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A contribution to the Neogene history of Fagaceae in the Central Balkan area*

EMANUEL PALAMAREV and DIMITER IVANOV

Institute of Botany, Bulgarian Academy of Sciences 23, Acad. G. Bonchev Str., 1113 Sofia, Bulgaria;
e-mail: palam@bio.bas.bg, dimiter@bio.bas.bg

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ABSTRACT. The evolution of the Fagaceae is studied for the Late Oligocene – Late Pliocene time interval, based on macro- and pollenrecords from the palaeofloristic area of the Central Balkan Range. The time interval includes floras from different stratigraphic levels: Late Oligocene/Earliest Miocene, Middle and Late Miocene (Badenian-Sarmatian-Maeotian-Pontian), and Pliocene (Dacian-Romanian).

Representatives of the genera *Fagus*, *Quercus*, *Castanea*, *Castanopsis*, *Lithocarpus*, *Trigonobalanopsis*, *Cyclobalanopsis*, *Pasaniopsis*, and *Eotrigonobalanus* are analyzed from the taxonomic and ecological point of view. Taxonomic diversity comprises 28 species of fossil plants. The following species: *Quercus sosnowskyi*, *Q. pseudocastanea*, *Q. gigas*, *Castanopsis elisabethae*, and *Fagus pristina* played the role of dominants in the fossil plant communities during different stages and substages. The following genera of the family Fagaceae are identified by pollen analysis: *Fagus*, *Quercus*, *Castanea*, and cf. *Castanopsis*. The genus *Quercus* displays the highest taxonomic diversity among them.

KEY WORDS: macroremains, pollen, Fagaceae, Neogene, Bulgaria

INTRODUCTION

Representatives of the family Fagaceae played an important role in the composition of the European Tertiary flora. As a principal component of biodiversity throughout the middle-late Tertiary, they are considered of great significance for the reconstruction of palaeoecosystems and for understanding their evolution in time and space, as well as the internal ecosystem dynamics. All this is due to the fact that many Fagaceae species predominated in forest palaeocoenoses (Palamarev & Mai 1998).

The Neogene represents a prominent time in the family's evolution. During that geological period significant events took place, namely from the viewpoint of changes in the floristic and syntaxonomic composition of palaeofloras and the resulting migration and extinction of species and genera. The Bulgarian Neogene floras bring important data to the above-mentioned changes, which are discussed in the present paper.

28 local palaeofloras in total (Fig. 1) representing several facies, e.g. marine, brackish or fresh-water, were analyzed. In relation to their age, they belong to the following stratigraphic levels: Late Oligocene/Earliest Miocene, Badenian, Sarmatian, Maeotian, Pontian, Dacian, and Romanian (Tab. 1).

In relation to species diversity, these floras varied in taxonomic richness. The Pontian flora was the richest, with 18 identified species (macroremains), followed by the Dacian (13) and the Volhynian (12) floras. The Late Oligocene/Earliest Miocene flora comprises only 3 species (macroremains), thus being the poorest flora studied. These differences in floristic richness could be explained both by the level of studying of the floras and by the importance of Fagaceae species in fossil com-

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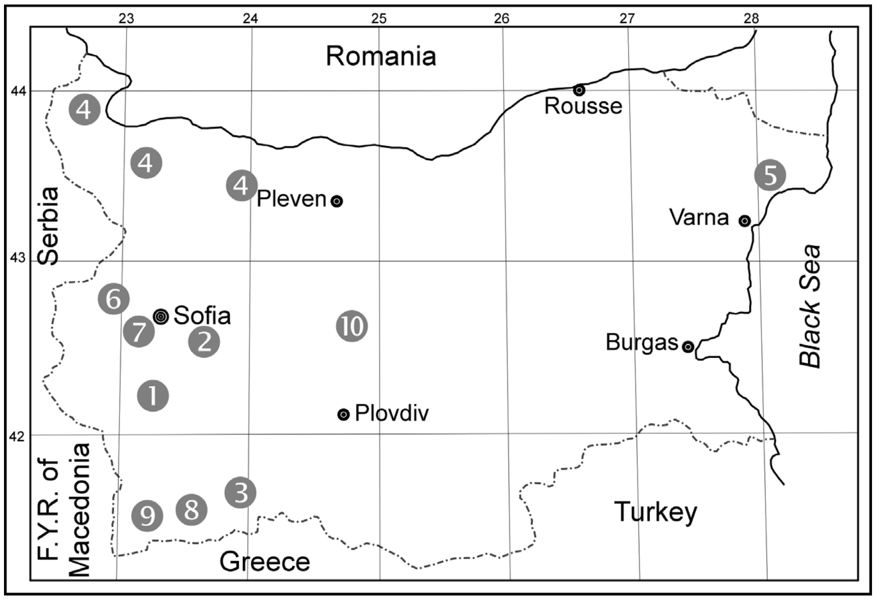

