

The early Oligocene flora and palaeo-environment of the Tard Clay Formation — latest results

Lilla HABLY & Boglárka ERDEI

Hungarian Natural History Museum, Botanical Department, Budapest, H–1476,
POB222, Hungary; e-mail:hably@bot.nhmus.hu

Abstract

The early Oligocene flora of the Tard Clay Formation is one of the most significant fossil floras of Hungary. Although, the investigation of the highly diverse flora started as early as the 1940s, the numerous, both exotic and extinct genera and species are still raising many questions. The significant development in the application of microscopic methods for cuticular examinations as well as morphometric analyses helped to resolve many taxonomical and systematic questions in the last decades. Recent research activities have been focussing mainly on revealing the botanical affinities of fossil genera in order to provide more realistic ecological and climate reconstructions. This paper provides a summary of the latest results achieved by studies of the Tard Clay floras highlighting conclusions of systematic, palaeoclimate and palaeoecological analyses.

Keywords: *early Oligocene flora, systematics, palaeoclimatology, palaeoecology, Tard Clay, Hungary*

Introduction

The remarkable early Oligocene flora fossilized in the sediments of the Tard Clay Formation is one of the most significant fossil floras of Hungary. Plant remains were found partly in the Óbuda region of Budapest, in abandoned clay pits of former brickyards, in the course of building operations, and drillings for underground constructions, and partly in the sediments of the Kiseged Hill, near Eger, which became well-known as Eger-Kiseged in the relevant palaeobotanical papers.

Although, the investigation of the well-preserved and highly diverse flora started as early as the 1940s, the numerous, both exotic and extinct species and genera are still raising many questions even nowadays. The flora flourishing in the early Oligocene was composed of ancient, “palaeotropical” elements including various thermophilous, partly lauraceous taxa which are related to species confined to subtropical, tropical regions today. These genera and species are often unidentifiable based solely on macromorphological traits since many characters are shared by various, often unrelated taxa. This is the main reason for uncertainties regarding the composition of the flora and conclusions based on mis-identified plant remains in the former decades.

The fossil flora yielded by the localities in Budapest was studied first by GÁBOR ANDRÉANSZKY and KLÁRA RÁSKY.

ANDRÉANSZKY (1963) mentioned many species from the Budapest — Batthyány Square, and the Bohn brickyard in Óbuda. Subsequently, PÁLFALVY (1978) described partly new taxa from the drill cores B1 and B2. Fossil plants from the Budaújlak brickyard in Óbuda were published by ANDRÉANSZKY (1949, 1952, 1956, 1959, 1965a), ANDRÉANSZY & NOVÁK (1957), VARGA (1956), and later by PÁLFALVY (1981). The flora of the Csillaghegy brickyard in Óbuda was presented in novel papers by RÁSKY (1943), VARGA (1956), and ANDRÉANSZKY (1959, 1963, 1965a). Plant remains found in the course of constructional works in Kapás Street and Moszkva Square (now Széll Kálmán Square) were studied by PÁLFALVY (1978). The flora of the Szépvölgyi Street and Nagybátony-Újlak brickyard in Budapest were initially investigated exclusively by RÁSKY (1943, 1950, 1956, 1962, 1965). Fossil remains excavated somewhat later, in the course of drillings for underground constructions from the Vörösvári Street and from the Kiscell–1 borehole were published by HABLY (1979, 1985a, 1986). In addition to the localities in Budapest the flora of Eger-Kiseged turned out to be significant and was published by ANDRÉANSZKY and his students (ANDRÉANSZKY 1949, 1951, 1954, 1955, 1956, 1959, 1964, 1965b, 1967a, b, NOVÁK 1950, ANDRÉANSZKY & NOVÁK 1957, ANDRÉANSZKY & CZIFFERY 1964).

Although, numerous papers have been published on the systematic study of most of the localities, many questions

have not been resolved mainly due to the diverse floristic spectrum comprising many extinct as well as exotic flora elements. Numerous form genera were established with uncertain or unresolved botanical affinities; therefore the ecological and climatological requirements of these taxa are not available for environmental, ecological and climatological reconstructions.

The vast development of microscopic methods applied in cuticular examinations helped to resolve many taxonomical and systematical questions in the last decades. The application of microscopes capable of higher magnifications, the more thorough and detailed taxonomical studies as well as the higher number of research papers serving as a basis for comparisons all helped to enhance our knowledge on the fossil floras including the Oligocene ones. Furthermore, some unique findings, for instance the organic attachment of leaves and fruits on the same twig providing direct evidence of their systematic relation (e.g. *Cedrelospermum* in MANCHESTER 1989), served as a supplement for systematic studies. These all promoted the taxonomical revision of many formerly published findings and the investigation of new outcrops as well as numerous unstudied plant remains stored in museum collections. This paper provides a summary of the latest results in the field of studies of the Tard Clay floras highlighting conclusions of systematic, palaeoclimate and palaeoecological analyses.

Material and methods

The fossil flora of the Tard Clay Formation is one of the best dated assemblages in Hungary. The marine or even brackish sediments contain rich nannoflora assemblages. According to the nannoplankton examinations (NAGYMAROSY & BÁLDI-BEKE 1988) the Tard Clay Formation belongs to the nannoplankton zones NP 21–23. Three levels of the Tard Clay Formation — lower, middle and upper — are distinguished (BÁLDI 1980, BÁLDI et al. 1984). Most of the plant-bearing layers belong to the upper level. Besides plant remains, skeletons of small fishes and fish scales are also common in the fossiliferous sediments.

Preservation of fossils from localities in Budapest (Budapest, Óbuda: Nagybátony-Újlak brickyard, Csillaghegy brickyard, Szépvölgy brickyard, Bohn brickyard, Kiscell brickyard, Vörösvári Street, Bécsi Street; Budapest: Budaújlak, Kiscell-1 borehole) enabled cuticular examinations but in some rare cases specimens from the Eger-Kiseged flora were also suitable for micromorphological analyses. Morphometric analyses were also helpful in resolving some taxonomical problems. Recent research activities have focussed mainly on revealing the botanical affinities of fossil genera in order to provide more realistic ecological and climate reconstructions. Abbreviations: BP —Hungarian Natural History Museum, Botanical Department, Palaeobotanical Collection

The fossil flora of the Tard Clay Formation

The list provided here is an account of those taxa that contributed with essential information to the systematics of the Tard Clay floras. The relations, distribution, floristic significance, and climate indicator value of these taxa are shortly discussed in the next chapter. In addition to the references of the species, the synonym lists include data documented exclusively from the Hungarian early Oligocene.

Ceratozamia floersheimensis (ENGELHARDT) KVAČEK

2002a *Ceratozamia floersheimensis* (ENGELHARDT) KVAČEK; KVAČEK, p. 305, figs 7–9, 19–21.

Material: Budapest, Óbuda, Nagybátony-Újlak brickyard: BP 2000.75.1.,

Doliostrobus taxiformis (STERNBERG) KVAČEK var. *hungaricus* (RÁSKY) KVAČEK & HABLY

1833 *Cystoseirites taxiformis* STERNBERG; STERNBERG, p. 35, pl. 18, figs 1–3.

1943 *Sequoia sternbergii* GÖPPERT; RÁSKY, p. 510, pl. 13, fig. 8, pl. 22, fig. 1.

1943 *Araucaria hungarica* RÁSKY; RÁSKY, p. 524, pl. 21, figs 3–4.

1968 *Doliostrobus hungaricus* (RÁSKY) BŮŽEK, HOLÝ & KVAČEK; BŮŽEK, HOLÝ & KVAČEK, p. 155.

1979 *Doliostrobus hungaricus* (RÁSKY) BŮŽEK, HOLÝ & KVAČEK; HABLY, p. 39, pl. 1, fig. 4, pl. 2, figs 3, 6.

1992a *Doliostrobus certus* BŮŽEK, HOLÝ & KVAČEK; HABLY, p. 371, pl. 1, fig. 3.

1998 *Doliostrobus taxiformis* (STERNBERG) KVAČEK var. *hungaricus* (RÁSKY) KVAČEK & HABLY; KVAČEK & HABLY, p. 6, pl. 1, figs 1–2.

2002b *Doliostrobus taxiformis* (STERNBERG) Z. KVAČEK var. *hungaricus* (RÁSKY) KVAČEK & HABLY; KVAČEK, p. 54.

Material: Budapest, Óbuda, Vörösvári Street, boreholes H: BP 78.108.2., 78.115., 78.190., 78.342.1., Eger-Kiseged: BP 97.132.1., 97.133.1., 97.134.1.

Chamaecyparites hardtii (GÖPPERT) ENDLICHER

1950 *Sequoia Sternbergii* (GÖPPERT) HEER; NOVÁK, p. 52, pl. 1, fig. 7.

1971 *Chamaecyparites hardtii* (GÖPPERT) ENDLICHER; KVAČEK, pp. 115–126, pl. 31, fig. 21, pl. 32., fig. 8.

1979 *Doliostrobus hungaricus* (RÁSKY) BŮŽEK, HOLÝ & KVAČEK; HABLY, pl. 1, fig. 4, pl. 2, fig. 6.

