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The early Miocene flora of Güvem (Central Anatolia, Turkey): a window into early Neogene vegetation and environments in the Eastern Mediterranean

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ABSTRACT. The early Burdigalian (MN3) plant assemblage of the Güvem area (northwestern Central Anatolia) is preserved in lacustrine sediments of the Dereköy pyroclastics. Its age is well constrained by radiometric dates of basaltic rocks bracketing the pyroclastics, making the Güvem flora one of the extremely few precisely dated early Miocene floras in the Mediterranean region. The rich assemblage of impression fossils comprises ferns and fern allies (2 species), gymnosperms (12 spp.) and angiosperms (129 spp.). *Ilex miodipyrena* sp. nov. is described as a new fossil-species. The most diverse families in the assemblage are the Fagaceae with 12 taxa and the Fabaceae with 12 leaf morphotypes and one fruit taxon. Aquatic plants are represented by seven taxa, riparian (including palms) and swamp forest elements by >35 taxa, and lianas by three taxa (*Smilax* spp., *Chaneya*). The relatively large number of aquatic and riparian/swamp elements is congruent with the rich fish, amphibian and reptile record of the Güvem area. Another characteristic feature of the plant assemblage is the presence of various lobed leaves which show similarities with modern species of different families (e.g. *Alangium*, various Malvales). Trees and shrubs growing on well-drained soils and forming closed-canopy and open-canopy forests are the most diversified group (>70 taxa). In terms of number of specimens in the collection and based on field observations, by far the most abundant leaf fossils belong to evergreen oaks of *Quercus drymeja* and *Q. mediterranea* and to various types of foliage that cannot be assigned to a particular extant or extinct genus of Fagaceae. These sclerophyllous trees must have covered vast areas surrounding the wetlands that developed during the early Miocene in the Güvem Basin. Based on a recent reassessment of the ecology and taxonomic affinity of these trees, they are considered to reflect humid temperate climatic conditions but with a brief drier season during the winter months. These forests are more similar to the laurel forests of the southeastern United States and those stretching in a narrow belt south of the Himalayas to eastern central China. The large number of Fabaceae may indicate the presence of warm subtropical environments but this is difficult to assess, as they are known for having wide ecological ranges today and in the past. All in all, a larger part of the plant taxa point to forested vegetation. This is in agreement with previous palynological studies which detected only small amounts of herbaceous and grass pollen. Open patches of vegetation may have been restricted to river banks and to rocky areas in a volcanic landscape. The biogeographic patterns detected for the early Miocene of the Güvem assemblage are manifold; most taxa are widespread Northern Hemispheric elements. A substantial part of the species migrated from Asia into Europe during the (late) Paleogene and reached Anatolia during the early Miocene (*Fagus*, *Paliurus*, *Chaneya*, *Ailanthus*, *Quercus kubinyii*, *Davallia haidingeri*, *Acer angustilobum*, *A. palaeosaccharinum*). Fewer taxa may have been in Anatolia before they migrated to Europe (e.g. *Nerium*, *Smilax miohavanensis*, *Quercus sosnowskyi*). Finally, very few taxa are Anatolian endemics (e.g. *Ilex miodipyrena*).

KEYWORDS: macrofossils, palaeobotany, palaeoenvironment, palaeobiogeography, Miocene, Turkey

INTRODUCTION

The Miocene period was the last period in the Earth's history when particularly warm conditions favoured rich forest vegetation in the Northern Hemisphere, including the subarctic region (Mai 1995, Zachos et al. 2001, Denk et al. 2011). In the early Miocene, tropical waters flowed between the Indian Ocean and Atlantic, causing mild and equable conditions in western Eurasia (Rögl 1998). In Turkey, the Pontides to the north and the Taurids to the south were not as high as today, and the Anatolian Plateau comprised lowlands, freshwater lakes, and marshes (Popov et al. 2004, Schildgen et al. 2012, 2014). Subsequently, intermittent collision of the Afro-Arabian plate with Eurasia created a physical connection between Africa and western Eurasia (Harzhauser et al. 2007) which enabled migration of a wide range of large mammals into western Eurasia (*Gomphotherium* landbridge).

There are remarkably few early Miocene plant macrofossil localities in the Mediterranean region that have been thoroughly studied in more recent times and that are species-rich. From Spain, the macrofloras of La Rinconada (Ribesalbes, Castellón) and Mora de Rubielos (Teruel) have been described by Barrón and Postigo-Mijarra (2011), Postigo-Mijarra and Barrón (2013), and Barrón and Diéguez (2001). The Chattian/Aquitanian flora of Armissan (Aude, southern France) described by Saporta (1865) has never been revised. The same is true for the Chattian floras of Aix-en-Provence and Manosque/Bois d'Asson (see Nury 1988 for the age of the Chattian floras). From Bosnia, Kvaček et al. (1993) described a moderately rich leaf flora. From Greece, Velitzelos (2002) published a preliminary revision of the rich flora of Kimi (Unger 1867), and Velitzelos et al. (1981) described leaf fossils of Lesvos. In addition, a number of early Miocene localities with displaced and *in situ* wood remains have been described from the island of Lesbos (e.g. Süss & Velitzelos 2010) and from Turkey (Akkemik et al. 2009, 2016).

The fossil sites in the vicinity of Güvem (Kızılcahamam district, Ankara Province; northwestern Central Anatolia; Fig. 1) have been studied by palaeontologists for almost 50 years. Vertebrates were studied by Paicheler et al. (1978), Hoek Ostende (2001),

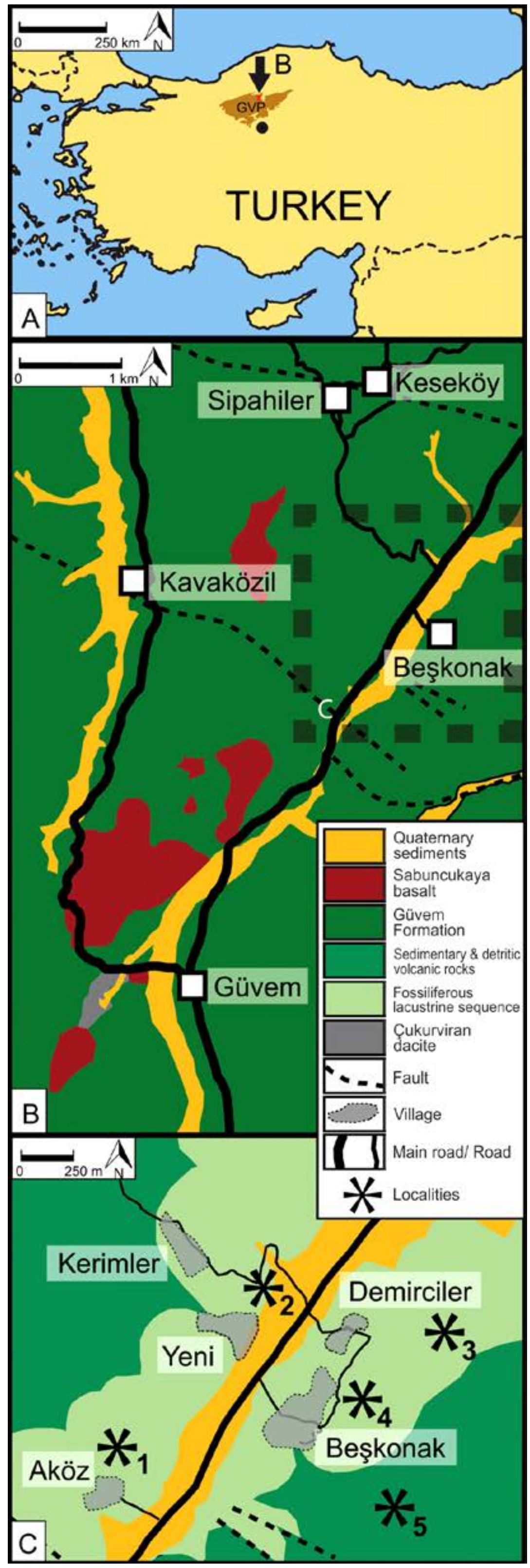

Fig. 1. **A–C**. Geographical and regional geological setting of early Miocene fossil localities in the Güvem area. **A**. Map showing the geographical position of the Galatia Volcanic Province (GVP) and the Güvem Basin (B). **B**. Regional geological map (simplified map based on Paicheler 1978; Tankut et al. 1998). **C**. Map showing Kasaplıgil's collection localities (simplified map based on Paicheler 1978); **1** – Aköz locality (= vertebrate locality of Paicheler et al. 1978); **2** – Çerkeş road "lone pine near the cemetery" locality; **3** – Demirciler locality; **4** – Beşkonak locality; **5** – Karga creek locality

Rückert-Ülkümen (2003), Lopez et al. (2004), and Dubois et al. (2010), among others. Among the recovered animal fossils are fishes, tadpoles, frogs, turtles, insectivores, and rodents. Most are typical of temperate and equatorial monsoon climates in Southeast Asia (Hoek Ostende 2001). One exception is the Ctenodactylidae, rodents that are today typical of arid landscapes in Africa but which, based on their fossil record, are thought to have possibly undergone substantial niche evolution.

Plant fossils discovered and collected by Baki Kasaplıgil in the late 1960s are now stored at the University of California Museum of Paleontology (UCMP). They form the basis of the present study. Kasaplıgil intended to publish a monograph on the flora of Güvem but unfortunately he died before he could complete his monograph (http://ucmp.berkeley.edu/blog/archives/939). A preliminary report was published by Kasaplıgil in 1977. At around the same time, Paicheler and Blanc (1981) published the plant fossils they collected from the Güvem area. This work is the most comprehensive published account on the early Miocene flora of the area and is accompanied by numerous photographs of the plant fossils. More recently, Yavuz-Işık (2008) investigated dispersed pollen and spores from the Güvem Formation taken from a 40 m section at the Keseköy mammal locality.

The aims of the present study were (*i*) to document, describe and determine the plant fossils collected by Baki Kasaplıgil, (*ii*) to compare Kasaplıgil's fossil plant collection to the one recovered and published by Paicheler & Blanc (1981) from the same area; (*iii*) to compare the early Miocene flora of Güvem to other published Miocene floras in the Mediterranean region and to Miocene floras across western Eurasia; (*iv*) to discuss the biogeographic relationships of the Güvem flora; and finally, (*v*) to infer the palaeoecology of the Güvem area during the early Miocene, using evidence from macrofossils and published data from dispersed pollen and spores.

MATERIAL AND METHODS

AGE AND GEOLOGIC SETTING

The age of the plant fossils is well constrained, as they are from the so-called Galatia Volcanic Province (also Galatean Volcanic Province, GVP; Fig. 1A), which belongs to the Pontide Tectonic Belt (Toprak et al. 1996, Wilson et al. 1997, Tankut et al. 1998). The GVP evolved as a consequence of the collision of the Afro-Arabian and Eurasian plates (Rögl 1998). Potassium-argon dating of volcanic rocks determined that the major phase of volcanic activity was during the early Miocene (17–20 Ma; Wilson et al. 1997). The Güvem Basin is one of several volcanic complexes within the GVP. It is characterized by thick fluvio-lacustrine sedimentary infills alternating with pyroclastics. The ca 1100 m thick Güvem Formation (Tankut et al. 1998) unconformably overlies Çukurviran dacite that has been dated to 19.7 ± 0.6 Ma (Wilson et al. 1997). The Dereköy pyroclastics (300 m; Fig. 2) lie at the base of the Güvem Fm, built up by effusive volcanic material (andesitic blocks, ash flows, lapilli tuffs) and interfingered by lacustrine sediments (claystones, diatomite). From this lacustrine sequence (Beşkonak sequence in Paicheler 1978) originate vertebrate, insect and plant fossils. On top of the Dereköy pyroclastics follow the Balta rhyolite (70 m), Bakacak andesite (200 m) and Oğlakcı dacite (50 m; Fig. 2). The latter two formations yielded K-Ar ages

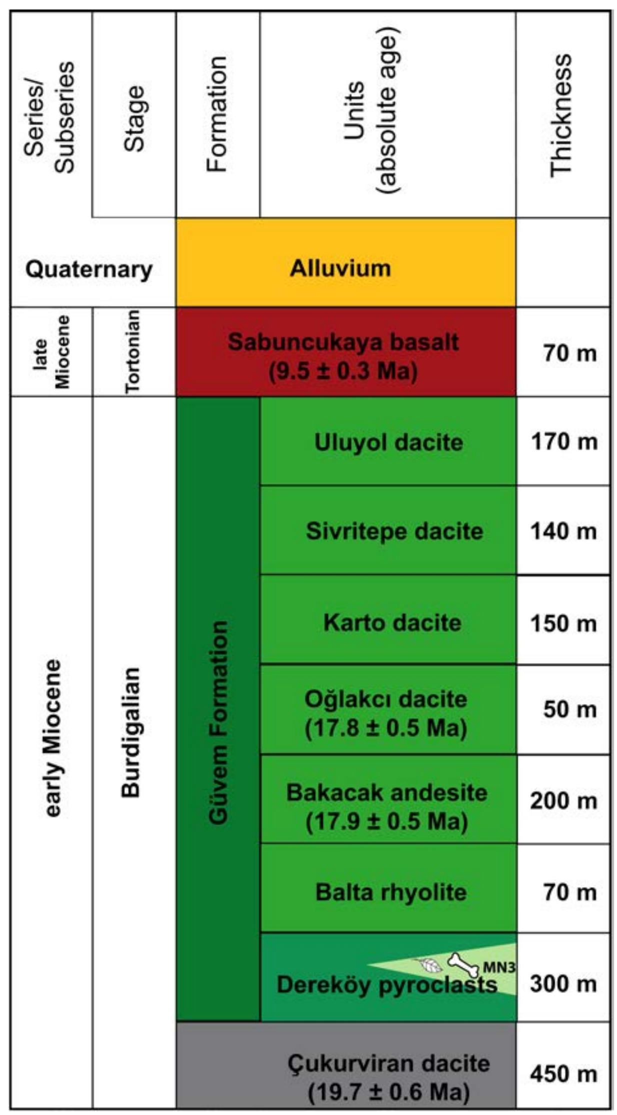

Fig. 2. Generalized/simplified stratigraphic column of the Güvem Formation (redrawn, based on Tankut et al. 1998); colour coding corresponds to legend in Fig. 1

of 17.9 ± 0.5 Ma and 17.8 ± 0.5 Ma (Wilson et al. 1997). Thus the age of the plant macrofossils investigated here is 20–18 Ma, early Burdigalian (or MN3). The mammals recovered from the Keseköy locality also have been referred to MN3 (De Bruijn et al. 1992, Hoek Ostende 2001, Wessels 2009, Fortelius 2016).

MATERIAL INFORMATION AND STORAGE

The plant fossil material investigated for the present study is from the Güvem area (Fig. 1; Kızılcahaman district, Ankara Province). It was collected by Baki Kasaplıgil (1918–1992) in the 1960s from five sites in the vicinity of Beşkonak village on both sides of the Çerkeş river (Fig. 1C). Specifically, Kasaplıgil collected most of the material in the vicinity of the villages of Aköz, Demirciler and Beşkonak, from the Karga creek site, and along the road from the Çerkeş valley to Yukarıkese (for detailed specimen information see **Supplementary Information File SI1*** on the *Acta Palaeobotanica* website). The material described by Paicheler & Blanc (1981) probably comes from essentially the same sites as that collected by Kasaplıgil. The material is stored at the University of California Museum of Paleontology (UCMP) in Berkeley.

In addition, in early summer 2017 we investigated and revised the J. C. Paicheler collection that formed the basis for Paicheler & Blanc (1981) and is housed at the Galerie de Paléobotanique du Muséum d'Histoires Naturelles (MNHN) in Paris. Although the focus of this paper is on the Kasaplıgil collection, a few taxa that were not recovered by Kasaplıgil but are in the Paicheler collection are included in this study. All the taxa housed in Paris are listed, along with their revised taxonomy, in **Supplementary Information File SI2**** on the *Acta Palaeobotanica* website.

SYSTEMATIC PALAEOBOTANY

In this section the material collected by Kasaplıgil and stored at UCMP and the material figured by Paicheler and Blanc (1981) and stored at MNHN are reconsidered. Taxa are organized as follows: Fern and fern allies, gymnosperms, and angiosperms (families in alphabetical order). The UCMP specimens (collection Kasaplıgil) were renumbered to follow the style of the UCMP database. For each UCMP number the corresponding specimen number as indicated by Kasaplıgil is provided in **Supplementary Information File SI1**. Leaf descriptions mainly follow Ash et al. (1999).

* File SI1 available on page http://botany.pl/images/ibwyd/acta_paleo/Acta_Palaeobotanica_57_2_Denk_et_al_SI_1.xls

** File SI2 available on page http://botany.pl/images/ibwyd/acta_paleo/Acta_Palaeobotanica_57_2_Denk_et_al_SI_2.xls

Family EQUISETACEAE Michaux ex DeCandolle

Genus *Equisetum* L.

***Equisetum* sp.**

1981 *Equisetum* sp. – Paicheler & Blanc: pl. 1, fig. 16.

Description. Fragment of aerial stems with nodes with leaves in whorls and fused into a sheath.

Remarks. The specimen figured in Paicheler & Blanc (1981) could not be found in the Paris collection. It cannot be ruled out that the figured specimen actually represents the axis of a monocot. One specimen (Kasaplıgil 5764 b) identified as *Equisetum* by Kasaplıgil is a small twiglet of *Populus*.

Family DAVALLIACEAE M.R.Schomb.

Genus *Davallia* (L.) Sm.

Davallia haidingeri Ettingsh.

Pl. 1, figs 1–5

1858 *Davallia haidingeri* Ettingsh. – Ettingshausen: p. 518, pl. 2, fig. 5.

1977 *Cryptogramma* aff. *crispa* (L.) R.Br. ex Hook. – Kasapligil: p. 29.

1981 *Hymenophyllum dilatatum* Sw. – Paicheler & Blanc: pl. 1, figs 12, 13.

1981 *Dryopteris* sp. – Paicheler & Blanc: pl. 1, figs 14, 15.

Material. Specimens UCMP202001, 202002, 202473; MNHN20123, 20125-02, 20299.

Description. Small fern fronds; petiole long, smooth, with prominent, adaxial, longitudinal groove; lamina triangular in outline, tripinnate-pinnatifid to quadripinnate; basal pinna pair opposite, succeeding pinnae subopposite to alternating towards apex, triangular in outline, arising at ca 45° angles; second- and third-order pinnae alternating, anadromous, close to attachment to rachis, narrow-triangular, stalked; ultimate segments stalked, simple or ± fused into bi- to trilobate segments; segments or segment lobes elliptic, obovate, or rounded-rhombic, usually somewhat asymmetrical, tapering to rounded or slightly pointed tip.

Remarks. The type material of this fossil fern has been described from Sotzka (Socka, Slovenia; late Eocene/early Oligocene;

Plate 1. **1–5**. *Davallia haidingeri* Ettingsh; **1**. Frond, overview, specimen UCMP202001 (6011); **2**. Pinnae, detail, specimen UCMP202001 (6011); **3**. Pinnae and stipe, detail, specimen UCMP202001 (6011); **4**. Frond, overview, specimen MNHN20125-02; **5.** Ultimate segments, detail, specimen MNHN20125-02

Plate 2. **1–3**. *Ephedra* sp.; **1**. Branch, overview, specimen UCMP202003 (5893); **2**. Branch, detail, specimen UCMP202003 (5893); **3**. Branch, detail, specimen UCMP202003 (5893). **4**, **5**. *Glyptostrobus europaeus* (Brongn.) Unger; **4**. Branch and leafy twigs, overview, specimen UCMP202004 (5941); **5**. Leafy twigs, detail, specimen UCMP202004 (5941)

Plate 3. **1–3**. *Glyptostrobus europaeus* (Brongn.) Unger; **1**. Branch, detail, specimen UCMP202005 (5929); **2**. Cones on fertile twig, specimen UCMP202006_01 (5944); **3**. Cones on fertile twig, specimen UCMP202007_01 (5923); **4**. *Sequoia abietina* (Brongn.) Erw.Knobloch, (?Male) Cones on fertile twigs, specimen UCMP202008 (5940)

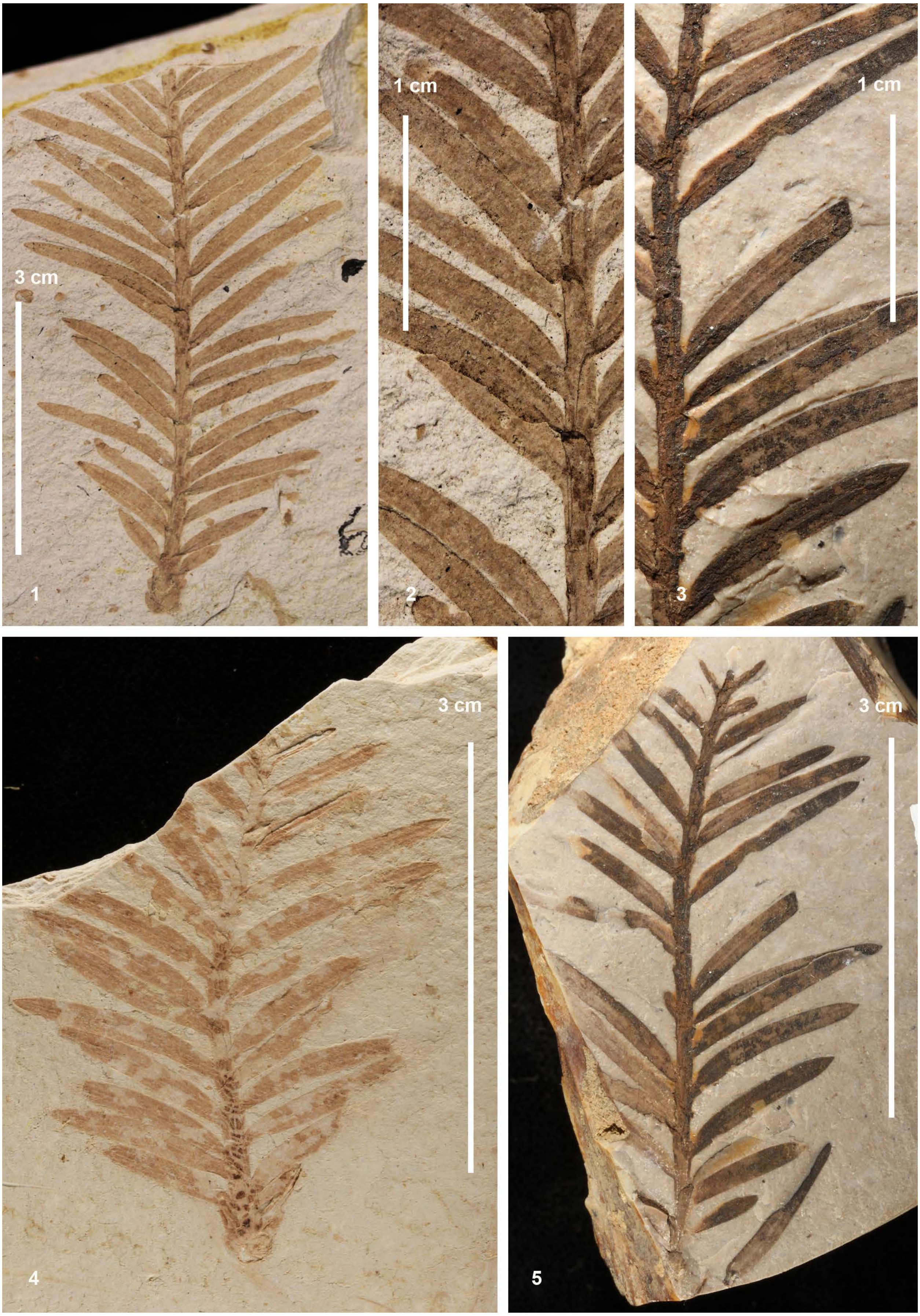

Plate 4. **1–5**. *Sequoia abietina* (Brongn.) Erw.Knobloch; **1**. Leafy twig, overview, specimen UCMP202009_01 (6921); **2**. Leafy twig, detail, specimen UCMP202009_01 (6921); **3**. Leafy twig, detail, specimen UCMP202010 (6010); **4**. Leafy twig, overview, specimen UCMP202011_01 (6003); **5**. Leafy twig, detail, specimen UCMP202010 (6010)

Ettingshausen 1858) and is very similar to the modern Macaronesian *Davallia canariensis* (L.) Sm. native to the Iberian Peninsula, Morocco, Canary Islands and Madeira. The extant genus occurs in the tropics and subtropics of Eurasia, Africa and Australia-New Zealand. Fossils from early Miocene deposits of New Zealand with preserved sori were described by Conran et al. (2010). Although the gross morphological similarity of the here-described fronds with *Davallia* is conspicuous, according to H. Schneider (pers. comm., 2015-02-24) an unequivocal generic determination is not possible without information from the rhizome, sori and indumenta. Bozukov and Ivanov (1995) investigated sori and spores of *Davallia haidingeri* from middle Miocene deposits of Bulgaria (Satovcha Graben) and found close similarity with the modern genus. It is worth noting that a time-calibrated phylogenetic study (Liu & Schneider 2013) suggested rapid diversification of Davalliaceae during the Miocene, with likely onset in the Oligocene. This would be consistent with the age of the fossils from Socka, Satovcha and Güvem.

The fern frond figured in Paicheler and Blanc (1981) as *Hymenophyllum* (Pl. 1, figs 4, 5) probably also represents *Davallia haidingeri*. Paicheler and Blanc (1981) assigned the fossil specimen to the modern *Hymenophyllum dilatatum* (G.Forst.) Sw. from New Zealand, Tahiti, the Juan Fernández Islands (Chile) and Yunnan (China; with the variety *amplum* Christ), but the terminal portions of the leaflets in this modern species are more rounded apically and the segments are oblong, while the segments in the fossil specimen (refigured in Pl. 1, figs 4, 5) are more elliptic and with a pointed apex. These features make the specimen more similar to the specimens assigned to *Davallia* in the present study.

GYMNOSPERMAE

Family EPHEDRACEAE Dumortier

Genus *Ephedra* L.

***Ephedra* sp.**

Pl. 2, figs 1–3

1977 *Ephedra* aff. *major* Host – Kasaplıgil: p. 29, fig. 14.

M a t e r i a l. Specimens UCMP202003, 202011_02.

D e s c r i p t i o n. Axis rigid, with nodes and internodes, nodes with remnants of scaly leaves, oppositely arranged.

R e m a r k s. A similar specimen was described by MacGinitie (1953) and compared with the extant *Ephedra nevadensis* S.Watson. The genus was also encountered in the pollen record of Güvem (Yavuz-Işık 2008).

Family CUPRESSACEAE Rich. ex Bartling

Genus *Glyptostrobus* Endlicher

Glyptostrobus europaeus (Brongn.) Unger

Pl. 2, figs 4, 5; Pl. 3, figs 1–3

1833 *Taxodium europeum* Brongn. – Brongniart: p. 175.

1850b *Glyptostrobus europaeus* (Brongn.) Unger – Unger: p. 435.

1977 *Glyptostrobus europaeus* (Brongn.) Unger – Kasaplıgil: figs 8, 9.

1981 *Glyptostrobus europaeus* (Brongn.) Unger – Paicheler & Blanc: pl. 2, figs 3–7.

M a t e r i a l. Specimens UCMP202004, 202005, 202006_01, 202007_01, 202008, 202138_02, 202148_02, 202173_02, 202317, 202378, 202379, 202381–202387, 202389, 202390_01, 202391, 202392, 202394, 202448_02, 202462; (cone) MNHN20345–20347, 20350a & b; (leafy axis) 172b, 20157, 20164, 20159-01, 20327–20333, one unnumbered specimen.

D e s c r i p t i o n. Leafy twig, branching alternate, two types of twigs distinguishable: "long shoots" with helically arranged scale-like leaves, "short shoots" with basal scale-like leaves replaced by needle-like leaves, helically arranged; seed cones terminal, solitary on fertile shoots with helically arranged scale-like leaves, cones obovate, scale complex consisting of a basal bract with a distinct tip and an apical ovuliferous scale with a series of distal lobes (Takaso & Tomlinson 1990).

R e m a r k s. The seed cones are virtually identical to the ones from Kimi-Aliveri (Euboea, MN4). According to Kvaček et al. (2002), early Miocene fertile twigs of *Glyptostrobus* differ slightly from younger forms (e.g. late Miocene of Vegora, northern Greece).

Genus *Sequoia* Endlicher

Sequoia abietina (Brongn.) Erw.Knobloch

Pl. 3, fig. 4, Pl. 4, figs 1–5

1822 *Phyllites abietinus* Brongn. – Brongniart in Cuvier: p. 360, pl. 11, fig. 13.
1964 *Sequoia abietina* (Brongn. in Cuvier) Erw.Knobloch – Knobloch: p. 602.
1977 *Sequoia langsdorfii* (Brongn.) Heer – Kasapligil: fig. 11.
1981 *Sequoia langsdorfii* (Brongn.) Heer – Paicheler & Blanc: pl. 6, figs 1–10.

Material. Specimens UCMP202008, 2022009_01, 2022010, 2022011_01, 202237, 202388, 202424, 202426, 202427, 202455, one unnumbered specimen; MNHN110, 111, 20150, 20153, 20154, 20155-01, 20160, 20168, 20311–20326, 20348, 20349.

Description. Leafy twig, basalmost part of twig with scale-like appressed leaves, followed by divergent linear-lanceolate needle leaves; leaves spirally arranged, leaf base adnate-decurrent and its lower part twisted, leaves straight to slightly curved, margins entire, apex acute, midrib present. One leafy twig with linear-lanceolate leaves and terminal young female cones with long bracts.

Remarks. The decurrent base and twisted lower part of the needle is very similar to leaves in *Sequoia* (Farjon 2005). The twig with young female cones shown in Pl. 3, fig. 4 is very similar to a twig figured in Teodoridis and Sakala (2008) from the early Miocene of Bilina as *Taxodium*. Based on observations of modern trees, we tentatively assign this specimen to *Sequoia* because the pollen cones in *Taxodium* are differently organized.

Genus *Calocedrus* Kurz

Calocedrus suleticensis
(Brabenec) Kvaček

Pl. 5, figs 1–4

1909 *Libocedrus suleticensis* Brabenec – Brabenec: p. 60, text fig. 42.
1999 *Calocedrus suleticensis* (Brabenec) Kvaček – Kvaček: p. 241, figs 1–6, 16–26.
1981 ? Cupressaceae – Paicheler & Blanc: pl. 7, figs 1, 2.

Material. Specimens UCMP202012, 202013_01, 202195; maybe MNHN20162, 20351, 20352.

Description. Branched twig with decurrent scale leaves, scale leaves falcate on main axis; scale leaves shorter on side branches, decussate, lateral ones boat-shaped, facial ones with triangular tip.

Remarks. The branches show some similarity with modern [*Calocedrus decurrens* (Torr.) Florin, *C. formosana* (Florin) Florin; Farjon 2005] and fossil (e.g. Kvaček & Hably 1998) species of *Calocedrus*. A single specimen that might represent a cone scale (Pl. 41, fig. 2) is 3 cm long, striate, with a small apical/subapical mucro. In size and shape, the striate inner surface and small distinct mucro, it fits with the modern North American *C. decurrens* (Farjon 2005), but it might also represent an insect remain.

The genus *Calocedrus* has a modern disjunction, with one species in western North America and one species in western China and Taiwan (Flora of North America Editorial Committee 1993, Wu & Raven 1999).

***Thuja* sp. ?**
(or ***Chamaecyparis*** or ***Cupressus***)

Pl. 5, figs 5–7

Material. Specimens UCMP202014, 202015.

Description. Twigs with opposite-decussate scale leaves; facial scale leaves similar to lateral ones, lateral leaves with free ending tip.

Remarks. Similar leaf arrangement and leaf shape is found in several Cupressaceae. Based on the material at hand, we are unable to assign the twigs to a particular genus.

Genus *Juniperus* L.

***Juniperus* sp.**

Pl. 6, figs 1, 2

Material. Specimens UCMP202016_01, one unnumbered specimen.

Description. Leafy twig, leaves arranged in dense whorls, leaves acicular, mainly straight to slightly lanceolate, apex sharply pointed.

Remarks. The twiglet labelled "*Picea*" by Kasaplıgil clearly belongs to *Juniperus*. The acicular leaves are arranged in whorls of three, as is characteristic of *Juniperus* (Farjon 2005).

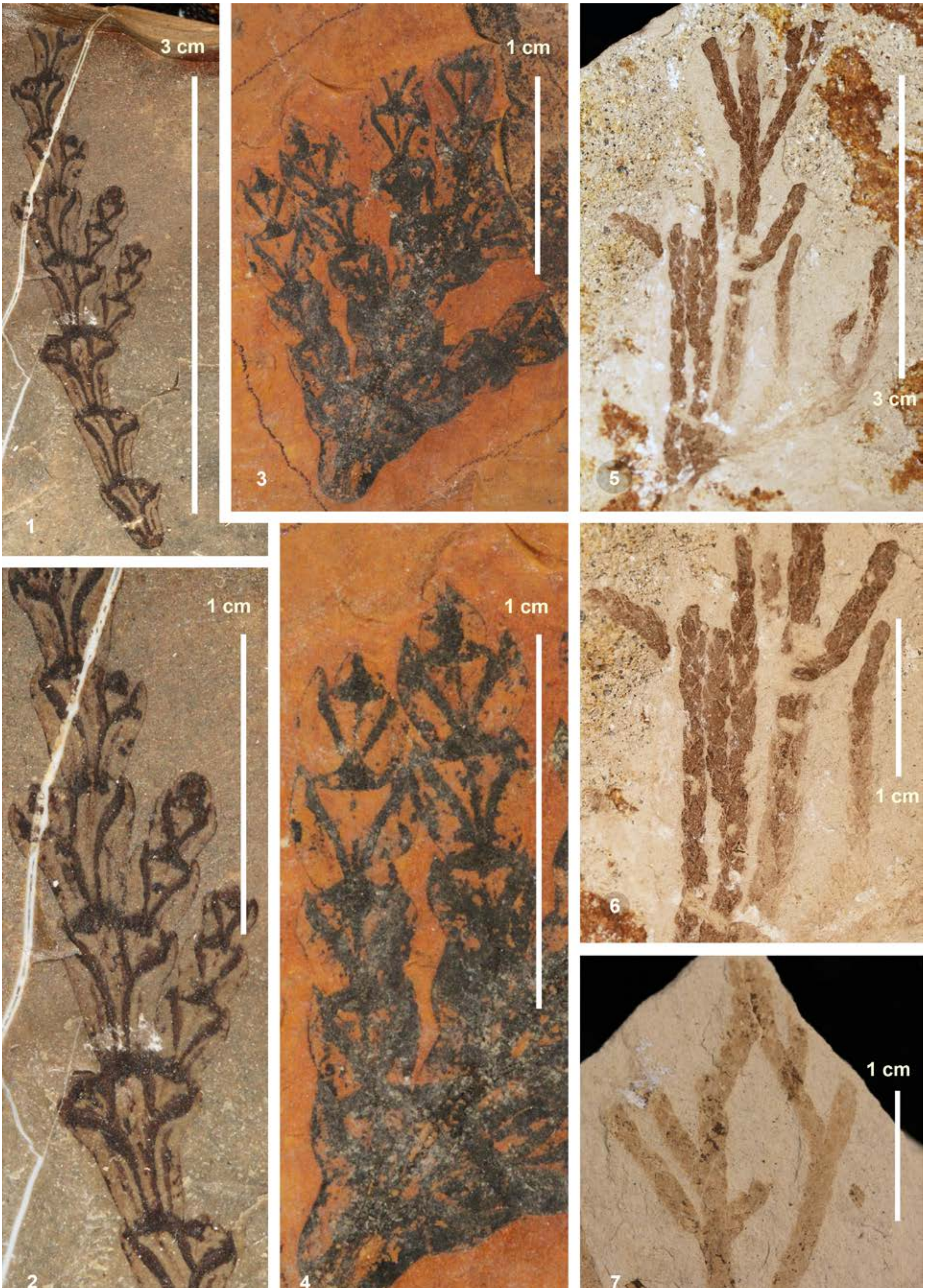

Plate 5. **1–4**. *Calocedrus suleticensis* (Brabenec) Kvaček; **1**. Branch, specimen, UCMP202012 (*n.n.*); **2**. Branch, detail, specimen, UCMP202012 (*n.n.*); **3**. Branch, specimen UCMP202013_01 (5500); **4**. Branch, detail, specimen UCMP202013_01 (5500). **5–7**. *Thuja* sp. ?; **5**. Branch, specimen UCMP202014 (5792); **6**. Branch, detail, specimen UCMP202014 (5792); **7**. Branch, detail, specimen UCMP202015 (6925)

Plate 6. **1**, **2**. *Juniperus* sp.; **1**. Leafy twig, specimen UCMP202016_01 (PA-312-n.n.); **2**. Leafy twig, detail, specimen UCMP202016_01 (PA-312-n.n.). **3**, **4**. *Cedrus* sp.; **3**. Winged seed, specimen UCMP202017_01 (5616a); **4**. Seed, detail, specimen UCMP202017_01 (5616a). **5**, **6**. *Pinus* sp. 1; **5**. Cone, (cast) specimen UCMP202018 (MTA 5530); **6**. Cone, detail, (cast) specimen UCMP202018 (MTA 5530). **7–9**. *Pinus* sp. 2; **7**. Cone, (cast) specimen UCMP202019 (MTA 5620); **8**. Cone, detail, (cast) specimen UCMP202019 (MTA 5620); **9**. Cone, detail, (cast) specimen UCMP202019 (MTA 5620)

Plate 7. **1–10**. *Torreya* sp.; **1**. Leaf, adaxial side, specimen MNHN20077; **2**. Leaf, abaxial side with two narrow stomatal bands, specimen MNHN20074; **3**. Leafy axis, specimen MNHN20342; **4**. Leafy axis, specimen MNHN20343a; **5**. Leafy axis with terminal bud, specimen MNHN20340; **6**. Leafy axis with terminal bud, specimen MNHN20341b; **7**. Leafy axis, specimen UCMP202020 (6004); **8**. Leafy axis, detail, specimen UCMP202020 (6004); **9**. Leafy axis, specimen UCMP202021 (*n.n.* MAT 434); **10**. Leafy axis, specimen UCMP202022 (5858)

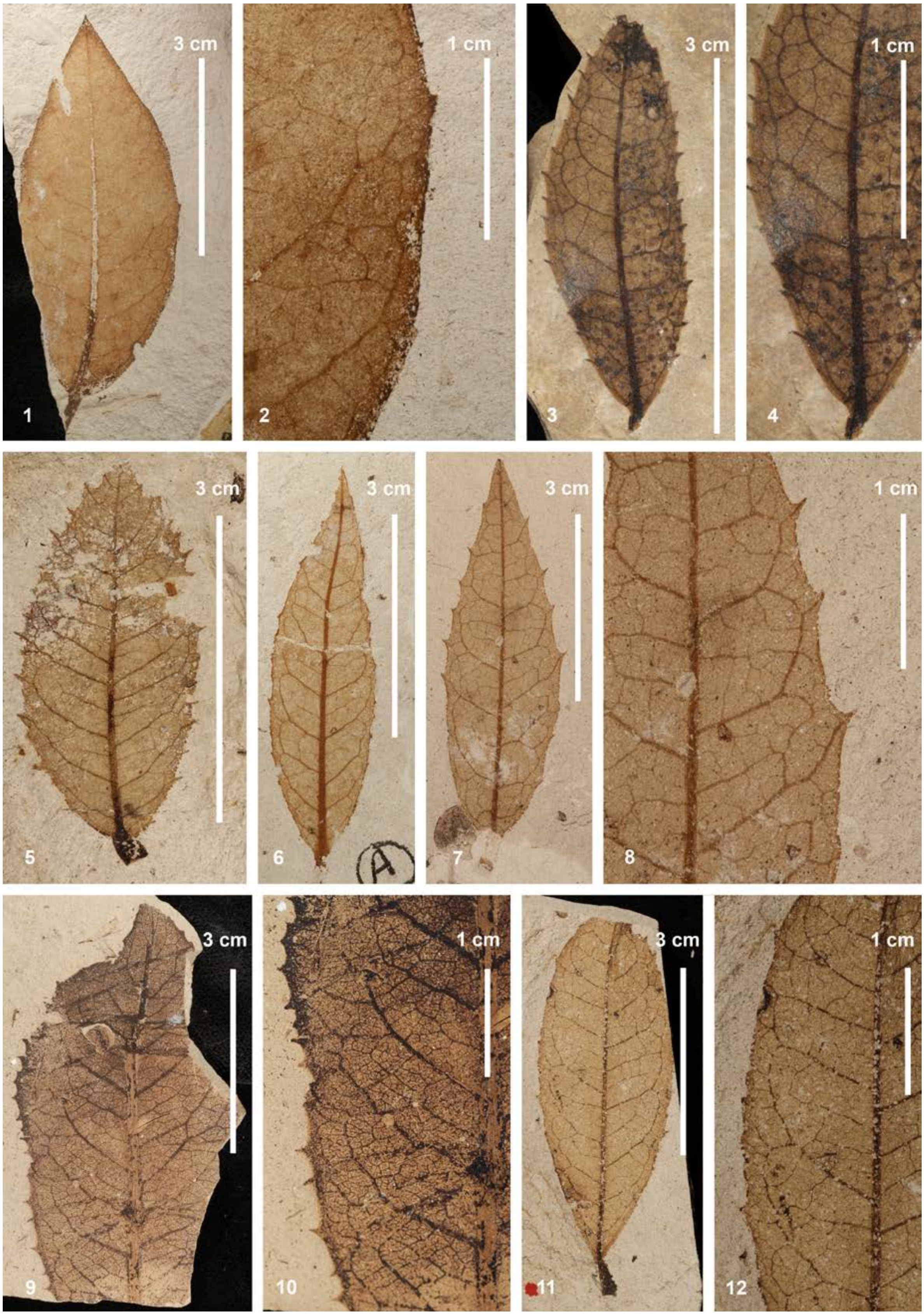

Plate 8. *Ilex miodipyrena* sp. nov.; **1**. Leaf, almost entire-margined, specimen UCMP202023 (5449); **2**. Leaf venation and margin, detail, specimen UCMP202023 (5449); **3**. Leaf, young leaf with many teeth, specimen UCMP202024 (5502); **4**. Leaf, venation, detail, specimen UCMP202024 (5502); **5**. Leaf, markedly dentate, specimen UCMP202025 (*n.n.* MTA 72-434); **6**. Leaf, inconspicuous dentition, specimen UCMP202026_01 (*n.n.* MTA 72-434); **7**. Leaf, holotype, regularly dentate leaf, specimen UCMP202027_01 (5794); **8**. Leaf, holotype, detail of venation and margin, specimen UCMP202027_01 (5794); **9**. Leaf, large leaf with irregular dentition, specimen UCMP202028 (5718); **10**. Leaf, venation and margin detail, specimen UCMP202028 (5718); **11**. Leaf, inconspicuous dentition, specimen UCMP202029 (5417b); **12**. Leaf, venation and margin detail, specimen UCMP202029 (5417b)

Family PINACEAE
Sprengel ex F.Rudolphi

Genus *Cedrus* Trew

Cedrus sp.

Pl. 6, figs 3, 4

Material. Specimen UCMP202017_01, 202283_01.

Description. Winged seed, ca 2.2 cm long, 1.6 cm wide, seed 8 mm long, 3 mm wide, reniform, wing broad obovate, apex obtuse.

Remarks. Paicheler and Blanc (1981, plate 6, fig. 11) referred a possibly male catkin to *Cedrus*. In addition, pollen of *Cedrus* has been reported from the Güvem Basin (Yavuz-Işık 2008).

Genus *Pinus* L.

Pinus sp. 1

Pl. 6, figs 5, 6

1981 *Pinus leucodermis* Ant. – Paicheler & Blanc: pl. 6, figs 12, 13.

Material. Artificial cast from original stored at MTA Ankara (on label: molded 1978_9). Specimen UCMP202018; MNHN20156, 20264.

Description. Seed cone, obovate, slightly curved, 12 cm long, 5 cm wide; dorsal, mucronate umbo, mucro not very distinct.

Remarks. Kasaplıgil (1977) lists *Pinus pinaster* in the text but does not figure a corresponding specimen. The specimen figured here was labeled as "*Pinus pinaster mioneyrensis* Kasapligil"; such a taxon is not listed in Kasaplıgil (1977). A cone very similar to the one figured here was called *P. leucodermis* Antoine by Paicheler & Blanc (1981). This name is a synonym of *P. heldreichii* H.Christ. *Pinus heldreichii* is a modern pine endemic to the Balkans and southern Italy. Overall, the dorsal, mucronate umbo suggests that this cone belongs to *Pinus* subgenus *Pinus* L.

Pinus sp. 2

Pl. 6, figs 7–9

Material. Artificial cast from original stored at MTA Ankara (on label: molded 1979-9). Specimen UCMP202019.

Description. Seed cone, 6 cm long, 3 cm wide; dorsal, mucronate umbo, mucro distinct.

Remarks. The figured specimen was labelled *Pinus firatii* Kasapligil. A larger specimen figured by Kasaplıgil (1977) as *P. canariensis* C.Smith ex Buch *fossilis* is similar to the present specimen in outline. The dorsal, mucronate umbo suggests that this cone belongs to *Pinus* subgenus *Pinus*.

Pinus sp. 3

Material. Specimen UCMP202281_02.

Description. Three-needled fascicle of *Pinus*.

Remark. Kasaplıgil compared this fragmentary short shoot to the modern *P. canariensis* C.Sm.

Pinus sp. 4

1981 *Pinus* sp. – Paicheler & Blanc: pl. 7, fig. 3.

Material. Specimen MNHN20148, 20257.

Description. Twig with five fascicles and isolated fascicle, fascicles five-needled, needles ca 6 cm long.

Remarks. Five-needled fascicles are found in pines of *Pinus* subgenus *Strobus* Lemmon, section *Quinquefoliae* Duhamel.

Family TAXACEAE S.F.Gray

Genus *Torreya* Arn.

Torreya sp.

Pl. 7, figs 1–10

1981 *Saxegothaea conspicua* Lindl. – Paicheler & Blanc: pl. 7, figs 7–10.

Material. Specimens UCMP202020–202022, 202260, 202274, 202397–202402, 202425, 202475, one unnumbered specimen; MNHN20074, 20077, 20434-01, 20336–20340, 20341a & b, 20342, 20343a & b.

Description. Leafy branch, axis appearing angular because of markedly decurrent leaf bases; leaf attachment appearing opposite possibly decussate, leaf organisation simple; laminar size nanophyll; laminar shape elliptic to slightly ovate, lamina symmetrical, laminar L:W ratio 4:1; base angle acute, apex angle acute, base shape cuneate to decurrent, position of leaf attachment marginal, short petiole twisted, apex shape straight; margin type entire; 1° vein category pinnate; two narrow parallel bands on one (abaxial) side of leaf, one distinct midvein on adaxial side of leaf.

Remarks. Such leafy branches were referred to the Podocarpaceae genus *Saxegothaea* by Paicheler and Blanc (1981), and to the water plant *Egeria*, the Cupressaceae *Metasequoia*, and the Taxaceae *Torreya* by Kasaplıgil. The opposite arrangement of leaves and the presence of two parallel stomatal bands on the abaxial leaf side are indicative of a closer relationship with Taxaceae. Saporta and Marion (1876) argued that a twiglet figured by Ettingshausen (1866) from Oligocene deposits of Žichov near Bilina as *Sequoia langsdorfii* actually belongs to *Torreya* and established the species *Torreya bilinica*. This name was adopted in later studies for dispersed leaves very similar to the ones reported here (e.g. Kvaček & Walther 1998, Walther & Kvaček 2007, early Oligocene of Central Europe; Barrón & Diéguez 2005, late Miocene of Spain). This is the first record of *Torreya* for the eastern Mediterranean Cenozoic. Based on the original figure of *Torreya bilinica* (Ettingshausen 1866, pl. 13, fig. 9) the specimens from Güvem may also belong to this species. The twiglet shown in Ettingshausen (1866) has the same ridged axis and the leaves are arranged oppositely to alternate. A single detached needle of short-leaved *Torreya* was published by Kolakovsky (1964, p. 31, pl. 3, figs 1, 2) from the late Miocene of Abkhasia as *T. nucifera* Sieb. et Zuccarini *fossilis* Kinkelin. More complete records are known from the Pliocene of France and described as *T. nucifera* var. *brevifolia* Saporta & Marion (1876).

Additional notes. The cuticular structure was obtained from specimen MNHN20313a. The preservation is poor, the surface seems to be covered by a thick papillation in stomatal areas, stomata are broadly elliptic, 30 μm wide and 45 μm long, hidden between papillae; non-stomatal areas consist of parallel-sided straight-walled cells 10–12 μm wide, only thinly cutinized (? prosenchymatous tissue). Such structure is typical of the genus *Torreya* and clearly rules out the Podocarpaceae.

ANGIOSPERMAE

Family AQUIFOLIACEAE DC. ex A.Rich.

Genus *Ilex* L.

Ilex miodipyrena **sp. nov.**

Pl. 8, figs 1–12

Diagnosis. Leaf elliptic, petiole twisted and proximally dilated, apex spinose, margin spinose or nearly entire, secondary venation brochidodromous, prominent intersecondary veins present.

Holotype. UCMP202027_01 (Pl. 7, figs 7, 8).

Etymology. Referring to the morphological similarity with the extant species *Ilex dipyrena* Wall. and the Miocene age of the type stratum.

Type locality. Beşkonak village on the bank of Cerkes, 1100 m. Kızılcahaman district, Ankara Province, Turkey.

Stratigraphy. Güvem Formation, lacustrine sediments of the Dereköy pyroclastics.

Age. ca 18–20 Ma. Early Burdigalian. MN 3.

Paratype. Material. Specimens UCMP202023, 202024, 202025, 202026_01, 202027_01, 202028, 202029, 202052_02, 202143_02, 202297.

Description. Leaf, simple, lamina size microphyll, shape elliptic, ± symmetrical, L:W ratio (1.3–) 3–4:1, base angle acute, apex angle acute, base shape cuneate to convex, position of petiolar attachment marginal, petiole slightly twisted and proximally dilated, apex shape straight to slightly acuminate, apex spinose; margin hyaline, serrate, regular to irregular spiny or nearly entire, tooth shape apical side straight, basal side concave, sinus rounded to angular, tooth apex spinose; primary venation pinnate, secondary venation brochidodromous (to semicraspedodromous), secondary loops present from which small veinlets enter teeth, secondary vein spacing irregular, secondary vein angle smoothly increasing towards base, strong intersecondaries present; tertiary veins regular polygonal reticulate, quaternary vein category regular polygonal reticulate.

