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Paleobotanical evidences of the Tertiary history and origin of the Mediterranean sclerophyll dendroflora

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Abstract: The evolution of important woody plant groups, ancestral to the modern Mediterranean dendroflora, is surveyed. Altogether, the history and phytogeography of 86 fossil species or species-groups is considered. The major part of the Paleomediterranean woody plants appears in Miocene mixed mesophyllous and mesoxerophyllous, evergreen and deciduous forests. The initial formation of basic Mediterranean sclerophyllous woody vegetation types is referred to periods from the Late Sarmatian to the Late Pontian, in geographic areas between 37° and 45° N latitude.

The history of the flora and vegetation of the Mediterranean region as remnants of the ancient Mediterranean of Tethyan floristic subkingdom (TAKHTAJAN 1978) has been intensively studied. Some of the authors have built their hypotheses on the basis of floristic or phytogeographic considerations (STOJANOFF 1925 & 1930, RECHINGER 1950, CONTANDRIOPOULOS 1962, POPOV 1963, MEUSEL 1969a & b, FAVARGER 1971, GREUTER 1971, etc.), whereas other have also used regional paleofloristic or paleogeographic facts (WULF 1944, HORVAT 1959, CREUTZBURG 1963, ANDREANSZKY 1963b, PALAMAREV 1967, GREUTER 1970, 1975, PACHOMOV 1976, LOVRIČ 1979, etc.). AXELROD (1975) has pointed to some similarities between the development of the Madro-Tethyan sclerophyll vegetation of California and the Tertiary Tethyan-Mediterranean plant formations.

The present paper gives a detailed representation of the origin and history of the basic ligneous plant species which built the Ancient Tethyan and Paratethyan sclerophyllous communities. The latter develop into the present-day Mediterranean forest vegetation by the end of their Tertiary history. More than 80 megataphofloras have been analysed and compared on the basis of own and literature data. These are distributed in different areas in Europe, Southwestern Asia, Kazakhstan and Western Siberia. They belong to 33 regions (Fig. 1) and a stratigraphic range from the Middle Eocene to the Late Pliocene, i.e. from 45 to 2 million years ago.

The floristic and phytogeographic synthesis includes 86 species or species-groups, belonging to 52 genera and 32 families. These species are considered as ancestral to about 100 extant Mediterranean and also some Submediterranean species

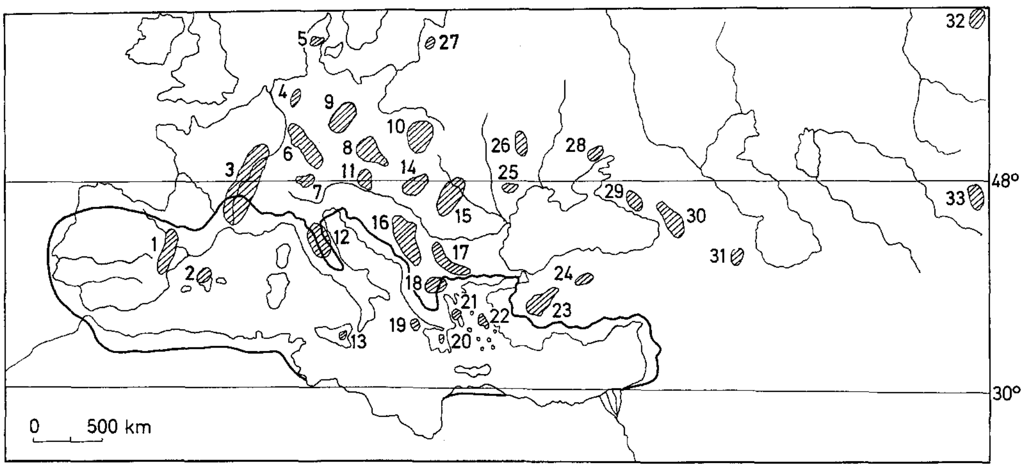

Fig. 1. Geographical location of the Tertiary macrofloras containing Paleomediterranean sclerophyll woody elements in Eurasia, (E Eocene, O Oligocene, M Miocene, P Pliocene), i.e. in Spain (1, O, M), the Balearic Islands (2, M), France (3, O, M, P), the Netherlands (4, P), Denmark (5, M), the Federal Republic of Germany (6, O, M, P), Switzerland (7, M), Czechoslovakia (8, O, M), the Democratic Republic of Germany (9, E, O, M, P), Poland (10, M, P), Austria (11, E, O, M), Italy (12 – 13, O, M), Hungary (14, O, M); Romania (15, O, M, P), Yugoslavia (16, O, M, P), Bulgaria (17, E, O, M, P); Greece (18 – 22, M, P), Turkey (23 – 24, O, M, P), and the Soviet Union (25 – 33, O, M, P). The bold line marks the recent Mediterranean floristic region

(Table 1). The eco-coenotic features of the paleofloras analysed elucidate the milieu in which the Paleomediterranean xerothermic elements studied appear and develop. Their "chronoareas" (after ZHILIN 1984) during the Tertiary (Table 1) are determined on the basis of their geographic distribution in Eurasia.

The paleofloristic data are presented in four groups according to the first appearance of the paleotaxa. As they are morphogenetically linked with their recent derivatives, but described as separate fossil species, they are here combined into species-groups.

