

The role of central Italy as a centre of refuge for thermophilous plants in the late Cenozoic

EDOARDO MARTINETTO

Dipartimento di Scienze della Terra, 5, via Accademia delle Scienze, I-10123 Torino, Italy, e-mail: martinetto@dst.unito.it

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ABSTRACT. Several fruit and seed assemblages have been gathered from the Pliocene and Early Pleistocene deposits of central Italy. Ongoing research on this material has led to the identification of relevant thermophilous taxa, also known in the Neogene of central Europe, but mostly in older sediments. This emphasizes the role of central Italy as a centre of refuge for thermophilous plants, in particular during the phases of climatic deterioration of the Middle and Late Pliocene. The group of species which persisted until the Middle Pliocene in the study area includes: *Tetraclinis salicornioides*, *Cryptomeria rhenana*, *Trigonobalanopsis exacantha*, *Itea europaea*, *Litsea? sonntagii*, *Magnolia allasoniae*, *M. ludwigii*, *Cyclea palatinati-bavariae*, *Ficus potentilloides*, *Cephalanthus pusillus*, *Toddalia latisiliquata* (possibly passing into the Late Pliocene), *T. naviculaeformis*, *T. rhenana*, *Zanthoxylum ailanthiforme*, *Meliosma canavesana*, *M. wetteraviensis*, *Sabia europaea*, *Sapindoidea margaritifera*, *Eurya stigmosa* and *Sparganium nanum*. A few thermophilous species persisted into the Late Pliocene (*Sequoia abietina*, *Sinomenium cantalense* and *Symplocos lignitarum*) while *Liriodendron geminata* was probably still extant into the Early Pleistocene (only pollen records), as *Liquidambar cf. europaea* and *Leitneria venosa* undoubtedly were.

KEY WORDS: fossils, fruit and seed, floristic refuge, Pliocene, Early Pleistocene, central Italy

INTRODUCTION

In central Italy several late Cenozoic continental basins are present, and their alluvial, fluvial or lacustrine deposits often contain different kinds of terrestrial plant remains, including fruits and seeds, which have been poorly studied until now. Since the late 1980^s, the present author has been visiting several outcrops and collecting a few sediment samples containing fossil fruits and seeds (“carpoids”) from selected layers, mostly in the Upper Valdarno and Tiberino basins (Fig. 1). The same type of research has been extended to two well-dated marine successions, which are rich in terrestrial plant remains: Marecchia and San Miniato). These samples have been processed and analysed according to the standard method employed by the author (Martinetto 1995, Basilici et al. 1997) and most of them gave positive results, so that a few dozen carpological species have been

identified in each fossil site (only 4 species in San Miniato). These floras are still mainly unpublished, so it seems pertinent to give here a short report on some important occurrences of plant mega/mesofossil taxa, with particular emphasis on those exotic elements which seem to have extended their stratigraphic range further than was formerly believed.

These data are particularly meaningful because the stratigraphic and geochronological assessment of central Italian continental successions has seen considerable advances in the last decade: many sections provided mammal assemblages (Gliozzi et al. 1997) and good magnetostratigraphic records, as well as long pollen sequences which highlight the patterns of vegetation change in the late Cenozoic, in particular during the onset of glacial/interglacial cycles in the Late Pliocene (Abbazzi et al. 1997, Bertini & Roiron 1997, Pontini & Bertini 2000).

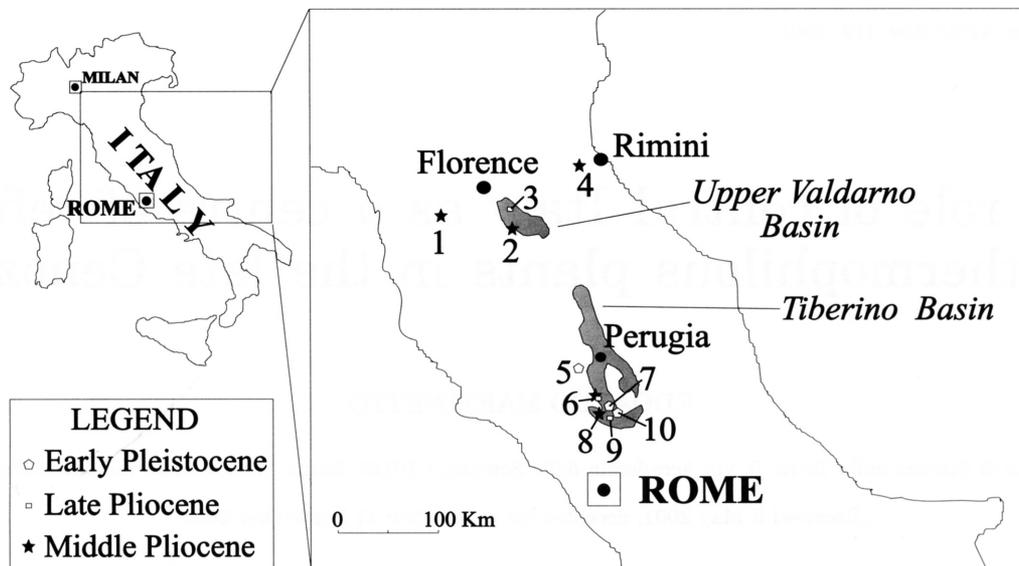


Fig. 1. Location of the Pliocene and Early Pleistocene study sites in central Italy. **1** – San Miniato, **2** – Santa Barbara, **3** – Poggiorosso near Matassino, **4** – Marecchia near Villa Verrucchio, **5** – Pietrafitta, **6** – Cava Toppetti-Todi, **7** – Collevalenza and Monticello, **8** – Dunarobba, **9** – Torre di Picchio, **10** – Villa San Faustino

STUDY SITES

One of the successions which has been more actively investigated in the last decade is the “first lacustrine phase” (Albianelli et al. 1995) of the Upper Valdarno Basin (Toscana), assigned to the Middle Pliocene. The whole succession is nearly 250 m thick and is divided into three formations: Spedalino Sands and Gravels, Meleto Clays and San Donato Sands (Torre et al. 1996). In particular the Meleto Clays contain well-preserved leaf assemblages which had already attracted the attention of several authors of the 19th century (Gaudin & Strozzi 1859, Ristori 1886, review in Mori Secci 1992).

More recently, Gregor (1990) published a list of carpological species (additional unpublished material is stored at the Naturmuseum of Augsburg, Germany) and Mai (1994) investigated the cones of a few pinaceous species, mainly originating from a 10 m thick sandy succession at the transition between the Meleto Clays and the overlying San Donato Sands, cropping out in the vicinity of a country house named La Tassinaiia. Several samples from this outcrop, indicated as Gregor’s section in this work, have been prepared by the present author, and the resulting collection of identified fruits and seeds has been deposited at the Earth Sciences Dept. of Torino.

The present author also collected a few fruits and seeds in the lower part of the Meleto Clays, at an outcrop close to the hamlet of Le Matole. Furthermore, Bertini and Roiron (1997) provided information on the leaf assemblages of the Meleto Clays.

All these 20th century records are referred to the succession which had been exposed until the late 1990^s in the Santa Barbara brown coal open-cast mine (Fig. 1: 2). In addition, a diversified macroflora (leaves, fruits and seeds) from an outcrop of the same formation in the vicinity of the village of Meleto has been described by Fischer and Butzmann (in press).

Albianelli et al. (1995, 1997) and Torre et al. (1996) demonstrated, on the basis of magnetic stratigraphy and mammal biochronology, that the Meleto Clays were deposited within the Gauss normal magnetochron (Middle Pliocene), and that the transition to the Matuyama reversed magnetochron (Late Pliocene) falls within the San Donato Sands.

