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Lower Miocene plant assemblage with coastal-marsh herbaceous monocots from the Vienna Basin (Slovakia)

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Abstract: A new plant assemblage of Cerová-Lieskové from Lower Miocene (Karpatian) deposits in the Vienna Basin (western Slovakia) is preserved in a relatively deep, upper-slope marine environment. Depositional conditions with high sedimentation rates allowed exceptional preservation of plant remains. The plant assemblage consists of (1) conifers represented by foliage of *Pinus hepios* and *Tetraclinis salicornioides*, a seed cone of *Pinus* cf. *ornata*, and by pollen of the Cupressaceae, Pinaceae, *Pinus* sp. and *Cathaya* sp., and (2) angiosperms represented by *Cinnamomum polymorphum*, *Platanus neptuni*, *Potamogeton* sp. and lauroid foliage, by pollen of *Liquidambar* sp., *Engelhardia* sp. and *Craigia* sp., and in particular by infructescences (so far interpreted as belonging to cereal ears). We validate genus and species assignments of the infructescences: they belong to *Palaeotriticum* Sitár, including *P. mockii* Sitár and *P. carpaticum* Sitár, and probably represent herbaceous monocots that inhabited coastal marshes, similar to the living grass *Spartina*. Similar infructescences occur in the Lower and Middle Miocene deposits of the Carpathian Foredeep (Slup in Moravia), Tunjice Hills (Žale in Slovenia), and probably also in the Swiss Molasse (Lausanne). This plant assemblage demonstrates that the paleovegetation was represented by evergreen woodland with pines and grasses in undergrowth, similar to vegetation inhabiting coastal brackish marshes today. It also indicates subtropical climatic conditions in the Vienna Basin (central Paratethys), similar to those implied by other coeval plant assemblages from Central Europe.

Key words: Early Miocene, Karpatian, Vienna Basin, Western Slovakia, paleobotany, palynology.

Introduction

The Lower Miocene deposits of the Karpatian stage (late Burdigalian) in the Central Paratethys contain rare plant macrofossils, with only a few directly dated localities in Austria and Moravia (Knobloch 1967, 1968; Kvaček 2003). However, diverse Miocene plant assemblages of Western Europe (Mai 1995, p. 367) that are not directly dated may be actually coeval with the late Early–Middle Miocene and may correspond to the “Early-Middle Miocene Optimum” (Flower & Kennett 1994; Zachos 2001).

Although highly detailed palynological datasets are available from the Karpatian in Slovakia (Planderová 1967, 1990) and Moravia (Doláková & Slamková 2003), macrofloral assemblages of the Karpatian in the Central Paratethys remain largely unknown. Our goal is to describe a new, relatively-well preserved plant assemblage of Early Miocene age from the Vienna Basin (western Slovakia) and to reconstruct paleovegetation and ecosystem conditions during the late Early Miocene in the eastern part of the Vienna Basin (Central Paratethys). The new plant assemblage implies that it was probably derived from coastal-marsh habitats and allows comparisons with other assemblages in the Central Paratethys (e.g. Kovar Eder et al. 1998, 2008; Bruch et al. 2004, 2011; Kern et. al. 2011). Our study also contributes to better understanding of climate during the Early and Middle Miocene in this region.

Geographical and geological setting

Samples were collected in the western part of the Slovak Republic at the Cerová-Lieskové locality. The outcrop is situated in the foothills of the Malé Karpaty Mountains, which represent the eastern margin of the central part of the Vienna Basin (Fig. 1A–C). The Vienna Basin was a part of the Central Paratethys Sea during the Miocene. Karpatian (late Burdigalian) sediments, assigned to the Lakšárska Nová Ves Formation (Špička & Zapletalová 1964), are well exposed in a former clay pit. These sediments are represented by massive, locally laminated, calcareous clays and clayey silts with thin tempestite intercalations (up to 10 mm thick) and several thin sandstone/siltstone layers. The section is almost 20 meters thick. The macrofossil assemblage consists of vertebrates, mainly teleosts, and a wide spectrum of invertebrates — bivalves, gastropods, scaphopods, cephalopods, decapods, isopods, and barnacles (Harzhauser & Schlögl 2012), regular and irregular echinoids, asteroids, siliceous sponges (Lukowiak et al. 2013), and solitary corals. Plant remains are also locally abundant. Microfossil assemblages include benthic and planktonic foraminifera, radiolarians,