Paleobotanical record

Group 1: species of an Eocene appearance. The data in Table 1 suggest an Eocene origin for nine species (10,4%), including members of the genera *Pinus, Tetraclinis, Periploca, Platanus, Rhamnus, Chamaerops* and *Smilax*. Very early, i.e. already in the Middle Eocene, the area of *Smilax websteri* (*S. excelsa:* the species presented here and afterwards in brackets correspond to recent derivatives) became apparent. Its expansion reached a maximum during the Miocene with an almost continuous European distribution reaching 56° N latitude. The remaining species of this group appear in the Late Eocene and change to some extent during the following periods of the Tertiary. As examples, one can point to *Pinus hepios* (*P. halepensis* s. str.), *P. thomasiana* (*P. pallasiana*) and *Tetraclinis brachyodon* (*T. articulata*) with vast areas of long duration. Throughout the Oligocene and Early Miocene they occupy large regions of W., C., S. and SE. Europe and SW. Asia. *Pinus thomasiana* reaches furthest north with its borderline in Europe and W. Siberia situated at 56 – 60° N

Table 1. Geochronological ranges and geographical distribution of Paleomediterranean woody plants in the Tethys and Paratethys region, together with their present equivalent taxa. *A* Austria, *Ba* Balearic Islands, *Bu* Bulgaria, *Cz* Czechoslovakia, *Dk* Denmark, *F* France, *Gd* German Democratic Republic, *Gf* German Federal Republic, *Gr* Greece, *H* Hungary, *I* Italy, *N* The Netherlands, *Pl* Poland, *Ro* Romania, *S* Spain, *Sua* Soviet Union (Armenia), *Suaz* Soviet Union (Azerbaijan), *Suf* Soviet Union (Russian Soc. Federal Sov. Republic), *Sug* Soviet Union (Georgia), *Suk* Soviet Union (Kazakhstan), *Sum* Soviet Union (Moldavia), *Suu* Soviet Union (The Ukraine), *Suw* Soviet Union (Western Siberia), *Sw* Switzerland, *T* Turkey, *Yu* Yugoslavia; E Eocene, O Oligocene, M Miocene, P Pliocene. The taxa are listed in alphabetical order.

Ancestral taxon	Tertiary					Present equivalent taxon
	E	O	M	P	Area	
Gnetopsida						
Ephedraceae						
Ephedra campylopoda CAM. foss.				+	Bu	*E. fragilis* DESF. subsp. *campylopoda* (CAM.) A. & G.
Pinopsida						
Cupressaceae						
Cupressus palaeosempervirens KOLAK. & SHAKR.		+	+	+	F-I-Pl-H-Gr-Bu	*C. sempervirens* L.
Juniperus bessarabica NEGRU			+		Sum	*J. macrocarpa* (SIEBTH. & SM.) BALL
J. drupacea-pliocenica RÉR.			+	+	S-F-Pl-Bu-Sug	*J. drupacea* LABILL.
J. excelsa L. foss.				+	Bu	*J. excelsa* L.
J. foetidissima WILLD. foss.			+	+	Bu	*J. foetidissima* WILLD., *J. thurifera* L.
J. oxycedrus L. foss.			+	+	Pl-Bu	*J. oxycedrus* L.
Tetraclinis brachyodon (BRONGN.) MAI & WALTHER	+	+	+		F-Gf-Gd-I-Yu-A-H-Pl-Cz-Ro-Bu	*T. articulata* (VAHL) MAST.
Pinaceae						
Abies ramesii SAP.		+	+		Ba-F	*A. numidica* CARR., *A. cilicica* (ANT. & KOTSCHY) CARR.
A. saportana RÉR.			+	+	S-Pl-Bu	*A. pinsapo* BOISS., *A. cephalonica* LOUD.
Cedrus vivariensis N. BOUL. (= *C. miocenica* LAUBY)			+	+	F-Pl-Bu	*C. libanii* RICH., *C. atlantica* (ENDL.) MAN.
Picea omoricoides WEB. (= *P. palaeoomorica* MÜLL.-STOLL)		+		+	Gf-Pl	*P. omorica* (PANČ.) PURK.
Pinus geanthracis (GOEPP.) REICH.			+	+	Gf-Gd-Pl-Bu-Sug-Suu	*P. peuce* GRISEB.
P. hepios UNG. sensu MAI & WALTHER (incl. *P. halepensis* MILL. foss.)	+	+	+	+	F-I-Gd-A-H-Yu-Ro-Bu-Gr-Suf	*P. halepensis* MILL. sensu stricto
P. laricioides MENZEL			+	+	S-F-Gf-Gd-A-Cz-Ro-Bu	*P. nigra* ARN. sensu lato

Table 1 (continued)

