

The first report of palaeobotanical remains from Zakynthos Island, Western Greece

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Received: April 12, 2019 ▷ Accepted: July 02, 2019

Abstract. This work represents the first interdisciplinary approach on the relationship between travertines (as discharges of terrestrial geothermal fields related to the Neogene magmatism and active faulting) and plant fossils in Greece. The present contribution brings the first scientific data for the Quaternary – Pleistocene – Holocene palaeoflora of Zakynthos Island based on leaf imprints. Nine fossil plant taxa are identified for the first time on this island, eight of them are new for the Greek Quaternary and five of them are identified for the first time in Greece: *Equisetum* aff. *fluviatile*, *Laurus nobilis* L. foss., *Ocotea* cf. *heeri*, *Populus nigra*, *Cydonia* aff. *oblonga*.

Key words: plant fossils, leaf imprints, geobiology, travertine, Quaternary, Porto Zorou fault.

Introduction

Zakynthos Island is situated in the Western Greece, it belongs to the Ionian Islands situated at the western margins of the Hellenic arc. It is the third largest of the Ionian Islands and covers an area of 405.55 km². This study focuses on the palaeobotanical findings from the area of Porto Zorou (SE Zakynthos Island).

The geology of the island has been studied by several scientists (Dermitzakis 1977; Triantaphyllou 1996; Zelilidis & al. 1998; Papanikolaou & al. 2011; Karakitsios & al. 2013, 2016, 2017), consisting of Alpine rocks belonging mainly to the Pre-Apulian (Paxos) and partly to the Ionian. According to the above-mentioned scientists the Pre-Apulian zone in Zakynthos Island consists of upper Cretaceous

to Pleistocene sediments, while the Ionian zone is represented by Triassic breccias and gypsum. These sediments are followed by similar Neogene and Quaternary deposits as those of the Pre-Apulian zone, which are however less thick and characterized by unconformities. The recent works by Karakitsios & al. (2013, 2016, 2017) in Zakynthos Island showed the influence of the diapiric movements of the Ionian Triassic evaporites on the configuration and the overall subsidence of the Zakynthos foreland basin and the Messinian Salinity Crisis expression in this area, as well as the subsequent evolution of the Basin.

The studied area of the present paper is close to Porto Zorou normal fault (Fig. 1). According to Zelilidis & al. (1998) the southeastern part of Zakyn-