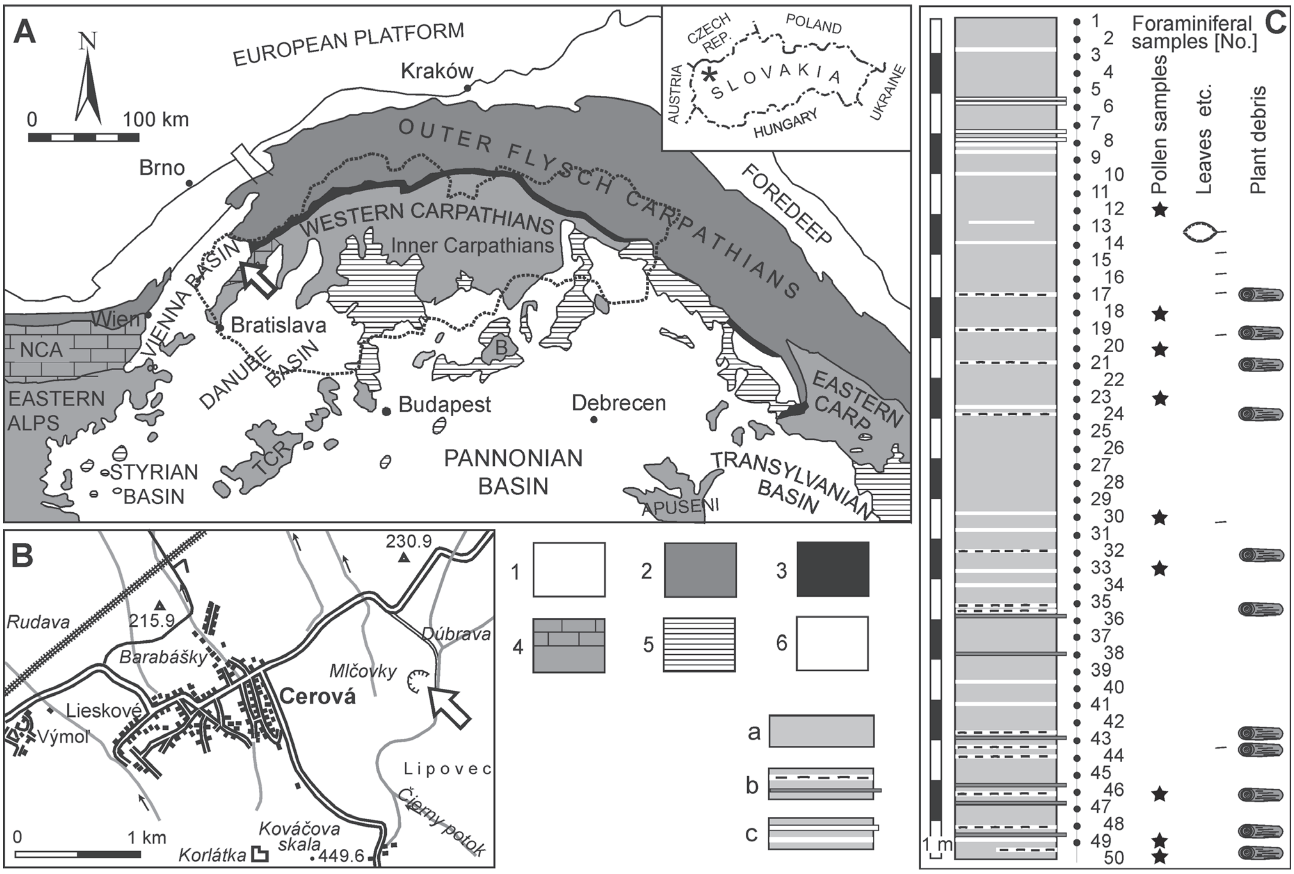


Fig. 1. A — Position of the Vienna Basin in the Carpathian-Pannonian system: 1 — European platform units, 2 — Carpathian-Alpine externides, 3 — Pieniny Klippen Belt, 4 — Alpine-Carpathian-Dinaride and Pannonian internids, 5 — Neogene volcanics, 6 — Neogene basins; B — Bükk, NCA — Northern Calcareous Alps, TCR — Transdanubian Central Range. **B** — Location of the Cerová-Lieskové clay pit, indicated by arrow. **C** — Simplified section through the Cerová-Lieskové clay pit: a — Massive calcareous clay, b — Thin tempestite layers with plant debris, and lithified clayey silt layers, c — Thin siltstone/sandstone layers, and silt lenses (modified from Łukowiak et al. 2013).

sponge spicules, bryozoans, ostracods, crinoid ossicles, coleoid statoliths, fish otoliths, shark teeth (Underwood & Schlögl 2013), and locally extremely abundant diatoms.

These clays and silts were deposited under upper bathyal conditions in a relatively oxygen-depleted environment (Schlögl et al. 2011). Foraminiferal assemblages from the intervals 14–20 (Fig. 1C) were analysed with the two-step depth equations of Hohenegger (2005) and yielded a paleodepth range between 240 and 330 meters (Schlögl et al. 2011). The upper bathyal aphotic zone is also reflected by gastropod and bivalve assemblages, with the predominance of carnivorous gastropods (along with scavengers and parasites), and bivalves composed mainly of chemosymbionts, and detritus and suspension feeders (Harzhauser et al. 2011). The shark fauna mainly of small-sized bathyal squaliform sharks, with pelagic lamniform sharks and sharks from the Centrophoridae and Hexanchidae families completely absent (Underwood & Schlögl 2013). Decapods (Hyžný & Schlögl 2011) and siliceous sponges (Lukowiak et al. 2013) also imply bathyal conditions. Assemblages of benthic foraminifera are dominated by infaunal and deep-infaunal, suboxic/dysoxic taxa, in some samples only with minor contribution of oxiphyllic taxa. Benthic Foraminiferal Oxygen Index (BFOI) of Kaiho (1994) indicates dysoxic and low-oxic conditions during the deposition of the intervals 14–20 (Schlögl et al. 2011).

The exceptional preservation of easily disarticulating animals such as ghost shrimps, minute pilumnid crabs, or cirolanid isopods implies a relatively high net sedimentation rate (Hyžný & Schlögl 2011; Hyžný et al. 2013). Thin sandstone/siltstone layers (up to 5 cm), silt "pavements" or laterally restricted thin silt lenses generally very poor for organic remains probably represent distal turbiditic deposits. Thin laminae up to 10 mm in thickness, rich in molluscs, echinoderms and wood debris most probably represent tempestite deposits. These are frequently dominated by one or two fossil groups, most commonly irregular echinoids and/or pteropods. Deposits also contain various redeposited microfossils from areas surrounding the Vienna Basin, including well preserved, most probably Lower Cretaceous freshwater ostracods (Pipík et al. 2010). These allochthonous remains and plant material were apparently transported by rivers from adjacent emerged land into the basin.

Co-occurrence of the foraminifera *Uvigerina graciliformis* Papp & Turnovsky, 1953 and *Globigerinoides bisphericus* Todd *in* Todd, Cloud, Low & Schmidt, 1954 and the absence of the genus *Praeorbulina* Olsson, 1964 suggest Late Karpatian age (Cicha & Rögl 2003; Berggren et al. 1995; see also Schlögl et al. 2011). The regional Paratethyan Karpatian stage is the time-equivalent of the latest Burdigalian (Rögl et al. 2003; Piller et al. 2007).

Material and methods

Several stratigraphic intervals contain dispersed or accumulated plant debris that shows two major preservation states (Fig. 1C). The first one is represented by abundant plant debris associated with various invertebrate remains within thin, most probably tempestite layers. The debris is poorly preserved, more or less fragmented due to transport and mainly conposed of wood fragments. The second one represents scattered, but generally better preserved leaves, grass-blades, fir-needles and wood fragments. These well-preserved remains are studied here (coming from intervals 13–14, 14–15, 15–16, 16–17, 19–20, 30–31, 43, see Fig. 1C). Nine intervals were selected for the palynological analysis out of 47 intervals sampled for benthic and planktonic foraminifers (samples 12, 18, 20, 23, 30, 33, 46, 49, and interval 49–50). Most of the samples are either barren or contain very few and poorly preserved pollen grains. Therefore, palynological data are inappropriate for statistical evaluation and paleoenvironmental interpretation.

Sample preparation followed standard laboratory methods (Erdtman 1954; Faegri & Iversen 1989; Moore et al. 1991). The description of the taxa follows the system based on molecular phylogeny (e.g. Judd et al. 2002; Reveal 2012). Leaf architecture is described using current terminology published by Ash et al. (1999) and Ellis et al. (2009). Below, we document the composition of the flora and rectify the nomenclature of the previously published data (Sitár 2001). All the investigated material is housed in the Slovak National Museum in Bratislava (SNM B). We compare this assemblage with similarly preserved plant remains from the Karpatian Slup holostratotype locality (southern Moravia), housed in the Moravian Museum, Brno (MZM).

Systematic paleobotany

Pinaceae

Pinus L.
Pinus hepios (Unger) Heer
Fig. 2.1

1850 *Pinites hepios* Unger, p. 362
1852 *Pinites hepios* Unger — Unger, p. 97, pl. 35, figs. 6–8, 9
1855 *Pinus hepios* (Unger) Heer, p. 57, pl. 21, fig. 7

Material: A single incomplete fascicle of needles (SNM B 1792/a,b), several needle fragments.

Description: A single isolated two-needled fascicle, needles fragmentary, 56.5 to 37.8 mm long and 0.6 to 0.8 mm broad, straight or slightly curved, secondarily compressed, needle apices, bases and the sheath not preserved, margin entire, venation consisting of one medial vein (to 0.3 mm broad), parallel striation poorly observed.

