Pollen Morphology of the Genus *Abies* in Japan

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The pollen morphology of 5 species of *Abies* (*A. firma, A. homolepis, A. mariesii, A. sachalinensis, A. veitchii*) in Japan is described using light and scanning electron microscopy. These species can be distinguished by the combination of various pollen morphological characters including sculpture of the cappa such as the triradiate streak, ornamentation of the cappula and the saccus, and grain size and proportion.

Key words: *Abies* pollen, Japan, Exine sculpture, Species distinction.

Introduction

Five species of *Abies* now grow in Japan, namely *Abies firma* Sieb. et Zucc., *A. homolepis* Sieb. et Zucc., *A. mariesii* Masters, *A. sachalinensis* (Fr. Schm.) Masters and *A. veitchii* Lindley[1]. They have different ecological amplitudes and are found in the different ranges of elevation in a certain district except for *A. sachalinensis*. For example, *A. firma* occurs below 600 m in altitude, *A. homolepis* between 1200 and 1600 m, *A. mariesii* and *A. veitchii* between 1500 and 2700 m in Nagano Prefecture, central Japan. *A. sachalinensis* has a distinct distribution, and grows in Hokkaido.

Fossil pollen of *Abies* is one of the common elements of Quaternary pollen flora in Japan. Pollen grains of the genus are not transported so long by the wind[2]. Therefore the ability to identify *Abies* species among pollen grains could enhance the paleoenvironmental information extracted from Quaternary sediments.

Numerous comprehensive studies on saccate pollen have been published. Many of them examined the pollen morphology of *Abies* species using light microscopy (LM), such as works by Wodehouse[3], Van Campo[4], Erdtman[5,6], Ueno[7], and Ting[8]. Yamazaki and Takeoka[9] clarified the detail sculpture of some species of the genus through transmission electron microscopy with a replica method. Some works[10-14] include illustrations and descriptions of the pollen grains of some *Abies* species using scanning electron microscopy (SEM).

SEM provides the potential to identify pollen grains below the genus level. Bagnell[12] studied the pollen grains of *Abies* species in the Rocky Mountain area and concluded that the morphology of the triradiate streak on the proximal surface of the corpus was the diagnostic character for species distinction.

The present study examines the pollen morphology of *Abies* species in Japan using SEM and LM, and attempts to separate the five species on the basis of pollen morphology.

Materials and Methods

Materials

The sources of the materials studied are as follows. *Abies firma* : polliniferous material collected by Tohru Yamanoi at the campus of Yamagata University, Yamagata Prefecture in June 1980. *A. homolepis* : herbarium material of Liberal Arts of Shinshu University, collected by M. Hotta at Mt. Tsurugisan, Tokushima Prefecture on May 29, 1962. *A. mariesii* : polliniferous material collected by Osamu Yamagata at Hakkoda, Aomori Prefecture in 1979. *A. sachalinensis* : polliniferous material collected by Yaeko Igarashi at Kuriyama, Hokkaido. *A. veitchii* : herbarium material of Faculty of Liberal Arts of Shinshu University, collected by the Seminar class 1979 at Mt. Hachimori, Nagano Prefecture on August 12, 1979.

Preparation

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

A part of treated grains was ultrasonificated to disrupt the grains for SEM observation of inner sculpture and/or exine structure of the grains.

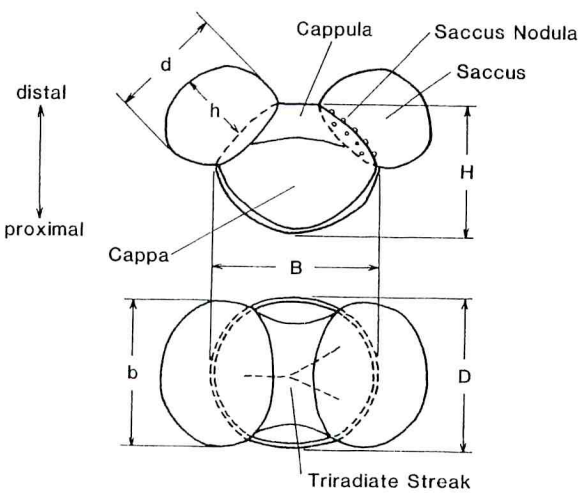

Fig. 1. Diagrammatic illustrations of *Abies* pollen grain showing terminology and measurements in lateral longitudinal view (upper) and distal polar view (lower) (modified from Erdtman[5]). H = corpus height, B = corpus depth, D = corpus depth, h = saccus height, b = saccus breadth, D = saccus depth.

