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Cuticular study of *Ptilophyllum* leaves from the Lower Cretaceous Choshi Group, in the Outer Zone of Japan

By

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Abstract This paper deals with the description of *Ptilophyllum acinacifolium*, sp. nov., *P. choshiense*, sp. nov., *P. subulatum*, sp. nov. and some unnamed forms, *P.* sp. A and *P.* sp. B, together with the redescription of *P. elongatum* KIMURA et OHANA, all collected from the Lower Cretaceous Choshi Group of marine origin. The preserved cuticles of these leaves were studied with light and scanning electron microscopes.

Ptilophyllum leaves known from the Jurassic-Early Cretaceous plant-beds of India, the Middle East and southern Europe have heavily papillate cuticles, but in those of the Choshi Group, papillae and trichomes are less prominent.

Key words: *Ptilophyllum*, Early Cretaceous, Choshi Group, Ryoseki-type flora, Japan

Introduction

More than 60 *Ptilophyllum* species have been described from the Mesozoic plant-beds, but it is difficult to make their specific identity only on the basis of external morphology, unless some very prominent features are observed. However, it is rather easy to determine the specific identification of *Ptilophyllum* leaves by using cuticular features [e. g. HARRIS (1969), BOSE and KASAT (1972)].

Cuticles of most *Ptilophyllum* leaves in Japan are not preserved except those from the Lower Cretaceous Choshi Group of marine origin in the Outer Zone of Northeast Japan. Therefore, most small *Ptilophyllum* leaves in Japan had been regarded by the previous authors as *P. pecten* (PHILLIPS) (e. g. OISHI, 1940), an European species.

In 1984, one of us (KIMURA) and OHANA investigated the cuticles of *Ptilophyllum* leaves and described a new species as *P. elongatum* (non DOUGLAS). Recently OBATA and his coworkers and also we collected many fossil leaf-fragments with preserved cuticle, from the Choshi Group. Some of them had already been described by us and by others as follows:

Sagenopteris inequilateralis OISHI: KIM and KIMURA, 1987
Stenopteris cyclostoma SAIKI, KIMURA et HORIUCHI, 1991 (MS)
Zamites choshiensis KIMURA et OHANA, 1985
Nilssonia dictyophylla KIMURA et OKUBO, 1985
Cupressinocladus obatae OKUBO et KIMURA, 1991
Frenelopsis choshiensis KIMURA, SAIKI et ARAI, 1985

In this paper, we identified 5 types of *Ptilophyllum* leaves on the basis of macro- and microscopic observations. This paper deals with the description of these types of *Ptilophyllum* leaves including three newly proposed species and two distinct forms together with the redescription of *P. elongatum* (non DOUGLAS) on the basis of the SEM observation.

Material and methods

Ptilophyllum leaves are common in occurrence mainly in the calcareous (ammonite) nodules found in the Barremian beds of the Choshi Group, in association with other plant taxa including pollen and spores. The geological age of the fossil beds is determined as the late early Barremian according to the associated ammonites and other marine fossils [OBATA *et al.* (1975) and OBATA *et al.* (1982)].

The material was macerated by regular method using SHULTZ's solution and dilute KOH solution and then prepared for microscopic observation. All specimens and slides described herein are kept in the National Science Museum, Tokyo.

Acknowledgements

We express our deep gratitude to Dr. Ikuwo OBATA of the National Science Museum, Tokyo who have collected and provided the specimens from the museum on loan for the present study. Our thanks are extended to Dr. Shya CHITALEY of the Cleveland Museum of Natural History, Ohio for her linguistic check of the manuscript. This study was partly supported by the Grant-in-Aids for Scientific Research from the Ministry of Education, Science and Culture of Japan (no. 02640615 given to KIMURA, and no. 63916012 given to OKUBO).

Description

Order Bennettitales

Genus *Ptilophyllum* MORRIS, 1840

Ptilophyllum acinacifolium KIMURA et OKUBO, sp. nov.

(Pl. 1, Fig. 5; Pl. 3, Figs. 1–6; Figs. 1a-e)

Holotype: NSM PP-8982 (collected by I. OBATA and others). *Stratum typicum*: Kimigahama Formation (upper lower Barremian), Choshi Group. *Locus typicus*:

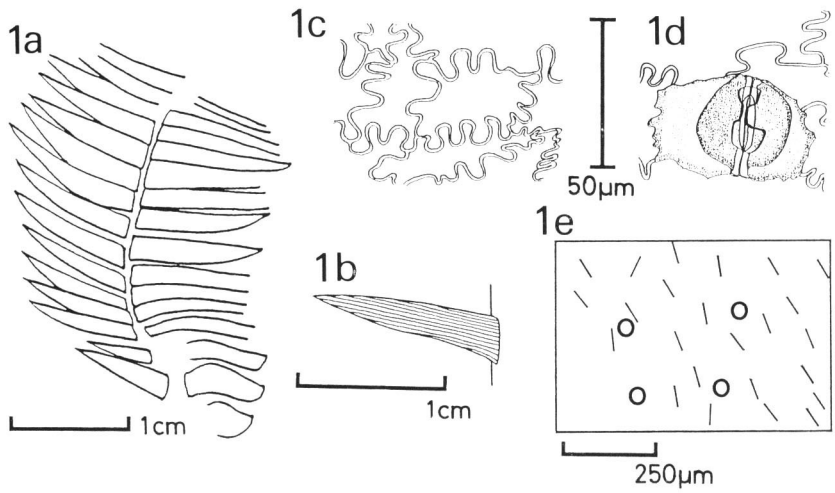


Fig. 1. *Ptilophyllum acinacifolium* KIMURA et OKUBO, sp. nov.:
1a. External leaf form (Holotype; NSM PP-8982). 1b. A pinna enlarged from Fig. 1a. 1c. A sketch of lower ordinary cells (slide no. NSM PP-8982-L11). 1d. A sketch of a stomatal complex (slide no. NSM PP-8982-L11). 1e. Distribution of the trichome-bases (open circle) and orientation of the stomatal apertures (dashed line) on the lower culicle (slide no. NSM PP-8982-L11).

Isejigaura-Coast along the Pacific Ocean (Loc. no. 7405 of OBATA *et al.*, 1975; roughly 140°52′48″E, 35°43′28″N), Choshi City, Chiba Prefecture. *Derivatio nominis*: After scimitar- or sword-like form of pinna. *Occurrence*: Rare (a single broken leaf was obtained).

Diagnosis: Leaf pinnate (whole shape and length unknown), up to 2 cm wide, narrowing downward. Pinnae closely set, attached subopositely to the upper sides of rachis at an angle of 70–90 degrees, scimitar-like in form, sometimes falcate; 10–12 mm long and up to 1.5–2.0 mm wide but becoming shorter proximally, 4–6 mm long and up to 1.5–2.0 mm wide; acroscopic basal margin straight or slightly contracted and basiscopic basal margin slightly decurrent but occasionally concealed by the basal acroscopic margin below; apex acuminate. Veins arising from whole base, running in parallel, simple, ending mostly at both margins, 11 in number in each pinna (50 per cm in density).

Cuticle hypostomatic. Upper cuticle ca. 3 μm thick, consisting only of ordinary cells. Ordinary cells rectangular or sometimes squarish, typically 35–90 μm long and 13–19 μm wide. Anticlinal walls strongly folded to form marked loops; sinuousity 8–10 μm long (crest to crest) and 9–11 μm wide (amplitude). Inner periclinal walls granulated; granules small, ca. 1 μm in diameter.

Lower cuticle ca. 4 μm thick, consisting of non-stomatal band on the vein-course and stomatal band between veins. Stomata paracytic (or syndetocheilic), densely scattered (ca. 120 per square mm) but forming 2–4 files in a stomatal band; aperture

transversely oriented or slightly oblique. Guard cells sunken; dorsal thickening of guard cells crescent-shaped, each 40–48 μm long and 16–18 μm wide, inner surface smooth. Subsidiary cells thickly cutinized; outer anticlinal walls slightly wavy and inner anticlinal walls non-specialized; papilla originated from outer periclinal wall of subsidiary cells and overarching the guard cell. Non-stomatal band 2–4 cells wide (ca. 70–100 μm wide), consisting of ordinary cells. Ordinary cells on the stomatal bands varied in form and size; squarish to rectangular, generally elongated longitudinally but sometimes laterally, 30–60 μm long and 20–50 μm wide. Other features like those of upper cuticle. Periclinal walls not papillate. Trichome bases scattered on the stomatal band, ca. 10–15 in number per square mm, arranged in rather regular lows; anticlinal wall being developed markedly on inner side of trichome base. Trichome base flared skirt-shaped, 60–70 μm in diameter in front-view, having 4–7 suture lines running from base to distal end; periclinal wall thin and hollowed. (reproductive organs not known.)

Discussion and *comparison*: Although obtained specimen is a single broken leaf, its external pinna form is distinct. So we created *Ptilophyllum acinacifolium*, sp. nov. to accommodate our leaf. No leaf comparable to our species has been found in the Japanese Mesozoic.

Ptilophyllum jabalpurensis JACOB et JACOB known from the Jabalpur Series and *P. sakrigaliense* SAH from the Rajmahal and Jabalpur Series somewhat resemble *P. acinacifolium* in pinna form, but both species are distinguished from the present species by their heavily papillate lower cuticles.

Cuticular features of *Ptilophyllum acinacifolium* and *P. choshiense* described in this paper are very similar to each other: both have, 1) a pair of papillae originated from subsidiary cells found in the stomatal apertures (Figs. 1d and 2e), 2) the same shaped anticlinal wall of trichome base (Pl. 2, Fig. 5 and Pl. 3, Fig. 5), and 3) similar periclinal walls (Pl. 2, Fig. 8 and Pl. 3, Fig. 6). However, the external features of the leaf are quite different from each other.

Ptilophyllum sparsifolium SHARMA from the Rajmahal Series (SHARMA, 1967) resembles *P. acinacifolium* in pinna form, but is different in its pinnae with rounded basal margins.

Ptilophyllum choshiense KIMURA, OKUBO et MIYAHASHI, sp. nov.