Ancestral taxon	Tertiary					Present equivalent taxon
	E	O	M	P	Area	
P. robustifolia SAP. sensu MAI & WALTHER 1985	+	+	+		S-I-F-Gf-Gd-Yu-GraBu-T	*P. pinaster* AIT.
P. salinarum PARTSCH.			+		Pl-Sum	*P. brutia* TEN.
P. thomasiana (GOEPP.) REICH.	+	+	+	+	Gf-Gd-Dk-Cz-A-Pl-Ro-Bu-Suu	*P. pallasiana* LAMB.
Magnoliopsida						
Aceraceae						
Acer campylopterix-group (*A. campylopterix* UNG., *A. opulifolium-pliocenicum* SAP., *A. obtusilobum* UNG.)			+	+	F-Gf-Yu	*A. opalus* MILL. sensu lato
A. crenatifolium ETT.			+	+	Gd-Cz-A-Pl	*A. hyrcanum* F. & M., *A. reginae-amaliae* BOISS.
A. angustilobum-group (*A. angustilobum* HEER, *A. haselbachensis* WALTHER, *A. berganum* MAI)		+	+		Gf-Gd-Sw-Cz-Bu-T	*A. heldreichii* ORPH.
A. pseudomonspessulanum-group (*A. pseudomonspessulanum* UNG., *A. loclense* HANTKE, *A. pseudocreticum* ETT., *A. hercynicum* MAI)		+	+	+	F-Gf-Gd-Sw-Cz-A-H-Pl-Ro-Bu-Gr-T	*A. monspessulanum* L., *A. orientale* L., *A. creticum* L.
Anacardiaceae						
Cotinus orbiculatus (HEER) BUDANTS. (= *Rhus palaeocotinus* SAP., *R. palaeoradicans* SAP.)		+	+	+	F-Gf-A-H-Pl-Bu-Sug-Suk-Sum-Suu	*C. coggygria* SCOP.
Pistacia acuminata-group (*P. acuminata* C. & E. M. REID, *P. lentiscoides* ANDR. & CZIFF.)			+	+	S-Gf-N-H-Ro-Pl-Yu-Gr-Sua	*P. lentiscus* L.
P. miocenica SAP.			+	+	Ba-F-Bu-Suu-Sum	*P. terebinthus* L., *P. palestina* L.
P. reddita (SAP.) SAP. & MAR.		+	+		F-H-Bu	*P. mutica* F. & M.
Rhus coriaria L. foss.			+		H	*R. coriaria* L.
Apocynaceae						
Nerium oleander-pliocenicum SAP. (= *N. oleander* L. foss.)			+	+	Ba-F-Ro-Bu	*N. oleander* L.
Aquifoliaceae						
Ilex balearica DESF. foss.				+	Ba-F	*I. balearica* DESF.
Asclepiadaceae						
Marsdenia takhtajanii STEPHYRTZA			+		Sum	*M. erecta* (L.) R. BR.
Betulaceae						
Alnus cycladum UNG.			+	+	Gr-Sug	*A. cordata* (LOISEL) DESF.

Table 1 (continued)

Ancestral taxon	Tertiary					Present equivalent taxon
	E	O	M	P	Area	
Carpinus neilreichii-group (*C. neilreichii* Kov., *C. bergeri* Giv., *C. polonica* Zabl., *C. europaea* Negru, *C. suborientalis* Sap.)		+	+	+	F-Gf-Gd-Cz-A-H-Pl-Ro-Bu-Gr-Sug-Sum-Suu	*C. orientalis* Mill.
Ostrya kryshtofovichii-group (*O. kryshtofovichii* Baik., *O. tenerrimum* Sap., *O. carpinifolia* Scop. foss.)		+	+	+	F-H-Pl-Bu-Gr-Suk-Sum-Suu	*O. carpinifolia* Scop.
Buxaceae						
Buxus pliocenica Sap. & Mar. sensu Palamarev & Kitanov 1988			+	+	S-F-Gf-Gd-A-Cz-Pl-Ro-Yu-Bu-Gr-T-Sug-Sum-Suu	*B. sempervirens* L. sensu lato
Caprifoliaceae						
Lonicera lipthyana Andr.			+		H	*L. arborea* Boiss.
Viburnum čukurovense Palam.			+		Bu	*V. orientalis* Pall.
V. pseudotinus Sap. & Mar. (= *V. tinus* L. foss.)		+	+		F-H-Ro	*V. tinus* L.
Coriariaceae						
Coriaria longaeva-group (*C. longaeva* Sap., *C. collinsonae* Gregor, *C. myrtifolia* L. foss.)		+	+	+	F-Gf-Ro-Bu	*C. myrtifolia* L.
Ericaceae						
Arbutus elegans Kolak.			+	+	Ro-Bu-Sug	*A. andrachne* L.
A. praeunedo Andr. (= *A. unedo* L. foss.)		+	+		H-Pl-Bu	*A. unedo* L.
Fabaceae sensu lato						
Anagyris foetida L. foss.			+		Pl-Bu	*A. foetida* L.
Ceratonia emarginata Heer		+	+	+	Gf-H-Bu-Sug-Suk	*C. siliqua* L.
Cercis cyclophylla Heer (= *C. virgilliana* Massal.)		+	+	+	F-I-Gf-H-Yu-Suk-Sum	*C. siliquastrum* L.
Colutea macrophylla Heer (= *C. parcefolia* Sap.)			+	+	S-F-Gf-Ro-Bu-Sug	*C. arborescens* L., *C. cilicica* Boiss. & Bal.
Fagaceae						
Castanea pliosativa Kolak. (= *C. sativa* Mill. foss., *C. atavia* Ung. p.p.)			+	+	F-I-Gf-Gd-Dk-Pl-Cz-H-Yu-Ro-Bu-Sug-Suu	*C. sativa* Mill.
Quercus cardanii Massal. sensu Palamarev & Kitanov 1988			+	+	F-I-Gd-N-H-Ro-Bu-Gr-Sug	*Q. canariensis* Willd., *Q. hartwissiana* Stev.
Q. equitrojanii Andr. (incl. *Q. trojana* Webb foss.)			+	+	H-Bu-T	*Q. trojana* Webb

