Acta Palaeobot. Suppl. 2: 129–151, 1999 — Proceedings 5th EPPC

TWO CONIFERS (TAXODIACEAE) OF THE BOHEMIAN CENOMANIAN (CZECH REPUBLIC, CENTRAL EUROPE)

JIŘÍ KVAČEK

National Museum, Prague, Department of Palaeontology, Václavské nám. 68, 115 79, Prague, Czech Republic; e-mail: jiri.kvacek@nm.cz

ABSTRACT. Two most frequent Taxodiaceous conifers *Quasisequoia crispa* (Velenovský) comb. n. and *Cunninghamites lignitum* (Sternberg) comb. n. of the Bohemian Cenomanian are revised and described on the basis of their leaf cuticles and ovuliferous cones. The definition of the genus *Cunninghamites* Presl in Sternberg is emended. The description of *Quasisequoia crispa* is enlarged basing on numerous foliage shoots and several cones and cone scales. Its sterile foliage consists of compressions of *Pagiophyllum*-like amphistomatic leaves arranged in helix. Impressions, compressions and three-dimensionally preserved specimens of ovuliferous cones consist of about 30 helically arranged cone scales. Each cone scale bears seeds probably in two rows. *Cunninghamites lignitum* is nomenclaturally revised. Its definition is emended basing on numerous foliage shoots and several ovuliferous cones. Sterile leaves are acicular, flattened, amphistomatic and helically arranged. Its ovuliferous cones are preserved three dimensionally as compressions, or impressions. They consist of helically arranged peltate cone scales, each bearing four seeds.

KEY WORDS: Conifers, Taxodiaceae, *Quasisequoia, Cunninghamites,* Cretaceous, Cenomanian

INTRODUCTION

Numerous conifers belonging to Taxodiaceae appeared during the Late Cretaceous reflecting high diversification of this family (e.g. Srinivasan & Friis 1989). Members of Taxodiaceae occurring in the Peruc-Korycany Formation of Cenomanian age were described e.g. by Velenovský (1885, 1887, 1888, 1889), Mařík (1901), Bayer (1914, 1920), Velenovský and Viniklář (1926, 1931), Kvaček (1997, 1998), Knobloch (in press), and their seeds were examined and published by Knobloch & Mai (1984, 1986).

In this article, two members of Taxodiaceae are described on the basis of their sterile leafy twigs and fertile parts: ovuliferous and pollen cones and cone scales. They are assigned to the genera *Cunninghamites* and *Quasisequoia*. At least one specimen with an ovuliferous cone found attached to a sterile leafy twig has been found in each taxon. The studied material is mostly coalified and compressed, and there are also impressions and charcoalified specimens available. The genus *Quasisequoia* was described from the Senonian of Sweden (Srinivasan & Friis 1989). *Cunninghamites* is based on the lectotype material from the Cenomanian of Saxony, Germany (Presl in Sternberg 1838, Kvaček & Straková 1997).

Localities, from which the studied specimens have been recovered, belong to the Peruc-Korycany Formation of the Bohemian Cretaceous Basin as defined by Čech *et al*. (1980). Palynological studies indicate a late middle Cenomanian age of this formation (Pacltová 1977). These deposits are a product of continental/marine sedimentation and show a change in palaeoenvironment from fluvial, sea-influenced to marine conditions (Uličný *et al*. 1997).

MATERIAL AND METHODS

Fossil material has been newly collected at the localities Pecínov, Praha – Hloubětín-Hutě and Horoušany – Kamenná Panna in the central Bohemia. Collections of the National Museum, Prague were used for the study of historical specimens from old localities Praha – Hloubětín (abandoned excavation), Lidice, Mšené (Bohemia) and Niederschöna (Saxony). Material newly collected during the years 1990–1996 consists of compressions, sometimes charcoalified or fusainized. The material has been compared to earlier collections housed in the National Museum, Prague, particularly to the type material of *Lycopodiolites lignitum* Sternberg and *Sequoia crispa* Velenovský represented by impressions.

The specimens were mostly studied directly on slabs of sediment. A part of well preserved hand-specimens were dissolved in HF or H_2O_2 in order to isolate coalified fossil remains. After this treatment the fossils were washed in water and carefully picked up manually. Some of them were dried and prepared for SEM studies, others were stored in glycerine in boxes or on preparation glasses and covered by plastic film. Cuticle preparations were made from both types of specimens, i.e. hand specimens and bulk-macerated remains using standard technique: Schulze´s solution followed by rising in water and KOH.

The material was observed and documented by Tesla SEM and Olympus BX light microscope in the National Museum, Prague. All specimens and preparations are deposited in the palaeobotanical collections of the National Museum, Prague (NM). Material

for comparison was studied from the collections of the Naturhistoriska riksmuseet, Stockholm (NRS), and Staatliches Museum für Mineralogie und Geologie, Dresden (MMG) and Charles University, Faculty of Science (PŘFUK).

SYSTEMATIC PART

Quasisequoia Srinivasan et Friis 1989: 8

Type species. *Quasisequoia florinii* Srinivasan et Friis 1989: 9, pl. 1, fig. 1 (No. S100193 coll. NRS)

The genus *Quasisequoia* was established by Srinivasan & Friis (1989) on the basis of fossil shoots, ovuliferous cones and seeds from the Senonian of Scania, Sweden (type locality Ĺsen). The conifer described below matches well with the type of *Quasisequoia* although the transversal groove mentioned in the discussion of Srinivasan & Friis (1989) is more prominently developed in the material at hand.

Quasisequoia crispa (Velenovský) comb. n.

Pls 1–3

Basionym: *Sequoia crispa* Velenovský 1885, Die Gymnospermen der böhmischen Kreideformation, p. 22, pl. 10, figs 5–7, 9, 14, 16

1885 *Sequoia crispa* Velenovský: 22, pl. 10, figs 5–7, 9, 14, 16
1888 *Sequoia major* Velenovský; Velenovský: 594, Pl. 1, fig. 6 (non figs 4, 5)
1901 *Sequoia crispa* Velenovský; Frič & Bayer: 102, fig. 57
1901 *Sequoia major* Velenovský; Frič & Bayer: 104, fig. 59c, (non figs 59a, b)
1903 *Sequoia crispa* Velenovský; Frič & Bayer: 102, fig. 57
1903 *Sequoia major* Velenovský; Frič & Bayer: 103, fig. 59c, (non figs 59a, b)
1931 *Sequoia crispa* Velenovský; Velenovský & Viniklář: 9, 68, pl. 26, figs 3, 4
1992a *Sequoia major* Velenovský; J. Kvaček: 302, pl. 1, figs 2, 4
1992b *Sequoia major* Velenovský; J. Kvaček: 42

Lectotype. F 262, Velenovský 1885, pl. 10, fig. 5 (selected herein Pl. 1, fig. 1), coll. NM.

Type locality. Lidice (Liditz) near Slaný, central Bohemia, Czech Republic.

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

Emended diagnosis. Shoots of unlimited growth, straight, richly branched, bearing leaves of the *Pagiophyllum* type born in helix; leaves appressed, decurrent, with abaxial surface convex, rounded, sometimes keeled; leaf apex blunt or acute, curved towards stem. Leaves amphistomatic, adaxial cuticle thin showing polygonal or tetragonal, slightly elongate cells. Stomata arranged in two bands reaching usually the apex, monocyclic or amphicyclic (di- to tricyclic) surrounded by 4–6 subsidiary cells. Stomata sunken in deeper or shallower pits, scattered in bands and irregularly orientated (in some rows orientated more transversely, in others with tending to be orientated longitudinally to the leaf margin). Inner subsidiary cells of the tricyclic stomata narrow, more cutinized forming a rim around the stomatal pit. Abaxial cuticle thin, smooth, ordinary cells polygonal, isodiametric, sometimes slightly elongate, anticlinal walls straight; irregularly orientated stomata of the same type as adaxially arranged in two stomatal bands, distributed in groups and frequently lacking in the apical part. Ovuliferous cones rounded or ovoid consisting of up to 30–35 helically arranged, rhomboidal cone-scales; escutcheon narrowly rhomboidal slightly pronounced, with a narrow transverse groove beneath the short tip. Cone scales with papillate inner surfaces, bearing probably two rows of seeds.

Specimens studied: F 260, F 261, F 262, F 263, F 616, F 620, F 622, F 1453, F 1980, F 2029, F 2033, 2035, F 2070, F 2346, F 2457, F 2488, F 2489, F 2496c, F 2522, F 2523a, F 2525, F 2526, F 2527, F 2529, F 2720 – F 2722, F 2874, dispersed material from Praha – Hloubětín-Hutě (numbers prefixed by "HU").

Occurrence. Lidice, Lipenec, Praha – Hloubětín -Hutě.

