



Research papers

New Pliocene records of plant fossil-taxa from NW Portugal and their relevance for the assessment of diversity loss patterns in the late Cenozoic of Europe



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ABSTRACT

The section of São Pedro da Torre (NW Portugal) is relevant because its rich pollen content, chronologically correlated to the late Pliocene assemblages of the reference section of Rio Maior. The purpose of this study was to carry out, for the first time in the area, a taxonomic analysis of the carpological remains and integrate the results with those of the previous palynological studies. Our carpological analysis pointed out several taxa not recorded previously in the area, mostly belonging to genera extirpated from Europe, such as *Azolla* cf. *aspera*, *Hypericum tertiarum*, *Itea europaea*, *Eurya stigmosa*, *Proserpinaca reticulata*, *Symplocos casparyi*, *Symplocos germanica* and *Tetraclinis salicornioides*. This taxonomic composition was only detected in Piacenzian deposits from Italy, the area of southern Europe where the chronological sequence of fruit and seed assemblages is less discontinuous. For most of these taxa the occurrence at São Pedro da Torre constitutes a westward extension of the distribution during Neogene. *Symplocos germanica* occurs for the first time in the Pliocene and is recorded much more westwards and southwards than previously known. The integrated plant record shades light on the vegetation, paleoenvironments and plant extirpation patterns throughout the Pliocene in the Iberian Peninsula. Although limited, the results from this contribution are intended to stimulate the search for fruit and seed assemblages in Portugal as well as in similar poorly studied areas, where Pliocene successions keep a future potentiality in documenting further the late occurrences in Europe of extirpated plant taxa, which are relevant for paleoclimatic and biogeographic reconstructions.

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1. Introduction

Throughout the Neogene, some European sites record very rich and diverse (leaves, seeds-fruits, pollen, wood) floras. However, they are not equally distributed over the continent but rather clustered in regions with appropriate sedimentation; some areas largely lack a fossil record, as different plant organ assemblages are bound to specific taphonomic conditions (Kovar-Eder, 2003).

The Pliocene constitutes a key period for understanding the origin of current vegetation associations across Europe. During this period, the European continent experienced a profound transformation of its vegetation, largely due to climate change. In southern Europe, these changes led to the disappearance of the subtropical tree vegetation, giving way to the Mediterranean vegetation that exists today. According to Vieira

et al. (2018) the Atlantic coast of the Iberian Peninsula appears to have maintained a warm and humid climate throughout the Pliocene. The relatively high precipitation reconstructed for most of the Rio Maior palynological record is substantially different from Piacenzian reconstructions on the Mediterranean side of the Iberian Peninsula. Mainly, these coastal areas served as a refuge mostly for thermophilous plants that otherwise would have vanished from Eurasia by the end of the Miocene or after the first Zanclean cooling events (Postigo-Mijarra et al., 2009; Vieira and Zetter, 2020). Genera like *Cercidiphyllum*, *Craigia*, *Mortoniendron*, *Diplopanax*, *Zanthoxylum*, Sapotaceae, *Trigonobalanopsis* or *Leitneria* have been recorded as part of the megathermal and mesothermal elements recorded in Piacenzian strata of West Portugal (Vieira and Zetter, 2020).

In this article we present the Pliocene record of several genera later extirpated (Smith-Patten et al., 2015) from Europe in the frame of the associated flora from the São Pedro da Torre (SPT) deposits in North-west Portugal. The records from such an extreme south-western location in Europe are relevant in the frame of the ongoing discussion about the extent and timing of Plio-Pleistocene plant extirpations and

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extinctions (Svenning, 2003; Biltekin et al., 2015; Magri et al., 2017; Momohara, 2016; Martinetto et al., 2017).

2. Geological setting

The SPT section is located in Northwest Portugal, close to the Spanish border (Fig. 1). This region is part of the greater Iberian Massif which comprises Precambrian–Paleozoic basement rocks. The deposits preserved at this location are part of the River Minho Basin. This basin extends from Galicia (Spain) into the North of Portugal over an area of approximately 17,080 km² and includes the Sil sub-basin, which, prior to the confluence with the Minho River, is more extensive draining from the Galician Range.

The Minho River extends 300 km in a NE-SW orientation. It runs from Lugo (Spain), in the North, and terminates at the Atlantic Ocean after a 70 km course defining the border between Portugal and Spain. In the terminal sector, the Minho valley is strongly controlled by variscan faults and by tectonic depressions related to the movement of some post Alpine related faults (Fig. 1).

The pre-Pleistocene Cenozoic deposits in the North-West Iberian Peninsula are limited and the sediments primarily infill small strike-slip basins running along N-S to NW-SE trending fault corridors. The younger Pleistocene and Holocene terraced fluvial deposits are located in the fluvial valleys (mainly in Minho valley) and close to the coast. These are composed of conglomerates with thin beds of sand and clay (Pereira, 1991).

