

# Late Miocene to Early Pliocene vegetation of southern Europe (7–4 Ma) as reflected in the megafossil plant record

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## Abstract

Assemblages of plant megafossils from the Late Miocene to Early Pliocene sites in southern Europe have been re-evaluated in order to get data for reconstructing the development of vegetation and climate during this time interval (7–4 Ma). Main areas of the survey are centred in Greece and adjacent countries, Italy, southern France and Spain. As a product of this study, maps of the studied area for the Late Miocene have been produced showing main physiognomic features of the forests expressed in the proportions of broad-leaved deciduous, broad-leaved evergreen, legume-type and sclerophyllous components, respectively.

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## 1. Introduction

Local plant fossil assemblages (often called “floras” in the European Cenozoic, or “taphofloras” by Russian palaeobotanists) do not reflect exactly the composition of the original floras nor do they give a true picture of the surrounding vegetation. Still these are the only sources of information from the point of view of palaeobotany and palynology to follow changes of the plant cover and derived climatic oscillations in time and space.

The following survey is focused on the latest Miocene to Early Pliocene history of vegetation in an area covering Greece and adjacent countries in the eastern Mediterranean, Italy, southern France and some other parts of the western Mediterranean, basing generally on megafossil records, such as foliage, fruits and seeds. Pollen records have been exceptionally and incompletely used for comparison and only in the analytical part of the text, not for the maps. We are aware of drawbacks of this approach and expect improved reconstructions of palaeovegetation, when a synthesis of palaeobotanical and palynological data is accomplished in the future. The main limitation to the use of palynological data more broadly over Europe is the fact that sporomorphs have been identified in various parts of Eurasia using either a morphological or botanical approach. In many cases, identified pollen

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taxa remain unpublished and the results are available only in summary synthetic pollen diagrams. Although not all sites of plant megafossils have been newly revised in this vast area, we have updated basic taxonomy of elements, which are employed for the suggested reconstructions.

This first attempt to show changes in aspects of woody vegetation is expressed on geographic maps using a new classification of forest elements developed recently for the purposes of the EEDEN program (Kovar-Eder and Kvaček, 2003). This taxonomic/physiognomic method enables us to include also taxa of uncertain systematic position by using physiognomic characters. The maps have been prepared only for the Late Miocene due to scarcity of widely dispersed sites dated to the Early Pliocene. There is still an inadequate number of Late Miocene assemblages that cover the area resulting in various anomalies, partly inconsistent with more detailed palynological research (compare Fauquette et al., 2006–this volume). However, such inconsistencies always happen, when widely scattered assemblages (e.g. of mammals) serve as a basis for this kind of map. The palaeobotanical data come mostly from our personal investigations in respective regions (Greece–Zlatko Kvaček, Italy–Edoardo Martinetto, southern France–Paul Roiron) or from published sources. Our attempt must be taken as a preliminary survey, which needs more work on other sites in the future to make the network denser. We very much hope to elaborate, in cooperation with the colleagues working in palynology, a more general and common palaeobotanical and palynological methodology for producing overview maps of main plant formations and biomes. In any case, the two methods can be regarded complementary (see e.g. Meller et al., 1999; Kovar-Eder et al., 2001a). To follow processes of vegetation dynamics more objectively, assemblages of all three categories of plant fossils, i.e. leaf and fruit megafossils, sieved fruit and seed mesofossils as well as sporomorphs should be simultaneously evaluated from the levels studied, each reflecting different and complementary parts of vegetation that covered the surrounding landscapes. However, such data are mostly only available from central Europe for earlier periods, e.g. Wackersdorf, Germany, Oberdorf, Austria, Rhenish Embayment, Germany, Cyprus Shale, Czech Republic (see Kovar-Eder et al., 2001a,b for references).

## 2. Survey and analysis of plant fossil assemblages

Our survey is selective because only recently circumscribed and well-dated sites have been analysed.

In some cases, the pollen record is also taken for comparison. The following abbreviations are employed below for the climatic proxies, if available: MAT=mean annual temperature, CMT=coldest month mean temperature, WMT=warmest month mean temperature, MART=mean annual range of temperature, MAP=mean sum of annual precipitation.

### 2.1. Greece and adjacent areas<sup>2</sup>

The area of eastern Mediterranean and adjacent regions encompasses several plant assemblages in Greece, Bulgaria, the former Yugoslavia, Romania and Abchasia. Their dating method is variable, partly by radiometrical data and partly by independent biostratigraphy.

The southernmost assemblage of Makrillia in Crete (Sachse, 1997) deviates somewhat from our scheme, being dated into the Tortonian (ca. 7.7–8.6Ma). It is characterised by foliage, diaspores as well as sporomorphs. The elements based on foliage are only partly well documented due to poor preservation of impressions without epidermal anatomy. Consequently the affinities of many leaf fossils are not recognisable. The conifers are represented by a few pine needles, a *Cathaya*-like cone scale, a *Taxodium* fragmentary twig and *Tetraclinis salicornioides* cladode-like segments. Broad-leaved elements are mostly arboreal with the most diversified being Fagaceae (*Fagus*, sclerophyllous oaks), Leguminosae (including *Podocarpium*) and abundant maples of the *Goniocarpa* group. Also Lauraceae, as far as it can be determined from foliar gross morphology, was probably well diversified. Of the Juglandaceae, *Engelhardia* (*Palaeocarya*), *Carya* and some other deciduous representatives were present. It seems likely that the assemblage includes more ancient elements coming from the northern part of western Eurasia and surviving from the Middle Miocene. This is illustrated by one very typical element—the octomeric flower called *Asterocalyx styriacus* Ett. (not identified but illustrated by Sachse, 1997, pl. 17, Figs. 18–19) occurring typically at Parschlug, Magyaregregy, Leoben and Randeck (Kovar-Eder et al., 2004). The reconstructed vegetation corresponds to the evergreen to mixed-mesophytic forests of the subtropical zone. The estimated climatic parameters as inferred by Sachse (1997) are MAT 17–20°C, CMT 10–12°C, MART 10–20°C, MAP 800–1600mm. Summer dryness was only weakly developed.

<sup>2</sup> By Z. Kvaček.

The Messinian/Pontian occurrences of plant fossils in northern Greece are mainly restricted to the Florina-Kozani basin (Vegora, Prosilion, Lava) extending up to western and southern Bulgaria (Podgumer, Garmen, Gaber, Goljam Manastir). Studies of epidermal anatomy contributed in some cases (Vegora–Kvaček et al., 2002) to more precise recognition of the affinities of various elements.

The lignite mine of Vegora has yielded the most diversified plant assemblage of a Late Neogene age in Greece. The locality situated south of Amintion, Florina District in western Macedonia belongs to the graben system of Florina–Kozani–Ptolemais. The fossiliferous layers are marls occasionally containing diatoms exposed above the lignite seams. Independent dating is provided by a radiometric (isotopic) dating of  $5.97 \pm 0.07$  Ma obtained from an ash layer close to the upper edge of the fossiliferous marls, indicating a Messinian/Pontian age. Most plant fossils studied are preserved as leaf compressions, rarely as carbonized cones, seeds and fruits. The assemblage comprises one fern (*Osmunda*), one *Ginkgo* species, one species of *Torreya* (Taxaceae), 6 species of Pinaceae documented by seed cones, 4 Cupressaceae (including Taxodiaceae), and more than 40 angiosperms (shrubs and trees, rarely herbs), when the elements are counted in combination of foliage and fruits.

The Fagaceae, Betulaceae, and Aceraceae are most diversified. Three woody plants—*Glyptostrobus*, *Fagus gussonii* and *Quercus sosnowskyi*—predominate in the assemblage in terms of number of specimens. Also common are remains of *Taxodium*, *Pterocarya*, *Quercus mediterranea*, *Quercus drymeja*, *Quercus kubinyii*, *Alnus ducalis*, *Zelkova zelkovifolia*, *Populus populina*, and *Acer pyrenaicum*. This is a heterogenous mixture of plants with widely different autecologies today. Riparian-swampy elements (taxodioids, *Pterocarya*, and probably *Alnus* and *Populus*) formed a belt of riparian azonal forest along the lake borders and disemboguing streams, while mesic woody plants (*Fagus*, *Q. kubinyii*, *Zelkova*, *A. pyrenaicum*) formed an open deciduous gallery forest around the lake. Evergreen oaks (*Q. mediterranea*, *Q. sosnowskyi*), cupressoids and *Pinus* formed scrub-like sclerophyllous woodland on drier substrates. We may assume a mosaic of woody vegetation related to the landscape relief. Accessory elements are found in various vegetation types. *Pinus* (pro parte), *Cupressus*, *Carpinus orientalis*-type, Leguminosae, *Acer integrilobum*, *Acer pseudomonspensulanum*, *Chamaerops humilis* were probably associated with subxeric woodland while *Ginkgo*, *Keteleeria*, Lauraceae, deciduous oaks/chestnut, *Alnus gaudinii*,

*Betula*, *Ulmus*, *Hedera*, *Acer subcampestre* enriched mesic gallery forests. Also *Cedrus*, confined today to mountains, was growing in lowland mesic forests, as is apparent from its rich occurrence at Drymos associated with *Cryptomeria* and other taxodioids (Velitzelos et al., 2000). *Platanus*, *Craigia*, *Alnus cecropiifolia*, *A. julianiformis*, *Acer tricuspidatum* and *Fraxinus* thrived together with *Glyptostrobus* and *Taxodium* stands on moist substrates along waters, with *Osmunda* in the undergrowth. This suggested reconstruction is purely intuitive, based on the inferred autecology of individual elements, as they behave elsewhere in the European Neogene. The reconstructed vegetation profile consists of three various types beginning from the lake: (1) the azonal riparian forest dominated by taxodioids and hygrophilic broad-leaved deciduous trees (*Alnus*, *Pterocarya*, *Populus*) with helophytic herbs (*Osmunda*, Monocotyledonae) in the undergrowth; (2) the mesic gallery forest (“Fagetum gussonii/Quercetum mixtum”) consisting of diversified deciduous trees of Fagaceae, Ulmaceae, *Acer*, *Platanus*, and others; and (3) the mesic-xeric woodland (“Quercetum mediterraneum”) dominated by evergreen sclerophyllous oaks, *Pinus* and Cupressaceae. Climatic estimates obtained by the co-existence approach suggest a subtropical climate: MAT 13.3–14.6°C, CMT 0.4–4.5°C, WMT 23.8–24.6°C, MAP 897–1018mm; the CLAMP analysis gives lower proxies: MAT 9.9–12.3°C, CMT 0.1–3.9°C, WMT 19.5–22.7°C, sum of growing season precipitation 398–1070mm.