The “second lacustrine phase” of the Upper Valdarno basin has been investigated near the village of Matassino, at the Poggiorosso site (SO.LA.VA. Quarry, Fig. 1: 3), where some fluvial-alluvial layers yielded very rich mammal assemblages (Mazzini et al. 2000). Here, interesting plant macroremains were collected from two sandy beds, which provide a detailed record not only of the local vegetation, but also of

the one growing on the slopes around the depositional basin. According to Mazzini et al. (2000) the age of the Poggiorosso succession is latest Pliocene, since the magnetostratigraphic analysis suggests it was formed during the Olduvai subchron.

Further south, in between the Apennine ranges, another large depression filled up by Pliocene and Early Pleistocene continental deposits occurs: the Tiberino Basin of the Umbria region. In its southwestern branch, running from Perugia to Todi, Basilici (1997) distinguished a few formations deposited in lacustrine or fluvial-alluvial palaeoenvironments. Each formation includes layers with a more or less good record of plant remains, which have been sampled by the present author in selected sites:

1) the Fosso Bianco Formation provided meaningful remains in the Cava Toppetti I site near Todi (Fig. 1: 6) and especially in several layers of the muddy-sandy deposits embedding the Fossil Forest of Dunarobba I (Fig. 1: 8, uncertain age, but probably Middle or Late Pliocene: Ambrosetti et al. 1995b). Actually the richest carpoflora has been found in a section (Dunarobba II, B, Ambrosetti et al. 1995b) which is located 400 m to the NW of the Fossil Forest site, and which is thought to be stratigraphically higher, and therefore a bit younger, than the Fossil Forest. The fossil fruits and seeds of the Cava Toppetti I site have been extracted by sandy sediments rich in mummified plant remains, which are enclosed in a big sub-lacustrine landslide, located above the top of the 140 m thick muddy succession drawn by Basilici (1997), which spans the late Middle Pliocene and the early Late Pliocene (ca. 3 to 2.1 Ma: Abbazzi et al. 1997). Despite the precise calibration of the underlying succession, the age of the deposits enclosed in the landslide is problematic: it may be more or less synchronous to the upper part of the muddy succession (early Late Pliocene) or a bit older (i. e. Middle Pliocene);

2) the Ponte Naja Formation, in the Cava Toppetti II site (Fig. 1: 6) is a 150 m thick alluvial fan succession, which includes a planar-concave sandy-gravelly body (channel filling) with abundant mummified "carpoids" in its middle part. Taxonomic analysis of this flora has so far permitted the identification of 37 species of woody and herbaceous plants. The

age of this succession has been determined as Late Pliocene using palaeomagnetic data, combined with the biochronologic interpretation of the mammal assemblages (Abbazzi et al. 1997);

3) four sites of the fluvial-alluvial Santa Maria di Ciciliano Formation provided carpological material, even if the floras contained fewer than 30 species. The most important floras are those of Torre di Picchio (Fig. 1: 9; Girotti et al. in press) and Villa San Faustino (Fig. 1: 10; Ambrosetti et al. 1995a); both sites provided important mammal assemblages, which made it possible to fix their age respectively to the latest Pliocene (C. Petronio pers. comm.) and to the Early Pleistocene. Useful information on fossil "carpoids" is available also for Monticello near Todi and Collevaenza (Fig. 1: 7). These sites are regarded by Basilici (1997) as Early Pleistocene, but there are no reliable dating elements to support this view.

Furthermore, in the same Umbria region, a few layers of the Pietrafitta site (Tavernelle basin, Fig. 1: 5) provided a diversified assemblage of freshwater macrophytes, associated with just a few remains coming from the terrestrial palaeoenvironment, so that the flora and vegetation of the dry land cannot be reconstructed on the basis of macroscopic remains alone. In the brown coal, which was being excavated at this site in the late 20th century (Lona & Bertoldi 1973), a variety of spectacular mammal remains has been recovered. The rich faunal assemblage suggests a latest Early Pleistocene age (Gliozzi et al. 1997).

Finally, the two marine deposits sampled for fossil "carpoids" are:

(I) a Middle Pliocene (ca. 3.0 to 2.9 Ma) portion of the well-calibrated Marecchia section (Fig. 1: 4; near Rimini, Adriatic coast), which according to Rio et al. (1997) covers a time interval from 3.1 to 2.2 Ma as a whole;

(II) another Middle Pliocene section in the vicinity of San Miniato (Fig. 1: 1; Lower Valdarno basin, Toscana), where four carpological species were found by S. Dominici in the residue of a bulk sample for mollusc analysis in a lagoonal layer (CSL1). The age of this section is based on the general sequence stratigraphic interpretation of the Lower Valdarno basin, where multiple data sets are available: index foraminifers, molluscs, continental mammals, magnetic stratigraphy (Benvenuti et al. 1995, Dominici 1994).

SYSTEMATIC PART

Some aspects of the fossil record of selected exotic species which have been detected in the studied floras are discussed below; in addition Table 1 shows the occurrences of further exotic elements. A complete overview of the floristic composition of the Pliocene/Early Pleistocene fruit and seed assemblages from central Italy is not yet available.

Gymnospermae

Cupressaceae

Tetraclinis salicornioides (Unger) Kvaček

Pl. 1 fig. 1, Pl. 2 figs 1a, b

1840 *Hellia salicornioides* Unger, p. 375.

1986 *Tetraclinis salicornioides* (Unger) Kvaček, p. 48, Pl. 1 fig. 11, Pl. 2 figs 2–14, Pl. 3 figs 3, 4.

The problematic nomenclature and taxonomy of Cenozoic leaf whorls and cones of *Tetraclinis* have been discussed by Mai (1997), who suggested using different specific names for these two types of remains, even when they are found in the same layer. Here, in agreement with former works on the Italian floras (Martinetto 1999) both cones and leaf whorls are designated with the single, widely used, binomial *Tetraclinis salicornioides* (Unger) Kvaček. A few remains of this species have been found in the "New Quarry" of Dunarobba II: 2 cones in one layer and 6 characteristic twig segments in another. In central Europe this species does not occur in Pliocene sites (Mai 1997), whereas it is rather common in the Early Pliocene of NW Italy (Martinetto 1999). The fossils of Dunarobba II prove that this species survived in central Italy at least until the Middle Pliocene, and its absence in the younger floras seems to indicate that later it either disappeared or became very rare.

Taxodiaceae

Cryptomeria rhenana Kilpper

Pl. 2 fig. 2

1968 *Cryptomeria rhenana* Kilpper, p. 104–106, Pl. 34 figs 23–30, Pl. 35 figs 1–8, Pl. 38 figs 3, 4; Figs 1–4.

In northern Italy this species occurs in several Early and Middle Pliocene sites (Marti-

netto 1999); in central Italy it is found in Santa Barbara (Gregor's section), Dunarobba II and Cava Toppetti I. Here it is mostly documented by seeds, which are readily recognizable for the trapezoidal to sub-rhombic outline and peculiar cell pattern. The seeds are associated with *Cryptomeria*-type shoot fragments, while the cones are absent or badly preserved.

Sequoia abietina (Brongniart) Knobloch

Pl. 1 figs 2–4

1822 *Phyllites abietina* Brongniart, p. 362, Pl. 15 fig. 16.

1964 *Sequoia abietina* (Brongniart) Knobloch, p. 601.

