

Late Neogene leaf assemblage from Bełchatów Lignite Mine (central Poland)

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ABSTRACT. Leaf macroremains collected in the Bełchatów Lignite Mine (central Poland) were investigated. The fossil assemblage consists of leaves of *Acer*, *Betula*, *Carpinus*, *Dicotylophyllum*, *Fagus*, ?*Magnolia*, “*Parrotia*”, *Pinus*, *Quercus*, and *Zelkova*. Mesophytic (zonal) elements dominate, with admixture of riparian (azonal) leaf taxa. The floristic composition points to late Neogene (late Miocene to late Pliocene) age and suggests favourable temperate climate with mild winters.

KEYWORDS: leaf macroremains, macromorphology, cuticular micromorphology, palaeovegetation, palaeoclimate, Neogene, Poland

INTRODUCTION

In the course of geological investigations of overburden in the Bełchatów Lignite Mine in 1997, a fragment of a borehole core of Neogene deposits with plant macroremains was collected. The excellent state of preservation of the plant remains enabled an extensive study of the fossil leaves, aimed at determining the palaeofloristics and palaeoecology of the assemblage in order to document the biodiversity of the Neogene flora and vegetation of this area of central Poland.

GEOLOGY

The Bełchatów Lignite Mine is situated in the southern part of the Central European Lowlands, in central Poland, ca 15 km south of Bełchatów (Fig. 1). In this area, Neogene deposits with lignite seams occur within a series of tectonic depressions named the Kleszczów Graben (Stuchlik et al. 1990). Czarnecki et al. (1992) and Matl (2000) distinguished four main lithological units of the



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

Neogene deposits filling the Kleszczów Graben: the subcoal unit (PW); the coal unit (W) with the main seam (PG), seam B, and seam C; the clayey-coal unit (I-W) with seam A; and the youngest clayey-sandy unit (I-P). The studied leaf assemblage was found in the drill core taken from borehole No. 1326/B from the

Bełchatów Lignite Mine. The sandy silt core sample with fossil leaf litter comes from 18.8–19.0 m depth below sea level and is underlain by silt and mud with leaf compressions. It lies several metres above the main seam (PG). Its stratigraphical position corresponds to the clayey-coal unit (I-W). However, the complicated tectonic structures in this part of the outcrop, with many complex faults, make it difficult to establish the exact geological position of the leaf assemblage and, in turn, its age.

MATERIAL AND METHODS

The leaf assemblage was preserved as an accumulation of compressed leaf litter. To isolate the plant remains, the leaf litter was rinsed in 15% solution of H₂O₂. After a few minutes of maceration the swollen mass of plant remains was transferred to a large container and rinsed in tap water. After washing, the mass of plant remains was searched for determinable plant remains. Isolated leaves were mounted in glycerine jelly; 27 leaf slides were made. Small fragments of isolated leaf compressions were used for cuticular analysis. The laminar fragments were cleaned with hydrofluoric acid, washed in water, macerated using NaClO solution (Bielnar commercial bleach), and finally mounted on slides with glycerine jelly; 24 slides of leaf epidermis were made. All studied fossil specimens are housed in the W. Szafer Institute of Botany, Polish Academy of Sciences (Kraków) under catalogue number KRAM-P 226. Leaf macromorphological descriptions mostly follow Ellis et al. (2009) and cuticular descriptions (micromorphology) follow Dilcher (1974) and Wilkinson (1979). The method of measuring the micromorphological structures depended on the shape of the object. Diameter was measured for regular, round, and broadly elliptic objects; length and width were measured for all roughly rectangular objects. For structures of irregular or variable shape (mainly epidermal cells) the longest dimension was measured. Macrophotographs were taken with a Nikon Coolpix 995 digital camera and a Nikon SMZ 800 stereomicroscope fitted with a Nikon DS-5M-U1 digital camera. Microphotographs were taken with a Nikon Eclipse E400 microscope fitted with a Canon A640 digital camera.

RESULTS

SYSTEMATIC PALAEOBOTANY

The classification of gymnosperms follows Christenhusz et al. (2011). The classification of angiosperms and author names of families follows APG III (2009).

GYMNOSPERMS

Pinaceae Spreng. ex Rudolphini

Pinus L.

Pinus sp.

Pl. 1, figs 1a, b, Pl. 4, figs 1a, b

Material. KRAM-P 226: 19

Description. **Macromorphology.** One fascicle and 3 isolated fragments of needles. Fascicle composed of 2 needles with persistent fascicle sheath 1.0 cm long. Needle fragments up to 5.0 cm long and 1.3–1.6 mm wide. Needle apex acuminate. Needle margins up to 3.5 cm above fascicle base, minutely serrate with small, partly irregularly spaced teeth (if regularly spaced, every 0.3 mm), remaining part of needle entire-margined.

Micromorphology. Epidermal cells rectangular, rather elongate, 80–370 µm long and 15–25 µm wide. Short walls of cells oblique or perpendicular to longer walls of cells. On epidermis, scattered papillae, 40 × 50 µm, parallel to axis of needle. Ca 7 stomatal bands present on every side of needle. All stomatal bands composed of single row of stomata. Longer axes of stomata parallel to midvein. Stomata cyclocytic, elliptic, 52–62 µm long and 42–45 µm wide. Outer stomatal ledge aperture narrow elliptic or spindle-shaped, 17–30 µm long and 5.0–7.5 µm wide. Polar T-shaped cuticular thickenings always visible, strongly developed.

Remarks. Fossil needles identified as undoubtedly belonging to genus *Pinus* L. Pine needles similar both to *Pinus hampeana* (Unger) Heer and to *Pinus laricioides* Menzel, broad-needled fossil taxa of *Pinus* with fascicles composed of two needles. *Pinus* sp. from Bełchatów differs from two-needled fossil-taxon *Pinus hepios* (Unger) Heer having wider needles (usually 1.3–1.5 mm wide as compared with needles up to 1.0 mm wide in *Pinus hepios*, see Kvaček et al. 2014). The occurrence of *Pinus* in the studied plant assemblage from Bełchatów is also confirmed by remains of peeled bark.

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

Bark of *Pinus* sp.

Pl. 1, fig. 2, Pl. 4, fig. 2

1969 *Pinus* – Rindengewebe, Schneider, p. 30, pl. 10, figs 2–4.

2010 *Pinus* morphospec. (bark), Schneider, p. 46, 47, pl. 1, figs 1, 2.

Material. KRAM-P 226: 8

Description. Macromorphology. Two fragments (3 × 2 cm and 3 × 3 cm) of exfoliated bark of conifer.

Micromorphology. Cells isodiametric or slightly elongated, cell walls undulate, sclerenchymatic, rather thick, cells 50–70 µm across.

Remarks. These plant remains represent exfoliated bark of *Pinus*. Similar remains were described as pine bark by, for example, Schneider (1969, 2010) during investigations of *cuticulae dispersae* from Miocene lignite deposits from Germany. Kvaček et al. (2011) mistakenly reported remains of pine bark as cf. *Rhizocaulon* sp.

ANGIOSPERMS

Betulaceae Gray

Alnus Miller*Alnus menzelii* Raniecka-Bobrowska

Pl. 1, figs 3a, b, 4, Pl. 4, figs 3a–3c

1954 *Alnus menzelii* Raniecka-Bobrowska, p. 11, Fig. 4, Phot. 11–13.

Material. KRAM-P 226: 5, 16, 17

Description. Macromorphology. Small fragments of leaves, up to 4.7 cm long and up to 3.6 cm wide, leaf base cordate. Leaf margin serrate, teeth badly preserved, secondary veins terminate in teeth apex. Only fragments of elongated petioles preserved, up to 2 cm long. Venation pinnate, primary vein straight, of moderate thickness. Secondary venation simple craspedodromous, up to 7 pairs of secondaries preserved, veins almost straight, slightly up-curved near leaf margin, distributed at intervals of 0.2–0.3 cm near leaf base to 0.6–0.7 cm in middle of lamina. First pair of secondary veins forms ca 110° angle with the primary vein, the next pair ca 90°; angle

decreases to 40–60° in middle part of leaf blade. Tertiary venation percurrent, ca 8 tertiary veins per 1 cm of secondary vein length. Tertiary venation forms ca 135° angle with primary vein. Higher-order venation orthogonal and partly random reticulate. Areoles well developed, 0.35–0.65 mm across, veinlets branched. Marginal ultimate venation looped.

Micromorphology. Adaxial epidermis composed of isodiametric to elongate, variably shaped cells 15–27(35) µm across. Anticlinal cell walls mainly straight, very rarely rounded. Adaxial epidermis cells over veins more elongated and narrow, usually tetragonal or similar shape. Abaxial epidermis cells usually slightly elongated, tetra- to polygonal, 12–27 µm across. Anticlinal cell walls usually straight, rarely rounded, sometimes characteristically undulate. Abaxial epidermis cells over veins usually rather elongated and narrow, up to 55 µm long and 10–15 µm wide. Leaves hypostomatic. Stomata anomocytic, very rarely cyclocytic, elliptic, 18–30 µm long and 15–20 µm wide. Outer stomatal ledge aperture spindle-shaped or wide spindle-shaped, distinctly cutinised, sometimes sharpened at poles, rather variable in size, 10–22 µm long and 4.0–7.5 µm wide. On the abaxial epidermis, mostly 4-celled trichome bases 25–32 µm across. Peltate trichome shields, rarely preserved, 60–85 µm in diameter.

Remarks. Leaves of *Alnus menzelii* Raniecka-Bobrowska are characterised by typical cordate bases. The studied leaf remains match the description of *Alnus menzelii* from the Miocene of Konin (Raniecka-Bobrowska 1954). Leaves of this species can be mistaken as other fossil members of the family Betulaceae, such as *Alnus kefersteinii* (Goeppert) Unger, *Betula brongniartii* Ettingshausen, *Betula prisca* Ettingshausen (Zastawniak & Walther 1998), or *Betula macrophylla* Heer (Worobiec 2003).

Modern equivalents. *Alnus menzelii* is most similar to two contemporary alder species, *A. serrulata* (Ait.) Willd. from the eastern part of North America and *A. subcordata* C.A. Meyer endemic to Hyrcanian forests (Raniecka-Bobrowska 1954, Browicz 1989).

Ecology. Arctotertiary, temperate element. *Alnus menzelii* was a typical component of riparian and swampy forests (Zastawniak & Walther 1998).

Occurrence. *Alnus menzelii* was previously reported from only a few Neogene localities, though according to Zastawniak and Walther (1998) it was rather common (see also Worobiec & Szykiewicz 2007). Quite recently, Hably (2013) reported this alder as a common species in the late Miocene vegetation of Hungary, often as a dominant element of fossil swamp associations. In Poland it occurred from the Middle Miocene to the late Miocene/early Pliocene (Worobiec et al. 2008).

