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Permineralized *Brachyphyllum* Leafy Branches from the Upper Yezo Group (Coniacian-Santonian), Hokkaido, Japan

By

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Abstract Permineralized *Brachyphyllum* leafy branches were collected from the Coniacian-Santonian beds of the Upper Yezo Group of marine origin in Hokkaido, Japan. This paper deals with the histological description of these coniferous leafy branches in detail. The present *Brachyphyllum* leafy branches are quite similar to and indistinguishable from *B. vulgare* (STOPES et FUJII) JEFFREY (formerly *Yezonia vulgaris* STOPES et FUJII) in internal anatomy. The taxonomic affinity of the present *Brachyphyllum vulgare* can not be precisely made clear, until its reproductive organs in organic connection are found.

Introduction

The Upper Yezo Group of marine origin is extensively exposed to the west of a meridional geotectonic zone (nearly N-S direction) of Hokkaido (see OHANA & KIMURA, 1991, p. 946, fig. 1A). This group (Upper Cretaceous) yields abundant permineralized plant fragments together with such marine animals as ammonites indicating Coniacian and Santonian ages for the calcareous nodules. Some of these fossil plants were already described by various authors. In this paper, we describe permineralized *Brachyphyllum* leafy branches on the basis of 12 specimens from the three localities, as follows:

From the middle to upper courses of the Obirashibe River: NSM PP-9017 (A, B), 9022, 9024, 9025 and 9026 (collected by H. TAKAHASHI) (Fig. 1A).

From the upper course of the Yubari River and its tributaries: NSM PP-9018 (A, B), 9020 (A–C) and 9021 (collected by Y. KERA); 9019 (A–C) (collected by M. KERA); 9028 (collected by H. TAKAHASHI) (Fig. 1B).

From the Kumaoizawa Valley: NSM PP-9023 and 9027 (collected by Y. KERA and M. KERA respectively) (Fig. 1B).

The specimens examined in this paper are permineralized mainly by calcium carbonate, but are well preserved externally and internally. The specimens were cut and sliced by diamond saw with a blade of 0.4 mm thick along the necessary surfaces and were polished by 500 mesh carborundum. The polished surfaces were then etched

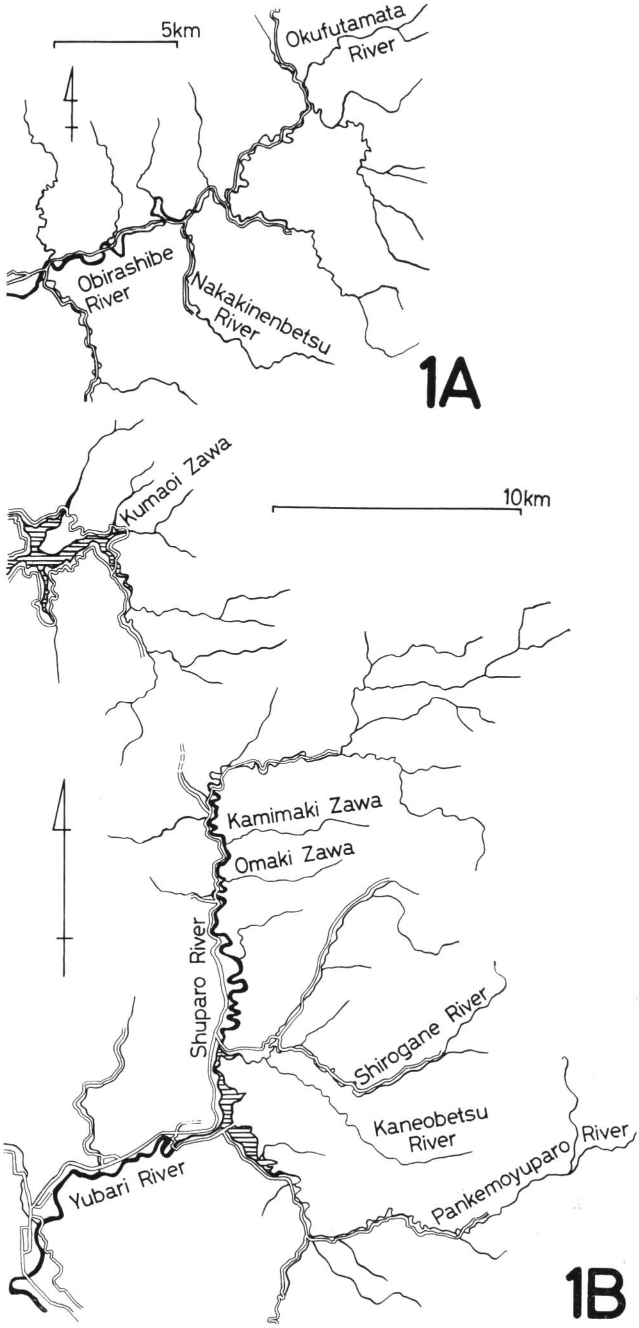

Fig. 1. Map showing the locations of the main rivers and valleys from which the fossil plants-sites are known. 1A; middle-upper courses of the Obirashibe River and its tributaries. 1B; upper course of the yubari River and its tributaries and the Kumaoizawa Valley (for details, see OHANA & KIMURA, 1991, p. 946).

by ca. 5% HCl solution for 40 to 50 seconds. Peels were made using cellulose acetate film ('Bioden R. F. A.'; 0.034 mm thick). Cuticular preparations for the light microscopy were made by the ordinary or bulk maceration procedures. For SEM observation, cuticles were coated with platinum and photographed with a Hitachi S-430 at accelating voltage of 15 kv.

All the specimens and cuticular slides and stages are stored in the National Science Museum, Tokyo.

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Description of *Brachyphyllum* leafy branches

Fragments of *Brachyphyllum* leafy branches extensively occur in the Upper Yezo Group. The genus *Brachyphyllum* LINDLEY et HUTTON ex BRONGNIART 1828 has been regarded as a form-genus redefined by HARRIS (1969, 1979). This generic name was given to the sterile leafy branches.

All the specimens here examined show the same external and internal features. In this paper we describe both features of our leafy branches on the basis of the specimens NSM PP-9018 and 9024. Cuticular features are also described on the basis of the leaves buried in the rock matrix in the specimen NSM PP-9018. These two are the most well preserved spercimens in our collection.

External Morphology

The leafy branches described here are represented by penultimate (median) and ultimate ones. All the external features agree well with those redefined by HARRIS (1969, 1979). A detailed sketch of the largest leafy branch amongst the collection shows a penultimate (a median one in this specimen) branch, 1.5 cm wide with adnate leaves, gives pinnate and subopposite or alternate, closely set ultimate branches at an angle of 50 degrees. These branch axes are covered by close helicals of adnate leaves. Unfortunately we have been unable to show the precise phyllotaxy of leaves, although we knew the 'simple method for determining the contact parastichies of a compressed fossil or cone' proposed by WATSON *et al.* (1987).

The penultimate branches examined are at least 4 cm long, becoming gradually narrower toward the roundish apex. The leaves are rhomboidal in surface wiew,

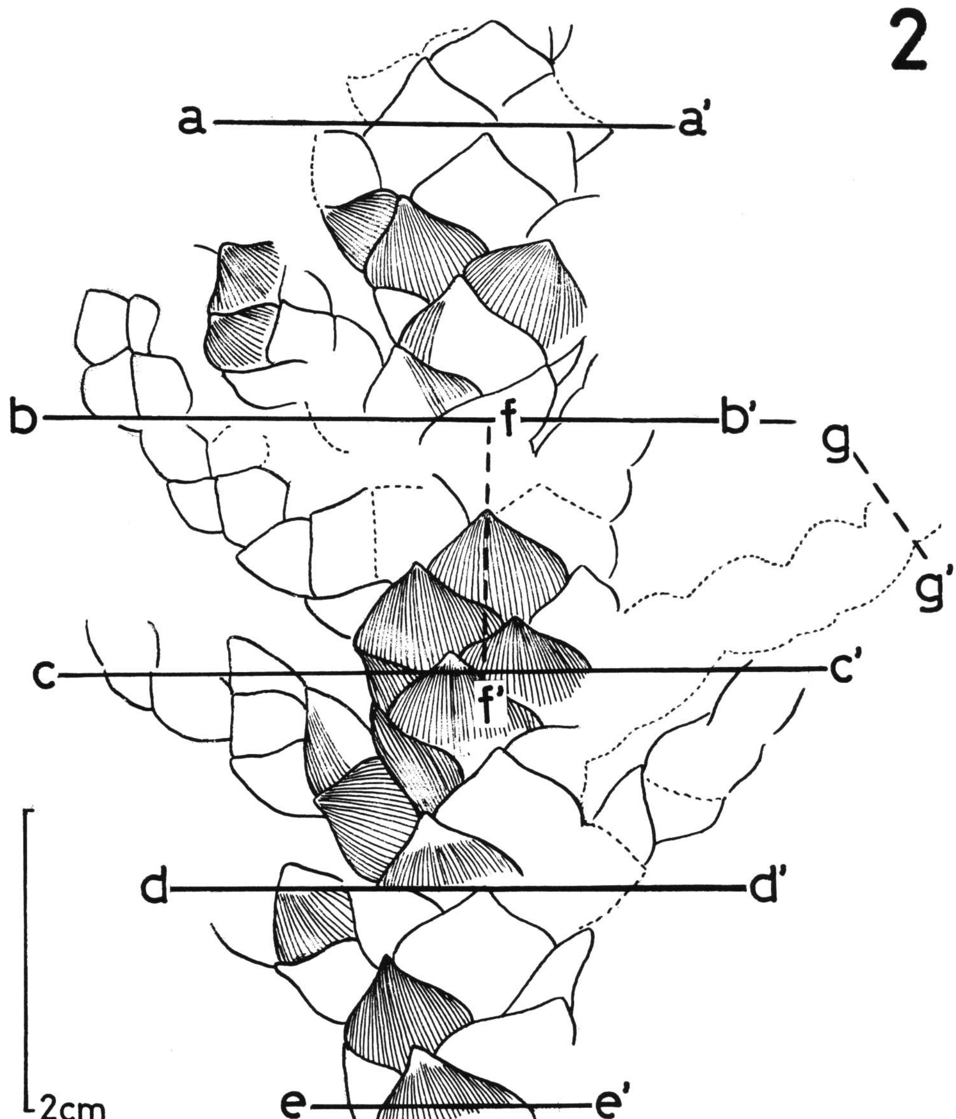

Fig. 2. A detailed sketch of the exposed and eroded surface of leafy branches (NSM PP-9018A). The a–a′, b–b′, c–c′, d–d′, e–e′ and g–g′ lines indicate the positions of transversely cut planes, and the f–f′ line indicates the position of longitudinally cut plane.

