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THE LATE EARLY PLEISTOCENE FLORA OF ORIOLO, FAENZA (ITALY): ASSEMBLY OF THE MODERN FOREST BIOME

This study is a tribute to the life and work of Zlatko Kvaček (1937 – 2020).

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Abstract: The late Early Pleistocene was the last time of equable climate in northern Central Italy, reflected in its large mammal fauna and numerous palynological records. Reliably dated leaf fossils from this time are rare, but provide crucial information on local and regional vegetation, biogeographic relationships, and species turnover coinciding with the assembly of modern forest biomes. Here we investigated a rich assemblage of leaf and fruit impressions (63 fossil-taxa) from the Oriolo quarry, Faenza (Ravenna), dated to the latest Calabrian, preserved in transgressive coastal deposits. The fossil assemblage represents riparian vegetation and xeric alluvial habitats in the lowlands and forest vegetation above the alluvial plain. Forest-building trees were deciduous, but comprised several taxa characteristic of open scrubland or forest edges. The composition of the flora reflects a dynamic process of assembling modern forest biomes in western Eurasia. While most taxa correspond to modern submediterranean and temperate woody species, some others represent late occurrences of taxa today confined to refugia outside Italy (*Parrotia*, *Gleditsia*, *Pterocarya*), and a few are Miocene/Pliocene relics indicating final floristic links with East Asia (Japan) and/or North America (*Tsuga* cf. *chiarugii*, *Carya* cf. *minor*) and Pleistocene endemism in Italy (*Berberis auriolensis*, *Acer aemilianum*).

Key words: Angiosperms, leaves, fruits, Early to Middle Pleistocene, Italy, Integrated Plant Record (IPR) vegetation analysis, statistical tool Drudge 1, Pleistocene relict taxa

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Introduction

The Mediterranean and submediterranean region experienced a shift from humid warm temperate climate, according to the Köppen-Geiger climate classification, to the modern summer-dry climate during the Pliocene and Early Pleistocene, which resulted in the disappearance of humid warm temperate forest in coastal lowlands (Suc 1984, Combourieu-Nebout et al. 2015). From ca. 2.6 Ma onwards, the Mediterranean region experienced greater dryness in glacial periods (Suc 1984, Leroy et al. 2011). During the most severe parts of the glacial periods, European temperate trees became restricted to local refugia in mountains and moist valley-bottoms in southern Europe (Willis 1996). The loss of temperate trees and shrubs from the Pliocene (Zanclean and Piacenzian) and Pleistocene floras of Europe and the dynamic change from glacial to interglacial phases has been the subject of numerous studies (e.g., Martinetto 2001, Bertini 2010, 2013, Leroy et al. 2011, Martinetto et al. 2012, 2014, 2015, Pini et al. 2014a, Combourieu-Nebout et al. 2015, Pross et al. 2015, Magri et al. 2017, Denk et al. 2021, Donders et al. 2021). One explanation for the successive disappearance of warmth-loving temperate woody taxa from the European flora suggested that extirpation from the European flora was determined by climate requirements still seen in the congeners of these extirpated taxa in the modern floras of East Asia and/or North America (niche conservatism; Svenning 2003). Comparative studies of palynological records through the Pleistocene showed that persistence and disappearance of taxa across Europe did not follow a North to South and West to East trend but were highly complex (Magri et al. 2017). Specifically, these authors suggested that the seemingly stochastic distribution of Pleistocene and Recent relict areas across the Mediterranean region might be related to genetic gradients in widespread Pleistocene populations such as *Taxodium*. All these studies were mainly concerned with patterns of extinction/extirpation, and less so

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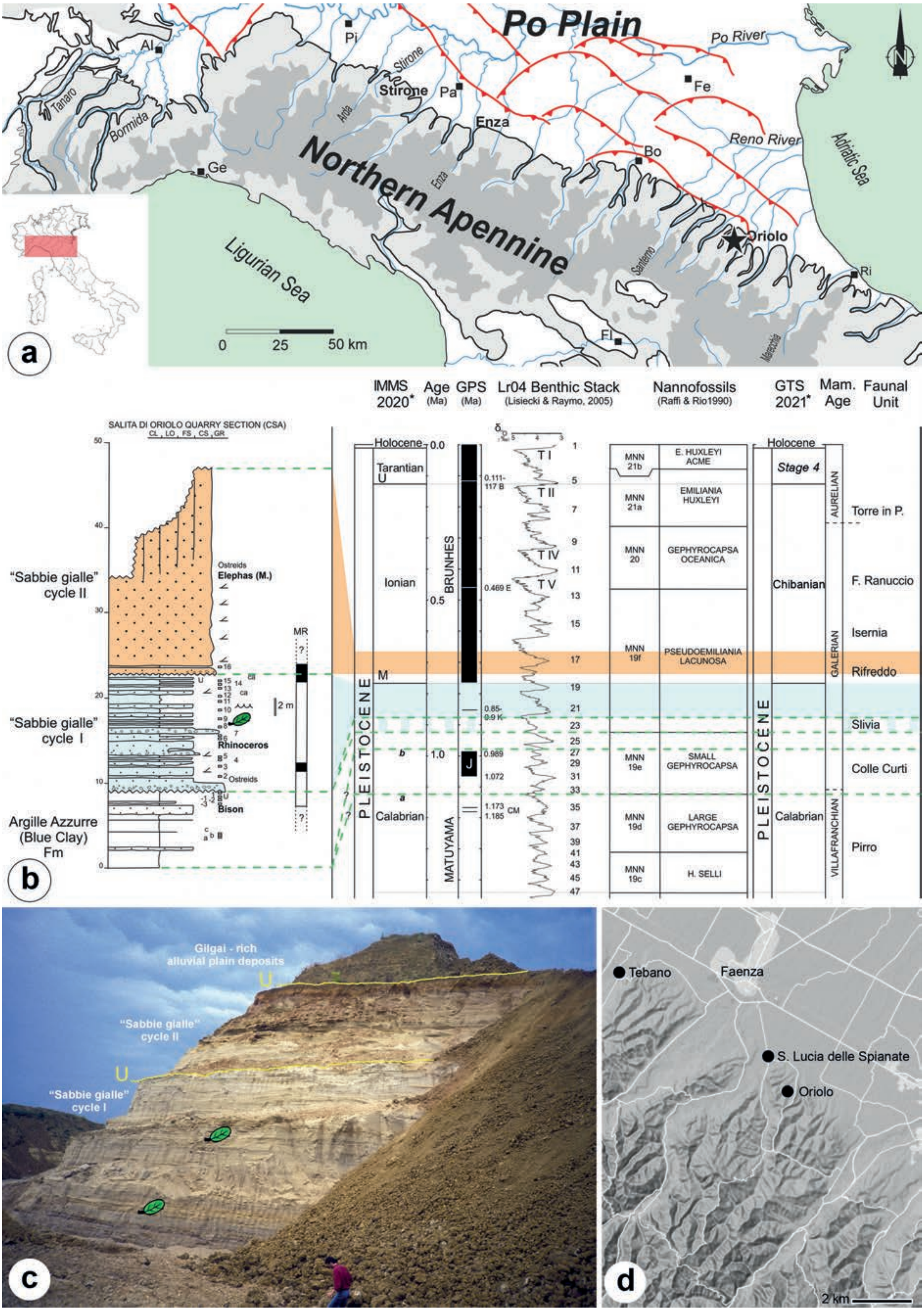


Text-fig. 1. a: Po Plain and foothills of the Northern Apennine in Northern Italy (inset) with the location of Oriolo (black star) and other Early and Middle Pleistocene plant localities, Enza and Stirone. Red lines indicate the frontal thrust arcs (modified from Martinetto et al. 2015). b: The "La Salita" section, Oriolo and chronology of the two "Sabbie gialle" cycles based on large mammals and palaeomagnetic correlation (modified from Toniato et al. 2017; IMMS 2020* [Italian Mediterranean Marine Stages] updated from Cohen and Gibbars 2020; GTS 2021* [Global Time Scale] updated from Head et al. 2021). c: Quarry "La Salita", Oriolo, in 1987. Main unconformities (U) separating the two "Sabbie gialle" cycles and terrestrial deposits on top are shown. Leaf symbols indicate the positions of some of the layers rich in fossil leaves (photo by G. B. Vai, modified). d: Surroundings of Faenza with the location of Oriolo and adjacent coeval sites yielding plant macrofossils.

with the assembly of modern forest ecosystems in western Europe.

Pollen-based comparative studies use genus-level similarities and can establish last occurrence dates with high precision, as the dispersed pollen record is much more complete than the leaf record. In contrast, leaves offer morphological information that allows comparisons with fossil-species and extant taxa at species level. For example, the morphological variability of Pliocene records of *Fagus* pollen does not differ from Pleistocene and recent ones, whereas leaves of *Fagus* allow pinpointing the appearance of the modern *Fagus sylvatica* s. str. L., 1753, in Europe. In the present study, we used macrofossils (leaves and fruit impressions) to establish species-level patterns of survival (Pleistocene relict distributions) and emergence of modern species. We investigated a rich leaf (and fruit) assemblage from well-dated latest Calabrian deposits (Toniato et al. 2017) in Northern Italy (Oriolo, Ravenna). Further, we assessed genus-level similarity of the late Calabrian Oriolo flora with extant Northern Hemisphere floras (using the *Drudge* application; Teodoridis et al. 2020) in order to document persisting floristic links with Northern Hemisphere floras outside Europe during the latest Calabrian. Finally, we compared the biogeographic histories of Pleistocene relict taxa in the Oriolo flora and discussed the assembly of modern forest biota in Europe.

Geological and palaeontological background

During the late 1980s and early 1990s, a quarry near the village of Oriolo (Faenza municipality, Ravenna province; Text-fig. 1a, d) was opened to exploit the Pleistocene sandy deposits for building materials. The Pleistocene strata yielded remains of large continental vertebrates, including *Mammuthus meridionalis* cf. *vestinus* (Azzaroli, 1972), *Bison* (*Eobison*) sp., *Stephanorhinus hundsheimensis* (Toula, 1902), *Hippopotamus* cf. *antiquus* Desmarest, 1822, and *Pseudodama* sp. This faunal assemblage, despite coming from slightly different levels, was tentatively assigned to the late Villafranchian (Early Pleistocene) or the early Galerian (early Middle Pleistocene; Marabini et al. 1987a, Masini et al. 1995, Ferretti 1999). Reinvestigation of the mammal remains established different ages for the skulls of *Bison* (*Eobison*) sp., MIS 31 (close to the base of Jaramillo subchron, ca. 1–1.1 Ma), *Stephanorhinus*, MIS 21, ca. 0.87–0.85 Ma, and *Mammuthus meridionalis* (Nesti, 1825), part of MIS 17 and 18, ca. 0.74–0.66 Ma (Toniato et al. 2017). In addition, from the Oriolo quarry, about 300 fossil leaves were recovered and prepared by one of the authors (MS) and deposited at the Civic Museum of Natural Sciences of Faenza. This fossil plant assemblage was initially studied by Martinetto and Sami (2001), and is the subject of the present investigation.

Geology, stratigraphy and age constraints of the Oriolo section

The section of the Oriolo quarry consists of several predominantly sandy layers belonging to the so-called “Sabbie gialle di Imola Auctt.” (Yellow Sands) (Amorosi et al. 1998, Marabini et al. 1987a, 1987b, Vai 1988; Text-fig. 1b, c), which represent the most recent transgressive marine episode along the Po Plain-Apennine margin between the end of the Early and the beginning of the Middle Pleistocene. In the territory of Faenza, these coastal deposits are mainly made up of medium and medium-fine yellowish sands (due to the presence of iron oxides), with parallel and crossed-concave stratification; they are not more than 40–50 m thick. In the quarry “La Salita” of Oriolo, the Sabbie gialle, exposed to a thickness of about 20 m, are characterized by an overall sub-horizontal stratification, dipping on average 7° towards the plain, with a direction of about 120° N. The sedimentary environment was a coastal setting with lagoon deposits and subordinate alluvial plains. The outcrop La Salita is composed of two dominantly sandy marine cycles bounded by unconformity surfaces. The two cycles unconformably overlay regressive sandy pelites and mud at the top of the more tectonically deformed Argille Azzurre (“Blue Clay”) Formation, and are overlain by Middle Pleistocene terrestrial deposits – mainly pelitic, and partly pedogenic (Toniato et al. 2017).

The lower (I) cycle contains some lenticular gravel lags and many thin, muddy beds intercalated between the sands, suggesting alternation of littoral and lagoonal/bay environment with significant fluvial activity. Fluvial activity is also indicated by some layers rich in well-preserved and diverse floated-leaf assemblages (Martinetto and Sami 2001), and by mammal bone fragments. The upper (II) cycle is more monotonously dominated by medium to coarse well-sorted littoral sand, suggesting a more stable and wider foreshore environment and a drier climate: also this sand body yielded various fossil remains of mammals, including a *Mammuthus* skull.

The “Sabbie gialle” cycle I for the most part is magnetically reversed, while cycle II is magnetically normal. Cycle I is best correlated with the upper part of the Matuyama reversed chron, and most probably corresponds to the time following the Jaramillo subchron, while the normal polarity interval at the top of the latter cycle probably represents the beginning of the Brunhes Chron (Marabini et al. 1996, Torre et al. 1996).

The sand body with layers containing fossil leaves shows reversed magnetism (Marabini et al. 1996, Muttoni et al. 2011), and hence the Oriolo plant assemblage can be correlated with the final Early Pleistocene, above the Jaramillo subchron (1.07–0.99 Ma), with a dating certainly between MIS 25 and MIS 19, but more probably MIS 21 (0.86–0.81 Ma). In contrast, in the “Sabbie gialle” cycle II the beginning of the Brunhes Chron dated to 0.781 Ma suggests an early Middle Pleistocene age for the deposits containing the *Mammuthus meridionalis* skull (Vai 1995, Amorosi et al. 1998, Toniato et al. 2017). Presently, only a small portion of cycle I is exposed from the original outcrop.

Two other outcrops of “Sabbie gialle” near Faenza, Tebano (Falcona quarry) and Santa Lucia delle Spianate (Text-fig. 1d) yielded less diverse but taxonomically similar leaf assemblages.

Taphonomy

The fossil leaves do not come from a single fossiliferous horizon, but from several levels of variably silty and sometimes sandy (fine sands) massive pelites of a yellowish colour, with a lentiform geometry and a maximum thickness of a few decimetres. They are interspersed within sandy layers with frequent crossed lamination and wave-ripples belonging to the 1st cycle of the Sabbie gialle (Martinetto and Sami 2001, Toniato et al. 2017). Although several blocks of sedimentary rock bear up to eight co-occurring taxa, it is difficult to determine whether the whole leaf assemblage from Oriolo represents a single warm stage or different portions of a glacial/interglacial cycle (discussed below). In view of the high sedimentation rate characterising similar depositional environments (coastline close to a river mouth), the various pelitic layers with plant remains most likely were deposited during a relatively short time. Therefore, the fossil plant assemblage from Oriolo likely represents a chronologically homogeneous flora. Plant macrofossils are preserved as ochre-coloured imprints due to the presence of iron oxides and hydroxides. Stereomicroscope investigations showed that iron minerals commonly encrusted the mesophyll of the leaf laminas.

In some cases, mostly intact leaves are concentrated on horizontal surfaces. These surfaces do not show any change in grain size and the leaves do not generally assume a plane-parallel, but rather a wavy arrangement, so that they often overlap each other, or are even preserved as folded impressions; this exceptional type of preservation has previously been reported by Sordelli (1896: 98) for another "yellow sands" site (Longone). This kind of preservation along with the accumulation of leaf fossils suggest a "mass" transportation followed by sudden sedimentation of leaf material, possibly related to episodes of flooding.

A few cones of *Tsuga* are preserved as three-dimensional external imprints in marly-calcareous concretions. They might have developed in pelitic sediments quite distinct from those containing most of the leaf remains, and hence it is uncertain whether these specimens are contemporary to the angiosperm leaves (Martinetto and Sami 2001).

Material and methods

Plant material

The plant material investigated in the present study is housed at the Faenza Museum (specimen labels MSF). The focus is on plant remains from the Oriolo quarry. However, in the section Systematic palaeobotany (below), records from two neighbouring sites of the same age, Tebano (Falcona quarry) and Santa Lucia delle Spianate, are mentioned as well.

Taxonomy and botanical nomenclature

Fossil leaves, fruits, seeds and related structures from Neogene sediments commonly are assigned to fossil-species. This is a relatively easy practice, because the specimens to be classified share relevant characteristics with a particular fossil-species; fossil-species may be based on leaf remains, carpological remains etc. Conversely, the same type of fossils from Pleistocene sediments have long been compared with extant species (see Sordelli 1896). This approach is justified since now there are many species-level molecular phylogenies available, suggesting that several European woody species originated before the Middle Pleistocene (e.g., Gömöry et al. 2018). However, to assign a fossil to an extant biological species in a meaningful way is a more complex undertaking than assigning it to a fossil-species, because the definition and delimitation of the biological species is often based on characters that are usually not available in the fragmentary, fossilized parts. When a fossilized part is extremely similar to the same part of an extant species, the natural question is whether the fossil offers sufficient morphological evidence to prove the presence of the extant species at the time of formation of the fossil-bearing deposit. In the present study, such a question often remains without a definite answer, and this is reflected in using an open nomenclature (Bengston 1988), where the species name is accompanied by such qualifiers as "aff." and "cf.". These qualifiers are not used in a consistent way in the literature (Bengston 1988, Sigovini et al. 2016, Turland et al. 2019), and we must specify our approach. If leaf or fruit remains were indistinguishable from modern species in western Eurasia, we indicated this similarity by "aff." preceding the species name. The usage of aff. (affinis) follows Turland (2019), meaning "akin, related to". By this we imply that such specimens with high probability either are crown or stem lineage members of an extant species. Reference to modern species appears reasonable, in view of published time-calibrated phylogenies for a number of plant taxa (e.g., *Fagus*, Gömöry et al. 2018; *Acer*, Renner et al. 2008; *Pterocarya*, Maharramova et al. 2018). For specimens that resembled previously described fossil-taxa, we indicated closer similarity with "cf." (confer, compare – imperative; Turland 2019).

To verify taxonomic identifications, we made use of numerous online herbaria, which provide high-resolution scans of millions of herbarium sheets. We mainly consulted herbaria of the Royal Botanic Garden Edinburgh (herbarium acronym **E**; https://data.rbge.org.uk/search/herbarium/), Muséum national d'Histoire naturelle (herbarium acronym **P**; https://science.mnhn.fr/institution/mnhn/collection/p/item/search/form?lang=en_US) and Smithsonian National Museum of Natural History (herbarium acronym **NMNH**; https://collections.nmnh.si.edu/search/botany/) for comparison of modern and fossil taxa. In addition, the collection of cleared leaf specimens **NMNS** Cleared Leaf Database (https://www.kahaku.go.jp/research/db/geology-paleontology/cleared_leaf/database/?lg=en) was used for comparison of leaf venation details in modern and fossil-taxa. For names of plant species and authorities, including the spelling of authorities, we used the International Plant Names Index (IPNI; https://www.ipni.org/).

The new *Berberis* species is registered with a unique PFN number in the Plant Fossil Names Registry, hosted and operated by the National Museum, Prague for the International Organisation of Palaeobotany (IOP).

Integrated Plant Record (IPR) vegetation analysis

The IPR vegetation analysis is a semi-quantitative technique that takes into account leaf physiognomy and plant autecology to characterise major zonal vegetation types/formations for late Paleogene and Neogene plant assemblages. Zonal vegetation types are defined by their proportions of key zonal components, i.e., broad-leaved deciduous (BLD), broad-leaved evergreen (BLE), sclerophyllous and legume-like (SCL+LEG), and dry and mesophytic herbs (DRY and MESO HERBS) – see for example Kovar-Eder et al. (2008) and Teodoridis et al. (2011a). The method was later validated and improved using modern vegetation sites from China and Japan (Teodoridis et al. 2011a, 2012) and through building an internet platform with an interactive database (Teodoridis et al. 2011b, Teodoridis et al. 2011–2022).

Drudge 1 and 2 tools

Teodoridis et al. (2020) developed the statistical tools "Drudge 1" and "Drudge 2", which add information from taxonomic similarity to the IPR vegetation analysis. The tools mathematically combine proportions of major zonal components (IPR Similarity) and taxonomic similarity at the genus level (Taxonomic Similarity) for a studied fossil flora. This proportion is compared with the reference dataset of modern plant assemblages from China and Japan, as well as from Europe and the Caucasus to determine close modern vegetation analogues for the studied fossil plant assemblage (Teodoridis et al. 2020). The tools were recently re-designed by Teodoridis et al. (2021) and are now provided as on-line applications (Teodoridis et al. 2011–2022; http://www.iprdatabase.eu/).

Systematic palaeobotany

The descriptions of fossil-taxa start with gymnosperms followed by angiosperms. Angiosperms are arranged following APG IV (2016).

Gymnosperms
Family Pinaceae Spreng. ex F.Rudolphi, 1830 nom. cons.

Genus *Tsuga* (Endl.) Carrière, 1855

Tsuga cf. *chiarugii* Tongiorgi, 1936

Text-fig. 2d, e

1936 *Tsuga chiarugii* Tongiorgi, p. 800, pl. 11, figs 1–4, 7, pl. 12, figs 5–10.
2014b *Tsuga chiarugii* Tongiorgi; Pini et al., p. 303, fig. 11.1.10, P, Q.
2015 *Tsuga* cf. *chiarugii* Tongiorgi; Martinetto et al., p. 155.

Material. Oriolo MSF 638, 976, 979.

Description. Two cone impressions accompanied by reddish iron minerals originate from the typical leaf-bearing sediments; another specimen is a 3-dimensionally preserved cast within a globose concrection originating from another layer of the Oriolo section. Cones are 28 mm long and 11 mm wide.

Remarks. The two cone impressions are compatible with the characters shown by mummified cones of *Tsuga chiarugii* from Ghirlanda, a deposit of possible Early Pleistocene age in Central Italy (Tongiorgi 1936), a species that has a mass occurrence in the Northern Italian site of Steggio (Ghiotto 2010, Pini et al. 2014b). *Tsuga* was common and diverse during the Early and Middle Pleistocene of southern Europe (Magri et al. 2017, Denk et al. 2021). From the older Calabrian site of Bezhan in Albania, Denk et al. (2021) reported three pollen taxa of *Tsuga* with affinities to modern Chinese, Japanese, and North American species. According to Magri et al. (2017), *Tsuga* disappeared from Northern Italy (north of 44°) during the latest Calabrian, while it persisted slightly longer in Central Italy. Pini et al. (2014a: 299) stated that pollen of *Tsuga* is "almost absent" in Northern Italy after 0.87 Ma; hence, sporadic records in the earliest Chibanian cannot be excluded.

Genus *Pinus* L., 1753
Subgenus *Pinus* subg. *Strobus* (Lemmon) A.E.Murray, 1983

Pinus aff. *peuce* Griseb., 1846

Text-fig. 2a, b

2009 *Pinus peuce* Griseb.; Martinetto, p. 27, fig. 4(5).

Material. Oriolo MSF 643, Tebano MSF n.n., a single specimen from Tebano.

Description. Cone fragmented, narrow oblong, 79–110 mm long, 21–25 mm wide, cone scales smooth or appearing to have a slightly reflexed apical part.

Remarks. The size, shape, number and thickness of the scales indicate that these cones belong to *Pinus* subgenus *Strobus* (five needle pines; Mai 1986). The only representative of this group known in the late Cenozoic of Italy is closely similar to the extant species *Pinus peuce* Griseb. from the Balkans. This kind of pinecone was already frequent in the Pliocene, and is also known from Pleistocene strata of Pianico (Sordelli 1896, Martinetto 2009) and Steggio (Ghiotto 2010). The bad preservation suggests that this taxon grew at some distance from the depositional area.

Genus *Abies* Mill., 1754

Abies aff. *alba* Mill., 1756

Text-fig. 2c

Material. Oriolo MSF 988.

Description. Cone scale, 15 mm long, 19 mm wide, wedge-shaped, apically rounded.

Remarks. The cone scale from Oriolo is markedly similar to the extant European *Abies alba*. According to Linares (2011), an *Abies alba* ancestor inhabited Italy at least since the Pliocene. The second species of *Abies* in the modern flora of Italy, the Sicilian endemic *A. nebrodensis* Mattei may have originated through a past hybridization event or through genetic drift resulting from the prolonged isolation of southern populations during post-glacial times (Linares 2011).

