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REVISION OF THE EARLY OLIGOCENE FLORA OF HRAZENÝ HILL (FORMERLY PIRSKENBERG) IN KNÍŽECÍ NEAR ŠLUKNOV, NORTH BOHEMIA

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Abstract: The early Oligocene flora of Hrazený hill in Knížecí village at Šluknov, the topic of Erwin Knobloch's diploma thesis, is revised and new elements not previously encountered are included, partly thanks to the use of cuticular analysis: among conifers *Pinus* cf. *rigios* (Unger) Ettingshausen, *Taxus engelhardtii* Kvaček and *Torreya bilinica* Saporta et Marion, among angiosperms *Laurophyllum medimontanum* Bůžek et al., *Platanus neptuni* (Ettingshausen) Bůžek et al., *Engelhardia orsbergensis* (Weber) Jähnichen et al., *Betula alboides* Engelhardt emend. Kvaček et Walther, *B. buzekii* Kvaček et Walther, *Alnus gaudinii* (Heer) Knobloch et Kvaček, *Carpinus roscheri* Walther et Kvaček, *C. mediomontana* Mai, *C. cordataeformis* Mai, *Ampelopsis hibschii* Bůžek et al., *Hydrangea microcalyx* Sieber, *Oleinites hallbaueri* (Mai) Sachse and *Saportaspemum* cf. *occidentale* Mayer et Manchester. Updated taxonomy has been proposed for several other fossil species including a new combination *Parvileguminophyllum haeringianum* (Ettingshausen) Kvaček comb. n. for the small legume foliage previously called *Mimosites*. The plant assemblage containing 60 fossil species (1 bryophyte, 5 conifers and 54 angiosperms) has been assigned to the early Oligocene (based on age of the radiometrical dated lava flow immediately covering the fossiliferous diatomite). The reconstructed vegetation type is interpreted as a warm-temperate mixed-mesophytic to broad-leaved deciduous forest with a high proportion of deciduous woody elements. The flora is very similar in its spectrum to adjacent sites of a similar age occurring in Seifhennersdorf in Saxony and Kundratice in the České středohoří Mountains and fits into the previously defined floral assemblage of Seifhennersdorf-Kundratice.

■ Early Oligocene, plant macrofossils, České středohoří Mountains, North Bohemia, palaeoclimate

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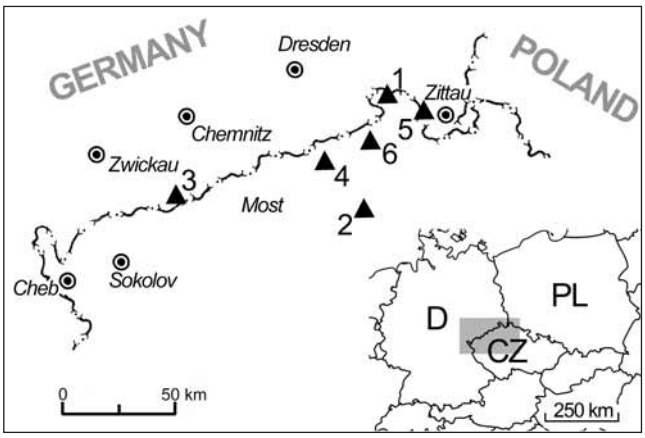
Introduction

Several Palaeogene sites of plant and animal assemblages connected with the magmatic complex of the České středohoří Mountains (Böhmisches Mittelgebirge in German) and adjacent Saxony well known since Sternberg's times have been newly revisited and reviewed in several monographs (e.g. Bůžek et al. 1976, Kvaček and Walther 1995, 1998, 2004, Walther and Kvaček 2007, Kvaček and Teodoridis 2011). All these studies contributed new information on the palaeo-world of this region. In addition to the classic localities we return now to those recovered and studied in detail after the Second World War, situated on the northern periphery of the mountains. A monograph on the early Oligocene flora of Seifhennersdorf-Varnsdorf was published in 2007 (Walther and Kvaček 2007) along with diatoms, fishes and insects. Another site – Hrazený hill (formerly Pirskenberg or Pirsken) in Knížecí near Šluknov – has also yielded numerous plant fossils, but so far no new revised data have been available (Text-fig. 1). The plant



Text-fig. 1. Location of the discussed early Oligocene sites in the northern part of the Bohemian Massif (the Czech Republic and Saxony) – 1. Knížecí, Hrazený hill, 2. Kundratice, 3. Hammerunterwiesenthal, 4. Holý Kluk, 5. Seifhennersdorf, 6. Bechlejovice.

material was collected from the diatomite layers there and worked out by Knobloch (1958, 1961) but the data are outdated and required revision. Beside the original material housed in the National Museum in Prague in 2014 we also sorted out and examined numerous additional fossils collected by Knobloch, which he had left aside for future study but never returned to these collections. Contrary to observations by Knobloch (1961, p. 248), some of the plant remains yielded cuticles that have enabled more precise identification (see Table 1).

Besides fossil plants, co-occurring fishes are known also from this locality (Obrhelová 1961, Gaudant in Bellon et al. 1998, Böhme 2007, Přikryl 2014) and some new specimens were recovered from the collections and offered to our colleague Tomáš Přikryl (Geological Institute CAS, v. v. i., Prague) for a re-evaluation. A few other animal remains (e.g. beetle wing-cases) found at the same time are too incomplete and have not as yet been subjected to detailed study.

Geological setting and age

The site of Hrazený hill, previously known as Pirskenberg or Pirsken in the village of Knížecí in North Bohemia (Knobloch 1961, Oberhelová 1961) lies ca. 10 km NW from the town of Rumburk and 4 km SSW from Šluknov (Plate 21). It lies on the periphery of the České středohoří magmatic complex in Šluknov hills (Bellon et al. 1998), where Hrazený hill is the highest peak at an altitude of 609.7 m above sea level. The fossiliferous diatomite lies under basaltoid (Kopecký in Knobloch 1959) and tephritic (Bellon in Bellon et al. 1998) lava flows and reaches about 5 m in thickness. It is not accessible in outcrops but samples are available from old waste heaps in Knížecí village following an unsuccessful search for lignite in the 19th century.

The first reports on fossil plant remains from this area were published by Weise (1890). Further geological and palaeontological data were obtained during geological mapping by Herrmann and Beck (1897) who also provided a list of recovered fossil plants identified by H. Engelhardt from Dresden. This collection was not illustrated nor described in detail. Another site of fossiliferous diatomite is situated near the village of Lipová (formerly Heinspach) mentioned by Herrmann and Beck (1897), where also fossil plants occur (see Jeremies 2006).

Knobloch (1959, p. 102–103) reported on his geological mapping in the area of Hrazený hill and the village of Knížecí in the following text (shortened translation from Czech): "The freshwater Tertiary deposit was not visible in the complete section. The thickness is very variable (from 0.3 m to 3–5 m on average). It starts with fine-grained green-brown tuffitic clay and continues upwards as variegated clay with interbeds of sandy and clayey bedded diatomite. It also includes a black layer of bituminous clay 0.2 m thick, which was obviously interpreted as poor quality lignite. The layers are not laid horizontally and incline towards the basin center at maximum angles of ca. 50° or less. The richest fossiliferous layers are represented by bedded reddish to light brown diatomite with abundant fossil flora showing regular bedding similar to the diatomite at Bechlejovice and Varnsdorf. The Tertiary complex ends with an eruption of basaltoid magma. L. Kopecký who kindly assessed thin sections of the magmatic rock from Hrazený hill identified it as common basalt sensu stricto. However, the existence of 2–3 flows cannot be ruled out."

An extensive correlative study of the České středohoří Mountains by Bellon et al. (1998) assigned the flora of Knížecí to the early Oligocene and concluded that the nearest plant assemblages were described from the slightly older sites of Seifhennersdorf-Varnsdorf and Kundratice (Kvaček and Walther 1998, Walther and Kvaček 2007). Bellon (in Bellon et al. 1998) attempted radiometric dating of several sites in the České středohoří magmatic complex by a detailed petrological and geochemical study. He carried out K-Ar dating on whole rock samples and obtained data suggesting an age from 23.7 to 38.3 Ma. He also analyzed one sample of a lava flow immediately covering the diatomite layer at Hrazený hill and an age of 29.5±1.5 Ma was suggested. Böhme (2007, p. 189) estimated the ectothermic vertebrate fauna from Knížecí also to be early Oligocene.

Material and methods

The collecting activities of Erwin Knobloch between the years 1956 – 1957 on waste dumps left after old mining attempts in the village of Knížecí (50°58'33''N, 14°24'51''E) provided almost all the study material (Knobloch 1958, 1959, 1961, Oberhelová 1961). A few plant specimens were added by Kotlaba and Bartoš later (collections in the National Museum in Prague). The exact position and lithology of the fossiliferous diatomite at Knížecí was described in detail by Knobloch (1958, 1959, 1961) who also personally excavated most of the material studied. Some of the layers are thinly bedded, fine grained and quite hard; the mechanical preparation to reveal complete plant impressions was obviously difficult because many specimens show traces left by a knife (Knobloch 1961, pl. 8, fig. 3 etc.). In addition to the thinly bedded diatomite we also noticed in the collections samples of coarser diatomite facies with accumulations of disintegrated *Tetraclinis* twigs and fragmentary plant fossils. The majority of the specimens studied represents flat leaf impressions, occasionally infructescences (*Platanus neptuni*, *Alnus*) and catkins (*Alnus*), fruits (*Acer*, *Craigia*, etc.) or seeds (*Carpolithes* spp.). In rare cases a detached stamen and fruitlets of *Platanus neptuni* were recovered. Conifer needles and a smaller proportion of leaf fossils are impressions/compressions with preserved coaly material and cuticle on the surface. The material is heavily oxidized. We used a shortened maceration procedure, in which the leaf fragments were first treated in diluted HF, rinsed in water and then in diluted 5% KOH. The coaly material was mostly naturally oxidized and could be dissolved without any additional maceration. The cuticles were then transferred into a drop of water on a slide, embedded in glycerol and sealed with a cover glass bordered with nail varnish.

The illustrated specimens and cuticle preparations have been transferred to the collections of the palaeontological department of the National Museum in Prague (numbers prefixed by NM), duplicate material is housed in the Czech Geological Survey, Prague (numbers prefixed by EK and without numbers) together with unidentified or fragmentary

Table 1. Current taxonomic assignements compared with the designations of Knobloch (1961).

Present treatment	Knobloch (1961)
Muscites sp.	*Muscites* sp.
Pinus cf. *rigios*	
Taxodium dubium	*Taxodium distichum miocenicum*
Tetraclinis salicornioides	*Libocedrus salicornioides*
Taxus engelhardtii	
Torreya bilinica	
Liriodendron haueri	*Liriodendron haueri*
Laurophyllum mediomontanum	*Salix longa*
Laurophyllum sp.	*Laurus princeps* + *Laurophyllum* sp. + ? *Benzoin attenuatum* +cf. *Laurus primigenia*
Daphnogene cinnamomifolia	*Cinnamomum scheuchzeri*
Smilax weberi	*Smilax grandifolia*
"*Typha*" *latissima*	*Typha latissima*
Poacites sp.	*Poacites* cf. *aequalis*
Platanus neptuni	*Ceratopetalum bilinicum* + *Comptonia difformis* p.p.
Cercidiphyllum crenatum	*Cercidiphyllum crenatum*
Ampelopsis hibschii	*Platanus* cf. *aceroides* + *Vitis* sp. + *Zelkova ungeri* p.p.
Phaseolites sp. 1	*Leguminosites* sp. p.p.
Phaseolites sp. 2	*Leguminosites* sp. p.p.
Phaseolites sp. 3	? *Cassia* sp.
Phaseolites sp. 4	*Dalbergia bella*
Parvileguminophyllum haeringianum	*Mimosites* cf. *haeringiana*
Rosa lignitum	*Rosa* sp. + *Engelhardia macroptera* p.p. + ? *Rhus pyrrhae*
Crataegus pirskenbergensis	*Crataegus pirskenbergensis*
Ulmus fischeri	cf. *Ulmus braunii* var. *plurinervia* + *Zelkova ungeri* p.p.
Zelkova zelkovifolia	
Celtis pirskenbergensis	*Celtis begonioides* + *Celtis begonioides* var. *pirskenbergensis*
Comptonia difformis	*Comptonia difformis* p.p.
Engelhardia orsbergensis	*Myrica lignitum* p.p.
Engelhardia macroptera	*Engelhardtia macroptera*
Carya fragiliformis	*Carya serraefolia*
Cyclocarya sp.	*Cyclocarya cyclocarpa* + *Juglans (Carya) bilinica* p.p.
Betula alboides	*Betula* cf. *dryadum*
Betula buzekii	*Betula prisca*
Alnus gaudinii	? *Pterocarya denticulata* + cf. *Alnus kefersteinii*
Alnus kefersteinii	*Alnus* sp. + *Betula* sp. p.p.
Carpinus grandis	*Carpinus orientalis*
Carpinus roscheri	*Betula brongniartii*
Carpinus cordataeformis	
Carpinus mediomontana	*Carpinus* cf. *neilreichii*

Table 1. [continued]

Populus zaddachii	*Populus zaddachii*
Salix sp.	*Populus rottensis*
Toxicodendron herthae	*Rhus herthae*
Acer angustilobum	*Acer* cf. *angustilobum*
Acer palaeosaccharinum	*Acer palaeosaccharinum*
Acer integrilobum	
Acer sp.	*Acer* sp.
Craigia bronnii	*Pteleaecarpum bronnii*
Cornus studeri	*Cornus studeri* + *Rhamnus graeffii*
Hydrangea microcalyx	*Paliurus thurmannii*
Oleinites hallbaueri	*Myrica lignitum* p.p. + cf. *Ilex rottensis*
Saportaspermum cf. *occidentale*	
Dicotylophyllum cf. *heerii*	
Dicotylophyllum sp. 1	*Juglans acuminata* + *Ficus arcinervia* + cf. *Rhus pteleaefolia*
Dicotylophyllum sp. 2	*Leguminosites* sp. p.p.
Dicotylophyllum sp. 3	*Juglans* (*Carya*) *bilinica* p.p.
Dicotylophyllum sp. 4	*Sibirea rottensis*
Dicotylophyllum sp. 5	*Aesculus* cf. *palaeocastanum*
Dicotylophyllum sp. 6	*Celastrus persei*
Carpolithes sp. 1	? *Pisonia eocenica*
Carpolithes sp. 2	*Carpolithes* sp.

specimens. The cuticle preparations transferred to the National Museum bear the same collection numbers as the macrofossil, from which they were taken, but with additional letters a–x. Most of the specimens described by Knobloch (1961) were available and re-examined here, except for some which were obviously lost, e.g. illustrated fruits of *Craigia*, *Engelhardia*, foliage of *Rosa* and some impressions of angiosperms.

Systematic palaeontology

The general characteristics of the flora were described by the late Erwin Knobloch who submitted it as a diploma thesis (Knobloch 1958) and later published it in an abbreviated form (Knobloch 1961). The cuticle analysis allowed the addition of several new elements not recognized in Knobloch's study and treated here in detail anew. The nomenclature published by Knobloch (1961) was rectified and notes on affinities of some other specimens were included according to present knowledge. English translations of the descriptions given in Czech by Knobloch (1958) are used in selected cases and new descriptions are provided, where necessary. Extensive synonym lists have been avoided and references to the basionyms and previous monographs are quoted instead. The chapter "Material studied" refers to the specimens investigated personally by the present authors. For the systematic arrangement of taxa newly proposed classifications and linear sequence of extant gymnosperms and angiosperms (Christenhusz et al. 2011, Reveal 2012) have been adopted.

Bryophytes

***Muscites* Brongniart**

***Muscites* sp.**

Pl. 1, Fig. 1–3

1961 *Muscites* sp. (*Hypnum heppii* Heer); Knobloch, p. 249, pl. 10, fig. 1.

Delicate impressions of sterile moss gametophyte plants monopodially branched and covered with leaflet appendages less than 1 mm in size showing thin midribs.

Discussion. The preservational state of the examined moss remains is quite poor, anatomical and morphological details that would allow a more precise identification are not visible. Similar but better preserved are impressions published as *Hypnum lycopodioides* Weber by Weyland (1937, p. 69, pl. 9, fig. 1–3) from the upper Oligocene of Rott, Rhineland, and housed in the collections of the Geological-Palaeontological Institute of the University in Bonn, which we could examine personally. The branching pattern seems to correspond to both fossil records. Before the Rhineland material is revisited no definite judgment can be made about the material from Knížecí.

Material. Fragmentary moss gametophytes, NM-G2888, NM-G11514 and a few un-numbered EK specimens.

Conifers

Pinaceae Lindley

Pinus Linnaeus
Pinus (subgen. *Pinus*) cf. *rigios* (Unger) Ettingshausen

Pl. 1, Fig. 4–5

? 1866 *Pinus rigios* (Unger) Ettingshausen, p. 41, pl. 13, fig. 11–12.

Fragmentary pine needles in ternate fascicle, ca. 0.5–0.7 mm thick, trigonal in cross section, the maximum preserved length 45 mm, sheath permanent, 2 mm long.

Discussion. Fossil pine needles are rare in the Palaeogene deposits of the České středohoří Mountains (e.g. Žichov and Matrý – see Ettingshausen 1866, Akhmetiev et al. 2009, as *Pinus rigios* (Unger) Ettingshausen). Some previously reported needle-like fossils assigned by Menzel (1901) to pines from Suletice-Berand turned out to represent monocots (Kvaček and Walther 1995). The occurrence of pine pollen noted in several cuticle preparations confirms pine stands nearby the site of Knížecí during the time when the fossiliferous diatomite was deposited.

P. rigios was originally described from the lower Miocene of Bílina in the North Bohemian Basin, where it is associated with seed cones of *P. engelhardtii* Menzel. A more accurate determination of the present material is not really possible because of its fragmentary nature. Co-occurring seed cones, which would more reliably characterise this pine, have not been so far recovered. The needles can be referred to subgen. *Pinus* and may represent the same species as those recovered at Žichov and Matrý.

Material. Two needle fascicles, EK 237a, b, 238.

Cupressaceae Richard ex Bartling sensu lato

Taxodium Richard
Taxodium dubium (Sternberg) Heer

Pl. 1, Fig. 6–7, Pl. 2, Fig. 1

1823 *Phyllites dubius* Sternberg, tent., p. 39, pl. 36, fig. 3.
1855 *Taxodium dubium* (Sternberg) Heer, p. 49–50, pl. 17, fig. 5–15.
1961 *Taxodium distichum miocenicum* Heer; Knobloch, p. 250, pl. 2, fig. 8, pl. 10, fig. 2.
1976 *Taxodium dubium* (Sternberg) Heer; Kvaček, p. 290, fig. 5–7.

The *Taxodium* twigs from Knížecí were described by Knobloch (1958) as follows (translated from Czech): "Leaves are acicular, entire-margined and acuminate at the apex, with a clearly distinct midrib. They are attached very regularly at angles of ca. 45° on either side of the twig axis. The longest twig reaches 12 cm." The twigs are on the average 60 mm long and 7 to 19 mm wide. Kvaček (1976, fig. 7b) was able to prepare the cuticle from one of the twigs from Knížecí previsouly published by Knobloch (1961, pl. 2, fig. 8, as *Taxodium distichum miocenicum* Heer) and interpreted it as ordinary epidermal structure of *Taxodium dubium* with stomata mostly transversally orientated to the leaf length.

Discussion. Similar twigs from Seifhennersdorf exhibited only poorly preserved epidermal structure (Walther and Kvaček 2007). According to Kunzmann et al. (2009), the European Oligocene populations of *Taxodium* belong to the same fossil species as occurring in the European Neogene and differ only in details of the cone scales.

Material. Leafy twigs, NM-G2815a, b with cuticle, NM-G2892, EK numerous specimens without number.

Tetraclinis Masters
Tetraclinis salicornioides (Unger) Kvaček

Pl. 1, Fig. 8–10, Pl. 2, Fig. 2–3

1847 *Thuites salicornioides* Unger, p. 11, pl. 3, fig. 1–4.
1961 *Libocedrus salicornioides* (Unger) Heer; Knobloch, p. 251, pl. 1, fig. 12, pl. 14, fig. 9.
1989 *Tetraclinis salicornioides* (Unger) Kvaček, p. 48, pl. 2, fig. 3, 10, 12, 14.

Knobloch (1958, as *Libocedrus salicornioides*) described some of the recovered remains as follows (translated from Czech): "Leaves on the twigs strongly adpressed, so that they look as if fused, forming the twig itself. They are approximately rhombic in form. The wider end bears a blunt tip, or it has projections on both sides and a medial small depression, where the next leaf is attached, or it is semicircular with six small projections. The leaves are scaly and show 2–6 (mostly 3) longitudinal ribs. They are verticillate and vary in size, the smallest being 2 mm long, the longest 12 mm." The newly obtained epidermal structure matches other records of this conifer from North Bohemia (see e.g. Kvaček 1989, Kvaček et al. 2014).

Discussion. Numerous specimens at hand have yielded cuticle structure and one specimen removed from rock shows even the typical stomatal topography of this species. It widely differs from the xeromorphic disposition of stomata in the narrow areas sunk between leaves in *T. brachyodon* (Brongniart) Mai et Walther (Kvaček et al. 2000).

Material. Short fragments of twigs, many isolated segments, NM-G2810, NM-G8584, NM-G11495b, c, NM-G11496a, b, NM-G11507, EK 240–245, further specimens not numbered.

Taxaceae Gray

Taxus Linnaeus
Taxus engelhardtii Kvaček

Pl. 1, Fig. 11–13, Pl. 2, Fig. 4–5

1976 *Taxus engelhardtii* Kvaček, p. 294, fig. 8–9.

Needle-like leaves isolated, flattened, univeined, only reaching 1 mm in width and 6–12 mm in length. Epidermal

structure shows adaxially rectangular cells with straight anticlines. Abaxial cuticle reflects two stomatal bands and three non-stomatal zones; medial non-stomatal zone papillate, lateral only beside stomata covered with low papillae. Stomatal apparati longitudinally arranged, monocyclic, composed of a pair of sunken guard cells and usually four papillate subsidiary cells.

D i s c u s s i o n . Knížecí is the third site, from which proven foliage of *Taxus engelhardtii* has been recorded. The first occurrence is from the type locality at Kundratice, where whole twigs are preserved (Kvaček and Walther 1998).Thanks to the very typical epidermal structure we can record the presence of this conifer based on separated needles with very particular papillate monocyclic stomata on the lower leaf side. In addition to the type locality it was only recorded in the upper Oligocene of Enspel in western Germany (Köhler and Uhl 2014). The needles of *Cephalotaxus parvifolia* (Walther) Kvaček et Walther are morphologically indistinguishable but differ decidedly by the absence of papillae on the stomata (Kvaček and Wather 1998, Walther and Kvaček 2007). According to Spjut (2007) *Taxus engelhardtii* is very similar to the extant *T. mairei* (Lemée et H. Léveillé) S.Y. Hu ex T.S. Liu native in subtropical laurophyllous forests of southern China.

M a t e r i a l . Isolated needles with cuticle structure, NM-G11481a, b, NM-G11482a, b, NM-G11501a–c.

Torreya Arnott

Torreya bilinica Saporta et Marion

Pl. 1, Fig. 14–16, Pl. 2, Fig. 6–8

1866 *Sequoia langsdorfii* Ettingshausen (non (Brongniart) Heer), p. 39, pro parte, pl. 13, fig. 9.
1876 *Torreya bilinica* Saporta et Marion, p. 221.
1984 *Torreya bilinica* Saporta et Marion; Kvaček, p. 478, fig. 5–6.

Needles linear, up to 20 mm long, 1.5 mm wide, apex bluntly acute, with a single broad midrib, epidermis prosenchymatous, cells straight-walled, very narrow, ca. 10–15 µm wide and more than 250 µm long, with blunt cuneate ends, abaxially papillate near stomatal bands, with two stomatal bands much more strongly papillate, ca. 120 µm wide, elliptic outlines of stomata barely visible under the thick papillate cover, stomata monocyclic, longitudinally aligned, otherwise scattered, not forming lines, guard cells sunken, with thinly demarcated elongate stomatal pit surrounded by a ring of ca. 8 subsidiary cells forming the broadly oval apparatus up to 80 µm wide and 110 µm long.