with a mucronate apex, usually broader than length (height), typically up to 1 cm wide and 0.8 cm high, and imbricated. Their lower parts are covered with free parts of the lower leaves. The free part of leaf is extended from the apex to the lateral

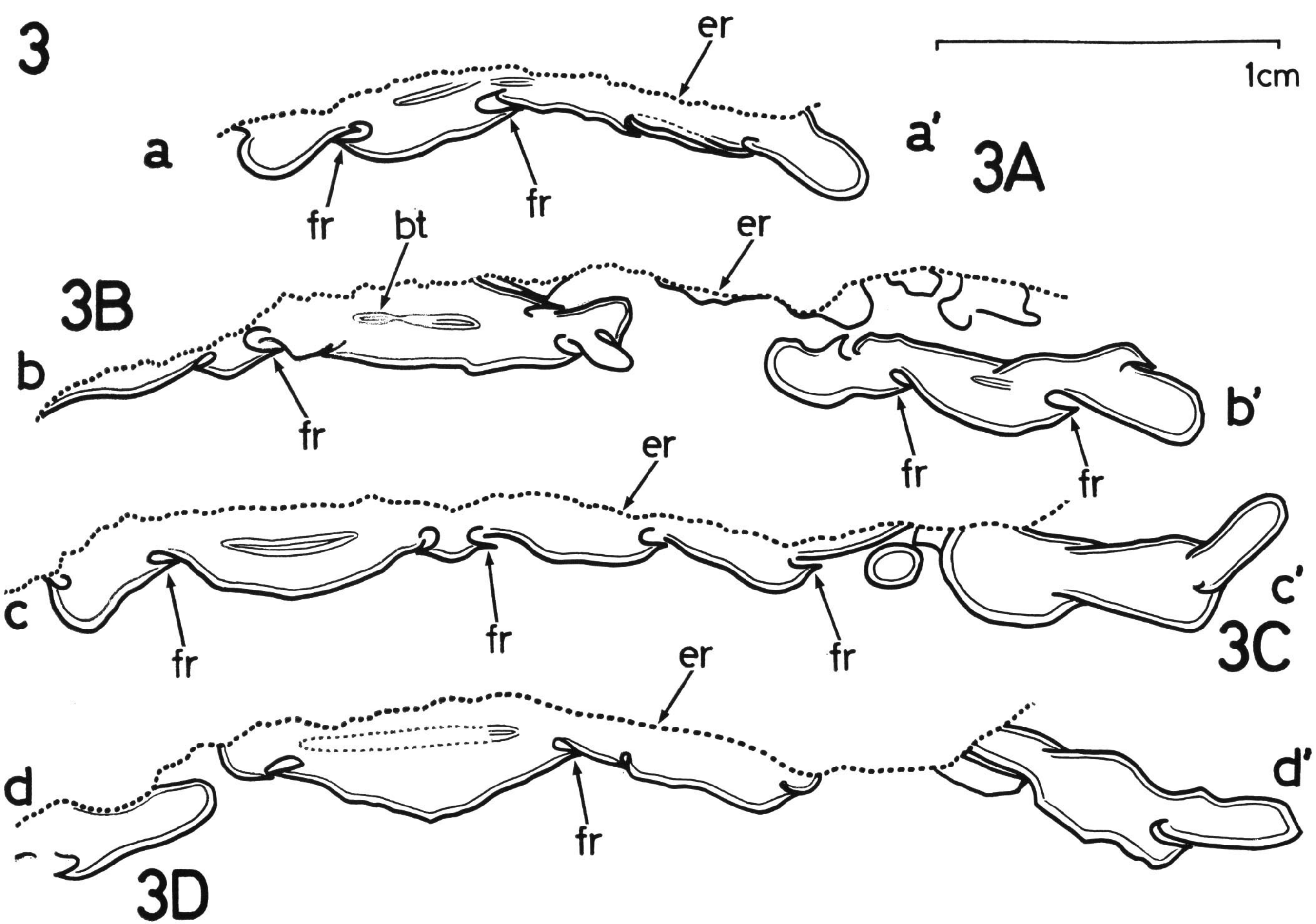

Fig. 3. The sketches of transverse sections of penultimate (median) and ultimate leafy branches (except for e–e′ section) drawn from Pl. 1 (A–D), showing the exposed and eroded surfaces (er: dotted lines), flattened ('lip'-shaped) wood cylinders, and helically arranged and adnate leaves with remarkable free part of leaves (fr). In places branch traces are shown (bt).

margins (like narrow wing). The margins are entire. The abaxial surface is ornamented by alternating fine longitudinal furrows and ridges, converging to the apex. In Fig. 2, solid lines drawn on the abaxial surface of leaves correspond to the stomatal rows.

Internal Anatomy

We cut the specimen NSM PP-9018 along the a–a′, b–b′, c–c′, d–d′ and e–e′ lines as shown in Fig. 2 to make five transverse sections of leafy branches (Pl. 1, Figs. 1A–E). They show detailed internal anatomy of the leafy branches, and their rough sketches are shown in Fig. 3 (except e–e′ section). The exposed surface of this specimen was partly eroded ('er' in Pl. 1 and Fig. 3), but fortunately the opposite surface was totally well preserved in the rock matrix. Each leafy branch consists of centrally flattened wood cylinder with pith, cortex and surrounding leaves. The central axes of the branches are compressed vertically, comprizing laterally elongated oval pith, 'lip-shaped' flattened wood cylinder and cortex (Fig. 3; Pl. 1, Figs. 1A–E; Pl. 2, Figs. 1–5).

Pith: The pith is composed of sclereids, resin passages and parenchymatous cells (Pl. 2, Figs. 1–5). Sclereids (or stone cells) are irregular, variable in form, thick-walled and often grouped to form sclereid nests (Pl. 2, Figs. 2–4; Pl. 5, Fig. 5).

Transverse view of the wood cylinder (vascular bundles): The xylem is endarch. The protoxylem and metaxylem are in contact with the outer margin of pith with some gaps (Pl. 2, Fig. 4). The secondary xylem forms a flattened cylinder (Pls. 1–2) except at the tip of younger branches (Pl. 3). The secondary wood cylinder consists of xylem tracheids of the same size, but is uneven in its thickness according to the position. For instance, in one radial view the number of tracheids is 40, and in the other of the same cylinder, it is 29 (Pl. 2, Figs. 5–6). Furthermore, the tracheids are considerably variable in thichness of their walls; some are very thick walled with a very small lumen and the others are quite thin. These thick- and thin-walled tracheids produce concentric or irregularly concentric zones in the secondary wood cylinder. The relative disposal of the thick- and thin-walled tracheids in this secondary wood is a distinguished feature of the present wood cylinder. There is no sign of any normal annual rings nor of any wood parenchyma. The cambium and phloem, which presumably lie in the crushed region just outside the secondary wood, are too poorly preserved. Sclerized bast fibres are absent in the phloem.

Young leafy branch: Figure 1 in Pl. 3 shows a transverse section cut along the g–g′ line as shown in Fig. 2. In the apical part of this ultimate branch, the vascular tracheids do not form a contiguous ring of wood, but they do form separate bundles around the pith. Each bundle consists of numerous groups of 18 to 22 primary xylem tracheids of small diameter, with one or two protoxylem tracheids at the innermost side of each bundle. Outside each bundle, there is a patch of phloem (Pl. 3, Fig. 3). No irregularity in a bundle is seen as in the secondary wood cylinder.

Radially longitudinal section of a leafy branch: A section of a rather thick branch

(NSM PP-9024) (Pl. 4, fig. 1; its transverse section is shown in Pl. 2, figs. 5–6) reveals that the wood cylinder consists mainly of thick-walled tracheids (kw) on the left (darkened zone) and thin-walled tracheids (tw) with two narrow rows of thick-walled tracheids on the right. Most region was lost along the cutting plane (z–z′) in this section. An oblique longitudinal section of the same branch shows that the wood cylinder consists of thick-walled tracheids on the left and mostly of thin-walled tracheids on the right, putting the pith (pi) between them (Pl. 4, Fig. 2). High-magnified observation of the area indicated as 'p' (Pl. 4, Fig. 1) reveals that both darkened sides consist of thick-walled tracheid zones, with a thin walled tracheid zone between the two (Pl. 4, Fig. 3). Bordered pits are seen on the radially cut, thick-walled tracheids. They are circular in shape, arranged in a single row and are separated from one another. In the same section, thin-walled tracheid zone is also visible in the area indicated as 'q' (Pl. 4, Fig. 1) where bordered pits are seen on the radial wall of thin-walled tracheids (Pl. 4, Fig. 4). They are also arranged in a single row, larger than those of the thick-walled tracheids, and are spaced more closely with each other, but they are not flattened laterally.

So far as our observation is concerned, most rows of the bordered pits are single. The rays are numerous and consist only of thin-walled parenchymatous cells, they are one cell wide and mostly one cell high (rarely two cells high) (Pl. 4, Figs. 3–4; Pl. 5, Fig. 5).

The cross fields are poorly preserved, sometimes showing that small-sized pits are arranged in 2 or 3 horizontal rows, each row with 2 to 4 pits in a field.