Carpinus L.

Carpinus grandis Unger emend. Heer

Pl. 1, figs 5a–5c, Pl. 4, figs 4a, b

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 226: 20

Description. Macromorphology. Leaf probably ovate, 3.6 cm long and 2.6 cm wide with cordate base. Leaf margin double serrate, teeth small, numerous, ± the same size, apical and basal side of teeth usually acuminate. Teeth apex acute. Secondary veins and their branches terminate at teeth apex. Venation pinnate, primary vein straight and thin. Secondary venation simple craspedodromous. Preserved 7 pairs of secondary veins. Secondaries straight, near leaf margin slightly up-curved, distributed at intervals of 0.2 cm near leaf base and ca 0.6 cm in middle part of lamina. Secondary veins form 45–55° angle with primary vein, and close to leaf margin produce numerous branches entering nearest teeth. Tertiary venation percurrent, forms ca 130° angle with primary vein. Ca 10 tertiary veins per 1 cm secondary vein length. Higher-order venation orthogonal reticulate. Areoles well developed, 0.20–0.35 mm across. Veinlets usually absent. Marginal ultimate venation looped.

Micromorphology. Adaxial epidermis composed of usually slightly elongated cells 20–32 µm across, with straight, rounded or slightly undulate anticlinal cell walls. Over vein cells are elongated and usually rectangular, 22–62 µm long. Walls of abaxial epidermis

cells mostly not visible, probably due to method of maceration. Leaves hypostomatic. Stomata anomocytic, wide elliptic or rounded, 17–25 µm in diameter. Stomatal pore almost always visible. Outer stomatal ledge aperture elliptic or wide elliptic, 7.5–13.0 µm long and 5.0–8.5 µm wide. Trichomes not found.

Remarks. The elliptic shape of the leaf blade, the dense, small teeth, and the shape of the leaf base and areoles without veinlets are characteristics of 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. With respect to the macromorphology and micromorphology of the epidermis, *Carpinus grandis* 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 Poland, reported from the early Miocene to early Pliocene (Hummel 1991, Krajewska 1998, Worobiec et al. 2008).

Fagaceae Dumort.

Fagus L.

Fagus silesiaca Walther & Zastawniak

Pl. 2, figs 1–3, 7, Pl. 5, figs 1a, b

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

Material. KRAM-P 226: 1, 6, 10, 12–15

Description. Macromorphology. Leaves elliptic, up to 4.5 cm long and 2.2–2.8 cm wide, with acute leaf base and acuminate leaf apex. Leaf margin simple serrate, teeth up-curved, apical sides of teeth concave, basal sides acuminate or convex, teeth apex acute

or rounded. Venation pinnate, primary vein often characteristically undulate. Secondary venation simple craspedodromous, in basal part often brochidodromous, secondaries preserved in up to 10 pairs, straight, near leaf margin often up-curved, distributed at intervals of 0.5–0.7 cm (near base 0.3 cm). Secondary veins form 40–50° angle with primary vein. Tertiary venation percurrent, forms 130–140° angle with primary vein. 7–10 tertiary veins per 1 cm of secondary vein length. Higher-order venation at least partly orthogonal reticulate. Areoles well developed, ca 0.3 mm across. Veinlets none, simple, or (rarely) once branched. Marginal ultimate venation looped.

Micromorphology. Adaxial epidermis composed of usually slightly elongated cells with distinctly undulate cell walls, 30–47 µm across. Adaxial epidermis cells over veins exclusively straight-walled, rectangular, rather elongate and thin, 7.5–10.0 µm wide. Abaxial epidermis consists of variable-shaped cells with straight, rounded or slightly undulate cell walls, 20–30 µm across. Abaxial epidermis cells over veins elongated and thin, 7.5–10.0 µm wide. Leaves hypostomatic. Stomata probably cyclocytic, usually roundish to wide elliptic, 20–25 µm in diameter. Outer stomatal ledge wide elliptic to elliptic, 8.5–12.5 µm long and 5.0–8.5 µm wide. Ill-defined T-piece (T-shaped cuticular thickenings) visible at poles of guard cells only on some cuticular slides. Stomatal pore occasionally visible. On lower epidermis, unicellular trichome bases, elliptic to roundish, 12.5–15.0 µm in diameter. Preserved remains of trichomes suggest solitary (unbranched) shape.

Remarks. The venation network, leaf margin serration and leaf epidermis micromorphology are typical for leaves of the genus *Fagus*. On the basis of their shape and number of secondary veins, the fossil beech leaf fragments described above belong to *Fagus silesiaca* Walther & Zastawniak (Walther & Zastawniak 1991).

Modern equivalents. The macromorphology and micromorphology of *Fagus silesiaca* leaves are comparable to those of the recent Chinese *Fagus hayatae* Palibin ex Hayata (Dyjor et al. 1992). North American beech, *Fagus grandiflora* Ehrh., morphologically

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

Quercus L.

Quercus gigas Goeppert emend. Walther & Zastawniak

Pl. 2, figs 4a, b, 5, Pl. 5, figs 2a, b, 3

1991 *Quercus gigas* Goeppert emend. Walther & Zastawniak, Figs 3–7; pl. 4, figs 1–3; pl. 5, figs 1–3; pl. 6, figs 1–5; pl. 7, figs 1–3; pl. 8, figs 1–5; pl. 9, figs 1–4; pl. 10, figs 1–3.

Material. KRAM-P 226: 2, 3, 11, 18

Description. Macromorphology. Small fragments of leaves (up to 5 cm long and up to 3 cm wide) with decurrent, obtuse and also acute leaf base. Leaf margin regularly simple serrate, teeth moderate or large, apical sides of teeth concave, basal sides concave, occasionally acuminate, tooth apex always acute, passing into a bristle which constitutes a spinose tooth termination. Secondary veins terminate in tooth apex bristles. Venation pinnate, primary vein mostly straight or slightly curved and of moderate thickness. Secondary venation simple craspedodromous; only at leaf base, lowermost pair of secondary veins brochidodromous, interconnected in loops. Secondaries preserved in up to 9 pairs, straight, near leaf margin sometimes slightly up-curved, departing primary vein at intervals of 0.3–0.8 cm (near base 0.3 cm) and usually forming 50° angle with primary vein. Tertiary venation percurrent, usually forming 140° angle with primary vein. Ca 8 tertiary veins per 1 cm of secondary vein length. Higher-order venation partly orthogonal reticulate. Areoles well developed, 0.3–0.5 mm across. Veinlets present, branched or multiple-branched. Marginal ultimate venation looped.

Micromorphology. Adaxial epidermis composed of tetragonal to polygonal cells 25–42 μm across, cells over veins elongated. Anticlinal cell walls straight. Abaxial epidermis consists of variably-shaped, usually somewhat elongated cells 15–25 μm across. Anticlinal cell walls curved or slightly undulate. Leaves hypostomatic. Stomata anomocytic, elliptic, wide elliptic, occasionally roundish, 20–30 μm long and 17–22 μm wide. Outer stomatal ledge aperture narrow elliptic to spindle-shaped, 7.5–17.0 μm long and 2.5–5.0 μm wide. Stomatal pore usually visible. T-piece at poles of guard cells usually visible. On abaxial epidermis, numerous (forming dense cover) stellate trichomes composed of several arms up to 100 μm long. Trichome base irregularly elliptic to roundish, (15)20–30(35) μm across.

Remarks. The macromorphology of the discussed leaves (especially the serrate margin with spinose teeth apices, is characteristic of several fossil fagaceous species such as *Castanea atavia* Unger, *C. gigas* (Goeppert) Ilnskaya, *C. kubinyii* Kováts ex Ettingshausen sensu Knobloch & Z. Kvaček, *Quercus kubinyi* (Kováts ex Ettingshausen) Czecczot, and *Q. gigas* Goeppert emend. Walther & Zastawniak. The macromorphology of the leaves from Bełchatów is rather similar to both “*Castanea*” *kubinyii* and *Quercus gigas* but the epidermis micromorphology is typical for leaves of *Quercus gigas* (Walther & Zastawniak 1991). *Quercus gigas* has numerous stellate trichomes in the abaxial epidermis, whereas leaves of “*Castanea*” *kubinyii* completely lack them (Knobloch & Kvaček 1976, Worobiec 2003). Another fossil oak common in the Neogene, *Quercus pseudocastanea* Goeppert emend. Walther & Zastawniak, differs markedly by having marginal lobes.

Modern equivalents. Macro- and micro-morphologically, *Quercus gigas* resembles recent oaks of section *Cerris* Oersted (Hummel 1983, Walther & Zastawniak 1991).

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

Occurrence. *Quercus gigas* is common in the Neogene floras of Europe. In Poland it occurred from the middle Miocene to Pliocene (Walther & Zastawniak 1991).

***Quercus pseudocastanea* Goeppert emend.
Walther & Zastawniak**

Pl. 2, figs 6a, b, Pl. 5, figs 4a, b

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

Material. KRAM-P 226: 4, 9

Description. Macromorphology. Small fragments of leaves (up to 4 cm long and up to 3.6 cm wide) with obtuse, decurrent and asymmetric leaf base. Leaf margin lobate, lobes small, apical sides of lobes convex, basal sides convex, occasionally acuminate, lobe apex always rounded with acute terminal part. Secondary veins terminate at lobe apex. Venation pinnate, secondary venation simple craspedodromous, lowermost secondaries brochidodromous (connected in loops as they do not terminate in lobes). Secondary veins diverge from main vein at ca 50° angle at intervals of 0.3 cm near leaf base and up to 1.2 cm in middle part of lamina. Tertiary venation percurrent and forming variable angles of ca 130–140° with primary vein. Ca 6–8 tertiary veins per 1 cm secondary vein length. Higher-order venation reticulate. Areoles well developed, 0.2–0.4 mm across. Veinlets present, branched. Marginal ultimate venation looped but imperfect fimbrial vein probably present.

Micromorphology. Adaxial epidermis composed of usually polygonal cells 30–37 μm across. Anticlinal cell walls straight, rarely rounded. Abaxial epidermis consists of isodiametrical or slightly elongated cells 17–35 μm across. Anticlinal cell walls straight, rounded or even slightly undulate. Leaves hypostomatic. Stomata anomocytic, elliptic to wide elliptic, 15–25 μm (commonly 20–25 μm) across. Outer stomatal ledge aperture elliptic, ca 7.5 μm long. Stomatal pore sometimes visible. T-piece at poles of guard cells usually visible. On abaxial epidermis, fasciculate and stellate trichomes, sometimes numerous, composed of several arms up to 123 μm long. Trichome bases roundish, 10–15 μm across.