DESCRIPTION

The lectotype (Pl. 1, fig. 1) suggested herein is represented by a shoot impression (25 mm long) with an attached ovuliferous cone (25 × 20 mm). The shoot bears helically arranged appressed leaves 4–5 mm long. The ovuliferous cone consists of 14 scales preserved only as impressions of rhomboidal escutcheons (8–10 × 4–7 mm) with irregularly ornamented surface and a short leafy tip in the middle. The type material from the localities Lidice and Lipenec shows two other cone impressions (one of them figured on Pl. 1, fig. 2) and three shoot impressions (F 616, F 620, and F 622 figured on Pl. 1, fig. 3). Several attempts to obtain cuticles from the type specimens have failed. Compressed material was recorded in Velenovský´s type locality of *Sequoia major* Praha – Hloubětín (F 1980, F 2529, Pl. 2, fig. 4, Pl. 2, fig. 1) and Praha – Hloubětín-Hutě (F 2029, F 2033, F 2035 (Pl. 1, fig. 5). The most common type of foliage is represented by a large shoot F 2029 (Pl. 1, fig. 5). Leaves are lanceolate, without a sharp keel. They vary from moderately narrow forms with abruptly incurved apices to broader leaves with a gradually incurved apices. The adaxial cuticle shows polygonal to elongate cells (20–30 × 25–40 μm) and two stomatal bands (Pl. 3, fig. 6) reaching the leaf apex. The stomatal apparati are 50–60 μm in diameter (Pl. 2, fig. 6), sunken in circular pits (Pl. 1, fig. 8). They are monocyclic or amphicyclic,

surrounded by 4–5 subsidiary cells (15–25 × 30–50 μm, Pl. 2, fig. 7). They are slightly specialised and more cutinized, forming a rim the around stomatal pit resembling the Florin ring (Pl. 1, fig. 8). Stomata are irregularly orientated. In some places stomatal files are transversely orientated (Pl. 1, fig. 7, Pl. 2, fig. 9, Pl. 3, fig. 6). In others places longitudinally or obliquely orientated stomata with leaf margin occur (Pl. 1, fig. 6). Abaxial cuticle shows nearly isodiametric tetragonal ordinary cells (25–40 × 45–75 μm) in short rows with straight and thin anticlinal walls (Pl. 7, fig. 5, Pl. 3, fig. 6). Stomata are scattered in groups in the basal leaf part (Pl. 2, fig. 4), and seem to be lacking in the medial part and apex (Pl. 3, fig. 6). They are amphicyclic, but smaller, 25–40 μm in diameter, surrounded by 3–5 subsidiary cells. They are shallowly sunken in oval, poorly developed pits (Pl. 2, fig. 3).

The ovuliferous cones from the type locality Lidice (F 260, F 261, F 262, F 263, F 616, F 620, F 622 etc.) are preserved as impressions (Pl. 1, figs 1, 2). Cone compressions come from the locality Praha – Hloubětín-Hutě (F 2720, F 2721). A cone compression born terminally on the shoot (F 2035) is shown on Pl. 1, fig. 4. The ovuliferous cones are ovoid, 20–25 mm long and 20–23 mm wide, attached terminally to the twigs (Pl. 1, figs 1, 2, 4). It is estimated that they consist of 30–35 cone scales. Four detached cone scales (F 2827 – Pl. 3, fig. 1; F 2826 – Pl. 3, figs 2, Pl. 2, fig. 8; F 2829, F 2830) were found in the locality Praha – Hloubětín-Hutě. The cone scales (7–9 × 4–6 mm) have deltoid shape (Pl. 3, fig. 1). Their escutcheons are broadly rhomboidal a with slightly pronounced transverse groove and clearly visible flattened leafy tip (Pl. 3, fig. 2). They show a well-outlined fleshy escutcheon and papillate adaxial and abaxial surfaces (papillae 30–70 μm in diameter). The escutcheon is ornamented with radial wrinkles which meet the margin of the escutcheon at right angles, and is sharply delimited from the scale body (Pl. 3, fig. 2). It bears poorly preserved stomata. The adaxial surface of the scale shows impression of two rows of seeds (Pl. 2, fig. 8, Pl. 3, fig. 1). Although it was searched for seeds none was recovered.

Male cones are terminal and solitary. A pollen cone (No. F 2722) with remnants of sterile foliage of *Quasisequoia crispa* was recovered from among bulk macerated specimens in the locality Praha – Hloubětín-Hutě. The cone is 32 mm × 5 mm and bears helically arranged cone scales with unknown anatomy. The pollen grains in situ are of the *Taxodiaceaepollenites* type, rounded, smooth, 25–35 μm in diameter, sometimes splitting longitudinally.

Discussion: *Quasisequoia crispa* is a well-outlined taxon distinct even in sterile state. Although some minor differences between the syntypes from Lidice and Lipenec exist, e.g. the specimens from Lidice have shorter, densely arranged leaves on shoots, both populations are considered to fall within variation of a single species. Velenovský (1888) later decided to designate a new species *Sequoia major* Velenovský (1888, pl. 1, figs 4–6). He based this species on the material from two localities: Praha – Hloubětín and Kralupy. I consider the syntype material from the Praha – Hloubětín locality (Pl. 2, figs 5, 6) to be identical with *Quasisequoia crispa*. On the other hand, the material from Kralupy, although poorly preserved in sandstone, does differ from *Quasisequoia crispa* in larger cone scales (12–15 × 5–8 mm). The specimens *Sequoia major* from Praha – Hloubětín have the same shape of leaves and the type of sterile twigs as *Quasisequoia crispa*. The recently collected ovuliferous cones from Praha – Hloubětín-Hutě have a very similar escutcheon ornamentation and leafy tips identical with the type material of *Quasisequoia crispa* (compare Pl. 3, fig. 2 and Pl. 1, fig. 1). The syntype of *Sequoia major* (Velenovský 1888, pl. 1, fig 6 – F 1980, F 2529) from Hloubětín is identical in cuticle pattern with *Quasisequoia crispa* from Praha – Hloubětín-Hutě (Pl. 2, fig. 6) and shows stomata surrounded by 4–5 subsidiary cells and polygonal ordinary cells (compare Pl. 2, fig. 6 and Pl. 1, fig. 6). Frequent determinations as *Sequoia major* ? *crispa* ? on old museum labels enclosed to the specimens of shoots from the locality Hloubětín illustrate that also later authors expressed doubts about the proper name for the Hloubětín conifer. An ovuliferous cone (F 2346) from the locality Hloubětín figured as a reconstruction (Velenovský 1888 pl. 1, fig. 5) differs a little from the type in larger size. It is highly probable that it is just a disintegrating cone of *Quasisequoia crispa*.

Quasisequoia crispa is recorded from several localities (Lipenec, Lidice, Praha – Hloubětín, Praha – Hloubětín-Hutě) and occurs probably also at Praha – Vidoule (teste Velenovský 1889). It is similar to some other *Sequoia*-like species of the Bohemian Cenomanian, but none of them have the cuticle preserved. *Sequoia fastigiata* (basionym *Caulerpites fastigiatus* Sternberg 1833, nomen superfluum to *Thuites alienus* Sternberg 1825= *Sequoia aliena* (Sternberg) Knobloch – compare J. Kvaček & Straková 1997), is known from impressions in sandstones (Velenovský 1885, pl. 11, fig. 1). It may be identical with *Quasisequoia crispa* showing only different kind of preservation. The holotype of this taxon from Smečno (Bohemia, Turonian) is missing (Kvaček & Straková 1997). Another specimen from the Sternberg's type collection (F 344) available in the National Museum, Praha is a poorly preserved impression in the Turonian sandy marlstone.

Sequoia affinis Velenovský & Viniklář (1926, pl. 1, figs 6, 7) differs in smaller, straight and sharply pointed leaves. Its type material lacks cuticle.

Sternberg (1825, pl. 46, fig. 2) described an ovuliferous cone impression under the name *Conites familiaris*

from the Turonian of the Bohemian Cretaceous Basin (F 347). It is a cone of taxodiaceous affinity which can be used as an organ genus for Cretaceous taxodiaceous cone impressions. (For inconsistences in aplication of the genus *Conites,* see Kvaček & Straková 1997). On the other hand, details preserved do not allow a precise comparison with the cones of *Quasisequoia crispa*, although agrees in size and approximately the same number of scales per cone.

The type of *Sequoia reichenbachii* (Geinitz) Heer (Geinitz 1842, pl. 24, fig. 4) was not available for this study. As interpreted by Velenovský 1885 (pl. 9, figs 5, 5a, 10, 12–14) it has long leaves (*Geinitzia* – type) quite different from those of *Quasisequoia crispa* .

Sequoia minor Velenovský (1887, pl. 1, figs 11, 13) differs from *Quasisequoia crispa* in much smaller cones and more delicate foliage.

Sequoia heterophylla Velenovský 1885, pl. 12, fig. 12, pl. 13, figs 2–4, 6–9 differs in much longer leaves (*Elatocladus*-type) and in cuticle structure showing monocyclic stomata orientated longitudinally to the leaf margin.

Quasisequoia florinii Srinivasan & Friis (1989, pl. 1, figs 1–8, pl. 7, figs 1–4) from the Upper Cretaceous of Sweden differs from *Quasisequoia crispa* in monocyclic stomata with more (5–7) subsidiary cells and in the absence of adaxial stomatal rows.

The Tertiary *Sequoia couttsiae* Heer = *Athrotaxis couttsiae* (Heer) Gardner (Pingen 1994) differs from *Quasisequoia crispa* in peltate cone scales having escutcheons with radial wrinkles, which reach nearly the centre of the apophysis, and also in a more spiny mucro on the escutcheon.

