

A NEW OLIGOCENE FLORA FROM LUDVÍKOVICE NEAR DĚČÍN (ČESKÉ STŘEDOHOŘÍ MTS., THE CZECH REPUBLIC)

This paper is dedicated to our friend and teacher, Zlatko Kvaček, who will be very much missed by all of us.

VASILIS TEODORIDIS^{1,*}, †ZLATKO KVAČEK², MIROSLAV RADOŇ³, VLADISLAV RAPPRICH⁴, ANGELA A. BRUCH⁵

- ¹ Department of Biology and Environmental Studies, Faculty of Education, Charles University, Magdalény Rettigové 4, 116 39 Praha 1, the Czech Republic; e-mail: vasilis.teodoridis@pedf.cuni.cz.
- ² Institute of Geology and Palaeontology, Faculty of Science, Charles University, Albertov 6, 128 43 Praha 2, the Czech Republic.
- ³ Regional Museum in Teplice, Zámecké náměstí 14, 415 01 Teplice, the Czech Republic; e-mail: rmtep@seznam.cz.
- ⁴ Czech Geological Survey, Klárov 3, 118 21 Praha 1, the Czech Republic; e-mail: vladislav.rapprich@geology.cz.
- ⁵ Heidelberg Academy of Sciences and Humanities, Research Center 'The Role of Culture in Early Expansions of Humans' at Senckenberg Research Institute and Natural History Museum Frankfurt, Senckenberganlage 25, 603 25 Frankfurt am Main, Germany; e-mail: abruch@senckenberg.de.
- *corresponding author

Teodoridis, V., Kvaček, Z., Radoň, M., Rapprich, V., Bruch, A. A. (2020): A new Oligocene flora from Ludvíkovice near Děčín (České středohoří Mts., the Czech Republic). – Fossil Imprint, 76(2): 297–314, Praha. ISSN 2533-4050 (print), ISSN 2533-4069 (on-line).

Abstract: A recently recovered site of plant macrofossils, Ludvíkovice, in the České středohoří Mts. is situated on Sokolí vrch hill, belonging to the Děčín Formation (radiometrically dated to 30.8–24.7 Ma), according to regional stratigraphy. The flora has yielded a fern, *Rumohra recentior*, and several angiosperms, but no conifers. The prevailing foliage is preserved without cuticles. Noteworthy are records of *Daphnogene cinnamomifolia*, *Laurophyllum* cf. *acutimontanum*, *Platanus neptuni*, *Sloanea artocarpites*, *Carya fragiliformis* / *C. quadrangula*, *Alnus rhenana*, *Trigonobalanopsis rhamnoides*, *Eotrigonobalanus furcinervis* and cf. *Quercus* sp. Several foliage specimens of dicots could not be identified to species level, i.e., *Leguminophyllum* sp., *Pungiphyllum* cf. *cruciatum* and *Dicotylophyllum* sp. div. The fossil plant assemblage of Ludvíkovice corresponds to zonal mesophytic vegetation accompanied by riparian elements. This is corroborated by the Integrated Plant Record vegetation analysis, which reconstructs a zonal broad-leaved evergreen forest similar to the living broad-leaved evergreen sclerophyllous forest from Southern Hunan and Northern Guangxi in SE China. The vegetation thrived under a humid climate characterized by average values of MAT (14.6–24.1 °C), WMMT (24.7–28.3 °C), CMMT (2.2–18.8 °C) and MAP (979–1724 mm). The fossil flora of Ludvíkovice is similar in composition to the floras of Markvartice, Veselíčko, also from the Oligocene Děčín Formation of the České středohoří Mts. and the Hrazený hill.

Key words: fossil, leaves, fruit, morphology, vegetation, climate, North Bohemia, Palaeogene

Received: July 13, 2020 | Accepted: September 22, 2020 | Issued: December 30, 2020

Introduction

In the last two decades, several Oligocene sites of plant assemblages known from the volcanic complex of České středohoří Mts. and adjacent Saxony have been reviewed in a number of papers, e.g., Suletice-Berand (Kvaček and Walther 2004), Seifhennersdorf (Walther and Kvaček 2007), Hrazený hill (Kvaček et al. 2015), Matrý at Sebuzín (Kvaček et al. 2018). All these studies produced new information about the palaeoenvironmental aspects of this region. The recently recovered plant assemblage from Ludvíkovice, introduced below, is another piece of the puzzle. The aim of

our study is to contribute to understanding the variability of environments associated with emerging volcanic complexes during the Oligocene.

The studied plant assemblage is located in an abandoned quarry on the northern slope of the Sokolí vrch hill (formerly Falkenberg, elevation 506 m alt.). The Sokolí vrch hill has the form of a flat table-rock, which rises some 200 m above the village Ludvíkovice (formerly Loosdorf) situated on its western slope, about 2 km north-northeast from Děčín (GPS: 50° 47′ 04″ N, 14° 16′ 44″ E – see Text-fig. 1). The abandoned quarry, which is divided into one high and four smaller benches, was operated by Ludvíkovice village since the

DOI 10.37520/fi.2020.024 297

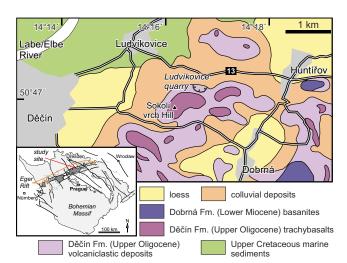
1870s. The quarry was later named after a local master-paver Robert Siebiger from Ludvíkovice, who operated the quarry before World War I. The last tenant of the quarry was Ernst Strache from Ludvíkovice during the 1940s, and exploitation terminated before the end of World War II. The quarry was temporarily re-opened between 2002 to 2010, when it was operated by Zemní a dopravní stavby Hrdý Milan, Ltd. in Dobrná. The fossil flora is known since 1930s (Rehnelt 1957), but its re-discovery by a private fossil-collector, Jan Stodola, from Horní Habartice occurred in 2003. These new findings, including those of Jan Stodola, were later published by Radoň (2006: 96–97) as a list of taxa. The present study describes the fossil flora from Ludvíkovice and tries to evaluate its palaeoenvironmental character.

Geological setting

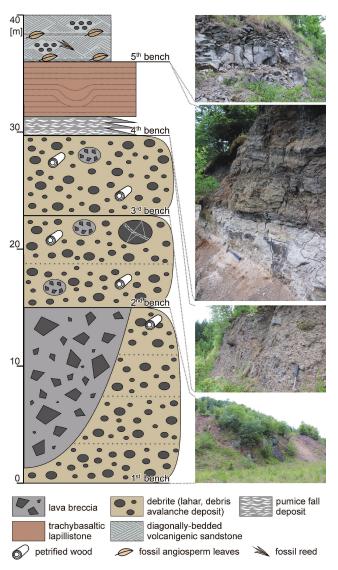
The palaeontological record of late Eocene to early Miocene in Northern Bohemia is associated with volcaniclastic rocks or sediments of intervolcanic lakes within two prominent volcanic complexes set within the Ohře Rift. Whereas the Doupovské hory Volcanic Complex is dominated by lava flows (e.g., Rapprich and Holub 2008), frequent volcaniclastic fossiliferous sequences can be found in the volcaniclastic deposits of the České středohoří Volcanic Complex. The volcanic activity in the latter complex lasted from the late Eocene until the late Miocene. Its superficial eruptive products represent a sequence of four formations, i.e., upper Eocene to lower Oligocene basanitic Ústí Fm. (available K-Ar geochronological data gave a range of 36.1–25.5 Ma – see Cajz 2000, Cajz et al. 2009), Oligocene trachybasaltic Děčín Fm. (30.8–24.7 Ma), lower Miocene basanitic Dobrná Fm. (24.0-19.3 Ma), and upper Miocene basanitic Štrbice Fm. (13.9-9.0 Ma), respectively. The magmatic centre for the earlier two formations was represented by the Roztoky Intrusive Complex occupying the Roztoky caldera and its immediate vicinity, with an activity span dated to 33–25 Ma (Ulrych and Balogh 2000).

The sequence of volcaniclastic deposits exposed in the abandoned Ludvíkovice quarry is associated with trachybasaltic lavas and therefore belongs to the Oligocene Děčín Fm. (possibly late Rupelian, but mainly Chattian). Lavas and pyroclastic rocks of the Děčín Fm. were mainly produced from a central stratovolcano (Cajz 2000), but the existence of smaller monogenetic volcanoes was also documented on the southern margin of the České středohoří Volcanic Complex (e.g., Rapprich et al. 2010). A large intrusive body associated with the Děčín Fm. on the southern margin of the České středohoří Volcanic Complex was recently dated to 29.12 ± 0.63 Ma (K-Ar, see Mysliveček et al. 2018).

The volcaniclastic sequence, with a total thickness reaching 40 m, can be subdivided into three main units (Textfig. 2). The total thickness of the first, gravitational unit, comprising debrites, reaches almost 30 m. The debrites are chaotic mostly matrix-supported, occasionally with boulders up to 4×2 m. Despite boundaries between individual flow-units not being clearly exposed, the variability in textures suggests that the debrites were deposited from several (6–8) debris flows, i.e., lahars. In the lowermost part of this unit, a body of lava breccia fills a fossil canyon within the lahar



Text-fig. 1. Geological sketch-map of the Ludvíkovice quarry area (adopted from the on-line geological map 1:50 000 scale of the Czech Geological Survey – https://mapy.geology.cz/geocr50/).



