

Wetland vegetation from the Miocene deposits of the Bełchatów Lignite Mine (central Poland)

Grzegorz Worobiec and Elżbieta Worobiec

ABSTRACT

Fossil plant remains (mainly leaves) of 18 species from the genera *Acer*, *Alnus*, *Betula*, *Carpinus*, *Carya*, cf. *Cercidiphyllum*, *Dicotylophyllum*, *Fagus*, *Gleditsia*, *Laria*, *Leguminophyllum*, *Myrica*, *Phragmites*, *Pinus*, *Potamogeton*, and *Sequoia* were found in upper Miocene deposits of the Bełchatów Lignite Mine (Central Poland). The fossil assemblage KRAM-P 225 is dominated by plant remains of bottomland forest type riparian vegetation. Some taxa point to the presence of water body and mesophytic upland communities. The composition of the fossil plant assemblage suggests warm temperate and moderately wet climatic conditions, comparable to the Cfa climate type (warm temperate, fully humid with hot summer) in the Köppen-Geiger climate classification. The mean annual temperature of 13.5°C–16.5°C was estimated by the coexistence approach method on the basis of plant macroremains. The deposits bearing these fossils are considered to be of latest middle Miocene to late Miocene age.

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Keywords: fossil leaves; new species; palaeovegetation; palaeoclimate; Neogene; Central Europe

Submission: 26 March 2018. Acceptance: 23 September 2019.

INTRODUCTION

Lignite deposits exploited by the Bełchatów Lignite Mine (central Poland) are amongst the largest Neogene lignite deposits in Europe mined for power plant industry purposes. They were discovered as a result of a geological investigation at the

beginning of the 1960s (Stuchlik et al., 1990). Neogene alluvial sediments with lignite seams that fill the tectonic depression named the Kleszczów Graben contain plant macro- and microremains. From 1960 to 1977 only palynological investigations of Neogene deposits from the Bełchatów mine were carried out. Ziemińska-Tworzydło (1966) consid-

Worobiec, Grzegorz and Worobiec, Elżbieta. 2019. Wetland vegetation from the Miocene deposits of the Bełchatów Lignite Mine (central Poland). *Palaeontologia Electronica* 22.3.63 1-38. <https://doi.org/10.26879/871>
palaeo-electronica.org/content/2019/2761-miocene-vegetation-of-poland

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ered the main coal seam to be of middle Miocene age based on palynological investigations. Starting from 1977, comprehensive palaeobotanical investigations of plant macroremains were carried out in the exposure. The results of investigations of plant macro- and microremains performed from 1977 to 1990 were summarised by Stuchlik et al. (1990). They established the age of deposits filling the Kleszczów Graben as Neogene, the main coal seam as late Miocene, and the overburden deposits as late Miocene–Pliocene (Stuchlik et al., 1990). Palaeobotanical investigations of the assemblages of plant macroremains from the Bełchatów Lignite Mine were then continued (Wójcicki and Zastawniak, 1998; Worobiec and Lesiak, 1998; Otto et al., 2001; Worobiec, 2003b; Worobiec and Worobiec, 2005; Worobiec, 2007; Worobiec and Szyrkiewicz, 2007; Worobiec and Worobiec, 2008; Worobiec et al., 2012; Worobiec, 2014; Worobiec and Szyrkiewicz, 2016; Worobiec and Worobiec, 2016). Besides fossil plant remains, fossil insects (Wegierek, 1995), snails (Stworzewicz and Szyrkiewicz, 1988; Stworzewicz, 1995), freshwater fishes (Jerzmańska and Hałuszczak, 1986), and mammals (Kowalski, 1993; Rzebik-Kowalska and Kowalski, 2001; Kowalski and Rzebik-Kowalska, 2002) preserved in the Neogene infilling of Kleszczów Graben were investigated.

During the investigations of Neogene deposits exposed in the Bełchatów Lignite Mine in October 1996, an interesting fossil leaf assemblage was found, although it has not yet been fully studied. Only the remains of Malvaceae *sensu lato* preserved in the discussed assemblage (fossil leaves of *Laria ruemianiana* (Heer) G. Worobiec and Kvaček) were investigated (Worobiec et al., 2010). The very good state of preservation of the plant fossils allows extensive palaeofloristical studies of the leaf remains. The current investigations are aimed at a comprehensive analysis of the palaeofloristics of the fossil assemblage followed by reconstruction of palaeovegetation. The results obtained form the basis for palaeoclimatic reconstructions and discussion of the age of the fossil assemblage. Data obtained by investigations of the discussed fossil plant assemblages from the Bełchatów mine contribute to reconstructing the Neogene flora and vegetation of Poland and to assessing and to documenting the biodiversity of Central Europe during the Neogene period.

GEOLOGY

Bełchatów Lignite Mine is situated in central Poland (51°15'46.4"N 19°18'49.2"E), south of the

town of Bełchatów (Figure 1). Neogene deposits with lignite seams occur within tectonic depressions of the Kleszczów Graben (Stuchlik et al., 1990). Four lithological units (subcoal unit [PW], coal unit [W], clayey-coal unit [I-W], and clayey-sandy unit [I-P]; Figure 2) were distinguished in the Neogene sedimentary series of the Kleszczów Graben (Czarnecki et al., 1992; Matl, 2000). The discussed leaf assemblage was found on October 24, 1996, in the Neogene deposits of the overburden escarpment 3 on the western slope of the open pit of the Bełchatów Lignite Mine, near spans 100–110 of conveyor belt B-302, southwest to borehole no. 1315. In the floor of the profile of the plant-bearing deposits were sands, clayey sands, and sandy clays covered by an erosional layer of flintstones and sands. The clay layer on top of this level contained the discussed plant assemblage covered by sands with silts. The discussed deposits belong to the clayey-sandy (I-P) unit considered to be of late Miocene age (Burchart et al., 1988; Stuchlik et al., 1990; Kowalski, 1993; Szyrkiewicz, 2000; Kowalski and Rzebik-Kowalska, 2002).

Wilczyński (1992) and Krzyszkowski and Winter (1996) considered the sedimentary series of the lower part of the clayey-sandy unit as having been formed in a fluvial environment of braided to meandering rivers with lush vegetation along the river banks.

MATERIAL AND METHODS

Fossil leaves from the discussed assemblage are preserved both as compressions and impressions. The best-preserved leaf compressions were isolated from the rock matrix and mounted on glass slides following the procedure described by Wor-



FIGURE 1. Location of the Bełchatów Lignite Mine.

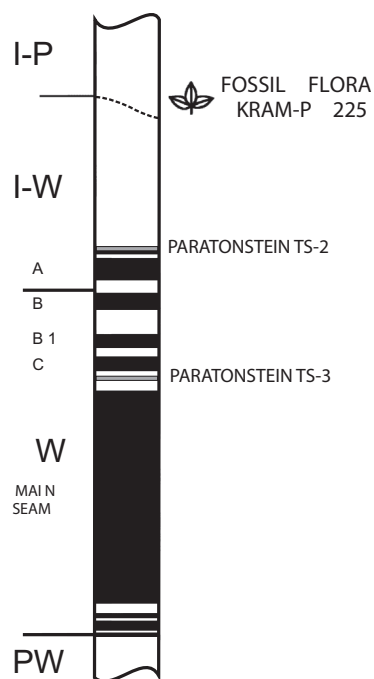


FIGURE 2. Schematic geological profile of Neogene deposits of the Bełchatów Lignite Mine (modified after Worobiec, 2007). PW, subcoal unit; W, coal unit; I-W, clayey-coal unit; I-P, clayey-sandy unit; A, B, B1, C, other coal seams. Black pattern, coal seams; grey pattern, paratonsteins (tuffaceous horizons).

biec (2003a). Thirty-seven slides of isolated leaves were made.

The remaining fossil leaves were slowly dried. In the case of isolated leaves and selected leaf compressions, small fragments of leaf blades were taken for cuticular analysis. These fragments were then cleaned with hydrofluoric acid, washed in water, macerated using NaClO solution (Bielnar commercial bleach), and finally mounted on slides with glycerine jelly. Altogether, 61 cuticular slides were made. All of the studied fossil leaves as well as the cuticular slides are housed in the W. Szafer Institute of Botany, Polish Academy of Sciences (Kraków) under catalogue number KRAM-P 225. The total number of specimens of all taxa is greater than the total number of rock samples with plant remains because in many cases remains belonging to different taxa were preserved in one rock sample. In such cases an alphanumerical specimen number is used. In total, 95 samples were studied.

Macromorphological descriptions of leaves mostly follow Hickey (1973, 1979) and Ellis et al. (2009), and micromorphological cuticular descriptions follow Dilcher (1974) and Wilkinson (1979). Macroscopic objects (specimens) were measured

with a ruler while microscopic ones (epidermal structures) were measured using microscope eyepiece with a scale (reticle). The measurements taken on the epidermal structures (e.g., cells, stomata) depended on their shape. The diameter was measured for round or broadly elliptic objects, while the length and width were used for all roughly rectangular objects. For objects of irregular 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.

For palynological analysis eight samples from clays, containing the plant macroremains of the KRAM-P 225 collection, were taken. The palynological samples were processed in the Laboratory of the W. Szafer Institute of Botany, PAS, using hydrochloric acid and sulfuric acid (Moore et al., 1991). Additionally, hydrofluoric acid was used to remove mineral matter and the residuum was sieved at 5 µm on a nylon mesh. From each sample, microscope slides were made, using glycerine jelly as a mounting medium. In each sample, more than 600 pollen grains and spores were identified, and for this purpose, one to three microscope slides were studied from each sample. The palynological residues and slides are stored in the W. Szafer Institute of Botany, PAS (Kraków).

SYSTEMATIC PALAEOBOTANY

The classification for gymnosperms follows Christenhusz et al. (2011), and for angiosperms and the author names of their families, it follows APG IV (2016), the IPNI (2018), and Farr and Zijlstra (2018). Plant families, genera, and species are listed following Chase and Reveal (2009), Haston et al. (2009), and Christenhusz et al. (2011).

Clade ACROGYMNOSPERMAE Cantino and Donoghue, 2007, in Cantino et al. (2007)

Family PINACEAE Sprengel ex F. Rudolphi, 1830
Genus *PINUS* Linnaeus, 1753

Type species. *Pinus sylvestris* Linnaeus, 1753

Pinus sp.
Figures 3.5, 4.1

Description

Macromorphology. Two fragments (up to 6 cm) of exfoliated bark.

Micromorphology. Cell walls strongly undulate, sclerenchymatic, rather thick.

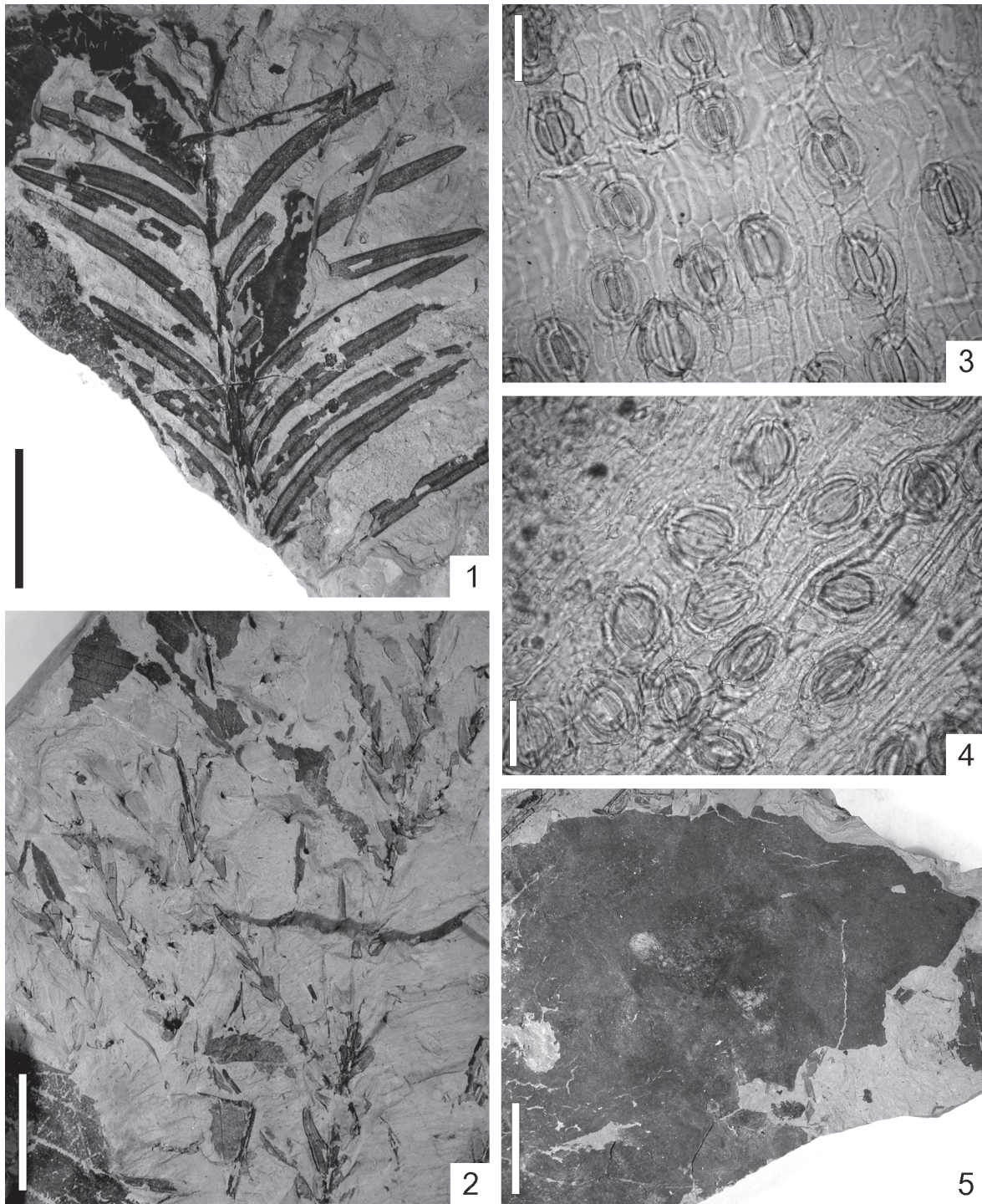


FIGURE 3. *Sequoia abietina* (Brongniart) Knobloch: 1. Taxodioid twig, KRAM-P 225/108; 2. Cryptomerioid twig, KRAM-P 225/86/VII; 3. Epidermis of needle from taxodioid twig, note parallel arrangement of longer axes of stomata in stomatal rows, KRAM-P 225/115; 4. Epidermis of needle from cryptomerioid twig, note variable arrangement of longer axes of stomata in stomatal rows, KRAM-P 225/86/VII. *Pinus* sp.: 5. Bark fragment, KRAM-P 225/99/II. Scale bar equals to 1 cm for (1), (2), and (5), and 50 μ m for (3) and (4).

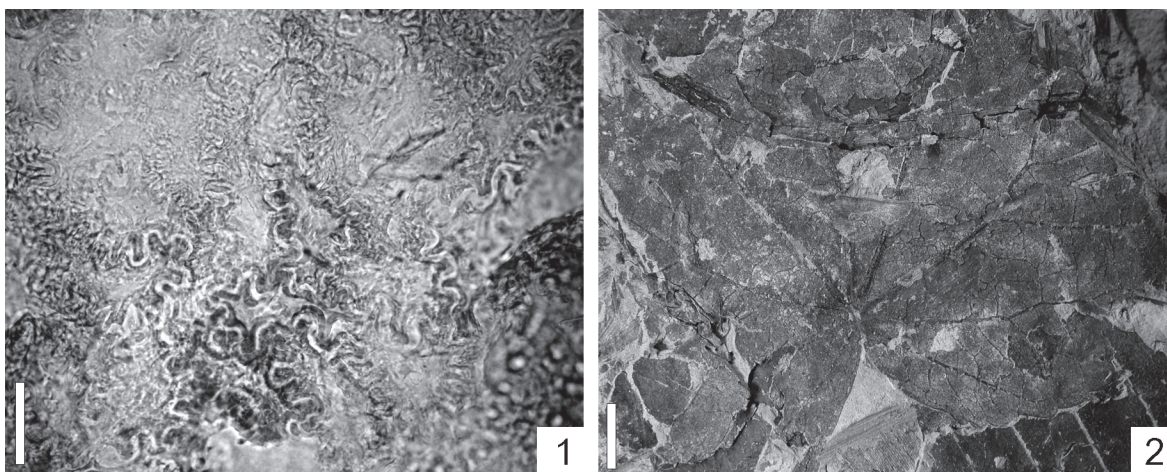


FIGURE 4. *Pinus* sp.: 1. Sclerenchymatic cells of bark, KRAM-P 225/99/II. cf. *Cercidiphyllum crenatum* (Unger) R. W. Brown emend. Z. Kvaček and Konzalová: 2. Leaf fragment, KRAM-P 225/44/II. Scale bar equals to 0.5 cm for (2), and 50 μ m for (1).

