

# Tracing the Eocene–Oligocene transition: a case study from North Bohemia

ZLATKO KVAČEK, VASILIS TEODORIDIS, KAREL MACH, TOMÁŠ PŘIKRYL & ZDENĚK DVOŘÁK



Geology and palaeontology of the Roudníky area, situated between the Most Basin and the České středohoří Mountains in North Bohemia, the Czech Republic, is treated in detail. The volcano-sedimentary structure underlying the basin with the included fossiliferous layers is newly interpreted as a maar-diatreme. The radiometric age of the basalts was determined to  $35.4 \pm 0.9$  Ma and  $37.1 \pm 0.9$  Ma – late Eocene, Priabonian. The fish fauna consists of amiids characteristic of other adjacent late Eocene sites while the co-occurring macroflora includes many elements that are typical of the Oligocene. Closest relations are to the fauna and flora of the Větruše Hill at Ústí nad Labem. Based on palaeoclimatic estimates the major turnover from subtropical to warm-temperate climatic regimes in North Bohemia appears to have initiated in the late Eocene by an increase of seasonality and the resulting vegetation change from the evergreen to mixed mesophytic forest types well before the maximum temperature drop of mean annual temperature at ca 33.5 Ma. • Key words: flora, fauna, climate, vegetation, late Eocene, early Oligocene, boundary.

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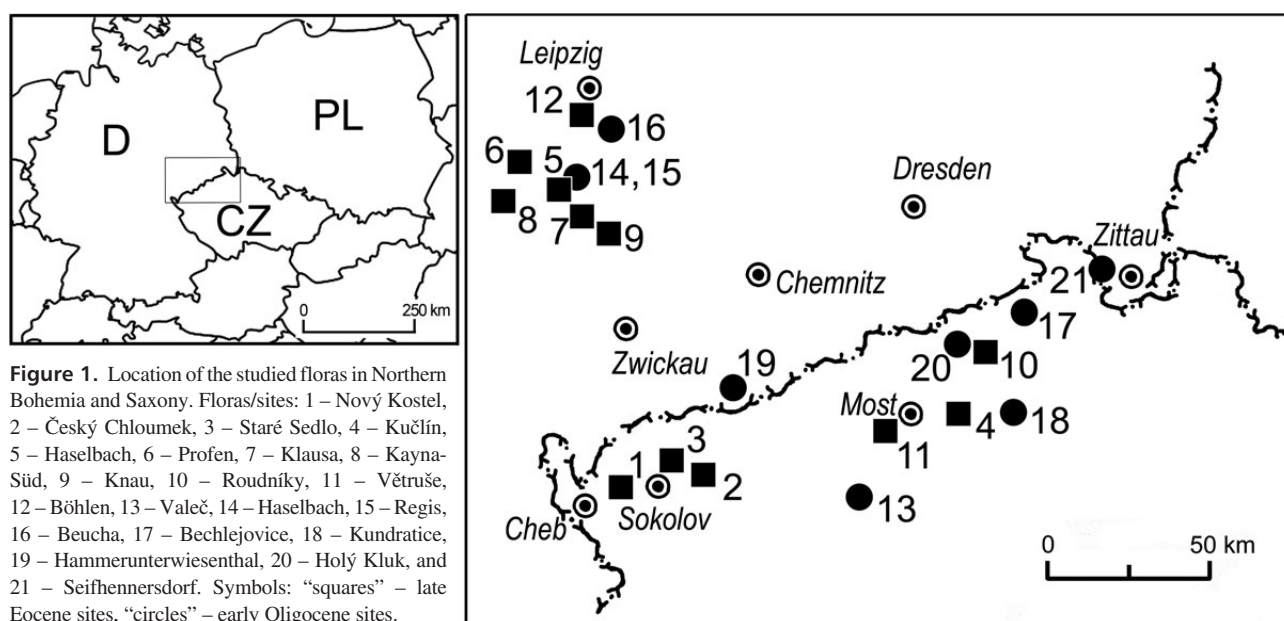
The palaeoclimatic event at the Eocene–Oligocene transition has attracted the attention of many palaeobotanists and researchers of palaeoenvironmental science (e.g., Collinson 1992, Collinson *et al.* 2010, Kvaček 2010, Teodoridis *et al.* 2012). In general, the pronounced cooling in this time interval (e.g., Zanzani *et al.* 2007, Hren *et al.* 2013) induced also changes in palaeovegetation, although this event manifested variously in the mid-northern latitudes (Mai 1995, Graham 1999, Akhmetiev *et al.* 2009). In this paper we will contribute to the discussion on this topic (Katz *et al.* 2008, Eldrett *et al.* 2009) and offer new palaeontological datasets based on the radiometrically (K–Ar) dated fossil plant and fish assemblages from North Bohemia that may add information on the timing and overall character of this event in Central Europe. This study includes revisions of the previously published tentative data (Bellon *et al.* 1998, Akhmetiev *et al.* 2009), supplemented by newly collected material from the same area at Roudníky. Much attention is devoted to exact evaluation of the geological position of the recovered fossils from the edge of the Most Basin and the České středohoří Mountains. More stress is also given to obtain objective pa-

laeoenvironmental signals from plant assemblages of the late Eocene to early Oligocene deposits of North Bohemia and Saxony by newly developed techniques, i.e., Integrated Plant Record Vegetation Analysis, Leaf Margin Analysis, Climate Leaf Analysis Multivariate Program and Coexistence Approach. The recently published monographs on the Eocene and Oligocene plant records in Central Europe (e.g., Walther & Kvaček 2007, Kvaček & Teodoridis 2011) allow us to correlate the studied sites more precisely.

The authors participated on the text as follows: Karel Mach and Zdeněk Dvořák – geology, Zlatko Kvaček and Vasilis Teodoridis – palaeobotany, Vasilis Teodoridis – palaeoenvironmental interpretations, Tomáš Přikryl – zoopalaeontology.

## Geological setting

The village of Roudníky is situated on the border of the Ústí part of the Most Basin and the České středohoří Mts approximately 10 km southwest from the town of Ústí nad



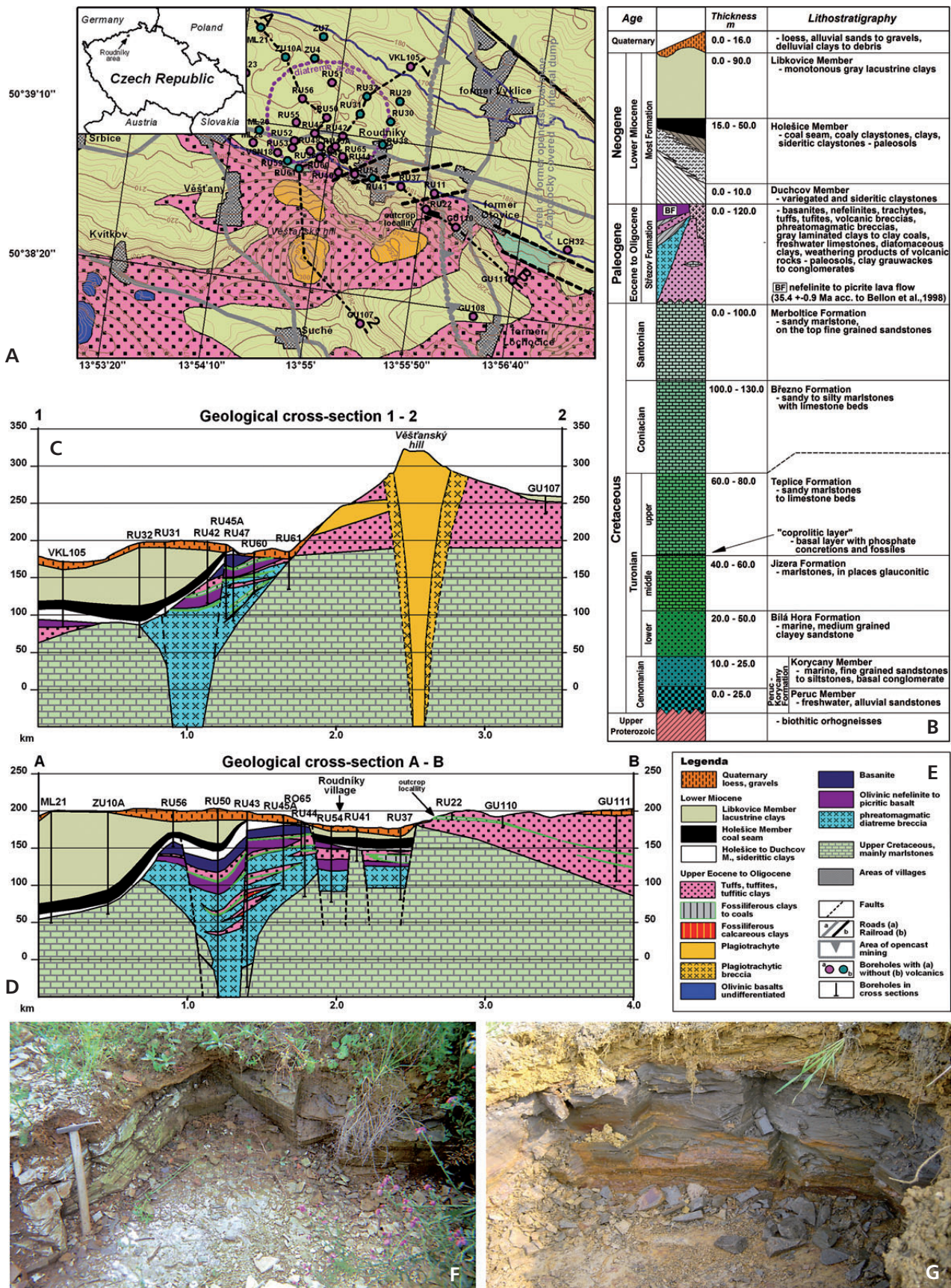
Labem. The fossils described in this paper come from several deep drill-cores in the vicinity of Roudníky (Figs 1, 2A) and from two outcrops southeast of the village (Fig. 2F, G). Most of the drill-cores that yielded fossils are located in the area within the Miocene fill belonging to the Most Formation of the Most Basin. The studied fossiliferous strata belong to the underlying volcano-sedimentary unit – the Střezov Formation of late Eocene to Oligocene age. Until 1992 the geology of the Roudníky area was known only from several drill-cores, and from the data of historical underground mining and working of the adjacent coal opencast mine. During 1990–1992, the geologic setting of the Roudníky area was studied in detail by a team of authors that issued the final report on coal deposit Chabařovice II reserves calculation (Vácha *et al.* 1992). During the prospection stage of their work several tens of new boreholes were made and the cores were examined by many specialists. A unique feature of the drilling program was the fact that many of boreholes reached not only the bottom of the Miocene coal seam, as necessary for the coal reserves calculation, but continued under the bottom of Miocene sediments or Eocene to Oligocene volcanic rocks and often reached even the contact with Cretaceous sediments (Fig. 2A–E). Use of complex methods during the drill-core evaluation and geophysical methods led to an extraordinarily high degree of understanding about subsurface geological structure and development of the area. Information on the general geological position of the deposit is given in the state

geological map 1:25,000 sheet 02-322 Krupka and its explanatory text (Jiránek 1991).

The Palaeogene fossil-bearing volcano-sedimentary units that are treated here belong either to the Střezov Formation or the volcano-sedimentary complex of the České středohoří Mts. In the vicinity of Roudníky the Střezov Formation consists mainly of various types of tuffs, tuffites and tuffitic clays, volcanic breccias and basaltic (olivinic basalts, basanites, nefelinites) or trachytic to phonolitic lavas. Many of these volcanic products are strongly weathered, changed into a tens-of-meters-deep kaolinic to smectitic weathering crust. Volcanic products are associated by several more or less continuous layers of clayey sediments. Clays rich in organic matter, rarely calcareous or diatomaceous clays, form several decimeters to 2.5 m thick deposits passing both laterally and vertically into tuffitic clays, tuffites or just tuffs, partly into thin coal seams. Some of them are very similar to early Miocene clays from the coal seam overburden (Cajz 1990). These clastic sediments are often laminated, containing various fossils (Bůžek 1990, Bellon *et al.* 1998). Among animal remains, freshwater bivalves, gastropods, crustaceans, insects, fishes, rare frogs, vertebrae of deer, teeth and coprolites of crocodiles (the last three mentioned items known from Větruše only) were identified. In the northern part of the Roudníky area products of volcanism are covered by early Miocene sediments of the Most Formation (Čadek *et al.* 1990). Several hundred meters east from

**Figure 2.** A – geological map of the Roudníky area (contour lines show a terrain state before mining); B – stratigraphic column of the Roudníky area; C – geological cross section 1–2; D – geological cross section A–B; E – explanation to Fig. 2A–D; F, G – outcrops of Roudníky.







the village, this early Miocene coal deposit was completely exhausted by the huge opencast mine Chabařovice (former A. Zápotocký) during the 70s to 80s of the 20<sup>th</sup> century. Today the exploited part of the coal deposits is filled by removed overburden clays. The mine was closed in 1993 and today an extensive lake arose in its deepest part and the area is completely reclaimed without any perspective of future mining.

The studied fossiliferous layers were documented mainly by drill-cores. They are represented by coals, bituminous clays, calcareous clays, diatomaceous clays, tuffitic clays and tuffites and reach from several cm to 2.5 m in thickness. The layers belong to the volcano-sedimentary unit of late Eocene to Oligocene age, partly called the Střezov Formation *sensu* Domáci (1977) and to the Ústí and Děčín formations of the České středohoří Mts *sensu* Cajz (1999, 2000). In fact we can consider the Střezov unit as a lateral continuation of the České středohoří units under the early Miocene cover. These units were dated by the <sup>40</sup>K-<sup>40</sup>Ar method (Bellon *et al.* 1998). The age of the analyzed sample of basaltic rock from the drill-core RU 60 (depth 21.4 m) was determined as  $35.4 \pm 0.9$  Ma and  $37.1 \pm 0.9$  Ma corresponding to the Priabonian, late Eocene.

The newly proposed interpretation of the volcano-sedimentary structure, which includes fossiliferous layers, envisages a maar-diatreme structure. Earlier interpretations by Cajz (1990) did not recognize the maar-diatreme structure in spite of noting breccias and tuffaceous rocks associated with a high content of xenolithic material formed by Cretaceous marlstones, late Proterozoic gneisses and Cainozoic clays. This previous interpretation generally led to an idea of repeated volcanic eruptions into the water basin accompanied by tectonic subsidence of the basin. Phreatomagmatic diatreme breccias that form majority of the diatreme body were described as a hyaloclastite or pepperite (Cajz 1990). The reinterpretation of drill-core material and maps of coal seam structure (Vácha *et al.* 1992) allows to support the new concept of the maar – diatreme structure by the following facts: (1) the circular form of the structure in plan – see Fig. 2A; (2) funnel-shape form of the body of breccias (Fig. 2C, D); (3) composition of breccia – high contents of xenoliths; (4) downward coarsening of dimensions of breccia fragments; (5) internal inclination of sedimentary layers to the center of the structure; (6) presence of the central depression originated by diagenetic subsidence of the central part filling; (7) the presence of two thick basalt lava bodies overlying lacustrine to palustrine clay and coal sediment on the top of the maar-diatreme structure; and (8) occurrence of laminated fossiliferous layers within the maar. All these facts do not exclude the possibility of surface water sources or small basins in the area during volcanic activity and documented reaction of ba-

saltic magma with the water either in the depth or on the surface of the maar lake.

The large maar-diatreme structure (Fig. 2C, D) has a champagne glass form (Lorenz 2003) typical for diatremes formed in relatively soft rock environments. In that topmost part the diameter of the structure reaches more than 1 km, while at the depth of 250 m it looks very narrow (100–150 m). Two continuous distinct basaltic bodies were documented in the studied drill-cores. The upper basaltic body, reaching a thickness of 15 m, is formed by basanite (Mag 1992) the lower one has the similar thickness and is formed by picritic basalt (Bellon *et al.* 1998) to olivinic nefelinite (Mag 1992). Both basalt bodies are separated by the upper fossiliferous layer of tuffites and clays. These bodies form the youngest volcanic filling (lava lakes) of the maar-diatreme structure and in fact they saved the maar-diatreme filling and fossiliferous deposits from more intensive destruction by erosion. The two fossiliferous horizons are developed in such a way that the lower one is covered by lower basaltic body and the upper one is localized between the lower and upper basaltic body. Other basalt occurrences within the maar-diatreme structure found in the drill-core profiles are much smaller in dimensions and have very irregular position within the profile. Three other irregular fossiliferous horizons under the basaltic bodies within the brecciated fill of the maar are localized only in its upper widening part. According to clay composition, laminated textures and content of fish scales, all the fossiliferous layers represent products of lacustrine and also palustrine (coal facies) environments. The deepest position has the layer of calcareous clays with remains of gastropods (drill-core RU 43, depth 110–165 m), while the deepest localized organic-rich layer is known from the central part of the diatreme depression (drill-core RU 50, depth 141.25–143.00 m). The position and correlation of the fossiliferous clays in the drill-cores and the outcrop SE from Roudníky is uncertain being partly based only on local correlation by the palaeontological markers (*Juniperus pauli*, *Cyclurus* sp.).

Several fossil localities are known in the wider surroundings of Roudníky that roughly correspond to this site. Fossiliferous clay and diatomite of the Větruše Hill 10 km to the east from Ústí nad Labem (see Radoň 2001) has yielded fossil plants and fish remains of amiids. This locality is characterized by 25 cm thick diatomaceous clay layer outcropping between two basaltic bodies similar to the Roudníky locality. The profile at Větruše was proposed as the holostratotype of the Ústí Formation (Cajz 2000) and the aquatic environment during the effusion was mentioned. The position and the association of fossils recovered in this clay layer partly coincide with those recovered in the Roudníky area (see below).

## Material and methods

Palaeontological material of Roudníky was collected from the drill-cores by the late Čestmír Bůžek and the first author during the geological exploration in 1987–1989. Later, Zdeněk Dvořák and his brother Pavel Dvořák during the years 1996 to 2003 succeeded to get important fossils from the outcrops. The plant fossils are preserved partly as compressions in pelitic volcanogenic deposits. Most of the specimens are housed in the collections of the National Museum in Prague (NM G, NM Pc), the others are in private collections of Zdeněk Dvořák (ZD), and the Regional Museum in Teplice (RMT).

In case of coaly leaf material attempts have been made to macerate cuticles by a routine technique of Schulze mixture. However, surface of most compressions are finely fractured due to desiccation, so that only well cutinized (evergreen) foliage yielded satisfactory structures.

To get independent palaeoenvironmental proxy-datasets for a comparison and validation of the Roudníky flora within the studied late Eocene to early Oligocene fossil floras/vegetation types of the Bohemian Massif and Saxony (Germany), five different palaeoenvironmental methods of Phytosociological approach, Integrated Plant Record vegetation analysis (IPR-vegetation analysis), Leaf Margin Analysis (LMA), Climate Leaf Analysis Multivariate Program (CLAMP) and Coexistence Approach (CA) have been used. The phytosociological approach (for details see Mai 1995) and IPR-vegetation analysis (e.g., Kovar-Eder et al. 2008; Teodoridis et al. 2011a, b) help to evaluate the studied plant assemblages. The other techniques were used to predict palaeoclimatic proxy-datasets based on physiognomic characters of foliage (LMA, CLAMP) and environmental requirements of the nearest living relatives (CA) of the studied fossil floras. The present study used linear regression equations by Wolfe (1979) –  $LMA_{MAT1} = 30.6 \times P + 1.41$ ; ( $r^2 = 0.98$ ), and by Su et al. (2010) –  $LMA_{MAT2} = 27.6 \times P + 1.038$ ; ( $r^2 = 0.79$ ) for LMA method, where MAT (mean annual temperature), P (proportion of n species with entire margin,  $0 < P < 1$ ) and  $r^2$  (coefficient of determination). To verify the obtained estimates, the value of sampling errors (SE1) and (SE2) were calculated following Wilf (1997) –  $SE1_{MAT} = c \sqrt{[(P(1-P))/n]}$  and Miller et al. (2006) –  $SE2_{MAT} = \sqrt{[(1 + \phi(n-1)P(1-P)) \times (P(1-P))/n]}$ , where the following symbols are used: c (slope of the MAT vs. leaf margin regression, equals 30.6 here), n (total species number), P (proportion of n species with entire margin,  $0 < P < 1$ ) and  $\phi = 0.052$  (dispersion factor). An updated version (see Teodoridis et al. 2012) of the special tool developed by Teodoridis et al. (2011c) was used to select relevant physiognomical datasets for using CLAMP, as characterized by e.g., Wolfe & Spicer (1999), Spicer et al. (2009), and Yang et al. (2011). Physiognomic characteristics of the studied floras are presented in Appendix 1.

The lastly used palaeoclimatic technique was Coexistence Approach (CA) developed by Mosbrugger & Utescher (1997) and updated by Utescher et al. (2000).

## Systematic palaeontology

The arrangement of plant taxa corresponds to the phylogenetic system based on molecular phylogeny (Judd et al. 2002, Christenhusz et al. 2011, Reveal 2012).

Plantae

Conifers

Family Pinaceae

### Genus *Pinus* L.

#### *Pinus* sp.

Figure 3A, B

*Material.* – Seeds, outcrop (ZD RUP 79a, 90).

*Description.* – One of the winged conifer seeds available is clearly assignable to *Pinus* because of the laterally adhering large seed and only slightly constricted wing (cf. Wolfe & Schorn 1990, pp. 7–8). Specific determination is equivocal because of very limited amount and incompleteness of material. The other specimen shows only the wing without the seed part.

Family Cupressaceae

### Genus *Juniperus* L. sect. *Sabina* (Mill.) Spach

#### *Juniperus pauli* Kvaček

Figures 3C, 7K

2002a *Juniperus pauli* Kvaček, p. 493, figs 1–3.

2009 *Juniperus pauli* Kvaček; Akhmetiev et al., p. 95, pl. 9, fig. 4.

*Material.* – Fertile twigs, outcrop (NM G 7904a and ZD RUP 6B – holotype and counterpart), sterile twigs and fragments, isolated male cones and seeds, drill-cores RU 44, depth 18 m (NM G 8777, G 8783), RU 60, depth 27.5–28 m (NM G 9412b – RU 60-7, NM G 9416, G 9417, RU 60-1), outcrop (ZD RUP 1A, B, 2, 3A, B, 4A, B, 5A).

*Description.* – The juniper from Roudníky is the earliest record of this genus in Europe. It is endemic in the North Bohemian Palaeogene, where it occurs besides Roudníky also at the Větruše Hill at Ústí/L. (pl. 9, figs 1–3; for detailed treatment see Kvaček 2002a). Its holotype represents a

fertile twig on a slab with attached seed cones confirming the affinity to the multi-seeded group of sect. *Sabina* Spach with smooth-edged leaves. The detached coaly twig fragments from drill-cores yielded epidermal anatomy corresponding to the Mediterranean *J. thurifera* L. The multi-seeded cones are similar to those of *Juniperus thurifera* var. *thurifera* distributed in the mountains of Spain and French Alps (Adams 2008).

## Genus *Taxodium* Rich.

### *Taxodium dubium* (Sternberg) Heer

Figures 3D–F, 7L

1853 *Taxodium dubium* (Sternberg) Heer, p. 136.

2009 cf. *Taxodium dubium* (Sternberg) Heer; Akhmetiev *et al.*, p. 95, pl. 9, fig. 5.

**Material.** – Sterile twigs, outcrop (ZD RUP 50, 93, 94, 95), partly with epidermal anatomy, drill-cores RU 43, depth 116.3 m (NM G 8810), RU 48, depth 16 m (NM G 8793b – RU 48-11B, NM G 9441 – RU 48-12), RU 60, depth 47.5–50 m (NM G 9427 – RU 60-20).