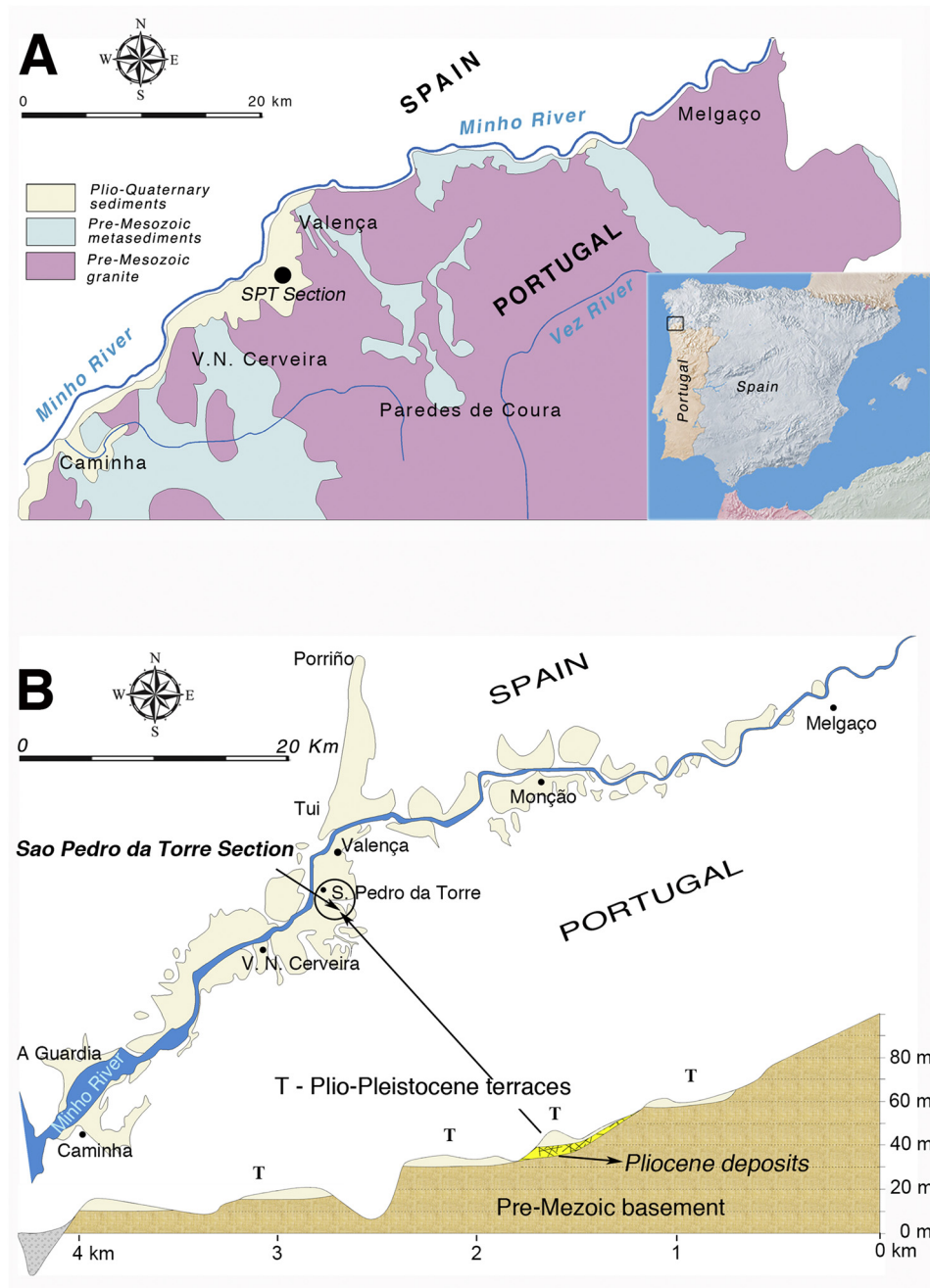


Fig. 1. Geological map and stratigraphy of São Pedro da Torre area. A - Regional geological map of Northwest Portugal (adapted from the Geological Map of Portugal 1:1,000,000, LNEG); B - Fluvial deposits from Minho River Basin. The transverse profile represents the sediments from S. Pedro da Torre area. The studied samples are from the Pliocene sediments, underneath the Plio-Pleistocene fluvial terraces (adapted from Vieira et al., 2011).

This study focused on the SPT fossiliferous level from the Cenozoic fluvial sedimentary record. It is preserved in a 4 km wide depression between Porriño (Spain) and V.N. Cerveira (Portugal) and is related to the N-S trending Pontevedra–Ponte de Lima fault corridor (Fig. 2). The geology of this region has been studied by several authors since 1944 (Teixeira, 1944; Lautensach, 1945; Nonn, 1966, 1967; Carvalho, 1981; Pereira, 1989, 1991; Alves and Pereira, 2000). In this location, a lower unit comprising clays with rich local horizons of lignites, sands and gravel, is covered by extensive fluvial gravel. These gravels are largely attributed to terraced fluvial deposits of Pleistocene age (Pereira, 1989, 1991). In order to date the basal lignite layers Nonn (1966) conducted a palynological study, the flora recovered contained *Palmae*, *Nyssa*, *Myrica*, *Rhus*, *Symplocos*, *Lygodium*, *Capparaceae* and *Cupressaceae* together with temperate elements like *Castanea*.

2.1. São Pedro da Torre flora

Some macrofossil remains recovered from the Barrocas site (São Pedro da Torre, Valença) have been partly studied in the late 1980's by João Pais and H.-J. Gregor but were never published (Pais et al., unpublished manuscript). They reported abundant leaves of *Taxodium* and *Liquidambar* (see Vieira et al., 2011 – fig. 5), fruits and seeds of *Taxodium*, *Symplocos*, *Eurya*, *Salvinia*, *Tilia*, *Rubiaceae* and *Apiaceae*. Also, in a preliminary palynological evaluation, when the outcrop was exposed, J. Pais recognized pollen grains of *Pinus*, *Picea*, *Taxodiaceae*, *Symplocos*, *Engelhardia*, *Carya*, *Liquidambar*, *Quercus*, *Salvinia*, *Ericaceae* and *Poaceae* (Vieira et al., 2011).

Poças (2004) analyzed two samples for palynology from the same levels and identified 28 different taxa and a high content of charcoal and amorphous organic matter. The described pollen assemblage was constituted by spores of *Lycopodium*, *Anthoceros*, *Polypodiaceae*, pollen of such gymnosperms as *Pinus*, *Cathaya*, *Tsuga*, *Taxodiaceae*, *Ephedra* and diverse angiosperm pollen of *Castanea*, *Quercus*, *Alnus*, *Engelhardia*, *Myrica*, *Carya*, *Liquidambar*, *Juglans*, *Pterocarya*, *Acer*, *Oleaceae*, *Tilia*, *Ilex*, *Ericaceae*, *Poaceae*, *Amaranthaceae*/*Chenopodiaceae*, *Cistaceae*, *Asteraceae* and *Cyperaceae*.

Vieira et al. (2011), studied three extra samples and applied a procedure with sodium perborate to remove the charcoal content from the samples to facilitate the pollen identification. Some pollen grains have been separated for single grain observation under Light Microscope (LM) and Scan Electronic Microscope (SEM), following the procedure outlined by Vieira et al. (2009) for comparative morphologic study. This technique allowed the recognition of 40 additional pollen and spore taxa for the first time in these sediments. The pollen assemblages revealed spores of *Pteridaceae* (most abundant), *Selaginellaceae*,

Polypodiaceae, and less numbers of *Osmundaceae*, *Cyatheaceae*, *Gleicheniaceae*, *Sphagnum*, *Anthocerochytes* and *Riccia*.

Pinaceae pollen is very abundant in the assemblage and other gymnosperms such as *Picea*, *Tsuga* and *Cupressaceae* (*Taxodiaceae* included), are present in small quantities. *Taxodium* leaves are more frequent in the sediment than the pollen, which is probably due to the poor preservation of the *Taxodiaceae* grains within the samples studied (Vieira et al., 2011).

Angiosperm tree and shrub pollen is abundantly recorded and diverse within the pollen assemblage and is essential in the characterization of the local vegetation types. The herbs are represented in lesser proportions, thus testifying to a dominance of forest-type vegetation in the areas surrounding the paleo-lake/channel. *Liquidambar* and *Juglandaceae* are relatively abundant, including the genera *Engelhardia* and *Juglans*, with subordinate *Carya*, *Platycarya* and *Pterocarya*. Vieira et al. (2011) noted that *Engelhardia* pollen record has a higher abundance when compared to *Quercus*. Pollen grains of *Symplocos* and *Nyssa* are also abundant, whereas those of other genera extirpated from Europe, e.g. *Diplopanax* and *Cercidiphyllum*, occur sporadically. The pollen record also revealed aquatic plants, such as *Typha*, *Myriophyllum* and *Nuphar*. Herbaceous angiosperms are also represented by several taxa from the family *Asteraceae*, *Cistaceae*, *Apiaceae*, *Poaceae*, etc. Woody climbers such as *Hedera* and *Parthenocissus* also have been reported (Vieira et al., 2011).