1992a *Chamaecyparites hardtii* (GÖPPERT) ENDLICHER; HABLY, p. 370, pl. 1, figs 1–2.

Material: Budapest, Óbuda, Vörösvári Street, borehole H-15: BP cf. 78.71.2., 78.86.2., 78.108.2., 78.113.1., 78.198.1.

***Tetraclinis salicornioides* (UNGER)
KVAČEK**

- 1950 *Libocedrus salicornioides* (UNGER) HEER; NOVÁK, p. 52, pl. 1, fig. 6, pl. 2, fig. 10.
- 1962 *Libocedrus salicornioides* (UNGER) HEER; RÁSKY, p. 31, pl. 2, figs 4–6, pl. 5, fig. 7.
- 1979 *Libocedrites salicornioides* (UNGER) ENDLICHER; HABLY, p. 39, pl. 2, fig 1, pl. 3, figs 3–4, pl. 4, fig. 2.
- 2000 *Tetraclinis salicornioides* (UNGER) KVAČEK; HABLY & MANCHESTER, p. 94.

Material: Budapest, Óbuda, BP: 62.65.1., 62.66.1., 62.68.1., Budapest, Óbuda, Vörösvári Street, boreholes H: BP 78.167.2., 78.173.3., 78.179.1., 78.189.2.

***Tetraclinis brachyodon* (BRONGNIART)
MAI & WALTHER**

- 1822 *Equisetum brachyodon* BRONGNIART; BRONGNIART, p. 328, pl. 16, fig. 3.
- 1985 *Tetraclinis brachyodon* (BRONGNIART) MAI & WALTHER; MAI & WALTHER, p. 30 (non pl. 3, figs 17–19).
- 1998 *Tetraclinis brachyodon* (BRONGNIART) MAI & WALTHER; KVAČEK & HABLY, p. 7, pl. 1, figs 3–5, text-fig. 1.

Material: Eger-Kiseged: BP 70.402.1., BP 97.130.1, BP 97.131.1, BP 97.136.1.

***Calocedrus suleticensis* (BRABENEC) KVAČEK**

- 1998 *Calocedrus suleticensis* (BRABENEC) KVAČEK; KVAČEK & HABLY, p. 7, pl. 1, fig. 6, text-fig. 2.

Material: Eger-Kiseged: BP 97.186.1.

***Laurophyllum acutimontanum* MAI**

- 1992a *Laurophyllum acutimontanum* MAI; HABLY, p. 371, pl. 4, fig. 4.
- 1998 *Laurophyllum acutimontanum* MAI; KVAČEK & HABLY, p. 8, pl. 2, figs 1–6, text-fig. 3.

Material: Budapest, Óbuda, Vörösvári Street, boreholes H-11, H-15: 78.2.1., 78.41.2., 78.109.1., Eger-Kiseged: BP 97.124.1., 97.125.1.

***Laurophyllum hradekense* KVAČEK & BÚŽEK**

- 1992a *Laurophyllum kvačekii* HABLY; HABLY, p. 371, pl. 2, figs 1–3.

Material: Budapest, Óbuda: BP. 2002.455.1., Budapest, Kiscell-1 borehole: cf. BP 81.10.1.

***Laurophyllum kvacekii* HABLY**

- 1992a *Laurophyllum kvačekii* HABLY; HABLY, p. 372, pl. 3, figs 1–5, pl. 4, figs 1–3.

Material: Budapest, Óbuda, Vörösvári Street, borehole H-11: BP 78.309.1., 78.314.2., 78.344.4., Kiscell-1 borehole: 81.2.1., 2005.238.1.

***Laurophyllum markvarticense* KVAČEK**

- 1992a *Laurophyllum markvarticense* KVAČEK; HABLY, p. 371, pl. 1, fig. 4.
- 1998 *Laurophyllum markvarticense* KVAČEK; KVAČEK & HABLY, p. 8, pl. 3, figs 1–3, 5, text-fig. 4.

Material: Eger-Kiseged: BP 97.129.1., Budapest, Óbuda, Vörösvári Street, borehole H-11: BP 78.2.1., Kis-cell-1 borehole: BP 81.2.1., 81.8.2.

***Laurophyllum medimontanum* BÚŽEK,
HOLÝ & KVAČEK**

- 1992a *Laurophyllum medimontanum* BÚŽEK, HOLÝ & KVAČEK; HABLY, p. 372, pl. 1, figs 5, 6.

Material: Budapest, Óbuda, Vörösvári Street, boreholes H-15, H-18: BP 78.109.1., 78.130.1., 78.314.2.

***Platanus neptuni* (ETTINGSHAUSEN)
BÚŽEK, HOLÝ & KVAČEK**

- 1957 *Cunonia oligocaenica* ANDRÉÁNSZKY & NOVÁK; ANDRÉÁNSZKY & NOVÁK, p. 47, pl. 2, fig. 5.
- 1964 *Ulmus affinis* MASSALONGO; ANDRÉÁNSZKY & CZIFFERY, p. 123, pl. 2, fig. 10, text-fig. 5.
- 1965a *Cupanites neptuni* (UNGER) SCHIMPER; ANDRÉÁNSZKY, p. 69, fig. 15, pl. 5, figs 5, 6.
- 1965a *Elaeocarpus agriensis* ANDRÉÁNSZKY; ANDRÉÁNSZKY, p. 72 [partly], pl. 6, fig. 4.
- 1965b *Cunonia oligocaenica* ANDRÉÁNSZKY & NOVÁK; ANDRÉÁNSZKY, p. 13, fig. 3.
- 1965b *Cupanites neptuni* (UNGER) SCHIMPER; ANDRÉÁNSZKY, p. 13, fig. 4.
- 1979 *Platanus neptuni* (ETTINGSHAUSEN) BÚŽEK, HOLÝ & KVAČEK; HABLY, pl. 8, figs 1–5, pl. 9, figs 1–3, 5, 6, pl. 10, figs 1–5, pl. 11, figs 1, 3, 4.
- 1980b *Platanus neptuni* (ETTINGSHAUSEN) BÚŽEK, HOLÝ & KVAČEK; HABLY, pp. 300–303, pl. 2, figs 3–9, pl. 3, figs 1–6, pl. 4, figs 1–5, pl. 5, figs 1, 3, pl. 6, figs 1–4, pl. 8, figs 1–4, pl. 9, figs 1–4, pl. 10, figs 1–4.
- 1985a *Platanus neptuni* (ETTINGSHAUSEN) BÚŽEK, HOLÝ & KVAČEK; HABLY, p. 37, fig. 2.

Material: Budapest, Óbuda, Vörösvári Street, boreholes H: BP 78.7.1., 78.15.1., 78.62.2., 78.67.2., 78.78.2., 78.98.3., 78.112.2., 78.121.1., 78.124.2., 78.185.2., 78.195.2., 78.202.1., 78.204.2., 78.205.2., Eger-Kiseged: BP 2002.74.1–2002.79.1., 2004.278.1–2004.282.1., 2004.665.1., 2004.667.1–2004.678.1., 2005.599.1–2005.601.1., 2006.28.1–2006.34.1., 2010.29.1., 2010.49.1–2010.53.1., 2010.62.1., 2010.63.1., 2014.61.1., 2014.191.1., 2015.81.1–2015.84.1.

***Sloanea olmediaefolia* (UNGER)
KVAČEK & HABLY**

- 1956 *Grewiopsis ellipticus* ANDRÉÁNSZKY; ANDRÉÁNSZKY, p. 226, pl. 4, fig. 12, pl. 5, fig. 17.
- 1962 *Sloaneaephylloides grambastii* RÁSKY; RÁSKY, p. 34, pl. 3, fig. 1.
- 1962 *Sloaneaephylloides obudaense* RÁSKY; RÁSKY, p. 37, pl. 4, figs 2–3.

- 1962 *Sloaneaephylum hungaricum* RÁSKY; RÁSKY, p. 39, pl. 3, fig. 2.
- 1962 *Actinidiophyllum ovatum* (MACGINITIE) RÁSKY; RÁSKY, p. 41, text-fig. 2.
- ?1962 *Banara eocenica* BERRY; RÁSKY, p. 43, pl. 5, figs 5–6.
- 1963 *Grewiopsis ellipticus* ANDRÉANSZKY; ANDRÉANSZKY, p. 253, pl. 3, figs 1, 2.
- 1964 *Alnus antiquorum* SAPORTA; ANDRÉANSZKY & CZIFFERY, p. 117, pl. 1, figs 1–2.
- 1964 *Populus mutabilis* HEER; ANDRÉANSZKY & CZIFFERY, p. 120, pl. 1, figs 5–6.
- 1965a *Elaeocarpus* cf. *ramiflorus* MERR.; ANDRÉANSZKY, p. 70, pl. 6, fig. 1.
- 1965 *Macarangaephylum palaeomonandrum* RÁSKY; RÁSKY, p. 85, pl. 5, figs 15–16.
- 1965 *Alchorneaephylum grambastii* (RÁSKY) RÁSKY; RÁSKY, p. 85, pl. 6, figs 19–20.
- 1966 *Alchorneaephylum grambastii* (RÁSKY) RÁSKY; RÁSKY, p. 265, pl. 1, fig. 2.
- 1966 *Alchorneaephylum chandleri* RÁSKY; RÁSKY, p. 264, pl. 1, fig. 3.
- 1966 *Baliospermophyllum kraueselii* RÁSKY; RÁSKY, p. 266, pl. 2, figs 4–5.
- 1967a *Tetragymnophyllum agriense* ANDRÉANSZKY; ANDRÉANSZKY, p. 38, pl. 3, figs 11–12, pl. 4, figs 15–16.
- 1995 *Icaciniphyllum agriense* (ANDRÉANSZKY) KVAČEK & BŮŽEK; KVAČEK & BŮŽEK p. 136, pl. 5, figs 1–5, pl. 6, figs 15–16.
- 2001 *Sloanea elliptica* (ANDRÉANSZKY) KVAČEK, HABLY & MANCHESTER; KVAČEK, HABLY & MANCHESTER, p. 117, pl. 2, figs 1–5, pl. 3, figs 1–5, pl. 4, figs 1–5, pl. 6, figs 1–7.
- 2008 *Sloanea olmediaefolia* (UNGER) KVAČEK & HABLY; HABLY & KVAČEK, p. 140, Fig. 1:1–5.