**Description.** – Sterile taxodioid foliage recovered at Roudníky belongs according to the epidermal anatomy to *Taxodium*: thin-walled quadrangular non-modified cells with smooth anticlines, amphicyclic stomata mostly perpendicularly oriented to the leaf midrib, with narrow elongate pit (Kunzmann *et al.* 2009). A morphologically similar Eocene conifer *Chamaecyparites hardtii* (Göpp.) Endl. emend. Kunzmann differs in epidermal anatomy by widely scattered, mostly longitudinally arranged amphicyclic stomata with darker cutinized subsidiary cells (Kunzmann 1999).

## Genus *Tetraclinis* Masters

### *Tetraclinis salicornioides* (Unger) Kvaček

Figures 3G, H, 7M

1989 *Tetraclinis salicornioides* (Unger) Kvaček, p. 48, pl. 1, fig. 11, pl. 2, figs 2–14, pl. 3, figs 1–4, text-fig. 1.

**Material.** – Twig fragments, drill-core RU-60, depth 28–28.5 m (NM G 9420a–c, unnumbered).

**Description.** – The cladode-like foliage of this conifer represented at Roudníky by the compressions with epidermal structure differs from the similar Cretaceous to early Palaeogene *Ditaxocladus* S.X. Guo & Z.H. Sun by thick papillate cuticles showing irregularly scattered stomata with very pronounced Florin rings (Guo *et al.* 2012). Similar records are known from the European Palaeogene and Neogene, more rarely from the Oligocene and Miocene of North America (Kvaček *et al.* 2000).

Family Taxaceae

## Genus *Cephalotaxus* Siebold & Zucc.

### cf. *Cephalotaxus parvifolia* (Walther) Kvaček & Walther

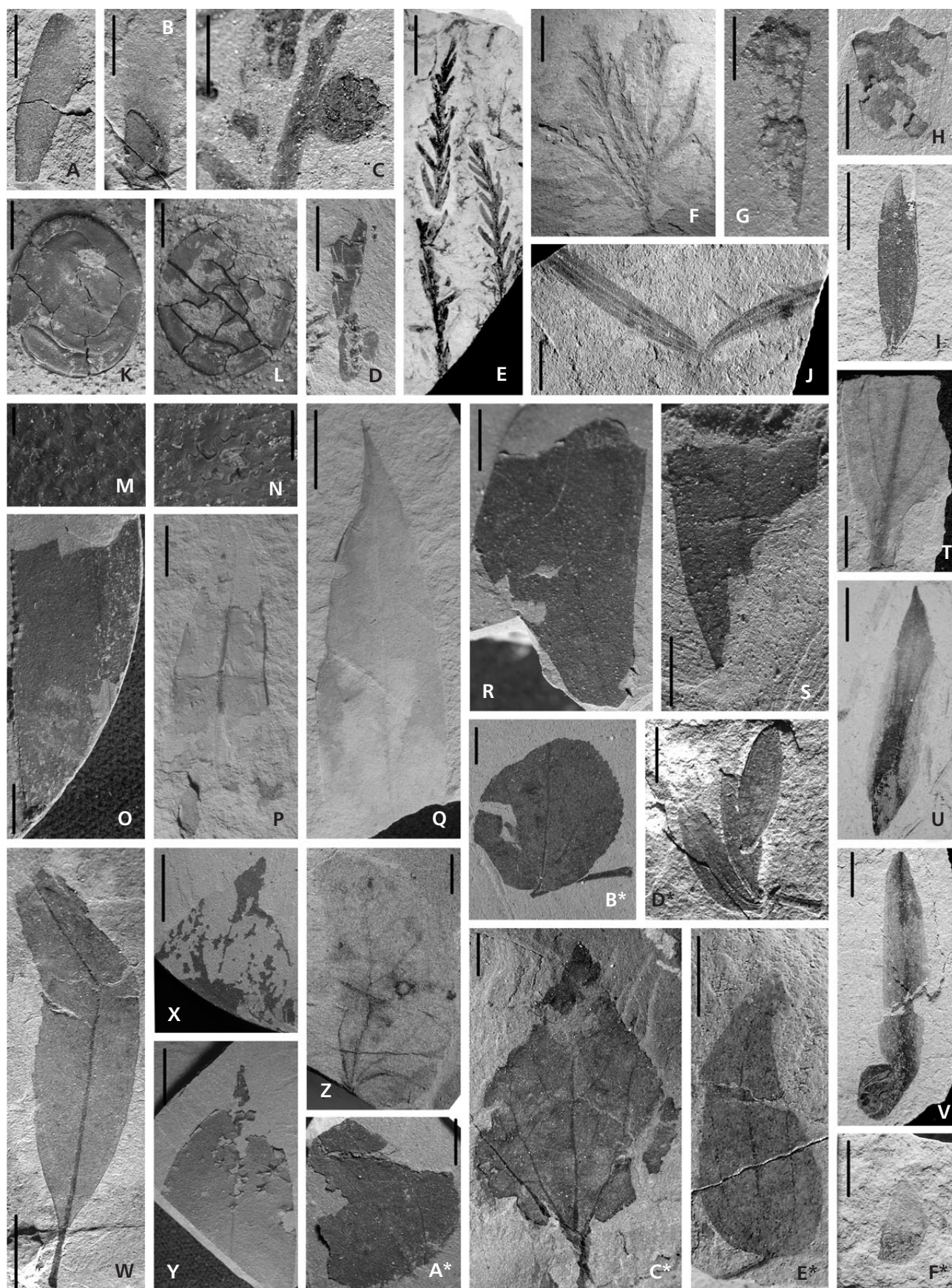
Figure 3I

? 1998 *Cephalotaxus parvifolia* (Walther) Kvaček & Walther, p. 11, pl. 4, figs 1–3.

**Material.** – Isolated needle, outcrop (ZD RUP 80).

**Figure 3.** Locality Roudníky. • A – *Pinus* sp., seed, ZD RUP 79a. • B – *Pinus* sp., seed, ZD RUP 90. • C – *Juniperus pauli* Kvaček, branch with seed cone, holotype, NM G7904a. • D – *Taxodium dubium* (Sternberg) Heer, leafy twig, NM G 8793, RU48-11B. • E – *Taxodium dubium* (Sternberg) Heer, leafy twig, ZD RUP 50. • F – *Taxodium dubium* (Sternberg) Heer, leafy twig, ZD RUP 93. • G – *Tetraclinis salicornioides* (Unger) Kvaček, two leafy segments, NM unnumbered, RU 60. • H – *Tetraclinis salicornioides* (Unger) Kvaček, leafy segment, NM G 9420a, RU 60. • I – ?*Cephalotaxus parvifolia* (Walther) Kvaček & Walther, incomplete needle, ZD RUP 80. • J – *Torreya bilinea* Saporta & Marion, leafy branch with two needles, ZD RUP 61. • K – cf. *Sabrenia* sp., seed, NM G 9448, RU 44. • L – cf. *Sabrenia* sp., seed, NM G 9449a, RU 44. • M – cf. *Sabrenia* sp., detail of testa, NM G 9448, RU 44. • N – cf. *Sabrenia* sp., structure of testa, NM G 9449a, RU 44. • O – *Laurophyllum acutimontanum* Mai, leaf compression, NM G 9404a, RU 60. • P – *Laurophyllum acutimontanum* Mai, fragmentary leaf, NM G 8808a, outcrop. • Q – *Laurophyllum acutimontanum* Mai, leaf impression with cuticle, NM G 8786a, RU 44. • R – *Laurophyllum pseudoprinceps* Weyland & Kilpper, fragmentary leaf compression, NM G 8772a, RU 44-9A. • S – *Laurophyllum pseudoprinceps* Weyland & Kilpper, fragmentary leaf compression, NM G 8762a, RU 43-1. • T – *Laurophyllum pseudoprinceps* Weyland & Kilpper, leaf base, NM G 8809a, outcrop. • U – *Liriodendron* sp., winged samara, ZD RUP 63A. • V – *Liriodendron* sp., winged samara, ZD RUP 28. • W – *Platanus neptuni* (Ettingshausen) Bůžek, Holý & Kvaček, leaf impression, ZD RU 12A. • X – *Platanus neptuni* (Ettingshausen) Bůžek, Holý & Kvaček, leaf apex with preserved epidermal anatomy, NM G 8794a, RU 48-10. • Y – *Platanus neptuni* (Ettingshausen) Bůžek, Holý & Kvaček, entire-margined leaf apex, NM G 9403a, RU 60-9. • Z – *Tilia brassicoides* (Saporta) Kvaček & Walther, bract, ZD RUP 133. • A\* – *Cercidiphyllum crenatum* (Unger) R. Brown, rounded leaf of mature branch, NM G 9414a, RU 60-13.A. • B\* – *Cercidiphyllum crenatum* (Unger) R. Brown, petiolate rounded leaf, ZD RUP 105. • C\* – *Cercidiphyllum crenatum* (Unger) R. Brown, leaf with acute apex, ZD RUP 18. • D\* – *Cercidiphyllum crenatum* (Unger) R. Brown, cluster of fruits, ZD RUP 22A. • E\* – cf. *Matudaea menzelii* Walther, petiolate leaf impression, ZD RUP 134. • F\* – *Cercidiphyllum crenatum* (Unger) R. Brown, winged seed, ZD RUP 89. Scale bars: A–J, O, P, R–V, Z–E\* = 5 mm; K, L = 1 mm; M, N = 50 µm; Q, W–Y = 10 mm; F\* = 3 mm.





**Description.** – Due to absence of epidermal traits the identification of this single needle is not straight-forward. Noteworthy are invisible stomatal bands on the impression. Similar sterile remains occurring in the Oligocene of North Bohemia and Saxony (Seifhennersdorf, Kundratice – Kvaček & Walther 1998, Walther & Kvaček 2007) have been assigned to *Cephalotaxus* on account of stomatal topography and match in gross morphology.

## Genus *Torreya* Arnott

### *Torreya bilinica* Saporta & Marion

Figure 3J

1876 *Torreya bilinica* Saporta & Marion, p. 221.

2009 *Torreya bilinica* Saporta & Marion; Akhmetiev *et al.*, p. 95, pl. 9, fig. 1.

**Material.** – Two needles attached to the twig, outcrop (ZD RUP 61).

**Description.** – Although lacking epidermal features the recovered impression of a twig fragment is referred to *Torreya* because of needle morphology and very narrow abaxial stomatal bands. Similar needle fossils have often been recorded in the Oligocene of North Bohemia, *e.g.*, at Žichov, Kundratice and in Saxony at Seifhennersdorf (Kvaček 1984, Walther & Kvaček 2007). This conifer has not been documented so far in the Eocene.

Angiosperms

Family Nymphaeaceae

## Genus *Sabrenia* M. Collinson

### *cf. Sabrenia* sp.

Figure 3K–N

**Material.** – Dispersed carbonized seeds – drill-cores RU 44, depth 39.5 m (G 9448, G 9449a, b), RU 60/94, depth 30.6–31.4 m (NM G 9431a–c).

**Description.** – Compressions of originally globose to ovoid seeds are variously deformed, disc-shaped, mostly rounded, *ca* 2–3.5 mm in diameter, rarely broadly elliptic, 2.5 mm wide and 3.6 mm long with slightly thickened peripheral rim and poorly preserved tiny embryotega (cap). The raphe ridge is obscured; surface of testa is finely granulate (granules *ca* 30 µm in diameter), more distinctly in larger specimens. At places the cell structure of testa is visible showing cells *ca* 60 µm long and 30 µm wide with more or less regularly deeply lobate-digitate anticlinal walls (usually 8–10 sinuses per cell).

The anatomical structure as far as it is preserved and gross morphology refers the material of Roudníky to seeds described in detail from the late Eocene Bembridge marls (Collinson 1980) as *Sabrenia chandlerae*. In the absence of further anatomical details we refrain from more accurate identification and comparisons with similar fossil seeds partly assigned to other *Brasenia*-like fossil taxa. Among seeds of the Nymphaeaceae *s. l.* recovered in the Kučlín diatomite (Kvaček & Teodoridis 2011), some match in the size and form those from Roudníky and Bembridge, although surface details necessary for more precise identification have not been available due to poor preservation of the Kučlín material as impressions. Similar small reticulate-granulate seeds, which were described as *Palaeonymphaea circumcincta* (Menzel) Mai from Germany (Ringsberg, ?early Oligocene – Mai 1988), differs in finely undulating anticlinal cell walls of testa. The Oligocene records of Nymphaealean seeds assigned to *Dusembaya seifhennersdorfensis* (Engelhardt) Mai (Mai 1988) differ in smooth surface.

Family Lauraceae

## Genus *Laurophyllum* Göpp.

### *Laurophyllum acutimontanum* Mai

Figures 3O–Q, 7N

1963 *Laurophyllum* (*Tetradenia*) *acutimontanum* Mai, p. 72, pl. 8, figs 7–9, 12 (non 10), pl. 9, figs 1–4, text-figs 11f–h.

**Material.** – Leaf compressions with epidermal anatomy, drill-cores RU 44, depth 18m (NM G 8786), RU 60, depth 27.5–28 m (NM G 9404 – RU 60-11A), outcrop (NM G 8808).

**Description.** – Thanks to preserved epidermal anatomy (amphicyclobrachyparacytic stomata with deeply sunken guard and inner subsidiary cells), a few lauroid compressions are assignable to this Palaeogene evergreen element. It evolved in the late Eocene (upper part of the Staré Sedlo Formation – Knobloch *et al.* 1996, Teodoridis *et al.* 2012) and spread typically in the Oligocene (Walther & Kvaček 2007).

### *Laurophyllum pseudoprinceps* Weyland & Kilpper

Figures 3R–T, 7O, P, 8A

1963 *Laurophyllum pseudoprinceps* Weyland & Kilpper, p. 100, pl. 23, figs 14–19, text-fig. 6.

**Material.** – Leaf compressions with epidermal anatomy, drill-cores RU 43, depth 36–37 m (NM G 8762 – RU 43-1),



RU 44, depth 18 m (NM G 8772 – RU 44-9a), outcrop (NM G 8809).

**Description.** – Lauroid leaf compressions with slightly more pronounced subbasal secondaries show diagnostic traits of *Laurophyllum pseudoprinceps*: bead-like thickenings of the anticlinal walls and amphibrachyparacytic stomata with broad ledges not reaching the stomatal poles (Weyland & Kilpper 1963, Kvaček 1971). This element occurs exceptionally in the Eocene (Knobloch et al. 1996). It was widely spread in the Oligocene of Central Europe, survived to the Miocene and accompanied mainly thermophilous plant assemblages (Holý et al. 2012).

Family Magnoliaceae

### Genus *Liriodendron* L.

#### *Liriodendron* sp.

Figure 3U, V

2009 *Liriodendron haueri* Ettingshausen; Akhmetiev et al., p. 95, pl. 9, fig. 8.

**Material.** – Fruitlets, drill-cores RU 44, depth 18 m (NM G 8788), RU 60, depth 27.5–28 m (NM G 9418), outcrop (ZD RUP 18, 28, 63A, 91).

**Description.** – The recovered dispersed winged samaras typical of this genus are assigned to the same genus as the record from the Oligocene of Markvartice (Bůžek et al. 1976, as *Liriodendron haueri* Ettingshausen). The basal part shows occasionally pairs of finely tuberculate seeds. No co-occurring foliage referable to the same genus has been found to help a more precise specific identification, although several records are known from the Bohemian Palaeogene (Ettingshausen 1869, as *Liriodendron haueri*, Žichov, Knobloch 1961, as *Liriodendron procaccinii* Ung., Hrazený, Kvaček & Teodoridis 2011, as *Liriodendron* sp., Kučlín).

Family Platanaceae

### Genus *Platanus* L.

#### *Platanus neptuni* (Ettingshausen)

Bůžek, Holý & Kvaček

Figures 3W–Y, 8B, C

1967 *Platanus neptuni* (Ettingshausen) Bůžek, Holý & Kvaček, p. 205, pl. 1, figs 1–4, 6 (non 5 – *Sloanea arto carpites*), pls 2–4.

2009 *Platanus neptuni* (Ettingshausen) Bůžek, Holý & Kvaček; Akhmetiev et al., p. 95, pl. 9, fig. 3.

**Material.** – Simple leaves, partly with epidermal anatomy, outcrop (ZD RUP12A), drill-cores RU 48, depth 49 m (NM G 8794 – RU 48-10), RU 60, depth 27.5–28 m (NM G 9403 – RU 60-9).

**Description.** – Foliage of this extinct plane tree is preserved in the material studied as impressions of dentate simple leaves and fragmentary compressions of sub-entire margined leaves with typical epidermal anatomy: deeply undulate anticlines of epidermal cells, stomata with large apertures and compound trichome bases. However, remains of infructescences have not been recovered. This deciduous element was distributed in Europe in the Palaeogene, in the Eocene more often in its trifoliate form, and reached even the Miocene (Kvaček & Manchester 2004).

Family Cercidiphyllaceae

### *Cercidiphyllum* Siebold & Zucc.

#### *Cercidiphyllum crenatum* (Unger) R. Brown

Figure 3A\*–D\*, F\*

1935 *Cercidiphyllum crenatum* (Unger) R. Brown, p. 575, pl. 68, figs 1, 6, 8–10.

2009 *Cercidiphyllum crenatum* (Unger) R. Brown; Akhmetiev et al., p. 95, pl. 9, fig. 9.

2009 *Daphnogene cinnamomifolia* (Brongniart) Unger; Akhmetiev et al., p. 95, pl. 9, fig. 8.

**Material.** – Leaves, fruits, seeds, drill-cores RU 60, depth 28–28.5m (NM G 9414 – RU 60-13), outcrop (ZD RUP 18, 19, 21A, 22A, 56A, 89, 105, 134).

**Description.** – This element is represented by clustered follicles, dispersed winged seeds and typically dimorphous foliage: rounded cordate crenate leaves of mature branches and narrow elliptic juvenile forms recalling foliage of *Ziziphus*. Similar variation is known elsewhere (Kvaček & Walther 2004, Bechlejovice). *C. crenatum* is common in the Oligocene to Neogene of Europe. In the Eocene only the related extinct *Trochodendroides*, associated with a different type of fruits (*Nyssidium*), occurred (e.g., in the Spitsbergen Palaeogene – Budantsev & Golovneva 2009).

Family Hamamelidaceae

### Genus *Matudaea* Lundell

**cf. *Matudaea menzelii* Walther**

Figure 3E\*

? 1978 *Matudaea menzelii* Walther in Mai & Walther, p. 51, pl. 3, figs 1–4, pl. 11, figs 2–3, pl. 24, figs 1–9.

**Material.** – Leaf impression, outcrop (ZD RUP 134).

**Description.** – The long petiolate entire-margined basally triveined leaf matches *Matudaea menzelii* known from several Oligocene sites in Germany (Walther in Mai & Walther 1978, Walther 1999). The identification of the record is not supported by epidermal anatomy. Similar fragments, also without cuticle structure, were described from other parts of the České středohoří Mts, e.g., Bechlejovice, Kundratice and Suletice (see Kvaček & Walther 2004).

Family Fabaceae

**Genus *Gleditsia* L.**

***Gleditsia* sp.**

Figure 4A

**Material.** – Detached leaflets, outcrop (ZD RUP 52A, 109).

**Description.** – Some indistinctly widely toothed legume leaflets of the Roudníky flora match in form fossils ascribed to *Gleditsia* (e.g., Guo & Zhou 1992).

**Genus *Leguminosites* Bowerbank emend. Schimper**

***Leguminosites* sp.**

Figure 4B

2009 Leguminosae gen. et sp. indet.; Akhmetiev *et al.*, p. 95, pl. 9, fig. 17.

**Material.** – Impressions of detached leaflets, outcrop (ZD RUP 52A).

**Description.** – Ordinary detached leaflets of legumes are not identifiable to the natural genus and are summarized here in this artificial category. They may represent some more distinct morphotypes.

**Genus *Palaeolobium* Unger**

***Palaeolobium* sp.**

Figure 4C, D

**Material.** – Impressions of detached leaflets (?), outcrop (ZD RUP 113, 135).

**Description.** – The foliage assigned to this taxon may not belong to legumes although it matches in gross morphology (spatulate lamina, longer stalk) with this morphotype known from other Palaeogene localities (Häring, Socka, Kundratice). The material at hand is devoid of epidermal anatomy. Similar specimens from Kundratice (Kvaček & Walther 1998) yielded epidermal patterns unlike legumes. A more detailed study of this taxon is required to clarify its affinities.

**Genus *Mimosites* Bowerbank emend. Ettingshausen**

***Mimosites haeringianus* Ettingshausen**

Figure 4E

1853 *Mimosites haeringianus* Ettingshausen, p. 92, pl. 30, figs 23–37 (“*haeringiana*”).

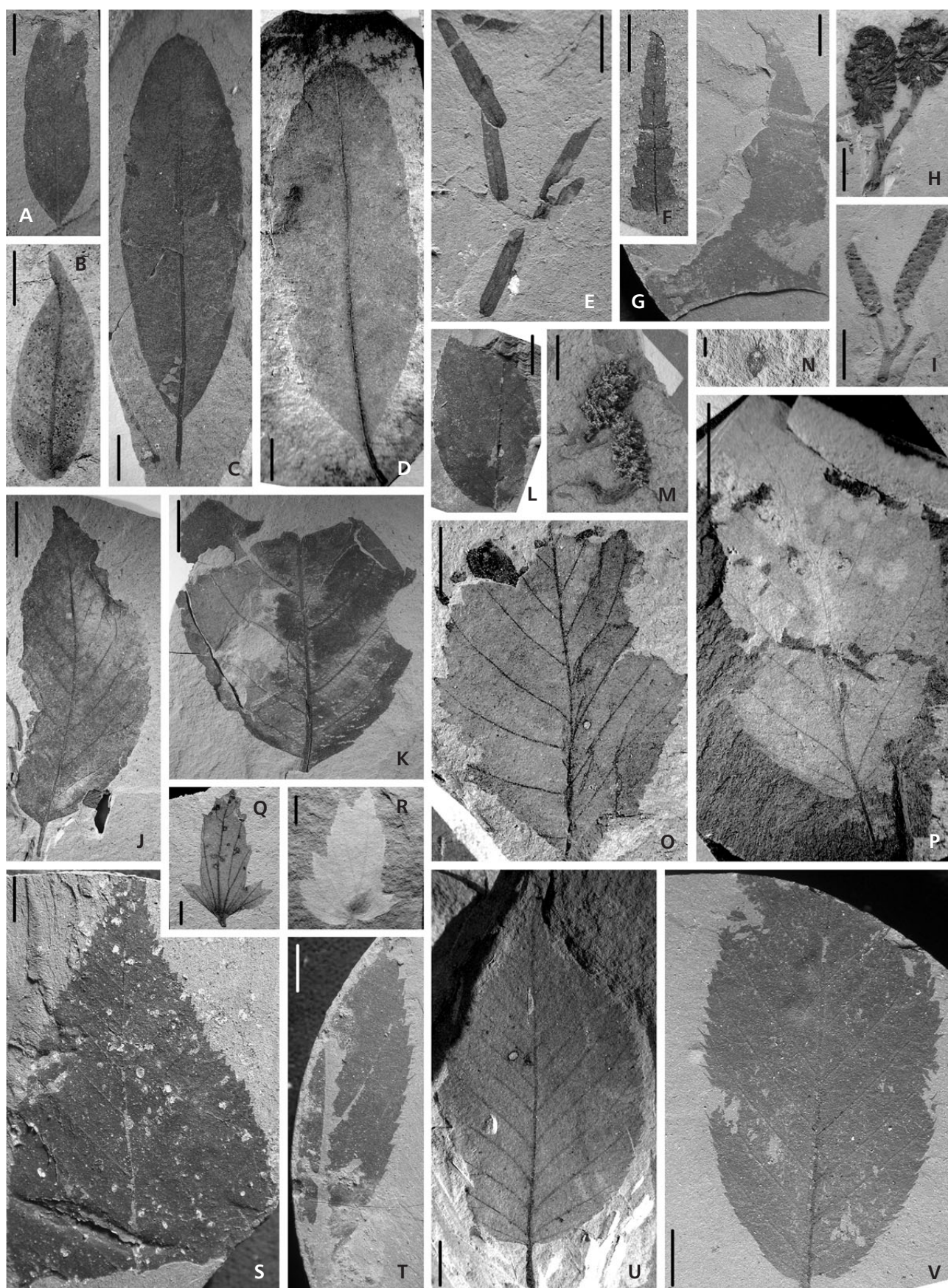
2009 *Mimosites haeringianus* Ettingshausen; Akhmetiev *et al.*, p. 95, pl. 9, fig. 21.