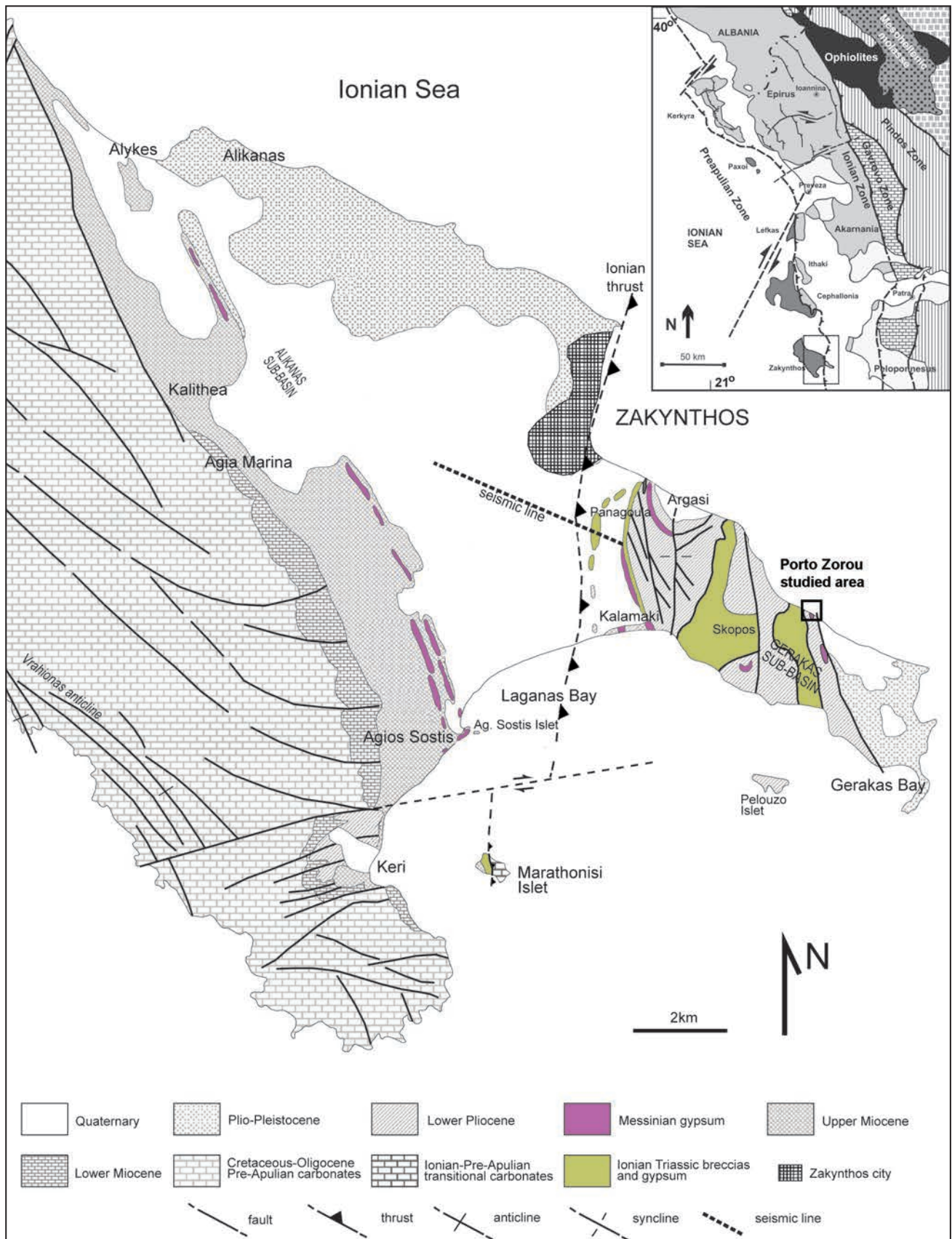


Fig. 1. Geological map of Zakynthos Island (modified from Karakitsios & al. 2017) with the fossiliferous travertine formation of Porto Zorou (studied area) indicated with a rectangle.

thos Island (and Porto Zorou area) has a Plio-Pleistocene age and is divided in five Formations: Agios Nikolaos, Porto Roma, Kalogeras, Gerakas, Akra Davia. Our material is probably belonging to the Upper Pleistocene of Porto Zorou, which is part of the lower tectonic block of the Porto Zorou normal fault that is now covered partially by the sea, presented as near shore isolated rocks. The hosting rock of the leaves consists of travertine, which is actually considered (Pentecost, 2005) as a chemically-precipitated continental limestone formed around seepages, springs and along streams and rivers, occasionally in lakes and consisting of calcite or aragonite.

Material and Methods

The specimens were collected from Porto Zorou area. The leaves imprints were photographed with a Panasonic Lumix and Canon EOS camera.

Among the recovered specimens leaf impressions, mostly fragmented prevail.

The studied plant material is housed in the collection of the Department of Historical Geology-Palaeontology, Faculty of Geology and Geoenvironment, University of Athens. The specimens are numbered and the frontal letters of their codes (ZPZ) refer to the island of Zakynthos and the Porto Zorou section.

The determination of leaf types followed the scheme for leaf morphology of the angiosperms plants of Dilcher (1974). The arrangement of the corresponding taxa in the systematic part of the article follows the scheme for Magnoliophyta of Takhtajan (1987).

Results

Fourteen plant imprints were studied. Eleven of them are Magnoliophyta leaf imprints of varying degrees of conservation and three are horsetail stem imprints. These imprints are situated on five rock fragments. The preserved leaf morphology allowed us to establish seven plant taxa. Because of the fragmentation of most of the material investigated, we have used combinations that allow for some approximation to fossil and recent species. To mark the proximity to fossil taxa, we have used the abbreviation cf., and aff. to the recent ones.

Equisetophyta

Equisetaceae, *Equisetum* L.

Equisetum aff. *fluviatile* L. (Pl. 1, Fig. 5).

Material: Two stem imprints.

The fossil material consists of a transversal section of two stems impressions (0.5 cm in diameter). Judging by the preserved ribs, it can be assumed that the number of all is over 30. Based on the stem's size and the ribs' number, it could be suggested that this specimen is related to the contemporary *E. fluviatile* L. which ranges throughout the temperate Northern Hemisphere.

Members of the genus *Equisetum* are commonly found into sediment basin layers, because of the specific habitat of the species of this genus – humid environments or coastal areas.

Equisetum sp. (Pl. 1, Fig. 6)

Material: One stem imprint.

The fossil material consists of an oblique section of a stem impression (0.2 cm in diameter). Judging by the preserved ribs, it can be assumed that the number of all is approximately eight. Based on the stem's size and the ribs' number, it could be suggested that this specimen is related to two contemporary species *E. palustre* L. or *E. arvense* L. For this reason, we prefer to define this material as a genus. *Equisetum* sp. has been reported from several Greek localities (Velitzelos & al. 2014) including: Makrilia (SW Crete, Middle Tortonian), Pitsidia (S. Crete, Tortonian), Patra (Peloponnese, Pliocene), Eastern Kos (late Miocene).

Magnoliophyta

Lauraceae, *Laurus* L.

Laurus nobilis L. foss. (Pl. 1, Fig. 7)

1935. Stefanov & Jordanov, p. 48, Pl. 16, Fig. 8; Fig.-text 45.

1984. Kitanov, p. 53, Fig. 8.5.

1974. *L. nobilis* L., Imchanitzkaja in Takhtajan, p. 44, Pl. 20, Figs 3-4.

1959. *Laurus* cf. *nobilis* L., Andreanszky, p. 65, Pl. 13, Fig. 2; Fig.-text 21.

Material: Four leaf imprints.

