Fossil *Gordonia* (s.l.)–like (Theaceae) winged seeds from the early Miocene of the Mecsek Mts, W Hungary

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Abstract

Winged seeds were recovered from two sites of the late early Miocene (Karpatian) flora of Magyaregregy, Mecsek Mts, W Hungary. The seeds are assigned to the fossil-genus and species, *Mecsekispermum gordonoides* Hably and Erdei gen. nov. et sp. nov., and are tentatively related to the family Theaceae. Based on the overall character of the winged seeds and the isodiametric surface pattern of the seed coat, the seeds are most comparable with species of *Gordonia* J. Ellis (s.l.) in Theaeae (*Laplacea* Kunth or *Polyspora* Sweet). A comparison with winged seeds of other fossil genera, e.g. *Saportaspermum* Meyer and Manchester, and winged seeds of modern genera in various families is also given. The fossil flora is preserved in the fish scale-bearing clay marl belonging to the Feked Formation and Komló Claymarl Member and dated as Karpatian (late Burdigalian, standard chronostratigraphy).

Keywords Fossil flora · Magyaregregy · *Saportaspermum* · *Mecsekispermum* · Fish scale-bearing clay marl · Karpatian

Introduction

Winged fruits or seeds have frequently been reported in the European fossil record. Disseminules having an apical or lateral wing have been described variously as *Cedrelospermum* Saporta, *Gordonia* J. Ellis, *Saportaspermum* Meyer and Manchester, or *Embothrites* Unger and have been assigned to various plant groups, e.g. Ulmaceae, Theaceae, and Malvales (Unger 1850; Manchester 1987; Meyer and Manchester 1997; Kvaček and Walther 1998; Kvaček and Wilde 2010). Fruits or seeds assigned to Theaceae are rare not only in the European fossil record but also worldwide. Grote and Dilcher (1989, 1992) gave a summary of fossil specimens reported as remains of Theaceae. The earliest fossil fruits assigned to *Gordonia* (*Gordonia lamkinensis* Grote and Dilcher and *Gordonia warmanensis* Grote and Dilcher) were described from the middle Eocene Claiborne flora in

Kentucky and Tennessee (Grote and Dilcher 1992; Martínez-Millán 2010).

The classification of the family Theaceae varied in many authors, according to the characters emphasised (Prince and Parks 2001). In the Cronquist system, the family involves ~40 genera and 600 species in four subfamilies (Cronquist 1981). Molecular data showed the family as non-monophyletic (e.g. Morton et al. 1996; Soltis et al. 2000), and APG (1998) suggested a narrow definition of the family with Theaceae s.str. and a separate Ternstroemiaceae (Ternstroemieae in Pentaphylacaceae). Based on molecular data, three main lineages of Theaceae s.str. were identified, i.e. Theaeae, Stewartieae, and Gordonieae (Prince and Parks 2001). According to the same study, the monophyly of the genus *Gordonia* was not supported, and sequence data placed its species in Gordonieae (*Gordonia* s. str.) and Theaeae (*Laplacea* Kunth and *Polyspora* Sweet). Although a common character of the seeds of *Gordonia* s.l. species is a prominent flattened apical wing, micromorphological study of the seed coat was used to corroborate the above placement of *Gordonia* s.l. species (Gunatillake et al. 2015).

Leaves of Theaceae have been reported from some localities in the Northern Hemisphere fossil record during the Cenozoic. Today the area of the family occupies subtropical-tropical Asia and America (Prince and Parks 2001); however, palaeofloristic data indicate the presence of the family also in Europe. Leaf records of Theaceae (s.l.) have been documented