Remarks. The shape of the leaf fragments (especially the marginal lobes with acute apical termination) is characteristic of the fossil oak *Quercus pseudocastanea* Goeppert emend. Walther & Zastawniak. Cuticular

micromorphology also corresponds to *Quercus pseudocastanea*. Another fossil oak with rather similar macromorphology, *Quercus roburoides* Gaudin, differs in having lobes with a retuse apex (Van der Burgh 1993, Belz and Mosbrugger 1994). *Quercus gigas* Goeppert emend. Walther & Zastawniak differs markedly in having a serrate margin with spinose teeth apices.

Modern equivalents. Macro- and micro-morphologically the leaves of *Quercus pseudocastanea* resemble recent oaks of section *Cerris* Oersted (Walther & Zastawniak 1991).

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

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

Hamamelidaceae R.Br. in C. Abel

"*Parrotia*" *pristina* (Ettingshausen) Stur

Pl. 3, figs 1a, b, Pl. 5, fig. 5

1852 *Styrax pristinum* Ettingshausen, p. 10, pl. 2, fig. 10.

1855 *Quercus fagifolia* Goeppert, p. 14, pl. 6, figs 9–12.

1859 *Parrotia fagifolia* (Goeppert) Heer, p. 306.

1867 *Parrotia pristina* (Ettingshausen) Stur, p. 192, pl. 5, figs 2, 3.

1971 "*Parrotia*" *pristina* (Ettingshausen) Stur; Bůžek, p. 52, Fig. 4, pl. 16, figs 8–12, pl. 17, figs 1–11.

Material. KRAM-P 226: 21

Description. **Macromorphology.** One very small (2 × 2 cm) fragment of basal part of leaf, entire-margined. Leaf base probably obtuse and decurrent. Two secondary veins depart opposite primary vein just above leaf base. Tertiary venation apparently percurrent. Higher-order venation random reticulate. Areoles imperfect, large, variable in size, 0.6–1.2 mm across. Veinlets present, branched. Marginal ultimate venation looped.

Micromorphology. On small fragments of abaxial epidermis without preserved cell walls, some outer stomatal ledge apertures

visible, usually spindle-shaped, rarely elliptic, 12–20 µm long and 5–10 µm wide. Two strongly cutinised trichome bases of unspecified trichome type found on unspecified layer of leaf epidermis.

Remarks. The characteristic structure of the leaf base (shape, venation) of the specimen is typical for leaves of the fossil species "*Parrotia*" *pristina* (Krajewska 1998). Moreover, on the leaf from Bełchatów were trichome bases rather similar to those from leaves of "*Parrotia*" *pristina* reported by Knobloch and Kvaček (1976) and Hably and Kvaček (1997). The architecture of higher-order venation (large, imperfectly developed areoles, branched veinlets) corresponds to the recent genus *Parrotia* C.A. Mey (Bisht et al. 1989). However, leaf morphology very similar to that of *Parrotia* is also found in other genera belonging to the family Hamamelidaceae: *Fothergilla* L., *Hamamelis* L., and *Shaniodendron* Deng et al. (Krajewska 1998, Teodoridis 2003, Walther & Eichler 2010). For this reason it is difficult to assign these fossil leaves to any of the four mentioned recent genera of Hamamelidaceae on the basis of leaf macromorphology and cuticle micromorphology (Knobloch & Kvaček 1976, Walther & Eichler 2010). To solve this problem, Bůžek (1971) introduced the collective name "*Parrotia*" *pristina* for fossil leaves of similar morphology.

Modern equivalents. The closest modern equivalents to "*Parrotia*" *pristina* may be recent *Parrotia persica* C.A. Mey and *Shaniodendron subaequale* (Chang) Deng et al. *Parrotia persica* occurs in alluvial and lowland deciduous Hyrcanian forests in the south-western and southern shores of the Caspian Sea and adjacent mountains (Akhani et al. 2010, Sefidi et al. 2011). Endemic to Eastern China and critically endangered *Shaniodendron subaequale* grows mainly in gravelly areas in valleys and barren areas near mountain ridges where drought frequently occurs, but sometimes also near mountain rivulets (Yue 2006). Hao and Wei (1998) maintained that *Shaniodendron subaequale* belongs to the genus *Parrotia* and proposed the new combination *Parrotia subaequalis* (Chang) Hao & Wei.

Ecology. Arctotertiary, warm temperate element. Usually considered a riparian element (member of the association *Parrotia-Ulmus*

pyramidalis sensu Kvaček & Bůžek 1982), also as a component of mesophytic forests (Belz & Mosbrugger 1994, Walther & Eichler 2010).

Occurrence. "*Parrotia*" *pristina* is known from the early Miocene to late Pliocene of Europe (Hably & Kvaček 1997, Walther & Eichler 2010). In Poland, reported from the middle Miocene of Stare Gliwice (Szafer 1961, as *Parrotia fagifolia* (Goeppert) Heer), late Miocene of Bełchatów (Stuchlik et al. 1990) and Sośnica (Meyer 1919 as *Parrotia fagifolia* (Goeppert) Heer), Miocene-Pliocene of Gnojna (Krajewska 1998) and Pliocene of Domański Wierch (Zastawniak 1972) and Ruszów (Hummel 1983).

Magnoliaceae Jussieu

Magnolia L.

?*Magnolia* sp.

Fig. 2, Pl. 3, fig. 2, Pl. 6, figs 1a, b

Material. KRAM-P 226: 27

Description. Macromorphology. One very small (ca 0.7 cm) leaf fragment, entire-margined. Secondary venation brochidodromous. Tertiary venation probably weakly percurrent. Higher-order venation reticulate. Areoles well developed, 0.5–0.8 mm across. Veinlets usually present, simple, exceptionally branched. Marginal ultimate venation looped.

Micromorphology. Adaxial epidermis consists of irregular-shaped, usually elongated cells 40–70 µm across. Anticlinal cell walls usually Ω -undulate. Adaxial epidermis cells over veins rather elongated and straight-walled. Abaxial epidermis consists of irregular-shaped, elongated cells 42–57 µm across. Anticlinal cell walls undulate. Leaf hypostomatic. Stomata brachyparacytic, of characteristic roundish-rhomboidal (frequently distinctly rhomboidal) shape, 30–35 µm long and 22–25 µm wide. Outer stomatal ledge aperture indistinct, rather thin, 2.5–5.0 µm wide, surrounded by distinct ledges raised above surface cuticle. On abaxial epidermis and exclusively over veins, unicellular trichome bases, roundish to irregular-shaped, 12–20 µm in diameter. Fruiting bodies of epiphyllous, microthyriaceous fungus also found on abaxial epidermis (Fig. 2A). In leaf mesophyll, scattered, roundish idioblast

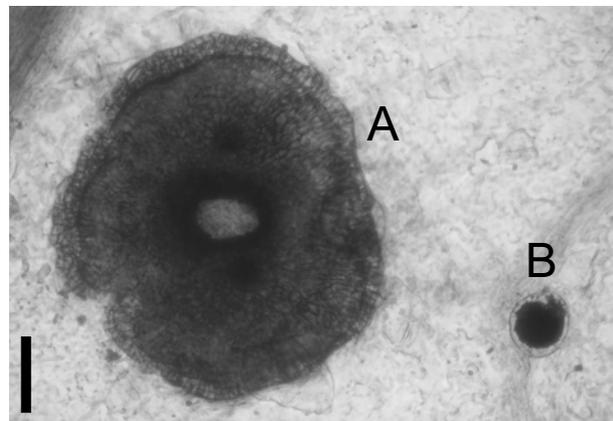


Fig. 2. ?*Magnolia* sp.: specimen No. KRAM-P 226/27. A – fruiting body of microthyriaceous epiphyllous fungus; B – idioblast secretory cell. Scale bar – 20 µm

secretory cells 30–45 µm in diameter are preserved (Fig. 2B).

Remarks. The structure of the stomatal complex and the presence of idioblast secretory cells in leaf mesophyll suggest its affinity to the Lauraceae family. The Ω -undulate cell walls of the adaxial epidermis and the shape of stomata somewhat resemble those of the genus *Laurus*. However, the leaf from Bełchatów differs from leaves of both fossil *Laurus abchatica* and recent *Laurus nobilis* in having lower stomatal density. The structure of higher-order venation resembles that of the genus *Sassafras* but the network of third-order venation differs from that of *Sassafras*. In respect of epidermal structure the studied leaf fragment also resembles representatives of the family Magnoliaceae. Such an affinity may be inferred from the presence of idioblast secretory cells. The course of third-order venation is also similar to that in the genus *Magnolia*. The structure of the stomatal complex of this leaf fragment differs somewhat from that of recent Magnoliaceae genera as *Liriodendron* and *Magnolia*, but this difference does not seem to rule out affinity with Magnoliaceae. The specimen's macro- and micromorphology suggest that the genus *Magnolia* is its closest counterpart.

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

Ecology. Warm temperate or subtropical element.

Occurrence. Macroremains of representatives of the genus *Magnolia* are common in the Neogene floras of Europe. In Poland, almost

exclusively carpological remains of *Magnolia* are reported from middle Miocene to Pliocene deposits (Zastawniak et al. 1996).

Sapindaceae Jussieu

Acer L.

Acer cf. *aegopodifolium* (Goepfert)

Baikovskaya ex Ilinskaya

Pl. 3 figs 3a, b, Pl. 6, figs 2a, b

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

Material. KRAM-P 226: 23

Description. Macromorphology. Small fragments of leaflet with serrate margin. Branches of veins terminate in tooth apex. Tertiary venation on preserved leaflet fragment orthogonal reticulate. Higher-order venation \pm orthogonal reticulate. Areoles well developed, 0.20–0.35 mm across. Veinlets simple or branched. Marginal ultimate venation looped.

Micromorphology. Adaxial epidermis composed of usually slightly elongated cells 27–57 μm across with strongly undulated walls. Cells over veins have straight, rarely rounded and never undulate walls, elongated and narrow, 40–56 μm long and 13–17 μm wide. Abaxial epidermis composed of isodiametric or slightly elongated cells 20–32 μm across, with straight or rounded cell walls. Leaves hypostomatic. Stomata anomocytic (seemingly paracytic, see Hummel 1983), from narrow to wide elliptic, 22–29 μm long and 20–22 μm wide. Outer stomatal ledge aperture rather distinct and of characteristic elliptic-oblongate shape, 16–20(24) μm long and 5.0–7.5 μm wide.