The presence of *Sequoia* in the Pliocene of central Italy had been generally assumed on the basis of the abundance of *Sequoia*-type pollen in several sections. Paganelli (1995) even attempted the reconstruction of a Pliocene *Sequoia* forest and its ecological conditions. Surprisingly, records of *Sequoia* cones have been scarce until now; in the present work cones of *Sequoia abietina* were retrieved from the samples of Gregor's section at Santa Barbara, and from both carpological assemblages of Cava Toppetti (I and II), where they are rather common. On the other hand, macrofossils of *Sequoia* are absent in Dunarobba (I and II), and this seems to be a good reason for rejecting the hypothesis that the large trunks forming the spectacular Fossil Forest might belong to *Sequoia* (Biondi & Brugiapaglia 1991, Paganelli 2000). They are more likely to represent remains of the *Glyptostrobus europaeus* plant, whose cones and shoots are very common in this site (Martinetto 1994, 2000). The source of the abundant *Sequoia*-type pollen found in the swamp sediments (Ambrosetti et al. 1995b) of the Fossil Forest might be both *Cryptomeria* and *Sequoia* plants growing in neighbouring, better-drained palaeoenvironments. Incidentally, *Sequoia* shoots have been collected in the sediments of the Fosso Bianco Formation not far from Dunarobba (Basilici 1997). In conclusion, *Sequoia* still ought to be an important tree in the Middle and Late Pliocene of central Italy, and some pollen diagrams suggest that it survived in southern Italy (Calabria) after the Pliocene/Pleistocene boundary (Combourieu-Nebout 1993); unfortunately no macrofossil record is presently available to support this view.

Table 1. Occurrence of some exotic species in the Pliocene and Early Pleistocene sites of central Italy. Age abbreviations: L – Late, Ist – latest, E – Early, M – Middle, Pli – Pliocene, Ple – Pleistocene

Species	Site	Age
<i>Actinidia faveolata</i> C. & E.M. Reid	Dunarobba II	M? Pli
<i>Alangium</i> sp.	Dunarobba II	M? Pli
<i>Ampelopsis malvaeformis</i> (Schlotheim) Mai	Dunarobba II, Cava Toppetti I, Monticello	M? Pli (?E Ple)
<i>Boehmeria</i> sp.	Torre di Picchio	Ist Pli
<i>Carya</i> sp.	Santa Barbara	M Pli
<i>Cathaya van-der-burghii</i> Gossmann in Mai	Santa Barbara, Poggiorosso	M Pli-Ist Pli
<i>Cephalanthus pusillus</i> Friis	Dunarobba I-II	M? Pli
<i>Cephalotaxus</i> sp.	Santa Barbara, Cava Toppetti II, Poggiorosso	M Pli-Ist Pli
<i>Craigia brononii</i> (Unger) Kvaček, Bůžek & Manchester	Meleto	M Pli
<i>Decodon</i> spp.	Dunarobba II, Torre di Picchio, Pietrafitta	M? Pli-E Ple
<i>Cryptomeria rhenana</i> Kilpper	Santa Barbara, Dunarobba II	M Pli
<i>Cyclea palatinati-bavariae</i> Gregor	Santa Barbara, Dunarobba II	M Pli
<i>Eurya stigmosa</i> (Ludwig) Mai	Santa Barbara, Dunarobba II	M Pli
<i>Fagaropsis?</i> sp.	Poggiorosso, Torre di Picchio	Ist Pli
<i>Ficus potentilloides</i> Mai	Dunarobba II, Cava Toppetti I	M? Pli
<i>Glyptostrobus europaeus</i> (Brongniart) Unger	Santa Barbara, Dunarobba I-II, Cava Toppetti I	M Pli
<i>Halesia</i> cf. <i>crassa</i> (C. & E.M. Reid) Kirchheimer	Poggiorosso	Ist Pli
<i>Ilex</i> cf. <i>protogea</i> Mai	Torre di Picchio	Ist Pli
<i>Itea europaea</i> Mai	Dunarobba I	M? Pli
<i>Juglans bergomensis</i> (Balsamo-Crivelli) Massalongo	Santa Barbara, Poggiorosso, Torre di Picchio	M Pli-Ist Pli
<i>Leitneria venosa</i> (Ludwig) Dorofeev	Villa San Faustino	E Ple
<i>Liquidambar</i> cf. <i>europaea</i> A. Braun	Santa Barbara, Dunarobba II, Cava Toppetti I, Poggiorosso, Torre di Picchio, Pietrafitta	M Pli-E Ple
<i>Liriodendron geminata</i> Kirchheimer	Dunarobba II, Poggiorosso, Torre di Picchio	M? Pli-Ist Pli
<i>Litsea?</i> <i>sonntagii</i> Gregor	Marecchia, San Miniato, Santa Barbara, Dunarobba I-II	M Pli
<i>Lobelia pliocenica</i> (Dorofeev) Mai	Dunarobba II, Poggiorosso, Torre di Picchio	M? Pli-Ist Pli
<i>Magnolia cor</i> Ludwig	Cava Toppetti II, Torre di Picchio	L Pli-Ist Pli
<i>Magnolia allasoniae</i> Martinetto	Santa Barbara, Dunarobba I-II	M Pli
<i>Magnolia ludwigii</i> Ettingshausen	Marecchia, Santa Barbara, Dunarobba II	M Pli
<i>Mahonia staphyleaeformis</i> Mai & Walther	Cava Toppetti II	L Pli
<i>Melissa elegans</i> E.M. Reid	Torre di Picchio	Ist Pli
<i>Meliosma canavesana</i> Martinetto	Santa Barbara, Dunarobba II	M Pli
<i>Meliosma wetteraviensis</i> (Ludwig) Mai	Dunarobba I	M? Pli
<i>Myrica</i> sp.	San Miniato, Dunarobba II	M Pli
<i>Nyssa disseminata</i> (Ludwig) Kirchheimer	Santa Barbara	M Pli
<i>Ocotea</i> sp. A	Santa Barbara	M Pli
<i>Paleocarya macroptera</i> (Brongniart) Jännichen, Friedrich & Takáč	Meleto	M Pli
<i>Parrotia</i> sp.	Poggiorosso	Ist Pli
<i>Phellodendron</i> cf. <i>elegans</i> (C. & E.M. Reid) C. & E.M. Reid	Cava Toppetti II	L Pli
<i>Proserpinaca reticulata</i> C. & E.M. Reid	Dunarobba II	M? Pli
<i>Pseudoeuryale limburgensis</i> (C. & E.M. Reid) Dorofeev	Villa San Faustino	E Ple
<i>Pseudolarix schmidtgenii</i> Kräusel	Santa Barbara, Meleto	M Pli
<i>Pseudotsuga</i> sp.	Cava Toppetti I	M? Pli
<i>Pterocarya</i> sp.	Marecchia, Santa Barbara, Dunarobba I-II, Poggiorosso, Torre di Picchio	M Pli-Ist Pli

Table 1. Continued.