The sites connected with the diatomite marl overlying the lignite seams at Lava and Prosilion are more like those of Vegora in floristic composition. At Lava, *Glyptostrobus*, Betulaceae, Fagaceae and *A. tricuspidatum* occur in the same frequency as at Vegora. *Engelhardia* is new for this part of Greece. At Prosilion, which is situated close to Lava (D. Velitzelos, personal communication, 2001), many of the elements are shared with the Vegora assemblage: *F. gussonii*, *Q. mediterranea*, *Q. sosnowskyi* and species of *Populus*, *Zelkova* and *Acer*, but in different frequencies. *Fagus* is scarcely represented, and so are *Glyptostrobus* and other Taxodiaceae. Prosilion is the only locality in Greece that has yielded *Taxus*. There are some plants not known at Vegora, but they are at Lava, e.g. *Engelhardia*, *Salix*.

The characteristics of the latest Pontian plant assemblages in Bulgaria can be summarised as follows (according to Palamarev et al., 1999).

The floras included in this group (Sofia Basin, Podgumer, Noviiskar Formation) are similar to that in northern Greece in floristic composition but they are more diversified. Important groups are the Pinaceae,

Betulaceae, Ericaceae, *Quercus* and *Acer*. There are many elements in common with the Vegora assemblage, e.g. *Osmunda*, *Ginkgo*, *Fagus*, *Q. mediterranea*, *Q. sosnowskyi*, deciduous oaks, *Craigia bronnii*, *A. ducalis*, *A. pseudomonspessulanum* and other maples, but Lauraceae, Leguminosae, Rosaceae and Ericaceae seem to be better represented.

The reconstructed vegetation is manifold including helophytic herbaceous communities, swamp forests with *Glyptostrobus* and *Taxodium*, mixed mesophytic humid forests in lowland as well as upland habitats including laurel-oak components, *Ginkgo*, Juglandaceae, *Liquidambar* in the canopy and Ericaceae, *Buxus*, *Ilex*, *Cornus*, *Daphne*, *Lonicera*, and other shrubs in the undergrowth. As in Greece, the mesic-subxeric open woodland was also recognised, being represented by sclerophyllous oaks, pines and other elements of this community. In the Eklichovo Basin, open landscape herbaceous communities with *Chenopodium*, *Polycnemum*, *Crataegus*, *Polygonum*, and Asteraceae were documented by pollen and diaspore assemblages (Palamarev et al., 1999, p. 32). Climatic estimates inferred from the autecology of important elements are: MAT 13–14°C, CMT 3–5°C, WMT 22–24°C, MAP 800–1000 mm.

Early Pliocene (Dacian) plant assemblages are few in Bulgaria, e.g. Kurilo, Lom, Gaber and Trojanovo (Palamarev et al., 1999). Laurophyllous elements were almost absent in the zonal vegetation and beech-deciduous oak-hornbeam forests predominated. The most diversified families are the Pinaceae, Fagaceae, Juglandaceae, Ulmaceae and Betulaceae, and, of the genera, *Quercus* and *Salix*. Evergreen elements are only poorly represented, mostly as a shrubby undergrowth (*Laurocerasus*, *Buxus*, *Rhododendron*, *Arbutus*, and evergreen oaks). Two walnuts—*Juglans bergomensis* and *J. kitanovii*—are noteworthy. In the zonal forests two communities are recognized: (1) Deciduous broad-leaved forest with *Taxus*, *Picea*, *Abies*, *Pinus*, *Tsuga*, *Thuja*, *Carya*, *Betula*, *Alnus*, *Carpinus*, *Fagus*, *Castanea*, *Quercus*, *Ulmus*, *Zelkova*, *Magnolia*, *Sassafras*, *Acer*, and *Fraxinus* in the canopy storey and *Buxus*, *Lonicera*, *Viburnum*, *Laurocerasus* and Ericaceae in the undergrowth; (2) Subxeric woodland with Aleppo pine, *Cupressus*, *Ephedra*, sclerophyllous oaks and other elements (*Carpinus* sect. *Orientalis*, *Cotinus*, *Arbutus*, *Acer* sect. *Gonicarpha*, *Smilax*). Climatic proxies inferred from the autecology of important elements are: MAT 12–13°C, CMT 3–5°C, WMT 20–22°C, MAP 800–1200 mm. The climatic character corresponds to humid warm-temperate regime with only a short period of precipitation deficiency.

The well-known site of plant fossils in Romania, Borsec, has newly been dated to the latest Pontian to Dacian (Givulescu, 1997). The assemblage is diversified, but has not been thoroughly analysed. It is dominated by deciduous Fagaceae, including *Castanea*, roburoid *Quercus* and *Fagus*, with additional Ulmaceae, Rosaceae, Leguminosae, and *Acer*. The occurrences of elements surviving from the Middle Miocene, e.g., *Daphnogene*, *Myrica*, *Paliurus*, *A. gaudinii* (as *Salix* spp. in Pop, 1936), “*Parrotia*” are noteworthy. Sclerophyllous elements are less pronounced than in more southerly sites of Bulgaria and Greece. The approximate MAT is estimated as 15.6°C, MAP 1361 mm.

The Late Miocene–Pliocene assemblages in Ukraine, e.g. Berezinka (Iljinskaya, 1968) reflect predominantly broad-leaved deciduous forests, in which some of the taxa are shared with southern Europe, e.g. *A. pyrenaicum* (including *A. ilnicense*). Thermophilic evergreen humid as well as subhumid sclerophyllous elements are not present.

Similar characteristics can be given for most Late Pontian plant assemblages in the former Yugoslavia (Mihajlović, 1990), where subhumid as well as humid subtropical elements only occasionally occur. An exception is the flora of the Kolubar Basin (Mihajlović and Lazarević, 1998, 1999), where the frequency and diversity of humid subtropical elements increased.

The Late Miocene–Early Pliocene assemblages in Abchasia (e.g. Kodor, Duab, Pitsunda, etc.; Kolakovskii, 1956, 1961, 1964; Kolakovskii and Ratiani, 1967) share many elements with the Pontian assemblage of Vegora. This is particularly true for the Kodor flora (also Pontian), where deciduous trees, e.g. *Ginkgo*, *A. integrilobum*-type, *Liquidambar*, *A. ducalis*, *A. gaudinii* (as *angustifolia*), *Platanus leucophylla*, *Fagus*, *Q. kubinyii*, *Q. petraea*-type, are accompanied by some thermophilic elements typical of Vegora: sclerophyllous *Q. sosnowskyi*, *Q. drymeja* (as *Castanopsis elisabethae*) and evergreen *Hedera*. However, there are also pronounced differences both in the flora and vegetation of Abchasia in contrast to the Messinian/Pontian of northern Greece, obviously due to more humid and less continental climatic conditions in Transcaucasia, which is a well-known refugium of the pre-Pontian plants. Diversified Lauraceae, Theaceae and other mesophytic elements like *Tetraclinis*, *Myrica*, *Daphnogene* and *Laurophyllum* (*Ocotea*) spp. and *Brassaiopsis*, which required humid summers, survived till the late Neogene as relicts in this part of the eastern Paratethys region. Among the deciduous trees, *Platanus* is represented by two species—*P. leucophylla* and *P. academiae* (i.e. *P.*

*lineariloba*, more similar to foliage of extant *P. orientalis*). Sclerophyllous oaks of the *Q. mediterranea* group can be traced in Transcaucasia only from the Pliocene (Kolakovskii in Takhtajan, 1982).

## 2.2. Northern and central Italy<sup>3</sup>

The thick and well-exposed Late Miocene successions of northern and central Italy often include a few layers with leaves and, sometimes, fruits and seeds of terrestrial plants, which have been sampled and studied in selected sites of the Po Basin and the Apennine foredeep.

On the Tirrenian side of Italy a section with abundant plant remains is known at Gabbro, western Tuscany (Berger, 1958). As a whole, nearly 20 local assemblages are known, which span in age from 7.2 to 5.3 Ma, according to the chronostratigraphic scheme of Roveri et al. (2001).

The state of knowledge of the palaeoflora is very variable from one locality to another. The assemblages of Ancona (Paolucci, 1896), Guarene (Sismonda, 1865; Peola, 1899a), Monte Castello (Peola, 1899b), Senigallia (Massalongo, 1854, 1858; Massalongo and Scarabelli, 1859), Stradella (Viviani, 1833; more properly called Montescano by Sordelli, 1896) and Polenta (Principi, 1926) were extensively sampled and taxonomically described so long ago, that an up-to-date revision is needed. The plant macrofossils from Carbonara Scrivia, Piobesi-Scaparoni and Nizza Monferrato have been sampled and studied more recently, but the lack of cuticular investigations hampers the identification of many entire-margined leaf types. In addition, a few rich localities, such as Banengo, Monte Castello, Palena, Roddi and Tossignano, have just been sampled and not yet studied in detail. In general, the quality of taxonomic identifications is variable, and a comparative revision of all the assemblages is badly needed, and essential to a correct palaeoclimatic interpretation.

