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Late persistence and deterministic extinction of "humid thermophilous plant taxa of East Asian affinity" (HUTEA) in southern Europe

Edoardo Martinetto¹, Arata Momohara², Roberto Bizzarri³, Angela Baldanza³, Massimo Delfino^{1,4}, Daniela Esu⁵, Raffaele Sardella⁵

1 - Dipartimento di Science della Terra, Università di Torino, via T. Valperga Caluso 35, I-10125 Torino, Italy.

2 - Graduate School of Horticulture, Chiba University, 648 Masudo, Chiba 271-8510, Japan.

3 – Dipartimento di Fisica e Geologia, Università di Perugia, Via A. Pascoli snc, I-06123 Perugia, Italy.

4 - Institut Català de Paleontologia Miquel Crusafont, Universitat Autònoma de Barcelona, Edifici Z (ICTA-ICP), Carrer de les Columnes s/n, Campus de la UAB, E-08193 Cerdanyola del Valles, Barcelona, Spain

5 - Dipartimento di Scienze della Terra, Sapienza Università di Roma, Piazzale Aldo Moro snc, Roma, Italy.

Key words

carpological remains, phytogeographic-climatic characterization, exotic elements, climate change, late Cenozoic, Italy

Abstract

Several terrestrial plant fossils found in the late Cenozoic of Europe belong to thermophilous genera or infrageneric taxa which do not grow in this continent today, and are usually called "exotic elements". Within this large group we singled out three more precisely defined categories based on the hypothesis that the change of geographic distribution between the late Cenozoic and the present is the result of deterministic extinctions caused by climate change. Among the taxa shared by the modern East Asian and the Plio-Pleistocene European flora, the "humid thermophilous taxa of East Asian affinity" (HUTEA) represent the central category in our study. These were traditionally considered "Pliocene" elements in Europe. In our analysis of 13 reliably dated Italian assemblages the percentage of species belonging to the HUTEA category was found to be higher in Pliocene sites, and very low to null in Pleistocene ones. Also early Pleistocene assemblages across all of Europe did not contain any HUTEA, apart from *Eucommia*, and *Glyptostrobus* and *Symplocos* sect. *Lodhra* in the refugial area of the Colchis.

Our analysis of fruit and seed assemblages in the San Lazzaro section (Umbria, central Italy), recently assigned to the early Pleistocene, provided contrasting evidence, which required a reconsideration of the stratigraphic and palaeontological context of two well known sites in central Italy, Cava Toppetti II and Dunarobba. Using vertebrate and continental mollusc biochronology the age of these sections was established and they were compared with other assemblages in central Italy and Europe. We show that in central Italy at least three HUTEA species (*Sinomenium cantalense*, *Symplocos casparyi*, *Toddalia rhenana*) persisted after the Pliocene/Pleistocene boundary. We conclude that central-southern Italy offered a refugial niche that was warm and wet enough to assure the longer survival of some HUTEA, in contrast to central Europe.

1. Introduction

In the course of the stratigraphical and palaeontological study of the San Lazzaro section in central Italy (Fig. 1), recently assigned to the early Pleistocene (Baldanza et al., 2014), one of us (A.B.) found an endocarp of *Sinomenium cantalense*. The finding of this species, readily assignable to the humid thermophilous taxa of East Asian affinity in an early Pleistocene section was the starting point for further collecting efforts to find evidence for the role of central Italy as a centre of refuge for such thermophilous taxa in the Plio-Pleistocene (Martinetto, 2001a). In this paper we adopt the

52 definition of the Pliocene and Pleistocene of Gibbard et al. (2010), with the boundary fixed at 2.6
 53 Ma, and we accept their indication for the chronologic boundaries of the four stages Zanclean,
 54 Piacenzian, Gelasian and Calabrian. Therefore, the terms middle Pliocene, late Pliocene and early
 55 Pleistocene used in previous works (among others, Ambrosetti et al., 1995a, 1995b; Abbazzi et al.,
 56 1997; Martinetto, 2001a) have a chronologic connotation which differs from that adopted here.
 57 It is well known that many plant fossils found in the late Cenozoic of Europe belong to
 58 thermophilous genera or infrageneric taxa which do not grow in this continent today (Mai, 1989;
 59 Qian et al., 2006; Rodriguez Sanchez and Arroyo, 2008). Such fossils are usually called "exotic
 60 elements" (Reid, 1920) and this term corresponds more or less with "extinct plants" for the Plio-
 61 Pleistocene interval (Svenning, 2003). The climatic requirements are not considered in the
 62 definition of both exotic and extinct; however, several attempts have been made to assign the exotic
 63 (or extinct) elements to a few distinct plant groups that involve a climatic characterization and/or a
 64 phytogeographic aspect (Mai, 1989, 1991, 1995a; Grichuk, 1997; Grimsson et al., 2015). Examples
 65 of names which have been used include: "Palaeotropical flora/element", "Arcto-Tertiary" or
 66 "Arctotertiary flora/element" (Engler, 1879–1882; Mai, 1989, 1991; Grimsson et al., 2015),
 67 "subtropical elements" (Mai, 1970; Zagwijn, 1990), "Mastixioideen" (Kirchheimer, 1957; Mai,
 68 1964), "Boreotropical flora" (Wolfe, 1975), "Taxodiaceae group" (Bertoldi et al., 1994), "Tethyan
 69 plants (or Tethys flora)" (Szafer, 1961; Mai, 1989; Rodriguez Sanchez and Arroyo, 2008), "Mega-
 70 mesothermic elements" (e.g. Popescu et al., 2010), "humid subtropical elements" (Bertini and
 71 Martinetto, 2011). All these names leave some uncertainty as to what is included and what is
 72 excluded from the definition, firstly because the phytogeographic information, both past and
 73 present, is superimposed to, and variously intermingles with, the climatic one, and secondly because
 74 of the very difficult, not unambiguous, climatic characterisation of the fossil-taxa (Kvaček, 2007;
 75 Grimm and Denk, 2012; Utescher et al., 2014). Also the modern reference models may be
 76 ambiguous, for example the qualitative term "subtropical" is used with very different temperature
 77 boundaries by Chinese (e.g. Hou, 1983) and Japanese authors (e.g. Kira, 1991).
 78 The different extant distribution of plant taxa that grew together in the Cenozoic of Europe have
 79 often been given considerable relevance in the analysis of palaeofloras (see Reid and Reid, 1915;
 80 Szafer, 1961; Mai, 1964, 1989, 1995a). However, in our opinion most previous analyses and
 81 descriptions of the floral change in the Plio-Pleistocene of Europe suffered from the lack of
 82 precisely defined categories whose chronological analysis would adequately point out timing and
 83 entity of the large Plio-Pleistocene mass extinction (Tallis, 1991; Svenning, 2003). Additionally, the
 84 descriptions of Plio-Pleistocene floral changes mostly relied on pollen data (e.g. Tzedakis et al.,
 85 2006; Postigo-Mijarra et al., 2009; Magri, 2010; Orain et al., 2013), particularly in Italy (Bertini,
 86 2010; Combourieu-Nebout et al., 2015). However, by combining pollen and carpological records
 87 (Bertini and Martinetto, 2011) it was noticed that pollen assemblages mainly reflect anemophilous
 88 plants, while they do not accurately represent the assemblages of "subtropical humid forest" type
 89 (*sensu* Hou, 1983, and Bertini and Martinetto, 2011), which are very rich in entomophilous plants
 90 and were present in southern Europe right at the time when major extinction events are
 91 hypothesized (Bertini and Martinetto, 2011). As recently confirmed by Goring et al. (2013), taxa
 92 that are pollinated by insect or animal vectors (entomophilous or zoophilous, respectively), and
 93 species with limited dispersal ability are rarely recorded in fossil pollen records. Some works on
 94 modern fruit and seed assemblages (e.g. Thomasson, 1991; Vassio and Martinetto, 2012 and
 95 references therein) indicate a less biased representation of plant diversity, in particular for several
 96 entomophilous (e.g. *Actinidia*, *Frangula*, *Paulownia*, *Rubus*, *Sambucus*) and herbaceous plants
 97 (e.g. *Ajuga*, *Cyperaceae*, *Hypericum*, *Potamogeton*, etc.). For these taxa, the plant elements that
 98 enter the fossil record and allow species-level identification are fruits and/or seeds. Thus, the works
 99 which exclude carpological data definitely underestimate past plant species diversity and the extent
 100 of Plio-Pleistocene plant extinctions, and the focus of this paper will be on fossil fruits and seeds.
 101 The analysis of the San Lazzaro material led us to reconsider the bulk of information accumulated
 102 for the Italian late Cenozoic fruit and seed assemblages in the last 30 years (in particular: Gregor,

1990; Martinetto, 1994, 1995, 1999, 2001a, 2001b, 2009, in press; Bertoldi and Martinetto, 1995; Mai, 1995b; Basilici et al., 1997; Ghiotto, 2010; Martinetto et al., 2007, 2015). Consequently, we felt the need to introduce precisely defined categories, which would permit us to better appreciate the chronological steps of the dramatic southern European floral change in the Plio-Pleistocene. One of the necessary operations was to combine in a clear manner the modern phytogeography and the climatic requirements of several taxa. Therefore, we focused on geographical and ecological characteristics of modern relatives of fossil taxa: partly shared geographic range, minimum thermic tolerance and moisture requirement. Since the geographic area where most of the "exotic" taxa of the European late Cenozoic are still living today is definitely East Asia (Tralau, 1963; Martinetto, 1998; Qian et al., 2006; Manchester et al., 2009), we considered it to be important for the definition of the new categories.

1.1. Definition of "humid thermophilous extinct European taxa of East Asian affinity" (HUTEA)

The taxonomic similarity between Neogene European floras and modern East Asian ones are rooted at least into the Miocene (Mai, 1989). As known from various studies at a global and regional scale, Cenozoic climates were generally warmer and more humid than at present, and were characterized by shallow latitudinal gradients (Utescher et al., 2011 and references therein). Several authors (Bruch et al., 2011, Liu et al., 2011, Xing et al., 2012; Jacques et al., 2013) pointed out that the climate was wetter and warmer than the present one during the Miocene in both central Europe and China. Even central and northern Eurasian areas, such as Kazakhstan (Bruch and Zhilin, 2006) and Siberia (Popova et al., 2012), were wetter and warmer during the Miocene, despite the relatively higher seasonality and continentality.