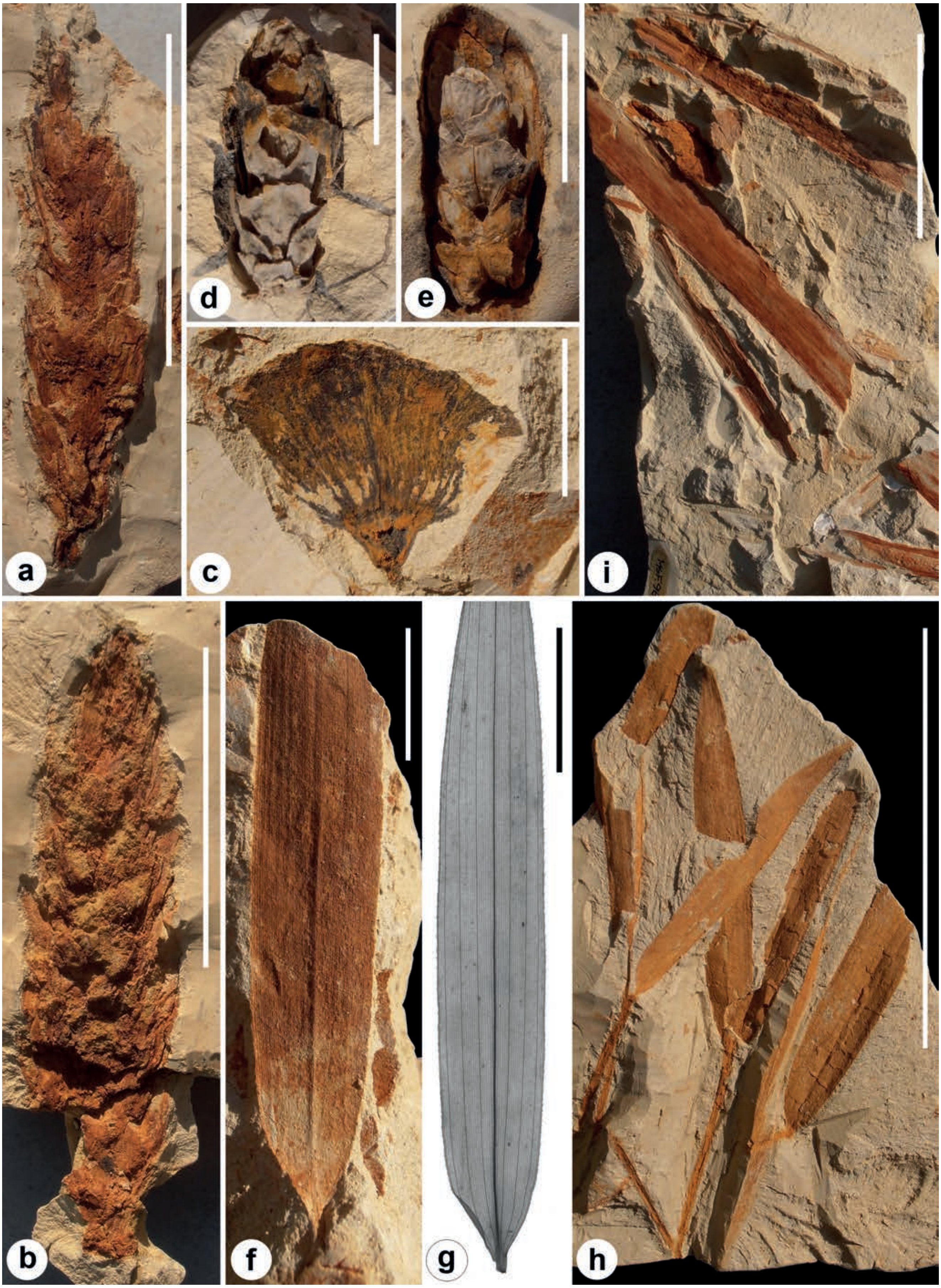
Angiosperms
Family Poaceae Barnhart, 1895 nom. cons.
Subfamily Bambusoideae Luerss., 1893
Tribe Arundinarieae Asch. et Graebn., 1902

"*Bambusa*" cf. *lugdunensis* Saporta, 1869

Text-fig. 2f, h

1869 *Bambusa lugdunensis* Saporta, p. 760.
1876 *Bambusa lugdunensis* Saporta; Saporta and Marion, p. 224, pl. 23, figs 8–16.

Material. Oriolo MSF 651, 651-1, 970, 973, n.n., Tebano MSF n.n.



Text-fig. 2. a, b: *Pinus* aff. *peuce* cones. a: Oriolo, MSF 643. b: Tebano, MSF 1021. c: *Abies* aff. *alba* cone scale, Oriolo MSF 988. d, e: *Tsuga chiarugii* cones. d: Oriolo MSF 638. e: Oriolo MSF 979. f, h: *Bambusa lugdunensis* leaves and leafy axis. f: Oriolo MSF 937. h: Oriolo MSF 651. g: Modern leaf of *Yushania* for comparison (NMNS Cleared Leaf Database specimen U1347). i: *Phragmites* sp. Oriolo MSF n.n. Scale bars 50 mm (a, b, h, i), 10 mm (c–g).

Description. Axis leafy, dispersed leaves, leaves alternate, petiolate, pseudopetiole <1 mm long, lamina base constricted, apex elongate acute, lamina 40–50 mm long, 6–10 mm wide, venation parallelodromous, midvein more prominent than lateral veins.

Remarks. *Bambusa lugdunensis* was described from Pliocene strata of Meximieux by Saporta (1869). The leaves of this fossil-species are known mainly from the Pliocene of southern France (Saporta 1869, Saporta and Marion 1876, Boulay 1892, Laurent 1904–1905), and they occur rarely in Upper Miocene and Pliocene deposits of Northwestern Italy (Martinetto 2003, Teodoridis et al. 2015). Comparable leaves, lacking genus diagnostic features, have been described from several Miocene localities across Europe (Berger and Zaubusch 1953, Grangeon 1958, Worobiec and Worobiec 2005), and from the Pliocene of Abkhazia (Georgia; Kolakovskii 1964).

We follow Worobiec and Worobiec (2005) in using the genus name "*Bambusa*" with quotation marks, indicating that assignment to a particular genus is difficult (see Text-fig. 2g for an example of a modern bamboo in tribe Arundinarieae). We tentatively assign the leaf remains from Oriolo to tribe Arundinarieae, the temperate woody bamboos (North Temperate clade; Bamboo Phylogeny Group 2012).

Genus *Phragmites* Adans., 1763

Phragmites sp.

Text-fig. 2i

Material. Oriolo MSF 969.

Description. Leaves and axes with nodes and internodes, leaves parallelodromous, ca. 15 mm wide.

Remarks. Such monocot leaf remains are usually ascribed to the genus *Phragmites*. They represent riparian vegetation and tolerate permanent flooding.

Family Berberidaceae Juss., 1789 nom. cons.

Genus *Berberis* L., 1753

Berberis auriolensis Denk et Sami sp. nov.

Text-fig. 3a–e

2001 *Berberis* sp.; Martinetto and Sami, p. 20, text-fig. 12.

Material. Oriolo MSF 644, 784, 788, 789, 790-1, 791, 792, 793, 794, 795?; Santa Lucia delle Spianate MSF n.n., Tebano MSF n.n.

Holotype. Here designated MSF 644; paratypes MSF 784, 788, 789, 790-1, 791, 792, 793, 794.

Plant Fossil Names Registry Number. PFN002946.

Diagnosis. Leaf, petiolate, lamina obovate or elliptical, micro to notophyll, base long cuneate, apex rounded, secondary venation brochidodromous, three distinct loops and secondary loops, margin subentire or dentate.

Etymology. The species name derives from the village Oriolo, the medieval name of which was Auriolus.

Type locality. Oriolo, Salita di Oriolo quarry, Italy.

Type stratum and age. "Sabbie gialle" cycle I, latest Calabrian.

Description. Leaf, petiolate, petiole 3–5 mm, lamina obovate or elliptical, 46–66 mm long, 27–43 mm wide, base acute, cuneate, apex rounded or bluntly acute, secondary venation distinctly brochidodromous, 3 main loops followed by secondary loops towards lamina margin, small veins entering teeth or forming marginal loops, margin appearing bent downward in some specimens and hence teeth obscured, ca. 5 teeth per 10 mm margin, teeth with long basal and short apical side.

Remarks. The leaves from Oriolo superficially resemble the European extant species *B. vulgaris* L., 1753. However, in the latter, the lobing of the secondary veins is steeper and the brochidodromous venation is generally less conspicuous. Dentition is variable in *B. vulgaris*, and the condition as found in the leaves from Oriolo is also met in living plants. In terms of leaf size, shape, and secondary venation, the northeastern Asian *B. amurensis* Rupr., 1857, is very similar to the fossil leaves (Text-fig. 3f), whereas *Berberis koreana* Palib., 1899, from Korea, and *B. canadensis* Mill., 1768, from North America are more similar in features of the leaf margin (Text-fig. 3g, h). These extant species belong to a modern clade comprising European, Asian and North American species (clade 5 of Adhikari et al. 2015). Remarkably, this clade also contains several narrow endemic relic species in western Eurasia (e.g., *B. aetnensis* C.Presl, 1826, *B. cretica* L., 1753, *B. maderensis* Lowe, 1856). Givulescu and Olos (1973) described *Berberis goinai* Givul. et Olos, 1973 from Late Miocene strata of Romania (Chiuzbaia). This fossil species is based on a single leaf that is similar to some specimens from Oriolo (obvate leaf, entire margin in basal part of the lamina, few teeth in apical part). However, as in *B. vulgaris*, the loops formed by the secondary veins are steeper and do not reach close to the margin, as they do in the specimens from Oriolo. Consequently, the fossil taxon from Oriolo is here described as a new species.

Genus *Epimedium* L., 1753

Epimedium cf. *praeaspera* (Andr.) Givul., 1979

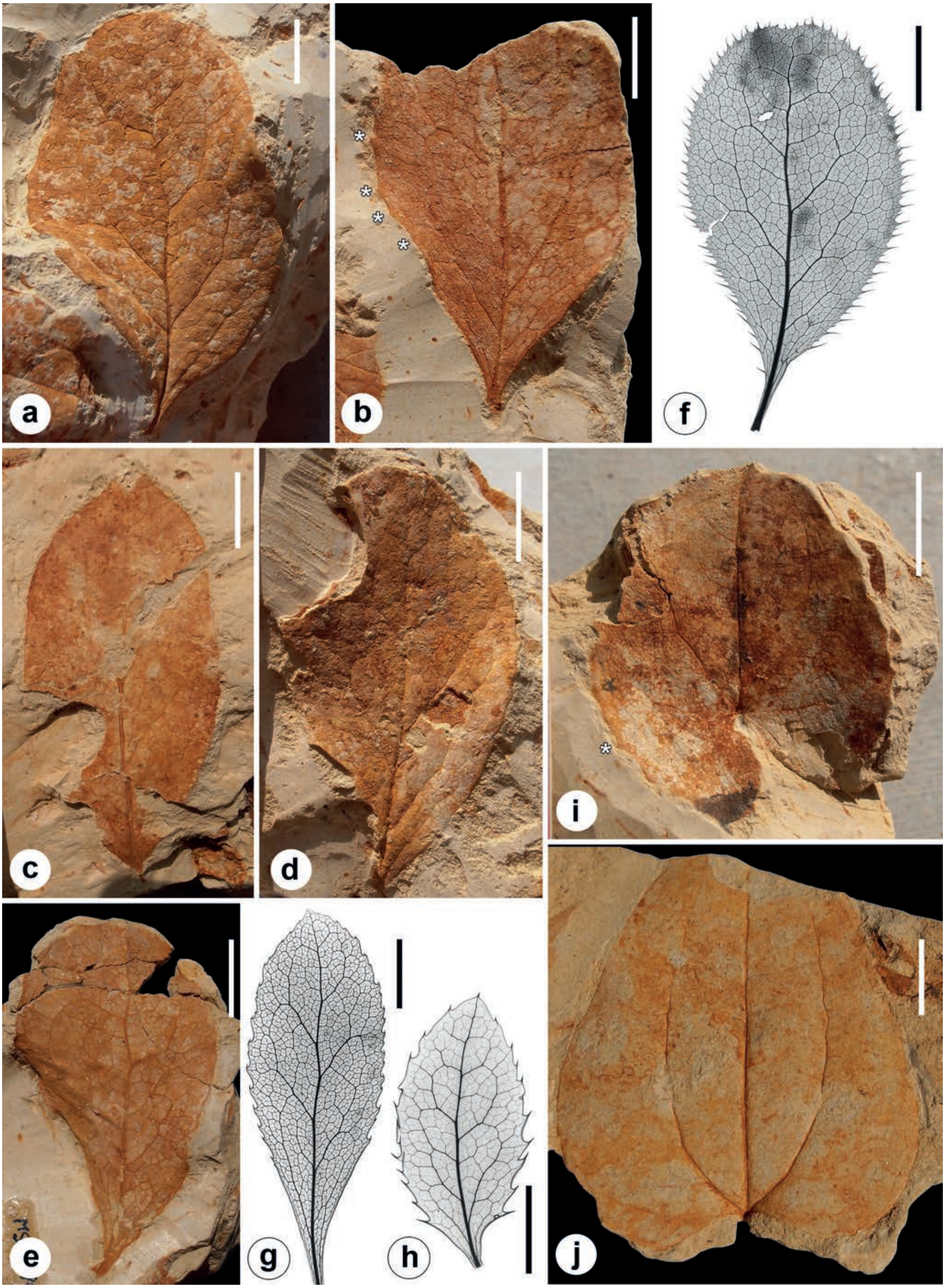
Text-fig. 3i

1956 *Smilax praeaspera* Andr., p. 228, pl. 5, fig. 19.
1959 *Smilax praeaspera* Andr.; Andreanszky, p. 182, text-fig. 236, pl. 58, fig. 5.
1979 *Epimedium praeaspera* (Andr.) Givul., p. 99, pl. 41, figs 9, 10.
1998 *Epimedium praeaspera* (Andr.) Givul.; Knobloch, p. 16, pl. 5, figs 8, 9.

Material. Oriolo MSF 778.

Description. Leaflet, lamina cordate, 35 mm long, 25 mm wide, base strongly cordate, lobate, apex acuminate, venation festooned brochidodromous, leaf margin spiny, ca. 3 spines/1 cm lamina margin.

Remarks. The leaves from Oriolo are very similar to the specimens of *Epimedium praeaspera* from the Pliocene flora of Willershausen (Knobloch 1998). According to Givulescu (1979), this species is closely related to the extant *E. alpinum*



Text-fig. 3. **a–e: *Berberis auriolensis* sp. nov. a: Oriolo MSF 644, Holotype. b: Oriolo MSF 794, asterisks indicate position of teeth. c: Oriolo MSF 784. d: Oriolo MSF 789. e: Oriolo MSF 790. f–h: Modern leaves of *Berberis*. f: *Berberis amurensis* var. *japonica* modern leaf (NMNS Cleared Leaf Database specimen T 0454). g: *Berberis koreana* modern leaf (NMNS Cleared Leaf Database specimen T 1646). h: *Berberis canadensis* modern leaf (NMNS Cleared Leaf Database specimen T 1670). i: *Epimedium* cf. *praeaspera* Oriolo MSF 778, asterisk indicates position of tooth. j: *Clematis* aff. *vitalba* Oriolo MSF 630. Scale bars 10 mm (a–j).**

L. native to broad-leaved deciduous mountain forests from Albania northwards to Austria and Piedmont (Italy).

Family Ranunculaceae Juss., 1789 nom. cons.

Genus *Clematis* L., 1753

Clematis aff. *vitalba* L., 1753

Text-fig. 3j

Material. Oriolo MSF 630-1, 710-1.

Description. Leaflet, lamina ovate, cordate, 43 to >50 mm long, 30–46 mm wide, primary venation acrodromous, one midvein, two lateral veins, secondary venation brochidodromous.

Remarks. The leaflet is very similar to the extant liana *C. vitalba* (cf. modern specimen E00440433, herbarium E). In contrast, similarities with *Smilax* are weak. The key candidate among modern *Smilax* spp. to compare against our fossil would be *Smilax excelsa* L. (modern relict distribution in the Euxinian-Hyrcanian forest region). However, this species differs in the number of primary veins (usually 2–3 pairs of lateral primary veins), and in the secondary venation. In *Smilax*, brochidodromous loops of secondary veins typically join to form an additional lateral primary vein (see for example specimen E00325946, herbarium E).

Family Hamamelidaceae R.Br., 1818 nom. cons.

Genus *Parrotia* C.A.Mey., 1831

Parrotia aff. *persica* (DC.) C.A.Mey., 1831

Text-fig. 4a–e

Material. Oriolo MSF 654-1, 678, 726, 727, 728, 729, 730-1, 731, 734, 743, 849, 853-1, 991, 993, Tebano MSF n.n.

Description. Leaf, petiolate, petiole >10 mm long, lamina obovate, elliptic to nearly orbicular, 45–87 mm long, 35–67 mm wide, apex obtuse, rarely acute, base acute to obtuse, rounded, base asymmetrical, lamina starting above point of divergence between primary vein and basal pair of secondary veins (Text-fig. 4c–e), secondary venation (pseudo)craspedodromous to brochidodromous, secondary vein spacing irregular, the first two pairs of secondary veins usually with several abmedial veins, leaf margin wavy.

Fruits, 2 valved capsules (Text-fig. 4a) and seeds (Text-fig. 4b), seed 6.5 mm long.

Remarks. *Parrotia* was widespread in the Neogene of western Eurasia and represented by a single fossil-species, *Parrotia pristina* (Ettingsh.) Stur, 1867 (Adroit et al. 2020). The fossil leaves from Oriolo are very similar to the modern *P. persica*. However, based on leaf imprints, it is nearly impossible to distinguish *Parrotia* leaves from those of some *Hamamelis* spp. (e.g., *H. vernalis* Sarg.). Because the leaves co-occur with fruits of *Parrotia*, we assigned both leaf and fruit remains to *Parrotia*. The fruits are about 10 mm long, as is the fruit from Enza described by Martinetto (2015). This specimen, assigned to *Parrotia* cf. *persica*, shares two relevant characters with the fruits from Oriolo (Text-fig. 4a): the two style bases are prominent and close to each other. In the smaller Pliocene fruits of *Parrotia reidiana* Kirchh., 1957, from Northwestern Italy (Martinetto 2015), associated with leaves of *Parrotia pristina* (Martinetto 2003), the two style bases are less prominent and usually more broadly spaced. The Pleistocene fossil leaves and fruits from Oriolo agree in morphology with the modern western Eurasian species (see also Roiron 1983, Leroy and Roiron 1996). Hence, we use the open nomenclature merely because the fossil record of *Parrotia* in the Pleistocene of Italy is more extensive than presently known, and not yet adequately studied. Wood of *Parrotia persica* has been reported from another section of the late Early Pleistocene, the Arda section (Pini et al. 2014a), and fruits have been noticed there in the field (Martinetto, pers. obs.), but not yet sampled.

Family Vitaceae Juss., 1789 nom. cons.

Genus *Vitis* L., 1753

Vitis sp.

Text-fig. 4f

Material. Oriolo MSF 838.

Description. Leaf, simple, palmate, 3-lobed, lamina broad ovate, 63 mm long, 74 mm wide, apex acute, pointed, primary venation actinodromous, secondary venation (semi) craspedodromous, lateral lobe with prominent abmedial veins, basal-most abmedial veins with an additional set of abmedial veins, margin serrate, teeth bluntly triangular.

Remarks. Sharply acute teeth are typical of *Vitis* (see for example Ardeghi et al. 2014), whereas other lianas in the Vitaceae such as *Ampelopsis* and *Parthenocissus* have coarser and blunter teeth usually with a small cuspidate tip. The extant woody liana *Vitis vinifera* subsp. *sylvestris* (Willd.) Hegi, 1925, grows in a wide range of habitats including wetlands, seasonal stream sides in closed forests, alluvial beds of large rivers, sand dune shrublands and forested wetlands (alder forests). In temperate forests of northern Iran, *Parrotia persica* and *Carpinus betulus* are the most frequent host species for *Vitis* (Naqinezhad et al. 2018).

Family Fabaceae Lindl., 1863 nom. cons.

Genus *Gleditsia* J.Clayton, 1753

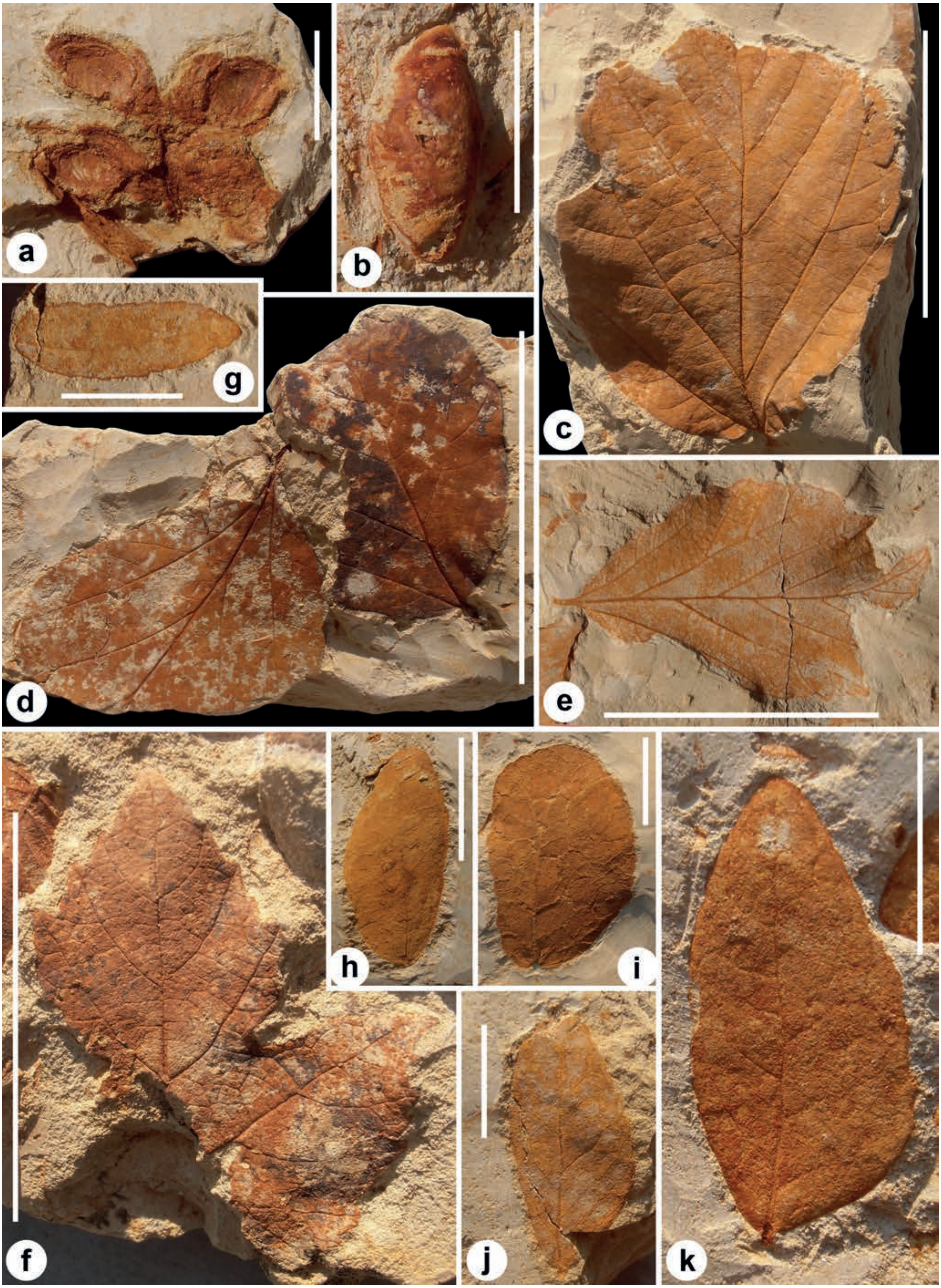
Gleditsia aff. *caspica* Desf., 1809

Text-figs 4h–k, 5a

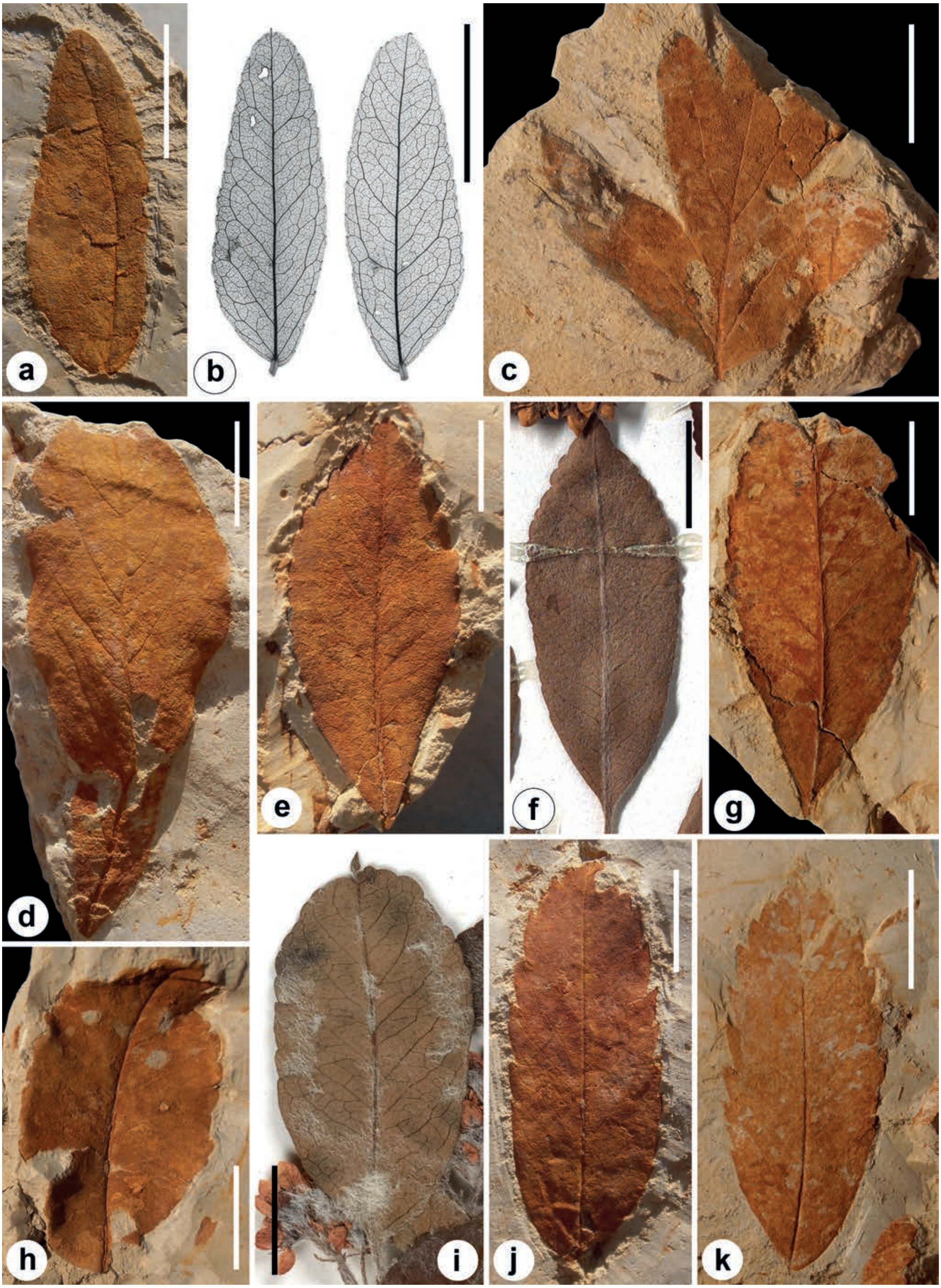
Material. Oriolo MSF 787, 847, 910-1, 914-1, 915-1, 917-1, 918-1, 919-1, 920-1, 922-1, 923, 925, 926, 927, 928, 929, 931, 932, 933, 934, 935, Santa Lucia delle Spianate MSF n.n.