Fig. 1. Localities of studied palaeofloras: **1** – Bobovdol Basin, open coal mine Mlamolovo, Upper Oligocene – ?Lower Miocene; **2** – Chukurovo Basin, Middle Miocene (Lower Badenian); **3** – Satovcha and Slasten Basins, Middle Miocene (Badenian); **4** – Forecarpathian Basin, localities: Ruzhinci, Kladorub, Tolovica, Gramada, Pelovo, Telish and Studeno buche – Volhynian (Lower Sarmatiam); Karbinci, Koshava and Belo pole – Bessarabian (Middle Sarmatian); Deleina – Badenian and Sarmatian; **5** – Euxinian Basin, Sarmatian; **6** – Beli-brjag Basin, Pontian – Dacian; **7** – Sofia Basin, localities: Podgumer – Upper Pontian, Balsha – Lower-Middle Pontian; Kurilo – Dacian; Gniljane, Lozenets and Zemljane – Romanian; **8** – Gotse-Delchev Basin, Pontian; **9** – Sandanski Basin, Upper Maeotian – Pontian; **10** – Karlovo Basin, Pontian-Pliocene

Table 1. Age and number of studied palaeofloras

Stage	Number of studied floras	Macroflora	Microflora
L. Oligocene/ E. Miocene	1	+	+
Badenian	3	+	+
Volhynian	8	+	+
Bessarabian	4	+	+
Chersonian	2	–	+
Meotian	1	–	+
Pontian	5	+	+
Dacian	2	+	+
Romanian	2	+	–

munities. The results obtained (Fig. 2) in this study show a distinct tendency for the Neogene evolution of the family, both in terms of taxonomic composition and of palaeoecology, which is the subject of the following discussion.

STAGES IN THE FAMILY EVOLUTION

The earliest stage in Neogene evolution of the family (Late Oligocene/Earliest Miocene) was characterized by a strong reduction in numbers and disappearance of ancient representatives of the genera *Dryophyllum*, *Eotrigonobalanus*, *Castaneophyllum*, *Pasaniopsis*, and *Quercus* (sections *Macrobalanus*, *Quercus*, and *Glauca*). The only known species were *Trigonobalanopsis exacantha*, *Fagus silesiaca*, and *Quercus neriifolia*: all characteristic species for the Late Oligocene and Early Miocene in central Europe. Records of these species in Bulgaria as early as in the Late Oligocene/Earliest Miocene make it the first locality outside their central European area for that time period.

After that early stage, the role of the Fagaceae increased during the Middle Miocene, and seven species of the genera *Fagus*, *Castanea*, *Castanopsis*, *Quercus*, and *Trigonobalanopsis* were identified (Tab. 2).

A significant event in the history of the family was the emergence of *Castanopsis pliovariabilis* (Kolak.) Kolak., *Quercus sosnowskyi* Kolak., and *Q. ilex* L. foss. in the Middle Miocene. The first species was characteristic of the Pontian flora of Abkhazia, and its record on the Balkan Peninsula has extended both its geographic and its stratigraphic distribution. Appearance of *Quercus sosnowskyi* was another interesting event in the Balkan Neogene. It belongs to sect. *Heterobalanus*