This climatic situation was probably suitable for the formation of latitudinal vegetation belts with a similar floristic composition in both western and eastern Eurasia (Mai, 1989, 1991; Kovar-Eder et al., 2008), and strong floristic affinities with East Asia have also been encountered for North American floras (Liu and Jacques, 2010). Several authors explained that the modern East Asian woody flora is richer than the European (and North American) one (e.g., Kubitzki and Krutzsch, 1996; Manchester, 1999; Tiffney and Manchester, 2001; Wen, 1999; Wen et al., 2010) mainly due to a minor impact of extinctions, even if several woody species got extinct also in East Asia during the Plio-Pleistocene (Momohara, 2015).

Some close relatives of most European extinct species were already present in the warm temperate belt of East Asia before the Pliocene (e.g., *Cathaya*, *Cephalotaxus*, *Craigia*, *Cryptomeria*, *Cyclocarya*, *Eucommia*, *Ginkgo*, *Glyptostrobus*, *Pseudolarix*, *Taiwania*; Manchester et al., 2009) or possibly migrated there during the Pliocene (e.g., *Hemiptelea*, *Rehderodendron*; Manchester et al., 2009), and could survive the Pleistocene climatic crisis because of the presence of niches that were wet (atmospheric humidity) and warm enough, even in sites not related to rivers and swamps. Based on the concept of "physiological uniformitarianism" (Tiffney and Manchester, 2001) we can assume that the climatic tolerances of the living relatives of Neogene European taxa that survived in the humid and warm temperate to tropical areas of East Asia roughly correspond (maybe only in part) to those of the extinct European forms of the same genus, subgenus or section. Svenning (2003) pointed out a deterministic effect in late Cenozoic plant extinctions and recognized three important groups of taxa for the analysis of the ancient European floras: 1) widespread taxa; 2) relictual taxa; 3) extinct taxa. In referring to extinct taxa, Svenning (2003) restricted his analysis to cool-temperate tree genera, but recently Eiserhardt et al. (2015) carried out an analysis on more thermophilous plants. Actually, several Plio-Pleistocene taxa occurring in Europe are more thermophilous than "cool-temperate" (Martinetto et al., 2015) so that we now consider it important to single out a new group of thermophilous taxa with a partly shared (as for eastern Asia) current distribution outside Europe and a common, definite climatic boundary. The thermophilous characterization of several taxa documented by fossils is provided by the minimum Mean Annual Temperature (MAT) requirement of their modern relatives (Table 1).

Consequently, we define as "**HU**mid **T**hermophilous extinct European taxa of **E**ast Asian affinity", in short HUTEA, those plant taxa which have well-documented fossil records in the late Cenozoic of Europe, which do not grow spontaneously in this continent and West Asia at present (unless as aliens), which do not tolerate a Mean Annual Temperature below 8°C and a Mean Annual Precipitation (MAP) below ca. 800-1000 mm/year, and which belong to genera or infrageneric taxa that presently grow in East Asia (Wang, 1961; Qian et al., 2006; Manchester et al., 2009; Fang et al., 2009, 2011; Grimm and Denk, 2012; Eiserhardt et al., 2015; Utescher and Mosbrugger, 2015). We single out the 8°C value of MAT because this is the boundary of the distribution of boreal (subarctic) and thermophilous (temperate) taxa in East Asia. The lower limit of fir and spruce forest and the upper limit of deciduous forest is 7.8 °C MAT in China (Fang and Yoda, 1989). Although the lower MAT limit of the thermophilous evergreen arboreal Fagaceae and Lauraceae (dominant tall trees of temperate broadleaved evergreen forests in East Asia) is between 9 and 12°C (Hattori and Nakanishi, 1985; Fang and Yoda, 1989; Fang et al., 2011), we decided that adding 1°C of tolerance would admit sporadic occurrences of thermophilous plants above the 9°C MAT isotherm. The focus on MAT for the definition of the HUTEA is justified by the large availability of data (Grimm and Denk, 2012; Utescher and Mosbrugger, 2015) for most of the plant genera documented by fossils in Europe, and by the determinant role of this parameter for plant extinction or survival in the late Cenozoic of Europe (Svenning, 2003; Eiserhart et al., 2015). Conversely, we did not manage to gather precise values of minimum precipitation requirements for all the exotic Neogene plant taxa of Europe; nevertheless we consider important to include in the HUTEA definition a rule that excludes those plants which tolerate a low precipitation (below ca. 800-1000 mm/year). In fact it has been pointed out that the extinction of several Neogene taxa in Europe depended from a scarce tolerance not only of low temperature, but also of low precipitation (Svenning, 2003; Eiserhart et al., 2015). The thermophilous genera that survived in southern Europe until present time (e.g. *Laurus*, *Olea*) are mainly adapted to dry (Mediterranean) climate, whereas several thermophilous genera extinct in Europe are now growing in areas affected by the East Asian Monsoon that supplies higher precipitation to plants during the growing season. In East Asia the main evergreen forest formation, dominated by Fagaceae and Lauraceae, is called "lucidophyllous forest" and differs from the south European (Mediterranean) sclerophyllous forest formation by its less xeromorphic characteristics, such as larger shiny leaves, larger tree size and higher species diversity with many epiphytes and woody lianas (Kira, 1991). We are aware that other parameters (e.g. Warmth Index, Coldness Index; Kira, 1991) could be more appropriate to define a category such as HUTEA. Nevertheless, the minimum MAT requirement is an important factor determining the possibility for a plant taxon to overcome a climatic bottleneck. The climatic characteristics of the refugia might have been decisive for the possibility of a plant species to survive (Magri, 2010; Gavin et al., 2014) and obviously it would have gone extinct if its minimal thermal or humidity requirements would no longer have been present in the last refugium. In this respect, groups of taxa with similar requirements may be expected to go extinct together (Tallis, 1991; Grichuk, 1997; Eiserhardt et al., 2015). However, some extinctions are certainly controlled by complex and multiple factors. For example it has been suggested that *Cedrus* (Su et al., 2013) and *Sequoia* (Zhang et al., 2015) disappeared from China because of seed ecological aspects, triggered by climate change.

Three examples, concerning genera which do not tolerate a MAT below 8°C (Table 1), may be useful to support the above definition of HUTEA: *Toddalia* is assigned to the HUTEA because it is distributed in the tropical-warm temperate zone of East Asia and in Africa, but not in Europe and West Asia (Gregor, 1979). *Symplocos* sect. *Lodhra* is assigned to the HUTEA because it is distributed in the tropical-warm temperate zone of East Asia, but not in Europe and West Asia (Fritsch et al., 2015). *Rehderodendron* is assigned to the HUTEA because it is distributed only in the "subtropical" zone (*sensu* Hou, 1983) of East Asia.

203 The genera *Cathaya* and *Pseudolarix* meet all the requirements to be classified as HUTEA, but they
204 are excluded for their present highly relictual distribution, which may provide an inaccurate
205 representation of their past climatic requirements, similarly as for *Tetraclinis* (Kvaček, 2007).
206 *Azolla* is not considered a HUTEA because it is a water plant rather independent from atmospheric
207 humidity.

(TABLE 1 approximately here)

209 According to the above definition and to the data (e.g., minimum thermic requirements: MAT_{min})
210 reported in Table 1, the following HUTEA have so far been documented for the late Cenozoic of
211 Italy (Martinetto, 1995, 1998, 1999, 2001a; 2001b; Follieri, 2010; Martinetto et al., 2015):
212 *Amentotaxus*, *Cephalanthus*, *Cinnamomum*, *Craigia*, *Cyclea*, *Cyclocarya*, *Ehretia*, *Engelhardia*,
213 *Eucommia*, *Glyptostrobus*, *Mallotus*, *Meliosma* subgen. *Kingsboroughia*, *Paulownia*,
214 *Rehderodendron*, *Sabia*, *Sargentodoxa*, *Saurauia*, *Sinomenium*, *Stemona*, *Symplocos* sect. *Lodhra*,
215 *Taiwania*, *Ternstroemia*, *Tetrastigma*, *Toddalia*, *Trichosanthes*, *Turpinia* and *Wikstroemia*.

216

217

218

219 1.2. Other categories (CTEA, TEWA)

220

221 Other taxa documented in the late Cenozoic of southern Europe have the correct geographic
222 distribution nowadays to be considered HUTEA (i.e. embracing East Asia and excluding Europe
223 and West Asia), but they are not considered, because the modern representatives do tolerate a Mean
224 Annual Temperature below 8°C (e.g. *Actinidia*, *Alangium*, *Ampelopsis*, etc.: Table 1). These taxa
225 will be named CTEA ("Cool-Tolerant extinct European taxa of East Asian affinity") in this paper
226 and belong to the somehow ambiguous [changing on the basis of the extent of territory considered]
227 category of the "exotic" taxa (Reid, 1920; see the more precisely defined "category E" in
228 Martinetto, in press).

229 The HUTEA category already has a satisfactory climatic connotation, which we deem to be useful
230 for an analysis of the climatic determinism in their extinction. Conversely, the CTEA category
231 certainly contains a very heterogeneous mix of species with different climatic tolerances. In fact,
232 *Magnolia* provides a good example of a cool-tolerant CTEA genus that contains several modern
233 species (Grimm and Denk, 2012; Mosbrugger and Utescher, 2015), which are absolutely
234 thermophilous and not cool-tolerant (tropical-subtropical). Similarly, a diversified climate tolerance
235 has been also hypothesized for different European fossil-species (Mai, 1975). Given this situation, it
236 is not surprising that several CTEA would show a HUTEA-like extinction pattern. However, in this
237 paper our attention has been focused on the species that show a delayed disappearance time in
238 comparison to the HUTEA.