Terminology

The used terminology follows Erdtman[5], but that of exine structure and sculpture follows Faegri and Iversen[15]. The term "saccus nodula" is defined by Klaus[16]. Figure 1 shows main terms for the pollen grain of *Abies*.

Measurements

The sizes of the corpus and saccus were measured: their height, breadth and depth (Fig. 1). But saccus height cannot be measured on SEM micrographs. Two size data were averaged for the grain with unequal sacci. We used an ocular micrometer in LM and a ruler on the SEM micrographs, respectively. The slides for LM observation were examined within four days after preparation.

Results

Following description is based mainly on SEM observation and partly on LM examination. The results of measurements are presented in Table 1 and Fig. 2.

Generic description

Form: Pollen grain consists of a corpus and two sacci. Most grains are bilateral, a few having unequal sacci. The outline of the proximal side of the corpus is rounded or slightly angular in lateral longitudinal view, and that in polar view is circular or elliptic. The shape of the saccus is flattened ellipsoidal, and saccus breadth is larger than its depth (Table 1). The saccus-cappa junction is clearly defined.

Exine sculpture: The cappa surface is covered with poorly-defined tectal elements and displays rugulate-scabrate sculpture with a few perforations (see Pl. 2, figs. 6-10). Proximal surface of the cappa, however, is sometimes nearly psilate with sparse perforations. The cappa surface is knobby in the area near the cappula and the saccus. The triradiate streak is present or absent on the proximal face (see Pl. 3). This character, if present, is often species specific. The morphology of the junction area of the three streaks is related to the thickness of the exine at the proximal pole (cf. remarks of *Abies sachalinensis*).

The cappula has microverrucate elements (see Pl. 2, figs. 1-5). The element is less than 1 μm in breadth, frequently between 0.5 and 0.7 μm. A small pit is present near the center of the element. The elements often fuse to each other. Density of the elements is variable within each species. Interspaces of the elements are nearly psilate, but are sculptured by much smaller elements.

The saccus surface is nearly psilate or indistinctive rugulate-scabrate with many perforations except in *Abies sachalinensis* (see Pl. 2, figs. 11-15). This character varies within each species, but it is sometimes species specific (cf. remarks below). The saccus-cappula junction is bordered by a thickened ridge (see Pl. 1, figs. 1-5; Pl. 2, figs. 1-5). The ridge is scabrate and/or rugulate.

Exine structure and inner sculpture: The cappa exine is tectate, but it is difficult to describe in detail (see Pl. 4, figs. 6, 7). Thickness of the cappa exine becomes thinner toward the proximal pole and toward the junction area with the saccus except in *Abies sachalinensis* (see Pl. 1, figs. 6-10). Maximum thickness of the cappa exine is variable within each species, being 5 μm or more except in *A. firma*. Inner surface of the corpus is psilate but displays very fine dimple-shaped sculpture (see Pl. 4, figs. 6, 7).

Table 1. Size data of *Abies* pollen (Avg = average, SD = standard deviation, Min = minimum, Max = maximum, N = number)

	Corpus (in μm)			Saccus (in μm)		
	Height	Breadth	Depth	Height	Breadth	Depth
(LM)						
A. firma						
Avg	80.1	112.9	92.4	30.2	78.7	62.8
SD	6.8	6.8	5.3	2.8	8.0	3.8
Min	67.5	96.3	82.5	25.0	63.8	57.5
Max	88.8	125.0	100.0	35.0	92.0	68.8
N	22	49	8	14	7	14
A. homolepis						
Avg	81.3	100.4	87.1	34.0	79.6	68.4
SD	4.0	4.1	5.9	3.5	4.4	3.9
Min	73.8	90.0	77.5	27.5	75.0	60.0
Max	87.5	107.0	95.0	37.5	82.5	75.0
N	18	50	10	10	7	10
A. mariesii						
Avg	86.8	122.3	99.6	40.9	93.4	76.8
SD	5.2	5.0	6.2	5.2	10.1	5.2
Min	77.5	112.5	92.5	27.5	71.2	68.8
Max	102.5	132.5	110.0	47.5	110.0	87.5
N	27	49	7	22	9	24
A. sachalinensis						
Avg	84.8	111.0	99.2	38.5	84.6	68.9
SD	7.3	8.2	4.7	7.4	6.4	5.8
Min	70.5	90.0	90.0	27.5	75.0	57.5
Max	102.5	123.8	105.0	58.8	96.3	85.0
N	19	48	6	20	7	22
A. veitchii						
Avg	72.0	98.8	97.4	39.0	87.3	66.2
SD	7.5	10.5	10.7	4.4	8.3	9.0
Min	57.5	65.0	70.0	30.0	67.5	47.5
Max	77.5	120.0	131.3	43.8	102.5	73.8
N	10	39	30	10	29	10

Table 1. (Cont.)