Protosequoia primaria (Miki 1969) from the Tertiary of Central Honshu (Japan) differs from *Quasisequoia crispa* in smaller cones bearing thick, convex cone scales. Twigs of *P. primaria* bear scale leaves that differ in shape from incurved leaves of *Quasisequoia crispa*. Both genera seem to be similar in general cuticle pattern judging from an indistinct photograph of the cuticle of *P. primaria* (Miki 1969, fig. 1B).

Quasisequoia crispa recalls in epidermal structure the recent *Sequoiadendron giganteum*, which differs from *Quasisequoia crispa* by bicyclic stomata and a well pronounced transversal groove on the ovuliferous cone scale escutcheon (Pl. 9, fig 3, Pl. 7, fig. 1). *Sequoia sempervirens* differs in distichous, flat, acicular leaves and in the presence of the transversal groove on the escutcheon.

Cunninghamites Presl in Sternberg 1838: 203

1926 *Kettneria* Velenovský & Viniklář: 11, 38, pl. 1, figs 12–15, pl. 3, fig. 6

Type species. *Cunninghamites oxycedrus* Presl in Sternberg 1838: 203, pl. 49, figs 1a-b (No. F 642, coll. NM) selected by Kvaček & Straková (1997) – see also Brongniart (1849: 68).

Emended diagnosis. Conifer shoots bearing linear-lanceolate, dorsiventrally flattened leaves with 3 or 5 ribs, helically arranged, diverging from shoot, widest at its basal third. Leaf margin bearing minute irregularly spaced teeth; older branches showing conspicuous leaf cushions. Leaf hypostomatic; leaf cushion bearing isodiametric cells and few stomata, abaxial cuticle showing elongate cells; adaxial cuticle with two stomatal bands bearing monocylic to incompletely dicyclic stomata. Pollen cones of conical shape born singly and terminally on leafy twigs, its surface covered by short imbricate distal ends of microsporophylls. Ovuliferous cone born terminally; mature cone ovoid, bearing helically arranged cone scales, peltate, with hexagonal escutcheon, cone scales bearing up to 4 seeds.

Discussion. The genus *Cunninghamites* differs from *Elatocladus* in the absence of any contraction of the leaf base, in number of ribs (? veins) per needle and in the presence of conspicuous leaf cushions, and from the genus *Geinitzia* in having needles flattened, not quadrangular in cross section. *Cunninghamites* does not represent a typical form-genus used only for sterile coniferous foliage. The lectotype of *C. oxycedrus* shows a terminal pollen cone (Niederschöna, Germany, Cenomanian). The newly included *Lycopodiolites lignitum* Sternberg based on the material from the Bohemian Cenomanian offers additional characters of ovuliferous cones and epidermal structure.

Kräusel (1922) and Velenovský & Viniklář (1926) correctly pointed out that the genus *Cunninghamites* Presl in Sternberg has nothing in common with the genus *Cunninghamia* R. Brown in L.C. Richard, contrary to Corda's (in Reuss 1846) and Velenovský's (1885) views. On the other hand, this fact does not rule out the name *Cunninghamites* from the nomenclatural usage as stated by Kräusel (1922) and Velenovský & Viniklář (1926). Therefore the name *Kettneria* Velenovský & Viniklář 1926 is included into the synonymy of *Cunninghamites* Presl in Sternberg.

Cunninghamites lignitum (Sternberg) comb. n.

Pls 4–6

1825 *Lycopodiolites lignitum* Sternberg, Flora der Vorwelt, vol. I, 4: (tentamen) VIII (Basionym)

?1838 *Cunninghamites oxycedrus* Presl in Sternberg: 203, pl. 48, figs 3a-c, pl. 49, figs 1a-c

?1849 *Cunninghamites oxycedrus* Presl in Sternberg; Brongniart: 68

?1850 *Cunninghamites oxycedrus* Presl in Sternberg; Göppert: 240 pro parte, pl. 47, fig. 2 (non pl. 47, figs 3,4)

1846 *Cunninghamia elegans* Corda in Reuss: 93, pl. 49, figs 29–31

1846 *Cunninghamia planifolia* Corda in Reuss: 93, pl. 50, figs 1–3
1847 *Cunninghamites elegans* (Corda) Endlicher: 201
1885 *Cunninghamia elegans* Corda in Reuss; Velenovský: 14, pl. 4, fig. 5, pl. 5, figs 1, 7, pl. 6, fig. 5
?1880 *Cunninghamites elegans* (Corda) Endlicher; Hosius & Marck: 142, pl. 25, fig. 22
?1880 *Cunninghamites elegans* (Corda) Endlicher var. *densifolus* Hosius & Marck: 178, pl. 37, figs 139–141
?1880 *Cunninghamites elegans* (Corda) Endlicher var. *linearis* Hosius & Marck: 179, pl. 37, fig. 142
?1885 *Cunninghamites elegans* (Corda) Endlicher; Hosius & Marck: 227, pl. 19, figs 1,2
1887 *Cunninghamia elegans* Corda in Reuss; Velenovský 634, figs 1–5
?1896 *Cunninghamia elegans* Corda in Reuss; Kerner: 50, pl. 4, fig. 4
1892 *Cunninghamia elegans* Corda in Reuss; Engelhardt: 89(11)
1901 *Cunninghamia elegans* Corda in Reuss; Frič & Bayer: 97, text-fig. 49
1903 *Cunninghamia elegans* Corda in Reuss; Frič & Bayer: 95, text-fig. 49
?1905 *Cunninghamites elegans* (Corda) Endlicher; Zeiller: 15, pl. 7, fig. 14
1919 *Elatocladus elegans* (Corda) Seward: 433, text-figs 804, 805
?1922 *Elatocladus elegans* (Corda) Seward; Kräusel: 10, pl. 1, figs 4–10, pl. 2, figs 1–5, pl. 3, figs 1, 2, text-figs 4, 5
?1923 *Elatocladus elegans* (Corda) Seward; Kräusel: 147, pl. 5, figs 2,3
1926 *Kettneria elegans* (Corda) Velenovský & Viniklář: 11, 38, pl. 1, figs 12–15, pl. 3, fig. 6
1931 *Kettneria elegans* (Corda) Velenovský & Viniklář; Velenovský & Viniklář: 7, 66, pl. 24, figs 1–3
?1939 *Elatocladus elegans* (Corda) Seward; Hartung: 110, pl. 3, figs 5, 6, pl. 5, figs 1–4, pl. 6, figs 2, 6
?1946 *Geinitzia elegans* (Corda) Stockmans: 15, pl. 2, figs 4, 10, 15, 16
1968 *Kettneria elegans* (Corda) Velenovský & Viniklář; Němejc: 393, pl. 46, fig. 3, text-fig. 299
1971 *Cunninghamites oxycedrus* Presl in Sternberg; Knobloch: 46
1992a *Cunninghamites oxycedrus* Presl in Sternberg; Kvaček: 302
1992b *Cunninghamites oxycedrus* Presl in Sternberg; Kvaček: 42
?1997 *Cunninghamites oxycedrus* Presl in Sternberg; Kvaček & Straková: 116, pl. 39, figs 1,3
1997 *Lycopodiolites lignitum* Sternberg; Kvaček & Straková: 94

Lectotype. F 636, (Sternberg's original No. 316), Sternberg 1825: 8 (tentamen); selected herein – pl. 4, fig. 1a, coll. NM.

Type locality. Mšené ("Msseno") near Litoměřice ("Litomeritz"), central – north Bohemia, Czech Republic.

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

Emended diagnosis: [partly according to Velenovský 1885]. Leafy axes of unlimited growth, straight, branching occasionally; linear-lanceolate, dorsiventrally flattened leaves born in helix, overlapping, bearing three or five ribs, needles at angles 20° to 50° to stem, widest at basal third; apical parts of axes formed by needles overlapping densely to form a bud; leaf margins bearing minute, irregularly placed teeth; older branches showing conspicuous leaf cushions. Leaf hypostomatic; leaf cushion bearing isodiametric cells and few stomata surrounded by 4 subsidiary cells, abaxial cuticle showing elongate cells; adaxial cuticle with two stomatal bands bearing monocylic to incompletely dicyclic stomata surrounded by 4–6 subsidiary cells.

Pollen cone of conical shape born singly at the end of a leafy twig, its surface covered by short, helically arranged, imbricating distal ends of microsporophylls.

Ovuliferous cone born terminally; mature cone ovoid bearing helically arranged cone scales, peltate, each with long stalk and large hexagonal escutcheon with risen spine on umbo, cone scales bearing up to 4 oval, wingless seeds.

Specimens studied: F 249, F 251, F 252, F 627, F 628, F 636, F 640, F 642, F 1455, F 2045, F 2047, F 2068, F 2069, F 2113, F 2277, F 2278a, F 2343b, F 2344, F 2612, F 2613, F 2614, F 2703 – F 2715, F 2718, F 2832 – F 2835.

Occurrence. Praha – Hloubětín, Praha – Hloubětín-Hutě, Praha – Vidoule; Vyšehořovice, Lipenec, Peruc, Mšené-lázně, Lidice, Otruby, Pecínov – quarries Babín north and Babín middle (unit 3, unit 5), Horoušany – Kamenná Panna.

