



# Niche evolution versus niche conservatism and habitat loss determine persistence and extirpation in late Neogene European Fagaceae

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## ABSTRACT

An increasing body of palaeobotanical data demonstrates a series of Pliocene and Pleistocene extirpations and extinctions of plant lineages in western Eurasia, which are believed to have been determined by the climatic properties of their related East Asian and North American sister lineages. We investigated the diversity of a widespread northern hemispheric plant family, Fagaceae, during the Late Pliocene of Portugal. We found a high diversity of Fagaceae comprising extant and extinct lineages. Dispersed pollen of *Castanopsis* and *Quercus* sect. *Cyclobalanopsis* represent the youngest records of these Himalayan-Southeast Asian groups in western Eurasia. Likewise, fossil-species of *Quercus* sect. *Lobatae* and the North American clade of sect. *Quercus* are the youngest records of these modern New World groups in western Eurasia. For the extinct *Trigonobalanopsis*, the pollen record of Portugal is the youngest known of this genus. Climate data of modern representatives demonstrate that a deterministic model can explain only a part of the Pliocene and Pleistocene extirpations. Modern cold month mean temperatures of *Castanopsis* and *Quercus* sect. *Cyclobalanopsis* and their last occurrences in western Eurasia in the Pliocene fit with a deterministic model (niche conservatism). In contrast, survival or extirpation of groups with high cold tolerance appear to have been more complex. Here, niche evolution, abundance and diversity of a lineage during pre-Pleistocene times, and habitat availability/loss determined the fate of Fagaceae lineages in western Eurasia.

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## 1. Introduction

The Late Pliocene (Piacenzian, 3.6–2.58 Ma) marked an important change in the northwestern Mediterranean region altering the forest structure and composition (Suc, 1984; Barrón et al., 2010; Jiménez-Moreno et al., 2010; Ezquerro et al., 2022). Across western Portugal, a coastal association dominated by taxodiaceous Cupressaceae (“Taxodiaceae”), *Myrica* L., *Symplocos* Jacq., *Nyssa* L., and others, disappeared and gave way to woody vegetation dominated by *Alnus* Mill. and Ericaceae (Vieira et al., 2018). The forest vegetation of the hinterland also changed from assemblages with Engelhardioideae, *Carya* Nutt., and Sapotaceae towards oak dominated forests with both deciduous and sclerophyllous evergreen

species of *Quercus* L. and modern Mediterranean elements such as *Pteris* Gled., *Ephedra* L., *Phillyrea* L., *Olea* L. and *Cistus* L. and increased Asteraceae (Suc, 1984; Diniz, 1984a; Vieira et al., 2018). At the same time, climate model simulations and climate reconstructions based on pollen data suggested that during the “middle Pliocene” (~3 Ma) the climate in the western Mediterranean and southwestern (Atlantic) Europe was warmer and wetter, and less seasonal than today (Fauquette et al., 1999; Haywood et al., 2010; Jiménez-Moreno et al., 2010; Vieira et al., 2018). This is expressed, for example, in the Piacenzian sequences of the Rio Maior pollen assemblage, which contain high amounts of Ericaceae pollen, unlike the more continental Pliocene pollen assemblages from the rest of the Iberian Peninsula (Barrón et al., 2010; Jiménez-Moreno et al., 2010). Hence, it has been proposed that while the climate of the northwestern Mediterranean region evolved towards a seasonal rhythm during the Piacenzian, the summer drought typical of the modern Mediterranean climate became established

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during the Early Pleistocene Gelasian stage (Suc, 1984; Barrón et al., 2010; Jiménez-Moreno et al., 2010; Velitzelos et al., 2014).

Regions such as the area north and south of the Strait of Gibraltar (Rodríguez-Sánchez et al., 2008), and Central Italy (Martinetto, 2001; Martinetto et al., 2017) have previously been pointed out as climate refugia based on the long persistence of warmth-loving taxa during the Pliocene and Early Pleistocene and the modern relict distribution of humid warm-temperate woody plants such as *Rhododendron ponticum* L., *Laurus nobilis* L., and *Prunus lusitanica* L. along with a high level of endemic woody species in the mesic mountains north of the Strait of Gibraltar (Monte Aljibe; Rodríguez-Sánchez et al., 2008). Likewise, the Black Sea region has been identified as long-term refuge for warmth-loving plants (Biltekin et al., 2015). More recently, several studies demonstrated the importance of the Atlantic region of Portugal as plant refuge during the Late Pliocene (Vieira, 2009; Vieira et al., 2011, 2018, 2022; Martinetto and Vieira, 2020; Vieira and Zetter, 2020). These studies found that several taxa currently confined to either East and Southeast Asia or North America, or having a wider pantropical distribution, persisted into the Piacenzian in Portugal. Examples for East and Southeast Asian elements included the genera *Cercidiphyllum* Siebold et Zucc., *Diplopanax* Hand.-Mazz., and *Craigia* Smith et Evans (Vieira and Zetter, 2020). East Asian–North American disjunct elements included *Itea* L. and North American elements (extending into Central and South America) included, among others, the genera *Proserpinaca* L., *Mortoniadendron* Standl. et Steyerl., and *Leitneria* Chapm. (Martinetto and Vieira, 2020; Vieira and Zetter, 2020). In addition, a few pantropical taxa were recorded (*Zanthoxylum* L., Sapotaceae, *Eurya* Thunb., and *Symplocos* Jacq.). Among pantropical taxa, the genus *Sideroxylon* L. is biogeographically interesting, as it also occurs on the Macaronesian islands (Lobin et al., 2005).

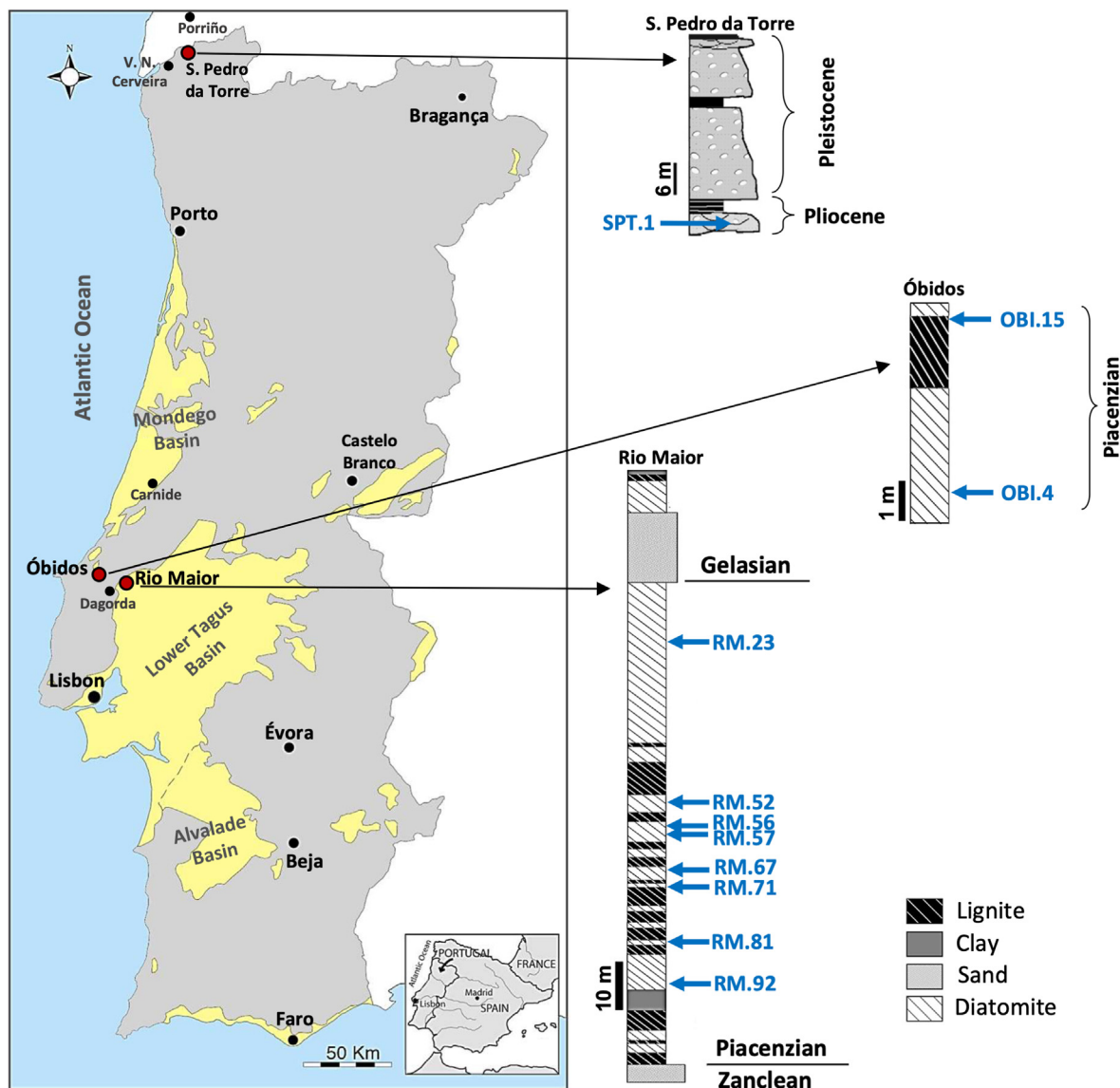
In the present study, we investigate the diversity of Fagaceae (oak family) in Portugal (Lusitania) during the Late Pliocene. Fagaceae are key elements in the modern tree flora of the Iberian Peninsula and are represented mainly by oaks (*Quercus* spp.). In contrast, *Fagus* L. and *Castanea* Mill. play only marginal roles in the modern flora of Portugal (<https://flora-on.pt/>). Previous papers distinguished four taxa of Fagaceae in the Pliocene of Portugal: *Fagus*, *Quercus*, *Castanea*, and the extinct genus *Trigonobalanopsis* Kvaček et H. Walther (Vieira, 2009; Vieira et al., 2011, 2018; Vieira and Zetter, 2020). In the present paper, we investigated dispersed pollen of the family Fagaceae using a combined light microscopy (LM) and scanning electron microscopy approach (SEM; Halbritter et al., 2018). Such a combined LM/SEM investigation is most beneficial in ecologically diverse groups such as oaks (genus *Quercus*) as it allows recognition of subgenera and sections within oaks and a clear distinction between extinct and extant groups of Fagaceae. Thus, we evaluated the ratio between extinct, extirpated, and surviving Fagaceae taxa during a time of transition to modern environments. Specifically, we were asking why some lineages in Fagaceae became extinct or extirpated in western Eurasia following the Pliocene, while others persisted. A previous study (Svenning, 2003) found that the current European status of cool temperate tree species in Europe (extinct/extirpated, relictual or widespread) can be predicted from modern climate requirements of their East Asian and North American congeners (climate niche conservatism) and that widespread European taxa are more cold tolerant (measured by the mean temperature of the coldest month) than relictual and extirpated taxa. We tested this deterministic model using the western Eurasian fossil record of the Fagaceae family during the Late Pliocene and subsequent stages. Finally, we placed the Late Pliocene Fagaceae of Portugal in a biogeographic context and evaluated the persistence of links across the North Atlantic versus continental Eurasia.

## 2. Geological background

Pliocene sediments in Portugal are preserved in large Cenozoic basins, the Lower Tagus Basin, Mondego Basin, and the Alvalade Basin, across the west coast as well as in smaller outcrops in the interior regions of the country. Sedimentological and lithostratigraphical evidence suggests a marine transgression took place along the Atlantic coast of Portugal during the late Zanclean – early Piacenzian (dated to 3.6–3.5 Ma) (Pena dos Reis et al., 1992; Cunha, 1992; Cunha et al., 1993; Ramos and Cunha, 2004). Palaeontological studies using calcareous nannofossils (Cachão, 1990), mollusc remains (Silva, 2001), and dinoflagellate cysts (Vieira et al., 2006) as well as isotopic analyses (Silva, 2001) lend further credibility to the dating of this transgression. When the sea level dropped, the progradation of fluvial systems deposited vast sandstones and conglomerates with localized lacustrine deposits comprising diatomites and lignites. These sediments have been defined as Sequence SLD13 by Ramos and Cunha (2004), representing one of the last Pliocene depositional sequences in the area that is successively topped by Pleistocene fluvial deposits.