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in the European floras from the middle Eocene up to the late Miocene. From the middle Eocene flora of Messel (Germany; Wilde 1989) and from the early Oligocene flora of Flörsheim (Mainz Basin, Germany; Kvaček 2004), leaves of two genera, *Gordonia* and *Ternstroemites* Berry, were mentioned. Leaves preserved with cuticle were reported as *Gordonia hradekensis* (Kvaček and Bůžek) Božukov and Palamarev, *Gordonia pseudoknauensis* Kvaček, and *Ternstroemites floersheimensis* Kvaček and Walther from the rich, thermophilous flora. From the early Miocene flora of Hrádek (North Bohemia, Czech Republic; Holy et al. 2012) and from the flora of the Cyprus Shale (Western Bohemia, Czech Republic; Bůžek et al. 1996), leaf remains of *Gordonia hradekensis* were mentioned. From the early Miocene (Ottnangian) flora of Köflach (Austria) ?*Gordonia oberdorfensis* Kovar-Eder and ?*Cleyera schilcheriana* Kovar-Eder (Kovar-Eder and Meller 2001) were described based on leaf remains and preserved cuticle. From the late early/early middle Miocene flora of Parschlug (Austria; Kovar-Eder et al. 2004), there are also some leaves assigned to Theaceae, cf. ?*Gordonia oberdorfensis* and *Ternstroemites pereger* (Unger) Kovar-Eder and Kvaček. From the middle Miocene (Badenian) of the Satovcha Graben in the Western Rhodopes (Bulgaria), Božukov and Palamarev (1995) described a flora as a rich refuge of the representatives of Theaceae (s.l.), e.g. *Eurya* aff. *acuminatissima* Merrill and Chun, *Gordonia hradekensis*, *Gordonia stefanovii* Palamarev and Božukov, *Hartia palaeorhodopensis* Božukov and Palamarev, *Stewartia stefanovii* Palamarev and Božukov, and *Stewartia submonadelpha* Tanai and Onoe. In Europe, Theaceae presumably survived up to the late Miocene or Pliocene based on reports from the Sessenheim flora in France (Geissert et al. 1990), Fritzlar (Hessen) in Germany (Hottenrott et al. 1996), and refuge areas of the Pannonian Basin. A rich late Miocene thermophilous flora was described from Mataschen (Austria, Kovar-Eder and Hably 2006) with four species assigned to Theaceae. *Gordonia emanuelii* Kovar-Eder, *Gordonia panonica* Kovar-Eder, *Gordonia styriaca* Kovar-Eder, and *Schima mataschensis* Kovar-Eder were described based on leaf remains with cuticle. The flora of Magyaregregy also yielded leaf remains described as *Ternstroemites pereger*, which may be related to the Theaceae (s.l.) family (Hably 2020).

Geology

The area of the Mecsek Mts 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 Mecsek area was summarised by Hámor (1970), Chikán (1991), and Barabás (2010, 2011). Widespread lower Miocene fluvial clastics (Szászvár Formation) are overlain

by the Budafa Formation, traditionally regarded as of Karpatian (late Burdigalian) age (Gyalog 1996; Gyalog and Budai 2004; Budai et al. 2015). The Budafa Formation consisted of three members, the Komló Claymarl Member, Pécsvárad Limestone Member, and the overlying Budafa Sandstone Members. The succession is overlain by Badenian (Langhian) Leitha limestones in the littoral zone and offshore sands and silts in the basins, locally with coal-bearing swamp deposits along the shores. Based on the absence of marine fossils in the Pécsvárad Limestone and in most part of the Komló Claymarl, Sebe et al. (2019) concluded that these rocks are lacustrine deposits. As suggested by the lake sediments and its fauna, instead of a system of smaller lakes, a contiguous water body, called “Lake Mecsek”, existed in the area from the Karpatian up to the early Badenian according to K/Ar age and biostratigraphic dating of the overlying marine deposits (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 and Komló Claymarl Member, dated as Karpatian (late Burdigalian) (Sebe et al. 2019). 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).

Palaeontological research of the Mecsek Mts dates back to decades, attested by numerous studies, e.g. nannoplankton (Báldi-Beke 1963), foraminifers (Korecz-Laky 1968), and palynology (Nagy 1969). After floristic works published by Staub (1882), Andreánszky (1955), and Pálfalvy (1953, 1961, 1964, 1967), Hably L. and her colleagues have contributed with studies to the knowledge on the Miocene flora of the Mecsek Mts (Hably 1992, 2001, 2002; Hably and Thiébaud 2002). A monographic study of the plant fossils of Magyaregregy is going to be published by Hably (2020). The Magyaregregy flora is extremely diverse with more than 100 taxa hitherto described, including *Glyptostrobus europaeus* (Brongniart) Unger, *Zizyphus paradisiaca* (Unger) Heer, *Daphnogene cinnamomifolia* (Brongniart) Unger, *Laurophyllum* sp., *Myrica lignitum* (Unger) Saporta, *Engelhardia orsbergensis* (P. Wessel and C. O. Weber) Jähnichen, Mai and Walther, *Cedrelospermum flichei* (Saporta) Hably and Thiébaud, *C. aquense* Saporta, *Zelkova zelkovifolia* (Unger) Bůžek and Kotlaba, legumes (*Podocarpium podocarpum* (A. Braun) Herendeen, Leguminosae gen. et sp.), *Ailanthus confucii* Unger, and *Ailanthus mecsekensis* Hably.

