Final Report (NKFIH K108664): Thermophilous elements of the Cenozoic floras in the Pannonian Basin and the Northern Hemisphere
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Summary of project objectives: Fossil flora and vegetation serve as one of the best tools for the evaluation of terrestrial climate and its change. The fossil record of various flora elements is of special significance from this point of view. Thermophilous flora elements are especially good indicators of climate, appearing with varying diversity in the Paleogene and Neogene fossil plant assemblages.
The current project focussed on the record of thermophilous plants by means of studying selected plant groups and Paleogene-Neogene floras of the Pannonian Basin and the Northern Hemisphere and assessed their importance for palaeoclimatic and palaeoecological interpretations.

Output of project: A main target of project studies in the Pannonian Basin was the Miocene flora of the Mecsek Mts. As regards Northern Hemisphere studies a special group of plants, cycads were focussed on. The study of the Miocene flora of the Mecsek Mts revealed an early Miocene flora dominated by thermophilous elements and a late Miocene flora demonstrating the last occurrence of many thermophilous plants in the Hungarian floras. Additional thermophilous elements were documented from the Oligocene flora of Környe and the late Miocene flora of Gratkorn. The study gave evidence that both floras are unique having extremely high ratio of thermophilous elements. Cycad research contributed to the knowledge on the palaeoecology of extinct cycad groups (*Dioonopsis*), on the palaeobiogeography, distribution and appearance of some both modern and extinct cycads (*Zamia* and *Ctenis*) in the fossil record as well as on cycad ontogeny and evolution. The most important outcome of the project is a monograph on the Miocene flora of the Mecsek Mts (submitted to Acta Palaeobotanica) and the first record of a cycad seedling (published in Biology Letters).
During the research period 11 papers were published (cummulative impact factor: 13; according to Scimago journal ranking D1: 1, Q1: 2, Q2: 5, Q3:2), and 9 abstracts were included in conference abstract volumes (7/2 – international/national conferences). One of the papers was published open access, other papers are accessible through the Repository of the Academy's Library (REAL) and the "Researchgate" website. The manuscript of a monograph on the Miocene flora of the Mecsek Mts was submitted to an international journal for publication. Its review is in progress. (A résumé of the manuscript is included at the end of the report.)

Collecting activities: During the project period fossil plant collections were made from Miocene localities near Magyaregregy (Mecsek Mts), Balatonszentgyörgy, Verőce, and Erdőbénye in order to record termophilous elements through the Miocene. A herbarium collection of seedlings of modern cycads was compiled for the Herbarium of the Hungarian Natural History Museum. All collections are available for future botanical and palaeobotanical studies.

Project Results

1. Palaeofloristic studies of Paleogene and Neogene floras of the Pannonian Basin

1.1. Fossil flora of the Mecsek Mts

1.1.1. The Karpatian fossil plant assemblage of the Mecsek Mts is an extremely diverse flora with more than a hundred taxa outnumbering most of the well-known Miocene floras of Europe. Studies included both the collections made during the project period and earlier collections stored in the Hungarian Natural History Museum and the Mining and Geological Survey of Hungary, i.e. Magyaregregy- Vágyom-völgy, Leánykői-árok, Farkasordító-árok, Almás-patak; Kisbattyán; Abaliget - Kiskő-hegy, Nyáras-völgy; Kisbeszterce (more than 10 000 specimens). The systematic results show a flora abundant in elements which are either rare in the northern hemisphere floras or have not been recorded so far from other fossil floras, thus potentially endemics, e.g. new species of *Leguminocarpum, Ailanthus, Nyssa*, *Clematis, Gordonia, Carpolithes*. The first Hungarian occurrence of several species was recorded in the Mecsek flora. Some of them are of high significance, such as *Quercus kubinyii, Podocarpium podocarpum*, *Liquidambar europaea,* and *Populus populina,* which became dominant in the middle Miocene (Sarmatian) floras and even later during the late Miocene (Pannonian) were significant members of the riparian vegetation. Considering the Hungarian fossil floras, the genera *Cedrelospermum* and *Zizyphus* had their last occurrence. The first and often the only Hungarian appearance of some species were recorded in this flora which are rare even in the European Miocene, i.e. *Ternstroemites pereger*, *Prinsepia serra, Populus zaddachii, Antholites stiriacus.* The ratio of definitely warm demanding members was very high in the flora, i.e. *Daphnogene*, *Laurophyllum*, Lauraceae, *Engelhardia*, *Cedrelospermum*, *Ailanthus*, and some species of the Fabaceae family that were dominant or frequent elements of the flora. Additional thermophilous elements were *Ternstreomites*, *Smilax*, *Palmacites*, and members of Malvaceae and Theaceae. Thermophilous elements dominated the floras indicating warm temperate climate conditions. Even the swamp elements attest for a definitely warm climate. The forests composed of *Glyptostrobus – Nyssa- Myrica* must have been formed in warm climate conditions. Based on the above a warm-subtropical climate is assumed in the early Miocene of the Mecsek Mts. The quantitative climate analysis of the Magyaregregy flora based on a preliminary, incomplete list of taxa by Erdei et al. (2007) characterizes well the temperature intervals of the climate (mean annual temperature 15.6-16.6 ^{o}C, temperature of the coldest and warmest months: 5-6.2 ^{o}C, and 24.7-27.9 ^{o}C). Floristic composition implies that rainfall was not evenly distributed and seasonal dry periods occurred during the year.

Results were presented in the 20th Annual Palaeontological Meeting of the Hungarian Geological Society (2 abstracts, 20. Magyar Őslénytani Vándorgyűlés, 2017.05.25-27., Tata-Tardos) and a manuscript (monograph) has been submitted to the international journal "Acta Palaeobotanica" (Scimago rank: Q2). The manuscript consists of 100 pages, with nearly 300 photos arranged in photo plates. A résumé and a photo plate sample of the manuscript are added at the end of the report.