Material: Budapest, Óbuda, Nagybátony-Újlak brick-yard: BP 60.1248.1., 62.71.1., 62.72.1=62.73.1., 62.74.1., 62.76.1=62.77.1., 62.80.1., 62.81.1., 62.913.1., 62.914.1., 62.915.1., 62.916.1=62.917.1., 62.918.1=62.919.1., 65.28.1=65.29.1., 65.31.1., 67.900.1., 67.901.1., 69.484.2., 69.485.1., 69.493.1., 70.257.1., 70.264.1., 70.291.1., 97.199.2., 97.200.2., 97.201.1., 97.202.1.; Budapest, Óbuda, Bohn brickyard: 60.1296.1.; Budapest, Óbuda, Bécsi Street: BP 97.203.2., 97.204.1., 97.205.2.; Eger-Kiseged: BP 70.178.1., 70.179.1., 70.183.1., 70.185.1., 70.186.1., 70.189.1., 70.191.1., 70.196.1., 70.197.1., 70.198.1., 70.199.1., 70.201.1., 70.202.1., 70.204.1., 70.205.1., 70.206.1., 70.209.1., 70.210.1., 70.211.1., 70.212.1., 70.214.1., 70.215.1., 70.216.1., 70.217.1., 70.219.1., 70.250.1., 70.283.1., 70.284.1., 70.285.1., 83.279.1.

Sloanea eocenica (RÁSKY) KVAČEK, HABLY & MANCHESTER

- 1962 *Sloaneaecarpum eocenicum* RÁSKY, RÁSKY p. 34, pl. 2, figs 1–3.
- 2001 *Sloanea eocenica* (RÁSKY) KVAČEK, HABLY & MANCHESTER; KVAČEK, HABLY & MANCHESTER, p. 115, pl. 1, figs 1–5.

Material: Budapest, Óbuda, Nagybátony-Újlak brick-yard: BP 62.64.1, 62.63.1, 63.978.1, 63.1004.1, 63.1014.1, 63.1016.1

Tetrapteris harpyiarum UNGER

- 1850a *Tetrapterys harpyiarum* UNGER; UNGER, p. 46, pl. 29, fig. 8.
- 1850b *Tetrapteris harpyiarum* UNGER; UNGER, p. 455.
- 1956 *Tetrapteris harpyiarum* UNGER; RÁSKY, p. 173. pl. 28, figs 1–3.
- 1959 *Abelia* sp.; ANDRÉANSZKY, p. 16, pl. 2, fig. 10, pl. 4, fig. 16.
- 1962 *Tetrapteris harpyiarum* UNGER; RÁSKY, p. 32, pl. 1, fig. 4.
- 1965 *Calyx quadripartitus* ANDRÉANSZKY; ANDRÉANSZKY, p. 16, pl. 2, fig. 8.
- 1979 *Abelia* cf. *quadrialata* REID & CHANDLER; HABLY, p. 39, pl. 9, fig. 4.
- 1986 *Abelia quadrialata* REID & CHANDLER; HABLY, p. 35, pl. 1, fig. 3, pl. 2, fig. 2.
- 2000 *Tetrapteris harpyiarum* UNGER; HABLY & MANCHESTER, p. 95, pl. 1, figs 2–9, pl. 2, fig. 1.
- 2000 *Tetrapteris harpyiarum* UNGER; HABLY, KVAČEK & MANCHESTER, p. 65, pl. 3, fig. 5.

Material: Budapest, Óbuda, Nagybátony-Újlak brick-yard: BP 56.3.1., 56.6.1–56.10.1., 56.16.1., 56.17.1., 56.20.1., 56.22.1., 56.24.1., Budapest, Óbuda, Vörösvári Street, boreholes H: BP 78.181.2., 78.149.2., Eger-Kiseged: BP 97.177.1.

Ziziphus zizyphoides (UNGER) WEYLAND

- 1956 *Zizyphus zizyphoides* (UNGER) WEYLAND; RÁSKY, p. 174, pl. 29, figs 1–3.
- 1979 *Zizyphus zizyphoides* (UNGER) WEYLAND; HABLY, pl. 6, figs 1, 4, pl. 7, figs 1, 2, pl. 8, figs 2, 3.
- 1986 *Zizyphus zizyphoides* (UNGER) WEYLAND; HABLY, p. 35, pl. 1, fig. 2.
- 2000 *Ziziphus zizyphoides* (UNGER) WEYLAND; HABLY, KVAČEK & MANCHESTER, p. 65, pl. 3, fig. 4.

Material: Budapest, Óbuda, Vörösvári Street, boreholes H: BP 78.24.2., 78.40.1., 78.120.2., 78.171.1., 78.192.2., 78.200.4.

Eotrigonobalanus furcinervis (ROSSMÄSSLER) WALTHER & KVAČEK

- 1943 *Myrica lignitum* (UNGER) SAPORTA; RÁSKY, p. 511, pl. 13, fig. 5.
- 1943 *Quercus furcinervis* (ROSSMÄSSLER) HEER; RÁSKY, p. 512, pl. 15, fig. 1.
- 1943 *Quercus goepperti* WEBER; RÁSKY, p. 514, pl. 15, fig. 2, pl. 16, figs 1, 2.
- 1963 *Dryophyllum* sp.; ANDRÉANSZKY, p. 238, pl. 2, fig. 1, text-fig. 6.
- 1963 *Castanopsis furcinervis* (ROSSMÄSSLER) KRÄUSEL & WEILAND; ANDRÉANSZKY, p. 237.
- 1964 *Quercus excelsior* ANDRÉANSZKY & KOVÁCS; ANDRÉANSZKY, p. 29, fig. 21.
- 1965a *Castanopsis furcinervis* (ROSSMÄSSLER) KRÄUSEL & WEILAND; ANDRÉANSZKY, p. 10, pl. 1, fig. 5.
- 1978 *Castanopsis furcinervis* (ROSSMÄSSLER) KRÄUSEL & WEILAND; PÁLFALVY, p. 316, pl. 1, fig. 2.
- 1978 *Dryophyllum* sp.; PÁLFALVY, p. 318, pl. 2, fig. 2.
- 1979 *Dryophyllum furcinerve* (ROSSMÄSSLER) SCHMALHAUSEN; HABLY, pl. 11, figs 2, 5, pl. 12, figs 1–4.

2010 *Eotrigonobalanus furcinervis* (ROSSMÄSSLER) WALTHER & KVAČEK; HABLY, p. 408, pl. 1, figs 8–11.

Material: Budapest, Óbuda, Vörösvári Street, boreholes, H: BP 78.32.2., 78.77.1., 78.172.2., 78.85.2., 78.215.1., 78.217.2., Budapest, Óbuda, Nagybátony-Újlak brickyard: BP 99.28.1., 99.29.1., 99.31.1., 99.35.1., 99.37.1., 99.39.1., 99.41.1–99.44.1., 99.61.1., 99.67.1., 2007.107.1–2007.214.1., Budapest, Óbuda: BP 2000.755.1., 756.1., 2002.203.1–2002.212.1., 2002.389.1–2002.407.1., 2002.439.1–2002.444.1., 2003.82.1., 2003.276.1., 2003.282., 2007.770.1–2007.773.1., 2007.782.1., 2007.783.1., 2007.938.1., 2014.252.1., Budaújlak: BP 2004.197.1–2004.199.1., 2004.856.1., 2004.858.1–2004.861.1., 2004.863.1., 2004.864.1., 2004.866.1., 2004.876.1., 2004.877.1., 2004.879.1., Budapest, Óbuda, Kiscell brickyard: BP 2007.752.1–2007.761.1., 2007.804.1., 2007.805.1., Eger-Kiseged: BP 95.491.1., 2000.99.1–2000.190.1., 2001.365.1., 2001.561.1–2001.578.1., 2002.143.1–2002.163.1., 2002.165.1–2002.202.1., 2004.324.1–2004.364.1., 2004.494.1–2004.500.1., 2004.878.1., 2005.545.1–2005.554.1., 2005.566.1–2005.580.1., 2005.582.1., 2006.12.1., 2006.68.1–2006.70.1., 2010.67.1–2010.76.1., 2010.859.1–2010.864.1., 2014.100.1., 2015.112.1., 2015.113.1.