Description. Leaflet, petiolate, petiole very short, lamina asymmetrical, broad to narrow elliptical, 12–27 mm long, 6–17 mm wide, secondary venation brochidodromous, small veins departing from secondary veins enter small crenulations, margin crenulate.

Remarks. Givulescu (1979: 102, pl. 41, fig. 14) assigned a leaflet from Late Miocene strata of Chiuzbaia (Romania), very similar to the material from Oriolo, to *Gleditsia allemanica* Heer, 1859. According to Givulescu (1979), *G. allemanica* was present in middle and Late Miocene floras of Germany, Hungary, Romania and Ukraine. Recently, well-preserved



Text-fig. 4. a–e: ***Parrotia*** **aff.** ***persica*****. a: Oriolo MSF 991 capsule. b: Oriolo MSF 994 endocarp. c: Oriolo MSF 654. d: Oriolo MSF 743. e: Oriolo MSF 678. f:** ***Vitis*** **sp. Oriolo MSF 838. g–k:** ***Gleditsia*** **aff.** ***caspica*****. g: Oriolo MSF 920. h: Oriolo MSF 939. i: Oriolo MSF 787. j: Oriolo MSF 917. k: Oriolo MSF 925. Scale bars 10 mm (a, h–k), 5 mm (b), 50 mm (c–f).**



Text-fig. 5. a: ***Gleditsia*** **aff.** ***caspica*** **Oriolo MSF 935. b:** ***Gleditsia caspica*** **modern leaflet (NMNS Cleared Leaf Database specimen T 1484). c:** ***Crataegus*** **aff.** ***monogyna*** **Oriolo MSF 836. d:** ***Mespilus*** **aff.** ***germanica*** **Oriolo MSF 785. e, g, h:** ***Pyracantha*** **aff.** ***coccinea*****. e: Oriolo MSF 627. g: Oriolo MSF 627. h: Oriolo MSF 684. f:** ***Pyracantha coccinea*** **modern leaf for comparison (NMNH 03695728). i:** ***Pyracantha coccinea*** **modern leaf for comparison (E00408203). j, k:** ***Sorbus*** **aff.** ***domestica*****. j: Oriolo MSF 636. k: Oriolo MSF 824. Scale bars 10 mm (a–k).**

leaflets of *Gleditsia* have been reported from Late Miocene and Pliocene localities in Poland and Germany. Worobiec and Worobiec (2019) reported *Gleditsia europaea* G.Worobiec, 2019, from the Bełchatów Lignite Mine (Poland), which they considered most closely related to the modern North American species *G. aquatica* Marshall, 1785. From the Pliocene of Frankfurt, Kvaček et al. (2020) reported *Gleditsia pliocaenica* Kvaček, Teodoridis et Denk, 2019, which they compared to the western Eurasian *G. caspica*. The Pliocene specimens are very similar to the material from Oriolo.

Leaflets of *Gleditsia* differ from the Neogene extinct genus *Podocarpium* (Herendeen 1992) by their crenulate margin.

Family Rosaceae Juss., 1789 nom. cons.

Genus *Crataegus* L., 1753 nom. cons.

Crataegus aff. *monogyna* Jacq., 1775

Text-fig. 5c

Material. Oriolo MSF 639-1, 832-1, 833, 834, 835, 836, 837.

Description. Leaf, simple, lamina ovate to deltoid, deeply lobed, 2–3 lobes per side, leaf lobe apices acute, base round to cuneate, lamina 18–29 mm long, 17–29 mm wide.

Remarks. The leaves are very similar to the modern *C. monogyna*. Another modern European species, *C. laevigata* (Poir.) DC., 1825, differs by obtuse lobe apices and shallower sinuses.

Genus *Sorbus* L., 1753

Sorbus aff. *domestica* L., 1753

Text-fig. 5j, k

1983 *Sorbus domestica* L.; Roiron, p. 705, pl. 9, figs 7, 8.
2001 *Sorbus domestica* L.; Martinetto and Sami, p. 21, fig. 6.

Material. Oriolo MSF 636, 823?, 824, 825?, 826, 827, 828 F, 830?, Tebano MSF n.n.

Description. Leaflet, sessile, lamina elliptical, lamina length 27–51 mm, lamina width 11–19 mm, ratio lamina length to width ca. 3/1, apex acute or obtuse, base slightly asymmetrical, acute to obtuse, basal part of lamina with entire margin, upper 2/3 to 1/2 with serrate margin, secondary venation craspedodromous, secondary veins departing from primary vein at acute angles, roughly uniform, teeth rosoid.

Remarks. Fossil leaves of *S. domestica* have previously been reported from Plio-Pleistocene strata of Crespià (Spain; Roiron 1983). Leaflets of *S. aucuparia* Poir., 1806, may look very similar to *S. domestica* when growing on dry sites.

cf. *Sorbus* sp.

Text-fig. 6b, c

Material. Oriolo MSF 677, 821.

Description. Leaflet, lamina ovate or ovate-elliptic, 24–27 mm long, 13–17 mm wide, base obtuse or bluntly acute, apex obtuse with a cusp, secondary venation craspedodromous, margin coarsely serrate, teeth usually with secondary teeth, tooth basal side long convex, apical side shorter concave, straight or convex.

Remarks. The leaflets are fairly similar to the extant species *Sorbus aucuparia* L., 1753. *Sorbus aucuparia* displays a marked leaf polymorphism with leathery leaves approaching the morphology of *S. domestica*, while chartaceous leaflets of seedlings and shade conditions commonly show the coarse dentition with secondary teeth, as seen in the fossil material.

Genus *Mespilus* L., 1753

Mespilus aff. *germanica* L., 1753

Text-fig. 5d

Material. Oriolo MSF 785.

Description. Leaf, simple, lamina elliptic oblong, 50 mm long, 19 mm wide, base acute, secondary venation brochidodromous, tertiary veins perpendicular or slightly oblique to secondary veins, margin entire.

Remarks. A single specimen resembles leaves of *M. germanica* based on the leaf shape, venation and margin. However, the morphological characteristics preserved in the fossil leaf are not sufficient to unambiguously assign the fossil to the modern species.

Genus *Pyracantha* M.Roem., 1847

Pyracantha aff. *coccinea* M.Roem., 1847

Text-fig. 5e, g, h

2009 *Pyracantha coccinea* M.Roem.; Martinetto, p. 27, fig. 3 (6).

Material. Oriolo MSF 627-1, 684-1.

Description. Leaf, simple, petiolate, lamina elliptic, 30–48 mm long, 20–21 mm wide, base acute, apex bluntly acuminate, secondary venation mixed, tertiary veins running perpendicular or oblique to secondary veins, margin dentate, teeth appressed, with long basal and short apical side, tooth type rosoid.

Remarks. The morphological variation of the fossil leaves (narrow and wide elliptic, mixed secondary venation, margin) matches the one found in the modern species *P. coccinea* (Text-fig. 5f, i). The modern species is native to southeastern Europe and western Asia and is ecologically very flexible. It can be an element of dry forests with *Zelkova*, *Carpinus orientalis*, or of woody associations on fixed sand dunes with *Malus*, *Hippophae*, *Berberis*, *Mespilus*, and *Paliurus* in western Georgia (Denk et al. 2001). In Italy, fossil leaves and fruits of *P. coccinea* were reported from the early Middle Pleistocene of Pianico-Sellere (Martinetto 2009).

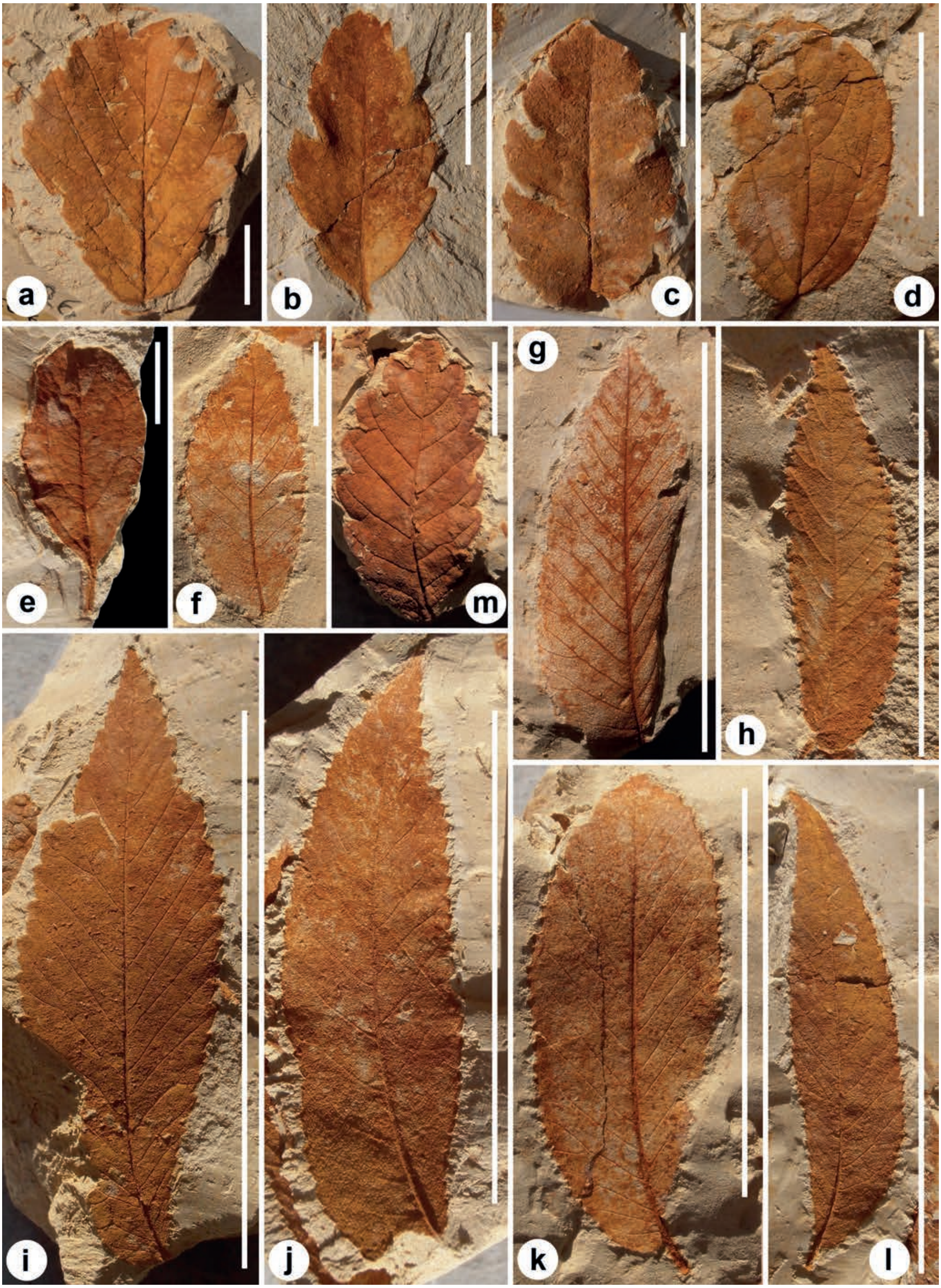
Genus *Spiraea* L., 1753

Spiraea aff. *cana* Waldst. et Kit., 1812

Text-fig. 6d

Material. Oriolo MSF 644, 944.

Description. Leaf, simple, petiolate, petiole short and bent, lamina obovate, 17 mm long, 9 mm wide, base obtuse, apex obtuse, secondary vein spacing irregular, two opposite basal secondary veins running to upper third of



Text-fig. 6. a: cf. *Rubus* sp., leaflet Oriolo MSF 676. b, c: cf. *Sorbus*. b: Oriolo MSF 821. c: MSF 677. d: *Spiraea* aff. *cana* Oriolo MSF 944. e: *Rhamnus* aff. *cathartica* Oriolo MSF 909. f–l: *Ulmus affinis*. f: Oriolo MSF 717. g: Oriolo MSF 725. h: Oriolo MSF 724. i: Oriolo MSF 721. j: Oriolo MSF 723. k: Oriolo MSF 637. l: Oriolo MSF 722. m: *Zelkova zelkovifolia* Oriolo 28 MSF 633. Scale bars 10 mm (a–f, m), 50 mm (g–l).

lamina, secondary venation brochidodromous, upper half or upper third of lamina with teeth, teeth with long basal and short apical side.

Remarks. The fossil leaves are very similar to the modern species *S. cana* native to Northeastern Italy and the northwestern Balkan Peninsula (Plants of the World Online, Royal Botanic Gardens, Kew. http://www.plantsoftheworldonline.org/ retrieved September 18th, 2021). Similarities also exist with *S. blumei* G.Don, 1832 (East Asia).

Rosaceae unspecified

cf. *Rubus* sp.

Text-fig. 6a

Material. Oriolo MSF 676, 677, 680.

Description. Leaflet, lamina rhombic obovate, 31–36 mm long, 21–29 mm wide, base rounded, secondary venation craspedodromous, first two pairs of secondary veins with prominent abmedial veins which run into teeth, teeth compound.

Remarks. The leaflet shown in Text-fig. 6a possible represents a terminal leaflet. The assignment to the genus *Rubus* is tentative, as we cannot exclude that these leaves belong to another rosaceous genus. However, the presence of distinct abmedial veins departing from the second pair of secondary veins and running into prominent teeth is typical of many *Rubus* spp. Terminal leaflets in the modern *R. caesius* L. collected by us from the wild in some cases look very similar to the fossil leaflet from Oriolo.

Family Rhamnaceae Juss., 1789 nom. cons.

Genus *Rhamnus* L., 1753

Rhamnus aff. *cathartica* L., 1753

Text-fig. 6e

Material. Oriolo MSF 909, 3 unnumbered specimens.

Description. Leaf, petiolate, lamina elliptic, 20–40 mm long, 14–25 mm wide, base acute, apex bluntly acuminate, secondary veins irregular, secondary veins in middle part of lamina widely spaced, intersecondary veins present, secondary venation brochidodromous, margin appearing entire because deflexed.

Remarks. The margin in this specimen is not well preserved. It seems somewhat crenulate, though, and this is also seen in *R. cathartica*. *Rhamnus cathartica* may be part of riparian vegetation, as well as forest edge communities and drier sites. It also forms part of (sub)Mediterranean scrub (Šibljak; Adamovic 1909, Horvat et al. 1974) with *Berberis*, *Acer* spp. and different deciduous oaks.

Family Ulmaceae Mirb., 1815 nom. cons.

Genus *Zelkova* Spach, 1841

Zelkova zelkovifolia (Unger) Bůžek et Kotl., 1963

Text-figs 6m, 7a–d

1847 *Ulmus zelkovifolia* Unger, p. 94 pro parte, pl. 24, figs 9–13, not fig. 8.

1963 *Zelkova zelkovifolia* (Unger) Bůžek et Kotl. in Kotlaba, p. 59, pl. 3, figs 7, 8.

Material. Oriolo MSF 633, 639, 675, 681?, 682-1, 683, 685?, 811, 812, 813, 814, 815, 816, 817 ?, 818, 819-1, 820, 850; Tebano MSF n.n.; Santa Lucia delle Spianate MSF n.n.

Description. Leaf, petiolate, lamina elliptical to ovate, lamina length 25–49 mm, width 16–25 mm, apex acute, base obtuse, sometimes slightly asymmetrical, margin serrate with coarse teeth (appearing crenate in case of blunt tooth apices), secondary venation craspedodromous, secondary veins commonly branching.

Remarks. The leaves of Oriolo are similar to both the modern *Z. carpinifolia* (Pallas) K.Koch, 1849, ranging from Turkey to northern Iran, and to the narrowly endemic *Z. sicula* Di Pasq., Garfi et Quézel, 1992, native to small areas in Sicily. For example, the leaf figured in Text-fig. 7d matches well leaves of *Z. carpinifolia,* while the leaf in Text-fig. 7b closely resembles leaves of *Z. sicula* (Denk and Grimm 2005). This last fossil is extremely similar to two fossil leaves from Riano Romano, figured by Follieri et al. (1986). Molecular data indicate that *Z. sicula* might be the result of a relatively recent hybridisation, with parents close to the ancestral species of *Z. abelicea* (Lam.) Boiss. (Crete) and the widespread Euxinian-Hyrcanian *Z. carpinifolia* (Christe et al. 2014, Rucinska 2012). Roiron (1983) referred *Zelkova* leaves of the Plio-Pleistocene of Crespià to the modern species *Z. crenata* Spach., 1841 (= *Z. carpinifolia*). Because the present leaves show a mosaic of characteristics typical of two modern species, we consider them to represent the fossil-taxon *Z. zelkovifolia*.

Genus *Ulmus* L., 1753

Ulmus affinis A.Massal., 1853

Text-fig. 6f–l

1853 *Ulmus affinis* A.Massal., p. 19.

1854 *Ulmus affinis* A.Massal.; Massallongo, p. 19, pl. 4, fig. 8.

1858 *Ulmus affinis* A.Massal.; Massallongo, p. 41.

1859 *Ulmus affinis* A.Massal.; Massallongo and Scarabelli, p. 212.

1859 *Ulmus braunii* Heer; Massalongo and Scarabelli, p. 211, pl. 21, fig. 10.

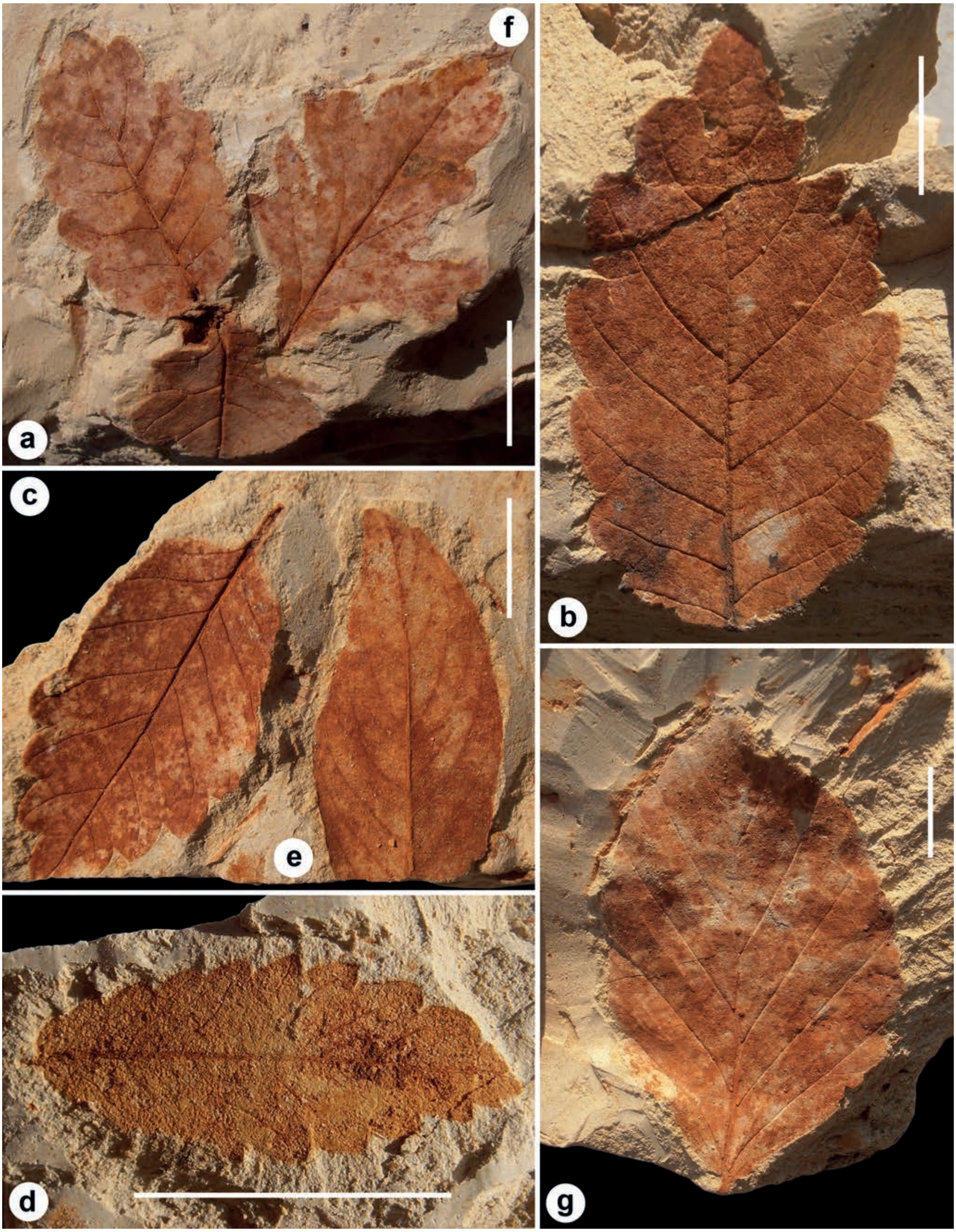
2001 *Ulmus* cf. *pyramidalis* Göpp.; Martinetto and Sami, p. 17, fig. 7.

2003 *Ulmus affinis* A.Massal.; Martinetto, p. 102, pl. 8, figs 2–4 (not fig. 1 = *U. pyramidalis* Göpp.).

Material. MSF 637, 705, 717, 718, 719, 720, 721, 722, 723, 724, 725, 726, 786.

Description. Leaf simple, petiolate, lamina elliptical, elliptical-lanceolate, commonly asymmetrical, lamina 19–64 mm long, 14–34 mm wide, length to width ratio ca. 2/1 to >4/1, apex acute, acuminate, base strongly asymmetrical, acute to cordate-auriculate, secondary venation craspedodromous, usually at least some secondary veins splitting halfway or close to lamina margin, margin serrate, teeth double serrate, the secondary tooth commonly inconspicuous.