Remarks. The leaf dimorphism (spinose or entire), the apex always ending in a spine,

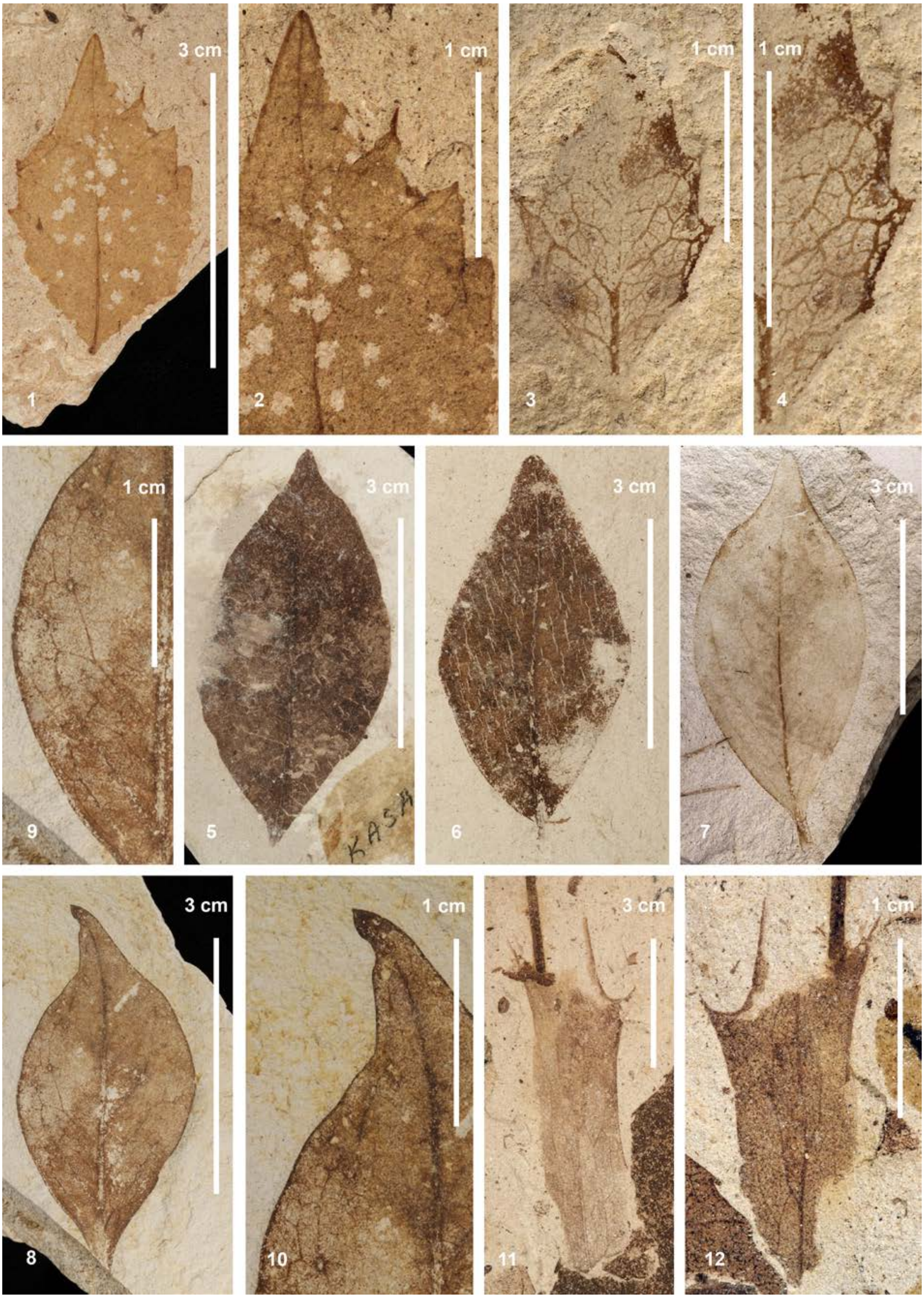

Plate 9. **1–4**. *Berberis* sp. vel *Ilex* aff. *I. pernyi* Franch. **1**. Leaf, specimen UCMP202030 (6916); **2**. Leaf tip, venation and margin, detail, specimen UCMP202030 (6916); **3**. Leaf, specimen UCMP202031 (5478); **4**. Leaf, venation and margin detail, specimen UCMP202031 (5478). **5–10**. cf. *Ilex* sp.; **5**. Leaf, specimen UCMP202032 (5855); **6**. Leaf, rhombic lamina shape, specimen UCMP202033 (5856b); **7**. Leaf, specimen UCMP202034 (5447); **8**. Leaf, specimen UCMP202035 (5737); **9**. Leaf, venation detail, specimen UCMP202035 (5737); **10**. Leaf, apex detail, specimen UCMP202035 (5737). **11**, **12**. *Mahonia grimmii* T.Güner & Denk; **11**. Leaf, specimen UCMP202036_02 (5460a); **12**. Leaf, counterpart, specimen UCMP202037_02 (5460b)

Plate 10. **1**. Arecaceae gen. indet., toothed rachis fragment, vel *Stratiotes* sp., leaf fragment, specimen MHNH20108; **2**. Arecaceae gen. indet., pinnate leaf fragment, specimen MHNH20130; **3**. Arecaceae gen. indet., leaflet-rachis attachment, detail, specimen MHNH20130; **4**. Arecaceae gen. indet., leaflet, parallel venation, detail, specimen MHNH20130; **5**. *Celtis japeti* Unger, leaf, specimen MHNH20058

and the secondary venation and twisted petiole suggest that these leaves belong to *Ilex*. In modern herbarium material (**Supplementary Information File SI3*****) the same morphological variability as in the fossil material can be observed. There are also some leaf similarities with *Berberis* section *Wallichianae* Schneider but in modern members of this section the leaf base commonly is cuneate.

Kasaplıgil considered these specimens to belong to *Ilex gracilis* Kolakovsky. This species was based on leaf fossils from the late Miocene flora of Kodor (Abkhasia; Kolakovsky 1964). However, *Ilex gracilis* has a distinctly fine-crenate margin which is not like the margin encountered in *I. miodipyrena* (see Kolakovsky 1964, text-figure page 46). One specimen with a L:W ratio of 1.3:1 (Pl. 29, figs 5, 6), labelled *Osmanthus* sp. by Kasaplıgil most likely also belongs to *Ilex miodipyrena*. The modern species *I. dipyrena* Wall. in Roxb. occurs from Pakistan to southwest China. “Himalayan Holly” occurs from 1700 to 3100 m a.s.l. in moist, shady places such as ravines in forests (Flora of Pakistan, http://www.tropicos.org/Project/Pakistan).

cf. *Ilex* sp.

Pl. 9, figs 5–10

Material. Specimens UCMP202025–202032, 202348_02.

Description. Leaf, simple; laminar size nano- to microphyll; shape elliptic to rhombic, symmetrical, L:W ratio 1.5–2:1; base angle acute, apex angle acute, base shape cuneate to decurrent, position of petiolar attachment marginal, apex shape straight to acuminate, apex pointed; margin type entire; 1° vein category pinnate, 2° vein category brochidodromous to camptodromous, 2° vein spacing decreasing towards base, 2° vein angle smoothly decreasing towards base, weak intersecondaries present, 3° vein category regular polygonal reticulate.

Remarks. Kasaplıgil compared these specimens to the modern *Ilex rotundata* Thunb. var. *microphylla* (Lindl. & Paxton) Hu. It is unclear which modern taxon this name refers to, but probably it is misspelled for *I. rotunda* Thunb. var. *microcarpa* (Lindl. & Paxton) S.Y.Hu. While two specimens (Pl. 9, figs 5, 6) do resemble *I. rotunda*, two other specimens with similar lamina shape have distinctly eucamptodromous venation (Pl. 9, figs 7–9). They could represent a different taxon which might not belong to *Ilex*.

*** File SI3 available on page http://botany.pl/images/ibwyd/acta_paleo/Acta_Palaeobotanica_57_2_Denk_et_al_SI_3.pdf

Family ARECACEAE Bercht. & J.Presl

Genus *Phoenicites* Brongn.

Phoenicites sp.

Pl. 10, figs 2–4

1981 *Phoenicites* sp. – Paicheler & Blanc: pl. 7, fig. 12.

Material. Specimens MNHN20130a & b.

Description. Pinnate leaf, rachis with attached induplicate leaflets.

Remarks. The specimens figured by Paicheler and Blanc (1981) as *Phoenicites* sp. and refigured here most likely belong to this fossil-genus.

?Arecaceae (rachis) vel ***Stratiotes* sp.** (leaf)

Pl. 10, fig. 1

1981 *Bromelia* L. – Paicheler & Blanc: pl. 7, fig. 11.

Material. MNHN20108.

Description. Rachis or leaf fragment, >8 cm long, 1.5–2.1 cm wide, with sharp emergent spines, the spines ca 1 cm apart.

Remarks. The axis may belong to a palm. Emergent spines are common along the margins of petioles in various groups of palms, for example in Borasseae (e.g. *Hyphaene* Gaertn.), Corypheae (*Corypha* L.) and Trachycarpeae (e.g. *Chamaerops* L., *Livistona* R.Br., *Washingtonia* H.Wendl.; Dransfield et al. 2008). A spiny petiole of *Hyphaene* has been reported from the late Oligocene of Ethiopia (Garcia Massini et al. 2010). The present specimen is more similar to members of Trachycarpeae. Alternatively, the specimen may represent a leaf fragment of Stratiotes. In the upper right margin of the specimen, the dentate leaf margin is folded in. This may indicate that the leaf texture was delicate as in Stratiotes and not coriaceous as in Arecaceae.

Family BERBERIDACEAE Juss.
vel AQUIFOLIACEAE DC. ex A.Rich.

Genus *Berberis* L. vel *Ilex* L.

Berberis* sp.** vel ***Ilex* aff. *I. pernyi Franch.

Pl. 9, figs 1–4

Material. Specimens UCMP202030, 202031.

Description. Leaf, leaf organisation simple; laminar size nano- to microphyll; laminar shape elliptic to rhombic, laminar symmetrical, laminar L:W ratio 1.5–2:1; base angle acute, apex angle acute, base shape cuneate, position of petiolar attachment marginal, apex shape straight; margin type serrate, tooth shape apical side concave, basal side straight to concave, sinus mainly rounded to angular, tooth apex spinose; 1° vein category pinnate, 2° vein category semicraspedodromous, weak intersecondaries present; 3° vein category regular polygonal reticulate, 4° vein category regular polygonal reticulate.

Remarks. The few leaves resemble small-leaved species of *Berberis*, for example *B. ilicifolia* L.f. but also the East Asian *Ilex perryana* S.Y.Hu and *I. pernyi*.

Family BERBERIDACEAE Juss.

Genus *Mahonia* Nutt.

Mahonia grimmii T.Güner & Denk

Pl. 9, figs 11, 12

1981 *Mahonia* sp. – Paicheler & Blanc: pl. 10, fig. 6.
2012 *Mahonia grimmii* T.Güner & Denk – Güner & Denk: p. 35, pl. 1, figs 1–4.

Material. Specimens UCMP202036_02, 202037_02; MNHN20073.

Description. Leaflet fragment; laminar size nano- to microphyll; laminar shape elliptic to rhombic, lamina symmetrical, laminar L:W ratio 2:1; base angle acute, apex angle acute, base shape cuneate, position of petiolar attachment marginal, apex shape straight; margin type serrate, tooth shape apical side concave, basal side concave, sinus rounded to angular, tooth apex spinose; 1° vein category pinnate, 2° vein category semicraspedodromous.

Remarks. The single specimen present in the collection of Kasaplıgil matches *Mahonia grimmii* described from the middle Miocene (MN6) of the Yatağan Basin (Güner & Denk 2012). This species occurs in early to middle Miocene strata of Turkey (Güvem, Ören Basin, Soma, Yatağan Basin).

Family BETULACEAE Gray

Genus *Alnus* Mill.

Alnus cycladum Unger

Pl. 11, fig. 6

1867 *Alnus cycladum* Unger – Unger: p. 47, pl. 3, figs 11–22.

Material. Specimen UCMP202040.

Description. Leaf, leaf organisation simple; laminar size nanophyll; laminar shape ovate, lamina symmetrical, laminar L:W ratio 1.5:1; base angle obtuse, apex angle acute to obtuse, base shape rounded to convex, position of petiolar attachment marginal, apex shape convex; margin type crenate, two orders of teeth present, teeth with convex basal and apical side, sinus angular, tooth apex simple; 1° vein category pinnate, 2° vein category craspedodromous, 2° vein spacing increasing towards base, 2° vein angle smoothly increasing towards base; 3° vein category mixed opposite/alternate.

Remarks. This small leaf matches very well the material from Kimi (Unger 1867). Similar leaves are encountered in a number of modern species, for example in *Alnus tenuifolia* Nutt., *A. oregana* Nutt. (USA), *A. tinctoria* Sarg. (Japan) and *A. incana* (L.) Moench, but particular relationships to these species remain to be established.

aff. *Alnus palaeojaponica* Weyland

Pl. 11, figs 7, 8

1943 *Alnus palaeojaponica* Weyland – Weyland: p. 103, pl. 17, figs. 4, 9, 10, Pl. 18, figs 1–4.

Material. Specimen UCMP202041.

Description. Leaf, leaf organisation simple; laminar size notophyll; laminar shape elliptic, lamina symmetrical, laminar L:W ratio 3:1; base angle acute, apex angle acute, base shape cuneate to convex, position of petiolar attachment marginal, apex shape convex to slightly acuminate; margin type serrate, two orders of teeth present, teeth with concave basal and apical side, sinus angular to rounded, tooth apex simple; 1° vein category pinnate, 2° vein

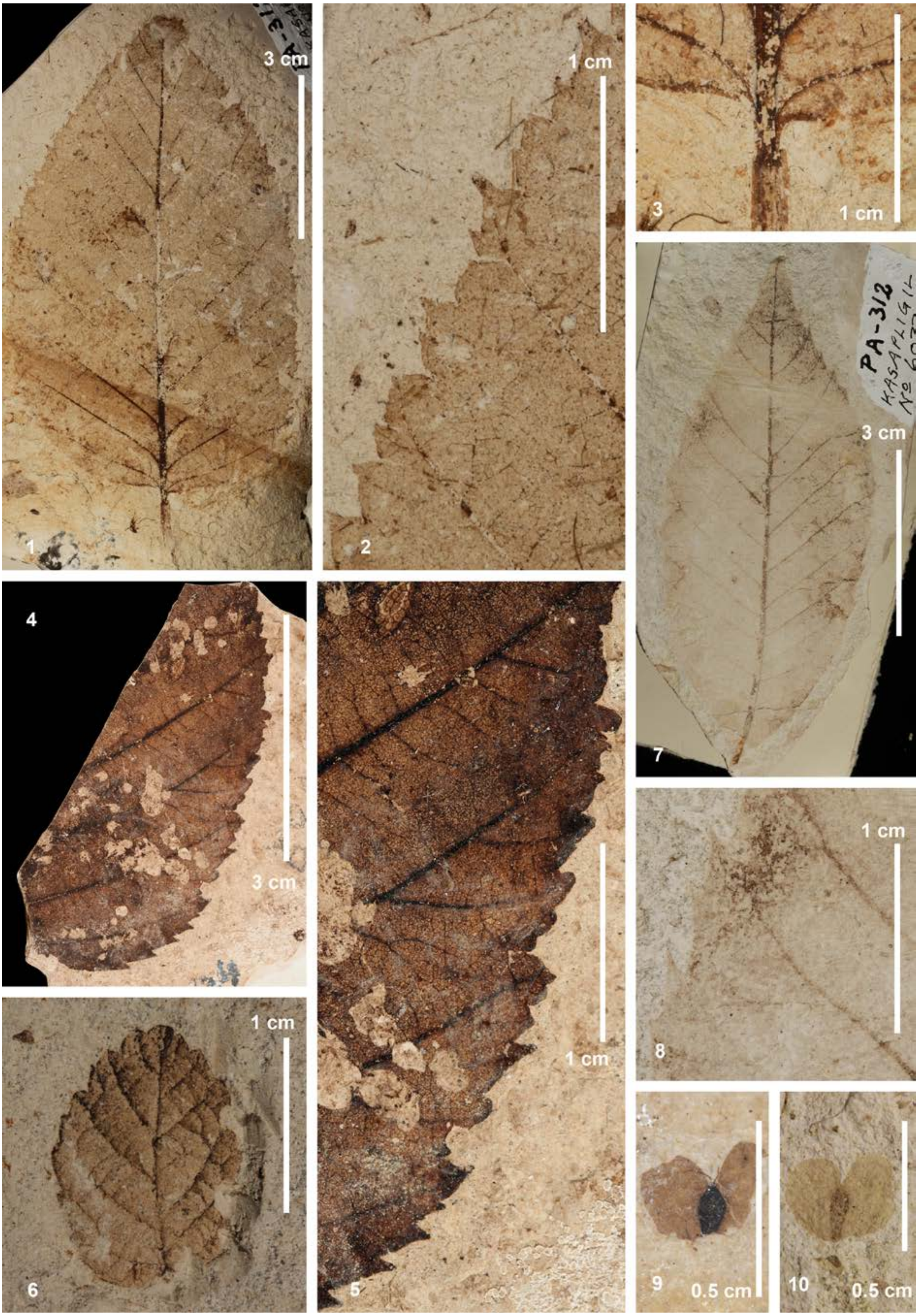

Plate 11. 1–5. *Betula* sp.; **1**. Leaf, specimen UCMP202038 (6035); **2**. Leaf venation and margin, detail, specimen UCMP202038 (6035); **3**. Leaf base, detail, specimen UCMP202038 (6035); **4**. Leaf, specimen UCMP202039 (6924); **5**. Leaf venation and margin, detail, specimen UCMP202039 (6924). **6**. *Alnus cycladum* Unger, leaf, specimen UCMP202040 (5419); **7**, **8**. *Alnus palaeojaponica* Weyland; **7**. Leaf, specimen UCMP202041 (6033); **8**. Leaf venation and margin, detail, specimen UCMP202041 (PA-312-6033). **9**, **10**. *Betula* sp. (seeds); **9**. Seed, specimen UCMP202042_01 (*n.n.*); **10**. Seed, specimen UCMP202009 (6921)

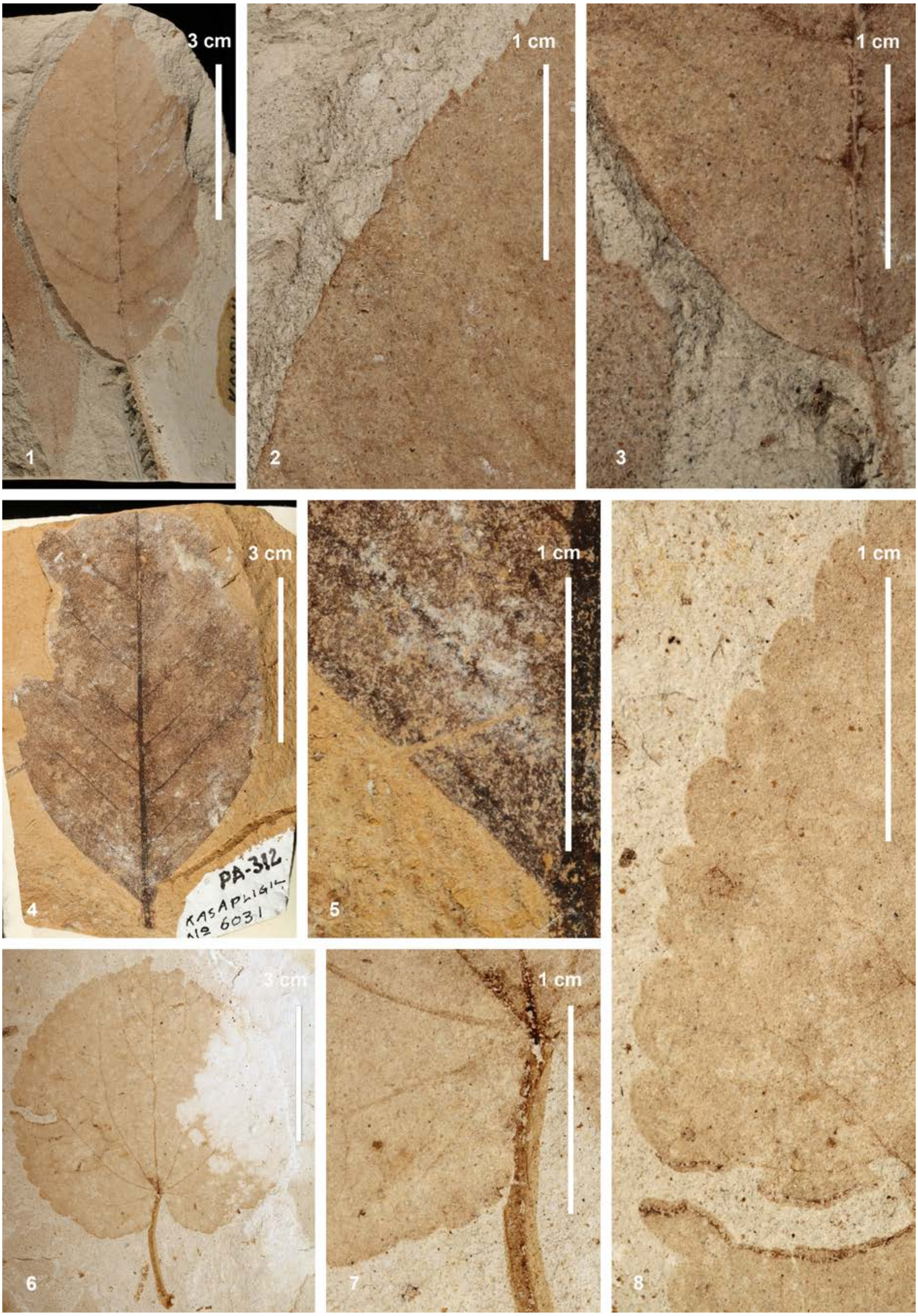

Plate 12. **1–5**. *Alnus gaudinii* (Heer) Erw.Knobloch & Kvaček; **1**. Leaf, specimen UCMP202043 (5534); **2**. Leaf venation and margin, detail, specimen UCMP202043 (5534); **3**. Leaf base, detail, specimen UCMP202043 (5534); **4**. Leaf, specimen UCMP202044 (6031); **5**. Leaf base and margin, detail, specimen UCMP202044 (6031). **6–8**. *Cercidiphyllum crenatum* (Unger) Brown; **6**. Leaf, specimen UCMP202045_01 (5968); **7**. Leaf base, detail, specimen UCMP202045_01 (5968); **8**. Leaf margin, margin feeder trace, detail, specimen UCMP202045_01 (5968)

category craspedodromous, 2° vein spacing ± uniform, 2° vein angle smoothly increasing towards base.

Remarks. This leaf resembles the modern Japanese species *Alnus firma* Siebold & Zucc. and *A. sieboldiana* Matsum. by its type of dentition (few sharp teeth; Liu 1996). *A. formosana* (Burkill) Makino sometimes has very similar leaves.

Alnus gaudinii (Heer) Erw.Knobloch & Kvaček

Pl. 12, figs 1–5

1859 *Rhamnus gaudinii* Heer – Heer: p. 79, pl. 124, figs 4–15, pl. 125, figs 1, 7, 13.
1867 *Alnus sporadum* Unger – Unger: p. 47, pl. 3, fig. 8.
1867 *Carpinus betuloides* Unger – p. 48, pl. 3, figs 29–34 (non 23–28, 35–37).
1867 *Quercus kamischinensis* Göpp. – Unger: p. 49, pl. 5, figs 18–20.
1868 *Alnus sporadum* Unger var. *phocaensis* Saporta – Saporta: p. 21, pl. 2, figs 1–5.
?1943 *Alnus rottensis* Weyland – Weyland: p. 101, pl. 17, fig. 1.
1981 *Alnus rottensis* Weyland – Paicheler & Blanc: pl. 5, figs 5–7.
1993 *Alnus phocaensis* Saporta – Gemici et al.: p. 95, pl. 5, fig. 3.
1993 *Fagus orientalis* Lipsky – Gemici et al.: p. 99, pl. 6, figs 2, ?3.

Material. Specimens UCMP202043, 202044; MNHN59, 20089.

Description. Leaf, leaf organisation simple; laminar size notophyll; laminar shape elliptic, lamina symmetrical, laminar L:W ratio 2:1; base angle acute, apex angle acute, base shape convex, position of petiolar attachment marginal; margin type serrate, two orders of teeth present, teeth with concave basal and straight apical side, sinus angular, tooth apex simple; 1° vein category pinnate, 2° vein category craspedodromous.

Remarks. Similar leaf morphotypes of *Alnus* from Central and Southern Europe have been described under several different names (see taxa listed under *A. gaudinii*). Because the original material figured by Heer (1859) is morphologically diverse, it appears most appropriate to include several species that were established later within *A. gaudinii*.

It is noteworthy that some of the leaves described by Grubov (in Kryshtofowicz et al. 1956; *Alnus schmalhausenii* Grub.) from late Oligocene strata of Ashutas (Kazakhstan) closely resemble those of *A. gaudinii*. According to Mai and Walther (1991), *A. schmalhausenii* is very similar to the roughly contemporaneous (Chattian/Aquitanian) *A. rostaniana* Saporta from Central Europe.

The closest similarities of *A. gaudinii* are with the modern western Himalayan *Alnus nitida* (Spach.) Endl. and the North American narrow endemic *A. maritima* Nutt. (Knobloch & Kvaček 1976). Saporta (1868) compared this leaf type with the modern western Eurasian species *A. orientalis* Decne. and *A. subcordata* C.A.Mey. In general, modern species of *Alnus* – except species of subgenus *Alnaster* – show weak molecular differentiation (Navarro et al. 2003). This and possibly their conserved ecological niche may explain the high degree of leaf morphological convergence in modern and fossil species of *Alnus*.

Genus *Betula*

Betula sp.

Pl. 11, figs 1–5

1977 *Betula luminifera* Winkl. *fossilis* – Kasaplıgil: fig. 40.
1981 *Betula alba* L. – Paicheler & Blanc: pl. 5, fig. 8.

Material. Specimens UCMP202038, 202039.

Description. Leaf, leaf organisation simple; laminar size notophyll; laminar shape ovate, lamina symmetrical, base slightly asymmetrical, laminar L:W ratio 2–2.5:1; base angle obtuse, apex angle acute, base shape rounded to truncate, position of petiolar attachment marginal, apex shape straight; margin type serrate, two orders of teeth present, teeth in basal part of leaf mainly with straight basal and apical side, teeth in middle apical part of leaf with flexuous basal and apical side, sinus angular, tooth apex simple; 1° vein category pinnate; 2° vein category craspedodromous, 2° vein spacing ± uniform, 2° vein angle smoothly increasing towards base; 3° vein category mixed opposite/alternate.

Remarks. The leaves are well comparable to the extant East Asian *Betula luminifera* H.Winkler and to the Himalayan *Betula utilis* D.Don by their shape, number and course of secondary veins, and teeth. These modern species belong to distantly related clades within *Betula* according to a molecular phylogenetic study by Wang et al. (2016). Leaves of *B. dryadum* figured by Saporta (1891) from Chattian strata of Manosque are very similar to the specimen from Güvem.

***Betula* sp.** (seeds)

Pl. 11, figs 9–10

1981 *Betula alba* L. – Paicheler & Blanc: pl. 5, figs 9–12 (seeds).

Material. Specimens UCMP202009, 202042; MNHN20200.

Description. Fruit samaroid, outline elliptic; seed with two lateral wings, wings wider and longer than seed, wings symmetric, seed elliptic to oblanceolate, with two linear styles.

Remarks. The shape of the wings is very similar to that of seeds of the modern *Betula pendula* Roth.

Family CANNABACEAE Martynov

Genus *Celtis* L.

Celtis japeti Unger

Pl. 10, fig. 4

1852 *Celtis japeti* Unger – Unger: p. 44, pl. 20, figs 25, 26.
1981 *Celtis* sp. – Paicheler & Blanc: pl. 15, figs 6, 7.

Material. Specimens MNHN20019-02, 20058, 20072, 20241; maybe 20242-02

Description. Leaves, simple, asymmetric, 2.5–4 cm long, 1.5 cm wide, base distinctly asymmetrical, rounded, margin serrate, primary venation acrodromous, one lateral primary vein straight, the other distinctly curved, secondary venation semicraspedodromous.

Remarks. Paicheler and Blanc (1981) figured small leaves of *Celtis* and compared them with the modern Caucasian *C. caucasica* Willd. and *C. tourneforti* Lam. We follow Knobloch (1998) and refer these leaves to *C. japeti*, while larger leaves with coarser dentition would correspond to *C. trachytica* Ettingsh.

Family CERATOPHYLLACEAE Gray

Genus *Ceratophyllum* L.

***Ceratophyllum* sp.**

Pl. 39, fig. 1

Material. Specimen UCMP202056.

Description. Achene with two pronounced lateral spines.

Remarks. The morphology of the achenes is similar to those encountered in *Ceratophyllum platyacanthum* Chamisso (Les 1989). Paicheler and Blanc (1981; pl. 1, fig. 11) refer a slender branch of a water plant to *C. submersum* L.

Family CERCIDIPHYLLACEAE Engl.

Genus *Cercidiphyllum* Siebold & Zucc.

Cercidiphyllum crenatum (Unger) R.W.Brown

Pl. 12, figs 6–8

1850c *Dombeyopsis crenata* Unger – Unger: p. 448.
1935 *Cercidiphyllum crenatum* (Unger) R.W.Brown – Brown: p. 575. Pl. 68, figs 1, 9, 10.
1977 *Cercidiphyllum crenatum* (Unger) R.W.Brown – Kasaplıgil: fig. 27.

Material. Specimen UCMP202045_01.

Description. Leaf, leaf organisation simple; laminar size notophyll; laminar shape nearly circular, lamina symmetrical, laminar L:W ratio 1:1; base angle wide obtuse, apex angle obtuse, base shape cordate, position of petiolar attachment marginal, apex shape convex; margin type crenate, teeth with convex basal and apical side, sinus angular, tooth apex simple; 1° vein category actinodromous, 2° vein category brochidodromous with secondary loops from which small veinlets enter the teeth, combined agrophic veins present, nine basal veins present, 2° vein spacing irregular, 2° vein angle ± uniform.

Remarks. This fossil species is very similar in gross morphology and leaf architecture to the modern species of *Cercidiphyllum* (Bugge 2005).

Family ERICACEAE Juss.

Genus *Rhododendron* L.

***Rhododendron* sp.**

Pl. 13, figs 1–4

Material. Specimens UCMP202046, 202047_01.

Description. Leaf, leaf organisation simple;

laminar size notophyll; laminar shape obovate, lamina symmetrical, laminar L:W ratio 3:1; base angle acute, apex angle obtuse, base shape convex to decurrent, position of petiolar attachment marginal, apex shape convex; margin type entire; 1° vein category pinnate, 2° vein category weak brochidodromous, 2° vein spacing ± uniform, 2° veins ± uniform; 3° vein category regular polygonal reticular.

R e m a r k s. This foliage resembles modern leaves of *Rhododendron*. Among western Eurasian (*R. ponticum* L.) and East Asian (e.g. *R. fortunei* Lindl.) species, some produce leaves virtually identical to the fossil ones, but a number of other families may produce similar types of foliage (e.g. Sapotaceae).

aff. Ericaceae gen. et spec. indet. 1

Pl. 13, fig. 5

M a t e r i a l. Specimen UCMP202048.

D e s c r i p t i o n. Leaf, leaf organisation simple; laminar size nanophyll; laminar shape ovate, lamina symmetrical, laminar L:W ratio

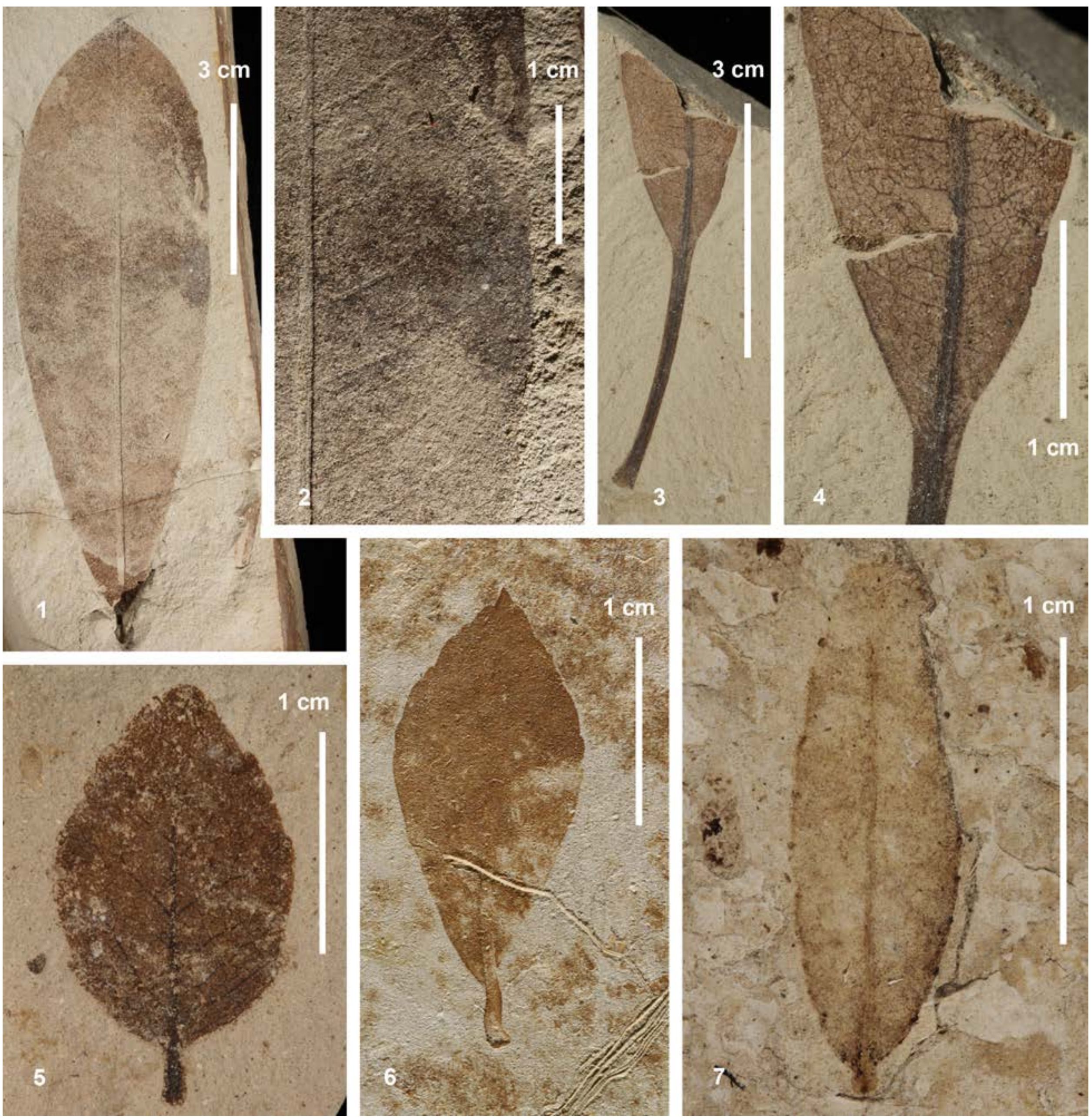

Plate 13. **1–4**. *Rhododendron* sp.; **1**. Leaf, specimen UCMP202046 (5552); **2**. Leaf, detail, specimen UCMP202046 (5552); **3**. Leaf, specimen UCMP202047_01 (5798); **4**. Leaf, detail, specimen UCMP202047_01 (5798); **5**. aff. Ericaceae gen. et spec. indet. 1, leaf, specimen UCMP202048 (5728); **6**. aff. Ericaceae gen. et. spec. indet. 2, leaf, specimen UCMP202049_01 (5454); **7**. aff. Ericaceae gen. et spec. indet. 3, leaf, specimen UCMP202050 (5834)

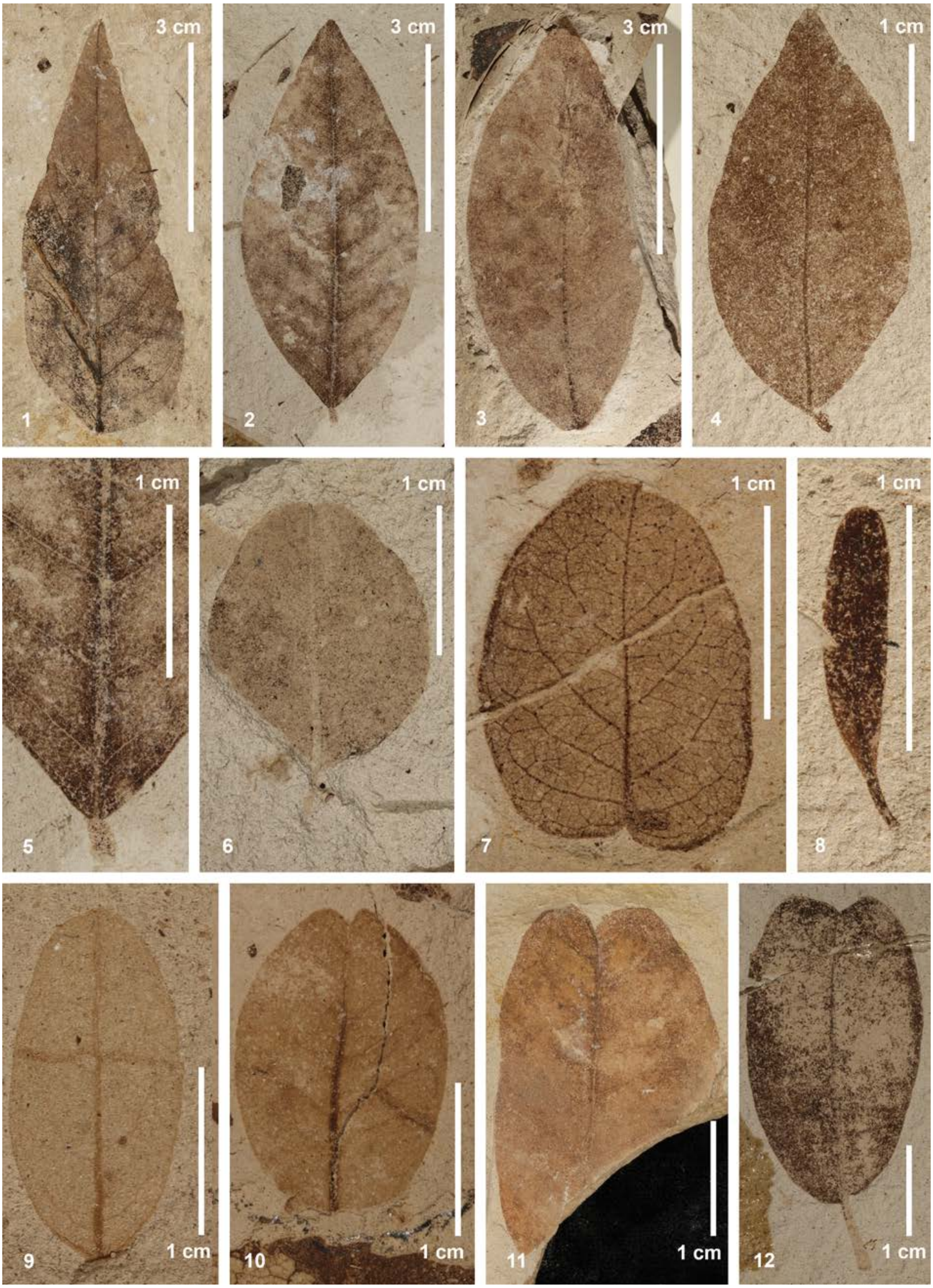

Plate 14. **1**. *Leguminophyllum* sp. 1, leaf, specimen UCMP202051 (*n.n.* MTA 72.434); **2**, **4**, **5**. *Leguminophyllum* sp. 2; **2**. Leaf, specimen UCMP202047_02 (5798); **4**. Leaf, specimen UCMP202052_01 (6049); **5**. Leaf base and venation, detail, specimen UCMP202047 (5798); **3**. *Leguminophyllum* sp. 3, leaf, specimen UCMP202053 (5974); **6**. *Leguminophyllum* sp. 4, leaf, specimen UCMP202054 (5733); **7**. *Leguminophyllum* sp. 5, leaf, specimen UCMP202055 (5732); **8**. *Leguminophyllum* sp. 6, leaf, specimen UCMP202056_02 (5812); **9**. *Leguminophyllum* sp. 7, leaf, specimen UCMP202057_01 (5452); **10**. *Leguminophyllum* sp. 8, leaf, specimen UCMP202057_02 (5452); **11**, **12**. *Leguminophyllum* sp. 9; **11**. Leaf, specimen UCMP202058 (5457); **12**. Leaf, specimen UCMP202059 (5453)

1.5–2:1; base angle obtuse, apex angle acute, base shape convex, position of petiolar attachment marginal, apex shape straight; margin type crenate, teeth with concave basal and apical side, sinus angular, tooth apex simple; 1° vein category pinnate, 2° vein category weak brochidodromous, 2° vein spacing irregular, 2° vein angle irregular; 3° vein category regular polygonal reticular.

Remarks. Kasaplıgil labelled this specimen *Vaccinium* or *Arctostaphylos uva-ursi*. It is doubtful whether this specimen belongs to Ericaceae.

aff. Ericaceae gen. et. spec. indet. 2

Pl. 13, fig. 6

Material. Specimen UCMP202049_01.

Description. Leaf, leaf organisation simple; laminar size nanophyll to microphyll; laminar shape rhombic obovate to oblong, laminar symmetry symmetrical, base slightly asymmetrical, laminar L:W ratio 2–2.5:1; base angle acute, apex angle acute, base shape cuneate, position of petiolar attachment marginal, apex shape straight to slightly acuminate; margin type crenate, teeth with convex basal and apical side, sinus angular, tooth apex simple; 1° vein category pinnate.

Remarks. Kasaplıgil labelled this specimen *Vaccinium*. It is doubtful whether this specimen belongs to Ericaceae. There are, however, similarities with some small-leaved swamp rhododendrons, for example *Rhododendron serrulatum* (Small) Millais. There are similarities with the North American *Vaccinium stamineum* L.

aff. Ericaceae gen. et spec. indet. 3

Pl. 13, fig. 7

Material. Specimen UCMP202050.

Description. Leaf, leaf organisation simple; laminar size nanophyll; laminar shape elliptic, lamina symmetrical, base slightly asymmetrical, laminar L:W ratio 4:1; base angle acute, apex angle acute, base shape convex, position of petiolar attachment marginal; margin type serrate, sinus angular; 1° vein category pinnate.

Remarks. Somewhat resembles leaves of *Vaccinium* (*vitis-idaea* L.) by its reduced glandular teeth.

Family FABACEAE Lindl.

Various types of foliage most probably belong to the family Fabaceae but cannot be assigned to particular genera. Traditionally, such leaves and leaflets have been determined down to genus level (e.g. Unger 1867, Paicheler & Blanc 1981). The high degree of convergent evolution of leaf morphology in the Fabaceae renders such an undertaking very difficult, however. We follow Wang (2012) and use the validly published generic names *Leguminocarpum* Dotzler for fossil legume fruits and *Leguminophyllum* A.Escalup-Bassi for fossil legume leaves.

Genus *Leguminophyllum* A.Escalup-Bassi

Leguminophyllum sp. 1

Pl. 14, fig. 1, Pl. 15, figs 1–3

1981 *Cassia hyperborea* Unger – Paicheler & Blanc: pl. 15, figs 11.

Material. Specimens UCMP202051, 202060, 202061.

Description. Leaf, leaf organisation simple; laminar size microphyll; laminar shape ovate, lamina symmetrical to asymmetrical, laminar L:W ratio 2–3:1; base angle acute, apex angle acute, base shape convex to rounded, position of petiolar attachment marginal, apex shape straight; margin type entire; 1° vein category pinnate, 2° vein category weak brochidodromous, 2° vein spacing ± uniform, 2° vein angle ± uniform.

Remarks. Heer (1859, pl. 137, figs 57–60) considered similar leaflets from various Miocene localities of Central Europe to belong to *Cassia hyperborea*. *Cassia* L. is a taxonomically difficult genus which contains between 500 and close to 1000 species. A closer taxonomic relationship of the leaflets from Güvem and the leaflets previously assigned to *Cassia* in several papers by Unger and Heer cannot be established based on impression fossils of leaflets.

Leguminophyllum sp. 2

Pl. 14, figs 2, 4, 5

1981 *Gymnocladus* sp. – Paicheler & Blanc: pl. 15, fig. 12.

Material. Specimens UCMP202047_02, 202052_01; MNHN20090.

Description. Leaf, leaf organisation simple;

laminar size microphyll; laminar shape elliptic-ovate, slightly rhombic, lamina symmetrical, laminar L:W ratio 2–2.5:1; base angle acute, apex angle acute, base shape cuneate, position of petiolar attachment marginal, apex shape straight; margin type entire; 1° vein category pinnate, 2° vein category weak brochidodromous, 2° vein spacing ± uniform, 2° vein angle ± uniform.

Remarks. The leaf corresponds to a general legume leaf type.

Leguminophyllum sp. 3

Pl. 14, fig. 3

Material. Specimen UCMP202053.

Description. Leaf, leaf organisation simple; laminar size microphyll; laminar shape elliptic, lamina symmetrical, laminar L:W ratio 2.5:1; base angle acute, apex angle acute, base shape convex, position of petiolar attachment marginal, apex shape straight; margin type entire; 1° vein category pinnate, 2° vein category weak brochidodromous, 2° vein spacing ± uniform, 2° vein angle ± uniform.

Remarks. Kasaplıgil labelled this specimen *Sophora*. We are unable to assign this Fabaceae-like leaf(let) to a modern genus.

Leguminophyllum sp. 4

Pl. 14, fig. 6

1864 *Physolobium orbiculare* Unger – Unger: p. 22, pl. 5, fig. 3.

Material. Specimen UCMP202053.

Description. Leaf, leaf organisation simple; laminar size nanophyll; laminar shape ovate to nearly circular, lamina slightly asymmetrical, laminar L:W ratio 1:1; base angle obtuse, apex angle obtuse, base shape convex, position of petiolar attachment marginal, apex shape retuse; margin type entire; 1° vein category pinnate.

Remarks. We are unable to assign this Fabaceae-like leaf(let) to a modern genus.

Leguminophyllum sp. 5

Pl. 14, fig. 7

1981 *Sophora europaea* Unger – Paicheler & Blanc: pl. 16, figs 4, 5.

Material. Specimen UCMP202055; MNHN20062.

Description. Leaf, leaf organisation simple; laminar size nanophyll; laminar shape oblong to ovate, lamina slightly asymmetric, laminar L:W ratio 1.5:1; base angle obtuse, apex angle obtuse, base shape slightly cordate, position of petiolar attachment marginal, apex shape rounded with minute tip; margin type entire; 1° vein category pinnate, 2° vein category brochidodromous, 2° vein spacing decreasing towards base, 2° vein angle smoothly increasing towards base; 3° veins alternate percurrent.

Remarks. No particular relationships can be established for this Fabaceae-like leaf(let). Such leaves are also found in Ericaceae.

Leguminophyllum sp. 6

Pl. 14, fig. 8

Material. Specimen UCMP202056_02.

Description. Leaf, leaf organisation simple; laminar size nanophyll; laminar shape oblong, lamina symmetrical, laminar L:W ratio 1:0.2; base angle acute, apex angle acute, base shape cuneate, position of petiolar attachment marginal, apex shape rounded; margin type entire; 1° vein category pinnate.

Remarks. Such leaves resemble leaves of modern brooms, such as *Spartium junceum* L.

Leguminophyllum sp. 7

Pl. 14, fig. 9

Material. Specimen UCMP202057_01.

Description. Leaf, leaf organisation simple; laminar size nanophyll; laminar shape oblong to elliptic, lamina symmetrical, laminar L:W ratio 2:1; base angle acute, apex angle acute, base shape convex to rounded, position of petiolar attachment marginal, apex shape convex to rounded; margin type entire; 1° vein category pinnate, 2° vein category camptodromous to brochidodromous, 2° vein spacing ± uniform, 2° vein angle ± uniform.

Remarks. Such leaflets are present in many genera of Fabaceae; we are unable to assign it to any particular modern genus.

Leguminophyllum sp. 8

Pl. 14, fig. 10

Material. Specimen UCMP202057_02.

Description. Leaf, leaf organisation simple; laminar size nanophyll; laminar shape elliptic, lamina symmetrical, laminar L:W ratio 1.5:1; apex angle obtuse, apex shape retuse; margin type entire; 1° vein category pinnate, 2° vein category brochidodromous, 2° vein spacing ± uniform, 2° vein angle ± uniform.

Remarks. Such leaflets are present in many genera of Fabaceae; we are unable to assign it to any particular modern genus.

Leguminophyllum sp. 9

Pl. 14, figs 11, 12; Pl. 15, fig. 7

Material. Specimens UCMP202058, 202059, 202064.

Description. Leaf, leaf organisation simple; laminar size microphyll; laminar shape oblong to slightly obovate, lamina slightly asymmetrical, asymmetrical base possible, laminar L:W ratio 1.5–2:1; base angle acute, apex angle obtuse, base shape convex to slightly rounded, position of petiolar attachment marginal, apex shape retuse; margin type entire; 1° vein category pinnate, 2° vein category brochidodromous.

Remarks. Such leaflets are present in many genera of Fabaceae; we are unable to assign them to any particular modern genus.

Leguminophyllum sp. 10

Pl. 15, figs 4, 5

Material. Specimen UCMP202062.

Description. Leaf, leaf organisation simple; laminar size microphyll; laminar shape obovate, lamina symmetrical, laminar L:W ratio 3:1; base angle acute, apex angle acute, apex shape convex with minute acuminate tip; margin type entire; 1° vein category pinnate.

Remarks. Kasaplıgil considered this leaf to belong to *Cassiophyllum*. Similar leaflets are found in many genera of Fabaceae.

Leguminophyllum sp. 11
"Acacia parschlugiana Unger"

Pl. 15, figs 9, 10

1864 *Acacia parschlugiana* Unger – Unger: p. 35, pro parte, pl. 11, fig. 20.

1981 *Gleditsia wesseli* Weber – Paicheler & Blanc: pl. 15, figs 9, 10.

Material. Specimen UCMP202066; MNHN20126

Description. Leaf, leaf organisation even-pinnate compound; compound leaf size microphyll, leaflet laminar size nanophyll; laminar shape oblong to slightly ovate, lamina asymmetrical, laminar L:W ratio 2–3:1; base angle acute, apex angle acute, base shape rounded, position of petiolar attachment marginal, apex shape rounded to convex; margin type entire; 1° vein category pinnate.

Remarks. This compound leaf with minute leaves corresponds to *Acacia parschlugiana*. According to Kovar-Eder et al. (2004), such leaf remains belong to Mimosoideae.

Leguminophyllum sp. 12

Pl. 15, fig. 6

1981 *Sophora europaea* Unger – Paicheler & Blanc: pl. 16, figs 2, 3.

Material. Specimen UCMP202063; MNHN20107-02.

Description. Leaf, leaf organisation simple; laminar size microphyll; laminar shape elliptic, lamina asymmetrical, base symmetrical, laminar L:W ratio 1:1; base angle obtuse, apex angle wide obtuse, base shape rounded to truncate, position of petiolar attachment marginal, apex shape retuse; margin type entire; 1° vein category pinnate, 2° vein category weak brochidodromous, 2° vein spacing decreasing towards base, 2° vein angle increasing towards base.

Remarks. Kasaplıgil compared this leaf with the fossil species *Ceratonia emarginata* A.Braun (e.g. Heer 1859) and with *Colutea macrophylla* Heer. Based on the secondary venation (secondary veins branch soon after departing the primary vein), this leaf(let) does not match any fossil or living *Ceratonia*. Paicheler & Blanc (1981) noted similarities with *Sophora*. *Sophora europaea* from Socka (Sotzka; Unger 1850a) is based on five isolated leaflets, one of which is somewhat similar to the material from Güvem.

While Unger compared the fossil species with the pantropical *S. tomentosa* L., closer similarities to this modern species cannot be confirmed for the leaflets from Güvem.

Genus *Leguminocarpum* Dotzler

Leguminocarpum **sp.**

Pl. 24, fig. 1

1981 *Sophora europaea* Unger – Paicheler & Blanc: pl. 15, figs 13, 14.

Material. Specimen MNHN20212.

Description. Pod, fragmented and lacking the proximal and distal ends, not contracted between the seeds.

Remarks. The pods figured in Paicheler and Blanc (1981) and re-figured here cannot be assigned to "*Leguminosites*" *palaeogaeus* (Unger) Kovar-Eder & Kvaček, which has a long stalk, or to "*L.*" *hesperidum* (Unger) Kovar-Eder & Kvaček, which has contracted pods (Kovar-Eder et al. 2004).

Family FAGACEAE Dumort.

Genus *Fagus* L.

Fagus castaneifolia Unger

Pl. 16, figs 1–5

1847 *Fagus castaneifolia* Unger – p. 104, pl. 28, fig. 1.
1867 *Fagus pristina* Saporta – Saporta: p. 69, pl. 6, figs 1–3.
1981 *Fagus pristina* Saporta – Paicheler & Blanc: pl. 11, fig. 15.
2004 *Fagus castaneifolia* – Denk: p. 6, fig. 10, A–M, fig. 11, A–G.

Material. Specimens UCMP202067, 202068_01, 202069, 202236, 2020321_01, 2020439, 202463; MNHN35, 36, 39–43, 45–47, 50, 51, 61, 67, 71, 73, 75, 20040, 20044, 20129, 20144, 20443–2044, five unnumbered specimen.

Description. Leaf, leaf organisation simple; laminar size microphyll to notophyll; laminar shape elliptic to slightly ovate, lamina symmetrical, laminar L:W ratio 3:1; base angle acute, apex angle acute, apex shape straight; margin type serrate, tooth apex simple, tooth shape apical side concave, basal side retroflexed, sinus rounded; 1° vein category pinnate, 2° vein category craspedodromous, 2° vein spacing uniform, 2° vein angle uniform; 3° vein category regular polygonal reticulate.

Remarks. Oligocene to middle Miocene foliage of *Fagus* from Central Asia to Europe has traditionally been split into a number of different species (*F. attenuata* auct. non Göppert, *F. antipofii* Heer in Abich, *F. pristina* Saporta, *F. saxonica* Kvaček & Walther; Kvaček & Walther 1991). Morphologically these species are very similar, and we follow the concept of Denk (2004) to unite these taxa within a single species, *F. castaneifolia*.

Quercus drymeia Unger

Pl. 16, figs 6–11; Pl. 17, figs 1–4

1847 *Quercus drymeja* Unger – Unger: p. 113, pl. 32, figs 1, 2, 4. 1867 *Quercus lonchitis* Unger – Unger: p. 50, pl. 5, figs 1, 2, 4–13, 16, 17.
1867 *Quercus zoroastri* Unger – Unger: p. 52, pl. 6, fig. 23.
1977 *Quercus drymeia* Unger – Kasaplıgil: fig. 30.
1981 *Myrica acuminata* Unger – Paicheler & Blanc: pl. 3 figs 6–9.
1981 *Myrica* sp. – Paicheler & Blanc: pl. 3, fig. 10.
1981 *Quercus drymeia* Unger – Paicheler & Blanc: pl. 10, figs 11–14; pl. 11, figs 1, 2.
2017a *Quercus drymeia* Unger Güvem Morphotype – Denk et al.: pl. 1, pl. 2; pl. 3, figs 1–3.
2017a *Quercus drymeia* Unger Floribunda Morphotype – Denk et al.: pl. 3, figs 4–10, pl. 4, pl. 5, pl. 6, fig. 6.

Material. Specimens UCMP202070–202073, 202074_01, 202075, 202100, 202153_02, 202238, 202240_01, 202241_01, 202242_02, 202251, 202256, 202261, 202265, 202275_01, 202278, 202281_01, 202282, 202291, 202292, 202294, 202295_01, 202296, 202298, 202299, 202303, 202306, 202313_02, 202359, 202362, 202365, 202367–202375, 202449–202452, 202454, 202456, 202458, 202464, 202466, eight unnumbered specimens; MNHN20001, 20045, 20050, 20052, 20067, 20094, 20098-03, 20102-01, 20103, 20111, 20125-01, 20132-01, 20136–20140, 20146, 20149, 20159-02, 20161, 20165-02, 20167, 20173-01, 20178, 20182, 20183, 20187, 20198, 20202, 20242-01, 20253-02, 20275-02, 20284, 20285-01, 20286, 20287, 20290, 20335, 20435, 20438, one unnumbered specimen.