Specimens examined

KRAM-P 225: 48/II, 99/II.

Remarks

These plant remains represent the peeled bark of *Pinus*. Worobiec (2014) and Worobiec and Szyrkiewicz (2016) reported the same type of exfoliated bark of *Pinus* associated with the needles of *Pinus* sp. from late Miocene leaf assemblages from the Belchatów mine.

Family CUPRESSACEAE Gray, 1821

Genus *SEQUOIA* Endlicher, 1847

Type species. *Sequoia sempervirens* (D. Don) Endlicher, 1847

Sequoia abietina (Brongniart) Knobloch, 1964
Figure 3.1-4

Description

Macromorphology. Shoots trimorphous. Taxodioid shoots bearing flat, entire-margined needles with distinctly marked midvein, up to 3.1 (rarely to 3.5) cm long and 0.15 cm–0.22 cm wide, apex acute, base obtuse or cuneate. Presence of two stomatal bands one on each side of the midvein. Needles arranged in one plane on both sides of shoots. Sabre-shaped cryptomerioid and cupressoid shoots bearing distinctly smaller, entire-margined needles, up to 0.6 cm long and 0.10 cm–0.15 cm wide with an acute apex and distinctly decurrent base.

Micromorphology. Features of epidermal cells of taxodioid, cryptomerioid, and cupressoid shoots similar, differing mostly in the shape and size of the stomatal bands and arrangement of the stomata.

Epidermal cells usually rectangular, between stomatal bands up to 180 μ m long (taxodioid) and up to 73.5 μ m long (cryptomerioid) and 12.3 μ m–24.5 μ m wide. Epidermal cells of the stomatal bands of all morphotypes up to 80 μ m long. Cell walls straight, sometimes rounded, end walls usually oblique. Cuticle thick and covered by epicuticular wax granules. Hypodermis present, poorly preserved. Taxodioid shoots with wide stomatal bands composed of several stomatal rows, longer axes of these stomata more or less parallel to the midvein of needle. Stomatal bands of cryptomerioid type arranged in narrow bands, longer axes of stomata randomly oriented to midvein. Stomata monocyclocytic, elliptic to wide elliptic, 41 μ m–66 μ m long and 24.0 μ m–41.7 μ m wide. Outer stomatal ledge aperture elliptic-oblongate (sausage-like), 17.0 μ m–39.2 μ m long (taxodioid) and 14.7 μ m–17.1 μ m long (cryptomerioid) and 7.3 μ m–14.7 μ m wide. Polar T-shaped cuticular thickening always present, distinct.

Specimens Examined

KRAM-P 225: 40/III, 44/VI, 70/II, 86/VII, 91/IV, 92/III, 93/VI, 96/III, 105/IV, 108, 110/III, 115, 116, 120/III.

Remarks

The discussed remains of the conifer are macromorphologically most similar to fossil *Sequoia abietina* (Brongniart) Knobloch. However, *Taxodium dubium* (Sternberg) Heer also displays a similar macromorphology. Nevertheless, shoots of *Taxodium dubium* have shorter and narrower needles and the orientation of the longer axes of stomata is perpendicular or slightly oblique to the

longer axis of a needle in *Taxodium*, whereas in taxodioid shoots of *Sequoia abietina* the longer axes of stomata are parallel to the needle axis, similar to the above described remains from Bełchatów. *Sequoia abietina* typically displays polymorphous shoots: taxodioid, cryptomerioid, and cupressoid (Dyjur et al., 1992).

Modern Equivalents

The fossil *Sequoia abietina* is comparable to recent *Sequoia sempervirens* (D. Don) Endl. from western North America (Knobloch, 1969). This species grows on the slopes of the Coastal Range Mountains, mainly in California (Roy, 1966; Watson, 1993).

Ecology

The taxon is considered as a riparian element (Kovar-Eder et al., 2001) or as a tree typical of the raised bog stage of the succession of the coal-forming vegetation (Schneider, 1992). Extant *Sequoia sempervirens* from California grows in a warm-summer mediterranean climate (Csb type in the Köppen-Geiger climate classification, Kottek et al., 2006), usually in moist places where summer fogs occur (Roy, 1966).

Occurrences

Sequoia abietina commonly occurs in Neogene plant assemblages of Central Europe (Dyjur et al., 1992). In Poland it is found from the early to late Miocene (Worobiec et al., 2008).

Clade ANGIOSPERMAE Lindley, 1830

Family CERCIDIPHYLLACEAE Engler, 1907

Genus CERCIDIPHYLLUM Siebold and Zuccarini, 1846

Type Species. *Cercidiphyllum japonicum* Siebold and Zuccarini ex J. J. Hoffmann and J. H. Schultes, 1852

cf. *Cercidiphyllum crenatum* (Unger) R. W. Brown emend. Z. Kvaček and Konzalová, 1996

Figure 4.2

Description

Macromorphology. Leaf fragment ca. 5 cm, base cordate. Margin crenate, veins terminating in sinus between teeth. Venation palmate: actinodromous, perfect, basal. Primary vein branched into nine branches. Tertiary venation weakly percurrent.

Specimens Examined

KRAM-P 225: 44/II.

Remarks

Crenate margin and palmate venation are consistent with fossil *Cercidiphyllum crenatum* (Unger) R.W. Brown emend. Z. Kvaček and Konzalová. However, due to the poor state of preservation, taxonomical determination is only provisional.

Modern Equivalents

Probably extant *C. japonicum*, growing in Japan and China in moist valley mountainous forests (Kvaček and Konzalová, 1996; Wei et al., 2010), the only extant relative of *C. crenatum*.

Ecology

Cercidiphyllum crenatum is considered to be a component of the Neogene wetland vegetation (Kvaček and Konzalová, 1996; Kovar-Eder et al., 1998).

Occurrence

Cercidiphyllum crenatum is found in the Neogene deposits in Europe, Asia, and North America. In Poland it is rarely found in Miocene assemblages (Worobiec et al., 2008).

Family MYRICACEAE Richard ex Kunth, 1817, in Bonpland et al. (1817)

Genus MYRICA Linnaeus, 1753

Type Species. *Myrica gale* Linnaeus, 1753

Myrica lignitum (Unger) Saporta, 1865

Figure 5.1-8

Description

Macromorphology. Usually fragmentary, elongated leaves, up to 9 cm long and 1.2 cm–2.4 cm wide. Leaf apex acute to attenuate, leaf base cuneate to decurrent. Presence of both entire-margined and simple serrate leaves. Apical and basal sides of teeth usually acuminate. Teeth apex acute. Secondary veins terminating at the teeth apex. Petiole up to 1.0 cm long. Venation pinnate. Primary vein straight, stout. Secondary venation brochidodromous. Numerous thin secondary veins running off primary vein at intervals of 0.4 cm–0.8 cm and forming an angle of 60°–90° with it. Secondaries curved upwards and near the leaf margin, interconnected in loops. Intersecondary veins present, distinct. Tertiary venation composite intersecondary to random reticulate. Higher-order venation random reticulate. Areoles well developed, 0.42 mm–1.20 mm in size. Veinlets always multiple branched. Numerous glandular trichome shields often attached to the surfaces of leaf impressions.

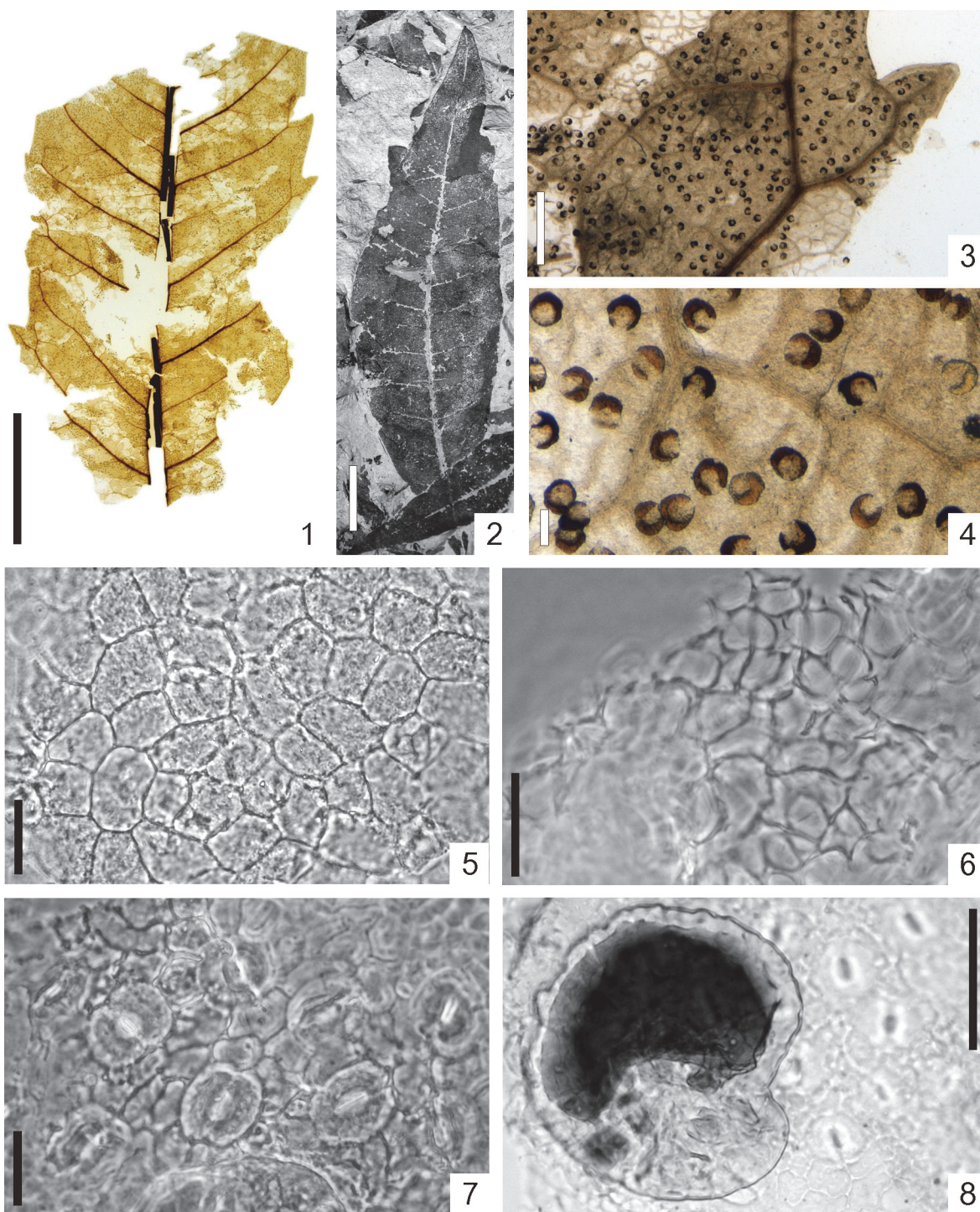


FIGURE 5. *Myrica lignitum* (Unger) Saporta: 1. Leaf fragment, KRAM-P 225/35; 2. Nearly whole leaf, KRAM-P 225/119/III; 3. Detail of tooth, KRAM-P 225/35; 4. Glandular trichome shields on leaf epidermis, KRAM-P 225/35; 5. Adaxial epidermis, KRAM-P 225/33; 6. hypodermis below adaxial epidermis, KRAM-P 225/34; 7. Abaxial epidermis with stomata, KRAM-P 225/35; 8. Glandular peltate trichome with remains of resinous secretion, KRAM-P 225/35. Scale bar equals to 1 cm for (1) and (2), 1 mm for (3), 100 μ m for (4), 50 μ m for (8), and 20 μ m for (5), (6), and (7).

Micromorphology. Adaxial epidermis composed of more or less isodiametric cells, 12.3 μm –27.0 μm in size. Anticlinal cell walls straight to rounded. Cuticle covered by epicuticular wax. Presence of hypodermis below adaxial epidermis, composed of roundish cells, 7.3 μm –12.3 μm . Abaxial epidermis consisting of irregular-shaped, isodiametric to elongated cells, 12.3 μm –19.6 μm in size. Anticlinal cell walls rounded. Cuticle covered by epicuticular wax. Leaves hypostomatic. Stomata anomocytic, rounded or widely elliptic, 20 μm –25 μm in diameter. Outer stomatal ledge aperture wide elliptic or rounded, 7.3 μm –12.3 μm in size. Polar T-shaped cuticular thickening visible on undermacerated cuticular fragments. On the abaxial epidermis, presence of numerous glandular peltate trichomes. Trichome shield multicellular, composed of radially arranged cells, 86 μm –118 μm in diameter. Remains of resinous secretion preserved inside some trichomes. Two-celled trichome bases, irregularly-elliptic, 20 μm –25 μm in size.

Specimens Examined

KRAM-P 225: 33, 34, 35, 40/II, 41/II, 43/II, 44/IV, 47/IV, 49/II, 54/II, 55/II, 58/V, 60/VI, 63/II, 68/IV, 69/II, 71/III, 72/IV, 74/II, 77/II, 80, 81/II, 82/II, 83/IV, 85/II, 86/V, 87/II, 88/V, 90, 91/III, 93/III, 94/II, 95/II, 96/II, 97/II, 99/I, 104/IV, 105/III, 106/II, 110/II, 119/III, 129, 130, 131.

Remarks

The described leaves are macro- and micro-morphologically similar to *Myrica lignitum* (Unger) Saporta *sensu lato*. The shape of both entire-margined and serrate leaves, venation pattern, and epidermal structure (stomata, peltate glandular trichomes) are typical for this fossil species. The fossil leaves of *Myrica* are macromorphologically very similar to fossil leaves of the genus *Engelhardia* Lesch. ex Bl. from the Juglandaceae family. *Engelhardia* differs from *Myrica* in the asymmetrical shape of the leaflets, which are usually smaller than *Myrica* leaves, and in the one-celled bases of glandular trichomes.

Modern Equivalents

Macromorphologically *Myrica lignitum* resembles several extant species of the same genus from North America, East Asia, and tropical mountain forests of Africa (Ilinskaya, 1964; Knobloch, 1969).

Ecology

Usually considered as a component of acid, swampy communities (Zidianakis et al., 2015).

Occurrence

Myrica lignitum is a common element of Neogene fossil floras (Knobloch and Kvaček, 1976).

Family BETULACEAE Gray, 1821

Genus *ALNUS* Miller, 1754

Type Species. *Alnus glutinosa* (Linnaeus) J. Gærtner, 1791 .

Alnus ducalis (Gaudin) Knobloch, 1969

Figure 6.1-4

Description

Macromorphology. Leaves up to 6.5 cm long and 5.2 cm wide. Leaf apex strongly emarginate, leaf base obtuse and slightly decurrent, mostly without teeth. Leaf margin serrate, teeth large, apical and basal sides of teeth acuminate. Teeth apex acute. Secondary veins and subsidiary veins terminating at the teeth apex. Venation pinnate, primary vein straight, of moderate thickness. Secondary venation simple craspedodromous, preserving up to seven pairs of secondaries, veins curved upwards, distributed at intervals of 0.3 cm near leaf base to 0.6 cm–0.9 cm in the middle of the lamina. Secondary veins diverging from midvein at an angle of 60°–80° near leaf base, 45°–60° in the middle of the lamina, and decreasing to 30° near leaf apex. Tertiary venation percurrent, ca. 5–8 tertiary veins occurring per 1 cm of secondary vein length. Tertiary venation with the primary vein forming an angle of 145° near leaf base, 125° in the middle of the lamina, and 100°–115° near leaf apex. Higher-order venation often orthogonal reticulate. Areoles well developed, ca. 0.4 mm in size.

Micromorphology. Adaxial epidermis composed of isodiametric to slightly elongate cells, 19 μm –39 μm in size. Anticlinal cell walls mainly straight. Adaxial cuticle covered by rather distinct epicuticular wax layer, sometimes cuticle also with striate ornamentation. Abaxial epidermis cells usually slightly elongated, 19.6 μm –31.9 μm in size, anticlinal cell walls usually straight, rarely rounded. Leaves hypostomatic. Stomata rather poorly preserved. Outer stomatal ledge aperture wide elliptic or spindle-shaped, ca. 15 μm long and 5.0 μm –7.3 μm wide. On the abaxial epidermis, 4-celled (very rarely 5–6 celled) roundish trichome bases, 22.0 μm –29.4 μm in size.

