

Pollen Morphology and Species-level Distinction of the Genus *Fagus* from the Hachiya Formation (Lower Miocene), Mizunami Group, Japan

Takeshi SAITO

*Department of Earth and Planetary Sciences, School of Science,
Nagoya University, Nagoya 464-01, Japan
(Received September 22, 1992 / Accepted November 11, 1992)*

ABSTRACT

Pollen morphology of the genus *Fagus* from the Hachiya Formation (Lower Miocene) is described using light and scanning electron microscopy (SEM), and that of modern *Fagus* in Japan is also examined to set up criteria for species-level distinction. Exine sculpture of modern two species, *Fagus crenata* Blume and *F. japonica* Maximowicz, is uniform within each species and resembles each other. Small outliers of the grain size distribution and smaller grains exhibit slightly different exine sculpture from that of normal grains. Each of the two species has specific ranges of grain size and polar area index.

More than 100 grains of fossil *Fagus* pollen are examined and divided into four types, A, B, C and D, on the basis of exine sculpture observed in SEM. Type A includes two species of the genus. Types B, C and D are morphological variation of type A species pollen, or are other species. Two or more *Fagus* species occurred in Japan in Early Miocene age.

INTRODUCTION

Fagus L. is one of the characteristic genera of the temperate zone flora in the Northern Hemisphere. About fifteen species occur in North America (U. S. A., Canada, Mexico), Europe, and Asia (Iran, Caucasus, Asia Minor, China, Japan). This genus is also one of the common constituents of the Neogene and Quaternary fossil flora of the Northern Hemisphere. Tanai (1974) summarized the fossil records of *Fagus* of east Asia and western North America, and proposed the phylogeny of the genus on the basis of leaf morphology.

The pollen of fossil *Fagus* is common in the Neogene and Quaternary strata as well as the macrofossils of the genus. There are, however, no studies of the phylogeny of the genus on the basis of pollen morphological feature. Crepet and Nixon (1989) suggested that exine sculpture observed in scanning electron microscopy (SEM) was a useful character to understand the phylogeny of the family Fagaceae. Species-level distinction of fossil *Fagus* pollen is primarily necessary to estimate the phylogeny of the genus on the basis of pollen morphology. SEM observation often makes possible the identification of pollen grains to species. Some works illustrated and described the

pollen morphology of living *Fagus* using SEM. These works are listed in Table 1 with respective species. A few works described the pollen morphology of fossil *Fagus* with SEM observation (Mohr, 1984; Gortemaker, 1986; Miyoshi and Uchiyama, 1987). This study examines the pollen morphology of the modern *Fagus* species in Japan, *F. crenata* Blume and *F. japonica* Maximowicz to set up criteria for species-level

Table 1. List of previous works which illustrated and described the pollen morphology of living *Fagus* on SEM observation.

Species	Works
<i>Fagus crenata</i> Bl.	Hanks and Fairbrothers (1976) Miyoshi (1982) Pragłowski (1982) Gortemaker (1986) Miyoshi and Uchiyama (1987) Crepet and Nixon (1989)
<i>F. engleriana</i> Seemen	Hanks and Fairbrothers (1976) Pragłowski (1982)
<i>F. grandifolia</i> Ehrh.	Hanks and Fairbrothers (1976) Pragłowski (1982) Gortemaker (1986)
<i>F. hayatae</i> Palib.	Hanks and Fairbrothers (1976) Miyoshi et al. (1991)
<i>F. japonica</i> Maxim.	Hanks and Fairbrothers (1976) Miyoshi (1982) Pragłowski (1982) Gortemaker (1986) Miyoshi and Uchiyama (1987)
<i>F. longipetiolata</i> Seemen	Hanks and Fairbrothers (1976)
<i>F. lucida</i> Rehd. & Wilson	Hanks and Fairbrothers (1976)
<i>F. mexicana</i> Martinez	Hanks and Fairbrothers (1976) Pragłowski (1982)
<i>F. multinervis</i> Nakai	Hanks and Fairbrothers (1976) Miyoshi et al. (1991)
<i>F. orientalis</i> Lipsky	Hanks and Fairbrothers (1976) Pragłowski (1982) Gortemaker (1986)
<i>F. sylvatica</i> L.	Hanks and Fairbrothers (1976) Pragłowski (1982) Gortemaker (1986)
<i>F. taurica</i> Popl.	Pragłowski (1982)

distinction and attempts to distinguish fossil *Fagus* pollen from the Hachiya Formation (Lower Miocene) at the species level.

MATERIALS AND METHODS

Recent materials

Polliferous material of *Fagus crenata* was collected by Tohru Yamanoi at Mt. Gassan, Yamagata Prefecture, in 1978; and that of *F. japonica* was collected by Seiju Yamaguchi at Kamiyahagi, Gifu Prefecture, in 1990.

Fossil material and locality data

The samples for this study come from the Nogami Volcaniclastic Member (Kodera and Nomura, 1988), which occupies the uppermost part of the Hachiya Formation, Mizunami Group (Itoigawa, 1980), Gifu Prefecture, Japan. The Hachiya Formation consists mainly of volcaniclastic rocks of rhyolite, andesite and basalt with intercalated sandstones, mudstones and lignite-bearing sedimentary rocks. This formation is of lacustrine origin.

The sampling locality is Yaotsu Town, Gifu Prefecture (137° 6' 48" E, 35° 28' 35" N). The columnar section in Fig. 1 shows the horizons of the two samples.

The K-Ar age dating is 22.2 Ma for the rhyolite of the lower part of the Hachiya Formation (Torii, 1982), 20.6 ± 2.1 Ma and 19.8 ± 2.1 Ma for the andesitic autobrecciated

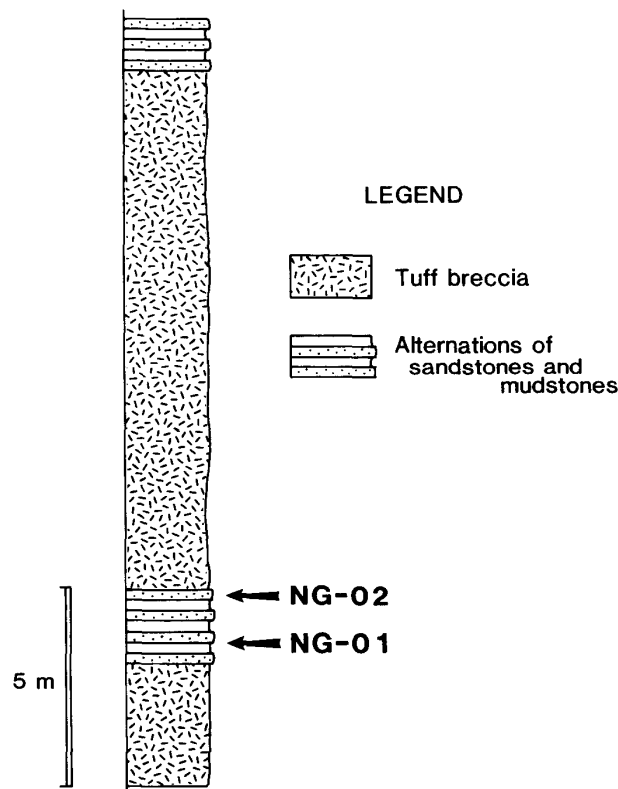


Fig. 1. Columnar section showing sampling horizons.

Table 2. Fossil pollen assemblage and abundance from samples studied.

Taxa	Abundance (%)	
	NG-01	NG-02
<i>Abies</i>	3.6	7.2
<i>Picea</i>	6.8	13.1
<i>Pinus</i>	—	3.3
<i>Tsuga</i>	3.6	6.0
<i>Pterocarya</i>	2.0	0.9
<i>Carya</i>	5.6	7.8
<i>Engelhardtia</i>	1.2	1.2
<i>Alnus</i>	12.4	5.4
<i>Betula</i>	10.0	5.7
<i>Carpinus</i>	7.2	5.1
<i>Fagus</i>	36.0	29.3
<i>Ulmus</i>	2.0	0.6
<i>Zelkova</i>	4.4	3.6
<i>Acer</i>	—	0.6
<i>Tilia</i>	2.0	2.4
Taxodiaceae	1.2	2.1
<i>Rhus</i>	0.4	0.9
<i>Liquidambar</i>	0.4	—
<i>Hemitrapa</i> ?	1.2	4.5
<i>Aesculus</i>	—	0.3
<i>Sparganium</i>	—	0.3

lavas of the middle and the upper part of the formation, respectively (Nomura, 1986).

Ina et al. (1983, 1985) described plant macrofossils of 65 species from the Hachiya Formation. They correlated “the Hachiya flora” with the Early Miocene “Aniai-type flora” (Huzioka, 1964). Hujiyama and Nomura (1986) described fossil insects, and Koderu and Nomura (1988) reported fossil of fresh-water fish. Table 2 shows the fossil pollen assemblage and abundance obtained from the two samples.

Preparation

The pollen grains from the recent material were acetolysed for about ten minutes, and treated with KOH (10%) for about five minutes. The treated grains were divided into two parts. One part was treated with HCl (36%), and mounted in glycerine jelly on glass slides for LM examination. The other was dehydrated with ethanol and added isoamyl acetate. The mounted grains on stabs were sputter-coated with gold for SEM observation.

The crushed samples which contain fossil pollen grains were treated with KOH (10%), HF (46%) and the acetolysis method for about ten minutes. Then, a solution of ZnCl₂ (s. g. 1.9) was added to concentrate pollen grains. The treated residue was mounted on glass slides in glycerine jelly for LM examination. For SEM observation, a part of this residue was dehydrated and sputter-coated by the same method as for recent materials.

Measurement

Mean axis and polar area index were measured with an ocular micrometer in LM observation and with a ruler on the SEM micrographs, respectively. The slides for LM observation of the recent materials were studied within four days after preparation, those of fossil materials were examined within four days. But the fossil materials were prepared about six months before.

(1) Mean axis (Mx)

Mean axis is defined as follows in this paper.

For equatorial view,

$$Mx=(P+E)/2$$

where P: polar axis, E: equatorial diameter.

For polar view,

$$Mx=E.$$

For oblique view,

$$Mx=(P'+E')/2$$

where P': longitudinal axis on the oblique projection,

E': axis falling at right angle with P' on the oblique projection.

Mean axis represents a grain size. These three alternative measurements are almost equivalent to each other for nearly spheroidal grains such as *Fagus* pollen. This method is not strictly accurate but practical.

(2) Polar area index (Pi)

Polar area index represents the relative extent of an apocolpium. This index is defined as follows with reference to Faegri and Iversen (1989: p.233).

For equatorial view and polar view,

$$Pi=d/E$$

where d: greatest distance between the ends of two colpi.

For oblique view,

$$Pi=d/E'.$$

POLLEN MORPHOLOGY OF MODERN *FAGUS* IN JAPAN

One hundred or more grains of *Fagus crenata* and *F. japonica* were examined at random with LM and SEM.

Description of pollen morphology

Genus *Fagus* L.

General aspect: Pollen grain nearly spheroidal, radially symmetrical, isopolar, 3-colporate. Apertures consist of colpi, colpus membranes and ora. Exine surface psilate, scabrate or verrucate in LM, densely packed with many elongated columnar tectal elements having rounded ends in SEM. The elements frequently overlap and intertwine (vermicular-rugulose exine structure; Pragłowski, 1982).

Remarks: A further description may be found in Pragłowski (1982).

