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A NEW EARLY MIOCENE (OTTNANGIAN) FLORA OF THE "RZEHAKIA BEDS" FROM BRNO-LÍŠEŇ

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Abstract: The fossil flora from brackish late Burdigalian (Ottnangian) sediments in Brno-Líšeň (the Czech Republic) contributes to our knowledge of floristic evolution and palaeoclimatic changes in the Western Carpathians. The fossil material investigated for this study comprises fragmentary leaf imprints, few fruits/seeds, and dispersed pollen from a single palynomorph-rich sample. Macro remains include 3 ferns (*Osmunda parschlugiana*, *Salvinia reussii*, ?Polypodiaceae gen. et sp. indet.) and 17 angiosperms (e.g., *Daphnogene polymorpha*, "*Parrotia*" *pristina*, *Leguminophyllum* spp., *Podocarpium podocarpum*, cf. *Engelhardia orsbergensis*, *Ulmus* sp., *Schoenoplectiella* cf. *ragozinii*). The palynospectrum comprises 106 taxa, including abundant palaeotropical elements of zonal evergreen forest, i.e., Sapotaceae, Palmae, *Engelhardia*, *Platycarya*, Fagaceae, Araliaceae and *Cornus-Mastixia*, accompanied by arctotertiary elements of deciduous zonal forest (*Quercus*, *Carpinus*, *Fagus*, *Carya*, *Juglans*, *Tilia*, *Betula*, *Parrotia*) and deciduous azonal (riparian) forest (e.g., *Alnus*, *Salix*, *Ulmus*). Aquatic plants, algae (Prasinophyceae, *Botryococcus*) and marine dinoflagellates indicate a marine environment with freshwater impact. Plant taxa possibly representing open areas such as *Olea*, *Celtis*, *Buxus*, *Ephedra*, Rosaceae and Poaceae are sporadic, as well as conifers of extrazonal forest such as *Cedrus*, *Tsuga*, *Picea*. The studied palynospectrum contains abundant thermophilic elements and does not point to a cooling event, as reported by previous authors from the Polish part of the Carpathian Foredeep.

Key words: fossil flora, leaves, fruits, pollen, palaeoenvironment, Early Miocene, Carpathian Foredeep, Paratethys

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Introduction

The late Burdigalian flora (Ottnangian, Central Paratethys stage) is not well known from southern Moravia, the Czech Republic, where sediments poor in organic matter are not favourable for fossil flora preservation. Macrofloral finds and palynomorphs from temporary excavations from the eastern part of Brno (district Líšeň) offered an exceptional opportunity to improve our knowledge of this stage of floristic evolution in the area.

The fossil record of the Ottnangian "Rzehakia Beds" from Brno-Líšeň was the subject of a presentation on the "Conference on Early Tertiary" held in Brno in 1995. Zlatko Kvaček contributed with the identification of macrofloral imprints, and Nela Doláková by the preliminary evaluation of the palynospectrum from the single exceptionally rich sample. Since that time, we repeatedly planned to write a paper each time we met. Sadly, Zlatko Kvaček passed away suddenly on the 25th of October, 2020.

We dedicate this paper as a small memorial to Zlatko for his life-long expertise in Cenozoic palaeobotany.

Geological setting

Lower Miocene strata with fossil flora are a part of the Miocene sedimentary infill of the Carpathian Foredeep – a foreland basin flanging the nappe system of the Carpathians. The basin was formed by the Savian orogenetic movements in the Burdigalian. The marine transgression penetrated the seacoast with highly differentiated relief configurations. The marine facies interchanged rapidly with those of lagoons and deltas (Nehyba et al. 1997, Doláková et al. 1999). A marine transgression was followed by the deposition of brackish, lacustrine and regressive sediments in the late Burdigalian (Ottnangian), due to continuing pressure of Carpathian nappes. In the study area, the depositional environment can be interpreted as brackish lagoonal to freshwater lacustrine and deltaic on the margins of the basin.

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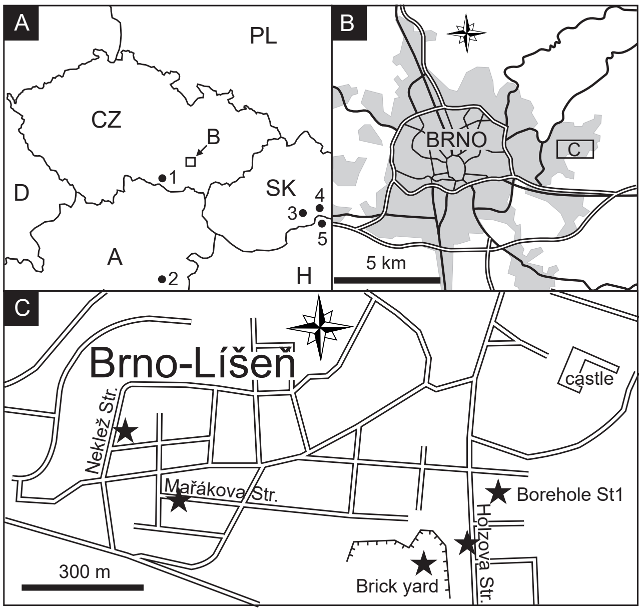


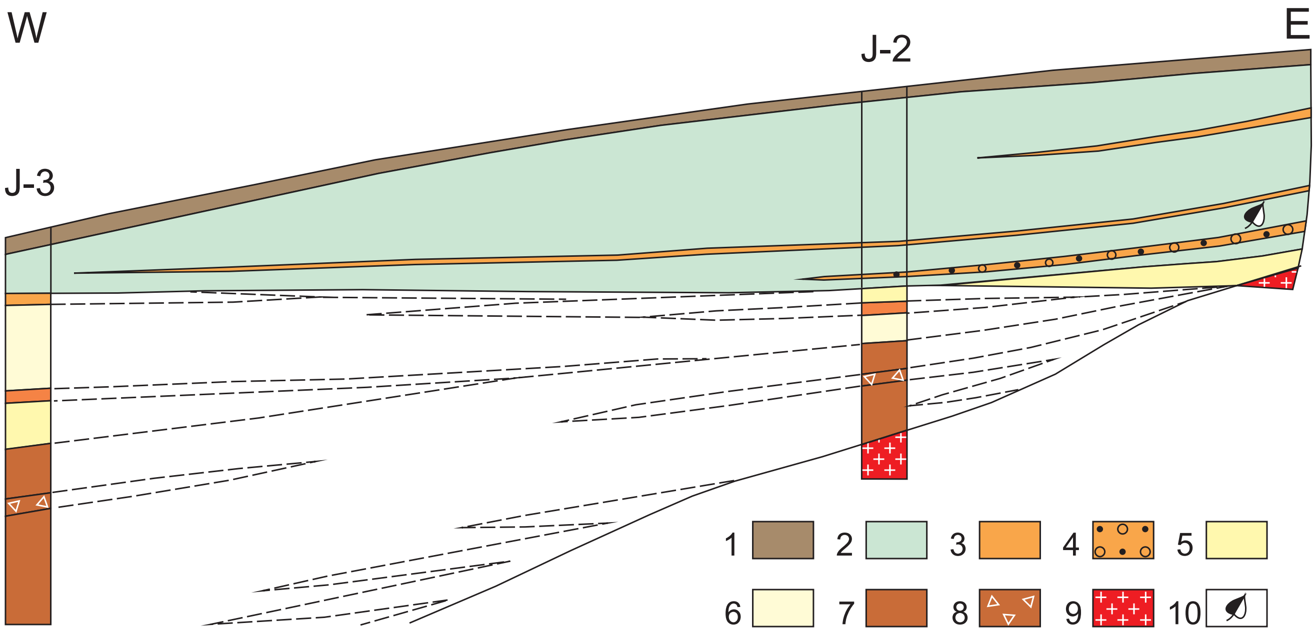
Text-fig. 1. Situation of Early Miocene plant localities. a: Central Europe with Brno area and other fossil sites mentioned in text (1 – Znojmo and Přímětice, 2 – Oberdorf, 3 – Modrý Kameň Basin, 4 – Lipovany, 5 – Ipolytarnóc; CZ – the Czech Republic, PL – Poland, SK – Slovakia, H – Hungary, A – Austria, D – Germany). b: Brno area with Líšeň municipal district indicated. c: Líšeň municipal district with fossil sites indicated by asterisk.

Text-fig. 2. Excavation at Nekležstreet in Brno-Líšeň in 1994.

The Ottnangian strata overlay the Proterozoic granodiorite of the Brno Massif. Ottnangian brackish clays, silts and sands have traditionally been called "Rzehakia Beds", referring to the endemic assemblage of molluscs dominated by the bivalve *Rzehakia socialis* (Rzehak, 1882). Čtyroký (1972) interpreted the mollusc assemblage as brachyhaline. This fauna was reported from Líšeň in previous studies (Čtyroký 1972, Čtyroký et al. 1973), and was also found in one of the herein-studied localities (borehole St1). A poor microfauna of ostracods, few poorly preserved benthic foraminifera, fish teeth and elasmobranch placoid scales indicate a brackish environment.

Material and methods

The fossiliferous sediments are represented by grey and rusty-coloured clays and silty clays. All macro remains were collected at several temporary outcrops in Brno-Líšeň (Text-fig. 1). The most representative plant collection came from excavations at Nekležstreet (49° 12′ 09.6″ N, 16° 40′ 56.2″ E; CGS point BU003; Text-figs 2, 3). A smaller collection of plant remains, mostly unidentified, came from



Text-fig. 3. "Rzehakia beds" at Líšeň-Nekležlocality. 1 – topsoil, 2 – greenish-gray clay, locally yellow-brown, 3 – ochre-brown coarse sand, 4 – conglomerate with clasts of granodiorite, 5 – grey-brown medium-grained sand, 6 – light yellowish fine sand, 7 – re-sedimented red-brown eluvium of granodiorite, 8 – re-sedimented red-brown granodiorite debris, 9 – granodiorite, 10 – fossil macroflora.

sewer excavations at Mařákova street (49° 12′ 04.7″ N, 16° 41′ 03.4″ E; CGS point BU019) and Holzova street (49° 12′ 02.9″ N, 16° 41′ 40.2″ E; CGS point BU012). The studied material was collected by the first author (M.B.) during the years 1993 – 1995.

The specimens are housed in the palaeontological collections of the Czech Geological Survey in Brno (MB80–MB112). The fossil leaf and fruit materials studied are preserved as impressions. The identification relied on gross morphological features. Attempts to obtain epidermal structures from these impressions failed.

Clays with leaf imprints did not contain palynomorphs. The palynomorph association was obtained from borehole St1 (depth 8.9–15.0 m), which was drilled in 1991 as water source along a football ground in Líšeň. The drill core comprises grey clay, brown-grey calcareous silt with *Rzehakia socialis*, brown-grey calcareous clay and subordinate grey non-calcareous clay with palynomorphs.

The sediment was subjected to chemical maceration for palynological study. The sample was treated with cold HCl (30%) and HF (70%), dissolving carbonates and silica. Separation of the palynomorphs from the rest of the residue was carried out using $ZnCl_2$ (density = 2 g/cm^3). Pure glycerine was used as the observation medium. A transmitted light microscope Alphaphot 2 with 200, 400, 1000 (oil immersion) magnifications and a SEM microscope (JEOL JSM – 649 OLV, Institute of Geological Sciences, Masaryk University, Brno) were used for pollen identification.

Plant communities were reconstructed following the ecological interpretation of the fossil plant assemblage, using information from leaf morphological characteristics and taxonomy. Abbreviations used to describe the vertical stratification of the plant community are, E1 (herbs), E2 (shrubs and lianas), E3 (trees up to 25 m tall), and E4 (trees over 25 m tall). The Integrated Plant Record vegetation analysis (Kovar-Eder et al. 2008, Teodoridis et al. 2011a, b) was applied to the leaf, carpological and pollen records. The pollen spectrum was interpreted using the Palaeotropical/Arctotertiary concept (P/A), applied according to Mai (1981, 1991), Planderová (1990) and Stuchlik (1994). The terminology of vegetation units – vegetation type (zonal, azonal, extrazonal) was used according to Kvaček et al. (2006), Kovar-Eder et al. (2008) and Kovar-Eder and Teodoridis (2018).