The first Hungarian occurrence of some taxa was recorded in this flora, such as *Quercus kubinyii* (Kováts ex Ettingshausen) Czecczot, *Podocarpium podocarpum*, *Liquidambar europaea* A. Braun, and *Populus populina* (Brongniart) Knobloch. Some rare elements are noteworthy as well, such as *Ternstroemites pereger* (leaves, Theaceae), cf. *Prinsepia serra* (Unger) Kovar-Eder and Kvaček, *Populus zaddachii* Heer, *Antholites stiriacus* Kovar-Eder and Kvaček, and some *Nyssa* L. species. The ratio of warm elements in the flora seems to be considerably high, and a warm subtropical climate is assumed in the early Miocene of the Mecsek Mts (Erdei et al. 2007; Hably 2020).

Material and methods

The fossil seeds (14 specimens) are preserved mostly as impressions in the fish scale-bearing clay marl. Owing to the fine-grained sediment, morphological details of some seeds are well-preserved. Fossils are stored in the palaeobotanical collection of the Hungarian Natural History Museum, inventoried with an epithet “HNHM-PBO”. For microscopic studies, an Olympus SZX9 dissecting microscope equipped with an Olympus DP72 digital camera was used. For comparisons, modern seed material of the herbarium of the HNHM and digitized herbarium material through JSTOR Global Plants (<https://plants.jstor.org>) were used (Royal Botanic Gardens Kew; Conservatoire et Jardin botaniques de la Ville de Genève; Queensland Herbarium; Royal Botanic Garden Edinburgh; Herbarium Trinity College, Dublin; Botanische Staatssammlung München; National Botanic Garden of Belgium; Herbarium of the Arnold Arboretum; Herbarium Museum Paris; Muséum National d’Histoire Naturelle; Singapore Botanic Gardens).

Results: systematic part

?Theaceae Ker Gawler, *nom. cons.*

?Theaceae Szyszlowicz.

Mecsekispermum Hably and Erdei, gen. nov.

Type species: *Mecsekispermum gordonoides* Hably and Erdei, sp. nov.

Etymology: The generic name refers to the geographic location, the Mecsek Mountains, where the fossil seeds were collected and *spermum* (= seed, Greek).

Diagnosis: Winged seed, consisting of asymmetric, elongate ovate seed body and an apical, flattened, elongate wing. Wing swelling on ventral side (ventral side concave). Wing distally rounded. Wing without veins, scars or any ornamentation, wing margin smooth. Seed body oriented with long axis at

about 20° angle to long axis of wing. Basal part of seed body rounded, apical part acute, pointed.

Mecsekispermum gordonoides Hably and Erdei, sp. nov.

Holotype: HNHM-PBO 2017.98.1; here designated; Fig. 1a–b

Repository: Hungarian Natural History Museum, Palaeobotanical collection (HNHM-PBO), Budapest, Hungary

Paratypes: HNHM-PBO 97.142.1, HNHM-PBO 2007.22.1, HNHM-PBO 2017.100.1, HNHM-PBO 2017.101.2, HNHM-PBO 2019.14.1; Fig. 1c–f, h

Repository: Hungarian Natural History Museum, Palaeobotanical collection (HNHM-PBO), Budapest, Hungary

Etymology: The species name refers to the similarity of the seeds to those of *Gordonia* s.l. species.

Type horizon and locality: Outcrop near the village Magyaregregy, Baranya County, Mecsek Mts, Hungary; fish-scale-bearing clay marl, Feked Formation, Komló Claymarl Member, dated as Karpatian (late Burdigalian).