The leaf traces: A longitudinal section of NSM PP-9018A cut along the f–f′ line as in Fig. 2 and its counterpart (NSM PP-9018B) shows a rather narrower wood cylinder (Pl. 5, Figs. 1–2). In the longitudinal section the left side is burried in the rock matrix and the right side is exposed and eroded. Detailed structures of the areas indicated by 'p' and 'q' (Pl. 4, Fig. 1) are shown on Plate 5, Figs. 3–5.

The leaf traces originate at a very small angle from the central wood cylinder as very slender bundles. They at first run almost in parallel to the central cylinder, then branching several times (Pl. 6, Figs. 1–2). Some leaf traces run horizontally and the others toward the leaf apex and leaf margin (Pl. 6, Figs. 3–4). The leaf trace tracheids have dense spiral or scalariform thickening. Small pits are sometimes found in a single row. These traces merge with the transfusion tissue of leaf. No bundle sheath is observed. Branch traces are frequently found in some places (Fig. 3B; Pl. 10, Fig. 5).

The leaves: The leaves are thick and appear to be freshy. The leaf base surrounds the branch axis. The free part of leaf is extended from the apex to the lateral margins, pointing inwardly rather than outwardly.

The abaxial surface of the leaves shows regular cuticle, epidermis of one cell thick with stomatal complexes, thick hypodermis, outer mesophyll layer represented by palisade cells, transfusion tissue zone and inner mesophyll layer corresponding to the usual spongy cell layer with many resin passages (Pl. 2, Fig. 1; Pl. 5, Figs. 1–4; Pl. 6,

Fig. 1; Pl. 7). The precise boundary between the inner mesophyll of the leaf and the cortex of the axis, and the periderm layer of the axis could not be detected.

The hypodermis consists of thick-walled, fibrous cells, they are variable in thickness from 40 to 50 μm according to the position. These cells are typically shown on Plate 7, Figs. 1–4. Stomata are not found on the hypodermis (Pl. 7, Fig. 4). Two to three storied palisade cell layers consist of vertically elongated parenchymatous cells. Its thickness varies from 100 to 200 μm according to the position. In some places, this layer is less or not developed at all.

The transfusion tissue is scattered, forming a zone inside the palisade cell layer. Each consists of a group of small-sized tracheids (Pl. 7, Figs. 1–2).

The inner mesophyll layer consists of parenchymatous cells and large and irregular sclereids which are often in groups, and numerous resin passages. They are closely packed each other with small intercellular spaces. In the resin passages, epitherial cells, lining the inside of passage, are not observed.

The free part of the leaf is thin, wing-like, becomes gradually narrower and thinner to the scarious or nearly scarious margins which encircle the axis to some extent, are not frilled, and lack trichomes (Pl. 2, Fig. 1; Pl. 4, Fig. 1; Pl. 5, Figs. 1–4; Pl. 7, Fig. 5). *The leaf cuticle*: The cuticle is hypostomatic and rather thick 7–9 μm at its fold (Pl. 8, Fig. 1). The adaxial cuticle consists only of ordinary cells and can be only seen on the adaxial surface of the free part of the leaf. The abaxial cuticle consists of longitudinal stomatal rows and ordinary cell files. The stomatal rows tend to converge at the apex of the free part of a leaf (Pl. 10, Figs. 1–3). They are separated by 3 to 6 ordinary cell files. The stomata are separated by one to 6 ordinary cells longitudinally. They are occasionally in contact with each other, but do not share their subsidiary cells.

The ordinary cells are small, thick-walled, isodiametric or slightly elongated rectangular or sometimes polygonal in surface view. The anticlinal walls are 3 to 5 μm thick, straight, not interrupted by pits. The periclinal walls are smooth, but thinly cutinized pad is discernible on the center of each inner wall (Pl. 9, Figs. 1, 4).

The stomatal complexes are haplocheilic, consist of guard cells sunken at the base (bottom) of epistomatal pits formed by subsidiary and monocyclic or incompletely monocyclic encircling cells. They are orientated randomly rather than longitudinally. The outer surface of guard cells are thinly cutinized and are often lost in the course of maceration.

The subsidiary cells are 4 to 6 (typically 4 to 5) in number, forming a ring observed by the light microscopy (Pl. 10, Figs. 1–4) and not specialized at the poles (Pl. 9). Encircling cells are similar in form and size to the ordinary cells.

The shallow epistomatal pits are inversely conical in sectional view, about 20 μm deep from the abaxial surface to the aperture of guard cells (Pl. 7, Fig. 4). Inside guard cells, there is a vertically elongated and irregularly shaped stomatal chamber (Pl. 7, Fig. 4). This chamber, confusable with a palisade cell, is distinguished by its large size and much broader in sectional view (Pl. 7, Figs. 1–4).

In the SEM observation, the surface rim made up of encircling cells is slightly raised from the general surface (Pl. 8, Figs. 5–6). These raised encircling cells are partly overlapped on the subsidiary cells. Accordingly, the subsidiary cells are not exposed on the abaxial surface, but located inside the epistomatal pit forming a ring (Pl. 8, Figs. 3–4) that surrounds the guard cells (Pl. 7, Fig. 4). However, in the light microphotographic observation, these encircling cells (forming a rim, and a ring of subsidiary cells) are seen overlapped (Pl. 10, Figs. 1–4).

The epistomatal pits in surface view is oblong, 19 to 29 μm in diameter, and the long axis corresponds to the sunken aperture (Pl. 8, Figs. 1–4). The inner view of abaxial cuticle reveals that most guard cells are incompletely preserved or lost (Pl. 9, Figs. 1–5).

In the wood of this plant, septate tracheid has not been noticed. Reproductive organs and woody stems in organic connection have not been found so far.

Discussion

So far as we know, there are two *Brachyphyllum* species whose external and internal features are very close to the present leafy branches, as discussed below.

Comparison with Yezonia vulgaris *STOPES et FUJII*: STOPES and FUJII (1910) made glorious studies on the internal anatomy of 18 plant taxa preserved in the calcareous nodules from Hokkaido, Japan. They gave detailed description on a conifer *Yezonia vulgaris* on the basis of sterile leafy branches. They did not mention their exact collecting localities, but it is obvious that the specimens they studied came from the Upper Yezo Group in the Yubari area (Fig. 1B). Although they did not show the external features of leafy branches in *Yezonia vulgaris*, the flattened ('lip-shaped') wood cylinder and detailed internal anatomy of *Yezonia vulgaris* agree well with our observation of the present leafy branches. We are therefore of the opinion that both leafy branches belong to the same species. STOPES and FUJII (1910) mentioned that the leafy branches are 'infrequent branching'. However, our observation evidently shows that the branching is frequent (Fig. 2). It is most likely that STOPES and FUJII's (1910) leafy branches correspond to our ultimate branches which do not further lamify.

In the same year, JEFFREY (1910) regarded *Yezonia vulgaris* as belonging to the genus *Brachyphyllum*. The reassignment was followed in part by STOPES (1911) and by SEWARD (1919). We also agree with JEFFREY's generic reassignment.

Comparison with Brachyphyllum 'macrocarpum' *NEWBERRY*: HOLLICK & JEFFREY (1906, 1909) and JEFFREY (1910) investigated the external and internal features of leafy branches in *Brachyphyllum macrocarpum*. This specific name was proposed by NEWBERRY, but not published by himself.

The anatomical features described by HOLLICK and JEFFREY (1906, 1909) are similar to those of *Brachyphyllum vulgare*. In the American leafy branches, however, HOLLICK and JEFFREY (1906, 1909) noticed the presence of annual rings in the secondary wood cylinder, and also noticed the periderm between the cortex of axis and the inner mesophyll layer of leaf. The resin passages of the American species appear to be larger in diameter and less in number than those of the Japanese leafy branches. In addition, in the American wood cylinder, rays are higher, 5 cells high (HOLLICK & JEFFREY, 1906, pl. 5, fig. 2). Furthermore, the American ultimate leafy branches are club-shaped and constricted at base, while those from Japan are parallel-sided.

As discussed above, the Japanese leafy branches do not agree exactly with the American leafy branches, so that we at present regard both as specifically distinct from each other and use the name *Brachyphyllum vulgare* for the Japanese leafy branches. At any rate, we assume that similar *Brachyphyllum* leafy branches existed in Hokkaido, the northern part of Japan and the eastern North America during Late Cretaceous time.

The specific name '*macrocarpum*' was controversial (SEWARD, 1919). But now we do not like to have anything to do with it, because the controversy of the specific names has no connection with the present study.

Female reproductive organs, *Yezostrobus oliveri* STOPES et FUJII (STOPES & FUJII, 1910) from Hokkaido and *Protodammara speciosa* HOLLICK et JEFFREY (HOLLICK & JEFFREY, 1906) from eastern North America have been found, both associated with *Brachyphyllum* leafy branches in occurrence. However, we have yet clarified features in detail, so that their taxonomic affinities are still uncertain. We assume that the enigmatic organ HOLLICK and JEFFREY (1909) regarded as 'a cone of *Brachyphyllum* sp. ?' is impossible to determine.

A number of 'species' have been described under the form-genus *Brachyphyllum*, and some are externally indistinguishable from another form-genus *Pagiophyllum*. Most of the *Brachyphyllum* 'species' described are represented only by impressions of sterile leafy branches. In some cases cuticles have remained in the compressions (*e.g.* KENDALL, 1947; WESLEY, 1956; LORCH, 1968; ASH, 1973; HARRIS, 1979; FISHER & WATSON, 1983; WATSON *et al.*, 1987), and in few cases, their reproductive organs in organic connection and/or in close association are known (*e.g.* KENDALL, 1947, 1949; HARRIS, 1979; Van KONIJNENBURG-Van CITTERT, 1987). Amongst them, *Brachyphyllum mamillare* LINDLEY et HUTTON (the type species of *Brachyphyllum*) was placed in the family Araucariaceae (KENDALL, 1947, 1949; HARRIS, 1979). The transverse section of its leaves are rhomboidal in shape rather than oval in *Brachyphyllum vulgare*.