Remarks. *Ulmus* leaves are very common in the late Cenozoic of Europe, and their taxonomy has been confusing. In the nineteenth century, numerous fossil-species were established (e.g., Göppert 1855). The leaves from Oriolo agree well with Unger's type *U. longifolia* Unger, 1847.



Text-fig. 7. a–d: *Zelkova zelkovifolia*. a: Fruiting twig, Oriolo MSF 639. b: Oriolo MSF 685. c: Oriolo MSF 859. d: Oriolo MSF 947. e: Unknown leaf fragment resembling *Lonicera nigra* L., 1753, Oriolo MSF 859. f: *Crataegus* aff. *monogyna* Oriolo MSF 639-1. g: *Fagus* aff. *sylvatica* Oriolo MSF 648. Scale bars 10 mm (a–g).

This taxon is problematic, as the name *U. longifolia* UNGER is illegitimate (younger homonym). The same name had previously been used for the modern species *U. longifolia* RAF., 1838. To solve this problem, Knobloch (1969) included *U. longifolia* in *Ulmus pyramidalis* GÖPP., 1855. However, in the emended description of *U. pyramidalis*, the leaf base is described as weakly asymmetric, and the original specimens of Göppert's (1855) *U. pyramidalis* have a symmetrical lamina with a symmetrical or weakly asymmetrical leaf base. The base is described as rounded or cuneate, rarely asymmetric by Hably and Zastawniak (2001), who consider the most characteristic features of *U. pyramidalis* the densely spaced secondary veins, particularly in the upper part of the lamina, and the regular shape. Hence, in our opinion, *U. longifolia* Unger nom. illeg. considerably differs from *U. pyramidalis* and should not be synonymised with the latter. The former would need a replacement name and a new taxonomic, geographic, and stratigraphic circumscription.

The similarity of *U. affinis* with *U. longifolia* was also noticed by Massalongo (1854) and Massalongo in Massalongo and Scarabelli (1859: 213). In the latter work, Massalongo noted that some specimens of *Ulmus braunii* Heer from Öhningen should be included within *U. affinis*, and that the name *U. braunii* possibly would need to be treated as junior synonym of *U. affinis*. He further was uncertain as to how to distinguish the specimens from Sośnica (Schossnitz), figured by Göppert (1855) as *U. longifolia*, from *Ulmus affinis*. In the present investigation, we include in *U. affinis* Messinian material from Senigallia, Pliocene material from Northwestern Italy (Martinetto 2003), and the present late Early Pleistocene material (App. I, Text-fig. A1). More work is needed to resolve the question of whether the lineage leading to *U. affinis* from Oriolo dated back to the Late Miocene (as in the concept of the present study), or whether it dated back to the Early Miocene (*U. longifolia* of Bílina).

According to Webenau (1995), the shape of leaves traditionally assigned to *U. longifolia* has no analogues in the current European flora, and the living species with the most similar leaves are *U. castaneifolia* Hemsl., 1891, and *U. lancifolia* Roxb., 1814, both from East Asia. *Ulmus lancifolia*, although somewhat similar in shape (elongate apex, narrow leaves), differs by its evergreen foliage, simple-serrate margin, and weakly asymmetrical leaf base (App. I, Text-fig. A2). Leaves with a distinctly asymmetrical leaf base and elliptic-lanceolate shape are found in a clade of western Eurasian species of sect. *Ulmus* (Wiegrefe et al. 1994): *Ulmus glabra* Huds., 1762, *U. minor* Mill., 1768, and their hybrids, e.g., *U.* × *hollandica* Mill., 1768 (App. I, Text-fig. A2), as well as in the Caucasian *U. elliptica* K.Koch, 1849.

Family Fagaceae Dumort., 1829

Genus *Fagus* L., 1753

Fagus aff. *sylvatica* L., 1753

Text-fig. 7g

Material. Oriolo MSF 648, n.n.

Description. Leaf, simple, petiolate, petiole 9 mm long, lamina elliptic 54–60 mm long, 34–46 mm wide, broad elliptic, base and apex acute, secondary venation pseudocraspedodromous, number of secondary veins 6–8, tertiary veins perpendicular to secondary veins.

Remarks. The two leaves are identical to modern leaves of *Fagus sylvatica* subsp. *sylvatica* populations typical of Central, southern and western Europe. Earlier Pliocene leaf assemblages of *Fagus* in Europe (e.g., northern Greece, Atalanti, Velitzelos et al. 2014; Northern Italy, Martinetto 2003; Frankfurt, Germany, Kvaček et al. 2020) show a mosaic of leaf morphological characteristics, like that found in the modern East Asian species *F. pashanica* C.C.Yang, *F. longipetiolata* Seemen, *F. crenata* Blume, and the western Eurasian *F. sylvatica* s.l. The leaves from Oriolo fall within the morphological variability of the modern European species *F. sylvatica* s. str. This is in agreement with molecular studies, which suggest that the modern species *Fagus sylvatica* s. str. diverged from its sister populations in Asia Minor at ca. 800 ky BP (Gömöry et al. 2018). Further genetic differentiation in Europe and the Balkans might have occurred even later, but these are not captured in the leaf morphology of modern populations.

Genus *Quercus* L., 1753
Section *Quercus* sect. *Cerris* Dumort., 1829

Quercus aff. *cerris* L., 1753

Text-fig. 8a, b

Material. Oriolo MSF 982, 984.

Description. Cupule, diameter 22–27 mm, oblong to spathulate scales, reflexed, ca. 2–3 mm long.

Remarks. The cupules resemble those of modern *Quercus* sect. *Cerris* by their reflexed scales. Such scales are also found in some *Q.* sect. *Ilex* (e.g., *Q. coccifera* L., 1753). Cupules in *Q. cerris* usually have more prominent scales, but they may look similar to the fossils from Oriolo when collected from the leaf litter.

Quercus aff. *cerris* L., 1753

Text-fig. 8c–e

Material. Oriolo MSF 657, 659, 689.

Description. Leaf, simple, petiolate, petiole 6–10 mm, lamina 60–80 mm long, 30–35 mm wide, ovate to elliptic, shallowly to deeply lobed, base acute-rounded, cordate, apex acute, lamina shallowly lobed, lobes with pointed apical tip (MSF 657), lamina irregular, deeply lobed, lobes pointed-triangular elongated (MSF 689), lamina deeply lobed, lobes with secondary lobes (MSF 659), number of lobes 5–8.

Remarks. The leaf morphological variability in the specimens from Oriolo fits well with the modern variability encountered in *Q. cerris* and in fossils from other Pleistocene localities from the Submediterranean region (Denk et al. 2021). Deeply lobed leaves with secondary lobes are also found in *Q. pubescens*, but they normally have fewer lobes (Schwarz 1937).

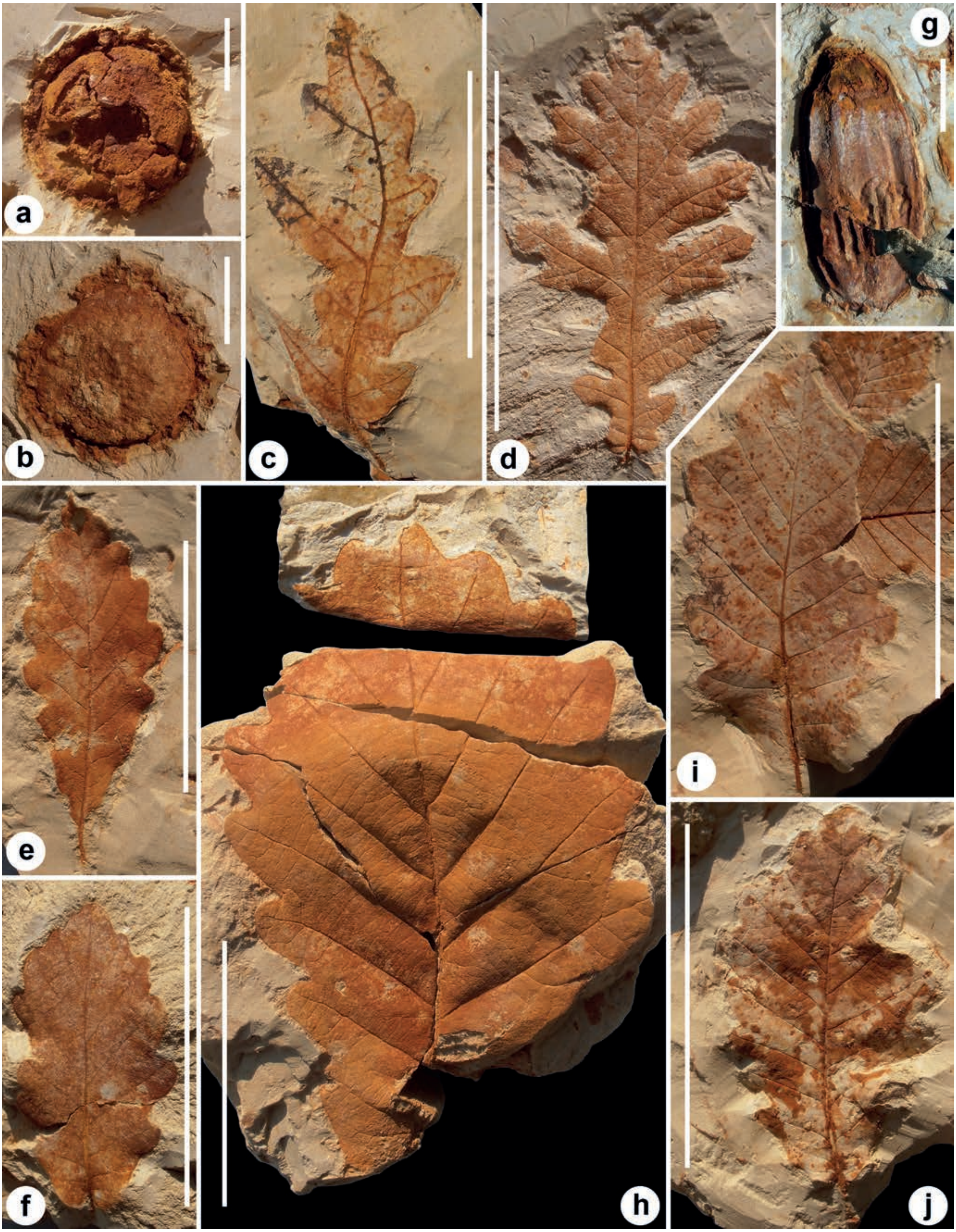
Section *Quercus* sect. *Quercus*

Quercus sect. *Quercus* sp. indet.

Text-fig. 8g

Material. Oriolo MSF 658, 658-1.

Description. Acorn, 38 mm long, 15 mm wide, oblong-elliptic in outline, with furrows running parallel with the long axis of the acorn.



Text-fig. 8. a–e: *Quercus* aff. *cerris*. a: Cup, Oriolo MSF 984. b: Cup, Oriolo MSF 982. c: Leaf, Oriolo MSF 689. d: Leaf, Oriolo MSF 659. e: Oriolo MSF 657. f: *Quercus* aff. *pubescens* Oriolo MSF 688. g: *Quercus* sect. *Quercus* acorn, Oriolo MSF 658. h–j: *Quercus iberica*. h: Oriolo MSF 694. i: Oriolo MSF 639. j: Oriolo MSF 698. Scale bars 10 mm (a, b, g), 50 mm (c–f, h–j).

Remarks. Acorns of this type are produced by several western Eurasian species of *Quercus* sect. *Quercus*, *Q. ilex* L., 1753, and *Q. coccifera* L., 1753, of sect. *Ilex*.

Quercus aff. *pubescens* Willd., 1796

Text-fig. 8f

Material. Oriolo MSF 633, 688, ?697, ?701.

Description. Leaf, simple, petiolate, lamina elliptic, 50–62 mm long, 25–30 mm wide, shallowly lobed, number of lobes 5–6, base cordate, auriculate, apex rounded acute.

Remarks. The distinction between *Quercus pubescens* and *Q. petraea* L. is not straightforward. *Quercus pubescens* leaves commonly have a cordate or auriculate base and broadly rounded lobe apices. In Europe, *Q. petraea* leaves never have a cordate base, and lobes are rounded triangular. However, eastern populations of the closely related *Q. iberica* M.Bieb., 1808 (syn. *Q. petraea* subsp. *polycarpa* (Schur) Soó, 1943) commonly have cordate leaf bases, but differ from *Q. pubescens* in their higher number of secondary veins and lobes.

Quercus aff. *petraea* (Matt.) Liebl., 1784

Text-fig. 8h–j

Material. Oriolo MSF 639, 656, 656-1, 692, 692-1, 694, 697, 698, 702-1, 702-2.

Description. Leaf, simple, petiolate, petiole up to 8 mm long, stout, lamina elliptic, 56–118 mm long, 30–80 mm wide, shallowly lobed, number of lobes 8–10, base obtuse-cordate to wide acute with rounded asymmetric very-base, apex acute rounded, secondary venation craspedodromous, number of secondary veins 9–11.

Remarks. These leaves resemble *Q. iberica* M.Bieb., 1808 (syn. *Quercus petraea* subsp. *polycarpa* (Schur) Soó, 1943) in their regular shape, absence of intersecondary veins, and the cordate-auriculate leaf base.

Family Juglandaceae DC. ex Perleb, 1818 nom. cons.

Genus *Carya* Nutt., 1818

Carya cf. *minor* Saporta, 1873

Text-fig. 9a–e

1873 *Carya minor* Saporta, p. 217.
1876 *Juglans minor* (Saporta) Saporta et Marion, p. 166, pl. 37, figs 1–6.
1970 *Carya* cf. *minor* Saporta; Pavia, pl. 3, fig. 5.
2001 *Carya* cf. *minor* Saporta; Martinetto and Sami, p. 17, text-fig. 10.

Material. Oriolo MSF 631, 631-1, 631-2, 634, 634-1, 635, 639, 690, 691, 755, 756, 757-1, 758, 759, 760, 761, 762, 763, 764, 765, 766, 767, 768, 769, 770, 771, 772, 773, 774, 775, 777.

Description. Leaflet, petiolate, petiole <2 mm long, lamina elliptic, ovate or obovate, 39–124 mm long, 18–57 mm wide, base cuneate decurrent, acute rounded, apex acute or acuminate, secondary venation mixed brochidodromous, semicraspedodromous, secondary veins branching close to leaf margin or rarely close to primary vein, secondary veins and intersecondary veins spaced 2–4 per 1 cm primary vein, margin sharply serrate.

Remarks. The material from Oriolo is closely similar to leaves/leaflets of *C. minor* from the Pliocene of Meximieux (France) and Willershausen (Germany) in some instances (densely spaced, regular secondaries forming a brochidodromous pattern of loops), while other leaflets have a more irregular pattern of secondary veins. From Miocene strata of France and Crete, Kvaček et al. (2011) and Zidianakis et al. (2020) described dispersed leaves and leaflets of *Carya* as *Carya* sp., accounting for differences in secondary venation with known western Eurasian Neogene species of *Carya*. Pavia (1970) reported a very similar leaflet from Arboschio (Pliocene).

Genus *Pterocarya* Kunth, 1824

Pterocarya aff. *fraxinifolia* (Poir.) Spach, 1834

Text-fig. 9f, g

Material. Oriolo MSF 632, 632-1, 632-2.

Description. Leaflet, fruits, leaflet oblong, 62 mm long, 30 mm wide, apex acuminate, secondary venation brochidodromous, margin bluntly serrate, fruit a winged nut, nut and lateral wings 15 mm wide.

Remarks. It is difficult to decide, on the basis of fruit and leaflet morphology, when the fossil-species name *P. limburgensis* has to be abandoned in favour of the name of the modern Euxinian-Hyrcanian species, *P. fraxinifolia*. Middle Pleistocene material from Central Italy has previously been referred to as *P. fraxinifolia* (Follieri 1958). Population genetic studies of *P. fraxinifolia* (Maharramova et al. 2018) suggest that the most recent common ancestor of *P. fraxinifolia* dates back to 0.91 Ma (1.94–0.04 Ma 95 % highest posterior density). Within the species, haplotypes of the Colchic-Caucasian region diverged at 0.69 Ma (1.94–0.04 95 % highest posterior density). This suggests that the leaflet and fruit from Oriolo might well represent early members of the modern species.

Family Betulaceae Gray, 1822 nom. cons.

Genus *Alnus* Mill., 1754

Alnus aff. *barbata* C.A.Mey., 1831 (*Alnus* aff. *glutinosa* subsp. *barbata* (C.A.Mey.) Yalt., 1967)

Text-fig. 9h–j

Material. Oriolo MSF 850, 852, 987.

Description. Leaf, seed cone; leaf, simple, petiolate, petiole 5 mm long, lamina broad elliptic, 55 mm long, 45 mm wide, base obtuse to shallowly cordate, secondary venation craspedodromous, basalmost secondaries departing from primary vein at right angle, following secondaries departing at steeper angles, abmedial veins usually departing from lower secondary veins, margin finely dentate; seed cone 15 mm long, 7 mm wide.

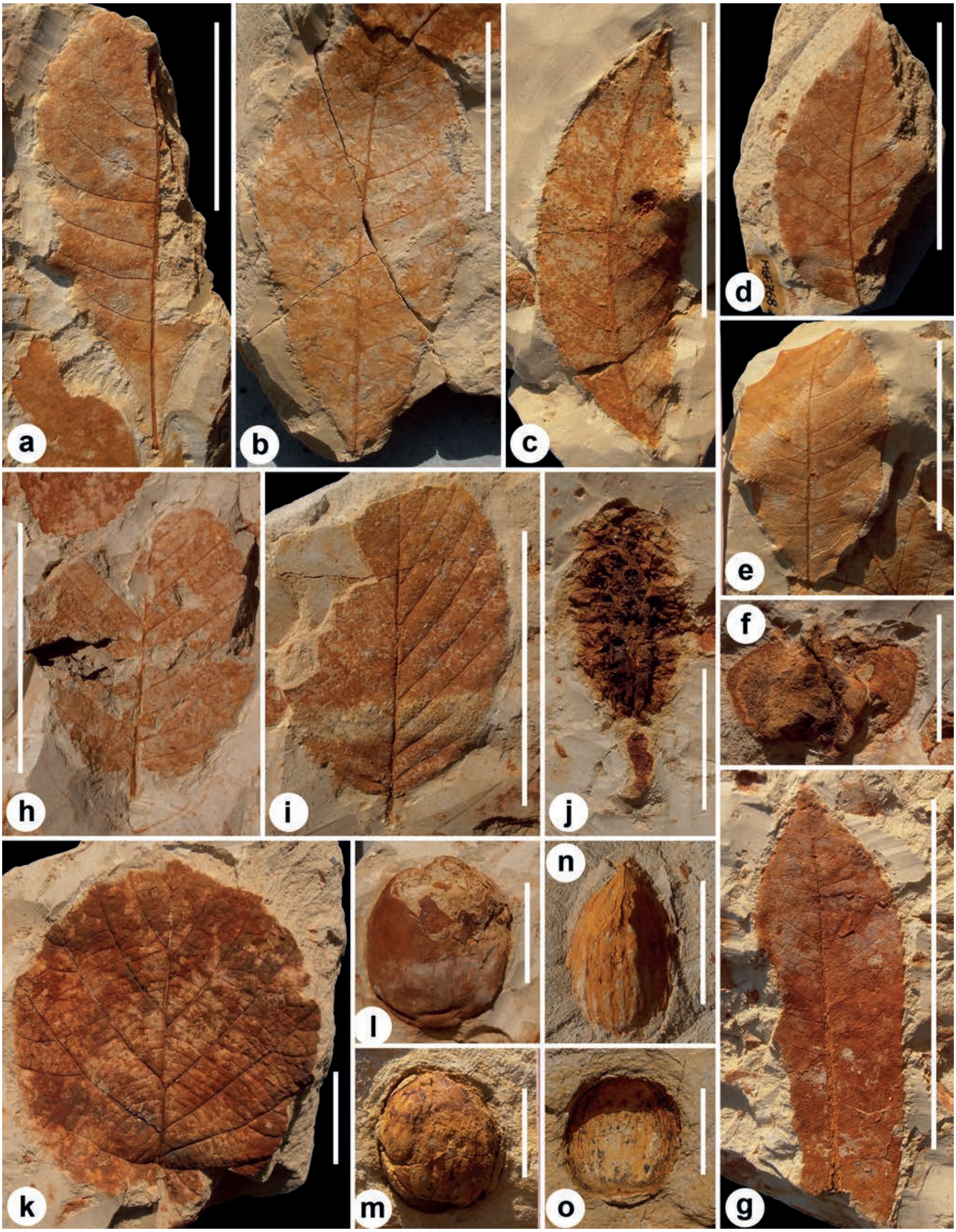
Remarks. The higher number of secondary veins (ca. 10 pairs) and the lamina apex that is not retuse, as in subsp. *glutinosa*, suggest closer affinities with the extant Euxinina-Hyrcanian subsp. *barbata*. Again, the shift from the fossil-species *A. cecropiifolia* (Ettingsh.) W.Berger to the modern *Alnus glutinosa* s.l. is difficult to determine, as the morphology of these two taxa overlaps in the eastern modern range of *A. glutinosa*.

Genus *Carpinus* L., 1753

Carpinus aff. *betulus* L., 1753

Text-fig. 10a, b

Material. Oriolo MSF 640-1, 642, 848, 851, 892, 893, 898, 985.



Text-fig. 9. a–e: *Carya* aff. *minor*. a: Terminal leaflet, Oriolo MSF 755. b: Oriolo MSF 755. c: Oriolo MSF 766. d: Oriolo MSF 768. e: Oriolo MSF 635. f, g: *Pterocarya* aff. *fraxinifolia*. f: Fruit, Oriolo MSF 632. g: Leaflet, Oriolo MSF 632a. h–j: *Alnus* aff. *glutinosa* subsp. *barbata*. h: Oriolo MSF 852. i: Oriolo MSF 850. j: Seed cone, Oriolo MSF 987. k–o: *Corylus* aff. *avellana*. k: Leaf, Oriolo MSF 841. l: Fruit, Oriolo MSF 1001. m: Fruit, Oriolo MSF 1022. n: Fruit, Oriolo MSF 1003. o: Fruit, Oriolo MSF 1022. Scale bars 50 mm (a–e, g–i), 10 mm (f, j–o).

Description. Leaf, fruit; leaf, simple, petiolate, petiole 7 mm, lamina ovate-elliptic, 33 to >60 mm long, 20–50 mm wide, base obtuse, apex acute, 11–12 densely spaced secondary veins, secondary venation craspedodromous, margin finely serrate; fruit subtended by a trilobate bract, central lobe oblong, 24 mm long, 6 mm wide, apex rounded, venation brochidodromous, margin entire, lateral lobes much shorter, 11 mm long.

Remarks. Separate leaves, fruit-bracts and fruits assigned to *C. betulus* commonly occur in Italy since the Late Miocene. However, hundreds of fossil fruits that occur in several Pliocene and Pleistocene sites of Italy (Martinetto 2015) always show a smaller mean size than the extant fruit samples of *C. betulus*, so Martinetto (2015) suggested assigning them to their own subspecies.

***Carpinus* aff. *orientalis* Mill., 1768**

Text-fig. 10c–g

Material. Oriolo MSF 639, 894, 896, 899, 900, 901, 902, 903, 904, 905, 906, 907, 985, 986.

Description. Leaf, fruit; leaf simple, petiolate, lamina ovate elliptic, 20–36 mm long, 12–21 mm wide, base acute, apex acute rounded, secondary venation craspedodromous, secondary veins densely spaced, regular, 11 pairs, margin serrate, teeth with convex basal and convex, concave or straight apical side; fruit subtended by a flabellate bract, shortly petiolate, 15 mm long, 10 mm wide, lamina obovate-rhombic, asymmetric, venation craspedodromous, margin dentate.

Remarks. Such leaves and fruits are common in Pliocene and Pleistocene plant assemblages across the Mediterranean region. Very similar fruits are known from Bernasso (France; Leroy and Roiron 1996) and Crespià (northern Spain; Roiron 1983).

Genus *Corylus* L., 1753

***Corylus* aff. *avellana* L., 1753**

Text-fig. 9k–o

Material. Oriolo MSF 639, 643, 644, 653, 838, 840, 841, 1000, 1001, 1003, 1022.

Description. Leaf, fruit; leaf, simple, petiolate, lamina broad elliptic to round, 37–50 mm long, 34–43 mm wide, base cordate, apex obtuse, secondary venation craspedodromous, secondary veins with prominent abmedial veins, margin shallowly lobed, serrate; secondary, abmedial and small higher order veins departing from tertiary veins entering teeth, teeth with short convex basal and apical side; fruit is a nut, 10–15 mm long, 10 mm wide.