Discussion: Foliage of *Pinus hepios* (Unger) Heer is usually associated with seed cones of *P. ornata* (Sternberg) Brongniart (e.g. Engelhardt 1876a; Menzel 1901). *P. hepios* usually represents a cumulative taxon name for pines with two-needle fascicles. It was based by Unger (1850, 1852) on foliage and seeds from the locality Parschlug (e.g. Kovar-Eder et al. 2004). Recently, Teodoridis & Sakala (2008) revised cone and foliage records of *P. hepios/P. ornata* from the Paleogene and Neogene deposits of the Czech Republic described by Sternberg (1825), Engelhard (1876a), Menzel (1901) and Knobloch et al. (1996). They considered morphological affinities to other pine species assigned to *P. engelhardtii* Menzel emend. Mai/*P. rigios* (Unger) Ettingshausen, *Pinus urani* (Unger) Schimper and *Pinus* sp. div. described from North Bohemia. Bůžek et al. (1996) recorded isolated 2 or 3-needled fascicles as *P. hepios* from several drill-cores of the Lower Miocene Cypris Formation in the Cheb and Sokolov basins of North Bohemia. This record of *P. hepios* is of Ottnangian to Karpatian age and corresponds stratigraphically to the plant assemblage of Cerová-Lieskové. It is associated with foliage of *P. rigios* and *P.* cf. *saturni* Unger, and with male and female cones and isolated seeds of *Pinus* sp. div. (Bůžek et al. 1996). Other coeval deposits of the Berzdorf Basin (Saxony, Germany) contain foliage of *P.* cf. *hepios*, *P.* cf. *palaeostrobus* Ettingshausen and *P.* cf. *rigios* associated with seed cone of *P. spinosa* Herbst (Czaja 2003). Mai (1986) revised the type and original material of *Pinus* species from the Paleogene and Neogene strata of Europe, stressing that mainly seed cones allow reliable identification to species level. Teodoridis & Sakala (2008) suggested that the xerophytic *P. halepensis* Mill. (Mediterranean and Western Asia) and *P. merkusii* Jungh. & de Vries (Vietnam, Laos, Cambodia, China, Philippines, Malaysia and Indonesia) are the extant species that are most comparable to the pine represented by the fossil species of *P. hepios/P. ornata*.

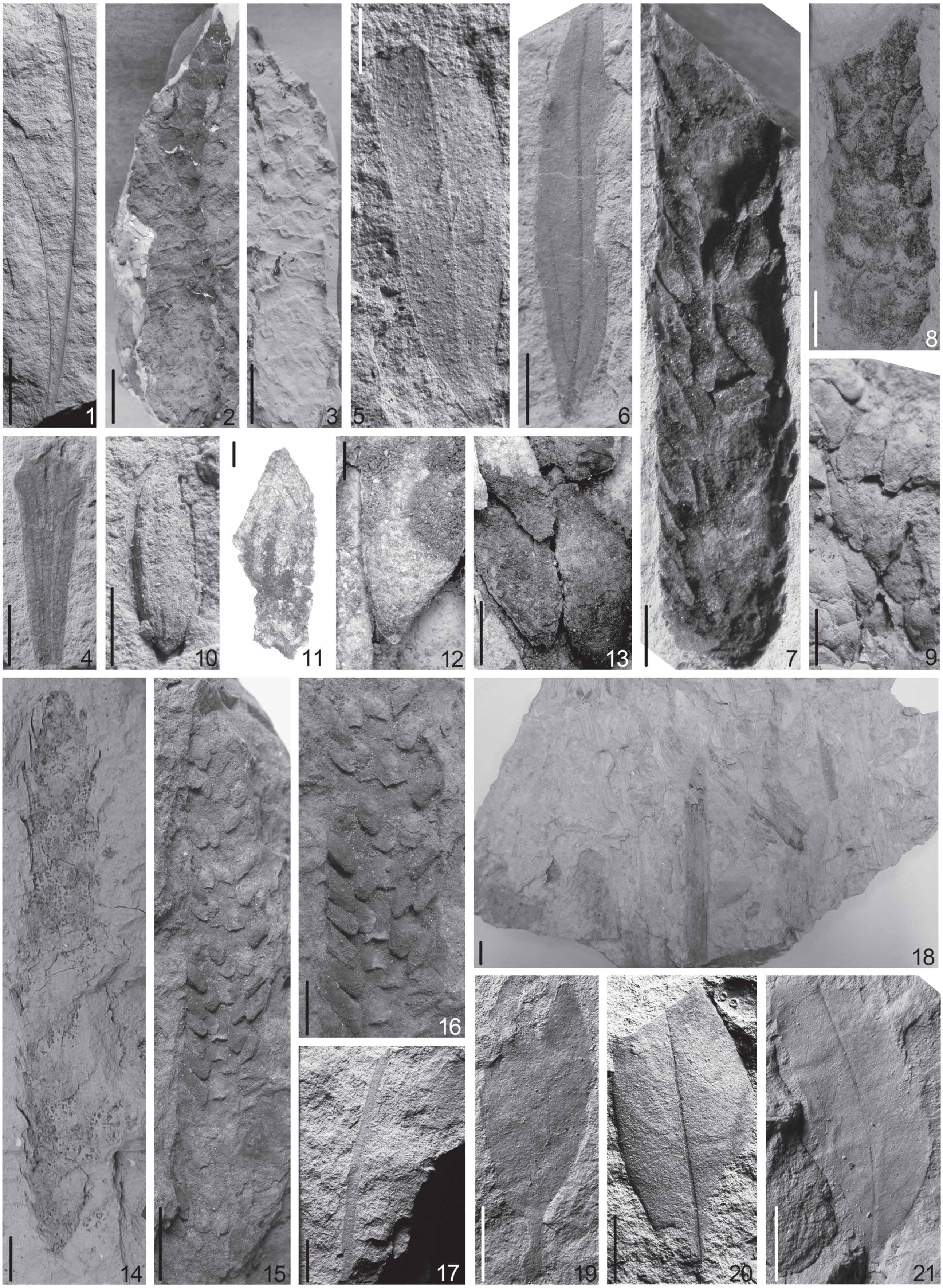
Pinus cf. *ornata* (Sternberg) Brongniart
Fig. 2.2–3

1825 *Conites ornatus* Sternberg, p. 39, pl. 55, figs.1, 2
1828 *Pinus ornata* (Sternberg) Brongniart, p. 107
1901 *Pinus ornata* Sternberg — Menzel, p. 54, pl. 2, figs. 6–7, 9
1994 *Pinus ornata* (Sternberg) Brongniart — Mai, p. 213, pl. 3, figs. 1–3, text-fig. 1b

Material: An incomplete seed cone (SNM B 1809).

Description: Incomplete seed cone symmetrical, probably oblong, 79.0 mm long, 16.8 mm broad, apophysis rhombic, flat to slightly arched, 5.9–(6.9)–8.1 mm long and 5.8–(7.1)–9.9 mm broad, distinctly keeled and radially striated, umbo rhombic up to 3.4 mm in diameter flat to slightly arched, excentro-denticulatomucronate, mucro small and indistinctly erected.

Remarks: *P. ornata* was described on the basis of a seed cone from the Lower Oligocene locality Valeč (Sternberg 1825, p. 39, pl. 55, figs. 1–2) but the holotype disappeared in the late 19th century. Additional seed cones were described later from North Bohemia, particularly from the Valeč type locality (Menzel 1901), but also from other Lower Eocene to Lower Miocene localities of the České středohoří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Mts, Staré Sedlo, Český Chloumek and Žitenice (Engelhardt 1876b; Knobloch 1962; Knobloch et al. 1996; Teodoridis et al. 2012) and the Most Basin, Hradiště near Černovice (Engelhardt 1876a, 1877) and Břešťany (Menzel 1901). Němejc (1968, p. 384, pl. 39, fig. 3) re-figured Menzel's cone from Valeč which was suggested as the neotype by Kvaček & Kvaček (1992, pl. 4, fig. 1).

