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# The conifer *Brachyphyllum squammosum* from the Bohemian Cenomanian

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ABSTRACT. *Brachyphyllum squammosum* (Velenovský) Palibin from the Bohemian Cenomanian (Czech Republic) is revised. New material, represented by conifer twigs, from the locality of Pecínov (60 km west of Prague) is described including the well-preserved micromorphology of its epidermis. Similar *Brachyphyllum* species from the Cretaceous and Jurassic are discussed. A marked similarity was recorded between *B. squammosum* and *B. vulgare* (Stopes & Fujii) Jeffrey from the Upper Cretaceous of Japan. The misinterpretation by Velenovský and Bayer of reproductive structure putatively associated with *B. squammosum* is briefly discussed. The lectotype of *B. squammosum* is designated. The palaeoecological conditions of growth for *B. squammosum* are briefly discussed.

KEY WORDS: *Brachyphyllum,* conifer, Cenomanian, Upper Cretaceous, Czech Republic

## INTRODUCTION

The conifer *Brachyphyllum squammosum* is a rather rare fossil plant of the Bohemian Cenomanian. It was described by Velenovský (1885) from the locality of Vyšehořovice. For a long time this locality was its unique occurrence in the Bohemian Cenomanian. In the seventies of the last century, Němejc and Kvaček (1975) recorded the species from the Santonian of South Bohemia. Finally, in the period between 1993 and 2003, several compressed specimens of *Brachyphyllum squammosum* were recovered in the Pecínov quarry. Although its systematic affinity remains unresolved, the material is interesting for its well-preserved cuticle and overall rarity. Its description and typification is the topic of the following report.

## LOCATION, GEOLOGY AND MATERIAL

The Bohemian Cretaceous Basin, as defined by Čech et al. (1980), located in the Bohemian Massif, the Czech Republic, Central Europe (Fig. 1), is infilled by Upper Cretaceous freshwater, brackish and marine sediments of Cenomanian to Campanian age.

The Peruc-Korycany Formation is situated in the basal most position of the Bohemian Cretaceous Basin. The locality of Vyšehořovice, 30 km east of Prague, comprising several sandstone quarries that were a source of palaeobotanical material for nearly one century, is now completely abandoned and preserved as a Natural monument. The Pecínov quarry, situated 60 km west of Prague, is a working quarry where the entire Peruc-Korycany Formation is exposed. The sedimentary succession in Pecínov was divided by Uličný and Špičáková (1996) into 5 units. Units 1–2 typically include fluvial pebbly sandstones, conglomerates and sandstones with interbedded mudstones. Unit 3 consists of mudstones rich in pyrite concretions. They are the products of marginal marine and brackish sedimentation in back swamps and in supratidal marshes. Unit 4 is represented by cross-bedded sandstones, mudstones and laminites, products of sedimentation on a tidal flat crossed by mean-