Text-fig. 2. Scheme of volcaniclastic sequence exposed in Ludvíkovice abandoned quarry.

deposits (Text-fig. 2). In the middle part of the debrite unit (around the base of the 2nd bench), the radial cracks around



Text-fig. 3. Textures of main volcaniclastic deposits exposed in abandoned Ludvíkovice quarry. a: radial cracks surrounding some boulders (see arrows) in hot lahar deposit. b: jig-saw fit of fractures (see arrows) within a mega-block of debris-avalanche deposit. c: pseudo-fiamme texture of compacted argillized pumice-fall deposit. d: trachybasaltic lapilli-stone of phreato-magmatic eruption. e: palaeo-relief developed and buried within the pyroclastic unit. f: diagonal bedding in fluvial volcanigenic sandstones. g: diluted and fine-grained lahars embedded in volcanigenic sandstones.

some boulders (Text-fig. 3a) suggest that at least some of the lahars were deposited as hot lahars. Below the base of the 3rd bench, the debrites contain large (> 4 m) mega-blocks displaying shattered texture with a jig-saw fit of cracks (Text-fig. 3b). Such texture in shattered mega-blocks, where individual sub-grains did not migrate apart, is characteristic for high-velocity water-undersaturated debris avalanches resulting from sector collapses of volcanic edifices. The uppermost part of this unit (3rd bench) is then represented by finer debrites dominated by ground-mass enclosing well-rounded boulders not exceeding 40 cm in diameter. Such structure corresponds to water-saturated debris-flows (lahars). The debrites of the gravitational unit contain randomly distributed fragments of mineralized woods. Altogether, this unit records processes associated with instability and gravitational decay of a large volcanic edifice.

The second unit, exposed on the 4th bench, exceeds 6 m in thickness. This unit is of pyroclastic origin and consists of several pyroclastic fall beds. The lowermost part (35 cm) differs from the rest of this unit in its whitish colour. This whitish bed consists of three layers, each of them with normal grading (lapillistone to lapilli-tuff) and good to moderate sorting (Text-fig. 3c). The coarser-grained parts display obvious clast-supported structure, while the clasts are represented by trachytic/phonolitic "pseudo-fiamme". As "pseudo-fiamme" we identify here fragments of trachtic/ phonolitic pumice which were flattened due to compaction of argillized glass and not due to welding of high-grade pyroclastic-flow deposits, as in the case of common fiamme. This deposit (note, this is the first report of a trachytic/ phonolitice superficial pyroclastic deposit in the Eger Rift) reflects a sub-Plinian eruption of larger semi-distant source vent with differentiated composition - possibly the Roztoky caldera (ca. 12 km SSW from Ludvíkovice, e.g., Kopecký 2010). The remaining portion of this unit is dominated by trachybasaltic lapillistones, locally with thin trachyte/phonolite pumice intercalations or admixtures. The lapillistones are well-sorted, clast-supported, and individual clasts (5-10 mm in diameter) are angular and free of any vesicles (Text-fig. 3d). The angular and nonvesiculated character of the pyroclasts suggests hydroclastic fragmentation during a phreatomagmatic eruption. The grain-size and sorting correspond to eruption(s) of nearby monogenetic volcano(es) of tuff-cone type. Within the sequence of trachybasaltic lapillistones, several disconformities follow the palaeotopography developed upon unconsolidated pyroclastic deposits (Text-fig. 3e). The sharp geometry of these palaeo-gullies indicates their formation in subaerial conditions during heavy rains. Continuous thickness and grain-size of the following beds covering the palaeo-gullies is clear evidence for deposition of these pyroclastic deposits as fall deposits under subaerial conditions. During this stage, a previously formed debritefan on the foothill of a larger complex volcano was penetrated and covered by pyroclastic deposits of a monogenetic volcanic field erupting on dry-land, but in water-saturated conditions. At the base of the pyroclastic unit, rare fossil rooting systems (rooted into lahar deposits) can be found.

The presented study focuses on the thinnest, uppermost unit of greyish colour. Well-sorted sandstones with diagonal bedding dominate this unit. Whereas the lower part is characterized by low-angle diagonal bedding, the upper part is characterized by high-angle diagonal bedding (Text-fig. 3f). Locally, the sandstones enclose channels filled with matrixsupported, ill-sorted gravels with well-rounded basaltic pebbles (1–5 cm, occasionally up to 20 cm; Text-fig. 3g). These gravels represent the diluted distal facies of lahars, deposited in a braiding river system. Two horizons within the volcanigenic sandstones contain abundant fossil leaves. The leaves are folded and deformed as they were rolled into the sediment during deposition in a fluvial system. Uncertain remnants of fossil reed (monocots) can be found across this unit. The entire unit is dominated by volcaniclastic sandstones and therefore corresponds to sedimentation in an alluvial fan on the foothills of the volcanic system, which buried previous volcaniclastic strata. The full sequence corresponds to deposition on a plain at the foothills of a large central volcano, with the influence of local smaller (parasitic?) cones.

Material and methods

The fossiliferous sediment is represented by greyish volcanogenic fine-grained sandstones with well-developed diagonal bedding. The fossil foliage and fruit material studied are preserved as impressions, usually moulded into the sediment and intensively folded, which makes their classification more challenging. Identification of the palaeobotanical material relies on gross morphological features. Attempts to obtain epidermal structures from these impressions failed. The studied fossils were collected by the third author (MR) between 2018 to 2020. The specimens are housed in the palaeobotanical collections of the Regional Museum in Teplice, the Czech Republic (PA) and National Museum in Prague, the Czech Republic (NM). Vegetation associations were reconstructed following the ecological interpretation of the fossil flora based on their specific leaf "character" and on the authors' experience. Abbreviations used to describe the vertical stratification of the fossil community are: E1 (herbs), E2 (shrubs and lianas), E3 (trees up to 25 m height) and E4 (trees over 25 m height). Three palaeoenvironmental techniques were applied to the material. The Integrated Plant Record vegetation analysis (IPRvegetation analysis - Kovar-Eder et al. 2008, Teodoridis et al. 2011) including the newly developed diagnostic tool of Drudge 1 sensu Teodoridis et al. (2020), Leaf Margin Analysis (LMA) sensu Su et al. (2010) and the Coexistence Approach sensu Utescher et al. (2014) were used to obtain independent palaeoenvironmental estimates.

Systematic palaeobotany

The arrangement of taxa follows the system introduced by the Angiosperm Phylogeny Group IV (APG IV 2016).

Family Dryopteridaceae HERTER, 1949 nom. cons.

Genus Rumohra Raddi, 1819

Rumohra recentior (UNGER) BARTHEL, 1976 Pl. 1, Figs 1–4

1847 Sphenopteris recentior UNGER, p. 123, pl. 37, fig. 4.

1976 Rumohra recentior (UNGER) BARTHEL, p. 457, text-fig. 6a-d, pls 80, 81.

Material. Fragments and incomplete sterile fern fronds, impressions PA 1618, PA 1619, PA 1620, PA 1621–28, PA 1625, NM-G 12803, NM-G 12804, NM-G 12806.

Description. Incomplete sterile fern fronds, apex with a lateral pinna and a detached pinna, preserved length up to 100 mm, rachis strong, surface smooth, pinna almost perpendicular, pinnules ovate, slightly asymmetrical, deeply irregularly dentate, up to 15 mm long and 5 mm wide, segments broadly attached, admedially oriented, shallowly dissected, secondary veins alternate, 3 times forked, the lowermost admedially reaching the margin.

Remarks. These fragments are up to now the first records of this fern in the Oligocene of the České středohoří Mts. and Saxony. From the Palaeogene of North Bohemia, it is only known from the Doupovské hory Mts., the locality Valeč (Bůžek et al. 1990) and from the České středohoří Mts., localities Kučlín (Kvaček and Teodoridis 2011) and Holý Kluk (Radoň et al. 2006). The new finds from Ludvíkovice morphologically fully correspond to the above mentioned material from the Czech Republic. For more detailed analysis of morphology and affinities see Barthel (1976).

Family Lauraceae Juss., 1789 nom. cons.

Genus Daphnogene Unger, 1850

Daphnogene cinnamomifolia (Brongn.) Unger, 1850 Pl. 1, Figs 5, 6

1822 *Phyllites cinnamomifolia* Brongn. in Cuvier, p. 359, pl. 11, fig. 12.

1850 Daphnogene cinnamomifolia (Brongn.) Unger, p. 424.

M a t e r i a l .14 incomplete simple leaves and fragments, impressions PA 1623, PA 1638, PA 1663A, PA 1665, PA 1673, PA 1678, PA 1679, NM-G 12797, NM-G 12802, NM-G 12805, NM-G 12807, NM-G 12812, NM-G 12815.

Description. Leaves lanceolate to widely oval, up to 120 mm long and 52 mm wide, apex not preserved probably shortly acuminate and blunt, base cuneate with fragmentary petiole, margin entire, venation suprabasal acrodromous, midrib strong, moderate, straight or curved, lateral veins thinner, alternate, running along the margin, usually connecting with secondaries at 2/3 of the blade length, secondary veins thinner, alternate, originating at 40° to 50°, curved and looping by margin or between midrib and lateral veins, tertiary veins alternate perpendicular, straight to sinuous, often forked, venation of the higher orders poorly preserved.