Systematic palaeobotany

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

Pteridophytes
Family Osmundaceae Martinov, 1820

Genus *Osmunda* L., 1753

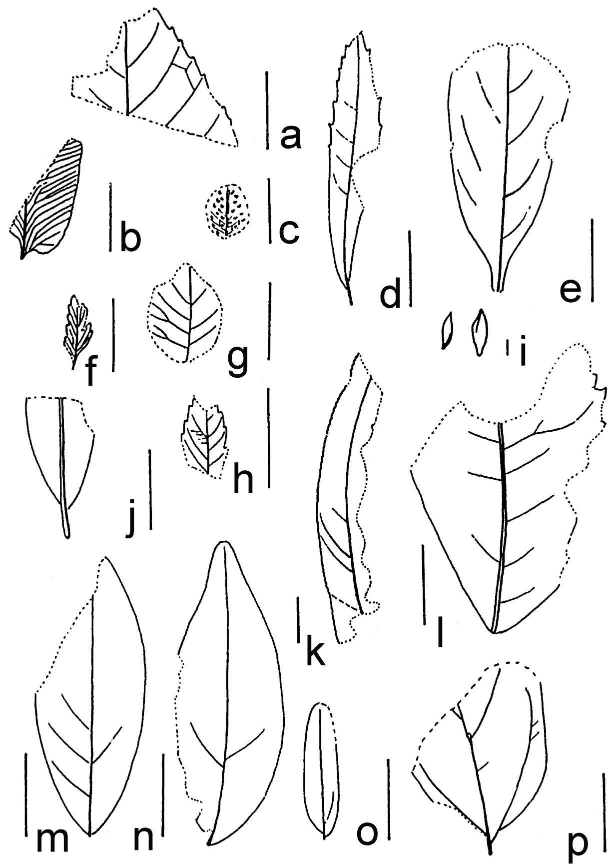
***Osmunda parschlugiana* (Unger) Andr., 1959**
Text-fig. 4b, Pl. 1, Figs 1, 2

1847 *Pteris parschlugiana* Unger, p. 122, pl. 36, fig. 6.
1959 *Osmunda parschlugiana* (Unger) Andr., p. 45.

M a t e r i a l . 4 specimens, Líšeň-Neklež (MB80–MB83).

D e s c r i p t i o n . Incomplete pinnules 13 to 22 mm long by 8 to 10 mm wide, shortly elliptic, acuminate, margin entire, midrib straight to slightly S-shaped, secondary veins free, bending towards pinnule apex, simple or forked.

R e m a r k s . *O. parschlugiana* is known from many Miocene sites of Europe. It is typified based on material from the Early/Middle Miocene flora of Parschlug (Unger 1847, Kovar-Eder et al. 2004). The pinnules are commonly known from the Early Miocene Most Formation (e.g., Bůžek 1971, Sakala 2000, Teodoridis 2006) and morphologically close to *Blechnum dentatum* (Göpp.) Heer (Kvaček and Hurník 2000). Knobloch (1969: 55) reported this fern from Uhelná, Silesia, the Czech Republic. It has also been recorded from Arctic regions, Kazakhstan, Iran and elsewhere associated with Turgayan "Arcto-tertiary" leaf assemblages (Kvaček and Bubík 2016).



Text-fig. 4. Original floral picture of locality Líšeň-Neklež drawn by Zlatko Kvaček, scale bars 10 mm. a: *Alnus* cf. *julianiformis* (Sternb.) Kvaček et Holý, MB102; b: *Osmunda parschlugiana* (Unger) Andr., MB81; c: *Salvinia reussii* Ettings., MB86; d: cf. *Engelhardia orsbergensis* (P.Wessel et C.O.Weber) Jähnichen, Mai et H.Walther, MB104; e: *Laurophyllum* sp., MB89a; f: ?Polypodiaceae gen. et sp. indet., MB84; g: *Ulmus* sp., MB105a; h: *Ulmus* sp., MB106; i: *Schoenoplectiella* cf. *ragozinii* (P.I.Dorof.) Doweld, MB88a; j: *Leguminophyllum* sp. 1, MB96; k: *Salix varians* Göpp., MB107; l: ?*Carya* sp., MB89b; m: *Leguminophyllum* sp. 1, MB97; n: *Leguminophyllum* sp. 1, MB87; o: *Podocarpium podocarpum* (A.Braun) Herend., MB100; p: "*Parrotia*" *pristina* (Ettingsh.) Stur, MB92.

Family Salviniaceae Martinov, 1820

Genus *Salvinia* Ség., 1754

***Salvinia reussii* Ettingsh., 1866**
Text-fig. 4c, Pl. 1, Fig. 3

1866 *Salvinia reussii* Ettingsh., p. 18, pl. 2, figs 21, 22.

M a t e r i a l . 1 specimen, Líšeň-Neklež (MB86).

D e s c r i p t i o n . Leaf incomplete, rounded, 9 mm long by 8 mm wide, margin entire, venation poorly preserved, secondary and intersecondary veins thin, parallel, creating an intermarginal vein, venation of higher order creating irregular nets of small tetragonal areoles with characteristic tubercles.

R e m a r k s . *Salvinia reussii* is a typical aquatic floating fern overgrowing the water surface of oxbow lakes or other calm waters characterized by typical foliage accompanied by floats (rarely) and generative organs (Bůžek et al. 1971).

Family ?Polypodiaceae J.Presl et C.Presl, 1822

?Polypodiaceae gen. et sp. indet.
Text-fig. 4f, Pl. 1, Fig. 4

M a t e r i a l . 2 specimens, Líšeň-Neklež (MB84–MB85).

D e s c r i p t i o n . Incomplete pinnules 9 and 10 mm long, 4 and 5 mm wide, shortly elliptic, acuminate, margin markedly dentate, midribs straight to slightly curved in upper part, secondary veins free, departing at acute angles, bending towards pinnule apex, simple or forked.

R e m a r k s . The fragmentary pinnules resemble fern foliage, due to their specific venation, but the character of the margin makes a more precise determination equivocal.

Angiosperms
Family Lauraceae Juss., 1789 nom. cons.

Genus *Daphnogene* Unger, 1850

***Daphnogene polymorpha* (A.Braun) Ettingsh., 1851**
Pl. 1, Figs 7, 8

1845 *Ceanothus polymorphus* A.Braun, p. 171.
1851 *Daphnogene polymorpha* (A.Braun) Ettingsh., p. 16, pl. 12, figs 22–25.

M a t e r i a l . 2 specimens, Líšeň-Neklež (MB90) and Líšeň-Mařákova (MB111).

D e s c r i p t i o n . Leaves incomplete lanceolate to widely oval, up to 25 mm long by 15 mm wide, apex not preserved probably shortly acuminate or blunt, base cuneate with fragmentary petiole (up to 7 mm), margin entire, venation suprabasal acrodromous, midrib moderate, straight or curved, lateral veins thinner, alternate, running along margin, usually connecting with secondaries at 2/3 of blade length, secondary veins thinner, alternate, departing from midrib at angles of 40° to 50°, curved and forming loops towards margin or located between midrib and lateral veins, tertiary veins alternate perpendicular, straight to sinuous, often forked, venation of higher order veins poorly preserved.

R e m a r k s . The typically tri-veined leaves of *Daphnogene polymorpha* are known from most Miocene localities of Europe (e.g., Knobloch and Kvaček 1976, Bůžek et al. 1996).

Genus *Laurophyllum* Göpp., 1854

***Laurophyllum* sp.**
Text-fig. 4e, Pl. 1, Fig. 9

M a t e r i a l . 1 specimen, Líšeň-Neklež (MB89a).

D e s c r i p t i o n . Incomplete leaf, lamina lanceolate to elliptic, 32 mm long by 22 mm wide, apex not preserved, base cuneate with fragmentary petiole, margin entire, venation brochidodromous, midrib straight, secondary veins thin, alternate, departing from midrib at angles of 40° to 60°, forming loops, tertiary veins alternate perpendicular, straight to sinuous, venation of higher order veins regular polygonal reticulate, poorly preserved.

R e m a r k s . Lauroid leaves with entire margin and brochidodromous venation with preserved epidermal structure are known in Early Miocene floras of Northern Bohemia and Moravia as *Laurophyllum pseudoprinceps* Weyland, *L. pseudovillense* Kvaček, *L. rugatum* Kvaček et Bůžek, *L. nechranicense* Bůžek et Kvaček, *L. saxonicum* Litke or *Laurophyllum* sp. (e.g., Bůžek et al. 1996, Kvaček and Hurník 2000, Kvaček and Teodoridis 2007, Holý et al. 2012).

Family Cyperaceae Juss., 1789 nom. cons.

Genus *Schoenoplectiella* Lye, 2003

***Schoenoplectiella* cf. *ragozinii* (P.I.Dorof.) Doweld, 2018**
Text-fig. 4i, Pl. 1, Fig. 5

1963 *Scirpus ragozinii* P.I.Dorof., p. 123, pl. 13, figs 38–45.
2018 *Schoenoplectiella* cf. *ragozinii* (P.I.Dorof.) Doweld, pp. 137–138.

M a t e r i a l . Numerous specimens, Líšeň-Neklež (MB88a).

D e s c r i p t i o n . Fruits 1.6–2.1 mm long, 0.7 to 1.2 mm wide, elliptical to obovate in outline, plano-convex to irregularly trigonous, often dorsoventrally flattened, apex widely round, rarely very small stalk base preserved, stalk distinct, cylindrical, truncate, surface longitudinally striate.

R e m a r k s . According to Doweld (2018), this fossil-species resembles the extant species *Schoenoplectiella mucronata* (L.) J.Jung et H.K.Choi.

Monocotyledonae gen. et sp. indet.
Pl. 1, Fig. 6

M a t e r i a l . 1 specimen, Líšeň-Mařákova (MB112).

D e s c r i p t i o n . Fragmentary strap-like leaf, apex and base not preserved, 23 mm long by 17 mm wide, margin entire, venation parallel, poorly preserved.

R e m a r k s . Due to the absence of the epidermal structure and incomplete preservation, the affinity of this monocot leaf fragment remains equivocal. The remains may belong to any of various groups of monocots, e.g., Poaceae Barnhart, Cyperaceae Juss., Sparganiaceae Hanin or Typhaceae Juss.

Family Hamamelidaceae R.Br., 1818 nom. cons.

Genus *Fothergilla* L., 1774 vel *Parrotia* C.A.Mey., 1831 vel *Shaniodendron* M.B.Deng, H.T.Wei et X.Q.Wang, 1992

"*Parrotia*" *pristina* (Ettingsh.) Stur, 1867
Text-fig. 4p, Pl. 1, Figs 10, 11

1851 *Styrax pristinum* Ettingsh., p. 19, pl. 3, fig. 9.
1867 *Parrotia pristina* (Ettingsh.) Stur, p. 4, pl. 40, figs 24, 25.

Material. 5 specimens, Líšeň-Nekležž (MB91–MB95).

Description. Incomplete leaves broadly elliptic to ovate, 19 to 26 mm long, 14 to 23 mm wide (maximum in upper third of lamina), apex round to acute, base rounded with fragmentary petiole, margin in upper part distinctly undulate, basal part entire, venation simple craspedodromous, midrib strong, straight or curved, secondary veins straight or curved upward, alternate, departing from primary vein at acute angles, basal pair distinct and opposite, tertiary veins often straight or forked, poorly preserved.

Remarks. This fossil-species is a common riparian element of Miocene plant assemblages in Europe (e.g., Bůžek 1971, Teodoridis 2003, 2006, Zidianakis et al. 2007, Worobiec 2014, Kovar-Eder and Schweigert 2018), and shows affinity to the genera *Fothergilla*, *Parrotia* and *Shaniodendron* (Kvaček and Hurník 2000, Worobiec 2014). Kvaček and Bůžek (1983) defined a plant association of *Parrotia-Ulmus pyramidalis* from the Most Basin, representing riparian vegetation along rivers and deltas.

Family Leguminosae Juss., 1789

Genus *Leguminophyllum* Escalup-Bassi, 1971

***Leguminophyllum* sp. 1**
Text-fig. 4j, m, n, Pl. 1, Figs 13, 14

Material. 3 specimens, Líšeň-Nekležž (MB87, MB96, MB99).

Description. Incomplete leaflets elliptic, 36 and 37 mm long, 14 and 13 mm wide, base asymmetric, widely cuneate, petiolule fragmentary and short, relatively thick, apex incomplete obtuse or slightly emarginate, margin entire, venation brochidodromous, midrib moderate, straight, secondary veins thinner, straight, forming loops, alternate, originating at angles of 40–50°, intersecondaries rarely discernible, thinner, parallel with secondaries, tertiary veins alternate percurrent, curved to sinuous, higher order venation regularly polygonal reticulate, poorly preserved.

Remarks. This morphotype represents relatively large and deciduous leaflets resembling legume leaflets, due to a slightly asymmetric base with fragmentary petiolule. Legume leaflets are relatively common in late Eocene to Miocene strata of Central Europe, and are described under different generic names such as *Leguminosites* Bowerb., *Leguminosae* s. l., *Robinia* L., *Cassia* L., *Dalbergia* L.f. and/or *Leguminosae* gen. et sp. (e.g., Knobloch 1969, Bůžek 1971, Bůžek et al. 1996, Teodoridis 2004, Teodoridis and Kvaček 2006, Kvaček and Walther 1998, Kvaček and Teodoridis 2011). Without knowledge of the epidermal structure and/or associated fruits, the systematic affinity is ambiguous.