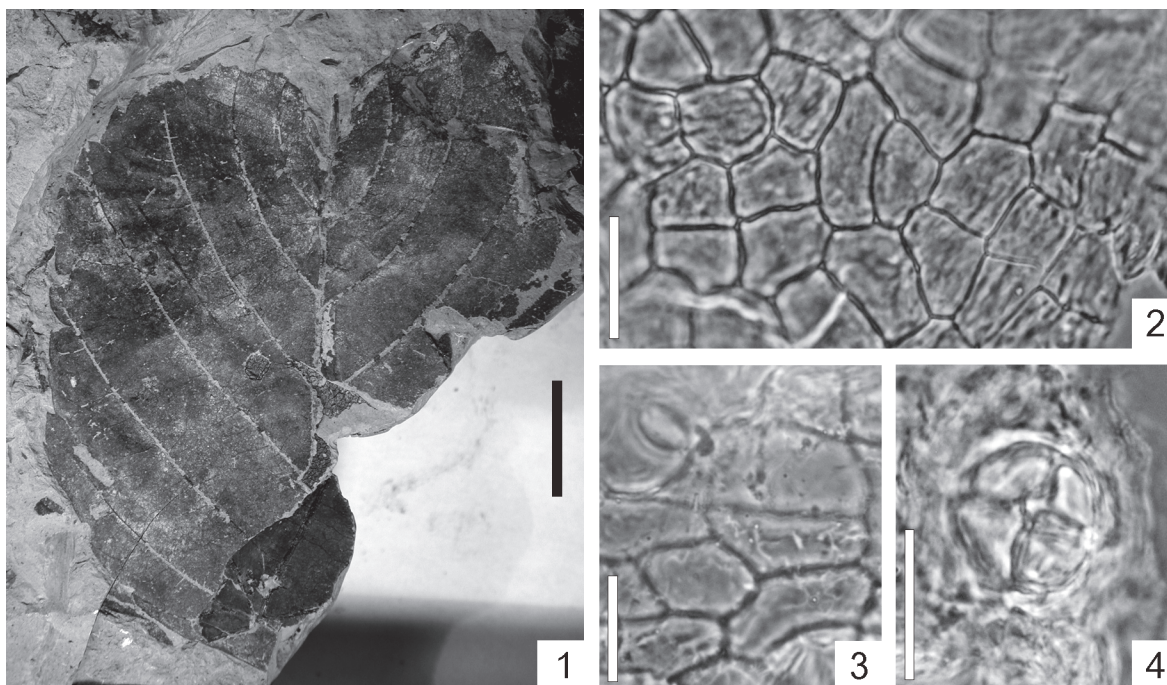


FIGURE 6. *Alnus ducalis* (Gaudin) Knobloch: 1. Leaf fragment, KRAM-P 225/88/I; 2. Adaxial epidermis, KRAM-P 225/122/I; 3. Abaxial epidermis with stoma, KRAM-P 225/88/I; 4. Four-celled base of glandular trichome, KRAM-P 225/122/I. Scale bar equals to 1 cm for (1), and 20 µm for (2), (3), and (4).

Specimens Examined

KRAM-P 225: 88/I, 122/I.

Remarks

The unique shape of this leaf type with strongly emarginate apex along with venation network unambiguously point to the fossil alder species *Alnus ducalis* (Gaudin) Knobloch.

Modern Equivalents

Extant *Alnus matsumurae* Callier from Japanese montane forests displays an almost identical morphology of leaves, especially emarginate apex (Kovar-Eder et al., 1996).

Ecology

Temperate element. Hably and Kovar-Eder (1996) and Kovar-Eder et al. (1996) considered it to be a component of riparian plant assemblages.

Occurrence

Alnus ducalis is an element of middle to late Miocene plant assemblages (Kovar-Eder et al., 1996). In Poland *Al. ducalis*, was previously reported only from middle Miocene localities, namely Czernica, Kokoszyce, and Młyny (Kovar-Eder et al., 1996). Stuchlik et al. (1990) mistakenly reported a leaf fragment of *Carya* from Belchatów as

being *Alnus ducalis* (Worobiec and Szyrkiewicz, 2007).

Genus *BETULA* Linnaeus, 1753

Type Species. *Betula alba* Linnaeus, 1753

Betula cf. *plioplatyptera* Hummel, 1991

Figure 7.1

Description

Macromorphology. Leaf fragments, up to 6 cm long and 1.8 cm–4.6 cm wide. Leaf apex probably acute, leaf base obtuse, mostly without teeth. Leaf margin double serrate, apical and basal sides of teeth more or less acuminate. Teeth apex acute. Secondary veins and subsidiary veins terminating at the teeth apex. Venation pinnate, primary vein straight, of moderate thickness. Secondary venation simple craspedodromous, preserving up to eight pairs of secondaries, veins first straight then curving upwards near leaf margin, distributed at intervals of 0.3 cm–0.4 cm near leaf base to 0.4 cm–0.5 cm in the middle of the lamina. Secondary veins diverging from midvein at an angle of 60°–70° near leaf base to 40°–55° in the middle of the lamina. Tertiary venation percurrent, ca. eight tertiary veins occur per 1 cm of secondary vein length. Tertiary venation forming an angle of ca. 140° with the primary vein. Higher-order venation

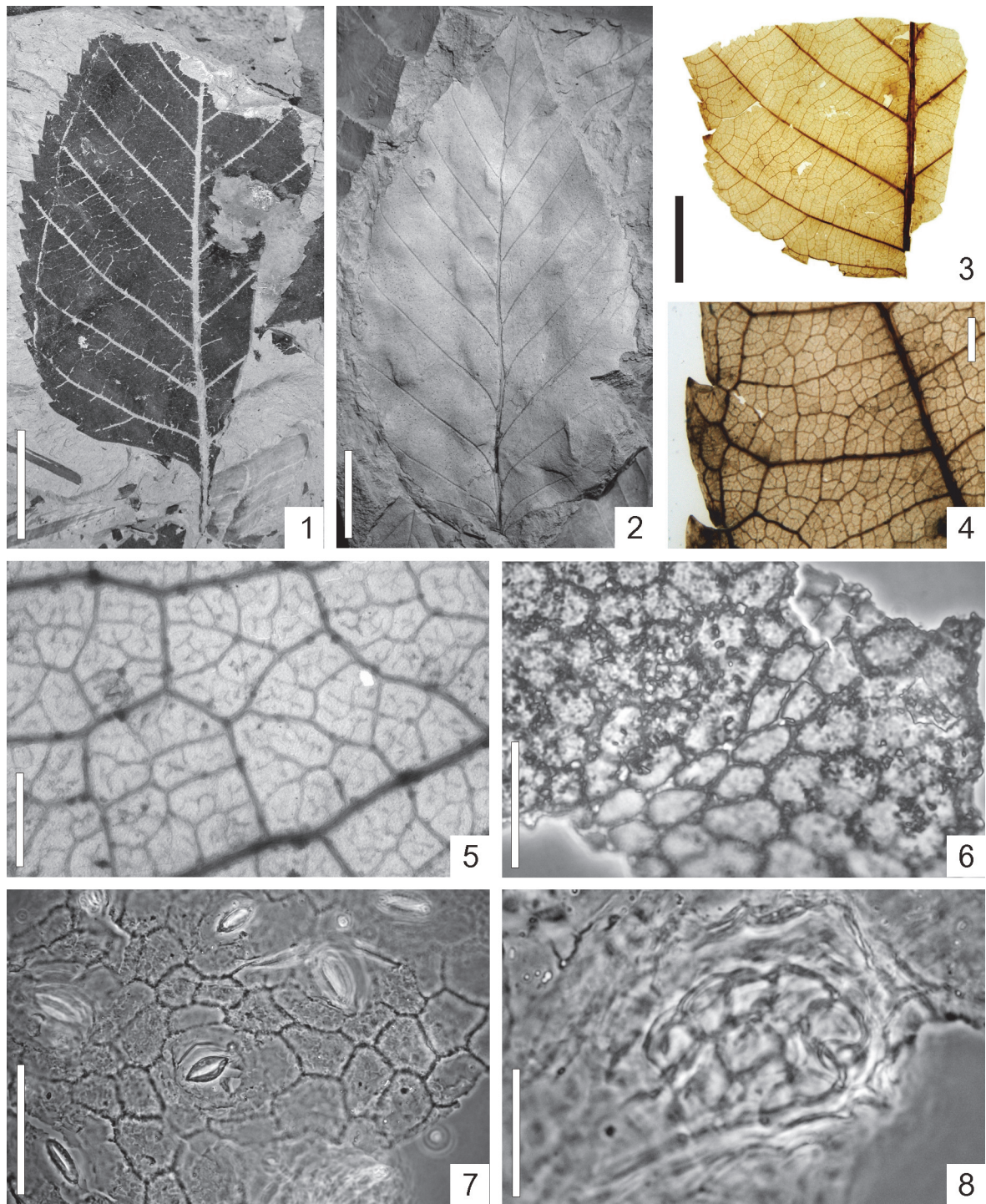


FIGURE 7. *Betula* cf. *plioplaptera* Hummel: 1. leaf, KRAM-P 225/106/I. *Betula subpubescens* Goeppert emend. Worobiec: 2. leaf, KRAM-P 225/104/I; 3. Fragment of basal part of leaf, KRAM-P 225/26; 4. Detail of leaf margin and teeth venation, KRAM-P 225/26; 5. Detail of leaf areolation, KRAM-P 225/26; 6. Adaxial epidermis, KRAM-P 225/26; 7. Abaxial epidermis with stomata, KRAM-P 225/26; 8. Multicellular glandular trichome base, KRAM-P 225/27. Scale bar equals to 1 cm for (1), (2), and (3), 1 mm for (4), 0.5 mm for (5), 50 μ m for (6) and (7), and 20 μ m for (8).

reticulate. Areoles well developed, 0.4 mm–0.6 mm in size. Veinlets multiple branched. Numerous glandular trichome shields often attached to the surfaces of leaf impressions exclusively on the impressions of leaf veins.

Specimens Examined

KRAM-P 225: 73, 93/I, 94/I, 106/I.

Remarks

The macromorphological features of the above described leaf fragments (e.g., shape of the leaves, large primary teeth) are most similar to *Betula plioplaptera* Hummel. However, the diagnostic features of the latter fossil species given by Hummel (1991) do not clearly separate it from *Betula subpubescens* Goeppert emend. Worobiec. Thus, it should not be overlooked that *Betula plioplaptera* could in fact be conspecific with *Betula subpubescens* and that the differences between these two fossil species could result from the natural morphological variability of their leaves.

Modern Equivalents

Betula plioplaptera resembles the extant North American species *B. papyrifera* Marsh. However, it differs considerably in respect of the structure of epidermis (Hummel, 1991).

Ecology

Similarly to extant *Betula papyrifera*, fossil *Betula plioplaptera* is considered as a temperate element.

Occurrence

In Poland the taxon is found in the Miocene deposits of Bełchatów (Worobiec and Szyrkiewicz, 2007) and the early Pliocene of Ruszów (Hummel, 1991).

Betula subpubescens Goeppert emend.
Worobiec, 2007
Figure 7.2-8

Description

Macromorphology. Leaves elliptic to ovate, up to 6.2 cm long and 2.5 cm–4.0 cm wide. Leaf apex acute to attenuate, base obtuse, rounded, rarely cuneate. Petiole (rarely entirely preserved) up to 0.9 cm long. Leaf margin double serrate, leaf base often entire-margined. Apical and basal sides of teeth mostly acuminate, teeth apex acute. Secondary veins and subsidiary veins terminating at teeth apex. Venation pinnate, primary vein straight, of

moderate thickness. Secondary venation simple craspedodromous, up to 9–11 pairs of secondaries preserved, arising at intervals of 0.4 cm–0.5 cm near leaf base and 0.4 cm–1.0 cm in the middle of the lamina. Secondaries more or less straight or curved upwards near leaf margin, diverging from midvein at an angle of 60°–70° near leaf base and 40°–55° in the middle of the lamina. Tertiary venation percurrent, convex, 5–10 tertiary veins occurring per 1 cm of secondary vein length and forming an angle of ca. 140° with the primary vein. Higher-order venation reticulate. Areoles well developed, 0.3 mm–0.6 mm in size. Veinlets multiple branched. Marginal ultimate venation incompletely looped. On some leaf impressions, presence of glandular trichome shields attached to the specimen surfaces exclusively on the impressions of leaf veins.

Micromorphology. Adaxial epidermis composed of more or less isodiametric cells, 15.0 µm–29.6 µm in size with usually straight, rarely rounded, anticlinal cell walls. Adaxial cuticle covered by a distinct epicuticular wax layer. Abaxial epidermis composed of isodiametric to elongated cells, 12.3 µm–36.8 µm in size, over the veins strongly elongated with straight to rounded anticlinal cell walls. Abaxial cuticle also covered by an indistinct epicuticular wax layer. Leaves hypostomatic. Stomata anomocytic, elliptic to narrow elliptic, 19.6 µm–34.3 µm long and 12.3 µm–19.6 µm wide. Outer stomatal ledge aperture wide elliptic or rounded, 14.7 µm–22.0 µm long and 4.9 µm–9.8 µm wide. Presence of glandular peltate trichomes on the abaxial epidermis. Trichome shield ca. 74 µm in diameter. On the abaxial epidermis, presence of glandular trichome bases, multicellular (5- to 10-celled, very rarely 4-celled), 27.0 µm–36.7 µm in size.

Specimens Examined

KRAM-P 225: 26, 28, 39/I, 42/I, 47/I, 60/I, 64/III, 66/I, 67/I, 68/I, 71/I, 72/I, 74/I, 88/II, 89/I, 91/I, 95/I, 104/I, 117, 125/I, 126, 128. cf. *Betula subpubescens*: 27.

Modern Equivalents

Betula subpubescens is comparable to recent *Betula pubescens* Ehrh., *B. utilis* D. Don., *B. davurica* Pall. (Hummel, 1991), and to *B. verrucosa* Ehrh. (Němejč, 1949).

Ecology

Similarly to modern equivalents, fossil *Betula subpubescens* is considered as a temperate element.

Occurrence

In Poland the species is found in middle Miocene to lower Pliocene deposits (Krajewska, 1998).

Betula sp.

Description

Badly preserved fragments of leaves of *Betula*.

Specimens Examined

KRAM-P 225: 44/I, 83/I, 86/I, 105/I, 123/I.

Remarks

These remains of leaves of fossil birch are so badly preserved that a precise identification is not possible. One scale of birch catkin was also found (specimen KRAM-P 225/125/II).

Genus *CARPINUS* Linnaeus, 1753

Type Species. *Carpinus betulus* Linnaeus, 1753.

Carpinus grandis Unger emend. Heer, 1856
Figure 8.1-4, 8.6-7

Description

Macromorphology. Leaves usually ovate, up to 5.7 cm long and 1.8 cm–3.0 cm wide with attenuate apex and obtuse, rounded, or slightly cordate base. Leaf margin double serrate, teeth small, numerous (especially in basal part of leaf), more or less of the same size, apical side of teeth acuminate (rarely concave), basal side acuminate (rarely convex). Teeth apex sharply acute, teeth often hook-shaped towards leaf apex. Secondary veins and their branches terminating at the teeth apex. Venation pinnate, primary vein straight, of moderate thickness or thin. Secondary venation simple craspedodromous. Secondaries preserved in up to 13 pairs, more or less straight or curved upwards near leaf margin, distributed at intervals of ca. 0.3 cm near leaf base and 0.4 cm–0.6 cm in the middle part of the lamina. Secondary veins diverging from midvein at an angle of 60°–70° near leaf base and 40°–55° in the middle of the lamina, usually producing numerous branches entering the nearest teeth close to the leaf margin. Tertiary venation percurrent, forming an angle of 120°–125° with the primary vein. Ten to 12 (sometimes 14) tertiary veins occurring per 1 cm of secondary vein length. Higher-order venation predominately orthogonal reticulate. Areoles well developed, 0.36 mm–0.60 mm in size. Veinlets simple or absent. Marginal ultimate venation incompletely looped.

Micromorphology. Adaxial epidermis composed of isodiametric or slightly elongated cells 12.3 µm – 29.4 µm in size, with straight, rounded, or sometimes slightly undulate anticlinal cell walls. Adaxial cuticle covered by a distinct epicuticular wax layer. Walls of abaxial epidermis cells mostly not visible, straight to rounded, ca. 30 µm in size. Leaves hypostomatic. Stomata roundish, 14.7 µm–19.6 µm in diameter. Outer stomatal ledge aperture elliptic, narrow elliptic, sometimes spindle-shaped, 6.1 µm–9.8 µm long and 3.7 µm–4.9 µm wide. Trichomes not found.

Specimens Examined

KRAM-P 225: 29, 30, 31, 32, 39/II, 40/IV, 41/I, 47/II, 58/I, 60/II, 64/I, 70/I, 71/II, 72/II, 75/I, 76, 77/I, 79/I, 83/II, 86/II, 88/III, 93/II, 96/I, 98, 102, 104/II, 105/II, 107/I, 120/I, 122/II, 123/II, 125/III, 132.

Remarks

Double serrate leaf margin with considerably small teeth, secondary veins branching, and venation of the leaf base are characteristics of the fossil species *Carpinus grandis* Unger emend. Heer. This is probably a collective species (Mai and Walther, 1978, 1988; Hummel, 1991; Zastawniak and Walther, 1998).