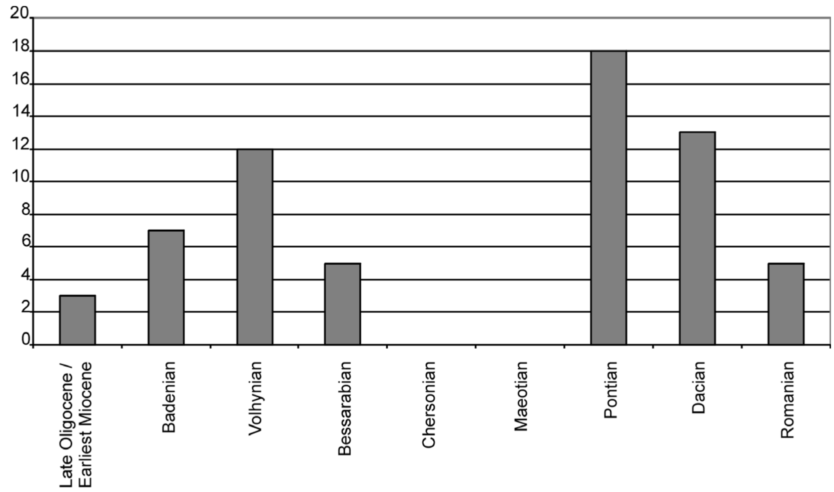

Fig. 2. Number of Fagaceae species from different stages (macroremains)

Table 2. Taxonomic composition of Fagaceae in Badenian of Bulgaria

Fossil species	Recent relative
Castanea sativa Mill.foss.	*C. sativa* Mill.
Castanopsis pliovariabilis (Kolak.) Kolak.	*C. chinensis* Hance
Quercus ilex L. foss.	*Q. ilex* L.
Q. lyellii Heer.compl.	*Q. flagellifera* Trel., *Q. laurifolia* Michx.
Q. neriifolia A. Br.	*Q. imbricaria* Michx., *Q. phellos* L.
Q. sosnowskyi Kolak.	*Q. suber* L.,*Q. alnifolia* Poech.
Trigonobalanopsis rhamnoides (Rossm.) Kvaček & Walther	*Trigonobalanus* (*Colombobalanus*) *excelsa* Lozano & al. vel *Castanopsis wallichii* King., *C. tribuloides* DC

(Oerst.) Menits. and is allied to *Q. suber* L. and *Q. alnifolia* Poech. Kolakovsky (1964) identified this species for the first time in the Pontian flora of Abkhazia; later on it was found in Bulgaria, both in Badenian and Pontian sediments, as well as in the Late Miocene of Greece and Turkey (Kvaček et al. 2002, Erdei et al. 2002). This fossil species is remarkable for its considerable morphological variability, which is also true for its Bulgarian representatives. It is known by the forms *sosnowskyi*, *angustifolia* and *palaeoacuta* (Bozukov 1999). Both *Castanopsis pliovariabilis* and *Quercus sosnowskyi* give evidence for a Neogene floristic exchange between Asia Minor and southeastern Europe. These data reveal *Q. sosnowskyi* as a characteristic Neogene element of the Balkan-southwest Asian area.

The presence of *Quercus ilex* foss. in the Middle Miocene (Badenian) and later on in the Late Pontian sediments indicates a tendency in the family evolution towards development of sclerophyll dendroflora of Mediterranean type, a tendency that intensified with time. Four more species were identified in the Badenian flora: *Castanea sativa* Mill. foss., *Quercus neriifolia* A. Br., *Q. lyellii* Heer. compl., and *Trigonobalanopsis rhamnoides* (Rossm.) Kvaček & Walther. The three latter ones were components in most Late Paleogene and Neogene European floras, and so did not present any special interest. *Castanea sativa* foss. appeared in the Badenian, but during the rest of the Neogene played a limited role in the forest structure.