239 Finally, a few taxa which do not tolerate a MAT below 8°C are not assigned to the HUTEA because
240 of the modern geographic range: *Coriaria*, *Datisca*, *Ficus*, *Laurus*, *Liquidambar*, *Morella*, *Ocotea*,
241 *Olea*, *Platanus*, *Sideroxylon*, *Styrax*, *Tetraclinis* and *Visnea* grow in southern Europe, North Africa
242 (incl. Macaronesia) and/or West Asia. These taxa will be indicated as TEWA, Thermophilous
243 European, West Asian and/or African elements, in this paper. *Pterocarya*, *Parrotia* and *Zelkova* are
244 not assigned to the HUTEA nor to the CTEA or TEWA, because they grow in relict niches of
245 south-eastern Europe and/or West Asia (southern shores of the Black Sea and Caspian Sea),
246 commonly including sites with a Mean Annual Temperature below 8°C.

247 Finally, late Cenozoic south European taxa that today only survive in America are not many
248 (*Decodon*, *Dulichium*, *Leitneria*, *Proserpinaca*, *Sequoia*, *Taxodium*) and will not be specifically
249 dealt with in this paper.

250 It is apparent that the HUTEA and CTEA concepts have much to do with a change of geographic
251 distribution between the Plio-Pleistocene and the present. The main aim of this work is to present
252 new fossil data from Italy and an updated state-of-the-art regarding the timing of disappearance of

253 HUTEA and CTEA species from Europe. Furthermore, we newly consider the possibility of
254 deterministic extinctions (Svenning, 2003; Eiserhardt et al., 2015).

255

256 2. Geological setting

257 The post-Miocene, NW-SE oriented South Valdichiana Basin (Fig. 1), enclosed between the Meso-
258 Cenozoic Rapolano-Mt. Cetona and Narnese-Amerina Apennine anticlines and bounded by
259 extensional faults, occupies a wide area between south-eastern Tuscany and western Umbria, in
260 central Italy. In the Pliocene-Pleistocene interval, the Narnese-Amerina ridge separated the mainly
261 marine domain of South Valdichiana from the continental deposits of the Southern Tiberino Basin
262 (Figs. 1, 2), while, during the early Pleistocene, a wide delta in what is now the Città della Pieve
263 area divided the continental (northwards) and the marine Valdichiana (southwards) (Bizzarri and
264 Baldanza, 2009; Bizzarri et al., 2015).

265 (FIGURE 1 approximately here)

266 South Valdichiana marine deposits in the study area, including the San Lazzaro section (Fig. 1),
267 clearly mark a regressive trend, from offshore transition silty sands to lower shoreface sands, and
268 finally to a gravel beachface with evidence of a river mouth in the uppermost part (Baldanza et al.,
269 2011). The same main trend is recognized in other sections nearby, such as the Monteleone section
270 and the Città della Pieve section (Bizzarri and Baldanza, 2009). All these sections are referred to
271 alternatively river- and wave-dominated shallow coastal marine environments (Bizzarri et al.,
272 2015), and attributed to the “Deltaic coast” inside the “Chiani-Tevere” Unit (Fig. 2, Baldanza et al.,
273 2014; Martinetto et al., 2014). On the other hand, through late Pliocene and early Pleistocene, the
274 Southern Tiberino Basin evolved from a wide lacustrine environment to a river-drained valley
275 system (Ambrosetti et al., 1995a; Basilici, 1997, 2000a, 2000b; Martinetto et al., 2014). The
276 sections Cava Toppetti II (Abbazzi et al., 1997) and Dunarobba (Ambrosetti et al., 1995b) are
277 representative of this second context.

278 (FIGURE 2 approximately here)

279 3. Materials and methods

280 This work integrates the analysis of freshly collected material from the San Lazzaro section with the
281 reinterpretation of the stratigraphic and palaeontological data from the sites Cava Toppetti II
282 (Abbazzi et al., 1997; Argenti, 1999, 2004; Martinetto, 2001a; Petronio et al., 2003; Sardella et al.,
283 2003) and Dunarobba (Ciangherotti et al., 1998; Manganelli and Giusti, 2000; Manganelli et al.,
284 2008; Martinetto et al., 2014).

285 In the San Lazzaro section, as well as in the neighbouring sections (Fig. 3), a close, about 1 m
286 spaced, sampling for marine microfossils ("biostratigraphic samples") was carried out in the
287 lowermost deposits, in order to provide an integrated biostratigraphical datum. Similarly, more
288 widely spaced biostratigraphic samples were collected in the upper part of the section, in
289 correspondence of fine-grained deposits. For each sample, 100 g of sediment were processed with
290 H₂O₂ solution, washed through a 63 µ size mesh, and the residue observed using a
291 stereomicroscope. Smear slides for nannoplankton analysis were prepared using the standard
292 technique proposed by Bown and Young (1998), and observed under a polarizing-light microscope
293 at 1000x magnification.

294 (FIGURE 3 approximately here)

295 The above-mentioned finding, in a biostratigraphic bulk sample (FU6, ca. 100 g) collected at 14 m,
296 of a fruit part (endocarp) of *Sinomenium cantalense* was the starting point for a more extensive
297 sampling effort in the San Lazzaro section. A few concentrations of compressed plant fragments
298 were noticed in the portion from 5.5 m to 8.5 m of the section (Fig. 4), and three bulk sediment
299 samples FU3 and FU4, ca. 400 g, and FU5, ca. 2000 g; these are named "carpological samples")
300 have been collected there and processed with the palaeocarpological method illustrated in Basilici et
301 al. (1997).

302 The methods for the identification of plant materials are the same as those recently described in
303 Martinetto et al. (2015). However, the climatic characterisation of each plant fossil-species was

304 carried out differently. We did not use only the data available in the Paleoflora Database (PFDB:
305 Utescher and Mosbrugger, 2015) and in the GrimClim Database (CG: Grimm and Denk, 2012),
306 because these data have several biases depending from their literature sources: the PFDB does not
307 indicate references for the thermal boundary values referred to each taxon, and the boundary
308 temperatures of Fang (2011), largely used by the CG, were defined from very rough distribution
309 data at county level (several Chinese provinces are larger than Japan). Therefore, whenever
310 possible, we used in Table 1 the more precise data from different literature sources (Alternative
311 MATmin in Appendix 1). Those include local floras and vegetation survey reports in China and
312 Japan, in which distribution of taxa are described and/or mapped on the altitudinal scale of at least
313 100 m based on herbarium specimens and/or field observations (Appendix 1).

(FIGURE 4 approximately here)

316 Deposits in the area of Fabro Scalo (Fig. 1) have been investigated with the aim to: 1) reconstruct a
317 lithostratigraphic section for the area, 2) better document the palaeofloral assemblages inside the
318 phytodebris-rich horizons of the San Lazzaro outcrop, 3) establish the age of these deposits, and 4)
319 compare the plant assemblages with other possibly coeval assemblages in central Italy, first of all
320 those of the dated Cava Toppetti II section (Abbazzi et al., 1997; Martinetto, 2001a), and secondly
321 those of poorly dated Dunarobba succession (Martinetto et al., 2014). To reevaluate the age of these
322 three sections, data on vertebrate and continental mollusc biochronology were reconsidered
323 (Abbazzi et al., 1997; Gliozzi et al., 1997; Ciangherotti et al., 1998; Petronio et al., 2003; Sardella et
324 al., 2003; Argenti, 2004; Manganelli et al., 2008).

325 In addition, continental mollusc and vertebrate records were investigated as complementary
326 palaeoclimatic evidence to terrestrial plants. In particular we analysed the history of the HUTEA
327 plants in parallel with that of the terrestrial ectothermic vertebrates, whose distribution is clearly
328 related to historical variations of temperature and humidity more directly than that of other
329 vertebrates (Delfino, 2002; Kotsakis et al., 2004; Venczel and Sanchiz, 2005; Delfino et al., 2006;
330 Delfino and Sala, 2007; Piras et al., 2007; Delfino et al., 2008).

331
332 Even if we base our analysis on the climatic determinism of plant extinctions, the correlation of the
333 disappearance events with the standard climatic curves (e.g. Zachos et al., 2001; Lisecki and Raymo,
334 2005; De Shepper et al., 2013; Prescott et al., 2014) requires more information and is beyond the
335 scope of this work.

336 337 3.2. Carpological and floristic analyses

338
339 The San Lazzaro sediment samples FU3, FU4 and FU5 were prepared according to a standard
340 palaeocarpological method (Martinetto, 1994; Basilici et al., 1997). The definition of the HUTEA
341 category allowed us to carry out a new floristic analysis, both for the San Lazzaro assemblage and
342 for several other Pliocene and early Pleistocene floras of Italy: we selected 13 reliably dated
343 assemblages (2 of the Zanclean, 5 of the Piacenzian, 2 of the Gelasian, 3 Calabrian, 1 early Middle
344 Pleistocene) and we analysed the percentage of species belonging to the HUTEA category, referred
345 to the total number of species (Table 2). Furthermore, since our focus was on the early Pleistocene,
346 we also analyzed the floral lists of all the main carpofloras of the rest of Europe (Baas, 1932;
347 Chochieva, 1965; Buzek et al., 1985; Mai and Walther, 1988; Günther and Gregor, 1990;
348 Velichkievich and Zastawniak, 2003; Mai and Velitzelos, 2007) whose age was proved or supposed
349 to fall within that time interval (Table 3).

(TABLE 2 approximately here)

(TABLE 3 approximately here)

352
353 In order to get an overview of the disappearance times of themophilous plants at the south European
354 scale, the occurrence and suggested extinction time of HUTEA were also checked in synthetic

355 palynological papers dealing with the following areas: whole area (Popescu et al., 2010), Iberian
356 peninsula (Postigo-Mijarra et al., 2009), Italy (Bertini, 2010; Magri, 2010; Combourieu-Nebout et
357 al., 2015), Balkan Peninsula (Tsedakis et al., 2006; Biltekin et al., in press), Colchis area (Shatilova
358 et al., 2014) and Turkey (Biltekin et al., in press).