R e m a r k s . The leaves of *Daphnogene cinnamomifolia* are known from most Oligocene localities of Europe and obviously represent lineal to oval lanceolate "sun" and larger oval "shade" leaves distinguished as two foliage forms "*cinnamomifolia*" and "*lanceolata*" (e.g., Kvaček and Walther 1995). In volcanic floras this element usually occurs abundantly (lacking at Bechlejovice). In Hammerunterwiesenthal (Krušné hory / Erzgebirge Mts.) and Valeč (Doupovské hory Mts.) it occurs in lacustrine

sediments with volcaniclastic admixture as a possible "pioneer" plant (Kvaček and Walther 1995).

Genus Laurophyllum Göpp., 1854

Laurophyllum cf. acutimontanum MAI, 1963 Pl. 1, Fig. 7

M a t e r i a l . 12 incomplete simple leaves and fragments, impressions PA 1623, PA 1650, PA 1662, PA 1665, PA 1679, NM-G 12808.

Description. Leaves lanceolate to elongate, up to 69 mm long and up to 18 mm wide, apex not preserved probably shortly attenuate to acute or blunt, base cuneate with fragmentary petiole (up to 7 mm), margin entire, venation brochidodromous, midrib straight, secondary veins thin, alternate, at 40° to 60°, looping, tertiary veins alternate perpendicular, straight to sinuous, venation of the higher orders regular polygonal reticulate, poorly preserved.

Remarks. The lauroid leaves with entire margin and brochidodromous venation are typical lanceolate to elongate in outline and in gross morphology match slender leaves of *Laurophyllum* cf. *acutimontanum*, which are common elements of late Eocene to Oligocene floras in Central Europe, e.g., Staré Sedlo, Bechlejovice, Kundratice, Suletice-Berand, Holý Kluk, Seifhennersdorf (Kvaček and Walther 1995, 1998, 2004, Knobloch et al. 1996, Radoň et al. 2006). However, the lack of epidermal structure does not allow for a clear assignment because the foliage of *Laurophyllum pseudoprinceps* Weyland et Kilpper and *Laurophyllum medimontanum* Bůžek, Holý et Kvaček have similar leaf morphology and co-occurred with *Laurophyllum acutimontanum* at Suletice-Berand, Kundratice and Bechlejovice (Kvaček and Walther 1995, 1998, 2004).

Family Platanaceae T.LESTIB., 1826 nom. cons.

Genus *Platanus* L., 1753 Subgenus *Platanus* subg. *Glandulosa* Kvaček, Manchester et Shuang X.Guo, 2001

> Platanus neptuni (Еттіндін) Bůžek, Holý et Kvaček, 1967 Pl. 2, Figs 1–3

1866 Sparganium neptuni Ettingsh., р. 31, pl. 7, figs 10–13, 17, 18.
 1967 Platanus neptuni (Еттіngsh.) Bůžek, Holý et Kvaček, р. 205, pl. 1, figs 1–4, 6, pls 2–4.

Material. Several incomplete simple leaves, impressions PA 1633, PA 1648, PA 1650, PA 1652, PA 1672, PA 1674, PA 1681, NM-G 12798, NM-G 12800.

Description. Fragmentary leaves elliptic to ovate or obovate, 52 to 118 mm long and 22 to 59 mm wide, apex not preserved, probably acute, base cuneate, margin widely blunt regularly dentate, entire in basal part, venation semicraspedodromous, partly eucamptodromous, secondary veins thinner, alternate, straight, originating at 40° to 60°, intersecondaries rarely obvious, thinner, tertiary veins alternate to opposite percurrent, straight to sinuous, venation of the higher orders regular polygonal reticulate, areolation well-developed, 3 to 4 sided, veinlets branching dichotomously.

Remarks. This extinct plane tree was widespread in the Palaeogene floras of the České středohoří Mts. starting from the late Eocene (Kučlín, Roudníky – Kvaček and Teodoridis 2011, Kvaček et al. 2014). It was a very common element during the Oligocene (Roudníky, Bechlejovice, Hrazený, Suletice-Berand and Seifhennersdorf – see Kvaček and Walther 1995, 2004, Walther and Kvaček 2007, Kvaček et al. 2014, 2015) to early Miocene of North Bohemia and Germany (Kvaček and Manchester 2004). The leaf morphology was corroborated by the cuticle structure, e.g., at Roudníky, Bechlejovice and Seifhennersdorf (Kvaček and Walther 2004, Walther and Kvaček 2007, Kvaček et al. 2014). The *Platanus neptuni* complex was monographically defined by Kvaček and Manchester (2004).

Family Fabaceae Lindl., 1836 nom. cons. Genus Leguminophyllum Escalup-Bassi, 1971

Leguminophyllum sp. Pl. 1, Figs 5–8

Material. 2 almost complete leaflets and their fragmentary counterparts, impressions PA 1625, PA 1664, PA 1668, PA 1675, PA 1676, NM-G 12796, NM-G 12799.

Description. Leaflets and fragments, widely elliptic to ovate, 32 to 95 mm long, 25 to 40 mm wide, base widely cuneate or rounded, apex shortly attenuate to acute, margin entire, venation brochidodromous, midrib thick, straight, secondary veins thinner, slightly bent and looping, regularly spaced, alternate to subopposite, originating at 40°, tertiary veins percurrent, curved to sinuous, venation of the higher orders regular polygonal reticulate, areolation well-developed, 3 to 4 sided.

Remarks. The almost complete leaflets are relatively big, and their morphology shows an affinity to deciduous elements of Leguminosae. Legume leaflets from the late Eocene to Oligocene of the Staré Sedlo Fm., the České středohoří Mts. and the Doupovské hory Mts. are not rare. They may represent several morphotypes, e.g., Kučlín (cf. Leguminosites sp. 1 and 2 - Kvaček and Teodoridis 2011), Matrý (? Leguminosae gen. indet. resembling Trigonobalanopsis Kvaček et H.Walther or Sapindus L. – Kvaček et al. 2018), Hrazený (*Phaseolites* spp. 1-4 - Kvaček et al. 2015) as well as from Bechlejovice (Leguminosites sp. 1, Leguminosites cladrastioides KVAČEK et H.Walther - Kvaček and Walther 2004) and Kundratice (Leguminosae gen. et sp., forma 1-5 - Kvaček and Walther 1998). Similarly, the plant assemblage of Seifhennersdorf contains many legumes, i.e., Leguminosites sp. 1 to 5 (Walther and Kvaček 2007). However, none of the above mentioned morphotypes match the material studied here. Leaflets with similar morphology are described as Cassiophyllum berenices (UNGER) KRÄUSEL from the Miocene of Chiuzbaia in Romania (Givulescu 1990) and as Leguminophyllum kvacekii G.Worobiec from the Miocene of Bełchatów in Poland (Worobiec and Worobiec 2019). We assign our studied material to the genus Leguminophyllum (Escalup-Bassi 1971), taking the view of Wang (1961) that the name Leguminosites should not be used for fossil legume leaflets.

Family Fagaceae Dumort., 1829

Genus Quercus L., 1753

cf. *Quercus* **sp.** Pl. 2, Figs 4–6

Material. 2 complete leaves and 1 incomplete leaf, impressions PA 1632, PA 1639, PA 1646.

Description. Leaves widely elliptic, incomplete leaf obovate, 50 mm to 61 mm long, 34 to 39 mm wide, apex acute, base widely cuneate, margin simple dentate, teeth acute, sinus rounded, venation craspedodromous, secondary veins thinner, slightly curved, alternate, originating at 40° to 60°, tertiary veins alternate to opposite percurrent, straight to sinuous, venation of the higher orders regular polygonal reticulate, areolation well-developed, 3 to 4 sided, veinlets lacking.

Remarks. The acute to short spiny teeth show an affinity to *Quercus*, however the widely elliptic outline is not typical for Fagaceae and may also resemble Betulaceae (see below). Relatively common leaves described as *Quercus lonchitis* UNGER (typified in Sotzka – Unger 1850, also occurring in Seifhennersdorf, Suletice, Lochočice and Stadice – Walther and Kvaček 2007) show similar features of the margin, however, the leaf outline is more elongate. Generally, the studied leaves also resemble the stratigraphically younger morphotypes of younger *Quercus drymeja* UNGER and *Q. mediterranea* UNGER. The incomplete obovate leaf (PA 1646) may morphologically resemble the basal part of "roburoid" oaks.

Genus Eotrigonobalanus H.Walther et Kvaček in Kvaček and Walter 1989

Eotrigonobalanus furcinervis (ROSSM.) H.WALTHER et Kvaček in Kvaček and Walter 1989

Pl. 2, Figs 6-8

1840 *Phyllites furcinervis* ROSSM., p. 33, pl. 6, fig. 25, pl. 7, figs 26–31.

1989 *Eotrigonobalanus furcinervis* (Rossm.) H.Walther et Kvaček in Kvaček and Walther, p. 581, text-figs 3–10, pls 33–36, 38–46, pl. 47, figs 1–3.

Material. Incomplete simple leaves, impressions PA 1645, PA 1661.