Description. Leaf, leaf organisation simple; laminar size microphyll; laminar shape elliptic, oblong and ovate; lamina symmetrical,

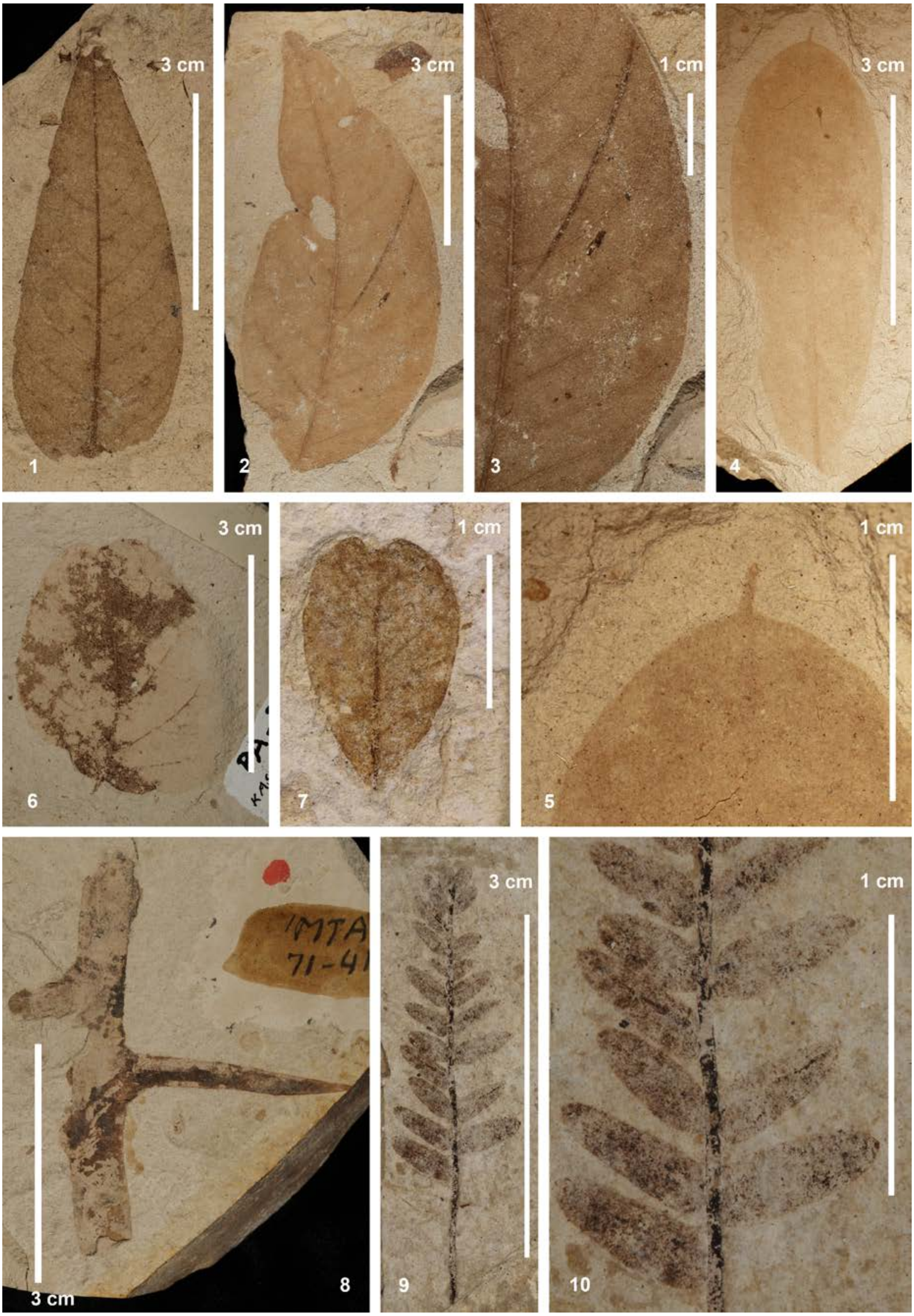

Plate 15. **1–3**. *Leguminophyllum* sp. 1; **1**. Leaf, specimen UCMP202060 (5758); **2**. Leaf, specimen UCMP202061 (5756); **3**. Leaf margin and venation, detail, specimen UCMP202061 (5756); **4**, **5**. *Leguminophyllum* sp. 10; **4**. Leaf, specimen UCMP202062 (5685); **5**. Leaf tip, detail, specimen UCMP202062 (5685); **6**. *Leguminophyllum* sp. 12, leaf, specimen UCMP202063 (5975); **7**. *Leguminophyllum* sp. 9, leaf, specimen UCMP202064 (*n.n.*); **8**. Indet. axis with thorns, twiglet, specimen UCMP202065 (*n.n.* MTA 71-416); **9**, **10**. *Leguminophyllum* sp. 11; **9**. Compound leaf, specimen UCMP202066 (5716); **10**. Compound leaf, detail, specimen UCMP202066 (5716)

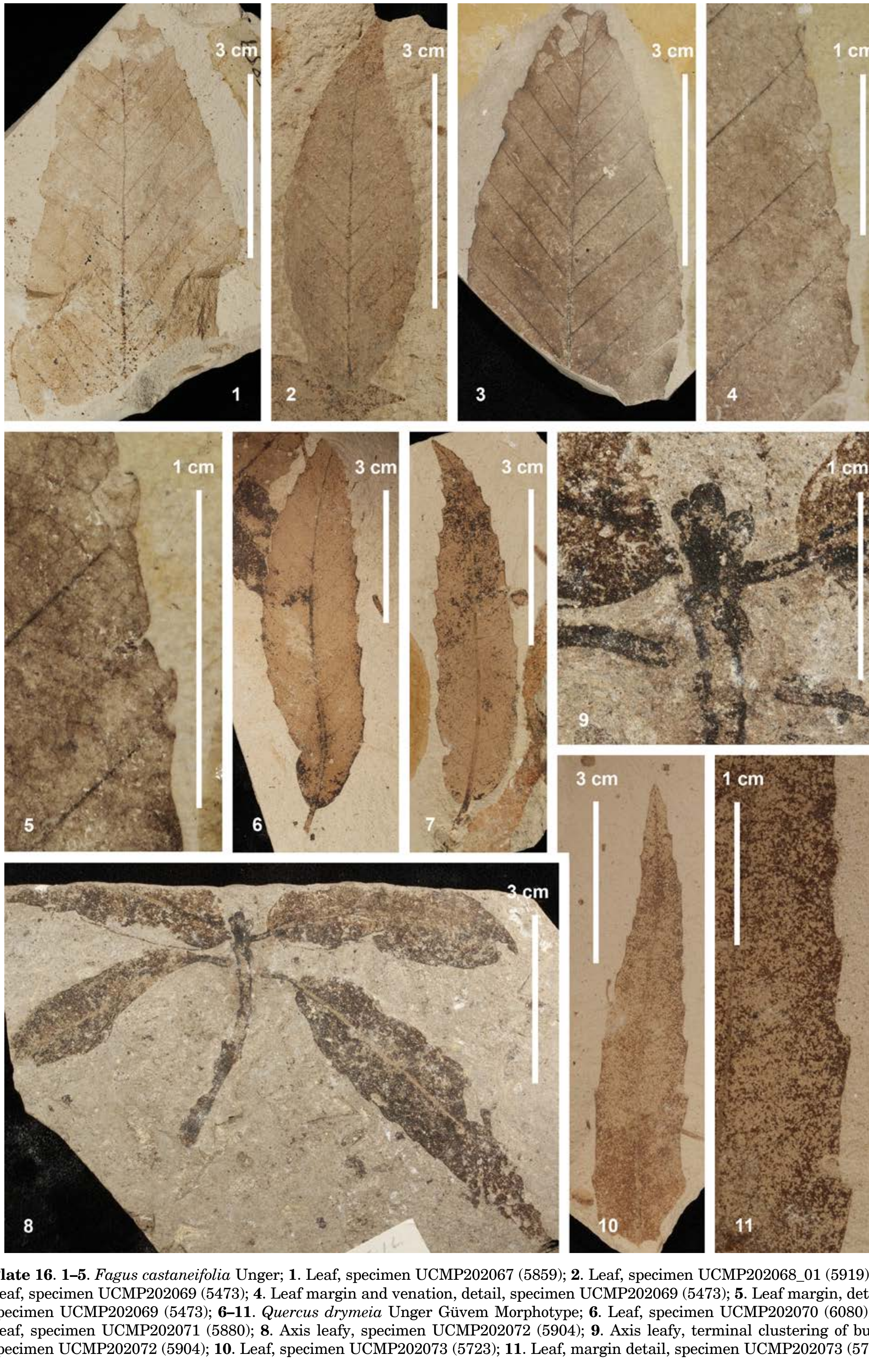

Plate 16. **1–5**. *Fagus castaneifolia* Unger; **1**. Leaf, specimen UCMP202067 (5859); **2**. Leaf, specimen UCMP202068_01 (5919); **3**. Leaf, specimen UCMP202069 (5473); **4**. Leaf margin and venation, detail, specimen UCMP202069 (5473); **5**. Leaf margin, detail, specimen UCMP202069 (5473); **6–11**. *Quercus drymeia* Unger Güvem Morphotype; **6**. Leaf, specimen UCMP202070 (6080); **7**. Leaf, specimen UCMP202071 (5880); **8**. Axis leafy, specimen UCMP202072 (5904); **9**. Axis leafy, terminal clustering of buds, specimen UCMP202072 (5904); **10**. Leaf, specimen UCMP202073 (5723); **11**. Leaf, margin detail, specimen UCMP202073 (5723)

laminar L:W ratio 4–8:1; base angle acute, apex angle acute, base shape rounded and convex, position of petiolar attachment marginal, apex shape straight to slightly acuminate; margin type serrate, tooth apex simple to mucronate, tooth shape apical side concave, basal side retroflexed, sinus rounded; 1° vein category pinnate, 2° vein category craspedodromous, 2° vein spacing mainly uniform, 2° vein angle uniform; 3° vein category regular polygonal reticulate.

Remarks. *Quercus drymeja* belongs to *Quercus* subgenus *Cerris* section *Ilex* (see Denk et al. 2017b for a revised classification of *Quercus*). *Quercus drymeja* has a long stratigraphic range (early Miocene to Pliocene; Velitzelos et al. 2014, Denk et al. 2017a). According to Denk et al. (2017a), two morphotypes are recognized in the Güvem leaf assemblage, one of which (Güvem Morphotype) is restricted to early Miocene sites, while the other (Floribunda Morphotype) is the most common morphotype within *Q. drymeja* and is present throughout the stratigraphic and geographic range of the species.

Quercus* cf. *kubinyii (Kováts ex Ettingsh.) Czeczott

Pl. 17, figs 5, 6

1852 *Castanea kubinyii* Kováts ex Ettingsh. – Ettingshausen: p. 5, pl. 1, fig. 12.
1951 *Quercus kubinyii* (Kováts) Czeczott – Czeczott: p. 392, fig. 7.
2017 *Quercus kubinyii* (Kováts ex Ettingsh.) Czeczott – Güner et al.: pl. 5, figs 8, 9.

Material. Specimen UCMP202076.

Description. Leaf fragment, leaf organisation simple; laminar shape elliptic, lamina symmetrical to asymmetrical, base angle acute, apex angle acute, base shape convex, position of petiolar attachment marginal, margin type serrate, tooth apex mucronate to spinose, tooth shape apical side concave, basal side retroflexed to concave, sinus rounded; 1° vein category pinnate, 2° vein category craspedodromous, 2° vein spacing irregular, 2° vein angle smoothly increasing towards base.

Remarks. Typical *Q. kubinyii* is similar to the modern species *Q. libani* G.Olivier and *Q. variabilis* Blume from Asia Minor and East Asia (cf. Kováts 1856). The specimens at hand do not show the prominent spiniform teeth, are smaller than the typical foliage of *Q. kubinyii*, and possibly fall within the morphological variability of *Q. drymeia*. Despite this, the specimen figured here is similar to small leaves assigned to *Q. kubinyii* from the middle (?) Miocene locality of Arjuzanx (Kvaček et al. 2011), and we tentatively include it within this fossil species. Specimens figured in Kasaplıgil (1977, figs 16, 34, 35) as *Q. kubinyii* most probably do not belong to this species. *Quercus kubinyii* belongs to *Quercus* subgenus *Cerris* section *Cerris* (see Denk et al. 2017b for a revised classification of *Quercus*). Pollen of this section has been recorded from Güvem by Denk et al. (2017a).

Quercus mediterranea Unger

Pl. 17, figs 7–11

1847 *Quercus mediterranea* Unger – Unger: p. 114, pl. 32, figs 5–9.
1977 *Quercus sclerophyllina* Heer – Kasaplıgil: fig. 32.
1981 *Quercus mediterranea* Unger – Paicheler & Blanc: pl. 9, figs 4–11.
2017a *Quercus mediterranea* Unger – Denk et al.: pl. 7, figs 7, 8, pl. 8.

Material. Specimens UCMP202077–202080, 202252, 202305, 202349, 202358_02, 202363_02, 202366, 202417_02, 202417_02 & 03; MNHN164, 20051, 20059, 20068, 20071a & b, 20188, 20195, 20223, 20236, 20239, 20240, 20289; maybe 20109, 20253 69B.

Description. Leaf, leaf organisation simple; laminar size microphyll; laminar shape ranging from elliptic to ovate to obovate; lamina symmetrical to slightly asymmetrical, laminar L:W ratio 2–3:1; base angle acute, apex angle acute, base shape convex to rounded, position of petiolar attachment marginal, apex shape straight; margin type serrate, tooth apex simple, tooth shape apical side concave, basal side retroflexed to concave, sinus rounded; 1° vein category pinnate, 2° vein category craspedodromous, 2° vein spacing irregular, 2° vein angle smoothly increasing towards base, 3° vein category regular polygonal reticulate.

Remarks. Kasaplıgil (1977 and unpublished labels) referred to these specimens as *Q. boissieri* subsp. *pesmenii*, *Q. calliprinos* Webb, *Q. coccifera* L., *Q. haidingeri* Ettingsh., *Q. kubinyii*, *Q. mediterranea*, *Q. sclerophyllina* Heer, and *Q. semecarpifolia* Smith. *Quercus mediterranea* belongs to *Quercus* subgenus *Cerris* section *Ilex* (see Denk et al. 2017b for a revised classification of *Quercus*).

Quercus sosnowskyi Kolak.

Pl. 18, figs 1, 2

1964 *Quercus sosnowskyi* Kolak. – Kolakovsky: p. 89, pl. 25, figs 3–11, pl. 26, figs 2–4, pl. 27, fig. 3, pl. 31, figs 2–7, pl. 32, figs 1–10, pl. 33, figs 1–5, pl. 34, figs 1–5, pl. 35, figs 1–10.

2002 *Quercus sosnowskyi* Kolak. – Kvaček et al.: p. 68, pl. 8, figs 1–5, pl. 9, figs 1–6, pl. 10, figs 1, 2, 4, pl. 15, figs 8, 9, pl. 29, figs 5, 6, pl. 30, figs 1, 2.

2017 *Quercus sosnowskyi* Kolak. – Güner et al.: pl. 6, figs 5–10.

Material. Specimens UCMP202081.

Description. Leaf fragment, leaf organisation simple; laminar size notophyll; margin type serrate, tooth apex simple, tooth shape apical side concave, basal side retroflexed to straight, sinus rounded; 1° vein category pinnate, 2° vein category craspedodromous, 2° vein spacing irregular, in upper two thirds 2° vein angle ± uniform, strong intersecondaries present; 3° vein category mixed opposite/alternate percurrent, 4° vein category regular polygonal reticulate.

Remarks. Kasaplıgil (1977) refers a specimen to *Q. sosnowskyi* f. *angustifolia* Kolak. (Kasaplıgil 1977; fig. 29) but this leaf specimen has a sharply serrate margin in the upper half of the lamina and does not correspond to Kolakovsky's variety (cf. Kolakovsky 1964). The few specimens described here represent the earliest occurrence of this East Mediterranean endemic Neogene species (see Güner et al. 2017). *Quercus sosnowskyi* belongs to *Quercus* subgenus *Cerris* section *Ilex* (see Denk et al. 2017b for a revised classification of *Quercus*).

***Quercus* sp.,** male inflorescence

Pl. 18, fig. 3

1981 *Quercus* sp. – Paicheler & Blanc: pl. 10, figs 7–10.

Material. Specimens UCMP202082, 202281_03, 202307, 202422_02; MNHN20175, 20176, 20412–20432.

Description. Lax male inflorescences, >5 cm long, with alternating, single, staminate flowers, perianth bell-shaped, lobed, ca 5 stamens per flower, anthers ca 1 mm long, with rounded or slightly mucronate apex, filaments slender, ca 2 mm long, longer than perianth lobes.

Remarks. Male inflorescences (perianth lobes and perianth shape, apical parts of anthers) may provide additional information for an infrageneric classification of oaks but are not well studied in extant oak species. Species of section *Cyclobalanopsis* tend to have male flowers that are clustered on the inflorescence axis (Wu & Raven 1999).

***Quercus* sp.,** cups

Pl. 18, figs 4–8

1981 *Quercus* sp. – Paicheler & Blanc: pl. 9, figs 13–20, pl. 11, figs 5–12.

Material. Specimens UCMP202083–202087; MNHN20221, 20222, 20225, 20227–20230, 20232, 20234-01, 20235, 20237, 20238, 20261, 20357–20373, 20374a & b.

Description. Dispersed cups, or cups paired on a short stalk, cup diameter 2–3 cm, bracts imbricate, narrowly triangular at base and linear towards apex.

Remarks. Cupules with similar scales occur in *Quercus* section *Quercus* (e.g. *Q. aliena* Blume) and section *Ilex* (e.g. *Q. floribunda* Wall.), while the scales are different in sections *Cerris* and *Cyclobalanopsis* (Flora of North America Editorial Committee 1997; Menitsky 2005).

***Quercus* sp.**

Pl. 19, figs 1–5

Material. Specimens UCMP202088, 202089_01, 202090.

Description. Leaf, leaf organisation simple; laminar size microphyll; laminar shape elliptic to oblong, lamina symmetrical, laminar L:W ratio 2.5–3.5:1; base angle acute to obtuse, apex angle acute, base shape convex, position of petiolar attachment marginal, apex shape straight; margin type serrate, tooth apex simple, tooth shape apical side concave, basal side straight to retroflexed; 1° vein category pinnate, 2° vein category craspedodromous, 2° vein spacing irregular, 2° vein angle smoothly increasing towards base.

Remarks. Kasaplıgil labelled these specimens *Q. kubinyii* but the dentition and course of secondary veins differ markedly from *Q. kubinyii*. Similar leaf morphology is found in members of *Quercus* section *Quercus* (white oaks, e.g. *Q. infectoria* Oliv.), and section *Ilex* (e.g. *Q. franchetii* Skan).

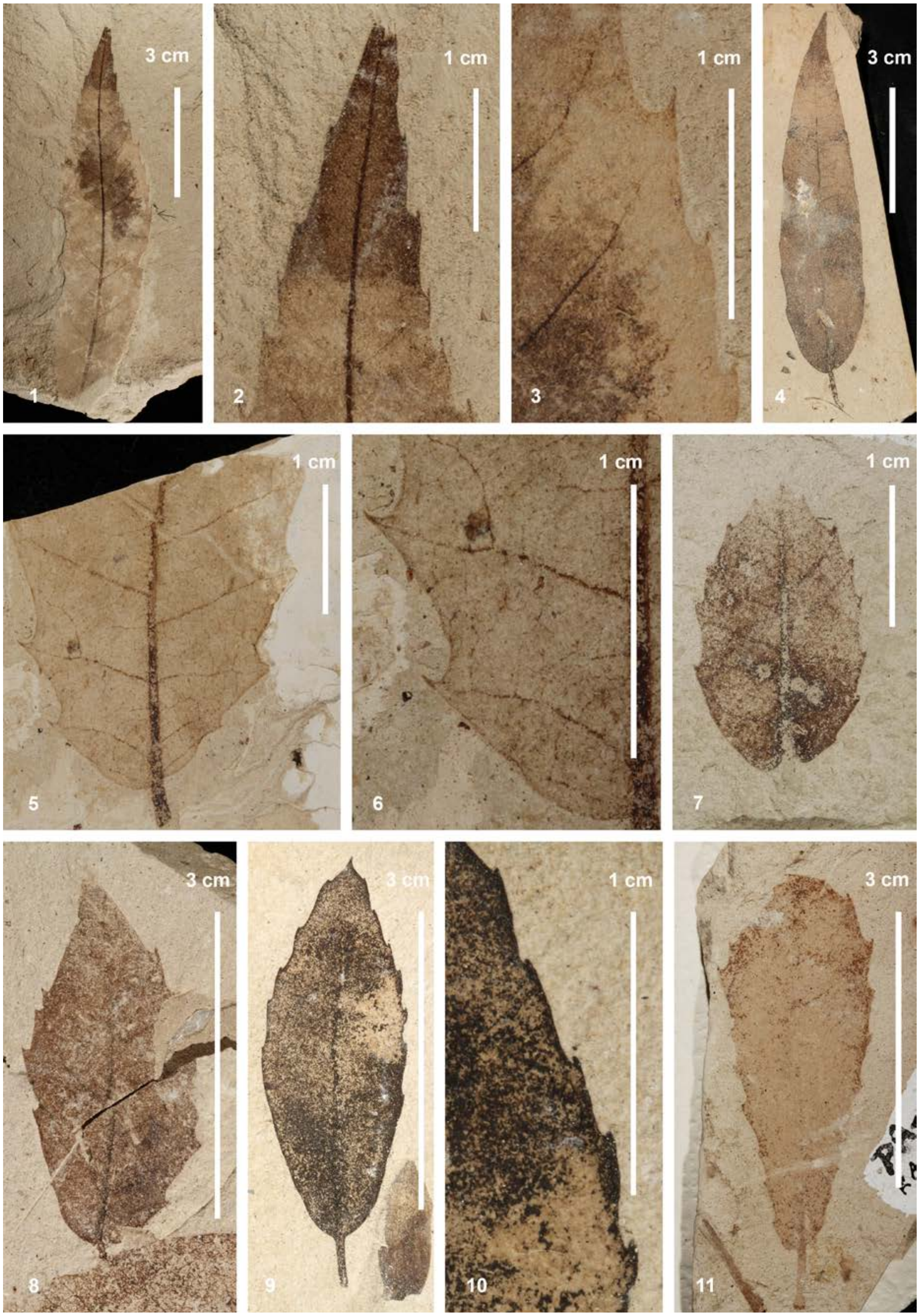

Plate 17. **1–4**. *Quercus drymeia* Unger Floribunda Morphotype; **1**. Leaf, specimen UCMP202074_01 (5910); **2**. Leaf, apical part of lamina, detail, specimen UCMP202074_01 (5910); **3**. Leaf, margin detail, specimen UCMP202074_01 (5910); **4**. Leaf, entire margined leaf, specimen UCMP202075 (5472); **5**, **6**. *Quercus* cf. *kubinyii* (Kováts ex Ettingsh.) Czeczott; **5**. Leaf, specimen UCMP202076 (5966); **6**. Leaf, detail of margin, specimen UCMP202076 (5966); **7–11**. *Quercus mediterranea* Unger; **7**. Leaf, specimen UCMP202077 (6061); **8**. Leaf, specimen UCMP202078 (5179); **9**. Leaf, specimen UCMP202079 (5476); **10**. Leaf, margin, detail, specimen UCMP202079 (5476); **11**. Leaf, inverted pear-shaped lamina, specimen UCMP202080 (6066)

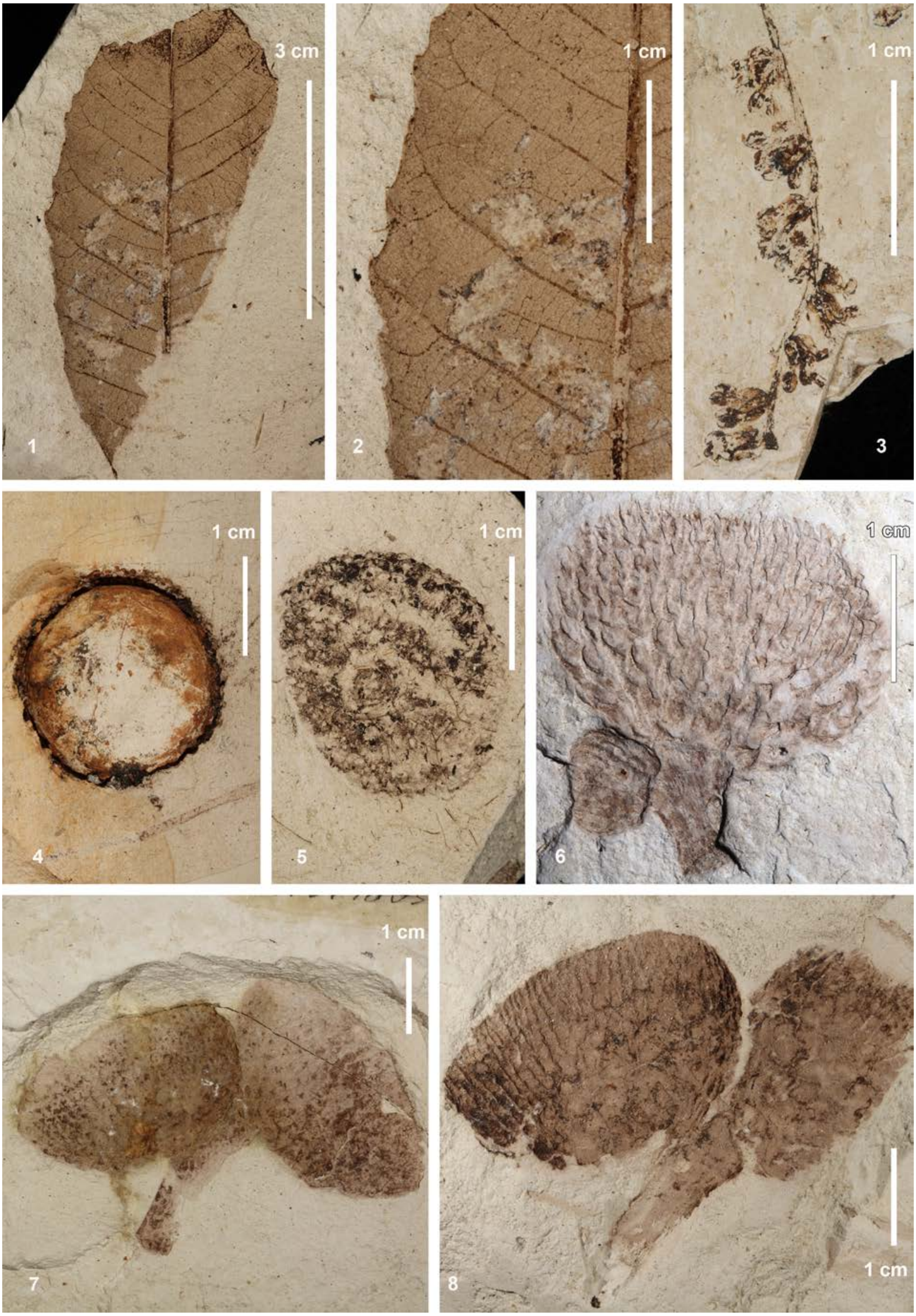

Plate 18. 1, **2**. *Quercus sosnowskyi* Kolak.; **1**. Leaf, specimen UCMP202081 (5445); **2**. Leaf margin and venation, detail, specimen UCMP202081 (5445); **3**. *Quercus* sp. male inflorescence, catkin, specimen UCMP202082 (*n.n.* MAT72-434); **4–8**. *Quercus* sp. cups; **4**. Specimen UCMP202083 (5989); **5**. Specimen UCMP202084 (*n.n.*); **6**. Specimen UCMP202085 (5913); **7**. Specimen UCMP202086 (5908); **8**. Specimen UCMP202087 (5914)

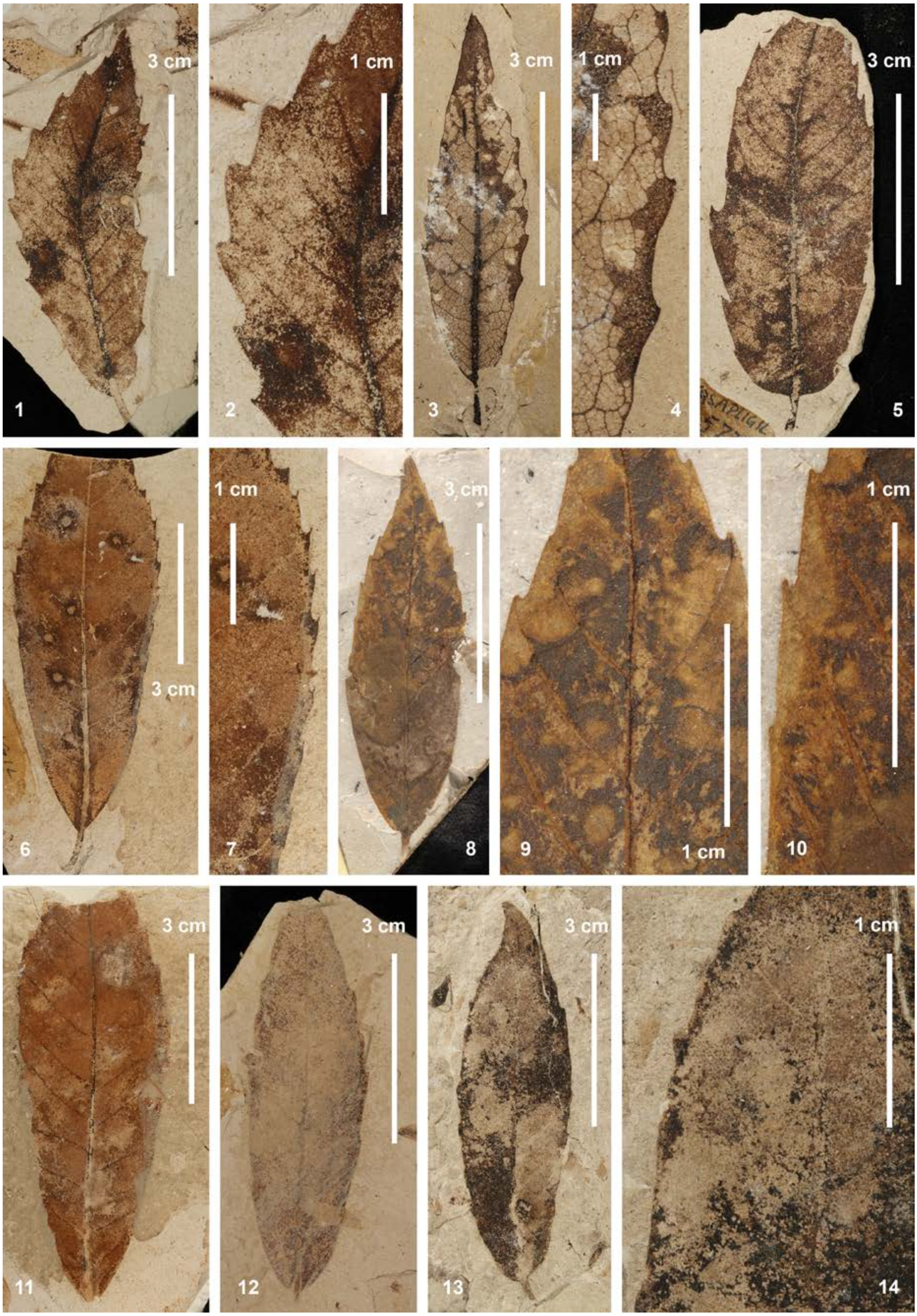

Plate 19. **1–5**. *Quercus* sp.; **1**. Leaf, specimen UCMP202088 (6045); **2**. Leaf, margin detail, specimen UCMP202088 (6045); **3**. Leaf, specimen UCMP202089_01 (5807); **4**. Leaf, margin detail, specimen UCMP202089_01 (5807); **5**. Leaf, specimen UCMP202090 (5736); **6–14**. Fagaceae gen. et spec. indet. 1; **6**. Leaf, specimen UCMP202091 (5918); **7**. Leaf, margin detail, specimen UCMP202091 (5918); **8**. Leaf, specimen UCMP202092 (5896); **9**. Leaf, margin detail, specimen UCMP202092 (5896); **10**. Leaf, margin detail, specimen UCMP202092 (5896); **11**. Leaf, specimen UCMP202093 (6052); **12**. Leaf, specimen UCMP202094_01 (5889); **13**. Leaf, specimen UCMP202095_01(5748); **14**. Leaf, margin detail, specimen UCMP202095_01 (5748)

Plate 20. **1**, **2**. Fagaceae gen. et spec. indet. 2; **1**. Leaf, specimen UCMP202096 (5699); **2**. Leaf, venation and margin, detail, specimen UCMP202096 (5699); **3–7**. Fagaceae gen. et spec. indet. 3; **3**. Leaf, specimen UCMP202097 (6037); **4**. Leaf, venation, detail, specimen UCMP202097 (6037); **5**. Leaf, specimen UCMP202098 (6055); **6**. Leaf, specimen UCMP202099_01 (5873a); **7**. Leaf, venation and margin, detail, specimen UCMP202099 (5873a); **8–11**. Fagaceae gen. et spec. indet. aff. *Eotrigonobalanus*; **8**. Leaf, specimen UCMP202100 (5897); **9**. Leaf margin, detail, specimen UCMP202100 (5897); **10**. Leaf, specimen UCMP202037_01 (5460a); **11**. leaf, margin detail, specimen UCMP202037_01 (5460a)

Fagaceae gen. et spec. indet. 1

Pl. 19, figs 6–14

Material. Specimens UCMP202091–202093, 202094_01, 202095_01.

Description. Leaf, leaf organisation simple; laminar size notophyll; laminar shape elliptic, lamina symmetrical to slightly asymmetrical, laminar L:W ratio 2.5–3.5:1; base angle acute, apex angle acute, base shape convex, position of petiolar attachment marginal, apex shape straight to slightly acuminate; margin type entire (basal part of lamina) to serrate (apical portion of lamina), tooth apex simple, tooth shape apical side concave, basal side straight, sinus rounded; 1° vein category pinnate, 2° vein category craspedodromous, 2° vein spacing decreasing towards base, 2° vein angle smoothly increasing towards base.

Remarks. These specimens show similarities with a number of genera within Fagaceae. For example, leaves of the Southeast Asian *Lithocarpus areca* (Hick. & A.Camus) A.Camus may produce very similar leaves; among *Quercus*, leaves of *Q. engleriana* Seem. (section *Ilex*; Denk & Grimm 2010) may be virtually identical to the ones included here.

Fagaceae gen. et spec. indet. 2

Pl. 20, figs 1, 2

Material. Specimen UCMP202096.

Description. Leaf, leaf organisation simple; laminar size notophyll; laminar shape narrow elliptic, lamina symmetrical to slightly asymmetrical, laminar L:W ratio >4:1; base angle acute, base shape convex; margin type entire; 1° vein category pinnate, 2° vein category weak brochidodromous, 2° vein spacing irregular, a few intersecondaries present.

Remarks. We are unable to assign this leaf to a particular modern genus within Fagaceae. Similar leaf types occur in various genera of Castaneoideae and in *Quercus*.

Fagaceae gen. et spec. indet. 3

Pl. 20, figs 3–7

1981 *Quercus* sp. – Paicheler & Blanc: pl. 11, figs 3, 4.

Material. Specimens UCMP202097, 202098, 202099_01; MNHN20038_01, 20047.

Description. Leaf, leaf organisation simple; laminar size notophyll; laminar shape narrow elliptic, lamina symmetrical to slightly asymmetrical, laminar L:W ratio 3.5–5:1; base angle acute, base shape convex; margin type entire; 1° vein category pinnate, 2° vein category weak brochidodromous, 2° vein spacing irregular, a few intersecondaries present.

Remarks. Kasaplıgil used different names for these specimens, including *Quercus lonchitis* Unger, *Q. sosnowskyi* Kolak. forma *angustifolia*, and *Castanopsis* sp.

There are similarities with a few species of *Castanopsis* and *Lithocarpus*, particularly with respect to secondary venation and general leaf shape. These are, for example, *Castanopsis fargesii* Franch., China [P00713408, for reference] and *Lithocarpus henryi* Rehder & E.H.Wilson [P00744423, for reference]. Among extinct Castaneoideae, *Trigonobalanopsis* has similar leaf shapes.

Fagaceae gen. et spec. indet. aff. *Eotrigonobalanus*

Pl. 20, figs 8–11

?1981 *Quercus drymeja* Unger – Paicheler & Blanc: pl. 11, figs 1, 2.

?2014 *Eotrigonobalanus furcinervis* (Rossm.) Walther & Kvaček – Velitzelos et al.: pl. 3, figs 4–9.

2017a *Quercus drymeja* Güvem Morphotype – Denk et al.: pl. 2, figs 8, 9.

Material. Specimens UCMP202037_01, 202100; MNHN20045.

Description. Leaf, leaf organisation simple; laminar size notophyll; laminar shape narrow elliptic, lamina symmetrical to slightly asymmetrical, laminar L:W ratio 3.5–5:1; base angle acute to obtuse, base shape convex to slightly cordate, apex angle acute, apex shape straight; margin type serrate, tooth apex simple, tooth shape apical side concave, basal side retroflexed; 1° vein category pinnate, 2° vein category craspedodromous, secondary veins occasionally branching well inside margin, 2° vein spacing uniform, a few intersecondaries present, vein angle uniform.

Remarks. Few fagaceous leaves from Güvem resemble the extinct genus *Eotriogonobalanus*. However, although the morphological variability of this genus is enormous (e.g. Kvaček & Walther 1989), the specimens from Güvem are quite distinct. Not knowing exactly what they are, we nevertheless point out their resemblance to the extinct genus. Dispersed pollen grains of *Eotrigonobalanus* have recently been described from Güvem (Denk et al. 2017a).

Family HYDROCHARITACEAE Juss.

Genus *Stratiotes* L.

Stratiotes kaltennordheimensis (Zenker) Keilhack

Pl. 39, figs 3, 4

1833 *Folliculites kaltennordheimensis* Zenker – Zenker: p. 177, pl. 4, figs A3–7.
1896 *Stratiotes kaltennordheimensis* (Zenker) Keilhack – Keilhack: p. 504.
1923 *Stratiotes kaltennordheimensis* (Zenker) Keilhack – Chandler: p. 130, pl. 5, fig. 15, pl. 6, figs 9–11, 27.
1981 *Stratiotes thalictroides* (Brongn.) Chandler – Paicheler & Blanc: pl. 1, figs. 9, 10.

Material. MNHN20204, 20300.

Description. Seed, oblong, 6.4–7.1 mm long, 3– 3.6 mm wide, bent at the base, collar truncated, testa with elongated tubercles.

Remarks. The seeds figured by Paicheler and Blanc (1981) and refigured here correspond to the specimens from the lower Miocene of Germany described in detail and figured by Chandler (1923). In contrast, *S. thalictroides* (Brongn.) Chandler, differs by much narrower, and oblong seeds.

Family JUGLANDACEAE DC. ex Perleb

aff. *Engelhardia* sp.

Pl. 21, figs 1, 2

Material. Specimen UCMP202101.

Description. Leaf, leaf organisation even-pinnate; laminar size microphyll; laminar shape ovate; lamina symmetrical, laminar L:W ratio 3:1; base angle acute, apex angle acute, base shape convex to rounded, position of petiolar attachment marginal, apex shape straight; margin type serrate, tooth apex simple, glandular, tooth shape apical side concave, basal side straight, sinus in basal area angular, in upper leaf part rounded; 1° vein category pinnate, 2° vein category semicraspedodromous, 2° vein spacing decreasing towards base, 2° vein angle smoothly decreasing towards base, weak intersecondaries present.

Remarks. This leaf resembles the modern East and Southeast Asian *Engelhardia apoensis* Elmer ex Nagel (cf. Manchester 1987; herbarium P) and *E. serrata* Blume China (herbarium P), based on the even-pinnate leaf organisation, the secondary venation and the minute teeth with a glandular tip. It differs from *E. apoensis* by the strictly opposite arrangement of the leaflets. It has nothing in common with other leaves from European Neogene strata referred to as *E. orsbergensis* (P.Wessel et Weber) Jähnichen, Mai et Walther. The latter show more resemblance with New World species of subfamily Engelhardioideae and not with modern (East Asian) species of *Engelhardia*. Kasaplıgil suggested affinities with *Rhus* or *Pistacia* but the dentition and course of secondary veins in the fossil leaf do not match leaves of these genera.

Genus *Juglans* L.

***Juglans* sp.**

Pl. 21, figs 3–6

1981 *Juglans acuminata* A.Braun – Paicheler & Blanc: pl. 16, figs 15, 16.

Material. Specimens UCMP202102, 202103; MNHN20032, 20035–20037, 20110, 20433.

Description. Leaf fragment, leaf organisation simple; laminar size noto- to mesophyll; lamina symmetrical, laminar L:W ratio 3–4:1; apex angle acute, apex shape straight; margin type serrate, tooth apex simple, tooth shape apical side concave, basal side retroflexed to concave, sinus rounded; 1° vein category pinnate, 2° vein category eucamptodromous, 2° vein spacing ± uniform, strong intersecondaries present; 3° vein category regular polygonal reticulate.

Remarks. Two leaflets belong to *Juglans*. Kasaplıgil considered the two specimens to be *J. shanwangensis* Hu & Chaney from the middle Miocene Shanwang locality in eastern China (Hu & Chaney 1940). This fossil species shares the presence of small remote teeth with the material from Güvem. In *J. acuminata* A.Braun the leaflets are entire-margined.

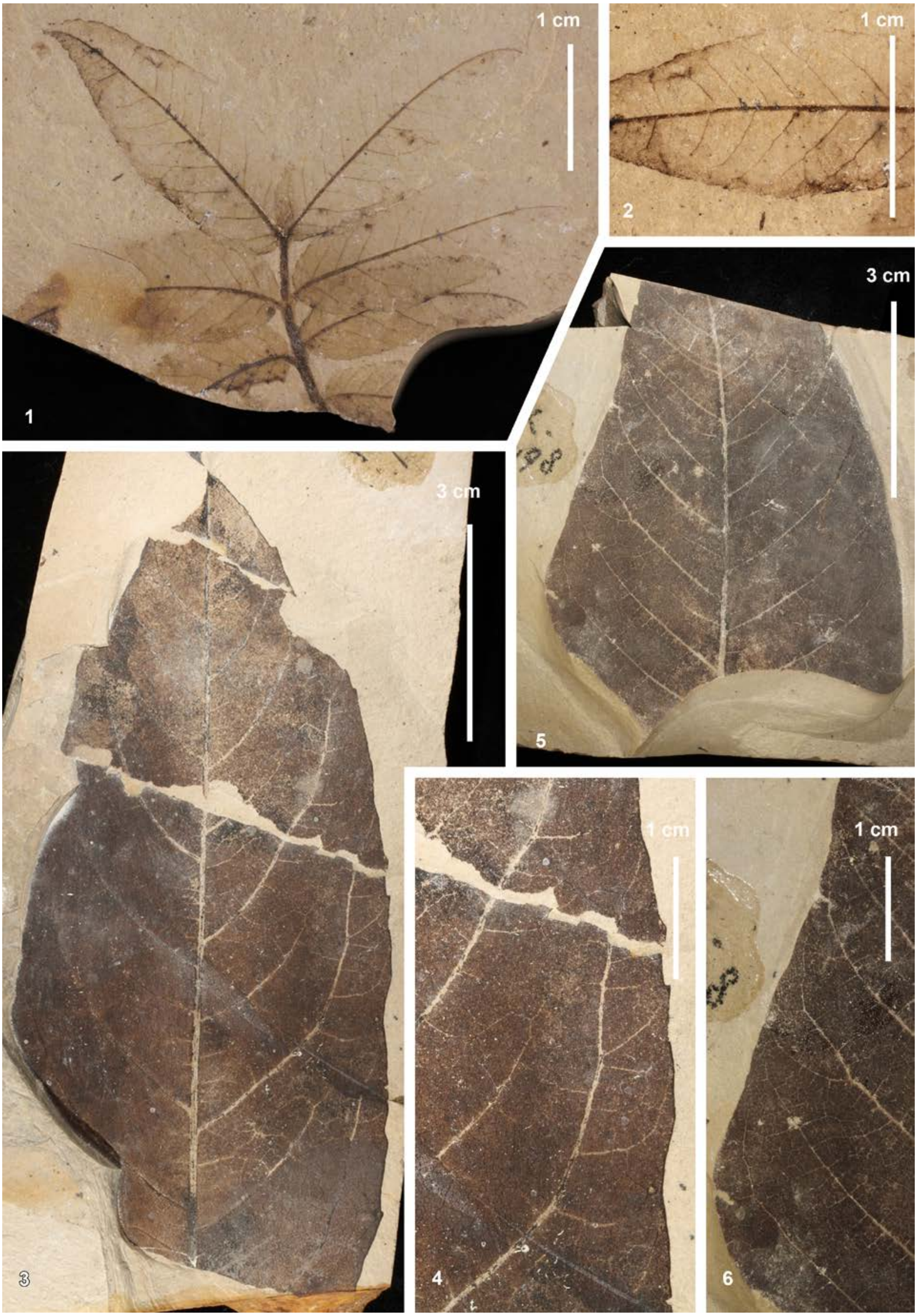

Plate 21. **1**, **2**. aff. *Engelhardia* sp.; **1**. Even pinnate leaf, specimen UCMP202101 (*n.n.*/2657?); **2**. Leaflet, detail, specimen UCMP202101 (*n.n.*/2657?); **3–6**. *Juglans* sp.; **3**. Leaf, specimen UCMP202102 (5499); **4**. Leaf, venation and margin, detail, specimen UCMP202102 (5499); **5**. Leaf, specimen UCMP202103 (5498); **6**. Leaf venation and margin, detail, specimen UCMP202103 (5498)

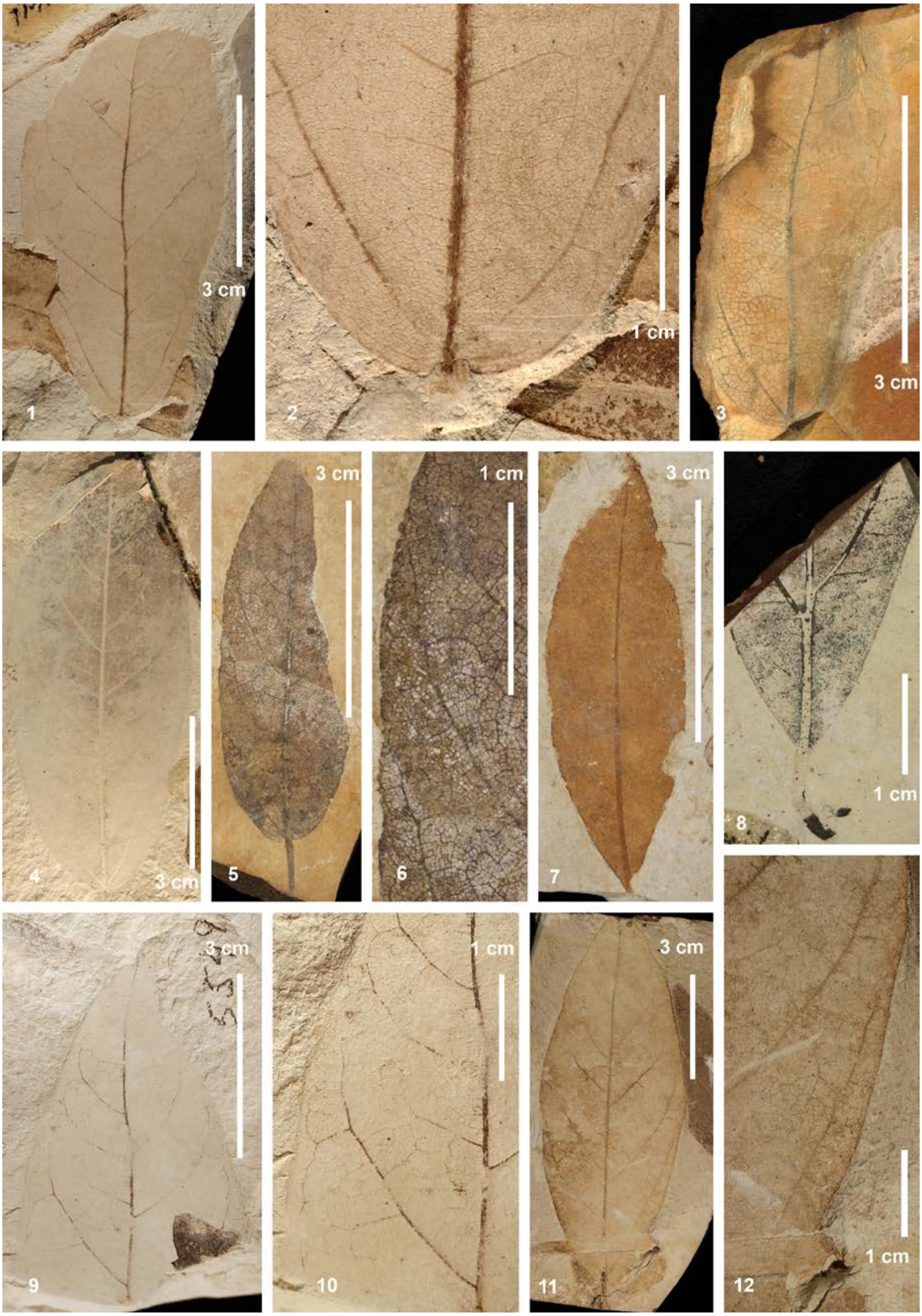

Plate 22. **1–6**. Lauraceae gen. et spec. indet. 1; **1**. Leaf, specimen UCMP202049 (5454); **2**. Leaf base and venation, detail, specimen UCMP202049 (5454); **3**. Leaf, specimen UCMP202104 (5428); **4**. Leaf, specimen UCMP202105 (5558); **5**. Leaf, specimen UCMP202106 (5709); **6**. Leaf venation and margin, detail, specimen UCMP202106 (5709); **7**. Lauraceae gen. et spec. indet. 2, cf. *Laurophyllum pseudoprinceps* Weyland & Kilpper, leaf, specimen UCMP202107 (5538); **8**. *Daphnogene polymorpha*, leaf, specimen UCMP202108 (5712); **9**, **10**. Lauraceae gen. et spec. indet. 3; **9**. Leaf, specimen UCMP202109 (5549); **10**. Leaf venation and margin, detail, specimen UCMP202109 (5549); **11**, **12**. *Laurophyllum* sp.; **11**. Leaf, specimen UCMP202110 (5912); **12**. Leaf venation and margin, detail, specimen UCMP202110 (5912)

Based on the leaf morphological variability in modern *Juglans regia*, this difference would not appear to be sufficient to discriminate species. In the modern species, entire-margined leaflets co-occur with serrate leaflets on the same tree.

In Kasaplıgil's collection there are a few remains of male catkins probably belonging to this genus (Pl. 41, figs 5, 6); the specimens figured by Paicheler and Blanc (1981, pl. 16, figs 7–12) most likely also represent *Juglans*.

Family LAURACEAE Juss.

Genus *Daphnogene* Unger

Daphnogene polymorpha (A.Braun) Erw.Knobloch

Pl. 22, fig. 8; Pl. 23, figs 3–5

1845 *Ceanothus polymorpha* A.Braun – Braun: p. 171.
1968 *Daphnogene polymorpha* (A.Braun) Erw.Knobloch – Knobloch: p. 138.
1981 *Cinnamomum polymorphum* Heer – Paicheler & Blanc: pl. 8, fig. 3.
1993 *Cinnamophyllum scheuchzeri* (Heer) Kräusel & Weyland – Gemici et al.: p. 99, pl. 8, fig. 5.
1993 *Cinnamophyllum polymorphum* (A.Braun) Kräusel & Weyland – Gemici et al.: p. 99, pl. 8, fig. 6.

Material. Specimens UCMP202108, 202111–202113; MNHN20054.

Description. Leaf, leaf organisation simple; laminar size microphyll; laminar shape elliptic; lamina symmetrical, laminar L:W ratio 3–3.5:1; base angle acute, apex angle acute, base shape cuneate, position of petiolar attachment marginal, apex shape straight; margin type entire; 1° vein category pinnate with one pair of suprabasal acute secondaries, 2° vein category eucamptodromous, 2° vein spacing decreasing towards apex, 2° vein angle smoothly decreasing towards apex.

Remarks. The leaves shown in Pl. 23 (figs 4, 5) were labelled *Litsea* and *Neolitsea* by Kasaplıgil.

Genus *Laurophyllum* Göppert

Laurophyllum sp.

Pl. 22, figs 11, 12; Pl. 23, figs 1, 2

1981 *Populus mutabilis* Heer – Paicheler & Blanc: pl. 5, fig. 2.
1981 *Ocotea heeri* Gaudin – Paicheler & Blanc: pl. 8, figs 4, 6.
1993 *Laurophyllum primigenium* (Unger) Kräusel & Weyland – Gemici et al.: p. 99, pl. 8, fig. 3.

Material. Specimens UCMP202089, 202110; MNHN20033a & b.

