section Prinus, whereas Axelrod (1983) suggested a close relationship with the section Cerris. In such characters as lanceolate to oblong lobe, narrow and deep sinus, and intersecondary veins that run along the lobe margin or embrace the sinus, *Q. sichotensis* is more similar to some extant species of Prinus (e.g., *Q. alba* L., *Q. macrocarpa* Michx. and *Q. garryana* Dougl. ex Hook.) than those of Cerris. On the one hand, the lobe apex of the fossil is usually acute with a pointed tip as in the extant *Q. cerris*. However, all these comparable extant species typically have fewer lobes than in the fossil leaves.

The extant species most closely similar to *Q. sichotensis* are found in the section Quercus; leaves of *Q. pyrenaica* Willd. and *Q. frainetto* Tenn. of southern Europe are similar to the fossil leaves in having many lobes (5 to 7 in pairs), narrowly deep sinus with acute bottom and well-developed intersecondary veins, although the fossils are more deeply indented in sinus and acutely tipped in lobe apex.

Occurrence.—Rettikhovka, southern Prymorye; Kobe, West Honshu; Kitami, Hokkaido.

Collection.—NSM-PP 16358 (Kitami); NSM-PP 16356, 16357 (Kobe); DVGI 650/11, /36, /73 (Rettikhovka).

Quercus ussuriensis Kryshtofovich

Figures 2-3, 5-1—4, 8-1—4

Quercus ussuriensis Kryshtofovich, 1937, p. 54, pl. 7, fig. 1 ; Iljinskaya, in Takhtajan, ed., 1982, p. 94, pl. 57, figs. 1-3, text-fig. 72 ; Ablaev *et al.*, 1993, p. 77, pl. 17, fig. 6, pl. 18, fig. 3.

Quercus kodairae Huzioka, 1954 (part), p. 196, pl. 25, fig. 7.

Quercus endoana Huzioka, 1972. p. 53, pl. 5, figs. 3, 4 ; Hori, 1987; pl. 62, figs, 8, 9 ; Ablaev *et al.*, 1993, p. 74, pl. 4, fig. 8.

Quercus arsenjevii auct. non Ablaev et Gorovoi, Ablaev. 1978, pl. 20, fig. 2.

Quercus sp., Huzioka, 1954, p. 197, pl. 25, fig. 11.

Quercus sp., Ablaev and Gorovoi, 1974, p. 167, fig. 2.

Quercus sp., Suzuki, Narita, Omi and Obara, 1974, pl. 1, fig. 1.

Type.—Holotype DNIGRM no. 5065 ; Kraskino, Primorye ; the "coal bearing formation" (Oligocene).

Supplementary Description.—Leaves wide ovate to very wide oblong in general outline, 9 to 20 (estimated) cm long and 6 to 16 cm wide ; apex acute with sharply pointed tip ; base somewhat inequilateral, typically obtuse to truncate, sometimes shallowly cordate ; petiole stout, 2 to 3 cm long ; texture thick. Margin dentate with large lobe-like teeth ; teeth elongate-triangular in shape, typically A2 and sometimes C1, separated by broadly opened and acute sinus ; tooth apex acute to attenuate with sharply pointed or shortly aristate tip, often curving apically or basally; a small subsidiary teeth rarely present on adaxial side of principal teeth. Venation pinnate; midvein stout, nearly straight but sometimes flexuous; secondary veins stout, entering teeth centrally, 7 to 9 pairs, opposite to subalternate, varying in divergence angles from midvein (at nearly right angle in the base of leaf, then gradually at smaller angles toward apex, and at about 30° in apical part); 1 or 2 basal pairs of secondary veins bending basally, most secondary veins of middle part nearly straight, and those of apical part curving apically; intercostal tertiary veins thin, convex percurrent, sometimes branched, about 3 per 1 cm distance; marginal tertiary veins thin, forming a series of brochidodromous loops within tooth; quaternary veins forming rectangular to pentagonal meshes; areoles formed by quinternary veins, four- or five-sided, 0.4 to 0.5 mm across; veinlets irregulary more than twice branching; fimbrial vein distinctly present, of third or fourth order in thickness.

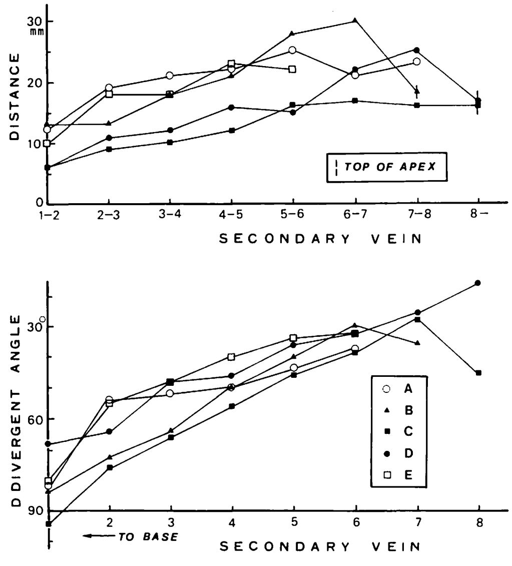


Figure 6. Each interval and divergent angles of the secondary veins in *Quercus ussuriensis* of Kitami. A. NSM-PP 16350, B. NSM-PP 16352, C. NSM-PP 16353, D. NSM-PP 16363, E. NSM-PP 16335.

Discussion.—Based on a single peculiar leaf lacking the apical portion, *Quercus ussuriensis* was first established by Kryshtofovich (1937) from Kraskino, southern Primorye. It was recently supplemented by Iljinskaya (in Takhtajan, *ed.*, 1982) on the basis of an additional specimen from Rettikhovka. From the Oligocene of Kitami, northeastern Hokkaido we collected many leaf specimens identical to *Q. ussuriensis*, some of which well preserve the finer venation. The above description is based principally on these Kitami specimens.

The simply dentate margin, trigonal or narrowly trigonal teeth with attenuate or short bristle tip, inequilateral base, long petiole, and irregularly more than twice branching veinlets (Fig. 2-3) are characteristic

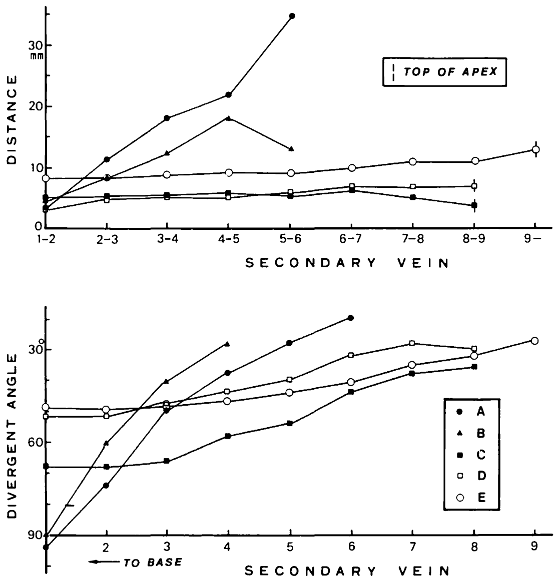


Figure 7. Each interval and divergent angles of the secondary veins in *Quercus ussuriensis* and *Q. kodairae* of North Korea and South Primorye. The measured values for Primorye specimens were obtained from the illustrations published. A, B. *Q. ussuriensis*, A: Kryshtofovich (1937), pl. 7, fig. 1, DNIGRM 5065, B: Huzioka (1972), pl. 5, fig. 3, IGPS 92335, C-E. *Q. kodairae*, C: Huzioka (1954), pl. 25, fig. 10, AKMG 6674-(8), D: Huzioka (1972), pl. 5, fig. 5, IGPS 92332, E: Akhmetyev in Takhtajan, *ed.* (1982), pl. 71, fig. 1.

features of *Q. ussuriensis*. The marginal indentation varies from 1/5 to 1/2 of the distance to the midvein; the apical side of lobe is usually longer than the basal side. The craspedodromous secondary veins appear to be irregularly arranged at a glance, but they show a uniform change from the base to apex in divergent angles and each interval (Fig. 6).

Quercus endoana Huzioka from Kogeonweon of North Korea (Huzioka, 1972) are inseparable from *Q. ussuriensis* in the margin and venation features, though the original specimens are somewhat incomplete in tooth apex. Two leaves illustrated as *Q. endoana* from Kobe, western Honshu (Hori, 1987) are also included in *Q. ussuriensis* by the features of margin and secondary venation. A single leaf described as *Quercus* sp. from Rettikhovka (Ablaev and Gorovoi, 1974) is closely similar to *Q. ussuriensis* in leaf shape, large trigonal lobes with a pointed tip and features of secondary venation, although it has a small subsidiary tooth on the adaxial side of the principal lobe. The subsidiary tooth is, however, also observed in our Kitami specimens, although in less frequency, and the above Rettikhovka leaf falls within the variation that *Q. ussuriensis* displays.

Quercus kodairae discussed in the preceding pages resembles *Q. ussuriensis* in general appearance but is distinguishable in having evenly spaced, nearly parallel secondary veins (Fig. 7) and an acute or obtuse lobe apex with no bristle tip. Kryshtofovich (1937) compared *Q. ussuriensis* with North American Miocene oaks, *Q. merriami* Knowlton and *Q. ursinae* Knowlton, both of which were later synonymized to *Q. pseudolyrata* Knowlton (Chaney and Axelrod, 1959; Wolfe, 1964). *Quercus pseudolyrata*, which represents a Miocene black oak in western North America, is highly variable in foliar shape, but it is distinguished from *Q. ussuriensis* in having a deeply lobed lamina that is usually broadly dissected with rounded sinuses. No fossil oak similar to *Q. ussuriensis* has been known from the Tertiary of North America.

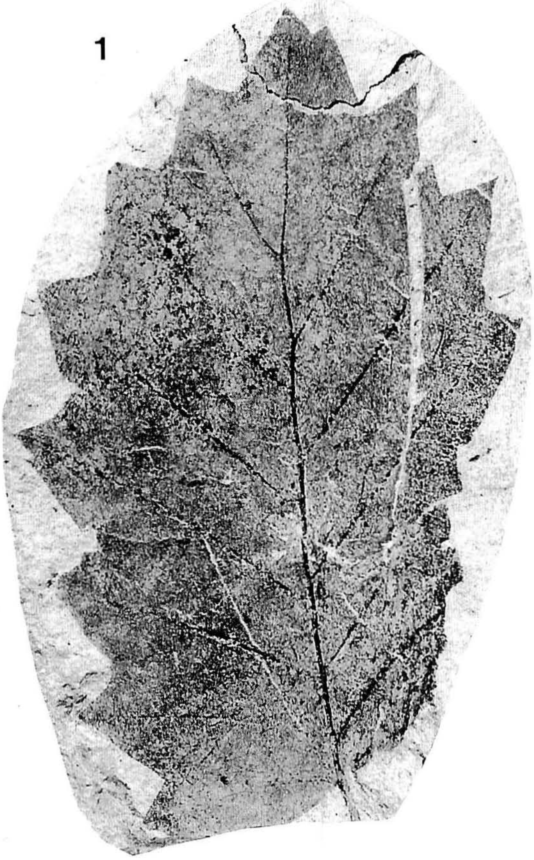
The typically wide-oblong shape with dentate or shallowly lobed margin, evenly spaced secondary veins, deltoid teeth with acute or shortly aristate tip and irregularly more than twice branching veinlets indicate clearly that *Q. ussuriensis* is closely similar to leaves of the section Cerris, especially to *Q. macrolepis* Kotschy and *Q. pyrami* Kotschy living in southeastern Europe to West Asia. The sometimes flexuous midvein also supports the resemblance of these fossil and extant species. Leaves of *Q. castaneaefolia* C.A. Mey. of Europe and *Q. trojana* Webb. of Asia Minor are also similar to those of *Q. ussuriensis*, but these extant leaves are distinguished in having usually narrow-oblong shape, more secondary veins and mucronate-tipped teeth.

Quercus ussuriensis may appear to be related to the subgenus *Erythrobalanus*, especially some of the section Rubrae and Nigrae, in having aristate teeth, but it distinctly differs in foliar shape and feature of ultimate veinlets. All the extant species of *Erythrobalanus* are typically lacking or single in the ultimate veinlets except some species having once branching veinlets.

Occurrence.—Wakamatsuzawa and Minamigaoka, Kitami, Hokkaido; Kobe, West Honshu; Kogeonweon and Kungshim, North Korea; Kraskino, Rettikhova and Rechnoi, southern Primorye.

Collections.—NSM-PP 16345-16349, 16352, 16355 (Minamigaoka), 16335-16342, 16343a, 16350, 16353 (Wakamatsuzawa); IGPS 92336, AKMG 6675 (Kogeonweon); IGPS 92335 (Kungshim).

→ **Figure 8.** (All figures in natural size unless otherwise stated). **1-4.** *Quercus ussuriensis* Kryshtofovich, 1: NSM-PP 16353, loc. Wakamatsuzawa, Kitami City, 2: IGPS 92335, loc. Kogeonweon, North Korea, 3: Enlargement of Fig. 5-4, showing fine venation, × 14, 4: NSM-PP 16352, Minamigaoka, Kitami City.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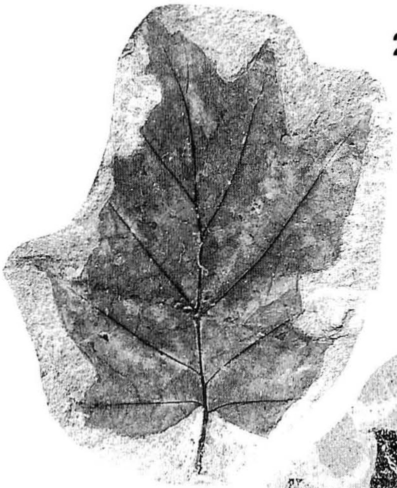
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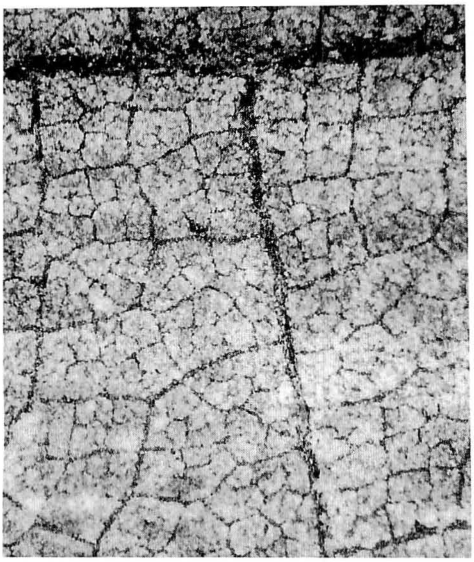
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Phytogeographic significance

Quercus is the largest genus in the Fagaceae, and is estimated as 450 (Willis, 1973) or 500-600 (Elias, 1971, Soepadmo, 1972) species. It is widely distributed in the temperate regions of the Northern Hemisphere and in higher altitudes of the tropics including Central America; some species extend further into northern Africa and northern Columbia. Of three (or four) subgenera of this genus, *Erythrobalanus* and *Protobalanus* are confined to the New World, while *Cyclobalanopsis* is to East Asia in modern distribution. The subgenus *Quercus* (*Lepidobalanus*) inhaibts both the Old and New Worlds.

The lobe-leaved species are included in the subgenus *Erythrobalanus* (sections Nigrae and Rubrae) and *Quercus* (sections Cerris, Quercus and Prinus). The aristate tip of the lobe may be a useful key for separating the subgenus *Erythrobalanus* from the subgenus *Quercus* within the American oaks (e.g., Trelease, 1924), but it is also observed in several species of *Quercus* (Cerris). Accordingly, all characters of leaves have to be considered for the interpretation of modern relationships of fossil leaves. A number of lobed oak leaves have been described from the Tertiary of Eurasia and North America, but the interpretation of their modern relationships is still far from complete. The Tertiary phytogeographic significance of lobed oaks that are described at this time is here briefly discussed, because the deeply lobed oaks are now not native to East Asia.

The section Cerris which is confined to Eurasia, extending into northernmost Africa, seems a relatively homogeneous group, because of little variability in leaf architecture. All the species, with the exception of *Q. spathulata* Seem., are more than twice branching with irregularly dendroid pattern in veinlets, and are serrate to dentate (sometimes lobed in some species) on the margin. In the feature of tooth apex, the extant species are grouped into two types; aristate-tipped species and acute-tipped (with a mucro) species.

Quercus ussuriensis belongs to the aristate-tipped group of Cerris, and is related to the South European-West Asian species such as *Q. macrolepis* Kotschy. and *Q. pyrami* Kotschy., not to East Asian species such as *Q. variabilis* Bl., *Q. acutissima* Carr. and *Q. chenii* Nakai. *Quercus ussuriensis* is confined to the Oligocene of East Asia; no fossil oaks of other regions have been known to be comparable to this species, although leaves referred to Cerris are widely known in the Neogene of Eurasia (e.g., Kolakovski, 1974). In the Neogene, especially the Upper Miocene to the Lower Pliocene, of southern Europe and West Asia including Kazakhstan, there are many species which have been considered to belong to Cerris; for instance, the common species are *Q. pseudocastanea* Goeppert, *Q. kubinyi* (Kovats) Berger and *Q. cerris* L. *fossilis*. However, these species to which various authors referred contain diverse leaf forms, respectively, and their taxonomy has been controversial (e.g., Knobloch, 1964, 1986; Kolakovski, 1974; Kolakovski in Takhtajan, *ed*., 1982; Kovar-Eder, 1988). Some of the specimens referred to these species seem to include some leaf characters of Cerris, although this needs to be reinvestigated. *Quercus kubinyi* represented by serrate leaves with aristate-tipped teeth is similar to the modern *Q. variabilis* Bl. or *Q. libani* Oliv. The modern species related to *Q. pseudocastanea* and *Q. cerris fossilis* have been considered to be related to *Q. castaneifolia* C.A. May. and *Q. cerris* L., respectively, by many authors; however, these extant species have bimorphic leaf forms, especially from dentate to lobed on the margin, and such bimorphic features have made difficult the interpretation of modern relationships of fossil leaves only by gross characters. Our brief survey indicates that fossils referred to Cerris are abundantly known from the Middle Miocene to the Pliocene in Europe, West Asia and Kazakhstan, and that they can be traced back to the Lower Miocene in Kazakhstan (Kornilova, 1960).

Except for *Q. ussuriensis*, fossil leaves of Cerris have been known commonly from the late Early Miocene to the Pliocene in East Asia ; they are *Q. miovariabilis* and its related species, which are similar to the extant *Q. variabilis* Bl. or *Q. acutissima* Carr. (e.g., Hu and Chaney, 1938 ; Tanai, 1961 ; Ozaki, 1991), and they can be traced back to the Oligocene (Hori, 1987 ; Tanai and Uemura, 1991 ; Ablaev and Iljinskaya in Takhtajan, *ed*., 1982). However, the acute-tipped group such as *Q. cerris* and *Q. castaneaefolia* is unknown in East Asia both in the past and present.

No species of Cerris, fossil or extant, is known in the New World. Accordingly, the fossil record may indicate that the section Cerris, at least the aristate-tipped group, originated in East Asia, and extended its distribution into Europe across the disappeared Turgai Depression since the Early Miocene, and that the acute-tipped group developed in Europe and West Asia since the Late Miocene.

Quercus ussuriensis is closely similar to *Q. macrolepis* and *Q. pyrami*, but it is not the direct progenitor of these extant species. These two extant species, as well as other species of Cerris, now inhabit the dry-summer, Mediterranean climate. *Quercus ussuriensis* is, however, associated with many temperate, mesic trees such as *Glyptostrobus, Metasequoia, Engelhardia, Carya, Cyclocarya, Alnus, Betula, Carpinus, Fagus, Platanus* and others ; it was under a wet-summer, temperate climate.

The section Quercus is now distributed from Europe to West Asia, while the Prinus is in East Asia and North America. These two sections include species with both lobed and serrate/dentate margined leaves, and also with both acute and rounded apices of lobes or teeth. Leaves of these sections are sometimes difficult to separate only by gross characters, or even by venation details such as ultimate veinlets. The lobed oak fossils here described, *Q. kobatakei, Q. kodairae* and *Q. sichotensis*, are difficult to assign to either section Prinus or Quercus, although they are similar to some extant species of North America or southern Europe/West Asia. However, many dentate/serrate margined leaves of the East Asiatic Prinus are well known in the Oligocene of East Asia, accompanied by lobed oaks (e.g., Huzioka, 1972 ; Uemura and Tanai, 1981 ; Ablaev and Iljinskaja in Takhtajan, *ed*., 1982), and these leaves were also known from the Lower Oligocene of eastern Kazakhstan (Iljinskaja, 1991). The lineage of the sections Prinus/Quercus may be traced back to the Late Eocene, if a Kamchatka species, *Q. bozhedomovii* Fotj. (Fotjanova, 1984), is accepted as Prinus. Fossil leaves of Prinus are common in the Neogene of East Asia, especially in the Upper Miocene and the Pliocene (Tanai, 1961), but they include no deeply lobed species.

