The Eocene flora of Tatabánya “marl-mine” (N Hungary)

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Abstract

The middle Eocene (Lutetian) fossil plant assemblage from Tatabánya (N Hungary) comprises plant remains preserved mostly as impressions. Remains of angiosperms are represented by Lauraceae (*Laurophyllum* div. sp., *Daphnogene* Unger), Rhamnaceae (*Ziziphus* Miller), Malvaceae s.l. (*Byttneriopsis* Z.Kvaček et Wilde), Leguminosae, and Palmae, and the occurrence of other families, i.e., Dioscoreaceae, Myrtaceae, Fagaceae, Anacardiaceae, Berberidaceae, Juglandaceae, and Theaceae, is uncertain. The scarcity of gymnosperms is a character similar to the coeval floras of Csordakút (N Hungary) and Girbou in Romania. The presence of *Ziziphus ziziphoides* (Unger) Weyland, high number of linear shaped leaves with entire margin and coriaceous texture (Lauraceae vel Fagaceae), and small-leaved Leguminosae suggests a “subhumid” character of the vegetation, which is recognisable also in early Palaeogene floras of eastern Central and Southeastern Europe, e.g., the Tard Clay floras in Hungary and floras of Serbia/Macedonia. In contrast, the Eocene floras from Central/Western Europe are indicative of a generally non-xerophytic character, e.g., Staré Sedlo in Bohemia, Messel, Geiseltal, and the Weissenster Basin floras in Germany. A frost-free climate with high mean annual temperatures similar to that estimated for coeval European floras may also be inferred for the Tatabánya flora.

Keywords Palaeobotany · Eocene · Lutetian · Plant macrofossils · Hungary

Introduction

Plant fossil record from the Eocene of Hungary

Reports on Eocene plant fossils from Hungary are scarce and often deal with few or even single specimens, which have exclusively been recorded from the Transdanubian region. From the middle Eocene of Budapest (Martinovics Hill), a palm fruit, *Actinorhytis eocaenica* (Tuzson) Rásky (*Juglandites eocaenica* Tuzson in Tuzson 1913), and a dicotyledonous flower, *Monotes oeningiensis* (Heer) Weyland, were recorded by Rásky (1956a). Furthermore, fruits of the “mangrove palm” *Nypa* Wurm (‘‘*Nipa burtinii* (Brongniart)

Ettingshausen’’) were reported (Schafarzick and Vendl 1929; Andreánszky 1954; Pálfalvy 1965).

From west of Budapest, *Nypa* (*Nipadites burtini* Brongniart) was documented from Dudar in the Bakony Mts. (Rásky 1948), a fruit from Tokod was described as *Xylopiacarpum eocaenicum* Rásky (Annonaceae) (Rásky 1956b), and a fragment of a leaf from Felsőgalla (Rásky 1956b) was determined as *Apocynophyllum plumieroides* Staub. Furthermore, ferns were described from the same area, including a fragment of *Acrostichum lanzaeanum* (Visiani) Reid et Chandler (Pálfalvy 1966a) from the Solymár Basin, and a fragment of a frond from Balinka, which was identified as *Stenochlaena palustris* (Burman) Beddome by Kovács (1957a). Another middle Eocene flora comprising more taxa was recorded from Látatlan in the Dorog Basin, N Hungary. Kovács (1961) published a huge list with taxa like *Blechnum* Linnaeus, *Buettneria apiculata* Kovács, *Castanopsis furcinervis* (Rossmäessler) Kräusel and Weyland, *Cedrela* P.Browne, *Cedrelospermum* Saporta, *Cinnamomum polymorphum* Heer, *Dryophyllum* Debey, *Eucalyptus* L’Héritier de Brutelle, Leguminosae, *Magnolia* Linnaeus, *Myrica* Linnaeus, Palmae, *Pterocarya* Kunth, *Quercus* Linnaeus, and *Sequoia* Endlicher from the locality. However, only a limited number of taxa from the assemblage were figured by Kovács.

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The flora of Lábátlan was revisited by Z. Kvaček during a visit to Budapest in 1989. Z. Kvaček (in Knobloch et al. 1996) mentioned the similarity of a predominant leaf type (“*Eucalyptus*” *transdanubica* Kovács) to *Apocynophyllum helveticum* Heer and proved the occurrence of Juglandaceae by cuticular analysis.

From the Lutetian of Csordakút (Gerecse Mts), a fossil flora was published by Erdei and Rákosi (2009). Remains of gymnosperms are absent from the fossil plant assemblage. Angiosperms were identified as *Daphnogene* sp., cf. *Eotrigonobalanus furcinervis* (Rossmässler) Walther et Z. Kvaček, *Cedrelospermum* div. sp., *Myrica* sp., *Comptonia* div. sp., Leguminosae (leaves and fruit), ?*Ziziphus ziziphoides* (Unger) Weyland, *Sloanea nimrodii* (Ettingshausen) Z. Kvaček et Hably, *Sloanea* sp. (fruit), *Smilax* div. sp.

Kedves studied the palynoflora of numerous Eocene sections from the region of Halimba (Bakony Mountains, Kedves 1961), the Dorog Basin (Kedves 1960), Solymár (Pilis Mountains, Kedves 1966a), and the Tatabánya Basin (Kedves 1962a) and recorded Palmae, *Castanea* Miller, *Quercus*, Myricaceae, Fagaceae, Taxodiaceae–Cupressaceae, Nyssaceae, *Pinus* Linnaeus, Sterculiaceae, Ericaceae, Aquifoliaceae, *Engelhardia* Leschenault de la Tour ex Blume, Anacardiaceae, Cycadales, etc. (Kedves 1963a; Kedves and Kolosváry 1966).

Fossil plants from Tatabánya

The first report on plant fossils from Tatabánya (Hosszúhajtai Valley in Pálfalvy 1966b) was published by Andreánszky (1951). The fossils were recovered from the *Operculina*-bearing clay marl and the overlying sandstones. According to Pálfalvy (1966b), the plant assemblage from the sandstones is richer than that from the clay marl. From the clay marl, Andreánszky (1951) especially mentioned Leguminosae (both fruits and leaves, including *Mimosocarpum* Andreánszky). Later Pálfalvy (1966b) added *Cinnamomophyllum* Kräusel et Weyland (Lauraceae), *Myrica* (Myricaceae), Palmae, *Quercus* (Fagaceae), Sapotaceae, and *Engelhardia* to the list. According to palynological studies (Kedves 1962a, 1963b, 1966b), spores of Osmundaceae, Polypodiaceae, and Schizaeaceae predominate in the clay marl, but pollen assigned to Palmae (e.g., *Calamus* Linnaeus), Ericaceae, Fagaceae, Juglandaceae, Meliaceae, Myricaceae, Sapotaceae, and Sterculiaceae were also mentioned. Based on the thin-shelled molluscs of the clay marl and the predominance of pteridophyte spores, Pálfalvy (1966b) suggested a calm nearshore depositional environment.