**Material.** – Detached leaflets, outcrop (ZD RUP 13), drill-core RU 60 (unnumbered).

**Description.** – Narrow linear blunt leaflets with a characteristic asymmetrical base and venation do not differ from other records of this legume typical of the Palaeogene (for detailed discussion see Kvaček & Walther 1998).

**Figure 4.** Locality Roudníky. • A – *Gleditsia* sp., leaflet, ZD RUP 109. • B – *Leguminosites* sp., leaflet, ZD RUP 52A. • C – *Palaeolobium* sp., leaf, ZD RUP 113. • D – *Palaeolobium* sp., leaf, ZD RUP 135. • E – *Mimosites haeringianus* Ettingshausen, part of leaf disintegrated into leaflets, ZD RUP 13. • F – ?*Castaneophyllum lonchitiforme* Kvaček & Walther, leaf apex, ZD RUP 107. • G – *Alnus gaudinii* (Heer) E. Knobloch & Kvaček, leaf fragment, NM G 9407a. • H – *Alnus kefersteinii* (Göppert) Unger, two female infructescences on a common stalk, ZD RUP 21a. • I – *Alnus kefersteinii* (Göppert) Unger, two male catkins, ZD RUP 16. • J – *Alnus gaudinii* (Heer) E. Knobloch & Kvaček, leaf impression, ZD RUP 131. • K – *Alnus gaudinii* (Heer) E. Knobloch & Kvaček, leaf base, ZD RUP 130. • L – *Alnus gaudinii* (Heer) E. Knobloch & Kvaček, leaf compression, NM G 8798a, RU 48-16. • M – *Betula dryadum* Brongniart, catkin, ZD RUP 147. • N – *Betula dryadum* Brongniart, winged fruitlet, ZD RUP 78. • O – *Betula alboides* Engelhardt emend. Walther & Kvaček, leaf impression, ZD RUP 148. • P – *Betula alboides* Engelhardt emend. Walther & Kvaček, leaf impression, ZD RUP 150. • Q – *Carpinus mediomontana* Mai, involucre, ZD RUP 14a. • R – *Carpinus mediomontana* Mai, involucre, ZD RUP 58a. • S – *Carpinus* sp., leaf apex, NM G 8766, RU 44. • T – *Ostrya atlantidis* Unger, leaf compression, NM G 9442, RU 48. • U – *Carpinus* sp., leaf, ZD RUP 104. • V – *Ostrya atlantidis* Unger, leaf base, NM G 9425, RU 60-17. Scale bars: A–M, O, Q–V = 5 mm; N = 1 mm; P = 10 mm.





Family Fagaceae

**Genus *Castaneophyllum* Dilcher & Jones**

**? *Castaneophyllum lonchitiforme* Kvaček & Walther**

Figure 4F

?2012 *Castaneophyllum lonchitiforme* Kvaček & Walther, p. 251, pl. 3, figs 1–5, 8–10, pl. 4, figs 1–6, pl. 6, figs 1–6.

*Material.* – Outcrop (ZD RUP 107).

*Description.* – A single leaf apex recalls in slender form and simple dentate margin oak-like foliage previously assigned to *Quercus lonchitis* Unger and occurring mainly in the Oligocene of Seifhennersdorf, Suletice, Lochočice and Stadice (Walther & Kvaček 2007). More detailed comparisons of the compression material from the above mentioned sites revealed morphological differences to the type specimens from the late Eocene locality Socka and epidermal features leading to the Castaneoideae (Kvaček & Walther 2012). The specimen at hand does not show any cuticle structure.

Family Betulaceae

**Genus *Alnus* Mill.**

***Alnus gaudinii* (Heer) E. Knobloch & Kvaček**

Figures 4G, J–L, 8D

1976 *Alnus gaudinii* (Heer) E. Knobloch & Kvaček, p. 33, pl. 6, figs 1, 3, pl. 7, figs 1, 5, pl. 13, fig. 4, pl. 15, figs 1–4, 7, 8, 10, 11, 13, 15, 17, pl. 16, figs 1–5, pl. 19, fig. 15, pl. 20, fig. 10, text-figs 11, 12.

*Material.* – Leaves, outcrop (ZD RUP 130, 131, 149), drill-cores RU 43, depth 116.3 m (NM G 8776, G 8792 – RU 43-2), RU 48, depth 49 m (NM G 8793 – RU 48-11, NM G 8797 – RU 48-13, NM G 8798 – RU 48-16), RU 60, depth 27.5–28 m (NM G 8812, G 9407a, G 9409 – RU 60-4).

*Description.* – Several ovate finely bluntly serrate long petiolate leaves with cuneate bases belong to alder foliage and match in morphological details and partly even in epidermal anatomy (large stomata of the laterocytic type) to the other records of *Alnus gaudinii* from the České středohoří Mts (Kundratice – Kvaček & Walther 1998, Bechlejovice – Kvaček & Walther 2004) and Saxony (Seifhennersdorf – Walther & Kvaček 2007). Similar leaf impressions differing in rounded bases were assigned also to *Alnus pho-*

*caeensis* Saporta (Seifhennersdorf – Mai 1963, Kleinsaubernitz – Walther 1999).

***Alnus kefersteinii* (Göppert) Unger**

Figure 4H, I

1847 *Alnus kefersteinii* (Göppert) Unger, p. 113, *pro parte*, pl. 33, fig. 2 (non pl. 33, figs 1, 3–4).

*Material.* – Infructescence, outcrop (ZD RUP 21, 85a), male catkin, outcrop (ZD RUP 16).

*Description.* – These infructescences and inflorescences belong obviously to the above foliage and accompany *A. gaudinii* in several other sites (*e.g.*, Kundratice – Kvaček & Walther 1998).

**Genus *Betula* L.**

***Betula alboides* Engelhardt**

**emend. Walther & Kvaček**

Figure 4O, P

2007 *Betula alboides* Engelhardt emend. Walther & Kvaček, p. 103, pl. 9, figs 2–7, text-fig. 5b.

*Material.* – Leaves, outcrop (ZD RUP 145, 146, 148).

*Description.* – Birch foliage occurring in the outcrop of Roundíky compares well with the records from Seifhennersdorf (Walther & Kvaček 2007) and Kundratice (Kvaček & Walther 1998), the latter assigned to *Betula buzekii* Kvaček & Walther, which was reduced into synonyms for priority reasons.

***Betula dryadum* Brongniart**

Figure 4M, N

1828 *Betula dryadum* Brongniart, p. 49, pl. 3, fig. 5.

*Material.* – Fruitlet, outcrop (ZD RUP 78), male catkin (ZD RUP 147).

*Description.* – The double winged fruitlet at hand confirms other remains of this kind occurring in Saxony (Mai 1963, Walther & Kvaček 2007) and but rarely in the České středohoří Mts (Kvaček & Walther 1998, as *Betula* sp.). The associated male catkin belongs obviously to the same plant. Foliage of the same plant described above accompanies these fruit remains at most localities.



## Genus *Carpinus* L.

### *Carpinus mediomontana* Mai

Figure 4Q, R

- 1978 *Carpinus mediomontana* Mai in Mai & Walther, p. 68, pl. 6, figs 6a–c, d (holotype), e–g, pl. 28, figs 21–27.  
2009 *Carpinus mediomontana* Mai; Akhmetiev et al., p. 95, pl. 9, fig. 6.

**Material.** – Involucres, drill-core RU 60, depth 27.5–28 m (NM G 8811), outcrop (ZD RUP 14A, 58A, 99, 100, 101).

**Description.** – Well preserved involucres of hornbeam show variations in morphology of this plant common in the Oligocene of North Bohemia and Saxony but so far lacking in the Eocene (for discussion of the taxonomy see Walther & Kvaček 2007).

### *Carpinus* sp.

Figure 4S, U

**Material.** – Leaves, drill-cores RU 44, depth 52 m (NM G 8795, G 8766), RU 48, depth 51 m (NM G 9438, 9441), RU 60, depth 27.5–28 m (NM G 9414c, G 9426, 9436), outcrop (ZD RUP 98, 102, 103, 104, 106, 111, 114, 119).

**Description.** – Various leaf fossils recovered in the Roudníky flora show affinities to foliage usually ascribed to *Carpinus grandis* Ung. As stated by Walther & Kvaček (2007) this morphotaxon may correspond to more species and in our case it surely belongs to the associated fruit remains described below.

## Genus *Ostrya* Scop.

### *Ostrya atlantidis* Unger

Figures 4T, V, 5A, B

- 1850 *Ostrya atlantidis* Unger, p. 408.  
2009 *Ostrya atlantidis* Unger; Akhmetiev et al., p. 95, pl. 9, figs 11–12.

**Material.** – Leaf impressions, drill-cores RU 43, depth 116.3 (NM G 8784), RU 44, depth 18 m (NM G 8763, G 8765, G 8766, G 8789a, G 8802), RU 45a, depth 44–45 m (NM G 8778a, G 9444c), RU 48, depth 50 m (NM G 9442), RU 60, depth 27.5–28 m (NM G 8760a, G 9410 – RU 60-8, G 9425 – RU 60-17), outcrop, fruit bracts, drill-core

RU 60, depth 27.5–28 m (NM G 8832), outcrop (ZD RUP 15A, 32, 33, 124, 125, 126).

**Description.** – Both fruits, partly only bracts enveloping the fruits and foliage typically double serrate mucronate at margin occur in all sites at Roudníky. The record well corresponds to others from Saxony (Seifhennersdorf – Walther & Kvaček 2007) and North Bohemia (Kundratice, Bechlejovice – Kvaček & Walther 1998, 2004).

Family Juglandaceae

## Genus *Carya* Nutt.

### *Carya fragiliformis* (Sternberg) Kvaček & Walther in Walther & Kvaček

Figure 5C, D

- 2007 *Carya fragiliformis* (Sternberg) Kvaček & Walther in Walther & Kvaček, p. 110, pl. 11, figs 1–3, pl. 23, figs 8–10, text-fig. 6b.  
2009 *Carya fragiliformis* (Sternberg) Kvaček & Walther; Akhmetiev et al., p. 95, pl. 9, fig. 10.

**Material.** – Leaflets, drill-cores RU 48, depth 48 m (NM G 8796 – RU 48-7), RU 60, depth 28.0–28.5 m (NM G 9414b), outcrop (ZD RUP 51, 128).

**Description.** – The juglandaceous foliage from the Roudníky area is somewhat arbitrarily assigned either to *Carya* or *Cyclocarya* according to the leaflet morphology as characterized by Walther & Kvaček (2007). The accompanying fruits or any details of epidermal structure are not available in the Roudníky flora. The present records are similar to those recovered at many sites of Oligocene age in North Bohemia and Saxony (Bůžek et al. 1976; Kvaček & Walther 1998, 2004; Walther & Kvaček 2007). Only scanty and equivocal remains similar to *Carya* leaflets have been recorded also in the late Eocene diatomites of Kučlín (Kvaček & Teodoridis 2011).

## Genus *Cyclocarya* Iljinskaya

### *Cyclocarya* sp.

Figure 5E, F

- 2009 *Cyclocarya* sp.; Akhmetiev et al., p. 95, pl. 9, fig. 18.

**Material.** – Leaflets, outcrop (ZD RUP 48, 127).

**Description.** – See above under *Carya fragiliformis* for comments.

Family Rhamnaceae

## Genus *Ziziphus* Miller

### *Ziziphus ziziphoides* (Unger) Weyland

Figure 5G

1943 *Ziziphus ziziphoides* (Unger) Weyland, p. 113.

**Material.** – Leaf impression, outcrop (ZD RUP 81).

**Description.** – A single leaf impression recovered in the outcrop of Roudníky belongs according to gross morphology (basally triveined blade with entire base and very finely serrate apex) to *Ziziphus* foliage as known from the European late Eocene (Bembridge – Reid & Chandler 1926, Kučlín – Bůžek *et al.* 1990, Kvaček & Teodoridis 2011) and Oligocene floras (for distribution see Mai 1995, p. 275, for taxonomical treatment Kvaček & Walther 2004). Broader morphotypes occurring in the Kučlín and Bechlejovice diatomites were separated as *Ziziphus ziziphoides* forma *bi-linica* (Ettingshausen) Kvaček & Walther (2004).

Family Rosaceae

## Genus *Rosa* L.

### *Rosa milosii* Kvaček & Walther

Figure 5H, J, K

2004 *Rosa milosii* Kvaček & Walther, p. 38, pl. 17, figs 4–8.

2009 *Rosa milosii* Kvaček & Walther; Akhmetiev *et al.*, p. 95, pl. 9, fig. 15.

**Material.** – Fruits, partly attached to thorny twigs and isolated twigs, drill-core RU 48: depth 48 m (G 9440a, b), outcrop (ZD RUP 35, 36A, 37, 83a).

**Description.** – Abundant fruits (“rose hips”) partly attached

to thorny twigs or isolated thorny twigs (Fig. 5H) occur in the Roudníky area and correspond well with the record from Bechlejovice (Kvaček & Walther 2004).

### *Rosa lignitum* Heer

Figures 5L, M, 8E

1869 *Rosa lignitum* Heer, p. 99, pl. 30, fig. 33.

**Material.** – Leaflets, drill-cores RU 44, depth 18 m (NM G 8771 – RU 44-3), RU 48, depth 51 m (NM G 8781 – RU 48-3, G 9440), RU 60, depth 51.75 m (NM G 8761, G 9424a – RU 69-18), outcrop (ZD RUP 38, 39, 40, 41A, 42, 46).

**Description.** – The foliage belonging to the above discussed fruits fits into the concept of a morphotype called *Rosa lignitum* Heer, and even corresponds in leaf epidermal anatomy: anomocytic stomata with slightly thickened ledges forming a lanceolate aperture. A similar structure was found in the record from Haselbach (Walther *in* Mai & Walther 1978).

## Genus *Pyracantha* M. Roem.

### *Pyracantha kraeuselii* Walther

Figures 5O–P, 8F, G

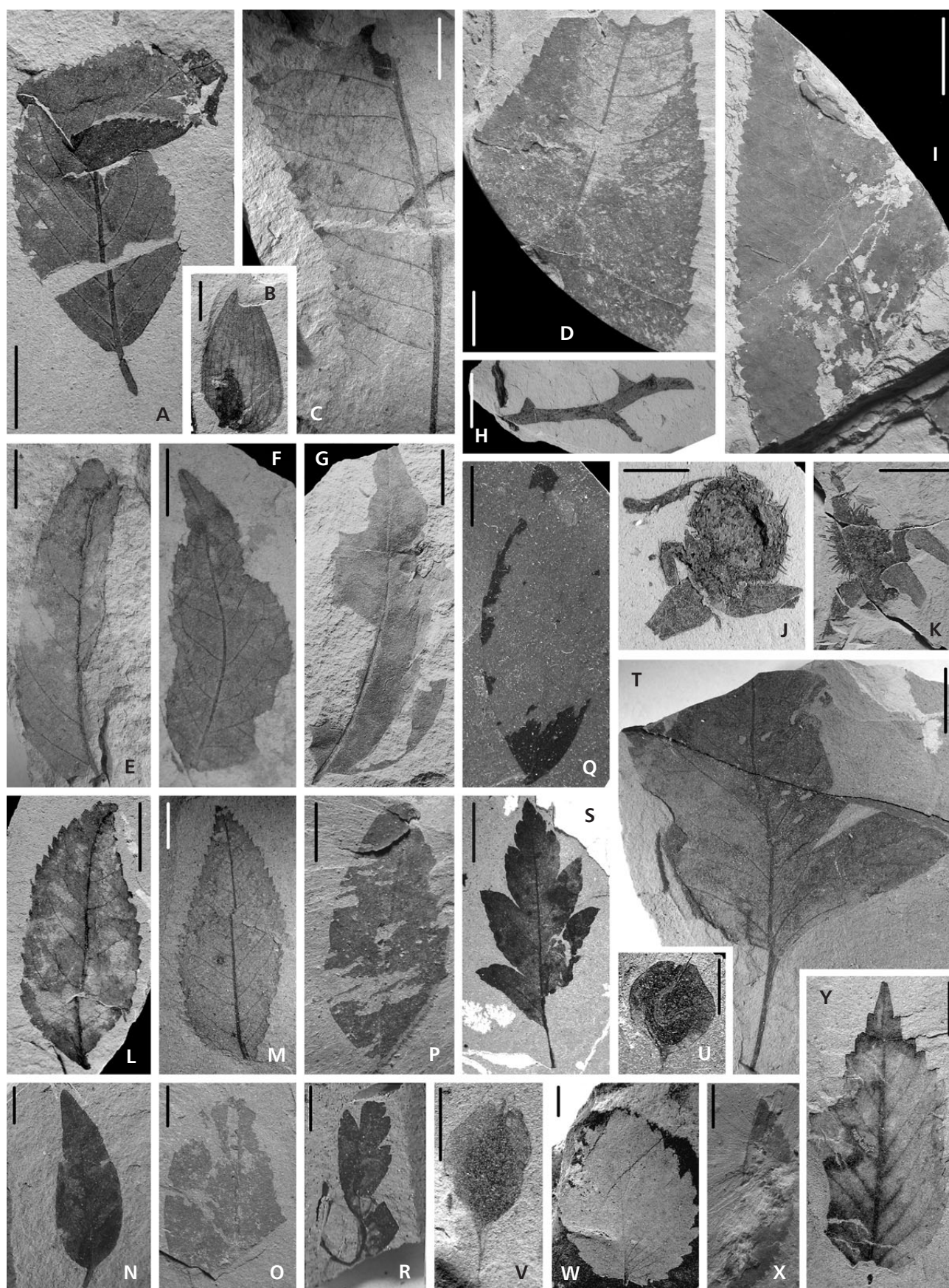
1978 *Pyracantha kraeuselii* Walther *in* Mai & Walther, p. 98, pl. 7, fig. 11, pl. 11, fig. 4, pl. 35, figs 7–9, pl. 39, figs 1–7.

**Material.** – Leaves with epidermal structure, drill-cores RU 43 m, depth 36–37 m (G 8767 b – RU 43-3B), RU 60, depth 27.5–28 m (NM G 9405 – RU 60-3, G 9415 – RU 60-6, G 9432 – RU 60-16).

**Description.** – This not easily recognizable element is characteristic by tough narrow subentire-margined leaves with anomocytic (?) round-oval stomata showing thickened

**Figure 5.** Locality Roudníky. • A – *Ostrya atlantidis* Unger, leaf base, ZD RUP 33. • B – *Ostrya atlantidis* Unger, fruit bract enveloping fruit, ZD RUP 32. • C – *Carya fragiliformis* (Sternberg) Kvaček & Walther, fragmentary leaflet, ZD RUP 128. • D – *Carya fragiliformis* (Sternberg) Kvaček & Walther, leaflet apex, NM G 8796, RU 48-7. • E – *Cyclocarya* sp., leaflet, ZD RUP 127. • F – *Cyclocarya* sp., leaf, ZD RUP 48. • G – *Ziziphus ziziphoides* (Unger) Weyland, leaf, ZD RUP 49. • H – *Rosa milosii* Kvaček & Walther, thorny twig, ZD RUP 38. • I – cf. *Dicotylophyllum ungeri* (Engelhardt) Walther & Kvaček, leaf, NM G 8805, RU 43. • J – *Rosa milosii* Kvaček & Walther, fruit, ZD RUP 36a. • K – *Rosa milosii* Kvaček & Walther, fruit, ZD RUP 37. • L – *Rosa lignitum* Heer, leaflet, ZD RUP 41a. • M – *Rosa lignitum* Heer, leaflet, ZD RUP 92a. • N – *Rosa lignitum* Heer, leaflet, ZD RUP 108. • O – *Pyracantha kraeuselii* Walther *in* Mai & Walther, fragmentary leaf compression with cuticle, NM G 9405a. • P – *Pyracantha kraeuselii* Walther *in* Mai & Walther, leaf compression with cuticle, NM G 8767b, RU 43-38. • Q – cf. “*Viburnum*” *atlanticum* Ettingshausen, leaf compression with cuticle, NM G 9439a. • R – *Crataegus pirkenbergensis* E. Knobloch, fragmentary leaf impression, ZD RUP 120. • S – *Crataegus pirkenbergensis* E. Knobloch, leaf impression, ZD RUP 11. • T – *Crataegus pirkenbergensis* E. Knobloch, base of larger leaf, ZD RUP 129. • U – *Ulmus* sp., fruit, ZD RUP 25. • V – cf. *Ulmus* sp., fruit, ZD RUP 26. • W – *Ulmus fischeri* Heer, small leaf impression, ZD RUP 132. • X – *Ulmus fischeri* Heer, leaf fragment, NM G 8764, RU 48. • Y – *Ulmus fischeri* Heer, leaf impression, ZD RUP 34. Scale bars: A, C–L, S, T, Y = 10 mm; A–J, M–R, U–X = 5 mm.





stomatal ledges reaching the poles. Besides the type locality Haselbach (Walther *in* Mai & Walther 1978) this is the second record of this species. Similar leaf remains from the Oligocene of Flörsheim have been recorded as *Andromediphyllum* Kvaček (2004a) but they clearly differ in circular stomata.

### Genus *Crataegus* L.

#### *Crataegus pirskenbergensis* E. Knobloch

Figure 5R–T

- 1961 *Crataegus pirskenbergensis* E. Knobloch, p. 26, pl. 7, figs 2–5.  
2009 *Crataegus pirskenbergensis* E. Knobloch; Akhmetiev *et al.*, p. 95, pl. 9, fig. 13.

**Material.** – Leaves, drill-core RU 44, depth 18 m (NM G 8785a – RU 44-4A), outcrop (ZD RUP 11, 120, 129).

**Description.** – Leaves of this *Crataegus* are recognized on the basis of pinnately sected to pinnately lobed lamina divided into triangular finely toothed lobes in 3 pairs diminishing in size from the base towards the apex. Such morphotypes occur in the Oligocene at the type locality Hrazený (Knobloch 1961) and Bechlejovice (Kvaček & Walther 2004).

### ?Rosaceae gen.

#### cf. *Dicotylophyllum ungeri* (Engelhardt)

Walther & Kvaček

Figure 5I

- ? 2007 *Dicotylophyllum ungeri* (Engelhardt) Walther & Kvaček, p. 116, pl. 15, figs 5–7.

**Material.** – Leaves, drill-cores RU 43, depth 114 m (NM G 8805), RU 44, depth 16 m (NM G 8806).

**Description.** – Some narrow elliptic leaf remains recalling Betulaceae or Juglandaceae differ in regularly bluntly simple serrate margin. Similar morphotypes of foliage from Seifhennersdorf and Bechlejovice were tentatively compared with the Rosaceae (Kvaček & Walther 2004, as Rosaceae gen. et sp. 2 and Rosaceae gen. et sp. 4, Walther & Kvaček 2007, as *Dicotylophyllum ungeri*).

