Plant assemblage from the Upper Miocene deposits of the Bełchatów Lignite Mine (Central Poland)

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ABSTRACT. The Upper Miocene plant macroremains (mainly leaves) collected in the Bełchatów Lignite Mine (Central Poland) were investigated and supplemented with palynological analysis. In the fossil flora there were found macroremains of *Acer, Betula, Carpinus, Dicotylophyllum, Fagus, Laria, Liquidambar, Populus, Pterocarya, Quercus, Reevesia, Salix, Taxodium, Trapa, and Ulmus.* Four new fossil leaf species to the Polish tertiary were reported: *Quercus roburoides* Gaudin, *Reevesia hurnikii* Kvaček, *Dicotylophyllum* sp. 1, and *Dicotylophyllum* sp. 2. The fossil plant assemblage is composed of mesophytic (zonal) and riparian (azonal) elements. The floristic composition confirms the Late Miocene age of the clayey-sandy unit of the Bełchatów Lignite Mine and suggests warm temperate climate conditions.

KEYWORDS: plant macroremains, macromorphology, plant cuticles, micromorphology, palynology, palaeovegetation, Late Miocene, Poland

INTRODUCTION

In the course of palaeobotanical survey in the outcrop of the Bełchatów Lignite Mine in 2004, an assemblage of abundant accumulations of plant macroremains, mainly fossil leaves, have been found. Good state of preservation of plant fossils made possible an extensive study of plant macroremains combined with palynological analysis. The investigations were aimed at palaeofloristics and palaeoecology of the assemblage to document biodiversity of the Neogene flora and vegetation of the Bełchatów Lignite Mine.

GEOLOGY

The Bełchatów Lignite Mine is situated in Central Poland, in the region between the rivers Warta and Pilica, ca 15 km south of the town Bełchatów (Fig. 1). Lignite seams occur within a tectonic depression named the Kleszczów Graben that is filled with Neogene and Quaternary deposits (Gotowała & Hałuszczak 1999). A lithostratigraphic profile of the Neogene deposits filling the Kleszczów Graben (Fig. 2) with four main lithological units: subcoal unit (PW), coal unit (W) including the main seam (PG), clayey-coal unit (I-W), and the youngest clayey-sandy unit (I-P) has been established (Stuchlik et al. 1990, Czarnecki et al. 1992, Szynkiewicz 2000, Matl 2000). Multiproxy studies (geological, palaeobotanical and palaeozoological) of the Neogene deposits at the Belchatów Lignite Mine allowed determination of the age of the main coal seam (PG) as Early Miocene, and those of the overburden sedimentary series of the clayey-sandy unit as Late Miocene (Burchart 1985, Burchart et al. 1988, Stuchlik et al. 1990, Kowalski 1993, Kowalski & Rzebik-Kowalska 2002, Stuchlik and Szynkiewicz 1998, Szynkiewicz 2000).



Fig. 1. Location of the Bełchatów Lignite Mine in Poland

Investigated plant assemblages were collected from the Bełchatów Lignite Mine outcrop. Material was found in July, 2004 on the western slope of the open pit of the Bełchatów Lignite Mine, on the overburden escarpment 3,



Fig. 2. Schematic geological profile showing the Neogene deposits of the Bełchatów Lignite Mine (modified after Worobiec 2007). Leaf drawing marks the stratigraphic position of the fossil plant assemblage KRAM-P 250. **TS-3** – paratonstein TS-3, dated at 18.1 ± 1.7 Ma BP or at 17.25 ± 0.4 Ma BP (Burchart 1985, Burchart et al. 1988); **TS-2** – paratonstein TS-2, dated at 16.5 ± 1.3 Ma BP or at 17.05 ± 0.69 Ma BP (Burchart 1985, Burchart et al. 1988); **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)

near the conveyor belt B-301. Its stratigraphical position corresponds to the lower part of the clayey-sandy unit of Late Miocene age (Fig. 2).

MATERIAL AND METHODS

Fossil specimens were slowly dried and prepared in the laboratory at the Władysław Szafer Institute of Botany, Polish Academy of Sciences. Plant macroremains are preserved mostly as compressions, often fragmented and deformed. The state of preservation of remains is usually good allowing preparation of fossil cuticles, exceptionally even isolation of leaf blades (Pl. 2, fig. 6). However, most of leaf compressions were strongly cracked which made the isolation of cuticles very difficult, in many cases even impossible.

From the selected leaf compressions fragments of coalified leaf lamina were sampled for cuticular analysis. The laminar fragments were cleaned with hydrofluoric acid, washed in water, macerated using a NaClO solution (a commercial bleach, called "Bielnar"), and finally mounted on slides with glycerine jelly.

All studied fossil specimens are housed at the W. Szafer Institute of Botany Polish Academy of Sciences, Kraków under the catalogue number KRAM-P 250. The total number of specimens from all taxa is greater than the total number of deposit fragments with plant remains because on some specimens several taxa were preserved. In such cases alphanumerical specimen number is used. In total 159 deposit samples were investigated.

Leaf macromorphological descriptions follow mostly Ellis et al. (2009) and cuticular descriptions (micromorphology) follows Dilcher (1974) and Wilkinson (1979). The way of measuring the size of micromorphological structures depended on the shape of the object. The diameter was measured in regular, round, and broadly elliptic objects, but the length and the width were measured in all rectangular objects. In structures of irregular or variable shape (mainly unmodified epidermal cells) the longest dimension was measured.

The drawings were made using a Carl Zeiss stereomicroscope with *camera lucida* attachment. Macrophotographs were taken using a NIKON Coolpix 995 digital camera and NIKON SMZ 800 stereomicroscope fited with NIKON DS-5M-U1 digital camera and microphotographs were taken using NIKON Eclipse E400 microscope fitted with CANON A640 digital camera.

Macroremains were identified on the basis of macrofossil morphology and cuticular analysis. Plant remains were compared to other related fossil taxa and herbarium material for more precise identifications. Cuticles from the fossil specimens were compared to cuticles of fossil and extant plants to further support the taxonomic affinity of the fossils. The reference herbarium and collections of epidermal preparations from fossil and recent leaves are housed in the Department of Palaeobotany, W. Szafer Institute of Botany Polish Academy of Sciences, Kraków. Two samples from the sediments containing leaf macroremains were used for palynological study (dr. E. Worobiec). The samples were prepared following a modified Erdtman's acetolysis method (Moore et al. 1991), using hydrofluoric acid to remove clay minerals. Two slides from each sample were prepared, using glycerine jelly as a mounting medium. The palynomorphs were identified using comparative material from previous publications (e.g. Stuchlik et al. 2001, 2002, 2009, in press) and the reference palynological collection of the Department of Palaeobotany, W. Szafer Institute of Botany Polish Academy of Sciences, Kraków.

RESULTS

SYSTEMATIC PALAEOBOTANY

The classification for gymnosperms follows Gadek et al. (2000). The classification of angiosperms and author names of families follows the APG III (2009). Plant families, genera, and species are listed alphabetically.

Gymnosperms

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. 1, fig. 5, Pl. 6, fig. 1

- 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 5-15.

Material. KRAM-P 250: 27/II, 30/I, 31/I and 32/I (counterparts), 35/I, 36/I, 46/II, 77/III, 129/III.

Description. Macromorphology. Fragments of leafy shoots, up to 5.3 cm long, vestigial needles at a base of shoot. Needles above base entire-margined, 0.7–1.2 cm long and 0.10–0.12 cm wide, decreasing in length towards base of shoot, apex of needle acute, rarely acuminate, base decurrent. Midvein clearly visible; epidermal cells mostly rectangular or square, 40–75 μ m long and 20–32 μ m wide. Cell walls thick, straight or rounded, end walls perpendicular or oblique to the long axis of cells. Hypodermis present, composed of cells lar wax. Stomata irregularly-emptic, $45-50 \mu m$ long. Long axis of stomata irregularly oriented, usually oblique to the long axis of needle and only sporadically parallel. Distinct T-shaped thickenings at the stomatal poles. Outer stomatal ledge aperture elongate-elliptic, about 20 μm long and 5–7 μm wide.

Remarks. The *Taxodium* shoots are morphologically similar to those of Sequoia abietina (Brongniart) Knobloch, but differ from the latter by having slightly narrower and longer needles. However, the needle morphology of both Sequoia and Taxodium is highly variable. For a reliable identification, the epidermal micromorphology of the needles from Bełchatów was analysed. Epidermis of Taxodium shows that the long axes of stomata are oblique to the axis of the needle. In case of taxodioid shoots of Sequoia the long axis of stomata is more or less parallel to the axis of the needle. In addition, the cuticle of *Taxodium* needles is rather delicate and was strongly damaged during preparation procedure, while the epidermis of Sequoia abietina needles is strongly cutinized and resistant to overmaceration.

Modern equivalents. Taxodium dubium is comparable with two extant species from North America: T. distichum (L.) Rich. and T. mucronatum Tenore (Hummel 1983). Taxodium distichum grows in swamps and on river banks in the south-western USA while T. mucronatum is associated with wet habitats on banks of mountain rivers and streams in Mexico (Krüssmann 1972).

E cology. Arctotertiary, warm temperate element. Woody species representing part of the azonal vegetation, probably growing in swamp and riparian forests. *Taxodium* has been suggested as being the dominant component of *Taxodium-Nyssa* swamp forests (Boulter et al. 1993, Belz & Mosbrugger 1994, Mai 1995, Kunzmann et al. 2009).

Occurrence. *Taxodium dubium* was a common component of European tertiary azonal vegetation. It occurred from the Late Eocene to Late Miocene in the (Atlantic-) Boreal province sensu Mai of Central Europe and from the Late Oligocene to Late Pliocene in the Transeuropean Paratethys province sensu Mai (Kunzmann et al. 2009). In Poland it occured from the Early Miocene to the Early Pliocene (see Worobiec et al. 2008).

Dicotyledones

Altingiaceae Horan., nom. cons.

Liquidambar L.

Liquidambar europaea A. Braun

Fig. 3: 1–2, Pl. 1, figs 1–3

- 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 250: 7/I, 8/I, 10/I, 17/I, 27/I, 136/III. cf. *Liquidambar europaea* 18/I.

Description. Macromorphology. Leaves palmately lobed, 3–5 lobed, up to 7.5 cm across. Apex of lobes attenuate. Leaf margin simple serrate, teeth small, apical side of teeth very short, concave, basal side long, acuminate, teeth apex round. Veins terminate in sinus between teeth. Primary venation palmate-actinodromous, perfect, primary vein branched into 5 branches. Secondariy venation semicraspedodromous, secondaries curved upwards, interconnected near leaf margin, forming loops, sending of fine veins towards teeth. Tertiary veins percurrent or weakly percurrent.

Remarks. Shape of leaf, distinctive serration of margin and network of venation are characteristic for the genus *Liquidambar* L. and the fossil species *Liquidambar europaea* A. Braun with typically 5-lobate leaves.

Modern equivalents. According to Hummel (1983) extant species from the section *Euliquidambar* Harms (especially the North American *Liquidambar styriaciflua* L. and *L. orientalis* Mill. from Asia Minor) are closely related to the fossil species *L. europaea*.

Ecology. Arctotertiary, warm temperate element. Like its extant relatives, *Liquidambar europaea* was most likely a typical element 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 it is known from the Middle Miocene to Pliocene (for localities see Hummel 1983).

Betulaceae Gray, nom. cons.

Betula L.

Betula plioplatyptera Hummel

Fig. 3: 4, Pl. 1, figs 4, 6

1991 Betula plioplatyptera Hummel, pp. 82–87, Fig. 6: 1–7, pl. 3, figs 1–3, pl. 4, figs 1–1a, pl. 5, figs 1–4.

Material. KRAM-P 250: 13/I, 83/I, 97/I. Betula cf. plioplatyptera: 156/I.