The fossil material consists of three leaf impressions. The first one preserves the lower half of its

leaf lamina (2.2 cm length and 1.0 cm width), while the other two preserve their medial sections (2.0 cm length and 1.0 and 0.8 cm width). The leaf lamina's form is elliptical, while the saved base is cuneate. The leaf margin is entire. The venation type is brochidodromous, where the secondary veins (five to six pairs) are angled in 40–45° according to the midvein. Inter-secondary veins are also registered and they are developed almost between all secondary ones. The fossil of this species is known from a sediment dated to the late Pontian – early Dacian from Bulgaria (Stefanov & Jordanov 1935, Kitanov 1984) and Pontian, Pliocene and Pleistocene in Georgia (Imhanitskaya 1974). Similar material is known from the Sarmatian in Hungary (Andreanszky 1959), while the recent species exists in the Mediterranean.

Litsea Juss.

- Litsea* cf. *primigenia* (Unger) Takhtajan (Pl. 1, Fig. 3)
1963. *Litsea primigenia* (Unger) Takhtajan, p. 202, Pl. 6, Fig. 9.
1987. Palamarev & Petkova, p. 39, Pl. 9, Figs 2, 4; Pl. 10, Fig. 9.
2014. as Lauraceae vel Fagaceae gen. et spec. indet, Velitzelos & al., p. 67.
1850b. *Laurus primigenia* Unger, p. 38, Pl. 40, Figs 1-4.
Material: Two leaf imprints.

The fossil material consists of two impressions of narrow elliptic leaves. The apex of the leaf lamina of the first specimen (4.5 cm length and 1.5 cm width) is not preserved. The apex of the second specimen (4.0 cm length and 1.5 cm width) is not preserved either, but it consists of the upper half of the leaf. The venation type is brochidodromous, where the sum of the preserved secondary vein pairs is six with an angle of 50° according to the midvein. The first pair of secondary veins situated at the leaf's base is angled in 30°. The majority of the secondary veins showed intersecondary veins developed in-between them; in addition the tertiary veins are perpendicular to the secondary ones. According to the above mentioned morphological data, it could be concluded that the leaf impression could be related to *L. primigenia*, but because of the fragmentary material is could be identified as *Litsea* cf. *primigenia*. The fossil species distribution covers Central, East and South-east Europe. Its stratigraphic sequence relates to Lower Eocene – Upper Miocene. *L. cubeba* (Lour.) Pers. has been accepted as its nearest living relative (Palamarev & Petkova 1987).

Ocotea Aubl.

- Ocotea* cf. *heeri* (Gaudin) Takhtajan (Pl. 1, Fig. 2)
1963. *Ocotea heeri* (Gaudin) Takhtajan, p. 199.
1987. Palamarev & Petkova, p. 36, Pl. 10, Figs 3, 6, 8.
1858. *Oreodaphne heeri* Gaudin in Gaudin & Strozzi, p. 35, Pl. 10, Figs 5-9; Pl. 11, Figs 1-7.

Material: One leaf imprint.

The fossil material consists of an elliptical leaf impression, with 2.2 cm length and 1.5 cm width probably. The apex and the base of the leaf blade are not preserved and this is why an absolute identification of the fossil is not possible. The leaf margin is entire, the secondary veins are angled in 40° according to the midvein and the venation type is brochidodromous. Based on this morphology, it could be suggested that the species relates to *O. heeri*. In support to this identification is also the lower angle of the first pair of secondary veins (30°) according to the midvein, than the rest secondary veins. The direction of the first pair of secondary veins suggests that they are diverging from a single point. These features are characteristic for the nearest living relative of the fossil *O. foetens* (Ait) Baill, despite its polymorphism of the leaf lamina. This species exists in Macaronesia. The fossil species distribution covers South-west, Central, South and South-east Europe. Its stratigraphic sequence is Upper Oligocene – Upper Pliocene (Palamarev & Petkova 1987).

The only report of *Ocotea* from Greece (Velitzelos & al. 2014) is: cf. Lauraceae [as *Ocotea laurifolia* Vassilevska identified in Butzmann & al. (2007)] from Rupelian-Chatian age, Evros.

Platanaceae, *Platanus* L.

- Platanus* cf. *leucophylla* (Unger) Knobl. (Pl. 1, Fig. 1)
1971. *Platanus leucophylla* (Unger) Knobl., p. 267.
2002. Kvaček & al., p. 58, Pl. 5, Figs 1-2.
1850a. *Populus leucophylla* Unger, p. 417.
1852. Unger, p. 118, Pl. 44, Figs 7-8.
1964. *Platanus platanifolia* (Ettingsh.) Knobl., p. 601.
1984. Kitanov, p. 53, Fig. 8: 1.
1987. Palamarev & Petkova, p. 52, Pl. 15, Fig. 2.

Material: One leaf imprint.

The fossil material consists of partially preserved leaf base of low sized leaf (0.8 cm length and 1.0 cm width). It is very likely that before the process of fossilization it has not yet reached its mature size. Despite this, based on the morphological features of the specimen, it could be identified as *Platanus* cf. *leucophylla*. The preserved section identifies the

Plate 1.