Species	Site	Age
<i>Rehderodendron ehrenbergii</i> (Kirchheimer) Mai	Santa Barbara	M Pli
<i>Sabia europaea</i> Czezzott & Skirgiello	Santa Barbara, Dunarobba II	M Pli
<i>Sapindoidea margaritifera</i> (Ludwig) Kirchheimer	San Miniato	M Pli
<i>Sassafras ludwigii</i> Mai	Dunarobba II	M? Pli
<i>Sequoia abietina</i> (Brongniart) Knobloch	Santa Barbara, Cava Toppetti I-II	M Pli-L Pli
<i>Sinomenium cantalense</i> (Reid) Dorofeev	Meleto, Dunarobba II, Cava Toppetti II	M Pli-L Pli
<i>Sparganium nanum</i> Dorofeev in Kolakovsky	Dunarobba II, Cava Toppetti I	M? Pli
<i>Spirella</i> sp.	Dunarobba II	M? Pli
<i>Swida gorbunovii</i> (Dorofeev) Negru	Dunarobba I-II	M? Pli
<i>Symplocos casparyi</i> Ludwig	Marecchia	M Pli
<i>Symplocos lignitarum</i> (Quenstedt) Kirchheimer	Marecchia, Dunarobba II, Cava Toppetti I-II	M Pli-L Pli
<i>Symplocos schererii</i> Kirchheimer	Santa Barbara	M Pli
<i>Taxodium dubium</i> (Sternberg) Heer	Santa Barbara, Meleto	M Pli
<i>Tetraclinis salicornioides</i> (Unger) Kvaček	Dunarobba II	M? Pli
<i>Toddalia latisiliquata</i> (Ludwig) Gregor	San Miniato, Dunarobba II, Cava Toppetti I-II	M Pli (L Pli?)
<i>Toddalia naviculaeformis</i> (Reid) Gregor	Marecchia	M Pli
<i>Toddalia rhenana</i> Gregor	Marecchia, Dunarobba II, Cava Toppetti I	M Pli
<i>Trichosanthes fragilis</i> E.M. Reid	Marecchia	M Pli
<i>Trigonobalanopsis exacantha</i> (Mai) Kvaček & Walther	Santa Barbara	M Pli
<i>Zelkova</i> sp.	Torre di Picchio	Ist Pli

Angiospermae – Dicotyledones

Fagaceae

Trigonobalanopsis exacantha
(Mai) Kvaček & Walther

Pl. 1 fig. 5

1970 *Trigonobalanus exacantha* Mai, p. 385, Pl. 1 figs 19–26, Pl. 2 figs 1–18, Pl. 3 figs 1, 15–19.1988 *Trigonobalanopsis exacantha* (Mai) Kvaček & Walther, p. 404, Pl. 47 figs 1–14, Pl. 48 figs 1–3.

In central Italy the occurrence of the characteristic cupules of this species is restricted to the Middle Pliocene sediments of the Upper Valdarno basin (Gregor's outcrop of Santa Barbara and Meleto; Gregor 1990, Fischer & Butzmann 2000). In northern Italy this species is a constant component of the floras of the Ca' Viettone complex (Martinetto 1999), and is often so common as to suggest that it was an important element of the mixed evergreen and broadleaf forest which covered the margins of the Po Basin in the Early Pliocene. At the meantime it was certainly still growing on the Atlantic coast of Europe too (Zagwijn 1990).

Altingiaceae

Liquidambar* cf. *europaea A. Braun

Pl. 1 fig. 6

1847 *Liquidambar europaea* A. Braun in Unger, p. 120, Pl. 35 figs 1–5.1959 *Liquidambar magniloculata* Czezzott & Skirgiello, p. 93, Pl. 15 figs 1–4.

Fruiting heads of *Liquidambar* have been found at Santa Barbara, in the Fosso Bianco Formation of Dunarobba II and Cava Toppetti I (Middle or Late Pliocene), as well as in the Torre di Picchio and Poggiorosso sites (latest Pliocene). Other badly preserved, much compressed fruiting heads, collected in the latest Early Pleistocene of the Pietrafitta site, have been observed in the Boldrini private collection (Pietrafitta, Perugia). These last specimens originate from the muddy layers above the main brown coal seam, where Lona and Bertoldi (1973) detected rather high pollen percentages of *Liquidambar*. These records prove that *Liquidambar* persisted in the Italian Peninsula longer than in transalpine Europe, where it seems to have disappeared in the Late Pliocene (Mai 1997). However, the specimens from central Italy have not yet been

submitted to a careful comparative analysis in order to assess their specific status. The well-preserved specimens from Cava Toppetti and Poggiorosso seem to be identical to analogous remains, rather common in the Early Pliocene of NW Italy (Martinetto 1995, Basilici et al. 1997), which had been assigned to *Liquidambar magniloculata* Czechtz & Skirgiello. However, according to Mai (1997), the valid name of this species is *L. europaea* A. Braun.

Hydrangeaceae

Itea europaea Mai

1985 *Itea europaea* Mai, p. 84, Pl. 6 fig. 1.

A few seeds and one fruit of this species were found in two samples of muddy sediment from the Fossil Forest of Dunarobba. In north-western Italy, this species occurs, always with a few seeds and/or fruits, in two sites of Early or Middle Pliocene age (Boschi and Pranzalito) and three ones of probable Middle Pliocene age (Martinetto 1999). These records suggest it was an accessory element of the mid-Pliocene swamp forest. Fossil pollen of *Itea* has been detected in a short section of the Sarzana Basin (north-western part of central Italy), tentatively assigned to the Miocene-Pliocene transition (Bertoldi et al. 1994). In this site carpological data are not yet available, but the high pollen percentages (12%) suggest that *Itea* was an important element in the local vegetation.

Mai (1985) showed that the nearest living relative of *Itea europaea* is the American species *I. virginica* L., which is the most cool-tolerant species (northern limit in Illinois) of this mainly tropical-subtropical genus. For this reason it is not surprising to find *I. europaea* in the Middle Pliocene of both northern and central Italy, and even of NW Europe (Belfeld: Mai 1985). Up to the present there is no evidence in favour of the longer persistence of this species in southern Europe.

Lauraceae

Litsea? sonntagii Gregor

Pl. 1 fig. 7

1980 *Litsea sonntagii* Gregor, p. 21, Pl. 4 figs 14–21.

The identification of lauraceous endocarps is often problematic, but in the floras of the

Ca' Viettone complex (Early Pliocene) of north-western Italy, a very characteristic type occurs, which probably represents a single species. In earlier works (Martinetto 1995, 1999) this species had erroneously been regarded as similar to *Gironniera carinata* Mai. Later it was recognized as a member of the Lauraceae, of which the most similar type described in the literature seemed to be *Litsea sonntagii* Gregor (Gregor 1980) of the Bavarian Miocene. Meller (Meller et al. 1999) already stated that the generic identification of "*Litsea? sonntagii*" was questionable and I agree with her because I collected some endocarps with a very similar morphology from a living lauraceous plant in Sichuan (China), most probably belonging to the genus *Lindera*. Therefore it will be necessary to investigate further the generic assignment of this species by looking for exceptionally well-preserved specimens. The recent discovery of a few complete fruits of *Litsea? sonntagii* Gregor, still attached to the pedicels, in a new fossil site near Fossano (NW Italy) could help in the assessment of its correct generic placement.

Despite the uncertain generic status, the specific assignment of the Italian material is well-defined: some specimens have been sent to Dr. H.-J. Gregor, who compared them with the German material, thus confirming the identification as *Litsea? sonntagii*. In central Italy *Litsea? sonntagii* is rather common in the deposits of Dunarobba (both the Fossil Forest and the "New Quarry"), it is rare at Marecchia and in Gregor's section of Santa Barbara, and it occurs as a single endocarp in the San Miniato site (Lower Valdarno, Middle Pliocene).

Leitneriaceae

Leitneria venosa (Ludwig) Dorofeev

Pl. 1 figs 8, 9

1857 *Lobelia venosa* Ludwig, p. 97, Pl. 21 figs 6a-c.

1960 *Leitneria venosa* (Ludwig) Dorofeev, p. 660.

A single, strongly compressed endocarp has been collected from the sediments of the Villa San Faustino site. This isolated specimen demonstrates that *Leitneria venosa* persisted in Italy until the Early Pleistocene. Actually its presence in the Pliocene was suggested by Gregor (1990), who listed a *Leitneria* sp. in the Early Pliocene San Gimignano flora. In northern Italy several endocarps of *L. venosa* have

recently been found at the top of the Cervo River section (Martinetto 1998: ?Late Pliocene). In conclusion *Leitneria* is a rare element in the late Cenozoic floras of Italy, and its ecological and climatic significance cannot as yet be fully appreciated.