Table 1 (continued)

Ancestral taxon	Tertiary					Present equivalent taxon
	E	O	M	P	Area	
Q. grandidentata UNG.			+	+	Gf-Cz-Pl-H-Ro-Yu-T	*Q. aegilops* L., *Q. brantii* LINDL.
Q. kubinyi-group (*Q. kubinyi* (ETT.) CZECZOTT, *Q. saperi* (MENZEL) HUMMEL)			+	+	F-A-H-Pl-Ro-Bu-Sug-Suu-Suw	*Q. libanii* OLIV.
Q. mediterranea UNG. sensu PALAMAREV & PETKOVA 1987		+	+	+	S-F-I-Gf-A-H-Ro-Yu-Bu-Gr-T-Sug	*Q. coccifera* L. sensu lato
Q. palaeocerris SAP. (= *Q. cerris-fossilis* KOLAK.)			+	+	F-Gd-H-Ro-Bu-Suf-Sug	*Q. cerris* L.
Q. praeilex SAP. (= *Q. praecursor* SAP., *Q. ilex* L. foss.)		+	+	+	S-F-H-Ro-Pl-Bu-Gr-T-Sug	*Q. ilex* L., *Q. baloot* GRIFF.
Q. pseudoalnus ETT.			+		A-H-Yu	*Q. alnifolia* POECH.
Q. pseudocastanea GOEPP. (= *Q. mioaxelrodii* KASAPLIGIL)		+	+	+	F-I-Gd-Pl-Cz-H-A-Ro-Bu-Gr-T-Sug-Suk-Suu	*Q. castaneifolia* CAM., *Q. afares* POMEL.
Q. pubescens L. foss.			+	+	Pl	*Q. pubescens* L.
Q. sosnowskyi-group (*Q. sosnowskyi* KOLAK., *Q. suber-pliocenica* N. BOUL. *Q. pseudosuber* SANTI foss., *Q. cerrisicarpa* KOLAK.)			+	+	F-Pl-Ro-Bu-T-Sug	*Q. suber* L.
Q. venturii MASSAL. (= *Q. boissieri* REUT. subsp. *pesmenii* KASAPLIGIL)			+		I-H-Ro-T	*Q. infectoria* OLIV., *Q. faginea* LAM.
Lauraceae						
Laurus nobilis L. foss.		+	+	+	F-H-Yu-Ro-Bu-Suk	*L. nobilis* L.
Moraceae						
Ficus europaea NEGRU			+		Pl-Sum	*F. carica* L.
Myrtaceae						
Myrtus rectinervis SAP. (= *M. bossniaca* ENGEL., *M. aquensis* SAP.)		+	+		F-Pl-Yu-Sug	*M. communis* L.
Oleaceae						
Fraxinus ornus L. foss.			+	+	F	*F. ornus* L.
F. praedicta HEER (= *F. grossidentata* LAURENT)			+	+	F-Gf-Pl-Ro-Suk	*F. angustifolia* VAHL sensu lato
Jasminum contiguum C. & E. M. REID				+	N	*J. fruticans* L.
Olea notii-group (*O. notii* UNG., *O. oleastroides* ZABL., *O. moldavica* NEGRU)		+	+		I-Gr-Cz-Pl-Gf-Bu-Sum	*O. oleaster* HOFFM. & LINK
Phillyrea lanceolata N. BOUL.			+		F-Sug	*P. angustifolia* L.

Table 1 (continued)