Fig. 1. *Platanus* cf. *leucophylla* (ZPZ-1a); **Fig. 2.** *Ocotea* cf. *heeri* (ZPZ-1b); **Fig. 3.** *Litsea* cf. *primigenia* (ZPZ-2a); **Fig. 4.** *Cydonia* aff. *oblonga* (ZPZ-1c); **Fig. 5.** *Equisetum* aff. *fluviatile* (ZPZ-1d); **Fig. 6.** *Equisetum* sp. (ZPZ-3a); **Fig. 7.** *Laurus nobilis* foss. (ZPZ-1e); **Fig. 8.** *Populus alba* (ZPZ-3b); **Fig. 9.** *Populus nigra* (ZPZ-3c) (measuring bar 1 cm).

leaf lamina as trilobate and there were prominent central vein and basal veins. The secondary veins of the right basal vein are also very prominent and straight; this is typical rather for genus *Platanus*, than for genus *Acer* or species of the Vitaceae family. The basal veins are angled in 30° according to the midvein. This is identical to the fossil *P. leucophylla* from the Late Miocene flora of Vegora (Kvaček & al. 2002). In support of this identification is the preserved part of toothed leaf margin which is a serration related to this species. The fossil species distribution includes South-west, Central and South-east Europe. Its stratigraphic sequence covers the Lower Oligocene – Upper Pliocene. The North-American *P. occidentalis* L. has been accepted as the nearest living relative (Palamarev & Petkova 1987). This species is distributed in the southeast states of the United States. In its native range, it is often found in riparian and wetland areas.

Platanus leucophylla is a widespread species in the Greek Neogene flora (Velitzelos & al. 2014) reported from 1) the Upper Miocene of Prosilio, Likoudi and Drymos (N. Greece), 2) the Middle to Upper Miocene of Nennita, Chios island (previously identified as *Platanus aceroides* Göppert), 3) the Upper Miocene of Strymon basin, previously described as *Platanus platanifolia* (Ettingshausen) Erw. Knobloch, 4) Pitsidia (S. Crete, Tortonian) as *Populus populina* (Brongniart) Erw. Knobloch vel *Platanus leucophylla* (Unger) Erw. Knobloch [previously described as *Populus crenata* Unger], 5) the Pliocene of Patra (Peloponnese), 6) the Upper Pliocene of Megalopolis (Velitzelos & al. 2014).

Salicaceae, *Populus* L.

Populus alba L. (Pl. 1, Fig. 8)

1929. *Populus alba* L., Stojanoff & Stefanoff, p. 28, Pl. 4, Figs 5-6; Figs-text 7, 4, 6.

2005. Gabriyan & Gohtuni (in Budantsev), p. 143, Pl. 78, Figs 4-8; Figs-text 81, 1-4.

1993. *Populus populina* (Brongniart) Knobloch (= *Populus latior* Al. Braun), Velitzelos, p. 10.

Material: Two leaf imprints.

The fossil material consists of a basal fragment of leaf with dimensions 2.0 cm × 1.5 cm and an almost whole preserved leaf – 3.0 cm length and 2.5 cm width. The whole width of the leaf lamina is approximately 3.0 cm. The leaf lamina form is very wide ovate. The apex is acute. The base is most proba-

bly cordate. The leaf margin is partially preserved, but it is clearly visible that it is irregular serrate. Bigger teeth are acute, smaller ones are obtuse. Sinuses between teeth are rounded. The venation is brochidodromous. Secondary veins are in four pairs, arciforming, at an angle of 50° towards the midvein. Tertiary veins form random reticulate pattern. All registered veins are sinuous, identically to the recent species.

The fossils of *P. alba* have been registered in Bulgaria and West Asia in sediments dated to the late Pontian – early Dacian (Stojanoff & Stefanoff 1929) and Pliocene – Middle Pleistocene (Budantsev 2005). Palamarev and Petkova (1987) interpret some of the available data as related to the fossil finds of *P. alba* in Europe and they place them as synonymous to *P. alba – pliocenica* Saporta. The described by Palamarev & Petkova (1987) leaf laminae are of ovate form, while the reviewed here fossil specimen suggest wide ovate form as the one presented by Stojanoff & Stefanoff (1929). *P. alba* is native to Morocco and the Iberian Peninsula through Central Europe (north to Germany and Poland) and Central Asia. It grows in humid environments, often by watersides, in regions with hot summers and cool to mild winter temperatures. It represents a riparian forest.

In Velitzelos & al. (2014: Plate 32, Fig. 11) there is a picture of *Populus alba* as *Populus sp.* as a representative of a small fossil assemblage of late Pliocene age from Megalopolis. The first reference of this assemblage and this fossil (reported as *Populus populina* (Brongniart) Knobloch) was made in Velitzelos (1993) and it was not accompanied with a photo/figure/plate and a detailed description.

Populus nigra L. (Pl. 1, Fig. 9)

1935. Stefanoff & Jordanoff, p. 31, Pl. 7, Fig. 4; Fig.-text 30.

1956. Kitanov & Nikolova, p. 89, Fig.-text 4.

Material: One leaf imprint

The fossil material consists of an almost whole preserved leaf – 3.0 cm length and 2.2 cm width. The whole width of the leaf lamina is approximately 3.0 cm. The leaf lamina form is very wide ovate. The apex is acuminate. The base is most probably cordate. The leaf margin is partially preserved, but it is clearly visible that it is regular serrate. Teeth are with obtuse apical angle and rounded sinuses between them. Basal veins form an angle of 50°

towards the midvein. The secondary veins are in four pairs, arciforming, at an angle of 60° towards the midvein. They are almost straight or arciform. Some of them bifurcate. Tertiary veins form percurrent pattern.