Magnoliaceae

Liriodendron geminata Kirchheimer

Pl. 2 fig. 3

1957 *Liriodendron geminata* Kirchheimer, p. 532, Fig. 147.

The seeds of this species are rather common in the Early and Middle Pliocene of northern Italy (Martinetto 1999), whilst in central Italy they are rare: a few pairs of seeds have been found in the sites of Dunarobba II and Torre di Picchio. The Pliocene pollen record does not provide clear indications: Paganelli (2000) reports low percentages of a *Araucaria-Liriodendron* pollen type in the Fossil Forest of Dunarobba, while Pontini and Bertini (2000) did not find *Liriodendron* in their Late Pliocene pollen diagram. Lona & Bertoldi (1973) detected *Liriodendron* pollen in the "Tiberian phase" of Pietrafitta, assigned by them to the Late Pliocene, but now unanimously referred to the late Early Pleistocene. In conclusion, *Liriodendron* probably survived until the Early Pleistocene in central Italy, even if its macrofossil evidence is restricted to the Plio-Pleistocene boundary (Torre di Picchio).

Magnolia allasoniae Martinetto

Pl. 2 fig. 4

1995 *Magnolia allasoniae* Martinetto, p. 90, Pl. 1 figs 4–7.

The rugose seeds of this species are rather common in the Pliocene of Italy, but so far I am unaware of any occurrence outside the country. In central Italy a few dozen seeds have been collected at Dunarobba I and II, two other seeds occurred in the basal part of the Meleto Clays at Santa Barbara (Le Matole section), and a single specimen was found in the Marecchia site. In conclusion this species occurs in the Middle Pliocene in central Italy, whereas in northern Italy it is restricted to the Early Pliocene (Martinetto 1999).

Magnolia ludwigii Ettingshausen

Pl. 1 figs 10, 11

1861 *Anona lignitum* Unger, p. 25, Pl. 10 fig. 7.

1868 *Magnolia ludwigii* Ettingshausen von, p. 871.

1975 *Magnolia lignita* (Unger) Mai, p. 571, Pl. 35–37 figs 34–38, 39–49, 50–58.

This species mostly occurred in central Europe before the Late Miocene (Salzhausen, Unger 1861, Ettingshausen 1868), with a single exception in the Early Pliocene of southern Poland (Mai 1975). On the other hand, in northern Italy it is commonly found in the Early Pliocene (Martinetto 1999). In central Italy its typical thick-walled seeds, with smooth external surface, are found in Marecchia, Santa Barbara (Gregor's section) and Dunarobba II, therefore the stratigraphic range of this species has to be extended to the Middle Pliocene.

Menispermaceae

Cyclea palatinati-bavariae Gregor

Pl. 2 figs 6, 7

1977 *Cyclea palatinati-bavariae* Gregor, p. 207, Pl. 18 figs 3–6; Fig. 3.

Two endocarp fragments, one from Gregor's section of Santa Barbara and the second from a sandy layer of the "New Quarry" of Dunarobba II, indicate that this species survived in central Italy at least until the Middle Pliocene. It was formerly known to occur in the Miocene of southern Germany and in three Early Pliocene sites of NW Italy (Martinetto 2001).

Sinomenium cantalense (Reid) Dorofeev

Pl. 2 fig. 5

1920 *Menispermum cantalense* Reid, p. 66, Pl. 3 figs 24, 25.

1955 *Sinomenium cantalense* (Reid) Dorofeev, p. 129.

In central Italy it is known to occur in the Middle Pliocene of the Upper Valdarno (Fischer & Butzmann 2000), in the "New Quarry" of Dunarobba II (Middle? Pliocene) and, very commonly, in the middle part of the Ponte Naja Formation at the Cava Toppetti II site (Late Pliocene). This last occurrence would suggest that *S. cantalense* survived the important extinction phase of the Middle-Late Pliocene transition (end-Reuverian), which

seemed to cause its disappearance from northern Italy (Martinetto 1999).

Moraceae

Ficus potentilloides Mai

Pl. 2 figs 8a, b

1964 *Ficus potentilloides* Mai, p. 23, Pl. 2 fig. 17; Fig. 3.

The tiny seeds show a variable and scarcely diagnostic shape, however they agree perfectly with the type material (observed at the Natural History Museum of Humboldt University in Berlin in 1993) of the species described by Mai (1964). Their moraceous character is confirmed by the characteristic cell pattern (Pl. 2 fig. 8b). The material presently known in central Italy consists of several seeds from the "New Quarry" of Dunarobba II and a few ones from the Cava Toppetti I site. This species was formerly known in a few localities of central European Miocene and of the north Italian Lower to Middle Pliocene (Martinetto & Mai 1996, Martinetto 1999).

Naucleaceae (Rubiaceae)

Cephalanthus pusillus Friis

Pl. 2 figs 9a, b

1985 *Cephalanthus pusillus* Friis, p. 69, Pl. 21 figs 1–7.

Mai (2000) proposed to use the name *Cephalanthus pusillus* Friis (= *C. dorofeevi* Arbuzova & Zhilin) as a valid synonym for *C. kirevskianus* Dorofeev (published without description). The type specimens described by Friis (1985) had been differentiated on the basis of the comparatively small size, although they bear essentially the same characters as the bulk of the Cenozoic specimens of *Cephalanthus* L. found in Europe and Siberia (Dorofeev 1963, Mai 2000). In this broader sense the species includes Eocene to Late Miocene records from central and eastern Europe and Early-Middle Pliocene records from northern Italy (Mai 1995a, Martinetto 1995, Cavallo & Martinetto 1996). In central Italy several fruits of this species (including tiny specimens identical to the Danish type material) have been detected in the Dunarobba I and II sites.

Rutaceae

Toddalia latisiliquata (Ludwig) Gregor

Pl. 1 figs 12a, b, 13

1860 *Cytisus latisiliquatus* Ludwig, p. 145, Pl. 58 fig. 17.

1978 *Toddalia latisiliquata* (Ludwig) Gregor, p. 25, Pl. 2 figs 3–5, Pl. 3 figs 1–6, Pl. 4 figs 1–6, Pl. 5 fig. 1; Fig. 1d.

A species characterized by its mid-sized (5–6 mm), thick-walled, bean-like seeds of rather variable shape. A few specimens occurring at San Miniato, Dunarobba II and Cava Toppetti I prove that *Toddalia latisiliquata* persisted until the Middle Pliocene in central Italy, thus post-dating its extinction time in northern Italy (Early-Middle Pliocene: Martinetto 1999) and central Europe (Late Miocene: Gregor 1979). Moreover, the presence of two seeds of this species in the Cava Toppetti II flora would suggest that it was still present in central Italy during the Late Pliocene, yet it would be better to wait for confirmation, as it is not possible to exclude that these specimens might have been reworked from older sediments.

Toddalia naviculaeformis (Reid) Gregor

Pl. 1 figs 14, 15

1920 Leguminosae g. (?), Reid, p. 69, Pl. 3 fig. 29a-b.

1923 *Martyia naviculaeformis* Reid, p. 327, Fig. 5a.

1975 *Toddalia naviculaeformis* (Reid) Gregor, p. 132, Pl. 7 figs 4, 5.

This species with large seeds (7–9 mm long) occurs only in the Marecchia site where six specimens were found. The occurrences in transalpine Europe, reported by Gregor (1978), include several sites of Miocene age (also Pont-de-Gail, the type locality of this species, is Upper Miocene after Gibert et al. 1977). However, this species had already been found in a Middle Pliocene site of NW Italy (Martinetto & Mai 1996), so that the record from Marecchia does not post-date its hypothetical extinction time from Europe, i. e. the Middle-Late Pliocene transition.

Toddalia rhenana Gregor

Pl. 1 figs 16, 17

1979 *Toddalia rhenana* Gregor, p. 325, 327, Figs 38, 39.