Sarmatian manifested a new stage in Fagaceae evolution and twelve species of the genera *Fagus*, *Castanea*, *Castanopsis*, *Lithocarpus*, *Pasaniopsis*, *Quercus*, and *Trigonobalanopsis* were identified in the Volhynian floristic complexes (Tab. 3). Most important for the history of the family were the species: *Fagus pristina* Sap., *Castanopsis elisabethae* Kolak., *Lithocarpus palaeobalcanicus* Palam. & Petkova, *Pasaniopsis decurrens* (Andr.) Palam. & Mai, *Quercus gigas* Goepp. (incl. *Q. pontica-miocenica*

Table 3. Taxonomic composition of Fagaceae in Volhynian of Bulgaria

Fossil species	Recent relative
Fagus pliocaenica Sap.	*F. orientalis* Lip.
Fagus pristina Sap.	*F. grandifolia* Ehrh.
Castanea sativa Mill.foss.	*C. sativa* Mill.
Castanopsis elisabethae Kolak.	*C. fabri* Hance, *C. ounbiensis* Hickel & Cam.
Lithocarpus palaeobalcanicus Palam. & Petkova	*L. conocarpa* (Oudem.) Rehd., *L. hui* Camus
Pasaniopsis decurrens (Andr.) Palam. & Mai	*Lithocarpus* spp.vel *Quercus* ssp. ex sect. *Acuta* Menits.
Quercus lyellii Heer. compl.	*Q. flagellifera* Trel., *Q. laurifolia* Michx.
Q. mediterranea Ung.	*Q. infectoria* Oliv., *Q. brantii* Lindl.
Q. neriifolia A. Br.	*Q. imbricaria* Michx., *Q. phellos* L.
Q. gigas Goepp.	*Q. griffithii* Hook. & Thoms., *Q. aliena* Bl.
Quercus pseudocastanea Goepp.	*Q. castaneifolia* C.A. Mey., *Q. aegilops* L.
Trigonobalanopsis rhamnoides (Rossm.) Kvaček & Walther	*Trigonobalanus* (*Colombobalanus*) *excelsa* Lozano & al. vel *Castanopsis wallichii* King., *C. tribuloides* DC

Kubat), and *Q. pseudocastanea* Goepp. (Palamarev & Petkova 1987).

The Neogene species *Fagus pristina* Sap. is related to the recent North American species *Fagus grandifolia* Ehrh. (Palamarev & Petkova 1987). The *F. pristina* differs in very specific leaf morphology, e.g. large leaves, with between 15–20 secondary veins, and thus it strongly differentiates from the so-called southeuropean Neogene species *Fagus gussonii* Mass. as well as from *F. orientalis* Lipsky which is its presumable extant analogue (Knobloch & Velitzelos 1986, Kvaček et al. 2002, Denk 2002). This is the reason for us to accept *F. pristina* as a separate species, not in the frame of *F. gussonii*. As the extant analogue of *F. pristina*, namely *F. grandifolia* do not have any recent European relatives, the fossil species represented an extinct evolution lineage. According to the available data on the distribution of this species, it was a specific South European Neogene element

Castanopsis elisabethae Kolak. and *Castanopsis pliovariabilis* (Kolak.) Kolak. represent the palaeocolchician element in the Bulgarian Neogene flora, thus evidencing a floristic exchange between East and Central Parathetys in the Badenian-Volhynian time period.

Lithocarpus palaeobalcanicus Palam. & Petkova was an endemic Balkan element, which appeared first in the Volhynian, and later on in the Pontian flora. Its presumable affiliation to the section of *Pasania* (Miq.) Barnett refers it to the most ancient lineages of the genus.

As an ancient representative of Fagaceae, *Pasaniopsis decurrens* (Andr.) Palam. & Mai seems to be a Palaeogene relict in the Neogene flora.

Quercus gigas Goepp. and *Q. pseudocastanea* Goepp. were the first species in the Bulgarian Neogene flora of the so-called alienoid-roburoid (sect. *Quercus*) and cerroid oaks (sect. *Cerris*). They marked a new evolution trend: emergence of a younger lineage, closely connected to evolutionarily more advanced oak species, such as *Q. griffithii* Hook. & Thoms., *Q. aliena* Bl., and *Q. aegilops* L. (Palamarev & Petkova 1987).

Geological history of the oak family evolution was poorly documented in the Bessarabian stage (Tab. 4), of a total of five investigated species, only *Quercus cardanii* Massal. is a representative of alienoid (roburoid) oaks, morphologically close to recent *Quercus hartwissiana* Stev. and *Q. canariensis* Willd. That species continued the trend in evolution of alienoid oaks, which had started at the beginning of the Sarmatian.