Description. The lectotype (F 636, Sternberg's coll. No. 316) of *Cunninghamites lignitum* (Sternberg) comb. n. selected herein is at the same time also a syntype of *Cunninghamites elegans* Corda in Reuss 1846: 93, pl. 49, fig. 29. It represents a once branched shoot showing a broad axis with helically arranged leaf cushions bearing dorsiventrally flattened leaves (Pl. 4, fig 1a). The main branch is 85 mm long, 10 mm in diameter; branchlet is 130 mm long, 5–6 mm in diameter. Broken leaves on the main axis show three veins. Due to the mode of preservation (see Harris 1979: 58) only a limited number of complete leaves is exposed. Corda (in Reuss 1846) considered them to be single-veined. Leaves are up to 22 mm long on the primary branch and up to 16 mm long on the branchlet. Careful maceration of very tiny pieces of carbonised matter preserved on the type specimen has provided fragments of cuticle obtained from leaf cushion showing thickly cutinized (anticlinal walls 3 μm thick), isodiametric ordinary cells ((15)–20–(25 × (25)–30–(50) μm in size, Pl. 4, fig. 4) and three stomata. Each stoma is surrounded by 4–5 subsidiary cells (25–30 × 30–50 μm, Pl. 4, fig. 3). Another type specimen of C. *lignitum* (Corda in Reuss 1846, pl. 49, fig. 29 above) is situated on the same slab as the lectotype (Pl. 4, fig. 1b – top) and shows a young branch with densely appressed leaf cushions. The attached leaves are incomplete, 1–2 mm wide, the longest 12 mm in length.

The lectotype of *Cunninghamites oxycedrus* Presl in Sternberg represents a leafy shoot (55 mm long) terminated by a pollen cone (Pl. 5, fig. 3). The leaf impression, bears helically arranged needle-like leaves (up to 18 mm long). The leaves are linear lanceolate, widest in the basal third, attached to the basal cushion without forming a distinct petiole, midrib well-pronounced – conspicuous accompanied by 4 ribs (?veins) running parallel to the leaf margin. The pollen cone is 18 × 8 mm in size, conical to ovoid, born singly at the end of the leafy branch. It bears small (2–3 mm long) helically arranged microsporophyls with imbricate distal ends. The only other preserved syntype (F 2612) figured by Presl (in Sternberg 1838) is a branched shoot (impression) bearing helically arranged leaves showing well-preserved 5 ribs (?veins). Another specimen (F 640) from the type locality Niederschöna was figured by Velenovský (1885, pl. 4, fig. 5) under the name *Cunninghamia elegans* Corda in Reuss (Pl. 5, fig. 6). Velenovský incorrectly determined the locality as Peruc (in the publication by Velenovský 1885 and also on the label). The type of sediment, the mode of preservation and the number of Sternberg's collection 331 refer clearly to the locality Niederschöna. There are several other specimens from that locality in the National Museum collection (F 2613, F 2614), one of them also incorrectly labelled as Peruc (F 2703).

Velenovský's study material figured under the name *Cunninghamia elegans* consists of the the above mentioned specimen (F 640) from the locality Niederschöna (Velenovský 1885, pl. 4, fig. 5 and probably its detail pl. 5, fig. 7) and two additional specimens from the locality Vyšehořovice (Velenovský 1885, pl. 5, fig. 1; pl. 6, fig. 5). The specimen F 640 shows the terminal part of a leafy branch bearing helically arranged leaves which are conspicuously ribbed (Pl. 5, fig. 6). The specimens F 627 and F 628 (part and counterpart) show the main axis bearing densely appressed leaf cushions in the helix; branchlets bear several leaves which are slightly ribbed. The specimen F 641 shows a forked leafy branch bearing needles up to 24 mm long and 2 mm wide.

The material studied by Velenovský & Viniklář (1926), which was available in PŘFUK, consists of two sterile twigs (B 61, B 15) and one isolated ovuliferous cone (B 196, Pl. 6, fig. 2). Their leaves are up to 28 mm long, and 1–1.5 mm wide. The oval ovuliferous cone figured by Velenovský & Viniklář (1931, pl. 24, fig. 2) is poorly preserved (35 × 60 mm) showing questionable traces of attached seeds (Pl. 6, fig. 2). Poor preservation does not allow to determine their number. Estimated number of scales exceeds 40 per cone.

Well-preserved compression material was collected from the localities Pecínov, Babín – north (unit 5); Praha – Hloubětín-Hutě and Horoušany-Kamenná Panna. The specimens from the localities Pecínov, Babín – middle (e.g. F 2278a, Pl. 6, fig. 1), Lipenec (F 646, F 652) and some others from Peruc show slightly shorter leaves (10) – 12 – (15) mm long and up to 1 mm wide. The specimens from Pecínov and Praha – Hloubětín-Hutě show hypostomatic leaves bearing small marginal teeth (Pl. 4, fig. 7) 10–15 μm long. Their cuticle is of medium thickness. The adaxial cuticle shows two stomatal bands, each 250 μm broad (Pl. 5, fig. 5) narrowing to the leaf base and apex (120 μm). The bands are separated by an intercostal zone (200–350 μm) showing elongate ordinary cells (5)–10–(20) × (45)–90–(125) μm in size. Stomatal bands consist of quadrangular to polygonal ordinary cells (15)–20–(30) × (25)–30–(50) μm in size (anticlinal walls 4–10 μm thick) and stomata (Pl. 5, fig. 9). These are mostly monocyclic, often incompletely dicyclic or incompletely monocyclic with stomatal axis orientated longitudinally or slightly obliquely to the leaf margin (Pl. 5, figs 5, 9). The guard cells are surrounded by 4–6 subsidiary cells (10)–15–(20) × (30)–40–(60) μm in size. The external surface of the adaxial cuticle is smooth (Pl. 5, fig. 1) showing slightly sunken stomata (Pl. 5, fig. 4). The abaxial cuticle shows elongate cells (8)–15–(20) × (35)–80–(100) μm in size (Pl. 5, fig. 8), with thinner anticlinal walls (1–2 μm thick). Rhomboidal leaf cushions (Pl. 4, figs 5, 6) show different cuticle pattern (Pl. 4, figs 2–4, 6) with isodiametric cells (10)–20–(30) × (10)–25–(40) μm in size, which have thickly cutinized anticlinal walls (3–5 μm thick) with few scattered dicyclic stomata surrounded by 4 subsidiary cells (Pl. 4, figs 3, 6).

The ovuliferous cones of *Cunninghamites lignitum* are ovoid and considerably large (25–35 × 55–65 mm). The best ovuliferous cones for morphological study were collected in the locality Pecínov. Two of them are isolated (F 2706b,c; F 2708a,b, Pl. 6, fig. 3) and two (F 2706a, F 2707) are attached to the leafy branches (Pl. 5, fig. 2). The specimen F 2707 shows a cone consisting of 35–45 cone scales with hexagonal or polygonal, helically arranged escutcheons (6–8 × 8–10 mm). Several cone scales obtained from bulk-maceration, have been prepared for SEM observations. One entirely preserved cone scale F 2834, 7 × 8 mm in size is deltoid in shape and bears a keel and four scars after detached seeds on the adaxial surface (Pl. 5, fig. 7).

Remarks to nomenclature. The species *Lycopodiolites lignitum* Sternberg [=*Cunninghamites lignitum* (Sternberg) comb. n.] was described without any illustration for the first time by Sternberg (1825) from the Bohemian Cenomanian – surroundings of Litoměřice. Later on, Presl (in Sternberg 1838) described another, probably conspecific conifer as *Cunninghamites oxycedrus* Presl in Sternberg from the Cenomanian locality Niederschöna (Saxony, Germany). Corda (in Reuss 1846) obviously

considered *Lycopodiolites lignitum* not adequately described or overlooked its name written on the type-specimen and introduced (on the same type) a new species *Cunninghamia elegans* Corda (in Reuss 1846). This superfluous name *Cunninghamia elegans* was in use for a longer time (see Heer 1883, Kräusel 1922, Hartung 1939). Knobloch (1971) included *Cunninghamia elegans* into the synonymy of *Cunninghamites oxycedrus* and than this name prevailed in usage (Kvaček 1992a,b, 1998, Knobloch 1999). Morphological differences in foliage of *Cunninghamites oxycedrus* from *Cunninghamites lignitum* (and *Cunninghamia elegans*) together with other reasons (absence of cuticle in the type specimen of *Cunninghamites oxycedrus* and in any other specimen from the type locality, lack of associated ovuliferous cones in the type locality) result in restriction of the usage of the name *Cunninghamites oxycedrus* to the material from the locality Niederschöna. Because *Cunninghamia elegans* is illegitimately published (Greuter *et al.* 1994, Art 52.1) it is recommended here to reintroduce the earliest published epithet in a new combination *Cunninghamites lignitum.*

N o t i c e. The genus *Lycopodiolites* (Schlotheim) ex Sternberg was used for the first time by Schlotheim (1820, pre-starting point name, no generic diagnose) under a modified spelling *Lycopodiolithes*. The name was validated by Sternberg 1825 (page VIII in Tentamen). The genus *Licopodiolites* should be retained for foliage shoots of *Lepidodendron* and included in its synonymy. The genus *Lycopodites* Brongniart 1822 which is in current use for such fossils requires conservation being typified by coniferous remains (see Seward 1910).