Family Ulmaceae

### Genus *Ulmus* L.

#### *Ulmus fischeri* Heer

Figure 5W–Y

- 1856 *Ulmus fischeri* Heer, p. 57, pl. 57, figs 1–3.  
2009 *Ulmus fischeri* Heer; Akhmetiev *et al.*, p. 95, pl. 9, fig. 20.

**Material.** – Leaf impressions, outcrop (ZD RUP 34, 132).

**Description.** – Coarsely double dentate leaf impressions with typical ulmoid venation occur rarely in outcrops of Roudníky. They correspond to the species identified as *Ulmus fischeri* commonly recorded in the Oligocene of North Bohemia and Germany (see Kvaček & Walther 2004).

#### *Ulmus* sp.

Figure 5U, V

**Material.** – Fruits, outcrop (ZD RUP 25, 26).

**Description.** – The bicornate winged elm samaras from Roudníky correspond in small size and basal position of the large nutlet with fruits accompanying the above foliage also at Kundratice (Kvaček & Walther 1998) and Bechlejovice (Kvaček & Walther 2004). The specimens are not well preserved and identification is partly equivocal (Fig. 5V). This fruit material is the first record from the Eocene of this region.

### Genus *Zelkova* Spach

#### *Zelkova zelkovifolia* (Unger) Bůžek & Kotlaba

Figure 6A, B

- 1963 *Zelkova zelkovifolia* (Unger) Bůžek & Kotlaba *in* Kotlaba, p. 59, pl. 3, figs 7, 8.  
2009 *Zelkova zelkovifolia* (Unger) Bůžek & Kotlaba; Akhmetiev *et al.*, p. 95, pl. 9, fig. 14.

**Material.** – Leaves, drill-cores RU 43, depth 37–38 m (NM G 8800), RU 44, depth 18 m (NM G 8768b), RU 48, depth 52 m (NM G 8773 – RU 48-14.), RU 60, depth 28–28.5 m (NM G 9424b, G 9435), outcrop (ZD RUP 8, 170).

**Description.** – Coarsely simple dentate leaf impressions at hand represent typical large specimens of *Zelkova* as known from the lower position of mature foliage shoots of extant species. Smaller morphotypes conforming to fruiting branches are rare in the Roudníky flora. The record of Roudníky is the oldest so far known in Europe. It



is most comparable with that from Bechlejovice (Kvaček & Walther 2004). *Zelkova* is quite rare elsewhere in the Oligocene of Central Europe (Kvaček & Walther 1998).

Family Malvaceae

### *Tilia* L.

#### *Tilia brassicoides* (Saporta) Kvaček & Walther

Figure 3Z

2004 *Tilia brassicoides* (Saporta) Kvaček & Walther, p. 40, pl. 21, figs 4–7, text-fig. 11.11.

**Material.** – A single bract, outcrop (ZD RUP 133).

**Description.** – A deeply cordate entire-margined bract, with several asymmetrically disposed basal veins, matches similar fossils assigned to *Tilia brassicoides* from Bechlejovice (Kvaček & Walther 2004). The only other known record is from the French Oligocene at Manosque (Saporta 1890, as *Rumex brassicoides*). Corresponding foliage does not co-occur at Roudníky, but is well known from other sites (Bechlejovice, Suletice, Kundratice, Žichov, Seifhennersdorf – Kvaček & Walther 2004).

### Genus *Craigia* W.W. Smith & W.E. Evans

#### *Craigia bronnii* (Unger) Kvaček, Bůžek & Manchester

Figure 6C, D

1991 *Craigia bronnii* (Unger) Kvaček, Bůžek & Manchester, p. 522.

2009 *Craigia bronnii* (Unger) Kvaček, Bůžek & Manchester; Akhmetiev et al., p. 95, pl. 9, fig. 7.

**Material.** – Capsule valves, drill-cores RU 48, depth 50 m (NM G 8764b, c), RU 60, depth 60 m (NM G 9413b, G 9414d, G 9419a, b, G 9420b, d, G 9437a, b), outcrop (ZD RUP 29, 30, 31, 420).

**Description.** – Several impressions of rounded and broadly oval capsule valves of *Craigia* fruits with characteristic venation radiating from the medial fusiform locule are represented in the studied outcrop and core material by well preserved specimens. These valves, like at Bechlejovice (Kvaček & Walther 2004), are usually smaller than those from the Miocene populations (Kvaček 2004b). This species has not been identified so far from the Eocene in central Europe.

### Genus *Dombeyopsis* Unger

#### *Dombeyopsis lobata* Unger

Figure 6E

1850 *Dombeyopsis lobata* Unger, p. 447.

**Material.** – Leaf impressions, outcrop (ZD RUP 29, 30).

**Description.** – As in other occurrences of this plant, also at Roudníky, trilobate entire-margined foliage of the *Dombeyopsis lobata* type accompanies the above described *Craigia bronnii* fruit remains and obviously belongs to the same plant. The fruits are smaller than in the Miocene populations (e.g., the Bílina Mine – Kvaček 2004b) and match the records at Bechlejovice (Kvaček & Walther 2004).

Family Anacardiaceae

### Genus *Toxicodendron* Mill.

#### *Toxicodendron herthae* (Unger) Kvaček & Walther

Figure 6F

1998 *Toxicodendron herthae* (Unger) Kvaček & Walther, p. 27, pl. 15, figs 3–8, text-fig. 13.16.

**Material.** – Leaflet, outcrop (ZD RUP 126).

**Description.** – The single simple bluntly serrate leaflet conforms with the ordinary morphotypes of this species as known from the early Miocene and Oligocene sites (see Kvaček & Walther 1998), which are quite variable according to the position in compound leaves. Records older than early Oligocene are not known so far.

Family Sapindaceae

### Genus *Acer* L.

#### *Acer angustilobum* Heer

Figure 6G, H

1859 *Acer angustilobum* Heer, p. 57, pl. 117, fig. 25a, pl. 118, figs 4–9.

2009 *Acer angustilobum* Heer; Akhmetiev et al., p. 95, pl. 9, fig. 2.

**Material.** – Leaves, drill-cores RU 44, depth 16 m (NM G 8791 – RU 44-12), RU 48, depth 51 m (NM G 9774, RU 48-9), outcrop (ZD RUP 44).



**Description.** – Maple leaves assigned to *Acer angustilobum* Heer morphologically match abundant records of this species from Kundratice (Kvaček & Walther 1998). In two cases, the epidermal structure has been obtained showing dense papillae on the abaxial side.

***Acer palaeosaccharium* Stur**

Figure 6I

1867 *Acer palaeosaccharinum* Stur, p. 177, pl. 5, fig. 8.

**Material.** – Leaf, drill-core 48, depth 51 m (NM G 8774a – RU 48-9), outcrop (ZD RUP 62).

**Description.** – Incomplete foliage at hand fits into the variation of *Acer palaeosaccharinum*, as known from the flora of Bechlejovice (Kvaček & Walther 2004).

***Acer* cf. *tricuspidatum* Bronn**

Figure 6J

? 1838 *Acer tricuspidatum* Bronn, p. 865, pl. 35, figs 10a, b.

**Material.** – Leaf impressions, outcrop (ZD RUP 34, 53).

**Description.** – Some impressions of maple foliage recall in broader and irregularly dentate lobes *Acer tricuspidatum* Bronn, as known from the monograph by Walther (1972). Epidermal structure to support this suggestion has not been obtained from the impression material. Similar morphotypes were often recorded in the Oligocene of North Bohemia and Saxony (Walther & Kvaček 2007).

***Acer* sp.**

Figure 6K–M

**Material.** – Fruits, flower, drill-cores RU 44, depth 16 m (NM G 8791 – RU 44-12), RU 45a, depth 44–45 m (NM

G 9443a, b), RU 60, depth 30.6–31.4 m (NM G 9429 – RU 60-19), outcrop (ZD RUP 53, 54).

**Description.** – No attempt is made to assign the reproductive material to the above described leaf taxa.

Family Cornaceae

**Genus *Nyssa* Gronov. ex L.**

***Nyssa disseminata* (Ludwig) Kirchheimer**

Figure 6N

1937 *Nyssa disseminata* (Ludwig) Kirchheimer, p. 916.

**Material.** – Endocarp compression, outcrop (ZD RUP 23).

**Description.** – The single available endocarp fits within the variation of *Nyssa disseminata* known from Seifhensdorf (Mai 1963). Such fossils are rare in the Palaeogene of North Bohemia (e.g., at Markvartice – Bůžek *et al.* 1976).

Family Ebenaceae

**Genus *Diospyros* L.**

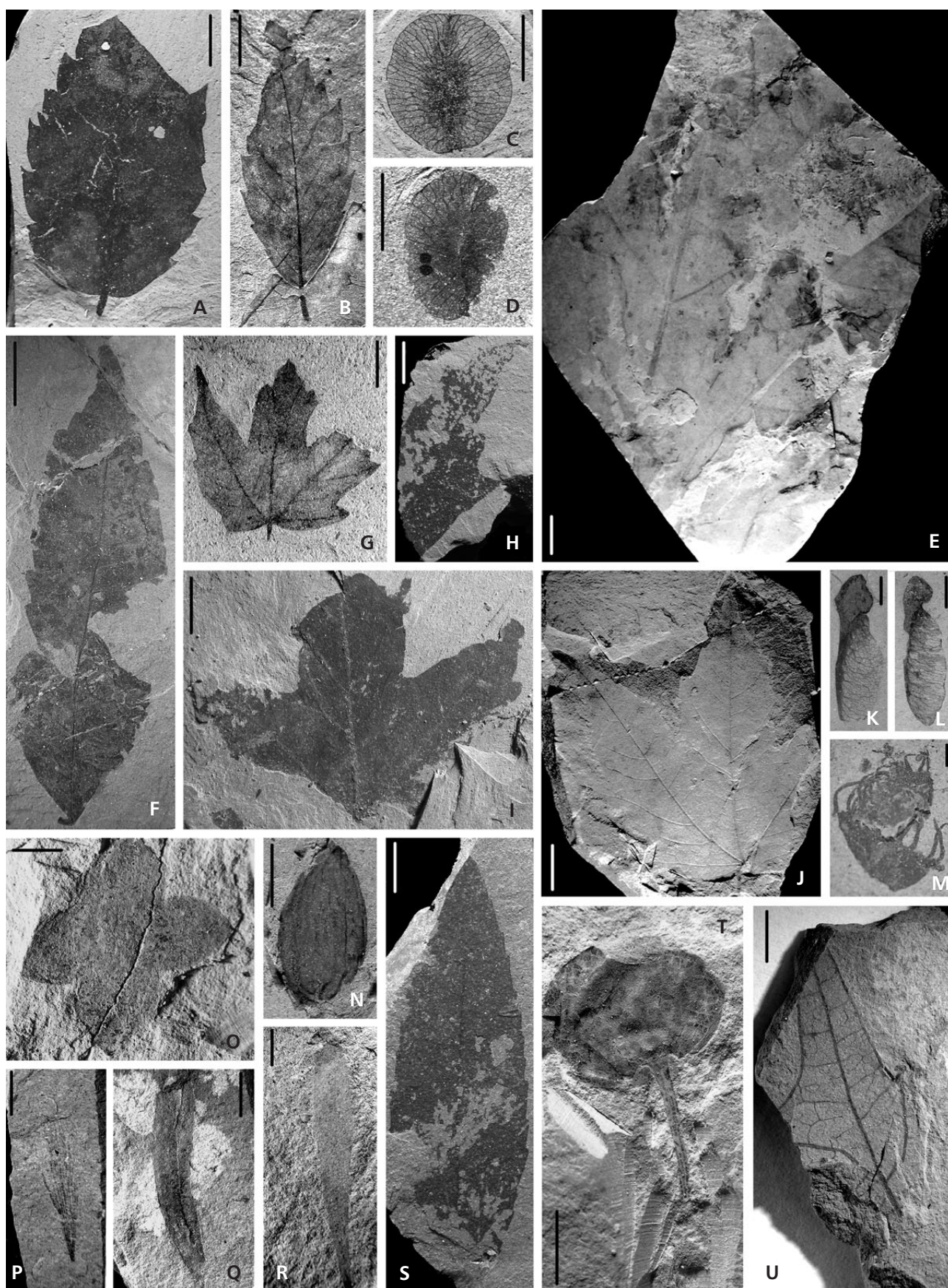
***Diospyros* sp.**

Figure 6O

**Material.** – Calyx, outcrop (ZD RUP 77a).

**Description.** – The single calyx impression referable to *Diospyros* does not differ from other findings of this sort from the Oligocene identified as *Diospyros brachysepala* A. Braun (see Walther & Kvaček 2007). However, it differs pronouncedly from smaller morphotypes abundant in the late Eocene diatomite of Kučlín and assigned with hesitation to *Diospyros* (Kvaček & Teodoridis 2011, as *Diospyros* ? *microcalyx*).

**Figure 6.** Locality Roudníky. • A – *Zelkova zelkovifolia* (Unger) Bůžek & Kotlaba, petiolate leaf impression, ZD RUP 8. • B – *Zelkova zelkovifolia* (Unger) Bůžek & Kotlaba, slender petiolate leaf, ZD RUP 17a. • C – *Craigia bronnii* (Unger) Kvaček, Bůžek & Manchester, capsule valve, ZD RUP 30. • D – *Craigia bronnii* (Unger) Kvaček, Bůžek & Manchester, capsule valve, ZD RUP 31. • E – *Dombeyopsis lobata* Unger, incomplete leaf base, ZD RUP 57a. • F – *Toxicodendron herthae* (Unger) Kvaček & Walther, leaflet, ZD RUP 126. • G – *Acer angustilobum* Heer, leaf impression, ZD RUP 44. • H – *Acer angustilobum* Heer, leaf compression, NM G 8791. • I – *Acer palaeosaccharium* Stur, leaf, NM G 8774a, RU 48-9. • J – *Acer* cf. *tricuspidatum* Bronn, leaf impression, ZD RUP 34. • K – *Acer* sp., samara, ZD RUP 53. • L – *Acer* sp., samara, ZD RUP 54. • M – *Acer* sp., flower, ZD RUP 55. • N – *Nyssa disseminata* (Ludwig) Kirchheimer, impression of fruit endocarp, ZD RUP 23. • O – *Diospyros* sp., calyx, ZD RUP 77a. • P – *Fraxinus* sp., fruit base, ZD RUP 143. • Q – *Fraxinus* sp., fruit with incomplete wing, ZD RUP 144. • R – *Fraxinus* sp., winged fruit base, ZD RUP 122. • S – *Symplocos oligocaenica* Kvaček, leaf compression with cuticle, NM G 9408a, RU 60-12. • T – *Carpolithes* sp., enigmatic fruit remain on stalk, ZD RUP 84a. • U – *Pungiphyllum cruciatum* (A. Braun) Frankenhäuser & Wilde, impression of lobed leaf fragment, ZD RUP 97. Scale bars: A, B, E–J = 10 mm; C, D, K, L, N–U = 5 mm; 13 = 1 mm.





Family Symplocaceae

**Genus *Symplocos* Jacq.**

***Symplocos oligocaenica* Kvaček**

Figures 6S, 8H, I

2004a *Symplocos oligocaenica* Kvaček, p. 17, pl. 14, figs 1, 10–12.

**Material.** – Leaf compression with epidermal anatomy, drill-core RU 60, depth 27.5–28 m (NM G 9408 – RU 60-12).

**Description.** – Fragmentary widely crenulate-toothed leaf compression is referred to *Symplocos* on account of brachyparacytic stomata in the abaxial cuticle. The reduced size of non-modified cells with almost straight anticlinal walls in comparison with stomata leads to the identification with the recently described *S. oligocaenica* Kvaček from the early Oligocene flora of Flörsheim (Kvaček 2004a). *S. volkeri* Kvaček from the same site neatly differs by still much smaller non-modified cells in comparison with stomata. *Dicotylophyllum deichmuelleri* Kvaček & Walther (1998) from the late Eocene and early Oligocene of the České středohoří Mts (Roudníky, Kundratice, Bechlejovice – see below) belongs also to this group of *Symplocos*-like foliage.

Family Oleaceae

**Genus *Fraxinus* L.**

***Fraxinus* sp.**

Figure 6P–R

**Material.** – Winged fruits, outcrop (ZD RUP 143, 149).

**Description.** – Fragmentary winged samaras with the basal seed-containing part usually aborted are recognizable in the sub-parallel venation of the wing. These coincide with

other similar records (Kundratice – Kvaček & Walther 1998, as *Fraxinus* sp.). The corresponding foliage has not been recovered at Roudníky yet.

Angiosperms fam. inc.

**Genus *Carpolithes* Sternberg**

***Carpolithes* sp.**

Figure 6T

**Material.** – Fruit impression, outcrop (ZD RUP 84a).

**Description.** – An enigmatic fruit impression on stalk is strange to us and does not show much of the internal structure. Its affinities remain open for further comments.

**Genus *Pungiphyllum* Frankenhäuser & Wilde**

***Pungiphyllum cruciatum* (A. Braun)**

**Frankenhäuser & Wilde**

Figures 6U, 7A, B

1995 *Pungiphyllum cruciatum* (A. Braun) Frankenhäuser & Wilde, p. 101.

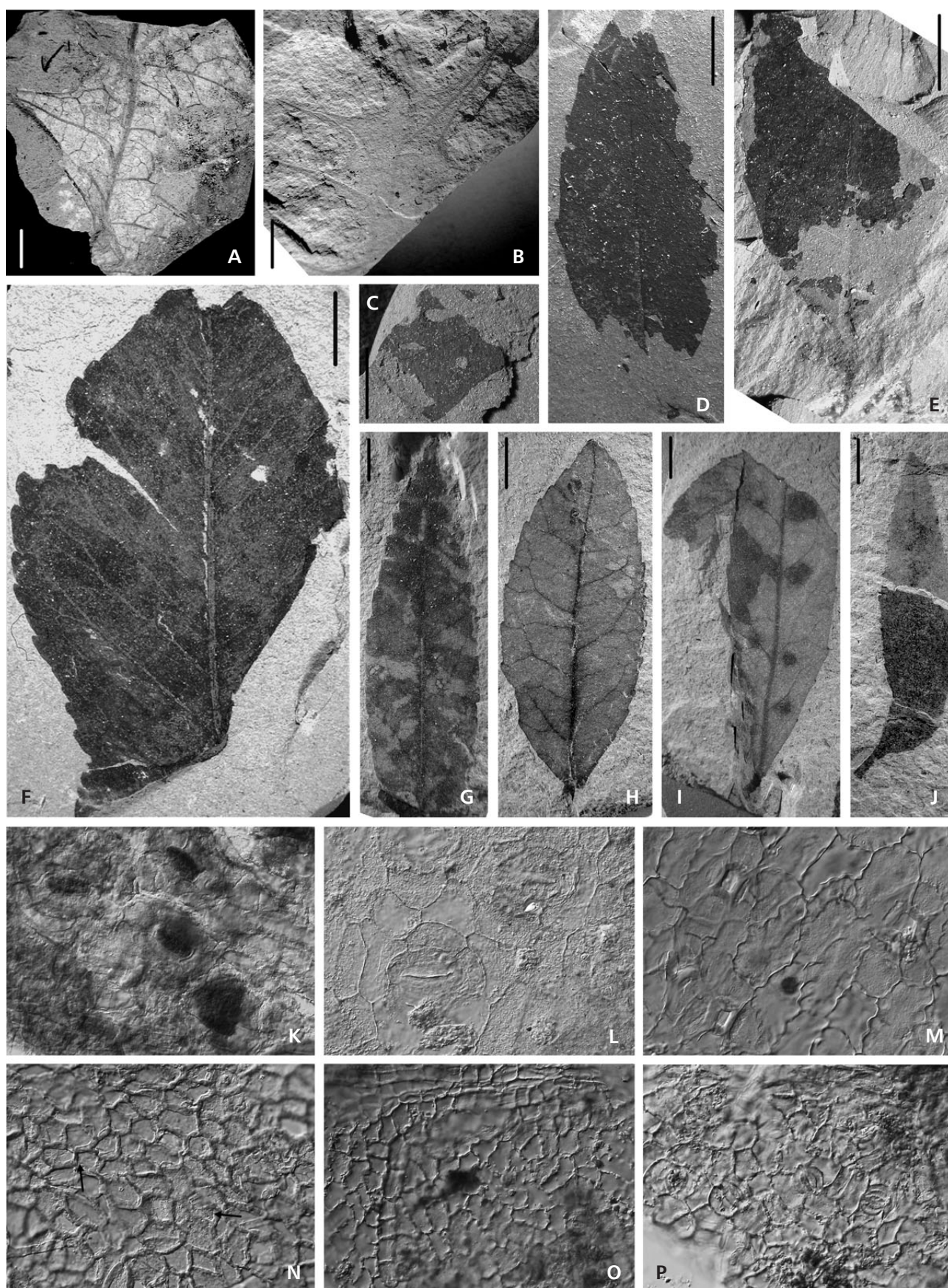
2009 *Pungiphyllum cruciatum* (A. Braun) Frankenhäuser & Wilde; Akhmetiev *et al.*, p. 95, pl. 9, fig. 19.

**Material.** – Leaves, outcrop (ZD RUP 60, 96, 97).

**Description.** – Several leaf impressions are assigned to this morphotype on account of deeply lobed lamina with spiny lobes on margin. Individual populations of this enigmatic plant vary in leaf shape from small shallow lobed forms of the middle Eocene (*Pungiphyllum waltheri* Frankenhäuser & Wilde 1995 from Messel) to shallow lobed elongate forms of the late Eocene diatomites from Kučlín [*Pungiphyllum heerii* (Sieber) Kvaček & Teodoridis, 2011] to the typically variable foliage distributed in the Oligocene to

**Figure 7.** Locality Roudníky. • A – *Pungiphyllum cruciatum* (A. Braun) Frankenhäuser & Wilde, incomplete impression of lobed leaf, ZD RUP 17a. • B – *Pungiphyllum cruciatum* (A. Braun) Frankenhäuser & Wilde, impression of leaf showing long spiny lobes, ZD RUP 96. • C – ?cf. “*Viburnum*” *atlanticum* Ettingshausen, incomplete leaf compression with cuticle, NM G 9433b, RU 60-14. • D – cf. “*Viburnum*” *atlanticum* Ettingshausen, leaf compression, NM G 9439a, RU 45. • E – cf. “*Viburnum*” *atlanticum* Ettingshausen, fragmentary leaf compression, NM RU 48-6. • F – cf. “*Viburnum*” *atlanticum* Ettingshausen, leaf impression showing details of venation, ZD RUP 47. • G – *Dicotylophyllum deichmuelleri* Kvaček & Walther, leaf impression, ZD RUP 115. • H – *Dicotylophyllum deichmuelleri* Kvaček & Walther, leaf impression, ZD RUP 123. • I – *Dicotylophyllum deichmuelleri* Kvaček & Walther, leaf impression, ZD RUP 139. • J – *Dicotylophyllum deichmuelleri* Kvaček & Walther, leaf impression, ZD RUP 116. • K – *Juniperus pauli* Kvaček, cuticle showing monocyclic stomata, NM G8783b, RU 44-11. • L – *Taxodium dubium* (Sternberg) Heer, cuticle showing rows of stomata, NM G8793e, RU 48-11B. • M – *Tetraclinis salicornioides* (Unger) Kvaček, cuticle with scattered stomatal pits, NM G 9420b, RU 60. • N – *Laurophyllum acutimontanum* Mai, abaxial cuticle with sunken amphicycloparacytic stomata, NM G8808c. • O – *Laurophyllum pseudoprinceps* Weyland & Kilpper, adaxial cuticle, NM G8762b, RU 43-1. • P – *Laurophyllum pseudoprinceps* Weyland & Kilpper, abaxial cuticle with brachyparacytic stomata, NM G8762c, RU 43.1. Scale bars: A, B = 10 mm; C–J = 5 mm. Magnification: K–P × 300.