Description. Leaf, leaf organisation simple; laminar size notophyll; laminar shape elliptic; lamina symmetrical, laminar L:W ratio 3–4:1; base angle acute, apex angle acute, base shape convex, position of petiolar attachment marginal, apex shape straight; margin type entire to serrate; tooth apex simple, tooth shape apical side concave, basal side concave, sinus rounded, 1° vein category pinnate with one pair of suprabasal acute secondaries, 2° vein category eucamptodromous, 2° vein spacing irregular, 2° vein angle ± uniform, weak intersecondaries present; 3° vein category alternate percurrent; 4° vein category regular polygonal reticulate; areolation well developed, four- to five-sided.

Remarks. Lauraceous leaves are difficult to assign to a particular modern or extinct genus based on leaf imprints alone. Nevertheless, the specimens from Güvem fit fairly well with the circumscription of this fossil genus.

Lauraceae gen. et spec. indet. 1

Pl. 22, figs 1–6

Material. Specimens UCMP202049, 202104–202106.

Description. Leaf, leaf organisation simple; laminar size micro- to notophyll; laminar shape elliptic to oblong; lamina symmetrical, laminar L:W ratio 3:1; base angle acute, base shape rounded, position of petiolar attachment marginal; margin type entire; 1° vein category pinnate with one pair of suprabasal acute secondaries reaching up to one fourth to one third of lamina; 2° vein category eucamptodromous, 2° vein spacing irregular, 2° vein angle irregular, weak intersecondaries present; 3° vein category regular polygonal reticulate; areolation well developed, four- to five-sided.

Remarks. The specimens included within Lauraceae gen. et spec. indet. 1 are characterized by the prominent pair of suprabasal secondaries at the base of the lamina. The specimen figured in Pl. 20 (figs 5, 6) is markedly similar to a leaf figured in Meyer and Manchester (1997, pl. 6, figs 2, 3) from late Oligocene deposits of Oregon as *Litsaeophyllum praesanguinea* (Chaney & Sanborn) Wolfe.

Lauraceae gen. et spec. indet. 2, cf. *Laurophyllum pseudoprinceps* Weyland & Kilpper

Pl. 22, fig. 7

1963 *Laurophyllum pseudoprinceps* Weyland & Kilpper – Weyland & Kilpper: p. 100, text fig. 6, pl. 23, figs 14–19.

Material. Specimen UCMP202107.

Description. Leaf, leaf organisation simple; laminar size microphyll; laminar shape elliptic; lamina symmetrical, laminar L:W ratio 2.5:1; base angle acute, apex angle acute, base shape cuneate, position of petiolar attachment marginal, apex shape straight; margin type entire; 1° vein category pinnate, 2° vein category eucamptodromous, 2° vein spacing irregular, 2° vein angle ± uniform, one pair of acute 2° veins suprabasal, weak intersecondaries present.

Remarks. This specimen corresponds to *Laurophyllum pseudoprinceps* as figured by Kvaček et al. 2011) from middle Miocene deposits of western France.

Lauraceae gen. et spec. indet. 3

Pl. 22, figs 9, 10

Material. Specimen UCMP202109.

Description. Leaf fragment, leaf organisation simple; apex angle acute, apex shape straight; margin type entire; 1° vein category pinnate, 2° vein category weak brochidodromous, 2° vein spacing irregular, 2° vein angle irregular, weak intersecondaries present; 3° vein category regular polygonal reticulate.

Remarks. Kasaplıgil labelled this specimen *Persea* aff. *indica* (L.) Spreng. Indeed, various species of *Persea* closely resemble the specimen from Güvem by their size, brochidodromous secondary venation, additional loops and weak intersecondaries (Klucking 1987). Despite this, no closer relationship with a particular genus of Lauraceae can be established.

Family MAGNOLIACEAE Juss.

Genus *Magnolia* L.

Magnolia sturii V.Sitar

Pl. 23, figs 6–8, Pl. 24, figs 2, 3

1973 Magnolia sturii V.Sitar – Sitar: p. 16, pl. 4, fig. 6, pl. 6, figs 1, 3, pl. 7, figs 1, 2.

1977 *Magnolia sprengeri* Pamp. – Kasaplıgil: fig. 28.

1981 *Magnolia sturii* V.Sitar – Paicheler & Blanc: p. 30, pl. 9, figs 1–3.

1981 ?*Bumelia florissanti* Lesq. – Paicheler & Blanc: p. 38, pl. 18, fig. 6.

Material. Specimens UCMP202114, 202115, 202273, 202408; MNHN20029; maybe 20031, 20093, 20097.

Description. Leaf fragment, leaf organisation simple; laminar size notophyll; lamina symmetrical; base angle acute, base shape cuneate, position of petiolar attachment marginal; margin type entire; 1° vein category pinnate, 2° vein category eucamptodromous, 2° vein spacing irregular, 2° vein angle uniform, weak intersecondaries present, 3° vein category regular polygonal reticulate.

Remarks. Kasaplıgil (1977) ascribed the fossil foliage to the extant *Magnolia sprengeri* native to China and also compared the fossil with the modern *M. cylindrica* Wils. Both these species show only limited similarity with the fossil leaves. Paicheler and Blanc (1981) referred a few leaves to *M. sturii* described by Sitar (1973) based on material from middle Miocene deposits of Slovakia. Sitar compared the fossil species with the extant East Asian species *M. stellata* (Siebold & Zucc.) Maxim. and *M. kobus* DC. The leaf shown in Pl. 23 (figs 7, 8) is similar to Paicheler and Blanc's (1981) *M. sturii* (refigured in Pl. 24, fig. 3). These specimens might well correspond to Sitar's fossil species. Tertiary veins running distinctly oblique to the secondaries as seen in the specimen in Pl. 21, fig. 6 are not common in the extant species but occasionally do occur in fossil foliage (Z. Kvaček, pers. observ.).

Genus *Magnoliostrobus* Seward & Conway

Magnoliostrobus sp.

Pl. 23, figs 9, 10

2000 *Magnoliostrobus* sp. – Fischer & Butzmann: p. 66, pl. 20, fig. 1.

Material. Specimen UCMP202116.

Description. Cone on short axis, axis 1 cm long, stout, cone >3 cm long and ca 2 cm wide, with follicles.

Remarks. The cone, though not very well preserved, might well belong to *Magnolia*.

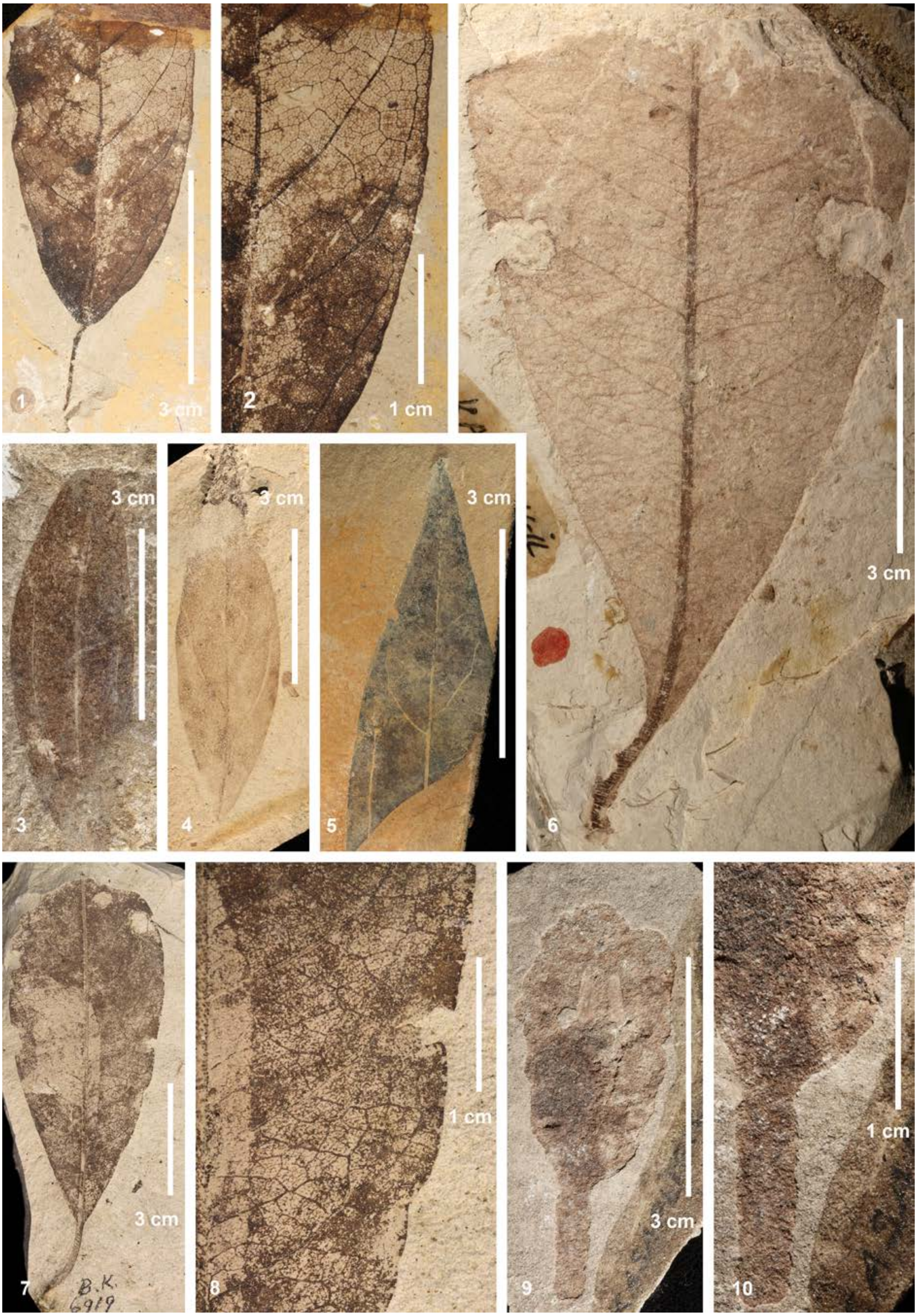

Plate 23. **1**, **2**. *Laurophyllum* sp.; **1**. Leaf, specimen UCMP202089 (5807); **2**. Leaf, venation and margin, detail, specimen UCMP202089 (5807); **3–5**. *Daphnogene polymorpha*; **3**. Leaf, specimen UCMP202111 (*n.n.*); **4**. Leaf, specimen UCMP202112 (5509); **5**. Leaf, specimen UCMP202113 (5722); **6–8**. *Magnolia sturii* V.Sitar; **6**. Leaf, specimen UCMP202114 (5557); **7**. Leaf, specimen UCMP202115 (6919); **8**. Leaf venation and margin, specimen UCMP202115 (6919); **9**, **10**. *Magnoliostrobus* sp.; **9**. Strobilus, specimen UCMP202116 (5797); **10**. Strobilus, detail, specimen UCMP202116 (5797)

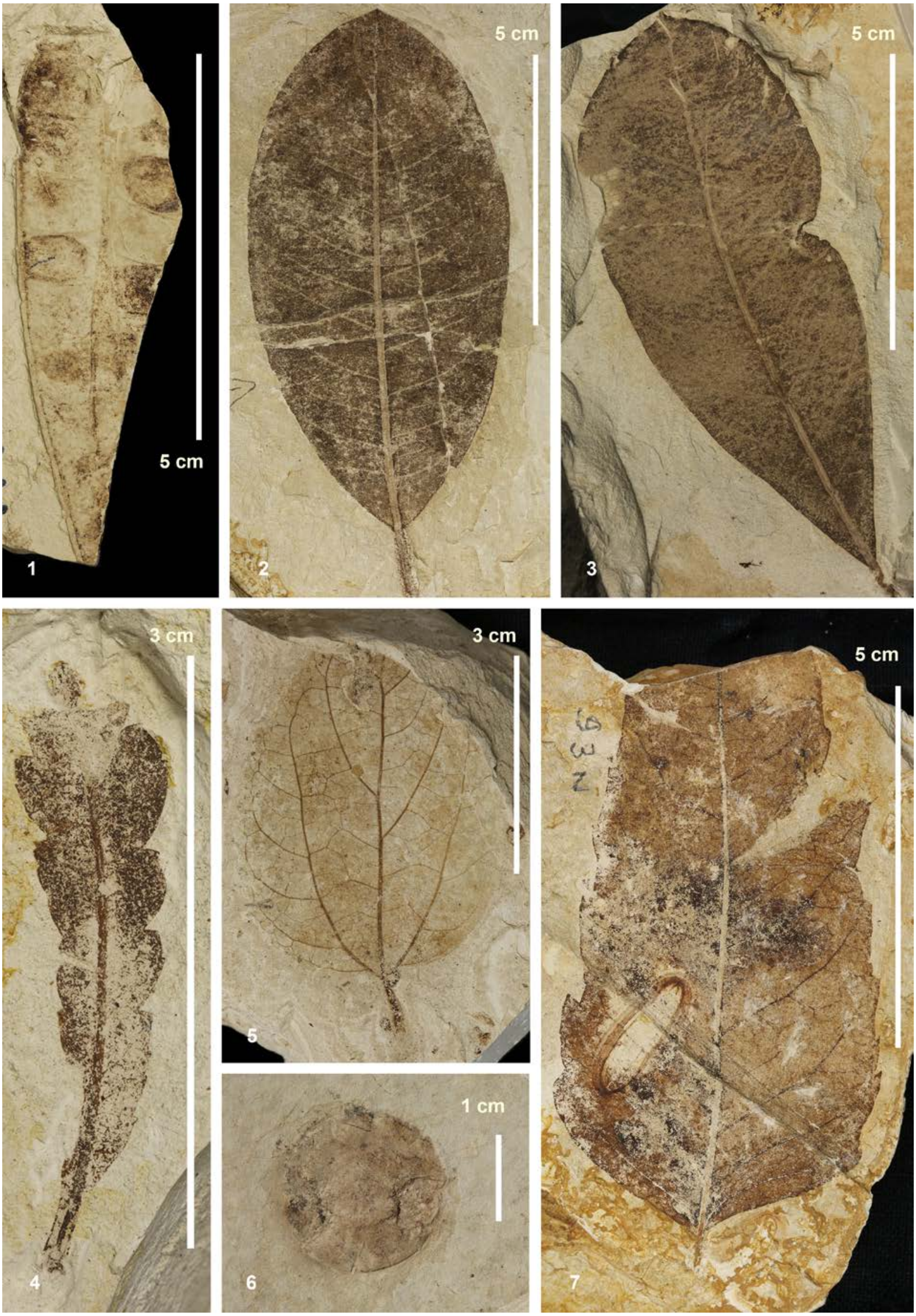

Plate 24. **1**. *Leguminocarpum* sp., pod, specimen MNHN20212; **2**, **3**. *Magnolia sturii* V.Sitar; **2**. Leaf, specimen MNHN20029; **3**. Leaf, specimen MNHN20031; **4**. *Comptonia oeningensis* A.Braun, leaf, specimen MNHN20106; **5**. *Paliurus tiliifolius* Mill., leaf, specimen MNHN20063; **6**. *Paliurus favonii* Unger, fruit, specimen MNHN20226; **7**. *Oleinites hallbaueri* (Mai) Sachse, leaf, specimen MNHN20046

Family MALVACEAE Juss.

Genus *Tilia* L.

***Tilia* sp.**

Pl. 24, figs 1–3, 7, 8

1981 *Ulmus* sp. – Paicheler & Blanc: pl. 15, fig. 8.

Material. Specimens UCMP202117, 202414; MNHN20024-01, 20025, 20285-02; maybe 20120.

Description. Leaf, leaf organisation simple; laminar size noto- to mesophyll; laminar shape elliptic to circular; lamina asymmetrical, laminar L:W ratio 1:1; base angle obtuse, apex angle obtuse, base shape convex and concave, position of petiolar attachment marginal, apex shape acuminate; margin type serrate, tooth apex simple, teeth with concave to convex apical and flexuous to convex basal side, sinus angular; 1° vein category pinnate, 2° vein category craspedodromous, 2° vein spacing increasing toward base, 2° vein angle ± uniform, slightly agrophic veins present in basal area; 3° vein category mixed opposite/alternate.

Remarks. The few leaves fall within the morphological variability of the western Eurasian *Tilia platyphyllos* Scop. Similar leaves have been reported from early Miocene deposits of Lesbos (Velitzelos et al. 2014).

Tilia knoblochii Velitzelos & Gregor

Pl. 25, figs 4, 5 (bracts), 6 (fruit)

1981 *Tilia platyphyllos* Scop. – Paicheler & Blanc: pl. 18, figs 12, 13.
2005 *Tilia knoblochii* Velitzelos, D.Velitzelos & Gregor – Velitzelos et al.: p. 5, pl. 3, figs 1–6, pl. 4, figs 6, 7.
2014 *Tilia knoblochii* Velitzelos, D.Velitzelos & Gregor – Velitzelos et al.: pl. 10, fig. 1.

Material. Specimens UCMP202118, 202119 (bracts), UCMP202120, 202304 (fruits); MNHN20076, 20214, 20413–20417 (fruits).

Description. Bracts and fruits, isolated bract >8 cm long, basal and apical parts spatulate, peduncle fused with central vein of bract along ca one fourth of bract lamina (indicated by much thicker central vein of bract in basal part of lamina), bract venation pinnate, secondary venation irregular, brochidodromous; fruits capsules, subglobose, 7–8 mm long, consisting of four valves.

Remarks. The bracts correspond morphologically (bract fused in lower ¼ – ½ with peduncle, bract oblong) to Manchester's (1994) type C. Based on the distinct shape of the bract with a spatulate apical and basal part, and the dimensions of bract and fruits, the specimens from Güvem appear to be very similar to bracts with attached capsules from early Miocene deposits of Kimi (Euboea, Greece), which were described as *Tilia knoblochii* (Velitzelos et al. 2005). According to Manchester (1994), type C, although being the most common type in extant *Tilia*, is not known from Europe before the Pliocene, while from Central Asia, Oligocene bracts from Kazakhstan correspond to type C. The bracts illustrated by Kryshtofowicz et al. (1956, pl. 59, figs 2, 4) are fused with the peduncle along 1.5 and 2 cm, similar to the bracts from Güvem, but are not distinctly spatulate at the apex and base. Thus, the specimens from Güvem and Kimi appear to mark the first occurrence of type C bracts of *Tilia* in Asia Minor and Europe.

Family MYRICACEAE A.Rich.
ex Kunth

Genus *Comptonia* (L.) J.M.Coult.

Comptonia oeningensis A.Braun

Pl. 24, Fig. 4

1845 *Comptonia oeningensis* A.Braun – Braun: p. 168.
1850a *Comptonia oeningensis* A.Braun – Unger: p. 32 (162), pl. 8 (29), fig. 3.
1850a *Comptonia meneghinii* Unger – Unger: p. 32 (162), pl. 8 (29), fig. 10.
1856 *Myrica oeningensis* (A.Braun) Heer – Heer: p. 33, pl. 70, figs 1–4.
1859 *Myrica oeningensis* (A.Braun) Heer – Heer: p. 175, pl. 150, fig. 18.
1867 *Dryandra ungeri* Ettingsh. – Unger: p. 59, pl. 9, fig. 17 (not figs 16, 18).
1981 *Comptonia acutiloba* Brongn. – Paicheler & Blanc: pl. 2, figs 11, 12.
2002 *Comptonia difformis* (Sternb.) Berry forma *dryandroides* (Unger) Velitzelos et al. – Velitzelos: pl. 9, fig. 17 (not figs 16, 18).

Material. Specimen MNHN20106.

Description. Leaf fragment, leaf simple, pinnatifid, lamina linear-lanceolate, with rounded to pointed lobes, lobes finely toothed, served by two secondary veins.

Remarks. The specimen figured in Paicheler and Blanc (1981) and refigured here is fragmentary but very similar to one specimen figured by Unger (1867; pl. 9, fig. 17) from Kimi. The latter has been referred to as *Comptonia difformis* (Sternb.) Berry forma *dryandroides* (Unger) by Velitzelos (2002). This taxon is based on late Eocene/early Oligocene material from Socka (Sotzka; Unger 1850a). It is characterized by several secondary veins per lobe and deeply incised lobes. The lobes are commonly finely toothed (see, e.g. Kvaček & Hably 1991). Although the latter character is shared between *C. dryandroides* and the specimen figured in Paicheler and Blanc (1981), the lobes are not deeply incised and they are severed by only two secondary veins. Therefore the closer similarities are with *C. oeningensis* A.Braun *sensu* Berry (Berry 1906). This fossil species is based on material from middle Miocene deposits of Germany.

Genus *Myrica* L.

Myrica sp.

Pl. 26, figs 1–11, Pl. 30, figs 9, 10

?1974 *Myrica longifolia* Unger – Zhilin: p. 74, pl. 45, fig. 5, pl. 46, fig. 4, pl. 49, figs 3, 4, pl. 52, fig. 4; not pl. 48, fig. 2.
1977 *Myrica banksiaefolia* Unger – Kasaplıgil: fig. 24.
1981 *Myrica banksiaefolia* Unger – Paicheler & Blanc: pl. 3, fig. 5.
1981 *Aralia* L. – Paicheler & Blanc: pl. 10, fig. 5.

Material. Specimens UCMP202121–202125, 202258, 202263_01, 202283_02, 202355_01, 202363, 202421_01; MNHN145, 146, 176, 20000, 20274, 20276, 20277, 20280–20282, 20288, 20107-01, 20275-01, 20278a & b, 20279-01, 20283-01; maybe 20041-01.

Description. Twigs with leaves alternate and aggregated at apex of shoot, dispersed leaves; leaf organisation simple; laminar size microphyll to notophyll; shape elliptic; symmetry symmetrical, laminar L:W ratio 5–8:1; base angle acute, apex angle acute, base shape cuneate, position of petiolar attachment marginal, apex shape straight; margin type entire or serrate, tooth apex simple, teeth with convex apical and retroflexuous to convex basal side, sinus angular; 1° vein category pinnate, 2° vein category craspedodromous, strong intersecondaries present, 2° vein spacing ± uniform, 2° vein angle ± uniform.

Remarks. The specimens figured by Paicheler and Blanc (1981) as four different species of *Myrica* do not belong to this genus. Most of the leaves belong to *Quercus drymeja* (see Denk et al. 2017a, SI 1); pl. 3, fig. 5 is a *Salix* leaf. The leaves from Güvem differ in tooth morphology (retroflexous basal side) from many Central European species of *Myrica*. Similar leaves were figured by Zhilin (1974) from late Oligocene strata of western Kazakhstan as *Myrica longifolia*. In our opinion these leaves differ from *M. longifolia* described by Unger (1850a) from late Eocene/early Oligocene strata. *M. longifolia* has almost linear leaves. Nevertheless, the similarity to Central Asian late Oligocene leaf types may indicate that these leaves belong to an entity different from the widespread *M. lignitum* (cf. Kovar-Eder 1982).

Family OLEACEAE Hoffmanns. & Link

Genus *Fraxinus* L.

***Fraxinus* sp.** (fruits)

Pl. 29, figs 1–4

1981 *Fraxinus* L. – Paicheler & Blanc: pl. 5, figs 13, 14.

Material. Specimens UCMP202094_02, 202139, 202140, 202141_01, 202142_02, 202230_02, 202241_02; MNHN20218, 20437.

Description. Samara fragments, 0.5–2 cm long, elliptic, veins running parallel.

Remarks. The samaras match those of modern and fossil *Fraxinus*.

Genus *Oleinites* Sachse

aff. *Oleinites hallbaueri* (Mai) Sachse

Pl. 24, fig. 7

1963 *Myrica hallbaueri* Mai – Mai: p. 46, text figs 3a, 3c, pl. 2, figs 4–6.
1981 *Knightia* sp. – Paicheler & Blanc: pl. 18, fig. 10.
2001 *Oleinities hallbaueri* (Mai) Sachse – Sachse: p. 319, pl. 2, figs 8, 9.
2007 *Oleinites hallbaueri* (Mai) Sachse – Walther & Kvaček: p. 122, pl. 17, figs 8, 9.

Material. Specimen MNHN20046.

Description. Leaf, >7.8 cm long, 4.5 cm wide, narrow ovate, petiolate, petiole 5 mm

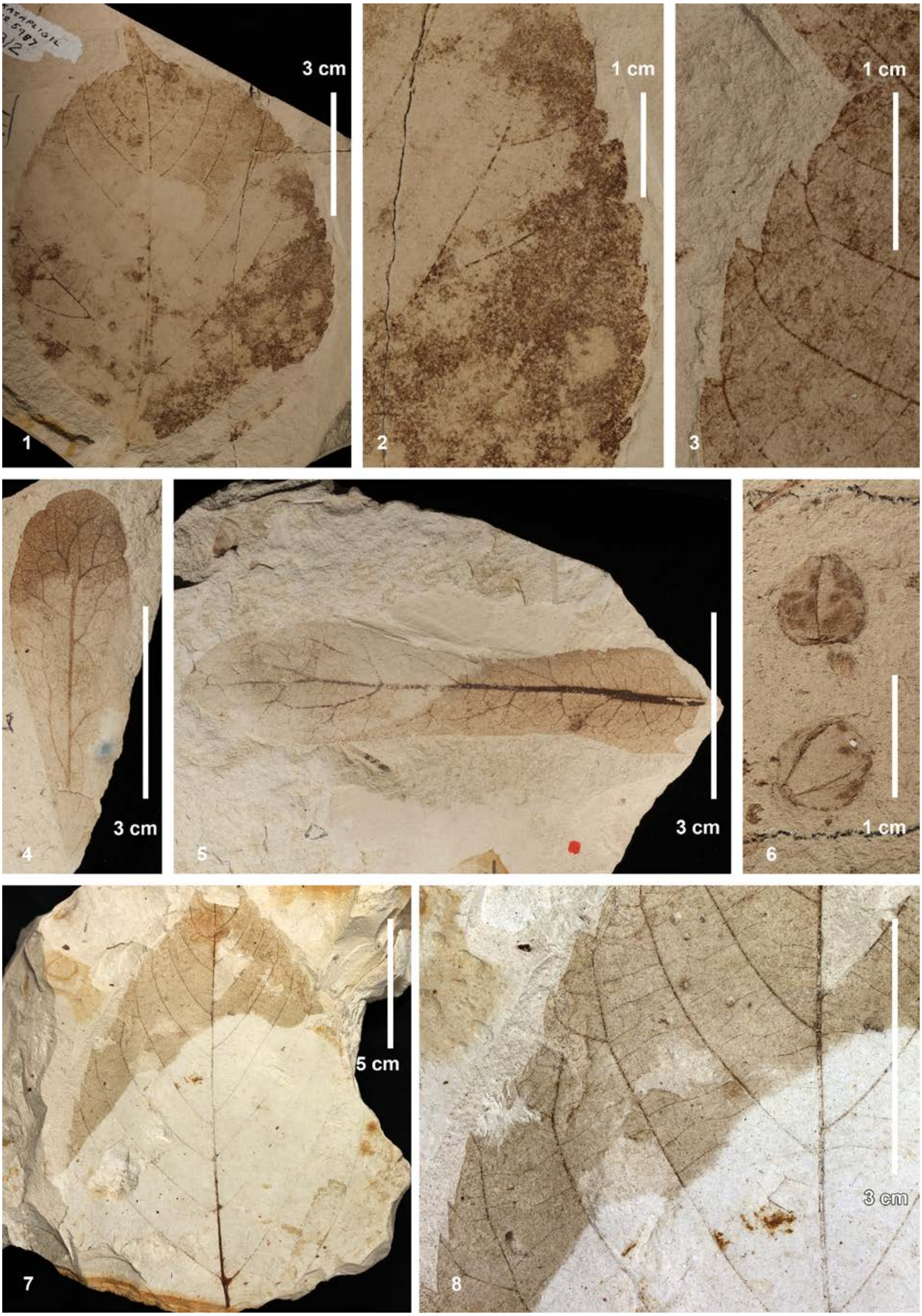

Plate 25. **1–3**, **7**, **8**. *Tilia* sp.; **1**. Leaf, specimen UCMP202117 (5987a); **2**. Leaf, margin, detail, specimen UCMP202117 (5987a); **3**. Leaf, venation and margin, detail, specimen UCMP202117 (5987a); **7**. Leaf, specimen MNHN20025; **8**. Leaf, venation and margin, detail, specimen MNHN20025; **4–6**. *Tilia knoblochii* Velitzelos & Gregor; **4**. Bract, specimen UCMP202118 (5507); **5**. Bract, specimen UCMP202119 (5715); **6**. Fruits, specimen UCMP202120 (5727a)

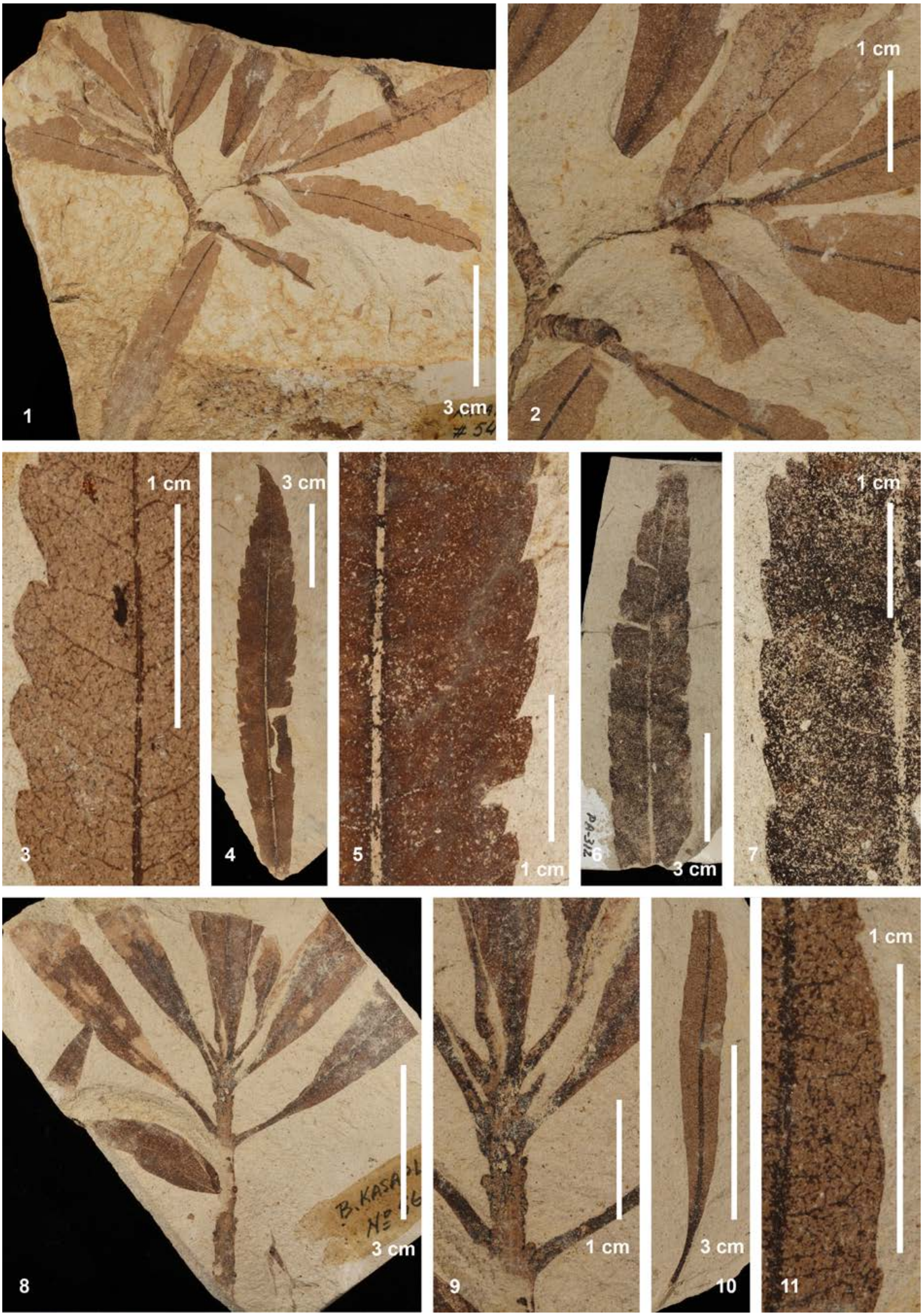

Plate 26. **1–11**. *Myrica* sp.; **1**. Branch with leaves, specimen UCMP202121 (5426); **2**. Leaves, specimen UCMP202121 (5426); **3**. Leaf, venation and margin, detail, specimen UCMP202121 (5426); **4**. Leaf, specimen UCMP202122 (5446); **5**. Leaf, margin, detail, specimen UCMP202122 (5446); **6**. Leaf, specimen UCMP202123 (5970); **7**. Leaf, margin, specimen UCMP202123 (5970); **8**. Branch with leaves, specimen UCMP202124 (5694); **9**. Branch with petioles and buds, detail, specimen UCMP202124 (5694); **10**. Leaf, specimen UCMP202125 (5757); **11**. Leaf, margin and venation, detail, specimen UCMP202125 (5757)

long, base cuneate to truncate, asymmetric, margin simple serrate to dentate, secondary venation craspedodromous to semicraspedodromous, secondaries and abmedial veins entering teeth, secondary vein spacing irregular, intersecondary veins present, teeth with straight to slightly convex basal side and straight to concave apical side.

Remarks. The leaflet figured by Paicheler and Blanc (1981) most likely belongs to the extinct Oleaceae *Oleinites*. The relatively sharp teeth at the asymmetrical base of the leaflet match those occurring in *Oleinites hallbaueri* (Mai) Sachse from Oligocene strata of Central Europe. Sachse (2001) transferred leaves of *Myrica hallbaueri* Mai to the extinct genus *Oleinites* Cookson based on leaf epidermal features.

Family POTAMOGETONACEAE Rchb.

Genus *Potamogeton* L.

Potamogeton bruckmanni A.Braun

Pl. 39, figs 7, 8

1851 *Potamogeton bruckmanni* A.Braun in Stitzenberger – Stitzenberger: p. 76.
1855 *Potamogeton bruckmanni* A.Braun – Heer: p. 102, pl. 47, figs 7, 7a.
1981 *Vaccinium* – Paichler & Blanc: pl. 18, fig. 5.

Material. Specimens UCMP202188, 202246; MNHN20057.

Description. Leaf, leaf organisation simple; laminar size nanophyll; laminar shape elliptic, lamina symmetrical, laminar L:W ratio 2:1; base angle acute, apex angle obtuse, base shape cuneate, position of petiolar attachment marginal, apex shape retuse; margin entire; 1° vein category pinnate, 2° vein category acrodromous to eucamptodromous, 2° vein spacing decreasing towards base, 2° vein angle uniform, 3° vein category mixed opposite/alternate.

Remarks. The specimens from Güvem represent submersed leaves of *Potamogeton* and are very similar to the one from Öhningen figured in Heer (1855). A number of fossil species described from Miocene strata of Central Europe are fairly similar to *P. bruckmanni* (e.g. *P. praenatans* Knoll, *P. stiriacus* Knoll; Teodoridis 2007) and all represent submersed and floating leaves.

Potamogeton geniculatus A.Braun

Pl. 39, figs 5, 6, Pl. 40, figs 1–3

1851 *Potamogeton geniculatus* A.Braun in Stitzenberger – Stitzenberger: p. 75.
1855 *Potamogeton geniculatus* A.Braun – Heer: p. 102, pl. 47, figs 1–6.
1981 *Potamogeton* sp. – Paicheler & Blanc: pl. 1, figs 3, 4 (5, 6 are fruits).

Material. Specimens UCMP202164_02, 202187, 202189; MNHN20145a-01, 20145b-01, 20208-02.

Description. Rhizome, axis with leaves; infructescence with leaves; leaf organisation simple; laminar size microphyll; laminar shape oblong linear, lamina symmetrical; base angle acute, no petiole present; margin entire; 1° vein category paralellodromous; infructescence umbel-like, with one or two flower axes originating from centre of umbel and surrounded by linear leaves.

Remarks. The specimens shown here are very similar to the illustration in Heer (1855, pl. 47, figs 1–6) but Heer's specimens do not have a rhizome. Heer (1855) and Paicheler and Blanc (1981) compared *Potamogeton geniculatus* with the extant *P. pusillus* L.

***Potamogeton* sp.**

Pl. 41, fig. 1

Material. Specimen UCMP202194; MNHN20201.

Description. Axis with oppositely arranged small (to 4 mm long), sessile leaves.

Remarks. Based on the parallelodromous venation, we tentatively assign this specimen to *Potamogeton*.

Erroneous genus *Zannichellia* L.

aff. *Daphnia* sp.

Pl. 39, fig. 2

1981 *Zannichellia palustris* L. – Paicheler & Blanc: pl. 1, figs 7, 8.

Material. Specimens MNHN20209, 20376, 20377.

Description. Less than a mm long ephippia with two dormant eggs.

Remarks. Paicheler and Blanc (1981) assigned these structures to the aquatic plant genus *Zannichellia*. It is, however, clear that they represent dormant eggs in ephippia of the planktonic crustacean order Cladocera, possibly of the genus *Daphnia*.

Family RHAMNACEAE Juss.

Genus *Paliurus* Mill.

Paliurus tiliifolius (Unger) Bůžek

Pl. 24, fig. 5

1847 *Paliurus favonii* Unger – p. 147, pro parte, pl. 50, figs 7, 8.
1971 *Paliurus tiliifolius* (Unger) Bůžek – Bůžek: p. 74, pl. 33, figs 1–21; pl. 34, figs 1–17.
1981 Rhamnaceae – Paicheler & Blanc: pl. 17, fig. 5.
2004 *Paliurus tiliifolius* (Unger) Bůžek – Kovar-Eder et al.: p. 76, pl. 11, fig. 1.

Material. Specimen MNHN20063-02.

Description. Leaf, simple, broad ovate, 4.5 cm long, 3.5 cm wide, petiolate, petiole 7 mm long, base obtuse, margin appearing slightly undulate, primary venation acrodromous, secondary venation brochidodromous.

Remarks. The leaf figured by Paicheler & Blanc (1981) and refigured here clearly belongs to *Paliurus tiliifolius* as originally described from the early Miocene of Bilina (Unger 1847). This species also occurs in Parschlug (Kovar-Eder et al. 2004). The fossil foliage is similar to the modern western Eurasian *P. spina-christi* Mill. and to *Ziziphus mucronata* Willd. from South Africa. Both these extant species are part of open or shrubby vegetation but their sister species are characteristic forest species (Chen et al. 2017).

Paliurus favonii Unger

Pl. 24, fig. 6

1847 *Paliurus favonii* Unger – p. 147, pro parte, pl. 50, fig. 6.
1981 *Paliurus* sp. – Paicheler & Blanc: pl. 17, fig. 3.

Material. Specimen MNHN20226.

Description. Fruit, central endocarp and mesocarp including a wing, wing with radial venation.

Remarks. Such fruits are commonly referred to *Paliurus favonii* and had a wide geographical and stratigraphic range throughout the Cenozoic (Burge & Manchester 2008).

Family ROSACEAE Juss.

Genus *Crataegus* Tourn. ex L.

***Crataegus* sp.**

Pl. 27, figs 6, 7

Material. Specimen UCMP202128.

Description. Leaf, leaf organisation simple; laminar size microphyll; laminar shape ovate; lamina symmetrical, laminar L:W ratio 1–1.5:1; base obtuse, apex angle acute, base shape slightly concave, position of petiolar attachment marginal; margin type serrate, multiple orders of teeth present, tooth apex simple, teeth with concave apical and flexuous to concave basal side; 1° vein category pinnate, 2° vein category craspedodromous, 2° vein spacing ± uniform, 2° vein angle increasing towards base.

Remarks. This foliage corresponds to that of extant species of *Crataegus* based on the concave shape of the leaf base. Similar leaves are also found in species of *Sorbus*. The specimen figured in Paicheler and Blanc (1981, pl. 17, fig. 16) as *Crataegus* actually is a lobe of *Acer palaeosaccharinum*.

Genus Prunus L.

***Prunus* sp.**

Pl. 27, figs 1–3

1981 *Ptelea* sp. – Paicheler & Blanc: pl. 16, fig. 20.

Material. Specimen UCMP202126; MNHN20060.

Description. Leaf, leaf organisation simple; laminar size microphyll to notophyll; laminar shape elliptic; lamina symmetrical, base slightly asymmetrical, laminar L:W ratio 3:1; base angle acute, apex angle acute, base shape convex, position of petiolar attachment marginal, nectaries on petiole present, apex shape straight; margin type crenate to serrate, tooth apex nonspecific glandular, teeth with convex apical and flexuous to convex basal side, sinus rounded; 1° vein category pinnate, 2° vein category brochidodromous.

Remarks. While there is no doubt that this leaf belongs to *Prunus* (presence of nectaries on the petiole), we cannot assign this leaf to any particular natural group of species within this large genus.

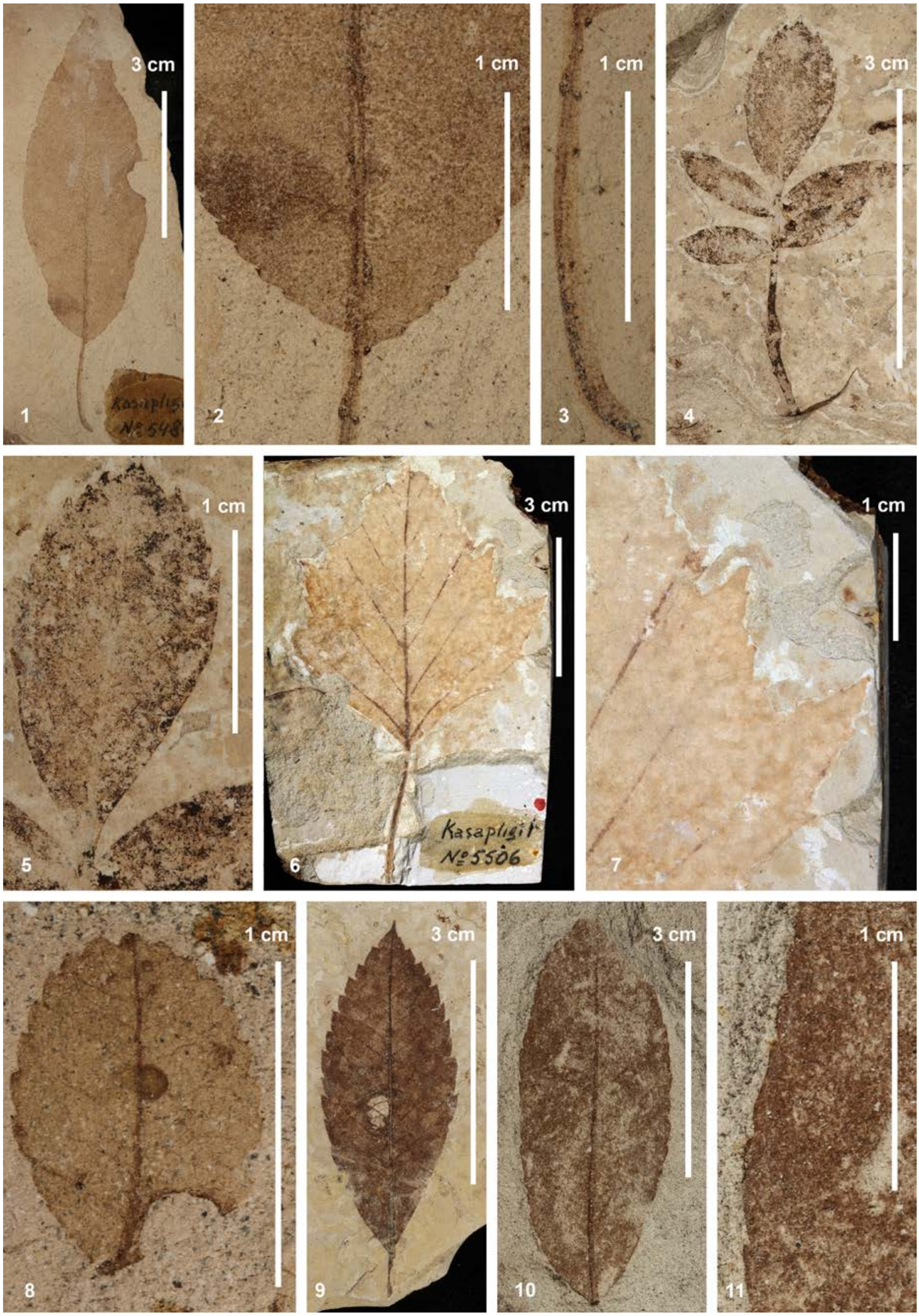

Plate 27. **1–3**. *Prunus* sp.; **1**. Leaf, specimen UCMP202126 (5486); **2**. Leaf base, detail, specimen UCMP202126 (5486); **3**. Petiole with nectaries, specimen UCMP202126 (5486); **4**, **5**. *Rosa* sp. aff. *Rosa mairei* H.Lév.; **4**. Pinnate leaf, specimen UCMP202127 (*n.n.* MAT72-434); **5**. Leaflet, detail, specimen UCMP202127 (*n.n.* MAT72-434); **6**, **7**. *Crataegus* sp.; **6**. Leaf, specimen UCMP202128 (5506); **7**. Leaf, margin detail, specimen UCMP202128 (5506); **8**. *Rosa* sp., leaf, specimen UCMP202129_01 (5717); **9**. cf. *Sorbus* sp., leaflet, terminal leaflet, specimen UCMP202130 (*n.n.*); **10**, **11**. cf. *Prunus* sp.; **10**. Leaf, specimen UCMP202131_01 (5808); **11**. Leaf, margin, detail, specimen UCMP202131_01 (5808)

cf. *Prunus* sp.

Pl. 27, figs 10, 11

Material. Specimen UCMP202131_01.

Description. Leaf, leaf organisation simple; laminar size microphyll to notophyll; laminar shape elliptic; lamina only base slightly asymmetrical, laminar L:W ratio 2–3:1; base angle acute, apex angle acute, base shape cuneate to convex, position of petiolar attachment marginal, apex shape straight to slightly acuminate; margin type finely serrate, tooth apex simple, teeth with flexuous apical and flexuous basal side; 1° vein category pinnate, 2° vein category probably brochidodromous to semicraspedodromous, strong intersecondaries present, 2° vein spacing irregular, 2° vein angle decreasing towards base.

Remarks. We tentatively include this leaf within *Prunus*, based on the course of secondary veins and the leaf margin.

Genus *Rosa* L.

Rosa sp. aff. *Rosa mairei* H.Lév.

Pl. 27, figs 4, 5

Material. Specimen UCMP202127.

Description. Leaf, leaf organisation odd-pinnate; leaflet laminar size nanophyll; leaflet laminar shape elliptic to obovate; lamina symmetrical, laminar L:W ratio 2.5–4:1; base angle acute, apex angle acute, base shape cuneate, position of petiolar attachment marginal, apex shape convex to slightly acuminate; margin type entire to serrate, tooth apex simple, teeth with straight to flexuous apical and convex to flexuous basal side, sinus angular; 1° vein category pinnate, 2° vein category semicraspedodromous.

Remarks. The leaf of this specimen is attached to a twiglet, suggesting that the plant producing the leaf was woody. The leaf organisation is similar to that found in the Chinese (Sechuan) species *R. mairei*, a species that grows in forests along streams (Wu et al. 2003).

aff. *Rosa* sp.

Pl. 27, fig. 8

Material. Specimen UCMP202129_01.

Description. Leaf, leaf organisation simple; laminar size nanophyll; laminar shape obovate; lamina symmetrical, laminar L:W ratio 1.5:1; base angle obtuse, apex angle obtuse, base shape cuneate, position of petiolar attachment marginal, apex shape rounded; margin type serrate, tooth apex simple, teeth with convex to flexuous apical and convex to flexuous basal side, sinus angular; 1° vein category pinnate, 2° vein category craspedodromous.

Remarks. The leaflet may represent the genus *Rosa*.

Genus *Sorbus* L.

Subgenus *Sorbus*

Sorbus sp.

Pl. 27, fig. 9, 28, figs 1–9

1981 *Sorbus aucuparia* L. – Paicheler & Blanc: pl. 17, figs 11–15.

2017 *Sorbus* sp. – Güner et al.: p. 14, pl. 8, fig. 5.

Material. Specimens UCMP202056_05, 202130, 202132–202137, 202138_01, 202178_02, 202242_03, 202257_02, 202267_02, 202335–202341, 202406, 202407; MNHN20115-01, 20115-02, 20116, 20122, 20283-02, one unnumberd specimen.

Description. Leaf, leaf organisation odd-pinnate; leaflet laminar size microphyll; leaflet laminar shape elliptic, elongate to obovate; lamina symmetrical, asymmetrical base can be present, laminar L:W ratio 3–5:1; base angle acute, apex angle acute, base shape cuneate to convex, position of petiolar attachment marginal, apex shape straight to convex; margin type serrate, tooth apex simple, teeth with flexuous apical and convex to flexuous basal side, sinus angular; 1° vein category pinnate, 2° vein category craspedodromous, strong intersecondaries present, 2° vein spacing irregular, 2° vein angle ± uniform; 3° vein category regular polygonal reticulate.

Remarks. These leaves and leaflets clearly belong to *Sorbus*. *Sorbus* species with pinnate leaves are widely distributed in North America and Eurasia and are accommodated within subgenus *Sorbus*; hence we refrain from comparing the fossil to a particular modern species.

Similar complete leaves are known from the early Miocene of Spain (Barrón et al. 2010). Recently, Güner et al. (2017) described leaflets

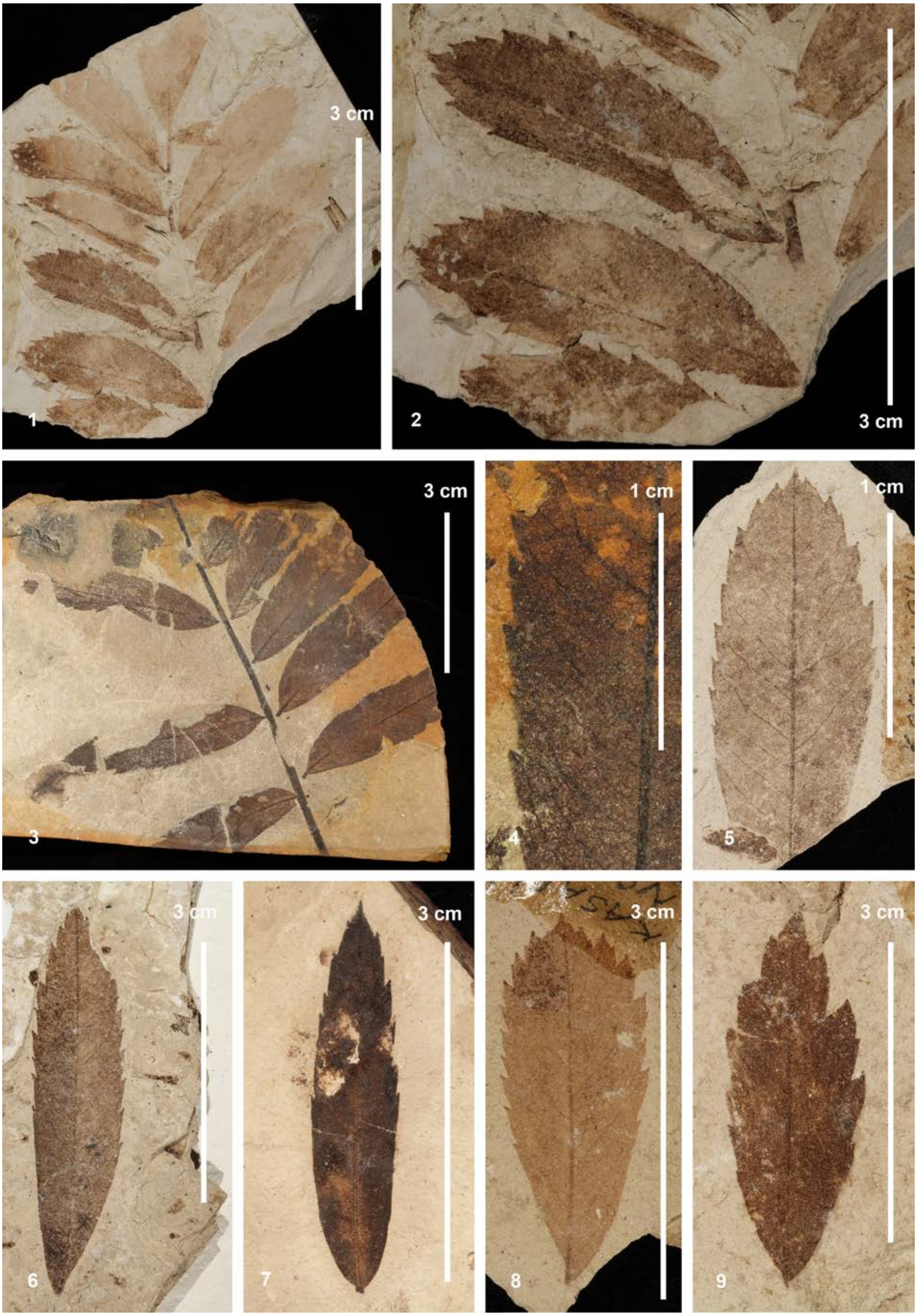

Plate 28. **1–9**. *Sorbus* sp. **1**. Pinnate leaf, specimen UCMP202132 (5826); **2**. Leaflets, detail, specimen UCMP202132 (5826); **3**. Pinnate leaf, specimen UCMP202133 (5827); **4**. Leaflet, margin and venation, detail, specimen UCMP202133 (5827); **5**. Leaflets, detail, specimen UCMP202134 (*n.n.*); **6**. Leaflets, detail, specimen UCMP202135 (5971); **7**. Leaflets, detail, specimen UCMP202136 (5838); **8**. Leaflets, detail, specimen UCMP202137 (5823); **9**. Leaflets, detail, specimen UCMP202138_01 (5928)

of *Sorbus* from middle Miocene deposits of southwestern Turkey which are very similar to the ones described here.