Description. Leaves simple, incomplete, oblong to elliptic, 70 mm and 102 mm long, 22 mm and 24 mm wide, base cuneate without petiole, apex not preserved probably shortly attenuate to acute, margin entire, venation eucamptodromous, midrib thick, almost straight, secondary veins thinner, slightly bent and looping along the margin, regularly spaced, alternate to subopposite, originating at 40°, tertiary veins percurrent, venation of the higher orders regular polygonal reticulate, areolation well-developed, 3 to 4 sided.

R e m a r k s . The leaves morphologically clearly match *Eotrigonobalanus furcinervis*, but the identification is tentative due to the lack of leaf epidermal anatomy. The leaves of this extinct fagaceous element are common in the late Eocene fluviatile sandstones of the Staré Sedlo Fm. (Knobloch et al. 1996, Teodoridis et al. 2012), Kučlín (Kvaček

2002, 2010, Kvaček and Teodoridis 2011) and other sites of this kind in Germany and elsewhere in Europe (Kvaček and Walther 1989). The occurrence of *Eotrigonobalanus* in Seifhennersdorf (Walther and Kvaček 2007) is the oldest evidence of this genus in volcanic floras of Central Europe during the early Oligocene. Regionally, this element is also known from the late Oligocene at Kleinsaubernitz (Walther 1999).

Genus Trigonobalanopsis Kvaček et H.Walther, 1988

Trigonobalanopsis rhamnoides (Rossm.) Kvaček et H.Walther, 1988

Pl. 2, Fig. 9

1840 Phyllites rhamnoides Rossm., p. 35, pl. 8, figs 30, 31.

1988 *Trigonobalanopsis rhamnoides* (Rossm.) Kvaček et H.Walther, p. 405, text-figs 2–4, pl. 2, figs 1–8, pls 50–54, pl. 55, figs 2–7, pl. 56, figs 1–4, pl. 57.

Material. 2 complete and 2 incomplete leaves, impressions PA 1651, PA 1665, PA 1667, NM-G 12813.

Description. Leaves oblong to ovate, 32 to 86 mm long, 11 to 30 mm wide, base cuneate, apex shortly attenuate and blunt, margin entire, venation brochidodromous, midrib straight, slightly curved in its upper third, secondaries very regularly spaced, subopposite, originating at 30° to 40° , venation of higher order not preserved.

Remarks. This extinct element of the Fagaceae has usually been determined mainly according to its rhamnoid (brochidodromous) venation. Occurrences in the late Eocene Staré Sedlo Fm. are rare (Knobloch et al. 1996) as well as in Kučlín (Kvaček and Teodoridis 2011). The early Oligocene flora of Bechlejovice contains two leaves described as cf. *Quercus bavarica* (Knobloch et Kvaček) Kvaček, which may show a morphological affinity to *Trigonobalanopsis*. In the volcanic facies *Trigonobalanopsis* was usually poorly represented (Rott, Kleinsaubernitz, Lower Rhine Basin), while it became a dominant element in the Miocene mastixioid floras (e.g., Kvaček and Walther 1988, Walther 1999, Winterscheid 2018).

Family Juglandaceae DC. ex Perleb, 1818 nom. cons.

Genus Carya Nutt., 1818

Carya fragiliformis (Sternb.) Kvaček et H.Walther in Walter and Kvaček 2007 / Carya quadrangula (Kirchh.) J.-F.Leroy, 1955

Pl. 3, Figs 6–9, Pl. 4, Fig. 1

- 1825 *Phyllites fragiliformis* Sternb., p. 42, index iconum, pl. 50, fig. 1.
- 1936 Caryojuglans quadrangular KIRCHH., pp. 82–85, text-fig. 13, pl. 12, fig. 36a–l.
- 1955 *Carya quadrangular* (KIRCHH.) J.-F.LEROY, pp. 162–163, text-fig. 81.
- 2007 *Carya fragiliformis* (STERNB.) KVAČEK et H.WALTHER in Walter and Kvaček, p. 110, text-fig. 6b, pl. 11, figs 1–3, pl. 23, figs 8–10.

Material. Incomplete leaflets and one incomplete endocarp, impressions PA 1627, PA 1644, PA 1659, PA 1660, PA 1682 (fruit).

Description. Detached incomplete leaflets, lanceolate to oblanceolate, 35 to 63 mm long, 12 to 26 mm wide, apex acute to acuminate, base cuneate with fragmentary petiolule up to 5 mm, often asymmetrical, margin irregularly serrate, teeth triangular, sharp, bent admedially, venation craspedodromous, to semicraspedodromous, midvein straight or curved, secondaries opposite in the basal part then alternate, originating at 40° to 60°, tertiary veins percurrent, venation of the higher orders regular polygonal reticulate, areolation well-developed, 3 to 4 sided. Incomplete endocarp widely elliptic in outline, apex acute, upper surface and distinct longitudinal ribs are not visible, base not preserved, 22 mm long and 18 mm wide, thickness of the nutshell 2.8 mm, the primary and secondary septum fragmentary. Seed body (kernel) oval incomplete, 2 lateral symmetric parts preserved.

Remarks. The material corresponds to the holotype of this fossil species based on a single specimen from Žichov (Kvaček and Straková 1997, Walther and Kvaček 2007). The hickory leaves and/or leaflets described as C. fragiliformis or C. serrifolia (GÖPP.) KRÄUSEL are relatively common elements from Oligocene localities in Central Europe, known from e.g., Bechlejovice (Kvaček and Walther 2004), Suletice-Berand (Kvaček and Walther 1995), Seifhennersdorf (Walther and Kvaček 2007) and Matrý (Kvaček et al. 2018). According to Walther and Kvaček (2007: 110), C. serrifolia, which in most cases was assigned to Oligocene - early Miocene material from Central Europe, may represent a descendant of this lineage in the late Neogene. Koutecký et al. (2019) associated this type of foliage with fruits of C. quadrangula (Kirchh.) J.-F. LEROY and wood of Eucaryoxylon crystallophorum Müll.-STOLL et MÄDEL following the whole plant concept. The fruit find from Ludvíkovice morphologically corresponds to C. quadrangula. On the other hand, some poorly preserved leaf material may show affinity to Engelhardia orsbergensis (P.Wessel et C.O.Weber) Jähnichen, Mai et H.Walther.

Family Betulaceae GRAY, 1822 nom. cons.

Genus Alnus Mill., 1754

Alnus rhenana (P.Wessel et C.O.Weber) Winterscheid et Kvaček, 2014

Pl. 2, Fig. 10, Pl. 3, Figs 1–5

- 1856 Corylus rhenana P.WESSEL et C.O.WEBER, p. 134, pl. 22, fig. 5.
- 2014 Alnus rhenana (P.Wessel et C.O.Weber) Winterscheid et Kvaček, p. 22, pl. 4, figs 1–5, pl. 11, figs 4–6.

M a t e r i a 1. Several fragments and incomplete leaves, impressions PA 1628, PA 1629, PA 1632, PA 1633, PA 1635–38, PA 1640, PA 1642, PA 1643, PA 1650, PA 1655–56, PA 1657, PA 1658, PA 1663A, NM-G 12814.

Description. Incomplete leaves and fragments are ovate to obovate, 23 to 85 mm long, 17 to 75 mm wide, apex acute to shortly attenuate, base rounded or slightly cordate, margin finely widely serrate, venation craspedodromous to semicraspedodromous, midrib thick, secondaries, subopposite to alternate, widely spaced, curved, originating at 30° to 50°, tertiary veins percurrent, straight, curved or

forked, venation of the higher orders regular polygonal reticulate, areolation well-developed, 4 sided.

R e m a r k s . The foliage in the samples from Ludvíkovice is very similar to the leaf material described from Matrý and Žichov as *Alnus rhenana*, which is typically long petiolate and variable in shape (Ettingshausen 1869, Winterscheid and Kvaček 2014). In addition to *A. rhenana*, narrow elliptic leaves of *Alnus gaudinii* (HEER) ERW.KNOBLOCH et KVAČEK known from Bechlejovice, Kundratice (Kvaček and Walther 1998, 2004), Holý Kluk (Radoň et al. 2006), Hrazený (Kvaček et al. 2015) and Seifhennersdorf (Walther and Kvaček 2007), are also a very common Oligocene elements of North Bohemia and Saxony.

Family Elaeocarpaceae Juss., 1816 nom. cons.

Genus Sloanea L., 1753

Sloanea artocarpites (Ettingsh.) Kvaček et Hably in Kvaček et al. 2001

Pl. 3, Figs 10-13

1869 Quercus artocarpites Ettingsh., p. 63, pl. 55, figs 19–19a.
 2001 Sloanea artocarpites (Ettingsh.) Kvaček et Hably in Kvaček et al., p. 117.

Material. Incomplete leaves and fragments, impressions PA 1630, PA 1631, PA 1634, PA 1641, PA 1654, PA 1666, PA 1667, PA 1671, PA 1677.

Description. Leaves incomplete, without petiole, lamina elliptic to ovate, 61 to 161 mm long and 38 to 76 mm wide, base widely cuneate to rounded, apex not preserved, probably acute or attenuate, margin subentire, with widely spaced minute teeth, venation camptosemicraspedodromous, midrib straight, secondaries subopposite, curved, originating at 40° to 60°, looping very near margin, with abmedial veinlets entering teeth, tertiary veins percurrent, venation of the higher orders regular polygonal reticulate, areolation well-developed, 3 to 4 sided.