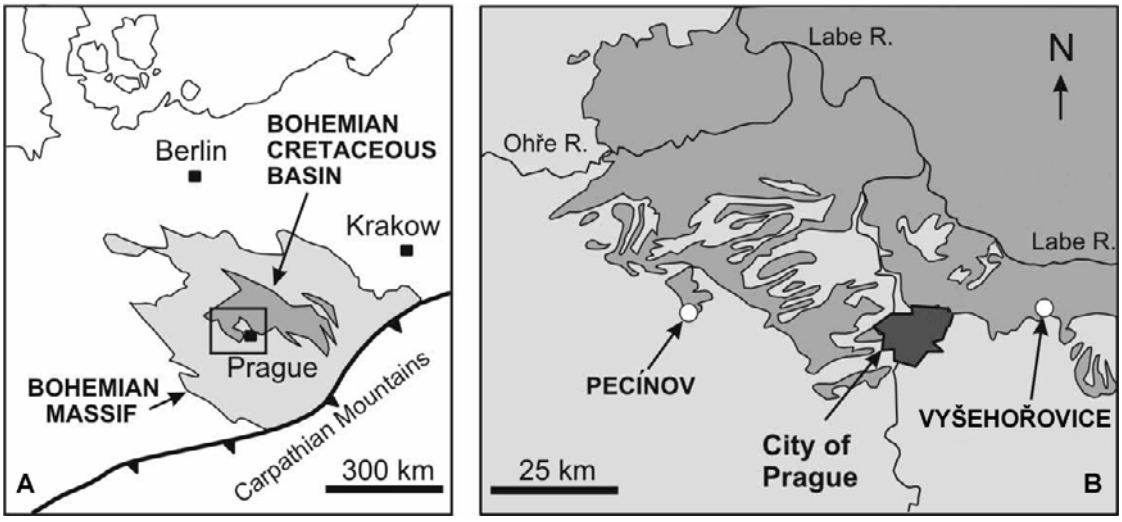


**Fig. 1. A** – Location of the Bohemian Cretaceous Basin in Central Europe; dark grey area indicates the Cretaceous basin, light grey area indicates the Bohemian Massif. **B** – Location of the two fossil sites mentioned in this paper, Czech Republic (after Uličný et al. 1997)

dering tidal creeks. The lower part of unit 5 is built of sandstones containing a rich marine fauna and occasionally preserved stems of tree ferns and poorly preserved leaf impressions. Intertidal to supratidal mudstones bearing a rich megaflora are locally preserved in the uppermost part of unit 5 (Uličný et al. 1997), and reflect local regression. Detailed biostratigraphical studies based on pollen spectra (Pacltová 1977) date the Peruc – Korycany Formation to the upper part of the middle Cenomanian.

## METHODS

Pieces of carbonised material were carefully picked from twig compressions with a preparation needle and treated for cuticle analysis. Carbonized material obtained by needle sampling was cleaned by treatment in HF. After cleaning, it was ready for a bleaching procedure that included maceration with Schulze's reagent: $HNO_3$ + $KClO_3$, neutralisation in water, and treatment in a low concentration solution of KOH, which was used for washing out the oxidized coal matter. The time for oxidation was about 15 minutes. After chemical treatment, cuticles were washed in water in Petri dishes. Some preparations were stained by a 2% safranine solution in water. Cuticles for light microscopy were embedded in glycerine framed by Noyere framing cement. Usually, preparations with needles under a binocular microscope were necessary to separate lower (abaxial) and upper (adaxial) cuticles and to adjust them properly on the preparation glass before covering. In this phase of the work, resin bodies and other remains of mesophyllous tissues were isolated and removed.

Cuticles prepared for SEM observations were treated in the same way in the Schulze's reagent, and then were washed in distilled water. Before drying, cuticles were removed in a drop of distilled water on an emulsion surface of pieces of glossy negative film. The small sheets were air-dried and mounted on SEM stubs.

Cuticle preparations were studied by light microscopy using Nomarski DIC (Olympus BX50) and by SEM (Tesla BS340). All studied material is housed in the collections of the National Museum, Prague.

## SYSTEMATICS

### Genus: ***Brachyphyllum*** Brongniart 1828

1825 *Thuites* Sternberg, p. 38 [pro parte].
1870 *Echinostrobus* Schimper, p. 331.

T y p e. 1828 *Brachyphyllum mamillare* Brongniart, p. 109.

The form genus, which I understand in the sense of the emendations by Kendall (1947) and Harris (1969), is characterized by coniferous twigs bearing leaves that have along their total length leaf cushions that are shorter than the width of the leaf cushions. Species of this form genus belong to the families Cheirolepidiaceae (Harris 1979, Watson 1988), Araucariaceae (Harris 1979) and Taxodiaceae as pointed out by Clement-Westerhof and Van Konijnenburg-Van Cittert (1991).

### ***Brachyphyllum squammosum*** (Velenovský) Palibin

Pl. 1, figs 1–4, Pl. 2, figs 1–6

B a s i o n y m. *Echinostrobus squammosus* Velenovský 1885, p. 16, pl. 6, figs 3, 6–8.