Family SALICACEAE Mirb.

Genus *Populus* L.

Populus populina (Brongn.) Erw.Knobloch

Pl. 29, figs 7–10

1822 *Phyllites populina* Brongn. – Brongnart: p. 237, pl. 14, fig. 4.
1964 *Populus populina* (Brongn.) Erw.Knobloch – Knobloch: p. 601.
1977 *Populus tremula* L. – Kasaplıgil: fig. 41.
1981 *Populus populina* (Brongn.) Erw.Knobloch – Paicheler & Blanc: pl. 4, fig. 5.
1981 *Populus tremula* L. – Paicheler & Blanc: pl. 4, figs 7, 8 (non fig. 6).

Material. Specimens UCMP202045, 202144, 202145, 202149_01; MNHN20020, 20022, 20023.

Description. Leaf, leaf organisation simple; laminar size microphyll to notophyll; laminar shape ovate; lamina symmetrical, laminar L:W ratio 1–1.5:1; base angle obtuse, apex angle obtuse, base shape truncate, position of petiolar attachment marginal, apex shape convex to rounded; margin type crenate, tooth apex rounded, teeth with retroflexuous apical and convex to retroflexuous basal side, sinus rounded; 1° vein category pinnate with two strong 2° basal veins, 2° vein category craspedodromous, simple agrophic veins present, 2° vein spacing irregular, 2° vein angle smoothly decreasing towards base; 3° vein category alternate percurrent.

Remarks. This fossil species occurs in late Oligocene to Pliocene strata. According to Iljinskaya (2005), it is closely similar to the extant *Populus tremula* L., *P. tremuloides* Michx. and *P. davidiana* Dode, all of which belong to a basal grade within *Populus* (Eckenwalder 1996, Hamzeh & Dayanandan 2004).

***Populus* sp.**

Pl. 40, figs 7, 8

1981 *Populus* sp. – Paicheler & Blanc: pl. 4, figs 9–12.

Material. Specimen UCMP202194; MNHN20173, 20179, 20191b.

Description. Catkins, pendulous; bracts alternating, floral bract apex deeply cut, ciliate.

Remarks. In addition, Paicheler and Blanc (1981, pl. 4, figs 15, 16) figure a nice specimen of an infructescence of *Populus*.

Genus *Salix* L.

Salix angusta A.Braun

Pl. 30, figs 1, 2

1851 *Salix angusta* A.Braun– Stitzenberger: p. 77.
1856 *Salix angusta* A.Braun – Heer: p. 31, pl. 69, figs 1–11.
1954 *Salix angusta* A.Braun– Hantke: p. 58, pl. 6, figs 1–4.

Material. Specimen UCMP202146.

Description. Leaf, leaf organisation simple; laminar size microphyll; laminar shape elliptic; lamina symmetrical, laminar L:W ratio 12:1; base angle acute, apex angle acute, base shape cunate, position of petiolar attachment marginal, apex shape straight; margin type entire, 1° vein category pinnate, 2° vein category possibly reticulodromous, 2° vein spacing irregular.

Remarks. The steep, reticulate venation seen in the basal part of the lamina suggests that this leaf belongs to *Salix* rather than to *Myrica*. We tentatively include this specimen within *S. angusta* described and figured from Öhningen (Heer 1856).

Salix varians Göpp.

Pl. 30, figs 3–6

1855 *Salix varians* Göpp. – Göppert: p. 26, pl. 19, figs 17, 18, pl. 20, figs 1, 2.
1859 *Salix varians* Göpp. – Heer: p. 174, pl. 150, fig. 6.
1981 *Salix haidingeri* Ettingsh. – Paicheler & Blanc: pl. 3, figs 11, 12.

Material. Specimens UCMP202147, 202148_01; MNHN20121.

Description. Leaf, leaf organisation simple; laminar size microphyll; laminar shape elliptic; lamina symmetrical, base asymmetrical, laminar L:W ratio 6–9:1; base angle acute, base shape cunate, position of petiolar attachment marginal; margin type crenate, tooth apex simple, teeth with convex apical and convex basal side, sinus angular; 1° vein category pinnate, 2° vein category semicraspedodromous.

Remarks. Fragmentary leaves assigned to *Salix haidingeri* (Paicheler & Blanc 1981) may belong to *S. varians* as well. Superficially

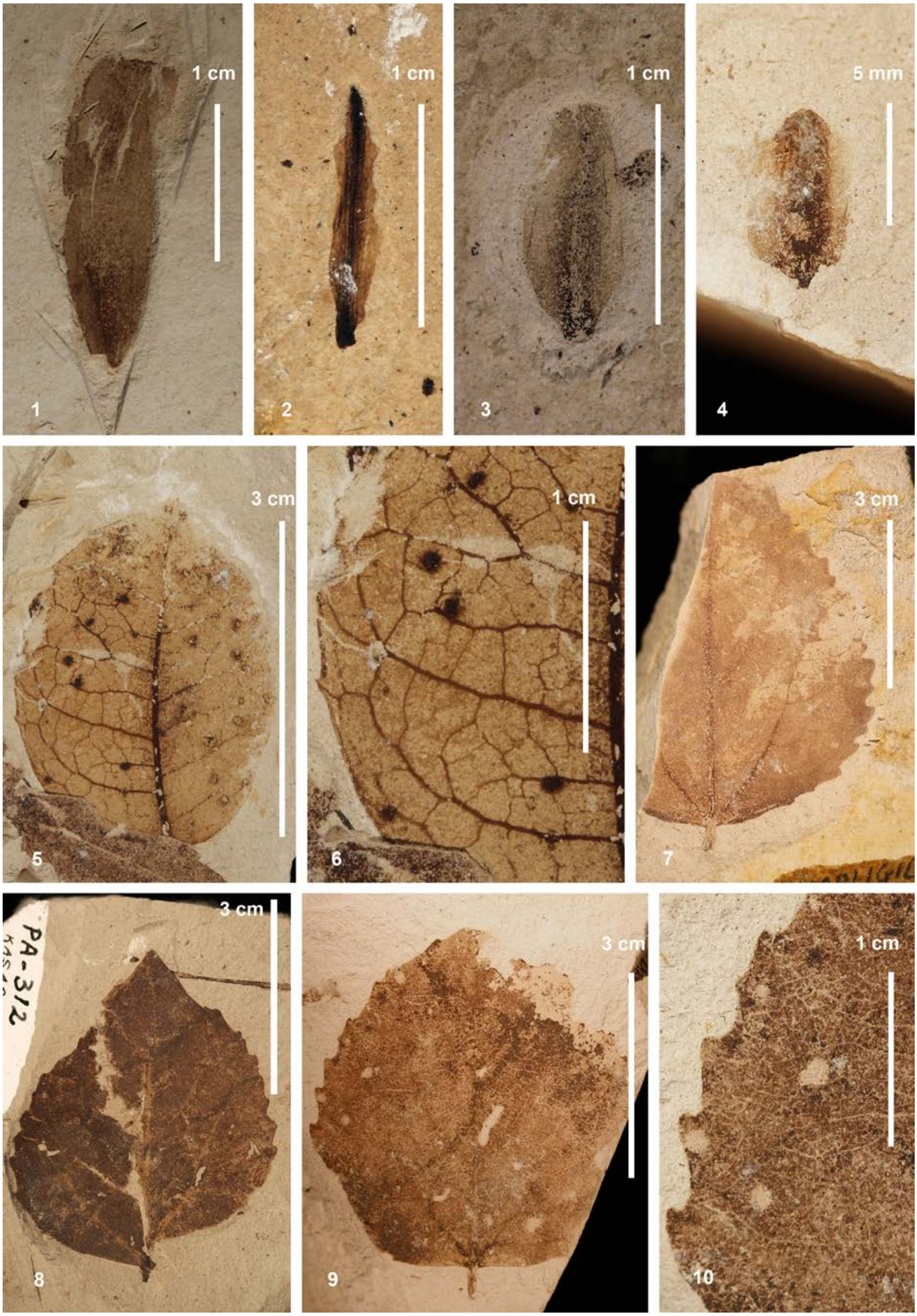

Plate 29. **1–4**. *Fraxinus* sp.; **1**. Fruit, specimen UCMP202139 (5481); **2**. Fruit, specimen UCMP202140 (*n.n.*); **3**. Fruit, specimen UCMP202141_01 (5701); **4**. Fruit, specimen UCMP202142_01 (5693); **5**, **6**. cf. *Ilex miodipyrena* sp. nov.; **5**. Leaf, specimen UCMP202143_01 (5977); **6**. Leaf venation, detail, specimen UCMP202143_01 (5977); **7–10**. *Populus populina* (Brongn.) Erw. Knobloch.; **7**. Leaf, specimen UCMP202144 (5386); **8**. Leaf, specimen UCMP202045 (5968); **9**. Leaf, specimen UCMP202145 (5436); **10**. Leaf venation and margin, detail, specimen UCMP202145 (5436)

Plate 30. **1**, **2**. *Salix angusta* A.Braun.; **1**. Leaf, specimen UCMP202146 (5863); **2**. Leaf base, detail, specimen UCMP202146 (5863); **3–6**. *Salix varians* Göpp.; **3**. Leaf, specimen UCMP202147 (5416); **4**. Leaf margin, detail, specimen UCMP202147 (5416); **5**. Leaf fragment, specimen UCMP202148_01 (5865); **6**. Leaf margin, detail, specimen UCMP202148_01 (5865); **7**, **8**. cf. *Salix* sp.; **7**. Leaf, specimen UCMP202149 (5536); **8**. Leaf venation, detail, specimen UCMP202149 (5536); **9**, **10**. *Myrica* sp.; **9**. Leaves, specimen UCMP202150 (5703); **10**. Leaf venation and margin, detail, specimen UCMP202150 (5703)

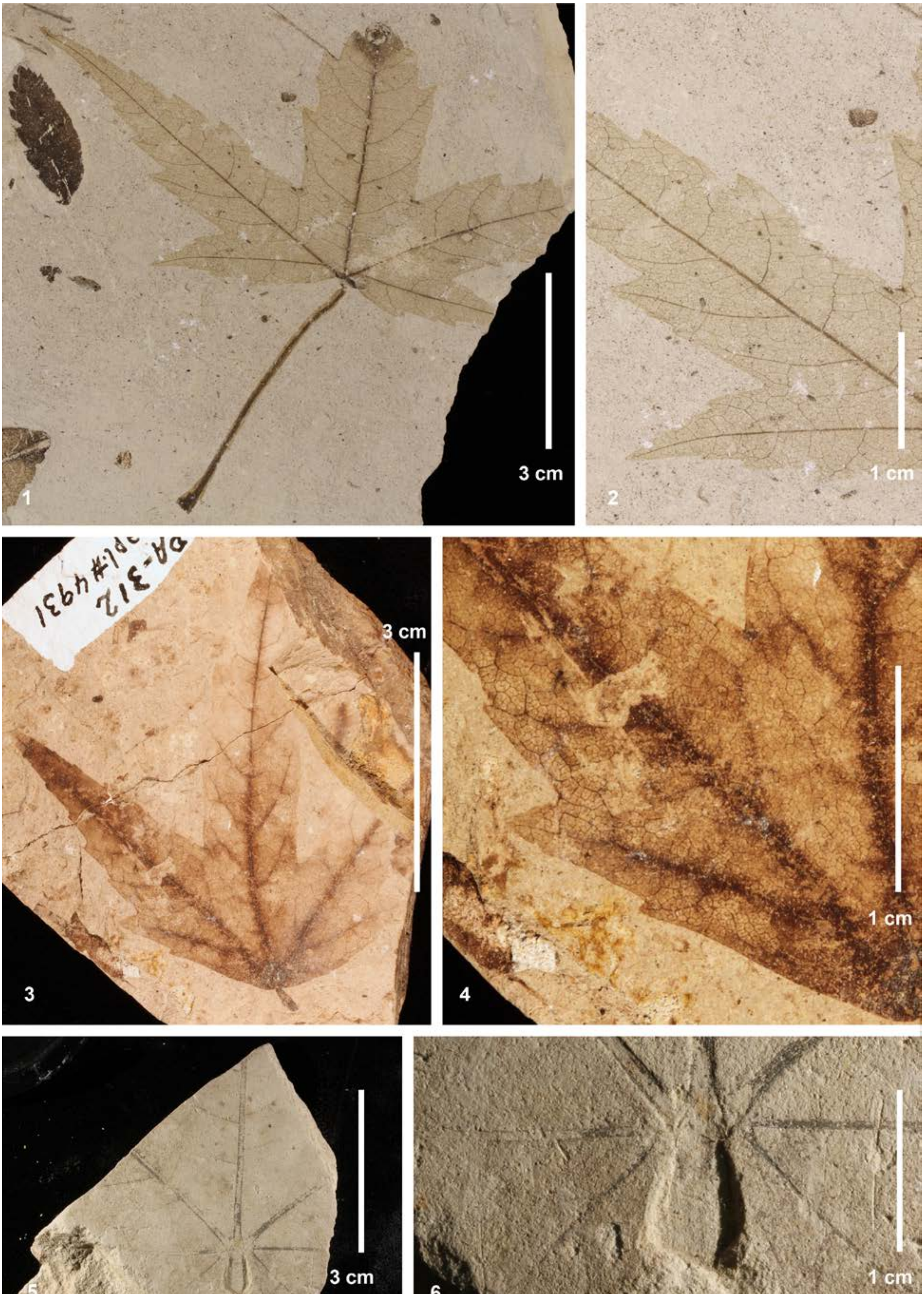

Plate 31. **1–4**. *Acer angustilobum* Heer *sensu* Hantke; **1**. Leaf, specimen UCMP202151_01 (5839); **2**. Leaf venation, detail, specimen UCMP202151_01 (5839); **3**. Leaf, specimen UCMP202152 (PA-312-4931); **4**. Leaf venation, specimen UCMP202152 (PA-312-4931); **5**, **6**. *Acer* sp.; **5**. Leaf fragment, specimen UCMP202153 (5906); **6**. Leaf base, detail, specimen UCMP202153 (5906)

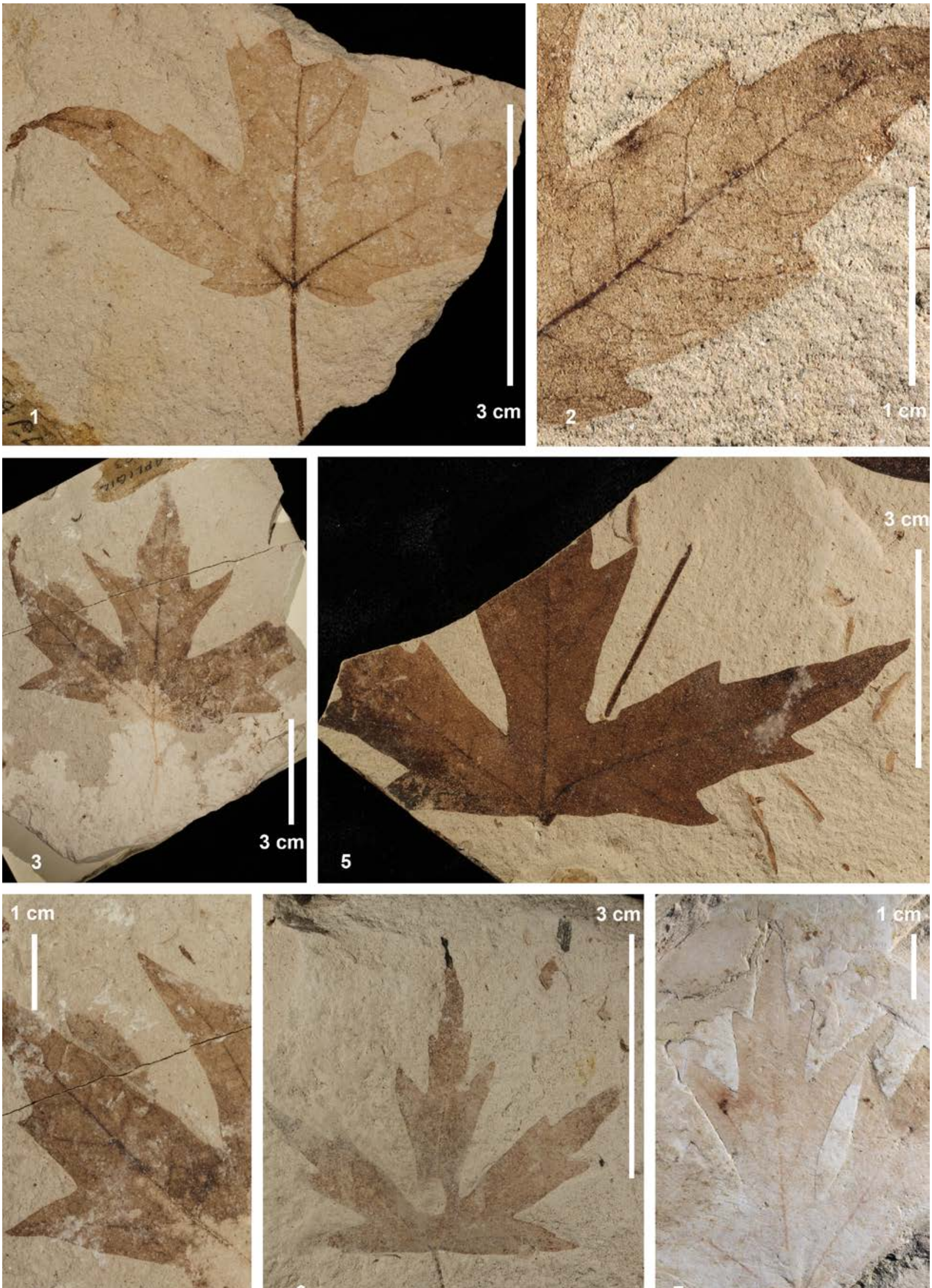

Plate 32. **1–7**. *Acer palaeosaccharinum* Stur; **1**. Leaf, specimen UCMP202154 (5818); **2**. Leaf venation, detail, specimen UCMP202154 (5818); **3**. Leaf, specimen UCMP202155 (5803); **4**. Leaf venation, detail, specimen UCMP202155 (5803); **5**. Leaf, specimen UCMP202056 (5812); **6**. Leaf, specimen UCMP202156 (4926); **7**. Leaf, specimen UCMP202157 (4930)

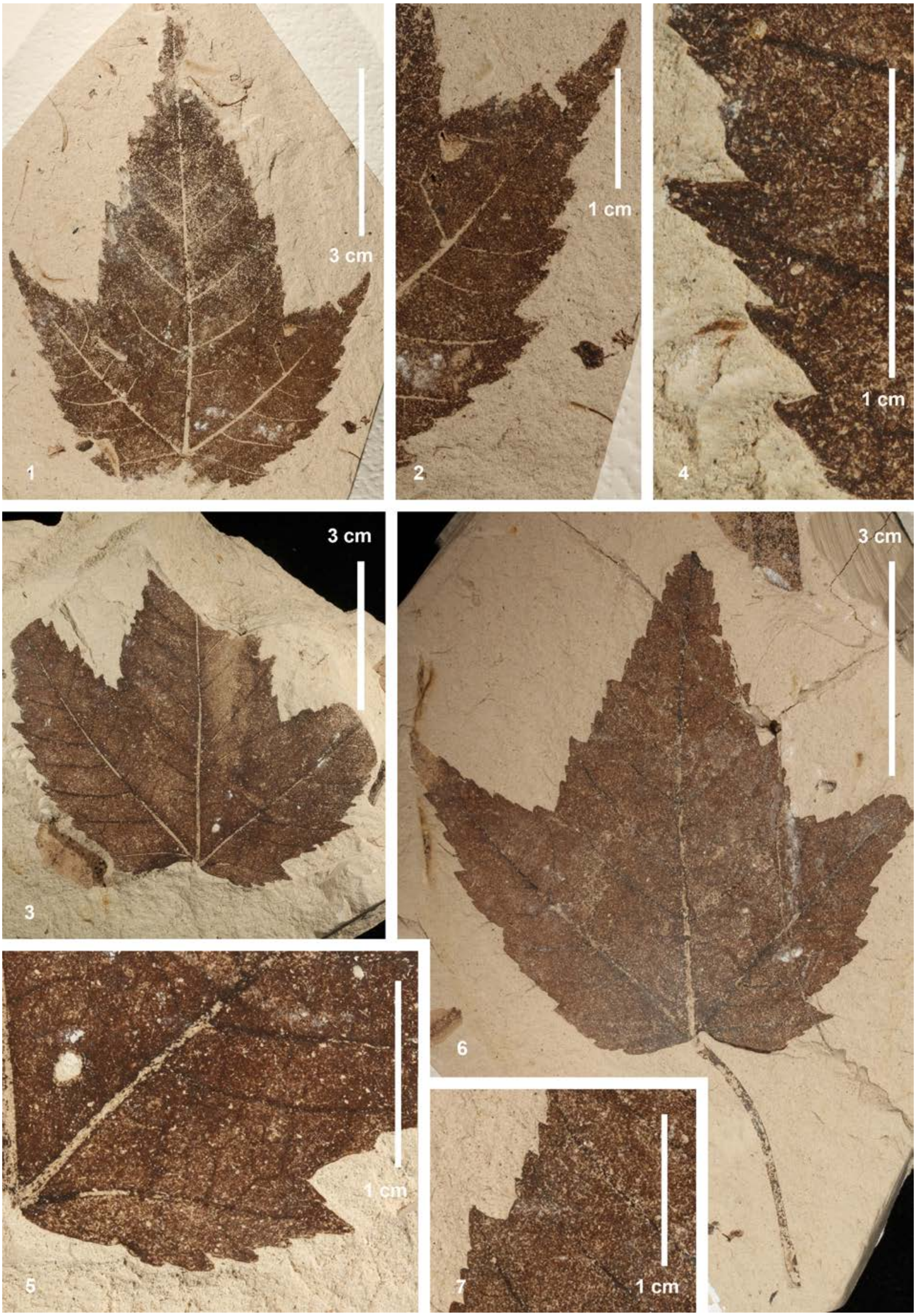

Plate 33. **1–7**. *Acer tricuspidatum* Bronn; **1**. Leaf, specimen UCMP202158 (4933); **2**. Leaf venation and margin, detail, specimen UCMP202158 (4933); **3**. Leaf, specimen UCMP202159 (6001); **4**. Leaf margin, detail, specimen UCMP202159 (6001); **5**. Leaf base and venation, detail, specimen UCMP202159 (6001); **6**. Leaf, specimen UCMP202160 (4932); **7**. Leaf margin, detail, specimen UCMP202160 (4932)

similar specimens figured in Pl. 30 (figs. 9, 10) differ in secondary venation and the remotely dentate margin which fit better with *Myrica* sp.

cf. *Salix* sp.

Pl. 30, figs 7, 8

Material. Specimen UCMP202149_01.

Description. Leaf, leaf organisation simple; laminar size microphyll; laminar shape elliptic lanceolate; lamina symmetrical, laminar L:W ratio 5:1; base angle acute, apex angle acute, base shape cunate, position of petiolar attachment marginal, apex shape straight; margin type entire, 1° vein category pinnate, 2° vein category possibly reticulodromous, 2° vein spacing irregular.

Remarks. We tentatively include this small leaf within *Salix*. Similar leaves occur in, for example, the extant *Salix purpurea* L.

Salix sp. (flower catkins)

Material. Specimens MNHN20173-02, 20185.

Paicheler and Blanc (1981) figure flower catkins that they refer to *Salix* (pl. 4, figs 1–4).

Family SAPINDACEAE Juss.

Genus *Acer* L.

Acer angustilobum Heer *sensu* Hantke

Pl. 31, figs 1–4

1859 *Acer angustilobum* Heer – Heer: p. 57, pl. 117, fig. 25, pl. 118, figs 4–9.
1972 *Acer angustilobum* Heer – Walther: p. 40, pl. 3, pl. 4, pl. 5, pl. 6, figs 1–5, pl. 33, pl. 34, pl. 35, pl. 36.
1981 *Acer dasycarpoides* Heer – Paicheler & Blanc: only pl. 12, fig. 9.

Material. Specimens UCMP202151, 202152, 202315; MNHN20011.

Description. Leaf, leaf organisation simple; petiole base swollen; laminar size micro- to notophyll; laminar shape elliptic, lamina symmetrical, laminar L:W ratio 1:1–1.5; base angle wide obtuse, apex angle acute, base shape lobate, position of petiolar attachment marginal, apex shape straight; margin type serrate, tooth apex simple, tooth shape apical side straight to concave, basal side ranging from concave to convex, sinus angular; lobation palmate, 3-lobed with two additional small basal lobes; 1° vein category palinactinodromous, three basal veins, 2° vein category craspedodromous, 2° vein spacing irregular, 2° vein irregular, strong intersecondaries present, in lobe sinus area 2° veins join, no 2° veins ending in lobe sinus; 3° vein category regular polygonal reticulate; 4° vein category regular polygonal reticulate; areolation well developed, five-sided; F.E.V.S. branching once.

Remarks. The specimens from Güvem fit with the original material from Öhningen (Heer 1859, Hantke 1965). According to Walther (1972), *Acer angustilobum* has a distinctly papillate abaxial epidermis. This feature is typical of some species in section *Acer* (Grimm et al. 2007), for example the western Eurasian *A. heldreichii* Orph. ex Boiss. and *A. trautvetteri* Medw. *Acer angustilobum* occurs in early Oligocene to middle Miocene strata of western Eurasia (Walther 1972).

Acer palaeosaccharinum Stur

Pl. 32, figs 1–7

1867 *Acer palaeosaccharinum* Stur – Stur: p. 177, pl. 5, fig. 8.
1972 *Acer palaeosaccharinum* Stur – Walther: p. 97, pl. 19, pl. 20, pl. 21, pl. 52, pl. 53.
1977 *Acer angustilobum* Heer – Kasaplıgil: fig. 26.
1981 *Acer tricuspidatum* Bronn – Paicheler & Blanc: pl. 12, fig. 4.
1981 *Acer dasycarpoides* Heer – Paicheler & Blanc: pl. 12, figs 8, 10, 11.
1981 *Acer palaeosaccharinum* Stur – Paicheler & Blanc: pl. 13, figs 1, 2.
1981 *Crataegus* sp. – Paicheler & Blanc: pl. 17, fig. 16.

Material. Specimens UCMP202056, 202131_02, 202154–202157, 202230_01, 202233, 202235, 202225_02, 202328, 202329, 202331_01; MNHN20006, 20010, 20027, 20041-02, 20081–20083.

Description. Leaf, leaf organisation simple; laminar size microphyll; laminar shape elliptic, lamina symmetrical, laminar L:W ratio 1:1–1.5; base angle obtuse, apex angle acute, base shape lobate to truncate, position of petiolar attachment marginal, apex shape straight; margin type serrate, tooth apex simple, tooth shape apical side straight to concave, basal side straight to concave, sinus angular; lobation palmate, 3-lobed, two additional minute basal lobes can be present; 1° vein category palinactinodromous, three basal veins, 2° vein category brochidodromous and craspedodromous, 2° vein spacing irregular, 2° vein angle smoothly decreasing towards base, strong intersecondaries present, 2° veins joining and forming a loop in lobe sinus area.

Remarks. *Acer palaeosaccharinum* has a stratigraphic range from the Oligocene to

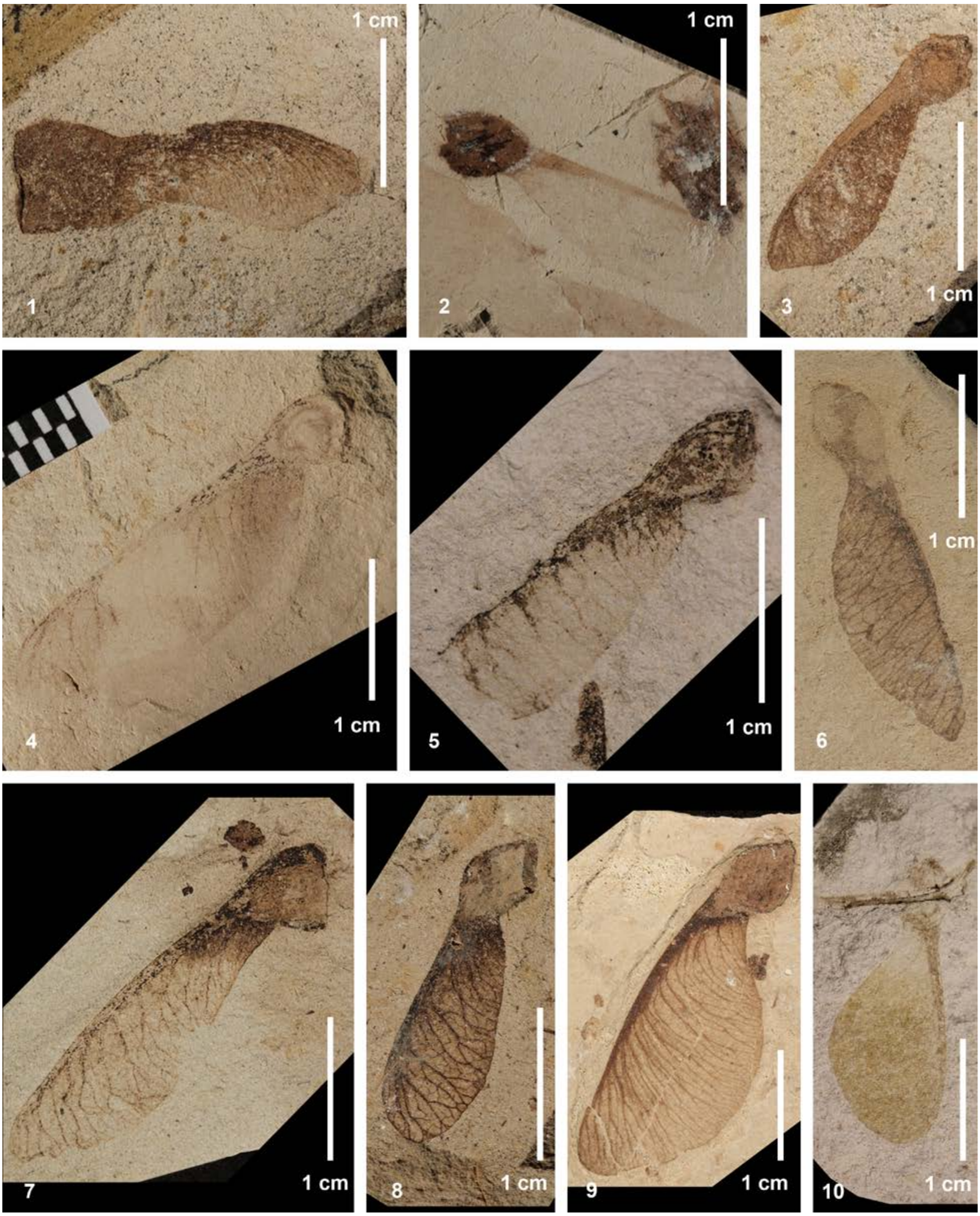

Plate 34. 1–10. *Acer* spp. (samaras); **1**. Samara, specimen UCMP202161 (5810); **2**. Samara, specimen UCMP202162 (5811); **3**. Samara, specimen UCMP202129_02 (5717); **4**. Samara, specimen UCMP202163 (5480); **5**. Samara, specimen UCMP202164_01 (5720a); **6**. Samara, specimen UCMP202165 (5479); **7**. Samara, specimen UCMP202166 (5433); **8**. Samara, specimen UCMP202167 (5431); **9**. Samara, specimen UCMP202168 (5822b); **10**. Samara, specimen UCMP202169 (5719)

Pliocene (e.g. Kvaček & Walther 2004, Velitzelos & Gregor 1990). According to Ströbitzer-Hermann (2002), this species typically occurs in volcanic deposits and can be interpreted as an element of mesophytic forests rather than riparian communities. This fossil species is most similar to the extant North American *Acer saccharum* Marsh. (Walther 1972).

The small leaves figured by Paicheler and Blanc (1981) in pl. 12, figs 2, 4, 11 and pl. 13, figs 8–10 under the names *A. tricuspidatum*, *A. dasycarpoides*, *A. integerrimum* Viviani and *A. pseudomonspessulanum* Unger most likely all belong to *A. integrilobum* Weber sensu Walther (1972) or may represent small leaves of either *A. angustilobum* or *A. palaeosaccharinum*.

Acer tricuspidatum Bronn

Pl. 33, figs 1–7

1838 *Acer tricuspidatum* Bronn – Bronn: pl. 35, figs 10a, 10b.
1845 *Acer trilobatum* Bronn – Braun: p. 172.
1845 *Acer productum* Bronn – Braun: p. 172.
1845 *Acer tricuspidatum* Bronn – Braun: p. 172.
1977 *Acer trilobatum* (Sternberg) A.Braun – Kasaplıgil: fig. 25.
1981 *Acer tricuspidatum* Bronn – Paicheler & Blanc: pl. 12, figs 1, 3.
1981 *Acer dasycarpoides* Heer – Paicheler & Blanc: pl. 12, fig. 12.

Material. Specimens UCMP202158–202160, 202231_01, 202277, 202315, 202330, 202332_02; MNHN20002, 20005, 20013-01, 20038-02, 20080, 20084, 20085, 20087.

Description. Leaf, leaf organisation simple; laminar size notophyll; laminar shape ovate, lamina symmetrical, laminar L:W ratio 1.5:1; base angle wide obtuse, apex angle acute, base shape lobate, position of petiolar attachment marginal, apex shape straight; margin type serrate, tooth shape apical side concave, basal side convex; lobation palmate, 3-lobed, two additional minute basal lobes can be present; 1° vein category palinactinodromous, five basal veins, 2° vein category craspedodromous, 2° vein spacing irregular, 2° vein angle smoothly decreasing towards base, strong intersecondaries present.

Remarks. This species has a stratigraphic range from the upper Oligocene to Pliocene (Walther 1972). Based on leaf epidermal features, the fossil species is closely related to the extant *Acer rubrum* L. and *A. saccharinum* L. (Ströbitzer-Hermann 2002).

Acer sp.

Pl. 31, figs 5, 6

1981 *Acer opalus* Mill. – Paicheler & Blanc: pl. 13, figs 7, 11.

Material. Specimen UCMP202153.

Description. Leaf; base angle wide obtuse, base shape lobate, position of petiolar attachment marginal; 1° vein category palinactinodromous, agrophic veins present, seven basal veins, 2° vein spacing irregular, strong intersecondaries present.

Remarks. A single leaf fragment, possibly 5-lobed with two additional small basal lobes. The complete leaves figured in Paicheler and Blanc (1981) are very similar to leaves from middle Miocene strata of southwestern Turkey referred to *Acer ilnicense* Iljinskaya (Güner et al. 2017). According to these authors, similar leaves are encountered in the extant *A. sterculiaceum* Wall., and *A. opalus* Mill.

Acer spp. (samaras)

Pl. 34, figs 1–10

1981 *Acer campestre* L. – Paicheler & Blanc: pl. 13, figs 13, 14.
1981 *Picea* sp. – Paicheler & Blanc: pl. 7, fig. 6.

Material. Specimens UCMP202129_02 & 03, 202161–202163, 202164_01, 202165–202169, 202287, two unnumbered specimens; MNHN7, 37a, 37c, 63F, 63R, 20190, 20256, 20301, 20378–20399, 20440-01, one unnumbered specimen; maybe 11.

Description (Pl. 34, fig. 1). Fruit samaroid, nutlet at basal end; nutlet diameter 0.5–0.8 cm; outline circular to slightly elliptic; attachment scar length 0.6–0.8 cm, attachment angle ca 90°; nutlet angle 10°–20°. Wing extending completely along apical margin of nutlet to attachment scar; length 2.4–2.6 cm, width 0.6–0.8 cm; proximal margin convex, distal margin sinuous, apex narrowly rounded; veins coalesced along proximal margin; wing veins diverging at 10°–30°, bifurcating acutely and anastomosing several times, some veinlets visible.

Description (Pl. 34, fig. 2): Fruit samaroid, nutlet at basal end; nutlet length 0.4–0.6 cm, nutlet width 0.3–0.4 cm; outline slightly

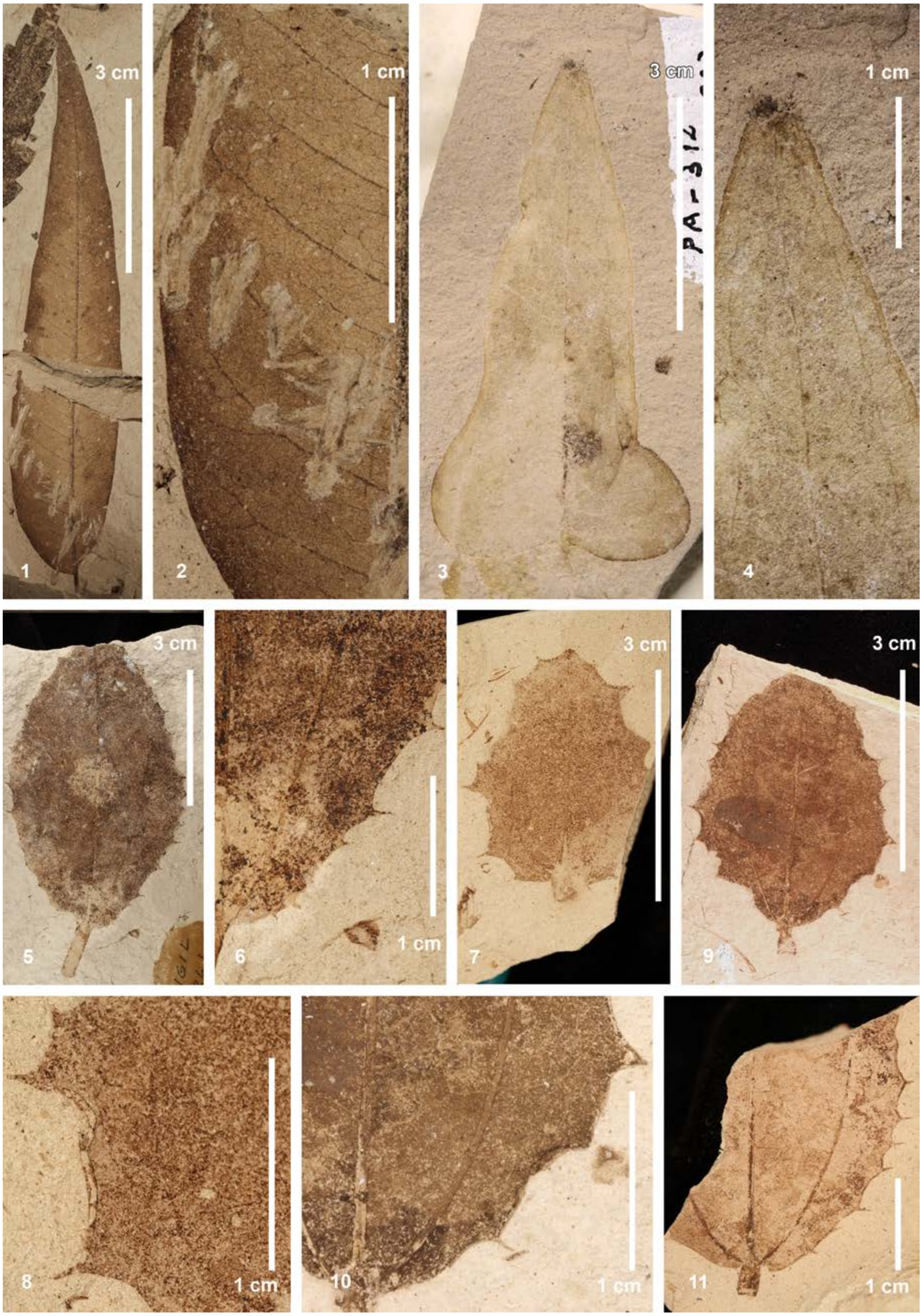

Plate 35. **1**, **2**. *Sapindus falcifolius* (A.Braun) A.Braun; **1**. Leaf, specimen UCMP202170 (5755); **2**. Leaf margin and venation, detail, specimen UCMP202170 (5755); **3**, **4**. *Smilax weberi* P.Wessel; **3**. Leaf, specimen UCMP202171 (4923); **4**. Leaf tip and venation, detail, specimen UCMP202171 (4923); **5–11**. *Smilax miohavanensis* Denk, D.Velitzelos, T.Güner & Ferrufino-Acosta; **5**. Leaf, specimen UCMP202172 (5861); **6**. Leaf base, venation and margin, detail, specimen UCMP202172 (5861); **7**. Leaf, specimen UCMP202164_05 (5720a); **8**. Leaf margin, detail, specimen UCMP202164_05 (5720a); **9**. Leaf, (holotype) specimen UCMP202173_01 (6914); **10**. Leaf base, venation and margin, detail, (holotype) specimen UCMP202173_01 (6914); **11**. Leaf fragment, specimen UCMP202164_06 (5720a)

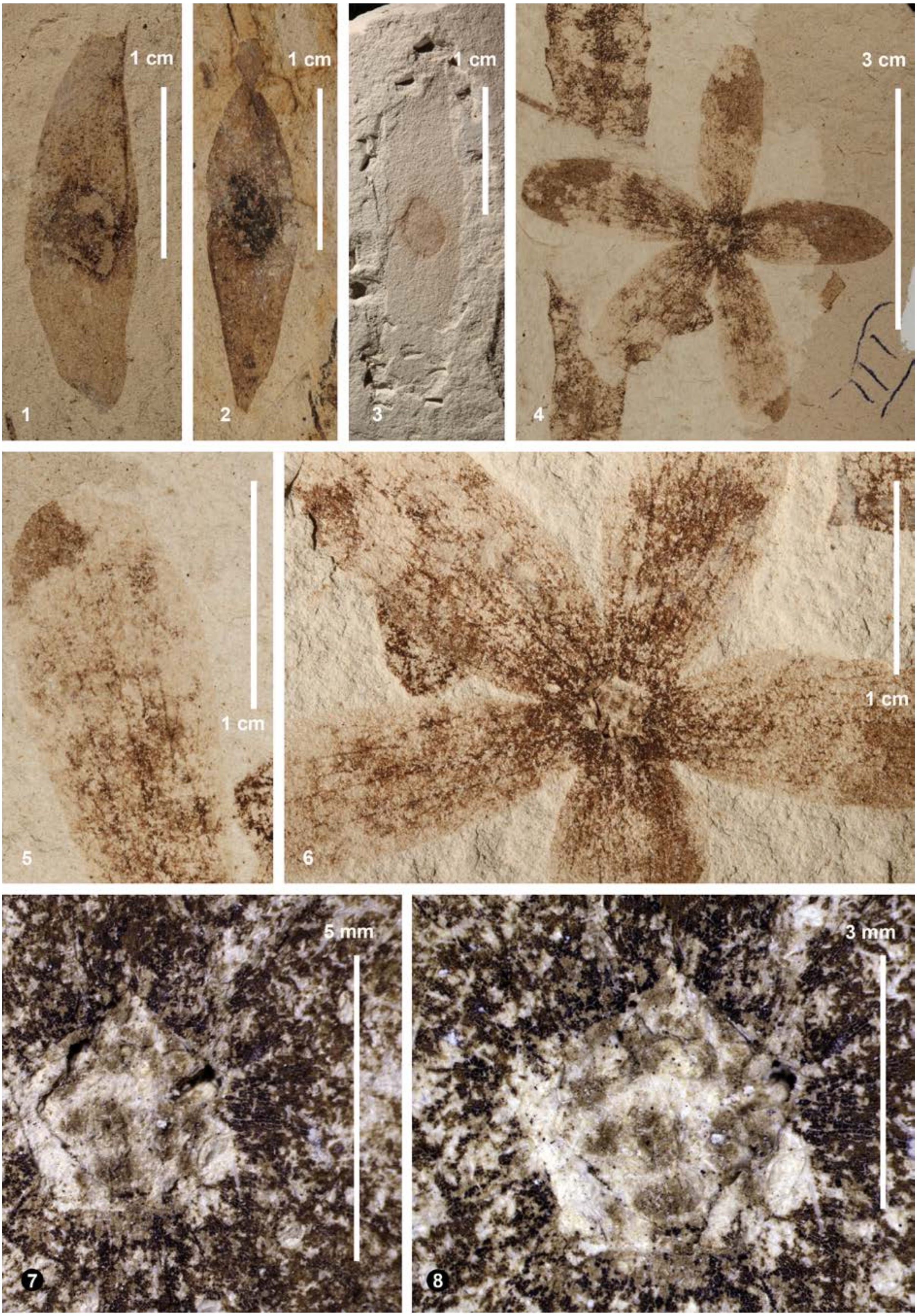

Plate 36. **1**. *Ailanthus tardensis* Hably type, fruit, specimen UCMP202174_01 (5387b); **2**, **3**. *Ailanthus confucii* Unger type; **2**. Fruit, specimen UCMP202174_02 (5387a); **3**. Fruit, specimen UCMP202175 (5916); **4–8**. *Chaneya* sp.; **4**. Flower, specimen UCMP202176_01 (5986); **5**. Petal, venation detail, specimen UCMP202176_01 (5986); **6**. Flower, detail, specimen UCMP202176_01 (5986); **7**. Flower, pentagonal central discus detail, specimen UCMP202176_01 (5986); **8**. Flower, pentagonal central discus detail, specimen UCMP202176_01 (5986)

obovate; attachment scar length 0.3–0.4 cm, attachment angle 60°–70°; nutlet angle 0°–10°. Wing extending partly along distal margin of nutlet; length 1.8–2 cm, width 0.6–0.8 cm; proximal margin straight, distal margin convex, apex rounded; veins not preserved.

Description (Pl. 34, figs 3, 7). Fruit samaroid, nutlet at basal end; nutlet diameter 0.4–0.6 cm; outline slightly elliptic; attachment scar length 0.3–0.5 cm, attachment angle ca 35°–45°; nutlet angle 15°–25°. Wing attached partly along apical margin of nutlet to attachment scar; length 2–2.6 cm, width 0.5–0.8 cm; proximal margin straight, distal margin convex, apex narrowly rounded; veins coalesced along proximal margin; wing veins diverging at 45°–55°, bifurcating acutely and anastomosing several times, reticulate veinlets visible.

Description (Pl. 34, figs 4, 5, 6, 8). Fruit samaroid, nutlet at basal end; nutlet diameter 0.4–0.6 cm; outline slightly elliptic; attachment scar length 0.3–0.5 cm, attachment angle ca 35°–45°; nutlet angle 15°–25°. Wing attached partly along apical margin of nutlet to attachment scar; length 2–2.6 cm, width 0.5–0.8 cm; proximal margin straight, distal margin convex, apex narrowly rounded; veins coalesced along proximal margin; wing veins diverging at 45°–55°, bifurcating acutely and anastomosing several times, reticulate veinlets visible.

Remarks. The samaras encountered in the fossil material belong to more than one species. For example, the specimen shown in Fig. 34: 1 resembles samaras found in section *Platanoidea*. The samaras figured by Paicheler and Blanc (1981) as *Acer campestre* L. (Paicheler & Blanc, pl. 13, figs 13, 14) do not belong to *A. campestre*. They are similar to the specimens shown in Pl. 34, figs 4, 5, 7, 8.

Genus *Sapindus* L.

Sapindus falcifolius (A.Braun) A.Braun

Pl. 35, figs 1, 2

1836 *Juglans falcifolia* A.Braun ex Buckland – Buckland: p. 513.
1851 *Sapindus falcifolius* (A.Braun) A.Braun in Stitzenberger – Stitzenberger: p. 87.
1981? *Sapindus falcifolius* (A.Braun) A.Braun – Paicheler & Blanc: pl. 14, figs 1, 2.

Material. Specimen UCMP202170; maybe MNHN20098-01, 20099, 20293.

Description. Leaf, leaf organisation simple; laminar size notophyll; laminar shape ovate, lamina base asymmetrical, laminar L:W ratio 7:1; base angle acute, apex angle acute, base shape convex and cuneate, position of petiolar attachment marginal, apex shape straight; margin type entire; 1° vein category pinnate, 2° vein category eucamptodromous, 2° vein spacing irregular, 2° vein angle ± uniform, weak intersecondaries present.

Remarks. Similar leaflets are found in various genera of the Sapindaceae. Because such leaves commonly co-occur with fruits of *Koelreuteria*, Kvaček et al. (2011) suggested that the foliage of "*Sapindus*" may actually belong to *Koelreuteria*. However, leaflets of *Koelreuteria* are partly lobed and coarsely to finely toothed.

Family SIMAROUBACEAE DC.

Genus *Ailanthus* Desf.

aff. *Ailanthus confucii* Unger

Pl. 36, figs 2, 3

1850c *Ailanthus confucii* Unger – Unger, p. 23.
1859 *Ailanthus confucii* Unger in Heer – Heer: p. 87, pl. 127, fig. 36.
1981 *Ailanthus altissima* Sw. – Paicheler & Blanc: pl. 16, figs 17–19.
2001 *Ailanthus confucii* Unger – Hably: p. 208, pl. 1, figs 1–10.
2004 *Ailanthus confucii* Unger – Corbett & Manchester: fig. 4, A–I.

Material. Specimens UCMP202174_02, 202175, 202276; MNHN20063-01, 20193, 20194, 20234-02, 20375, 20400–20402.

Description. Samaras, elliptic lanceolate, 20–30 mm long, 5–8 mm wide, proximal and distal end acute, central seed, ventral vein running marginally.

Remarks. These samaras are very similar to those of the modern *Ailanthus altissima* (Mill.) Swingle.

aff. *Ailanthus tardensis* Hably

Pl. 36, fig. 1

2001 *Ailanthus tardensis* Hably – Hably: p. 210, pl. 3, figs 1–7.
2004 *Ailanthus tardensis* Hably – Corbett & Manchester: fig. 4, J, K.

Material. Specimen UCMP202174_01.

Description. One samara, elliptic to narrow obovate, 25 mm long, 5–6 mm wide, proximal end acute, distal end rounded, seed central, ventral vein running from seed to proximal end of samara, ventral vein inset from margin.

Remarks. Based on the position of the ventral vein, Corbett and Manchester (2004) distinguished two types of fruits for Asia and Europe, corresponding to *A. confucii* and *A. tardensis* (Hably 2001). In *Ailanthus confucii* the ventral vein runs along the margin of the wing, whereas in *A. tardii* the ventral vein is well inset from the margin. The latter condition is seen in the extant species *A. excelsa* Roxb., *A. fordii* Noot. and *A. triphysa* (Dennst.) Alston. These species occur in India and Sri Lanka, China and northern and eastern Australia.

Family SIMAROUBACEAE DC.
vel RUTACEAE JUSS.

Genus *Chaneya* Wang & Manchester

***Chaneya* sp.**

Pl. 36, figs 4–8, Pl. 48, fig. 1

1977 *Astronium truncatum* (Lesquereux) MacGinitie – Kasaplıgil: fig. 24.
1981 *Astronium* sp. – Paicheler & Blanc: pl. 14, figs 5, 6.

Material. Specimen UCMP202176_01; MNHN20213b.

Description. Five-lobed corolla with thickened, pentagonal, central disc, ca 45 mm in diameter (a second specimen figured in Paicheler and Blanc, 1981, measures 31 mm in diameter), petals >20 mm long, elliptic, with 5–7 parallel longitudinal veins, longitudinal veins connected by anastomosing higher-order veins that depart at steep angles, central disc with whorl of carpels.

Remarks. The two flowers from the Güvem area are of different size; the one figured by Paicheler has shorter lobes but most probably they belong to the same species. Most of the previously described species of *Chaneya* have markedly smaller flowers. One exception is *Chaneya kokangensis* (Endo) Wang & Manchester from middle Miocene strata of Shanwang, eastern China (Wang & Manchester 2000, Teodoridis & Kvaček 2005). These specimens are almost identical in petal size to the ones from Turkey. The taxonomic affinities of *Chaneya* are with the extant Rutaceae and Simaroubaceae (*Picrasma*; Wang & Manchester 2000, Teodoridis & Kvaček 2005). Although it is impossible to infer the precise palaeoecology of this genus, Wang and Manchester (2000) speculated that this extinct genus may have been a liana.

Family Smilacaceae Vent.

Smilax weberi P.Wessel

Pl. 35, figs 3, 4

1856 *Smilax weberi* Wessel in Wessel & Weber – Wessel & Weber: p. 127, pl. 21, fig. 1.
1977 *Smilax aspera* L. – Kasaplıgil: fig. 16.

Material. Specimen UCMP202171.

Description. Leaf, leaf organisation simple; laminar size notophyll; laminar shape ovate-auriculate, lamina symmetrical, laminar L:W ratio 3:1; base angle wide obtuse, apex angle acute, base shape concave rounded, position of petiolar attachment marginal, apex shape straight; margin type entire; lobation base lobed; 1° vein category arcodromous, 2° vein category brochidodromous, strong intersecondaries present.

Remarks. Similar morphotypes of *S. weberi* have been reported from early Miocene deposits of Soma and from early Miocene deposits of Kimi (Denk et al. 2014, 2015).

Smilax miohavanensis Denk, D.Velitzelos, T.Güner & Ferrufino-Acosta

Pl. 35, figs 5–11

1981 *Populus tremula* L. – Paicheler & Blanc: pl. 4, fig. 6 (non figs 7, 8).
2004? *Mahonia aspera* (Unger) Kovar-Eder & Kvaček – Kovar-Eder et al.: p. 57, pl. 13, figs 1–6, 8.
2015 *Smilax miohavanensis* Denk, D.Velitzelos, T.Güner & Ferrufino-Acosta – Denk et al.: p. 426, figs 4–7.