Eotrigonobalanus andreanszkyi (MAI)
KVAČEK & WALTHER

1998 *Eotrigonobalanus andreanszkyi* (MAI) KVAČEK & WALTHER; KVAČEK & HABLY, p. 10, pl. 2, figs 7–9, pl. 4, fig. 9, text-fig. 6.

Material: Eger-Kiseged: BP 67.271., 67.279.1., 67.277.1., 67.278.1., 67.395.1., 67.400.1., 67.912.1.

Engelhardia orsbergensis (WESSEL & WEBER)
JÄHNICHEN, MAI & WALTHER

1957 *Schinus oligocaenicum* ANDRÉÁNSZKY & NOVÁK; ANDRÉÁNSZKY & NOVÁK, p. 49, pl. 2, figs 6–7.
1963 *Schinus oligocaenicum* ANDRÉÁNSZKY & NOVÁK; ANDRÉÁNSZKY, p. 246.
1998 *Engelhardia orsbergensis* (WESSEL & WEBER) JÄHNICHEN, MAI & WALTHER; HABLY & FERNANDEZ MARRON, p. 72, pl. 3, fig. 21.

Material: Budapest, Óbuda, Nagybátony-Újlak brickyard: BP 55.2130.1., 83.390.1–83.483.1., 84.116.1., 84.117.1., 99.179.1., 2004.446.1., 2006.176.1–2006.178.1. Eger-Kiseged: BP 83.272.1., 2002.39.1–2002.50.1., 2003.253.1–255.1., 2004.283.1–291.1., 2004.531.1., 2004.532.1., 2004.607.1–2004.622.1., 2004.682.1., 2005.508.1., 2006.13.1–2006.27.1., 2014.95.1., 2015.72.1., 2015.73.1.

Engelhardia macroptera (UNGER)
BRONGNIART

1956 *Engelhardtia brongniarti* SAPORTA; RÁSKY, p. 169, pl. 27, fig. 1.
1963 *Engelhardtia brongniarti* SAPORTA; ANDRÉÁNSZKY, p. 228, pl. 1, fig. 4.
1964 *Engelhardtia brongniarti* SAPORTA; RÁSKY, p. 77, pl. 7, figs 5–7.

1965 *Engelhardtia brongniarti* SAPORTA; RÁSKY, pl. 7, figs 5–7.
1965 *Engelhardtia brongniarti* SAPORTA; RÁSKY, p. 86, pl. 4, fig. 11.
1978 *Engelhardtia macroptera* (BRONGNIART) ETTINGSHAUSEN; PÁLFALVY, p. 314, pl. 2, fig. 3.

Material: Budapest, Óbuda, Bécsi Street: BP 2002.447.2., Budapest, Budaújlak: BP 2004.151.1., Eger-Kiseged: BP 2001.610.1., 2004.624.1., 2004.625.1–2004.628.1., 2005.533.1., 2005.534.1., 2010.54.1., 2010.55.1., 2010.57.1.

Ailanthus tardensis HABLY

1938 *Ailanthus confucii* UNGER; WEYLAND, p. 100, pl. 12, fig. 14, text-fig. 40.
1956 *Ailanthus confucii* UNGER; RÁSKY, p. 172., pl. 27, figs 2, 3.
2001 *Ailanthus tardensis* HABLY; HABLY, p. 210, pl. 3, figs 1–7.

Material: Budapest, Óbuda, Nagybátony-Újlak brickyard: BP 55.1738.1–55.1744.1., 55.1748.1–55.1750.1., 55.2002.1., BP 55.2003.1., BP 55.2005.1–55.2007.1., 55.2009.1–55.2027.1., 55.2029.1–55.2036.1., 55.2040.1–55.2044.1., 55.2046.1–55.2048.1., 55.2050.1–55.2052.1., 55.2054.1., 55.2057.1., 55.2058.1., 55.2060.1., 55.2062.1–55.2064.1., 55.2067.1., 55.2068.1., 55.2070.1., 55.2072.1., 55.2074.1., 55.2076.1–55.2080.1., 55.2082.1–55.2089.1., 55.2092.1–55.2098.1., 55.2100.1–55.2106.1., 55.2108.1–55.2120.1., 56.89.1., 56.90.1., 62.93.1., 2000.191.1–2000.198.1.

Craigia bronnii (UNGER) KVAČEK,
BŮŽEK & MANCHESTER

1845 *Ulmus bronnii* UNGER; UNGER, p. 79, pro parte, pl. 25, figs 2–4 (not fig. 1).
1964 *Ulmus*-Früchte; ANDRÉÁNSZKY & CZIFFERY, p. 125.
1991 *Craigia bronnii* (UNGER) KVAČEK, BŮŽEK & MANCHESTER; KVAČEK, BŮŽEK & MANCHESTER, p. 522.
1998 *Craigia bronnii* (UNGER) KVAČEK, BŮŽEK & MANCHESTER; KVAČEK & HABLY, p. 10, pl. 5, figs 7–9.

Material: Eger-Kiseged: BP 67.347.1.–67.354.1.

Cedrelospermum aquense (SAPORTA) SAPORTA

1956 *Embothrites borealis* UNGER; RÁSKY, p. 174, pl. 28, figs 4–8.
1963 *Embothrites* sp.; ANDRÉÁNSZKY, p. 230, text-fig. 2.
1978 "Embothrites" borealis UNGER; PÁLFALVY, p. 313, non fig.
1998 *Cedrelospermum* sp.; KVAČEK & HABLY, p. 11, pl. 4, fig. 8.
2002 *Cedrelospermum aquense* (SAPORTA) SAPORTA; HABLY & THIÉBAUT, p. 80, pl. 5, figs 1–6.

Material: Budapest, Óbuda, Nagybátony-Újlak brickyard: BP 56.32.1., 56.33.1., 56.34.1., 56.35.1., 56.36.1., 56.37.1., 56.38.1., 56.39.1., 56.40.1., 56.41.1., 56.42.1., 56.43.1., 56.44.1., 56.45.1., 56.46.1., 56.47.1., 56.48.1., 56.49.1=56.50.1., 56.51.1., 56.52.1., 56.54.1., 56.55.1., 56.56.1., 56.57.1=56.58.1., 56.59.1., cf. 56.60.1., 56.61.1., 56.62.1., 56.63.1., 56.64.1., 56.65.1., 56.66.1. Budapest, Óbuda, Bécsi Street: 99.148.1., 99.176.2. Eger-Kiseged: 67.795.1., 67.841.1., 67.844.1., 67.819.1.

Cedrelospermum flichei (SAPORTA)
HABLY & THIÉBAUT

- 1891 *Hemiptelea flichei* SAPORTA; SAPORTA, pp. 74–75, pl. 20, fig. 5.
1891 *Microptelea reperta* SAPORTA; SAPORTA, p. 74, pl. 17, fig. 2.
1998 *Cedrelospermum* sp., KVAČEK & HABLY, p. 11, pl. 4, fig. 7.
2002 *Cedrelospermum flichei* (SAPORTA) HABLY & THIÉBAUT;
HABLY & THIÉBAUT, p. 82, pl. 7, figs 1, 2.

Material: Budapest, Óbuda, Nagybátony-Újlak brick-yard: BP 99.156.2., 99.157.2., 99.187.1., 99.188.1., 99.189.1., Eger-Kiseged: BP 71.254.1., 2015.105.1.

Acherniaephylum hydrarchos (UNGER)
HABLY

- 1850a *Ficus hydrarchos* UNGER; UNGER, p. 165 (35), 33 (12): 2.
1960 *Acherniaephylum kraeuseli* RÁSKY; RÁSKY, p. 427, 1: 2, 3.
1960 *Passifloriaephylum kraeuseli* RÁSKY; RÁSKY, p. 433, 4: 16.
2010 *Acherniaephylum hydrarchos* (UNGER) HABLY; HABLY, p. 410, pl. 5, figs 6–8.

Material: Budapest, Óbuda, Nagybátony-Újlak brick-yard: BP 60.33.1., 60.34.2=60.35.1., 60.36.1=60.37.1., 60.38.1., 2006.131.2., 2007.216.2., 2007.217.2., 2007.575.2., 2007.576.1., 2007.577.1., 2007.578.1., 2007.579.1., 2007.580.1., 2007.581.2., 2007.582.1., 2007.583.1., 2007.584.1., 2007.585.1.; Eger-Kiseged: BP 83.296.1., 2007.570.2., BP 2007.571.1., 2007.572.1., 2007.573.2., 2007.574.1.