***Leguminophyllum* sp. 2**
Pl. 1, Fig. 12

Material. 1 specimen, Líšeň-Nekležž (MB88b).

Description. Leaflet ovate, 18 mm long, 14 mm wide, base asymmetric, rounded to slightly cordate with fragmentary petiolule, apex shortly attenuate and blunt, margin entire, venation brochidodromous, midrib moderate, straight, secondary veins thinner, straight, looping, alternate to subopposite, originating at angles of 40–50°, intersecondaries rarely obvious, thinner, parallel with secondaries, tertiary veins alternate percurrent, curved to sinuous, higher order venation poorly preserved.

Remarks. This morphotype represents probably more than one biological species.

Genus *Podocarpium* A.Braun, 1851

***Podocarpium podocarpum* (A.Braun) Herend., 1992**
Text-fig. 4o, Pl. 2, Figs 1, 2

1836 *Gleditschia podocarpa* A.Braun in Buckland, p. 513.
1971 *Podogonium oeningense* (K.D.Koenig) Kirchh.; Bůžek, pp. 98–99, text-fig. 16, pl. 47, fig. 9, pl. 50, figs 1–27, pl. 51, figs 1–12.
1992 *Podocarpium podocarpum* (A.Braun) Herend., p. 732.

Material. 2 leaflets, Líšeň-Nekležž (MB100, MB101).

Description. Leaflets shortly petiolulate, oval, 17 and 12 mm long, 4.5 and 5 mm wide, apex acute, base asymmetric, round, margin entire, midrib strong, straight; secondary veins poorly preserved, only one camptodromous basal vein.

Remarks. The leaflets of *Podocarpium podocarpum* known from the Cheb, Sokolov and Most Basins, the Czech Republic and from Parschlug, Austria are often associated with pods (Bůžek 1971, Bůžek et al. 1996, Teodoridis 2002, 2003, 2006, Kovar-Eder et al. 2004). Gregor and Hantke (1980) suggested a close affinity between fruits of the genus *Podogonium* Heer (i.e., *Podocarpium*) and stalked fruits of *Gleditsia aquatica* Marshall and *Gleditsia heterophylla* Bunge nom. illeg., distributed in swamps in southeast USA. In contrast, Herendeen (1992) compared it with African tropical to subtropical representatives of the genera *Gilletiodendron* Vermoesen, *Cryptosepalum* Benth. and *Tessmannia* Harms. According to Kovar-Eder et al. (2004), this legume inhabited mostly gallery forests under subtropical and warm-temperate climates.

Family Betulaceae Gray, 1822 nom. cons.

Genus *Alnus* Mill., 1754

***Alnus* cf. *julianiformis* (Sternb.) Kvaček et Holý, 1974**
Text-fig. 4a, Pl. 2, Fig. 3

1823 *Phyllites julianaeformis* Sternb., pp. 37, 39, pl. 36, fig. 2.
1974 *Alnus julianaeformis* (Sternb.) Kvaček et Holý, p. 367, text-fig. 1, pls 1, 2, 3, pl. 4, fig. 1.

Material. 1 specimen, Líšeň-Nekležž (MB102).

Description. Leaf fragment, 12 mm long by 22 mm wide, apex shortly acute, base not preserved, margin simple serrate, teeth acute, sinuses acute, venation simple craspedodromous, midrib strong, secondary veins thin, distinct, alternate, curved towards the apex and margin, departing from primary vein at angles of 30° to 50°, tertiary veins often straight or forked, higher order venation poorly preserved.

R e m a r k s . *A. julianiformis* was widely distributed in Europe during the Miocene. The leaves are usually associated with infructescences of *Alnus gracilis* Unger (e.g., Knobloch and Kvaček 1996). It is a warmth-loving element with taxonomic affinities to the extant *A. trabeculosa-A. formosana* group of Southeast Asia (Kovar-Eder et al. 2004). Ecologically it is a swamp or riparian element that can survive periodical long-lasting flooding (Teodoridis 2003).

Family Myricaceae Rich. ex Kunth, 1817 nom. cons.

Genus *Comptonia* L'Hér., 1789

***Comptonia comptoniifolia* (Brongn.) Doweld, 2017**
Pl. 2, Fig. 4

1825 *Aspleniopteris difformis* Sternb., p. 33, pl. 24, fig. 1.
1906 *Comptonia difformis* (Sternb.) E.W.Berry, p. 495.
2017 *Comptonia comptoniifolia* (Brongn.) Doweld, pp. 223–224.

M a t e r i a l . 1 specimen, Líšeň-Neklež (MB103).

D e s c r i p t i o n . Fragment of pinnately lobed lamina, lobe 11 mm long by 8 mm wide, ovate, apex acute, margin entire, venation eucamptodromous, secondary veins thin, innervating one lobe, venation of higher orders poorly preserved.

R e m a r k s . The leaf fragment is safely assigned to *Comptonia comptoniifolia*, based on the characteristic venation of the entire lobe. This taxon is a typical shrub element of the Most Basin, e.g., Břešťany clay and sand-clay facies of the Žatec delta (Bůžek 1971, Kvaček and Bůžek 1983, Teodoridis 2002, 2006).

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

Genus *Carya* Nutt., 1818

?*Carya* sp.
Text-fig. 4l, Pl. 2, Fig. 5

M a t e r i a l . 1 specimen, Líšeň-Neklež (MB89b).

D e s c r i p t i o n . Incomplete leaflet asymmetric, widely elliptic, 38 mm long by 27 mm wide, base widely cuneate, apex not preserved, margin regularly simple serrate, teeth acute, sinuses angular, venation craspedodromous or semicraspedodromous, midrib strong, straight or slightly curved, secondary veins distinct, alternate, numerous, originating at 60° to 70°, thin tertiary veins numerous, alternate percurrent, straight to curved or forked, higher order venation poorly preserved.

R e m a r k s . The incomplete leaflet resembles *Carya* sp. on the basis of leaflet morphology, i.e., teeth, partly venation and secondaries originating at relatively obtuse angles. However, an affinity to other genera of Juglandaceae or Fagaceae Dumort. cannot be excluded.

Genus *Engelhardia* Lesch. ex Blume, 1826 nom. cons.

cf. *Engelhardia orsbergensis* (P.Wessel et C.O.Weber) Jähnichen, Mai et H.Walther
Text-fig. 4d, Pl. 2, Figs 6, 7

1856 *Banksia orsbergensis* P.Wessel et C.O.Weber, p. 146, pl. 25, fig. 9a–d.
1977 *Engelhardia orsbergensis* (P.Wessel et C.O.Weber) Jähnichen, Mai et H.Walther, p. 326, text-figs 1–3, pls 38–49.

M a t e r i a l . 2 specimens, Líšeň-Neklež (MB104, MB105b).

D e s c r i p t i o n . Leaflet narrow elliptic to slightly ovate, 38 mm long, 8 mm wide, apex acute, base asymmetric, cuneate, shortly petiolulate, margin in the lower part entire, higher up simply widely serrate, teeth acute, sinus angular, venation camptodromous to semicraspedodromous, midrib strong, moderately narrowed, straight to slightly curved, secondary veins distinctly thinner, numerous and dense, mostly straight, alternate, departing from midvein at angles of 50° to 80°, forming loops near margin, intersecondaries parallel with secondaries, thinner, tertiary veins straight to sinuous, higher order venation poorly preserved.

R e m a r k s . This fossil-species is widely distributed in warmer floras of the Oligocene and Miocene of Europe (e.g., Knobloch and Kvaček 1976, Kvaček and Walther 1995, Kovar-Eder et al. 2004, Walther and Kvaček 2007, Kvaček et al. 2011). Its affinities are clearly with the tribe Engelhardieae W.E.Manning, close to the living *Oreomunnea* Oerst. Due to its intermediate taxonomical position, it has been variously assigned to *Engelhardia* s. l., *Palaeocarya* Saporta or *Oreoroa* Dilcher et Manchester (Knobloch and Kvaček 1976, Jähnichen et al. 1977, 1984).

Family Salicaceae Mirb., 1815 nom. cons.

Genus *Salix* L., 1753 nom. cons.

***Salix varians* Göpp., 1855**
Text-fig. 4k, Pl. 2, Fig. 8

1855 *Salix varians* Göpp., p. 26, pl. 19, figs 17, 18, pl. 20, figs 1, 2.

M a t e r i a l . 1 specimen, Líšeň-Neklež (MB107).

D e s c r i p t i o n . Incomplete leaf lanceolate, 52 mm long by 8 mm wide, base and apex not preserved, margin crenulate to serrate with fine teeth, venation eucamptodromous to brochidodromous, midrib strong, moderate, secondary veins alternate, numerous, curved towards margin, originating at 40° to 60°, tertiary veins and higher order venation poorly preserved.

R e m a r k s . The material is assigned to *Salix varians* based on the leaf morphology. Another species, *S. haidingeri* Ettingsh., differs in more slender leaves. *S. varians* is comparable to the living *S. bonplandiana* Kunth on the basis of its leaf epidermal structure (Bůžek 1971), and is usually interpreted as a shrub element of swamps and their periphery (Kvaček and Bůžek 1983).

Family Ulmaceae Mirb., 1815 nom. cons.

Genus *Ulmus* L., 1753

***Ulmus* sp.**
Text-fig. 4g, h, Pl. 2, Figs 10, 11

Material. 2 specimens, Líšeň-Neklež (MB105a, MB106).

Description. Leaves asymmetric, ovate, 12 and 6 mm long, 9 and 5 mm wide, base incomplete round or slightly cordate, apex incomplete shortly attenuate to acute, margin double-dentate with rectangular primary teeth, secondary teeth usually finer; venation simple craspedodromous, midrib strong, moderate, straight, secondary veins thin, distinct, alternate to opposite, originating at 30° to 60°, curved towards to apex and margin, rarely forked, tertiary veins often straight or forked, venation of higher orders regular polygonal reticulate, areolation well-developed, 3 to 4 sided, veinlets branching dichotomously.

Remarks. The leaf material shows a close affinity to *Ulmus pyramidalis* Göpp. due to the distinctly dentate margin and closely spaced parallel secondary veins, but the specimens are extremely small. *Ulmus pyramidalis* can be compared to the recent species *U. americana* L., distributed in east and southeast areas of the USA as a characteristic element of riparian forests (Kvaček and Bůžek 1983). *U. pyramidalis* was a typical element of riparian forests, and probably grew on elevated habitats along rivers (levees).

Angiosperms incertae familiae

Genus *Dicotylophyllum* Saporta, 1892

***Dicotylophyllum* sp.**
Pl. 2, Fig. 9

Material. 1 specimen, Líšeň-Neklež (MB108).

Description. Incomplete leaf widely elliptic, 72 mm long by 42 mm wide, base widely cuneate, petiole fragmentary, apex not preserved, margin preserved only at basal part, entire, venation simple craspedodromous, midrib moderate, straight, secondary veins thin, distinct, alternate or opposite at basal part, 8 pairs preserved, interspaced at wide distances (up to 12 mm), curved towards apex and margin, originating at 40° to 60°, tertiary veins percurrent often straight or forked, higher order venation regular polygonal reticulate, areolation well-developed, 3- to 4-sided.

Remarks. This leaf resembles Betulaceae due to its relatively large lamina and widely spaced secondary vein pairs. However, the absence of the margin does not allow a specific assignment. Bůžek (1971) described leaves as *Alnus* sp. from Čermníky (North Bohemia, the Czech Republic), which morphologically resemble our material and leaves of *A. menzelii* Ran.-Bobr. and *A. rostaniana* Saporta emended by Mai and Walther (1991) known from the late Oligocene and Early Miocene of Europe (Teodoridis 2002).

Genus *Carpolithes* Brongn., 1822

***Carpolithes* sp. 1**
Pl. 2, Fig. 12

Material. Incomplete fruit or seed, Líšeň-Neklež (MB109).

Description. Fruit/seed elliptic, 3.5 mm long by 1.8 mm wide, upper surface smooth.

Remarks. An affinity remains open.

***Carpolithes* sp. 2**
Pl. 2, Fig. 13

Material. Incomplete fruit or seed, Líšeň-Neklež (MB110).

Description. Fruit/seed ovate, 4 mm long by 2 mm wide apex acute, base probably rounded, upper surface smooth.

Remarks. Affinity remains open.

Palynology

Over 1,330 palynomorphs representing 106 taxa were identified in the sample from borehole St1. The palynospectrum includes 24 taxa of pteridophytes, 11 taxa of gymnosperms and 67 angiosperms. Cysts of marine and brackish cyanobacteria and algae have also been identified. Systematic determination, botanical affiliation and numbers of individual taxa are given in Table 1.