Early Messinian assemblages (7.2–5.96 Ma) are preserved in laminated marine sediments in the localities of Banengo, Roddi, Senigallia p. p., Gabbro I and Palena. Detailed stratigraphical studies are needed to confirm or better assess their chronostratigraphic position. The collection from Senigallia was gathered from a few sites, without stratigraphical information, in the early 19th century (Massalongo and Scarabelli, 1859). It includes both early and mid-Messinian material, which is not easy to separate. However, the

majority of the leaf impressions originate from the Gessoso Solfifera Formation, so that the mixed flora of Senigallia will be treated together with the “mid”-Messinian floras (Table 1). Similarly, Berger (1958) omitted to separate in his systematic treatment the material from two layers at Gabbro, the first referable to the early Messinian and the second, most likely, to the “mid”-Messinian (Landini, personal communication). Falorni (1988–1989) listed separately the taxa occurring in the lower layer (Gabbro I: Villa Nardi); but still the precise occurrence of several species in the upper layer (Gabbro II: Pane e Vino) is not clear (hence the many question marks in Table 1). Re-examining the properly labelled original material preserved at the University of Pisa could solve this problem.

Such early Messinian assemblages are formed by both deciduous and evergreen broad-leaved elements. The northern sites (Banengo, Roddi) show a peculiar prevalence of leaves of deciduous Fagaceae (*Fagus* and *Quercus*), while the southern one of Palena shows more sclerophyllous types. Also the evergreen oak *Q. mediterranea* is common at Gabbro I, while it is doubtful in the northern sites (even those of the “mid” Messinian; Table 1). *Cercis virgiliana*, occurring at Gabbro I, seems to be a southern element, since it was elsewhere recorded only at Senigallia, either in the early or “mid” Messinian (also present at Ancona). Palms are recorded at Roddi (cf. *Sabal*) and Palena (cf. *Calamus*). The best-known assemblage of Gabbro I points to a warm-temperate humid (to sub-humid?) climate, and the others do not provide contrasting evidence, except for a clue to less humidity at Palena suggested by small leaf size and generalized sclerophylly.

In the “mid”-Messinian, favourable conditions for leaf preservation occurred in marginal basins, where deposition of gypsum layers and marls took place (Gessoso Solfifera Formation). Such marls often contain scattered leaves, sometimes concentrated in a few selected horizons. At Stradella, leaf impressions are directly preserved in gypsum.

Leaves have been sampled in a series of sites from Piedmont (Alba area) to Marches (Ancona). Taxonomic data have been published for the assemblages of the Alba area (Sismonda, 1865; Peola, 1899a; Cavallo et al., 1986; Guglielmetto and Iguera, 1994; Martinetto et al., 2000), Nizza Monferrato (Brambilla and Gallo, 2002), Carbonara Scrivia (Brambilla et al., 1982), “Stradella” (Viviani, 1833; more properly called Montescano by Sordelli, 1896), Portalbera (Brambilla, 1992a), Polenta (Principi, 1926), Monte Castellaro (Gentilini, 1989), Senigallia (Massalongo, 1854, 1858; Massalongo and Scarabelli, 1859), and “Ancona”

<sup>3</sup> By E. Martinetto.

Table 1

Distribution of selected plant megafossil taxa (mostly leaves) in the main early and “mid” Messinian floras of Italy

Taxa	P	C	AL	N	ST	T	SE	AN	G1	G2
<i>Acer integerrimum</i>	o	o	o		o		o	o	o	?
<i>Acer tricuspidatum</i> ssp. <i>lusaticum</i>	o		o		o			?	o	?
<i>Acer</i> (other species)	o		o				f	o	o	?
<i>Alnus cecropiaefolia</i>			o		*			?		
<i>Alnus ducalis</i>	o	o	o	?					o	
“ <i>Bambusa</i> ”				o		o				
cf. <i>Betula</i>	o		o					o		?
<i>Carpinus</i>			o		o	o	?	o	o	
<i>Carya minor</i>	o		o				o	?		
<i>Celtis trachytica</i>		o	o							
<i>Cercis virgiliana</i>							o	o	o	
<i>Craigia brononii</i>			o						o	?
<i>Cunninghamia</i>	o		o			o	o			
<i>Daphnogene polymorpha</i>	o	o	o	o	o	o	f	o	f	
<i>Fagus</i>	f	f	f	f	f	o	f	f	o	o
<i>Ginkgo adiantoides</i>	o		o		o		o			
<i>Glyptostrobus europaeus</i>	o				o	o	o	o	o	o
<i>Hedera</i> cf. <i>helix</i>		o	o			o				
<i>Liquidambar europaea</i>	o		o	o	o	o	o		o	
<i>Liriodendron procaccinii</i>							o	o		
<i>Magnolia</i>	o	o	o	o			?		?	?
<i>Myrica lignitum</i>	o	o	o	?				o	o	?
<i>Ocotea heerii</i>	o	o	o		o	o	o	o	o	
<i>Palaeocarya macroptera</i>		o	o			o	o		o	
<i>Parrotia pristina</i>			o							
<i>Pinus</i>			o	f		o	o	o	f	f
<i>Platanus leucophylla</i>	o	o	o	o	f	f	f	o	f	o
<i>Podocarpium podocarpum</i>	o	o	o	?						
<i>Populus</i> ( <i>P. nigra</i> type)	o		o		?		o	o	o	o
<i>Populus</i> ( <i>P. tremula</i> type)	o		o		o				o	o
<i>Pterocarya paradisiaca</i>	o	o	o		o		o	o		
<i>Quercus drymeja</i>	o	o	o		o		o	o	o	?
<i>Quercus gigas</i>	o	o	o			o		?		
<i>Quercus</i> gr. <i>kubinyii</i>	o		o		o	o	o	o	o	?
<i>Quercus mediterranea</i>				?			?	o	o	f
<i>Quercus</i> (deciduous)	o	o	o	o	o	f	f	f	o	f
<i>Rubus</i> sp.		o	o							
<i>Salix</i>	o	o	o	o	o			o	o	o
<i>Sassafras ferretianum</i>							o	o		
<i>Sequoia abietina</i>	o	o	o		o	o	o	o	f	f
<i>Smilax</i>	o		o				o	o	o	o
<i>Taxodium dubium</i>	?		o			?	o	o	o	o
<i>Tetraclinis salicornioides</i>	o		o	o		o	o	o	o	o
<i>Thuja saviana</i>	?	?	o						o	o
<i>Tilia</i>			?				o	?		o
<i>Trigonobalanopsis rhamnoides</i>	o		o	?	?	?	?	?	?	?
<i>Ulmus</i>	o	o	o		?		o	o	o	o
<i>Zelkova zelkovaefolia</i>	o		o	o	f		f	o		f
Evergreen? Lauraceae	f	o	f	f	o	f	f	f	o	
Leguminosoid types	f	o	o	o	o	o	f	o	o	o
No-toothed,?evergreen dicots	o	o	o	f	o	f	f	f	o	o

P=Piobesi-Scaparoni; C=Castagnito; AL=composite list of all the leaf floras of the Gessoso Solifera Formation near Alba; N=Nizza Monferrato; S=Stradella, more precisely called the Montescano flora; T=Tossignano; SE=Senigallia; AN=Ancona; G1=Gabbro I, early Messinian; G2=Gabbro II, probably “mid” Messinian.

\**A. cecropiaefolia* occurs at Portalbera, close to Stradella.

(Paolucci, 1896, collection from a few localities in the vicinity of the town having the same name). Another important assemblage, preliminarily cited by Knobloch and Gregor (1997), is known from Tossignano near Imola (Province of Bologna). As reported above, the flora of Gabbro II is also likely referable to the “mid”-Messinian.

Due to the high number of localities, a detailed list of taxa would be totally unsuitable for this synthetic overview, thus only the most important re-evaluated occurrences in the main sites are reported in Table 1. The revised floral lists of Ancona, Stradella and Nizza Monferrato are exclusively based on re-examination of the published drawings and pictures. Those of Gabbro and Senigallia are also mainly based on re-examination of the illustrations (Berger, 1958; Massalongo and Scarabelli, 1859; Brambilla, 1995), although a tentative survey of the original collections has been carried out. The remaining lists refer to the collections which have been directly analysed by one of the authors (E.M.).

The identification of Neogene leaf specimens on the basis of drawings and pictures is rather hazardous, however, a few taxa, well known in the European Neogene (e. g. those listed at the species level in Table 1), can be reliably recognized thanks to their peculiar gross-morphological characters (venation and margin). This method also permits identifications at the genus level for some common taxa (*Carpinus*, *Fagus*, *Populus*, *Pinus*, etc.) that are affected by problems of taxonomy and nomenclature at the species level.

On the other hand, the same method of identification cannot be applied to the so-called “leguminosoid” types and, particularly, to the entire-margined leaves with a coriaceous texture, suggesting an evergreen habit (“non-toothed ?evergreen dicots”). Some leaf types (“evergreen pinnately veined ?Lauraceae”) can tentatively be separated from this latter group on account of a strong affinity to some modern Lauraceae bearing pinnate-campitodromous venation and a dense reticulum of isodiametrical areoles (*Apollonias*, *Laurus*, *Persea*, etc.). The future development of cuticular investigation will probably be the key to the botanical identification of these problematic groups.

Actually, Brambilla (1995) and Brambilla and Gallo (2002) proposed a very precise botanical identification of some “non-toothed ?evergreen dicots” from Senigallia and Nizza Monferrato by comparisons only to the leaf venation patterns of modern tropical–subtropical taxa without leaf epidermal evidence. The present authors hesitate to accept such identifications due to the peculiar climatic requirements of some genera

(*Annona*, *Cryptocarya*, *Eugenia*, *Friesodielsia*, *Polialthia*, *Terminalia*) which are in conflict with those of the bulk of the Messinian floras.