359

360 4. Results

361

362 4.1. The San Lazzaro section and its age constraints

363

364 The composite sedimentological and stratigraphic reconstruction proposed for the Fabro Scalo area
365 integrates old observations (Baldanza et al., 2011, 2014; Bizzarri et al., 2015) and newly collected
366 data. The general geological and sedimentological pattern, from the base to the top, is organized as
367 follows (Fig. 3):

- 368 - about 10 m (cropping out) of structureless, mollusc-rich clayey and silty sand (offshore transition
369 deposits); the lowermost layers are covered by recent alluvial deposits;
- 370 - up to 30-40 m of highly fossiliferous (mainly molluscs) fine sand (lower shoreface deposits);
- 371 - up to 25 m of intermingled coarse sand and gravel (gravel beachface deposits);
- 372 - a minimum of 20 m of channelled gravel with minor sand (river mouth deposits).

373 The about 27 m-thick San Lazzaro section represents approximately the lower/intermediate part of
374 this composite section (Fig. 3); deposits grade up from poorly sorted silty sand, referred to the
375 offshore transition, to moderately sorted fine sand of lower shoreface. Throughout the section, a
376 rich and diversified fossil record (Baldanza et al., 2014; Bizzarri et al., 2015), dominated by
377 molluscs, echinids, lunulite bryozoans, benthic foraminifera and decapod crustaceans was
378 documented; both macro- and micropaleontological assemblages are dominated by benthic taxa,
379 mostly referred to warm shallow water conditions.

380 As for the Monteleone and the Città della Pieve sections, deposits in the Fabro Scalo area are
381 mainly referred to the MNN 18 - MNN 19a zones (*sensu* Rio et al., 1990) on the basis of
382 nannofossil assemblages: rare small-sized *Gephyrocapsa* spp. (*sensu* Raffi, 2002), *Helicosphaera*
383 *sellii*, *Calcidiscus macintyreii*, very rare and broken *Discoaster brouweri* and *Coccolithus pelagicus*.
384 Through the composite lithostratigraphic section, two calcareous nannofossil biostratigraphic events
385 are recognized (Fig. 3): the LO of *Discoaster brouweri* (top of MNN 18 zone, *tDb sensu* Raffi,
386 2002) in the lowermost part of the Fabro-Carnaiola section, and the FO of medium-sized
387 *Gephyrocapsa* spp. (base of MNN19b subzone, *bmG sensu* Raffi, 2002) at about the top (22 m) of
388 the San Lazzaro section. Therefore, the biostratigraphic data permit to assign deposits to the
389 Gelasian *pro parte* - Calabrian *p.p.* interval. This transition is also marked by the occurrence, in the
390 lowermost deposits, of marine ostracods such as *Aurila cruciata*, *Loxoconcha glabra*, *Argilloecia*
391 sp., and *Ruggieria longecarenata*, usually documented from the end of the Gelasian and the base of
392 the Calabrian (Faranda and Gliozzi, 2008). The occurrence, throughout Gelasian-Calabrian sections,
393 of taxa of previously supposed “Pliocene affinity”, such as *Amphistegina* spp. and *Persististrombus*
394 cf. *coronatus*, is not surprising, nor sufficient to suggest an older (Piacenzian) age: in fact, the
395 persistence of these taxa into Gelasian to Calabrian deposits has been documented in other sites of
396 this area (Bizzarri and Baldanza, 2006; Monaco et al., 2011). The two horizons with carpological
397 remains, inside the San Lazzaro section (Fig. 3), are attributed to the MNN 19a subzone, well inside
398 the early Pleistocene, and are still referable to the Gelasian stage.

399

400 4.1.1. The San Lazzaro carpological assemblage

401 The preparation of the San Lazzaro carpological samples yielded plant assemblages mainly made
402 up of woody fragments, particularly abundant in sample FU5. However, a careful observation
403 allowed us to separate also a few, mostly fragmentary, fruits and seeds. Samples FU3 and FU4 had
404 a very poor carpological content, reported in Table 4, whereas FU5 yielded more abundant
405 carpological material that allowed us to identify five definite fossil-species (ICN, McNeill et al.,

2012) well-known in the Pliocene of Italy (see Table 4 for the number of specimens): *Magnolia allasoniae*, *Sinomenium cantalense*, *Symplocos casparyi*, *Toddalia rhenana* and *Zanthoxylum ailanthiforme*. The occurrence of 3 HUTEA out of 6 species forming the San Lazzaro plant assemblage (Table 4) represents a very high percentage (50%). So, the precise identification at species level allowed by fruit morphology give to these few remains a relevant importance, due to the stratigraphic context in which they have been found. These taxa have been described and figured in Martinetto (2001a, 2001b), Mai and Martinetto (2006) and Martinetto et al. (2014, 2015). A single species has been left in open nomenclature for the reason discussed below:

- *Vitis* cf. *vinifera* L. subsp. *sylvestris* Gmelin - seeds of *Vitis* with distinct similarities to the modern Mediterranean wild grape *V. vinifera* subsp. *sylvestris* are abundant in several tens of Italian fossil sites spanning from the Zanclean to the Holocene (Martinetto, 1994; Basilici et al., 1997; Cavallo and Martinetto, 2001). However, their assignment to the modern species (and subspecies) is not straightforward because a similar fossil-species has also been described (*Vitis parasyvestris* Kirchheimer 1957) and often reported in the Neogene of Europe (Geissert et al., 1990; Martinetto, 1994; Mai, 2001). The diagnostic features of this last species are said to be the length up to 7 mm and the small seed body associated to a narrow cylindrical basis, somehow similar to that of the Holocene cultivated forms of *V. vinifera* subsp. *vinifera*. The consistent variability of morphological characters observed in rich fossil populations makes a precise assignment at species level problematic, in the absence of a detailed statistical and morphometric study. However, the dimensions and the shape of the base in the Plio-Pleistocene Italian seeds is mostly the same as in the modern Mediterranean species, so that a major affinity to *Vitis vinifera* subsp. *sylvestris* than to *V. parasyvestris* is suggested also for the specimen of San Lazzaro.

(TABLE 4 approximately here)

4.1.2. Taphonomical considerations

Almost the whole carpological record of San Lazzaro comes from a thin lens of mixed shells and compressed phytodebris (FU5 in Table 4). Several lenses of this type are usually well exposed and recognizable after periods of intense rain (Fig. 5). Each lens is concave upwards, up to 40 cm wide, less than 10 cm thick, and filled by structureless clastic-bioclastic very fine sand, just a little coarser than the enclosing silty sand deposits. Mollusc shells and fragments are usually found at the bottom or in the lateral parts, while thin wood fragments are more randomly dispersed. In the 4-9.5 m interval (Fig. 3), such lenses are frequent, interposed to both shell lags and spotted mollusc specimens. Millimetric, isolated wood fragments (compressions) are locally spread through the rest of the section. A speditive anatomical analysis (stereomicroscope) proves that most of the phytodebris consists of heteroxylous and homoxylous xylem fragments, thus proving their origin from terrestrial or at least coastal woody plants. The abundance of such plant remains in a shallow marine nearshore environment probably reflects river flood events from neighboring areas. Distally, from the prodelta to the offshore marine environment, major events may trigger remobilization of sediments (sediment-gravity flows *sensu* Lowe, 1982 and Nemec and Steel, 1984), including density currents (turbidity currents). Several plant fragments horizons inside massive to laminated sandy sediments are interpreted as part of turbidites *s.l.* and even diagnostic of hyperpycnal flows (hyperpycnites: Zavala et al., 2012). On the other hand, the San Lazzaro deposits were referred to lower shoreface/offshore transition by means of sedimentological features (Baldanza et al., 2014; Bizzarri et al., 2015), and no evidences of deposits related to turbidity currents and/or hyperpycnal flows was found. Thus, the depositional models proposed by Zavala et al. (2012) to account for the richness of plant remains, leaves, charcoal or other very light land-derived materials in distal to deep marine deposits cannot be applied here. As well as the shell lags, these lenses can be interpreted as storm layers: plant remains transported to the sea during intense floods (in mass transport) by small rivers, depending on their size and density, may more or less longer float or quickly settle to the seafloor. As for other bioclasts, woody fragments and even larger branches and

trunks (Monaco et al., 2011) are remobilized during storm events, and redistributed inside storm layers. The small dimensions of fragments (up to few centimetres, usually <1 cm), the lack of whole leaves, the partially abraded aspect of carpological remains, their concentration inside lenses of very fine sands, surrounded by silty sand-dominated deposits, all indicate discontinuous, wave-induced sedimentation events (tempestites) in a relatively low energy environment. The possibility of reworking of plant material in marine environments was already discussed in Martinetto et al. (2015).

(FIGURE 5 approximately here)

4.2. The Dunarobba section

An updated overview of the stratigraphic information on several sections of the Dunarobba site can be found in Martinetto et al. (2014), and here we concentrate on two types of rich and well-diversified molluscan assemblages from the Dunarobba Forest Section (DF). The first, coming from the silty clays encrusting the trunks, is dominated by extinct hygrophilous land prosobranchs and pulmonates, such as *Hydrocena dubrueilliana*, *Carychium* (*Saraphia*) *pachychilum*, *C. (S.) pseudotetrodon*, *Negulus villafranchianus*, *Leiostyla gottschicki*, *Gastrocopta* (*Albinula*) *acuminata fossanensis* (= *G. (A.) acuminata*), *Gastrocopta* (*Vertigopsis*) *dehmi* (= *G. (V.) moravica*), *Eostrobilops aloisii*, *Staurodon cianfanellianus*, *Laminifera* (*Laminiplicata*) *villafranchiana* (= *Laminiplica villafranchiana*) (Manganelli et al., 1989, 1990; Esu and Girotti, 1991; Esu et al., 1993; Ciangherotti et al., 1998; Manganelli and Giusti, 2000; Manganelli et al., 2008). These species are of high palaeobiogeographical and biochronological interest. Most of them, such as *H. dubrueilliana*, *C. pseudotetrodon*, *N. villafranchianus*, *G. (V.) dehmi* (= *G. (V.) moravica*), *G. (A.) acuminata fossanensis* (= *G. (A.) acuminata*), *L. gottschicki*, *E. aloisii*, *L. villafranchiana*, are in common with the NW Italian assemblages of the late Pliocene (Piacenzian of the marine chronostratigraphy) deposits of Villafranca d'Asti (RDB section) or Ceresole d'Alba and other Pliocene sites (Ciangherotti, 1997; Esu and Ciangherotti, 2004; Ciangherotti et al., 2007), and mostly got extinct during the late Pliocene (Piacenzian)/early Pleistocene (Gelasian) transition.