Description. Macromorphology. Leaf fragments, up to 5.5 cm long and 2.5-2.8 cm wide. Leaf apex acute, base acute and decurrent, usually without teeth. Leaf margin double serrate, apical and basal sides of teeth acuminate, sometimes rounded. Tooth apex mostly acute, sometimes slightly rounded. Secondary veins and subsidiary veins terminating at the teeth apex. Venation pinnate, primary vein straight, of moderate thickness. Secondary venation simple craspedodromous, preserved up to 8 pairs of secondaries, veins first straight curve upwards near leaf margin, distributed at intervals of 0.3 cm near leaf base to 0.4-0.7 cm in the middle of the lamina. Secondary veins diverging from midvein at an angle of $40-55^{\circ}$. Tertiary venation percurrent, ca. 8-10 tertiary veins occur per 1 cm of secondary vein length. Tertiary venation forms an angle of 120–135° with the primary vein.

Remarks. The macromorphological features of leaf fragments, e.g. shape of the leaves, large primary teeth, minor secondary teeth and an irregularly serrate leaf margin allowed its identification as *Betula plioplatyptera* Hummel. Specimen no. 156/I only presumably belongs to *Betula plioplatyptera* as it is badly preserved. This species differs from *Betula subpubescens* Goeppert emend. Worobiec in shape, outline of leaf base, arrangement of teeth, and course of the tertiary venation (Hummel 1991, Worobiec & Szynkiewicz 2007).

Modern equivalents. *Betula plioplatyptera* resembles the extant North American species *B. papyrifera* Marsh., particularly its form *elongata* Schneider though it is considerably



Fig. 3. 1–2 – *Liquidambar europaea* A. Braun: 1 – specimen KRAM-P 250/7/I, 2 – specimen KRAM-P 250/17/I; 3 – *Dicotylophyllum* sp. 2: specimen KRAM-P 250/48/I; 4 – *Betula plioplatyptera* Hummel: specimen KRAM-P 250/83/I; 5 – *Betula subpubscens* Goeppert emend. Worobiec: specimen KRAM-P 250/133/I; 6 – *Dicotylophyllum* sp. 1: specimen KRAM-P 250/111/I; 7 – *Carpinus grandis* Unger emend. Heer: specimen KRAM-P 250/113/I; 8 – *Fagus silesiaca* Walther & Zastawniak: specimen KRAM-P 250/131/I. Scale bar – 1 cm

different when regarding the structure of epidermis (Hummel 1991).

Ecology. Arctotertiary, temperate element. Most probably component of riparian or mesophytic forests.

Occurrence. In Poland it is found in Miocene deposits of Bełchatów (Worobiec & Szynkiewicz 2007) and Early Pliocene of Ruszów (Hummel 1991).

Betula subpubescens Goeppert emend. Worobiec

Fig. 3: 5, Pl. 1, fig. 7, Pl. 6, fig. 2

- 1855 Betula subpubescens Goeppert, p. 11, Pl. 3, fig. 9.
- 1991 Betula subpubescens Goeppert; Hummel, pp. 87–91, Pl. 6, figs 1–4, Pl. 7, figs 1–4, Pl. 8, figs 1–5; Fig. 7: 1–13.
- 2007 Betula subpubescens Goeppert emend. Worobiec, Worobiec & Szynkiewicz, pp. 43–45, Pl. 6, figs 2, 3a–3c, Pl. 7, figs 2a–2e.

Material. KRAM-P 250: 38/I, 40/I, 60/I, 74/I, 82/I, 99/III, 123/IV, 127/II, 133/I and 134/I (counterparts), 136/I, 138/II, 144/I, 149/I. *Betula* cf. *subpubescens*: 53/II and 54/I (counterparts), 70/I, 94/III, 97/I.

Description. Macromorphology. Leaves elliptic to ovate, up to 5.0 cm long, 1.4-3.2 cm wide, leaf apex acute to acuminate, base obtuse, often decurrent. Petiole, rarely preserved, up to 1.4 cm long. Leaf margin double serrate, leaf base often entire-margined. Primary teeth served by secondary veins are large, subsidiary teeth (2-3) small, apical and basal sides of teeth usually acuminate, tooth apex acute or acuminate. Secondary veins and subsidiary veins terminate at apex of teeth. Venation pinnate, primary vein straight, of moderate thickness. Secondary venation simple craspedodromous, 8–11 pairs of secondaries preserved, arise at intervals of 0.2–0.3 cm near leaf base and 0.3-0.9 cm in middle of the lamina, initially ± straight and curved upwards near leaf margin, diverging from midvein at an angle of 55–60° near leaf base and $40–55^{\circ}$ (commonly 40–50°) in the middle of the lamina. Tertiary venation percurrent.

Micromorphology. Adaxial epidermis composed of more or less isodiametric cells, $20-25 \mu m$ across with usually straight anticlinal cell walls. Leaves hypostomatic. There are only visible some outer stomatal ledge apertures, wide spindle-shaped, about 18 μm long and 10 μm wide. On the abaxial epidermis glandular trichome bases, multicellular (8–10 cells), 30–35 μm across were found.

Remarks. Macro- and micromorphologically the above described leaf remains correspond to leaves of *Betula subpubescens* Goeppert emend. Worobiec. Some specimens only presumably belong to *Betula subpubescens* as they are badly preserved.

Modern equivalents. Betula subpubescens is comparable to recent Betula pubescens Ehrh. (= Betula alba Roth), B. bhojpathra Wall. (= B. utilis D.Don.) and B. davurica Pall. (Hummel, 1991), as well as according to Němejc (1949) to B. verrucosa Ehrh. (= B. pendula Roth).

Ecology. Arctotertiary, temperate element. Most probably a component of riparian or mesophytic forests.

Occurrence. In Poland it is found from the Middle Miocene to Early Pliocene (Krajewska 1998).

Betula sp.

Material. KRAM-P 250: 2/I, 5/III, 45/I, 58/I, 66/I, 72/I, 73/I, 75/I, 85/I, 100/II, 101/I, 119/I, 121/I, 122/III, 155/I.

Description. Macromorphology. Fragments of leaves with *Betula* type of teeth. Leaf margin double serrate, primary teeth served by secondary veins are large, apical and basal sides of teeth acuminate, apex of tooth acute or moderate acute.

Remarks. The leaves undoubtedly represent the genus *Betula*. Identification to species level is impossible due to the incompleteness of the specimens, but doubtless among them are represented species *Betula plioplatyptera* Hummel and *Betula subpubescens* Goeppert emend. Worobiec and perhaps also *Alnus adscendens* (Goeppert) Zastawniak & Walther.

Carpinus L.

Carpinus grandis Unger emend. Heer

Fig. 3: 7, Pl. 2, figs 2, 4a-4b

1850 Carpinus grandis Unger, p. 408.1852 Carpinus grandis Unger, p. 39, Pl. 20, figs 4, 5.

1856 Carpinus grandis Unger; Heer, Pl. 71, figs 19b,
c-e, Pl. 72, figs 2–11, 14, 16, 17, 19, 20, 22–24,
Pl. 73, figs 2–4.

Material. KRAM-P 250: 4/II, 15/I, 23/II, 64/I, 90/I, 99/II, 113/I, 129/II, 148/II, 153/I.

Description. Macromorphology. Leaf blade frequently characteristically wavy. Leaves elliptic or ovate, up to 5.0 cm long and 2.5–3.4 cm wide with acute, obtuse, rounded, or rarely slightly cordate base. Petiole up to 1.0 cm long. Leaf margin double serrate, teeth small, numerous, more or less of the same size, apical and basal side of teeth acuminate or rounded. Teeth apex acute, teeth often slightly hook-shaped. Secondary veins and their branches terminate at the teeth apex. Venation pinnate, primary vein straight of moderate thickness. Secondary venation simple craspedodromous. Secondaries preserved in up to 8 pairs, straight, near leaf margin slightly upward curved, distributed at intervals of 0.3-0.4 cm near leaf the base and 0.5–0.8 cm in the middle part of lamina. Secondary veins form an angle of 40–50° with the primary vein, close to the leaf margin produce numerous branches entering the nearest teeth. Tertiary venation percurrent, forms an angle of 120-140° with the primary vein. About 9 to 10 tertiary veins occur per 1 cm of secondary vein length.

Remarks. The elliptic shape, double serrate leaf margin, arrangement of secondary veins, and venation of the leaf base are characteristic of the genus *Carpinus* L. The leaves under discussion belong to the fossil species *Carpinus grandis* Unger emend. Heer, most probably a collective species that includes several morphotypes of fossil leaves (Mai & Walther 1978, 1988, Hummel 1991, Zastawniak & Walther 1998).

Modern equivalents. Leaves of *Carpinus* grandis from Bełchatów correspond to recent representatives of section *Eucarpinus* (comp. Krüssmann 1976) and with respect to macromorphology and micromorphology of epidermis could be compared to *Carpinus betulus* L. (Heer 1856, Zastawniak 1972, Hummel 1991, Krajewska 1998), *Carpinus caucasica* Grossh. (Hummel 1991), and *Carpinus orientalis* Mill. (Ilinskaya 1968).

Ecology. Arctotertiary, temperate element. Component of mesophytic and probably also riparian vegetation. Occurrence. *Carpinus grandis* is known in tertiary floras of Europe from the middle Oligocene to the Late Pliocene (Mai & Walther 1978, 1988, Hummel 1991, Zastawniak & Walther 1998). In the territory of Poland found from Early Miocene to Early Pliocene (Hummel 1991, Krajewska 1998, Worobiec et al. 2008).

Carpinus grandis Unger sensu Berger

Pl. 2, fig. 7

1850 Carpinus grandis Unger, p. 408.

1953 Carpinus grandis Unger sensu Berger; Berger, p. 14, Figs 5: A–G.

Material. KRAM-P 250: 5/II, 53/III, 54/IV, 122/II.

Description. Fragments of fruit involucre.

Remarks. These remains of fruits of fossil hornbeam represent species *Carpinus grandis* Unger sensu Berger compared with involucres of recent *Carpinus betulus* L. (Krajewska 1998).

Betulaceae indet.

Material. KRAM-P 250: 8/III, 11/I, 13/III, 24/I, 29/I, 34/I, 41/I, 61/I, 62/I, 67/I, 78/I, 81/I, 84/I, 86/II, 114/I, 117/I, 151/I, 155/II.

Remarks. On the basis of the type of serration of leaf margins, these fragments of leaves could be categorised as belonging undoubtedly to the family Betulaceae. Due to poor state of preservation identification of the genera position is uncertain.

Dicotyledones incertae sedis

Dicotylophyllum sp. 1

Fig. 3: 6, Pl. 2, figs 5–6, Pl. 6, figs 3a–3b

Material. KRAM-P 250: 98/I, 99/I, 100/I, 103/I, 104/I, 105/I, 106/I, 107/I, 108/I, 109/I (counterpart to 112/II), 110/I, 111/I, 112/II.

Description. Macromorphology. Fragments of entire-margined leaves, up to 4.5 cm long and 1.4–2.6 (3.6) cm wide. Leaf apex probably attenuate, leaf base obtuse. Venation pinnate, primary vein straight, and of moderate thickness. Secondary venation brochidodromous. Secondaries upwardly curved and interconnected in loops, arranged alternately, distributed at intervals of 0.5-1.0 (commonly 0.6-0.8) cm. Secondary veins form an angle of $50-70^{\circ}$ with primary vein. Tertiary venation reticulate. Higher order venation random reticulate. Areoles well developed, 0.20-0.45 mm across, veinlets usually simple, rarely once branched or lacking. Marginal ultimate venation looped.

Micromorphology. Cells of abaxial epidermis with usually straight, rarely rounded walls, about 20 μ m across. Leaves hypostomatic. Stomata anomocytic, narrow elliptic to elliptic, 15–25 μ m across. Outer stomatal ledge aperture spindle-shaped, usually rather narrow, 9–17 μ m long and 2.5–6.0 μ m wide. On the abaxial epidermis, unicellular, strongly cutinised, rounded to elliptic trichome bases were found, 12–22 μ m in diameter. Trichome bases are located both over the veins and on vein-free area.

Remarks. Systematic position of the described leaf fragments is unknown. Some similarities in macromorphology could be observed in comparison with leaves described by Kvaček et al. (2011) as species of morphogenus *Leguminosites* Bowerbank emend. Schimper, especially with *Leguminosites* sp. A. However, they differ from *Dicotylophyllum* sp. from Bełchatów in the development of veinlets and micromorphology of epidermis.

Dicotylophyllum sp. 2

Fig. 3: 3, Pl. 4, fig. 1, Pl. 6, fig. 4

 $M\,a\,t\,e\,r\,i\,a\,l.$ KRAM-P 250: 48/I and 152/I (counterparts).