In the Pontian a boom of the Fagaceae occurred, as corroborated by identification of

Table 4. Taxonomic composition of Fagaceae in Bessarabian of Bulgaria

Fossil species	Recent relative
Castanea sativa Mill.foss.	*C. sativa* Mill.
Quercus cardanii Massal.	*Q. hartwissiana* Stev., *Q. canariensis* Willd.
Q. lyellii Heer. compl.	*Q. flagellifera* Trel., *Q. laurifolia* Michx.
Q. mediterranea Ung.	*Q. infectoria* Oliv., *Q. brantii* Lindl.
Q. pseudocastanea Goepp.	*Q. castaneifolia* C.A. Mey., *Q. aegilops* L.

Table 5. Taxonomic composition of Fagaceae in Pontian of Bulgaria

Fossil species	Recent relative
Fagus decurrens E.M. Reid	*F. sieboldii* Endl.
Fagus pliocaenica Sap.	*F. orientalis* Lip.
Fagus silesiaca Walther & Zastawn.	*F. longipetiolata* Seem.
Castanea sativa Mill.foss.	*C. sativa* Mill.
Castanopsis elisabethae Kolak.	*C. fabri* Hance, *C. ounbiensis* Hickel & Cam.
Cyclobalanopsis stojanovii Palam. & Kitan.	*C. glaucoides* Schottky, *C. myrsinifolia* (Bl.) Oerst.
Lithocarpus palaeobalcanicus Palam. & Petk.	*L. conocarpa* (Oudem.) Rehd., *L. hui* Camus
Quercus bulgarica Kitan.fill.	*Q. cerris* L., *Q. castaneifolia* C.A. Mey.
Q. cardanii Massal.	*Q. hartwissiana* Stev., *Q. canariensis* Willd.
Q. cerris L. foss.	*Q. cerris* L.
Q. coccifera L. foss.	*Q. coccifera* L.
Q. ilex L. foss.	*Q. ilex* L.
Q. lonchitis Ung. s. l.	*Q. serrata* Thunb.,*Q. gilva* Bl.
Q. neriifolia A. Br.	*Q. imbricaria* Michx. ,*Q. phellos* L.
Q. gigas Goepp.	*Q. griffithii* Hook. & Thoms., *Q. aliena* Bl.
Q. pseudocastanea Goepp.	*Q. castaneifolia* C.A. Mey., *Q. aegilops* L.
Q. sosnowskyi Kolak.	*Q. suber* L.,*Q. alnifolia* Poech.
Q. cruciata A. Br.	*Q. falcata* Michx., *Q. triloba* Michx., *Q. macrocarpa* Michx., *Q. rubra* L.

18 species (Tab. 5). Representatives of the following genera were documented: *Fagus* (3 species), *Castanea* (1), *Castanopsis* (1). *Cyclobalanopsis* (1) *Lithocarpus* (1), and *Quercus* (11). The fact that palynological data (Ivanov 1995, Ivanov & Slavomirova 2000) also disclosed the morphological diversity of *Quercus* pollen, with four morphological types (Tab. 6) deserves mentioning. Along with the species known from earlier stages, new species emerged, including two endemic: *Cyclobalanopsis stojanovii* Palam. & Kitan. and *Quercus bulgarica* Kitan. fill. The first belongs to the ancient subgenus *Cyclobalanopsis* Oerst., and the second to the evolutionarily younger cerroid group. A characteristic feature of this period was the presence of species related to such palaeomediterranean elements as *Quercus ilex* L. foss., *Quercus coccifera* L., and *Quercus sosnowskyi* Kolak. (Steffanoff & Jordanoff 1935, Kitanov G. 1984, Palamarev & Kitanov 1988, Vatsev & Petkova 1996).