Miocene of Central Europe (Kvaček & Walther 1981, as “*Quercus*” *cruciata*).

**cf. “*Viburnum*” *atlanticum* Ettingshausen**

Figures 5Q, 7C–F, 8J, K

? 1868 *Viburnum atlanticum* Ettingshausen, p. 209, pl. 36, fig. 2.

**Material.** – Fragmentary compressions – impressions, drill-cores RU 44, depth 18 m (NM G 8768a, G 9433 – RU 44-5), RU 45a, depth 44–45 m (NM G 9439a, b, G 9444 b, d – RU 45a-1), RU 48, depth 52 m (RU 48-6), ? RU 60, depth 27.5–28 m (G 9433b – RU 60-14), outcrop (ZD RUP 47).

**Description.** – The leaf fragments assigned to this heterogeneous morphotype are typically widely bluntly toothed, with steep, dense semicraspedodromous venation, partly with preserved epidermal anatomy: thin cuticles showing adaxially polygonal cells with slightly wavy anticlines, abaxially with hardly discernible stomata of anomocytic type. The direct identification with the not yet revised type material from Žichov without epidermal anatomy is equivocal, although in the general form the fragments studied are similar. Bůžek (1971) introduced a broad concept of *V. atlanticum* on the basis of the Miocene material, but later Bůžek *et al.* (1976) added some other specimens from the Oligocene of Markvartice that clearly differ. None of the so far described records can be safely compared with the material from Roudníky.

**Genus *Dicotylophyllum* Saporta**

***Dicotylophyllum deichmuelleri* Kvaček & Walther**

Figures 7G–J, 8L

1998 *Dicotylophyllum deichmuelleri* Kvaček & Walther, p. 14, pl. 6, figs 7–12, text-figs 13.7, 13.30.

**Material.** – Fragmentary leaf compression, drill-core RU 48, depth 52 m (NM G 8790 – RU 48-4), impressions,

outcrop (ZD RUP 115, 116, 121, 123, 137, 138, 139, 140, 141, 142).

**Description.** – Petiolate, ovate leaves with widely dentate margin have been assigned to this element on account of a single compression with cuticle structure showing apparent paracytic stomata. Other impressions correspond in morphology with the records from Bechlejovice (Kvaček & Walther 2004) assigned to the same taxon. The type locality Kundratice (Kvaček & Walther 1998) yielded better preserved material with epidermal anatomy. This leaf element is obviously evergreen and likely belongs to *Symplocos*. It differs only in details of epidermal structure (larger cells with wavy anticlinal walls vs isometrical straight-walled cells smaller than stomata) from *Symplocos oligocaenica* Kvaček mentioned above.

Animalia

Pisces

Order Esociformes Nelson, 1994

Family Umbridae Bonaparte, 1846

**Genus *Umbra* Kramer, 1777**

***Umbra* sp.**

Figure 10A–D

**Material.** – NM Pc 02893–Pc 02896 and unnumbered specimens, cores RU 40/76 and RU 60/94; Roudníky.

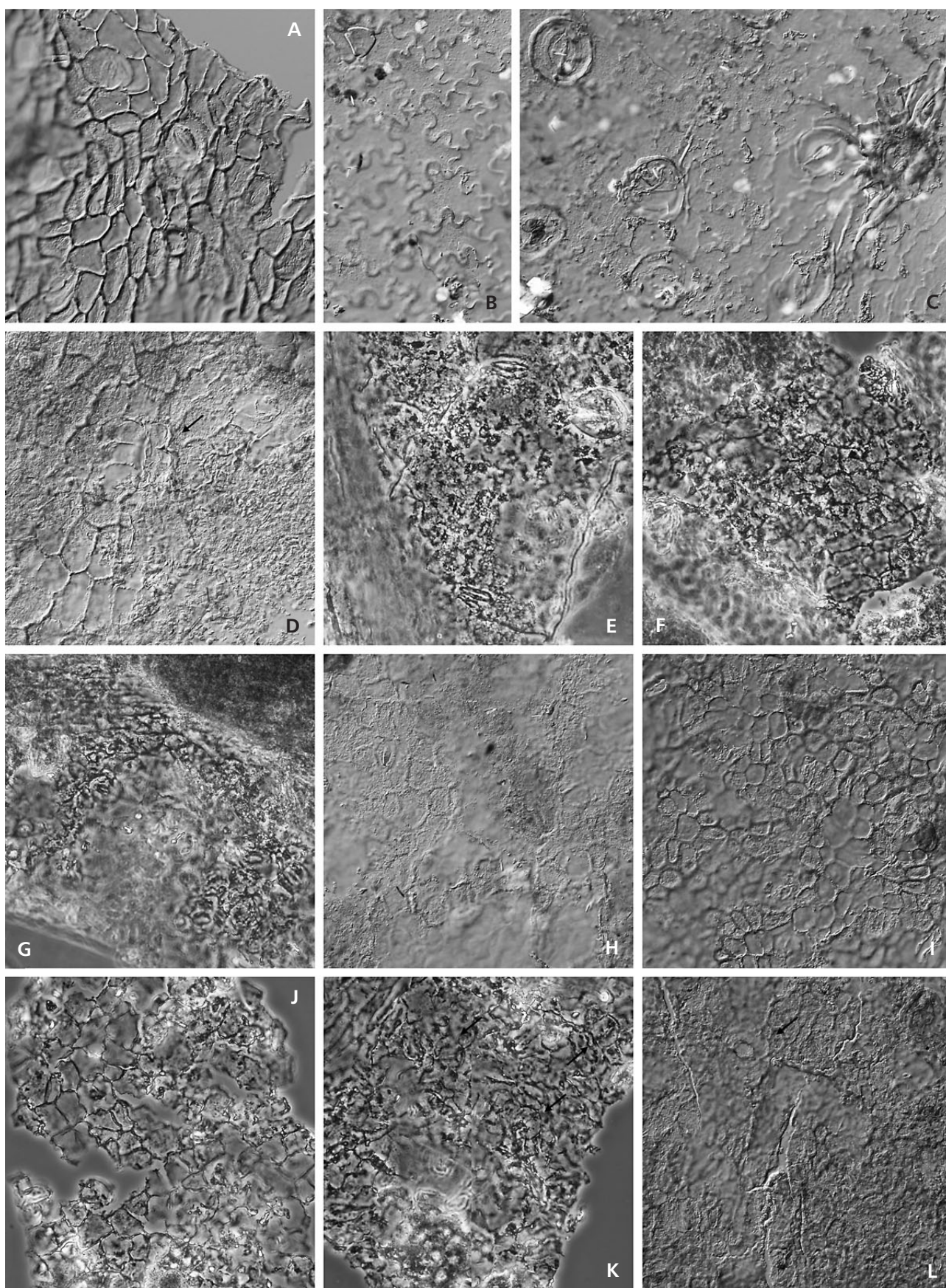
**Description.** – The scales are preserved as rounded imprints on the surface of the sediment. The nucleus is antero-posteriorly elongated. The circuli are arranged round the nucleus; they are joining together at the angle of about 50° in the posterior part of the scale. Radii are not presented.

**Remarks.** – The specimens from Roudníky were described by Gaudant in Bellon *et al.* (1998). The specific features of the umbrid scales are rather limited and it is quite problematic to distinguish umbrid and palaeoesocid scales, so the determination is tentative. Remains of the genus *Umbra* were found in the Oligocene deposits of the sites of Bechlejovice and Odeř (Obrhelová 1978), early Miocene deposits

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**Figure 8.** Locality Roudníky. • A – *Laurophyllum pseudoprinceps* Weyland & Kilpper, abaxial cuticle near midrib with brachyparacytic stomata, NM G8809b. • B – *Platanus neptuni* (Ettingshausen) Bůžek, Holý & Kvaček, adaxial cuticle with undulate anticlines, NM G 9403b, RU 60-9. • C – *Platanus neptuni* (Ettingshausen) Bůžek, Holý & Kvaček, abaxial cuticle with stomata and a compound trichome base, NM G9403b, RU 60-9. • D – *Alnus gaudinii* (Heer) E. Knobloch & Kvaček, abaxial cuticle with scattered stomata, NM G 8812c, RU 60-2. • E – *Rosa lignitum* Heer, abaxial cuticle with scattered stomata, NM G9424e, RU 60-18A. • F – *Pyracantha kraeuselii* Walther in Mai & Walther, adaxial cuticle, NM G 9432c, RU 60-16. • G – *Pyracantha kraeuselii* Walther in Mai & Walther, abaxial cuticle, NM G 9432c, RU 60-16. • H – *Symplocos oligocaenica* Kvaček, adaxial cuticle, NM G9408c, RU 60-12. • I – *Symplocos oligocaenica* Kvaček, adaxial cuticle, NM G 9408c, RU 60-12. • J – cf. “*Viburnum*” *atlanticum* Ettingshausen, abaxial cuticle, NM G 9444d, RU45a-1B. • K – cf. “*Viburnum*” *atlanticum* Ettingshausen, adaxial cuticle, NM G 9444d, RU45a-1B. • L – cf. *Dicotylophyllum deichmuelleri* Kvaček & Walther, abaxial cuticle with paracytic stoma, NM G8790c, RU48-4. Magnification: A–L × 300.







of the Mariana mine near Skyřice, the Merkur and Nástup mines (Obrhelová 1990) and from the Middle Miocene of Öhningen in Germany (Gaudant 2012). The species described as *Umbra weileri* (Martini 1965) from the Lower Oligocene of Sieblos was revised and moved to the genus *Palaeoesox* by Gaudant (2012).

Order Amiiformes Hay, 1929

Family Amiidae Bonaparte, 1832

### Genus *Cyclurus* Agassiz, 1844

#### *Cyclurus* sp.

Figures 10E–M, 11A–Q

**Material.** – NM Pc 02897, Pc 02898 and unnumbered specimens, drill-cores RU 43, RU 43/31 and RU 60 (depth 94 m), Roudníky, outcrop: disarticulated skull bones ZD RU 165, 166 (part and counterpart) ZD RU 167, 168 (part and counterpart); dentary ZD RU 152; prearticular ZD RU 161–164; parasphenoideum RU 153; gulare mediale ZD RU 154–158; ceratohyal anterior ZD RU 159, 160 (part and counterpart); articulated caudal part of the body ZD RU 169, 170 (part and counterpart); isolated scales ZD RU 171–186; Větruše collection: unnumbered dentary (ZD). Větruše collection: isolated scales: RMT PA1247, PA1248 (part and counterpart), RMT PA1478, MT PA1479, RMT PA1485, RMT PA1486; teeth: RMT PA1487, RMT PA1488; isolated vertebrae: RMT PA1489/1, RMT PA1489/2 (part and counterpart), RMT PA1490.

**Description.** – The specimens from the Větruše Hill comprise isolated scales, teeth, vertebral centra and jaw bone (Fig. 10E–K). The specimens from the Roudníky locality are represented by two groups: 1) the specimens from drill-cores (Fig. 10L, M) are typical isolated amioid scales (*sensu* Schultze 1966) that were described and figured in Bellon *et al.* (1998). 2) The specimens from the outcrop are represented mainly by isolated scales and by their

groups, isolated bones, and partly disarticulated skeletons. They are classified to the genus *Cyclurus* on the basis of the following features (which are typical for the genus according to the Grande & Bemis 1998 and Gaudant 2008): blunt-like coronoid teeth at the lower jaw (specimen ZD RU 165, Fig. 11B: the dark arrows show coronoid teeth; the white arrow shows one of the dentary tooth); the shape of the gulare mediale is subtriangular and truncated posteriorly (Fig. 11D); the heart-like shape of the tooth path on the ventral surface of the parasphenoideum (Fig. 11C). Other specimens are not taxonomically significant. The scales represent majority of the collected specimens (see selected specimens in the Fig. 11G–Q). They are typical amioid scales (*sensu* Schultze 1966), their morphology is same as of the specimens from the Kučlín locality (see Přikryl 2011). In some specimens it is possible to recognize annuli (*e.g.*, ZD RU 172, see arrows in the Fig. 11I).

**Remarks.** – Remains of the genus *Cyclurus* were found in the Eocene of the Kučlín diatomite (Grande & Bemis 1998, Gaudant 2008, Přikryl 2011) and the limestone of Kostomlaty (Obrhelová & Obrhel 1987, Böhme 2007) as well as in the Eocene of Germany (localities Geiseltal and Messel – Gaudant 1988). Other specimens of the genus *Cyclurus* are mentioned from the Late Cretaceous and Palaeocene of Canada, Palaeocene of Mongolia, upper Palaeocene and Eocene of France, Eocene deposits of the USA and Kazakhstan and exceptionally in the lowermost Oligocene of Germany at Sieblos (for details see Grande & Bemis 1998).

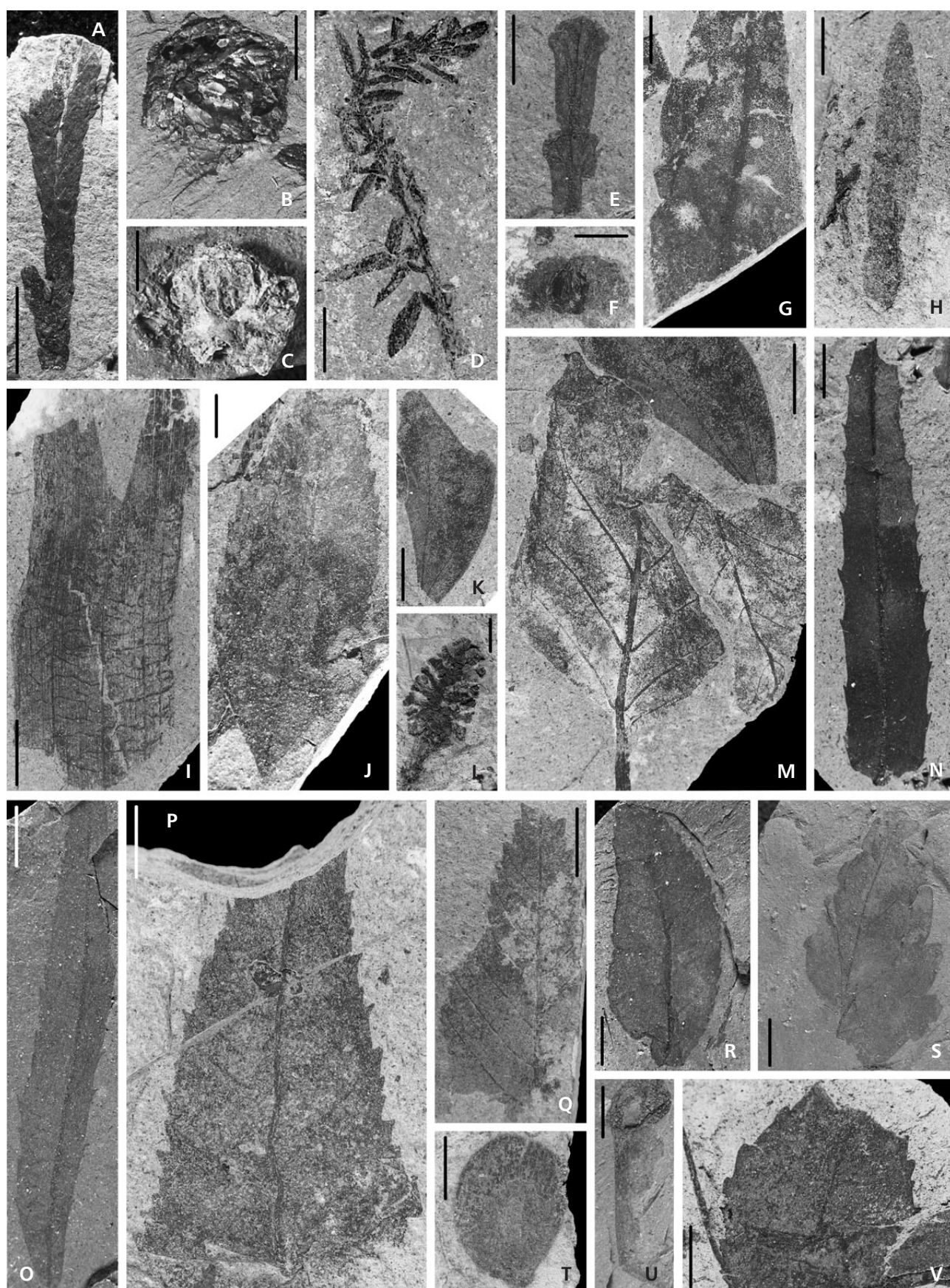
Besides the fish remains described above also fossils of frogs (Palaeobatrachidae) are associated at the locality of Větruše. They are not treated in detail in this paper. The palaeobatrachids were restricted to the European region (for details see Wuttke *et al.* 2012).

### Palaeofloristic signals of the Roudníky flora

The above described flora of Roudníky connected with the amiids fish assemblage and radiometrically dated to late

**Figure 9.** Locality Větruše. • A – *Juniperus pauli* Kvaček, leafy twig, RMT PA 1202/2. • B – *Juniperus pauli* Kvaček, seed cone, RMT PA 1201. • C – *Juniperus pauli* Kvaček, seed cone, RMT PA 1495/1. • D – *Taxodium dubium* (Sternberg) Heer, leafy twig, RMT PA 1204/1. • E – *Tetraclinis salicornioides* (Unger) Kvaček, leafy segment, RMT PA 1220. • F – *Tetraclinis salicornioides* (Unger) Kvaček, seed, RMT PA 1223. • G – *Laurophyllum* cf. *acutimontanum* Mai, fragmentary leaf, RMT PA 1226. • H – *Liriodendron* sp., winged samara, RMT PA 1222/1. • I – Monocotyledonae gen. indet., leaf fragment, RMT PA 1209. • J – *Platanus neptuni* (Ettingshausen) Bůžek, Holý & Kvaček, leaf, RMT PA 1224/1. • K – *Daphnogene cinnamomifolia* (Brongniart) Unger vel cf. *Matudaea menzelii* Walther, leaf fragment, RMT PA 1208. • L – *Alnus kefersteinii* (Göppert) Unger, female infructescence on a fragmentary stalk, RMT PA 1215/1. • M – *Ostrya atlantidis* Unger, incomplete leaf compression, RMT PA 1208. • N – *Engelhardia orsbergensis* (Wessel & Weber) Jähnichen, Mai & Walther, incomplete leaflet, RMT PA 1205. • O – *Engelhardia orsbergensis* (Wessel & Weber) Jähnichen, Mai & Walther, incomplete leaflet, RMT PA 1206. • P – *Carya fragiliformis* (Sternberg) Kvaček & Walther, fragmentary leaflet, RMT PA 1225/1. • Q – *Ulmus fischeri* Heer, leaf fragment, RMT PA 1214. • R – *Rosa lignitum* Heer, leaflet, RMT PA 1211. • S – *Zelkova zelkovifolia* (Unger) Bůžek & Kotlaba, incomplete leaf, RMT PA 1219. • T – *Craigia bronni* (Unger) Kvaček, Bůžek & Manchester, capsule valve, RMT PA 1221/1. • U – *Acer* sp., samara, RMT PA 1239. • V – *Acer* sp., incomplete leaf, RMT PA 1210/1. Scale bars: A–V = 5 mm.







Eocene (Bellon *et al.* 1998) is dominated by broad-leaved deciduous (“modern Arcto-Tertiary”) elements, *e.g.*, *Liriodendron*, *Ostrya*, *Alnus gaudinii*, *Betula* sp., *Carpinus medimontana*, *Tilia*, *Carya*, *Cyclocarya*, *Cercidiphyllum*, *Acer* sp., Ulmaceae (*Ulmus*, *Zelkova*) and Rosaceae (*Rosa*, *Crataegus*, *Pyracantha*). Thermophilic elements are also present, including Lauraceae (*Laurophyllum acutimontatum*, *L. pseudoprinceps*), *Symplocos*, *Nyssa*, Fabaceae (*Mimosites*, *Leguminosites*, *Gleditsia*) and *Platanus neptuni* with post-Grande Coupure immigrants of conifers (*Torreya*, *Cephalotaxus*) and *Craigia/Dombeyopsis*. In view of its dating to late Eocene, this assemblage deviates from the others of this time interval in central Europe. None of the extinct subtropical plant markers characteristic of the European Eocene (*Doliosstrobos* and *Chamaecyparites* of the conifers, extinct malvacean taxa of the group of *Byttneriopsis*, the juglandaceous *Hooleya*, the araceous *Nitophyllites*) have been found here. Only a few plants present at Roudníky cross the Eocene/Oligocene boundary elsewhere (*e.g.*, *Taxodium dubium*, *Tetraclinis salicornioides*, *Ziziphus ziziphoides*, *Pungiphyllum*). *Juniperus pauli* is a noteworthy endemic conifer not known outside North Bohemia. The associated pollen spectra corroborate the deciduous character of the vegetation. They are rich in cupressoid and carpinoid pollen, lack the early Oligocene marker *Boehlenipollis* but include *Intratipollenites microreticulatus* Mai known mainly from the Eocene (Konzalová 1989, 2003). Most Arcto-Tertiary elements listed above are shared with the early Oligocene floras of central Europe, but do not appear in the Eocene. On the other hand, the early Oligocene (Kiscellian) floras of Budapest-Csillaghegy, Eger-Kiseged (Hungary, Hably 1985) contain several elements such as *Doliosstrobos*, *Raskya*, *Acrostichum* characteristic of the late Eocene floras of the Bohemian Massif.

### Floristic comparison with the flora of the Větruše Hill and other late Eocene and early Oligocene sites of Central Europe

A florule most similar to Roudníky, which is connected with the amiids, has been recovered in the diatomite of the Větruše Hill at Ústí/L. (Bůžek 1967, 1991; Radoň 2001). Most of the recovered plant elements (Fig. 9A–J, L, M, P–V) are shared with Roudníky, particularly *Juniperis pauli* besides *Taxodium*, *Tetraclinis*, *Platanus neptuni*, *Liriodendron*, *Craigia*, *Zelkova*, *Alnus* and *Ostrya*. *Engelhardia* is present at Větruše as macrofossils and at Roudníky as the pollen (Konzalová 1989, 2003). This plant assemblage is too poor for a more detailed statistical evaluation. Moreover, the adjacent basalts are not radiometrically dated.