1889 *Echinostrobus squammosus* Velenovský, (ex parte), p. 9, pl. 1, figs 13, 14, (non figs 16–19); pl. 2, fig. 1, (non fig. 2).
1901 *Echinostrobus squammosus* Velenovský; Bayer in Frič & Bayer, p. 106, text-fig. 61, 1, 2 (non text-fig. 61, 3).
1903 *Echinostrobus squammosus* Velenovský; Bayer in Frič & Bayer, p. 105, text-fig. 61, 1, 2 (non text-fig. 61, 3).
1931 *Echinostrobus squammosus* Velenovský; (ex parte) Velenovský & Viniklář, p. 11 (70), (non pl. 25, figs 2–11).
1937 *Brachyphyllum squammosum* (Velenovský) Palibin, p. 177.
1968 *Echinostrobus squammosus* Velenovský; Němejc, p. 394, pl. 42, fig. 1.
1975 *Brachyphyllum squammosum* (Velenovský) Palibin; Němejc & Kvaček, p. 24, text-figs 3, 4; pl. 3, figs 7–10; pl. 15, figs 1–6.
2000 *Brachyphyllum squammosum* (Velenovský) Palibin; Kvaček & Dilcher, p. 22, pl. 1, fig. 2.

Lectotype. Designated herein, No. NM F 00267, F 00268 (part and counterpart), Velenovský 1885, pl. 6, fig. 3, (herein Pl. 1, fig. 1).

Type locality. Vyšehořovice, 30 km east of Prague.

Type horizon. Peruc Korycany Formation, Cenomanian, Upper Cretaceous.

Emended diagnosis. Leafy twigs, regularly branched in one plane; leaves rhomboidal, helically arranged, scale-like, appressed to the axis, bearing longitudinal grooves abaxially; free leaf tip very short. Branches of the last order short with blunt apex. Adaxial cuticle showing quadrangular or polygonal cells in rows, the cells transversely orientated. Abaxial cuticle bearing longitudinal interchanging stomatal and inter-stomatal rows converging towards the apex. Amphicyclic stomata arranged in rows, orientated transversely or obliquely, rarely longitudinally to the leaf axis. Stomata slightly sunken, surrounded by 4–5(6) subsidiary cells; stomatal apparati with bilobed polar extensions. External leaf surface smooth.

Specimens studied. F 00267, F 00268, F 00649, F 00650, F 00867, F 00868, F 02504, F 02515, F 02516, F 02838, F 02839.

Occurrence. Vyšehořovice, Pecínov quarry, unit 5.

Description. The lectotype, designated herein (Pl. 1, fig. 1), is preserved as an impression. It represents a part of a branched shoot 55 mm long. It is covered by helically arranged rhomboidal scale-like leaves (4 × 4 mm). Its branchlets are short, not exceeding 10 mm.

The most complete twig, although poorly preserved, is specimen F 00649 and its counterpart F 00650. It represents a 140 mm long main axis branched in three orders (Velenovský 1889, pl. 2, fig. 1). The illustration is largely modified and reconstructed.

Specimens known from the Pecínov locality (Kvaček & Dilcher 2000) are leaf compressions showing details of the micromorphology of the cuticle. The best-preserved specimen (F 02504) shows a 100 mm long twig branched in three orders, showing blunt terminal shoots (Pl. 1, fig. 3). Rhomboidal leaves (Pl. 1, fig. 2) are hypostomatic, arranged helically on the twig, and bear delicate grooves on the abaxial side.