Mai (1986, p. 575; 1994, p. 213) assigned the seed cones of *P. ornata* on the basis of the flat apophyses in the basal cone part and a relatively long stalk to the "*Merkusii*" group, together with other related fossil species and their synonyms, mainly known from Miocene localities of France.

Seed cones of a xerophytic extant species of *P. halepensis* Mill. from the Mediterranean and western Asia and those of the extant species *P. merkusii* Jung. & de Vries from Vietnam, Laos, Cambodia, China, Philippines, Malaysia and Indonesia are most comparable to *P. ornata*. Kvaček et al. (2004b) noted that *P. massoniana* Lamb. from Taiwan and China could represent an extant equivalent but this species differs by having shorter cones (only 40–(25)–70 mm long), which are also more shortly stalked (Fu et al. 1999). Teodoridis & Sakala (2008) applied principles of the holistic approach (i.e. the whole plant concept sensu Kvaček 2004) to the fossil coniferous remains from the Most Basin (Czech Republic) and defined the *Pinus ornata* plant which combines seed cones of *P. ornata* and foliage of *P. hepios.*

Cupressaceae

Tetraclinis Masters
Tetraclinis salicornioides (Unger) Kvaček
Fig. 2.4

1847 *Thuites salicornioides* Unger, p. 11, pl. 2, figs. 1–4, pl. 20, fig. 8
1866 *Libocedrus salicornioides* (Unger) Heer — Ettingshausen, p. 33, pl. 10, fig. 5 (non fig. 14)
1982 *Libocedrites salicornioides* (Unger) Endlicher — Kovar, p. 36, pl. 6, figs. 1, 2, 10, pl. 16, figs. 2–4, pl. 33, figs. 2, 3
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: One complete foliar segment (SNM B 1793/a,b).

Description: Isolated cladode-like branch segment, 15.3 mm long, 1.8 and 5.5 mm broad in its lower and upper part, corresponding to pseudo-whorl, composed of pairs of dimorphic facial and lateral leaves with bluntly mucronate apices and rounded base, simple pseudo-whorl obovate, margin entire, 5 prominent longitudinal lines on upper surface.

Discussion: Kovar (1982, as *Libocedrites*), Kvaček (1989), Mai & Walther (1991) and Kvaček et al. (2000) summarized morphology and taxonomy of *Tetraclinis.* The relatively robust foliage segment completely fused in the pseudo-whorl shows morphological affinity to *Tetraclinis salicornioides* rather than to the more xeromorphic *T. brachyodon* (Brongniart) Mai & Walther. Impressions of sterile foliage of *T. salicornioides* are almost indistinguishable from an unrelated extinct cupressoid conifer *Ditaxocladus* S.X. Guo & Z.H. Sun from the Upper Cretaceous to Paleocene of the Northern Hemisphere (Guo et al. 2012). The foliage of both conifers differs in the general shape of foliage sprays, which are slender, elongate in *Ditaxocladus* and widely spread in *Tetraclinis salicornioides*. The seed cone morphology and leaf anatomy is also significantly different (Guo et al. 2012).

T. salicornioides diverged from *T. brachyodon* during the Eocene and adapted to forest conditions in humid subtropical to warm temperate zones (Kvaček et al. 2000). Both species went extinct during the Pliocene. Fragments of foliage and cones of *Tetraclinis* also occur in the Cypris Formation (Cheb and Sokolov basins, Czech Republic) and in deposits of the Zittau and Berzdorf basins (e.g. Bůžek et al. 1996; Czaja 2003; Holý et al. 2012). The only living *Tetraclinis articulata* (Vahl) Masters is a sclerophyllous relict occurring in the western Mediterranean (native in the Atlas Mountains of Morocco, Algeria and Tunisia, in Malta and Cartagena in SE Spain) and cannot be considered as the most similar living relative to *T. salicornoides*. *T. salicornioides* may be ecologically more similar to *Calocedrus macrolepis* Kurz distributed in SE China, Myanmar (Burma), Thailand and Vietnam on the basis of its foliage physiognomy (Kvaček et al. 2011).

Angiosperms

Lauraceae
Cinnamomum L. sect. *Camphora* Nees
Cinnamomum polymorphum (A. Braun) Heer
Fig. 2.5–6

1845 *Ceanothus polymorphus* A. Braun, p. 171
1847 *Ceanothus bilinicus* Unger, p. 145, pl. 49, fig. 9
1851 *Daphnogene polymorpha* (A. Braun) Ettingshausen, p. 16, pl. 2, figs. 23–25
1855 *Camphora polymorpha* (A. Braun) Heer, p. 112, pl. 1, fig. 11

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Fig. 2. 1 — *Pinus hepios* (Unger) Heer, incomplete isolated double-needled fascicle, SNM B 1792/a, scale bar 10 mm. **2–3** — *Pinus* cf. *ornata* (Sternberg) Brongniart, seed cone with its latex mold SNM B 1809, scale bar 10 mm. **4** — *Tetraclinis salicornioides* (Unger) Kvaček, isolated cladode-like branch segment, SNM B 1793/a, scale bar 5 mm. **5–6** — *Cinnamomum polymorphum* (A. Braun) Heer: 5 — basal part of narrow leaf, SNM B 1795/1, scale bar 5 mm; 6 — almost complete narrow leaf with well-preserved venation, SNM B 1796, scale bar 5 mm. **7–13** — *Palaeotriticum mockii* Sitár: 7 — incomplete cylindrical infructescence, holotype, SNM B 1786, scale bar 5 mm; 8 — basal fragment of similar infructescence, SNM B 1787, scale bar 5 mm; 9 — poorly preserved fragment of infructescence with adhering ichnofossils on the basal part, SNM B 1788, scale bar 5 mm; 10 — detached spikelet, SNM B 1789, scale bar 5 mm; 11 — detail of a spikelet isolated from the holotype, SNM B 1786, scale bar 1 mm; 12–13 — details of spikelets, holotype, SNM B 1786, scale bar 2 mm. **14** — *Palaeotriticum carpaticum* Sitár, spiny cylindrical infructescence, holotype, SNM B 1791, scale bar 5 mm. **15–16** — *Palaeotriticum mockii* Sitár, Slup locality, MZM Ge 28923: 15 — cylindrical infructescence, scale bar 10 mm; 16 — detail of spikelets, scale bar 5 mm. **17–18** —Monocotyledonae fam. et gen. indet.: 17 — linear leaf fragment, SNM B 1795/2, scale bar 10 mm; 18 — accumulated leaf debris, SNM B 1798, scale bar 10 mm. **19** — *Potamogeton* sp., incomplete leaf, SNM B 1797, scale bar 10 mm. **20–21** — *Dicotylophyllum* sp. 1.: 20 — fragmentary leaf lamina, SNM B 1799, scale bar 10 mm; 21 — lower part of an incomplete leaf, SNM B 1802, scale bar 10 mm.

1856 *Cinnamomum polymorphum* (A. Braun) Heer, p. 88, pl. 91, fig. 11c–d, pl. 93, figs. 25–28, pl. 94, figs. 1–16

Material: Three incomplete leaves (SNM B 1794, B 1795/1, B 1796) and fragments of leaf lamina.