In the present study, we investigated pollen grains recovered from three Pliocene localities: Rio Maior, Óbidos, and S. Pedro da Torre (Fig. 1; see Supplementary data 1 for a full list of pollen and spore taxa counted for each sample). Palynologically, Rio Maior (RM) is the most studied Portuguese Pliocene locality to date (e.g., Andrade, 1944; Diniz, 1984a). Based on biostratigraphical correlations using pollen zones established by Zagwijn (1960) and Suc (1984), Diniz (1984b) proposed a Pliocene to Gelasian (Lower Pleistocene) age for the deposits at Rio Maior. Later, Vieira (2009) refined the age, observing that basal sands from the deepest cores (e.g. F98) record marine influence and some rare dinoflagellate cysts comparable with that of the site Vale do Freixo, Carnide (north of Rio Maior, Fig. 1; Vieira et al., 2006), which can be linked with the late Zanclean – early Piacenzian marine transgression. The sequence of lacustrine diatomites and lignites, from which the analysed samples were collected, correspond to Piacenzian (Late Pliocene) sedimentation (Zbyszewski, 1943, 1949, 1967; Vieira et al., 2018; Vieira and Zetter, 2020). Using magnetostratigraphy, the uppermost sediments at the site Abum (in Rio Maior) were dated to the 2.58 Ma Gauss – Matuyama reversal (Diniz and Möner, 1995). This provides an upper age constraint of early Gelasian for the final infilling at Rio Maior (Diniz, 2003). The locality at Óbidos (OBI) to the west of Rio Maior (Fig. 1) also preserves a sequence of diatomites and lignites, preserved in a small elongated synclinal extending between the Dagorda and S. Mamede localities. The pollen assemblages from Óbidos were correlated with the upper part of the deposits at Rio Maior (Vieira, 2009).

São Pedro da Torre (SPT) is located in northwest Portugal (Fig. 1), close to the border with Spain. In this region, pre-Pleistocene deposits are limited and sediments are primarily filling small strike-slip basins running along N–S to NW–SE trending fault corridors (Pereira, 1991). The outcrop at São Pedro da Torre occurs in a 4 km wide depression between Porriño (Spain) and V.N. Cerveira (Portugal), and comprises a lower unit consisting of clays, lignite layers, sands and gravel, covered by extensive fluvial deposits of Pleistocene age (Pereira, 1991). During the 1990's, the A3 highway construction exposed sediments with black and white clays containing plant macrofossils. A study of the pollen content from the clays suggests a mixed deciduous-evergreen broadleaved and conifer forests that thrived under humid warm-temperate climates during the Pliocene in that region (Vieira et al., 2011). The carpological record recently established by Martinetto and Vieira (2020) includes several taxa that are new for this period and geographical region. Some of these taxa belong to genera that are now extirpated from Europe, such as *Azolla* cf. *Aspera* P.I.Dorof., *Eurya stigmosa*



**Fig. 1.** Geographical location of Portugal showing the main Cenozoic basins and the three studied locations. Simplified lithological logs and the stratigraphic position of the analysed samples.

(R.Ludw.) Mai, *Hypericum tertiaerum* P. Nikitin, *Itea europaea* Mai, *Proserpinaca reticulata* C. Reid et E. Reid, *Symplocos casparyi* Mai, *Symplocos germanica* R. Ludw., and *Tetraclinis salicornioides* (Unger) Kvaček. To date, no carpological remains of Fagaceae have been found at this locality.

### 3. Materials and methods

Standard laboratory processing for palynomorphs with HCl (55%) and HF (37%) for acid maceration (Halbritter et al., 2018), followed by 125 µm and 10 µm sieving to remove coarse and fine fractions respectively was applied to all sedimentary rock samples. The final residues were diluted in liquid glycerine and mounted on slides without cover slips to allow selection and extracting of pollen grains. Several pollen grains were investigated using the single-grain method that combines light (LM) and scanning electron microscopy (SEM) (Zetter, 1989; Halbritter et al., 2018). In the initial pollen counts with LM, 420 pollen grains of Fagaceae were recognized. Of these, ca. 50 were selected for a combined LM and SEM

investigation (Supplementary data 1). This method allows for a more accurate systematic identification of pollen, compared to traditional counting analysis using LM only, resulting in a higher taxonomic resolution based on morphological features. Individual pollen grains were extracted from the residue using a micromanipulator, a preparation needle with an eyebrow hair fixed to it. Extracted pollen grains were transferred into a clean drop of glycerol on a separate slide for photography with LM. The same individual grains were then transferred to a SEM stub. To dissolve the remaining glycerol, the pollen grains were repeatedly washed with small drops of absolute ethanol. The stubs with the pollen grains were then coated with gold and the pollen grains studied and photographed with SEM (Zetter, 1989; Vieira et al., 2009; Halbritter et al., 2018). Morphological features of the pollen grains were noted in both LM and SEM, and the grains along with their peculiarities were measured and described following Punt et al. (2007; LM) and Halbritter et al. (2018; LM and SEM).

Climate data for modern species of Fagaceae were obtained using WorldClim vers. 2.1 (<https://www.worldclim.org/data/>)

worldclim21.html) at a resolution of 30 s (ca. 1 km<sup>2</sup>; Fick and Hijmans, 2017) from georeferenced occurrence data from GBIF (<http://www.gbif.org/>), and the atlases by Thompson et al. (2015) and Fang et al. (2011). Because the climate parameters for a particular plant species in Fang et al. (2011) are based on mean values of climate variables at county-level, we validated these data by comparing occurrence-based climate data from GBIF/WorldClim and Fang et al. (2011; Fig. 6).

#### 4. Results - systematic paleobotany

For the stratigraphic distribution of particular pollen taxa of Fagaceae in the Rio Maior, Óbidos, and S. Pedro da Torre localities, see Table 1.

Order: Fagales.

Family: Fagaceae Dumort.

Subfamily: not determined.

Genus: *Trigonobalanopsis* Kvaček et H. Walther (extinct).

*Trigonobalanopsis* sp. (Fig. 2, 1–3).

Description: Pollen, dispersal unit monad, outline trilobate in polar view, elliptic in equatorial view (LM), polar axis 15–18 μm long (LM, SEM), equatorial diameter 11–13 μm (LM, SEM), P/E ratio prolate, shape ellipsoid; aperture arrangement tricolporate, colpi long, pori small and indistinct; exine 0.7–0.9 μm thick, nexine thinner than sexine (LM); pollen wall tectate (SEM); sculpture psilate in LM, rugulate to microrugulate, and perforate in SEM, parallel (micro)rugulae forming irregularly arranged groups, (micro)rugulae 0.5–1.6 μm long, 120–150 nm wide, (micro)rugulae segmented (SEM).

Remarks: The segmented (micro)rugulae observed with SEM are a diagnostic feature for the extinct genus *Trigonobalanopsis*. Pollen of this type was identified adhering to fossil *T. schmidtii* Walther et Zetter leaves (Walther and Zetter, 1993). Dispersed *Trigonobalanus* pollen has since been described, using combined LM and SEM, from the late early Eocene (Ypresian) Princeton Chert, British Columbia, Canada (Grímsson et al., 2016a), the early Oligocene (Denk et al., 2012) and Early Miocene (Kmenta, 2011) of Germany, the Early to Late Miocene of Austria (Meller et al., 1999; Grímsson et al., 2016b), the Middle Miocene of Denmark (Denk and Bouchal, 2021) and Anatolia, Turkey (Bouchal et al., 2016, 2017), and the Late Miocene of Iceland (Denk et al., 2011). *Trigonobalanopsis* sp. Pollen from the Late Pliocene of Portugal is the youngest record of the genus up to date. In Lower Pliocene strata, carpological remains of *Trigonobalanopsis* are abundant in Central Italy and the Netherlands, while they are restricted to Central Italy in the “middle” Pliocene (Zagwijn, 1990; Martinetto, 2001).

Subfamily: Castaneoideae Oerst. (paraphyletic).

Genus: not determined.

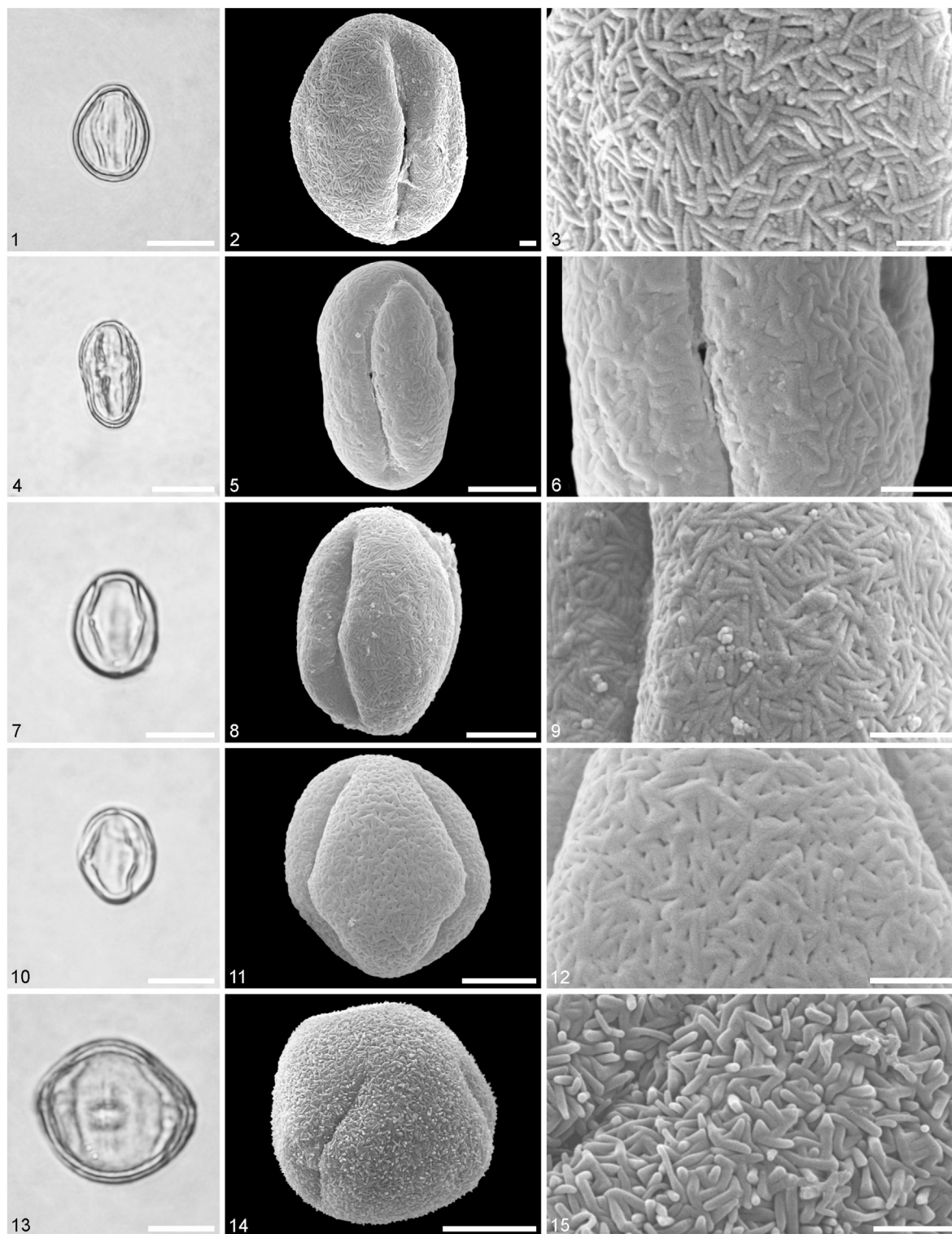
Castaneoideae gen. et spec. indet. 1, aff. *Castanea* Mill. (Fig. 2, 4–6).

Description. Pollen, dispersal unit monad, outline trilobate in polar view, elliptic in equatorial view (LM), polar axis 17–20 μm long (LM, SEM), equatorial diameter 10–12 μm (LM, SEM), P/E ratio prolate, shape ellipsoid; aperture arrangement tricolporate, colpi long, pori lalongate; exine 0.7–0.9 μm thick, nexine as thick as sexine (LM); pollen wall tectate (SEM); sculpture psilate in LM, rugulate, fossulate, and perforate in SEM.