(Pl. 1, Figs. 1–4; Pl. 2, Figs. 1–9; Figs. 2a-g)

1960. *Ptilophyllum pecten* (PHILLIPS): NISHIDA, p. 190, pl. 1, fig. 9; pl. 3, fig. 24. *Holotype*: NSM PP-8983. *Paratypes*: NSM PP-8984, 8985 and 8986. Other specimens examined: NSM PP-8991 and 17 other specimens (collected by I. OBATA and others). *Stratum typicum*: Kimigahama Formation (upper lower Barremian), Choshi Group. *Locus typicus*: Isejigaura-Coast along the Pacific Ocean (Loc. no. 7210 of OBATA *et al.*, 1975), Choshi City, Chiba Prefecture. *Derivatio nominis*: After Choshi City. *Occurrence*: Rather common but fragmental.

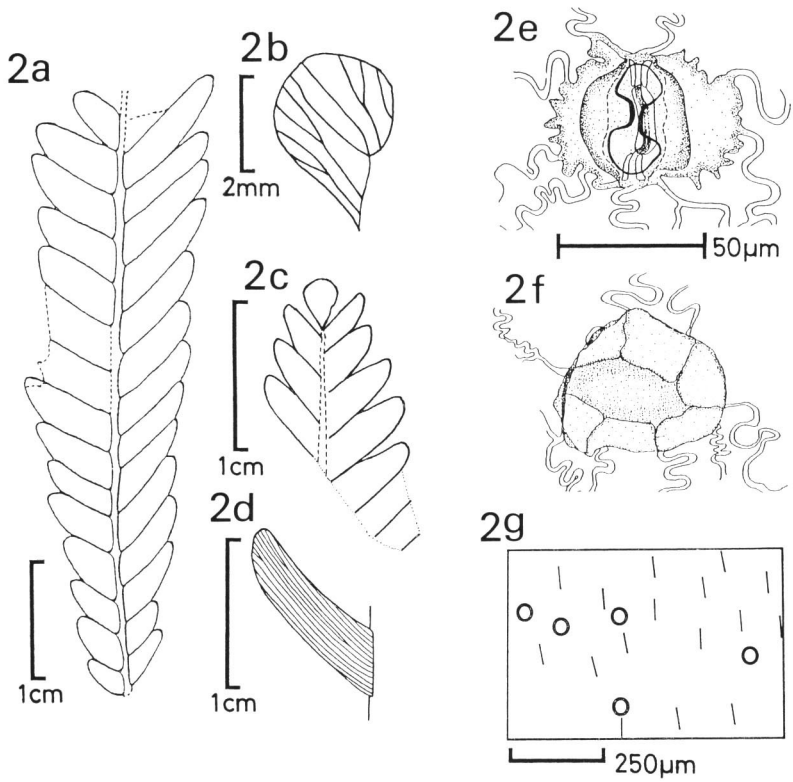


Fig. 2. *Ptilophyllum choshiense* KIMURA, OKUBO et MIYAHASHI, sp. nov.:
2a. External leaf form (Holotype; NSM PP-8983). 2b. A small pinna at the distal end of a leaf enlarged from Fig. 2c. 2c. An apical part of a leaf (Paratype; NSM PP-8986). 2d. A pinna enlarged from Fig. 2a, showing the venation. 2e. A sketch of a stomatal complex (slide no. NSM PP-8995-S1). 2f. A sketch of a trichome base (slide no. NSM PP-8996-L1). 2g. Distribution of the trichome-bases (open circle) and orientation of the stomatal apertures (dashed line) on the lower cuticle (slide no. NSM PP-8993-L1).

Diagnosis: Leaves small, oblanceolate; 0.6 (0.3–0.8) cm wide at base, 0.8 (0.6–1.1) cm wide at middle, and 0.8 (0.3–1.3) cm wide at apex (Petiole not known). Rachis slender, 0.5 mm wide, but usually concealed by the pinna bases. Pinnae attached alternately to the upper sides of rachis at an angle of 40–55 degrees at apex of a leaf and 50–70 degrees at base; linear or narrowly ovate, slightly falcate, sometimes rhomboidal and with obtusely pointed apex, margins entire; typically 10 mm long and 3 mm wide at the middle, rarely 5 mm long and 1.5 mm wide. Acroscopic basal margin straight or slightly rounded but never forming a definite auricle, and basiscopic basal margin straight or slightly decurrent. Nerves nearly parallel, typically 9 in number, but in larger pinna 12 in number, slightly diverging, some forking dichotomously in all levels; density 20–40 per cm.

Cuticle hypostomatic. Upper cuticle ca. 3 μm thick, consisting of rather regular rows of rectangular, squarish or rarely polygonal cells, typically 50 μm long (range noted 30–118 μm long) and 30 μm wide (range noted 20–68 μm wide); anticlinal walls markedly sinuous, sinuousity typically 8 μm long (crest to crest) and 15 μm wide (amplitude), outer periclinal walls smooth, but finely granulated inside; granules 0.5–1.3 μm in diameter. Trichome and papilla absent.

Lower cuticle ca. 3 μm thick, differentiated into alternate stomatal and non-stomatal bands, and marginal non-stomatal zones. A single stomatal band 150–250 μm wide, consisting normally of 2–4 regular stomatal files. Stomata paracytic (or syndetocheiric), regularly scattered, a few touching each other longitudinally or laterally. Aperture slit-like, transversely oriented or slightly oblique. Guard cells sunken; dorsal thickening of guard cells crescent-shaped, thickly cutinized, each 35–45 μm long and 14–16 μm wide, inner surface smooth. Subsidiary cells usually broad, each 40–50 μm long and 25–35 μm wide, outer anticlinal wall straight or sinuous and inner wall thickly cutinized; periclinal wall singly papillate, papilla overarching the guard cell, usually expanding from its base, apex rounded or flat. A single non-stomatal band 2–4 cells wide (100–180 μm wide), consisting only of ordinally cells. Ordinary cells squarish or rectangular, typically 30–100 μm long and 25–60 μm wide; anticlinal walls sinuous; sinuousity 11 μm long and 19 μm wide in longitudinal walls and 8 μm long and 14 μm wide in end walls; periclinal walls devoid of papillae. Ordinary cells in the stomatal bands smaller than those of the non-stomatal bands, generally broader, 52 μm long and 51 μm wide; anticlinal walls sinuous; sinuousity 10 μm long and 15 μm wide. Outer periclinal walls smooth, finely granulated inside. Marginal non-stomatal zone 3–5 cells wide, consisting only of ordinary cells; cells rectangular or squarish, sometimes polygonal, 50 μm long and 48 μm wide; anticlinal walls sinuous; sinuousity 10 μm long and 17 μm wide in lateral walls and 7 μm long and 11 μm wide in end walls. Trichome bases distributed on the stomatal bands, 12 per square mm in density, but not common on the non-stomatal bands, rarely touching each other. Peculiar anticlinal wall being developed inside of trichome base; flared skirt-shaped, dish-shaped or pyramid-shaped; circular, oblong or polygonal in outline in front-view, 60–70 μm in diameter, having 4 to 7 suture lines running from base to apex; periclinal wall thinner than adjacent parts, having a small pore on the centre of inner periclinal wall. (Reproductive organs not known.)

Discussion and *comparison*: BOSE and KASAT (1972) described 10 *Ptilophyllum* species with preserved cuticles on the basis of Indian material. Cuticular features of these Indian leaves are quite different from our leaves, because in these Indian species, cuticles are usually heavily cutinized and heavily papillate. On the contrary, our leaves are characterized by the non-papillate cuticle except for subsidiary cells.

Among over 60 *Ptilophyllum* species hitherto described, our leaves are externally most close to *P. cutchense* redescribed in detail by BOSE and KASAT (1972). But it is difficult to identify our leaves with *Ptilophyllum cutchense*, because unfortunately leaf cuticle of *P. cutchense* has not been known, in spite of the inserted long list of

synonyms of *P. cutchense* given by BOSE and KASAT (1972).

Under the circumstances we unavoidably separate our leaves from *Ptilophyllum cutchense* specifically and create the species, *P. choshiense* for our leaves.

Externally the leaves of *Ptilophyllum choshiense* are indistinguishable from the following leaves described by the previous authors from the Lower Cretaceous plant-beds in the Outer Zone of Japan:

Ptilophyllum pecten (PHILLIPS) MORRIS: OISHI, 1940, pl. 32, figs. 1, 1a, 2 (= YOKOYAMA's *Nilssonia pterophylloides*) from the Yuasa Formation, and pl. 32, fig. 3 from the Ryoseki Formation.

P. ex gr. *pecten* (PHILLIPS) MORRIS: KIMURA and KANSHA, 1978, p. 4, figs. 3–4; text-fig. 12a-b from the Yuasa and Arida Formations: KIMURA and MATSUKAWA, 1979, pl. 3, fig. 3 from the Sebayashi Formation.

However, we retain their specific identity with *Ptilophyllum choshiense* and regard them as *P. pterophylloides* (YOKOYAMA). *Ptilophyllum* cf. *pterophylloides* (YOKOYAMA) described by KON'NO (1967) from the Lower Cretaceous of Ulu Endau, Malaysia is also indistinguishable from *P. choshiense* in external leaf form.

The following species are comparable with *Ptilophyllum choshiense* in leaf form and in having shorter pinnae:

Ptilophyllum horridum ROY: BOSE and KASAT, 1972 from the Lower Cretaceous Jabalpur Series.

P. institacallum BOSE: BOSE, 1959; BOSE and KASAT, 1972; ditto.

P. pecten (PHILLIPS): HARRIS, 1969 from the Middle Jurassic of Yorkshire.

P. vasekgahense BARNARD et MILLER: BARNARD and MILLER, 1976 from the Middle Jurassic of Iran.

However, they are distinguished essentially from *Ptilophyllum choshiense* by their heavily papillate cuticles. *Ptilophyllum pectinoides* (PHILLIPS) is, according to HARRIS (1969), characterized by its cuticle which is flat and non-papillate, but it is distinguished by having both shorter and longer pinnae.

