



Taxonomy and palaeoecology of two widespread western Eurasian Neogene sclerophyllous oak species: *Quercus drymeja* Unger and *Q. mediterranea* Unger



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ABSTRACT

Sclerophyllous oaks (genus *Quercus*) play important roles in Neogene ecosystems of south-western Eurasia. Modern analogues ('nearest living relatives') for these oaks have been sought among five of six infrageneric lineages of *Quercus*, distributed across the entire Northern Hemisphere. A revision of leaf fossils from lower Miocene to Pliocene deposits suggests that morphotypes of the *Quercus drymeja* complex are very similar to a number of extant Himalayan, East Asian, and Southeast Asian species of *Quercus* Group Ilex and may indicate subtropical, relatively humid conditions. *Quercus mediterranea* comprises leaf morphotypes that are encountered in modern Mediterranean species of *Quercus* Group Ilex, but also in Himalayan and East Asian members of this group indicating fully humid or summer-wet conditions. The fossil taxa *Quercus drymeja* and *Q. mediterranea* should be treated as morphotype complexes, which possibly comprised different biological species at different times. *Quercus mediterranea*, although readily recognizable as a distinct morphotype in early to late Miocene plant assemblages, may in fact represent small leaves of the same plants that constitute the *Quercus drymeja* complex. Based on the available evidence, the species forming the *Q. drymeja* complex and *Q. mediterranea* thrived in fully humid or summer-wet climates. The onset of the modern vegetational context of Mediterranean sclerophyllous oaks is difficult to trace, but may have been during the latest Pliocene/early Pleistocene.

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1. Introduction

Quercus (oaks, Fagaceae) is among the most important tree genera in the Northern Hemisphere. With about 400–500 species, it is the largest genus in the order Fagales (Govaerts and Frodin, 1998). Species are distributed in temperate and subtropical regions; the northern limit of their distribution corresponds to the transition from snow climates with warm summers to snow climates with cool summers (*Dfb* to *Dfc*, and *Dwb* to *Dwc* climates according to the Köppen-Geiger classification; Kottek et al., 2006; Peel et al., 2007). Recent molecular phylogenetic and morphological studies recovered two well-supported main lineages within oaks, one comprising the white oaks (*Quercus* Group *Quercus*),

red oaks (*Quercus* Group *Lobatae*) and golden-cup oaks (*Quercus* Group *Protobalanus*), whereas the other group comprises the cycle-cup oaks (*Quercus* Group *Cyclobalanopsis*), the *Cerris* oaks (*Quercus* Group *Cerris*) and the *Ilex* oaks (*Quercus* Group *Ilex*; Denk and Grimm, 2010; Hubert et al., 2014; Hipp et al., 2015; Simeone et al., 2016). *Quercus* Groups *Lobatae* and *Protobalanus* are presently confined to North and Central America and *Quercus* Group *Quercus* occurs throughout the Northern Hemisphere, while *Quercus* Groups *Ilex*, *Cerris* and *Cyclobalanopsis* are Eurasian. These infrageneric groups are also recognized using pollen morphology (Denk and Grimm, 2009; Denk and Tekleva, 2014). In contrast, similar leaf morphologies have evolved in parallel in different groups. For example, the western North American golden-cup oaks and the American white oaks of section *Virentes* are only distantly related to species of the Eurasian *Ilex* oaks, but have morphologically highly similar evergreen leaves (Flora of North America Editorial Committee, 1997; Flora of China Editorial Committee, 1999; Menitsky, 2005).

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In the present study, we assess the taxonomy of two western Eurasian Neogene sclerophyllous leaf fossil-species of oaks and compare it to evidence from dispersed pollen and from the carpological record.

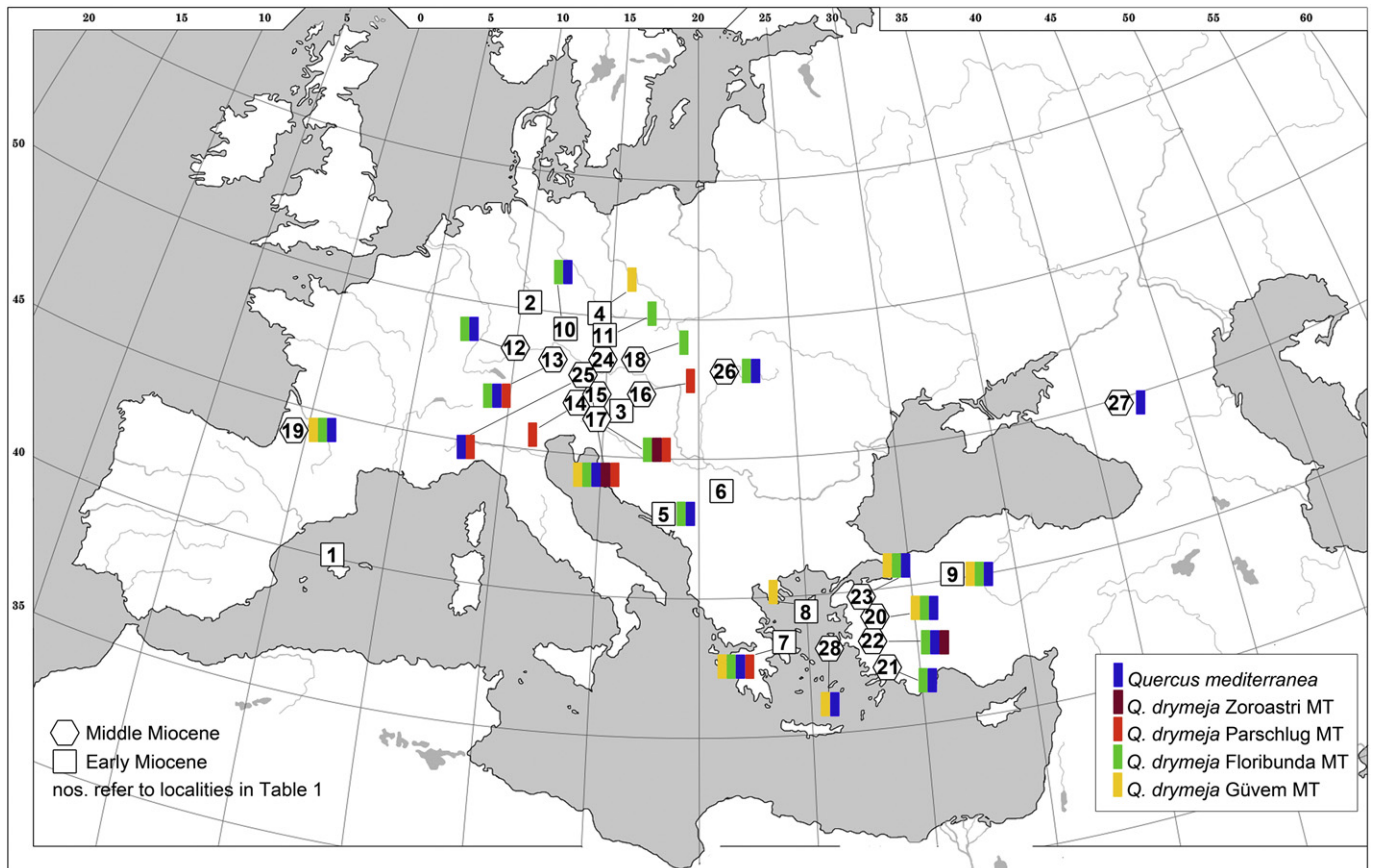
1.1. The fossil record of sclerophyllous oaks in Europe

In a seminal study, Unger (1841–1847) described two species of sclerophyllous oaks from middle Miocene deposits of Parschlug, Austria, *Quercus drymeja* Unger and *Q. mediterranea* Unger. Unger considered the taxonomic affinity of *Q. drymeja* to be with the western Asian *Q. libani* G.Olivier (*Quercus* Group Cerris), the Mexican and Central American *Q. lancifolia* Schlechter et Chamisso, and mainly with the Mexican and Central American *Q. xalapensis* Bonpland (both *Quercus* Group Lobatae, red oaks). In contrast, he considered *Q. mediterranea* as closely similar to the Mediterranean *Q. pseudococcifera* Desfontaines (= *Q. coccifera* L.; *Quercus* Group Ilex). Kvaček et al. (2002) investigated late Miocene plant fossils from northern Greece and based on epidermal features (almost hairless abaxial leaf surface with only dispersed massive trichome bases) also suggested that *Q. mediterranea* belongs to the “*Q. coccifera* group”. They noticed that distinguishing features of the leaf epidermis are shared between *Q. mediterranea* and *Q. drymeja*, but nevertheless compared the latter with the extant Mexican red oaks *Q. sartorii* Liebmann and *Q. xalapensis*. Kovar-Eder et al. (2004) re-studied the type material of *Q. drymeja* and *Q. mediterranea* from middle Miocene deposits of Parschlug and distinguished one additional sclerophyllous oak, *Q. zoroastri* Unger (1850). They agreed on the relationship between *Q. mediterranea* and the modern *Q. coccifera*, but did not indicate particular relationships of *Q. drymeja* and *Q. zoroastri* with modern oak species. More recently, Kvaček et al. (2011) studied middle Miocene leaf assemblages from southwestern France with abundant

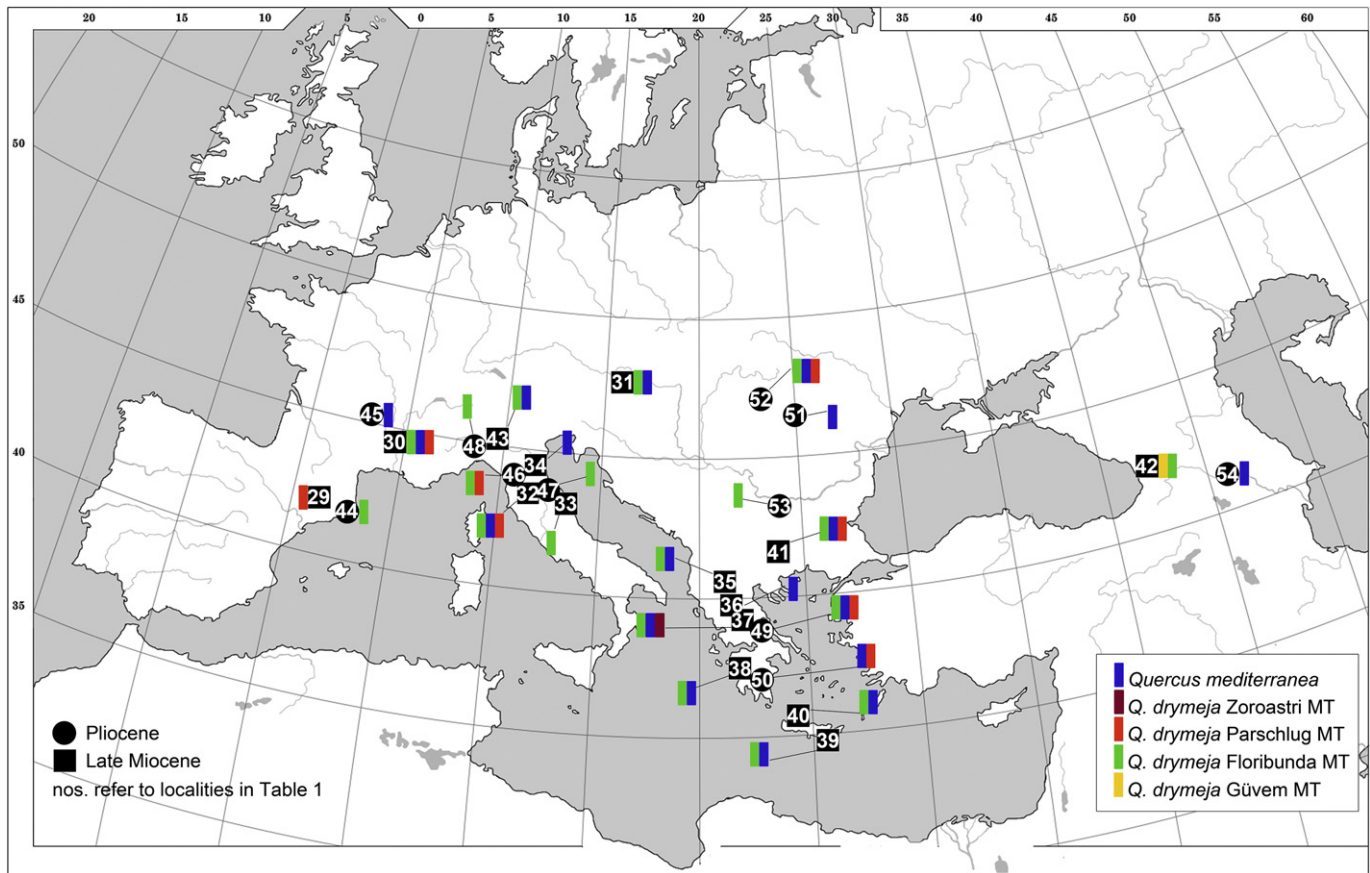
Q. drymeja and *Q. mediterranea*. They noticed that although the leaf epidermis of *Q. mediterranea* matches that of the extant *Q. coccifera* (Kvaček et al., 2002), the leaf shape, size, and tooth architecture differ. For *Q. drymeja*, they found identical leaf epidermal features in the material from southwestern France and the material from northern Greece. Most recently, Deng et al. (2017) investigated all living members of Group Ilex and concluded that based on the scanty record of leaf epidermal characteristics of *Q. drymeja* most similarities are with “less hairy species in mesophytic and broadleaved evergreen forests, e.g., *Q. cocciferoides* and *Q. baronii*.” (Deng et al., 2017, p. 33).

Notably, the records of *Q. drymeja* and *Q. mediterranea* have been substantially expanded after their original publication and currently cover an area from Spain to Georgia in western Eurasia and a stratigraphic range from lower Miocene to Pliocene (e.g. Givulescu and Ghiurca, 1969; Knobloch and Velitzelos, 1986a; Kvaček et al., 1993; Kvaček et al., 2002; Velitzelos, 2002; Velitzelos et al., 2014; Maps 1, 2).

In view of the great morphological variability among leaf fossils assigned to *Q. drymeja* and the large stratigraphic range of this fossil species, ca. 19 Ma to ca. 5 Ma (see, e.g. Velitzelos et al., 2014; Table 1), we were interested in assessing the morphological coherence of this taxon across its geographical and stratigraphical range as this may have implications for inferring their closest modern relatives (commonly called nearest living relatives). In addition, we were interested in the systematic relationships of the two fossil-species *Q. drymeja* and *Q. mediterranea*. We used a modern phylogenetic framework established for oaks, which includes a time calibrated phylogeny for the genus (Manos et al., 2001; Denk and Grimm, 2010; Hubert et al., 2014; Hipp et al., 2015). Finally, we discuss how niche evolution in oak lineages may impact palaeoecological inferences using nearest-living-relative approaches.



Map 1. Early and middle Miocene records of *Quercus drymeja* Unger and *Q. mediterranea* Unger (see also Table SI 1).



Map 2. Late Miocene and Pliocene records of *Quercus drymeja* Unger and *Q. mediterranea* Unger (see also Table SI 1).

2. Material and methods

The material investigated for this study partly comes from our own field work carried out between 2008 and 2014 (Likoudi, Greece; Soma, Şahımalı, Tınaz, Salihpaşalar, Turkey) or from existing museum/university and private collections (Parschlug and Lavanttal, Austria; Güvem, Turkey). In addition, a comprehensive review of published accounts was made (Table 1; Maps 1, 2).

Plant fossils recovered from middle and upper Miocene deposits of Likoudi, Soma, Şahımalı, Tınaz, and Salihpaşalar are stored at the Swedish Museum of Natural History (S), Stockholm, and the Department of Forestry, Istanbul University (ISTO-F), Bahçeköy. Material from the Austrian Parschlug and Lavanttal localities, middle Miocene, is stored at the Museum of Natural History Vienna (NHM), the palaeontological collection of the University of Vienna (as SU_LAV), the Geological Survey Vienna (GBA), the Universalmuseum Joanneum, Centre of Natural History (LMJ), Graz, and in private collections (collection Andreas Hassler, [SH]). The rich material from lower Miocene deposits of Güvem was collected by Baki Kasaplıgil during the late 1960s and 1970s and is stored at the University of California, Museum of Paleontology (UCMP), Berkeley.

Dispersed pollen grains were investigated from lower Miocene plant bearing deposits of Kimi (Greece) and Güvem (Turkey), in order to assess the contributions of different infrageneric groups of *Quercus* to the palynological assemblages of deposits rich in sclerophyllous *Quercus* foliage. Sedimentary rock was processed following the protocol described in Grímsson et al. (2008) and the same pollen grains were investigated with LM and SEM (single grain method; Zetter, 1989).

Modern species of *Quercus* were studied in the herbaria at Edinburgh (E; physical herbarium and online herbarium catalogue at <http://elmer.rbge.org.uk/bgbase/vherb/bgbasevherb.php>) and Paris (P; physical herbarium and online catalogue at <https://science.mnhn.fr/institution/mnhn/search/form>). Additional information from herbaria was retrieved

from the online herbarium catalogue from Kew (<http://apps.kew.org/hercat/navigator.do>) and New York Botanical Garden (<http://sweetgum.nybg.org/science/vh/>), and from the Oaks of the World website (<http://oaks.of.the.world.free.fr/>). Leaf litter of *Quercus ilex* was collected from a small grove on the foothills of Mount Olympus, above Katerini, Greece.

We also used the eight-gene time-calibrated phylogeny for *Quercus* of Hubert et al. (2014) to compare inferred biogeographic relationships of the fossil taxa with the estimated dates of infrageneric splits based on molecular data.

3. Results

3.1. Leaf morphology and taxonomic relationships of *Quercus drymeja* and *Q. mediterranea*

Quercus drymeja and *Q. mediterranea* display a wide range of morphological variation in early Miocene to Pliocene deposits across western Eurasia. They may be dominating elements of fossil plant assemblages (e.g. Güvem, Aydın/Şahımalı, Turkey; Kimi, Elasona/Likoudi, Vegora, Greece; Miljevina, Bosnia; Toscana, Italy; Lavanttal, Austria; Kodor, Georgia) or rare accessory elements at other localities (Table 1). In the following, a number of distinct morphotypes are described (Table 2) and compared to particular modern species in a phylogenetic context. The term ‘morphotype’ as used here refers to “any distinct, more or less stable morphological form of a given organism” (Lincoln et al., 1998).

3.2. *Quercus drymeja* Unger

Published records included within *Quercus drymeja* are listed under the morphotypes described below. For a complete list of records included within *Q. drymeja*, see Table SI 1.

Table 1Occurrences of *Quercus drymeja* [D] and *Q. mediterranea* [M] in the Neogene of western Eurasia. Numbers indicate position of localities on Maps 1 and 2.

Age	State, locality	Reference	Taxon (D, M)	Frequency	Remarks	
1	Early Miocene	Spain, Mallorca	Depape, 1928; Arènes and Depape, 1956	D	Rare	One leaf fragment
2	Early Miocene	Germany, Kaltennordheim (Escheri Formation)	Mai, 2007	D	Rare	Not figured
3	Early Miocene	Austria, Münzenberg/Leoben	von Ettingshausen, 1888	D M	Rare	As <i>Q. drymeja</i> Unger, <i>Q. lonchitis</i> Unger (D), <i>Q. palaeo-Ilex</i> Ettingshausen (M)
4	Early Miocene	Czech Republic, Cyprus Shale ^a	Bůžek et al., 1996	D	Rare	As <i>Q. cf. drymeja</i> (D)
5	Early Miocene	Bosnia, Miljevina	Kvaček et al., 1993	D M	Abundant	As <i>Q. ex gr. drymeja</i> (D), <i>Q. mediterranea</i> Unger (M)
6	Early Miocene	Serbia, Žagubica Basin	Lazarević and Milivojević, 2010	D	Rare	Leaf fragment
7	Early Miocene	Greece, Kimi, Aliveri	Unger, 1867; Velitzelos et al., 2014	D M	Abundant	As <i>Q. lonchitis</i> (D), <i>Q. mediterranea</i> (M), <i>Q. zoroastri</i> Unger (D)
8	Early Miocene	Greece, Lemnos	Berger, 1953b; Velitzelos et al., 2014	D	Rare	As <i>Q. lonchitis</i> (D)
9	Early Miocene	Turkey, Güvem area	Paicheler and Blanc, 1981	D M	Abundant	As <i>Myrica</i> spp., <i>Q. drymeja</i> (D), <i>Q. mediterranea</i> (M)
10	Early/middle Miocene	Germany, Wackersdorf ^b	Knobloch and Kvaček, 1976; Kovar-Eder et al., 2001	D M	Rare	As <i>Quercus</i> sp. (?D), <i>Q. mediterranea</i> vel <i>Castanea</i> sp. (M)
11	Early/middle Miocene	Czech Republic, Mydlovary Formation ^a	Knobloch and Kvaček, 1996	D	Rare	As <i>Q. cf. drymeja</i> (D)
12	Middle Miocene (Badenian)	Germany, Steinheim	Schweigert, 1993	D M	Abundant	As <i>Q. drymeja</i> (D), <i>Q. mediterranea</i> (M)
13	Middle Miocene (Badenian)	Germany, Entrischenbrunn	Schmitt and Butzmann, 1997	D M	Rare	As cf. <i>Quercus</i> sp. (M), <i>Myrica</i> sp. (D)
14	Middle Miocene (Badenian)	Austria, Lintsching	Ströbitzer, 1999	D	Rare	As <i>Q. drymeja</i> (D)
15	Middle Miocene (Badenian)	Austria, Parschlug	Unger, 1847, 1850, 1852; Kovar-Eder et al., 2004	D M	Abundant	As <i>Quercus drymeja</i> , <i>Q. zoroastri</i> (D), <i>Q. urophylla</i> Unger (D), ? <i>Q. gmelini</i> A.Braun (D), <i>Q. mediterranea</i> (M)
16	Middle Miocene (Badenian)	Austria, Weingraben	Berger, 1952a; Draxler and Zetter, 1991; Jechorek and Kovar-Eder, 2004	D	Rare	As <i>Q. drymeja</i> (D)
17	Middle Miocene (Badenian)	Austria, Lavanttal	Berger, 1955a	D M	Abundant	As <i>Q. drymeja</i> (D), <i>Q. mediterranea</i> (M)
18	Middle Miocene (Helvetium)	Austria, Teiritzberg	Berger, 1957a	D	Rare	As <i>Q. drymeja</i> (D)
19	Middle Miocene (Badenian)	France, Arjuzanx ^a	Kvaček et al., 2011	D M	Abundant	As <i>Q. drymeja</i> (D), <i>Q. cf. zoroastri</i> , <i>Q. mediterranea</i> (M)
20	Middle Miocene (Badenian)	Turkey, Soma	Gemici et al., 1991	D M	Abundant	As <i>Q. drymeja</i> , <i>Q. cf. trojana</i> Webb (D), <i>Q. ilex</i> L., <i>Q. mediterranea</i> (M)
21	Middle Miocene (Badenian)	Turkey, Yatagan Basin	Gemici et al., 1990	D M	Abundant	As <i>Q. drymeja</i> , <i>Q. goepperti</i> C.O.Weber vel <i>kubinyii</i> (D), <i>Q. ilex</i> (M)
22	Middle Miocene (Badenian)	Turkey, Aydin, Şahınlı	Gemici et al., 1993	D M	Abundant	As <i>Q. drymeja</i> , <i>Castanopsis</i> sp., <i>Q. cf. drymeja</i> (D), <i>Q. mediterranea</i> (M)
23	Middle Miocene (Badenian)	Turkey, Balya	Engelhardt, 1903	D M	Abundant	As <i>Myrica</i> spp., <i>Q. lonchitis</i> , <i>Pterocarya denticulata</i> Weber, <i>Q. mediterranea</i> , <i>Castanea kubinyii</i> Kováts, <i>Q. drymeja</i> , <i>Q. haidingeri</i> Ettingshausen (D), <i>Ilex ambigua</i> Unger (M)
24	Middle Miocene (Sarmatian)	Austria, Türkenschanze	Berger and Zabusch, 1952	D M	Rare	As <i>Q. drymeja</i> (D), <i>Q. mediterranea</i> (M)
25	Middle Miocene (Sarmatian)	Austria, Hernals	Berger, 1953a	D M	Rare	As <i>Q. drymeja</i> (D), <i>Q. mediterranea</i> (M)
26	Middle Miocene (Sarmatian)	Hungary, Erdöbénye	Kováts, 1856; Erdei et al., 2011	D M	Abundant	As <i>Q. szirmayana</i> Kováts (M), <i>Q. pseudoilex</i> Kováts (D), <i>Q. urophylla</i> (D)
27	Middle Miocene (Sarmatian)	Russia, Armavir	Kutuzkina, 1964	?M	Rare	As <i>Quercus neriifolia</i> A.Braun (M)
28	Middle Miocene (Sarmatian)	Greece, Chios, Nenita layers	Velitzelos et al., 2014	M	Rare	As <i>Q. mediterranea</i> (M)
29	Late Miocene	Spain, Cerdanya	Barrón, 1999a, 1999b	D	Abundant	As <i>Q. drymeja</i> (D)
30	Late Miocene	France, Ardèche	Boulay, 1887	D M	Abundant	As <i>Q. drymeja</i> (D), <i>Q. mediterranea</i> , <i>Q. coccifera</i> (M)
31	Late Miocene (Pannonian)	Austria, Brunn-Vösendorf	Berger, 1952b, 1955b	D M	Rare	As <i>Quercus cf. drymeja</i> (D), <i>Q. cf. mediterranea</i> (M)
32	Late Miocene (Messinian)	Italy, Tuscany (Gabbro, Monte Livornesi)	Berger, 1957b	D M	Abundant	As <i>Quercus drymeja</i> , ? <i>Q. goepperti</i> (Weber) Weyland, <i>Q. linguiformis</i> Boulay (D), <i>Q. mediterranea</i> (M)
33	Late Miocene	Italy, Senigallia	Massalongo and Scarabelli, 1859	D M	Rare	As <i>Juglans italica</i> Massalongo (D)
34	Late Miocene	Italy, Borgo Tossignano	Teodoridis et al., 2015	M	Rare	As <i>Quercus mediterranea</i> (M)
35	Late Miocene (Pontian)	Greece, Vegora ^a	Kvaček et al., 2002	D M	Abundant	As <i>Q. drymeja</i> (D), <i>Q. mediterranea</i> (M)
36	Late Miocene	Greece, Prosilio, Lava	Knobloch and Velitzelos, 1986b; Kvaček and Walther, 1989	M	Abundant	As <i>Quercus cf. mediterranea</i>
37	Late Miocene	Greece, Likoudi	Knobloch and Velitzelos, 1986a	D M	Abundant	As <i>Q. cf. drymeja</i> (D), <i>Q. cf. mediterranea</i> (M)
38	Late Miocene	Greece, Platana	Kleinhölter, 1994	D M	Abundant	As <i>Q. drymeja</i> (D), <i>Q. mediterranea</i> (M)

(continued on next page)

Table 1 (continued)

Age	State, locality	Reference	Taxon (D, M)	Frequency	Remarks
39	Late Miocene Greece, Crete, Messara Basin	Zidianakis et al., 2010	D M	Rare	As <i>Q. drymeja</i> (D), <i>Q. mediterranea</i> (M)
40	Late Miocene Greece, Crete, Vrysses Basin	Zidianakis et al., 2007	D	Rare	As <i>Q. drymeja</i> (D)
41	Late Miocene Bulgaria, Gotse Delchev Basin ^a	Palamarev and Tsenov, 2004	D M	Abundant (D)	As <i>Q. drymeja</i> , <i>Q. ilex fossilis</i> , <i>Q. lonchitis</i> , <i>Q. sosnowskiyi</i> Kolakovskiy (D), <i>Q. mediterranea</i> (M)
42	Late Miocene Georgia, Kodor	Kolakovskiy, 1964	D	Abundant	As <i>Castanopsis elisabethae</i> Kolakovskiy, <i>C. bifurcata</i> Kolakovskiy, <i>C. furcinervis</i> (Rossmässler) Kräusel et Weyland, <i>Q. sosnowskiyi</i> f. <i>angustifolia</i> Kolakovskiy (D)
43	Late Miocene/Pliocene Italy, Montescano, Lombardia	Sordelli, 1896	D M	Abundant?	As <i>Q. drymeja</i> (D), <i>Q. gaudinii</i> Lesquereux (D, M), <i>Q. praecursor</i> Saporta (D)
44	Pliocene Spain, Girona, Caldes de Malavella	Robles et al., 2013	D	Rare	As <i>Q. drymeja</i> (D)
45	Pliocene France, Montagne de Perrier	Mai, 1995	M	Rare	As <i>Q. mediterranea</i> (M)
46	Pliocene Italy, Valdarno	Gaudin and Strozzi, 1859	D M	Abundant	As <i>Quercus drymeja</i> , (? <i>Q. gaudinii</i>) (D), <i>Q. mediterranea</i> (M)
47	Pliocene Italy, Valdarno, Meleto	Fischer and Butzmann, 2000	D	Abundant	As <i>Q. drymeja</i>
48	Pliocene Italy, Piedmont, Valmanera/Asti	Martinetto, 2003	D	Rare	As cf. <i>Quercus ilex</i>
49	Pliocene Greece, Atalanti	Velitzelos et al., 2014	D M	Abundant	As <i>Q. drymeja</i> (D), <i>Q. mediterranea</i> (M)
50	Pliocene Greece, Skoura	Velitzelos et al., 2014	M	Rare	As <i>Q. mediterranea</i> (M)
51	Pliocene Romania, Borsec	Pop, 1936	M	Rare	As <i>Q. mediterranea</i> , <i>Q. cf. ilex</i>
52	Pliocene Romania, Chiuzbaia	Givulescu and Ghiurca, 1969	D M?	Rare	As <i>Quercus</i> cf. <i>glaucofolia</i> Andreánszky, <i>Q. drymeja</i> (D), <i>Q. cf. ilex</i> , <i>Q. aff. coccifera</i> , <i>Q. mediterranea</i> (M)
53	Pliocene (Dacian) Bulgaria, Beli Breg basin	Bozukov et al., 2011	D	Rare	As <i>Q. drymeja</i> , <i>Q. sosnowskiyi</i> , <i>Q. aff. acrodonta</i> Seemen (D)
54	Pliocene Georgia, Malye Shiraki	Kolakovskiy and Rationi, 1967	M	Rare	As <i>Q. mediterranea</i> (M)

^a Leaf epidermal features preserved.