In general, the leaf types found in the localities of the Gessoso Solifera Formation are rather uniform from north (“Alba”) to south (Ancona, Gabbro), as they largely include the same deciduous (e.g., *Acer*, *Alnus*, *Fagus*, *Ginkgo*, *Liquidambar*, *Platanus*, *Populus*, *Pterocarya*, *Quercus* p.p., *Salix*, *Zelkova*) and evergreen (e.g., Lauraceae, *Engelhardia* (*Palaeocarya*), *Smilax*, *Trigonobalanopsis* and many “non-toothed ?evergreen dicots”) broad-leaved taxa associated with several conifers (*Tetraclinis*, other Cupressaceae, *Taxodium*, *Sequoia*, other Taxodiaceae, *Pinus*, other Pinaceae). A few taxa have been exclusively detected in the northernmost localities (*Celtis trachytica*, *Hedera* cf. *helix*, *Parrotia pristina*), while *Liriodendron procaccinii* and *Sassafras ferretianum* are restricted to the southernmost sites. Palms have never been detected in the Gessoso Solifera Formation.

For the “mid-Messinian” both leaf physiognomy and taxonomic composition (Table 1) point to an arboreal vegetation growing under warm temperate and humid palaeoclimatic conditions (Martinetto et al., 2000). Nevertheless, two assemblages of Piedmont (Monticello, Piobesi, both near Alba) are very poor in evergreen taxa and may indicate a prevalently deciduous forest type, unless the representation of evergreen leaves has been strongly biased by selective transport.

The geochronology of the Lago-Mare episode, though rather well known (5.59–5.33 Ma), is still the object of discussion over whether it is later Messinian and/or earliest Pliocene in age (Roveri et al., 2001; Clauzon et al., in press). The Lago-Mare continental deposits often yield abundant plant macrofossils, which have been poorly studied till now. One of the present authors (E.M.) obtained taxonomical results (Table 2) from the investigation of fruits, seeds and, subordinately, leaves from two sites: Corneliano d’Alba (composite section Sioneri-Ciabot Cagna, close to Alba) and Scipione Ponte (section of the Stirone River, close to Fidenza).

The carpological assemblages at Corneliano d’Alba and Scipione Ponte are rather diverse and represent a rich assemblage of woody and herbaceous plants indicating a warm-temperate climate. Although the two assemblages differ in several occurrences (Table 2), they share a significant group of taxa which provides very similar palaeofloral context (cf. Cucurbitaceae, *Magnolia allasoniae*, Oleaceae, *Sambucus pulchella*, *Sapindoidea margaritifera*, *Solanum* aff. *nigrum*, *Toddalia latisiliquata*, *T. rhenana*, *Visnea germanica*).

Table 2

Taxonomic list and abundance of fruits and/or seeds in two latest Messinian(?) sites of northern Italy

Taxa	SP	CA
<i>Ampelopsis ludwigii</i>	6	3
Apiaceae	2	
Asteraceae	1	
cf. Capparaceae	3	
<i>Carpinus</i> cf. <i>miocenica</i>	4	1
<i>Carpolithes gratioloides</i>	1	
Chenopodiaceae		1
<i>Coriaria</i> cf. <i>collinsoniae</i>	1	
<i>Crataegus</i> sp.	1	
cf. Cucurbitaceae	3	1
<i>Cupressus</i> cf. <i>sempervirens</i>	18	
<i>Cyclea palatinati-bavariae</i>		2
<i>Daphne</i> sp.	1	
<i>Euphorbia</i> spp.	9	
<i>Fagaropsis</i> sp.		1
<i>Ficus potentilloides</i>	3	
<i>Hypericum</i> cf. <i>humifusum</i>	1	
<i>Hypericum</i> sp. 1	2	
<i>Hypericum</i> sp. 2	1	
<i>Ilex</i> cf. <i>saxonica</i>	4	
Lamiaceae (calyx)	3	
<i>Litsea sonntagii</i>		2
<i>Magnolia allasoniae</i>	9	f
<i>Magnolia</i> sp.	1	
<i>Mahonia staphyleaeformis</i>	1	
<i>Mallotus maii</i>	1	
<i>Medicago</i> sp.	2	
cf. <i>Myrtus</i>		1
<i>Najas</i> cf. <i>flexilis</i>		15
Oleaceae	1	1
cf. <i>Palaeocarya macroptera</i>	3	
<i>Pinus</i>	2	1
<i>Pinus</i> cf. <i>strozzii</i>	1	
Poaceae	1	
<i>Potamogeton</i> sp.		15
<i>Quercus</i> sect. <i>Cerris</i>	2	
<i>Ranunculus</i> cf. <i>reidii</i>	1	
<i>Rubus</i> cf. <i>laticostatus</i>	4	
<i>Sambucus pulchella</i>	1	1
<i>Sapindoidea margaritifera</i>	8	5
<i>Selaginella</i> e gr. <i>pliocenica</i>	1	
<i>Solanum</i> aff. <i>nigrum</i>	6	6
<i>Solanum</i> cf. <i>dulcamara</i>		1
cf. <i>Styrax</i>	6	
<i>Swida discimontana</i>	11	1
<i>Tetraclinis salicornioides</i>		f
<i>Teucrium</i> sp.		1
<i>Thymelea</i> sp.	3	
<i>Toddalia latisiliquata</i>	6	6
<i>Toddalia rhenana</i>	4	2
<i>Visnea germanica</i>	25	10
<i>Vitis teutonica</i>	7	
<i>Zanthoxylum</i> cf. <i>ailanthiforme</i>	1	1

SP=Scipione Ponte; CA=Corneliano d'Alba.

The reconstruction of the forest cover and humidity conditions is not easy on the basis of the available data sets. Some of the woody plant genera (*Cyclea*, *Litsea*, *Magnolia*) occur today only in humid forests, however, it is not too hazardous to imagine that in latest Messinian (?) palaeoenvironments they could find a suitable ecological niche in some sort of gallery forests along rivers. On well-drained soils, a sub-humid, more open forest probably was developed. In fact the humidity-requiring *Fagus*, so common in early-“mid” Messinian and Pliocene assemblages, has not been recorded from the Lago-Mare deposits. Additional clues for this reconstruction are the abundance of *Cupressus* and the occurrence of *Medicago* and *Vitex* (leaves at Corneliano d'Alba). Also the abundance of the legume *Podocarpium podocarpum* at Corneliano d'Alba may be due to peculiar environmental conditions, since this species never occurs in the many Pliocene floras of the same region.

The lower part of the Zanclean in the studied area is characterized by a sudden ingression and deposition of deep-marine sediments, which are poor in plant remains. For this reason the documentation of plant megafossils from 5.3 to 4.0 Ma is still lacking. A few poor leaf assemblages, assigned to the Early or Middle Pliocene, occur in Lombardy (Sordelli, 1896) and southern Switzerland (Canton Ticino–Brambilla, 1992b). One of these assemblages (Castel di Sotto) most probably is of a latest Early Pliocene age; it is characterised by a dominance of “non-toothed ?evergreen dicots” and certainly indicates a warm climate, even “subtropical” according to Brambilla (1992b).

A rich fruit and seed assemblage is known from a layer of the deep-marine section of Pocapaglia in Piedmont (updated list of taxa in Table 3), dated to the Early Pliocene (nannoplankton biozone NN14–NN15: 4.1–3.9 Ma). Other minor carpoflora-bearing localities in Piedmont, such as Breolungi, Crava di Morozzo (Cavallo and Martinetto, 1996) and Sento I (Basilici et al., 1997), also dated to the late Early Pliocene, yielded floras very similar to that of Pocapaglia. Actually, the richest assemblages of this type were provided by a few sites in Piedmont, which are not precisely dated (Basilici et al., 1997; Bertoldi and Martinetto, 1995; Martinetto, 1999), although their age must fall within the late Early Pliocene–early Middle Pliocene time interval (ca. 4.0–3.0 Ma). Further to the east, a poor Early Pliocene carpological assemblage has been preliminarily described by Gregor (1990) from Lugagnano (foraminifer biozones MPL 2–MPL3, 5.2–3.8 Ma: Iaccarino, personal communication).

Table 3

Updated taxonomic list of fruits and/or seeds gathered in an Early Pliocene marine layer at Pocapaglia, northern Italy

<i>Acer</i> spp.	<i>Cinnamomum costatum</i>	<i>Liriodendron geminata</i>	<i>Prunus</i> sp.	<i>Sinomenium cantalense</i>	<i>Ternstroemia reniformis</i>
<i>Actinidia</i> cf. <i>faveolata</i>	<i>Cladium</i> sp.	<i>Litsea sonntagii</i>	<i>Pterocarya limburgensis</i>	cf. <i>Solanum</i>	<i>Tetraclinis salicornioides</i>
<i>Alnus</i> sp.	<i>Coriaria</i> sp.	<i>Magnolia allasoniae</i>	cf. <i>Pyracantha</i>	<i>Sorbus herzogenrathensis</i>	<i>Thuja saviana</i>
<i>Ampelopsis ludwigii</i>	<i>Corylus avellana</i>	<i>Mahonia staphyleaeformis</i>	<i>Quercus</i> subgen. <i>Cerris</i>	<i>Sparganium nanum</i>	<i>Toddalia latisiliquata</i>
<i>Aralia</i> sp.	<i>Cryptomeria rhenana</i>	<i>Mallotus maii</i>	<i>Quercus</i> sp.	<i>Spiraea</i> sp.	<i>Toddalia rhenana</i>
Asclepiadaceae indet.	<i>Cymodocea</i> sp.	cf. <i>Meliosma miessleri</i>	<i>Ranunculus</i> cf. <i>reidii</i>	<i>Spirella</i> sp.	<i>Trigonobala-nopsis exacantha</i>
Asteraceae indet.	<i>Ehretia</i> sp.	<i>Morus germanica</i>	<i>Rehderodendron ehrenbergii</i>	<i>Staphylea bessarabica</i>	cf. <i>Viola</i>
cf. <i>Calluna</i>	<i>Eurya stigmosa</i>	<i>Myrica</i> sp.	<i>Rubus microspermus</i>	cf. <i>Styphelia</i>	<i>Visnea germanica</i>
<i>Carex</i> cf. <i>flagellata</i>	<i>Fagus</i> sp.	<i>Ocotea</i> sp.	<i>Sabia europaea</i>	cf. <i>Stratiotes</i>	<i>Vitis</i> sp.
<i>Carex</i> sp.	<i>Ficus potentilloides</i>	<i>Oxalis europaea</i>	<i>Sambucus pulchella</i>	<i>Styrax</i> cf. <i>maximus</i>	<i>Vitis teutonica</i>
<i>Carpinus betulus</i>	<i>Glyptostrobus europaeus</i>	<i>Paulownia cantalensis</i>	<i>Sapindoidea margaritifera</i>	<i>Symplocos gothanii</i>	<i>Zanthoxylum ailanthiforme</i>
<i>Carpinus</i> cf. <i>europaea</i>	<i>Ilex</i> cf. <i>cantalensis</i>	<i>Phellodendron</i> cf. <i>elegans</i>	<i>Sassafras ludwigii</i>	<i>Symplocos gothanii</i>	
<i>Cephalanthus pusillus</i>	<i>Ilex fortunensis</i>	<i>Phytolacca salsoloides</i>	cf. <i>Sassafras</i>	<i>Symplocos lignitarum</i>	
<i>Cephalotaxus rhenana</i>	<i>Ilex</i> sp.	Poaceae indet.	<i>Selaginella moravica</i>	<i>Symplocos minutula</i>	
<i>Chamaecyparis</i> sp.	<i>Liquidambar magniloculata</i>	<i>Potamogeton</i> sp.	<i>Sequoia abietina</i>	<i>Symplocos schereri</i>	