MIRANDA and CHAPHEKAR (1980) recognized nine patterns (A-I types) of sculptures on the inner periclinal surface of cuticle in the family Pinaceae with remarks that they are of systematic value. In the diagnosis of *Pilophyllum choshiense*, we showed the fine sculpture of the inner periclinal surface of ordinary cells (pl. 2, Fig. 8). Our sculpture pattern may correspond to the E-type observed in *Cedrus atlantica* (ENDLICHER) CARRUTHERS by MIRANDA and CHAPHEKAR (1980); besides it is similar to both *Ptilophyllum acinacifolium* and *P. pecten* (PHILLIPS) figured by ALVIN (1970). But we at present are not sure as to whether the sculpture patterns have systematic value or not in *Ptilophyllum* or other bennettitaleans.

The anticlinal wall of the trichome base develops markedly on the inner surface of lower cuticle (Pl. 2, Figs. 5–7 and Fig. 2f). This is also observed in *Ptilophyllum acinacifolium*, *P.* sp. B described in this paper and *P. elongatum* KIMURA et OHANA (non DOUGLAS) (Pl. 3, Fig. 5; Pl. 5, Figs. 5–6; Pl. 6, Figs. 5–6). Among these three species, *Ptilophyllum choshiense* is very similar to *P. acinacifolium*.

SINCOCK and WATSON (1988) discussed the form and structure of trichome-bases on the observations they made using light and scanning microscopes. They reported the same trichome-bases as in Choshi leaves. In their figs. 1, 8, 9 and 10, there is a circular pore in each inner periclinal wall. They wrote that the pore might suggest the involvement of the hypodermal cell below.

On the other hand, OKAZAKI *et al.* (1984) investigated cystoliths in the leaves of various higher plants, for example, Moraceae and Urticaceae. The cystolith generally consists of lithocyst, stalk and cystolith-body. In most cases, the cystolith is formed by calcium carbonate deposition.

The pore in the inner periclinal wall of trichome-base (Pl. 2, Fig. 6, indicated by an arrow) suggests the possibility of the trace of the cystolith stalk. The anticlinal wall on the inner side of the trichome-base is hence thought to be the preserved remains of the lithocyst after maceration. Similar pore is observed in the cuticle of *Ptilophyllum elongatum* (Pl. 6, Figs. 5–6).

OKAZAKI *et al.* (1984) suggested on the basis of their physiological experiments under dry condition, the transpiration is extremely suppressed, and the plant can not continue to photosynthesize, because the stomata close the apertures causing reduction of carbon-dioxide in the mesophyll. In such a case, calcium carbonate in the cystolith might become carbon-dioxide source to photosynthesize. This idea is in accordance with our suggestion as to which *Ptilophyllum* leaves might have lived under the dry and hot condition. The result of our further observation of this structure will be mentioned in our separate paper.

Ptilophyllum elongatum KIMURA et OHANA (non DOUGLAS)

(Pl. 6, Figs. 1–6)

1984. *Ptilophyllum elongatum* KIMURA et OHANA (non DOUGLAS), p. 381, figs. 1–9.

Emeded diagnosis: Leaf pinnate, 5 cm wide on lower part, and 4 cm wide on upper part, with thin rachis, 1.5 mm wide on proximal, and 0.9 mm wide on distal end. (Whole leaf unknown.) Pinnae set closely on upper part but rather remote on lower part, attached subopposite ly to the upper sides of rachis, directed forward on upper side but nearly perpendicular on lower side. Pinnae elongated, nearly parallel sided for the most part, with obtuse apex, acroscopic basal angle rounded and free to the rachis, basiscopic base straight or slightly decurrent, typically 2.5 cm long and 2 mm wide. Nerves densely crowded, some dichotomously forking once near the base, parallel, ending with distal part of pinna, not coverging, 11 in number (ca. 5 per mm in density) at the middle.

Upper cuticle 1–2 μm thick (measured in folds), without stoma or trichome, showing irregular rows of rectangular, squarish or sometimes polygonal cells. Anticlinal walls sinuous. (Sculpture-pattern of periclinal wall unknown.)

Lower cuticle, 2–3 μm thick, differentiated into stomatal and non-stomatal bands. Stomatal bands broader, each consisting normally of 2–4 long and rather regular

stomatal files. Marginal non-stomatal bands 7–8 cells wide. Cells rectangular or squarish, sometimes polygonal; anticlinal walls sinuous, 50–75 μm long and 18–25 μm wide. Other non-stomatal bands 2–3 cells wide between stomatal bands. Cells squarish or rectangular, 35–60 μm long and 15–25 μm wide; anticlinal walls sinuous, periclinal wall devoid of papillae or trichome-bases. Cells in stomatal band smaller than those of non-stomatal bands, mostly broader than long; anticlinal walls wavy or sinuons. Inner periclinal walls finely sculptured on both stomatal and non-stomatal bands. Trichome-bases being developed on the lower cuticle at intervals of 2–4 stomata, forming dish-shaped structure on the inner side of cuticle; orbiculate to elliptic in outline in front view, 50–70 μm in long diameter; inner periclinal wall rough and with a small pore in its center (ca. 8–10 μm in diameter). Stomata paracytic (or syndetocheiric), closely set, rather regularly scattered, often touching each other longitudinally, but a few touching each other laterally, transversely oriented but a few oblique. Guard cells crescent-shaped, thickly cutinized, 35–50 μm long and 30–35 μm wide, stomatal aperture oval or slit-like. Subsidiary cells usually broad, outer wall straight or wavy, sometimes partly sinuous, inner wall thickly cutinized, surface wall devoid of papillae. (Reproductive organs unknown.)

Discussion: This species was proposed by KIMURA and OHANA (1984) on the basis of its external leaf form (slender and elongated pinnae) and cuticular features observed by light microscope. In this paper, additional diagnostic features are given and its cuticular features are emended because of our subsequent observations with SEM.

The sculpture pattern of this species is finer than those of other three Choshi species and might be between the B- and E-types of MIRANDA and CHAPHEKAR (1980).

The dish-shaped structure exists on the inner surface of the lower cuticle according to our SEM-observation (Pl. 6, fig. 5). This structure is the same as 'trichome' described by KIMURA and OHANA (1984, figs. 7A-8B).

The specific name '*elongatum*' was wrongly given by KIMURA and OHANA (1984). It was used previously by DOUGLAS (1969) for a markedly elongate leaf with tiny pinnae described from the Lower Cretaceous Tyers Group of Australia. It is superfluous to mention but we feel that DOUGLAS' species is far remote in its pinna form, size and mode of attachment of pinnae, from the *Ptilophyllum* species known from the Northern Hemisphere. Several *Ptilophyllum* species described by DOUGLAS (1969) appear to deviate from the category of the emended generic diagnosis of *Ptilophyllum* given by HARRIS (1969).

Ptilophyllum subulatum KIMURA et OKUBO, sp. nov.

(Pl. 1, Fig. 6; Pl. 3, Figs. 7–8; Pl. 4, Figs. 1–3; Figs. 3a-g)

Holotype; NSM PP-9013. *Paratypes*; NSM PP-8987, 8988 and 9014 (collected by OBATA and others). *Stratum typicum*: Kimigahama Formation. *Locus typicus*: Isejigaura-Coast (Loc. no. 6482 of OBATA *et al.*, 1975). *Derivatio nominis*: After subulate pinnae. *Occurrence*: Rather rare. *Diagnosis*: Leaf pinnate, rather small-

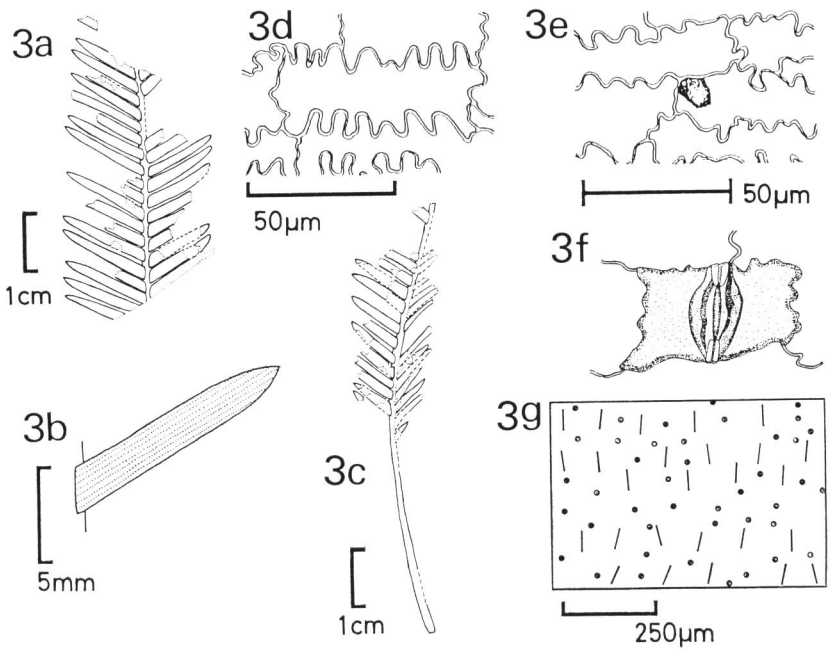


Fig. 3. *Ptilophyllum subulatum* KIMURA et OKUBO, sp. nov.:
3a. A part of leaf (Holotype; NSM PP-9013). 3b. A pinna enlarged from Fig. 3a, showing veins faintly preserved. 3c. A basal part of leaf (Paratype; NSM PP-9014). 3d. A sketch of upper ordinary cells (slide no. NSM PP-8987-L2). 3e. A sketch of lower ordinary cells; a small papilla exists on the periclinal wall of ordinary cell (slide no. NSM PP-8987-L23). 3f. A sketch of a stomatal complex (slide no. NSM PP-8987-L23). 3g. Distribution of the papillae or thickened areas (solid circles) and orientation of the stomatal apertures (dashed lines) on the lower cuticle (slide no. NSM PP-8987-L23).

sized (whole shape and length unknown), up to 2.5 cm wide, narrowing downward gradually. Rachis slender, 1.0–1.5 mm wide. Petiole longer, over 3 cm long and 1.5–2.0 mm wide. Pinnae closely set, attached at an angle of 50–60 degrees on the upper sides of rachis, subulate in form, typically 1.5 cm long and 2 mm wide; apex acute; both acroscopic and basiscopic margins straight. Veins generally obscure, arising from whole base, simple, running parallel with each other, not converging at apex, typically 7 in number in each pinna (35 per cm in density).