From the overlying sandstones, Pálfalvy (1966b) mentioned Annonaceae, Aquifoliaceae, Fagaceae, Lauraceae, Magnoliaceae, Myricaceae, Myrtaceae, Palmae, Sapotaceae, Sterculiaceae, *Zizyphus ziziphoides*, and some ferns including a new species, *Stenochlaena transdanubica* Pálfalvy, all from the Rozlozsnik collection, which is deposited in the former Hungarian Geological Survey, now Mining and Geological

Survey of Hungary (MBFSZ, Budapest). Kovács (1957b) published some additional plant remains from the brown coal deposits of Tatabánya (shafts IX and XI) which are underlying the clay marls and assigned them to the genus *Dracontomelon* Blume (*Dracontomelon minimum* Reid et Chandler) but Manchester (1994) reassigned both the London Clay and Tatabánya occurrences to the extinct anacardiaceous genus *Pentoperculum* Manchester.

According to Kovács (1968), a collection made by Skoflek in 1963–1964 at the so-called Tatabánya I and II localities and also stored in the MBFSZ includes taxa like *Actinodaphne* Nees, Anacardiaceae, *Apocynophyllum* Heer, *Buettneria apiculata* Kovács, *Castanopsis furcinervis* (Rossmässler) Kräusel et Weyland, *Cedrela*, *Cupania* Linnaeus, *Diospyros* Linnaeus, *Dodonaea* Miller, *Dryophyllum*, *Grewiopsis* De Wildeman et T.Durand, *Illicium* Linnaeus, Lauraceae, Leguminosae, *Lithocarpus* Blume, *Magnolia*, Magnoliaceae–Annonaceae, *Michelia* Linnaeus, *Myrica*, *Notelaea* Ventenat, Palmae, *Persea* Miller, *Plumeria* Linnaeus, *Quercus*, *Sapindus* Linnaeus, *Stenochlaena* J.Smith, *Strychnos* Linnaeus, and *Ziziphus ziziphoides*. Unfortunately, nothing was figured from the collection by the author except for only three types of leaves which were assigned to *Laurus assimilis* Saporta, Magnoliaceae, and *Sapindus* sp., respectively.

Later, Hably (1985) published some taxa from Tatabánya–Márgabánya (“marl-mine”) and noted that this locality is not identical with those mentioned above, i.e., *Castanopsis elisabethae* Kolakovsky, *Engelhardia orsbergensis* (Wessel et Weber) Jähnichen, Mai et Walther, *Nyssa* sp., *Ocotea obtusifolia* (Berry) La Motte, *Paliurus* cf. *tiliaefolius* (Unger) Bůžek, *Sabal major* (Unger) Heer, and *Zizyphus ziziphoides*.

The present paper focuses on specimens which were collected by Skoflek in Tatabánya in the 1980s. A reinvestigation and revision of the collections mentioned above is beyond the scope of this study.

Geology, stratigraphy, and age of the locality

In Hungary, Eocene rocks discordantly overlie older (Mesozoic or Paleozoic) strata (Kecskeméti 1998). The total thickness of middle and upper Eocene sediments does not exceed 500–700 m. The rocks comprising the flora of Tatabánya “marl-mine” (Fig. 1) belong to the Csolnok Claymarl Formation and are called as well “Operculine marl” or “Nummulite marl” because of the sometimes high or even rock-forming quantities of foraminifera (Kecskeméti 1998). Based on the occurrence of *Nummulites subplanatus* Hantken and *N. variolarius* Lamarck, which are indicating the first marine sediments of the Eocene transgression, Kecskeméti (in Hably 1985) assigned the fossiliferous sediments to the Lutetian (middle Eocene). On the other hand, the “Operculine marl” (cited as belonging to the Dorog Formation

Fig. 1 Geographic position of the Tatabánya “marl-mine” locality and a simplified geological map for the area of Tatabánya (modified after Selmeczi in Hably et al. 2015)

Geographic position of the Tatabánya “marl-mine” locality and a simplified geological map for the area of Tatabánya (modified after Selmeczi in Hably et al. 2015).

in Báldi-Beke 1984) was dated as NP16 nannoplankton zone (upper Lutetian) based on the occurrence of *Reticulofenestra placomorpha* (Kamptner) Stradner in Stradner et Edwards, *Pemma papillatum* Martini, and *Sphenolithus furcatolithoides* Locker (Báldi-Beke 1984).

Material and methods

Fossils included in this study were collected by István Skoflek in the 1980s from the Tatabánya “marl-mine” locality (Fig. 1). The collection at our disposal consists of nearly 400 specimens that are housed in the Kuny Domokos Museum, Tata (N Hungary) (abbreviation “TB”). Fossils are almost exclusively leaves; fruits are only represented by a couple of poorly preserved specimens.

Fossils are preserved in yellowish, often reddish carbonaceous sandy clay. Leaves are mostly preserved as impressions

and rarely as blackish compressions; however, our attempts to prepare cuticles mostly failed. Leaves are often fragmented, and entire specimens with apex, base, and leaf margin preserved are rare. The margin of the leaves is often damaged. This suggests transport and/or decay of the plant material before final burial; however, incompleteness of leaves is often caused by the irregular cleavage of the rock.

Rarely, leaves are characterised by a texture more resistant to decay and retained cuticles showing epidermal details. Cuticles were isolated following the conventional method including rock-digestion by HCl/HF, oxidation with HNO₃ (instead of Schulze’s solution), and leaching by an aqueous solution of KOH.

The cuticles were studied with transmitted light, interference contrast, and epifluorescence microscopy (Nikon Eclipse E600 type microscope equipped with a SPOT digital camera). Digital photos were processed with the software “Image-Pro Plus Ver. 4.”

◀ **Fig. 2** **a** Pteridophyta, fragment of a pinna or pinnule; TB.83.587.1; scale bar 1 cm. **b** ?Cupressaceae s.l., twig fragment; T.B.83.484.1, scale bar 1 cm. **c–e** *Laurophyllum* ?*kinkelinii* (Engelhardt) Kvaček; TB.83.293.1; **c** leaf fragment, scale bar 1 cm, **d** abaxial cuticle showing stomata and trichome bases, fm, scale bar 30 µm. **e** Abaxial cuticle showing stomata and trichome bases, fm, scale bar 30 µm. **f–h** cf. *Ocotea hradekensis* (Kvaček et Bůžek) Kvaček; TB.83.385.1; **f** fragmented leaf, scale bar 1 cm. **g** Abaxial cuticle showing stomata, lm, scale bar 30 µm. **h** Abaxial cuticle showing stomata, lm, scale bar 30 µm. **i** *Laurophyllum* sp., leaf; TB.83.369.1.; scale bar 1 cm. **j** *Laurophyllum* sp., leaf; TB.83.493.1.; scale bar 1 cm

Results

Pteridophyta

Figure 2a

Material: TB.83.587.1

Description: A tiny fragment from the marginal part of a pinna or pinnule.