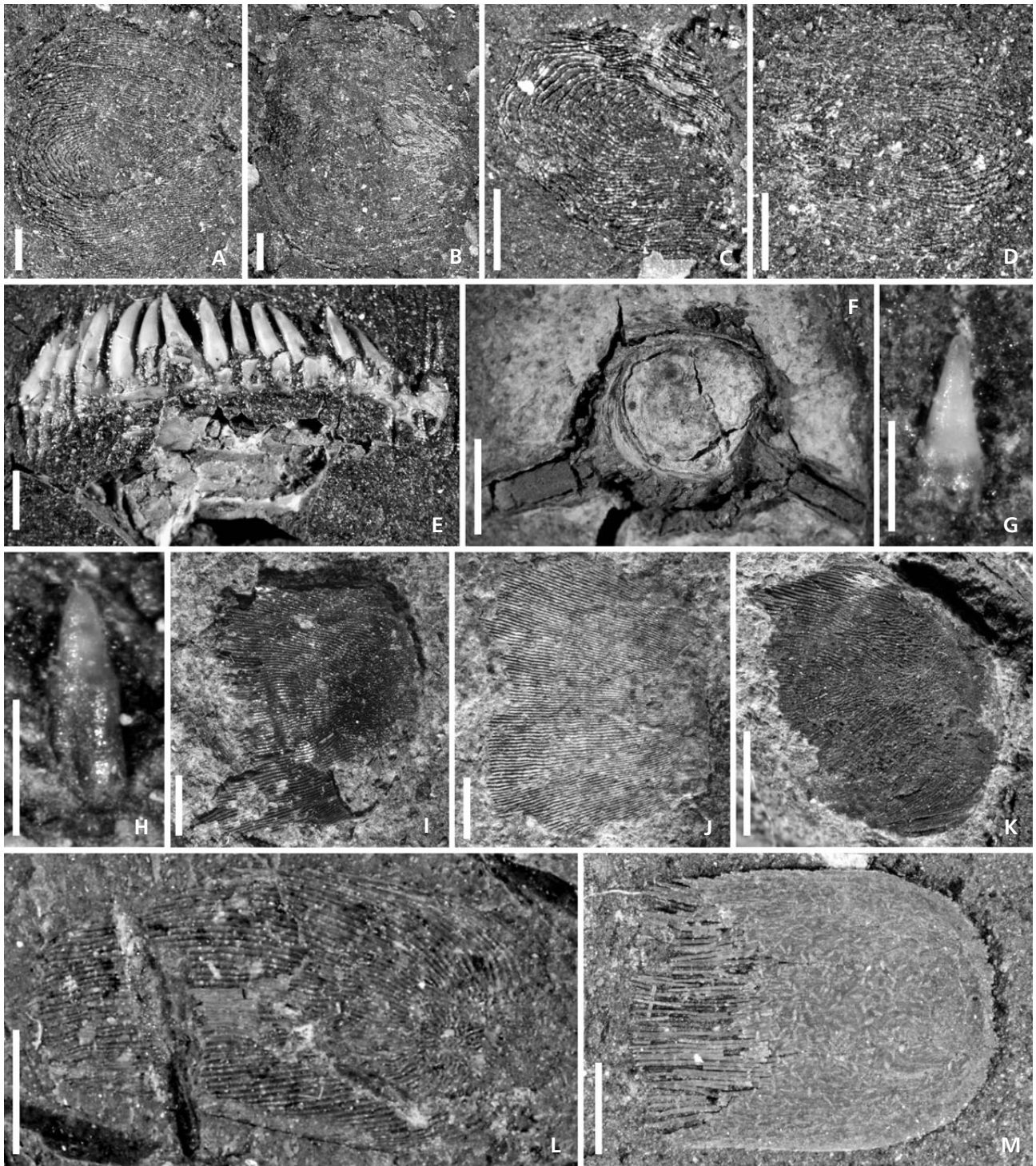
The late Eocene flora of Kučlín (Kvaček 2002b, Kvaček & Teodoridis 2011), which is stratigraphically and

geographically close to Roudníky, is strikingly different, although only *ca* 2 million years older. The Kučlín assemblage does not show many affinities to late Eocene floras of the Staré Sedlo Formation (Knobloch *et al.* 1996, Teodoridis *et al.* 2012) and the Weissester Basin (*e.g.*, Haselbach, Kayna-Süd, Klaus, Knau, Phönix-Nord and Profen – Mai & Walther 1985, 2000), probably due to difference in facies – volcanic assemblage of Kučlín vs. basinal assemblages of Staré Sedlo and the Weissester Basin. These basinal floras are characterized by several phytostratigraphical markers such as *Steinhauera subglobosa*, *Rhodomyrtophyllum reticulosum*, *Gordonia saxonica* and *Laurophyllum syncarpifolium* associated with the predominant *Eotrigonobalanus*, and *Daphnogene* allowing the correlation of these floras to the late Eocene floristic assemblage of Hordle-Zeitz *sensu* Mai (1995). However, *Doliosstrobos* is more often represented in late Eocene floras of Germany contrary to the Staré Sedlo Formation. The well diversified “volcanic” flora of Kučlín, according to the recent revision, includes many important Eocene, mostly extinct angiosperms, such as *Raskya*, *Hooleya*, and other, partly endemic or enigmatic elements, *e.g.*, *Nitophyllites*, *Trigonobalanopsis*, *Castaneophyllum*, *Byttneriopsis* and *Ternstroemites* (Kvaček & Teodoridis 2011, Teodoridis *et al.* 2012). Almost none of these plants are shared with the Roudníky assemblage.

The flora of Böhlen (Mai & Walther 2000, outcrops 1 and 2 only) is based mainly on the carpological material and is interpreted as the youngest flora within the late Eocene sediments of the Weissester Basin (Mosbrugger *et al.* 2005, level G\*). The flora is hardly comparable with predominantly leaf floras of the Palaeogene of North Bohemia because of absence of phytostratigraphical markers. The flora of Böhlen shows a mixture of coniferous and broad-leaved evergreen (BLE) elements (*Chamaecyparites*, *Tetraclinis*, *Phoebe*, *Visnea*, and *Zenobia*), of which only *Tetraclinis* is shared with Roudníky.

The above described phenomena of high abundance of the Arcto-Tertiary (broad-leaved deciduous) elements and the lack of *Doliosstrobos* in the Roudníky flora show distinct linkage to the early Oligocene floras of the Doupov volcanic (Valeč, Dvorce, Vrbice) and České středohoří Mts complexes (Bechlejovice, Kunderatice) rather than to the mentioned late Eocene floras of the Staré Sedlo Formation, Kučlín and the Weissester Basin. Bůžek *et al.* (1968, 1987) reported from the lowermost limestone deposits of Valeč belonging to the Doupov volcanic complex a rare occurrence of *Doliosstrobos*, which is an important marker related to the Eocene/Oligocene boundary and to the floristic assemblage of Bembridge *sensu* Mai (1995). Thin-bedded limestone and volcano-clastic rocks from the localities Valeč, Dvorce and Vrbice, which belong to higher parts of the Doupov complex, yielded floras showing a distinct early Oligocene character proved by occurrence of *Alnus*





**Figure 10.** A – *Umbra* sp., scale, Roudníky, NM Pc02893, RU 60/94: 30.6–31.4 m. • B – *Umbra* sp., scale, Roudníky, NM Pc02894, RU 40/76: 14.1–14.4 m. • C – *Umbra* sp., scale, Roudníky, NM Pc02895, RU 40/76: 14.1–14.4 m. • D – *Umbra* sp., scale, Roudníky, NM Pc02896, RU 60/94: 30.6–31.4 m. • E – *Cyclurus* sp., jaw, Větruše, ZD unnumbered. • F – *Cyclurus* sp., vertebral centra, Větruše, RMT PA1490. • G – *Cyclurus* sp., isolated tooth, Větruše, RMT PA1487. • H – *Cyclurus* sp., isolated tooth, Větruše, RMT PA1488. • I – *Cyclurus* sp., scale, Větruše, RMT PA1486. • J – *Cyclurus* sp., scale, Větruše, RMT PA1248. • K – *Cyclurus* sp., scale, Větruše, RMT PA1247. • L – *Cyclurus* sp., scale, Roudníky, NM Pc02897, RU 43/31: 36–37 m. • M – *Cyclurus* sp., scale, Roudníky, NM Pc02898, RU 60/94: 41.5–41.7 m. Scale bars: E, F, K = 2 mm; G, H = 0.5 mm; A–D, I, J, L, M = 1 mm.

*rostaniana* (cf. *nostratum sensu* Bůžek *et al.* 1987), *Zelkova*, *Mahonia* and *Ulmus* (Bůžek *et al.* 1990). The most diversified early Oligocene floras are known from the magmatic complex of the České středohoří Mts and Saxony, such as the floras of Bechlejovice (Kvaček & Walther 2004), Kundratice (Kvaček & Walther 1998), Knížecí-Hrazený (Knobloch 1961), Suletice-Berand (Kvaček & Walther 1995), Holý Kluk (Radoň *et al.* 2006), Markvartice-Veselíčko (Bůžek *et al.* 1976), and Seifhennersdorf (Walther & Kvaček 2007). These floras lack *Doliosrobis*, but include other coniferous elements, such as *Torreya bilinica*, *Cephalotaxus parvifolia*, *Calocedrus sulticensis*, in the combination with thermophilic broad-leaved elements (*Platanus neptuni*, “*Acer*” *sotzkianum*, *Sloanea*, *Palaeohosiea*, *Engelhardia*, *Laurophyllum acutimontanum* *etc.*) as well as newly appearing Arcto-Tertiary elements, e.g., *Alnus gaudinii*, *Acer palaeosaccharinum*, *Acer angustilobum*, *Cercidiphyllum*, *Carya*, *Betula*, *Ostrya*, *Carpinus*, *Craigia*, *Zelkova*, *Ulmus fischeri* *etc.* (Kvaček & Walther 2001, 2003). Due to invasion of the mentioned deciduous “modern” Arcto-Tertiary elements into central Europe (e.g., *Ostrya*, *Carpinus*, *Carya* and *Acer*) associated with persisting *Tetraclinis*, Lauraceae and other thermophilic (“palaeosubtropical”) elements, such as *Engelhardia*, *Sloanea*, *Palaeohosiea*, these floras are correlated to the floristic assemblage of Seifhennersdorf-Kundratice *sensu* Kvaček & Walther (1998). The flora of Hammerunterwiesenthal in Saxony outside the Doupov volcanic complex (Walther 1998) is radiometrically dated to the early Oligocene (Rupelian) and can also be correlated to the floristic assemblage of Seifhennersdorf-Kundratice *sensu* Kvaček & Walther (1998).

In scarcity of *Daphnogene* and low diversity of other Lauraceae and domination of Arcto-Tertiary elements, the Roudníky flora deviates from other late Eocene floras of the Bembridge-Spechbach floristic assemblage *sensu* Mai (1995). It does not resemble any of the so far known late Eocene sites in North Bohemia (Kostomlaty, Mrtvý vrch, Hlinná, Lbín) and adjacent regions.

## Fauna of Roudníky and Větruše

The late Eocene fish localities are rather scarce in North Bohemia (compared with Oligocene localities, see Böhme

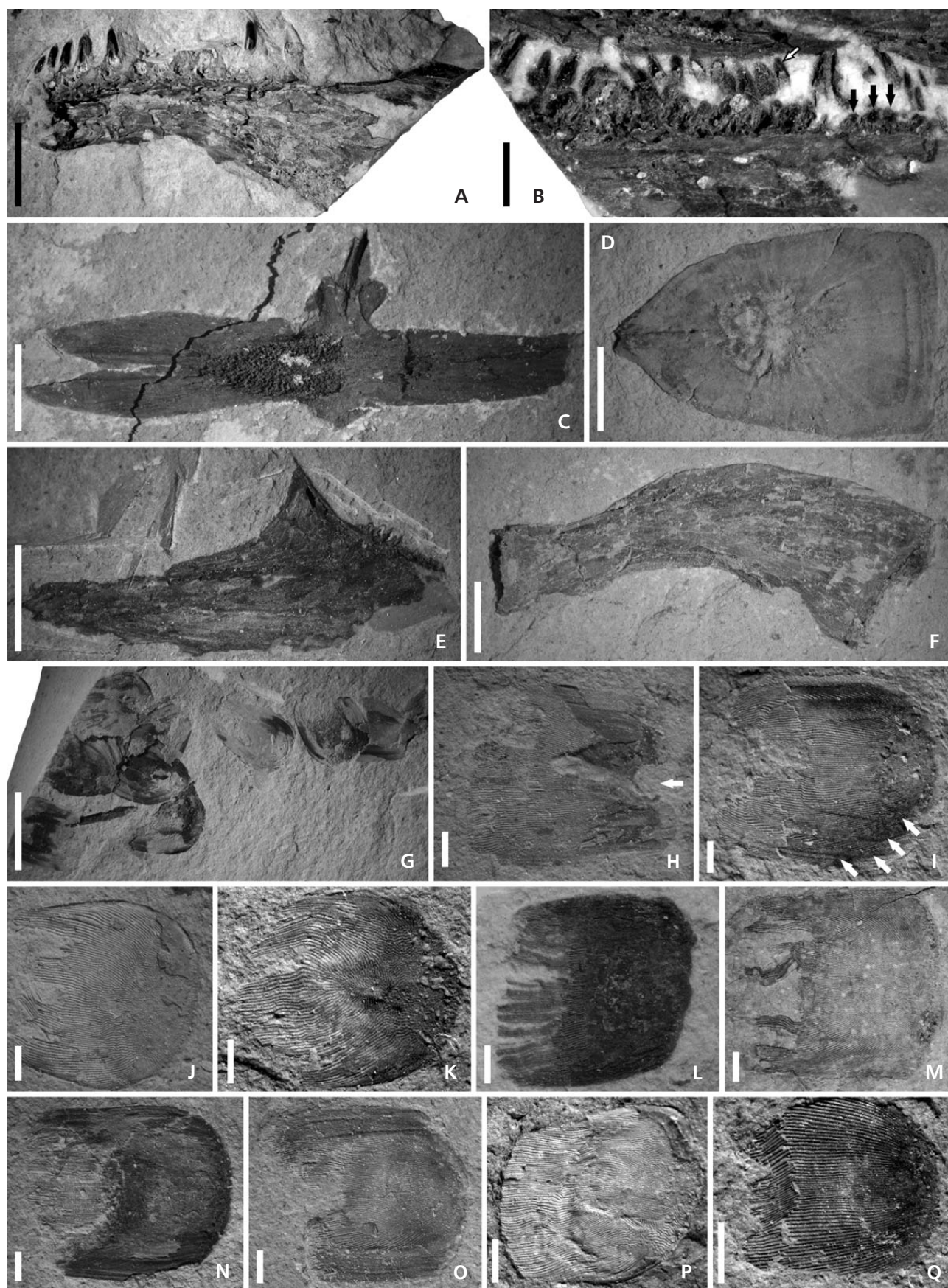
2007, table 2) being represented only by Roudníky, Kundratice (drill-core KU 1), Kostomlaty, and Kučlín. These are characterized mainly by the lack of the Cyprinidae fishes, which is in accordance with the situation in all of Europe. This remarkable absence was explained by Chang & Chen (2000) as a time period before the Cyprinidae distribution from the source area to Europe.

The fish scale specimens from the Roudníky drill-cores were described by Bellon *et al.* (1998) who suggested Eocene age on the basis of the composition of the fish fauna and the radiometric dating. The fish fauna of the Roudníky area and the Větruše Hill is characterized by an overwhelming majority of amiid remains, that were also described from the Kučlín and Kostomlaty localities (late Eocene) in North Bohemia, where the amiids are accompanied also by thumaturids (Thumaturidae, Esociformes) and/or by other fish groups. The thumaturids (as a subgroup of esociform order, see Gaudant & Meunier 2004) are missing at the both localities studied, but at Roudníky the esociformes are represented by umbrids (specimens from the drill-cores). The today living umbrids are known for their ability to accept lower oxygen levels in water (Geyer & Mann 1939a, b). The recent amiid bowfin *Amia calva* is also known for the ability to use the atmospheric air for respiration in an insufficiently oxygenated environment (e.g., Wilder 1878, Bevelander 1934). Such a poor diversity of the fish fauna can suggest the presence of a lake with sub-oxygenated waters that was inhabited by fishes able to accept such specific conditions. For the same reason other fish groups, for which the respiratory needs are higher, are missing.

The presence of the archaic amiid genus *Cyclurus* is typical of the Eocene localities in North Bohemia and elsewhere in Europe. The genus is not represented at the Kundratice outcrop (just perciform fish *Properca bispinnella* is present; Obrhelová 1976), but this irregularity may be caused by the fact that the material from Roudníky comes mainly from the drill-cores. The Kučlín fish fauna is, together with *Cyclurus macrocephalus*, characterized by the thumaturids, Percichthyidae and Moronidae (e.g., Obrhelová 1971, 1975; Micklich 1988, 1990; Micklich & Bohme 1997; Gaudant 2008; Přikryl 2008). The genus *Cyclurus* is accompanied just by thumaturids at the Kostomlaty locality (Obrhelová & Obrhel 1987).

**Figure 11.** Locality Roudníky. • A – *Cyclurus* sp., dentary, ZD RU 152. • B – *Cyclurus* sp., detail of dentition, ZD RU 165 (the black arrows show coronoidal teeth, the white arrow shows tip of dentary’s tooth). • C – *Cyclurus* sp., parasphenoideum, ZD RU 153. • D – *Cyclurus* sp., gulare mediale, ZD RU 154. • E – *Cyclurus* sp., prearticular, ZD RU 163. • F – *Cyclurus* sp., ceratohyal anterior, ZD RU 159. • G – *Cyclurus* sp., group of isolated scales, ZD RU 182. • H – *Cyclurus* sp., isolated scale of lateral line, ZD RU 174 (the arrow shows external opening of the lateral line system). • I – *Cyclurus* sp., isolated scale, ZD RU 172 (the arrows show growing marks). • J–Q – *Cyclurus* sp., isolated scales showing variability of the specimens; J – *Cyclurus* sp., ZD RU 177; K – *Cyclurus* sp., ZD RU 178; L – ZD RU 175; M – *Cyclurus* sp., ZD RU 171; N – *Cyclurus* sp., ZD RU 183; O – *Cyclurus* sp., ZD RU 186; P – *Cyclurus* sp., ZD RU 180; Q – *Cyclurus* sp., ZD RU 179. Scale bars: A, C–G = 5 mm; B, H–Q = 1 mm.





**Table 1.** Results and predicted zonal vegetation types defined by IPR-vegetation analysis for the studied fossil sites from late Eocene to early Oligocene of Northern Bohemia and Saxony (*sensu* Teodoridis *et al.* 2011b, table 8) including their GPS location and floristic sources.

Age	Localities	GPS	Reference	Dating	IPR-vegetation results			
					% of BLD	% of BLE	% of SCL + LEG	ZONPALM
Early Oligocene	Seifhennersdorf	N 50° 56' 7.02", E 14° 36' 26.99"	Walther & Kvaček (2007)	30.44 ± 1.25 Ma	59.44	33.54	5.10	1.92
	Hammerunterwiesenthal	N 50° 34' 36.89", E 13° 0' 17.52"	Walther (1998)	30.5 Ma	54.64	36.08	3.09	6.19
	Holý Kluk	N 50° 40' 6.23", E 13° 50' 8.55"	Radoň <i>et al.</i> (2006)	30.9 ± 1.5 Ma	64.56	29.09	6.36	0.00
	Kundratice	N 49° 24' 8.94", E 16° 8' 6.76"	Kvaček & Walther (1998)	32.75 ± 0.82 Ma	58.37	35.29	6.34	0.00
	Bechlejovice	N 50° 45' 23.77", E 14° 14' 16.55"	Kvaček & Walther (2004)	?	62.51	26.60	9.92	0.93
	Haselbach (Haselbach FA)	N 51° 8' 24.00", E 12° 24' 36.00"	Mai & Walther (1978)	33.0–33.7	50.03	42.48	4.26	3.23
Late Eocene	Větruše	N 50°39' 17.94", E 14°2' 22.81"	this paper	?	73.91	26.09	0.00	0.00
	Roudníky	N 50° 38' 57.96", E 13° 55' 10.51"	this paper	35.4 ± 0.9 Ma	59.09	28.79	12.12	0.00
	Böhlen	N 51°12' 10.38", E 12°23' 12.94"	Mai & Walther (1985, 2000)	35.5–37.0	33.33	66.67	0.00	0.00
	Kayna-Süd	N 51° 16' 32.38", E 11° 56' 48.59"			18.42	81.58	0.00	0.00
	Klausau	N 50° 57' 34.42", E 12° 30' 43.03"			23.53	64.71	0.00	11.76
	Knau	N 50°39' 10.02", E 11°43' 17.15"			8.11	91.89	0.00	0.00
	Profen	N 51°7' 32.45", E 12°12' 56.56"			21.43	76.79	0.00	1.79
	Haselbach (Zeitz Sand)	N 51° 8' 24.00", E 12° 24' 36.00"			12.96	79.63	0.00	7.41
	Kučlín	N 50° 31' 54.78", E 13° 47' 46.27"	Kvaček & Teodoridis (2011)	38.3 Ma	45.81	40.65	12.26	1.29
	Staré Sedlo	N 50° 10' 54.39", E 12° 43' 11.37"	Knobloch <i>et al.</i> (1996), Teodoridis <i>et al.</i> (2012)	?	25.00	59.21	2.63	13.61
	Český Chloumek	N 50° 6' 51.89", E 12° 56' 50.54"		?	21.88	65.63	0.00	6.91
	Nový Kostel	N 50° 12' 58.36", E 12° 26' 45.45"		?	33.90	66.10	0.00	0.00

The Roudníky fish fauna does not show much in common with the North Bohemian Oligocene fish localities. The only exception is that of Bechlejovice, which preserves umbrids (Obrhelová 1978) connecting both sites. At Roudníky a few isolated umbrid scales were found (Fig. 10J–M). Nevertheless, their presence shows indications of inhabitation of this area by umbrids, well documented later from the Oligocene and then successively to the Miocene (Obrhelová 1978, 1990; Kvaček *et al.* 2004).

Besides fish remains, the fauna of the Větruše Hill includes abundant teeth of crocodile *Diplocynodon* sp. (Radoň 2001). Quite rare frog remains (Palaeobatrachidae) from the Větruše locality correspond to other findings of anura in North Bohemia, both the Eocene (*i.e.*, Kučlín) and the Oligocene in age (*e.g.*, Bechlejovice). It seems that palaeobatrachids were not affected by the Eocene/Oligocene transition (Wuttke *et al.* 2012).