Results of palaeobotanical studies also contributed to a complex research led by Krisztina Sebe investigating syn-rift deposits in the Mecsek Mts from a tectono-

sedimentary aspect using results of stratigraphy, palaeontology and structural observations. Based on all available data and information a single water body ‘‘Lake Mecsek’’ was indicated covering the present-day Mecsek Mts and their surroundings in the Karpatian-early Badenian. Results have been published in the international journal ”Swiss Journal of Geosciences” (Scimago rank: Q2), (Hably involved as co-author).

1.1.2. A late Miocene (Pannonian) flora from the Mecsek Mts, Pécs-Danitz-puszta represents the oldest among the Pannonian floras of Hungary so far recorded, and comprises thermophilous elements in relatively high number, i.e. *Daphnogene pannonica*, Lauraceae gen. et sp., and *Tetraclinis salicornioides*, which occurs exclusively in this flora during the Pannonian. The dominance of lauraceous elements, and other thermophilous taxa, e.g. *Myrica lignitum* indicates the warmest conditions during the late Miocene of Hungary. The occurrence of *Quercus kubinyii, Tetraclinis salicornioides* and the partly laurophyllous vegetation suggest mesophytic habitats adjacent to the lake and its swamps and lowlands in the area of the Mecsek Mts at 10-11 mya.
Results were presented at the Annual Palaeontological Meeting of the Hungarian Geological Society. Two papers on the results have been published in the international journals “Neues Jahrbuch für Geologie und Paläontologie Abhandlungen” (Scimago rank: Q2) and “Studia botanica hungarica”.

1.2. An Oligocene thermophilous flora from Környe
In the course of the groundworks of the ’Környe Industrial Park’ near Tatabánya (N Hungary), fossiliferous beds of the Oligocene Mány Formation were exposed. Plant remains excavated represent the abundant occurrence of thermophilous elements, among others a rare taxon of Mastixioideae. The flora consists of typical Oligocene species, such as “*Rhamnus*” *warthae*, *Alnus oligocaenica* accompanied by elements thriving in humid habitats, e.g. the fern *Pronephrium stiriacum* in large quantities, and the conifer *Glyptostrobus europaeus*. The floristic composition suggests a warm subtropical climate. The single, so-called “Arctotertiary” element of this flora, *Alnus oligocaenica* does not seem to indicate climate cooling, instead, it appeared in the swamp vegetation as an intrazonal element.
Results have been published in the international journal “Neues Jahrbuch für Geologie und Paläontologie Abhandlungen” (Scimago rank: Q2).

1.3. Fossil plants from the middle Miocene of Verőce
Fossil plants have recently been discovered and collected from the Miocene (?Badenian) locality in Verőce. If further studies corroborate the age and stratigraphy of the site, the locality will contribute with essential data to middle Miocene flora and vegetation of Hungary, since Badenian layers known so far are almost devoid of plant fossils. This locality contributes with new data also to the Miocene of the Börzsöny region. Based on the study of more than 200 leaf impressions, a floodplain forest of *Populus populina*, *Populus balsamoides*, *Acer angustifolia,* and other *Acer* species was reconstructed. As an accessory element *Equisetum parlatorii* occurred in habitats with high water supply, and other rare elements *Pterocarya denticulata* and *Liquidambar europaea* are also noteworthy. Although these associations are constrained first of all by edaphic factors, some definitely thermophilous elements, e.g. *Pterocarya denticulata* and *Liquidambar europaea*, indicate warm climate conditions. The dominant species of *Populus* and *Acer* must have favoured a climate

significantly warmer than today as proven by many other European occurrences. Results will be published in "Studia botanica hungarica" (in progress).

1.4. Gratkorn – a unique middle Miocene flora

The St. Stefan clay-pit at Gratkorn is an extraordinary fossil locality, due to its diverse and unique plant and animal records. The fossil flora from Gratkorn (north-western margin of the Pannonian Basin, Austria) representing dominantly an aquatic vegetation was investigated. The age of the plant-bearing sediment is Sarmatian, late Middle Miocene. The flora is composed of mainly aquatic plants, i.e. *Ceratophyllum schrotzburgense*, *Caldesia europaea* sp. nov., which is the first leaf record of *Caldesia* in Europe, *Stratiotes* sp., *Hydrochariphyllum kvacekii* sp. nov., Hydrocharitaceae gen. et sp. indet, *Potamogeton martinianus* and Monocotyledonae gen. et sp. indet. Wetland habitats were represented by *Pteris oeningensis*, *Podocarpium podocarpum*, *Myrica lignitum*, *Ulmus carpinoides*, cf. *Alnus* sp., *Salix varians*, *Salix* sp. 1., *Populus balsamoides*, *Decodon* sp., *Acer integrilobum*, Asclepiadaceae vel Cucurbitaceae gen. et sp. indet. The zonal vegetation is represented by *Buxus pliocenica*. According to the floristic composition the climate at Gratkorn was subtropical and frost-free. The fossil assemblage is abundant in endemic elements as well as thermophilous ones, e.g. *Podocarpium*.
Results were published in the international journal "Palaeontographica Abt. B." (Scimago rank: Q2).

1.5. Early Oligocene floras of the Tard Clay Formation.

A summary was given on the latest results of the palaeobotanical investigations of Hungarian Early Oligocene floras and was published in the international journal "Hantkeniana" (Scimago rank: Q3).

1.6. Overview of Greguss' fossil wood types.

Initiated by a palaeobotanist from Charles University, Prague, the fossil wood collection made by Greguss Pál and stored by the palaeobotanical collection of the Hungarian Natural History Museum was reviewed and published in the international journal "Fossil Imprint" (Scimago rank: Q3), (Hably involved as co-author).