Modern Equivalents

Carpinus grandis corresponds to recent hornbeam species of section *Eucarpinus* (comp. Krüssmann, 1976) and could be compared to *Carpinus betulus* L. (Heer, 1856; Zastawniak, 1972; Hummel, 1991; Krajewska, 1998), *Carp. caucasica* Grossh. (Hummel, 1991), and *Carp. orientalis* Mill. (Ilinskaya, 1968).

Ecology

Similarly to modern equivalents, fossil *Carpinus grandis* is considered as a temperate element.

Occurrence

Carpinus grandis is known from the middle Oligocene to the late Pliocene plant assemblages from Europe (Mai and Walther, 1978, 1988; Hummel, 1991; Zastawniak and Walther, 1998). In Poland this fossil taxon can be found from the early Miocene to the early Pliocene (Hummel, 1991; Krajewska, 1998; Worobiec et al., 2008).

Carpinus sp.
Figure 8.5

Description

Badly preserved fragments of fruit involucre.

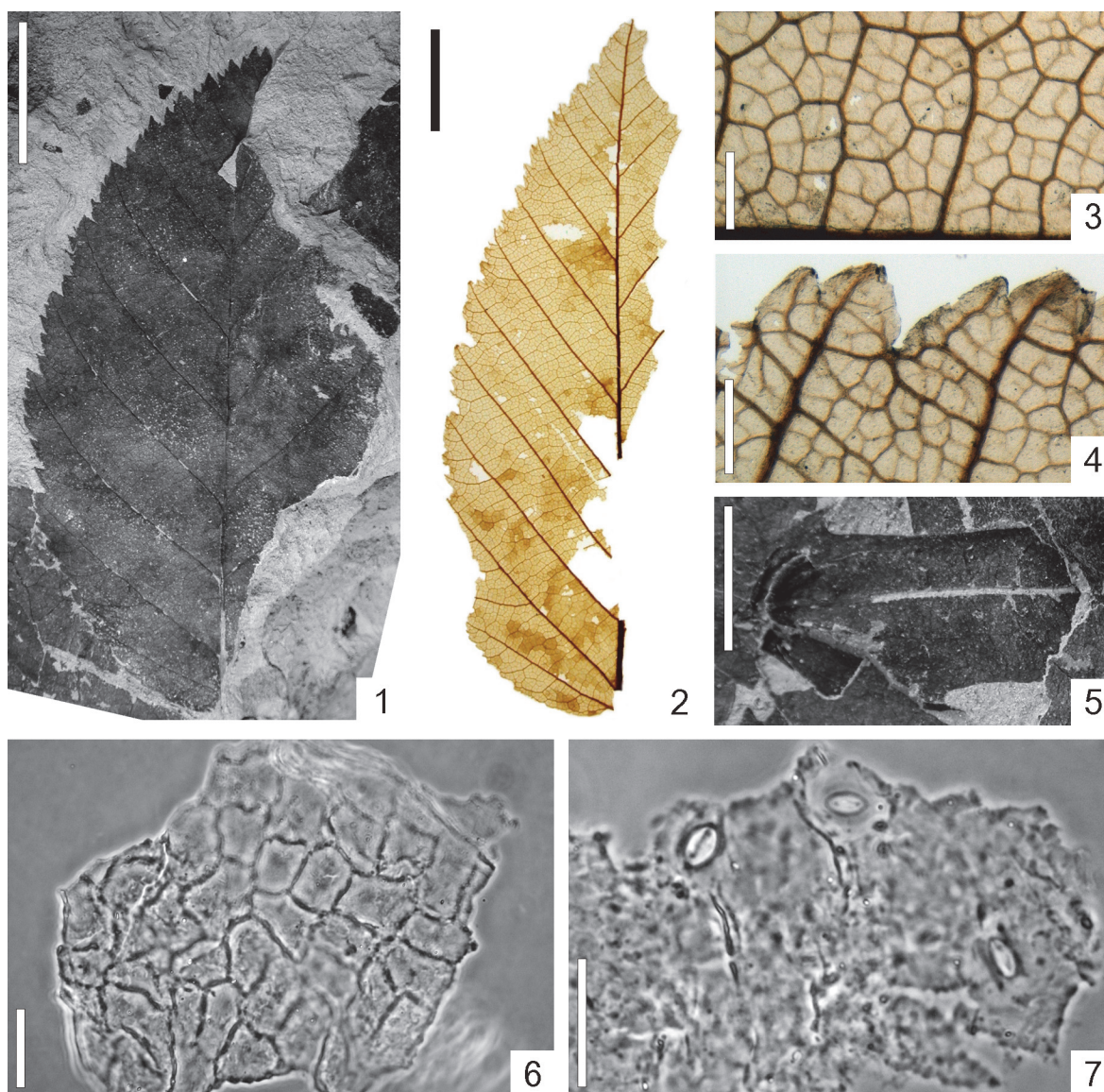


FIGURE 8. *Carpinus grandis* Unger emend. Heer: 1. Leaf, KRAM-P 225/40/IV; 2. Leaf, KRAM-P 225/30; 3. Detail of leaf areolation, KRAM-P 225/30; 4. Detail of leaf margin and teeth venation, KRAM-P 225/30; 6. Adaxial epidermis, KRAM-P 225/31; 7. Abaxial epidermis with stomata, KRAM-P 225/31. *Carpinus* sp.: 5. Fragment of fruit involucre, KRAM-P 225/91/II. Scale bar equals to 1 cm for (1), 0.5 cm for (2) and (5), 0.5 mm for (3) and (4), and 20 μ m for (6) and (7).

Specimens Examined

KRAM-P 225: 91/II, 119/I.

Remarks

Remains of fruits of fossil hornbeam. Due to the poor state of preservation, a more precise identification is not possible.

BETULACEAE indet.

Specimens Examined

KRAM-P 225: 41/III, 45/II, 49/III, 51/III, 52/II, 55/III, 60/VIII, 67/IV, 68/I, 69/III, 72/V, 78/II, 82/III, 91/V, 101, 105/V.

Remarks

On the basis of the serration of leaf margin typical of Betulaceae members, these leaf fragments undoubtedly belong to the Betulaceae family. Due to the rather poor state of preservation, a more precise identification is not possible.

Family FAGACEAE Dumortier, 1829

Genus *FAGUS* Linnaeus, 1753

Type Species. *Fagus sylvatica* Linnaeus, 1753.

Fagus silesiaca Walther and Zastawniak, 1991
Figure 9.1-6

Description

Macromorphology. Leaves elliptic, up to 6.8 cm long and 3.0 cm–3.5 cm wide. Leaf apex attenuate, leaf base obtuse. Leaf margin simple serrate, teeth upwardly curved, apical side of teeth concave, basal side acuminate or straight, teeth apex rounded. Venation pinnate, primary vein thin, sometimes sinuous (zig-zag). Secondary venation simple craspedodromous. Secondaries alternate, preserved in up to ten pairs, straight, right on leaf margin sometimes upwardly curved, distributed at intervals of 0.5 cm–0.9 cm. Secondary veins diverging from midvein at an angle of 40°–50°. Tertiary venation percurrent, forming an angle of 125°–135° with the primary vein. Eight to 10 tertiary veins occurring per 1 cm of secondary vein length. Four-order venation orthogonal reticulate. Areoles well developed, 0.36 mm–0.48 mm in size. Veinlets simple or absent. Marginal ultimate venation looped.

Micromorphology. Adaxial epidermis composed of usually slightly elongated cells with undulate cell walls (sometimes straight-walled), 25.0 µm–41.7 µm in size. Over veins cells straight-walled. Abaxial epidermis consisting of variable-shaped cells with straight (rarely rounded) cell walls, 19.6 µm–36.8 µm in size. Leaves hypostomatic. Stomata cyclocytic, roundish, sometimes wide elliptic, 20 µm–25 µm in diameter. T-shaped cuticular thickenings usually slightly visible at poles of guard cells. Outer stomatal ledge elliptic, 9.8 µm–12.3 µm long and 4.9 µm–7.4 µm wide. On abaxial epidermis, presence of unicellular trichome bases, roundish, 9.8 µm–13.5 µm in diameter.

Specimens Examined

KRAM-P 225: 12, 15, 24, 67/II, 79/II, 89/II, 104/III, 121.

Remarks

The venation network, the serration of the leaf margin, and the stomatal complex are typical of leaves of the genus *Fagus*. The shape of the leaves and the number of secondary veins are consistent with the fossil species *Fagus silesiaca* Walther and Zastawniak (Walter and Zastawniak, 1991).

Modern Equivalents

In terms of macro- and micromorphology, the leaves of *Fagus silesiaca* are similar to the leaves of the extant Chinese beech *Fagus hayatae* Palibin ex Hayata (Dyjur et al., 1992). The leaves of *Fagus grandiflora* Ehrh. from North America, macromorphologically similar to *Fagus silesiaca*, differ in having anomocytic stomata (Kvaček and Walther, 1991).

Ecology

Fossil *Fagus silesiaca* is considered as a warm temperate element (Worobiec, 2014).

Occurrence

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

Family JUGLANDACEAE de Candolle ex Perleb,
1818 Juglandaceae DC. ex Perleb, nom. cons.
Genus *CARYA* Nuttall, 1818

Type Species. *Carya tomentosa* (Lamarck) Nuttall, 1818.

Carya serrifolia (Goeppert) Kräusel, 1920
Figure 10.1-7

Description

Macromorphology. Only fragments of leaflets, up to 8.5 cm long and 3.5 cm–6.5 cm wide, leaflet base obtuse. Leaflet margin simple serrate, apical side of teeth acuminate or concave, basal side acuminate (sometimes convex or concave), teeth apex acute, nearly spinose. Branches of secondary veins terminating at teeth apex. Venation pinnate, primary vein straight and of moderate thickness. Secondary venation mixed craspedodromous. Secondaries alternate, preserved in up to 17 pairs distributed at intervals of 0.4 cm–0.5 cm near leaflet base and 0.5 cm–1.3 cm in the middle part of the lamina, slightly upwardly curved, near the leaflet margin strongly curved and interconnected in loops sending fine veins towards teeth. Secondary veins diverging from midvein at an angle of 80°–90° near leaflet base to 55°–80° in the middle of the lamina. Tertiary venation percurrent, 4–6 tertiary veins occurring per 1 cm of secondary vein length and forming an angle of 130°–160° with the primary vein. Higher-order venation reticulate. Areoles well developed, 0.18 mm–0.30 mm in size. Veinlets simple or absent (rarely branched once). Marginal ultimate venation looped. Numerous glandular trichome

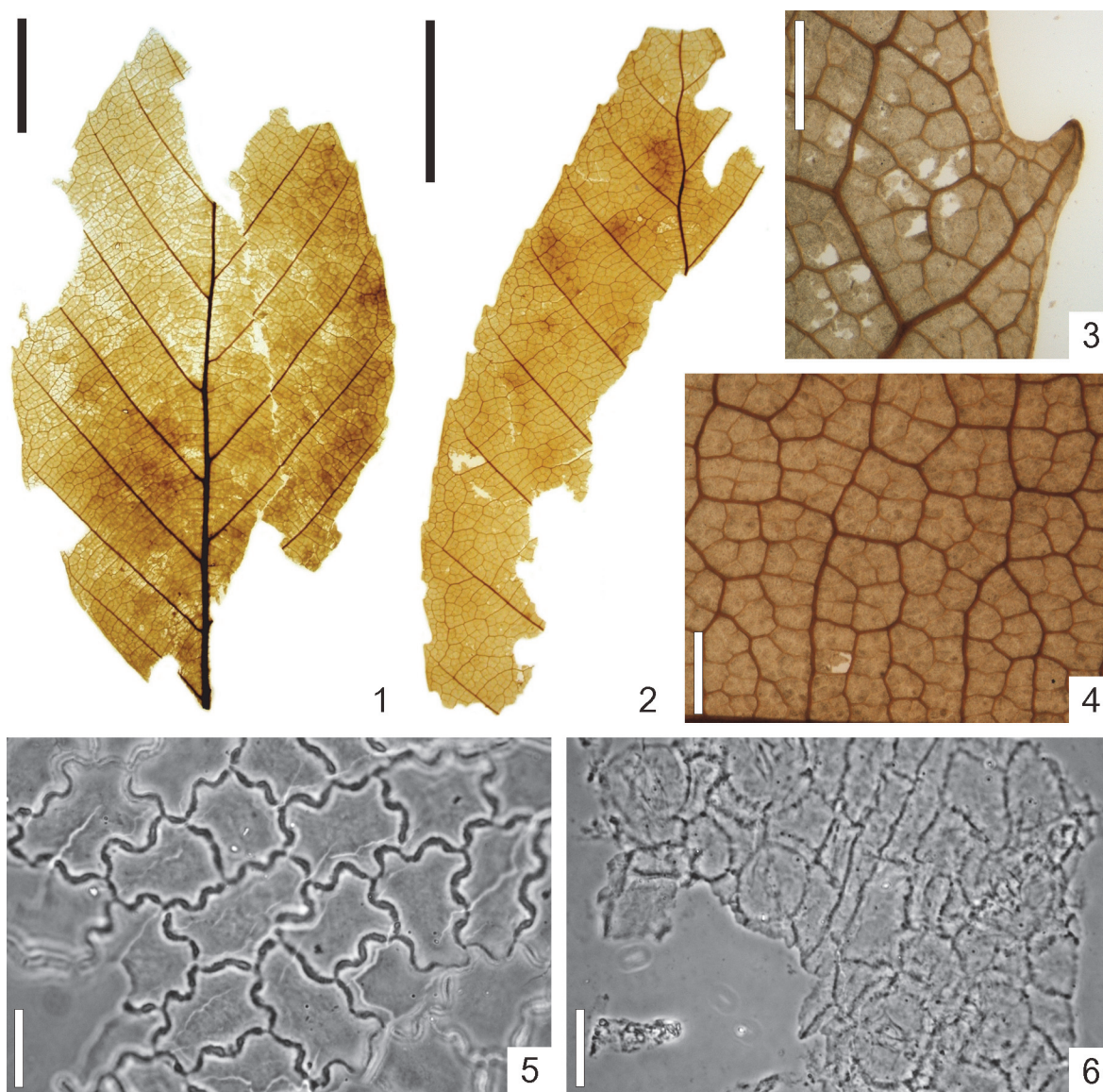


FIGURE 9. *Fagus silesiaca* Walther and Zastawniak: 1. Leaf fragment, KRAM-P 225/15; 2. Leaf fragment, KRAM-P 225/12; 3. Detail of leaf margin and tooth venation, KRAM-P 225/24; 4. Detail of leaf areolation, KRAM-P 225/24; 5. Adaxial epidermis, KRAM-P 225/24; 6. Abaxial epidermis with stomata, KRAM-P 225/12. Scale bar equals to 1 cm for (1) and (2), 1 mm for (3) and (4), and 20 μm for (5) and (6).

shields often attached to the surfaces of leaflet impressions.

Micromorphology. Adaxial epidermis consisting of slightly elongated cells with straight, rounded (or more seldom, slightly undulate) cell walls, 22.0 μm –41.7 μm in size. Abaxial epidermis rather badly preserved, cells isodiametric or slightly elongated, straight-walled, ca. 30 μm in size. Leaflets hypostomatic. Stomata elliptic to wide elliptic, 22 μm –24 μm in size. Indistinct T-shaped cuticular thickenings at poles of guard cells. On abaxial epidermis, presence of peltate trichome shields (scales), 134 μm –171 μm in diameter. Trichome

bases unicellular (rarely two-celled), roundish to elliptic, 22 μm –29 μm in diameter.

Specimens Examined

KRAM-P 225: 2, 8, 18, 19, 78/I, 84, 88/IV, 103, 109, 111, 112, 114, 118, 120/II.