Palaeoenvironmental signals

The leaf and fruit flora of Brno-Líšeň so far includes 20 vascular plant taxa – 3 ferns and 17 angiosperms (including 3 taxa of uncertain systematic affinity). Three specific vegetation assemblages can be distinguished based on the phytosociological approach. The first vegetation assemblage is a riparian vegetation preferring sandy soils and usually influenced by sporadic and repeated floodings. It includes mainly azonal elements: "*Parrotia*" *pristina* (E2), *Alnus* cf. *julianiformis* (E2), cf. *Engelhardia orsbergensis* (E3), *Salix varians* (E2), *Ulmus* sp. (E3) and azonal fern of *Osmunda parschlugiana* (E1). The second plant assemblage of reed and aquatic vegetation is characterized by azonal elements, such as *Schoenoplectiella* cf. *ragozinii* (E1), Monocotyledonae gen. et sp. indet. (E1) and *Salvinia reussii* (E1). The third vegetation assemblage corresponds to a zonal mesophytic (mesic) forest, restricted to well-drained habitats. It is characterized by the co-occurrence of the following angiosperms: *Daphnogene polymorpha* (E3), *Laurophyllum* sp. (E3), *Leguminophyllum* spp. (E3), *Podocarpium podocarpum* (E2), cf. *Carya* sp. (E3–4), *Dicotylophyllum* sp. (E2–3) and *Comptonia comptoniifolia* (E2), along with the fern of ?Polypodiaceae gen. et sp. indet. (E1) in the understorey. The mentioned vegetation assemblages depend on specific ecological conditions of the biotopes and overlap in their ecotones.

The pollen spectrum is characterized by evergreen elements (palaeotropical – 26 %), such as Sapotaceae Juss., Palmae, *Engelhardia* + *Platycarya* Siebold et Zucc. (11 %), evergreen Fagaceae (represented by pollen grains of the fossil-species *Quercoidites henrici* (R.Potonié) R.Potonié, P.W. Thomson et Thierg., *Quercoidites microhenrici* (R.Potonié) R.Potonié, P.W. Thomson et Thierg.), *Trigonobalanopsis* Kvaček et H.Walther, *Tricolporo-*

Table 1. List of determined palynomorphs from locality Brno-Líšeň (Neklež) with number of grains and percentages of relevant groups (x – rare, xxx – abundant). Palynomorphs systematically classified according to Nagy (1985), Zetter (1989), Planderová (1990), Stuchlik et al. (1994, 2014), Hofmann et al. (2002), Kvaček et al. (2002), Bouchal (2019), Denk et al. (2012), Denk and Bouchal (2021), The Palaeoflora Database (www.geologie.unibonn.de/Palaeoflora) and a palynological database PalDat (2000 onwards; www.paldat.org).

palynomorph affiliation		palynological taxa	number	%
Microforaminifera			x	
marine Dinophyta	several types	types with branched projections	xxx	
other Dinophyta	*Ovoidites*	several types	xxx	
Cyanophyta	gen. indet.	*Sigmopollis laevigatoides* Krutzsch et Pacltová	xxx	
Chlorophyta	Tasmanaceae	*Pterospermella* sp., *Pleurozonaria* sp., *Mecsekia* sp.	x	
	Botryococcus	*Botryococcus braunii* Kütz.	x	
?	gen. indet.		xxx	
Sporophyta				
Sphagnaceae	*Sphagnum*	*Stereisporites stereoides* (R.Potonié et Venitz) P.W.Thomson et Pflug	2	
		Stereisporites pseudopsilatus Krutzsch	1	
?Cyatheaceae, ?Lygodiaceae	unknown	*Toroisporis* sp.	3	
?Polypodiopsida	Filicopsida	*Leiotriletes* sp., *Triplanosporites sinuosus* Pflug ex P.W.Thomson et Pflug	18	
?Polypodiaceae	Filicopsida	*Laevigatosporites haardti* (R.Potonié et Venitz) P.W.Thomson et Pflug	28	
Davalliaceae	*Davallia*	*Verrucatosporites alienus* (R.Potonié) P.W.Thomson et Pflug	1	
Davalliaceae, Dryopteridaceae Polypodiaceae	*Davallia*, *Polypodium*	*Verrucatosporites tenellis* (Krutzsch) Krutzsch	1	
Polypodiaceae	*Polypodium*	*Verrucatosporites megafavus* Krutzsch	1	
Dennstaedtiaceae	*Paesia*	*Verrucatosporites favus* (R.Potonié) P.W.Thomson et Pflug	1	
	gen. indet.	*Foveotriletes verrucatoides* Krutzsch	1	
Gleicheniaceae, Cyatheaceae	gen. indet.	*Neogenisporis neogenicus* Krutzsch	6	
Lycopodiaceae	*Lycopodium*	*Retitriletes* sp.	1	
	Lycopodiella	*Camarozonosporites decorus* (Herb.Wolf) Krutzsch	4	
Lygodiaceae	*Lygodium*	*Leiotriletes wolffi* Krutzsch	4	
	Lygodium	*Corrugatosporites multivallatus* (P.W.Thomson et Pflug) Planderová	2	
Lygodiaceae	gen. indet.	*Leiotriletes* sp., *Triplanosporites sinuosus* Pflug ex P.W.Thomson et Pflug	11	
Osmundaceae	*Osmunda*	*Baculatisporites primarius* (Herb.Wolff) P.W.Thomson et Pflug	10	
Pteridaceae	gen. indet.	*Undulozonosporites semiverrucatus* (Krutzsch) L.Stuchlik	2	
Pteridaceae	*Pteris*	*Polypodiaceoisporites simplex* E.Nagy, *P. gracillimusv* E.Nagy, *P. helveticus* E.Nagy	25	
	Pteris	*Polypodiaceoisporites muricinguliformis* E.Nagy	1	
	Pteris	*Polypodiaceoisporites corrutoratus* E.Nagy	7	
Selaginellaceae	*Selaginella*	*Echinatisporis miocenicus* Krutzsch et Sontag	15	
	Selaginella	*Echinatisporis echinoides* Krutzsch et Pacltová	6	
	Selaginella	*Echinatisporites* cf. *bockwitzensis* Krutzsch	2	
	Selaginella	*Muerrigerisporis monstrans* Krutzsch	6	
Schizaeaceae, Dicksoniaceae	gen. indet.	*Polypodiaceoisporites marxheimensis* (Mürrig. et Pflug ex P.W.Thomson et Pflug) Krutzsch	4	
Σ of determined spores			150	11%
Gymnospermae				
Pinaceae	*Pinus*	*P. haploxylon* and *sylvestris* types	300	
	Cathaya	*Cathayapollenites krutzschi* (Sivak) Planderová	50	
Σ of *Pinus*, *Cathaya*			350	25%
	Keteleeria	*Keteleeriapollenites dubius* (Chlonova) Słodk.	2	
	Picea	*Piceapollis* sp.	5	
	Abies	*Abiespollenites* sp.	8	
	Cedrus	*Cedripites miocaenicus* Krutzsch	9	
	Tsuga	*Zonalapollenites maximus* (Raatz) Krutzsch	3	
Sciadopitaceae	*Sciadopitys*	*Sciadopityspollenites serratus* (R.Potonié et Venitz) Raatz	8	

Table 1. continued

palynomorph affiliation		palynological taxa	number	%
Taxodiaceae	*Taxodium*, *Glyptostrobus* type	*Inaperturopollenites hiatus* (R.Potonié) Thomson et Pflug, *I. concepidites* (Wodehouse) Krutzsch	30	
Ephedraceae	*Ephedra*	*Ephedripites* div. sp.	2	
Angiospermae	**Magnoliopsida**			
Altingiaceae	*Liquidambar*	*Liquidambarpollenites stigmosus* (R.Potonié) Krutzsch	6	
Amaranthaceae	aff. *Gomphrena*	*Vaclavipollis soiana* E.Nagy	1	
Aquifoliaceae	*Ilex*	*Ilexpollenites iliacus* (E.Potonié) Thierg. ex R.Potonié	12	
	Ilex	*Ilexpollenites margaritatus* (R.Potonié) Raatz ex R.Potonié	15	
	Ilex	*Ilexpollenites propinquus* (R.Potonié) R.Potonié	12	
Araliaceae	*Acantopanax*, *Aralia*	*Araliaceoipollenites euphorii* (R.Potonié) R.Potonié	2	
Betulaceae	*Alnus*	*Alnipollenites verus* R.Potonié	27	
	Betula	*Betulaepollenites betuloides* (Pflug) E.Nagy	70	
	Carpinus	*Carpinidites carpinoides* (Pflug) E.Nagy	2	
Buxaceae	*Buxus*	*Buxapollis buxoides* Krutzsch	3	
Cannabaceae	*Celtis*	*Celtipollenites* sp.	31	
Cornaceae	Cornoideae, Mastixioideae	*Cornaceaepollis satzveyensis* (Pflug) Ziemb.-Tworz.	2	
Cornaceae, Mastixioideae, Vitaceae		*Cornaceaepollis minor* (Stuchlik) Stuchlik, *C. major* (Stuchlik) Stuchlik	2	
Cyrillaceae, Clethraceae	gen. indet.	*Tricolporopollenites megaexactus* (R.Potonié) Thomson et Pflug	21	
	gen. indet.	*Tricolporopollenites exactus* (R.Potonié) Grab.	10	
?Droseraceae		*?Drosera*	1	
Ericaceae	*Erica*	*Ericipites ericius* (R.Potonié) R.Potonié	2	
	gen. indet.	*Ericipites* div. sp.	1	
Eucommiaceae	*Eucommia*	*Eucommioipollis parmularius* (R.Potonié) Ziemb.-Tworz.	2	
Fagaceae	?Castaneoideae, ?*Trigonobalanopsis*	*Tricolporopollenites cingulum* subsp. *oviformis* (R.Potonié) P.W.Thomson et Pflug	12	
	?Castaneoideae × Lythraeae (*Decodon*)	*Tricolporopollenites cingulum* subsp. *pusillus* (R.Potonié) P.W.Thomson et Pflug	50	
	Trigonobalanus	*Fususpollenites fusus* (R.Potonié) Kedves	1	
	Castaneoideae × *Eotrigonobalanus*	*Tricolporopollenites pseudocingulum* (R.Potonié) P.W.Thomson et Pflug	10	
	Quercoideae gen. indet.	*Quercoidites henrici* (R.Potonié) R.Potonié, P.W.Thomson et Thierg.	19	
	Quercoideae gen. indet.	*Quercoidites microhenrici* (R.Potonié) R.Potonié, P.W.Thomson et Thierg.	51	
	Quercus	*Quercoidites granulatus* (E.Nagy) Słodk., *Quercoidites* sp.	9	
	Fagus	*Faguspollenites verus* Raatz	3	
Fabaceae, Fagaceae, Combretaceae	gen. indet.	*Tricolporopollenites falax* (R.Potonié) Krutzsch	5	
	gen. indet.	*Tricolporopollenites liblarensis* (P.W.Thomson) Grab.	52	
Haloragaceae	*Myriophyllum*	*Myriophyllum* sp.	1	
Hamamelidaceae	*Parrotia-Distylium type*	*Tricolporopollenites indeterminatus* (Romanovicz) Ziemb.-Tworz.	2	
Juglandaceae	*Carya*	*Caryapollenites simplex* (R.Potonié) Raatz	59	
	Pterocarya/Cyclocarya	*Pterocaryapollenites stellatus* (R.Potonié) Thierg.	18	
	Juglans	*Juglanspollenites verus* Raatz	32	
	Engelhardia	*Engelhardtioidites punctatus* (R.Potonié) R.Potonié, *E. quietus* (R.Potonié) R.Potonié	120	
	Platycarya	*Platycaryapollenites miocaenicus* E.Nagy	25	
Loranthaceae, Santalaceae	*Loranthus*	*Gothanipoll gothani* Krutzsch	2	
Myricaceae	*Myrica*	*Myricipites* sp.	43	
Nyssaceae	*Nyssa*	*Nyssapollenites kruschi* (R.Potonié) E.Nagy	2	
Oleaceae	*Olea*	*Oleaidearumpollenites* sp.	70	
	Fraxinus	*Fraxinus* sp.	40	
	Ligustrum/Syringa type	*Ligustrum/Syringa* type	1	
Plantaginaceae	*Plantago*	*Plantaginacearumpollenites miocaenicus* E.Nagy	1	
Platanaceae	*Platanus*	*Platanipollis ipelensis* (Pacltová) Grab.	9	