Description: Leaves simple, lanceolate, elliptic to obovate, 22–89 mm long, 5–34 mm broad, base slightly asymmetric, cuneate to broadly cuneate, petiole not preserved, apex incomplete, acuminate and blunt, margin entire, venation suprabasal acrodromous, midrib strong, straight or slightly curved in the apical part, lateral veins thinner, alternate, originating at an angle of 20–35°, running along the margin, secondary veins thinner, alternate or opposite, at an angle of 40–55°, curved and looping near margin or straight to forked between midrib and lateral veins, venation of higher orders poorly preserved.

Discussion: Holý et al. (2012) followed the original view of Heer (1856) refreshed by Ferguson (1971) and associated the fruits of the *Cinnamomum* sect. *Camphora* type with variable leaves usually identified as *Daphnogene polymorpha* (e.g. Mai 1960, 1999; Holý 1977; Pingen et al. 1994). The whole plant is closely related to the extant species of *Cinnamomum camphora* L. Remains of *Daphnogene*/*Cinnamomum* are dominant elements in many Oligocene and Miocene floras of Europe, including mastixioid ones (e.g. Bůžek et al. 1996; Kvaček & Walther 1974; Mai & Walther 1978, 1991; Kvaček et al. 2004; Holý et al. 2012). Kvaček & Walther (1974) revised morphologically variable leaf forms (i.e. narrow lanceolate to broadly oval forms) into a single species of *C. polymorphum* that produced the above mentioned type of fruits. The leaf variability was considered as an ecotypical variation (Kvaček & Walther 1974). However, Kvaček & Walther (1974) treated leaves of *Daphnogene cinnamomifolia* (Brongniart) Unger from the Paleogene localities separately from *Cinnamomum polymorphum*, which is preserved in branches with attached fruits and differs in details of epidermal anatomy. Knobloch (1967, 1969) described abundant leaves of *Daphnogene bilinica* (Unger) Kvaček & Knobloch and one broader incomplete leaf of *D. cinnamomeum* (Rossmässler) Knobloch from the Karpatian flora of Dolní Dunajovice, which morphologically corresponds to those from the Cerová-Liesková site.

Platanaceae

Platanus L.

Platanus neptuni (Ettingshausen) Bůžek, Holý & Kvaček
Fig. 3.1–3, 3.5–7

1967 *Platanus neptuni* (Ettingshausen) Bůžek, Holý & Kvaček, p. 205, pl. 1. figs. 1–4, 6 (non 5 — *Sloanea artocarpites*), pls. 2–4 (for a full synonymy see Kvaček & Manchester 2004)

Material: Leaf impressions (SNM B 1801-1802, 1804), fruitlets impressions partly with counterparts (SNM B 1806-8).

Description: Leaves simple ovate to slightly obovate, up to 80 mm long and max. 25 mm broad, margin sub-entire or fine widely dentate on the upper part, midrib strong, almost straight, venation eucamptodromous to semicraspedodromous, secondary veins regularly spaced, at an angle of 45–60°, looping near the margin, quite thin, interspaced partly with single intersecondaries, higher-order veins indistinct. Sessile narrow ovoid to obovoid fruitlets, 6 mm long and up to 3 mm broad, ending into 0.5 mm thick and 3 mm long blunt slender and bent style, the body showing a few indistinct longitudinal ribs.

Discussion: Foliage of this extinct plane tree is preserved as impressions of almost entire-margined leaves and disintegrated remains of infructescences. This deciduous element occurred in Europe in the Paleogene and continued up to the middle Miocene (Kvaček & Manchester 2004).

Monocotyledonae

Palaeotriticum Sitár, gen. nov.
Palaeotriticum Sitár (2001), pp. 115–116, nom. inval.
(typification lacking)

The genus name *Palaeotriticum* was proposed by Sitár (2001, p. 115) for: “imprints of grass ears”.....“related to modern *Triticum*”. The diagnosis of this taxon needs to be validated as follows:

Diagnosis: Infructescences spike-like, cylindrical, consisting of serially arranged ovoid, tightly crowded bodies corresponding to spikelets with glume-like bracts.

Type: *Palaeotriticum mockii* Sitár.

The material consists of several specimens of cylindrical spike-like infructescences preserved as compressed moulds. Two fossil species are recognized: *Palaeotriticum mockii* Sitár (form A) and *Palaeotriticum carpaticum* Sitár (form B). After a more detailed study of the material, the following characteristics are offered to complement the original descriptions.

Palaeotriticum mockii Sitár
Fig. 2.7–13, 2.15–16

1850 *Pinites spiciformis* Unger, p. 529, pro parte
1852 *Pinites spiciformis* Unger, p. 28, pro parte, pl. 14, fig. 14 (non fig. 15)
1967 *Spirematospermum* cf. *wetzleri* (Heer) Chandler — Knobloch, p. 253, pl. 1E, fig. 4
1969 *Spirematospermum* cf. *wetzleri* (Heer) Chandler — Knobloch, p. 48, pl. 13, fig. 3
2001 *Palaeotriticum mockii* Sitár, pp. 115–116, fig. 2 (generotypus)

Diagnosis: Sessile cylindrical infructescence with rounded base containing slender ovoid bi-serially arranged bodies interpreted as single-seeded spikelets with tri-veined unarmed glumes recalling bracts stretching over the seed by a short sharp tip.

Holotype: The specimen illustrated in Sitár (2001, fig. 2) and re-illustrated here in Fig. 2.6, housed in the Slovak National Museum in Bratislava under inventory number SNM B 1786.

Additional material: 2 fragments of infructescences (SNM B 1787, B 1788) and 2 isolated spikelets (SNM B 1789, B 1790).

Description: The holotype is the most complete specimen attaining the maximum width near the rounded base of 12 mm and very slightly narrowing upwards. It is preserved in the length of ca. 60 mm, which may represent half of the complete infructescence. It shows an arrangement of spikelets coming obliquely from the center in three visible rows. The median row apparently covers the spindle. The spikelets are obviously one-seeded, devoid of surface tissue. Incomplete remnants of glumes are seen on some bodies and appear ventrally to be tri-veined (Fig. 2.11). The tightly crowded spikelets are exposed and show smooth surface of the seed, which is not preserved. Spikelets of the lateral rows are sub-parallel, attached at an angle of ca. 35°. Spikelets of the medial row are compressed longitudinally. The spikelet separated mechanically from one lateral row (Fig. 2.11) is obovoid, 8 mm long and max. 3 mm broad, bluntly pointed at the apex, wedge-shaped and flattened on the basis. On the ventral side, it shows the remnant of the glume with 3 darker lines of veins that disappeared during the treatment in diluted hydrofluoric acid. The specimen was damaged during the preparation. The loose spikelet (Fig. 2.10) is spindle-shaped, 12 mm long and 3 mm broad, smooth on the surface, without apparent details except for slight striation on the lower part coming from a stout short stalk on the base. Another incomplete specimen (Fig. 2.8) represents a basal fragment of the same spike-like infructescence. It is 10 mm wide, and rounded at the base, without any stalk, showing less distinctly ovoid tightly crowded bodies interpreted as single-seeded spikelets. The last specimen (Fig. 2.9), showing probably the middle part of a spike-like infructescence, includes only 2 rows of wedge-shaped spikelets with smooth surface.