Leaves petiolate; petiole stout, to 2.5 cm long; lamina up to 12 cm long, narrow ovate to lanceolate, broad to narrow elliptical, narrow oblong; base acute to rounded to cordate; apex acute to acuminate, more rarely attenuate; primary vein stout; leaf margin entire or dentate; teeth conspicuous or inconspicuous, occasionally ending in bristle-like spine, basal side straight, sigmoid, or convex, apical side concave; secondary veins regularly or irregularly spaced, departing from primary vein at low to steep angles, occasionally intersecondary veins present, secondary venation camptodromous (usually close to the leaf base), semicraspedodromous, or craspedodromous; tertiary veins mixed opposite/alternate percurrent, more or less perpendicular to secondary veins except for close to the primary vein, where they are bent and inserting the primary vein at right angle, fourth order venation alternate percurrent, areolation well developed, 4-sided to polygonal.

3.2.1. *Quercus drymeja* morphotypes (MT)

3.2.1.1. *Quercus drymeja* Güvem Morphotype.

Plates I (Güvem), II (Güvem), III, 1–3 (Soma, Parschlug)

- 1867 *Quercus lonchitis* Unger — Unger, p. 50, pl. 5, fig. 3
 1903 *Myrica acuminata* Unger — Engelhardt, p. 57, pl. 7, fig. 3
 1903 *Myrica banksiaefolia* Unger — Engelhardt, p. 58, pl. 7, fig. 4
 1903 *Quercus lonchitis* Unger — Engelhardt, p. 58, pl. 7, figs. 6–8
 1903 *Quercus haidingeri* Ettingshausen — Engelhardt, p. 59, pl. 7, fig. 17
 1903 *Pterocarya denticulata* Weber — Engelhardt, p. 63, pl. 7, fig. 9
 1903 *Myrica acuminata* Unger — Engelhardt, pl. 7, fig. 3
 ?1953 *Quercus lonchitis* Unger — Berger, p. 37, figs. 2, 3
 1981 *Myrica acuminata* Unger — Paicheler and Blanc, pl. 3, figs. 7–9
 1981 *Myrica* sp. — Paicheler and Blanc, pl. 3, fig. 10

Table 2

Distinguishing morphological features for *Quercus drymeja* morphotypes recognized in the present study, and for *Quercus mediterranea*.

Taxon	Lamina length	Lamina shape	Lamina base	Intersecondary veins	Dentition	Tooth type	Subsidiary teeth
<i>Quercus drymeja</i> Güvem Morphotype (MT)	Up to 10+ cm	Elliptic to lanceolate	Rounded	Rarely present	Present along entire margin of lamina	Inconspicuously hooked	Occasionally present
<i>Quercus drymeja</i> Floribunda MT	Up to 10+ cm	Narrow oblong to long narrow ovate, elliptic	Acute to rounded	Commonly present	Absent, present along entire margin, or restricted to upper half of lamina	Spinose, bristle-like extension curved apically	Commonly present
<i>Quercus drymeja</i> Parschlug MT	Up to 10+ cm	Lanceolate to elliptic	Acute to cuneate	Rarely present	Present along entire margin of lamina	Spiny	Rarely present
<i>Quercus drymeja</i> Zoroastri MT	Up to 10+ cm	Broad elliptic to ovate/rhombic	Acute to rounded	Usually absent	Present along entire margin, or restricted to upper half of lamina	Coarse	Rarely present
<i>Quercus mediterranea</i>	Up to 5+ cm	Ovate, elliptic, oblong, obovate	Acute, rounded, cordate, inverted pear-shaped	Occasionally present	Absent, present along entire margin, or restricted to upper half of lamina	Coarse or fine	Present or absent

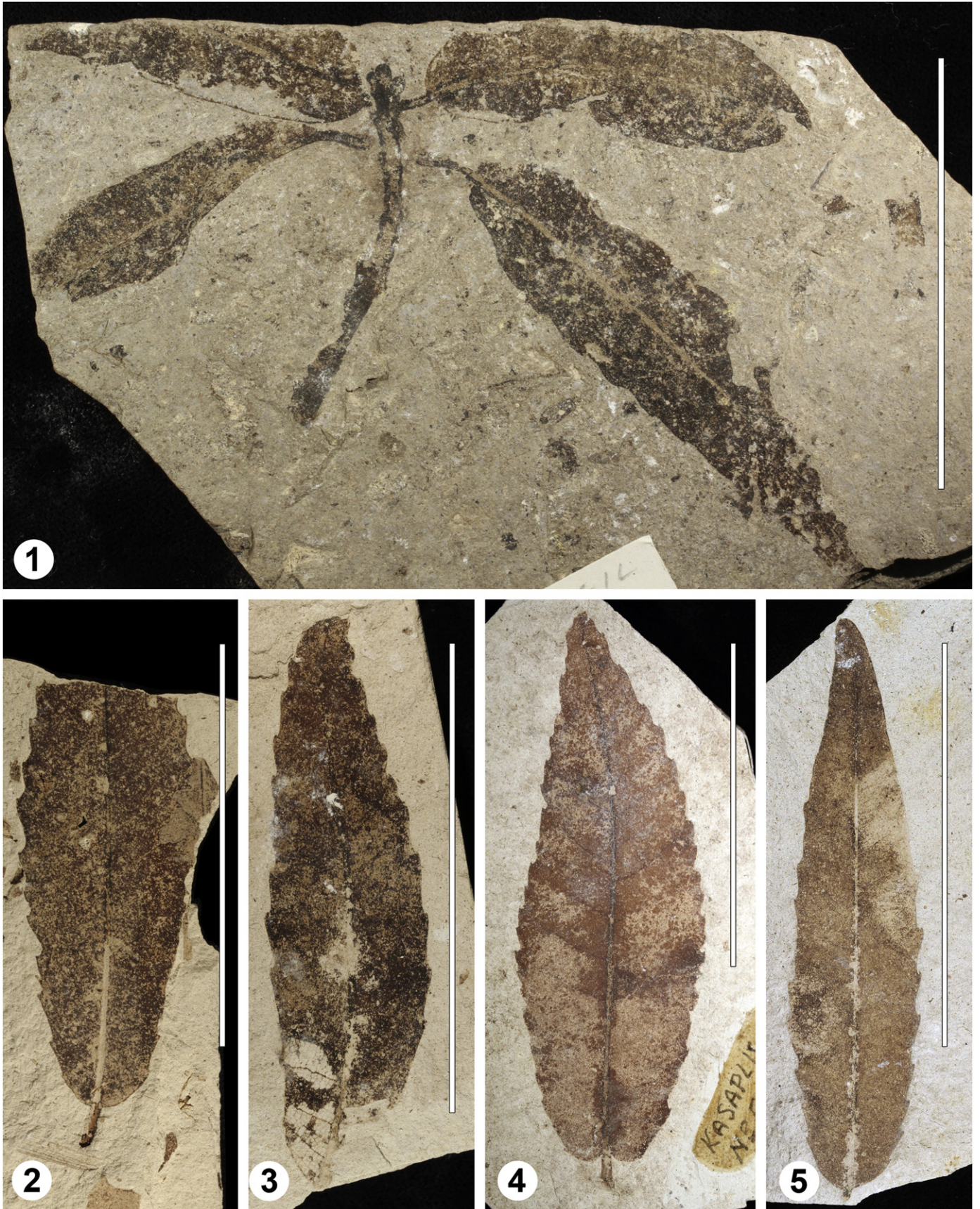


Plate I. *Quercus drymeja* Unger, Güvem Morphotype. Early Miocene, Güvem area, Turkey; palaeobotanical collection UCMP. 1. Kasapligil 5904, leafy twig with terminally clustered buds. 2. Kasapligil 5812. 3. Kasapligil 5692, typical leaf with regularly dentate margin. 4. Kasapligil 5450. 5. Kasapligil s.n., note elongate acute apex. Scale bar is 5 cm in 1–5.

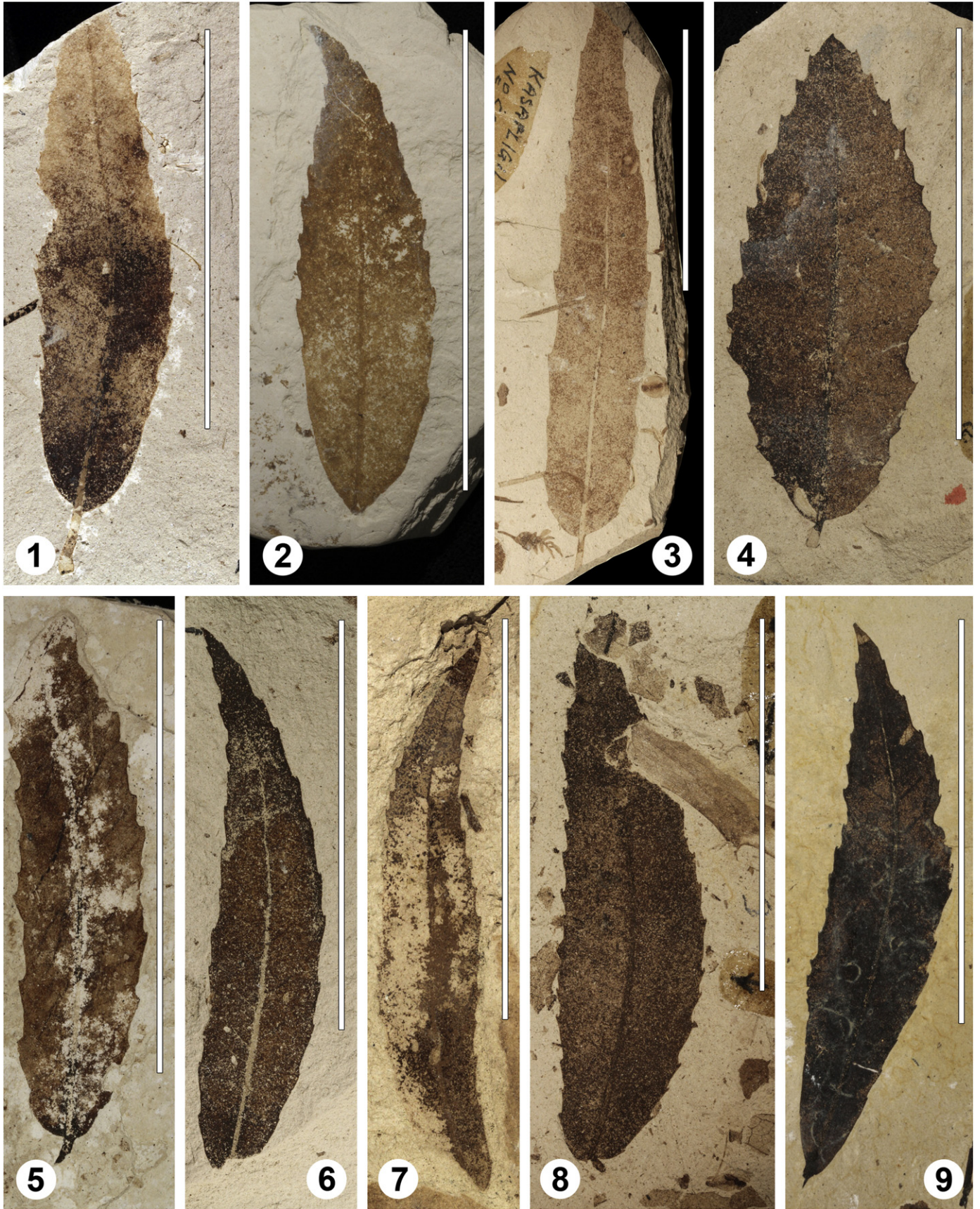


Plate II. *Quercus drymeja* Unger, Güvem Morphotype. Early Miocene, Güvem area, Turkey; palaeobotanical collection UCMP. 1. Kasapligil 5795. 2. Kasapligil 6057. 3. Kasapligil 5411, note flower of *Populus* sp. in the lower left-hand corner. 4. Kasapligil 5450. 5. Kasapligil 5995. 6. Kasapligil 6048. 7. Kasapligil 5849. 8. Kasapligil 5460a, note leaflet of *Mahonia grimmii* Güner et Denk on the right side. 9. Kasapligil 5897, leaf resembling the extinct fagaceous genus *Eotrigonobalanus*. Scale bar is 5 cm in 1–9.

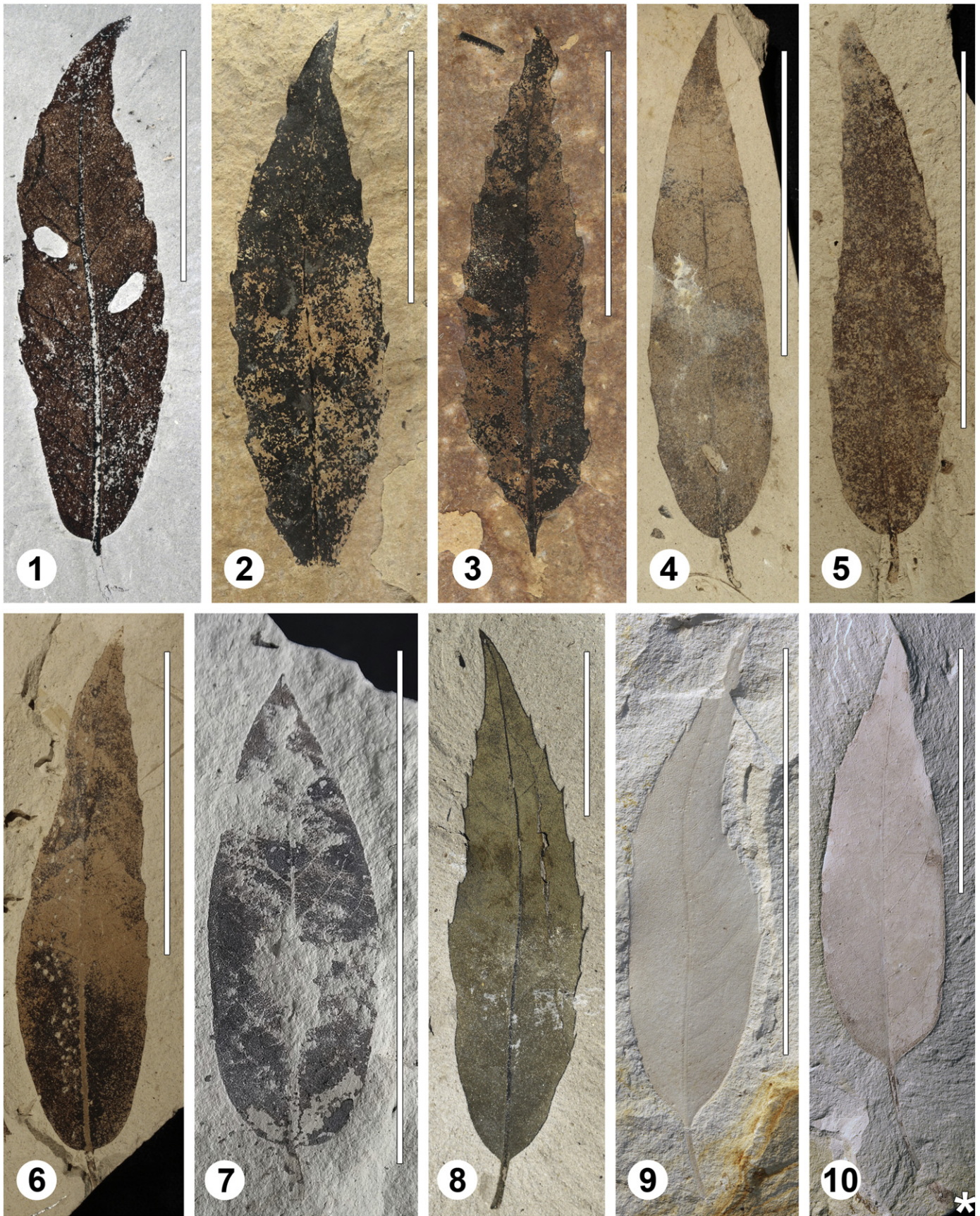


Plate III. *Quercus drymeja* Unger, Floribunda Morphotype. Early to late Miocene. 1. Soma. 2, 3. Parschlug. 4–6. Güvem. 7. Tmaz. 8. Şahımalı. 9, 10. Likoudi. 1. ISO-F.s.n. 2. GBA.s.n. 3. GBA.s.n. 4. UCMP Kasaplıgil 5472. 5. UCMP Kasaplıgil 5902. 6. UCMP Kasaplıgil 5396. 7. ISTO-F 00548. 8. ISTO-F.s.n. 9. S116570. 10. S116701. Asterisk denotes end of long petiole. Scale bar is 5 cm in 4–7, 9, 10; 3 cm in 1–3, 8.

- 1981 *Quercus drymeja* Unger — Paicheler and Blanc, pl. 10, figs. 11–14, non pl. 11, figs. 1, 2 (= aff. *Eotrigonobalanus furcinervis*)
 1991 *Quercus drymeja* Unger — Gemici et al., p. 172, pl. 8, fig. 9
 1991 *Quercus* cf. *trojana* Webb — Gemici et al., p. 173, pl. 9, fig. 7
 2011 *Quercus drymeja* Unger — Kvaček et al., p. 30, pl. 6, figs. 1–6, pl. 11, figs. 12, 13, pl. 17, figs. 4, 5

Lamina shape narrow elliptic to lanceolate; base rounded to bluntly acute or shallowly cordate; apex acute to elongated acute; margin dentate along entire margin; teeth small, hooked, regular, basal side straight to convex, apical side straight to concave; occasionally subsidiary teeth; secondary veins departing from primary vein at low to steep angles, angle typically increasing towards base.

Remarks: This MT is common in the early Miocene assemblages of the Güvem area (Plates I, II) and occurs sporadically in Kimi (Unger, 1867). It is also found in Soma (Gemici et al., 1991; Plate III, 1), Parschlug (Plate III, 2, 3) and in middle Miocene deposits of Arjuzanx (Kvaček et al., 2011).

Small teeth as in this MT are also seen in leaves of the highly polymorphic species *Quercus phillyreoides* A.Gray (*Quercus* Group Ilex), the only member of the group found in Japan, and in leaves of the Mediterranean *Q. ilex* (e.g. Plate XI, 2). Rounded teeth as present in the specimens from Arjuzanx are also seen in the modern *Q. kingiana* Craib (Group Ilex). Further, this early Miocene foliage of *Q. drymeja* superficially resembles the extinct Paleogene Fagaceae *Castaneophyllum lonchitiforme* (Kvaček and Walther, 2012) but differs from these leaf types by straight secondary veins, smaller number of secondary veins, and different leaf base (roundish to bluntly acute versus cuneate to acute). It is noteworthy that among the dispersed pollen grains investigated from the plant-bearing layers in the Güvem area one form appears to represent the extinct Fagaceae *Eotrigonobalanus furcinervis* (Rossmässler) Walther et Kvaček (Plate SI I, figs. 7–9). Likewise, a few leaves resembling *Q. drymeja* Güvem MT may actually represent *Eotrigonobalanus* (e.g. Plate II, 9). Similar leaves of *Eotrigonobalanus* were figured in Velitzelos et al. (2014; pl. 3, figs. 5, 7) from Oligocene layers of eastern Greece.

Modern analogue: *Quercus* Group Ilex.

3.2.1.2. *Quercus drymeja Floribunda* Morphotype.

Plates III, 4–10, IV, V (Güvem, Likoudi, Salihpaşalar, Soma, Şahınlı, Tinaz), ?VI, 6 (Parschlug)

- 1856 *Quercus urophylla* Unger — Kováts, p. 22, pl. 2, fig. 7
 1859 *Quercus drymeja* Unger — Gaudin and Strozzi, p. 44, pl. 4, figs. 2, 4, 6, 7, 8
 1859 *Quercus gaudinii* Lesquereux — Gaudin and Strozzi, p. 43, pl. 6, fig. 2 (not 3)
 1859 *Juglans italica* Massalongo — Massalongo and Scarabelli, p. 396, pl. 33, figs. 2, 13
 1867 *Quercus zoroastri* Unger — Unger, p. 52, pl. 6, fig. 23
 1887 *Quercus drymeja* var. *integribasis* N.Boulay — Boulay, p. 258
 1896 *Quercus drymeja* Unger — Sordelli, p. 125, pl. 21, figs. 1–4
 1896 *Quercus praecursor* Saporta — Sordelli, p. 127, pl. 20, fig. 11
 1896 *Quercus gaudinii* Lesquereux — Sordelli, p. 128, pl. 20, figs. 8, 10
 1903 *Quercus mediterranea* Unger — Engelhardt, p. 59, pl. 7, fig. 10
 1903 *Castanea kubinyi* Kováts — Engelhardt, p. 60, pl. 7, figs. 12, 15
 1903 *Quercus drymeja* Unger — Engelhardt, p. 59, pl. 7, figs. 13, 14
 1952b *Quercus* cf. *drymeja* Unger — Berger, p. 92, pl. 1, figs. 48–50
 1955a *Quercus drymeja* Unger — Berger, p. 408, fig. 7
 1957a *Quercus drymeja* Unger — Berger, p. 91, fig. 2
 1957b *Quercus drymeja* Unger — Berger, p. 21, pl. 4, figs. 69, 71
 1957b *Quercus linguiformis* Boulay — Berger, p. 34, pl. 11, fig. 165
 1964 *Castanopsis elisabethae* Kolakovsky — Kolakovsky, p. 79, pl. 24, fig. 5
 1964 *Castanopsis bifurcata* Kolakovsky — Kolakovsky, p. 78, pl. 24, fig. 6
 1964 *Castanopsis furcinervis* (Rossmässler) Kräusel et Weyland — Kolakovsky, p. 80, pl. 24, figs. 7, 8, pl. 25, figs. 1, 2
 1964 *Quercus sosnowskyi* forma *angustifolia* Kolakovsky — Kolakovsky, p. 90, pl. 25, figs. 3–11

- 1969 *Quercus drymeja* Unger — Givulescu and Ghiurca, p. 39, pl. 9, fig. 11
 1976 *Quercus* sp. — Knobloch and Kvaček, p. 43, pl. 17, figs. 15, 18, pl. 19, fig. 9, pl. 21, figs. 8, 9
 1981 *Myrica lignitum* (Unger) Saporta — Paicheler and Blanc, pl. 3, fig. 3
 1986a, *Quercus* cf. *drymeja* Unger “Group 1”, “Group 2” — Knobloch and Velitzelos, p. 10, pl. 3, figs. 2–4, 7, 8, 10, pl. 4, figs. 6, pl. 5, figs. 2, 7, 8
 ?1986a, *Quercus dubia* Knobloch et Velitzelos — Knobloch and Velitzelos, p. 11, pl. 3, fig. 1
 1990 *Quercus goeppertii* vel *kubinyi* — Gemici et al., p. 33
 1993 *Quercus drymeja* Unger — Gemici et al., p. 99, pl. 6, fig. 1
 1993 *Quercus* cf. *drymeja* Unger — Gemici et al., p. 99, pl. 7, figs. 1, 3
 1993 *Castanopsis* sp. — Gemici et al., p. 95, pl. 6, fig. 5
 1993 *Quercus* ex gr. *drymeja* Unger — Kvaček et al., p. 61, text fig. 4a, b, pl. 2, figs. 4–7, pl. 3, figs. 1–4
 1993 *Quercus drymeja* Unger — Schweigert, p. 66, pl. 2, fig. 5
 1994 *Quercus drymeja* Unger — Kleinhöfner, figs. 2, 6
 1996 *Quercus* cf. *drymeja* Unger — Knobloch and Kvaček, p. 52, pl. 7, figs. 1, 2, 5, pl. 8, figs. 4, 4a, pl. 9, fig. 7, pl. 15, fig. 9, text figs. 7, 8
 1997 cf. *Myrica* sp. — Schmitt and Butzmann, p. 59, pl. 3, figs. 7, 8
 2000 *Quercus drymeja* Unger — Fischer and Butzmann, p. 45, pl. 11, figs. 6–11, text-figs. 63–66
 2002 *Quercus drymeja* Unger — Kvaček et al., p. 66, pl. 10, figs. 8, 12, pl. 11, figs. 1–6, pl. 15, figs. 2, 7, pl. 30, figs. 5–6 (Vegora, Messinian).
 2003 *Quercus* cf. *ilex* L. — Martinetto, p. 96, pl. 3, fig. 10
 2004 *Quercus zoroastri* Unger — Kovar-Eder et al., p. 62, pl. 5, fig. 2
 2004 *Quercus sosnowskyi* Kolakovsky — Palamarev and Tsenov, p. 149, pl. 1, fig. 3, pl. 2, fig. 5, pl. 3, figs. 1, 2
 2004 *Quercus ilex fossilis* — Palamarev and Tsenov, p. 149, pl. 1, fig. 6
 2004 *Quercus drymeja* Unger — Palamarev and Tsenov, p. 150, pl. 2, fig. 3, pl. 3, figs. 3, 4
 2007 *Quercus* sp. — Zidianakis et al., p. 359, figs. 3a, 5q
 2010 *Quercus drymeja* Unger — Zidianakis et al., fig. 20
 2011 *Quercus* aff. *acrodonta* Seemen — Bozukov et al., p. 8, pl. 2, figs. 1, 2
 2011 *Quercus drymeja* Unger — Bozukov et al., p. 8, pl. 2, fig. 4
 2011 *Quercus sosnowskyi* Kolakovsky — Bozukov et al., p. 9, pl. 2, figs. 5, 6
 2013 *Quercus drymeja* Unger — Robles et al., p. 79, pl. 1, figs. 14, 15
 2014 *Quercus drymeja* Unger — Velitzelos et al., pl. 28, figs. 9, 10, pl. 29, figs. 1, 2

Lamina shape narrow lanceolate, oblong, narrow to broad elliptic; base acute to rounded, symmetrical or \pm asymmetrical; apex acute to acuminate; margin dentate or nearly entire; teeth regular, inconspicuously spinose with bristle-like extensions pointing towards apex; secondary veins irregularly spaced, simple or branched; intersecondary veins present; secondary veins departing from primary vein at steep to low angles.