During the last two decades, studies of cheirolepidiaceous conifers have been remarkably progressed, and the concept of this family has become larger and broader (see reviews by ALVIN, 1982; WATSON, 1982, 1988; CLEMENT-WESTERHOF & Van KONIJNENBURG-Van CITTERT, 1991).

These authors have regarded that *Brachyphyllum crusis* KENDALL and *B. scottii* KENDALL belong to the Cheirolepidiaceae, and that *B. ardenicum* HARRIS, *B. carpentieri* FISHER et WATSON, *B. castatum* WATSON, FISHER et HALL, *B. hegewaldia* ASH, *B. ningshiaense* CHOW et TSAO and *B. pulcher* LORCH are probably cheirolepidoaceous.

In addition, ARCHANGELSKY and FUEYO (1989) established a new genus *Squa-*

matostrobus on the basis of leafy branches, and pollen- and seed-cones, and placed it in the family Podocarpaceae. Its sterile leafy branches were formerly regarded as *Brachyphyllum tigrense* TRAVERSO.

At present it is difficult to determine the taxonomic position of *Brachyphyllum* only on the basis of sterile leaf form and cuticular features. This is because that these cuticles have a wide variation in form among the fossil Araucariaceae and Cheirolepidiaceae which include such form-genera as *Pagiophyllum* and *Cupressinocladus* and such genera as *Androvettia*, *Frenelopsis*, *Pseudofrenelopsis*, *Hirmeriella* and *Tomaxellia*. However, at least the sterile leafy branches of such genera as *Androvettia*, *Frenelopsis*, *Pseudofrenelopsis* and *Geinitzia* can be distinguished from *Brachyphyllum* leafy branches by their unique leaf forms. But it is difficult to distinguish *Hirmeriella* and *Tomaxellia* from *Brachyphyllum* by the feature of sterile leafy branches.

Brachyphyllum vulgare has leaf cuticle closely similar to those of some fossil Araucariaceae, Cheirolepidiaceae, Podocarpaceae, and Taxodiaceae, thereby making difficult to attribute *B. vulgare* to any conifer families based only on sterile leaf cuticle and internal anatomy of leafy branches.

HOLLICK and JEFFREY (1909) established a wood genus *Brachyoxylon* and described *B. notabile* on the basis of wood pieces (lignite) from the same locality where their *Brachyphyllum macrocarpum* occurs. They assumed that their *Brachyoxylon* is the stem of *Brachyphyllum macrocarpum*. These wood pieces were formerly regarded as *Brachyphyllum macrocarpum* and '*Araucarioxylon* sp.' (HOLLICK & JEFFREY, 1906), and 'Wood of *Brachyphyllum*' (JEFFREY, 1906). However, such wood pieces referable to *Brachyoxylon* have not been found from the Upper Yezo Group.

JEFFREY (1910) regarded *Brachyphyllum vulgare* as araucariaceous, while ALVIN *et al.* (1981) referred *Brachyphyllum macrocarpum* and *Brachyoxylon notabile* to the Cheirolepidiaceae.

Under such circumstances, we reserve to make further discussion on the affinity of *Brachyphyllum vulgare* until its reproductive organs in organic connection are obtained.

Finally we suggest that the flattened wood cylinder is a unique feature in *Brachyphyllum vulgare* and *B. macrocarpum*, and also that these flattened cylinder are natural rather than sediment compression; the cells in leafy branches of *Brachyphyllum vulgare* are mostly intact from compression. Such a vew is also supported by the observation that the ammonites and inoceramids in the same nodules are also intact from compression. In addition, it would be suggested that the present flattened leafy branches had a dorsiventral habit (Pl. 10, Fig. 5).

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Explanation of plates

All figures belong to *Brachyphyllum vulgare* (STOPES et FUJII) JEFFREY.

Plate 1: Five transverse sections of a leafy branch (NSM PP–9018) cut along the lines as shown in Fig. 2.
The position of a flattened ('lip'-shaped) wood cylinder of the penultimate (median) leafy branch is indicated between x–x′ and y–y′ lines. er; exposed and eroded surface.

Plate 2: Transverse sections of the pith, flattened wood cylinder and supposed cortex.
Fig. 1. A penultimate (median) leafy branch, enlarged from the counterpart of Pl. 1 (1C).
Fig. 2. A right half of the flattened wood cylinder, enlarged from Pl. 1 (1C).
Fig. 3. The central part of a wood cylinder, enlarged from Fig. 1 of this plate.
Fig. 4. A part of a wood cylinder, enlarged from the counterpart of Pl. 1 (1B). Figs. 1–4 were sectioned from NSM PP–9018A.
Fig. 5. Slightly flattened wood cylinder sectioned from NSM PP–9024.
Fig. 6. A part of wood cylinder, enlarged from Fig. 5 of this plate. er; exposed and eroded surface, pi; pith, kw; thick-walled tracheids, tw; thin-walled tracheids, fr; free part of leaf, scl; sclereids, px; primary xylem, rp; resin passage.

Plate 3: Vascular bundles of the tip of an ultimate younger branch, transversely sectioned along the g–g′ line in Fig. 2 (NSM PP–9018A).
Fig. 1. Transverse section of the tip of an ultimate branch.
Fig. 2. Separated bundles and a leaf trace (lt), shown by enclosed white lines.
Fig. 3. Enlarged from Fig. 2 of this plate. xy; xylem tracheids, ph; phloem.
Fig. 4. Separated central bundles and three leaf traces (lt) originated from the central bundles. All figures are enlarged from Fig. 1 of this plate. pi; pith with sclereids nest and resin passages.

Plate 4: Radial longitudinal section of a leafy branch (NSM PP–9024).
Fig. 1. Rather thick leafy branch. The wood cylinder consists of thick and thin walled tracheids.
Fig. 2. Oblique longitudinal section (the same as Fig. 1 of this plate).
Fig. 3. Enlarged from the area indicated by 'p' in Fig. 1 of this plate, showing vascular tracheids with bordered pits and rays.
Fig. 4. Enlarged from the area indicated by 'q' in Fig. 1 of this plate. kw; thick walled tracheids, tw; thin walled tracheids, pi; pith, bp; bordered pit, ry; ray, cf; cross field.

Plate 5: Radial longitudinal section cut along the f–f′ line in Fig. 2 (NSM PP–9018A).
Fig. 1. Slender wood cylinder.
Fig. 2. Counterpart of Fig. 1 of this plate.
Fig. 3. Enlarged from the area indicated by 'p' in Fig. 1 of this plate.
Fig. 4. Enlarged from the area indicated by 'q' in Fig. 1 of this plate.
Fig. 5. Enlarged from the area indicated by 'r' in Fig. 2 of this plate. pi; pith.

Plate 6: Leaf traces (or veins).
Fig. 1. Enlarged from the area indicated by 's' in Pl. 5, fig. 2, showing very slender leaf traces (lt); some run nearly longitudinally and the others horizontally.
Fig. 2. Enlarged from Pl. 5, fig. 1, showing the leaf traces (lt).
Fig. 3. Further enlarged from the area 'p' in Fig. 2 of this plate, showing the branched leaf trace.
Fig. 4. Transverse section enlarged from Pl. 10, fig. 5 (counterpart of Pl. 1–1B), showing leaf traces with scalariform pittings (or thickenings).

Plate 7: Transverse and longitudinal sections of leaves, showing the leaf forming cells.

Fig. 1. Transverse section, showing leaf forming cell layers or zones, enlarged from Pl. 10, fig. 5. co and sp; cortex and inner mesophyll, tf; transfusion tissue zone, ph; crushed phloem, rp; resin passage, lt; leaf trace.

Fig. 2. Longitudinal section of a leaf, showing the transfusion tissue (tf) zone inside, outer mesophyll (palisade) zone, hypodermal layer and thin epidermal layer (small arrows indicate the positions of stomata). Enlarged from Pl. 5, fig. 2.

Fig. 3. The same as Fig. 2 of this plate. pa; palisade layer, hy; hypodermal layer.

Fig. 4. Enlarged partly from the area indicated by the enclosed dotted line in Fig. 3 of this plate, showing a section of stoma. sc; stomatal chamber, gc; guard cell, ss; subsidiary cell, esc; epistomatal pit.

Fig. 5. Transverse section of the free part of a leaf (fr), enlarged from Pl. 2, fig. 1.

Plate 8: Surface (abaxial) view of leaf cuticle (SEM microphotograph)

Fig. 1. Lower half shows outer surface of abaxial cuticle with epistomatal pits, and upper half shows the inner view of abaxial cuticle folded over the outer surface from the left side, in the course of maceration and preparation (stage no. 201).

Fig. 2. Abaxial surface of cuticle, showing stomatal pits in rows and thick walled ordinary cells (stage no. 202).

Fig. 3. Enlarged from Fig. 2 of this plate, showing a stomatal pit with a surrounding rim formed by the encircling cells, a slightly sunken ring formed by the subsidiary cells and thick walled ordinary cells. Guard cells are seen at the bottom of a pit with obliquely disposed aperture.

Fig. 4. The same as Fig. 3 of this plate, but guard cells are poorly preserved.

Figs. 5–6. Tilted surface view of two epistomatal pits, their rims are sligntly raised (stage no. 202).

Plate 9: Inner view of abaxial leaf cuticle (SEM microphotograph)

Fig. 1. Three stomatal rows and thick walled ordinary cells. The central part of inner periclinal wall of each cell is slightly thickened (pad-like).

Figs. 2–3. Tilted view of stomata (stage no. 201). In Fig. 3, guard cells were lost.

Figs. 4–5. In Fig. 4, a stoma with 5 subsidiary cells (1–5) and encircling ordinary cells (a–j), enlarged from Fig. 1 of this plate.