2. Thermophilous elements in the Cenozoic of the Northern Hemisphere: cycads

During the research period new pieces of information were revealed and published that help to infer the Cenozoic diversity and distribution of cycads (Cycadales) with strong emphasis on their palaeoecology including their climate tolerance and requirements. (Basic information on the background of this research is included at the end of this paragraph.)

2.1. The Cenozoic record of a "Mesozoic" extinct cycad.

Leaves of *Ctenis*, an extinct cycad known formerly from Mesozoic floras, were described from the Eocene of western North America (Clarno Formation, Oregon). Although the leaves are similar in gross form and organization to some other extant and Cenozoic fossil cycads, it differs in its venation, demonstrating an anastomosing pattern. The record of *C. clarnoensis* and other fossil cycad genera with anastomosing venation pattern from the Paleogene implies that an extinct lineage or lineages of cycads previously considered to be restricted to the Mesozoic, may have persisted into

the Paleogene. Some physiognomic features of the leaves of *Ctenis* from the Clarno Formation suggest periodically dry conditions. By the present record the stratigraphic range of *Ctenis* is significantly extended from its previously known latest records in the Early Cretaceous up to as late as the Eocene.
Results were published in the "International Journal of Plant Sciences" (Scimago rank: Q2).

2.2. The first fossil record of the modern cycad genus, *Zamia*
All "*Zamia*" (one of the largest genera of modern cycads) specimens published hitherto in the fossil record were reviewed and the first fossil occurrence of the genus was identified based on foliage remains from Eocene deposits of Panama. Morphological comparisons of macro- and micromorphological traits of modern and fossil cycads proved that the fossil foliage is related to the modern *Zamia* genus. Morphometric analysis adopted for the comparison of the fossil epidermal features with those of modern *Zamia* species (35 species representing all major *Zamia* clades) showed that the fossil foliage is the most comparable to species of the Caribbean clade of the genus. These results also implied new scenarios on *Zamia* evolution. Results were presented in the international conference of cycad biology, CYCAD2015, in Colombia, and have been published by the international journal "Bulletin of Geosciences" (Scimago rank: Q1).

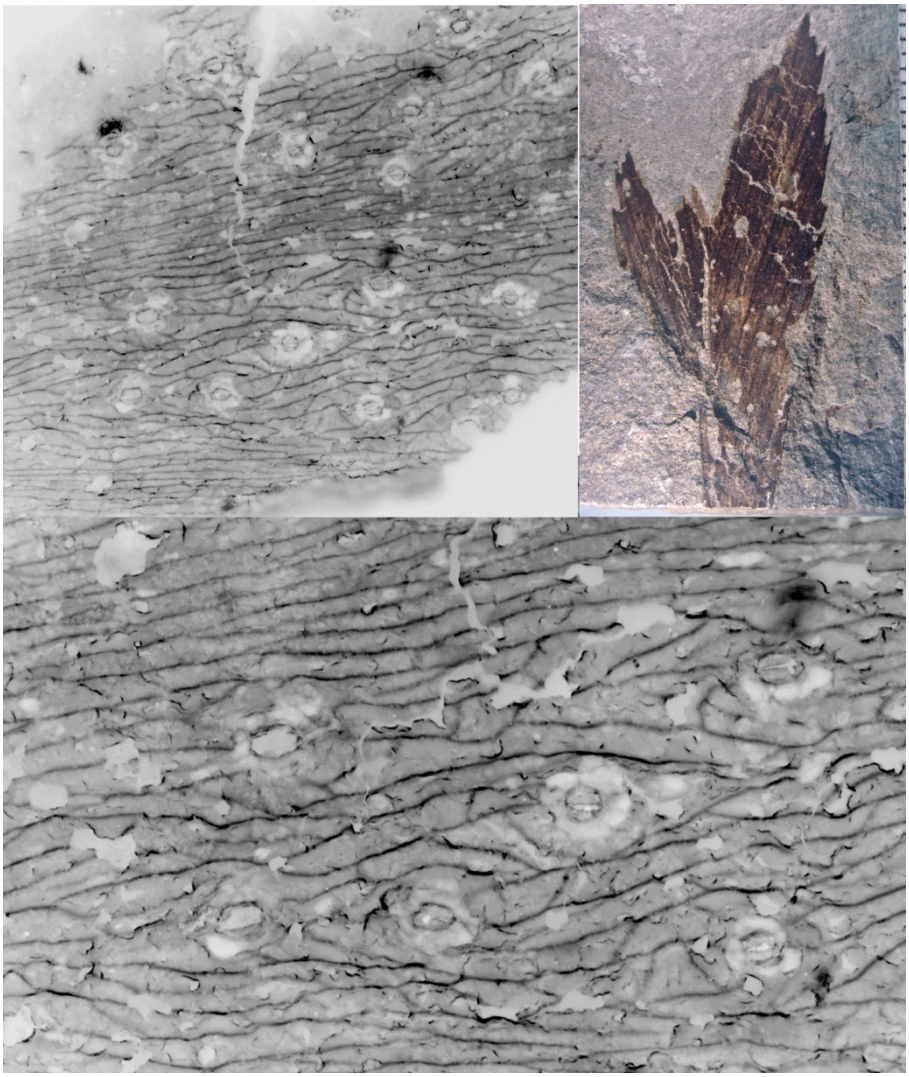
2.3. The first fossil record of a cycad seedling
Exceptional fossils, seedling foliage and an adult specimen of the extinct cycad *Dioonopsis* were described and studied from the early Paleocene Castle Rock flora, Denver Basin, Colorado, USA. Fossils of early ontogenetic stages of plants may preserve morphological characters to facilitate our understanding of the relationships between extinct groups. However, these, especially seedlings, are rarely fossilized. The fossil seedling foliage from the Castle Rock flora is particularly important because it is the first cycad seedling in the fossil record and furthermore, the late and early ontogenetic stages (the seedling and the adult specimens) belong to the same species of the extinct genus *Dioonopsis* (Cycadales) based on shared epidermal micromorphology. The fossil cycad seedling shows characters unknown among modern cycad genera and its phylogenetic analysis implies that extinct lineages of cycads were present and widespread during the early Cenozoic. The apparent scarcity of modern forms in both the Paleogene and Mesozoic fossil record of cycads may be interpreted by a younger evolutionary radiation of modern cycads, as suggested by Nagalingum et al. (2011). The fossil record from the Castle Rock flora further expands the distribution of *Dioonopsis* during the Paleogene. The megafloras accompanying *Dioonopsis* provide information on the ecological tolerance of the genus. The Castle Rock flora has been interpreted as a high diversity, subtropical rain forest (Johnson & Ellis 2002), whereas during the Paleocene, *Dioonopsis* achieved higher palaeolatitudes (the Beringial passage) estimated at 75°–80°N, thus its adaptation to extreme light variations was probably established. Considering these ecological factors, *Dioonopsis* had an ecological tolerance greater than any extant cycad genus. During the study seedlings of modern cycads were studied using the living collection of the Montgomery Botanical Center, Florida, USA and a reference collection was made for the Hungarian Natural History Museum, as well.
Results have been summarized in a paper published "open access" in the international journal "Biology Letters" (Scimago rank: D1).