Remarks

The leaflet shape, the mixed craspedodromous venation, and the secondary veins branching point to the fossil species *Carya serrifolia* (Goeppert) Kräusel. Leaflets of fossil *Pterocarya paradisiaca* (Unger) Ilinskaya, somewhat similar to those of

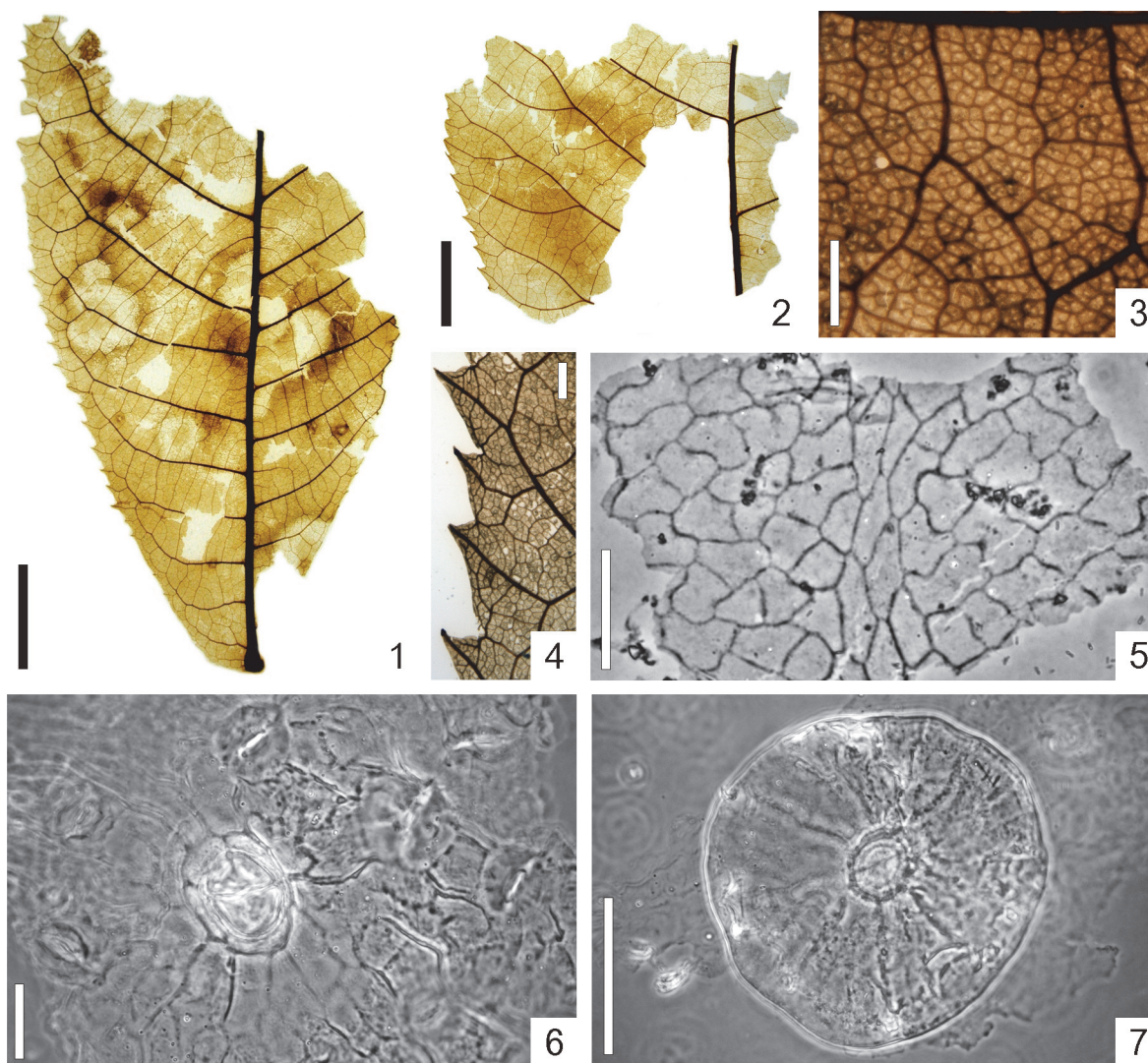


FIGURE 10. *Carya serrifolia* (Goeppert) Kräusel: 1. Leaflet, KRAM-P 225/18; 2. Leaflet fragment, KRAM-P 225/19; 3. Detail of leaflet areolation, KRAM-P 225/8; 4. Detail of leaflet margin and teeth venation, KRAM-P 225/19; 5. Adaxial epidermis, KRAM-P 225/8; 6. Abaxial epidermis with stomata and one-celled glandular trichome base, KRAM-P 225/8; 7. Glandular peltate trichome, KRAM-P 225/18. Scale bar equals to 1 cm for (1) and (2), 1 mm for (3) and (4), 50 µm for (5) and (7), and 20 µm for (6).

Carya serrifolia, usually differ in displaying an oblongated shape.

Modern Equivalents

Carya serrifolia is usually compared with extant North American species *Carya aquatica* (F.Michx.) Nutt., *Carya illinoensis* (Wangenh.) K. Koch., and *Carya tomentosa* Nutt. (Teodoridis, 2002).

Ecology

Fossil *Carya serrifolia* is considered as a warm temperate element (Hably and Kvaček, 1998).

Occurrence

Carya serrifolia is common in Neogene European fossil plant assemblages (Knobloch, 1969; Palamarev and Petkova, 1987). In Poland, this fossil species is found from the middle Miocene to the early Pliocene (Worobiec, 2003b).

Family SAPINDACEAE Jussieu, 1789
Genus *ACER* Linnaeus, 1753

Type Species. *Acer pseudoplatanus* Linnaeus, 1753.

Acer tricuspidatum Bronn sensu Procházka and Bůžek, 1975
Figure 11.1-4

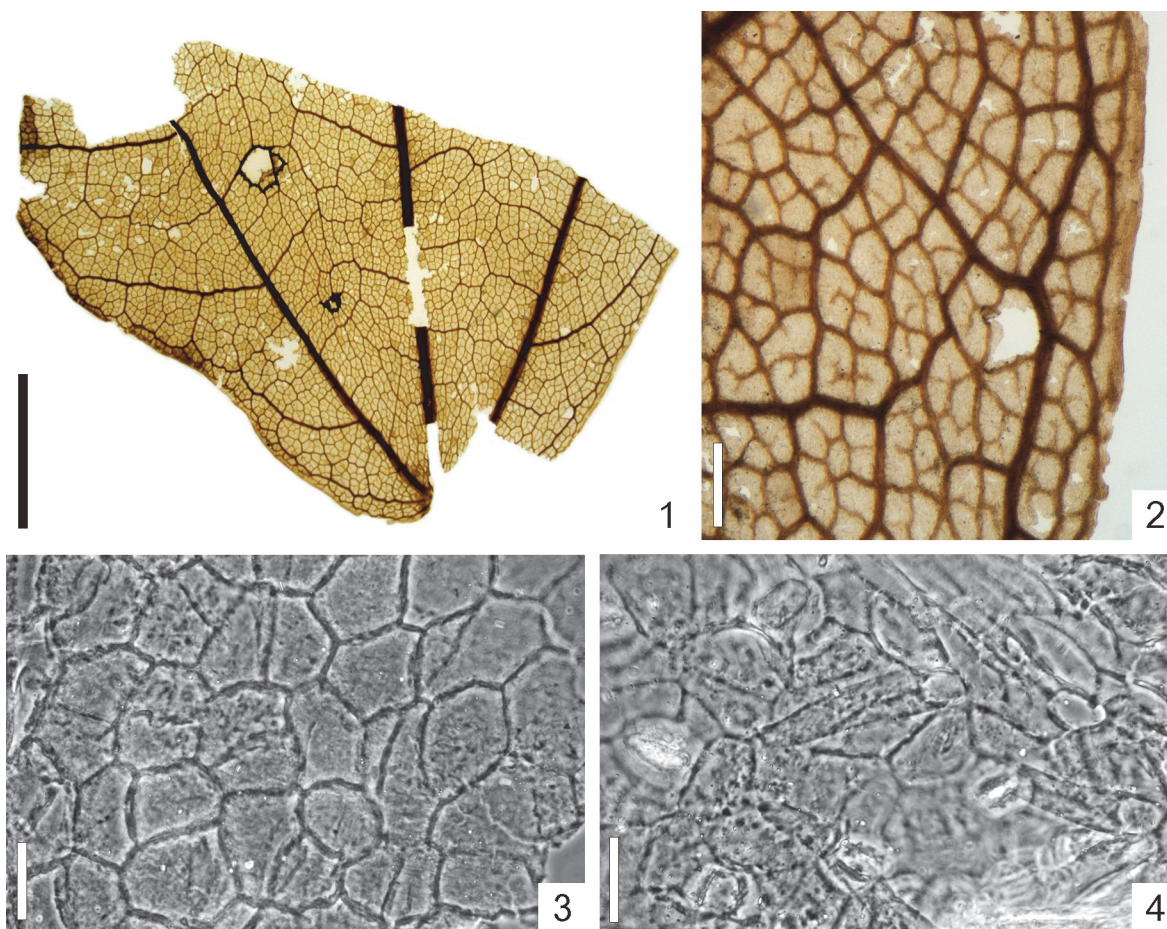


FIGURE 11. *Acer tricuspidatum* Bronn sensu Procházka and Bůžek: 1. Fragment of basal part of leaf, KRAM-P 225/1; 2. Detail of leaf margin venation and areolation, KRAM-P 225/1; 3. Adaxial epidermis, KRAM-P 225/1; 4. Abaxial epidermis with stomata and solitary, unicellular trichomes, KRAM-P 225/1. Scale bar equals to 0.5 cm for (1), 0.5 mm for (2), and 20 μm for (3) and (4).

Description

Macromorphology. Small fragment of leaf, 1.5 cm by 2.2 cm. Leaf base more or less rounded. Venation palmate, actinodromous, basal. Primary vein branched into three branches. Tertiary veins composite intersecondary. Higher-order venation random reticulate. Areoles well developed, 0.24 mm–0.42 mm in size. Veinlets simple or once branched. Marginal ultimate venation looped.

Micromorphology. Adaxial epidermis composed of isodiametric or slightly elongated cells with mostly straight walls, 24.0 μm –51.5 μm in size, with indistinct cuticle ornamentation of parallel striae. Over veins, cells more elongated and narrow. Abaxial epidermis composed of isodiametric or slightly elongated cells, 17 μm –37 μm in size, with straight or rounded cell walls. Leaves hypostomatic. Stomata anomocytic or sometimes brachyparacytic, round-

ish to elliptic, 17 μm –22 μm in size. Outer stomatal ledge aperture rather distinct and of characteristic elliptic-rectangular shape, 9.8 μm –17.0 μm long and 7.4 μm –9.8 μm wide. On abaxial epidermis, presence of numerous unicellular, simple trichomes, 54 μm –63 μm long and ca. 10 μm wide with unicellular trichome bases, ca. 12 μm in size. Similar trichome bases also rarely found on adaxial epidermis.

Specimens Examined

KRAM-P 225: 1.

Remarks

The described leaf fragment is rather small, although the stomatal shape and abundant pubescence of abaxial epidermis are typical of the fossil species *Acer tricuspidatum* Bronn sensu Procházka and Bůžek.

Modern Equivalents

Acer tricuspidatum is related to the extant eastern North American maple species *Acer rubrum* L. and *Ac. saccharinum* L. (Hantke, 1954; Kräusel and Weyland, 1959; Holý et al., 2012). The cuticular micromorphology of extant *Ac. rubrum*, *Ac. saccharinum*, and *Ac. hyrcanum* Frisch. and Mey is similar to that of *Ac. tricuspidatum* (Walther, 1972).

Ecology

Similarly to modern equivalents, fossil *Acer tricuspidatum* is considered as a warm temperate element.

Occurrence

Acer tricuspidatum is known from middle Oligocene to Pliocene plant assemblages from Europe (Procházka and Bůžek, 1975) and is frequently found in the Neogene of Poland (Worobiec et al., 2008).

Family MALVACEAE Jussieu, 1789

Fossil-genus *LARIA* G. Worobiec and Kvaček, 2010, in Worobiec et al. (2010)

Type Species. *Laria rueminiana* (Heer) G. Worobiec and Kvaček, 2010.

Laria rueminiana (Heer) G. Worobiec and Kvaček, 2010

Specimens Examined

KRAM-P 225: 7, 11, 38, 39/III, 40/I, 42/II, 43/I, 44/III, 45/I, 46, 47/III, 48/I, 49/I, 50, 51/I, 52/I, 53, 54/I, 55/I, 56, 57, 58/III, 59, 60/IV, 61, 62, 63/I, 64/II, 65, 66/II, 67/III, 68/II, 69/I, 86/III, 87/I, 97/I. cf. *Laria rueminiana*: 81/I, 82/I, 107/II, 110/I.

Remarks

The discussed remains of leaves of *Laria rueminiana* were thoroughly described, discussed, and illustrated earlier in Worobiec et al. (2010).

Family FABACEAE Lindley, 1836

Genus *GLEDITSIA* Clayton, J. Clayton in Linnaeus, 1753

Type Species. *Gleditsia triacanthos* Linnaeus, 1753.

Gleditsia europaea sp. nov. G. Worobiec
Figure 12.1-8

Holotype

Specimen KRAM-P 225/16, illustrated in Figure 12.1, 12.4, 12.7-8. Stored in W. Szafer Institute

of Botany, Polish Academy of Sciences, Kraków, Poland.

Further Type Material

KRAM-P 225: 3, 36, 37, 58/II, 60/III.

Further Tentatively Referred Material

cf. *Gleditsia europaea* sp. nov.: 100, 119/II.

Synonymy

- ? 1998 *Ternstroemites* sp., Worobiec and Lesiak, p. 192-193, Pl. 2, figs. 2, 2a
- 2014 *Dicotylophyllum* sp. 1, Worobiec, p. 258, Pl. 3 fig. 5, Pl. 6, figs. 3a-3b
- 2016 *Dicotylophyllum* sp. 1 sensu Worobiec (2014), Worobiec and Szykiewicz, p. 457, Pl. 5, figs. 1a-1b

Repository

W. Szafer Institute of Botany, Polish Academy of Sciences, Kraków, Poland, collection KRAM-P 225.

Type Locality

Bełchatów Lignite Mine, Poland.

Stratigraphic Horizon

Latest middle Miocene to late Miocene.

Etymology

Species named after Europe.

Diagnosis

Leaflets elliptic-ovate, asymmetric. Leaflet apex acute to mucronate, leaflet base obtuse to rounded, distinctly asymmetric, almost sessile. Petiolule rather short, thick. Leaflet margin crenate, veins loop reaching glands on leaflet margin. Venation pinnate. Secondary venation semicraspedodromous. Secondaries alternate, irregularly arranged, curved upwards, and interconnected in loops. Intersecondary veins sometimes present. Tertiary venation usually random reticulate, rarely composite intersecondary. Higher-order venation random reticulate. Areoles imperfectly developed, large, and rather diverse in size. Veinlets multiple branched. Marginal ultimate venation looped. Adaxial epidermis cells with straight, sometimes rounded, and thick walls. Abaxial epidermis cells with straight, rounded, or rarely wide, undulate walls. Leaflets hypostomatic. Stomata elliptic, cyclocytic, anisocytic, and paracytic. Outer stomatal ledge aperture spindle-shaped. Both adaxial and abaxial epidermis with unicellular, simple, solitary trichomes with unicellular, elliptic to roundish trichome bases.

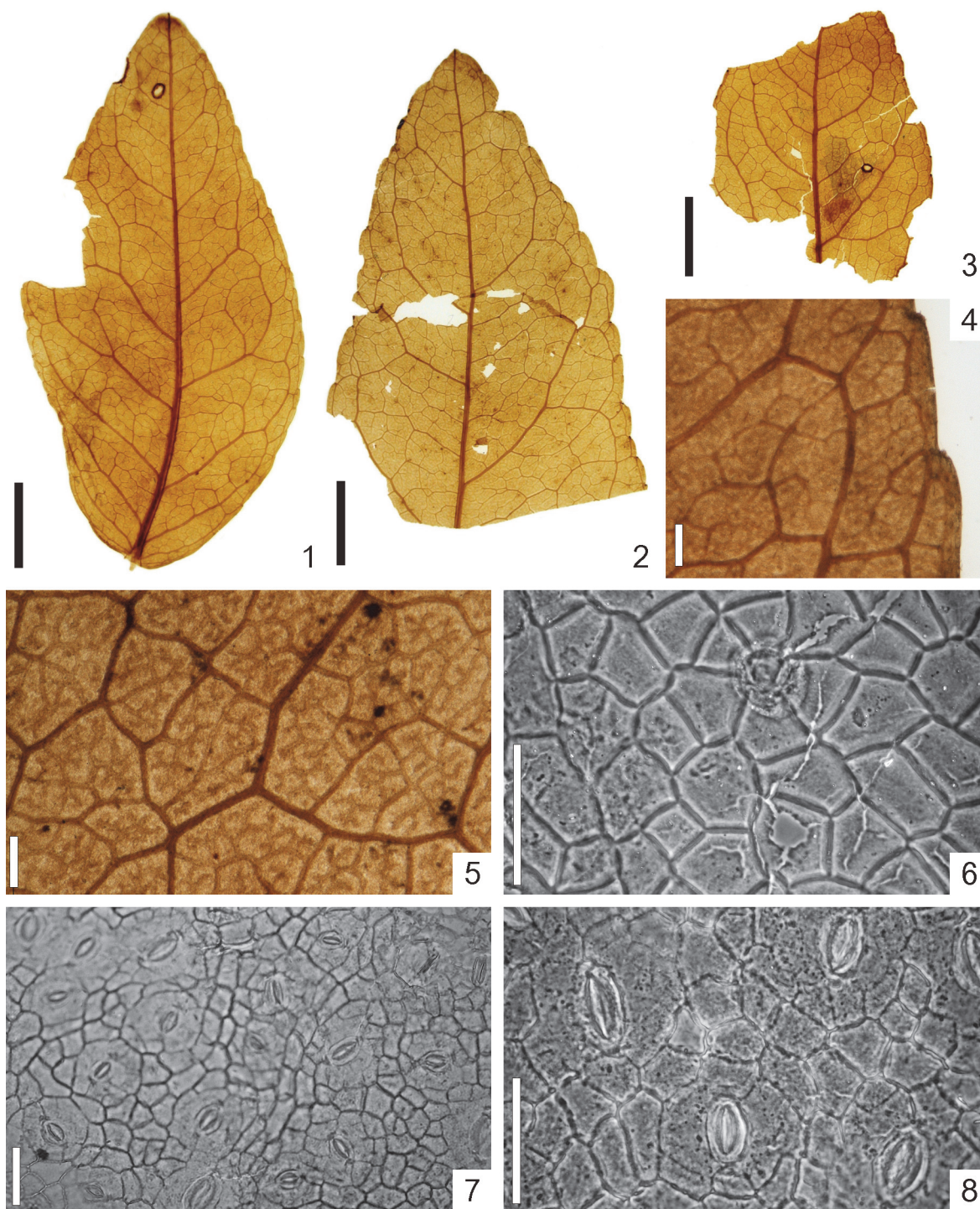


FIGURE 12. *Gleditsia europaea* sp. nov.: 1. Holotype, leaflet, KRAM-P 225/16; 2. Leaflet fragment, KRAM-P 225/8; 3. Leaflet fragment, KRAM-P 225/37; 4. Holotype, detail of leaflet margin and teeth venation, KRAM-P 225/16; 5. Detail of leaflet areolation, KRAM-P 225/3; 6. Adaxial epidermis, KRAM-P 225/3; 7. Holotype, abaxial epidermis with stomata, KRAM-P 225/16; 8. Holotype, abaxial epidermis with stomata, KRAM-P 225/16. Scale bar equals to 0.5 cm for (1), (2), and (3), 0.5 mm for (4) and (5), and 50 µm for (6), (7), and (8).