The specimen F 02504 provided most of the material for cuticle analysis. Areas of adaxial and abaxial leaf cuticles are uneven. The adaxial cuticle is confined to the narrow area in the apex of the leaf only. It shows quadrangular or polygonal cells (15–35 × 30–65 μm, Pl. 1, fig. 4) in rows and a narrow cuticular crista (120 μm high, Pl. 1, fig. 2). Ordinary epidermal cells in rows are often orientated transversely, but sometimes obliquely or even parallel to the leaf axis with anticlinal walls bent or straight, 1–4 μm thick. The abaxial cuticle shows stomata arranged in rows, which converge towards the leaf apex (Pl. 1, fig. 2). Stomatal rows are quite regular (Pl. 2, fig. 1). The non-stomatal areas are one to four cells wide (Pl. 2, fig. 2). Ordinary cells are elongate to isodiametric (10–25 × 20–65 μm) with straight or bent anticlinal walls. They are arranged in short rows. Stomata are monocyclic or incompletely dicyclic (Pl. 2, figs 2, 3). Their orientation is not stable. In the apical and basal regions of the leaf lamina the stomata are usually orientated obliquely or longitudinally to the leaf margin while transversally in the central part. The stomata are surrounded by 4–5(6) subsidiary cells (20–30 × 30–55 μm) forming a circular stomatal apparatus (60–100 μm in diameter, Pl. 2, figs 3, 4). The remains of guard cells are rarely preserved and form a pore 40–45 μm long (Pl. 2, fig. 3). Sometimes two nodulous polar extensions are preserved projecting through the subsidiary cells (Pl. 2, fig. 3). SEM study of the outer abaxial surface of the leaf has documented a rather smooth surface with numerous perforations

representing stomatal pits (30–35 μm) without any rim (Pl. 2, figs 5, 6).

## DISCUSSION

*Brachyphyllum squammosum* is a unique taxon known thus far only from the Bohemian Cretaceous. Besides the Cenomanian, it was also recorded in the South Bohemian Senonian (Němejc & Kvaček 1975). This material, from the locality of Řídká Blana, agrees in macromorphology with the type material and also with the material from Pecínov, including the presence of hypostomatic leaves. It differs slightly in cuticle structure. Stomata of the Cenomanian specimens are not as strictly transversely orientated to the leaf margin. This character is considered here as an intraspecific variation. *Brachyphyllum squammosum* described from the Campanian of North Carolina (Raubeson & Gensel 1991) is very similar in macromorphology, but differs slightly from *B. squammosum* of the Czech Republic in cuticle pattern, having a lower density and strictly perpendicular orientation of stomata in rows.

*Echinostrobus minor* described by Velenovský (1889), is a fragment of a conifer twig impression of *Brachyphyllum* type. Its leaves are much smaller, showing pointed apices. It probably represents a different taxon. Without information about its cuticle, comparison with *B. squammosum* is difficult.

Most of the Cretaceous species of *Brachyphyllum* are preserved as leaf impressions or their cuticles have not yet been studied: *B. obesiforme* Saporta, *B. confusum* Saporta (Cretaceous of Portugal, Teixeira 1948), *B. crassicaule* Fontaine, (US Cretaceous, Potomac F., Fontaine 1889), *B. crassum* Lesquereux = *B. macrocarpum* Newberry nom. inval. (US Cretaceous, Dakota F., Lesquereux 1892), *B. araxenum* Palibin (Cretaceous of Dalaragez, Armenia, Palibin 1937). *Brachyphyllum* sp. from the Cretaceous of Aachen (Stockmans 1946), is very similar to *B. squammosum* in macromorphology (as far as it is possible to recognize from the simplified illustration), but it is an impression specimen. Ohana and Kimura (1993) described material labelled as *Brachyphyllum vulgare* (Stopes & Fujii) Jeffrey from the Upper Cretaceous of Japan. It agrees in many characters with *B. squammosum*, particularly in having hypostomatic leaves and stomata in rows. It differs from *B. squammosum* in the presence of the free part of the leaf tip, which is well pronounced. It is also better preserved – petrified, showing a flattened wood cylinder. Kunzmann et al. (2004) described *Brachyphyllum obesum* Heer sensu Duarte from the Early Cretaceous of the Crato Formation in Brazil, which is also similar to *B. squammosum*. It has a similar cuticle pattern showing stomata in rows, but its leaves are amphistomatic.