## Palaeoenvironmental analysis

### Phytosociological approach

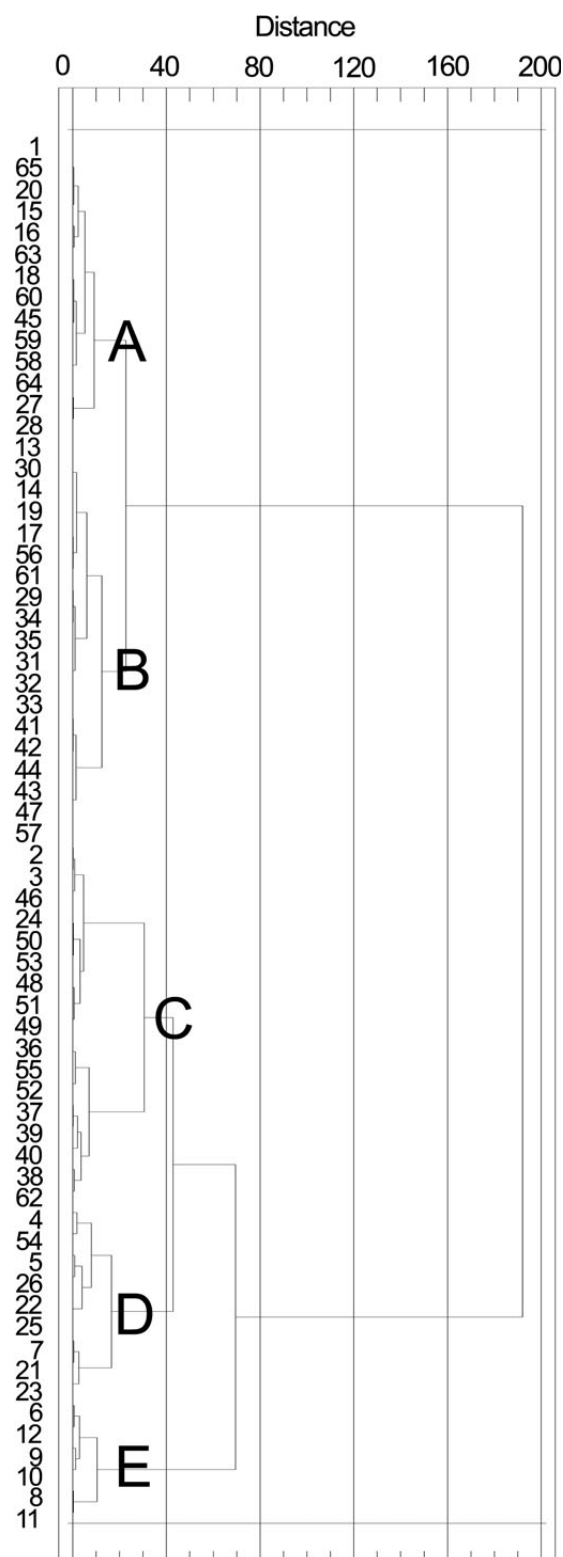
Generally, Kvaček (2010) defined the zonal vegetation type of Mid-latitude Notophyllous Broad-leaved Evergreen Forest typified by the middle Eocene floras of Eckfeld (Germany) and Lábatlan (Hungary) and the late Eocene floras of Hordle (England) and Kučlín (Czech Republic). The zonal vegetation type was interpreted as the upland vegetation analogue of the more azonal late Eocene floras known from the Staré Sedlo Formation and Weisselster Basin. They were assigned by Kvaček (2010) to the broad-leaved evergreen riparian gallery forest with palms (Staré Sedlo) and mixed *Doliosirobus* and/or *Quasisequoia* and broad-leaved evergreen swamp forest (Weisselster Basin). Comparing the above mentioned plant assemblages – with the early Oligo-



Table 1. continued

% DRY HERB	% MESO HERB	% of zonal herbs of zonal taxa	IPR-vegetation results				Vegetation type <i>sensu</i> Teodoridis <i>et al.</i> (2011b)
			Number of zonal taxa	Number of zonal woody angiosperms	Total number of taxa	Problematic taxa	
0.00	2.65	2.60	58	52	82	3	MMF/BLEF
0.00	0.00	0.00	18	16	23	1	MMF/BLEF
0.00	3.56	3.56	42	37	53	2	MMF
0.00	0.84	0.84	60	55	75	5	MMF/BLEF
0.00	3.64	3.64	55	51	68	0	MMF
2.90	4.35	7.25	34	30	64	1	BLEF
0.00	0.00	0.00	14	12	17	0	MMF
0.00	0.00	0.00	38	33	45	1	MMF
0.00	11.11	11.11	9	6	14	1	BLEF (excluded)
0.00	11.36	11.36	22	19	36	0	BLEF
0.00	5.41	5.41	19	16	26	0	BLEF
0.00	4.76	4.76	30	19	21	3	BLEF
0.00	0.00	0.00	31	28	45	0	BLEF
0.00	4.69	4.69	32	26	49	3	BLEF
0.81	2.64	3.45	82	78	106	6	BLEF
0.00	3.37	3.37	45	38	47	1	BLEF
0.00	0.00	0.00	17	16	18	0	BLEF
0.00	0.00	0.00	30	30	32	0	BLEF

cene vegetation types of the Doupov volcanic complex (locality Valeč) and the České středohoří Mts (Bechlejovice, Kunderatice), a distinct decrease of broad-leaved evergreen elements close to the Eocene/Oligocene boundary is obvious. It corresponds to an enormous immigration of riparian deciduous broad-leaved elements from Asia to Europe (Kvaček & Teodoridis 2007). This trend is now reported from the specific floras of Roudníky (this paper) and Böhlen (Mai & Walther 1985, 2000), where the floristic composition is significantly different from Kučlín and Staré Sedlo and its vegetation character corresponds to the modern Mixed-Mesophytic Forest vegetation type from SE Asia. The same vegetation type is supposed for the mentioned early Oligocene sites of Bechlejovice (Kvaček & Walther 2004, p. 51), Kunderatice (Kvaček & Walther 1998, p. 31), Hammerunterwiesenthal (Walther 1998, p. 252) and Seifenhennersdorf (Walther & Kvaček 2007, p. 131).



**Figure 12.** Dendrogram (Ward's method, squared Euclidean distance) showing one defaulted cluster based on the percentage of the BLD, BLE, and SCL+LEG components (*sensu* Teodoridis *et al.* 2011b, 2012) on the studied fossil and modern sites from China and Japan. Numbers represent the studied sites (DATA source in Appendix 3). Five subclusters (A to E) are distinguished.

**Table 2.** Palaeoclimate proxy datasets of the Leaf Margin Analysis (LMA) and Climate Leaf Analysis Multivariate Program (CLAMP) for the studied floras from Northern Bohemia and Saxony. Symbols: SE (sampling error), *n* (total species number), MAT (mean annual temperature), WMMT (warmest month mean temperature), CMMT (coldest month mean temperature), 3-WET (precipitation during 3 consecutive wettest months), 3-DRY (precipitation during 3 consecutive driest months), GROWSEAS (length of the growing season), GSP (growing season precipitation), MMGSP (mean monthly growing season precipitation), RH (relative humidity), SH (specific humidity) and ENTHAL (enthalpy), and STDEV Residuals (standard deviations).

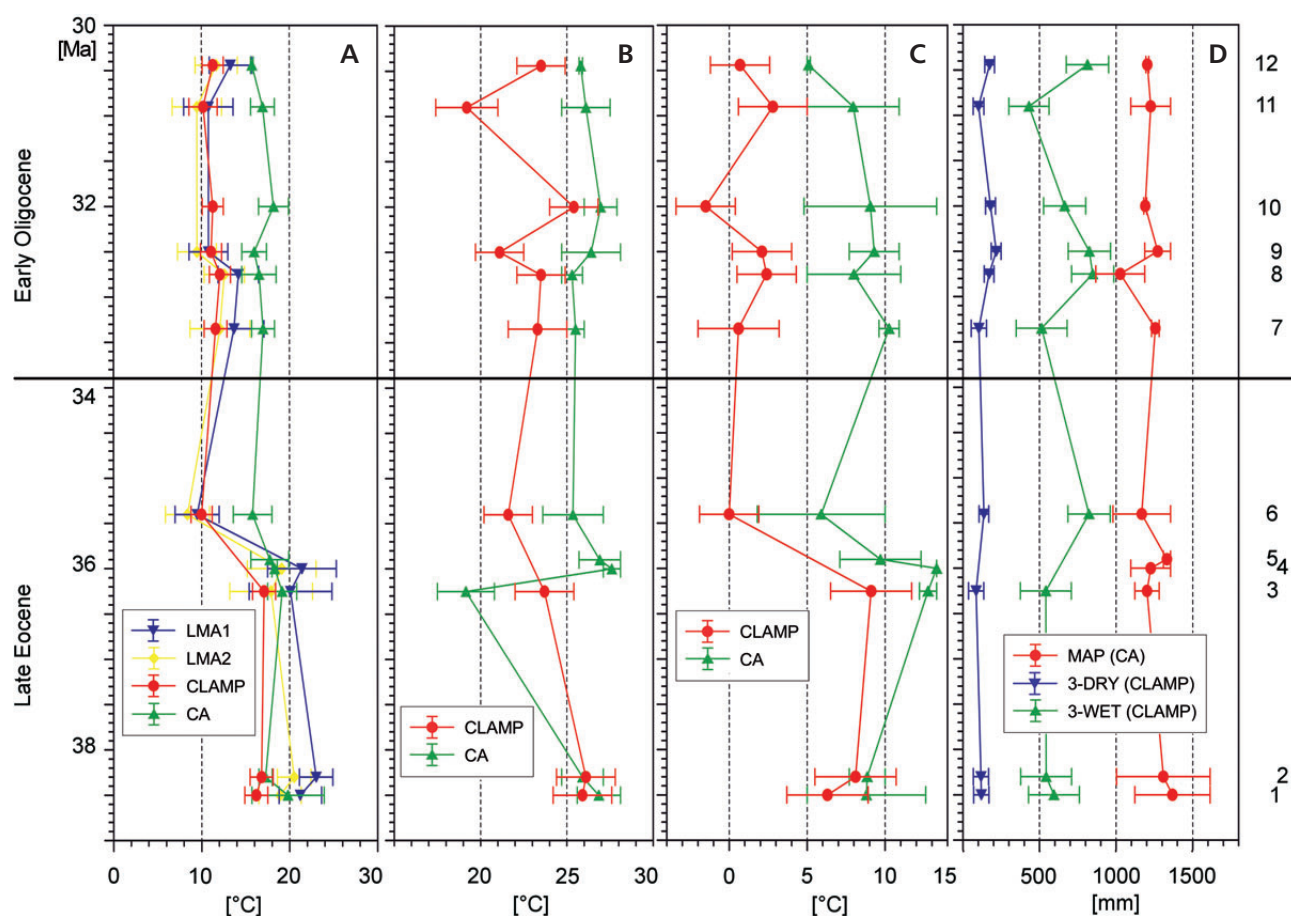
Age	Localities	Palaeoclimatic estimates											References
		LMA					CLAMP						
		MAT 1 [°C] <i>sensu</i> Wolfe (1979)	MAT 2 [°C] <i>sensu</i> Su <i>et al.</i> (2010)	SE 1 [°C] <i>sensu</i> Wilf (1997)	SE 2 [°C] <i>sensu</i> Miller <i>et al.</i> (2006)	n	MAT [°C] (STDEV)	WMMT [°C] (STDEV)	CMMT [°C] (STDEV)	3-WET [cm] (STDEV)	3-DRY [cm] (STDEV)	CLAMP calibration datasets	
Early Oligocene	Seifhennersdorf	13.3	11.7	2.1	2.4	49	11.3 (1.2)	23.5 (1.4)	0.7 (1.9)	81.3 (13.8)	17.4 (3.2)	144	this paper
	Holý Kluk	10.8	9.5	2.8	2.8	26	10.2 (1.6)	19.2 (1.8)	2.8 (2.2)	43.1 (13.1)	10.2 (3.5)	173	this paper
	Hammerunterwiesenthal	–	–	–	–	–	11.3 (1.2)	25.4 (1.4)	-1.5(1.9)	66.4 (13.8)	18.0 (3.2)	144	this paper
	Kundratice	14.2	12.6	1.9	2.3	61	12.1 (1.2)	23.5 (1.4)	2.4 (1.9)	84.7 (13.8)	17.1 (3.2)	144	this paper
	Bechlejovice	10.8	9.5	2.0	2.2	52	11.1 (1.2)	21.1 (1.4)	2.1 (1.9)	82.5 (13.8)	21.7 (3.2)	144	this paper
	Haselbach 1, Beucha (Haselbach FA)	13.7	12.1	3.4	3.4	20	11.6 (1.3)	23.3 (1.7)	0.6 (2.6)	51.4 (16.6)	10.4 (5.0)	189	this paper
Late Eocene	Roudníky	9.5	8.4	2.4	2.5	32	10.0 (1.2)	21.6 (1.4)	0.0 (1.9)	82.3 (13.8)	13.7 (3.2)	144	this paper
	Haselbach (Zeitz FA)	20.1	17.9	5.0	4.7	9	–	–	–	–	–	–	Teodoridis <i>et al.</i> (2012)
	Knau (Zeitz FA)	21.4	19.1	4.2	3.9	10	–	–	–	–	–	–	
	Haselbach, Klaus, Knau (Zeitz floristic assemblage – FA)	22.7	20.2	3.3	3.3	18	17.1 (1.3)	23.7 (1.7)	9.1 (2.6)	54.1 (16.6)	8.6 (5.0)	189	
	Kučlín	23.0	20.5	1.6	1.9	78	16.8 (1.3)	26.1 (1.7)	8.1 (2.6)	54.3 (16.6)	11.8 (5.0)	189	Kvaček & Teodoridis (2011)
	Staré Sedlo	21.2	18.9	2.2	2.4	44	16.2 (1.3)	25.9 (1.7)	6.3 (2.6)	59.4 (16.6)	12.0 (5.0)	189	Teodoridis <i>et al.</i> (2012)
	Český Chloumek	21.4	19.1	4.0	3.9	13	–	–	–	–	–	–	
	Nový Kostel	26.1	23.3	2.9	2.7	18	–	–	–	–	–	–	

## IPR-vegetation analysis

The fossil plant assemblages of Roudníky and Větruše were compared using IPR-vegetation analysis (*e.g.*, Kovar-Eder *et al.* 2008, Teodoridis *et al.* 2011b) of the following characteristic key components: broad-leaved deciduous (BLD) – 59.1% and 73.9%, broad-leaved evergreen (BLE) – 28.8% and 26.1%, sclerophyllous + legume-like (SCL+LEG) – 12.1% and 0%, dry herbaceous + mesophytic herbaceous /zonal herbaceous/ (D-HERB+M-HERB/ZONAL HERB/) – both 0% (for a detailed taxa scoring see Appendix 2). According to the thresholds for the key components detailed above for defining vegetation types (modified by Teodoridis *et al.* 2011b, table 8), the floras of Roudníky and Větruše belong to the mixed mesophytic forest (MMF) vegetation type. Results of the IPR-vegetation analysis from the late Eocene and early Oligocene floras from the Bohemian Massif and Saxony (Germany) are presented in Table 1. According to these results, the studied late Eocene floras correspond to the broad-leaved evergreen forest (BLEF) vegetation type

as a possible zonal vegetation cover for upland environments. However, the studied vegetation assemblages of BLEF from the Weissester Basin are characterized by a relatively high percentage of the BLE elements (65 to 92%) contrary to those from the Staré Sedlo Formation, Kučlín and Roudníky, which varies from 40 to 66% (Teodoridis *et al.* 2012; partly Table 1). Moreover, the assemblages of Kučlín and Roudníky also show a high percentage of sclerophyllous and legume-like elements (12.1% and 14.2%), which is a rare phenomenon in the late Eocene floras of Europe. The results of IPR-vegetation analysis from the studied early Oligocene sites from the Bohemian Massif and Saxony (*i.e.*, Haselbach, Bechlejovice, Kundratice, Hammerunterwiesenthal, Holý Kluk and Seifhennersdorf) show relatively low percentage of BLE components (27–42%) and higher percentage of BLD components (50–59%) contrary to those from the late Eocene sites of the Staré Sedlo Formation and the Weissester Basin. The percentage of SCL+LEG component varies from 3 to 10%. The ratios of the key components (Table 1) permit assign-





**Figure 13.** Palaeoclimatic changes and trends based on the proxy-datasets of the studied parameters derived from the LMA, CLAMP and CA techniques during late Eocene to early Oligocene. Palaeoclimatic parameters: A – MAT (mean annual temperature); B – WMMT (mean temperature of the warmest month); C – CMMT (mean temperature of the coldest month); D – MAP (mean annual precipitation); 3-WET (precipitation during 3 consecutive wettest months) and 3-DRY (precipitation during 3 consecutive driest months). Symbols: 1 – Staré Sedlo, 2 – Kučlín, 3 – Haselbach, Klaus, Knau (Zeit FA), 4 – Knau (Zeit FA), 5 – Böhlen, 6 – Roudníky, 7 – Haselbach 1, Beucha (Haselbach FA), 8 – Bechlejovice, 9 – Kundratice, 10 – Hammerunterwiesenthal, 11 – Holý Kluk and 12 – Seifhennersdorf.

ment to the vegetation type of mixed mesophytic forest (MMF) at Bechlejovice and Holý Kluk sites and to the ecotonal vegetation of BLEF/MMF at Kundratice, Hammerunterwiesenthal and Seifhennersdorf sites. Only the early Oligocene vegetation type of Haselbach corresponds to BLEF (see Table 1).

According to Teodoridis *et al.* (2012) a modern living vegetation analogue of the studied late Eocene vegetation of Nový Kostel, Český Chloumek, Staré Sedlo, Žitenice, Klaus, Phönix-Nord, and Profen is the subtropical broad-leaved evergreen forest of Mt. Emei (Sichuan, China) and of Mt. Longqi (Fujian, China) based on the results of the cluster analysis comparing 47 modern vegetation units from subtropical and tropical zones of China and Japan and 14 late Eocene fossil vegetation types from the Weisselster, Cheb and Sokolov basins (for details see Teodoridis *et al.* 2012; partly Fig. 13 – clusters “A”, “B”, source Appendix 3). However, a dendrogram (Fig. 12) derived from the cluster analysis (Ward’s method, Euclidean

square distance *sensu* Teodoridis *et al.* 2011b, 2012) does not prove the above mentioned statements for the vegetation of Větruše (54), Roudníky (55) and Kučlín (62). The two latter sites show the closest relation to the early Oligocene flora of Bechlejovice (52) in a cluster marked as “C” (Fig. 12). Focusing on the structure of cluster “C”, it is obvious that the late Eocene sites of Roudníky and Kučlín are related to the studied early Oligocene sites rather than to the late Eocene sites from the Staré Sedlo Formation and the Weisselster Basin. The cluster “C” shows an affinity of the early Oligocene floras such as Holý Kluk (49), Kundratice (51), Seifhennersdorf (48), Haselbach (53), and Hammerunterwiesenthal (50), to the modern vegetation assemblages of specific vegetation samples of the BLEF type from Mt. Fuji, Japan (24), Mixed Mesophytic Forest vegetation type from Mt. Emei, China (2, 3) and Monsoon vegetation type from Xishuangbanna, China (46). Similarly, cluster “C” presents close relation of the modern MMF vegetation associations of *Eurya-Cryptomeria japonica*

**Table 3.** Palaeoclimate proxy datasets of the Coexistence Approach (CA) for the studied floras from Northern Bohemia and Saxony. Symbols: MAT (mean annual temperature), WMMT (mean temperature of the warmest month), CMMT (mean temperature of the coldest month), and MAP (mean annual precipitation).

Age	Localities		Palaeoclimatic estimates								References	
			MAT [°C]		WMMT [°C]		CMMT [°C]		MAP [mm]			
			min. value	max. value	min. value	max. value	min. value	max. value	min. value	max. value		
Early Oligocene		Seifhennersdorf	15.6	15.9	25.7	25.9	5.0	5.2	1194.0	1213.0	Mosbrugger <i>et al.</i> (2005)	
		Holý Kluk	15.6	18.3	24.7	27.5	5.0	10.9	1096.0	1355.0	Utescher (personal communication 2013)	
		Hammerunterwiesenthal	16.5	19.9	26.0	27.9	4.8	13.3	1180.0	1200.0	Utescher (personal communication 2013)	
		Kundratice	14.6	18.5	24.7	25.9	5.0	11.0	867.0	1187.0	Utescher (personal communication 2013)	
		Bechlejovice	14.6	17.4	24.7	28.1	7.7	10.9	1187.0	1355.0	Utescher (personal communication 2013)	
		Haselbach FA	Beucha	15.6	16.1	24.7	25.6	5.0	5.8	897.0	1206.0	Roth-Nebelsick <i>et al.</i> (2004)
		Regis		16.5	23.9	26.0	27.9	9.6	13.6	1187.0	1281.0	Roth-Nebelsick <i>et al.</i> (2004)
		Haselbach		15.7	18.3	25.0	26.0	9.6	10.9	1231.0	1281.0	Roth-Nebelsick <i>et al.</i> (2004)
	Valeč		9.3	21.7	22.3	28.6	2.7	13.6	979.0	1741.0	Utescher (personal communication 2013)	
Late Eocene		Roudníky	13.6	18.0	23.6	27.1	1.8	10.0	979.0	1355.0	Utescher (personal communication 2013)	
		Böhlen	15.6	19.9	25.7	28.1	7.1	12.3	1308.0	1355.0	Mosbrugger <i>et al.</i> (2005)	
		Haselbach (Zeitz FA)	17.5	20.8	27.1	27.9	12.2	13.3	1122.0	1281.0	Mosbrugger <i>et al.</i> (2005)	
		Knau	18.0	18.6	27.1	28.1	13.3	13.3	1096.0	1355.0	Mosbrugger <i>et al.</i> (2005)	
		Kučlín	16.5	18.0	24.7	27.1	7.7	10.0	1003.0	1613.0	Kvaček & Teodoridis (2011)	
		Staré Sedlo	15.7	23.9	25.6	28.1	5.0	12.6	1122.0	1613.0	Teodoridis <i>et al.</i> (2012)	

from the Yakushima Island, Japan only (38–40) to the mentioned fossil vegetation of Roudníky (55), Kučlín (62), and Bechlejovice (52). The remaining clusters “D” and “E” in Fig. 12 group together modern vegetation types of broad-leaved deciduous forest (BLDF) from China and Japan associated with the studied vegetation type of Větruše (54). The vegetation of Větruše shows the closest relationship to the modern broad-leaved deciduous forest of the Mt. Emei (4) – Tang & Ohsawa (1997). This clustering was influenced by a relatively higher percentage of the BLD component (73.9%), which is secondarily caused by low value of zonal woody angiosperms (but still acceptable for use of IPR-vegetation analysis).

### Palaeoclimatic proxy-datasets

The plant assemblage of Roudníky was evaluated using a combination of the physiognomic (LMA, CLAMP) and Nearest Living Relatives (CA) techniques. The CLAMP method uses the physiognomic characteristics of the Roudníky assemblage presented in Appendix 1 and 144 physiognomic and gridded meteorological calibration datasets (Physg3brcAZ, GRIDMet3brAZ) selected by a new statistical tool published by Teodoridis *et al.* (2012). The palaeoclimatic proxy-datasets for the Roudníky are as follows: CLAMP estimates – MAT 10.0 °C, WMMT 21.6 °C, CMMT 0.0 °C, 3-WET 82.3 cm and 3-DRY 13.7 cm; LMA estimates – MAT<sub>1</sub> is 9.5 °C (*sensu* Wolfe 1979) and MAT<sub>2</sub>

is 8.4 °C (*sensu* Su *et al.* 2010), and values of the sampling error *sensu* Miller *et al.* (2006) is 2.5 °C and 2.4 °C *sensu* Wilf (1997); CA proxy data intervals: MAT 13.6–18.0 °C, WMMT 23.6–27.1 °C, CMMT 1.8–10.0 °C, and MAP 979–1355 mm (see Tables 2, 3). Contrary to the estimates of Roudníky, palaeoclimatic proxies from the other late Eocene floras of the Bohemian Massif and Saxony (partly Teodoridis *et al.* 2012, Kvaček & Teodoridis 2011, Tables 2, 3) show higher and almost balanced results in comparison with the used techniques, *i.e.*, MAT: 16.2–17.1 °C (CLAMP), 22.9 °C and 20.5 °C (LMA<sub>MAT1</sub> and LMA<sub>MAT2</sub> – average values), 15.7–23.9 °C (CA); WMMT: 23.7–26.1 °C (CLAMP), 24.7–28.1 °C (CA); CMMT: 6.3–9.1 °C (CLAMP), 5–13.3 °C (CA); and MAP: 1003–1613 mm (CA) – see detailed in Tables 2, 3. The results of LMA from Český Chloumek, Haselbach and Knau were excluded due to a low number of the evaluated taxa (from 9 to 13) which is also obvious from the values of the sampling errors (SE 1, SE 2) exceeding 3.9 °C (Table 2). However, the used techniques have unequivocally proved a decreasing trend in the all studied palaeoclimatic parameters by the time of “the latest” flora of Roudníky (Fig. 13). An additional palaeoclimatic parameter, the mean annual range of temperature (MART), based on the CLAMP proxies, arose from 14.6 °C (floras of the Zeitz floristic assemblage) and/or 19.6 °C (Staré Sedlo) to 21.6 °C (Roudníky) and based on the CA estimates increased from 14.3 °C (Knau) and/or 18.1 °C (Staré Sedlo) to 19.5 °C (Roudníky). Mosbrugger *et al.* (2005) published CA proxy-datasets for the flora of Böhlen



(Weisselster Basin, Saxony, 37 Ma) showing well comparable estimates with Roudníky (Table 3). However, the CA analysis is based on only 9 taxa and the floristic characters of Böhlen and Roudníky do not correspond (see above).