Description

Macromorphology. Fragments of leaflets, elliptic-ovate, up to 3.4 cm long and 1.2 cm–2.0 cm wide, asymmetric. Leaflet apex acute to mucronate, leaflet base obtuse to rounded, distinctly asymmetric, almost sessile. Petiolule rather short, thick. Leaflet margin crenate, veins loop reaching glands on leaflet margin. Venation pinnate, primary vein straight, and of moderate thickness. Secondary venation semicraspedodromous. Secondaries alternate, irregularly arranged, curved upward, and interconnected in loops, forming an angle of 50°–65° with the primary vein. Intersecondary veins sometimes present. Tertiary venation usually random reticulate (rarely composite intersecondary). Higher-order venation random reticulate. Areoles imperfectly developed, large, and rather diverse in size, 0.7 mm–2.4 mm. Veinlets multiple branched. Marginal ultimate venation looped. Presence of numerous trichomes in leaf margin of isolated leaves.

Micromorphology. Adaxial epidermis composed of isodiametric or slightly elongated cells, with straight, sometimes rounded thick walls, 17.0 µm–51.5 µm in size. Abaxial epidermis composed of isodiametric or slightly elongated cells with straight, rounded, or rarely even wide undulate walls, 19.6 µm–44.1 µm in size, over the veins cells elongated and rectangular. Leaflets hypostomatic. Stomata cyclocytic, anisocytic, and paracytic, elliptic, 25 µm–42 µm long and 14.7 µm–19.6 µm wide. Outer stomatal ledge aperture spindle-shaped, 17.2 µm–34.3 µm long and 4.9 µm–17.2 µm wide. On both adaxial and abaxial epidermis, presence of unicellular, simple, solitary trichomes (on abaxial epidermis, 90 µm–245 µm long and 9.0 µm–14.7 µm wide). Unicellular, elliptic to roundish trichome bases, 25 µm–32 µm (adaxial epidermis) and 19.6 µm–24.5 µm (abaxial epidermis) in diameter.

Remarks

Characteristically asymmetrical leaflet base, short petiolule, crenate margin, and network of secondary and third order venation are overall similar to the condition seen in extant species of the genus *Gleditsia* L. Cuticular micromorphology also matches well extant species of *Gleditsia* (Barclay et al., 2017). Similar fossil leaflets were described from Miocene deposits of Europe and Japan as *Gleditsia* sp. (Hably and Kvaček, 1997; Kvaček et al., 2011), *Gleditsia miosinensis* Hu and Chaney (Yabe, 2008), and *Leguminosites* sp. (Kvaček et al., 2008). Among them only *Gleditsia* sp. described from the Miocene flora of Arjuzanx, France (Kvaček et al., 2011) and

Leguminosites sp. found in the Pliocene flora of Auenheim, France (Kvaček et al., 2008) are sufficiently well preserved to be reliably compared with *Gleditsia* leaflets from Bełchatów. Moreover, leaflets of *Leguminosites* sp. from Auenheim are accompanied by thorn remains described as cf. *Gleditsia* sp. Macromorphologically, leaflets from Arjuzanx, Auenheim, and Bełchatów are rather similar and the observed differences between them could be caused both by intra- and inter-specific variability. However, there are no data about the cuticular micromorphology of the discussed legume leaflets from Arjuzanx and Auenheim. Contrary to these fossils, the leaflets of *Gleditsia* from Bełchatów display excellently preserved cuticular structures. Considering this, we decide to erect a new taxon. The remaining fossil record of the *Gleditsia* genus (leaflets, woods, spines, pollen grains) is rather scarce, partly poorly preserved, and in many cases, taxonomical determination of these fossils is doubtful. The oldest fossils of *Gleditsia* are known from Oligocene, and the best documented is the Miocene record from North America, Eastern Asia, and Caucasus (Schnabel et al., 2003).

Modern Equivalents

The fossil *Gleditsia europaea* sp. nov. is most similar to the extant North American species *Gleditsia aquatica* Marshall in terms of leaflet shape, margin crenation, and density of secondary veins as well as the cuticular micromorphology. *Gleditsia aquatica* is an obligatory wetland species (Lichvar, 2013) found in wetland forest vegetation of south and southeastern USA (USDA Plants Database, 2017).

Ecology

Similarly to extant *Gleditsia aquatica* Marshall, fossil *Gleditsia europaea* sp. nov. is considered as a warm temperate element, component of wetland vegetation.

Fossil-genus *LEGUMINOPHYLLUM* A. Escalup-Bassi, 1971

Type Species. *Leguminophyllum emarginatum* A. Escalup-Bassi, 1971.

Leguminophyllum kvacekii sp. nov. G. Worobiec
Figure 13.1-8

Holotype

Specimen KRAM-P 225/22, illustrated on Figure 13.1. Stored in W. Szafer Institute of Botany, Polish Academy of Sciences, Kraków, Poland.

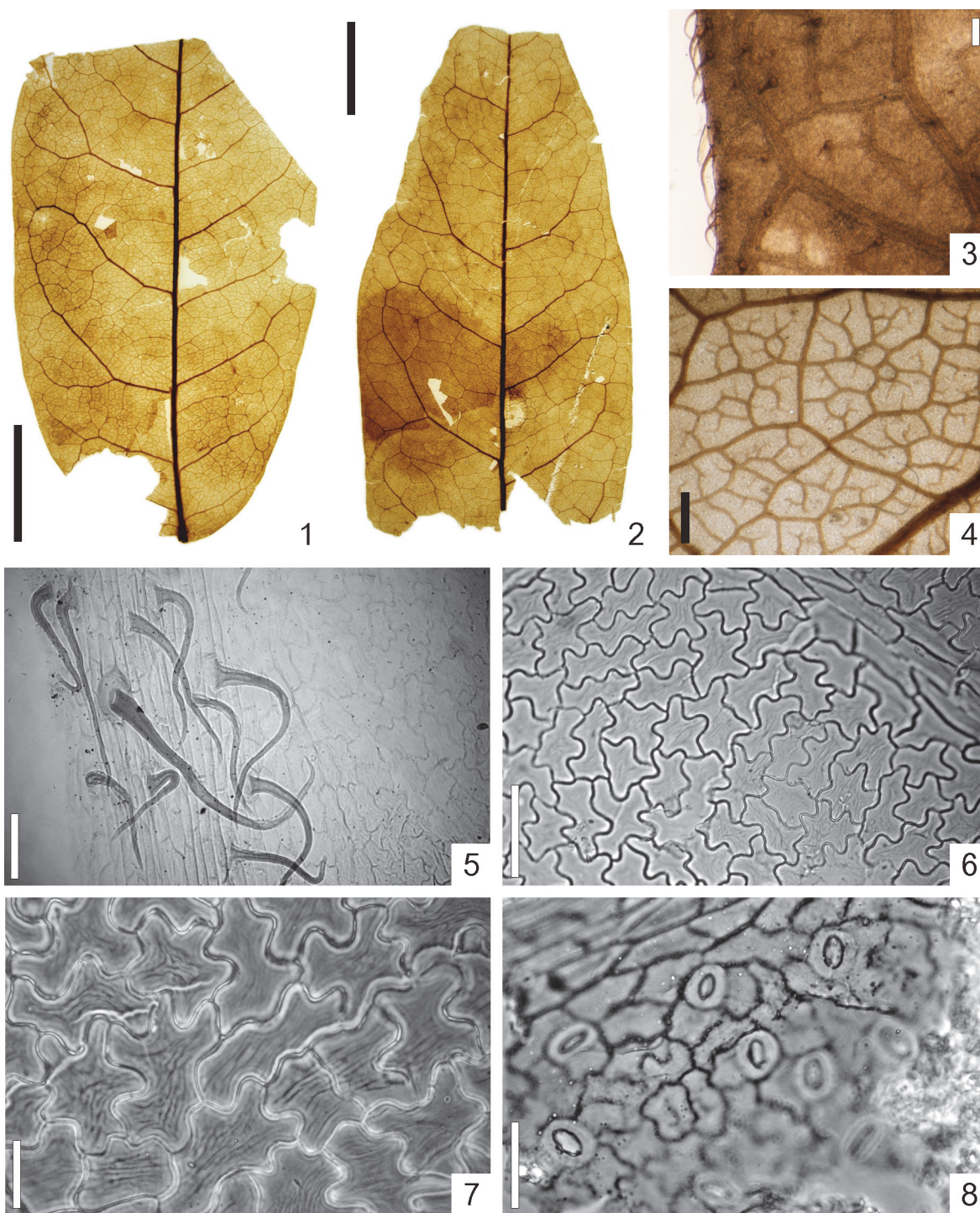


FIGURE 13. *Leguminophyllum kvacekii* sp. nov.: 1. Holotype, leaflet fragment, KRAM-P 225/22; 2. Leaflet fragment, KRAM-P 225/14; 3. Detail of leaflet margin with large trichomes, KRAM-P 225/14; 4. Detail of leaflet areolation, KRAM-P 225/5; 5. Adaxial epidermis with large trichomes over the veins, KRAM-P 225/4; 6. Adaxial epidermis, undulate cell walls, KRAM-P 225/17; 7. Adaxial epidermis, note striate ornamentation of cuticle, KRAM-P 225/17; 8. Abaxial epidermis with stomata, KRAM-P 225/17. Scale bar equals to 1 cm for (1) and (2), 0.5 mm for (4), 0.1 mm for (3), 50 µm for (5) and (6), and 20 µm for (7) and (8).

Further Type Material

KRAM-P 225: 4, 5, 6, 9, 10, 14, 17, 20, 21, 25, 51/II, 58/IV, 60/V, 66/III, 68/III, 72/III, 75/II, 85/I, 86/IV, 107/III, 113, 127.

Synonymy

? 2016 *Dicotylophyllum* sp. 4, Worobiec and Szynkiewicz, p. 458–459, pl. 5, figs. 4a–b, pl. 13, figs. 4a–4c

Repository

W. Szafer Institute of Botany, Polish Academy of Sciences, Kraków, Poland, collection KRAM-P 225.

Type Locality

Bełchatów Lignite Mine, Poland.

Stratigraphic Horizon

Latest middle Miocene to late Miocene.

Etymology

Named after the eminent Czech palaeobotanist Professor Zlatko Kvaček in recognition of his contribution to Paleogene and Neogene palaeobotany on the occasion of his eighteenth birthday.

Diagnosis

Leaflets asymmetric, entire-margined, margin covered by large trichomes. Leaflet base distinctly asymmetric, obtuse sometimes rounded or nearly cordate, short petiolulate or sessile. Venation pinnate, primary vein straight or bent. Secondary venation brochidodromous. Secondaries curved upwards and interconnected in loops, distributed at irregular intervals. Intersecondary veins present, distinct. Tertiary venation composite intersecondary. Higher-order venation reticulate. Areoles well developed, diverse in size. Veinlets usually multiple branched, sometimes simple. Marginal ultimate venation looped. Adaxial epidermis cells walls undulate, rarely straight and rounded, cuticle with distinct striate ornamentation. Abaxial epidermis cells with straight, rounded to undulate cell walls. Leaves hypostomatic. Stomata anomocytic, elliptic. Outer stomatal ledge aperture elliptic, sometimes wide spindle-shaped. Unicellular, simple, solitary trichomes in abaxial epidermis, unicellular trichome bases in both adaxial and abaxial epidermis.

Description

Macromorphology. Entire-margined (sometimes margin sinuous) leaflets, asymmetric, up to 5.7 cm long and 2.6 cm–3.7 cm (rarely 4.0 cm) wide. Leaflet

margin covered by large trichomes. Leaflet base obtuse sometimes rounded or nearly cordate, distinctly asymmetric, short petiolulate or sessile. Venation pinnate, primary vein straight or bent, and of moderate thickness. Secondary venation brochidodromous. Secondaries curved upwards and interconnected in loops, preserved in up to seven pairs, distributed at irregular intervals of 0.3 cm–0.4 cm near leaflet base and 0.6 cm–1.4 cm in the middle of the lamina, forming an angle of 60°–80° with the primary vein. Intersecondary veins present, distinct. Tertiary venation composite intersecondary. Higher-order venation reticulate. Areoles well developed, diverse in size, 0.4 mm–1.0 mm (rarely 1.2 mm). Veinlets usually multiple branched, sometimes simple. Marginal ultimate venation looped.

Micromorphology. Adaxial epidermis composed of isodiametric or slightly elongated cells, with undulate, rarely straight or rounded walls, 22.0 µm–58.8 µm in size. Cuticle of adaxial epidermis with distinct striate ornamentation. Abaxial epidermis composed of isodiametric or slightly elongated cells with straight, rounded to undulate cell walls, 19.6 µm–36.8 µm in size. Over the veins, cells elongated and rectangular. Leaves hypostomatic. Stomata anomocytic, elliptic to wide elliptic, 22.0 µm–26.9 µm in size. Stomatal pore usually visible. Outer stomatal ledge aperture elliptic, sometimes wide spindle-shaped, 11.0 µm–19.6 µm long and 4.9 µm–9.8 µm wide. Presence of unicellular, simple, solitary trichomes, 98 µm–245 µm long and up to 17 µm wide in the basal part of the abaxial epidermis. Presence of presumably unicellular trichome bases, 34.3 µm–44.1 µm in size, on both adaxial and abaxial epidermis.

Remarks

The above described leaflets are short petiolulate or sessile, which is typical for fossil legume leaflets usually assigned to the fossil-genus *Leguminosites* Bowerbank emend. Schimper. The initial name *Leguminosites* was used for legume carpological remains but later also for leaflets. However, according to Wang (2012), fossil-genus *Leguminosites* name, due to nomenclatural rules, should not be used for legume leaflet fossils. Instead, Wang (2012) suggested using the fossil genera names *Leguminophyllum* A. Escalup-Bassi and *Parvileguminophyllum* Herendeen and Dilcher for fossil leaflets of Fabaceae. Considering this, we decided to attribute the legume leaflets from Bełchatów to the fossil-genus *Leguminophyllum*, which has priority over *Parvileguminophyllum*. The epidermal micromorphology of *Leguminophyllum*

kvacekii sp. nov. matches well the micromorphology of various members of extant (Barclay et al., 2017) and fossil (e.g., Kvaček et al., 2011) Fabaceae. *Leguminophyllum kvacekii* sp. nov. leaflets are nearly identical in both macromorphology and cuticular structure to leaflets earlier described from middle to late Miocene leaf assemblage from the Bełchatów mine as *Dicotylophyllum* sp. 4 (Worobiec and Szyrkiewicz, 2016), and they are therefore likely conspecific. Another fossil taxon of legume leaflets from the Neogene deposits of Bełchatów, *Dicotylophyllum* sp. 1 (Worobiec et al., 2012), probably conspecific with *Dicotylophyllum* sp. 3 (Worobiec and Szyrkiewicz, 2016), differs from *Leguminophyllum kvacekii* sp. nov. mainly in its considerably smaller areoles. The well-preserved legume leaflets described as *Leguminosites* sp. B, *Leguminosites* sp. G, and *Leguminosites* sp. H from the Miocene flora of Arjuzanx, France (Kvaček et al., 2011), are also similar to *Leguminophyllum kvacekii* sp. nov. Among them, *Leguminosites* sp. H seems to be macromorphologically closest to *Leguminophyllum kvacekii* sp. nov. Unfortunately, there are no data on the epidermal structure of *Leguminosites* sp. H and, therefore, the relationships between those two fossil taxa cannot be conclusively clarified. *Leguminophyllum kvacekii* sp. nov. differs from the fossil-genera of similar Fabaceae leaflets, *Podocarpium* A. Braun ex Stizenberger and *Phaseolites* Unger, in density and the course of the secondary venation network. In addition, for most of the leaflets described as *Phaseolites* and *Podocarpium*, there are no data on their epidermis. Other fossil genera considered as legume leaflets, such as *Bauhinites* Seward and Conway, *Dalbergites* E. W. Berry, *Diphyllites* Heer, *Diplophyllum*

Velenovsky and Viniklar, *Fontainea* Newberry, and *Podalyriophyllum* Ettingshausen, were reported mostly from Cretaceous deposits, usually have no data on cuticles, and therefore their placement among Fabaceae seems doubtful.