2.4. Ecological adaptation of *Dioon*: implication of fossils

The ecological adaptation of species of the modern cycad genus *Dioon* and its implications for the evolution of the genus were investigated in cooperation with colleagues of the Naples Botanical Garden, Italy. Some characters, such as the degree of stomatal protection, reflect ecological specializations in species, e.g. volcanic stress. Results suggest that the fossil record of *Dioon* is highly incomplete and many Cenozoic taxa previously associated with the genus need to be reconsidered. A paper was published in the international journal "Botanical Journal of the Linnaean Society" (Scimago rank: Q1) (Erdei involved as co-author).

2.5. The fossil record of the extinct cycad *Eostangeria* from Romania

Based on the study of fossil leaf material from the early Miocene of Romania (Ciocadia Valley) the occurrence of the extinct cycad genus *Eostangeria* was documented. This record attests for a broader stratigraphic and spatial occurrence of this extinct cycad in Europe than it was previously thought. Results will be published in "Studia botanica hungarica" (in progress).



A leaf fragment and cuticular details of *Eostangeria*, an extinct cycad from the early Miocene of Romania (Ciocadia Valley).

***Background of research*:** Cycads (Cycadales) are primitive gymnosperms with species confined today to small, threatened populations in subtropical-tropical regions (Hill 1998-2004 - http://plantnet.rbgsyd.nsw.gov.au), mostly in areas between the Tropics of Cancer and Capricorn. However, cycads were flourishing during the Mesozoic, in both hemispheres (Taylor et al. 2009). Modern cycads have long been seen as the relicts of this formerly flourishing and diverse, thermophilous group of plants (Norstog & Nichols 1997). Challenging the "living fossil" theory, latest molecular phylogenetic studies of modern taxa imply a late Paleogene/Neogene (40-20 million years ago) origin of most modern genera (Nagalingum et al. 2011). Nevertheless, there is only limited amount of fossil data supporting molecular estimations. Approximately half of the modern genera have not been documented in the fossil record and at the same time there are many unknown, extinct genera that have been described from the Cenozoic (Barthel 1976; Hill 1980; Horiuchi & Kimura 1987; Kvaček & Manchester 1999; Erdei et al. 2010, 2012, 2015; Wilf et al. 2016), suggesting a cycad spectrum basically different from both the Mesozoic and the modern ones. It is still unclear how end-Cretaceous extinction and Cenozoic climate cooling affected cycads, which lineages survived the Cretaceous/Paleogene boundary, and when modern forms appeared. The role of cycads in the European Cenozoic floras is also a topic requiring future research.

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***Résumé*:**
The early Miocene (Karpatian) flora of the Mecsek area.

Introduction

The palaeontological research of the Mecsek Mts dates back to decades. Palynological studies were carried out by Nagy (1969). The first floristic study of the Miocene flora of the Mecsek Mts was published by Staub (1882). The relatively few specimens were collected from several sites. The author mentioned the localities Rákpatak-völgy near Ó-Falu, Nádasd, Hidas, Magyar-Hidas, Német-Hidas, Váralja, Puszta-Szobák, Komlóvölgy, Abaliget, Tekeres, and Rákos, which all, except Váralja, represent marl with fish scales. In Váralja, deposits preserving the plant remains were described as quartz-andesitic tuff. The figures showing drawings of the fossil specimens help to recognize some genera and species, i.e. *Pinus*, *Daphnogene* (mentioned as *Cinnamomum* by Staub), *Zizyphus paradisiaca*, *Zelkova zelkovifolia* (*Planera Ungeri* by Staub), *Ailanthus confucii*, *Myrica,* and Leguminosae *gen*. et *sp*. (mentioned as *Cassia* by Staub). The occurrence of these genera and species in the small fossil assemblage suggests that these taxa were frequent members of the Miocene flora of the Mecsek Mts. Unfortunately, many of the drawings could not be identified and the often invalid, old names help their taxonomic assignment neither.

Later Andreánszky (1955) and Pálfalvy (1953, 1961, 1964, 1967) published floristic data of the Miocene Mecsek flora, however, often merely flora lists without figures and descriptions were provided. Nevertheless, a survey of the Mecsek flora has hitherto not been accomplished. In the two decades Hably and her colleagues have made collections. Meanwhile several taxa have been studied and many among them were revised (Hably 1992, 2001, 2002, Hably & Thiébaut 2002). Currently, first of all collections made by Sebe contribute with essential data to our knowledge on the Miocene flora of the Mecsek Mts.