Fossil leaves referred to the section Quercus are known mainly from Upper Miocene and Pliocene of Europe to Kazakhstan ; for instance, the dentate leaves such as *Q. kodorica* Kolakov. (Kolakovski, 1964), *Q. macrantheoides* Andreansz. (e.g., Andreanszky, 1959 ; Givulescu, 1979) and *Q. pontica-miocenica* Kubât (e.g., Knoblock, 1986), and the lobed leaves such as *Q. praeerucifolia* Straus (Straus, 1956) and *Q. pseudorobur* Kovat (e.g., Kryshtofovich and Baikovskaya, 1965). Most of these species seem to be similar to some extant leaves of the section Quercus in gross characters, but their comparisons are conjectural. Some of them were considered to be Cerris (e.g., Kovar-Eder, 1988 ; Hummel, 1983), while some are assigned to Prinus (e.g., Iljinskaja, 1968). Leaves referred hitherto to the section Quercus need to be further reinvestigated.

The fossil record of the sections Prinus and Quercus in Eurasia suggests that the ancestral complex of these two sections originated in East Asia and eastern Kazakhstan by the

Early Oligocene, including both the deeply lobed and dentate/serrate margined types. The dentate/serrate type has flourished as Prinus in East Asia since the Early Miocene, while both types developed as Quercus in Europe and West Asia since the Late Miocene.

Fossil leaves of Prinus have been commonly known from the Early Miocene to the Pliocene of western North America. Although they have been called by various epithets, they are grouped by two lineages (Wolfe, 1980); *Q. prelobata* Condit represented by deeply lobed leaves (e.g., Condit, 1944; Chaney and Axelrod, 1959) and *Q. columbiana* Chaney and its probable descendant, *Q. winstanleyi* Chaney, both of which are represented by dentate/shallowly lobed leaves (e.g., Chaney, 1920; Chaney and Axelrod, 1959). Late Eocene leaves of Prinus from Colorado (Cockerell, 1908) and Montana (Becker, 1969) seem to be dubious, but acorns of the subgenus *Quercus* are known from the Oligocene of Texas (Daghlian and Crepet, 1983), although uncertain at the sectional level. Accordingly, Prinus may be traced back to the Oligocene in North America.

Both the lineage of *Q. columbiana* and a Beringian species, *Q. furuhjelmi* Heer, are related to some of East Asiatic Prinus (Wolfe and Tanai, 1980; Wolfe, 1980), and some interchange in this section between East Asia and North America was considered (Wolfe, 1980). This interchange is also documented by the Oligocene deeply lobed oaks, *Q. kobatakei* and *Q. sichotensis* of East Asia, which are related to some extant species of North American Prinus. Prinus is widely distributed with diverse species in North America, including both the dentate/shallowly lobed and deeply compound lobed leaves. It is noteworthy that the western North American species of Prinus are, regardless of foliar shape, more than twice branching in veinlets, distinct from the eastern North American and East Asian species which are none or single in veinlets. It may be documented from the venation study of fossil leaves when the modern type of the western North American Prinus appeared.

The section Rubrae characterized by widely or deeply lobed leaves with aristate tips have been commonly known in the Neogene of western North America. All these fossils are related to the extant species of western North America (Wolfe, 1980). The pre-Miocene records of Rubrae are few; a late Eocene specimen from Montana (Becker, 1969) is dubious, and the Oligocene leaves from Texas (Daghlian and Crepet, 1983) are probably the oldest record in North America.

Few fossils of *Erythrobalanus* have been known in Eurasia with the exception of *Q. cruciata* Al. Braun (synonym: *Q. gigantum* Ettings.). This species, represented by diverse shaped leaves with aristate-tipped lobes, has been known from the Lower Oligocene to the Pliocene in Europe to western Kazakhstan, but its generic assignment is still controversial (e.g., Hantke, 1965; Andreanszky, 1966; Kvaček and Walther, 1981; Hably, 1983). It is noteworthy that some of *Q. cruciata* from central Europe were suggested to be probably referable to *Nyssa* and *Ilex* in the anatomical characters (Kvaček and Walther, 1981), although most of other specimens still remain uncertain. A peculiar oak, *Q. alexeevii* Pojarkova, from the Oligocene to the Lower Miocene of eastern Kazakhstan, has been referred to *Erythrobalanus*, similar to a Mexican extant oak (Kryshtofovich *et al*., 1956; Iljinskaja in Takhtajan, *ed*., 1982). However, this Kazakhstan species is closely similar to the shallowly lobed leaf of *Nyssa aquatica* L. (oral communication from Wolfe, 1993). Thus, these two fossil species of Eurasia, which hitherto were referred to *Erythrobalanus*, are of dubious generic assignment.

Conclusion

The deciduous broad-leaved forest associated commonly with conifers such as the Pinaceae, Taxodiaceae and Cuppressaceae was widely distributed in northeastern Asia (Primorye, North Korea and North Japan) and eastern Kazakhstan during the Oligocene. This forest included many deciduous oak species with various leaf forms, from serrate to deeply lobed margins. Pre-Oligocene oaks have a moderate record in East Asia, although the Eocene forests were composed commonly of broad-leaved trees. It is noteworthy in the evolution of the Fagaceae that the genus *Quercus* considerably diversified since the Early Oligocene in East Asia and eastern Kazakhstan.

Of the various Oligocene oaks, the lobed species of the subgenus *Quercus* characteristically appeared ; they are members of phylads of the sections Cerris and Prinus/Quercus. Deeply lobed oaks are, however, lacking since the Miocene to the present, although the sections Cerris and Prinus are now growing with many species in East Asia. On the other hand, the subgenus *Quercus*, with both the lobed and serrate leaved species, developed in Europe, West Asia and North America since Miocene time (especially Middle or early Late Miocene), and still grows luxuriantly in these regions.

Fossils of the subgenus *Erythrobalanus* are known commonly from the Early Miocene to the Pliocene in North America, and are native with diverse species there today, extending into Central America. The oldest record of this subgenus is from the Oligocene of southern United States. However, the fossil record of *Erythrobalanus* is meager in Eurasia, with two exceptions which have been controversial in taxonomy. A brief survey of the fossil oak record in the Northern Hemisphere suggests that some oaks such as the section Cerris originated in East Asia, and then dispersed into Europe. On the one hand, the origin of the section Prinus and Quercus is as yet indeterminable, because the fossil taxonomy of these two sections is still controversial.

It is now an unsolved problem why the deeply lobed species appeared first in East Asia in the evolution of the genus *Quercus*, and disappeared there since the Early Miocene, although still growing in North America, southern Europe and West Asia. That lobation in oak leaves is an atavistic phenomenon from the Late Cretaceous distant ancestors of Hamamelididae, was suggested by some authors (Rüffle and Knappe, 1977 ; Rüffle, 1980). We need, however, to investigate the intergeneric phylogeny and phytogeographic relationships and past environments under which *Quercus* evolved in the Northern Hemisphere.

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ence.

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Futamata 二股, Hamg'yeong-Bukudo 咸鏡北道, Hoeryeong 会寧, Husehata 布施畑, Kitami 北見，Kizu 木津，Kobe 神戸，Kogeonweon 古乾原，Kungshim 弓心，Kyeongweon 慶源，Minamigaoka 南ケ丘，Ochiai 落合，Okuhata 奥畑，Sanda 三田，Wakamatsuzawa 若松沢，Yongpukdong 龍北洞.

東アジアの第三系産コナラ属の浅裂状葉化石と，その北半球における植物地理学的考察：温帯性落葉広葉樹と針葉樹から主としてなり，浅裂状，歯状〜歯牙状縁の多様な葉のコナラ属を特徴的に含む漸新世植物相が，日本，北朝鮮，ロシヤのプリモリヤ地方に分布する。浅裂状の葉をもつコナラ属の漸新世化石を分類学的に再検討し，*Quercus kobatakei* Tanai and Yokoyama, *Q. kodairae* Huzioka, *Q. sichotensis* Ablaev and Gorovoiおよび*Q. ussuriensis* Kryshtofovichのコナラ亜属に属する4種を識別した。*Q. ussuriensis*はCerris節に属し，東アジアよりもむしろヨーロッパ〜西アジアの現生種に近似し，残りの3種はPrinusまたはQuercus節に属し，北アメリカのPrinus節またはヨーロッパ〜西アジアのQuercus節の現生種に似ている。次いで，コナラ亜属の北半球における化石記録を概観して，上記の4種の植物地理学的な意義を考察した。Cerris節は東アジア及びカザック東部に漸新世初期に出現し，中新世以降西アジアやヨーロッパに分布を広げたが，アメリカ大陸には及んでいない。一方，PrinusとQuercus節の化石記録は東アジア起源を示唆しているが，この両節は葉のみでは区別が十分ではないので，これらの植物地理的な歴史は必ずしも明らかではない。
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966. SKELETAL APPARATUS AND ITS EVOLUTIONARY TRENDS IN A TRIASSIC CONODONT *ELLISONIA DINODOIDES* (TATGE) FROM THE TAHO LIMESTONE, SOUTHWEST JAPAN*

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Abstract. A Triassic conodont *Ellisonia dinodoides* (Tatge) from pelagic carbonate rocks of the Taho Limestone in Ehime Prefecture, Southwest Japan is reconstructed as a quadrimembrate apparatus with the M, Sa, Sb and Sc elements. The elements represent well marked evolutionary trends in the length of the processes during the Smithian to Norian. The anterior or anterolateral and posterior processes of the elements decrease in total length from the Smithian to Anisian but seem to keep the size distribution constantly until the Norian. The inferred ratio of the M, Sa, Sb, and Sc elements is 2 : 1 : 2 : 6 in the Smithian to Anisian. The Sa element, however, is very rare or absent in the Norian. The correlation coefficient between the number of the denticles on the processes and the size of the processes varies from 0.09 to 0.75 and does not represent any evolutionary trends during the Triassic. The decrease in size of the processses during the Triassic seems a common phenomenon in long-ranged ramiform conodonts.

Key words. Ehime Prefecture, *Ellisonia dinodoides* (Tatge), evolutionary trend, skeletal apparatus, Taho Limestone, Triassic conodont.

Introduction

The form species of conodonts, *Chirodella dinodoides* (Tatge), *Diplododella meissneri* (Tatge), *Neoplectospathodus muelleri* Kozur and Mostler, and *Neohindeodella triassica* (Müller) have been reported from Lower to Upper Triassic strata of various areas in the world. These form species also occur abundantly in the Taho Limestone exposed at Tahokamigumi, Shirokawa-cho, Higashiuwa-gun, Ehime Prefecture. As a result of the present investigation based on numerous specimens from various levels of this limestone, it becomes clear that these four form species are the elements of a conodont apparatus. I propose *Ellisonia dinodoides* (Tatge) for this quadrimembrate skeletal apparatus and describe the elements with reference to the type species of *Ellisonia, E. triassica* Müller reconstracted by Koike (1990).

Ellisonia dinodoides is one of the long-ranging Triassic conodonts and the elements of the apparatus represent rather conspicuous trends in morphologic variation during Early to Middle or Late Triassic. No evolutionary trends in Triassic conodonts have ever been described or discussed in detail. I show the evolutionary trends observed in the elements of *E. dinodoides* (Tatge).

All of the described specimens are kept in the Institute of Geology, Yokohama National University.

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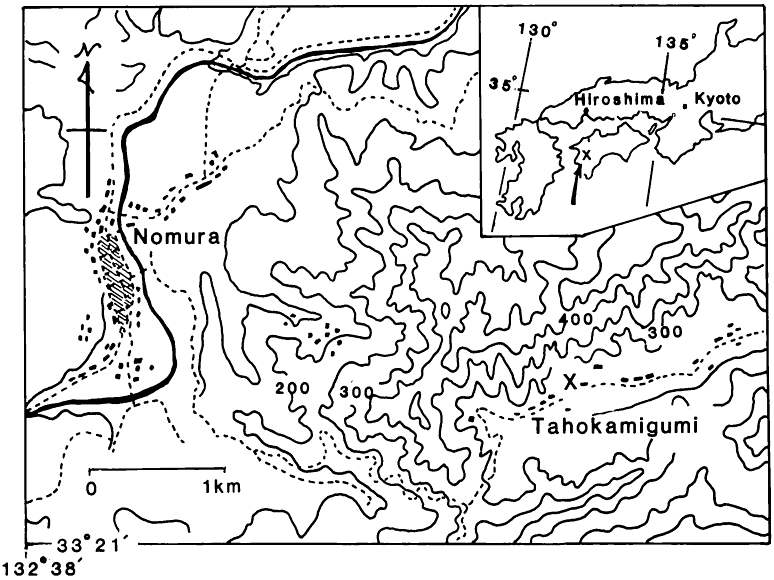

Figure 1. Index map showing the location (×) of the Taho Limestone at Tahokamigumi, Shirokawa-cho, Higashiuwa-gun, Ehime Prefecture, Southwest Japan.

Geologic setting

The Taho Limestone occurs as an exotic block in Jurassic clastic rocks associated with Triassic bedded chert and Permian limestone blocks. The limestone block of the Taho Limestone attains 54 meters in thickness at the type section. It corresponds to the Smithian to middle Anisian and late Carnian to Norian (Koike, 1981). The Ladinian to lower Carnian strata are absent due to a fault (Figure 2). The Smithian limestone (*Neospathodus waageni—N. conservativus* Zone) is composed of 10 m thick, gray, massive biomicrite and 6 m thick dolomitized biomicrite, and 2 m thick thin-bedded biomicrite in ascending order. The lower and upper half of dolomitic biomicrite are thin- to medium-bedded and massive, respectively. Skeletal debris comprising biomicrite is mainy thin-shelled bivalves and subordinate echinoderm spines and crusts, and ammonoids. The upper part of the Smithian yields bivalves *Anodontophora* and *Eumorphotis* associated with ammonoids *Meekoceras* and *Anasibirites* (Yehara, 1925). The Spathian limestone (*Neospathodus triangularis—N. homeri* Zone, 7 m thick) and lower to middle Anisian limestone (*Neogondolella timorensis* and *N. bulgarica* Zones, 11 m thick) are composed of dark gray, thin- to medium-bedded biomicrite including abundant thin-shelled bivalves and radiolarians and subordinate echinoderm crusts, small gastropods, and foraminifers. The upper Carnian limestone (*Neogondolella nodosa* Zone, 3 m thick) and Norian limestone (*Epigondolella spatulata* Zone, 15 m thick) are characterized by white massive biomicrite with abundant radiolarians and thin-shelled bivalves. In the upper part of the Anisian and the base of the Carnian limestones, there occur thin layers which may represent discontinuity surfaces. The layers contain glauconite, limonite, pyrite, apatite, fluorite, barite, and hydrocarbons which are of biogenic or chemical origin.

It is difficult to reconstract the sedimentary environment of the Taho Limestone because the limestone is an exotic block in Jurassic clastic rocks, and the distribution is very limited, and both underlying and overlying strata are absent or unexposed. The Taho

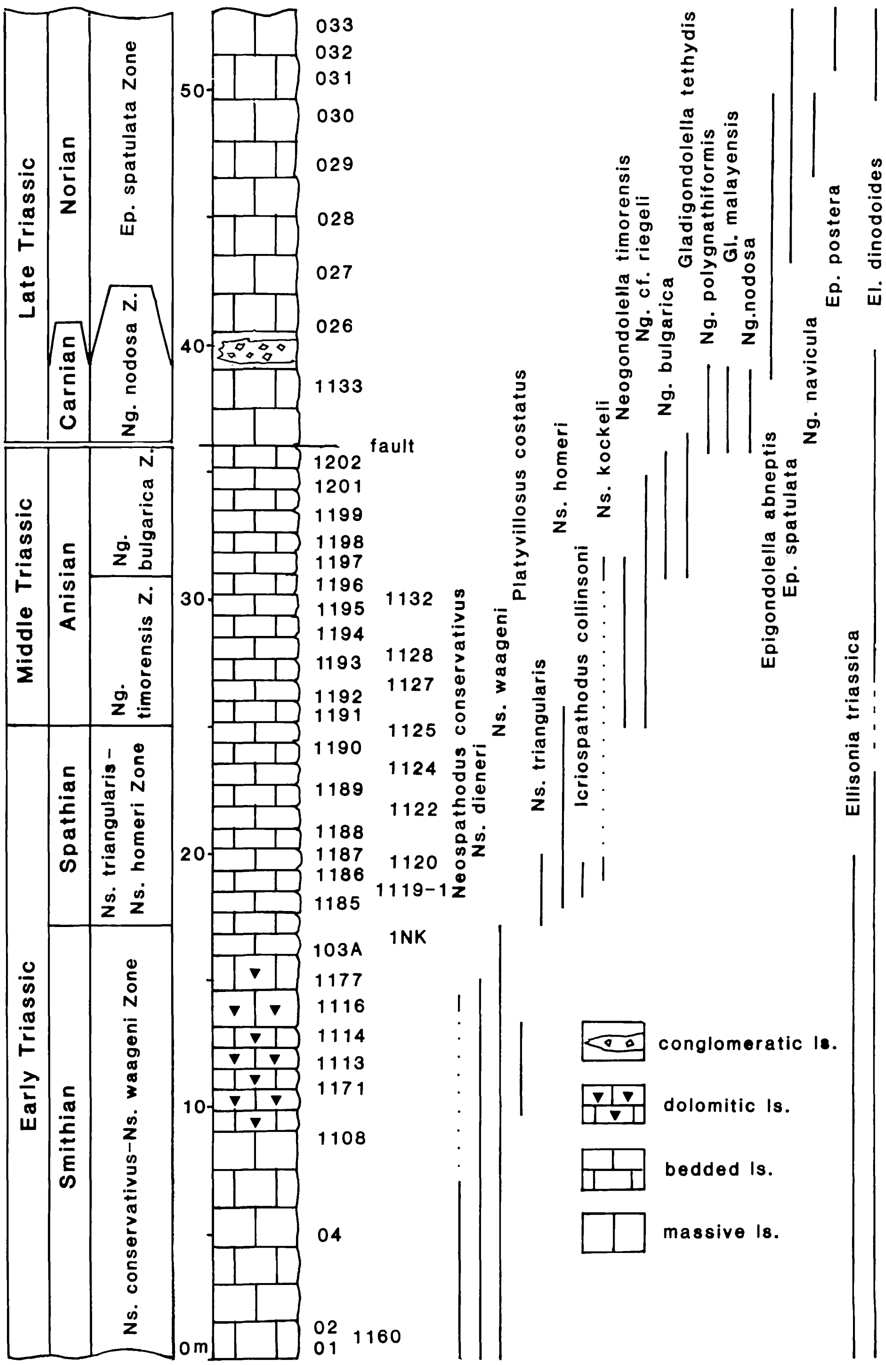

Figure 2. Stratigraphic section and vertical distribution of *Ellisonia* and important pectiniform conodonts.

Limestone shows almost the same lithofacies throughout and consists of pelagic limestone intercalating layers concentrated with thin-shelled bivalves and radiolarian remains. Thin-shelled bivalves are hardly identified but may be referred to *Halobia, Daonella, Bositra* and other monotids (Kanmera, 1969). These bivalves are considered to be of planktonic and/or pseudoplanktonic habitat (Hayami, 1969). The dolomitic limestone of the Smithian is originated from dolomitized thin-shelled bivalve-bearing micrite. The limestone contains no terrigenous sand and indicates a condensed sequence. An estimated sedimentation rate is about 0.5–0.8 g/cm^2/1,000 yr.

The Taho Limestone is quite similar in lithofacies and thickness to those of the Triassic Kamura Limestone exposed at Shioinouso, Takachiho-cho, Miyazaki Prefecture, Kyushu. The Smithian limestone of the Kamura Limestone unconformably overlies the Upper Permian limestone of the Mitai Formation (Watanabe *et al.*, 1979). Therefore, it is probable that the Taho Limestone was deposited on the Permian carbonate platform. The Permian limestone crops out as exotic blocks near the type section of the Taho Limestone. On the other hand, the limestone might have been deposited on the deep sea-floor where the accumulation rate was low. In the former case, carbonate sediment of the Taho Limestone was accumulated under a deeper sea environment than the Permian limestone, which includes calcareous algae, calcareous foraminifers, and fecal pellets.

Occurrence of *Ellisonia dinodoides* (Tatge)

Ellisonia dinodoides is a cosmopolitan species and the elements of the species have been reported from various areas in the world. The earliest occurrence of this species is in the Griesbachian of China (Ding, 1983) and Iran (Hirsch and Sussli, 1973). The specimens assigned to this species, however, were not described or illustrated in their reports. The Smithian specimens of this species have been described and illustrated in many papers (e.g. Bryii, 1989, Gedik, 1975, Koike, 1982, Mosher, 1968, 1973, Müller, 1956). This species ranges into the interval of the Carnian and Norian (e.g. Huckriede, 1958, Mosher, 1968, Mock, 1971, Budurov and Stefanov, 1974, Mirauta and Gheorghian, 1978, Wang and Dai, 1981, Onder, 1984).

Ellisonia triassica, the type species of *Ellisonia,* is also a cosmopolitan species and it occurs earlier than *E. dinodoides,* namely, in the Late Permian in Pakistan, Iran, Kashmir (Sweet, 1970a, 1973), and Utah (Paull, 1982). The occurrence of this species is restricted to the interval of the Griesbachian to Spathian of Europe, North America, and Asia (e.g. Hirsch and Sussli, 1973, Mosher, 1973, Wang and Wang, 1976, Clark and Hatleberg, 1983, Duan, 1987).