Vieira et al. (2011) correlated the SPT floral association with the lower part (early Piacenzian) of the Rio Maior succession (the reference basin for the Portuguese Pliocene re-studied by Vieira (2009) on the basis of the shared abundance of pollen of *Engelhardia*, *Symplocos* and *Nyssa* (Vieira, 2009; Vieira et al., 2009; Vieira et al., 2018)). The pollen assemblages of both these localities characterize a diverse, mixed, forest dominated by several evergreen taxa intermixed with deciduous elements. The abundance of *Taxodium*-type pollen suggested the presence of swamp environments along the Portuguese Atlantic coast during most of the Pliocene, developed in a very moist (due to the proximity to the Atlantic) subtropical climate.

3. Material and methods

The sample analyzed for this study was collected from a sedimentary level of black clay intercalated with white clays containing visible plant macrofossils, which was exposed during the A3 highway construction during the 1990's. The construction allowed the collection of samples from the fossiliferous bed, shortly before the outcrop was reburied (Fig. 2).

A sample from the fossiliferous bed of laminated blue-grey consolidated mud (sediment volume c. 1.2 dm³) was selected for the detailed study of the macroremains. The sediment was dry, since it was stored since several years in the Earth Science Department at Minho University (Braga, Portugal). The bulk sample has been dried and sunk in 3% H₂O₂. After complete reaction of H₂O₂ with the sediment, both the fraction floating on the surface of the solution and the sunken one have been sieved with a final mesh size of 0.3 mm. Morphologically interesting plant parts (mainly fruits and seeds) have been picked up from the residues, separated in small plastic boxes, identified, counted, and finally stored in the paleocarpological collection of the Earth Sciences Department of the University of Turin. Furthermore, selected specimens were observed under SEM. The taxonomic identification procedures and nomenclature used are in agreement with those described in Martinetto (2015).

4. Results

The analyses revealed a species-poor carpological assemblage due to sediment facies and small volume available, but the presence of some relevant taxa previously never reported from this latitude have allowed a comparison of the flora with others in western territories of Eurasia.



Fig. 2. Photo of the outcrop during the construction of the A3 highway, in São Pedro da Torre (Valença, Portugal) highlighting the fossiliferous bed.

The list of taxa identified in SPT is detailed in Table 1. The more relevant species have been selected for a detailed discussion regarding their importance to understand the Pliocene floras.

4.1. Systematic paleontology

Plant families according to Stevens (2001 onwards).

Family: SALVINIACEAE

Genus: **Azolla**

Species: *Azolla* cf. *aspera* P.I.Dorof.

Plate I, 1–3

Description: See Nikitin and Hvalj (2011).

Remarks: The species of *Azolla* occurring at SPT shows megaspores very similar to those of *A. pyrenaica* Florschütz and Menéndez Amor, a poorly known fossil-species described from the Pliocene of Rousillon (SE France), and whose name validity is questioned by Nikitin and Hvalj (2011): “designatio typi omissa”. The abundant megaspores of SPT were directly compared with material collected in the type locality Ille-sur-Têt and found to correspond in all the details. However, they also seemingly resemble the megaspores of the valid Russian species *Azolla aspera*, whose accurate comparison to *A. pyrenaica* does not seem to have been carried out yet, thus forcing us to treat them as the *A. aspera*-*A. pyrenaica* type of megaspores. In the absence of an accurate taxonomic overview in southern and western Europe, the open nomenclature *Azolla* cf. *aspera* could be of practical use to accommodate specimens with affinity to *A. aspera* (Nikitin and Hvalj, 2011).

Distribution: *Azolla* cf. *aspera* occurs in two Italian localities, considered of Zanclean age (Benasso and Canton Talentino: Martinetto, 1994), hence the record of SPT is the only one in western and southern Europe assessing the persistence until Piacenzian of this plant or group of plants. *Azolla* cf. *aspera* seems to disappear from the fossil record of the whole Europe at the end of the Pliocene (Nikitin and Hvalj, 2011). Another fossil-species with larger megaspores, *A. tegeliensis* Florschütz, occurs in the Gelasian of central Europe and Italy (Mai and Walther, 1988; Martinetto et al., 2007), and disappears (probably meeting with extinction) before the Middle Pleistocene (Field, 1992).

Family: CUPRESSACEAE

Genus: **Tetraclinis**

Species: *Tetraclinis salicornioides* (Unger) Kvaček.

Plate I, 9–12

Description: See Kvaček (1989) and Kvaček et al. (2000) for the diagnostic features of *Tetraclinis salicornioides* and its distinction from the related fossil-species *Tetraclinis brachyodon* (Brongn.) Mai et H. Walther. Both species differ mainly in epidermal structure of their scaly leaves, four of which are combined in flattened decussate pairs, called “cladode-like segments”. *T. salicornioides* is distinguished from *T. brachyodon* also for the generally broader cladode-like segments. This species is considered to have been a thermophilous element living in the undergrowth of mixed evergreen and deciduous forests (Kovar-Eder et al., 1996), requiring high atmospheric humidity. Conversely, *T. brachyodon* was most likely a more xeromorphic element growing mainly in lowland forests along seacoasts (Kvaček, 1989).

Remarks: The highly diagnostic fossil remains from the Pliocene of SPT constitute the record of *Tetraclinis* which is youngest and closest to its present relict stands. Presently, the genus *Tetraclinis* comprises a single extant species, *Tetraclinis articulata* (Vahl) Mast., also known as Cartagena Cypress, which is native from warm and dry areas of North Africa, but also found in the islands of Malta and Cyprus, and in southern Spain (Sierra de Cartagena, Murcia) (Morte and Honrubia, 1996). However, the genus *Tetraclinis* has a good fossil record comprising cones, seeds, and foliage (Kvaček, 1989; Kovar-Eder and Kvaček, 1995; Mai, 1985; Zidianakis et al., 2007), particularly in the Oligocene and Miocene strata across Europe.

Distribution: The fossil-species *T. brachyodon* has been recorded, mainly in Europe, in early Eocene to early Pliocene sediments. *T. salicornioides* is more common than the foregoing species in Europe,

occurring from middle Eocene to late Pliocene. Meyer and Manchester (1997) reported the occurrence of *Tetraclinis* in North America and a posterior publication from Kvaček et al. (2000) discussed the recognition of *T. salicornioides* in western North America and its dispersal across the North Atlantic during the Paleogene or Miocene.

Family: HALORAGACEAE

Genus: **Proserpinaca**

Species: *Proserpinaca reticulata* C.Reid & E.Reid.

Description: See Reid and Reid (1915) and Mai and Walther (1988). The extinct diversity of *Proserpinaca* in Europe is uncertain: Dorofeev (1976) proposed three fossil-species on the basis of small variations in fruit morphology, that should be accurately re-evaluated. One of these species, *P. brevicarpa* P.I.Dorof. has been accurately documented from the middle Miocene of Denmark (Friis, 1985). Fruits from Pliocene localities, with very similar morphology, but longer and with a different surface sculpture, have been assigned to *P. europaea* P.I.Dorof.