Remarks. The leaves are characterized by a specific marginal venation of campto-semicraspedodromous type which allows the unambiguous identification of this mesophytic and thermophilous element. *Sloanea artocarpites* was widespread at most sites of the České středohoří Mts. such as Suletice-Berand (Kvaček and Walther 1995), Holý Kluk (Radoň et al. 2006) and Matrý (Kvaček et al. 2018) and Seifhennersdorf in Saxony (Walther and Kvaček 2007). Similar foliage is known from the early Oligocene sites of Hungary and Slovenia accompanied by fruits of the *Sloanea*-type (Kvaček et al. 2001).

Angiosperms inc. fam.

Genus Dicotylophyllum SAPORTA, 1892

Remarks. Several morphotypes from Ludvíkovice are not assignable to any well-known fossil genus or species of angiosperm foliage.

Dicotylophyllum sp. 1 Pl. 4, Figs 2, 3

Material. 2 incomplete leaves/leaflets, impressions PA 1628.

Description. Leaves/leaflets incomplete, lamina elliptic and obovate, 41 and 93 mm long, 19 and 21 mm wide, base cuneate, apex shortly attenuate, margin entire or ? finely crenulate in apical part, venation brochidodromous or semicraspedodromous, midrib straight, secondary veins subopposite to alternate, numerous, originating at 40° to 60°, looping, intersecondaries parallel, venation of higher order not preserved.

Remarks. The leaves/leaflets resemble *Carya* leaflets based on the lamina shape, size and numerous secondary veins, however a typical margin is not preserved. On the other hand, an affinity to Lauraceae or Leguminosae cannot be excluded due to the resemblance in shape, a relatively distinct midrib and the "evergreen" character of the leaf/leaflet lamina.

Dicotylophyllum sp. 2 Pl. 4, Fig. 4

Material. Incomplete leaf, impression PA 1650.

Description. Incomplete leaf, elliptic, 49 mm long, 21 mm wide, base not preserved, apex incomplete probably blunt or shortly attenuate, margin entire, venation brochidodromous, midrib straight, secondary veins subopposite to alternate, originating at 40° to 60°, 9 pairs preserved, looping by the margin, venation of higher order not preserved.

Remarks. The preserved fragmentary leaf lamina seems to have a coriaceous character, which may also be proven by the entire margin and should indicate an evergreen character of the element. The spacing of secondary veins shows an affinity to Fagaceae rather than to Lauracaeae, therefore an assignment to *Trigonobalanus* or *Quercus bavarica* (Knobloch et Kvaček) Kvaček may be acceptable but cannot be proven without knowledge of the epidermal structure.

Dicotylophyllum rossmaessleri Erw. Knobloch et Kvaček in Knobloch et al. 1996

Pl. 4, Figs 5, 6

1996 Dicotylophyllum rossmaessleri Erw.Knobloch et Kvaček in Knobloch et al., p. 114, pl. 8, fig. 2, text-fig. 59f.

Material. Almost complete leaf, impression PA 1663B.

Description. Almost complete leaf, linear-ovate in outline, 110 mm long and 27 mm wide, base cuneate, apex long attenuate, margin entire, venation eucampto-brochidodromous, midrib straight, secondary veins alternate, originating at 30° to 40°, tertiary veins perpendicular higher-order venation regular polygonal reticulate, areolation well-developed.

Remarks. The specific type of venation in combination with the almost linear character of the leaf lamina and an extremely attenuate apex allow an assignment to *Dicotylophyllum rossmaessleri* without any doubt. The element is typified in the late Eocene flora of Staré Sedlo and probably has an affinity to evergreen Fagaceae such as *Eotrigonobalanus* (Knobloch et al. 1996).

Genus Pungiphyllum Frankenh. et V.Wilde, 1995

Pungiphyllum cf. cruciatum (A.Braun) Frankenh. et V.Wilde, 1995 Pl. 4, Figs 7, 8

1850 Quercus cruciata A.Braun in Bruckmann, p. 228.

1995 *Pungiphyllum cruciatum* (A.Braun) Frankenh. et V.Wilde, p. 101.

Material. 2 incomplete leaves, impressions PA 1670, NM-G 12812.

Description. Incomplete leaves widely oblong to oval, 67 and 81 mm long, 34 and 65 mm wide, apex not preserved, base probably widely cuneate, margin entire at the base, coarsely dentate towards the apex, teeth large, spiny, palmately disposed, sinus rounded, venation craspedodromous, midrib strong, moderate, straight to curved, secondary veins alternate, straight or slightly curved, originating at 40° to 70°, tertiary veins distinct, straight to convex, alternate, percurrent, often looping by the margin, venation of the higher orders regular polygonal reticulate, areolation well developed, 3- to 4-sided.

Remarks. The morphotype of *Pungiphyllum* cruciatum occurs in several late Eocene and Oligocene sites in Bohemia, e.g., at Kučlín, Kundratice, Bechlejovice, Suletice-Berand, Matrý (see Kvaček and Walther 1995, 1998, 2004, Kvaček and Teodoridis 2011, Kvaček et al. 2018). Systematic affinities have not been resolved so far, even though the epidermal structure is known from Kundratice and Eckfeld (Germany) and helped to exclude the original assignment to *Quercus* (Frankenhäuser and Wilde 1995, Kvaček and Walther 1998).

Palaeoenvironmental and phytostratigraphical signals

The flora of Ludvíkovice, preserved as leaf and carpological material, so far includes 15 vascular plant taxa – 1 fern, 14 angiosperms (including 4 taxa with uncertain systematic affinities). The fossil plant assemblage at Ludvíkovice represents mainly zonal mesophytic elements accompanied by partly riparian elements. In the studied material, taxa producing foliage with a dentate margin prevailed (53.9 %). Most elements represent trees. As mentioned earlier, two specific vegetation assemblages can be distinguished based on the phytosociological approach. The first vegetation assemblage, limited to well-drained habitats, is a zonal mesophytic (mesic) forest characterized by the associated occurrence of the following angiosperms: Daphnogene cinnamomifolia (E3), Laurophyllum cf. acutimontanum (E3), Leguminophyllum sp. (E3), Sloanea artocarpites (E3-4), Carya fragiliformis / C. quadrangula (E3-4), Alnus rhenana (E3), Pungiphyllum cf. cruciatum (E2-3), Trigonobalanopsis rhamnoides (E3), cf. Quercus sp. and Dicotylophyllum sp. div. (E2-3), Rumohra recentior (E1). The second one is a riparian vegetation preferring a waterlogged substrate, which includes partly azonal elements, i.e., Platanus neptuni (E3) and Eotrigonobalanus furcinervis (E3). Both vegetation assemblages depend on

specific ecological conditions of the biotopes and mutually integrate on their ecotons. Focusing on results derived from the Integrated Plant Record (IPR) vegetation analysis (see Kovar-Eder et al. 2008, Teodoridis et al. 2011), the predicted zonal vegetation type for Ludvíkovice is a zonal broad-leaved evergreen forest (BLEF), where the specific pattern of the key components is as followed: broad-leaved deciduous (BLD) – 42.3 %, broad-leaved evergreen (BLE) – 53.9 %, sclerophyllous + legume-like (SCL+LEG) – 3.9 % and zonal herbaceous/ (ZONAL HERB) - 7.1 %, number of zonal taxa (14), number of zonal woody elements (13). Kovar-Eder and Teodoridis (2018) changed the minimum number of zonal elements required for this analysis from 10 to 15 to obtain the most reliable results possible from IPR vegetation analysis. As Ludvíkovice possess 14 zonal elements only, the required number of taxa is almost achieved, and the predicted zonal cover may be accepted with some caution. The newly developed "Drudge 1" tool was also applied. This enables the closest modern analogue plant assemblage to be determined from a calibration dataset (containing 505 modern plant assemblages from Europe, Caucasus, China, Mongolia and Japan) for fossil vegetation by combining IPR Similarity and Taxonomical Similarity parameters (see Teodoridis et al. 2020). The Drudge 1 system indicates "Broad-leaved Evergreen Sclerophyllous Forest from Southern Hunan and Northern Guangxi" from SE China (see Wang 1961: 145, 148) as the closest modern analogue plant assemblage to the fossil plant assemblage of Ludvíkovice. With its predicted vegetation type of BLEF and a modern analogue from SE China, the Ludvíkovice flora shows a close affinity to late Oligocene plant assemblages from Kleinsaubernitz, Počerny-Podlesí and Borna-Ost, which were estimated as Broad-leaved Evergreen Forest (see Teodoridis and Kvaček 2015: tab. 3).

Palaeoclimatic estimates for Ludvíkovice derived from Leaf Margin Analysis (LMA – equation sensu Su et al. 2010, sampling error "SE" sensu Miller et al. 2006) predicted a mean annual temperature (MAT) of 14.8 °C \pm 4.0 °C. The Climate Leaf Multivariate Program (CLAMP sensu Wolfe and Spicer 1999) could not be applied here due to the low number of dicotyledonous elements. Similarly this issue may also have influenced the result derived from LMA including the value of SE. Palaeoclimatic data derived from the Coexistence Approach (e.g., Mosbrugger and Utescher 1997, Utescher et al. 2014) are as follows: MAT 14.6-24.1 °C, warmest month mean temperature (WMMT) 24.7-28.3 °C, coldest month mean temperature (CMMT) 2.2-18.8 °C, mean annual precipitation (MAP) 979-1724 mm, wettest month precipitation (MPwet) 164–434 mm, driest month precipitation (MPdry) 8–61 mm, and warmest month precipitation (MPwarm) 125-196 mm. These palaeoclimatic estimates are very similar to those based on Oligocene plant assemblages from Kleinsaubernitz and Flörsheim (see Teodoridis and Kvaček 2015).