Description. Macromorphology. Leaf fragment up to 4.5 cm long and 3.2-3.4 cm wide. Leaf margin simple serrate, teeth of variable size, apical sides acuminate, rarely convex or straight, basal sides acuminate or convex, teeth apex acute or moderate acute. Venation pinnate, primary vein straight of moderate thickness. Secondary venation simple craspedodromous to semicraspedodromous. Up to 7 pairs of secondary veins preserved, arranged at intervals of 0.4-0.8 cm, forming an angle of $50-60^{\circ}$ with the primary vein. Secondaries first straight then curved upward, close to the leaf margin characteristically distinctly forked, branches enter the teeth. Tertiary venation percurrent.

Remarks. Systematic position of the described leaf fragment is unknown.

Dicotyledones indeterminatae

Material. KRAM-P 250: 7/III, 52/I, 87/I, 91/I, 116/I, 120/III, 148/I.

Remarks. Fragments of dicotyledonous leaves, preserved in such a poor state that determination of their systematic position is completely impossible.

Fagaceae Dumort., nom. cons.

Fagus L.

Fagus silesiaca Walther & Zastawniak Fig. 3: 8, Pl. 6, fig. 5

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

Material. KRAM-P 250: 5/I, 13/II, 15/II, 16/I, 22/I, 23/III, 33/II, 35/II, 37/I, 44/II, 46/I, 53/I, 64/II, 68/I, 72/II, 76/I, 90/II, 115/I, 117/II, 123/II, 126/III, 129/I, 131/I and 132/I (counterparts), 137/I and 138/I (counterparts), 139/I and 140/I (counterparts), 142/I, 143/I, 150/III, 152/II.

Description. Macromorphology. Leaves usually elliptic, rarely ovate, up to 6.0 cm long and 2.6-3.8 (commonly 3.0-3.5) cm wide with acute or obtuse, exceptionally even asymmetric leaf base. Leaf margin simple serrate, teeth upwardly curved, apical sides of teeth concave, basal sides acuminate or convex, teeth apex acute or slightly rounded. Venation pinnate, primary vein in apical part of leaf often characteristically undulate. Secondary venation simple craspedodromous, secondaries preserved in 8-10 pairs, straight or near leaf margin slightly upwardly curved, distributed at intervals of 0.5-1.0 (commonly 0.6-0.8) cm. Secondary veins form an angle of (35) 40-50 (55)° with primary vein. Tertiary venation percurrent, forms an angle of $120-140^{\circ}$ with the primary vein. 8-12 (commonly 10-12) tertiary veins occur per 1 cm of secondary vein length. Higher order venation orthogonal reticulate. Areoles well developed, 0.3-0.5 mm across, veinlets simple or none. Marginal ultimate venation looped.

Micromorphology. Adaxial epidermis composed of usually slightly elongated cells with



Fig. 4. 1, 4, 5 – Laria rueminiana (Heer) G. Worobiec & Kvaček: 1 – specimen KRAM-P 250/50/I, 4 – specimen KRAM-P 250/80/I, 5 – specimen KRAM-P 250/94/I; 2 – Salix sp.: specimen KRAM-P 250/93/I; 3 – Pterocarya paradisiaca (Unger) Ilinskaya: specimen KRAM-P 250/147/I; 6 – Salix varians Goeppert sensu lato: specimen KRAM-P 250/150/II; 7 – Populus populina (Brongniart) Knobloch: specimen KRAM-P 250/118/I. Scale bar – 1 cm

distinctly undulate cell walls, about 37 μ m across. Leaves hypostomatic. Abaxial epidermis consists of variable-shaped cells with rounded or slightly undulate cell walls, 25–30 μ m across. Stomata usually roundish, rarely wide elliptic, 20–25 μ m in diameter. Outer stomatal ledge elliptic-oblongate, 7–11 μ m long and 5–7 μ m wide. Indistinct polar cuticular thickness usually visible.

Remarks. The fragments of fossil beech leaves described above belong to Fagus silesiaca Walther & Zastawniak. It differs from the leaves of Fagus kraeuselii Z. Kvaček & Walther in having a greater number of secondary veins (8–10 pairs) and from middle Oligocene – Early Miocene species Fagus saxonica Z. Kvaček & Walther in having fewer secondary veins (comp. Kvaček & Walther 1991). Rather similar to that of Fagus silesiaca is Fagus menzelii Z. Kvaček & Walther (Kvaček & Walther 1991). The present author confirms his earlier opinion (Worobiec 2003) that there are no significant taxonomic differences between Fagus silesiaca and F. menzelii and both morphotypes most probably represent one taxon. As the description of Fagus silesiaca is earlier, the name of Fagus silesiaca has been given preference, in accordance with the International Code of Botanical Nomenclature. Discussed leaves of Fagus silesiaca Walther & Zastawniak differ from Neogene Iceland species F. friedrichii Grímsson & Denk having less number of secondary veins and form F. gussonii Massalongo in generally smaller leaves (Grímsson & Denk 2005).

Modern equivalents. The macromorphology and micromorphology of leaves of *Fagus silesiaca* is comparable to that of the recent *Fagus hayatae* Palibin ex Hayata that grows in the Mixed Mesophytic Forests of central China (Dyjor et al. 1992). *Fagus grandiflora* Ehrh. (= *Fagus ferruginea* Ait.) from the eastern USA is morphologically very similar to *Fagus silesiaca*, but differs in having anomocytic stomata (Kvaček & Walther 1991).

Ecology. Arctotertiary, warm temperate element. According to Kvaček and Walther (1991) it grew in mixed mesophytic or deciduous forests.

Occurrence. *Fagus silesiaca* is frequently found from the Late Miocene to the Early Pliocene of Central Europe (Walther 1994) and was usually reported under the incorrect names *Fagus attenuata* Goeppert and *Fagus haidingeri* Kováts sensu Knobloch. In the territory of Poland found from Middle Miocene to Pliocene (see Worobiec 2003).

Quercus L.

Quercus pseudocastanea Goeppert emend. Walther & Zastawniak

Pl. 3, figs 2a-2b

1991 Quercus pseudocastanea Goeppert emend. Walther & Zastawniak, p. 169, Fig. 8, pl. 2, figs 2-6, pl. 3, figs 1-6.

Material. KRAM-P 250: 14/II, 28/I, 39/I, 51/II, 77/II, 94/II, 136/II, 154/I.

Description. Macromorphology. Usually small fragments of leaves (up to 5 cm). Leaf margin lobate, lobes 0.8 cm high and up to 1.2 cm in diameter in basal part, apical and basal sides of lobes convex, lobes apex always acute. Secondary veins terminate at the lobes apex. Venation pinnate, secondary venation on preserved fragments simple craspedodromous. Secondary veins diverge from the main vein at an angle of about 50° at intervals of 0.9–1.0 cm. Tertiary venation percurrent and forms an angle of about 135° with the primary vein.

Remarks. The shape of the leaf fragments and the marginal lobes with always acute apex are characteristic of the species *Quercus pseudocastanea* Goeppert emend. Walther & Zastawniak. *Quercus gigas* Goeppert emend. Walther & Zastawniak differs markedly by having serrate margin with spinose teeth apex.

Modern equivalents. With respect to the macro- and micromorphology *Quercus pseudocastanea* resembles recent oaks from section *Cerris* Oersted (Walther & Zastawniak 1991).

Ecology. Arctotertiary, warm temperate element. Most probably component of mesophytic forests (Belz & Mosbrugger 1994).

Occurrence. *Quercus pseudocastanea* is common in the tertiary of Europe. It is found from the Middle Miocene to the Upper Pliocene. In the territory of Poland found from the Middle Miocene to Pliocene (see Walther & Zastawniak 1991).

Quercus roburoides Gaudin

Pl. 3, figs 1a–1b

1859 Quercus roburoides Gaudin; Gaudin & Strozzi, p. 44, pl. 3, fig. 14.

Material. KRAM-P 250: 1/I, 9/I, 12/I, 20/I and 21/I (counterparts), 36/II, 63/I, 101/III, 105/II, 112/III, 122/I, 127/I, 135/I, 141/II, 150/IV.

Description. Macromorphology. Fragments of leaves up to 8.0 cm long and presumably 8.0 cm wide, leaf base rounded. Leaf margin lobate, lobes 0.3 to 1.3 cm high and 0.8 to 2.0 cm in diameter in basal part, apical and basal sides of lobes convex, lobes apex always rounded, often retuse (with apical cleft). Secondary veins terminate at the lobes apex. Venation pinnate, secondary venation on preserved fragments simple craspedodromous. Secondary veins more or less straight, irregularly spaced at intervals of 0.5-2.0 cm, diverge from the main vein at an angle of 30-60°, the angle of divergence of the secondary veins considerably decrease from base (60°) to apex (30°). Tertiary venation percurrent, on one specimen about 7 tertiary veins occur per 1 cm of secondary vein length.

Micromorphology. On the unsuccessful cuticular slide there are only visible scattered stomata, $17-25 \ \mu m$ across with T-shaped thickenings at the stomatal poles.

Remarks. These leaves are similar to leaves of the fossil oak Quercus pseudocastanea Goeppert emend. Walther & Zastawniak. However, some differences in macromorphology between them could be found. Leaves of Quercus pseudocastanea from the same locality are rather regular in shape and always have lobes with acute apex. The discussed leaves are usually of less regular shape and always have lobes with rounded, often even retuse apex. This last feature concerning lobes is according to Belz and Mosbrugger (1994) typical for Quercus roburoides Gaudin. Detailed description and comparison of macro- and micromorphology of leaves of both Quercus pseudocastanea and Quercus roburoides was made by Van der Burgh (1993). In his opinion Quercus pseudocastanea has regular shape, numerous secondary veins with almost absent intersecondaries and smaller lobes contrary to *Quercus roburoides* which leaves are more irregular in shape and less number of lobes. Van der Burgh (op. cit.) has

not found any differences in the micromorphology of cuticles between these two discussed species.

Modern equivalents. In the respect of macromorphology, recent oaks *Quercus petraea* (Matt.) Liebl. and *Quercus canariensis* Willd., members of the section *Robur* are most similar to *Quercus roburoides* (Belz & Mosbrugger 1994).

Ecology. Arctotertiary, temperate element. Most probably component of mesophytic forests (Belz & Mosbrugger 1994).

Occurrence. Taxon new for the fossil floras of Poland. Leaves reported as *Quercus pseudorobur* Kovats (should be treated as a synonym of *Quercus roburoides*) from the Middle Miocene (Sarmatian) locality of Młyny (Zastawniak 1980) belong to species *Quercus pseudocastanea* (Walther & Zastawniak 1991). *Quercus roburoides* is a typical species of the late Neogene floras of Europe, found in the Pliocene deposits (Van der Burgh 1993, Walther 1994).

Quercus sp.

Material. KRAM-P 250: 128/I, 153/II, 113/III.

Remarks. Leaves macromorphologically similar both to *Quercus pseudocastanea* Goeppert emend. Walther & Zastawniak and *Quercus roburoides* Gaudin, but too poorly preserved for unambiguous identification.

Juglandaceae DC. ex Perleb, nom. cons.

Pterocarya Kunth.

Pterocarya paradisiaca (Unger) Ilinskaya

Fig. 4: 3, Pl. 3, figs 6a–6b, Pl. 6, figs 6a–6b

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

Material. KRAM-P 250: 147/I. cf. *Pterocarya* paradisiaca: 54/II, 149/II.

Description. Macromorphology. Oblongate leaflet, 3.8 cm long and 1.3 cm wide. Leaflet margin simple serrate, apical side of teeth concave, basal side convex, straight, teeth apex acute. Branches of secondary veins terminate at the teeth apex. Venation pinnate, primary vein straight, and of moderate thickness. Secondary venation semicraspedodromous. Secondary veins, preserved in up to 7 pairs, depart the primary vein at intervals of 0.35–0.55 cm and form an angle of 60–90° with the primary vein. Secondary veins are upwardly curved and interconnected in loops. Intersecondary veins rarely present. Tertiary venation weakly percurrent or composite intersecondary.