Gymnosperms

?Cupressaceae s.l.

Figure 2b

Material: T.B.83.484.1

Description: The only putative record of gymnosperms is a poorly preserved twig fragment with ?helically arranged scale-like leaves; however, cuticle was not retained.

Angiospermae

Lauraceae

Laurophyllum Göppert

Laurophyllum ?*kinkelinii* (Engelhardt) Kvaček

Figure 2c–e

Material: TB.83.293.1; TB.83.435.1; TB.83.479.1

Description (TB.83.293.1): Fragment from the upper half of leaf, up to 7 cm long and 2.2 cm wide, entire margined. Shape of lamina narrow, ?elliptic. Apex attenuate. Venation camptodromous, midrib moderate. Six pairs of secondary veins arise at angles of 45–50°. Tertiary venation not visible.

Adaxial cuticle not preserved, arrangement of epidermal cells on abaxial cuticle barely recognisable (therefore epifluorescence was applied to reveal more details).

Anticlinal cell walls slightly thickened, curved, epidermal cells isodiametric, 13–28 µm in diameter. Randomly arranged stomata and single-celled trichome bases occur in high number. Elongated cells and trichomes (trichome bases) clearly indicate the course of the veins. Stomata paracytic, 15–20 µm wide and 13–18 µm long, stomatal pore 4–5 µm long, stomatal ledges not thickened. Trichome bases with 6–9 surrounding cells, basal cell thickened with bright fluorescence, trichomes not preserved.

Discussion: The above description fits best to leaves of Lauraceae and the fossil leaf is therefore assigned to the form

genus *Laurophyllum*. The epidermal details, namely, the structure of epidermal cells and stomata, the hardly discernible outlines of ordinary cells and stomata, and the high number of trichome bases are most comparable to *L. kinkelinii* as described from the early Oligocene flora of Flörsheim (Kvaček 2004). However, in the lack of more macromorphological details, the assignment of the leaf fragment to the species is uncertain.

Considering *Laurophyllum* species reported so far from this area (equivalent to the later central Paratethys), *L. acutimontanum* Mai and *L. markvarticense* Kvaček show some similarities in having elongate leaves and apex. *L. acutimontanum* has similar trichome bases but these occur only sparsely. The species differs also in having more or less papillate cells encircling the stomata and slightly overlapping the stomatal pore (Mai 1963; Kvaček 1971). *L. markvarticense* has very scanty trichome bases (Kvaček 1971) in contrast to the present leaf which is characterised by a high number of them.

The epidermal characters of *L. pseudovillense* Kvaček show the greatest similarity, i.e., quite small paracytic stomata and trichome bases of more or less similar structure (Kvaček 1971). However, such a density of trichome bases has neither been reported from the type material of *L. pseudovillense* (Kvaček 1971) nor in later reports of the species (Kovar-Eder et al. 1998; Meller et al. 1999). Furthermore, a rim around the basal cell of the trichomes is not so expressed in our material. A somewhat similar epidermal structure may be observed in *Laurophyllum* sp. leaves from the Oligocene flora of Csolnok, Hungary (Erdei and Wilde 2004), although stomata are slightly smaller for the present material than those of the Csolnok leaves (length 15–20 µm, width 18–25 µm). The leaves from Csolnok are less elongate and have an acute apex contrasting with the *Laurophyllum* leaves from Tatabánya having long attenuate apex and narrow lamina. In addition, unlike on those from Csolnok, a large number of trichome bases and no papillate structures have been observed on the cuticle of the leaf from Tatabánya. It should be noted, however, that the density of trichomes may be the result of different ecological constraints (e.g., sun/shade leaves, lower humidity; see Johnson 1975).

Kvaček (2004) compared the fossil leaves of *L. kinkelinii* with extant *Persea* leaves based on leaf shape, venation, and epidermal structure.

Laurophyllum sp.

Figures 2i–j and 3a

Material: TB.83.369.1; TB.83.380.1; TB.83.399.1; TB.83.493.1; TB.83.508.1; TB.83.533.1; TB.83.540.1

Description (based on TB.83.369.1. and TB.83.493.1.): Fragmentary leaves, length of the fragments more than 5 cm, width 2.3–3 cm. Apex not preserved, base acute. Margin entire. Venation camptodromous, with secondaries arising at angles of 40–60°. Secondaries curved and

Fig. 3 **a** *Laurophyllum* sp., leaf; TB.83.533.1.; scale bar 1 cm. **b** *Daphnogene* sp., leaf; TB.83.327.1.; scale bar 0.5 cm. **c** *?Eotrigonobalanus furcinervis* (Rossmässler) Walther et Z. Kvaček, leaf; TB.83.257.1.; scale bar 1 cm. **d** *?Engelhardia orsbergensis* (Weber) Jähnichen, Mai et Walther, leaf; TB.83.540.1.; scale bar 1 cm. **e** *Ziziphus ziziphoides* (Unger) Weyland, leaf; TB.83.522.1.; scale bar

1 cm. **f** *Ziziphus ziziphoides* (Unger) Weyland, leaf; TB.83.445.1.; scale bar 1 cm. **g** *Byttneriopsis daphnogenes* (Ettingshausen) Kvaček et Wilde, leaf; TB.83.432.1.; scale bar 1 cm. **h** cf. *Byttneriopsis* sp., leaf; TB.83.429.1.; scale bar 1 cm. **i** *?Mahonia* sp., leaf; TB.83.442.1.; scale bar 1 cm. **j** *Leguminosites* sp., leaflets; TB.83.548.1.; scale bar 1 cm. **k** *?Rhodomyrtophyllum* sp., leaf; TB.83.315.1.; scale bar 1 cm

forming weak loops close to the margin. Epidermal details not preserved.

Discussion: Leaf morphology, entire margin and venation recall leaves of Lauraceae (see Klucking 1987).

?*Ocotea* Aublet

cf. *Ocotea hradekensis* (Kvaček et Bůžek) Kvaček

Figure 2f–h

Material: TB.83.385.1

Description: A fragmentary leaf with well-preserved cuticle. Length of the fragment 10 cm, width 2.5 cm. Margin entire, apex and base not preserved. Secondary and higher order venation not preserved.

Adaxial cuticle not preserved. Abaxial cuticle thick and showing a well recognisable arrangement of epidermal cells. Anticlinal cell walls straight and moderately thickened. Epidermal cells isodiametric and 12–30 µm in diameter. Stomata randomly arranged, paracytic, 18–24 µm wide and 16–22 µm long. Strongly cutinized outer stomatal ledges surround the 8–12 µm long stomatal pore. No trichomes, trichome bases, or any special ornamentation of the cuticle observed. Amorphous fluorescent patches (?oil glands) appear when using epifluorescence.