	Corpus (in μm)			Saccus (in μm)		
	Height	Breadth	Depth	Height	Breadth	Depth
(SEM)						
A. firma						
Avg	49.3	74.1	61.1	.....	53.8	40.6
SD	2.4	3.2	1.9	.....	7.8	2.4
Min	43.8	66.0	58.4	.....	45.1	35.4
Max	52.8	80.5	63.6	.....	68.4	45.1
N	26	44	5	.....	5	23
A. homolepis						
Avg	50.6	66.9	58.5	.....	57.6	44.9
SD	1.0	3.2	1.9	.....	4.1	2.8
Min	49.3	60.4	54.9	.....	50.9	41.3
Max	52.5	73.1	60.4	.....	62.0	50.1
N	9	30	5	.....	4	7
A. mariesii						
Avg	55.8	86.1	67.3	.....	64.3	55.1
SD	3.7	5.9	0.5	.....	3.4	4.0
Min	48.5	70.8	66.8	.....	59.6	47.7
Max	62.0	96.2	68.1	.....	69.2	64.0
N	18	30	4	.....	6	22
A. sachalinensis						
Avg	53.5	74.4	66.0	.....	60.0	47.6
SD	3.0	4.1	1.6	.....	1.2	4.9
Min	47.7	62.8	64.4	.....	58.8	40.5
Max	58.0	83.5	67.6	.....	61.2	63.6
N	21	41	2	.....	2	25
A. veitchii						
Avg	45.1	66.6	64.0	.....	55.6	43.1
SD	.....	2.8	3.6	.....	7.4	6.8
Min	.....	62.0	58.8	.....	52.3	35.4
Max	.....	71.6	70.0	.....	70.4	44.7
N	1	15	7	----	11	7

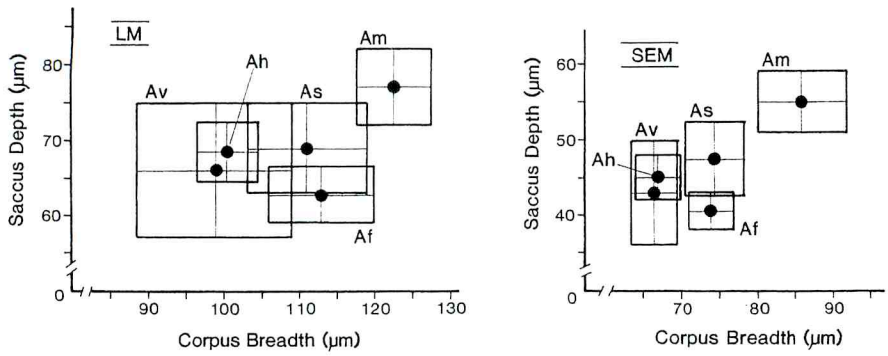

Fig. 2. Size range of corpus breadth against saccus depth. Solid circle represents the average value. Vertical line shows the range of saccus depth (± 1 standard deviation). Horizontal line shows the range of corpus breadth (± 1 standard deviation). Af = *Abies firma*, Ah = *A. homolepis*, Am = *A. mariesii*, As = *A. sachalinensis*, Av = *A. veitchii*.

The saccus has beehive-like chambers in it (see Pl. 4, fig. 5). The chambers are truncated abruptly, center of the saccus being empty. Surface of the chamber wall is slightly knobby, and small pores are present. The saccus nodula occur on the floor of the saccus (saccale area). The nodula consist of microverrucate, microbaculate, microclavate, microechinate and/or other irregular form elements. Microechinate elements are restricted near the junction area with the saccus. The pattern of the saccus nodula is characteristic for each species.