Remarks. The pollen morphology (LM, SEM) and ultrastructure (SEM) of Castaneoideae, including *Castanea*, *Castanopsis* (D.Don) Spach, *Chrysolepis* Hjelmq., *Lithocarpus* Blume, and *Notholithocarpus* Manos, Cannon et S.H.Oh, has been studied in detail by, among others, Crepet and Daghljan (1980), Miyoshi (1982), Prąglowski (1984), Wang and Pu (2004), and Manos et al. (2008).

**Table 1** Distribution of Fagaceae pollen taxa identified from different stratigraphic levels from Rio Maior, Óbidos, and S. Pedro da Torre. Sample site abbreviations as in Fig. 1.

Sample	Castaneoideae gen. et spec. indet. 1, aff. <i>Castanea</i>	Castaneoideae gen. et spec. indet. 2, aff. <i>Castanopsis</i>	<i>Trigonobalanopsis</i> sp.	<i>Fagus</i> sp.	<i>Quercus</i> sect. <i>Cyclobalanopsis</i> sp.	<i>Quercus</i> sect. <i>Cerris</i> sp. 1	<i>Quercus</i> sect. <i>Cerris</i> sp. 2	<i>Quercus</i> sect. <i>Ilex</i> sp.	<i>Quercus</i> sect. <i>Lobatae</i> sp. 1	<i>Quercus</i> sect. <i>Lobatae</i> sp. 2	<i>Quercus</i> sect. <i>Lobatae</i> sp. 3	<i>Quercus</i> sect. <i>Lobatae</i> vel <i>Quercus</i> sp. 1	<i>Quercus</i> sect. <i>Lobatae</i> vel <i>Quercus</i> sp. 2
SPT.1													
OBI.15													
OBI.4													
RM.23													
RM.52													
RM.56													
RM.57													
RM.67													
RM.71													
RM.81													
RM.92													



**Fig. 2.** Fossil Fagaceae pollen from Rio Maior. (1–3) *Trigonobalanopsis* sp., same grain, sample RM.71, (1) Equatorial view in LM, (2) Equatorial view in SEM, (3) Close-up of sculpture in SEM, (4–6) Castaneoideae gen. et spec. indet. 1, aff. *Castanea*, same grain, sample RM.57, (4) Equatorial view in LM, (5) Equatorial view in SEM, (6) Close-up of sculpture in SEM, (7–9) Castaneoideae gen. et spec. indet. 1, aff. *Castanopsis*, same grain, sample RM.92 (10) Equatorial view in LM, (11) Equatorial view in SEM, (12) Close-up of sculpture in SEM, (10–12) Castaneoideae gen. et spec. indet. 1, aff. *Castanopsis*, same grain, sample RM.67, (13) Equatorial view in LM, (14) Equatorial view in SEM, (15) Close-up of sculpture in SEM, (13–15) *Fagus* sp., same grain, sample RM.23 (7) Equatorial view in LM, (8) Oblique equatorial view in SEM, (9) Close-up of sculpture in SEM. Scale bar = 10  $\mu\text{m}$  in 1, 4, 7, 10, 13 and 14; 5  $\mu\text{m}$  in 5, 8, and 11; 2  $\mu\text{m}$  in 6, 9, 12, and 15; 1  $\mu\text{m}$  in 2, and 3.

Pollen from most of these genera is similar in size and shape as well as sculpture when observed with SEM. However, *Castanea* pollen is usually smaller and narrower, and the rugulate sculpture appears flattened and fused (e.g., Prąglowski, 1984). Castaneoideae gen. et spec. indet. 1 pollen from the Pliocene of Portugal has short and broad rugulae that are indistinct, the rugulae are fused and show little relief suggesting it belongs to the genus *Castanea*. Fossil Castaneoideae pollen, documented mostly with LM, has been described from the Upper Cretaceous (Santonian/Campanian) and throughout the Cenozoic of North America and Europe from mid to high latitudes (e.g., Muller, 1981; Stuchlik et al., 2014; Grímsson et al., 2016a; Suc et al., 2020). Fossil “*Castanea*” type pollen grains studied with LM and SEM have been reported from the middle Eocene (late Lutetian to early Bartonian) of Hareøen, western Greenland (Grímsson et al., 2015), the late Eocene of Florissant, Colorado, United States (Bouchal et al., 2014), and the Middle Miocene of Austria (Grímsson et al., 2016b).

Castaneoideae gen. et spec. indet. 2, aff. *Castanopsis* (Fig. 2, 7–12).

Description. Pollen, dispersal unit monad, outline trilobate in polar view, elliptic in equatorial view (LM), polar axis 14–18 µm long (LM, SEM), equatorial diameter 11–15 µm (LM, SEM), P/E ratio prolate, shape ellipsoid; aperture arrangement tricolporate, colpi long, pori small but distinct; exine 0.7–0.9 µm thick, nexine thinner than sexine (LM); pollen wall tectate (SEM); sculpture psilate in LM, rugulate to microrugulate, and perforate in SEM, parallel (micro) rugulae forming irregularly arranged groups, (micro)rugulae distinct to indistinct, 0.8–2.1 µm long, 100–150 nm wide (SEM).

Remarks. This pollen type shows a constant grain size and aperture arrangement as well as pollen wall features observed with LM, but there is a considerable range in the sculpture observed with SEM. The (micro)rugulae range from being distinct with their outline clearly traceable (Fig. 2, 9) to almost completely covered by sporopollenin (Fig. 2, 12). This variation may reflect species differences, but since similar variability of the pollen sculpture is known from several other Fagaceae, for example *Fagus* and *Quercus* (e.g., Denk, 2003; Denk and Grimm, 2009; Makino et al., 2009; Denk and Tekleva, 2014), we assign them to the same fossil-taxon. As mentioned before, Castaneoideae type pollen is difficult to differentiate at genus level and impossible using LM only (e.g., Prąglowski, 1984). Nevertheless, based on the sculpture observed with SEM, in combination with the aperture arrangement in LM, Castaneoideae gen. et spec. indet. 2 pollen resembles pollen from particular extant species of the genus *Castanopsis*, especially *C. cuspidata* (Thunb.) Schottky, as figured by Naryshkina and Evstigneeva (2017). *Castanopsis cuspidata* is currently native to Korea and southern Japan (POWO, 2022). Furthermore, there are similarities of Castaneoideae gen. et spec. indet. 2 with a number of extant and Quaternary *Castanopsis* spp. Based on the equatorial outline and P/E ratio (see, for example, Wang and Pu, 2004; Tang et al., 2020). Fossil *Castanopsis* pollen identified using combined LM and SEM are rare in the palynological record. The only finds we are aware of include dispersed grains from the late Eocene (Priabonian) of Florissant, Colorado, United States (Bouchal et al., 2014). SEM observations include early Eocene (Ypresian) grains from the Russian Far East (Naryshkina and Evstigneeva, 2020) and late Eocene grains of the Baltic amber, Kaliningrad (Sadowski et al., 2020). Based on previously figured fossil Castaneoideae type pollen, Castaneoideae gen. et spec. indet. 2 pollen from Portugal is most similar to dispersed grains from the Holocene of the Sea of Japan (see plate 14, Figs. 9 and 10 in Naryshkina and Evstigneeva, 2017) and to pollen extracted from anthers of Castaneoideae, gen. indet. from the Baltic amber (plate 17 in Sadowski et al., 2020).

Subfamily: Fagoideae K. Koch.

Genus: *Fagus* L.

*Fagus* sp. (Fig. 2, 13–15).

Description. Pollen, dispersal unit monad, outline circular to trilobate in polar view, circular in equatorial view (LM), polar axis 22–25 µm long (LM, SEM), equatorial diameter 22–25 µm (LM, SEM), P/E ratio isodiametric, shape spheroidal; aperture arrangement tricolporate, colpi  $\frac{2}{3}$  of polar axis length, pori large, nexine thickened around pori; exine 1.0–1.3 µm thick, nexine thinner than sexine (LM); pollen wall tectate (SEM); sculpture scabrate in LM, microrugulate to rugulate and fossulate in SEM, (micro)rugulae diverging and protruding, 0.5–2 µm long, 190–310 nm wide (SEM).

Remarks. The LM and/or SEM based pollen morphology of all living *Fagus* species has been studied/illustrated by Prąglowski (1982), Saito (1992), Denk (2003), and Wang and Pu (2004). Just over half of the extant species have been investigated using TEM (e.g., Prąglowski, 1982; Wang and Pu, 2004). *Fagus* pollen from all extant species is similar and overlaps regardless whether investigated with LM or SEM. One exception is the pollen of subgenus *Engleriana* that differs by narrow and long colpi that extend between the poles and the smaller grain size. The colpi are wider and shorter and the pollen grains are larger in subgenus *Fagus*. Occasionally, long and narrow colpi occur in *F. grandifolia* Ehrh. and *F. longipetiolata* Seemen, and small pollen occurs in *F. hayatae* Palib., all of subgenus *Fagus* (Prąglowski, 1982; Denk, 2003). The small size of the fossil *Fagus* pollen suggests they belong to subgenus *Engleriana*, but the short colpi suggest they belong to subgenus *Fagus*. A few species in subgenus *Fagus* have small pollen as well, e.g. *Fagus hayatae*. The oldest *Fagus* pollen record, based on combined LM and SEM, is from the Paleocene (Danian) of Agatdalen, Nuussuaq Peninsula, western Greenland (Grímsson et al., 2016a). Other geographically important Cenozoic *Fagus* pollen records based on combined LM and SEM include the early Eocene of British Columbia, Canada (Manchester and Dillhoff, 2004; Grímsson et al., 2016a), the early Eocene (Ypresian) of the Primorskii Region, Russian Far East (Naryshkina and Evstigneeva, 2020), the middle Eocene (late Lutetian to early Bartonian) of Hareøen, western Greenland (Grímsson et al., 2015), the early Oligocene of Germany (Denk et al., 2012), the Early Miocene of Japan (Saito, 1992), and the Middle Miocene of Iceland (Denk et al., 2011).

Genus: *Quercus*.

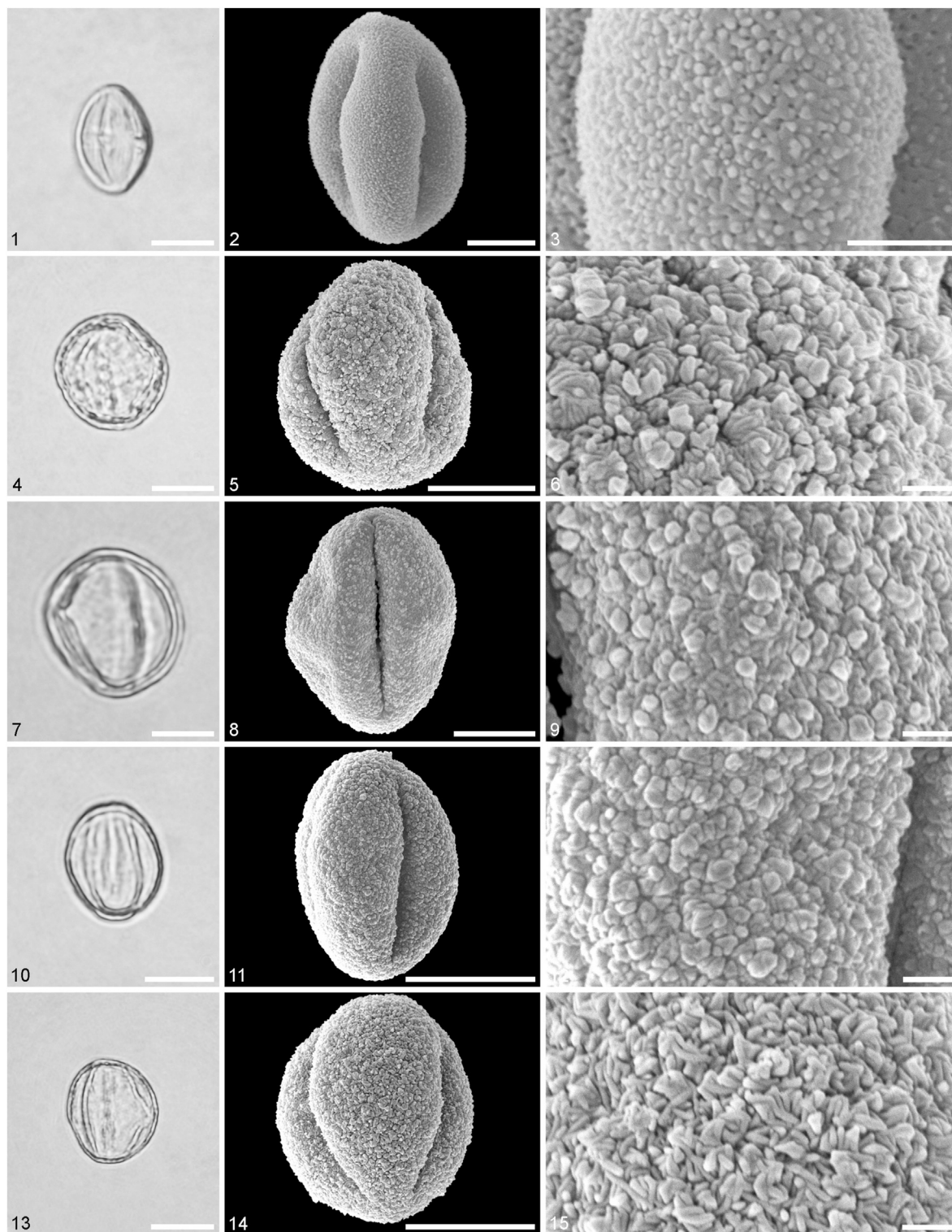
Subgenus: *Cerris*.