Remarks: Within the family Haloragaceae, of possible Australian origin (Chen et al., 2014), the genus *Proserpinaca* currently comprises three species of herbaceous plants distributed from Eastern North America towards Central America and into Colombia and Brazil. It is commonly found in shallow water environments, along shores of lakes and streams. (Schmidt-Mumm and Posada, 2000).

Distribution: Reid and Reid (1915) were the first authors to recognize the occurrence of *P. reticulata* in the Cenozoic of Europe. This occurrence was later confirmed by several studies (e.g., Szafer, 1954; Zagwijn, 1963; Geissert, 1967; Mai and Walther, 1988; Martinetto, 1994) that pointed out a distribution of fossils since the Oligocene-Miocene transition in western Siberia and since the middle Miocene in central Europe, where they surely occur up to the late Piacenzian (Martinetto, 1994; Martinetto et al., 2015). However, the time of disappearance from Europe is somehow uncertain due to the poor dating of the youngest findings: Nordhausen in East Germany and Zuurland in The Netherlands, both sites of probable Gelasian age (Kuijper, 1988; Mai and Walther, 1988). Another fossil-species with a late occurrence in Europe is *P. europaea* (Gelasian of Rippesroda, East Germany). According to the compilation of studies reported by Birks (2019), the genus *Proserpinaca* may have persisted for a long time during Pleistocene in Europe, but the documentation seems to be somehow uncertain.

We are not aware of other records of *Proserpinaca* in the Iberian Peninsula, where the single fruit found at SPT constitutes the first and unique record to date. Differently from other taxa, the south European records do not support a longer persistence of *Proserpinaca* at lower latitude, since the youngest published records are from central Europe. A possible explanation for the extirpation of this genus across Europe might have been the low humidity recorded in southern Europe, which could have had a more determinant effect than the lower temperatures registered in central Europe. The presence of *Proserpinaca* in STP also agrees with the existence of humid warm-temperate climate across the western part of the Iberian Peninsula (Vieira, 2009).

Family: HYPERICACEAE

Genus: **Hypericum**

Species: *Hypericum tertiarum* P. Nikitin.

Plate I, 7–8

Description: See Velichkevich and Zastawniak (2003), Nikitin (2006) and Martinetto et al. (2012); furthermore, Meseguer and Sanmartín (2012) provided a synthetic description of seed characters and an overview of the fossil record of *Hypericum*. Although the distinction from the similar fossil-species *H. pleistocenicum* Wielicz. has never been discussed in detail, we may argue that the ornamentation formed by the transversely elongated external cells may be distinctive: isodiametrical to slightly elongated in *H. pleistocenicum* (Velichkevich and Zastawniak, 2008) versus consistently elongated in *H. tertiarum* (Nikitin, 2006).

Remarks: Velichkevich and Zastawniak (2003) pointed out that three extant species of *Hypericum* produce seeds that most closely resemble those of *H. tertiarum*. The three species belong to the

Table 1

Comprehensive floral list of the SPT plant remains. e/n: exotic/native genus; LEAF-TYPE CATEGORY: DC, deciduous conifer; EC, evergreen conifer; E, broadleaved evergreen; D, broadleaved deciduous; HABITUS: t, tree; s, shrub; h, herb. ECOLOGY: m, mesic; hy, hygrophilous; a, aquatic.

Taxon	Author	Family	e / n	LEAF-TYPE	Habitus	Ecology	Part (type of remain)	Abundance S1	Abundance S2
<i>Alisma</i> sp.		ALISMATACEAE	n	/	h	hy	Seed		1
<i>Alnus</i> sp.		BETULACEAE	n	D	s/t	hy	Various	6	1
Apiaceae indet.		APIACEAE	/	/	h	/	Fruit	1	2
<i>Azolla</i> cf. <i>aspera</i>	P.I. Dorofeev	AZOLLACEAE	e	/	h	a	Megaspores	20	8
<i>Cladium</i> sp.		CYPERACEAE	n	/	h	hy	Endocarp	1	
Ericaceae cf. <i>Erica</i>	L.	ERICACEAE	n	E	h/s	m	Seed	1	
<i>Eurya stigmosa</i>	(Ludwig) D.H. Mai	PENTAPHYLACEAE	e	E	s	m	Seed	7	3
<i>Hypericum tertiarum</i>	P. Nikitin	GUTTIFERAE	n	E/D	h/s	m	Seed	12	8
<i>Itea europaea</i>	Mai	ITEACEAE	e	E/D	s	m/hy	Seed		3
<i>Juncus</i> sp.		JUNCEAE	n	/	h	m/hy	Seed	1	3
<i>Oenanthe</i> cf. <i>lachenalii</i>	C.C. Gmel.	APIACEAE	n	/	h	hy	Fruit	1	
<i>Proserpinaca reticulata</i>	C. Reid et E.M. Reid	HALORAGACEAE	e	/	h	a	Fruit	1	
<i>Salvinia</i> sp.		SALVINIACEAE	n	/	h	a	Megaspores	34	11
cf. <i>Saxifraga</i>		cf. SAXIFRAGACEAE	n	/	h	?	Seed		1
<i>Scirpus</i> sp.		CYPERACEAE	n	/	h	hy	Fruit		2
<i>Symplocos casparyi</i>	R. Ludw.	SYMPLOCACEAE	e	E	t/s	m	Endocarp	1	
<i>Symplocos germanica</i>	Mai	SYMPLOCACEAE	e	E	t/s	m	Endocarp		3
<i>Taxodium dubium</i>	(C. Presl) A. Braun	CUPRESSACEAE	e	DC	hy	hy	Shoots, leaves	> 100	> 100
<i>Taxodium dubium</i>	(C. Presl) A. Braun	CUPRESSACEAE	e	DC	t	hy	Seeds	7	6
<i>Taxodium dubium</i>	(C. Presl) A. Braun	CUPRESSACEAE	e	DC	t	hy	Scales	3	2
<i>Tetraclinis salicinioides</i>	(Unger) Z. Kvaček	CUPRESSACEAE	n	EC	s	m	Shoot portions	8	5
<i>Typha</i> sp.		TYPHACEAE	n	/	h	hy	Fruit		1

well-supported *Triadenum* clade (Nürk et al., 2015, 2018), that was considered as a separate genus by some authors. It occurs today only in North America and East Asia, but the fossil record demonstrates a common occurrence across Europe, particularly during Neogene. The divergence from the other clades of *Hypericum* is estimated to have occurred in the Oligocene (about 30 Ma) on the basis of molecular evidence. Other aspects of the phylogeny of *Hypericum*, with a good synthesis on the fossil records, have been reported by Meseguer et al. (2013).

Distribution: The seeds identified in SPT allow extending to the Iberian Peninsula the geographic range of *H. tertiarum* and demonstrate a persistence, at least until the Piacenzian, in this area. This species is commonly recorded in several Neogene sites of Europe and Siberia (Nikitin, 2006), and was certainly still present in Europe during Gelasian, as testified at first by fossil specimens from a sample of the classical carpollological deposit of the Egypt Pit of Tegelen in The Netherlands (Mai and Walther, 1988), stored at the Museum für Naturkunde of Berlin (coll. Mai 6911). Other Gelasian records were reported by Martinetto et al. (2012, 2015) from Italy. The assessment of the last occurrence of *H. tertiarum* implies an attention in distinguishing the similar fossil-species *H. pleistocenicum*, occurring in the Middle Pleistocene of eastern Europe.

