

Neogene wetland vegetation based on a leaf assemblage from the Bełchatów Lignite Mine (Central Poland)

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ABSTRACT. Well-preserved leaf macroremains collected in the Bełchatów Lignite Mine (Central Poland) were investigated. Fossil leaves of *Acer*, *Dicotylophyllum*, *Fagus*, *Eucommia*, *Laria*, *Laurophyllum*, *Liquidambar*, *Pinus*, *Populus*, *Pterocarya*, *Quercus*, *Salix*, *Salvinia*, *Taxodium*, *Ulmus*, *Vitis*, and *Zelkova*, and fossil fruit of *Eucommia* were found in fossil assemblage KRAM-P 218 formed in a fluvial sedimentary environment. The fossil assemblage is dominated by plant remains of riparian vegetation of bottomland hardwood forest type. Some taxa point to the presence of mesophytic upland communities. The floristic composition points to warm temperate climate with mild winters, comparable to Cfa type (warm temperate, fully humid with hot summer) in the Köppen-Geiger climate classification. Mean annual temperature of 13.5–16.5°C was reconstructed by the coexistence approach method. Middle to late Miocene age (late Sarmatian to early Pannonian) is suggested for the plant-bearing deposits.

KEYWORDS: plant macroremains assemblage, macromorphology, cuticular micromorphology, palaeovegetation, palaeoclimate, Neogene, Poland

INTRODUCTION

An assemblage of mainly fossil leaves was found in the course of geological mapping of Neogene deposits in an outcrop of the Bełchatów Lignite Mine on 17 July 1995. The plant fossils were generally in a very good state of preservation, allowing extensive palaeofloristic studies. Previously only Betulaceae leaf remains from the assemblage were studied in detail (Worobiec & Szynkiewicz 2007). Our investigation of the remaining fossils involves a comprehensive analysis of the palaeofloristics of the assemblage, followed by reconstruction of the palaeovegetation in order to document the biodiversity of the Neogene flora and vegetation of the area around the present-day city of Bełchatów. This work and the earlier study of Betulaceae macroremains (Worobiec & Szynkiewicz, op. cit.) are the basis for the present palaeoclimatic reconstruction and discussion of the age of the fossil assemblage.

GEOLOGY

The Bełchatów Lignite Mine is in central Poland, south of the city of Bełchatów (Fig. 1) in the southern part of the Central European Lowlands. Neogene deposits of the Bełchatów Lignite Mine occur within the Kleszczów Graben (Stuchlik et al. 1990). Czarnecki et al. (1992) and Matl (2000) distinguished four main lithological units: subcoal unit (PW); coal unit (W) with the main seam (PG), seam B and seam C; clayey-coal unit (I-W) with seam A; and the youngest clayey-sandy unit (I-P) of the Neogene deposits of the Kleszczów Graben. Earlier investigations of the Neogene deposits of the Bełchatów Mine (Burchart 1985, Burchart et al. 1988, Stuchlik et al. 1990, Kowalski 1993, Kowalski & Rzebik-Kowalska 2002, Szynkiewicz 2000) determined early Miocene age of the main coal seam (PG) and late



Fig. 1. Location of Bełchatów Lignite Mine in Poland

Miocene age of the sedimentary series of the clayey-sandy (I-P) unit.

The discussed leaf assemblage was found on 17 July 1995 on the western slope of the open pit of the Bełchatów Lignite Mine, on

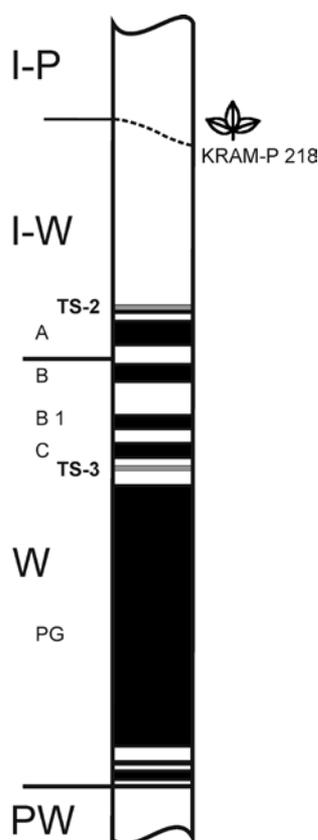


Fig. 2. Schematic geological profile showing Neogene deposits of Bełchatów Lignite Mine (modified after Worobiec 2007). Leaf drawing marks stratigraphic position of fossil plant assemblage KRAM-P 218. TS-3 – paratonstein TS-3, TS-2 – paratonstein TS-2, PW – subcoal unit, W – coal unit, I-W – clayey-coal unit, I-P – clayey-sandy unit; A, B, B1, C and PG – coal seams (PG – main coal seam). Black shading – coal seams, grey shading – paratonsteins

overburden escarpment 4/5, at 93–100 m a.s.l. near borehole 70/21.5. The lower part of the fossil site held coal seam I(A) covered by paratonstein TS-2 (Fig. 2). Above were dusty sands and sands with plant detritus belonging to the clayey-coal unit (I-W). The deposits were later eroded, and on the underlying clayey-coal unit deposits were then deposited quartzite sands with abundant plant detritus with striped flintstones, covered by one-metre-thick grey silts with accumulation of leaf macroremains (assemblage KRAM-P 218). These deposits were then covered by fine-grained sands, white quartzite sands, clayey sands, and sandy clays. The northern part of the deposits with the leaf assemblage was cut by a fault. The discussed plant macroremains assemblage was deposited several hundred metres from fossil assemblage KRAM-P 217, considered to be late Miocene (Worobiec 2003a). Fossil plant assemblages VI, Xa, and XIIIa probably are of similar age (Stuchlik et al. 1990). Deposits with fossil assemblage KRAM-P 218 were left in an eroded depression (Fig. 3) representing abandoned channel fill. This is in accordance with Wilczyński (1992) and Krzyszkowski and Winter (1996), who stated that the deposits belonging to the lower part of the clayey-sandy unit and the upper part of the clayey-coal unit were formed in a fluvial environment of braided to meandering rivers with dense vegetation along river banks.

MATERIAL AND METHODS

The state of preservation of the fossil leaves collected in the Bełchatów Lignite Mine outcrop varied from compressions (mainly) to impressions. The best-preserved specimens of leaf compressions were isolated from the rock matrix following the procedure described by Worobiec (2003b). Eighty slides of isolated leaves were made.

The remaining compressions and impressions were slowly dried. Small fragments of leaf blades were taken from selected leaf compressions (isolated ones and others adhered to rock matrix) for cuticular analysis. The laminar fragments were cleaned with hydrofluoric acid, washed in water, macerated using NaClO solution (Bielnar commercial bleach), and finally mounted on slides with glycerine jelly. Altogether, 109 slides of leaf epidermis were made. All studied fossil specimens are housed in the W. Szafer Institute of Botany, Polish Academy of Sciences (Kraków) under catalogue number KRAM-P 218.

The total number of specimens of all taxa is greater than the total number of rock samples with plant remains because several remains belonging to different taxa were preserved on some samples. In such cases an



Fig. 3. View of overburden escarpment 4/5 in Belchatów Lignite Mine outcrop, 17 July 1994. Arrow points to location of deposits with fossil assemblage KRAM-P 218. (Photo A. Szyrkiewicz)

alphanumeric specimen number is used. In total, 105 deposit samples were studied.

Macromorphological descriptions of leaves mostly follow Ellis et al. (2009), and micromorphological cuticular descriptions follow Dilcher (1974) and Wilkinson (1979).

The method of measuring the micromorphological objects (cells, stomata, trichomes) depended on their shape. Diameter was measured for regular, round, and broadly elliptic objects. Length and width were measured for all roughly rectangular objects. For objects of irregular shape (mainly epidermal cells) the longest dimension was measured.

Drawings were made using a Carl Zeiss stereomicroscope with a camera lucida attachment. Macro photographs were taken with a Nikon Coolpix 995 digital camera and a Nikon SMZ 800 stereomicroscope fitted with a Nikon DS-5M-U1 digital camera. Micro photographs were taken with a Nikon Eclipse E400 microscope fitted with a Canon A640 digital camera.

RESULTS

SYSTEMATIC PALAEOBOTANY

The classification follows Ruggiero et al. (2015) for Bryophyta, and Christenhusz et al. (2011) for ferns and gymnosperms. The classification of angiosperms and author names of their families follows APG III (2009). Plant families, genera and species are listed following Chase & Reveal (2009), Haston et al. (2009), and Christenhusz et al. (2011).

Bryophyta

Bryopsida

Bryidae Engl.

Pl. 8, figs 4, 5

Material. Two palynological slides from samples taken from specimens KRAM-P 218/109 and KRAM-P 218/104

Description. Only small, badly preserved fragments, presumably of moss leaves (phylloids) of two different types. Leaf fragment (Pl. 8, fig. 4) consists of rhomboidal, elongated cells 31–36 μm long and 10–12 μm wide. Cell walls sinuous, up to 2.5 μm thick. Second fragment (Pl. 8, fig. 5) consists of usually rhomboidal cells 17–27 μm long and 7–10 μm wide, papillose, with one to two roundish papillae. Cell walls straight or sinuous, thin or thick, up to 1.5 μm .

Remarks. The cell structure of these plant remains is typical for moss leaves, but their systematic position remains unknown due to the absence of distinctive features and the poor state of preservation. Moss remains were earlier reported both from Belchatów (Stuchlik et al. 1990) and from other Neogene localities of Poland (e.g. Szafran 1958, 1964).

Polypodiidae Cronquist, Takht. & Zimmerm.

Salviniales Bartl. in Mart.

Salviniaceae Martinov

Salvinia Séguier

Salvinia sp.

Pl. 6, fig. 1

Material. KRAM-P 218: 123/III, 142/II, 145/IV

Description. Macromorphology. Only floating leaves preserved, small, up to 0.7 cm long and up to 0.5 cm wide. On leaf blade impressions, visible network of secondary veins and characteristic, distinct tubercles or hollows on areolae. Midvein indistinct.

Remarks. The characteristic morphology of these remains is typical for the water fern *Salvinia*, whose morphology is unique among ferns (Bonnet 1955, Croxdale 1978, 1979, 1981). The small size of the floating leaves suggest affinity with fossil *Salvinia mildeana* Goeppert typical for the younger Neogene. Another species of this genus, *Salvinia reussii* Ettingshausen, typical for Oligocene and Early Miocene floras, has distinctly larger leaves (Collinson et al. 2001). However, the morphological characters of *Salvinia* leaves should be used with caution for the taxonomy of fossil material of this genus (see Bůžek et al. 1971). Usually found in the fossil state are megaspores of *Salvinia* and remains of floating leaves; submerged segments of the plant are much more rarely found.

Modern equivalents. The modern genus *Salvinia* comprises ca 10 species that occur in Europe, America, Africa and Madagascar, and Asia (Tryon & Tryon 1982, Collinson et al. 2001). Most of them are in the tropics and subtropics except for *Salvinia natans* (L.) Allioni, which is distributed in temperate regions (Wang et al. 2014).

Ecology. Warm temperate element. Modern representatives of *Salvinia* typically grow in lakes, rivers, ponds in stagnant water, and sometimes also in slightly brackish waters. *Salvinia* usually occurs among aquatic vegetation but sometimes forms large floating mats (Tryon & Tryon 1982). Fossil *Salvinia* is considered a component of the

Salvinia-Azolla water plant community (Kunzmann & Walther 2012).

Occurrence. Fossil floating leaves of *Salvinia* or *Salvinia*-like plants are widespread in the fossil record beginning from the Late Cretaceous (Shaparenko 1956, Collinson et al. 2001, Wang et al. 2014), but Collinson (1991, 1996) pointed out that most of the recorded fossils of *Salvinia* are doubtful due to the absence of reproductive organs (see Wang et al. 2014). In Poland the remains of floating leaves of *Salvinia* are reported from Miocene deposits (Zastawniak et al. 1996).

Gymnosperms

Pinaceae Spreng. ex Rudolphini

Pinus L.

Pinus sp.

Pl. 1, fig. 1, Pl. 9. figs 1a, b

Material. KRAM-P 218: 18, 105, 124/III

Description. Macromorphology. One needle with preserved remnants of a persistent fascicle sheath measuring ca 1 cm long, and numerous needle fragments up to 5.0 cm long and 1–2 mm wide with acute/attenuate apex. Needles mostly entire-margined; only on small fragment minutely serrate with small, partly irregularly spaced teeth.

Micromorphology. Epidermal cells strongly cutinised, rectangular, rather elongate, up to 270 µm long and 20–25 µm wide. Short walls of cells often oblique to longer walls of cells. On one side of the needle epidermis, scattered papillae 40–85 × 20–30 µm, parallel to axis of needle. Ca 7 stomatal rows present on every side of needle. All stomatal rows composed of single row of stomata. Longer axes of stomata parallel to midvein. Stomata cyclocytic, elliptic, 50–60 µm long and 35–40 µm wide. Outer stomatal ledge aperture narrow elliptic, 20–25 µm long and 10.0–12.5 µm wide. Polar T-shaped cuticular thickenings always visible, strongly developed.

Remarks. The macromorphology of these needle remains is typical for *Pinus*, as confirmed by the distinctive structure of the stomatal

rows composed of a single row of stomata. The absence of preserved whole fascicles precludes reliable classification of these pine needles to a given species. The remains of peeled bark of *Pinus* were also found in the studied plant assemblage.

Ecology. Probably a temperate element.

Occurrence. Remains of pine needles are common in the Neogene deposits of Europe.

Bark of *Pinus* sp.

Pl. 1, fig. 2, Pl. 9, fig. 2

- 1969 *Pinus* – Rindengewebe, Schneider, p. 30, pl. 10, figs 2–4.
 2010 *Pinus* morphospec. (bark), Schneider, p. 46, 47, pl. 1, figs 1, 2.
 2014 Bark of *Pinus* sp., Worobiec, p. 251, pl. 1, fig. 2, pl. 4, fig. 2

Material. KRAM-P 218: 4

Description. Macromorphology. Two fragments (3 and 4 cm across) of exfoliated bark.

Micromorphology. Cells isodiametric or slightly elongated, 55–85 µm across, cell walls strongly undulate, sclerenchymatic, rather thick.

Remarks. These plant remains represent peeled bark of *Pinus*. Remains of pine bark were earlier reported by Schneider (1969, 2010) from Miocene lignite deposits from Germany. Kvaček et al. (2011) mistakenly classified them as remains of cf. *Rhizocaulon* sp. Worobiec (2014) reported the same type of exfoliated bark of *Pinus* associated with needles of *Pinus* sp. from presumably a late Miocene leaf assemblage from the Bełchatów mine.

Cupressaceae s.l. *sensu* Gadek et al. 2000

Taxodioideae Endl. ex K. Koch *sensu*
 Gadek et al. 2000

Taxodium Rich.

Taxodium dubium (Sternberg) Heer

Pl. 6, fig. 2, Pl. 9, figs 3, 4

- 1823 *Phyllites dubius* Sternberg; Sternberg, p. 37, Pl. 36, fig. 3.
 1853 *Taxodium dubium* (Sternberg) Heer; Heer, p. 136.
 1855 *Taxodium dubium* (Sternberg) Heer; Heer, p. 49, Pl. 17, figs 515.

Material. KRAM-P 218: 82/I, 85/V, 86/I, 89/I, 90/II, 99/II, 100/I, 101, 103, 107, 108/I, 115, 117, 118, 123/I, 124/I, 126/I, 131, 132/I, 135, 137/I, 142/I, 145/I, 148/I, 174/I, 176/I, 184, 185/II, 186

Description. Macromorphology. Fragments of leafy shoots up to 5.5 cm long and up to 2.5 cm wide. Needles entire-margined, 1.0–2.0 cm long and 1.1–1.6 mm wide, decreasing in length towards base and apex of shoot. Apex of needle acute, base obtuse and decurrent.

Micromorphology. Epidermal cells mostly rectangular, 54–86 µm long and 17–25 µm wide. Cell walls thick, straight or rounded, end walls perpendicular or oblique to long axis of cells. Cuticle thick, slightly granulate. Stomata irregularly elliptic, 40–50 µm long and 22–32 µm wide. Long axis of stomata irregularly oriented, usually oblique to long axis of needle. Present are distinct T-shaped thickenings at stomatal poles. Outer stomatal ledge aperture elongate-elliptic, 16–20 µm long and ca 12 µm wide.

Remarks. *Taxodium* shoots, morphologically similar to those of *Sequoia abietina* (Brongniart) Knobloch, differ in having slightly narrower and longer needles, though the needle morphology of both *Sequoia* and *Taxodium* is highly variable. However, an analysis of the epidermal micromorphology of the needles made it possible to distinguish the two genera. *Taxodium dubium* from Bełchatów has the long axes of stomata oblique to the axis of the needle, unlike in *Sequoia* where the long axes of stomata are more or less parallel to the needle axis (Hummel 1983, Worobiec 2003a).

Modern equivalents. *Taxodium dubium* is comparable with two extant species: *T. distichum* (L.) Rich. and *T. mucronatum* Tenore from North America (Hummel 1983). *Taxodium distichum* grows in swamps and in riparian communities of the south-eastern USA, while *T. mucronatum* occurs on banks of mountain rivers and streams in Mexico (Krüssmann 1972).

Ecology. Warm temperate element. *Taxodium dubium* represents azonal vegetation and grew in swamp and riparian forests. It is considered a dominant component of *Taxodium-Nyssa* swamp forests (Boulter et al. 1993, Belz & Mosbrugger 1994, Mai 1995, Kunzmann et al. 2009).

Occurrence. In Europe, *Taxodium dubium* was reported from the late Eocene to late Miocene deposits in the (Atlantic-) Boreal province sensu Mai of Central Europe, and from the late Oligocene to late Pliocene in the Trans-European Paratethys province sensu Mai (Kunzmann et al. 2009). In Poland it is found in early Miocene to early Pliocene deposits (see Worobiec et al. 2008).

Angiosperms

Lauraceae Juss. nom. cons.

Laurophyllum sp.

Pl. 1, figs 3a–3c, Pl. 6, fig. 3, Pl. 9, figs 5a, b

2014 ?*Magnolia* sp., Worobiec, p. 256, 257, Fig. 2, Pl. 3, fig. 2, Pl. 6, figs 1a, b

Material. KRAM-P 218: 39, 42, 100/II, 113 (fragments of one leaf).

Description. Macromorphology. One leaf 9.5 cm long and 5 cm wide, entire-margined. Leaf base cuneate to decurrent. Venation pinnate, primary vein straight and of moderate thickness (up to 1 mm wide). Secondary venation brochidodromous. Secondaries distributed at irregular intervals of 1.6–2.6 cm, curved upward and interconnected in loops, forming irregular 50–60° angle with primary vein. Intersecondary veins present. Tertiary venation weakly percurrent or composite intersecondary. Higher-order venation random reticulate. Areoles well developed, 0.3–0.6 mm across. Veinlets usually none, if present simple. Marginal ultimate venation forms distinct fimbrial vein.

Micromorphology. Adaxial epidermis consisting of usually elongated cells 35–50 µm across. Anticlinal cell walls usually Ω -undulate. Abaxial epidermis consisting of irregular-shaped, usually elongated cells 35–63 µm across. Anticlinal cell walls undulate, sometimes Ω -undulate. Leaf hypostomatic. Stomata brachyparacytic of characteristic roundish-rhomboidal (frequently distinctly rhomboidal) shape, of rather uniform size, 22–25 µm wide. Outer stomatal ledge aperture indistinct, rather thin, surrounded by distinct ledges raised above surface of cuticle, 17–20 µm long and 12–15 µm wide. In leaf mesophyll, numerous roundish idioblast secretory cells 35–43 µm in diameter.

Remarks. The structure of the stomatal complex (brachyparacytic) and the presence of idioblast secretory cells in the leaf mesophyll are characteristic of leaves of the Lauraceae family. The Ω -undulate cell walls of the adaxial epidermis and the shape of the stomata somewhat resemble those of the genus *Laurus*. However, these leaves from Bełchatów differ from leaves of both the fossil species *Laurus abchasicus* and extant *Laurus nobilis* in having lower stomatal density. The structure of the higher-order venation resembles that of the genus *Sassafras* but the network of the third-order venation seems to differ from that of *Sassafras*. The moderately cutinised epidermis suggests deciduousness of this fossil lauroid. A rather small leaf remain with the same epidermis micromorphology was earlier reported from late Neogene deposits of the Bełchatów Mine as ?*Magnolia* sp. (Worobiec 2014). However, the macromorphology of this new material of lauroid leaves from Bełchatów, especially the higher-order venation, seems to differ from fossil leaves of *Magnolia* known from the European Neogene. It should be added that the adaxial epidermis of *Laurophyllum* sp. from Bełchatów is almost identical to that of the fossil-taxon *Cornus graeffii* (Heer) Hantke reported from Neogene deposits of the Lower Rhine Embayment (Belz & Mosbrugger 1994), suggesting that both fossil remains represent the same fossil species. The macromorphology of these leaf remains also matches well.

Modern equivalents. Warm temperate to subtropical representatives of the family Lauraceae (e.g. Nitta & Ohsawa 1997).