D i s c u s s i o n. The type specimens of *Cunninghamites oxycedrus* Presl in Sternberg from the Cenomanian strata in Germany, locality Niederschöna, show a very similar morphology to *Cunninghamites lignitum*. Corda discussing morphological differences distinguishes *C. oxycedrus* and *Cunninghamia elegans* basing on the length and width of leaves and twig gross-morphology. The width of leaves depends obviously on the mode of preservation. This kind of conifer leaves are folded, appearing narrower, as already pointed out by Harris (1979). The leaves of *C. lignitum* vary in length. On the other hand, similarity of ovuliferous cones found attached to the twigs bearing long leaves (Praha-Vidoule, Velenovský & Viniklář 1926, pl. 1, fig. 13) and shorter leaves (Pecínov) provides a good reason for unifying of long-leaf and short-leaf forms. No ovuliferous cone from the Niederschöna locality is available for the present study. Moreover, all the studied material of *C. oxycedrus* from the locality Niederschöna is preserved as impressions. No comparison of cuticle anatomy was therefore possible. For this moment I suggest to consider *C. oxycedrus* probably synonymous with C. *lignitum*, in view of the above mentioned facts and keeping with Knobloch's opinion (Knobloch 1971). For the definite solution, a detailed study of more complete and better preserved material from Niederschöna is needed.

The holotype of *Cunninghamia planifolia* Corda (in Reuss 1846, pl. 50, figs 1–3) from the locality Peruc has not been available for the present study and is probably lost. This taxon is very probably identical with *Cunninghamites lignitum* being very similar in gross-morphology.

Cunninghamia stenophylla Velenovský 1885 is a heterogeneous taxon consisting of cf. *Cunninghamites lignitum* from Lipenec figured by Velenovský (1885, pl. 5, figs 2, 4, 4a, 10) and *Cyparissidium minimum* Velenovský, Velenovský's pl. 5, fig. 16). The twigs and needles figured by Velenovský on plate 2 (figs 2, 4, 4a, 10) shows a conifer probably identical with *C. lignitum* and is classified herein as cf. *Cunninghamites lignitum*. They are similar in appearance with the short-leaf form occurring in Pecínov, Babín middle. *C. stenophylla* Velenovský (1885, pl. 5, fig. 16) from Lanšperk (F 253) differs from *C. lignitum* in cuticle structure. It shows elongate cells with sinuate anticlinal walls and stomata resembling those of *Cyparissidium minimum* (see Kvaček 1998). An ovuliferous cone from Lanšperk figured by Velenovský (1887, pl. 1, fig. 1) and labelled as *Cunninghamia elegans* is surely not of *Cunninghamites lignitum*. Its structure resembles ovuliferous cones of the *Pityostrobus*-type. Moreover, the figure by Velenovský (1887) seems to be only a reconstruction. The cone F 629 has no shoot attached.

The available specimens of *Kettneria elegans* (Corda) Velenovský & Viniklář published by Velenovský & Viniklář (1926, pl. 1, figs 12–15, pl. 3, fig. 6) from the locality of Praha-Vidoule are mostly poor leaf impressions. Several important ovuliferous cones and seeds (Velenovský & Viniklář 1926, pl. 1, figs 12, 13; Velenovský & Viniklář 1931, pl. 24, figs 1, 3) are depicted of which the specimen showing a twig with the attached ovuliferous cone is missing in the collection of PŘFUK. Another ovuliferous cone available in this collection from the same locality (B 196, Pl. 6, fig. 2) shows morphological details of *C. lignitum*: peltate cone scales and spiny polygonal escutcheons.

The specimens described as *Cunninghamia elegans* by Kräusel (1922, pl. 1, figs 4, 6, 10, pl. 2, figs 1–5) from Swalmen (Cretaceous of the Netherlands) agrees well with *C. lignitum* in gross-morphology and cuticle pattern. Also the material described by Kräusel (1923, pl. 1, figs 2, 3) from the Limburg Cretaceous in the Aachen Sands seems to be identical in cuticle structure with C. *lignitum*.

The specimens described by Stockmans (1946) as *Geinitzia elegans* (Stockmans 1946, pl. 2, figs 4, 10, 15, 16)

from the Cretaceous of Belgium are identical in cuticle pattern. Also the shoot morphology seems to be very similar.

The specimens described as *Cunninghamia elegans* by Zeiller (1905, pl. 7, fig. 14) from Bodoshti and by Hartung (1939, pl. 3, figs 5, 6, pl. 5, figs 1–4, pl. 6, figs 2, 6) from the Upper Cretaceous between Gabrovo and Sliven in Bulgaria are very similar to C. *lignitum* although the cuticle pattern is necessary for definite decision.

Cunninghamites squamosus Heer is suggested by Kräusel (1922) to be identical with *Cunninghamia elegans* = *C. lignitum*. The similarity in gross-morphology supports this opinion which is followed also here. The taxon differs in shorter leaves, but C. *lignitum* shows considerably higher degree of heterophylly.

Cunninghamites elegans (Hosius & Marck 1880, pl. 25, fig. 22), *Cunninghamia elegans* var. *densifolus* (Hosius & Marck 1880, pl. 37, figs 139–141), *Cunninghamia elegans* var. *linearis* (Hosius & Marck 1880, pl. 37, fig. 142), *C. squamosus* (Hosius & Marck 1880, pl. 25, 20–22, pl. 37, 137, 138) and *C. recurvatus* (Hosius & Marck 1880, pl. 37, figs 143, 144) are probably also identical with C. *lignitum* as already stated by Kräusel (1922). These leaf shoots described from the Upper Cretaceous of Westphalen represent a similar morphological type of twigs as *Cunninghamia elegans* described by Kräusel (1922, 1923) from the Limburg and the Aachen Cretaceous and probably represent twigs in various stages of maturity of the same conifer.

The following coniferous twigs showing curved, less densely arranged leaves and preserved as impressions have been described as *Cunninghamites elegans* from North America and Greenland. They are considered to represent the *Elatocladus*-type of foliage different from *Cunninghamites*:

1869 *Cunninghamites elegans* (Corda) Endlicher; Schenk: 17, pl. 4, fig. 3

1883 *Cunninghamites elegans* (Corda) Endlicher; Heer: 17, pl. 53, fig. 1a

1895 *Cunninghamites elegans* (Corda) Endlicher; Newberry: 48, pl. 5, figs 1–7

1900 *Cunninghamites elegans* (Corda) Endlicher; Fliche: 10, pl. 1, fig. 1

1902 *Cunninghamites elegans* (Corda) Endlicher; Hollick: 402, pl. 41, fig. 11

1905 *Cunninghamites elegans* (Corda) Endlicher; Knowlton in Stanton & Hatcher: 135, pl. 15, fig. 1

1906 *Cunninghamites elegans* (Corda) Endlicher; Hollick: 41, pl. 3, fig. 1

1914 *Cunninghamites elegans* (Corda) Endlicher; Berry: 24, 106

A coniferous twig described by Heer (1883, pl. 53, fig. 1a) from Greenland has been newly discussed by Boyd (1992) who placed it with a question mark to the genus *Elatocladus*.

Coniferous twigs from the Judith River Beds in the USA (Upper Cretaceous) assigned by Knowlton to *Cunninghamites elegans* (Knowlton in Stanton & Hatcher 1905, pl. 15, fig. 1) and to *Cunninghamites recurvatus* (Knowlton in Stanton & Hatcher 1905, pl. 16, fig. 6) have less dense leaves attached nearly perpendicularly to the axis. They probably represent a separate and distinct taxon.

ACKNOWLEDGEMENTS

I am grateful to my father Zlatko Kvaček (Charles University, Prague) and Johanna van Konijnenburg – van Cittert (Utrecht University) for their numerous consultations in the field on fossil plant morphology and taxonomy. My thanks go to Blanka Pacltová (Charles University, Prague) and Marcela Svobodová (Geological institute, The Czech Academy of Science, Prague) for their help in palynology, Zdeněk Pouzar (NM, Prague), for consultations on nomenclature. I am also grateful to Lutz Kuntzmann (MMG, Dresden) for supply of specimens of *Cunninghamites oxycedrus*. My thanks go to David Chiller for English editing, Ivana Čejková and my wife Helena for their help with SEM work and Helena Pražanová for her help with preparing the plates of the manuscript. The project was supported by the Czech Grant Agency (grant No. 205/96/0529).

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PLATES

Plate 1

Quasisequoia crispa (Velenovský) comb. n.