Micromorphology. Abaxial epidermis consists of irregularly-shaped cells with rounded to slightly undulate cell walls, 25–37 μ m across. Stomata probably anomocytic, wide elliptic, about 20 μ m across. Outer stomatal ledge aperture spindle-shaped, about 12 μ m long and 7 μ m wide. On the abaxial epidermis glandular, peltate trichomes (scales), 100–125 μ m in diameter were found. These trichomes have unicellular, elliptic bases, 12–17 μ m in diameter. Also one unicellular, globose trichome with unicellular base was found.

Remarks. The venation pattern of leaflets and characteristic peltate trichomes with unicellular bases point to species *Pterocarya paradisiaca* (Unger) Ilinskaya. *Carya serrifolia* (Goeppert) Kräusel differs in branched secondary veins having craspedodromous endings (comp. Hummel 1983, Manchester 1987). Two other leaflets (250/54/II and 250/149/II) only presumably belong to *Pterocarya paradisiaca* as they are badly preserved.

Modern equivalents. *Pterocarya paradisiaca* is similar to the contemporary *P. fraxinifolia* Spach (Ilinskaya 1968, Knobloch 1969), distributed in the Euxine-Hyrcanian area where it grows along river and stream valleys in riparian forests (Boratyński & Boratyńska 1975, Akhani & Salimian 2003).

Ecology. Arctotertiary, warm temperate element. *Pterocarya paradisiaca* is a frequent component of riparian communities in the Palaeogene and Neogene of Eurasia.

Occurrence. Common in azonal vegetation of Neogene of Europe, known from the Late Oligocene to the Late Pliocene (Zastawniak et al. 1996). In the territory of Poland found from the Early Miocene to Pliocene (see Worobiec et al. 2008). Lythraceae Jaume Saint-Hilaire, nom. cons.

Trapa L.

Trapa sp. Pl. 3, fig. 5

Material. KRAM-P 250: 68/II.

Description. Only one small, characteristic fragment of fruit from *Trapa* – barbed spine (also named harpoon) was preserved.

Remarks. *Trapa* is an arctotertiary, warm temperate element, a typical water plant. Fruits of several taxa of *Trapa* are common in the Neogene floras of Europe (Wójcicki & Zastawniak 2003).

Malvaceae Jussieu, nom. cons. sensu lato

? Helicteroideae Griseb.

Laria G. Worobiec & Kvaček

Laria rueminiana (Heer) G. Worobiec & Kvaček

Fig. 4: 1, 4–5, Pl. 3., figs 3a–4, Pl. 7, figs 1a–4

- 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 250: 7/II, 49/I and 50/I (counterparts), 54/III, 79/I, 80/I, 82/II, 94/I, 96/I, 150/I. cf. *Laria rueminiana*: 51/I.

Description. Macromorphology. Only leaf fragments, up to 6.0 cm long and up to 5.7 cm wide. Leaves entire-margined, leaf base truncate to cordate. Petioles elongated, often with well developed pulvinus. Venation palmate: actinodromous, basal. Primary vein branched into 5 (usually) or 6 (rarely) branches. Secondary venation brochidodromous. Tertiary venation percurrent. About 5 tertiary veins occur per 1 cm of secondary vein or branches of primary vein. Higher-order venation more or less orthogonal reticulate. Areoles well developed, about 0.3 mm across. Veinlets absent or simple. Marginal ultimate venation looped.

Micromorphology. Adaxial epidermis composed of isodiametric or slightly elongated

cells, (20) 25-45 (50) µm across. Cell walls in some leaves mostly straight or rounded, in others undulate. Cuticle of adaxial epidermis in some leaves with distinct ornamentation in form of striae while in other leaves without ornamentation. Abaxial epidermis composed of cells 25-42 µm across, anticlinal cell walls usually almost invisible, rounded or straight. Leaves hypostomatic. Stomata probably anomocytic, elliptic and of variable size, 15-32 µm in diameter, cell walls of guard cells mostly invisible. Some stomata are surrounded by cuticular striations perpendicular to the stomatal pore. Outer stomatal ledge aperture usually spindle-shaped, rarely narrow elliptic, and of very variable size, 11–22 µm long and 4–10 µm wide. On the abaxial epidermis two types of trichomes were found. Most numerous were glandular, clavate-like trichomes, composed of about 4 cells (usually fragmentarily preserved), up to about 52 µm long and 12-20 µm wide with unicellular base, 12-17 (usually 15) μm in diameter. There was also found one, simple, ensiform, unicellular trichome, 57 µm long.

Remarks. The leaves under discussion, both macro- and micromorphologically correspond to the leaf morphotaxon *Laria rueminiana* (Heer) G. Worobiec & Kvaček that was described as a new combination on the basis of material from the Polish Neogene localities of Bełchatów Lignite Mine and Ruja near Legnica (Worobiec et al. 2010).

Modern equivalents. Fossil Laria rue*miniana* could be compared with many extant members of Malvaceae s.l. (Worobiec et al. 2010). However, results of investigations on fossil fruits of Reevesia hurnikii Kvaček and associated plant organs (leaves of "Ficus" truncata = Laria rueminiana and winged seeds of Saportaspermum sp.) found in the Early Miocene flora from the Most Basin in North Bohemia, Czech Republic (Kvaček 2006) suggest close relationship between Reevesia and Laria rueminiana. Micromorphologically most of extant Reevesia species differ from Laria rueminiana in dominance of brachyparacytic stomatal complex and in low variability of stomatal size (Worobiec et al. 2010).

E cology. Palaeotropical, subtropical element. Extant *Reevesia*, which is considered to be a relative to *Laria rueminiana*, exists over an area of paratropical to subtropical evergreen

forests of the eastern Himalavas and southeastern Asia (Kvaček 2006). In the earlier investigation of Bełchatów Lignite Mine and Ruja lignite deposit, Laria rueminiana was found within hygrophilous, mainly swampy and riparian vegetation (Worobiec 2003, Worobiec et al. 2008). However, the assemblage under discussion from Belchatów points to be riparian and mesophytic similarly as vegetation of the North Bohemian Basin locality Čermníky where numerous leaves of Laria rueminiana were found (Bůžek 1971). Besides, in the Bílina Mine (Czech Republic) leaves of Laria ruemi*niana* were found in assemblages representing vegetation of drier riparian forests on fertile alluvial soils (Parrotia-Ulmus association of Kvaček & Boulter in Boulter et al. 1993). Therefore it can be concluded that Laria rueminiana should be considered as a component of mesophytic to riparian vegetation.

Occurrence. Rare element of the Neogene floras of Europe, in the territory of Poland infrequently found in Middle to Late Miocene assemblages (Worobiec et al. 2010).

Helicteroideae Griseb.

Reevesia Lindl.

Reevesia hurnikii Kvaček

Pl. 4, figs 2a-2b

2006 *Reevesia hurnikii* Kvaček, pp. 434–436, 439–440, Figs. 1–8.

Material. KRAM-P 250: 77/I.

Description. Coalified detached capsule valve with strongly thickened dorsal edge (see Kvaček 2006), 2.5 cm long and 1.0 cm high.

Remarks. The detached capsule valve is identical with impressions described under the name of *Reevesia hurnikii* Kvaček by Kvaček (2006) from the Bilina Mine. Kvaček (op. cit.) suggested that fruit valves of *Reevesia hurnikii* judging to the character of impressions should be woody, and it is confirmed in the material from Belchatów. Of a special interest is cooccurrence of leaves of *Laria rueminiana* (Heer) G. Worobiec & Kvaček and fruit valves of *Reevesia hurnikii* Kvaček in the investigated locality from Belchatów. They are accompanied there by relatively numerous pollen grains of genus *Reevesiapollis* Krutzsch (Table 1). Only in the Bílina Mine were found leaves of *Laria ruemi*niana and fruit valves of *Reevesia hurnikii* with rather scarce pollen material. Co-occurrence of pollen grains of *Reevesiapollis* with *Laria rueminiana* and *Reevesia hurnikii* is another evidence in support of the idea that leaves of *Laria rueminiana* belong to a fossil representative of the genus *Reevesia*. Moreover, it is very probable that leaves of *Laria rueminiana*, fruit valves of *Reevesia hurnikii* and pollen grains of *Reevesiapollis* represent organs of the same plant.

Modern equivalents. The fossil valves of *Reevesia hurnikii* correspond in respect of size and shape to those of several extant species of genus *Reevesia*, e.g. *Reevesia pubescens* Mast. or *R. thyrsoidea* Lindl. (Kvaček 2006).

E cology. Palaeotropical, subtropical element. Extant representatives of *Reevesia* exists over an area of paratropical to subtropical evergreen forests of eastern Himalayas and southeastern Asia (Kvaček 2006). Similarly as in case of co-occurring leaf morphospecies *Laria rueminiana*, *Reevesia hurnikii* should be considered as an element of mesophytic to riparian vegetation.

Occurrence. Taxon new for the fossil floras of Poland. Previously found only in the Early Miocene of the Czech Republic (Kvaček 2006).

Salicaceae Mirb.

Populus L.

Populus balsamoides Goeppert

Pl. 4, figs 3-4b, Pl. 7, fig. 5

1855 Populus balsamoides Goeppert, p. 23, pl. 15, figs. 5–6.

Material. KRAM-P 250: 102/I and 112/I (counterparts), 120/I and 126/I (counterparts), 135/III. *Populus* cf. *balsamoides*: 42/I and 43/I (counterparts), 59/I, 101/IV.

Description. Macromorphology. Leaf fragments up to 6.5 cm long, and about 5.0 cm wide. Leaf apex attenuate, base rounded. Margin simple serrate, teeth 2–4 mm long, apical side of teeth very short, concave, basal side long, convex or acuminate, teeth apex rounded. Veins terminate in sinus between teeth. Venation pinnate, primary vein straight and stout. Secondary venation semicraspedodromous, secondaries distributed at intervals of 0.4 cm near leaf base and up to 1.0 cm in the middle of the lamina. Secondary veins upwardly curved diverging from midvein at an angle of $50-60^{\circ}$, branching towards leaf margin forming agrophic (pectinal) veins. Tertiary veins percurrent or composite intersecondary, forms an angle of $90-100^{\circ}$ with the primary vein; ca. 8 tertiary veins occur per 1 cm of secondary vein.

Micromorphology. Adaxial epidermis consisting of polygonal cells with straight walls, 21–30 μ m across. Abaxial epidermal cells 20–35 μ m across, cell wall rounded or straight. Leaves probably hypostomatic. Stomata elliptic to elliptic-elongated, varying in size, 15–25 μ m long and 10–15 μ m wide. Outer stomatal ledge aperture spindle-shaped, ledges strongly cutinised, 15–20 μ m long and 4–9 μ m wide.

Remarks. Macromorphology of the discussed leaves (shape, network of venation, type and shape of teeth) undoubtedly points to the genus *Populus* and the species *Populus balsamoides*. On the shape of teeth this taxon differs markedly from another fossil poplar, *Populus populina* (Brongniart) Knobloch.

Modern equivalents. Extant leaves of Populus balsamifera L. are morphologically comparable to P. balsamoides. Populus balsamifera is North American member of the section Tacamahaca Spach, component of riparian forests (Hantke 1954, Krüssmann 1976, Belz & Mosbrugger 1994). Poplars from the section Tacamahaca are indigenous to Eastern Asia and North America (Teodoridis et al. 2009). Contrary to this opinion, some of authors compare Populus balsamoides with recent Chinese Populus lasiocarpa Oliv. from section Leucoides Spach. (Ilinskaya 1968, Zastawniak 1972).

Ecology. Arctotertiary, temperate element. Woody species of azonal vegetation of riparian forests (Belz & Mosbrugger 1994).

Occurrence. Common in the Neogene floras of Europe. In Poland it is found from the Middle Miocene to Pliocene (Zastawniak 1972, Stuchlik et al. 1990, Krajewska 1998).

Populus populina (Brongniart) Knobloch

Fig. 4: 7, Pl. 4, figs 7a–7b

1822 Phyllites populina Brongniart, p. 237, pl. 14, fig. 4.

- 1836 Populus latior A. Br.; A. Braun in Buckland, p. 512.
- 1964 Populus populina (Brongniart) Knobloch, p. 601.

Material. KRAM-P 250: 118/I.