Ecology. Warm temperate or subtropical element.

Altingiaceae Horan., nom. cons.

Liquidambar L.

Liquidambar europaea A. Braun

Pl. 6, figs 4a, b, Pl. 9, fig. 6

1836 *Liquidambar europaeum* A. Braun in Buckland, p. 513.

1969 *Liquidambar europaea* A. Braun; Knobloch, p. 94, pl. 44, figs 1, 3, 4–7, pl. 45, figs 1, 2, 6, pl. 46, figs 1, 4, pl. 59, fig. 2.

Material. KRAM-P 218: 110/II

Description. Macromorphology. Leaf palmately 3-lobed, 4.5 × 4 cm. Leaf base truncate/cordate. Leaf margin simple serrate, teeth small, apical side of teeth very short, convex, basal side long, straight/convex, tooth apex round. Veins terminate in sinus between teeth. Primary venation palmate, actinodromous, perfect. Primary vein branched into 3 branches. Secondary venation semicraspedodromous, secondaries interconnected near leaf margin, forming loops, sending fine veins towards teeth.

Micromorphology. Adaxial epidermis composed of isodiametric or slightly elongated cells 25–42 µm across, with straight and thick cell walls. Anticlinal cell walls of abaxial epidermis not visible. Leaves hypostomatic. Stomata elliptic, ca 30 µm long and ca 20 µm wide. Outer stomatal ledge spindle-shaped, ca 15 µm long and ca 5 µm wide.

Remarks. The leaf shape, distinctive serration of the margin, network of venation, and epidermal features are characteristic for the fossil species *Liquidambar europaea* A. Braun.

Modern equivalents. North American *Liquidambar styraciflua* L. and *L. orientalis* Mill. from Asia Minor are closely related to the fossil *L. europaea* (Hummel 1983).

Ecology. Warm temperate element. *Liquidambar europaea*, like its extant relatives, most probably was a component of azonal riparian forests (Kovar-Eder 1988, Belz & Mosbrugger 1994, Mai 1995, Kovar-Eder et al. 2001).

Occurrence. Common in the Neogene floras of Europe. From Poland, known from middle Miocene to Pliocene deposits (for localities see Hummel 1983).

Vitaceae Juss. nom. cons.

Vitis L.

Vitis strictum (Goeppert) Knobloch

Pl. 1, figs 4a–4c, Pl. 10, figs 1a–1c

1855 *Acer strictum* Goeppert, p. 35, Pl. 23, figs 1–5.

1969 *Vitis strictum* (Goeppert) Knobloch, p. 125, Fig. 269, Pl. 64, fig. 9.

Material. KRAM-P 218: 33, 38, 40, 55, 83, 92/III, 106/IV, 108/III, 116

Description. Macromorphology. Leaves lobate, up to 7.5 cm long and 6.0 cm wide, some

of best-preserved specimens seem asymmetric. Lobe apex attenuate, leaf base deeply cordate. Fragment of petiole 1.8 cm long. Leaf margin simple serrate. Teeth upwardly curved (hooked). Apical side of teeth acuminate, basal side acuminate or convex, tooth apex acute. Venation palmate, actinodromous, perfect, basal. Primary vein of moderate thickness (up to 0.5 mm), branched into 7–8 branches. Secondary venation mostly craspedodromous, secondaries usually curved upward. Secondary veins or their branches usually terminate in teeth, but some (the lowermost) connected in imperfect loops. Tertiary venation composite intersecondary. Higher-order venation random reticulate. Areoles well developed, 0.20–0.45 mm across. Veinlets usually none, if present simple. Marginal ultimate venation looped.

Micromorphology. Adaxial epidermis composed of isodiametric or slightly elongated cells with mostly straight walls, 25–42 µm across. Cuticle covered by epicuticular wax layer. Cells over veins elongated, up to 90 µm long. Abaxial epidermis composed of isodiametric or slightly elongate cells 15–25 µm across, with usually straight, sometimes rounded cell walls, cells over veins strongly elongated. Leaves hypostomatic. Stomata probably anomocytic, rounded to wide elliptic, 15–20 µm in diameter. Stomatal pore often visible. Radial striae found around large stomata. Very rarely, giant stomata up to 32 µm in diameter found on abaxial epidermis. Outer stomatal ledge aperture imperfectly spindle-shaped or narrow elliptic to oblongate, 5.0–7.5 µm long and 2.5–4 µm wide. On abaxial epidermis, scattered trichome bases ca 30 µm across. Trichome type unknown.

Remarks. The macromorphology of these leaves (lobate leaf blade with characteristic hook-shaped teeth) and the cuticular features are most typical for leaves of the genus *Vitis*. They best match the fossil species *Vitis strictum* (Goeppert) Knobloch (= *Vitis teutonica* Al. Braun, Zastawniak 1978). Their asymmetry, tooth shape and venation are typical of this species (Knobloch 1969, Zastawniak 1978, Teodoridis 2002). The cuticular micromorphology well matches those of leaf remains described as *Vitis* sp. from late Neogene deposits of the Lower Rhine Embayment, which are considered to be macromorphologically similar to *Vitis strictum* (Belz & Mosbrugger 1994). Belz and Mosbrugger (op. cit.), however, state that

the adaxial epidermis of *Vitis* sp. leaves differs from that of *Vitis strictum* described earlier by Mai and Walther (1991) in having straight cell walls. It cannot be excluded that the differences in cell wall undulation between the discussed vine leaves are caused by the effects of different environmental conditions, as in the case of leaves of *Liquidambar* (Xiao et al. 2011), and all the discussed fossil leaves represent the fossil-species *Vitis strictum*.

Modern equivalents. Contemporary North American vine species *Vitis vulpina* L. (= *V. cordifolia* Michx.) can be compared with *Vitis strictum* (Knobloch 1969, Zastawniak 1978, Teodoridis 2002).

Ecology. Warm temperate element. *Vitis strictum* was a climber, probably a component of riparian communities (Teodoridis 2002).

Occurrence. Common species of Tertiary fossil leaf assemblages (Kvaček et al. 2004), known from the late Oligocene to Pliocene (Zastawniak 1978, Teodoridis 2002). In Poland reported only from Miocene deposits from Chłapowo, Mirostowice, Pierusza, Ruprechtów, Sośnica (Zastawniak 1978), and Bełchatów (Stuchlik et al. 1990).

Rosaceae Juss. nom. cons.

Crataegus L.

cf. *Crataegus* sp.

Pl. 7, fig. 1

Material. KRAM-P 218: 106/II

Description. Macromorphology. More or less ovate leaf 3 cm long and ca 2 cm wide, with acute leaf base. Fragment of petiole 0.5 cm long. Leaf margin lobate and serrate, teeth small, lobes up to 0.8 cm long and 0.2–0.3 cm high, apical and basal sides of lobes convex. Secondary veins terminate at lobe apex. Venation pinnate, primary vein of moderate thickness. Secondary venation simple craspedodromous. Secondary veins preserved in 3–4 pairs, straight, distributed at 0.4–0.6 cm intervals, forming 45–50° angle with primary vein.

Remarks. The shape of this leaf is similar to that in the genus *Crataegus* and similar to fossil leaves described as *Crataegus* sp. 1 from Pliocene deposits of Willershausen (Knobloch 1998)

and *Crataegus* sp. 1 from Miocene deposits of Hungary (Andreánsky 1959). Rather similar are morphotype LX (*Quercus* cf. *pseudocastanea* Goepfert and *Rhus quercifolia* Goepfert) described by Ferguson (1971) from the Miocene flora of Kreuzau. As the fossil-species *Rhus quercifolia* is a synonym of *Acer aegopodifolium* (Goepfert) Baikovskaya ex Ilinskaya, it cannot be excluded that these remains considered to be *Crataegus* sp. in fact represent a terminal leaflet of the compound leaf of *Acer aegopodifolium*.

Modern equivalents. Probably recent representatives of the genus *Crataegus*.

Ecology. Temperate element.

Occurrence. Fossil leaves of *Crataegus* are found in Oligocene to Pliocene plant assemblages from Europe (Andreánsky 1959, Knobloch 1998, Kvaček & Walther 2004). Leaves of *Crataegus* have not been reported from fossil floras of Poland, whereas fossil hawthorn fruits have been found in some localities from the Miocene to Pliocene (Szafer 1961).

Ulmaceae Mirb.

Ulmus L.

Ulmus sp.

Pl. 1, figs 5a–5c, Pl. 7, figs 2a, b, Pl. 10, fig. 2

Material. KRAM-P 218: 16, 37, 82/II, 104/III, 111, 119, 127/III, 141/IV, 161, 165, 166, 171/III, 172/I

Description. Macromorphology. Only leaf fragments, usually small, up to 6 cm long and 5 cm wide, with obtuse to cordate and asymmetric leaf base. Leaf margin usually double serrate, teeth hook-shaped, apical side of teeth concave, basal side usually acuminate. Tooth apex acute. Secondary veins or their branches terminate in tooth apex. Venation pinnate, primary vein straight, of moderate thickness. Secondary venation simple craspedodromous. Secondary veins rather numerous (up to 9 pairs preserved), run off primary vein at 0.2–0.6 cm intervals in middle part of lamina. Secondaries form variable 40–60° angle with primary vein. Secondary veins usually straight, or directly on leaf margin slightly curved upward. Tertiary venation percurrent, forming 130–150° angle with primary vein, 7–9 tertiary veins per 1 cm

of secondary vein length. Higher-order venation more or less orthogonal reticulate. Areoles well developed, 0.38–0.68 mm across. Veinlets present, multiple-branched. Marginal ultimate venation looped or incomplete.

Micromorphology. Adaxial epidermis consisting of isodiametric or slightly elongated cells 12–35 µm across. Anticlinal cell walls usually straight. Stomata elliptic, 20–25 µm across. Outer stomatal ledge aperture narrow elliptic, 10–15 µm long and ca 5 µm wide. On undetermined side of epidermis, unicellular trichome bases, roundish to elliptic, 10–12 µm in diameter.

Remarks. These leaves with serrate margins, hook-shaped teeth and dense secondary venation are typical for *Ulmus*. The incompleteness of the discussed leaf precludes an unequivocal assignment to any fossil species.

Ecology. Probably a temperate element.

Zelkova Spach

Zelkova zelkovifolia (Unger) Bůžek & Kotlaba

Pl. 2, figs 1a–1c, Pl. 10, fig. 3

1841 *Ulmus zelkovaefolia* Unger, p. 94, 95, pl. 24, fig. 7 pro parte, figs 9–12, pl. 26, fig. 7.

1963 *Zelkova zelkovaefolia* (Unger) Bůžek & Kotlaba; Kotlaba, p. 59–62, pl. 3, figs 7, 8.

Material. KRAM-P 218: 13, 19 and 151 (counterparts), 27, 57, 77, 92/IV, 93/I, 94, 112, 171/IV, 172/II, 173/III

Description. Macromorphology. Leaves of various size, up to 2.3 cm long and 1.0–4.0 cm wide. Leaf apex acute to attenuate, leaf base obtuse to slightly cordate, sometimes asymmetric. Petiole very short, 0.1 cm long. Leaf margin simple serrate, teeth large, apical and basal side of teeth predominantly acuminate, tooth apex acute. Secondary veins terminate in tooth apex. Venation pinnate, primary vein of moderate thickness (not exceeding 1 mm). Secondary venation simple craspedodromous. Secondaries straight or slightly curved upward, distributed at 0.3–1.0 cm intervals, forming 40–50° angle with primary vein. Tertiary venation weakly percurrent, ca 5 tertiary veins per 1 cm of secondary vein length. Higher-order venation more or less orthogonal reticulate. Areoles well

developed, ca 0.38–0.95 mm across. Veinlets present, multiple-branched. Marginal ultimate venation looped or incomplete.

Micromorphology. Adaxial epidermis consisting of usually elongated cells 37–62 µm across. Depending on specimen, anticlinal cell walls undulate or straight to rounded. Stomata extremely rarely preserved, elliptic, ca 25 µm across. Outer stomatal ledge aperture slightly spindle-shaped, ca 17 µm long and 5 µm wide. On undetermined side of epidermis, unicellular trichome bases, roundish to elliptic, 12–15 µm in diameter.

Remarks. The serrate margins with simple, large teeth and the venation network of this material are typical for leaves of the genus *Zelkova*. The shape and size of these *Zelkova* leaves correspond to the fossil species *Z. zelkovifolia* (Unger) Bůžek & Kotlaba.

Modern equivalents. *Zelkova carpinifolia* (Pallas) K. Koch from the Euxine forests (Eastern Anatolia, Transcaucasia) and Hircanian forests on the southern shores of the Caspian Sea (Kvavadze & Connor 2005) is considered to be most similar to the fossil *Zelkova zelkovifolia*.

Ecology. Warm temperate element. This species is considered a component of European Palaeogene and Neogene riparian vegetation (Kovar-Eder 2003).

Occurrence. *Zelkova zelkovifolia* is known from the Oligocene to Plio-Pleistocene (Zastawniak et al. 1996). In Poland, found from the middle Miocene to Pliocene (Worobiec et al. 2008).

Fagaceae Dumort.

Fagus L.

Fagus silesiaca Walther & Zastawniak

Pl. 2, figs 2a–2c, 3, Pl. 10, figs 4, 5

1991 *Fagus silesiaca* Walther & Zastawniak, p. 156–160, Fig. 1, pl. 1, figs 1–6, pl. 2, fig. 1.

Material. KRAM-P 218: 1, 22–26, 28, 29, 35, 36, 61–69, 71–74, 84, 85/II, 87/III, 89/III, 99/III, 104/I, 110/I, 121, 123/II, 128, 129, 138/III, 141/I, 145/III, 155, 158, 170/II, 173/I, 175/II, 176/II, 182

Description. Macromorphology. Leaves elliptic or ovate, up to 6.3 cm long and 2.2–4.5 cm

wide. Leaf base acute or obtuse, leaf apex acuminate, rarely acute. Leaf margin simple serrate, teeth upwardly curved, apical sides of teeth concave, basal sides acuminate or convex, tooth apex rounded. Venation pinnate, primary vein of moderate thickness or thin, often sinuous. Secondary venation simple craspedodromous, in basal part often brochidodromous. Secondaries alternate, preserved in up to 11 pairs, straight, right on leaf margin upwardly curved entering nearest tooth, distributed at 0.5–0.9 cm intervals. Secondary veins form 35–50° angle (average 40–45°) with primary vein. Tertiary venation percurrent, forms 120–140° angle with primary vein, 6–10 tertiary veins per 1 cm of secondary vein length. Higher-order venation orthogonal reticulate. Areoles well developed, ca 0.2–0.3 mm across. Veinlets simple, rarely none, occasionally branched once. Marginal ultimate venation looped.

Micromorphology. Adaxial epidermis composed of isodiametric or slightly elongated cells with usually distinctly undulate cell walls (rarely with rounded walls), 20–45 µm across. Over veins, cells exclusively straight-walled, rectangular, elongate, up to 47 µm long and 7.5–12.0 µm wide. Abaxial epidermis consisting of variable-shaped cells with straight or rounded cell walls, 15–27 µm across, cells elongated over veins. Leaves hypostomatic. Stomata cyclocytic, roundish to wide elliptic, 20–25 µm in diameter. Outer stomatal ledge roundish to wide elliptic (oblong), rarely wide spindle-shaped, 7.5–12.0 µm long and 4–9 µm wide. T-piece (T-shaped cuticular thickenings) usually visible at poles of guard cells, occasionally very distinct. On lower epidermis, unicellular trichome bases, elliptic to roundish, 7.5–12.0 µm in diameter. Trichomes solitary (unbranched), composed of few cells, fragmentarily preserved, up to 50 µm.

Remarks. The venation network, the serration of the leaf margin and the stomatal complex are distinctive for leaves of the genus *Fagus*. The shape of the leaves and the number of secondary veins point to the fossil-species *Fagus silesiaca* Walther & Zastawniak (Walther & Zastawniak 1991).

Modern equivalents. Macro- and micromorphologically, the leaves of *Fagus silesiaca* are comparable to extant leaves of the Chinese species *Fagus hayatae* Palibin ex Hayata (Dyjur et al. 1992). Leaves of *Fagus grandiflora* Ehrh.

from North America are macromorphologically similar to *Fagus silesiaca* but differ in having anomocytic stomata (Kvaček & Walther 1991).

Ecology. Warm temperate element.

Occurrence. *Fagus silesiaca* is common in late Miocene to early Pliocene leaf assemblages of Central Europe (Walther 1994). In Poland, reported from middle Miocene to Pliocene floras (Worobiec 2003a).

Quercus L.

Quercus pseudocastanea Goepfert emend. Walther & Zastawniak

Pl. 2, figs 4a, b, Pl. 10, fig. 6, Pl. 11, fig. 1

1991 *Quercus pseudocastanea* Goepfert emend.
Walther & Zastawniak, p. 169, Fig. 8, pl. 2, figs 2–6, pl. 3, figs 1–6.

Material. KRAM-P 218: 3, 11, 85/IV, 109/III, 110/III, 114, 122

Description. **Macromorphology.** Fragments of leaves up to 9.2 cm long and up to 5.3 cm wide. Leaf margin lobate, lobes small, apical sides of lobes convex, basal sides convex, occasionally acuminate, lobe apex always rounded with acute terminal part. Secondary veins terminate at lobe apex. Venation pinnate. Secondary venation simple craspedodromous. Secondaries straight, sometimes upwardly curved near leaf margin, preserved in up to 9 pairs, distributed at 0.9–1.4 cm intervals. Secondary veins form 40–50° angle with primary vein. Tertiary venation percurrent, forming ca 140–150° variable angle with primary vein, ca 5–7 tertiary veins per 1 cm of secondary vein length. Higher-order venation mostly orthogonal reticulate. Areoles well developed, 0.25–0.50 mm across. Veinlets present, simple or branched. Marginal ultimate venation forms imperfect fimbrial vein.

Micromorphology. Adaxial epidermis composed of usually irregular-shaped cells 22–33 µm across. Anticlinal cell walls rounded, curved or (rarely) undulate. Abaxial epidermis consists of irregular-shaped cells 20–30 µm across. Anticlinal cell walls curved or undulate. Leaves hypostomatic. Stomata anomocytic, elliptic to wide elliptic, 17–22 µm long and 12–16 µm wide. Outer stomatal ledge aperture elliptic-oblongate, ca 5–8 µm long. Stomatal pore often visible. T-piece usually visible at poles of guard

cells. On abaxial epidermis, two types of trichomes: most numerous, stellate trichomes composed of 4–5 arms, 98–150 μm across, with roundish trichome bases composed of several cells, ca. 12–15 μm across; rarely, uniseriate trichomes with unicellular base.

Remarks. Fossil oak leaves with marginal lobes and acute termination of the apex are characteristic of the fossil-species *Quercus pseudocastanea* Goepfert emend. Walther & Zastawniak. The micromorphology of the epidermal cells of these leaves corresponds to *Quercus pseudocastanea*. The rather similar fossil oak *Quercus roburoides* Gaudin differs from *Quercus pseudocastanea* in having lobes with a retuse apex.

Modern equivalents. In respect of macro- and micromorphology the leaves of *Quercus pseudocastanea* are comparable to extant oaks from section *Cerris* Oersted (Walther & Zastawniak 1991).

Ecology. Warm temperate element.

Occurrence. *Quercus pseudocastanea* is common in Neogene floras of Europe from the middle Miocene to late Pliocene. In Poland, found from the middle Miocene to Pliocene (Walther & Zastawniak 1991).

Juglandaceae DC. ex Perleb, nom. cons.

Carya Nuttall

Carya serrifolia (Goepfert) Kräusel

Pl. 3, figs 1a–1c, Pl. 7, fig. 3, Pl. 11, fig. 2

1855 *Quercus serraefolia* Goepfert, p. 17, pl. 5, fig. 14.

1920 *Carya serraefolia* (Goepfert) Kräusel, p. 389, pl. 5, fig. 2.

Material. KRAM-P 218: 9, 31, 34, 85/I, 87/I, 89/II, 108/II, 149, 171/I, 177, 181, cf. *Carya serrifolia*: 109/II

Description. **Macromorphology.** Only fragments of leaflets, up to 8.5 cm long and 5.0 cm wide. Leaflet margin simple serrate, apical and basal side of teeth acuminate, tooth apex acute, almost spinose. Branches of secondary veins terminate at tooth apex. Venation pinnate, primary vein straight and of moderate thickness. Secondary venation mixed craspedodromous: both semicraspedodromous and simple craspedodromous. Secondary veins

preserved in up to 11 pairs, departing primary vein at 0.6–1.3 cm intervals and forming 60–80° angle with primary vein. Secondary veins upwardly curved, branched, branches interconnected in loops or directly enter nearest tooth. Tertiary venation percurrent, forming 130–140° angle with primary vein. 4–5 tertiary veins per 1 cm of secondary vein length. Higher-order venation orthogonal reticulate. Areoles well developed, 0.20–0.35 mm across. Veinlets simple or absent, rarely branched once. Marginal ultimate venation looped.