Discussion: Although, it represents about two thirds of the original size, its macromorphological traits are hardly recognisable and reveal no details of the venation type. Overall character of the cuticle, type and size of stomata, and the lack of trichome bases fit best to the description of *Laurophyllum hradekense* Kvaček et Bůžek (Kvaček and Bůžek 1966; Kvaček 1971) later recombined as *Ocotea hradekensis* (Kvaček in Bůžek et al. 1996). The fossil leaf from Tatabánya is only tentatively assigned to *O. hradekensis* since the anticlinal cell walls are less thickened (though this may be the result of habitat variation) and less undulate compared to *O. hradekensis* (Knobloch and Kvaček 1976; Holý et al. 2012). Stomata are a bit smaller, similar to the size displayed by the stomata of *Laurophyllum pseudoprinceps* Weyland et Kilpper. However, the latter species has characteristic bead-like thickenings unlike our fossil. Due to the poorly preserved macromorphology of the leaf, the axillary glands at the base of the lower secondaries which were described by Bůžek et al. (1996) as characteristic for the species (see below) cannot be recognised in our specimen.

O. hradekensis has been recorded so far mainly from Miocene localities such as in the Oberpfalz (Bavaria, Germany) together with co-occurring thermophilous elements (e.g., Pandanaceae, Zingiberaceae) (Peters 1963), the Lower Lusatian coal seam, the Žitava Basin, N Bohemia, as an element of a rich mastixioid flora of subtropical character (Kvaček 1971; Holý et al. 2012), from Ledenice (South Bohemian Basins, Knobloch and Kvaček 1996), and from the early Miocene Cypris Shale (Western

Bohemia, Bůžek et al. 1996). Based on similar epidermal patterns and associated fruit remains, Kvaček (1971) compared the fossil taxon with recent *Ocotea* (*O. foetens* Benthams et Hooker). Kvaček (in Bůžek et al. 1996) therefore directly assigned the species to the genus *Ocotea* as *Ocotea hradekensis* (Kvaček et Bůžek) Kvaček based on a combination of characters such as type of stomata and axillary glands (at the axils of the basal pair of secondary veins). He mentioned a younger record of the species from the early Pannonian of Romania. An older, Palaeogene occurrence was reported by Hably (1992) from the early Oligocene Tard Clay Formation in Hungary. However, considering the long stratigraphic record, it seems hardly probable that the same species persisted without any changes from the middle Eocene up to the Miocene.

Daphnogene Unger

Daphnogene sp.

Figure 3b

Material: TB.83.327.1

Description: A small fragmentary leaf of 1.5 cm width and 2.7 cm preserved length. Shape elliptic and asymmetric, margin entire. Base obtuse, petiole and apex not preserved. Venation basal acrodromous. The strong basal pair of secondary veins runs into the upper half of the lamina. Relatively strong tertiary veins (at least three on both sides) depart from the basal secondaries and form loops. Higher order venation reticulate.

Discussion: The morphology of the fossil resembles those leaves that are commonly assigned to the collective extinct genus *Daphnogene*. Although leaves of *Daphnogene* mostly display a suprabasal pair of strong secondary veins and a more acute base, the overall character of the fossil leaf still is most comparable to this lauraceous genus. However, acrodromous venation occurs in a great number of angiosperm families, e.g., Lauraceae, Hamamelidaceae, Rhamnaceae, Melastomataceae, and Malvaceae. A similar three-veined fossil leaf taxon, *Majanthemophyllum* Weber has an opposite pair of basal secondaries, but it differs in its tertiary venation (Knobloch et al. 1996).

Fagaceae

?*Eotrigonobalanus* Walther et Kvaček

?*Eotrigonobalanus furcinervis* (Rossmässler) Walther et Kvaček

Figure 3c

Material: TB.83.257.1

Description: Upper half of a fragmentarily preserved lanceolate leaf. Preserved length 7.1 cm, width 1.5 cm. Apex not preserved. Margin toothed, teeth small, acute. Venation semicraspedodromous. Midrib straight and moderate,

◀ **Fig. 4** **a** ?Dioscoreaceae gen. et sp. indet., fruit; TB.83.205.2.; scale bar 1 cm. **b** Palmae gen. et sp. indet., leaf; TB.83.851.1.; scale bar 1 cm. **c, d** ?Theaceae gen. et sp. indet., leaf; TB.83.551.1.; C, scale bar 1 cm; D, scale bar 0.5 cm. **e** ?Theaceae gen. et sp. indet., leaf; TB.4; scale bar 1 cm. **f** *Dicotylophyllum* sp. 1., leaf; TB.83.596.1.; scale bar 1 cm. **g** *Dicotylophyllum* sp. 2., leaf; TB.83.567.1.; scale bar 1 cm. **h** *Dicotylophyllum* sp. 3., leaf; TB.83.356.1.; scale bar 1 cm

secondaries arise at angles of 45–55° and curve upwards. Higher order veins not preserved.

Discussion: The leaf recalls the morphology of *Eotrigonobalanus furcinervis*. A wide morphological range of the species was recorded (Kvaček and Walther 1989), i.e., lanceolate to ovate forms, entire to toothed margin, craspedodromous to semicraspedodromous and craspedodromous venation. Due to insufficiently preserved morphological details the leaf is only tentatively assigned to the species.

Eotrigonobalanus furcinervis is a frequent member of Palaeogene floras in Europe (for details, see Kvaček and Walther 1989; Knobloch et al. 1996). Further records of the species based on macromorphology are known from the Eocene flora of Ovce Polje, Macedonia (Mihajlovič and Ljubotenski 1994) and uncertain records from the Eocene flora of Csordakút, Hungary (Erdei and Rákosi 2009). Macro- and micromorphologically supported records of the taxon have been reported from the early Oligocene floras of the Hungarian Tard Clay Formation at Budapest—Nagybátony-Újlak brickyard and H-boreholes (Hably 1986; Hably and Manchester 2000).

Juglandaceae

?*Engelhardia* Leschenault de la Tour ex Blume

?*Engelhardia orsbergensis* (Weber) Jähnichen, Mai et Walther

Figure 3d

Material: TB.83.540.1.; TB.83.506.1.

Description (TB.83.540.1.): Asymmetric leaf(let), apical part not preserved. Length of the fragment 5 cm, width 2 cm, lamina and base asymmetric, cuneate, with a short petiolule(?) of 3 mm length. Margin serrate, teeth small, acuminate. Midvein slightly bent, secondaries arise at angles of 45–50°.

Discussion: The overall character of the leaf fragment is comparable to *Engelhardia orsbergensis*; however, the species has no distinct petioles. The short petiolule-like structure of the fossil may have formed due to infolding of the lamina (see in Jähnichen et al. 1977); however, some extant *Engelhardia* species, e.g., *E. roxburghiana* Lindley, carry leaflets with short petiolules. Nevertheless, since no epidermal details are available the fragment is only tentatively assigned to the species.