D i s c u s s i o n . The fossil record of needles of *Torreya* from the Czech Republic was reviewed by Kvaček (1984) who used evidence from epidermal anatomy to confirm the view of Saporta and Marion (1976) that the fragmentary twig from the Oligocene site of Žichov in North Bohemia, which had been misidentified as *Sequoia* by Ettingshausen (1866), should belong to *Torreya* in spite of the aberrant blunt apex of the needles. Similar rounded apices as in other occurrences of *Torreya bilinica* at Seifhennersdorf and also at Knížecí appear in ancient representatives of the genus (*Torreya gracilis* Florin, 1958) while the Neogene records (e.g. Kvaček et al. 2008) share the cuspidate apex with all living species (Florin 1948, Li et al. 2001). The Palaeogene of North Bohemia (Žichov – Kvaček 1984, Kundratice – Kvaček and Walther 1998, Matrý – Akhmetiev et al. 2009, Roudníky – Kvaček et al. 2014, Knížecí – present paper) and Saxony (Kleinsaubernitz – Walther 1999, Seifhennersdorf – Walther and Kvaček 2007) is the limited area of this species, which is not known elsewhere.

M a t e r i a l . Fragmentary needles with cuticle structure, NM-G11508a, b, NM-G11509a, b, NM-G11510a, b, all with cuticle, EK 246.

Magnoliaceae Jussieu

Liriodendron Linnaeus
Liriodendron haueri Ettingshausen

Pl. 3, Fig. 1–4, Pl. 6, Fig. 1

1869 *Liriodendron haueri* Ettingshausen, p. 9, pl. 41, fig. 10–10b.
1961 *Liriodendron procaccinii* Unger; Knobloch, p. 273, pl. 7, fig. 1, 3.
1961 *Styrax* sp.; Knobloch, p. 288, pl. 14, fig. 4.

Leaves broadly ovate with four lobes arising from a point one third of the blade width or only shallowly bilobate, leaf blade 41–82 mm long and 21 – ca. 90 mm wide, base widely cuneate, petiolate, petiole maximum 50 mm long. Midrib strong and straight, secondary veins arising at an angle of 40–50°, opposite or alternate, every second joined by a broken tertiary vein to the next vein above and then looping. Lowermost pairs sending fine outer loops towards the margin. Tertiary venation forms polygonal fields. Mesophyll tissue with small lens-shaped secretory cells, cuticles smooth, the abaxial surface with scattered stomata openings, otherwise cell structure poorly preserved.

D i s c u s s i o n . One aberrant leaf impression with only two shallow lobes was referred to *Styrax* by Knobloch (1961) but a similar leaf impression from Markvartice was assigned to *Liriodendron* on account of its epidermal anatomy (Bůžek et al. 1976, pl. 3, fig. 8). Of the available names for fossil species of *Liriodendron* (see e.g. Archenegg 1894) we prefer here *Liriodendron haueri* Ettingshausen rather than *L. procaccinii* Unger (selected by Knobloch 1958, 1961) because the former name is based on a leaf impression from the Oligocene of North Bohemia (see Hably et al. 2001, p. 27, pl. 20, fig. 2, Akhmetiev et al. 2009, pl. 13, fig. 3) and was accepted by the previous authors dealing with other Palaeogene occurrences of Tulip tree foliage in this region (see e.g. Bůžek et al. 1976, Walther 1998). *L. procaccinii* is a common designation for fossil foliage of *Liriodendron* distributed mainly in Europe during the late Neogene (see Saporta and Marion 1876 – Meximieux, Knobloch 1998 – Willershausen). *L. haueri* differs from *L. procaccinii* in acute lobes contrary to mostly rounded lobes in the Italian Neogene populations (Knobloch 1998, p. 14). Revision of the latter species type material from Senigallia, Italy (Massalongo and Scarabelli 1859, Kustatcher et al. 2014) is required. Two extant species differ in the surface sculpture of the abaxial

cuticle. The leaves in *L. tulipifera* L. from E and SE North America are abaxially smooth, in *L. chinense* (Hemsley) Sargent from eastern China and Vietnam are papillate. In this respect our material looks to be similar to *L. tulipifera*.

It is noteworthy that in living species of Tulip tree the fruitlets survive in large quantities after the season under the trees while foliage readily decomposes over the winter. This is perhaps a reason why leaf impressions are less common than fruitlets in the fossil state (e.g., at Markvartice – Bůžek et al. 1976, Roudníky – Kvaček et al. 2014). This is however not the case at the Knížecí site, where no fruitlets have yet been recovered.

Material. Leaf impressions, NM-G2856a–f with cuticle, NM-G2859, NM-G2997, NM-G8591.

Lauraceae Jussieu

Laurophyllum Göppert
Laurophyllum medimontanum Bůžek, Holý et Kvaček

Pl. 4, Fig. 1–2, Pl. 6, Fig. 2

1961 *Salix longa* Al. Braun; Knobloch, p. 252, pl. 8, fig. 9.
1976 *Laurophyllum medimontanum* Bůžek, Holý et Kvaček, p. 98, pl. 9, fig. 1–5, pl. 16, fig. 1–6, pl. 17, fig. 1–2.

Leaves elongate, entire-margined, 70–110 mm long and 15 mm wide, midrib straight, gradually narrowing towards the base apex, secondary veins thin, long ascending and looping, intersecondaries ending in tertiary veins that form a polygonal network. Abaxial cuticle moderately papillate, reflecting brachyparacytic stomata.

Discussion. This fossil species was at first compared with *Laurophyllum villense* (Weyland et Kilpper) Kvaček, 1971 but later recognized as an independent fossil species (Bůžek et al. 1976), widely distributed at Markvartice, outside the Bohemian Massive also found in Hesse (Flörsheim – Kvaček 2004, as *Laurophyllum* cf. *villense*).

Material studied. Leaf impressions, partly with cuticles, NM-G2863, NM-G2995, NM-G2996, NM-G3002a–c, NM-G3003.

Laurophyllum sp.

Pl. 4, Fig. 3–7, Pl. 6, Fig. 3

1961 *Laurus princeps* Heer; Knobloch, p. 275, pl. 10, fig. 4.
1961 *Laurophyllum* sp.; Knobloch, p. 276, pl. 10, fig. 8.
1961 ? *Benzoin attenuata* Heer; Knobloch, p. 276.
1961 cf. *Laurus primigenia* Unger; Knobloch, p. 276, pl. 10, fig. 7.

Leaves elongate to oval, 48–106 mm long, 17–19 mm wide, entire-margined, venation camptodromous to brochidodromous lauroid, secondaries irregularly disposed.

Discussion. Lauroid leaf impressions described by Knobloch (1961, p. 275–276) are mostly preserved without clearly discernible cuticle structure and thus their identification to species level is very imprecise. One specimen (NM-G2885) yielded a very thinly cutinized abaxial epidermis, which is similar to the material from Markvartice assigned to Magnoliaceae (?) gen. et sp. by Bůžek et al. (1976).

Material studied: Leaf impressions, NM-G2884, NM-G2885a, b, NM-G2890a, b, NM-G2977, NM-G2890a, b, NM-G11998a, b, EK 258.

Daphnogene Unger
Daphnogene cinnamomifolia (Brongniart) Unger

Pl. 5, Fig. 1–4, Pl. 6, Fig. 4

1822 *Phyllites cinnamomifolia* Brongniart in Cuvier, p. 359, pl. 11, fig. 12.
1850 *Daphnogene cinnamomifolia* (Brongniart) Unger, p. 424.
1961 *Cinnamomum scheuchzeri* (Heer) Frentzen; Knobloch, p. 276, pl. 1, fig. 7, pl. 10, fig. 9.

Knobloch (1961) identified cinnamomoid leaves from Knížecí according to the slender form as *Cinnamomum scheuchzeri* from the middle Miocene of Öhningen and described them as follows: (translated from Czech) "Leaves lanceolate, entire. Midrib straight, conspicuous. Basal veins running near the margin. In the leaves' lower two thirds they end and connect with the secondary veins, which depart from the midrib. Basal veins are connected with the leaf margin by tertiaries either perpendicular or oblique or broken. In the leaves' upper third secondary veins arise from the midrib and interconnect by loops. Higher-order venation is formed by a reticulum of polygonal fields." The leaves vary in size from very small, 21 mm long and 13 mm wide to slightly broader, ca. 40 mm wide, fragmentary in length. The mesophyll tissue contains numerous lens-shaped secretory cells. The recently obtained structure of the adaxial cuticle shows polygonal cells with straight anticlinale walls or occasionally only very shallowly wavy, the abaxial cuticle is densely hairy and the trichomes are only 5 µm thick, very narrow, and ca 100 µm long.

Discussion. The record of *Daphnogene* from Knížecí is similar in epidermal patterns to those known from other Oligocene localities in Europe (e.g. Kvaček and Knobloch 1967, Bůžek et al. 1976). The abaxial epidermal structure, namely long narrow trichomes, corresponds to that described from the Oligocene material of Markvartice (Kvaček in Bůžek et al. 1976). As any connection between Palaeogene foliage with fruits of *Cinnamomum* has not yet been proven, we continue including the above fossil species in the fossil genus *Daphnogene*.

Material studied: Leaf impressions-compressions, NM-G2811, NM-G2851a, b, NM-G8600, NM-G11497, NM-G11498, NM-G11499, NM-G11500, NM-G11513, EK 247, 248, partly with cuticles.

Smilacaceae Ventenat

Smilax Linnaeus
Smilax weberi Wessel

Pl. 5, Fig. 9–10

1856 *Smilax weberi* WESSEL; Wessel and Weber, p. 17, pl. 2, fig. 1.
1961 *Smilax grandifolia* (UNGER) HEER; Knobloch, p. 251, pl. 13, fig. 7, pl. 15, fig. 9.

Leaves entire-margined, blade 37 to ca. 65 mm long, 29 to 34 mm wide, ovate, at base more or less cordate, towards the apex gradually narrowing. Midrib straight, with one or two arch-like basal veins on either side, the outermost interconnected by large fields. Tertiary venation consists of polygonal fields of variable size.

Discussion. The newly studied type material from the upper Oligocene of Rott (Winterscheid et al., personal communication) confirms the correct identification of the Knížecí material, as suggested above.

Material studied: Leaf impression, NM-G8581a, b, NM-G8608, EK 249.

Monocotyledonae inc. fam.

"*Typha*" *latissima* A. BRAUN

Pl. 5, Fig. 5–6, 8

1961 *Typha latissima* A. BRAUN; Knobloch, p. 251, pl. 12, fig. 7.

Strap-like fragmentary foliage with parallel venation attaining a mean width of 10–15 mm, parallel veins of two orders; between slightly thicker veins 1 mm apart run 2–4 thinner veins. Cross veins almost perpendicular, 1.5–2 mm apart.

Discussion. The generic affinity of the foliage described above is open and due to fragmentary nature of fossils uncertain.

Material studied: Leaf fragments, NM-G8593, EK 250–254.

Poacites HEER (non SCHLOTHEIM)
Poacites sp. div.

Pl. 5, Fig. 7

1961 *Poacites* cf. *aequalis* ETTINGSHAUSEN; Knobloch, p. 252.

Strap-like fragmentary leaves with parallel venation, attaining a meanwidth 6 to 17 mm. Thicker veins irregularly interspaced with thinner veins.

Discussion. The affinity of these fragments to monocots is obvious but otherwise not determinable more exactly. Heer (1855) was the first who connected the fossil genus *Poacites* correctly with angiosperms, contrary to previous authors, who had applied it mostly to lycopod foliage (see Andrews 1955, 1970). Hence the name *Poacites* in the sense of Heer (1855) requires conservation.

Material studied: Leaf impressions, NM-G3001, EK 255–257.

Platanaceae LESTIBOUDOIS ex DUMORTIER

Platanus LINNAEUS
Platanus neptuni (ETTINGSHAUSEN) BŮŽEK, HOLÝ et KVAČEK

Pl. 6, Fig. 5, Pl. 7, Fig. 1–7

1866 *Sparganium neptuni* ETTINGSHAUSEN, p. 31, pl. 7, fig. 9–15.
1961 *Comptonia diforme* (STERNBERG) BERRY; Knobloch, p. 257, pro parte, pl. 3, fig. 9 left [NM-G2830b].
1961 *Ceratopetalum bilinicum* ETTINGSHAUSEN; Knobloch, p. 277, pl. 10, fig. 12.
1967 *Platanus neptuni* (ETTINGSHAUSEN) BŮŽEK, HOLÝ et KVAČEK, p. 205, pl. 1–4.

Fragmentary leaves obovate, 37–42 mm long and 7–11 mm wide, on the margin widely blunt regularly toothed, partly entire, venation semicraspedodromous, partly eucamptodromous, adaxial cuticle composed of polygonal cells with regularly sinuate anticlines, abaxial cuticle showing large anomocytic stomata and compound trichome bases dispersed on abaxial leaf side. Female infructescence ca. 10 mm in diameter composed of narrow fruitlets projected by a short style out of the infructescence outline. Isolated stamen obconical, with two longitudinal pollen sacks and a terminal thickened cap. Strap-like stipules parallel-veined, cut at the base.

Discussion. The single available infructescence was wrongly interpreted as belonging to *Comptonia* by Knobloch (1961). All the other organs fit within the characteristics recognized previously in this species (Bůžek et al. 1976, Kvaček and Manchester 2004). The affinity of these foliage fragments is confirmed by the epidermal structure showing large anomocytic stomata with widely open ledges and compound trichome bases (Pl. 6, Fig. 5) recorded in the previous studies.

Material studied: Fragmentary leaves, partly with cuticle structure, NM-G2887, NM-G11503a, b, NM-G11504a, b, EK 259–262; female infructescence, NM-G2830b; isolated stamen, NM-G11998c; stipule, EK 263.

Cercidiphyllaceae VAN TIEGHEM

Cercidiphyllum SIEBOLD et ZUCCARINI
Cercidiphyllum crenatum (UNGER) R. BROWN

Pl. 7, Fig. 8–9

1850 *Dombeyopsis crenata* UNGER, p. 448.
1935 *Cercidiphyllum crenatum* (UNGER) R. BROWN, p. 575, pl. 68, fig. 1, 6, 8–10.
1961 *Cercidiphyllum crenatum* (UNGER) R. BROWN; Knobloch, p. 274, pl. 15, fig. 1, 3, 4, 11.

Leaves of *Cercidiphyllum* were characterized by Knobloch (1958, translation from Czech) as follows: "Leaf blade cordate to elliptical, widest in the lower half. Leaf margin crenulate, base cordate to rounded. 1–3 basal veins run on either side of the main vein. They are broken in places,

where other veins emerge. A row of thinner veins start from basal veins and run towards the leaf margin, they loop and send veinlets into marginal teeth. Tertiary venation consists of variously sized fields". Leaf blades attain 30 to 64 mm in length and 21 to ca. 50 mm in width.

Discussion. The typical variation in leaf form from narrower elliptical to rounded and broadly cordate is developed in the plant assemblage of Knížecí in the same way as in some other records of this species in the České středohoří Mountains, e.g. at Bechlejovice (Kvaček and Walther 2004).

Material studied: Leaf impressions, NM-G8580, NM-G8595, NM-G8599, NM-G11492, EK 264–266.

Vitaceae Jussieu

Ampelopsis Michaux
Ampelopsis hibschii Bůžek, Kvaček et Walther

Pl. 8, Fig. 1–6

1961 *Platanus* cf. *aceroides* Göppert; Knobloch, p. 277, pl. 10, fig. 3 [NM-G2891].
1961 *Vitis* sp.; Knobloch, p. 288, pl. 8, fig. 3 [NM-G2869].
1961 *Zelkova ungeri* Kováts; Knobloch, p. 270, pro parte, pl. 7, fig. 7 [NM-G2855].
1981 *Ampelopsis hibschii* Bůžek, Kvaček et Walther, p. 127, pl. 1–6, text-fig. 1–7.

Knobloch (1958) described the material as follows (translated from Czech): "Base slightly cordate, leaf probably palmately veined and trilobate. From the base three basal veins and secondaries emerge, which are slightly wavy and end in the marginal teeth. Tertiary veins are perpendicular or oblique between secondaries and form variable large fields. Petiole 18 mm long" (under *Platanus* cf. *aceroides*). "A rounded leaf, probably shallowly trilobed (leaf margin and apex not preserved). Base cordate, basal veins slightly arched, secondaries also wavy. Tertiaries forked between secondaries producing a broken line. Quaternary venation composed of a network of polygonal areoles" (under *Vitis* sp.). Morphologically variable fragmentary foliage attains 38 to ca. 78 mm in length and 68 to ca. 80 mm in width.

Discussion. Besides large fragmentary leaves and a petiolate base assigned to *Platanus* cf. *aceroides*, *Vitis* and partly *Zelkova* by Knobloch (1961), we recovered from the additional fragmentary material from Knížecí leaf apices with a separated tip, a diagnostic feature of *A. hibschii* (Bůžek et al. 1981). We assume that other fragmentary leaf fossils apparently belonging to Vitaceae, as listed in the synonymy, belong to this species known from Bechlejovice, Kundratice and elsewhere. One impression assigned to *Zelkova* (Knobloch 1961, pl. 7, fig. 7) may represent a leaflet of a compound leaf only rarely encountered in this species (e.g. Walther in Mai and Walther 1978, pl. 7, fig. 2–3, as *Ampelopsis* sp.).

Material studied: Leaf impressions, NM-G2855, NM-G2869, NM-G2891, EK 267–271, more specimens not numbered.

Leguminosae Jussieu

Phaseolites Unger
Phaseolites sp. 1

Pl. 9, Fig. 4

1961 *Leguminosites* sp.; Knobloch, p. 279, pro parte, pl. 5, fig. 15.

Leaflets entire-margined, oval, symmetric to slightly oblique, rounded at base, rounded at apex, attaining at maximum 30 mm in length and 22 mm in width, sessile to very shortly petiolulate, venation very fine, dense, eucamptodromous.

Discussion. Similar legume leaflets have been described from Bechlejovice (Kvaček and Walther 2004, p. 31, pl. 13, fig. 5–7, as *Leguminosites* sp. 1) and Kundratice (Kvaček and Walther 1998, p. 20, pl. 10, fig. 9–10, as Leguminosae gen. et sp., forma 1–2). We use the fossil taxon *Phaseolites* for such legume foliage instead of *Leguminosites*, which is typified by carpological material (Bowerbank 1840).

Material studied: Leaflet impressions, NM-G2839, EK 273–275.

Phaseolites sp. 2

Pl. 9, Fig. 7–8

1961 *Leguminosites* sp., Knobloch, p. 279, pro parte, pl. 8, fig. 10.

Leaflets entire-margined, ovate, almost sessile, obliquely attached and asymmetric at base, fragmentary in length, 20 mm wide.

Discussion. Knobloch (1961) stated that he did not find any reference to similar legume foliage in the literature and we share his opinion.

Material studied: Impressions of isolated leaflets, NM-G2983, NM-G2868, EK 276.

Phaseolites sp. 3

Pl. 9, Fig. 5

1961 ? *Cassia* sp.; Knobloch, p. 280, pl. 11, fig. 5.

Fragmentary compound leaf, with leaflets entire-margined, ovate (?), obviously belonging to but detached from a long straight petiole, sessile, showing two basal veins starting asymmetrically from the rounded base.

Discussion. Knobloch (1961) believed that this incomplete fossil remain may resemble *Dalbergia rottensis* Weyland (1937, p. 98, pl. 11, fig. 11–14, text-fig. 39). Due to its very fragmentary nature the generic affinity of this single specimen is very uncertain.

Material studied: Incomplete leaf impression, NM-G2903.

Phaseolites sp. 4

Pl. 9, Fig. 6

1961 *Dalbergia bella* HEER; Knobloch, p. 280, pl. 10, fig. 10.

Leaflet sessile, entire-margined, emarginate, obovate, 24 mm long, 12 mm wide, midrib thin, straight, secondary veins eucamptodromous, steep, closely spaced, occasionally forked near margin, tertiary venation reticulate.

Discussion. The generic affinity of this single leaflet obviously belonging to legume foliage is uncertain.

Material studied: Leaflet impression, NM-G2862a, b.

Parvileguminophyllum HERENDEEN et DILCHER

1990 *Parvileguminophyllum* HERENDEEN et DILCHER, p. 348.

Type: *Parvileguminophyllum georgianum* (BERRY) HERENDEEN et DILCHER.

Parvileguminophyllum haeringianum (ETTINGSHAUSEN) KVAČEK comb. nov.

Pl. 9, Fig. 1–3

1853 *Mimosites haeringiana* ETTINGSHAUSEN, p. 92, pl. 30, fig. 23–37 (basionym).
1961 *Mimosites* cf. *haeringiana* ETTINGSHAUSEN; Knobloch, p. 280, pl. 12, fig. 1, pl. 14, fig. 8.
2010 *Mimosites haeringiana* ETTINGSHAUSEN; Meller, p. 140–141, pl. 41, fig. 7–8, pl. 42, fig. 1–9.

Lectotypus selected here: leaflet illustrated by Ettingshausen (1853, pl. 30, fig. 31) and Meller (2010, pl. 42, fig. 6a, b), GBA 1853/001/0173/8 at the Geologische Bundesanstalt, Vienna (Häring, Lower Oligocene).

Linear basally asymmetrical leaflets of delicate legume foliage, blunt at the apex and with asymmetrical basal venation, 11–19 mm long and 4 mm wide.

Discussion. Previous records of this legume, elsewhere often occurring as compound leaves (e.g. at Kundratice – Kvaček and Walther 1998, Bechlejovice – Kvaček and Walther 2004, as *Mimosites haeringianus*) were described from the České středohoří Mountains under the designation *Mimosites haeringianus* ETTINGSHAUSEN (Kvaček and Walther 1998, 2004). Because the generic name *Mimosites* is based on pods (Bowerbank 1840), a newly introduced fossil genus *Parvileguminophyllum* for morphologically similar foliage of uncertain affinities (Herendeen and Dilcher 1990) is given preference. The late Eocene flora of Florissant includes very similar leaf impressions known as *Prosopis linearifolia* (LESQUEREUX) MACGINITIES (1953, p. 126, pl. 46, fig. 1, 5 (non pl. 73, fig. 7); Meyer 2003, p. 105, fig. 95). A more precise comparison has not yet been done.

Material studied: Leaflet impressions, NM-G8583, NM-G8592, NM-G11487, EK numerous not numbered.

Rosaceae JUSSIEU

Rosa LINNAEUS
Rosa lignitum HEER

Pl. 10, Fig. 1–9

1869 *Rosa lignitum* HEER, p. 99, pl. 30, fig. 33.
1961 *Rosa* sp.; Knobloch, p. 278, pl. 8, fig. 4.
1961 *Engelhardtia macroptera* (BRONGNIART) ETTINGSHAUSEN; Knobloch, p. 311, pro parte, only pl. 4, fig. 4.
1961 ? *Rhus pyrrhae* UNGER; Knobloch, p. 287, pl. 8, fig. 2, pl. 11, fig. 11.

Leaflets mostly ovate, small-sized, 19–54 mm long, 22–19 mm wide, crenulate to finely denticulate on margin, sub-sessile, venation dense, semi-craspedodromous. Knobloch (1961) characterized the material very briefly: (translated from German): "Leaflets oval, simple dentate, at base slightly asymmetrical, teeth apically orientated, secondary veins steep and entering the marginal teeth."

Discussion. Knobloch (1961) refered to a monograph of fossil roses, predicted to have been accomplished by the Czech expert Dr. Ivan Klášterský but which was never finished, and therefore treated the remains of roses very superficially. Detached leaflets of similar type and crenulate margin as well as complete compound leaves had been since known from other localities in the České středohoří Mountains, e.g. Kundratice (Kvaček and Walther 1998), Roudníky (Kvaček et al. 2014) and in particular Bechlejovice (Kvaček and Walther 2004).

Material studied: Leaflet impressions, NM-G2865, NM-G2871, NM-G2876b, EK 277–286.

Crataegus Linnaeus
Crataegus pirskenbergensis KNOBLOCH

Pl. 10, Fig. 10–11

1961 *Crataegus pirskenbergensis* KNOBLOCH, p. 278, pl. 8, fig. 7–8.

Leaves broadly ovate, divided into 3 lobes, 32 to 78 mm long, 26 to ca. 60 mm wide, finely serrate. For a more detailed description and diagnosis see Knobloch (1961).

Discussion: Similar leaf impressions have also been recorded in the Oligocene floras at Bechlejovice (Kvaček and Walther 2004), Roudníky (Kvaček et al. 2014) and probably at Seifhennersdorf (Walther and Kvaček 2007).