Raskya vetusta (ETTINGSHAUSEN)
MANCHESTER & HABLY

- 1880 *Tetrapteris vetusta* (ETTINGSHAUSEN) SEIBER; SEIBER, p. 19, pl. 4, figs 29–30.
1926 *Abelia quadrialata* E. M. REID & CHANDLER; E. M. REID & CHANDLER, p. 133, pl. 8, figs 29–31, text-fig. 11.
1959 *Abelia* sp.; ANDREÁNSZKY, p. 16, pl. 2, fig. 11, pl. 3, figs 13, 14, pl. 4, fig. 17, text-fig. 8.
1960 *Abelia quadrialata* E. M. REID & CHANDLER; RÁSKY, p. 435, pl. 1, fig. 1.
1963 *Abelia* sp.; ANDREÁNSZKY, p. 250, pl. 3, fig. 5.
1997 *Raskya vetusta* (ETTINGSHAUSEN) MANCHESTER & HABLY; MANCHESTER & HABLY, p. 236, pl. 1, figs 1–5, pl. 2, figs 1–9, text-fig. 1.
2000 *Raskya vetusta* (ETTINGSHAUSEN) MANCHESTER & HABLY; HABLY, KVAČEK & MANCHESTER, p. 65, pl. 3, figs 7–8.

Material: Budapest, Óbuda: BP 62.1.1., 78.306.2., 78.312.4., 81.18.2., 2001.376.1., 2002.435.2., 2004.449.1., 2005.620.1., 2005.621.1., Eger-Kiseged: BP 2001.255.1., 2002.82.1., 2004.746.1., 2004.747.1., 2005.612.2., 2006.182.2., 2006.183.1–2006.186.1.

Kydia kraeuseli (RÁSKY)
HABLY

- 1943 *Ficus kräuseli* RÁSKY; RÁSKY, p. 516, pl. 17, fig. 1.
1943 *Cercis parvifolia* LESQUEREUX; RÁSKY, p. 527, pl. 24, fig. 1.
1943 *Cercis hungarica* RÁSKY; RÁSKY, p. 528, pl. 24, figs 2, 4.
1943 *Cercis spokanensis* KNOWLTON; RÁSKY, p. 529, pl. 24, fig. 3.
1956 *Kydia palaeocalycina* RÁSKY; RÁSKY, p. 176, pl. 31, figs 1, 2.

- 1966 *Ficus latsonoides* ANDREÁNSZKY; ANDREÁNSZKY, p. 79, figs 71, 72.
2010 *Kydia kräuseli* (RÁSKY) HABLY, HABLY, p. 412, pl. 4, figs 1, 5, 7.

Material: Budapest, Óbuda, Nagybátony-Újlak brick-yard: BP: 56.138.1= 56.139.1. (Holotype of *Kydia palaeocalycina* RÁSKY with counterpart), 56.140.1., 56.141.1., 56.142.1., 56.143.1., 56.143.1., 60.31.1., 60.32.1., 63.1052.1., 63.1054.1., 64.414.1=64.415.1. (counterpart), 2004.440.1., 2004.439.1., 2004.448.1., 2006.96.2., 2006.97.2., 2006.98.2., 2006.99.1., 2006.100.2., 2006.101.1., 2006.102.2., 2006.103.2., 2006.104.1., 2006.105.1., 2006.106.1., 2006.107.2., 2006.108.1., 2006.109.1., 2006.110.1., 2006.111.1., 2006.112.1., 2006.113.1., 2006.114.1., 2006.115.2., 2006.116.1., 2006.117.2., 2006.118.2., 2006.119.1., 2006.120.1., 2006.121.2., 2006.122.1., 2006.123.1., 2006.124.1., 2006.125.1., 2006.16.2., 2006.127.2., 2006.128.1., 2006.129.1. Budapest, Óbuda, Csillaghegy brickyard: BP: 61.22.1., 61.23.1., 61.24.1. (Holotype of *Cercis hungarica* RÁSKY), Budapest, Óbuda, Szépvölgy brickyard: BP: 61.16.1=61.17.1., (Holotype of *Ficus kräuseli* RÁSKY with counterpart).

Apocynospermum sp.

- 2000 *Apocynospermum* sp.; HABLY, KVAČEK & MANCHESTER, p. 65, pl. 3, fig. 9.

Material: Budapest, Óbuda, Nagybátony-Újlak brick-yard: BP 63.1039.1.

Composition of the flora based on recent taxonomical revisions

The early Oligocene flora of Hungary is a quite rich assemblage comprising a high diversity of “palaetropical” flora elements. Pteridophytes, gymnosperms and angiosperms are all well represented in the flora. The former is relatively diverse with numerous genera, i.e. *Acrostichum aureum* L., *Antrophytes egedensis* ANDREÁNSZKY, *Aspidites* sp., *Blechnum dentatum* (GÖPPERT) AL. BRAUN, *Lygodium gaudinii* HEER, *Osmunda leganyii* ANDREÁNSZKY, *Osmunda lignitum* (GIEBEL) STUR, *Pteris budensis* ANDREÁNSZKY, *Rhipidopteris palaeopeltata* ANDREÁNSZKY.

The diversity of gymnosperms is also noteworthy with high abundance of some species such as *Tetraclinis salicornioides* (UNGER) KVAČEK and *Doliostrobus taxiformis* (STERNBERG) KVAČEK var. *hungaricus* (RÁSKY), KVAČEK & HABLY. Other characteristic elements are *Pinus tuzsonii* NOVÁK and *Pinus palaeostrobus* ETTINGSHAUSEN. Cuticular studies were inevitable to identify the species, *Chamaecyparites hardtii* (GÖPPERT) ENDLICHER, with certainty (HABLY 1992a) since its macromorphological traits are shared by the twigs of *Doliostrobus*. The first fossils of the modern cycad genus *Ceratozamia* were proved from the early Oligocene of Hungary (KVAČEK 2002a), which indicates a neotropical affinity of the fossil flora. The modern genus is confined to the southernmost part of North America (Mexico) and Central America.

Among angiosperms members of Lauraceae were significant with various species of *Daphnogene* and *Laurophylloides*. The identification of species of the latter, *L. medimontanum* BÚŽEK, HOLÝ & KVAČEK, *L. hradekense* KVAČEK & BÚŽEK, and a new species, *L. kvacekii* HABLY, was based on cuticular examinations therefore these species could be proved only based on the better preserved specimens from the H- boreholes (Budapest). Recent studies showed that specimens from the Eger-Kiseged flora are occasionally preserved with fragments of the cuticle, thus two additional *Laurophylloides* species, *L. acutimonitanum* MAI and *L. markwarticense* KVAČEK, could be identified, both from the H- boreholes in Budapest and Eger-Kiseged.

A significant fagaceous species predominate the flora in nearly all the localities is *Eotrigonobalanus furcinervis*, which possesses leaves showing quite variable morphological traits, i.e. many transitional forms have been documented between the broad leaved and the elongate-lanceolate forms. The fruits of this species were recorded for the first time from Eger-Kiseged (KVAČEK & HABLY 1998). The specimen from Eger-Kiseged is the most complete one collected so far, some intact fruits attached to twigs are well observable. One of the most characteristic elements of the Tard Clay flora, *Ziziphus zizyphoides* is abundant in each locality, and its northernmost occurrence is proved from here. The leaves and fruits of *Engelhardia*, *E. orsbergensis* and *E. macroptera*, show varying frequency, they are dominant, accessory or absent in the localities. The occurrence of *Hooleya hermis* (UNGER) E. M. REID & CHANDLER and *Ailanthes tardensis* is noteworthy in the flora of Budaújlak (HABLY 2001), these species are absent from the other localities. A winged fruit, *Tetrapteris harpyiarum* (HABLY & MANCHESTER 2000) is presumably an endemic element since it has exclusively been recorded from the localities of the Tard Clay Formation and from stratigraphically related sediments in Slovenia. A relatively high number of specimens (~50) of another winged fruit, *Raskya vetusta* (MANCHESTER & HABLY 1997), having unknown affinity, was recorded from Eger-Kiseged and the Nagybátony-Újlak brickyard in Óbuda. In addition to the Hungarian record the extinct *Raskya* genus has so far been described from the Eocene floras of Bembridge (England) and Kučlín (Czech Republic) (MANCHESTER & HABLY 1997). A species of *Ailanthes*, *A. tardensis* was described from the Nagybátony-Újlak brickyard in Óbuda and published along with a discussion on characters distinguishing it from *A. confucii* UNGER, which is typical in the early Miocene floras of Hungary (Mecsek Mts) (HABLY 2001). *Ailanthes* has not been documented in Eger-Kiseged. A higher number of leaves of *Platanus neptuni* (ETTINGSHAUSEN) BÚŽEK, HOLÝ & KVAČEK were collected from the H- boreholes than from Eger-Kiseged, however the species is not a dominant element of the floras. Although, species of *Platanus* are usually listed among "arctotertiary" elements, *P. neptuni* is rather an ancient, thermophilous, "palaeotropical" species. The *Leguminosae* fossils which

may represent arboreal taxa are noteworthy elements of the floras in all the localities. Numerous leaflets of legume genera, such as *Dalbergia bella* HEER, were found both in Eger-Kiseged and Budapest; however a closer identification would be uncertain due to the absence of cuticular details. Legume pods occurring first of all in Eger-Kiseged serve as clear evidence of *Leguminosae*. These are the earliest evidence of the group from the Hungarian Cenozoic and remains became more numerous during the late Oligocene.