Ancestral taxon	Tertiary					Present equivalent taxon
	E	O	M	P	Area	
P. pschechensis Kutuzk. (= *P. latifolia* L. foss.)			+		Suf-H	*P. latifolia* L.
Periplocaceae						
Periploca kryshtofovichii Korn. (incl. *P. graeca* L. foss.)	+	+	+	+	I-Ro-Bu-Sua-Suf-Sug-Suk	*P. graeca* L.
Platanaceae						
Platanus academiae-group (*P. academiae* Gaudin, *P. schimperi* Sap., *P. lineariloba* Kolak.)	+	+	+	+	I-Gr-Bu-Sug-Suu	*P. orientalis* L.
Punicaceae						
Punica palaeogranatum-group (*P. palaeogranatum* Kutuzk., *P. tertiaria* Gregor, *P. granatum* L. var. *planchonii* Sap.)		+	+		S-F-Gf-Pl-Bu-Suf-Sug	*P. granatum* L.
Rhamnaceae						
Paliurus ovoideus-group (*P. ovoideus* (Goepp.) Herr, *P. thurmanii* Heer, *P. orbiculatus* Sap.)			+		F-Gf-Pl-Ro-Bu-Gr-Sug-Suk-Sum	*P. spina-christii* Mill.
Rhamnus colubrinoides Ett. (= *R. alaternoides* Heer, *R. alaternus* L. foss.)	+		+		Gf-A-H-Pl-Bu-Sua	*R. alaternus* L.
Rosaceae						
Cerasus mahaleb L. foss.			+		Pl	*C. mahaleb* L.
Prunus insitita L. var. *pliocenica* Mädler				+	F-Gf-Gd-Pl	*P. insitita* L.
P. palaeocerasus Ett.			+	+	Cz-Suu	*P. cerasus* L.
Pyracantha acuticarpa C. & E. M. Reid (incl. *P. coccinea* L. foss.)			+	+	Gf-N-Dk-Cz-Pl-Ro-Sug-Sum-Suu	*P. coccinea* L.
Styracaceae						
Styrax maximus-group (*S. maximus* (Web.) Kirchh., *S. pristinum* Ett., *S. pseudoofficinalis* Baik.)			+	+	Gf-Gd-F-N-A-H-Pl-Sug-Suu	*S. officinalis* L.
Tamaricaceae						
Tamarix kryshtofovichii Takht. & Kutuzk.			+		Sua	*T. ramosissima* Led.
Thymelaeaceae						
Daphne kimmerica Kolak.			+	+	Pl-Suaz-Sug	*D. laureola* L.
D. oeningensis A. Br.			+		Gf-A-Pl-Suu	*D. oleoides* Schreb.
Ulmaceae						
Celtis lacunosa-group (*C. lacunosa* Kirchh., *C. japetii* Ung., *C. begonioides* Goepp., *C. vulcanica* Kov., *C. cernua* Sap.)		+	+	+	F-Gf-Cz-Pl-H-A-Bu-Suk-Sum	*C. australis* L.

Table 1 (continued)

Ancestral taxon	Tertiary					Present equivalent taxon
	E	O	M	P	Area	
Verbenaceae						
Vitex paucidenticulata KUTUZK.			+		Suf	*V. agnus-castus* L.
Liliopsida						
Arecaceae						
Chamaerops helvetica FRIEDR. (incl. *C. humilis* L. foss.)	+	+	+	+	Gd-Pl-Gr-Sug-Sum	*C. humilis* L.
Ruscaceae						
Ruscus subaculeatus BERGER			+		A	*R. aculeatus* L.
Smilacaceae						
Smilax hastata (BRONGN.) SAP. sensu PALAMAREV & PETKOVA 1987		+	+	+	S-I-F-Gf-Cz-H-Ro-Yu-Bu-T-Sug-Sum	*S. aspera* L.
S. websteri WESSEL sensu PALAMAREV & PETKOVA 1987	+	+	+	+	S-F-I-Gf-Gd-Dk-Cz-H-Ro-Yu-Bu-Suu	*S. excelsa* L.

latitude. The most eastern partial area of this species is situated in W. Siberia during the Late Oligocene (GORBUNOV 1958). The area of *Pinus robustifolia* (*P. pinaster*) is the most diffuse. Its partial areas exist during the following stages: a) Upper Eocene – Middle Oligocene in C. Europe (GDR, MAI & WALTHER 1985), b) Upper Oligocene in W. Europe (France, SAPORTA 1865) and c) Upper Oligocene in SE. Europe (Bulgaria, PALAMAREV 1962).

The above mentioned Eocene species significantly reduce their areas and gradually disappear during the Late Miocene and Early Pliocene, to be replaced by their present-day derivatives with the S. European flora.

Group 2: species of an Oligocene appearance. 23 species (26,8%) are placed in this group (Table 1). They are from the genera *Abies, Cupressus, Picea, Pinus, Acer, Arbutus, Carpinus, Celtis, Ceratonia, Cercis, Coriaria, Cotinus, Laurus, Myrtus, Olea, Ostrya, Pistacia, Punica, Quercus, Viburnum* and *Smilax*. *Pistacia reddita* (*P. mutica*) and *Punica palaeogranatum* (*P. granatum*) from the Lower Oligocene are the earliest. It is worth noting that the most ancient find of *Punica palaeogranatum* is from the early Oligocene flora of the Rhodope region in Bulgaria (PALAMAREV & PETKOVA unpubl.).

The remaining species apparently start their evolution from the Middle and Late Oligocene. Some aspects concerning the development of their areas are of interest. There are taxa with large and continuous areas, including regions of almost the whole of Europe (except the north), as well as parts of the Caucasus, Asia Minor and Kazakhstan, e.g., *Acer pseudomonspessulanum*-group (*A. monspessulanum*-group), the *Carpinus neilreichii*-group (*C. orientalis*), *Cercis cyclophylla* (*C. siliquastrum*), *Cotinus orbiculatus* (*C. coggygria*), *Quercus mediterranea* (*Q. coccifera*