Table 1. continued

palynomorph affiliation		palynological taxa	number	%
Rosaceae	*Rubus* type	cf. *Rubus* type	2	
Rutaceae	gen. indet.	*Rutacearumpollenites* sp.	5	
Rutaceae	gen. indet.	*Rutacearumpollenites rutaceoides* Kohlm.-Adam. et Ziemb.-Tworz.	2	
Salicaceae	*Salix*	*Salixpollenites* sp.	3	
Sapotaceae	gen. indet. – several types	*Sapotaceoidaepollenites* div. sp.	11	
Staphyleaceae	*Staphylea*	*Staphylea* sp.	1	
Sterculiaceae	*Reevesia*	*Reevesiapollis triangulus* (Mamczar) Krutzsch	3	
Symplocaceae	*Symplocos*	*Symplocoidites latiporis* (P.W.Thomson et Pflug) Słodk.	5	
	Symplocos	*Symplocoidites vestibulum* (R.Potonié) R.Potonié	8	
Tamaricaceae	?*Tamarix*	*Tamarixpollenites* sp.	2	
Malvaceae, Tilioideae	cf. *Craigia*	*Intratriporopollenites insculptus* Mai	2	
	Tilia	*Intratriporopollenites instructus* (R.Potonié) P.W.Thomson et Pflug	10	
Theaceae	Gordonieae	*Gordonipollenites microreticulatus* Kohlm.-Adam. et Ziemb.-Tworz.	1	
Tricolporopollenites indet.	gen. indet. – several types	*Tricolporopollenites* indet.	100	
Ulmaceae	*Ulmus*	*Ulmipollenites undulosus* Herb.Wolf	42	
	gen. indet., *Zelkova*?			
Vitaceae	*Parthenocissus*	*Tricolporopollenites marcodurensis* P.W.Thomson et Pflug	2	
	Liliopsida			
Arecaceae	gen. indet.	*Arecipites* sp.	5	
	Calamus	*Dicolpopollis kockeli* Pflanzl	8	
Cyperaceae	gen. indet.	*Cyperaceaepollis* Krutzsch	4	
Poaceae	gen. indet.	*Graminidites* sp.	29	
Potamogetaceae	*Potamogeton*	*Potamogeton* sp.	12	
Sparganiaceae	*Sparganium*	*Sparganiaceaepollenites* sp.	10	
Σ of determined grains			**1,706**	
Σ of determined grains without *Pinus*, *Cathaya*			**1,356**	**100%**
evergreen woody elements (palaeotropical)			**351**	**26%**
deciduous woody (arctotertiary) elements			**197**	**15%**
azonal elements without ferns			**656**	**48%**

pollenites liblarensis (P.W.Thomson) Grab., Araliaceae Juss., *Symplocos* Jacq., *Reevesia* Lindl., *Cornus-Mastixia*, Rutaceae Juss., *Parthenocissus* Planch. (Pls 3, 4, 5). Deciduous woody (arctotertiary) elements, i.e., *Quercus* L. – "deciduous oak types", *Carpinus* L., *Fagus* L., *Carya*, *Juglans* L., *Tilia* L., *Betula* L., *Zelkova* Spach, *Parrotia* and *Eucommia* Oliv. (Pls 3, 4, 5) make up 15 % of the assemblage. Various communities of moisture-loving vegetation are significantly represented. Occurrences of coastal swamp elements (Taxodioideae Endl. ex K.Koch, Cyrillaceae Lindl., Myricaceae Rich. ex Kunth, *Decodon* J.F.Gmel., infrequent *Nyssa* L.) and deciduous riparian forest elements (*Alnus*, *Salix*, *Ulmus*, *Fraxinus* L., *Liquidambar* L., *Pterocarya* Kunth, *Platanus* L.) are indicated. Typical for this association is a higher proportion (11 %) of thermophilic as well as temperate ferns: *Pteris* L., *Davallia* Sm., *Osmunda* L., Gleicheniaceae C.Presl, Lygodiaceae C.Presl, Schizaeaceae Kaulf., Dennstaedtiaceae Pic.Serm, Polypodiacea J.Presl et C. Presl. The high proportion and diversity of morphologically distinct spores of *Selaginella* is a striking feature of the studied palynospectrum (Pl. 3). Findings of spore couplets of the genus *Lycopodiella* Holub are also interesting (Pl. 3, Fig. 5, Pl. 5, Fig. 4a–c). Aquatic flora – *Sparganium* L., *Potamogeton* L., single grains of *Myriophyllum* L. – and elements of waterlogged areas – Cyperaceae Juss., sporadic *Sphagnum* L., unique tetrads closely similar to *Drosera* L. (Pl. 3, Fig. 25) – is represented as well. Pollen grains representing plants that can occur in open areas and heliophytes (*Olea* L., *Celtis* L., Ericaceae Juss., *Buxus* L., Rosaceae Juss., *Ephedra* L., Poaceae Barnhart, *Salvia* L.) are scarce. Conifers represented mainly by *Pinus* L. and *Cathaya* Chun et Kuang (21 %) complement the image of the vegetation. Elements of extrazonal mountain forest such as *Cedrus* Trew, *Tsuga* (Endl.) Carrière, *Picea* A.Dietr., *Abies* Mill., *Keteleeria* Carrière are also present, but in low numbers. The marine dinoflagellates (Pl. 3, Fig. 27), green algae Prasinophyceae, sporadically *Botryococcus* Kütz., together with some aquatic plants mentioned above, indicate a marine environment with freshwater impact. Several findings of Normapolles group pollen (Pl. 3, Fig. 26) indicate re-deposition from older, probably Cretaceous sediments.

Numerous structured rounded objects were found, somewhat resembling pollen grains of *Potamogeton*. However, SEM studies revealed an almost smooth surface morphology, quite different from *Potamogeton*. Probably these objects are bodies or cysts of planktonic green algae (Pl. 3, Fig. 24, Pl. 5, Fig. 5a, b).

Focusing on the results derived from the Integrated Plant Record (IPR) vegetation analysis applied on the leaf, carpological and pollen records, the predicted zonal vegetation type for Brno-Líšeň is a transitional vegetation (ecotone) between zonal subtropical broad-leaved evergreen forest (BLEF) and zonal warm-temperate to subtropical mixed mesophytic forest (MMF). The specific pattern of the key components is as follows: broad-leaved deciduous (BLD) – 53.3 %, broad-leaved evergreen (BLE) – 32.2 %, sclerophyllous + legume-like (SCL+LEG) – 12 % and zonal herbaceous (ZONAL HERB) – 23.5 %; number of zonal taxa – 90, number of zonal woody elements – 60 (App. I).

Discussion and floristic correlation with some Early Miocene localities of Central Europe

Regarding the representation of different types of palynomorphs in previous studies dealing with the Carpathian Foredeep (Doláková et al. 1999, Doláková 2004, Kováčová et al. 2011), several interesting similarities were found. The higher representation of *Symplocos* and Rutaceae pollen in the samples of Eggenburgian – Ottnangian (Aquitanian – Burdigalian) age is interesting, and is not recorded from the younger stages (Karpatian, Badenian, i.e., upper Burdigalian, Langhian). *Ulmus* and *Fraxinus* predominate over *Alnus* in riparian communities. At the Eggenburgian/Ottnangian and Ottnangian/Karpatian transitions, higher proportions and diversity of morphologically conspicuous spores of *Selaginella* accompanied by an increased frequency of other pteridophytes were already revealed by previous palynological studies of the Carpathian Foredeep, and may be related to higher climate and substrate humidity during transgressions. Mountain conifer elements such as *Tsuga* are markedly rarer than in younger strata, which may reflect the gradual emergence of the Carpathian mountain ridges.

Macroflora (dispersed leaves, fruits and seeds) findings are very rare from the Early Miocene period of the southern part of the Carpathian Foredeep. A unique oryctocoenosis from Lower Miocene strata from Znojmo and Přímětice (southern part of the Carpathian Foredeep in Czech Republic; Text-fig. 1) has been described by Knobloch (1969, 1982, 1984), who recognised several ecologically different associations:

a) Shrub-herbaceous heliophilous vegetation with representatives of evergreen sclerophyllous woody plants.

b) Swamp vegetation similar to our locality, with *Glyptostrobus* Endl., *Myrica* L., an aquatic flora with *Salvinia*, *Potamogeton*, *Nymphaea* L., and coastal reed with *Typha* L., *Decodon*, *Sparganium*, were identified.

Palynological investigations of the *Rzehakia* beds (Ottnangian – Karpatian, i.e., upper Burdigalian) in the Slovak part of the Modrý Kameň Basin (Novohrad-Nógrad Basin, Salgótraján Formation; Text-fig. 1) indicated a temperate to subtropical climate with few arctotertiary elements (Planderová 1973, Doláková 2004). Typical is the presence of pollen of the fossil-genus *Pentapollenites* Krutzsch (Nagy 1985, Planderová 1990). The palynospectra are similar to the ones from the Carpathian Foredeep, except for the presence of *Pentapollenites*, which has not been recorded from the Carpathian Foredeep.

Němejc and Knobloch (1973) regarded the macroflora from the Salgótraján Formation from Lipovany (Faziostratotypus of the Ottnangian Stage; Text-fig. 1) as subtropical humid. They considered this association as evidence of a major warm oscillation in the Early Miocene.

Rich plant Ottnangian assemblages (leaf, palynomorphs and diaspores) were studied from the basal layers of the lignite-bearing sequence in the opencast mine Oberdorf (Styria, Austria; Text-fig. 1) (Meller et al. 1999). Elements of open-water habitats, reed associations, peatbogs, swamp and riparian forest, as well as mesophytic forest were detected; the latter was classified as "Younger Mastixoid" assemblage sensu Mai (1964). The plant assemblages from all overlying layers are of lower diversity then in the basal strata. This was interpreted to be due to differences in the depositional facies. However, some of the subtropical taxa characteristic of "Younger Mastixoid" assemblages (e.g., *Mastixia* Blume, *Symplocos*, *Toddalia* Juss., *Zanthoxylum* L. (Rutaceae)) occur not only in the basal layers but in the upper part of the sequence as well. Climatic conditions were interpreted as subtropical humid. This interpretation is very similar to our results as concerns the Carpathian Foredeep and the Brno-Líšeň locality (Doláková et al. 1999, Doláková 2004, Kováčová et al. 2011).

According to Nagy (1969, 2005), the Early Miocene was the warmest sub-epoch of the Miocene in the Pannonian Basin, and its palynomorphs indicate a warm subtropical climate. During the Ottnangian in the Mecsek Mountains (Hungary), the number of temperate elements increased, but relatively numerous tropical ferns also occurred. In northern Hungary, brown coal-forming swamp forests were typical of this period.

At Ipolytarnóc (lower Ottnangian, Nógrád Basin, Hungary), the mass co-occurrence of lauraceous leaves, needle leaves and cones of Pinaceae Spreng. ex F.Rudolphi and palms indicates extensive lauraceous forests with abundant Pinaceae near the shore (Hably 1985; Text-fig. 1). The large size of the *Laurus* L. and *Platanus neptuni* leaves and frequent ferns testify to development under humid conditions. At the beginning of the Ottnangian, a warm subtropical climate prevailed in Ipolytarnóc. Erdei et al. (2007) evaluated the flora of Ipolytarnóc as the complex interrelation of tectonic-palaeogeographic evolution, climate, flora and vegetation development through the Neogene of the Pannonian domain. These authors infer warmer climate conditions and slightly higher mean annual precipitation than for floras younger than Karpatian stage. Similar humid conditions can also be assumed for the studied locality Brno-Líšeň, based on the high number and increased diversity of fern spores there.

In the uppermost Ottnangian-lower Karpatian interval, plant assemblages with higher proportion of arctotertiary elements (markedly cooler) were described by several authors from the Carpathian Foredeep in the Polish Lowland (Oszast and Stuchlik 1977, Stuchlik 1980, Sadowska 1989, Ważyńska 1998, Hably 2020). The decrease in thermophilous elements in the Ottnangian-lower Karpatian has been recognized and defined as the microfloristic Zone MF-3 by Planderová (1990) and Planderová et al. (1993a, b). This cooling event has never been observed in palynospectra of the Carpathian Foredeep in Moravia (Doláková et al. 1999, Doláková 2004, Kováčová et al. 2011). Floristic changes recorded from the Polish Lowland may reflect differences in palaeogeography.

Conclusions

Macroflora remains (leaf imprints, fruits/seeds) and a rich palynomorph association were recovered from brackish sediments of the Burdigalian (Ottnangian) "*Rzehakia* beds", which have previously been considered to be generally poor in plant fossils. The study of this fossil material generated valuable information on vegetation at the margin of the Western Carpathian foreland basin during the Early Miocene:

1) Macro remains include three ferns (*Osmunda parschlugiana*, *Salvinia reussii*, ?Polypodiaceae indet.) and 17 angiosperms (e.g., *Daphnogene polymorpha*, "*Parrotia*" *pristina*, *Leguminophyllum* spp., *Podocarpium podocarpum*, cf. *Engelhardia orsbergensis*, *Ulmus* sp., *Schoenoplectiella* cf. *ragozinii*).