Remarks for each species

Abies firma (Pl. 1, figs. 1, 6; Pl. 2, figs. 1, 6, 11; Pl. 3, figs. 1, 6; Pl. 4, figs. 1, 5): Fifty-one grains were examined in SEM and LM. Microverrucate elements on the cappula are relatively small. The saccus surface is psilate. The cappa surface is relatively smooth, and the proximal face is nearly psilate. The triradiate streak is absent in many grains. Some grains have indistinctive raised streaks, which disappear near the proximal pole (see Pl. 3, fig. 1). Saccus depth is small relative to corpus breadth (Fig. 2). Maximum thickness of the cappa exine is less than 5 μm in LM. The proximal side of the corpus shows a relatively rounded outline in lateral longitudinal view. The saccus nodula consist mainly of microclavate elements, surface of the saccale area being knobby.

Ueno[11] has reported the triradiate streak expressed as shallow grooves on the all grains of this species which he examined. The morphological character of the streak of Ueno's specimen is different from that of our specimen.

A small abnormal grain has a different sculptural pattern from that of normal grains mentioned above.

Abies homolepis (Pl. 1, figs. 2, 7; Pl. 2, figs. 2, 7, 12; Pl. 3, figs. 2, 7; Pl. 4, figs. 2, 6): Thirty-seven grains were examined in SEM, and 50 grains in LM. All grains showing proximal face in SEM have the triradiate streak. The streak is a pronounced raised ridge, and each side is narrowly depressed. Three streaks meet at the proximal pole, where the streaks are indistinctive. The angles made by three streaks are variable. Some grains have the fourth ridge on the proximal

face of the cappa (see Pl. 3, fig. 7). The thickened ridge along the saccus-cappula junction is less developed. Microverrucate elements on the cappula are relatively small. The saccus surface sometimes displays rugulate-scabrate sculpture (see Pl. 2, fig. 12). This sculpture is coarser than the cappa surface. The proximal side of the cappa shows a relatively angular outline in lateral longitudinal view. The saccus are often compressed, and the surface of the cappa undulates. These two characters may result from insufficiency of the effect of chemical treatments. The saccus nodula are dense, most nodula being microverrucate.

Abies mariesii (Pl. 1, figs. 3, 8; Pl. 2, figs. 3, 8, 13; Pl. 3, figs. 3, 8; Pl. 4, figs. 3, 7): Thirty-nine grains are examined in SEM, and 50 grains in LM. Microverrucate elements on the cappula are relatively large. The triradiate streak is absent on most of the grains examined, and the area of proximal pole exhibits an indistinctive depression. Some grains display the indistinctive triradiate streak expressed as a shallow groove and/or a faint ridge (see Pl. 3, fig. 8). Corpus breadth is large (Fig. 2) and the outline of the proximal side of the corpus is slightly angular in lateral longitudinal view. On many of the grains examined, the proximal root of the saccus meets the cappa at proximal half of the corpus in lateral longitudinal view. The saccus nodula consist mainly of microbaculate and microverrucate elements.

Ueno[7] measured corpus breadth of this species, but his size data is nearly equal to that of other species he examined. According to the size data of Nakamura[17], this species has the largest corpus breadth of all species he examined.

Abies sachalinensis (Pl. 1, figs. 4, 9; Pl. 2, figs. 4, 9, 14; Pl. 3, figs. 4, 9; Pl. 4, fig. 4): Fifty-one grains were examined in SEM and LM. This species is clearly distinguished from other species in having thick exine at the proximal pole in LM. Some grains have the triradiate streak. The streak is a raised ridge, and the junction area of three streaks is not depressed. This fact is due to thickness of the exine at the proximal pole (see Pl. 1, fig. 9). The surface of the saccus is finely scabrate with few perforations. This character is consistent and is specific for the species. Microverrucate elements on the cappula are relatively large. Few to no saccus nodula appear on the saccale area.

Abies veitchii (Pl. 1, figs. 5, 10; Pl. 2, figs. 5, 10, 15; Pl. 3, figs. 5, 10): Fifty-one grains were examined in SEM and LM. The triradiate streak is absent, the proximal pole being depressed. Microverrucate elements are relatively small. The outline of the corpus is more circular than that of other species in polar view. In the slides for LM, many of observed grains were in polar view position. The saccus nodula, unfortunately, could not be examined in SEM due to a small amount of material. But the pattern of the saccus nodula seems to be similar to that of *A. sachalinensis* according to LM observation.

Conclusion and Discussion

Exine sculpture and structure, and grain size and proportion vary for each species. *Abies* pollen cannot be identified to species on the single character. But the combination of many characters enables us to distinguish the pollen grains of the genus to species.