In the Taho Limestone, *Ellisonia dinodoides* occurs in the lowest part (Smithian) to the uppermost part (Norian). The elements of this species attain in frequency from 150 to 350 in approximately 3 kg of limestone. They are absent in certain levels of the Smithian and the lower part of the Anisian (*Neogondolella timorensis* Zone). Jaccard coefficient is 1 among the elements in the Smithian to Carnian. As mentioned below, however, one of the elements (Sa element) is absent or very rare in the Norian although the other elements always occur together.

The apparatus of *Ellisonia dinodoides* (Tatge)

The skeletal apparatus of *E. dinodoides* reconstracted is quadrimembrate and composed of the M, Sa, Sb, and Sc elements.

The M element is a breviform digyrate type with lateral processes of markedly unequal length. It is identical with the form species *Chirodella dinodoides* (Tatge, 1956).

Table 1. Occurrence of M, Sa, Sb and Sc elements of *Ellisonia dinodoides* (Tatge) and their ratio.

Norian				
Loc.	M	Sa	Sb	Sc
033	88	1	13	106
032	10	0	3	15
031	110	0	27	111
030	78	0	36	136
029	4	0	7	23
028	10	0	13	31
027	9	0	3	24
026	6	0	2	12
total	315	1	104	458
ratio	2 :	0 :	0.7 :	2.9

Carnian				
Loc.	M	Sa	Sb	Sc
1133	3	1	2	4

Anisian				
Loc.	M	Sa	Sb	Sc
1202	70	34	50	101
1201	29	12	24	54
1199	14	8	19	19
1198	23	6	12	42
1197	52	26	93	172
1191	22	13	26	80
total	210	99	224	468
ratio	2.1 :	1 :	2.3 :	4.7

Spathian				
Loc.	M	Sa	Sb	Sc
1125	24	11	40	77
013	5	3	12	20
1124	65	38	132	245
1189	12	5	10	30
012	16	8	13	56
1122	40	25	43	129
1188	68	32	82	251
011	34	16	47	107
1187	32	19	69	135
056′	37	27	42	163
1186	49	29	54	139
1119′	3	4	10	23
total	385	217	554	1375
ratio	1.8 :	1 :	2.6 :	6.3

Smithian				
Loc.	M	Sa	Sb	Sc
1177	42	32	70	148
1116	23	24	62	146
1171	2	3	6	18
1108	3	4	5	18
04	24	25	55	123
1160	18	20	39	70
02	60	39	75	230
total	172	147	312	753
ratio	1.2 :	1 :	2.1 :	5.1

The Sa element is an alate type with a pair of very short anterolateral processes and a short posterior process. It is identical with the form species *Diplododella maissneri* (Tatge, 1956).

The Sb elements is an extensiform digyrate type with a pair of laterally extended long lateral processes. It is identical with the form species *Neoplectospathodus muelleri* proposed by Kozur and Mostler (1970) and *Neohindeodella kobayashii* (Igo and Koike, 1965).

The Sc element is a bipennate type with a short anterior process and a long posterior process. This element is identical with the form species *Neohindeodella triassica* (Müller, 1956). Sweet (1970b) ascribed the form species *N. triassica* to the Lb (Sc) element of multielement species *Ellisonia triassica. Neohindeodella triassica* proposed by Müller (1956), however, carries 11 denticles on the posterior process and falls under the category of the Sc element of *E. dinodoides* as described below.

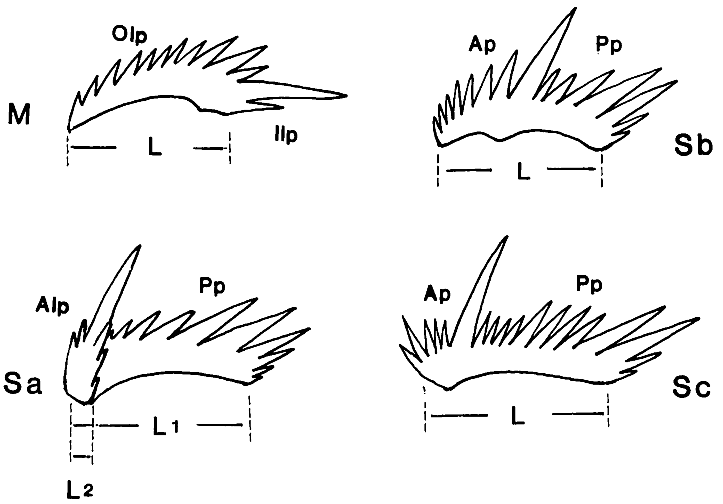

Figure 3. *Ellisonia dinodoides* (Tatge) showing the characters measured and their nomenclature. L : length of process, L_1 : length of posterior process, L_2 : length of anterolateral process, Olp : Outerlateral process, Ilp : Innerlateral process, Ap : Anterior process, Pp : Posterior process.

The number of elements of *E. dinodoides* occurring in each level is shown in Table 1. The frequency of the M, Sa, Sb, and Sc elements from 7 samples of the Smithian, 12 samples of the Spathian, and 6 samples of the Anisian is 172, 147, 312, 753 (1.2 : 1 : 2.1 : 5.1 in ratio), 385, 217, 554, 1375 (1.8 : 1 : 2.6 : 6.3), and 210, 99, 230, 468 (2.1 : 1 : 2.3 : 2.3 : 4.7), respectively. The number of *E. dinodoides* is very low in the Carnian. The total number of the M, Sa, Sb, and Sc elements from 25 samples ranging from the Smithian to Anisian attains to 767, 463, 1,090, 2,596, respectively and the ratio is 1.7 : 1 : 2.4 : 5.6. Therefore, the inferred ratio can be regarded as 2 : 1 : 2 : 6 (Table 1). On the other hand, the frequency of the M, Sa, Sb, and Sc elements from 8 samples in the Norian is 315, 1, 104, and 458, respectively and the ratio among the elements is 2 : 0 : 0.7 : 2.9. Therefore, the Sb and Sc elements are fairly small in number against the M element compared with those from the Smithian to Anisian. This may be interpreted as meaning that the Sb and Sc elements are more fragile than the M element and poorly preserved in sediment and/or mechanically broken during the preparation process. Absence or rare occurence of the Sa elements in the Norian samples is difficult to explain. The same phenomenon can be recognized in the specimens from the Norian limestone in the Southern Alps, Austria. Thus, absence of the Sa element in the Norian may be a general tendency in the apparatus of *E. dinodoides.*

Evolutionary trends in *Ellisonia dinodoides* (Tatge)

Statistical analysis on morphology of *E. dinodoides* reveals evolutionary trends in variation of the size of the elements in the apparatus during the Early to Late Triassic. A general trend of decrease in range of size distribution and shifting to decrease in maximum size of the processes can be recognized in each of four elements (Figure 4). It should be specified that conodont samples treated herein are from limestone layers of about 10 cm thick and size distribution of the elements from each location may be of mixed populations which lived over hundreds of thousands of years. The total length of the anterior and posterior processes of the Sc

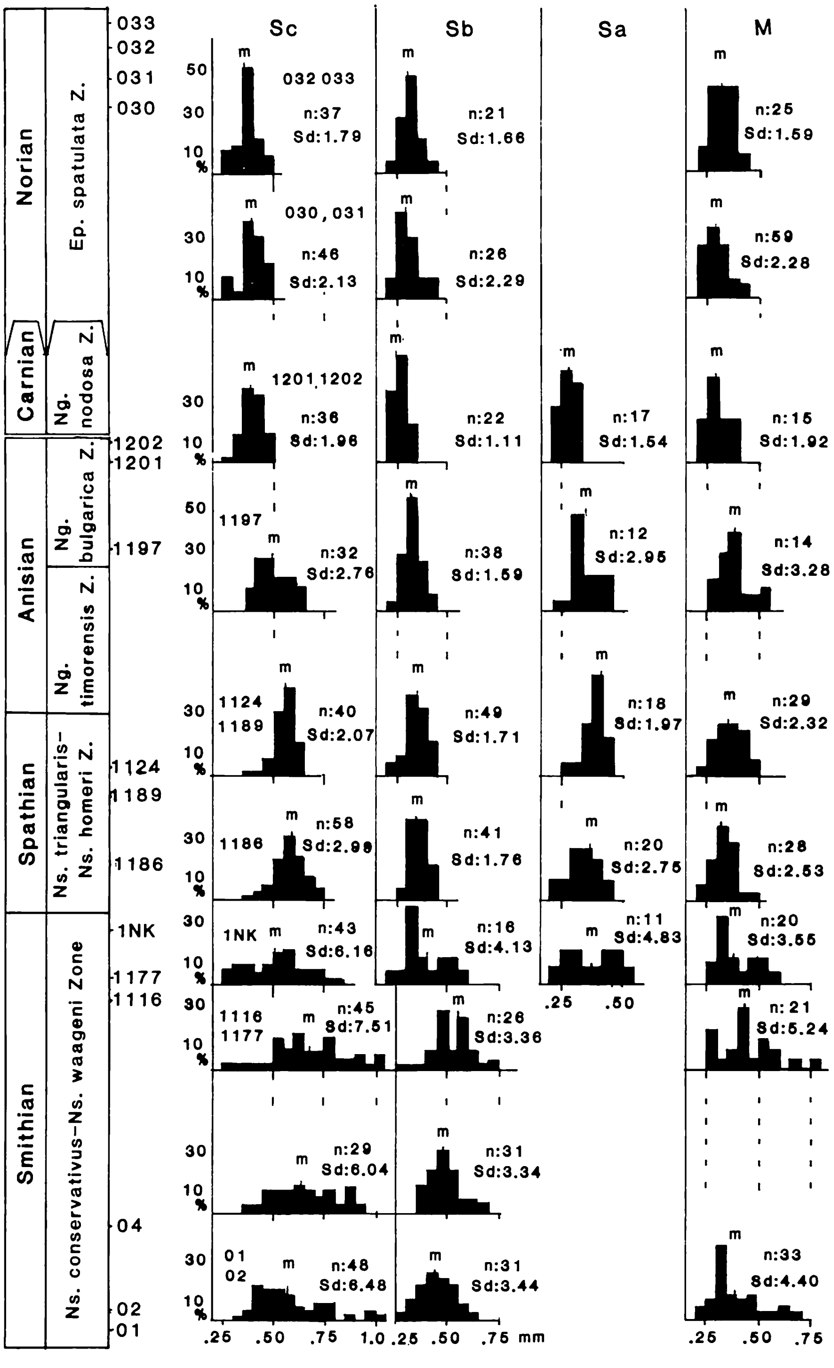

Figure 4. Evolutionary trends of the Sc, Sb, Sa and M elements of *Ellisonia dinodoides* (Tatge). The length of the processes was measured. n : number of specimens measured, m : arithmetic mean, sd : standard deviation.

element ranges from 0.26 to 1.13 mm in the Smithian and 0.26 to 0.84 mm in the late Smithian or early Spathian, 0.33 to 0.61 or 0.73 mm in the Spathian, 0.28 to 0.63 or 0.65 mm in the early Anisian, and 0.25 to 0.48 mm in the middle Anisian. The range of size distribution remains from 0.25 to 0.45 or 0.48 mm in the Norian. Thus, the processes seem to be constant in range of size distribution from the middle Anisian to Norian, although unfortunately there is no information on the late Anisian and Ladinian materials.

The same tendency can be observed in other element. In the Sb element the total length of the anterior and posterior processes ranges from 0.24 to 0.70 mm in the Smithian and the maximum value decreases to 0.60 mm in the late Smithian to early Spathian, 0.53 mm in the Spathian, 0.41 mm in the eary Anisian, 0.33 mm in the middle Anisian, and 0.40 to 0.43 mm in the Norian.

In the M element the inner and outer lateral processes range in total length from 0.26 to 0.80 mm in the Smithian and the maximum value decreases to 0.60 mm in the late Smithian to early Spathian, 0.46 mm in the Spathian and early Anisian, 0.35 mm in the middle Anisian, and 0.34 to 0.38 mm in the Norian.

Statistical analysis on the Sa element is possible only for the materials from the late Smithian to Anisian because the Sa element is small in number and poorly preserved in the Smithian and very rare or absent in the Norian. As far as observed, the Sa element also represents a tendency toward decrease in total length of the posterior and one side of the anterolateral processes, namely, 0.20 to 0.55 mm in the late Smithian, 0.23 to 0.47 mm in the late Spathian and early Anisian, and 0.21 to 0.34 mm in the middle Anisian.

This fact proves that ontogenetic development of the size retreated during the Smithian to middle Anisian and probably almost ceased during the middle Anisian to Norian. The same evolutionary trend can be recognized in *E. dinodoides* from the Kamura Limestone of Kyushu. The decrease in size of the processes during the Triassic can be also observed in other long-ranged ramiform form species *Neohindeodella suevica* (Tatge) (Sc element), *Enantiognathus ziegleri* (Diebel) (M element), and *Diplododella acroforme* (Mosher and Clark) (Sa element).

There is a probability that the size of

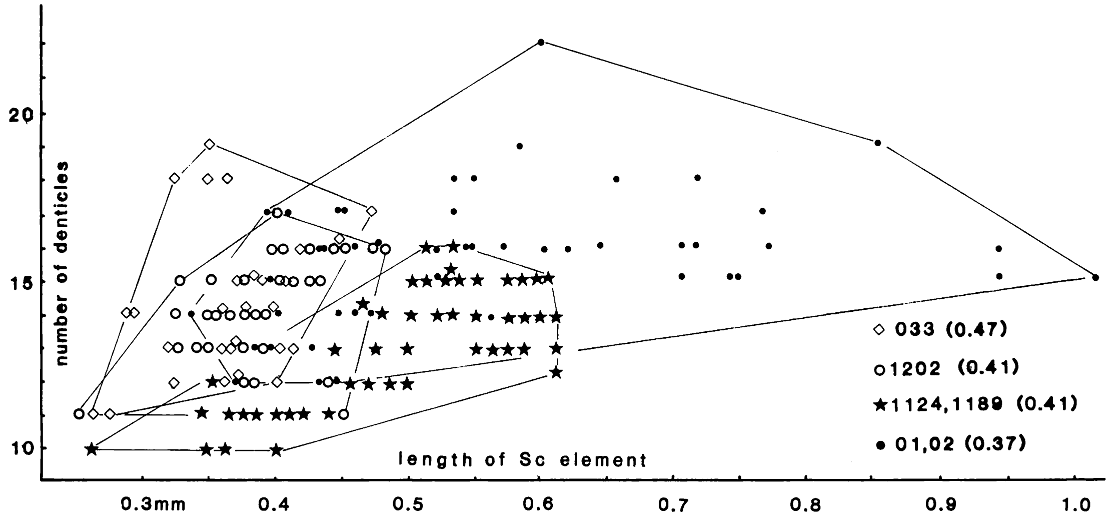

Figure 5. Comparison of the length of the processes with the number of denticles in the Sc element of *Ellisonia dinodoides* (Tatge). Values in parentheses represent the correlation coefficient.

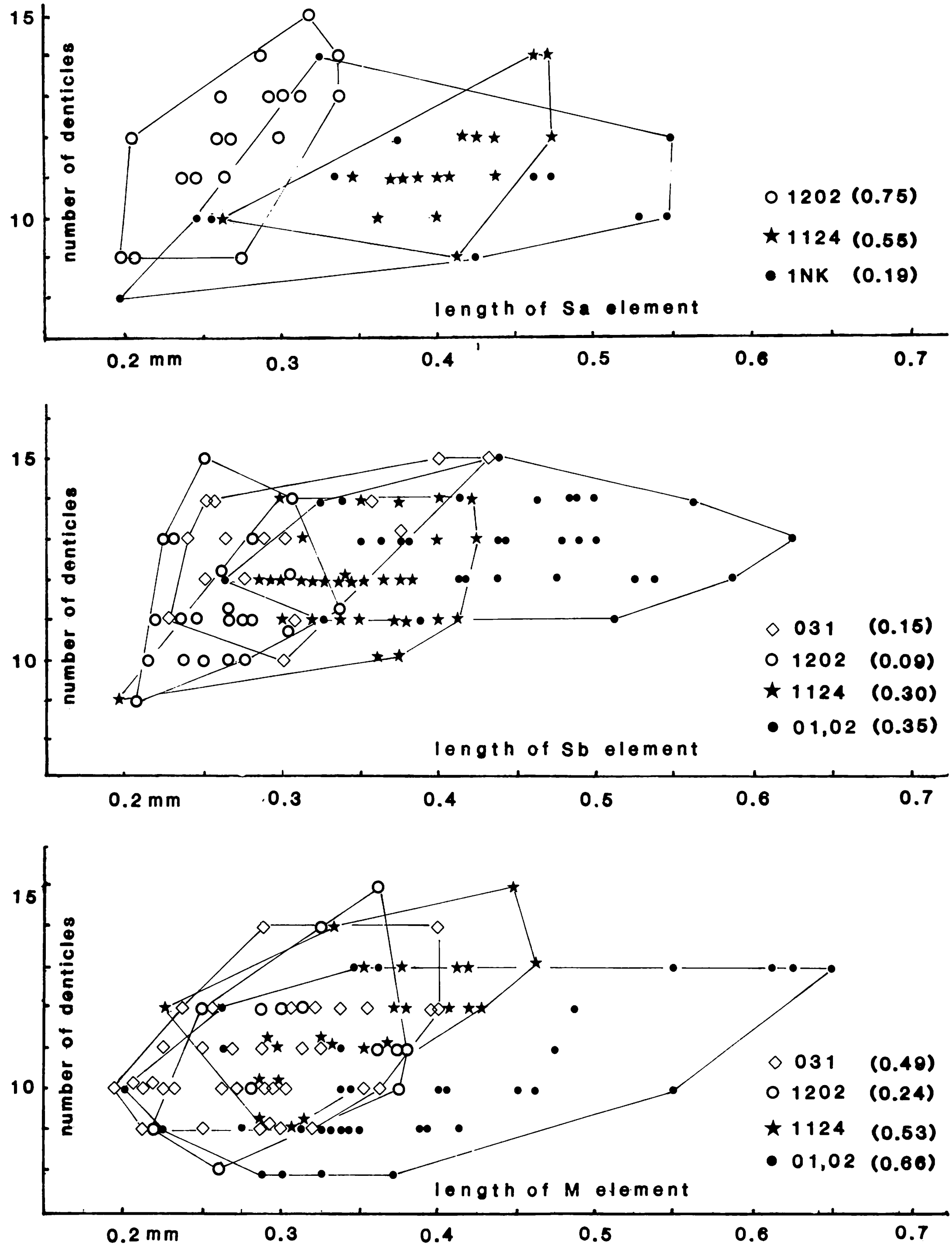

Figure 6. Comparison of the length of the processes with the number of denticles in the M, Sb and Sa elements of *Ellisonia dinodoides* (Tatge). Values in parentheses represent the correlation coefficient.

ramiform elements which may have a function of internal support for ciliated tissue in the food-gathering system (Nicoll, 1987) has a relationship to the size of the conodont animals. In that case conodont animals with *E. dinodoides* apparatuses might have decreased in size of the soft body and become very small in the Middle to Late Triassic.

The relationship between the number of the denticles and the length of the processes was analyzed for each of four elements (Figures 5, 6). The correlation coefficient between two characters in the Sc element ranges from 0.37 to 0.47 in four populations and it is fairly constant from the Smithian to Norian. The M element represents a more widely ranging correlation coefficient of 0.24 to 0.66. The correlation coefficient in the Sb and Sa elements varies from 0.09 to 0.35 and 0.19 to 0.75, respectively.

The correlation coefficient between two characters of these ramiform elements is considerably low compared with that of the pectiniform element studied by some workers (e.g. Rhodes, Williams, and Robinson, 1973; Koike, 1992). The range in number of the denticles for the length of the processes is very wide. This factor makes the correlation coefficient low. The number of denticles increases somewhat rapidly with the length of the processes and attains its maximum in the early growth stage but keeps constant in the late stage in the elements of the Smithian. The maximum total number of the denticles is almost the same in each element throughout the Triassic and the characters of the elements from the Spathian, Anisian, and Norian coincide with those of the early staged elements from the Smithian.

Systematic paleontology

Genus *Ellisonia* Müller, 1956
Type species: *Ellisonia triassica* Müller, 1956

Remarks: Sweet (1970b) proposed a multielement genus *Ellisonia* and recognized seven multielement species based on specimens from the Lower Triassic of Pakistan. According to his description, these species are quadrimembrate or quinquimembrate types characterized by a skeletal apparatus that includes some combination of kladognathus-, hibbardella- (or ellisonia-), lonchodina-, enantiognathus-, and prioniodina-like elements. Sweet (1970b) did not provide, however, any emended diagnosis of the genus *Ellisonia* which was originally erected to include only a hibbardella-like conodont element. The reason was that a large number of species, ranging from the Ordovician through Triassic, had skeletons composed of combinations of the intergradational forms that were distinguished from the multielement groups assigned to *Ellisonia*.