Description. Macromorphology. Fragment of a single leaf, 5.5×5.3 cm. Leaf margin simple serrate. Apical side of teeth concave, very rarely straight, basal side convex, very rarely straight, teeth apex acute, sometimes attenuate. Venation pinnate, primary vein bent and of moderate thickness. Secondary venation craspedodromous, secondaries run off primary vein at intervals of 1.2-1.5 cm, diverging from midvein at an angle of $30-50^{\circ}$. Secondaries curved upwards, strongly branched, intersecondary veins present. Tertiary venation weakly percurrent, irregular. Higherorder venation random reticulate.

Remarks. Leaf margin with straight or hookshaped teeth with acute apex are characteristic of fossil poplar *Populus populina* (Brongniart) Knobloch.

Modern equivalents. In the respect of macromorphological and micromorphological features to the *Populus populina* are related two extant poplar species, *Populus alba* L. and *Populus tremula* L. from the section *Leuce* Duby (Knobloch & Kvaček 1976).

Ecology. Arctotertiary, temperate element. Component of bottomland vegetation of riparian forests (Belz & Mosbrugger 1994).

Occurrence. Neogene floras of Europe. In Poland it occurs from the Middle Miocene to the Pliocene (see Worobiec et al. 2008).

Populus sp.

Pl. 4, fig. 5

Material. KRAM-P 250: 13/IV, 25/I, 55/I, 69/II, 71/I, 123/I and 124/I (counterparts), 129/III, 139/II, 145/I and 146/I (counterparts), 157/I, 159/I.

Description. Macromorphology. Fragments of sometimes rather large leaves (preserved remains measure up to 8.0 cm). Leaf apex attenuate, base rounded. Leaf margin simple serrate. Apical side of teeth concave, basal side more or less acuminate, teeth apex rounded, hook-shaped. Venation pinnate. Secondary venation craspedodromous, secondary veins diverging from midvein at an angle of 90–100°, secondaries strongly curved upwards. Intersecondary veins present.

Micromorphology. Two very poor cuticular slides from specimens 250/71 and 250/123 were obtained. Walls of cells of adaxial epidermis straight. Stomata elliptic. Outer stomatal ledge aperture spindle-shaped, 12–19 μ m long and 4–9 μ m wide. There were also found (specimen 250/71) numerous unicellular trichome bases on the small fragments of the cuticle from unspecified laminar side.

Remarks. The fossil leaf fragments clearly belong to the genus *Populus*, but are too poorly preserved to be assigned to a particular species. Cuticles features observed are very similar to those of *Populus balsamoides* from the same locality.

Salix L.

Salix varians Goeppert sensu lato

Fig. 4: 6, Pl. 7, fig. 6, Pl. 8, fig. 1

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

Material. KRAM-P 250: 150/II.

Description. Macromorphology. Fragment of single, elongated leaf, 3.5 cm long, ca 1.0 cm wide. Leaf apex probably attenuate. Leaf margin simple serrate, teeth rather small, 1.0-1.5 mm long. Apical side of teeth concave, basal side convex. Teeth apex acute, hook-shaped. Secondary vein branches terminate in sinuses between teeth. Venation pinnate, primary vein straight, of moderate thickness. Secondary venation semicraspedodromous, secondaries distributed at intervals of 0.6–0.7 cm, diverging from midvein at an angle of ca 45°, Secondaries curving upwards, running almost parallel to the leaf margin. Intersecondary veins present. Tertiary veins composite intersecondary or percurrent, forming angle of about 100° with primary vein, 10-15 tertiary veins occur per 1 cm.

Micromorphology. Cells of abaxial epidermis with straight, rounded, or occasionally undulate walls. Cuticle of abaxial epidermis is covered by epicuticular wax of characteristic micromorphology. Stomata brachyparacytic, narrow elliptic and varying in size, 15–22 μ m long and 7–15 μ m wide. Outer stomatal ledge aperture narrow spindle-shaped, strongly cutinized, varying in size, 12–19 μ m long and $2.5{-}9.0~\mu m$ wide. On the abaxial epidermis, unicellular trichome bases, roundish, 10–15 μm in diameter were found.

Remarks. The macro- and micromorphology of these leaves allowed their identification as *Salix varians* Goeppert. The leaves of *S. varians* show significant morphological variability (Krajewska 1998) and it is possible that this morphospecies includes leaves from more than a single biological species.

Modern equivalents. *Salix varians* is usually compared with the extant Eurasian species of *S. fragilis* L. and *S. triandra* L. (Bůžek 1971, Krajewska 1998).

Ecology. Arctotertiary, temperate element. Salix varians was typical species of azonal vegetation of riparian forests (Belz & Mosbrugger 1994).

Occurrence. Common species in the Palaeogene and Neogene floras of Europe, found from the Oligocene to the Pliocene (Krajewska 1998). In the territory of Poland found in the Middle and Late Miocene floras (see Worobiec & Kasiński 2009).

Salix sp.

Fig. 4: 2, Pl. 5, fig. 1

Material. KRAM-P 250: 93/I.

Description. Macromorphology. Small fragment $(2.5 \times 2.2 \text{ cm})$ of elongated leaf. Leaf margin serrate, teeth hook-shaped. Venation pinnate, secondary venation semicraspedodromous, secondaries curving upward. Tertiary venation composite intersecondary, forming angle of about 100–110° with primary vein.

Remarks. Leaf fragment with margin serration and venation network (especially tertiary venation) typical for willow. The poor state of preservation precludes an unequivocal assignment to any fossil species.

Sapindaceae Jussieu, nom. cons.

Acer L.

Acer aegopodifolium (Goeppert) Baikovskaya ex Ilinskaya

Fig. 5: 1, 3, Pl. 5, figs 3–4b, Pl. 8, figs 2–3b

1855 Rhus quercifolia Goeppert, p. 37, pl. 25, figs 6–9.

- 1855 Rhus aegopodifolia Goeppert, p. 37, pl. 25, fig. 10.
- 1959 Monopleurophyllum hungaricum Andreánszky,
 p. 168, pl. 48, fig. 6, pl. 50, fig. 2, pl. 52, fig. 7,
 pl. 53, figs 3–4.
- 1963 Monopleurophyllum quercifolium (Goeppert) Kotlaba, p. 63, pl. 5, figs 4, 5.
- 1965 Acer aegopodifolium (Goeppert) Baikovskaya; Shvareva, p. 953.
- 1968 Acer aegopodifolium (Goeppert) Baikovskaya; Ilinskaya, p. 67, pl. 9, figs 12–15, pl. 20, figs 4, 5.
- 1974 Acer aegopodifolium (Goeppert) Baikovskaya ex Ilinskaya; Zhilin, pp. 56, 30.
- 1988 Acer quercifolium (Goeppert) Kovar-Eder, pp. 51–52, pl. 6, figs 14–16.

Material. KRAM-P 250: 3/I and 4/I (counterparts), 8/II, 22/III, 44/I, 47/I and 49/II (counterparts), 113/II, 120/II. cf. *Acer aegopodifolium*: 12/II.

Description. Macromorphology. Several leaflets of compound leaf, often preserved in original position. Leaflets strongly asymmetric, 2.8-4.0 (4.5) cm long and 2.0-2.5 cm wide, apex acute to rounded, leaf base acute or obtuse. Leaflet margin simple serrate and lobed, teeth rather rare, usually one distinct lobe visible just above leaflet base, apical and basal side of teeth and lobes rounded, apex also rounded. Venation pinnate, midvein straight. Secondary venation mixed craspedodromous, secondary veins irregularly spaced and in the terminal parts characteristically minute bend, strongest branch entering the lobe, some secondaries terminate in teeth and lobe apex, the remaining interconnected in loops. Intersecondary veins present, indistinct. Tertiary and higher order venation more or less random reticulate. Areoles well developed, veinlets present, probably branched. Marginal ultimate venation looped.

Micromorphology. Adaxial epidermis composed of isodiametric or elongated cells, with usually undulate, rarely straight or rounded walls, 32–62 μ m across. There are leaflets both with strie ornamentation and without ornamentation of cuticle. Abaxial epidermis composed of isodiametric or elongate cells, with straight or rounded cell walls, 17–27 μ m across. Leaflets hypostomatic. Stomata anomocytic, wide elliptic, 20–25 μ m long and 17–22 μ m wide. Outer stomatal ledge aperture from wide spindle-shaped to elliptic oblongate, 15–17 μ m long and 6–8 μ m wide.

Remarks. The discussed remains represent



Fig. 5. 1, 3 – Acer aegopodifolium (Goeppert) Baikovskaya ex Ilinskaya: 1 – specimen KRAM-P 250/113/II, 3 – specimen KRAM-P 250/120/II; 2 – Ulmus pyramidalis Goeppert: specimen KRAM-P 250/33/I; 4–5 – Ulmus cf. plurinervia Unger: 4 – specimen KRAM-P 250/88/I, 5 – specimen KRAM-P 250/88/I. Scale bar – 1 cm

leaflets of compound leaf of the fossil species Acer aegopodifolium (Goeppert) Baikovskaya ex Ilinskaya. Baikovskaya (in Shvareva 1965) was the first to identify discussed fossil leaf morphotype as Acer. This opinion was confirmed by Ilinskaya (1968). Of the two Goeppert's species names ("quercifolia" and "aegopodifolia"), name "aegopodifolium" was used to to avoid confusion with the species Rulac quercifolium Hollick (Ilinskava 1968, Walther & Zastawniak 2005), described from the Upper Cretaceous deposits of Alaska (Hollick 1930). For the same morphotype of leaf remains as from Belchatów, Kovar-Eder (1988) proposed a new combination, Acer quercifolium (Goeppert) Kovar-Eder. However, name Acer aegopodifolium (Goeppert) Baikovskaya ex Ilinskaya has priority and Acer quercifolium (Goeppert) Kovar-Eder should be treated as synonym. Schmitt and Kvaček (1999) were the first who published data on the micromorphology of the fossil epidermis of the Acer aegopodifolium from the Late Miocene deposits of Hambach. Epidermal features of leaflets from Belchatów are much the same. The only found difference is strie ornamentation of the cuticle of leaflets of Acer aegopodifolium from Belchatów, yet it is found only in part of leaflets.

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

E cology. Arctotertiary, warm temperate element. Considered to be an accessory species in azonal forest communities (Walther & Zastawniak 2005).

Occurrence. Acer aegopodifolium is known from the Middle and Upper Miocene of central and eastern Europe (Walther & Zastawniak 2005). From the territory of Poland it is known from Middle Miocene (Młyny, as Monopleurophyllum quercifolium (Goeppert) Kotlaba in Zastawniak 1980) and Late Miocene (Sośnica, as Rhus quercifolia Goeppert, R. aegopodifolia Goeppert in Goeppert 1855, and as Acer aegopodifolium in Walther & Zastawniak 2005; Bełchatów as Monopleurophyllum quercifolium (Goeppert) Kotlaba in Stuchlik et al. 1990; Stare Bystre as Acer quercifolium (Goeppert) Kovar-Eder in Worobiec 1994).

Acer cf. tricuspidatum Bronn sensu Procházka & Bůžek

Pl. 5, fig. 2

- ? 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 250: 26/I.

Description. Macromorphology. One badly preserved fragment of lobed and probably entire-margined leaf. Venation palmate, actinodromous. Primary vein branched into 5 branches. Network of tertiary venation typical of genus *Acer*.

Remarks. This leaf most probably represent the species *Acer tricuspidatum* Bronn sensu Procházka & Bůžek which is confirmed on the basis of its morphology.

Modern equivalents. Acer tricuspidatum is classified within section Rubra Pax (Walther 1972, Procházka & Bůžek 1975) and is related to the contemporary species Acer rubrum L. and A. saccharinum L. (Hantke 1954, Kräusel & Weyland 1959). The cuticular micromorphology of extant A. rubrum, A. saccharinum and A. hyrcanum Frisch. & Mey is similar to that of fossil A. tricuspidatum (Walther 1972).

E cology. Arctotertiary, temperate element. Usually considered to be a component of swampy vegetation in the Neogene of Central Europe (Walther 1972). As a riparian element it was reported by Kovar-Eder et al. (2001) in the Miocene flora of Oberdorf.