According to the above-mentioned floristic composition, the plant assemblage of Ludvíkovice deviates from most of the known floras of the České středohoří Mts. and is perhaps more similar to the previously described floras of Markvartice and Veselíčko (Bůžek et al. 1976) and Hrazený (Kvaček et al. 2015), which show a more thermophilous

and "younger" character pointing to the late Rupelian climatic optimum (Kvaček and Walther 2001, Walther and Kvaček 2007) and/or late Oligocene. Similarly, Oligocene floras of Flörsheim (Kvaček 2004) and Kleinsaubernitz (Walther 1999) have close affinities to Ludvíkovice due to the occurrences of the thermophilous evergreen elements of Fagaceae and Lauraceae.

Acknowledgement

We are grateful to both reviewers, i.e., Boglárka Erdei and Dieter Uhl for their critical comments and suggestions. Curators of the palaeontological collections of the National Museum in Prague are also acknowledged for technical assistance, namely Lenka Váchová and Jiří Kvaček. This study was supported by the grant projects of GA ČR No. P18-25057S, Charles University, Prague, Progres Q16, and the Czech Geological Survey (project No. 310410). This work is a contribution to NECLIME (Neogene Climate Evolution in Eurasia).

References

- Angiosperm Phylogeny Group (2016): An update of the Angiosperm Phylogeny Group classification for the orders and families of flowering plants: APG IV. Botanical Journal of the Linnean Society, 181: 1–20. https://doi.org/10.1111/boj.12385
- Barthel, M. (1976): Eozäne Floren des Geiseltales. Farne und Cycadeen. Abhandlungen des Zentralen Geologischen Institutes, 26: 439–498.
- Bruckmann, A. E. (1850): Flora oeningensis fossilis. Jahreshefte des Vereins für Vaterländische Naturkunde in Württemberg, 6(2): 215–238.
- Bůžek, Č., Fejfar, O., Konzalová, M., Kvaček, Z. (1990): Floristic changes around Stehlin's Grande Coupure. – In: Knobloch, E., Kvaček, Z. (eds), Proceedings of the Symposium: Palaeofloristic and Palaeoclimatic Changes in the Cretaceous and Tertiary, Prague 1989. Czech Geological Survey, Prague, pp. 167–181.
- Bůžek, Č., Holý, F., Kvaček, Z. (1967): Eine bemerkenswerte Art der Familie Platanaceae Lindl. (1836) im nordböhmischen Tertiär. Monatsberichte der Deutschen Akademie der Wissenschaften, 9: 203–215.
- Bůžek, Č., Holý, F., Kvaček, Z. (1976): Tertiary flora from Volcanogenic Series at Markvartice and Veselíčko near Česká Kamenice (České středohoří Mts.). – Sborník geologických věd, Paleontologie, 18: 69–132.
- Cajz, V. (2000): Proposal of lithostratigraphy for the České středohoří Mts volcanics. – Bulletin of the Czech Geological Survey, 75: 7–16.
- Cajz, V., Rapprich, V., Erban, V., Pécskay, Z., Radoň, M. (2009): Late Miocene volcanic activity in the České středohoří mountains (Ohře/Eger Graben, northern Bohemia). Geologica Carpathica, 60: 519–533. https://doi.org/10.2478/v10096-009-0038-8
- Cuvier, G. (1822): Recherches sur les ossements fossiles, vol. III. G. Dufour et E. d'Ocagne, Paris, 412 pp. + 80 pls. [Brongniart, A.: Description des végétaux fossiles du terrain de sédiment supérieur, pp. 351–369]

- Escalup-Bassi, A. (1971): Sur deux empreintes des grès à sables d'Anjou. Comptes Rendus du Congrès des Sociétés Savantes de Paris et des Départements, Section des Sciences, 94: 93–98.
- Ettingshausen, C. v. (1866): Die fossile Flora des Tertiärbeckens von Bilin, I. [Preprint from] Denkschriften der Kaiserlichen Akademie der Wissenschaften, Mathematisch-naturwissenschaftliche Classe, 26: 1–98.
- Ettingshausen, C. v. (1869): Die fossile Flora des Tertiärbeckens von Bilin, III. [Preprint from] Denkschriften der Kaiserlichen Akademie der Wissenschaften, Mathematisch-naturwissenschaftliche Classe, 29: 1–110.
- Frankenhäuser, H., Wilde, V. (1995): Stachelspitzige Blätter aus dem Mitteleozän von Eckfeld (Eifel). Abhandlungen des Staatlichen Museums für Mineralogie und Geologie zu Dresden, 41: 97–115.
- Givulescu, R. (1990): Upper Miocene fossil floras from Chiuzbaia, Maramureș County (in Romanian). Editura Academiei Române, București, 236 pp.
- Kirchheimer, F. (1936): Beiträge zur Kenntnis der Tertiärpflanzen. Palaeontographica, Abteilung B, 82: 71–141.
- Knobloch, E., Konzalová, M., Kvaček, Z. (1996): Die obereozäne Flora der Staré Sedlo-Schichtenfolge in Böhmen (Mitteleuropa). Rozpravy Českého geologického ústavu, 49: 1–260.
- Kopecký, L. (2010): České Středohoří Mts. and Ambient Young Alkaline Volcanic Complexes in the Ohře Rift, Czech Republic: Volcanology, Petrology and Rift Evolution. Czech Geological Survey, Prague, pp. 1–188.
- Koutecký, V., Teodoridis, V., Čáp, P., Mantzouka, D., Sakala, J. (2019): Fossil wood from the Doupovské hory and České středohoří volcanic complexes: latest overview and new angiosperms from the locality Dvérce Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen, 293(3): 283–306. https://doi.org/10.1127/njgpa/2019/0842
- Kovar-Eder, J., Jechorek, H., Kvaček, Z., Parashiv, V. (2008): The Integrated Plant Record: an essential tool for reconstructing Neogene zonal vegetation in Europe. Palaios, 23: 97–111.
 - https://doi.org/10.2110/palo.2006.p06-039r
- Kovar-Eder, J., Teodoridis, V. (2018): The Middle Miocene Central European plant record revisited; widespread subhumid sclerophyllous forests indicated. Fossil Imprint, 74(1-2): 115–134.
 - https://doi.org/10.2478/if-2018-0009
- Kvaček, J., Straková, M. (1997): Catalogue of fossil plants described in works of Kašpar M. Sternberg. National Museum, Prague, 201 pp.
- Kvaček, Z. (2002): Late Eocene landscape, ecosystems and climate in north Bohemia with particular reference to the locality Kučlín near Bílina. Bulletin of the Czech Geological Survey, 77: 217–236.
- Kvaček, Z. (2004): Revisions to the Early Oligocene flora of Flörsheim (Mainz Basin, Germany) based on epidermal anatomy. – Senckenbergiana lethaea, 84: 1–73. https://doi.org/10.1007/BF03043465
- Kvaček, Z. (2010): Forest flora and vegetation of the European early Palaeogene a review. Bulletin of Geosciences, 85(1): 3–16. https://doi.org/10.3140/bull.geosci.1146

- Kvaček, Z., Hably, L., Manchester, S. R. (2001): Fruits and foliage of *Sloanea* (Elaeocarpaceae) from the Early Oligocene of Hungary and Slovenia. Palaeontographica, Abt. B., 159: 113–124.
- Kvaček, Z., Manchester, S. R. (2004): Vegetative and reproductive structure of the extinct *Platanus neptuni* from the Tertiary of Europe and relationships within the Platanaceae. Plant Systematics Evolution, 244: 1–29. https://doi.org/10.1007/s00606-003-0082-2
- Kvaček, Z., Teodoridis, V. (2011): A Late Eocene flora of Kučlín near Bílina in North Bohemia revisited. Acta Musei Nationalis Pragae, Series B Historia Naturalis, 67(3-4): 77–82.
- Kvaček, Z., Teodoridis, V., Mach, K., Přikryl, T., Dvořák, Z. (2014): Tracing Eocene-Oligocene transition: a case study from North Bohemia. Bulletin of Geosciences, 89(1): 21–66.
 - https://doi.org/10.3140/bull.geosci.1411
- Kvaček, Z., Teodoridis, V., Radoň, M. (2018): Review of the late Oligocene flora of Matrý at Sebuzín (České středohoří Mts.). Fossil Imprint, 74(3-4): 292–316. https://doi.org/10.2478/if-2018-0018
- Kvaček, Z., Teodoridis, V., Zajícová, J. (2015): Revision of the early Oligocene flora of the Hrazený hill (former Pirskenberg) at Knížecí near Šluknov, North Bohemia. Acta Musei Nationalis Pragae, Series B Historia Naturalis, 71(1-2): 55–102. https://doi.org/10.14446/AMNP.2015.55
- Kvaček, Z., Walther, H. (1988): Revision der mitteleuropäischen tertiären Fagaceen nach blattepidermalen Charakteristiken. II. Teil. *Castanopsis* (D. Don) Spach, *Trigonobalanus* Forman, *Trigonobalanopsis* Kvaček and Walther. Feddes Repertorium, 99: 395–418. https://doi.org/10.1002/fedr.4910990904
- Kvaček, Z., Walther, H. (1989): Revision der mitteleuropäischen tertiären Fagaceen nach blattepidermalen Charakteristiken. III. Teil. *Dryophyllum* Debey ex Saporta und *Eotrigonobalanus* Walther and Kvaček gen. nov. Feddes Repertorium, 100: 575–601. https://doi.org/10.1002/fedr.4911001102
- Kvaček, Z., Walther, H. (1995): The Oligocene volcanic flora of Suletice-Berand near Ústí nad Labem, North Bohemia a review. Acta Musei Nationalis Pragae, Series B Historia Naturalis, 50(1-4): 25–54.
- Kvaček, Z., Walther, H. (1998): The Oligocene volcanic flora of Kundratice near Litoměřice, České středohoří Volcanic complex (Czech Republic). Acta Musei Nationalis Pragae, Series B Historia Naturalis, 54: 1–43.
- Kvaček, Z., Walther, H. (2001): The Oligocene of Central Europa and the development of forest vegetation in space and time based on megafossils. – Palaeontographica, Abt. B, 259: 125–149.
- Kvaček, Z., Walther, H. (2004): Oligocene flora of Bechlejovice at Děčín from the neovolcanic area of the České Středohoří Mountains, Czech Republic. – Acta Musei Nationalis Pragae, Series B – Historia Naturalis, 60: 9–60.
- Leroy, J.-F. (1955): Étude sur les Juglandaceae. Mémoires du Muséum national d'histoire naturelle, series B, 6: 1–246.
- Miller, I. M., Brandon, M. T., Hickey, L. J. (2006): Using leaf margin analysis to estimate the mid-Cretaceous (Al-