Plate 10 (Figs. 1–4): Surface view of the abaxial cuticle (light microphotograph)

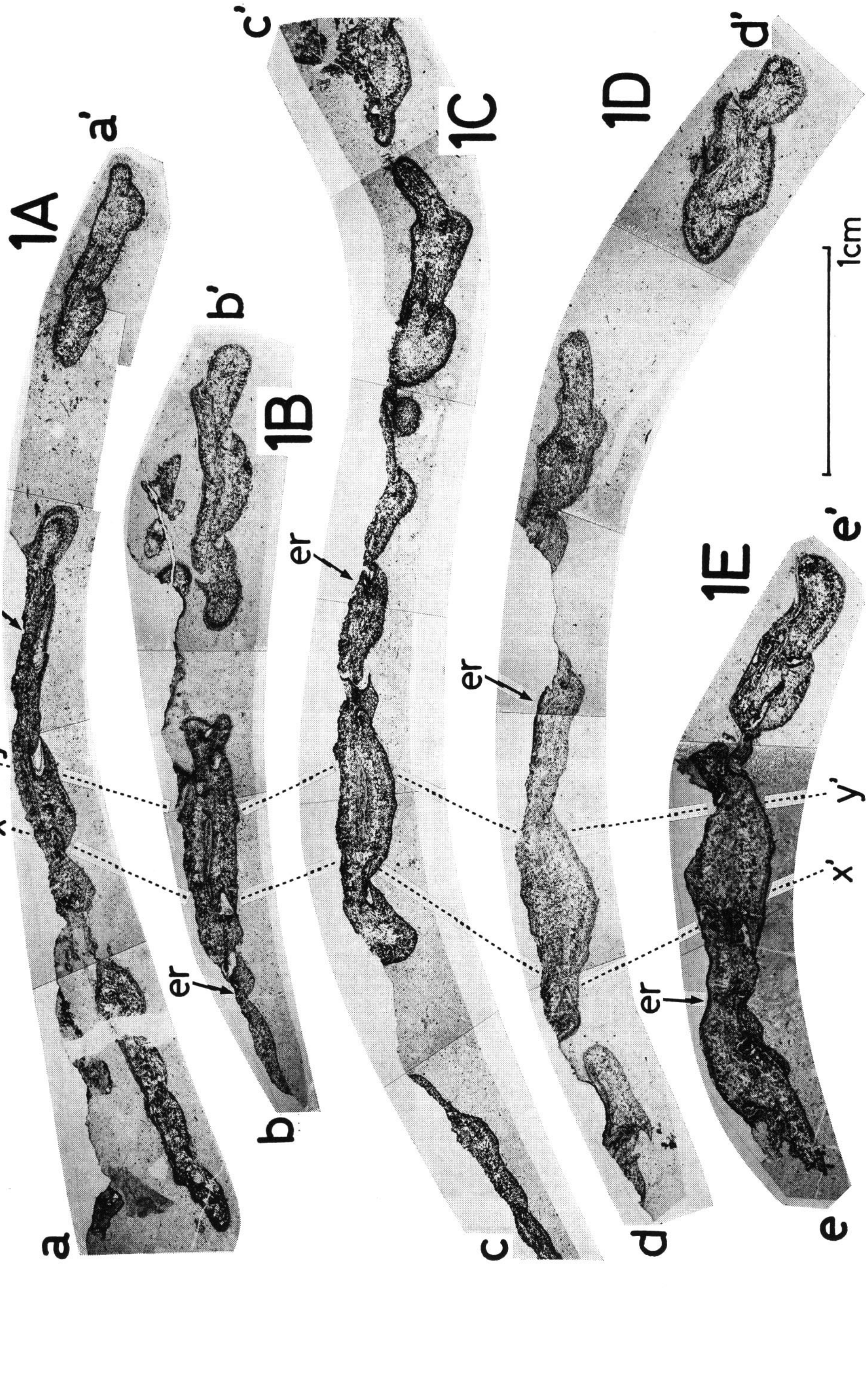
Fig. 1. Stomatal rows tending to converge toward the apex of a free part of leaf (slide no. 103).

Fig. 2. The same as Fig. 1 of this plate, showing rather regularly disposed stomatal rows and ordinary cell files (slide no. 101).

Fig. 3. Enlarged partly from Fig. 1 of this plate. Randomly orientated apertures are seen.

Fig. 4. Further enlarged view of the stomata. In the light microphotograph, a rim of encircling cells and a ring of subsidiary cells are vertically overlapped and subsequently they are seen as a wider loop enclosing the guard cells.