Remarks. The leaflet is assigned to genus *Acer* L. on the basis of the morphology of higher-order venation and especially epidermal structure (the rather characteristic shape of stomata). The epidermal characters of this specimen differ markedly from those in the fossil species *Acer tricuspdatum* Bronn sensu Procházka

& Bůžek, common in the Neogene, which has numerous solitary trichomes on the abaxial epidermis and usually straight-walled adaxial epidermis cells. The undulate cell walls of the adaxial epidermis, the structure of stomata, the absence of trichomes on the abaxial epidermis, and the dimensions of epidermal structures are much the same as in fossil *Acer aegopodifolium* (Goepfert) Baikovskaya ex Ilinskaya (Schmitt & Kvaček 1999, Worobiec et al. 2012). Leaflet venation architecture (course of higher-order veins, size and shape of areoles, veinlets development) is also similar to that of *Acer aegopodifolium*. However, the very fragmentary nature of this specimen makes its taxonomic assignment only presumptive.

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

Ecology. Arctotertiary, warm temperate element. An accessory species in azonal forest communities (Walther & Zastawniak 2005).

Occurrence. *Acer aegopodifolium* is known from the middle and late Miocene of Central and Eastern Europe (Walther & Zastawniak 2005). From Poland it is reported from middle and upper Miocene deposits (Worobiec et al. 2012).

Ulmaceae Mirbel

Zelkova Spach

Zelkova zelkovifolia (Unger)

Bůžek & Kotlaba

Pl. 3, fig. 4

- 1841 *Ulmus zelkovaefolia* Unger, p. 94, 95, pl. 24, fig. 7 pro parte, figs 9–12, pl. 26, fig. 7.
 1963 *Zelkova zelkovaefolia* (Unger) Bůžek & Kotlaba; Kotlaba, p. 59–62, pl. 3, figs 7, 8.

Material. KRAM-P 226: 7

Description. Macromorphology. Three small leaf fragments up to 2.3 cm long and up to 2.0 cm wide, with acute, cordate and asymmetric leaf base. Petiole short, 0.5–0.7 cm long. Leaf margin simple serrate, teeth large, apical and basal side of teeth acuminate, tooth apex acute. Secondary veins terminate in teeth apices. Venation pinnate, primary vein

of moderate thickness. Secondary venation simple craspedodromous. Secondary veins straight or slightly up-curved, distributed at intervals of 0.1–0.2 cm near leaf base and up to 0.6 cm in the middle part of lamina, forming 40–50° angle with primary vein. Some secondary veins are characteristically dichotomous branched. Tertiary venation weakly percurrent, ca 6 tertiary veins per 1 cm of secondary vein length. Higher-order venation reticulate. Areoles well developed, ca 0.5–0.8(1.0) mm across. Veinlets present, branched. Marginal ultimate venation looped.

Remarks. The venation network of these leaf fragments is typical for both *Ulmus* and *Zelkova* but they have serrate margins with simple, large teeth, typical for leaves of the genus *Zelkova* and the fossil species *Z. zelkovifolia* (Unger) Bůžek & Kotlaba.

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

Ecology. Arctotertiary, warm temperate element. It was a component of European Palaeogene and Neogene riparian vegetation (Kovar-Eder 2003).

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

Dicotyledones incertae sedis

***Dicotylophyllum* Saporta**

***Dicotylophyllum* sp. 1**

Pl. 3 fig. 5, Pl. 6, figs 3a, b

Material. KRAM-P 226: 22

Description. **Macromorphology.** One small fragment (1.5 cm) of leaf without margin. Venation pinnate. Tertiary venation weakly percurrent or composite intersecondary. Higher-order venation random reticulate. Areoles imperfect or incomplete.

Micromorphology. Adaxial epidermis composed of isodiametric or slightly elongated cells, quadrangular to polygonal, with straight, sometimes rounded walls, 27–40 µm across. Cell structure of abaxial epidermis not visible. Leaves hypostomatic. Stomata elliptic, 25–37 µm long and 15–20 µm wide. Outer stomatal ledge aperture distinct, spindle-shaped, 17–25 µm long and 5–11 µm wide. On abaxial epidermis are unicellular, simple, solitary trichomes, 50–62 µm long, with unicellular, elliptic to roundish, strongly cutinised trichome base, 20–22 µm in diameter.

Remarks. The shape of the leaf fragment somewhat resembles *Terntroemites* sp. sensu Worobiec & Lesiak (1998) but it differs in respect of venation and epidermis structure. Its systematic position is undetermined due to the absence of distinctive characters.

***Dicotylophyllum* sp. 2**

Pl. 3, figs 6a, b, Pl. 6, figs 4, 5

Material. KRAM-P 226: 24–26

Description. **Macromorphology.** Three small leaf fragments up to 2 cm across. Leaf base obtuse or rounded. Leaf entire-margined in preserved fragments. On leaf margin, rather large solitary trichomes spaced every 0.15–0.20 mm. Venation pinnate, primary vein of moderate thickness. Secondary venation brochidodromous. Secondaries irregularly distributed, up-curved and interconnected in loops. Intersecondary veins present, weakly developed. Tertiary venation weakly percurrent or reticulate. Higher-order venation reticulate. Areoles well developed, 0.25–0.45 mm across. Veinlets present, simple, rarely branched. Marginal ultimate venation looped.

Micromorphology. Adaxial epidermis composed of usually slightly elongated cells with straight or rounded cell walls, 25–42 µm across. Adaxial epidermis cells over veins straight-walled, rectangular, elongate, up to 50 µm long and 10–15 µm wide. Cuticle surface covered by ornamented epicuticular wax. Abaxial epidermis consists of irregular-shaped cells with rounded or straight cell walls, 12–27 µm across. Leaves hypostomatic. Stomata roundish to wide elliptic, of rather regular size and shape, 17–20 µm in diameter. Outer stomatal ledge spindle-shaped, 7.5–12.0 µm long and

2.5–5.0 µm wide. On lower epidermis, bases of unknown trichome type.

Remarks. The studied dicotyledonous leaf remains are poorly preserved. Their systematic position cannot be determined due to the absence of distinctive characters.

RESULTS OF INVESTIGATIONS OF PLANT MACROREMAINS

GENERAL FINDINGS

Study of the 27 leaf slides revealed 12 taxa of the genera *Acer*, *Alnus*, *Carpinus*, *Dicotylophyllum*, *Fagus*, ?*Magnolia*, “*Parrotia*”, *Pinus*, *Quercus*, and *Zelkova*. Two fossil species new for the Polish tertiary are reported: *Dicotylophyllum* sp. 1 and *Dicotylophyllum* sp. 2.

TAPHONOMY

The investigated leaf remains were isolated from a thin layer of fossil leaf litter composed of humified plant remains, mostly leaves. This kind of litter could have resulted from rapid accumulation of fallen leaves that grew in vegetation surrounding a sedimentary reservoir, probably an abandoned river channel. A leaf accumulation (thanatocoenosis) can originate from seasonal leaf fall or storm damage, followed by transport in rainfall or flood waters to sedimentary reservoirs, and finally mass deposition on the bottom (Worobiec et al. 2008). The state of preservation (usually well preserved leaf fragments) suggests moderate compaction of litter without extensive cracking and/or faulting, and rapid burial in sediment.

CHARACTERISTICS OF PALAEOVEGETATION

Study of the plant macroremains preserved in leaf assemblage KRAM-P 226 allowed a reconstruction of the local vegetation of this Neogene locality from the Bełchatów Lignite Mine. The area surrounding the sedimentary reservoir in which the fossil leaf litter assemblage formed was covered mainly by mesophytic (zonal) forests. Only a few taxa are characteristic of azonal riparian (“*Parrotia*” and *Zelkova*) and swamp (*Alnus menzelii*) vegetation. The mesophytic forests were composed of *Carpinus grandis*, *Acer aegopodifolium*, *Fagus silesiaca*, ?*Magnolia* sp., *Pinus* sp., *Quercus*

gigas, and *Q. pseudocastanea*. The mesophytic forests most probably correspond to deciduous broad-leaved forests of the *Quercus-Carpinus-Castanea* association sensu Mai (1995). Their modern analogues might be the floristically rich mesophytic deciduous forests of the eastern part of North America (Braun 1964, Knapp 1965, Barnes 1991), northern China (Wang 1961), and the Euxine-Hyrcanian area (Colchis, Talysh, southern shore of Caspian Sea; Nakhutsrishvili et al. 2011). The representatives of riparian vegetation (“*Parrotia*” *pristina*, *Zelkova zelkovifolia*) suggest the presence of riparian forests corresponding to the extant riparian arboreal vegetation of river valleys and banks of the Euxine-Hyrcanian area (Tutayuk 1975, Rastin 1983, Akhani et al. 2010). The only swamp forest species in the discussed leaf assemblage is *Alnus menzelii*. This typical swamp fossil alder points to the presence of at least remnants of swamp forests of the *Glyptostrobus-Alnus-Byttneriophyllum* association, present in Europe beginning from the late Oligocene to the Pliocene (Mai 1995). Swamp forest of this type dominated in the Miocene of the Polish Lowlands (Worobiec 2009). Interestingly, remains of aquatic vegetation were completely absent. Possibly the water body of the sedimentary reservoir in which leaf assemblage KRAM-P 226 was preserved was shallow and/or existed only periodically after flooding.

RECONSTRUCTION OF PALAEOCLIMATE

All fossil taxa present in the studied leaf assemblage represent the arctotertiary geofloristic element (Mai 1995), typical for extant temperate and warm temperate climate areas in the Northern Hemisphere. The absence of more thermophilous taxa representing a palaeotropical element point to temperate climate during the accumulation of these plant remains. The presence of some taxa whose extant relatives are typical for warm temperate climate areas (?*Magnolia* sp., “*Parrotia*” *pristina*, *Zelkova zelkovifolia*) indicates favourable climatic conditions with mild winters. On the ?*Magnolia* leaf fragment were found some fruiting bodies of epiphyllous, microthyriaceous fungus (Fig. 2A). The presence of epiphyllous fungi is generally correlated with humid and warm, even subtropical climate. However, the presence of only one taxon of these fungi on one leaf points only to humid but not necessarily

warm climate (Worobiec & Worobiec 2013). The palaeoclimate might be compared to the contemporary climate of Euxine-Hyrcanian lowlands. Riparian forests of this region are characterised by the presence tertiary relicts such as *Parrotia persica* and *Zelkova carpinifolia* (Pall.) K. Koch, comparable to the fossil "*Parrotia*" *pristina* and *Zelkova zelkovifolia* found in Bełchatów. Both taxa occur together in the Hyrcanian area (Nakhutsrishvili et al. 2011). The Hyrcanian area has favourable climatic conditions for vegetation, with ca 15°C mean annual temperature and high annual precipitation evenly distributed throughout the year (very short or absent dry season). The average minimum coldest month temperature in this area is higher than 0°C (Akhani et al. 2010, Nakhutsrishvili et al. 2011).