Micromorphology. Adaxial epidermis consists of isodiametric or slightly elongated cells with usually straight cell walls 17–25 μm across. Abaxial epidermis rather badly preserved. Leaves hypostomatic. Stomata elliptic to wide elliptic, 20–30 μm across. Radial striae around large stomata. Outer stomatal ledge aperture wide to narrow elliptic, 10–18 μm long and 5–8 μm wide. On abaxial epidermis, unicellular, roundish to elliptic trichome bases 15–20 (25) μm in diameter. Very rarely, pelate trichomes (scales) ca 100 μm in diameter over veins.

Remarks. The mixed craspedodromous venation pattern and the branching character of the secondary veins at the leaf margin are typical for leaves of the genus *Carya* Nutt. Leaf shape and size point to the fossil-species *Carya serrifolia* (Goepfert) Kräusel. Leaves of the fossil wing nut *Pterocarya paradisiaca* (Unger) Ilinskaya, somewhat similar to those of *Carya serrifolia*, differ in having semicraspedodromous secondary venation, oblongate shape, and different shape of the teeth.

Modern equivalents. Extant representatives of the genus *Carya* (ca 17 species) show a disjunct distribution and occur in tropical to temperate regions of East Asia and eastern North America (Zhang et al. 2013, Knor et al. 2015). *Carya serrifolia* is usually compared with some recent North American species of this genus: *Carya aquatica* (F. Michx.) Nutt., *Carya illinoensis* (Wangenh.) K. Koch., and *C. tomentosa* Nutt. (Teodoridis 2002).

Ecology. Warm-temperate element.

Occurrence. *Carya serrifolia* is common in Neogene European floras (Knobloch 1969, Palamarev & Petkova 1987). In Poland, found from the middle Miocene to early Pliocene (Worobiec 2003a).

Pterocarya* Kunth.**Pterocarya paradisiaca*
(Unger) Ilinskaya**

Pl. 8, figs 2a, b

- 1849 *Prunus paradisiaca* Unger, p. 7, pl. 14, fig. 22.
 1897 *Pterocarya castaneifolia* (Goepfert) Schlechtendal; Schlechtendal, p. 22, pl. 5, figs 1–3b, pl. 6, figs 5, 6.
 1962 *Pterocarya paradisiaca* (Unger) Ilinskaya, p. 104.

Material. KRAM-P 218: 144/I

Description. Macromorphology. Fragment of probably oblongate leaflet, 4.0 cm long and 1.9 cm wide. Leaflet margin simple serrate, apical side of teeth concave, basal side straight or acuminate, tooth apex acute. Venation pinnate, primary vein straight and of moderate thickness. Secondary venation semicraspedodromous. Secondary veins preserved in up to 9 pairs, departing midvein at 0.3–0.5 cm intervals and forming 70–80° angle with primary vein. Secondary veins upwardly curved and interconnected. Tertiary venation percurrent, ca 8 tertiary veins per 1 cm of secondary vein length.

Remarks. The semicraspedodromous secondary venation pattern and the oblongate shape are typical for leaflets of the genus *Pterocarya*. Leaflet shape and size point to the fossil-species *Pterocarya paradisiaca* (Unger) Ilinskaya. *Carya serrifolia* (Goepfert) Kräusel differs in having secondary veins with craspedodromous endings and in tooth shape (cf. Hummel 1983, Manchester 1987).

Modern equivalents. *Pterocarya paradisiaca* is compared to the extant *P. fraxinifolia* Spach (Ilinskaya 1968, Knobloch & Kvaček 1976, Belz & Mosbrugger 1994), distributed in the Euxine-Hyrcanian area where it grows in riparian forests (Boratyński & Boratyńska 1975, Akhani & Salimian 2003).

Ecology. Warm temperate element. *Pterocarya paradisiaca* is considered a component of riparian forests in the Neogene of Eurasia (Kovar-Eder 2003).

Occurrence. *Pterocarya paradisiaca* occurred in Europe from the late Oligocene to late Pliocene (Zastawniak et al. 1996). In Poland, found in Neogene (lower Miocene to Pliocene) deposits (Worobiec et al. 2008).

Salicaceae Mirb.***Populus* L.*****Populus balsamoides* Goepfert**

Pl. 3, figs 2a, b, Pl. 7, fig. 4, Pl. 11, fig. 3

- 1855 *Populus balsamoides* Goepfert, p. 23, pl. 15, figs 5, 6.

Material. KRAM-P 218: 43, 46, 85/III, 92/II, 98, 120 and 140 (counterparts), 139. *Populus* cf. *balsamoides*: 127/II, 136/II, 157

Description. Macromorphology. Leaf fragments up to 8.5 cm long and 8 cm wide. Leaf apex attenuate, base rounded to slightly cordate. Margin simple serrate, teeth 2–4 mm long, apical side of teeth very short, basal side long, convex, tooth apex rounded. Veins terminate in tooth apex. Venation pinnate, primary vein straight and of moderate thickness or stout. Secondary venation semicraspedodromous, secondaries distributed at intervals from 0.5 cm near leaf base to 2.3 cm in middle of lamina. Secondary veins upwardly curved, diverging from midvein at ca 50° angle, branching towards leaf margin, forming agrophic (pectinal) veins. Tertiary veins percurrent, forming 110–100° angle with primary vein, ca. 5 tertiary veins per 1 cm of secondary vein. Higher-order venation reticulate. Areoles well developed, ca 0.5 mm across. Veinlets branched. Marginal ultimate venation looped.

Micromorphology. Adaxial epidermis not preserved. Abaxial epidermal cells 17–25 µm across, cell walls straight. Cuticle usually covered by epicuticular wax granules. Stomata elliptic to elliptic-elongated, rather diverse in size, 15.0–27.5 µm long and ca 12 µm wide. Stomata surrounded by striae perpendicular to longer axis of stoma. Outer stomatal ledge aperture spindle-shaped, extremely diverse in size, ledges strongly cutinised, 12.5–35 µm long and 2.5–17.5 µm wide. Some probable trichomes or trichome bases found, strongly cutinised, 20–30 µm across.

Remarks. Leaf shape, tooth type and shape, and the venation network are characteristic for the fossil species *Populus balsamoides*. The tooth shape and abaxial epidermis structure of this species differ from those of another fossil Neogene poplar, *Populus populina* (Brongniart) Knobloch.

Modern equivalents. Extant leaves of *Populus balsamifera* L., a North American riparian species and member of section *Tacamahaca* Spach, are morphologically comparable to *P. balsamoides* (Hantke 1954, Krüssmann 1976, Belz & Mosbrugger 1994). Some authors compare *Populus balsamoides* with the recent Chinese *Populus lasiocarpa* Oliv. from section *Leucoides* Spach. (Ilinskaya 1968, Zastawniak 1972).

Ecology. Probably a temperate element.

Occurrence. Common in Neogene floras of Europe. In Neogene deposits of Poland, found from the middle Miocene to Pliocene (Worobiec et al. 2012).

Salix L.

Salix varians Goeppert *sensu lato*

Pl. 3, figs 3a–3c, Pl. 11, figs 4a–4c

1855 *Salix varians* Goeppert, p. 26, pl. 19, figs 17, 18, pl. 20, fig. 1.

Material. KRAM-P 218: 54, 91, 97/II, 106/III, 156 and 164 (counterparts), 171/II, 173/II

Description. Macromorphology. Fragments of elongated leaves up to 5.5 cm long and up to 2.5–3.0 cm wide. Leaf base obtuse, rounded to slightly cordate. Leaves mostly entire-margined, rarely simple serrate. Apical sides of teeth very short, basal sides long and acuminate. Tooth apex acute or rounded. Petiole up to 1 cm long, bent. Venation pinnate, primary vein straight, rather stout. Secondary venation semicraspedodromous, secondaries considerably thinner than primary vein, distributed at 0.3–0.9 cm intervals, diverging from midvein at 60–80° angle (commonly 70°). Secondaries curving upwards, near leaf margin (almost parallel to leaf margin) strongly interconnected by tertiary veins. Intersecondary veins present. Tertiary venation percurrent, forming 120–100° angle with primary vein, 10–12 tertiary veins per 1 cm. Higher-order venation reticulate. Areoles imperfectly developed, diverse in size, 0.40–0.75 mm across. Veinlets branched. Marginal ultimate venation looped.

Micromorphology. Adaxial epidermis composed of strongly cutinised, rather regular, isodiametric, occasionally slightly elongated, polygonal cells 10–20 µm across. Anticlinal

cell walls predominately straight, sometimes rounded. Abaxial epidermis consists of isodiametric or slightly elongated cells 15–20 µm across. Anticlinal cell walls straight, rarely rounded. Cuticle of abaxial epidermis covered by epicuticular wax of characteristic reticulate micromorphology, usually rather abundant and thus occluding epidermal cell outlines almost completely. Leaves hypostomatic. Stomata brachyparacytic, elliptic, 15–20 µm across. Outer stomatal ledge aperture spindle-shaped, strongly cutinised, 10–12.5 µm long and 5.0–7.5 µm wide. Both on adaxial and abaxial epidermis, unicellular trichome bases, elliptic to rounded, 7.5–11 µm in diameter, surrounded by 4–7 cells. Unicellular trichomes, preserved only on adaxial epidermis, measure ca 11 µm.

Remarks. The macromorphology of these leaves identifies them as the fossil species *Salix varians* Goeppert. Leaves of *S. varians* with their characteristic layer of epicuticular wax of similar reticulate micromorphology were described earlier only from Bełchatów (Worobiec et al. 2012). This fossil species shows significant macromorphological (Krajewska 1998) and micromorphological (Worobiec et al. 2008, Worobiec & Kasiński 2009) variability; this fossil-taxon very likely includes leaves from more than a single biological species.

Modern equivalents. *Salix varians* is usually compared with the extant Eurasian *S. fragilis* L. and *S. triandra* L. (Bůžek 1971, Krajewska 1998). In respect of venation architecture, margin serration and epidermal micromorphology, however, some authors compare *Salix varians* with *Salix bonplandiana* Kunth (Mai & Walther 1978, Walther & Kvaček 2007) found in riparian communities of Arizona, eastern Mexico and Guatemala (Brown et al. 1977, Caballero Deloya 1977, Thompson et al. 1999).

Ecology. Probably a temperate element. *Salix varians* is considered a component of azonal vegetation of riparian forests (Belz & Mosbrugger 1994).

Occurrence. A fossil-taxon frequently found in tertiary floras of Europe from the Oligocene to Pliocene (Krajewska 1998). In Poland, found in middle and late Miocene leaf assemblages (Worobiec & Kasiński 2009).

Sapindaceae Jussieu, nom. cons.

***Acer* L.**

Acer aegopodifolium

(Goepfert) Baikovskaya ex Ilinskaya

Pl. 7, fig. 5, Pl. 11, fig. 5

- 1855 *Rhus quercifolia* Goepfert, p. 37, pl. 25, figs 6–9.
 1855 *Rhus aegopodifolia* Goepfert, p. 37, pl. 25, fig. 10.
 1965 *Acer aegopodifolium* (Goepfert) Baikovskaya; Shvareva, p. 953.
 1968 *Acer aegopodifolium* (Goepfert) Baikovskaya; Ilinskaya, p. 67, pl. 9, figs 12–15, pl. 20, figs 4, 5.

Material. KRAM-P 218: 138/I, 150/I.

Description. Macromorphology. Two leaflets of compound leaf. One leaflet seems asymmetric, up to 4.2 cm long and up to 1.8 cm wide, apex probably attenuate. Leaflet margin simple serrate, teeth rare, apical and basal sides of teeth rounded. Venation pinnate, mid-vein slightly bent. Secondary venation mixed craspedodromous, secondary veins irregularly spaced and in terminal parts a characteristically minute bend, some secondaries terminate in teeth, the remaining interconnected in loops. Tertiary and higher-order venation more or less random reticulate. Areoles well developed.

Micromorphology. Abaxial epidermis composed of cells with rounded walls. Stomata anomocytic, wide elliptic, 17–22 µm long and 17–20 µm wide. Outer stomatal ledge aperture from wide spindle-shaped to elliptic oblongate, 17–20 µm long and 8–10 µm wide.

Remarks. This material represents leaflets of the fossil-species *Acer aegopodifolium* (Goepfert) Baikovskaya ex Ilinskaya. Schmitt and Kvaček (1999) were the first to describe fossil epidermis of *Acer aegopodifolium* from upper Miocene deposits of Hambach (Germany). Worobiec et al. (2012) discussed the variability of leaf epidermis micromorphology in *Acer aegopodifolium*.

Modern equivalents. Macromorphologically, *Acer aegopodifolium* could be compared to extant maples from section *Trifoliata* Pax (Walther & Zastawniak 2005), especially to *Acer griseum* (Franchet) Pax and *A. trifolium* Komarov.

Ecology. Warm temperate element.

Occurrence. *Acer aegopodifolium* is known from middle to upper Miocene deposits of

Central and Eastern Europe (Kovar-Eder et al. 1994, Walther & Zastawniak 2005). In Poland, found in middle and late Miocene leaf assemblages (Worobiec et al. 2012, Worobiec 2014).

Acer tricuspidatum

Bronn sensu Procházka & Bůžek

Pl. 3, fig. 4, Pl. 4, figs 1a, b, Pl. 11, fig. 6, Pl. 12, fig. 1

- 1838 *Acer tricuspidatum* Bronn, p. 865, pl. 35, figs 10a, b.
 1845 *Acer trilobatum* Al. Braun, p. 172.
 1975 *Acer tricuspidatum* Bronn sensu novo, Procházka & Bůžek, p. 24, Figs 2, 3, 4d, 5–13, pl. 22, figs 1–7, pl. 23, figs 1–6, pl. 24, figs 1–4.

Material. KRAM-P 218: 5, 124/II, 132/II, 145/II, 150/II, 159, 162, cf. *Acer tricuspidatum*: 134, 137/II.

Description. Macromorphology. Leaves mostly trilobate, up to 8.5 cm wide. Lobe apex attenuate, leaf base cordate. Leaf margin simple serrate. Teeth upwardly curved (hooked). Apical side of teeth concave, basal side acuminate, tooth apex rounded. Secondary veins or their branches terminate in tooth apex. Venation palmate, actinodromous, perfect. Primary vein branched into usually 5 branches. Secondary venation mixed craspedodromous. Most secondary veins terminating in teeth but some connecting with other secondary veins in imperfect loops. Tertiary veins form characteristic network of interconnected veins. Higher-order venation both orthogonal and random reticulate. Areoles well developed, diverse in size, 0.2–0.4 mm across. Marginal ultimate venation looped.

Micromorphology. Adaxial epidermis composed of isodiametric or slightly elongated cells with mostly straight walls, 22–44 µm across, with indistinct cuticle ornamentation of parallel striae. Cells elongated over veins, up to 62 µm long and 10–12 µm wide. Abaxial epidermis composed of isodiametric or slightly elongate cells 10–29 µm across, with straight or rounded cell walls, cells over veins strongly elongated. Leaves hypostomatic. Stomata anomocytic, elliptic, 15–20 µm long and 13–15 µm wide. Outer stomatal ledge aperture rather distinct and of characteristic elliptic-rectangular shape, 10–14 µm long and 4–7 µm wide. On abaxial epidermis, numerous unicellular simple trichomes up to 135 µm long,

with unicellular, elliptic-roundish trichome bases 7–12 μm across (in only one specimen 16–17 μm across).

Remarks. These leaf remains represent the fossil species *Acer tricuspdatum* Bronn sensu Procházka & Bůžek. The leaf macromorphology (especially leaf blade shape and tooth structure) and cuticular features (stomata shape and abundant pubescence of abaxial epidermis) are typical for that fossil maple species.

Modern equivalents. *Acer tricuspdatum*, classified within section *Rubra* Pax (Walther 1972, Procházka & Bůžek 1975), is related to extant *Acer rubrum* L. and *A. saccharinum* L. from section *Rubra* from eastern North America (Hantke 1954, Kräusel & Weyland 1959, Holý et al. 2012). The cuticular micromorphology of extant *A. rubrum*, *A. saccharinum*, and *A. hyrcanum* Frisch. & Mey is similar to that of fossil *A. tricuspdatum* (Walther 1972).

Ecology. Probably warm temperate element. Usually considered a component of wetland vegetation in the Neogene of Central Europe (Walther 1972).

Occurrence. In Europe, *Acer tricuspdatum* is known from the middle Oligocene to Pliocene, commonly found in Miocene floras (Procházka & Bůžek 1975). In the Neogene of Poland, *Acer tricuspdatum* was frequently found in fossil assemblages (see Worobiec et al. 2008).

Acer sp.

Pl. 4, figs 2a–2c, Pl. 12, figs 2a, b

Material. KRAM-P 218: 60, 95 and 96 (counterparts), 104.

Description. Macromorphology. Fragments of leaves up to 7.5 cm long and up to 3.5 cm wide. Leaf margin simple serrate. Teeth indistinct and infrequent, located usually in apical part of leaf, irregularly spaced. Apical and basal sides of teeth convex, tooth apex rounded. Indistinct branches of veins terminate in tooth apex. Venation pinnate, primary vein straight and of moderate thickness. Secondary venation brochidodromous to semicraspedodromous. Secondaries distributed at 0.6–1.3 cm intervals, curved upward and interconnected in indistinct loops, forming irregular 60–70° angle with primary vein. Intersecondary veins usually present. Tertiary venation

composite intersecondary. Higher-order venation both orthogonal and random reticulate. Areoles well developed, 0.30–0.60 mm across. Veinlets branched. Marginal ultimate venation looped.

Micromorphology. Adaxial epidermis composed of more or less elongated cells 42–62 μm across, with undulated cell walls. Cuticle with striate ornamentation covered by rather distinct epicuticular wax layer. Abaxial epidermis composed of variable-shaped cells 20–32 μm across, with straight or rounded cell walls. Cuticle of abaxial epidermis covered by epicuticular wax. Leaves hypostomatic. Stomata anomocytic, often apparently paracytic, wide elliptic to rounded, 22.5–27.5 μm in diameter. Outer stomatal ledge aperture narrow elliptic, oblongate, exceptionally spindle-shaped, 15–20 μm long and (6) 10–15 μm wide.

Remarks. The characteristic stomata shape and the tertiary venation architecture of these leaves identify them as belonging to the genus *Acer*. The poor state of preservation precludes an unequivocal assignment to any fossil species or erection of a new fossil species.

Ecology. Probably a temperate element.

Malvaceae Jussieu, nom. cons. *sensu lato*

? Helicteroideae Griseb.

Laria G. Worobiec & Kvaček

Laria rueminiana

(Heer) G. Worobiec & Kvaček

Pl. 4, figs 3a, b, Pl. 8, fig. 4, Pl. 12, figs 3a–3c

1859 *Ficus rueminiana* Heer, p. 183, pl. 152, figs. 11, 12.

1859 *Ficus truncata* Heer, p. 183, pl. 152, fig. 15.

2010 *Laria rueminiana* (Heer) G. Worobiec & Kvaček; Worobiec et al., pp. 903–907, Fig. 6A–6J, Fig. 7A–7H, Fig. 9B.

Material. KRAM-P 218: 44, 170/III.

Description. Macromorphology. Only one leaf divided into two specimens ca 7 × 8 cm, entire-margined. Leaf base truncate. Venation palmate, actinodromous, basal. Primary vein branched into 7 branches. Secondary venation brochidodromous. Tertiary venation percurrent, ca 3 tertiary veins per 1 cm of secondary vein or branches of primary vein. Higher-order venation reticulate. Areoles well developed,

0.20–0.35 mm across. Veinlets absent, simple or branched once. Marginal ultimate venation looped.

Micromorphology. Adaxial epidermis composed of more or less isodiametric cells 20–38 µm across. Cell walls mostly straight. Cuticle of adaxial epidermis with distinct striate ornamentation. Anticlinal cell walls of abaxial epidermis usually almost invisible. Cells over veins strongly elongated and thin, 10–12 µm wide. Leaves hypostomatic. Stomata elliptic and of variable size, cell walls of guard cells mostly not visible. Some stomata surrounded by cuticular striations perpendicular to outer ledges. Outer stomatal ledge aperture spindle-shaped and of very diverse size, 10–20 µm long and 4–10 µm wide. On abaxial epidermis, two types of trichomes: stellate trichomes most numerous, up to 200 µm in diameter, composed of several arms with multicellular base of 25–33 µm in diameter, located mostly over veins; occasional glandular, clavate trichomes composed of 4 cells, 35–47 µm long and 15–20 µm wide, with unicellular base 12–15 µm in diameter.

Remarks. Both macro- and micromorphologically, the leaves correspond to those of the fossil taxon *Laria rueminiana* (Heer) G. Worobiec & Kvaček, which was erected as a new combination on the basis of material from the Bełchatów Lignite Mine and Ruja near Legnica (Worobiec et al. 2010).