Fagus crenata Blume
(Pl. I, figs. 1-6; Pl. III, figs. 1-3, 8)

General aspect : Pollen grain relatively large; spheroidal or oblate-spheroidal, occasionally prolate-spheroidal; circular or rounded triangular in polar view, circular or transversely elliptic, occasionally longitudinally elliptic in equatorial view. Colpi relatively short, narrow, having acute ends; ora nearly circular. Apocolpia compara-

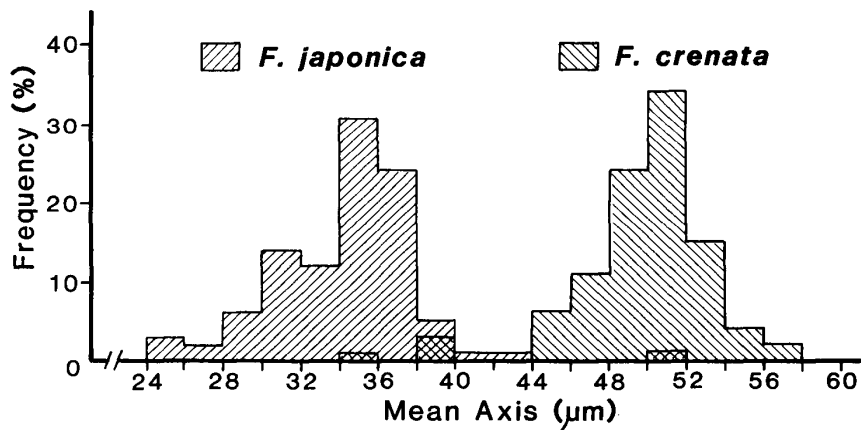


Fig. 2. Histograms showing size frequency of the pollen grains of *Fagus crenata* and *F. japonica* in LM. *F. crenata* : N=100, av=49.7μm, sd=3.5μm ; *F. japonica* : N=100, av=34.3μm, sd=3.7μm (av: average, sd: standard deviation).

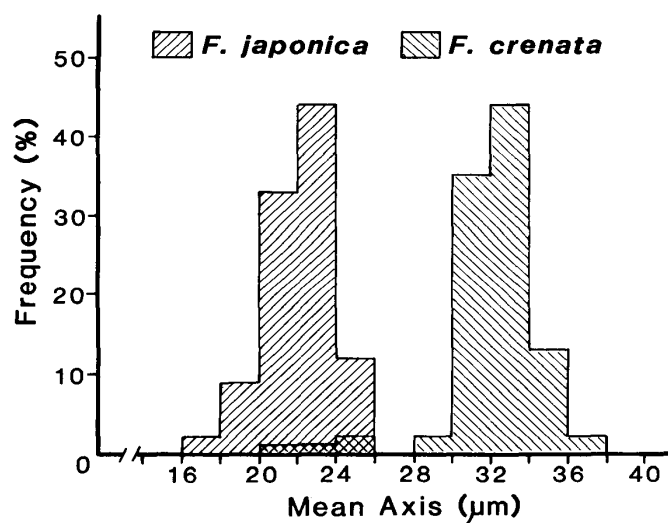


Fig. 3. Histograms showing size frequency of pollen grains of *Fagus crenata* and *F. japonica* in SEM. *F. crenata* : N=105, av=32.3μm, sd=2.2μm ; *F. japonica* : N=100, av=22.1μm, sd=1.6μm (abbreviations in Fig. 2).

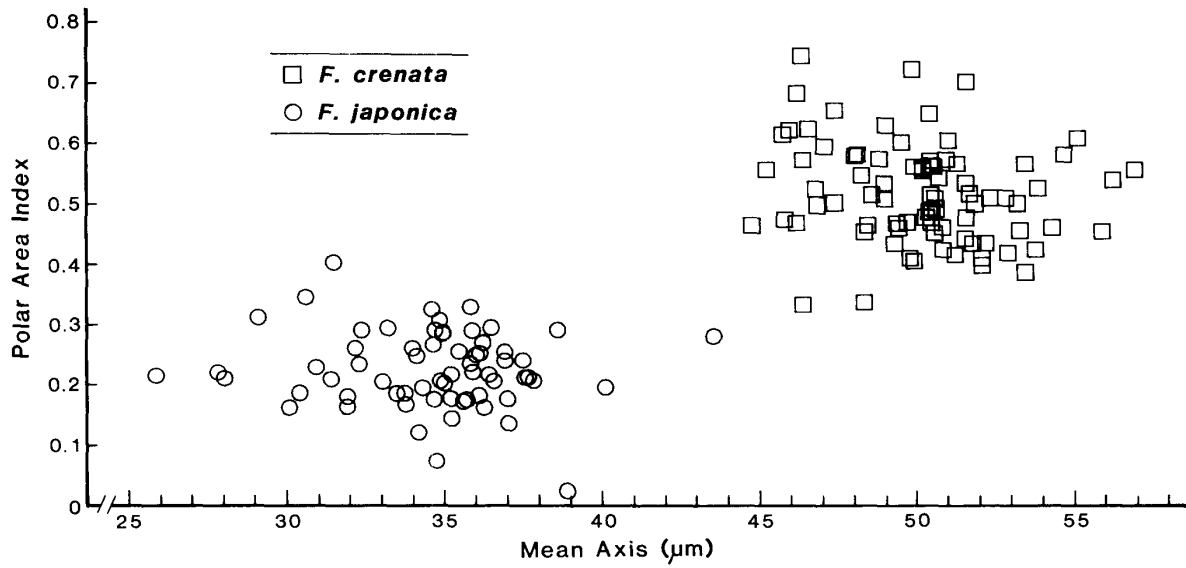


Fig. 4. Pollen grain size of *Fagus crenata* and *F. japonica* plotted against their polar area index in LM. *F. crenata*: N=82; $r = -0.19$; polar area index, $av = 0.52$, $sd = 0.08$; *F. japonica* : N=64; $r = -0.10$; polar area index, $av = 0.22$, $sd = 0.05$ (r : correlation coefficient, others in Fig. 2).

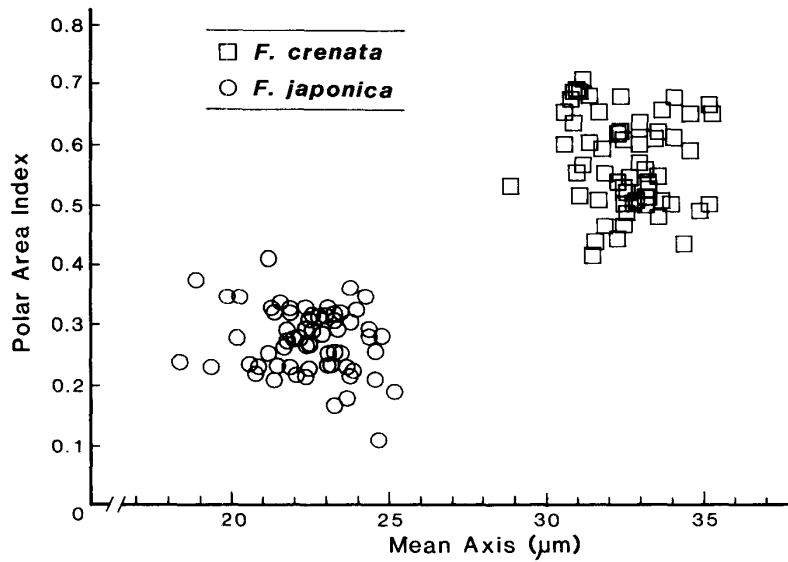


Fig. 5. Pollen grain size of *Fagus crenata* and *F. japonica* plotted against their polar area index in SEM. *F. crenata* : N=61 ; $r = -0.13$; polar area index, $av = 0.57$, $sd = 0.08$; *F. japonica* : N=65 ; $r = -0.21$; polar area index, $av = 0.27$, $sd = 0.06$ (abbreviations in Fig. 4).

tively large.

Exine surface scabrate in LM. In SEM, tectal elements essentially elongated columnar, more or less fused to each other; straight or gently curved, having smooth surface. Transverse diameter of the elements about 0.10 to 0.30 μm , frequently about 0.20 μm . Trends of the elements may vary, but many parts of exine surface are covered with horizontal elements.

Pattern of exine sculpture uniform around whole grain except near colpus. Tectal elements more or less fused. Fusion is most conspicuous at the area covering ora, reducing toward poles and mesocolpia. Tectal elements of the fused area often irregular in shape.

Colpus membrane sculptured by fused, indefinite, columnar (?) elements. The elements may be more narrow and shorter than those of exine surface.

Variability: Frequency of mean axis is presented in Fig. 2 (in LM) and Fig. 3 (in SEM). Relationship between polar area index and mean axis is shown in Fig. 4 (in LM) and Fig. 5 (in SEM). There is little correlation between the two measurements.

One of 100 grains subjected to LM observation is 4-colporate. Five grains possess an unequal colpus whose length is shorter than that of the other two.

Exine sculpture is uniform, but 4 of 105 grains examined with SEM show slightly different exine sculpture. They are small outliers of the grain size distribution. In addition to these 4 grains, six smaller grains were intentionally observed. These smaller grains can be divided into two types on the basis of exine sculpture. One type is comprised of pollen grains which have slightly different tectal elements from those of normal grains (see Pl. III, figs. 1, 2). The elements of this type are more densely packed than those of normal grains, and shape of the elements is rather irregular. Another type has the same tectal elements as those of normal ones (see Pl. III, fig. 3). This type resembles normal grains in exine sculpture. But tectal elements are more densely packed than those of normal grains, and vertical elements rather abundant.

Remarks: Grain size measured in LM is larger than any other size data from the works listed in Table 1, Shimakura (1973) and Uchiyama (1986). Grain size in dry condition was reported only by Miyoshi and Uchiyama (1987). Their size data are slightly larger than those in this study.

Uchiyama (1986) examined four grains for the measurements of polar area index. They range from 0.41 to 0.71. His data are concordant with the results of this study.

Fagus japonica Maxim.

(Pl. II, figs. 1-6; Pl. III, figs. 4-7, 9)

General aspect: Pollen grain relatively small; spheroidal or oblate-spheroidal, occasionally prolate-spheroidal; circular or rounded triangular in polar view, circular or transversely elliptic, occasionally longitudinally elliptic in equatorial view. Colpi long, narrow, having rather obtuse ends; ora nearly circular. Apocolpia small.

Exine surface scabrate in LM. In SEM, tectal elements essentially elongated columnar, more or less fused to each other; straight or gently curved, having smooth surface. Transverse diameter of most elements about 0.12 to 0.20 μm . Trends of the elements vary, but many parts of exine surface are covered with horizontal elements.

Pattern of exine sculpture uniform around whole grain except near colpus. At the colpal margin, tectal elements sometimes fused to each other, and they packed more densely than those of the rest of grain surface; and occasionally, the elements form a slight elevation like margo. Some grains have ektexinous bridges covering ora (see Pl. II, figs. 5, 6).

Colpus membrane sculptured by fused, indefinite, columnar (?) elements. The elements may be more narrow and shorter than those of exine surface. On the membrane, orbicular or subangular granules often exist (see Pl. III, fig. 9). The granules abundant near os. Subangular granules have traces of being made of columnar elements like tectal elements on the exine surface. These granules may result from dirt.

Variability: Frequency of mean axis is presented in Fig. 2 (in LM) and Fig. 3 (in SEM). Relationship between polar area index and mean axis is shown in Fig. 4 (in LM) and Fig. 5 (in SEM). There is little correlation between the two measurements.

One of 100 grains subjected to LM observation have no ora, two grains lacking in both ora and colpi.

Exine sculpture is uniform, but 2 of 100 grains examined with SEM show rather different exine sculpture. They are smaller in the grain size distribution. In addition to these 2 grains, I intentionally observed 14 smaller grains. Exine surface of those grains have no recesses between the tectal elements (see Pl. III, figs. 4-7).

Remarks: Grain size in dry condition is smaller than the size data from Miyoshi and Uchiyama (1987), whereas that in glycerine jelly is concordant with other data.

Uchiyama (1986) examined four grains for the measurements of polar area index. They range from 0.25 to 0.29. His data are within the results of this study.

Pollen grains of this species are primarily distinguished from those of *Fagus crenata* by grain size and polar area index. Exine sculpture of *F. japonica* resembles that of *F. crenata*, but the tectal elements for the former are more uniform and slightly more narrow than those for the latter. Fusion at the colpal margin of *F. japonica* is not more conspicuous than that of *F. crenata*. Ektexinous bridges are absent in *F. crenata*. Shape of the colpal ends of *F. japonica* is often more obtuse than that of *F. crenata*.

Gortemaker (1986) recognized the cluster pattern in the arrangement of the tectal elements of this species, but other works including this study do not discern the pattern.

Discussion

On the basis of above results, it is possible to set up the criteria for species-level distinction of fossil *Fagus* pollen.

Mean axis and polar area index have specific range for each species. The amplitude of mean axis is about 15 μm in LM (Fig. 2), and 10 μm in SEM (Fig. 3); that of polar area index about 0.3 both in LM and SEM (Figs. 4, 5).