- bian) paleolatitude of the Baja BC block. Earth and Planetary Science Letters, 245: 95–114. https://doi.org/10.1016/j.epsl.2006.02.022
- Mosbrugger, V., Utescher, T. (1997): The coexistence approach a method for quantitative reconstructions of Tertiary terrestrial palaeoclimate data using plant fossils. Palaeogeography, Palaeoclimatology, Palaeoecology, 134: 61–86.
 - https://doi.org/10.1016/S0031-0182(96)00154-X
- Mysliveček, J., Rapprich, V., Kochergina, Y. V., Magna, T., Halodová, P., Pécskay, Z., Poňavič, M. (2018): Petrology of weakly differentiated alkaline, high-level intrusive rocks in the Záhořany-Chotiněves Belt near Litoměřice (Czech Republic). Journal of Geosciences, 63(4): 317–331. https://doi.org/10.3190/jgeosci.278
- Radoň, M. (2006): Nové paleontologické nálezy v terciérních intravulkanických sedimentech Českého středohoří [New paleontological findings in sedimentary intercalations within the volcanic complex of the České středohoří Mts.]. Zprávy o geologických výzkumech 39(for 2005): 94–97. (in Czech)
- Radoň, M., Kvaček, Z., Walther, H. (2006): Oligocene megafossil plant remains and environment from the newly recovered locality of the Holý Kluk hill near Proboštov (České středohoří Mountains, Czech Republic). – Acta Universitatis Carolinae, Geologica, 47: 95–124.
- Rapprich, V., Cajz, V., Kycl, P., Suchý, J., Radoň, M. (2010): Nové poznatky o vulkanickém stylu děčínského souvrství, získané dokumentací příležitostných odkryvů při stavbě dálnice D8 u Radejčína [New observations on style of volcanic activity of the Děčín Formation, based on temporary exposures during the D8 highway construction near Radejčín]. Zprávy o geologických výzkumech, 43(for 2009): 39–42. (in Czech with English abstract)
- Rapprich, V., Holub, F. V. (2008): Geochemical variations within the Upper Oligocene-Lower Miocene lava succession of Úhošť Hill (NE margin of Doupovské hory Mts., Czech Republic). Geological Quarterly, 52: 253–268.
- Rehnelt, K. (1957): Der Aschenregen des Schiechenbergvulkans. Ein neuer Fundort von Pflanzenresten aus der sudetendeutschen Braunkohlenformation. – Trei da Hejmt, 10(3): 3.
- Rossmässler, E. A. (1840): Die Versteinerungen des Braunkohlensandsteins aus der Gegend von Altsattel in Böhmen (Elnbogener Kreises). – Arnold Buchhandlung, Dresden, Leipzig, 42 pp. https://doi.org/10.5962/bhl.title.147139
- Sternberg, K. (1825): Versuch einer geognostisch-botanischen Darstellung der Flora der Vorwelt. Bd. I, H. 4. Ernst Brenck's Wittwe, Regensburg, 48 pp.
- Su, T., Xing, Y. W., Liu, Y. S., Jacques, F. M. B., Chen, W. Y., Huang, Y. J., Zhou, Z. K. (2010): Leaf margin analysis: a new equation from humid to mesic forests in China. Palaios, 25(3-4): 234–238. https://doi.org/10.2110/palo.2009.p09-129r
- Teodoridis, V., Kovar-Eder, J., Mazouch, P. (2011): The IPR-vegetation analysis applied to modern vegetation in SE China and Japan. Palaios, 26(10): 623–638. https://doi.org/10.2110/palo.2010.p10-149r

- Teodoridis, V., Kvaček, Z. (2015): Palaeoenvironmental evaluation of Cainozoic plant assemblages from the Bohemian Massif (Czech Republic) and adjacent Germany. Bulletin of Geosciences, 90(3): 695–720. https://doi.org/10.3140/bull.geosci.1553
- Teodoridis, V., Kvaček, Z., Zhu, H., Mazouch, P. (2012): Environmental analysis of the mid-latitudinal European Eocene sites of plant macrofossils and their possible analogues in East Asia. Palaeogeography, Palaeoclimatology, Palaeocology, 333-334: 40–58. https://doi.org/10.1016/j.palaeo.2012.03.008
- Teodoridis, V., Mazouch, P., Kovar-Eder, J. (2020): The Integrated Plant Record (IPR) analysis: Methodological advances and new insights into the evolution of European Palaeogene/Neogene vegetation. Palaeontologia Electronica, 23(1): a16 (19 pp.). https://doi.org/10.26879/1055
- Ulrych, J., Balogh, K. (2000): Roztoky Intrusive Centre in the České středohoří Mts.: Differentiation, emplacement, distribution, orientation and age of dyke series. Geologica Carpathica, 51: 383–398.
- Unger, F. (1847): Chloris protogaea. 1–10. W. Engelmann, Leipzig, 149 pp.
- Unger, F. (1850): Genera et species plantarum fossilium. W. Braunmüller, Vindobonae, XL + 627 pp.
- Utescher, T., Bruch, A. A., Erdei, B., François, L., Ivanov, D., Jacques, F. M. B., Kern, A. K., Liu, Y. S., Mosbrugger, V., Spicer, R. A. (2014): The Coexistence Approach Theoretical background and practical considerations of using plant fossils for climate quantification. Palaeogeography, Palaeoclimatology, Palaeoecology, 410: 58–73. https://doi.org/10.1016/j.palaeo.2014.05.031

- Walther, H. (1999): Die Tertiärflora von Kleinsaubernitz bei Bautzen. Palaeontographica, Abt. B, 249: 63–174.
- Walther, H., Kvaček, Z. (2007): Early Oligocene flora of Seifhennersdorf (Saxony). Acta Musei Nationalis Pragae, Series B Historia Naturalis, 63(2-4): 85–174.
- Wang, Ch. W. (1961): The forests of China (Maria Moors Cabot Foundation, Publication No. 5). Harvard University Press, Cambridge (MA), 313 pp.
- Wessel, P., Weber, O. (1856): Neuer Beitrag zur Tertiär- Flora der niederrheinischen Braunkohlenformation. Palaeontographica, 4: 1–57.
- Winterscheid, H. (2018): Revision of a late Oligocene florule from the south-western edge of the Lower Rhine Basin (western Germany). Acta Palaeobotanica, 58(1): 49–60.
 - https://doi.org/10.2478/acpa-2018-0004
- Winterscheid, H., Kvaček, Z. (2014): Revision der Flora aus den oberoligozänen Seeablagerungen von Orsberg bei Unkel am Rhein (Rheinland-Pfalz, Deutschland). Palaeontographica, Abt. B, 291(1-3): 1–83.
- Wolfe, J. A., Spicer, R. A. (1999): Fossil leaf character states: multivariate analysis. In: Jones, T. P., Rowe, N. P. (eds), Fossil Plants and Spores: Modern Techniques. Geological Society, London, pp. 233–239.
- Worobiec, G., Worobiec, E. (2019): Wetland vegetation from the Miocene deposits of the Belchatów Lignite Mine (central Poland). Palaeontologia Electronica, 22(3): 63 (38 pp.).
 - https://doi.org/10.26879/871

Explanation to the plates

PLATE 1

Rumohra recentior (UNGER) BARTHEL, Oligocene, Ludvíkovice

- Two most complete specimens of sterile fern fronds, PA 1618.
- 2. Fragment of sterile fern frond with slightly asymmetrical attached ovate irregularly dentate pinnules, PA 1620.
- Detail of irregularly dentate, shallowly dissected pinnules including 3-times forked secondary veins, PA 1618.
- 4. Detail of irregularly dentate, shallowly dissected pinnule including 3-times forked secondary veins, PA 1620.