The species is widespread in the European Palaeogene and Neogene floras, and a frequent element of the Hungarian Cenozoic floras from the early Oligocene (Tard Clay floras) up to the Pliocene (Hably and Kvaček 1998).

Rhamnaceae

Ziziphus Miller

Ziziphus ziziphoides (Unger) Weyland

Figure 3e–f

1847 *Ceanothus ziziphoides* Unger, p.145, Taf. 49, fig. 10

1853 *Ceanothus ziziphoides* Unger, Ettingshausen, p. 76, Taf. 25, figs. 9–39

1948 *Ziziphus ziziphoides* (Unger) Weyland, Weyland, pp. 113–118

1975 *Ziziphus ziziphoides* (Unger) Weyland; Palamarev et Petkova, p. 205, Pl. 3, fig. A

Material: TB.83.206.1; TB.83.207.1; TB.83.223.1; TB.83.227.1; TB.83.255.1; TB.83.275.1; TB.83.286.1; TB.83.297.1; TB.83.300.1; TB.83.378.1; TB.83.399.1; TB.83.445.1; TB.83.522.1

Description: Leaves fragmentarily preserved, lanceolate, length of the fragments 2–2.8 cm, width 1.1–1.6 cm, petiole not preserved. Base acute, slightly asymmetric, apex not preserved. Margin crenate. Venation basal acrodromous. Midrib moderate and slightly bent. Apart from a pair of stout secondary veins arising at the base finer venation not preserved.

Discussion: The species is a common element of the early Oligocene floras of Hungary (Tard Clay floras; Andreánszky 1963, Hably 1979). Other unequivocal records of the species are not known from the Hungarian Eocene, although an equivocal record was reported from the Eocene of Csordakút (Erdei and Rákosi 2009). Another species, *Ziziphus bilinica* Ettingshausen, is often merged with *Z. ziziphoides* or maintained as a separate taxon (e.g., Kučlin; Kvaček and Teodoridis 2011) indicating that the European fossils of the genus still require revision (Kvaček and Teodoridis 2011).

The frequent occurrence of the species in Palaeogene assemblages of the eastern part, such as Häring (Austria; Ettingshausen 1853), Sotzka (Slovenia; Unger 1847), Ovce Polje (Macedonia; Mihajlovič and Ljubotenski 1994), and Bulgaria (Palamarev and Petkova 1975), may indicate a sub-humid character of the vegetation of parts of Central and Southeastern Europe for the respective time.

Malvaceae s.l.

Byttneriopsis Kvaček et Wilde

Byttneriopsis daphnogenes (Ettingshausen) Kvaček et Wilde

Figure 3g

Material: TB.83.432.1, ?TB.2.

Description: Fragmentarily preserved leaf (lower half) of 3.2 cm length and 2.8 cm width. Leaf with long petiole (more than 1 cm long, robust, 2 mm wide, pulvinate and geniculate). Leaf entire margined, base cuneate, venation basal acro-dromous with three strong primaries (three-veined). Higher order venation not preserved.

Discussion: The morphological description of the leaf is well comparable to that of the fossil genus *Byttneriopsis* (Kvaček and Wilde 2010). It accommodates simple, non-lobate, entire margined leaves with a characteristic long petiole, basal acrodromous venation, and barrel shaped glandular trichomes suggesting malvacean affinities (Kvaček and Wilde 2010). The leaf is assigned to *Byttneriopsis daphnogenes* based on the distinctly pulvinate and geniculate petiole, triveined venation, and cuneate base). This morphospecies was reported from various Eocene sites of Europe, including Lábátlan in Hungary, Messel in Germany, and Kučlín in the Czech Republic (Kvaček and Wilde 2010). The putative modern analogues of *Byttneriopsis* grow under subtropical-paratropical conditions (Kvaček and Wilde 2010).

cf. *Byttneriopsis* sp.

Figure 3h

Material: TB.83.429.1

Description: Leaf of 6.5 cm length and 2.9 cm width, ovate with entire margin, apex acuminate, base cuneate, petiole not preserved. Venation basal acrodromous with the basal veins arising directly from the base of the lamina, midrib moderate, basal veins curved, reaching up to nearly the half of the lamina, giving off loop-forming lateral veins. Higher order venation dense, orthogonal reticulate.

Discussion: The morphological description of the leaf fits well to that of the morphogenus *Byttneriopsis* (Kvaček and Wilde 2010). Since petiole and characteristic epidermal details of the leaf are not preserved the leaf is only tentatively assigned to the genus.

Leaves with similar morphology were described as cf. *Matudaea menzelii* Walther from the Tard Clay Formation (early Oligocene, Kiscellian) of Hungary (p. 9, Pl. 5, Figs. 1–6; Kvaček and Hably 1998). However, they differ in having two strong lateral veins arising slightly above the base (suprabasal acrodromous). Unfortunately, the material from the Tard Clay also lacks cuticles. Leaves of *Daphnogene* may show some similarities in their acrodromous venation (see, e.g., Wilde 1989), but venation is mostly suprabasal.

Berberidaceae

?*Mahonia* Nuttall

?*Mahonia* sp.

Figure 3i

Material: TB.83.442.1.

Description: Leaf(?) fragmentary, 3.1 cm long and 2 cm wide. Shape ovate, apex and base not preserved. Margin toothed, dentate, with few coarse teeth. Venation not preserved except for a stout midvein.

Discussion: The overall character of the fossil with its shape, margin, and texture, recalls *Mahonia* leaflets. Due to its fragmentary state and the lack of preservation in higher order venation, the fossil cannot be assigned to *Mahonia* with certainty. The earliest *Mahonia* fossils in Europe were described from the early Oligocene (Bůžek et al. 1990; Güner and Denk 2012).

Leguminosae

Leguminosites Bowerbank emend. Schimper

Leguminosites sp.

Figure 3j

Material: TB.83.548.1.

Description: Leaf compound, 8 leaflets preserved. Basal and apical parts of leaf not preserved. Leaflets sessile, narrow oblong, 0.6–0.8 cm long and 0.2–0.3 cm wide. Base acute, asymmetric, apex rounded. Margin entire. Venation not preserved.

Discussion: The compound leaf strongly recalls Leguminosae; however, closer affinities are uncertain.

Myrtaceae

?*Rhodomyrtophyllum* Rüffle et Jähnichen

?*Rhodomyrtophyllum* sp.

Figure 3k

Material: TB.83.315.1; TB.83.453.1.

Description: Narrow elliptic leaves, length of the fragments 3.8–4.2 cm, width 1.8–1.9 cm, petiole not preserved. Base acute, or nearly obtuse, apex not preserved. Margin entire. Venation eucamptodromous with dense and comparatively fine secondary and intersecondary venation. Midrib moderate and straight. Secondaries arise at angles of 70–80°, join the adjacent secondaries near the leaf margin and form loops. Finer intersecondary veins arise at the same angles between the secondaries. Tertiary venation appears reticulate. Cuticle not preserved.