Exine sculpture except in the colpal margin is generally uniform for each species, but trends of the tectal elements and the degree of fusion are rather variable. Small outliers or some smaller grains have slightly different sculpture. They are probably immature grains or those which escaped chemical treatments. Exine sculpture at the colpal margin is variable, and occasionally, margo-like structure is present.

The criteria are based on only two species. They should be modified when other *Fagus* species are quantitatively studied.

POLLEN MORPHOLOGY OF EARLY MIOCENE *FAGUS*

More than 100 grains of fossil *Fagus* pollen were examined at random with LM and SEM. These grains can be divided into the following four types on the basis of exine sculpture observed with SEM.

Fossilized pollen grains are generally compressed and/or broken. Therefore the error of measurements is larger than that for recent grains. The results of measurements in LM are presented in Figs. 6 and 7. These figures are not illustrated for each type because the following four types cannot be clearly distinguished from each other with LM.

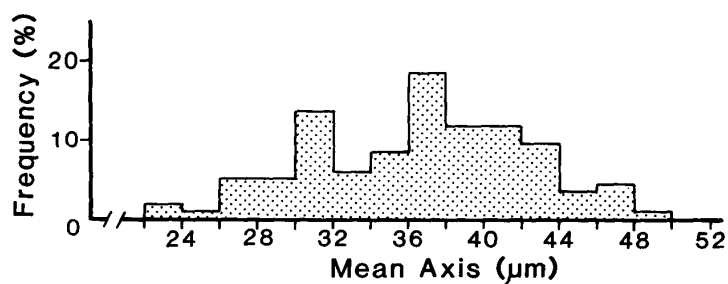


Fig. 6. Histograms showing size frequency of the pollen grains of Early Miocene *Fagus* in LM. N=119.

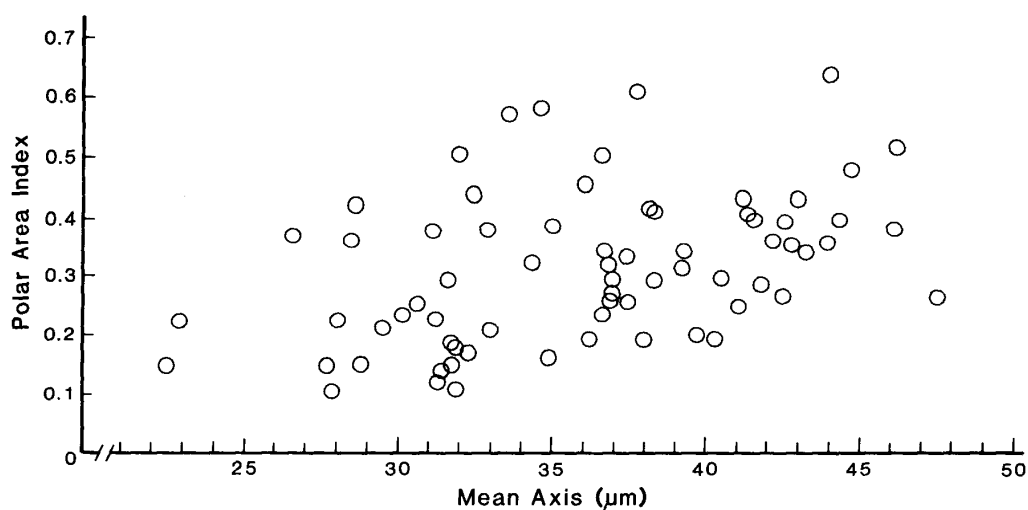


Fig. 7. Pollen grain size of Early Miocene *Fagus* plotted against its polar area index in LM. N=70.

Type A
(Pl. IV, figs. 1-4; Pl. V, figs. 1-4)

Description : Pollen grain spheroidal, oblate-spheroidal or prolate-spheroidal; circular or rounded triangular in polar view, circular, transversely elliptic or longitudinally elliptic in equatorial view. Colpi moderate length or long, narrow, having acute or rather obtuse ends. Apocolpia moderate extent or small.

Tectal elements essentially elongated columnar, sometimes fused to each other;

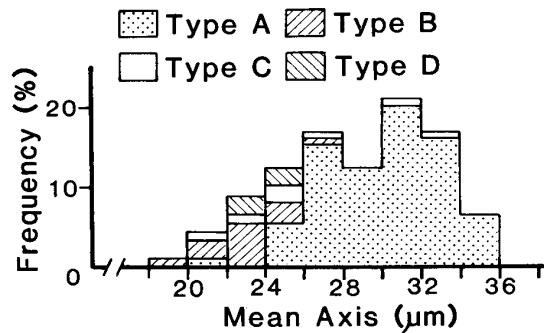


Fig. 8. Histograms showing size frequency of the pollen grains of Early Miocene *Fagus* for each type in SEM. $N=113$, Type A : $N=87$; $av=30.6\mu\text{m}$, $sd=2.5\mu\text{m}$ (abbreviations in Fig. 2).

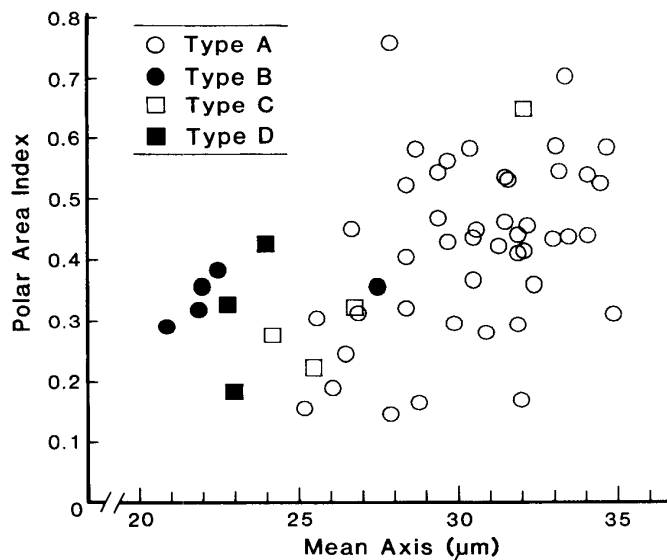


Fig. 9. Pollen grain size of Early Miocene *Fagus* plotted against its polar area index for each type in SEM. Type A : $N=45$; $r=0.39$; polar area index, $av=0.43$, $sd=0.14$ (abbreviations in Fig. 4).

straight or gently curved, having smooth surface or bearing small processes. Transverse diameter of most elements 0.10 to 0.30 μm , frequently about 0.20 μm . Trends of the elements vary, but many part of exine surface are covered with horizontal elements.

Pattern of exine sculpture uniform around whole grain except near colpus. At the colpal margin, tectal elements more or less fused, sometimes forming a slight elevation, occasionally margo (see Pl. IV, fig. 1, Pl. V, fig. 3). Ektexinous bridges sometimes exist (see Pl. V, figs. 1, 4).

Colpus membrane sculptured by fused, indefinite, columnar (?) elements. The elements may be more narrow and shorter than those of the exine surface.

Remarks: Eighty seven grains (77%) were observed with SEM. Frequency of mean axis is presented in Fig. 8. Relationship between polar area index and mean axis is shown in Fig. 9. There is weak correlation between the two measurements.

Pattern of exine sculpture of this type is rather variable grain by grain. It is difficult, however, to distinguish these grains into further pollen types because of their continuous differences in exine sculpture.

This type resembles *Fagus crenata* and *F. japonica*. But the transverse diameter of the tectal elements of this type is more variable than that of the two recent species of Japan. Surface of the elements of the modern species is more smooth than that of this type.

Type B (Pl. VI, figs. 1-3)

Description: Pollen grain relatively small; spheroidal or prolate-spheroidal; circular in polar view, circular or longitudinally elliptic in equatorial view. Colpi moderate length or long, narrow, having acute ends. Apocolpia moderate extent or small.

Tectal elements well or poorly defined. The elements essentially elongated columnar, often fused, more or less irregular in shape; straight or gently curved, having smooth surface or bearing small processes. Vertical elements relatively abundant. Transverse diameter of the elements about 0.12 to 0.25 μm . Pattern of exine sculpture uniform around whole grain. Several grains have ektexinous bridges. Colpus membrane unobserved.

Remarks: Fifteen grains (13%) were observed with SEM. Frequency of mean axis is presented in Fig. 8. Relationship between polar area index and mean axis is shown in Fig. 9. This type is distinguished from Type A by trends of the tectal elements and irregular tectal elements.

Type C (Pl. VI, fig. 4; Pl. VII, figs. 1, 2)

Description: Pollen grain spheroidal, circular both in polar and equatorial view. Colpi moderate length or long, narrow, having acute ends. Apocolpia moderate extent or small.

Tectal elements well or poorly defined. The elements, essentially elongated

columnar, mostly straight, occasionally gently curved, having smooth surface of bearing small processes. Two or more elements arrange parallel, more or less fused to each other, showing cluster pattern. These clusters occasionally form insular structures. Transverse diameter of most elements about 0.15 to 0.20 μm .

Pattern of exine sculpture uniform around whole grain except near colpus. At the colpal margin, tectal elements more or less fused, forming a slight elevation or occasionally conspicuous margo (see Pl. VII, fig. 1). Colpus membrane unobserved.

Remarks: Seven grains (6%) are observed with SEM. Frequency of mean axis is presented in Fig. 8. Relationship between polar area index and mean axis is shown in Fig. 9. One grain has short colpi and large apocolpia (see Pl. VII, fig. 2). This is an exception.

This type is clearly distinguished from others by its cluster pattern. In LM, the exine sculpture of the grain which displays insular structures is probably recognized as verrucate. These grains resemble form-species *Fagus granulata*, which was established by Martin and Rouse (1966) on the basis of pollen morphology from Mio-Pliocene in Canada. But accurate comparison cannot be made because they did not examine the pollen grains with SEM.

Gortemaker (1986) discerned the cluster pattern on the exine surface of *Fagus japonica* and Miocene fagoid pollen from U.S.A.

Exine sculpture of this type appears to be intermediate ornamentation between that of *Amentoplexipollenites catahoulaensis* Crepet and Nixon and Type A pollen. *A. catahoulaensis* is an extinct Oligocene Fagaceae taxon from U.S.A. Pollen grain of the species are prolate, having clustered and twisted tectal elements (Crepet and Nixon, 1989).

Type D (Pl. VII, figs. 3, 4)

Description: Pollen grain relatively small; spheroidal, prolate-spheroidal or oblate-spheroidal; circular or rounded triangular in polar view, circular, longitudinally elliptic or transversely elliptic in equatorial view. Colpi rather long, narrow, having acute ends. Apocolpia rather small.

Tectal elements well or poorly defined. The elements essentially shortly columnar, more or less fused to each other, packed densely. Transverse diameter of many of elements about 0.18 μm . These elements result in relatively fine sculpturing. Pattern of exine sculpture uniform around whole grain except near colpus. At the colpal margin, tectal elements more or less fused.

Colpus membrane unobserved. The state of transformations suggests the thick endexine near colpus.

Remarks: Four grains (4%) were observed with SEM. Frequency of mean axis is presented in Fig. 8. Relationship between polar area index and mean axis is shown in Fig. 9.

This type is distinguished from others by its fine sculpture. This feature is recognizable at lower magnification rather than higher magnification. In LM, this type probably resembles the pollen of *Cyclobalanopsis*. But the exine sculpture differs

from those of *Cyclobalanopsis* on SEM observation.

CONCLUSION AND DISCUSSION

I attempt to classify these four types at the species level on the basis of the criteria derived from the investigation of the recent species.

The exine sculpture of Type A has greater variation than that found in pollen of present day species. It is known that sculptural pattern varies in relation to temperature and humidity during growth of a tree (Hebda and Lott, 1974). Pollen grains involved in one sample have been deposited during hundreds or thousands of years. Therefore it must be taken into consideration that the morphological variation of recent pollen which was derived from a tree is not equivalent to that of fossil grains which had been derived from many trees during a long time. The ranges of polar area index and mean axis of this type, however, are considerably greater than those of one species. And the grain size distribution of this type shows bimodal pattern (Fig. 8). Furthermore, there is weak correlation between mean axis and polar area index (Fig. 9). Such weak correlation between the two measurements is recognizable in the assemblage of two recent species as a whole while not in each species (Figs. 4, 5). These facts suggest that Type A includes two species: one is larger size and has larger polar area index (*Fagus* sp. 1), and the other is smaller size and has smaller polar area index (*F.* sp. 2). These two species cannot be clearly distinguished from each other. Morphological relationship between *F.* sp. 1 and *F.* sp. 2 resembles that between *F. crenata* and *F. japonica*.