Table 6. Distribution of the fossil Fagaceae pollen in Neogene of Bulgaria (according to Ivanov 1995, 1996, 1997, 2001, Ivanov & Slavomirova 2000, Kamenov & Kojumdgieva 1983). **1** – Aquitanian; **2** – Badenian; **3** – Sarmatian: **3a** – Volhynian; **3b** – Bessarabian; **3c** – Chersonian; **4** – Maeotian; **5** – Pontian; **6** – Pliocene

Fossil species	Recent relative	1	2	3a	3b	3c	4	5	6
Faguspollenites verus Raatz	*Fagus* sp.	+	+	+	+	+	+	+	
F. gemmatus Nagy	*Fagus* sp.							+	
Fagus sp.									+
Tricolporopollenites cingulum ssp. *oviformis*(Pot.) Th. & Pfl.	*Castanea* sp.	+	+	+	+	+	+	+	
T. cingulum ssp. *pussilus* (Pot.) Th. & Pfl.	*Castanea* pp., *Lithocarpus* pp., *Castanopsis* pp.	+	+	+	+	+	+	+	
T. liblarensis (Th.) Grabowska	*Castanopsis, Lithocarpus*	+	+	+	+	+	+	+	
Castanea sp.									+
Quercoidites asper (Pfl. & Th.) Slodk.	*Quercus* sp.; *Q. robur* type	+	+	+	+	+	+	+	
Q. henrici (Pot.) Pot., Th. & Tierg.	*Quercus* sp.	+		+	+			+	
Q. microhenrici Pot.	*Quercus* sp.	+							
Q. granulatus (Nagy) Slodk.	*Quercus* sp.							+	
Querecopollenites petra typus Nagy	*Quercus petraea* type							+	
Quercus sp.									+
Tricolporopollenites cf. *villensis* (Th.) Th. & Pfl.	Fagaceae	+							

Table 7. Taxonomic composition of Fagaceae in Dacian of Bulgaria

Fossil species	Recent relative
Fagus decurrens E.M. Reid	*F. sieboldii* Endl.
Fagus pliocaenica Sap.	*F. orientalis* Lip.
Castanea sativa Mill.foss.	*C. sativa* Mill.
Cyclobalanopsis stojanovii Palam. & Kitan.	*C. glaucoides* Schottky, *C. myrsinifolia* (Bl.) Oerst.
Quercus cardanii Massal.	*Q. hartwissiana* Stev., *Q. canariensis* Willd.
Q. cerris L. foss.	*Q. cerris* L.
Q. glaucifolia Andr.	*Q. glauca* Thunb.
Q. ilex L. foss.	*Q. ilex* L.
Q. kubinyi (Ett.) Czeczott	*Q. libani* Oliv., *Q. acutissima* Carr.
Q. mediterranea Ung.	*Q. infectoria Oliv.*, *Q. brantii* Lindl.
Q. gigas Goepp.	*Q. griffithii* Hook. & Thoms., *Q. aliena* Bl.
Q. pseudocastanea Goepp.	*Q. castaneifolia* C.A. Mey., *Q. aegilops* L.
Q. trojana Webb. foss.	*Q. trojana* Webb.

During the Pontian two new *Fagus* species emerged, namely *Fagus decurrens* E.M. Reid and *Fagus silesiaca* Walther & Zastawn. The first one related to a recent Japanese species *Fagus sieboldii* Endl. and the second to the East Asian *Fagus longipetiolata* Seem. and *F. hayata* Palib. But these species were widely distributed in Europe and did not represent any special interest. One more oak species, *Quercus lonchitis* Ung. (incl. *Q. drymeja* Ung.), deserves mentioning, which might be regarded as a Palaeogene relict in the Pontian flora of Bulgaria and as a member of the ancient sections *Semiserrata* Menits. or *Gilva* Menits. (Menitzkyi 1984, Palamarev & Mai 1998, Denk & Meller 2001).

The Pontian witnessed a further development of species of the genera *Castanea*, *Castanopsis*, *Lithocarpus*, alienoid and cerroid oaks. Along with them, *Quercus neriifolia* A. Br. also existed as a transitional Palaeogene-Neogene species of section *Phellos* Michx. Another species related to North American oaks contributed to the Pontian flora, namely *Q. cruciata* A. Br. That species was probably closely related to some species of the sections *Rubrae* Michx. and *Albae* Rehd. (Palamarev & Kitanov 1975).