Section: *Cyclobalanopsis*.

*Quercus* section *Cyclobalanopsis* sp. (Fig. 3, 1–3).

Description. Pollen, dispersal unit monad, outline trilobate in polar view, elliptic in equatorial view (LM), polar axis 18–20 µm long (LM, SEM), equatorial diameter 12–15 µm (LM, SEM), P/E ratio prolate, shape ellipsoid; aperture arrangement tricolporate, colpi long, pori lalongate and distinct, nexine thickened around pori (LM); exine 0.8–1.0 µm thick, nexine thinner than sexine (LM); pollen wall tectate (SEM); sculpture psilate in LM, nanorugulate to nanoechinate and perforate in SEM, nanorugulae/echini distinct, irregularly arranged, often protruding, up to 0.5 µm long (SEM).

Remarks. The pollen morphology (LM and SEM) of oaks from section *Cyclobalanopsis* has been portrayed by Crepet and Daghighian (1980), Miyoshi (1982), Wang et al. (1995), Wang and Pu (2004), Fujiki and Ozawa (2007), Makino et al. (2009), Denk and Grimm (2009), Miyoshi et al. (2011), and Zhang et al. (2018). Based on the LM micrographs provided by Wang and Pu (2004) it is evident that the endopori in section *Cyclobalanopsis* are variable ranging from pollen with minute indistinct pori to pollen with large endopori that are clearly lalongate and with or without a thickened nexine. Based on the sculpture seen in SEM, *Quercus* section *Cyclobalanopsis* sp. pollen from Portugal shows similar sculpture



**Fig. 3.** Fossil Fagaceae pollen from Rio Maior. (1–3) *Quercus* section *Cyclobalanopsis* sp., same grain, sample RM.81, (1) Equatorial view in LM, (2), Equatorial view in SEM, (3) Close-up of sculpture in SEM, (4–6) *Quercus* section *Cerris* sp. 1, same grain, sample RM.56, (4) Equatorial view in LM, (5) Equatorial view in SEM, (6) Close-up of sculpture in SEM, (7–9) *Quercus* section *Cerris* sp. 1, same grain, sample RM.56, (7) Equatorial view in LM, (8) Equatorial view in SEM, (9) Close-up of sculpture in SEM, (10–12) *Quercus* section *Cerris* sp. 2, same grain, sample RM.56 (10) Equatorial view in LM, (11) Equatorial view in SEM, (12) Close-up of sculpture in SEM, (13–15) *Quercus* section *Ilex* sp., same grain, sample RM.56, (13) Equatorial view in LM, (14) Equatorial view in SEM, (15) Close-up of sculpture in SEM. Scale bar = 10 µm in 1, 4, 5, 7, 8, 10, 11, 13, and 14; 5 µm in 2; 2 µm in 3; 1 µm in 6, 9, 12, and 15.

arrangement as documented by Makino et al. (2009; plate 6) for some pollen of *Quercus gilva* Blume. There are only few fossil pollen records based on combined LM and SEM assigned to *Quercus* section *Cyclobalanopsis*. The earliest record is from the Eocene of Hainan, China (Hofmann, 2010), that is closely followed by pollen discovered from the late Eocene of Florissant, Colorado, United States (Bouchal et al., 2014) and (possibly) the late Eocene Baltic amber (Sadowski et al., 2020). Then there is a gap in the pollen record until the Miocene of Zhejiang, China (Liu et al., 2007), but there is also a putative record from the Middle Miocene of Lavanttal, Austria (Grímsson et al., 2016b). Compared to these fossil records, the Pliocene *Quercus* section *Cyclobalanopsis* sp. pollen type from Portugal shows similar sculpture in SEM to Pollen Type 7 illustrated by Hofmann (2010), but the endoaperture arrangement is different. The general SEM sculpture of *Quercus* section *Cyclobalanopsis* sp. pollen from Portugal is also similar to that observed in *Quercus* Morphotaxon 4 from the Miocene of China (Liu et al., 2007), but the endoaperture in the Chinese pollen is not elongate nor does it show the typical nexine thickening around the pori as observed in the pollen from Portugal.

#### Section: *Cerris*.

##### *Quercus* section *Cerris* sp. 1 (Fig. 3, 4–9).

Description. Pollen, dispersal unit monad, outline trilobate in polar view, elliptic in equatorial view (LM), polar axis 18–26 µm long (LM, SEM), equatorial diameter 18–24 µm (LM, SEM), P/E ratio isodiametric to prolate, shape spheroidal to ellipsoid; aperture arrangement tricolporate, colpi long, pori small but distinct; exine 1.1–1.3 µm thick, nexine thinner than sexine (LM); pollen wall tectate (SEM); sculpture psilate in LM, nano- to microrugulate (rod-shaped) and perforate in SEM, nano/microrugulae distinct to indistinct, agglomerating and forming protruding groups, basal nano/microrugulae as well as protruding groups partly covered by secondarily sporopollenin (SEM).

Remarks. The pollen morphology (LM and/or SEM) of all c. 12 extant species of *Quercus* section *Cerris* has been described and illustrated by Miyoshi (1982), Reille (1992–1998), Beug (2004), Wang and Pu (2004), Denk and Grimm (2009), Makino et al. (2009), Li et al. (2011), and Miyoshi et al. (2011). The sculpture of *Quercus* section *Cerris* sp. 1 pollen is typical of the section and there are several extant Eurasian species that produce pollen with similar sculpture when studied with SEM (e.g., Denk and Grimm, 2009). The fossil pollen record of *Quercus* section *Cerris*, based on SEM, dates back to the early Eocene (Ypresian) of the Primorskii Region, Russian Far East (see *Quercus* sp. 4 in Naryshkina and Evstigneeva, 2020). Younger records based on combined LM and SEM include dispersed pollen from the late Oligocene of south-western Siberia (Denk et al., 2021a), the late Oligocene to Pliocene of Germany (Ferguson et al., 1998; Van der Burgh and Zetter, 1998; Kmenta, 2011), the Miocene of eastern China (see plate I, figs. 1–3 and 7–12 in Liu et al., 2007), the Early to Middle Miocene of Austria (Hofmann et al., 2002; Grímsson et al., 2016b); the Early to Middle Miocene of Anatolia, Turkey (Bouchal et al., 2016, 2017; Bouchal, 2019; Denk et al., 2019), the Middle Miocene of Denmark (Denk and Bouchal, 2021), the Late Miocene of northwestern Greece (Bouchal et al., 2020), the Pleistocene of Albania (Denk et al., 2021b), and the Holocene of the Sea of Japan (Tekleva et al., 2014). Most of these Eurasian fossil records portray pollen showing SEM sculpture comparable to that of the *Quercus* section *Cerris* sp. 1 and/or sp. 2 pollen types from Portugal. *Quercus* section *Cerris* sp. 1 pollen was the most frequent Fagaceae pollen occurring in the samples from Portugal. Based on the varying grain size and the variability of the SEM sculpture it is uncertain if the pollen grains assigned to this type are representing a single biological taxon or more. Studies on modern oak pollen have shown that a single species can produce

pollen of varying size that also show a considerable variability in sculpture in SEM. In the same way, different oak species are also known to produce comparable pollen that overlap completely in both size, aperture arrangement, and sculpture observed with SEM (e.g., Solomon, 1983a, 1983b; Denk and Grimm, 2009; Makino et al., 2009; Denk and Tekleva, 2014).

##### *Quercus* section *Cerris* sp. 2 (Fig. 3, 10–12).

Description. Pollen, dispersal unit monad, outline trilobate in polar view, elliptic in equatorial view (LM), polar axis 17–19 µm long (LM, SEM), equatorial diameter 13–15 µm (LM, SEM), P/E ratio prolate, shape ellipsoid; aperture arrangement tricolporoidate, colpi long, pori small and indistinct; exine 0.9–1.1 µm thick, nexine thinner than sexine (LM); pollen wall tectate (SEM); sculpture psilate in LM, nanorugulate to microrugulate (rod-shaped) and perforate in SEM, nano/microrugulae indistinct, agglomerating and forming protruding groups, basal nano/microrugulae as well as protruding groups partly covered by secondarily sporopollenin (SEM).

Remarks. The *Quercus* section *Cerris* sp. 2 pollen type differs from the previous type by the smaller size, thinner pollen wall, and the features of the endoapertures.

#### Section: *Ilex*.

##### *Quercus* section *Ilex* sp. (Fig. 3, 13–15).

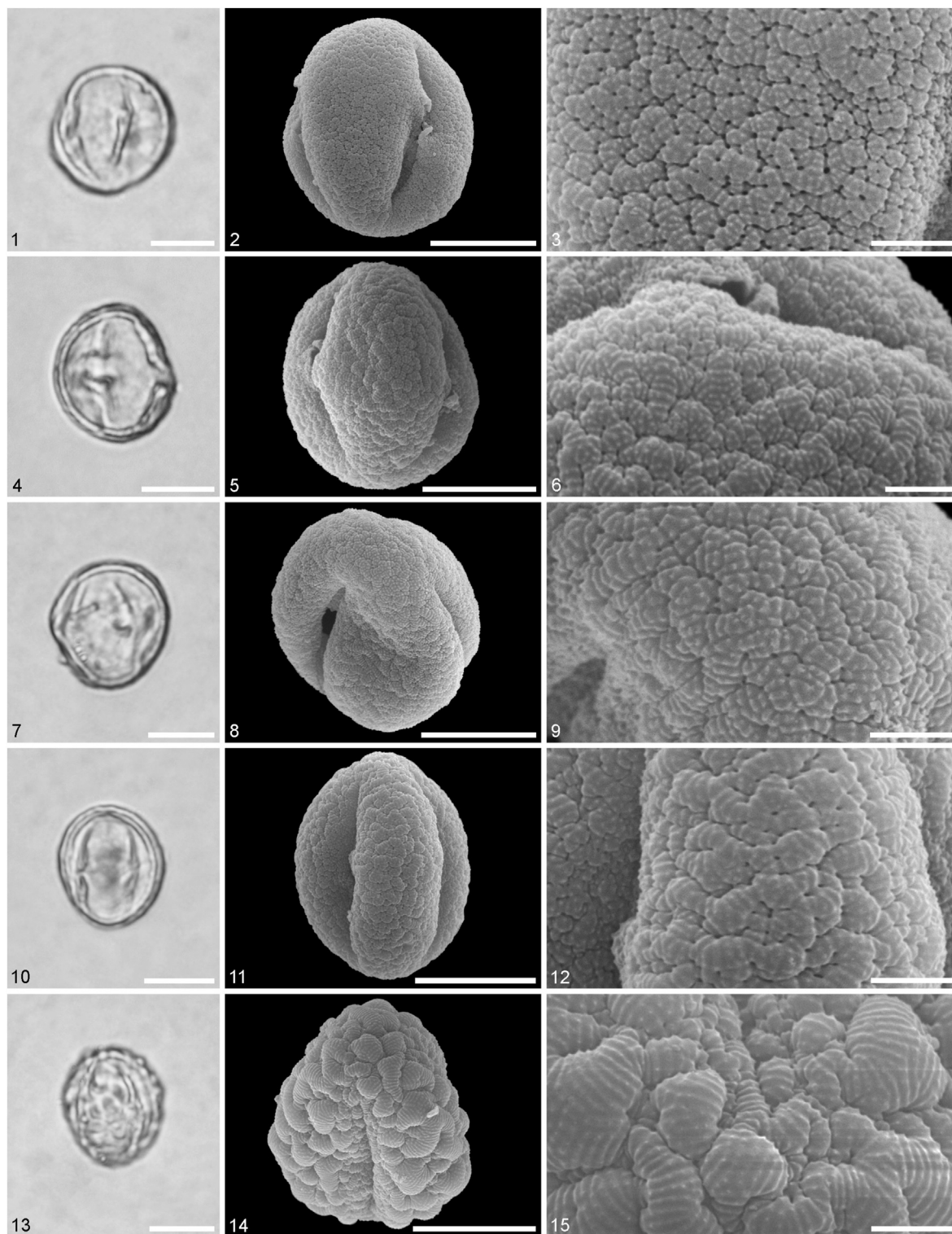
Description. Pollen, dispersal unit monad, outline trilobate in polar view, elliptic in equatorial view (LM), polar axis 18–20 µm long (LM, SEM), equatorial diameter 15–18 µm (LM, SEM), P/E ratio prolate, shape ellipsoid; aperture arrangement tricolporate, colpi long, pori small but distinct; exine 0.9–1.1 µm thick, nexine thinner than sexine (LM); pollen wall tectate (SEM); sculpture psilate in LM, nanorugulate to rugulate (rod-shaped) and perforate in SEM, nanorugulae distinct, irregularly arranged in groups, nano/rugulae 1.2–0.4 µm long, 100–150 nm wide (SEM).