Modern equivalents. The leaf macromorphology of *Laria rueminiana* can be compared with that of many extant members of Malvaceae s.l. (Worobiec et al. 2010). Investigations of fossil fruits of *Reevesia hurnikii* Kvaček and associated leaves of *Laria rueminiana* found in the early Miocene flora from the Most Basin in North Bohemia, Czech Republic (Kvaček 2006), suggest a close relationship between *Reevesia* and *Laria rueminiana*. Remains of *L. rueminiana* and *Reevesia hurnikii* associated with pollen grains of *Reevesiapollis* were also found in the Bełchatów Lignite Mine (Worobiec et al. 2012). In view of this, the *L. rueminiana* leaves, *Reevesia hurnikii* fruits, and *Reevesiapollis* pollen grains probably in fact represent organs of the same plant and should be treated as one fossil-taxon. However, most extant *Reevesia* species differ from *Laria rueminiana* in their dominance of the brachyparacytic stomatal complex and in their low variability of stomatal size (Worobiec et al. 2010). Extant

representatives of *Reevesia* exist over an area of paratropical to subtropical evergreen forests of the eastern Himalayas and South-east Asia (Kvaček 2006).

Ecology. Probably a subtropical element.

Occurrence. A rare element of the Neogene floras of Europe. In Neogene deposits of Poland, infrequently found in middle to late Miocene leaf assemblages (Worobiec et al. 2010).

Eucommiaceae Engler nom. cons.

Eucommia D. Oliver

Eucommia europaea Mädlar

Pl. 4, figs 4a, b

1939 *Eucommia europaea* Mädlar, p. 103, Pl. 8, figs 29–31, Pl. 9, figs 9–11.

Material. KRAM-P 218: 78–80, 153, 169.

Description. **Macromorphology.** Fragments of samaras up to 4.5 cm long and up to 1.5 cm wide. Preserved stipe ca 0.5 cm long, seeds up to 2 cm long and ca 0.5 cm wide.

Micromorphology. Epidermis of samara composed of elongated cells up to 70 µm long, with undulate cell walls. Cuticle ornamentation: parallel, thin, elongated, undulate striae. On epidermis, scattered elliptic stomata ca 30 µm across. Samaras filled with network of latex (guttapercha) strands, still elastic.

Remarks. The shape and particularly the presence of latex (guttapercha) strands inside samaras are distinctive features of fossil fruits of *Eucommia*. The best match is with the fossil-species *Eucommia europaea* Mädlar.

Modern equivalents. Extant *Eucommia* is a monotypic genus with the species *Eucommia ulmoides* Oliver, endemic to mountain forests of central and southern China at 200–2500 m a.s.l. (Ying et al. 1993, Wang et al. 2003). *Eucommia ulmoides* is similar in respect to the size and symmetry to fossil *Eucommia europaea* (Call & Dilcher 1997).

Ecology. Warm temperate element.

Occurrence. *Eucommia europaea* in Europe is known from Miocene and Pliocene deposits (Call & Dilcher 1997). Since there are no records of fossil remains of *Eucommia* older than Miocene in Europe, Geng et al. (1999) suggest that

the appearance of *Eucommia* in Europe only in the Neogene resulted from the closing of the Turgai Strait in the Oligocene. In the Neogene of Poland, *Eucommia europaea* was found in late Miocene to Pliocene assemblages (Zastawniak et al. 1996).

***Eucommia* sp.**

Pl. 8, fig. 4, Pl. 12, figs 4a, b

Material. KRAM-P 218: 56, 174/II, cf. *Eucommia* sp.: 168.

Description. Macromorphology. Rather small fragments of leaf. Leaf margin simple serrate, teeth small, apical side of teeth concave, basal side convex, tooth apex acute. Secondary veins reach sinus between teeth and give branches terminating in tooth apex. Secondary venation semicraspedodromous. On preserved leaf fragment, secondary vein branches interconnected in loops. Branches from loops terminate in teeth. Tertiary venation weakly percurrent or composite intersecondary.

Micromorphology. Cellular structure of both the adaxial and abaxial epidermis almost not evident. On preserved fragments of adaxial epidermis, dense striate cuticular ornamentation. Leaves hypostomatic. Stomata regularly elliptic, 25–30 µm long and 17–20 µm wide. Outer stomatal ledge aperture rather distinct, very narrow elliptic or spindle-shaped, 12.5–22.5 µm long and 4.0–7.5 µm wide. Inside leaf blade, remnants of network of latex (guttapercha) strands (filaments). Filaments ca 2.5 µm wide, with clavate endings.

Remarks. The presence of latex (guttapercha) strands inside the leaf blade is exclusively a trait of the genus *Eucommia*.

Modern equivalents. *Eucommia ulmoides* Oliver, endemic to mountain forests of central and southern China (Ying et al. 1993, Wang et al. 2003).

Ecology. Warm temperate element.

Occurrence. In Poland, fossil leaf remains of *Eucommia* were reported from Miocene deposits of Sośnica (Micek 1959), Gdów Bay (Łańcucka-Środoniowa 1966), Wieliczka and Zakrzów (Wąs in: Łańcucka-Środoniowa 1966), and Pliocene deposits of Mizerna (Szafer 1952, 1954).

Dicotyledones incertae sedis

***Dicotylophyllum* Saporta**

***Dicotylophyllum* sp. 1**
sensu Worobiec (2014)

Pl. 5, figs 1a, b

Material. KRAM-P 218: 7, 97/III, 109/IV.

Description. Macromorphology. Fragments of leaves up to 3.5 cm long and 1.8 cm wide. Leaf base acute to decurrent. Leaf margin simple serrate to crenate. Apical and basal side of teeth convex, tooth apex rounded. Venation pinnate, primary vein straight and thin (up to 0.5 mm wide). Secondary venation brochidodromous. Secondaries curved upward, forming ca. 60° angle with primary vein. Intersecondary veins present, distinct. Tertiary venation weakly composite intersecondary. Higher-order venation random reticulate. Areoles imperfectly developed, very large and rather diverse in size, 1.0–2.5 mm across. Veinlets multiple branched.

Micromorphology. Adaxial epidermis composed of usually tetragonal cells 25–30 µm across, with straight cell walls. Cell walls of abaxial epidermis straight. Leaves hypostomatic. Stomata of rather regular elliptic shape, 32–37 µm long and 17–25 µm wide. Outer stomatal ledge aperture distinctly spindle-shaped, 22–32 µm long and 7–12 µm wide.

Remarks. Macromorphologically these leaf remains are much the same as leaves of *Dicotylophyllum* sp. 1 reported earlier from the Bełchatów Mine (Worobiec 2014). They also show some similarities with the leaf of *Ternstroemites* sp. also described from the Bełchatów Mine (Worobiec & Lesiak 1998), but the systematic position of these leaf remains is unknown.

Ecology. Unknown.

***Dicotylophyllum* sp. 2**

Pl. 5, figs 2a–2c, Pl. 13, figs 1a, b

Material. KRAM-P 218: 2, 47 and 86/II (counterparts), 144/II.

Description. Macromorphology. Fragments of entire-margined, obovate to ovate leaves, up to 9.0 cm long and up to 3.5 cm wide. Leaf base acute to obtuse. Venation pinnate, primary vein straight and of moderate

thickness (up to 1 mm wide). Secondary venation brochidodromous, secondaries preserved in up to 9 pairs, distributed at diverse intervals of 0.7–1.5 cm, curved upward and interconnected in loops. Intersecondary veins sometimes present. Tertiary venation weakly percurrent or composite intersecondary, ca. 3–4 tertiary veins per 1 cm of secondary vein length. Higher-order venation random reticulate. Areoles well developed, 0.75–1.15 mm across. Veinlets branched. Marginal ultimate venation looped.

Micromorphology. Adaxial epidermis composed of usually slightly elongated cells 10–15 µm across, with mostly rounded, sometimes curved walls. Cuticle covered by distinct layer of epicuticular wax. Cellular architecture of abaxial epidermis strongly effaced, only cuticular layer preserved. Leaves hypostomatic. Stomata narrow elliptic, ca 25 µm long and 15–17 µm wide. Outer stomatal ledge aperture distinctly spindle-shaped, 17.5–22.5 µm long and ca 5 µm wide. On adaxial epidermis, scattered one-celled trichome bases ca 17 µm across. Trichome type unknown.

Remarks. The systematic position of these leaf remains is unknown.

Ecology. Unknown.

***Dicotylophyllum* sp. 3**

Pl. 5, figs 3a, b, Pl. 13, figs 2a, b, 3

Material. KRAM-P 218: 6, 21, 32, 45, 163.

Description. Macromorphology. Fragments of entire-margined leaves up to 5.0 cm long and 5.0 cm wide. Venation pinnate, primary vein straight and of moderate thickness (up to 1 mm wide). Secondary venation brochidodromous. Secondaries preserved in up to 4 pairs, distributed at variable intervals of 0.6–1.4 cm, curved upward and interconnected in loops, forming 60–70° angle with primary vein. Intersecondary veins sometimes present, indistinct. Tertiary venation weakly percurrent or composite intersecondary, ca 3–4 tertiary veins per 1 cm of secondary vein length. Higher-order venation random reticulate. Areoles well developed, 0.20–0.38 mm across. Veinlets none or simple, exceptionally branched. Marginal ultimate venation looped or forming incomplete fimbrial vein.

Micromorphology. Adaxial epidermis composed of usually irregular-shaped cells

17–35 µm across, with rounded, curved, sometimes also undulate cell walls. Cuticle covered by distinct layer of granular epicuticular wax. Cell walls of abaxial epidermis indistinct, strongly undulate, cells irregular-shaped and elongated. Leaves hypostomatic. Stomata probably anomocytic, elliptic to narrow elliptic, 20–26 µm long and 12–15 µm wide. Outer stomatal ledge aperture spindle-shaped, 14–17 µm long and 4–7 µm wide. On both adaxial and abaxial epidermis, trichome bases ca 30 µm across. Trichomes rarely preserved, solitary and most probably one-celled.

Remarks. The systematic position of these leaf remains is unknown.

Ecology. Unknown.

***Dicotylophyllum* sp. 4**

Pl. 5, figs 4a, b, Pl. 13, figs 4a–4c

Material. KRAM-P 218: 12, 14.

Description. Macromorphology. Two leaf fragments up to 4.0 cm long and 3.0 cm wide, entire-margined. Leaf margin covered by large trichomes. Venation pinnate, primary vein straight and of moderate thickness. Secondary venation brochidodromous, secondaries curved upward and interconnected in loops. Secondaries distributed at irregular intervals of 0.7–1.3 cm, forming irregular ca 60° angle with primary vein. Intersecondary veins present, distinct. Tertiary venation composite intersecondary. Higher-order venation random reticulate. Areoles well developed, rather diverse in size, 0.35–0.84 mm across. Veinlets branched. Marginal ultimate venation looped.

Micromorphology. Adaxial epidermis composed of usually elongated cells 27–42 µm across, with undulate cell walls. Cuticle of adaxial epidermis with distinct striate ornamentation. Abaxial epidermis composed of irregular-shaped cells with rounded to undulate cell walls. Leaves hypostomatic. Stomata probably anomocytic, elliptic, sometimes roundish, 20–30 µm long and 17–20 µm wide. Stomatal pore usually visible. Outer stomatal ledge aperture elliptic, sometimes slightly spindle-shaped, 10–17 µm long and 5–10 µm wide. On both adaxial and abaxial epidermis, found trichome bases similar as in *Dicotylophyllum* sp. 2, 37–40 µm across. Trichome type unknown.

Remarks. The systematic position of these leaf remains is unknown.

Ecology. Unknown.

Dicotyledones incertae sedis
= Dicotyledones indet.

Pl. 5, fig. 5

Material. KRAM-P 218: 41, 75, 90/III, 93, 102, 148/II, 167/II.

Remarks. The systematic position of these plant remains is unknown.

TAPHONOMY

These plant remains usually were preserved in fine-grained sediment, mostly as slightly coalified (humified) specimens, the leaves usually as compressions or adpressions (compressed leaf blades associated with impressions, Shute & Cleal 1986). An accumulation of leaves (thanatocoenosis) may originate from seasonal leaf fall from trees and shrubs that directly surround a waterbody and subsequently settle in a mass deposit on the bottom. Transport of fallen leaves into a waterbody by flood waters and by strong winds from more distant places should be considered as one possibility. The plant assemblage studied here presumably was formed in a waterbody of an abandoned channel of a meandering or braided river (oxbow lake?). Detritic material deposited in an oxbow lake (Citterio & Piégay 2009, Toonen et al. 2012) would have buried the accumulated plant macroremains on the reservoir bottom, leading directly to their preservation by preventing extensive decay or complete decomposition. A thanatocoenosis of this type is considered to be parautochthonous (Gastaldo et al. 1996).

CHARACTERISTICS OF PALAEOVEGETATION

Ferguson et al. (1998) pointed out that a proper analysis of palaeovegetation on the basis of a given fossil assemblage should be based above all on (1) the ecology of the nearest living relatives of fossil taxa, (2) the sedimentary environment that limits the possible habitats suggested by the ecology of the

nearest living relatives, and (3) the type of fossil remains (macroremains as leaves, carpological remains, microremains as palynomorphs) which limited the range of transport by wind or water. We consider these three bases fundamental to a reliable reconstruction of plant communities, not only for the assemblage from Bełchatów Mine but for all fossil plant associations.

The first element to consider in our reconstruction of the palaeovegetation must be the type of fossil remains. Almost all fossils analysed (except for the moss remains) from assemblage KRAM-P 218 from the Bełchatów mine are macroremains. Ferguson (1985) found that most macroscopic plant parts have limited dispersal potential; for leaves fallen from trees it does not exceed 20–50 m from the arborescent source plant. The second consideration is the type of sedimentary environment. In the case of a fluvial sedimentary environment, the leaf litter of the riparian vegetation surrounding a sedimentary reservoir bears little resemblance to the vegetation as whole (Spicer 1980, Ferguson 1985). In an analysis of a Miocene plant assemblage from Kreuzau, Germany, Ferguson et al. (1998) suggested that the leaf floras in accumulations of plant macroremains in deposits of abandoned channels reflected only the autochthonous water plants of the waterbody and the vegetation cover of surrounding habitats such as point bars or natural levees. Oryctocoenoses of this type are then treated as parautochthonous (Gastaldo et al. 1996). As the deposits of an abandoned channel with fossil assemblage KRAM-P 218 were formed in a fluvial sedimentary environment of a braided or meandering river with well-developed vegetation along the river banks (Krzyszowski & Winter 1996) and contain mostly leaf macroremains, this oryctocoenosis most probably reflects only the local azonal wetland vegetation surrounding a sedimentary reservoir. The third element of the fossil plant communities reconstruction is an analysis of the ecology of the nearest living relatives of fossil taxa. In the case of plant assemblages from abandoned channels this analysis will help distinguish taxa as components of swamp, riparian, or more mesophytic but still wetland communities. Finally, it should be stressed that fossil plant assemblages from fluvial environments formed in abandoned channels usually almost exclusively represent remains of azonal wetland vegetation. Zonal mesophytic plant

communities can be reconstructed only indirectly on the basis of taxa representing the “mesophytic” component of riparian plant communities.

Both the ancient and extant wetland vegetation of a fluvial (riverine) environment is shaped mostly by periodic or perennial effects of flood waters and by variation of groundwater levels associated with flood periods (Theriot 1993, Cooper & Merritt 2012). The frequency and duration of flood and groundwater levels depend directly on the lateral geomorphology (elevational gradient) of the river floodplain. Based on the frequency and duration of flood inundation and soil saturation, the National Wetland Technical Council (NWTC, USA) proposed a zonal classification of floodplain forests, with six hydrological zones (Clark & Benforado 1981, Wharton et al. 1982, Theriot 1993, Sharitz & Mitsch 1993). Zone 1 represents open water (aquatic) communities (river channels, oxbow lakes, permanently inundated places). Zones 2 to 5 cover the bottomland hardwood ecosystem: zone 2 represents swamp sites (flooded every year), zone 3 lower hardwood wetland (semi-permanently flooded), zone 4 medium hardwood wetland (seasonally flooded), and zone 5 higher hardwood wetland (only temporarily flooded). Last, zone 6 represents the transition from floodplain hygrophilous vegetation to mesophytic upland communities.

The effects on plant physiology exerted by the frequency and duration of flood inundation and groundwater levels strongly influence the distribution of plant species in wetland communities. Besides plants growing exclusively in wetland habitats (mostly aquatic plants inhabiting waterbodies), most wetland species can also be found in more mesic localities, often in mesophytic upland communities (Tiner 1993). The United States Fish and Wildlife Service in cooperation with other United States Federal agencies developed the *National Wetland Plant List* (Reed 1988, Tiner 1993, Lichvar 2012, 2013, Lichvar et al. 2012). It established five wetland indicator status ratings for plants occurring in natural conditions: obligate wetland plants (OBL) almost always occur in wetlands; facultative wetland plants (FACW) usually occur in wetlands but occasionally are found in non-wetlands; facultative plants (FAC) are found equally in wetland and non-wetlands; facultative upland plants (FACU) typically are found in non-wetland habitats

but occasionally inhabit wetlands; and upland species (UPL) growing on mesophytic upland communities are almost never found in wetlands (Lichvar et al. 2012).

In an analysis of fossil plant communities from macroremains, such a detailed rating of wetland indicator status for individual taxa and for an analysis of plant community zonation does not seem credible. Nonetheless, some general rating of wetland species and the corresponding plant communities is possible on the basis of fossil macroremains assemblage KRAM-P 218 from the Bełchatów Mine. Two wetland ranks of plant species were established for it: obligate wetland plants (OW) that occur almost exclusively in wetlands, found in open water and swamp habitats (corresponding to zones 1 and 2 of NWTC), and facultative wetland plants (FW) inhabiting drier bottomland hardwood communities found both in wetland (especially riparian) and in upland mesic localities. Upland species in macroremains assemblages found as the result of long-range transport of leaves, fruits, and seeds by wind or flowing water from mesophytic communities inhabiting elevations surrounding the river floodplain probably were absent in this fossil assemblage.

Using the above groups, Table 1 lists wetland species from assemblage KRAM-P 218, including data from previous research on macroremains of Betulaceae (Worobiec & Szyrkiewicz 2007). This grouping is grounded on the flood tolerance characteristics of modern equivalents of the fossil taxa, based partly on *National Wetland Plant List* of the USA (Lichvar 2012, 2013). Taking into account the wetland statuses of the fossil taxa assembled in Table 1, we can reconstruct the local wetland vegetation surrounding the sedimentary reservoir of the abandoned channel for assemblage KRAM-P 218 from the Bełchatów Mine. The only obligate wetland plants (OW) found, *Salvinia* and *Taxodium*, may suggest that permanently inundated areas covered by vegetation probably were limited. On the other hand, the remains of water ferns *Salvinia* confirm the presence of a water reservoir with stagnant or slowly moving water. Fossil *Taxodium*, like its extant equivalents *Taxodium distichum* (bald cypress) and the closely related *T. ascendens* Brongn. (pond cypress), occupied permanently inundated places in and around a water reservoir (Burns & Honkala 1990). The remaining

Table 1. Wetland indicator status ratings: obligate wetland (OW), facultative wetland (FW) for fossil species from assemblage KRAM-P 218 and their modern equivalents. * – taxa reported in Worobiec & Szyrkiewicz (2007)

Fossil taxon	Obligate wetland (OW)	Facultative wetland (FW)	Modern equivalent(s) (North American equivalents are in boldface)	Wetland indicator status ratings for modern equivalents from North America (Lichvar 2013)
<i>Acer aegopodifolium</i>		+	<i>Acer</i> sectio <i>Trifoliata</i> : <i>A. griseum</i> , <i>A. trifolium</i>	–
<i>Acer</i> sp.		+	<i>Acer</i> sp.	–
<i>Acer tricuspdatum</i>		+	<i>Acer</i> sectio <i>Rubra</i> : <i>A. rubrum</i> , <i>A. saccharinum</i>	Facultative/Facultative Wetland
<i>Alnus julianiformis</i> *		+	<i>Alnus trabeculosa</i> , <i>A. japonica</i>	–
<i>Betula plioplaptera</i> *		+	<i>Betula</i> spp.	–
<i>Betula subpubescens</i> *		+	<i>Betula pubescens</i>	Facultative Wetland/Facultative
Betulaceae indet. (gen. et sp. div.)*	?	?	unknown	–
<i>Carpinus grandis</i> *		+	<i>Carpinus betulus</i>	–
<i>Carpinus</i> sp. (fruit)*		+	<i>Carpinus</i> spp.	–
<i>Carya serrifolia</i>		+	<i>Carya aquatica</i> <i>C. illinoensis</i> <i>C. tomentosa</i>	Obligate /Facultative Wetland/ Facultative/ Facultative Upland
cf. <i>Crataegus</i> sp.		+	? <i>Crataegus</i> spp.	–
<i>Dicotyledones</i> incertae sedis	?	?	unknown	–
<i>Dicotylophyllum</i> sp. 1 sensu Worobiec (2014)	?	?	unknown	–
<i>Dicotylophyllum</i> sp. 2	?	?	unknown	–
<i>Dicotylophyllum</i> sp. 3	?	?	unknown	–
<i>Dicotylophyllum</i> sp. 4	?	?	unknown	–
<i>Eucommia europaea</i>		+	<i>Eucommia ulmoides</i>	–
<i>Eucommia</i> sp. (leaf)		+	<i>Eucommia ulmoides</i>	–
<i>Fagus silesiaca</i>		+	<i>Fagus hayatae</i>	–
<i>Laria rueminiana</i>		+	<i>Reevesia</i> spp.	–
<i>Laurophyllum</i> sp.		+	Lauraceae	–
<i>Liquidambar europaea</i>		+	<i>Liquidambar styriaciflua</i> , <i>L. orientalis</i>	Facultative/Facultative Wetland
Mosses remains	?	?	unknown	–
<i>Pinus</i> sp.		+	<i>Pinus</i> spp.	–
<i>Populus balsamoides</i>		+	<i>Populus balsamifera</i>	Facultative Wetland/Facultative
<i>Pterocarya paradisiaca</i>		+	<i>Pterocarya fraxinifolia</i>	–
<i>Quercus pseudocastanea</i>		+	<i>Quercus</i> sectio <i>Cerris</i>	–
<i>Salix varians</i>		+	<i>Salix fragilis</i> , <i>S. triandra</i> , <i>S. bonplandiana</i>	Facultative Wetland
<i>Salvinia</i> sp.	+		<i>Salvinia natans</i>	Obligate
<i>Taxodium dubium</i>	+		<i>Taxodium distichum</i> , <i>T. mucronatum</i>	Obligate
<i>Ulmus</i> sp.		+	<i>Ulmus</i> spp.	–
<i>Vitis strictum</i>		+	<i>Vitis vulpina</i>	Facultative
<i>Zelkova zelkovifolia</i>		+	<i>Zelkova carpinifolia</i>	–

fossil plant taxa suggest that a riparian community of periodically flooded bottomland hardwood forest dominated there. The stand of riparian forest in moist places probably was dominated by *Acer tricuspdatum*, *Carya serrifolia*, *Liquidambar europaea*, *Pterocarya paradisiaca*, *Populus balsamoides*, *Salix varians*, and *Zelkova zelkovifolia*, and accompanied by lianas such as *Vitis strictum*. This community corresponds to vegetation of zone 3 (lower hardwood wetland, semipermanently flooded)

in the zonal classification of floodplain forests (NWTC, USA) (Clark & Benforado 1981, Wharton et al. 1982, Theriot 1993, Sharitz & Mitsch 1993). In drier places, the riparian forest of the KRAM-P 218 locality was enriched with more mesophytic taxa such as *Acer aegopodifolium*, *Alnus julianiformis*, *Betula plioplaptera*, *Betula subpubescens*, *Carpinus grandis*, *Eucommia europaea*, *Fagus silesiaca*, *Quercus pseudocastanea*, and *Ulmus* sp., and probably also *Laria rueminiana*, *Laurophyllum* sp., and

Pinus sp. This community probably developed on elevations such as natural levees, and occupied habitats equivalent to NWTC zones 4 and 5 (medium to higher hardwood wetland, rarely flooded).