Fossils of *P. nigra* have been registered in Bulgaria in sediments dated to the late Pontian – early Dacian (Stefanoff & Jordanoff 1935) and Romanian (Kitanov & Nikolova 1956). Fossils associated with this recent species are known from the Hungarian Sarmatian – *Populus* cf. *nigra* (Andreanszky 1959) and Late Miocene of Greece – *Populus* sp.2 (Kvaček & al. 2002). An interesting fact is that in the late Miocene flora of Vegora (Greece), taxa have been established related to both the *P. alba* (*Populus* sp.1) and *P. nigra* (*Populus* sp.2) (Kvaček & al. 2002). *P. nigra* has a large distribution area throughout Europe (without its northern parts) and is also found in northern Africa and central and west Asia. The distribution area also includes the Caucasus and large parts of the Middle East. This species grows in low-lying areas of moist ground (flood-plain forests and riparian ecosystems, Richardson & al. 2014:95).

Rosaceae, *Cydonia* Mill.

Cydonia aff. *oblonga* Mill. (Pl. 1, Fig. 4)

1935. *C. vulgaris* Pers.; Stefanoff & Jordanoff, p. 57, Pl. 20, Fig. 4; Fig.-text 54.

1956. *C. oblonga* Mill.; Kitanov & Nikolova, p. 104, Pl. 7, Fig. 1; Fig.-text 17.

Material: One leaf imprint.

The fossil material consists of a base of a wide ovate leaf lamina (1.3 cm length, 2.7 cm width) with an entire leaf margin and cordate base. The secondary veins are angled in 50° according to the central one. There are brochidodromous veins originating from the basal veins towards the leaf lamina margin. Similar characteristic features are related to the leaves of *Cydonia oblonga*. Because of the insufficiency of the material, the specimen was identified as *Cydonia* aff. *oblonga* Mill. The fossil of *C. oblonga* has been registered in the Sofia basin (Bulgaria) and was dated to the late Pontian – early Dacian (Stefanov & Jordanov 1935) and Romanian (Kitanov & Nikolova 1956); it was also found in Pliocene sediments from Romania (Pop 1936). Today it is commonly accepted that the recent species originates from South-west Asia and it is widely grown as a cultural plant.

Discussion

This paper presents preliminary results of a study during which a new locality of palaeobotanical interest was discovered in Porto Zorou area in Zakynthos Island. The study of the collected samples brings new data to the Quaternary of Zakynthos Island and of Greece, since, the review of the palaeobotanical record of Greece (Velitzelos & al. 2014) during the Pleistocene includes until now only the areas of: Megalopoli (Arcadia, Peloponnese), Rhodes, Kos and Santorini (South Aegean). As stated recently in Mantzouka & al. (2019) several inconsistencies remain concerning the palaeobotanical research in Greece. By conducting this study we would like to contribute to the palaeobotanical research in Greece, by illuminating new plant fossiliferous localities of interest related with the findings' identification, with the age and the palaeoenvironment and palaeoclimate they represent.

The species identified in the present paper belong to a travertine formation in Porto Zorou area, SE Zakynthos Island with a late Pleistocene age, or younger.

The studies of Greek travertines include the areas of Aidhipsos (Anagnostidis & Golubic 1966), Edhessa, Naoussa (Faugeres 1981, regarded as “tufa” sensu Ford & Pedley 1996), Sidirokastro, Rhodope Mountains and northern Greece (Vavliakis & al. 1983) and more recently to Attica (Kampouroglou & Economou-Eliopoulos 2016) and northern Euboea Island and Sperchios area (Kanellopoulos & al. 2017), while their occurrence on a substantial scale has been studied in detail in Turkey as a result of Quaternary volcanic activity, e.g. Pammukale (Pentecost 1995).

This work represents the first interdisciplinary approach on the relationship between travertines (as discharges of terrestrial geothermal fields related to the Tertiary-Quaternary magmatism and active faulting) and plant fossils in Greece.

This is the first identification of plant fossils from Zakynthos Island and the first report of the taxa *Equisetum* aff. *fluviale* L., *Laurus nobilis* L. foss., *Litsea* cf. *primigenia* (Unger) Takhajan, *Ocotea* cf. *heeri* (Gaudin) Takhtajan, *Platanus* cf. *leucophylla* (Unger) Knobl., *Populus alba* L., *P. nigra* L. and *Cydonia* aff. *oblonga* Mill. for the Quaternary of Greece. Studies on the palaeoflora of Zakynthos Island should continue. If new and well-preserved material confirms the presence of the species *Litsea primigenia*, *Ocotea heeri*, *Platanus*

leucophylla, this will mean that the stratigraphic range of these species will be expanded to the Upper Pleistocene – Holocene.

Concerning the plant fossils, the relationship between plants and travertines is a challenging topic (Pentecost 2005) and the connection between plant assemblages in fossiliferous travertine and the palaeoclimatic interpretation of the area has been also a subject of discussion in palaeobotanical research (e.g. for the case study of Murviel-lès-Béziers in Kovar-Eder & al. 2006).