Remarks: This MT is the most common among the *Quercus drymeja* morphotypes.

We included within this MT also leaves that slightly differ by more rigid dentition; similar leaves are commonly found in the East Asian *Q. engleriana* (e.g. Kolakovsky, 1964, pl. 24–26, as *Castanopsis* spp.). Modern plants of *Quercus engleriana* have, in addition, leaves with inconspicuously spinose leaf margin (Plate XIV, 4–8), as typical for this MT.

The distinct leaf morphology of this MT links it to four modern species of *Quercus* Group Ilex, *Q. floribunda* Wallich ex Lindley (junior syn. *Q. dilatata* Royle) from the Himalayan region (eastern Afghanistan to western Nepal; Plates XIII, XIV, 1), *Q. setulosa* Hickel et A.Camus (southern China, Laos, Thailand, Vietnam, Plate XIV, 2, 3), *Q. tarokoensis* Hayata (Taiwan), *Q. spinosa* subsp. *miyabei* (Hayata) A.Camus (syn. *Q. tatakaensis* Tomiya; Taiwan) and *Q. engleriana* Seemen (Assam, Tibet, southern China; Plate XIV, 4–6). Some leaves considered by Unger (1867) to belong to *Q. zoroastri* clearly fall within this MT while those figured by Unger (1852) and the neotype of this taxon selected by Kovar-Eder et al. (2004) do not (see below 3.2.1.4.).

Modern analogues: *Quercus floribunda* (syn. *Q. dilatata*), *Q. setulosa*, *Q. tarokoensis*, *Q. spinosa* subsp. *miyabei* (syn. *Q. tatakaensis*), and *Q. engleriana*.

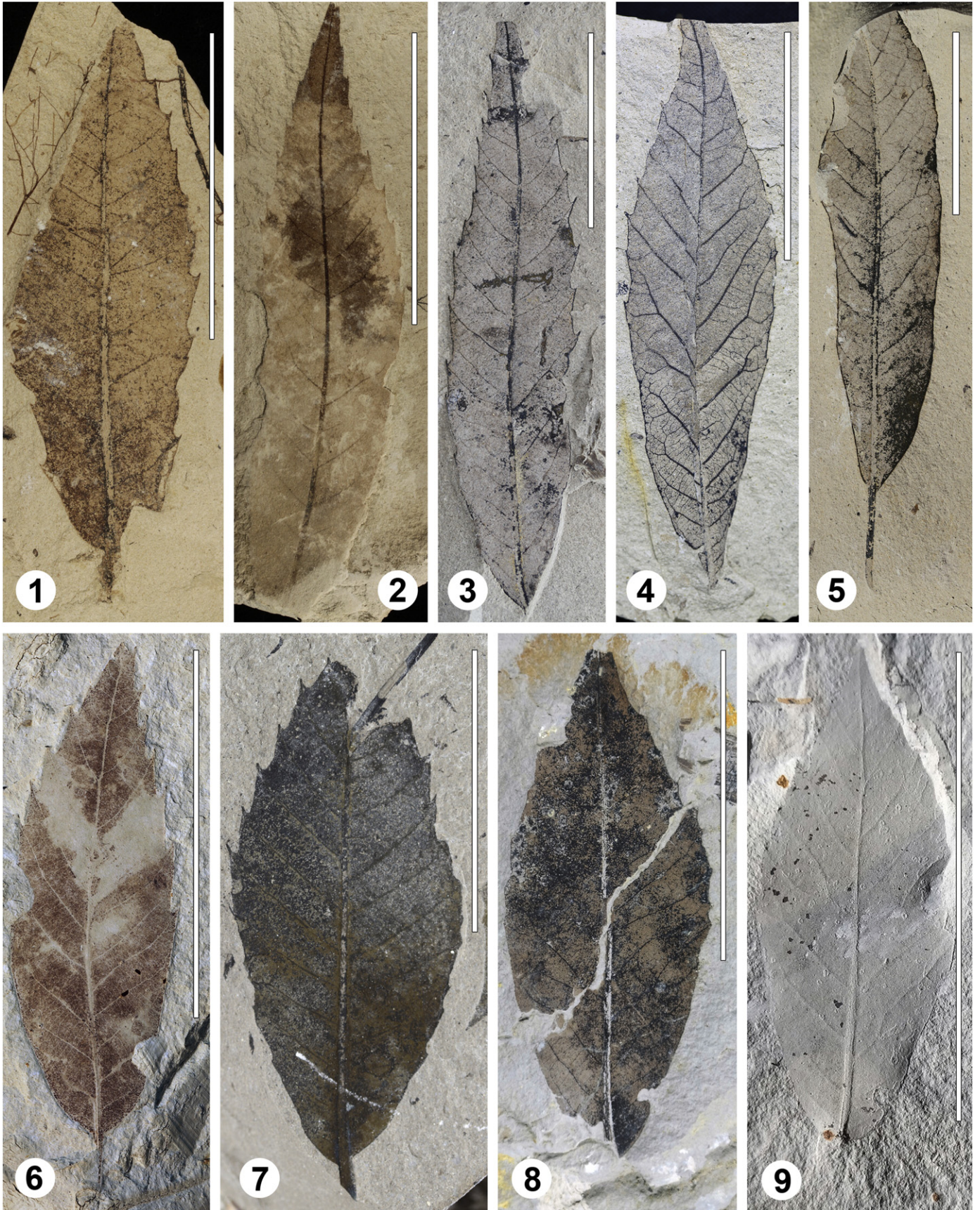


Plate IV. *Quercus drymeja* Unger, Floribunda Morphotype. Early to late Miocene. 1, 2. Güvem. 3–5, 7. Şahınlı. 6. Likoudi. 8. Salihpaşalar. 9. Tınaz. 1. UCMP Kasaplıgil 5550. 2. UCMP Kasaplıgil s.n. 3–5. ISTO-F s.n. 6. S116569. 7. ISTO-F s.n. 8. ISTO-F 01520. 9. ISTO-F 01239. Scale bar is 5 cm in 1, 2, 6, 8, 9; 3 cm in 3–5, 7.

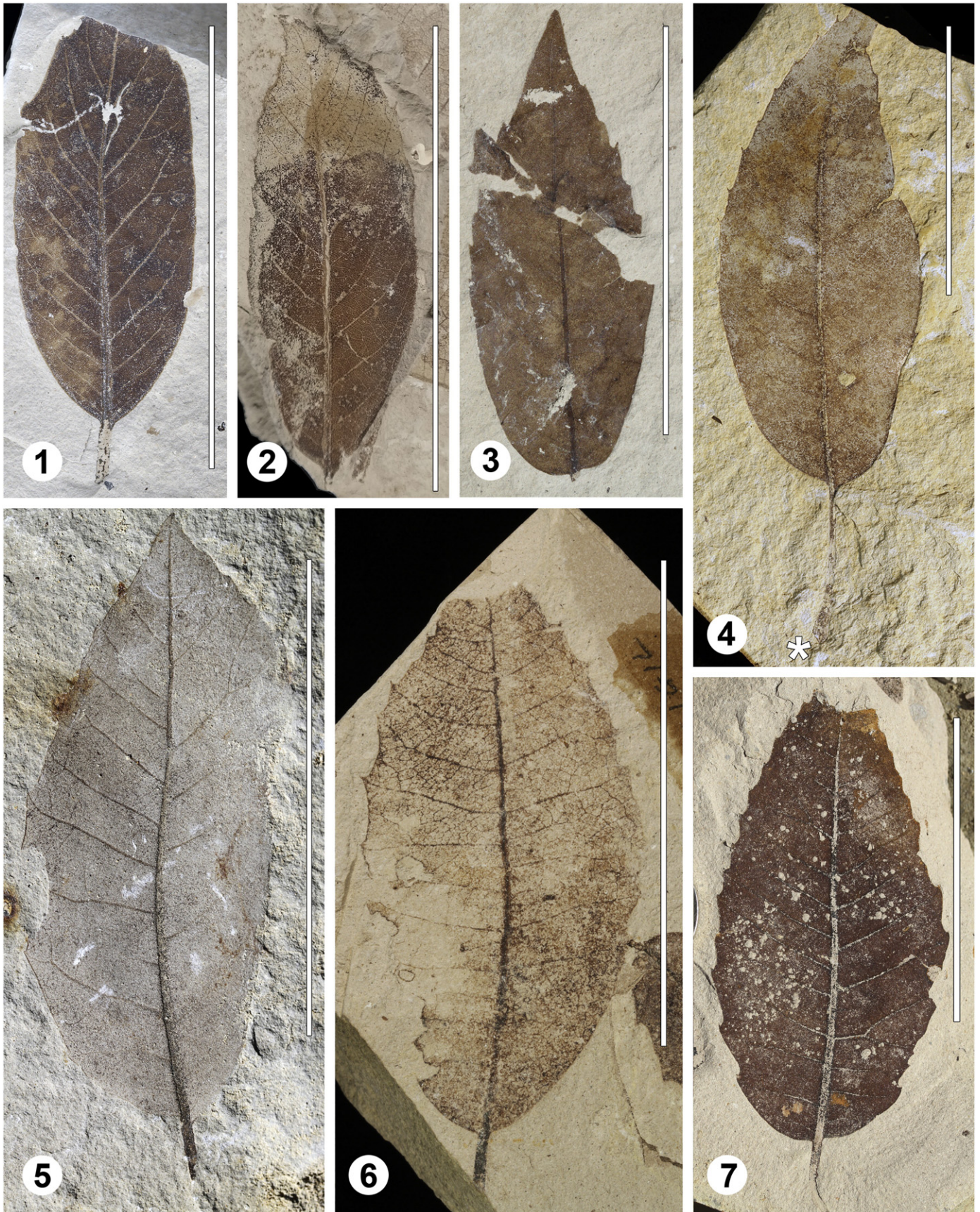


Plate V. *Quercus drymeja* Unger, Floribunda Morphotype. Early to late Miocene. 1–3. Salihpaşalar. 4. Likoudi. Asterisk denotes end of long petiole. 5. Soma. 6. Güvem. 7. Şahinalı. 1. ISTO-F 01866. 2. ISTO-F 01856. 3. ISTO-F 01494. 4. S116575. 5. ISTO-F s.n. 6. UCMP Kasapligil 5879. 7. ISTO-F s.n. Scale bar is 5 cm in 1–7.

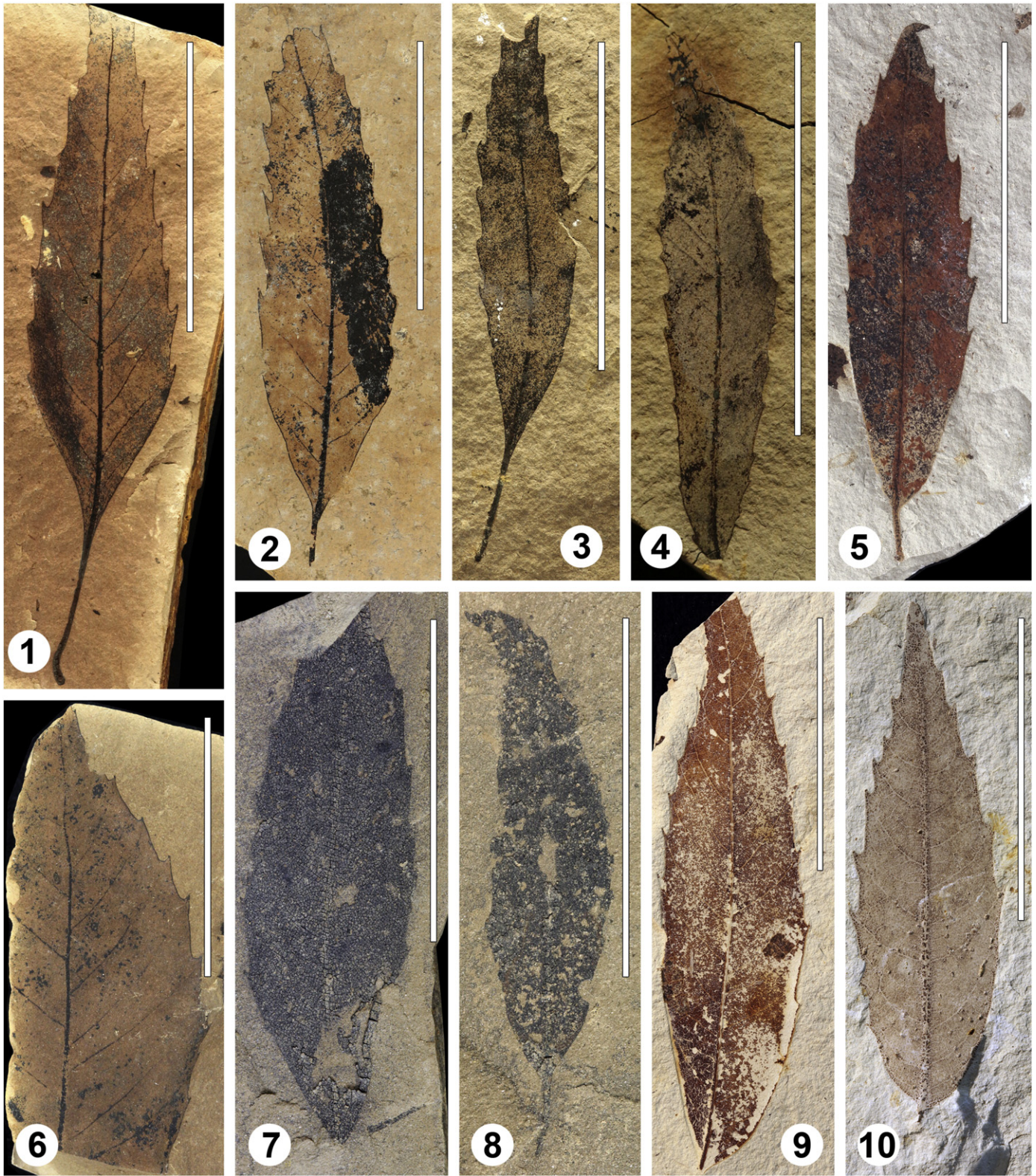


Plate VI. *Quercus drymeja* Unger, Parschlug Morphotype (MT). Middle and late Miocene. 1–4, 6. Parschlug. 5. Soma. 7, 8. Schaßbach. 9, 10. Şahinalı. 1. LMJ303. 2. GBA2002_040, figured in Kovar-Eder et al. (2004, pl. 4, fig. 4). 3. LMJ s.n. 4. NHM 9390. 5. ISTO_F s.n. 6. S133952, Floribunda MT. 7. SH073. 8. SH077. 9. S116564. 10. S116573. Scale bar is 3 cm in 1–10.

3.2.1.3. *Quercus drymeja* Parschlug Morphotype.

Plate VI (Parschlug, Soma, Schaßbach, Likoudi)

- 1847 *Quercus drymeja* Unger – Unger, p. 113, pl. 32, figs. 1, 2, 4, not fig. 3
- 1852 *Quercus gmelini* A.Braun – Unger, p. 36, pl. 18, fig. 10

- 1859 *Quercus drymeja* Unger – Gaudin and Strozzi, p. 44, pl. 4, fig. 1
- 1867 *Quercus lonchitis* Unger – Unger, p. 50, pl. 5, figs. 1, 2, 4–13, 16, 17
- 1887 *Quercus drymeja* Unger var. *ungeri* – Boulay, p. 258
- ?1952a *Quercus drymeja* Unger – Berger, p. 18, figs. 9, 10
- 1953 *Quercus drymeja* Unger – Berger, p. 144, fig. 7
- 1955a *Quercus drymeja* Unger – Berger, p. 409, figs. 10–12

1957b *Quercus drymeja* Unger — Berger, p. 21, pl. 4, figs. 70, 72–74
 ?1969 *Quercus* cf. *glaucofolia* Andreánszky — Givulescu and Ghiurca, p. 35, pl. 9, fig. 7

1997 cf. *Myrica* sp. — Schmitt and Butzmann, p. 59, pl. 4, fig. 2

1999a *Myrica drymeja* Unger — Barron, fig. 4d

?2002 *Quercus drymeja* Unger — Kvaček et al., p. 66, pl. 11, fig. 7

2004 *Quercus drymeja* Unger — Kovar-Eder et al., p. 61, pl. 4, figs. 1–7

?2004 *Quercus lonchitis* Unger — Palamarev and Tsenov, p. 150, pl. 1, fig. 4

Lamina shape narrow lanceolate to ovate lanceolate; base markedly cuneate to acute; apex acute to attenuate; margin dentate; teeth regular, spiny; secondary veins departing from primary vein at acute angles.

Remarks: This distinct MT is most typical of the Parschlug plant assemblage (Unger, 1841; Kovar-Eder et al., 2004; Plate VI, 1–4, 6). It is also common in Kimi (Unger, 1867). In Schaßbach (Plate VI, 7, 8), Valdarno (Gaudin and Strozzi, 1859), Soma (Plate VI, 5), and Likoudi (Plate VI, 9, 10) it is only rarely encountered.

Relationships of this MT with modern species are difficult to establish. Except for *Quercus* Group Ilex, leaf morphological similarities are also with extant species of Group Cyclobalanopsis, particularly with the Himalayan *Q. glauca* Thunberg in Murray. Secondary veins are, however, different in species of Group Cyclobalanopsis: vein spacing typically decreases towards the apex and secondary veins are more curved than in species of Group Ilex. Aside from this, no pollen of Group Cyclobalanopsis has been recovered from sediments of Kimi, and the characteristic cups with bracts arranged in concentric rings (“cycle-cup oaks”) are not known from the fossil record of western Eurasia (e.g. Mai, 1995). Among species of *Quercus* Group Ilex, the Himalayan species *Q. lanata* Smith in Rees and *Q. leucotrichophora* A.Camus (incl. *Q. incana* Roxburgh) are most similar to this MT (Plate XV).

Modern analogue: East Asian (Himalayan to Chinese) members of *Quercus* Group Ilex.

3.2.1.4. *Quercus drymeja* Zoroastri Morphotype.

Plate VII, 1–6 (Parschlug, Schaßbach, Likoudi)

1852 *Quercus zoroastri* Unger — Unger, p. 36, pl. 18, figs. 7, 8 not fig. 9

1955a *Quercus mediterranea* Unger — Berger, p. 408, fig. 8

1986a, *Quercus* cf. *drymeja* Unger “Group 2” — Knobloch and Velitzelos, p. 10, pl. 4, fig. 3

2004 *Quercus zoroastri* Unger — Kovar-Eder et al., p. 62, pl. 5, figs. 1, 3, 4

?2011 *Quercus* cf. *zoroastri* Unger — Kvaček et al., p. 30, pl. 6, figs. 12, 13

Lamina shape broad elliptic, rhombic, to ovate; with relatively wide base, basal part tapering into an elongate apical part; base bluntly acute, cuneate, to rounded; apex acute to acuminate; margin dentate along upper two thirds of lamina; teeth regular, coarse or spinose, basal side straight, apical side concave; occasionally subsidiary teeth; secondary veins departing from primary vein at acute angles.

Remarks: This MT is rarely found in specimens from Parschlug and Schaßbach. Specimens that match this morphotype are also present in Likoudi (Plate VII, 6). There are several transitions of such leaves to the Floribunda MT and to *Quercus mediterranea*. For example, the specimen from Parschlug figured in Plate VII, 1 has more bristle-like spinose teeth (Plate VII, 2 and the specimens figured in Unger, 1852) and approaches the Floribunda MT.

Quercus zoroastri was described in 1850 (Unger, 1850) and subsequently figured in various papers (e.g. Unger, 1852, 1867). In our opinion, the specimens figured by Unger (1867) from Kimi better match the Floribunda MT. Kvaček et al. (2011, pl. 6, figs. 12, 13) figured two leaves from Arjuzanx as *Q. cf. zoroastri*. These leaves differ from typical Zoroastri MT by hooked teeth, a comparatively higher number of secondary veins, and small lamina size. Similar dentition as in these latter specimens is sometimes seen in *Q. phillyreoides*. Further, the leaves from Arjuzanx ascribed to *Q. cf. zoroastri* are so similar in dentition to the specimens referred to as *Q. mediterranea* (Kvaček et al., 2011, plate 6, figs. 12, 13 [as cf. *zoroastri*], plate 6, fig. 16 [as *mediterranea*]) that

they might have originated from the same plant. Notably, a few specimens from Parschlug (e.g. Plate VIII, 11) appear to have similar dentition as well.

The morphological affinities of the Zoroastri MT might be the same as for the Floribunda MT. For example, extant *Q. engleriana* may have slender leaves with entire margin or bristle-like teeth, or broad leaves with coarse teeth (Plate XIV, 4–8). Hence, the Zoroastri MT might represent coarser leaves produced by the same plants as Parschlug and Floribunda MT leaves.

Modern analogue: *Quercus* Group Ilex or same as for Floribunda MT.

3.3. *Quercus mediterranea* Unger

Plate VII, 7, 8, VIII

1847 *Quercus mediterranea* Unger — Unger, p. 114, pl. 32, figs. 5–9

1852 *Quercus mediterranea* Unger — Unger, p. 35, pl. 18, figs. 1–6

1856 *Quercus szirmayana* Kováts — Kováts, p. 21, pl. 2, figs. 1–5

1867 *Quercus mediterranea* Unger — Unger, p. 52, pl. 6, figs. 1–22

1887 *Quercus mediterranea* Unger — Boulay, p. 259

1887 *Quercus coccifera* L. — Boulay, p. 259

?1896 *Quercus gaudinii* Lesquereux — Sordelli, p. 128, pl. 20, fig. 9

1903 *Ilex ambigua* Unger — Engelhardt, p. 63, pl. 7, fig. 19

1936 *Quercus mediterranea* Unger — Pop, p. 70, pl. 17, fig. 3

1936 *Quercus* cf. *ilex* L. — Pop, p. 71, pl. 2, fig. 4, pl. 3, fig. 5, pl. 17, figs. 4–7

1953a *Quercus mediterranea* Unger — Berger, p. 144, fig. 8

1955b *Quercus* cf. *mediterranea* Unger — Berger, p. 76, figs. 9–11

1957b *Quercus mediterranea* Unger — Berger, p. 33, pl. 11, figs. 155–164

1967 *Quercus mediterranea* Unger — Kolakovsky and Ratiani, pl. 4, figs. 2–4

1969 *Quercus mediterranea* Unger — Givulescu and Ghiurca, p. 38, pl. 9, fig. 9

?1969 *Quercus* cf. *ilex* L. — Givulescu and Ghiurca, p. 38, pl. 17, figs. 13a, b

1976 *Quercus mediterranea* Unger vel *Castanea* sp. — Knobloch and Kvaček, p. 42, pl. 21, fig. 7, pl. 30, fig. 10

1981 *Quercus mediterranea* Unger — Paicheler and Blanc, pl. 9, figs. 4–11

1986a *Quercus* cf. *mediterranea* Unger — Knobloch and Velitzelos, p. 11, pl. 2, fig. 5

1986b *Quercus* cf. *mediterranea* Unger — Knobloch and Velitzelos, p. 30, pl. 14, figs. 4, 11, pl. 15, fig. 7

1990 *Quercus ilex* L. — Gemici et al., p. 33, fig. 3c

1991 *Quercus mediterranea* Unger — Gemici et al., p. 173, pl. 9, fig. 6

1993 *Quercus mediterranea* Unger — Gemici et al., p. 99

1993 *Quercus mediterranea* Unger — Kvaček et al., p. 62, pl. 3, figs. 5–7, pl. 8, fig. 4, text figs. 4c–g

1993 *Quercus mediterranea* Unger — Schweigert, p. 67, pl. 2, fig. 2

1994 *Quercus mediterranea* Unger — Kleinhöfner, p. 265

1997 cf. *Quercus* sp. — Schmitt and Butzmann, p. 59, pl. 2, fig. 11

2002 *Quercus mediterranea* Unger — Kvaček et al., p. 65, pl. 10, figs. 7, 9–11, pl. 31, figs. 1, 2

2004 *Quercus mediterranea* Unger — Kovar-Eder et al., p. 62, pl. 4, figs. 8–16

2004 *Quercus mediterranea* Unger — Palamarev and Tsenov, p. 149, pl. 1, fig. 5

2007 *Quercus mediterranea* Unger — Zidianakis et al., p. 358, figs. 2h–k, 5j

2010 *Quercus mediterranea* Unger — Zidianakis et al., fig. 2m

2011 *Quercus mediterranea* Unger — Kvaček et al., p. 32, pl. 6, figs. 14–17

2014 *Quercus mediterranea* Unger — Velitzelos et al., pl. 25, fig. 13

?2014 *Quercus* aff. *mediterranea* Unger — Velitzelos et al., pl. 28, fig. 11

2015 *Quercus mediterranea* Unger — Teodoridis et al., pl. 261, pl. 7, figs. 7–9

Leaves petiolate, petiole stout, ≤1 cm long; lamina up to 6 cm long, lamina shape ovate, roundish-obovate, elliptical, or inverted pear-shaped; base acute to round to cordate; apex acute to acuminate; primary vein stout, becoming slightly thinner towards apex; leaf margin entire or dentate; teeth conspicuous or inconspicuous, occasionally ending in bristle-like spine or almost reduced to spine, basal side