AGE OF THE PLANT ASSEMBLAGE

The discussed leaf assemblage from the Bełchatów Lignite Mine is situated in Neogene deposits overlying the main coal seam, possibly in a coal-clayey unit of early to middle Miocene age. Possibly, however, the leaf assemblage originated from the lower part of a sandy-clayey unit whose age is estimated as late Miocene (see Geology). The composition of leaf assemblage KRAM-P 226 well matches late Miocene leaf assemblages from the sandy-clayey unit of the Bełchatów Lignite Mine (Stuchlik et al. 1990, Worobiec & Lesiak 1998, Worobiec 2003, Worobiec et al. 2012). The absence of palaeotropical taxa among the leaf remains (e.g. members of the family Lauraceae, palms) excludes early Miocene age of the leaf flora. The composition of leaf assemblage KRAM-P 226, with domination of the temperate, deciduous floristic element, is typical of the late Neogene vegetation of Central Europe. Most of the taxa found occur from the Miocene to Pliocene, usually in upper Miocene deposits.

COMPARISON OF THE PLANT ASSEMBLAGE KRAM-P 226 FROM BEŁCHATÓW WITH OTHER NEOGENE LEAF FLORAS OF POLAND AND CENTRAL EUROPE

The leaf flora of the KRAM-P 226 specimens from late Neogene deposits of Bełchatów shows low species richness but the material can be compared with other Neogene leaf floras from Poland and neighbouring countries.

Taxonomically the leaf assemblage corresponds to leaf floras described from late Neogene deposits of Poland (Tab. 1). All taxa (except for *Dicotylophyllum* sp. 1 and 2) were reported earlier from late Miocene fossil plant assemblages from the Bełchatów Lignite Mine (Stuchlik et al. 1990, Worobiec & Lesiak 1998, Worobiec 2003, Worobiec & Szynekiewicz 2007, Worobiec et al. 2010, Worobiec et al. 2012). Besides the Bełchatów assemblages, the most similar ones are Pliocene fossil leaf assemblages representing mostly mesophytic and riparian vegetation from Ruszów (Hummel 1983, 1991), Domański Wierch (Zastawniak 1972), and transitional Miocene/Pliocene flora of Gnojna (Krajewska 1998). Other localities have fewer taxa in common (Tab. 1), but that is usually the result of the different sedimentary environments of these assemblages, mostly representing swampy communities. Leaf floras similar to the KRAM-P 226 assemblage from Bełchatów have been reported from numerous localities in Central Europe. The discussed assemblage resembles late Neogene (late Miocene or early Pliocene) leaf floras from Willershausen (Knobloch 1998), Precarpathians (Shvareva 1983), Ottendorf-Okrilla (Walther & Eichler 2010), and the Molassezone of Austria (Kovar-Eder 1988). The differences between those localities and leaf assemblage KRAM-P 226 from Bełchatów seem to be a result of differences in the sedimentary environments of these localities. Assemblage KRAM-P 226 is much less comparable with floras from lower/middle Miocene deposits (Tab. 2) such as Kreuzau (Ferguson 1971) and Achldorf (Knobloch 1986).

CONCLUSIONS

– In this study of 27 leaf slides, 12 taxa of the genera *Acer*, *Alnus*, *Carpinus*, *Dicotylophyllum*, *Fagus*, *?Magnolia*, "*Parrotia*", *Pinus*, *Quercus*, and *Zelkova*, belonging to 7 families of gymnosperms and angiosperms, were identified.

– Two fossil species new for the tertiary of Poland are reported: *Dicotylophyllum* sp. 1 and *Dicotylophyllum* sp. 2.

– The area surrounding the sedimentary reservoir in which the fossil leaf litter assemblage formed most probably was dominated by mesophytic (zonal) vegetation with only a small

Table 1. Taxa shared between the KRAM-P 226 assemblage and selected leaf floras from the Neogene of Poland. (+) – taxon given under another name

Taxon	LATE MIOCENE		PLIOCENE	
	BELCHATÓW (Stuchlik et al. 1990, Worobiec & Lesiak 1998, Worobiec 2003, Worobiec & Szykiewicz 2007, Worobiec et al. 2010)	GNOJNA (Krajewska 1998)	RUSZÓW (Hummel 1983, 1991)	DOMAŃSKI WIERCH (Zastawniak 1972)
<i>Pinus</i> sp.	+			
Bark of <i>Pinus</i> sp.	+			
<i>Alnus menzelii</i>	+	+	+	
<i>Carpinus grandis</i>	+	+	+	+
<i>Fagus silesiaca</i>	+		+	(+)
<i>Quercus gigas</i>	+	+	+	(+)
<i>Quercus pseudocastanea</i>	+		+	+
“ <i>Parrotia</i> ” <i>pristina</i>	+	+	+	+
? <i>Magnolia</i> sp.	?			
<i>Acer</i> cf. <i>aegopodifolium</i>	+	+	?	
<i>Zelkova zelkovifolia</i>	+			+

Table 2. Taxa shared between the KRAM-P 226 assemblage and selected leaf floras from the Neogene of Central Europe. (+) – taxon given under another name

Taxon	MIDDLE MIOCENE		MIDDLE MIOCENE/ LATE MIOCENE	LATE MIOCENE	LATEST MIOCENE	PLIOCENE
	KREUZAU (Ferguson 1971)	PRECARPATHIANS (Shvareva 1983)	ACHLDORF (Knobloch 1986)	MOLASSEZONE OF AUSTRIA (Kovar-Eder 1988)	OTTEN- DORF-OKRILLA (Walther & Eichler 2010)	WILLERSHAUSEN (Knobloch 1998)
<i>Pinus</i> sp.			+	+		
Bark of <i>Pinus</i> sp.						
<i>Alnus menzelii</i>			+			
<i>Carpinus grandis</i>		+	+	+	+	+
<i>Fagus silesiaca</i>		+		(+)	(+)	
<i>Quercus gigas</i>	(+)	(+)	(+)			+
<i>Quercus pseudocastanea</i>		+		+	+	
“ <i>Parrotia</i> ” <i>pristina</i>		+	+	+		+
? <i>Magnolia</i> sp.		(+)				+
<i>Acer</i> cf. <i>aegopodifolium</i>		+		(+)		+
<i>Zelkova zelkovifolia</i>	(+)	+	(+)	+		+

share of azonal riparian and swamp communities. Mesophytic forests were composed of *Carpinus grandis*, *Acer aegopodifolium*, *Fagus silesiaca*, ?*Magnolia* sp., *Pinus* sp., *Quercus gigas*, and *Q. pseudocastanea*. Riparian vegetation is represented by two taxa, “*Parrotia*” *pristina* and *Zelkova zelkovifolia*, and swamp by only one, *Alnus menzelii*. Remains of water reservoir vegetation were completely absent, suggesting that the water body was shallow and/or existed only periodically after flooding.

– All fossil taxa present in the discussed leaf assemblage represent the arctotertiary geofloristic element. The absence of thermophilous, palaeotropical taxa points to temperate climate during the accumulation of these deposits with plant remains. Taxa typical for areas with warm temperate climate (?*Magnolia* sp., “*Parrotia*” *pristina*, *Zelkova zelkovifolia*) indicate warm climate with mild winters. The palaeoclimate during the period in which sedimentation of plant assemblage KRAM-P

226 occurred may have been similar to the contemporary climate of the Euxine-Hyrcanian lowlands.

– The composition of the leaf assemblage, with domination of the temperate, deciduous floristic element typical of the late Neogene vegetation of Central Europe, suggests its late Miocene age.

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PLATES

Plate 1

Pinus sp.

- 1a. Three needles and one two-needled fascicle, specimen No. KRAM-P 226/19
- 1b. Details of serrate needle margin, specimen No. KRAM-P 226/19

Bark of *Pinus* sp.

- 2. Fragment of exfoliated bark, specimen No. KRAM-P 226/8

Alnus menzelii Raniecka-Bobrowska

- 3a. Leaf, specimen No. KRAM-P 226/5
- 3b. Detail of higher-order venation architecture, areolation and veinlets, specimen No. KRAM-P 226/5
- 4. Basal part of leaf, specimen No. KRAM-P 226/16

Carpinus grandis Unger emend. Heer

- 5a. Leaf, specimen No. KRAM-P 226/20
- 5b. Detail of higher-order venation architecture and areolation, specimen No. KRAM-P 226/20
- 5c. Detail of teeth and leaf margin venation, specimen No. KRAM-P 226/20

1a: scale bar – 1 cm; 2, 3a, 4, 5a: scale bar – 0.5 cm; 3b, 5b, 5c: scale bar – 0.5 mm; 1b: scale bar – 100 µm