1. Lectotype, ovuliferous cone born on shoot, Lidice; F 262, × 1
2. Syntype, ovuliferous cone born on shoot, Lidice; F 260, × 1
3. Syntype, shoot, Lipenec; F 622, × 1.1
4. Ovuliferous cone born on shoot, Praha – Hloubětín-Hutě; F 2035, × 1
5. Shoots compressions, Praha – Hloubětín-Hutě; F 2029, × 1
6. LM of adaxial cuticle, Praha – Hloubětín-Hutě; F 2828 (HU 22/144/6a), × 200
7. LM of adaxial cuticle, Praha – Hloubětín-Hutě; F 2828 (HU 22/144/6a), × 200
8. SEM of adaxial cuticle, inner surface, Praha – Hloubětín-Hutě; F 2720 (5137), × 250


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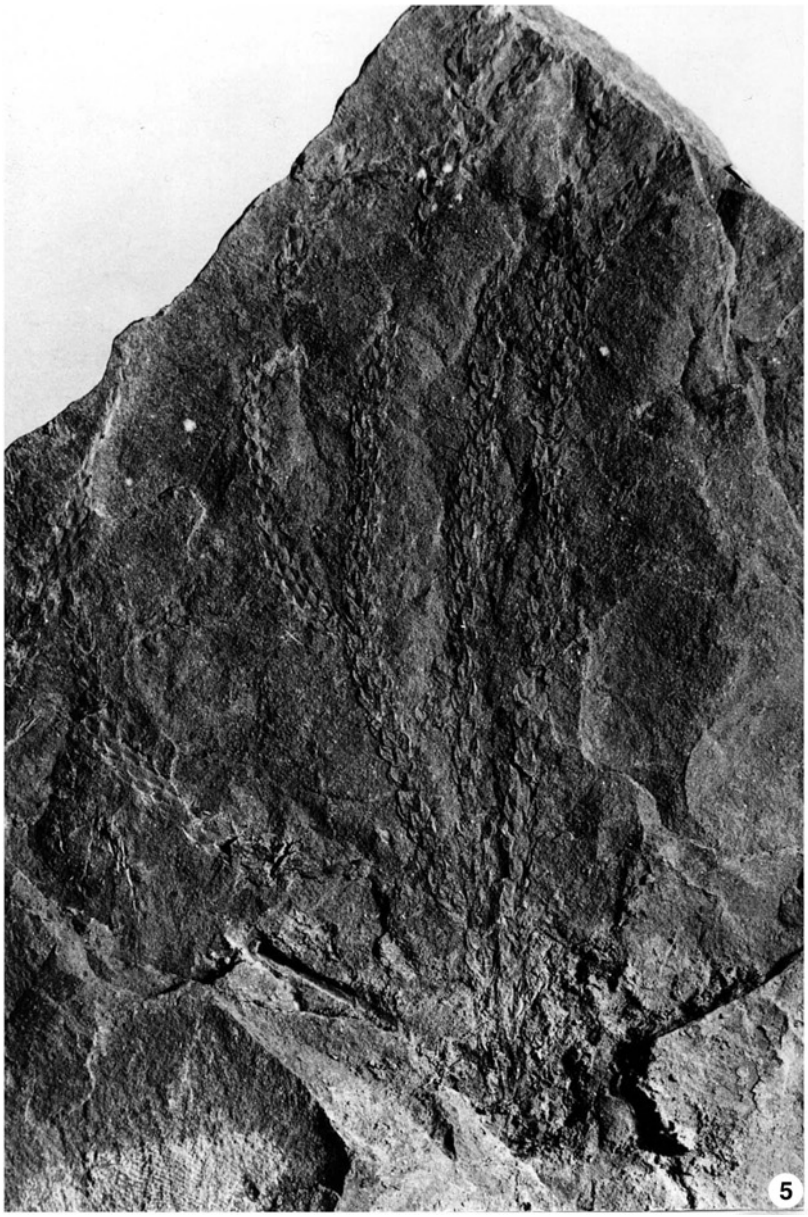
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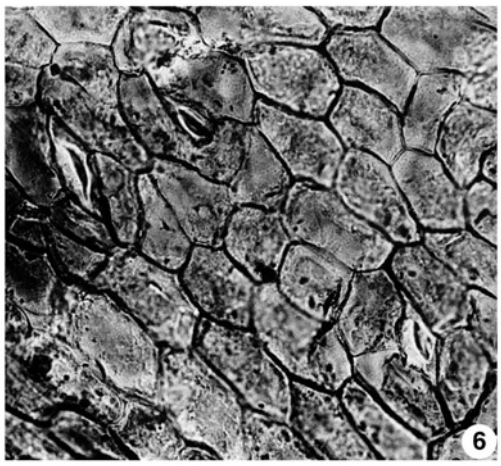
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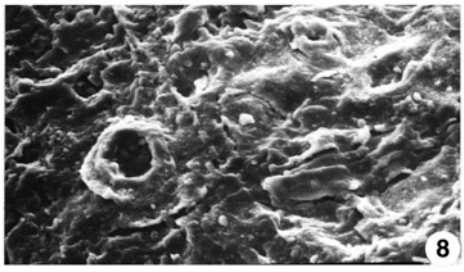
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Plate 2

Quasisequoia crispa (Velenovský) comb. n.

1. SEM of shoot, Praha – Hloubětín-Hutě; F 2720 (5134), × 10
2. SEM of abaxial cuticle, outer surface, Praha, Hloubětín– Hutě; F 2720 (5156), × 50
3. SEM of abaxial cuticle, stoma, outer surface, Praha, Hloubětín- Hutě; F 2721 (5241), × 50
4. LM of abaxial (left) and adaxial (right) cuticle, Praha – Hloubětín-Hutě; F 2874, × 50
5. Shoot, Syntype of *Sequoia major* (Velenovský 1888b, Pl. 1, fig. 6), Praha, Hloubětín; F 2529, × 1
6. LM of adaxial cuticle, syntype of *Sequoia major* (Velenovský 188b, pl. 1, fig. 6), Praha, Hloubětín; F 1980b, × 200
7. LM of adaxial cuticle, stoma, Praha – Hloubětín-Hutě; F 2828 (HU 22/144/6a), × 500
8. SEM of ovuliferous cone scale, adaxail part, Praha, Praha – Hloubětín-Hutě; F 2826 (4392), × 15
9. SEM of adaxial cuticle, stoma, inner surface, Praha – Hloubětín-Hutě; coll. NM (5213), × 500

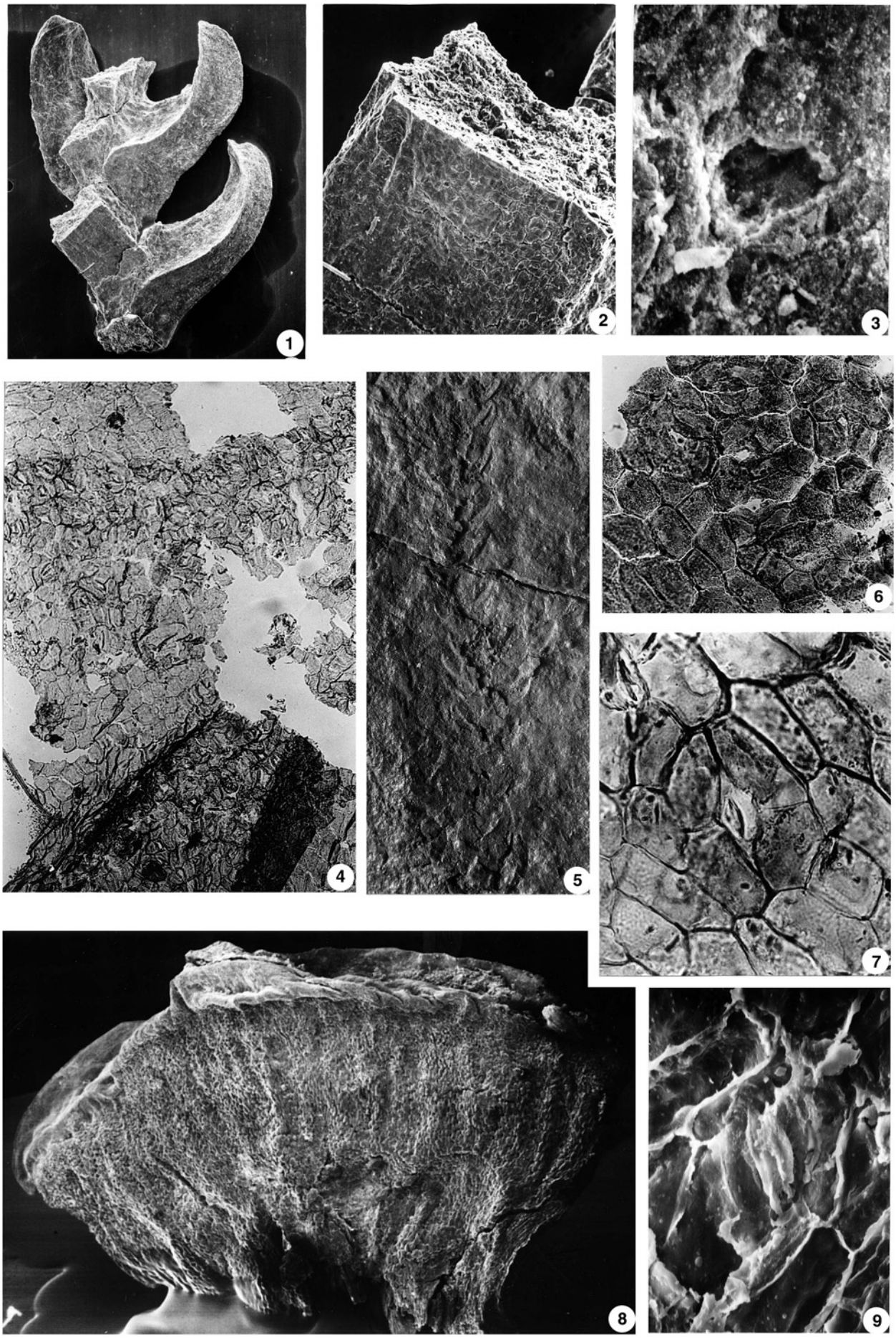
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Plate 3

Quasisequoia crispa (Velenovský) comb. n.