2) The rich palynological record contained 106 taxa (24 pteridophytes, 11 gymnosperms and 67 angiosperms). It comprises abundant palaeotropical elements of zonal evergreen forest, accompanied by arctotertiary elements of deciduous zonal forest, azonal coastal swampy and deciduous riparian forests. Vegetation of open areas and heliophytes, as well as conifers of extrazonal forest, are sporadic. Aquatic plants, algae (Prasinophyceae, *Botryococcus*) and marine dinoflagellates indicate the marine environment with freshwater impact.

3) Based on the leaf, carpological and pollen records, the Integrated Plant Record (IPR) vegetation analysis predicts the zonal vegetation type ecotone (transitional vegetation) between zonal subtropical broad-leaved evergreen forest (BLEF) and zonal warm-temperate to subtropical mixed mesophytic forest (MMF) for Brno-Líšeň. Compared to other localities of fossil plants from the vicinity of the Central Paratethys similar in age, the plant communities are of similar character. The studied palynospectrum contains a large proportion of thermophilous elements, and does not point to a cooling event during the late Burdigalian (Ottnangian) in the studied area.

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Explanations of the plates

PLATE 1

Osmunda parschlugiana (Unger) Andr.
1. Incomplete pinnule, Líšeň-Nekležˇ, MB80.
2. Incomplete pinnule, Líšeň-Nekležˇ, MB81.

Salvinia reussii Ettingsh.
3. Incomplete rounded leaf, Líšeň-Nekležˇ, MB86.

?Polypodiaceae gen. et sp. indet.
4. incomplete pinnule with markedly dentate margin, Líšeň-Nekležˇ, MB84.

Schoenoplectiella cf. *ragozinii* (P.I.Dorof.) Doweld
5. Fruits, Líšeň-Nekležˇ, MB88a.

Monocotyledonae gen. et sp. indet.
6. Leaf fragment, Líšeň-Mařákova, MB112.

Daphnogene polymorpha (A.Braun) Ettingsh.
7. Incomplete leaf, Líšeň-Nekležˇ, MB90.
8. Incomplete leaf, Líšeň-Mařákova, MB111.

Laurophyllum sp.
9. Incomplete leaf, Líšeň-Nekležˇ, MB89a.

"*Parrotia*" *pristina* (Ettingsh.) Stur
10. Incomplete leaf, Líšeň-Nekležˇ, MB91.
11. Incomplete leaf, Líšeň-Nekležˇ, MB92.

Leguminophyllum sp. 2
12. Complete leaflet, Líšeň-Nekležˇ, MB88b.

Leguminophyllum sp. 1
13. Incomplete leaf, Líšeň-Nekležˇ, MB97.
14. Incomplete leaf and its counterpart, Líšeň-Nekležˇ, MB96.

Scale bars 5 mm.

PLATE 2

Podocarpium podocarpum (A.Braun) Herend.
1. Complete leaflet, Líšeň-Nekležˇ, MB100.
2. Incomplete leaflet, Líšeň-Nekležˇ, MB101.

Alnus cf. *julianiformis* (Sternb.) Kvaček et Holý
3. Leaf fragment, Líšeň-Nekležˇ, MB102.

Comptonia comptoniifolia (Brongn.) Doweld
4. Leaf fragment, Líšeň-Nekležˇ, MB103.

? *Carya* sp.
5. Incomplete leaflet, Líšeň-Nekležˇ, MB89b.

cf. *Engelhardia orsbergensis* (P.Wessel et C.O.Weber) Jähnichen, Mai et H.Walther
6. Leaflet fragment with simply widely serrate margin, Líšeň-Nekležˇ, MB105b.
7. Isolated leaflet, Líšeň-Nekležˇ, MB104.

Salix varians Göpp.
8. Incomplete leaf, Líšeň-Nekležˇ, MB107.

Dicotylophyllum sp.
9. Incomplete leaf, Líšeň-Nekležˇ, MB108.

Ulmus sp.
10. Incomplete leaf, Líšeň-Nekležˇ, MB105a.
11. Incomplete leaf, Líšeň-Nekležˇ, MB106.

Carpolithes sp. 1
12. Incomplete fruit or seed, Líšeň-Nekležˇ, MB109.

Carpolithes sp. 2
13. Incomplete fruit or seed, Líšeň-Nekležˇ, MB110.

Scale bars 5 mm for Figs 1–11 and 2 mm for Figs 12, 13.

PLATE 3

Palynomorphs, Líšeň, borehole St1

1. *Muerrigerisporis monstrans* Krutzsch.
2. *Echinatisporis miocenicus* Krutzsch et Sontag.
3. *Polypodiaceoisporites muricinguliformis* E.Nagy.
5. *Camarozonosporites decorus* (Herb.Wolf) Krutzsch.
6. *Potamogeton* sp.
7. *Ilexpollenites iliacus* (R.Potonié) Thierg. ex R.Potonié.
8. *Ilexpollenites propinquus* (R.Potonié) R.Potonié.
9. *Myriophyllum* sp.
10. *Rutacearumpollenites* sp.
11. *Tricolporopollenites indeterminatus* (Romanowicz) Ziemb.-Tworz.
12. *Gordonipollenites microreticulatus* Kohlm.-Adam. et Ziemb.-Tworz.
13. *Tricolporopollenites cingulum* subsp. *pusillus* (R.Potonié) P.W.Thomson et Pflug.
14. *Symplocoidites vestibulum* (R.Potonié) R.Potonié.
15. *Platycaryapollenites miocaenicus* E.Nagy.
16. *Salixpollenites* sp.
17. *Araliaceoipollenites euphorii* (R.Potonié) R.Potonié.
18. *Quercoidites henrici* (R.Potonié) R.Potonié, P.W.Thomson et Thierg.
19. *Gothanipollenites gothani* Krutzsch.
20. *Celtipollenites* sp.
21. *Oleaidearumpollenites* sp.
22. *Fraxinus* sp.
23. Rosaceae *Rubus* type.
24. ?Chlorophyta.
25. ?*Drosera*.
26. Normapolles group.
27. Marine Dinophyta.

Figs 1–26 magnification 1,000×, Fig. 27 magnification 500×.

PLATE 4

Palynomorphs, Líšeň, borehole St1

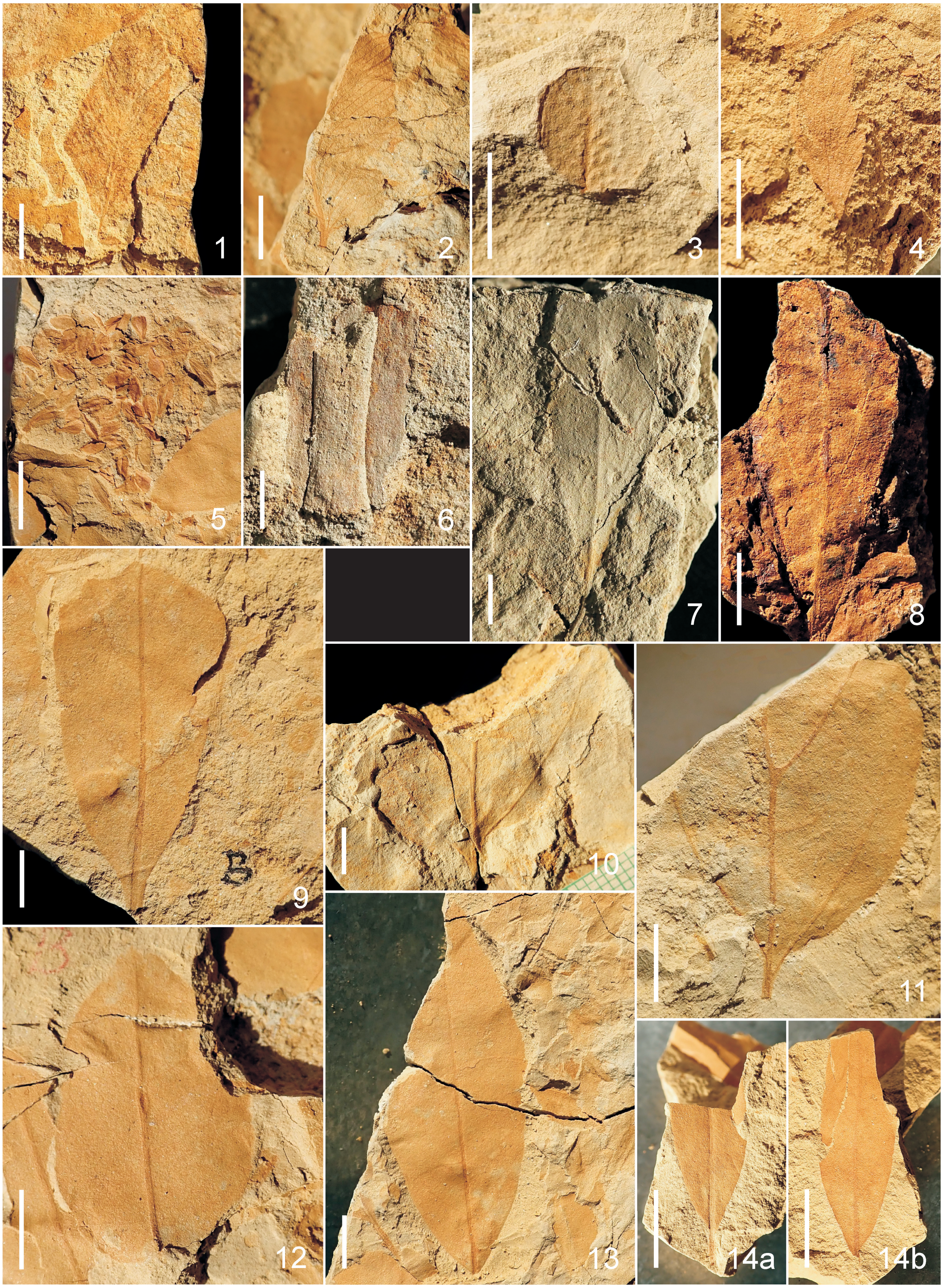
1. *Quercoidites microhenrici* (R.Potonié) R.Potonié, P.W.Thomson et Thierg. (affiliation: *Quercus*, infrageneric group *Quercus* vel Lobatae 1; Denk et al. 2012); a: LM 1,000×, b, c: SEM.
2. *Quercoidites microhenrici* (R.Potonié) R.Potonié, P.W.Thomson et Thierg. (affiliation: *Quercus*, infrageneric group *Cerris*; Denk et al. 2012); a: LM 1,000×, b, c: SEM.
3. *Quercoidites granulatus* (E.Nagy) Słodk. (affiliation: *Quercus*, infrageneric group *Quercus* vel Lobatae 2; Denk et al. 2012); a: LM 1,000×, b, c: SEM.
4. *Tricolporopollenites pseudocingulum* (R.Potonié) P.W.Thomson et Pflug (affiliation: Castaneoideae; Kohlman-Adamska and Ziembinska-Tworzydlo 2000 × *Eotrigonobalanus*; Denk et al. 2012); a: LM 1,000×, b, c: SEM.
5. *Sapotaceoidaepollenites* sp. (affiliation: Sapotaceae); a: LM 1,000×, b, c: SEM.

PLATE 5

Palynomorphs, Líšeň, borehole St1

1. *Tricolporopollenites liblarensis* (P.W.Thomson) Grab. (affiliation: Fabaceae × Fagaceae × Vitaceae); a: LM 1,000×, b, c: SEM.
2. *Platanipollis ipelensis* (Pacltová) Grab. (affiliation: *Platanus* sp.); a: LM 1,000×, b, c: SEM.
3. *Ligustrum*/*Syringa* type; a: LM 1,000×, b, c: SEM.
4. *Camarozonosporites decorus* (Herb.Wolf) Krutzsch (affiliation: *Lycopodiella*); a: LM 1,000×, b, c: SEM.
5. Chlorophyta type; a: LM 1,000×, b: SEM.
6. *Leiotriletes wolffi* Krutzsch (affiliation: *Lygodium*); a: LM 1,000×, b: SEM.