Remarks. The most comprehensive morphological (LM, SEM) and ultrastructural (TEM) study on *Quercus* section *Ilex* pollen is by Denk and Tekleva (2014) and Zhang et al. (2018). Additional literature containing descriptions as well as LM and SEM micrographs of *Quercus* section *Ilex* pollen include Crepet and Daghlian (1980), Miyoshi (1982), Reille (1992–1998), Beug (2004); Wang and Pu (2004; also TEM), Fujiki and Ozawa (2007), Denk and Grimm (2009), Li et al. (2011), and Miyoshi et al. (2011). Fossil *Quercus* section *Ilex* sp. pollen from the Pliocene of Portugal shows identical SEM sculpture and LM morphology typical of several Mediterranean and Asian species of *Quercus* section *Ilex* (e.g., Denk and Tekleva, 2014). The earliest dispersed fossil *Quercus* section *Ilex* type pollen grains, documented with combined LM and SEM, are from the early Eocene of the Primorskii Region, Russian Far East (Naryshkina and Evstigneeva, 2020). Additional Paleogene records include pollen from the Eocene of Hainan, China (Hofmann, 2010) and the early Oligocene of Germany (Denk et al., 2012). Neogene pollen records of *Quercus* section *Ilex* include grains from the Early Miocene of Turkey (Denk et al., 2019), Middle Miocene of Austria (Grímsson et al., 2016b) and Turkey (Bouchal et al., 2016a; 2017; Bouchal, 2019), the Late Miocene of NW Greece (Bouchal et al., 2020), the Pleistocene of Albania (Denk et al., 2021a,b), and from the Holocene of the Sea of Japan (Tekleva et al., 2014). *Quercus* section *Ilex* sp. pollen from the Pliocene of Portugal is comparable to most of these much older as well as ± contemporaneous fossil pollen records. The general size range of the grains is similar, so is the aperture arrangement, and the sculpture in most of them is more or less identical when studied with SEM.

#### Subgenus: *Quercus*.

##### Section: *Lobatae*.





**Fig. 4.** Fossil Fagaceae pollen from Rio Maior. (1–3) *Quercus section Lobatae* sp. 1, same grain, sample RM.67. (1) Equatorial view in LM, (2) Equatorial view in SEM, (3) Close-up of sculpture in SEM, (4–6) *Quercus section Lobatae* sp. 1, same grain, sample SPT.1. (4) Equatorial view in LM, (5) Equatorial view in SEM, (6) Close-up of sculpture in SEM, (7–9) *Quercus section Lobatae* sp. 1, same grain, sample RM.67. (7) Equatorial view in LM, (8) Oblique equatorial view in LM, (9) Close-up of sculpture in SEM, (10–12) *Quercus section Lobatae* sp. 1, same grain, sample RM.67. (10) Equatorial view in LM, (11) Equatorial view in SEM, (12) Close-up of sculpture in LM, (13–15) *Quercus section Lobatae* sp. 2, same grain, sample SPT.1. (13) Equatorial view in LM, (14) Equatorial view in SEM, (15) Close-up of sculpture in SEM. Scale bar = 10  $\mu\text{m}$  in 1, 2, 4, 5, 7, 8, 10, 11, 13, and 14; 2  $\mu\text{m}$  in 3, 6, 9, 12, and 15.

*Quercus section Lobatae* sp. 1 (Fig. 4, 1–12).

Description. Pollen, dispersal unit monad, outline trilobate in polar view, elliptic in equatorial view (LM), polar axis 18–23  $\mu\text{m}$

long (LM, SEM), equatorial diameter 15–21  $\mu\text{m}$  (LM, SEM), P/E ratio prolate, shape ellipsoid; aperture arrangement tricolporate, colpi long, pori large and distinct, nexine thickened around pori; exine

1.3–1.6  $\mu\text{m}$  thick, nexine thinner than sexine (LM); pollen wall tectate (SEM); sculpture psilate to scabrate in LM, microareolate to areolate, fossulate, and perforate in SEM, (micro)areolae segmented, ridges of segments with nanoechinate suprasculpture, nanoechini arranged in rows of 2–8 per segment (SEM).

Remarks. Pollen morphology of *Quercus* section *Lobatae* has mainly been studied with SEM by Martin and Drew (1969), Adams and Morton (1972), Lewis et al. (1983), Solomon (1983b), and Jones et al. (1995). Fossil pollen assigned to section *Lobatae* commonly have distinct and large pori, which look somewhat elongate, and sometimes even a thickened nexine. This seems to be a typical feature of sect. *Lobatae* (see Stuchlik et al., 2014; van Benthem et al., 1984). In addition, the variability of the sculpture observed with SEM (compare panels 3, 6, 9, and 12 in Fig. 4) and the size range of the pollen assigned to the *Quercus* section *Lobatae* sp. 1 pollen type from Portugal is comparable with that portrayed by Solomon (1983a, b) for several different red oaks in North America. These include for example *Quercus imbricaria* Michx., *Q. laurifolia* Michx., and *Q. phellos* L. (see Figs. 10–12 in Solomon, 1983b), all occurring in Central or Southeast United States (Hélaridot, 2022). Similar pollen grains were also described from Holocene strata in the USA (Tekleva and Haselwander, 2016). Fossil pollen records of *Quercus* section *Lobatae*, based on combined LM and SEM, where dispersed pollen was assigned solely to this section and not to section *Quercus* as well, are rare. Interestingly, most of the pollen records are of Eocene age, from the Russian Far East (Naryshkina and Evstigneeva, 2020), China (Hofmann, 2010), Baltic amber (Sadowski et al., 2020), Greenland (Grímsson et al., 2015), and from British Columbia, Canada (Grímsson et al., 2016a). Then there is a gap in the pollen record until the Miocene of Poland (Stuchlik et al., 2014) and the Holocene of the Sea of Japan (Tekleva et al., 2014). The fossil *Quercus* section *Lobatae* sp. 1 pollen type from Portugal is not comparable to any of the previously recorded Eocene to Holocene pollen. The segmented areolate sculpture, and especially the nanoechinate suprasculpture observed with SEM in the pollen from Portugal is unique, and so far only known from pollen of extant oaks currently occurring in the United States (Solomon, 1983b, fig. 11b). Somewhat similar pollen grains from the Miocene/Pliocene boundary of Iceland (5.5 Ma Selárgil locality; Denk et al., 2010) have previously been compared to extant North American red or white oaks. They differ from the grains from Portugal by the lack of perforations and are unlike the Paleogene records mentioned above and Eurasian modern members of sect. *Quercus*.

#### *Quercus* section *Lobatae* sp. 2 (Fig. 4, 13–15).

Description. Pollen, dispersal unit monad, outline trilobate in polar view, elliptic in equatorial view (LM), polar axis 19–21  $\mu\text{m}$  long (LM, SEM), equatorial diameter 17–19  $\mu\text{m}$  (LM, SEM), P/E ratio prolate, shape ellipsoid; aperture arrangement tricolporate, colpi long, pori large and distinct; exine 1.5–1.7  $\mu\text{m}$  thick, nexine thinner than sexine (LM); pollen wall tectate (SEM); sculpture verrucate in LM, verrucate to areolate, fossulate, and perforate in SEM, verrucae/areolae segmented or striate, ridges of segments/stria with nanoechinate suprasculpture (SEM).

Remarks. We tentatively assign pollen showing this unique sculpture into *Quercus* section *Lobatae* and as a separate fossil-species. However, it is possible that the *Lobatae* sp. 2 grains represent aberrant pollen of the section *Lobatae* sp. 1 pollen type.

#### *Quercus* section *Lobatae* sp. 3 (Fig. 5, 1–3).

Description. Pollen, dispersal unit monad, outline trilobate in polar view, elliptic in equatorial view (LM), polar axis 27–29  $\mu\text{m}$  long (LM, SEM), equatorial diameter 22–24  $\mu\text{m}$  (LM, SEM), P/E ratio prolate, shape ellipsoid; aperture arrangement tricolporate, colpi long, pori large and distinct; exine 2.0–2.3  $\mu\text{m}$  thick, nexine thinner

than sexine (LM); pollen wall tectate (SEM); sculpture scabrate in LM, verrucate to areolate, fossulate, and perforate in SEM.

Remarks. The sculpture observed with SEM is typical for that documented in other dispersed fossil pollen of section *Lobatae* from both the Eocene of the Northern Hemisphere (e.g., Hofmann, 2010; Grímsson et al., 2015, Grímsson et al., 2016b; Naryshkina and Evstigneeva, 2020) and the Holocene of the Sea of Japan and Missouri, USA (Tekleva et al., 2014; Tekleva and Haselwander, 2016). Among living red oaks, similar psilate areolae/verrucae are found, for example, in *Q. palustris* (cf. Solomon, 1983a, fig. 16) or *Q. rubra* (Solomon, 1983b, fig. 17b). Psilate verrucae also occur in white oaks (*Quercus* sect. *Quercus*; e.g. *Q. frainetto*, *Q. bumelioides*, T. Denk, pers. observ.).