The studied palaeoclimatic proxy-datasets derived from the early Oligocene assemblages/sites in the Bohemian Massif and Saxony show only a slightly different character comparing to Roudníky (see Tables 2, 3). The palaeoclimatic proxy-datasets derived by CA for probably the oldest early Oligocene flora of Valeč in the Bohemian Massif has a very approximate value due to the long range of the CA intervals (exceeded 10 °C by MAT and CMMT parameters). But it also shows a significant decreasing trend of temperature in comparison to the above mentioned late Eocene floras, *e.g.*, differences of MAT are 4.3 °C higher (Staré Sedlo), 3.7 °C (Haselbach), and 0.3 °C (Roudníky). The mean value of MAT proxy-data at Valeč (15.5 °C) seems to be very low comparing those to the average value of MAT (17.7 °C) estimated for Haselbach, Regis and Beucha (Table 3) and/or Bechlejovice and Kundratice (16.0 °C and 16.6 °C). The presented palaeoclimatic proxy-datasets of Roudníky estimated by the LMA, CA and CLAMP techniques correspond in all studied parameters to those of the early Oligocene sites of Bechlejovice, Kundratice, Beucha, Regis, Haselbach, Hammerunterwiesenthal, Holý Kluk, and Seifhennersdorf rather than to those from the studied late Eocene sites from the Bohemian Massif and Saxony (Tables 2, 3; Fig. 13). The averaged values of the important palaeoclimatic parameters of the mentioned early Oligocene sites summarizing LMA, CLAMP and CA estimates (Tables 2, 3) are characterized as follows, *i.e.*, MAT: 13.7 °C (LMA<sub>MAT 1</sub>), 12.1 °C (LMA<sub>MAT 2</sub>), 11.3 °C (CLAMP), 17.1 °C (CA); WMMT: 22.7 °C (CLAMP), 26 °C (CA); CMMT: 1.2 °C (CLAMP), 8.3 °C (CA); and MAP: 1182 (CA). Kvaček & Walther (2004) published palaeoclimatic estimates for Bechlejovice derived from CLAMP and CA. These original values show warmer characteristics and are here re-evaluated using extended NLR's database (CA) as well as the gridded meteorological calibration datasets (Table 3).

Zachos *et al.* (2001, 2008) characterized palaeoclimatically the Eocene epoch as follows: It starts by a significant peak of the Early Eocene Climatic Optimum (EECO; 52 to 50 Ma) expressed by a 1.5‰ decrease in  $\delta^{18}\text{O}$ . This event was followed by a 17 Ma long trend towards cooler conditions (3.0‰ rise in  $\delta^{18}\text{O}$ ), with much of the change occurring during the early–middle Eocene (50 to 48 Ma) into the early Oligocene (35 to 34 Ma). The cooling trend is also proved in terrestrial ecosystems by the presented changes in palaeovegetation and palaeoclimate during the late Eocene and/or on the boundary of late Eocene/early Oligocene (Tables 1–3; Fig. 13) in the Bohemian Massif (Staré Sedlo, Kučlín, Roudníky) as well as in Saxony (Knau, Haselbach, Böhlen – see Mosbrugger *et al.* 2005, Figs 2, 3).

Palaeoclimatic studies of this time interval from other parts of the Northern Hemisphere are partly contradictory. The terrestrial spore and pollen assemblages recovered in the Norwegian–Greenland Sea indicate at the Eocene–Oligocene transition increased seasonality and the shift to cooler winters (Eldrett *et al.* 2009). European climatic proxies derived from the terrestrial records are regionally heterogeneous (Hren *et al.* 2013). Climatic characters of vegetation boundaries changed in Europe with the palaeogeographical position and influence of oceanic *vs.* continental climate (Kvaček 2010). The different signals of terrestrial plant fossils and fish fauna/radiometric dating in the area of Roudníky and Větruše may reflect environmental conditions on the land due to volcanic activities, transport from the vegetation cover at higher altitudes or even atmospheric “cooling” effect of volcanic activity. We favour the explanation by an increased seasonality of climate, as suggested for high latitude Europe (Eldrett *et al.* 2009), which allows for overrepresentation of deciduous over evergreen and more sensitive plant elements.

## Conclusions

1. Concerning the floristic composition, the floras of Roudníky and Větruše are closer to those of early Oligocene age known from adjacent areas. They both widely deviate from those of the late Eocene (Kučlín). This floristic difference may not be so strongly expressed in their leaf physiognomy. On the contrary, the fish fauna includes *Cyclurus* typical of the European Eocene, which is in line with the radiometric dating of adjacent basalts.
2. Based on the megafossil flora and fish fauna of Roudníky and Větruše, the major turnover in ecosystems from subtropical to warm temperate climatic regimes in North Bohemia is to be placed as early as within the late Eocene pending the radiometric datation is correct. The increased seasonality of climate may have played a more important role than the drop of mean annual temperature.
3. According to the results of IPR-vegetation analysis corroborated by cluster analysis (Ward's method, Euclidean square distance), the vegetation type of Roudníky shows the closest affinity to early Oligocene vegetation of Bechlejovice and late Eocene vegetation of Kučlín, as well as to modern MMF vegetation classified to the association of *Eurya-Cryptomeria japonica* from the Yakushima Island (Japan). The cluster analysis proves a close relationship of Roudníky (as well as Kučlín) to early Oligocene sites rather than the late Eocene sites from the Staré Sedlo Formation and the Weisselster Basin.

4. The higher value of % SCL+LEG components in Roudníky (*Gleditsia* sp., *Mimosites haeringianus*, *Pyracantha krauselii*, *Ziziphus ziziphoides*) should indicate “more open” upland vegetation (light forest). It corresponds also to relatively low values of SH, RH, MAP contrary to those estimated for the other studied late Eocene sites of the Staré Sedlo Formation and the Weisselster Basin.

5. The vegetation change, which is expressed by drastically decreased proportion of BLE and increase of BLD elements at Roudníky (as detected by phytosociological approach and IPR-vegetation analysis) during the latest Eocene in the Bohemian Massif, corresponds to a significant cooling trend of wintermean temperatures, independently proven by LMA, CLAMP, CA and geochemical techniques.

6. Palaeoclimatic estimates of Roudníky are best comparable to those of the studied early Oligocene sites rather than to late Eocene palaeoclimatic proxy-datasets of the Staré Sedlo Formation and the Weisselster Basin.

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## Appendix 1

Percentages of foliar physiognomic characters of the studied floras.

Foliar Physiognomic Characters [%]		Roudníky	Haselbach 1, Beucha (Haselbach F/A)	Bechlejovice	Kundratice	Hammerunterwiesenthal	Holý Kluk	Seifhemsdorf
Margin Character States	Lobed	15.63	25.00	19.23	11.48	20.00	15.38	16.33
	No Teeth	26.56	40.00	30.77	41.80	53.85	30.77	38.78
	Teeth Regular	46.88	47.50	47.12	38.52	23.08	55.77	28.57
	Teeth Close	33.59	22.50	34.62	25.41	26.92	46.15	20.41
	Teeth Round	27.34	27.50	24.04	15.57	0.00	36.54	14.29
	Teeth Acute	45.31	37.50	47.12	42.62	38.46	40.38	47.96
	Teeth Compound	10.94	7.50	6.73	10.66	0.00	3.85	11.22
Size Character States	Nanophyll	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	Leptophyll I	0.00	0.00	0.00	0.00	0.00	1.92	0.00
	Leptophyll II	3.13	0.00	1.92	3.28	11.36	5.77	0.00
	Microphyll I	13.28	6.65	6.08	16.93	18.91	14.73	12.06
	Microphyll II	35.78	28.70	28.46	33.05	46.18	54.46	29.22
	Microphyll III	32.66	44.95	44.15	30.18	14.36	16.00	36.88
	Mesophyll I	15.16	18.30	78.79	14.89	9.09	3.19	19.71
	Mesophyll II	0.00	1.25	3.19	0.82	0.00	1.92	1.02
	Mesophyll III	0.00	0.00	0.00	0.82	0.00	1.92	1.02
Apex Character States	Apex Emarginate	0.63	0.00	0.00	0.00	0.00	46.15	1.69
	Apex Round	25.09	10.00	11.54	25.67	0.00	38.46	14.96
	Apex Acute	44.31	45.00	61.54	49.44	66.67	59.62	44.55
	Apex Attenuate	29.94	45.00	26.92	24.85	33.33	1.92	38.78
Base Character States	Base Cordate	10.94	9.15	22.12	11.48	54.17	19.23	19.71
	Base Round	37.50	31.65	37.50	30.33	12.50	57.69	35.02
	Base Acute	51.56	59.15	39.42	58.20	33.33	23.08	45.22
Length to Width Character States	L : W < 1 : 1	4.69	6.25	3.85	5.74	4.55	19.23	9.18
	L : W 1–2 : 1	17.97	13.75	26.92	18.85	43.91	25.00	18.37
	L : W 2–3 : 1	30.16	27.50	25.63	30.87	16.64	25.00	26.51
	L : W 3–4 : 1	37.03	25.00	33.33	34.97	34.82	13.46	29.57
	L : W > 4 : 1	10.16	25.00	10.25	9.56	0.00	17.31	16.31
Shape Character States	Obovate	0.63	2.50	1.60	2.46	0.00	15.38	2.04
	Elliptic	33.59	40.00	33.33	54.92	83.33	34.62	31.63
	Ovate	65.78	57.50	65.06	42.62	16.67	50.00	66.33

## Appendix 2A

List of plant taxa occurring in the studied floras from Roudníky and their scoring according to the IPR-vegetation analysis.

site: Roudníky		ZONAL								AZONAL				
Taxa	CONIF	BLD	BLE	SCL	LEG	Zonal arboreal PALM	Zonal arboreal ferns	D-HERB	M-HERB	AZONAL WOODY	Azonal non-woody elements	AQUATIC	problematic taxa	comments
<i>Acer angustilobum</i>	1.00	1.00												1.00
<i>Acer</i> cf. <i>tricuspidatum</i>		0.25								0.75				1.00
<i>Acer palaeosaccharium</i>		1.00												1.00
<i>Alnus gaudinii</i> / <i>A. kefersteinii</i>		1.00												1.00
<i>Betula alnoides</i> / <i>B. dryadum</i>		1.00												1.00
cf. <i>Sabrenia</i> sp.													1.00	1.00
<i>Carpinus</i> sp. / <i>C. mediomontana</i>		1.00												1.00
<i>Carpolithes</i> sp.														1.00
<i>Carya fragiliformis</i>		1.00												1.00
cf. <i>Cephalotaxus parvifolia</i>														1.00
<i>Cercidiphyllum crenatum</i>			0.25								0.75			1.00
<i>Craigia bronii</i> / <i>Dombeyopsis lobata</i>			0.50								0.50			1.00
<i>Crataegus pirskenbergensis</i>			1.00											1.00
<i>Cyclocarya</i> sp.			1.00											1.00
<i>Dicotylophyllum deichmuelleri</i>				1.00										1.00
<i>Diospyros</i> sp.			1.00											1.00
<i>Fraxinus</i> sp.			0.50								0.50			1.00
<i>Gleditsia</i> sp.					0.50	0.50								1.00
<i>Juniperus pauli</i>														1.00
<i>Laurophyllum acutimontanum</i>				1.00										1.00
<i>Laurophyllum pseudoprinceps</i>			1.00										1.00	
<i>Leguminosites</i> sp.					1.00								1.00	
<i>Liriodendron haueri</i>		1.00											1.00	
cf. <i>Matudaea menzelii</i>			1.00										1.00	
<i>Tilia brassicoides</i>		1.00											1.00	
<i>Mimosites haeringianus</i>					1.00								1.00	
<i>Nyssa disseminata</i>		0.50								0.50			1.00	
<i>Ostrya atlantidis</i>		1.00											1.00	
<i>Paeolobium</i> sp.		0.50	0.50										1.00	
<i>Pinus</i> sp.													1.00	
<i>Platanus neptuni</i>		0.50								0.50			1.00	
<i>Pungiphyllum cruciatum</i>			1.00										1.00	
<i>Pyracantha kraeuselii</i>			0.50	0.50									1.00	
? <i>Castaneophyllum lonchitiforme</i>			1.00										1.00	
<i>Rosa lignitum</i> / <i>R. milosii</i>		0.50	0.50										1.00	
<i>Symplocos oligocaenica</i>			1.00										1.00	
<i>Taxodium dubium</i>										1.00			1.00	
<i>Tetraclinis salicornioides</i>													1.00	



site: Roudníky		ZONAL								AZONAL				
Taxa	CONIF	BLD	BLE	SCL	LEG	Zonal arboreal PALM	Zonal arboreal ferns	D-HERB	M-HERB	AZONAL WOODY	Azonal non-woody elements	AQUATIC	problematic taxa	comments
<i>Torreya bilinica</i>	1.00													1.00
<i>Toxicodendron herthae</i>		1.00												1.00
<i>Ulmus fischeri</i>		0.50								0.50				1.00
cf. “ <i>Viburnum</i> ” <i>atlanticum</i>		0.50	0.50											1.00
<i>Zelkova zelkovifolia</i>		1.00												1.00
<i>Ziziphus ziziphoides</i>			0.50	0.50										1.00
cf. <i>Dicotylophyllum ungeri</i>		1.00												1.00
														44.00
Sum of taxa	5.00	19.50	9.50	1.50	2.50	0.00	0.00	0.00	0.00	5.00	0.00	1.00	1.00	45.00
Sum zonal taxa														38.00
Percentage of zonal taxa	13.16	51.32	25.00	3.95	6.58	0.00	0.00	0.00	0.00					100.00
Sum zonal woody angiosperms														33.00
Percentage of zonal woody angiosperms		59.09	28.79	4.55	7.58	0.00								100.00
Sum of % SCL+LEG	12.12													
Sum of % D-HERB+M-HERB	0.00													

## Appendix 2B

List of plant taxa occurring in the studied floras from Větruše and their scoring according to the IPR-vegetation analysis.

site: Větruše		ZONAL								AZONAL			
Taxa													
	CONIF	BLD	BLE	SCL	LEG	Zonal arboreal PALM	Zonal arboreal ferns	D-HERB	M-HERB	AZONAL WOODY	Azonal non-woody elements	AQUATIC	problematic taxa
<i>Acer</i> sp.		1.00											1.00
<i>Alnus kefersteinii</i>		1.00											1.00
<i>Carya fragiliformis</i>		1.00											1.00
<i>Craigia bronii</i>		0.50								0.50			1.00
<i>Daphnogene cinnamomifolia</i> vel cf. <i>Matudaea menzelii</i>			1.00										1.00
<i>Engelhardia orsbergensis</i>		0.50	0.50										1.00
<i>Juniperus pauli</i>	1.00												1.00
<i>Laurophyllum</i> cf. <i>acutimontanum</i>			1.00										1.00
<i>Liriodendron</i> sp.		1.00											1.00
Monocotyledonae gen. indet.											1.00		1.00
<i>Ostrya atlantidis</i>		1.00											1.00
<i>Platanus neptuni</i>		0.50								0.50			1.00
<i>Rosa lignitum</i>		0.50	0.50										1.00
<i>Taxodium dubium</i>										1.00			1.00
<i>Tetraclinis salicornioides</i>	1.00												1.00
<i>Ulmus fischeri</i>		0.50								0.50			1.00
<i>Zelkova zelkovifolia</i>		1.00											1.00
Sum of taxa	2.00	8.50	3.00	0.00	0.00	0.00	0.00	0.00	0.00	2.50	1.00	0.00	17.00
Sum zonal taxa													13.50
Percentage of zonal taxa	14.81	62.96	22.22	0.00	0.00	0.00	0.00	0.00	0.00				100.00
Sum zonal woody angiosperms													11.50
Percentage of zonal woody angiosperms		73.91	26.09	0.00	0.00	0.00							100.00
Sum of % SCL+LEG		0.00											
Sum of % D-HERB+M-HERB		0.00											



## Appendix 3

Results of the IPR-vegetation analysis and cluster analysis (Ward's method, squared Euclidean distance) of the studied late Eocene and early Oligocene floras from Northern Bohemia and Saxony and modern tropical, subtropical and temperate vegetation types from China and Japan (*sensu* Teodoridis *et al.* 2011b, 2012). DATA source for the cluster analysis was values of the percentage of BLD, BLE and SCL+LEG components. Abbreviations: BLDF (broad-leaved deciduous forests), MMF (mixed mesophytic forests), BLEF (broad-leaved evergreen forests), ShSF (subhumid sclerophyllous forests), MMF/BLEF (transitional/ecotonal/zonal vegetation types of MMF and BLEF), and BLDF/MMF (transitional/ecotonal/zonal vegetation types of BLDF and MMF).

Time/Zone/Age	Country	Area	Vegetation type – empirical classification	Studied modern vegetation units [region, (sub)community, (sub)association] and fossil floras / studied fossil floras <i>sensu</i> Teodoridis <i>et al.</i> (2011b, 2012)	Site numbers – Cluster analysis	Cluster (Fig. 13)	IPR-vegetation analysis			
							% of BLD	% of BLE	% of SCL+LEG	Classification <i>sensu</i> Teodoridis <i>et al.</i> (2011b)
RECENT SUBTROPICAL and TEMPERATE ZONE	China	Mt. Emei	BLEF	plots (Tang & Ohsawa 1997, Tang <i>et al.</i> 2007)	1	A	34	66	0	BLEF
			MMF	1 plot (Tang & Ohsawa 1997)	2	C	65	36	0	MMF/BLEF
				vegetation description (Li & Shi 2007)	3	C	67	31	1	MMF/BLEF
			BLDF	2 plots (Tang & Ohsawa 1997)	4	D	80	17	4	BLDF
		Meili Snow Mts	BLDF	<i>Betula</i> spp., <i>Acer</i> spp., <i>Sorbus</i> spp. comm.	5	D	100	0	0	BLDF
				summarized communities of <i>Hippophae rhamnoides</i> , <i>Prunus mira</i> , <i>Salix luctuosa</i> and <i>Zanthoxylum simulans</i> , and <i>Populus haoana</i> var. <i>haoana</i>	6	E	68	6	26	ShSF
				Summary for BLDF	7	D	84	3	13	BLDF
			ShSF	<i>Quercus guyavifolia</i> comm.	8	E	56	12	33	ShSF
				<i>Quercus aquifolioides</i> comm., <i>Q. aquifolioides</i> and <i>Pinus armandii</i> subcomm.	9	E	55	21	24	ShSF
				<i>Quercus aquifolioides</i> comm., <i>Q. aquifolioides</i> subcomm.	10	E	64	14	22	ShSF
				<i>Quercus aquifolioides</i> comm., <i>Q. aquifolioides</i> and <i>Populus davidiana</i> subcomm.	11	E	54	15	31	ShSF
				Summary for ShSF	12	E	62	12	26	ShSF
		Mt. Longqi	BLEF	<i>Phoebe bournei</i> comm.	13	B	17	80	3	BLEF
				<i>Altingia chinensis</i> comm.	14	B	14	82	3	BLEF
				<i>Castanopsis fargesii</i> comm.	15	A	38	60	1	BLEF
				<i>Castanopsis eyrei</i> comm.	16	A	29	69	3	BLEF
				<i>Castanopsis carlesii</i> comm.	17	B	17	83	0	BLEF
				<i>Lithocarpus polystachys</i> comm.	18	A	23	77	0	BLEF
				plots (He <i>et al.</i> 1998)	19	B	14	84	2	BLEF
				Summary for BLEF	20	A	35	64	1	BLEF
	Japan	Shirakami Sanchi	BLDF	<i>Lindera membranacea</i> - <i>Fagus crenata</i> comm.	21	D	78	9	13	BLDF/MMF
				<i>Quercus mongolica</i> var. <i>grosseserrata</i> - <i>Lindera umbellata</i> var. <i>membranacea</i> comm.	22	D	87	6	6	BLDF
				<i>Ilex-Thuja standishii</i> comm.	23	D	77	5	18	BLDF/MMF
		Mt. Fuji	BLEF	<i>Camellia japonica</i> region	24	C	55	42	3	BLEF
			BLDF	<i>Fagus crenata</i> region	25	D	89	5	6	BLDF
				<i>Vaccinium-Picea</i> region	26	D	95	2	3	BLDF
		Nara	BLEF	<i>Podocarpus nagi</i> assoc., typical subassoc.	27	A	33	57	6	BLEF
				<i>Podocarpus nagi</i> assoc.	28	A	38	53	6	BLEF
		Shiroya-ma	BLEF	<i>Elaeocarpus sylvestris</i> var. <i>ellipticus</i> assoc.	29	B	17	73	6	BLEF

Time/Zone/Age	Country	Area	Vegetation type – empirical classification	Studied modern vegetation units [region, (sub)community, (sub)association] and fossil floras / studied fossil floras <i>sensu</i> Teodoridis <i>et al.</i> (2011b, 2012)	Site numbers – Cluster analysis	Cluster (Fig. 13)	IPR-vegetation analysis			
							% of BLD	% of BLE	% of SCL+LEG	Classification <i>sensu</i> Teodoridis <i>et al.</i> (2011b)
RECENT	SUBTROPICAL and TEMPERATE ZONE	Japan	BLEF	<i>Ficus superba</i> var. <i>japonica</i> - <i>Persea thunbergii</i> assoc.	30	B	17	81	2	BLEF
				<i>Tarennia-Castanopsis sieboldii</i> assoc.	31	B	16	80	5	BLEF
				<i>Hydrangea-Castanopsis sieboldii</i> assoc.	32	B	14	80	6	BLEF
				<i>Distylium-Quercus salicina</i> assoc., typical subassoc.	33	B	14	81	6	BLEF
				<i>Distylium-Quercus salicina</i> assoc., <i>Maesa japonica</i> subassoc.	34	B	19	76	5	BLEF
				Summary for <i>Distylium-Quercus salicina</i> assoc.	35	B	20	75	5	BLEF
			MMF	<i>Eurya-Cryptomeria japonica</i> assoc., <i>Dryopteris nipponensis</i> subassoc.	36	C	56	32	12	MMF/BLEF
				<i>Eurya-Cryptomeria japonica</i> assoc., typical subassoc.	37	C	56	27	17	MMF
				<i>Eurya-Cryptomeria japonica</i> assoc., <i>Tsuga sieboldii</i> subassoc.	38	C	43	42	15	BLEF
				<i>Eurya-Cryptomeria japonica</i> assoc., <i>Carex morrowii</i> var. <i>laxa</i> subassoc.	39	C	53	31	16	MMF/BLEF
				Summary for <i>Eurya-Cryptomeria japonica</i> assoc.	40	C	43	38	19	MMF/BLEF
	TROPICAL ZONE	China	Jianfengling	Tropical lowland rain forest	41	B	5	95	1	BLEF
				Tropical montane rain forest	42	B	1	98	0	BLEF
			Xishuangbanna	Tropical seasonal rain forest	43	B	9	89	0	BLEF
				Tropical montane rain forest	44	B	3	97	0	BLEF
				Tropical seasonal moist forest	45	A	26	73	1	BLEF
				Monsoon forest	46	C	59	40	1	BLEF
				Tropical montane broad-leaved evergreen forest	47	B	9	91	0	BLEF
FOSSIL	Early Oligocene	D	Seifhennersdorf		48	C	59	34	5	MMF/BLEF
		CZ	Holý Kluk		49	C	65	29	6	MMF
		D	Hammerunterwiesenthal		50	C	55	36	3	MMF/BLEF
		CZ	Kundratice		51	C	58	35	6	MMF/BLEF
			Bechlejovice		52	C	63	27	10	MMF
		D	Haselbach (Haselbach FK)		53	C	50	42	4	BLEF
	Late Eocene	CZ	Větruše		54	D	74	26	0	MMF
		CZ	Roudníky		55	C	58	30	13	MMF
		D	Kayna-Süd		56	B	18	82	0	BLEF
			Knau		57	B	8	92	0	BLEF
			Klausau		58	A	24	65	0	BLEF
			Phönix-Nord		59	A	25	74	1	BLEF
			Profen		60	A	21	77	0	BLEF
			Haselbach (Zeitz Sand)		61	B	13	80	0	BLEF
		CZ	Kučlín		62	C	46	41	12	BLEF
			Staré Sedlo		63	A	25	59	3	BLEF
			Český Chloumek		64	A	22	66	0	BLEF
			Nový Kostel		65	A	34	66	0	BLEF