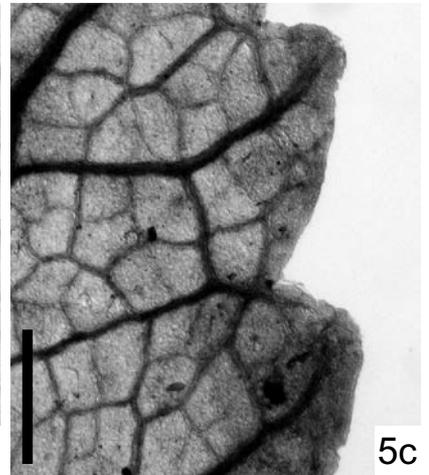
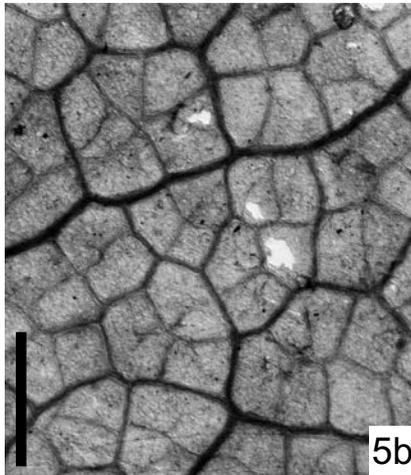
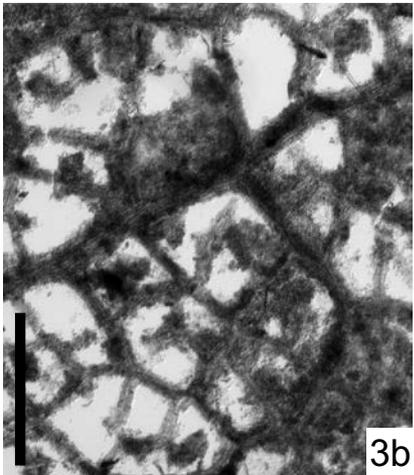
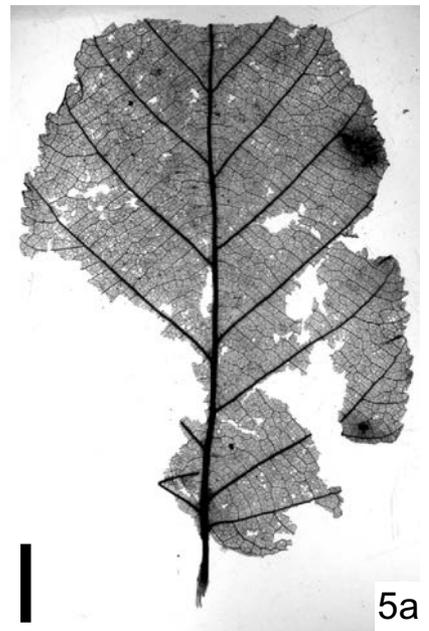
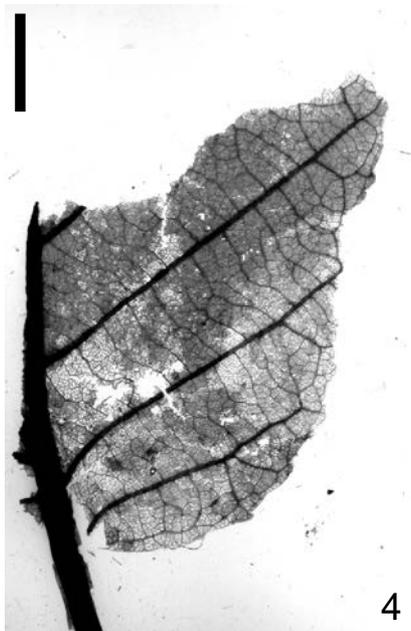
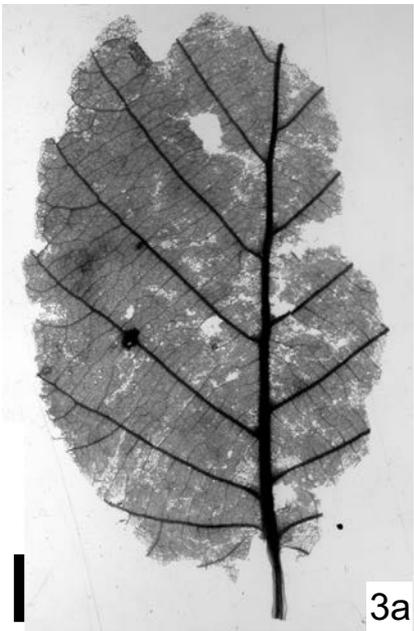
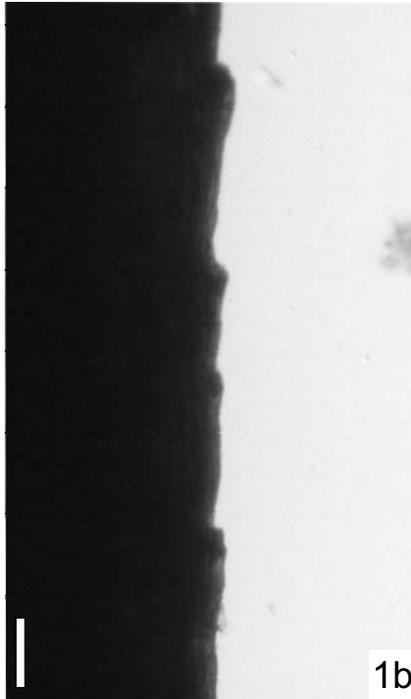


Plate 2

Fagus silesiaca Walther & Zastawniak

1. Leaf, specimen No. KRAM-P 226/12
2. Leaf, specimen No. KRAM-P 226/6
3. Leaf, specimen No. KRAM-P 226/13
7. Detail of teeth and leaf margin venation, specimen No. KRAM-P 226/10

Quercus gigas Goepfert emend. Walther & Zastawniak

- 4a. Leaf, specimen No. KRAM-P 226/2
- 4b. Detail of higher-order venation architecture, areolation and veinlets, specimen No. KRAM-P 226/2
5. Leaf, specimen No. KRAM-P 226/3

Quercus pseudocastanea Goepfert emend. Walther & Zastawniak

- 6a. Leaf, specimen No. KRAM-P 226/4
- 6b. Detail of lobe shape and venation, specimen No. KRAM-P 226/4

1–3, 4a, 5, 6a: scale bar – 0.5 cm; 4b, 6b, 7: scale bar – 0.2 mm

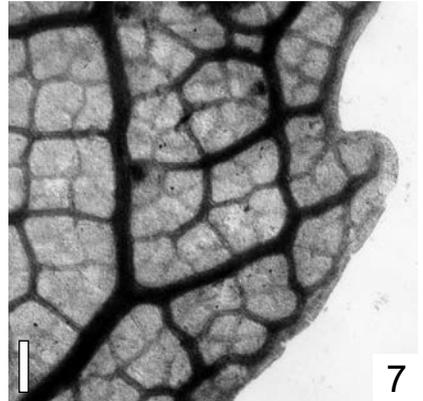
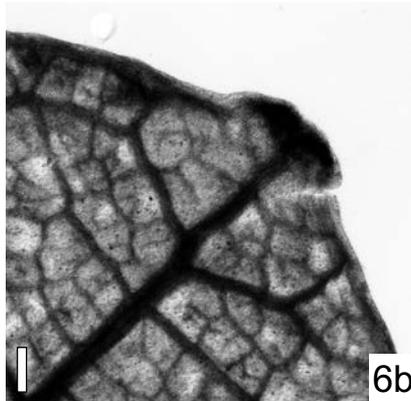
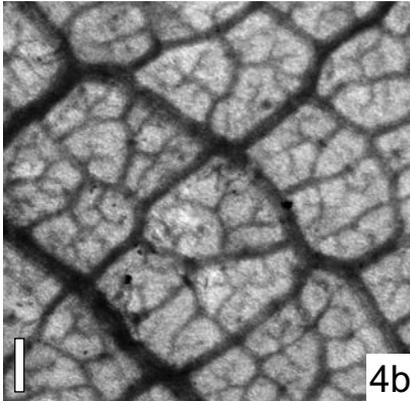
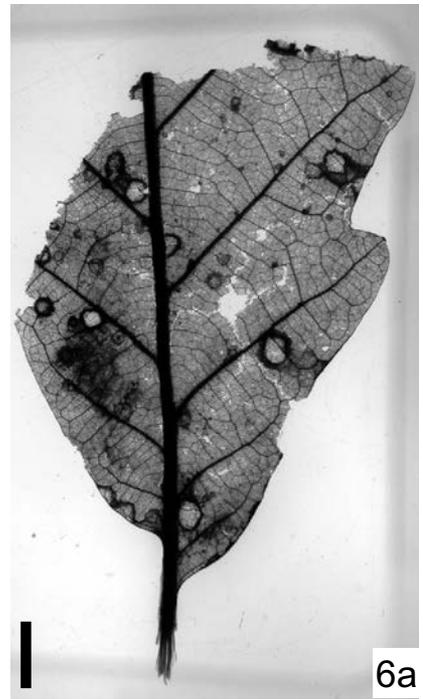
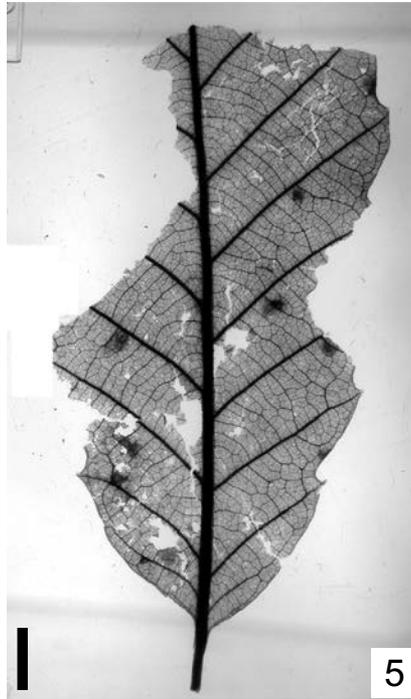
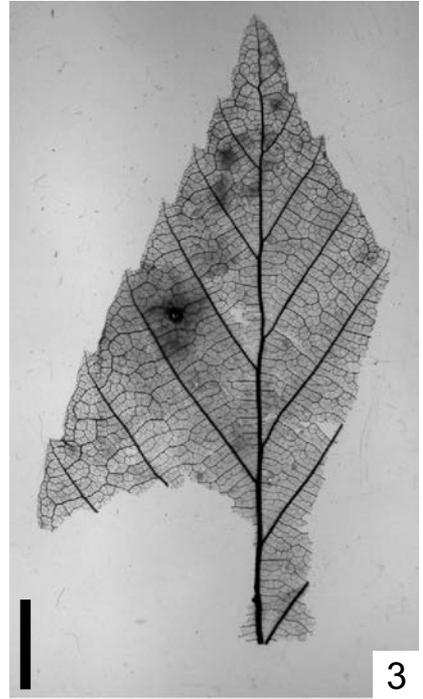
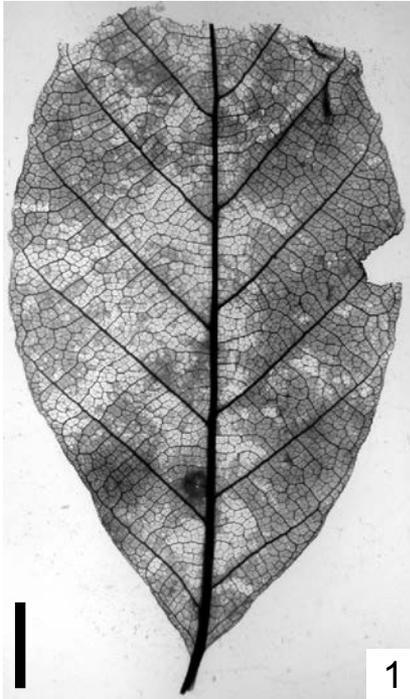


Plate 3

“Parrotia” pristina (Ettingshausen) Stur

- 1a. Leaf base, specimen No. KRAM-P 226/21
- 1b. Detail of higher-order venation architecture, areolation and veinlets, specimen No. KRAM-P 226/21

?Magnolia sp.