#### Section: *Quercus* vel *Lobatae*.

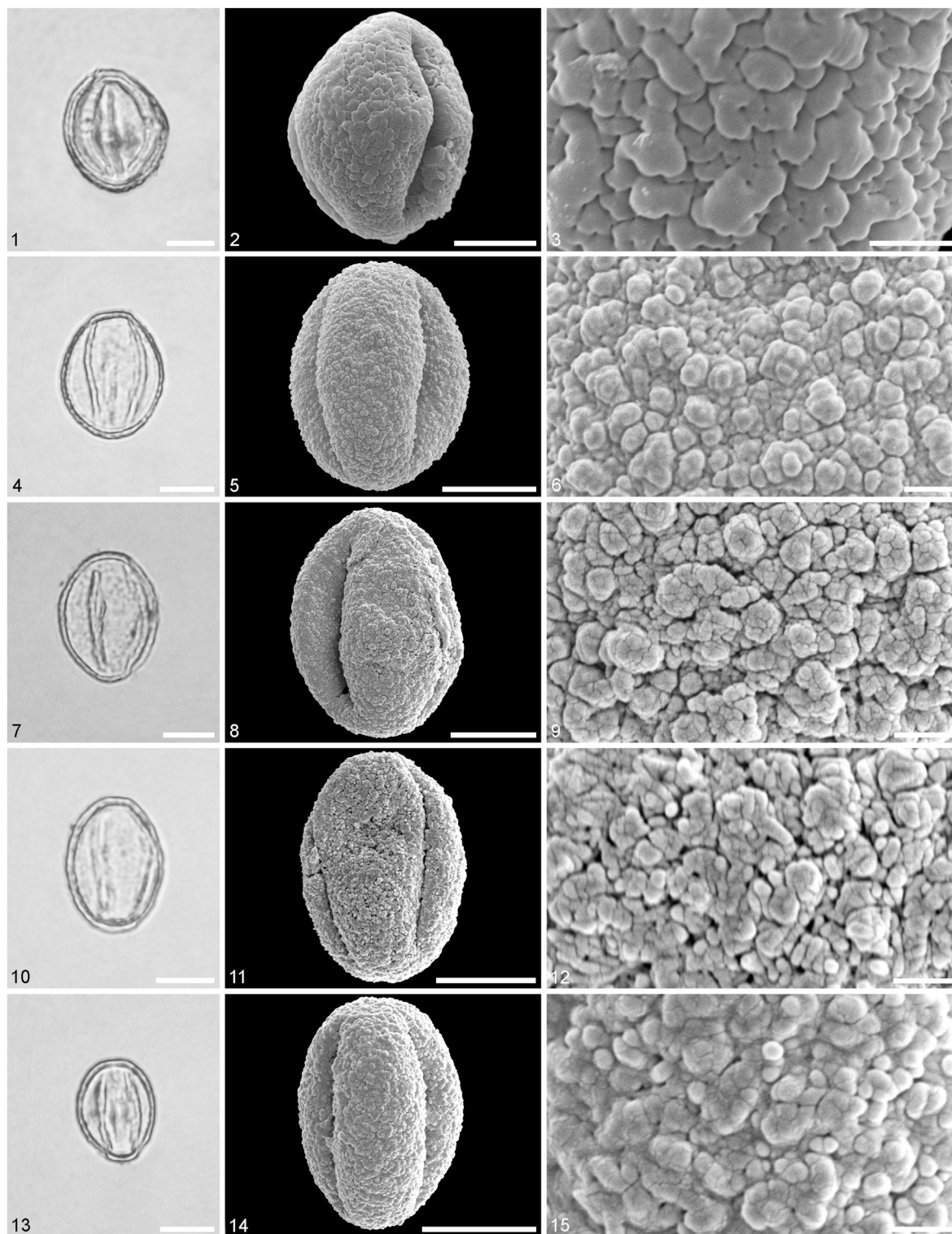
*Quercus* section *Quercus* vel *Lobatae* sp. 1 (Fig. 5, 4–9).

Description. Pollen, dispersal unit monad, outline trilobate in polar view, elliptic in equatorial view (LM), polar axis 25–27  $\mu\text{m}$  long (LM, SEM), equatorial diameter 19–22  $\mu\text{m}$  (LM, SEM), P/E ratio prolate, shape ellipsoid; aperture arrangement tricolporoidate, colpi long, pori small and indistinct; exine 0.9–1.1  $\mu\text{m}$  thick, nexine thinner than sexine (LM); pollen wall tectate (SEM); sculpture psilate to scabrate in LM, nano- to microverrucate, fossulate, and perforate in SEM, the nano/microverrucae composed of agglomerated nanorugulae, all sculpture elements partly masked by sporopollenin (SEM).

Remarks. For notes on literature regarding the pollen morphology and ultrastructure of pollen from *Quercus* section *Lobatae* see Remarks for the *Quercus* section *Lobatae* sp. 1. pollen type. The pollen morphology (LM and SEM) and ultrastructure (TEM) of *Quercus* section *Quercus* has been thoroughly documented by Martin and Drew (1969), Adams and Morton (1972), Crepet and Daghljan (1980), Miyoshi (1982), Lewis et al. (1983), Solomon (1983b), Jones et al. (1995), Wang and Pu (2004), Denk and Grimm (2009), Makino et al. (2009), Li et al. (2011), Miyoshi et al. (2011), Panahi et al. (2012), and Denk and Tekleva (2014). Based on the literature it is clear that both sections *Lobatae* and *Quercus* can produce medium to large sized pollen with indistinct endoapertures (LM) as well as the very typical “cauliflower” sculpture (sensu Denk and Grimm, 2009) observed with SEM. Therefore, pollen showing this combination of features cannot be assigned to only one of the two sections with certainty (e.g., Denk and Grimm, 2009). The fossil pollen record representing *Quercus* section *Quercus* vel *Lobatae*, based on combined LM and SEM investigations, comprises dispersed pollen grains from the middle Eocene of Hareøen, western Greenland (Grímsson et al., 2015), the late Eocene of Colorado, United States (Bouchal et al., 2014), the late Oligocene of southwestern Siberia (Denk et al., 2021a,b), the Miocene of eastern China (Liu et al., 2007), the Middle Miocene of Turkey (Bouchal et al., 2016a; 2017; Bouchal, 2019), the Late Miocene of Iceland (Denk et al., 2010) and northwestern Greece (Bouchal et al., 2020), the Late Miocene–Early Pliocene of Tennessee, United States (Liu and Quan, 2020), the Pleistocene of Albania (Denk et al., 2021a,b), and the Holocene of the Sea of Japan (Tekleva et al., 2014). The typical “cauliflower” sculpture observed with SEM in the *Quercus* section *Quercus* vel *Lobatae* sp. 1 pollen type is known from all mentioned Eocene to Holocene fossil records.

#### *Quercus* section *Quercus* vel *Lobatae* sp. 2 (Fig. 5, 10–15).

Description. Pollen, dispersal unit monad, outline trilobate in polar view, elliptic in equatorial view (LM), polar axis 20–25  $\mu\text{m}$  long (LM, SEM), equatorial diameter 15–19  $\mu\text{m}$  (LM, SEM), P/E ratio prolate, shape ellipsoid; aperture arrangement tricolporoidate, colpi long, pori small and indistinct; exine 0.8–1.1  $\mu\text{m}$  thick, nexine thinner than sexine (LM); pollen wall tectate (SEM); sculpture



**Fig. 5.** Fossil Fagaceae pollen from Rio Maior. (1–3) *Quercus* section *Lobatae* sp. 3, same grain, sample SPT.1, (1) Equatorial view in LM, (2) Equatorial view in SEM, (3) Close-up of sculpture in SEM, (4–6) *Quercus* section *Quercus vel Lobatae* sp. 1, same grain, sample RM.56, (4) Equatorial view in LM, (5) Equatorial view in SEM, (6) Close-up of sculpture in SEM, (7–9) *Quercus* section *Quercus vel Lobatae* sp. 1, same grain, sample RM.52, (7) Equatorial view in LM, (8) Equatorial view in SEM, (9) Close-up of sculpture in SEM, (10–12) *Quercus* section *Quercus vel Lobatae* sp. 2, same grain, sample OBI.4, (10) Equatorial view in LM, (11) Equatorial view in SEM, (12) Close-up of sculpture in SEM, (13–15) *Quercus* section *Quercus vel Lobatae* sp. 2, same grain, sample OBI.4, (13) Equatorial view in LM, (14) Equatorial view in SEM, (15) Close-up of sculpture in SEM. Scale bar = 10  $\mu$ m in 1, 2, 4, 5, 7, 8, 10, 11, 13, and 14; 2  $\mu$ m in 3; 1  $\mu$ m in 6, 9, 12, and 15.

psilate to scabrate in LM, nano-to microverrucate, nanorugulate (rod-shaped), fossulate, and perforate in SEM, the nano/microverrucae composed of agglomerated nanorugulae, individual nanorugulae (rod-shaped) present between nano/microverrucae, all sculpture elements partly masked by sporopollenin (SEM).

Remarks. *Quercus* section *Quercus* vel *Lobatae* sp. 2 pollen differs from sp. 1 by its smaller pollen and the size and arrangement of sculpture elements observed with SEM. The “cauliflower” sculpture is less prominent and the individual nanorugulae composing the nano/microverrucae as well as those nanorugulae positioned between the nano/microverrucae are larger and more distinct than in *Quercus* section *Quercus* vel *Lobatae* sp. 1 pollen, especially in specimens where sporopollenin is not masking the main sculpture (compare Fig. 5, 6 to Fig. 5, 12). Although we assign the *Quercus* section *Lobatae* vel *Quercus* pollen into two different fossil-species, it is unclear how many biological taxa are represented by these pollen types. Pollen belonging to section *Quercus* vel *Lobatae* was the second most frequent Fagaceae pollen type in the Portuguese samples, just after the section *Cerris* type. As with other oak groups, different species can produce highly similar pollen and a single oak species can produce pollen showing considerable size range and wall thickness as well as differences in sculpture observed with SEM (see e.g., Solomon, 1983a, 1983b; Denk and Grimm, 2009; Makino et al., 2009).

## 5. Discussion

### 5.1. Modern versus Late Pliocene Fagaceae diversity of Portugal

At present times, the native flora of Portugal includes only a single genus of Fagaceae (*Quercus*, 8 spp.; sections *Quercus*, *Cerris*, *Ilex*; <https://flora-on.pt/>). *Fagus* occurs rarely as naturalized tree (<https://www.euforgen.org/species/fagus-sylvatica/>; Rübél and Rübél, 1932) and *Castanea sativa* despite being widely cultivated may not be native to Portugal either (Krebs et al., 2019). This diversity is lower than the diversity of Fagaceae during the Pliocene. From the Late Pliocene Rio Maior, Óbidos, and S. Pedro da Torre localities, we identified five sections of *Quercus* representing at least nine species, *Fagus*, and two fossil-species with strong morphological affinities to the Castaneoideae genera *Castanopsis* and *Castanea*. In addition, we recognized a species of the extinct

genus *Trigonobalanopsis*.

An increased taxonomic diversity during the Late Pliocene and Early Pleistocene in Portugal has also been reported for extinct and extirpated conifers (e.g. *Cedrus*, *Taxodium*, *Cathaya*, Magri et al., 2017, and possibly the extinct conifer *Quasisequoia couttsiae* (Heer) L. Vieira, 2009). The persistence of humid warm temperate Himalayan to Southeast Asian elements (*Quercus* sect. *Cyclobalanopsis* and genus *Castanopsis*) might be attributable to prolonged equable climate conditions in the Atlantic part of the Iberian Peninsula (Haywood et al., 2010; Jiménez-Moreno et al., 2010; Vieira et al., 2018).

### 5.2. Contrasting biogeographic links of Pliocene Fagaceae in Portugal

The Late Pliocene pollen assemblage of the Rio Maior region in western Portugal is particularly rich in Fagaceae taxa both at the genus and species levels. These fossil-taxa represent various contrasting biogeographic links of the Late Pliocene flora of Portugal (Table 2). Most conspicuous are final links of the European flora with the extant North American flora and with the extant East and Southeast Asian flora.

*Quercus* sections *Quercus* and *Lobatae* are common in Cenozoic strata of western Eurasia (e.g. Stuchlik et al., 2014; Grímsson et al., 2016b; Sadowski et al., 2020). Previous scanning electron microscopy studies of the pollen sculptures within and among members of these large and ecologically diverse oak sections (e.g. Solomon, 1983a, b; Denk and Grimm, 2009; Makino et al., 2009) demonstrated some morphological overlap in pollen sculpture between the sections. This makes it sometimes difficult drawing a clear boundary between these sections based on dispersed fossil pollen. Biogeographically, the American sect. *Lobatae* had a Paleogene distribution including western and eastern North America (Daghlian and Crepet, 1983; Bouchal et al., 2014), Europe (Sadowski et al., 2020), and East Asia (Tanai and Uemura, 1994; as sect. *Cerris*). The sect. *Lobatae* pollen identified in the present paper (Fig. 4, 4–9) and the previously identified sect. *Lobatae* vel *Quercus* pollen from Pliocene strata of Iceland (Denk et al., 2010) have in common that they correspond in micromorphology exclusively to pollen from (North) American extant members of *Quercus*. This indicates prolonged links of the European woody flora with North America in

**Table 2**  
Youngest stratigraphic ranges of Fagaceae lineages in western Eurasia.

Taxon/Time	Modern	Pleistocene	L Pliocene	E Pliocene	Miocene	Reference
<i>Trigonobalanopsis</i>	xx	xx	Portugal	Italy	Present (incl. Iceland)	1, 2, 3
<i>Fagus</i>	Present	Present	Present	Present	Present	
<i>Fagus gussonii</i>	xx	xx	xx	xx	Iceland, Spain, Italy, Greece	1, 4-8
<i>Castanea</i>	Present	Present	Present	Present	Present	1, 9
<i>C. sativa</i> lineage	Present	Present	Absent	Absent	Absent	10
Western Eurasian lineage	xx	xx	Portugal	?	Greece	
<i>Castanopsis</i>	x	x	Portugal	Bulgaria	Bulgaria, Germany	1, 11-13
<i>Quercus</i> sect. <i>Ilex</i>	Present	Present	Present	Present	Present	
<i>Quercus</i> sect. <i>Cerris</i>	Present	Present	Present	Present	Present	
<i>Quercus</i> sect. <i>Cyclobalanopsis</i>	x	x	Portugal	?	Austria?	1, 14
<i>Quercus</i> sect. <i>Lobatae</i>	x	x	Portugal	?	Present	1, 14, 15
<i>Quercus</i> sect. <i>Quercus</i>	Present	Present	Present	Present	Present	
<i>Q.</i> sect. <i>Quercus</i> East Asian type	x	x	Germany	?	?	16
<i>Q.</i> sect. <i>Quercus</i> New World type	x	x	Portugal	?	Iceland	1, 4

Note: L: Late, E: Early, xx: Extinct, x: Extirpated, Present: Widespread in western Eurasia, Boxes: Genetic bottlenecks and/or hybridization leading to extinction of old lineages and formation of modern species, Blue shading: “Atlantic link”, Orange shading: “East Asian link”. References: 1: this study, 2: Martinetto and Vieira (2020), 3: Vieira and Zetter (2020), 4: Denk et al. (2011), 5: Grímsson and Denk (2005), 6: Barrón and Diéguez (1994), 7: Knobloch and Velitzelos (1987), 8: Kvaček et al. (2002), 9: Mai and Velitzelos (1997), 10: Fernández-Lopez et al. (2021), 11: Mantzouka et al., 2021, 12: Gee et al. (2003), 13: Sadowski et al. (2018), 14: Grímsson et al. (2016b), 15: Stuchlik et al. (2014), 16: Kvaček et al. (2020).