Material. Specimens UCMP202164_05, 202164_06, 202172, 202173_01, 202266, 202279, 202470; MNHN20021, 20024-02, 20048, 20053, 20196; maybe 20243.

Description. Leaf, leaf organisation simple; laminar size microphyll; shape ovate, symmetrical, L:W ratio 1.5–2:1; base angle acute to obtuse, apex angle acute, base shape concave to rounded, position of petiolar attachment marginal, short and stout petiole, apex shape rounded to convex; margin type serrate, tooth apex spinose, tooth shape apical side concave, basal side straight to concave; 1° vein category acrodromous.

Remarks. The new combination *Mahonia* (?) *aspera* (Kovar-Eder et al. 2004) is based on Unger's (1847) *Quercus aspera*. More recently, Denk et al. (2015) revised the original material from Parschlug and abundant material from Güvem; they placed these leaves in the genus *Smilax*.

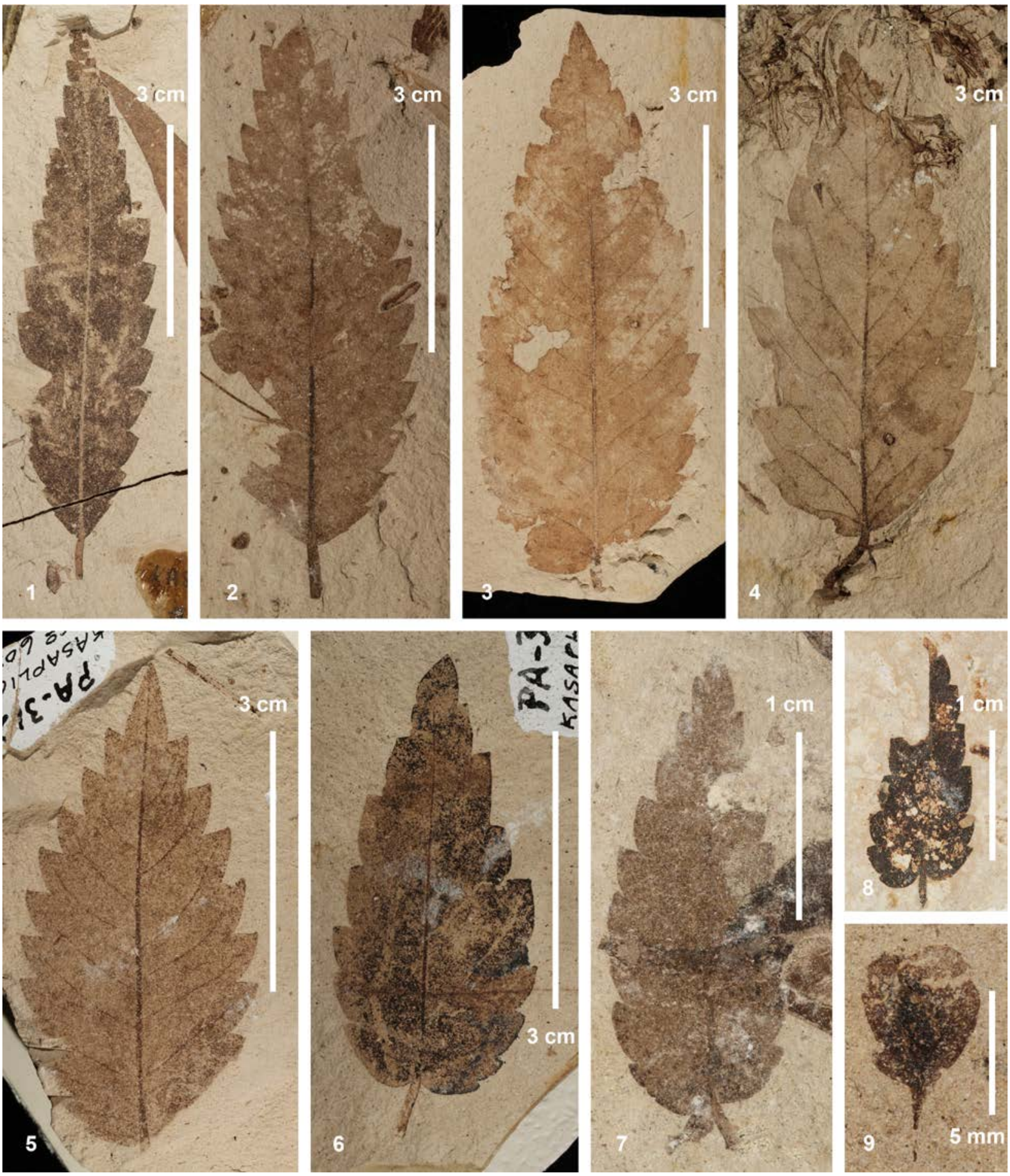

Plate 37. 1–8. *Zelkova zelkovifolia* (Unger) Bůžek & Kotlaba; **1**. Leaf, specimen UCMP202170_02 (5755); **2**. Leaf, specimen UCMP202174_03 (5387c); **3**. Leaf, specimen UCMP202177 (5844); **4**. Leaf, specimen UCMP202178_01 (5849a); **5**. Leaf, specimen UCMP202179 (6024); **6**. Leaf, specimen UCMP202180 (6017); **7**. Leaf, specimen UCMP202181 (5853); **8**. Leaf, specimen UCMP202182_01 (5995); **9**. *Ulmus* sp., fruit, specimen UCMP202183 (5953)

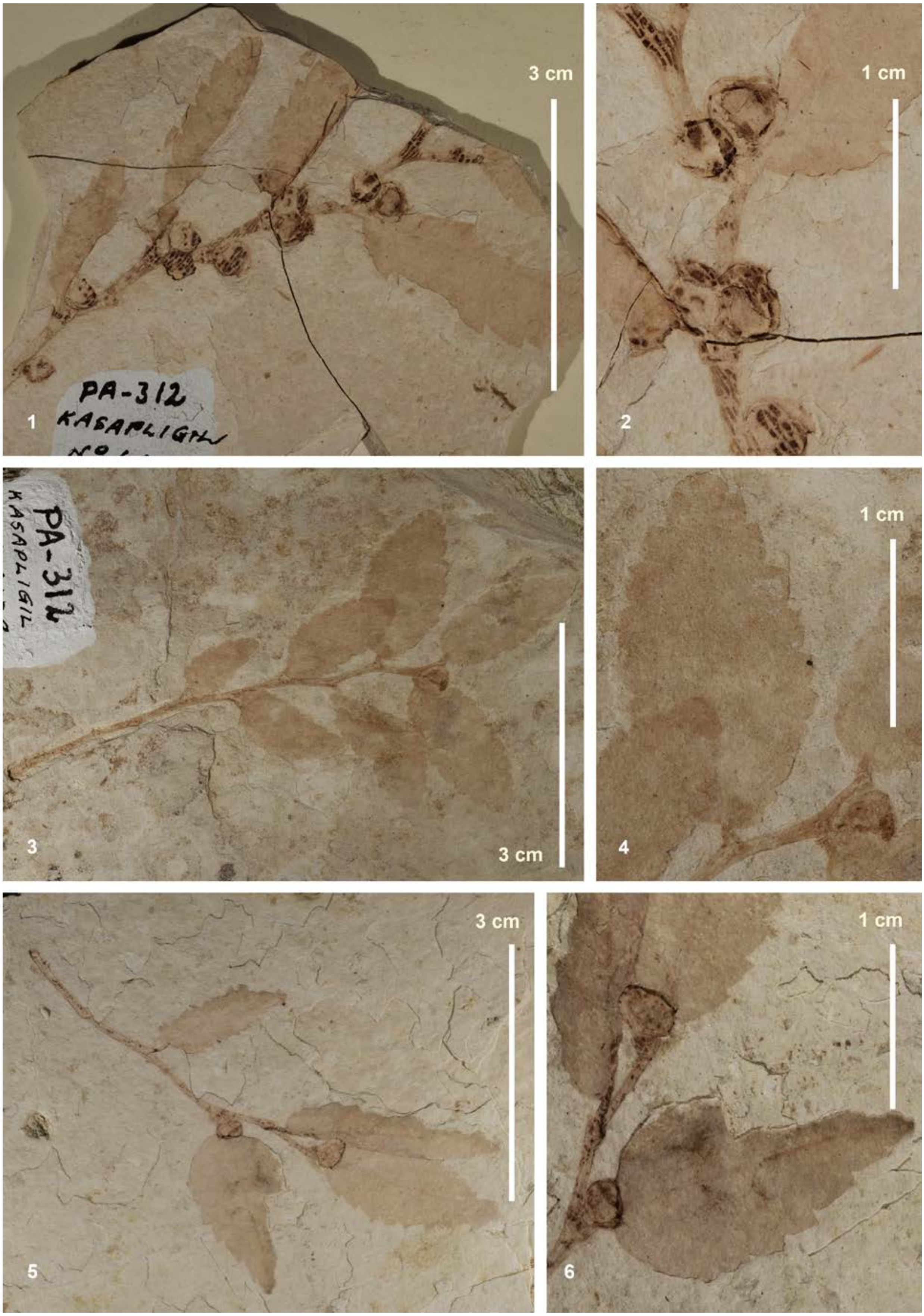

Plate 38. **1–6**. *Zelkova zelkovifolia* (Unger) Bůžek & Kotlaba; **1**. Fruiting branch, specimen UCMP202184 (PA-312-6023); **2**. Fruits, detail, specimen UCMP202184 (PA-312-6023); **3**. Fruiting branch, specimen UCMP202185 (PA-312-6028); **4**. Fruit, detail, specimen UCMP202185 (PA-312-6028); **5**. Fruiting branch, specimen UCMP202186 (6027); **6**. Fruits, detail, specimen UCMP202186 (6027)

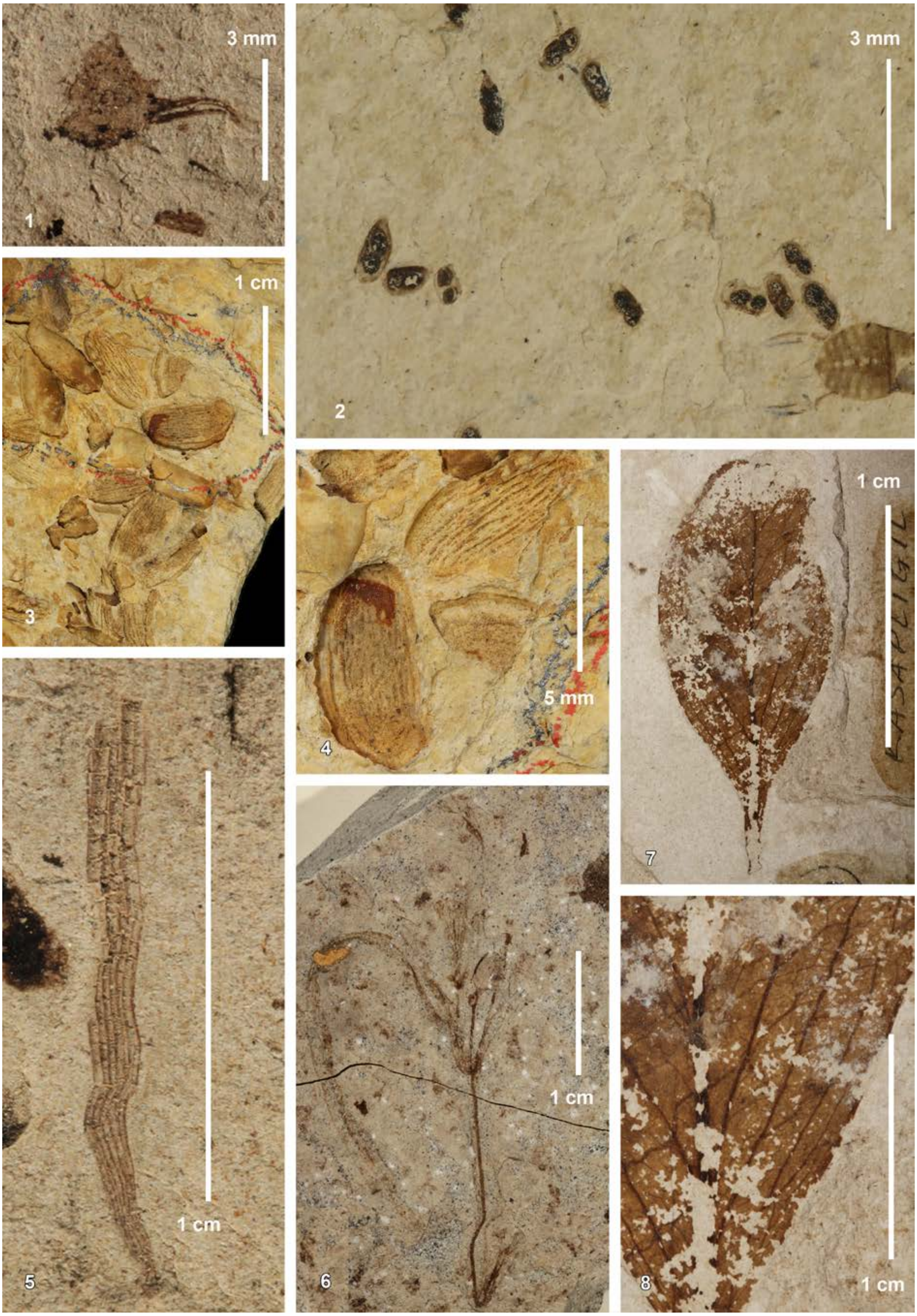

Plate 39. 1. *Ceratophyllum* sp., fruit, specimen UCMP202056 (5812); **2**. aff. *Daphnia* sp., dormant eggs in ephippia, specimen MNHN20209; **3**, **4**. *Stratiotes kaltennordheimensis* (Zenker) Keilhack; **3**. Seeds, specimen MNHN20204; **4**. Seeds, detail, specimen MNHN20204; **5**, **6**. *Potamogeton geniculatus* A.Braun; **5**. Narrow leaf, specimen UCMP202164 (5720a); **6**. Narrow leaves, specimen UCMP202187 (*n.n.*); **7**, **8**. *Potamogeton bruckmanni* A.Braun; **7**. Wide leaf, specimen UCMP202188 (5860); **8**. Leaf venation, detail, specimen UCMP202188 (5860)

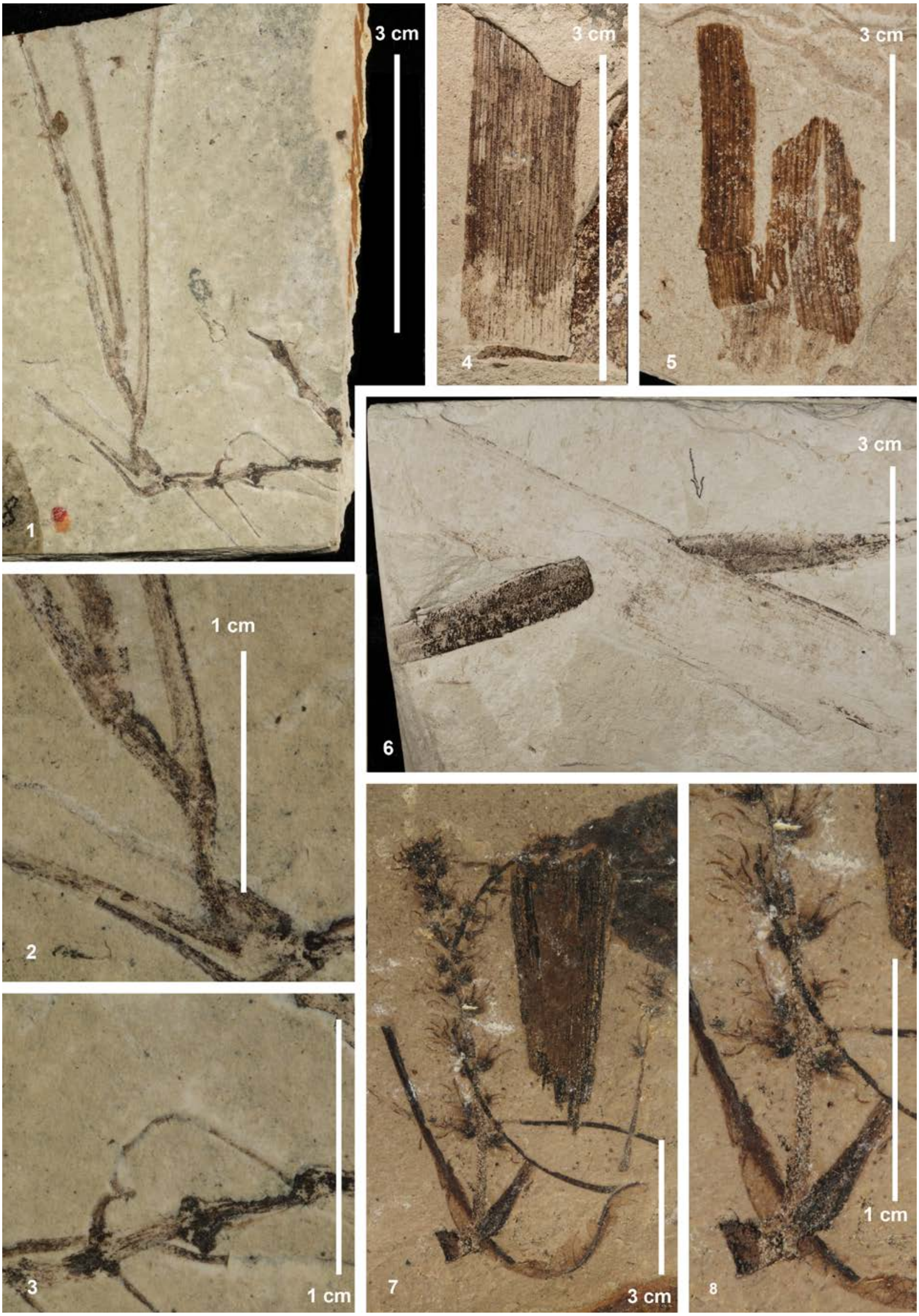

Plate 40. 1–3. *Potamogeton geniculatus*; **1**. Roots, stem and petioles, specimen UCMP202189 (5708); **2**. Stem and petioles, detail, specimen UCMP202189 (5708); **3**. Roots and stem, detail, specimen UCMP202189 (5708); **4–6**. *Typha* sp.; **4**. Leaf fragment, specimen UCMP202190 (*n.n.*); **5**. Leaf fragment, specimen UCMP202191_01 (5546); **6**. Leaf fragment, specimen UCMP202192_01 (5871); **7**, **8**. *Populus* sp.; **7**. Catkin, specimen UCMP202194 (5874); **8**. Catkin, detail, specimen UCMP202194 (5874)

Family TYPHACEAE Juss.

Typha sp.

Pl. 40, figs 4–6

1981 *Typha* L. – Paicheler & Blanc: pl. 2, figs 8, 9.

Material. Specimens UCMP202190, 202191_01, 202192_01, 202219_01.

Description. Leaf fragment, laminar shape oblong, lamina symmetrical; margin type entire; unlobed; venation parallelodromous.

Remarks. Parallelodromous leaves with short perpendicular veins connecting the main veins are assigned to Typha.

Family ULMACEAE Mirb.

Ulmus sp. (fruits)

Pl. 37, fig. 9

1981 *Ulmus* sp. – Paicheler & Blanc: pl. 15, figs 1–5 (fruits), non fig. 8 (leaf).

Material. Specimen UCMP202183; MNHN20169, 20170, 20199, 20403, 20404, 20406–20409, 20412.

Description. Samara, round to elliptic, 6–10 mm long, winged, wings wide, apex with notch, venation reticulate in proximal part and radial in distal part of wing, perianth 2–3 mm long, shallowly lobed.

Remarks. The winged samaras in Kasaplıgil's material and figured by Paicheler and Blanc (1981) clearly belong to *Ulmus*.

Zelkova zelkovifolia (Unger) Bůžek & Kotlaba

Pl. 37, figs 1–8; Pl. 38, figs 1–6

1843 *Ulmus zelkovifolia* Unger – Unger: pl. 24, figs 9–13, not fig. 8.
1845 *Ulmus zelkovifolia* Unger – Unger: p. 94, pro parte.
1963 *Zelkova zelkovifolia* (Unger) Bůžek & Kotlaba in Kotlaba – Kotlaba: p. 59, pl. 3, figs. 7, 8.
1977 *Zelkova* – Kasaplıgil: figs 20–23.
1981 *Quercus polymorpha* Cham. & Schl. – Paicheler & Blanc: pl. 11, fig. 13.
1981 *Quercus infectoria* Oliv. – Paicheler & Blanc: pl. 11, fig. 14.
1981 *Zelkova ungeri* Kováts – Paicheler & Blanc: pl. 14, figs 7–15.

Material. Specimens UCMP202170_02, 202174_03, 202177, 202178_01, 202179–202181, 202182_02–3, 202184–202186, 202240_03, 202242_01, 202262, 202288, 202333, 202342–202345, 202376, 202428–202434, 202435_01, 202436_01, 202453; MNHN20043, 20049, 20069, 20070, 20118, 20251, 20254, 20262, 20267, 20269, 20439, 20208-01, 20253-01, 20441.

Description. Leaf, leaf organisation simple; laminar size microphyll to notophyll; laminar shape elliptic to ovate, lamina asymmetrical, laminar L:W ratio 2–3.5:1; base angle acute to slightly obtuse, apex angle acute, base shape cuneate to convex, position of petiolar attachment marginal, apex shape straight to slightly acuminate; margin type serrate, tooth shape apical side slightly flexuous, basal side convex; 1° vein category pinnate, 2° vein category craspedodromous, 2° vein spacing irregular, 2° vein angle smoothly increasing towards base.

Remarks. *Zelkova* is a common element of many Oligocene to Pliocene plant assemblages in western Eurasia.

Incertae sedis – reproductive structures

Unknown cupule

Pl. 41, fig. 3

Material. Specimen UCMP202164.

Description. A cup-like structure on a short stalk.

Remarks. The specimen may represent a fagaceous young cupule.

Unknown ?flower

Pl. 41, fig. 4

Material. Specimen UCMP202196.

Description. Four sepal-like structures, basally fused, each sepal ca 5 mm long, elliptic.

Remarks. We are unable to suggest affinities to a modern family or genus.

Unknown male catkin, aff. *Juglans*

Pl. 41, figs 5, 6

1981 *Juglans* sp. – Paicheler & Blanc: pl. 16, figs 6–12.

Material. Specimen UCMP202197, 202351; MNHM20171, 20174, 20197.

Description. Male catkin, 2.5 cm long,

consisting of many densely packed staminate flowers.

Remarks. Similar catkins occur in *Juglans*.

Unknown flower (?Lauraceae)

Pl. 41, fig. 7

Material. Specimen UCMP202142_01.

Description. Perianth, ca 5 mm in diameter, consisting of six undifferentiated segments.

Remarks. Four to six sepal-like segments are found in many flowers of Lauraceae but it is impossible to infer particular relationships for the flower at hand.

aff. *Antholithes stiriacus* Kovar-Eder & Kvaček or *Nuphar* sp. (stigmatic disc)

Plate 41, fig. 8

Material. Specimen UCMP202198.

Description. Disc-like structure with radiating arms.

Remarks. The specimen resembles flower remains referred to as *Antholithes stiriacus* by Kovar-Eder et al. (2004, pl. 15, figs 14, 15). The specimen is also very similar to one described and figured in Meyer and Manchester (1997, pl. 75, figs 9, 10) from the Oligocene of western North America. Meyer and Manchester (1997) considered these structures to be the remains of the stigmatic disc of a *Nuphar* fruit.

Incertae sedis – foliage

Foliating whorl of leaves, aff. *Daphniphyllum* Blume

Pl. 41, figs 9, 10

Material. Specimen UCMP202199.

Description. Several small leaves arranged in a whorl, leaf organization simple, laminar size nanophyll, laminar shape elliptic, lamina symmetrical, L:W ratio 2:1, base and apex angle acute, base shape convex, apex shape convex, margin entire, 1° vein category pinnate, primary vein stout, 2° vein category weak brochidodromous, vein spacing uniform, vein angle uniform.

Remarks. Grímsson et al. (2015a) recorded dispersed pollen of *Daphniphyllum* from middle Miocene sediments of Austria. Modern species of *Daphniphyllum* occur in East and Southeast Asia, India and New Guinea.

Lobed leaf no. 1

Pl. 42, figs 1–3

Material. Specimen UCMP202042, 202200.

Description. Leaf, leaf organisation simple; laminar size mesophyll; laminar shape elliptic, laminar L:W ratio 1:1.5; base angle obtuse, apex angle acute, base shape truncate, position of petiolar attachment marginal, apex shape convex to rounded; margin type entire; lobation palmate; 1° vein category basal actinodromous, five basal veins, 2° vein category brochidodromous, 2° vein spacing increasing towards base, 2° vein angle smoothly increasing towards base, 3° vein category regular polygonal reticulate; 4° vein category regular polygonal reticulate; areolation well developed, five-sided; F.E.V.S. ranging between not branching to branching once.

Remarks. We are unable to place this leaf remain within a modern family. The patterns of lobation and secondary venation are very similar to leaves of *Alangium*.

Lobed leaf no. 2 (aff. *Dombeyopsis lobata* Unger)

Pl. 42, figs 4–6, ?Pl. 48, fig. 6

1981 *Acer opalus* Mill. – Paicheler & Blanc: pl. 13, fig. 7.

Material. Specimen UCMP202201, 202202; MNHN20007, 20095a &b.

Description. Leaf fragment, leaf organisation simple; laminar size mesophyll; margin type entire to crenulate; lobation palmate; 2° vein category brochidodromous, 3° vein category mixed alternate/opposing decurrent; 4° vein category regular polygonal reticulate.

Remarks. The material from Güvem resembles extinct species of Malvaceae, in particular *Dombeyopsis lobata* Unger (Knobloch & Kvaček 1964, Kvaček & Walther 2004, Worobiec et al. 2010). This very large leaf also resembles modern leaves of *Paulownia* (Paulowniaceae, Lamiales) with about seven species in China, Laos and Vietnam. Smiley (1961) reported similar

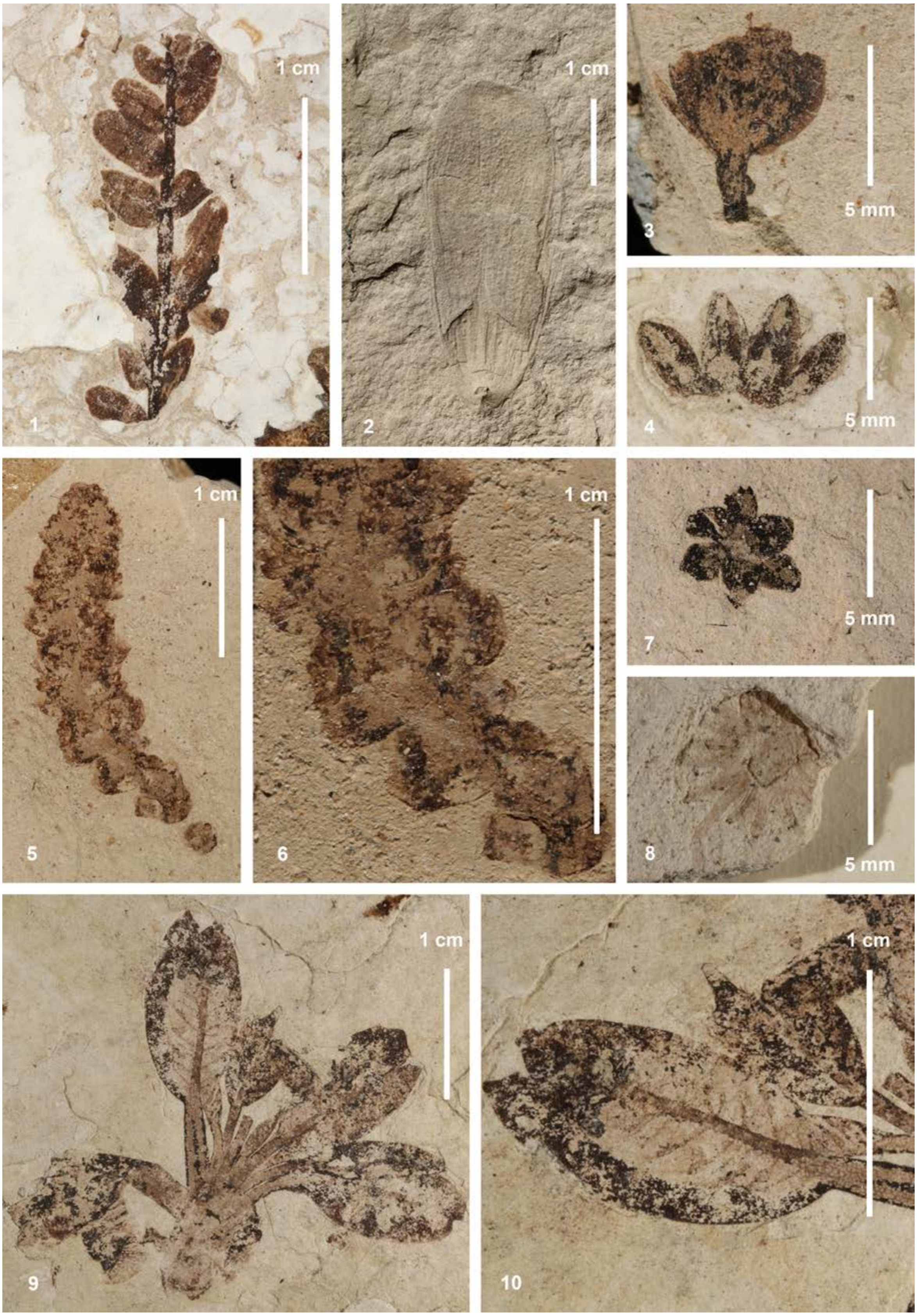

Plate 41. **1**. *Potamogeton* sp., axis leafy, specimen UCMP202194 (5978); **2**. Indet. cone scale (aff. *Calocedrus* sp.) or insect remain, specimen UCMP202195 (5494); **3–8**. Unidentified reproductive organs; **3**. Cupule, specimen UCMP202164_03 (5720a); **4**. Flower, specimen UCMP202196 (5983); **5**. Male catkin aff. *Juglans*, specimen UCMP202197 (5866a); **6**. Male catkin aff. *Juglans*, detail, specimen UCMP202197 (5866a); **7**. Flower (?Lauraceae), specimen UCMP202142_01 (5693); **8**. Flower, aff. *Antholithes stiriacus* Kovar-Eder & Z.Kvaček or *Nuphar* sp., specimen UCMP202198 (5962); **9–10**. Incertae sedis – foliage; **9**. Foliating whorl of leaves, aff. *Daphniphyllum* Blume, specimen UCMP202199 (*n.n.* MAT72-434); **10**. Foliating whorl of leaves, aff. *Daphniphyllum* Blume, detail, specimen UCMP202199 (MAT72-434)

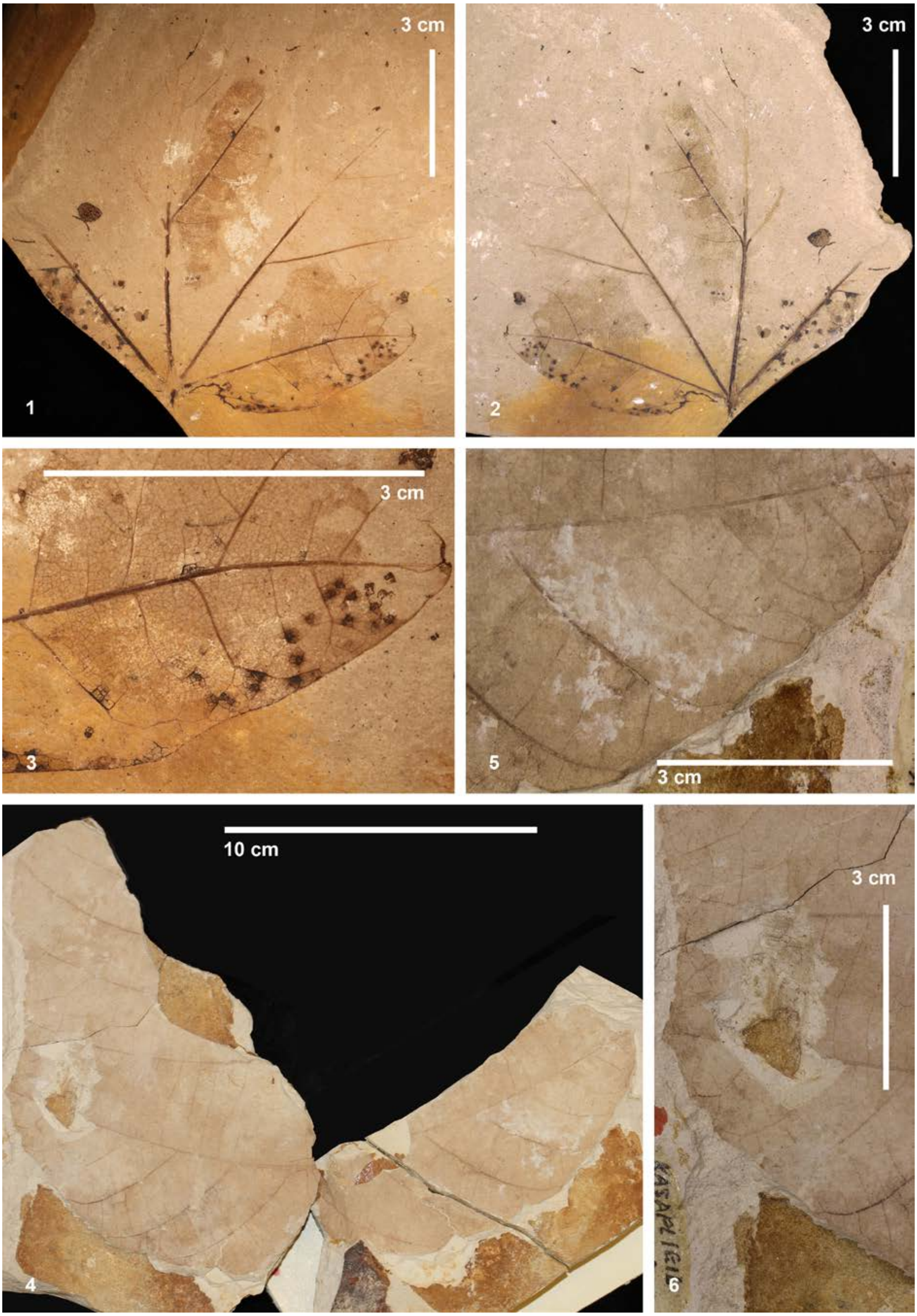

Plate 42. **1–6**. Incertae sedis – foliage; **1**. Lobed leaf no. 1, specimen UCMP202200 (*n.n.*); **2**. Lobed leaf no. 1, counterpart, specimen UCMP202042 (*n.n.*); **3**. Lobed leaf no. 1, venation, detail, specimen UCMP202200 (*n.n.*); **4**. Lobed leaf no. 2 (cf. *Dombeyopsis lobata* Unger), specimen UCMP202201, 202202 (5541); **5**. Lobed leaf no. 2 (cf. *Dombeyopsis lobate* Unger), venation, detail, specimen UCMP202201, 202202 (5541); **6**. Lobed leaf no. 2 (cf. *Dombeyopsis lobate* Unger), venation, detail, specimen UCMP202201, 202202 (5541)

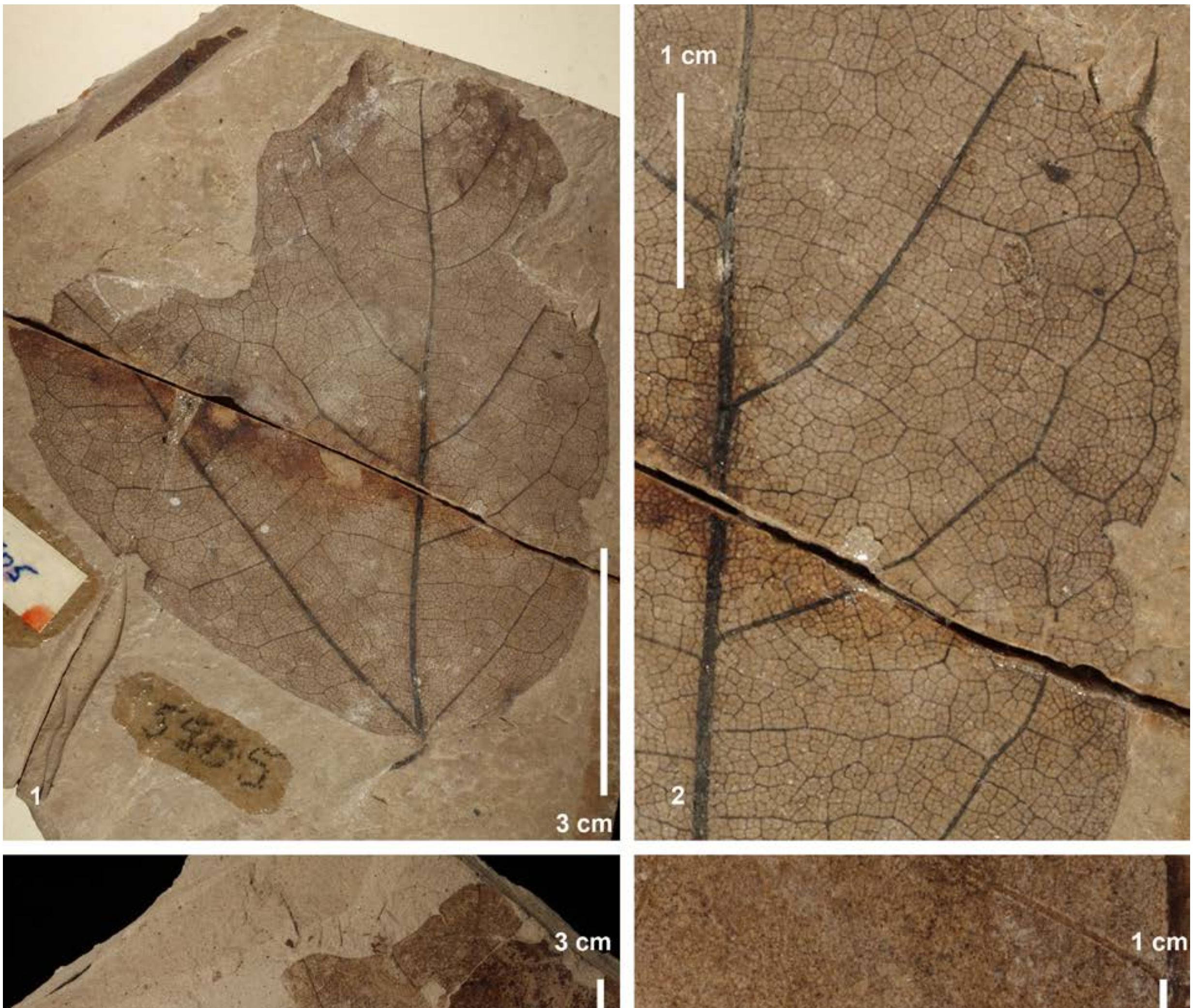

Plate 43. **1–4**. Incertae sedis – foliage; **1**. Lobed leaf no. 3 aff. *Alangium platanifolium* (Siebold & Zucc.) Harms, specimen UCMP202203 (5505); **2**. Lobed leaf no. 3 aff. *Alangium platanifolium* (Siebold & Zucc.) Harms, venation, detail, specimen UCMP202203 (5505); **3**. Lobed leaf no. 4, specimen UCMP202204_01 (5533); **4**. Lobed leaf no. 4, venation, detail, specimen UCMP202204_01 (5533)

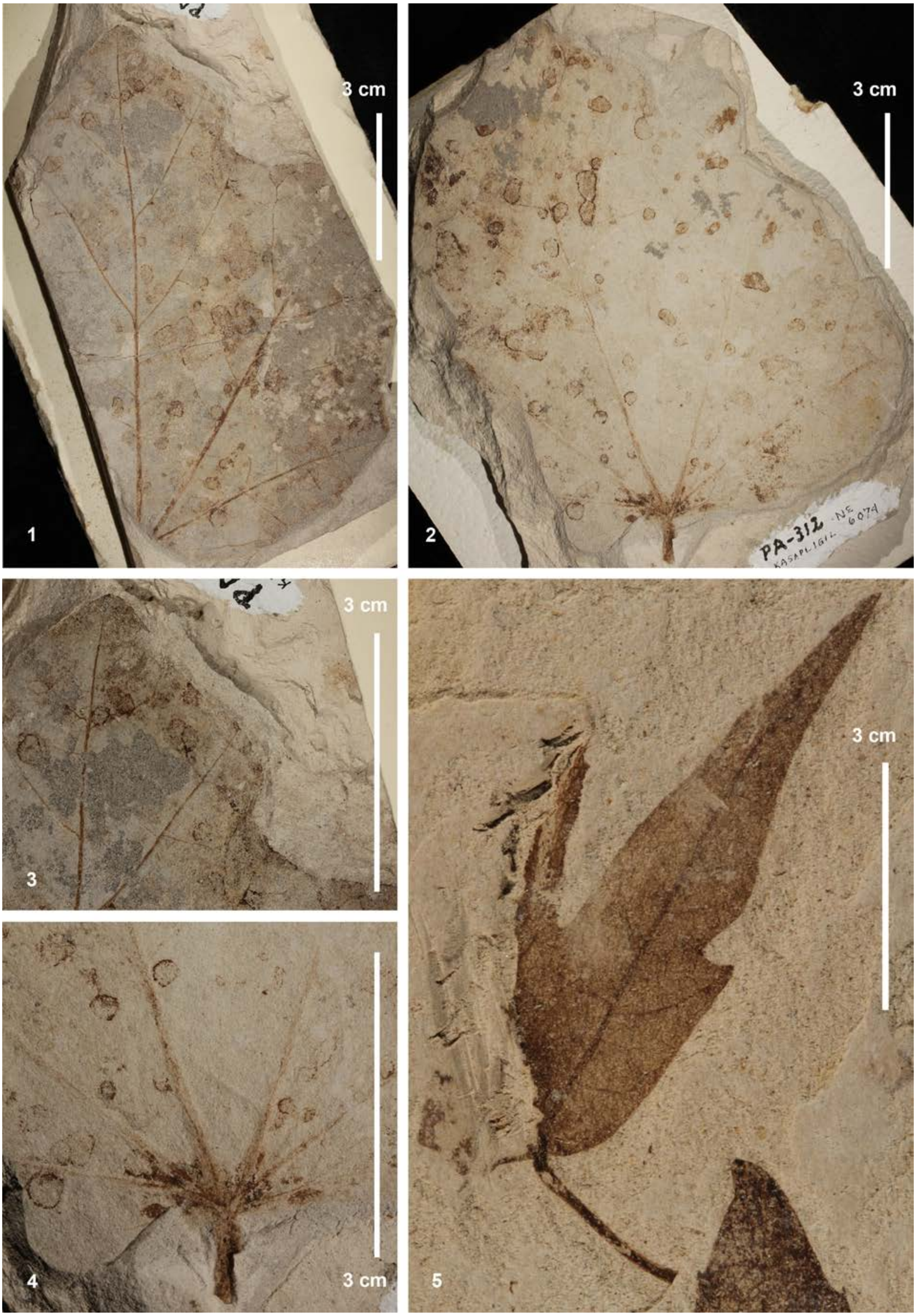

Plate 44. **1–6**. Incertae sedis – foliage; **1**. Lobed leaf no. 5 (aff. *Alangium chinense* (Lour.) Harms), specimen UCMP202205(6073); **2**. Lobed leaf no. 5 (aff. *Alangium chinense* (Lour.) Harms), specimen UCMP202206 (6074), counterpart to UCMP202205 (6073); **3**. Lobed leaf no. 5 (aff. *Alangium chinense* (Lour.) Harms), detail, specimen UCMP202205 (6073); **4**. Lobed leaf no. 5 (aff. *Alangium chinense* (Lour.) Harms), base, detail, specimen UCMP202206 (6074); **5**. Lobed leaf no. 6, specimen UCMP202074 (5910)

leaves of *Paulownia* from the Neogene of western North America. Fruit remains are known from Neogene deposits of Europe (e.g. Fischer & Butzmann 1997).

Lobed leaf no. 3 (aff. *Alangium platanifolium* (Siebold & Zucc.) Harms)

Pl. 43, figs 1, 2

Material. Specimen UCMP202203.

Description. Leaf, leaf organisation simple; laminar size notophyll; laminar shape elliptic, lamina asymmetrical; laminar L:W ratio 1.5:1; base angle obtuse, apex angle acute, base shape convex, position of petiolar attachment marginal; margin type serrate, tooth apex simple, tooth shape apical side concave, basal side straight, sinus rounded; lobation asymmetrical palmate; 1° vein category basal actinodromous, two basal veins, 2° vein category brochidodromous to semicraspedodromous, 2° vein spacing irregular, 2° vein angle irregular, strong intersecondaries present; 3° vein category mixed opposite/alternate percurrent; 4° vein category regular polygonal reticulate; areolation well developed, four- to five-sided; F.E.V.S. absent.

Remarks. Kasaplıgil labelled this specimen Moraceae. This asymmetrically lobed leaf is most similar to leaves of the genus *Alangium* (Cornaceae), particularly to leaves of the East Asian *A. platanifolium* and to a lesser degree *A. chinense* (Loureiro) Harms.

Lobed leaf no. 4

Pl. 43, figs 3, 4

Material. Specimen UCMP202204_01.

Description. Leaf fragment, leaf organisation simple; laminar size notophyll; base angle obtuse, apex angle acute, base shape convex, position of petiolar attachment marginal; margin type entire; lobation palmate; 1° vein category basal actinodromous, five (?) basal veins, 2° vein in spacing irregular, 2° vein angle irregular, strong intersecondaries present.

Remarks. Kasaplıgil labelled this specimen *Broussonetia miocenica* Hu & Chaney (Moraceae), described from the middle Miocene Shanwang flora (eastern China; Hu & Chaney 1940). There are closer similarities with the genus *Alangium* and possibly also with the extinct Malvaceae *Laria rueminiana*.

Lobed leaf no. 5 (aff. *Alangium chinense* (Lour.) Harms)

Pl. 44, figs 1–4

1981 *Acer opalus* Mill. – Paicheler & Blanc: pl. 13, figs 7, 11.

Material. Specimens UCMP202205, 202206; MNHN20016, 20017.

Description. Leaf fragment; laminar size mesophyll; laminar L:W ratio 1:1.5; base angle obtuse, apex angle acute, base shape truncate, position of petiolar attachment marginal, apex shape straight; margin type entire; lobation palmate; 1° vein category basal actinodromous, seven basal veins, 2° vein category craspedodromous, strong intersecondaries present.

Remarks. Kasaplıgil labelled this specimen *Brassaiopsis mirabilis* Kol., an extinct Araliaceae from late Miocene deposits of Georgia (Abkhasia; Kolakovsky 1964). *Brassaiopsis* has deeply lobed leaves, while the material from Güvem is shallowly lobed. Again, similarities with *Alangium chinense* and *A. platanifolium* are noted. Further similarities are with modern and extinct genera of Malvaceae, namely with the East Asian *Firmiana simplex* (L.) W.F.Wight and the extinct *Laria* (Worobiec et al. 2010) and "*Ficus*" *tiliifolia* forma *lobata* Heer (Heer 1859).

Lobed leaf no. 6

Pl. 44, fig. 5

Material. Specimen UCMP202074.

Description. Leaf fragment; leaf organisation simple, laminar size micro- to notophyll; laminar L:W ratio 1:1.5; base angle obtuse, apex angle acute, base shape convex, position of petiolar attachment marginal, apex shape straight; margin type entire with single tooth, tooth apex simple, tooth with concave apical and straight basal side, sinus angular; lobation palmate; 1° vein category basal actinodromous, 2° vein category brochidodromous, rarely craspedodromous, strong intersecondaries present, 2° vein spacing irregular, 2° vein angle smoothly increasing towards base.

Remarks. The single specimen resembles some leaves of the East Asian *Alangium platanifolium* (cf. herbarium sheet P00542829, herbarium P).

'Dicotylophyllum' sp. 1–26

Unless stated otherwise, we are unable to assign the following leaf specimens to a particular modern taxon.

Dicotylophyllum 1

Pl. 45, fig. 1

Material. Specimen UCMP202207_01.

Description. Leaf, leaf organization simple, lamina size microphyll; lamina shape elliptic, lamina symmetry symmetrical, lamina L:W ratio 2:1; base angle acute, apex angle acute, base shape concave, position of petiolar attachment marginal; margin type entire; 1° vein category pinnate, 2° vein category weak brochidodromous, 2° vein angle smoothly decreasing towards base.

Dicotylophyllum 2 cf. *Pistacia* aff. *P. therebinthus* L.

Pl. 45, figs 2, 3

Material. Specimen UCMP202209.

Description. Leaf, leaf organization simple, lamina size microphyll; lamina shape elliptic, lamina symmetry only base asymmetrical, lamina L:W ratio 4:1; base angle acute, apex angle acute, base shape convex to concave, position of petiolar attachment marginal; margin type entire; 1° vein category pinnate, 2° vein category cladodromous, 2° vein spacing irregular, 2° vein angle ± uniform, strong intersecondaries present; 3° vein category random reticulate.

Remarks. The venation pattern in this leaf/leaflet is similar to that in the extant deciduous *Pistacia therebinthus*.

Dicotylophyllum 3 aff. *Buxus*

Pl. 45, figs 4, 5

Material. Specimen UCMP202141_02.

Description. Leaf, leaf organization simple, lamina size microphyll; lamina shape obovate, lamina symmetry symmetrical, lamina L:W ratio 3:1; base angle acute, apex angle acute, base shape cuneate, position of petiolar attachment marginal, apex shape rounded; margin type entire; 1° vein category pinnate, 2° vein category brochidodromous, 2° vein spacing irregular, 2° vein angle ± uniform.

Remarks. The leaf shape, margin and venation are similar to some species of *Buxus*.

Dicotylophyllum 4

Pl. 45, figs 6, 7

1981 *Cercidiphyllum* sp. – Paicheler & Blanc: pl. 17, figs 6, 7.

1981 *Sibiera* sp. – Paicheler & Blanc: pl. 18, figs 1, 2.

Material. Specimen UCMP202209; MNHN20056, 20092.

Description. Leaf, leaf organization simple, lamina size microphyll; lamina shape elliptic, lamina symmetry symmetrical, lamina L:W ratio 3:1; base angle acute, apex angle acute, base shape cuneate to convex, position of petiolar attachment marginal, apex shape straight; margin type entire; 1° vein category pinnate, 2° vein category eucamptodromous, 2° vein spacing irregular, 2° vein angle decreasing towards base.

Dicotylophyllum 5

Pl. 45, fig. 8

Material. Specimen UCMP202210.

Description. Leaf, leaf organization simple, lamina size notophyll; lamina shape ovate, lamina symmetry symmetrical, lamina L:W ratio 2.5:1; base angle acute, apex angle acute, base shape convex, position of petiolar attachment marginal, apex shape straight; margin type entire; 1° vein category pinnate, 2° vein category eucamptodromous, 2° vein spacing ± uniform, 2° vein angle increasing towards base.

Dicotylophyllum 6

Pl. 45, figs 9, 10, Pl. 48, fig. 2

1981 *Hedera* sp. – Paicheler & Blanc: pl. 10, fig. 3.

Material. Specimen UCMP202211; MNHN20026.