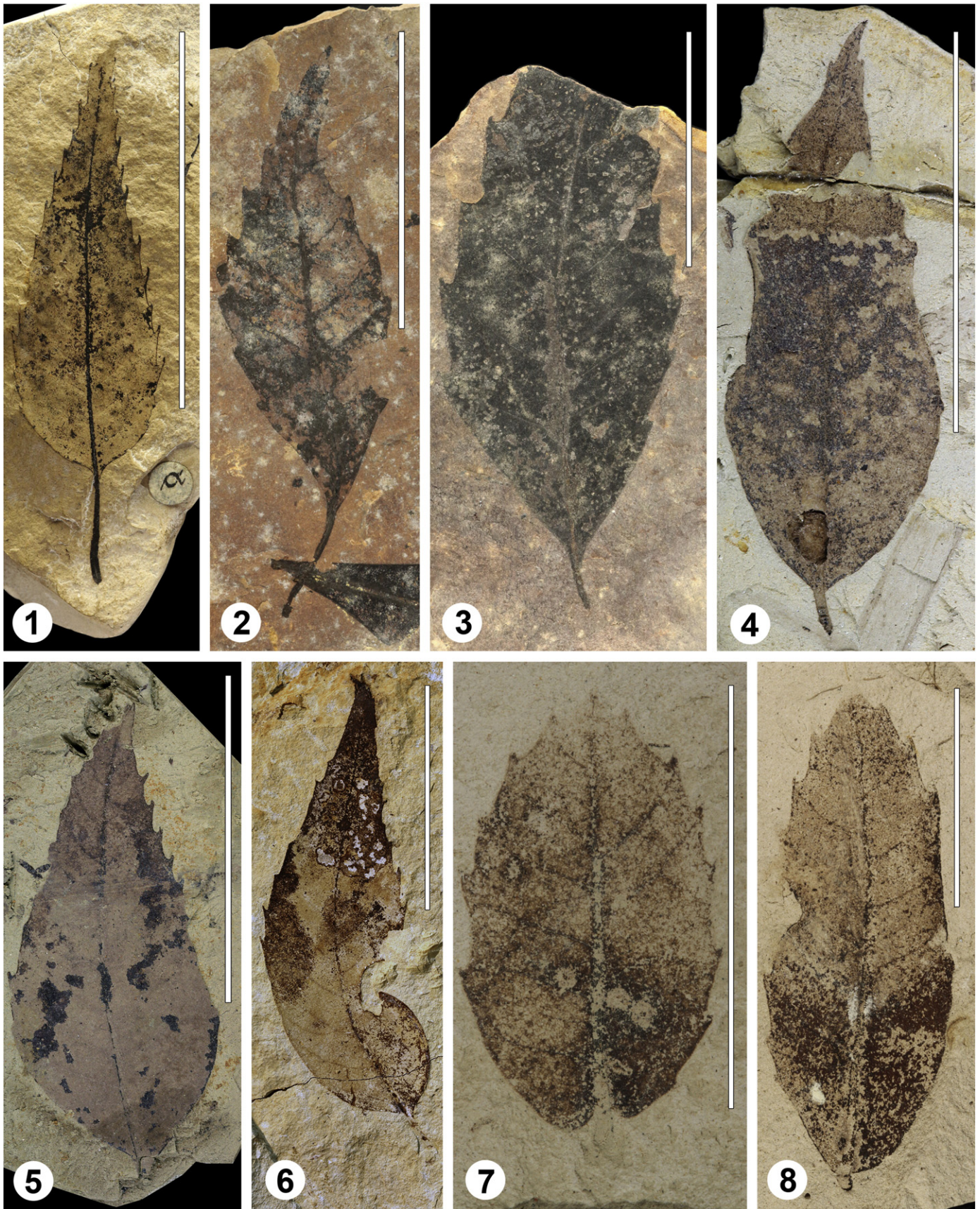


Plate VII. 1–6. *Quercus drymeja* Zoroastri morphotype. 7–8. *Quercus mediterranea* Unger. 1. Parschlug, LMJ76866, figured in Kovar-Eder et al. (2004, pl. 5, fig. 2). Note that this leaf is very similar to some specimens assigned to *Quercus drymeja* Floribunda morphotype. 2. Parschlug, GBA2002_042, figured in Kovar-Eder et al. (2004, pl. 5, fig. 4). 3. Parschlug, GBA s.n. 4. Schaßbach, SH060A. 5. Schaßbach, SU_LAV3685. 6. Likoudi, S116551, very similar to specimens assigned to Floribunda MT. 7. Güvem, UCMP Kasapligil 6061. 8. Güvem, UCMP Kasapligil 6076. Scale bar is 5cm in 1, 6; 3 cm in 2–5; 2 cm in 7–8.

straight, sigmoid, or convex, apical side concave; secondary veins regularly or irregularly spaced, departing from primary vein at low to steep angles, usually vein angle increasing towards base; secondary venation craspedodromous and semicraspedodromous to camptodromous (close to the leaf base), secondary venation camptodromous in entire margined leaves; tertiary veins mixed opposite/alternate percurrent, more or less perpendicular to secondary veins except for close to the primary vein, where they are bent and inserting the primary vein at right angles, fourth order venation alternate percurrent, areolation well developed, 4-sided to polygonal, freely ending ultimate veins unbranched.

Remarks: Specimens of *Quercus mediterranea* are morphologically fairly stable throughout the Neogene of western Eurasia. Compared to *Q. drymeja*, the morphological variability among specimens of *Q. mediterranea* across western Eurasia shows a weaker spatial or temporal pattern. The leaf types encountered in *Quercus mediterranea* are very similar to those seen in a number of modern species of *Quercus* Group Ilex (cf. Plate VII, 7, 8, VIII versus Plates IX, XVI, XVII).

Particular leaf types, such as the inverted pear-shaped one (Plate VIII, 1–4, Güvem, Şahımalı, Parschlug, Soma), are encountered in various modern species (e.g. Plate XVI, 6, *Q. acrodonta*, 7, *Q. cocciferoides*, 11, *Q. franchetii*). Distinctly spiny leaves as encountered in Salihpaşalar (Plate VIII, 15–17) occur in small leaves of the Himalayan *Q. floribunda* (Plate XVII, 3, 4). Some specimens of *Q. mediterranea* (e.g. Unger, 1852, pl. 18, 1) are markedly similar to modern leaves of *Q. ilex* (Plate IX, 2) and *Q. coccifera* (Plate XVI, 9).

Modern analogue: Miocene and Pliocene, *Quercus* Group Ilex; latest Pliocene (?) and Pleistocene, *Q. aucheri*, *Q. coccifera*, and *Q. ilex*.

3.4. *Quercus* Group Ilex: fossil vegetation context

In Oligocene deposits of western Eurasia, the sclerophyllous *Quercus* Group Ilex is only represented by pollen (Denk et al., 2012). The palynoflora of Cospuden (Germany) reflects lowland swamp forests and well-drained lowland and upland forests in a humid warm temperate climate (Cf, Cw climate types according to the Köppen-Geiger climate classification; for explanation of all climate types mentioned in the text see Kottek et al., 2006, and Peel et al., 2007). Genera of Aquifoliaceae, Araliaceae, Arecaceae, Juglandaceae, Mastixioideae, Oleaceae, Rubiaceae, Rutaceae, Sapotaceae, Simaroubaceae, Sterculioideae, Styracaceae, and Symplocaceae, among others, belong to humid warm temperate and subtropical lineages. Ericaceae were diverse (Denk et al., 2012). Oligocene leaf fossils assigned to *Quercus* Group Ilex from Yunnan, China, were part of broadleaved evergreen forests with dominance of oaks in a “subtropical, warm, wet climate” (Liu et al., 1996). There is, however, no conclusive evidence that these leaf remains indeed belong to *Quercus* Group Ilex (see below, Section 4.2).

Several localities with abundant sclerophyllous oaks of *Quercus* Group Ilex are known from the early Miocene of western Eurasia. Kvaček et al. (1993) described an early Miocene leaf assemblage from Bosnia dominated by riparian elements (*Glyptostrobus*, *Alnus*, *Myrica*). Among plants of well-drained soils, *Quercus drymeja* is the most abundant, followed by *Q. mediterranea* and *Fagus*. The latter is an inclusive indicator of fully humid, subtropical or temperate climates with warm or hot summers (Cfa, Cfb, Dfb). Similarly, the roughly coeval flora of Kimi (Greece) is dominated by riparian *Alnus* and *Myrica* with *Quercus drymeja* and *Q. mediterranea* being most abundant among plants of well-drained soils. *Fagus* is moderately abundant in the flora of Kimi (Unger, 1867; Velitzelos, 2002). The early Miocene flora of Güvem (Anatolia; this study; T. Denk, unpublished data) is dominated by *Quercus*

drymeja with minor contributions of *Q. mediterranea* and *Fagus*. Among riparian elements, *Acer* and *Myrica* are very abundant (Paicheler and Blanc, 1981). *Quercus drymeja* and *Q. mediterranea* are rare or absent in early Miocene assemblages of southern France (Mai, 1995) and on the Greek islands of Lemnos and Lesbos (Velitzelos et al., 2014). These assemblages are possibly representing subtropical lowland stands with palms playing an important role.

Middle Miocene floras containing various amounts of sclerophyllous oaks have been interpreted as representing swamp and riparian forests with Taxodioideae, and humid (*Fagus*) and subhumid mesophytic forests (sclerophyllous oaks; e.g. Şahımalı, Yatağan Basin, Gemici et al., 1990, 1993; Akgün et al., 2007; Parschlug, Lavanttal, Berger, 1955a; Kovar-Eder et al., 2004). Local expansion of subhumid sclerophyllous forests in the Paratethyan region was attributed to high summer mean temperatures and dry edaphic conditions (Kvaček et al., 2006; see also Rögl, 1999). Late Miocene and early Pliocene plant assemblages with abundant sclerophyllous oaks are commonly also rich in *Fagus* and have been interpreted as mesophytic forests (Kolakovsky, 1964; Knobloch and Velitzelos, 1986a, 1986b; Fischer and Butzmann, 2000; Kvaček et al., 2002; Velitzelos et al., 2014). Overall, this suggests that sclerophyllous oaks of *Quercus* Group Ilex occurred in humid subtropical forests during the Oligocene and early Miocene, and in humid temperate forests during the middle and late Miocene and Pliocene.

3.5. Modern analogues of *Quercus drymeja* and *Q. mediterranea*: vegetation context

Closest morphological similarities of *Quercus drymeja* were encountered with the modern species *Q. floribunda* (syn. *Q. dilatata*), *Q. setulosa* (incl. *Q. laotica*), *Q. engleriana*, *Q. tarokoensis*, and with *Q. lanata* and *Q. leucotrichophora* (all members of *Quercus* Group Ilex).

These species are mainly distributed south of the Himalayas (*Q. floribunda*) to China and Southeast Asia (*Q. lanata*, *Q. leucotrichophora*). *Quercus engleriana* is widespread in southwestern China, south-central China and eastern China (Huang et al., 1999; Menitsky, 2005), *Q. tarokoensis* and *Q. spinosa* subsp. *miyabei* (syn. *Q. tatakaensis*) are endemic species of Taiwan, and *Q. setulosa* occurs in southern China, Laos, Thailand and Vietnam (Table 4).

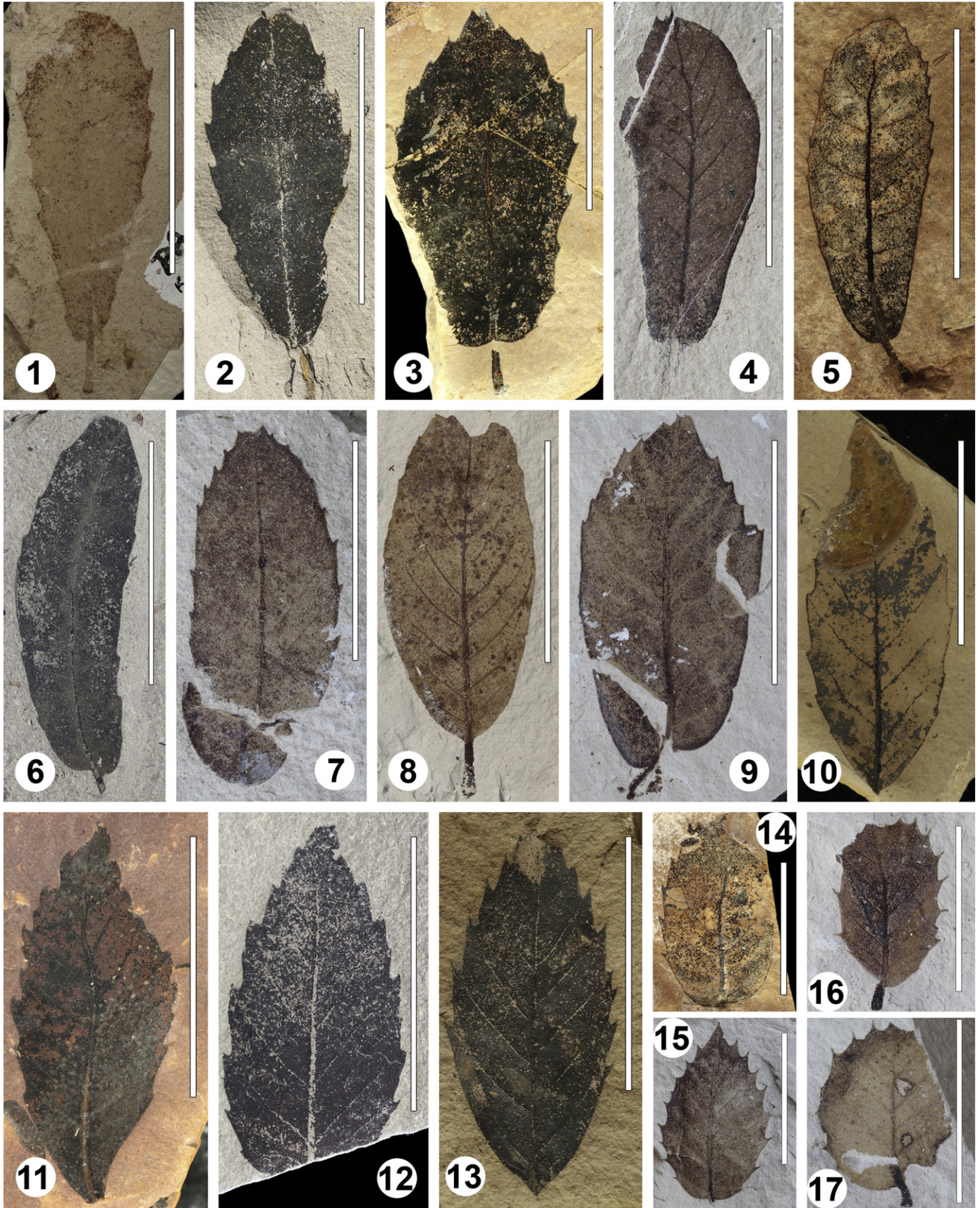
Quercus floribunda dominates or forms part of mesophytic forests in regions with sufficient or high amounts of summer precipitation and annual precipitation between 800 and 1200 mm (Afghanistan; Freitag, 1972) and to 3000 mm (India, Nepal; Menitsky, 2005). Co-occurring tree species in eastern Afghanistan belong to the genera *Pinus*, *Cedrus*, *Acer*, *Celtis*, and *Juglans*; a rich shrub layer comprises species of *Viburnum*, *Syringa*, *Lonicera*, *Rhamnus*, and others (Supplementary Information, Table SI 2). In northern India (Kangra) and Nepal, *Quercus floribunda* occurs in the montane vegetation belt, between ca. 1500 and 2400 m. Annual precipitation ranges from ca. 1000 to 3000 mm. The climate is a warm temperate summer-wet climate (Cfa, Cwa, Cwb). At its lower vertical distribution *Q. floribunda* co-occurs with *Q. lanata*, large-leaved *Rhododendron*, *Lyonia* (Ericaceae), *Myrica* (Myricaceae), *Litsea*, *Machilus* (Lauraceae), *Symplocos* (Symplocaceae), and *Rhus* (Anacardiaceae). Higher up, oak-conifer forests comprise *Pinus*, *Cedrus*, *Abies*, *Cupressus*, and *Acer* spp., *Betula*, *Lonicera*, *Myrsine*, *Olea*, *Populus*, *Rhus*, and *Viburnum* (Menitsky, 2005; Schroeder, 1998; Table SI 2).

While *Quercus lanata* and *Q. floribunda* may form pure stands or be accessory elements in mixed broadleaved and conifer forests, *Q. engleriana* is an accessory element in mixed mesophytic forests of China under a fully humid Cfa or summer-wet Cwa climate (Table SI

Plate VIII. *Quercus mediterranea* Unger. 1–4. Inverted pear-shaped leaves. 1. Güvem, UCMP Kasapligil 6066. 2. Şahımalı, ISTO-F s.n. 3. Parschlug, LMJ76507, figured in Unger (1852, pl. 18 fig. 1), Kovar-Eder et al. (2004, pl. 4, fig. 10). 4. Soma, ISTO-F s.n. 5. Parschlug, LMJ79517. 6. Şahımalı, ISO-F s.n. 7. Salihpaşalar, ISTO-F 01482. 8. Salihpaşalar, ISTO-F 01514. 9. Salihpaşalar, ISTO-F 01490. 10. Parschlug, NHM 9370. 11. Parschlug, GBA2002_019, note coarse, hooked teeth; similar forms are known from middle(?) Miocene deposits of Arjuzanx, SW France (Kvaček et al., 2011). 12. Soma, ISTO-F s.n. 13. Parschlug, NHM 9381, figured in Kovar-Eder et al. (2004, pl. 4, fig. 15). 14. Parschlug, LMJ76524B. Lectotype of *Quercus mediterranea* (Unger, 1847, pl. 32, fig. 1; Kovar-Eder et al., 2004, pl. 4, fig. 8). 15. Salihpaşalar, ISTO-F 01483. 16. Salihpaşalar, ISTO-F 01481. 17. Salihpaşalar, ISTO-F 01526. Scale bar is 3 cm in 1–6, 8–13; 2 cm in 7, 14–17.

3). These forests comprise temperate and a few subtropical elements. Typically, species of *Fagus* and *Cathaya* along with diverse Lauraceae are found. Overall, these forests share a number of taxa with Oligocene

western Eurasian forests with *Quercus* Group *Ilex* (Denk et al., 2012; see above: *Cathaya*, *Ilex*, Araliaceae, Ericaceae, *Rhododendron*, *Symplocos*, *Zanthoxylum*) and with early Miocene floras (e.g. diverse Lauraceae).



Quercus tarokoensis is part of montane evergreen sclerophyllous forests in eastern Taiwan (Song and Xu, 2003) where it co-occurs with another sclerophyllous oak of *Quercus* Group Ilex, *Q. spinosa* David. The climate in this area is distinctly warm temperate and fully humid (Cfa, Cfb climates). Similarly, *Quercus spinosa* subsp. *miyabei* (syn. *Q. tatakaensis* Tomiya) forms part of montane laurophyllous forests in eastern and central Taiwan (Yang et al., 2008). Also here, the climate is distinctly temperate (Cfb).

Quercus setulosa grows in the montane vegetation belt above tropical monsoon forests. Drier forests including this species are pine-oak forests with Poaceae in the understorey. Wet subtropical forests are mixed evergreen-deciduous forests with ferns and epiphytes; they commonly occur along rivers. Oaks co-occur with subtropical tree species of Theaceae, Styracaceae, Magnoliaceae, Myrtaceae, Juglandaceae (*Engelhardia*), and Rutaceae, and with temperate species of Betulaceae (*Carpinus*) and Ericaceae (*Rhododendron*, *Vaccinium*; Menitsky, 2005; Table SI 4). The predominating climate is a tropical monsoon climate type, Aw, and a warm temperate monsoon climate type, Cwa.

In addition, a number of modern species that typically produce medium sized to small leaves can specifically be compared with *Quercus mediterranea*. Among these are the modern Mediterranean species *Q. coccifera*, *Q. ilex*, and *Q. aucheri* (see Plate IX and Plate XVI, 9, for modern leaves closely matching *Q. mediterranea*). Further, a number of Himalayan and East Asian species produce leaves similar to the fossil-species *Quercus mediterranea* (Plates XVI, XVII). It is, however, noteworthy that in assemblages that contain both *Quercus drymeja* and *Q. mediterranea*, most leaves assigned to *Q. mediterranea* might represent small leaves of the same plants that produced the leaves of *Q. drymeja*. This suggests that the entities *drymeja* and *mediterranea* may in many cases have been produced by the same plants.

4. Discussion

4.1. Taxonomic affinity and phylogenetic context of sclerophyllous oaks in the Neogene of western Eurasia

Previous authors have suggested close relationships of *Q. drymeja* with New World representatives of *Quercus* Group Quercus (white oaks) and Group Lobatae (red oaks; Table 3). Such relationships can be rejected based, firstly, on leaf morphological grounds: extant New World species although resembling *Q. drymeja* display a different range of leaf variability only marginally overlapping with that of *Q. drymeja* (see below). Further, in the few cases, where leaf cuticles were preserved (e.g. Gotse Delchev Basin, late Miocene, Palamarev and Tsenov, 2004; Vegora, late Miocene, Arjuzanx, middle Miocene, Kvaček et al., 2002, 2011), closest similarities of the leaf epidermis was found with modern species belonging to *Quercus* Group Ilex (see Deng et al., 2017). Secondly, early Miocene localities with abundant *Q. drymeja* yield abundant dispersed pollen of *Quercus* Group Ilex but none of Group Quercus/Lobatae (supplementary information, Plates SI I, SI II). For similar reasons, closer similarities with modern *Quercus* Group Cyclobalanopsis (cycle cup oaks) as suggested by e.g. Kolakovsky (1964) can be rejected. The characteristic cups of cycle-cup oaks have never been found in western Eurasian Cenozoic sediments (Mai, 1995). Also pollen of *Quercus* Group Cyclobalanopsis has never been encountered in western Eurasia (own observations). Thus, we here consider *Q. drymeja* and *Q. mediterranea* to belong to *Quercus* Group Ilex.

Quercus drymeja and *Q. mediterranea* have been compared to extant species of five of the six infrageneric groups within *Quercus* (Table 3). Knobloch and Velitzelos (1986a) compared *Q. drymeja* with the East Asian *Q. serrata* Thunberg (*Quercus* Group Quercus) and *Q. setulosa* (Group Ilex). *Quercus serrata* may have narrow elliptical leaves with lobes that approach dentitions (subsp. *serrata*). However, these leaf

shapes are commonly co-occurring with broad-obovate lobed leaves; the lobes typically end in a prominent glandular tip. *Quercus serrata* belongs to deciduous white oaks (Menitsky, 2005; Denk and Grimm, 2010) that do not possess prominent compound trichome bases. Among North American white oaks, a number of (evergreen) species are somewhat similar to *Q. drymeja* (*Q. arizonica* Sargent, *Q. corrugata* Hooker, *Q. germana* Schlechter et Chamisso, *Q. tamaiapensis* C.H.Muller, and *Q. vicentensis* Trelease). These species differ from *Q. drymeja* by much coarser dentition and generally broader laminae. However, single specimens of *Q. drymeja* are closely similar with these New World white oaks. Based on palynological evidence, also in this case, it appears more likely that these leaves belong to *Quercus* Group Ilex or Group Cerris and that gross morphological similarities are the result of convergent evolution in leaves of distantly related oak lineages.

Kvaček et al. (2002), although noting that *Q. mediterranea* and *Q. drymeja* do not differ significantly in leaf epidermal features, suggested the deciduous red oak *Q. xalapensis* (incl. *Q. sartorii*; *Quercus* Group Lobatae) as modern analogue for *Q. drymeja*. *Quercus xalapensis* has narrow elliptical to obovate leaves with bristle-like teeth. As in many red oaks, these leaf shapes co-occur with such ones with asymmetrical, broad apical parts of the lamina with prominent teeth (lobes ending in long bristles) never met in *Q. drymeja* leaf assemblages. Similar leaf shapes and patterns of leaf variability are found in several red oaks (*Q. depressa* Humboldt et Bonpland, *Q. eduardii* Trelease, *Q. flocculenta* C.H.Muller, *Q. galeanensis* C.H.Muller, *Q. hypoxantha* Trelease). These species typically have bristle-like teeth and their range of leaf variability commonly includes lobed leaves. Although a few fossil leaves from GÜvem are fairly similar to some of the leaves encountered in these modern species, they are by no means representative. In a later study, Kvaček et al. (2011) suggested *Q. coccifera* as modern analogue for both *Q. mediterranea* and *Q. drymeja*.

Overall, it is remarkable that Unger's (1841, 1850) original concept of *Q. xalapensis* (incl. *Q. sartorii*) and *Q. lancifolia* being closely related to *Q. drymeja* has been adopted by many subsequent authors (Table 3). In contrast, only few studies suggested closer relationships with *Quercus* Group Cyclobalanopsis, the evergreen oaks of the monsoonal parts of tropical and subtropical East Asia. *Quercus mediterranea* was considered to be more closely related with the modern *Q. coccifera* by most authors, and this relationship was later supported by leaf epidermal characteristics (Kvaček et al., 2002, 2011). Most of the studies listed in Table 3 compared *Q. mediterranea* with Mediterranean species of *Quercus* Group Ilex. A few exceptions are the studies by Sordelli (1896), Paicheler and Blanc (1981), Knobloch and Velitzelos (1986a), and Bozukov et al. (2011), which suggested relationships also with East and Southeast Asian members of *Quercus* Group Ilex.

Quercus drymeja and *Q. mediterranea* represent two extremes of a morphological cline, recognized at the inter-specific but also intra-specific level in their potential modern analogues of *Quercus* Group Ilex (according to Denk and Grimm, 2010; Menitsky, 2005). Long and slender leaves commonly co-occur with small, roundish to elliptical leaves in the same species (e. g. Plates XIII, XIV versus XVII, *Q. floribunda*, and Plates IX versus X, *Q. ilex*). A few modern species of *Quercus* Group Ilex exclusively have small, *mediterranea*-like, leaves. These are typically found at high elevations from Afghanistan to south-western China (e.g. *Quercus semecarpifolia* Smith, *Q. guyavifolia* Léveillé, *Q. rehderiana* Handel-Mazzetti, *Q. senescens* Handel-Mazzetti; *Q. monimotricha* (Handel-Mazzetti) Handel-Mazzetti) and in the fully Mediterranean species *Q. aucheri* and *Q. coccifera*. Based on the modern situation, we have to consider that the two fossil-taxa *Quercus drymeja* and *Q. mediterranea* represent different (two or more) biological species in some assemblages, and a single species in others. Aside from this, they clearly fall within the range of the well-circumscribed *Quercus* Group Ilex (leaf morphology, pollen morphology; Kvaček et al., 2002; Menitsky, 2005; Denk and Grimm, 2009; Denk et al., 2010; Denk and Tekleva, 2014; Deng et al., 2017).