Southwest Europe and Iceland. At the same time, links with the East Asian (modern) clade of *Quercus* sect. *Quercus* have recently been reported for oak foliage of the Late Pliocene flora of Frankfurt am Main (Germany; Kvaček et al., 2020).

In contrast, *Castanopsis* currently occurs from the southern Himalayas to Japan and Southeast Asia. In Europe, fossil records derive from Eocene to Pliocene strata (Sadowski et al., 2018, 2020). Hence, the present record from Late Pliocene deposits of Portugal represents a final link of the Pliocene western Eurasian with the current Himalayan-East Asian distribution of this genus. Recently, Mantzouka et al. (2021) carried out a broad comparative anatomical study of fossil wood from the Late Miocene to Early Pliocene of southwestern Bulgaria and modern wood of Fagaceae. These authors concluded that the largest similarities with the fossil wood was with the extant *Castanopsis*. Along with the presence of this genus in Early Miocene deposits of Germany (Gee et al., 2003), this suggests that *Castanopsis* persisted in western Eurasia at least from late Eocene to Late Pliocene times before it became extirpated in its last climate refuge.

Similarly, *Quercus* sect. *Cyclobalanopsis* is a group of evergreen oaks currently confined to the Himalayas and East and Southeast Asia (Grímsson et al., 2016b). It has a sparse record in Europe with possible occurrences in the late Eocene Baltic amber floras (Sadowski et al., 2020) and the Middle Miocene of southern Central Europe (Grímsson et al., 2016b). As for *Castanopsis*, the late persistence in Portugal might be due to the prolonged warmth and humidity in this part of South Europe.

The remaining members of extant groups of Fagaceae, *Quercus* sect. *Cerris*, *Quercus* sect. *Ilex*, *Castanea*, and *Fagus* have Eurasian (sect. *Cerris*) and Northern Hemispheric modern distributions, respectively. *Quercus* section *Cerris* sp. 1 pollen was the most frequent Fagaceae pollen occurring in the samples from Portugal. Today, only *Quercus suber* L., the cork oak, is native to Portugal. This morphologically and ecologically derived species was inferred to diverge from its sister species *Quercus crenata* Lam. during the Pliocene (Denk et al., 2022). Also, the evergreen sect. *Ilex* is today represented with two or more species in Southwest Europe. The modern western Eurasian members of this section evolved during the Pliocene and Pleistocene from its Himalayan sister taxa (Jiang et al., 2019). Consequently, the Late Pliocene records of sections *Cerris* and *Ilex* may belong to the extant lineages thriving today in Portugal.

The fossil record of *Castanea* is obscure and the origin of this widely cultivated species in western Eurasia is unclear. A main obstacle to detect *Castanea* in the leaf fossil record is the lack of discriminative characters of the leaf morphology and micromorphology against species of *Quercus* sect. *Libani* (Kvaček et al., 2002; Denk et al., 2022). Recent population genetic studies (Fernández-Lopez et al., 2021) suggest that the modern *C. sativa* evolved from a global Cenozoic population that experienced a genetic bottleneck during Late Miocene to Early Pliocene times. A split between a western and eastern portion of the ancestral western Eurasian population would have occurred during the Early to Middle Pleistocene. During subsequent interglacial intervals of the Middle and Late Pleistocene, the extant Iberian populations of *C. sativa* originated in a hybrid zone between the western and eastern populations. Such a scenario is in accordance with Messinian records of *Castanea* (based on fruits and leaves) from Northern Greece (Mai and Velitzelos, 1997; Kvaček et al., 2002) and a Pliocene record of abortive nuts from Germany (Van der Burgh, 1978). A similarly complex evolutionary origin (and lack of fossil record) has recently been demonstrated for the Persian walnut, *Juglans regia* (Zhang et al., 2019).

*Fagus* is a common element in Late Pliocene floras across Europe (e.g. Kvaček et al., 2008, 2020); an earlier link between Atlantic

floras of the Iberian Peninsula with the North Atlantic floras of Iceland existed in the form of the Late Miocene fossil-species *Fagus gussonii* A. Massal.). *Fagus* is absent from the extant flora of Portugal and became extirpated in Portugal during the late Chibanian stage (Magri et al., 2017).

Finally, the Late Pliocene flora of Rio Maior hosts the youngest known record of the fossil-genus *Trigonobalanopsis*. This genus is known from Late Cretaceous strata of Siberia (cf. Denk and Bouchal, 2021) and Paleogene strata of western North America (Grímsson et al., 2016a). Youngest records of *Trigonobalanopsis* have previously been documented from some Italian localities dating to the Early and “middle” Pliocene represented by carpological remains or leaves (Basilici et al., 1997; Martinetto, 1996; Martinetto, 1999, 2001; Kvaček, 2007). Hence, the present record from the Piacenzian of Portugal is the youngest records of this taxon; it is absent from coeval floras of Central Europe (e.g. Auenheim, Frankfurt; Kvaček et al., 2008; Kvaček et al., 2020).

### 5.3. Differential extinction/extirpation during the pliocene/pleistocene

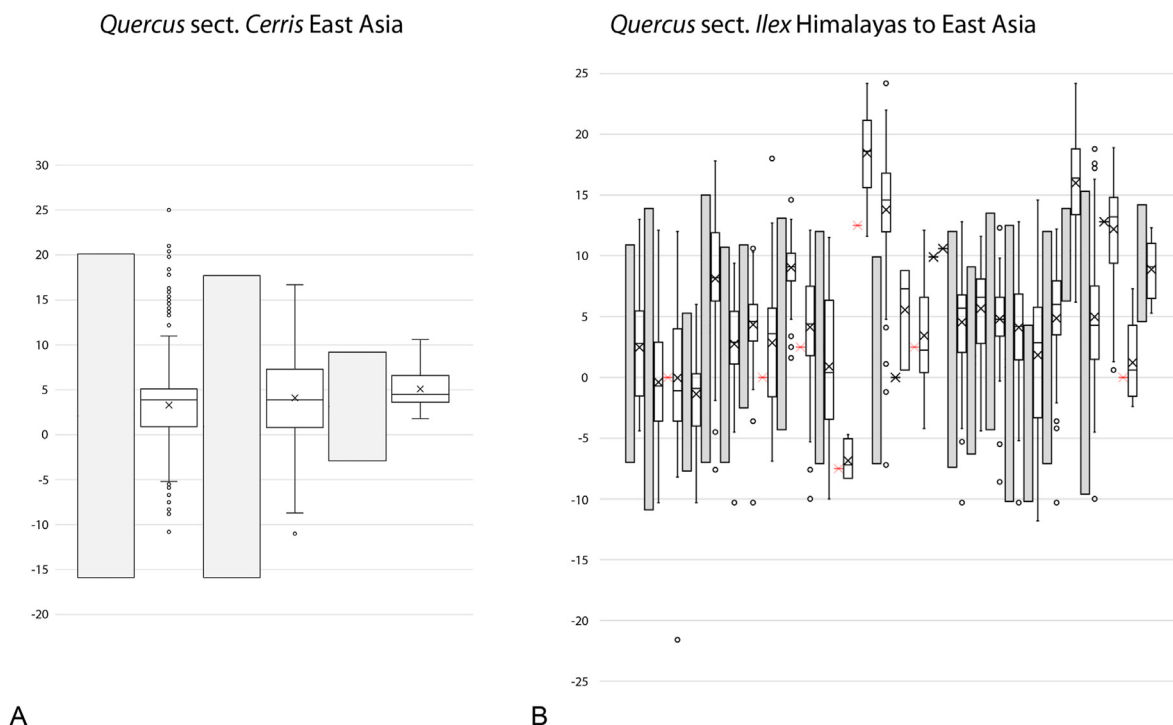
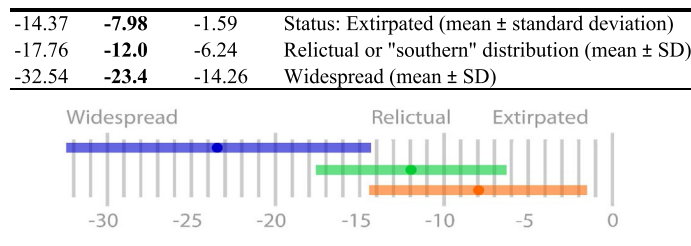
For the Pleistocene, deterministic extirpation has been suggested to explain why some plant groups disappeared from western Eurasia whereas others persisted in refugia (Svenning, 2003). Specifically, this study suggested that climatic requirements of modern extra-European woody taxa could explain whether their European congeners survived, have a current relict distribution, or were extirpated (Table 3).

In our study, the extirpation of *Castanopsis* and *Quercus* sect. *Cyclobalanopsis* from the tree flora of Europe after the Late Pliocene fits with the deterministic model of Svenning (2003; Fig. 7A and B and Supplementary data 2). Both taxa have several species occurring in tropical climates (CMT  $\geq 18$  °C). While *Castanopsis* rarely thrives in areas with winter frosts, some species of *Quercus* sect. *Cyclobalanopsis* extend into areas with coldest month mean temperatures (CMT) below  $-10$  °C. Hence, the lower range of CMT in sect. *Cyclobalanopsis* is similar to another evergreen section in *Quercus*, sect. *Ilex* (Fig. 6B). However, members of sect. *Ilex* adapted to seasonally dry climates (climate niche evolution) and persisted in southern refugia of the Mediterranean region; in addition, sect. *Ilex* was diverse and widespread across western Eurasia during the Neogene. In contrast, *Castanopsis* and *Q.* sect. *Cyclobalanopsis* did not shift from their humid warm temperate climate niches and became extirpated in western Eurasia. Both groups were rare during the Neogene in western Eurasia.

Also, the persistence of *Quercus* sect. *Cerris* (Fig. 6A), *Castanea* (Fig. 7C), and *Fagus* (Fig. 7D) fit with a deterministic model. *Quercus* sect. *Cerris* was widespread and diverse during the Neogene in western Europe and adapted to different environments; *Fagus*, despite its CMT lower range being between the predicted status relictual and widespread (Table 3), is widespread in present western Eurasia and was diverse and widespread throughout the Neogene and Pleistocene. The present state of *Castanea* (relictual, southern refugia – overprinted by its wide current cultivation in Europe) corresponds with the CMT threshold predicted for relictual taxa (Table 3).