The floras of Pocapaglia and related sites are partly made up by genera still living in Europe, as well as by genera presently absent in the native flora in this continent. The present distribution of the latter is mostly restricted to East Asia and/or North America. Genera with an Asian-American disjunction, occurring in Pocapaglia and, partly, in the remaining sites are: *Chamaecyparis*, *Thuja*, *Ampelopsis*, *Aralia*, *Cephalanthus*, *Liquidambar*, *Liriodendron*, *Magnolia*, *Mahonia*, *Meliosma*, *Sassafras* and *Symplocos*. Additionally, *Sequoia* is presently confined to North America. The exclusively East Asian component is represented by many genera, such as *Cephalotaxus*, *Cryptomeria*, *Glyptostrobus*, *Actinidia*, *Cinnamomum*, *Eurya* s. s., *Hartia*, *Mallotus*, *Paulownia*, *Phellodendron*, *Pterocarya*, *Rehderodendron*, *Sabia*, *Sinomenium* and *Toddalia*. This observation suggests that modern plant communities of East Asia, and particularly of China, can act as a model for the reconstruction of the Pliocene zonal vegetation and climate in the Po Basin.

The occurrence of *Cinnamomum*, *Eurya*, *Fagus*, *Hartia*, *Magnolia* and *Ternstroemia* makes it possible to trace a parallelism between the zonal palaeovegetation of the late Early Pliocene of northern Italy and some living plant communities of the “Evergreen Broad-

Leaved Forest” of China (Wang, 1961; Hou, 1983). In analogy with the Chinese model (Wang, 1961; Hou, 1983; Ying, 1983), we can reconstruct a high-diversity closed forest community with a simultaneous cover of evergreen (*Cinnamomum*, *Distylium*, *Eurya*, *Ficus*, *Hartia*, *Magnolia* p. p., *Meliosma* subgen. *Meliosma*, *Symplocos*, *Ternstroemia*, *Trigonobalanopsis*, *Visnea*) and deciduous (*Ehretia*, *Liquidambar*, *Liriodendron*, *Magnolia* p. p., *Mallotus*, *Nyssa*, *Engelhardia* (*Palaeocarya*), *Paulownia*, *Quercus*, *Rehderodendron*) trees and shrubs. Conifers also played a role in the forest cover, especially *Cathaya*, *Chamaecyparis*, *Cryptomeria*, *Pinus*, and *Tetraclinis*.

Thus, during the Early Pliocene climatic optimum the regional vegetation in northwestern Italy was represented by mixed warm-temperate forests similar to the modern *Laurisilvae* of central China. Nevertheless, the abundance of “mid”-temperate genera (*Carpinus*, *Liquidambar*, *Pterocarya*, *Vitis*) restricts maximum analogy to the northern (cooler) part of this “subtropical vegetation zone” (Hou, 1983). This recent Asian analogue also allows us to better define the climatic conditions of the Early Pliocene. In fact comparable plant communities are developed under a warm-temperate humid climate with MAT 15–17°C, and MAP above 1000mm/year (Wang, 1961; Hou, 1983;

Satoo, 1983). Occasional winter frost can occur under such conditions.

### 2.3. Southern France and NW Spain<sup>4</sup>

Plant assemblages studied in southern France and NW Spain occur at localities variously dated and in various stages of exploration. The sites of Cerdanya, Murat in the French Massif Central and Murviel-lès-Béziers in Languedoc are of Late Miocene age, while those of Cessenon, Papiol in Catalonia and Pichegu are of Early Pliocene age.

The rich plant assemblage of Cerdanya has been studied for a long time since Rérolle in 1884.

It includes, according to Rérolle (1884–85), Menendez Amor (1955), Sanz de Siria (1985), Arroyo Garcian (1995) and Barron (1996), the following plant taxa: *Osmunda parrishii*, *Lygodium gaudini*, *Pteridium oeningense*, *Equisetum* sp., *Abies saportana*, *Pinus palaeostrobos*, *Cathaya vanderburghii*, *Taxodium distichum*, *Glyptostrobus europaeus*, *Juniperus drupacea*, *Ostrya oeningensis*, *Betula insignis*, *Alnus kefersteinii*, *A. occidentalis*, *A. prisca*, *Carpinus grandis*, *C. neireichii*, *Corylus* sp., *F. gussonii*, *F. pristina*, *Castanea ungeri*, *C. palaeopumila*, *Quercus denticulata*, *Q. drymeja*, *Q. elaena*, *Quercus hispanica*, *Q. mediterranea*, *Myrica lignitum*, *M. marginalis*, *Juglans acuminata*, *J. vetusta*, *Carya bilinica*, *Pterocarya denticulata*, *Populus tremulaefolia*, *Salix lavateri*, *S. sp.*, *Ulmus braunii*, *Zelkova zelkovaefolia*, *Bytneriophyllum tiliae-folium*, *F. lanceolata*, *F. pulcherrima*, *Ficus* sp., *Embotrium microspermum*, *Conospermum macrophyllum*, *Buxus pliocenica*, *Acer integerrimum*, *A. pyrenaicum*, *A. subcampestre*, *A. sp.*, *Platanus* sp., *P. pristina*, *Daphnogene eugeniae*, *Cinnamomum polymorphum*, *Persea princeps*, *S. ferretianum*, *Mahonia malheurensis*, *Berberis rhopaloides*, *Callicoma microphylla*, *Pirus phytali*, *Cotoneaster* sp., *Crataegus nicotiana*, *Caesalpinia* sp., *Cassia lignitum*, *C. sp.*, *Gleditsia allemanica*, *G. wesseli*, *Robinia regeli*, *Colutea macrophylla*, *Podocarpium* sp., *Leguminosites* sp.1, *L. sp.2*, *Calpurnia europaea*, *Terminalia miocenica*, *Punica granatum*, *Melastomites radobojanus*, *Trapa ceretana*, *Tilia vidali*, *T. expansa*, *Fraxinus numana*, Monocotyledons—*Potamogeton orbiculare*, *Smilax hastata*, *Juncus* sp., *Phragmites* sp., *Cyperites* sp., Poaceae, *Typha latissima*.

According to Martin-Closas (1995), several communities can be distinguished. Hydrophytic and swamp

communities are well documented by *Ceratophyllum*, *Potamogeton*, *Trapa*, *Juncus*, *Phragmites*, *Typha*, *Taxodium* and others. Mesophilic taxa are represented on the margins of the palaeolake and the lower part of mountain slopes, as *Alnus*, *Betula*, deciduous *Quercus*, *Fagus*, *Zelkova*, *Carya*, *Acer*, *Tilia* and probably *Cathaya*.

The laurel forest is poorly developed with *Cinnamomum*, *Daphnogene*, *Sassafras* and *Persea*. This assemblage, where the megathermal taxa are absent, still indicates a more thermophilic type of vegetation than the extant one or a lower elevation of this basin than today. The microflora (Bessedik, 1985) is also in agreement and includes numerous conifers (*Pinus*, *Abies*, Taxodiaceae, *Cathaya* and others), deciduous broad-leaved trees (*Quercus*, *Fagus*, *Alnus*, *Ulmus* and *Zelkova* and others), some mediterranean taxa (*Quercus ilex-coccifera*, *Olea* and others) and only a few thermophilic elements (e.g. Sapotaceae).

The plant assemblage of Murat in the French Massif Central is preserved in lacustrine diatomite deposits, which are dated by the Potassium/Argon (K/Ar) method to  $5.34 \pm 0.3$  Ma. It includes the following elements (Roiron, 1991, corrected): *G. europaeus*, *Sequoia abietina*, *Abies ramesi*, *Pinus* sp., *Picea* sp., *A. ducalis*, *A. cecropiifolia*, *Alnus viridis*, *Alnus* sp. (cf. *A. kefersteinii*), *Betula* sp., *Carpinus suborientalis*, *Carpinus betulus*, *C. orientalis*, *Q. hispanica*, *Q. sp.* (cf. *Q. macranthera*), *Q. kubinyi*, *Z. zelkovifolia* (aff. *Z. crenata* and *Z. acuminata*), *Ulmus campestris*, *U. sp.* (cf. *U. fulva*), *Celtis australis*, *Populus tremula*, *Carya minor*, *Juglans regia*, *Phellodendron* sp. (cf. *P. amurense*), *Cedrela* sp., *A. integerrimum*, *A. sanctae-crucis*, *A. campestre*, *A. opulifolium*, *A. platanoides*, *A. tricuspidatum*, *H. helix*, *Ilex* sp. (aff. *Ilex cornuta*), *Tilia tomentosa*, *Dombeyopsis lobata*, *Berberis* sp. (cf. *B. regeliana*), *Ceratophyllum demersum*, *Crataegus* sp. (cf. *C. douglasii*), *Prunus acuminata*, *Rosa* sp. (cf. *R. californica*), cf. *Photinia*, *Bambusa* sp.