Occurrence. Acer tricuspidatum is known from Central Europe from the middle Oligocene to the Pliocene, most frequently found in the Miocene floras (Procházka & Bůžek 1975). In the territory of Poland, Acer tricuspidatum was a common element of Neogene plant communities (see Worobiec et al. 2008).

Acer sp.

Pl. 5, figs 5–6

Material. KRAM-P 250: 86/I and 101/II (counterparts).

Description. Macromorphology. Maple samara, 2.8-3.2 cm long and 1.2 cm wide (in

the widest place). The seed impression about 1 cm long.

Remarks. Some morphological similarities could be found with samaras of extant *Acer* griseum (Franchet) Pax, relative of fossil *Acer* aegopodifolium (Goeppert) Baikovskaya ex Ilinskaya, common in the investigated plant assemblage form Belchatów. However, differences found between discussed taxa and scarcity of material (one specimen) excluded reliable assessment to a certain taxon.

Ulmaceae Mirb.

Ulmus L.

Ulmus cf. plurinervia Unger

Fig. 5: 4–5, Pl. 5, fig. 7

? 1847 Ulmus plurinervia Unger, p. 95, pl. 25, figs 1–4.

Material. KRAM-P 250: 88/I and 89/I (counterparts), 92/I.

Description. Macromorphology. Leaf fragments, up to 3.0 cm long and 2.2–2.4 cm wide with obtuse and strongly asymmetric leaf base. Leaf margin serrate, teeth apex moderate acute. Secondary veins terminate in teeth apex. Venation pinnate, primary vein slightly bent, of moderate thickness. Secondary venation simple craspedodromous. Secondary veins, more or less straight, usually opposite, preserved in 10 pairs, run off primary vein at intervals of 0.2–0.3 cm and form an angle of about 60–90° with it.

Remarks. Macromorphology of specimens described above is typical for *Ulmus*, e.g. serrate margins with characteristic teeth and dense secondary venation. Relatively small size of leaves and their shape indicate that they could represent a fossil elm *Ulmus plurinervia* Unger.

Modern equivalents. East Asiatic species *Ulmus parvifolia* Jacq. and *Ulmus pumila* L. are most similar to *Ulmus plurinervia* Unger (Krajewska 1998).

Ecology. Arctotertiary, temperate element. Most probably component of riparian or mesophytic forests.

Occurrence. Taxon not very common in the Neogene of Europe. In the territory of Poland rarely found in the Middle Miocene to Late Miocene floras (see Krajewska 1998).

Ulmus pyramidalis Goeppert

Fig. 5: 2, Pl. 5, figs 8–9b

1855 Ulmus pyramidalis Goeppert, p. 28, pl. 13, figs 10–12.

Material. KRAM-P 250: 14/I, 19/I, 23/I, 33/I, 56/I and 57/I (counterparts), 65/I, 79/II, 123/II, 130/I and 158/I (counterparts). cf. *Ulmus pyra-midalis*: 65/I, 54/IV.

Description. Macromorphology. Only leaf fragments, up to 5.0 cm long and 2.6-3.6 cm wide with cordate, sometimes rounded and asymmetric leaf base. Petiole, rarely preserved, short (about 0.5 cm) and bent. Leaf margin serrate, teeth characteristic hookshaped, apical side of teeth concave, basal side convex or acuminate. Teeth apex acute. Secondary veins or their branches terminate in teeth apex. Venation pinnate, primary vein more or less straight, of moderate thickness. Secondary venation simple craspedodromous. Secondary veins rather numerous, up to 15 pairs, run off primary vein at intervals of 0.10-0.15 cm near leaf base and 0.2–0.7 cm (commonly 0.4–0.6 cm) in the middle part of lamina. Secondaries form with primary vein an angle of about 60-90° near leaf base and $30-60^{\circ}$ in the middle part of lamina. Secondary veins usually straight or, near the leaf margin, slightly curved upward. Tertiary venation percurrent forming angle of 120–140° with primary vein, 7–12 (commonly 10) tertiary veins occur per 1 cm of secondary vein length. Higher order venation orthogonal reticulate.

Remarks. Leaves described above with serrate margins, hook-shaped teeth and dense secondary venation are typical for *Ulmus*. Characteristic features of the above described leaves are rather numerous secondary veins together with elongate shape which are typical for fossil *Ulmus pyramidalis* Goeppert (Hably & Zastawniak 2001).

Modern equivalents. Ulmus pyramidalis is usually compared with the extant North American species Ulmus alata Michx., Ulmus americana L., and Chinese Ulmus castaneifolia Hemsl. (see Krajewska 1988).

Ecology. Arctotertiary, temperate element. Most probably a component of riparian or mesophytic forests. In the Early Miocene (Egerian) floras of Hungary was a dominant element of the riparian vegetation (Hably 1994).

Occurrence. Common in the Neogene European floras (Krajewska 1988). In the territory of Poland rarely reported from Early to Late Miocene floras (Krajewska op. cit.).

Ulmus sp.

Material. KRAM-P 250: 6/I, 13/IV, 22/II, 69/I, 127/III, 135/II and 141/I (counterparts).

Remarks. The characteristic teeth shape, secondary and third order venation of these leaf fragments allow to place them in *Ulmus* L. It is very probable that most of them represent the species *Ulmus pyramidalis* Goeppert, a dominating species of elm in this locality. Nonetheless, the condition of preservation of discussed remains does not allow more precise identification.

DISCUSSION

COMPOSITION OF THE FLORA

As the result of investigation of 159 deposit samples with plant macroremains, 21 species from genera Acer, Betula, Carpinus, Dicotylophyllum, Fagus, Laria, Liquidambar, Populus, Pterocarya, Quercus, Reevesia, Salix, Taxodium, Trapa, and Ulmus were found. Four new fossil leaf species to the Polish tertiary were reported: Quercus roburoides Gaudin, Reevesia hurnikii Kvaček, Dicotylophyllum sp. 1, and Dicotylophyllum sp. 2.

Of special interest is the co-occurrence of morphotaxa from the family Malvaceae s.l. (Tables 1, 2): Laria rueminiana (leaves), Reevesia hurnikii (fruit), and Reevesiapollis (pollen). This finding is important for the whole plant concept (see Sakala 2004 and Kvaček 2008) of fossil Malvaceae s.l. In the Bílina Mine (Czech Republic) leaves of Laria rueminiana were found along with fruits of Reevesia hurnikii, winged seeds of Saportaspermum sp. (Kvaček 2006), and also Reevesiapollis pollen, but the pollen are rather scarce and were only reported from a single sample (Worobiec et al. 2010). In Bełchatow, Laria rueminiana and Reevesia hurnikii occur **Table 1**. Results of palynological analysis (number of palynomorphs) of two samples from plant assemblage KRAM-P 250.Palaeofloristic elements: P2 – subtropical, P – generally palaeotropical, A1 – warm-temperate, A2 – temperate, A – generally
arctotertiary, P/A – cosmopolitan. Palaeofloristic elements according to "Atlas of pollen and spores of the Polish Neogene"
(Stuchlik et al. 2001, 2002, 2009, in press)

Taxon	Botanical affinity	Element	Sam- ple 1	Sam- ple 2
SPORES				
Baculatisporites primarius + Rugulatisporites sp.	Osmundaceae	P/A	2	2
Cryptogrammasporis magnoides (Krutzsch) Skawińska	Pteridaceae: Cryptogramma	A1	1	1
Laevigatosporites spp.	Polypodiaceae, Davalliaceae	P/A	7	2
Leiotriletes sp.	Lygodiaceae	Р	3	1
Retitriletes sp.	Lycopodiaceae: Lycopodium	А		1
other spores	ferns	unknown	1	
GYMNOSPERMS				
Abiespollenites sp.	Pinaceae: Abies	А	1	
Cathayapollis spp.; Pinuspollenites sp.	Pinaceae: Cathaya; Pinus haplohylon type	A1	11	7
Inaperturopollenites spp.	Cupressaceae: Taxodium, Glyptostrobus	P2/A1	19	33
Piceapollis spp.	Pinaceae: Picea	Α	1	5
Pinuspollenites labdacus (Potonié) Raatz	Pinaceae: Pinus; Pinus sylvestris type	А	33	29
Sciadopityspollenites sp.	Sciadopityaceae: Sciadopitys	A1		1
Sequoiapollenites sp.	Cupressaceae: Sequoia, Sequoiadendron, Metasequoia	A1	2	-
Zonalapollenites spp.	Pinaceae: Tsuga	Α	6	4
ANGIOSPERMS				
Aceripollenites striatus (Pflug) Thiele-Pfeiffer	Sapindaceae: Acer	A1	5	8
Alnipollenites verus Potonié	Betulaceae: Alnus	P2/A	23	15
Caprifoliipites sp.	Adoxaceae: Sambucus, Viburnum	P/A1	1	1
Carpinipites carpinoides (Pflug) Nagy	Betulaceae: Carpinus	P2/A1	20	33
Caryapollenites simplex (Potonié) Raatz	Juglandaceae: Carya	A1	4	2
Cupuliferoipollenites oviformis (Potonié) Potonié	Fagaceae: Castanea, Castanopsis, Lithocarpus	P2/A1	2	2
Celtipollenites sp.	Ulmaceae: Celtis	P/A1	4	3
Cyperaceaepollis neogenicus Krutzsch	Cyperaceae	P/A	6	10
Ericipites spp.	Ericaceae	Α	2	3
Faguspollenites sp.	Fagaceae: Fagus	Α	31	62
Graminidites spp.	Poaceae: Pooideae	P/A	. 3	5
Ilexpollenites margaritatus (Potonié) Raatz	Aquifoliaceae: <i>Ilex</i>	P/A1	1	
Intratriporopollenites sp.	Malvaceae: Tilioideae	A1	1	•
Juglanspollenites verus Raatz	Juglandaceae: Juglans	A1	. 1	6
Myricipites sp.	Myricaceae	P2/A1	4	1
Nyssapollenites sp.	Cornaceae: Nyssa	P2/A1		. 3
Oleoidearumpollenites sp.	Oleaceae: ?Fraxinus	A1	3	2
Periporopollenites stigmosus (Potonié) Thomson & Pflug	Altingiaceae: Liquidambar	A1	1	
Polvatriopollenites stellatus (Potonié) Pflug	Juglandaceae: Pterocarva	A1		
Potamogetonacidites sp.	Potamogetonaceae: Potamogeton	P/A	2	2
<i>Quercoidites henrici</i> (Potonié) Potonié, Thomson & Thiergart	Fagaceae: Quercoideae	P/A1	2	•
Quercopollenites sp.	Fagaceae: Quercus	A1	. 21	
Reevesiapollis sp.	Malvaceae: Reevesia	P	2	7
Salixipollenites sp.	Salicaceae: Salix	A2		4
Sparganiaceaepollenites sp.	Sparganiaceae, Typhaceae	P/A	2	. – 1
Tricolporopollenites exactus (Potonié) Grahowska	Cyrillaceae. Clethraceae	P2/A1		
?Tricolporopollenites pseudocingulum (Potonié) Thomson & Pflug	?Styracaceae	P/A1	-	1
Tricolporopollenites sp.	Rosaceae	P/A	•	. 1
	-		-	

Table 1. Continued

Taxon	Botanical affinity	Element	Sam- ple 1	Sam- ple 2
Triporopollenites coryloides Pflug	Betulaceae: Corylus	А		2
Trivestibulopollenites betuloides Pflug	Betulaceae: Betula	Α	52	58
Ulmipollenites sp. + ?Zelkovaepollenites sp.	Ulmaceae: Ulmus, ?Zelkova	A2, A1	26	34
Umbelliferoipollenites sp.	Apiaceae	A2		
Vitispollenites sp.	Vitaceae: Vitis	A1	3	2
VARIA	pollen and spores indet.	unknown	9	11
Sum of sporomorphs			342	406

along with *Reevesiapollis* pollen which are rather abundant (Table 1). This pollen type was also present in one of the cuticular slides of *Laria rueminiana*, occurring in clumps. The co-occurence of the three malvalean morphotaxa in Bełchatów suggests that they might represent vegetative and reproductive organs of a single biological species and undoubtedly confirming the presence of *Reevesia* in the fossil flora from the Late Miocene of Bełchatów Mine.