Material studied: Leaf impressions, NM-G2861a, b, NM-G2867 a, b.

Ulmaceae MIRBEL

Ulmus LINNAEUS
Ulmus fischeri HEER

Pl. 11, Fig. 1–4

1856 *Ulmus fischeri* HEER, p. 57, pl. 57, fig. 1–3.

1961 cf. *Ulmus braunii* HEER var. *plurinervia* (UNGER) STANDFEST; Knobloch, p. 270, pl. 1, fig. 3, 5.
1961 *Zelkova ungeri* KOVÁTS; Knobloch, p. 270, pl. 1, fig. 2, pl. 7, fig. 4, 7.

Leaves shortly petiolate, lamina broadly ovate to ovate-elongate or oval, 13–45 mm long, 15–31 mm wide, simple or double dentate. Midrib straight, up to 11 secondary veins, straight to slightly bent, partly forked, tertiary veins perpendicular to secondary veins.

Discussion. Knobloch (1961) incorrectly assigned some coarsely simple dentate elm leaves to *Zelkova* which differs in having less densely spaced secondary veins. These simple dentate leaves fall into the normal variation of *Ulmus fischeri* foliage which is widely distributed in the Oligocene of the České středohoří Mountains (e.g. Bechlejovice – Kvaček and Walther 2004) and Saxony (Walther and Kvaček 2007).

Material studied: Leaf impressions, NM-G2804, NM-G2807, NM-G2808, NM-G2809, NM-G2855, NM-G2858, EK 287, some other fragments not numbered.

Zelkova SPACH
Zelkova zelkovifolia (UNGER) BŮŽEK et KOTLABA

Pl. 11, Fig. 5

1844 *Ulmus zelkovifolia* UNGER, p. 94, pl. 24, fig. 7 right, 9–13.
1845 *Ulmus zelkovifolia* UNGER; Unger, p. 95, pl. 26, fig. 7 (lectotype).
1963 *Zelkova zelkovifolia* (UNGER) BŮŽEK et KOTLABA in KOTLABA, p. 59, pl. 3, fig. 7–8.

Two leaf fragments showing coarsely dentate margins and which prove the occurrence of this fossil species at Knížecí.

Discussion. In general both fragments match a much more diversified record from Kundratice and Bechlejovice (Kvaček and Walther 1998, 2004). They differ from the simple dentate elm foliage, e.g. *Ulmus fischeri* HEER, in having fewer secondary veins, although in some critical cases the differentiation might be arbitrary.

Material studied: Leaf impressions, EK 288, 289.

Celtidaceae LINK

Celtis TOURNEFORT
Celtis pirskenbergensis (KNOBLOCH) KVAČEK et WALTHER

Pl. 12, Fig. 1–6

1961 *Celtis begonioides* GÖPPERT var. *pirskenbergensis* KNOBLOCH, p. 273, pl. 6, fig. 3, 5, 8 (holotype).
1961 *Celtis begonioides* GÖPPERT; Knobloch, p. 273, pl. 6, fig. 9, pl. 12, fig. 4.
2006 *Celtis* sp.; Radoň et al., p. 101, pl. 5, fig. 5–7.
2007 *Celtis pirskenbergensis* (KNOBLOCH) KVAČEK et WALTHER; Walther and Kvaček, p. 101, pl. 7, fig. 1–8, text-fig. 4a–c.

Leaves short petiolate, ovate to elongate, up to 64 mm long and 16 to ca. 45 mm wide, oblique at base, on margin coarsely serrate, slightly asymmetrical. Three basal veins arise from below the lamina base at sharp angles. Outer basal veins ascend upwards to about one half of the leaf length and then loop with higher almost straight secondary veins. Tertiary veins are perpendicular (translated from Knobloch 1958, 1961, emended).

Discussion. Kvaček and Walther (in Walther and Kvaček 2007) merged all specimens of *Celtis* recovered from Knížecí and elsewhere in the Palaeogene of North Bohemia and Saxony into a single fossil species *C. pirskenbergensis* (KNOBLOCH) KVAČEK et WALTHER. The same large sized kind of foliage also occurs at the other Oligocene sites Holý Kluk (Radoň et al. 2006) and Seifhennersdorf (Walther and Kvaček 2007). We agree with this treatment leaving separately other fossil species known from the Miocene, which clearly differ morphologically (see e.g. Němejc et al. 2003).

Material studied: Leaf impressions, NM-G2850a, b (holotype), NM-G2851a, b, NM-G2852, NM-G2853a, b, NM-G2979, NM-G8600.

Myricaceae RICHARD ex KUNTH

Comptonia L´HÉRITIER
Comptonia difformis (STERNBERG) BERRY

Pl. 6, fig. 6, Pl. 13, Fig. 1–8

1961 *Comptonia difformis* (STERNBERG) BERRY; Knobloch, p. 257 pro parte (non infructescence on pl. 3, fig 6 left = *Platanus neptuni*), pl. 3, fig. 4–7, 9–10, pl. 12, fig. 6, pl. 15, fig. 8.

Leaves coriaceous, variable in size from minute specimens hardly attaining 21 mm in length and 5 mm in width to larger, up to 80 mm long, acuminate, at base abruptly narrowing into a short petiole. Leaf lamina pinnately dissected into triangular rounded segments (lobes) at base reaching usually to the midrib, opposite to alternate, variable in size and form in this respect matching the living *Comptonia peregrina* L. Segments at apex usually blunt, but also mucronate; 2–8 perpendicular secondaries entering the lobes, three of them are usually thicker than the others and stretch to the margin from the straight midrib. They are connected by oblique tertiary veins that form a polygonal field (Knobloch 1958, translated from Czech, emended). The newly obtained epidermal structure is very fragmentary. Adaxial cuticle is smooth and shows outlines of cells ca. 20–25 µm in diameter with almost straight to wavy anticlines. Abaxial cuticle is extremely thin, hairy, and shows rounded short uniseriate stalks ca. 12 µm in diameter and even disc-shaped glandular trichomes up to 50 µm in diameter.

Discussion. The occurrence of *Comptonia* in the European Palaeogene is connected with two fossil species, *C. difformis* later widely spread in the Neogene and the more xeromorphic, small-leaved *C. dryandrifolia* BRONGNIART (= *C. schrankii* (STERNBERG) BERRY). The population from

Knížecí corresponds to *C. difformis* morphologically, as stated by Knobloch (1961), as well as in epidermal anatomy. In general the epidermal structure matches that obtained from leaves of *Comptonia difformis* from the upper Oligocene of Kleinsaubernitz (Walther 1999).

Material studied: Leaf compressions-impressions, NM-G2826, NM-G2827, NM-G2829, NM-G2831, NM-G2986, NM-G2987, NM-G2988, NM-G2989, NM-G2830, NM-G11502a, b, EK 290–302, numerous specimens not numbered.

Juglandaceae A. Richard ex Kunth

***Engelhardia* Leschenaux ex Blume**
***Engelhardia orsbergensis* (Wessel et Weber) Jähnichen, Mai et Walther**

Pl. 6, Fig. 9, Pl. 14, Fig. 1–5

1856 *Banksia orsbergensis* Wessel et Weber, p. 146, pl. 25, fig. 9a–d.
1961 *Myrica lignitum* (Unger) Saporta; Knobloch, p. 256, pro parte, pl. 1, fig. 13, pl. 2, fig. 10, pl. 2, fig. 3, pl. 12, fig. 5.
1977 *Engelhardia orsbergensis* (Wessel et Weber) Jähnichen, Mai et Walther, p. 326, pl. 38–49, text-fig. 1–3.

Leaflets narrow elongate, 34–55 mm long and 13 mm wide, straight to slightly bent, minutely widely dentate, base asymmetrical. The epidermal structure rarely preserved on delicate leaflets, showing rounded stalks of peltate trichomes and sunken stomata.

Discussion. The material from Knížecí was partly identified as *Myrica lignitum* (Knobloch 1961, p. 256, morphotype 1, cf. *Dryandroides acuminata*). All specimens studied correspond morphologically to the variation in *Engelhardia orsbergensis* as known from the type locality Orsberg in the Rhineland (Jähnichen et al. 1977, Winterscheid and Kvaček 2014) and other occurrences in the České středohoří Mountains (e.g. Kvaček and Walther 1995, 1998). Similar leaflets, but lacking epidermal structure, have been described from the early Oligocene site Häring in Austria under several fossil species, e.g. *Rhus prisca* Ettingshausen and *R. juglandogene* Ettingshausen.

Material studied: Leaflets, NM-G2805, NM-G2824, NM-G8582, NM-G11511a, b, EK 303–311, some more not numbered.

***Engelhardia macroptera* (Brongniart) Unger**

Pl. 14, Fig. 5

1828 *Carpinus macroptera* Brongniart, p. 48, pl. 3, fig. 6.
1866 *Engelhardia macroptera* (Brongniart) Unger, p. 52, pl. 16, fig. 9–12.
1961 *Engelhardia macroptera* (Brongniart) Unger; Knobloch, p. 261, pl. 4, fig. 4, 10.

Fruits are rounded nuts attached to a four-winged involucrum. The main three wings are triveined, the medial wing is longer, rounded at the apex, the very short forth wing envelopes the fruit basally. Venation consists of elongate fields along the main veins, forming smaller areoles towards the lobe margin (translated and emended from Knobloch 1958).

Discussion. The fruits of *Engelhardia* occur only rarely in the Knížecí plant assemblage and match other occurrences in the European Tertiary (see Mai in Jähnichen et al. 1977).

Material studied: Fragmentary involucres, EK 312.

***Carya* Nuttal**
***Carya fragiliformis* (Sternberg) Kvaček et Walther**

Pl. 14, Fig. 70

1825 *Phyllites fragiliformis* Sternberg, p. 42, index iconum, pl. 50, fig. 1.
1961 *Carya serraefolia* (Göppert) Kräusel; Knobloch, p. 260, pl. 9, fig. 9, 12, pl. 11, fig. 1–3.
2007 *Carya fragiliformis* (Sternberg) Kvaček et Walther; Walther and Kvaček, p. 110, pl. 11, fig. 1–3, pl. 23, fig. 8–10, text-fig. 6b.

Leaflets ovate-oval, 36–115 mm long and 26–36 mm wide, on margin double serrate, base decurrent, asymmetrical, midrib straight or slightly bent, distinct, secondary veins at almost right angle at leaflet base, higher up at a more steep angle. Often forked near margin, sometime twice, particularly those from near the leaflet base, tertiary veins running perpendicularly or slightly oblique, higher-order venation areolate (Knobloch 1958, translated from Czech, modified).

Discussions: The material assigned by Knobloch (1961) to *Carya* represents variable foliage, which is partly difficult to distinguish from leaflets of *Cyclocarya*, as described below.

Material studied: Impressions of leaflets, NM-G2878, NM-G2878, NM-G2894, NM-G2895, NM-G2978, EK 313–316.

***Cyclocarya* Iljinskaya**
***Cyclocarya* sp.**

Pl. 14, Fig. 8

1897 *Pterocarya cyclocarpa* D.H.R. Schlechtendal, p. 20, pro parte, pl. 4, fig. 1–3.
1961 *Cyclocarya cyclocarpa* (D.H.R. Schlechtendal) Knobloch, p. 262, pl. 15, fig. 5–7.
1961 *Juglans (Carya) bilinica* A. Braun; Knobloch, p. 258, pl. 4, fig. 5–9.

Leaflets lanceolate to narrow ovate, cuneate at base, 33–70 mm long, 14–22 mm wide, margin fine serrate, midrib bent, secondary veins widely regularly spaced, looping near margin, semicraspedodromous, tertiary veins forming polygonal fields (Knobloch 1961, emended).

Discussion. Knobloch (1961) was the first who corrected Iljinskaya's combination of *Cyclocarya* "*cycloptera*"

for this species (Iljinskaya 1953) to "*cyclocarpa*". The morphology of foliage corresponds in general with the records from Bechlejovice (Kvaček and Walther 2004) and Seifhennersdorf (Walther and Kvaček 2007). So far no associated fruits of *Cyclocarya* have been recovered in the České středohoří Mountains and thus an open nomenclature is applied (see also Walther and Kvaček 2007).

Material studied: Impressions of leaflets, NM-G2833, NM-G2836, NM-G2837, NM-G2929, NM-G2932, NM-G2984, NM-G8589, EK 317–319.

Betulaceae Gray

Betula Linnaeus
Betula alboides Engelhardt

Pl. 15, Fig. 1–2

1870 *Betula alboides* Engelhardt, p. 16, pl. 3, fig. 22–23.
1961 *Betula* cf. *dryadum* Brongniart; Knobloch, p. 266, pl. 14, fig. 3.

Leaves broadly ovate or oval, rounded at base, 26–30 mm long, 13–22 mm wide, margin simple to double dentate, midrib thin, secondary vein in 6–7 pairs, craspedodromous, at medium acute angles (47–62°).

Discussion. The smaller leaves of birch recovered at Knížecí and assigned by Knobloch (1961) to *Betula dryadum* Brongniart match the newly studied lectotype of *B. alboides* from Seifhennersdorf (Walther and Kvaček 2007). However, we do not follow use of this fossil species also for larger forms, as suggested by Walther and Kvaček (2007), and apply a separate species *B. buzekii* for them, as explained below.

Material studied: Leaf impressions, NM-G8588, EK 324–327.

Betula buzekii Kvaček et Walther

Pl. 15, Fig. 3–4

1961 *Betula prisca* Ettingshausen; Knobloch, p. 265, pl. 2, fig. 5, 7, pl. 5, fig. 1–13, pl. 10, fig. 11.
1998 *Betula buzekii* Kvaček et Walther, p. 9, pl. 3, fig. 8–10, text-fig. 5, 13.1.

Leaves long petiolate, ovate to ovate elongate, ca 40 mm long and 25 mm wide, on the apex acute to acuminate, at base rounded to subcordate or slightly decurrent, margin simple to double serrate; midrib straight or slightly bent, secondary veins diverging at angles of (25–) 30–40 (–45)°, mostly opposite, 7–9, 3–5 mm apart, craspedodromous, tertiary veins slightly bent between secondary veins (Knobloch 1961, as *Betula prisca*, emended).

Discussion. The prevailing birch foliage from Knížecí was assigned by Knobloch (1961) to *Betula prisca* Ettingshausen. It corresponds well in gross leaf morphology to the newly established species *B. buzekii* Kvaček et Walther (1998) based on another early Oligocene population from Kundratice.

Material studied: Leaf impressions, NM-G2821, NM-G2822, NM-G2823, NM-G2838, NM-G2841, NM-G2842, NM-G2843, NM-G2844, NM-G2845, NM-G2846, NM-G2847, NM-G2848, NM-G2849, NM-G2882, NM-G2980, NM-G2982, NM-G2994, NM-G4839, NM-G4840, NM-G4841, EK 320–323, some more not numbered.

Alnus Miller
Alnus gaudinii (Heer) Knobloch et Kvaček

Pl. 15, Fig. 5–7

1859 *Rhamnus gaudinii* Heer, p. 79, pl. 124, fig. 4–15, pl. 125, fig. 1, 7, 13.
1961 ? *Pterocarya* aff. *denticulata* (Göppert) Schlechtendal; Knobloch, p. 264, pl. 11, fig. 10.
1961 cf. *Alnus kefersteinii* (Göppert) Unger; Knobloch, p. 267, pl. 2, fig. 9, 11.
1976 *Alnus gaudinii* (Heer) Knobloch et Kvaček, p. 33, pl. 6, fig. 1, 3, pl. 7, fig. 1, 5, pl. 13, fig. 4, pl. 15, fig. 1–4, 7–8, 10–11, 15, 17, pl. 16, fig. 1–5, pl. 19, fig. 15, pl. 20, fig. 10, text-fig. 11–12.

Leaves oblong to narrow ovate, incomplete in length, 23–30 mm wide, on margin simple serrate, teeth blunt, almost glandular, quite widely spaced, secondary veins eucamptodromous-semicraspedodromous, at angles of 30–35°, partly looping, tertiary veins oblique or perpendicular, prominent, higher-order venation distinct.

Discussion. Knobloch (1961) compared some alder leaf impresions from Knížecí with *Alnus kefersteinii*, which is based on generative organs, and erroneously compared some leaf impressions with the Juglandaceae (as ? *Pterocarya* aff. *denticulata* (Göppert) Schlechtendal). Similar foliage occurs e.g. at Kundratice, from where the epidermal structure has also been obtained (Kvaček and Walther 1998).

Material studied: Leaf impressions-compressions, NM-G8603a, b, EK 328–341.

Alnus kefersteinii (Göppert) Unger

Pl. 15, Fig. 8–9

1838 *Alnites kefersteinii* Göppert, p. 364, pl. 41, fig. 1–19.
1847 *Alnus kefersteinii* (Göppert) Unger, p. 115, pro parte, pl. 33, fig. 1–3.
1961 *Betula* sp.; Knobloch, p. 267, pro parte, pl. 5, fig. 14 (non pl. 10, fig. 8 = indeterminable object).
1961 *Alnus* sp.; Knobloch, p. 268, pl. 2, fig. 3, 12.

Alder infructescences 14–21 mm long, 10–12 mm wide, catkins containing in situ pentaporate pollen of *Alnus*.

Discussion. Both female and male reproductive organs are assigned to the same fossil species following the original Göppert's (1838) concept. The same type of *A. gaudinii* foliage has been found in association with similar infructescences at many other Oligocene sites, e.g. Kundratice (Kvaček and Walther 1998) and Seifhennerdorf (Walther and Kvaček 2007).

Material studied: Infructescences and catkins with pollen in situ, NM-G2819, NM-G2820, NM-G2840, EK 342–343.

Carpinus Linnaeus
Carpinus grandis Unger

Pl. 16, Fig. 1

1850 *Carpinus grandis* Unger, p. 409.
1961 *Carpinus orientalis* Gaudin et Strozzi; Knobloch, p. 269, pl. 13, fig. 6, pl. 14, fig. 1.

Leaves ovate, 27–35 mm long, 12–18 mm wide, fine simple or double serrate on margin, subcordate to rounded at base, midrib straight, secondary veins craspedodromous, parallel, densely spaced, tertiary veins not preserved.

Discussion. The above described hornbeam foliage may not be placed without question in the above relatively formal taxon, as it is accompanied at various sites either by fruits of the *C. betulus* type or the *C. orientalis* type described below.

Material studied: Leaf impressions, NM-G8587, NM-G8601, EK 345–348, 358.

Carpinus roscheri Kvaček et Walther

Pl. 16, Fig. 2–3

1961 *Betula brongniartii* Ettingshausen; Knobloch, p. 266, pl. 2, fig. 1–2, 6.
2007 *Carpinus roscheri* Kvaček et Walther; Walther and Kvaček, p. 105, pl. 10, fig. 1–5, text-fig. c–e.

Leaves broadly ovate, 45–65 mm long, 31–39 wide, base rounded to subcordate, margin coarsely double serrate, midrib almost straight, thick, secondary veins regularly parallel, at angles of 50°, in leaf base up to 70°, opposite or slightly alternate, in 10 pairs ca. 6 mm apart.

Discussion. Foliage similar to the newly described fossil species *C. roscheri* from Seifhennersdorf (Walther and Kvaček 2007) was recovered by Knobloch (1961, as *Betula brongniartii*) also at Knížecí. As at Seifhennersdorf this type of foliage is accompanied by involucres, assigned to *Carpinus cordataeformis* and differing from the *C. orientalis* – type in shallow lobed margins.

Material studied: Leaf impressions, NM-G2816a, b, NM-G2817, NM-G2818, NM-G2821, NM-G2825, NM-G2981, EK 344.

Carpinus cordataeformis Mai

Pl. 16, Fig. 6–7

1963 *Carpinus cordataeformis* Mai, p. 55, pro parte, pl. 4, fig. 1–2, text-fig. 6a–b.

Involucrum elongate, very shallow bluntly dentate on one side partly covering the fruit, and almost entire on the opposite side.

Discussion. Similar fruits accompany leaves of *C. roscheri* at Seifhennersdorf (Walher and Kvaček 2007).

Material studied: Involucres, NM-G2995b, EK 349.

Carpinus mediomontana Mai

Pl. 16, Fig. 4–5

1961 *Carpinus neilreichii* Kováts; Knobloch, p. 268, pl. 12, fig. 3.
1963 *Carpinus cordataeformis* Mai, p. 55, pro parte, pl. 4, fig. 3–4, text-fig. 6d.
1978 *Carpinus mediomontana* Mai; Mai and Walther, p. 68, pl. 6, fig. 6, pl. 28, fig. 21–27.

According to Knobloch (1958, translated from Czech) the involucres are asymmetric, not divided into lobes, on one side entire, on the opposite coarsely dentate with double denticulate larger teeth, venation palmate, including up to 7 basal primary veins, thicker stretching to the teeth, thinner veinlets ending before margin at about 2/3 of the involucre, higher order veins perpendicular or slightly oblique.

Discussion. Similar involucres and fruits have been found at Seifhennersdorf associated with foliage of *C. grandis* (Walther and Kvaček 2007). At Knížecí they occur quite often and clearly prevail over *Carpinus cordataeformis*.

Material studied: Involucres, partly with fruits, NM-G2998b, NM-G8586, EK 350–356, 405, some more not numbered.

Salicaceae Mirbel

Populus Linnaeus
Populus zaddachii Heer

Pl. 17, Fig. 4–6

1859 *Populus zaddachii* Heer, p. 307
1869 *Populus zaddachii* Heer; Heer, p. 30, pl. 5, pl. 6, fig. 1–7, pl. 12, fig. 1c.
1961 *Populus zaddachii* Heer; Knobloch, p. 254, pl. 12, fig. 9, pl. 13, fig. 5, pl. 14, fig. 2, 7.

According to Knobloch (1958, translated from Czech), the leaves are broadly ovate elongate to cordate with crenulate-serrate margin, at base rounded to slightly cordate; the midrib is straight extending into a flattened petiole up to 2 mm broad and accompanied by two lateral primaries, from which thin secondary veins arise. They attain a size ranging from 36 mm to more than 120 mm in length and 29–73 mm in width.

Discussion. Knobloch (1961, p. 254) stressed the large variation in leaf morphology of *P. zaddachii* and compared it with the living *P. balsamifera* L. This fossil species typical of the European Oligocene (see Mai and Walther 1978) is known from several other Oligocene sites in North Bohemia and Saxony (see Walther and Kvaček 2007).

Material studied: Leaf impressions, NM-G2990, NM-G2991, NM-G8578, NM-G8579a, b, NM-G8590, NM-G8604a, b, EK 359.

Salix Linnaeus
Salix sp.

Pl. 17, Fig. 1–3

1961 *Populus rottensis* Weyland; Knobloch, p. 254, pl. 1, fig. 9, pl. 11, fig. 9.

Leaves narrow lanceolate, up to 85 mm long and 16–18 mm wide, base rounded with thick petiole, margin glandular serrate. Midrib thick, secondary veins quite steep, camptodromous to semicraspedodromous, bent along the margin, lower pair almost opposite. Tertiary veins reticulate.

Discussion. Knobloch (1961) followed Weyland (1937) who suggested similar material from Rott to belong to *Populus* and assigned also his fragmentary impressions to *Populus*, mainly because of lacking intersecondary veinlets. In our opinion these leaf impressions are more comparable with foliage of willows, described from other Oligocene sites as *Salix varians* Göppert with preserved epidermal anatomy important for distinguishing both genera (see Walther in Mai and Walther 1978, Walther and Kvaček 2007).

Material studied: Leaf impressions, NM-G2806, NM-G2893a, b, EK 360a, b, more fragments not numbered.

Anacardiaceae Lindley

Toxicodendron Miller
Toxicodendron herthae (Unger) Kvaček et Walther

Pl. 18, Fig. 1

1849 *Rhus herthae* Unger, p. 6 (non pl. 14, fig. 21= *Fagus* sp.).
1850 *Rhus herthae* Unger; Unger, p. 473.
1961 *Rhus herthae* Unger; Knobloch, p. 286, pl. 13, fig. 4.
1998 *Toxicodendron herthae* (Unger) Kvaček et Walther, p. 27, pl. 15, fig. 3–8, text-fig. 13.16.

Leaflets oval, very fragmentary, on the apex bluntly acute, on margin irregularly bluntly coarsely serrate, midrib straight, distinct, secondary veins bent, craspedodromous, accompanied by single intersecondaries, not reaching the margin, tertiary veins oblique. Resin ducts have been recorded in the mesophyll during maceration. Epidermal structure not preserved except distinct and dense wavy cuticle striation.