Fig. 5. A transverse section of the penultimate (median) leafy branch (counterpart of Pl. 1–1B). In this figure, palisade cell layer is well developed on the upper side and consists mainly of thin walled tracheids, and its lower side mainly of thick walled tracheids. This feature would suggest that the present flattened leafy branches had a dorsiventral habit. bt; a branch trace.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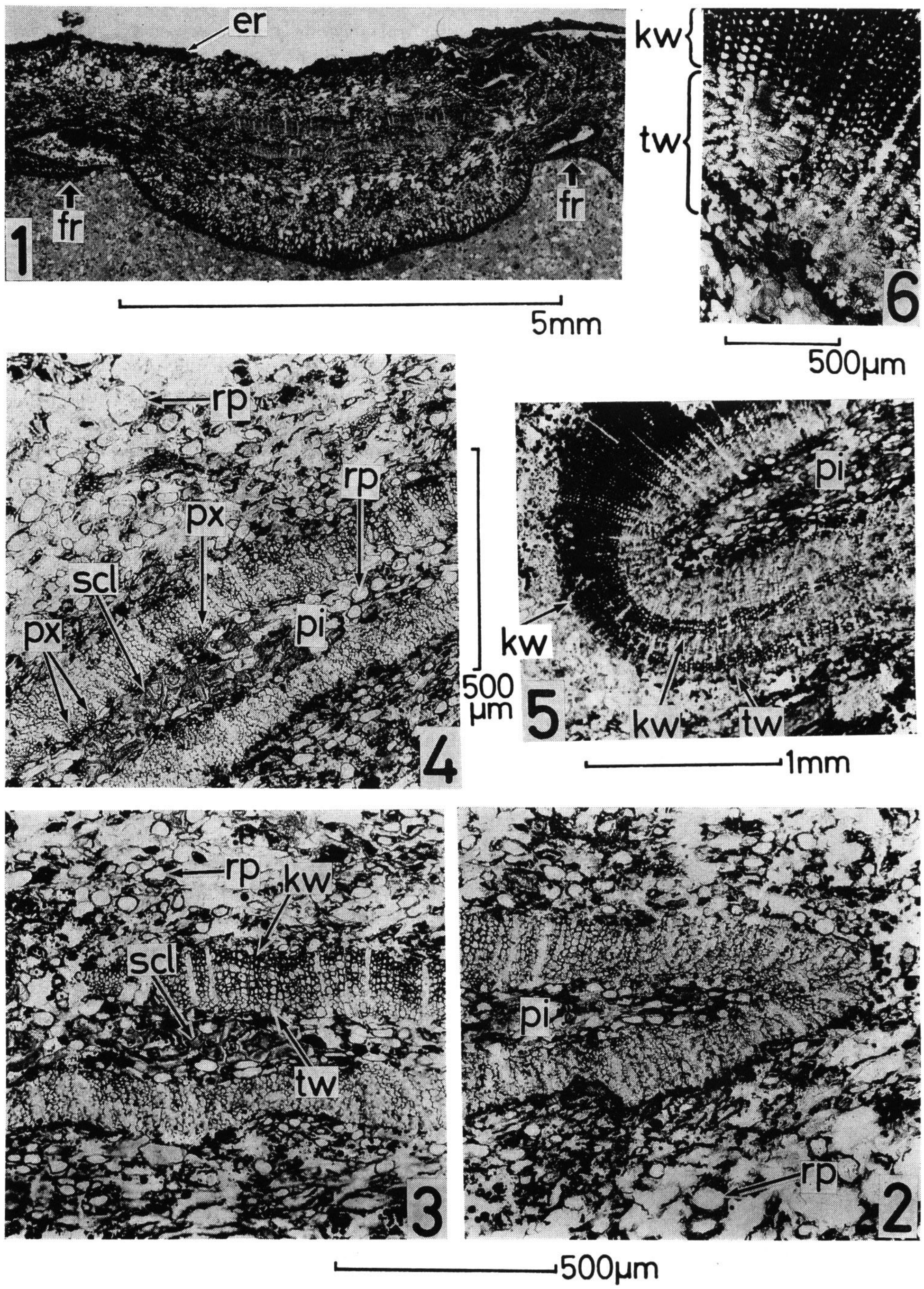