The second assemblage, coming from the sediments around the trunks of the Forest Section (Martinetto et al., 2014), is characterized by aquatic prosobranchs, such as *Theodoxus groyanus*, *Emmericia umbra*, *Prososthenia paulae*, *Tournouerina belnensis*, *Melanopsis affinis*, *Micromelania* (*Goniochilus*) *zitteli*, mainly endemic to central Italy and getting extinct in the late early Pleistocene (Ambrosetti et al., 1995b; Ciangherotti et al., 1998; Esu and Girotti, 2001).

Thanks to a high percentage of extinct molluscs of Pliocene character and to the findings of land species common to the late Pliocene molluscan fauna of NW Italy and other European Pliocene sites, it is possible to suggest a late Pliocene age (Piacenzian) for the Dunarobba molluscan fauna, even if a late Pliocene-earliest Pleistocene age (Piacenzian-Gelasian) cannot be excluded. The climatic indications of these molluscs, based on the modern relatives, indicate a warm temperate climate with a high atmospheric humidity, e.g. the genus *Eostrobilops* lives in East Asia, South of 40° N, and *Negulus* in East Africa (Ethiopia) (Esu and Ciangherotti, 2004).

The occurrence of several fruit and seed assemblages in different sections of the Dunarobba site has been recently reported by Martinetto et al. (2014). The most diverse plant assemblage, originating from a sandy bed indicated as DC1b, included 41 species, 8 of which are recognized as HUTEA with a resulting percentage of 20%.

4.3. The Cava Toppetti II section

The Cava Toppetti site, a few kilometers south-west of Todi (Fig. 1), was comprehensively investigated during the two last decades, and several sedimentological, stratigraphic, palaeontological and palaeoenvironmental data were collected (Ambrosetti et al., 1995a; Basilici, 1995; Abbazzi et al., 1997; Gliozzi et al., 1997; Pontini, 1997; Leone et al., 2000; Pontini et al., 2002; Martinetto et al., 2014). Due to the presence of two completely different successions, cut through by a main extensional fault, the various records were referred to either Cava Toppetti I, the older succession made up by the Fosso Bianco Unit (FBU), or Cava Toppetti II, the younger

508 succession made up by the Ponte Naja Unit (PNU). Both the FBU and PNU (Fig. 2: Ambrosetti et
509 al., 1995a; Basilici, 1995) were well exposed through the quarry fronts in the 1980s-1990s, but later
510 the outcrop was deteriorated by the lack of quarrying activities, the successive backfilling and the
511 slope restoration.

512 (FIGURE 6 approximately here)

513 The about 150 m thick Cava Toppetti II section pertained to the uppermost PNU; it was composed
514 (Fig. 6) of prevailing clayey-sandy silt deposits (fine-grained sheet flow deposits), with interposed
515 silty clay (palaeosol), planar-concave sandy gravel (stream ribbon channels) and tabular sandy
516 gravel deposits (coarse-grained sheet-flow deposits). A complete sedimentological description and
517 interpretation of PNU deposits can be found in Basilici (1995) and Abbazzi et al. (1997). The
518 palaeoenvironment was reconstructed on a sedimentological basis as the medial and distal portion
519 of an alluvial fan. Several types of sediments locally bear molluscs, whereas fragments of large
520 vertebrates and micromammals were mainly collected inside palaeosols. According to Abbazzi et
521 al. (1997), deposits of Cava Toppetti II section originally overlie the about 300 m thick lacustrine
522 laminated silty clay deposits of the FBU, attributed to late Pliocene-early Pleistocene by means of
523 magnetostratigraphy (Late Gauss to Early Matuyama Chrons).

524 At Cava Toppetti II an important biochronological datum is given by the occurrence of the
525 micromammal *Apodemus dominans* (Argenti, 1999; Sala and Masini, 2007). In the southwestern
526 branch of the Tiberino Basin such occurrence has been recorded also at the Pantalla site, together
527 with a diversified vertebrate assemblage (Gentili et al., 1997; Cherin et al., 2013a, 2013b, 2014a,
528 2014b). All the vertebrate data support a biochronological framework with Cava Toppetti II and
529 Pantalla referable to the middle-late Villafranchian transition (Coste San Giacomo or Olivola
530 Faunal Units), i.e. to the late Gelasian (Cohen et al., 2013). Recently, Bellucci et al. (2014) provided
531 new data on the Coste San Giacomo faunal assemblage, including also small vertebrates. The age of
532 this deposit, reference locality of the Coste San Giacomo Faunal Unit, has been approximately
533 assessed at 2.1 Ma. The ongoing researches will allow a more detailed comparison of the Cava
534 Toppetti II mammal assemblage to those of Coste San Giacomo and of the other Umbrian localities
535 mentioned above.

536 The molluscs collected in the alluvial fan deposits of the Cava Toppetti II section (Abbazzi et al.,
537 1997) are characterized by a few extinct freshwater prosobranchs, such as *T. groyanus*, *E. umbra*,
538 *Choerina tudertis*, *M. affinis*, *Prososthenia augusti*, *P. tasso*, which are endemic to central Italy,
539 and by a few extinct species of land snails, such as *Carychium* (*Carychiella*) *puisseguri*, *Carychium*
540 (*Saraphia*) *pachychilum*, *Carychium* (*S.*) *pseudotetrodon* and *Negulus villafranchianus*. Among
541 these, only three species are shared with the Dunarobba assemblage, whilst all the species of
542 freshwater prosobranchs were recovered also at Dunarobba. The PNU land molluscan fauna results
543 impoverished in extinct molluscs compared with the Dunarobba one indicating a slightly younger
544 age, that is early early Pleistocene (Gelasian). The lack of most of the thermophilous taxa occurring
545 at Dunarobba, such as the representatives of the genera *Hydrocena*, *Eostrobilops*, *Staurodon*,
546 *Laminiplica*, suggests a cooler climate during the deposition of the PNU unit in comparison to the
547 Dunarobba Fossil Forest one (Ciangherotti et al., 1998). Furthermore, these taxa are also less
548 exigent in terms of atmospheric humidity.

549 As for the macroscopic plant remains, the record of the Cava Toppetti II section is rather poor, but
550 an important fruit and seed-bearing deposit (Fig. 7) has been located in the middle part of the
551 section (Fig. 6) and the occurrence of several species had been reported by Martinetto (2001a). As a
552 whole 40 species have been identified, 8 of which are recognized as HUTEA with a resulting
553 percentage of 7%.

554
555 (FIGURE 7 approximately here)

556
557 All the data presented above call for a reconfirmation of the chronological position of the Cava
558 Toppetti II section. We know that some recent papers challenged the reliability of several old

paleomagnetic data, due to some bias on magnetic minerals (e.g. the issue related to the Jaramillo subchron discussed in Muttoni et al., 2014). However, the bulk of data collected in the Tiberino Basin, their correlation with part of the Valdarno Basin sequence, which is also time-calibrated by means of radiometric data (Bertini, 2013), and the magnetic susceptibility-based high-resolution cyclostratigraphy (Pontini et al., 2002; Napoleone et al., 2003, 2004), make the chronologic interpretation of the Cava Toppetti II succession reliable in the light of current knowledge. Thus, on the basis of its palaeontological content and stratigraphic position, the section is thought to be early Pleistocene (Gelasian) in age, younger than the Reunion Event and older than the Olivola Faunal Unit, which is placed at the end of the normal polarity subchron Olduvai (Torre et al., 1996; Napoleone et al., 2003; Bellucci et al., 2014). The sedimentological features suggest a high sedimentation rate (>1.3 mm/y: Basilici, 1995; Abbazzi et al., 1997), and a time span of about 100 ky to 300 ky is presumed for the whole Cava Toppetti II section, inside the 2.1-1.9 Ma range; (Abbazzi et al., 1997; Leone et al., 2000; Martinetto et al., 2014).

4.4. Frequency of the HUTEA since 5 Ma and last occurrence of CTEA

The percentages of species belonging to the HUTEA category in the well-dated reference floras of Italy (Fig. 8, Table 2) show that the Zanclean-Piacenzian assemblages have a higher value (7-31%), and the HUTEA are constantly present in all the floras that are well dated within this time interval, and also in those tentatively assigned to it (Martinetto et al., 2015; Martinetto, in press). A single HUTEA (*Eucommia*) occurs in one (Arda-AD3) of the two Gelasian reference assemblages (2% HUTEA), whereas the other Gelasian assemblage (Casnigo) and all of the Calabrian-Middle Pleistocene ones are devoid of HUTEA. Also the main European carpofloras definitely or possibly dated to the Gelasian-Calabrian would be devoid of HUTEA (Table 2), if not for the occurrence of *Eucommia* at Tegelen and Schwanheim.

Another late occurrence of two HUTEA species has been reported for a fossil flora of the Colchis area (Kvarbeti, Georgia): *Glyptostrobus europaeus* and *Symplocos casparyi* (*Symplocos* sect. *Lodhra*). This flora was referred by Chochieva (1975) to the Gurian local stage, which is now correlated to the Calabrian (Shatilova et al., 2014). Biltekin et al. (in press) even suggest the persistence of *G. europaeus* in the Holocene of the southern Black Sea.

(FIGURE 8 approximately here)

Our newly recovered Gelasian assemblage of San Lazzaro, with 50% HUTEA, is an exception at the European scale, but it must be considered that the low number of species may have biased this value. The other Gelasian assemblage available in central Italy, Cava Toppetti II, has 7% HUTEA and the Piacenzian or Gelasian Dunarobba assemblage has 20% HUTEA. These floras, similar to other Gelasian-Calabrian ones of Italy (Girotti et al., 2003, Martinetto, 2001a; Martinetto et al., 2015) and Europe (Table 2) are still very rich in CTEA, commonly associated with *Parrotia*, *Pterocarya* and *Zelkova*. By merging the occurrence data of HUTEA (Fig. 9), CTEA (compare Table 1 with data in Martinetto, 2001a, and Martinetto et al., 2015) and TEWA (Martinetto, 2001a; Martinetto et al., 2015) it is apparent that at least 70 plant species disappeared from southern Europe in the time interval between latest Zanclean (3.7 Ma) and early Middle Pleistocene (0.5 Ma).