TAPHONOMY

Plant macroremains were preserved as dispersed in fine-grained deposits. The structure of deposits suggests that the assemblage was formed in water reservoir with stagnant or slow-flowing water, probably oxbow lake of meandering river or abandoned channel of braided river. Presence of shallow, stagnant waters is confirmed by occurrence of Trapa macroremain and pollen grains of *Potamogeton*, plants typical of this environment (Table 1). The rate of sedimentation was especially high during periodical floods. Swelled rivers delivered detritic material that had immediately buried plant remains accumulated on the reservoir bottom and prevented extensive decay or complete decomposition of them. The discussed fossil flora was parautochtonous with considerable admixture of allochtonous taxa (comp. Gastaldo et al. 1996). It is confirmed by the mixture of taxa characteristic of azonal (riparian) and zonal (mesophytic) vegetation. Such a mixture of taxa could indicate that the sedimentary reservoir was situated at floodplain covered by riparian forests near elevated and drier river terraces or levee being typically covered with mesophytic vegetation. The same mixture of vegetation could be inferred from the results of palynological investigations.

PALYNOLOGY OF PLANT ASSEMBLAGE

Both studied samples yielded rich and well-preserved sporomorph assemblages suitable for detailed pollen analysis. The palynoflora is composed of 12 gymnosperm pollen, 36 angiosperm pollen, and 8 spore morpho-taxa (Table 1). The identified sporomorph taxa represent plants that probably occurred in the following plant communities:

Azonal vegetation communities:

Swamp forest (composed mainly of Taxodioideae, including *Taxodium* and *Glyptostrobus*, as well as *Nyssa* and *Alnus*)

Riparian forest (*Pterocarya*, Ulmus, Acer, Juglans, Salix, Alnus, Celtis, Carya, Fraxinus, *Reevesia*, and others)

Reeds and surrounding vegetation (mainly Cyperaceae, Poaceae, and Sparganium)

Aquatic plants (*Potamogeton*)

Zonal vegetation community:

Mesophytic forest (composed mainly of deciduous trees Fagus, Quercus, Carpinus, Betula, Ulmus, Castanea, Juglans, Acer, and coniferous trees Pinus, Cathaya, Tsuga, Picea, and others).

The identified sporomorph taxa have been classified to an appropriate palaeofloristic element (see Table 1), mainly on the basis of Atlas of pollen and spores of the Polish Neogene (Stuchlik et al. 2001, 2002, 2009, in press), and the checklist of selected pollen and spore taxa from the Neogene deposits proposed by Ziembińska-Tworzydło et al. (1994). In the studied material the following palaeofloristic elements have been distinguished: palaeotropical (P), including subtropical (P2); arctotertiary (A), including: warm-temperate (A1) and temperate (A2), as well as cosmopolitan (P/A). The composition of sporomorph associations from the studied samples shows an apparent dominance of arctotertiary (including warmtemperate and temperate) and cosmopolitan palaeofloristic elements (Table 1). Palaeotropical elements are represented by a few taxa only (mainly subtropical), all occurring as rare specimens. A few spores of *Leiotriletes* sp. and pollen grains of *Cupuliferoipollenites* oviformis, Ilexpollenites margaritatus, Reevesiapollis sp., Tricolporopollenites exactus, as well as probably Quercoidites henrici and Tricolporopollenites pseudocingulum, have been encountered.

CHARACTERISTICS OF PALEOVEGETATION

On the basis of investigations on plant macroremains and palynological analyses, reconstruction of the local vegetation of the discussed Late Miocene locality from Bełchatów Lignite Mine has been performed. The area surrounding the sedimentary reservoir in which formed the fossil assemblage was covered by riparian (azonal) and mesophytic (zonal) forests.

Riparian vegetation was composed of Acer cf. tricuspidatum, Laria rueminiana, Liquidambar europaea, Populus balsamoides, Populus populina, Populus sp., Pterocarya paradisiaca, Reevesia hurnikii, Salix sp., and Salix varians sensu lato. Palynological analysis supplemented the list of riparian taxa of discussed assemblage with genera Alnus, Carya, Fraxinus, Sequoia, and Vitis. Riparian forests of this type occurred in the European tertiary from the middle Palaeocene to the end of Pliocene (Mai 1995). Recent equivalents to the Late Miocene riparian vegetation from Belchatów exist in south-eastern North America (Knapp 1965, Barnes 1991) as well as in the Euxine-Hyrcanian area (Anatolia, Colchis, Talysh, southern coast of the Caspian Sea; Tutayuk 1975, Rastin 1983, Akhani et al. 2010) occupying river valleys, river banks within the range of episodic flooding.

Elevated, drier areas in surroundings of fossil assemblage reservoir, placed above the maximum level of periodical flood inundation, were covered by zonal mesophytic forests. Forests of this type were composed of angiosperms such as Acer aegopodifolium, Betula plioplatyptera, Betula sp., Betula subpubescens, Carpinus grandis, Fagus silesiaca, Quercus pseudocastanea, Quercus roburoides,

Ulmus cf. plurinervia, Ulmus pyramidalis, and Ulmus sp. Pollen analysis revealed also presence of gymnosperms (Picea, Pinus, Tsuga, probably also Abies, and Sciadopitys) accompanied by angiosperms not found among macroremains (Castanea, Celtis, Corylus, and Juglans). These Mesophytic forests correspond to deciduous broad-leaved forests (Kovar-Eder 2003) of the Quercus-Carpinus-Castanea association sensu Mai (1995). As their modern analogues could be considered floristically rich mesophytic deciduous forests from the eastern part of North America (Braun 1964, Knapp 1965, Barnes 1991), northern China (Wang 1961), and Euxine-Hyrcanian area (Akhani et al. 2010).

Among macroremains swamp forests taxa are represented only by *Taxodium dubium*. Pollen analysis revealed also scarcity of swamp elements in the fossil assemblage, confirming only the presence of Taxodioideae (*Taxodium*/ *Glyptostrobus*) and *Nyssa*. These trees occurred there as remnants of swamp forests of the *Glyptostrobus-Alnus-Byttneriophyllum* association (Mai 1995) which existed in Europe from the Upper Oligocene to the Pliocene, dominating in the Miocene of the Polish Lowlands area.

Presence of harpoon from a *Trapa* fruit and pollen grains of *Potamogeton* and Sparganiaceae/Typhaceae suggests that the fossil plant assemblage accumulated in a water reservoir surrounded by reed (Sparganiaceae/ Typhaceae) vegetation. The water surface was most likely covered by floating leaves of *Trapa* and *Potamogeton*. The occurrence of *Trapa* and *Potamogeton* suggest stagnant or only slow running water pointing to the existence of an oxbow lake.

RECONSTRUCTION OF PALAEOCLIMATE

Most of the fossil taxa of plant macroremains represent the arctotertiary geofloristic element (Mai 1995). Extant taxa that are closely related to the fossil species are presently thriving under warm temperate climate in the northern hemisphere. Taxa representing palaeotropical element like *Reevesia* are rare both in macroand microremains. Absence of thermophilous taxa such as Lauraceae or palms, the rarity of palaeotropical species, and the dominance of arctotertiary element indicates a warm temperate climate during the accumulation of the fossil plant assemblage.

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The palaeoclimate may have been comparable to contemporary climates of the area of Euxine-Hyrcanian forests. In riparian forests of this region *Pterocarya fraxinifolia* C.A. Mey occurs that is comparable to the fossil Pterocarya paradisiaca (Unger) Ilinskaya from Belchatów. The Euxine-Hyrcanian area has favourable climatic conditions for vegetation, and according to Akhani et al. (2010) it endures high amounts of annual precipitation that is evenly distributed throughout the year (very short or absent dry season). The average minimum temperature for the coldest month is higher than 0°C. According to Tutayuk (1975) the climatic values of this area are as follows: mean annual temperatures around +14°C, mean temperature of the coolest month above 0°C, mean annual precipitation more than 1000 mm.

The palaeoclimate as reconstructed from the fossil assemblage from Belchatów could also be compared to that of south-eastern North America, especially along the Atlantic coastline. For instance, *Acer rubrum* var. *drummondii* (Hook & Arnott) Sarg. occurs in this area and is believed to be closely related to the fossil *Acer tricuspidatum*. The climate of this region is characterised by a mean annual temperature varying between +14 and +19°C, the mean temperature of the coolest month \geq +5°C, and high annual precipitation, up to 1200–1500 mm (Knapp 1965, Barnes 1991).

AGE OF THE PLANT ASSEMBLAGE

From the geological point of view, the discussed fossil assemblage from the Bełchatów Lignite Mine is situated at the lower part of clayey-sandy unit which age is estimated as Late Miocene (see Geology). This is in accordance with results of our palaeobotanical investigations. Early Miocene age is excluded due

Table. 2. Taxa shared between the KRAM-P 250 plant assemblage and selected leaf floras from the Neogene of Poland. (+) – taxon given under another name

	Middle Miocene		Late Miocene			Pliocene		
Taxon	Dobrzyń on Vistula River (Kownas 1956, 1959)	Konin (Raniecka-Bobrowska 1954)	Stawiany, Młyny (Zastawniak 1980)	Bełchatów (Stuchlik et al. 1990, Worobiec & Lesiak 1998, Worobiec 2003, Worobiec & Szynkiewicz 2007, Woro- biec et al. 2010)	Gozdnica (Dyjor et al. 1992)	Stare Bystre (Worobiec 1994)	Domański Wierch (Zastawniak 1972)	Ruszów (Hummel 1983, 1991)
Acer cf. tricuspidatum	(+)		+	+				+
Acer aegopodifolium			(+)	(+)		(+)		
Betula plioplatyptera				+				+
Betula subpubescens	(+)	(+)	+	+	+			+
Carpinus grandis	+			+			+	+
Fagus silesiaca			+	+	+	(+)	(+)	+
Laria rueminiana				+				
Liquidambar europaea			+	+			+	+
Populus balsamoides	+	+		+			+	
Populus populina							(+)	+
Pterocarya paradisiaca			+	+		+	+	
Quercus pseudocastanea				+			+	
Quercus roburoides								
Reevesia hurnikii								
Salix varians	+			+			+	?
Taxodium dubium	+			+	+			+
Trapa sp.		(+)		+				
Ulmus cf. plurinervia								
Ulmus pyramidalis								

to absence of the members of the family Lauraceae and palms (Arecaceae) and scarcity of palaeotropical elements both in macro- and microremains. Floristic composition of the plant assemblage is generally typical of late Neogene floras of Central Europe. Most of the taxa occur from Miocene to Pliocene, but most frequently in Middle and Late Miocene. Morphotaxa of representative of the genus Reevesia (leaves of Laria rueminiana and fruit capsule valve of Reevesia hurnikii) are restricted to Miocene floras of Europe. Acer aegopodifolium found in the discussed locality from Bełchatów, were reported only from deposits older than Pliocene. Quercus roburoides is the only one species typical of Pliocene floras of Europe (van der Burgh 1993). However, rarely it is also found in slightly older deposits, for example of uppermost Miocene to lowermost Pliocene of the Lower Rhine Embayment (Hauptkies Serie, Belz & Mosbrugger 1994). Taking into consideration domination of the warm temperate, deciduous floristic element among plant remains and earlier discussion, we suggest Late Miocene age of plant macroremains.

Moreover, composition of pollen spectra along with low frequency of sporomorphs representing palaeotropical element points to the Late Miocene age of the sediment studied and thereby of the corresponding horizons with plant macroremains. Therefore, the results of palynological investigations definitely confirm the Late Miocene age of this part of clayey-sandy unit of Neogene deposits of the Bełchatów Lignite Mine.