One of the dominant and most characteristic elements of the flora is *Sloanea olmediaefolia* (KVAČEK et al. 2001). The fossil occurrence of the modern *Sloanea* genus was documented in the fossil record for the first time. Since then the genus has been found in many other European, mainly Oligocene floras (HABLY 2007, HABLY et al. 2007, HABLY & KVAČEK 2008, ERDEI & RÁKOSI 2009). It is noteworthy that ANDRÉÁNSZKY & CZIFFERY (1964) evaluated some species as „microtherm” elements, for instance *Alnus antiquorum* and *Populus mutabilis*, which were later proven to belong to *Sloanea olmediaefolia*. Many specimens of other species indicated as "arctotertiary" elements by ANDRÉÁNSZKY and CZIFFERY (1964) are poorly preserved and unidentifiable remains. Others, for instance *Ulmus minuta* (p. 122, text-fig. 4.) and *Ulmus affinis* (p. 123, text-fig. 5.) belong to the genus *Quercus* and to the species *Platanus neptuni*, respectively. Another example is some fruits initially documented as *Ulmus* (ANDRÉÁNSZKY & CZIFFERY 1964) which later were revisited and assigned to *Craigia bronnii* (KVAČEK & HABLY 1998).

Floristic comparison of the floras from Óbuda and Eger-Kiseged

Although the species composition of the individual floras of the Tard Clay Formation is basically similar, some differences between the Eger-Kiseged and Budapest area are clearly observable. The flora of Eger-Kiseged may be regarded as a small-leaved flora since species, even those shared by the two areas, possess leaves of smaller size. The most typical species of the Tard Clay, i.e. *Ziziphus zizyphoides*, *Eotrigonobalanus furcinervis*, *Engelhardia orsbergensis*, *Sloanea olmediaefolia* have leaves in Eger-Kiseged that are smaller, mainly narrower with a couple of centimetres on the average than leaves of the same taxa in Óbuda (Budapest). Morphometric analyses evaluated the size difference of the leaves between the two areas as significant (TAMÁS & HABLY 2005). Studies applied on leaves of modern plants show that comparable morphometric difference may be attributable to drier climatic conditions in Kiseged than in Óbuda. Nevertheless, the Kiseged and Óbuda areas were situated in lower latitudes during the Oligocene than their current geographic coordinates and even their relative geographic position was different from the modern one (CSONTOS et al. 1992, CSONTOS 1995). As a summary, the morphometric analyses carried out on a couple of species suggest climatic

difference between the Kiseged and Óbuda areas (TAMÁS & HABLY 2009, ERDEI et al. 2012). Species composition, at the same time, is quite similar with only a couple of distinctive species, e.g. *Ailanthus tardensis* and *Hooleya hermis* occasionally abundant in Óbuda, but missing from Eger-Kiseged.

Floristic change at the turn of the early and late Oligocene in the Paratethys area

The floristic turn during the Oligocene was one of the most robust floristic changes of the Paleogene.

The flora appearing in the late Oligocene was attributed to the general spread of “arctotertiary” elements induced by the deterioration of climate, mainly by the decrease of mean annual temperatures. However, our current knowledge suggests other factors playing important role in the floral development of the Oligocene.

As regards the occurrence of species some trends are clearly observable. Many species are not found in the late Oligocene floras, these presumably did not survive. The most significant taxa are *Eotrigonobalanus furcinervis*, *Ziziphus zizyphoides*, *Raskya vetusta*, *Tetrapteris harpiarum*, *Hooleya hermis*, *Ailanthus tardensis*, *Dolistrobus taxiformis* var. *hungaricus*, many fern species and other accessory elements (*Chamaecyparis hardtii*, *Laurophyllum* spp., etc.) (HABLY 1985b, ERDEI & HABLY 2010). Some species survived and were present in the late Oligocene but they became less significant or their importance remained unchanged. A good example is *Tetraclinis salicornioides*, which occurs sporadically in the late Oligocene floras but later, in the early Miocene flora and vegetation (Ipoltarnóć) it plays an important role again. Another species, *Sassafras tenuilobatum* is rare in both the early and late Oligocene floras.

There are four plant groups that gained higher importance during the late Oligocene. One of these is the Lauraceae family, which, although, played already an important role in the early Oligocene floras, became dominant with its increased species and specimen numbers in the late Oligocene (Egerian) floras.

Another species with increasing importance is *Platanus neptuni*, which was already a member of early Oligocene floras, though with low number of specimens but in the late Oligocene became dominant in nearly all the localities. A characteristic species, *Engelhardia orsbergensis* was a dominant element of some early Oligocene floras, e.g. Budaújlak, however it became a typical element of the late Oligocene and even the early Miocene floras, e.g. Ipoltarnóć (HABLY 1985a), where, accompanied by *Platanus neptuni* it predominates the fossil assemblage. The fourth group displaying increasing importance through the late Oligocene is the arboreal Leguminosae. Some of these were members of the Tard Clay floras but others appeared in the Egerian floras. Nevertheless, the first main flourish of the group took place in the late Oligocene (HABLY 1992b). The

group of plants appearing in the late Oligocene comprises many taxa, such as *Platanus neptuni* forma *fraxinifolia*, *Ulmus pyramidalis*, *Rosa* sp., *Trigonobalanopsis rhamnoides* (ROSSMÄSSLER) KVAČEK & WALTHER, *Acer* div. sp., “*Rhamnus*” *warthae*, *Betula* div. sp., *Alnus* div. sp. etc.

Apparently, the floristic change was much more complex than just the appearance of “arctotertiary” elements. Some of the “palaeotropical” elements gain also higher importance or appear as late as the late Oligocene in the Palaeogene basin area. The “reorganization” of the flora and vegetation cannot be fully explained by the deterioration of climate. Some geological events must have taken place that had an impact on the terrestrial flora and vegetation by means of changing their habitat and climatic environment.

The early Oligocene terrestrial climate and palaeoecology based on the fossil plant record

Since climate and environment determine and limit the distribution of plants, the systematic, morphometric and various other palaeoecological analyses of terrestrial plants help us to estimate palaeoclimate and its variables. The systematics-based Coexistence Approach (CA) method (MOSBRUGGER & UTESCHER 1997) was applied to the fossil floras in order to obtain quantitative palaeoclimate data. The method follows the nearest living relative concept. Based on the climatic requirements of the nearest living relatives of the fossil plant taxa it calculates ‘coexistence intervals’ for various climate parameters. The mean annual temperature (MAT), mean temperature of the warmest (WMT) and coldest (CMT) months, and mean annual precipitation (MAP) were calculated based on the floras from Budapest and Eger-Kiseged resulting in the following values: MAT — 15.6–22 °C; CMT — 7.7–19.8 °C; WMT — 24.7–28.2 °C; MAP — 1194–1520 mm (ERDEI et al. 2007, 2012). The values prove a much warmer climate compared to the current conditions. The difference is even more pronounced when considering the early Oligocene values of CMT well above freezing conditions. The climate analysis of late Oligocene (Egerian) macrofloras of Hungary (ERDEI & BRUCH 2004) indicated lower mean annual and cold month temperatures (9.3–20.5 °C / –3.3–13.3 °C) compared to the early Oligocene climate data suggesting a cooling of climate.

The morphometric analysis of leaves belonging to taxa from the Hungarian as well as Italian and Slovenian early Oligocene floras showed a significant morphological difference of the Eger-Kiseged flora suggesting different climatic (lower humidity) conditions of the latter (ERDEI et al. 2012).

Palaeoatmospheric CO₂ level calculations adopting the method by KONRAD et al. (2008) on *Sloanea* leaves from the Hungarian and Slovenian early Oligocene sites resulted in (overlapping) values between 503–839 ppm during NP23 (ERDEI et al. 2012), which shows an overlap with results obtained from other proxy data (BERNER & KOTHAVALA

2001, ROTHMAN 2002, PAGANI et al. 2005). The obtained values in the early Oligocene are higher than the pre-industrial value but much lower than values usually calculated for the Eocene with maximum values of 2000 ppm or more in several proxy data sets (PEARSON & PALMER 2000, PAGANI et al. 2005).

Acknowledgements

The authors are grateful to Prof Zlatko Kvaček for useful comments and suggestions.

The study was supported by the Hungarian Scientific Research Fund (OTKA 108664).