Discussion: Such ovate leaves with dense secondary and intersecondary venation arising nearly perpendicular from the midvein resemble leaves that were assigned to Myrtaceae, e.g., *Rhodomyrtophyllum reticulosum* (Rossmässler) Knobloch et Kvaček in Knobloch et al. (1996), *R. sinuatum* (Bandulska) Walther in Mai and Walther (1985), or *R. rossmässleri* Rüffle et Jähnichen (1976). The fossils may well belong to *Rhodomyrtophyllum*; however, we refrained to assign the leaves with certainty due to the lack of cuticular details. *Rhodomyrtophyllum* leaves were mainly described from Eocene localities of Europe; those confirmed by cuticular structures are from Messel (Wilde 1989), the Weißenster Basin (Mai and Walther 1985), Staré Sedlo (Knobloch et al. 1996), and the Geiseltal (Rüffle and Jähnichen

Fig. 5 **a** *Dicotylophyllum* sp. 4., leaf; TB.5.; scale bar 1 cm. **b** *Dicotylophyllum* sp. 5., leaf; TB.83.417.1.; scale bar 1 cm. **c** *Dicotylophyllum* sp. 6., leaf; TB.83.378.1.; scale bar 1 cm. **d** *Dicotylophyllum* sp. 6., leaf; TB.83.378.1.; scale bar 1 cm. **e**

Carpolithes sp. 1., fruit or seed; TB.83.421.1; scale bar 1 cm. **f** *Carpolithes* sp. 2., ?fruit; TB.83.339.1; scale bar 1 cm. **g** *Carpolithes* sp. 3. (?*Ailanthus* sp.), fruit; TB.83.474.1; scale bar 1 cm

1976), etc. The only Hungarian record (also lacking cuticular details) of *Rhodomorphophyllum* (*R. rossmässleri*) was published from the early Oligocene Tard Clay floras (Budapest, H-boreholes, Hably 1979).

Theaceae

?Theaceae gen. et sp. indet.

Figure 4c–e

Material: TB.83.551.1; TB.4.

Description (TB.83.551.1): Fragmentary leaf, length 6.2 cm, width 2.5 cm. Leaf elliptic, slightly obovate, base cuneate,

apex not preserved, margin ?entire. Venation camptodromous, midvein stout, secondaries irregularly spaced, decurrent along midvein, arising at angles of 45–50°. Mostly fine intersecondaries, irregularly spaced, arising at various angles. Tertiary veins reticulate, between tertiaries freely ending branched veinlets.

Another leaf fragment (TB.4.) is petiolate and more ovate than the previous leaf, but shows a venation pattern with decurrent secondaries well comparable to the first leaf.

Discussion: Venation pattern, especially decurrent secondary veins, and overall leaf morphology resemble leaves of Theaceae (e.g., *Adinandra* Jack, *Eurya* Thunberg, *Gordonia*

J. Ellis, *Stewartia* I. Lawson).

Dioscoreaceae

?Dioscoreaceae gen. et sp. indet.

Figure 4a

Material: TB.83.205.2.

Description: Impression of a winged fruit of 1.4 cm length and 1.7 cm width. Fruit symmetrical, widely elliptic, with persistent epigynous calyx, at least two wings. Base narrowing into a pedicel, endocarp centrally positioned. Wing margin entire, marginal vein or thickening present. Venation pattern dichotomizing and anastomosing, veins radiating outwards, no suture observable.

Discussion: The clearly preserved epigynous perianth and the overall structure of the fruit recalls Dioscoreaceae (?*Dioscorea* L.) fruits. However, a strong median suture as seen in the modern fruits is not observable, which may be due to preservation. In Dioscoreaceae, fruits develop from a tricarpellate inferior ovary and an epigynous perianth often persists (Manchester and O’Leary 2010). Other fruits with epigynous perianth resembling the fossil belong to Combretaceae or Lecithydaceae. The wings of comparable fruits in Combretaceae have usually no distinct marginal vein/thickening. Fruits of *Petersianthus* Merrill (Lecithydaceae) are much larger than our fossil and have characteristic but different venation patterns of the wings (see Manchester and O’Leary 2010).

Comparable fruits (but with definite median suture) were described as *Dioscoreocarpum marginatum* Andreánszky from the early Oligocene flora of Eger-Kiseged (Tard Clay; Andreánszky 1959; see also Raz 2017). Other fruits were reported as ?*Dioscorea* from the late Eocene flora of Kučlin (Czech Republic; Kvaček and Teodoridis 2011). Today, members of Dioscoreaceae are plants with a liana-like or climbing habit.

Arecaceae

Palmae gen. et sp. indet.

Figure 4b

Material: TB.83.202.1; TB.83.204.1; TB.83.391.1; TB.83.535.1; TB.83.851.1

Description: Fragmentary remains of leaf segments, width of individual segments 1.2–1.5 cm, margin of segments entire. Basal or apical parts of segments not preserved.

Discussion: The fossil leaves probably represent a sabaloid palm; however, precise identification is not possible since the basal part of the segments is not preserved. Palms are represented in the Palaeogene of Hungary, though, not frequently. No palms were recorded in the coeval flora of Csordakút (Erdei and Rákosi 2009). From the early Oligocene floras of the Tard Clay Formation, some fossils were assigned to (sabaloid) palms, e.g.,

Sabal haeringiana Unger (Rásky 1943).

Angiospermae fam. indet.

Dicotylophyllum Saporta

Dicotylophyllum sp. 1.

Figure 4f

Material: TB.83.199.1; TB.83.361.1; TB.83.596.1.

Description (TB.83.596.1): Leaf fragmented, lamina elliptic, length 5.8 cm, width 2 cm. Apex and base not preserved but presumably both acute (?cuneate). Margin hardly observable, damaged, seems toothed, teeth details not available. Venation seems craspedodromous, midvein slightly curved, moderate, secondaries regularly spaced, at least 12 pairs, arise at 45–50°, run slightly bent toward the margin. Higher venation not preserved.

Discussion: According to shape and venation, these leaves may represent Fagaceae or Ulmaceae.

Dicotylophyllum sp. 2.

Figure 4g

Material: TB.83.567.1.

Description: Leaf asymmetric, lanceolate, 4.7 cm long and 1.2 cm wide. Base asymmetric, acute, apex attenuate. Margin entire. Venation cladodromous, midvein moderate, slightly curved. Secondaries (min. 11 pairs) arising at angles of 60–70°, run straight and fork near the margin. Delicate intersecondaries arise at the same angles as secondaries and run straight. Higher order venation not preserved.

Discussion: Leaf shape, entire margin, and type of venation may refer to Anacardiaceae.