Additional material: Magyaregregy: HNHM-PBO 2017.97.1, HNHM-PBO 2017.142.2, HNHM-PBO 2018.251.2, HNHM-PBO 2018.258.1, HNHM-PBO 2018.291.1, HNHM-PBO 2018.369.1; Magyaregregy, Vágyom-völgy: HNHM-PBO 2017.156.1, HNHM-PBO 2017.157.2; Fig. 1g.

Repository: Hungarian Natural History Museum, Palaeobotanical collection (HNHM-PBO), Budapest, Hungary.

Diagnosis: Winged seed, consisting of asymmetric, elongate ovate seed body and apical, flattened, elongate wing. Length of winged seeds 0.9–1.7 cm, width up to 0.6 cm, wing distally rounded. Wing swelling on ventral side (ventral side concave). Wing without scars, veins or any ornamentation, wing margin smooth. Length of seed body up to 0.7 cm, width up to 0.25 cm, oriented with long axis at about 20° angle to long axis of wing. Basal part of seed body rounded, apical part acute. Surface cell pattern of seed coat on wing isodiametric, without ridges or protrusions.

Discussion

The remains are most probably seeds suggested by the lack of veins on the wing (see argumentation by Meyer and Manchester 1997). Some of the seeds (e.g. the holotype, HNHM-PBO 2017.98.1; Fig. 1a–b) show a somewhat angular seed body which may refer to its development in a fruit. The dorsal margin of the wing seems to be more thickened than the ventral margin.

Winged fruits or seeds showing comparable gross morphology to *Mecsekispermum* seeds (i.e. equipped with an apical or lateral wing) have been variously described in the fossil record as *Cedrelospermum*, *Gordonia*, *Saportaspermum*, or

Fig. 1 **a–h** Winged seeds of *Mecsekispermum gordonii* Hably and Erdei gen. nov. et sp. nov. from the early Miocene of Magyaregregy, Mecsek Mts (Hungary). **a–b** holotype HNHM-PBO 2017.98.1, **b** Enlargement of seed body of holotype. **c–d** paratype HNHM-PBO

2017.100.1, **d** Isodiametric surface cell pattern of seed coat on wing. **e** paratype HNHM-PBO 2007.22.2. **f** paratype HNHM-PBO 97.142.1. **g** HNHM-PBO 2018.251.2. **h** paratype HNHM-PBO 2017.101.2. Scale bar (a, c, e–h) 1 cm, (b) 5 mm, (d) 1 mm

Embothrites (Unger 1850; Manchester 1987; Meyer and Manchester 1997; Kvaček and Walther 1998; Kvaček and Wilde 2010). Seeds were described as cf. *Gordonia* sp. in Kundratice (Czech Republic), but Kvaček and Walther (1998) noted that similar seeds have been described as *Saportaspermum occidentale* Meyer and Manchester from the Oligocene Bridge Creek flora of OR, USA (Meyer and Manchester 1997). Later, Kvaček and Walther (2004) described winged seeds resembling the material from Kundratice as *Saportaspermum* sp. from the nearby locality of Bechlejovice (Czech Republic) and noted that “Similar seeds are produced by various Sterculiaceae (e.g. *Reevesia* Lindl.)”. The seeds described from Kundratice as cf. *Gordonia* sp. and from Bechlejovice as *Saportaspermum* sp. show similar morphology and most probably represent the same species of *Saportaspermum*. This is supported also by the fact that sediments of the two localities represent the same formation (Ústí Formation) of the České Středohoří (Cajz 2000); they are coeval, early Oligocene and floristically quite similar in sharing many taxa (Teodoridis and Kvaček 2015). Studies published later assign *Saportaspermum* to the Malvaceae family (Kvaček 2006), but its taxonomical position is uncertain. This extinct genus was typified with *Saportaspermum occidentale* (Meyer and Manchester 1997) from North America.