Sweet (1981, 1988) provided a diagnosis for this genus probably on the basis of the type species *Ellisonia triassica* Müller and revised his earlier view on the skeletal apparatus of *Ellisonia*, now regarding this genus as a seximembrate type with the M (digyrate), Sa (alate), Sb (digyrate), Sc (bipennate), Pb (digyrate), and Pa (angulate) elements.

Koike (1990) studied *E. triassica* Müller collected from the Lower Triassic part of the Taho Limestone and reconstructed the species as a trimembrate apparatus composed of the M or Pb (digyrate), Sa (alate), and Sc (bipennate) elements in the ratio of 1 : 2 : 4. Recent restudy of *E. triassica* based on many specimens newly found from the same limentone revealed that the apparatus agrees well with the above-mentioned conclusion.

The M, Sa, and Sc elements of *Ellisonia dinodoides* (Tatge) proposed herein are usually easily distinguishable from the M, Sa, and Sc elements of *E. triassica* in many respects as mentioned below. There seem some transitional forms, however, between each element of both species, especially of the Smithian. For example, the M element with a short innerlateral process, the Sa element with horizontally extended anterolateral processes and the Sc element with a short anterior process of *E. triassica* which represents wide morphologic variation (Koike, 1990, Figs. 2, 4, 6) are somewhat transitional with the M, Sa, and Sc elements of *E. dinodoides,* respectively. The Sc element with subequal anterior and posterior processes in the *E. triassica* apparatus (Koike, 1990, Fig. 4, e) is somewhat similar to the Sb element of *E. dinodoides.*

It is difficult to show common morphologic characters between *E. dinodoides* or *E. triassica* and other Triassic *Ellisonia* species (*E. clarki, E. delicatula, E. gradata, E. robusta, E. torta*) proposed by Sweet (1970b). I collected many specimens from the Taho Limestone which can be correlated with almost all elements of these *Ellisonia* species but did not reconstruct the elements to certain conodont apparatuses. Further study is necessary to obtain information about not only the *Ellisonia* species but also the genera *Xaniognathus* and *Cypridodella* erected by Sweet (1981), which contain almost the same formed elements with those of the *Ellisonia* species.

I offer herein a diagnosis of *Ellisonia* based on *E. triassica* and *E. dinodoides* as follows. The apparatus is trimembrate or quadrimembrate, composed of the M (breviform digyrate), Sa (alate), Sc (bipennate), and Sb (extensiform digyrate) elements. The processes of the elements are stout in large specimens. The denticles are stout and discrete or indiscrete. The cusp is stout and long. Zone of recessive basal margin is prominent and occupies more than one half of the height of the processes beneath the cusp.

Ellisonia dinodoides (Tatge)

Figures 7-10.

Metalonchodina ? *dinodoides* Tatge, 1956, p. 135, pl. 6, fig. 4 : *Prioniodina* ? *dinodoides* (Tatge), Budurov and Vrabljanski, 1964, p. 536-537, pl. 1, figs. 13, 15-18 : *Chirodella dinodoides* (Tatge), Mosher, 1968, p. 918, pl. 113, fig. 1 (M element).

Roundya meissneri Tatge, 1956, p. 143, pl. 6, fig. 11 ; *Diplododella meissneri* (Tatge), Mosher, 1968, p. 924, pl. 113, fig. 34 (Sa element).

Hindeodella kobayashii Igo and Koike, 1965 p. 10, pl. 1, fig. 4 : *Neoplectospathodus muelleri* Kozur and Mostler, 1970, p. 449, pl. 3, figs. 3, 5, 7 (Sb element).

Hindeodella triassica Müller, 1956, p. 826, pl. 26, figs. 4-5 ; *Hindeodella* (*Neohindeodella*) *triassica triassica* (Müller), Kozur, 1968, p. 1077, pl. 2. figs. 10-11 (not 5, 14, 15, 19), pl. 3, fig. 3 : *Neohindeodella triassica triassica* (Müller), Kozur and Mostler, 1972, p. 24, pl. 1, fig. 24, pl. 4, fig. 13, pl. 7, figs. 12-13, pl. 8, fig. 30, pl. 13, fig. 10, 13 ; *Neohindeodella triassica* (Müller), Kozur and Mock, 1973, pl. 1, fig. 11 (Sc element).

Description

M element : The outerlateral process ranges in length from 0.25 mm to 0.6 mm and bears 9 to 15 denticles. The denticles extend anteriorly and curve slightly inward and tend to decrease in size toward the posterior and the largest denticle adjacent to the cusp is sometimes almost the same size as the cusp. The innerlateral process ranges in length from 0.03 mm to 0.2 and posesses 1 to 3 denticles. One of the denticles is sometimes as large as the cusp. The cusp is thick and long particularly on large and stout processes and curves inward in a hooklike shape. Zone of recessive basal margin is well developed and occupies about one half of the height of the lateral processes on the inner side.

Sa element : Length of the anterolateral process ranges from 0.02 mm to 0.2 mm. The basal margin of the processes is horizontal or turns gently upward. The denticles on the process range in number from 1 to 5. The posterior process is 0.2 mm to 0.5 mm in length and bears 5 to 10 denticles. The denticles tend to increase in size posteriorly and increase in inclination posteriorly, changing angle between the process from about 45

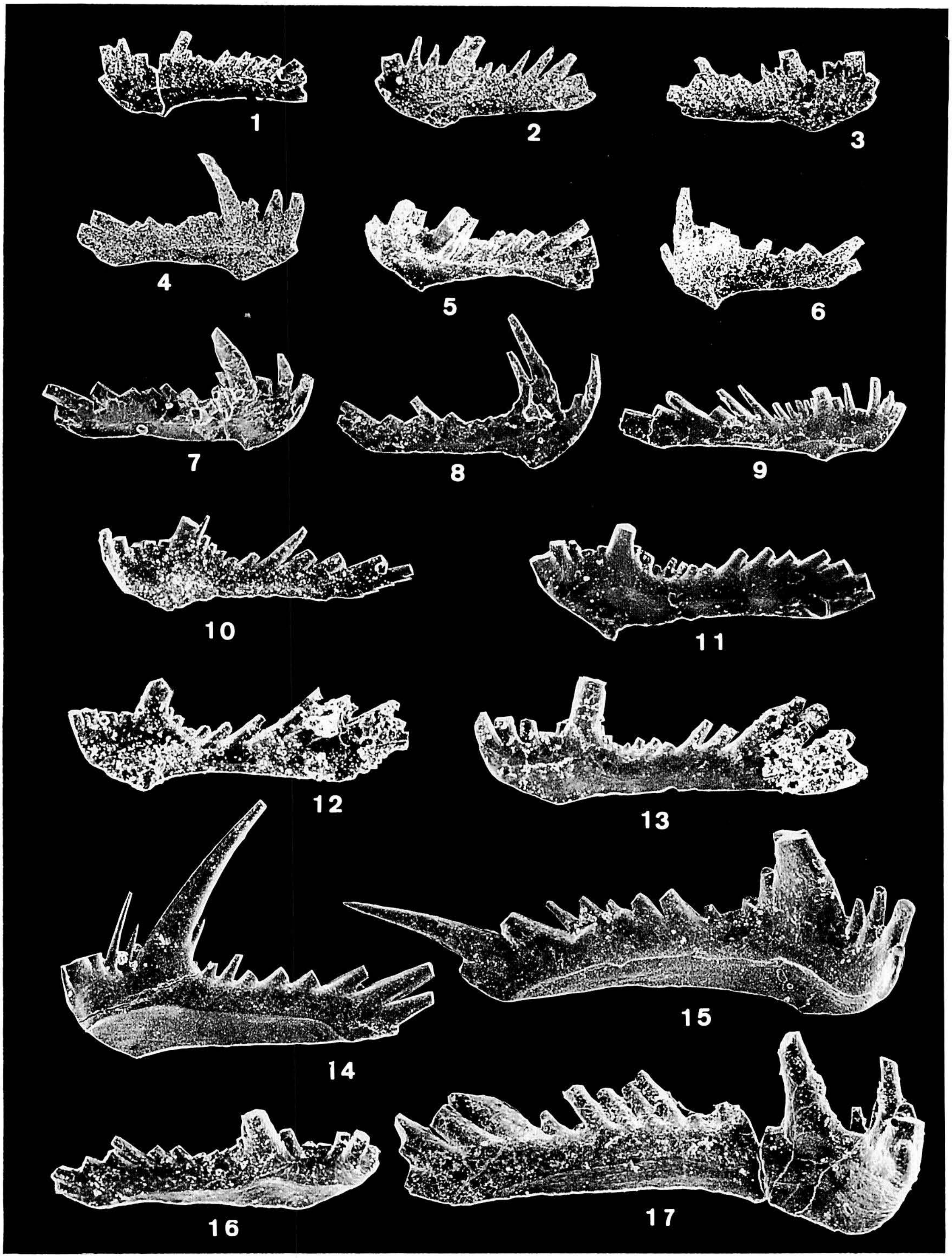

Figure 7. Sc element of *Ellisonia dinodoides* (Tatge). 1, 2: YNUC15670, 15671 from Loc. 33; 3: YNUC15672 from Loc. 32; 4: YNUC15673 from Loc. 31; 5: YNUC15674 from Loc. 30; 6: YNUC15675 from Loc. 28; 7, 8: YNUC15676, 15677 from Loc. 1202; 9–11: YNUC15678–15680 from Loc. 1191; 12: YNUC15681 from Loc. 1124; 13: YNUC15682 from Loc. 1122; 14, 15: YNUC15683, 15684 from Loc. 1 NK; 16, 17: YNUC15685, 15686 from Loc. 04. All figures are ×70.

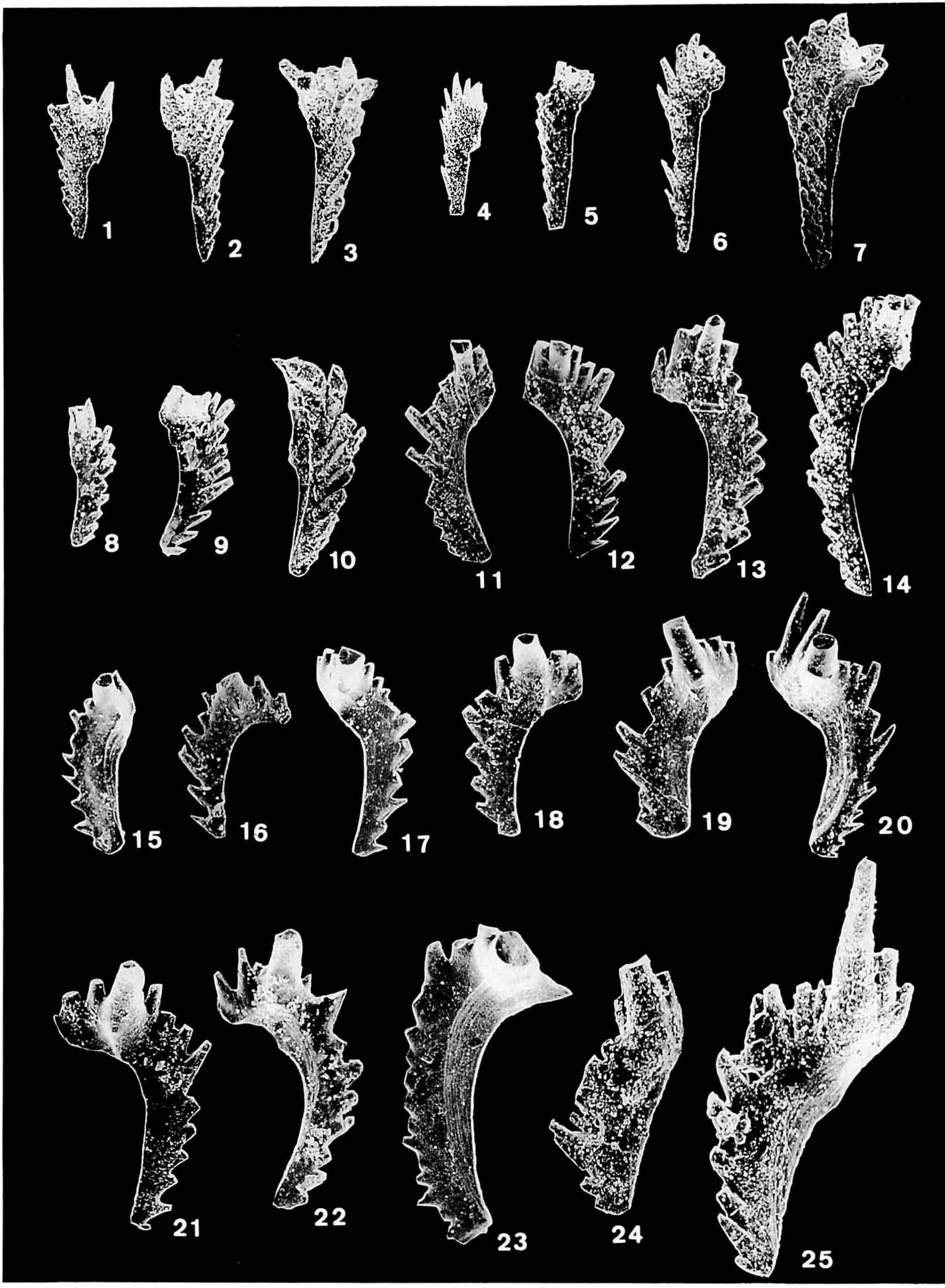

Figure 8. M element of *Ellisonia dinodoides* (Tatge). 1–3: YNUC15687–15689 from Loc. 33; 4–7: YNUC15690–15693 from Loc. 30; 8–10: YNUC15694–15696 from Loc. 1202: 11, 12: YNUC15697, 15698 from Loc. 1191; 13, 14: YNUC15699, 15700 from Loc. 1124; 15–23: YNUC15701–15709 from Loc. 1 NK; 24, 25: YNUC15710, 15711 from Loc. 04. All figures are ×70.

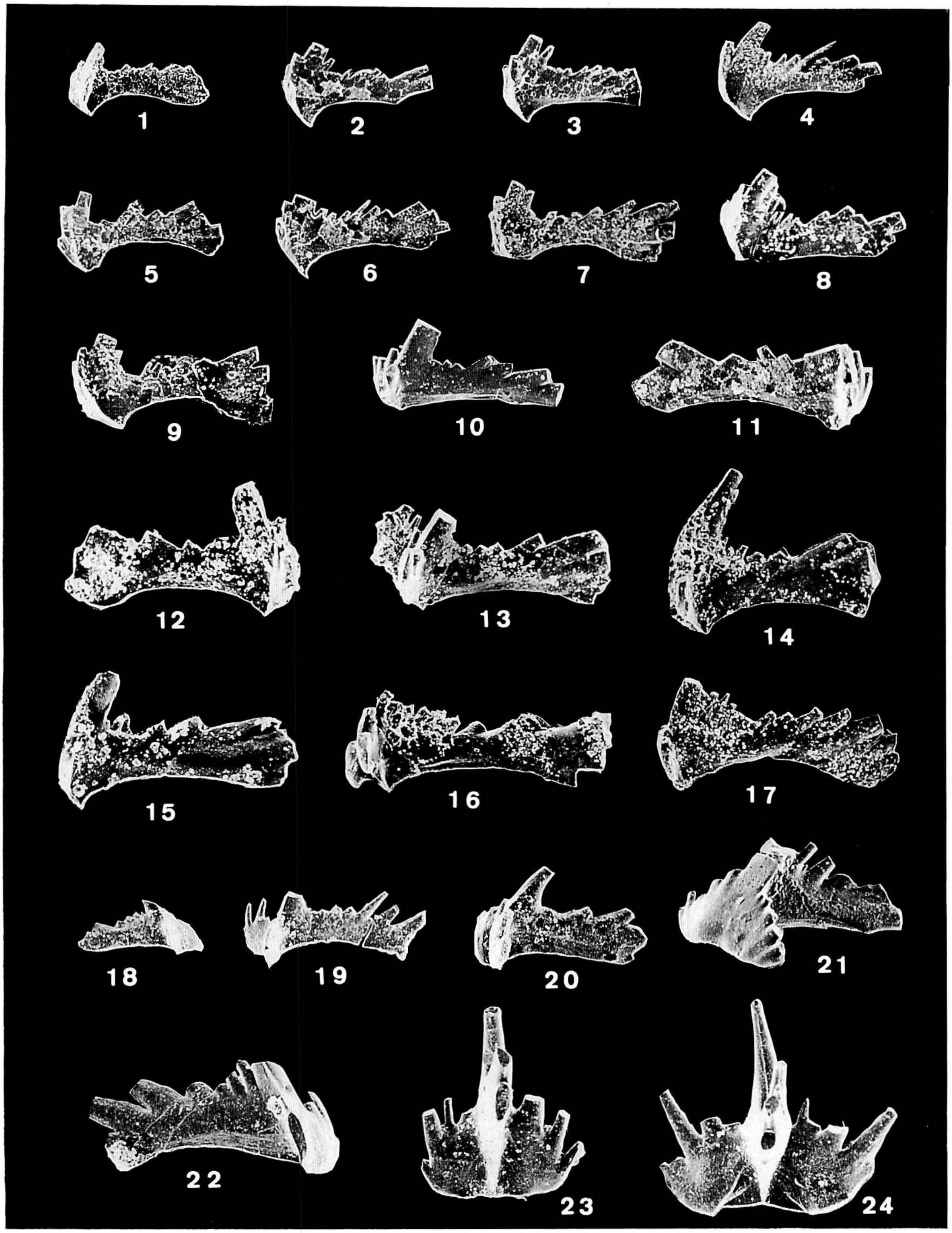

Figure 9. Sa element of *Ellisonia dinodoides* (Tatge). 1 : YNUC15712 from Loc. 31 ; 2–9 : YNUC15713–15720 from Loc. 1202 ; 10–13 : YNUC15721–15724 from Loc. 1124 ; 14–16 : YNUC15725–15727 from Loc. 1122 ; 17 : YNUC15728 from Loc. 1197 ; 18–24 : YNUC15729–15735 from Loc. 1 NK. All figures are ×70.

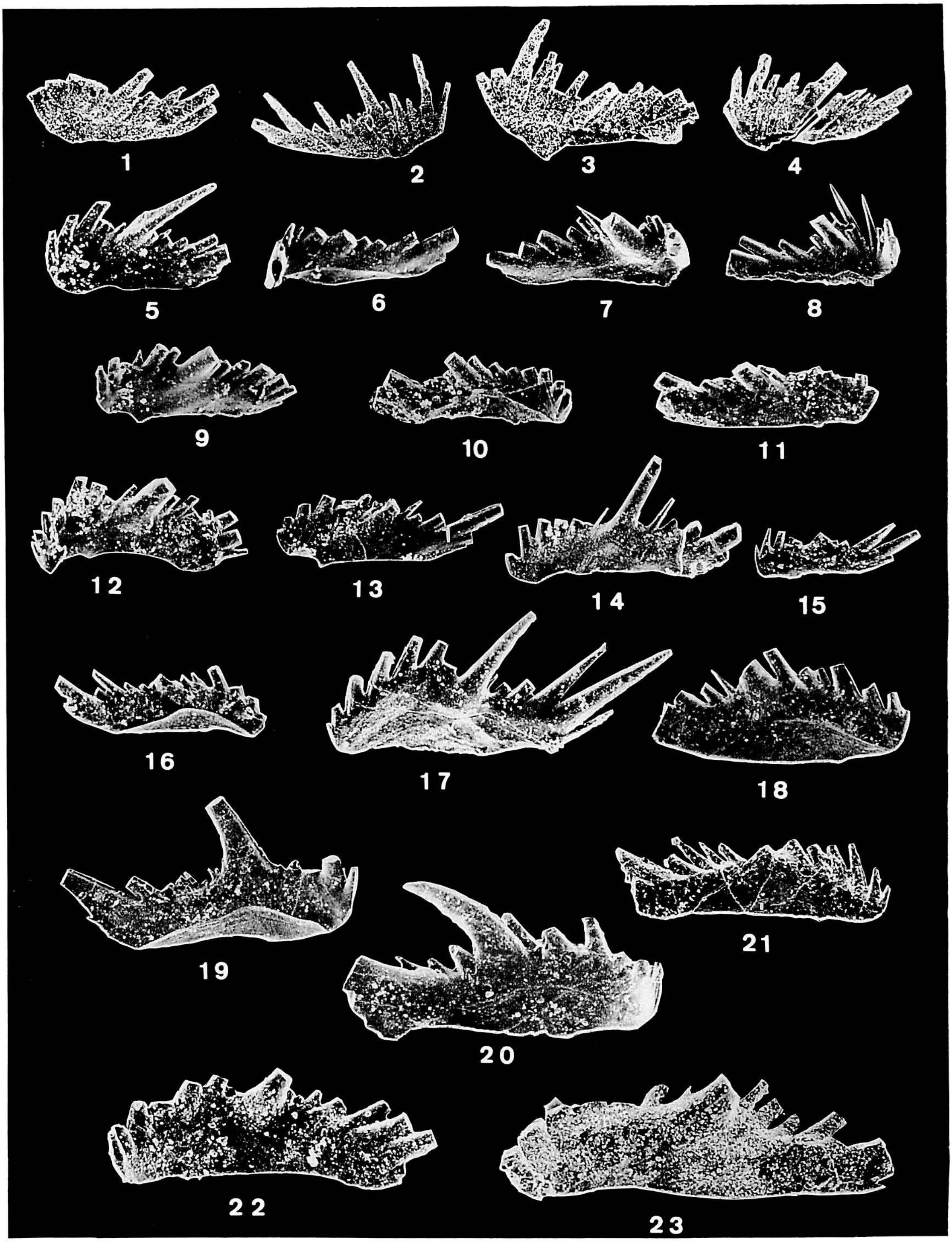

Figure 10. Sb element of *Ellisonia dinodoides* (Tatge). 1 : YNUC15736 from Loc. 33 ; 2 : YNUC15737 from Loc. 31 ; 3 : YNUC15738 from Loc. 30 ; 4 : YNUC15739 from Loc. 29 ; 5. 6 : YNUC 15740, 15741 from Loc. 1197 ; 7, 8 : YNUC15742, 15743 from Loc. 1191 ; 9–12 : YNUC15744–15747 from Loc. 1124 ; 13, 14 : YNUC15748, 15749 from Loc. 1122 ; 15–20 : YNUC15750–15755 from Loc. 1 NK : 21–23 : YNUC15756–15758 from Loc. 04. All figures are ×70.

degrees in the anterior portion to 10 degrees in the posterior portion. Two to four minute denticles are present behind the large denticle at the posterior end in some specimens. Zone of recessive basal margin occupies one half of the height of the anterolateral and posterior processes beneath the cusp.