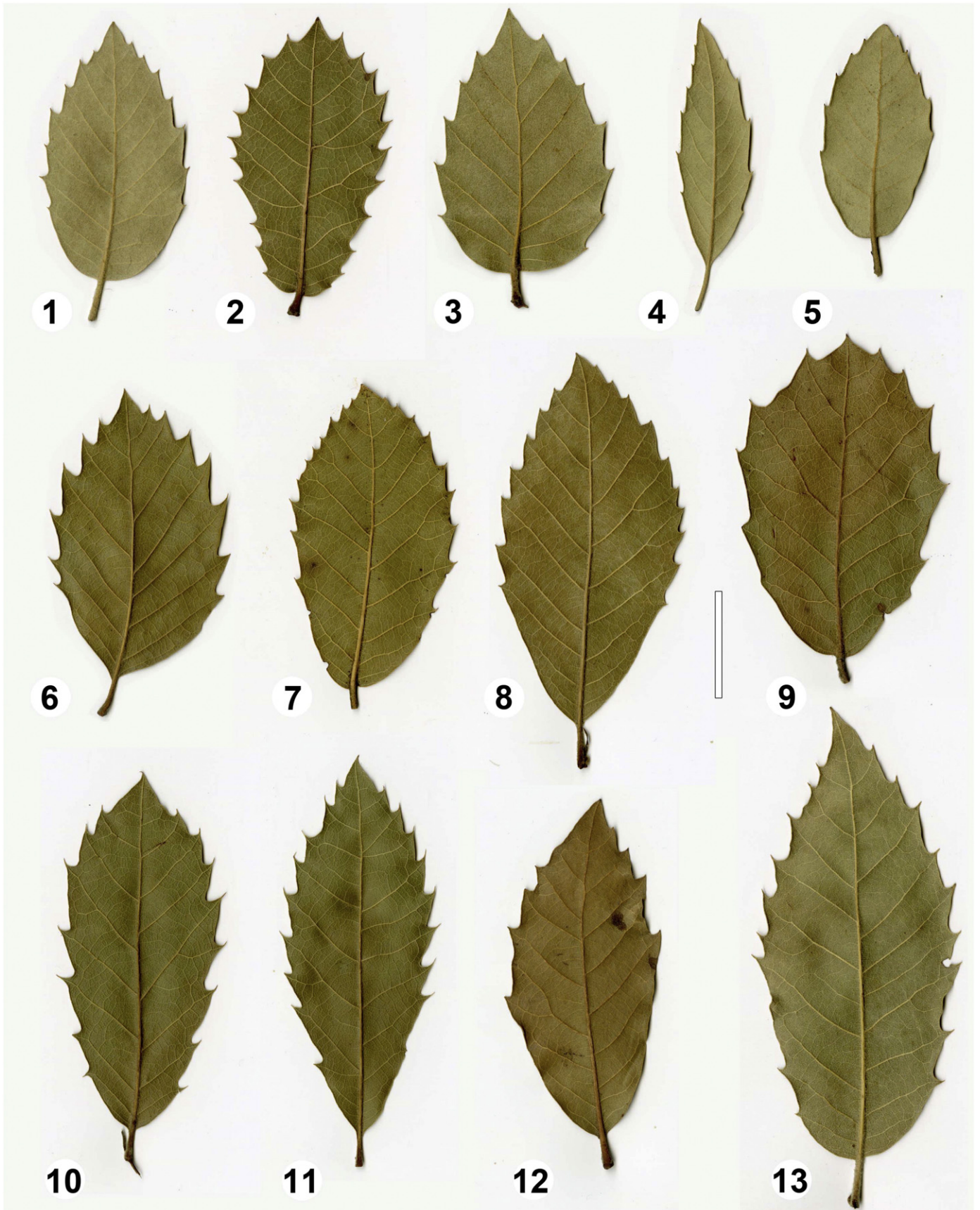


Plate IX. Extant *Quercus ilex* L. Litter sample, Katerini to Mt. Olympos, above Vrontou, Greece. 1–13. Leaves matching *Quercus mediterranea*. Scale bar is 2 cm in 1–13.

Table 3
Inferred modern analogues (nearest living relatives, NLR) for *Q. drymeja* ([D], including *Q. zoroastri*, [Z]) and *Q. mediterranea* [M]. Sorted chronologically after year of publication. Cerris, Cyclobalanopsis, Ilex, Lobatae, Quercus refers to infrageneric groups in *Quercus* recognized in molecular phylogenies and morphology (Denk and Grimm, 2009, 2010).

Reference	Taxon (D, M)	NLR Cerris	NLR Cyclobalanopsis	NLR Ilex	NLR Lobatae (red oaks)	NLR Quercus (white oaks)
Unger, 1841, 1850	D M	<i>Q. persica</i> Jaubert et Spach (= <i>Q. brantii</i> Lindley) (Z), <i>Q. libani</i> Olivier (D)		<i>Q. pseudococcifera</i> Desfontaine (= <i>Q. coccifera</i> L.) (M)	<i>Q. calophylla</i> Schlechter et Chamisso (= <i>Q. candicans</i> Née) (Z), <i>Q. xalapensis</i> Humboldt et Bonpland (D)	<i>Q. lancifolia</i> Schlechter et Chamisso (D)
Kováts, 1856	D M			<i>Q. alnifolia</i> Poech (M), <i>Q. ilex</i> L. (D)		
Massalongo and Scarabelli, 1859	D M			<i>Q. pseudococcifera</i> (M)	<i>Q. xalapensis</i> (D)	
Unger, 1867	D M	<i>Q. persica</i> (= <i>Q. brantii</i>) (Z)		<i>Q. pseudococcifera</i> (M)		<i>Q. lancifolia</i> (D)
Sordelli, 1896	D M	Section <i>Cerris</i> (D)		<i>Coccifera</i> group (D), <i>Q. ilex</i> (D, M), <i>Q. phyllireoides</i> A. Gray (D), section <i>Cerris</i> (D) <i>Q. ilex</i> (D), <i>Q. pseudococcifera</i> (M)	<i>Q. sartorii</i> Liebmann (D)	<i>Q. lancifolia</i> (D)
Engelhardt, 1903	D M					
Depape, 1928; Arènes and Depape, 1956	D	<i>Q. chinensis</i> Bunge (= <i>Q. variabilis</i> Blume)			<i>Q. sartorii</i> , <i>Q. xalapensis</i>	<i>Q. serrata</i> Thunberg, <i>Q. lancifolia</i>
Pop, 1936	M			<i>Q. coccifera</i>		
Berger, 1952a	D		[<i>Q. turbinata</i> Blume (= <i>Q. gemelliflora</i> Blume)]			Berger meant <i>Q. turbinata</i> Liebmann (= <i>Q. polymorpha</i> Schlechter et Chamisso)
Berger and Zabusch, 1952	D M			<i>Q. ilex</i> (M)		
Berger, 1953a	D M	<i>Q. suber</i> L. (M)		<i>Q. coccifera</i> (M), <i>Q. ilex</i> (M)		
Berger, 1952b, 1955b	D M			<i>Q. ilex</i> (M)		
Berger, 1955a	D M			<i>Q. ilex</i> (M)	<i>Q. xalapensis</i> (D)	<i>Q. turbinata</i> (= <i>Q. polymorpha</i>) (D)
Berger, 1957a	D				“Various evergreen oaks of S North America”	“Various evergreen oaks of S North America”
Berger, 1957b	D M		<i>Q. turbinata</i> (= <i>Q. gemelliflora</i>) (D), <i>Q. glauca</i> Thunberg (D)	<i>Q. ilex</i> (M)		<i>Q. lancifolia</i> (D), <i>Q. corrugata</i> Hooker (D)
Kutuzkina, 1964	?M				<i>Q. phellos</i> L. (?M), <i>Q. imbricata</i> Michaux (?M)	
Kolakowski, 1964	D	<i>Q. suber</i>		<i>Q. alnifolia</i> (refers to <i>Q. sosnowskyi</i> various forms but not f. <i>angustifolia</i>), <i>Q. ilex</i> <i>Q. coccifera</i> , <i>Q. ilex</i>		
Kolakovsky and Ratiani, 1967	M					
Givulescu and Ghiurca, 1969	D M?					<i>Q. serrata</i> (D)
Paicheler and Blanc, 1981	D M		<i>Q. myrsinifolia</i> Blume (D)	<i>Q. ilex</i> (M), <i>Q. coccifera</i> (M), <i>Q. floribunda</i> Wallich (D) <i>Q. coccifera</i> (M), <i>Q. ilex</i> (M), <i>Q. setulosa</i> (D) <i>Q. coccifera</i> , <i>Q. ilex</i>		<i>Q. lancifolia</i> (D), <i>Q. serrata</i> (D)
Knobloch and Velitzelos, 1986a	D M					<i>Q. serrata</i> (D)
Knobloch and Velitzelos, 1986b; Kvaček and Walther, 1989	M					
Gemici et al., 1991	D M	<i>Q. castaneifolia</i> C.A.Meyer (D)		<i>Q. coccifera</i> (M), <i>Q. ilex</i> (M), <i>Q. pseudococcifera</i> (M)	<i>Q. sartorii</i> (D)	
Gemici et al., 1993	D M	<i>Q. castaneifolia</i> (D)		<i>Q. coccifera</i> (M)	<i>Q. sartorii</i> (D)	
Bůžek et al., 1996	D	<i>Q. chinensis</i> (= <i>Q. variabilis</i>)				<i>Q. serrata</i>
Barrón, 1999a, 1999b	D	E Asia	E Asia	E Asia		E Asia
Kvaček et al., 2002	D M			<i>Q. coccifera</i> (M)	<i>Q. xalapensis</i> (D)	
Kvaček et al., 2011	D M			<i>Q. coccifera</i> (M, D)		
Bozukov et al., 2011	D			<i>Q. acrodonta</i> Seemen		
Velitzelos et al., 2014	D M			<i>Quercus</i> Group Ilex (M, D)		
This study	D M			<i>Quercus</i> Group Ilex (M, D)		

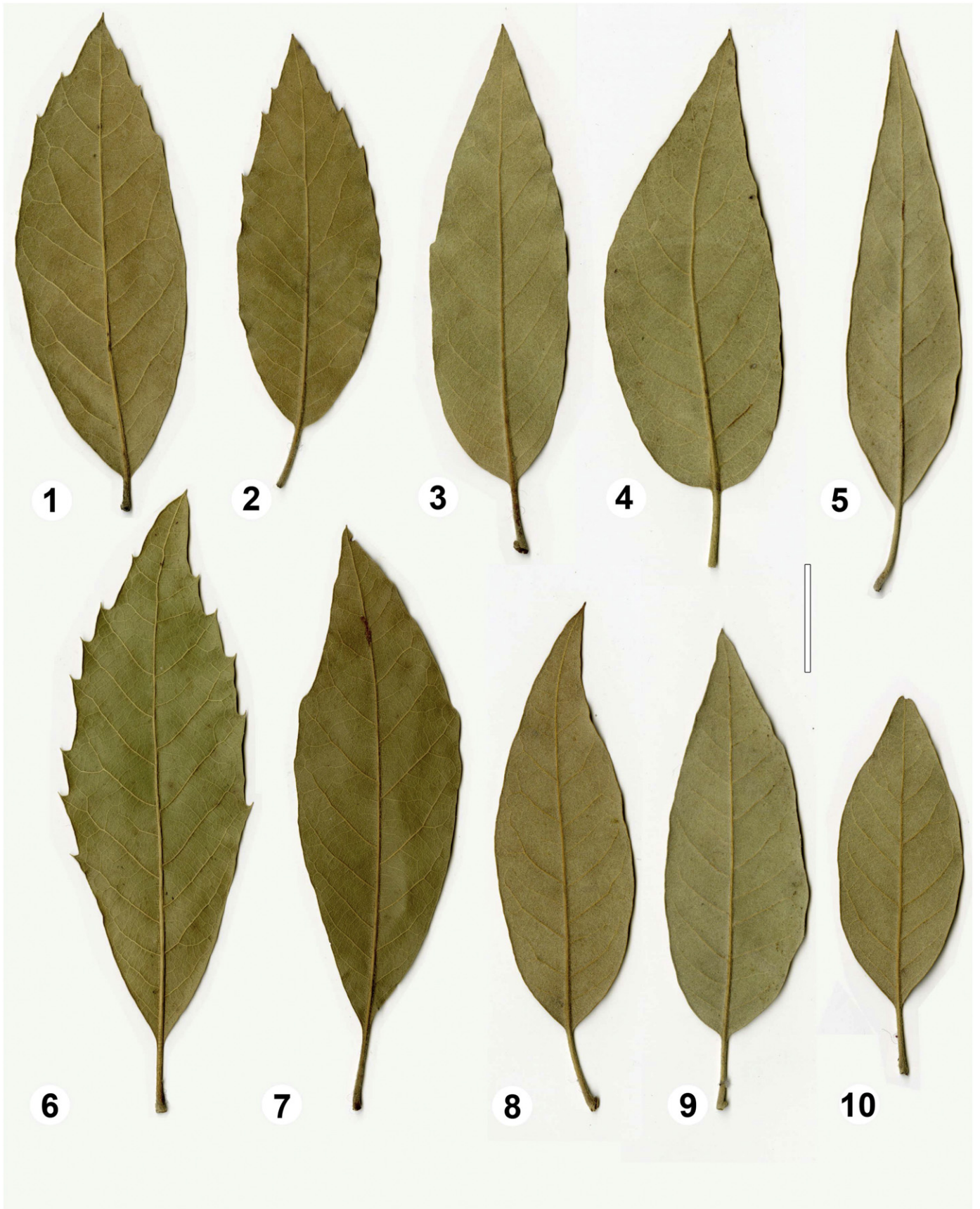


Plate X. Extant *Quercus ilex* L. Litter sample, Katerini to Mt. Olympos, above Vrontou, Greece. 1–10. Leaves resembling *Quercus drymeja* Floribunda Morphotype. Scale bar is 2 cm in 1–10.

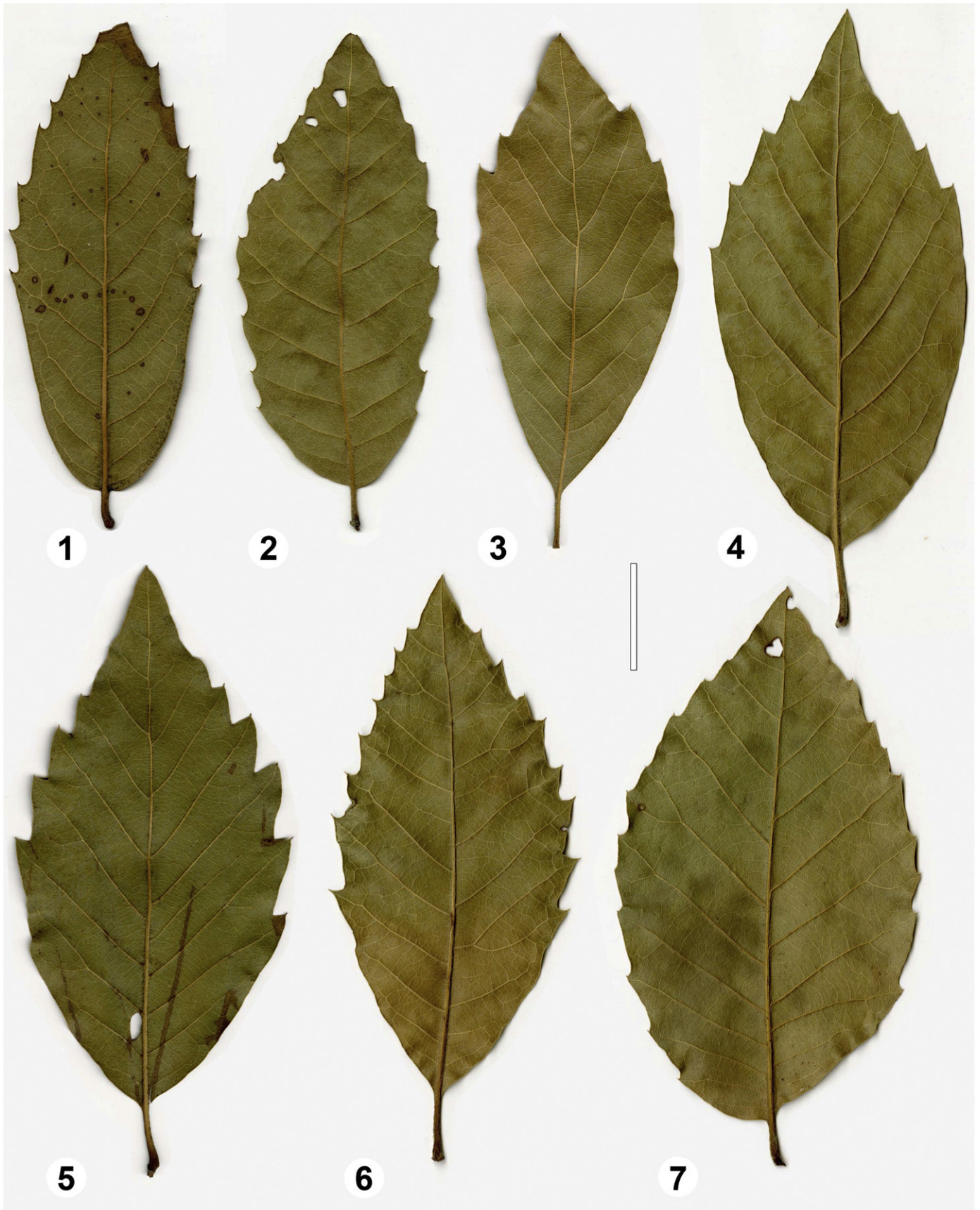


Plate XI. Extant *Quercus ilex* L. Litter sample, Katerini to Mt. Olympos, above Vrontou, Greece. 1–10. Leaves resembling *Quercus drymeja* morphotypes (MT). 1. *Quercus drymeja* Floribunda MT. 2. *Quercus drymeja* Güvem MT. 3–7. *Quercus drymeja* Zoroastri MT. Scale bar is 2 cm in 1–7.

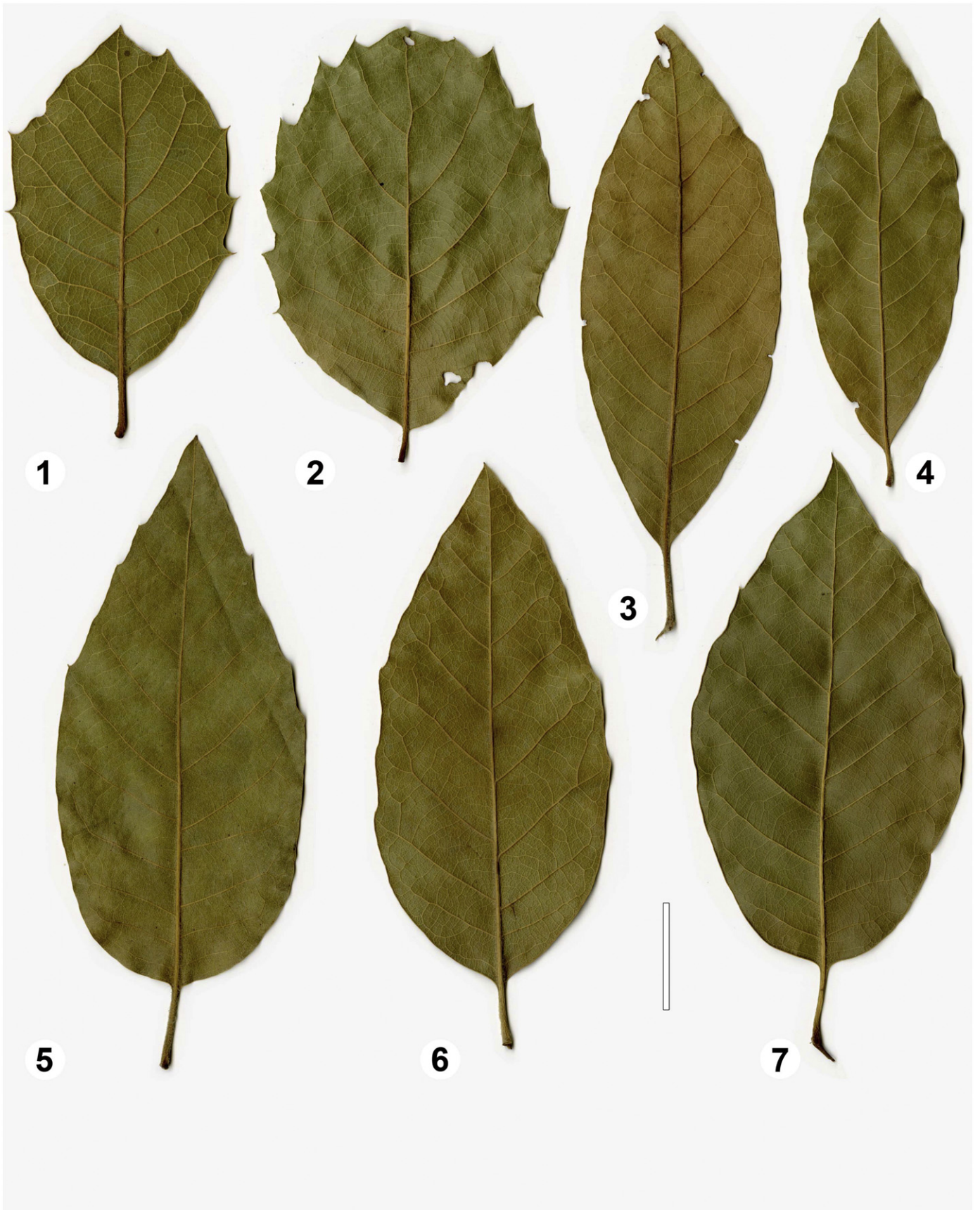


Plate XII. Exant *Quercus ilex* L. Litter sample, Katerini to Mt. Olympus, above Vrontou, Greece. 1–7. Leaves do not match a particular (fossil) morphotype. Scale bar is 2 cm in 1–7.

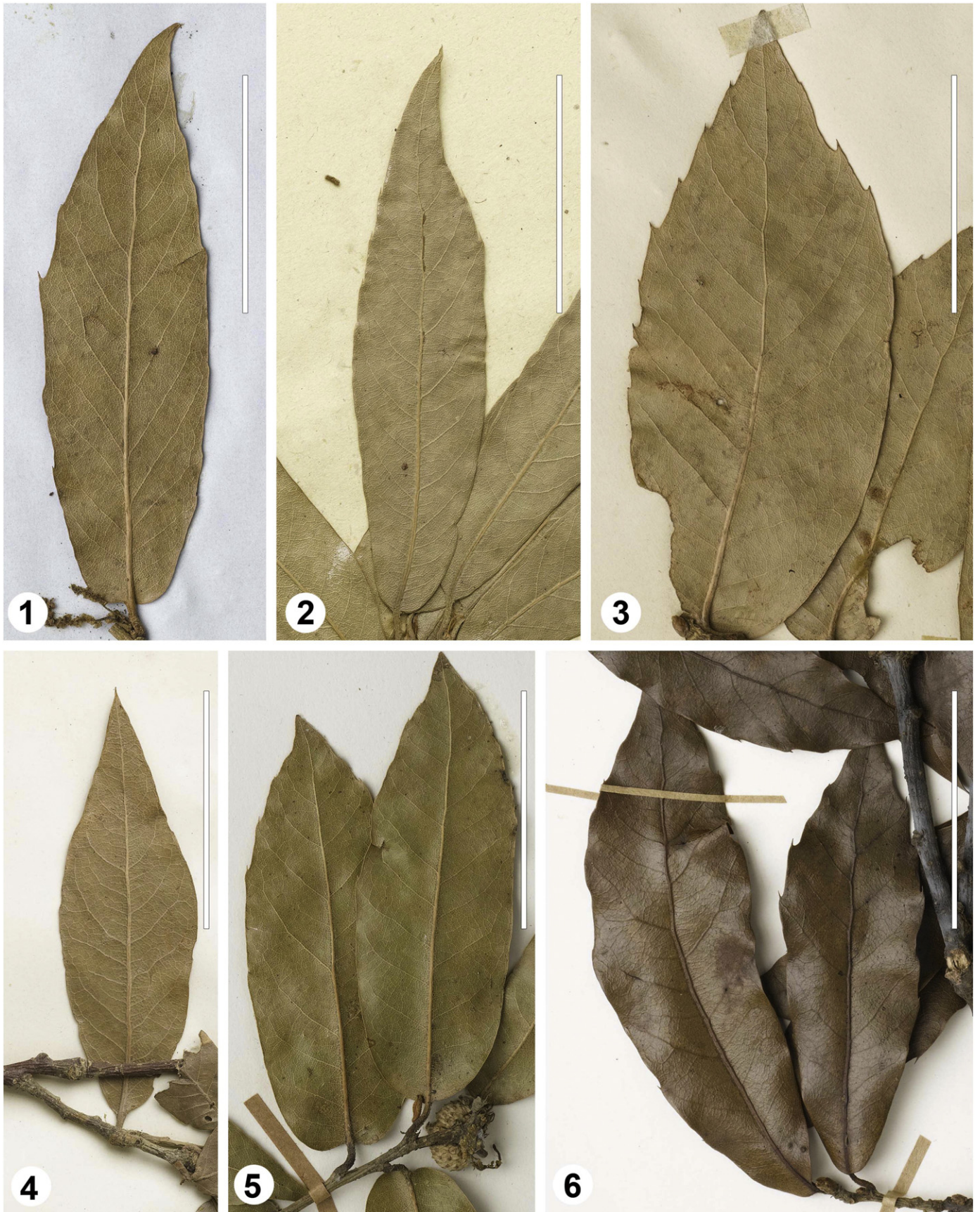


Plate XIII. Extant *Quercus floribunda* Wallich, southern foothills of Himalaya. Herbarium E. 1. E00671614, westernmost Nepal. 2. E00671621. 3. E00671626, N India. 4. E00671620. 5. E00451993, W Nepal. 6. E00132049, W Nepal. Scale bar is 5 cm in 1–6.