References

- ANDREÁNSZKY G. 1949: Néhány páfrány a Kárpát-medence harmadkorából. (Quelques fougères de l'époque tertiaire du bassin Carpathique). — *Index horti bot. Univ. Bud.* **7**, 1–9.
- ANDREÁNSZKY G. 1951: Adatok a hazai harmadkori flóra ismeretéhez. (Contributions à l'étude de la Flore tertiaire de la Hongrie). — *Földtani Közlöny* **81**, 320–328.
- ANDREÁNSZKY G. 1952: Újabb harmadidőszaki páfrányok. (Nouvelles fougères de Tertiaire de la Hongrie). — *Földtani Közlöny* **82/10–12**, 397–402.
- ANDREÁNSZKY G. 1954: Mangrovepáfrány a hazai alsóoligocénből. (Mangrove-fern in Hungary from the Oligocene). — *Botanikai Közlemények* **44/1–2**, 135–139.
- ANDREÁNSZKY, G. 1955: Neue und interessante tertiäre Pflanzenarten aus Ungarn I. — *Annales historico-naturales Musei nationalis hungarici* **6**, 37–50.
- ANDREÁNSZKY, G. 1956: Neue und interessante tertiäre Pflanzenarten aus Ungarn II. — *Annales historico-naturales Musei nationalis hungarici* **7**, 221–229.
- ANDREÁNSZKY, G. 1959: Contribution à la connaissance de la Flore de l'oligocène inférieur de la Hongrie et un essai sur la reconstitution de la Flore contemporaine. — *Acta Botanica Hungarica* **5/1–2**, 1–37.
- ANDREÁNSZKY, G. 1963: Beiträge zur Kenntnis der Unter-Oligozänen Flora der Umgebung von Budapest. — *Acta Botanica Hungarica* **9/3–4**, 227–257.
- ANDREÁNSZKY G. 1964: A tölgy rokonsági köre az Eger melletti Kiseged alsó-oligocén flórájában. (Der Verwandschaftskreis der Eiche in der unteroligozänen Flora von Kiseged bei Eger [Oberungarn]). — *Az Egri Múzeum Évkönyve* **2**, 7–42.
- ANDREÁNSZKY, G. 1965a: Neue und interessante tertiäre Pflanzenarten aus Ungarn IV. — *Annales historico-naturales Musei nationalis hungarici* **57**, 53–79.
- ANDREÁNSZKY G. 1965b: Középső-oligocén növénymaradványok Eger környékén. (Plantes fossiles d'âge rupelian des environs d'Eger [Hongrie septentrionale]). — *Az Egri Múzeum Évkönyve* **3**, 7–22.
- ANDREÁNSZKY, G. 1967a: Neue und interessante tertiäre Pflanzenarten aus Ungarn V. — *Annales historico-naturales Musei nationalis hungarici* **59**, 29–44.
- ANDREÁNSZKY G. 1967b: Hüvelyesek (Leguminosae) szerepe az Eger melletti Kiseged alsó-oligocén flórájában. (Die Rolle der Leguminosen in der unter-oligozänen Flora von Kiseged bei Eger [Ober-Ungarn]). — *Az Egri Múzeum Évkönyve* **5**, 7–30.
- ANDREÁNSZKY, G. & CZIFFERY, G. 1964: Reste einiger mikrothermen Gattungen aus der unter-oligozänen Flora von Kiseged bei Eger [Ober-Ungarn]. — *Annales historico-naturales Musei nationalis hungarici* **56**, 117–128.
- ANDREÁNSZKY, G. & NOVÁK, E. 1957: Neue und interessante tertiäre Pflanzenarten aus Ungarn III. — *Annales historico-naturales Musei nationalis hungarici* **8**, 43–55.
- BÁLDI, T. 1980: The early History of the Paratethys. — *Földtani Közlöny* **110**, 456–472.
- BÁLDI, T., HORVÁTH, M., NAGYMAROSY, A. & VARGA, P. 1984: The Eocene–Oligocene boundary in Hungary. The Kiscellian stage. — *Acta Geologica Hungarica* **27/1–2**, 41–65.
- BERNER, R. A. & KOTHAVALA, Z. 2001: GEOCARB III: a revised model of atmospheric CO₂ over Phanerozoic time. — *American Journal of Science* **301**, 182–204.
- BRONGNIART, A. 1822: Description des végétaux fossiles du terrain de sédiment supérieur. — In: *Description géologique des environs de Paris* M. M. G. Cuvier et A. Brongniart. Paris, 353–402.
- BŮŽEK, Č., HOLÝ, F. & KVAČEK, Z. 1968: Die Gattung *Doliostrobus* MARION und ihr Vorkommen im nordböhmischen Tertiär. — *Palaeontographica B* **123**, 153–172.
- CSONTOS, L. 1995: Tertiary tectonic evolution of the Intra-Carpathian area: a review. — *Acta Vulcanologica* **7/2**, 1–13.
- CSONTOS, L., NAGYMAROSY, A., HORVÁTH, F. & KOVAC, M. 1992: Tertiary evolution of the Intra-Carpathian area: a model. — *Tectonophysics* **208**, 221–241.
- ERDEI, B. & BRUCH, A. 2004: Climate analysis of Late Oligocene (Egerian) macrofloras from Hungary. — *Studia Botanica Hungarica* **35**, 5–23.
- ERDEI, B., HABLY, L., KÁZMÉR, M., UTESCHER, T. & BRUCH, A. 2007: Neogene flora and vegetation development of the Pannonian domain in relation to palaeoclimate and palaeogeography. — *Palaeogeography, Palaeoclimatology, Palaeoecology* **253**, 131–156.
- ERDEI, B. & RÁKOSI, L. 2009: The Middle Eocene flora of Csordakút (N Hungary). — *Geologica Carpathica* **60/1**, 43–57.
- ERDEI, B. & HABLY, L. 2010: Palaeogene and Neogene localities in the North-Hungarian Mountain Range (including introduction to the

- modern flora). — 8th European Palaeobotany–Palynology Conference 2010, 6–10 July 2010 Budapest, Hungary, Excursion guide, pp. 1–52.
- ERDEI, B., UTESCHER, T., HABLY, L., TAMÁS, J., ROTH-NEBELSICK, A. & GREIN, M. 2012: Early Oligocene Continental climate of the Palaeogene Basin (Hungary and Slovenia) and the surrounding area—a complex approach. — *Turkish Journal of Earth Sciences* **21**, 153–186.
- HABLY, L. 1979: Some Data to the Oligocene Flora of the Kiscellian Tard Clay, Hungary. — *Annales historico-naturales Musei nationalis hungarici* **71**, 33–53.
- HABLY, L. 1980a: Oligocén (Kiscellien) makroflóra az óbudai H-jelű fúrásokból. (Oligocene [Kiscellian] Macroflora from the H-boreholes of Óbuda). — *Őslénytani Viták (Discuss. Palaeont.)* **25**, 155–164.
- HABLY, L. 1980b: *Platanus neptuni* (ETT.) BUZEK, HOLÝ et KVÁČEK in the Hungarian Oligocene. — *Acta Botanica Hungarica* **26/3–4**, 299–316.
- HABLY, L. 1983: Az oligocén flórakutatás újabb eredményei. — *Botanikai Közlemények* **70/1–2**, 5–11.
- HABLY, L. 1985a: *Platanus neptuni* (ETT.) BÚŽEK, HOLÝ & KVÁČEK magyarországi előfordulása, rétegtani, környezet- és klímajelző szerepe. (The Hungarian occurrence of *Platanus neptuni* (ETT.) BÚŽEK, HOLÝ & KVÁČEK and its significance in stratigraphic, environment and climate indication). — *Botanikai Közlemények* **72/1–2**, 37–42.
- HABLY, L. 1985b: The flora of the Tard Clay and climatological changes round the turn of the Eocene/Oligocene. — *Őslénytani Viták (Discuss. Palaeont.)* **31**, 109–110.
- HABLY, L. 1986: The macroflora of the borehole Kisell–1 in Budapest. — *Annales historico-naturales Musei nationalis hungarici* **78**, 31–40.
- HABLY, L. 1992a: New Data to the Macroflora of the Tard Clay Formation on the Basis of Cuticular Analysis. — *Courier Forschungsinstitut Senckenberg* **147**, 369–381.
- HABLY, L. 1992b: Distribution of legumes in the Tertiary of Hungary. — *Advances in Legume Systematics: Part 4. Fossil Record*, 169—187. Kew.
- HABLY, L. 2001: Fruits and leaves of *Ailanthus* DESF. from the Tertiary of Hungary. — *Acta Palaeobotanica* **41**, 207–219.
- HABLY, L. 2007: New European records and first evidence of epidermal structures of *Sloanea* L. from Italy—revised type and original material of Principi 1916. — *Rivista Italiana di Paleontologia e Stratigrafia* **113/3**, 449–457.
- HABLY, L. 2010: The Early Oligocene flora of Santa Giustina (Liguria, Italy)—revision and comparison with the flora of the Tard Clay Formation. — *Rivista Italiana di Paleontologia e Stratigrafia* **116/3**, 405–420.
- HABLY, L. & FERNANDEZ MARRON, M. T. 1998: A comparison of the Oligocene floras of the Tethyan and Central-Paratethyan areas on the basis of Spanish and Hungarian macroflora. — *Tertiary Research* **18/3–4**, 67–76.
- HABLY, L. & KVÁČEK, Z. 2008: Nomenclatural types and taxonomy of UNGER's (1850) and ETTINGSHAUSEN's (1853) fossil leaves recognized as new *Sloanea* records in the European Paleogene. — *Neues Jahrbuch für Geologie und Paläontologie Abhandlungen Stuttgart* **249/2**, 139–142.
- HABLY, L. & MANCHESTER, S. R. 2000: Fruits of *Tetrapterys* (Malpighiaceae) from the Oligocene of Hungary and Slovenia. — *Review of Palaeobotany and Palynology* **111/1–2**, 93–101.
- HABLY, L. & THIÉBAUT, M. 2002: Revision of *Cedrelospermum* (Ulmaceae) fruits and leaves from the Tertiary of Hungary and France. — *Palaeontographica B* **262**, 71–90.
- HABLY, L., KVÁČEK, Z. & MANCHESTER, S. R. 2000: Shared Taxa of Land Plants in the Oligocene of Europe and North America in context of Holarctic Phytogeography. — *Acta Universitatis Carolinae, Geologica* **44/1**, 59–74.
- HABLY, L., BÁLDI T. & NAGYMAROSY A. 2007: Nosvaj, Kiseged. — In: PÁLFY J. & PAZONYI P. (szerk.) GeoKalauz I. Őslénytani kirandulások Magyarországon és Erdélyben. Hantken Kiadó, Budapest, 199–203.
- HABLY, L., TAMÁS, J. & CIOOPPI, E. 2007: *Sloanea peolai* n. comb. — a new European record of *Sloanea* (Elaeocarpaceae) in the Italian Oligocene. — *Review of Palaeobotany and Palynology* **146**, 18–28.
- KONRAD, W., ROTH-NEBELSICK, A. & GREIN, M. 2008: Modelling of stomatal density response to atmospheric CO₂. — *Journal of theoretical Biology* **253**, 638–658.
- KVÁČEK, Z. 1971: Supplementary notes on *Doliostrobus* MARION. — *Palaeontographica B* **135**, 115–126.
- KVÁČEK, Z. 2002a: A new Tertiary *Ceratozamia* (Zamiaceae, Cycadopsida) from the European Oligocene. — *Flora* **197**, 303–316.
- KVÁČEK, Z. 2002b: Novelties on *Doliostrobus* (Doliostrobaceae), an extinct conifer genus of the European Palaeogene. — *Journal of the National Museum (Prague), Natural History Series* **171/1–4**, 131–175.
- KVÁČEK, Z., & BÚŽEK, Č. 1995: Endocarps and foliage of the flowering plant family Icacinaceae from the Tertiary of Europe. — *Tertiary Research* **15/3**, 121–138.
- KVÁČEK, Z. & HABLY, L. 1998: New plant elements in the Tard Clay Formation from Eger-Kiseged. — *Acta Palaeobotanica* **38**(1), 5–23.
- KVÁČEK, Z., BÚŽEK, Č. & MANCHESTER, S. R. 1991: Fossil fruits of *Pteleaecarpum* WEYLAND — Tiliaceous, not Sapindaceous. — *Botanical Gazette* **152/4**, 522–523.
- KVÁČEK, Z., HABLY, L. & MANCHESTER, S. R. 2001: *Sloanea* (Elaeocarpaceae) fruits and foliage from the Early Oligocene of Hungary and Slovenia. — *Palaeontographica B* **259/1–6**, 113–124.
- MAI, D. & WALther, H. 1985: Die obereozänen Floren des Weißelster-Beckens und seiner Randgebiete. — *Staatliches Museum für Mineralogie und Geologie zu Dresden* **33**, 5–260.
- MANCHESTER, S. R. 1989: Attached reproductive and vegetative remains of the extinct American-European genus *Cedrelospermum* (Ulmaceae) from the early Tertiary of Utah and Colorado. — *American Journal of Botany* **76/2**, 256–276.
- MANCHESTER, S. R. & HABLY, L. 1997: Revision of “Abelia” fruits from the Paleogene of Hungary, Czech Republic and England. — *Review of Palaeobotany and Palynology* **96**, 231–240.

