



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.

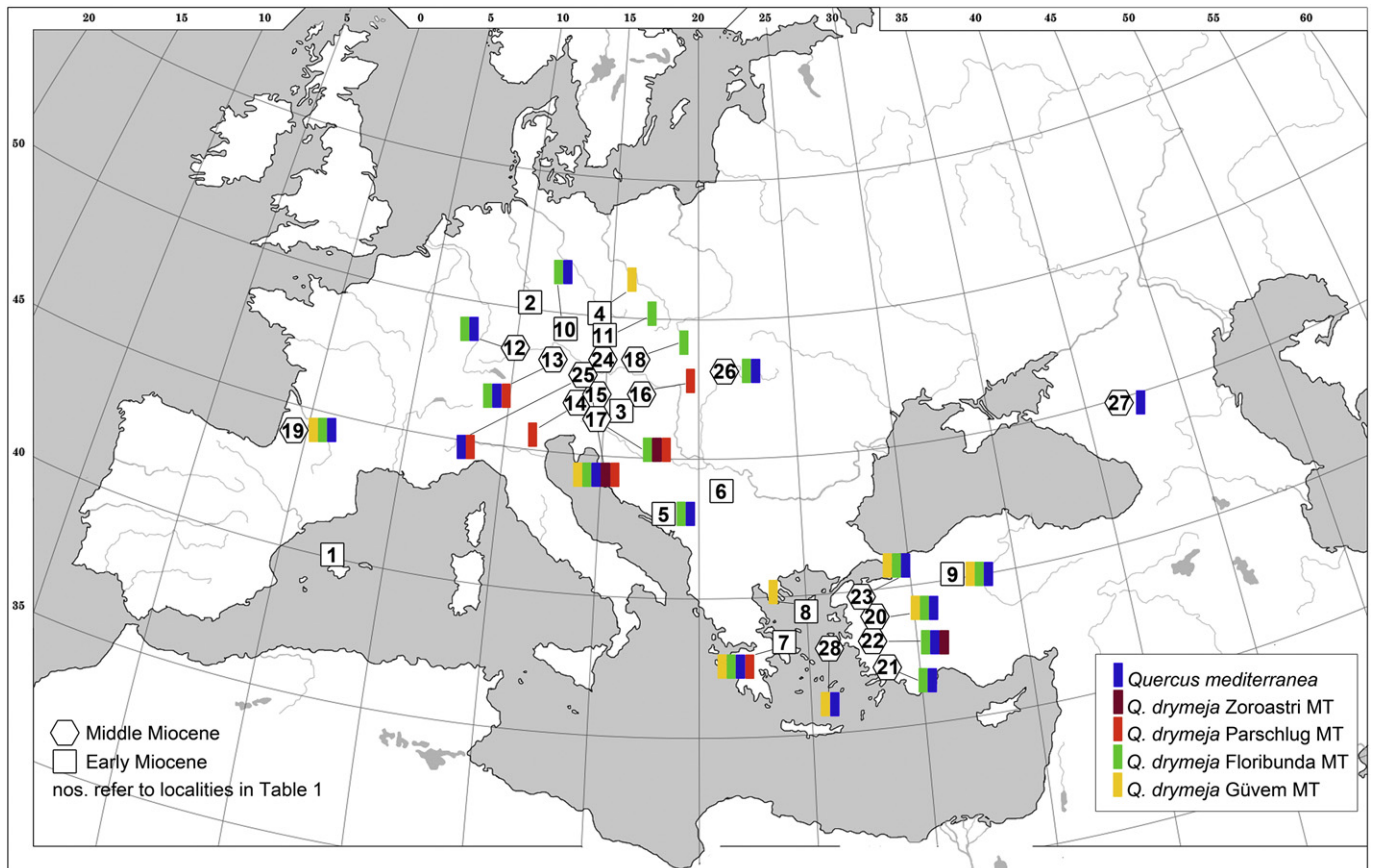
1.1. The fossil record of sclerophyllous oaks in Europe

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).

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