Seeds similar to *Saportaspermum* were mentioned from several Miocene floras under various names, e.g. *Embothrium parschlugianum* Ett. (Ettingshausen 1890) from Schönegg and Parschlug (Austria) and *Embothrium sotzkianum* (Unger) Ettingshausen and *E. salicinum* (Ettingshausen) Heer (Ettingshausen 1888) from the Leoben area (Austria). From Kymi (Greece), small winged seeds, originally published as *Embothrium salicinum*, were revised by Velitzelos et al. (2002) as *Saportaspermum* sp. Seeds of larger size than the above species were described as *Saportaspermum dieteri* Kvaček and Walther and *Saportaspermum kovacsiae* Kvaček and Wilde from the early Oligocene flora of Seifhennersdorf (Germany) and from the Eocene floras of Lábátlan (Hungary), Kučlín (Czech Republic), and Messel (Germany), respectively (Kvaček and Wilde 2010). These seeds were assigned to malvacean plants (Walther and Kvaček 2007, Kvaček and Wilde 2010).

In the flora of Parschlug (Austria), there are several specimens of *Saportaspermum* varying in morphology (Kovar-Eder et al. 2004). All the seeds mentioned above show characters similar to *Saportaspermum*, described by Meyer and Manchester (1997). We refrain to accommodate winged seeds from Magyaregregy in this genus since their morphological traits differ from characters mentioned in the protologue of *Saportaspermum* (Meyer and Manchester 1997). In *Saportaspermum* seeds, the seed body is more rounded contrasting the elongate ovate seed body of *Mecsekispermum*. In *Saportaspermum*, the

ventral and dorsal margin of the wing are more or less parallel contrasting *Mecsekispermum* seeds, in which the wing is swelling (rounded) on the ventral side of the seed giving a concave appearance to the ventral wing margin. In *Mecsekispermum* seeds, the wing is oriented with its long axis at a very shallow angle (up to 20°) to the long axis of the seed body contrasting seeds of *Saportaspermum* displaying larger angles (30–40°). Although seeds assigned to *Saportaspermum* may represent various plant groups, many of them seem to represent malvacean plants (Kvaček and Wilde 2010).

Samaras of *Cedrelospermum* (Ulmaceae, also occurring in Magyaregregy, see in Hably 2020) are different in showing a characteristic V-shaped stigmatic notch distally, in having, though not always, a secondary wing and subparallel veins converging towards the distal end of the wing (Manchester 1987).

Specimens described as *Embothrites borealis* Unger from the Eocene flora of Socka (Unger 1850) has rounded seed body, and the wing showing fine dichotomous venation is attached to the seed with a neck contrasting *Mecsekispermum* seeds. Some of the *E. borealis* specimens (Unger 1861) were transferred to the ulmaceous genus *Cedrelospermum* (Manchester 1987).

Fossil seeds along with the leaves of *Cedrela* P. Browne (*C. merrillii* (Chaney) Brown) were described by Meyer and Manchester (1997) from the Oligocene Bridge Creek flora in Oregon (North America). These seeds show similarities to the seeds of *Mecsekispermum* in the attachment of the seed body and wing; however, they are quite variable in the form of seed body and wing contrasting seeds from the Mecsek. The fossil *Cedrela* seeds show the characteristic form of modern *Cedrela* seeds, with crescent-form wing and elongate seed body (Fig. 2k–l).

Compared with modern genera, the fossil seeds from Magyaregregy display a gross morphology most comparable with the seeds with apical flattened wing of *Gordonia* s.l. species of Theae in the Theaceae family (*Polyspora* and *Laplacea* species) (Fig. 2a–c), e.g. *G. haematoxylon* Sw., *G. lanceifolia* Burkill, *G. luzonica* S.Vidal, *G. papuana* Kobuski, *G. tonkinensis* Pit., and *G. wrightii* (Griseb.) H.Keng). The attachment of seed body and wing including their relative orientation, the shape of seed body and wing, and their ratio agrees with those of modern *Gordonia* seeds. The isodiametric pattern of the seed coat above the wing (Fig. 1d) is in agreement with that observed in *Gordonia* s.l. species of Theae by Gunathilake et al. (2015). The seed coat of species in Gordonieae (*G. lasianthus* (L.) J.Ellis and *G. brandegeei* H.Keng) shows protrusions though it is not consequently present on the wing (Gunathilake et al. 2015). Our seeds show an intermediate size between the size ranges of *Gordonia* s.l. seeds in Gordonieae and Theae.