Discussion. Fragmentary specimens clearly correspond with the more complete material from Bechlejovice, Kundratice and other sites of North Bohemia and Saxony, from where this well recognizable accessory element has been reported (Kvaček and Walther 1998, 2004). For nomenclatural details see Kovar-Eder et al. (2004).

Material studied: Impressions of fragmentary leaflets, NM-G2916a, b, EK 361.

Sapindaceae Jussieu

Acer Linnaeus
Acer angustilobum Heer

Pl. 6, Fig. 7, Pl. 18, Fig. 2–3

1859 *Acer angustilobum* Heer, p. 57, pl. 117, fig. 25a, pl. 118, fig. 4–9.
1961 *Acer* cf. *angustilobum* Heer; Knobloch, p. 285, pl. 9, fig. 4, pl. 11, fig. 4.

Leaves deeply tricuspidate, blades 19 to more than 65 mm long and 22–74 mm wide, lobes of almost the same width, with subparallel margins, widely simple dentate. Abaxial cuticle fine papillate.

Discussion. Maple leaves with a prominently double dentate middle lobe have usually been assigned to *Acer palaeosaccharinum* Stur but transitional forms connect them with typical *Acer angustilobum* with only simple dentation on the main lobe. Both fossil morpho-types are connected with transition as expressed in the Procházka's monographs (Procházka 1952, Procházka and Bůžek 1975) by establishing infraspecific taxa (*Acer palaeosaccharinum* forma *subplatanoides* Procházka et Bůžek and forma *subdasycarpoides* Procházka et Bůžek). We apply the same system as in Knobloch (1961) and maintain both fossil species independently. The epidermal structure obtained from one fragmentary specimen corresponds exactly to the structure described for *A. angustilobum* from Seifhennersdorf (Walther and Kvaček 2007, p. 117). We follow this treatment stressing that foliage from the České středohoří Moutains assigned to *A. angustilobum* is difficult to discriminate from some forms of *A. palaeosaccharinum* as described below, which differ in epidermal anatomy (Walther 1972).

Material studied: Leaf impressions, NM-G2877, NM-G2993, NM-G8607, NM-G11505a, b, EK 363–371.

Acer palaeosaccharinum Stur

Pl. 18, Fig. 6–7

1867 *Acer palaeosaccharinum* Stur, p. 177, pl. 5, fig. 8.
1961 *Acer palaeosaccharinum* Stur; Knobloch, p. 284, pl. 1, fig. 11, pl. 9, fig. 3, 5–8, 10, pl. 9, fig. 6–7.

Knobloch (1958) described leaf forms which he assigned to *Acer palaeosaccharinum* Stur as follows (translation from Czech): "Leaves 3–5 lobed, base rounded to subcordate, margin widely simple to double dentate with teeth of different size. Venation palmate, basal veins at 40–50°, secondary veins craspedodromous, only slightly bent, tertiary veins forming polygonal fields." The blades are 16 to 76 mm long and 18 to 85 mm wide. The epidermal structure was not preserved.

Discussion. This species prevails in the Knížecí leaf assemblage. As noted above, aberrant leaf forms of *Acer palaeosaccharinum* can be misinterpreted as *A. angustilobum*.

Material studied: Leaf impressions, NM-G2814, NM-G2872, NM-G2874, NM-G2875, NM-G2876, NM-G2879, NM-G2880, NM-G2900, NM-G8605, EK several impressions not numbered.

Acer integrilobum Weber

Pl. 18, Fig. 4

1852 *Acer integrilobum* C.O. Weber, p. 196, pl. 22, fig. 5a–5b (non fig. 5c).

Leaf trilobate, ca. 20 mm long and fragmentary in width, lobes entire-margined.

Discussion. Such maple leaves with almost entire margin are rare in the Oligocene leaf assemblages of the České středohoří Mountains (Walther 1972, Kvaček and Walther 1998). They occur commonly in the Oligocene localities Rott and Seifhennersdorf and differ from entire-margined trilobed forms of *A. integerrimum* (Viviani) Massolongo in acuminate apices of lobes (Walther 1972).

Material studied: Leaf impression, EK 362.

Acer sp.

Pl. 18, Fig. 5

1961 *Acer* sp.; Knobloch, p. 286, pl. 7, fig. 8, pl. 11, fig. 8.

Isolated mericarps of winged double samaras, 22–45 mm long, 8–35 mm wide, seed part rounded, 5–7 mm in diameter, attachment scar at a very narrow angle to the fruit length.

Discussion. Knobloch (1961) proposed that the fruits occurring at Knížecí belong to foliage of *A. palaeo-saccharinum* which prevails in the Knížecí plant assemblage. Such fruits have been described as *Acer cyclospermum* Göppert from the upper Oligocene deposits in the Rhineland (Winterscheid and Kvaček 2014). The connection between fossil maple fruits and foliage has not so far been firmly resolved.

Material studied: Detached maple mericarps, NM-G2860, NM-G2992, NM-G8596, EK 372–373.

Malvaceae Jussieu

Craigia W.W. Smith et W.E. Evans
Craigia bronnii (Unger) Kvaček, Bůžek et Manchester

Pl. 19, Fig. 1–2

1845 *Ulmus bronnii* Unger, p. 79, pro parte, pl. 25, fig. 2–4 (non fig. 1).
1948 *Pteleaecarpum bronnii* (Unger) Weyland, p. 130, pl. 21, fig. 5, text-fig. 5–9.
1961 *Pteleaecarpum bronnii* (Unger) Weyland; Knobloch, p. 280, pl. 6, fig. 11, pl. 13, fig. 12.
1991 *Craigia bronnii* (Unger) Kvaček, Bůžek et Manchester, p. 522.

Winged broadly oval to rounded fruit valves 10–12 mm wide and 12–17 mm long with spindle-shaped medial locule, rarely with a small ovate seed inside. Venation of the wing composed of narrow elongated fields radiating from the locule, steeper in the upper part.

Discussion. These fruit remains agree in size and morphology with other records of the same species, commonly recovered from the Oligocene and Miocene of Central Europe (Kvaček et al. 2005).

Material studied: Detached fruit valves, EK 374–376.

Cornaceae Berchtold et J. Presl

Cornus Linnaeus
Cornus studeri Heer

Pl. 19, Fig. 4

1859 *Cornus studeri* Heer, p. 27, pl. 105, fig. 18–21.
1861 *Rhamnus graeffii* Heer; Heer, p. 287, pl. 10, fig. 13.
1961 *Cornus studeri* Heer; Knobloch, p. 288, pl. 13, fig. 1–3, 11.

Leaves rounded elliptical, blade 31–74 mm long, 17–50 mm wide, entire-margined, secondary veins very steep, directed subparallel towards the apex. Tertiary venation not preserved.

Discussion. The exact affinity of this morpho-type is equivocal (see discussion in Knobloch 1961, p. 288) and is not supported by any epidermal study.

Material studied: Leaf impressions, NM-G2999, NM-G8598, NM-G8606, NM-G2883a, b, EK 378–380.

Hydrangeaceae Dumortier

Hydrangea Linnaeus
Hydrangea microcalyx Sieber

Pl. 19, Fig. 3

1880 *Hydrangea microcalyx* Sieber, p. 16, pro parte, fig. 26–27, 31.
1961 *Paliurus thurmannii* Heer; Knobloch, p. 287, pl. 11, fig. 11.

Petaloid sepal entire-margined, described by Knobloch (1958, as *Paliurus thurmannii* translated from Czech) as follows: “The main vein is straight and accompanied on both sides by bent basal veins running towards the apex. The outer side of the basal veins is bordered by small loops. The inner area between main veins shows irregularly disposed areoles”. The only specimen available is 18 mm long and 13 mm wide,

Discussion. The single petaloid sepal recovered at Knížecí was erroneously assumed by Knobloch (1961) to represent a leaf impression. Similar, more complete remains of *Hydrangea microcalyx* are also known from Kučlín (Kvaček and Teodoridis 2011), Suletice-Berand (Kvaček and Walther 1995) and Seifhennersdorf (Walther and Kvaček 2007).

Material studied: One sepal impression, NM-G8585.

Oleaceae Hoffmann et Link

Oleinites Cookson
Oleinites hallbaueri (Mai) Sachse

Pl. 6, Fig. 8, Pl. 19, Fig. 5–7

1885 *Carya elaenoides* Unger; Engelhardt, p. 67, pl. 25, fig. 1–4.
1961 *Myrica lignitum* (Unger) Saporta; Knobloch, p. 256, pro parte, pl. 3, fig. 1–2.
1961 cf. *Ilex rottensis* Weyland; Knobloch, p. 282, pl. 13, fig. 10.
1963 *Myrica hallbaueri* Mai, p. 46, pl. 2, fig. 4–6, text-fig. 3a.
2001 *Oleinites hallbaueri* (Mai) Sachse, p. 319, pl. 2, fig. 8–9.

Leaves elongate, up to 142 mm long and 65 mm wide, widely coarsely dentate, acuminate at the apex, rounded at the base, venation semicraspedodromous, midrib straight. Secondary veins regularly spaced, at wide angles, at the ends abruptly looping, and sending side veinlet into the teeth. Simple intersecondaries occasionally present, tertiary venation very fine, forming irregular fields. The cuticle structure poorly preserved, showing straight-walled cells on the adaxial epidermis and peltate trichomes with unicellular base, which is reflected in the outline as a double line.

Discussion. Knobloch (1961) merged this morpho-type with *Myrica lignitum* but stressed the heterogeneity of this species in his concept. Mai (1963) separated it as a new species of *Myrica*. Later studies of the epidermal anatomy (Sachse 2001) confirmed the affinity to the Oleaceae and not to the Myricaceae. Our structure of the peltate trichomes from specimen NM-G2812 matches the pattern found on the holotype (Bůžek et al. 1976).

Material studied: Leaf impressions, NM-G2812, NM-G2828, NM-G2832, NM-G4859a, b, NM-G8602, EK 381–382, more specimens not numbered.

Dicotyledonae inc. fam.

Saportaspermum Meyer et Manchester
Saportaspermum cf. *occidentale* Meyer et Manchester

Pl. 20, Fig. 9

Winged seeds 10 mm long and 4 mm wide matching previous records from the Oligocene and Miocene of North America (Meyer and Manchester 1997) and Central Europe (see Walther and Kvaček 2007).

Discussion. The affinity of these winged seeds described above has not yet been resolved, although such remains regularly accompany similar leaf assemblages of Oligocene and Miocene age. As they have been dispersed by wind and occur sporadically, their parent plants may belong to elements growing far from the nearby vegetation.

Material studied: NM-G11483, EK 394.

Dicotylophyllum Saporta
Dicotylophyllum cf. *heeri* (Engelhardt) Kvaček et Walther

Pl. 20, Fig. 5

cf. 1998 *Dicotylophyllum heerii* (Engelhardt) Kvaček et Walther, p. 14, pl. 6, fig. 5–6, text-fig. 7–8, 13.28.

Fragments of (?) ovate leaves, rounded at base, long petiolate, with two glands next the leaf base, margin glandular serrate-crenate. Venation semicraspedodromous, midrib stout, secondary veins bent along the margin, at wider angles. Poorly preserved cuticle reflects only oval openings of stomata. Cuticle of the midrib is hairless and consists of isodiametric polygonal straight-walled cells.

Discussion. The affinity to *Prunus* is suggested by the presence of glands on the leaf base.

Material studied: Leaf fragments, NM-G11488a, b, NM-G11512.

Dicotylophyllum sp. 1

Pl. 20, Fig. 1

1961 *Juglans acuminata* A. Braun; Knobloch, p. 258, pl. 4, fig. 2.
1961 *Ficus arcinervia* (Rossmässler) Heer; Knobloch, p. 273, pl. 7, fig. 5–6.
1961 cf. *Rhus pteleaefolia* Weber; Knobloch, p. 286, pl. 8, fig. 1.

Leaflets (?) elongate oval, entire-margined, 45–81 mm long, 23–30 mm wide. Midrib straight, thick, secondary veins looping well within the margin. Tertiary veins almost perpendicular to the secondaries, forming loops along the margin. One specimen has a long tip.

Discussion. This entire-margined morpho-type has been assigned to various genera (e.g. *Cedrela* by Palamarev and Petkova 1987) but so far no definite solution has been reached. The foliage is chartaceous, not suitable for cuticle studies.

Material studied: Leaf impressions, NM-G2834, NM-G2857, NM-G2864.

Dicotylophyllum sp. 2

Pl. 20, Fig. 2–3

1961 *Leguminosites* sp.; Knobloch, p. 280, pl. 14, fig. 6.
1998 "*Palaeolobium*" sp. 1; Kvaček and Walther, p. 23, pl. 13, fig. 1–2, text-fig. 13.24.

Leaves long petiolate, entire-margined with narrow elliptical to elongate blade, 19 mm long, 9 mm wide, rounded at apex, cuneate at base.

Discussion. The affinity of these leaf forms is quite uncertain (Kvaček and Walther 1998); Knobloch (1961) believed that such morpho-types may represent foliage of legumes. Contrary to most legume leaflets, the discussed leaf remains are long petiolate and in our opinion may more likely represent simple leaves.

Material studied: Leaf impressions, NM-G8597a, b, EK 383–386.

Dicotylophyllum sp. 3

Pl. 20, Fig. 4

1961 *Juglans* (*Carya*) *bilinica* UNGER; Knobloch, p. 258, pro parte, pl. 4, fig. 9.

Along with specimens identified as *Juglans* (*Carya*) *bilinica* and included here to *Cyclocarya* (see above) one broader leaf fragment ca. 45 mm wide assigned by Knobloch (1961) to *Juglans* deviates in its forked secondaries.

Discussion. This fragmentary specimen may indeed represent a large leaflet, but a better interpretation would be as *Fraxinus* rather than *Juglans.*

Material studied: Leaf impression, NM-G2837.

Dicotylophyllum sp. 4

Pl. 20, Fig. 8

1961 *Sibirea rottensis* WEYLAND; Knobloch, p. 278, pl. 8, fig. 12.

Leaf elongate, entire-margined, in the preserved specimen a length of 50 mm, 11 mm wide, apex bluntly rounded. Venation brochidodromous, irregular, midrib straight, secondary veins very steep, almost parallel with the midrib, forming elongated fields. Tertiary venation very fine, reticulate (according to Knobloch 1958, 1961, emended).

Discussion. Knobloch (1961) compared the single fragment described above with foliage of *Sibirea rottensis* WEYLAND, 1941 from the upper Oligocene of Rott. This interpretation has not been confirmed so far.

Material studied: Leaf impression, NM-G2889.

Dicotylophyllum sp. 5

Pl. 20, Fig. 7

1961 *Aesculus* cf. *palaeocastanum* ETTINGSHAUSEN; Knobloch, p. 283, pl. 1, fig. 6, pl. 8, fig. 12.

Leaflets (?) elongate, shortly petiolulate, blades incomplete, more than 36 mm long, 31 mm wide, margin double serrate, midrib bent, quite thick. Secondary veins at narrow angles, craspedodromous. Tertiary veins perpendicular or oblique between secondary veins.

Discussion. Knobloch (1961) interpreted one leaf impression (NM-G2866) as a leaflet belonging to *Aesculus* and another fragment (NM-G8594) as a slightly different form of the same species (Knobloch 1958). In our opinion the affinity of both these impressions is very doubtful.

Material studied: Leaf impressions, NM-G2866, NM-G8594.

Dicotylophyllum sp. 6

Pl. 20, Fig. 5

1961 *Celastrus persei* UNGER; Knobloch, p. 281, pl. 8, fig. 6.

Leaf oval, 23 mm long, 17 mm wide, widely cuneate at base, apex bluntly acute, margin crenulate, venation semi-craspedodromous, secondary veins at wide angles, bent along the margin, sending out veinlets which end between the teeth.

Discussion. Knobloch (1961) believed according to the architecture and venation of this single impression that it certainly belonged to *Celastrus*. Perhaps more reasons should be put forward for such a determination, although the morpho-type is quite distinct and noteworthy.

Material studied: Leaf impression, NM-G2862.

Carpolithes STERNBERG
Carpolithes sp. 1

Pl. 20, Fig. 11

1961 ? *Pisonia eocenica* ETTINGSHAUSEN; Knobloch, p. 289, pl. 1, fig. 10

A minute narrow elliptical object with a long bent stalk or style.

Discussion. This fossil described from Knížecí resembles a separated fruitlet of *Platanus neptuni* but no additional material is available to support a more precise identification.

Material studied: ? fruitlet impression, NM-G2813 a, b.

Carpolithes sp. 2

Pl. 20, Fig. 10

1961 *Carpolithes* sp.; Knobloch, p. 289, pl. 8, fig. 11

Flattened rounded unidentifiable seeds (or fruits) ca. 2.5 mm in diameter, partly on a short stout stalk.

Discussion. The objects are poorly preserved and require a more detailed comparative study.

Material studied: Compressed seeds or fruits, NM-G2870, EK 396–398.

Excluded objects inc. sed.

1961 *Betula* sp.; Knobloch, p. 267, pro parte, pl. 10, fig. 6.

The fossil originally interpreted as a birch catkin did not yield any pollen. On detailed examination it seemed to be composed of fragments of fish scales and may represent a coprolite.

Material studied: One enigmatic fossil, NM-G2886a.

Comparison with other palaeobotanical sites in north Bohemia and adjacent Saxony

The Knížecí plant assemblage is from a recently examined site and the available collection is not so extentsive in comparison with historical localities, such as e.g.

Kundratice, Suletice and Kučlín in the České středohoří Mountains and Seifhennersdorf in Saxony. The flora falls undoubtedly into the Kundratice-Seifhennersdorf floral assemblage, as defined by Kvaček and Walther (1998, for a more detailed comparison see Walther and Kvaček 2007, p. 132–4). The flora with the closest relationship to the Knížecí flora appears to be the Seihennersdorf assemblage; this is also supported by the geographic and chronostratigraphic proximity. Several, new and only partly proven elements stress common features of both sites, namely the combination of conifers (*Taxodium*, *Tetraclinis*, *Torreya*) and angiosperms (*Platanus neptuni*, *Daphnogene*, *Toxicodendron*, the same species of *Ulmus*, *Carpinus*, *Betula*, Juglandaceae, *Acer*, *Rosa*, *Ampelopsis* etc.). There are only a few noteworthy differences. The occurence of *Taxus engelhardtii* in Knížecí is shared with Kundratice, *Liriodendron haueri* and *Pinus* cf. *rigios* with Žichov and *Comptonia* with Suletice. The restricted spectrum of the Lauraceae and other termophilous elements (e.g. *Sloanea*) is similar to that of Bechlejovice. Although the dating of Knížecí is not exact, the prevailing deciduous character of the angiosperms suggests that Knížecí can be assumed as being from the early stages of Oligocene floras in North Bohemia (Bechlejovice, Kundratice) and it shows similarities with the flora of Roudníky (Kvaček et al. 2014) dated into the latest Eocene. Significant differences can be found between Knížecí and Kučlín (Kvaček and Teodoridis 2011), the latter lacking most of the deciduous angiosperms noted above. This Eocene flora, together with some others from North Bohemia with *Doliostrobus* (drill cores Hlinná and Lbín), deserves more detailed analysis in the future based on evidence of angiosperms from sites adjacent to Kučlín. These floras may represent a new plant complex contemporaneous with that of Hordle-Zeitz sensu Mai (1995). Younger Oligocene sites (Markvartice, Flörsheim) indicate warming trends reflected in the higher diversity of termophilous elements, namely the Lauraceae. The Knížecí flora is in this respect quite poor, containing only *Daphnogene* and *Laurophyllum medimontanum*.

Implications on vegetation and palaeoclimatology

The IPR analysis of the plant assemblage of Knížecí produces the following scores for the key components, i.e. broad-leaved deciduous (BLD) – 78.7 %, broad-leaved evergreen (BLE) – 17.8 %, sclerophyllous + legume-like (SCL+LEG) – 3.6 % and zonal herbaceous (ZONAL HERB) – 2.1 %. This indicates a transitional zonal vegetation type between Mixed Mesophytic Forest and Broad-leaved Deciduous Forest sensu Teodoridis et al. (2011). The species diversity is not very high and some morphotypes included in the analysis may contain more natural species (e.g. *Laurophyllum* sp.), some others are not preserved well enough for accurate evaluation. However this ecotonal type of zonal vegetation was also estimated for the other early Oligocene plant assemblages of Kundratice (Kvaček and Walther 1998), Hammerunterwiesenthal (Walther 1998), Seifhennersdorf (Walther and Kvaček 2007), Suletice-Berand (Kvaček and Walther 1995) and Markvartice-Veselíčko (Bůžek et al. 1976) – for detail see Teodoridis and Kvaček (2015).

The studied material is in some cases fragmentary and not really suitable for statistical physiognomical studies, such as CLAMP and any results must be taken cautiously. The CLAMP results (using the 144 site calibration dataset) estimate the climatic character of Hrazený to be as follows: mean annual temperature (MAT) – 11.3 °C, warmest month mean temperature (WMMT) – 22.1 °C, coldest month mean temperature (CMMT) – 1.7 °C, precipitation during 3 consecutive wettest months (3-WET) – 1357 mm and precipitation during 3 consecutive driest months (3-DRY) – 254 mm. The MAT proxy derived from Leaf Margin Analysis sensu Su et al. (2010) shows a result comparable with CLAMP, i.e., 11.2 °C (Sampling Error is 2.5 °C). We are indebted to Torsten Utescher, who kindly provided parallel proxy data based on the Coexistence Approach (CA) for the following characters: MAT (14.6–18.9°C) WMMT (24.7–28.3°C), CMMT (5–12.2°C) and mean annual precipitation – MAP (979–1213 mm). The CA estimates produces higher values than those from physiognomic techniques. In general, the proxy-data from Knížecí fit well into the palaeoclimatic evolution of the Bohemian Massif during the Palaeogene, as formulated by Teodoridis and Kvaček (in press), corresponding to a slight warming trend after the late Eocene/early Oligocene climatic collapse.

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Explanation of the plates

PLATE 1

***Muscites* sp.**

1. Most complete specimen, NM-G11514 (scale bar 5 mm).
2. Counter-impression to the missing Knobloch's original (1961, pl. 10, fig. 1). NM-G2888 (scale bar 3 mm).
3. Magnified detail of the previous figure (scale bar 1 mm).

***Pinus* cf. *rigios* (Unger) Ettingshausen**

4. Fascicle of three needle leaves joined with sheat, EK 237a (scale bar 5 mm).
5. Three fragmentary needle leaves, obviously from the same fascicle, EK 238 (scale bar 5 mm).

***Taxodium dubium* (Sternberg) Heer**

6. Most complete shoot with cuticle structure shown in Pl. 2, Fig. 1, Knobloch's original (1961, pl. 2, fig. 8), NM-G2815a (scale bar 5 mm).
7. Impression of another shoot, Knobloch's original (1961, pl. 10, fig. 2), NM-G2892 (scale bar 5 mm).

***Tetraclinis salicornioides* (Unger) Kvaček**

8. Fragment of a branched twig composed of wide medial segments with attached simple ultimate segments, EK 243 (scale bar 5 mm).
9. Another branched twig fragment, EK 242 (scale bar 9 mm).
10. Simple twig segment with cuticle isolated from the rock shown in Pl. 2, Fig. 2–3, NM-G11507 (scale bar 3 mm).

***Taxus engelhardtii* Kvaček**

11. Needle base with cuticle, NM-G11482a (scale bar 3 mm).
12. Short needle with cuticle, NM-G11481a (scale bar 3 mm).
13. Needle base with cuticle, NM-G11501a (scale bar 3 mm).

***Torreya bilinica* Saporta et Marion**

14. Needle fragment with cuticle (see arrow), NM-G11508a (scale bar 3 mm).
15. Needle fragment with cuticle (see arrow), NM-G11510a (scale bar 1.5 mm).
16. Complete needle compression with cuticle, NM-G11509a (scale bar 5 mm).

PLATE 2

***Taxodium dubium* (Sternberg) Heer**

1. Cuticle of the specimen shown in Pl. 1, Fig. 6 reflecting stomata, NM-G2815b (scale bar 100 µm).

***Tetraclinis salicornioides* (Unger) Kvaček**

2. Cuticle of the specimen shown in Pl. 1, Fig. 10 reflecting stomatal zone, NM-G11507a (scale bar 100 µm).
3. Cuticle of the same specimen shown in Pl. 1, Fig. 10 reflecting non-stomatal zone, NM-G11507a (scale bar 100 µm).