Discussion: Unger (1850, 1852) described two infructescences as *Pinites spiciformis* from the Slovenian Tertiary locality of Saalberg at Stein, called now Žale at Kamnik (late Badenian, Tunjice Hills). One of these specimens (Unger 1852, pl. 14, fig. 14) strongly resembles our *Palaeotriticum mockii* and differs only by slightly larger dimensions of its spikelets (max. 10 mm long and 6 mm wide, if the illustration reflects the object in natural size). Unger believed that both figured specimens may represent slender conifer seed cones similar to *Pinus strobus* L. We were unable to inspect the type material from Slovenia, which is missing in the collections of Joanneum (Graz, Austria), where most of the Unger's original material is housed, and it is also not present in the collections of the Geologische Bundesanstalt, Vienna. From the same locality, Unger (1860, p. 41) listed fruits of *Carya costata* (Sternberg) Brongniart. The Žale site in Slovenia seems to be of the late Badenian age on the basis of the geological surroundings (Bogomir Jelen, personal communication Nov. 2013).

One of the type specimens of *Pinus lardyana* Heer (1855, p. 38, pl. 20, fig. 5e) from the Lower Miocene deposits of Lausanne also resembles *Palaeotriticum mockii* but the inspection of the actual specimen is required to achieve an accurate comparison. One of the illustrated specimens differs from our material in spikelets parallel to the main axis. The other type material from localities near Lausanne differs still more by crowded irregularly disposed bodies resembling *Spirematospermum* (see below). One of the syntypes shows a rhachis or a twig fully devoid of bracts or foliage and thus may partly belong to *Pinus*. The species requires a more detailed revision. Mai (1986, p. 577) assigns *Pinus lardyana* to invalid or insufficiently described species. Knobloch (1967, 1969) described an incomplete infructescence from the Karpatian locality Slup SE of Znojmo in southern Moravia (Carpathian Foredeep), fully corresponding to *Palaeotriticum mockii*. He assigned it with doubts to *Spirematospermum* and described it as a pod 85 mm long and 13 mm broad with serially arranged moulds of oval seeds (Knobloch 1967— p. 253, pl. 1E, fig. 6; 1969 — p. 48, pl. 13, fig. 5). The bodies, which we interpret as single-seeded spikelets, are arranged in one medial and two (or double) lateral rows. The overall shape of the fossil is cylindrical, slightly narrowing to the apex and rounded at the base. The surface is abraded, not showing glume-like processes but otherwise matching *Palaeotriticum mockii* (Fig. 2.15–16). This material is housed in the Moravské Zemské Museum Brno (MZM, Ge 28923).

The affinity of *Palaeotriticum mockii* is uncertain due to poor preservation. Spiral surface sculpture typical of seeds of *Spirematospermum* is not visible. One of the isolated bodies from the holotype does not show any sculpture under scanning electron microscope (SEM). The incomplete infructescenses widely deviate in form from capsules of *Spirematospermum*, in which the crowded seeds are arranged more chaotically and the capsules are clearly stalked (Fischer et al. 2009, pl. 3). The bodies in the holotype look like fillings of empty spaces.

We disagree with Unger's interpretation because the seed cones of conifers are woody but the plant remains from both localities in Slovakia and Moravia are devoid of any woody tissue or its possible traces. The arrangement of fruitlets also strongly differs from the structure of pine cones, in which the seeds are more loosely arranged, in the case of *Pinus strobus* L. with adnate wings. The fossils assigned to *Palaeotriticum mockii* resemble earls of grasses, namely the wheat with unarmed fruitlets. However diagnostic characters of caryopsides such as scales (glumes, lemmas) enclosing the fruitlet and seed are absent. The bodies are filled with the sediment, and thus were apparently hollow when buried, and their surfaces bear darker thin remnants of plant tissue.

The fruit remains of grasses described from the Miocene until now (e.g. Łańcucka-Środoniowa 1966, 1979) are much smaller and show inner structural traits of embryo. According to the morphological similarity of *Palaeotriticum* and its relatively good preservation implying a rather short-term transport from the coast, the most likely living analogue of *Palaeotriticum mockii* appears to be *Spartina alterniflora* Loisel., an invasive halophytic grass spread on salt marshes of the Americas from Canada to Argentina, which produces similar spikes. Another species with similar infructescences is *Spartina cynosuroides* (L.) Roth, called Big Cordgrass or Giant Cordgrass, which forms dense stands in brackish marshes on tidal wetlands of the Atlantic USA from the Gulf Coast to New England (see Hitchcock 1951).

Palaeotriticum carpaticum Sitár
Fig. 2.14

2001 *Palaeotriticum carpaticum* Sitár, p. 118, fig. 3

Diagnosis: Cylindrical infructescence well flattened covered by impressions of bract-like processes and showing long spines arising from the spikelet surface.


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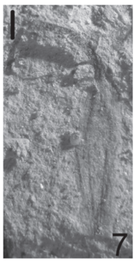
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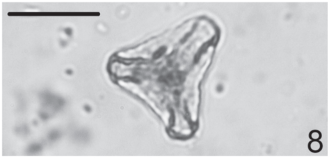
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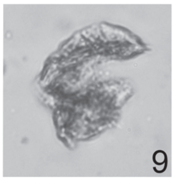
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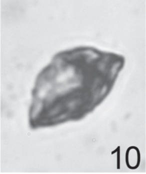
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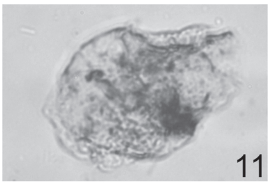
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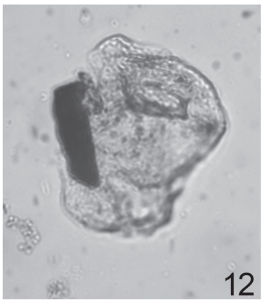
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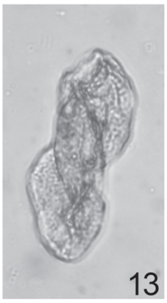
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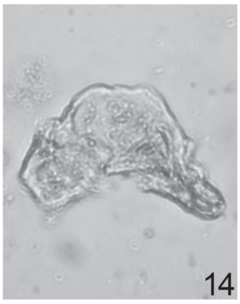
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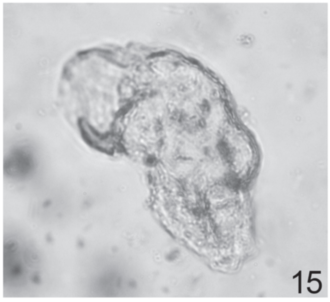
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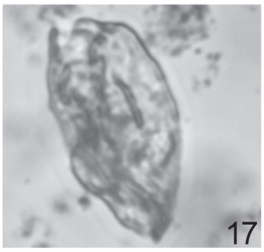
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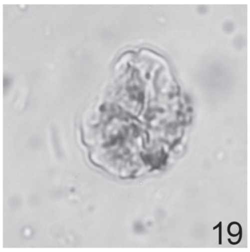
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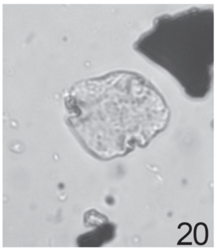
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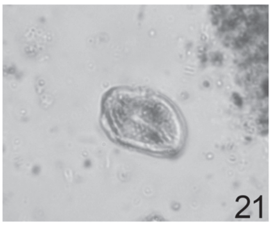
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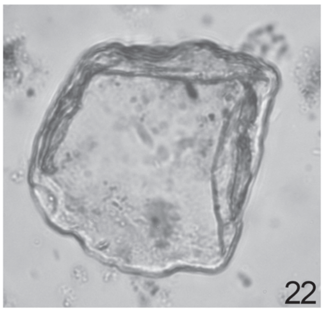
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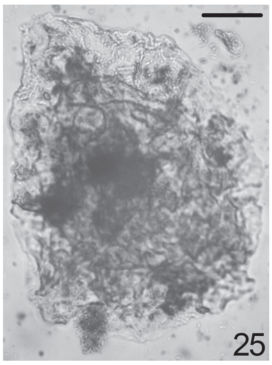
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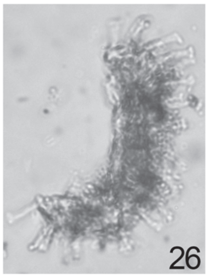
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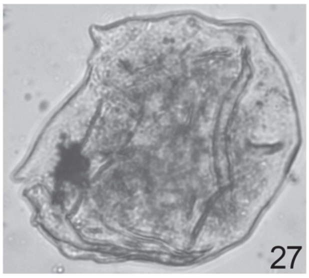
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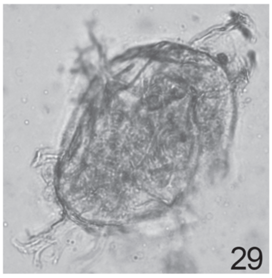
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Holotype: The specimen illustrated in Sitár (2001, fig. 3) and re-illustrated here in Fig. 2.14, housed in the Slovak National Museum in Bratislava under inventory number SNM B 1791.