Cuticle hypostomatic. Upper cuticle 4 μm thick, consisting only of squarish to rectangular cells, 25–80 μm long and 20–40 μm wide. Anticlinal walls folded to form loops, sinuousity 8–11 μm long and 7–10 μm wide, end walls less folded. Outer periclinal walls smooth but inner periclinal walls granulated; granules large, 4–6 μm in diameter.

Lower cuticle ca. 4 μm thick, consisting of stomatal bands between veins and non-stomatal bands on vein-courses. Stomatal bands 160–200 μm wide, consiting of

stomata and ordinary cells. Stomata paracytic (or syndetocheiric), densely scattered, 150 per square mm, but forming 2–3 files, aperture oriented transversely or somewhat oblique. Guard cells sunken, often narrow crescent-shaped, each 36–40 μm long and 12–16 μm wide, inner surface smooth. Non-stomatal band 2–4 cells wide (80–160 μm), consisting of squarish to rectangular cells, 30–110 μm long and 24–28 μm wide. Inner periclinal walls granulated; granules somewhat larger than those of upper cuticle (4–8 μm in diameter); other features like those of upper cuticle. Cells in the stomatal bands varied in form and size, squarish to rectangular but rarely polygonal, 24–96 μm long and 24–44 μm wide; other features like those of non-stomatal bands. Papillae or thickened areas scattered on the ordinary cells of both non-stomatal bands, 120 in number per square mm, lump-shaped and thickly cutinized. (Reproductive organs not known.)

Discussion and *comparison*: Our leaves are characterized by having subulate pinnae with acutely pointed apex, straight margins and with 7 indistinct, parallel and simple veins and by papillae or thickened areas on the lower cells of both non-stomatal and stomatal bands, in which character, our leaves are specifically distinguished from other leaves described in this paper.

Ptilophyllum caucasicum DOLUDENKO et SVANIDZE and *P. okribense* f. *ratchiana* DOLUDENKO et SVANIDZE (DOLUDENKO and SVANIDZE, 1969) from the Upper Jurassic (?) of Georgia resemble our *P. subulatum*, but is distinguished by their pinnae with heavily papillate lower cuticles.

An incompletely preserved leaf regarded by OISHI (1940) as *Ptilophyllum pecten* (PHLLIPS) from Nishinotani (Lower Monobegawa Formation, Kochi Prefecture, is similar in pinna form to that of *P. subulatum*. But it is difficult to make a precise comparison of OISHI's leaf with the present ones, because its cuticular features are not known. Thus we established *Ptilophyllum subulatum* sp. nov. to include our leaves.

Ptilophyllum sp. A

(Pl. 1, Fig. 7; Pl. 4, Figs. 4–8; Figs. 4a-f)

Specimen examined: NSM PP-8989 (collected by I. OBATA and others). *Horizon*: Kimigahama Formation (upper lower Barremian), Choshi Group. *Locality*: Isejigaura (the same as *Ptilophyllum subulatum*). *Occurrence*: Rare (only a single broken leaf).

Description: Leaf is pinnate, ca. 2.5 cm wide, sending off very closely set pinnae at an angle of 50–65 degrees. Pinnae are narrowly oblong with rounded apex, typically 10.5–13.5 mm long and 3–4 mm wide; both acroscopic and basiscopic basal margins are nearly straight, but sometimes the latter is slightly decurrent on the upper side of rachis and mostly concealed by the basal acroscopic margin of pinna below. Veins are originated from whole base, 8 in number at base, then slightly diverging and some are once forked; 35 per cm in density.

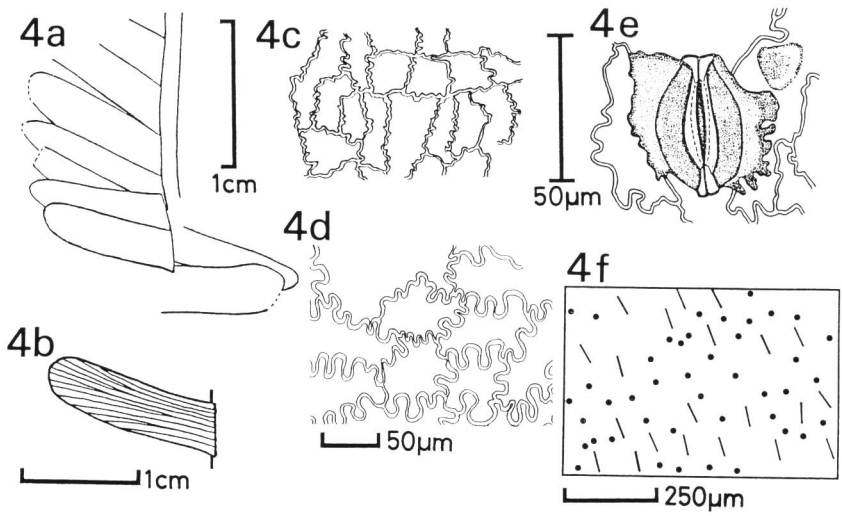


Fig. 4. *Ptilophyllum* sp. A:
4a. A part of leaf (NSM PP-8989). 4b. A pinna enlarged from Fig. 4a, showing the venation. 4c. A sketch of upper ordinary cells (slide no. NSM PP-8989-L1). 4d. A sketch of lower ordinary cells (slide no. NSM PP-8989-L1). 4e. A sketch of a stomatal complex and a small papillae on the ordinary cell (slide no. NSM PP-8989-L1). 4f. Distribution of the papillae or thickened areas (solid circle) and orientation of the stomatal apertures (dashed line) on the lower cuticle (slide no. NSM PP-8989-L1).

Cuticle is hypostomatic. Upper cuticle is ca. 3 μm thick, consisting of cells, rectangular and elongated laterally, but sometimes squarish or rarely polygonal, typically 25 μm long (range noted 15–43 μm) and 50 μm wide (range noted 30–75 μm). Anticlinal walls are folded; sinuousity is 5–8 μm long and 5–8 μm wide. Outer periclinal walls are smooth and inner periclinal walls are generally smooth and sparsely granulated; granules are large, 5–8 μm in diameter.

Lower cuticle is 4 μm thick, consisting of non-stomatal bands on the vein-courses and stomatal bands between veins. Stomatal band is 180–230 μm wide, consisting of stomata and ordinary cells. Stomata are paracytic (or syndetocheiric), forming two rather regular files; aperture is oriented transversely but sometimes oblique; density is 40–60 per square mm. Guard cells are sunken, large, crescent-shaped, each typically 65 μm long (range noted 55–75 μm) and 22 μm wide (range noted 19–25 μm). Subsidiary cells are rather small and non-papillate; inner periclinal walls are smooth. Non-stomatal bands are 3–5 cells wide (100–180 μm), consisting of cells which are varied in form and size like those in the stomatal bands. The cells in the non-stomatal and stomatal bands have anticlinal walls strongly folded to form loops; sinuousity is 8–15 μm long and 8–18 μm wide; end walls are less folded. Outer periclinal walls are papillate; papillae are 20–30 μm in diameter, scattered randomly,

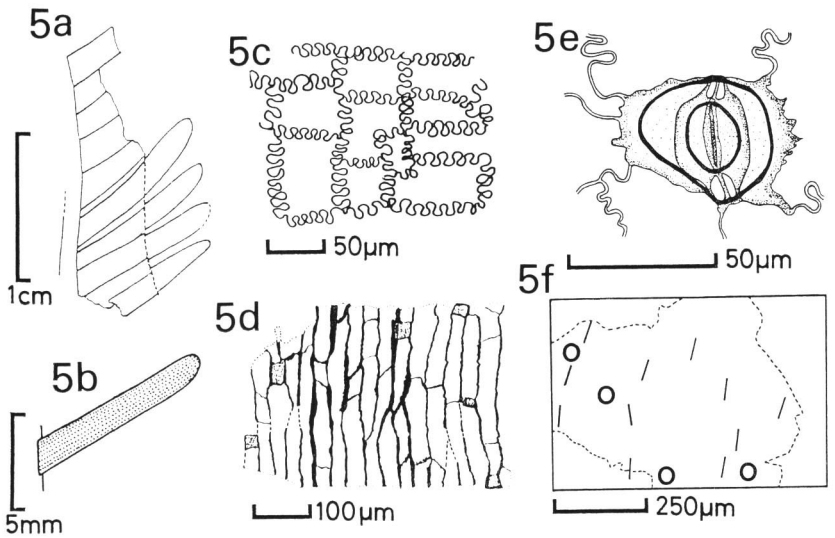


Fig. 5. *Ptilophyllum* sp. B:
5a. A part of leaf (NSM PP-8990). 5b. A pinna enlarged from Fig. 5a. 5c. A sketch of upper ordinary cells (slide no. NSM PP-8990-L7). 5d. Cuticle of rachis (slide no. NSM PP-8990-L10). 5e. A sketch of a stomatal complex, showing stomatal pit formed by subsidiary cells (slide no. NSM PP-8990-L3). 5f. Disritbution of the trichome-bases (open circle) and orientation of the stomatal apertures (dashed line) on the lower cuticle (slide no. NSM PP-8990-L3).

40–60 per square mm in density. Inner periclinal walls are generally smooth, but sometimes granulated; granules are large, 6–8 μm in diameter. Reproductive organs are not known.

Remarks: Our leaf is characterized by its narrow oblong pinnae, large-sized stomata and papillate lower cells which character is rare in most gymnospermous plants known from the Choshi Group.