*Brachyphyllum* sp. 2 from the Maastrichtian of the Netherlands (Kunrade Region, van der Ham & van Konijnenburg-van Cittert 2003), differs from *B. squammosum* in having amphistomatic leaves and stomata randomly distributed only locally arranged in rows. *Brachyphyllum patens* (Miquel) van der Ham et al. from the Maastrichtian of the Netherlands and Belgium differs from *B. squammosum* in having amphistomatic leaves and randomly oriented stomata (van der Ham et al. 2003). *Brachyphyllum punctatum* Miquel from the English and German Wealden differs from *B. squammosum* in having a thick cuticle with stomata on the abaxial side that are deeply sunken in stomatal tubes (Watson et al. 1987, 1988). *Brachyphyllum tigrense* Traverso (1966) from the Lower Cretaceous of Argentina differs from *B. squammosum* in having stomata irregularly distributed.

Cuticles of Jurassic members of the genus (e.g., *B. mamillare* Lindley & Hutton, *B. crucis* Kendall, *B. ardenicum* Harris) published by Kendall (1947), Harris (1979) and Orlovskaya (1971 – *B. mamillareforme* Orlovskaja) differ from *B. squammosum* in having amphistomatic leaves with stomata distributed irregularly or in short or irregular rows. Within Jurassic species, the macromorphology of *B. squammosum* resembles most *B. mamillare* associated with *Araucaria philipsii* (Carruthers) Schimper (Harris 1979).

The arrangement of stomata (orientated transversely to the leaf margin) of *Brachyphyllum squammosum* is more similar to the genus *Agathis,* particularly in the presence of stomatal polar extensions. However, Velenovský and Viniklář (1931) state that sterile twigs of *Brachyphyllum squammosum* were found attached to taxodiaceous cones at the locality of Jevíčko. Unfortunately, their material was not figured and was not available for the present study. At present there is no

clear evidence for the taxodiaceous affinity of *Brachyphyllum squammosum*. On the other hand, there is no robust support for its affinities with the family Araucariaceae.

In association with sterile foliage of *Brachyphyllum squammosum*, Velenovský (1885) described a cone-like reproductive structure consisting of bilobed "scales". The structure was classified by Bayer (1914) as *Strobilostrobus* nom. nud. and by Velenovský and Viniklář as *Diplostrobus stupeckyanus* Velenovský & Viniklář (1931). Although in both later publications the authors realised the independent status of a sterile twig (*B. squammosum*) and the reproductive structure, the problem of the systematic affinity of the reproductive organ consisting of bilobed structures remained unresolved. In both cases Bayer (1914) and Velenovský and Viniklář (1931) interpreted the structure as a problematical conifer cone. However, new studies (Eklund & Kvaček 1998, J. Kvaček unpublished data) indicate that *Diplostrobus* is an angiosperm inflorescence. As in the case of *Mauldinia* (Lauraceae), the bilobed structures of *Diplostrobus* probably represent cladodia of an inflorescence of a lauroid angiosperm.

Ecological remarks. *Brachyphyllum squammosum* (Velenovský) Palibin is typically found as small fragments. In Pecínov it occurs in a *Sphenolepis* assemblage together with *Sphenolepis pecinovensis* (Kvaček 1997) and *Cunninghamites lignitum* (Kvaček 2000). The presence of other mesophyte taxa (Gnetales, *Nilssoniopteris pecinovensis* Kvaček 1995) and its habit suggest that *Brachyphyllum squammosum* was probably a member of "upland" vegetation.

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# PLATES

Plate 1

*Brachyphyllum squammosum* (Velenovský) Palibin

1. Lectotype, shoot, × 2, Vyšehořovice; F 267
2. LM of apical part of leaf, × 40, Pecínov; F 2504b
3. Branched shoot, × 1, Pecínov; F 2504
4. LM of adaxial cuticle, × 200, Pecínov; F 2504c