Family: ITEACEAE

Genus: *Itea*

Species: *Itea europaea* Mai.

Plate I, 5-6

Description: The holotype of *I. europaea* was described by Mai (1985, pl. 6, 1) from lower Miocene sediments of the Berzdorf open-pit mine in Saxony, Germany (Mai, 2000). The species is characterized by ovoid to oblong, seeds, about 1.3 to 2 mm long and 0.8 to 1.2 mm wide, with a glossy testa covered by small polygonal cells with raised anticlinal walls. These seeds are somehow similar to those of Brassicaceae, but do not show a U-shaped embryo, and differ for the raised instead of sunken anticlinal walls on the seed surface. The three seeds recovered from SPT correspond in all details with the Italian material from Dunarobba (Pliocene or less probably Early Pleistocene), which had been directly compared with seeds of *Itea europaea* from the type locality Berzdorf at the Museum für Naturkunde of Berlin.

Remarks: Presently, *Itea* is a genus native to eastern Asia, and with one deciduous species from eastern North America. A single fossil-species, *I. europaea*, has been so far reported from Europe. The relevance

of fossil seeds for the historical biogeography and phylogeography of *Itea* has been recently pointed out in the monograph by Hermsen (2013).

Distribution: This species has been reported from several early Miocene to late Pliocene (Piacenzian) European carpofloras of the following areas: Belarus, Bulgaria, Germany, Italy (see Appendix 1), Poland, and western Russia (Hermsen, 2013). Even if it was already known that *I. europaea* persisted in southern Europe towards the end of the Piacenzian (Martinetto, 1999; Hermsen, 2013), the seeds recorded at SPT demonstrate that such persistence extends also to the Iberian Peninsula, and at the meantime allows to assess that the species was distributed across the whole Europe during Neogene. Occurrences of *Itea* from Italian (Appendix 1) and German sites demonstrate that this taxon was still present in Europe during Piacenzian and the youngest published records in South Europe occur close to the Piacenzian-Gelasian boundary (Bertini, 2010; Martinetto et al., 2007; Bertini and Martinetto, 2011).

Family: PENTAPHYLACEAE

Genus: *Eurya*

Species: *Eurya stigmosa* (R.Ludw.) Mai

Plate I, 4

Description: see Zhu et al. (2016) and Góis-Marques et al. (2019).

Remarks: The genus *Eurya* Thunb. comprises 130 extant species mainly distributed through tropical to subtropical Asia, South and Central America and in the western and southern Pacific Islands (Min and Bartholomew, 2007). They are a group of evergreen shrubs and mainly small trees, commonly found as dominant understory elements in tropical to subtropical broad-leaved evergreen forests (Min and Bartholomew, 2007).

Distribution: The *Eurya* fossil record is dominated mainly by seeds and ranges from the Cretaceous (Knobloch and Mai, 1986) to the Early Pleistocene (Martinetto et al., 2015). Occurrences of the genus have been reported in Europe (Austria, Bulgaria, Czech Republic, Denmark, Germany, England, Italy and Poland), Russia, Japan and China (Zhu et al., 2016). The Italian fossil record allows us to follow the decline of *E. stigmosa* in the late Cenozoic: its remains are common in the Zanclean, and became rare in the Piacenzian, being identified in six localities, one of which is dated to the upper part of this stage (Irace et al., 2017). A problematic record of a single seed has been reported from a long marine section (Arda) in Italy to be of Pleistocene age (Gelasian or Calabrian?), but according to Martinetto et al. (2015) there is no

