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Review paper

Review of the Cenozoic floras and vegetation of Greece ☆

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ABSTRACT

Oligocene to Pleistocene floras of Greece are reviewed based on published and unpublished material. Oldest plant-bearing sediments of Rupelian–Chattian age are exposed in eastern Thrace (Evros) and were deposited after the closure of the Turgai Seaway. They contain a blend of (*i*) taxa that migrated to western Eurasia from the East (*Alnus*, *Fagus*), (*ii*) characteristic Oligocene taxa (*Nyssa altenburgensis*, *Ampelopsis hibschii*), and (*iii*) extinct (*Eotrigonobalanus*, *Quasisequoia*) and modern genera (*Calocedrus*, *Quercus* Group Lobatae) from older epochs. Coastal palm swamps and laurel forests of the hinterland indicate a subtropical, fully humid to winter-dry climate (Cfa, Cwa according to Köppen). The Aquitanian–Burdigalian plant assemblage of Lesbos is intermediary between Evros and the Burdigalian floras of Euboea sharing taxa with Evros (palms), and with Euboea and early Miocene floras of Anatolia (Güvem, *Tilia*). In the early Miocene (Burdigalian) floras of Euboea, species of *Quercus* Group Ilex (*Quercus drymeja*, *Quercus mediterranea*) characteristic of fully humid or winter-dry (monsoon) climates (Cf, Cw) became dominant elements in well-drained forests. Floristic links are with late Oligocene to middle Miocene floras of Central Asia (*Tilia*), Asia Minor (cycads, *Quercus* Group Ilex, *Tilia*), and South and Central Europe (cycads, *Quercus* Group Ilex, palms). Middle Miocene floras are restricted to the Aegean Islands (Chios). Biogeographic links are with early to late Miocene floras of Central Europe (*Parrotia*, *Podocarpium*) and with middle Miocene floras of Anatolia (*Parrotia*). Upper Miocene plant-bearing sedimentary formations are most abundant in Greece and exposed on the Ionian Islands, Greece mainland to East Macedonia, Peloponnese, Aegean Islands, and Crete. Overall, the fossil plant assemblages from Greece mainland are indicative of fully humid conditions during this time (Cfa), with *Fagus* and oaks of *Quercus* Group Ilex being dominant elements. Seasonality may have been more pronounced on the Peloponnese and the Aegaean Islands and Crete, expressed by the rare occurrence of *Fagus* in the fossil records of these areas. The palaeobotanical records from Samos unambiguously point to the presence of forest vegetation during early Tortonian to Messinian (Cwa) when the famous vertebrate faunas of Samos were deposited. The Pliocene is characterized by the regional occurrence of modern types of deciduous oaks mainly of *Quercus* Group Cerris and *Quercus* subsect. *Galliferae*. East Asian links persist in *Fagus*, *Quercus*, and Cupressaceae, North American ones in *Sabal*; several other mesophytic taxa from previous periods are recorded as well. The modern sclerophyllous Mediterranean vegetation, thriving in a warm summer dry climate (Csa), cannot be traced prior to the Pleistocene based on the palaeobotanical record.

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☆ Dedicated to Professor Evangelos Velitzelos.

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1. Introduction

At present, most parts of Greece enjoy a Mediterranean climate with hot and dry summers caused by the Subtropical High and cyclonic rains in winter due to the North Atlantic Oscillation (Walter, 1973). Mediterranean sclerophyllous forests are the climax vegetation under such a climate (Schroeder, 1998). The modern Mediterranean climate and vegetation are a young phenomenon and cannot be traced further back than to the late Pliocene (e.g. Suc, 1984). Nevertheless, "Mediterranean elements" and sclerophyllous plant taxa that were interpreted to reflect truly Mediterranean conditions have been reported in western Eurasia from all periods of the Cenozoic (Palamarev, 1989; Mai, 1995). The origin of sclerophyllous vegetation and the evolution of the adaptive characters of its taxa have variously been discussed in a northern hemispheric context (Axelrod, 1975; Kadereit and Baldwin, 2012).