There are several modern genera in various families which produce winged seeds or fruits equipped with an

Fig. 2 a–l Winged seeds of modern genera compared to the fossil-genus *Mecsekispermum*. **a** *Gordonia lanceifolia* Burkill (Theaceae), Singapore Botanic Gardens (SING), SING0055529. (*Polyspora lanceifolia* (Burkill) Orel, Peter G.Wilson, Curry and Luu). **b** *Gordonia papuana* Kobuski var. *acuminata* Kobuski (Theaceae), Queensland Herbarium (BRI), BRI-AQ0024245. (*Polyspora papuana* (Kobuski) Orel, Peter G.Wilson, Curry and Luu). **c** *Gordonia wrightii* (Griseb.) H.Keng (Theaceae), Isotype of *Laplacea wrightii* Griseb., Conservatoire et Jardin botaniques de la Ville de Genève (G), G00354909. **d** *Eriolaena hookeriana* Wight and Arn. (Malvaceae), Herbarium Trinity College, Dublin, TCD00879. **e** *Eriolaena yunnanensis* W.W.Sm. (Malvaceae), Royal Botanic Garden Edinburgh, E00031272. **f** *Reevesia tomentosa* H.L.Li (Malvaceae), Muséum National d'Histoire Naturelle (P),

P02286055. **g** *Nesogordonia kabingaensis* (K.Schum.) Capuron var. *leplaei* (Vermoesen) L.C.Barnett (Malvaceae), National Botanic Garden of Belgium (BR), BR0000006295752. **h** *Pterospermum argenteum* Tardieu (Malvaceae), Herbarium of the Arnold Arboretum (A), A00062911. **i** *Luehea cymulosa* Spruce ex Benth. (Malvaceae), Botanische Staatssammlung München (M), M0210183. **j** *Carrierea calycina* Franch. (Salicaceae), Royal Botanic Gardens Kew, K000591300; <http://specimens.kew.org/herbarium/K000591300>, copyright of the Board of Trustees of the Royal Botanic Gardens, Kew. **k** *Cedrela huberi* Ducke (Meliaceae), Herbarium Museum Paris, P01819647. **l** *Cedrela odorata* L. (Meliaceae), National Botanic Garden of Belgium (BR), BR0000005798391 scale bar (a–l) 1 cm

apical (or lateral) wing and resembling to some degree seeds of *Mecsekispermum*, e.g. Malvaceae (*Eriolaena* D.C., *Luehea* Willd., *Nesogordonia* Baill., *Pterospermum* Schreb., *Pterygota* Schott and Endl., *Reevesia*), Theaceae (*Gordonia* s.l.), Salicaceae (*Carrierea* Franch.), Meliaceae (*Cedrela*), Celastraceae (*Kokoona* Thw.), and Proteaceae (*Embothrium* J.R. and G. Forst.) (see also Kvaček and Wilde 2010).

Most of these have characters different from *Mecsekispermum*, e.g. venation on wing, shape of seed, attachment of seed body and wing, and ratio of seed and wing.

In the family Malvaceae, winged seeds of *Eriolaena* species (e.g. *E. glabrescens* D.C., *E. hookeriana* Wight and Arn.; Fig. 2d–e) display an angular seed body and a short wing. Winged seeds of *Luehea* species (e.g. *L. conwentzii* K.Schum., *L. cymulosa* Spruce ex Benth., *L. grandiflora* Mart., *L. seemannii* Planch. and Triana; Fig. 2i) have an acute basal part of the seed body and a high ratio of the wing and seed; i.e. seed body is quite small compared with the wing. Seeds of species in *Nesogordonia* (e.g. *N. bernieri* Baill., *N. chrysocarpa* Rakotoar. and Callm., *N. kabingaensis* (K.Schum.) Capuron, *N. papaverifera* (A.Chev.) Capuron ex N.Hallé, *N. rakotovaioi*