The triradiate streak has been thought to be the species specific character[12,18]. This character

is also useful in species distinction in this study but is not definitive. Because many grains do not exhibit this streak. Furthermore, the difference between Ueno[11] and this study in the shape of the triradiate streak of *Abies firma* might suggest the streak is not consistent within one species.

Measurements are sometimes thought to be unreliable criteria because size of pollen grains varies geographically[19,20] and is influenced by chemical treatments[21]. Pollen grains also swell as time passed in glycerine jelly[22]. *Abies* pollen grains of each species, which were measured about six month before, were remeasured. The rates of increasing in size of corpus breadth, which are expressed average value based on ten grains, are as follows: *A. firma* (6.4 %), *A. homolepis* (5.4 %), *A. mariesii* (8.9 %), *A. sachalinensis* (6.2 %) and *A. veitchii* (10.4 %). Figured grains in Pl. 1 (figs. 6-10) are the swelling specimens. We think that relative measurements are more useful than simple size measurements. The average values of saccus depth are in nearly direct proportion to those of corpus depth if the data of *A. firma* are omitted. In other words, this relative measurements can be used in separating *A. firma* pollen from others mentioned above. But, as a matter of fact, the size ranges of *Abies* pollen grains overlap each other as seen in Fig. 2, which is expressed by the intervals of one standard deviation. Therefore we consider that measurements must be used as lower reliable criteria.

The pattern of the saccus nodula is different for each species in this study. But Klaus[16] stated that this character was influenced by ecological conditions. We think that the pattern of the saccus nodula will become a useful character for palynology or systematics in the future because this feature is visible in LM.

We can identify a part, not all, of *Abies* pollen grains to species at LM levels of resolution as follows. *Abies sachalinensis* is characteristic for the thick exine at the proximal pole. *A. homolepis* possesses the pronounced raised triradiate streak, which is visible in LM, and displays the undulated cappa surface. The proximal side of the corpus is slightly angular in outline in lateral longitudinal view. The saccus is often compressed. *A. firma* has the small sacci relative to its corpus breadth, and the proximal side of the corpus is rounded in outline in lateral longitudinal view. Maximum thickness of the exine is less than 5 μm. *A. mariesii* has larger corpus breadth and a slightly angular outline of the corpus. Position of the saccus to the corpus aids in its identification. *A. veitchii* has no definitive characteristics, but the outline of the cappa is circular in polar view. Grains of the species may be stable in polar view position in LM slides.

This study is the first step to the species distinction among *Abies* pollen grains in Japan. The results of this study should be emended when the variability are found in *Abies* pollen grains from many localities.

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日本産モミ属の花粉形態

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日本産モミ属5種（モミ，ウラジロモミ，オオシラビソ，トドマツ，シラビソ）の花粉形態を走査型電子顕微鏡と光学顕微鏡を使って調べ記載する．cappa の表面装飾，とくに triradiate streak，saccus や cappula の表面の模様，花粉粒の大きさや形などを総合的に判断すれば，花粉形態にもとづいてこれら5種を識別することが可能である．

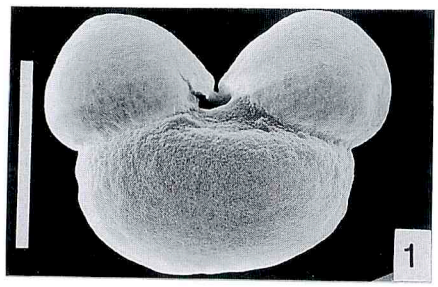
Plate 1. SEM (1-5) and LM (6-10) micrographs of *Abies* pollen in lateral longitudinal view. Magnification, 1-5: ca. × 500, scale bar = 50 μm; 6-10, ca. × 290, scale bar = 50 μm.
1, 6. *A. firma*; 2, 7. *A. homolepis*; 3, 8. *A. mariesii*; 4, 9. *A. sachalinensis*; 5, 10. *A. veitchii*.

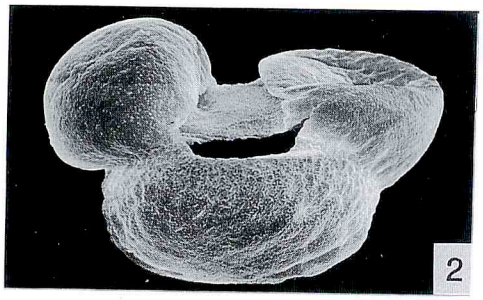
Plate 2. SEM micrographs of surface sculpture of *Abies* pollen in lateral longitudinal view: cappula (1-5), cappa (6-10), saccus (11-15). Arrows (1-5) indicate thickened ridges. Magnification, 1-5: ca. × 2350, scale bar = 5 μm; 6-15: ca. × 3000, scale bar = 5 μm.
1, 6, 11. *A. firma*; 2, 7, 12. *A. homolepis*; 3, 8, 13. *A. mariesii*; 4, 9, 14. *A. sachalinensis*; 5, 10, 15. *A. veitchii*.