Description: Only one specimen is available. Contrary to the infructescences assigned to *P. mockii*, its surface is flat compressed, not showing any distinct spikelets-like bodies. It comes from the same strata as the previous taxon. The compression is almost complete, 63 mm long and max. 10 mm broad, with a blunt apex without its very terminal part, and the slightly damaged base; this base is widely conical, without any sign of a stalk. On the sides of the infructescence, sharp ca. 2–3 mm long spine-like processes stretch apically recalling awns in some grasses.

Discussion: We are not aware of any similar fossil remains matching *Palaeotriticum carpaticum* Sitár. Our specimen may represent an empty infructescence of the previous species. It does not show any diagnostic trait that would allow a better comparison.

Potamogeton sp.
Fig. 2.19

Material: Incomplete leaf (SNM B 1797).

Description: Leaf simple, elliptic, 34 mm long and 13 mm broad, base almost complete, cuneate, narrowed continually into 7.8 mm long and 2 mm broad petiole, apex incomplete, probably acute or obtuse, margin entire, venation poorly preserved, ?paralellodromous, with 3 thin parallel veins bent towards the apex on either side of a thin midrib.

Discussion: The entire margin, the narrowed base with a broad petiole and paralellodromous venation type are morphological features that may correspond to leaves of *Potamogeton*. Broader leaf forms of this genus were rarely described, e.g. by Knobloch (1969) from the Karpatian of Moravia at Nový Jičín as *Potamogeton* sp. or by Sitár (1969) from the middle to upper Miocene deposits of the Turiec Basin as *P. martinianus* Sitár.

Monocotyledonae fam. et gen. indet.
Fig. 2.17–18

Material: Numerous leaf fragments (SNM B 1795/2, B 1798).

Description: Leaf fragments simple linear, various in size up to 170 mm long and 29 mm broad, base and apex not preserved, margin entire, venation paralellodromous and poorly preserved.

Discussion: Sitár (2001, Fig. 1; Fig. 2.17) described several incomplete leaf impressions (5–7 mm broad) with parallel venation, which co-occurred with *Paleotriticum* and were preliminary assigned to the Poaceae family. Similar leaf fragments are common in the Paleogene and Neogene plant assemblages of Europe and are usually interpreted as azonal herbaceous elements because they are accompanied by fruits of Cyperaceae, typical of moist habitats. Our specimen (Fig. 2.17) is poorly preserved and more slender. It could have some affinity to *Pinus*, but no morphological feature resembling leaf midrib is visible. Bands of leaf remains accompanying the infructescences of *Palaeotriticum* at Cerová-Lieskové as well as at Slup are not referable to any particular monocot.

Angiospermae incertae sedis

Dicotylophyllum Saporta
Dicotylophyllum sp. 1
Fig. 2.20–21

Material: Incomplete leaves and fragments (SNM B 1799, B 1802).

Description: Leaves simple, elliptic to obovate, 28–72 mm long, 11–24 mm broad, base cuneate, petiole not preserved, apex incomplete, probably shortly acuminate and blunt, margin entire, venation brochidodromous, midrib strong, straight or slightly curved in the apical part, secondary veins thinner, alternate, originating at an angle of 40–60°, curved and looping near margin, intersecondaries parallel to major secondaries, venation of higher orders poorly preserved.

Discussion: These remains show some affinity to Lower Miocene leaf morphotypes of the Lauraceae, Magnoliaceae and Fabaceae families. The leaves may not represent a single fossil species. The impression character and poor preservation do not allow discrimination of the leaf texture. The specimen shown in Fig. 2.20 is similar to the leaf material from several Miocene localities in the Rhineland and Lower Lusatia described as *Papilionaceophyllum liblarense* Kräusel & Weyland (=*Magnolia liblarensis* (Kräusel & Weyland)

◄

Fig. 3. 1–3 *Platanus neptuni* (Ettingshausen) Bůžek, Holý & Kvaček: 1 — negative impression of a complete leaf with fine serrate apex, SNM B 1800, scale bar 10 mm; 2 — positive incomplete leaf impression with distinctly serrate leaf margin and semicraspedodromous venation, SNM B 1801, scale bar 10 mm; 3 — incomplete leaf with poorly preserved venation, SNM B 1804, scale bar 5 mm. **4** — *Dicotylophyllum* sp. 2, very narrow fragmentary leaf lamina, SNM B 1803/a, scale bar 10 mm. **5–7** — *Platanus neptuni* (Ettingshausen) Bůžek, Holý & Kvaček: 5 — immature fruitlet with long slightly curved style, SNM B 1806/b, scale bar 1 mm; 6 — immature fruitlet with almost straight style, SNM B 1807, scale bar 1 mm; 7 — impression of an immature fruitlet with long and curved style showing a few indistinct longitudinal ribs, SNM B 1808, scale bar 1 mm. **8** — *Concavisporites* sp. (Gleicheniaceae), spore, interval 49–50. **9–10** — Cupressaceae, pollen grains, sample 12. **11–13** — Pinaceae, pollen grains, interval 49–50. **14–15** — *Pinus* sp., pollen grain, interval 49–50 and sample 18. **16** — cf. *Potamogeton*, pollen grain, interval 49–50. **17** — cf. *Liquidambar*, pollen grain, sample 46. **18** — Fagaceae, pollen grain, sample 23. **19** — *Engelhardia* sp., pollen grain, interval 49–50. **20** — *Craigia* sp. (*Intratriporopolenites* cf. *insculptus* type), pollen grain, interval 49–50. **21** — *Tricolporopollenites* sp., pollen grain, interval 49–50. **22** — Zygnemataceae, Algae, sample 46. **23** — Algae, sample 46. **24** — *Mecsekia* sp., Algae, interval 49–50. **25** — Dinoflagellata, Algae, sample 18. **26–27** Dinoflagellata, Algae, interval 49–50. **28** — Dinoflagellata, Algae, sample 46. **29** — Dinoflagellata, Algae, sample 23. 8–29 — scale bar 20 µm.