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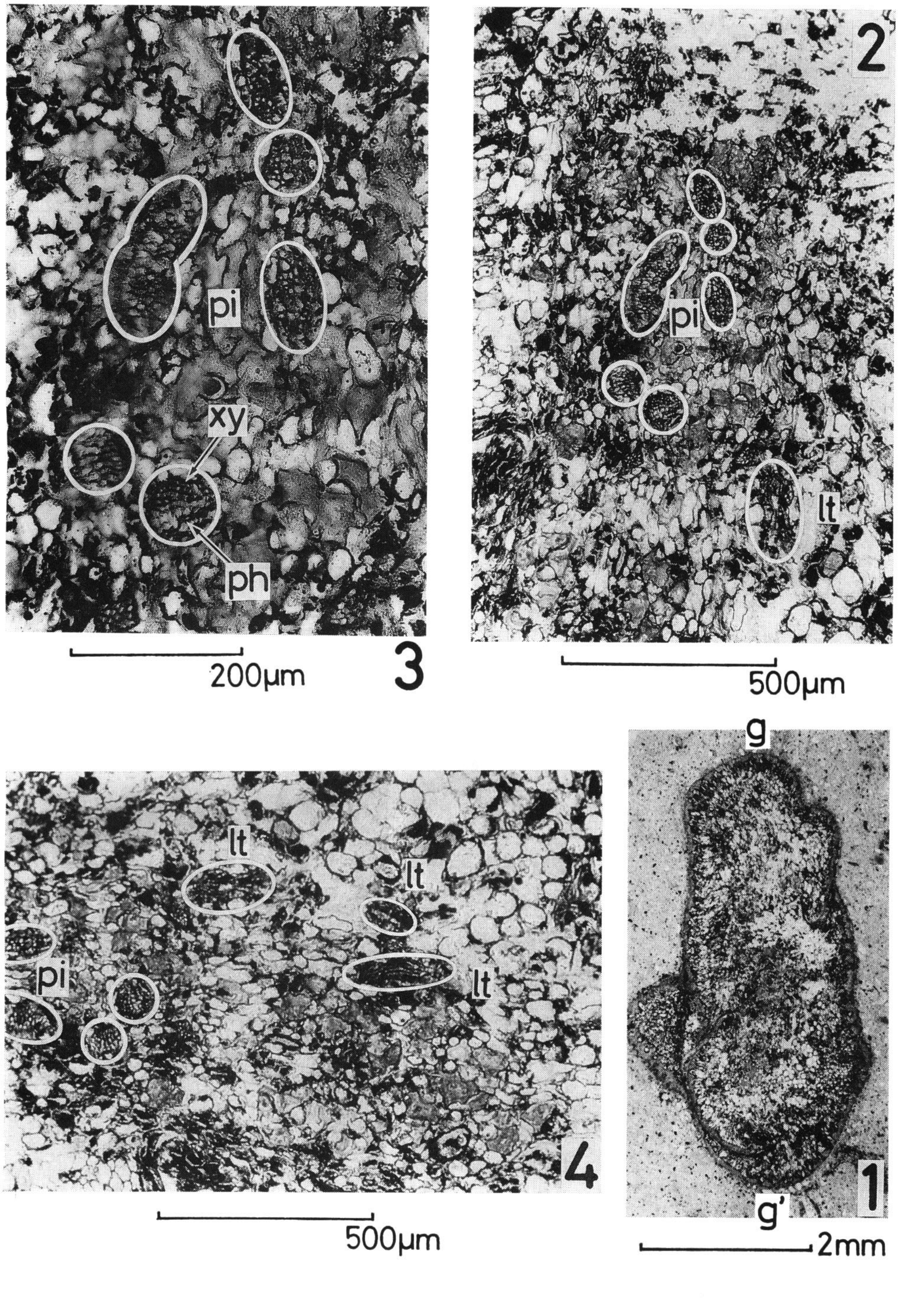
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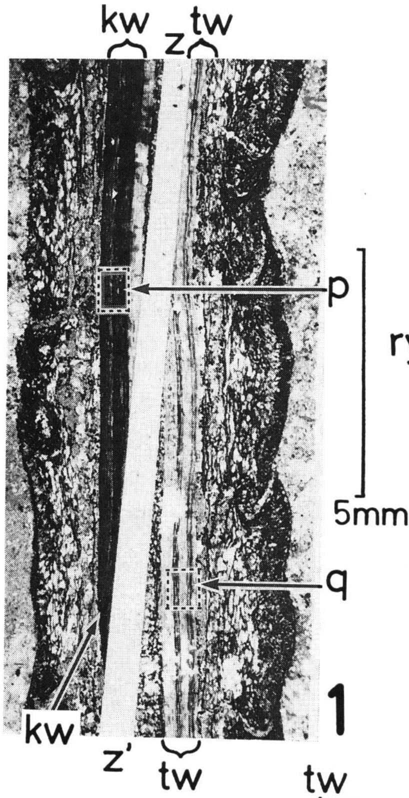
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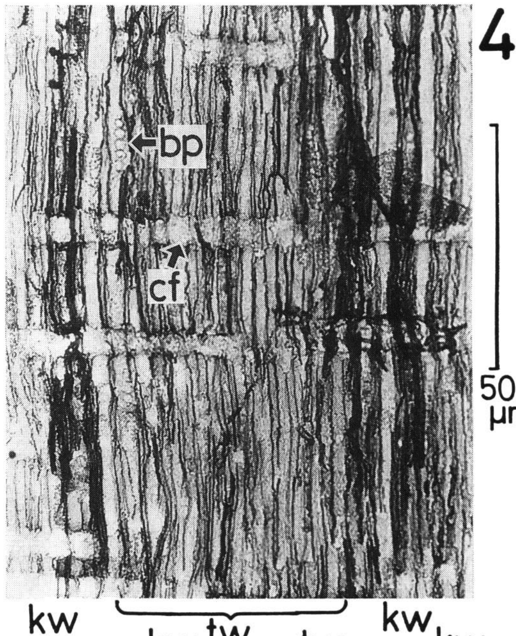
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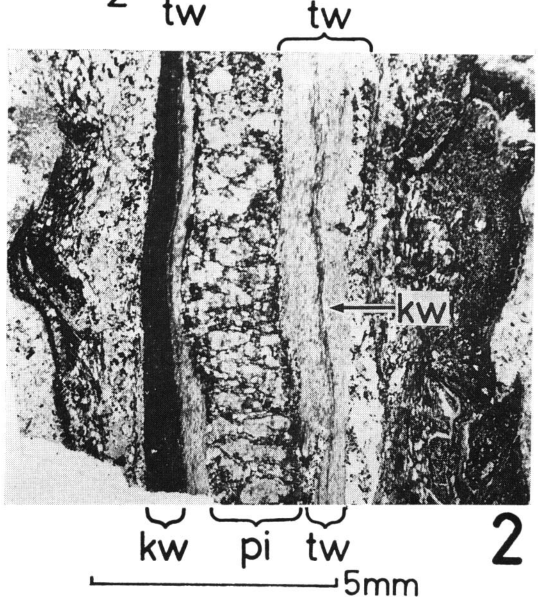
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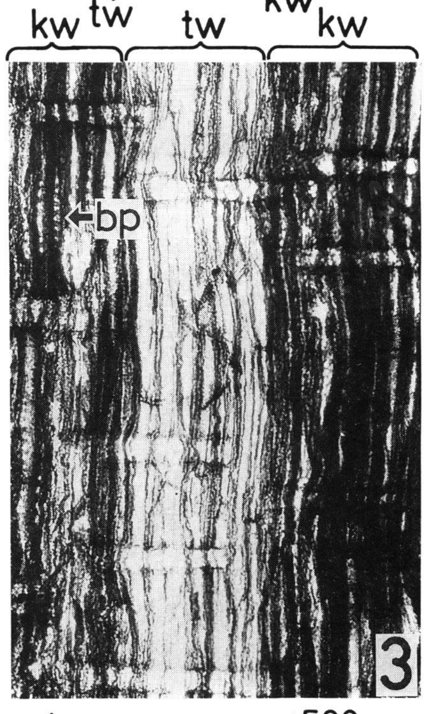
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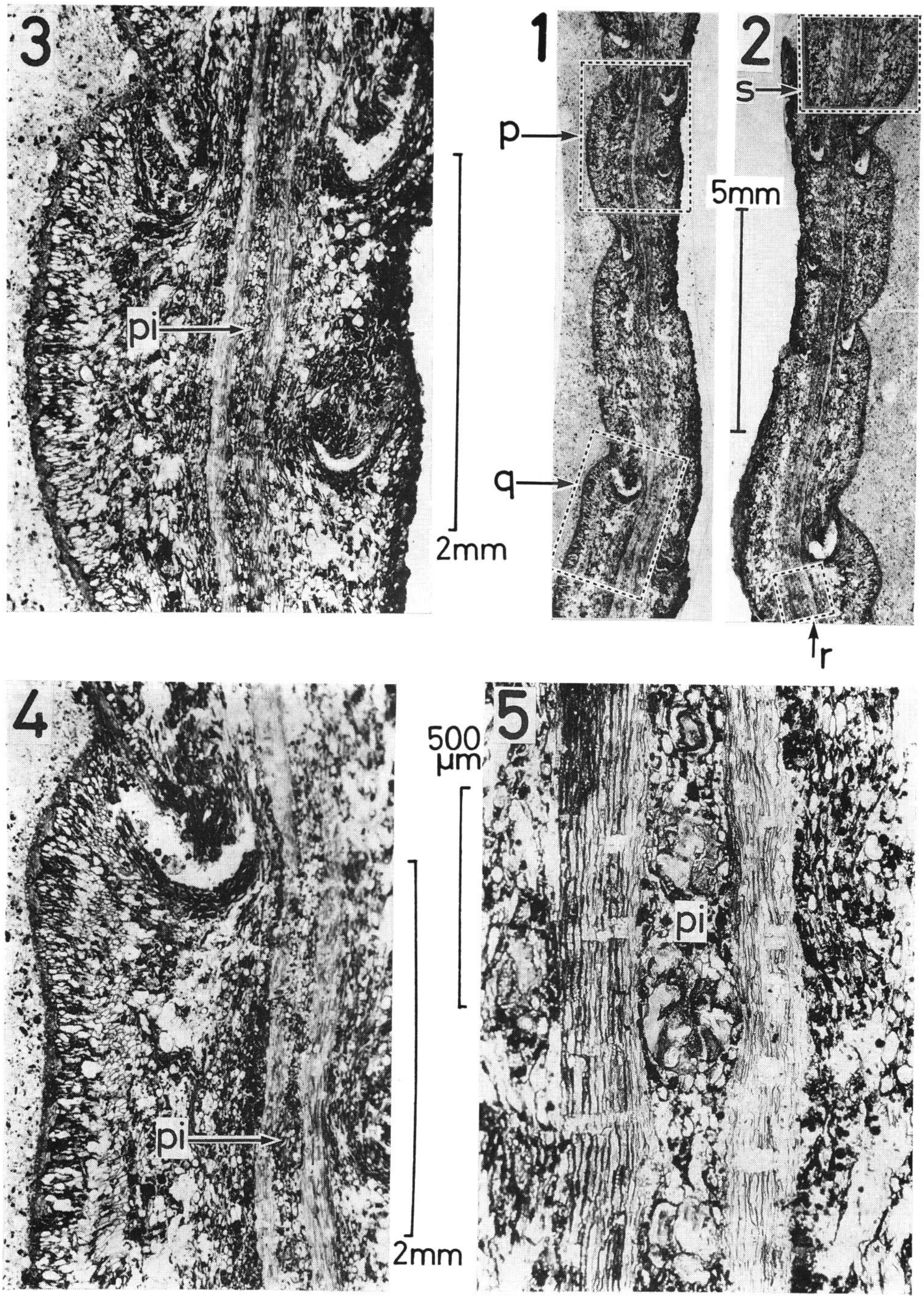