PLATE 1



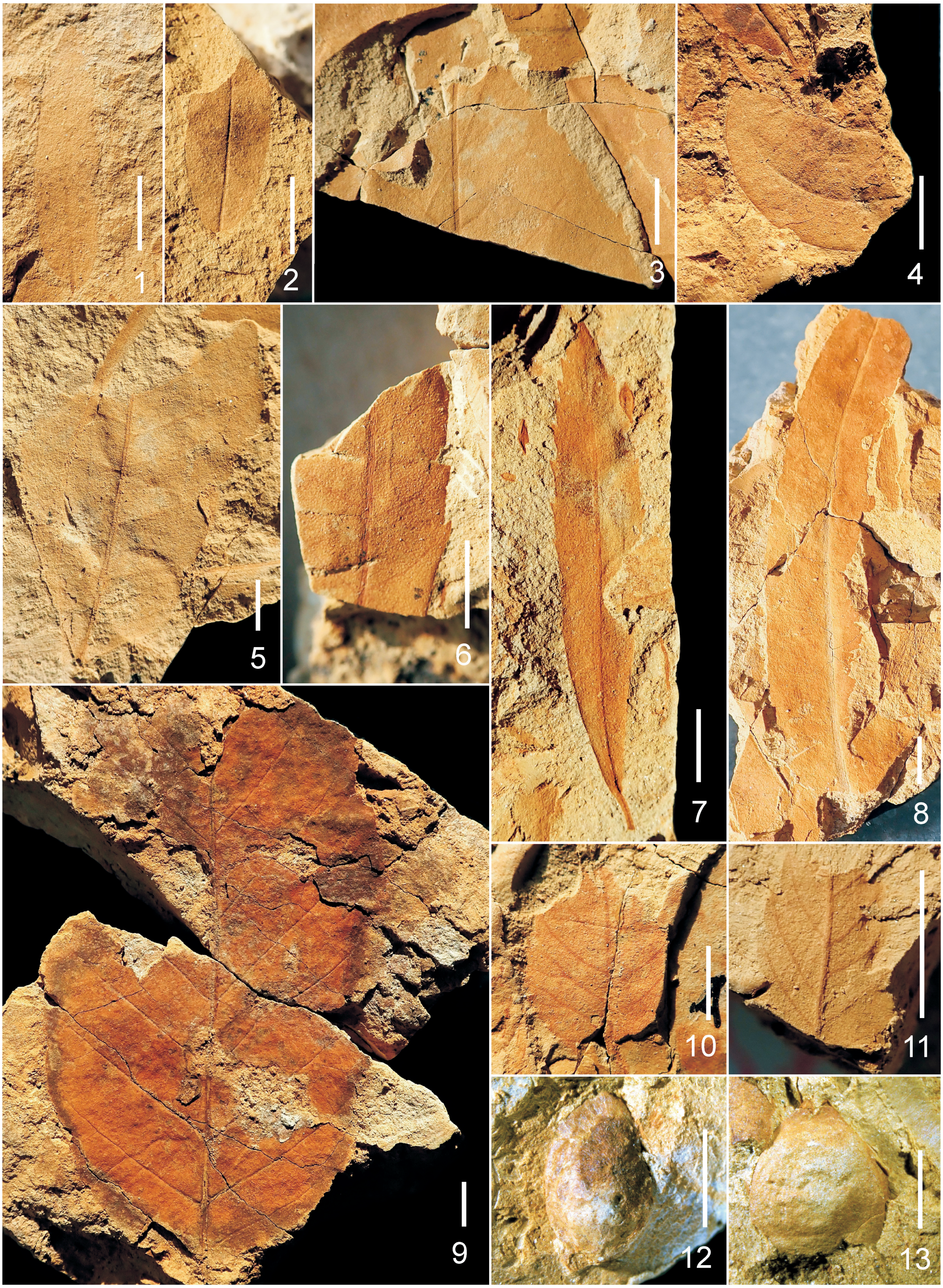

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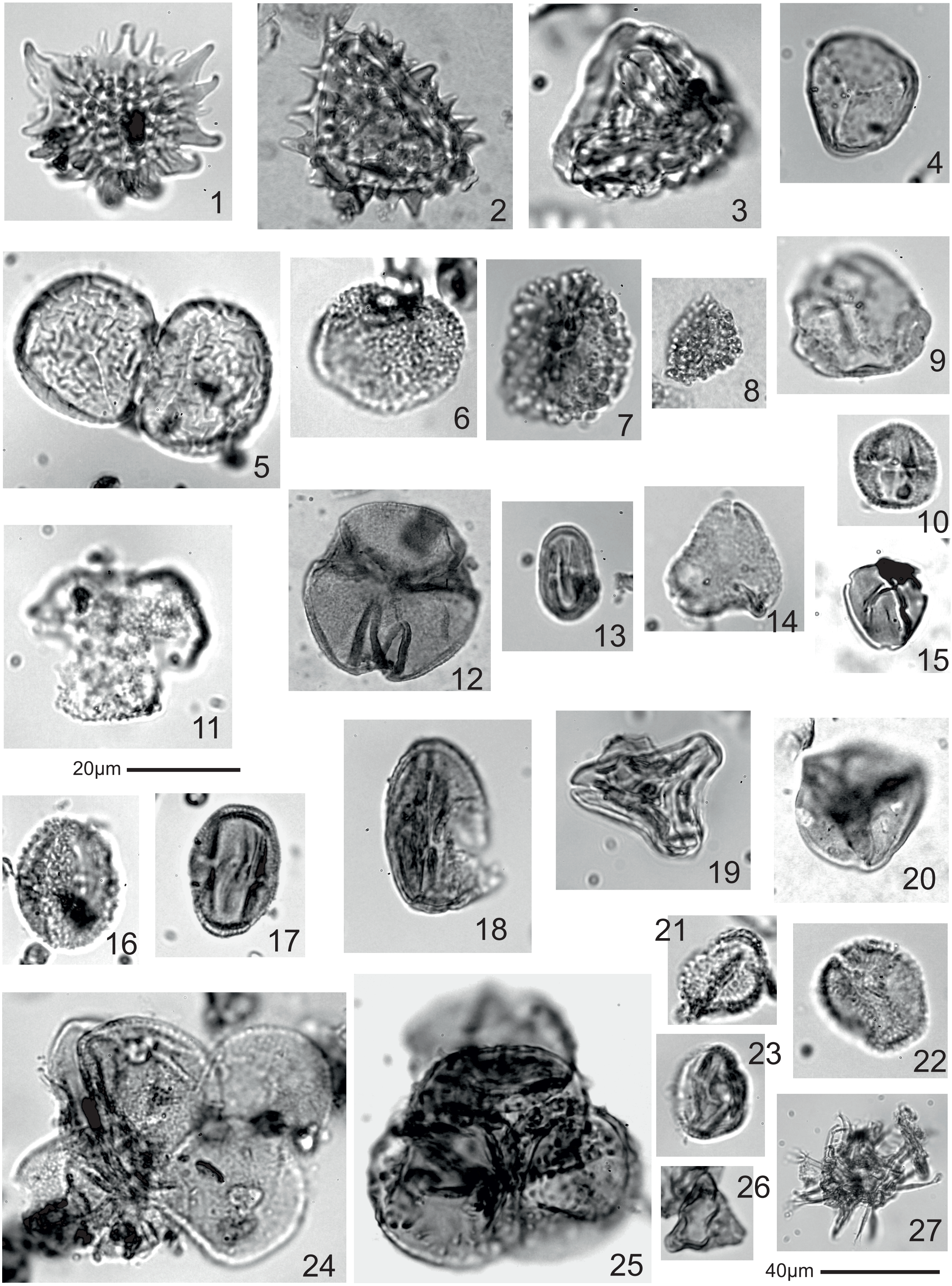
PLATE 3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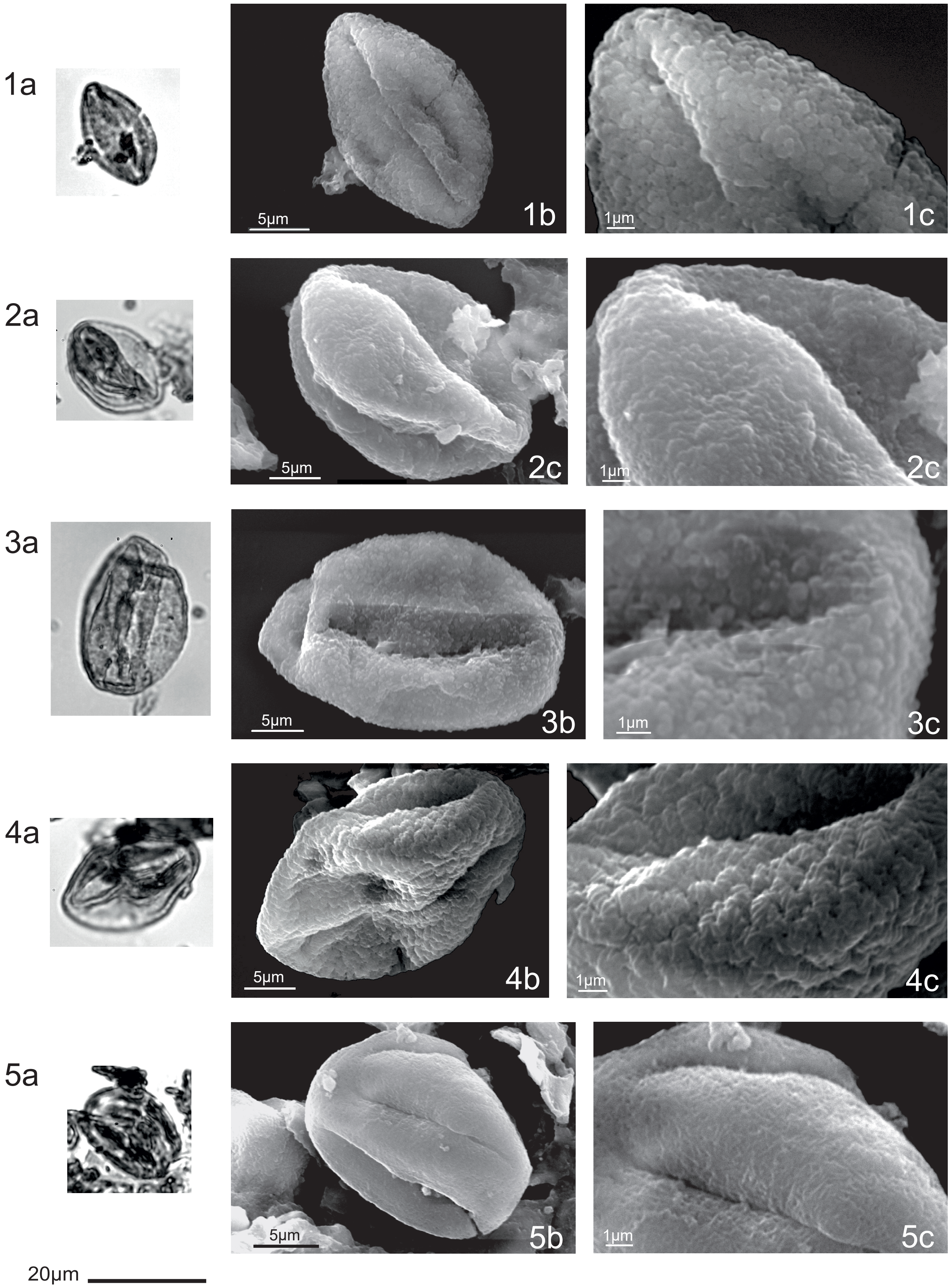
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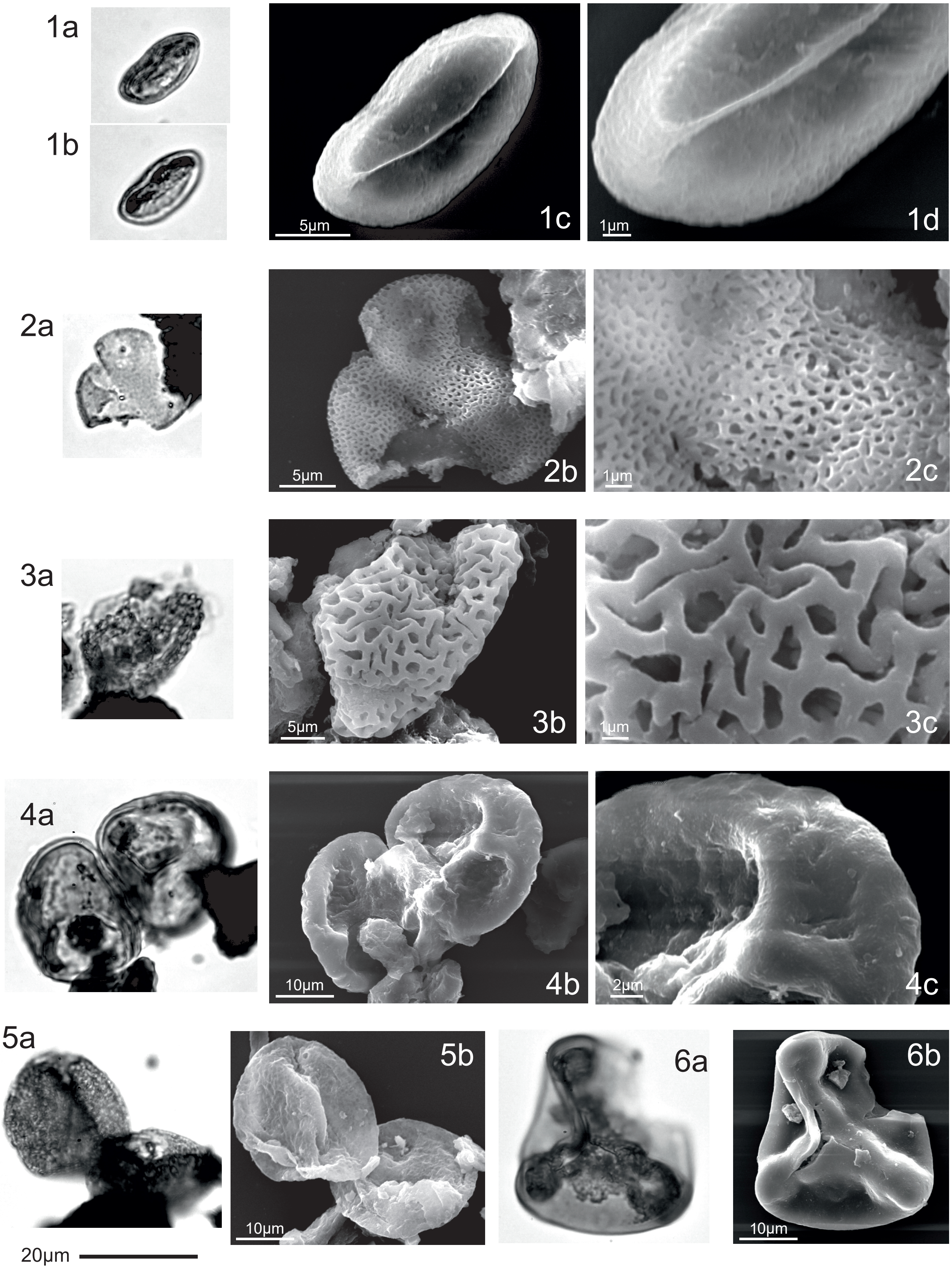
PLATE 5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Appendix I