Our leaf resembles externally and anatomically those of *Ptilophyllum sahnii* GUPTA et SHARMA (BOSE and KASAT, 1972), but at present it is difficult to identify it specifically, because our material is represented only by a single broken leaf. Hence we regard our leaf as *Ptilophyllum* sp. A.

Ptilophyllum hsiangshanense WU known from the Xiangxi Formation, West Hubei (WU *et al.*, 1980) also resembles in form and venation our *P.* sp. A. However, it is distinguished by the truncated pinna apices, instead of rounded ones as seen in ours.

Ptilophyllum sp. B

(Pl. 1, Fig. 8; Pl. 5, Figs. 1–8; Figs. 5a-f)

Specimen examined: NSM PP-8990 (collected by I. OBATA and others).

Horizon: Kimigahama Formation (upper lower Barremian), Choshi Group.
Locality: Isejigaura Coast (the same as *Ptilophyllum subulatum*).
Occurrence: Rare (a single broken leaf was obtained).
Description: Leaf is pinnate (whole shape and length unknown). Pinnae are closely set, attached to the upper sides of rachis at an angle of 45–60 degrees and are generally linear but sometimes lanceolate in form, 14 mm long and 2 mm wide, with rounded apex. Veins are obscure, arising from whole base, simple and run in parallel with each other.

Cuticle is hypostomatic. Upper cuticle is 3 μm thick, consisting of cells, rectangular and elongated laterally, sometimes squarish but rarely triangular in shape, typically 40 μm long (range noted 20–70 μm) and 70 μm wide (range noted 20–100 μm). Anticlinal walls are folded; sinuousity is 8–13 μm long and 7–12 μm wide.

Lower cuticle is 4 μm thick, consisting of non-stomatal bands on vein-courses and stomatal bands between veins. Stomatal band is 150–300 μm wide, consisting of stomata, trichome-bases and ordinary cells. Stomata are paracytic (or syndetocheiric), forming 2–3 regular files; aperture is oriented transversely but rarely oblique; density is 30–60 per square mm. Guard cells are sunken, crescent-shaped; each typically 62 μm long (range noted 58–66 μm) and 24 μm wide (range noted 19–29 μm), inner surface of dorsal thickening smooth. Subsidiary cells are highly cutinized; outer anticlinal walls wavy. Subsidiary cells form a pit and a circular thickened rim surrounding external stomatal aperture. Non-stomatal band consists of cells typically rectangular, 80–150 μm long and 35–50 μm wide. Cells on the stomatal bands are rectangular typically 55–95 μm long (range noted 40–155 μm long) and 40–50 μm wide (range noted 25–65 μm wide). Anticlinal walls are folded; sinuousity is 7–17 μm long and 10–18 μm wide. Periclinal walls are finely granulated (ca. 1 μm in diameter). Trichome-bases are scattered on the stomatal band, 20–30 in number per square mm, circular to semicircular or squarish in outline, 45–65 μm in major diameter and 30–60 μm in minor diameter; anticlinal walls are heavily cutinized and inner periclinal surface is smooth and not specialized.

Cuticle of rachis is rather thick, consisting of cells and trichome-bases. They are rectangular in shape, typically 70 μm long (range noted 50–130 μm) and 25 μm wide (range noted 20–35 μm); anticlinal walls are finely waved and thickly cutinized. Trichome-bases are scattered, 20–40 in number per square mm, squarish to rectangular in shape, 30–50 μm long and 25–30 μm wide; both anticlinal and periclinal walls are thickly cutinized. Reproductive organs are not known.
Remarks: Our leaf is characterized by its linear pinnae, forming stomatal pit with a circular thickened rim surrounding stomatal aperture and scattered trichome-bases on the lower cuticle.

No comparable leaf with *Ptilophyllum* sp. B has been found in the Japanese Mesozoic. In *Ptilophyllum* leaves found in the other regions, there is no comparable leaf cuticle with such stomatal pit and rim surrounding stomatal aperture. But such stomatal structure is observed normally in some coniferous cuticles.

HARRIS (1969) described *Ptilophyllum pecten* (PHILLIPS). In his fig. 26G, he figured a bulging cell (trichome-base ?) on the lower cuticle. The external shape of this structure is similar to the internal view of trichome-base of *Ptilophyllum* sp. B.

References

ALVIN, K. L., 1970. The study of fossil leaves by Scanning Electron Microscopy. Proc. 3rd Annual SEM Symposium, Chicago: 123–128.

BARNARD, P. D. W. & MILLER, J. C., 1976. Flora of the Shemshak Formation (Elburz, Iran). Part 3: Middle Jurassic (Dogger) plants from Katumbargah, Vesek Gah and Omam Manak. *Palaeontographica*, **155B**: 31–117, pls. 1–15.

BOSE, M. N., 1959. The fossil flora of the Jabalpur Group-1. *Ptilophyllum institacallum* n. sp. *Palaeobotanist*, **7**: 26–28, pl. 1.

——— & KASAT, M. L., 1972. The genus *Ptilophyllum* in India. *Ibid.*, **19**: 115–145, pls. 1–14.

DOUGLAS, J G., 1969. The Mesozoic floras of Victoria. Parts 1 and 2. Geol. Surv. Victoria Mem., **28**: 1–310, pls. 1–51.

DOLUDENKO, M. P. & SVANIDZE, C. I., 1969. The Late Jurassic flora of Georgia. Trans. Acad. Sci. USSR, Moscow, **178**: 1–115, pls. 1–81 (in Russian).

HARRIS, T. M., 1969. The Yorkshire Jurassic flora III. Bennettitales. 186 pp., 7 pls. Brit. Mus. (Nat. Hist.).

KIM, J. H. & KIMURA, T., 1987. Cuticle of *Sagenopteris* (Caytoniales), an extinct gymnospermous plant, first observed in Japan. *Proc. Japan Acad.*, **63B**: 179–182.

KIMURA, T. & KANSHA, M., 1978. Early Cretaceous plants from the Yuasa District and the Aridagawa Valley, Wakayama Prefecture, in the Outer Zone of Japan. Part 1. *Bull. Natn. Sci. Mus.*, Tokyo, C, **4**: 99–116, pls. 1–4: Part 2. *Ibid.*, C, **4**: 165–180.

——— & MATSUKAWA, M., 1979. Mesozoic plants from the Kwanto Mountainland, Gumma Prefecture, in the Outer Zone of Japan. *Ibid.*, **4**, 99–112, pls. 1–6.

——— & OKUBO, A., 1985. *Nilssonia dictyophylla* sp. nov., from the Lower Cretaceous Choshi Group, in the Outer Zone of Japan. *Proc. Japan Acad.*, **61B**: 430–432.

——— & OHANA, T., 1984. *Ptilophyllum elongatum* sp. nov., from the lower Barremian Kimigahama Formation, the Choshi Group, in the Outer Zone of Japan. *Ibid.*, **60B**: 381–384.

——— & ———, 1985. *Zamites choshiensis* sp. nov., from the Lower Cretaceous Choshi Group, in the Outer Zone of Japan. *Ibid.*, **61B**: 352–355.

———, SAIKI, K. & ARAI, T., 1985. *Frenelopsis choshiensis* sp. nov., a cheirolepidiaceous conifer from the Lower Cretaceous Choshi Group in the Outer Zone of Japan. *Ibid.*, **61B**: 426–429.

KON'NO, E., 1967: Some younger Mesozoic plants from Malaya. In 'Geol. Palaeont. SE-Asia, 3': 135–164, pls. 25–27.

MIRANDA, V. & CHAPHEKAR, M., 1980. SEM stydy of the inner periclinal surface of leaf cuticles in the family Pinaceae. *Bot. Journ. Linn. Soc.*, **81**: 61–78.

NISHIDA, M., 1960. Lower Cretaceous plants found in Choshi Peninsula, Chiba. *Bull. Fac. Lit. Sci., Chiba Univ.*, **3**: 187–193, pls. 1–3 (in Japanese with English description of a new species).

OBATA, I., HAGIWARA, S. & KAMIKO, S., 1975. Geological age of the Cretaceous Choshi Group. *Bull. Natn. Sci. Mus.*, Tokyo, C, **1**: 17–36, pls. 1–3 (in Japanese with English summary).

———, MAIYA, S., INOUE, Y. & MATSUKAWA, M., 1982. Integrated mega- and micro-fossil biostratigraphy of the Lower Cretaceous Choshi Group, Japan. *Ibid.*, **8**: 145–172, pls. 1–7.

OISHI, S., 1940. The Mesozoic floras of Japan. *Journ. Fac. Sci., Hokkaido Imp. Univ.*, 4, **5**: 123–480, pls. 1–48.

OKAZAKI, M., ISHIDA, Y. & SETOGUCHI, H., 1984. Calcification in higher plants and its physiological roles with special reference to cytolith. *Bull. Tokyo Gakugei Univ.*, 4, **36**: 67–81 (in Japanese

with English abstract).

OKUBO, A. & KIMURA, T., 1991. *Cupressinocladus obatae*, n. sp., newly found from the Lower Cretaceous Choshi Group, in the Outer Zone of Japan. *Bull. Natn. Sci. Mus.*, Tokyo, C, **17**: 91–109.

SINCOCK, C. A. & WATSON, J., 1988. Terminology used in the description of bennettitalean cuticle characters. *Bot. Journ. Linn. Soc.*, **97**: 179–187.

SHARMA, B. D., 1967 Investigations on the Jurassic flora of Rajmahal Hils, India. 3. A review of the genus *Ptilophyllum* of MORRIS, with description of two new species from Amarjola in the Rajmahal Hills. *Palaeontographica*, **120B**: 139–150, pls. 1–15.

WU, S. Q., YE, M. N. & LI, B. X., 1980. Upper Triassic and Lower and Middle Jurassic plants from the Hsiangchi Group, Western Hubei. Mem. Nanjing Inst. Geol. Palaeont., Acad. Sinica, no. **14**: 63–131, pls. 1–39 (in Chinese with English abstract).

Explanation of plates

Plate 1: External leaf forms of *Ptilophyllum* leaves from the Choshi Group. Scale bars show 1 cm long.