The geological reinvestigation of well-known plant fossiliferous localities and its correlation with a travertine formation could lead to the reappraisal of the potential origin of the material/fossiliferous stratum (from a geological/palaeoenvironmental point of view) along with new palaeobotanical findings (as in a recently published study by Koutecký & al. 2019).

Moreover, Pentecost (2005) includes as an example of the occurrence of plant impressions in travertines the finding of laurels (e.g. *Laurus nobilis*) from the Pleistocene and Holocene of Europe (especially from Italy and Malta, Pentecost 2005: 255). The latter species has been identified also in the present paper.

According to Ali & al. (2014) the native status of certain species can be enlightened by the leaves' impressions preserved in the travertine systems, as in the case of white poplar (*Populus alba*). Roiron & al. (2004) has investigated the occurrence of *P. alba* in travertine formations from the continental Europe (Weimar, Burgtonna) and Mediterranean since Pleistocene (e.g. southern France: Meyrargues, Aygalades, Spain: Beceite, Italy: Oriolo and Rome, Algeria: Algiers).

The present paper includes the first identification of *Populus alba* for Greece and supports the hypothesis that *P. alba* is an autochthonous species in central Europe and Mediterranean regions, at least since the Middle Pleistocene, not introduced in the western Mediterranean by Roman colonization (Roiron & al. 2004). The present study represents the first evidence of the indigenous status of this species also in the eastern Mediterranean Basin.

Moreover, an accurate date of the fossiliferous travertine formation of Zakynthos Island is crucial for the investigation of the occurrence of *P. alba* during the last ice age (Würm) in southern Europe. According to Roiron & al. (2004) the scarcity of travertine formations during the Würm period could be responsible for the absence of this species during this period. On

the other hand, *P. alba* is not sensitive to cold, so its presence during this period is possible.

Concerning the occurrence of *P. nigra* at the travertine formation, a similar case was the co-existence of *P. alba* and *P. nigra* from the Holocene of Saint-Guilhem-le-Désert (France, Hérault) (Roiron 2004; Ali & al. 2008) which had illuminated the hypothesis of a semi-humid environment (Lecoeuvre & al. 2008).

The colonization routes of black poplar in Europe have been studied through the EUFORGEN Network (Cottrell & al. 2005) taking into account the chloroplast DNA derived from the genebank collections of 11 laboratories in 9 countries (unfortunately the fact that Greece is not included in the above mentioned research could be crucial for the results). The occurrence of *Populus nigra* in Zakynthos Island as discussed here, should be of importance concerning also the distribution of the species.

The importance of palaeobotanical studies and of the right species' determinations is also pointed out in the present work. *Equisetum* has preserved its eco-physiological behavior (e.g. tolerance in high salinity, alkalinity, and heavy metal concentrations due to the vicinity with hot springs' environments) for the last 150 Ma (Channing & al. 2011). Fossil *Equisetum* species are indicators of specific habitat, paleoecology and paleoecophysiology reconstructions, representatives of physical and chemical conditions of modern hot spring systems, because this genus "enables the recognition of paleoflow directions from hot spring vent areas, across sinter aprons to geothermal wetlands, and from there into either peripheral terrestrial or lacustrine clastic depositional environments" (Guido & al. 2010).

Moreover, the present paper encourages the interdisciplinary methods on the study of evolutionary processes and biodiversity of species through time concerning the evaluation of the colonization effects, the geographic distance or the local adaptation (e.g. Dewoody & al. 2015) by the combined usage of macrofossils (as the leaf impressions of this work) their adaptive traits to environmental conditions and cpDNA for more accurate results (especially when palynological data cannot be used).

A stable isotope geochemical study of the studied area in the future would also supply information on the origin and depositional environment of Zakynthos travertine, following the example of recent studies at Pamukkale travertines, Turkey (Kele & al. 2011).

Finally, the present work in combination with the work on “travitonics” by Hancock & al. (1999) supports the establishment of the combined usage of travertines and palaeobotany, as the previously mentioned authors did for travertines and active faults.

Acknowledgments. Special thanks to G. Rigatos for his kind help on photo shooting. We are also thankful to the anonymous reviewers.