Riparian forest represented by assemblage KRAM-P 218 was common in the Miocene of the Polish Lowlands (Worobiec & Kasiński 2009). The Miocene vegetation from Bełchatów has much in common with riparian communities of eastern and south-eastern North America (Wilén & Tiner 1993, Hamel & Foti 1995), riparian forests of river valleys and banks of the Euxine-Hyrcanian area (Tutayuk 1975, Rastin 1983, Akhiani et al. 2010), and riparian communities of central China (Wei et al. 2010).

Plant remains of taxa considered exclusively upland (zonal, mesophytic) seem to be completely absent from this oryctocoenosis. Probably this floodplain was very flat and/or very wide, and the sedimentary reservoir may have been situated at some distance from any elevation such as river terraces or upland slopes covered by mesophytic communities. However, as most of the taxa in assemblage KRAM-P 218 were classed as facultative wetland species, at least a portion of them may also have been components of mesophytic upland communities (cf. Tiner 1993). The taxonomical composition of facultative wetland taxa suggests that the mesophytic deciduous forests from the eastern part of North America (Braun 1964, Knapp 1965, Barnes 1991), northern China (Wang 1961) and the Euxine-Hyrcanian area (Colchis, Talysh, southern coast of the Caspian Sea; Akhiani et al. 2010, Nakhutsrishvili et al. 2011) can be treated as recent equivalents of the Miocene upland vegetation surrounding the riparian environment of the Bełchatów Mine.

This reconstruction of fossil vegetation based on the macroremains assemblage is in accordance with the results of a pollen analysis of samples taken from assemblage KRAM-P 218 (Worobiec & Worobiec 2016). The pollen spectra show the dominant role of wetland, riparian, and swamp vegetation, and confirm the presence of a freshwater reservoir. Some genera recorded in both the pollen samples and the macroremains assemblage (*Acer*, *Betula*, *Eucommia*, *Fagus*, *Quercus*, *Ulmus*) could grow in both swamp and mesophytic plant communities, however.

RECONSTRUCTION OF PALAEOCLIMATE

Against the common view, thermal climatic conditions (mean annual temperature, cold-month mean, frosts) have an important influence on azonal wetland vegetation like that from this assemblage from Bełchatów (Tepley et al. 2004, Schnitzler et al. 2005). Most of the fossil taxa found in assemblage KRAM-P 218 represent the warm temperate element, equivalent to the former arctotertiary geofloristic element (Mai 1995, Grímsson et al. 2015). Extant taxa closely related to the fossil species generally are found in warm temperate climate areas of the Northern Hemisphere. The only presumably subtropical taxa seem to be *Laria rueminiana* and a representative of genus *Laurophyllum*, member of the Lauraceae family. However, as these *Laurophyllum* leaves are similar both to the extant *Laurus* and *Sassafras* genera, it is highly likely that *Laurophyllum* from Bełchatów represents a warm temperate member of the family Lauraceae (Nitta & Ohsawa 1997). The dominance of the warm temperate element and the absence of typically thermophilous plants (e.g. palms) point to a warm temperate climate during the accumulation of fossil plant assemblage KRAM-P 218 from Bełchatów. Nonetheless, *Laurophyllum*, *Laria rueminiana*, and some other taxa (e.g. *Zelkova zelkovifolia*) indicate rather favourable climatic conditions with mild winters. The pollen analysis similarly suggests warm temperate and moderately wet climatic conditions (Worobiec & Worobiec 2016).

To reconstruct mean annual temperature (MAT) from the leaf assemblage from Bełchatów we used the coexistence approach (CA) method (Mosbrugger & Utescher 1997). Table 2 presents data on the fossil-taxa and their recent counterparts with equivalent ranges of MAT (Utescher & Mosbrugger 2015), both for fossil-taxa from this paper and for representatives of Betulaceae, from Worobiec & Szyrkiewicz (2007). The obtained MAT of 13.5–16.5°C (lower limit for extant members of the genus *Reevesia* and upper limit for *Betula pubescens* and *Populus balsamifera*) seems probable.

Unlike thermal climatic conditions, reconstruction of palaeoprecipitation totals on the basis of this wetland assemblage from Bełchatów does not seem credible, as wetland, riparian,

Table 2. Fossil taxa found in assemblage KRAM-P 218 (* – taxa reported in Worobiec & Szyrkiewicz 2007), their nearest living relatives (NLR) and mean annual temperature (MAT) ranges of NLR. NLR and their MAT ranges based on *The Palaeoflora Database* (Utescher & Mosbrugger 2015)

Fossil taxon	NLR of fossil taxon	MAT lower limit of NLR	MAT upper limit of NLR
<i>Taxodium dubium</i>	<i>Taxodium</i> sp.	13.30	25.00
<i>Acer aegopodifolium</i>	<i>Acer</i> sp.	-1.10	24.00
<i>Acer tricuspdatum</i>	<i>Acer</i> sectio <i>Rubra</i> : <i>A. rubrum</i> , <i>A. saccharinum</i>	3.40	23.80
<i>Acer</i> sp.	<i>Acer</i> sp.	-0.40	24.00
<i>Alnus julianiformis</i> *	<i>Alnus trabeculosa</i> , <i>A. japonica</i>	6.20	22.10
<i>Betula plioplaptera</i> *	<i>Betula</i> sp.	-15.00	25.80
<i>Betula subpubescens</i> *	<i>Betula pubescens</i>	-6.70	16.50
<i>Carpinus grandis</i> *	<i>Carpinus betulus</i>	5.30	17.60
<i>Carpinus</i> sp. (fruit)*	<i>Carpinus</i> sp.	0.00	25.80
<i>Carya serrifolia</i>	<i>Carya</i> sp.	4.40	26.60
<i>Eucommia</i> sp. (leaf)	<i>Eucommia ulmoides</i>	10.60	19.40
<i>Eucommia europaea</i>	<i>Eucommia ulmoides</i>	10.60	19.40
<i>Fagus silesiaca</i>	<i>Fagus grandifolia</i> , <i>F. longipetiolata</i> , <i>F. hayatae</i>	4.40	23.10
<i>Laria rueminiiana</i>	<i>Reevesia</i> sp.	13.50	25.50
<i>Liquidambar europaea</i>	<i>Liquidambar styraciflua</i> , <i>L. orientalis</i>	12.50	21.30
<i>Laurophyllum</i> sp.	<i>Lauraceae</i>	–	–
<i>Pinus</i> sp.	<i>Pinus</i> sp.	-9.20	25.50
<i>Populus balsamoides</i>	<i>Populus balsamifera</i>	-5.50	16.50
<i>Pterocarya paradisiaca</i>	<i>Pterocarya fraxinifolia</i>	8.10	18.10
<i>Quercus pseudocastanea</i>	<i>Quercus</i> sectio <i>Cerris</i>	4.70	22.20
<i>Salix varians</i>	<i>Salix</i> sp.	-17.00	27.70
<i>Salvinia</i> sp.	<i>Salvinia</i> sp.	0.00	25.60
<i>Ulmus</i> sp.	<i>Ulmus</i> sp.	-4.90	26.60
<i>Vitis strictum</i>	<i>Vitis vulpina</i>	10.50	20.80
<i>Zelkova zelkovifolia</i>	<i>Zelkova</i> sp.	6.20	21.90
Obtained MAT range		13.5–16.5°C	

or swamp communities are not so sensitive to precipitation amounts as zonal vegetation is (Brinson et al. 1981).

The palaeoclimate experienced by plant assemblage KRAM-P 218 from Bełchatów may be comparable to the contemporary climate of areas of deciduous broad-leaved forests with warm temperate to subtropical, humid, often monsoon climate. The fossil plant communities may be related to the extant biome of temperate deciduous (summergreen) forests or even to evergreen broad-leaved (“laurel”) forests (Box and Fujiwara 2005a). Recent equivalents of fossil taxa from Bełchatów might be found in warm temperate deciduous forests of East Asia (central Japan, eastern central China – temperate deciduous forests, Mixed Mesophytic Forests), eastern North America (eastern deciduous forests, southern mixed hardwood forests), the Euxine-Hyrcanian region (deciduous Colchis and Hyrcanian forests) and the Sierra Madre Oriental, Mexico (Mexican holarctic dicotyledonous forest) (Greller 2013, Box and Fujiwara 2015b). The climate of the listed

areas generally can be classified as Cfa type (warm temperate, fully humid, with hot summer) in the Köppen-Geiger climate classification (Kottek et al. 2006).

AGE OF THE PLANT ASSEMBLAGE

The analysed leaf assemblage from the Bełchatów Lignite Mine is situated at the lowermost part of a sandy-clayey unit whose age is estimated as late Miocene (see Geology). The composition of leaf assemblage KRAM-P 218 well matches the late Miocene leaf assemblages from the sandy-clayey unit from the Bełchatów Lignite Mine (Stuchlik et al. 1990, Worobiec & Lesiak 1998, Worobiec 2003a, Worobiec et al. 2012, Worobiec 2014). The composition of leaf assemblage KRAM-P 218, with domination of the temperate, deciduous floristic element, is typical of the late Neogene vegetation of Central Europe (Mai 1995, Kovar-Eder 2003).

The overall results of the pollen analysis of samples taken from assemblage KRAM-P 218,

similar to the middle to late Miocene palynofloras of Poland (Worobiec & Worobiec 2016), generally correspond to the proposed late Miocene age of leaf assemblage KRAM-P 218. On the other hand, the palynoflora is most similar in its composition to the spore-pollen spectra of the X climatic phase – the *Nyssapollenites* spore-pollen zone (Piwocki & Ziemińska-Tworzydło 1995, 1997, Ziemińska-Tworzydło 1998). Deposits bearing such assemblages accumulated during the Sarmatian and early Pannonian. The studied palynoflora is very close in its composition to Gozdnicza profile 4 (Worobiec & Worobiec 2016). Thus, assemblage KRAM-P 218 could be either late Sarmatian or early Pannonian. It should be added that the flora of KRAM-P 218 represents the latest occurrence of the Lauraceae (*Laurophyllum* sp.) in the Neogene of Poland. The presence of a representative of the Lauraceae family (*Sassafras*) in the late Neogene (late Miocene to early Pliocene) has been confirmed from several Central and Western European localities: Gércse and Pula (Hably & Kvaček 1997), Willershausen (Knobloch 1998), and Sessenheim-Auenheim (Teodoridis et al. 2009).

CONCLUSIONS

From 186 specimens (80 slides with isolated leaf remains and fruits of *Eucommia* and 106 rock samples) we identified 18 species from the genera *Acer*, *Carya*, *?Crataegus*, *Dicotylophyllum*, *Eucommia*, *Fagus*, *Laria*, *Laurophyllum*, *Liquidambar*, *Pinus*, *Populus*, *Pterocarya*, *Quercus*, *Salix*, *Salvinia*, *Taxodium*, *Ulmus*, *Vitis*, and *Zelkova*. Moss remains were found as well.

Four fossil taxa new for the Polish tertiary were recorded: *Laurophyllum* sp. and *Dicotylophyllum* sp. 2 – 4.

Fossil assemblage KRAM-P 218 formed in a fluvial sedimentary environment of a braided or meandering river with well-developed vegetation along the river banks (Krzyszowski & Winter 1996), and probably reflects only local azonal wetland vegetation surrounding a sedimentary reservoir. On the basis of the proposed wetland indicator status ratings, the local wetland vegetation surrounding a sedimentary reservoir of an abandoned channel was reconstructed for assemblage KRAM-P 218. Remains of *Salvinia* point to the presence of a waterbody with

stagnant or slowly moving water. Most of the remaining taxa suggest dominance of a riparian community of the bottomland hardwood forest type, with *Acer tricuspidatum*, *Carya serrifolia*, *Liquidambar europaea*, *Pterocarya paradiasiaca*, *Populus balsamoides*, *Salix varians*, and *Zelkova zelkovifolia*, accompanied by lianas such as *Vitis strictum*. In drier places, *Acer aegopodifolium*, *Alnus julianiformis*, *Betula plioplastyptera*, *Betula subpubescens*, *Carpinus grandis*, *Eucommia europaea*, *Fagus silesiaca*, *Quercus pseudocastanea*, and *Ulmus* sp. were found, and probably also *Laria rueminiana*, *Laurophyllum* sp., and *Pinus* sp. Riparian forests of that type were common in the Miocene of the Polish Lowlands (Worobiec 2009). Riparian communities of eastern and south-eastern North America (Wilén & Tiner 1993, Hamel & Foti 1995), riparian forests of river valleys and banks of the Euxine-Hyrcanian area (Tutayuk 1975, Rastin 1983, Akhani et al. 2010), and riparian communities of central China (Wei et al. 2010) have much in common with the Miocene vegetation from Bełchatów. Some of the taxa of assemblage KRAM-P 218 could also be components of mesophytic upland communities similar to those of mesophytic deciduous forests of the eastern part of North America (Braun 1964, Knapp 1965, Barnes 1991), northern China (Wang 1961), and the Euxine-Hyrcanian area (Colchis, Talysh, southern coast of Caspian Sea; Akhani et al. 2010, Nakhutsrishvili et al. 2011).

Most of the taxa present in this leaf assemblage represent the warm temperate element. The dominance of the warm temperate element and the absence of typically thermophilous plants (e.g. palms) indicate that warm temperate climate prevailed during the accumulation of fossil plant assemblage KRAM-P 218. *Laurophyllum*, *Laria rueminiana*, and some other taxa indicate rather favourable climatic conditions with mild winters. A mean annual temperature (MAT) range of 13.5–16.5°C is suggested on the basis of the coexistence approach (CA) method (Mosbrugger & Utescher 1997). It does not seem plausible to make a quantitative reconstruction of palaeoprecipitation on the basis of this assemblage from Bełchatów. The palaeoclimate of plant assemblage KRAM-P 218 from Bełchatów may have been comparable to the contemporary climate of areas of deciduous broad-leaved forest with warm temperate to subtropical, humid, often monsoon climate,

classified as Cfa type (warm temperate, fully humid, with hot summer) in the Köppen-Geiger climate classification (Kottek et al. 2006). The fossil plant communities could be related to the extant biome of temperate deciduous (summer-green) forests or even to evergreen broad-leaved (“laurel”) forests (Box & Fujiwara 2005a).

The composition of leaf assemblage KRAM-P 218, its geological setting, and the findings from its palynological analysis suggest middle to late Miocene age (late Sarmatian to early Pannonian).

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PLATES

Plate 1

Pinus sp.

1. Two fragments of needles and one fascicle, specimen no. KRAM-P 218/18

Bark of *Pinus* sp.

2. Fragment of exfoliated bark, specimen no. KRAM-P 218/14

Laurophyllum sp.

- 3a. Leaf, specimen no. KRAM-P 218/42

- 3b. Detail of leaf margin, specimen no. KRAM-P 218/42

- 3c. Detail of higher-order venation. Visible are numerous idioblast secretory cells (arrow) in mesophyll, specimen no. KRAM-P 218/42

Vitis strictum (Goeppert) Knobloch

- 4a. Leaf, specimen no. KRAM-P 218/55

- 4b. Detail of teeth and leaf margin venation, specimen no. KRAM-P 218/55

- 4c. Detail of leaf areolation, specimen no. KRAM-P 218/55

Ulmus sp.

- 5a. Leaf, specimen no. KRAM-P 218/37

- 5b. Detail of teeth and leaf margin venation, specimen no. KRAM-P 218/37

- 5c. Detail of leaf areolation and veinlets, specimen no. KRAM-P 218/37

Scale bars: 1, 3a, 4a, 5a, 5b – 1 cm; 2 – 5 mm; 3b, 4b – 2 mm; 4c, 5c – 200 μ m; 3c – 100 μ m

Photos 4c, 5c – K. Cywa

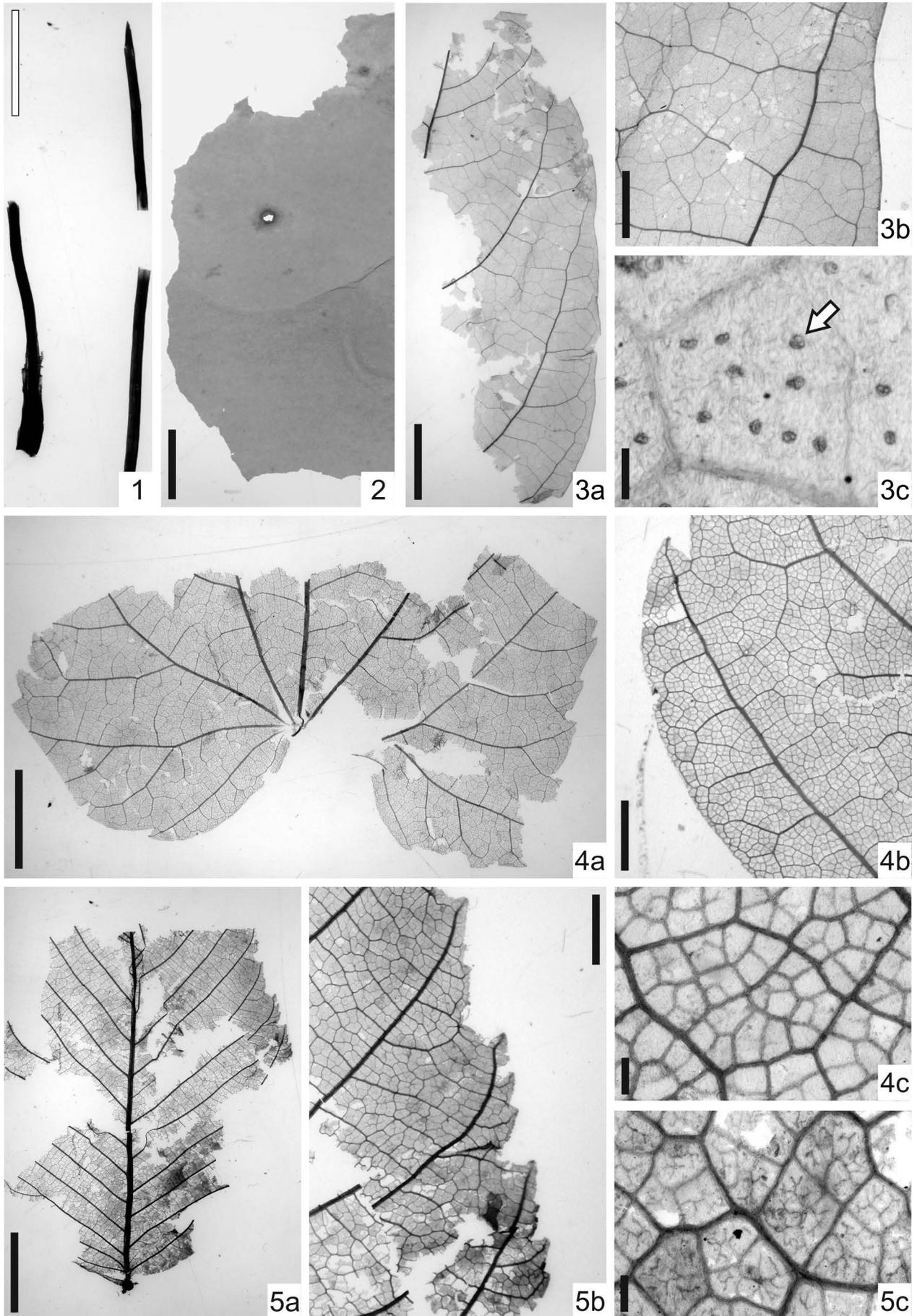


Plate 2

Zelkova zelkovifolia (Unger) Bůžek & Kotlaba

- 1a. Leaf, specimen no. KRAM-P 218/19
- 1b. Detail of teeth and leaf margin venation, specimen no. KRAM-P 218/19
- 1c. Detail of leaf areolation and veinlets, specimen no. KRAM-P 218/37