The seeds of this species are definitely smaller (length 3–4 mm) than those of *Toddalia latisiliquata*. In central Europe *T. rhenana*

is distributed in the Miocene and Early Pliocene (Gregor 1979), whereas in northern Italy it is rather common in the Early and Middle Pliocene. In central Italy it has been found at Marecchia, Dunarobba II and Cava Toppetti I, so it does not seem to have survived beyond the Middle-Late Pliocene boundary.

Zanthoxylum ailanthiforme

(Gregor) Gregor

Pl. 1 figs 18–21

- 1975 *Rutaspermum ailanthiforme* Gregor, p. 122, Pl. 6, fig. 5; Fig. 38.
 1978 *Zanthoxylum ailanthiforme* (Gregor) Gregor, p. 30, Pl. 1 figs 1–4.

Seeds of *Zanthoxylum* have been found at the following sites: Marecchia (11 specimens), Cava Toppetti I (7) and Dunarobba II (2). At first glance the seed populations from central Italy seemed to belong to *Z. ailanthiforme* (Gregor) Gregor. This species has been reported in the Early Pliocene of northern Italy, and in particular at the Ca' Viettone site (Bertoldi & Martinetto 1995), where a goodly number of specimens (ca. 30) occur. Remarkably, comparison of this material with the collections from central Italy showed that the two populations are readily distinguishable, even if individual specimens may be completely identical. The prevailing form in the population from northern Italy is characterized by its sub-circular outline and markedly curved hilum which always extends over the full width of the seed. The sculpture is coarse, with irregular tubercles and pustules. In the populations from central Italy, the prevailing form tends to be broader (mean dimensions: $4.3 \times 3.2 \times 2.2$ mm), semicircular or boat-like in outline, with a quasi-straight hilum extending over 3/4 of the seed width. The sculpture is quite variable, but often finer than in the north Italian specimens, and sometimes with short transverse ridges which traverse the slight depression below the hilar scar.

Probably the two populations should be assigned to separate taxonomic entities, but it is difficult to regard them as two species, since individual specimens of the two populations may be identical. However, the forms from central Italy agree quite well with the type specimens of *Z. ailanthiforme* (Gregor 1978), and are therefore assigned to this species, even though they are slightly larger (4.3×3.2

vs 3.5×2.6 mm). Taxonomic and nomenclatural assessment of the north Italian population will be the subject of future work.

Sabiaceae

Meliosma canavesana Martinetto

Pl. 1 figs 22, 23a, b

- 2001 *Meliosma canavesana* Martinetto 2001, p. 157, Pl. 3 figs 6–10, Pl. 4 fig. 4.

This recently described species (Martinetto 2001) occurs as two endocarps in Santa Barbara (Gregor's outcrop) and half an endocarp in a sandy layer of the "New Quarry" of Dunarobba II. This means that it survived in central Italy at least until the Middle Pliocene. The nearest living relatives are some tropical-subtropical species of SE Asia belonging to the subgen. *Meliosma*.

Meliosma wetteraviensis (Ludwig) Mai

- 1857 *Hamamelis wetteraviensis* Ludwig, p. 105, Pl. 20 figs 27a, b.
 1964 *Meliosma wetteraviensis* (Ludwig) Mai, p. 110.

The present author recently supported the view that only one fossil species of *Meliosma* subgen. *Kingsboroughia* is present in the late Cenozoic of Italy: *Meliosma wetteraviensis* (Martinetto 2001). This species occurs in the Dunarobba Fossil Forest represented by three small endocarps ("*M. pliocaenica*" morphotype, a specimen was illustrated by Martinetto 1994) and a single, larger one (5.5×5 mm). In NW Italy *M. wetteraviensis* is particularly common in the floras of the Stura complex (Middle Pliocene), being a probable member of the extensive *Glyptostrobus europaeus* swamp forest, an ancient plant community which has been well-recorded in the Dunarobba succession too (Martinetto 1994, 2000).

Sabia europaea Czechtz & Skirgiello

Pl. 1 figs 24, 25

- 1959 *Sabia europaea* Czechtz & Skirgiello, p. 122, Pl. 20 figs 9–12.

Two fragmentary, but readily recognizable endocarps of this species were found respectively in Gregor's outcrop of Santa Barbara and in a sandy layer of the "New Quarry" of Dunarobba II. *S. europaea* is very rare in Italy,

with single specimens only having been found in a few Early and Middle Pliocene floras of NW Italy (Martinetto 1998).

Sapindaceae?

Sapindoidea margaritifera (Ludwig)

Kirchheimer

Pl. 1 figs 26a, b

- 1860 *Taxus margaritifera* Ludwig, p. 73, Pl. 60 fig. 19.
 1936a *Sapindoidea margaritifera* (Ludwig) Kirchheimer, p. 89, Pl. 9 fig. 1a-f.
 1991 *Koelreuteria margaritifera* (Ludwig) Mai in Mai & Walther, p. 108, Pl. 13 fig. 17 [not accepted].

This species in northern Italy seems to be a rather constant and index taxon in the floras of the Ca' Viettone complex (Early Pliocene); its presence in the Middle Pliocene has not yet been proven. In central Italy, two specimens of *S. margaritifera* have been collected by Dr. S. Dominici in the San Miniato section, assigned to the Middle Pliocene (see above). Furthermore, Gregor (1990) reported *Sapindoidea globosa* from the Early Pliocene section of San Gimignano. This latter species has not been confirmed for Italy by research over the last decade, making it necessary to check if Gregor's material too can be assigned to *S. margaritifera*.

Symplocaceae

Symplocos lignitarum (Quenstedt)

Kirchheimer

Pl. 1 figs 27-29

- 1867 *Carpolithus lignitarum* Quenstedt, p. 914, Pl. 86 figs 35, 41.
 1949 *Symplocos lignitarum* (Quenstedt) Kirchheimer, p. 14, Pl. 1 fig. 4, Pl. 2 fig. 15.

It has been proved recently that, towards the end of the Pliocene, the genus *Symplocos* still survived in northern Italy, but it was represented there by a member of *Symplocos* sect. *Palura*, a deciduous group of frost-tolerant plants (Cavallo & Martinetto in press). On the other hand, *S. lignitarum* may be referred to the broad thermophilous group of *Symplocos*, represented by evergreen shrubs and small trees. Its occurrence at Cava Toppetti II indicates that at least one of the species which characterize the warmest Neogene floras of Europe ("younger Mastixioidean") survived the Middle to Late Pliocene extinction phase (Mar-

tinetto 1999). This occurrence may be very important for reconstructing the ecological conditions of Mediterranean refuges in the Late Pliocene. This species has also been found at Marecchia, Dunarobba II and Cava Toppetti I.

Symplocos schereri Kirchheimer

Pl. 1 fig. 30

- 1935 *Symplocos schereri* Kirchheimer, p. 291, Fig. 8.
 1936b *Symplocos schereri* Kirchheimer, p. 221, Pl. 14 fig. 1a-e.

A few endocarps have been found in the sandy layers of the Santa Barbara site (Gregor's outcrop). In northern Italy these fossils were found in the majority of Early Pliocene carpological assemblages, and an external mould of one endocarp occurred at the top of the Arboschio section, which is assigned to the Middle Pliocene (Martinetto & Mai 1996). Thus the available data point to the persistence of this species in the Middle Pliocene of southern Europe, while in north-western Europe its last appearance dates to the Early Pliocene ("Brunsumian": Van der Burgh 1978)

Theaceae

Eurya stigmosa (Ludwig) Mai

Pl. 2 fig. 10

- 1860 *Potamogeton stigmusus* Ludwig, p. 60, Pl. 8 fig. 13.
 1960 *Eurya stigmosa* (Ludwig) Mai, p. 79, Pl. 4 figs 8-17; Fig. 4.