- 2. Leaf fragment, arrow points to fructification of microthyriaceous, epiphyllous fungus, specimen No. KRAM-P 226/27

Acer cf. aegopodifolium (Goeppert) Baikovskaya ex Ilinskaya

- 3a. Leaf fragment, specimen No. KRAM-P 226/23
- 3b. Detail of higher-order venation architecture, areolation and veinlets, specimen No. KRAM-P 226/23

Zelkova zelkovifolia (Unger) Bůžek & Kotlaba

- 4. Leaf, specimen No. KRAM-P 226/7

Dicotylophyllum sp. 1

- 5. Leaf fragment, specimen No. KRAM-P 226/22

Dicotylophyllum sp. 2

- 6a. Leaf fragment, specimen No. KRAM-P 226/26
- 6b. Detail of higher-order venation architecture, areolation and veinlets, specimen No. KRAM-P 226/26

1a, 3a, 4: scale bar – 0.5 cm; 5, 6a: scale bar – 0.25 cm; 2: scale bar – 0.2 cm; 1b, 3b, 6b: scale bar – 0.2 mm

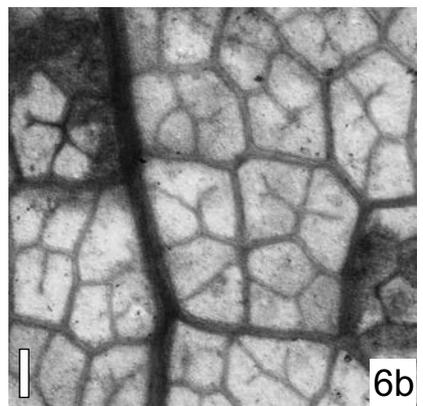
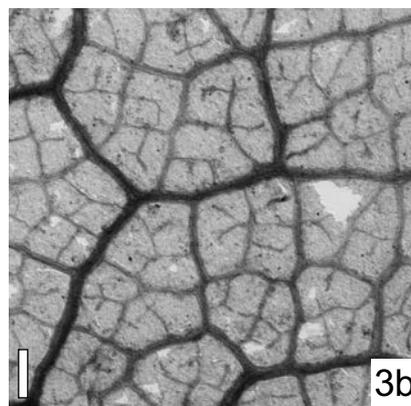
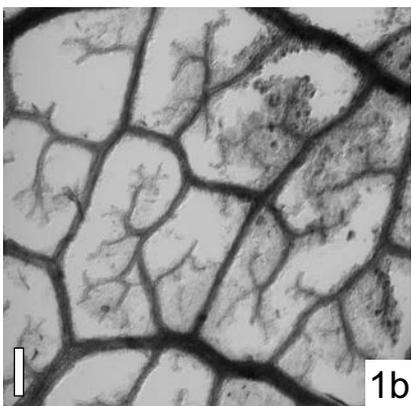
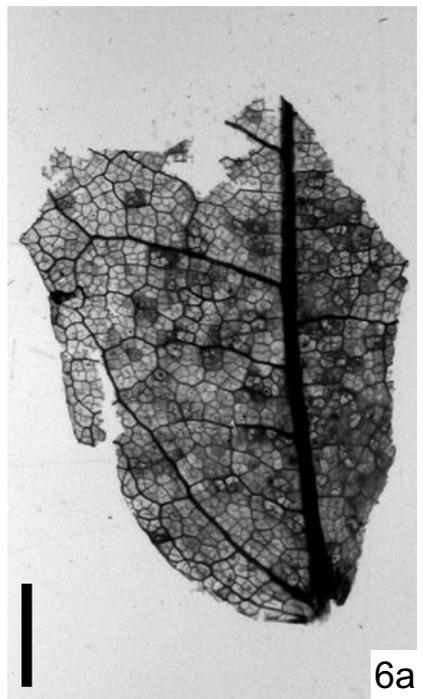
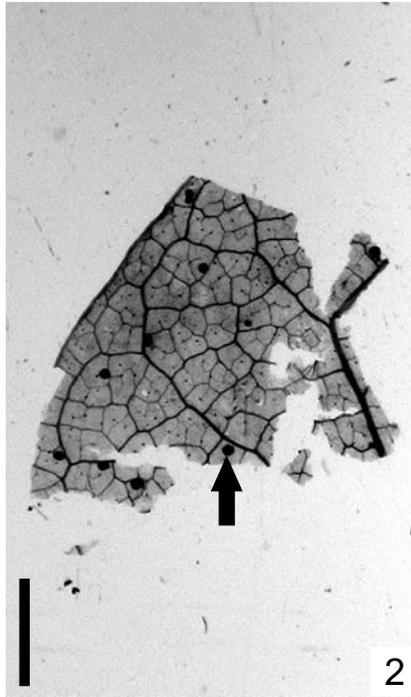


Plate 4

Pinus sp.

- 1a. Epidermis. Note the parallel arrangement of longer axes of stomata, specimen No. KRAM-P 226/19
- 1b. Epidermis. Note the presence of papillae (arrow), specimen No. KRAM-P 226/19

Bark of *Pinus* sp.

- 2. Detail of sclerenchymatic cells of bark, specimen No. KRAM-P 226/8

Alnus menzelii Raniecka-Bobrowska

- 3a. Adaxial epidermis, specimen No. KRAM-P 226/5
- 3b. Abaxial epidermis with stomata, specimen No. KRAM-P 226/5
- 3c. Abaxial epidermis with four-celled base of glandular trichome, specimen No. KRAM-P 226/5

Carpinus grandis Unger emend. Heer

- 4a. Adaxial epidermis, specimen No. KRAM-P 226/20
- 4b. Abaxial epidermis with stomata, specimen No. KRAM-P 226/20

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

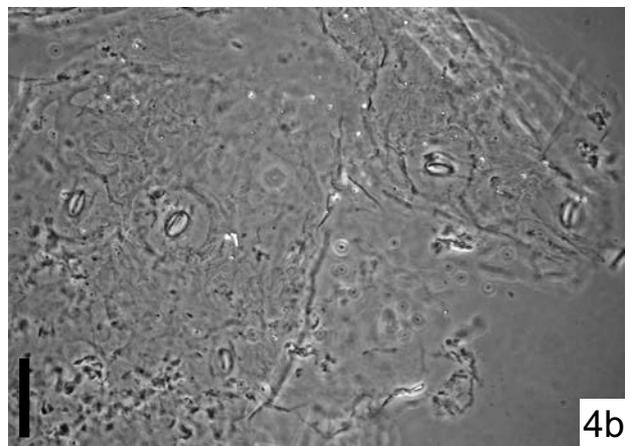
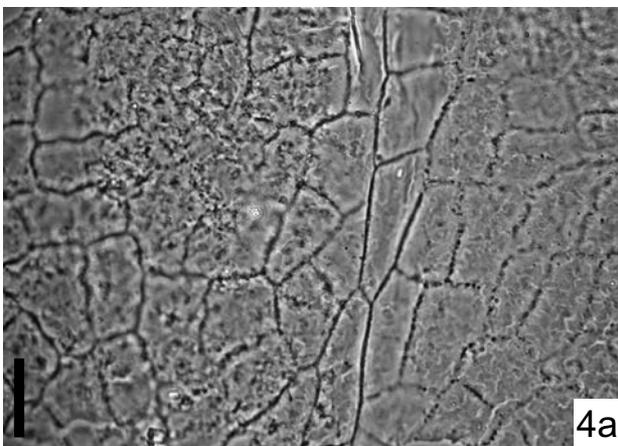
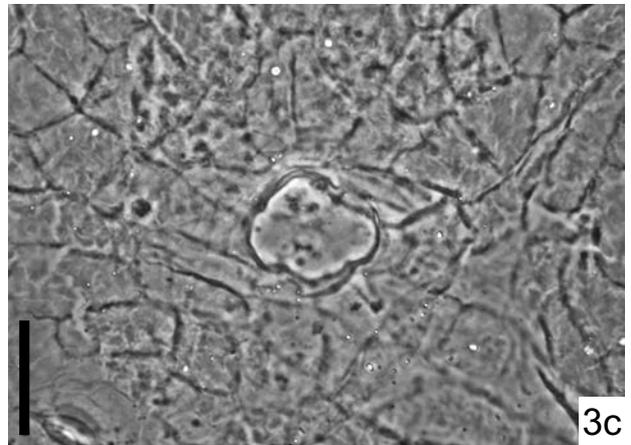
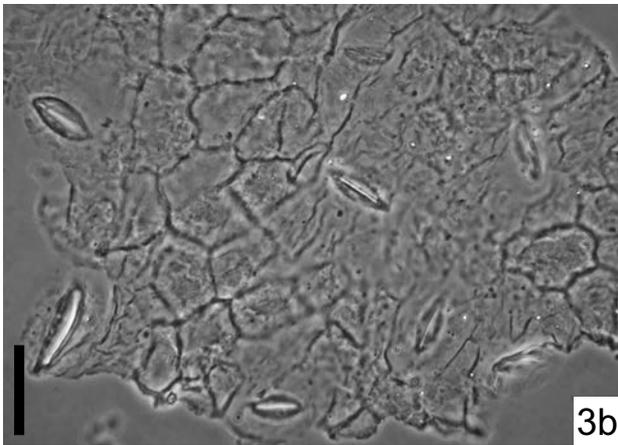
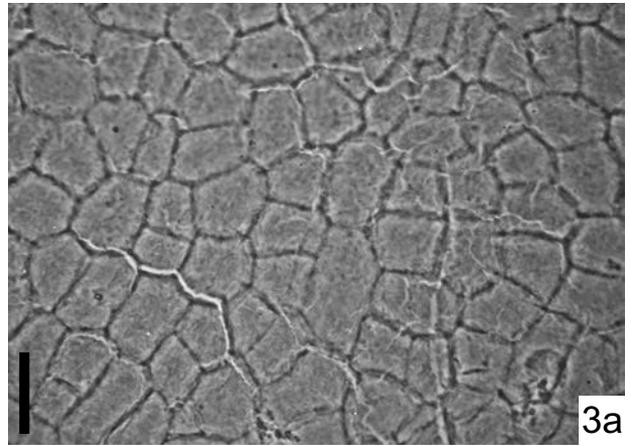
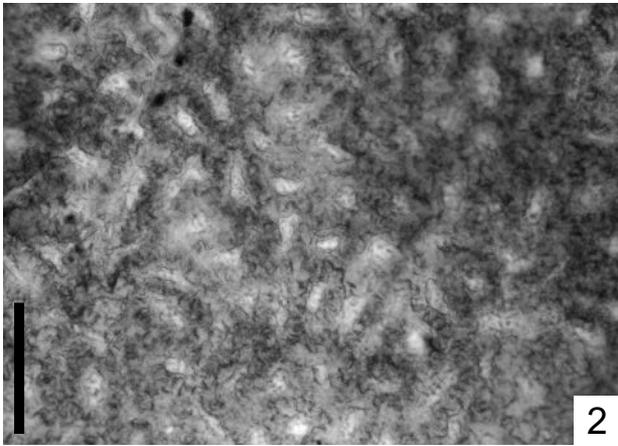
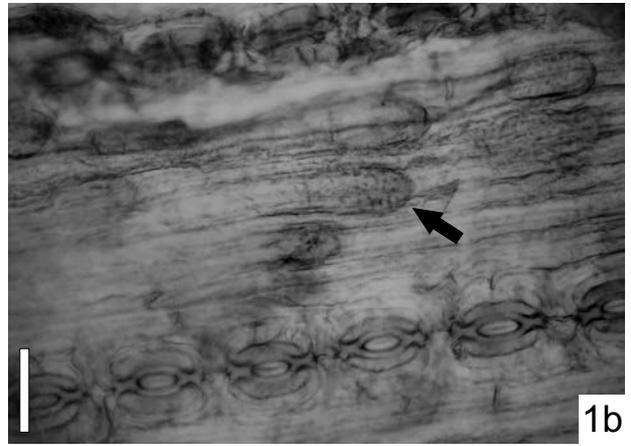
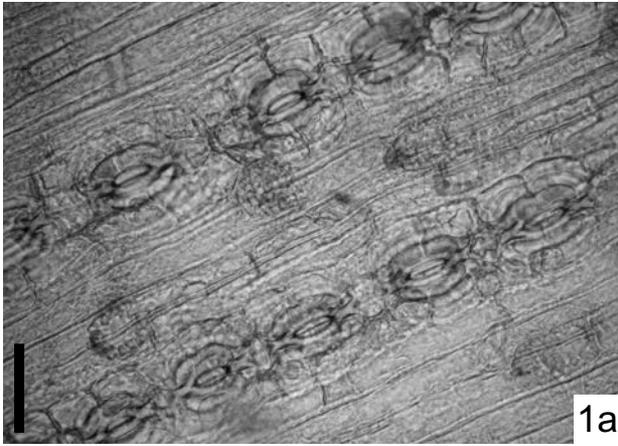