Dicotylophyllum sp. 3.

Figure 4h

Material: TB.83.356.1.

Description: Simple petiolate leaf. Lamina symmetric, 6 cm long, 3.2 cm wide, elliptic. Petiole short, 25 mm long and relatively stout. Base obtuse, apex obtuse, and nearly rounded. Margin entire, slightly wavy. Venation eucamptodromous, midvein relatively thin and straight. Secondaries (8 pairs) arising at angles of 45–60°, slightly irregular in course and spacing, the lowermost pair arises close to the base at an angle of about 70°. Most pairs of secondaries opposite, rarely alternate, running nearly straight, curved near the margin. Higher order venation not preserved.

Dicotylophyllum sp. 4.

Figure 5a

Material: TB.83.419.1; TB.83.494.1; TB.83.506.1;

TB.83.546.1; TB.5; TB.83.566.1

Description: Narrow elliptic to lanceolate, slightly asymmetric leaves, length of the only complete leaf 15.2 cm, width 2–2.3 cm, the others are fragmentary. Petiole 0.4 cm long. Base acute, cuneate, apex attenuate. Margin entire but irregularly wavy. Venation eucampto-dromous, midrib stout and slightly curved. Secondaries curved arising at angles of 60–70°, some intersecondary veins less steeply arising. Higher order venation not preserved.

Discussion: Such entire-margined leaves with eucampto-dromous venation may represent species of Lauraceae or Fagaceae.

Dicotylphyllum sp. 5.

Figure 5b

Material: TB.83.417.1; TB.83.438.1; (broken halves of a single specimen)

Description: Leaf asymmetric, lanceolate, 10.5 cm long and 2.3 cm wide. Base not preserved, apex attenuate. Margin entire. Venation eucamptodromous, midvein moderate, curved in the lower half. High number of upward curving secondaries (min. 16 pairs) arise at angles of 60–70°. Intersecondaries (sometimes even two) arise between secondaries at angles of 60–80°. Adjacent secondaries and intersecondaries join to form loops or run towards the margin. Tertiary venation reticulate.

Discussion: The morphological characters of the leaf recall some Lauraceae (e.g., *Litsea* Lamarck, see Klucking 1987).

Dicotylphyllum sp. 6.

Figure 5c–d

Material: TB.83.378.1.

Description: Fragment of a large leaf, lamina most probably elliptic, length of the fragment 16 cm, width 5 cm. Apex and base not preserved. Entire and irregularly wavy margin only preserved on a short length. Venation irregular, cladodromous. Midvein straight, relatively stout. Secondary veins slightly decurrent, arising at angles of 45–50°, irregularly running, forking once or twice close to the margin. Tertiary veins forming an irregularly ramified network.

Discussion: Size of the leaf and decurrent irregularly forking secondaries remind of some Magnoliaceae.

Carpolithes sp. 1.

Figure 5e

Material: TB.83.421.1.

Description: Mold of a fruit or seed, diameter 1.3 cm, with basal scar, no ornamentation preserved.

Carpolithes sp. 2.

Figure 5f

Material: TB.83.339.1

Description: Impression of an ?infructescence with a diameter 1.8 cm, elongate bracts or ?fruitlets radially arranged.

Carpolithes sp. 3. (?*Ailanthus* sp.)

Figure 5g

Material: TB.83.474.1.

Description: An incompletely preserved winged fruit, length of the fragment 32 mm, width 9 mm. Roundish seed of 4 mm diameter, centrally positioned. No venation preserved except for an intramarginal vein or thickening.

Discussion: Especially due to shape and centrally positioned seed the fossil may represent an *Ailanthus* Desfontaines samara. Fruits of *Ailanthus* were mostly recorded from the Oligocene and Miocene of Europe (see for details Hably 2001), including numerous samaras from the early Oligocene Tard Clay flora (Nagybátony-Újlak brickyard). *Ailanthus* fruits are also known from Eocene localities in Central Europe (e.g., Kučlin, Kvaček and Teodoridis 2011; Messel, Collinson et al. 2012; see also Corbett and Manchester 2004).

Flora and vegetation

The leaf assemblage from Tatabánya dominantly comprises remains of angiosperms. Gymnosperms may be represented by a single specimen of a coniferous twig and ferns by a single tiny fragment of a pinna or pinnule. Angiosperms represented by cuticles are two species of Lauraceae, *Laurophyllum* ?*kinkelinii* and cf. *Ocotea hradekensis*. Other leaves which are putatively regarded as Lauraceae based on leaf shape and venation were assigned to *Daphnogene* and *Laurophyllum*. Furthermore, there are leaves of Rhamnaceae (*Ziziphus ziziphoides*), Malvaceae s.l. (*Byttneriopsis*), Leguminosae, Myrtaceae, and Palmae and other taxa are regarded as probable, such as Berberidaceae (?*Mahonia*), Dioscoreaceae, Fagaceae (?*Eotrigonobalanus*), Anacardiaceae, Juglandaceae (?*Engelhardia*), and Theaceae.

The rarity of gymnosperms in the fossil assemblage may either reflect their subordinate role in the vegetation or can be attributed to the depositional setting. In any case, the poor preservation and fragmentation of most of the leaf fossils indicate considerable transport and sorting which could be an alternative explanation for the rarity of gymnosperms.

The taphocoenosis is dominated by long lanceolate leaves which are characterised by entire to slightly wavy margin. Lauraceae, Rhamnaceae (*Ziziphus*), and fragments of palm leaves are frequent elements of the assemblage; however, considering longer transport, some of them may be over-represented due to an originally resistant, coriaceous texture. As rare

elements, Malvaceae s.l., Myrtaceae, and Leguminosae as well as putative Berberidaceae, Dioscoreaceae, Anacardiaceae, Juglandaceae, and Theaceae should be mentioned.

The taphocoenosis is dominated by dicotyledonous arborescent plants and palms. Remains of herbaceous elements, e.g., ferns, are extremely rare and aquatic or helophytic plants are totally missing. Although a reconstruction of the composition of the original vegetation is hardly feasible based on the poor fossil record, an evergreen character may be indicated by the morphology of the leaves; entire-margined leaves are dominating and a high number of the taxa probably had a coriaceous texture originally (Lauraceae spp., ?*Mahonia* sp., ?*Rhodomorphophyllum* sp., *Dicotylophyllum* sp. 4). The frequent occurrence of *Ziziphus* and leaves with entire and slightly wavy margin and coriaceous texture (e.g., *Dicotylophyllum* sp. 4) as well as small-leaved Leguminosae may suggest subhumid conditions and a xerophytic character of the original vegetation.