References

- Ali, A.A., Ambert, P., André, J., Chabal, L., Gasco, J., Roiron, P. & Terral, J.F. 2008. Holocene hydrological and vegetation changes in southern France inferred by the study of an alluvial travertine system (Saint-Guilhemle-Désert, Hérault) C. R. Geosciences.
- Ali, A.A., Terral, J.-F., Girard, V. & Roiron, P. 2014. Les travertins à empreintes, témoins de la paléobiodiversité végétale (Plant imprints from travertines, witnesses of vegetation palaeobiodiversity). – *Quaternaire*, **25(2)**:157-161.
- Anagnostidis, K. & Golubic, S. 1966. Über die Ökologie einiger *Spirulina*-Arten. – *Nova Hedwigia*, **11**: 309-335.
- Andreanszky, M. 1959. Die Flora der Sarmatischen Stufe in Ungarn. Akademiai Kiado, Budapest.
- Brasier, A.T. 2011. Searching for travertines, calcretes and speleothems in deep time: Processes, appearances, predictions and the impact of plants. – *Earth-Science Reviews*, **104**: 213-239.
- Budantsev, L. 2005. Magnoliophyta fossiliorossiae etc. vitatum finitimarum. Vol. 4. *Nyctaginaceae – Salicaceae*. Mosquae – Petropoli (in Russian).
- Channing, A., Zamuner, A., Edwards, D. & Guido, D. 2011. *Equisetum thermale* sp. nov. (Equisetales) from the Jurassic San Agustín hot spring deposit, Patagonia: Anatomy, paleoecology, and inferred paleoecophysiology. – *Am. J. Bot.*, **98(4)**: 680-697.
- Cottrell, J.E., Krystufek, V., Tabbener, H.E., Milner, A.D., Connolly, T., Sing, L., Fluch, S., Burg, K., Lefèvre, F., Achard, P., Bordács, S., Gebhardt, K., Vornam, B., Smulders, M.J.M., VandenBroeck, A.H., Van Slycken, J., Storme, V., Boerjan, W., Castiglione, S., Fossati, T., Alba, N., Agúndez, D., Maestro, C., Notivol, E., Bovenschen, J. & van Dam, B.C. 2005. Postglacial migration of *Populus nigra* L.: lessons learnt from chloroplast DNA. – *Forest Ecol. Managem.*, **206**: 71-90.
- Denk, T., Güner, T.H., Bouchal, J.M. & Kallanxhi, M.-E. 2019. The Pleistocene flora of Bezhán, southeast Albania: early appearance of extant tree species. – *Historical Biology*, 1-23, DOI: 10.1080/08912963.2019.1615061.
- Dermitzakis, M. 1977. Stratigraphy and sedimentary history of the Miocene of Zakynthos (Ionian Islands, Greece). – *Ann. Geol. Pays Hell.*, **29**: 47-186.
- Dewoody, J., Trewin, H. & Taylor, G. 2015. Genetic and morphological differentiation in *Populus nigra* L.: isolation by colonization or isolation by adaptation? – *Molec. Ecol.*, **24**: 2641-2655.
- Dilcher, D. 1974. Approaches to the identification of Angiosperm leaf remains. – *Bot. Rev.*, **40(1)**: 1-157.
- Faugeres, L. 1981. Travertins quaternaires de Naoussa (Macedonie, Greece). – *Actes du Colloque de l'Association des Geographes Français*, 73-77.
- Ford, T.D. & Pedley, H.M. 1996. A review of tufa and travertine deposits of the world. – *Earth-Science Reviews*, **41**: 117-175.
- Gaudin, C. & Strozzi, C. 1858. Contribution à la flore fossile italienne. I. Mémoire sur quelques gisements de feuilles fossiles de la Toscane. – *Neue Denkschr. Schweiz. Ges. Naturwiss.*, **16**: 2-47.
- Guido, D.M., Channing, A., Campbell, K. & Zamuner, A. 2010. Jurassic geothermal landscapes and ecosystems at San Agustín, Patagonia, Argentina. – *J. Geol. Soc.*, **167**: 11-20.
- Hancock, P.L., Chalmers, R.M.L., Altunel, E. Z. & Çakir, Z. 1999. Travitronics: using travertines in active fault studies. – *J. Struct. Geol.*, **21**: 903-916.
- Kampouroglou, E.E. & Economou-Eliopoulos, M. 2016. Assessment of the environmental impact by As and heavy metals in lacustrine travertine limestone and soil in Attica, Greece: Mapping of potentially contaminated sites. – *Catena*, **139**: 137-166.
- Kanellopoulos, Chr., Mitropoulos, P., Valsami-Jones, E. & Voudouris, P. 2017. A new terrestrial active mineralizing hydrothermal system associated with ore-bearing travertines in Greece (northern Euboea Island and Sperchios area). – *J. Geochem. Exploration.*, **179**: 9-24.
- Karakitsios, V., Roveri, M., Lugli, S., Manzi, V., Gennari, R., Antonarakou A., Triantaphyllou, M., Agiadi, K. & Kontakiotis, G. 2013. Remarks on the Messinian evaporites of Zakynthos Island (Ionian Sea, Eastern Mediterranean). – *Bull. Geol. Soc. Greece*, **47**: 146-156.
- Karakitsios, V., Roveri, M., Lugli, S., Manzi, V., Gennari, R., Antonarakou, A., Triantaphyllou, M., Agiadi, K., Kontakiotis, G., Kafousia, N. & de Rafelis, M. 2017. A record of the Messinian salinity crisis in the eastern Ionian tectonically active domain (Greece, eastern Mediterranean). – *Basin Research*: 1-31.
- Kele, S., Özkul, M., Fórizs, I., Gökgöz A., Baykara M.O., Alçiçek, M.C. & Németh, T. 2011. Stable isotope geochemical study of Pamukkale travertines: New evidences of low-temperature non-equilibrium calcite-water fractionation. – *Sedimentary Geology*, **238 (1-2)**: 191-212.
- Kitanov, B. & Nikolova, A. 1956. Neues Untersuchungsmaterial über die fossile Flora von Lozenec in Sofia. – *Izv. Bot. Inst. (Sofia)*, **5**: 85-125 (in Bulgarian).
- Kitanov, G. 1984. Pliocene Flora Composition in the Gotche Delchev Region. – *Fitologiya*, **25**: 41-70 (in Bulgarian).
- Knobloch, E. 1971. Nomenklatorisch-taxonomische Bemerkungen zu *Platanus aceroides* Goepfert und *Quercus attenuate* Goepfert. – *Mitt. Bayer. Staatssamml. Paläont. Hist. Geol.*, **11**: 263-265.
- Koutecký, V., Teodoridis, V., Čáp, P., Mantzouka, D. & Sakala, J. 2019. Fossil wood from the Doupovské hory and České středohoří volcanic complexes: latest overview and new angiosperms from the locality Dvěrce. – *Jahrbuch für Mineralogie – Abhandlungen*, **293(3)**: 283-306.
- Kovar-Eder, J., Kvaček, Z., Martinetto, E. & Roiron, P. 2006. Late Miocene to Early Pliocene vegetation of southern Europe (7–4Ma) as reflected in the megafossil plant record. – *Palaeogeogr., Palaeoclim., Palaeoecol.*, **238**: 321-339.