- MOSBRUGGER, V. & UTESCHER, T. 1997: The coexistence approach — a method for quantitative reconstructions of Tertiary terrestrial palaeoclimate data using plant fossils. — *Palaeogeography, Palaeoclimatology, Palaeoecology* **134**, 61–86.
- NAGYMAROSY, A. & BÁLDI-BEKE, M. 1988: The position of the Paleogene formations of Hungary in the standard nannoplankton zonation. — *Annales Universitatis Scientiarum Budapestinensis de Rolando Eotvos Nominatae, Sectio Geologica* **28**, 3–25.
- NOVÁK E. 1950: A kisegedi oligocén-flóra fenyőféléi. (Die Koniferen der oligozänen Flora von Kiseged bei Eger [Ungarn]). — *Annales Universitatis Scientiarum Budapestinensis de Rolando Eotvos Nominatae, Sectio Biologica* **1/1**, 48–61.
- PAGANI, M., ZACHOS, J. C., FREEMAN, K. H., TIPPLE, B. & BOHATY, S. 2005: Marked decline in atmospheric carbon dioxide concentrations during the Paleogene. — *Science* **309**, 600–603.
- PÁLFALVY I. 1978: Alsóoligocén növénymaradványok a Metro szelvényének budai szakaszáról. (Unteroligozäne Pflanzenreste aus dem Budaer Abschnitt der Untergrundbahn (Metro). — *A Magyar Állami Földtani Intézet Évi Jelentése 1976-ról*, 311–320.
- PÁLFALVY I. 1981: A magyarországi Engelhardia fajok rétegtani, ökológiai és cönológiai szerepe. (Stratigraphische, ökologische und zönologische Rolle der Engelhardia-Arten aus Ungarn). — *A Magyar Állami Földtani Intézet Évi Jelentése 1979-ról*, 491–495.
- PEARSON, P. E. & PALMER, M. R. 2000: Atmospheric carbon dioxide concentrations over the past 60 million years. — *Nature* **406**, 695–699.
- RÁSKY, K. 1943: Die oligozäne Flora des Kiseller Tons in der Umgebung von Budapest. — *Földtani Közlöny* **73**, 508–610.
- RÁSKY K. 1950: *Tarrietia hungarica* n. sp. előfordulása Magyarországon. (*Tarrietia hungarica* n. sp. aus Ungarn). — *Földtani Közlöny* **80**, 192–194.
- RÁSKY K. 1956: Fosszilis növények a Budapest környéki „Budai” márgaösszletből (Fossil plants from the marl formation of the environs of Budapest). (in Hungarian). — *Földtani Közlöny* **86/2**, 165–179.
- RÁSKY, K. 1960: Pflanzenreste aus dem Obermiozäne Ungarns. — *Senckenbergiana Letheo* **41/1–6**, 423–449.
- RÁSKY, K. 1962: Tertiary Plant Remains from Hungary. (Upper Eocene and Middle Oligocene). — *Annales historico-naturales Musei nationalis hungarici* **54**, 31–55.
- RÁSKY, K. 1964: Studies of Tertiary Plant Remains from Hungary. — *Annales historico-naturales Musei nationalis hungarici* **56**, 63–96.
- RÁSKY, K. 1965: A Contribution to the Study of Tertiary Plant Remains from Hungary. — *Annales historico-naturales Musei nationalis hungarici* **57**, 81–94.
- RÁSKY, K. 1966: Some Plant Remains from the Tertiary of Hungary. — *The Palaeobotanist* **14**, 264–268.
- REID, E. M. & CHANDLER, M. E. J. 1926: Catalogue of Cainozoic plants in the Department of Geology vol. 1, The Bembridge Flora. — *British Museum of Natural History London*, 206 p.
- ROTHMAN, D. H. 2002: Atmospheric carbon dioxide levels for the last 500 million years. — *PNAS* **99**, 4167–4171.
- SAPORTA, G. 1891: Recherches sur la végétation du niveau aquitanien de Manosque. III. Amentacées, Salicinées et Urticinées. — *Mémoires de la Société géologique de France. Paléontologie*, 9 (II), fasc. **1, 2**, (III), fasc. **1, 2**, 35–83.
- SEIBER, J. 1880: Zur Kenntnis der nordböhmischen Braunkohlenflora. — *Sitzungsberichte der Kaiserlichen Akademie der Wissenschaften Wien*, Abt. 1, **82**, 67–101.
- STERNBERG, K. 1833: *Versuch einer geognostisch-botanischen Darstellung der Flora der Vorwelt. Fasc. 5–6.* — Leipzig, Prag, Regensburg, 80 p.
- TAMÁS, J. & HABLY, L. 2005: The morphometrical analysis of *Sloanea elliptica* (ANDREÁNSZKY) Z. KVAČEK & HABLY from the Oligocene of Buda and Bükk Mountains and its palaeogeographic implications — *Review of Palaeobotany and Palynology* **134**, 257–268.
- TAMÁS, J. & HABLY, L. 2009: Unidirectional shift in leaf morphology of coexisting species — a possible indicator of palaeoclimatic differences. — *Palaeogeography, Palaeoclimatology, Palaeoecology* **271/3–4**, 185–195.
- UNGER, F. 1845: *Chloris protogaea*, 6–7. — W. Engelmann. Leipzig.
- UNGER, F. 1850a: Die fossile Flora von Sotzka. — *Denkschriften math.-nat. K. K. Akademie Wissenschaften* **2**, 3–67.
- UNGER, F. 1850b: *Genera et Species Plantarum Fossilium*. — Vindobonae, Apud Wilhelmmum Braumüller. 627 p.
- VARGA I. 1956: A budaújlaki alsó-oligocén flóra páfrányai és fenyőféléi. (Die Farne und Koniferen der Funde bei Budaújlak aus dem unteren Oligozänen). — *Botanikai Közlemények* **46/3–4**, 291–299.
- WEYLAND, H. 1938: Beiträge zur Kenntnis der rheinischen Tertiärflora. II. Erste Ergänzungen und Berichtigungen zur Flora der Blätterkohle und des Polierschiefers von Rott im Siebengebirge. — *Palaeontographica B* **83**, 67–122.