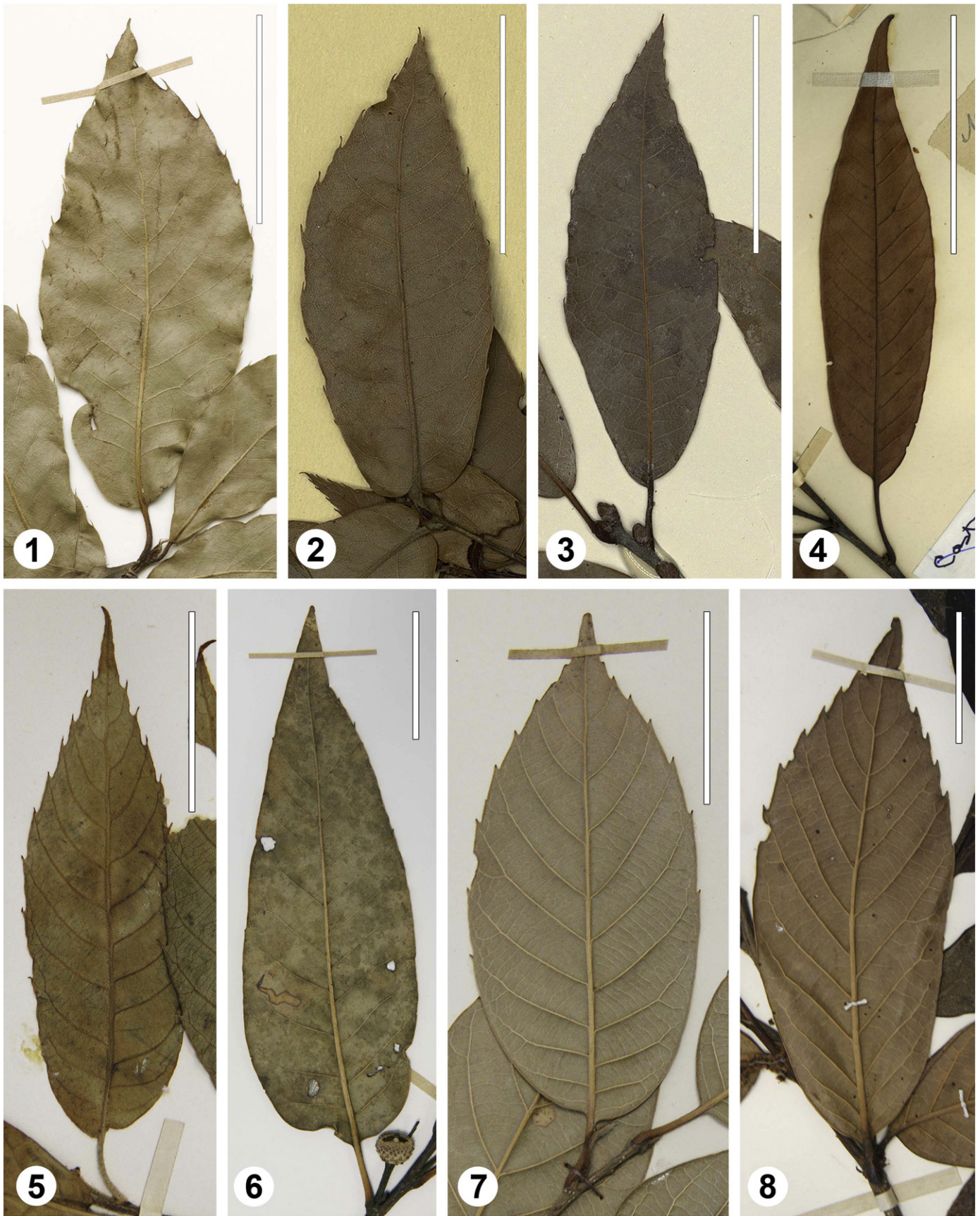


Plate XIV. Extant members of *Quercus* Group Ilex. 1. *Quercus floribunda* Wallich, Herbarium E. 2, 3. *Quercus setulosa* Hickel et A.Camus, Herbarium P. 4–8. *Quercus engleriana* Seemen, Herbarium E. 1. E00132035, westernmost Nepal. 2, 3. P06813203, Vietnam. 4. E00275658, Guizhou, China. 5. E.H. Wilson 3633, Sichuan, China. 6. Z.-Y. Li et al. 171, Henan, China. 7. W.K. Hu 8864, Sichuan, China. 8. W.P. Fang 948, Sichuan. Scale bar is 3 cm in 1–8.

Kvaček et al. (2002, 2011) found that the abaxial leaf epidermis in *Q. drymeja* from Vegora, Greece, differed from extant *Q. ilex* by its almost hairless abaxial leaf surface, and that leaf epidermal features of *Q. drymeja* and *Q. mediterranea* were fairly similar. Epidermal features of the fossil taxa suggested closer relationship with the Mediterranean

Q. coccifera. *Quercus drymeja* foliage from Arjuzanx, France, resembling the Güvem MT of the present study also showed leaf epidermal characteristics consistent with the material from Vegora. In a recent investigation, Deng et al. (2017) studied epidermal characteristics of all modern members of *Quercus* Group Ilex and stated that the fossil-species

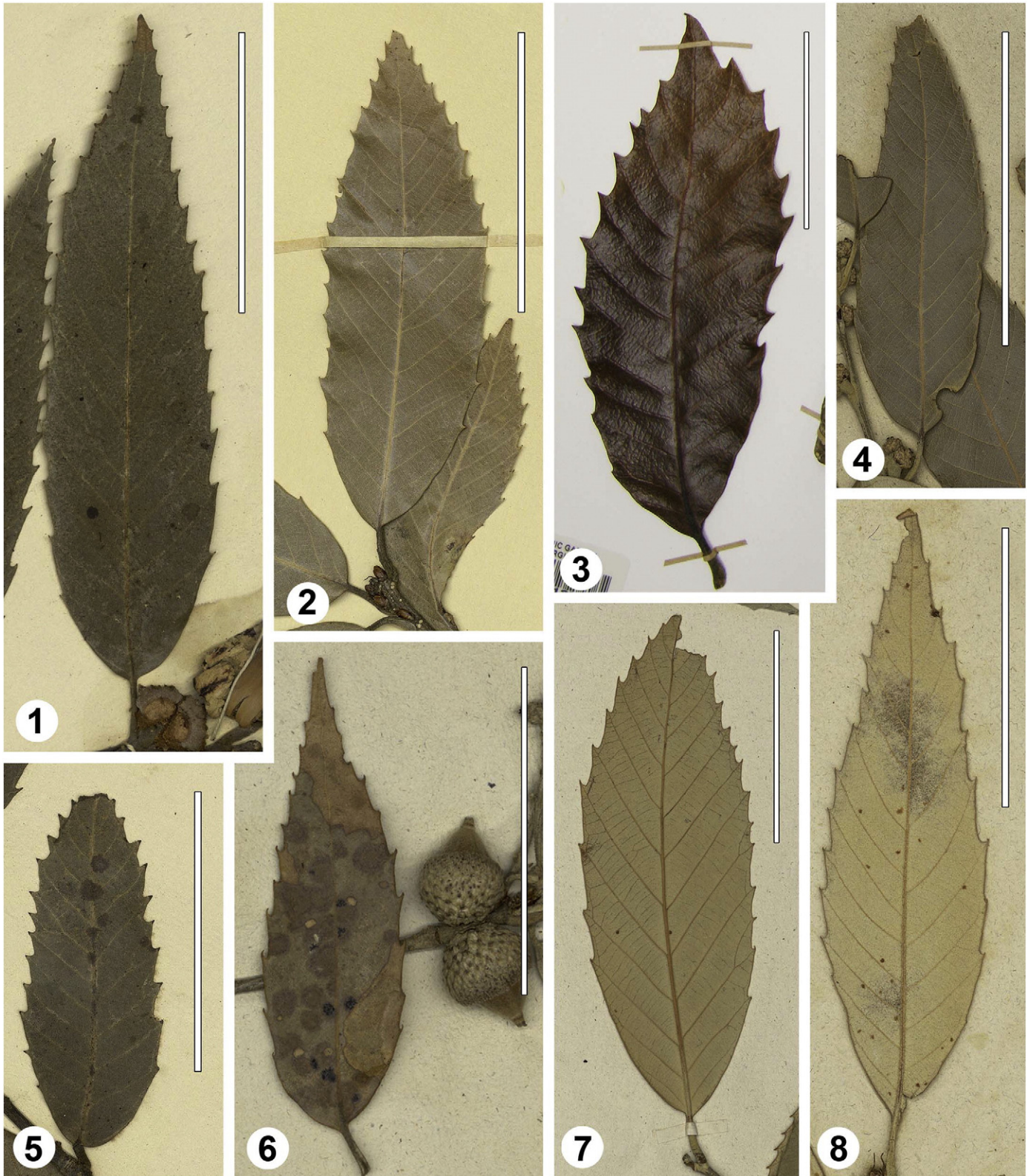


Plate XV. Extant species of *Quercus* Group Ilex. 1, 2, 4–8. *Quercus leucotrichophora* A.Camus, Herbarium P. 3. *Quercus lanata* Smith, Herbarium E. 1. P00164011, N Pakistan. 2. P00164028, Nepal. 3. [M Minaki et al 9105137] W Nepal. 4. P00164025, N India. 5. P00164011, N Pakistan. 6. P00164021. 7. P00164023. 8. P00164019. Scale bar is 5 cm in 1–8.

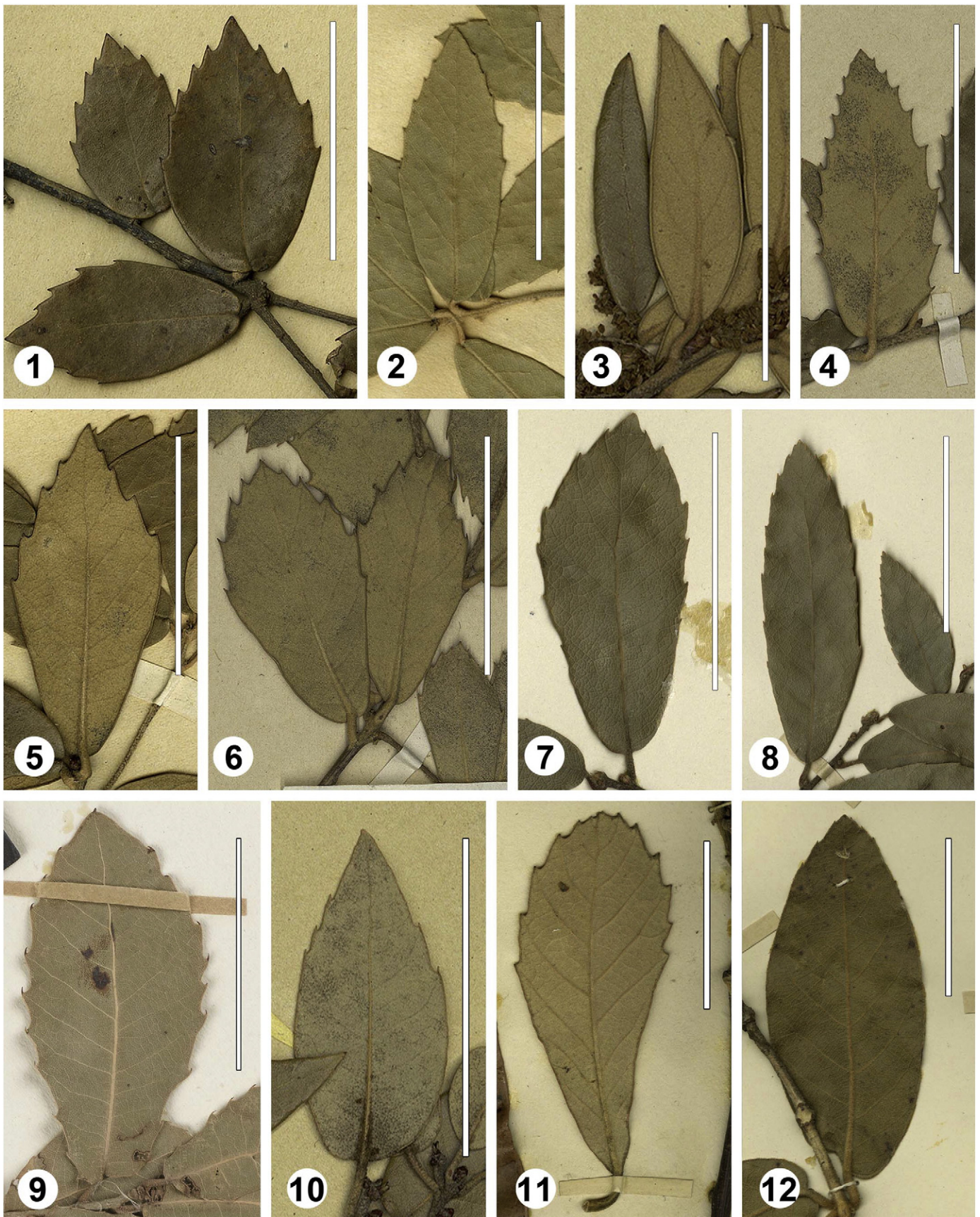


Plate XVI. Extant species of *Quercus* Group Ilex. 1–6. *Quercus acrodonta* Seemen, Herbarium P. 1, 2, 5. P00721863, Hubei, China. 3. P06856596, Shaanxi, China. 4. P06856603, Shaanxi, China. 6. P06856601, Shaanxi, China. 7, 8. *Quercus cocciferoides* Handel-Mazzetti, Herbarium E. E275420, NW Yunnan. 9. *Quercus coccifera* L. Herbarium E. E00404406, Israel. 10. *Quercus handeliana* A.Camus, Herbarium P. P06872352, Yunnan, China. 11. *Quercus franchetii* Skan, Herbarium E. E00275419, Yunnan, China. 12. *Quercus oxyphylla* (E.H.Wilson) Handel-Mazzetti, Herbarium E. E00275407, Anhui, China. Scale bar is 3 cm in 1–12.

Quercus drymeja might be related to “less hairy species in mesophytic and broadleaved evergreen forests”. A number of potential modern analogues of *Quercus drymeja* Floribunda MT recognized in the present study exactly match these criteria (*Q. floribunda*, *Q. tarokoensis*, *Q. tatakaensis*; see Deng et al., 2017, table 3). However, it needs to be kept in mind that within closely related species the type of indumentum may be very different (e.g. in *Q. ilex*, *Q. alnifolia*, *Q. coccifera* and *Q. calliprinos*; Deng et al., 2017). This suggests that particular indumentum types have evolved independently in different more or less closely related groups of oaks.

Molecular data suggest that the Mediterranean *Q. aucheri*, *Q. alnifolia*, *Q. coccifera* and *Q. ilex* share a common origin with the Himalayan *Q. floribunda* and *Q. baloot* (Denk and Grimm, 2010; Simeone et al., 2016). When viewed in a Eurasian context, *Q. floribunda* occurs nested in a group of East Asian Group Ilex oaks, which is sister to the western Eurasian Ilex oaks. Notably, *Q. coccifera* and the strongly pubescent *Q. aucheri* are genetically indistinguishable. This may suggest that the presence or absence of leaf pubescence is less useful to determine taxonomic relatedness than generally assumed.

Quercus drymeja and *Q. mediterranea* represent extinct member(s) of the *Quercus* Group Ilex lineage. The Güvem MT of the lower Miocene deposits of Güvem and Kimi might in principle also represent a taxon intermediary between Group Ilex and Cerris (cf. Denk and Grimm, 2010, for the molecular differentiation of *Quercus* Group Ilex and Group Cerris). Unambiguous fossil evidence for Group Cerris (early Oligocene, Russian Far East; Pavlyutkin et al., 2014) occurs later than for Group Ilex (middle Eocene, Hainan Island, southern China; Hofmann, 2010; Spicer et al., 2014), and all currently available molecular data indicate a (Miocene) budding scenario for the origin of Group Cerris from a Group Ilex stock (Denk and Grimm, 2010; Hubert et al., 2014; Hipp et al., 2015; Simeone et al., 2016).

A time-calibrated phylogeny of oaks based on eight nuclear gene regions (six single-copy genes, the polymorphic ITS region, and the 2nd and 3rd intron of the *CRC* gene), clade-consensus sequences, and a set of analyses, each using a different dating constraint (Hubert et al., 2014) suggested a late Oligocene to early Miocene crown age of the Group Ilex-Group Cerris lineage, with the two western Eurasian and the two East Asian members of Group Ilex included in the study by Hubert et al. (2014) diverging shortly after. The estimates correspond

well with the time of deposition of the Güvem and Kimi deposits and with changes in morphotype diversity during the Miocene. Floribunda MTs of early Miocene Turkish and Greek deposits have short petioles as in modern *Q. floribunda*, while late Miocene specimens of this MT have conspicuously long petioles. This could reflect the isolation and morphological lineage sorting of the western Eurasian populations from the common ancestor of Group Ilex. While the western Eurasian populations (Floribunda MT) went extinct during the course of the Pliocene, the Himalayan and East Asian populations persisted. It would be tempting to assume that Miocene populations of *Q. mediterranea* evolved directly into the modern populations of the sibling species *Q. aucheri*, *Q. coccifera*, and *Q. ilex*. But it is more likely that populations of both *Q. drymeja* and *Q. mediterranea* provided the stock for the three modern species as well as for some western Himalayan taxa; particularly with respect to the extreme morphological plasticity (Mount Olympus example, Plates IX to XII), the ambiguous climatic preference (summer-dry *Csa* climates, but also in *Cfa* climates), and the notable genetic diversity of the modern *Q. ilex* (e.g. Denk and Grimm, 2010; Simeone et al., 2016; Vitelli et al., 2017).

The Himalayan high-elevation species with leaves similar to *Q. mediterranea* are probably not closely related to the *Q. drymeja-mediterranea* complex. Leaf fossils very similar to modern *Q. monimotricha*, *Q. semecarpifolia* and others were recovered from 15 Ma deposits of the Namling Plateau, Tibet (Zhou et al., 2007), suggesting that this group of oaks had evolved by the middle Miocene and possibly before. Across their shared range, the modern *Q. aucheri* and *Q. coccifera* share genotypes with *Q. ilex* (Denk and Grimm, 2010; Vitelli et al., 2017), even in highly divergent, non-coding nuclear (ITS) and plastid (*trnH-psbA*) gene regions that have frequently been suggested as barcodes for species discrimination in plants. The three species can only be differentiated with the sequences of the highly divergent and polymorphic 5S intergenic spacer (Denk and Grimm, 2010). In the eastern Mediterranean region, *Q. coccifera* shares the plastid diversity of the Cypriot endemic *Q. alnifolia*, which has clearly distinct nuclear signatures even when growing in mixed stands (Neophytou et al., 2011a, 2011b). Further east, the western Himalayan species are genetically distinct. Overall, this points to a (very) recent origin of *Q. coccifera* from the general western Eurasian stock of *Quercus* Group Ilex. Thus, the *mediterranea*-type leaves of Mediterranean and

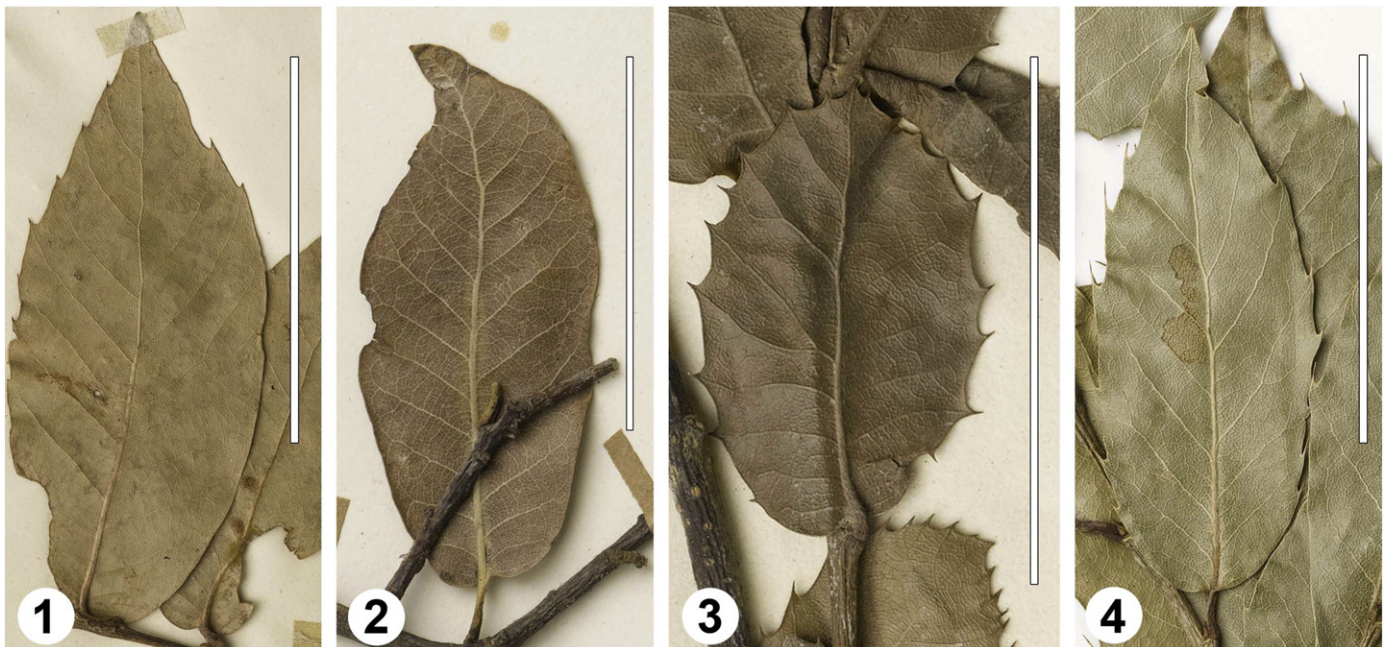


Plate XVII. Extant *Quercus floribunda* Wallich, Herbarium E. 1. E00671626. Southern foothills of the Himalaya. 2. E00671610. N Pakistan. 3. E00671616. Pakistan. 4. E00671618. N India. Scale bar is 5 cm in 1; 3 cm in 2–4.

Eastern Himalayan species are most likely the result of convergent evolution.

4.2. Earliest occurrences of sclerophyllous oaks in Eurasia

The earliest unambiguous evidence of *Quercus* Group Ilex in western Eurasia are pollen grains from the early Oligocene of Central Europe (Denk et al., 2012) and leaf remains from the early Miocene of the eastern Mediterranean region (Paicheler and Blanc, 1981; Velitzelos et al., 2014). In East Asia, earliest unequivocal evidence of sclerophyllous oaks of Group Ilex is from the middle Eocene Changchang Formation, Hainan (Hofmann, 2010, dispersed pollen; Spicer et al., 2014, foliage). Possibly, *Quercus* Group Ilex was present in Yunnan (China) by the Oligocene (Zhou, 1993; *Quercus haugii* Colani, leaf fossils), but this record would need to be re-examined (the specimen figured in Writing Group of Cenozoic Plants of China, WG CPC, 1978, is a fragment of a leaf and is inconclusive regarding the taxonomic relationships of this leaf type). Leaf records of *Quercus* Group Ilex are common from Miocene deposits of East Asia (e.g. WG CPC, 1978; Zhou, 1993). At the time when *Quercus* Group Ilex established in Eurasia, sclerophyllous oaks were already represented by at least two related lineages in North America. Bouchal et al. (2014) found unequivocal evidence for *Quercus* Group Quercus/Lobatae and Group Protobalanus in the latest Eocene of Florissant, central U.S.A.

Paleogene leaf fossils previously included within *Q. lonchitis*–*Q. drymeja* (Unger, 1852; Palamarev and Mai, 1998) were later transferred to the extinct genus *Castaneophyllum* Jones and Dilcher (Kvaček and Walther, 2012) based on leaf epidermal characteristics. These leaves also differ in gross morphology from the ones described here from Miocene deposits.

4.3. Niche evolution in Eurasian sclerophyllous oaks

Ackerly (2004) investigated adaptive leaf evolution in 12 lineages of Californian chaparral plants growing under distinct Mediterranean climate. Ten of the 12 chaparral plants originated from subtropical ancestors thriving in fully humid or summer-wet climates. Ackerly (2004) concluded that ancestors of chaparral plants were already pre-adapted and therefore were successful under Mediterranean (summer-dry) climates but had not necessarily evolved under Mediterranean climates. Table 4 summarizes the geographical, vertical and climatic distribution of modern species of *Quercus* Group Ilex, to which morphotypes of *Q. drymeja* and *Q. mediterranea* are compared in the present study. *Quercus baloot*, although not specifically compared to the fossil taxa is included as well, because it is considered to be closely related to both *Q. floribunda* and *Q. coccifera* (Simeone et al., 2016), connects the distribution ranges of these two species, and forms hybrids with *Q. floribunda* (Menitsky, 2005). Generally, the modern species have a large vertical range, with the exception of the Mediterranean *Q. coccifera* and the warm temperate to tropical *Q. setulosa*, both of which occur at lower elevations than the (typical) temperate species. Geographically, the species replace each other along a west-east and a north-south (in East Asia) axis. In addition, in the western range, different species are typical of certain altitudinal belts and ecologically distinct. For example, *Q. baloot* is markedly adaptable to different climate types, both in terms of seasonality and temperature extremes (Fig. SI 1). *Quercus floribunda* occurs in a vertical belt above *Q. baloot* in humid temperate climates (fully humid and summer-wet). To the east, *Quercus floribunda* is replaced by *Q. lanata* and *Q. leucotrichophora* occurring in similar climates and vegetation types (see Section 3.4). Still further east and northeast, *Q. engleriana* is also found in fully humid (Cf climates) and less so in summer-wet climates (Cw). *Quercus engleriana* may occur together with *Fagus* and various Tertiary relicts such as *Cercidiphyllum*, *Symplocos*, *Torreya*, *Zanthoxylum* and *Zelkova* (Table SI 3). Finally, *Q. setulosa* extends to the lowland tropics occurring above tropical dipterocarp forest. Hence, speciation processes and niche evolution in

Table 4 Geographic distribution, climatic characterisation, and vertical distribution of sclerophyllous oaks of *Quercus* Group Quercus. *Quercus coccifera* is anatomically most similar to the fossil taxa; *Q. baloot* is included because it connects the ranges of *Q. coccifera* with the eastern species and forms hybrids with *Q. floribunda*. Climate types according to Köppen-Geiger climate classification: C – temperate, s – summer-dry, f – fully humid, w – summer-wet; D – snow climate; B – steppe climate; Aw – tropical monsoon climate (for details see Kottrek et al., 2006; Peel et al., 2007). Sources: Browicz and Ziełinski (1982), IOP1 (1996-2007), Menitsky (2005), and <http://oaks.of.the.world.free.fr/index.htm>.

	Altitude m a.s.l.	Mediterranean	Afghanistan	Pakistan	Kashmir	Nepal	India	Bhutan	Assam	Myanmar	China	Taiwan	SE Tibet	Thailand	Laos	Vietnam	Borneo
<i>Quercus coccifera</i> ^a	0–1700	Cs, Cf															
<i>Quercus baloot</i>	500–3300				Cf, Cw		Cw										
<i>Quercus floribunda</i>	1200–3000		Cf, Ds	B	Cf, Cw												
<i>Quercus lanata</i> + <i>leucotrichophora</i> ^b	400–2700		Cf, Cw	Cf, Cw	Cw		Cw		Cw					Aw			?
<i>Quercus engleriana</i>	1000–2800		Cf, Cw	Cf, Cw			Cw		Cw				Cw				
<i>Quercus tarokoensis</i>	400–1300												Cw				
<i>Quercus spinosa</i> subsp. <i>miyabei</i>	1500–2600																
<i>Quercus setulosa</i>	(100)700–1000(1300)													Aw			Aw

^a Main distribution Mediterranean; a few populations behind the Turkish Black Sea coast occur in humid temperate climate.

^b Including *Q. incana*; <http://oaks.of.the.world.free.fr/index.htm> includes *Q. incana* and *Q. leucotrichophora* in *Q. lanata*.

^c Listed in <http://oaks.of.the.world.free.fr/index.htm>.

^d Record by Camus questioned by Menitsky.

sclerophyllous oaks of Group Ilex were likely triggered by ecological differentiation and geographical distance.

In addition to the western Eurasian fossil taxa investigated here, leaf fossils related to modern sclerophyllous oaks of high elevations on the outer slopes of the Himalayas and of southwestern China (e.g. *Q. semecarpifolia*, *Q. guyavifolia*, *Q. aquifolioides*, *Q. pannosa*) occurred on an already elevated southern Tibet Plateau (Wang et al., 2008) and in the Hengduan Mountains during the Miocene and Pliocene (Zhou, 1992; Zhou et al., 2007). As in the case of the Californian chaparral the sclerophyllous evergreen leaf morphology of the ancestral species of *Quercus* Group Ilex appears to have facilitated ecological radiation into diverse habitats already during the Miocene.