s. l.), *Q. pseudocastanea* (*Q. castaneifolia*, *Q. afares*), and *Smilax hastata* (*S. aspera*). Alternatively, there are species having restricted and discontinuous areas, e.g., *Abies saportana* (*A. pinsapo*, *A. cephalonica*), *A. ramesii* (*A. numidica*, *A. cilicica*), *Picea omoricoides* (*P. omorica*), *Arbutus praeunedo* (*A. unedo*), *Coriaria longaeva*-group (*C. myrtifolia*), *Myrtus rectinervis* (*M. communis*), *Viburnum pseudotinus* (*V. tinus*). The *Celtis lacunosa*-group (*C. australis*), *Ceratonia emarginata* (*C. siliqua*), the *Olea notii*-group (*O. oleaster*), the *Ostrya kryshtofovichii*-group (*O. carpinifolia*) and *Quercus praeilex* (*Q. ilex*, *Q. baloot*) occupy an intermediate position in this respect, being disjunct, i.e. SW. European-Caucasian, E. European-Kazakhstanian and Caucasian-Kazakhstanian. Besides, the Caucasian part of these areas is always younger than its other parts. This could be due to the existence of an European and a Kazakhstanian Paleogene centres of dispersal for semixerophytic or xerophytic elements, expanding to the East and West, respectively. It seems that the Caucasian part of these areas survived for a longer period in comparison to other parts which disappeared already before the Pliocene.

It is typical of the major part of the Oligocene Paleomediterranean species that their northermost borderline reached 50 – 53° N latitude during the different stages of their development.

Group 3: species of a Miocene appearance. This group is the most numerous, including 49 species or 57% (Table 1). It is represented by the genera *Abies*, *Cedrus*, *Juniperus*, *Pinus*, *Acer*, *Alnus*, *Anagyris*, *Arbutus*, *Buxus*, *Cerasus*, *Colutea*, *Daphne*, *Ficus*, *Fraxinus*, *Lonicera*, *Marsdenia*, *Nerium*, *Paliurus*, *Phillyrea*, *Pistacia*, *Prunus*, *Pyracantha*, *Quercus*, *Rhus*, *Styrax*, *Tamarix*, *Viburnum*, *Vitex* and *Ruscus*. Part of the species are of an Early Miocene appearance, i.e. *Pinus laricioides* (*P. nigra*), *Acer crenatifolium* (*A. hyrcanum*, *A. reginae-amaliae*), *Alnus cycladum* (*A. cordata*), *Colutea macrophylla* (*C. arborescens*), *Fraxinus praedicta* (*F. angustifolia* s. l.), *Paliurus ovoideus*-group (*P. spina-christii*), *Pistacia miocenica* (*P. terebinthus*, *P. palaestina*), *Quercus grandidentata* (*Q. aegilops*, *Q. brantii*), *Styrax maximus*-group (*S. officinalis*). Among these species, *Pinus laricioides*, *Fraxinus praedicta*, *Paliurus ovoideus* and *Styrax maximus* stand out with their quite extensive Tertiary areas; *Styrax maximus*, e.g., can be qualified as European – Southwest-asian – Kazakhstanian. The northern borderline of the species mentioned above coincides more or less with the northern boundary of C. Europe.

In contrast, some Early Miocene species have restricted or diffuse areas, e.g., *Acer crenatifolium* (C. Europe), *A. campylopterix*-group (*A. opalus* s. l., W. – SE. Europe), *Alnus cycladum* (S. Balkan – Georgia), and *Pistacia miocenica* (SW. – E. Europe – Georgia).

The major part of the species discussed appear during the Middle and particularly the Late Miocene. A more expanded European (E) or European – Southwestasian (ESWA) area is characteristic only of *Buxus pliocenica* (*B. sempervirens*-group): ESWA, the *Pistacia acuminata*-group (*P. lentiscus*): ESWA, *Pyracantha acuticarpa* (*P. coccinea*): ESWA, *Quercus cardanii* (*Q. canariensis*): ESWA, *Q. palaeocerris* (*Q. cerris*): ESWA, and *Castanea pliosativa* (*C. sativa*): ESWA. Concerning the subgroup of the Middle and Late Miocene Paleomediterranean elements, the more diffuse areas characterize *Cedrus vivariensis* (*C. libanii*, *C. atlantica*), *Juniperus drupacea-pliocenica* (*J. drupacea*), *Pinus salinarum* (*P. brutia*), *Anagyris foetida*-fossilis (*A. foetida*), *Arbutus elegans* (*A. andrachne*), *Daphne kimmerica* (*D. laureola*), *D. oeningensis* (*D. oleoides*), *Nerium oleander-pliocenica* (*N. oleander*), *Phillyrea* *lanceolata* (*P. angustifolia*), and *Prunus palaeocerasus* (*P. cerasus*). These species exhibit three types of disjunction, namely the SW. European – E. European type, the E. European – SW. Asian type and the C. European – Caucasian type. The smallest area has been found in *Viburnum čukurovense* (*V. orientalis*), regarded as a Bulgarian Miocene endemic.

Group 4: species of a Pliocene appearance. This is the smallest group with only five species or 5,8% (Table 1) and consists of the following taxa: *Ephedra campylopoda*-fossilis (*E. fragilis* subsp. *campylopoda*), *Juniperus excelsa*-fossilis (*J. excelsa*), *Ilex balearica*-fossilis (*I. balearica*), *Jasminum contiguum* (*J. fruticans*), and *Prunus insitita* var. *pliocenica* (*P. insitita*). A specific feature is their restricted Tertiary areas: the first four species have partial areas in Bulgaria, SW. France and the Netherlands, while the fifth has a SW. and C. European area.

The limited number of the Paleomediterranean elements having a Pliocene appearance could be attributed to the fact that the transformation of the major part of the pre-Pliocene species into their recent Mediterranean derivatives mostly took place during the Pliocene.