(FIGURE 9 approximately here)

4.5. Ectothermic vertebrate record (amphibians and reptiles)

The Italian peninsula hosted in the past a few reptile genera that went locally extinct (with a timing different from that of the HUTEA) and now survive in a stripe that extends eastward from the Balkan Peninsula to Indonesia, but still preserves in an exclusive way some amphibians that once had a much larger range. Examples are *Agama s.l.*, *Pseudopus*, *Tomistoma*, *Vipera* (oriental group), among thermophilous reptiles (Delfino, 2002; Kotsakis et al., 2004; Piras et al., 2007; Delfino et al., 2008), and *Salamandrina* and plethodontid salamanders among the amphibians that are tied to

humid terrestrial, non lentic or lotic, niches (Delfino, 2002; Venczel and Sanchiz, 2005; Delfino et al., 2006; Delfino and Sala, 2007). Particularly interesting is the case of the fully terrestrial plethodontid salamanders of the genus *Hydromantes* that have in the Italian biogeographic region the only Palaearctic representatives with their sister taxon living in Korea (Buckley et al., 2010). These lungless salamanders are tied to environments with high environmental humidity that allow gas exchanges through their skin, but the fact that they have interstitial habits could imply the influence of factors that go beyond those that controlled the survival of plants. It should also be mentioned that the last European occurrence of the frog genus *Latonia*, known since the Oligocene, is the one of Pietrafitta (Delfino, 2002; Rage and Rocek, 2003), a Calabrian site in Central Italy (Martinetto et al., 2014) and that this genus, described on the basis of fossil material and long considered extinct, was recently found alive in Israel (Biton et al., 2013).

5. Discussion

Depending on the concepts of "physiological uniformitarianism" (Tiffney and Manchester, 2001) and deterministic late Cenozoic plant extinctions in Europe (Svenning, 2003) we singled out three groups of plant fossil-species occurring in southern Europe: CTEA, HUTEA, TEWA. The CTEA and HUTEA include several species extinct in Europe, belonging to supraspecific plant taxa with a partly shared modern distribution in East Asia. The HUTEA are the descendants of the "exuberant laurophyllous flora" (Kubitzki and Krutzsch, 1996) growing in the warm temperate belt of southern Laurasia during the Eocene. At this time many taxa now distributed in eastern Asia were present in North America and Europe, but later survived only in the first and, partly, in the second continent. For this reason it would be more appropriate to speak about taxa "conserved in East Asia" rather than "of East Asian affinity".

Several taxa that tolerated cooler conditions (including many CTEA) tended to occupy a higher latitudinal belt during the Eocene and Early-Middle Miocene, and were able to survive both in eastern Asia and eastern North America, but not in Europe (Tiffney and Manchester, 2001; Wen et al., 2010). In fact, the present Asian-American biogeographic disjunction of several plant taxa (*Hamamelis*, *Liquidambar*, *Liriodendron*, *Magnolia*, ecc.) "mostly represents relict distributions of a wider distribution in the Tertiary. It is a product of complex processes such as migration/dispersal, extinction, speciation, vicariance, and perhaps also evolutionary convergence and stasis" (Wen et al., 2010).

Phylogenetic studies based on disjunct eastern Asian-eastern North American living plants (e.g. Magnoliaceae: Nie et al., 2008) pointed out that the divergence times mostly date back to Eocene-Miocene (Wen et al., 2010). The divergence times of extinct European taxa and their extant eastern Asian sister taxa is poorly understood, even if a few recent studies incorporated fossils in the phylogenies (e.g. Xiang et al., 2006; Denk and Grimm, 2009; Zhang et al., 2013; Fritsch et al., 2015).

Despite this lack of information, the available literature is sufficient to explain why it is convenient to separate the groups CTEA, HUTEA and TEWA: during the Eocene and/or Early-Middle Miocene, under equable climatic conditions (Wing and Greenwood, 1993; Zachos et al., 2001; Tiffney and Manchester, 2001; Grímsson et al., 2015), a north-south differentiation of the flora (and vegetation) was already present, so that the boreal regions were covered by cool-tolerant taxa (e.g. *Fagus*, *Juglans*: Aradhya et al., 2007; Denk and Grimm, 2009), some of which can be classified as CTEA (e.g. *Chamaecyparis*: Liu et al., 2009), and the middle latitudes were covered by more thermophilous taxa, including many HUTEA and TEWA, not adapted to regular and severe frost (e.g. *Cinnamomum*, *Engelhardia*, *Mastixia*, *Ocotea*, *Sideroxylon*, *Symplocos* sect. *Lodhra*, *Tetraclinis*, *Toddalia*, etc.). However, also several CTEA grew in these warm mid-latitude forests: in fact, even if we indicated the CTEA as a group of cool-tolerant plants, this applies only to the supraspecific taxa, and several CTEA species were probably as thermophilous as the HUTEA (see above the example of *Magnolia*). This hypothesis is corroborated by the observation that several

CTEA species display a HUTEA-like pattern of disappearance in Italy (see CTEA2 and CTEA3 in Fig. 9), which could suggest a similar thermophilous attitude.

The analysis of the percentage of HUTEA species in some well-dated early Pliocene to early Pleistocene carpofloras of Italy (excluded those newly analysed here) provided an interesting picture: values above 15% in the Zanclean, above 7% in the Piacenzian, 2-0% percent in the Gelasian and invariably 0% in the Calabrian (Figs 8, 9). Furthermore, an analysis of the early Pleistocene carpofloras of Europe (Table 2) showed that most of them do not contain HUTEA, apart *Eucommia* and possibly *Glyptostrobus* and *Symplocos* sect. *Lodhra* in the Colchis refugial area (Chochieva, 1975; Shatilova et al., 2014). Thus, our new record of the San Lazzaro section is of particular relevance, because for the first time an assemblage containing a very high percentage (50%) of HUTEA is documented in European sediments independently dated to the early Pleistocene. This is in agreement with a previous record (Martinetto, 2001a) of the same species occurring at San Lazzaro (*Sinomenium cantalense*, *Symplocos casparyi*, *Toddalia rhenana*) in the continental sediments of another early Pleistocene site of central Italy, Cava Toppetti II, even if in this second site the percentage of HUTEA is definitely lower (7%). The reconsideration of the stratigraphic data, in particular the biochronologic indications of continental molluscs and vertebrates, allows us to confirm a Gelasian age for the Cava Toppetti II section, the flora-bearing layer being most likely deposited between 2.1 and 1.9 Ma. The independent age assignments of the Cava Toppetti II and San Lazzaro sections point to a time-correlation of the warm and humid HUTEA-bearing phase detected in both of them. The combined record of the two sections is fundamental to prove that the three above-mentioned HUTEA species actually survived in central Italy after the Pliocene/Pleistocene boundary, and to rule out the suspect that the occurrence of their carpological remains in the marine San Lazzaro section could be due to the reworking from older (Pliocene) sediments (Martinetto et al., 2015).

Even if most of the HUTEA documented in the Pliocene (Fig. 9) are not yet reported in the early Pleistocene, it may be argued that this is a bias due to the scarcity of records. Indeed, the proved occurrence in the early Pleistocene of such thermophilous and humidity-requiring plants as *Symplocos* sect. *Lodhra* and *Toddalia* suggests the possibility that also other HUTEA would have crossed the Pliocene/Pleistocene boundary. Chiarini et al. (2009) reported fruits of *Engelhardia* from a poorly dated section that could be of early Pleistocene age. Pollen data suggest the persistence of *Engelhardia* in central Italy until the Middle Pleistocene (Biltekin et al., in press) and in Spain till to the early Pleistocene (Postigo-Mijarra et al., 2009). These late occurrences are in agreement with the suggestion by Kvaček (2007) that the European *Engelhardia* is an extinct phylogenetic clade that was more cool-tolerant than the extant Asian species, and possibly it should be excluded from the HUTEA in future analyses.

The possible late occurrence of a few potential HUTEA is also implicit in other South European palynological assemblages (Tsedakis et al., 2006; Postigo-Mijarra et al., 2009; Bertini, 2010; Magri, 2010; Popescu et al., 2010; Orain et al., 2013; Shatilova et al., 2014; Biltekin et al., in press; Combourieu-Nebout et al., 2015), reporting *Eucommia*, *Symplocos* and "Taxodiaceae" pollen up to the Calabrian, and in some areas to the Middle Pleistocene (Shatilova et al., 2014; Biltekin et al., in press) or Holocene ("Taxodiaceae": Biltekin et al., in press). However, the identification at genus (for the "Taxodiaceae") or section level (for *Symplocos*), which is necessary for the assignement to the CTEA or HUTEA, is mostly not provided in such works (except Biltekin et al., in press).

To our knowledge the single macrofossil of a HUTEA in the Middle Pleistocene of Europe is a wood of *Amentotaxus* sp. (Follieri, 2010) from central Italy, associated to several taxa that later went extinct in Europe (*Taxodium*, the CTEA *Cephalotaxus* and *Torreya*, and the TEWA *Ocotea*). We cannot exclude that central-southern Italy may have offered a refugial niche that was warm and wet enough to assure the longer survival of a few HUTEA, in contrast to central Europe. In fact pollen data document the persistence of potential HUTEA ("Taxodiaceae") and humidity-requiring CTEA (*Carya*) till to the Middle Pleistocene in central and southern Italy (Manzi et al., 2011; Magri and Palombo, 2013; Orain et al., 2013; Biltekin et al., in press). However, most of the CTEA have

the last macrofossil record (Martinetto, 1999, 2001a; Martinetto et al., 2015) in the time span from 1.4 to 0.8 Ma (Fig. 9).