Rakotoar. and Andriamb. and Callm.; Fig. 2g) show somewhat similar morphology to *Mecsekispermum* seeds, but dorsal and ventral margins of the wing run parallel and straight. The long axes of the seed body and the wing are oriented at higher, 60–80° angle to each other. In the seeds of *Pterygota* Schott and Endl., the wing is ornamented. Winged seeds of *Pterospermum* species (e.g. *P. aceroides* Wall., *P. argenteum* Tardieu, *P. greuiifolium* Pierre, *P. lanceifolium* Roxb. ex DC., *P. heterophyllum* Hance, *P. macrocarpum* Hochr., *P. pecteniforme* Kosterm., *P. proteus* Burkill, *P. reticulatum* Wight and Arn., *P. semisagittatum* Roxb. ex DC., *P. truncatolobatum* Gagnep.; Fig. 2h) have a rounded seed body and a wing much longer compared with the seed body. In seeds of *Reevesia* species (e.g. *R. clarkii* (Monach. and Moldenke) S.L. Solheim ex Dorr, *R. glaucophylla* Hsue, *R. macrocarpa* H.L.Li, *R. pubescens* Mast., *R. tomentosa* H.L.Li; Fig. 2f) wing shape is different from that of the fossil seeds; ventral side of wing is straight, whereas dorsal side shows prominent swelling.

In the family Salicaceae, winged seeds of the genus *Carrierea* (e.g. *C. calycina* Franch.; Fig. 2j) have a broader wing compared with seed body and wing length.

In the family Meliaceae, seeds of some *Cedrela* (e.g. *C. angustifolia* DC., *C. balansae* C.DC., *C. fissilis* Vell., *C. dugesii* S.Watson, *C. montana* Moritz ex Turcz., *C. ngobe* Köcke, T.D.Penn. and Muellner, *C. oaxacensis* C.DC. and Rose, *C. odorata* L., *C. rehderiana* H.L.Li, *C. saltensis* M.A.Zapater and del Castillo; Fig. 2k–l) and *Toona* (Endl.) M.Roem. species (e.g. *T. hexandra* M.Roem., *T. sinensis* (Juss.) M.Roem., *T. sureni* (Blume) Merr.) have often larger (twice or more) and almost linear seeds. The morphology of the seeds is quite variable, and wing frequently shows a crescent form. The wing is often strongly concave and fragmented. Winged fruits in families Anacardiaceae (e.g. *Loxopterygium* Hook.f.), Malpighiaceae (e.g. *Banisteriopsis* C.B.Rob.), Fabaceae (e.g. *Tipuana* Benth.), Polygalaceae (e.g. *Securidaca* Mill.), Phytolaccaceae (e.g. *Seguieria* Loefl.), Ulmaceae (e.g. *Phyllostylon* Capan. ex Benth. and Hook.f.), and Sapindaceae (e.g. *Acer* L., *Serjania* Plum. ex Mill.) are quite different from *Mecsekispermum*. A basic difference is that these fruits show venation on the wing.

Since the morphology of the winged seeds from Magyaregregy does not agree with any fossil winged seeds described hitherto, we establish a new genus, *Mecsekispermum*. Winged seeds (with apical wing) from Paleogene and Neogene floras have usually been included in the genus *Saportaspermum*. We think that seeds from Magyaregregy, which are morphologically distinct from *Saportaspermum* seeds described so far, should not be assigned to this genus. In addition most of the *Saportaspermum* seeds seem to have malvalean affinities, and describing seeds of presumably non-malvalean affinities in this genus would not be practical. The similarity of *Mecsekispermum* seeds to seeds of some modern *Gordonia* species is emphasised, but with the lack of clear evidence, we do not assign them to the modern genus *Gordonia*. There are other, co-occurring leaf and

fruit (capsule) remains at the locality, described as *Ternstroemites pereger* and *Carpolithes gergoei* Hably and Erdei (Hably 2020), which may be related to the Theaceae family; however these, due to uncomplete or poor preservation, do not contribute with additional information to the systematic assignment of the seeds.

Conclusions

Winged seeds are described from the early Miocene flora of Magyaregregy, Mecsek Mts, Hungary. Since the seeds are different from other fossil-winged seeds and unequivocal evidence for the systematic relation of the fossils to modern genera does not exist, a new fossil genus and species *Mecsekispermum gordonoides* is established. Based on some shared characters including seed body and wing morphology and the surface pattern of the seed coat, the seeds are tentatively compared with *Gordonia* s.l. species in Theaceae (Theaceae).

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Compliance with ethical standards

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

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