Cenozoic floras of Greece have been in the focus of palaeobotanical research since the middle of the 19th century (e.g. Brongniart, 1833; Sauvage, 1846; Heer, 1859; Brongniart, 1861; Unger, 1862, 1867; Saporta, 1868; Fuchs, 1877; Teller, 1880; Fritel, 1921a,b). One of the most representative Cenozoic plant taxa of the Northern Hemisphere, *Glyptostrobus europaeus*, was originally described from the lower Miocene of Allonisos (as île d'Iliodroma), an island of the Northern Sporades (Brongniart, 1833). Major biogeographic questions have been addressed by Unger (1867), who compared plant fossils from the lower Miocene of Kimi to southern hemispheric genera of the family Proteaceae, long before Wegener's theory of the continental drift had been formulated, and hence suggesting that plant groups that are today confined to areas outside Europe may have had a much wider distribution in the past.

Intensified research on the Cenozoic floras of Greece started in the 1970ies (Velitzelos, 1974) and since then a great number of new floras have been discovered and described (e.g. Knobloch and Velitzelos, 1986a, 1986b; Kleinhölter, 1994a, 1994b, 1995b; Sachse, 1997; Mai and Velitzelos, 2002) including a monograph on the late Miocene flora of Vegora from northern Greece (Kvaček et al., 2002). Overviews about Greek floras have previously been compiled by Velitzelos and Gregor (1990) and Velitzelos (1993), and Gregor (1990) reviewed the Cenozoic vegetation and climate history in the Mediterranean region.

In the present paper we provide updated and new flora lists for most of the known Cenozoic Greek plant fossil localities along with illustrations of representative taxa. We review previous work and discuss more than 50 Oligocene to latest Pleistocene plant assemblages from Greece in a Mediterranean, western Eurasian, and northern hemispheric context. Major taxonomic changes in plant communities are discussed in view of regional and large scale environmental and climatic changes. Temporal and spatial changes of vegetation across Greece are traced and the timing of the origin of the modern Mediterranean vegetation is discussed.

2. Material and methods

The present paper is based on plant fossil material stored at the University of Athens. Most of the material has been collected since the 1970s by various people. Major collections were assembled by Evangelos and Dimitrios Velitzelos in collaboration with Erwin Knobloch, Dieter Hans Mai, Herbert Süss, Hans-Joachim Gregor, Thomas Denk and others. In addition, important material from the Peloponnese was collected by Klaus Kleinhölter and from Crete by Markus Sachse and Giannis Zidianakis. Historical collections assembled in the course of Brongniart's, Unger's and other studies of the fossil flora of Kimi are stored at various European museums and universities, e.g. Paris and Vienna.

Published accounts on Cenozoic plant assemblages from Greece are reviewed and the nomenclature and determinations revised when necessary. This is particularly important to enable comparability between fossil plant assemblages and to avoid taxonomic redundancy. In addition to the revised floral lists, a number of unpublished floras are presented.

In order to assess the broad palaeoecology of fossil plant taxa, the ecology of their potential modern analogs was considered. Depending on the taxonomic resolution, modern analogs may be species, infrageneric groups, genera, or families. For systematic evaluation of fossil taxa, phylogenetic frameworks were considered when available (e.g. Denk and Grimm, 2009a, 2010).

In addition, sedimentary context and context of fossil plant assemblages was used to infer the palaeoecology of fossil taxa (e.g. Walther, 1972, for *Acer*; Walther, 1989, for *Cunninghamia*; Kvaček and Walther, 1989, for *Eotrigonobalanus*; Kunzmann, 1999, for *Quasisequoia*; Kvaček et al., 2005, for *Craigia*; Denk and Grimm, 2009b, for *Fagus*).

The fossil plant assemblages were qualitatively compared to contemporaneous Greek and western Eurasian plant assemblages to