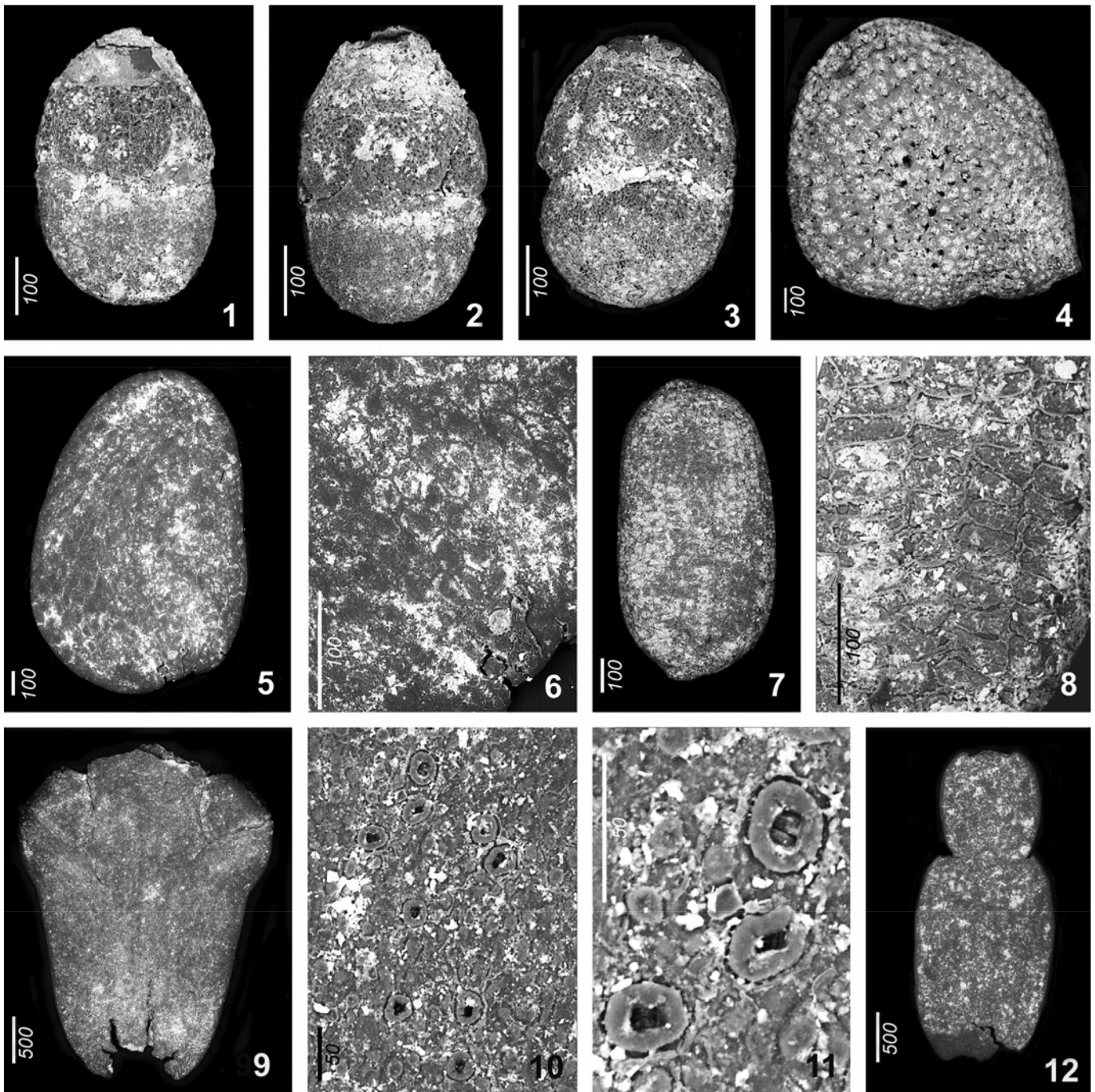


Plate I. Examples of plant macrofossils from SPT, Piacenzian. SEM photos. The measures given next to the scale bars are micrometers. (1–3) *Azolla cf. aspera* P.I.Dorof.: megaspores showing variation in shape (CCN8401, CCN8402, CCN8403). (4) *Eurya stigmosa* (R.Ludw.) Mai: seed, CCN8404; (5, 6) *Itea europaea* Mai: seed and detail of the surface showing subhexagonal cells with thin and raised anticlinal walls, CCN8405; (7, 8) *Hypericum tertiarum* P.Nikitin: seed and detail of the surface showing transversally elongated cells, CCN8406; (9–11) *Tetraclinis salicornioides* (Unger) Kvaček: broad shoot segment (CCN8407) and detail of the external side of the cuticle with stomata. (12) *Tetraclinis salicornioides* (Unger) Kvaček: shoot fragment comprised of the two terminal segments (CCN8408).

possibility to exclude the reworking of this seed into the marine sediments. Pandolfi et al. (2017) also reported, from a Gelasian deposit of central Italy, a seed similar to *E. stigmosa*, but not so well preserved to show diagnostic characters, and therefore treated as cf. *Eurya*. We have to conclude that, although abundant, the fossil record from Italy does not provide definitive evidence for the persistence of *E. stigmosa* in the Pleistocene.

The last record of *E. stigmosa* in continental Europe is represented by a seed from the Calabrian of Georgia, although not accurately

documented (Chochieva, 1975; see comments in Martinetto et al., 2017). Recently, Góis-Marques et al. (2019) reported a solid fossil record of *E. stigmosa* from the Calabrian of Madeira and suggested that this record would represent a population in refugium. Our new record from SPT testifies that the distribution of the species in the Piacenzian reached a point not too far from Madeira.

Family: SYMPLOCACEAE

Genus: **Symplocos**

Species: *Symplocos germanica* Mai and *Symplocos casparyi* R.Ludw.

Description: See Mai and Martinetto (2006). The strongly compressed specimens of SPT are considered diagnostic for the identification of both *S. germanica* and *S. casparyi* because of the combination of outline, dimensions, diagnostic ornamentation and strong lignification.

Remarks: *Symplocos* is the main genus of family Symplocaceae (Thorne, 2000; Fritsch et al., 2008) and nowadays comprises approximately 300 species of woody flowering plants (trees and shrubs) distributed through Southeast Asia to north-eastern Australia, as well as in the Americas, where they are mostly restricted to the Neotropics (Fritsch et al., 2008). It is found primarily in humid tropical montane forests and humid subtropical (= warm temperate) forests. The earliest known record of *Symplocos* is from Late Cretaceous fossil pollen from the western United States (Fritsch et al., 2008). During the Tertiary, this genus was common and widely distributed in Europe (Mai and Martinetto, 2006; Manchester and Fritsch, 2014; Tiffney et al., 2018). In southern Europe, pollen of *Symplocos* has been reported in several localities (e.g., Bertini, 2002; Bertoldi et al., 1994; Vieira, 2009; Vieira et al., 2018; Vieira and Zetter, 2020) and Vieira et al. (2011) described two pollen types of *Symplocos* also from SPT. Pollen records are generally not assigned to precise fossil-species, whereas carpological records are, and also allow a better assessment of the modern botanical affinities of the fossil forms (Fritsch et al., 2015; Tiffney et al., 2018). Two clearly distinct fossil-species occur at SPT, one is *S. casparyi*, whose fruit morphology and anatomy (Mai and Martinetto, 2006) correspond to several extant species of subgenus *Symplocos*, sect. *Lodhra*, the best match being with species of the East and Southeast Asian *Symplocos nakaharae* complex (Liu and Qin, 2013). The second fossil-species is *S. germanica*, that represents an extinct European plant whose fruits show possible affinities (Mai and Martinetto, 2006) to both subgenus *Symplocos*, sect. *Lodhra* (Asia) and subgenus *Symplocos*, sect. *Symplocos*, ser. *Urbaniocharis* (central America) (Fritsch et al., 2008).

Distribution: The fossil record of *S. casparyi* is abundant in the Neogene of Europe, and it was already known to persist in central Italy until the Gelasian (Martinetto et al., 2017). Conversely, the youngest record of *S. germanica* was so-far from the late Miocene of Germany (Mai and Martinetto, 2006; Fritsch et al., 2008) and it was never reported from southern Europe, including Italy, even at the light of the most recent advances in research. We can suppose that this fossil-species did not manage to cross the Alps but was able to follow the Atlantic coast and reach Portugal during Neogene. The record of SPT also testifies that *S. germanica* persisted longer here than in central Europe, at least until the Piacenzian.

5. Discussion

5.1. Novel contributions of the carpological record from SPT in comparison with other plant records

The knowledge of the floristic assemblage recorded in SPT was enhanced with this study. From the 19 different taxa recorded in the carpological record, only 6 (*Alnus*, *Taxodium*, Ericaceae, *Symplocos*, *Typha* and Apiaceae) have been identified in the palynological study by Vieira et al. (2011). Plant species like *Eurya stigmosa*, *Hypericum tertiaerum*, *Itea europaea* and *Proserpinaca reticulata* cannot be mentioned in any pollen assemblage because the identification of these fossil-species relies on carpological characters. Nevertheless, not a single fossil pollen grain from SPT can be associated with the same ancient plants that produced these carpological remains. These plants being entomophilous, probably had a too scarce pollen production to leave any fossil palynological record. A different reason can be envisaged for the lack of pollen of *Tetraclinis salicornioides*, and this is the scarcely diagnostic morphology of cupressaceous pollen, which is present in the SPT deposit. Taphonomy can explain why the sediment collected contained abundant leaves of *Taxodium* and *Liquidambar* but the abundance of pollen only concerned *Liquidambar* (missing in the carpological record); the *Taxodium*-type pollen wasn't very frequent. The absence of

fruits and seeds of particular extirpated genera (*Cercidiphyllum*, *Craigia*, *Mortoniendron*, etc.), whose pollen was recorded in small quantity in the Pliocene of Portugal, can be easily explained by the combination of the fine grain (short transport of plant remains) and small quantity of sediment analyzed at SPT. Only an extensive sampling with focus on sandy sediments (long-transported remains) would have allowed the detection of rare, far-growing and/or large-fruited (e.g., *Diplopanax*, *Liquidambar*) plant taxa (Vassio and Martinetto, 2012).