1–4. *Ptilophyllum choshiense* KIMURA, OKUBO et MIYAHASHI, sp. nov.: 1. Holotype (NSM PP-8983). 2. Middle part of a leaf (one of the paratypes; NSM PP-8984). 3. Middle part of a leaf (one of the paratypes; NSM PP-8985). 4. Apical part of a leaf (one of the paratypes; NSM PP-8986).

5. *Ptilophyllum acinacifolium* KIUMRA et OKUBO, sp. nov.: (Holotype; NSM PP-8982).

6. *Ptilophyllum subulatum* KIMURA et OKUBO, sp. nov.: (Holotype; NSM PP-9013).

7. *Ptilophyllum* sp. A: (NSM PP-8989).

8. *Ptilophyllum* sp. B: (NSM PP-8990).

Plate 2: Cuticle of *Ptilophyllum choshiense* KIMURA, OKUBO et MIYAHASHI, sp. nov. Scale bars show 10 μm long except for Figs. 1 and 2 where they show 100 μm long.

1. SEM-photograph. Internal view of lower cuticle (stage no. NSM PP-8991-S1). 2. Light micrograph of the lower cuticle (slide no. NSM PP-8991-L25). 3. Light micrograph of a stoma (slide no. NSM PP-8992-L2). 4. SEM-photograph. Internal view of a stoma (stage no. NSM PP-8991-S1). 5. Light micrograph of a trichome-base (slide no. NSM PP-8991-L25). 6. SEM-photograph. Internal view of a trichome-base. The presence of a small pore indicated by an arrow (stage no. NSM PP-8985-S1). 7. Fluorescence micrograph. External surface view of trichome-base (NSM PP-8994). 8. SEM-photograph. Internal view of periclinal wall of lower ordinary cell (stage no. NSM PP-8991-S1). 9. SEM-photograph. External view of a stomatal aperture with a pair of papillae indicated by arrows (stage no. NSM PP-8983-S1).

Plate 3: Cuticle of *Ptilophyllum acinacifolium* KIMURA et OKUBO, sp. nov. (Figs. 1–6) and *P. subulatum* KIMURA et OKUBO, sp. nov. (Figs. 7–8): Scale bars show 10 μm long except for Figs. 1, 2, 7 and 8 where they show 100 μm long.

1. SEM-photograph. Internal view of the lower cuticle (stage no. NSM PP-8982-S1). 2. Light micrograph of the lower cuticle (slide no. NSM PP-8982-L11). 3. Light micrograph of a stoma (slide no. NSM PP-8982-L11). 4. SEM-photograph. Internal view of a stoma (stage no. NSM PP-8982-S1). 5. Light micrograph of a trichome base on the lower cuticle (slide no. NSM PP-8982-L11). 6. SEM-photograph. Internal view of periclinal wall of the lower ordinary cell (stage no. NSM PP-8982-S1). 7. SEM-photograph. Internal view of the lower cuticle (stage no. NSM PP-8988-S2). 8. Light micrograph of the lower cuticle. Small papillae are scattered of which one is indicated by an arrow (slide no. NSM PP-8987-L23).

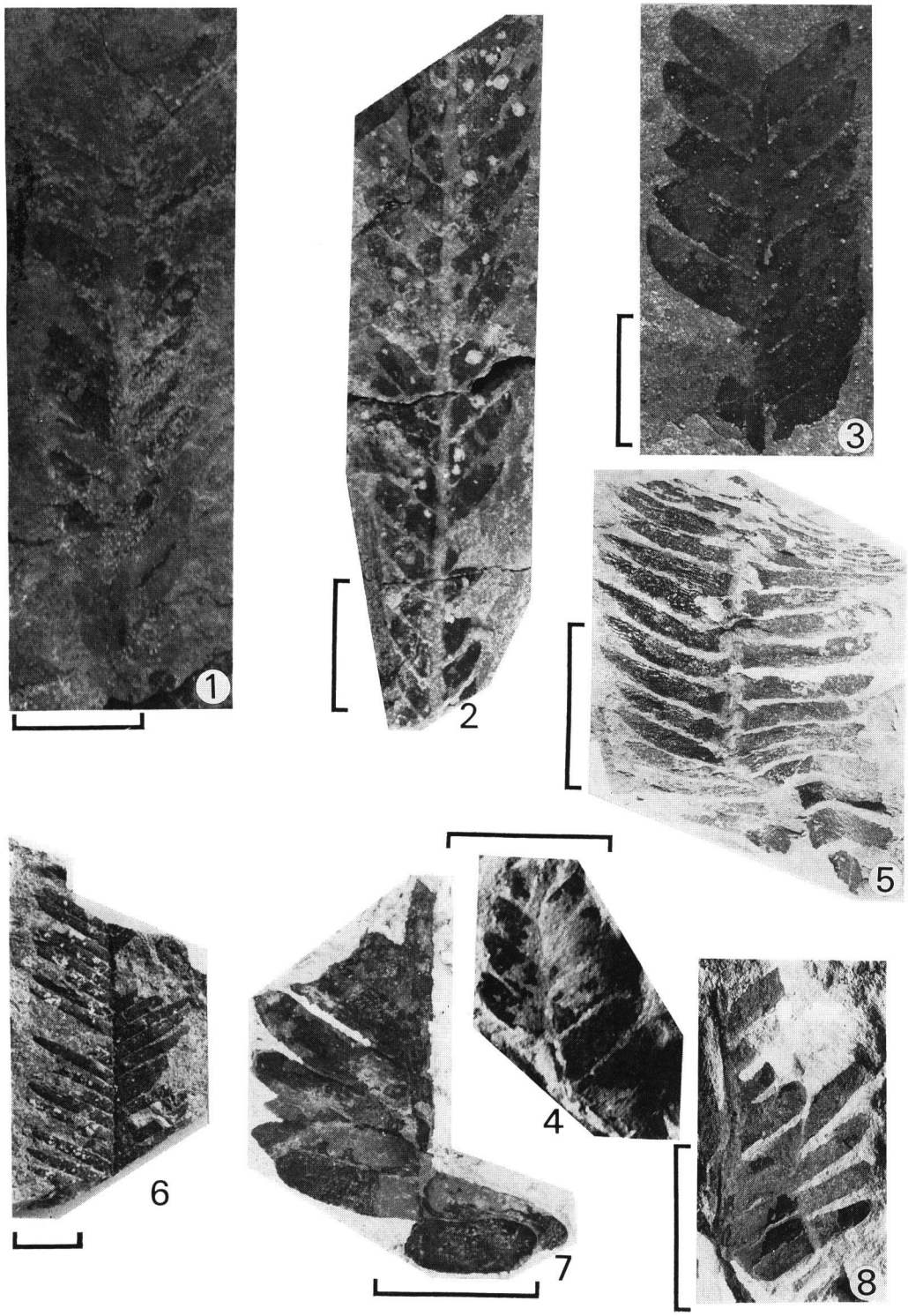
Plate 4: Cuticles of *Ptilophyllum subulatum* KIMURA et OKUBO, sp. nov. (Figs. 1–3) and *P.* sp. A (Figs. 4–8): Scale bars show 10 μm except for Figs. 5 and 6 where they show 100 μm long.

1. Light micrograph of a stoma (slide no. NSM PP-8987-L23). 2. SEM-photograph. Internal view of a stoma (stage no. NSM PP-8987-S2). 3. SEM-photograph. Internal view of periclinal wall of the lower ordinary cell (stage no. NSM PP-8987-S2). 4. SEM-photograph. Internal view of periclinal wall of the lower ordinary cell (stage no. NSM PP-8989-S1). 5. SEM-photograph. Internal view of the lower cuticle (stage no. NSM PP-8989-S1). 6. Light micrograph of the lower cuticle. Small papillae are scattered of which one is indicated by an arrow (slide no. NSM PP-8989-L1). 7. Light micrograph of a stoma

(slide no. NSM PP-8989-L1). 8. SEM-photograph. Internal view of a stoma (stage no. NSM PP-8989-S1).

Plate 5: Cuticle of *Ptilophyllum* sp. B: Scale bars show 10 μm long except for Figs. 1 where they show 100 μm long.
1. SEM-photograph. Internal view of the lower cuticle (stage no. NSM PP-8990-S2). 2. Light micrograph of the lower cuticle (slide no. NSM PP-8990-L3). 3. Light micrograph of a stoma (slide no. NSM PP-8990-L3). 4. SEM-photograph. Internal view of a stoma (stage no. NSM PP-8990-S2). 5. Light micrograph of a trichome base on the lower cuticle (slide no. NSM PP-8990-L3). 6. SEM-photograph. Internal view of a trichome base (stage no. NSM PP-8990-S2). 7. SEM-photograph. Internal view of periclinal wall of the lower ordinary cell (stage no. NSM PP-8990-S2). 8. SEM-photograph. External view of a stomatal aperture (stage no. NSM PP-8990-S1).