Type B is probably a small outlier of *Fagus* sp. 1 and/or *F.* sp. 2. The exine sculpture of Type B resembles that of the small outlier of *F. crenata* and *F. japonica*, and the grain size of this type is relatively small.

Type C seems to be a species different from *Fagus* sp. 1 and *F.* sp. 2 because the sculptural pattern is different. This type might relate to extinct Oligocene Fagaceae taxa. However, this type may be a variation of *F.* sp. 1 or *F.* sp. 2 because there is a possibility that sculptural pattern varies within one species such as *F. japonica*. Gortemaker (1986) discerned the cluster pattern in the arrangement of tectal elements of *F. japonica*, whereas other works including this study did not discern the pattern. The existence of the grain which has large apocolpia supports the possibility (Fig. 9).

Type D seems to be a species different from *Fagus* sp. 1 and *F.* sp. 2. But the possibility cannot be denied that Type D is a small outlier of *F.* sp. 1 and/or *F.* sp. 2.

The conclusion is that two or more *Fagus* species occurred in Japan during the deposition of the Hachiya Formation. According to the fossil records of leaves and cupules, only *F. antipofi* Heer grew in East Asia in Early Miocene time (Tanai, 1974). The leaf remains of *Fagus* from the Hachiya Formation are also assigned to *F. antipofi* (Ina et al., 1983). Therefore the conclusion of this study is different from that derived from leaf and cupule remains. *F.* sp. 1 or *F.* sp. 2 is probably assigned to *F. antipofi*.

This difference seems to be caused by the stratigraphic position of the Hachiya Formation. The formation is of early Early Miocene in age, and the stratigraphic position is lower than other formations which contain the typical Aniai-type Flora. It is considered that the Japanese Islands were situated at the eastern margin of the Asia

Continent at that time (Chiji and IGCP-246 National Working Group of Japan, 1990). Then, the paleoclimate represented by the Hachiya Flora was slightly warmer than that by the typical Aniai-type flora (Ina et al., 1983). These paleogeography and paleoclimate might make the second *Fagus* species migrate from the south to Japan. In western North America, *F. antipofi* and *F. washoensis* LaMotte occurred in Early Miocene time. These two species had separate geographical distribution at that time: the habitat of *F. antipofi* is northern area and that of *F. washoensis* is southern area (Tanai, 1974). According to the conclusion of this study, *F. antipofi* and other *Fagus* species might grow in separate habitat in East Asia as in western North America.

Recent *Fagus* species are grouped based on leaf morphology or pollen morphology by several workers (Tralau, 1962; Tanai, 1974; Hanks and Fairbrothers, 1976; Gortemaker, 1986). I attempt to group the living *Fagus* species on the basis of polar area index. Because I investigated only *Fagus crenata* and *F. japonica*, the data of other recent species listed in Table 1 have been taken from other works. Selected recent *Fagus* species are distinguished into two groups, the small apocolpia group and the large apocolpia group. The boundary value of polar area index between the two groups is decided at 0.4 for convenience, which is the boundary value between *F. crenata* and *F. japonica*. The former group includes *F. grandifolia*, *F. japonica* and *F. multinervis*; and the latter group *F. crenata*, *F. hayatae*, *F. orientalis* and *F. sylvatica*. This grouping is concordant with that of Tanai (1974). Pollen grains of Early Miocene *Fagus* in this study belong to both groups as well as recent *Fagus* in Japan.

ACKNOWLEDGMENTS

I am deeply indebted to Dr. Junji Itoigawa of Nagoya University for his valuable suggestions and critical reading the manuscript, and to Dr. Tohru Yamanoi of Yamagata University for offering me polliniferous material of *Fagus crenata*, critical reading the manuscript, and helpful suggestions. Thanks are due to Mr. Seiju Yamaguchi, Mizunami City, Gifu Prefecture, from whom I obtained the polliniferous material of *Fagus japonica*. Thanks are also due to Mr. Haruyuki Ina of Kyokuryo High School, Aichi Prefecture for his helpful suggestions.

I wish to express my special thanks to Dr. Joseph Praglowski of Swedish Museum of Natural History for critical reading the manuscript and valuable suggestions.

REFERENCES

- Chiji, M. and IGCP-246 National Working Group of Japan (1990) Paleogeography and environments during the opening of the Sea of Japan. In: Tsuchi R. ed., *Pacific Neogene events-their timing, nature and interrelationship*. Univ. Tokyo Press, 161-169.
- Crepet, W. L., and K. C. Nixon (1989) Extinct transitional Fagaceae from the Oligocene and their phylogenetic implications. *Amer. J. Bot.*, vol. **76**, 1493-1505.
- Faegri, K. and J. Iversen (1989) Textbook of pollen analysis. 4th ed. by K. Faegri, P. E. Kaland and K. Krzywinski. Wiley, 323 p.
- Gortemaker, R. E. (1986) A method to identify pollen of some recent and fossil species of *Fagus* L. (Fagaceae). *Rev. Palaeobot. Palynol.*, vol **47**, 263-292.
- Hanks, S. L. and D. E. Fairbrothers (1976) Palynotaxonomic investigation of *Fagus* L. and *Nothofagus*

- Bl.: light microscopy, scanning electron microscopy, and computer analyses. In: Heywood V. H. ed., *Botanical systematics. An occasional series of monographs*. Academic Press, 1-141.
- Hebda, R. J. and N. A. Lott (1974) Effects of different temperatures and humidities during growth on pollen morphology; an SEM study. *Pollen Spores*, vol. **15**, 563-572.
- Hujiyama, I. and T. Nomura (1986) Early Miocene insect fauna of the Hachiya Formation, Gifu Prefecture Japan. *Bull. Mizunami Fossil Mus.*, No. **13**, 1-13 (in Japanese with English abstract).
- Huzioka, K. (1964) The Aniai flora of Akita Prefecture, and the Aniai-type floras in Honshu, Japan. *J. Min. Coll., Akita Univ., Ser. A*, vol. **3**, 1-105.
- Ina, H., T. Nomura and I. Kimura (1983) Plants from the Miocene Hachiya Formation in Tono District, Gifu Prefecture, Japan. *Bull. Mizunami Fossil Mus.*, No. **10**, 1-22.
- Ina, H., T. Nomura and I. Kimura (1985) Additional plants from the Miocene Hachiya Formation of the Tono District, Gifu Prefecture, Japan. *Bull. Mizunami Fossil Mus.*, No. **12**, 1-26.
- Itoigawa, J. (1980) Geology of the Mizunami district, central Japan. *Monograph Mizunami Fossil Mus.*, No. **1**, 55p. (in Japanese).
- Kodera, H. and T. Nomura (1988) Early Miocene Cyprinid fishes collected from the Hachiya Formation, Gifu Prefecture, Japan. *Bull. Mizunami Fossil Mus.*, No. **14**, 1-12 (in Japanese with English abstract).
- Martin, H. A. and G. E. Rouse (1966) Palynology of Late Tertiary sediments from Queen Charlotte Islands, British Columbia. *Canadian J. Bot.*, vol. **44**, 171-208.
- Miyoshi, N. (1982) Pollen morphology by means of scanning electron microscope. 4. Fagaceae (Angiospermae). *Bull. Hiruzen Res. Inst., Okayama Univ. Sci.*, No. **7**, 55-60 (in Japanese with English summary).
- Miyoshi, N. and T. Uchiyama (1987) Modern and fossil pollen morphology of the genus *Fagus* (Fagaceae) in Japan. *Bull. Hiruzen Res. Inst., Okayama Univ. Sci.*, No. **13**, 1-6.
- Miyoshi, N., K. T. Choi and S. J. Kang (1991) Pollen grains of *Fagus hayatae* and *Fagus multinervis*. *Jpn. J. Palynol.*, vol. **37**, 183-184 (in Japanese).
- Mohr, B. A. R. (1984) Die Mikroflora der Obermiozänen bis Unterpliozänen Deckschichten der Rheinischen Braunkohle. *Palaeontographica, Abt. B*, **191**, 29-133.
- Nomura T. (1986) Preliminary report of the Miocene Hachiya Formation and its K-Ar ages. *Jour. Geol. Soc. Japan*, vol. **92**, 73-76 (in Japanese).
- Pragłowski, J. (1982) Fagaceae L.: Fagoideae. *World pollen and spore flora*. **11**, 1-28.
- Shimakura, M. (1973) Palynomorphs of Japanese Plants. *Osaka Museum of Natural History, Spec. Publ.* vol. **5**, 60 p. (in Japanese).
- Tanai, T. (1974) Evolutionary trend of the genus *Fagus* around the Northern Pacific Basin. In: *Symposium on origin and phytogeography of Angiosperms*, Birbal Sahni Inst. Palaeobot., Spec. Publ., No. **1**, 62-83.
- Torii, T. (1982) The history of Inuyama city, topography and geology. In: *The board of education of Inuyama City*, 23-56 (in Japanese).
- Tralau, H. (1962) Die spättertiären *Fagus*-Arten Europas. *Bot. Not.*, vol. **115**, 147-176.
- Uchiyama, T. (1986) Pollen morphology of *Quercus* and *Fagus* (Fagaceae) in Japan. *Jpn. J. Palynol.*, vol. **32**, 81-87 (in Japanese with English abstract).

Plate I

SEM micrographs of *Fagus crenata* pollen. Magnification, a: ca. x1350, scale bar: 10 μm ; b: ca. x6500, scale bar: 2 μm .

- 1a. Polar view, large apocolpium.
- 2a. Nearly polar view, moderate extent of apocolpium.
- 3a. Nearly polar view, small apocolpium.
- 1b, 2b, 3b. Apocolpium.
- 4a. Equatorial view, short colpus.
- 5a. Nearly equatorial view, moderate length of colpus.
- 6a. Nearly equatorial view, long colpus.
- 4b, 5b, 6b. Mesocolpium.