Fagus silesiaca Walther & Zastawniak

- 2a. Leaf, specimen no. KRAM-P 218/64
- 2b. Detail of teeth and leaf margin venation, specimen no. KRAM-P 218/64
- 2c. Detail of leaf areolation, specimen no. KRAM-P 218/64
- 3. Leaf, specimen no. KRAM-P 218/62

Quercus pseudocastanea Goepfert emend. Walther & Zastawniak

- 4a. Leaf, specimen no. KRAM-P 218/11
- 4b. Detail of leaf areolation, specimen no. KRAM-P 218/11

Scale bars: 1a, 2a, 3, 4a – 1 cm; 1b, 2b – 2 mm; 1c, 2c, 4b – 200 µm

Photos 1c, 2c, 4b – K. Cywa

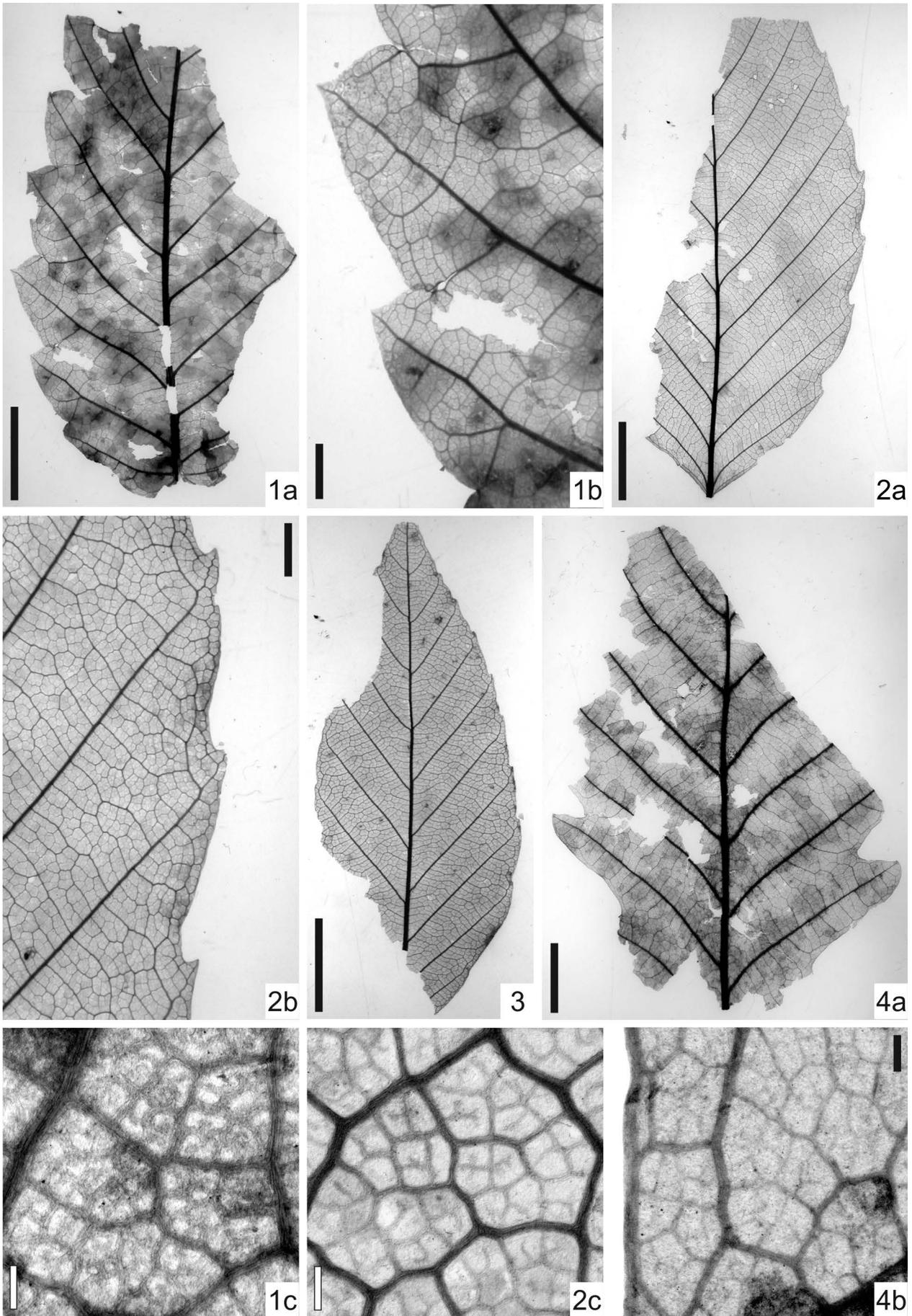


Plate 3

Carya serrifolia (Goeppert) Kräusel

- 1a. Leaflet, specimen no. KRAM-P 218/9
- 1b. Detail of teeth and leaflet margin venation, specimen no. KRAM-P 218/9
- 1c. Detail of leaflet areolation, specimen no. KRAM-P 218/9

Populus balsamoides Goeppert

- 2a. Leaf, detail of teeth and leaf margin venation, specimen no. KRAM-P 218/46
- 2b. Detail of leaf areolation, specimen no. KRAM-P 218/46

Salix varians Goeppert sensu lato

- 3a. Leaf, specimen no. KRAM-P 218/54
- 3b. Detail of teeth and leaf margin venation, specimen no. KRAM-P 218/54
- 3c. Detail of leaf areolation, specimen no. KRAM-P 218/54

Acer tricuspidatum Bronn sensu Procházka & Bůžek

- 4. Leaf, specimen no. KRAM-P 218/5

Scale bars: 1a, 3a – 1 cm; 2a, 4 – 5 mm; 1b, 3b – 2 mm; 1c, 2b, 3c – 200 µm

Photos 1c, 2b, 3c – K. Cywa

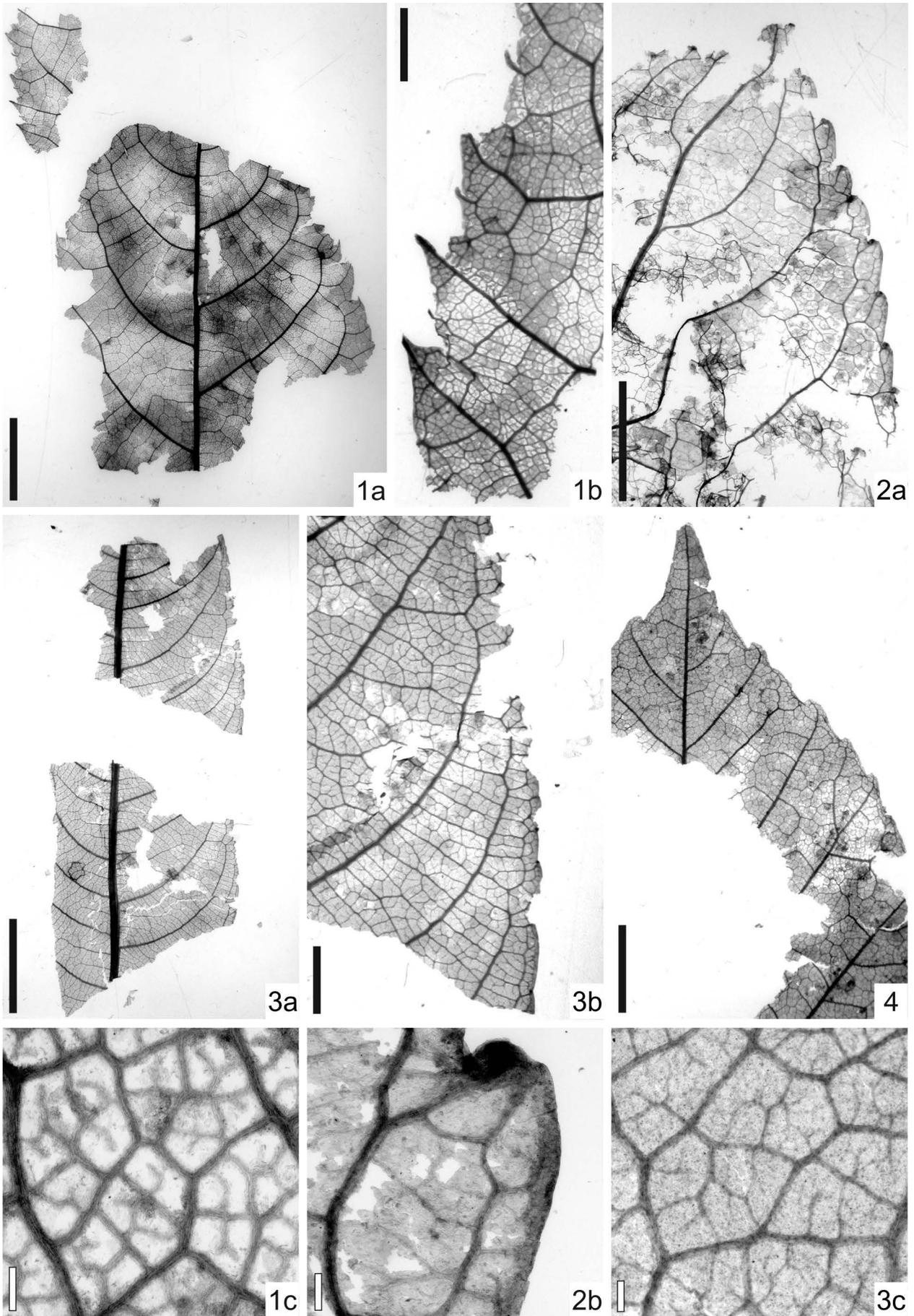


Plate 4

Acer tricuspidatum Bronn sensu Procházka & Bůžek

- 1a. Detail of teeth and leaf margin venation, specimen no. KRAM-P 218/5
- 1b. Detail of leaf areolation, specimen no. KRAM-P 218/5

Acer sp.

- 2a. Leaf, specimen no. KRAM-P 218/60
- 2b. Detail of teeth and leaf margin venation, specimen no. KRAM-P 218/60
- 2c. Detail of leaf areolation, specimen no. KRAM-P 218/60

Laria rueminiana (Heer) G. Worobiec & Kvaček

- 3a. Detail of higher order venation, specimen no. KRAM-P 218/44
- 3b. Detail of leaf areolation, specimen no. KRAM-P 218/44

Eucommia europaea Mädlar

- 4a. Samara, specimen no. KRAM-P 218/79
- 4b. Detail of samara. Visible network of latex (guttapercha) strands, specimen no. KRAM-P 218/79

Scale bars: 2a, 4a – 1 cm; 1a, 2b, 3a, 4b – 2 mm; 1b, 2c, 3b – 200 μ m

Photos 1b, 2c, 3b – K. Cywa

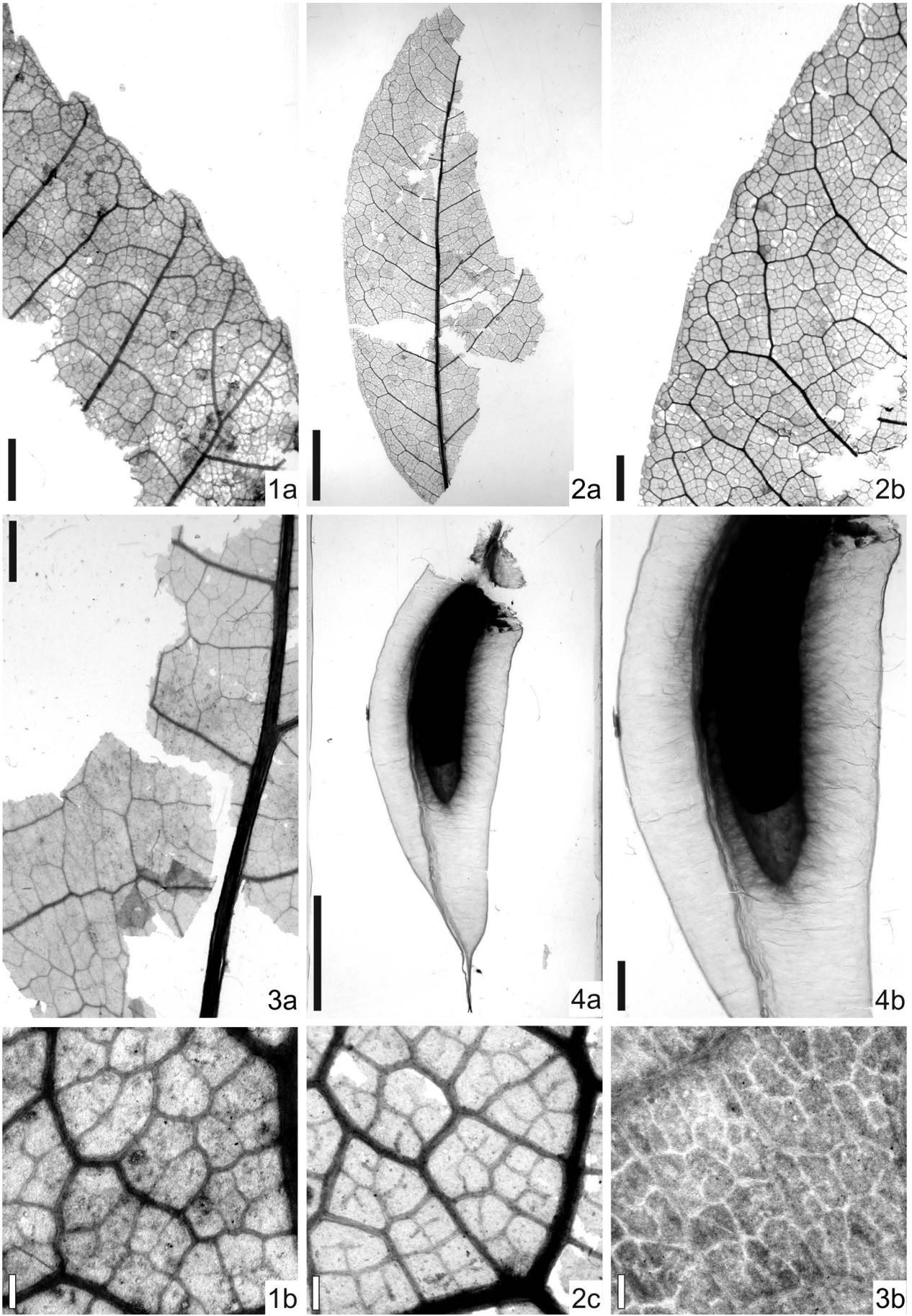


Plate 5

Dicotylophyllum sp. 1 sensu Worobiec (2014)

- 1a. Leaf, specimen no. KRAM-P 218/7
- 1b. Detail of leaf areolation, specimen no. KRAM-P 218/7

Dicotylophyllum sp. 2

- 2a. Leaf, specimen no. KRAM-P 218/2
- 2b. Detail of teeth and leaf margin venation, specimen no. KRAM-P 218/2
- 2c. Detail of leaf areolation, specimen no. KRAM-P 218/2

Dicotylophyllum sp. 3

- 3a. Leaf, specimen no. KRAM-P 218/45
- 3b. Detail of teeth and leaf margin venation, specimen no. KRAM-P 218/45

Dicotylophyllum sp. 4

- 4a. Leaf, specimen no. KRAM-P 218/14
- 4b. Detail of leaf areolation, specimen no. KRAM-P 218/14

Dicotyledones incertae sedis = Dicotyledones indet.

- 5. Leaf, specimen no. KRAM-P 218/41

Scale bars: 2a, 5 – 1 cm; 3a, 4a – 5 mm; 1a, 2b, 3b – 2 mm; 1b, 2c, 4b – 200 µm

Photos 1b, 2c, 4b – K. Cywa

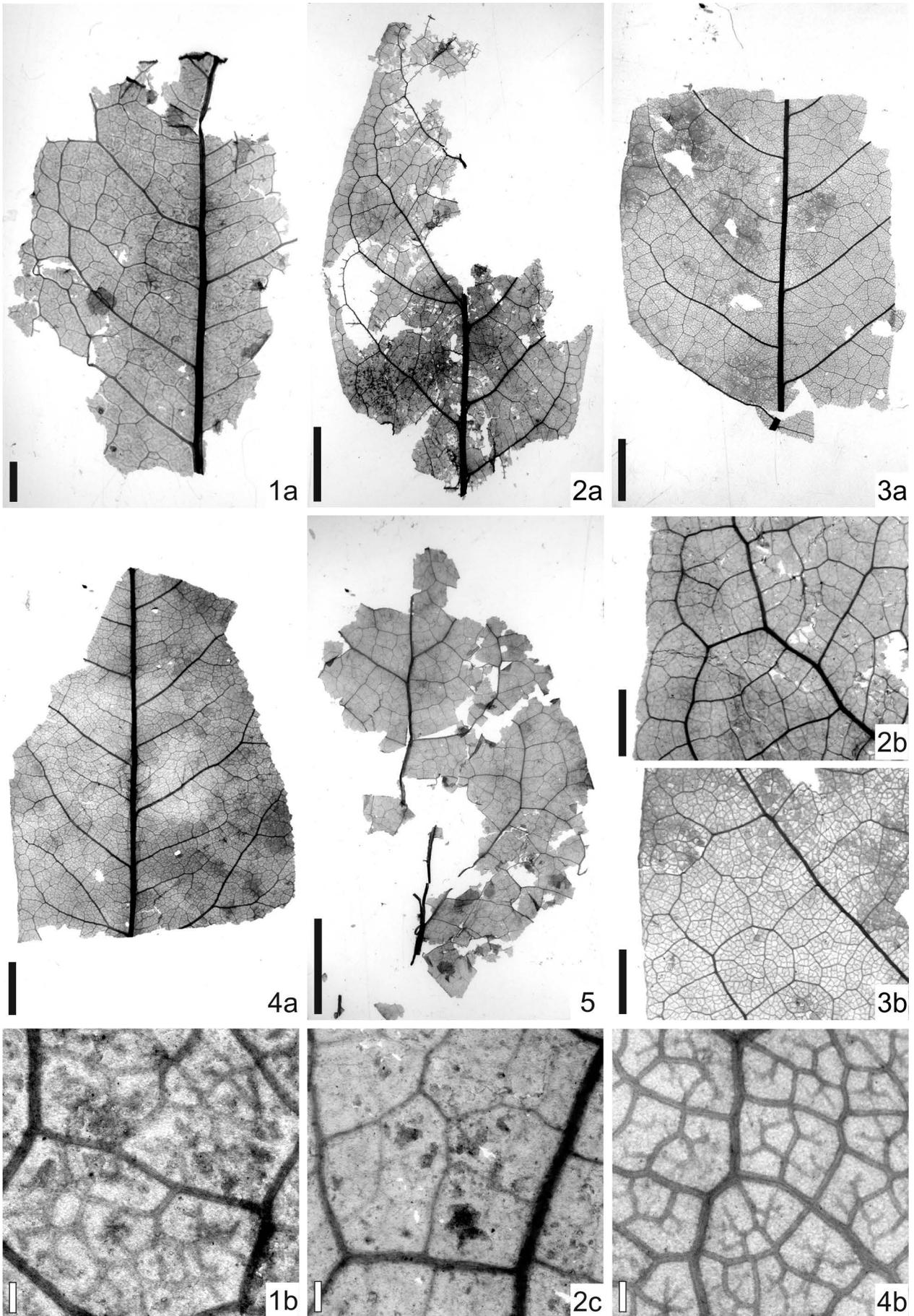


Plate 6

Salvinia sp.

1. Floating leaf impression, specimen no. KRAM-P 218/142/II

Taxodium dubium (Sternberg) Heer

2. Twig, specimen no. KRAM-P 218/131

Laurophyllum sp.