Remarks. The small size of the leaves may indicate that *Corylus* was part of the drier hinterland, possibly of a Šibljak type (deciduous scrub in submediterranean vegetation of southeastern Europe; Adamovic 1909). Specimen MSF 644 is on a slab with a leaf of *Berberis*. Fossil fruits of *C. avellana* occur in several Pliocene and Pleistocene sites of Italy (Martinetto 2015).

Family Coriariaceae DC., 1824 nom. cons.

Genus *Coriaria* L., 1753

***Coriaria* aff. *myrtifolia* L., 1753**

Text-fig. 11a, b

Material. Oriolo, MSF 647-1, 677, 704, 706, 707, 708, 709, 709-1, 711-1, 713.

Description. Leaf, simple, subsessile, lamina elliptic, broad lanceolate, 23–39 mm long, 9–17 mm wide, base acute to obtuse, apex acute, primary venation acrodromous, three primary veins, occasionally an additional lateral vein departing from a lateral primary vein, giving lamina an asymmetrical appearance (cf. Text-fig. 11b, right half of the lamina), secondary veins connecting central and lateral primary veins departing from central vein at steep angles, margin entire.

Remarks. Leaves of this type are found, although rare, in the Pliocene of the Piedmont; more frequent are the seeds of this genus, also present in the Pleistocene of Stirone (Gregor 1986). The latter are not related to *C. myrtifolia* of the Mediterranean region, but to Asian species.

Family Salicaceae Mirb., 1815 nom. cons.

Genus *Populus* L., 1753

***Populus* aff. *alba* L., 1753**

Text-fig. 11c, d

Material. Oriolo MSF 647, 649, 675, 711, 714, 725, 744-1, 745, 746, 747, 748, 749, 750, 752, 753, 754.

Description. Leaf, simple, petiolate, petiole >18 mm, lamina elliptic to rhombic, shallowly lobed, 33–50 mm long, 25–53 mm wide, base obtuse to bluntly acute, apex acute rounded, venation pinnate, basal pair of secondary veins usually more prominent than following secondaries, 3–5 pairs of secondary veins, secondary veins with prominent abmedial veins, of which some enter rounded teeth.

Remarks. The leaf morphological variability encountered in the fossil leaves is similar to the variability found in the modern species *P. alba* L. The ecology of this taxon comprises riparian stands and disturbed open stands.

***Populus* aff. *nigra* L., 1753**

Text-fig. 11f–h

Material. Oriolo MSF 629, 735, 736, 737, 738, 739, 740, 741, 742.

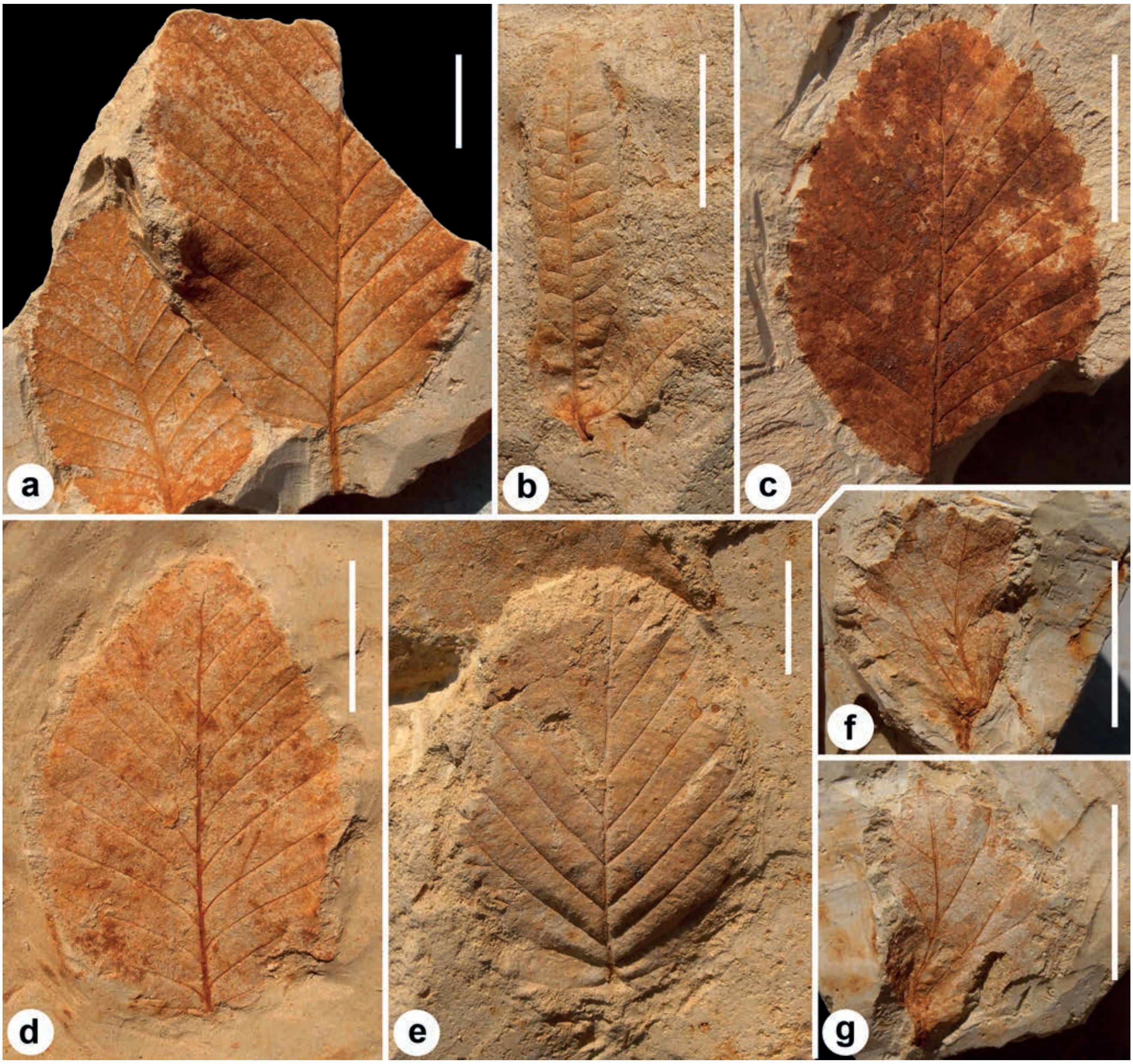
Description. Leaf, simple, petiolate, petiole >15 mm long, lamina deltoid, 36–77 mm long, 27–74 mm wide, base truncate, truncate-rounded or cordate, apex attenuate, number of secondary veins 5–7, occasionally basal secondary veins with prominent abmedial veins, margin finely crenate to prominently dentate, teeth inconspicuous or prominent with sigmoid basal side and straight or convex apical side.

Remarks. Similar leaves were reported from Calabrian deposits of northeastern Spain (Roiron 1983) and from the Pianico-Sèllere lacustrine deposits (Martinetto 2009).

***Populus* aff. *tremula* L., 1753**

Text-fig. 11e

Material. Oriolo MSF 749.



Text-fig. 10. a, b: *Carpinus* aff. *betulus*. a: Leaves, Oriolo MSF 640. b: Fruit, Oriolo MSF 985. c–g: *Carpinus* aff. *orientalis*. c: Oriolo MSF 895. d: Oriolo MSF 899. e: Oriolo MSF 848. f: Fruit, Oriolo MSF 986. g: Fruit, Oriolo MSF 985. Scale bars 10 mm (a–g).

Description. Leaf, simple, petiolate, petiole 30 mm long, lamina round, >33 mm long, >30 mm wide, base obtuse, 3 pairs of secondary veins, basal pair departing from leaf base, secondary veins and abmedial veins entering blunt, coarse teeth.

Remarks. Such leaves are also known from latest Pliocene (Reuverian) strata of Europe (e.g., Laurent and Marty 1923), and from Early and Middle Pleistocene strata of the Mediterranean region (Leroy and Roiron 1996, Martinetto 2009).

Genus *Salix* L., 1753 nom. cons.

Salix aff. *caprea* L., 1753

Text-fig. 12a, b

Material. Oriolo MSF 857, 860.

Description. Leaf, simple, petiolate, petiole 4–5 mm long, stout, thickened at proximal end, lamina elliptic, 42–44 mm long, 19 mm wide, base acute, apex acute, secondary venation eucamptodromous, intersecondary veins commonly present.

Remarks. Two leaves from Oriolo resemble the modern *S. caprea*, or a hybrid with participation of *S. caprea*, a widespread European riparian element.

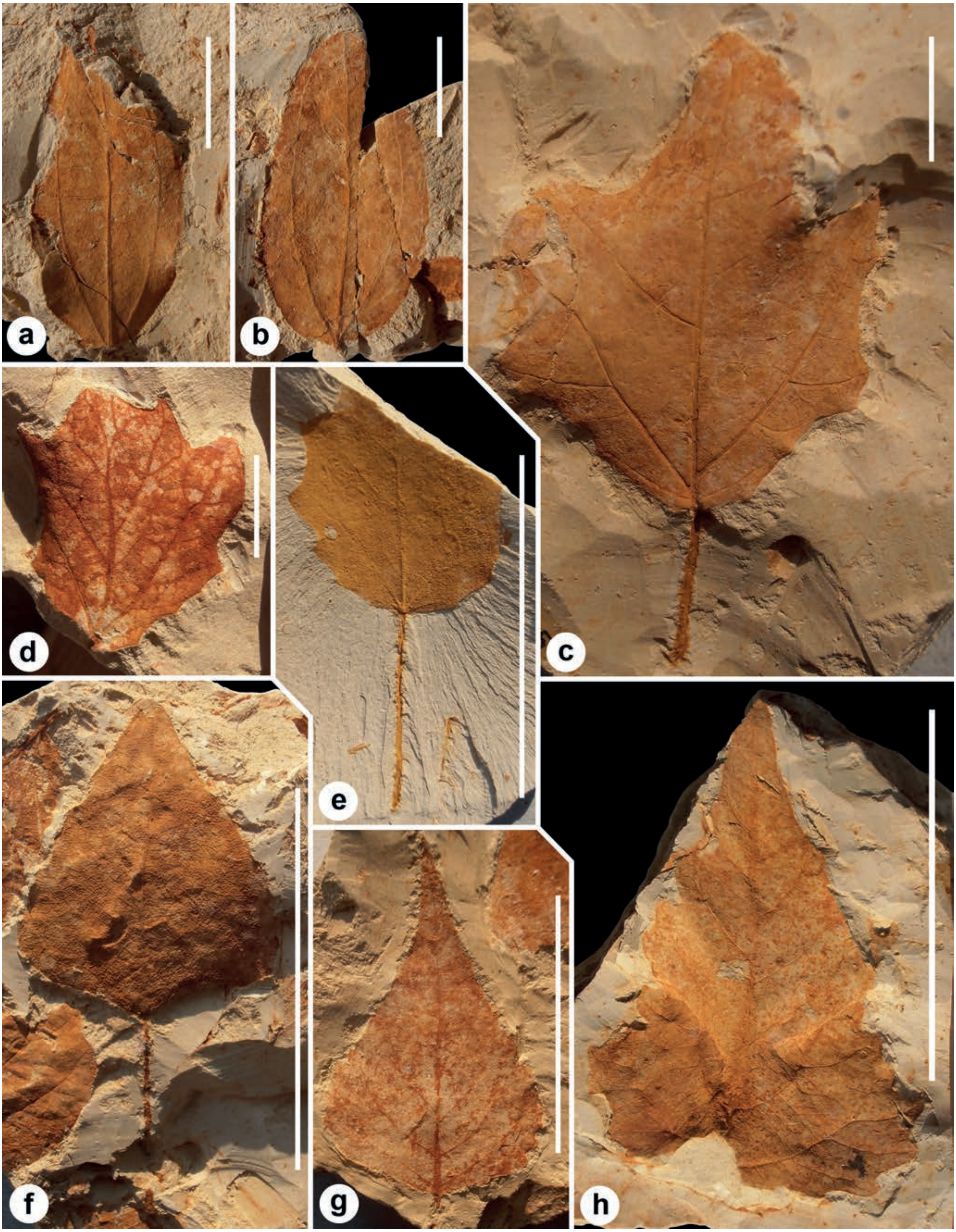
Salix aff. *alba* L., 1753

Text-fig. 12c–d

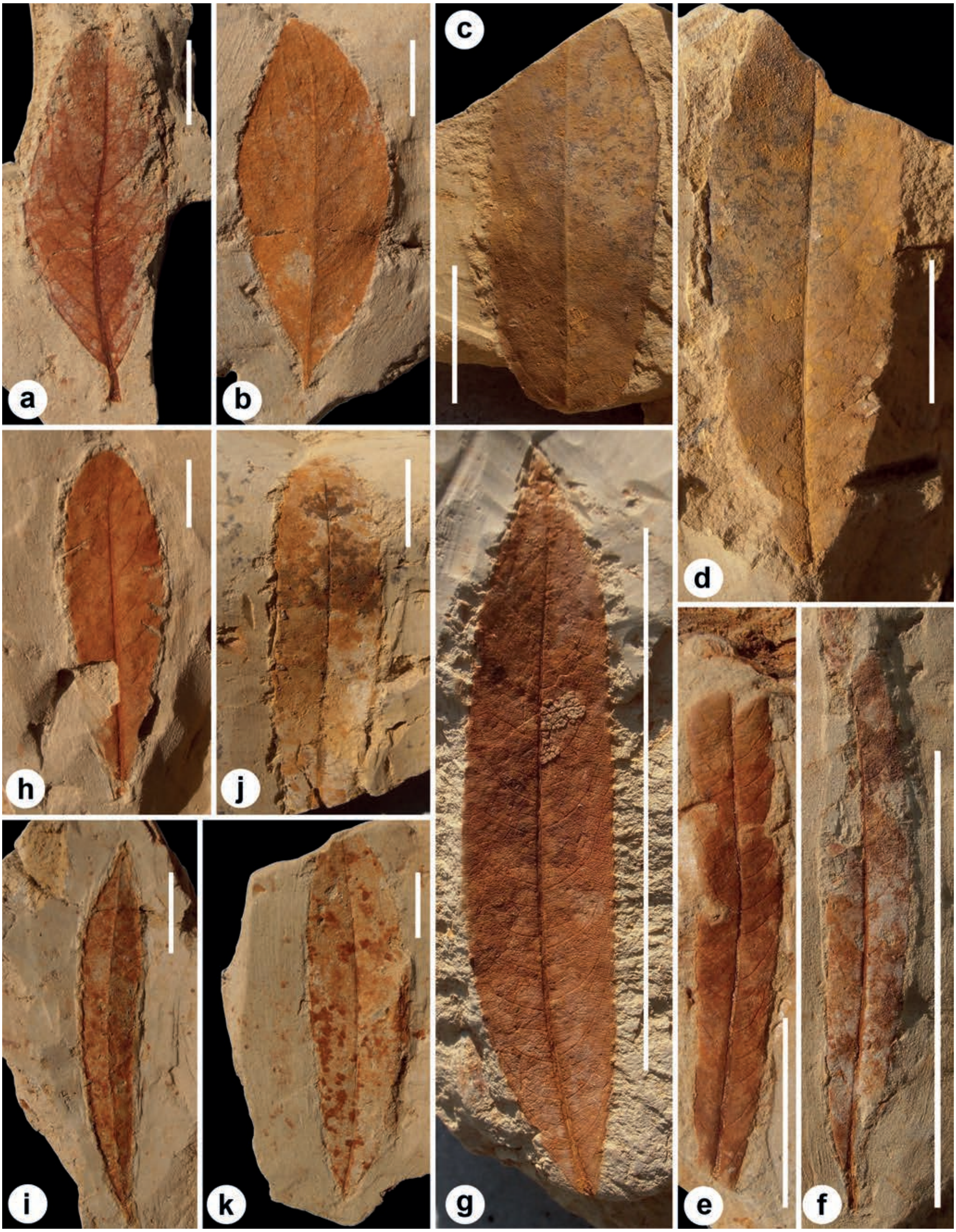
Material. Oriolo MSF 851, 851-1.

Description. Leaf, simple, lamina oblanceolate, >40 mm long, 14 mm wide, base acute, secondary venation eucamptodromous, small veins departing from secondary veins enter small, glandular teeth.

Remarks. Based on the course of the secondary veins, the lamina shape and the rare presence of intersecondary



Text-fig. 11. a, b: *Coriaria* aff. *myrtifolia*. a: Oriolo MSF 647. b: Oriolo MSF 704. c, d: *Populus* aff. *alba*. c: Oriolo MSF 745. d: Oriolo MSF 725. e: *Populus* aff. *tremula* Oriolo MSF 749. f–h: *Populus* aff. *nigra*. f: Oriolo MSF 737. g: Oriolo MSF 742. h: Oriolo MSF 738. Scale bars 10 mm (a–d), 50 mm (e–h).



Text-fig. 12. a, b: *Salix* aff. *caprea*. a: Oriolo MSF 857. b: Oriolo MSF 860. c, d: *Salix* aff. *alba*. c: Oriolo MSF 854. d: Oriolo MSF 854. e, f: *Salix* aff. *viminalis* vel *eleagnos*. e: Oriolo MSF 803. f: Oriolo MSF 801. g: *Salix* aff. *triandra* Oriolo MSF 626. h–k: *Salix* spp. div. indet. h: Oriolo MSF 865. i: Oriolo MSF 807. j: Oriolo MSF 804. k: Oriolo MSF 802. Scale bars 10 mm (a–e, h, i–k), 50 mm (f, g).

veins, the two leaf fragments from Oriolo match the modern species *S. alba*, or a hybrid with participation of this species.

Salix aff. *viminalis* L., 1753 vel. *S. eleagnos* Scop., 1771

Text-fig. 12e, f

Material. Oriolo MSF 801, 803.

Description. Leaf, simple, petiolate, lamina lanceolate, >65 mm long, 5–11 mm wide, base and apex narrow acute, secondary venation brochidodromous, secondary veins departing from primary vein at steep angles, 0–2 intersecondary veins between two consecutive secondary veins.

Remarks. Determination of *Salix* spp. based on leaf morphology is difficult because extant species frequently hybridise with other species, and the same can be expected for Pleistocene taxa. The leaves from Oriolo most probably belong to either *S. viminalis* or *S. eleagnos*. Pure *S. eleagnos* usually has narrower leaves with the leaf base tapering into the petiole, but various hybrids with other species match the fossil leaves. *Salix viminalis* is a typical element of riparian scrub (together with *S. triandra* L., see below), whereas *S. eleagnos* may be a riparian element or part of xeric alluvial vegetation (Ellenberg 1996, Schratt-Ehrendorfer 2000).

Salix aff. *triandra* L., 1753

Text-fig. 12g

Material. Oriolo MSF 626.

Description. Leaf, simple, lamina broad lanceolate, ca. 700 mm long, 15 mm wide, base acute, apex acute, secondary venation brochidodromous, secondary veins departing from primary vein at low angle and then bending upwards, typically two intersecondary veins between two consecutive secondary veins, intersecondaries nearly perpendicular to primary vein or departing at low angles, small veins departing from the looping secondary veins enter teeth, teeth small, glandular, regularly and densely spaced.

Remarks. This well-preserved leaf from Oriolo is virtually identical to modern leaves of *S. triandra* (verified by field observations [TD] and comparison with numerous herbarium material). Among other species, hybrids between *S. caprea* × *S. viminalis* sometimes look quite similar to the leaf from Oriolo, but differ in the crenulation of the leaf margin. *Salix triandra* has also been reported from the Reuverian (latest Pliocene) of Central Europe (Laurent and Marty 1923).

Salix indet. div. spp.

Text-fig. 12h–k

Material. Oriolo MSF 802, 804, 807, 865.

Remarks. We were unable to attribute these leaves to any particular modern or fossil species of *Salix*.

Family Sapindaceae Juss., 1789 nom. cons.

Genus *Acer* L., 1753
Section *Acer* sect. *Palmata* Pax, 1885

Acer aemilianum Sordelli, 1896

Text-fig. 13a, d–g

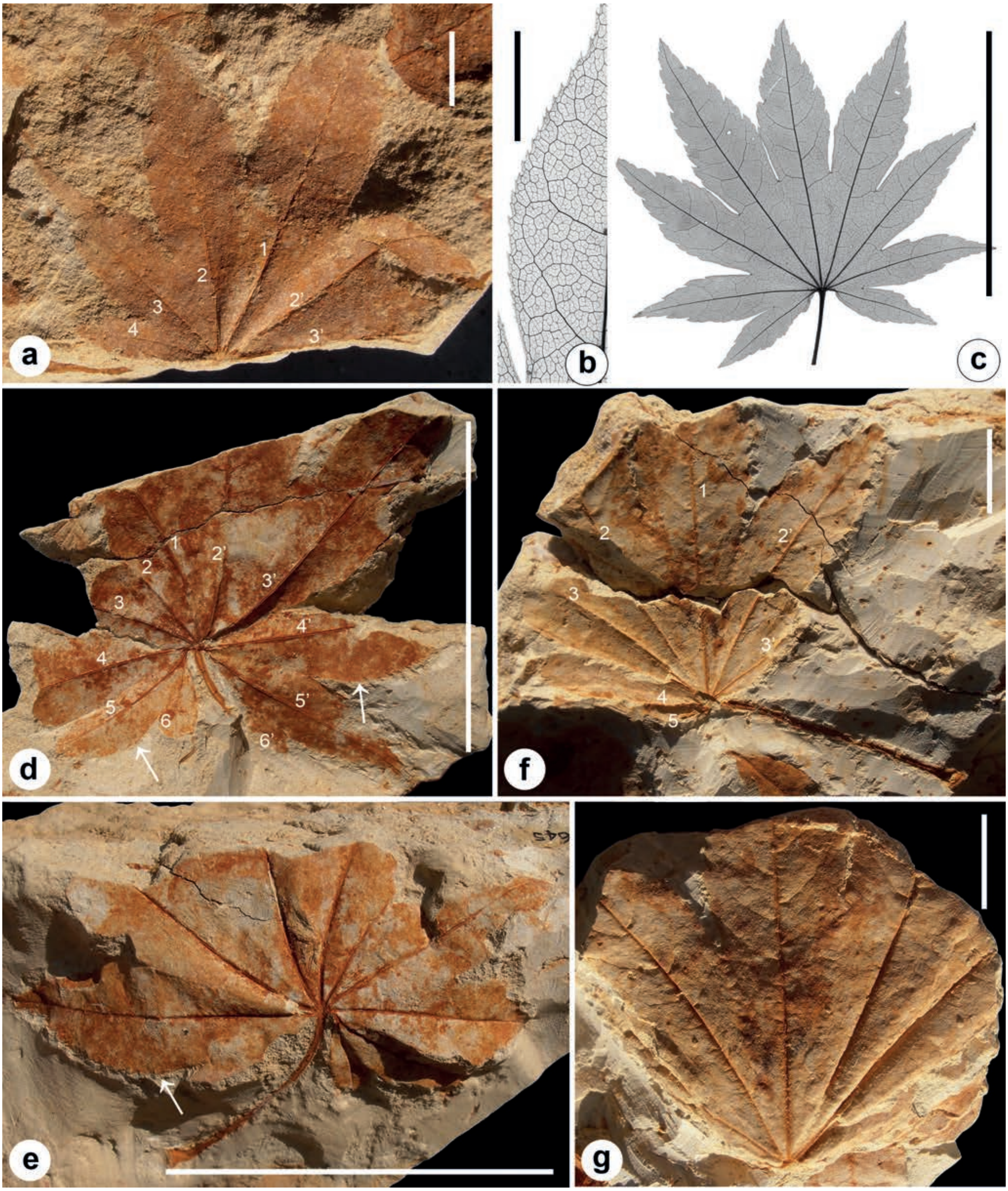
1896 *Acer aemilianum* Sordelli, p. 156, pl. 30, fig. 8.
1988 *Acer polymorphum* Siebold et Zucc. *pliocenica* Saporta; Jorda et al., p. 54, pl. 1, figs 10–13.

Material. Oriolo MSF 645, 645-1, 660, 660-1, 661, 661-1.

Description. Leaf, petiolate, petiole ca. 3 cm long, with widened proximal part, lamina up to 52 mm long, 71 mm wide, primary venation palmate, number of primary veins 7–9 (–11), number of lobes 7–9 (–11), lobe apex attenuate, secondary venation craspedodromous, margin finely serrate or double-serrate along the upper 2/3 or 4/5 of the free lobes.