The thermophilic elements, such as Taxodiaceae, are scarce while mesophilic taxa are abundant as *Alnus*, *Carpinus*, *Acer*, *Zelkova*, deciduous *Quercus*, *Carya* etc. Temperate elements, such as *Abies*, *Picea* or *Betula*, are frequent while Lauraceae and Hamamelidaceae are lacking. This vegetation can be compared with mesophilic forests covering the mountains of northeastern China. It may indicate a climatic cooling at the end of the Miocene in this region correlated with an Antarctic glaciation, but the overall cooler aspect of this assemblage may be due to higher palaeoelevation of the site (Fauquette, personal communication).

<sup>4</sup> By P. Roiron.

The plant assemblage of Murviel-lès-Béziers in the Orb Messinian valley is connected with marine Pliocene sediments. The profile of the Messinian and Pliocene formations shows that the fossiliferous travertine can be attributed to the final Messinian because it is situated at the top of the Miocene deposits between two linear incision phases showing the eustatic Messinian crisis. The list of elements (Roiron and Ambert, 1990, corrected) includes: cf. *Magnolia*, *P. leucophylla*, *Liquidambar europaea*, *Populus balsamoides*, *P. tremula*, *A. integerrimum*, *Cedrela* sp., *Zanthoxylum* sp., *Arundo* vel *Bambusa*.

This travertine contains impressions of leaves and fruits of mostly riparian plants such as *Populus*, *Platanus*, *Liquidambar*, but also of thermophilic taxa, e.g. *Zanthoxylum* and *Cedrela*. Leaves of *A. integerrimum* dominate the assemblage. Cool temperate and Mediterranean elements are lacking at Murviel. The overall aspects of the assemblage suggest warm and humid conditions near the site. This may apply perhaps to all lowlands of the northwestern Mediterranean basin. In fact, the erosional processes that produced the Messinian valley needed significant rainfall on the nearest mountains during the Messinian salinity crisis.

The plant assemblage of Cessenon is situated near Murviel. The Orb Messinian valley is filled there by the marine transgression at the beginning of the Pliocene. Above the Messinian breccias, the section is constituted by marine clays and coastal sands covered by continental sands and conglomerates. The marine and coastal sediments are rich in plant remains (leaves, fruits, seeds, wood and pollen). The so far recognised elements (Roiron, 1991, corrected) include: *Abies* sp., *Pinus* sp., *G. europaeus*, cf. *Sequoia*, *Cupressus* cf. *sempervirens*, *Laurus primigenia*, *P. leucophylla*, *Quercus coccifera*, *Quercus ilex*, *Q. hispanica* (aff. *sessiliflora*), *Q. kubinyii*, *A. ducalis*, *P. tremula*, *Salix* sp., *Prunus* sp., *Cedrela* sp., *Nerium oleander*, *Fraxinus* cf. *oxycarpa*.

The leaf assemblage contains only a few subtropical taxa, such as *Glyptostrobus* or *Cedrela*, some riparian elements, such as *Populus*, *Salix* and *Platanus*, and plants with mediterranean nearest relatives, such as *Cupressus*, *Laurus nobilis*, *Q. ilex*, *Q. coccifera*, *Nerium*, etc. The Californian vegetation is still a more similar extant model where subtropical humid taxa live mixed with more xerophilic plants.

The microflora of Cessenon is more diversified and includes conifers, such as *Cathaya* and *Cedrus*, mesophilic deciduous broad-leaved taxa, such as *Liquidambar*, *Parrotia*, *Carya*, and mediterranean

elements, such as *Pistacia*, *Olea* and *Phillyrea* (Suc, 1980). Hence at the beginning of the Pliocene, the climatic conditions in Languedoc show a decrease in summer rainfall.

The rich plant assemblage of Papiol in the Vallès-Penedès basin in Catalonia (NW Spain) is dated to the beginning of the Pliocene. It was studied first by Almera (1907) and later by Sanz de Siria (1985). It contains many mesophilic or Canarian (humid) elements but also a large group of taxa with mediterranean affinities, such as *N. oleander*, *Buxus sempervirens* and also *Chamaerops*, *Q. ilex*, *L. nobilis* and *Viburnum tinus*. The pollen spectrum of Papiol is also rich in mediterranean taxa (Suc and Cravatte, 1982). The climate at the beginning of the Pliocene in Catalonia became warm-temperate with dry summers like in Languedoc.

The Papiol plant assemblage (Sanz de Siria, 1985, corrected) includes: *Asplenium* sp., *P. aff. palaeostrobus*, *P. sp.*, *S. abietina*, *A. integrilobum*, *A. nicolai*, *A. tricuspdatum*, *A. sp.*, *Alnus stenophylla*, *A. sp.*, *Benzoin antiquum*, “*Bumelia*” *bohemica*, *B. sempervirens*, *C. minor*, *Cassiophyllum berenices*, *Cassia* sp., *Castanea atavia*, *Celastrus gardonensis*, *C. australis*, *C. polymorphum*, *Colutea crusafontii*, *Daphnogene ungeri*, *Diospyros anceps*, *D. protolotus*, *Fagus pliocenica*, *Fraxinus ornus*, *Ilex canariensis*, *I. golpei*, *J. acuminata*, *J. vetusta*, *Laurus canariensis*, *L. nobilis*, *L. europaea*, *L. procaccinii*, *Magnolia grandiflora*, *Myrica* sp., *Notelaea* (?) *excelsa*, *Ocotea heeri*, *Persea braunii*, *P. indica* var. *pliocenica*, *Phillyrea latifolia*, *P. leucophylla*, *Populus alba*, *P. mutabilis*, *Q. coccifera*, *Q. charpentieri*, *Q. drymeja*, “*Q.*” *gmelini*, *Q. ilex*, “*Q.*” *meriani*, *Q. pseudosuber*, *Rhamnus* sp., *Salix angusta*, *S. varians*, *S. sp.*, *Sapindus dubius*, *S. falcifolius*, *S. ferretianum*, *U. braunii*, *V. tinus*, *C. humilis*, *Phragmites* cf. *oeningensis*, *Poacites* sp., *T. latissima*.

The Early Pliocene plant assemblage of Pichegu (Gard, France) is preserved at the opening of the Rhône river in yellow coastal sand above marine clays. It includes (Roiron, 1991, corrected): *Ginkgo adiantoides*, *Abies* cf. *spectabilis*, *Tsuga* cf. *caroliniana*, *Thuja* vel *Chamaecyparis*, *C. polymorphum*, *D. ungeri*, *L. nobilis*, *L. primigenia*, *O. heeri*, cf. *Persea gratissima*, *P. leucophylla*, *L. europaea*, *Ulmus pyramidalis*, *Z. zelkovifolia* (aff. *Z. crenata* and aff. *Z. acuminata*), *C. minor*, *P. denticulata*, *F. gussonii*, *F. pliocenica*, *Quercus faginea*, *Q. hispanica* (aff. *Q. sessiliflora*), *Q. ilex*, *Q. kubinyii*, *Q. cf. castaneifolia*, *A. ducalis*, *C. betulus*, *C. orientalis*, *C. suborientalis*, *C. cf. tschonoskii*, *P. alba*, *P. balsamoides*, *P. nigra*, *P. tremula*, *Salix* sp., *C. gardonensis*, *A. tricuspdatum*, *A. sp.*, *Bambusa* sp.

The assemblage is rich in mesophilic taxa and riparian elements. Some xerophilic taxa, such as *C. orientalis*, *Q. ilex* and *L. nobilis*, are present. In addition, the assemblage contains mega-mesothermic taxa, such as subtropical Lauraceae and *Celastrus*. There are no taxodioids in the macrofossil record but the pollen diagram shows a decrease in Cupressaceae (including Taxodiaceae) from the base to the upper part of the section (Suc, 1980). The disappearance of taxodioids in Languedoc at that period is certainly caused by the Mediterranean-type climate with dry summers.

#### 2.4. Discussion

The eastern Mediterranean shows in the Pontian/Messinian two kinds of zonal forests, probably mixed or merging due to relief and exposition—humid gallery forests with dominating broad-leaved deciduous arboreal elements and some evergreen shrubs and lianas, and subxeric woodland with pines and sclerophyllous oaks. Humid subtropical elements are few (Lauraceae, *Craigia*), almost absent. The Early Pliocene vegetation is not much different, as far as it is documented (Bulgaria), with a lowering proportion of elements characteristic of subtropical climate and an open landscape.

In Italy the proportion of sclerophyllous oaks in the Early Messinian seems to increase towards southerly sites (Gabbro I), suggesting a warm-temperate humid to subhumid climate there. In the mid-Messinian, the vegetation grew under warm-temperate humid conditions, while the latest Messinian (?) Lago-Mare assemblage again includes elements of probably subhumid conditions (*Cupressus*, legumes including *Podocarpium*), and lacks *Fagus*. The Early Pliocene vegetation returned to humid subtropical evergreen forests with East Asian affinities.

The plant assemblages from southern France and Spain testify to a progressive decrease of more thermophilic plant elements during the studied time interval. In the northwestern part of the Mediterranean basin, the Messinian phase seems to be not so xeric as in the southern part.