Discussion

The appearance of ligneous sclerophyll Paleomediterranean species began during the second part of the Eocene. This process took place within the boundaries of the zonal vegetation composed of the subtropical woody vegetation (of the Dryophylleto-Daphnogenetum-sempervirentifruticosum type) which occupied large territories of the entire Tertiary Tethys region in Eurasia. These sclerophyll species played a secondary role, forming restricted azonal communities influenced by relatively dry edaphic and microclimatic conditions. However, the role of these Paleomediterranean elements increased during the Oligocene, when they formed specific tree and shrub coenoses in different areas of the Tethys. They arose, both from various subtropical and warm-temperate broad-leaved evergreen and deciduous communities, as well as from coniferous mixed coenoses. These communities are mainly composed of *Lauraceae, Fagaceae, Magnoliaceae, Theaceae* and some Conifers. Thus, Oligocene xerothermic centres are formed on the Iberian, Apenninian and Balkan Peninsulas, as well as in some C. European and French regions (SAPORTA 1862, 1865; PRINCIPI 1916, PANTIĆ 1956, GRANGEON 1958, ANDREANSZKY 1966, PALAMAREV 1967, FERNANDEZ MARRON 1971, 1979, etc.). The species of the genera *Quercus* (sectt. *Ilex* and *Heterobalanus*), *Arbutus, Pistacia, Ceratonia, Acer* (sect. *Goniocarpa*), *Periploca, Smilax* and *Pinus* (sect. *Banksia*) are best represented in these centres. They probably formed restricted and isolated formation types of Querceta mediterraneae, Querceta praeilicis and Pineta hepios.

The evolution of sclerophyllous coenoses of a Paleomediterranean type appears irregular during the subsequent phases of the Neogene. The phenomenon is more distinct during the Burdigalian of Balearic Islands, Greece and Kazakhstan (UNGER 1867, ARENES & DEPAPE 1956, KORNILOVA 1960); during the Sarmatian and Tortonian on territories of the Iberian, Apenninian, and Balkan Peninsulas (PRINCIPI 1926, MENENDEZ AMOR 1955, PANTIĆ 1956, BERGER 1957, PANTIĆ & MIHAJLOVIČ 1976, 1977; VELITZELOS & SCHNEIDER 1979, VELITZELOS & PETRESCU 1981, VELITZELOS & al. 1981, 1985, 1986; PALAMAREV & PETKOVA 1987), as well as in Hungary, Moldavia, and pre-Caucasus (ANDREANSZKY 1959, KUTUZKINA 1964,

1974; NEGRU 1972, STEPHYRTZA 1974, 1982); during the Late Aragonian in Asia Minor (MÄDLER & STEFFENS 1979); During the Messinian – Late Pontian period this developed further in different regions of the Tethys and Paratethys, as is supported by the concentration of Paleomediterranean species in some local paleofloras. Communities of a Mediterranean sclerophyllous type during this period contained evergreen oaks, species of *Arbutus, Ceratonia, Olea, Phillyrea, Pistacia, Pyracantha* and *Pinus hepios*. PANTIČ & MIHAJLOVIČ (1977, 1979) published data about the development of maquis-like coenoses in Yugoslavia during the Pannonian. HEIMANN & al. (1975) reported data about the existence of such vegetation in Greece during the Messinian, while TAKHTAJAN (1956), KOLAKOVSKYI (1964), and RATIANI (1972) have demonstrated the existence of sclerophyllous coenoses of the Mediterranean type during the Pontian and Akchagylian in Armenia and Georgia.

The process of evolution of sclerophyllous vegetation of the type discussed is supported also by the data from the Pannonian flora of Romania (GIVULESCU 1962), the Late Pontian flora of Bulgaria (STEFANOFF & JORDANOFF 1935, KITANOV 1984), and the Early Pliocene floras of France (DEPAPE 1922) and Turkey (KASAPLIGIL 1977, 1981).

The areas of the Paleomediterranean species appearing during the Miocene reach 47 – 49° N latitude during their evolution. This undoubtedly is an indication that the present-day border of the Mediterranean floristic region if a post-Miocene event. The drastic reduction of the areas probably begins during the Messinian, continues in the Pliocene and reaches the present extent during the Pleistocene.

When comparing the dynamics of the distribution areas of Tertiary ancestors and their modern derivatives, two opposite trends become obvious. On the one hand, there are cases where the areas of the Tertiary species are more extensive than those of the derivatives, e.g., in *Tetraclinis brachyodon – T. articulata, Pyracantha acuticarpa – P. coccinea, Quercus cardanii – Q. canariensis, Q. kubinyi – Q. libanii, Q. pseudocastanea – Q. castaneifolia*, and *Styrax maximus – S. officinalis*. On the other hand, the areas of the Tertiary ancestors are more restricted than those of their recent derivatives, comparing *Juniperus bessarabica – J. macrocarpa, J. foetidissima* fossilis – *J. foetidissima, J. oxycedrus* fossilis – *J. oxycedrus, Anagyris foetida* fossilis – *A. foetida, Cerasus mahaleb* fossilis – *C. mahaleb, Ficus europaea – F. carica, Fraxinus ornus* fossilis – *F. ornus, Jasminum contiguum – J. fruticans, Marsdenia takhtajanii – M. erecta, Quercus pubescens* fossilis – *Q. pubescens, Tamarix kryshtofovichii – T. ramosissima*, and *Ruscus subaculeatus – R. aculeatus*.