1. SEM of ovuliferous cone scale, adaxail part, Praha – Hloubětín-Hutě; F 2827 (4369) × 8
2. SEM of ovuliferous cone scale, escutcheon, Praha – Hloubětín-Hutě; F 2826 (4289), × 8
3. Male cone, Praha – Hloubětín-Hutě; F 2722, × 2
4. Pollen *Taxodiaceaepollenites*-type in situ from the male cone, Praha – Hloubětín-Hutě; F 2722a, × 1000
5. Cluster of pollens *Taxodiaceaepollenites*-type in situ from the male cone, Praha – Hloubětín-Hutě; F 2722a, × 400
6. LM of adaxial (left) and abaxial (right) cuticle, Praha – Hloubětín-Hutě; coll. NM (HU 22/45/6a), × 100

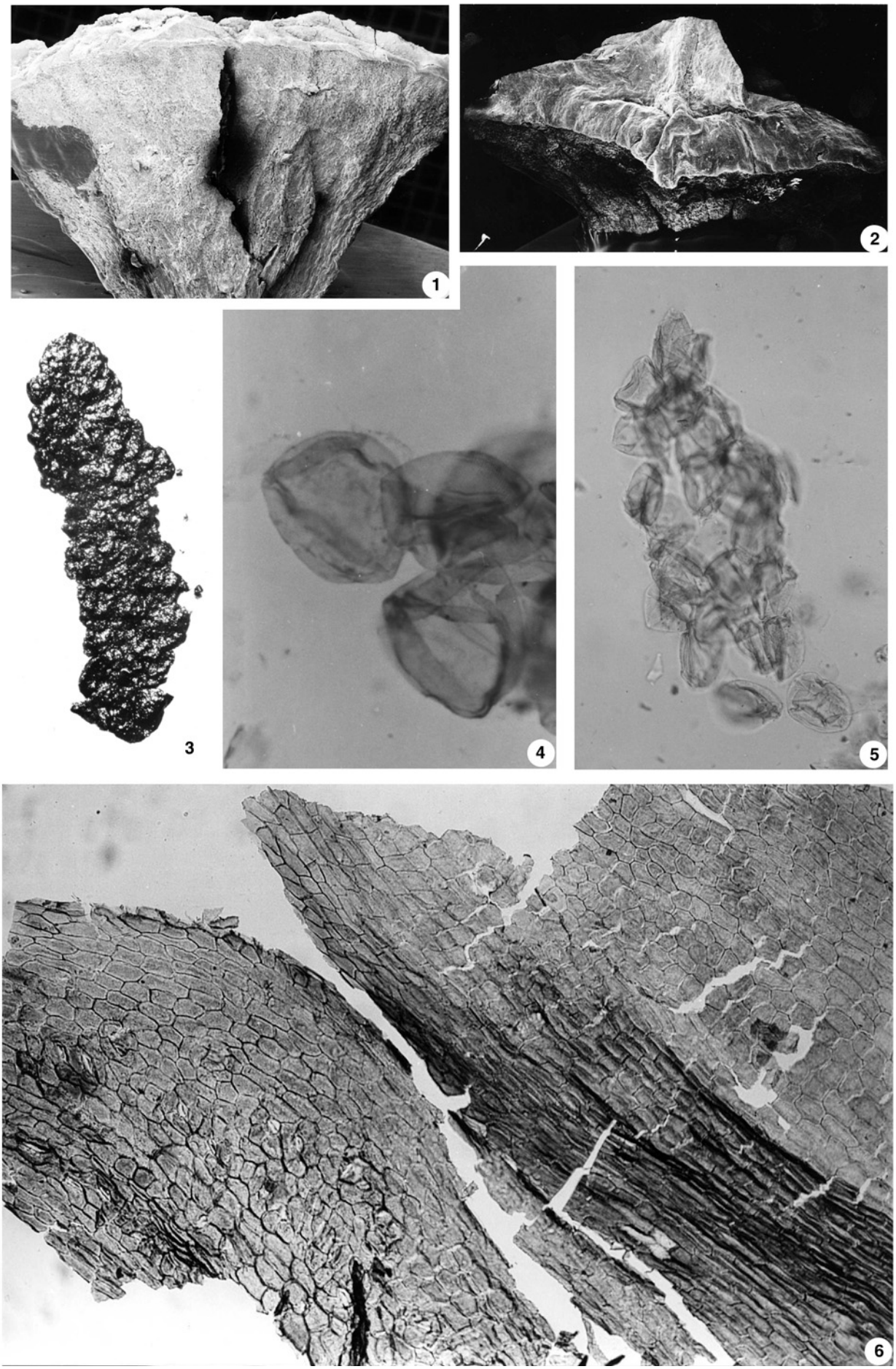
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Plate 4

Cunninghamites lignitum Sternberg

1. Lectotype Sternberg 1825, p. VIII; (type of *Cunninghamia elegans* Corda in Reuss 1846, pl. 49, fig. 29), Mšené-lázně, F 636, × 1
2. LM of abaxial cuticle of leaf-cushion, Pecínov; F 2709, × 200
3. Lectotype, LM of adaxial cuticle, stoma from leaf-cushion, Mšené-lázně; F 636b, × 400
4. Lectotype, LM of abaxial cuticle from leaf-cushion, Mšené-lázně; F 636c, × 400
5. SEM of leafy shoot showing leaf-cushion in middle, Pecínov; F 2832 (7074), × 30
6. SEM of same shoot as in fig. 3 showing detail of leaf cushion, Pecínov; F 2832 (7075), × 300
7. SEM of same leaf showing detail of marginal teeth, Pecínov; F 2833 (7072), × 1000

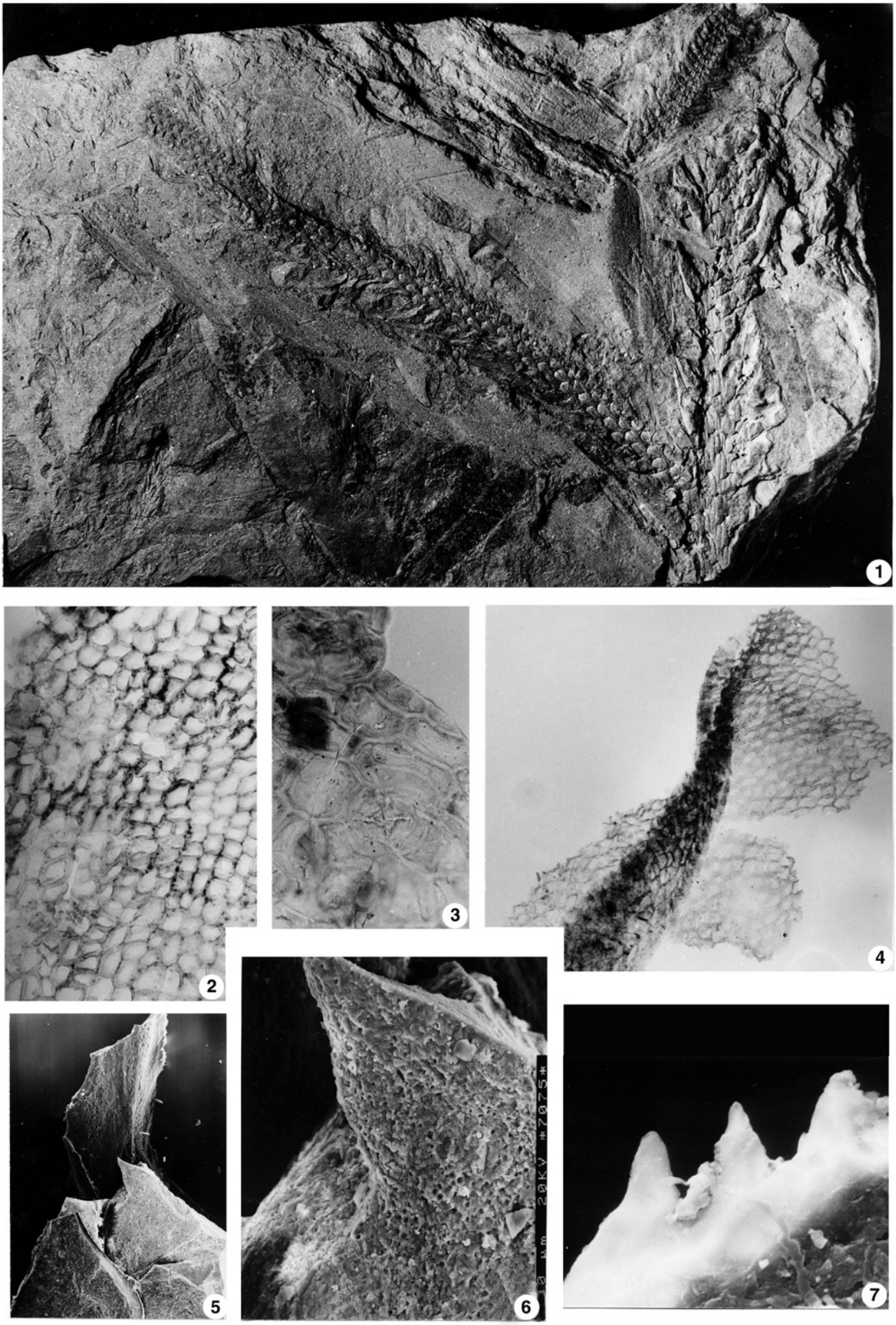
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Plate 5