Sb element: Length of the process ranges from 0.22 mm to 0.7 mm. The anterior process bends gently to sharply inward at the middle portion. The denticles on the anterior process are 5 to 8 in number and tend to increase in size and inclination posteriorly. The posterior process bears 4 to 7 denticles which tend to increase in size and inclination posteriorly. The largest denticle near the posterior end is sometimes as large as the cusp. Zone of recessive basal margin occupies one half to two thirds of the height of the process beneath the cusp.

Sc element: The anterior process ranges from 0.06 mm to 0.25 mm in length and bends gently to sharply inward at the middle portion. The denticles on the anterior process are 4 to 7 in number and tend to increase in size anteriorly. The denticles extend anteriorly in the anterior portion and incline posteriorly in the posterior portion. The posterior process is 0.2 mm to 0.75 mm in length and carries 7 to 13 denticles which increase in size and inclination posteriorly. The large denticles at the posterior end are sometimes as large as the cusp. Zone of recessive basal margin occupies more than one half of the height of the process beneath the cusp. The lower margin is almost horizontal throughout the posterior process and curves downward beneath the cusp and turns upward anteriorly on the anterior process and forms reverse-triangular shaped projection beneath the cusp.

Remarks: The innerlateral process of the M element of *E. triassica* is one third of the length of or subequal in length of the outerlateral process and relatively longer than that of *E. dinodoides.* The denticles on the innerlateral and outerlateral processes are 3 to 7 and 4 to 8 in number, respectively. The Sa element of *E. triassica* possesses longer and more strongly downwardly extended anterolateral processes with 3 to 10 denticles on each. The denticles on the posterior process range in number from 4 to 6 which are generally less than those of *E. dinodoides.* The Sc element of *E. triassica* possesses 4 to 8 denticles on the posterior process, which is less than in *E. dinodoides.* The anterior process of *E. triassica* shows remarkable morphologic variation in lateral curvature and relative length to that of the posterior process. The Sc element with strongly innerlaterally curved and/or relatively long anterior process resembles some Sb elements of *E. dinodoides.* The denticles on the anterior process, however, are 2 to 5 and generally less than those of *E. dinodoides.*

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田穂石灰岩産三畳紀コノドント *Ellisonia dinodoides* (Tatge) の構成エレメントならびに進化傾向：愛媛県東宇和郡城川町田穂上組に分布する，田穂石灰岩から産する *Ellisonia dinodoides* (Tatge) を検討したところ，M, Sa, Sb, Sc の4つの構成エレメントからなり，それらは2:1:2:6の割合の数で存在することが判明した。しかしSaエレメントがノリアンでは極めて少ないか，失われるようである。各エレメントは，スミシアンからアニシアンまで大きさが減少するが，アニシアンからノリアンにかけてはほぼ一定の大きさを保つ。エレメントの大きさと歯の数の相関係数は0.09から0.75で，標本ごとにかなりのばらつきを示す。この相関係数について，時代的な傾向は認められない。三畳紀において，個体の大きさが時代とともに減少するのは，比較的生存期間の長い複歯状コノドントに見られる一般的な傾向である。

小池敏夫

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967. EARLY SHELL FEATURES OF SOME LATE PALEOZOIC AMMONOIDS AND THEIR SYSTEMATIC IMPLICATIONS*

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Abstract. Microstructural characteristics of the early shell portion in 41 species of Late Paleozoic Goniatitina and Prolecanitina (Ammonoidea) are described based on optical and scanning electron microscopy of well-preserved specimens from the midcontinent of North America, England, and Urals (Russia). The results of observations reveal that the two suborders exhibit certain distinct features in the embryonic shell characters that help distinguish them. Species of the Goniatitina have an elliptical caecum in median section and a relatively large ammonitella angle, whereas those of the Prolecanitina have a rectangular caecum and a proximally constricted initial chamber in median section. Furthermore, in the species of the Goniatitina, the second septum is either close to or attached to the proseptum on the dorsal side, forming a necklike structure, and the embryonic shells are sculptured by longitudinal lirae instead of the microtubercles that are present in the Mesozoic Ammonitida. These observations and the available data on Mesozoic taxa suggest that the external and internal features of embryonic shells are useful for higher-level systematics of the Ammonoidea.

Key words. Goniatitina, Prolecanitina, early shell features, systematics, Late Paleozoic.

Introduction

Since the classical monograph by Branco (1879-80), many papers have been published describing the external and internal features of early whorls of various ammonoid taxa. As a result, it is clearly established that in all ammonoids, the early shell portion consists of a number of common characters and that at least in the Mesozoic Ammonoidea, their character states appear to be stable at higher taxonomic levels (Druschits and Khiami, 1969, 1970; Druschits and Doguzhaeva, 1974, 1981; Zakharov, 1974, 1977; Tanabe *et al*., 1979; Tanabe and Ohtsuka, 1985). As

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compared with Mesozoic ammonoids, Paleozoic ammonoids have been little studied for their early shell structures apart from a few papers (Böhmers, 1936; Miller and Unklesbay, 1943; Bogoslovskaya, 1959).

We have made an extensive survey of the external and internal features of the early shell portion in some Late Paleozoic ammonoids belonging to the Goniatitina and Prolecanitina. In this paper we describe the results of our observations and compare them with the available data on Mesozoic ammonoids, discussing the validity of the early shell features from the standpoint of higher-level systematics.

Material and methods

Thirty-nine species of the Goniatitina (27 genera of 20 families) and two species of the Prolecanitina listed in Appendix have been studied. Specimens of these species were collected from the Middle Carboniferous to Permian strata of the midcontinent of North America (Wyoming, Oklahoma, Arkansas, Missouri, Nevada, Kansas, Texas, and Mexico), England, and Urals (Russia) and were preserved in shales, limestones, and carbonate concretions. They include specimens studied and figured by Miller and Unklesbay (1943). Higher categories of these species were determined following the schemes of Kullmann (1981) and Glenister and Furnish (1981).

Most specimens were cut and polished along the median plane. The polished surface of each specimen was etched with 5% acetic acid for a few minutes, washed with distilled water, and then ion-coated with Pt-Pa after drying. These ion-sputtered specimens were observed for their early internal shell structures by means of Hitachi model S 2400 and Zeiss model DSM 940 scanning electron microscopes. Thin-sectioned specimens studied by Miller and Unklesbay (1943) were observed using a WILD optical microscope. Furthermore, we also measured certain internal shell characters (length of prosiphon, diameters of initial chamber and ammonitella, and ammonitella angle) in each specimen using a micrometer (accuracy ± 1 μm) attached to a Nikon model V16 profile projector and/or to an optical microscope (magnifications X50-200). Basic morphology, terminology and measurements of the ammonoid early shell portion in median section are diagramatically shown in Figure 1. The terminology of the embryonic shell characters applied in this paper is based on Branco (1879-80), Grandjean (1910), Druschits and Khiami (1969), and Landman and Waage (1982) (see Tanabe and Ohtsuka, 1985, figure 1). Measurements and character states of selected early shell structural elements in the species examined are summarized in Tables 2-3, in which the data of other species documented by Böhmers (1936) and Bogoslovskaya (1959) are included.

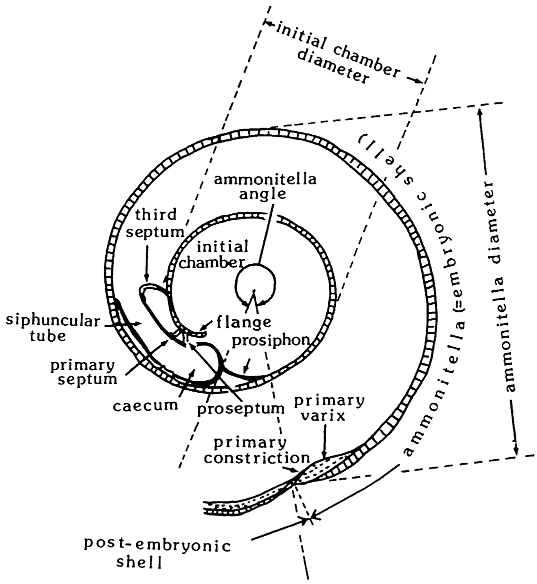

Figure 1. Basic morphology, terminology and measurements of the ammonoid internal shell structure at the early postembryonic stage (median section). After Branco (1879-80), Grandjean (1910), Druschits and Khiami (1969), and Landman and Waage (1982) for terminology of the embryonic shell characters.

The specimens utilized are reposited at the University of Iowa (SUI) for those described by Miller and Unklesbay (1943) and at the University Museum, University of Tokyo (UMUT) and the American Museum of Natural History (AMNH) for the remaining ones.

Notes on the ammonoid early shell features

To establish an adequate foundation, it is appropriate that we briefly discuss the general characteristics of the ammonoid early shell features based on the observations by previous authors and ourselves. The early shell portion of the Ammonoidea consists of a spindle-shaped to subspherical hollow initial chamber and subsequent whorls. The initial chamber has long been mistakenly called the protoconch, but it is not homologous with the protoconch of gastropods nor the prodissoconch of the Bivalvia that are formed during either embryogenesis or the post-hatching larval stage. A thick nacreous deposit termed the primary varix by Druschits *et al.* (1977) appears on the inner side of the ventral shell wall approximately one whorl from the base of the first whorl (pv; Figure 4-4b). The primary varix rapidly thins out adorally and is replaced by a clear constriction termed the primary constriction, from which marked changes in shell structure, whorl shape, and surface ornamentation occur synchronously (Figure 3E; Erben *et al.*, 1968, 1969; Birkelund and Hansen, 1968, 1974; Kulicki, 1979; Birkelund, 1981; Tanabe *et al.*, 1980; Bandel *et al.*, 1982; Landman and Bandel, 1985; Landman, 1987, 1988; Tanabe, 1989). The early shell portion of all ammonoids consists of such common structural elements as the prosiphon, caecum, flange, proseptum, septa, and siphuncle. Minute ammonoid shells consisting of an initial chamber and one subsequent whorl terminating at the primary varix rarely occur as fossils, and Druschits and Khiami (1969) termed them ammonitellas.

Relying on comparison of the early shell microstructure with extant shelled cephalopods, most recent authors regarded the ammonitella as the embryonic shell (Birkelund and Hansen, 1968; Druschits and Khiami, 1970; Druschits *et al.*, 1977; Kulicki, 1979; Tanabe *et al.*, 1980; Druschits and Doguzhaeva, 1981; Bandel, 1982, 1986; Landman, 1982; Tanabe and Ohtsuka, 1985; Tanabe, 1989). Detailed microscopic observations of preserved ammonitellas in Carboniferous goniatites (Tanabe *et al.*, 1993) and Cretaceous ammonites (Landman, 1982, 1985) have shown that only a small portion of the siphuncle and a few septa formed in the embryonic stage (see Figure 4-4a).

Observations

1. Goniatitina

Initial chamber.—In every species the initial chamber is nearly spherical to slightly elliptical in median section. It is unusually large (0.9-1.0 mm in median diameter) in *Perrinites* of the Perrinitidae. *Goniolobоceras welleri* of the Gonioloboceratidae may also have a large initial chamber in view of its large embryonic shell size, though we could not measure the exact initial chamber size in the specimen examined because of secondary breakage. The initial chamber in the other

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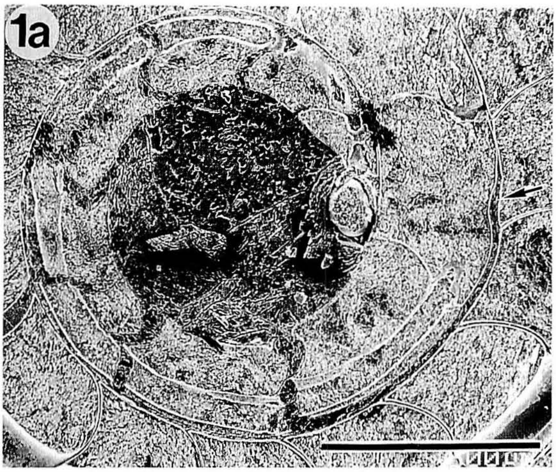
→ **Figure 2.** Scanning electron micrographs of the early internal shell structure in median section. Overall views of early whorls (1a, 2a, 3a) and close-up of the caecum area (1b, 2b, 3b). **1a-b.** *Goniatites* sp. aff. *G. crenistria* Phillips (Goniatitina: Goniatitaceae). UMUT PM 19019-2. **2a-b.** *Goniatites choctawensis* Shumard (Goniatitina: Goniatiaceae). UMUT PM 19020-2. **3a-b.** *Glaphyrites warei* (Miller and Owen) (Goniatitina: Gastrioceratacea). UMUT PM 19026-2. Scale bars: 500 μm for 1a, 2a and 100 μm for 1b, 2b and 3b. Arrows in 1a, 2a and 3a point to the primary constriction. psh: prosiphon, c: caecum, f: flange, pr: proseptum (1st septum), ps: primary septum (2nd septum).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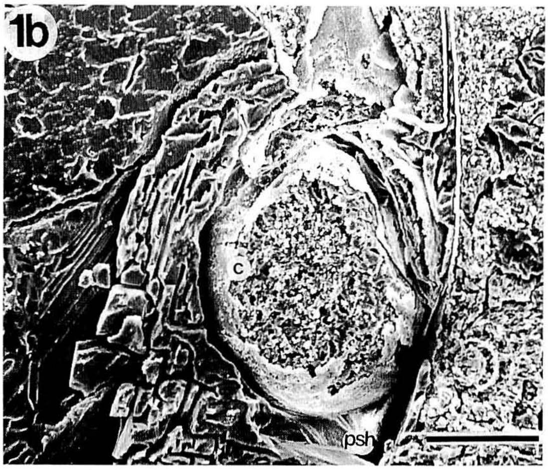
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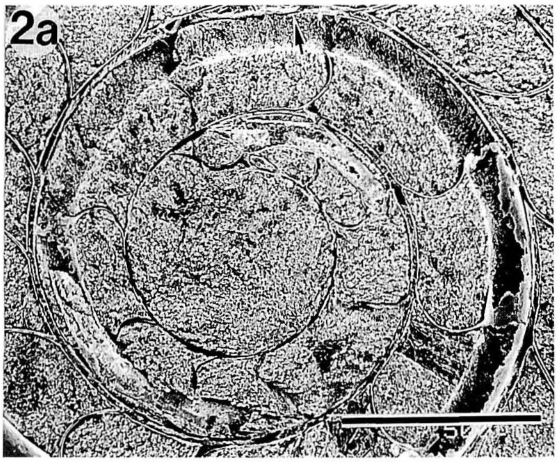
c
psh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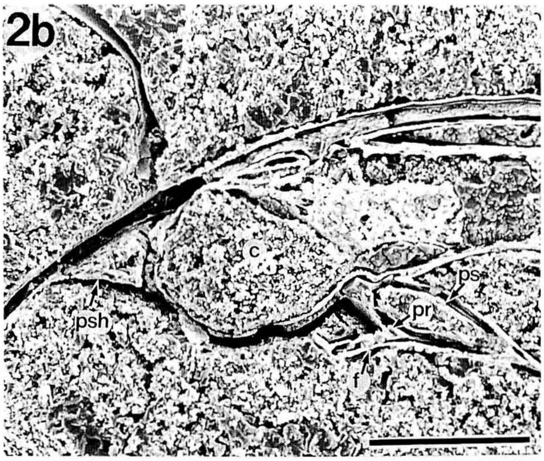
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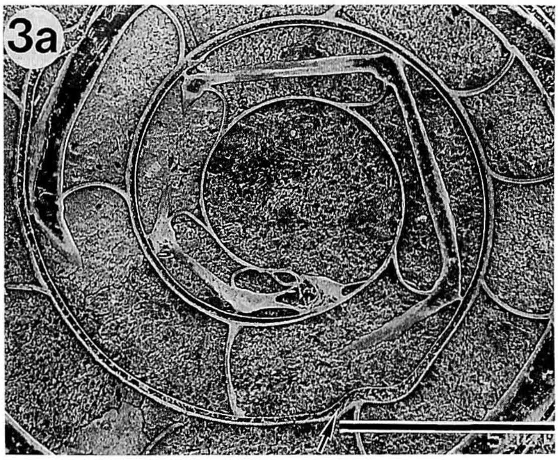
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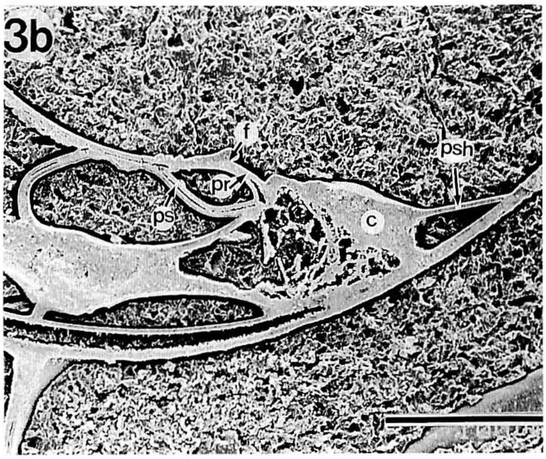
3b
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species ranges from 0.34 to 0.70 mm in median diameter. The microstructure of the initial chamber wall is not preserved in most specimens examined, but in the ammonitellas of *Aristoceras* sp. from Kansas it consists of a single prismatic layer (Tanabe *et al*., 1993). The flange, that is the inner lip of the initial chamber wall, is well developed in every species (see Figures 2-2b, 2-3b, 3-1b, and 4-1b).

Caecum.—The bulb-like earliest portion of the siphuncle is called the caecum. In median section, it is adapically convex and elliptical to spherical in outline in all species (Figures 2-1b, 2-2b, 2-3b, 3-2a, 3-3, 4-1b, 4-3, & 5-1b). In a specimen of *Goniatites* sp. aff. *G. crenistria*, the wall of the caecum is made up of multilayered black membranes, which might be originally organic (see Figure 2-1b).

Prosiphon.—The prosiphon is an organic sheet that extends from the adapical end of the caecum to the inner surface of the initial chamber. In every species it is relatively short (0.02-0.11 mm) in relation to the initial chamber size and gently curved ventrally. In many species, the prosiphon is frequently split into two or three sheets, of which the shorter ones appear on the ventral side of the caecum (see Figures 3-2b, 4-1b, and 6A).

Proseptum.—The constricted base of the caecum is enclosed by the first septum, currently called the proseptum. In all species examined, it is gently convex adapically in median section (Figures 2-2b, 2-3b, 3-1b, 3-2c) and has a short septal neck on the dorsal side of the caecum, which is directed both adorally and adapically (Figures 2-2b and 3-2c). Owing to the secondary recrystallization during fossilization we can not observe the original microstructure of the proseptum in the specimens examined. According to Erben *et al*. (1969), it is prismatic in the exceptionally well-preserved specimen of *Gastrioceras* from the Pennsylvanian Kendrick Shale of Kentucky.

Second septum (*primary septum*).—The second septum occurs in close vicinity to the proseptum. It is gently concave adapically, with a retrochoanitic septal neck, as in the third septum and after. In the species of the Goniatitidae and *Glaphyrites*, the second septum is united with the proseptum on the ventral side. It is connected with the proseptum on the dorsal side of the caecum, forming a necklike attachment (Figures 2-2b, 2-3b, 3- 1b, 3-2c, 4-1b, 5-1b, and 6A).