***Taxus engelhardtii* Kvaček**

4. Cuticle of the specimen shown in Pl. 1, Fig. 13 reflecting medial non-stomatal zone, NM-G11501b (scale bar 100 µm).
5. Cuticle of the specimen shown in Pl. 1, Fig. 13 reflecting medial stomatal zone, NM-G11501b (scale bar 100 µm).

***Torreya bilinica* Saporta et Marion**

6. Cuticle of the specimen NM-G11509a reflecting lateral non-stomatal zone showing papillae near stomatal band, NM-G11509b (scale bar 100 µm).
7. Stomatal band of the previous specimen, NM-G11509b (scale bar 100 µm).
8. Cuticle of the specimen shown in Pl. 1, Fig. 15 reflecting stomatal band devoid of distal parts of papillae, NM-G11510b (scale bar 100 µm).

PLATE 3

***Liriodendron haueri* Ettingshausen**

1. Long petiolate leaf base, Knobloch's original (1961, pl. 7, fig. 1), NM-G2859 (scale bar 10 mm).
2. Shallowly lobed small leaf, Knobloch's original (1961, pl. 14, fig. 4, as *Styrax* sp.), NM-G8591 (scale bar 10 mm).
3. Lobed leaf with cuticle shown in Pl. 6, Fig. 1, Knobloch's original (1961, pl. 7, fig. 3), NM-G2856a (scale bar 10 mm).
4. Incomplete lobed leaf with well-preserved venation, NM-G2997 (scale bar 10 mm).

PLATE 4

***Laurophyllum medimontanum* Bůžek, Holý et Kvaček**

1. Leaf compression with cuticle shown in Pl. 6, Fig. 2, NM-G3002a (scale bar 10 mm).
2. Leaf impression, Knobloch's original (1961, pl. 8, fig. 9, as *Salix longa* A. Braun), NM-G2563a (scale bar 10 mm).

***Laurophyllum* sp.**

3. Leaf impression, Knobloch's original (1961, pl. 10, fig. 7, as cf. *Laurus primigenia* Unger), NM-G2890a (scale bar 5 mm).
4. Impression of a leaf fragment, EK 258 (scale bar 5 mm).
5. Leaf compression with cuticle shown in Pl. 6, Fig. 3, Knobloch's original (1961, pl. 10, fig. 4, as *Laurus princeps* Heer), NM-G2885a (scale bar 10 mm).
6. Petiolate base of leaf impression, Knobloch's original (1961, not figured, as ? *Benzoin attenuatum* Heer), NM-G2977 (scale bar 10 mm).
7. Impression of leaf fragment, Knobloch's original (1961, pl. 10, fig 8), NM-G2884 (scale bar 10 mm).

PLATE 5

***Daphnogene cinnamomifolia* (Brongniart) Unger**

1. Leaf impression with cuticle, Knobloch's original (1961, pl. 1, fig. 7, as *Cinnamomum scheuchzeri* (Heer) Frenzen), NM-G2811a (scale bar 5 mm).

2. Broad leaf fragment with cuticle, NM-G11497 (scale bar 5 mm).
3. Small leaf compression with cuticle, NM-G11500a (scale bar 5 mm).
4. Narrow leaf impression, EK 247(scale bar 5 mm).

***"Typha" latissima* A. Braun**
5. Leaf impression with preserved venation, EK 250 (scale bar 5 mm).
6. Leaf impression with preserved venation, Knobloch's original (1961, pl. 12, fig. 7, as *Typha latissima* A. Braun), NM-G8593 (scale bar 5 mm).
8. Narrow leaf impression longitudinally torn in two parts, EK 253 (scale bar 5 mm).

***Poacites* sp.**
7. Narrow leaf impression, EK 255 (scale bar 5 mm).

***Smilax weberi* Wessel**
9. Impression of incomplete leaf base, Knobloch's original (1961, pl. 15, fig. 9, as *Smilax grandifolia* (Unger) Heer), NM-G8081a (scale bar 5 mm).
10. Impression of almost complete leaf, Knobloch's original (1961, pl. 13, fig. 7, as *Smilax grandifolia* (Unger) Heer), NM-G8608 (scale bar 5 mm).

PLATE 6

***Liriodendron haueri* Ettingshausen**
1. Smooth cuticle of lower leaf side reflecting outlines of stomata obtained from leaf impression published by Knobloch (1961, pl. 7, fig. 3), NM-G2856b (scale bar 50 µm).

***Laurophyllum medimontanum* Bůžek, Holý et Kvaček**
2. Strongly papillate abaxial cuticle of lower leaf side of leaf compression shown in Pl. 4, Fig. 1, NM-G3704c (scale bar 50 µm).

***Laurophyllum* sp.**
3. Thin cuticle with a trichome base from lower leaf side of leaf compression shown in Pl. 4, Fig. 5, NM-G2885b (scale bar 50 µm).

***Daphnogene cinnamomifolia* (Brongniart) Unger**
4. Hairy abaxial cuticle of leaf compression shown in Pl. 5, Fig. 1, NM-G2811b (scale bar 50 µm).

***Platanus neptuni* (Ettingshausen) Bůžek, Holý et Kvaček**
5. Abaxial cuticle of the specimen shown in Pl. 7, Fig. 2. NM-G11504b (scale bar 50 µm).

***Comptonia difformis* (Sternberg) Berry**
6. Abaxial cuticle with peltate trichomes from the specimen shown in Pl. 13, Fig. 3, NM-G11506b (scale bar 50 µm).

***Acer angustilobum* Heer**
7. Papillate abaxial cuticle from the specimen shown in Pl. 18, Fig. 3, NM-G11505b (scale bar 50 µm).

***Oleinites hallbaueri* (Mai) Sachse**
8. Adaxial cuticle with peltate trichome from the specimen shown in Pl. 19, Fig. 5, NM-G2812b (scale bar 50 µm).

***Engelhardia orsbergensis* (Wessel et Weber) Jähnichen, Mai et Walther**
9. Abaxial cuticle from the specimen shown in Pl. 14, Fig. 5, NM-G11511b (scale bar 50 µm).

PLATE 7

***Platanus neptuni* (Ettingshausen) Bůžek, Holý et Kvaček**
1. Leaf impression, Knobloch's original (1961, pl. 10, fig. 12, as *Ceratopetalum bilinicum* Ettingshausen), NM-G2887 (scale bar 5 µm).
2. Leaf compression with cuticle, NM-G11504a (scale bar 5 mm).
3. Leaf compression with cuticle, NM-G11503a (scale bar 10 mm).
4. Leaf compression with cuticle, EK 260 (scale bar 5 mm).
5. Isolated stamen, NM-G11918c (scale bar 1 mm).
6. Infructescence, Knobloch's original (1961, pl. 3, fig. 9 left, as *Comptonia difformis* (Sternberg) Berry), NM-G2830b (scale bar 5 mm).
7. Isolated stipule, EK 263 (scale bar 3 mm).

***Cercidiphyllum crenatum* (Unger) R. Brown**
8. Impression of broad leaf, Knobloch's original (1961, pl. 15, fig. 1), NM-G2998a (scale bar 10 mm).
9. Impression of elliptic leaf, Knobloch's original (1961, pl. 15, fig. 3), NM-G8595 (scale bar 10 mm).

PLATE 8

***Ampelopsis hibschii* Bůžek, Kvaček et Walther**
1. Leaf impression, Knobloch's original (1961, pl. 8, fig. 3, as *Vitis* sp.), NM-G2869 (scale bar 10 mm).
2. Impression of leaf apex with separated tip, EK 267 (scale bar 10 mm).
3. Impression of leaf base, EK 271 (scale bar 10 mm).
4. Leaf fragment with separated tip, EK 270 (scale bar 10 mm).
5. Leaf base with petiole, Knobloch's original (1961, pl. 10, fig. 3, as *Platanus* cf. *aceroides* Göppert), NM-G2891 (scale bar 10 mm).
6. Leaflet, Knobloch's original (1961, pl. 7, fig. 7, as *Zelkova ungeri* Kováts), NM-G2855 (scale bar 10 mm).

PLATE 9

***Parvileguminophyllum haeringianum* (Ettingshausen) Kvaček comb. n.**
1. Leaflet, Knobloch's original (1961, pl. 14, fig. 8, as *Mimosites* cf. *haeringiana* Etingshausen), NM-G8583 (scale bar 3 mm).
2. Leaflet, Knobloch's original (1961, pl. 12, fig. 1, as *Mimosites* cf. *haeringiana* Ettingshausen), NM-G8592 (scale bar 3 mm).
3. Leaflet, NM-G11487 (scale bar 3 mm).

***Phaseolites* sp. 1**
4. Leaflet base, Knobloch's original (1961, pl. 5, fig. 15), NM-G2839 (scale bar 5 mm).

***Phaseolites* sp. 3**
5. Fragmentary long petiolate leaf with fragmentary leaflets, Knobloch's original (1961, pl. 11, fig. 5, as ?*Cassia* sp.), NM-G2903 (scale bar 5 mm).

***Phaseolites* sp. 4**
6. Emarginate leaflet, Knobloch's original (1961, pl. 10, fig. 10, as *Dalbergia bella* Heer), NM-G2862b (scale bar 5 mm).

***Phaseolites* sp. 2**
7. Leaflet base, EK 276 (scale bar 5 mm).
8. Leaflet base, Knobloch's original (1961, pl. 8, fig. 10, as *Leguminosites* sp.), NM-G2868 (scale bar 5 mm).

PLATE 10

***Rosa lignitum* Heer**
1. Leaflet, Knobloch's original (1961, pl. 8, fig. 2, as ? *Rhus pyrrhae* Unger), NM-G2866 (scale bar 5 mm).
2. Leaflet, NM-G2876b (scale bar 5 mm).
3. Leaflet, EK 285 (scale bar 5 mm).
4. Leaflet, EK 282 (scale bar 5 mm).
5. Small leaflet, EK 284 (scale bar 5 mm).
6. Small leaflet, EK 283 (scale bar 5 mm).
7. Leaflet, EK 280 (scale bar 5 mm).
8. Leaflet, Knobloch's original (1961, pl. 9, fig. 11, as ? *Rhus pyrrhae* Unger), NM-G2871 (scale bar 5 mm).
9. Leaflet, EK 279 (scale bar 5 mm).

***Crataegus pirskenbergensis* Knobloch**
10. Leaf impression, Knobloch's original (1961, pl. 8, fig. 7), NM-G2861a (scale bar 10 mm).
11. Leaf impression, Knobloch's original (1961, pl. 8, fig. 8, holotype), NM-G2867a (scale bar 10 mm).

PLATE 11

***Ulmus fischeri* Heer**
1. Leaf impression, Knobloch's original (1961, pl. 1, fig. 7, as *Zelkova ungeri* Kováts), NM-G2807 (scale bar 10 mm).
2. Narrow leaf impression, Knobloch's original, (1961, pl. 1, fig. 2, as *Zelkova ungeri* Kováts), NM-G2804 (scale bar 5 mm).
3. Leaf base, Knobloch's original (1961, pl. 7, fig. 4, as *Zelkova ungeri* Kováts), NM-G2868 (scale bar 5 mm).
4. Leaf impression, EK 287 (scale bar 10 mm).

***Zelkova zelkovifolia* (Unger) Bůžek et Kotlaba**
5. Leaf base, EK 288 (scale bar 10 mm).

PLATE 12

***Celtis pirskenbergensis* (Knobloch) Kvaček et Walther**
1. Leaf base, Knobloch's original (1961, pl. 6, fig. 9, as *Celtis begonioides* Göppert), NM-G2851a (scale bar 10 mm).
2. Leaf apex, Knobloch's original (1961, pl. 6, fig. 5, as *Celtis begonioides* Göppert var. *pirskenbergensis* Knobloch), NM-G2852 (scale bar 10 mm).
3. Leaf impressions showing leaf apex and a part of the base, Knobloch's original (1961, pl. 6, fig. 8, as *Celtis begonioides* Göppert var. *pirskenbergensis* Knobloch, holotype), NM-G2850a (scale bar 10 mm).
4. Leaf fragment, NM-G2979, Knobloch's original (1961, not figured, as *Celtis begonioides* Göppert var. *pirskenbergensis* Knobloch) (scale bar 10 mm).
5. Leaf fragment, counterimpression to Knobloch's original (1961, pl. 6, fig. 3, as *Celtis begonioides* Göppert var. *pirskenbergensis* Knobloch), NM-G2853b (scale bar 10 mm).
6. Leaf base, Knobloch's original (1961, pl. 12, fig. 4, as *Celtis begonioides* Göppert), NM-G8600 (scale bar 10 mm).

PLATE 13

***Comptonia difformis* (Sternberg) Berry**
1. Leaf apex, EK 209 (scale bar 10 mm).
2. Middle part of leaf, Knobloch's original (1961, pl. 3, fig. 10), NM-G2827 (scale bar 10 mm).
3. Fragmentary leaf compression with cuticle, NM-G11506a (scale bar 5 mm).
4. Almost complete leaf, EK 298 (scale bar 10 mm).
5. Narrow leaf without apex, EK 300 (scale bar 10mm).
6. Lower part of leaf, Knobloch's original (1961, pl. 3, fig. 6), NM-G2826 (scale bar 10 mm).
7. Magnified base of the previous specimen NM-G2826 (scale bar 5 mm).
8. Minute leaf impression, NM-G2987 (scale bar 1.5 mm).
9. Narrow leaf without apex, EK 291 (scale bar 10 mm).

PLATE 14

***Engelhardia orsbergensis* (Wessel et Weber) Jähnichen, Mai et Walther**
1. Leaflet, Knobloch's original (1961, pl. 12, fig. 5, as *Myrica lignitum* (Unger) Saporta), NM-G8582 (scale bar 10 mm).
2. Leaflet fragment, Knobloch's original (1961, pl. 1, fig. 13, as *Myrica lignitum* (Unger) Saporta), NM-G2805 (scale 10 bar mm).
3. Large leaflet, NM-G11515b (scale bar 10 mm).
4. Leaflet fragment, Knobloch's original (1961, pl. 2, fig. 10, as *Myrica lignitum* (Unger) Saporta), NM-G2824 (scale bar 10 mm).
5. Fragmentary compression of base with cuticle, NM-G11511a (scale bar 5 mm).

***Engelhardia macroptera* (Brongniart) Unger**
6. Fragmentary involucre, EK 312 (scale bar 10 mm).

***Carya fragiliformis* (Sternberg) Kvaček et Walther**
7. Leaflet base, counter-impression to Knobloch's original (1961, pl. 9, fig. 12, as *Carya serraefolia* (Göppert) Kräusel), NM-G2878b (scale bar 10 mm).

***Cyclocarya* sp.**
8. Upper part of compound leaf, Knobloch's original (1961, pl. 15, fig. 6, as *Cyclocarya cyclocarpa* (Schlechtendal) Knobloch), NM-G2932 (scale bar 10 mm).

PLATE 15

***Betula alboides* Engelhardt**
1. Fragmentary leaf, Knobloch's original (1961, pl. 14, fig. 3, as *Betula* cf. *dryadum* Brongniart), NM-G8588 (scale bar 10 mm).
2. Almost complete leaf, EK 324 (scale bar 5 mm).

***Betula buzekii* Kvaček et Walther**
3. Almost complete leaf, Knobloch's original (1961, pl. 5, fig. 11, as *Betula prisca* Ettingshausen), NM-G2847 (scale bar 10 mm).
4. Almost complete leaf, Knobloch's original (1961, pl. 5, fig. 4, as *Betula prisca* Ettingshausen), NM-G2848 (scale bar 10 mm).

***Alnus gaudinii* (Heer) Knobloch et Kvaček**
5. Leaf base, EK 339 (scale bar 10 mm).
6. Leaf base, EK 330 (scale bar 10 mm).
7. Leaf impression, Knobloch's original (1961, pl. 11, fig. 10, as ? *Pterocarya* aff. *castaneaefolia* (Göppert) Schlechtendal), NM-G8603 (scale bar 10 mm).

***Alnus kefersteinii* (Göppert) Unger**
8. Infructescence, Knobloch's original (1961, pl. 2, fig. 12, as *Alnus* sp.), NM-G2819a (scale bar 5 mm).
9. Male catkin, Knobloch's original (1961, pl. 5, fig. 14, as *Betula* sp.), NM-G2840 (scale bar 5 mm).

PLATE 16

***Carpinus grandis* Unger**
1. Leaf impression, Knobloch's original (1961, pl. 14, fig. 1, as *Carpinus orientalis* Gaudin et Strozzi), NM-G8587 (scale bar 10 mm).

***Carpinus roscheri* Kvaček et Walther**
2. Smaller leaf fragment, Knobloch's original (1961, pl. 2, fig. 6, as *Betula brongniartii* Ettingshausen), NM-G2817 (scale bar 10 mm).
3. Base of leaf fragment, Knobloch's original (1961, not figured, as *Betula brongniartii* Ettingshausen), NM-G2981 (scale bar 10 mm).

***Carpinus medimontana* Mai**
4. Involucre, EK 256 (scale bar 5 mm).
5. Involucre, NM-G2998b (scale bar 5 mm).

***Carpinus cordataeformis* Mai**
6. Involucre, NM-G2995b (scale bar 5 mm).
7. Involucre, EK 349 (scale bar 5 mm).

PLATE 17

***Salix* sp.**
1. Almost complete leaf, Knobloch's original (1961, pl. 1, fig. 9, as *Populus rottensis* Weyland), NM-G2806 (scale bar 10 mm).
2. Leaf tip, EK 360a (scale bar 10 mm).
3. Upper part of leaf, NM-G2995c (scale 10 bar mm).

***Populus zaddachii* Heer**
4. Long petiolate leaf base, Knobloch's original (1961, not figured), NM-G8590 (scale bar 10 mm).
5. Leaf blade, Knobloch's original (1961, not figured), NM-G8579a (scale bar 10 mm).
6. Leaf apex, EK 359 (scale bar 10 mm).

PLATE 18

***Toxicodendron herthae* (Unger) Kvaček et Walther**
1. Leaflet apex, counter-impression to Knobloch's original (1961, pl. 13, fig. 4, as *Rhus herthae* Unger) NM-G2916b (scale bar 10 mm).

***Acer angustilobum* Heer**
2. Small leaf, EK 363 (scale bar 5 mm).
3. Leaf fragment with cuticle shown in Pl. 6, Fig. 9, NM-G11505a (scale bar 10 mm).

***Acer integrilobum* Weber**
4. Small leaf, EK 362 (scale bar 10 mm).

***Acer* sp.**
5. Winged mericarp, Knobloch's original (1961, pl. 11, fig. 8, as *Acer* sp.), NM-G8596 (scale bar mm).

***Acer palaeosaccharinum* Stur**
6. Long petiolate leaf, Knobloch's original (1961, pl. 9, fig. 5), NM-G2872 (scale bar 5 mm).
7. Broad leaf, Knobloch's original (1961, pl. 1, fig. 11), NM-G2814 (scale bar 10 mm).

PLATE 19

***Craigia bronnii* (Unger) Kvaček, Bůžk et Manchester**
1. Fruit valve, EK 374 (scale bar 5 mm).
2. Incomplete fruit valve, EK 375 (scale bar 5 mm).

***Hydrangea microcalyx* Sieber**
3. Petaloid sepal, Knobloch's original (1961, pl. 11, fig. 11, as *Paliurus thurmannii* Heer), NM-G8585 (scale bar 5 mm).

***Cornus studeri* Heer**
4. Basal part of leaf, Knobloch's original (1961, pl. 13, fig. 1), NM-G8606 (scale bar 10 mm).

***Oleinites hallbaueri* (Mai) Sachse**
5. Leaf fragment with cuticle, Knobloch's original (1961, pl. 1, fig. 8, as *Myrica lignitum* (Unger) Saporta), NM-G2812a (scale bar 10 mm).

6. Almost complete leaf, Knobloch's original (1961, pl. 3, fig. 1, as *Myrica lignitum* (Unger) Saporta), NM-G4859a (scale bar 10 mm).
7. Detailed venation of the previous specimens, NM-G4859a (scale bar 5 mm).

PLATE 20

***Dicotylophyllum* sp. 1**

1. Leaf fragment, Knobloch's original (1961, pl. 4, fig. 2, as *Juglans acuminate* A. Braun), NM-G2834 (scale bar 10 mm).

***Dicotylophyllum* sp. 2**

2. Long petiolate leaf base, EK 383 (scale bar 5 mm).
3. Petiolate leaf base, Knobloch's original (1961, pl. 14, fig. 6, as *Leguminosites* sp.), NM-G8597a (scale bar 5 mm).

***Dicotylophyllum* sp. 3**

4. Leaf fragment, Knobloch's original (1961, pl. 4, fig. 9, as *Juglands* (*Carya*) *bilinica* Unger), NM-G2837 (scale bar 10 mm).

***Dicotylophyllum* cf. *heerii* (Engelhardt) Kvaček et Wather**

5. Petiolate leaf base, NM-G11512 (scale bar 5 mm).

***Dicotylophyllum* sp. 6**

6. Small complete leaf, Knobloch's original (1961, pl. 14, fig. 6, as *Celastrus persei* Unger), NM-G2862 (scale bar 5 mm).

***Dicotylophyllum* sp. 5**

7. Leaf base, Knobloch's original (1961, pl. 1, fig. 6, as *Aesculus* cf. *palaeocastanum* Ettingshausen), NM-G2806a (scale bar 10 mm).

***Dicotylophyllum* sp. 4**

8. Leaf without base, Knobloch's original (1961, pl. 8, fig. 12, as *Sibirea rottensis* Weyland), NM-G28089 (scale bar 5 mm).

***Saportaspermum* cf. *occidentale* Mayer et Manchester**

9. Winged seed, NM-G11483 (scale bar 3 mm).

***Carpolithes* sp. 2**

10. Rounded seed?, Knobloch's original (1961, pl. 8, fig. 11, as *Carpolithus* sp.), NM-G2870 (scale bar 1 mm).

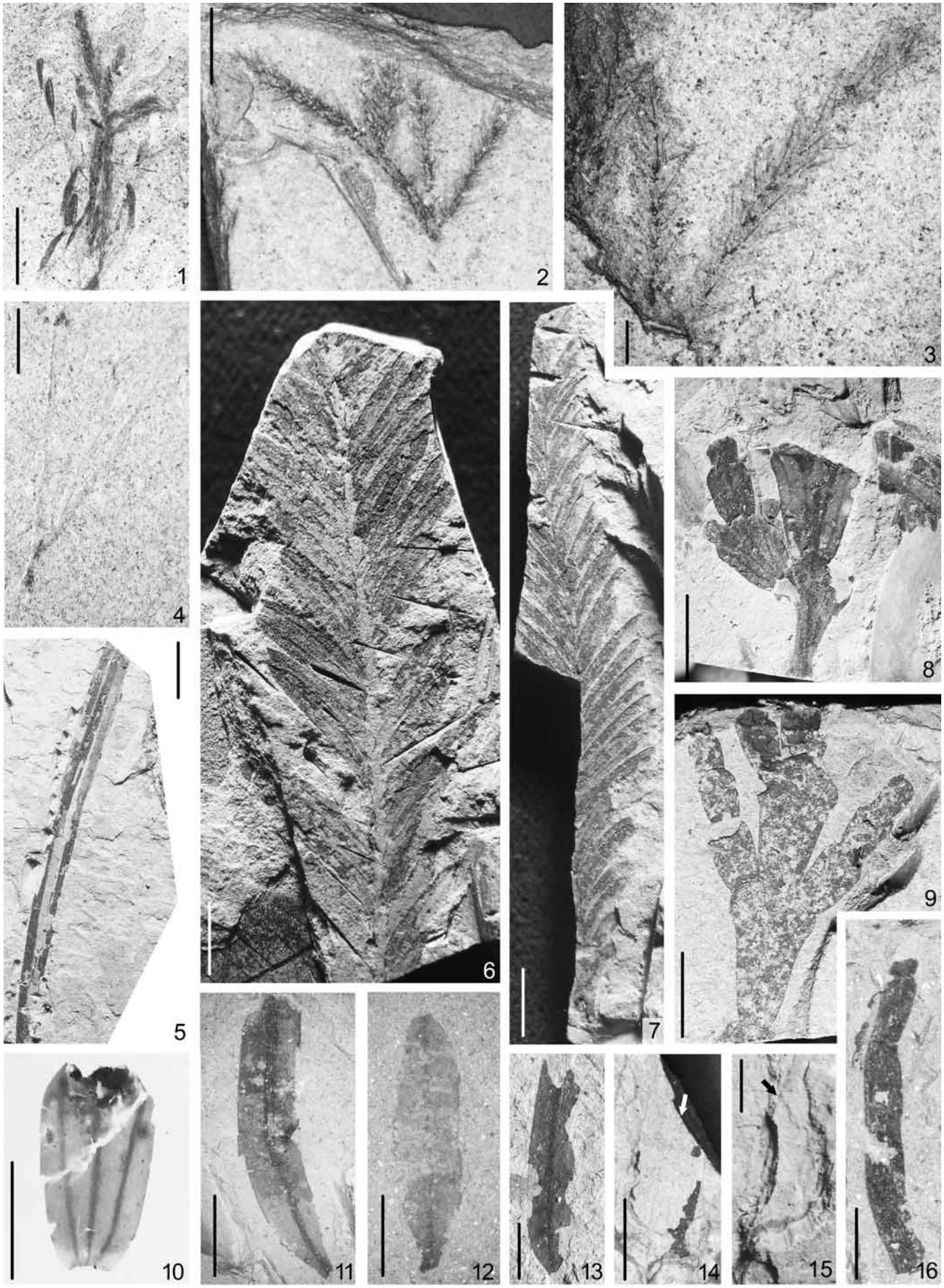
***Carpolithes* sp. 1**

11. Fruitlet?, Knobloch's original (1961, pl. 1, fig. 10, as ? *Pisonia eocenica* Ettingshausen), NM-G2813a (scale bar 1 mm).