Also a simple comparison of the fossil record and the current distribution of the terrestrial ectothermic vertebrates suggests that the Italian biogeographic region acted as a humid refugium. It is actually tempting to associate the history of plants with that of these animals, whose distribution is clearly related to historical variations of temperature and humidity more directly than that of other vertebrates. However, it seems that despite the possibility of identifying a general common trend there are significant differences that are only partly related to the incompleteness of the fossil records of both groups. Conversely, a particularly intriguing argument is the concomitant persistence in the San Lazzaro section of thermophilous terrestrial plants and unexpected (for the early Pleistocene) thermophilous marine benthic taxa, such as *Amphistegina* spp. and *Persististrombus* cf. *coronatus* (Bizzarri and Baldanza, 2006; Harzhauser and Kronenberg, 2008; Monaco et al., 2011).

It is well known that the Pliocene is characterized by intense climatic oscillations of increasing amplitude, also at the middle latitudes (De Shepper et al., 2013), with cold pulses at 3.7-3.6 Ma, 3.3 Ma (Zanclean/Piacenzian transition) and intense glaciations during late Piacenzian-early Gelasian, at 2.7-2.4 Ma (Zachos et al., 2001; Lisecki and Raymo, 2005; Prescott et al., 2014). The early Pleistocene is characterized by ~40 kyr lower-amplitude glacio-eustatic oscillations (Combourieu-Nebout et al., 2015), terminating in the mid Pleistocene 'climate revolution' with an abrupt shift to ~100 kyr higher-amplitude oscillations in the late Calabrian, between 0.9 and 0.8 Ma (MIS 23 and MIS 22: Muttoni et al., 2011). This event brought a cooler climate during glacial maxima at the middle latitudes (Ravazzi et al., 2005; Bertini, 2010; Muttoni et al., 2011).

The above-mentioned climatic crises were probably responsible for terrestrial plant extinctions (Svenning, 2003; Eiserhardt et al., 2015). In the Italian record (Martinetto, 1999, 2001a; Martinetto et al., 2015) the HUTEA still show a very high percentage in correspondence of the late Piacenzian "warm blip" (CQ1 assemblage: 31%), but a marked decrease in the percentage and number of species (Fig. 8) occurs soon after, in the transition from the Piacenzian to the Gelasian. The north Italian plant assemblages formed during the late Piacenzian cooling (Irace et al., 2012) are totally devoid of HUTEA, but this is not the time of their definitive disappearance from Europe. The new record from the independently dated marine section of San Lazzaro and the related continental record from Cava Toppetti II show that at least three species of HUTEA persisted in central Italy in the Gelasian (*Sinomenium cantalense*, *Symplocos casparyi*, *Toddalia rhenana*). Further macrofossil studies in the Calabrian and Middle Pleistocene are needed for a better assessment of the disappearance time of these and other HUTEA species. In parallel, a more precise dating of important fruit and seed bearing sections should be obtained. If the Dunarobba section would be proven to have an early Pleistocene age (Bizzarri et al., 2011; Martinetto et al., 2014), this would imply that at least 8 HUTEA species (20% of the species in Dunarobba's assemblage DC1b) overcome the Plio/Pleistocene boundary in central Italy (Fig. 9), and the warmest Gelasian peaks still had a flora of definite "Pliocene" character. Actually, the evidences provided by continental molluscs and the fruit and seed assemblages (Fig. 9) suggest a Piacenzian (or transitional Piacenzian-Gelasian) age of the Dunarobba deposits, but also in this case we cannot rule out the persistence of Pliocene taxa in a climatic refugium. In fact, uncertainties in the disappearance time from central Italy of several thermophilous and humid requiring organisms still exist, and further data should be collected. As for plants, particular attention should be addressed to southern Italy, where pollen assemblages (Biltekin et al., in press; Combourieu-Nebout et al., 2015) suggest a longer persistence of thermophilous exotic taxa. However, the lack of palaeocarpological investigations in such an area did not permit a verification of the eventual presence of several HUTEA that do not have a recognizable pollen record (Table 1).

The new data collected and the use of the new categories HUTEA, CTEA and TEWA allow us to provide a description of the massive late Cenozoic plant extinction in southern Europe, which is more detailed and effective than the previous ones. For example, Rodriguez Sanchez and Arroyo

(2008) recently provided this version of the story: "in the Piacenzian relict genera of the Tethyan flora still coexisted in southern Europe with ancestors of extant Mediterranean taxa. The onset of the Mediterranean climate in the Pliocene, with hot and dry seasons, and the glacial–interglacial cycles of the Quaternary, with recurrent periods of cold and arid conditions, ultimately caused the extinction of many members of the Tethyan Palaeogene flora in Europe and North Africa (Mai, 1989; Svenning, 2003)".

We suggest here a more articulated scenario: during the Miocene the humidity-requiring descendants of both the Palaeotropical ("Tethyan") and Arctotertiary floras coexisted in Europe (Mai, 1989, 1991), and most of them (TEWA excluded) did not develop an adaptation to aridity. A consistent group of plants, namely our HUTEA, also did not adapt to cool climate, whereas in other groups (our CTEA) cool-tolerant forms had been selected in the course of various Cenozoic cool phases (Zachos et al., 2001). The climatic tolerances of the HUTEA, TEWA (e.g. *Ficus*, *Laurus*, *Liquidambar*, *Ocotea*) and likely thermophilous CTEA species (i.e. CTEA2 in Fig. 9) were probably fixed by a selection under globally equable climates in the Eocene-Miocene time span (Mai, 1989; Wing and Greenwood, 1993; Svenning, 2003; Rodriguez Sanchez and Arroyo, 2008; Manchester et al., 2009; Grímsson et al., 2015), when some HUTEA (*Sargentodoxa*, *Sinomenium*) also grew in North America (Manchester et al., 2009), persisting into the Mio/Pliocene transition (Liu and Jacques, 2010).

In southern Europe the HUTEA, TEWA and thermophilous CTEA species still grew together in the same plant communities (see Martinetto and Vassio, 2010; Martinetto et al., 2015) during the Zanclean, Piacenzian and the Gelasian warm peaks, when the climate was favourable for all of them. Later, thanks to their major drought tolerance (Svenning, 2003; Grimm and Denk, 2012; Utescher and Mosbrugger, 2015), the TEWA found some relatively warm refuges in the Mediterranean (*Coriaria*, *Laurus*, *Liquidambar*, *Olea*, *Styrax*, *Tetraclinis*), North Africa (*Laurus*, *Olea*, *Tetraclinis* and, possibly, *Morella*, *Ocotea*, *Sideroxylon*, *Visnea*) and West Asia (*Olea*, *Sideroxylon*). Some TEWA are today conserved in Macaronesia (*Morella*, *Ocotea*, *Sideroxylon*, *Visnea*) but their arrival there could be as recent as Pleistocene (Kondrasov et al., 2015).

Conversely, the HUTEA did not manage to adapt either to the dry and cool European conditions (Manzi et al., 2011) or to the too dry North African-East Asian ones and survived only in East Asia; just a few of them also survived in wet parts of tropical Africa (e.g. *Toddalia*) and/or America (e.g. *Meliosma* subgen. *Kingsbouroghia*, *Sassafras*, *Saurauia*).

As for the chronology of the disappearance, the Italian record would suggest that the HUTEA were constantly present in the Zanclean-Piacenzian flora of southern Europe, had a small retreat at the Zanclean-Piacenzian transition, possibly affecting four species of HUTEA (Fig. 9), and a larger one at the Piacenzian-Gelasian transition (18 species of HUTEA: Fig. 9); three species of HUTEA (*Toddalia latisiliquata*, *T. rhenana*, *Sinomenium cantalense*) seem to disappear at the Gelasian/Calabrian transition, and there is poor evidence in Italy for the few HUTEA which survived in the Calabrian, even if at least two HUTEA species (*Glyptostrobus europaeus* and *Symplocos casparyi*) were still present during the Calabrian in the Colchidian refugium (Chochieva, 1975). *Engelhardia* and *Eucommia* still occurred in the Calabrian of Italy and Spain (Postigo-Mijarra et al., 2009; Bertini, 2010; Biltekin et al., in press; Martinetto in press PalB); the last southern European macrofossil record of an HUTEA which is presently known is that of *Amentotaxus* sp. in the Middle Pleistocene of central Italy (Follieri, 2010).

Similarly to the HUTEA, also the CTEA did not tolerate dry conditions (Svenning, 2003), but a few ones (*Carya*, *Tsuga*) still survived in the Middle Pleistocene of central-southern Italy (Magri, 2010), Turkey (Biltekin et al., in press) and the Balkan (Tsedakis et al., 2006; Biltekin et al., in press) and Iberian (Postigo-Mijarra et al., 2009) peninsulas, due to the presence of refugia (Combourieu-Nebout et al., 2015) which were humid enough, as demonstrated by the continuous presence of the draught-intolerant *Fagus* until today (Magri, 2008). *Parrotia*, *Pterocarya* and *Zelkova*, which had climatic requirements similar to the CTEA, survived until the present around the Black and Caspian

seas (*Zelkova* also in the Mediterranean). Another plant extinct in Europe, *Cedrus*, has particular requirements and histories (Magri, 2012; Su et al., 2013; Biltekin et al., in press). As a whole the carpological data, in connection with the abundant pollen data available, testify that in the late Piacenzian-Middle Pleistocene interval at least 70 plant species (Table 1), including HUTEA (Fig. 9), CTEA (Fig. 9, Table 1) and TEWA (Martinetto et al., 2015), disappeared from the fossil record. However, such a disappearance is not readily interpretable as extinction. By comparing our results with those of Bertoldi et al. (1994), Martinetto (1999, 2001a), Martinetto et al. (2007) and Bertini (2010) it is apparent that the rapidly increasing fossil evidence provided by the Italian carpological and pollen records determined a progressive shift of the last occurrence data of several taxa (e.g.: *Liriodendron*, *Magnolia*, *Sinomenium*, *Symplocos*, *Toddalia*), and there is still space for further changes based on new fossil evidence. We propose that, based on the present evidence, only the concomitant disappearance events of several species, such as the HUTEA2 + CTEA2 (Fig. 9), should be considered as reliably assessed. These concern only two main phases: The Piacenzian/Gelasian transition (main crisis of the HUTEA2 and CTEA2) and the late Calabrian/Middle Pleistocene (main crisis of the CTEA4, last occurrence of the HUTEA *Amentotaxus*). The disappearance events of plant macrofossils at the Zanclean/Piacenzian transition (a few HUTEA1) and Gelasian/Calabrian transition (a few HUTEA3 and CTEA3) appear of minor scale, as also confirmed by the relatively continuous pollen records (Tzedakis et al., 2006; Postigo-Mijarra et al., 2009; Bertini, 2010; Magri, 2010; Orain et al., 2013; Shatilova et al., 2014; Biltekin et al., in press; Combourieu-Nebout et al., 2015). These last events are not univocally interpretable as extinctions, since the taxa which seem to disappear could have become silent for the macrofossil record, though perhaps still present in small relict niches, as suggested by the late occurrence of *Eurya* cf. *stigmosa* (CTEA), *Glyptostrobus europaeus* (HUTEA) and *Symplocos casparyi* (HUTEA) in the Calabrian of the Colchis refugium (Chochieva, 1975; Mai and Martinetto, 2006) and also of *Amentotaxus* (HUTEA), *Cephalotaxus* (CTEA) and *Torreya* (CTEA) in the Middle Pleistocene of central Italy (Follieri, 2010).