A species which in central Europe is particularly common in the Miocene, and appears to have its last record in the Early Pliocene (Van der Burgh 1983). It is also very common in the Early Pliocene of northern Italy, where it is probably still present in the Middle Pliocene (Martinetto 1999). In central Italy Gregor (1990) reported seeds of *Eurya* sp. (probably *E. stigmosa*) from San Gimignano (Early Pliocene), and a few seeds of *E. stigmosa* have been found at Santa Barbara (Gregor's outcrop) and Dunarobba II. Therefore this species does not seem to cross the Middle/Late Pliocene boundary; however, in eastern Europe it is reported from the Chori site (Georgia), whose age is close to the Pliocene/Pleistocene boundary (Mai 1997).

Vitaceae

Ampelopsis malvaeformis (Schlotheim)
Mai in Mai & Gregor

Pl. 2 fig. 11

- 1822 *Carpolithus malvaeformis* Schlotheim, p. 98, Pl. 21 figs 9a-c.
1982 *Ampelopsis malvaeformis* (Schlotheim) Mai in Mai & Gregor, p. 418, Pl. 21 figs 1-3.

A few seeds occur in Dunarobba and Cava Toppetti I, and a single specimen in Monticello. In northern Italy this species is rather common in the Early and Middle Pliocene, but seems to disappear at the Middle/Late Pliocene boundary. The discovery at Monticello suggests that in central Italy *Ampelopsis malvaeformis* would still have been present in the Early Pleistocene, but such a hypothesis needs urgent confirmation, due to the absence of reliable dating elements for this site (Basilici 1997).

Angiospermae – Monocotyledones

Sparganiaceae

Sparganium nanum Dorofeev
in Kolakovsky

Pl. 2 figs 12, 13

- 1958 *Sparganium nanum* Dorofeev in Kolakovsky, p. 324, Pl. 17 figs 2-5.

This is one of the few species of herbaceous plant which disappeared rather early from the late Cenozoic record: Mai and Walther (1988) reported its occurrence in the Late Miocene and Pliocene of eastern Europe and in the Middle? Pliocene of Thuringia (Kranichfeld); in northern Italy it is very common in the Early and Middle Pliocene, but it never occurs after the Middle-Late Pliocene transition. Even in central Italy *S. nanum* occurs only in the older sites: the "New Quarry" of Dunarobba II (4 samples) and the Fosso Bianco Formation at Cava Toppetti I. We may conclude that this species was probably sensitive to a cool climate, and its persistence in the Pleistocene, even in central Italy, should be regarded as most unlikely.

CONCLUSION

At first glance, from a palaeobotanical point of view, it is difficult to accept that so many

elements, which in central Europe are reputed to characterize the Miocene or Early Pliocene floras, can be found in the Middle and even Late Pliocene in southern Europe. The temptation to propose an older age for the flora bearing sites is very strong (Gregor 1990, Günther & Gregor 1989, Fischer & Butzmann 2000). However, the non-palaeobotanical dating elements are in general so convincing that they can hardly be questioned on the basis of the scattered and incompletely studied palaeobotanical data which are available at present. Only an extensive survey of the late Cenozoic floras of central Italy would justify a re-assessment of the present chronostratigraphic interpretations. The single site at which current palaeobotanical data would seem to be crucial for defining the geochronologic position is Dunarobba. In this succession there are no reliable dating elements, and a Late Pliocene age, mainly suggested by continental snails (Ambrosetti et al. 1995b), seems to be in contrast with the high percentage of exotic and "subtropical" elements in the fossil flora which is comparable to that of the Santa Barbara site in the Upper Valdarno, reliably dated to the Middle Pliocene.

If we accept the chronostratigraphic assessment suggested by non-palaeobotanical dating elements for the remaining sites, the new palaeofloristic data reported above allow us to draw several conclusions about plant biogeography and biostratigraphy in central Italy, by comparison with the rich record available for central Europe:

1) Central Italy obviously belonged to the Western European floristic region in the Middle and Late Pliocene, since most of the species in the floras of Santa Barbara, Cava Toppetti I and II and Dunarobba are also present in the coeval, or slightly older, floras of central Europe; the same seems to be true for the Poggiorosso and Torre di Picchio floras (latest Pliocene). On the other hand, in the few floras of the Early Pleistocene (Villa San Faustino, Monticello), several herbaceous taxa appear, which are uncommon or absent in central Europe (cf. *Helianthemum*, *Ajuga*, *Eleocharis*, *Potentilla micrantha*, *Verbena officinalis*), thus suggesting that the flora was becoming different from the transapennine and transalpine ones. However, it is important to emphasize that those taxa which are now characteristic of the Mediterranean floristic

region are totally absent in all the Pliocene and Early Pleistocene macrofloras from central Italy. This is in agreement with the minor role played by Mediterranean plants in the pollen records from the Upper Valdarno (Bertini & Roiron 1997, Torre et al. 1996) and Tiberino Basins (Abbazzi et al. 1997, Follieri 1977, Pontini & Bertini 2000).

2) Despite the marked floristic affinity to central Europe and northern Italy, the stages of floristic change in central Italy seem to be well-differentiated. This is particularly clear because several species which disappeared from central Europe at the end of the Miocene (Early Pliocene in N Italy), were still present in the Middle Pliocene of central Italy (e. g. *Cyclea palatinati-bavariae*, *Daphnogene polymorpha*, *Sapindoidea margaritifera*). Likewise, in the Late Pliocene of the Ponte Naja Formation, three species which seem to disappear at the end of the Early Pliocene in central Europe (Middle Pliocene in N Italy) are still found: *Eurya* cf. *stigmosa*, *Symplocos lignitarum* and *Toddalia latisiliquata*. All these data suggest that central Italy acted as a refuge for Neogene thermophilous species (Southern French – Italian Refuge: Mai 1995b).

3) From the foregoing points it follows that the use of carpological species for biostratigraphical interpretations based on central-European records is unsafe at present. However, it will certainly constitute a useful and precise tool for continental biostratigraphy as soon as the carpological assemblages have been calibrated on a local scale, fitting the pattern of climate change which had been active in central Italy. The same problem occurs with pollen assemblages, which show repeated phases of expansion and retreat of “mega-mesothermic” elements in the Middle and Late Pliocene (Albianelli et al. 1995, Bertini & Roiron 1997, Pontini & Bertini 2000, Torre et al. 1996), thus hampering an age estimation based on floral composition (as proposed, for example, by Bertoldi et al. 1994). At present, the best way to exploit the biostratigraphic potential of plant remains in central Italy would seem to be a combined analysis of palynological and carpological data; this approach may permit, even in short sections, detection of the key features of a given vegetational phase.