Plate 6: SEM-photographs of leaf cuticle of *Ptilophyllum elongatum* KIMURA et OHANA (prepared from the holotype; CH-A1). Scale bars show 10 μm long except for Fig. 1 where it shows 100 μm.
1. Internal view of the lower cuticle (stage no. 86102301). 2. Internal view of a stoma (stage no. 86102301). 3. Internal view of the lower ordinary cells (stage no. 86051702). 4. Internal view of periclinal and anticlinal walls of the lower ordinary cells enlarged from Fig. 3. 5. Internal view of a trichome base. A small pore is indicated by an arrow (stage no. 86051702). 6. A small pore on the periclinal wall of a trichome base, enlarged from Fig. 5.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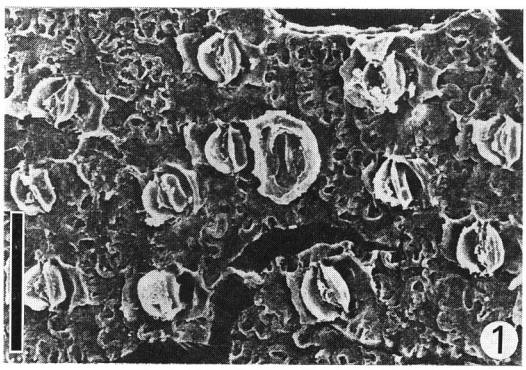
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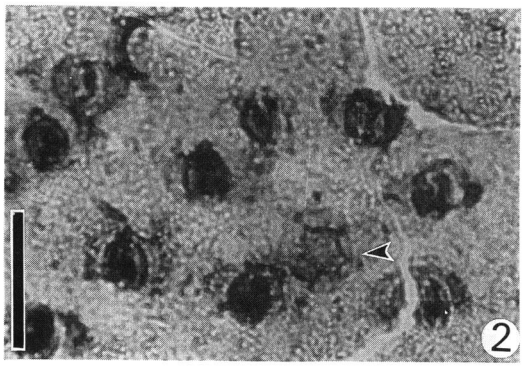
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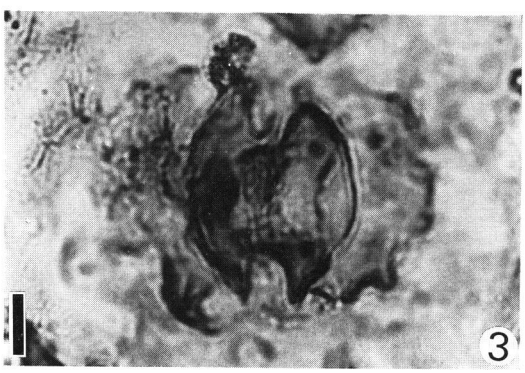
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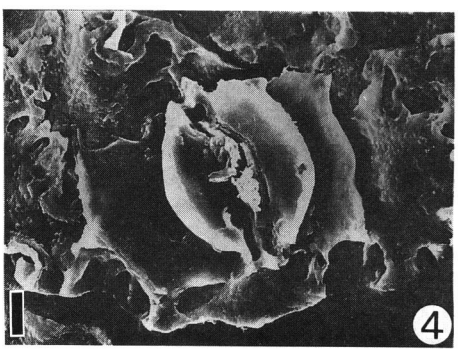
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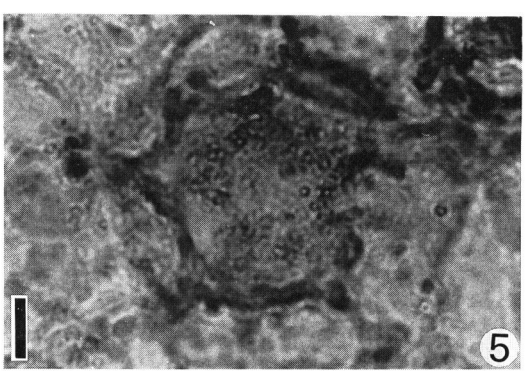
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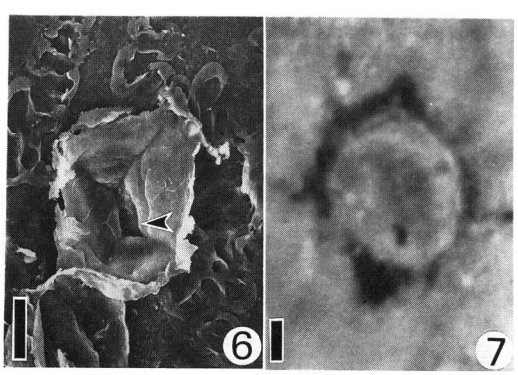
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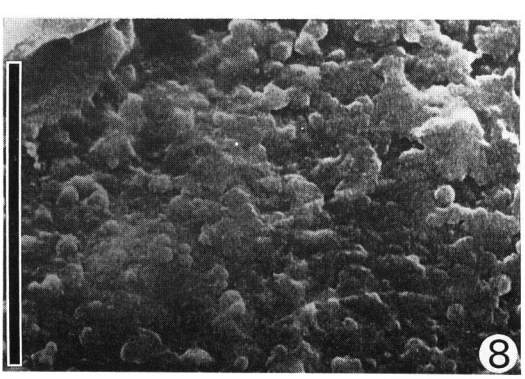
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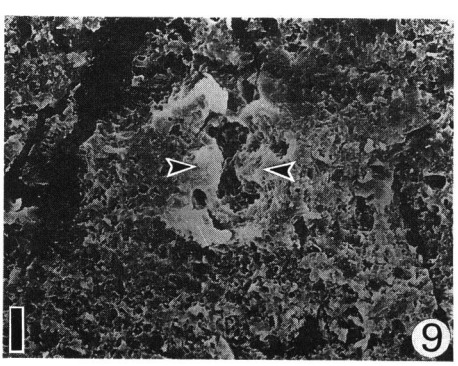
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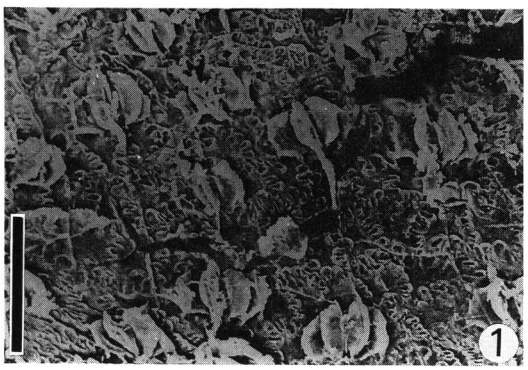
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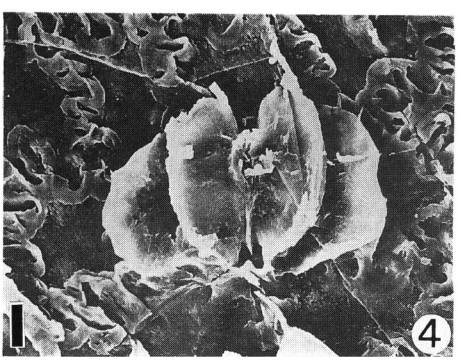
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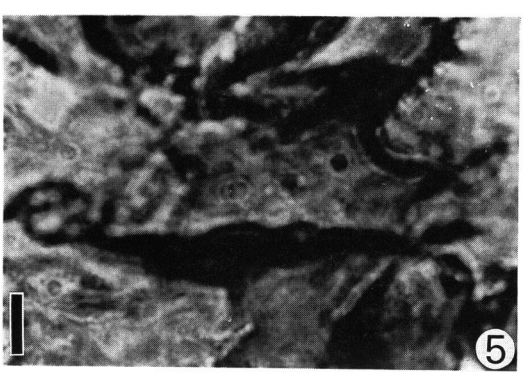
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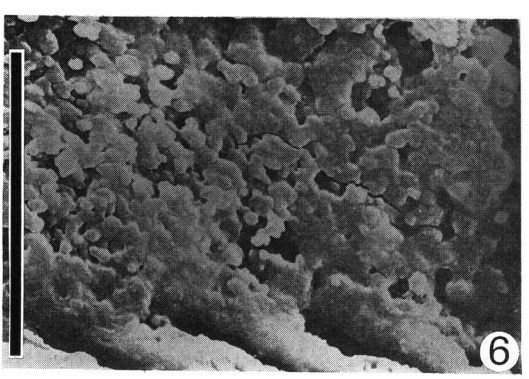
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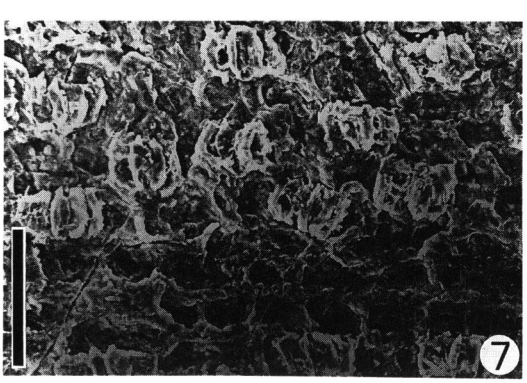