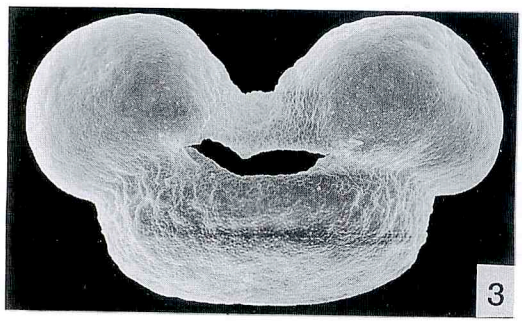
Plate 3. SEM micrographs of proximal face of *Abies* pollen. Magnification, ca. × 500, scale bar = 50 μm.
1, 6. *A. firma*; 2, 7. *A. homolepis*; 3, 8. *A. mariesii*; 4, 9. *A. sachalinensis*; 5, 10. *A. veitchii*.

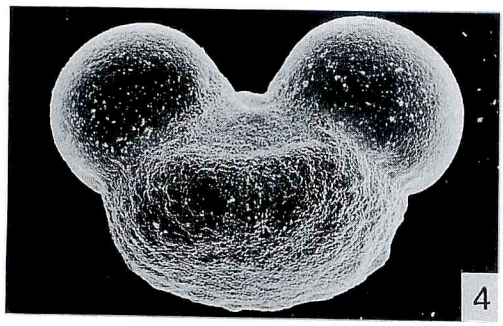
Plate 4. SEM micrographs of fractured grains of *Abies* pollen. Magnification, scale bar = 5 μm.
1. *A. firma*. Saccus nodula. ca. × 1600; 2. *A. homolepis*. Saccus nodula. ca. × 2350; 3. *A. mariesii*. Saccus nodula. ca. × 3400; 4a, 4b. *A. sachalinensis*. Saccale area. a: ca. × 1350, b: ca. × 3400; 5. *A. firma*. Inner structure of saccus. ca. × 1350; 6. *A. homolepis*. Exine structure of cappa. ca. × 5100; 7. *A. mariesii*. Exine structure of cappa. ca. × 5100.