Modern Equivalents

The exact systematic position of the leaflets attributed to *Leguminophyllum kvacekii* sp. nov. is unknown as leaflets of this macro- and micromorphology are common among extant Fabaceae genera and, as such, they are hardly assignable to any natural taxon.

Ecology

Unknown.

Dicotyledones incertae sedis

Fossil-genus *DICOTYLOPHYLLUM* Saporta, 1894

Type Species. *Dicotylophyllum cerciforme* Saporta, 1894.

Dicotylophyllum sp. 1

Figure 14.1-3

Description

Macromorphology. Badly preserved, small fragment (ca. 1 cm) of basal part of serrate leaf. Vein loop reaching sinus between teeth. Veinlets branched.

Micromorphology. Adaxial epidermis composed of slightly elongated cells with one papilla in each cell, with undulate walls, 41.7 μm –56.4 μm in size. Cuticle of adaxial epidermis covered by epicuticular wax. Abaxial epidermis similar in terms of morphology to adaxial epidermis, with undulate cell walls. Leaves hypostomatic. Stomata elliptic to wide elliptic, 26.9

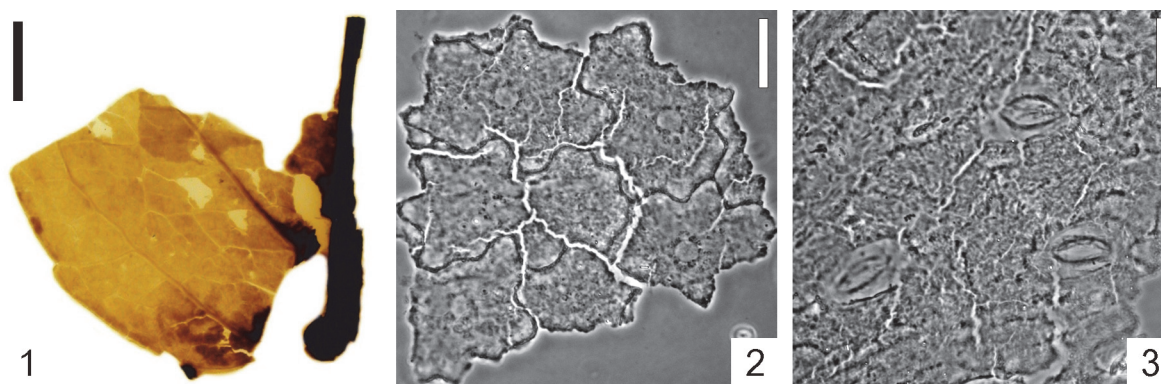


FIGURE 14. *Dicotylophyllum* sp. 1: 1. Fragment of basal part of leaf, KRAM-P 225/13; 2. Adaxial epidermis, note papillae in each cell, KRAM-P 225/13; 3. Abaxial epidermis with stomata, KRAM-P 225/13. Scale bar equals to 2 mm for (1), and 20 μm for (2) and (3).

µm–31.9 µm in size. Outer stomatal ledge aperture spindle-shaped to elliptic, 12.2 µm–22.0 µm long and 7.4 µm–11.0 µm wide.

Specimens Examined

KRAM-P 225: 13.

Remarks

The systematic position of the leaf remain is unknown.

Dicotyledones indet.

Specimens Examined

KRAM-P 225: 83/III, 92/I.

Remarks

The discussed leaf remains are poorly preserved, without distinctive characters. Their systematic position is unknown.

Clade PETROSAVIIDAE S.W. Graham and W.S.

Judd, 2007, in Cantino et al. (2007)

Family POACEAE Barnhart, 1895

Genus *PHRAGMITES* Adanson, 1763

Type Species. *Phragmites communis* Trinius, 1820.

Phragmites oeningensis A. Braun, Stizenberger, 1851

Figure 15.1

Description

Macromorphology. Rather small and badly preserved fragments of linear, entire-margined leaves, up to 8.0 cm long and ca. 0.8 cm wide. Venation parallelodromous. Midvein rarely preserved. Lateral veins spaced 0.7 mm–1.0 mm apart, with 3–4 (close to leaf margin) to 5–6 (in the middle part of the lamina) third order veins lying between them, spaced 0.12 mm–0.18 mm apart. Cross (transverse) veins absent.

Specimens Examined

KRAM-P 225: 44/V, 93/IV, 106/III.

Remarks

The above described monocotyledonous leaves with parallelodromous venation without cross veins point to the fossil species *Phragmites oeningensis* A. Braun.

Modern Equivalents

Common reed *Phragmites communis* Trin. is considered as a recent equivalent of fossil *Phragmites oeningensis* (Krajewska, 1998).

Ecology

Similarly to modern equivalent, fossil *Phragmites oeningensis* is considered as a temperate element.

Occurrence

Phragmites oeningensis was common in the Paleogene and Neogene of Europe. In Poland it was reported from middle to late Miocene deposits (Worobiec et al., 2008).

Family POTAMOGETONACEAE Berchtold and J. Presl, 1823

Genus *POTAMOGETON* Linnaeus, 1753

Type Species. *Potamogeton natans* Linnaeus, 1753.

Potamogeton sp.
Figure 15.2-7

Description

Macromorphology. Fragments of entire-margined leaves, up to 2.7 cm long and ca. 1 cm wide. Leaf apex acute to attenuate, leaf base decurrent, petiole broad and rather long. Leaf venation parallelodromous. Midvein present, straight and thin, 6–7 lateral veins spaced 0.12 mm–0.30 mm apart (close to leaf margin) to 0.50 mm–1.20 mm (in the middle part of the lamina) lying on each side of the midvein. Usually oblique transverse veins spaced 0.5 mm–1.0 mm, connecting adjacent lateral veins. Besides these comparatively broad leaves in some of the rock samples (e.g., 225/58, 225/71), presence of small fragments of narrow (up to 2 mm wide) linear leaves with venation typical of *Potamogeton*. Presumably narrow, submerged leaves or phyllodes of the same or other species.

Micromorphology. Leaves without stomata. Epidermis seemingly uniform on both sides of the leaves. Epidermal cells rectangular, up to 25 µm long and 5.0 µm–12.5 µm wide. Anticlinal cell walls straight or rounded. Surface of the epidermis covered by sparse grains of epicuticular wax.

Specimens Examined

KRAM-P 225: 23, 58/VI, 60/VII, 71/IV, 86/VI, 92/II, 93/V, 94/III, 106/IV, 119/IV, 124.

Remarks

The described leaf remains display venation architecture and epidermal cell arrangement typical of genus *Potamogeton*. The mixture of different morphological forms of *Potamogeton* leaf fossils could have originated from different species or could have resulted from the heterophylly of leaves

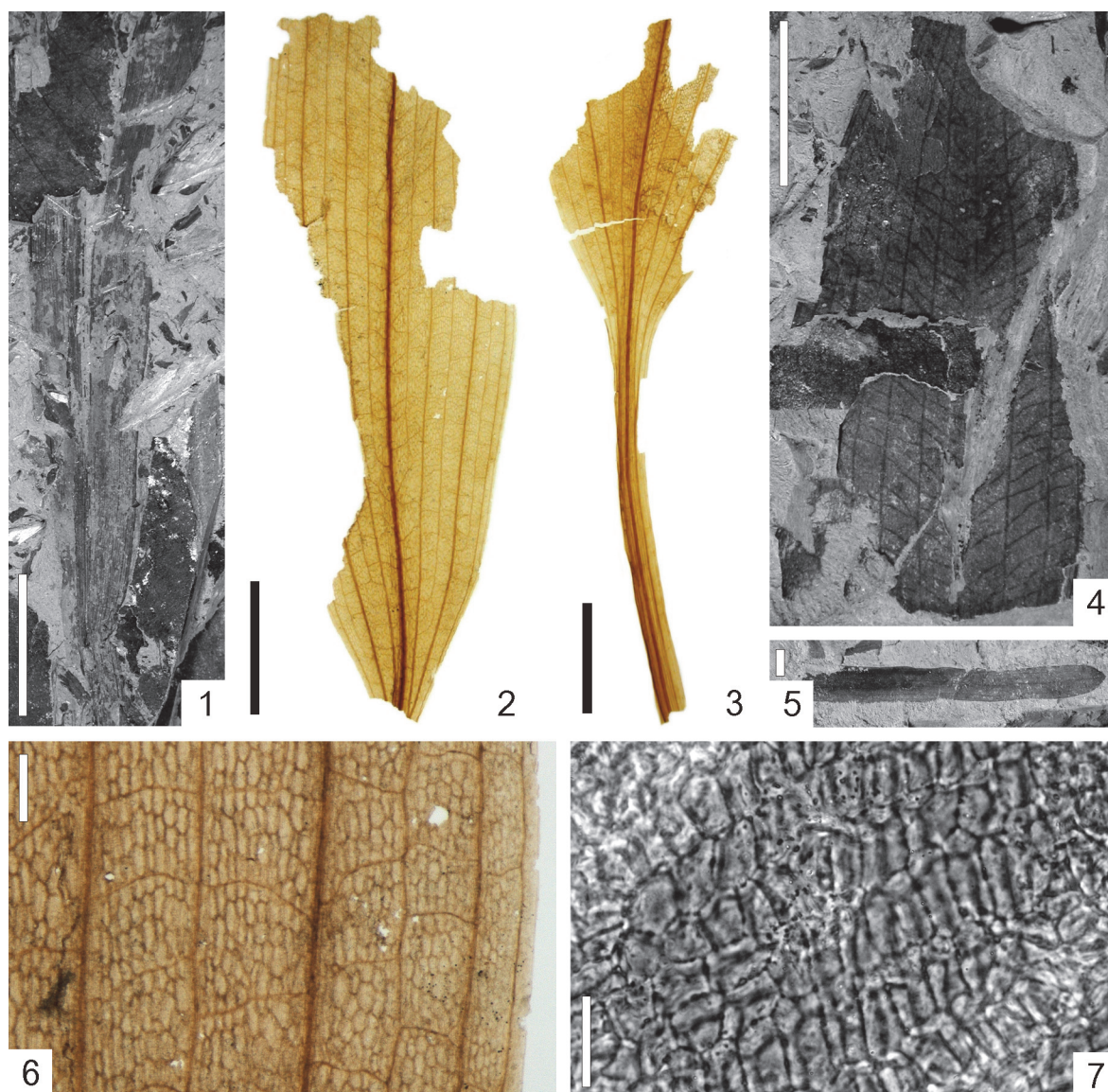


FIGURE 15. *Phragmites oeningensis* A. Braun: 1. Leaf fragment, KRAM-P 225/93/IV. *Potamogeton* sp.: 2. Leaf fragment, KRAM-P 225/23; 3. Leaf fragment, KRAM-P 225/23; 4. Leaf fragment, KRAM-P 225/106/IV; 5. Fragment of submerged leaf or phyllode, KRAM-P 225/58/VI; 6. Detail of leaf venation and leaf margin, KRAM-P 225/23; 7. Epidermis, KRAM-P 225/23. Scale bar equals to 1 cm for (1), 0.5 cm for (2), (3), and (4), 1 mm for (5), 0.5 mm for (6), and 20 μ m for (7).

typical of some species of *Potamogeton* (Les and Sheridan, 1990). They certainly represent pondweed species with submerged leaves, which is corroborated by a complete absence of stomata on both sides of the leaf epidermis (comp. Haynes et al., 1998). Miocene leaves of *Potamogeton martinianus* Sitár from Reith, Austria (Kovar-Eder and Krainer, 1991), *Potamogeton* sp. from Prosilio, Greece (Velitzelos et al., 2014), and *Potamogeton* sp. from Tossignano and Monte Tondo, Italy (Teodoridis et al., 2015) differ from *Potamogeton* sp. from Bełchatów in their considerably wider

leaves. Similar differences are observed with leaves of *Potamogeton* aff. *perfoliatus* L. from Konin, Poland (Raniecka-Bobrowska, 1954). The remaining fossils of *Potamogeton* leaves from Poland, *Potamogeton martinianus* Sitár (Zastawniak, 1980) and *Potamogeton* sp. (Kownas, 1956), both from middle Miocene deposits, are too badly preserved to be compared with pondweed leaves from Bełchatów. Leaves of *Potamogeton praenatans* Knoll from Most Basin, Czech Republic (Teodoridis, 2007) are somewhat similar in shape and width to *Potamogeton* sp. from Bełchatów.

Nevertheless, due to the rather fragmentary nature of *Potamogeton* leaf remains from Bełchatów, we cannot match the discussed remains and fossil leaves of *Potamogeton* from other localities.

Modern Equivalents

Due to the rather fragmentary nature of the leaves of *Potamogeton* sp., any recent pondweed equivalent could not be established.

Ecology

Potamogeton sp. from Bełchatów is considered to be a temperate element. Similarly to recent representatives of *Potamogeton*, pondweed from Bełchatów was certainly an aquatic plant (Haynes et al., 1998).

Occurrence

According to Daghlia (1981), the fossil remains of *Potamogeton* (mainly seeds) were reported worldwide from Oligocene deposits. The leaves of this genus in Europe, however, were reported beginning from the late Eocene, and they occur most frequently in Neogene deposits (Teodoridis, 2007). Pre-Cenozoic reports concerning macroremains of *Potamogeton* are considered to be doubtful (Daghlia, 1981). In Poland, fossil *Potamogeton* leaves were reported from middle Miocene deposits of Dobrzyń on the Vistula River (Kownas, 1956), Konin (Raniecka-Bobrowska, 1954), and Młyny (Zastawniak, 1980).

TAPHONOMY

The remains of leaves from the KRAM-P 225 assemblage were preserved as compressions and impressions. An accumulation of leaves may have originated from seasonal leaf fall from trees and shrubs directly surrounding a fluvial lake (most probably a water body with stagnant or slowly moving water). The transport of fallen leaves into a water body by flood waters or by strong winds from more distant places could also have happened. The plant assemblage studied here was presumably formed in an abandoned channel of a meandering river (oxbow lake) or braided river (comp. Wilczyński, 1992 and Krzyszkowski and Winter, 1996). A plant assemblage (oryctocoenosis) of this type is considered to be parautochthonous (Gastaldo et al., 1996).