Except for the plants with Mediterranean affinities, the Chinese humid subtropical forest is a good model for this Neogene vegetation of southern Europe. Most of the Mio-Pliocene taxa are present in the evergreen broad-leaved forest with *Pinus*, *Cathaya* and Ericaceae on the rocky slopes and evergreen and deciduous taxa, such as *Castanopsis*, *Quercus*, *Cunninghamia*, and Lauraceae elsewhere.

### 3. Vegetation reconstruction synthesis—the spotty record portrayed on geographic maps<sup>5</sup>

#### 3.1. Methodology

In this synthesis the regional record is placed into a broad European context. The plant record of fissile, i.e. splittable sediments (leaves and associated fruit macrofossils) is evaluated for main physiognomic features of forests as expressed in percentages of broad-leaved deciduous (BLD), broad-leaved evergreen (BLE), legume-type (LEG), and sclerophyllous (SCL) taxa (components). These four physiognomical kinds of foliage are indicative of prevailing factors of climate on the respective fossil site: broad-leaved deciduous and broad-leaved evergreen for humid, warm temperate to subtropic conditions and legume-type (i.e. microphyllous–nanophyllous size categories) and sclerophyllous taxa for sub-humid conditions.

Principally, the fossil plant record of every locality is grouped into a physiognomic/taxonomic scheme where azonal taxa are grouped separately (as their possible over-representation might distort the character of the zonal vegetation). Colour-interpolated maps are produced using the inverse distance-weighting algorithm in the GIS package MapInfo. This method has been described in detail in Kovar-Eder and Kvaček (2003). There, these results were compared to those which have been obtained in parallel by grouping the same floras independently to a sociological scheme (humid temperate, humid subtropical, sub-humid subtropical, azonal). As the BLD-component is characteristic of humid temperate, the BLE-component of humid subtropical, and the LEG- and SCL-components of sub-humid subtropical vegetation, we checked whether the results obtained from both grouping schemes are consistent. It was possible to demonstrate the close coherence of the results based on these two different groupings.

In the maps presented here, the percentages of the BLD, BLE, LEG, and SCL components are calculated from the zonal woody component (woody angiosperms including palms and conifers) while previously the calculations were restricted to the zonal woody dicotyledons only (Kovar-Eder and Kvaček, 2003). However, the resulting impact of this modification on the maps is not significant because palms are extremely rare and the diversity of conifers is rather low. Nevertheless, the inclusion of conifers and palms better

<sup>5</sup> By J. Kovar-Eder.

meets the intention to evaluate the plant record as completely as possible.

This attempt is restricted to well-(independently) dated floras of the younger Late Miocene only, because the Early Pliocene data set is not yet rich enough to meet the necessary requirements (Table 4).

### 3.2. Results

The presented maps (Fig. 1) show the following percentages of the BLD, BLE, SCL and LEG components of the zonal woody taxa (angiosperms, conifers) (Table 5).

#### 3.2.1. The BLD component

Its percentages range between 20% (Makrilia) and 100% (Berezinka and Odesti). With a few exceptions (Murviel-les-Beziers, Gabbro, Borsec, Vegora), it is dominant ( $\geq 50\%$ ) in eastern and southern regions of

Central Europe and the region of the Massif Central. A north–south gradient can be traced clearly in Central Europe only.

#### 3.2.2. The BLE component

It varies usually around 10–20% and a generally low north–south gradient can be discerned. In Murviel-les-Beziers the value of the BLE component is exceptionally high.

#### 3.2.3. The LEG component

It ranges from 0 to 20% and is generally very low on the Balkan Peninsula. In the region of the Massif Central in France its values are slightly higher. The highest percentage is in the assemblage from Makrilia.

#### 3.2.4. The SCL component

The values vary usually between 0 and 19%, except for Makrilia (30%). Low values are characteristic of

Table 4  
List of sites evaluated in the maps of Fig. 1

Locality no.	Name	Basin/Region	Epoch	Regional stage	Reference
32	Ilnica	Tshop Mukatchevo basin	Miocene, late	Pannonian, Pontian?	
33	Velikij Rakovec	Tshop-Mukatchevo basin	Miocene	Pannonian, Pontian	
34	Berezinka	Tshop-Mukatchevo basin	Miocene	Pannonian, Pontian?	
49	Osojna kod Kladovo	Paratethys, Pannonian basin	Miocene	Pontian, late	
50	Crevni Breg	Pannonian basin	Miocene	Pontian, late	
69	Gabbro near Livorno	Toscana	Miocene	Messinian	
73	Baita	Baia Mare basin	Miocene	Pontian	
74	Sinersig	Lugoj basin	Miocene	Pontian, early	
80	Odesti	Baia Mare basin	Miocene	Pontian, early	
83	Turt, Valea Chitasului	Oas basin	Miocene	Pontian	
123	Borsec	Transylvanian/Borsec basin	Miocene, Pliocene	Pontian, late, Dacian	
263	Prosilion near Kozani	Prosilion-Trigonikon/ Kozani-Servia basin	Miocene, late		
281	Pincina	Lucenec basin	Miocene	Pontian	
690	Kolubara	Kolubara coal basin	Miocene	Pontian, late	Mihajovic and Lazarević (1999)
694	Vegora	Vegora basin	Miocene	Messinian	
700	Pitsunda		Miocene	Pontian	
701	Murat	Cantal, Massif Central	Miocene	Messinian	
709	Joursac	Cantal, Massif Central	Miocene, late		Marty (1903)
710	Mougudo	Cantal, Massif Central	Miocene	Tortonian, Messinian	Laurent and Marty (1927)
711	St. Vincent	Cantal, Massif Central	Miocene	Tortonian, Messinian	Laurent and Marty (1927)
712	Andance	Massif Ardeche	Miocene	Tortonian	Brice (1965)
742	Cheylade	Cantal, Massif Central	Miocene	Messinian	Gilbert et al. (1977)
743	Niac	Cantal, Massif Central	Miocene	Tortonian, Messinian	Gilbert et al. (1977)
756	Makrilia-Flora	Ierapetra basin	Miocene	Tortonian, late	
760	Male Shirak	Kurinsk basin	Miocene, Pliocene	Pontian, Kimmerian	Kolakovskii and Rationi (1967)
761	Likudi near Elassona	Thessalia	Miocene, late		
762	Murviel-les-Beziers	Ria Pliocene de l'Orb, Languedoc	Miocene	Messinian, late	
771	Las Clausades	Cantal, Massif Central	Miocene	Tortonian, Messinian	Marty (1905)

References given only as far as they are neither included in Kovar-Eder et al. (1994) nor in the text of this paper.

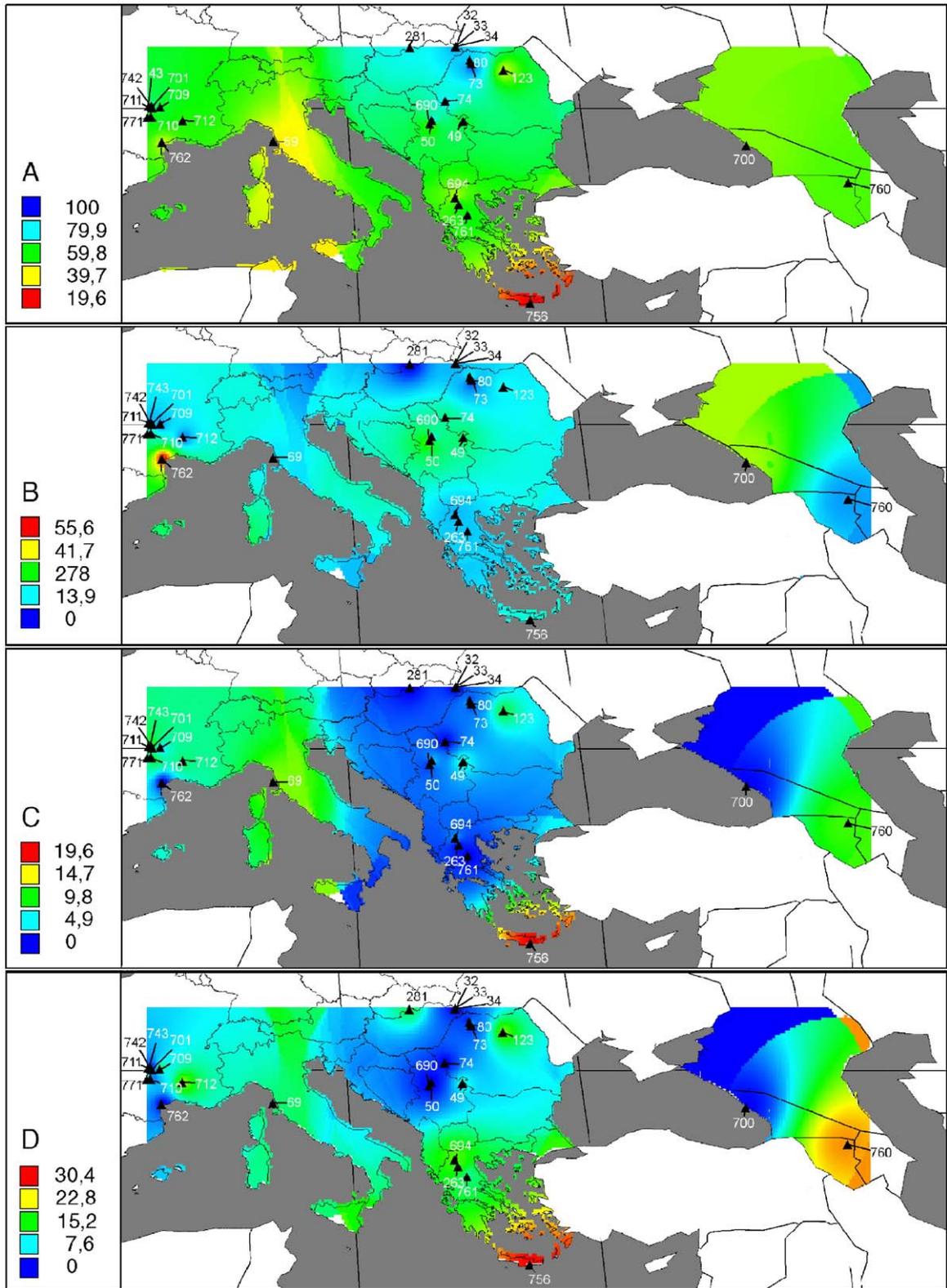


Fig. 1. Maps showing the percentages of the BLD component (A), the BLE component (B), the LEG component (C), and the SCL component (D) (locality numbers correspond with those in the Tables 4 and 5).