PLATE 21

View of the present landscape at the Hrazený locality, photo P. Gürtlerová 2014.

PLATE 1



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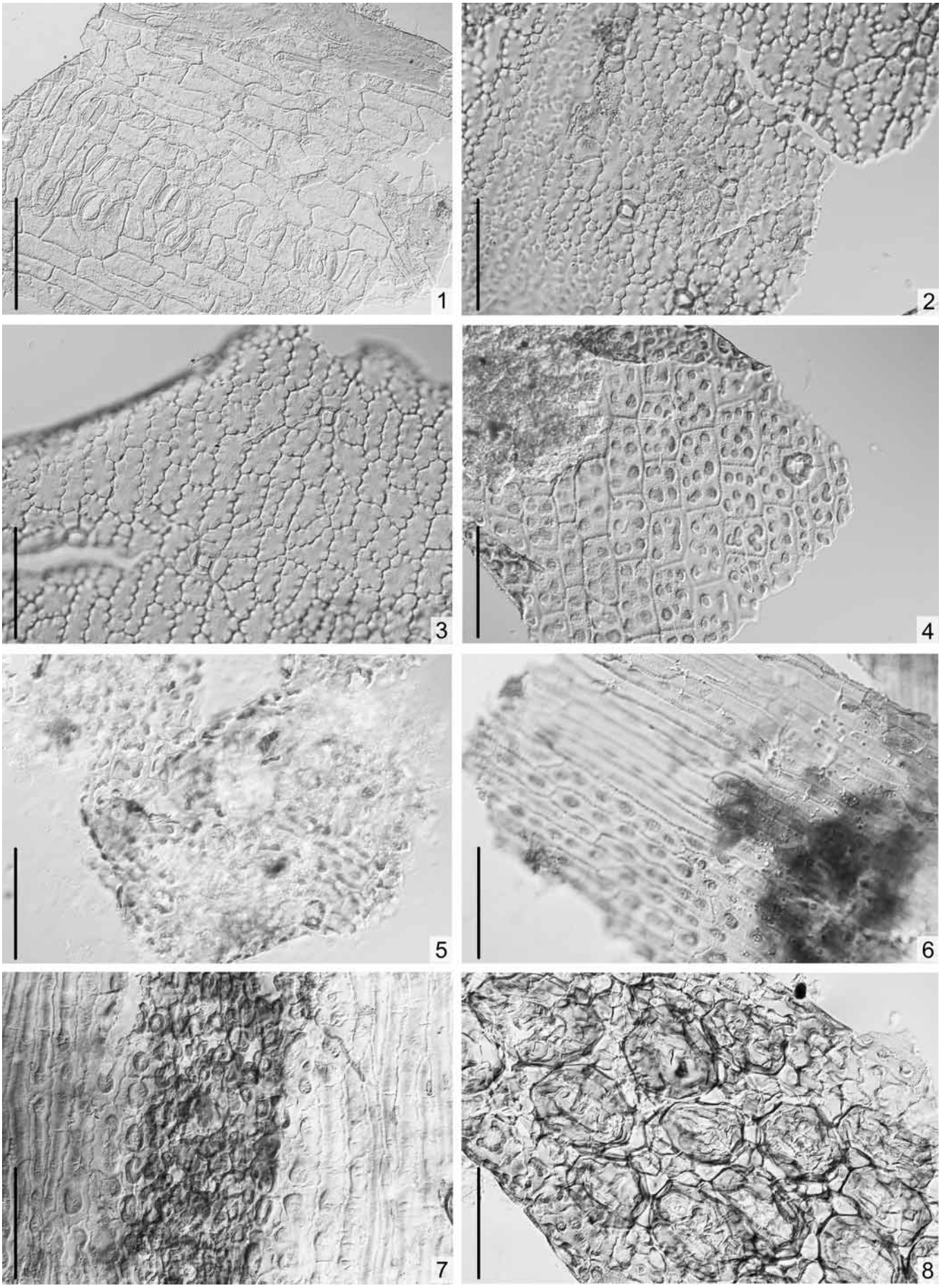

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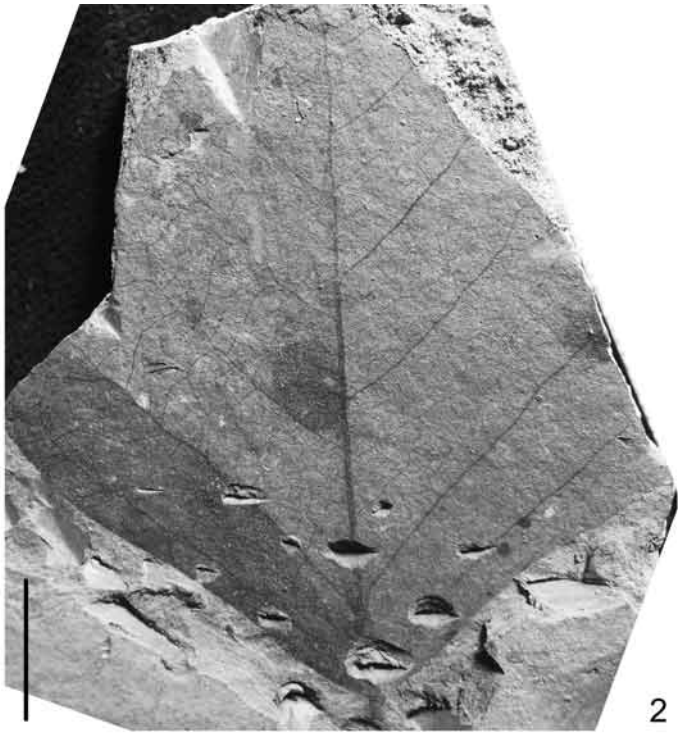

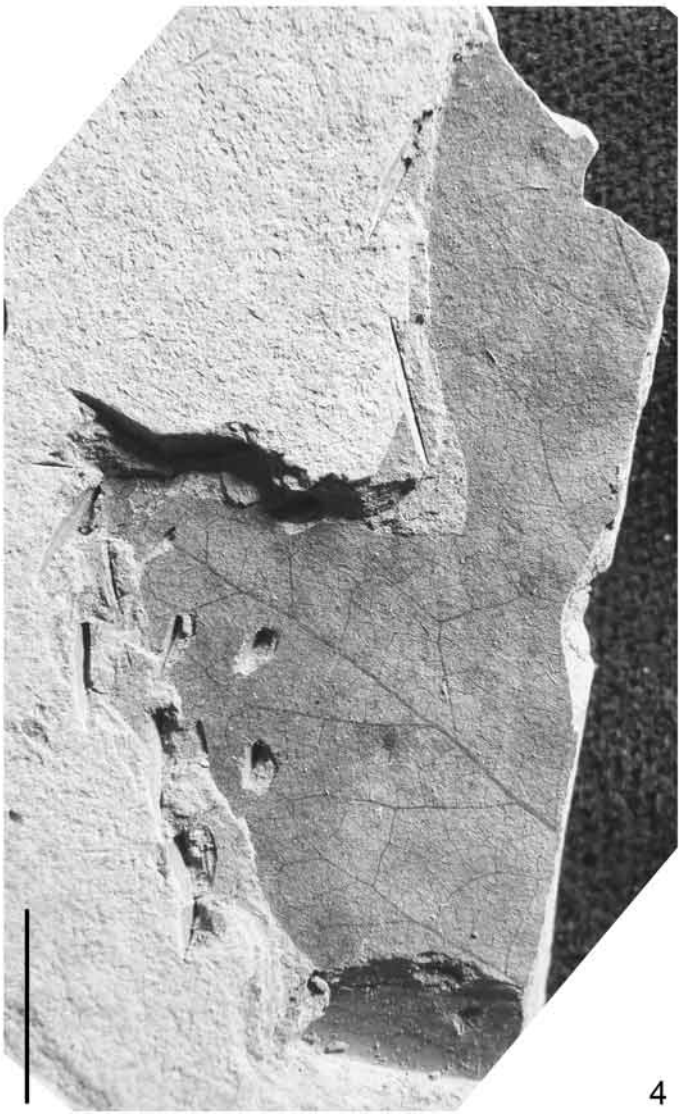

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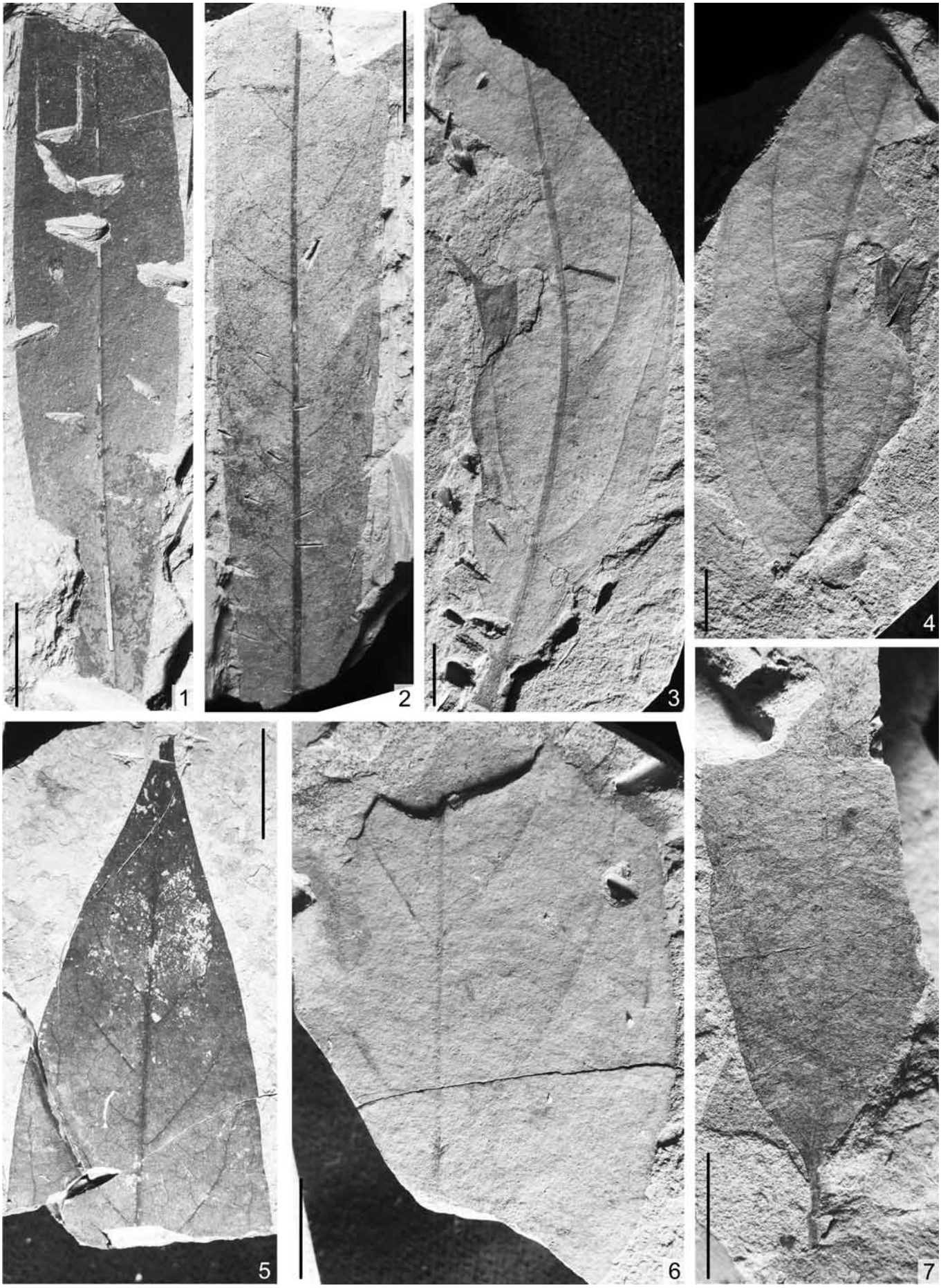

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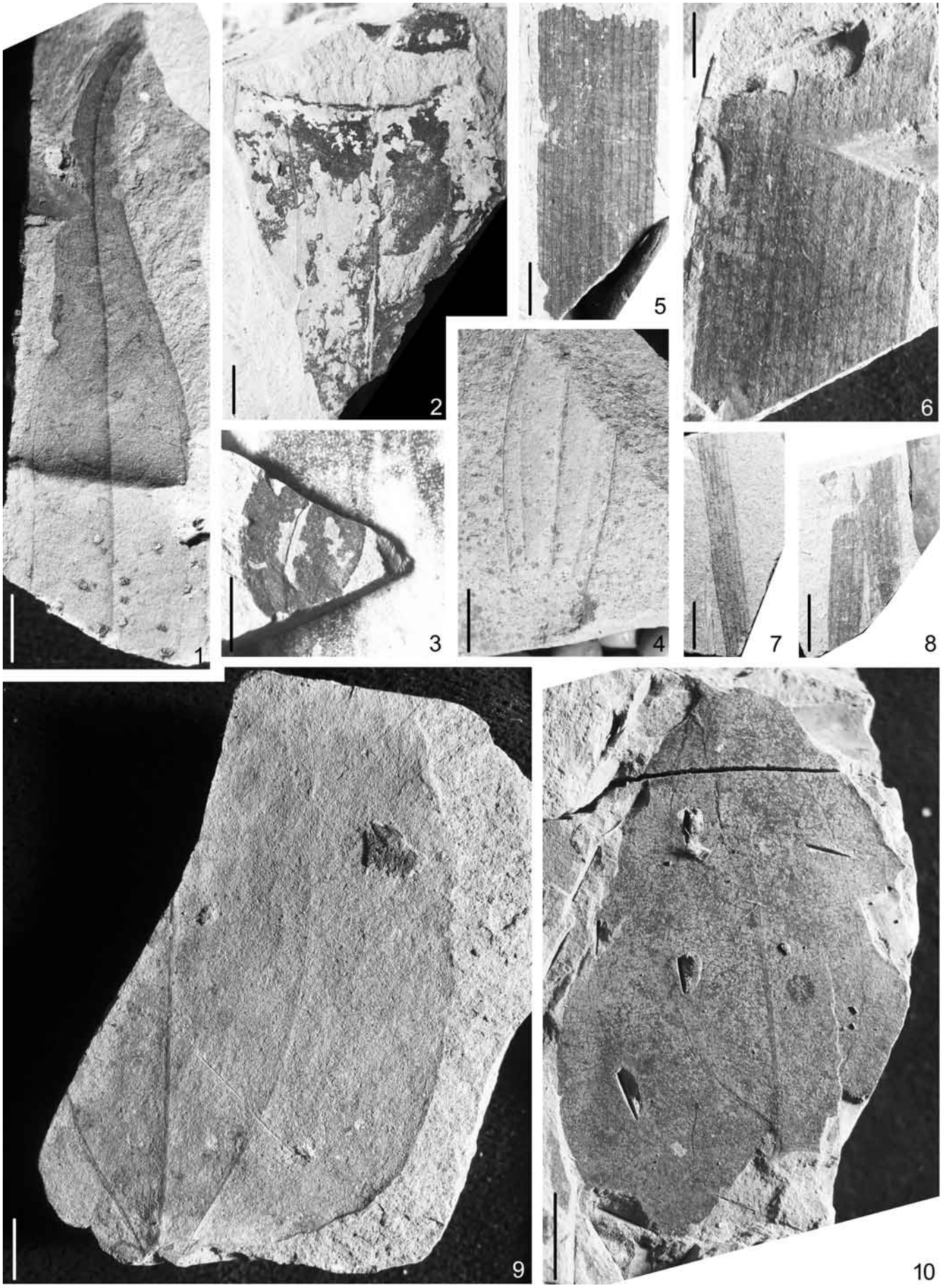

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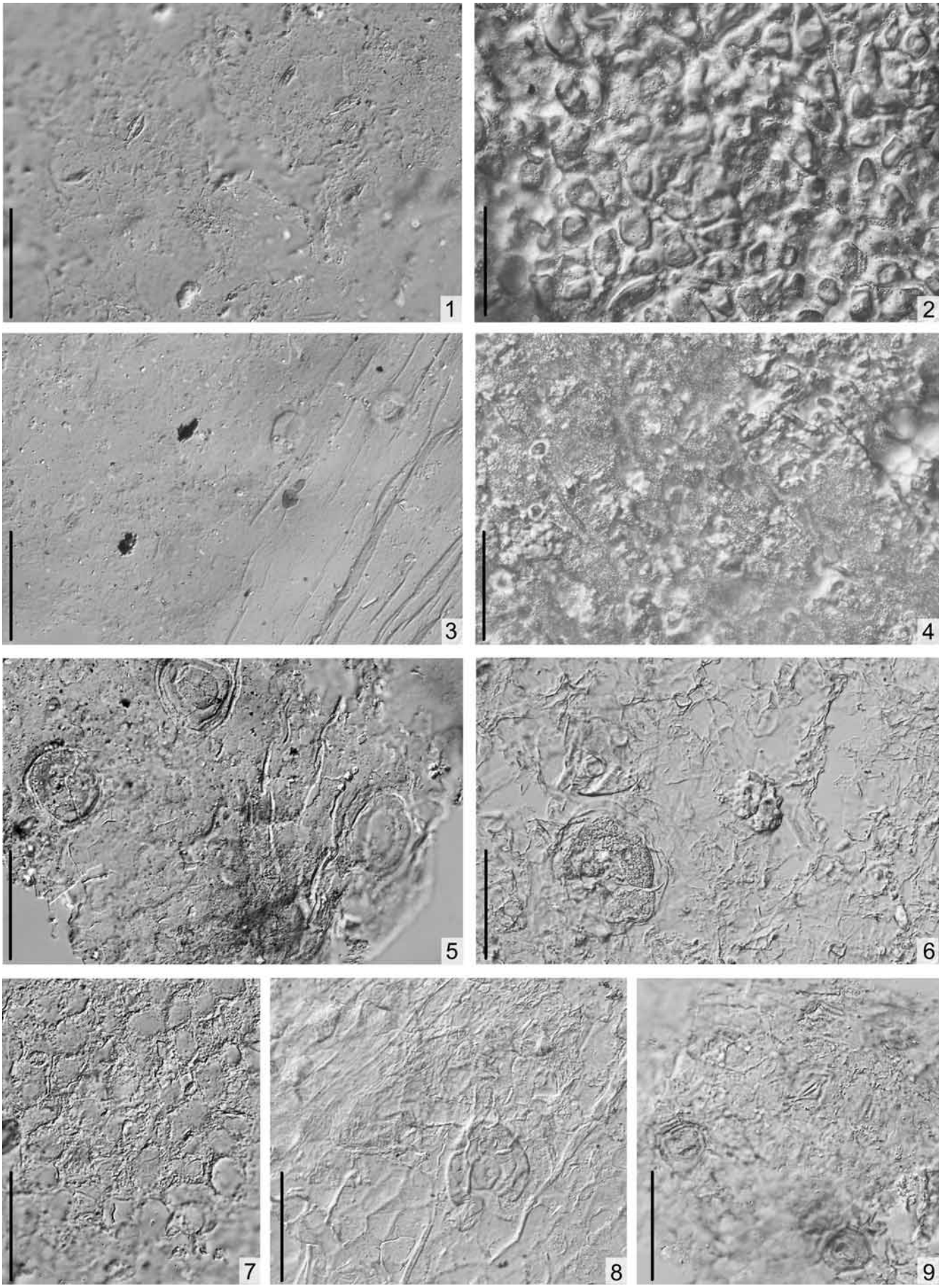

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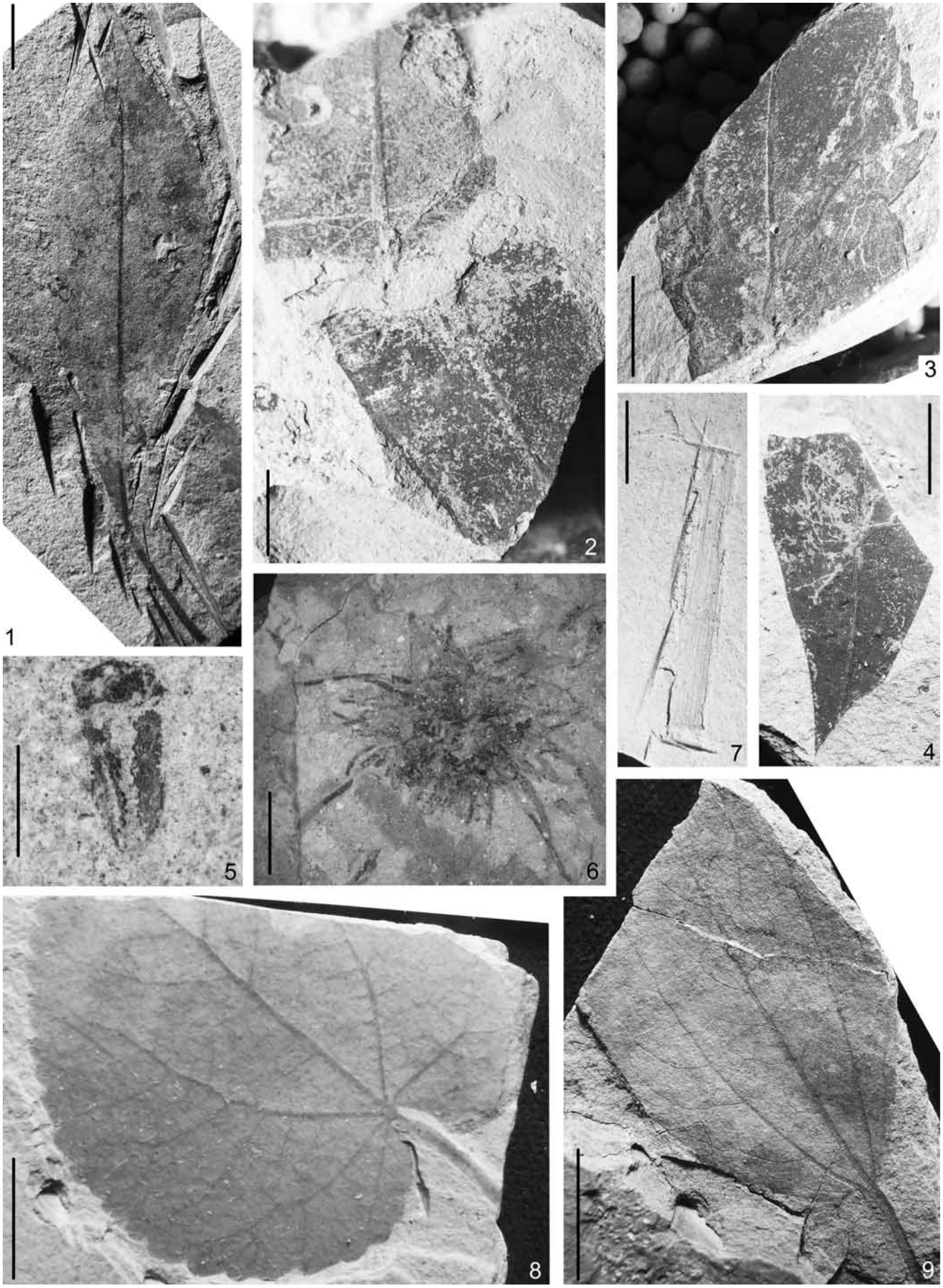