Cunninghamites lignitum Sternberg

1. SEM of isolated leaf, adaxial view, Pecínov; F 2831 (3071), × 20
2. Ovuliferous cone, Pecínov; F 2708a, × 2
3. Lectotype, ovuliferous cone impression, (Presl in Sternberg 1838, pl. 49, figs 1a,b), Niederschöna, Germany; F 642, × 1
4. SEM of same shoot as in fig. 3 showing stomatal band within abaxial part of leaf, Pecínov; F 2832 (7077), × 400
5. LM of adaxial cuticle, Pecínov; F 2278aA, × 200
6. Shoot, (Velenovský 1885a, pl. 4, fig. 5), Niederschöna, Germany; F 640, × 1
7. SEM of ovuliferous cone scale, adaxial part, Pecínov; F 2834 (4285), × 8
8. LM of abaxial cuticle, Pecínov; F 2709a, × 200
9. LM of adaxial cuticle, Pecínov; F 2278aA, × 400

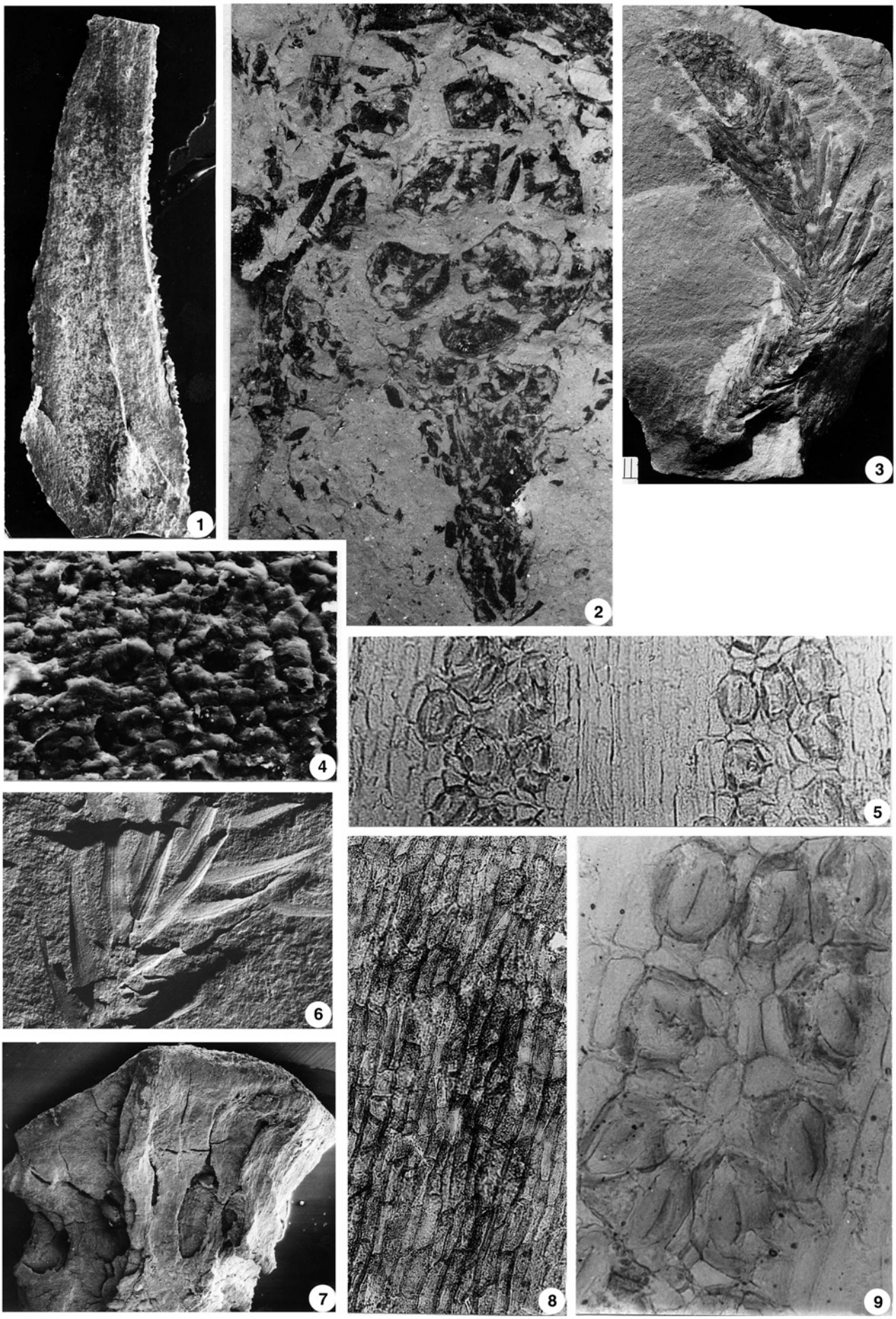
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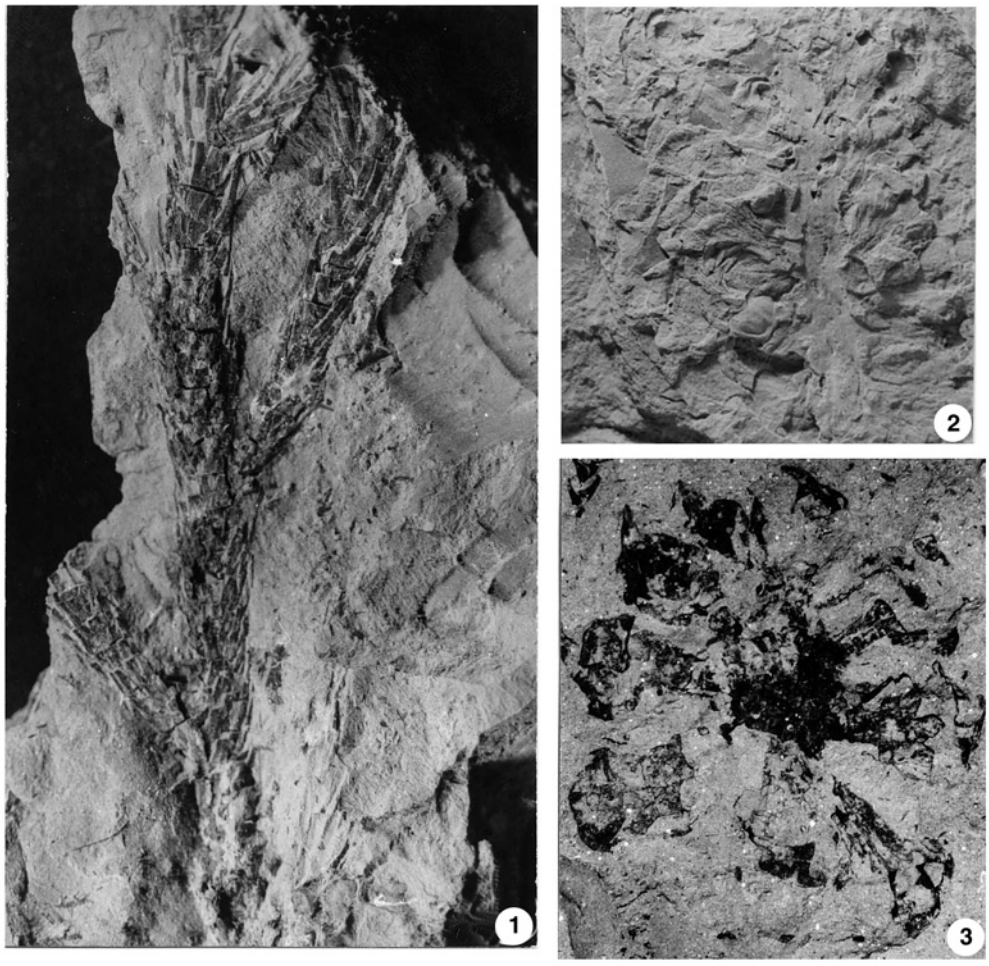
Plate 6

Cunninghamites lignitum Sternberg

1. Shoot, Pecínov; F 2278a, × 1
2. Ovuliferous cone (Velenovský & Viniklář 1931, pl. 24, fig. 2), Praha, Vidoule; B 196, × 1
3. Ovuliferous cone, Pecínov; F 2707, × 2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