Description. Leaf fragment, leaf organization simple, lamina size microphyll; apex angle acute, base apex shape straight; margin type entire; 1° vein category pinnate, 2° vein category

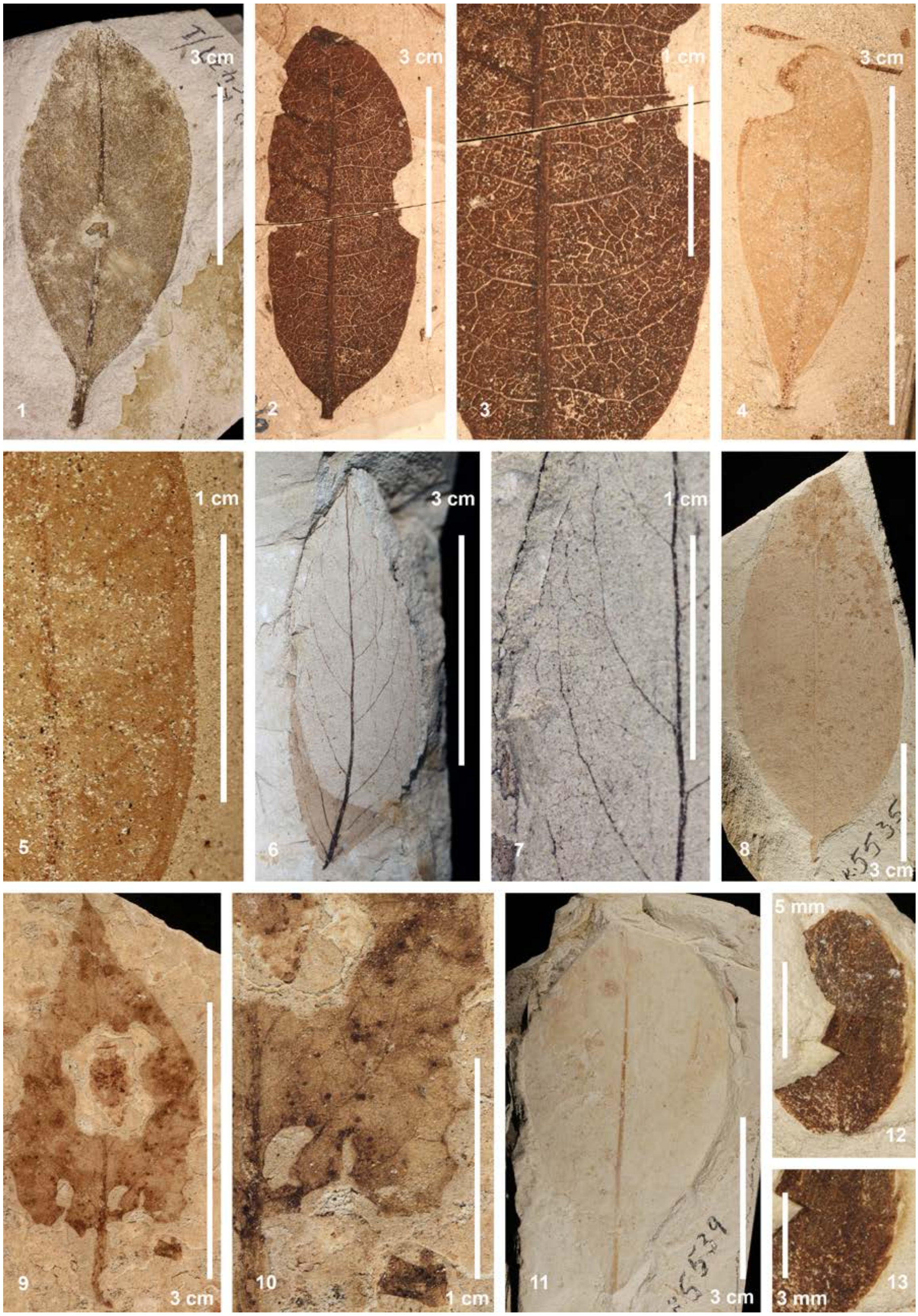

Plate 45. Incertae sedis – foliage; **1**. 'Dicotylophyllum' sp. 1, leaf, specimen UCMP202207_01 (5437); **2**, **3**. 'Dicotylophyllum' sp. 2 cf. *Pistacia* aff. *P. therebinthus* L.; **2**. Leaf, specimen UCMP202208_01 (6926); **3**. Leaf venation, detail, specimen UCMP202209 (6926); **4**, **5**. 'Dicotylophyllum' sp. 3 aff. *Buxus* sp.; **4**. Leaf, specimen UCMP202141_02 (5701); **5**. Leaf venation, detail, specimen UCMP202141_02 (5701); **6**, **7**. 'Dicotylophyllum' sp. 4; **6**. Leaf, specimen UCMP202209 (5555); **7**. Leaf venation, detail, specimen UCMP202209 (5555); **8**. 'Dicotylophyllum' sp. 5, leaf, specimen UCMP202210 (5535); **9**, **10**. 'Dicotylophyllum' sp. 6; **9**. Leaf fragment, specimen UCMP202211 (6915); **10**. Leaf venation, detail, specimen UCMP202211 (6915); **11**. 'Dicotylophyllum' sp. 7, leaf, specimen UCMP202212 (5539); **12**, **13**. 'Dicotylophyllum' sp. 8, leaf fragment, specimen UCMP202213 (*n.n.*); **13**. Leaf venation, detail, specimen UCMP202213 (*n.n.*)

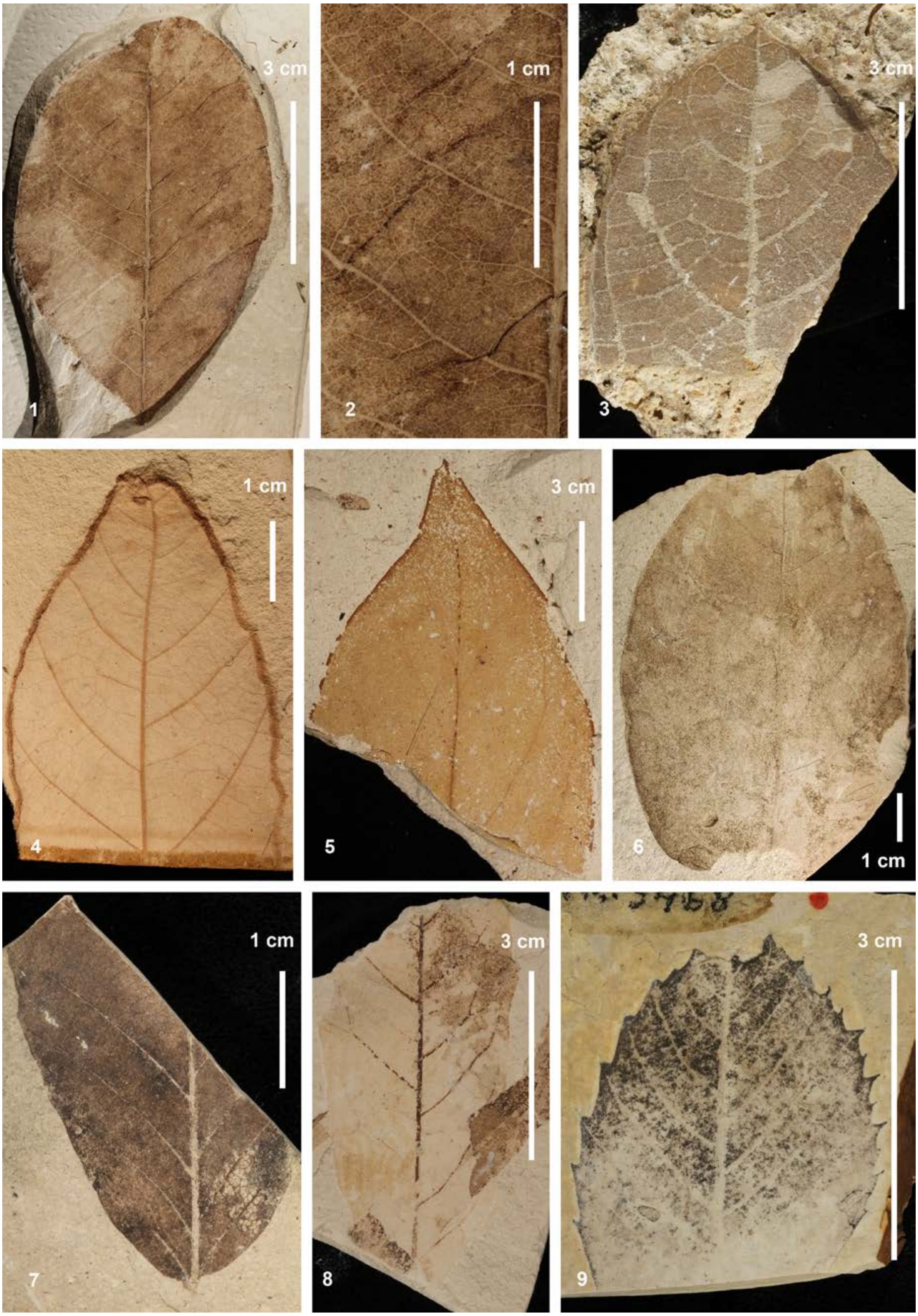

Plate 46. Incertae sedis – foliage; **1**, **2**. 'Dicotylophyllum' sp. 9; **1**. Leaf, specimen UCMP202214 (5979); **2**. Leaf venation, detail, specimen UCMP202214 (5979); **3**. 'Dicotylophyllum' sp. 10 aff. *Ficus* sp., leaf fragment, specimen UCMP202215 (5915); **4**. 'Dicotylophyllum' sp. 11, leaf fragment, specimen UCMP202216 (5730); **5**. 'Dicotylophyllum' sp. 12 aff. cf. *Ilex* sp., leaf fragment, specimen UCMP202217 (5753); **6**. 'Dicotylophyllum' sp. 13, leaf fragment, specimen UCMP202207_02 (5437); **7**. 'Dicotylophyllum' sp. 14 aff. *Fagus* sp., leaf fragment, specimen UCMP202218 (5710); **8**. 'Dicotylophyllum' sp. 15, leaf fragment, specimen UCMP202219_01 (5749); **9**. 'Dicotylophyllum' sp. 16 aff. *Quercus* sp., leaf fragment, specimen UCMP202220 (5468)

eucamptodromous, weak intersecondaries present; 3° vein category alternate percurrent.

Remarks. We are unable to assign this poorly preserved leaf specimen to a particular modern taxon; it resembles some species of *Calystegia* (Convolvulaceae), a genus of climbing herbs.

Dicotylophyllum 7 aff. *Cornus*

Pl. 45, fig. 11

Material. Specimen UCMP202212.

Description. Leaf fragment, leaf organization simple, lamina size notophyll; lamina symmetry symmetrical; base angle acute, base shape decurrent, position of petiolar attachment marginal; margin type entire; 1° vein category pinnate, 2° vein category weak brochidodromous, 2° vein spacing in lower two thirds decreasing towards base, 2° vein angle decreasing towards base.

Remarks. Kasaplıgil labelled this specimen "aff. *Cornus miowalteri* Hu & Chaney".

Dicotylophyllum 8

Pl. 45, figs 12, 13

Material. Specimen UCMP202213.

Description. Leaf fragment, leaf organization simple, lamina size nanophyll; lamina shape elliptic to oblong, lamina symmetry symmetrical, laminar L:W ratio 2:1; margin type serrate, tooth apex simple, teeth with straight apical and basal side, sinus angular; 1° vein category pinnate, 2° vein category semicraspedodromous, 2° vein angle decreasing towards base.

Remarks. This leaf fragment resembles Rosaceae or *Berberis*.

Dicotylophyllum 9

Pl. 46, figs 1, 2, Pl. 48, fig. 5

1981 *Periploca* sp. – Paicheler & Blanc: pl. 18, fig. 7.

Material. Specimen UCMP202214; MNHN20091.

Description. Leaf, leaf organisation simple; laminar size notophyll; laminar shape elliptic; lamina symmetrical, laminar L:W ratio 2:1; base angle acute, base shape decurrent; margin type entire; 1° vein category pinnate, 2° vein category weak brochidodromous, 2° vein spacing irregular, 2° vein angle smoothly decreasing towards base, strong intersecondaries present; 3° vein category mixed alternate/opposite percurrent; 4° vein category regular polygonal reticulate; areolation well developed, four- to five-sided.

Remarks. Kasaplıgil labelled this specimen *Diospyros*. The course of the secondary venation, however, does not fit with that in *Diospyros*. Paicheler and Blanc (1981) suggested this leaf to belong with *Periploca*. Also, this genus bears no similarity to the specimen at hand.

Dicotylophyllum 10 aff. *Ficus*

Pl. 46, fig. 3

Material. Specimen UCMP202215.

Description. Leaf fragment; apex angle obtuse, apex shape convex; margin type entire; 1° vein category pinnate, 2° vein category weak brochidodromous, 2° vein spacing in upper third irregular, 2° vein angle in upper third smoothly decreasing towards base, weak intersecondaries present; 3° vein category mixed alternate/opposite percurrent.

Remarks. Kasaplıgil labelled this specimen *Ficus*. There are striking similarities in leaf shape and leaf venation between some species of *Ficus* and the single fossil specimen from Güvem. For example, the modern Indian and Southeast Asian *Ficus mollis* Vahl (cf. herbarium sheet P06875784, herbarium P) includes leaves virtually identical to the fossil. Despite this, we do not think a generic determination is meaningful based on a single fragmentary leaf.

Dicotylophyllum 11

Pl. 46, fig. 4

Material. Specimen UCMP202216.

Description. Leaf fragment; apex angle acute; margin type serrate, tooth apex simple, sinus rounded; 1° vein category pinnate, 2° vein category craspedodromous, 2° vein spacing in upper third irregular, 2° vein angle in upper third smoothly increasing towards base, strong intersecondaries present; 3° vein category mixed alternate/opposite percurrent.

Dicotylophyllum 12 aff. cf. *Ilex* sp.

Pl. 46, fig. 5

Material. Specimen UCMP202217.

Description. Leaf fragment; apex angle acute, apex shape acuminate to convex; margin type entire; 1° vein category pinnate, 2° vein category eucamptodromous, 2° vein spacing in upper third irregular, 2° vein angle in upper third ± uniform, no intersecondaries present.

Remarks. This specimen resembles the leaves described above as cf. *Ilex* sp.

Dicotylophyllum 13

Pl. 46, fig. 6

Material. Specimen UCMP202207_02.

Description. Leaf fragment; leaf organisation simple; laminar size notophyll; laminar shape elliptic to ovate; lamina symmetrical, laminar L:W ratio 1.5–2:1; base angle obtuse; margin type entire; 1° vein category pinnate, 2° vein category weak brochidodromous, 2° vein spacing increasing towards base, 2° vein angle ± uniform, weak intersecondaries present.

Dicotylophyllum 14 aff. *Fagus*

Pl. 46, fig. 7

Material. Specimen UCMP202218.

Description. Leaf fragment; base angle acute, base shape convex, position of petiolar attachment marginal; margin type serrate; tooth apex simple, tooth shape apical side and basal side concave, sinus rounded; 1° vein category pinnate, 2° vein category pseudocraspedodromous, 2° vein spacing in lower third decreasing towards base, 2° vein angle ± uniform, no intersecondaries present; 3° vein category regular polygonal reticulate; 4° vein category regular polygonal reticulate; areolation well developed, four- to five-sided.

Remarks. This leaf remain may belong to *Fagus*.

Dicotylophyllum 15

Pl. 46, fig. 8

Material. Specimen UCMP202219_01.

Description. Leaf fragment; base angle acute; margin type serrate; tooth apex simple, tooth shape apical side and basal side concave, sinus rounded; 1° vein category pinnate, 2° vein category craspedodromous, 2° vein spacing in middle part irregular, 2° vein angle decreasing towards base, weak intersecondaries present.

Dicotylophyllum 16 aff. *Quercus*

Pl. 46, fig. 9

Material. Specimen UCMP202220.

Description. Leaf fragment; margin type serrate; tooth apex simple, tooth shape apical side concave, basal side concave to straight, sinus angular, 1° vein category pinnate, 2° vein category craspedodromous, 2° vein spacing ± uniform, 2° vein angle ± uniform, weak intersecondaries present.

Dicotylophyllum 17 aff. *Nerium* sp.

Pl. 47, figs 1, 2

Material. Specimen UCMP202221.

Description. Leaf fragment; laminar shape elliptic to oblong; margin type entire; 1° vein category pinnate, distinct primary vein, from which thin secondary veins depart at low angles towards margin.

Remarks. Such foliage has been referred to as *Nerium* sp. by Kovar-Eder et al. (2004) and by Velitzelos et al. (2014). Also, Kasaplıgil labelled this specimen cf. *Nerium*. The leaf morphology of the fossil specimen is virtually identical to leaves of the modern *Nerium oleander* L.

Dicotylophyllum 18

Pl. 47, fig. 3

Material. Specimen UCMP202222.

Description. Leaf fragment; margin type entire; 1° vein category pinnate, 2° vein category eucamptodromous, 2° vein spacing ± uniform, 2° vein angle smoothly increasing towards base.

Dicotylophyllum 19

Pl. 47, fig. 4

Material. Specimen UCMP202223.

Description. Leaf, leaf organisation simple; laminar size notophyll; laminar shape elliptic to oblong, lamina base slightly asymmetrical, laminar L:W ratio 3:1; base angle acute, apex angle acute, base shape rounded, position of petiolar attachment marginal; margin type serrate,

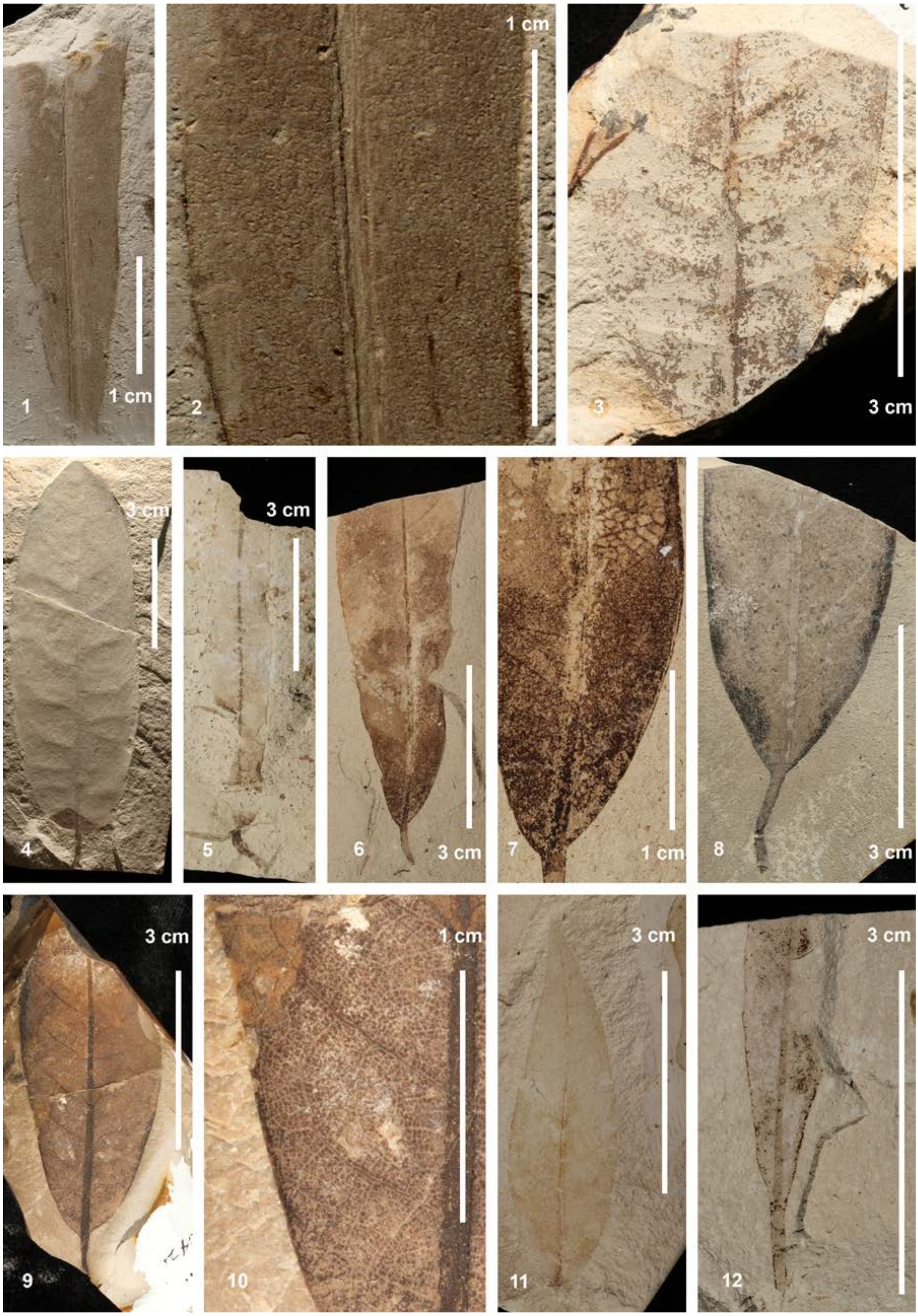

Plate 47. Incertae sedis – foliage; **1**, **2**. 'Dicotylophyllum' sp. 17 cf. *Nerium* sp.; **1**. Leaf fragment, specimen UCMP202221 (5857); **2**. Leaf venation, detail, specimen UCMP202221 (5857); **3**. 'Dicotylophyllum' sp. 18, leaf fragment, specimen UCMP202222 (6062); **4**. 'Dicotylophyllum' sp. 19, leaf fragment, specimen UCMP202223 (5551) (might belong to the same taxon as Dicotylophyllum sp. 18); **5**. 'Dicotylophyllum' sp. 20 aff. *Quercus neriifolia* A.Braun, leaf fragment, specimen UCMP202224_01 (5877); **6**, **7**. 'Dicotylophyllum' sp. 21, **6**. Leaf fragment, specimen UCMP202225_01 (5795); **7**. Leaf base and venation, detail, specimen UCMP202225_01 (5795); **8**. 'Dicotylophyllum' sp. 22, leaf fragment, specimen UCMP202226 (5497); **9**, **10**. 'Dicotylophyllum' sp. 23; **9**. Leaf fragment, specimen UCMP202227 (6042); **10**. Leaf venation, detail, specimen UCMP202227 (6042); 11. 'Dicotylophyllum' sp. 24, leaf fragment, specimen UCMP202228 (5484); **12**. 'Dicotylophyllum' sp. 25, leaf fragment, specimen UCMP202229 (5868)

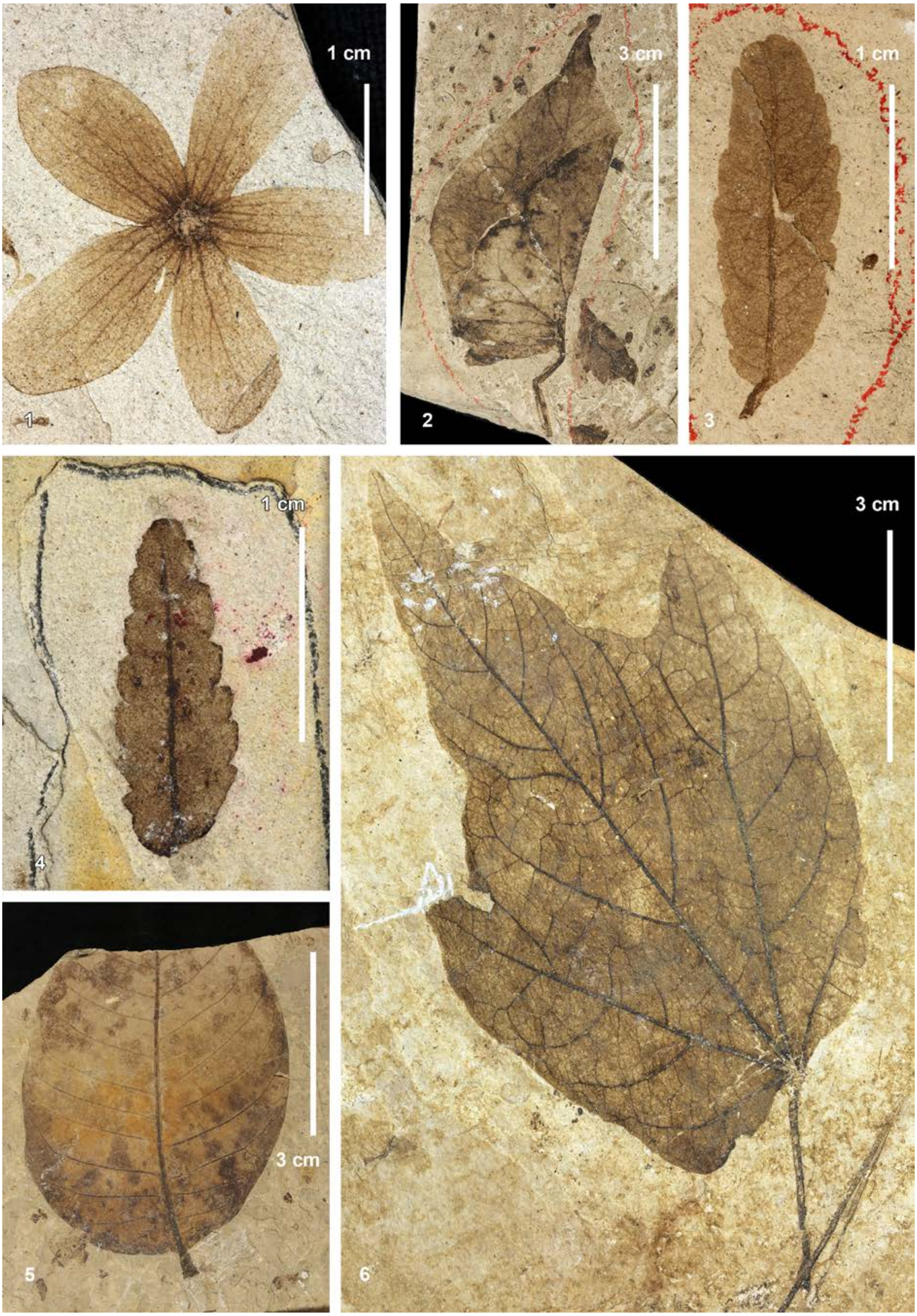

Plate 48. **1**. *Chaneya* sp., flower, specimen MNHN20213 [as *Astronium* sp.]; **2**. 'Dicotylophyllum' sp. 6, leaf, specimen MNHN20026 [as *Hedera* sp.]; **3**. 'Dicotylophyllum' sp. 26 aff. *Cedrelospermum* sp., leaf, specimen MNHN20100 [as *Rhus* sp.]; **4**. cf. *Zelkova zelkovifolia* (Unger) Bůžek & Kotlaba, small leaf, specimen MNHN20069 [as *Rhus* sp.]; **5**. 'Dicotylophyllum' sp. 6, leaf, specimen 20091 [as *Periploca*]; **6**. Lobed leaf no. 2 (aff. *Dombeyopsis lobata* Unger), leaf, specimen MNHN20007 [as *Acer tricuspidatum*]

tooth shape apical side and basal side concave, sinus rounded; 1° vein category pinnate, 2° vein category craspedodromous, 2° vein spacing irregular, 2° vein angle smoothly increasing towards base, strong intersecondaries present.

Dicotylophyllum 20 aff. *Quercus neriifolia* A.Braun

Pl. 47, fig. 5

Material. Specimen UCMP202224_01.

Description. Leaf fragment, leaf organisation simple; laminar size notophyll; laminar shape oblong, lamina base slightly asymmetrical; base angle acute, base shape cuneate to convex, position of petiolar attachment marginal; margin type entire; 1° vein category pinnate.

Remarks. Oblong leaves with an entire margin resemble some species of *Quercus*.

Dicotylophyllum 21

Pl. 47, figs 6, 7

Material. Specimen UCMP202225_01.

Description. Leaf fragment, leaf organisation simple; base angle acute, base shape cuneate to convex, position of petiolar attachment marginal; margin type entire, 1° vein category pinnate, 2° vein category eucamptodromous, strong intersecondaries present.

Dicotylophyllum 22

Pl. 47, fig. 8

Material. Specimen UCMP202226.

Description. Leaf fragment, leaf organisation simple; base angle acute, base shape cuneate to convex, position of petiolar attachment marginal; margin type entire; 1° vein category pinnate, 2° vein category eucamptodromous.

Dicotylophyllum 23

Pl. 47, figs 9, 10

Material. Specimen UCMP202227.

Description. Leaf, leaf organisation simple; laminar size notophyll; laminar shape obovate, lamina base slightly asymmetrical; base angle acute, base shape convex, position of petiolar attachment marginal; margin type entire; 1° vein category pinnate, 2° vein category brochidodromous, 2° vein spacing decreasing slightly towards base, 2° vein angle smoothly increasing towards base, no intersecondaries present; 3° vein category mainly opposite percurrent, 3° vein course sinuous.

Remarks. Similar leaves are found in *Rhododendron* and a great number of other genera and families.

Dicotylophyllum 24

Pl. 47, fig. 11

Material. Specimen UCMP202228.

Description. Leaf, leaf organisation simple; laminar size microphyll; laminar shape ovate, lamina symmetrical, laminar L:W ratio 3.5:1; base angle acute, apex angle acute, base shape convex, position of petiolar attachment marginal, apex shape straight; margin type entire; 1° vein category pinnate, 2° vein category brochidodromous, 2° vein spacing irregular, 2° vein angle abruptly increasing towards base, weak intersecondaries present.

Remarks. Kasaplıgil labelled this specimen *Sapindus*.

Dicotylophyllum 25

Pl. 47, fig. 12

Material. Specimen UCMP202229.

Description. Leaf fragment, leaf organisation simple; base angle acute, apex angle probably acute, base shape straight, position of petiolar attachment marginal; margin type entire; 1° vein category pinnate.

Dicotylophyllum 26 aff. *Cedrelopsermum*

Pl. 48, fig. 3

1981 *Rhus* sp. – Paicheler & Blanc: pl. 14, fig. 3.

Material. MNHN20100.

Remarks. The leaf refigured here corresponds fairly well with leaves of the extinct genus *Cedrelospermum* from Oligocene and Miocene deposits of France and Hungary (Hably 2002).

Indet. axis with thorns

Pl. 15, fig. 8

Material. Specimen MTA71-416.

Description. Part of twiglet, with two thorns.

Remarks. Kasaplıgil considered this axillar fragment to belong to *Gleditsia*. Also Heer (1859, pl. 133) included such remains within *Gleditsia*. The single specimen in Kasaplıgil's collection may also have originated from an entirely different plant, for example *Crataegus*.

DISCUSSION

COMPARISON OF EXISTING COLLECTIONS AND NEW COLLECTIONS

In this paper we provide a taxonomic assessment of the rich plant material collected by Baki Kasaplıgil from early Miocene strata in the Güvem area, northwestern Central Anatolia. We compare the material of Kasaplıgil with the collection of Paicheler and Blanc (1981) collected from the same sites. The fact that Kasaplıgil referred to his plant assemblage as originating from the vicinity of Güvem village (Kasaplıgil 1977) led to some confusion. For example, in Wang and Manchester (2000) and Teodoridis and Kvaček (2005), Güvem and Bes-Konak were treated as distinct localities of late and early Miocene age. In fact, the fossils collected by Kasaplıgil and Paicheler originate from a single small area in the vicinity of Beşkonak village (Fig. 1C), including the Keseköy vertebrate locality. Thus it is all the more interesting that the collection Kasaplıgil gathered during the 1960s and the one collected by Paicheler differ slightly in composition. For example, *Ilex miodipyrena* is present exclusively in the Kasaplıgil collection, where it is fairly abundant, while *Celtis*, *Comptonia*, infructescences of *Populus*, and leaves and fruits of *Paliurus* are represented only in the Paicheler collection. Also interesting is that *Fagus* is very rare in the Kasaplıgil collection but is represented by ca 30 leaves in the Paicheler collection. This is probably because the leaves in the Paicheler collection come from coarser-grained sediments and are less well preserved. During a short visit to the area in 2016 we found a few taxa recorded neither by Kasaplıgil nor by Paicheler. This clearly indicates the need for further field work.

RELIABILITY OF DETERMINATIONS

In this study we used a taxonomic approach to identify a diverse assemblage of leaf, fruit and flower remains from the early Miocene of northwestern Central Anatolia. It is important to note that the reliability of the determinations varies considerably across the fossil taxa. This is because the number of diagnostic morphological characters varies among leaf taxa. Thirty-four of the 143 taxa cannot be confidently assigned to a particular family (Table 1) but are distinct morphotypes; thus they convey an idea of the taxonomic diversity of the plant assemblage. About 80 taxa are assigned to genera and ca 40 taxa are determined to species level (including those for which affinities to particular modern species are indicated).

A number of taxa that are tentatively assigned to families (e.g. Ericaceae and aff. *Engelhardia* in the Juglandaceae) need further taxonomic investigation. This is also true for the large lobed leaves that occur scattered in the Kasaplıgil collection.

PALAEOENVIRONMENTS INFERRED FROM THE PLANT ASSEMBLAGE OF GÜVEM

According to the interpretation of Popov et al. (2004), the area of Güvem comprised lowlands with freshwater lakes surrounded by highlands to the north (Western Pontides) and to the west. In general, Anatolia and the Lower Caucasus to the east still formed an island north of the East Mediterranean Basin and south of Eastern Paratethys. Deposition of the plant-bearing strata occurred during the major phase of volcanic activity in the Galatia Volcanic Province in the early Miocene (Tankut et al. 1998). Hoek Ostende (2001) and de Bruijn et al. (1996) stated that a humid biotope is indicated by the relatively high amount of insectivores in the fauna of Keseköy (27% of the total fauna). Abundant Soricidae, in particular, are indicative of a warm and humid climate (Hoek Ostende 2001).

The rich plant assemblage described here has a mixed environmental signal, pointing to a heterogeneous landscape in the Güvem region. Despite this, based on the abundance of individual taxa in the Kasaplıgil and Paicheler collections and based on our own observations when revisiting the sites indicated in Figure 1C, two elements – various morphotypes of *Quercus drymeja* and Fagaceae gen. et sp. indet. (various types) – clearly must have been very widespread in the area surrounding the lake(s) in the lowlands. The evergreen broadleaved forests dominated by these two components may have

Table 1. Plant taxa recognized from the early Miocene Güvem Formation, and their affinities to particular vegetation units (VU)

Family	Taxon	Taxonomic affinities	Vegetation unit[a]
Equisetaceae	*Equisetum* sp.	*Equisetum*	VU2, VU3, VU4
Davalliaceae	*Davallia haidingeri*	*Davallia canariensis*	?VU6, VU7
Ephedraceae	*Ephedra* sp.	*Ephedra*	VU0, VU5b, VU7
Cupressaceae	*Glyptostrobus europaeus*	*Glyptostrobus*	VU3
Cupressaceae	*Sequoia abietina*	*Sequoia*	VU5a, VU6, VU7
Cupressaceae	*Calocedrus suleticensis*	*Calocedrus*	VU5a–VU7
Cupressaceae	*Thuja* sp. ? (or *Chamaecyparis* or *Cupressus*)	Cupressaceae	VU0, VU4–VU7
Cupressaceae	*Juniperus* sp.	*Juniperus*	VU0, VU7
Pinaceae	*Cedrus* sp.	*Cedrus*	VU7
Pinaceae	*Pinus* sp. 1	*Pinus*	VU7
Pinaceae	*Pinus* sp. 2	*Pinus*	VU7
Pinaceae	*Pinus* sp. 3	*Pinus*	VU7
Pinaceae	Unassigned Pinaceae seed	Pinaceae	VU7
Taxaceae	Torreya	Taxaceae	VU5, VU6, VU7
Apocynaceae	Dicotylophyllum 17	aff. *Nerium*	VU4
Aquifoliaceae	*Ilex miodipyrena*	*Ilex dipyrena*	VU6, VU7
Aquifoliaceae	cf. *Ilex* sp.	*Ilex*	VU4, VU5–VU7
Arecaceae	*Phoenicites* sp.	Arecaceae	VU0, VU3
Berberidaceae	*Berberis* sp. vel *Ilex* aff. *I. pernyi*	–	–
Berberidaceae	*Mahonia grimmii*	*Mahonia* Group Orientales	VU5a, VU6
Betulaceae	*Alnus cycladum*	*Alnus*	VU3, VU4
Betulaceae	*Alnus palaeojaponica*	E Asian large-leaved *Alnus*	VU3, VU4
Betulaceae	*Alnus gaudinii*	N Hemisphere large-leaved *Alnus*	VU3, VU4
Betulaceae	*Betula* sp.	*Betula luminifera*, *B. utilis*	VU5a
Betulaceae	*Betula* sp. (seeds)	*B. pendula*	VU5a, VU6
Anacardiaceae	Dicotylophyllum 2	cf. *Pistacia* aff. *P. therebinthus*	VU5b
Buxaceae	Dicotylophyllum 3	aff. *Buxus*	VU5a, VU6
Cannabaceae	*Celtis japeti*	*Celtis*	VU5
Ceratophyllaceae	*Ceratophyllum* sp.	*Ceratophyllum*	VU1
Cercidiphyllaceae	*Cercidiphyllum crenatum*	*Cercidiphyllum*	VU5, VU6
Cornaceae	Dicotylophyllum 7	aff. *Cornus*, *Cornus miowalteri*	?VU4, VU6
Ericaceae	*Rhododendron* sp.	*Rhododendron* large-leaved	VU6?
Ericaceae	aff. Ericaceae gen. et spec. indet. 1	–	–
Ericaceae	aff. Ericaceae gen. et spec. indet. 2	–	–
Ericaceae	aff. Ericaceae gen. et spec. indet. 3	–	–
Fabaceae	*Leguminophyllum* sp. 1	Fabaceae	VU0, VU3
Fabaceae	*Leguminophyllum* sp. 2	Fabaceae	VU0, VU3
Fabaceae	*Leguminophyllum* sp. 3	Fabaceae	VU0, VU3
Fabaceae	*Leguminophyllum* sp. 4	Fabaceae	VU0, VU3
Fabaceae	*Leguminophyllum* sp. 5	Fabaceae	VU0, VU3
Fabaceae	*Leguminophyllum* sp. 6	*Spartium junceum*	VU2
Fabaceae	*Leguminophyllum* sp. 7	Fabaceae	VU0, VU3
Fabaceae	*Leguminophyllum* sp. 8	Fabaceae	VU0, VU3
Fabaceae	*Leguminophyllum* sp. 9	Fabaceae	VU0, VU3
Fabaceae	*Leguminophyllum* sp. 10	Fabaceae	VU0, VU3
Fabaceae	*Leguminophyllum* sp. 11, *Acacia parschlugiana*	Mimosoideae	VU0
Fabaceae	*Leguminophyllum* sp. 12	Fabaceae	VU0, VU3
Fabaceae	*Leguminocarpum* sp.	Fabaceae	VU0, VU3
Fagaceae	*Fagus castaneifolia*	*Fagus*	VU6, VU7
Fagaceae	*Quercus drymeja*	*Quercus* sect. *Ilex*	VU5a
Fagaceae	*Quercus* cf. *kubinyii*	*Quercus* sect. *Cerris*	VU5a, VU6
Fagaceae	*Quercus mediterranea*	*Quercus* sect. *Ilex*	VU5
Fagaceae	*Quercus sosnowskyi*	*Quercus* sect. *Ilex*	VU5a
Fagaceae	*Quercus* sp., male inflorescence	*Quercus*	–
Fagaceae	*Quercus* sp., cups	*Quercus*	–
Fagaceae	*Quercus* sp. 1	*Quercus*	?VU5a

Table 1. Continued

Family	Taxon	Taxonomic affinities	Vegetation unit[a]
Fagaceae	Fagaceae gen. et spec. indet.1	Fagaceae	VU5a
Fagaceae	Fagaceae gen. et spec. indet.2	Fagaceae	VU5a
Fagaceae	Fagaceae gen. et spec. indet.3	Fagaceae	VU5a
Fagaceae	Fagaceae gen. et spec. indet. aff. *Eotrigonobalanus*	Fagaceae	VU5a
Hydrocharitaceae	*Stratiotes kaltennordheimensis*	*Stratiotes*	VU1
Juglandaceae	aff. *Engelhardia* sp.	*Engelhardia*	VU5a
Juglandaceae	*Juglans* sp.	*Juglans*	VU4
Juglandaceae	Unknown male catkin, aff. *Juglans*	*Juglans*	VU4
Lauraceae	*Daphnogene polymorpha*	Lauraceae	VU4, VU5a, VU6
Lauraceae	*Laurophhyllum* sp.	Lauraceae	VU4, VU5a, VU6
Lauraceae	Lauraceae gen. et spec. indet. 1	Lauraceae	VU4, VU5a, VU6
Lauraceae	Lauraceae gen. et spec. indet. 2, cf. *Laurophyllum pseudoprinceps*	Lauraceae	VU4, VU5a, VU6
Lauraceae	Lauraceae gen. et spec. indet. 3	Lauraceae	VU4, VU5a, VU6
Magnoliaceae	*Magnolia sturii*	*Magnolia*	VU4, VU5a, VU6
Magnoliaceae	*Magnoliostrobus*	*Magnolia*	VU4, VU5a, VU6
Malvaceae	*Tilia* sp.	*Tilia platyphyllos*	VU6
Malvaceae	*Tilia knoblochii*	*Tilia platyphyllos*	VU6
Moraceae	Dicotylophyllum 10	aff. *Ficus mollis*	VU0, VU4
Myricaceae	*Comptonia oeningensis*	*Comptonia*	VU4
Myricaceae	*Myrica* sp.	*Myrica*	VU3, VU4, VU5
Oleaceae	*Fraxinus* sp.	*Fraxinus*	VU4
Potamogetonaceae	*Potamogeton bruckmanni*	*Potamogeton*	VU1
Potamogetonaceae	*Potamogeton geniculatus*	*Potamogeton pusillus*	VU1
Potamogetonaceae	*Potamogeton* sp.	*Potamogeton*	VU1
Rhamnaceae	*Paliurus tiliifolius*	*Paliurus*	VU5, VU6
Rhamnaceae	*Paliurus favonii*	*Paliurus*	VU5, VU6
Rosaceae	*Crataegus* sp.	*Crataegus*	VU4, VU5
Rosaceae	*Prunus* sp.	Deciduous, large-leaved *Prunus*	VU4, VU5a, VU6
Rosaceae	cf. *Prunus* sp.	Deciduous, large-leaved *Prunus*	VU4, VU5a, VU6
Rosaceae	*Rosa* sp. aff. *Rosa mairei*	*Rosa mairei*	VU4–VU7
Rosaceae	*Rosa* sp.	*Rosa*	VU4–VU7
Rosaceae	*Sorbus* sp.	*Sorbus* subgenus *Sorbus*	VU5, VU6
Salicaceae	*Populus populina*	*P. tremula*, *P. tremuloides*, *P. davidiana*	VU4, VU7
Salicaceae	*Populus* sp.	*Populus*	VU4, VU7
Salicaceae	*Salix angusta*	*Salix*	VU4
Salicaceae	*Salix varians*	*Salix*	VU4
Salicaceae	cf. *Salix* sp.	*Salix*	VU4
Salicaceae	*Salix* sp. (flower catkins)	*Salix*	VU4
Sapindaceae	*Acer angustilobum*	*Acer heldreichii*, *A. trautvetteri*	VU6
Sapindaceae	*Acer palaeosaccharinum*	*Acer saccharum*	VU5a, VU6
Sapindaceae	*Acer tricuspidatum*	*Acer rubrum*	VU4, VU5a, VU6
Sapindaceae	*Acer* sp.	*Acer sterculiaceum*, *A. opalus*	VU5a, VU6
Sapindaceae	*Acer* spp. (samaras)	*Acer*	–
Sapindaceae	*Sapindus falcifolius*	–	–
Simaroubaceae	aff. *Ailanthus confucii*	*Ailanthus altissima*	VU4, VU5
Simaroubaceae	aff. *Ailanthus tardensis*	*Ailanthus excelsa*, *A. fordii*, *A. triphysa*	VU4, VU5
Simaroub. vel Rutaceae	*Chaneya* sp.	*Picrasma* (Simaroubaceae), Rutaceae	?VU3, VU4
Smilacaceae	*Smilax weberi*	*Smilax*	VU3, VU4, VU5a
Smilacaceae	*Smilax miohavanensis*	*Smilax* Havanensis group	VU3, VU4, VU5
Typhaceae	*Typha* sp.	*Typha*	VU1
Ulmaceae	*Ulmus* sp.	*Ulmus*	VU4, VU5
Ulmaceae	*Zelkova zelkovifolia*	*Zelkova*	VU4, VU5
Fam. indet.	Unknown cupule	–	–

Table 1. Continued

Family	Taxon	Taxonomic affinities	Vegetation unit[a]
Fam. indet.	Unknown ?flower	–	–
Fam. indet.	Unknown flower (?Lauraceae)	–	–
Fam. indet.	aff. *Antholithes stiriacus* or *Nuphar* sp.	–	–
Fam. indet.	aff. *Daphniphyllum*	–	VU4, VU5a
Fam. indet.	Lobed leaf no. 1 (aff. *Alangium*)	–	?VU6
Fam. indet.	Lobed leaf no. 2 (aff. *Dombeyopsis lobata*)	*Dombeyopsis lobata*, *Laria rueminiana*, *Paulownia*	?VU0, VU4–VU6
Fam. indet.	Lobed leaf no 3. (aff. *Alangium platanifolium*)	*Alangium platanifolium*, *A. chinense*	?VU6
Fam. indet.	Lobed leaf no. 4	*Alangium*, *Broussonetia miocenica*, *Laria rueminiana*	?VU0, VU6
Fam. indet.	Lobed leaf no. 5 (aff. *Alangium chinense*)	*Alangium platanifolium*, *Brassaiopsis mirabilis*, *Ficus tiliifolia* f. *lobata*, *Firmiana simplex*, *Laria*	–
Fam. indet.	Lobed leaf no. 6	*Alangium platanifolium*	?VU6
Fam. indet.	Dicotylophyllum 1	–	–
Fam. indet.	Dicotylophyllum 4	–	–
Fam. indet.	Dicotylophyllum 5	–	–
Fam. indet.	Dicotylophyllum 6	–	–
Fam. indet.	Dicotylophyllum 8	–	–
Fam. indet.	Dicotylophyllum 9	–	–
Fam. indet.	Dicotylophyllum 11	–	–
Fam. indet.	Dicotylophyllum 12	–	–
Fam. indet.	Dicotylophyllum 13	–	–
Fam. indet.	Dicotylophyllum 14	aff. *Fagus*	VU6, VU7
Fam. indet.	Dicotylophyllum 15	–	–
Fam. indet.	Dicotylophyllum 16	aff. *Quercus*	?VU5, VU6
Fam. indet.	Dicotylophyllum 18	–	–
Fam. indet.	Dicotylophyllum 19	–	–
Fam. indet.	Dicotylophyllum 20	aff. *Quercus neriifolia*	VU4, VU5a
Fam. indet.	Dicotylophyllum 21	–	–
Fam. indet.	Dicotylophyllum 22	–	–
Fam. indet.	Dicotylophyllum 23	–	–
Fam. indet.	Dicotylophyllum 24	–	–
Fam. indet.	Dicotylophyllum 25	–	
Fam. indet.	Dicotylophyllum 26	aff. *Cedrelospermum*	VU4, VU5
Fam. indet.	Indet. axis with thorns	Rosaceae	–

[a]slightly modified from Denk (2016): Vegetation Unit (**VU**) **0**: Subtropical, moist or dry light forest. **VU 1**: Aquatic. **VU 2**: Bog, wet meadow. **VU 3**: Swamp forest. **VU 4**: Riparian forest. **VU 5**: Well-drained lowland forest (**VU5a** – *Quercus drymeja*, Fagaceae gen. et spec. indet. various, **VU5b** – edaphically and aspect-wise dry forest). **VU 6**: Well-drained upland forest (*Fagus-Cathaya*). **VU 7**: Well-drained (lowland and) upland conifer forest including hummocks

covered large parts of the hinterland, including lowlands and uplands. We followed Denk (2016) in referring plant taxa to vegetation units (VUs, Fig. 3). A few plants are indicative of open landscape (VU0). Apart from taxa with a wide ecological range (*Zelkova*, *Ulmus*), the relatively large diversity of dispersed Fabaceae leaflets might indicate the presence of more open areas. The minor contribution of herbaceous plants including grasses in the palynological record (Yavuz-Işık 2008), however, suggests that no extensive open areas existed. In contrast, a rich fish, reptile and amphibian fauna (Paicheler et al. 1978, Rückert-Ülkümen 2003, Dubois et al. 2010, Vasilyan et al. 2016) attests to a wetland biome surrounding the lakes and rivers, which is also supported by the abundant presence of a taxodiaceous swamp element (*Glyptostrobus*) in the assemblage (VU1, 2, 3). Swamp forest communities and wet meadows may also have contained palms. Comparable ecosystems are present in, for example, the southeastern United States, where wet prairies change to *Pinus* forests with a rich understorey of palms (Duever et al. 1986). A rich riparian forest was present along the rivers and better-drained areas around the lake (VU4). Farther away from the deposition area, well-drained lowland forests comprised various broadleaved evergreen Fagaceae and *Quercus drymeja* (VU5). A further variant of

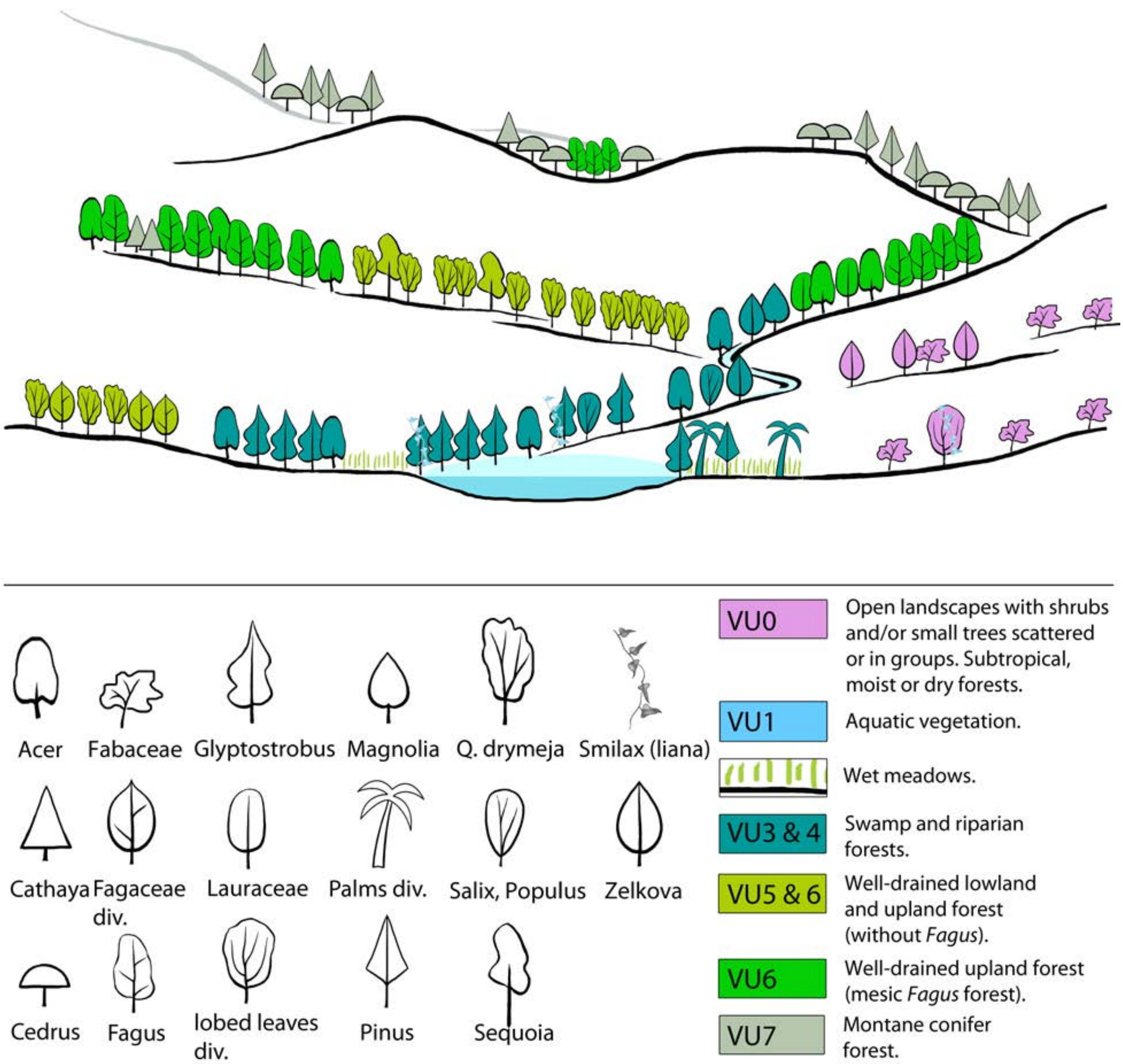

Fig. 3. Landscape reconstruction for the early Miocene of the Güvem area. A series of schematic vegetation transects from lowland well-drained and lowland aquatic and swamp forest, to riparian forest, to various types of upland forest described in the text. Note that herbaceous taxa and woody taxa recognized in the palynological record (Yavuz-Işık 2008) are not indicated in the sketches. One exception is the genus *Cathaya*, which is shown here as part of upland conifer forest and upland *Fagus* forest. Vegetation units correspond to the ones described in Table 1

lowland well-drained forest with *Carpinus* appears to be better captured in the palynological record (Yavuz-Işık 2008). Upland forests may have included *Quercus drymeja* (broad-leaved evergreen Fagaceae) forest, possibly also with *Sequoia* (VU6a) and a more mesic variant of *Fagus* forest (VU6b). A number of conifers (*Torreya*, *Cedrus* pollen and macrofossil record, *Cathaya* pollen) may have contributed to these more mesic upland forests. While there is a relatively good match between the macrofossil data presented here and the palynological record published by Yavuz-Işık (2008), naturally non-aquatic herbaceous taxa are almost absent from the macrofossil record. Herbaceous taxa including Poaceae have low shares in the palynological sequence investigated by Yavuz-Işık (2008) and indicate "that open areas were not widespread in the Güvem area during the Burdigalian". This is consistent with evidence from the macrofossil record.

Overall, the vegetation inferred from the macrofossil and from the palynological records suggests the presence of laurel forests according to Schroeder (1998) and broadleaved deciduous and conifer upland forests. It does not suggest the presence of sclerophyllous forest (see Denk et al. 2017a for a taxonomic and ecological evaluation of *Quercus drymeja* and *Q. mediterranea*). Laurel forest corresponds to the SCL plus LEG (sclerophyllous and legume) component/subhumid subtropical component and less so to the BLE (broadleaved evergreen)/humid subtropical component of Kovar-Eder and Kvaček (2002) and Jechorek and Kovar-Eder (2004). The subhumid or humid climatic signature of the "sclerophyllous" component in Neogene floras seems difficult to assess, because the ecological niches of taxa representing the SCL component may have changed markedly during the Neogene (cf. Ackerly 2004, Denk et al. 2017a). Likewise, the ecological niches of the LEG component are difficult to assess, because Fabaceae occur in a wide range of environments.

Overall, the inferred vegetation types would have thrived under humid warm temperate climate with a drier but not pronouncedly dry season in the winter (Cf climates according to Köppen, Peel et al. 2007).