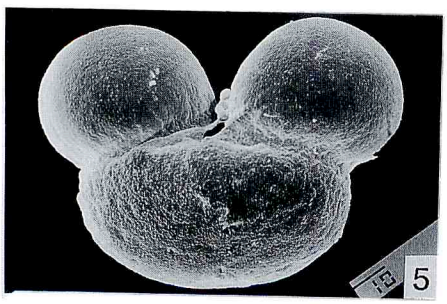
Plate 1

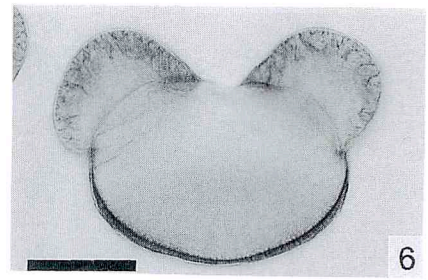


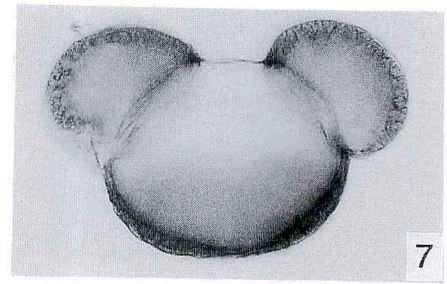


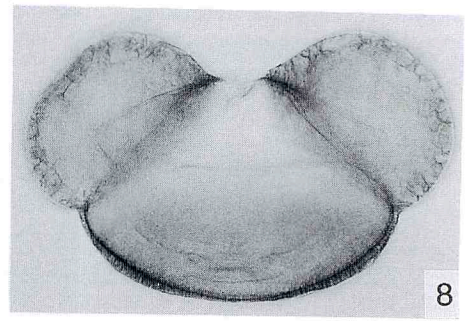