Remarks. The leaf remains from Oriolo clearly belong to *A. aemilianum* described by Sordelli (1896) from strata referred to as “Pliocene” (but possibly Early Pleistocene) in the surroundings of Fidenza (Emilia-Romagna). Leaves belonging to *Acer* section *Palmata* (Van Gelderen et al. 1994, Grimm et al. 2006, Renner et al. 2008; including close to 50 modern species) from Miocene and Pliocene strata of western Eurasia have been referred to as *Acer vindobonensis* (Ettingsh.) Berger, 1955 (Ettingshausen 1851, Berger 1955) and *A. sanctae-crucis* Stur, 1867 (Stur 1867, Knobloch 1998; Tab. 1). *Acer vindobonensis* was based on a leaf fragment from Late Miocene strata of Austria (Ettingshausen 1851; as *Sterculia vindobonensis* Ettingsh.) and described as palmate leaf with five entire margined lobes. *Acer sanctae-crucis*, described from Middle Miocene strata of Slovakia, has 7-lobed leaves, the lobes being elongate triangular with finely serrate margin. Subsequent authors either treated *A. sanctae-crucis* as synonym of *A. vindobonensis* (e.g., Menzel 1906, Zastawniak 1972, Kovar-Eder 1988, Kovar-Eder et al. 1996, Walther and Zastawniak 2005) or as distinct species (e.g., Berger 1955, Iljinskaya 1968, Knobloch 1998). In addition, two fossil-species of sect. *Palmata* originally described from East Asia were reported from Europe. Of these, *A. protojaponicum* Tanai et Onoe, 1959, is distinct by its shallowly lobed leaves, whereas *A. nordenskioeldi* Nath., 1883, reported by Berger (1955, 1957), resembles *A. vindobonensis* (Tab. 1). Further, Saporta (1873, 1879; see also Andreanszky 1959) used the name of a modern East Asian species for Pliocene (Cantal, France) maple leaves, *A. polymorphum* Siebold et Zucc., 1845 (synonym of *A. palmatum* Thunb., 1784), and added *pliocenicum* without indicating a taxonomic rank. Similarly, Menzel (1906) used the modern name *A. polymorphum* and added *miocenicum*.

While it is not the aim of this paper to revise western Eurasian *Acer* remains of sect. *Palmata*, we note that most of the taxonomic disagreement between previous authors discussing possible differences or conspecifity between *A. vindobonensis* and *A. sanctae-crucis* may be due to the fact that all previous authors compared these fossil-taxa (with the exception of the distinct *A. protojaponicum*) to a single modern species, *A. palmatum* (*A. polymorphum*). One exception is the work by Stur (1867), who indicated similarities with various species of sect. *Palmata*. Table 1 summarizes leaf characteristics of previously described fossil members of sect. *Palmata* from western Eurasia and lists similarities to modern species. This is highly informative



Text-fig. 13. **a, d–g:** ***Acer aemilianum*****. b, c:** ***Acer palmatum*** **and** ***A. sieboldianum*** **modern leaves (NMNS Cleared Leaf Database). a: Oriolo MSF 661, 7-lobed leaf. b: Specimen U 1049, lobe detail showing finely serrate leaf margin. c: Specimen T 0246, 9-lobed leaf with coarsely serrate leaf margin. d: Oriolo MSF 645-1, 9-lobed leaf with two small additional lobes. e: Oriolo MSF 645. f: Oriolo MSF 660, 9-lobed specimen. g: Oriolo MSF 660-1. White arrows indicate position along lamina lobes where marginal serration starts. Scale bars 10 mm (a–c, f, g), 50 mm (d, e).**

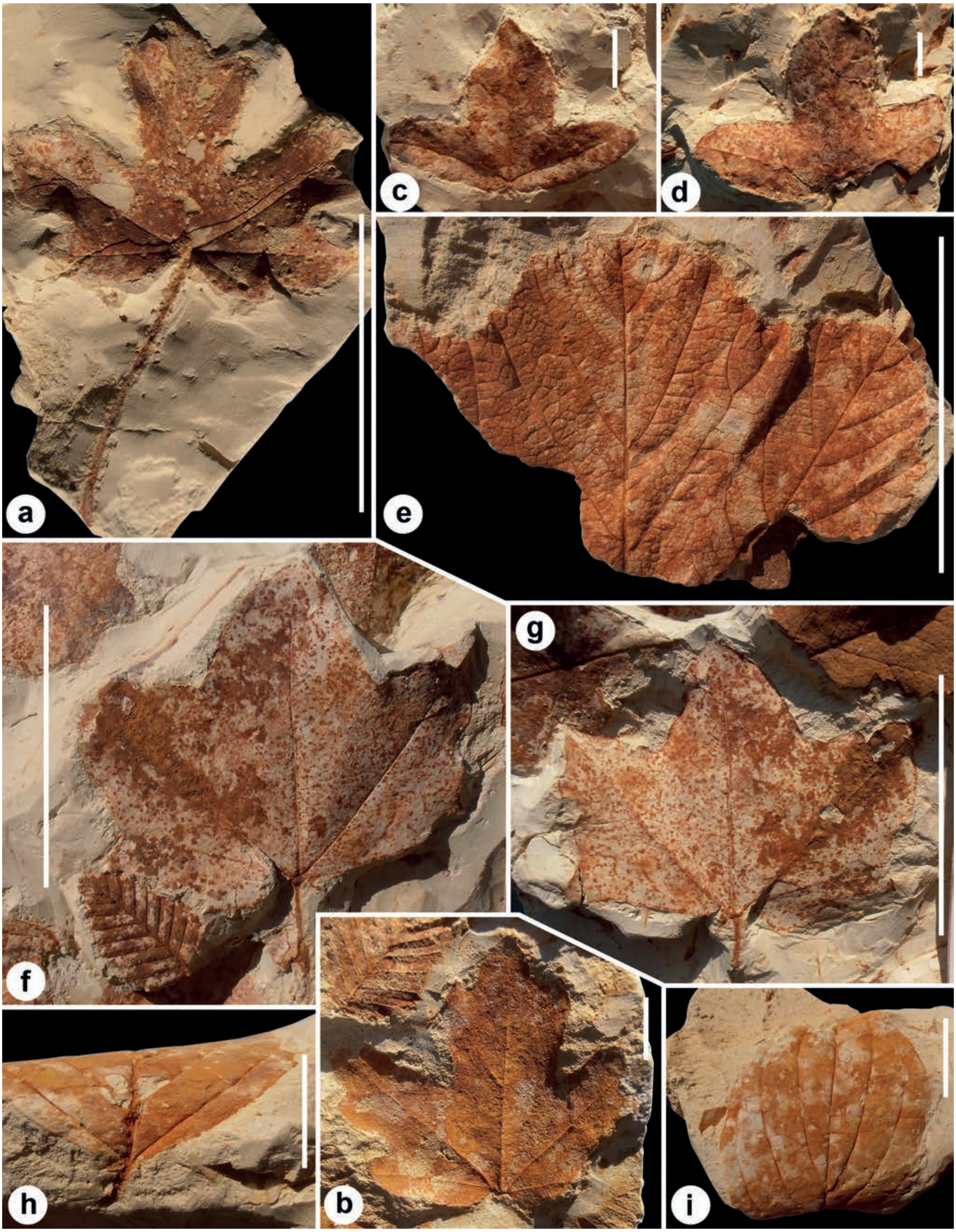
in the case of *A. vindobonense*, for which a subentire margin has been refuted (e.g., Walther and Zastawniak 2005), perhaps simply because such a margin is not found in the modern *A. palmatum*. However, there are other members of sect. *Palmata* that can be compared with the subentire to remotely serrate leaves of *A. vindobonensis*, such as *Acer sinense* (Tab. 1), which produces leaves nearly identical to *A. vindobonensis*. Thus, considering a broader set of modern species as possible modern analogues of fossil-taxa, we suggest that a thorough revision of both western Eurasian

Table 1. Comparative morphology of fossil-taxa of *Acer* sect. *Palmata*. [a]Berger 1955, [b]Berger 1955, 1957, [c]Givulescu and Ghiurca 1969, [d]Leroy and Roiron 1996, [e]Girard et al. 2019, [f]Tanai 1976, 1983, [g]Rayushkina 1979. Notes: Saporta (1873, 1879) assigned leaves from Pliocene strata of France (Cantal) to *Acer polymorphum* Siebold et Zucc., 1845 *pliocenicum* Saporta, 1873. These leaves are 7–9-lobed, have remotely dentate lobes, teeth distinct and simple; similar to *A. sinense* var. *longilobum* W.P. Fang, 1939. Menzel (1906) assigned leaves from the Late Miocene of Germany to *Acer polymorphum* Siebold et Zucc., 1845 *miocenicum* Menzel, 1906. These leaves are 5-lobed with two basal additional lobes and are remotely dentate; they would need to be re-examined for taxonomic assessment. Barrón and Diéguez (2001) described a leaf from Early Miocene deposits of Spain as *A. vindobonensis*. Although this leaf differs markedly from *A. vindobonense* by the rhombic shape of the lobes, it might belong to sect. *Palmata*.

	Western Eurasia Records of *Acer* sect. *Palmata*				
Taxon	*Acer vindobonensis* (Ettingsh.) Berger, 1955	*A. sanctae-crucis* Stur, 1867	*A. nordenskioeldi* Nath., 1883	***A. aemilianum*** **Sordelli, 1896**	*A. protojaponicum* Tanai et Onoe, 1959
Age	Middle Miocene to Pliocene	Middle Miocene, Pliocene	Late Miocene	Piacenzian to latest Early Pleistocene	Late Miocene, Early Pleistocene
Morphology:					
No. of lobes	5 lobed	7 lobed	7 lobed[b]	9 lobed, 7–11 lobed	9 lobed
Margin	Entire; weakly serrate[a]	Finely serrate	Subentire, remotely serrate[b]	Finely serrate upper 2/3 of lobe	Serrate
Lobation	Deeply disected	Deeply disected	Deeply disected	Deeply disected	Shallowly disected
Geography:	Austria, Poland, Romania, Czech Republic, Hungary	Slovakia, Germany, ?Romania, ?Ukraine	Austria, Italy	Italy, France	France, Romania[c, d, e]
Remarks	Similar to *Acer sinense* Pax, 1897 [*A campbellii* subsp. *sinense* (Pax) P.C.de Jong, 1994].	Similar to *Acer* sect. *Palmata*, incl. *A. palmatum* Thunb. ex Murray, 1784 subsp. *amoenum* (Carrière) H.Hara, 1954, *A. ceriferum* Rehder, 1911, but not *A. sinense.*	Similar to *Acer sinense* Pax, 1897 [*A. campbellii* subsp. *sinense* (Pax) P.C.de Jong, 1994]. Revision needed: These records may belong to *A. vindobonensis*.	Similar to *Acer* sect. *Palmata*, e.g. *Acer sieboldianum* Miq., 1865. Among fossil-taxa, leaves with 9 or more lobes are otherwise only seen in *A. polymorphum pliocenicum* (Saporta, 1873, 1879).	Similar to *Acer japonicum* Thunb. ex Murray, 1784.

	East Asian Records of *Acer* sect. *Palmata*			
Taxon	*A. nordenskioeldi* Nath., 1883	*A. protomatsumurae* Tanai, 1983	*A. protojaponicum* Tanai et Onoe, 1959	? *A. palmatum* var. *nordenskioeldi* (Nath.) Schmalh., 1887
Age	Early Miocene to Pliocene	Miocene	Early Miocene to Pliocene	Late Oligocene to Miocene
Morphology:				
No. of lobes	7 lobed, 5–7 lobed[f]	7–9 lobed	9–11 lobed	7 lobed
Margin	Dentate, finely to coarsely serrate[p]	Coarsely double-serrate	Double serrate	Subentire
Lobation	Deeply disected	Deeply disected	Shallowly disected	Deeply disected
Geography:	Japan, North Korea, China, Russian Far East	South Korea	Japan, North Korea	South Altai[g]
Remarks	Similar to *Acer sinense* Pax, 1897 [*A. campbellii* subsp. *sinense* (Pax) P.C.de Jong, 1994].	Similar to *A. palmatum* subsp. *matsumurae* Koidz., 1911.	Similar to *Acer japonicum* Thunb. ex Murray, 1784.	Similar to *Acer sinense* Pax, 1897 [*A. campbellii* subsp. *sinense* (Pax) P.C.de Jong, 1994].

Underlined character states and countries refer to original descriptions and from where the fossil-species were described.



Text-fig. 14. a, b: *Acer* aff. *campestre*. a: Oriolo MSF 664. b: Oriolo MSF 666. c, d: *Acer* aff. *monspessulanum*. c: Oriolo MSF 641. d: Oriolo MSF 662. e: *Acer* aff. *opulus* subsp. *obtusatum* Oriolo MSF 669. f, g: *Acer* aff. *cappadocicum* subsp. *lobelii*. f: Oriolo MSF 675. g: Oriolo MSF 631. h, i: *Cornus* sp. Oriolo MSF 655, two views of a strongly folded leaf impression. Scale bars 50 mm (a, e–g), 10 mm (b–d, h, i).

and East Asian fossil-taxa of sect. *Palmata* is needed (T. Denk, in preparation).

The specimens from Oriolo differ from previously described fossil-species of *Acer* section *Palmata* by the lobe margin, which is serrate along most of the lamina, and by the variable and high number of lobes. According to Tanai (1983), lobe number is taxonomically informative in extant and fossil species of *A.* sect. *Palmata*. For example, in *A. nordenskioeldi* from East Asia, a great number of examined specimens consistently had 5–7 lobes. Among modern members of sect. *Palmata*, *A. sieboldianum* produces leaves that match *A. aemilianum* by its number of lobes and the serrate margin.

During the Middle Miocene to Pliocene, representatives of sect. *Palmata* were rare elements of several floras in western Eurasia (Menzel 1906, Knobloch 1969, Kovar-Eder 1988).

Acer sanctae-crucis s. str. might have had its last occurrence in the Pliocene flora of Willershausen, and *Acer protojaponicum* in the Early Pleistocene of France (ca. 2 Ma; Bernasso; Leroy and Roiron 1996, Girard et al. 2019; Tab. 1). The new record from Oriolo extends the fossil record of sect. *Palmata* in Europe into the Pleistocene, ca. 0.84 Ma, before it was extirpated from Europe and Asia Minor.

A time-calibrated molecular phylogeny of maples suggested that the Asian members of the *Palmata* clade (Grimm et al. 2006) diverged from the single North American member during the Middle Miocene (Renner et al. 2008). The fossil record further provides evidence that the section was fairly diverse in western Eurasia before it was extirpated in the Pleistocene.

Section *Acer* sect. *Platanoidea* Pax, 1885

Acer aff. *campestre* L., 1753

Text-fig. 14a, b

Material. Oriolo MSF 646, 664, 665, 666.

Description. Leaf, palmate, petiolate, petiole up to 50 mm, distal part widened, lamina 5-lobed, 45–53 mm long, 50–62 mm wide, lobes oblong to rhombic, with few – usually one on each side of lobe – coarse, blunt teeth in upper part.

Remarks. The fossil-taxon *A. subcampestre* occurred in Central Europe at around the Middle Miocene (Ströbitzer-Hermann and Kovar-Eder 2002), and was a typical accessory element of riparian and mesophytic forest during the middle and Late Miocene. In analogy with the ecology of the modern *A. campestre*, Güner et al. (2017) suggested that the fossil-species could also have been part from drier, more open sites, in addition to riparian and mesophytic lowland forests. Adamovic (1909) mentions *A. campestre* as an element of Šibljak vegetation in the Balkans.

Acer aff. *lobelii* Ten., 1819 (*Acer* aff. *cappadocicum* subsp. *lobelii* (Ten.) A.E.Murray, 1982)

Text-fig. 14f, g

Material. Oriolo MSF 675, 631, n.n.

Description. Leaf, simple, petiolate, petiole >20 mm long, lamina rhombic, 5-lobed, with three main and two smaller lobes, lamina 55–60 mm long, 70–75 mm wide, base truncate-shallowly cordate, lobes triangular, with a blunt acuminate apex, margin entire or with few hook-like teeth approaching small lobes, primary venation actinodromous, 5 primary veins, secondary venation brochidodromous.

Remarks. *Acer lobelii* belongs to a clade of maples (several subspp. of *A. cappadocicum* ranging from Italy to Asia Minor, the Himalayas and East Asia). Within western Eurasia, modern species (subspecies) of *A. cappadocicum* is thought to have appeared in the Pleistocene, based on the inferred divergence time for *A. campestre* and *A. platanoides* L., 1753 (Renner et al. 2008).

Section *Acer* sect. *Acer*

Acer aff. *monspessulanum* L., 1753

Text-fig. 14c, d

Material. Oriolo MSF 662, 641.

Description. Leaf, simple, petiolate, 30–45 mm long, 40–60 mm wide, trilobed, lobes oblong triangular, lateral primary veins departing from central vein at wide angles, secondary venation brochidodromous, margin entire.

Remarks. The lineage leading to *A. monspessulanum* might date back to the middle and Late Miocene, represented by the fossil-species *A. pseudomonspessulanum* Unger, 1847 (Ströbitzer-Herrmann and Kovar-Eder 2002). This is in accordance with a dated phylogeny for *Acer* (Renner et al. 2008), which suggests differentiation in western Eurasian members of sect. *Acer* in the Late Miocene. The origin of the modern species *A. monspessulanum* might be of Pleistocene age, based on divergence times inferred for closely related western Eurasian species pairs of *Acer*.

Acer aff. *opalus* subsp. *obtusatum* (Waldst. et Kit. ex Willd.) Gams, 1925

Text-fig. 14e

Material. Oriolo MSF 669.

Description. Leaf, simple, lamina fragmented, 80 mm wide, shallowly 3-lobed, lobes with broad obtuse apex, margin bluntly serrate.

Remarks. The species *A. obtusatum* Waldst. et Kit. ex Willd., 1806, is commonly treated as a subspecies of *A. opalus* Mill., 1768. Similar leaf remains were referred to as *Acer* aff. *opalus* Mill., 1768 *fossilis* from Pliocene strata of Willershausen, Germany (Knobloch 1998). During the Pleistocene, leaves resembling *A. obtusatum* became more common (e.g., Roiron 1983, northeastern Spain; Leroy and Roiron 1996, France). The Middle Pleistocene site of Pianico in the Southern Alps yielded several leaves (*Acer* cf. *opalus*; Martinetto 2009), whose more prominent lobes with acute apex would point to *A. opalus* subsp. *opalus*.

Family Tiliaceae Juss., 1789 nom. cons.

Genus *Tilia* L., 1753

Tilia sp.

Text-fig. 15a–c

Material. Oriolo MSF 674, 679, 908, n.n.

Description. Leaf, bract; leaf simple, lamina broad ovate, 56–60 mm long, 50–66 mm wide, apex

Text-fig. 15. a–c: *Tilia* sp. a: Oriolo MSF 679. b: Oriolo MSF n.n., fruiting bract. c: Oriolo MSF 908. d: *Fraxinus* aff. *angustifolia* subsp. *oxycarpa* Oriolo MSF 782. e–i: *Hedera* aff. *helix*. Polymorphic leaves. e: Oriolo MSF 628. f: Oriolo MSF 650. g: Oriolo MSF 797. h: Oriolo MSF 799. i: Oriolo MSF 796. Scale bars 50 mm (a, c–e), 10 mm (b, f–i).

acute, venation pinnate, compound agrophic, basal pair of secondary veins with several prominent abmedial veins, basal abmedial veins with a series of further abmedial veins, secondary venation craspedodromous, margin serrate; bract >27 mm long, 9 mm wide, midvein branching 17 mm below apex.

Remarks. *Tilia* was likely part of well-drained lowland mixed forest.

Family Cornaceae Bercht. et J.Presl, 1825 nom. cons.

Genus *Cornus* L., 1753

Cornus sp.

Text-fig. 14h, i

Material. Oriolo MSF 655.

Description. Leaf, simple, petiolate, lamina broad elliptic, ca. 40 mm long, 28 mm wide, secondary venation distinctly eucamptodromous, three pairs of basal veins originating in lower third of lamina and curving steeply upwards, approaching the entire leaf margin.

Remarks. *Cornus* may have been an element of riparian vegetation, forest edges, and Šibljak.

Family Oleaceae Hoffmanns. et Link, 1809

Genus *Fraxinus* L., 1753

Fraxinus aff. *angustifolia* subsp. *oxycarpa* (Willd.) Franco et Rocha Afonso, 1971

Text-fig. 15d

Material. Oriolo MSF 782.

Description. Leaflet, lamina elliptic, 65 mm long, 20 mm wide, base acute decurrent, secondary venation brochidodromous, small veins departing from the looping secondary vein enter into teeth, teeth widely spaced, with long apical and short basal side, tooth apex possibly glandular.

Remarks. The single specimen from Oriolo is virtually identical to modern leaflets of *F. angustifolia* subsp. *oxycarpa*.

Family Araliaceae Juss., 1789 nom. cons.

Genus *Hedera* L., 1753

Hedera aff. *helix* L., 1753

Text-fig. 15e–i

Material. Oriolo MSF 628, 628-1, 650, 796, 797, 798, 799, 800.

Description. Leaf, simple, polymorphic, lamina cordate, roundish, rhombic or inverted trapezoid, 22–79 mm long, 18–52 mm wide, venation campylodromous, pinnate, or actinodromous, margin entire.

Remarks. Vegetative creeping stems of *Hedera* produce leaves that differ markedly from those on flowering axes. The ovate rhombic leaf in Text-fig. 15e might be a leaf from a flowering stem.

Angiospermae incertae sedis

App. II

Leaf morphotype 1

App. II, Text-fig. A3a

Material. Tebano SG 049.

Description. Leaf, petiolate, lamina ovate, ca. 50 mm long, 25 mm wide, base obtuse asymmetrical, apex bluntly acuminate, secondary venation eucamptodromous, occasionally branching, spacing between secondary veins narrow at basal and apical portions of lamina, much wider in middle part.

Leaf morphotype 2

App. II, Text-fig. A3b

Material. Oriolo MSF 631.

Description. Asymmetrical leaf or leaflet, 5 × 4 cm.

Leaf morphotype 3

App. II, Text-fig. A3c

Material. Oriolo MSF n.n.

Description. Cordate leaf with cordate base.

Remarks. This leaf remain resembles the modern *Alnus cordata* (Loisel.) Duby, 1828, by its cordate base and lowest secondary veins (pectinal veins) being gently curved and subparallel to basal margin.

Leaf morphotype 4

App. II, Text-fig. A3d–f

Material. Oriolo MSF 891, 856, 858.

Description. Elliptic leaves, ca. 50 mm long, 10–15 mm wide, base and apex acute, secondary venation eucamptodromous, possibly small glandular teeth along the margin.

Leaf morphotype 5

App. II, Text-fig. A3g

Material. Oriolo MSF 783.

Description. Leaf/leaflet, lamina oblong, >54 mm long, 24 mm wide, base round, secondary venation brochidodromous forming 3–4 steep loops, additional loops formed by higher order venation towards leaf margin.

Remarks. Somewhat similar leaf/leaflets are produced by Fabaceae and *Berberis*.

Leaf morphotype 6

App. II, Text-fig. A3h

Material. Oriolo MSF 952.

Description. A legume like leaflet, lamina obovate and oblong, 25 and >30 mm long.

Leaf morphotype 7

App. II, Text-fig. A3i

Material. Oriolo MSF 862.

Description. Leaf, petiolate, petiole 1 mm, lamina oblanceolate, 25 mm long, 6 mm wide at widest point, secondary venation steep eucamptodromous, margin entire.

Remarks. A small leaf resembling the extant species *Daphne gnidium* L., 1753.

Leaf morphotype 8

App. II, Text-fig. A3j–l

Material. Oriolo MSF 912, 912-1, 662-1.

Description. Leaf, petiolate, petiole 1 mm, bent, stout, lamina elliptic or elliptic-obovate, 11–14 mm long, 5–8 mm wide, base obtuse, apex obtuse cuspidate, secondary venation eucamptodromous to brochidodromous, margin entire.

Remarks. The leaves from Oriolo resemble modern leaves of *Cotoneaster*, Rosaceae. Similar leaves are produced by the modern species *Cotoneaster intermedius* (Lecoq. et Lamotte) H.J.Coste, 1893, native to France and Italy.

Leaf morphotype 9

App. II, Text-fig. A3m

Material. Oriolo MSF 715.

Description. Leaf, lamina roundish, ca. 22 mm long, 18 mm wide, base cordate, secondary venation perfect, basal acrodromous, two pairs of lateral primary veins, margin serrate (possibly of rosoid type).

Leaf morphotype 10

App. II, Text-fig. A3n

Material. Oriolo MSF 716.

Description. Leaf, lamina broad elliptic, ca. 18 × 13 mm, a primary vein is flanked by several pairs of acrodromous lateral veins, lateral veins are connected by transversal veins.