BIOGEOGRAPHIC AFFINITIES OF THE GÜVEM FLORA

A number of unrevised Cenozoic floras of the Mediterranean region are difficult to assess comparatively because it is not known whether taxa described under several different names belong to the same fossil species or not (see, for example, the case of *Alnus*). It is also difficult to compare taxonomic richness across regions, because early scholars of the early Miocene floras (e.g. Saporta, Unger, Kasaplıgil) had taxonomic concepts different from the ones usually followed today. Kasaplıgil distinguished close to 20 taxa of *Quercus*, whereas in the present study four species of *Quercus* are recognized. Unger (1867) recognized 17 species of Fabaceae, while Velitzelos (2002) collectively called these leaf and fruit remains 'Leguminosae gen. div.' Unger (1867) further described 12 species of the mainly Southern Hemispheric family Proteaceae. Modern revisions have demonstrated that none of these taxa belongs to Proteaceae (Kvaček & Erdei 2001, Velitzelos et al. 2014).

In the present study we made an initial effort towards a taxonomic correlation of Cenozoic floras across the Mediterranean and Parathetys region (see also Mai 1995, for extensive correlations expressed as "Florenkomplexe", floristic complexes). This effort is preliminary. In the following it is illustrated through the example of a number of biogeographically interesting taxa.

The phytogeographic patterns for early Miocene Anatolia are mostly cosmopolitan. The ***(i)*** "**cosmopolitan**" pattern describes taxa that had a wide Northern Hemispheric distribution during the early Miocene. The encountered distribution patterns are legacies of older radiations. This pattern holds for most phylogenetically old taxa (e.g. *Equisetum*, *Ephedra*, *Glyptostrobus*, *Sequoia*, *Cedrus*, *Pinus*, *Torreya*, *Arecaceae*, *Cercidiphyllum*, *Daphnogene*, and *Magnolia*).

The second most common pattern is the ***(ii)*** "**Europe into Anatolia**" pattern. This is mainly a variant of more complex biogeographic patterns such as Asia – Europe – Anatolia.

Fagus castaneifolia – *Fagus* has a complex biogeographic history (Manchester & Dillhoff 2004, Denk & Grimm 2009, Grímsson et al. 2016). The earliest unambiguous records are from Paleocene deposits in Greenland, from where it migrated both to East Asia and to western North America. From East Asia, *Fagus* migrated to Europe during the Oligocene. The earliest occurrences in western Eurasia are from Rupelian strata in Central Europe (Denk et al. 2012, dispersed pollen) and Thrace (Velitzelos et al. 2014, single leaf from Lagina, eastern Thrace, Greece; Nakoman 1966, fairly abundant pollen in Oligocene deposits of Thrace, Turkey) and Chattian strata of France (Saporta 1867). Thus, this genus may have migrated to Anatolia from Thrace. Early Miocene records are concentrated in the eastern Mediterranean region (Bosnia to Turkey) and in Central Europe, but rare or absent in the western Mediterranean region.

Paliurus tiliifolius, *P. favonii* – *Paliurus* was recently discovered from Late Cretaceous strata in India (Manchester & Kapgate 2014), suggesting that the genus evolved in India and dispersed into East Asia and western North America during the Paleogene. From there it dispersed into Europe during the Oligocene (late Oligocene of Germany). In the early Miocene, *Paliurus* was relatively common in Central Europe, from where it also must have entered Anatolia.

Chaneya sp. – The extinct genus *Chaneya*, with affinities to Rutaceae and Simaroubaceae (Wang & Manchester 2000, Teodoridis & Kvaček 2005), has a scattered distribution across the Northern Hemisphere. It first occurs in middle Eocene strata of western North America and East Asia (Wang & Manchester 2000, Feng & Jin 2012). The earliest records in western Eurasia are from late Eocene deposits of Bohemia (Kvaček & Teodoridis 2011) and from the Oligocene of Bavaria. In the early Miocene, *Chaneya* was present in Central Europe (e.g. Austria) and also in Anatolia.

Ailanthus confucii, *Ailanthus tardensis* – The earliest fossil records of the genus *Ailanthus* are from early Eocene strata of western North America and East Asia (Corbett & Manchester 2004). In Europe the earliest records are from middle Eocene deposits of Messel (Germany). *Ailanthus confucii* is known from Oligocene deposits of Kazakhstan and Croatia (Hably 2001, Corbett & Manchester 2004). *A. tardensis* is known from the late Eocene of Central Europe (Kvaček & Teodoridis 2011) and from early Oligocene strata of Hungary (Hably 2001).

Quercus kubinyii – This oak species belongs to *Quercus* section *Cerris*, and the Güvem material would be among the oldest representatives in western Eurasia. *Quercus* section *Cerris* originated in East Asia in the early Oligocene (Pavlyutkin et al. 2014), from where it migrated to Europe during the Oligocene and Miocene. The earliest records in Central Europe are from the Oligocene/Miocene boundary (Kmenta 2011); unambiguous records of leaves and pollen in Anatolia are from middle Miocene strata (Bouchal et al. 2016, 2017, Güner et al. 2017).

Davallia haidingeri – The fern *Davallia haidingeri* has been described from late Eocene/early Oligocene strata of Sotzka (Socka, Slovenia; Ettingshausen 1858) and is closely comparable to the modern species *D. trichomanoides* Blume from Nepal to Japan and Southeast Asia, and less so to *D. canariensis* (L.) Sm. from southwestern Europe and northwestern Africa including the Macaronesian Islands (Bozukov & Ivanov 1995). In addition to the type locality, this species is known only from the middle Miocene of southern Bulgaria (Bozukov & Ivanov 1995; foliage and *in situ* spores) and from Güvem. At the same time, *Davallia* is known from early Miocene deposits of New Zealand (Conran et al. 2010**).**

Acer angustilobum – *Acer angustilobum* belongs to *Acer* section *Acer* (Grimm et al. 2007) and was fairly widespread in volcanic floras of Central Europe during the Oligocene and early and middle Miocene (Walther 1972). *A. angustilobum* is closely related to the fossil species *A. haselbachensis* Walther from late Eocene to Oligocene strata of Central Europe. This is the first record of this species in the eastern Mediterranean region. *A. angustilobum* is also known from the Aquitanian of southwestern France (Saporta 1868, Bouches-du-Rhone, Marseille).

Acer palaeosaccharinum – *Acer palaeosaccharinum* belongs to *Acer* section *Rubra* (Walther 1972, Grimm et al. 2006). Unambiguous records of this species are known from early Oligocene strata of Central Europe. Leaves assigned to *A. palaeosaccharinum* from late Oligocene/early Miocene strata of Kazakhstan (Zhilin 1974) may also belong to *A. angustilobum*. In Europe this species has a long stratigraphic range from the Oligocene to the Pliocene (Ströbitzer-Hermann 2002). It is typically connected with volcanic deposits. It is noteworthy that both these maples are not known from the slightly younger (early MN4) strata of Kimi-Aliveri (Euboea, Greece; Velitzelos et al. 2014).

A rare but biogeographically highly significant pattern is the ***(iii)*** **"Anatolia into Europe"** pattern.

Aff. *Daphniphyllum* – The genus *Daphniphyllum* is known only from dispersed pollen from middle Miocene strata of Central Europe (Grímsson et al. 2015a). The cited authors specifically compared the fossil pollen to pollen of a modern Himalayan species of *Daphniphyllum*.

Nerium – Similar distinctive leaves have been recorded from European early/middle to late Miocene strata (Kovar-Eder et al. 2004) and from the late Miocene of Greece (Velitzelos et al. 2014). The fossil from Güvem may represent the oldest record of *Nerium* in western Eurasia. To establish a biogeographic pattern, however, the fossil record from early Miocene strata in France would need to be revised.

Smilax miohavanensis – This species is known from Güvem (MN3) and from late early Miocene deposits in Euboea (Kimi-Aliveri; MN4; Hoek Ostende et al. 2015), middle Miocene (MN6, Bouchal et al. 2017) deposits of the Yatağan Basin floras (Güner et al. 2017), and from Parschlug in Austria (possibly MN5, Kovar-Eder et al. 2004).

Quercus sosnowskyi – This oak species has its earliest fossil record in Güvem. From the Yatağan Basin floras (middle Miocene, MN6) a mass occurrence of *Q. sosnowskyi* is recorded

(Güner et al. 2017). From Anatolia the species extended its range during the late Miocene to northwestern Greece and Abkhasia (Georgia). *Quercus drymeja* may also have radiated from Anatolia (after entering western Eurasia from East Asia).

Only a few taxa represent the ***(iv)*** "**Anatolian endemism**" biogeographic pattern.

Ilex miodipyrena – *Ilex miodipyrena* is only known from Güvem, but a reinvestigation of the late Oligocene to early Miocene plant assemblages of southwestern France may show whether this element was also present in the western Mediterranean region, as has been shown for other elements (*Berberis kymeana* (Unger) Kvaček & Erdei; Kvaček & Erdei 2001).

Mahonia grimmii – *Mahonia grimmii* is also known from the Aquitanian flora of Soma and from the middle Miocene floras of the Yatağan Basin (Güner & Denk 2012, Güner et al. 2017). This species belongs to *Mahonia* Group Orientales, which may have originated in East Asia (Hu et al. 2017). *Mahonia* Group Orientales was also present in middle Miocene strata of southwestern Europe (*Mahonia* sp., Kvaček et al. 2011).

Rosa aff. *Rosa mairei* – *Rosa* aff. *Rosa mairei* is known only from Güvem. The only specimen in the Kasaplıgil collection is similar to the modern East Asian *R. mairei*.

A further, little-explored pattern is the ***(v)*** "**Mediterranean disjunctions (including excursions into Paratethys)**" pattern. This pattern is rarely encountered in the plant assemblage of Güvem but is known from, for example, Soma (Erdei et al. 2010, Denk et al. 2014). In Güvem, compound leaves of *Sorbus* subgenus *Sorbus* are common. Similar leaves/leaflets are known from the early Miocene of Spain (Barrón & Postigo-Mijarra 2011).

CONCLUSIONS AND OUTLOOK

Currently, a meaningful comparison of early Miocene floras in the Mediterranean region is hampered by a marked inflation of names and outdated generic associations for many of the classical localities. Taxonomic revisions of classical palaeobotanical work such as that of Saporta (e.g. Saporta 1865, 1867, 1868) are currently lacking; such a task will be time-consuming and difficult (cf. Gregor & Knobloch 2001). Modern investigations of early Miocene macro floras are very rare (e.g. preliminary revision of the Kimi flora, Greece, by Velitzelos 2002; flora of the Ribesalbes-Rincona Basin, eastern Spain, by Barrón & Postigo-Mijarra 2011, Postigo-Mijarra & Barrón 2013). In contrast, from Central Europe a fairly large number of comprehensively studied early Miocene macro floras are known (e.g. Mai & Walther 1991, Bůžek et al. 1996, Teodoridis & Kvaček 2006). Younger, middle Miocene floras from the Mediterranean and Paratethys regions also are rare (e.g. Arjuxanz flora, southwestern France, Kvaček et al. 2011; Parschlug flora, Kovar-Eder et al. 2004). Eventually the Miocene floras of the Mediterranean and Paratethys regions should be investigated comparatively. In view of the lack of revisions for some of the most important floras (e.g. Armissan, Bois d'Asson, Manosque, Leoben), it will take some time before this can be done in a meaningful way.

Our present study provides a platform for a number of forthcoming studies dealing with palaeoclimatic inferences and with palaeobiogeographic aspects of the early Miocene plant assemblage of Güvem. Using a taxon-free leaf physiognomic approach (CLAMP, Yang et al. 2011), broadleaved angiosperm morphotypes will be used in a forthcoming study to infer various climate parameters which can then be compared to the qualitative assessment made in the present study. In addition, based on modern analogues of the plant taxa recognized in the present study, Köppen signatures will be inferred (Denk et al. 2013, Grímsson et al. 2015b). To broaden the picture and to assess whether biogeographic and palaeoenvironmental signals from different organism groups are congruent, it will also be important to consider new evidence from micro- and macromammal assemblages from early Miocene strata in the eastern Mediterranean region (see e.g. Hoek Ostende et al. 2015).

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REFERENCES

ACKERLY D.D. 2004. Adaptation, niche conservatism, and convergence: comparative studies of leaf evolution in the California chaparral. Am. Nat., 16: 654–671.

AKKEMIK Ü., TÜRKOĞLU N., POOLE I., ÇIÇEK I., KÖSE N. & GÜRGEN G. 2009. Woods of a Miocene petrified forest near Ankara, Turkey. Turk. J. Agric. For., 33: 89–97.

AKKEMIK Ü., ARSLAN M., POOLE I., TOSUN S., KÖSE N., KARLIOĞLU KILIÇ N. & AYDIN A. 2016. Silicified woods from two previously undescribed early Miocene forest sites near Seben, northwest Turkey. Rev. Palaeobot. Palynol., 235: 31–50.

ASH A., ELLIS B., HICKEY L.J., JOHNSON K., WILF P. & WING S. 1999. Manual of Leaf Architecture – morphological description and categorization of dicotyledonous and net-veined monocotyledonous angiosperms by Leaf Architecture Working Group. Smithsonian Institution, Washington.

BARRÓN E. & DIÉGUEZ C. 2001. Estudio macroflorístico del Mioceno Inferior lacustre de la cuenca de Rubielos de Mora (Teruel, España). Bol. Geol. Min., 112(2): 13–56.

BARRÓN E. & DIÉGUEZ C. 2005. Cuticular study of leaf compressions from the Late Miocene (Vallesian) diatomites of Cerdaña Basin (Eastern Pyrenees, Spain). N. Jb. Geol. Paläont. Abh., 237(1): 61–85.

BARRÓN E. & POSTIGO-MIJARRA J.M. 2011. Early Miocene fluvial-lacustrine and swamp vegetation of La Rinconada mine (Ribesalbes-Alcora basin, eastern Spain). Rev. Palaeobot. Palynol., 165(1–2): 11–26.

BARRÓN E., RIVAS-CARBALLO R., POSTIGO-MIJARRA J.M., ALCALDE-OLIVARES C., VIEIRA M., CASTRO L., PAIS J. & VALLE-HERNÁNDEZ M. 2010. The Cenozoic vegetation of the Iberian Peninsula: a synthesis. Rev. Palaeobot. Palynol., 162(3): 382–402.

BERRY E.W. 1906. Living and Fossil Species of *Comptonia*. Am. Nat., 40: 485–524.

BOUCHAL J.M., GRÍMSSON F., ZETTER R. & DENK T. 2016. The middle Miocene palynoflora and palaeoenvironments of Eskihisar (Yatağan Basin, southwestern Anatolia): a combined LM and SEM investigation. Bot. J. Linn. Soc., 182: 14–79.

BOUCHAL J.M., MAYDA S., AKGÜN F., GRÍMSSON F., ZETTER R. & DENK T. 2017. Miocene palynofloras of the Tınaz lignite mine, Muğla, southwest Anatolia: taxonomy, palaeoecology and local vegetation change. Rev. Palaeobot. Palynol., 243: 1–36.

BOZUKOV V. & IVANOV D. 1995. *Davallia haidingeri* Ett., a new species to Bulgarian flora – leaf remain and spores in situ. Phytol. Balcan., 1(2): 15–18.

BRABENEC B. 1909. Souborná květena českého útvaru třetihorního. Arch. přírodověd. Prozk. Čech, 14(3): 1–144.

BRAUN A. 1845. Die Tertiär-Flora von Öhningen. N. Jb. Min. Geogn. Geol. Petref.-Kunde, 1845: 164–174.

BRONGNIART A. 1822. Sur la classification et la distribution des végétaux fossiles en général, et sur ceux des terrains de sédiment supérieur en particulier. Mém. Mus. Natl. Hist. Nat., 8: 203–240.

BRONGNIART A. 1833. Notice sur une Conifère fossile du terrain d'eau douce de l'île d'Iliodroma. Ann. Sci. Nat., ser. 1, 30: 168–176.

BRONN H.G. 1838. Lethaea Geognostica II. E. Schweizerbart's Verlagsbuchhandlung, Stuttgart.

BROWN R. 1935. Miocene leaves, fruits and seeds of *Cercidiphyllum*. J. Paleont., 13: 485–499.

BRUIJN H. DE, ÜNAY E. & HOEK OSTENDE L.W. VAN DEN. 1996. The composition and diversity of small mammal associations from Anatolia through the Miocene: 266–270. In: Bernor R.L., Fahlbusch V. & Mittman H.-W. (eds), The evolution of western Eurasian Neogene mammal faunas. Columbia Univ. Press, New York.

BUCKLAND W. 1836. Geology and mineralogy considered with reference to natural theology Vol. 1. William Pickering, London.

BUGGE G. 2005. *Cercidiphyllum*-like leaf fossils from the Palaeogene of Spitsbergen. Master thesis, University of Oslo.

BURGE D.O. & MANCHESTER S.R. 2008. Fruit morphology, fossil history, and biogeography of *Paliurus* (Rhamnaceae). Int. J. Pl. Sci., 169: 1066–1085.

BŮŽEK C. 1971. Tertiary flora of the northern part of the Pétipsy area. Věst. Ústř. Úst. geol., 36: 1–118.

BŮŽEK C., HOLÝ F. & KVAČEK Z. 1996. Early Miocene flora of the Cypris shale (Western Bohemia). Acta Mus. Nat. Pragae Ser. B., Hist. Nat., 52(1–4): 1–72.

CHANDLER M.E.J. 1923. The geological history of the genus *Stratiotes*: an account of the evolutionary changes which have occured within the genus during the Tertiary and Quaternary times. Quarterly J. Geol. Soc., London, 79: 117–138.

CHEN Y.-S., MESEGUER A.S., GODEFROID M., ZHOU Z., ZHANG J.-W., DENG T., KIM J.-H., NIE Z.-L., LIU Y.-S. & SUN H. 2017. Out-of-India dispersal of *Paliurus* (Rhamnaceae) indicated by combined molecular phylogenetic and fossil evidence. Taxon, 66(1): 78–90.

CONRAN J.G., KAULFUSS U., BANNISTER J.M., MILDENHALL D.C. & LEE D.E. 2010. *Davallia* (Polypodiales: Davalliaceae) macrofossils from Early Miocene Otago (New Zealand) with in situ spores. Rev. Palaeobot. Palynol., 162(1): 84–94.

CORBETT S.L. & MANCHESTER S.R. 2004. Phytogeography and fossil history of *Ailanthus* (Simaroubaceae). Int. J. Plant Sci., 165(4): 671–690.

CUVIER G. 1822. Recherches sur les ossemens fossiles. Vol. 2, 3. G. Dufour et E. D'Ocagne, Paris, Amsterdam.

CZECZOTT H. 1951. Środkowo-mioceńska flora Zalesiec koło Wiśniowca I. Acta Geol. Pol., 2: 349–445.

DE BRUIJN H., DAAMS R., DAXNER-HÖCK G., FAHLBUSCH V., GINSBURG L., MEIN P. & MORALES J. 1992. Report of the RCMNS working group on fossil mammals, Reisenburg 1990. Newsl. Stratigr., 26(2–3): 65–118.

DENK T. 2004. Revision of *Fagus* from the Cenozoic of Europe and South Western Asia and its phylogenetic implications. Doc. Nat., 150: 1–72.

DENK T. 2016. Palaeoecological interpretation of the late Miocene landscapes and vegetation of northern Greece: a comment to Merceron et al., 2016 (Geobios, doi:10.1016/j.geobios.2016.01.004). Geobios, 49: 135–146.

DENK T. & GRIMM G.W. 2009. The biogeographic history of beech trees. Rev. Palaeobot. Palynol., 158: 83–100.

DENK T. & GRIMM G.W. 2010. The oaks of western Eurasia: traditional classifications and evidence from two nuclear markers. Taxon, 59: 351–366.

DENK T., GRÍMSSON F. & ZETTER R. 2012. Fagaceae from the Early Oligocene of Central Europe: persisting New World and emerging Old World biogeographic links. Rev. Palaeobot. Palynol., 169: 7–20.

DENK T., GÜNER H.T. & GRIMM G.W. 2014. From mesic to arid: Leaf epidermal features suggest preadaptation in Miocene dragon trees (*Dracaena*). Rev. Palaeobot. Palynol., 200: 211–228.

DENK T., GRÍMSSON F., ZETTER R. & SÍMONARSON L.A. 2011. Late Cainozoic floras of Iceland. 15 million years of vegetation and climate history in the northern North Atlantic. Topics in Geobiology, 35. Springer, Dordrecht.

DENK T., GRIMM G.W., GRÍMSSON F. & ZETTER R. 2013. Evidence from "Köppen signatures" of fossil plant assemblages for effective heat transport of Gulf Stream to subarctic North Atlantic during Miocene cooling. Biogeosciences, 10: 7927–7942.

DENK T., VELITZELOS D., GÜNER H.T. & FERRUFINO-ACOSTA L. 2015. *Smilax* (Smilacaceae) from the Miocene of western Eurasia with Caribbean biogeographic affinities. Am. J. Bot., 102(3): 423–438.

DENK T., GRIMM G.W., MANOS P.S., DENG M. & HIPP A. 2017b. An updated infrageneric classification of the oaks: review of previous taxonomic schemes and synthesis of evolutionary patterns. In: Gil-Peregrin E., Peguero-Pina J.J. & Sancho-Knapik D. (eds) Oaks Physiological Ecology. Exploring the Functional Diversity of Genus Quercus. Tree Physiology, 7. Springer Nature, Cham, Switzerland.

DENK T., VELITZELOS D., GÜNER H.T., BOUCHAL J.M., GRÍMSSON F. & GRIMM G. 2017a. Taxonomy and palaeoecology of two widespread western Eurasian Neogene sclerophyllous oak species: *Quercus drymeja* Unger and *Q. mediterranea* Unger. Rev. Palaeobot. Palynol., 241: 98–128.

DRANSFIELD J., UHL N.W., ASMUSSEN C.B., BAKER W.J., HARLEY M.M. & LEWIS C.E. 2008. Genera Palmarum. The evolution and classification of palms. Royal Bot. Gard. Kew.

DUBOIS A., GROSJEAN S. & PAICHELER J.-C. 2010. Strange tadpoles from the Lower Miocene of Turkey: is paedogenesis possible in Anurans? Acta Palaeont. Polonica, 55(1): 43–55.

DUEVER M.J., CARLSON J.E., MEEDER J.F., DUEVER L.C., GUNDERSON L.H., RIOPELLE L.A., ALEXANDER T.R., MYERS R.L. & SPANGLER D.P. 1986. The Big Cypress National Preserve. National Audobon Society, New York.

ECKENWALDER J.E. 1996. Systematics and evolution of *Populus*: 7–32. In: Stettler R.F., Bradshaw H.D., Heilman P.E. & Hinckley T.M. (eds.), Biology of *Populus* and its implications for management and conservation. NRC Research Press, National Research Council of Canada, Ottawa, Ontario, Canada.

ERDEI B., AKGÜN F. & LUMAGA M.R.B. 2010. *Pseudodioon akyoli* gen. et sp. nov., an extinct member of Cycadales from the Turkish Miocene. Plant Syst. Evol., 285: 33–49.

ETTINGSHAUSEN von C. 1852. Fossile Pflanzenreste aus dem trachytischen Sandstein von Heiligenkreuz bei Kremnitz. Abh. Geol. Reichsanst., 1: 1–14.

ETTINGSHAUSEN von C. 1858. Beiträge zur Kenntnis der fossilen Flora von Sotzka.Sitzungsber. kaiserl. Akad. Wiss. Wien, math.–naturwiss. Cl., 28(6): 471–567.

ETTINGSHAUSEN von C. 1866. Die fossile Flora des Tertiär-Beckens von Bilin. Vol. 1. Karl Gerold's Sohn, Wien.

FARJON A. 2005. A monograph of Cupressaceae and *Sciadopitys*. Royal Bot. Gard., Kew.

FENG X.X. & JIN J.H. 2012. First record of extinct fruit genus *Chaneya* in low-latitude tropic of South China. Sci. China Earth Sci., 55: 728–732.

FISCHER T.C. & BUTZMANN R. 1997. Description of the fossil fruit *Paulownia inopinata* nov. sp. from the Middle Miocene of Unterwohlbach (Bavaria) and other possible occurrences of the genus in the Tertiary. Doc. Nat., 115: 1–13.

FISCHER T.C. & BUTZMANN R. 2000. Die mediterrane neogene Flora von Meleto (Valdarno, Italien). Paläobotanik, Paläoökologie und Pälaoklima. Flora Tertiaria Mediterranea, 5(6): 1–187.

FLORA OF NORTH AMERICA EDITORIAL COMMITTEE. 1993. Flora of North America North of Mexico. Volume 2. Pteridophytes and Gymnosperms. New York, Oxford, Oxford University Press.

FLORA OF NORTH AMERICA EDITORIAL COMMITTEE. 1997. Flora of North America North of Mexico. Volume 3. Magnoliophyta: Magnoliidae and Hamamelididae. New York, Oxford, Oxford University Press.

FORTELIUS M. (coord.) 2016. New and Old Worlds Database of Fossil Mammals (NOW). University of Helsinki. http://www.helsinki.fi/science/now/.

GARCÍA MASSINI J.L., JACOBS B.F. & TABOR N.J. 2010. Paleobotany and sedimentology of late Oligocene terrestrial strata from the northwestern Ethiopian Plateau. Palaeontologia Electronica, 13(1) 6A: 1–51. http://palaeo-electronica.org/2010_1/184/index.html

GEMICI Y., AKYOL E. & AKGÜN F. 1993. Şahınalı (Aydın) Neojen havzasinin fosil makro ve mikorflorasi. Doğa Turk. J. Bot., 17: 91–106.

GÖPPERT H.R. 1852. Ueber die Braunkohlefloren des nordöstlichen Deutschlands. Zeitschr. Deutschen geolog. Ges., 4(2): 484–496.

GÖPPERT H.R. 1855. Die tertiäre Flora von Schossnitz in Schlesien. Heyn'sche Buchhandlung (E. Remer.) Görlitz, Paris, Leipzig, London.

GREGOR H.J. & KNOBLOCH E. 2001. Kritische Bemerkungen zu Saporta's fossilen Floren in Süd-Frankreich, speziell in der Provence. Flora Tertiaria Mediterranea, 4: 1–57.

GRIMM G.W., DENK T. & HEMLEBEN V. 2007. Evolutionary history and systematics of *Acer* section *Acer* – a case of low-level phylogenetics. Plant Syst. Evol., 267: 215–253.

GRIMM G.W., RENNER S.S., STAMATAKIS A. & HEMLEBEN V. 2006. A nuclear ribosomal DNA phylogeny of *Acer* inferred with maximum likelihood, splits graphs, and motif analyses of 606 sequences. Evol. Bioinform., 2: 279–294.

GRÍMSSON F., MELLER B., BOUCHAL J.M. & ZETTER R. 2015a. Combined LM and SEM study of the middle Miocene (Sarmatian) palynoflora from the Lavanttal Basin, Austria: part III. Magnoliophyta 1 – Magnoliales to Fabales. Grana, 54: 85–128.

GRÍMSSON F., GRIMM G.W., ZETTER R. & DENK T. 2016. Cretaceous and Paleogene Fagaceae from North America and Greenland: evidence for a Late Cretaceous split between *Fagus* and the remaining Fagaceae. Acta Palaeobot., 56: 247–305.

GRÍMSSON F., GRIMM G.W., MELLER B., BOUCHAL J.M. & ZETTER R. 2015b. Combined LM and SEM study of the middle Miocene (Sarmatian) palynoflora from the Lavanttal Basin, Austria: part IV. Magnoliophyta 2 – Fagales to Rosales. Grana, 55: 101–163.

GÜNER T.H. & DENK T. 2012. The genus Mahonia in the Miocene of Turkey: taxonomy and biogeographic implications. Rev. Palaeobot. Palynol., 175: 32–46.

GÜNER T.H., BOUCHAL J.M., KÖSE N., GÖKTAS F., MAYDA S. & DENK T. 2017. Landscape heterogeneity in the Yatağan Basin (southwestern Turkey) during the middle Miocene inferred from plant macrofossils. Palaeontographica, B, 296(1–6): 113–171.

HABLY L. 2001. Fruits and leaves of *Ailanthus* Desf. From the Tertiary of Hungary. Acta Palaeobot., 41 (2): 207–219.

HABLY L. 2002. Revision of *Cedrelospermum* (Ulmaceae) fruits and leaves from the Tertiary of Hungary and France. Palaeontographica, B, 262(1–4): 71–90.

HAMZEH M. & DAYANANDAN S. 2004. Phylogeny of *Populus* (Salicaceae) based on nucleotide sequences of chloroplast trnT-trnF region and nuclear rDNA. Am. J. Bot., 91(9): 1398–1408.

HANTKE R. 1954. Die fossile Flora der obermiozänen Oehninger-Fundstelle Schrotzburg (Schienerberg, Süd-Baden). Denkschr. Schweiz. Naturf. Ges., 80: 27–118.

HANTKE R. 1965. Die fossilen Eichen und Ahorne aus der Molasse der Schweiz und von Oehningen (Süd-Baden). Neujahrsbl. Nat. Ges. Zürich, 167: 1–108.

HARZHAUSER M., KROH A., MANDIC O., PILLER W.E., GÖHLICH U., REUTER M. & BERNING B. 2007. Biogeographic responses to geodynamics: a key study all around the Oligo-Miocene Tethyan Seaway. Zool. Anz., 246(4): 241–256.

HEER O. 1855. Die tertiäre Flora der Schweiz. – Flora Tertiaria Helvetiae, vol. 1. Winterthur, Verlag Wurster & Co.

HEER O. 1856. Die tertiäre Flora der Schweiz. – Flora Tertiaria Helvetiae, vol. 2. Winterthur, Verlag Wurster & Co.

HEER O. 1859. Die tertiäre Flora der Schweiz. – Flora Tertiaria Helvetiae, vol. 3. Winterthur, Verlag Wurster & Co.

HOEK OSTENDE VAN DEN L.W. 2001. Insectivore faunas from the Lower Miocene of Anatolia – Part 8: Stratigraphy, palaeoecology, palaeobiogeography. Scripta Geol., 122: 101–122.

HOEK OSTENDE VAN DEN L.W., MAYDA S., OLIVER A., MADERN A., HERNÁNDEZ-BALLARÍN V., PELÁEZ-CAMPOMANES P. 2015. Aliveri revisited, a biogeographical appraisal of the early Miocene mammals from the eastern Mediterranean. Palaeobiod. Palaeoenv., 95: 271–284.

HU H.H. & CHANEY R.W. 1940. A Miocene flora from Shantung Province, China. Carnegie Inst. Wash. Publ., 507: 1–147.

HU Q., HUANG J., CHEN Y.-F., MANCHESTER S.R. 2017. *Mahonia* fossils from the Oligocene of South China: Taxonomic and biogeographic implications. Palaeoworld. http://dx.doi.org/10.1016/j.palwor.2017.03.004

ILJINSKAYA I.A. 2005. *Populus populina* (Brogn.) Knobloch: 135–138. In: Budantsev L. (ed.), Fossil Flowering Plants of Russia and Adjacent Countries. Russian Academy of Sciences, Moscow.

JECHOREK H. & KOVAR-EDER J. 2004. Vegetational characteristics in Europé around the late early to early middle Miocene based on the plant macro record. Cour. Forsch.-Inst. Senckenberg, 249: 53–62.

KASAPLIGIL B. 1977. A late Tertiary conifer–hardwood forest from the vicinity of Güvem village, near Kızılcahaman, Ankara. Bull. Miner. Res. Explor. Inst. Turk., 88: 25–33.

KEILHACK K. 1896. Über Folliculites. Naturw. Wochenschr., 11: 504.

KLUCKING E.P. 1987. Leaf venation patterns. Volume 2. Lauraceae. J. Cramer, Berlin, Stuttgart.

KMENTA M. 2011. Die Mikroflora der untermiozänen Fundstelle Altmittweida, Deutschland. Diploma thesis, Univ. Vienna. 102 p.

KNOBLOCH E. 1964. Haben *Cinnamomum scheuchzeri* Heer und *Cinnamomum polymorphum* (Al. Braun) Heer nomenklatorisch richtige Namen? N. Jb. Geol. Paläont. Mh., 10: 597–603.

KNOBLOCH E. 1968. Bemerkungen zur Nomenklatur Tertiärer Pflanzenreste. Acta Mus. Nat. Pragae Ser. B, 24(3): 121–151.

KNOBLOCH E. 1998. Der pliozäne Laubwald von Willershausen am Harz. Doc. Nat., 120: 1–302.

KNOBLOCH E. & KVAČEK Z. 1964. *Byttneriophyllum tiliaefolium* (Al. Braun) Knobloch et Kvaček in den tertiären Floren der Nordhalbkugel. Acta Mus. Nat. Pragae Ser. B, 5: 123–166.

KNOBLOCH E. & KVAČEK Z. 1976. Miozäne Blätterfloren vom Westrand der Böhmischen Masse. Rozpravy Ústøedního Ústavu Geologického, 42: 1–131.

KOLAKOVSKY A.A. 1964. The Pliocene flora of Kodor. Sukhumi Bot. Gard. Monogr., 1: 1–200.

KOTLABA F. 1963. Tertiary plants from three new localities in southern Slovakia. Acta Mus. Nat. Pragae Ser. B, 19(2): 53–72.

KOVAR-EDER J. 1982. Eine Blätter-Flora des Egerien (Ober-Oligozän) aus marinen Sedimenten der Zentralen Paratethys im Linzer Raum (Österreich). Beitr. Paläont. Österr., 9: 1–209.

KOVAR-EDER J. & KVAČEK Z. 2002. Towards vegetation mapping based on the fossil plant record. Acta Univ. Carol. – Geol., 46(4): 7–13.

KOVAR-EDER J., KVAČEK Z. & STRÖBITZER-HERMANN M. 2004. The Miocene flora of Parschlug (Styria, Austria) – revision and synthesis. Ann. Naturhist. Mus. Wien, 105(A): 45–159.

KOVÁTS J. 1856. Fossile Flora von Erdőbénye. Arb. Geol. Ges. Ung., 1: 1–38.

KRYSHTOFOWICZ A.N., PALIBIN I.V., SHAPARENKO K.K., YARMOLENKO A.V., BAYKOVSKAYA T.N., GRUBOV V.I., ILJINSKAYA I.A. 1956. Oligotsenovaya flora gory Ashutas v Kazakhstane (Oligocene flora of Ashutas Mount in Kazakhstan). Komarov Bot. Inst. Acad. Sci. SSSR, publ. 145, ser. 8. Palaeobotanica, 1: 1–241 (in Russian).

KVAČEK Z. 1999. An ancient *Calocedrus* (Cupressaceae) from the European Tertiary. Flora, 194: 237–248.

KVAČEK Z. & WALTHER H. 1989. Revision der mitteleuropäischen tertiären Fagaceen nach blattepidermalen Charakteristiken III. Teil *Dryophyllum* Debey ex Saporta und *Eotrigonobalanus* Walther & Kvaček gen. nov. Feddes Repert., 100: 575–601.

KVAČEK Z. & HABLY L. 1991. Notes on the Egerian stratotype flora at Eger (Wind brickyard), Hungary, Upper Oligocene. Ann. Hist.-Nat. Mus. Nat. Hung., 83: 49–82.

KVAČEK Z. & WALTHER H. 1991. Revision der mitteleuropäischen tertiären Fagaceen nach blattepidermalen Charakteristiken. IV. Teil: *Fagus* Linné. Feddes Repert., 102: 471–534.

KVAČEK Z., MIHAJLOVIĆ D. & VRABAC S. 1993. Early Miocene flora of Miljevina (eastern Bosnia). Acta Palaeobot., 33(1): 53–89.

KVAČEK Z. & HABLY L. 1998. New plant elements in the Tard Clay Formation from Eger-Kiseged. Acta Palaeobot., 38(1): 5–23.

KVAČEK Z. & WALTHER H. 1998. The Oligocene volcanic flora of Kundratice near Litoměřice, České středohoří Volcanic Complex (Czech Republic) – a review. Acta Mus. Nat. Pragae Ser. B, 54(1–2): 1–42.

KVAČEK Z. & ERDEI B. 2001. Putative proteaceous elements of the *Lomatites*-type reinterpreted as new *Berberis* of the European Tertiary. Plant Syst. Evol., 226: 1–12.

KVAČEK Z. & TEODORIDIS V. 2011. The late Eocene flora Kučlin near Bílina in North Bohemia revisited. Acta Mus. Nat. Pragae Ser. B, 67(3–4): 83–144.

KVAČEK Z. & WALTHER H. 2004. Oligocene flora of Bechlejovice at Děčín from the neovolcanic area of the České Středohoři Mountains, Czech Republic. Acta Mus. Nat. Pragae Ser. B, 60(1–2): 9–60.

KVAČEK Z., VELITZELOS, D. & VELITZELOS E. 2002. Late Miocene flora of Vegora, Macedonia, N. Greece. Korali Publications, Athens.

KVAČEK Z., TEODORIDIS V. & ROIRON P. 2011. A forgotten Miocene mastixioid flora of Arjuzanx (Landes, SW France). Palaeontographica, B, 285: 3–111.

LES D.H. 1989. The Evolution of achene morphology in *Ceratophyllum* (Ceratophyllacaea), IV. Summary of proposed relationships and evolutionary trends. Syst. Bot., 14(2): 254–262.

LIU H. & SCHNEIDER H. 2013. Evidence supporting *Davallia canariensis* as a late Miocene relict endemic to Macaronesia and Atlantic Europe. Austral. Syst. Bot., 26(5): 378–385.

LIU Y.-S. 1996. Foliar architecture of Betulaceae and a revision of the Chinese betulaceous megafossils. Palaeontographica, B, 239: 23–57.

LÓPEZ-ANTOÑANZAS R., SEN S. & SARAÇ G. 2004. A new large Ctenodactylid species from the Lower Miocene of Turkey. J. Vertebr. Paleont., 24 (3): 676–688.

MACGINITIE H.D. 1953. Fossil plants of the Florissant beds, Colorado. Carnegie Inst. Washington Publ., 599: 1–198.

MAI D.H. 1963. Beiträge zur Kenntnis der Tertiärflora von Seifhennersdorf (Sachsen). Jb. Staatl. Mus. Mineral. Geol., 1963: 39–114.

MAI D.H. 1995. Tertiäre Vegetationsgeschichte Europas. Gustav Fischer Verlag, Stuttgart.

MAI D.H. & WALTHER H. 1991. Die oligozänen und miozänen Floren NW-Sachsens und des Bitterfelder Raumes. Abh. Staatl. Mus. Mineral. Geol. Dresden, 38: 1–230.

MANCHESTER S.R. 1987. The fossil history oft he Juglandaceae. Monographs Syst. Bot., 21: 1–137.

MANCHESTER S.R. 1994. Fruits and seeds of the middle Eocene Nut Bed Flora, Clarno Formation, Oregon. Palaeontographica Am., 58: 1–205.

MANCHESTER S.R. & DILLHOFF R.M. 2004. *Fagus* (Fagaceae) fruits, foliage, and pollen from the Middle Eocene of Pacific northwestern North America. Can. J. Bot., 82: 1509–1517.

MANCHESTER S.R. & KAPGATE D. 2014. Fruits and seeds of the late Maastrichtian Deccan cherts of central India. Abstract 651, Botany 2014. http://2014.botanyconference.org/engine/search/index.php?func=detail&aid=651

MENITSKY Y. L. 2005. Oaks of Asia. Scientific Publishers, New Hamshire.

MEYER H.W. & MANCHESTER S.R. 1997.The Oligocene Bridge Creek flora of the John Day Formation. Univ. California Publ. Geol. Sci., 141: 1–195.

NAKOMAN E. 1966. Contribution à l'étude palynologique des formations tertiaires du Bassin de Thrace. Ann. Soc. Géol. Nord, 86: 65–107.

NAVARRO E., BOUSQUET J., MOIROUD A., MUNIVE A., PIOU D. & NORMAND P. 2003. Molecular phylogeny of *Alnus* (Betulaceae), inferred from nuclear ribosomal DNA ITS sequences. Plant and Soil, 254: 207–217.

NURY D. 1988. L'Oligocène de Provence méridionale. Stratigraphie, dynamique sédimentaire, reconstitutions paléogéographiques. Thèse de Doctorat d'Etat (1987). Université de Provence. Documents du BRGM, no. 163, 412 p.

PAICHELER J.-C. 1978. Volcanic paleoenvironment and examples of sedimentary incidences at Tertiary Beşkonak Lake (Northern Anatolia – Turkey). Bull. Geol. Soc. Turkey, 21: 11–25.

PAICHELER J.-C. & BLANC C. 1981. La flore du basin lacustre miocène de Bes-Konak (Anatolie septentrionale, Turquie). Géol. Mediterr., 8(1): 19–60.

PAICHELER J.-C., BROIN F. DE, GAUDANT J., MOURER-CHAUVIRE C., RAGE J.-C. & VERGNAUD-GRAZZINI C. 1978. Le bassin lacustrine miocène de Bes-Konak (Anatolie-Turquie): géologie et introduction a la paléontologie des vertébrés. Geobios, 11(1): 43–65.

PAVLYUTKIN B.I., CHEKRYZHOV I.U. & PETRENKO T.I. 2014. Geology and floras of lower Oligocene in the Primorye. Russ. Acad. Sci., Vladivostok. 236 p.

PEEL M.C., FINLAYSON B.L. & MCMAHON T.A. 2007. Updated world map of the Köppen-Geiger climate classification. Hydrol. Earth Syst. Sci., 11: 1633–1644.

POPOV S.V., RÖGL F., ROZANOV A.Y., STEININGER F.F., SHCHERBA I.G. & KOVAC M. (eds) 2004. Lithological-paleogeographic maps of Paratethys. 10 maps late Eocene to Pliocene. Cour. Forsch.-Inst. Senckenberg, 250: 1–46.

POSTIGO-MIJARRA J.M. & BARRÓN E. 2013. Zonal plant communities of the Ribesalbes-Alcora Basin (La Rinconada mine, eastern Spain) during the early Miocene. Bot. J. Linn. Soc., 172: 153–174.

RÖGL F. 1998. Palaeogeographic considerations for Mediterranean and Paratethys seaways (Oligocene to Miocene). Ann. Naturhist. Mus. Wien, 99 A: 279–310.

RÜCKERT-ÜLKÜMEN N. 2003. Fossil ranids from Miocene deposits of Central Anatolia. Istanbul Üniv. Müh. Fak. Yerbilimleri Dergisi, 16(2): 71–74.

SACHSE M. 2001. Oleaceous laurophyllous leaf fossils and pollen from the European Tertiary. Rev. Palaeobot. Palynol., 115: 213–234.

SAPORTA G. DE. 1865. Etudes sur la végétation du sud-est de la France à l'époque tertiaire. Deuxième partie, III. Ann. Sci. Nat. Bot., 5th Ser. 4: 5–264.

SAPORTA G. DE. 1867. Etudes sur la végétation du sud-est de la France à l'époque tertiaire. Troisième partie, I–III. Ann. Sci. Nat. Bot., 5th Ser. 8: 5–136.

SAPORTA G. DE. 1868. Etudes sur la végétation du sud-est de la France à l'époque tertiaire. Troisième partie, IV. Flore des argiles du bassin de Marseille. Ann. Sci. Nat. Bot., 5th Ser. 9: 5–62.

SAPORTA G. DE. 1891. Recherches sur la végétation du niveau Aquitanien de Manosque. Mém. Soc. Géol., 9: 1–83.

SAPORTA G. DE & MARION A.F. 1876. Recherches sur les végétaux fossiles de Meximieux. Arch. Mus. Hist. Nat., 1: 131–335.

SCHILDGEN T.F., YILDIRIM C., COSENTINO D. & STRECKER M.R. 2014. Linking slab break-off, Hellenic trench retreat, and uplift of the Central and Eastern Anatolian plateau. Earth-Sci. Rev., 128: 147–168.

SCHILDGEN T.F., COSENTINO D., BOOKHAGEN B., NIEDERMANN S., YILDIRIM C., ECHTLER H., WITTMANN H. & STRECKER M.R. 2012. Multi-phased uplift of the southern margin of the Central Anatolian plateau, Turkey: A record of tectonic and upper mantle processes. Earth Planet. Sci. Lett., 317/318: 85–95.

SCHROEDER G.-F. 1998. Lehrbuch der Pflanzengeographie. Quelle & Meyer, Wiesbaden.

SITAR V. 1973. Die fossile Flora sarmatischer Sedimente aus der Umgebung von Močiar in der mittleren Slowakei. Acta Geol. Geogr. Univ. Comenianae, Geologica, 26: 5–85.

SMILEY C.J. 1961. A record of *Paulownia* in the Tertiary of North America. Am. J. Bot., 48(2): 175–179.

STITZENBERGER E. 1851. Uebersicht der Versteinerungen des Grossherzogthums Baden. J. Diernfellner, Freiburg i. Br.

STRÖBITZER-HERMANN M. 2002. Results of cuticular-analytic, systematic-taxonomic, stratigraphic and palaeoecological investigations in fossil *Acer*-species. 6th European Palaeobotany-Palynology Conference. Athens, Greece, pp. 165–166.

STUR D. 1867. Beiträge zur Flora der Süßwasserquarze, der Congerien- und Cerithierenschichten im Wiener und Ungarischen Becken. Jb. Geol. Reichsanst., 17: 77–188.

SÜSS H. & VELITZELOS E. 2010. *Lesbosoxylon* gen. nov., eine neue Morphogattung mit dem Typus *Lesbosoxylon ventricosuradiatum* sp. nova aus dem Tertiär der Insel Lesbos, Griechenland. Feddes Repert., 121(1–2): 18–26.

TAKASO T. & TOMLINSON P.B. 1990. Cone and ovule ontogeny in *Taxodium* and *Glyptostrobus* (Taxodiaceae-Coniferales). Am. J. Bot., 77(9): 1209–1221.

TANKUT A., WILSON M. & YIHUNIE T. 1998. Geochemistry and tectonic setting of Tertiary volcanism in the Güvem area, Anatolia, Turkey. J. Volcan. Geotherm. Res., 85(1–4): 285–301.

TEODORIDIS V. 2007. Revision of *Potamogeton* fossils from the Most Basin and their palaeoecological significance (Early Miocene, Czech Republic). Bull. Geosc., 82(4): 409–418.

TEODORIDIS V. & KVAČEK Z. 2005. The extinct genus *Chaneya* Wang & Manchester in the Tertiary of Euorpe – a revision of Porana-like fruit remains from Ohningen and Bohemia. Rev. Palaeobot. Palynol., 134: 85–103.

TEODORIDIS V. & KVAČEK Z. 2006. Palaeobotanical research of the Early Miocene deposits overlying the main coal seam (Libkovice and Lom Members) in the Most Basin (Czech Republic). Bull. Geosci., 81(2): 93–113.

TEODORIDIS V. & SAKALA J. 2008. Early Miocene conifer macrofossils from the Most Basin (Czech Republic). N. Jb. Geol. Paläont. (Abh.), 250: 287–312.

TOPRAK V., SAVASCIN Y., GULEC N. & TANKUT A. 1996. Structure of the Galatean Volcanic Province, Turkey. Int. Geol. Rev., 38(8): 747–758.

UNGER F. 1841–1847. Chloris Protogaea. Beiträge zur Flora der Vorwelt. Wilhelm Engelmann, Leipzig.

UNGER F. 1850a. Die fossile Flora von Sotzka. Denkschr. k. Akad. Wiss., Math.-Naturwiss. Cl., 2: 127–197.

UNGER F. 1850b. Die Gattung *Glyptostrobus* in der Tertiär-Formation. Sitz. Ber. Akad. Wiss., Math.-Naturwiss. Cl., 5: 434–435.

UNGER F. 1850c. Genera et species plantarum fossilium. W. Braunmüller, Vindobonae.

UNGER F. 1852. Iconographica plantarum fossilium. Denkschr. k. Akad. Wiss., Math.-Naturwiss. Cl., 4: 73–118.

UNGER F. 1864. Sylloge Plantarum Fossilium. Pugillus Secundus. Sammlung fossiler Pflanzen besonders aus der Tertiär-Formation. Karl Gerold's Sohn, Vienna.

UNGER F. 1867. Die Fossile Flora von Kumi auf der Insel Euboea. Denkschr. k. Akad. Wiss., Math.-Naturwiss. Cl., 27: 27–90.

VASILYAN D., CLAESSENS L. & ZBYNEK R. 2016. Fish, amphibian and reptile faunas from Kargi 1-3, Harami 1, Harami 3, Hançili 1, Keseköy, Çandir, Bağiçi, Turkey, latest Oligocene – Middle Miocene: 21. In: Mayda S., Kaya T., Pelaez-Campomanes & Hoek Ostende L. W. van den (eds), Taking the Orient Express. RCMNS workshop on the role of Anatolia in Mediterranean Neogene palaeobiogeography EGE University, Izmir, 16–18 September 2016.

VELITZELOS D. (ed.). 2002. Field Guide to the Neogene of the Island of Evia– Early Miocene Flora of Kymi. Field Guide, 6th Europ. Palaeobot.-Palynol. Conf., University of Athens.

VELITZELOS E. & GREGOR H.-J. 1990. Some aspects of the Neogene floral history in Greece. Rev. Palaeobot. Palynol., 62: 291–307.

VELITZELOS D., BOUCHAL J.M. & DENK T. 2014. Review of the Cenozoic floras and vegetation of Greece. Rev. Palaeobot. Palynol., 204: 56–117.

VELITZELOS E., PETRESCU I. & SYMEONIDIS N. 1981. Tertiäre Pflanzenreste aus der Ägäis. Die Makroflora der Insel Lesvos (Griechenland). Ann. Géol. Pays Hellén., 30: 500–514.

VELITZELOS E., VELITZELOS D. & GREGOR H.-J. 2005. *Tilia knoblochii* nov. spec., the first occurrence of bracts with capsules in Greece, with remarks on the geology of the Aliveri–Kymi-Basin (Lower Miocene). Flora Tertiaria Mediterr., 6(9): 1–19.

WALTHER H. 1972. Studien über tertiäre *Acer* Mitteleuropas. Abh. Staatl. Mus. Mineral. Geol., 19: 1–309.

WALTHER H. & KVAČEK Z. 2007. Early Oligocene flora of Seifhennersdorf (Saxony). Acta Mus. Nat. Pragae Ser. B, 63(2–4): 85–174.

WANG Q. 2012. Nomenclatural notes on *Leguminosites* and several taxonomically relevant names (fossil Leguminosae). Taxon, 61(4): 871–877.

WANG Y.F. & MANCHESTER S.R. 2000. *Chaneya*, a new genus of winged fruit from the Tertiary of North America and eastern Asia. Int. J. Plant Sci., 161: 167–178.

WANG N., MCALLISTER H.A., BARTLETT P. & BUGGS R.J.A. 2016. Molecular phylogeny and genome size evolution of the genus *Betula* (Betulaceae). Ann. Bot., 117: 1023–1035.

WESSEL P. & WEBER O. 1856. Neuer Beitrag zur Tertiärflora der niederrheinischen Braunkohleformationen. Palaeontographica, 4: 111–168.

WESSELS W. 2009. Miocene rodent evolution and migration: Muroidea from Pakistan, Turkey and Northern Africa. Geologica Ultraiectina, 307: 1–290.

WEYLAND H. 1943. Beiträge zur Kenntnis der rheinischen Tertiärflora. Part 6. Palaeontographica, B, 87: 94–136.

WEYLAND H. & KILLPER K. 1963. Kritische Untersuchungen zur Kutikularanalyse tertiärer Blätter VI. Palaeontographica, B, 113: 93–116.

WILSON M., TANKUT A. & GULEÇ N. 1997. Tertiary volcanism of the Galatia Province, NW Central Anatolia, Turkey. Lithos, 42: 105–121.

WOROBIEC G., WOROBIEC E. & KVAČEK Z. 2010. Neogene leaf morphotaxa of Malvaceae s.l. in Europe. Int. J. Plant Sci., 171(8): 892–914.

WU Z.Y. & RAVEN P.H. 1999. Flora of China, Volume 4. Cycadaceae through Fagaceae. Beijing, Science Press, St. Louis, Missouri Botanical Garden Press.

WU Z.Y., RAVEN P.H. & HONG D.Y. 2003. Flora of China. Vol. 9 (Pittosporaceae through Connaraceae).

Beijing, Science Press, St. Louis, Missouri Botanical Garden Press.

YANG J., SPICER R.A., SPICER T.E.V. & LI C-S. 2011. 'CLAMP' Online: a new web-based palaeoclimate tool and its application to the terrestrial Paleogene and Neogene of North America. Palaeobiodiv. Palaeoenv., 91: 163–183.

YAVUZ-IŞIK N. 2008. Vegetation and climatic investigations in the EarlyMiocene lacustrine deposits of the Güvem Basin (Galatean Volcanic Province), NW Central Anatolia, Turkey. Palaeogeogr. Palaeoclimatol. Palaeoecol., 150: 130–139.

ZACHOS J., PAGANI M., SLOAN L., THOMAS E. & BILLUPS K. 2001.Trends, rhythms, and aberrations in global climate 65 Ma to present. Science, 292: 686–693.

ZENKER J.C. 1833. Folliculites Kaltennordheimensis, eine neue fossile Fruchtart. N. Jb. Min. Geogn. Geol. Petref.-Kunde, 1833: 177–179.

ZHILIN S.G. 1974. The Tertiary floras of the Plateau Ustjurt (Transcaspia) (in Russian). Komarov Botanical Institute of the Academy of Sciences of the USSR, Leningrad, 122 p.