COMPARISON OF THE PLANT ASSEMBLAGE FROM BEŁCHATOW WITH OTHER NEOGENE LEAF FLORAS OF POLAND AND CENTRAL EUROPE

The macroremains assemblage is taxonomically very similar to other late Neogene leaf floras of Poland (Table 2). Most similar floras are earlier described Late Miocene fossil plant assemblages from the Bełchatów Lignite Mine (Stuchlik et al. 1990, Worobiec & Lesiak 1998, Worobiec 2003, Worobiec & Szynkiewicz 2007, Worobiec et al. 2010). Pliocene floras from

	Middle	Miocene	Middle Miocene/ Late Miocene	Late Miocene	Pliocene
Taxon	Kreuzau (Ferguson 1971)	Precarpathians (Shvareva 1983)	Achldorf (Knobloch 1986)	Molassezone of Austria (Kovar-Eder 1988)	Willershausen (Knobloch 1998)
Acer cf. tricuspidatum		(+)	+	+	
Acer aegopodifolium		+			
Betula plioplatyptera					
Betula subpubescens		+	+	+	+
Carpinus grandis		+	+	+	+
Fagus silesiaca		(+)		(+)	
Laria rueminiana	?		(+)		
Liquidambar europaea	+	+	+	+	+
Populus balsamoides	+	+			
Populus populina	+	(+)		+	?
Pterocarya paradisiaca	?			+	
Quercus pseudocastanea		+	+	+	
Quercus roburoides					+
Reevesia hurnikii					
Salix varians	+				
Taxodium dubium	+		+		
Trapa sp.				?	
Ulmus cf. plurinervia					
Ulmus pyramidalis		+	+		

Table. 3. Taxa shared between the KRAM-P 250 plant assemblage and selected leaf floras from the Neogene of Central Europe. (+) – taxon given under another name

ans, Picea, Pint

Ruszów (Hummel 1983, 1991) and Domański Wierch (Zastawniak 1972) share many taxa with the Bełchatów flora (Table 2). Other localities have less taxa in common (Table 2), but it is usually due to low taxonomical diversity and different sedimentary environments as the other assemblages are mostly derived from swampy communities.

Macrofossil plant assemblages similar to the KRAM-P 250 from Bełchatów have been reported from numerous localities outside Poland (cf. Mai 1995). The taxonomic composition of the Bełchatów assemblage compares well with Middle/Late Miocene leaf floras of central and western Europe (Table 3), e.g. Precarpathians (Shvareva 1983), Achldorf (Knobloch 1986), and Molassezone of Austria (Kovar-Eder 1988). It compares much less with older floras (Table 3), e.g. Kreuzau (Ferguson 1971) and younger floras, e.g. Willershausen (Knobloch 1998).

CONCLUSIONS

- As the result of investigation of 159 rock samples with plant macroremains, 21 species, representing 15 genera, belonging to 10 families of gymnosperms and angiosperms have been identified.

- Four new fossil species are reported for the tertiary of Poland: *Quercus roburoides* Gaudin, *Reevesia hurnikii* Kvaček, *Dicotylophyllum* sp. 1, and *Dicotylophyllum* sp. 2.

- Palynological analysis show a mixture of taxa representing riparian (azonal) vegetation and zonal mesophytic forests. Sporomorphs representing azonal swamp forest vegetation are relatively rare. Taxa belonging to arctotertiary, warm temperate element prevail in the pollen spectra. Palaeotropical element is very rare.

- Local vegetation surrounding the sedimentary reservoir was dominated by riparian (azonal) and mesophytic (zonal) forests. Riparian forests were composed of Acer, Laria, Liquidambar, Populus, Pterocarya, Reevesia, Salix, and representatives of genera Alnus, Carya, Fraxinus, Sequoia, and Vitis as indicated by pollen analysis. Zonal vegetation of mesophytic forests from drier areas in the vicinity were composed of angiosperms such as Acer, Betula, Carpinus, Fagus, Quercus, Ulmus, as well as representatives of genera Castanea, Celtis, Corylus, Juglans, Picea, Pinus, and Tsuga, probably also Abies and Sciadopitys as revealed by palynological analysis. Swamp forests taxa were represented only by shoots of Taxodium and pollen grains of Nyssa and Taxodioideae, remnants of Glyptostrobus-Alnus-Byttneriophyllum association (Mai 1995). Macroremain of Trapa and pollen grains of Potamogeton and Sparganiaceae/Typhaceae suggest existence of a water reservoir with stagnant or only very slowly moving water.

- Fossil plant taxa found (both macro- and microremains) represent mainly warm temperate and temperate arctotertiary element and indicate warm temperate climate during the period of formation of plant assemblage. Palaeoclimatic condition could be similar to the contemporary climate of the area of Euxine-Hyrcanian forests and/or south-eastern part of North America.

- The stratigraphical position of the assemblage KRAM-P 250 in the profile of Neogene deposits of the Belchatów Lignite Mine and its floristic composition point to the Late Miocene age.

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PLATES

Plate 1

Liquidambar europaea A. Braun

1. Leaf, specimen No. KRAM-P 250/17/I

2. Detail of leaf margin, specimen No. KRAM-P $250/7/\mathrm{I}$

3. Leaf, specimen No. KRAM-P 250/10/I

Betula plioplatyptera Hummel

4. Detail of leaf margin, specimen No. KRAM-P 250/83/I

6. Leaf, specimen No. KRAM-P 250/13/I

Taxodium dubium (Sternberg) Heer

5. Twig, specimen No. KRAM-P 250/31/I

Betula subpubescens Goeppert emend. Worobiec

7. Leaf, specimen No. KRAM-P 250/74/I

1–3, 5–7: scale bar – 1 cm; 4: scale bar – 1 mm



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Betula subpubescens Goeppert emend. Worobiec

1. Leaf, specimen No. KRAM-P 250/133/I

Carpinus grandis Unger emend. Heer

2. Leaf, specimen No. KRAM-P 250/113/I/A

4a. Leaf, specimen No. KRAM-P 250/113/I/B

4b. Detail of leaf margin, specimen No. KRAM-P 250/113/I/B

Fagus silesiaca Walther & Zastawniak

3. Leaf, specimen No. KRAM-P 250/131/I

8. Detail of tooth venation, specimen No. KRAM-P 250/16/I

Dicotylophyllum sp. 1

5. Leaf, specimen No. KRAM-P 250/104/I

6. Detail of leaf margin venation, specimen No. KRAM-P 250/107/I

Carpinus grandis Unger sensu Berger

7. Fruit involucre, specimen No. KRAM-P 250/5/II

1, 2, 3, 4a, 5, 7: scale bar – 1 cm; 4b, 6, 8: scale bar – 1 mm



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Quercus roburoides Gaudin

1a. Leaf, specimen No. KRAM-P 250/21/I

1b. Detail of lobe shape and venation, specimen No. KRAM-P 250/21/I

Quercus pseudocastanea Goeppert emend. Walther & Zastawniak

2a. Leaf, specimen No. KRAM-P 250/136/II2b. Detail of lobe shape and venation, specimen No. KRAM-P 250/136/II

Laria rueminiana (Heer) G. Worobiec & Kvaček

3a. Leaf, specimen No. KRAM-P 250/94/I

3b. Detail of leaf base and petiole with pulvinus, specimen No. KRAM-P 250/94/I

3c. Detail of leaf margin venation, specimen No. KRAM-P 250/94/I

4. Leaf, specimen No. KRAM-P 250/50/I

Trapa sp.

5. Barbed spine of fruit, specimen No. KRAM-P 250/68/II

Pterocarya paradisiaca (Unger) Ilinskaya

6a. Leaflet, specimen No. KRAM-P 250/147/I6b. Detail of leaflet margin, specimen No. KRAM-P 250/147/I

1a, 2a, 3a, 3b, 4, 6a: scale bar - 1 cm; 1b, 2b, 5, 6b: scale bar - 1 mm; 3c: scale bar - 200 µm



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Dicotylophyllum sp. 2

1. Leaf, specimen No. KRAM-P 250/48/I

Reevesia hurnikii Kvaček

2a. Detached capsule valve, specimen No. KRAM-P 250/77/I 2b. Detached capsule valve, specimen No. KRAM-P 250/77/I

Populus balsamoides Goeppert

3. Leaf, specimen No. KRAM-P 250/112/I

4a. Leaf, specimen No. KRAM-P 250/102/I

4b. Detail of teeth and leaf margin venation, specimen No. KRAM-P 250/102/I

Populus sp.

5. Leaf, specimen No. KRAM-P 250/145/I

Salix varians Goeppert sensu lato

6a. Leaf, specimen No. KRAM-P 250/150/II6b. Detail of teeth and leaf margin venation, specimen No. KRAM-P 250/150/II

Populus populina (Brongniart) Knobloch

7a. Leaf, specimen No. KRAM-P 250/118/I7b. Detail of teeth and leaf margin venation, specimen No. KRAM-P 250/118/I

1–3, 4b, 5, 6a, 7a: scale bar – 1 cm; 4a, 6b, 7b: scale bar – 1 mm



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Salix sp.

1. Leaf, specimen No. KRAM-P 250/93/I

Acer cf. tricuspidatum Bronn sensu Procházka & Bůžek

2. Leaf, specimen No. KRAM-P 250/26/I

Acer aegopodifolium (Goeppert) Baikovskaya ex Ilinskaya

3. Fragment of compound leaf, specimen No. KRAM-P 250/83/I

4a. Fragment of compound leaf, specimen No. KRAM-P 250/120/II

4b. Detail of lobe venation, specimen No. KRAM-P 250/120/II

Acer sp.

5. Samara, specimen No. KRAM-P 250/86/I

6. Samara, specimen No. KRAM-P 250/101/II

Ulmus cf. plurinervia Unger

7. Leaf, specimen No. KRAM-P 250/88/I

Ulmus pyramidalis Goeppert

8. Leaf, specimen No. KRAM-P 250/56/I

9a. Leaf, specimen No. KRAM-P 250/33/I

9b. Detail of teeth and leaf margin venation, specimen No. KRAM-P 250/33/I

1–4a, 5–9a: scale bar – 1 cm; 4b, 9b: scale bar – 1 mm



Taxodium dubium (Sternberg) Heer

1. Epidermis. Note the oblique arrangement of longer axes of stomata, specimen No. KRAM-P 250/31/I Betula subpubescens Goeppert emend. Worobiec

2. Multicellular base of glandular trichome on abaxial epidermis, specimen No. KRAM-P 250/133/I

Dicotylophyllum sp. 1

3a. Abaxial epidermis with stomata, specimen No. KRAM-P 250/99/I3b. One-celled base of trichomes on abaxial epidermis, specimen No. KRAM-P 250/99/I

Dicotylophyllum sp. 2

4. One-celled base of trichomes on abaxial epidermis, specimen No. KRAM-P 250/152/I

Fagus silesiaca Walther & Zastawniak

5. Abaxial epidermis with stoma, specimen No. KRAM-P 250/126/III

Pterocarya paradisiaca (Unger) Ilinskaya

6a. Peltate glandular trichomes with unicellular base, specimen No. KRAM-P 250/147/I6b. Detail of peltate glandular trichome, specimen No. KRAM-P 250/147/I

6a: scale bar – 100 μm; 1, 4, 6b: scale bar – 50 μm; 2, 3a, 3b, 5: scale bar – 20 μm



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Laria rueminiana (Heer) G. Worobiec & Kvaček

- 1a. Adaxial epidermis, specimen No. KRAM-P 250/80/I
- 1b. Detail of adaxial epidermis, specimen No. KRAM-P 250/80/I
- 1c. Abaxial epidermis with stomata, specimen No. KRAM-P 250/80/I
- 2. Abaxial epidermis with stomata, specimen No. KRAM-P 250/94/I
- 3. Detail of stomata structure and striations, specimen No. KRAM-P 250/79/I
- 4. Four-celled glandular clavate trichome, specimen No. KRAM-P 250/54/III

Populus balsamoides Goeppert

5. Abaxial epidermis with stomata, specimen No. KRAM-P 250/120/I

Salix varians Goeppert sensu lato

6. Abaxial epidermis. Note brachyparacytic stomata and cover of epicuticular wax, specimen No. KRAM-P 250/150/II

1a, 1c, 2, 5, 6: scale bar – 50 μ m; 1b, 3, 4: scale bar – 20 μ m



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Salix varians Goeppert sensu lato

1. Details of brachyparacytic stomata and cover of epicuticular wax, specimen No. KRAM-P 250/150/II

Acer aegopodifolium (Goeppert) Baikovskaya ex Ilinskaya

2. Adaxial epidermis, specimen No. KRAM-P 250/47/I

3a. Details of adaxial epidermis. Note striae ornamentation of cuticle, specimen No. KRAM-P 250/4/I

3b. Abaxial epidermis with stomata, specimen No. KRAM-P $250/4/\mathrm{I}$

2: scale bar – 100 $\mu m;$ 1, 3a, 3b: scale bar – 20 μm