Leaf morphotype 11

App. II, Text-fig. A3o

Material. Oriolo MSF 880.

Description. Leaf, lanceolate, subsessile, primary vein thickening towards leaf base, lamina 26 mm long, 8 mm wide, base decurrent, apex cuspidate, secondary venation camptodromous, margin with remote reduced glandular teeth.

Various rosaceous leaves

App. II, Text-fig. A3p–z

Material. Oriolo MSF 874, 883, 890, 943, 948, 950, 956, 957, 958, 960, 961, 962, 966.

Description. Leaves vary in length from 10 to 40 mm, margins are crenulated or serrate.

Vegetation reconstruction and genus-level affinities with extant vegetation

The IPR vegetation analysis predicts a zonal, broad-leaved deciduous forest (BLDF) as the most representative zonal vegetation unit for the Oriolo assemblage, where the specific pattern of the key components is as follows: BLD (83.6 %), BLE (4 %), SCL+LEG (12.4 %), DRY + MESO HERBS (5.4 %), number of zonal taxa (38), number of zonal woody elements (32; App. III).

The underrepresentation of herbaceous elements (5 taxa in the Oriolo leaf assemblage) is accounted for by using Drudge 1 (focussing only on woody plants) to determine the closest modern analogue (zonal) plant assemblage at the genus level, from a calibration dataset containing 505 modern plant assemblages from Europe, Caucasus, China, Mongolia and Japan (Teodoridis et al. 2020). Drudge 1 indicates montane Broad-leaved Deciduous Forest – *Fagus crenata* region at 600–1,800 m a.s.l. on Mt. Fuji in Japan (Nakamura 2000, Teodoridis et al. 2011a) as a possible modern analogue zonal plant assemblage to the fossil plant assemblage of Oriolo (App. III).

The gridded climate proxies for the BLDF – *Fagus crenata* region at 600–1,800 m are as follows: Mean annual temperature 5.8–12 °C, warmest month mean temperature 16.9–23 °C, coldest month mean temperature -4.4–1.8 °C and mean annual precipitation 1,866 mm (Teodoridis et al. 2011a: tab. 5).

Discussion

Vegetation during the latest Calabrian in northern Central Italy

The diverse leaf assemblage of Oriolo is represented by a few hundred specimens with a lithological matrix of very homogeneous type. Such a matrix characterizes a few layers within the Sabbie gialle cycle 1, with a high sedimentation rate (Toniato et al. 2017), and is here taken as evidence that deposition of the plant assemblage happened during a short time span, not longer than several millennia (with the exception of *Tsuga* cones, see above). As a whole, this assemblage provides unique insights into the vegetation of a relatively warm and humid phase, possibly referable to a single interglacial (less probably an interstadial) around 0.84 Ma (Toniato et al. 2017) at the end of the Early Pleistocene. The attribution to an interglacial, i.e., either MIS 21 or MIS 19 (Toniato et al. 2017), is supported by the occurrence of such thermophilous elements as: *Acer* aff. *monspessulanum*, *Pyracantha* aff. *coccinea*, *Rhamnus* aff. *cathartica*, *Sorbus* aff. *domestica*. Therefore, within the limits of stratigraphic resolution that can be achieved with the data at hand, we conclude that the assemblage from Oriolo may document an interglacial forest phase in which the woody flora was still characterized by several taxa presently absent from mainland Italy (*Carya*, *Gleditsia*, *Parrotia*, *Pinus* aff. *peuce*, *Pterocarya*, *Zelkova*). The assemblage comprises at least 63 fossil-taxa, of which 51 can be assigned to species and/or genera. Twelve are unidentified dicot leaf types (Tab. 2). Three taxa are conifers (gymnosperms), two are monocots (angiosperms), and 58 (including 12 unidentified dicot leaf types) belong to other angiosperms. Among the 46 angiosperm taxa identified to species and genus level, most are woody plants, due to the taphonomic bias in the leaf fossil record towards woody plants. Only a single herbaceous plant and three woody lianas are recorded. Twenty taxa represent trees, ten shrubs, and twelve may have been trees or shrubs.

The qualitative assessment of the palaeoenvironment of the Oriolo area during the latest Calabrian (Tab. 2) suggests the presence of a rich riparian vegetation, with little indication of swamp forests (vegetation unit VU3 only represented by *Phragmites*, *Alnus glutinosa* subsp. *barbata* and *Quercus* sect. *Quercus*). Twenty-seven taxa are

Table 2. Plant fossil-taxa from Oriolo including information about life form, element, reliability of determination, closest modern analogue, and ecology. [a]Reliability of determination: moderate and low indicate that species diagnostic morphological characteristics are insufficient for allowing a reliable identification. [b]Vegetation units (Denk 2016): VU 0/a: Xeric alluvial habitats on water-permeable gravel (Schratt-Ehrendorfer 2000). VU 0/b: Dry woodland, well-drained soils above alluvial plain including Šibljak (Adamovic 1909). VU 1: Aquatic. VU 2: Bogs, wet meadows. VU 3: Swamp forest. VU 4: Riparian forest. VU 5: Well-drained lowland forest including levee forests. VU 6: Well-drained upland forest. VU 7: Well-drained (lowland and) upland conifer forest including hammocks and raised bogs within peat-forming vegetation.

Fossil-taxon	Life form	Element	Reliability[a]	Modern analogue	Ecology[b]	Dry sites
Tsuga cf. *chiarugii*	T conif.	Cone	High	*Tsuga* spp.	VU7	
Pinus aff. *peuce*	T conif.	Cone	High	*Pinus* subgenus *Strobus*	VU7	
Abies aff. *alba*	T conif.	Cone scale	High	Abies spp.	VU7	
"*Bambusa*" cf. *lugdunensis*	Monocot.	Leaf	High	Poaceae, subfam. Bambusoideae	VU4	
Phragmites sp.	Monocot.	Axis	Moderate	*Phragmites* spp.	VU2, VU3	
Berberis auriolensis	S	Leaf	High	*B. amurensis*, *B. canadensis*, *B. vulgaris* (clade 5 of Adhikari et al. 2015)	VU0	VU0a, b
Epimedium cf. *praeaspera*	H	Leaf	High	*Epimedium* spp.	VU5, VU6, VU7	
Clematis aff. *vitalba*	L	Leaf	Moderate	*Clematis* spp.	VU0, VU4, VU5	VU0a, b
Parrotia aff. *persica*	T	Leaf	High	*Parrotia persica*	VU5	
Vitis sp.	L	Leaf	High	*Vitis vinifera* subsp. *sylvestris*	VU0, VU4, VU5	VU0a, b
Gleditsia aff. *caspica*	T/S	Leaf	High	*Gleditsia caspica*	VU4, VU5	
Crataegus aff. *monogyna*	S	Leaf	High	*Crataegus monogyna*	VU0, VU4, VU5	VU0a, b
Sorbus aff. *domestica*	T/S	Leaflet	High	*Sorbus domestica*	VU5	
cf. *Sorbus* sp.	T/S	Leaflet	High	*Sorbus aucuparia*	VU5, VU6, VU7	
Mespilus aff. *germanica*	S	Leaf	Moderate	*Mespilus germanica*	VU5	
Pyracantha aff. *coccinea*	S	Leaf	High	*Pyracantha coccinea*	VU0	VU0a, b
Spiraea aff. *cana*	S	Leaf	High	*Spiraea cana*, [*Spiraea blumei*]	VU0, VU5, VU6	VU0a, b
cf. *Rubus* sp.	S	Leaf	Low	*Rubus* spp.	VU0, VU4	VU0a, b
Rhamnus aff. *cathartica*	S	Leaf	High	*Rhamnus cathartica*	VU5	
Zelkova zelkovifolia	T/S	Leaf	High	*Zelkova carpinifolia*, *Z. sicula*, *Z. abelicea*	VU0, VU5	VU0b
Ulmus affinis	T/S	Leaf	High	*Ulmus minor*, *U. glabra*, *U.* × *hollandica*	VU0, VU4, VU5	VU0a, b
Fagus aff. *sylvatica*	T	Leaf	High	*Fagus sylvatica*	VU6	
Quercus aff. *cerris*	T	Leaf	High	*Quercus cerris*	VU0, VU5	VU0b
Quercus aff. *cerris*	T	Fruit	High	*Quercus cerris*	VU0, VU5	VU0b
Quercus sect. *Quercus*	T	Fruit	High	*Quercus* sect. *Quercus*	VU0, VU3-VU7	VU0a, b
Quercus aff. *pubescens*	T	Leaf	Moderate	*Quercus pubescens*	VU0, VU5	VU0a, b
Quercus aff. *petraea* s.l.	T	Leaf	High	*Quercus petraea* s.l.	VU4, VU5, VU6	VU0a, b
Carya cf. *minor*	T	Leaf	High	*Carya* spp.	VU0, VU4, VU5	VU0a, b
Pterocarya aff. *fraxinifolia*	T	Leaf	High	*Pterocarya fraxinifolia*	VU4	
Alnus aff. *barbata* (*Alnus* aff. *glutinosa* subsp. *barbata*)	T	Leaf, cone	High	*Alnus glutinosa* subsp. *barbata*	VU3, VU4, VU5	
Carpinus aff. *betulus*	T	Leaf, fruit	High	*Carpinus betulus*	VU5	
Carpinus aff. *orientalis*	T/S	Leaf, fruit	High	*Carpinus orientalis*	VU0	VU0a, b
Corylus aff. *avellana*	S	Leaf, fruit	High	*Corylus avellana*	VU0, VU4, VU5	VU0a
Coriaria aff. *myrtifolia*	S	Leaf	High	*Coriaria myrtifolia*	VU0, VU5	VU0a, b
Populus aff. *alba*	T	Leaf	High	*Populus alba*	VU4	
Populua aff. *nigra*	T	Leaf	High	*Populus nigra*	VU4	
Populus aff. *tremula*	T	Leaf	High	*Populus tremula*	VU4	
Salix aff. *caprea*	T/S	Leaf	Moderate	*Salix caprea*, *Salix caprea* × *Salix* spp.	VU4	
Salix aff. *alba*	T/S	Leaf	Moderate	*Salix alba*, *Salix alba* × *Salix* spp.	VU4	
Salix aff. *viminalis/eleagnos*	T/S	Leaf	High	*Salix viminalis*, *Salix eleagnos*, *Salix eleagnos* × *Salix* spp.	VU0, VU4	VU0a
Salix aff. *triandra*	T/S	Leaf	High	*Salix triandra* [*S. caprea* × *viminalis*]	VU4	
Salix div. spp.	T/S	Leaf	Moderate	*Salix* spp.	VU4	

Table 2. continued

Fossil-taxon	Life form	Element	Reliability[a]	Modern analogue	Ecology[b]	Dry sites
Acer aemilianum	T	Leaf	High	Palmata clade (one N American, several E Asian spp.), *Acer sieboldianum*	VU4, VU5	
Acer aff. *campestre*	T	Leaf	High	*Acer campestre*	VU0, VU4, VU5	VU0a, b
Acer aff. *lobelii* (*Acer* aff. *cappadocicum* subsp. *lobelii*)	T	Leaf	High	*Acer lobelii* (*Acer cappadocicum* subsp. *lobelii*)	VU4, VU6	
Acer aff. *monspessulanum*	T/S	Leaf	High	*Acer monspessulanum*	VU0, VU5	VU0a, b
Acer aff. *opalus* subsp. *obtusatum*	T	Leaf	High	*Acer opalus* subsp. *obtusatum*	VU0, VU5	VU0b
Tilia sp.	T	Leaf, bract	High	*Tilia* spp.	VU5	
Cornus sp.	S	Leaf	High	*Cornus* spp.	VU0, VU4	VU0a
Fraxinus aff. *angustifolia* subsp. *oxycarpa*	T	Leaflet	High	*Fraxinus angustifolia* subsp. *oxycarpa*	VU0, VU4	VU0a
Hedera aff. *helix*	L	Leaf	High	*Hedera helix*	VU4, VU5, VU6	
Indet. Leaf morphotypes (MT1–MT11)	?	Leaf	Low			
Indet. “rosaceous” leaf remains	?	Leaf	Low			

Extinct species	Relictual distribution in submediterranean W Eurasia
Extirpated from Italy	Submediterranean taxa, forest undergrowth, open scrubland

elements of riparian vegetation tolerating temporal flooding (VU4), with the Salicaceae being the most diverse family (>8 species). Well-drained lowland forest (VU5) was also relatively rich (28 taxa). Dominating tree species were *Quercus* spp. and *Carpinus betulus*, with an admixture of *Acer* spp. and diverse Rosaceae in both the tree and shrub layers. This lowland forest was highly similar to present-day lowland forests in the submediterranean forest region of western Eurasia (see for example, Denk et al. 2001, Bergmeier et al. 2004, Talebi et al. 2014), with only a few exotic elements (*Acer aemilianum*). The qualitative inference of palaeoenvironments linked to the Oriolo leaf assemblage is in accordance with the semi-quantitative vegetation inference from the IPR analysis, suggesting the presence of broad-leaved deciduous forest (BLDF) with only a few evergreen taxa in the understorey (App. III).

According to Leroy et al. (2011), transitions from glacial to interglacial conditions during the Early Pleistocene facilitated colonization of Europe by early hominins, because the vegetation was relatively free of forests, whereas vegetation would have been too forested during transitions from interglacial to glacial conditions. The case of Oriolo might be an indication that even during periods favouring forests, a great diversity of environments related to alluvial landscapes might have provided open landscapes as well. These vegetation types could have provided suitable habitats for various large mammals roaming through the latest Calabrian landscapes of northern Italy.

Remarkably, the leaf assemblage of Oriolo is characterised by a high number of shrubs (Tab. 2). Of these, several are typical components of locally dry and/or open vegetation. One vegetation type common on gravelly soils in river and delta areas has been termed xeric alluvial vegetation (e.g., Amoros et al. 1987, Schratt-Ehrendorfer 2000; VU0/a in Tab. 2). Alluvial systems typically comprise various wet and moist habitats (VU1, 2, 3, [4]), but xeric alluvial vegetation can develop over coarse sediments with low available water capacity. Shrubs such as *Berberis*, *Crataegus*, *Corylus* and *Cornus* and trees that do not grow very tall (e.g., *Carpinus orientalis*, *Acer campestre*, *A. monspessulanum*) are typical for this vegetation type. A second type of more open vegetation found in Oriolo were dry woodlands on well-drained soils above the alluvial plain. In the submediterranean vegetation zone, such woodlands have been termed Šibljak (Adamovic 1909, Horvath et al. 1974) when dominated by broadleaf deciduous shrubs and small trees. Šibljak associations can be dominated by different shrub species, such as *Berberis*, *Quercus* spp., but can also be of a mixed character. Typical elements of the latter are, among others, *Crataegus*, *Mespilus*, *Pyracantha*, *Ulmus* spp., *Cornus* spp., *Quercus* spp., *Acer* spp., with lianas such as *Clematis* and *Vitis* (Adamovic 1909; VU0/b in Tab. 2). Similar species compositions are to be expected at forest edges and may form transitions to alluvial plains.

Finally, the composition of the leaf assemblage and the dispersed conifer cones of Oriolo suggest a hinterland vegetation of more mesic character, possibly corresponding to a mixed *Fagus*-*Abies* and (drier) *Pinus* forest (compare with the result of the Drudge 1 analysis).

Comparison with coeval floras

The dominance of leaf remains in the assemblages of Oriolo and the absence of mummified fruits and seeds hamper the comparison with other late Calabrian and early Chibanian floras of Northern Italy (Leffe, Steggio, Stirone-Laurano, Ranica, Arda, Enza; Ghiotto 2010, Martinetto et al. 2015, Martinetto 2015), which are dominated by carpological remains. Only the Middle Pleistocene locality Piànico-Sèllere yielded numerous well-preserved leaf remains (Martinetto 2009). Shared taxa with Oriolo are *Pinus peuce*, *Acer cappadocicum* s.l., and *Pyracantha coccinea*. Due to the younger age and the more northerly position, the leaf assemblage of Piànico-Sèllere has less extinct/extirpated elements (*Rhododendron ponticum* L. var. *sebinense* (Sordelli) Sordelli, 1896, *Pinus peuce*) than Oriolo. In contrast, the leaf assemblage of Oriolo is very similar to the Early Pleistocene flora of Crespià (age ca. 2.1–1.6 Ma), northeastern Spain (Roiron 1983; 18 potentially conspecific taxa). The only difference are evergreen shrubs and trees found only in Crespià that are typical of more maritime climates, such as *Laurus canariensis* Willd., 1809, *Ilex aquifolium* L., 1753, and evergreen oaks (*Quercus ilex* L., 1753). A further leaf assemblage similar to Oriolo is the Gelasian flora of Bernasso (Leroy and Roiron 1996), which shares >10 species with the leaf assemblage of Oriolo. There are also similarities with the leaf assemblage from Bezhan (Albania), for which a Calabrian age has been suggested (Denk et al. 2021). This flora shares with Oriolo *Phragmites*, *Quercus cerris*, *Populus alba*, *Acer monspessulanum*, and has a similar generic composition (*Ulmus* aff. *minor*, *Crataegus* sp., *Salix* sp.), but includes evergreen *Quercus*, which has not been reported from Oriolo. Finally, we note some similarity with Pleistocene floras of the Sisian region, Armenia (Ollivier et al. 2010). Conspecific and closely related taxa include *Quercus cerris*, *Q. iberica*, *Carpinus betulus*, *Populus alba*, *Salix alba*, *S. caprea*, *Tilia* sp., *Ulmus carpinifolia* (as *U. minor*), *Crataegus*, *Spiraea*, and *Acer campestre*. This underscores the assembly of the modern-day submediterranean forest vegetation during the Early Pleistocene across western Eurasia.

Biogeographic affinities

Using IPR vegetation analysis and taxonomic similarity, Drudge 1 inferred the highest similarity of the Oriolo plant assemblage with today's Japanese broad-leaved deciduous forest (BLDF). This is surprising at first, because the Oriolo leaf assemblage is markedly modern in appearance and the qualitative comparison with modern vegetation suggests a strong overlap with modern submediterranean western Eurasian vegetation (see above and Follieri 1958).

However, closer inspection of biogeographic affinities of the Oriolo flora can explain the Drudge 1 result. At the genus level, all taxa represented in the leaf assemblage of Oriolo also occur in East Asia. Fossil species that went extinct in western Eurasia belong to groups that became extirpated from the western Eurasian flora in the latest Cenozoic, and all have modern species in East Asia (a few also in North America; *Tsuga*, *Carya*). Hence, given the humid-temperate character of the Oriolo flora, the modern analogue BLDF on Mt. Fuji, Japan (MAT 5.8–12 °C, WMMT 16.9–23 °C, CMMT -4.4–1.8 °C and MAP 1866 mm) inferred by Drudge 1 is reasonable, and reflects the ultimate floristic-climatic links of the Pleistocene western Eurasian flora with the present-day East Asian (Japanese) one.

We identified three main biogeographic patterns in the flora of Oriolo: first, species native to Italy and adjacent regions (e.g., *Acer monspessulanum*, *Fagus sylvatica*); second, species absent from the modern Central and South European flora but with relict distributions in other parts of western Eurasia (e.g., *Parrotia*, *Pterocarya*); and third, extinct species belonging to groups extirpated in western Eurasia in the late Cenozoic persisting in East Asia (e.g., *Acer* sect. *Palmata*,) and/or North America (*Tsuga*, *Carya*; see Tab. 2).

In the following, we will discuss some biogeographically interesting patterns of recent western Eurasian extirpation. The most intriguing is probably the fossil record of *Acer* sect. *Palmata*, represented by *A. aemilianum* in the Oriolo flora. Sect. *Palmata* is one of the (genetically) most evolved, is the most speciose lineage of *Acer* (Van Gelderen et al. 1994, Grimm et al. 2006, Renner et al. 2008) and is today restricted to East Asia, except for the single species *A. circinatum* Pursh, which survived along the Pacific coast of North America. The fossil record of sect. *Palmata* in East Asia is not older than Early Miocene (Tanai 1983), and there are no Palmata-like fossils known from eastern North America, Greenland, or Iceland. In view of the molecularly-inferred age estimate for the split between the western North American *A. circinatum* and the East Asian members of sect. *Palmata* of 13.6–12 Ma (Renner et al. 2008), dispersal of sect. *Palmata* to North America via Beringia might have happened before the Middle Miocene. The oldest record of sect. *Palmata* in western Eurasia could be a leaf from Early Miocene strata of Spain (Barrón and Diéguez 2001). While the next youngest records from Western Europe are of Pliocene and Pleistocene age (France, Spain), scattered records of the section are known in Eastern and Central Europe from Middle Miocene to Pleistocene strata. To our knowledge, the Oriolo record is the by far youngest in western Eurasia, and is almost 1 million years younger than the next youngest (Bernasso; Leroy and Roiron 1996). *Acer* section *Palmata* persisted in western Eurasia into the Pleistocene, with two distinct fossil-species resembling the East Asian species *A. sieboldianum* (Sordelli 1896, this study) and *A. japonicum* (Givulescu and Ghiurca 1969, Leroy and Roiron 1996), before it became extirpated in western Eurasia (Tab. 1). The range expansion of this group from East Asia to western Eurasia appears to have occurred during the Oligocene, if we accept the Early Miocene record from the Rubielos de Mora leaf assemblage of Spain. A possible biogeographic link is a record from undated "late Oligocene or Miocene" deposits of the South Altai region (Schmalhausen 1887, Rayushkina 1979), but the specific identity of this leaf remain is somewhat questionable.

The fossil-species *Berberis auriolensis* is another taxon with possible biogeographic affinities with modern East Asian taxa. This taxon shows a mosaic of characters found in modern members of a monophyletic group within *Berberis* (Clade 5 in Adhikari et al. 2015). Members of Adhikari et al.'s Clade 5 show substantial morphological variability, possibly related to niche shifts from temperate into summer-dry Mediterranean climates. Several members of this clade survived in western Eurasia as narrow endemic species (e.g., *Berberis maderensis*, *B. aetnensis*, *B. cretica*), along with the widespread *B. vulgaris*. *Berberis auriolensis*, however, shows morphological affinities with Clade 5 species from North America (e.g., *B. canadensis* Mill., 1768), as well as the Himalayas-East Asia (e.g., *B. amurensis* Rupr., 1857). Hence, we consider this fossil-taxon a Pleistocene member of this clade, representing either an extirpated lineage or more ancestral morphology.

The pattern recognized for *Berberis auriolensis* also applies to the extinct *Tsuga* cf. *chiarugii*. *Tsuga* has a disjunct modern range, from the Himalayas to East Asia, and in North America. *Tsuga chiarugii* and associated dispersed pollen from possibly Early Pleistocene strata of Ghirlanda were initially compared to *T. americana* (Mill.) Farw., 1915 (a synonym of *T. canadensis* (L.) Carriére, 1855) native to eastern North America, and to *T. diversifolia* (Maxim) Mast., 1881, from Central and Southern

Japan (Tongiorgi 1936). In Early Pleistocene deposits from Albania, dispersed *Tsuga* pollen represents at least three lineages of *Tsuga*, corresponding to modern North American, Chinese, and Japanese species (Denk et al. 2021). The pollen record of *Tsuga* across South Europe and the Balkans indicates that this genus declined in Northern Italy at around 0.8 Ma (Pini et al. 2014a), while it persisted in other parts of Europe until 300 ka (Magri et al. 2017). In a similar fashion, *Carya* disappeared from Northern Italy, or became very rare at the end of the Calabrian, while persisting until the Late Pleistocene in the western Black Sea region (Magri et al. 2017).

The biogeographic pattern seen in *Ulmus affinis* may point to a western Eurasian origin of the wider group of elms to which this fossil-taxon belongs. Western Eurasian species of sect. *Ulmus* form a monophyletic group (Wiegrefe et al. 1994), which could be the surviving members of a clade that started to emerge during the Early Miocene and included species like *U. affinis* (see App. I).

Among taxa that became extirpated in Italy and adjacent regions, *Parrotia* was widespread during the Miocene and Pliocene across Europe (Mai 1995). The Pliocene fossil-species *P. reidiana* based on fruit remains differs in being smaller than the modern *P. persica*, native to the Hyrcanian region (Martinetto 2015). The material from Oriolo matches the modern species in terms of both leaf and fruit morphology, and is therefore attributed to *P. persica*. This would indicate that the modern species *P. persica* (native to Iran and Azerbaijan) had a much wider distribution in western Eurasia during the late Early Pleistocene.

Zelkova was also common and widespread during the Neogene in western Eurasia. The fossils from Oriolo are intermediate between the modern Euxinian-Hyrcanian *Z. carpinifolia* and *Z. sicula* from Sicily. Unlike *Parrotia*, speciation in *Zelkova* during the Pleistocene led to a narrow endemic species in South Europe (*Z. sicula*), in addition to the more widespread modern *Z. carpinifolia* and *Z. abelicea* (Crete).