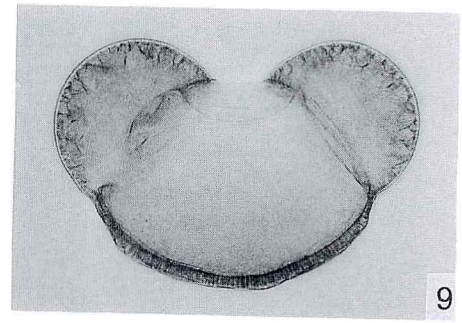












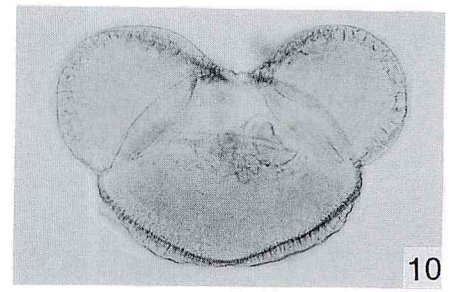


Plate 2

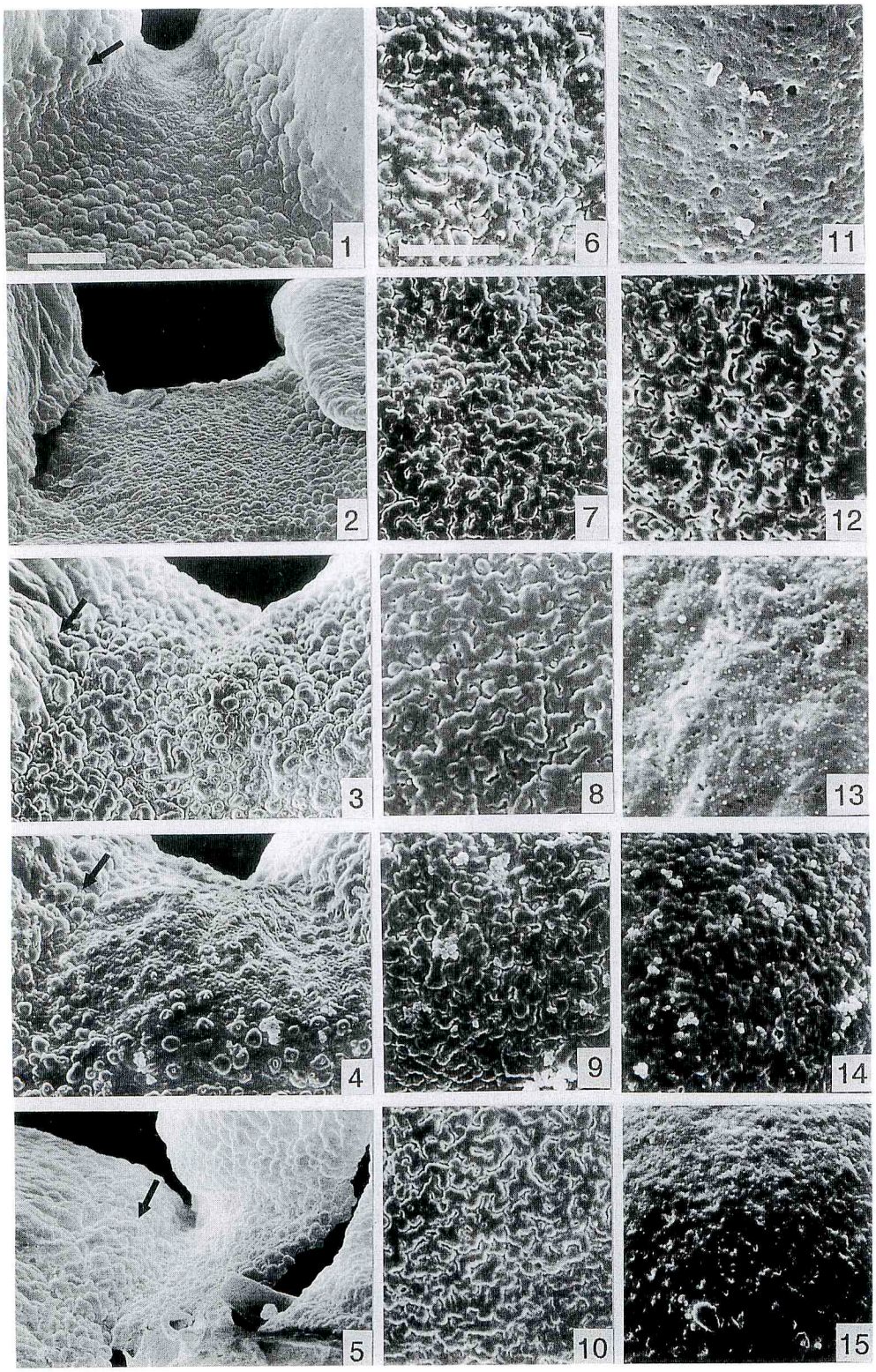


Plate 3

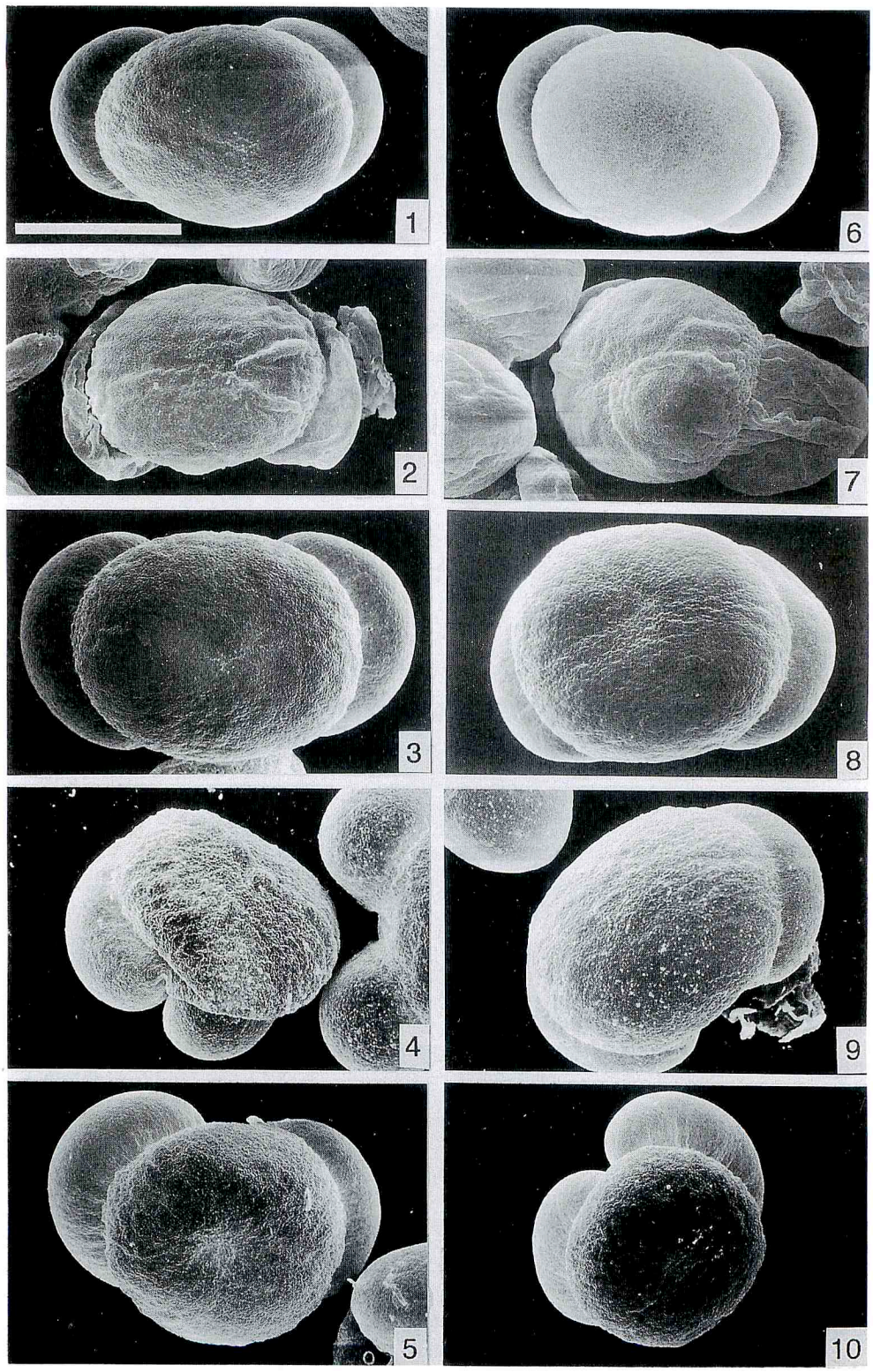


Plate 4