Daphnogene cinnamomifolia (Brongn.) Unger, Oligocene, Ludvíkovice

- 5. Incomplete widely oval "shade" leaf with cuneate base and suprabasal acrodromous venation, PA 1623.
- 6. Incomplete lanceolate "sun" leaf with cuneate base and incomplete acuminate apical part, PA 1678.

Laurophyllum cf. acutimontanum MAI, Oligocene, Ludvíkovice

7. Incomplete entire elongate leaf with cuneate base and brochidodromous venation, NM-G 12808.

Leguminophyllum sp., Oligocene, Ludvíkovice

- 8. Complete ovate leaflet with acute apex and widely cuneate base, PA 1625.
- 9. Counterpart of the leaflet PA 1625.
- Complete widely elliptic leaflet with rounded base and shortly attenuate to acute apex, PA 1664.
- 11. Counterpart of the leaflet PA 1664.

Scale bar 5 mm for Fig. 3 and 10 mm for Figs 1, 2, 4–11.

PLATE 2

Platanus neptuni (ETTINGSH.) BŮŽEK, HOLÝ et KVAČEK, Oligocene, Ludvíkovice

- 1. Incomplete leaf with cuneate base and regularly dentate margin, PA 1648.
- 2. Incomplete leaf with regularly dentate margin, PA 1652.
- 3. Detail of leaf margin, PA 1652.

cf. Quercus sp., Oligocene, Ludvíkovice

- 4. Complete widely elliptic leaf with simply dentate margin, PA 1639.
- 5. Detail of leaf margin, PA 1639.
- 6. Incomplete leaf with simply dentate margin, PA 1646.

Eotrigonobalanus furcinervis (ROSSM.) H.WALTHER et KVAČEK, Oligocene, Ludvíkovice

- 7. Incomplete oblong leaf, PA 1645.
- 8. Incomplete elliptic leaf, PA 1661.

Trigonobalanopsis rhamnoides (ROSSM.) H. WALTHER et KVAČEK, Oligocene, Ludvíkovice

Almost complete ovate leaf with attenuate and blunt apex, PA 1651.

Alnus rhenana (P.Wessel et C.O.Weber) Winterscheid et Kvaček, Oligocene, Ludvíkovice

10. Incomplete basal leaf part with detail of venation of higher order, PA 1640.

Scale bar 5 mm for Figs 3, 5, 9 and 10 mm for Figs 1, 2, 4, 6–8, 10.

PLATE 3

Alnus rhenana (P.Wessel et C.O.Weber) Winterscheid et Kvaček, Oligocene, Ludvíkovice

- 1. Incomplete leaf, PA 1629A.
- 2. Detail of finely widely serrate leaf margin, PA 1629.
- 3. Incomplete leaf, PA 1650.
- 4. Complete leaf with rounded base, PA 1657.
- 5. Incomplete leaf with shortly attenuate apex, PA 1632.

Carya fragiliformis (STERNB.) KVAČEK et H.WALTHER, Oligocene, Ludvíkovice

- 6. Almost complete asymmetrical leaflet with cuneate base, PA 1659.
- 7. Almost complete leaflet with attenuate apex and well-preserved margin, PA 1660.
- 8. Detail of incomplete leaflet with irregularly serrate margin, PA 1660.
- Incomplete leaflet with distinct higher order of venation, PA 1644.

Sloanea artocarpites (Ettingsh.) Kvaček et Hably, Oligocene, Ludvíkovice

- 10. incomplete leaf lamina with typical teeth and camptosemicraspedodromous venation, PA 1654.
- 11. Incomplete leaf with well-preserved apical part of lamina with venation and margin, PA 1630.
- 12. Detail of the lamina venation, PA 1630.
- 13. Incomplete leaf with well-preserved margin area, PA 1631.

Scale bar 5 mm for Figs 6, 8, 9 and 10 mm for Figs 1–5, 7, 10–13.

PLATE 4

Carya quadrangula (KIRCHH.) J.-F.LEROY, Oligocene, Ludvíkovice

1. Incomplete endocarp, PA 1682.

Dicotylophyllum sp. 1, Oligocene, Ludvíkovice

- 2. Incomplete elliptic and obovate leaves/leaflets, PA 1628.
- Detail of leaf/leaflet lamina with numerous secondaries, PA 1628.

Dicotylophyllum sp. 2, Oligocene, Ludvíkovice

4. Incomplete leaf with entire margin, PA 1650.

Dicotylophyllum rossmaessleri Erw.Knobloch et Kvaček, Oligocene, Ludvíkovice

- 5. Almost complete leaf with attenuate apex and entire margin, PA 1663B.
- 6. Detail of leaf lamina, PA 1663.

Pungiphyllum cf. cruciatum (A.Braun) Frankenh. et V.Wilde, Oligocene, Ludvíkovice

- Incomplete leaf with coarsely dentate margin, NM-G 12812.
- 8. Incomplete leaf with coarsely dentate margin, PA 1670.

Scale bar 5 mm for Figs 1, 4, 6 and 10 mm for Figs 2, 3, 5, 7, 8.

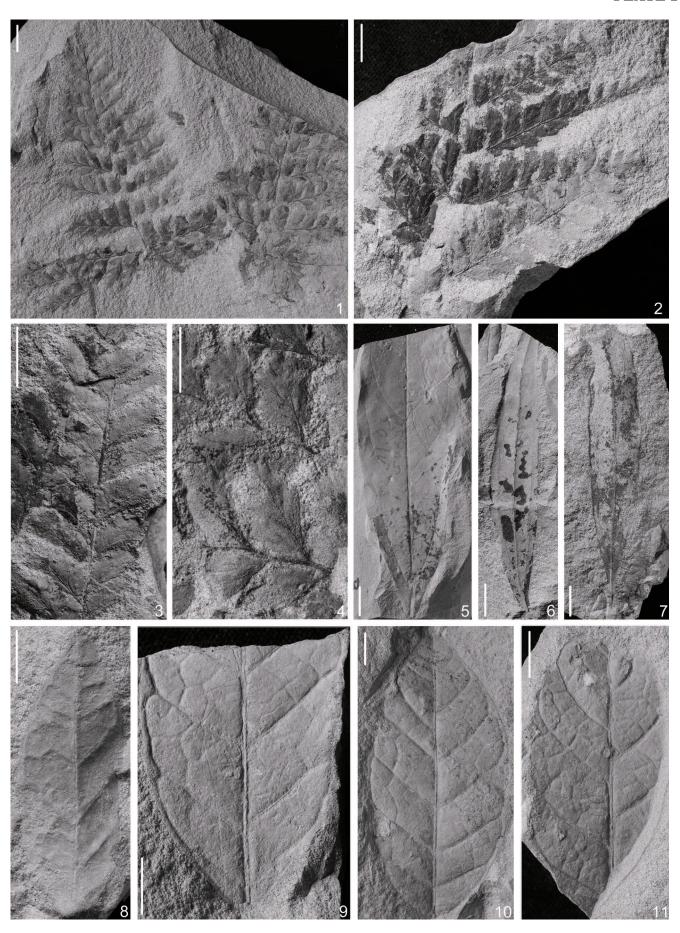


PLATE 2



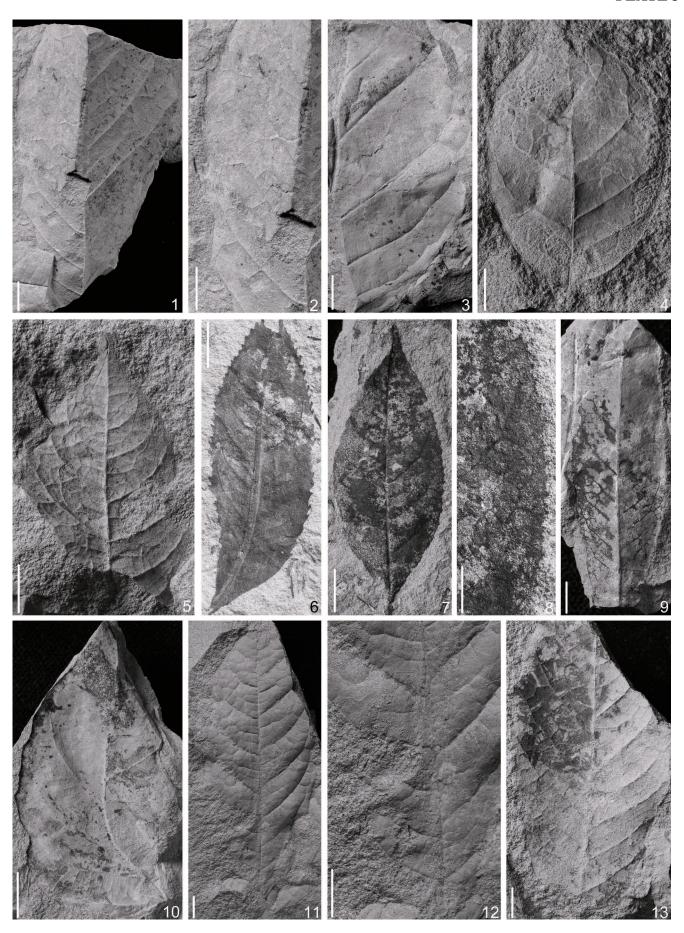


PLATE 4