KOLAKOVSKYI (1974) offers considerations concerning the altitudinal zonation of the vegetation of the Ancient Mediterranean area during the Neogene. According to the principle of actualismus, one can assume some of the Paleomediterranean conifers to have been an integral part of the sclerophyllous coastal, lowland or hilly phytocoenoses, which we now prefer the call "paleomediterranean sclerophyllous tree and shrub communities" (instead of the term "pre-maquis" introduced earlier: PALAMAREV 1967). Such Conifer elements are *Pinus hepios, P. salinarum, P. robustifolia, Juniperus bessarabica, J. drupacea-pliocenica* and *Tetraclinis brachyodon*. Other species probably have formed mixed mesoxerophyllous to mesophyllous forests at higher elevations, e.g., *Abies saportana, A. ramesii, Cedrus vivariensis, Cupressus palaeosempervirens, Picea omoricoides, Pinus geanthracis, P.*

laricioides, P. thomasiana. This type of paleocoenoses probably formed a montane Mediterranean vegetation belt.

The evergreen mesoxerophyllous oaks of the sectt. *Ilex* and *Heterobalanus* obviously have played an important role in the formation of the sclerophyllous coastal, lowland and hilly forests. The paleobotanical data suggest that they have given rise to the oak-chestnut woods and the so-called "oak-maquis" (MENITZKYI 1984) later on.

The Late Tertiary sclerophyllous coenoses also contain deciduous oaks (from sectt. *Quercus* and *Cerris*). These oaks are considered by MENITZKYI (1984) to appear first in the Tethyan subtropical flora at the beginning of the Miocene as montane elements and then to descend to the lower belts. According to this author, the dispersal of the numerous deciduous oaks into S. Europe and the Caucasus has taken place after the disappearance of the Himalayan sector of the Tethys during the latest Miocene (RÖGL & STEININGER 1983).

Some Paleomediterranean species groups have paticipated in the composition of the azonal riparian vegetation, e.g., members of *Nerium, Periploca, Platanus, Tamarix, Vitex,* and *Smilax.*

The evolution of the sclerophyllous woody communities composed of Paleomediterranean elements is closely connected with the aridity of the climate during the different phases of the Neogene. This aridity had a cyclic character and mainly affected regions of the Alpine-Himalayan Orogenic Belt. PAPP & STEININGER (1979) report data about a considerable aridity in the Tethys between 30° and 40° N latitude during the Messinian – Late Pontian period, probably as a result of the extensive Messinian regressive phases and corresponding increases in land surface. The dispersal of the xerophytic element probably was of a cyclic nature, just as the climate. This is supported by the mesophytic nature of the Pliocene. S. European floras, reconstituted after the "xeric period" from the Sarmatian to the Messinian. The last "xeric wave" effecting Paleomediterranean elements probably occurred during the latest Romanian (resp. Piacenzian) and the Pleistocene. These arid phases stimulated the formation of Neogene xerothermic centres on the Iberian, Apenninian and Balkan Peninsula, as well in Asia Minor. The composition of the paleofloras suggests a warm-temperate climate with a humidity of the present W. Mediterranean type. Its summer aridity is moderated by the relatively high air humidity, favoured by persisting air circulations. Such a type of climate made possible the long co-existence of laurophyllous, mesoxerophyllous and xerophyllous woody plants in the Neogene Tethyan and Paratethyan vegetation.

In the Late Pliocene the differences between the W. and E. Mediterranean floristic areas are already apparent, differences which further increase during the Pleistocene.

ANDREANSZKY (1963 a, b) in his hypothesis about the origin of the so-called "Atlantic xerophilic element" including the Paleomediterranean floristic element, postulates the presence of a xerothermic centre on the territory of the Maroccanian and Spanish Meseta (between 32 and 40° N latitude) from which the dispersal of the xerothermic ligneous element had started. However, there is no paleobotanical evidences for such a centre. Moreover, the paleofloras analysed by us support the presence of several Euroasiatic centres of different ages (from the Burdigalian to the Akchagylian) on the territories from the Iberian Peninsula to Kazakhstan, belonging to different paleofloristic phytochoria (Iberian, Ligurian, Pannonian, Karpathian, Balkanian, Krimea-Caucasian, Asia Minor, etc.). The considerations above mentioned makes it clear that the ANDREANSZKY's "Atlantic xerophilous element" should be regarded as a Tertiary Tethyan and Paratethyan sclerophyllous element.

In conclusion we would like to point out that the paleobotanic data indicate the presence of Paleomediterranean elements during the Middle and Late Paleogene in Eurasia which have been of subordinate significance for the composition and structure of the vegetation. Only during the Late Miocene and Pliocene, a semi-arid climatic zone was formed between 37° and 45 °N latitude with more prominent sclerophyllous woody coenoses. Their direct descendants nowadays constitute much of the woodland vegetation of the Mediterranean floristic area with their two basic coenotic units, Querceta ilicis and Oleo-Ceratonion.

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