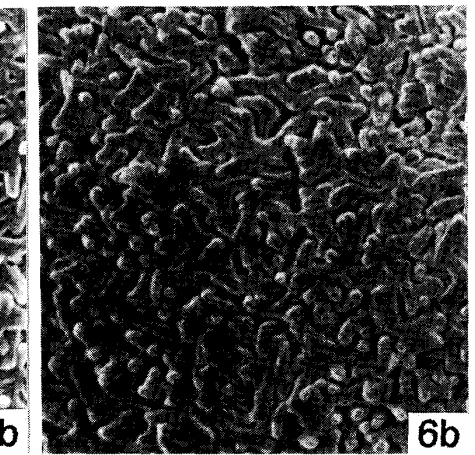
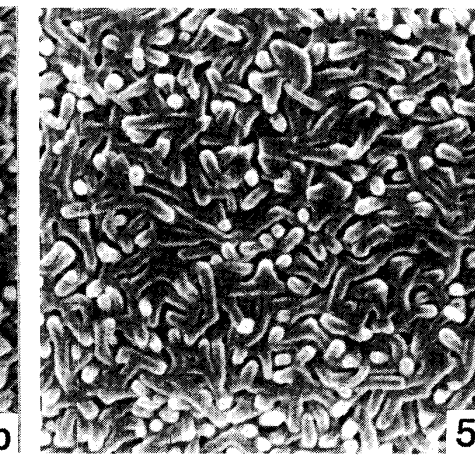
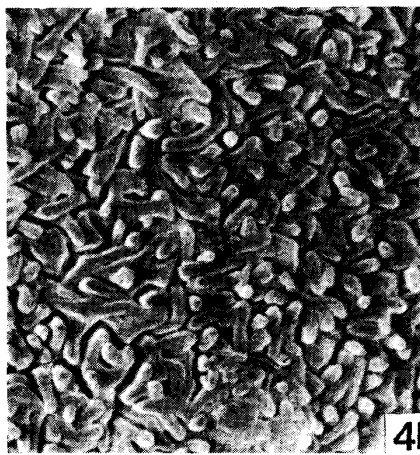
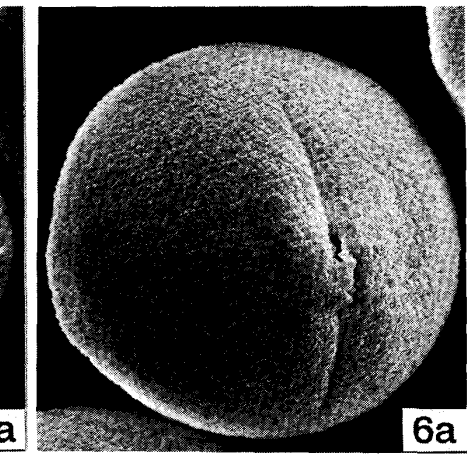
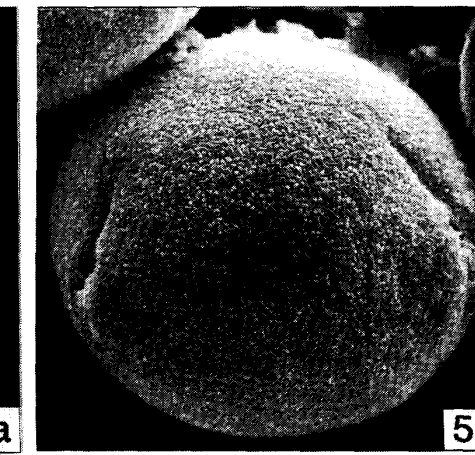
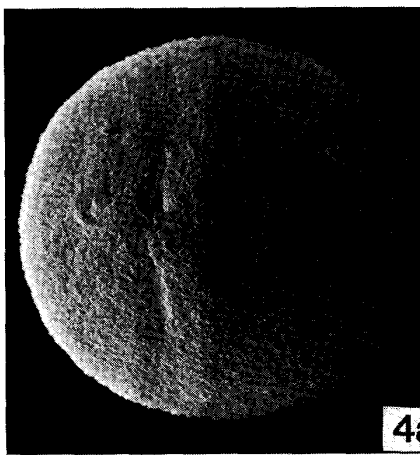
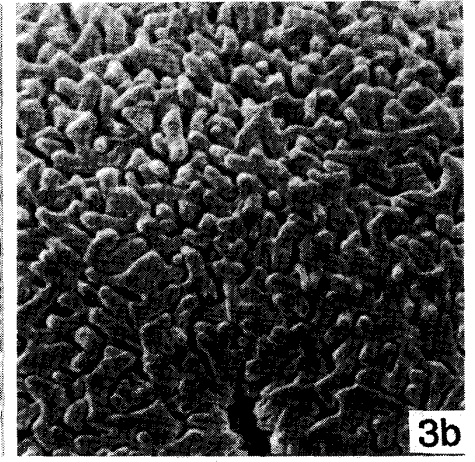
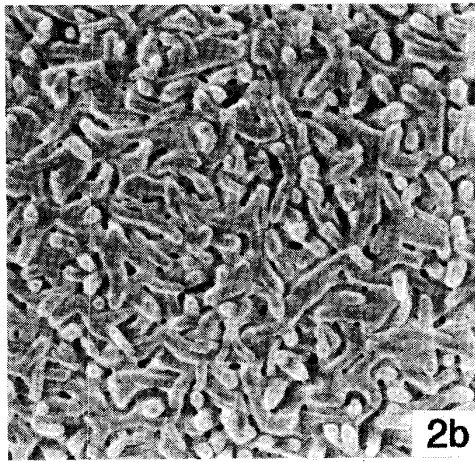
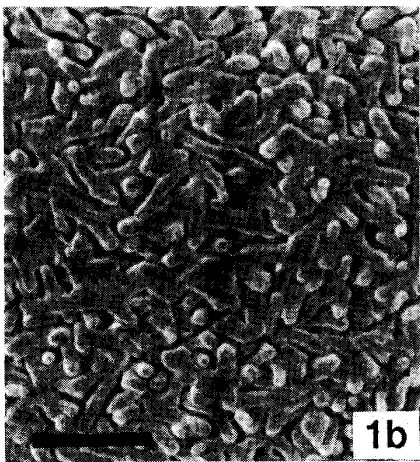
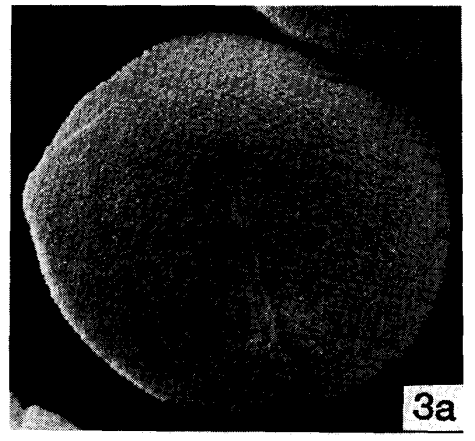
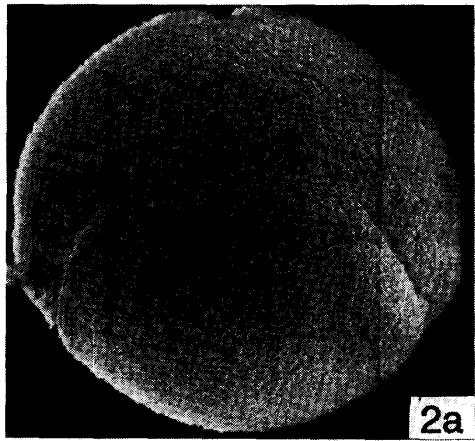
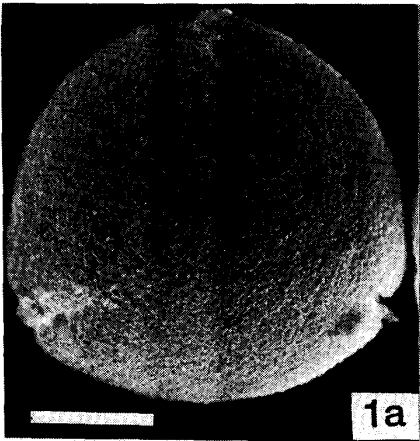


Plate II

SEM micrographs of *Fagus japonica* pollen. Magnification, a: ca. x1350, scale bar: 10 μ m; b: ca. x6500, scale bar: 2 μ m.

- 1a. Nearly polar view, very small apocolpium.
- 1b. Near apocolpium.
- 2a. Polar view, small apocolpium.
- 2b. Apocolpium.
- 3a, 4a. Oblique view.
- 3b, 4b. Mesocolpium.
- 5a, 6a. Equatorial view.
- 5b. Colpus membrane and ektexinous bridge covering os.
- 6b. Ektexinous bridge covering os.

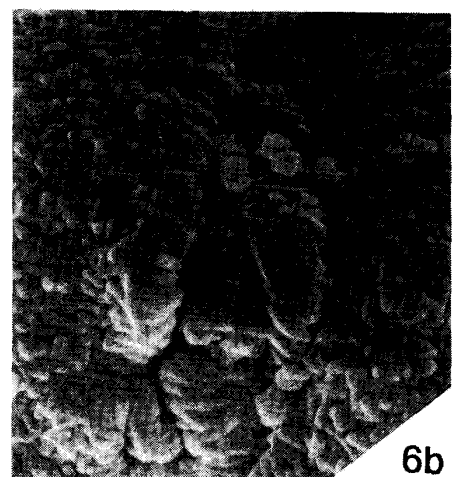
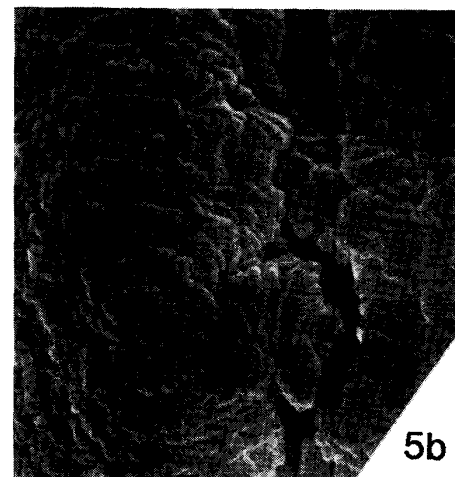
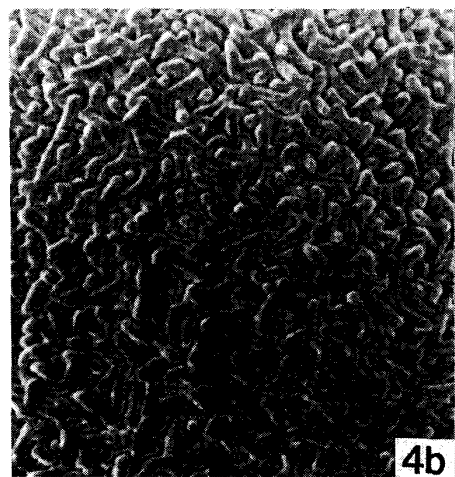
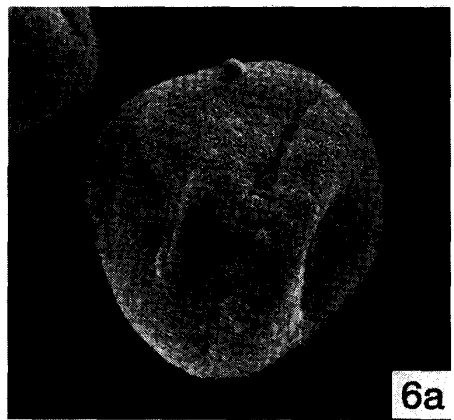
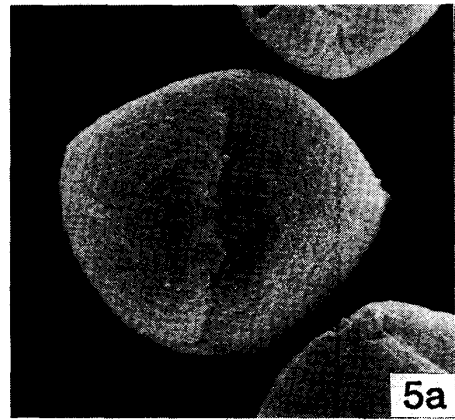
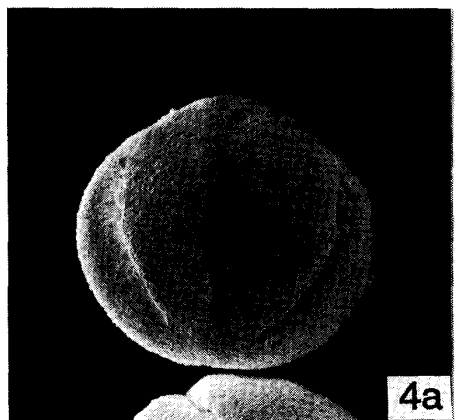
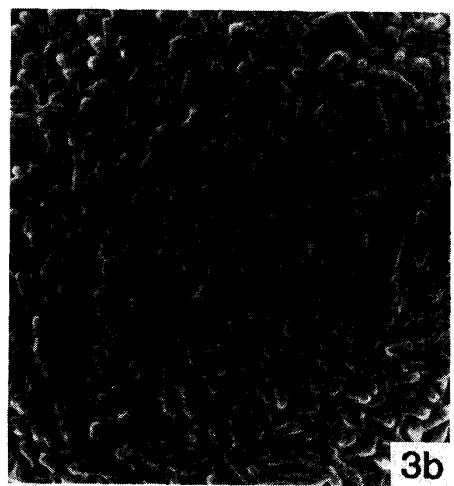
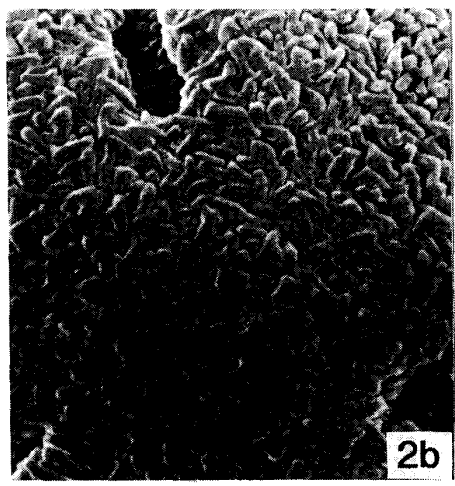
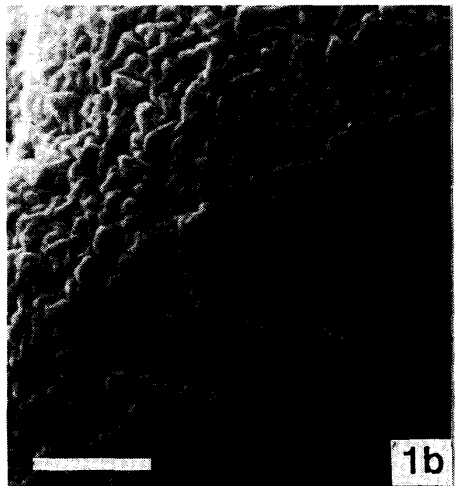
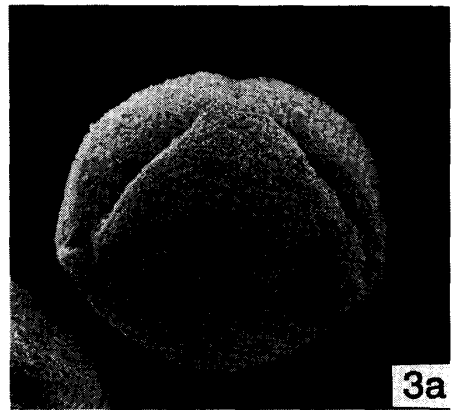
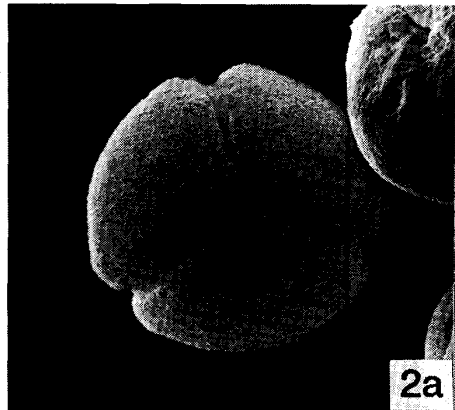
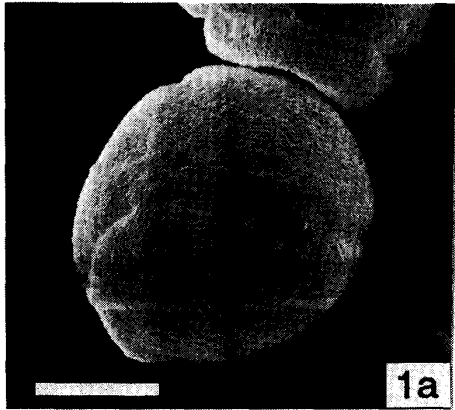