Table 5

The matrix spreadsheet of the evaluated floras (legend see Kovar-Eder and Kvaček, 2003)

Locality no.	Conifers	BLD	BLE	SCLE	LEG	Ferns	Mono	Aquatic	Palms	Excl.	Total excl. azonal	Total zonal+ azonal	Azonal woody	Percentage of BLD of BLD+ BLE+LEG+ SCL+conifers+ palms	Percentage of BLE of BLD+ BLE+LEG+ SCL+conifers+ palms	Percentage of LEG of BLD+ BLE+LEG+ SCL+conifers+ palms	Percentage of SCL of BLD+ BLE+LEG+ SCL+conifers+ palms
32	2.00	8.00	3.00	0.00	0.00	3.00	2.00	0.00	0.00	2.00	20.00	26.00	6	61.54	23.08	0.00	0.00
33	0.00	7.50	0.50	0.00	0.00	0.00	4.00	0.00	0.00	0.00	12.00	18.00	6	93.75	6.25	0.00	0.00
34	0.00	7.00	0.00	0.00	0.00	0.00	5.00	2.00	0.00	0.00	14.00	20.00	6	100.00	0.00	0.00	0.00
49	0.00	11.50	4.00	1.50	1.00	0.00	0.00	0.00	0.00	0.00	18.00	22.00	4	63.89	22.22	5.56	8.33
50	1.00	17.50	2.50	0.00	1.00	1.00	1.00	0.00	0.00	0.00	24.00	28.00	4	79.55	11.36	4.55	0.00
69	12.00	18.83	6.33	5.83	6.00	0.00	2.00	1.00	0.00	7.00	58.99	67.99	9	38.44	12.92	12.25	11.90
73	0.00	9.50	2.00	1.00	1.00	0.00	2.00	0.00	0.00	2.50	18.00	23.00	5	70.37	14.81	7.41	7.41
74	0.00	4.00	1.00	0.00	0.00	1.00	1.00	0.00	0.00	2.00	9.00	14.00	5	80.00	20.00	0.00	0.00
80	0.00	3.00	0.00	0.00	0.00	0.00	2.00	1.00	0.00	2.00	8.00	11.00	3	100.00	0.00	0.00	0.00
83	0.00	8.50	1.50	0.00	0.00	0.00	0.00	0.00	0.00	0.00	10.00	14.00	4	85.00	15.00	0.00	0.00
123	6.00	19.00	6.00	7.50	3.50	0.00	3.00	1.00	0.00	10.00	56.00	62.00	6	45.24	14.29	8.33	17.86
263	1.00	5.50	1.00	1.50	0.00	0.00	1.00	1.00	0.00	0.00	11.00	14.00	3	61.11	11.11	0.00	16.67
281	1.00	9.50	0.00	1.50	0.00	0.00	1.00	0.00	0.00	1.00	14.00	16.00	2	79.17	0.00	0.00	12.50
690	1.00	4.00	3.00	0.00	0.00	0.00	0.00	0.00	0.00	1.00	9.00	12.00	3	50.00	37.50	0.00	0.00
694	7.00	15.50	3.50	6.00	1.00	0.00	0.00	0.00	1.00	1.00	35.00	46.00	11	45.59	10.29	2.94	17.65
700	2.00	7.50	5.50	0.00	0.00	0.00	0.00	0.00	0.00	1.00	16.00	18.00	2	50.00	36.67	0.00	0.00
701	4.00	23.00	3.50	2.50	1.00	0.00	1.00	2.00	0.00	2.00	39.00	43.00	4	67.65	10.29	2.94	7.35
709	5.00	18.50	2.50	4.00	1.00	0.00	2.00	0.00	0.00	15.00	48.00	56.00	8	59.68	8.06	3.23	12.90
710	1.00	23.33	4.83	1.50	1.33	1.00	2.00	0.00	0.00	6.00	40.99	44.99	4	72.93	15.10	4.16	4.69
711	2.00	14.33	1.33	0.00	2.33	0.00	0.00	0.00	0.00	1.00	20.99	22.99	2	71.69	6.65	11.66	0.00
712	2.00	15.00	2.00	5.00	2.00	1.00	1.00	1.00	0.00	1.00	30.00	34.00	4	57.69	7.69	7.69	19.23
742	1.00	12.00	2.00	0.00	2.00	2.00	2.00	0.00	0.00	4.00	25.00	29.00	4	70.59	11.76	11.76	0.00
743	1.00	14.83	6.83	3.00	1.33	3.00	2.00	1.00	0.00	8.00	40.99	43.99	3	54.95	25.31	4.93	11.12
756	4.00	5.50	4.50	8.50	5.50	0.00	0.00	0.00	0.00	4.00	32.00	34.00	2	19.64	16.07	19.64	30.36
760	0.00	12.50	2.00	6.00	2.50	0.00	1.00	1.00	0.00	4.00	29.00	32.00	3	54.35	8.70	10.87	26.09
761	3.00	11.00	2.00	2.00	0.00	0.00	1.00	0.00	0.00	1.00	20.00	24.00	4	61.11	11.11	0.00	11.11
762	0.00	4.00	5.00	0.00	0.00	0.00	1.00	0.00	0.00	1.00	11.00	13.00	2	44.44	55.56	0.00	0.00
771	2.00	5.50	2.50	0.00	2.00	0.00	1.00	0.00	0.00	1.00	14.00	14.00	0	45.83	20.83	16.67	0.00

The different components are in absolute numbers of taxa.

assemblages from the Paratethys region especially and are worth mentioning for Pitsunda (Abchasia) at the eastern margin of the Black Sea. A slight north–south gradient can be diagnosed.

### 3.3. Discussion

The interpretation is biased by the widely spaced data net and the concentration of sites to sedimentation basins. Due to the stratigraphical high-resolution deficiency in the continental plant assemblages, we are unable to split the plant record into a finer succession. Moreover, the evaluation of some sites may be problematic due to poor preservation of the plant material there (Makrilia) or low species numbers as in Murviel-lès-Béziers where 4 sites, each with <10 species were summarised, yielding only 13 taxa in total.

The overall characteristic is the dominance of the BLD component over the region except for Crete. The north–south gradient of the BLD component (higher percentages in the north) is more distinct than that of the BLE component (low values in the north). The higher percentages of the BLE component in northern regions of the Balkan Peninsula and the eastern margin of the Black Sea indicate warm humid conditions. This interpretation is strongly supported by the pictures derived from the LEG and SCL components. Both maps show their absence or extremely low percentages in both regions. This reflects their special status favourable for a longer persistence of taxa surviving from the Middle Miocene, e.g. *T. salicornioides* (Cupressaceae) and *Trigonobalanopsis rhamnoides/exacantha*. From spotty floristic investigations, the eastern Black Sea and the (more southerly) Pannonian lake regions were already known as refuge areas during the Late Miocene/Pliocene (Givulescu, 1957; Shakryl, 1990; Palamarev and Ivanov, 1998; Stuchlik et al., 1999). Early Pontian palynological evidence from the southern Carpathian foredeep indicates, compared to the former Maeotian biota, a shift towards higher MAT and MAP values favourable for palaeotropical elements (Ivanov et al., 2002). A further aspect is the presence of mesic conifers not bound to wetlands: In the assemblages from Ukraine and the northern Balkan Peninsula this component is rarely represented while in the assemblages from the southern Balkan Peninsula and the Massif Central it occurs regularly, and thus influences the percentages of the components calculated.

The trends of the different components may also be interpreted in plant sociological terms: In regions with at least 70–75% of broad-leaved deciduous zonal woody taxa and a minor addition of temperate conifers, we

certainly deal with (mixed) deciduous, humid temperate forests. In this context it is noteworthy that palms are almost absent within the region except for Vegora and NW Spain (*Chamaerops*). However, five external molds of palm trunks are preserved in live position in an Upper Miocene travertine at Peyrolles (Durance valley, Provence) (Clauzon et al., 1990). An increase of broad-leaved evergreen taxa indicates humid warm-temperate to subtropical mixed deciduous-evergreen forests (northern Balkan Peninsula, eastern coast of the Black Sea). Presence and diversity of sclerophyllous taxa can be interpreted as indicative of increasingly sub-humid conditions.

### 4. Conclusions

The presented data sets show that vegetation dynamics between 7 and 4Ma proceeded slightly differently within the area studied most obviously due to changes in palaeogeography and global climate. The maps of the first part of this interval (i.e. the Messinian–Pontian) summarise reconstructed physiognomy of forests in the Late Miocene of the Mediterranean, as far as the dating of the sites of plant megafossils allowed. The fossil plant record investigated includes also the period of the Messinian salinity crisis. The overall intriguing question certainly to be addressed in the next collaborative research concerns its effects on the flora and vegetation: Tentatively, the data available to us do not indicate discernible effects of this crisis on the terrestrial vegetation. However, we are uncertain to what degree the still unsatisfactory stratigraphical resolution may bias possible effects and we cannot be certain about vegetation structure from wider surroundings where we lack a detailed (not synthetic) palynological framework including taxonomically valid descriptions of critical taxa. Additionally, we have to consider also the possibility that the plant record derives from humid intervals only. It will be premature to draw definite conclusions about the vegetation dynamics in the respective areas and to compare them before a more intimate combination of megafossil and palynological data and denser network of sites will be available to achieve more objective reconstruction of the plant cover.

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