4.4. Palaeoecological implications

Foliage of *Quercus drymeja* and in particular of *Q. mediterranea* has sometimes been connected to seasonally dry and Mediterranean climatic conditions or xerophytic plant communities (e.g. Berger, 1953a, Austria, Hernal, middle Miocene, as maquis and dry Mediterranean forest; Berger and Zabusch, 1952, Austria, Türkenschanz, middle Miocene, as Mediterranean maquis, savannah, and scrubland-steppe comparable to those in eastern and southern Africa; Berger, 1957b, Messinian Italy, as dry, light scrublands, savannah, and scrubland-steppe; Andreánszky, 1963, Hungary, middle Miocene, Erdöbénye, as Mediterranean sclerophyllous forest; Kvaček et al., 2002, Greece, late Miocene, Vegora, as ethesian summer-dry regime). Pollen with affinity to "*Quercus ilex/coccifera*" is commonly considered to represent an ecological group of "Mediterranean sclerophyllous" or "xeric" elements (e.g. Jiménez-Moreno et al., 2005, 2008).

These interpretations overlooked that woody angiosperms with sclerophyllous leaves have long been considered as remnants of laurophyllous humid vegetation from which they evolved into various subhumid vegetation types (Axelrod, 1975; Palamarev, 1989; Mai, 1995; Ackerly, 2004). Palamarev (1967) and Axelrod (1975) suggested that the sclerophyllous flora evolved as an understory element of humid subtropical (mesophytic) forests or on specific substrates in the Eocene and that increased seasonality since the early Oligocene (see, for example, Zachos et al., 2001) further promoted sclerophyllous plants that began to form independent vegetation units. According to Palamarev (1967), the maximum rainfall occurred during the warm summer months and the shift to summer-dry conditions as currently found in the Mediterranean region occurred during the latest Miocene or Pliocene (see also Suc, 1984). With respect to the overall molecular differentiation patterns in *Quercus* Group Ilex and, in particular, its western Eurasian members (e.g. Denk and Grimm, 2010; Simeone et al., 2016; Vitelli et al., 2017), it appears very unlikely that a xerophytic evergreen oak lineage should have persisted from the Miocene (*Q. mediterranea*) until today (*Q. coccifera*).

The results of the present study suggest that when members of *Quercus* Group Ilex (pollen and foliage) are dominating in Miocene plant assemblages of western Eurasia, they indicate substantial rainfall (Cfa-, Cwa-climates) but not summer draught. This explains why they commonly co-occur with humid temperate elements such as *Fagus* and *Cathaya* (e.g. Güvem-Keseköy; Vegora). Where they are rare or absent, *Fagus* also is rare or absent (e.g. Lesbos, Crete, possibly Soma). In the Miocene, this probably means aspect-wise drier stands (e.g. lee situations). This is in agreement with Kvaček et al.'s (2006) interpretation of what they called "subtropical sub-humid sclerophyllous forest". These authors clearly stated that these forests have nothing in common with the modern Mediterranean forest thriving under a summer-dry climate and instead suggested similarities with montane forests in drier parts of the Himalayas. It is difficult to pinpoint the origin of true Mediterranean sclerophyllous oaks (*Q. coccifera*, *Q. aucheri*, *Q. ilex*, *Q. alnifolia*). The late Pliocene flora of Atalanti (Lokris Basin, Central Greece; Velitzelos et al., 2014) still comprises "exotic" elements such as *Fagus haidingeri* and *Quercus drymeja* with Himalayan and East

Asian affinities. From the early Pleistocene of Rhodes and Zakynthos floras with high proportions of modern Mediterranean taxa have been reported and these may mark the origin of modern Mediterranean sclerophyllous oaks (Velitzelos et al., 2014).

4.5. Conclusions

We assessed taxonomic affinities of two widespread Neogene sclerophyllous oaks in western Eurasia. We notice that the inferred taxonomic relationships of the fossil leaf taxa *Quercus drymeja* (including *Q. zoroastri*) and *Q. mediterranea* have not changed much since the original description by Unger in the middle of the 19th century. Using leaf morphological characters of fossil and modern taxa, the available scattered information on leaf epidermal characteristics of the fossil taxa, and information from the record of dispersed pollen grains, we infer that both taxa represent a Eurasian infrageneric group of *Quercus*, Group Ilex, that occurs from western North Africa and southwestern Europe to Southeast Asia and Japan. In the light of leaf variation encountered in their modern relatives, we conclude that leaf remains assignable to *Q. drymeja* and *Q. mediterranea* may have belonged to a single species or to two or more species at different localities. This has implications for the usage of standardized modern analogue taxa to infer palaeoenvironments and palaeoclimate.

We also compared Miocene and Pliocene plant assemblages with sclerophyllous oaks of Group Ilex to modern vegetation containing morphologically closely related species. Analogous modern vegetation follows a humid transect of forest vegetation on the outer slopes of the Himalayas from northeastern Afghanistan to Nepal and into humid temperate China. This suggests that the two widespread sclerophyllous oaks *Q. drymeja* and *Q. mediterranea* indicate mostly general humid temperate conditions, fully humid or summer-wet, during the times when they were deposited rather than Mediterranean conditions as implied by their modern western Eurasian relatives.

Supplementary data to this article can be found online at <http://dx.doi.org/10.1016/j.revpalbo.2017.01.005>.

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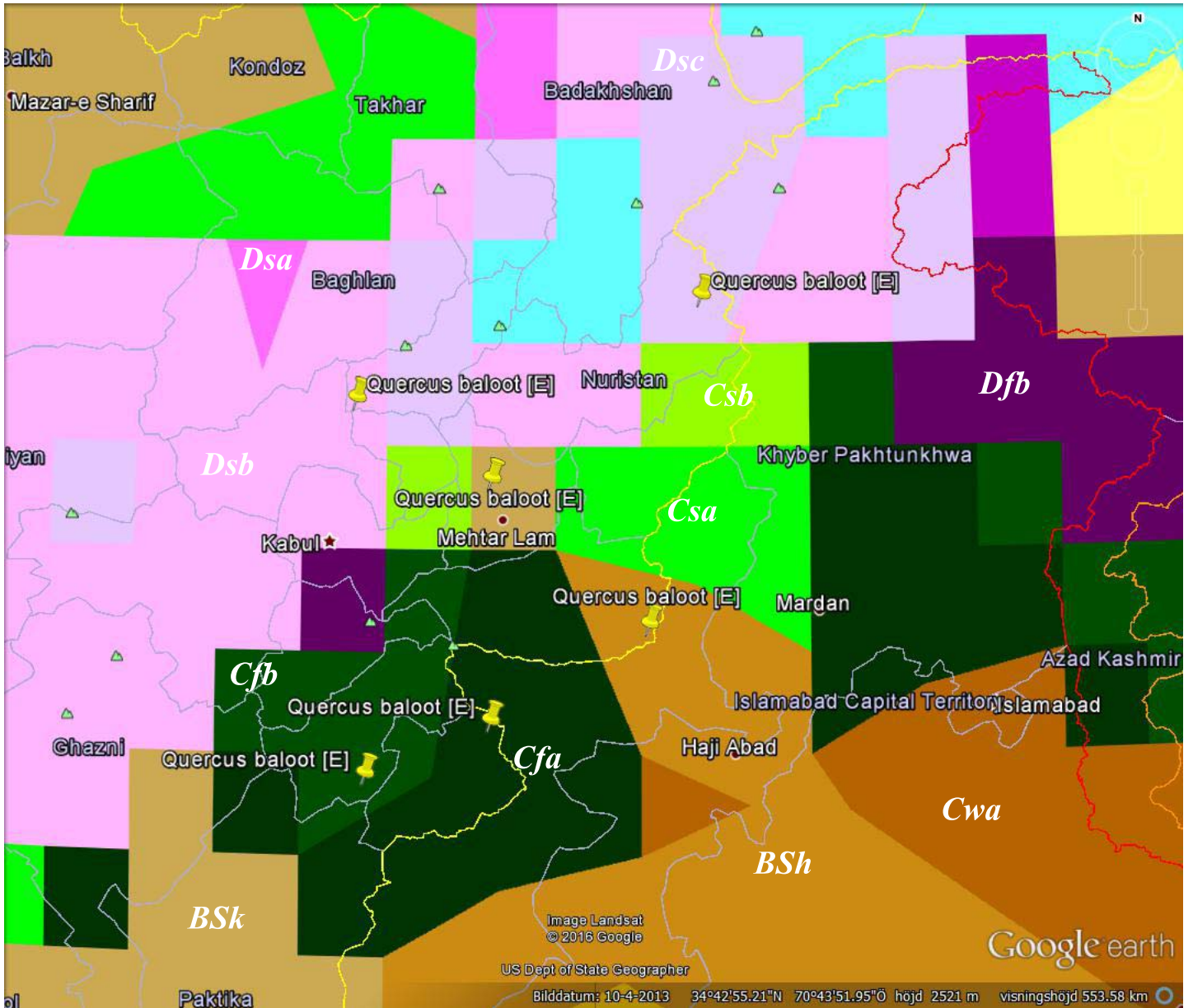
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Figure SI 1. Köppen-Geiger climate types mapped on a Google earth map using <http://koeppen-geiger.vu-wien.ac.at/data/Koeppen-Geiger-GE.kmz.zip>. Occurrences of *Quercus baloot* from herbarium Edinburgh (E) are mapped to show the ecological breadth of this taxon. The map shows the complex climatic situation in NE Afghanistan/NW Pakistan. Climate types: *C* – temperate, *s* – summer-dry, *f* – fully humid, *w* – summer-wet, *a* – hot summer, *b* – cool summer; *D* – snow climate; *BS* – steppe climate, *k* – cold, *h* – hot (for details see Kottke et al., 2006; Peel et al., 2007).



2 Denk et al_Figure SI 1

Supplementary Information

Plate SI I: Dispersed pollen from early Burdigalian deposits of Güvem, Ankara, Turkey.

1–3. *Quercus* Group Cerris. **4–6.** *Quercus* Group Ilex. **7–9.** *Eotrigonobalanus furcinervis* (Rossmässler) Walther et Kvaček. **1.** Grain 1, light microscopy (LM), overview equatorial view, tricolporoidate. **2.** Grain, scanning electron microscopy (SEM), equatorial view. **3.** Grain 1, SEM, detail of sculpturing, verrucate scattered with densely spaced tuft agglomerations. **4.** Grain 2, LM, overview, equatorial view, tricolporoidate. **5.** Grain 2, SEM, equatorial view. **6.** Grain 2, SEM, detail of sculpturing, sculpturing rod-like, (micro)rugulate, tuft agglomerations forming desert rose-like structures (green shading). **7.** Grain 3, LM, overview equatorial view, tricolporoidate. **8.** Grain 3, SEM, equatorial view. **9.** Grain 3, SEM, detail of sculpturing, sculpturing rod-like, micro(rugulate), tuft agglomerations forming braided structures (green shading). Scale bar is 10 μm in 1, 2, 4, 5, 7, 8; 1 μm in 3, 6, 9.

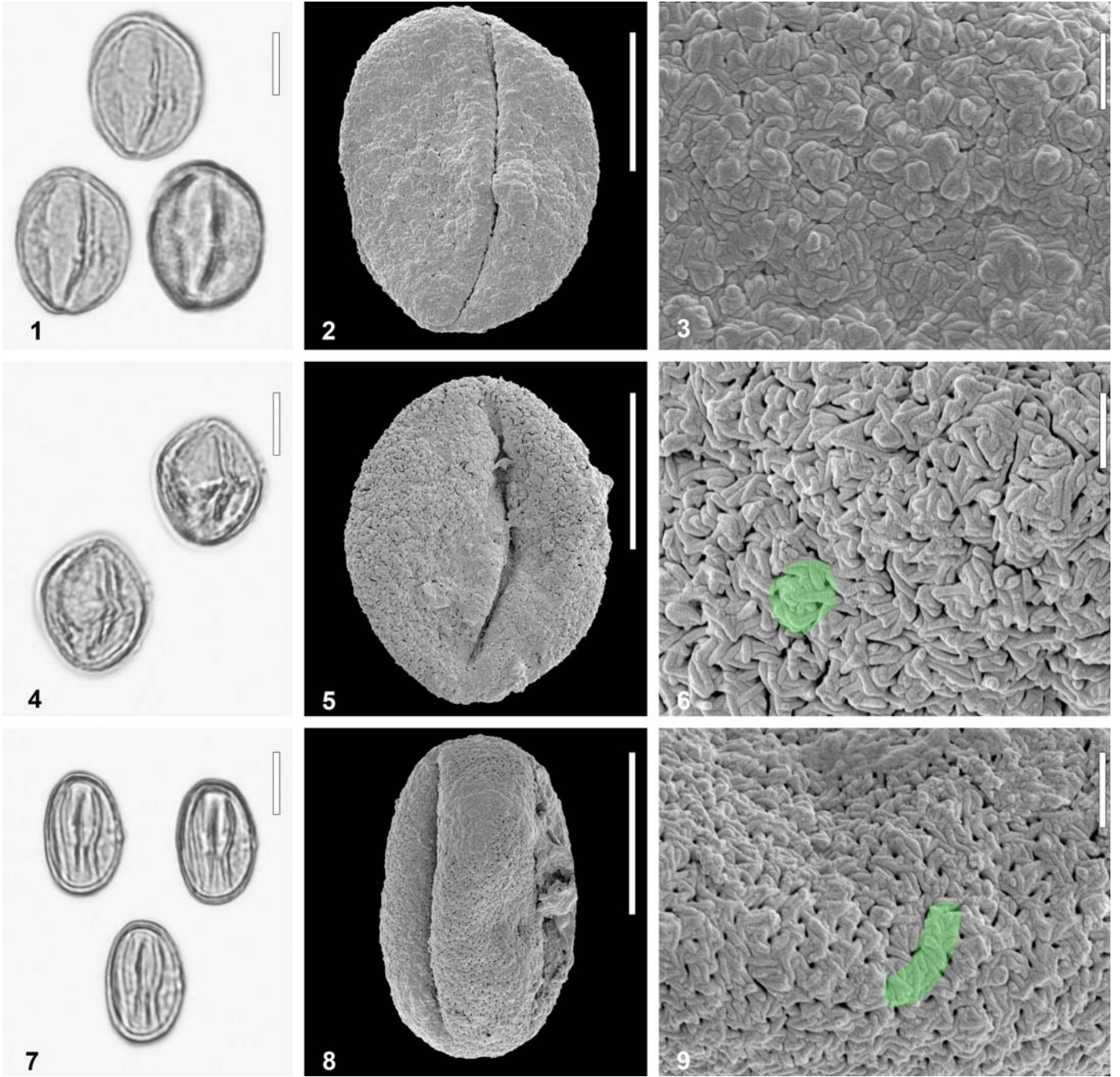
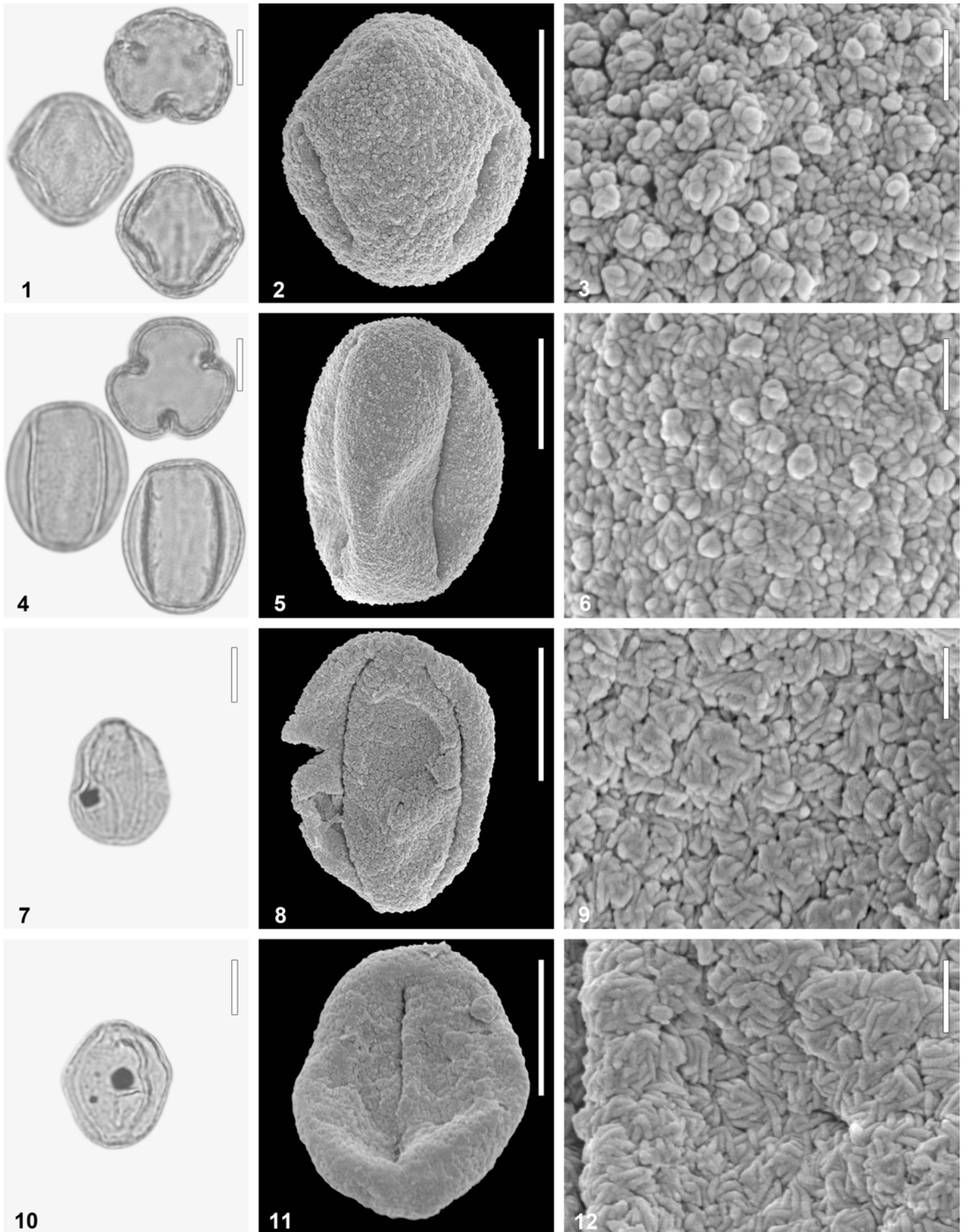


Plate SI II: Dispersed pollen from lower Burdigalian deposits of Kimi, Euboea, Greece.

1–6. *Quercus* Group Cerris. **7–12.** *Quercus* Group Ilex. **1.** Grain 1, light microscopy (LM), overview polar and equatorial view, tricolporoidate. **2.** Grain, scanning electron microscopy (SEM), oblique equatorial view. **3.** Grain 1, SEM, detail of sculpturing, verrucate scattered with densely spaced tuft agglomerations. **4.** Grain 2, LM, overview polar and equatorial view, tricolpate. **5.** Grain 2, SEM, equatorial view. **6.** Grain 2, SEM, detail of sculpturing, sculpturing verrucate scattered with tuft agglomerations. **7.** Grain 3, LM, overview, equatorial view, tricolp(oid)ate. **8.** Grain 3, SEM, equatorial view. **9.** Grain 3, SEM, detail of sculpturing, sculpturing rod-like, (micro)rugulate, tuft agglomerations in a single plane. **10.** Grain 4, LM, overview equatorial view, tricolp(oid)ate. **11.** Grain 4, SEM, equatorial view. **12.** Grain 4, SEM, detail of sculpturing, sculpturing rod-like, micro(rugulate), tuft agglomerations in a single plane. Scale bar is 10 μm in 1, 2, 4, 5, 7, 8, 10, 11; 1 μm in 3, 6, 9, 12.



Map ref.	Reference	Original determination	Revised determination (MT, morphotypes of <i>Quercus drymeja</i>)	Remarks
15	Unger 1847	<i>Quercus drymeja</i> p. 113, pl. 32, figs 1, 2, 4, (not 3) <i>Quercus mediterranea</i> p. 114, pl. 32, figs 5-9	Parschlug MT <i>Quercus mediterranea</i>	
15	Unger 1852	<i>Quercus mediterranea</i> p. 35, pl. 18, figs 1-6 <i>Quercus zoroastri</i> p. 36, pl. 18, figs 7, 8 (not 9) <i>Quercus gmelini</i> A.Braun p. 36, pl. 18, fig. 10 <i>Quercus urophylla</i> Unger p. 36, pl. 18, fig. 11	<i>Quercus mediterranea</i> Zoroastri MT Parschlug < > Zoroastri MT	
26	Kováts 1856	<i>Quercus szirmayana</i> Kováts p. 21, pl. 2, figs 1-5 <i>Q. pseudoilex</i> Kováts p. 22, pl. 2, fig. 6 <i>Q. urophylla</i> Unger p. 22, pl. 2, fig. 7	<i>Quercus mediterranea</i> Floribunda MT	
46	Gaudin & Strozzi 1859	<i>Quercus drymeja</i> p. 44, pl. 4, figs 1-18, Pl. 7, figs 1-2 <i>Quercus gaudini</i> p. 43, pl. 6, fig. 2 (not 3)	Parschlug MT Pl. 4, fig. 1 Floribunda MT Pl. 6, fig. 2	Floribunda MT Pl. 4, figs 2, 4, 6, 7, 8 a
33	Massalongo & Scarabelli 1859	<i>Quercus drymeja</i> p. 186, pl. 24, fig. 7, Pl. 42, fig. 10 <i>Juglans italica</i> Massalongo p. 396, pl. 33, figs 2, 13	uncertain if <i>Quercus</i> Floribunda MT	
7	Unger 1867	<i>Quercus lonchitis</i> p. 50, pl. 5, figs 1-17 <i>Quercus mediterranea</i> p. 52, pl. 6, figs 1-22 <i>Quercus zoroastri</i> p. 52, pl. 6, figs 23-28	Parschlug MT Pl. 5, figs. 1, 2, 4-13, 16, 17 <i>Quercus mediterranea</i> Floribunda MT Pl. 6, fig. 23	?Güvem MT Pl. 5, fig. 3
30	Boulay 1887	<i>Quercus drymeja</i> p. 258 <i>Quercus mediterranea</i> p. 259 <i>Quercus coccifera</i> L. p. 259	Parschlug MT <i>Quercus mediterranea</i> <i>Quercus mediterranea</i>	Floribunda MT b
43	Sordelli 1896	<i>Quercus drymeja</i> p. 125, pl. 21, figs 1-4 <i>Quercus praecursor</i> p. 127, pl. 20, fig. 11 <i>Quercus gaudinii</i> p. 128, pl. 20, figs 8-10	Floribunda MT Floribunda MT Floribunda MT	? <i>Q. mediterranea</i> Pl. 20, fig. 9

23	Engelhardt 1903	<i>Myrica acuminata</i> Unger	Güvem MT	
		p. 57, pl. 7, fig. 3		
		<i>Myrica banksiaefolia</i> Unger	Güvem MT	
		p. 58, pl. 7, fig. 4		
		<i>Quercus lonchitis</i> Unger	Güvem MT	
		p. 58, pl. 7, figs 6-8		
		<i>Pterocarya denticulata</i> Weber	Güvem MT	
		p. 63, pl. 7, fig. 9		
		<i>Quercus mediterranea</i>	Floribunda MT	
		p. 59, pl. 7, fig. 10		
23	Engelhardt 1903	<i>Castanea kubinyi</i> Kováts	Floribunda MT	
		p. 60, pl. 7, figs 12, 15		
23	Engelhardt 1903	<i>Quercus drymeja</i>	Floribunda MT	Güvem > Floribunda MT
		p. 59, pl. 7, figs 13, 14	Pl. 7, fig. 13	Pl. 7, fig. 14
23	Engelhardt 1903	<i>Quercus haidingeri</i> Ettingshausen	Güvem MT	
		p. 59, pl. 7, fig. 17		
		<i>Ilex ambigua</i> Unger	<i>Quercus mediterranea</i>	
		p. 63, pl. 7, fig. 19		
51	Pop 1936	<i>Quercus mediterranea</i>	<i>Quercus mediterranea</i>	
		p. 70, pl. 17, fig. 3		
51	Pop 1936	<i>Quercus cf. ilex</i>	? <i>Quercus mediterranea</i>	
		p. 71, pl. 2, fig. 4, Pl. 3, fig. 5, Pl. 17, figs 4-7		
16	Berger 1952a (Weingraben)	<i>Quercus drymeja</i>	? Parschlug MT	
31	Berger 1952b Berger 1955b	<i>Quercus cf. drymeja</i>	Floribunda MT	
		<i>Quercus cf. mediterranea</i>	<i>Quercus mediterranea</i>	
25	Berger 1953a (Hernals)	<i>Quercus drymeja</i>	Parschlug MT	
		<i>Quercus mediterranea</i>	<i>Quercus mediterranea</i>	
8	Berger, 1953b (Velitzelos et al., 2014)	<i>Quercus lonchitis</i> (<i>Q. drymeja</i>)	? Güvem MT	
17	Berger 1955a (Lavantt.)	<i>Quercus drymeja</i>	Parschlug MT	Floribunda > Parschlug MT
		<i>Quercus mediterranea</i>	Fig. 10-12 Floribunda MT	Fig. 9 Zoroastri MT
17	Berger 1955a (Lavantt.)	p. 408, figs 7, 8	Fig. 7	Fig. 8
		<i>Quercus goeppertii</i>	such leaves occur in Şahinalı	
32	Berger 1957b (Gabbro)	<i>Quercus drymeja</i>	Floribunda MT	Parschlug MT
		p. 21, pl. 4, figs 67, 68		
		<i>Quercus mediterranea</i>	Pl. 4, figs 69, 71	Pl. 4, figs 70, 72-74
		<i>Quercus linguiformis</i> N.Boulay	<i>Quercus mediterranea</i>	
32	Berger 1957b (Gabbro)	p. 33, pl. 11, figs 155-164	Floribunda MT	
		p. 34, pl. 11, fig. 165		