Scoring of plant taxa from Brno-Líšeň for IPR analysis. Every taxon has value 1, which may be split into several taxonomic-physiognomic groups: CONIF (zonal and extrazonal conifers), BLD (broad-leaved deciduous woody angiosperms), BLE (broad-leaved evergreen woody angiosperms), SCL (sclerophyllous woody angiosperms), LEG (legume-type woody angiosperms), ZONPALM (zonal palms), ARBFERN (arborescent ferns), DRY HERB (open woodland and grassland), MESO HERB (mesophytic herbs, undergrowth), AZONAL WOODY (trees and shrubs), AZNW (azonal non-woody elements, monocots/reeds), and AQUATIC (aquatic elements), PROBLEMATIC (non-specific taxa).
Results of IPR vegetation analysis from studied floras: ZONAL HERB (DRY HERB + MESO HERB), FERN (zonal and extrazonal ferns), AZONAL WOODY (azonal tree and shrubs), AZONAL NON-WOODY (azonal ferns and horsetails), REED/SEDGES (rooted monocots), AQUATIC (aquatic elements), MMF (Mixed Mesophytic Forest), BLEF (Broad-leaved Evergreen Forest) and BLDF (Broad-leaved Deciduous Forest).

site: Líšeň	ZONAL									AZONAL			PROBLEMATIC taxa	
Taxa	CONIF	BLD	BLE	SCL	LEG	ZONPALM	ARBFERN	DRY HERB	MESO HERB	AZONAL WOODY	AZNW	AQUATIC		
“Parrotia” pristina		0.50								0.50				1.00
Abies spp.	1.00													1.00
Alnus cf. *julianiformis*		0.50								0.50				1.00
Alnus sp.		0.50								0.50				1.00
Amaranthaceae								0.50			0.50			1.00
Anacardiaceae – Fagoideae – Styracaceae		0.50	0.50											1.00
Araliaceae gen. et sp. indet.		0.50	0.30							0.20				1.00
Betula spp.		0.50								0.50				1.00
Buxus sp.			0.50	0.50										1.00
Calamus sp.						0.50				0.50				1.00
Carpinus sp.		1.00												1.00
Carpolithes sp. 1													1.00	1.00
Carpolithes sp. 2													1.00	1.00
Carya sp.		0.50								0.50				1.00
Castanea sp.		1.00												1.00
Castanopsis sp.			1.00											1.00
Cathaya sp.	1.00													1.00
Cedripites miocaenicus	1.00													1.00
Celtis sp.		0.50		0.50										1.00
cf. *Carya* sp.		1.00												1.00
cf. *Comptonia comptoniifolia*		1.00												1.00
Cornaceae gen. et sp. indet.		0.50	0.50											1.00
Cornaceae, Mastixioideae, Vitaceae		0.50								0.50				1.00
Craigia sp.		0.50								0.50				1.00
Cyatheaceae gen. et sp. indet.							1.00							1.00
Cyperaceae sp.									0.50		0.50			1.00
Cyrillaceae vel Clethraceae gen. et sp. indet.		0.33	0.33							0.33				0.99
Daphnogene polymorpha			1.00											1.00
Davallia									1.00					1.00
Davalliaceae									1.00					1.00
Decodon spp.											1.00			1.00
Dennstaedtiaceae									1.00					1.00
Dicotylophyllum sp.		1.00												1.00
Distylium uralensis, *D. racemosum*			1.00											1.00
Drosera									0.50		0.50			1.00
Engelhardia orsbergensis		0.50	0.50											1.00
Engelhardia sp.		0.50	0.50											1.00
Eotrigonobalanus frucinervis / *E. andreanszkyi*			0.50							0.50				1.00
Ephedra sp.								1.00						1.00
Ericaceae gen. et sp. indet.		0.25	0.25	0.25						0.25				1.00

site: Líšeň	ZONAL									AZONAL			PROBLEMATIC taxa	
Taxa	CONIF	BLD	BLE	SCL	LEG	ZONPALM	ARBFERN	DRY HERB	MESO HERB	AZONAL WOODY	AZNW	AQUATIC		
Ericipites callidus		0.33		0.33						0.33				0.99
Eucommia sp.		1.00												1.00
Fabaceae gen. et sp. indet				0.50	0.50									1.00
Fagus sp.		1.00												1.00
Fraxinus sp.		0.50								0.50				1.00
Gleicheniaceae gen. et sp. indet.									1.00					1.00
Glyptostrobus sp.										1.00				1.00
Gordonia hradekensis			1.00											1.00
Ilex aquifolium				1.00										1.00
Ilex sp.		0.25	0.25	0.25						0.25				1.00
Juglans sp.		1.00												1.00
Keteleeria sp.	1.00													1.00
Laevigatosporites haardti ssp. *haardtioides*									1.00					1.00
Laurophyllum sp.			1.00											1.00
Leguminophyllum sp. 1		1.00												1.00
Leguminophyllum sp. 2		1.00												1.00
Ligustrum		0.25	0.25	0.25						0.25				1.00
Liquidambar sp.		0.50								0.50				1.00
Loranthophyllum lingulatum		1.00												1.00
Lycopodiella									0.50	0.50				1.00
Lycopodium sp., *L. annotinum*									1.00					1.00
Lygodiaceae									1.00					1.00
Lygodium sp.									1.00					1.00
Lygodium sp. 2									1.00					1.00
Mastixia – Cornus sp.			1.00											1.00
Monocotyledonae gen. et sp. indet.										1.00				1.00
Myrica spp.		0.33	0.33							0.33				0.99
Myriophyllum sp.												1.00		1.00
Nyssa sp.		0.50								0.50				1.00
Oleidearumpollenites sp.		0.25	0.25	0.25						0.25				1.00
Osmunda parschlugiana									0.50	0.50				1.00
Osmunda sp.									1.00					1.00
Palmae gen. et sp. indet.						1.00								1.00
Parrotia pristina		0.50								0.50				1.00
Parthenocissus sp.		0.80	0.20											1.00
Picea sp.	1.00													1.00
Pinus sp. – *haploxylon* type	1.00													1.00
Pinus sp. – *sylvestris* type	0.50									0.50				1.00
Plantago sp.								0.50	0.50					1.00
Platanus sp.		0.50								0.50				1.00
Platycarya sp.		1.00												1.00
Poaceae gen. et sp. indet.								0.33	0.33		0.33			0.99
Podocarpium podocarpum					1.00									1.00
Polypodiaceae gen. et sp. indet.									0.50		0.50			1.00
Polypodiaceaesporites gracilis									1.00					1.00
Polypodium									1.00					1.00
Potamogeton praenatus												1.00		1.00
Pteridaceae									1.00					1.00
Pteris oeningensis									0.50		0.50			1.00
Pterocarya sp.		0.50								0.50				1.00
Quercoidites henrici		0.33	0.33							0.33				0.99

site: Líšeň	ZONAL									AZONAL				
Taxa	CONIF	BLD	BLE	SCL	LEG	ZONPALM	ARBFERN	DRY HERB	MESO HERB	AZONAL WOODY	AZNW	AQUATIC	PROBLEMATIC taxa	
Quercoidites microhenrici		0.25	0.25	0.25						0.25				1.00
Quercus cerris		0.80		0.20										1.00
Quercus petraea		1.00												1.00
Quercus rhenana										1.00				1.00
Quercus spp.		0.25	0.25	0.25						0.25				1.00
Quercus vel *Castanea*		0.50	0.50											1.00
Reevesia sp.			1.00											1.00
Rubus sp. div.		0.33	0.33							0.34				1.00
Rutaceae gen. et sp. indet.		0.25	0.25	0.25						0.25				1.00
Salix sp.										1.00				1.00
Salix varians		0.50								0.50				1.00
Salvinia reussii												1.00		1.00
Sapotaceae gen. et sp. indet.			0.75	0.25										1.00
Sciadopitys sp.	0.50									0.50				1.00
Selaginella sp.									1.00					1.00
Schizaceae gen. et sp. indet.									1.00					1.00
Schoenoplectiella cf. *ragozinii*											1.00			1.00
Sparganium sp.											1.00			1.00
Sphagnum sp.											1.00			1.00
Staphylea sp.		1.00												1.00
Symplocos spp.		0.20	0.60							0.20				1.00
Symplocos spp. 2			1.00											1.00
Tamarix sp.		0.33	0.33	0.33										0.99
Taxodium dubium										1.00				1.00
Tilia sp.		1.00												1.00
Tricolporollenites liblarensis			0.50							0.50				1.00
Tricolporopollenites sp.													1.00	1.00
Trigonobalanopsis sp.			1.00											1.00
Trigonobalanus andreanszkyi			1.00											1.00
Tsuga sp.	1.00													1.00
Ulmaceae gen. et sp. indet.		0.33		0.33						0.33				0.99
Ulmus cf. *pyramidalis*		0.50								0.50				1.00
Sum of taxa	8.00	31.86	19.25	5.69	1.50	1.50	1.00	2.33	18.83	20.14	6.83	3.00	3.00	122.93
Sum of zonal taxa														89.96
Percentage of zonal taxa	8.89	35.42	21.40	6.33	1.67	1.67	1.11	2.59	20.93					100.00
Sum of zonal woody angiosperms														59.80
percentage of zonal woody angiosperms		53.28	32.19	9.52	2.51	2.51								100.00
Sum of % SCL + LEG	12.02													
Sum of % DRY HERB + MESO HERB (ZONAL HERB)	23.52													

<table>
<tr><th rowspan="2">Vegetation type</th><th colspan="3">Zonal woody components</th><th>Zonal herbaceous components (fossil record)</th><th>Zonal herbaceous components (modern record)</th></tr>
<tr><th>BLD</th><th>BLE</th><th>SCL + LEG</th><th>MESO + DRY HERB</th><th>MESO + DRY HERB</th></tr>
<tr><td>Broad-leaved decidous forests</td><td>> 80 %</td><td></td><td></td><td>≤ 30 %</td><td>40–70 %</td></tr>
<tr><td>Ecotone</td><td>75–80 %</td><td rowspan="2">< 30 %</td><td rowspan="3">< 20 %</td><td rowspan="3">< 30 %</td><td rowspan="3">40–55 %</td></tr>
<tr><td>Mixed mesophytic forests</td><td rowspan="2">< 75 %</td></tr>
<tr><td>Ecotone</td><td>30–40 %</td></tr>
<tr><td>Broad-leaved evergreen forests</td><td></td><td>> 40 %</td><td>(SCL + LEG) < BLE</td><td>< 25 %</td><td>10–45 %</td></tr>
<tr><td>Subhumid sclerophyllous forests</td><td></td><td></td><td>≥ 20 %</td><td>< 30 %</td><td>40–55 %</td></tr>
<tr><td>Xeric open woodlands</td><td></td><td>< 30 %</td><td>≥ 20 %</td><td>30–40%; MESO HERB > DRY HERB up to 10 % of all zonal herbs</td><td>n.a.</td></tr>
<tr><td>Xeric grasslands or steppe</td><td></td><td>< 30 %</td><td></td><td>≥ 40 %</td><td>n.a.</td></tr>
</table>