Plate 5

Fagus silesiaca Walther & Zastawniak

- 1a. Adaxial epidermis, specimen No. KRAM-P 226/10
- 1b. Abaxial epidermis with stomata, specimen No. KRAM-P 226/10

Quercus gigas Goeppert emend. Walther & Zastawniak

- 2a. Adaxial epidermis, specimen No. KRAM-P 226/11
- 2b. Adaxial epidermis, note stellate trichome base (arrow), specimen No. KRAM-P 226/11
3. Abaxial epidermis with stomata, specimen No. KRAM-P 226/3

Quercus pseudocastanea Goeppert emend. Walther & Zastawniak

- 4a. Abaxial epidermis with stomata and trichome base (arrow), specimen No. KRAM-P 226/9
- 4b. Detail of stellate trichome (arrow), specimen No. KRAM-P 226/9

“Parrotia” pristina (Ettingshausen) Stur

5. Trichome base, specimen No. KRAM-P 226/21

All photos: scale bar – 20 µm

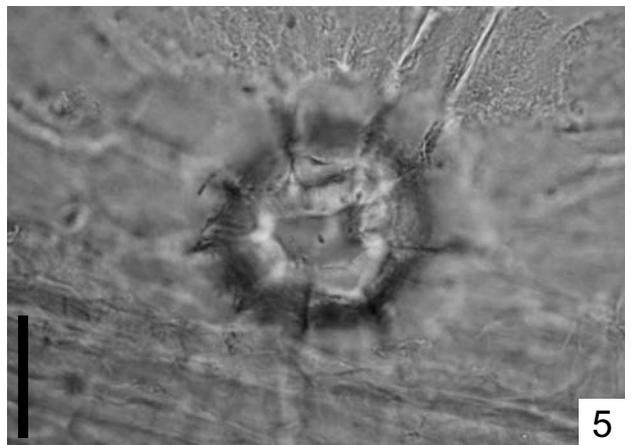
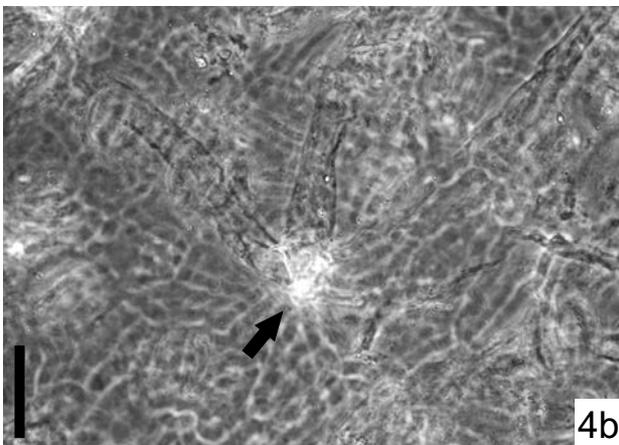
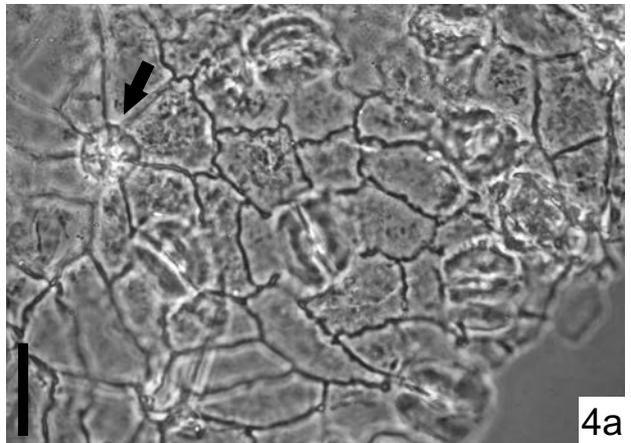
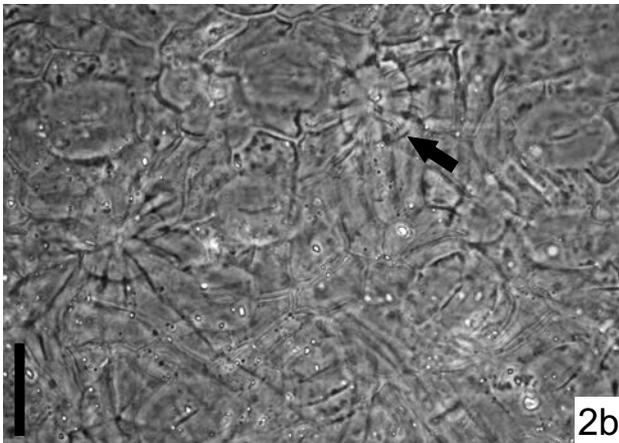
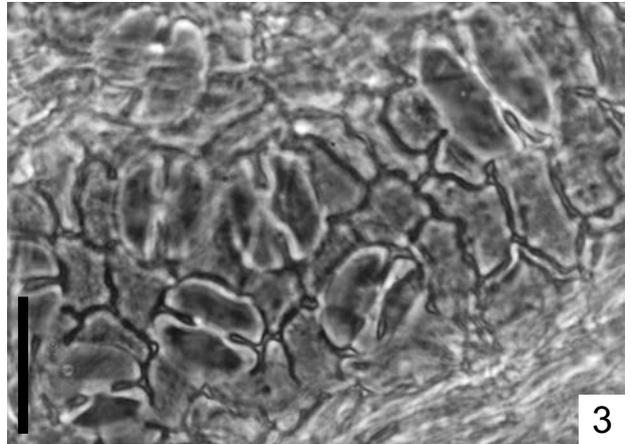
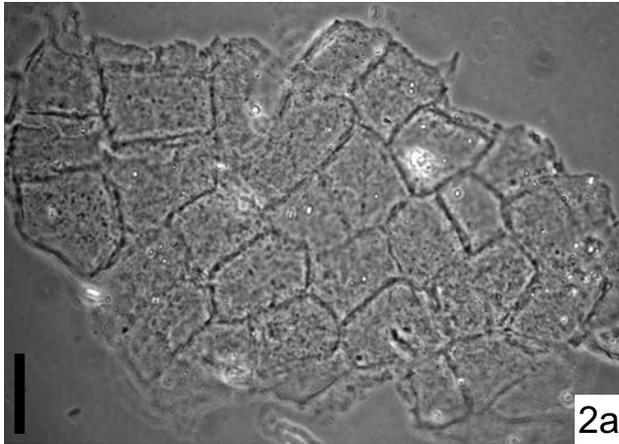
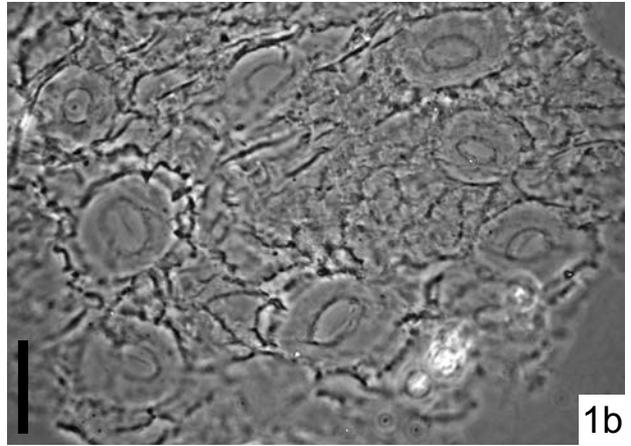
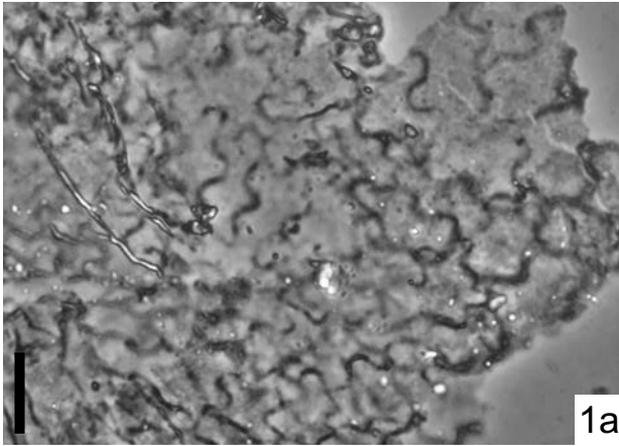


Plate 6

?Magnolia sp.

- 1a. Adaxial epidermis, specimen No. KRAM-P 226/27
- 1b. Abaxial epidermis with stomata, specimen No. KRAM-P 226/27

Acer cf. *aegopodifolium* (Goepfert) Baikovskaya ex Ilinskaya

- 2a. Adaxial epidermis, note striate ornamentation of cuticle, specimen No. KRAM-P 226/23
- 2b. Abaxial epidermis with stomata, specimen No. KRAM-P 226/23

Dicotylophyllum sp. 1

- 3a. Adaxial epidermis, note two unicellular, simple, solitary trichomes, specimen No. KRAM-P 226/22
- 3b. Abaxial epidermis with stomata, specimen No. KRAM-P 226/22

Dicotylophyllum sp. 2

- 4. Adaxial epidermis, specimen No. KRAM-P 226/26
- 5. Abaxial epidermis with stomata, specimen No. KRAM-P 226/25

1a, 1b: scale bar – 50 µm; 2a–5: scale bar – 20 µm