Plate III

SEM micrographs of smaller grains of *Fagus crenata* (1-3) and *F. japonica* pollen (4-7) and colpus and os of normal grains (8, 9). Magnification, a: ca. x1350, scale bar: 10 μ m; b, 8, 9: ca. x6500, scale bar: 2 μ m.

- 1-3. Small outliers in the grain size distribution of *F. crenata* pollen.
- 4-7. Smaller grains in the size distribution of *F. japonica* pollen.
8. Colpus membrane and os of a normal pollen grain of *F. crenata*.
9. Colpus, colpus membrane and os of a normal pollen grain of *F. japonica*.

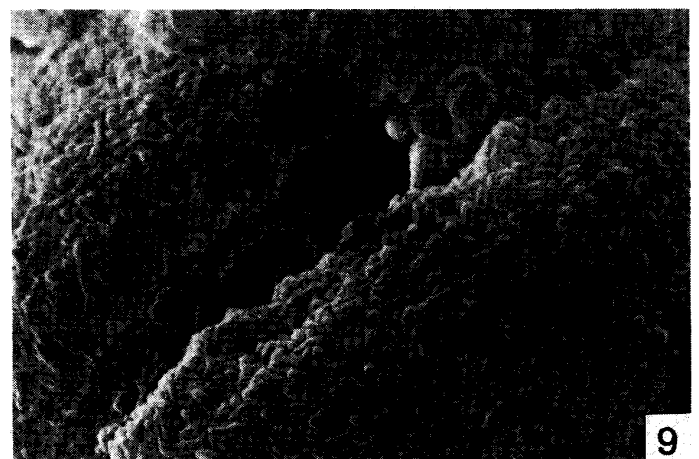
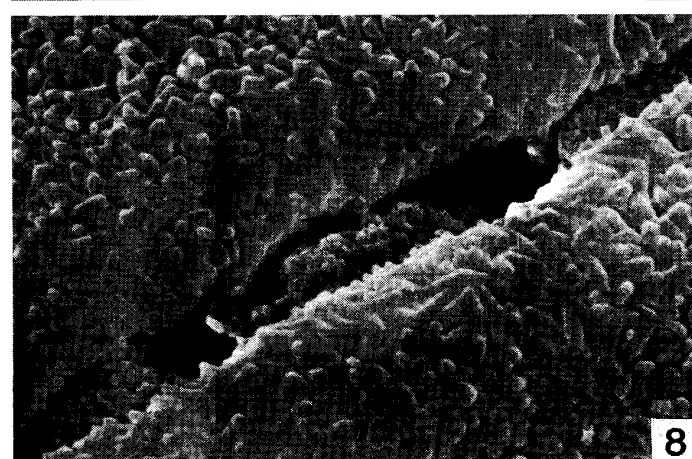
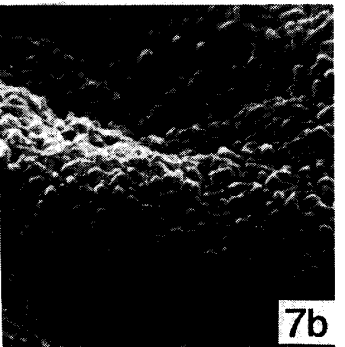
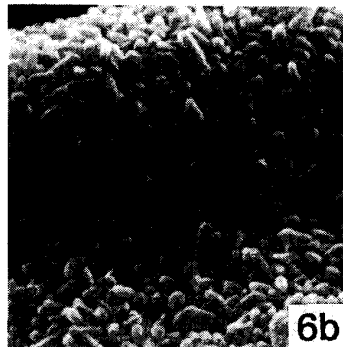
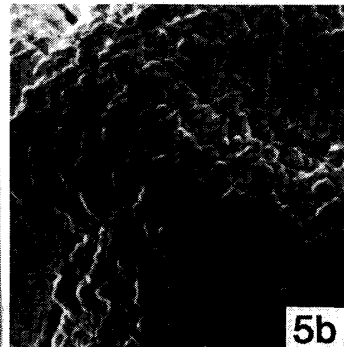
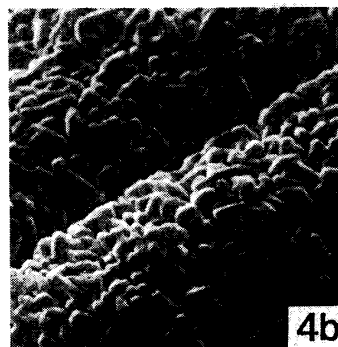
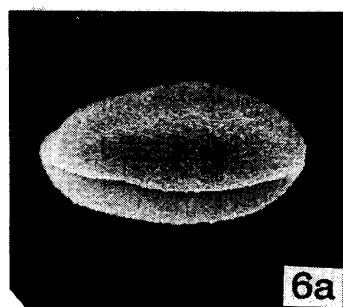
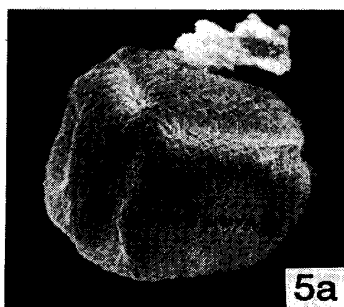
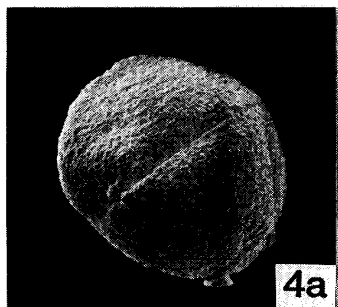
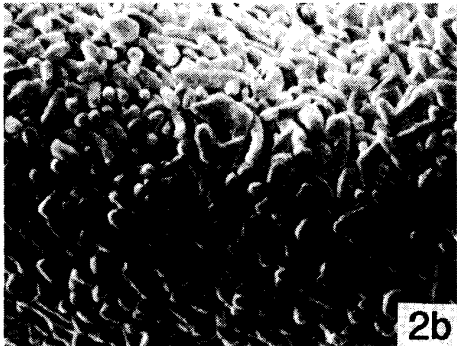
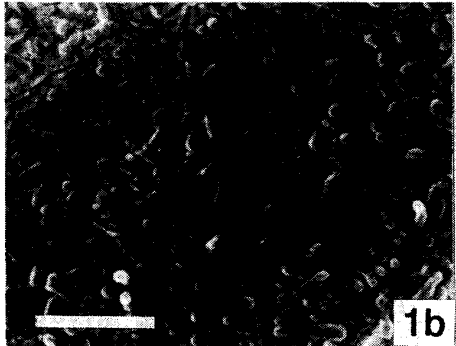
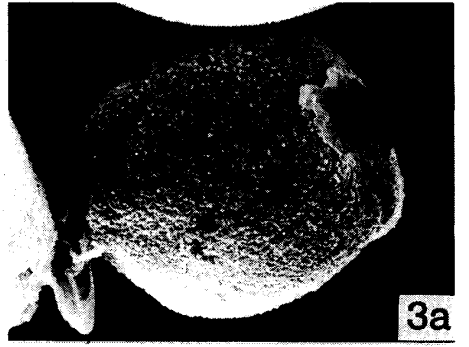
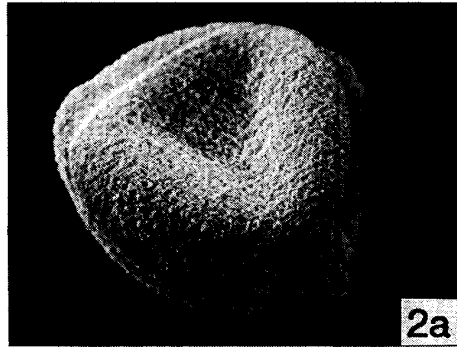
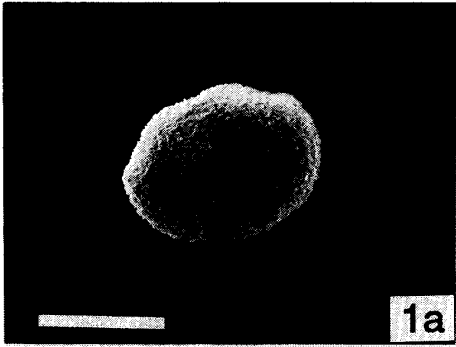


Plate IV

SEM micrographs of Type A pollen of Early Miocene *Fagus*. Magnification, a: ca. x1350, scale bar: 10 μ m; b: ca. x6500, scale bar: 2 μ m.

- 1a. Nearly polar view. NG-01.
- 1b. Colpus, colpus membrane, and margo-like structure.
- 2a. Nearly polar view. NG-02.
- 2b. Mesocolpium near colpus.
- 3a. Nearly equatorial view. NG-02.
- 3b. Mesocolpium.
- 4a. Equatorial view. NG-01.
- 4b. Mesocolpium.