Böhmers (1936) first documented these characteristic features of the second septum in some Permian Goniatitina and Prolecanitina and proposed the term prosepta for the first two septa. This terminology was subsequently applied in the description of the internal shell structure of Upper Paleozoic ammonoids by Miller and Unklesbay (1943). Erben *et al*. (1968, 1969) redefined the second septum as the primary septum based on the interpretation that it was secreted by the adapical epithelium unlike the secretion of the proseptum by the lateral, ventral and dorsal parts of the epithelium. According to Erben *et al*. (1968, 1969), the primary septum in the *Gastrioceras* specimen from the Kendrick Shale is prismatic like the proseptum, though we could not observe its original microstructure in the present material because of its insufficient preservation.

Siphuncle.—In most species the siphuncle is ventral throughout ontogeny (Table 3), but it keeps a central position at least in the first three whorls in *Agathiceras applini* of the Agathiceratidae (see Miller and Unklesbay, 1943, fig. 8A). A similar condition was described in *A. cancellatus* Haniel by Böhmers (1936, fig. 39). In *Bisatoceras* sp. of the Bisatoceratidae, the siphuncle occupies a central position in the first whorl, and then abruptly shifts its position to the ventral side in the earlier part of the second whorl (Figure 4-1a). In most species the siphuncular tube follows the spiral of the shell except in the species of *Glaphyrites* where it extends straight across each chamber in the first whorl (Figures 2-3a and 3-1a ; see also Miller and

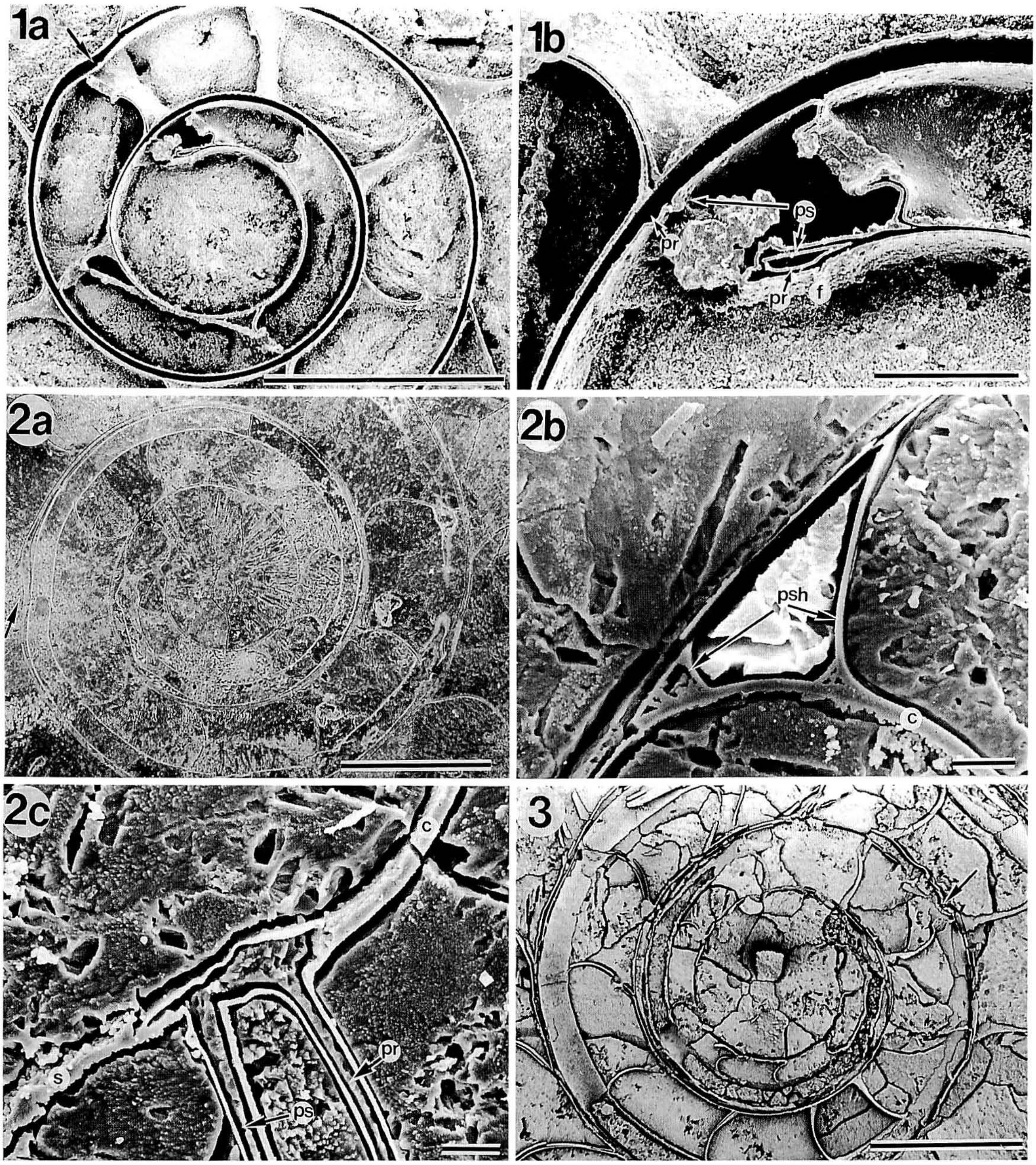
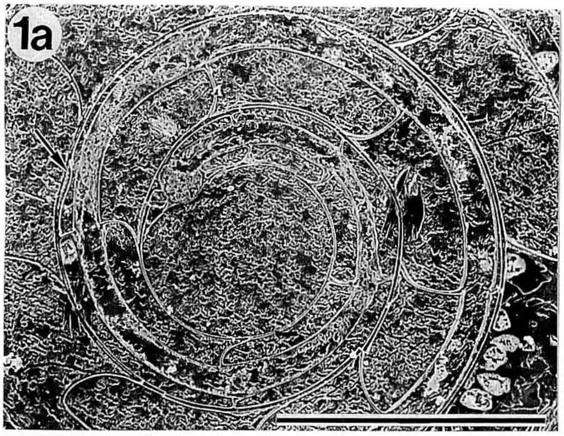


Figure 3. Scanning electron micrographs of the early internal shell structure in median section. **1a-b.** *Glaphyrites clinei* (Miller and Owen) (Goniatitina : Gastrioceratаceae). Overall view of early whorls (1a) and adapical end of the first whorl (1b). UMUT PM 19028. **2a-c.** *Glaphyrites hyattianus* Girty. Enlarged ventral (2b) and dorsal (2c) portions of the caecum area. UMUT PM 19025-2. **3.** *Arkanites relictus* (Quinn, McCaleb and Webb) (Goniatitina : Gastrioceratаceae). UMUT PM 19029. Scale bars : 500μm for 1a, 2a and 3, 100 μm for 1b, and 10 μm for 2b and 2c. Arrows in 1a, 2a and 3 point to the primary constriction. For abbreviations see the explanation of Figure 2.

Table 1. Measurement data of the species examined. PD : median diameter of initial chamber, AD : median diameter of ammonitella, AA : ammonitella angle, PL : length of prosiphon.

Sub-order	Superfamily	Family	Species	PD (mm)	AD (mm)	AA (deg.)	PL (mm)	PL/PD	Remarks
Goniatitina	Dimorphocerataceae	Dimorphoceratidae	*Dimorphoceras politum* (Shumard)	---	0.90	---	---	---	SUI 1755
		Girtyoceratidae	*Girtyoceras meslerianum* (Girty)	.45	.96	400	---	---	UMUT PM 19023-1
			Eumorphoceras plummeri Miller & Youngquist	---	1.04	---	---	---	UMUT PM 19030
			Gatherites morrowensis (Miller & Moore)	.42	.84	385	---	---	UMUT PM 19032
	Goniatitaceae	Goniatitidae	*Goniatites* sp. aff. *G. crenistria* Phillips	.48	.95	382	.11	.23	UMUT PM 19019-1
				.60	1.10	372	.08	.13	UMUT PM 19019-2
			Goniatites choctawensis Shumard	.56	1.06	345	---	---	UMUT PM 19020-1
				.55	1.09	386	.06	.07	UMUT PM 19020-2
			Goniatites multiliratus Gordon	.53	.94	384	---	---	UMUT PM 19033
		Agathiceratidae	*Agathiceras applini* Plummer & Scott	.48	1.03	---	.05	.10	SUI 1766
	Neoglyphiocerataceae	Cravenoceratidae	*Cravenoceras richardsonianum* (Girty)	.46	.80	367	---	---	UMUT PM 19021
			Cravenoceras incisum (Hyatt)	.53	.95	380	---	---	UMUT PM 19022-1
	Gastriocerataceae	Gastrioceratidae	*Pseudogastrioceras simulator* (Girty)	.40	.80	364	.04	.17	SUI 1740
			Owenoceras bellilineatum (Miller & Owen)	---	.87	355	---	---	SUI 1713
		Reticuloceratidae	*Arkanites relictus* (Quinn, McCaleb & Webb)	.51	.81	386	---	---	UMUT PM 19029
		Glaphyritidae	*Glaphyrites hyattianus* (Girty)	.59	1.03	405	.05	.08	UMUT PM 19025-2
			Glaphyrites warei (Miller & Owen)	.46	.88	385	.06	.13	UMUT PM 19026-1
				.45	.86	372	.05	.12	UMUT PM 19026-2
			Glaphyrites jonesi (Miller & Owen)	.54	.96	375	---	---	UMUT PM 19027
			Glaphyrites clinei (Miller & Owen)	.39	.71	382	---	---	UMUT PM 19028
				.52	.94	364	---	---	SUI 1735
			Glaphyrites welleri (Smith)	.35	.81	356	.03	.09	SUI 1726
		Homoceratidae	*Homoceras subglobosum* (Bisat)	.53	.91	385	.10	.19	UMUT PM 19024-2
	Goniolobocerataceae	Goniolobocetatidae	*Gonioloboceras welleri* Smith	---	1.92	384	---	---	SUI 1743
	Shumarditaceae	Perrinitidae	*Properrinites bakeri* (Plummer & Scott)	.70	1.19	---	---	---	SUI 1790
			Perrinites sp.	1.03	2.31	383	---	---	AMNH 41183a
				.89	2.00	382	.16	.18	AMNH 41183b
	Adrianitaceae	Adrianitidae	*Texoceras* sp.	---	.97	---	---	---	UMUT PM 19037-1
			Adrianites dunbari Miller & Furnish	.63	1.00	365	12	.19	SUI 1764
			Crimites elkoensis Miller, Furnish & Clarke	.37	.65	345	---	---	UMUT PM 19038
	Popanocerataceae	Popanoceratidae	*Popanoceras annae* Ruzhencev	---	.66	---	---	---	SUI 1777
			Peritrochia erebus Girty	.45	.88	410	---	---	UMUT PM 19039-1
	Neoicocerataceae	Metalegoceratidae	*Metalegoceras baylorense* White	.45	.85	365	.02	.05	UMUT PM 19035
	Cyclolobaceae	Cyclolobidae	*Mexicoceras guadalupense* (Girty)	.52	.93	378	---	---	SUI 1782
		Vidrioceratidae	*Vidrioceras* sp.	.44	.80	361	---	---	UMUT PM 19329
	Thalassocerataceae	Thalassoceratidae	*Eothalassoceras inexpectans* (Miller & Owen)	.37	.66	356	.03	.08	UMUT PM 19036-1
				.37	.66	360	---	---	UMUT PM 19036-2
			Aristoceras sp.	.36	.75	368	---	---	UMUT PM 19010
		Bisatoceratidae	*Bisatoceras* sp.	.34	.62	359	.11	.31	UMUT PM 19033-1
Prolecanitina	Medlicottiaceae	Pronoritidae	*Pronorites praepermicus* Karpinsky	.61	1.22	330	.26	.43	SUI 1686
			Neopronorites vulgaris (Karpinsky)	.44-.54	1-1.10	310-320	---	---	Bogoslovskaya (1959)
			Neopronorites permicus (Tschernow)	.44-.56	.96-1.1	340	---	---	Bogoslovskaya (1959)
		Medlicottiidae	*Artinskia electraensis* (Plummer & Scott)	.48	1.01	340	---	---	UMUT PM 19040-1
				.52	1.16	355	.05	.10	UMUT PM 19040-2
			Artinskia artiensis (Grünewaldt)	.43-.44	.90	345	---	---	Bogoslovskaya (1959)
			Medlicottia orbignyana (Verneuil)	.34	.72	326-330	---	---	Bogoslovskaya (1959)
	Prolecanitaceae	Daraelitidae	*Daraelites elegans* Tschernow	.45	1.06	---	---	---	Bogoslovskaya (1959)

⟶ **Figure 4.** Scanning electron micrographs of the early internal shell structure in median section. **1a-b.** *Bisatoceras* sp. (Goniatitina : Thalassocerataceae). Early whorls (1a) and close-up of the caecum area (1b). UMUT PM 19033-1. **2.** *Eothalassoceras inexpectans* (Miller and Owen) (Goniatitina : Thalassocerataceae). Overall view of early whorls. UMUT PM 19036-1. **3.** *Crimites elkoensis* Miller, Furnish and Clarke. Overall view of early whorls. UMUT PM 19038. **4a-b.** *Aristoceras* sp. (Goniatitina : Thalassocerataceae). Overall view (4a) and close-up of the apertural portion (4b) of a full-grown embryonic shell (ammonitella). UMUT 19010 (same specimen as figured by Tanabe *et al.*, 1993, fig. 7). Scale bars : 500 μm for 1a, 2, 3 and 4a, and 100 μm for 1b and 4b. Arrows in 1a, 2, 3 and 4a point to the primary constriction. pv : a thick nacreous swelling (primary varix). For other abbreviations see the explanation of Figure 2.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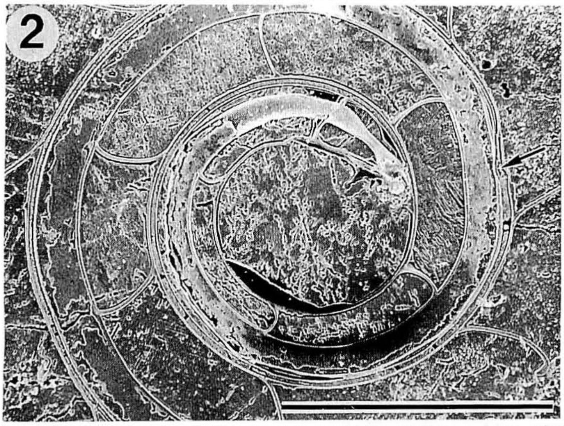
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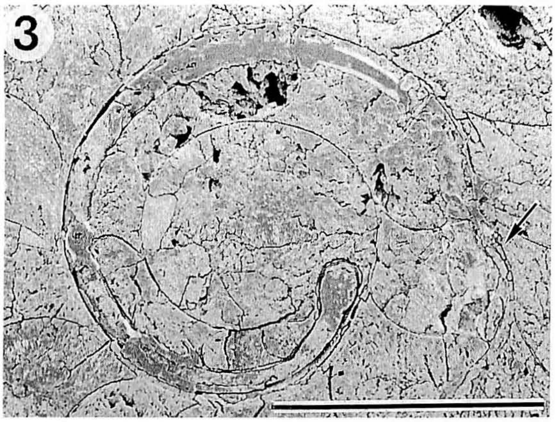
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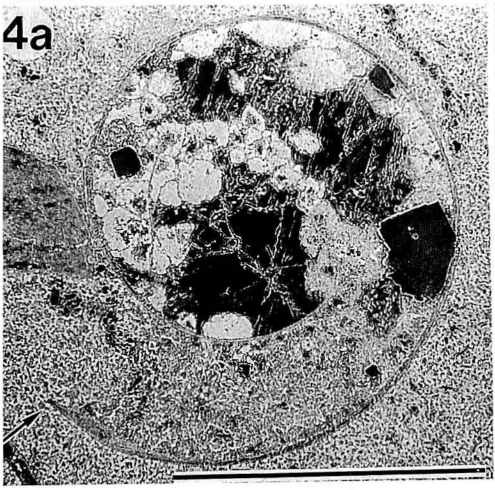
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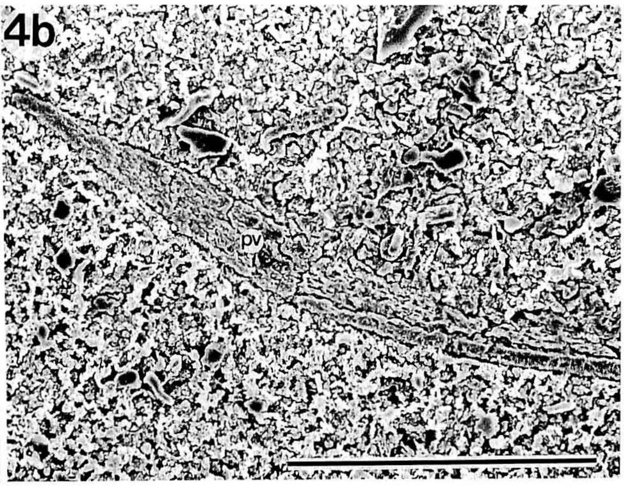

4b
pv

Unklesbay, 1943, pl. 2, fig. 2; fig. 6G).

Ammonitella.—The diameter of ammonitellas in median section ranges from 0.71 to 1.19 mm in most species. However, *Gonioloboceras welleri* (Goniolobocertidae) and *Perrinites* sp. (Perrinitidae) both have an extremely large ammonitella more than 1.9 mm in median diameter. The ammonitella angle ranges from 345° to 410° in the species examined (Table 1). There is a significant positive linear relationship between the ammonitella and initial chamber diameters (Figure 7). The ammonitella diameter, however, appears to be independent of the ammonitella angle (Figure 8). Similar conditions have been observed in Mesozoic ammonoids (Tanabe *et al.*, 1979, fig. 5; Tanabe and Ohtsuka, 1985, figs. 4, 5).

External and internal microstructures of the ammonitella wall are rarely preserved in Paleozoic ammonoids because of recrystallization. In the present material we could only observe these structures in the ammonitellas of *Aristoceras* sp. and *Vidrioceras* sp. from the Upper Carboniferous (Pennsylvanian) of Kansas. In the two species, the ammonitella wall is prismatic until the appearance of the nacreous primary varix (pv; Figure 4-4b; Tanabe *et al.*, 1993). Some ammonitellas of the latter species removed from the weathered portion of a carbonate concretion are ornamented with evenly spaced longitudinal lirae on their exposed surfaces (Figure 5-4). This ornament appears to be characteristic of the embryonic stage, since it is absent in medium-to-large-sized specimens. The outer surface of ammonitellas of *Aristoceras* sp. is smooth without any trace of ornamentation (Figure 4-3).

2. Prolecanitina

Initial chamber.—Pronorites praepermicus and *Artinskia electraensis* both belonging to the Medlicottiaceae have a slightly elliptical initial chamber, 0.48-0.61 mm in median diameter; its proximal portion is constricted in shape (Figure 5-2a). Bogoslovskaya (1959, pl. 2, figs. 1, 3) figured constricted initial chambers of *Artinskia artiensis* and *Medlicottia orbignyana* of the same superfamily. However, such a constriction is not clearly illustrated in Böhmers' (1936) drawings of some Prolecanitina in median section.