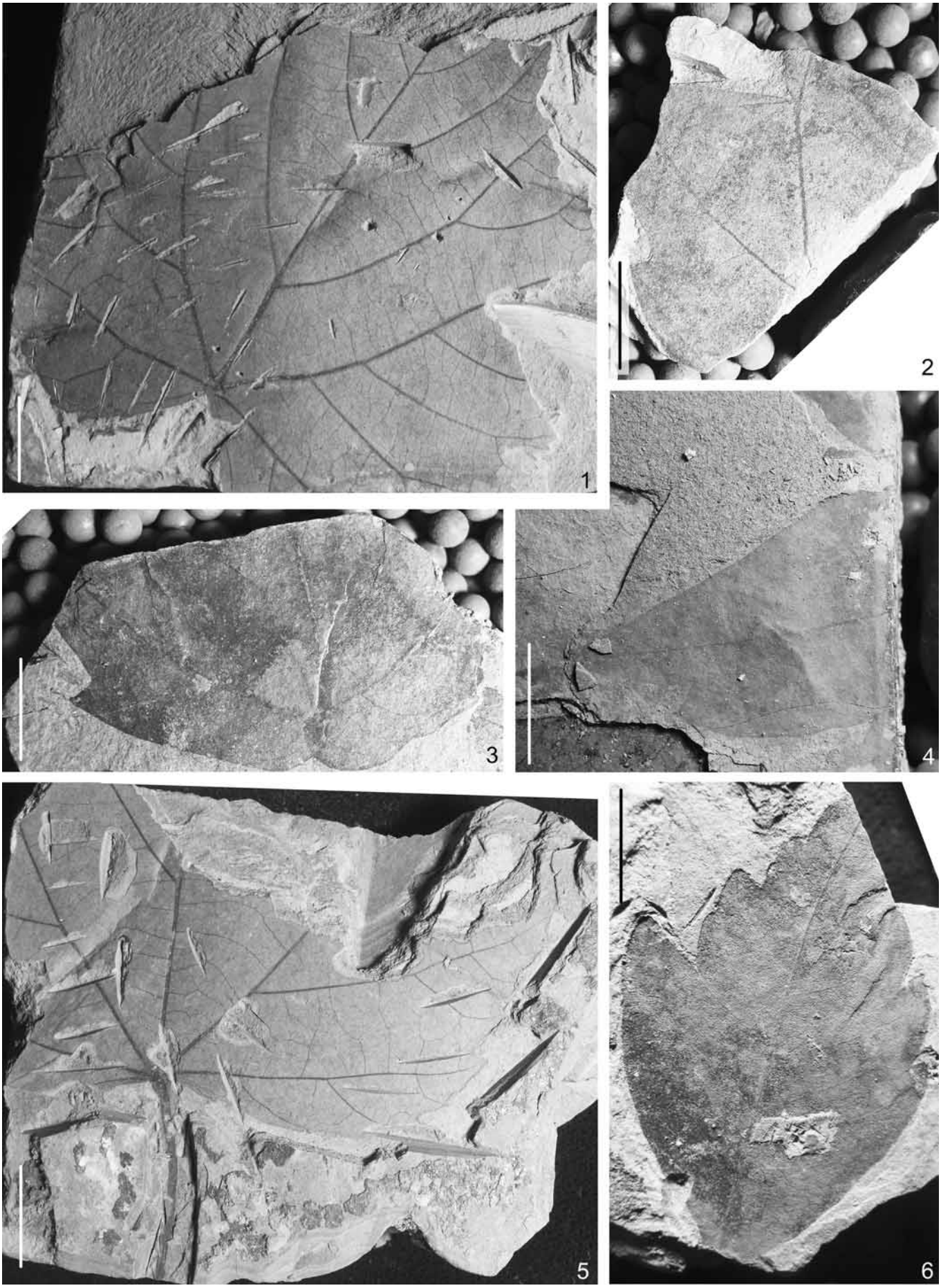
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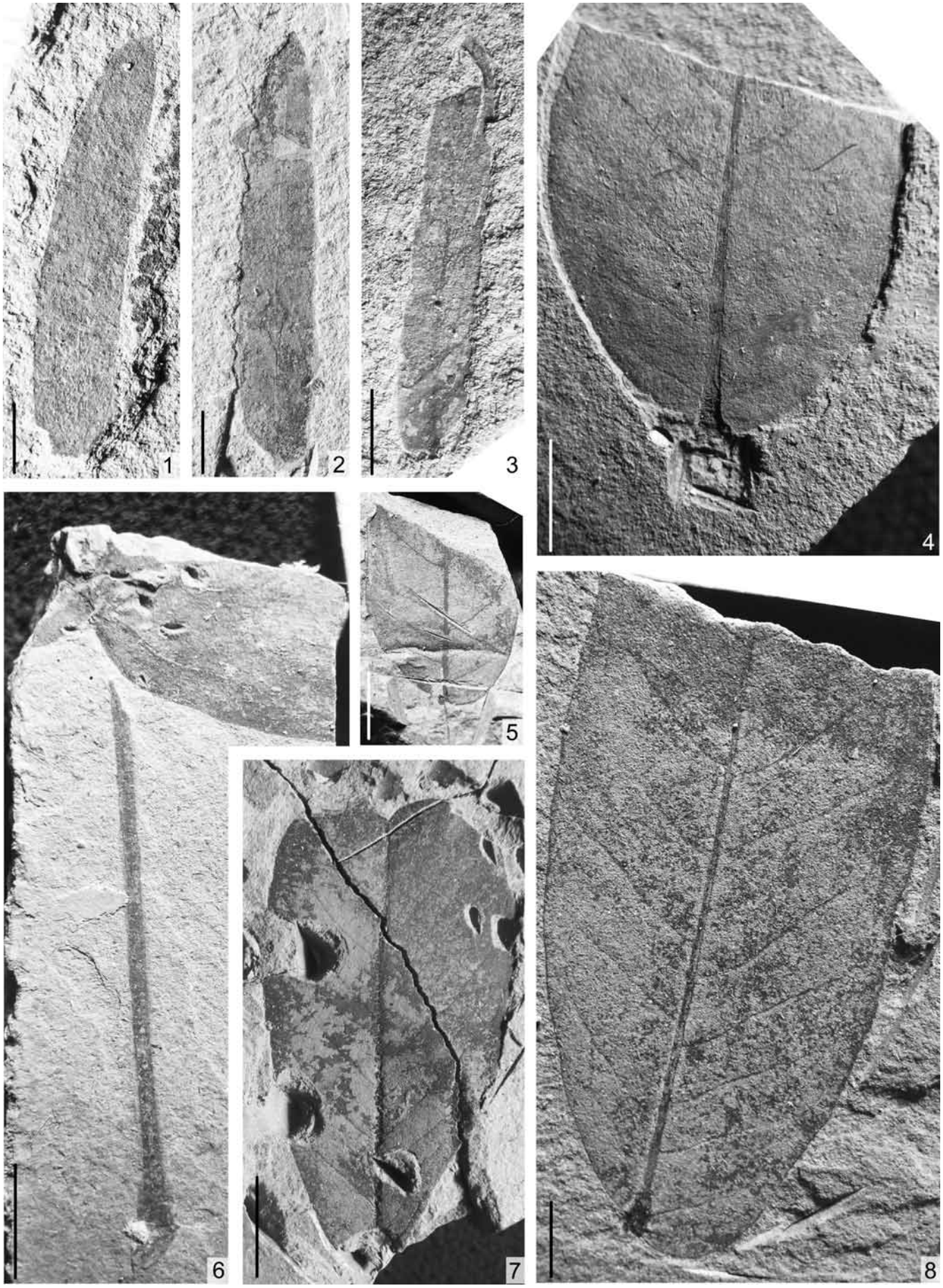

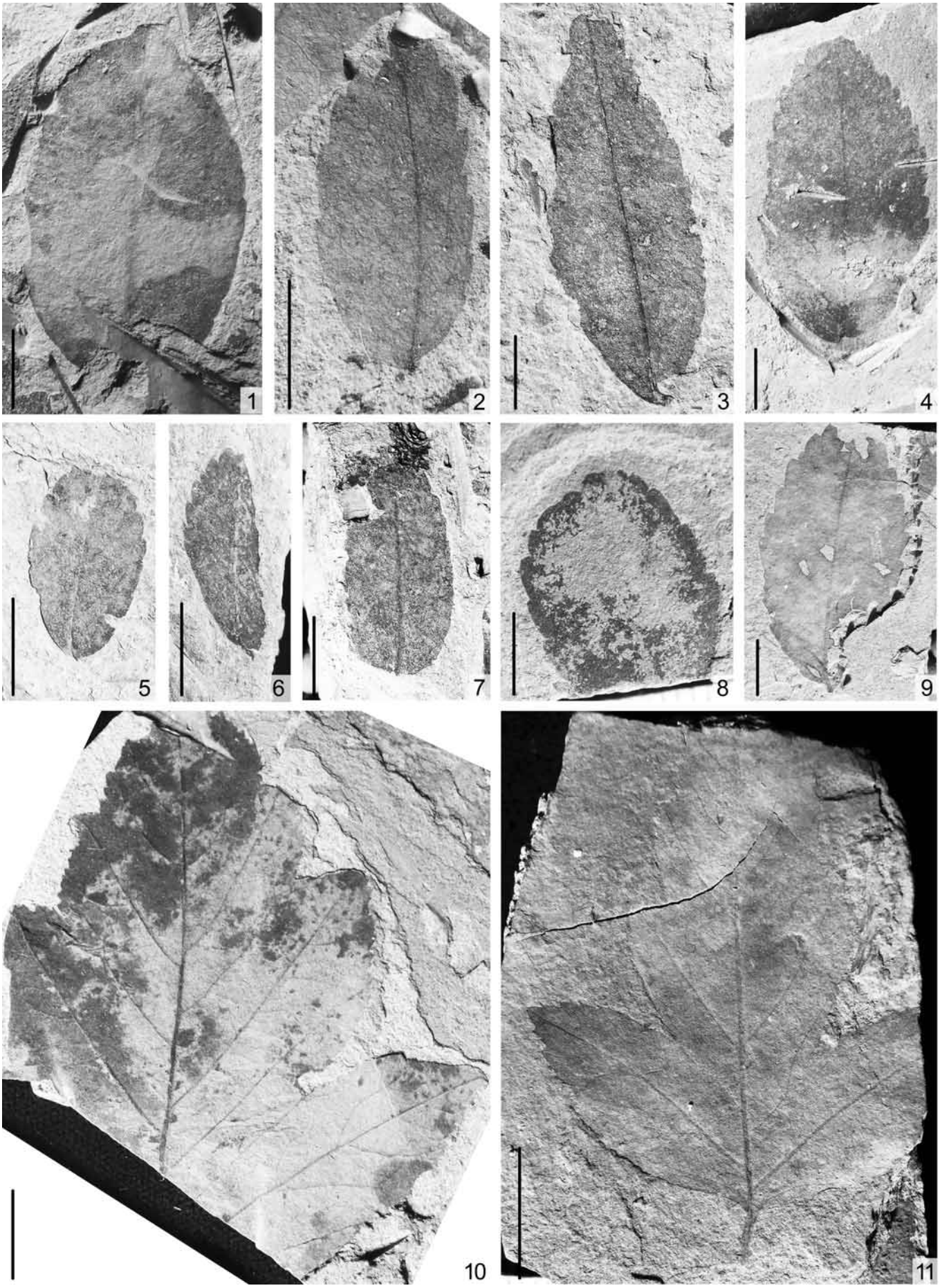
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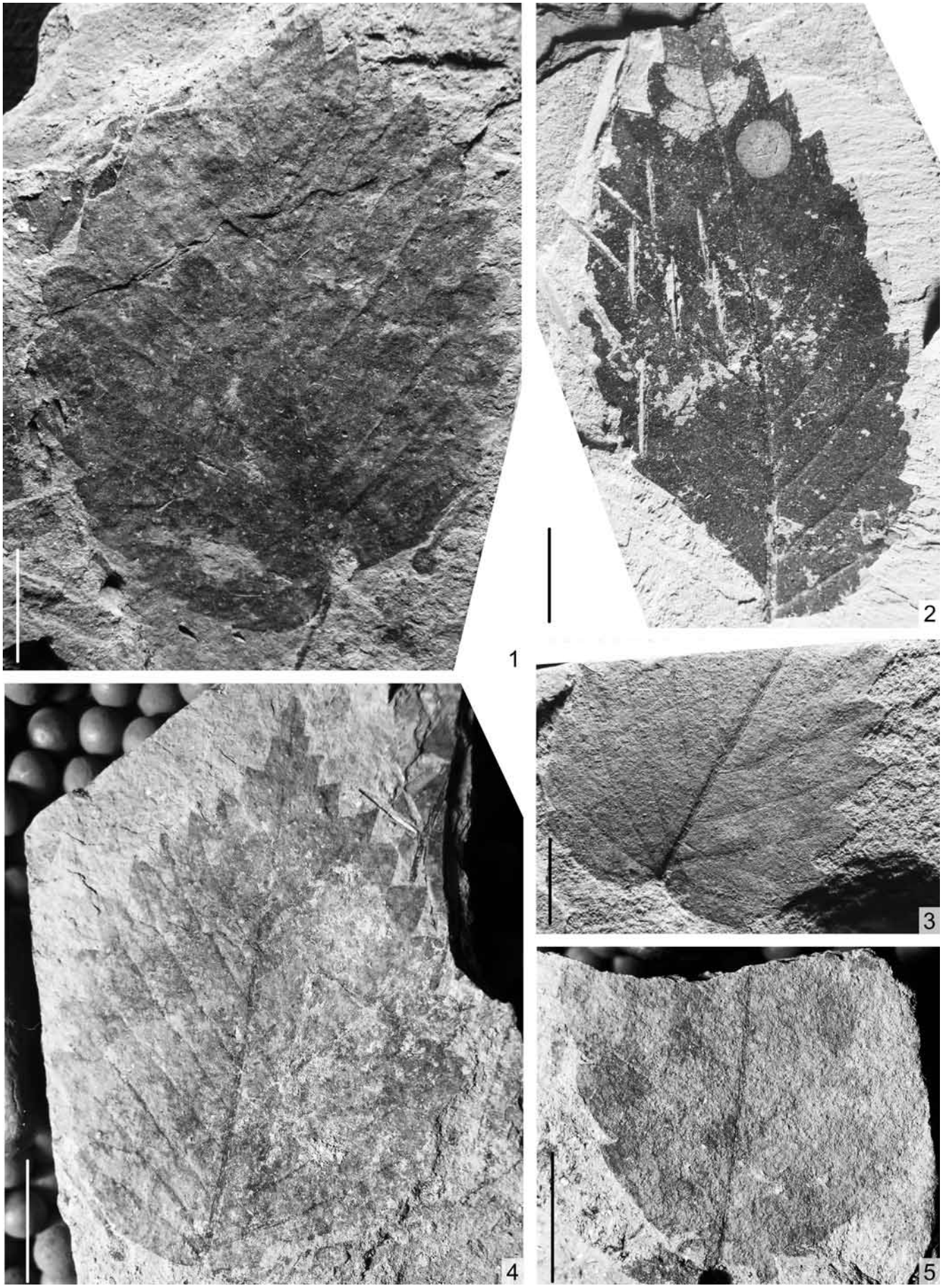


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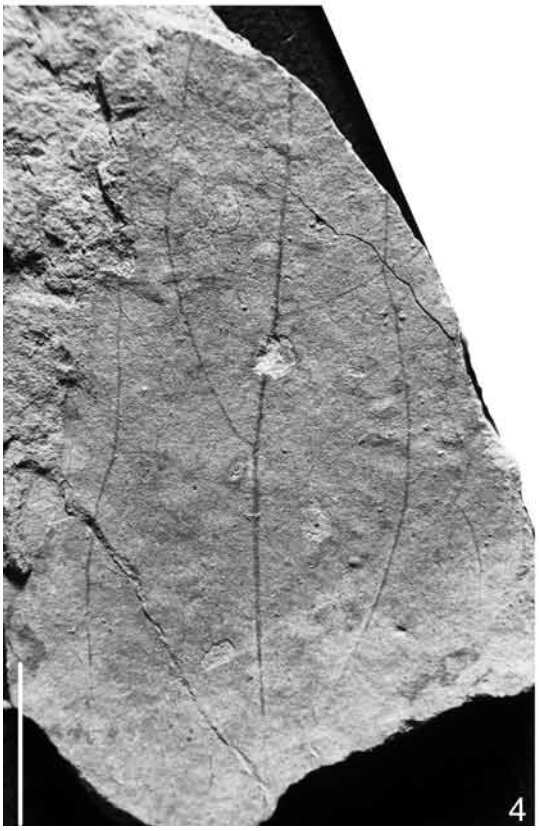
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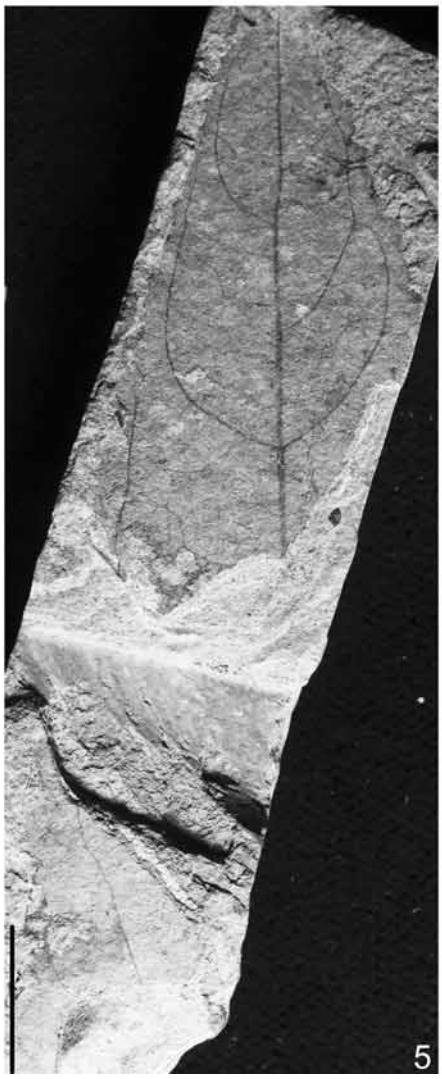
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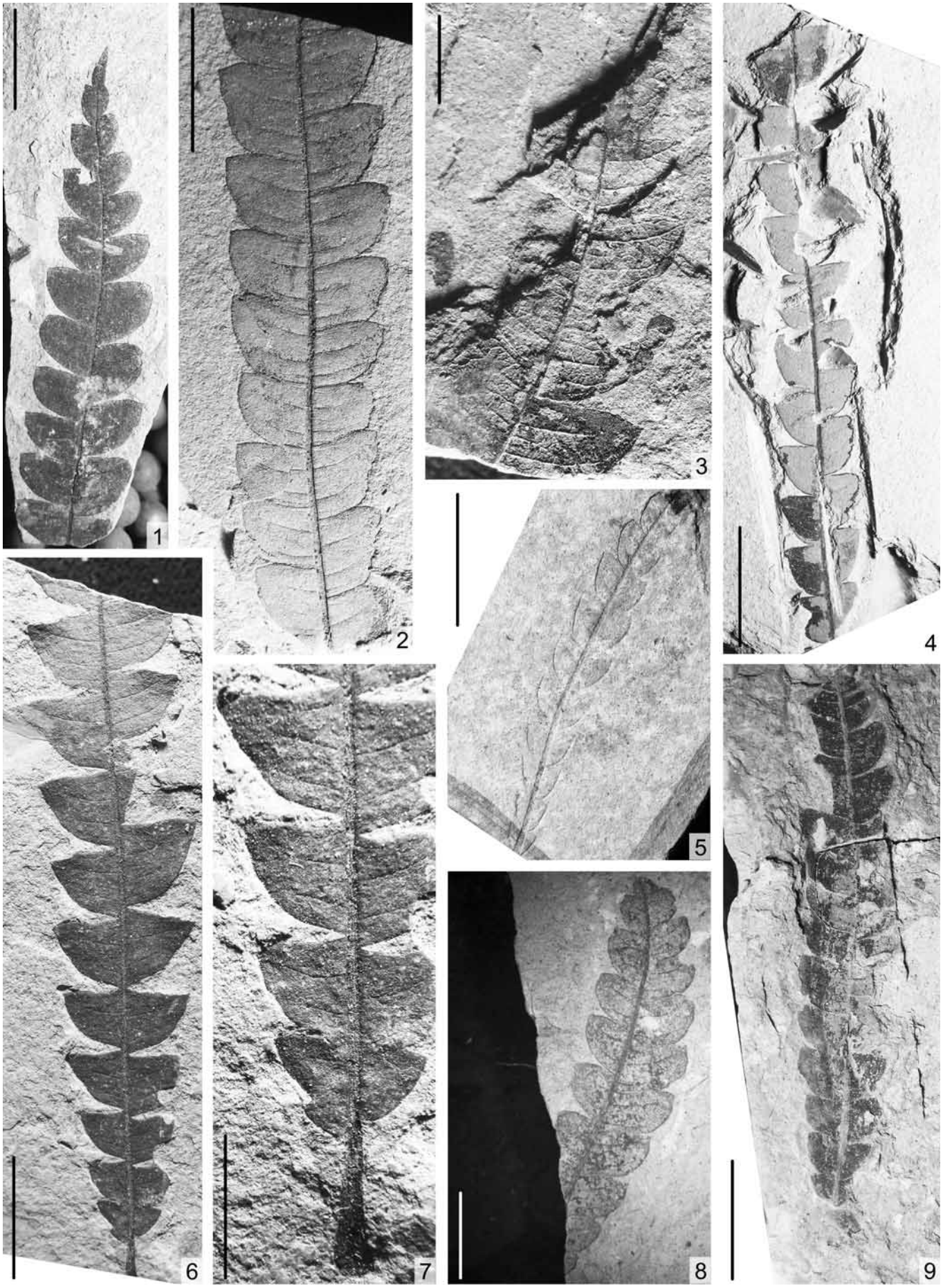