The palynological studies of Kedves (1962a, 1962b) provide additional information on the vegetation of the Tatabánya coal basin, which was not uniform according to his results. The palynoflora of the northern coal field shows similarities to that of Dorog, and the palynofloras of the southern and western coal fields are comparable to those of Halimba (and Dudar). Based on the palynological spectra, the Dorog, Halimba, and Dudar floral districts were distinguished by Kedves (1962a, 1962b) for the Eocene. He argued that Dorog was characterised by open swamp conditions in the littoral region together with Taxodiaceae–Cupressaceae swamp forests, palms, Myricaceae, and *Sequoia* forests. The Halimba sequences suggest *Castanea* on higher levels, as well as Myricaceae, Sapotaceae, and Palmae. Kedves attributed the disparity of these floral districts to different ecological conditions. The Eocene palynological spectra of Hungary led Kedves (1960) to infer a tropical climate for the area in general.

The results of our study of the macroflora show a picture with a high frequency of leaves representing Lauraceae and the extreme rarity of gymnosperms.

Comparisons with Eocene and early Oligocene assemblages of Hungary and Europe

The middle Eocene flora of Csordakút (Erdei and Rákosi 2009) was preserved in a lacustrine facies, while the Tatabánya assemblage in contrast was recovered from marine clays and marls. A similar character of the Tatabánya and Csordakút assemblages is the absence of gymnosperms. Shared taxa are Lauraceae, *Ziziphus ziziphoides*, Leguminosae, ?*Eotrigonobalanus*, and ?Anacardiaceae. Remains of palms are missing from Csordakút, whereas *Sloanea* Linnaeus, *Cedrelospermum*, and Myricaceae were not found at Tatabánya but recorded at Csordakút. Furthermore, the

lanceolate leaf type (*Dicotylophyllum* sp. 4: ?Lauraceae vel Fagaceae) which is characterised by an entire, slightly wavy leaf margin, and possibly had a coriaceous texture, dominates the Tatabánya assemblage but was not recognised in the taphocoenosis of Csordakút. Such disparities in the macroremains most probably reflect the different facies of the two localities. Although the Eocene flora of Lábatlan (Kovács 1959, 1961) needs future revision, it can be noted already that the subordinate role of gymnosperms is common to other Eocene macro-assemblages from Hungary.

In contrast to the Eocene macro-assemblages being devoid of gymnosperm remains, the flora of the early Oligocene Tard Clay Formation (NP23 nannoplankton zone) is well characterised by conifers (Kvaček and Hably 1998), like *Doliosrobis taxiformis* (Sternberg) Kvaček var. *hungaricus* (Rásky) Kvaček et Hably, and *Tetraclinis salicornioides* (Unger) Kvaček as well as *T. brachyodon* (Brongniart) Mai et Walther, *Calocedrus suleticensis* (Brabenec) Kvaček, *Chamaecyparites hardtii* (Göppert) Endlicher, etc. Even cycads are represented by the remains of *Ceratozamia floersheimensis* (Engelhardt) Kvaček (Kvaček 2002). Winged fruits, which show a high diversity in the Tard Clay flora, are nearly missing in the Tatabánya assemblage. Features shared by the Tard Clay floras and the Tatabánya assemblage are the abundance of Lauraceae (*Laurophyllum* div. sp.), and the occurrence of taxa, like *Ziziphus ziziphoides*, Palmae, ?*Eotrigonobalanus furcinervis*. Remains of *Sloanea* are quite characteristic of the Tard Clay floras, but were not recorded at Tatabánya. *Daphnogene* leaves are frequent in the Tard Clay flora, but only represented by a single specimen in the Tatabánya assemblage. The subhumid character of the Tard Clay assemblage (Erdei et al. 2012) can also be recognised at Tatabánya which is confirmed by the frequent occurrence of *Ziziphus* together with long narrow leaves with entire and slightly wavy margin (*Dicotylophyllum* sp. 4; Lauraceae vel Fagaceae) and small-leaved Leguminosae.

Since the Tatabánya assemblage is dominated by impressions and cuticles are rarely preserved, a systematic comparison with other European Eocene floras is limited. However, some general notes should be made. A subhumid character of the vegetation similar to Tatabánya is often suggested by the early Palaeogene floras of eastern Central Europe and Southeastern Europe, e.g., by the early Oligocene flora of Häring in Tirol (Ettingshausen 1853), the Tard Clay floras (Hably 2006; Erdei et al. 2012), Eocene to early Oligocene floras of Serbia and Macedonia (Mihajlovič and Ljubotenski 1994), and the late Eocene flora of Ovče Polje (Macedonia; Mihajlovič and Ljubotenski 1994). Similar to the Eocene macrofloras of Hungary, the Eocene Girbou assemblage in Romania (Petrescu et al. 1976) is devoid of gymnosperm remains.

The Eocene floras from Central/Western Europe generally do not show a subhumid character. The late Eocene flora of Staré Sedlo in Bohemia (Knobloch et al. 1996) and the early Palaeogene floras of the Weissenster Basin, Messel, and the

Geiseltal in Germany (Rüffle 1976; Rüffle et al. 1976; Mai and Walther 1978; Wilde 1989) are all devoid of *Ziziphus* but share Lauraceae, Leguminosae, Palmae, and (?)*Eotrigonobalanus* (missing in Messel) with the Tatabánya flora. Interestingly, the tropical-subtropical genus *Sloanea*, which preferred mesic habitats and was a frequent element of Eocene floras in Bohemia (Kučlin), the Weissensteiner Basin (Kvaček and Teodoridis 2011), Messel (Collinson et al. 2012), or even Csordakút in Hungary (Erdei and Rákosi 2009), is missing in the Tatabánya assemblage.

Climate and vegetation

Based on the leaf physiognomic characters, a broad-leaved evergreen forest thrived in the source area for the middle Eocene taphocoenosis of the Tatabánya region. The ratio of entire-margined leaves is quite high, 79% (total number of leaves 323), higher than measured for the Messel assemblage (57%, total number of leaves 1078) or the Tard Clay flora (61%, total number of leaves 2239) but close to values obtained for the flora of Kučlin (> 70%, Kvaček and Teodoridis 2011). The high ratio of entire-margined leaves in Tatabánya may be attributable to the relatively low sample size; however, taphonomic factors such as sorting and differential preservation may have been more important for selection. Palaeoclimate estimates of some European Eocene floras (e.g., Kučlin, Staré Sedlo, floras of the Weissensteiner Basin and Saxony, Messel) adopting CLAMP, LMA, or CA methods showed a frost-free climate with a mean annual temperature higher than 16°C (see Roth-Nebelsick et al. 2004; Mosbrugger et al. 2005; Kvaček and Teodoridis 2011; Grein et al. 2011). Comparable temperatures were obtained for the early Oligocene Tard Clay floras (Erdei et al. 2012) and may also be inferred for the Tatabánya flora.

Data accessibility

Specimens studied are housed in the palaeobotanical collection of the Kuny Domokos Museum, Tata, Hungary. Full details of studied collection material, inventory numbers, applied methodology, and locality data are provided in the text.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

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