Sampling sites occur at many points of the Mecsek Mts. Most of the fossil specimens (approximately 90%) were collected in the surroundings of Magyaregregy, dominantly from the fish scale marl, but some also from volcanic deposits. Fossils have been preserved in the so-called fish-scale marl in Magyaregregy, Vágyom-völgy; Kisbattyán; Magyaregregy, Leánykői-árok; Magyaregregy, Kisréti-árok; Magyaregregy, Farkasordító-árok; Abaliget, Kiskő-hegy; Abaliget, Nyáras-völgy. Fossils originated from rhiolitic tuff in Magyaregregy, Almás-patak; Kisbeszterce and Hetvehely, Kán. The late Miocene (Pannonian) flora of the Mecsek is not discussed here, details have been provided in papers by Hably (2013), Hably & Sebe (2016), and Hably, et al. (in press).

The main part of the monograph is the Systematic part, in which more than 100 taxa are described and discussed. The Mecsek flora is extremely diverse. Beside the well-known, common species, many rare taxa occur in the assemblage and the number of specimens that could not be identified is high, as well. In order to reinforce future research the unidentified specimens are both discussed and figured. Based on the extremely diverse assemblage, flora and vegetation reconstructions and climatic analysis were made.

Geological settings

The area of the Mecsek is situated in the SW Pannonian Basin, on the Tisza-Dacia Megaunit, a tectonic block south of the Mid-Hungarian Shear Zone. The Neogene stratigraphy of the eastern Mecsek area was summarised by Hámor (1970)

whereas the western part was studied by Chikán (1991) and Barabás (2010). Widespread lower Miocene fluvial clastics, including conglomerates to variegated clays (Szászvár Formation) are overlain by the Budafa Formation, traditionally regarded as of Karpatian (late Burdigalian) age (Gyalog 1996, Gyalog & Budai 2004, Budai et al. 2015), and consisting of three members, the Komló Claymarl Member, Pécsvárad Limestone Member, and the overlying Budafa Sandstone Members. The succession is overlain by Badenian (Langhian) with normal marine Leitha limestones (Lajta Limestone Formation Pécsszabolcs and Rákos Members) in the littoral zone and offshore sands and silts (Tekeres and Szilágy Formations) in the basins, locally with coal-bearing swamp deposits (Hidas Formation) along the shores.

Most of the fossil plant remains were fossilized in the Komló Claymarl Member („fish-scale bearing clay marl). It is composed of dark grey, greenish-grey, massive or laminated silty clay marl, calcareous silt and fine sands, with numerous fish scales and bones, and sometimes with tuff interbeds. K/Ar dating measurements from tuff interbeds within the Komló Claymarl showed an age of 16.82±0.65 Ma, i.e. Karpatian (late Burdigalian) (Sebe et al. 2019).

The absence of marine forms in the Pécsvárad Limestone and in most part of the Komló Claymarl indicates the lack of connections to normal salinity seas thus these rocks are lacustrine deposits (Sebe et al. 2019). The lake sediments and the fauna suggest that instead of a system of smaller lakes a contiguous water body, called „Lake Mecsek" existed in the area. A Karpatian to Early Badenian age of the lake is indicated according to the K/Ar age and biostratigraphic dating of the overlying marine deposits described above (Sebe et al 2019). The Pécsvárad and Komló Members are both interpreted as lake deposits and differ very much from the Budafa Sandstone Member, therefore Sebe et al (2019) united the two members as a separate formation, the Feked Formation.

Consequently, the „fish scale-bearing clay marl" sediments preserving the plant fossils belong to the Feked Formation, Komló Claymarl Member, dated as Karpatian (late Burdigalian) (Sebe et al. 2019).

Material and methods

Fossil specimens are dominantly impressions of leaves but fruits and seeds, mainly winged ones, also frequently occur. Impressions are generally well preserved in the fish-scale marl owing to the fine-grained sediment, however cuticles are not or only poorly preserved not suitable for cuticular analysis. In some cases twigs with some leaves or rarely with leaf and fruit remains are observable. A fossil flower is an exceptional remain with the stamens, both the theca and filaments, having been fossilized, however no pollen preserved. In addition to the plant fossils, numerous fish scales are observable, the name of the sediment also referring to these findings, and insect fossils have also been recovered during collecting.

The largest collection from the Miocene of the Mecsek, nearly 10.000 specimens, is stored in the palaeobotanical collection of the Hungarian Natural History Museum, inventoried as "HNHM-PBO". A smaller assemblage collected by Pálfalvy is stored in the collections of the Mining and Geological Survey of Hungary inventoried as "BK".

Fossil remains were studied using macromorphological methods. Descriptions followed Dilcher (1974) and Ellis et al. (2009). For microscopic studies an Olympus SZX9 dissecting microscope and a Nicon Eclips E600 microscope were used.