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PLATES

Plate 1

Tetraclinis salicornioides (Unger) Kvaček

1. Cone, Dunarobba II, Middle? Pliocene
Sequoia abietina (Brongniart) Knobloch
2. Cone, Cava Toppetti II, Late Pliocene
- 3, 4. Seeds, Cava Toppetti II, Late Pliocene
Trigonobalanopsis exacantha (Mai) Kvaček & Walther
5. Cupule, Gregor's section of Santa Barbara, Middle Pliocene
Liquidambar cf. *europaea* A. Braun
6. Fruiting head, Torre di Picchio, latest Pliocene
Litsea? *sonntagii* Gregor
7. Endocarp, Gregor's section of Santa Barbara, Middle Pliocene
Leitneria venosa (Ludwig) Dorofeev
- 8, 9. Endocarp from both sides, Villa San Faustino, Early Pleistocene
Magnolia ludwigii Ettingshausen
- 10, 11. Seed, external view and split seed, internal view, Gregor's section of Santa Barbara, Middle Pliocene
Toddalia latisiliquata (Ludwig) Gregor
- 12a, b. Split seed, internal and external views, Cava Toppetti II, Late Pliocene
13. Seed with deep hilar scar, external view, San Miniato (CSL1 bed), Middle Pliocene
Toddalia naviculaeformis (Reid) Gregor
- 14, 15. Seed, external view and broken seed, internal view, Marecchia, Middle Pliocene
Toddalia rhenana Gregor
- 16, 17. Seeds, lateral and hilar views, Dunarobba II, Middle? Pliocene
Zanthoxylum ailanthiforme (Gregor) Gregor
18. Seed, hilar view, Dunarobba II, Middle? Pliocene
19. Broken seed, internal view, Cava Toppetti I, Middle (or Late) Pliocene
20. Seed, lateral view, Cava Toppetti I, Middle (or Late) Pliocene
21. Seed, lateral view, Marecchia, Middle Pliocene
Meliosma canavesana Martinetto
22. Endocarp, oblique lateral view, Gregor's section of Santa Barbara, Middle Pliocene
- 23a, b. Split endocarp, internal and apical views, Gregor's section of Santa Barbara, Middle Pliocene
Sabia europaea Czacott & Skirgiello
24. Fragmentary endocarp, lateral view, Dunarobba II, Middle? Pliocene
25. Fragmentary endocarp, lateral view, Gregor's section of Santa Barbara, Middle Pliocene
Sapindoidea margaritifera (Ludwig) Kirchheimer
- 26a, b. Seed (?), lateral-ventral and dorsal views, San Miniato (CSL1 bed), Middle Pliocene
Symplocos lignitarum (Quenstedt) Kirchheimer
27. Endocarp, lateral view with three seed locules and basal pit, Cava Toppetti II, Late Pliocene
- 28, 29. Endocarps, oblique-lateral and lateral views, Cava Toppetti II, Late Pliocene
Symplocos schererii Kirchheimer
30. Curved endocarp, lateral view, Gregor's section of Santa Barbara, Middle Pliocene

Scale bar – 1 mm

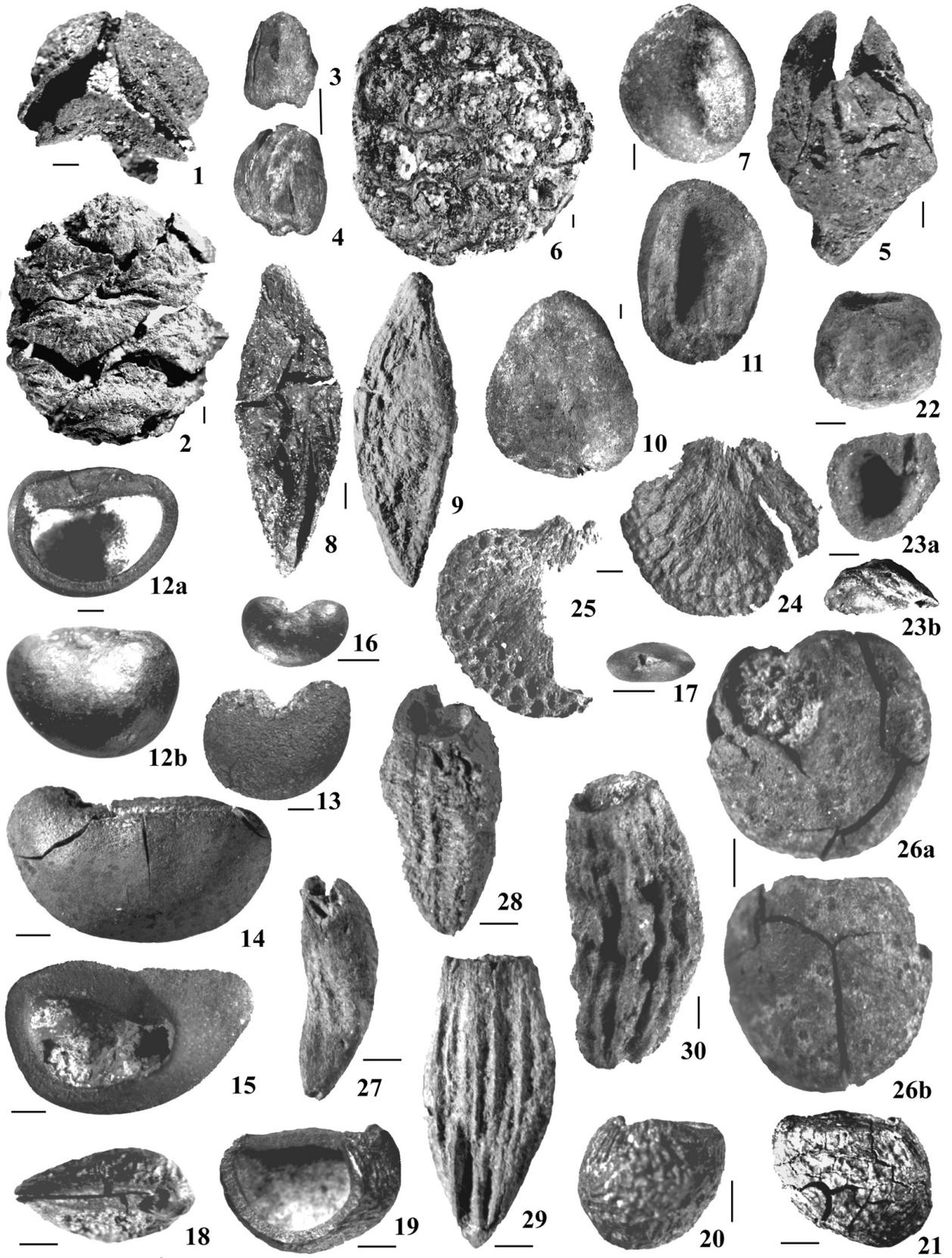


Plate 2

Tetraclinis salicornioides (Unger) Kvaček

1a, b. Leaf whorl and detail of stomata, Dunarobba II, Middle? Pliocene

Cryptomeria rhenana Kilpper

2. Seed, Cava Toppetti I, Middle (or Late) Pliocene

Liriodendron geminata Kirchheimer

3. Pair of seeds, Torre di Picchio, latest Pliocene (or earliest Pleistocene)

Magnolia allasoniae Martinetto

4. Seed, internal view, Dunarobba II, Middle? Pliocene

Sinomenium cantalense (Reid) Dorofeev

5. Endocarp, front view, Dunarobba II, Middle? Pliocene

Cyclea palatinati-bavariae Gregor

6. Fragment of endocarp, front view, Dunarobba II, Middle? Pliocene

7. Fragment of endocarp, side view, Dunarobba II, Middle? Pliocene

Ficus potentilloides Mai

8a, b. Seed, lateral view and detail of the surface structure, Dunarobba II, Middle? Pliocene

Cephalanthus pusillus Friis

9a, b. Fruit with dehiscence valve and detail of the surface structure. Dunarobba II, Middle? Pliocene

Eurya stigmosa (Ludwig) Mai

10. Seed with remains of the fruit tissue. Gregor's section of Santa Barbara, Middle Pliocene

Ampelopsis malvaeformis (Schlotheim) Mai in Mai & Gregor

11. Seed (pyrene), Dunarobba II, Middle? Pliocene

Sparganium nanum Dorofeev in Kolakovsky

12. Endocarp, lateral-apical view, Dunarobba II, Middle? Pliocene

13. Endocarp, lateral view, Dunarobba II, Middle? Pliocene

All SEM photos, figs 6 and 7 excepted; scale bar – 1 mm long where not specified