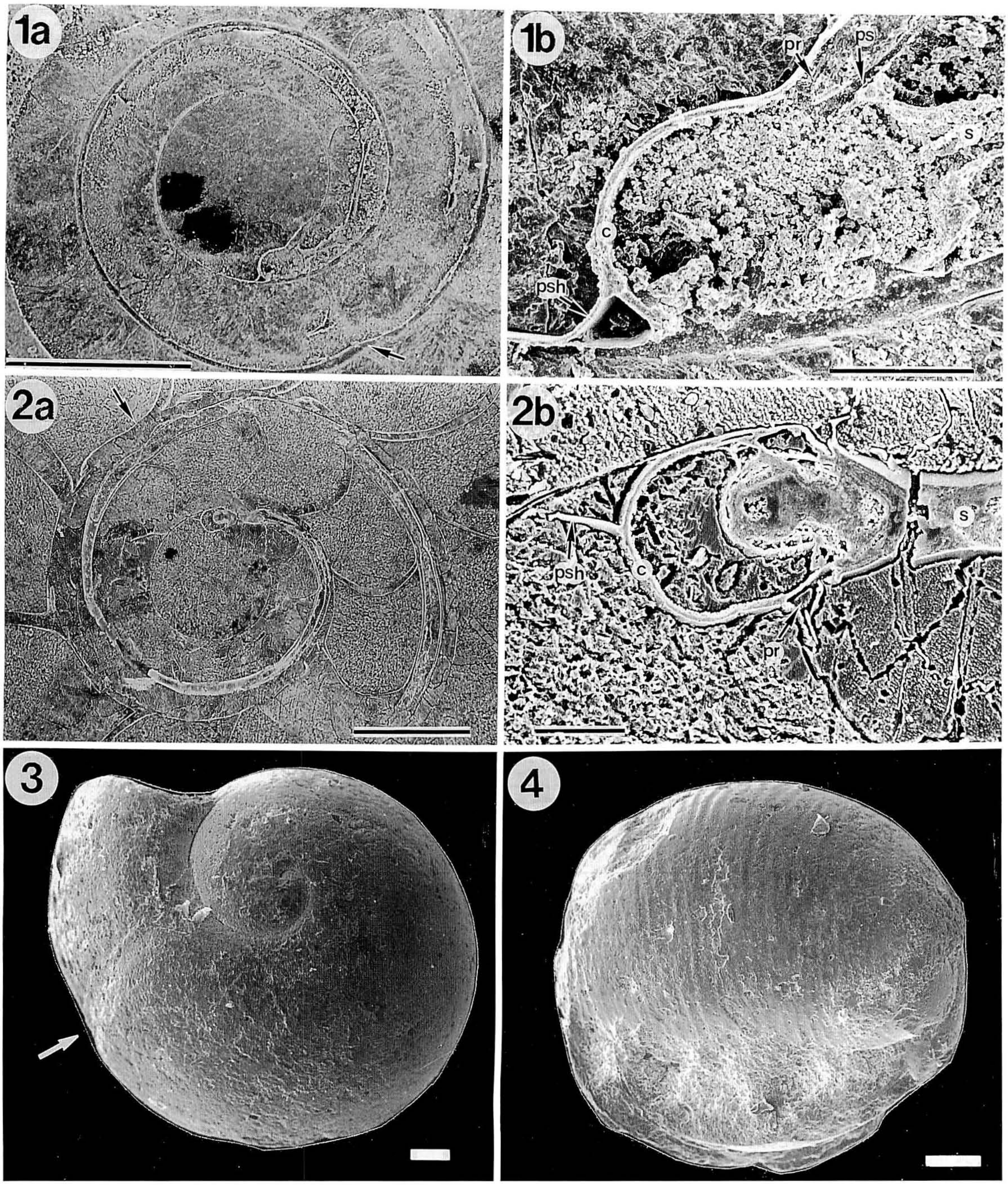
Caecum.—The two species examined possess a rectangular caecum in median section (Figure 5-2b). A similar shaped caecum was illustrated in other Prolecanitina (*A. artiensis, M. noetlingi*, and *Neopronorites vulgaris*) by Bogoslovskaya (1959, pl. 2)

Prosiphon.—The prosiphon is relatively long (0.26 mm) in *P. praepermicus* but is short (0.05 mm) in *A. electraensis* (Figures 5-2b & 6B). In both species, it is gently curved ventrally. Böhmers (1936) and Bogoslovskaya (1959) also described such a short and curved prosiphon in other Permian Prolecanitina.

Second septum.—The proseptum in *P. praepermicus* and *A. electraensis* examined is slightly convex adapically in median section, and its septal neck on the dorsal side is directed both adapically and adorally, as in the Goniatitina (Figures 5-2b and 6B). These features of the proseptum were reported in other Prolecanitina by Böhmers (1936).

Primary septum.—Unlike the Goniatitina,

→ **Figure 5.** Scanning electron micrographs of the early internal shell structure in median section (1, 2) and of isolated minute shell (3, 4). **1a-b.** *Homoceras subglobosum* (Bisat) (Goniatitina: Gastrioceraceae). Overall view of early whorls (1a) and close-up of the caecum area (1b). PM 19024-2. **2a-b.** *Artinskia electraensis* (Plummer and Scott) (Prolecanitina: 2a-b. *Artinskia electraensis* (Plummer and Scott) (Prolecanitina: Medlicottiaceae). Overall view of early whorls (2a) and close-up of the caecum area (2b). PM 19040-2. **3-4.** *Vidrioceras* sp. (Goniatitina: Cyclolobaceae). 3. Early postembryonic shell (lateral view). UMUT PM 19344. 4. Embryonic shell (ammonitella) with longitudinal lirae (frontal view). UMUT PM 19014. Scale bars: 500 μm for 1a and 2a, 100 μm for 3 and 4, and 50 μm for 1b and 2b. Arrows in 1a, 2a and 3 point to the primary constriction. s: siphuncular tube. For other abbreviations see the explanation of Figure 2.


1a
1b
pr
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4

Table 2. Character states of selected early internal shell structural elements in the species examined. Data sources: 1. Böhmers (1936), 2. Bogoslovskaya (1959).

Sub-order	Superfamily	Family	Species	Length and shape of prosiphon	Shape of caecum	Initial position of siphuncle
Goniatitina	Dimorphocerataceae	Girtyoceratidae	*Girtyoceras meslerianum* (Girty)	?	Elliptical	Ventral
	Goniatitaceae	Goniatitidae	*Goniatites* aff. *crenistria* Phillips	Short & curved	Elliptical	Ventral
			Goniatites choctawensis Shumard	?	Elliptical	Ventral
			Goniatites multiliratus Gordon	?	Elliptical	Ventral
		Agathiceratidae	*Agathiceras applini* Plummer & Scott	Short & curved	Elliptical	Central
			Agathiceras sundaicum Haniel[1]	Short & curved	Elliptical	Central
	Neoglyphiocerataceae	Neoglyphioceratidae	*Neoglyphiceras abramovi* Popow	Short & curved	Elliptical	Subcentral
		Cravenoceratidae	*Cravenoceras richardsonianum* (Girty)	?	Elliptical	Ventral
			Cravenoceras incisum (Hyatt)	?	Elliptical	Ventral
	Gastriocerataceae	Gastrioceratidae	*Pseudogastrioceras simulator* (Girty)	Short & curved	Elliptical	Ventral
			Owenoceras bellilineatum (Miller & Owen)	?	?	Ventral
		Reticuloceratidae	*Arkanites relictus* (Quinn, McCaleb & Webb)	?	Elliptical	Ventral
		Glaphyritidae	*Glaphyrites hyattianus* (Girty)	Short & curved	Elliptical	Ventral
			Glaphyrites warei (Miller & Owen)	Short & curved	Elliptical	Ventral
			Glaphyrites jonesi (Miller & Owen)	?	?	Ventral
			Glaphyrites clinei (Miller & Owen)	?	?	Ventral
			Glaphyrites celleri (Smith)	Short & curved	Elliptical	Ventral
		Homoceratidae	*Homoceras subglobosum* (Bisat)	Short & curved	Elliptical	Ventral
	Goniolobocerataceae	Gonioloboceratidae	*Gonioloboceras welleri* Smith	Short & curved	Elliptical	Ventral
	Shumarditaceae	Perrinitidae	*Properrinites bakeri* (Plummer & Scott)	?	Elliptical	Ventral
	Adrianitaceae	Adrianitidae	*Adrianites dunbari* Miller & Furnish	Short & curved	Elliptical	Ventral
			Adrianites cancellatus Haniel[1]	?	Elliptical	Ventral
			Crimites elkoensis Miller, Furnish & Clarke	?	Elliptical	Ventral
	Popanocerataceae	Popanoceratidae	*Popanoceras annae* Ruzhencev	?	?	Ventral
	Neoicocerataceae	Metalegoceratidae	*Metalegoceras baylorense* White	Short & curved	Elliptical	Ventral
	Cyclolobaceae	Cyclolobidae	*Mexicoceras guadalupense* (Girty)	Short & curved	?	Ventral
	Thalassocerataceae	Thalassoceratidae	*Eothalassoceras inexpectans* (Miller & Owen)	Short & curved	Elliptical	Subventral
		Bisatoceratidae	*Bisatoceras* sp.	Short & curved	Elliptical	Central
Prolecanitina	Prolecanitaceae	Prolecanitidae	*Prolecanites sepentinus* Phillips[1]	?	?	Ventral
		Daraelitidae	*Daraelites submeeki* Haniel[1]	?	?	Ventral
	Medlicottiaceae	Pronoritidae	*Pronorites praepermicus* Karpinsky	Long & curved	Rectangular	Ventral
			Pronorites timorensis Haniel[1]	?	?	Ventral
			Neopronorites vulgaris (Karpinsky)[2]	Short & curved	Rectangular	Ventral
		Medlicottiidae	*Artinskia electraensis* (Plummer & Scott)	Short & curved	Rectangular	Ventral
			Artinskia artiensis (Grünewaldt)[2]	Short & curved	Rectangular	Ventral
			Propinacoceras simile Haniel[1]	?	?	Ventral
			Medlicottia artiensis Grünew[1]	?	?	Ventral
			Medlicottia orbignyana (Verneuil)[2]	Short & curved	Rectangular	Ventral
			Episageceras noetlingi Haniel[1]	?	?	Ventral

the second septum in all Prolecanitina hitherto investigated does not appear in close vicinity to the proseptum (Figure 5-2a, b; Böhmers, 1936, figs. 3-8; Miller and Unklesbay, 1943, fig. 5F; pl. 1, fig. 3; Bogoslovskaya, 1959, pl. 2). Like the third septum, the second septum in *Artinskia* is convex adorally in median section, with a retrochoanitic septal neck (Figure 5-2a), so that it is more similar to subsequent septa than to the proseptum.

Siphuncle.—The siphuncle keeps a ventral position throughout ontogeny in the two species. The same evidence has been described in other Prolecanitina (Böhmers, 1936; Miller and Unklesbay, 1943; Bogoslovskaya, 1959).

Ammonitella.—The two medlicottiaceans have an ammonitella of similar size (1.01-1.22 mm in median diameter). Their ammonitella angles range from 330° to 355°, being much smaller than those of most Goniatitina (Table 1; Figure 8).

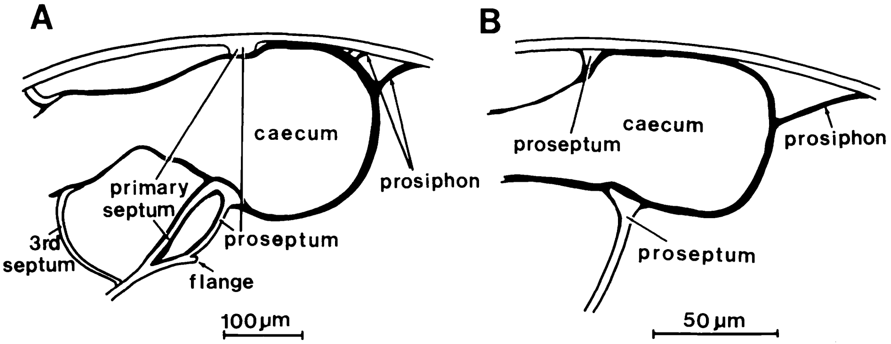

Figure 6. Diagrammatic drawings of the adoral portion of the initial chamber in *Glaphyrites hyattianus* (Girty) (Goniatitina : Gastriocerataceae) (A) and *Artinskia electraensis* (Plummer and Scott) (Prolecanitina : Medlicottiaceae) (B), showing the differences in the shape of the caecum and proseptum. A : UMUT PM 19025-2, B : UMUT PM 19040-2.

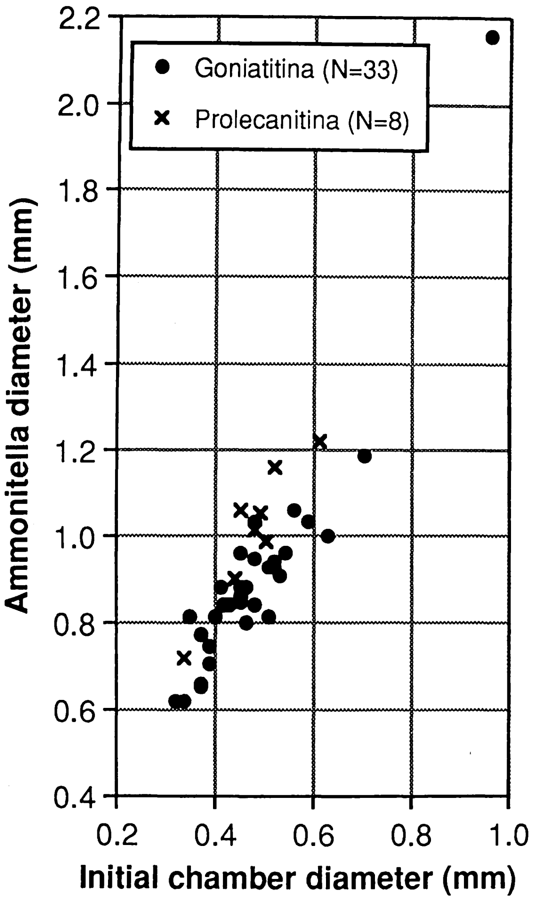

Figure 7. Scatter plot of ammonitella diameter versus initial chamber diameter in the Goniatitina and Prolecanitina examined.

Discussion

The results of this work are consistent with the data of previous authors (Böhmers, 1936 ; Miller and Unklesbay, 1943 ; Bogoslovskaya, 1959), and both indicate that the Goniatitina and Prolecanitina exhibit certain distinct features in their early shell characters. All species of the Goniatitina examined have a short and curved prosiphon, an elliptical caecum, and a relatively large ammonitella angle. Furthermore, their primary septum (second septum) is either close to or attached to the proseptum on the dorsal side. Species of the Prolecanitina also have a short and curved prosiphon, but unlike the Goniatitina, their caecum is rectangular in outline and their initial chambers have a distinct constriction in their proximal part.

As stated before, in the Prolecanitina and most Goniatitina examined, the siphuncle occupies a ventral position throughout ontogeny (Table 2). Many genera belonging to several different families of the Goniatitina (e.g. species of *Agathiceras, Bisatoceras, Maximites, Pseudohalorites, Neoaganites, Sosioceras, Shouchangoceras, Sangzhites, Elephantoceras*, and *Erinoceras*), however, possess a centrally or subcentrally located siphuncle during early to late ontogeny. This evidence was initially observed in sev-

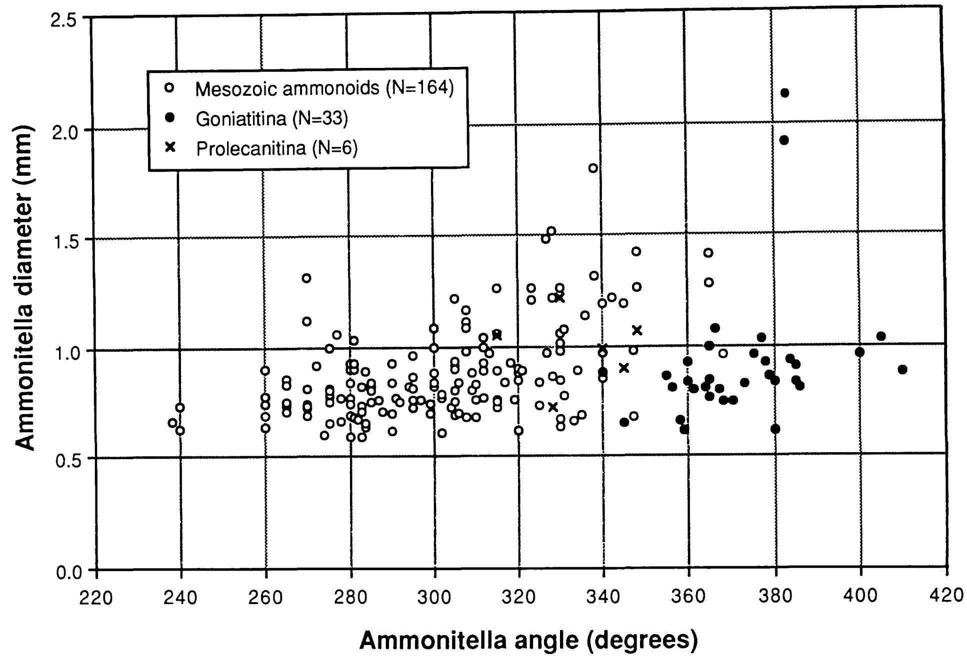

Figure 8. Scatter polt of ammonitella diameter versus ammonitella angle in the Goniatitina and Prolecanitina examined compared with the Mesozoic suborders. After Landman *et al.* (1994) for the measurements of Mesozoic suborders.

eral genera by Miller and Unklesbay (1943). Later studies by Nassichuk (1975), Zhou (1979) and the summary by Frest *et al.* (1981) clearly show that the primary siphuncular position is not useful for detailed systematics of the Goniatitina. There are no significant differences in the early internal shell structures below the superfamily level for the Goniatitina (Table 2).

Let us now compare the early shell features between Paleozoic and Mesozoic ammonoids. External and internal structures of embryonic shells in the Mesozoic Ammonoidea have been described and discussed by a number of authors from the viewpoint of higher taxonomy (e.g. Druschits and Doguzhaeva, 1974, 1981 ; Zakharov, 1974 ; Tanabe *et al.*, 1979 ; Tanabe and Ohtsuka, 1985 ; Ohtsuka, 1986 ; Tanabe, 1989 ; Landman *et al.*, 1994). These works have shown that species of the same Mesozoic suborder commonly exhibit distinct features and developmental patterns in their embryonic shell characters.

Although the embryonic shells of all ammonoids consist of a number of common structural elements, there is a significant difference in the surface ornamentation between Paleozoic and Mesozoic ammonoids. Namely, well-preserved embryonic shells of the Goniatitina occasionally retain evenly spaced longitudinal lirae on their exposed surface (Figure 5-4), whereas those in the Mesozoic Ammonitida (Phylloceratina, Lytoceratina, Ammonitina, and Ancyloceratina) possess a tuberculate microornamentation instead of longitudinal ornament (Tanabe, 1989, figures 1, 3 and 4). Embryonic shells of some Devonian Tornoceratina and Anarcestina are, by contrast, ornamented with transverse lirae (House, 1965). Embryonic shell ornamentation in the Ceratitina and Prolecanitina is still unknown.

On the basis of comparison of the embryonic shell structure with extant *Nautilus* and

Spirula, Tanabe (1989) explained the above difference in the embryonic shell ornamentation between Paleozoic and Mesozoic ammonoids from a morphogenetic viewpoint. According to his interpretation, Mesozoic Ammonitida passed through an endocochliate body plan during a limited interval in the embryonic stage, so that the outermost prismatic embryonic shell layer with microtubercles was secreted by the exterior epithelium of the reflected mantle, as in the case of extant *Spirula*. He also suggested that in Paleozoic ammonoids, embryonic shells were formed by the interior epithelium; accordingly, the growing ammonoid maintained an ectocochliate body plan throughout ontogeny.

Among the quantitative embryonic shell characters, ammonitella angle (=spiral length of the body chamber at hatching) shows the most taxonomic variation. In the Goniatitina, the angle ranges from 345° to 410°, with 365° on the average, which is larger by 45°~60° than the mean values of the other suborders (Figure 8). There is no marked difference in the mean initial chamber size between the Goniatitina and other suborders (Landman *et al*., 1994). These facts imply differences in the volume ratio of the initial chamber to the ammonitella. Like other suborders, hatchlings of goniatites were probably neutrally buoyant (see Tanabe *et al*., 1994 for details of hydrostatic analysis).

Relying on the data on ammonitella diameter in the species hitherto investigated, we have suggested that most ammonoids hatched with relatively small embryonic shells approximately 1 mm in diameter (Tanabe and Ohtsuka, 1985; Landman, 1988; Landman *et al*., 1994). Yet, there is some variation in the embryonic shell size among and within individual suborders. For example, the embryonic shell diameter is relatively large (0.8~1.8 mm) in the Lytoceratina, whereas it is relatively small (0.5~1.3 mm) in the Prolecanitina, Ceratitina, Phylloceratina, Ammonitina, and Ancyloceratina. Most species of the Goniatitina have also a relatively small embryonic shell ranging from 0.6 to 1.2 mm in diameter, but species of *Perrinites* and *Gonioloboceras* possess an unusually large embryonic shell ranging from 1.9 to 2.3 mm in diameter. In all probability, these goniatites had different early life histories from other ammonoids; possibly, they had a longer embryonic period and laid a smaller number of offspring than the latter in association with brooding.

Summary and conclusion

From the microscopic examinations of the embryonic shell characters in a total of 41 species of Carboniferous-Permian Goniatitina and Prolecanitina, it was revealed that the two suborders have their own characteristic features in the embryonic shell structures. Species of the Goniatitina have a short and curved prosiphon, an elliptical caecum in median section, and a relatively large ammonitella angle. Their primary septum (second septum) is either close to or attached to the proseptum on the dorsal side. Species of the Prolecanitina also possess a short and curved prosiphon, but are distinguished from the Goniatitina by having a rectangular caecum and an initial chamber with a constriction in the proximal part in median section. In well-preserved specimens of the Goniatitina and Devonian suborders (Tornoceratina and Anarcestina), the exposed surface of the embryonic shell is sculptured by longitudinal or transverse lirae, instead of microtubercles that are present in the Mesozoic Ammonitida. These observations strongly support the hypothesis that the external and internal features of embryonic shells can be as useful as suture patterns for higher-level systematics of the Ammonoidea.

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後期古生代アンモノイド類の初期殻形態とその系統学的意義：北米内陸部，英国およびウラル山地の石炭・ペルム系産の保存の良い標本に基づき，ゴニアタイト亜目とプロレカニテス亜目に属するアンモノイド類41種の初期殻体諸形質を検討した。その結果，調べた種は亜目ごとに独特の胚殻形態を持つことが判明した。ゴニアタイト亜目に属する種の胚殻はいずれも，(1) 正中断面上で楕円形をした盲管を持つこと，(2) アンモニテラ (孵化までにできる胚殻) の螺環が比較的長いこと，(3) 第2隔壁が原隔壁に接近または接合し，背側で頚状の構造をつくること，などで特徴づけられる。一方，プロレカニテス亜目に属する種の胚殻はいずれも，正中断面上で長四角形の盲管を持ち，初期室の基部には顕著なくびれが発達する。保存の良いゴニアタイト類の胚殻表面には成長方向に配列した多数の肋が認められ，中生代のアンモノイド類に普遍的に認められる疣状突起とは明瞭に識別される。これらの観察事実や中生代の部類に関する資料から判断して，胚殻の外部・内部諸形質はアンモノイド類の高次の系統分類にきわめて有効な基準となると結論される。

棚部一成・*Neil H. Landman*・*Royal H. Mapes*

Appendix. List of material. After Kullmann (1981) and Glenister and Furnish (1981) for higher systematics.