5.2. Paleobiogeographic and biochronologic relevance of sites with both pollen and carpological records

Indeed, fossil fruits and seeds associated with pollen studies help to get a wider understanding of the whole floral content, and recognizing taxa to a species level helps to understand the paleobiogeography in higher detail. Vieira et al. (2011) recorded common pollen from the genus *Symplocos* at SPT, although only with the carpological data was possible to determine the occurrence of two species *Symplocos germanica* and *Symplocos casparyi*, thus permitting to investigate the paleobiogeography and biochronology at the species level, instead of the less-accurate genus level. Wherever it has been possible, like at SPT, to combine rich pollen and carpological records (e.g., Bertini and Martinetto, 2011), the floristic composition and diversity of ancient vegetation has been more accurately estimated. These combined records also allowed to better understand the extent in time of the distribution of several plant taxa, and to point out the pattern of Plio-Pleistocene plant extirpations and extinctions. In southern Europe most of the information came so-far from the rich Italian fossil records (Bertini and Martinetto, 2011; Martinetto et al., 2014; Magri et al., 2017; Martinetto et al., 2018). As a whole, the combined carpo-palynological plant record testified that in the late Piacenzian-Chibanian interval at least 70 plant species disappeared from Italy, but the timing of such numerous disappearance events is not yet well-assessed. In fact, by comparing the results of Bertoldi et al. (1994), Martinetto (1999, 2001), Martinetto et al. (2007), Bertini (2010) and Martinetto et al. (2014, 2018) it is apparent that the rapidly increasing fossil evidence provided by the Italian carpological and pollen records determined a progressive delay of the last occurrence data of several taxa (e.g., *Liriodendron*, *Magnolia*, *Sinomenium*, *Symplocos*, *Toddalia*), and there is still space for further updates based on new fossil evidence.

In this paper we point out that the diagnostic macroremains from a poorly studied area (Portugal) can provide new contributions to the biogeography and biochronology of several Neogene plant fossil-species. The record of SPT represents both the westernmost and the most recent occurrence in Europe (Fig. 3) of *Symplocos germanica* and *Tetraclinis salicornioides* (the record of the almost contemporary Duna-robbia site in central Italy has an uncertain age, probably Piacenzian or Gelasian; Martinetto et al., 2014). Four additional fossil-species, *Hypericum tertiaerum*, *Itea europaea*, *Proserpinaca reticulata* and *Symplocos casparyi*, have at SPT their westernmost occurrence. Conversely, from the chronological point of view they occur elsewhere in deposits which are either contemporary or younger than those of SPT (Fig. 3). By analyzing the CENOFITA database (Martinetto and Vassio, 2010; Martinetto et al., 2018), based upon the above-mentioned Italian carpological records, the concomitant occurrence of the seven fossil-species (Table 1) shared by SPT and the Italian floras (apart *S. germanica*, lacking in Italy) was only detected in the Piacenzian time interval. Such biochronological indication agrees with the foregoing age interpretation based on the correlation of the pollen assemblage with the Rio Maior ones.

5.3. Significance of SPT flora for the knowledge of the Pliocene vegetation of the Iberian Peninsula and Europe

The current understanding shows that the SPT deposit may represent a small marshy pond connected to a main river channel. From the

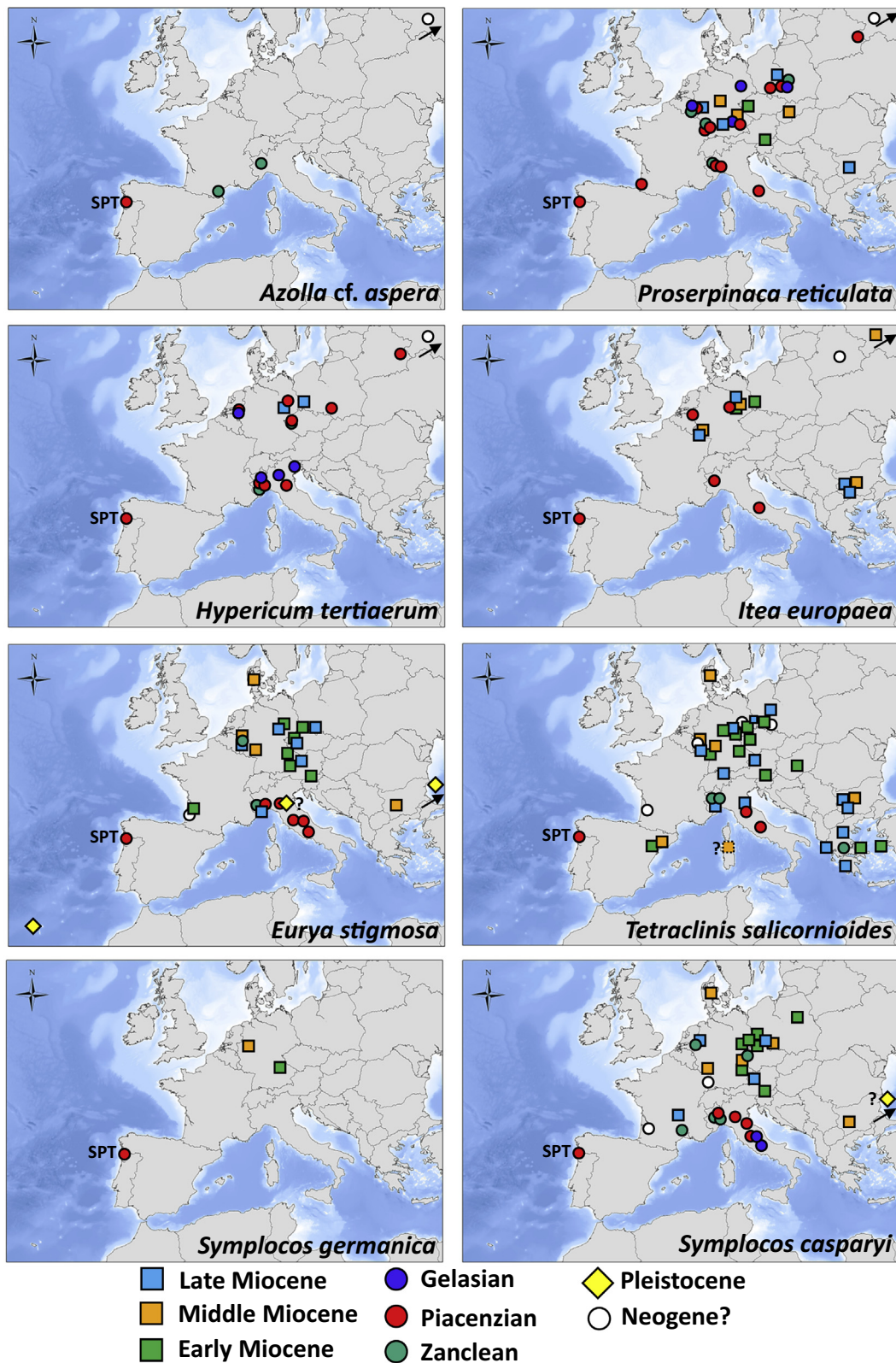


Fig. 3. Maps of the European post-Oligocene distribution of selected fossil-species occurring at SPT. The localities have been plotted on the maps by evaluating occurrence data reported by: Reid and Reid, 1915; Mai and Walther, 1988; Biondi and Filigheddu, 1990; Günther and Gregor, 1997; Meller, 1998; Kovar-Eder and Wojcicki, 2001; Velichkevich and Zastawniak, 2003; Meller and Hofmann, 2004; Mai and Martinetto, 2006; Meller, 2007; Barrón et al., 2010; CENOFITA database described by Martinetto and Vassio, 2010; Velitzelos et al., 2014.