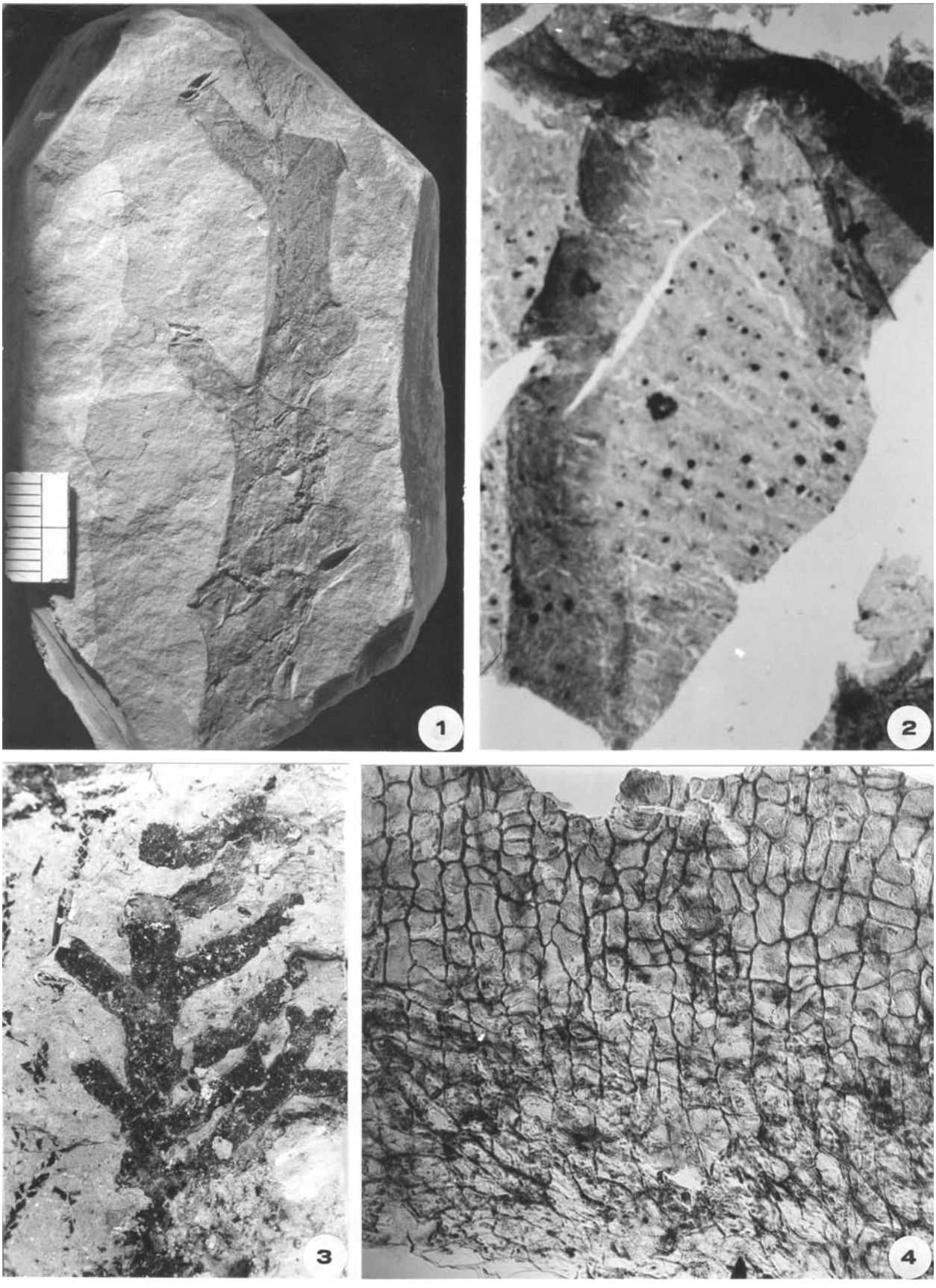
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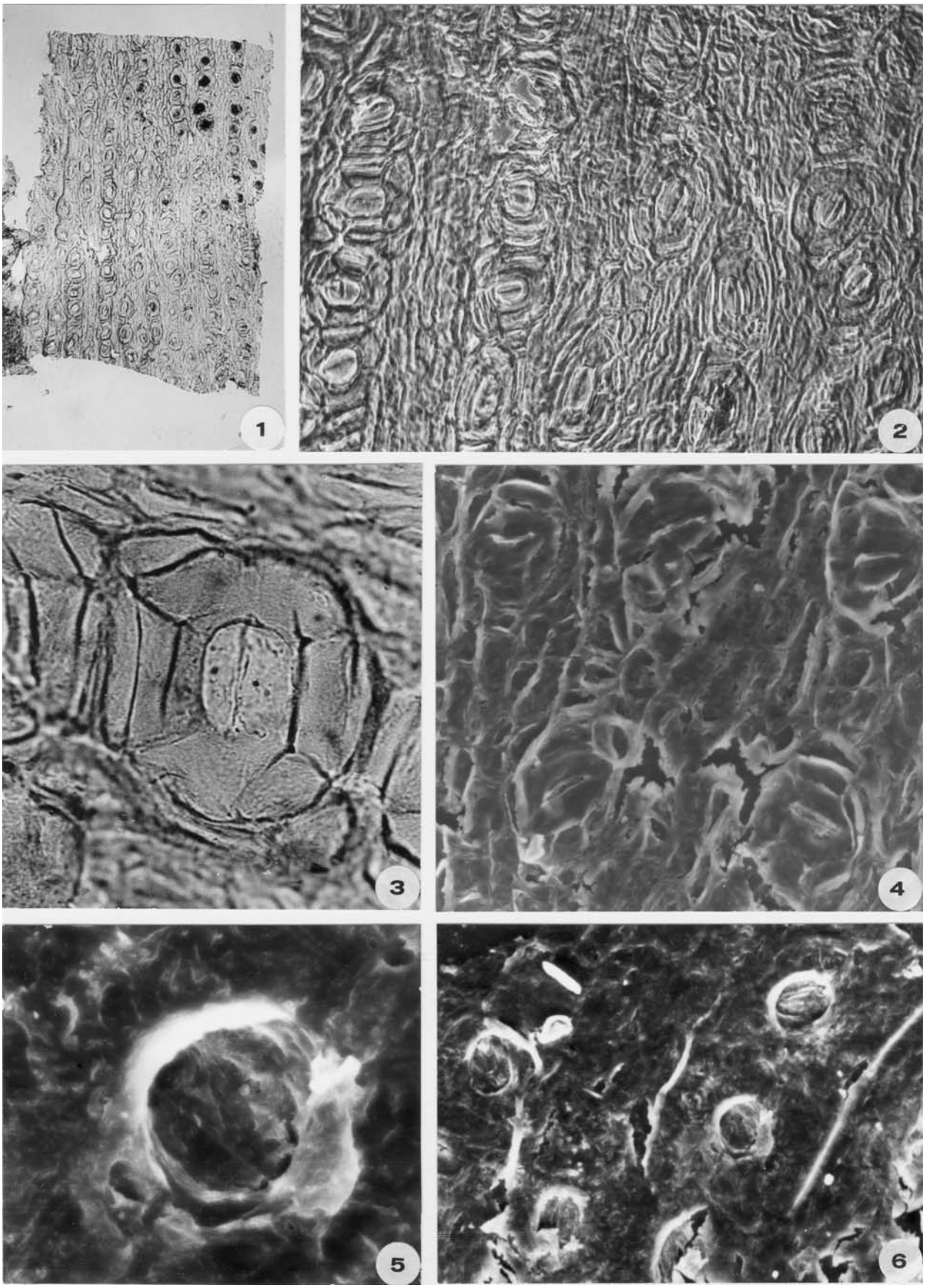
Plate 2

*Brachyphyllum squammosum* (Velenovský) Palibin

1. LM of abaxial cuticle, × 40, Pecínov; F 2504b
2. LM of abaxial cuticle, × 200, Pecínov; F 2504c,
3. LM of abaxial cuticle, stoma, × 900, Pecínov; F 2504c
4. SEM of abaxial cuticle, inner surface, × 300, Pecínov; F 2504d (7457)
5. SEM of abaxial cuticle, outer surface, stoma, × 1000, Pecínov; F 2504d (7480)
6. SEM of abaxial cuticle, outer surface, stomatal rows, × 300, Pecínov; F 2504d (7477)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