3. Leaf, specimens no. KRAM-P 218/100/II and KRAM-P 218/113

Liquidambar europaea A. Braun

- 4a. Leaf, specimen no. KRAM-P 218/110/II

- 4b. Detail of leaf margin with teeth, specimen no. KRAM-P 218/110/II

Scale bars: 2, 3 – 1 cm; 4a – 5 mm; 1, 4b – 2 mm

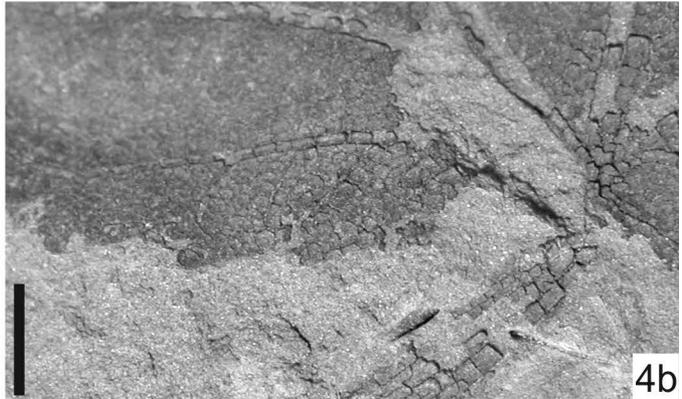
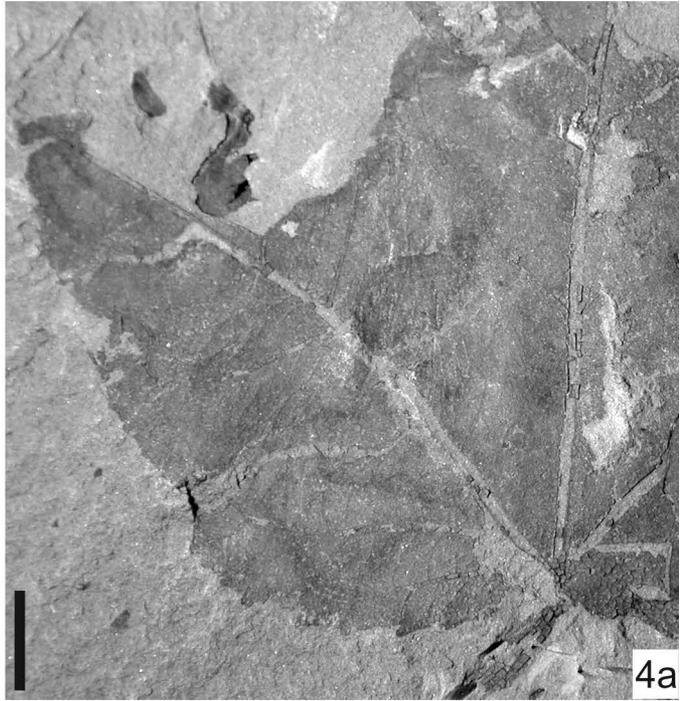
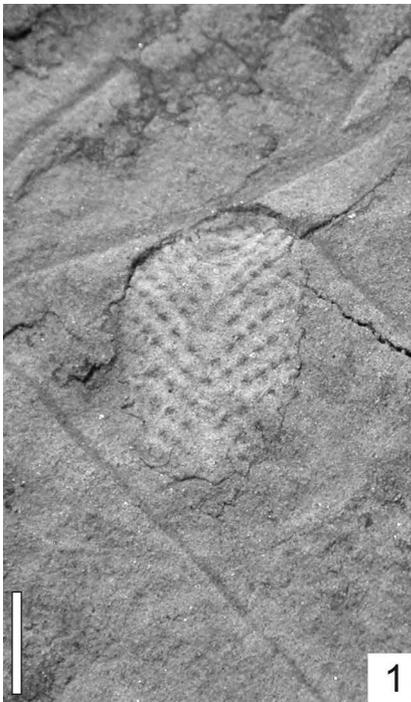


Plate 7

cf. *Crataegus* sp.

1. Leaf, specimen no. KRAM-P 218/106/II

Ulmus sp.

- 2a. Leaf, specimen no. KRAM-P 218/111

- 2b. Detail of leaf margin with teeth, specimen no. KRAM-P 218/111

Carya serrifolia (Goeppert) Kräusel

3. Leaflet, specimen no. KRAM-P 218/171/I

Populus balsamoides Goeppert

4. Leaf, specimen no. KRAM-P 218/120

Acer aegopodifolium (Goeppert) Baikovskaya ex Ilinskaya

5. Leaflet, specimen no. KRAM-P 218/138/I

Scale bars: 3, 4 – 1 cm; 1, 2a, 5 – 5 mm; 2b – 2 mm

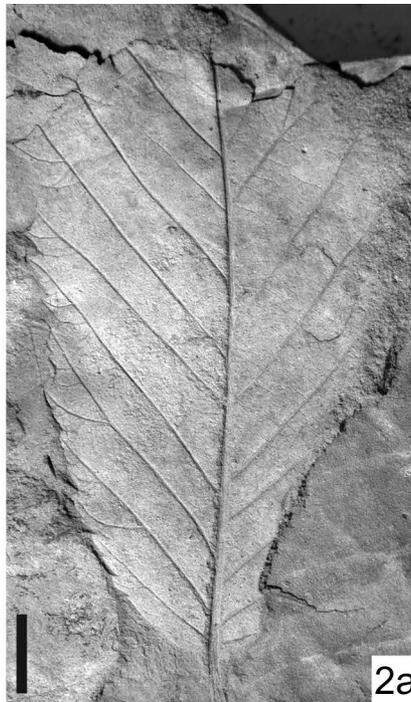


Plate 8

Pterocarya paradisiaca (Unger) Ilinskaya

- 1a. Leaf, specimen no. KRAM-P 218/144/I
- 1b. Detail of leaf margin with teeth, specimen no. KRAM-P 218/144/I

Eucommia sp.

2. Leaf, specimen no. KRAM-P 218/1174/II

Laria rueminiana (Heer) G. Worobiec & Kvaček

3. Leaf, specimen no. KRAM-P 218/170/III

Bryophyta

4. Fragment of probable moss leaf, palynological slide KRAM-P 218/109
5. Fragment of probable moss leaf, palynological slide KRAM-P 218/104

Scale bars: 1 – 1 cm; 1a, 2 – 5 mm; 1b – 2 mm; 4, 5 – 50 μ m

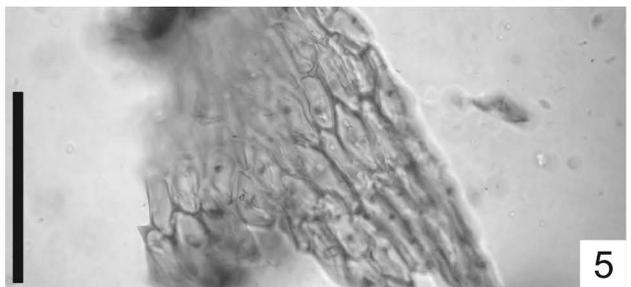
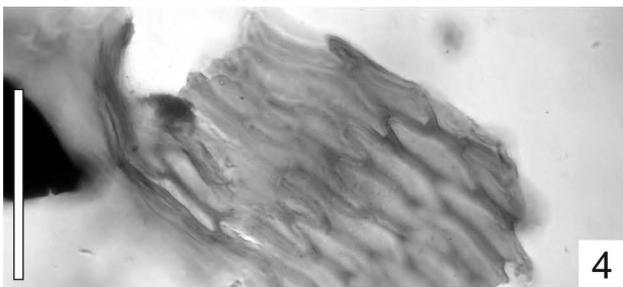
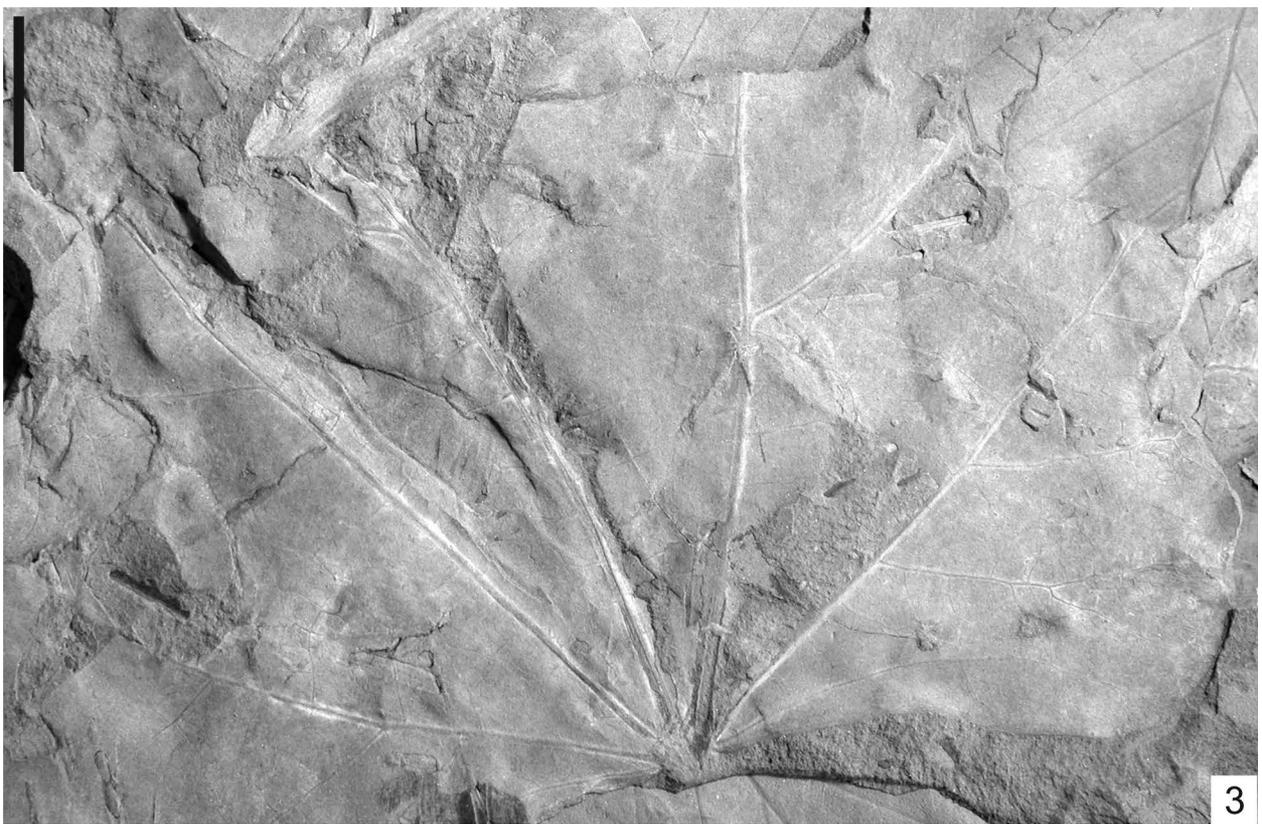


Plate 9

Pinus sp.

- 1a. Epidermis, stomatal rows. Note parallel arrangement of longer axes of stomata, specimen no. KRAM-P 218/18
- 1b. Epidermis. Detail of stomata, specimen no. KRAM-P 218/18

Bark of *Pinus* sp.

2. Detail of sclerenchymatic cells of bark, specimen no. KRAM-P 218/4

Taxodium dubium (Sternberg) Heer

3. Epidermis. Note perpendicular arrangement of longer axes of stomata, specimen no. KRAM-P 218/131
4. Epidermis. Note perpendicular arrangement of longer axes of stomata, specimen no. KRAM-P 218/145/I

Laurophyllum sp.

- 5a. Adaxial epidermis. Note Ω -undulate anticlinal cell walls and attached roundish, idioblast secretory cell (arrow), specimen no. KRAM-P 218/42
- 5b. Abaxial epidermis with stomata, specimen no. KRAM-P 218/42

Liquidambar europaea A. Braun

6. Strongly damaged abaxial epidermis with stoma, specimen no. KRAM-P 218/42

Scale bars: 1a, 3 – 50 μm ; 1b, 2, 4, 5a, 5b, 6 – 20 μm

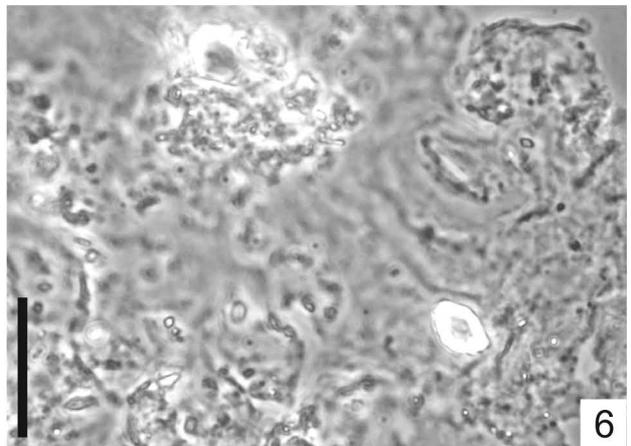
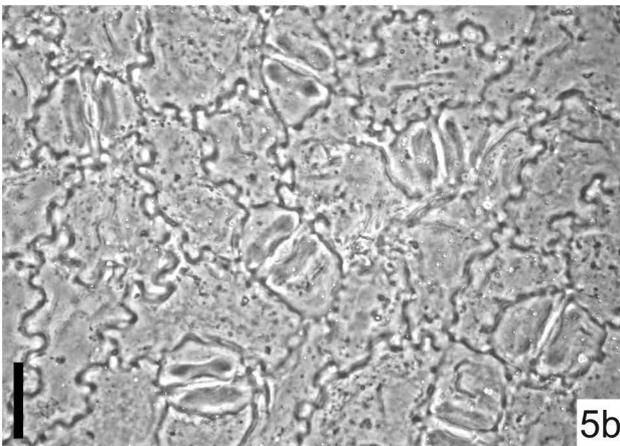
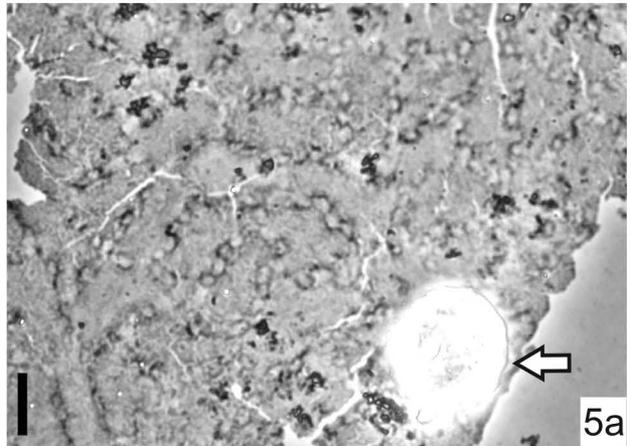
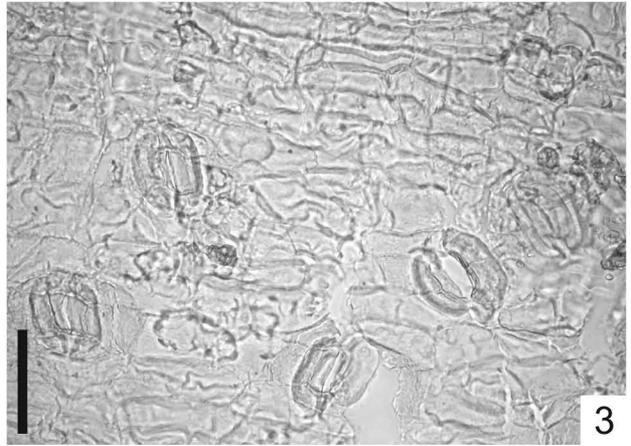
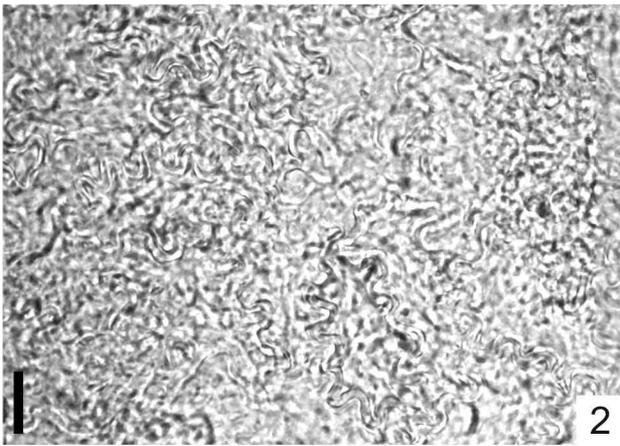
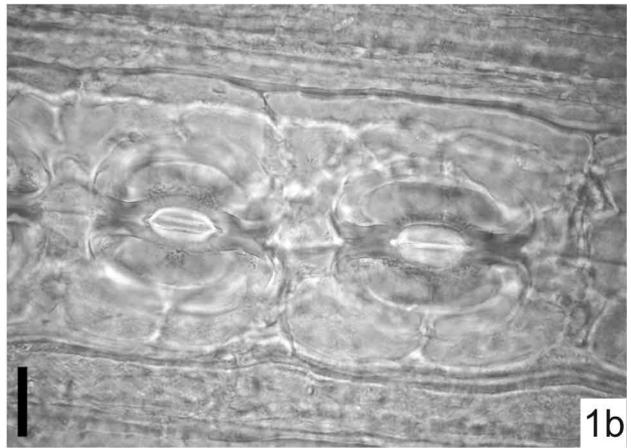
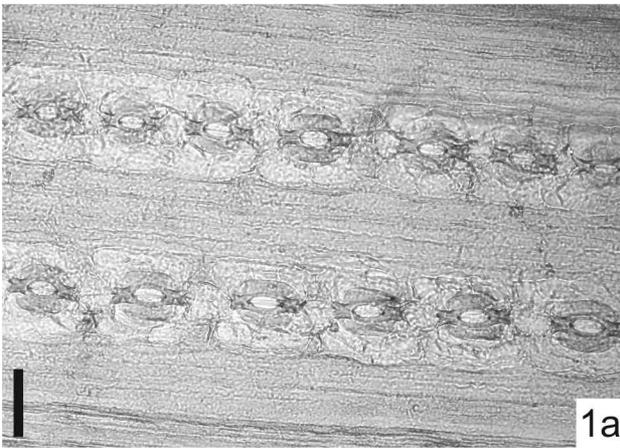


Plate 10

Vitis strictum (Goepfert) Knobloch

- 1a. Adaxial epidermis, specimen no. KRAM-P 218/38
- 1b. Abaxial epidermis. Note stomata and trichome base (arrow), specimen no. KRAM-P 218/38
- 1c. Abaxial epidermis with stomata, specimen no. KRAM-P 218/38

Ulmus sp.

