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

Boglárka Erdei 1 · Lilla Hably 1

Received: 3 March 2020 / Revised: 5 May 2020 / Accepted: 21 September 2020 / Published online: 7 January 2021
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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 gordonioides* 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 Theeae (*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; Martinez-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. *Theaceae*, 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 *Theaceae* (*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 (Gunathilake 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...
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) Bozukov and Palamarev, Gordonia pseudoknauensis Kvaček, and Ternstroemites floresheimensis Kvaček and Walther from the rich, thermophilous flora. From the early Miocene flora of Hradek (North Bohemia, Czech Republic; Holy et al. 2012) and from the flora of the Cypris Shale (Western Bohemia, Czech Republic; Bůžek et al. 1996), leaf remains of Gordonia hradekensis were mentioned. From the early Miocene (Ottangian) flora of Köflach (Austria) Gordonia oberdorffensis 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 (Unger) Kovar-Eder and Kvaček. From the middle Miocene (Badenian) of the Satovcha Graben in the Western Rhodopes (Bulgaria), Bozukov and Palamarev (1995) described a flora as a rich refuge of the representatives of Theaceae, cf. ?Gordonia oberdorffensis and Ternstroemites pereger (Unger) Kovar-Eder and Kvaček. From the middle Miocene (Badenian) of the Satovcha Graben in the Western Rhodopes (Bulgaria), Bozukov 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, Gordania stefanovii Palamarev and Bozukov, Hartia palaeorhodopensis Bozukov and Palamarev, Stewartia stefanovii Palamarev and Bozukov, and Stewartia submonadelph a 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, and refuge areas of the Pannonian Basin. A rich late Miocene Gordonia emanuelii Palamarev (1995) described a flora as a rich refuge of the

Consequently, the “fish scale-bearing clay marl” sediments preserving the plant fossils belong to the Feked Formation and Komló Claymarl Member, dated as Karpbian (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. Karpbian (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), Andréánszky (1955), and Pálfalvy (1953, 1961, 1964, 1967), Hably L. and her colleagues have contributed studies to the knowledge on the Miocene flora of the Mecsek Mts (Hably 1992, 2001, 2002; Hably and Thiébaut 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 ligitum (Unger) Saporta, Engelhardia orsbergensis (P.Wessel and C. O. Weber) Jähnichen, Mai and Walther, Cedrelosphermum flichei (Saporta) Hably and Thiébaut, C. aquense Saporta, Zelkova zelkovifolia (Unger) Bůžek and Kotlaba, legumes (Podocarpium podocarpum (A. Braun) Herendeen, Leguminosae gen. et sp.), Ailanthus confucii Unger, and Ailanthus mescensis Hably.
The first Hungarian occurrence of some taxa was recorded in this flora, such as *Quercus kubinyii* (Kováts ex Ettingshausen) Czeczott, *Podocarpium podocarpum*, *Liquidambar europaea* A. Braun, and *Populus populina* (Brongniart) Knobloch. Some rare elements are noteworthy as well, such as *Ternstroemites pereger* (leaves, Theaceae), *Prinsepia serra* (Unger) Kovar-Eder and Kvaček, *Populus zaddachi* 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 Edinborough; Herbarium Trinity College, Dublin; Botanische Staatssammlung München; National Botanic Garden of Belgium; Herbarium of the Arnold Arboretum; Herbier Museum Paris; Muséum National d’Histoire Naturelle; Singapore Botanic Gardens).

### Results: systematic part

*Theaceae* Ker Gawler, *nom. cons.*  
*Mecsekispernum* Hably and Erdei, gen. nov.  
**Type species:** *Mecsekispernum 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.  

*Mecsekispernum 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 Claymarm 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 *Mecsekispernum* 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 gordonioides* 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. Reesevia 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 Štědřohůří (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 setzkanum (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 kovsvaiae Kvaček and Wilde from the early Oligocene flora of Seifhennersdorf (Germany) and from the Eocene floras of Lábatlan (Hungary), Kučín (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 Mecsekispernum. In Saportaspermum, the ventral and dorsal margin of the wing are more or less parallel contrasting Mecsekispernum 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 Mecsekispernum 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 Mecsekispernum 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 Mecsekispernum 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. haematoxyylon 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 Theaeae.

There are several modern genera in various families which produce winged seeds or fruits equipped with an
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* lanceifolia Burkill, *Gordonia* papuana Kobuski var. acuminata Kobuski, *Gordonia* lanceifolia Burkill; *Polyspora* lanceifolia (Burkill) Orel, Peter G.Wilson, Curry and Luu.), 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), Herbier Museum Paris, P01819647. l *Cedrela odorata* L. (Meliaceae), National Botanic Garden of Belgium (BR), BR0000005798391 scale bar (a–l) 1 cm

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), Herbier Museum Paris, P01819647. l *Cedrela odorata* L. (Meliaceae), National Botanic Garden of Belgium (BR), BR0000005798391 scale bar (a–l) 1 cm

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. conventzii* 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. rakotovaoi*...
Rakotoar, and Andriamb. and Callm.; Fig. 2g) show somewhat similar morphology to Mecsekispernum 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 Pterogyta Schott and Endl., the wing is ornamented. Winged seeds of Pterospermum species (e.g. P. aceroides Wall., P. argenteum Tardieu, P. grewijfillum Pierre, P. lanceifolium Roxb. ex DC., P. heterophylum Hance, P. macroparum Hochr., P. pecteniforme Kosterm., P. proteus Burkii, 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. 2i) 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. dagesii S.Watson, C. montana Moritz ex Turezc, 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. Luxopterygium Hook.f.), Malpighiaceae (e.g. Banisteriopsis C.B.Rob.), Fabaceae (e.g. Tijuana Benth.), Polygalaceae (e.g. Securidaca Mill.), Phytolaccaceae (e.g. Seguiera 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 Mecsekispernum. 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, Mecsekispernum. Winged seeds (with apical wing) from Paleogene and Neogene floras have usually been included in the genus Saportaspernum. We think that seeds from Magyaregregy, which are morphologically distinct from Saportaspernum seeds described so far, should not be assigned to this genus. In addition most of the Saportaspernum seeds seem to have malvalean affinities, and describing seeds of presumably non-malvalean affinities in this genus would not be practical. The similarity of Mecsekispernum 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 incomplete 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 Mecsekispernum gordonioides 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).

Acknowledgements

We are grateful to Steven Manchester for his valuable suggestions. We thank Volker Wilde and an anonymous reviewer for the improvement of the manuscript. We are also grateful for the invitation to contribute to this special issue by the guest-editors Angela Bruch, Dieter Uhl and Torsten Utescher.

Funding

Open access funding provided by Hungarian Natural History Museum. The research was supported by the National Research, Development and Innovation Office (NKFIH K120123).

Compliance with ethical standards

Conflict of interest

The authors declare that they have no conflict of interest.

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