A similar case of extirpation of a widespread western Eurasian type along with speciation in Europe is seen in *Quercus* sect. *Quercus*. Late Early Pleistocene leaves from Oriolo assigned to *Q. petraea* are more similar to the eastern (Euxinian-Hyrcanian) subspecies *iberica* (syn. *Q. iberica*) than to the modern European *Q. petraea* s. str. Very similar leaf remains are known from slightly older deposits from Armenia (Ollivier et al. 2010). Therefore, *Quercus iberica* appears to have been more widespread in western Eurasia than at present. Modern populations of *Q. petraea* s. str. might have gone through multiple bottlenecks during subsequent cool periods, during which the eastern morphotype of *Q. petraea* subsp. *iberica* was lost in Europe, whereas some chloroplast DNA haplotypes are still shared between *Q. iberica* from western Georgia and *Q. petraea* s. str. from Europe (Ekhvaia et al. 2018). This pattern of extirpation and speciation is also seen in *Alnus barbata* (*Alnus glutinosa* subsp. *barbata*).

Extirpation of woody plant taxa in Italy and adjacent regions – deterministic or stochastic?

The latest Calabrian flora of Oriolo comprises 51 taxa identified to the species level (Tab. 2). 38 of these represent taxa currently found in Italy and adjacent regions, while 13 represent exotic (extinct and extirpated) taxa. Hence, 74.5 % of the taxa from Oriolo are part of the modern regional flora. The remaining 25.5 % comprise 8 extinct species belonging to genera with disjunct distribution in different parts of the Northern Hemisphere, and 5 species that became extirpated from the Italian flora during the Middle and Late Pleistocene.

According to Svenning (2003), CMMT played a crucial role in determining survival, extirpation or extinction of tree taxa in Europe during the late Neogene. By looking at climate requirements of present-day extra-European representatives of genera that are widespread, relictual, or extirpated in Europe, Svenning (2003) established thresholds that predict these three scenarios for European trees. CMMT for widespread European trees would be -23.4 ± 9.14 °C, for relictual trees -12.0 ± 5.76 °C, and for extirpated/extinct -7.98 ± 6.39 °C. Taking these numbers at face value, the modern analogue of *A. aemilianum*, the East Asian species *A. sieboldianum* requires minimum CMMT of ca. -8 °C (climate parameter extracted from occurrence data in https://www.gbif.org/). *Acer japonicum*, a modern analogue for *A. protojaponicum*, is much hardier and can tolerate CMMT of -12 °C. For *A. vindobonensis* and *A. sanctae-crucis*, current climate requirements of different modern analogues suggest slightly different scenarios: *Acer palmatum* (analogue for *A. sanctae-crucis*) clearly suggests that the European fossil-species was doomed to extinction. According to Fang et al. (2011), *A. palmatum* requires minimum CMMT of -2.9 °C. *Acer ceriferum* (analogue for *A. sanctae-crucis*) requires CMMT of -6.7 °C, and *A. sinense* (analogue of *A. vindobonensis*) CMMT of -7 °C (Fang et al. 2011). In contrast, present-day extra-European *Tsuga* spp. require minimum CMMT of -16.2 °C (Thompson et al. 2015) for the North American strain and -0.5 °C (Fang et al. 2011) for the East Asian. This would suggest that *Tsuga* had a good chance to survive in western Eurasia, and calls for alternative explanations why this conifer genus disappeared from Europe. Similarly, the modern climate requirements for North American members of *Carya* (minimum CMMT -14.7 °C; Thompson et al. 2015) would appear to be sufficient to enable survival of this genus in relict areas. Notably, Chinese species of *Carya* require much higher minimum CMMT (Fang et al. 2011).

For taxa that have refugia in Asia Minor, like *Gleditsia*, the North American *Gleditsia triacanthos* L., 1753, requires a minimum CMMT of -10.8 °C, and the East Asian *G. japonica* Miq., 1867, -18.8 °C (Thompson et al. 2015, Fang et al. 2011). This would qualify *Gleditsia* as a survivor, or at least as a potential Tertiary relict in Europe. In contrast, the presence of three subspecies of *Acer cappadocicum* Gled., 1785, in western Eurasia is surprising, as the Chinese subspecies requires a minimum CMMT of -9.1 °C (Fang et al. 2011).

Appearance of modern tree species as a further reason for Pleistocene extinction/extirpation

Overall, this suggests that in addition to climate requirements of present-day extra-European congeners of Pliocene and Pleistocene European tree taxa, other factors such as niche competition or stochasticity of population dynamics contributed to their survival or extirpation.

For the Mediterranean region, Pleistocene pollen records of critical taxa have been reviewed by Magri et al. (2017). They indeed found a strongly regional pattern of last local occurrences across the Mediterranean region, which does not fit with climate as the main trigger, but points to multicausality for survival-extirpation patterns. For the Northern Italian region, we note that the macrofossil record of Oriolo is exceptional, because several leaf records of "exotic" plant taxa are by far the youngest recorded for Europe.

A number of plant taxa that were part of the Miocene and Pliocene flora of western Eurasia belong to groups that thrive in cool temperate regions today, but despite this, became extirpated in Europe. For example, leaf remains of *Quercus* sect. *Quercus* from Pliocene strata of Willershausen and Frankfurt (*Quercus praecastaneifolia* Erw.Knobloch, 1998) are related to present-day East Asian species of sect. *Quercus*, with minimum requirements of CMMT of -15.9 °C (Fang et al. 2011, Kvaček et al. 2020). These taxa may have been outcompeted or introgressed by extant species, such as *Quercus petraea*, which went through a series of bottlenecks resulting in new geno- and morphotypes that were better adapted to climatic cycles of the Pleistocene. Likewise, *Quercus petraea* s. str. and *Fagus sylvatica* s. str. of Europe were more competitive in this region than their eastern subspecies/species *Q. iberica* and *F. orientalis* (Gömöry et al. 2021). Genera that became extirpated in Europe and western Eurasia, despite their North American and East Asian congeners being highly cold-tolerant, such as *Tsuga*, possibly were outcompeted by other conifers that speciated during the Pliocene and Pleistocene (e.g., *Abies*; Hrivnák et al. 2017), or by woody angiosperms that had gone through environmental bottlenecks and occupied similar ecological niches.

Conclusion

An increasing number of stratigraphically highly resolved palynological studies provide detailed information about the response of vegetation to Pleistocene glacial-interglacial cycles. These studies can identify regional patterns of last local occurrence of taxa that are absent from the present-day European flora. Leaf and carpological remains are not as common as dispersed spores and pollen, but can be used to trace biogeographic histories at the level of species. Specifically, such studies can trace the appearance of modern species in the fossil record (first local occurrence), which is not possible by means of the dispersed spore and pollen records. In the present study, we investigated an assemblage of leaf and fruit impression fossils from latest Early Pleistocene strata. Through detailed taxonomic assessment, we document modern species, and extinct and locally extirpated species in the Pleistocene flora of Oriolo, Northern Italy. Our study provides evidence that regional extirpation and extinction are to some degree the result of deterministic Plio-Pleistocene extinctions determined by climate tolerances of extra-European congeners of Plio-Pleistocene European plant taxa. In addition, we provide evidence for additional factors influencing extinction and extirpation: Biotic interactions between newly emerging taxa that had gone through bottlenecks and evolved new geno- and morphotypes (for example, modern species of *Quercus*, *Fagus*, *Acer*) and "old" elements in the flora of Europe (for example, *Carya*, *Liquidambar*, *Zelkova*) led to the extinction/extirpation of the latter and contributed to the assembly of modern European forest biomes.

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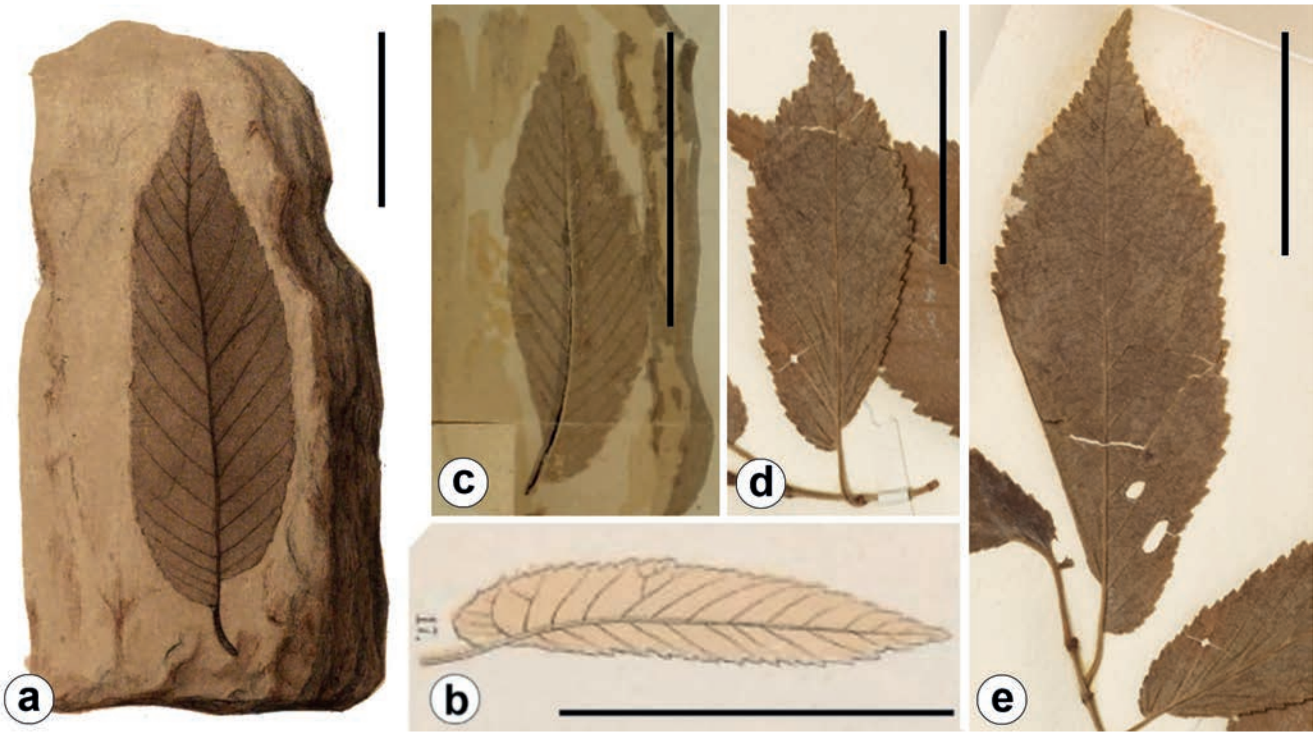
Appendix I

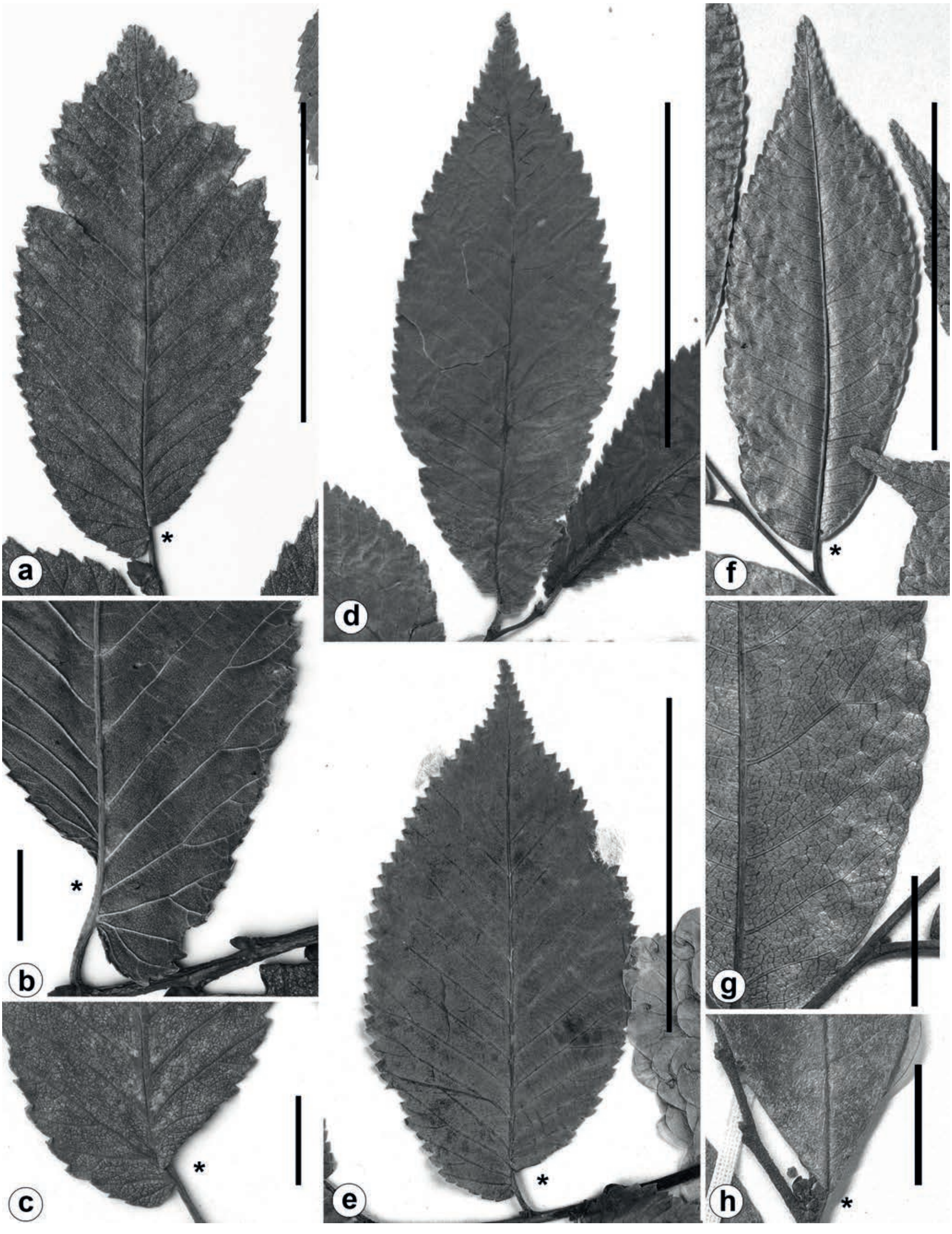
A hypothetical evolutionary scenario leading to Pleistocene representatives of the fossil-species *U. affinis*. *Ulmus longifolia* Unger, 1847 (nom. illeg.; Text-fig. A1a) from Early Miocene deposits of Bílina was described by Unger (1847). Subsequently, Heer (1856) described a highly polymorphic fossil-species *Ulmus braunii* Heer, 1856 (Text-fig. A1b) from Middle Miocene deposits of Öhningen. This taxon included broad to lanceolate leaves with strongly asymmetrical leaf base. *Ulmus affinis* Massal., 1853 (Text-fig. A1c) from Messinian deposits of Senigallia was described in 1853 and figured in 1854 (Massallongo 1853, 1854). Not shown here are the Pliocene leaf remains from Asti, northern Italy, and the Pleistocene specimens from Oriolo described in the present study (see Text-fig. 6g–l). Leaf morphotypes similar to the fossil-taxa mentioned above (narrow, strongly asymmetrical lamina, asymmetrical base) are rarely encountered in the modern species *Ulmus minor* Mill., 1768; Text-fig. A1d, e).

Consequently, the hypothetical lineage shown here may not be directly related to modern members of the western Eurasian *Ulmus* sect. *Ulmus*.

Modern species previously compared to *Ulmus longifolia* (see main text) and here compared to *Ulmus affinis* are illustrated in Text-fig. A2.



Text-fig. A1. a: *Ulmus longifolia* Unger, 1847 (Unger 1847: pl. 26, fig. 5). b: *Ulmus braunii* Heer, 1856 (Heer 1856: pl. 79, fig. 17). c: *Ulmus affinis* A.Massal., 1853 (Massallongo 1854: pl. 4, fig. 8). d, e: *Ulmus carpinifolia* Gled., 1773 syn. of *Ulmus minor* Mill., 1768, (herbarium K566057), UK. Scale bars 30 mm (a–e).



Text-fig. A2. a: *Ulmus carpinifolia* Gled., 1773 syn. of *Ulmus minor* Mill., 1768, (herbarium E00824885). b: *Ulmus carpinifolia* Gled., 1773 syn. of *Ulmus minor* Mill., 1768, (herbarium E00824885). c: *Ulmus carpinifolia* Gled., 1773 syn. of *Ulmus minor* Mill., 1768, (herbarium E00824885 detail of (a)). d, e: *Ulmus elliptica* K.Koch, 1849 (herbarium E00034393). f, g: *Ulmus lancifolia* Roxb., 1814, nom. inval. (herbarium NMNH03413489). h: *Ulmus lancifolia* Roxb., 1814, nom. inval. (herbarium NMNH03413488). Asterisks indicate different types of asymmetric leaf base. Scale bars 50 mm (a, d, e, f), 10 mm (b, c, g, h).

Appendix II

Angiosperms incertae sedis.

Text-fig. A3. a: Leaf morphotype 1 Tebano MSF SG 049. b: Leaf morphotype 2 Oriolo MSF 631. c: Leaf morphotype 3 Oriolo MSF n.n. d, f: Leaf morphotype 4. d: Oriolo MSF 891. e: Oriolo MSF 856. f: Oriolo MSF 858. g: Leaf morphotype 5 Oriolo MSF 783. h: Leaf morphotype 6 Oriolo MSF 952. i: Leaf morphotype 7 Oriolo MSF 862. j, l: Leaf morphotype 8. j: Oriolo MSF 912. k: Oriolo MSF 662. l: Oriolo MSF 662-1. m: Leaf morphotype 9 Oriolo MSF 715. n: Leaf morphotype 10 Oriolo MSF 716. o: Leaf morphotype 11, overview and detail of margin Oriolo MSF 880. p–z: Various rosaceous leaves/leaflets. p: Oriolo MSF 943. q: Oriolo MSF 890. r: Oriolo MSF 950. s: Oriolo MSF 958. t: Oriolo MSF 966 aff. *Sorbus*. u: Oriolo MSF 956. v: Oriolo MSF 961. w: Oriolo MSF 962. x: Oriolo MSF 874. y: Oriolo MSF 883. z: Oriolo MSF 960.

Appendix III

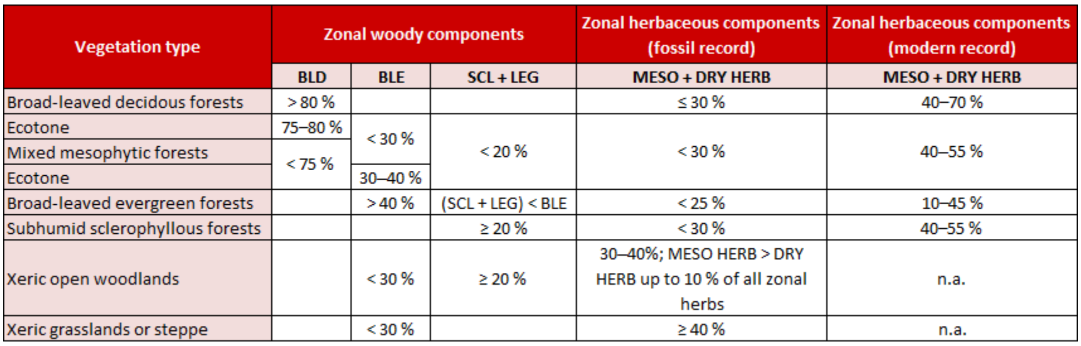
Results of IPR and Drudge 1 analyses.

Table A1. Coding of plant taxa from Oriolo for the IPR analysis.

site: Oriolo	ZONAL									AZONAL			PROBLEMATIC taxa	
Taxa	CONIF	BLD	BLE	SCL	LEG	ZONPALM	ARBFERN	DRY HERB	MESO HERB	AZONAL WOODY	AZNW	AQUATIC		
Tsuga sp.	1.00													1.00
Pinus aff. *peuce*	1.00													1.00
Abies sp.	1.00													1.00
Bambusa lugduensis											1.00			1.00
Phragmites sp.											1.00			1.00
Berberis sp.		0.50		0.50										1.00
Epimedium cf. *praeasper*								0.20	0.80					1.00
Clematis aff. *vitalba*									0.50		0.50			1.00
Parrotia aff. *persica*		0.80								0.20				1.00
Vitis sp.		0.50								0.50				1.00
Gleditsia aff. *caspica*		0.50								0.50				1.00
Crataegus aff. *monogyna*		1.00												1.00
Sorbus aff. *domestica*		1.00												1.00
Mespilus aff. *germanica*		1.00												1.00
Pyracantha aff. *coccinea*			0.50	0.50										1.00
Spiraea sp.		0.50		0.50										1.00
Rubus sp.		0.50						0.25	0.25					1.00
Rhamnus aff. *cathartica*		1.00												1.00
Zelkova zelkovifolia		1.00												1.00
Ulmus sp.		0.80								0.20				1.00
Fagus aff. *sylvatica*		1.00												1.00
Quercus aff. *cerris*		0.80		0.20										1.00
Quercus sect. *Quercus*		1.00												1.00
Quercus aff. *pubescens*		0.80		0.20										1.00
Quercus aff. *petraea* s.l.		1.00												1.00
Carya minor		1.00												1.00
Pterocarya aff. *fraxinifolia*		0.80								0.20				1.00
Alnus aff. *glutinosa* subsp. *barbata (Alnus* aff. *barbata)*		0.20								0.80				1.00
Carpinus aff. *betulus*		1.00												1.00
Carpinus aff. *orientalis*		0.50		0.50										1.00
Coriaria aff. *myrtifolia*		0.50		0.50										1.00
Populus aff. *alba*		0.40								0.60				1.00
Populua aff. *nigra*		0.50								0.50				1.00
Populus aff. *tremula*		0.50								0.50				1.00
Salix aff. *alba*		0.20								0.80				1.00
Salix aff. *eleagnos*		0.20								0.80				1.00
Salix aff. *caprea*		0.50		0.30						0.20				1.00
Salix sp.		0.50								0.50				1.00
Acer vindobonensis		1.00												1.00
Acer aff. *campestre*		0.80		0.20										1.00
Acer aff. *lobelii (Acer* aff. *cappadocicum* subsp. *lobelii)*		0.80								0.20				1.00
Acer aff. *monspessulanum*		0.50		0.50										1.00
Acer aff. *opalus* subsp. *obtusatum*		1.00												1.00
Tilia sp.		1.00												1.00

Table A1. continued

site: Oriolo	ZONAL									AZONAL			PROBLEMATIC taxa	
Taxa	CONIF	BLD	BLE	SCL	LEG	ZONPALM	ARBFERN	DRY HERB	MESO HERB	AZONAL WOODY	AZNW	AQUATIC		
Cornus sp.		0.90		0.10										1.00
Hedera aff. *helix*			0.80							0.20				1.00
Fraxinus aff. *angustifolia* subsp. *oxycarpa*		0.50								0.50				1.00
														47.00
Sum of taxa	3.00	27.00	1.30	4.00	0.00	0.00	0.00	0.45	1.55	7.20	2.50	0.00	0.00	47.00
Sum zonal taxa														37.30
Percentage of zonal taxa	8.04	72.39	3.49	10.72	0.00	0.00	0.00	1.21	4.16					100.00
Sum zonal woody angiosperms														32.30
percentage of zonal woody angiosperms		83.59	4.02	12.38	0.00	0.00								100.00
Sum of % SCL + LEG	12.38													
Sum of % DRY HERB + MESO HERB (ZONAL HERB)	5.36													



Vegetation type	Zonal woody components			Zonal herbaceous components (fossil record)	Zonal herbaceous components (modern record)
	BLD	BLE	SCL + LEG	MESO + DRY HERB	MESO + DRY HERB
Broad-leaved decidous forests	> 80 %			≤ 30 %	40–70 %
Ecotone	75–80 %	< 30 %	< 20 %	< 30 %	40–55 %
Mixed mesophytic forests	< 75 %				
Ecotone		30–40 %			
Broad-leaved evergreen forests		> 40 %	(SCL + LEG) < BLE	< 25 %	10–45 %
Subhumid sclerophyllous forests			≥ 20 %	< 30 %	40–55 %
Xeric open woodlands		< 30 %	≥ 20 %	30–40%; MESO HERB > DRY HERB up to 10 % of all zonal herbs	n.a.
Xeric grasslands or steppe		< 30 %		≥ 40 %	n.a.

Table A2. Drudge 1 analysis for the Pleistocene flora of Oriolo: Listed are similarities to modern vegetation types based on IPR and taxonomic (genus-level) similarity.

Table A2 is available as an electronic supplement only.