- Kvaček, Z., Velitzelos, D. & Velitzelos, E.** 2002. Late Miocene Flora of Vegora Macedonia N. Greece. Korali Publications, Athens.
- Lecoivre, C., Oris, F. & Wallon, S.** 2008. Paléoenvironnement au Néolithique à Saint Guilhem-le-Désert à travers l'étude de la flore fossile du travertin du gué des Gours. ORPAL
- Mantzouka, D., Sakala, J., Kvaček, Z., Koskeridou, E. & Karakitsios, V.** 2019. Petrified Forest of Lesbos Island (Greece): A Palaeobotanical Puzzle of a Unique Geopark and the New Discoveries. IOP Conf. Ser. – Earth Environm. Sci., **221**: 1-10.
- Papanikolaou, M.D., Triantaphyllou, M.V., Platzman, E.S., Gibbard, P.L., McNiocail, C. & Head, M.J.** 2011. A well-established Early–Middle Pleistocene marine sequence on south-east Zakynthos island, western Greece: magneto-biostratigraphic constraints and palaeoclimatic implications. – J. Quatern. Sci., **26**(5): 523-540.
- Pentecost, A.** 1995. The Quaternary travertine deposits of Europe and Asia Minor. – Quatern. Sci. Rev., **14**: 1005-1028.
- Pentecost, A.** 2005. Travertine. Springer.
- Pop, E.** 1936. Flora pliocenica de la Borsec. Tipografia Nationala, Cluj.
- Richardson, J., Isebrands, J.G. & Ball, J.B.** 2014. Ecology and physiology of Poplars and Willows. In: **Isebrands, J.G. & Richardson, J.(eds.)** 2014. Poplars and Willows-Trees for Society and the Environment. The Food and Agriculture Organization of the United Nations & CABI publ. pp.634.
- Roiron, P., Ali, A.A., Guendon, J.-L., Carcaillet, C. & Terral, J.-F.** 2004. Preuve de l'indigénat de *Populus alba* L. dans le Bassin méditerranéen occidental. – Compt. Rend. Biol., **327** (2):125-132.
- Stefanoff, B. & Jordanoff, D.** 1935. Studies upon the Pliocene Flora of the Plain of Sofia (Bulgaria). – Abh. Bulg. Akad. Wiss., **29**: 3-150.
- Stojanoff, N. & Stefanoff, B.** 1929. Beitrag zur Kenntnis der Pliozänflora der Ebene von Sofia. – Spis. Bulg. Geol. Druzh., **1**(3): 4-120.
- Takhtajan, A.** 1974. Magnoliophytafossilia URSS. Vol. **1**, Magnoliaceae – Eucomiaceae. Nauka, Leningrad (in Russian).
- Takhtajan, A.** 1987. Systema Magnoliophytorum. Nauka, Leningrad (in Russian).
- Takhtajan, A.** 1963. The Neogene flora of the Goderdzi Pass. I. – Paleobotanika, **4**: 189-204 (in Russian).
- Triantaphyllou, M.V.** 1996. Biostratigraphical and ecostratigraphical observations based on calcareous nannofossils of the eastern Mediterranean Plio-Pleistocene deposits. GAIA, **1**, pp. 229.
- Unger, F.** 1850a. Genera et Species Plantarum fossilium. Vindobonae.
- Unger, F.** 1850b. Die fossile Flora von Sotzka. – Ak. Wiss. Wien, Math.-Naturwiss. Kl., Denkschr., **2**: 131-197.
- Vavliakis, E., Sotiriadis, L. & Psilovikos, A.** 1983. The marginal Sidirokastro basin of the Rhodope Massif during the Neogene and the Quaternary. – Clausthaler Geol. Abh., **44**: 3-19.
- Velitzelos, D., Bouchal, J.M. & Denk, T.** 2014. Review of the Cenozoic floras and vegetation of Greece. – Rev. Palaeobot. Palynol., **204**: 56-117.
- Zelilidis, A., Kontopoulos, N., Avramidis, P. & Piper, D.J.W.** 1998. Tectonic and sedimentological evolution of the Pliocene-Quaternary basins of Zakynthos island, Greece: case study of the transition from compressional to extensional tectonics. – Basin Research, **10**: 393-408.
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