Kvaček) and related to the genus *Magnolia* L. (Kvaček 1979; Schneider 2007). In the absence of the epidermal anatomy, the affinity to this species or to other numerous species of *Laurophyllum*/Lauracaeae and Fabaceae is inconclusive (e.g. Bůžek et al. 1996; Kvaček 1971; Holý et al. 2012). A stratigraphically and geographically close plant assemblage from Dolní Dunajovice contains similar leaves with entire margins assigned to *Laurophyllum* sp. and *Dicotylophyllum* sp. 8 by Knobloch (1969).

Dicotylophyllum sp. 2
Fig. 3.4

Material: Fragment of leaf/leaflet lamina (SNM B 1803/a,b).

Description: Medial part of leaf/leaflet lamina, 53 mm long, 4 mm broad, base and apex not preserved, margin probably entire, venation probably brochidodromous, midrib strong, slightly curved, lateral veins thinner, alternate, originating at an angle of 40–55°, venation of higher orders poorly preserved.

Discussion: The incomplete character of the lamina does not allow any assignment to the genus and family levels. Similar leaf impressions from the Karpatian of Moravia (Dolní Dunajovice) were assigned to *Echitonium sophiae* O. Weber by Knobloch (1969).

Palynology

Terrestrial plants sporomorphs (Fig. 3.8–21) of Pinaceae, Cupressaceae, *Pinus* sp., *Engelhardia* sp., *Tricolporopollenites* sp., cf. *Potamogeton*, cf. *Craigia* sp. (*Intratriporopolenites* cf. *insculptus*) and aff. *Concavisporites* (Gleicheniaceae) occur in interval 49–50, in addition to palynomorphs of *Mecsekia* sp. (Fig. 3.24) and dinoflagellates (Fig. 3.25–29) typical of marine environment. Similarly, the samples 46 and 23 contain various dinoflagellates and marine algae remnants (46) as well as *Mecsekia* sp. (23) and freshwater algae (Zygnemataceae) (Fig. 3.22), which are associated with very rare and poorly preserved cf. *Liquidambar* and unidentified pollen *Tricolporopollenites* sp. (46) and single grains of Fagaceae, Cupressaceae and Pinaceae (23). Sporomophs occur rarely in sample 12, being represented by single grains of Cupressaceae and cf. *Potamogeton* sp. The sample 18 shows a palynological composition almost identical to that of sample 23 and is characterized by *Mecsekia* sp., dinoflagellates, Pinaceae, and by re-worked *Lygodium* spore. The samples 49 and 30 are totally barren of palynomorphs. Single and poorly preserved grains of Pinaceae and *Cathaya* sp. were found in samples 20 and 33.

Composition and habitat of source plant assemblage

The macrofossil plant assemblage of Cerová-Lieskové consists of two conifers and four morphotypes of angiosperm foliage as well as of several molds of spike-like infructescences of azonal monocots. The palynological assemblage is also not diverse and taxonomically matches the macrofossil plant assemblage. The low taxonomic richness and common co-occurrence of these taxa during the Miocene do not allow precise phytostratigraphical correlation with other plant assemblages in Central Europe. However, the occurrence of the infructescence of *Palaeotriticum mockii* at the locality of Slup near Znojmo implies floristic similarity between the Vienna Basin and the Carpathian Foredeep. The single specimen at this locality co-occurs with *Tetraclinis salicornioides* (cited by Knobloch 1969 as *Libocedrites salicornioides*), *Cinnamomum polymorphum* (as *Daphnogene bilinica*) and with several lauroid and betuloid leaf fragments. Knobloch (1967, 1969) described Karpatian plant assemblages from Dolní Dunajovice, Velké Dyjákovice and from the drill-core of Kl 147 at Žilina near Nový Jičín from the Czech part of the Carpathian Foredeep. Two other conifers — *Glyptostrobus europaeus* (Brongniart) Unger and *Pinus* sp. (cited in Knobloch 1969, p. 45, as *P.* aff. *goethanus* Unger, *P.* aff. *saturni* Unger) and several angiosperms (*Potamogeton* sp., *Arundo* sp. vel *Phragmites* sp., *Liquidambar europaea* A. Braun, *Carpinus* sp., Betulaceae gen. et sp. indet., *Echitonium sophiae* Weber, and *Dicotylophyllum* sp. div.) also occur in the Carpathian Foredeep. These plant assemblages consist of taxa that occur frequently during the Miocene at other sites in the Czech Republic (the Cypris Formation, the Kristina Mine in the Zittau Basin in North Bohemia, the Mydlovary Formation in South Bohemia — Bůžek et al. 1996; Holý et al. 2012), Germany (Berzdorf, Wackersdorf — Knobloch & Kvaček 1976; Czaja 2003), Poland (Turów — Czeczott & Skirgiełło 1959, 1961, 1967, 1975, 1980) and Austria (Kovar-Eder 1998; Meller 1998; Hofmann et al. 2002).

We suggest that the source vegetation of Cerová-Lieskové represents a mixture of azonal and zonal elements. Arboreal elements of *Tetraclinis salicornoides/*Cupressaceae, *Cathaya*, *Pinus* sp., *Cinnamomum polymorphum*, *Engelhardia*, *Platanus neptuni*, and probably lauroid elements of *Dicotylophyllum* sp. 1–2 belong to mesophytic vegetation of the Broad-leaved Evergreen or Mixed Mesophytic forest type (e.g. Kovar-Eder et al. 2008). These vegetation types are also captured by other Karpatian plant assemblages of Central Europe (Kovar-Eder et al. 2001; Holý et al. 2012). Azonal elements are represented by herbaceous monocots, including *Paleotriticum*, *Potamogeton* sp., and arboreal elements such as *Liquidambar* and partly mesophytic *Craigia* (Kvaček & Walther 2004) corresponding to riparian vegetation. The analogy with the *Spartina* type grasses allows reconstruction of the herbaceous vegetation type as coastal salt marshes and brackish marshes as known on tidal wetlands of North America.

Conclusions

Fully marine, upper slope bathyal clays and silts at Cerová-Lieskové locality contain relatively well-preserved plant remains that reflect terrestrial vegetation of the surrounding land. The plant assemblage corresponds to allochthonous remains transported by currents into the upper-slope environments. The macrofossil and pollen assemblages correspond to thermophile subtropical forests typical of the Karpatian (late Burdigalian) time interval in Europe (Brzobohatý et al. 2003). Enigmatic monocots resembling wheat infructescence probably belong to herbaceous salt marsh vegetation growing close to the shoreline, similar to the living grass *Spartina* Schreb. These monocots are similar to specimens described from Moravia (Early Miocene–Karpatian) and Slovenia (Middle Miocene–Badenian). These specimens were previously wrongly assigned to *Spirematospermum* fruits or Pinaceae seed cones, respectively. We suggest that these monocots represent herbaceous vegetation bounded to intra-tidal flats.

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