6. Conclusions

New data on early Pleistocene fossil fruit and seed assemblages from Italy allowed us to detect several extinct taxa that commonly went unnoticed in pollen analyses. The combined analysis of Pliocene and early Pleistocene occurrence data provided a detailed picture of the reduction of plant diversity in southern Europe. The possible explanation of the causes of plant extinction requires an excursion into deeper times: Several Neogene plants were mainly adapted to grow in thermophilous mesic forests, whose consistent water supply was guaranteed by atmospheric humidity more than groundwater. The climate deterioration of the Plio-Pleistocene cancelled the ecological space of growth of most thermophilous and humidity-requiring taxa. Provided that habitat shift occurred very rarely, most taxa did not manage to adapt to the harsh conditions either from 2.7 to 2.4 Ma or from 1.0 to 0.3 Ma, and went extinct. The chance to avoid extinction was not only a question of temperature, but a combination of this with humidity requirements. Southern Europe became extremely dry during the Pleistocene glacials and those plants requiring both higher temperature and consistent water supply had no chance to find a niche to survive, if not adapted to live along rivers (*Liquidambar*, *Parrotia*, *Platanus*, *Pterocarya*). A few humidity-requiring plants that had already developed an adaptation to cold climate in the Oligocene or Miocene, like *Carya*, could temporarily survive into the Middle Pleistocene also in the inhospitable Europe, possibly in small, not too dry refugia. A similar niche may have saved *Parrotia*, but in the south Caspian area. Our carpological data, in connection to the abundant pollen data available from the literature, testify that the late Zanclean-Middle Pleistocene interval has really been the theatre of a stepwise mass extinction in southern Europe: at least 70 plant species disappeared in two main phases: Piacenzian-Gelasian transition (main crisis of the HUTEA and CTEA2) and late Calabrian-Middle Pleistocene (main crisis of the CTEA4, last occurrence of the HUTEA *Amentotaxus*). The disappearance events at the Zanclean-Piacenzian transition (mostly HUTEA1) and Gelasian/Calabrian transition (a few

863 HUTEA3 and CTEA3) appear of minor entity and are not univocally interpretable as extinctions.
864 The chronological positions of the two main collective disappearance events coincide with two
865 well-known intervals of major climatic deterioration and support a climatic determinism in the
866 south European extinctions of the investigated plant taxa.

867
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1340
1341 Figure captions

1342 Figure 1 - Simplified geological scheme for the area of the San Lazzaro, Cava Toppetti and
1343 Dunarobba sections.

1344 Figure 2 - Reference lithostratigraphic schemes for the South Valdichiana and Tiberino Basins
1345 (modified after Baldanza et al., 2014). 1=San Lazzaro; 2=Cava Toppetti II; 3=Dunarobba.

1346 Figure 3 - Sedimentological/stratigraphic sections in the San Lazzaro area. Location of the
1347 biostratigraphic (dots) and carpological (FU3-6) samples is also reported. *tDb*=*Discoaster broweri*
1348 LO; *bmG*=medium-sized *Gephyrocapsa* sp. FO (sensu Raffi, 2002). CS = clay, silt; G = gravel.

1349 Figure 4 - Panoramic view of the San Lazzaro quarry. The richest fruit and seed bearing deposit
1350 (FU5) was located at the transition from the grey to the yellowish sediments (1/3 above the bottom
1351 of the image).

1352 Figure 5 - Detail of a lens of mixed shells and compressed phytodebris at ca. 8 m from the base of
1353 the San Lazzaro section (see FU4 in Fig. 3).

1354 Figure 6 - Resumed geological setting, sedimentological interpretation, magnetostratigraphic and
1355 biochronological calibration, and fossil record for the Cava Toppetti II site (redrawn after Abbazzi
1356 et al., 1997). Original vertebrates taxonomy reported by Abbazzi et al. (1997) is not revised nor
1357 further discussed herein.

1358 Figure 7 - Aspect of the deposits with compressed macroscopic plant remains in the Cava Toppetti
1359 II section as they appeared in the year 1998. The sampled fruit and seed bearing sediment
1360 (consolidated sandy mud, see NJ1 in Fig. 7) is shown in the detail below.

1361 Figure 8 - Histograms of the percentage of HUTEA species in some well-dated early Pliocene to
1362 Early Pleistocene floras of Italy (dark grey bars). Records from San Lazzaro, Dunarobba and Cava
1363 Toppetti II are also reported (pale grey bars). Numbers indicate the total of HUTEA species in each
1364 assemblage. See label explanations and locality data in Table 2.

1365 Figure 9 - Scheme summarizing the chronological distribution of carpological records of selected
1366 species in the Pliocene and early Pleistocene of northern-central Italy. The records from all the
1367 localities accessed into the CENOFITA database (Martinetto and Vassio, 2010; Martinetto et al.,

2015) are reported, according to data published by Basilici et al. (1997), Bertoldi and Martinetto (1995), Ghiotto (2010), Gregor (1990), Martinetto (1994, 1995, 1999, 2001a, 2001b, 2003, 2009, in press), Martinetto et al. (2015). Both the HUTEA and CTEA have been subdivided in groups according to the chronostratigraphic distribution, in such a way that the numbers 1 to 4 corresponds to the Groups 1 to 4 in Martinetto et al. (2015). All of the species referred to the HUTEA and CTEA4 have been reported, whereas for the CTEA2 and CTEA3 only selected examples have been shown. The age range for each species is indicated by black bars for the records originating from reliably dated localities (Martinetto, 1999, 2001a, 2003; Martinetto et al., 2007, 2015): Lugagnano (5.1-4.5 Ma), Canale (4.5-3.8 Ma), Cherasco (4.5-3.8 Ma), Pocapaglia (4.5-3.8 Ma), Breolungi (5.1-3.8 Ma), Morozzo (5.1-3.8 Ma), Sento I (3.8-3.6 Ma), Candelo (4.5-3.6 Ma), Baldichieri-Fornace (3.8-3.3), Roatto (3.3-3.2 Ma), RDB Quarry of Villafranca d'Asti (3.3 to 3.1 Ma), Stura di Lanzo Fossil Forest (3.1-3.0 Ma), Marecchia (3.0-2.9 Ma), San Miniato (3.0-2.8 Ma), Castell'Arquato-Monte Falcone (3.0-2.8 Ma), Meleto (2.9-2.8 Ma), Santa Barbara (2.9-2.7 Ma), Castell'Arquato-Arda-AD3 (2.5-2.4 Ma), Casnigo (2.1-1.9 Ma), Poggio Rosso (ca. 1.9 Ma), Santerno-Codrignano (1.8-1.7 Ma), Leffe 1st browncoal (1.6-1.4 Ma), Stirone-Laurano-LA1 (1.1-1.0 Ma), Enza-EZ38 (1.1-1.0 Ma), Ranica (1.1-1.0 Ma), Oriolo (1.0-0.8 Ma), Stirone-Laurano-LA3 (0.9-0.8 Ma), Pianico-BVC lithostratigraphic unit (0.8-0.7 Ma). Hatched bars indicate records from the following poorly dated localities (see Martinetto, 1999; Martinetto et al., 2015): Ca' Viettone (late Zanclean, possibly 3.8 to 3.6 Ma); Fossano (late Zanclean, possibly 4.0 to 3.6 Ma); Sento II (possibly late Zanclean, 3.8 to 3.6 Ma); Cossato (possibly late Zanclean-early Piacenzian, 3.8 to 3.2 Ma); Front (possibly Piacenzian, 3.3 to 3.0 Ma); Momello-Lanzo (possibly Piacenzian, 3.6 to 3.0 Ma); Castelletto Cervo I (possibly late Piacenzian, 2.8 to 2.6 Ma); Castelletto Cervo II (possibly Gelasian, 2.6 to 2.0 Ma); San Pietro di Ragona (Gelasian, 2.6 to 1.8 Ma); Buronzo (possibly Gelasian, 2.2 to 1.8 Ma); Steggio (Calabrian, 1.8 to 0.8 Ma). Abbreviations: c = climber; h = herb; MAT = Mean Annual Temperature; Mes = Messinian; MP = Middle Pleistocene; NLR = Nearest Living Relative; s = shrub; t = tree.

Table 1 - Mean Annual Temperature lower threshold values for modern plant genera or subgeneric taxa extinct in Europe ("exotic"), according to the Paleoflora database (PFDB, Utescher and Mosbrugger, 2015), the GrimClim database (CG, Grimm and Denk, 2012), and to different literature sources listed in Appendix 1 (Alternative MATmin). The list is limited to taxa of the HUTEA and CTEA categories with a proved occurrence in the late Cenozoic of Italy, selected as a representative territory for the evaluation of the southern European floral change.

Table 2 - List of the reference localities selected for the calculation of HUTEA species percentage reported in Fig. 8.

Table 3 - Occurrence of HUTEA and CTEA genera in the main Early Pleistocene carpofloras of Europe.

Table 4 - List of the carpological taxa identified in four sediment bulk samples from the San Lazzaro section, see Fig. 3. In brackets the number of specimens for each species.