Suborder & Family	Species	Horizon	Locality	Sample
Goniatitina				
Dimorphoceratidae	*Dimorphoceras politum* (Shumard)	M. Pennsylvanian	Henry Co., Missouri	N=1 (SUI 1755)
Girtyoceratidae	*Girtyoceras meslerianum* (Girty)	U. Miss. (Chesterian)	Jack Fork Creek, Pontotoc Co., Oklahoma	N=5 (UMUT PM 19023-1~5)
	Eumorphoceras plummeri Miller & Youngquist	U. Miss. (Chesterian)	San Saba, Texas	N=1 (UMUT PM 19030)
	Gatherites morrowensis (Miller & Moore)	L. Penn. (Morrowan)	Gather Mt., Arkansas	N=1 (UMUT PM 19032)
Goniatitidae	*Goniatites multiliratus* Gordon	U. Miss. (Chesterian)	Jack Fork Creek, Pontotoc Co., Oklahoma	N=5 (UMUT PM 19018-1~5)
	Goniatites sp. aff. *G. crenistria* Phillips	U. Miss. (Chesterian)	Ahloso, Pontotoc Co., Oklahoma	N=1 (UMUT PM 19019-1)
	Goniatites kentuckiensis Miller	U. Miss. (Chesterian)	Ada, Oklahoma	N=1 (SUI 1718)
	Goniatites choctawensis Shumard	M. Miss. (Meramecian)	Clarita, Coal Co., Oklahoma	N=1 (UMUT PM 19020-1)
Agathiceratidae	*Agathiceras applini* Plummer & Scott	L. Pennsylvanian	Coleman, Texas	N=1 (SUI 1766)
Cravenoceratidae	*Cravenoceras richardsonianum* (Girty)	U. Miss. (Chesterian)	Wapanucka, Johnston Co., Oklahoma	N=1 (UMUT PM 19021)
	Cravenoceras incisum (Hyatt)	U. Miss. (Chesterian)	San Saba, Texas	N=3 (UMUT PM 19022-1~3)
Schistoceratidae	*Schistoceras missouriense* (Miller & Faber)	U. Penn. (Missourian-Virgilian)	Jacksboro, Texas	N=1 (SUI 1746)
Gastrioceratidae	*Pseudogastrioceras simulator* (Girty)	L. - M. Permian	Sublette Range, Wyoming	N=2 (SUI 1738, 1740)
	Owenoceras bellilineatum (Miller & Owen)	U. Miss. (Chesterian)	Henry Co., Missouri	N=1 (SUI 1713)
Reticuloceratidae	*Retites semiretia* McCaleb	L. Penn. (Morrowan)	Thompson, Arkansas	N=1 (UMUT PM 19031)
	Arkanites relictus (Quinn, McCaleb & Webb)	L. Penn. (Morrowan)	Bradshaw Mt., Carroll Co., Arkansas	N=1 (UMUT PM 19029)
Glaphyritidae	*Glaphyrites hyattianus* (Girty)	M. Penn. (Desmoinesian)	Okmulgee, Oklahoma	N=3 (UMUT PM 19025-1~3)
	Glaphyrites warei (Miller & Owen)	M. Penn. (Desmoinesian)	Collinsville, Tulsa, Oklahoma	N=6 (UMUT PM 19026-1~6)
	Glaphyrites jonesi (Miller & Owen)	M. Penn. (Desmoinesian)	Collinsville, Tulsa, Oklahoma	N=2 (SUI 1735, UMUT PM 19027)
	Glaphyrites clinei (Miller & Owen)	M. Penn. (Desmoinesian)	Collinsville, Tulsa, Oklahoma	N=1 (UMUT PM 19028)
	Glaphyrites welleri (Smith)	M. Penn. (Desmoinesian)	Henry Co., Missouri	N=1 (SUI 1726)
Homoceratidae	*Homoceras subglobosum* (Bisat)	M. Carbon. (L. Namurian)	Stonehead Beck, Yorkshire, England	N=2 (UMUT PM 19024-1, 2)
Shumarditidae	*Shumardites cuyleri* Plummer & Scott	U. Penn. (Missourian-Virgilian)	Jacksboro, Texas	N=1 (SUI 1791)
Perrinitidae	*Properrinites bakeri* (Smith)	L. Permian	Dugout Mt., Brewster Co., Texas	N=1 (SUI 1790)
	Perrinites sp.	M. Permian	Clayslide, Iron Mt., Texas	N=1 (AMNH 41183-1)
Adrianitidae	*Texoceras* sp.	M. Permian	El Capitan, Texas	N=2 (UMUT PM 19037-1, 2)
	Adrianites dunbari Miller & Furnish	M. Permian	La Difunta, Coahuila, Mexico	N=1 (SUI 1764)
	Pseudagathiceras difuntense Miller	M. Permian	Unknown	N=1 (SUI 1790)
	Crimites elkoensis Miller, Furnish & Clarke	M. Permian	Buck Mt., Nevada	N=1 (UMUT PM 19038)
Popanoceratidae	*Popanoceras annae* Ruzhencev	M. Permian	Aktubinsk, Russia	N=1 (SUI 1777)
	Peritrochia erebus Girty	M. Permian	Bone Springs, Texas	N=2 (UMUT PM 19039-1, 2)
Metalegoceratidae	*Metalegoceras bakeri* (Miller & Parizek)	M. Permian	Buck Mt., Nevada	N=1 (UMUT PM 19034)
	Metalegoceras baylorense White	M. Permian	Buck Mt., Nevada	N=1 (UMUT PM 19035)
Cyclolobidae	*Mexicoceras guadalupense* (Girty)	M. Permian	South Wells, Culberson Co., Texas	N=1 (SUI 1782)
Thalassoceratidae	*Eothalassoceras inexpectans* (Miller & Owen)	M. Penn. (Desmoinesian)	Okmulgee, Oklahoma	N=3 (UMUT PM 19036-1~3)
Bisatoceratidae	*Bisatoceras greenei* Miller & Owen	L. Penn. (Morrowan)	Henry Co., Missouri	N=1 (SUI 1719)
	Bisatoceras sp.	M. Penn. (Desmoinesian)	Okmulgee, Oklahoma	N=2 (UMUT PM 19033-1, 2)
Prolecanitina				
Pronoritidae	*Pronorites praepermicus* Karpinsky	M. Permian (Artinskian)	Middle Urals, Russia	N=1 (SUI 1686)
Medlicottiidae	*Artinskia electraensis* (Plummer & Scott)	M. Permian	Buck Mt., Nevada	N=3 (UMUT PM 19040-1~3)

Trans. Proc. Palaeont. Soc. Japan, N.S., No. 173, pp. 401-404, 2 Figs., April 30, 1994

SHORT NOTES

30. A LARGE SPECIES OF *VERBEEKINA, V.* SP. A, FROM THE TAISHAKU LIMESTONE IN HIROSHIMA PREFECTURE, WEST JAPAN

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The Carboniferous and Permian Taishaku Limestone cropping out over a large area near Tojo Town, in Hiroshima Prefecture about 90 km to the northeast of Hiroshima, has been studied by many workers. However, only a few studies have been published describing the Permian fusulinaceans. Previous papers are: Hanzawa (1942), Akagi (1958), Hayasaka and Kato (1966), Sada and Yokoyama (1966), and Oho and Sada (1984).

The Permian of the Taishaku Limestone was studied by Sada (1974) and divided into five fusulinacean zones, the *Pseudoschwagerina* Zone, *Parafusulina* Zone, *Neoschwagerina* Zone, *Lepidolina multiseptata shiraiwensis* Zone and *Lepidolina elongata* Zone in ascending order.

We are now describing a large and unusual species of *Verbeekina, V.* sp. A, from the *Lepidolina multiseptata shiraiwensis* Zone cropping out at Ippaimizu in the eastern part of Taishaku Limestone Upland (Figure 1). This is the first time that *Verbeekina* has been described and illustrated from Taishaku. The most well known species of *Verbeekina* in Japan is *V. verbeeki* (Geinitz) and it is characterized by its large and spherical shell.

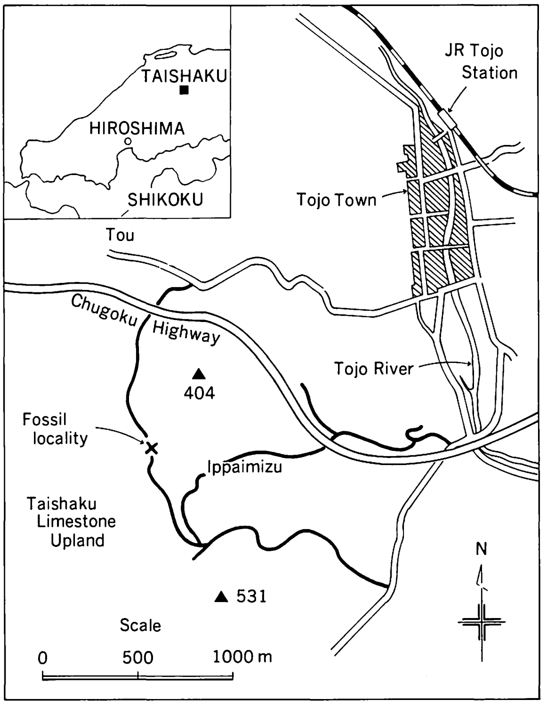

Figure 1. Map showing the fossil locality (Loc. A-IPV) at Ippaimizu, south of Tou near Tojo Town in Hiroshima Prefecture.

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The shell of *Verbeekina* sp. A, however, is larger than that of *V. verbeeki* (Geinitz).

In this paper the large species of *Verbeekina* is described as *Verbeekina* sp. A.

Description of species

Family Verbeekinidae Staff
and Wedekind, 1910
Subfamily Verbeekininae Staff
and Wedekind, 1910
Genus *Verbeekina* Staff, 1909
Type species.—Fusulina verbeeki
Geinitz, in Geinitz and
von der March, 1876

Verbeekina sp. A

Figures 1-1—2

Description.—The shell of the present species is large and spherical to subspherical with a straight axis of coiling. The shell of the illustrated specimen (UHA-IPV-8, Figure 2-1) is 10.95 mm in length and 8.5 mm in width, giving a form ratio of 1.28.

The proloculus is spherical and its diameter is 50 μm. The first volution coils at a large angle to the later volutions and in the second volution the shell becomes spherical to subspherical. Beyond the third volution the shell expands rapidly and almost uniformly.

The spirotheca is composed of a tectum and keriotheca. It is thin in the inner volutions but increases in thickness from the eleventh volution. The spirothecal thickness of the first to the seventeenth volution in a specimen illustrated as Figure 2-1 (UHA-IPV-8) measures 21, 21, 18, 11, 21, 21, 18, 13, 16, 21, 32, 27, 50, 48, 41, 59 and 75 μm, respectively.

The parachomata are not observed in the inner six volutions in a specimen illustrated as Figure 2-2 (UHA-IPV-22) but they appear in the seventh volution, though they are very rare and small. They are well developed in the outer two or three volutions and are one-third as high as the chambers.

Remarks.— *Verbeekina* sp. A somewhat resembles *V. verbeeki* (Geinitz) described by Toriyama (1958, p. 205-208, pl. 37, figs. 1-6, pl. 38, figs. 1-6) from the Akiyoshi Limestone in Yamaguchi Prefecture, by Nogami (1961, p. 167-169, Taf. 2, figs. 1-4) from the Atetsu Limestone in Okayama Prefecture, and by Toriyama and Pitakpaivan (1973, p. 50-53, pl. 6, figs. 1-6) and Toriyama and Kanmera (1977, p. 8-10, pl. 1, figs. 8-10) from central Thailand. However, the former species has a larger shell and greater number of volutions. The present species is similar in some respects to *Verbeekina crassispira* (Chen, 1956, p. 49-50, pl. 9, figs. 7-10; Sheng, 1958, p. 285-286, pl. 1, figs. 5-7) from China. The latter species, however, has a smaller shell, smaller form ratio and smaller number of volutions. *Verbeekina* sp. A somewhat resembles *V. douvillei* (Deprat) (Ozawa and Kobayashi, 1990, p. E26, pl. 11, fig. 10) reported from the *Lepidolina multiseptata shiraiwensis* Zone (AK 47) of Akiyoshi Limestone. However, the former species differs from the latter in having a larger shell and more volutions.

The present species is a large and unusual species of *Verbeekina* and is different from any of the known species of *Verbeekina*, although the inner structure of the shells is destroyed and incomplete. The present species may be a new species but the specific naming is postponed until more information is obtained.

The inner structure of *Verbeekina* sp. A is destroyed as stated above but that of its associated species is not. *Verbeekina* sp. whose shells were restructured was reported by Toriyama (1978) from Thailand and he considered that the selective destruction of *Verbeekina* might be caused by its extremely thin and fragile wall and septa. The destruction of *Verbeekina* sp. A of Taishaku may also have been caused by its thin and fragile spirotheca and septa.

Occurrence.—The specimens of *Verbeekina* sp. A is obtained from a black limestone at Ippaimizu in the eastern part of the Taishaku Limestone Upland, and is associated with

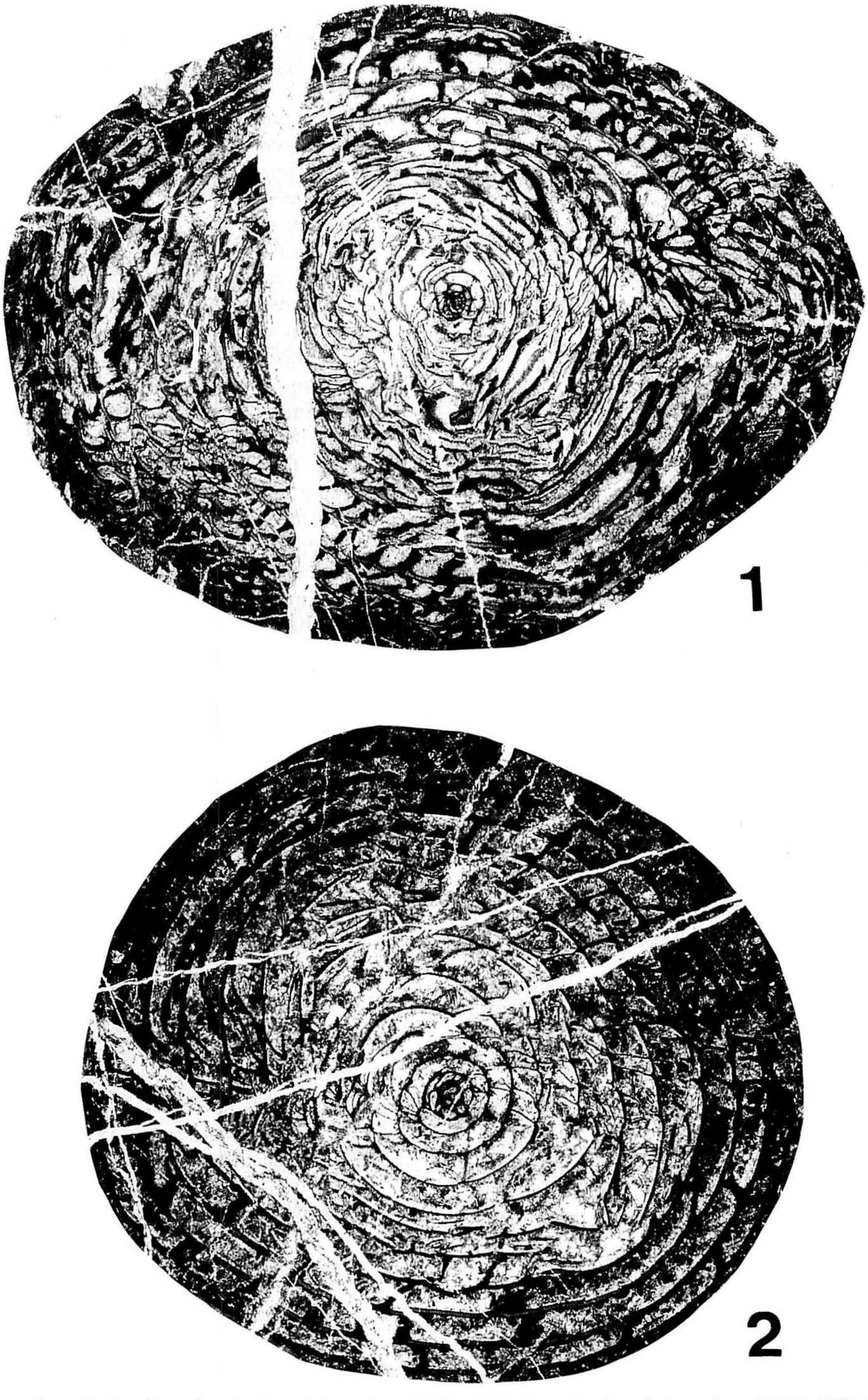

Figure 2. *Verbeekina* sp. A. **1,** axial section, UHA-IPV-8, × 10. **2,** axial section, UHA-IPV-22, × 10.

Lepidolina multiseptata shiraiwensis (Ozawa) and *Kahlerina* sp.

Locality.—Loc. A-IPV at Ippaimizu, south of Tou near Tojo Town in Hiroshima Prefecture.

Fusulinacean zone.—*Lepidolina multiseptata shiraiwensis* Zone.

Repository.—The figured specimens are preserved at Division of Geological Sciences in Department of Environmental Sciences, Faculty of Integrated Arts and Sciences, Hiroshima University (UH) under the repository number given (see Explanations of Figure 2).

Acknowledgments

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Trans. Proc. Palaeont. Soc. Japan, N.S., No. 173, pp. 405, 2 Figs., April 30, 1994

SHORT NOTES

31. *LEVENELLA*, A NEW NAME FOR *LEVENIA* UENO, 1991 (FORAMINIFERIDA, FUSULINACEA), *NON* GRAY, 1947*

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Dr. T. Kase has kindly called my attention to the fact that the name of fusulinacean subgenus *Levenia* established in Ueno (1991) is preoccupied by that of the cassid gastropod *Levenia* by Gray (1847). As the former is a primary junior homonym of the latter, I propose here the new name *Levenella* for *Levenia* Ueno, 1991, *non* Gray, 1847. This subgenus *Levenella* is named in honor of Professor E. Ya. Leven of the Geological Institute, Moscow for his great contributions to fusulinacean paleontology and younger paleozoic biostratigraphy.

I thank Dr. Tomoki Kase of National Science Museum, Tokyo for having pointed out this nomenclatural error.

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PROCEEDINGS OF THE PALAEONTOLOGICAL SOCIETY OF JAPAN

日本古生物学会　1994年年会・総会

日本古生物学会1994年年会・総会が，1月27-29日に国立科学博物館（上野本館および新宿分館）で開催された（参加者320名）.

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Palaeontological Society of Japan (PSJ) Council Actions

During its meeting on January 26, 1994, the PSJ Council enacted the following changes to PSJ membership.

New members elected :

Tomio Arakawa, Kouichi Fukuoka, Katsumi Hattori,
Toshihiko Ichihara, Kentarou Ikeda, Masaki Ishikawa,
Hiroshi Ito, Hitomi Kikuchi, Eiichi Kitabayashi,
Midori Matsumoto, Kazunori Miyata, Saori Nakai,
Yoshihisa Nohmi, Hidetoki Noguchi, Akira Ookubo,
Hideo Oomori, Kazuo Sakamoto, Makoto Shibata,
Toshio Shimanuki, Mineshi Suzuki, Masayuki Tagawa,
Hidenori Tanaka, Masaya Tsuchihashi, Osamu Tsujii,
Masaki Umeda, Shozo Yoshioka, Dewi Syavitri Husein,
Tuncer Güvenç, Manug Myo Myint, Leopoldo P. De Silver,
Zaw Win, Maybellyn A. Zepeda.

New Fellows approved :

Akito Asai, Hiroshi Nishi.

Resigned members :

(Ordinary member) :

Hiroyuki Maeda.

(Fellow)

Mosaburo Kanuma, Noriyuki Nasu, Yoshio Okazaki.

Deceased members :

(Fellow)

Kazuo Fuzioka, Kazuyoshi Okami, Kin-ichi Sakurai,
Keiji Suzuki.

New Honorary members approved by the general assembly at 1994 Annual Meeting of the Society held on 27 January, 1994.

Koichiro Ichikawa, Taro Kanaya, Saburo Kanno,
Tamio Kotaka.

行事予定

◎1994年例会（第143回例会）は熊本大学理学部で6月25日（土），26日（日）に開催されます。

◎1995年年会・総会は，名古屋大学理学部で開催予定です。

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