The Karpatian (late early Miocene) flora of the Mecsek Mts

The Miocene flora of the Mecsek is dominated by angiosperms and gymnosperms, whereas pteridophytes are subordinate elements. Among gymnosperms *Glyptostrobus europaeus* (Brongniart) Unger of the family Cupressaceae s.l. played the most significant role occupying swamp habitats as a typical element, though considering the entire flora the species was not dominant. Other representatives of the family Cupressaceae s.l., Cupressaceae gen. et sp. and *Tetraclinis salicornioides* (Unger) Kvaček were also recorded as rare accessory elements. Among Pinaceae, needles (two and three per fascicle) and seeds of *Pinus* and *Abies* were also described. Angiosperms predominate in the flora. Among Lauraceae the most important taxon is *Daphnogene* but other taxa described as *Laurophyllum* are also present. One species of this genus, *Laurophyllum markvarticense* Kvaček was identified based on cuticular analysis. Besides leaf remains a lauraceous fruit, *Laurocarpum* sp. was also recorded. The family Berberidaceae is also present as accessory element in the flora with *Berberis andreanszkyi* Kvaček & Erdei and *Mahonia*. The family Altingiaceae is represented by few remains of *Liquidambar europaea* Al. Braun, which is the first occurrence of the species in the Hungarian fossil floras. Later, during the middle Miocene (Sarmatian) the species became widespread in Northern Hungary, and during the late Miocene (Pannonian) it predominated the riparian vegetation through the Carpathian Basin. The family Betulaceae is represented by one genus, *Ostrya***,** with both leaves and involucres. From the family Fagaceae, *Fagus, Quercus kubinyii* and *Quercus drymeja* Unger were recorded. This is the first Hungarian occurrence of *Q. kubinyii*, which later became dominant in the Sarmatian floras of Northern Hungary. The family Theaceae is represented by a rare species *Ternstroemites pereger* described from the coeval flora of Parschlug, and with an endemic species, *Gordonia mecsekensis,* represented by winged fruits. The presence of the family Myricaceae is evidenced by the leaves of *Myrica lignitum*, which was a dominant element of the swamp vegetation. The family Juglandaceae played a significant role in the flora and vegetation. Besides the frequent species of Miocene floras, *Engelhardia orsbergensis* and *E. macroptera*, *Carya serrifolia* and other not identifiable species of the family, mentioned as Juglandaceae *gen*. et *sp*.1. and *sp*.2. were also recorded. The Tiliaceae family is present with *Tilia* sp. and *Craigia bronnii* as rare accessory elements. The family Ulmaceae shows high diversity, with dominant species of *Cedrelospermum*, *C. flichei* and *C. aquense*. In addition, *Zelkova zelkovifolia* is also present, first with such high number of specimens in the fossil record of Hungary. The genus *Ulmus* is proved by the species, *Ulmus braunii,* and other, not identifiable leaf and fruit remains of the genus. Members of the family Salicaceae are rare accessory elements with some species of *Populus.* Among them *Populus populina* and *P. balsamoides* show their first occurrence in the Hungarian fossil record as rare elements. The species *Populus populina* became widespread and dominant later in the late Miocene (Pannonian) (Hably 2013). Another species, *Populus zaddachii*, is a rare element, occurring in Hungary exclusively in the Miocene flora of the Mecsek Mts. The presence of the genus *Populus* is evidenced by its leaf, fruit, and catkin remains. Members of the Buxaceae family represented by the genus *Buxus* are rare accessory elements of the flora, likewise the Rosaceae family with the genus *Rosa* and the species *Prinsepia serra*. This latter is a rare species in Europe, first described from the flora of Parschlug (Kovar-Eder et al. 2004). This is the first occurrence of the species in Hungary. The Celastraceae family has few and uncertain occurrences in the Mecsek flora. The family Fabaceae is quite diverse in the flora with some dominant, characteristic taxa. Among them the species *Podocarpium podocarpum* predominates the flora having mainly leaflets, but also leaf and fruit

(pod) remains. Nearly all fossil sites of the Miocene Mecsek flora yielded high number of leaflets identified as Leguminosae gen. et sp. A fruit described as *Leguminocarpum mecsekense* is a characteristic element of the flora, and two species, *Acacia parschlugiana* and *Leguminosites palaeogaeus* occur as rare accessory elements. The family Thymelaeaceae is represented by the rare accessory element, *Daphne oeningensis*. *Zizyphus paradisiaca* is the most important species of the Rhamnaceae family and it is a dominant and characteristic element of the flora. In addition two species, *Paliurus favonii* and *Berchemia multinervis* are rare accessory elements of the flora. The Sapindaceae family is represented by the genus *Acer*. Its fruit remains outnumber leaf remains which may be attributable to long distance transport. From the family Anacardiaceae *Cotinus sp.*and *Rhus sp.*are present with small number of specimens. At the same time the family Simaroubaceae is significant with only one genus, *Ailanthus*. The fruit, *Ailanthus confucii* and leaflets of *Ailanthus mecsekensis* occur with high number of specimens, therefore dominant elements of the flora. The family Ebenaceae is represented by the reproductive structures described as *Diospyros*? *microcalix*. Members of the Malvaceae family are rare elements of the flora with *Sterculia* sp., *Tilia* sp., *Craigia bronnii*, and leaves described as *Dicotylophyllum* sp 1. The family Oleaceae is subordinate in the flora with some fruits of cf. *Fraxinus* sp. The presence of the family Apocynaceae is noteworthy with accessory remains of *Nerium* sp. This is the first occurrence of the genus in Hungary but earlier it was mentioned from the coeval flora of Parschlug (Kovar-Eder et al. 2004). The family Nyssaceae is noteworthy having leaf remains of several species, i.e. *Nyssa gyoergyi* n.sp., *Nyssa gergoei* n. sp., *Nyssa* sp. 1. , cf. *Nyssa* div. sp. and fruits as well. The family Ranunculaceae is represented by the species *Clematis csabae,* members of the family Ericaceae were recorded as leaf remains of *Arbutus* sp.

Among monocots noteworthy taxa are *Smilax* cf. *weberi* of the family Smilacaceae, *Cladiocarya* sp. of the family Cyperaceae, and leaves of *Palmacites* of the family Arecaceae. Several monocot remains mentioned as Monocotyledonae gen. et sp. were collected the closer affinities of which are uncertain.