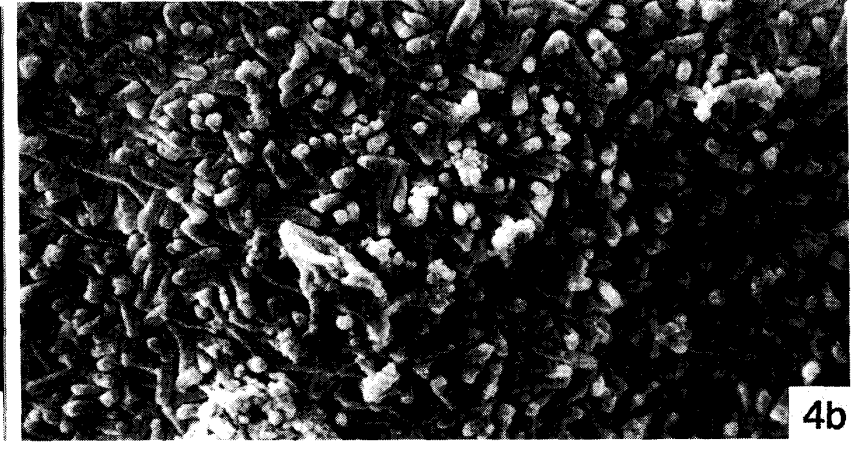
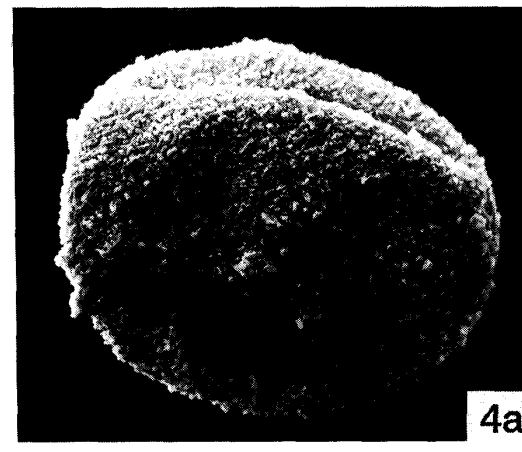
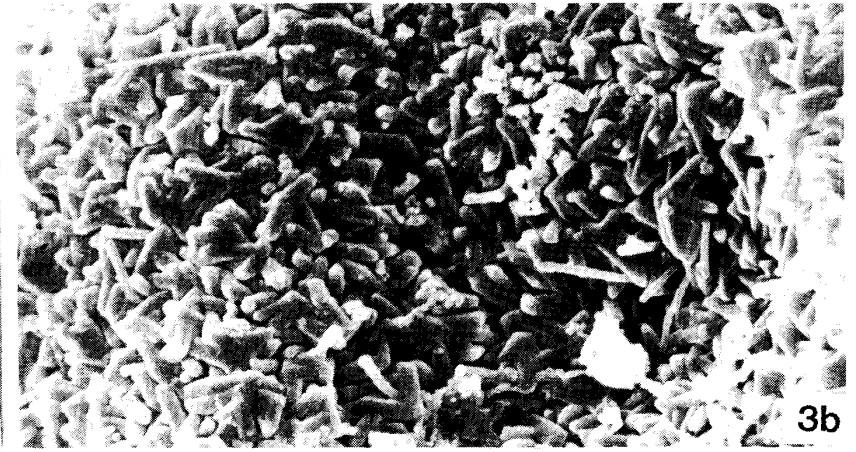
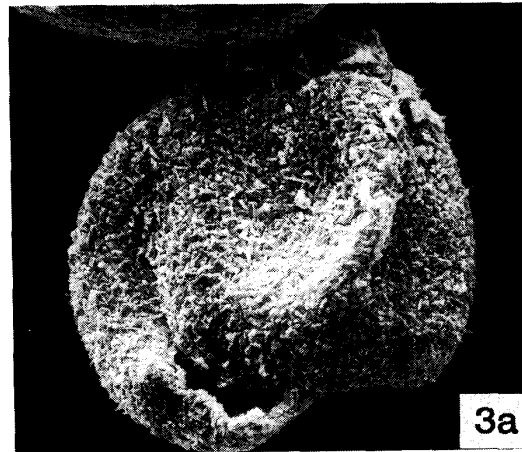
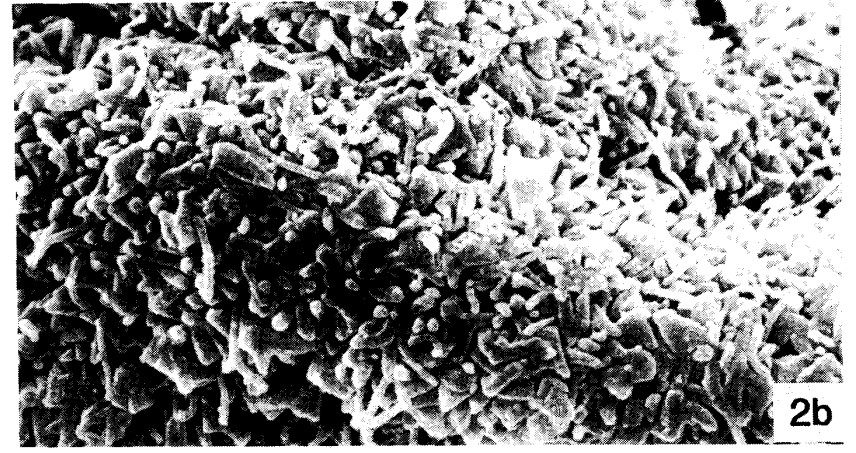
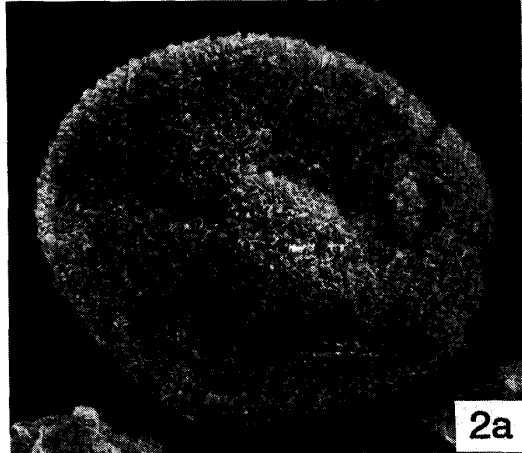
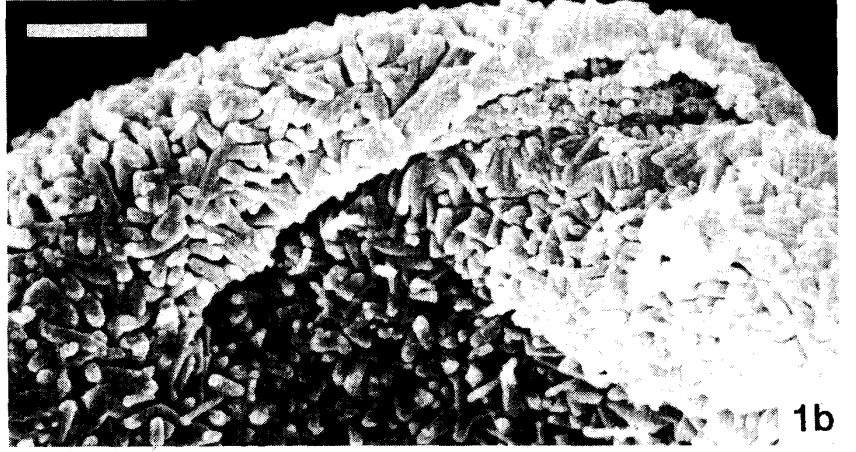
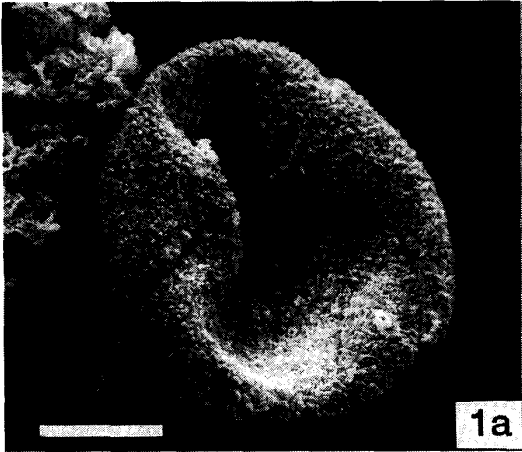


Plate V

SEM micrographs of Type A pollen of Early Miocene *Fagus*. Magnification, a: ca. x1350, scale bar: 10 μ m; b, c: ca. x6500, scale bar: 2 μ m.

- 1a. Equatorial view. NG-01.
- 1b. Colpus and ektexinous bridge.
- 2a. Nearly polar view. NG-01.
- 2b. Colpus and colpus membrane.
- 3a. Polar view. NG-01.
- 3b. Apocolpium.
- 3c. Colpus and margo formed by angular elements.
- 4a. Oblique view. NG-01.
- 4b. Near apocolpium.

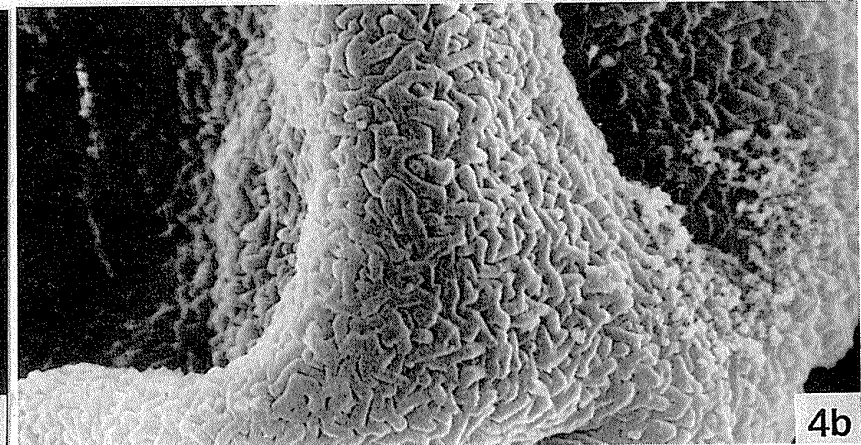
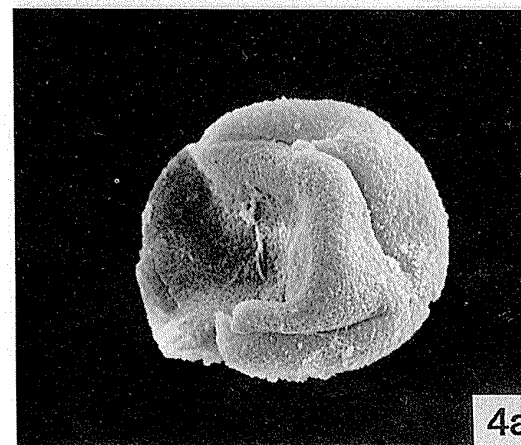
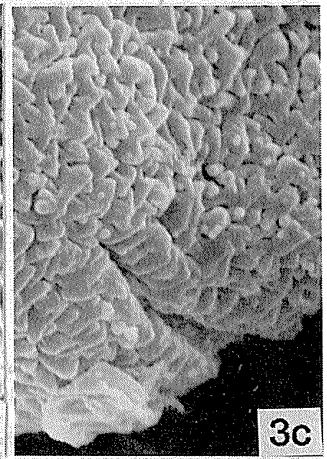
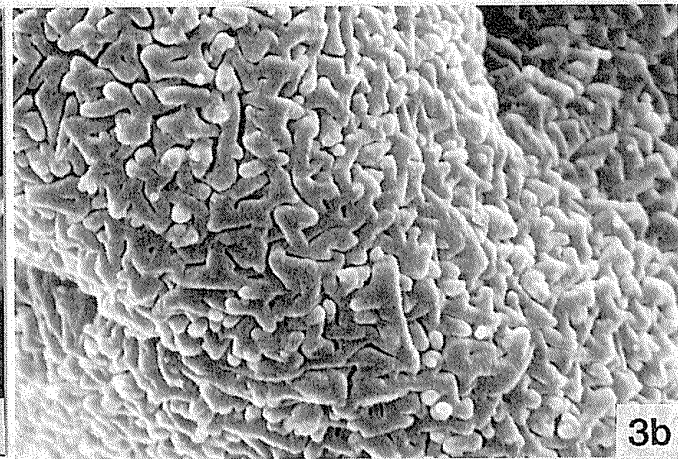
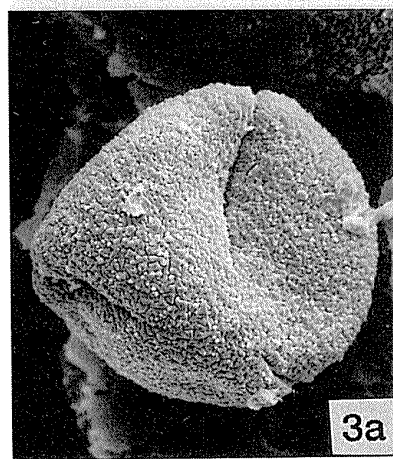
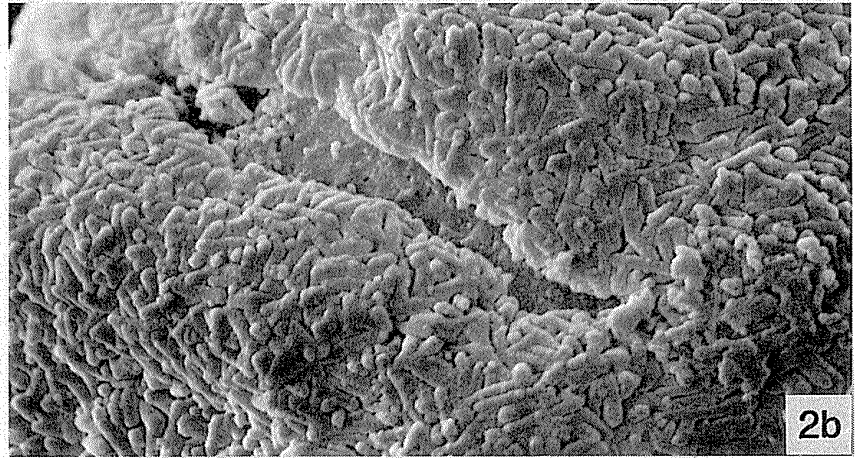
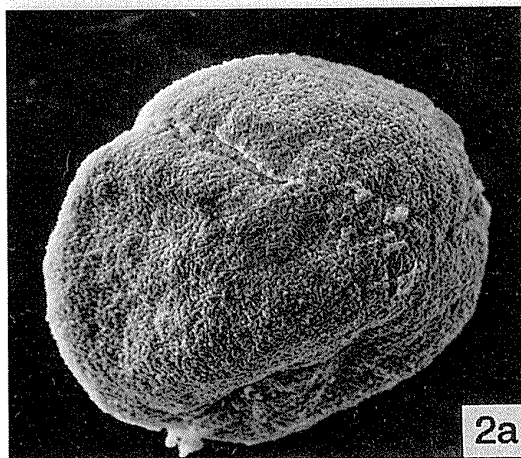
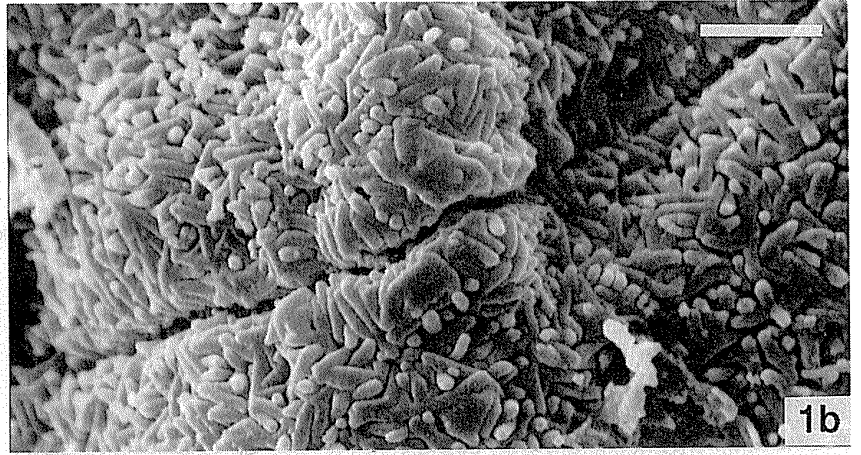
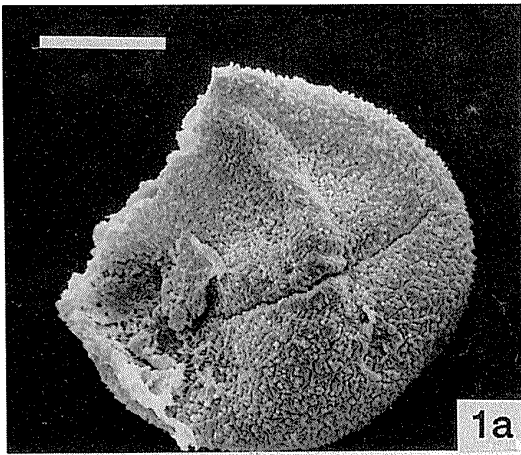