total pollen content, a broadleaved evergreen/warm mixed forest, with similarities to modern ones living today in eastern China or in Florida, was inferred, suggesting relatively stable climatic conditions under a humid warm-temperate climate and comparable with the most complete Pliocene record from Rio Maior (Lower Tagus Basin, Portugal) (Vieira et al., 2018). The most relevant taxa yielded in the carpological record in general agree with the paleoenvironment previously described for SPT. Particularly *Symplocos*, *Eurya* and *Tetraclinis* have been described as part of a broadleaved evergreen/warm mixed forest. This same type of vegetation seemingly had a regional extension, since it was reconstructed based on comparable records from the Atlantic coast (Rio Maior, Anadia and Barracão: Vieira, 2009). However, it is worth examining the possible significance of SPT flora in the frame of the Pliocene vegetation of the Iberian Peninsula and Europe.

Current PRISM4 vegetation reconstructions for the Piacenzian show the presence of warm-temperate mixed forest on the Atlantic margin of western Europe and temperate xerophytic shrubland on the Mediterranean coast of the Iberian Peninsula (Dowsett et al., 2016). Some studies of the Piacenzian from Catalonia reveal the existence of a diverse vegetation depending on soil conditions, altitude and proximity to the coast. In general, the record shows a progressive extinction of thermophilous taxa and an increase in Mediterranean elements. Salzmann et al. (2013) proposed that during cooler and drier intervals of the Piacenzian xerophytic shrubland might have been present on the Atlantic coast of the Iberian Peninsula. This cold-dry scenario is not supported by the new results from Rio Maior (Vieira et al., 2018). Instead, the Atlantic coast of Iberia appears to have maintained a warm and humid climate throughout the Piacenzian. The flora recovered from SPT helps to support the view that the Atlantic margin of Iberia kept favorable conditions to support some specific plant communities for longer time than other localities at the same latitude, even if a more complete assessment of the floral composition of such communities would need further research. In fact, the limited pollen evidence available for the Early-Middle Pleistocene of Portugal does not shade enough light on the destiny of several taxa needing a wet and warm temperate climate that were still growing in Portugal around 3 Ma, but later were extirpated. Obviously, they must have lost over time the suitable conditions fitting their ecological requirements and future studies should investigate the possible causes: did the climate become everywhere too dry in Portugal? or too cold? or a combination of both factors?

5.4. Future potentiality of carpological studies in the Iberian Peninsula and other poorly studied areas

The new carpological record from SPT (Portugal) shows the potentiality of the local Pliocene successions as a repository of paleofloral data that cannot be provided by pollen and leaf assemblages. One of the main bias explaining the present scarcity of carpological information is the lack of people with an adequate training or “search image” (see Tiffney, 1990), which is fundamental in locating, sampling and recovering abundant fruit and seed assemblages in occasional exposures such as the one presented here. These fossil assemblages are rare in the less humid climates of southern Europe, but the initial results obtained in this work, combined with the more conspicuous records provided by more than 30 years of research in Italy (Martinetto, 1999, 2001, 2015; Martinetto et al., 2014, 2015, 2017, 2018), testify for their importance in paleoclimatic and biogeographic reconstructions. Extensive sampling of similarly limited fossil-bearing deposits, such as those of continental small-vertebrate assemblages of the Neogene (Alba et al., 2001), provided an exceptionally rich fossil record of well-known relevance. Only the scarce sampling effort can explain the present poor evidence of carpological assemblages in the existing Iberian literature (Barrón et al., 2010). However, the temporary exposures of fruit and seed-bearing deposits should be considered as precious as the small-vertebrate assemblages for the wealth of information they can

provide before disappearing. The carpological fossil sites are as rare, vulnerable and ephemeral as the vertebrate assemblages, and the efforts of the few scientists active in their study are often not enough to search, gather and preserve all the potentially useful information. Although limited, the results of the present contribution are intended to stimulate the “search image” for fruit and seed assemblages in the Iberian Peninsula as well as in similar poorly studied areas.

Declaration of Competing Interest

None. No conflict of interest in this manuscript from any of the authors.

Declaration of Competing Interest

None.

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Appendix A. Appendix 1_ Revised records of *Itea europaea* in Italy

We deem it useful to point out some additions and corrections to the summary of the Italian occurrences of *Itea europaea* reported by Hermsen (2013).

1. *Itea europaea*, most probably Pliocene (mapped as Piacenzian in Fig. 3), otherwise Gelasian, Dunarobba (Umbria, Italy). Martinetto (2001). The material consists in a scarcely preserved fruit and 13 well-preserved seeds (only 5 specimens reported in the tables of Martinetto et al., 2014); the morphology of these remains is much diagnostic to assign them to *Itea europaea*.

2. *Itea europaea*, Pliocene (Piacenzian), Front Canavese (Piedmont, Italy). Martinetto (1999), Martinetto et al. (2007). Only two seeds with diagnostic characters are known.

3. *Itea europaea*, Pliocene (probably Piacenzian), Pranzalito (Piedmont, Italy). Martinetto (2001). Only one diagnostic seed is known.

4. *Itea europaea*, Pliocene (Piacenzian), Stura di Lanzo (Piedmont, Italy). Martinetto (1999), Martinetto et al. (2007). Only one diagnostic seed is known.

Deleted occurrences:

5. *Itea europaea*, Pliocene, Boschi di Barbania (Piedmont, Italy). Martinetto (2001). The material consists in two badly preserved fruits, whose morphology is not completely diagnostic to assess that these are capsules of *Itea europaea*, therefore it is better to treat them as “cf. *Itea*,” and the record is not reported in Fig. 3.

6. *Itea europaea*, Pliocene, Villafranca d'Asti (Piedmont, Italy). Hermsen (2013) correctly pointed out that “The evidence for this occurrence is ambiguous. Martinetto (1999) states in the text that this taxon is present in this flora [by real mistake, at page 507], but does not indicate that it is present in the accompanying table. Martinetto (2001) also seems to imply that the taxon may be present here.” Actually, a sentence reported in Martinetto (2001) should have been corrected as follows: “In northwestern Italy, this species occurs, always with a few seeds and/or fruits, in two sites of Early or Middle Pliocene age (Boschi and Pranzalito) and two [not three] ones of probable Middle [presently late = Piacenzian] Pliocene age (Martinetto, 1999)” [we add here that these sites were Front and Stura di Lanzo]. Therefore, *Itea europaea* was neither reported for the Pliocene of Villafranca d'Asti (RDB Quarry) in the 20th century nor it occurred there until the year 2020.

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