Several species were recorded in the Mecsek flora which had their first Hungarian occurrence. Some of them are of high significance, such as *Quercus kubinyii, Podocarpium podocarpum*, *Liquidambar europaea,* and *Populus populina,* which became dominant in the middle Miocene (Sarmatian) floras and even later during the late Miocene (Pannonian) were significant members of the riparian vegetation (Hably 2013, 2014). Considering the Hungarian fossil floras, the genera *Cedrelospermum* and *Zizyphus* had their last occurrence, i.e. *Cedrelospermum aquense, Cedrelospermum flichei*, and *Zizyphus paradisiaca*. The first and often the only Hungarian appearance of some species were recorded in the Mecsek which are rare even in the European Miocene, i.e. *Ternstroemites pereger*, *Prinsepia serra, Populus zaddachii, Antholites stiriacus.*

There are also endemic species, e.g. *Leguminocarpum mecsekense, Ailanthus mecsekensis, Nyssa gyoergyi* n.sp., *Nyssa gergoei* n. sp., *Nyssa* sp. 1. , *Clematis csabae, Gordonia mecsekensis, Carpolithes gergoei*.

The Karpatian assemblage of the Mecsek Mts is an extremely diverse flora with more than a hundred taxa outnumbering most of the well-known Miocene floras of Europe.

Vegetation of the Mecsek Mts in the Karpatian

The ecological requirements of plant taxa indicate the habitats they occupied and the vegetation type in which they flourished. Based on the Mecsek fossil

assemblage four main types of vegetation can be distinguished. The swamp vegetation included arboreal, shrub, and herbaceous plants, as well. Arboreal taxa of swamps were *Glyptostrobus europaeus, Myrica lignitum*, and *Nyssa*. The shrub level was composed of *Myrica*, whereas close to open water rich stands of herbaceous monocots must have thrived. Only few remains of *Salvinia*, Ceratophyllaceae, and *Cladiocarya* reflect aquatic vegetation. Another edaphic vegetation type was the riparian vegetation. In low riparian habitats *Populus* and *Carya*, in higher level habitats *Acer* and *Ulmus* formed arboreal vegetation. In wetland habitats *Liquidambar europaea* was a member of vegetation. Further from wetlands the zonal vegetation was composed of a probably drought-tolerant subxerophytic vegetation with numerous plant taxa, i.e. *Zizyphus paradisiaca*, *Cedrelospermum*, *Ailanthus*, *Buxus*, *Berberis*, *Mahonia*, *Rosa*, *Prinsepia serra*, Celastraceae, *Paliurus*, *Cotinus*, *Rhus*, *Nerium*, *Arbutus*. The family Fabaceae was represented in the zonal vegetation by *Acacia parschlugiana*, *Leguminosites palaeogaeus*, *Leguminocarpum mecsekense, Gleditsia,* Leguminosae gen. et sp.. *Gordonia mecsekensis* was probably also a member of this vegetation. Presumably, the arboreal zonal vegetation was not dense but rather parkland-like, which is supported by the fact that a significant part of the arboreal species develop winged fruits or seeds. Anemochor fruit and seed types are more frequent in open vegetation types due to more effective dispersal (Erdei & Hably 2000, Erdei et al. 2012). Influenced by local geomorphology and by other factors determining microclimate, definitely dry habitats were presumably formed, which is supported by the presence of taxa, e.g. *Buxus*, *Berberis*, *Mahonia*, *Rosa*, *Prinsepia serra*, Celastraceae, *Paliurus*, *Cotinus*, *Rhus*, *Nerium*.

Presumably, a vegetation type with higher rainfall requirements was also formed relatively close to the Lake Mecsek but not in the wetlands. Members of this vegetation were some lauraceous taxa, i.e. *Daphnogene*, *Laurophyllum*, the evergreen thermophilous *Engelhardia* of the Juglandaceae family*, Palmacites* and many other exotic taxa. Liana, e.g. *Smilax*, *Clematis* were also members of the forest vegetation. The fabaceous species, *Podocarpium podocarpum* presumably thrived in this vegetation, although it occurs in European floras suggesting relatively broad intervals of climate values. In the late middle Miocene (late Sarmatian) flora of Gratkorn (Austria) it is a member of a definitely wetland type of vegetation (Hably & Meller 2017), whereas in the nearly coeval Sarmatian flora of Erdőbénye (Hungary) *Podocarpium* is a predominant member of a vegetation suggesting definitely dry climate conditions (Kováts 1856, Erdei 1995).

Late early Miocene Climate of the Mecsek

Based on the climate requirements of plants, fossil floras can be applied in climate reconstructions. However, members of the azonal or edaphic associations are less suitable for the estimation of past climate conditions since the occurrence of such vegetation is influenced by local, e.g. soil factors. Most of the plant taxa of the Mecsek flora were members of the zonal vegetation thus they are suitable for a climate reconstruction. The ratio of Palaeotropical elements, which were definitely warm demanding members of the flora, was very high, i.e. *Daphnogene*, *Laurophyllum*, Lauraceae, *Engelhardia*, *Cedrelospermum*, *Ailanthus*, and some species of the Fabaceae family that were dominant or frequent elements of the flora. Additional thermophilous elements were *Ternstreomites*, *Smilax*, *Palmacites*, and members of Malvaceae and Theaceae.

Although edaphic associations are less suitable for climate reconstructions these also suggest climate conditions to a certain degree. Regarding temperature

requirements they are informative, however due to the usually abundant water supply amount and distribution of rainfall are not limiting factors.

In Magyaregregy, the swamp elements attest for a definitely warm climate. The forests composed of *Glyptostrobus – Nyssa- Myrica* must have been formed in warm climate conditions. As modern analogue, the *Taxodium* forests of Florida can be mentioned. Based on the above a warm-subtropical climate is assumed in the Miocene of the Mecsek Mts. According to the quantitative climate analysis (Erdei et al. 2007) of the Magyaregregy flora, the mean annual temperature was 15.6-16.6 ^{o}C, temperature of the coldest and warmest months were 5-6.2 ^{o}C, and 24.7-27.9 ^{o}C, respectively. Although the above analysis was based on a preliminary, incomplete list of taxa, estimated climate values characterize well the palaeoclimate. The reconstruction of rainfall and its distribution is more complicated. The flora represents riparian forests, subtropical laurel forests, deciduous forests with low rainfall demand, and even taxa appear that are characteristic of dry habitats, e.g. *Buxus*, *Berberis*, *Mahonia*, *Rosa*, *Prinsepia serra*, Celastraceae, *Paliurus*, *Cotinus*, *Rhus*, *Nerium*, *Arbutus*. *Zizyphus paradisiaca*, *Cedrelospermum* and *Ailanthus* may be also mentioned here. *Cedrelospermum* must have had a broad climatic tolerance; it was present in floras ranging from tropical or subtropical rain forests, e.g. Clarno Formation in Oregon, to seasonally dry tropical forests, e.g. Green River Formation in Colorado (Manchester 1989), Céreste in France, Tard Clay Formation in Hungary (Hably & Thiébaut 2002).