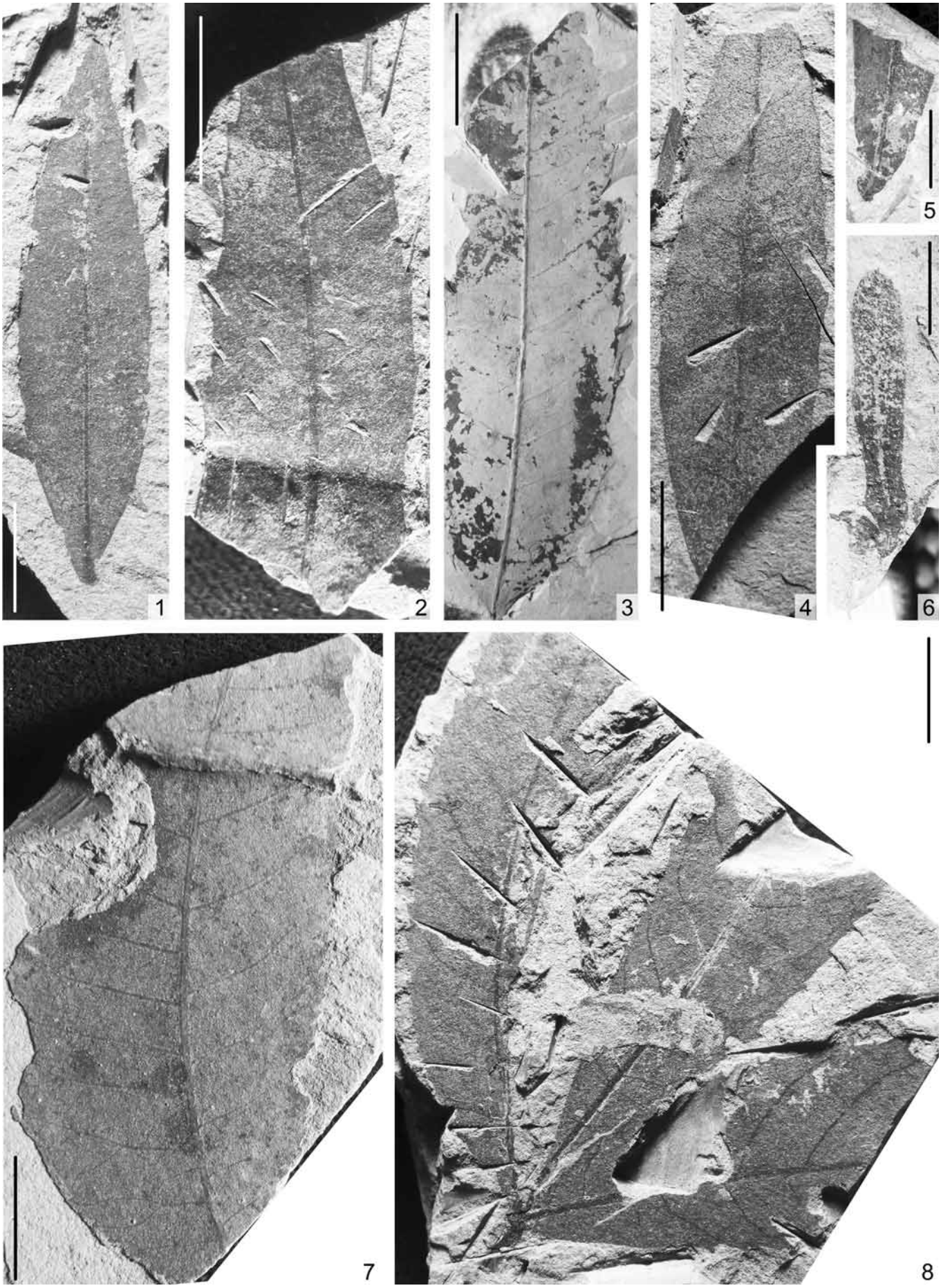
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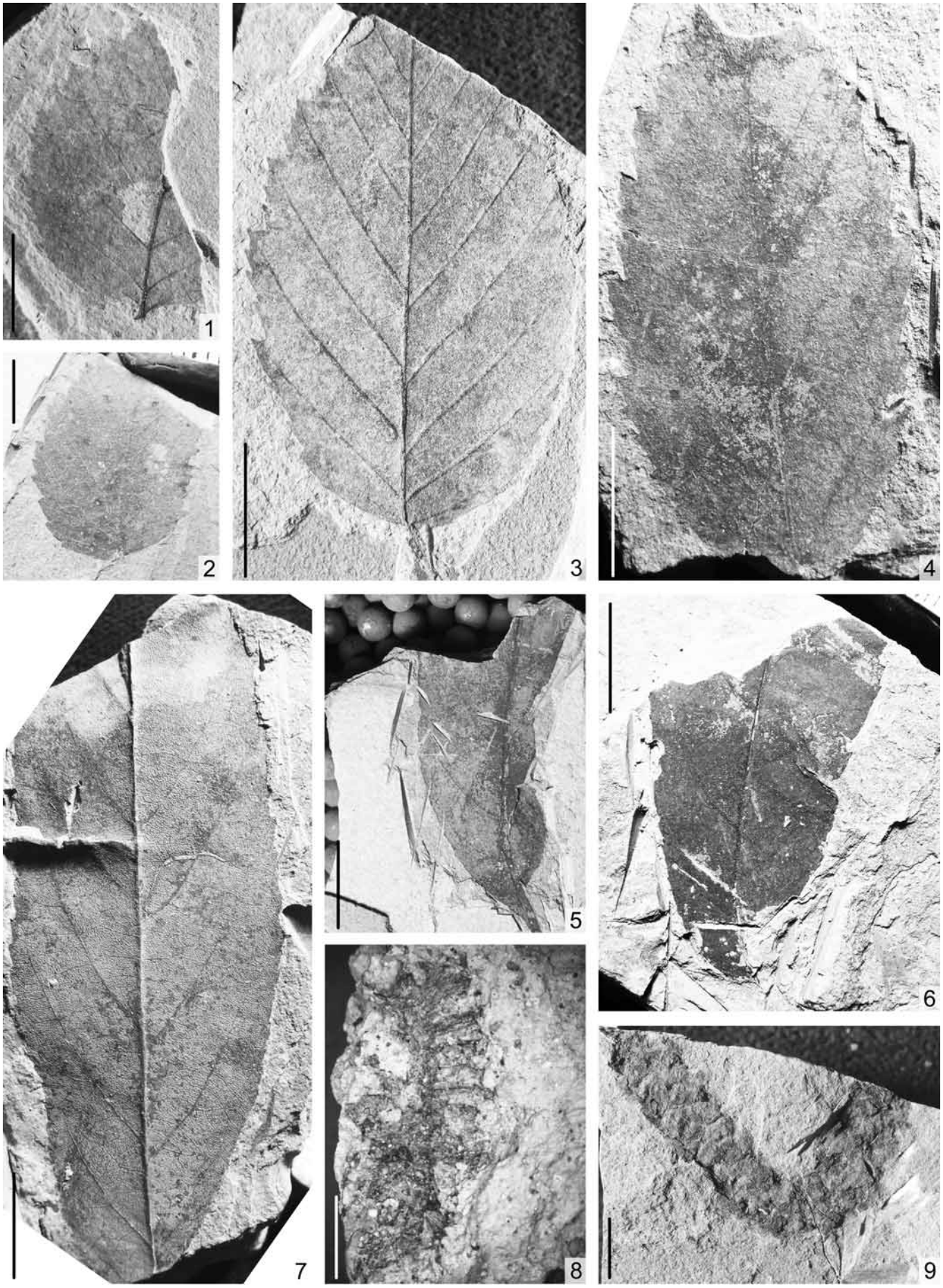

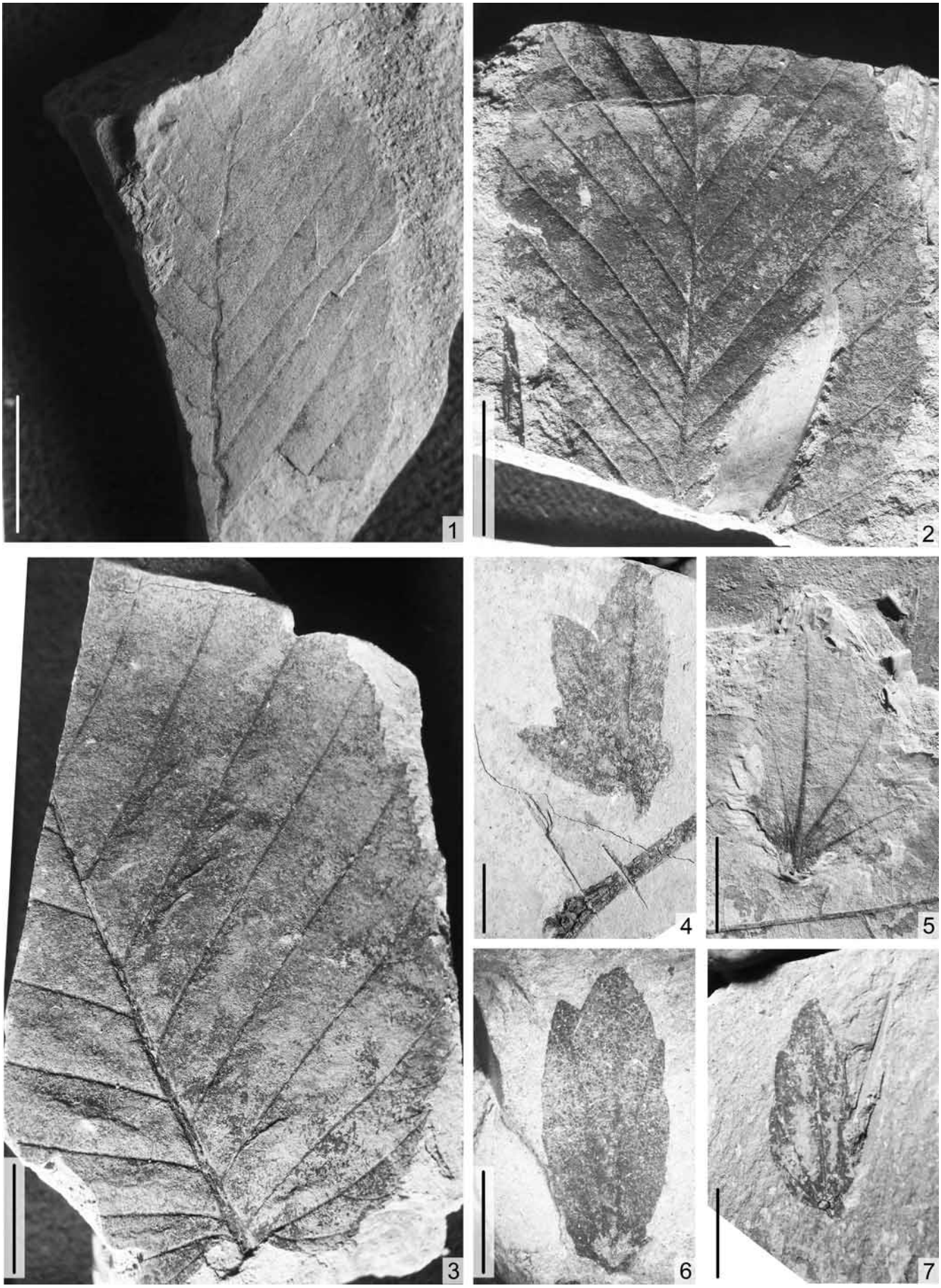
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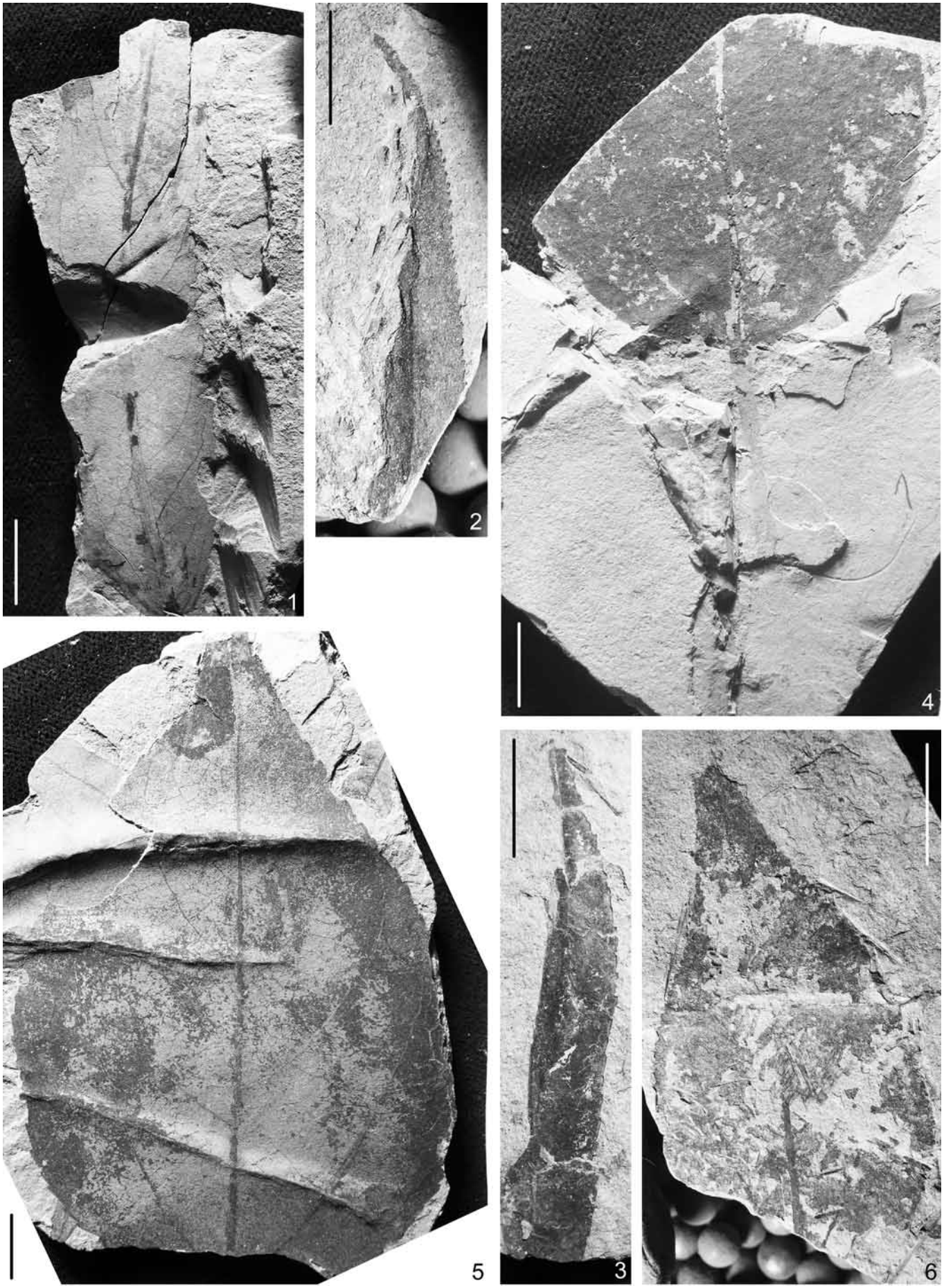

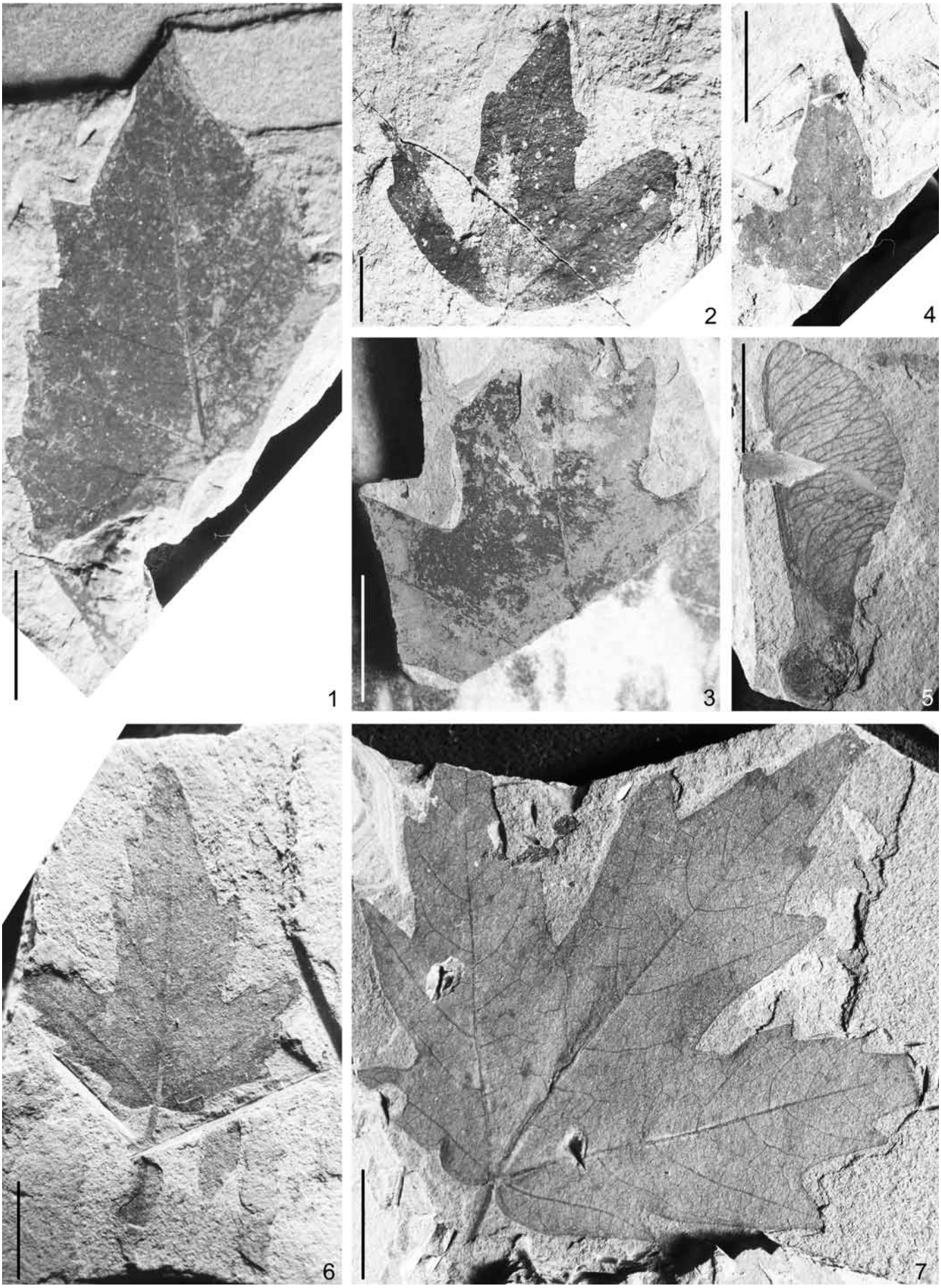
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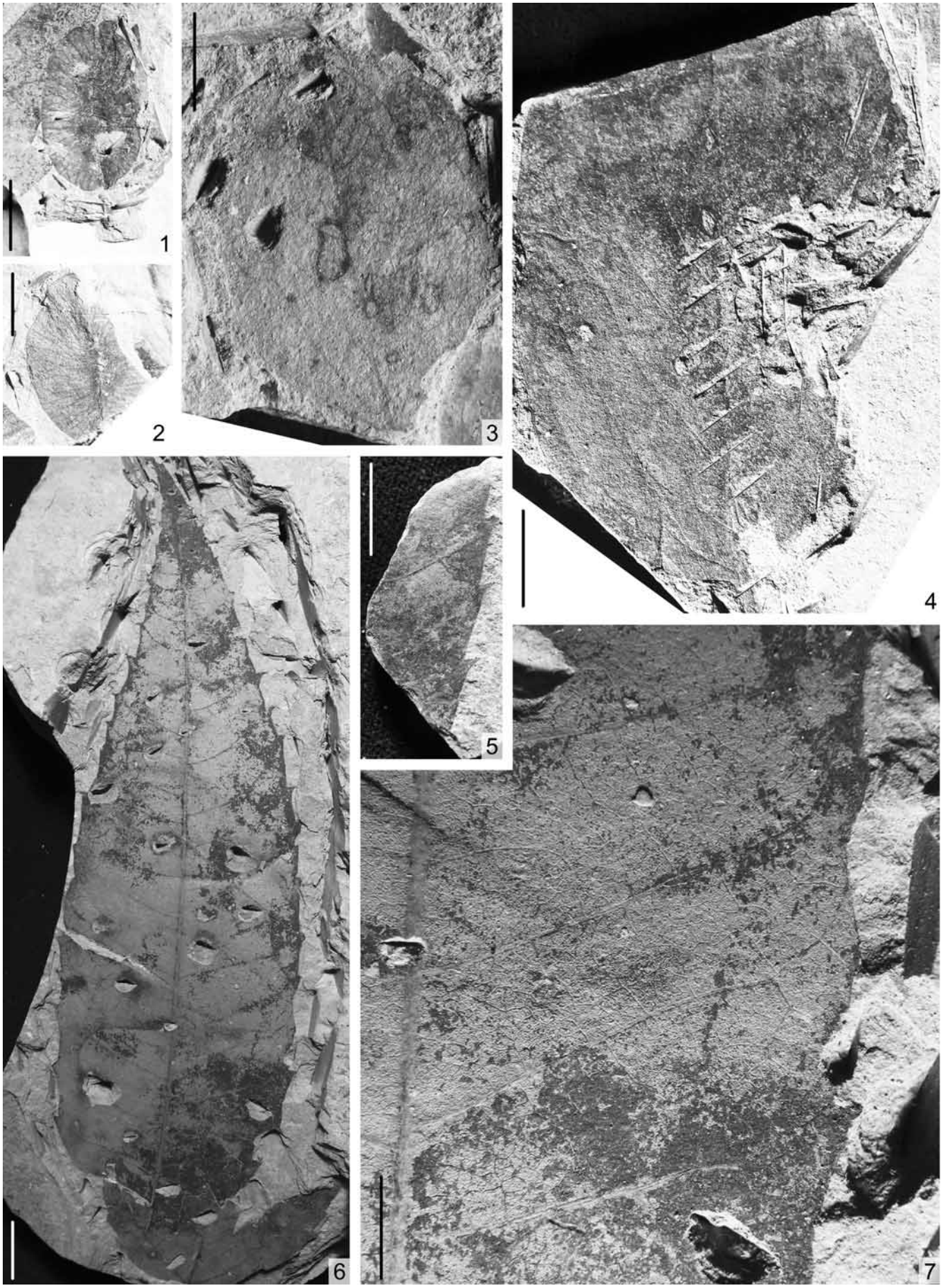

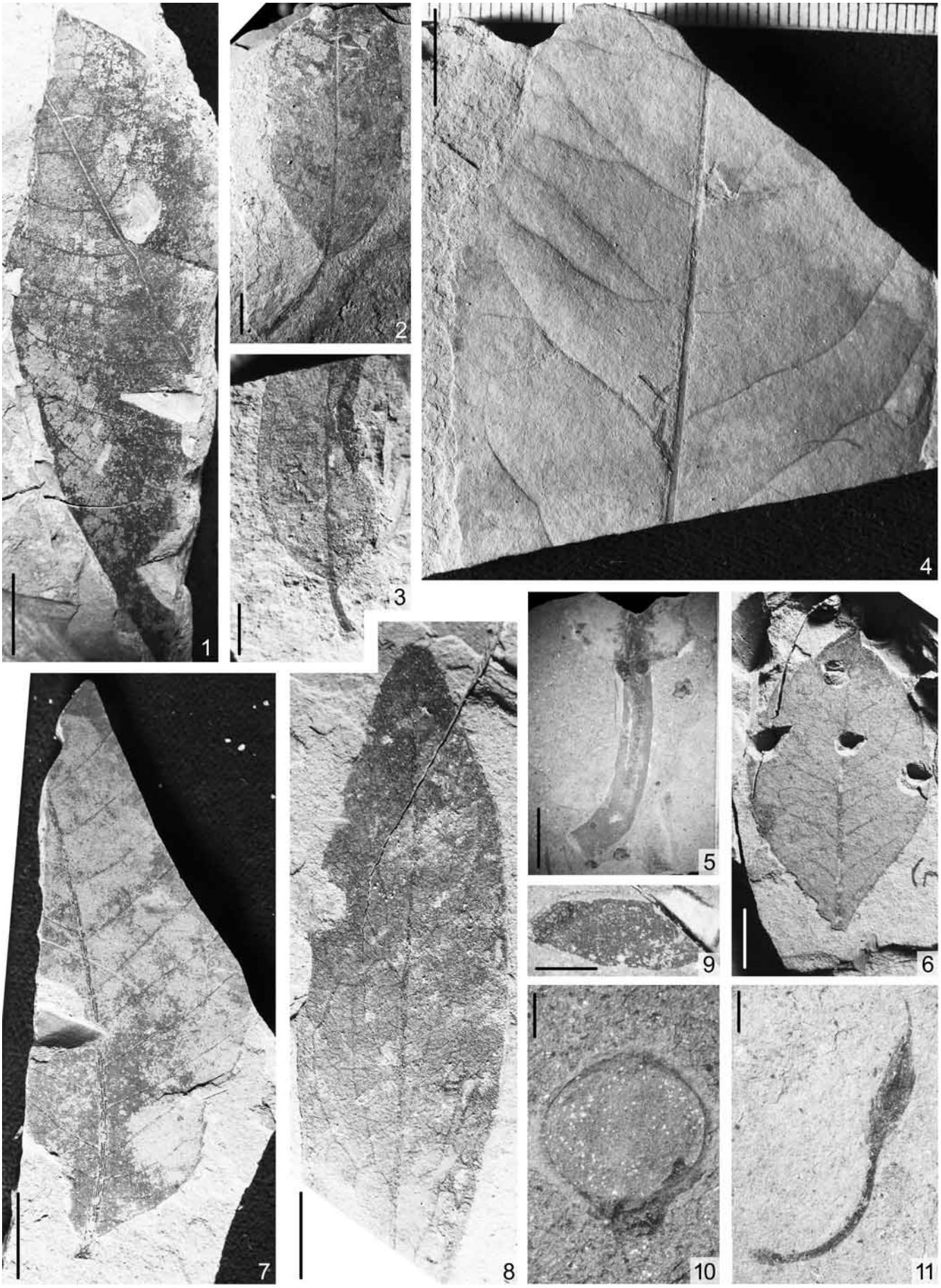
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PLATE 21