18	Berger 1957a (Teiritzberg)	<i>Quercus drymeja</i> p. 91, fig. 2	Floribunda MT
42	Kolakowski 1964	<i>Castanopsis elisabethae</i> Kolakovsky p. 79, pl. 24, fig. 5	Floribunda MT
		<i>Castanopsis bifurcata</i> Kolakovsky p. 78, pl. 24, fig. 6	Floribunda MT
		<i>Castanopsis furcinervis</i> p. 80, pl. 24, figs 7, 8, Pl. 25, figs 1, 2	Floribunda > Güvem MT
		<i>Quercus sosnowskyi</i> forma <i>angustifolia</i> p. 90, pl. 25, figs 3-11	Floribunda MT
54	Kolakovsky and Ratiani 1967	<i>Quercus mediterranea</i> pl. 4, figs 2-4	<i>Quercus mediterranea</i>
52	Givulescu and Ghiurca 1969	<i>Quercus</i> cf. <i>glaucofolia</i> p. 35, pl. 9, fig. 7	?Parschlug MT
		<i>Quercus</i> cf. <i>ilex</i> p. 38, pl. 17, figs 13a, b	? <i>Quercus mediterranea</i>
		<i>Quercus mediterranea</i> p. 38, pl. 9, fig. 9	<i>Quercus mediterranea</i> or Floribunda MT
		<i>Quercus</i> sp. aff. <i>Q. coccifera</i> ? p. 39, pl. 8, fig. 9	?
		<i>Quercus drymeja</i> p. 39, pl. 9, fig. 11	Floribunda MT
10	Knobloch & Kvaček 1976	<i>Quercus</i> sp. p. 43, pl. 17, figs 15, 18, Pl. 19, fig. 9, Pl. 21, figs 8, 9	?Floribunda MT
		<i>Quercus mediterranea</i> vel <i>Castanea</i> sp. p. 42, pl. 21, fig. 7, Pl. 30, fig. 10	<i>Quercus mediterranea</i>
9	Paicheler and Blanc, 1981	<i>Myrica lignitum</i> pl. 3, fig. 3	Floribunda MT
		<i>Myrica acuminata</i> pl. 3, figs 6-9	Güvem MT
		<i>Myrica</i> sp. pl. 3, fig. 10	Güvem MT
		<i>Quercus mediterranea</i> pl. 9, figs 4-11	<i>Quercus mediterranea</i>
		<i>Quercus drymeja</i> pl. 10, figs 11-14	Güvem MT
		<i>Quercus drymeja</i> pl. 11, figs 1, 2	cf. <i>Eotrigonobalanus</i> <i>furcinervis</i>

37	Knobloch & Velitzelos 1986a	<i>Quercus</i> cf. <i>drymeja</i> "Group 1" p. 10, pl. 3, fig. 10, Pl. 5, figs 2, 7, 8	Floribunda MT	
		<i>Quercus</i> cf. <i>drymeja</i> "Group 2" p. 10, pl. 3, figs 2-4, 7-8, Pl. 4, figs 3, 6	Floribunda MT	? Zoroastri MT
		<i>Quercus dubia</i> p. 11, pl. 3, fig. 1	?Floribunda MT	
		<i>Quercus</i> cf. <i>mediterranea</i> p. 11, pl. 2, fig. 5	<i>Quercus mediterranea</i>	
36	Knobloch & Velitzelos 1986b	<i>Quercus</i> cf. <i>mediterranea</i> p. 30, pl. 14, figs 4, 11, Pl. 15, fig. 7	<i>Quercus mediterranea</i>	
21	Gemici et al. 1990	<i>Quercus drymeja</i>	not figured	
		<i>Quercus goeppertii</i> vel <i>kubinyii</i>	Floribunda MT	
		<i>Quercus ilex</i> p. 33, fig. 3c	<i>Quercus mediterranea</i>	
20	Gemici et al. 1991	<i>Quercus drymeja</i> p. 172, pl. 8, fig. 9	Güvem MT	
		<i>Quercus ilex</i> L. p. 172, pl. 9, figs 1, 2		
		<i>Quercus mediterranea</i> p. 173, pl. 9, fig. 6	<i>Quercus mediterranea</i>	
		<i>Quercus</i> cf. <i>trojana</i> p. 173, pl. 9, fig. 7	?Güvem MT	
22	Gemici et al. 1993	<i>Quercus drymeja</i> p. 99, pl. 6, fig. 1	Floribunda MT	
		<i>Castanopsis</i> sp. p. 95, pl. 6, fig. 5	Floribunda MT	
		<i>Quercus</i> cf. <i>drymeja</i> p. 99, pl. 7, figs 1, 3	Floribunda MT	
		<i>Quercus mediterranea</i>		
5	Kvaček et al. 1993	<i>Quercus</i> ex gr. <i>drymeja</i> text fig. 4a, b, Pl. 2, figs 4-7, p. 61, pl. 3, figs 1-4	Floribunda MT	c
		<i>Quercus mediterranea</i> text fig. 4c-g, Pl. 3, figs 5-7, p. 62, pl. 8, fig. 4	<i>Quercus mediterranea</i>	
12	Schweigert 1993	<i>Quercus drymeja</i> p. 66, pl. 2, fig. 5	Floribunda MT	
		<i>Quercus mediterranea</i> p. 67, pl. 2, fig. 2	<i>Quercus mediterranea</i>	
38	Kleinhölter 1994	<i>Quercus drymeja</i> Fig. 2, 6	Floribunda MT	
		<i>Quercus mediterranea</i>	<i>Quercus mediterranea</i>	
4	Bůžek et al. 1996	<i>Quercus</i> cf. <i>drymeja</i> p. 21, pl. 11, figs 2, 4	? Güvem MT	
11	Knobloch & Kvaček 1996	<i>Quercus</i> cf. <i>drymeja</i> p. 52, pl. 7, figs. 1, 2, 5, pl. 8, figs 4, 4a, pl. 9, fig. 7, pl. 15, fig. 9, text figs 7, 8	Floribunda MT	

13	Schmitt & Butzmann 1997	cf. <i>Quercus</i> sp. p. 59, pl. 2, fig. 11 cf. <i>Myrica</i> sp. p. 59, pl. 3, figs 7, 8; pl. 4, fig. 2	<i>Quercus mediterranea</i> Floribunda MT Parschlug MT Pl. 3, figs 7, 8 Pl. 4, fig. 2
29	Barron 1999a, b	<i>Quercus drymeja</i> Fig. 4d	Parschlug MT
14	Ströbitzer 1999	<i>Quercus drymeja</i> p. 100, pl. 2, fig. 10, pl. 9, figs 7-9	Parschlug MT Pl. 2, fig. 10, Pl. 9, figs 7-9
47	Fischer & Butzmann 2000	<i>Quercus drymeja</i> p. 45, pl. 11, figs 6-11, text-figs 63-66	Floribunda MT
35	Kvaček et al. 2002	<i>Quercus mediterranea</i> p. 65, pl. 10, figs 7, 9-11, pl. 31, figs 1, 2 <i>Quercus drymeja</i> p. 66, pl. 10, figs. 8, 12, pl. 11, figs 1-7, pl. 15, figs 2, 7, pl. 30, figs 5, 6	<i>Quercus mediterranea</i> Floribunda MT ?Parschlug MT Pl. 11, fig. 7
48	Martinetto 2003	<i>Quercus</i> cf. <i>ilex</i> p. 96, pl. 3, fig. 10	Floribunda MT
15	Kovar-Eder et al. 2004	<i>Quercus drymeja</i> p. 61, pl. 4, figs 1-7 <i>Quercus mediterranea</i> p. 62, pl. 4, figs 8-16 <i>Quercus zoroastri</i> p. 62, pl. 5, figs. 1-4	Parschlug MT Pl. 4, figs 1-7 <i>Quercus mediterranea</i> Pl. 4, figs 8-16 Zoroastri MT Floribunda MT Pl. 5, figs. 1, 3, 4 Pl. 5, fig. 2
41	Palamarev & Tsenov 2004	<i>Quercus mediterranea</i> p. 149, plate 1, fig. 5 <i>Quercus sosnowskyi</i> p. 149, plate 1, fig. 3, Pl. 2, fig. 5, Pl. 3, figs 1, 2 <i>Quercus ilex</i> fossilis p. 150, pl. 1, fig. 6 <i>Quercus drymeja</i> p. 150, pl. 2, fig. 3, Pl. 3, figs 3, 4 <i>Quercus lonchitis</i> p. 150, pl. 1, fig. 4	<i>Quercus mediterranea</i> Floribunda MT Floribunda MT Floribunda MT Parschlug > Floribunda MT
40	Zidianakis et al. 2007	<i>Quercus mediterranea</i> p. 358, fig. 2h-k, 5j <i>Quercus</i> sp. p. 359, fig. 3a, 5q	<i>Quercus mediterranea</i> ?Floribunda MT
39	Zidianakis et al. 2010	<i>Quercus mediterranea</i> fig. 2m <i>Quercus drymeja</i> fig. 2o	<i>Quercus mediterranea</i> Floribunda MT
53	Bozukov et al. 2011	<i>Quercus</i> aff. <i>acrodonta</i> p. 8, pl. 2, figs 1, 2 <i>Quercus drymeja</i> p. 8, pl. 2, fig. 4 <i>Quercus sosnowskyi</i> p. 9, pl. 2, figs 5, 6	Floribunda MT Floribunda MT Floribunda MT

19	Kvaček et al. 2011	<i>Quercus drymeja</i>	Güvem MT	e
		p. 28, pl. 6, figs 1-6		
		<i>Quercus cf. zoroastri</i>	Parschlug <> Zoroastri MT	
44	Robles et al. 2013	<i>Quercus drymeja</i>	Floribunda MT	
		p. 79, pl. 1, figs 14, 15		
28	Velitzelos et al. 2014 (Chios)	<i>Quercus mediterranea</i>	<i>Quercus mediterranea</i>	
49	Velitzelos et al. 2014	<i>Quercus drymeja</i>	Floribunda MT	
		pl. 28, figs 9, 10, pl. 29, figs 1, 2		
34	Teodoridis et al. 2015	<i>Quercus aff. mediterranea</i>	? <i>Quercus mediterranea</i>	
		pl. 28, fig. 11		
34	Teodoridis et al. 2015	<i>Quercus mediterranea</i>	<i>Quercus mediterranea</i>	
		p. 261, pl. 7, figs 7-9		

Colour coding corresponds to that in Maps 1 and 2

Map nos. refer to Maps 1 and 2

^a pl. 4, figs 2, 8 extremely similar to modern *Q. floribunda*

^b Boulay lists 3 varieties: **var. ungeri** [Gaudin pl. 4, fig. 1] corresponds to Parschlug MT; **var. integrbasis** N.Boulay [Gaudin pl. 4, figs. 3, 6, 7] corresponds to Floribunda MT; **var. laharpü** N.Boulay [Gaudin Pl. 4, figs 5, 10]

^c Similar to the Likoudi specimens

^d Specimen S133952 Parschlug very similar to *Q. floribunda*

^e The *Q. mediterranea* leaves may well be from the same biological species as the *Q. drymeja* and *Q. zoroastri* leaves

<i>Quercus floribunda</i> E Afghanistan- NW Pakistan	N India-Nepal oak forests of the outer slopes of the Himalayas	<i>Quercus lanata</i> N India-Nepal
(1600) 1900-2400 (2900) m	1500-2400 (2850) m	600-1800 (2000) m
<i>Quercus floribunda</i> Lindley (<i>Q. dilatata</i> Royle)	<i>Quercus floribunda</i> Lindley (<i>Q. dilatata</i> Royle)	<i>Quercus lanata</i> Smith (<i>Q. incana</i> Roxburgh, <i>Q. leucotrichophora</i> A.Camus)
<i>Acer platanoides</i> subsp. <i>turkestanicum</i> (Pax) P.C.DeJong	<i>Acer caesium</i> Wallich ex Brandis	<i>Acer acuminatum</i> Wallich ex D.Don
<i>Celtis caucasica</i> Willdenow	<i>Acer cappadocicum</i> Gleditsch (<i>A. cultratum</i> Wallich)	<i>Acer caesium</i> Wallich ex Brandis
<i>Clematis</i> spp.	<i>Aesculus indica</i> (Wallich ex Camb.) Hook.f.	<i>Acer cappadocicum</i> Gleditsch (<i>A. cultratum</i> Wallich)
<i>Cotoneaster roseus</i> Edgeworth	<i>Berberis</i> spp.	<i>Acer oblongum</i> Wallich ex DC.
<i>Diospyros lotus</i> L.	<i>Betula alnoides</i> Buchanan-Hamilton ex D.Don	<i>Albizia chinensis</i> (Osbeck) Merrill
<i>Hedera helix</i> L.	<i>Buxus sempervirens</i> L.	<i>Alnus nepalensis</i> D.Don
<i>Indigofera heterantha</i> Brandis	<i>Carpinus viminea</i> Lindley in Wallich	<i>Betula alnoides</i> Buchanan-Hamilton ex D.Don
<i>Isodon rugosus</i> (Wallich ex Benth) Codd	<i>Cornus capitata</i> Wallich ex Roxburgh	<i>Camellia</i> sp.
<i>Jasminum humile</i> L.	<i>Cornus macrophylla</i> Wallich	<i>Carpinus viminea</i> Lindley in Wallich
<i>Juglans regia</i> L.	<i>Corylus colurna</i> L.	<i>Cornus capitata</i> Wallich ex Roxburgh
<i>Lonicera quinquelocularis</i> Hardwicke in Hooker f.	<i>Desmodium</i> sp.	<i>Cornus macrophylla</i> Wallich
<i>Parrotiopsis jacquemontiana</i> (Decaisne) Rehder	<i>Euonymus fimbriatus</i> Wallich	<i>Deutzia corymbosa</i> R.Brown
<i>Piptanthus nepalensis</i> (Hooker) D.Don	<i>Euonymus lucidus</i> D.Don	<i>Euonymus tingens</i> Wallich
<i>Prunus cornuta</i> (Wallich ex Royle) Steudel	<i>Euonymus tingens</i> Wallich	<i>Ficus neriifolia</i> var. <i>nemoralis</i> (Wallich ex Miq.) Corner
<i>Pyrus pashia</i> L.	<i>Indigofera heterantha</i> Brandis	<i>Fraxinus floribunda</i> Wallich
<i>Quercus baloot</i> Griffith [Ilex]	<i>Juglans regia</i> L.	<i>Ilex dipyrena</i> Wallich
<i>Rhamnus dahuricus</i> Wilson	<i>Lonicera quinquelocularis</i> Hardwicke in Hooker f.	<i>Neolitsea umbrosa</i> (Nees) Gamble
<i>Rosa moschata</i> Herrmann	<i>Lonicera unguistifolia</i> Wallich ex Candolle	<i>Lonicera quinquelocularis</i> Hardwicke in Hooker f.
<i>Rosa</i> spp.	<i>Lyonia ovalifolia</i> (Wallich) Drude	<i>Lyonia ovalifolia</i> (Wallich) Drude
<i>Rubus caesius</i> L.	<i>Machilus duthiei</i> King ex Hooker f.	<i>Machilus duthiei</i> King ex Hooker f.
<i>Syringa emodi</i> Wallich ex Royle	<i>Meliosma dilleniifolia</i> (Wallich ex Wight & Am.) Walpers	<i>Machilus odoratissima</i> Nees
<i>Viburnum cotinifolium</i> D.Don	<i>Neolitsea umbrosa</i> (Nees) Gamble	<i>Mallotus philippiensis</i> (Lamarck) Müller Argoviensis
<u>Conifers</u>	<i>Platanus orientalis</i> L.	<i>Myrsine africana</i> L.
<i>Cedrus deodara</i> (Roxburgh) G.Don	<i>Prunus cornuta</i> (Wallich ex Royle) Steudel	<i>Olea europaea</i> subsp. <i>cuspidata</i> (Wallich ex G.Don) Ciferri
<i>Pinus gerardiana</i> Wallich ex D.Don	<i>Quercus lanata</i> Smith [Ilex]	<i>Phoebe lanceolata</i> (Nees) Nees
<i>Pinus wallichiana</i> A.B.Jackson	<i>Quercus semecarpifolia</i> Smith [Ilex]	<i>Populus ciliata</i> Wallich ex Royle
	<i>Rhamnus purpurea</i> Edgeworth	<i>Pyrus pashia</i> L.
	<i>Rhododendron arboreum</i> Smith	<i>Quercus glauca</i> Thunberg [Cyclobalanopsis]
	<i>Rosa</i> spp.	<i>Quercus semecarpifolia</i> Smith [Ilex]
	<i>Salix denticulata</i> Andersson	<i>Rhamnus triquetra</i> (Wallich) Brandis
	<i>Sorbus lanata</i> (D.Don) Schauer	<i>Rhododendron arboreum</i> Smith
	<i>Staphylea emodii</i> Brandis	<i>Toxicodendron succedaneum</i> (L.) Kuntze
	<i>Ulmus wallichiana</i> Planchon	<i>Ulmus wallichiana</i> Planchon
	<i>Viburnum cotinifolium</i> D.Don	<i>Viburnum cotinifolium</i> D.Don
	<i>Viburnum nervosum</i> D.Don	<i>Viburnum nervosum</i> D.Don
	<i>Viburnum stellatum</i> (Oersted) Hemsley	<i>Woodfordia fruticosa</i> (L.) Kurz
	<u>Conifers</u>	<u>Conifers</u>
	<i>Abies pindrow</i> (Royle ex D.Don) Royle	<i>Cedrus deodara</i> (Roxburgh) G.Don
	<i>Abies spectabilis</i> (D.Don) Mirbel	<i>Cupressus torulosa</i> D.Don
	<i>Picea smithiana</i> (Wallich) Boissier	<i>Picea smithiana</i> (Wallich) Boissier
	<i>Pinus wallichiana</i> A.B.Jackson	<i>Pinus wallichiana</i> A.B.Jackson
	<i>Taxus baccata</i> L.	<i>Pinus roxburghii</i> Sargent
(Freitag, 1971; Menitsky, 2005)	(Menitsky, 2005)	(Menitsky, 2005)

Table SI 2: Oak forests of the outer slopes of the Himalaya. *Quercus floribunda* and *Q. lanata* dominated mesophytic montane forests in warm temperate climates (Cf and Cw climates according to Köppen and Geiger)

<i>Quercus engleriana</i>		
China, Omei Shan, Sichuan	Daba Shan, Hubei	Guizhou, Chongqing
deciduous evergreen mixed forest	deciduous evergreen mixed forest	relict forests with the conifer <i>Cathaya</i>
700-1600 m	1000-1800 m	1200-1800 m
<i>Quercus engleriana</i> Seemen	<i>Quercus engleriana</i> Seemen	<i>Quercus engleriana</i> Seemen
<i>Acer</i> spp.	<i>Acer maximowiczii</i> Pax	<i>Abelia engleriana</i> (Graebner) Rehder
<i>Acer davidii</i> Franchet	<i>Acer robustum</i> Pax	<i>Acanthopanax trifoliatum</i> (L.) Merr
<i>Ailanthus vilmoriniana</i> Dode	<i>Acer sterculiaceum</i> subsp. <i>franchetii</i> (Pax) A.E.Murray	<i>Acer davidii</i> Franchet
<i>Alnus cremastogyne</i> Burkill	<i>Aralia chinensis</i> L.	<i>Berberis fallaciosa</i> C.K.Schneider
<i>Betula insignis</i> Franchet	<i>Carpinus cordata</i> Blume	<i>Berchemia floribunda</i> (Wallich) Brongniart
<i>Betula luminifera</i> H.J.P.Winkler	<i>Castanopsis carlesii</i> (Hemsley) Hayata	<i>Blastanopsis pauciflorus</i> (Bentham) Guillaumin
<i>Carpinus fangiana</i> Hu	<i>Eleocarpus japonicus</i> Siebold & Zuccarini	<i>Camellia grijsii</i> Hance
<i>Castanopsis platyacantha</i> Rehder & E.H.Wilson	<i>Fagus engleriana</i> Seemen	<i>Cladrastis delavayi</i> (Franchet) Prain
<i>Celtis biondii</i> Pampanini	<i>Kerria japonica</i> (L.) DC.	<i>Cladrastis sinensis</i> Hemsley
<i>Celtis bungeana</i> Blume	<i>Lithocarpus viridis</i> (Schottky) Rehder & E.H.Wilson	<i>Cornus oblonga</i> Wallich in Roxburgh
<i>Cercidiphyllum japonicum</i> Siebold & Zuccarini	<i>Lonicera giraldii</i> Rehder	<i>Cotoneaster glaucophyllus</i> Franchet
<i>Corylus</i> spp.	<i>Machilus thunbergii</i> Siebold & Zuccarini	<i>Cotoneaster rhytidophyllus</i> Rehder & E.H.Wilson
<i>Davidia involucrata</i> Baillon	<i>Michelia wilsonii</i> Finet & Gagnepain	<i>Daphniphyllum macropodum</i> Miquel
<i>Fagus longipetiolata</i> Seemen	<i>Photinia glabra</i> (Thunberg) Maximowicz	<i>Dipelta yunnanensis</i> Franchet
<i>Fagus lucida</i> Rehder & E.H.Wilson	<i>Quercus acrodonta</i> Seemen [Ilex]	<i>Enkianthus chinensis</i> Franchet
<i>Juglans regia</i> L.	<i>Quercus baronii</i> Skan [Ilex]	<i>Enkianthus quinqueflorus</i> Loureiro
<i>Lithocarpus cleistocarpus</i> (Seemen) Rehder & E.H.Wilson	<i>Quercus dolicholepis</i> A.Camus [Ilex]	<i>Euonymus porphyreus</i> Loesener
<i>Lithocarpus megalophyllus</i> Rehder & E.H.Wilson	<i>Quercus glauca</i> Thunberg [Cyclobalanopsis]	<i>Gamblea ciliata</i> C.B.Clarke
<i>Lithocarpus viridis</i> (Schottky) Rehder & E.H.Wilson	<i>Quercus oxyphylla</i> (E.H.Wilson) Handel-Mazzetti [Ilex]	<i>Helwingia japonica</i> (Thunberg) F.Dietrich
<i>Machilus yunnanensis</i> Lecomte	<i>Quercus phillyreoides</i> A.Gray [Ilex]	<i>Hugeria vaccinoidea</i> (H.Léveillé) Hara
<i>Magnolia</i> sp.	<i>Quercus serrata</i> Murray [Quercus]	<i>Ilex franchetiana</i> Loesener
<i>Morus</i> sp.	<i>Schima superba</i> Gardner & Champion	<i>Ilex pedunculosa</i> Miquel
<i>Prunus</i> sp.	<i>Schisandra sphaenantha</i> Rehder & E.H.Wilson	<i>Lindera obtusiloba</i> Blume
<i>Pterocarya</i> sp.	<i>Symplocos paniculata</i> (Thunberg ex Murray) Miquel	<i>Litsea cubeba</i> (Loureiro) Persoon
<i>Pteroceltis tatarinowii</i> Maximovich	<i>Viburnum betulifolium</i> Batalin	<i>Litsea ichangensis</i> Gamble
<i>Quercus acutissima</i> Carruthers [Cerris]		<i>Lyonia ovalifolia</i> (Wallich) Drude
<i>Quercus aliena</i> Blume [Quercus]	<u>Conifers</u>	<i>Neolitsea aurata</i> (Hayata) Koidzumi
<i>Quercus baronii</i> Skan [Ilex]	<i>Tsuga chinensis</i> (Franchet) E.Pritzel	<i>Neolitsea chunii</i> Merrill
<i>Quercus dentata</i> Thunberg [Quercus]		<i>Quercus glauca</i> Thunberg [Cyclobalanopsis]
<i>Quercus glauca</i> Thunberg [Cyclobalanopsis]		<i>Rhamnus hemsleyana</i> C.K.Schneider
<i>Quercus oxyodon</i> Miquel [Cyclobalanopsis]		<i>Rhododendron longipes</i> Rehder & E.H.Wilson
<i>Quercus serrata</i> Murray [Quercus]		<i>Rhododendron mariesii</i> Hemsley & E.H.Wilson
<i>Quercus spinosa</i> David [Ilex]		<i>Rhododendron simsii</i> Planchon
<i>Rhus</i> sp.		<i>Rubus bambusarum</i> Focke
<i>Schima crenata</i> Korthals		<i>Rubus pinnatisepalus</i> Hemsley
<i>Schima superba</i> Gardner & Champion		<i>Schima sinensis</i> (Hemsley & E.H.Wilson) Airy-Shaw
<i>Sorbus</i> sp.		<i>Smilax discotis</i> Warburg
<i>Ternstroemia japonica</i> (Thunberg) Thunberg		<i>Sorbus folgneri</i> (C.K.Schneider) Rehder
<i>Tetracentron sinense</i> Oliver		<i>Sorbus hemsleyi</i> (C.K.Schneider) Rehder
<i>Tilia chinensis</i> Maximovich		<i>Symplocos sumuntia</i> Buchanan-Hamilton ex D.Don
<i>Zelkova sinica</i> C.K.Schneider		<i>Vaccinium henryi</i> Hemsley
		<i>Viburnum cylindricum</i> Buchanan-Hamilton ex D. Don
		<i>Zanthoxylum dimorphophyllum</i> Hemsley
<u>Conifers</u>		<u>Conifers</u>
<i>Taxus chinensis</i> (Rehder & E.H.Wilson) Rehder		<i>Cathaya argyrophylla</i> Chun & Kuang
		<i>Torreya fargesii</i> Franchet
(Schroeder, 1998; Menitsky, 2005)	(Menitsky, 2005)	(Ying et al., 1983; Qian et al., 2016)

Table SI 3: Oak forests of temperate China. *Quercus engleriana* occurs scattered in these forests.

References

Qian, S., Yang, Y., Tang, C. Q., Momohara, A., Yi, S., Ohsawa, M., 2016. Effective conservation measures are needed for wild *Cathaya argyrophylla* populations in China: Insights from the population structure and regeneration characteristics. *Forest Ecology and Management* 361, 358–367.

Ying, T., Ma, C., Li, L., Zhang, Z., Zhang, W., 1983. Studies on the *Cathaya* communities. *Acta Botanica Sinica* 25, 157–170.

Quercus setulosa**NW Thailand**

subtropical pine-oak open forest with grasses

600--1000 m*Quercus setulosa* Hickel & A.Camus*Anneslea fragrans* Wallich*Castanopsis diversifolia* (Kurz) King ex Hooker f.*Castanopsis indica* (Roxburgh ex Lindley) A.DC.*Helicia nilagirica* Beddome*Lithocarpus fenestratus* (Roxburgh) Rehder*Lithocarpus sootepensis* (Craib) A.Camus*Lithocarpus truncatus* (King ex Hooker f.) Rehder*Lyonia ovalifolia* (Wallich) Drude*Phyllanthus emblica* L.*Quercus acutissima* Carruthers [Cerris]*Quercus griffithii* J.D.Hooker & Thomson ex Miquel [Quercus]*Quercus helferiana* A.DC. [Cyclobalanopsis]*Quercus kerrii* Craib [Cyclobalanopsis]*Quercus kingiana* Craib [Ilex]Conifers:*Pinus kesiya* Royle ex Gordon*Pinus merkusii* Junghuhn & de Vriese

(Menitsky, 2005; Le Hardy de Beaulieu and Lamant, 2010)

N Thailand, Thanon Thong Chai Range

wet subtropical forest

600--1000 m*Quercus setulosa* Hickel & A.Camus*Calophyllum* sp.*Carpinus* sp.*Castanopsis acuminatissima* (Blume) A.DC.*Cinnamomum* sp.*Engelhardia* sp.*Eugenia* sp.*Euodia* sp.*Manglietia* sp.*Michelia* sp.*Pithecellobium* sp.*Quercus quangtriensis* Hickel & A.Camus [Cyclobalanopsis]*Rhododendron* sp.*Schima wallichii* (DC.) Korthals*Styrax* sp.*Vaccinium* sp.Conifers:*Cephalotaxus griffithii* Hooker f.*Podocarpus* sp.

(Menitsky, 2005)

Table SI 4: Subtropical forests of SE Asia with *Quercus setulosa*

Reference

Le Hardy de Beaulieu, A., Lamant, T., 2010. Guide illustré des chênes. 2 volumes. Geer, Edilens.