CHARACTERISTICS OF PALAEOVEGETATION

A reliable reconstruction of the palaeovegetation must take into account the form of fossil remains (which limits the range of possible transport by wind

or water), the sedimentary environment that limits the possible habitats, and the ecology of the nearest living relatives of fossil taxa (Ferguson et al., 1998). Most macroremains analysed from assemblage KRAM-P 225 are fossil leaves, usually from trees and shrubs, with a limited dispersal potential that did not exceed 20–50 m from the source plant (Ferguson, 1985). The plant assemblage KRAM-P 225 was most probably formed in the fluvial sedimentary environment of a water body with stagnant (fluvial lake in abandoned channel) or slowly flowing water (fluvial lake in abandoned channel partially or temporarily connected with river). In the case of a fluvial sedimentary environment, leaf assemblages of wetland vegetation surrounding a sedimentary reservoir bear little resemblance to the vegetation as a whole (Spicer, 1980; Ferguson, 1985). Leaf floras formed in deposits of a similar type of sedimentary environment reflect both the autochthonous aquatic vegetation (water plants) and the vegetation cover of habitats that directly surround the water body (Ferguson et al., 1998). The analysis of the ecology of the nearest living relatives of fossil taxa could help to distinguish taxa found in the discussed plant assemblage as components of swamp, riparian, or mesophytic plant communities. It should be stressed, however, that fossil plant assemblages from fluvial environments of abandoned channels are composed almost exclusively of remains of wetland vegetation that grow along the channel margins (Behrensmeyer and Hook, 1992). Thus, the presence and presumably composition of mesophytic (zonal) plant communities can be inferred only indirectly using taxa that represent the “mesophytic” component of wetland plant communities (Worobiec and Szykiewicz, 2016). Wetland vegetation of a fluvial (riverine) environment is shaped mostly by the duration of floods and the associated variation of groundwater levels (Theriot, 1993; Cooper and Merritt, 2012). The frequency and duration of flood inundation and raised groundwater levels depend directly on the elevational gradient of the river floodplain and strongly influence the distribution of plant species in wetland communities. Considering this, Reed (1988), Tiner (1993), and Lichvar (2013) established five wetland indicator status ratings for plants occurring in natural conditions for the USA's *National Wetland Plant List*. In the case of fossil plant communities, however, such a detailed rating of wetland taxa does not seem credible since most extant wetland species can be found both in rather wet and more mesic localities, even in mesophytic upland communities (Tiner, 1993). Therefore, Worobiec and Szykiewicz (2016) proposed a simplified

ranking for fossil wetland species with only two ranks: obligate wetland plants (OW), which occur exclusively or almost exclusively in wetlands, and facultative wetland plants (FW), which besides inhabiting drier bottomland hardwood communities also possibly grow in upland mesophytic communities. Table 1 ranks wetland species from assemblage KRAM-P 225, mainly on the basis of the flood tolerance of modern North American equivalents of the fossil taxa, partly based on the already noted American *National Wetland Plant List* (Lichvar, 2013), Stults and Axsmith (2015), and Elliott et al. (2016). *Potamogeton*, an obligate wetland plant found in the discussed assemblage, points to the presence of water body vegetation of stagnant or slowly moving water. The remaining fossil taxa suggest that the sedimentary reservoir was surrounded by wetland (riparian) communities of a periodically flooded bottomland hardwood forest. In moist places it was probably dominated by *Acer tricuspidatum*, *Betula* cf. *plioplatyptera*, *Betula subpubescens*, *Carpinus grandis*, *Carpinus* sp., *Carya serrifolia*, cf. *Cercidiphyllum crenatum*, *Gleditsia europaea* sp. nov., *Laria ruemianiana*, *Myrica lignitum*, *Phragmites oeningensis*, *Pinus* sp., and *Sequoia abietina*. *Gleditsia europaea* sp. nov. and *Phragmites oeningensis* most probably occupied the shore of

the water body and were accompanied by *Acer tricuspidatum*, *Carya serrifolia*, and *Myrica lignitum*. In drier places, the bottomland vegetation was presumably mixed with more mesophytic taxa such as *Carpinus grandis*, *Pinus* sp., and *Sequoia abietina*. The wetland (riparian) forests similar to assemblage KRAM-P 225 were common in the Miocene of the Polish Lowlands (Worobiec and Kasiński, 2009). The Miocene vegetation from Belchatów has much in common with riparian communities of eastern and south-eastern North America (Wilén and Tiner, 1993; Hamel and Foti, 1995). It also has some relationship (presumably presence of *Cercidiphyllum*) with the riparian communities of central China (Wei et al., 2010).

Taxa considered to be exclusively upland (zonal, mesophytic) seem to be completely absent from the discussed fossil assemblage. Presumably, the sedimentary reservoir may have been situated away from any elevations such as river terraces or upland slopes covered by mesophytic communities. Nonetheless, *Alnus ducalis* and *Fagus silesiaca*, whose remains were rather scarce, most probably occupied dry habitats in transition between riparian forest and upland mesophytic communities (Elliott et al., 2016). As most of the remaining taxa were classified as facultative wetland species, some of them

TABLE 1. Ranks of wetland species from assemblage KRAM-P 225. In the case of fossil taxa with modern equivalents from North America, the wetlands ranks are based on the flood tolerance of these equivalents (Lichvar, 2013; Stults and Axsmith, 2015; Elliott et al., 2016).

Fossil taxon	Obligate wetland	Facultative wetland
<i>Acer tricuspidatum</i>		+
<i>Alnus ducalis</i>		+
<i>Betula</i> cf. <i>plioplatyptera</i>		+
<i>Betula subpubescens</i>		+
<i>Carpinus grandis</i>		+
<i>Carpinus</i> sp.		+
<i>Carya serrifolia</i>		+
cf. <i>Cercidiphyllum crenatum</i>		+
<i>Dicotylophyllum</i> sp. 1	?	?
<i>Fagus silesiaca</i>		+
<i>Gleditsia europaea</i> sp. nov.	+	
<i>Laria ruemianiana</i>		+
<i>Leguminophyllum kvacekii</i> sp. nov.	?	?
<i>Myrica lignitum</i>		+
<i>Phragmites oeningensis</i>		+
<i>Pinus</i> sp.		+
<i>Potamogeton</i> sp.	+	
<i>Sequoia abietina</i>		+

may also have been components of mesophytic upland communities.

This reconstruction of fossil vegetation based on the macroremains assemblage is in accordance with the results of a pollen analysis of samples taken from assemblage KRAM-P 225. Among the pollen, Pinaceae (mainly *Pinus*, *Cathaya*, *Tsuga*, and *Abies*) and Cupressaceae (*Taxodium*/*Glyptostrobus* type and *Sequoia*/*Sequoiadendron*/*Metasequoia* type) prevail. Pollen grains of angiosperms from the genera *Betula*, *Fagus*, *Pterocarya*, *Carya*, *Myrica*, *Carpinus*, *Alnus*, *Ulmus*, and *Nyssa* are relatively frequent. In addition, the pollen grains of *Celtis*, *Liquidambar*, *Acer*, *Salix*, *Fraxinus*, *Eucommia*, *Reevesia*, *Cercidiphyllum*, and Fabaceae (fossil species *Tricolporopollenites fallax* and *Tr. liblarensis*) and others are also present. The occurrence of some freshwater algae as well as the pollen of *Potamogeton*, Sparganiaceae/Typhaceae type, and *Nuphar* confirm the presence of a freshwater body. The pollen spectra show the dominance of wetland, riparian, and swamp vegetation. However, some genera recorded in both pollen and macroremains assemblages (*Acer*, *Betula*, *Eucommia*, *Fagus*, *Quercus*, *Ulmus*) could grow in both swamp and mesophytic plant communities. Palynological assemblage will be discussed in detail in a separate article.

PALAEOCLIMATE RECONSTRUCTION

Thermal climatic conditions (e.g., cold-month mean temperature, lowest winter temperature) have an influence on azonal wetland vegetation (Tepley et al., 2004; Schnitzler et al., 2005). Almost all fossil taxa found in assemblage KRAM-P 225 represent temperate or warm temperate elements, equivalent to the former arctotertiary geofloristic elements (Mai, 1995; Grímsson et al., 2015). The nearest living relatives of these fossil species are found in temperate to warm temperate climate areas of the Northern Hemisphere characterised by “C” (warm temperate elements) and mild varieties of “D” (temperate elements) climate types in the Köppen-Geiger climate classification (Kottek et al., 2006). The absence of typically thermophilous plants (e.g., Lauraceae, palms) confirms climatic cooling during the late Miocene (Prista et al., 2015) and points to warm temperate climate conditions during the sedimentation of the deposits with the discussed leaf assemblage. All the same, the presence of *Gleditsia europaea* sp. nov., *Laria rueminiiana*, and *Sequoia abietina*, and presumably presence of *Cercidiphyllum crenatum* indicate favourable climatic conditions with presumably mild winters. We used the coexistence

approach (CA) method (Mosbrugger and Utescher, 1997) to estimate the mean annual temperature (MAT) for the discussed leaf assemblage. In Table 2 we compare data on the fossil taxa and their recent counterparts with their MAT ranges for most taxa based on Utescher and Mosbrugger (2017) and for *Cercidiphyllum japonicum* and *Fagus hayatae* on Fang et al. (2011). As a result we estimate the MAT range as 13.5°C–16.5°C (lower limit for *Reevesia* sp. and upper limit for *Betula pubescens*).

Unfortunately, reconstruction of palaeoprecipitation using macroremains as a basis for azonal, wetland vegetation from Bełchatów, does not seem credible. Contrary to the vegetation of mesophytic habitats that depends mostly on water from rainfall, wetland plants take advantage of the riverine water supply and thus are not so sensitive to precipitation amounts (Brinson et al., 1981).

The palaeoclimate experienced by plant assemblage KRAM-P 225 from Bełchatów may be comparable to the modern climate of areas of deciduous broad-leaved forests with a warm temperate and humid climate. The palaeovegetation of leaf assemblage KRAM-P 225 could correspond to the extant biome of temperate deciduous (summer-green) forests (Box and Fujiwara, 2013). Recent equivalents of the fossil taxa from Bełchatów might be found in warm temperate deciduous forests of eastern North America (eastern deciduous forests, southern mixed hardwood forests), East Asia (central Japan, eastern central China – temperate deciduous forests, Mixed Mesophytic Forests) and the Euxine-Hyrcanian region (deciduous Colchis and Hyrcanian forests) (Greller, 2013; Box and Fujiwara, 2015). The climate of these areas corresponds to the Cfa type (warm temperate, fully humid, and with a hot summer) in the Köppen-Geiger climate classification (Kottek et al., 2006).

AGE OF THE PLANT ASSEMBLAGE

The analysed leaf assemblage from the Bełchatów Lignite Mine is situated at the floor part of a sandy-clayey unit whose age is estimated as late Miocene. The composition of leaf assemblage KRAM-P 225 corresponds to late Miocene leaf assemblages found earlier in a sandy-clayey unit from the Bełchatów Lignite Mine (Stuchlik et al., 1990; Worobiec and Lesiak, 1998; Worobiec, 2003b; Worobiec et al., 2012; Worobiec, 2014). Taxa representing a warm temperate, deciduous floristic element present in leaf assemblage KRAM-P 225 are typical of the late Neogene vegetation of Central Europe (Mai, 1995; Kovar-Eder, 2003). The overall results of the pollen analysis of samples

TABLE 2. The nearest living relatives (NLR) of fossil taxa from leaf assemblage KRAM-P 225 and the mean annual temperature (MAT) ranges (°C) of NLR. Data on NLR and their MAT ranges based on Utescher and Mosbrugger (2017), and for *Cercidiphyllum japonicum* and *Fagus hayatae* on Fang et al. (2011).

Fossil taxon	NLR of fossil taxon	Lower limit of MAT of NLR	Upper limit of MAT of NLR
<i>Acer tricuspidatum</i>	<i>Acer</i> section <i>Rubra</i> (<i>Ac. rubrum</i> , <i>Ac. saccharinum</i>)	3.40	23.90
<i>Alnus ducalis</i>	<i>Alnus matsumurae</i> *	- 0.40	7.60
<i>Betula</i> cf. <i>plioplatyptera</i>	<i>Betula</i> sp.	- 15.00	25.80
<i>Betula subpubescens</i>	<i>Betula pubescens</i>	- 6.70	16.50
<i>Carpinus grandis</i>	<i>Carpinus betulus</i>	5.30	17.60
<i>Carpinus</i> sp.	<i>Carpinus</i> sp.	0.00	25.80
<i>Carya serrifolia</i>	<i>Carya</i> sp.	4.40	26.60
cf. <i>Cercidiphyllum crenatum</i>	<i>Cercidiphyllum japonicum</i>	2.00	18.20
<i>Dicotylophyllum</i> sp. 1	-	-	-
<i>Fagus silesiaca</i>	<i>Fagus hayatae</i>	9.30	21.10
<i>Gleditsia europaea</i> sp. nov.	<i>Gleditsia</i> sp.	5.70	21.70
<i>Laria ruemianiana</i>	<i>Reevesia</i> sp.	13.50	25.50
<i>Leguminophyllum kvacekii</i> sp. nov.	<i>Leguminosae</i>	-	-
<i>Myrica lignitum</i>	<i>Myrica</i> sp.	- 8.90	28.10
<i>Phragmites oeningensis</i>	<i>Phragmites</i> sp.	-	-
<i>Pinus</i> sp.	<i>Pinus</i> sp.	- 9.20	25.50
<i>Potamogeton</i> sp.	<i>Potamogeton</i> sp.	- 15.00	23.50
<i>Sequoia abietina</i>	<i>Sequoia sempervirens</i>	9.10	25.00
Obtained MAT range		13.5°C – 16.5°C	

* *Alnus matsumurae* is an outlier taxon, excluded from the calculation of MAT as it is a mountainous species, endemic to Japan.

taken from assemblage KRAM-P 225 generally correspond to the proposed late Miocene age of the leaf assemblage studied. The palynoflora is most similar in its composition to the spore-pollen spectra of the X and XI climatic phases distinguished by Ziemińska-Tworzydło (in Piwocki and Ziemińska-Tworzydło, 1997). Deposits bearing such assemblages accumulated during the late Serravalian and Tortonian. The studied palynoflora is also close in composition to assemblage KRAM-P 218 (Worobiec and Worobiec, 2016). Thus, assemblage KRAM-P 225 could be either late Serravalian or Tortonian (latest middle Miocene and late Miocene).

CONCLUSIONS

From 132 specimens (37 slides with isolated leaf remains and 95 rock samples), 18 species from the genera *Acer*, *Alnus*, *Betula*, *Carpinus*, *Carya*, cf. *Cercidiphyllum*, *Dicotylophyllum*, *Fagus*, *Gleditsia*, *Laria*, *Leguminophyllum*, *Myrica*, *Phragmites*, *Pinus*, *Potamogeton*, and *Sequoia* were identified.

Two new fossil species were described: *Gleditsia europaea* sp. nov. G. Worobiec and *Leguminophyllum kvacekii* sp. nov. G. Worobiec.

Plant assemblage KRAM-P 225 reflects only local azonal wetland vegetation and most probably was formed in the fluvial sedimentary environment of a water body with stagnant or slowly flowing water, which is indicated by the presence of *Potamogeton*. The water body was surrounded by wetland (riparian) communities of a periodically flooded bottomland hardwood forest. In moist places it was probably dominated by *Acer tricuspidatum*, *Betula* cf. *plioplatyptera*, *Betula subpubescens*, *Carpinus grandis*, *Carpinus* sp., *Carya serrifolia*, cf. *Cercidiphyllum crenatum*, *Gleditsia europaea* sp. nov., *Laria ruemianiana*, *Myrica lignitum*, *Phragmites oeningensis*, *Pinus* sp., and *Sequoia abietina*. *Gleditsia europaea* sp. nov. and *Phragmites oeningensis* most probably occupied the shore of the water body and were accompanied by *Acer tricuspidatum*, *Carya serrifolia*, and *Myrica lignitum*. In drier places, the bottomland vegetation was presumably mixed with more mesophytic taxa such as *Carpinus*

grandis, *Pinus* sp. and *Sequoia abietina*. Riparian vegetation similar to assemblage KRAM-P 225 was common in the Miocene of the Polish Lowlands (Worobiec and Kasiński, 2009) and has much in common with the riparian communities of eastern and south-eastern North America (Wilén and Tiner, 1993; Hamel and Foti, 1995), and also probably with the riparian forests of central China (Wei et al., 2010). Taxa considered to be exclusively upland (mesophytic) seem to be completely absent from the discussed assemblage. However, *Alnus ducalis*, *Fagus silesiaca*, and some of other taxa may also have been components of mesophytic upland communities. The reconstruction of fossil vegetation based on the macroremains assemblage is in accordance with the results of pollen analysis.

Almost all of the taxa present in this leaf assemblage represent the warm temperate element. The nearest living relatives of those fossil species are found in warm temperate climate areas of the Northern Hemisphere. The presence of cf. *Cercidiphyllum crenatum*, *Laria rueminiiana*, *Gleditsia europaea* sp. nov., and *Sequoia abietina* indicates favourable climatic conditions with presumably mild winters. The pollen analysis confirms a warm temperate climate and suggests moderately wet conditions. A mean annual temperature (MAT) range of 13.5°C–16.5°C is suggested on the basis of the

coexistence approach (CA) method (Mosbrugger and Utescher, 1997). Reconstruction of palaeoprecipitation on the basis of azonal, wetland vegetation from Bełchatów seems unreliable.

The palaeoclimate of plant assemblage KRAM-P 225 may have been comparable to the modern-day climate of the areas of deciduous broad-leaved forest with a warm temperate, humid (often monsoonal), climate, classified as the Cfa type (warm temperate, fully humid, with a hot summer) in the Köppen-Geiger climate classification (Kottek et al., 2006).

The composition of leaf assemblage KRAM-P 225, its geological setting, and the findings from its palynological analysis suggest a latest middle Miocene to late Miocene age.

ACKNOWLEDGEMENTS

The studies were supported by the W. Szafer Institute of Botany, Polish Academy of Sciences, Kraków, Poland through the statutory funds. We thank D. Zdebska, S. Florjan, and M. Wayda (former researchers of the Institute of Botany, Jagiellonian University, Kraków) for their help with fieldworks and collecting fossil leaves in the outcrop of the Bełchatów Lignite Mine.

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