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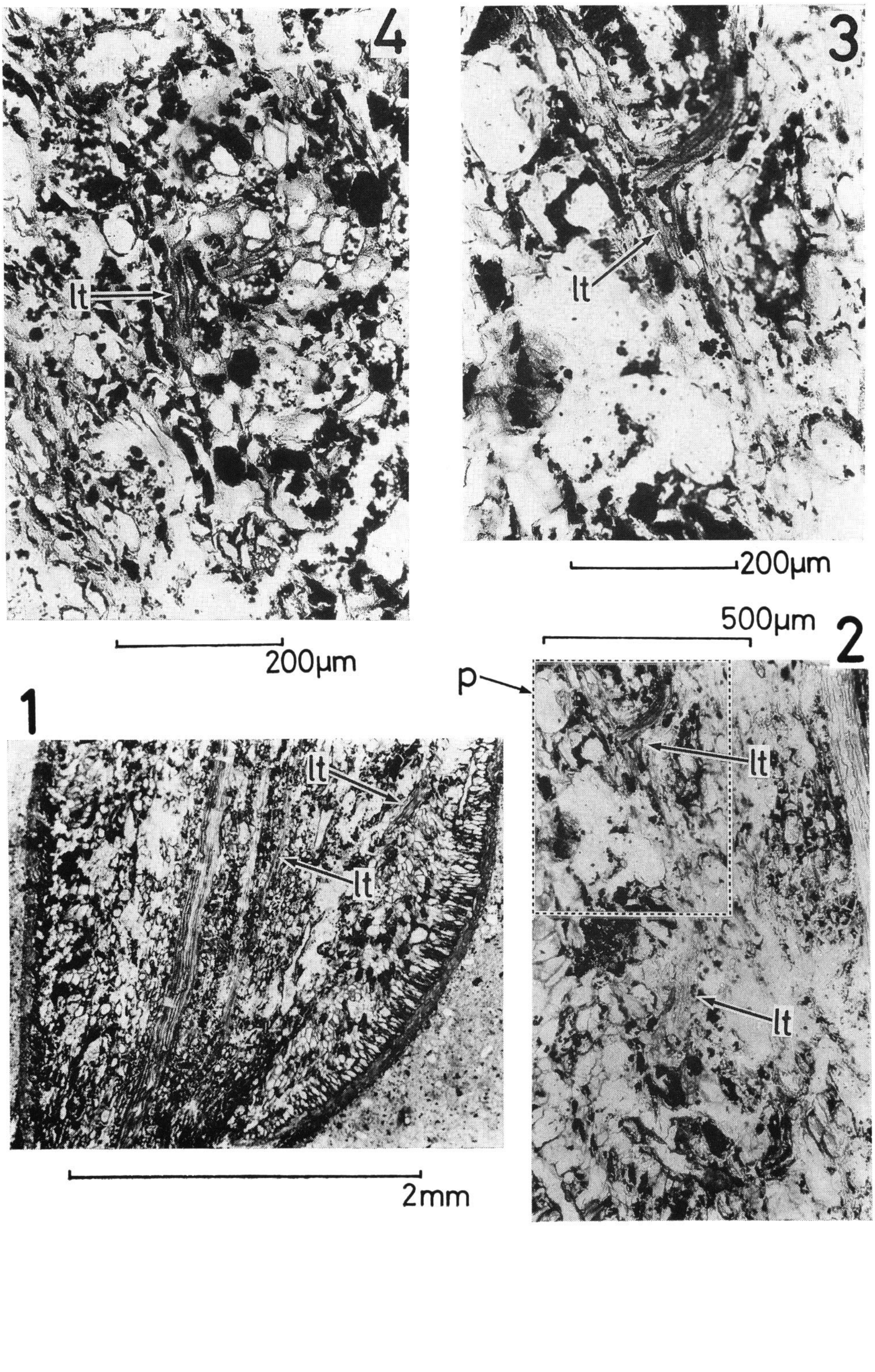
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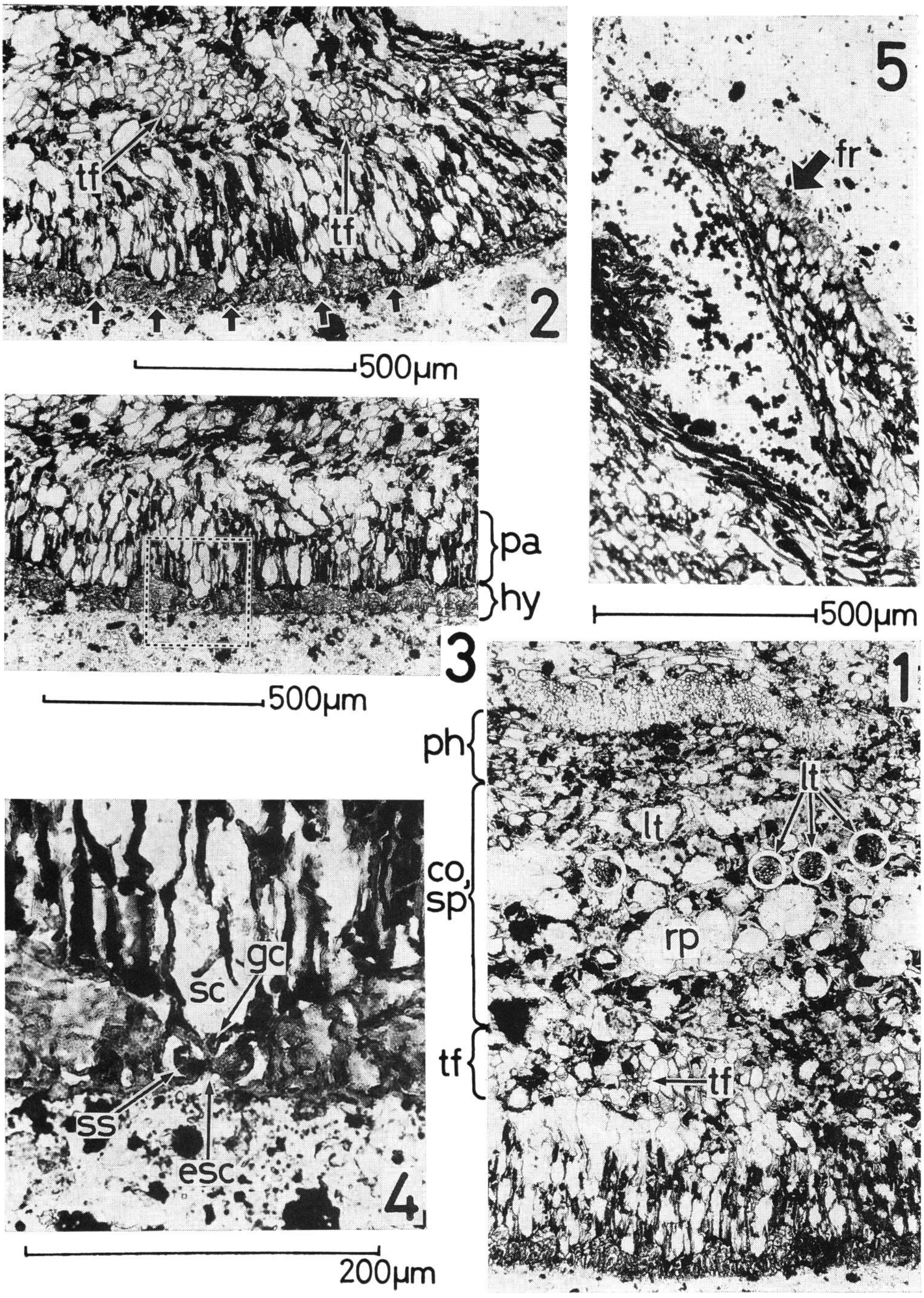
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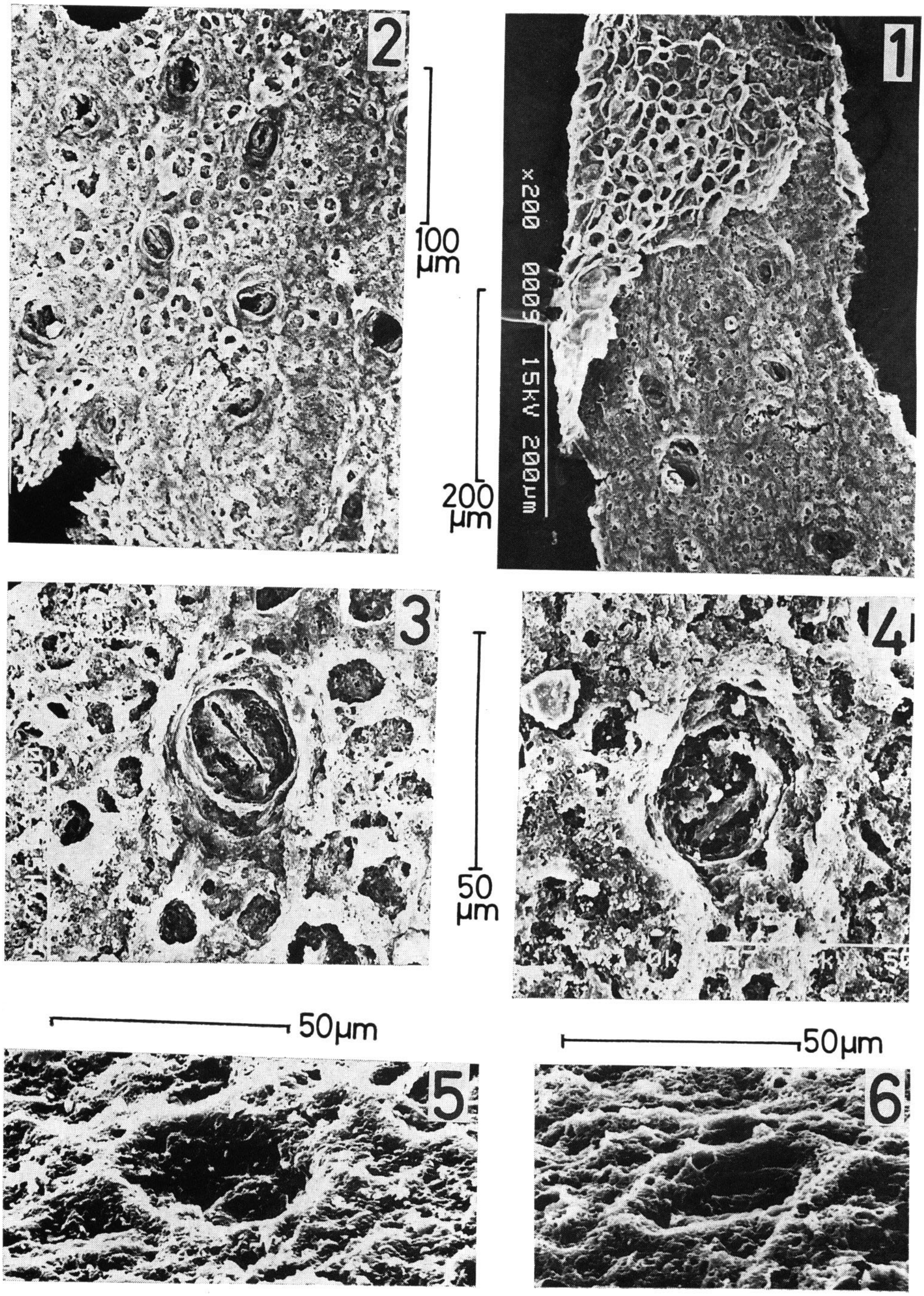
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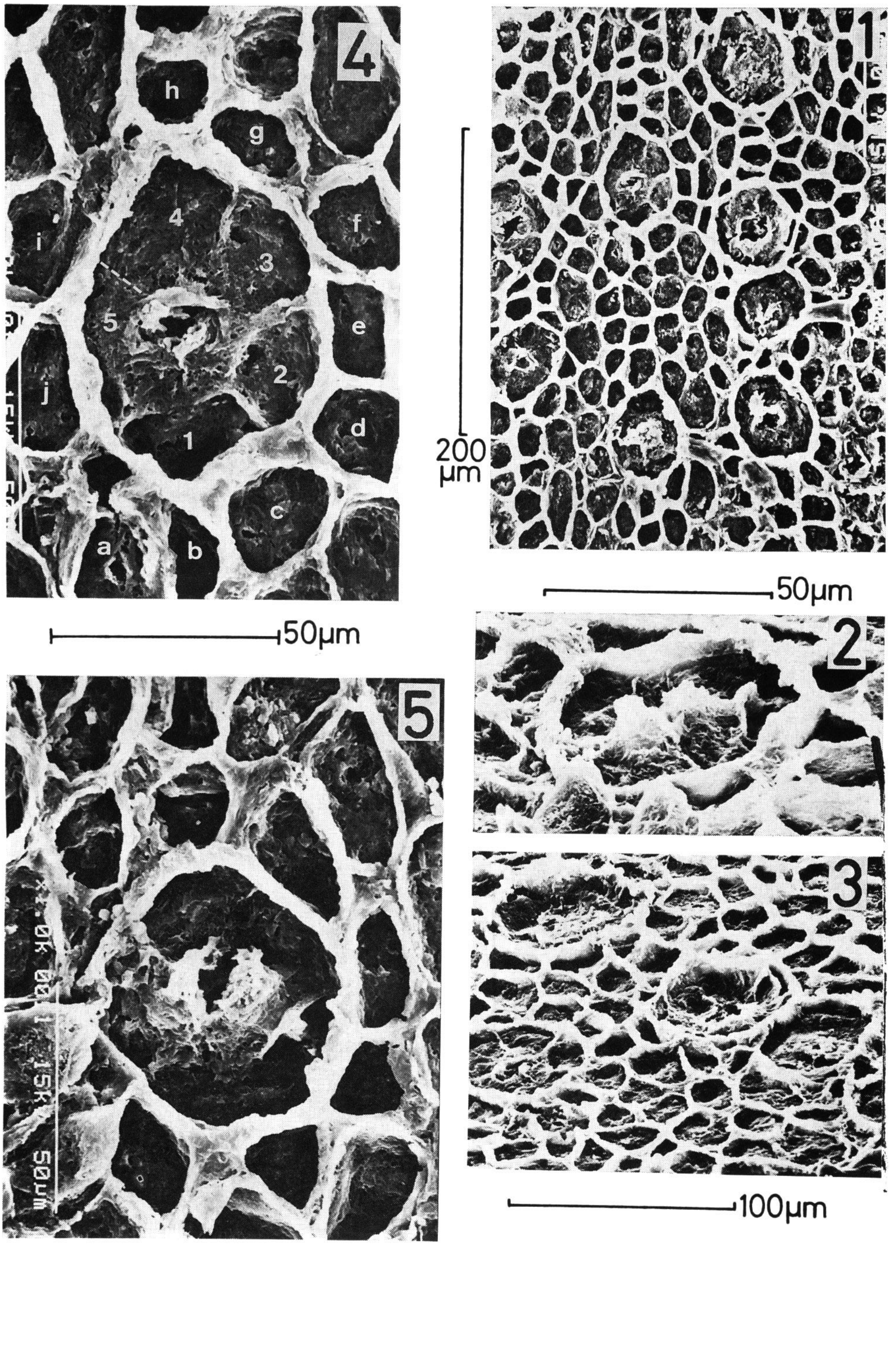
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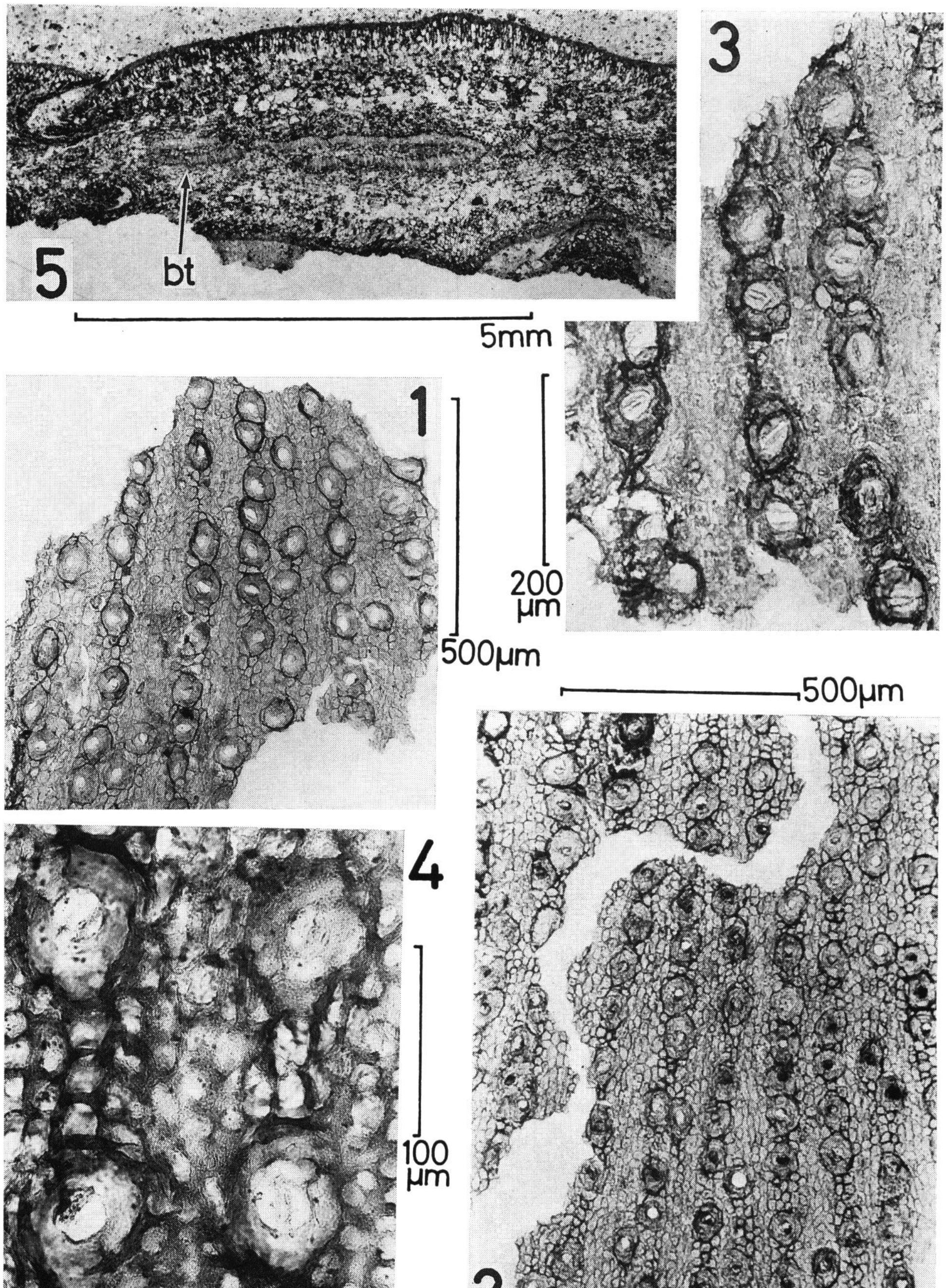
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