For three other groups extirpated in Europe, other reasons than a climatic determinism must be invoked to explain their current absence from western Eurasia. Modern CMT of extra-European members of *Quercus* sect. *Lobatae* would suggest that this group of oaks should have survived and being widespread in the modern tree flora of Europe. Likewise, members of the Chinese and North American clade of *Quercus* sect. *Quercus* should have survived in Europe (Fig. 7E and F and Table 3). Fossil-taxa corresponding with the Chinese clade of *Quercus* sect. *Quercus* are rarely encountered in

**Table 3**  
Coldest month mean temperature (CMT; °C) thresholds proposed in Svenning (2003) determining present European status (extirpated, relictual, widespread) of temperate trees.



**Fig. 6.** Coldest month mean temperatures (CMT; °C) of extra-European modern representatives of Fagaceae lineages identified from the Late Pliocene Rio Maior assemblage. Box plots (GBIF occurrence data and gridded WorldClim climate data) and ranges of CMT (grey bars; data from Fang et al., 2011). See Supplementary data 2 for taxon sampling. **A.** East Asian members of *Quercus* sect. *Cerris*. CMT from the two different databases are in good agreement, but ranges from Fang et al. (2011) tend to be biased towards cooler CMT. **B.** Himalayan to East Asian members of *Quercus* sect. *Ilex*. CMT from the two databases are in good agreement. Lower CMT range of Fang et al. (2011) commonly corresponds to extreme values from occurrence data. Red symbols indicate data are missing for this taxon in Fang et al. (2011)

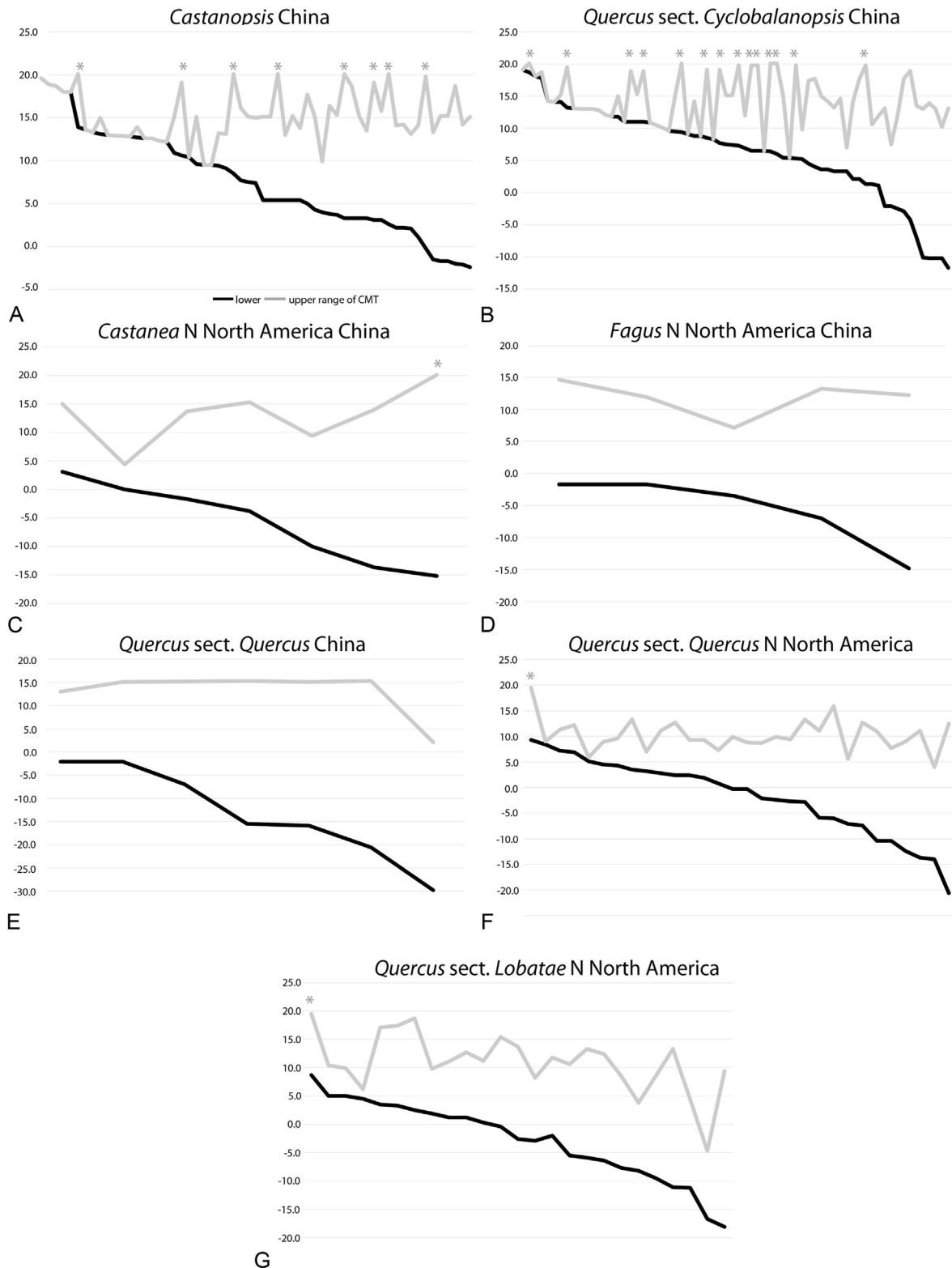
the Neogene fossil record of western Eurasia (Late Miocene to Late Pliocene; see discussion on the fossil-species *Quercus praecastaneifolia* Erw. Knobloch in Kvaček et al., 2020). Likewise, members of the North American clade of *Q.* sect. *Quercus* are extremely rare in the European fossil record (possibly the early Pliocene *Quercus* pollen morphotype 2 reported from Iceland (Denk et al., 2010).

*Quercus* sect. *Lobatae* is at present times confined to the Americas and climate properties of modern members would suggest that this group should have persisted in western Eurasia (Fig. 7G). *Quercus* sect. *Lobatae* is not frequently encountered in the Neogene record of western Eurasia and a possible reason for its extirpation here is loss of suitable habitats as these oaks may have been typical elements of lignite forming swamp vegetation in Europe.

Recent palaeobotanical work indicates further deviations from a strictly deterministic model of persistence versus extirpation. The conifer genus *Tsuga* with North American species thriving in areas with CMT below -16 °C (Thompson et al., 2015) disappeared from

most parts of Europe during the Pleistocene (Magri et al., 2017; Donders et al., 2021) and persisted until the Late Pleistocene in Anatolia (Biltekin et al., 2015). Similarly, *Carya* with CMT below -14 °C in North America (Thompson et al., 2015) disappeared in western Eurasia in the latest Pleistocene, despite being more cold-tolerant than some relict tree taxa in western Eurasia (e.g. *Aesculus*, *Liquidambar*, see Fang et al., 2011; Thompson et al., 2015). At the same time, Postigo-Mijarra et al. (2009) demonstrated that a number of warmth-loving taxa (Sapotaceae, Engelhardioideae, Mimosoideae) persisted in the Iberian Peninsula at least until the Gelasian and sometimes until the Early Pleistocene. Sapotaceae were reported to have persisted until the Early Pliocene in Anatolia and possibly into the Early Pleistocene on the island of Zakynthos and southern Italy, and Engelhardioideae until the Middle Pleistocene (Chibanian; Biltekin et al., 2015; Magri et al., 2017).

Somewhat counterintuitive, the last occurrence of *Acer* sect.



**Fig. 7.** Coldest month mean temperature (CMT; °C) ranges of modern representatives of Fagaceae from China (Fang et al., 2011) and northern North America (Thompson et al., 2015). See Supplementary data 2 for taxon sampling. Asterisks on upper CMT ranges indicate that a taxon enters the tropical zone (defined by CMT ≥ 18 °C). **A.** *Castanopsis*. Post-Pliocene extirpation in western Eurasia follows a deterministic model (niche conservatism in a warm temperate to tropical lineage). **B.** *Quercus* sect. *Cyclobalanopsis*. Post-Pliocene extirpation in western Eurasia despite relatively low CMT in some taxa (compare with *Q.* sect. *Ilex*; Fig. 6B). This warm temperate to tropical lineage was rare and not diversified in western Eurasia during the Neogene. **C.** Extra-European *Castanea*. Persistence in southern parts of western Eurasia; relatively low CMT; uncommon in fossil record throughout the Neogene. **D.** Extra-European *Fagus*; relatively cool CMT but warmer than *Castanea*. Persistence in cool parts of western Eurasia; widespread and diversified throughout western Eurasia during Neogene. **E.** Chinese clade of *Quercus* sect. *Quercus*. Extirpated in western Eurasia after the Pliocene; very low CMT. Rare in European Pliocene. **F.** Northern North American *Q.* sect. *Quercus*. Post-Pliocene extinction in western Eurasia; low CMT; very rare during late Neogene of Europe. **G.** *Quercus* sect. *Lobatae* northern North America. Post-Pliocene extirpation in western Eurasia despite relatively low CMT. Habitat loss (coal swamps) during late Neogene.

*Palmata* in Europe at 0.8 Ma (latest Early Pleistocene) prior to its final extinction in western Eurasia (Denk et al., 2022) also does not fit with the deterministic Plio-Pleistocene extinction hypothesis of Svenning (2003). Extra-European members of *Acer* sect. *Palmata* occur in areas with CMT not colder than  $-8\text{ }^{\circ}\text{C}$  in North America (*A. circinatum* Pursh.; Thompson et al., 2015) and  $-18.8\text{ }^{\circ}\text{C}$  (*A. pseudosieboldianum* (Pax) Kom.) in China (Fang et al., 2011). Denk et al. (2022) suggested that for some of the current relict taxa, complicated genetic bottlenecks including hybridisation may have been key to their survival. Examples are *Zelkova sicula* in Italy, but also several cultivated trees such as *Juglans regia* and *Castanea sativa* (Zhang et al., 2019; Fernández-Lopez et al., 2021).

## 6. Conclusion

In this study we described a high diversity of plant lineages belonging to the family Fagaceae in Late Pliocene deposits of Portugal. For both extinct and modern genera, the Pliocene records of Portugal are the latest ones in western Eurasia prior to their Pleistocene extinction (fossil-genus *Trigonobalanopsis*) and extirpation (fossil-taxa of *Castanopsis*, *Quercus* sections *Cyclobalanopsis* and *Lobatae*; North American clade of *Quercus* sect. *Quercus*). Further palynological studies with high taxonomic resolution would be needed in the Mediterranean region to establish a full chronology of extinctions and extirpations in this area. Based on the current data, we found that climate deterioration explains some of the Pleistocene extirpations of Fagaceae lineages in western Eurasia as has been previously suggested (deterministic model in which climate properties of extra-European congeneric taxa explain the state of these taxa in Europe – widespread, extinct, and relictual; Svenning, 2003). In addition, we found that for some groups climate alone does not explain whether these lineages became extirpated, persisted in refugia or continue to be widespread in western Eurasia. Main factors determining the fate of Fagaceae lineages during the Late Pliocene and Pleistocene were their ability of niche evolution, their abundance and/or taxonomic diversity during pre-Pleistocene times, and habitat availability (for example, lignite forming swamp vegetation for some *Quercus* sect. *Lobatae*). Lineages, which became extirpated in western Europe commonly showed niche conservatism (for example, humid warm temperate to tropical climate niches of *Castanopsis* and *Quercus* sect. *Cyclobalanopsis*). Cold adapted lineages that became extirpated (for example, East Asian clade of *Quercus* sect. *Quercus*) usually were rare in the Neogene fossil record of western Eurasia. A number of lineages with similar lower ranges of coldest month mean temperatures of their extra-European congeneric species (suggesting either extirpation or relictual distributions in Europe) nevertheless have different states in the modern flora of Europe: *Castanea* – relictual; rare during the Neogene. *Fagus* – widespread; diverse and common during the Neogene. *Quercus* sect. *Lobatae* – extirpated in Europe; rare during the European Neogene, typical element of lignite forming swamp forests. *Quercus* sect. *Cyclobalanopsis* – extirpated; rare during the European Neogene, niche conserved. *Quercus* sect. *Ilex* – relictual in southern, Mediterranean, refugia; widespread and diverse during the European Neogene.

## Author contributions

MV did the palaeontological fieldwork and collected the material; MV and FG described the plant material; MV, FG, RZ, and TD identified fossil dispersed pollen; TD compiled climate parameters for modern extra-European Fagaceae; MV, FG, and TD wrote the first drafts, all authors wrote and discussed the final paper.

## Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

## Data availability

All data used are made available in the main article and the Supplement.

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## Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.quascirev.2022.107896>.

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