Plate VI

SEM micrographs of Types B (1-3) and C (4) of Early Miocene *Fagus* pollen. Magnification, a: ca. x1350, scale bar: 10 μ m; b: ca. x6500, scale bar: 2 μ m.

- 1a. Type B. Equatorial view. NG-01.
- 1b. Mesocolpium.
- 2a. Type B. Equatorial view. NG-01.
- 2b. Mesocolpium and colpus.
- 3a. Type B. Oblique view. NG-01.
- 3b. Mesocolpium and colpus.
- 4a. Type C. Oblique view. NG-02.
- 4b. Mesocolpium and colpus.

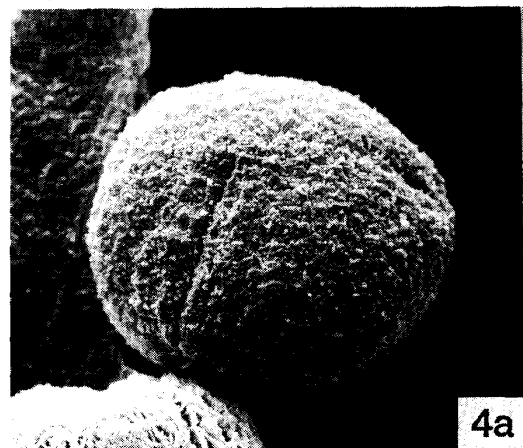
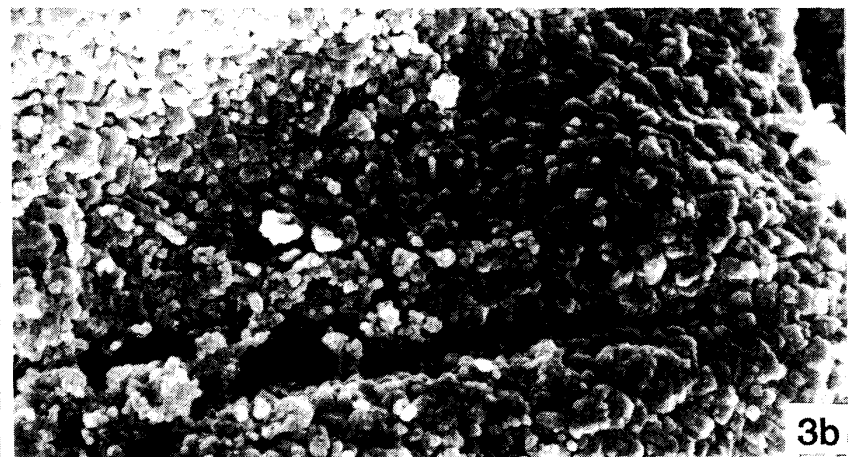
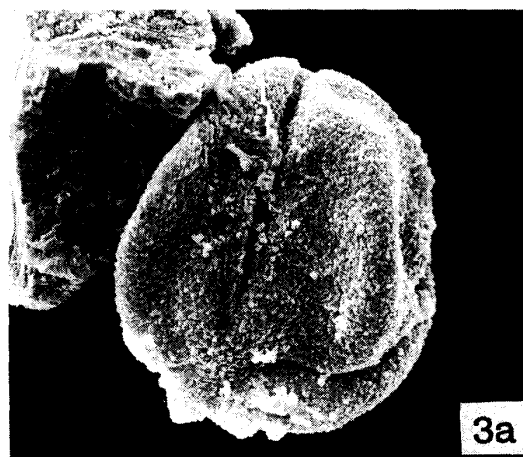
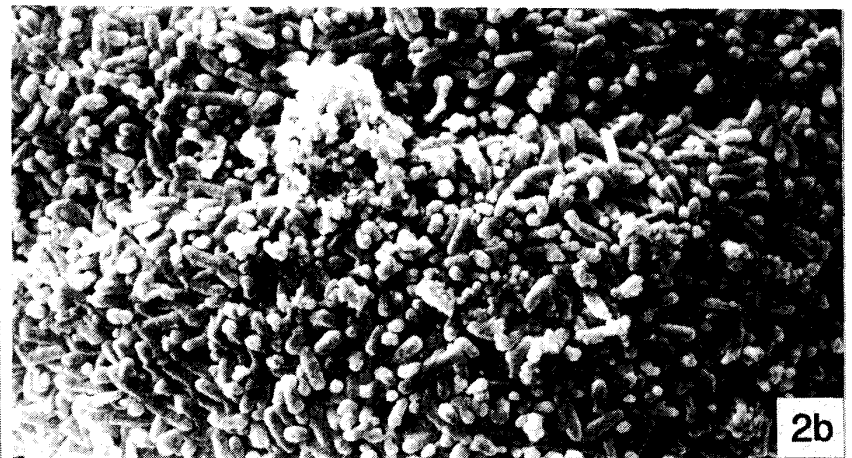
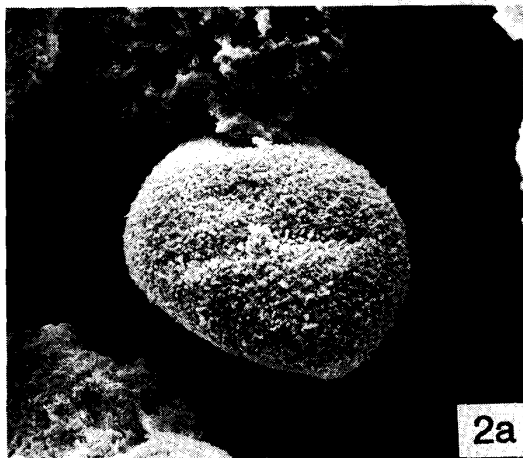
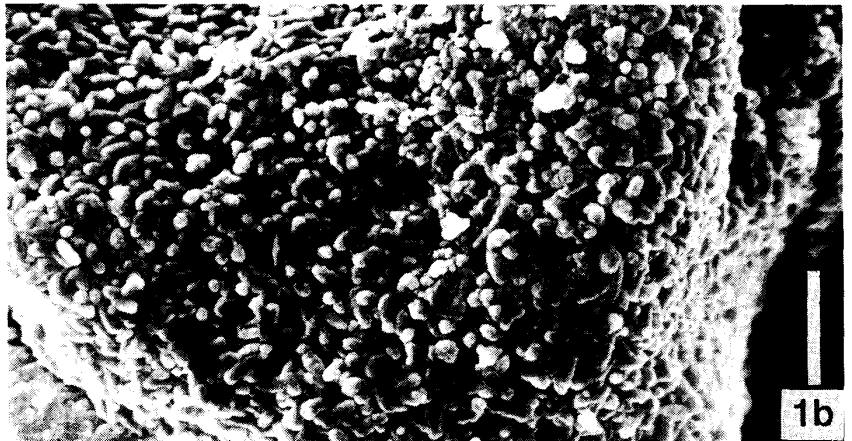
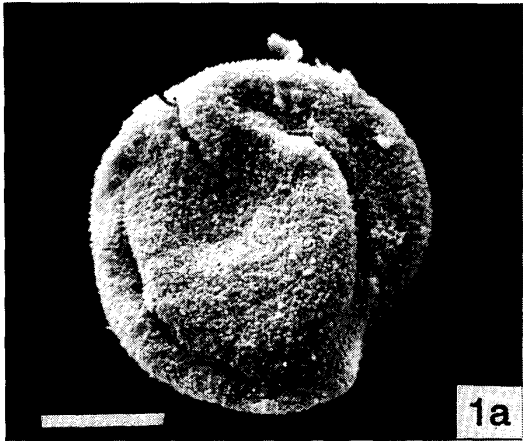


Plate VII

SEM micrographs of Types C (1, 2) and D (3, 4) of Early Miocene *Fagus* pollen. Magnification, a: ca. x1350, scale bar: 10 μ m; b: ca. x6500, scale bar: 2 μ m.

- 1a. Type C. Oblique view. Insular structures. NG-01.
- 1b. Mesocolpium.
- 2a. Exceptional form of Type C. Nearly polar view. NG-02.
- 2b. Apocolpium.
- 3a. Type D. Polar view. NG-02.
- 3b. Apocolpium.
- 4a. Equatorial view. NG-01.
- 4b. Mesocolpium.