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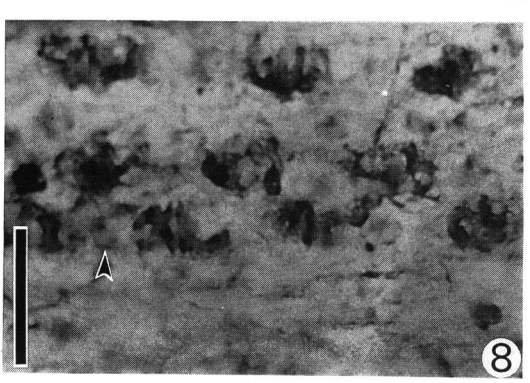
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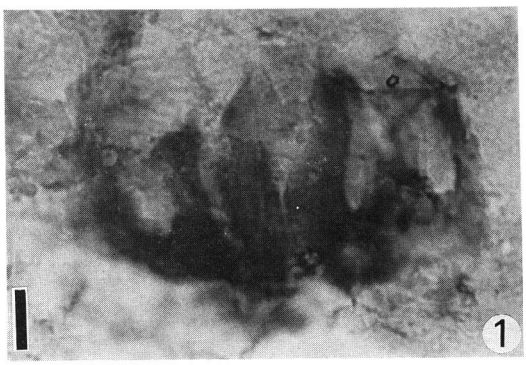
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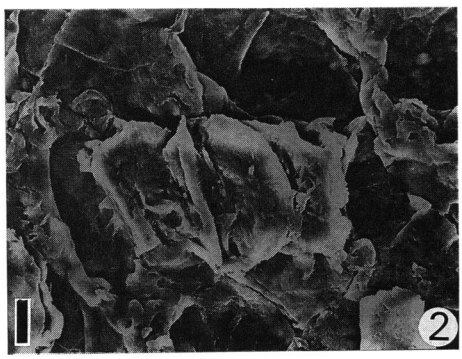
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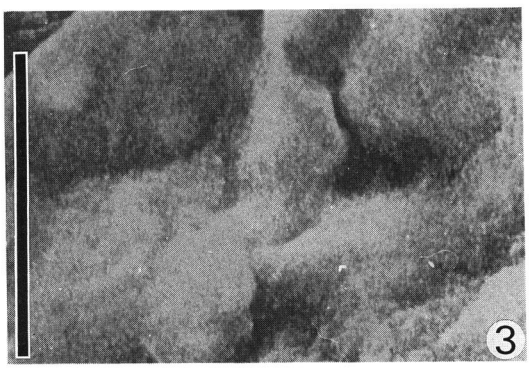
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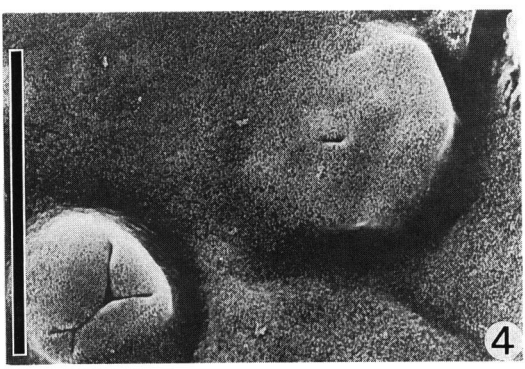
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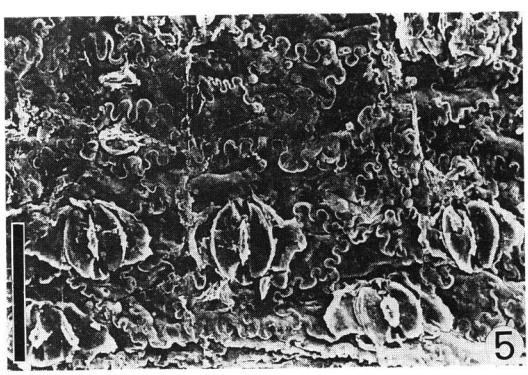
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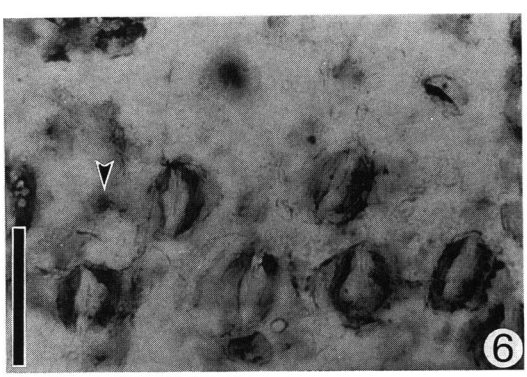
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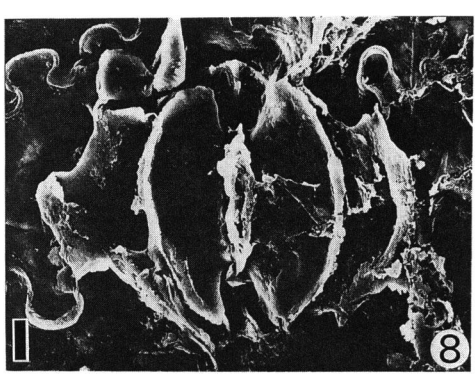
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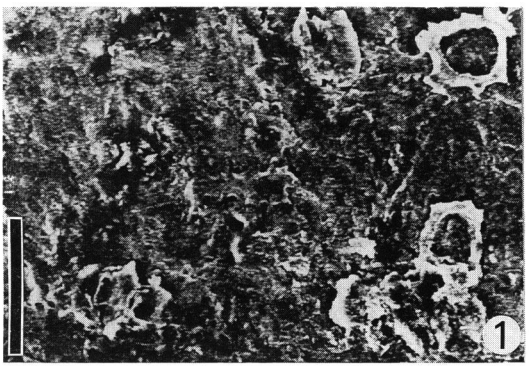
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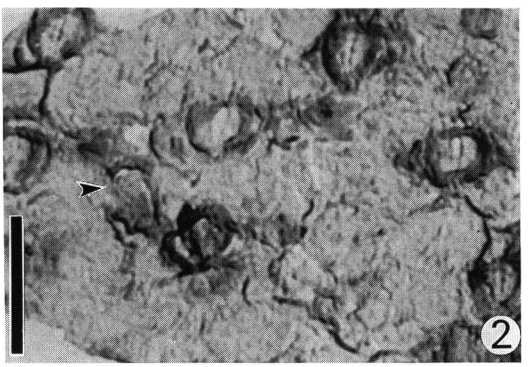
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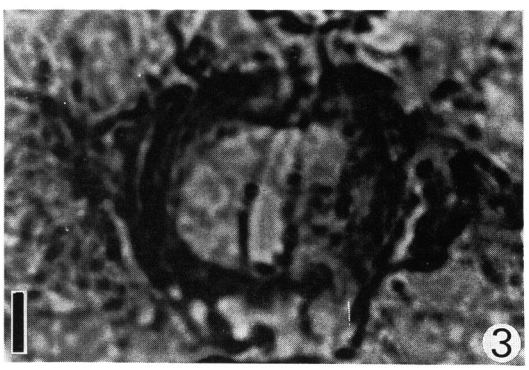
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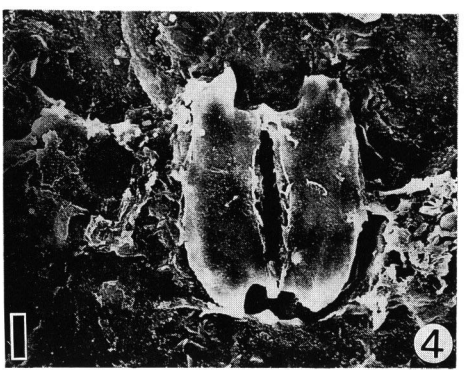
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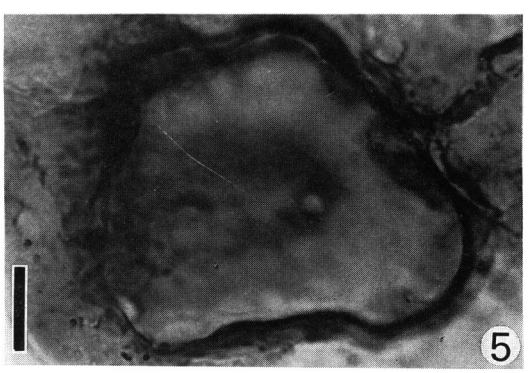
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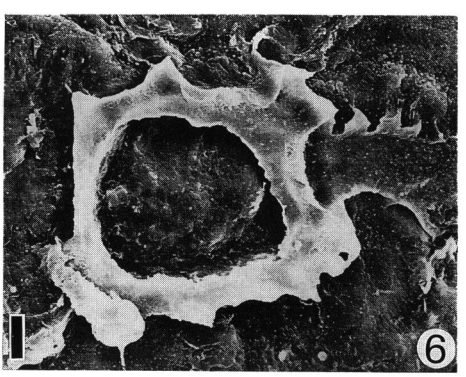
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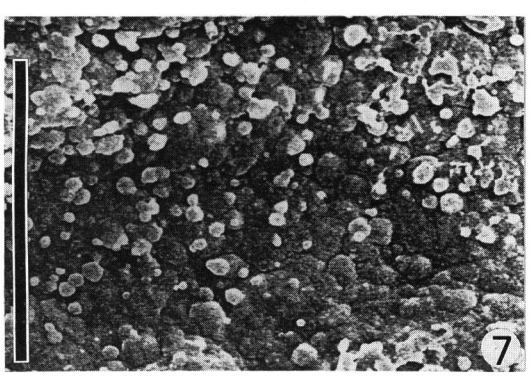
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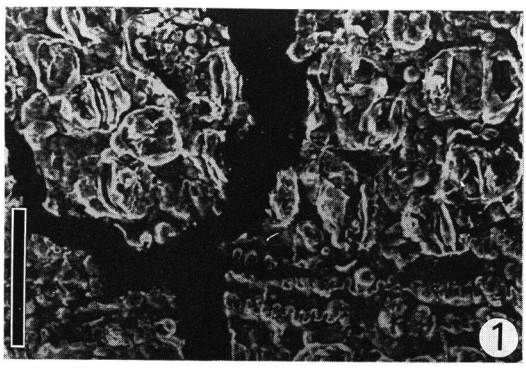
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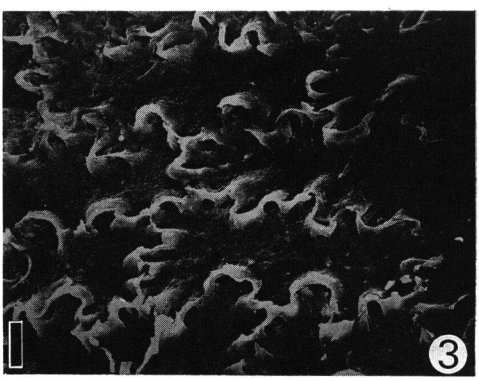
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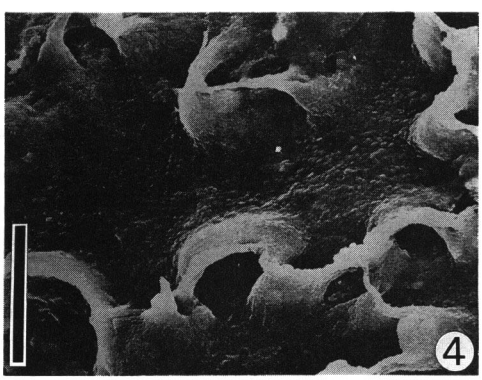
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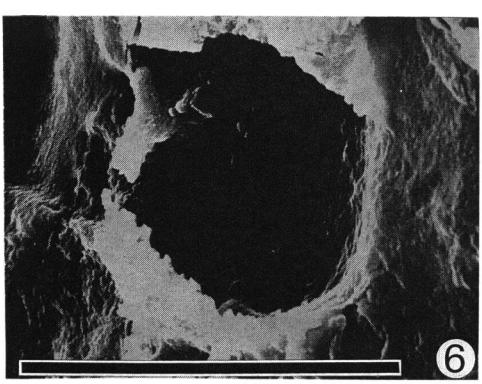
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