- 2. Adaxial epidermis, specimen no. KRAM-P 218/16

Zelkova zelkovifolia (Unger) Bůžek & Kotlaba

- 3. Adaxial epidermis, specimen no. KRAM-P 218/13

Fagus silesiaca Walther & Zastawniak

- 4. Adaxial epidermis, specimen no. KRAM-P 218/64
- 5. Abaxial epidermis with stomata, specimen no. KRAM-P 218/26

Quercus pseudocastanea Goepfert emend. Walther & Zastawniak

- 6. Adaxial epidermis, specimen no. KRAM-P 218/11

Scale bars: 3, 4 – 50 μm ; 1a, 1b, 1c, 2, 5, 6 – 20 μm

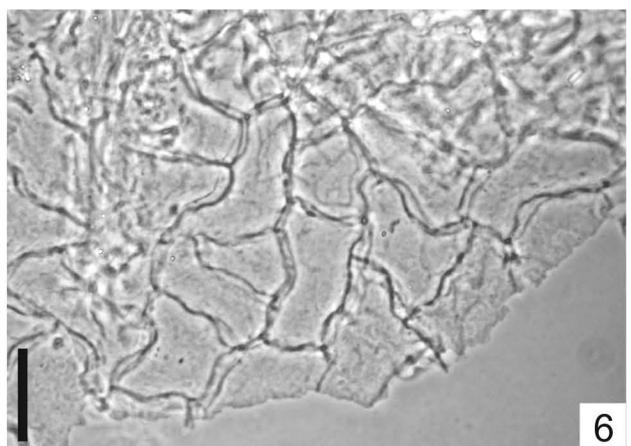
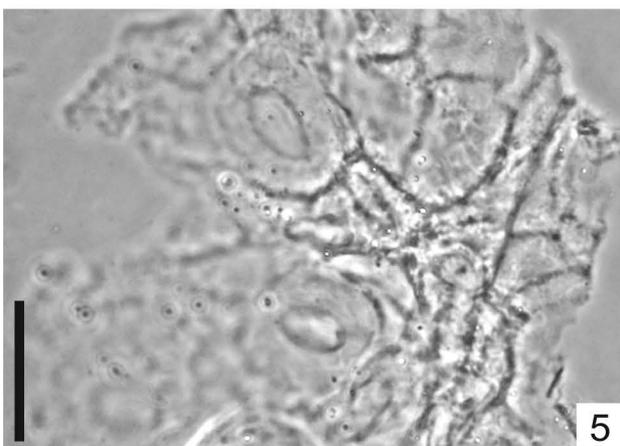
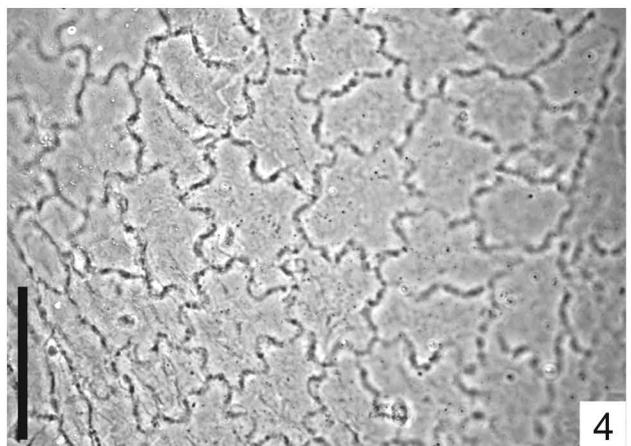
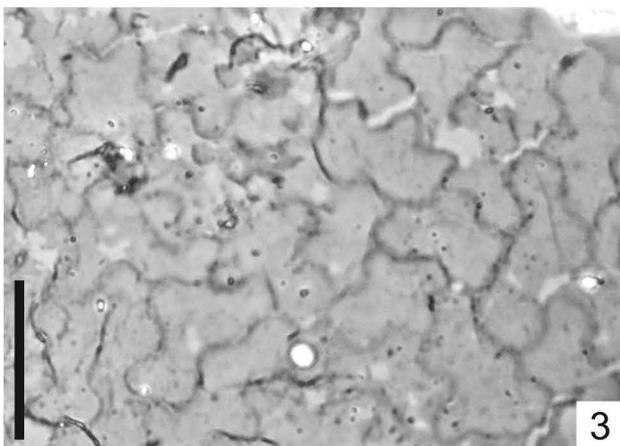
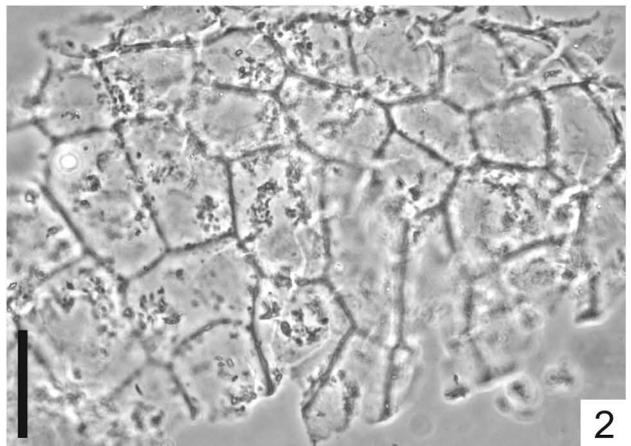
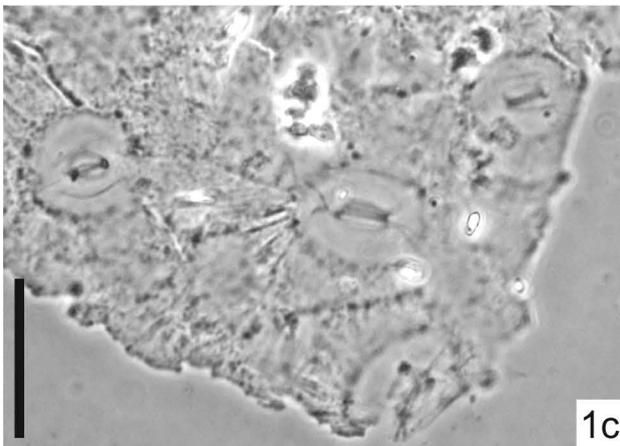
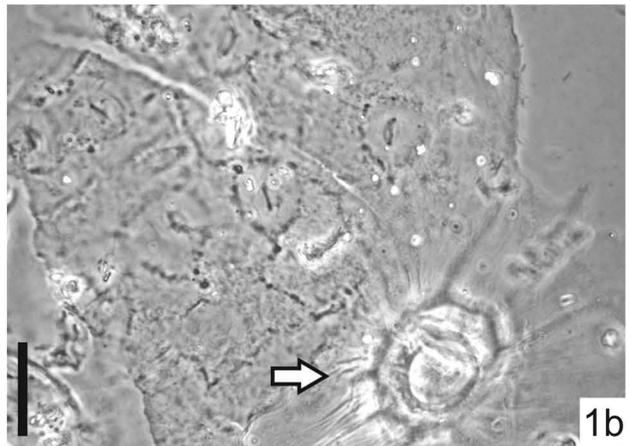


Plate 11

Quercus pseudocastanea Goepfert emend. Walther & Zastawniak

1. Abaxial epidermis with stomata, specimen no. KRAM-P 218/11

Carya serrifolia (Goepfert) Kräusel

2. Abaxial epidermis with stomata, specimen no. KRAM-P 218/9

Populus balsamoides Goepfert

3. Abaxial epidermis with stomata, specimen no. KRAM-P 218/46

Salix varians Goepfert *sensu lato*

- 4a. Adaxial epidermis, specimen no. KRAM-P 218/54

- 4b. Abaxial epidermis. Note stomata and cover of epicuticular wax, specimen no. KRAM-P 218/54

- 4c. Abaxial epidermis. Note brachyparacytic stomata, specimen no. KRAM-P 218/54

Acer aegopodifolium (Goepfert) Baikovskaya ex Ilinskaya

5. Strongly damaged abaxial epidermis with stomata, specimen no. KRAM-P 218/138/I

Acer tricuspidatum Bronn *sensu* Procházka & Bůžek

6. Adaxial epidermis. Note striate ornamentation of cuticle, specimen no. KRAM-P 218/162

All scale bars: 20 µm

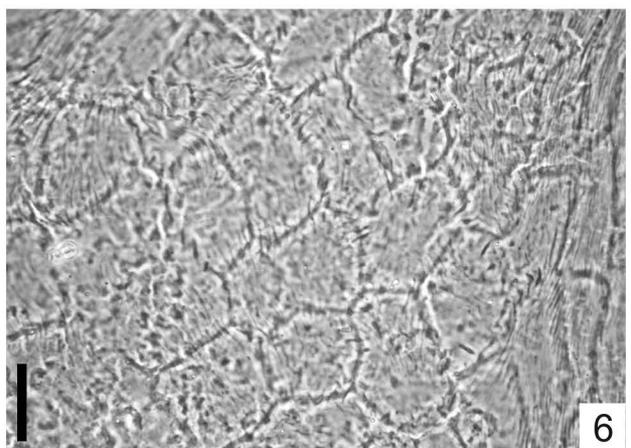
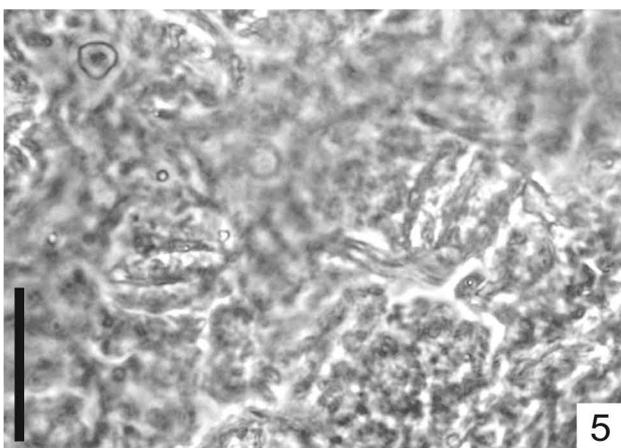
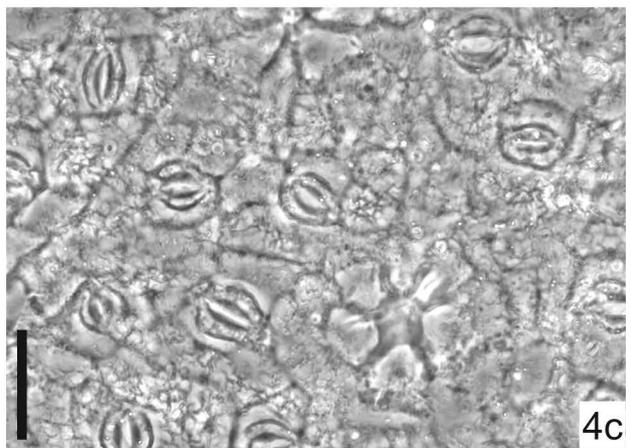
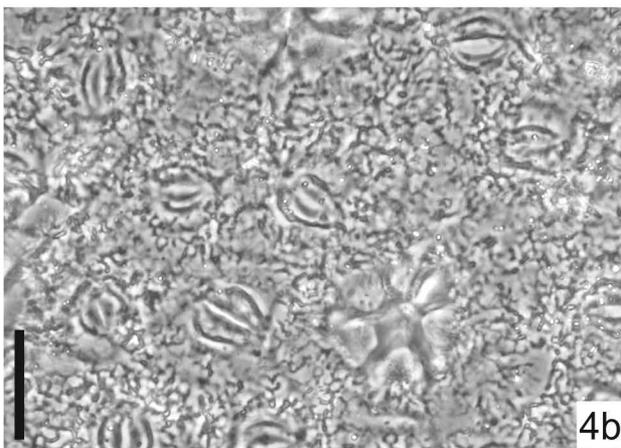
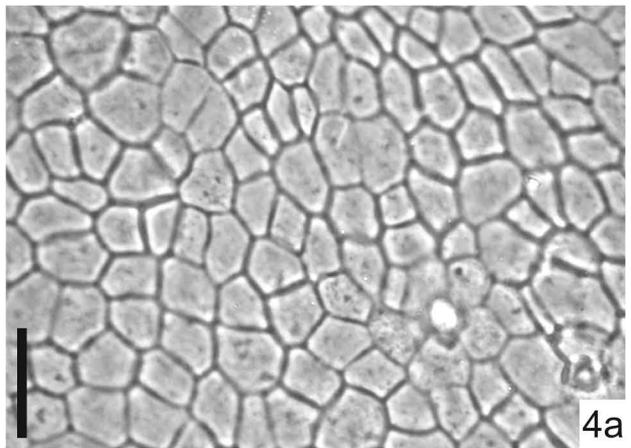
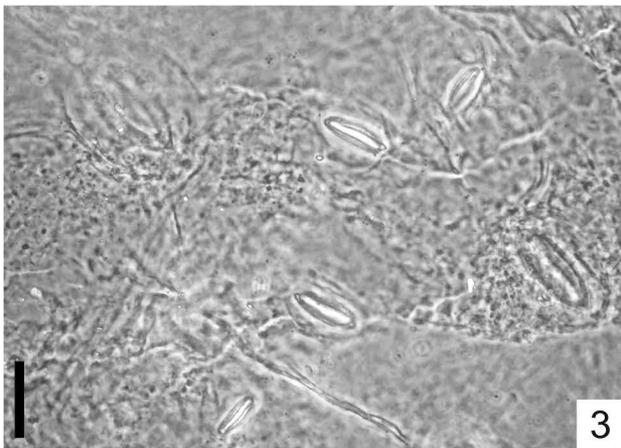
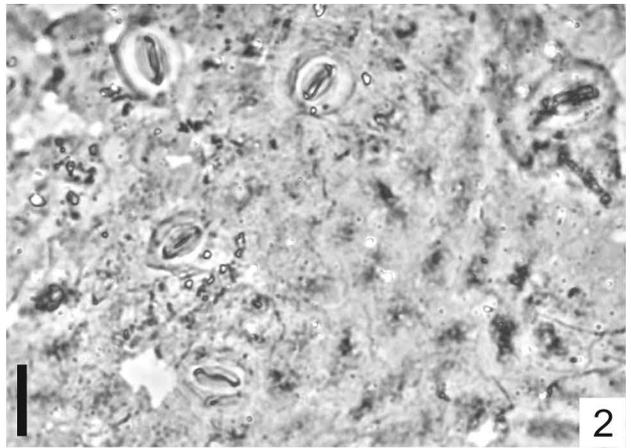
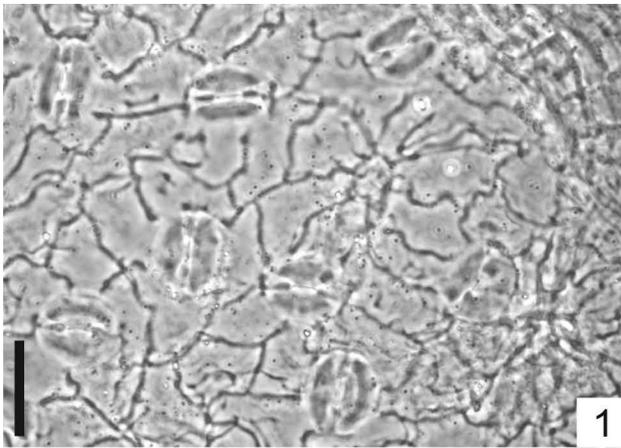


Plate 12

Acer tricuspidatum Bronn sensu Procházka & Bůžek

1. Abaxial epidermis with stomata, specimen no. KRAM-P 218/162

Acer sp.

- 2a. Adaxial epidermis, specimen no. KRAM-P 218/60
- 2b. Abaxial epidermis with stomata, specimen no. KRAM-P 218/60

Laria rueminiiana (Heer) G. Worobiec & Kvaček

- 3a. Adaxial epidermis. Note striate ornamentation of cuticle, specimen no. KRAM-P 218/44
- 3b. Abaxial epidermis with stomata. Note stellate trichome (A) and stellate trichome base (B), specimen no. KRAM-P 218/44
- 3c. Abaxial epidermis with stomata. Note four-celled glandular clavate trichome (arrow), specimen no. KRAM-P 218/44

Eucommia sp.

- 4a. Strongly damaged abaxial epidermis with stomata, specimen no. KRAM-P 218/56
- 4b. Isolated latex (guttapercha) filament with clavate ending, specimen no. KRAM-P 218/56

All scale bars: 20 µm

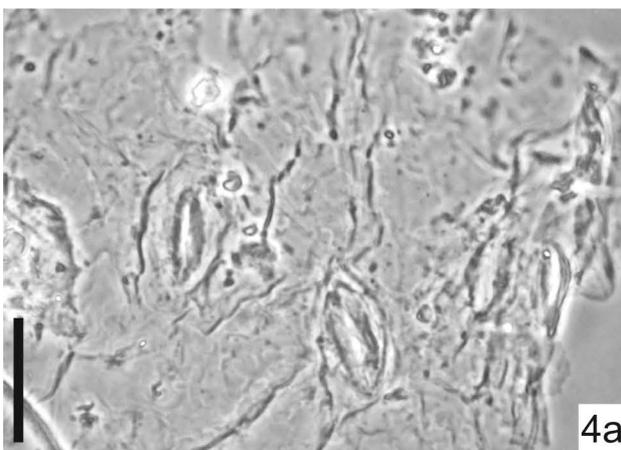
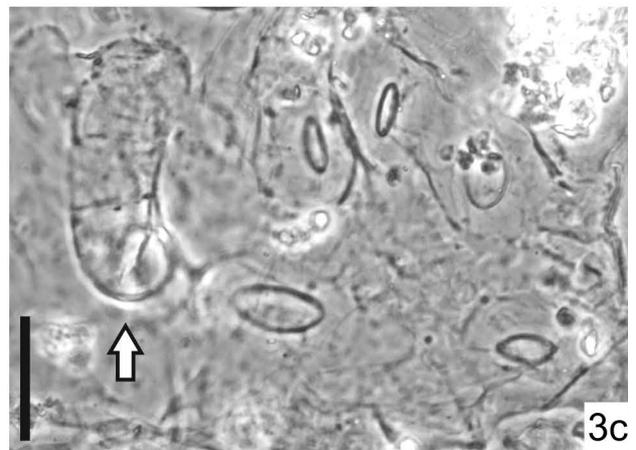
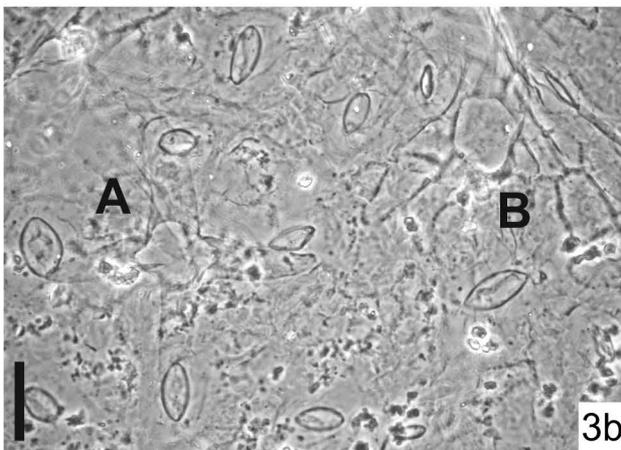
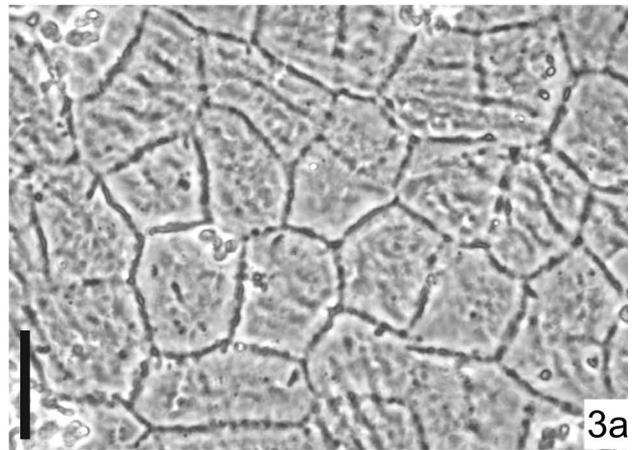
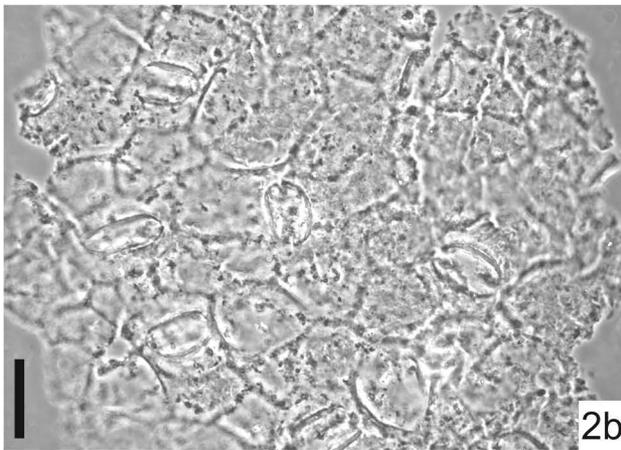
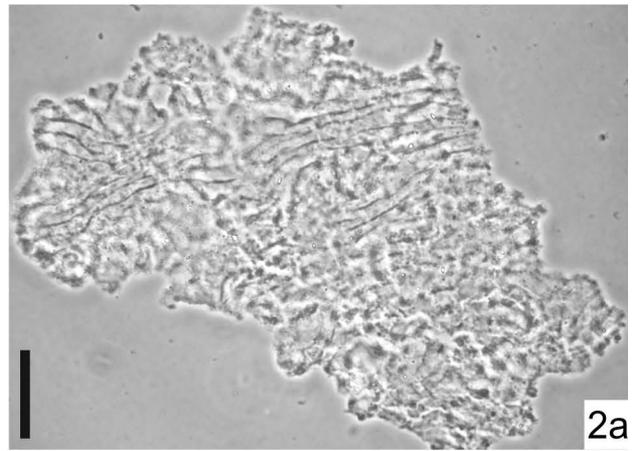
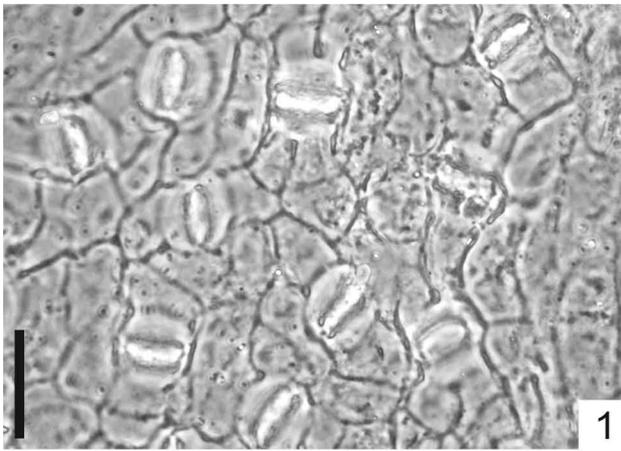


Plate 13

Dicotylophyllum sp. 2

- 1a. Adaxial epidermis, specimen no. KRAM-P 218/47
- 1b. Strongly damaged abaxial epidermis with stomata, specimen no. KRAM-P 218/47

Dicotylophyllum sp. 3

- 2a. Adaxial epidermis, specimen no. KRAM-P 218/21
- 2b. Trichome bases (arrow), specimen no. KRAM-P 218/21
- 3. Abaxial epidermis with stomata and trichome base (arrow), specimen no. KRAM-P 218/45

Dicotylophyllum sp. 4

- 4a. Adaxial epidermis. Note distinct striate ornamentation of cuticle, specimen no. KRAM-P 218/14
- 4b. Strongly damaged abaxial epidermis with stomata, specimen no. KRAM-P 218/14
- 4c. Adaxial epidermis with trichome base, specimen no. KRAM-P 218/14

All scale bars: 20 µm