This implies that rainfall was not evenly distributed but seasonal dry periods occurred during the year and habitats with seasonal water supply were present. Vegetation was rather subxerophytic, not xerophytic. Periodical dry seasons were replaced by rainy seasons with abundant rainfall, which meant a water supply enough both for the extended swamp and riparian vegetation, and the zonal vegetation.

Estimation of the mean annual precipitation shows broad intervals between 823 and 1356 mm (Erdei et al. 2007). This may be attributable to the presence of diverse associations, both zonal and azonal vegetation types, in the taphocoenosis.

Leaf morphology indicates both humid and dry habitat types. Large leaves and the occurrence of attenuate leaf apex imply warm and humid climate, e.g. *Dicotylophyllum* sp.1. and many specimens belonging to the Lauraceae family. Dry climate conditions may be indicated by the small size of leaves, e.g. *Buxus*, the occurrence of narrow, entire margined leaves, e.g. *Nerium* or the coupled appearance of small leaf size and toothed margin with teeth having attenuate or spinose apices, e.g. *Berberis*, *Mahonia*, *Rosa*, *Prinsepia serra, Quercus kubinyii*.

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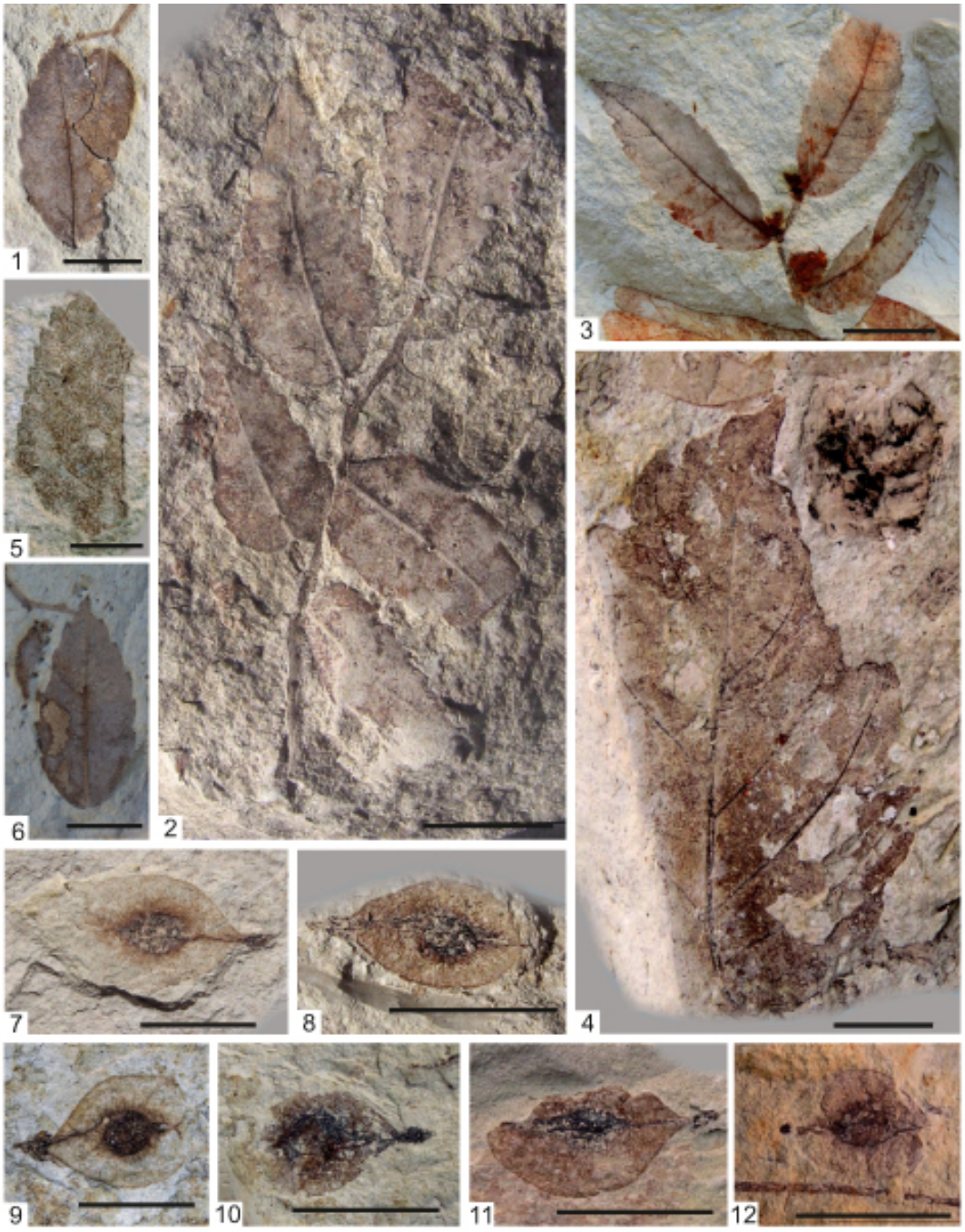

Plate 6. *Zelkova zelkovifolia*, leaves, (1-6); *Ulmus* sp., fruits, (7-12);