Thirteen species were identified in the Early Pliocene (Dacian), and the most important characteristic of that period was an increase in the numbers of cerroid oaks, e.g. *Quercus kubinyii* (Ett.) Czeczott and *Q. trojana* Webb. foss. (Tab. 7). The second species deserves special mentioning, because its extant analogue, *Q. trojana* Webb., grows in the Balkans and in Asia Minor as a component of Submediterranean Shibljaks (Palamarev 1989, Palamarev & Kitanov 1988). In that time the representatives of the genera *Castanopsis*, *Trigonobalanus* and *Cyclobalanopsis* disappeared from the fossil plant complexes. Also oaks from the sections *Glauca* Menits., *Gilva* Menits., *Semiserrata* Michx., *Phellos* Michx., and *Heterobalanus* (Oerst.) Menits. no longer existed.

Table 8. Taxonomic composition of Fagaceae in Romanian of Bulgaria

Fossil species	Recent relative
Fagus silesiaca Walther & Zastawn.	*F. longipetiolata* Seem.
F. pliocaenica Sap.	*F. orientalis* Lip.
Castanea sativa Mill.foss.	*C. sativa* Mill.
Quercus gigas Goepp.	*Q. griffithii* Hook. & Thoms., *Q. aliena* Bl.
Q. cerris L. foss.	*Q. cerris* L.
Q. cardanii Massal.	*Q. hartwissiana* Stev., *Q. canariensis* Willd.
Q. lonchitis Ung. s.l.	*Q. serrata* Thunb., *Q. gilva* Bl.
Q. coccifera L. foss.	*Q. coccifera* L.
Q. ilex L. foss.	*Q. ilex* L.
Q. trojana Webb. foss.	*Q. trojana* Webb.

There is very scanty information on the evolution of Fagaceae during the Late Pliocene. Only 10 species of the genera *Fagus*, *Castanea* and *Quercus* were identified (Tab. 8). Representatives of *Castanopsis*, *Lithocarpus*, *Trigonobalanopsis*, *Cyclobalanopsis*, and *Quercus* (sect. *Glauca*,*Gilva*, *Semiserrata*, *Heterobalanus*, and *Quercus*) disappeared completely. Only a limited number of oaks from the cerroid and alienoid groups remained (Kitanov B. 1940, 1956, 1960, Kitanov G. 1982).

ECOLOGY AND PALAEOCOENOLOGY

Taking into account the environmental requirements of the closest living relatives of the fossil species, the Neogene species of Fagaceae could be differentiated into the following ecological groups (Tab. 9):

1) Hygromesophytes: *Castanopsis elisabethae*, *C. pliovariabilis*, *Lithocarpus palaeobalcanicus*, *Quercus lyellii*, and *Q. neriifolia*.

2) Mesophytes: *Fagus decurrens*, *F. pristina*, *F. silesiaca*, *Castanea sativa*, *Cyclobalanopsis stojanovii*, *Quercus cardanii*, *Q. glaucifolia*, *Q. kubinyii*, *Q. pseudocastanea*, *Q. cruciata*, *Q. gigas*, *Trigonobalanopsis rhamnoides*, and *T. exacantha*.

3) Semixerophytes to xerophytes: *Quercus bulgarica*, *Q. ilex* foss., *Q. coccifera* foss., *Q. lonchitis*, *Q. mediterranea*, *Q. trojana* foss., and *Q. sosnowskyi*.

During the Late Oligocene/Earliest Miocene and Middle Miocene (Badenian and Volhynian), Fagaceae species grew as components of hygromesophytic and mesophytic forests of the subtropical, moderate hygrophilous type, and in laurophyllous coenoses. Semixerophytes and xerophytes played a subordinate role in the structure of intrazonal vegetation. During that time period pollen grains of Fagaceae appeared in the pollen spectra in small quantities for *Quercus* and sporadically for *Castanea* and *Fagus*.

At the turn from the Badenian to Sarmatian, climatic changes occurred, resulting in the reduction in numbers and disappearance of hygromesophyte and some mesophyte species in favour of semixerophyte and xerophyte ones. That tendency was also well expressed at the end of Sarmatian. The regression of water basins at the end of Sarmatian s.l. led to aridization of climate and disappearance of hygromesophytes. The pollen of *Quercus* and *Ulmus* dominated in the pollen spectra. A new change in the taxonomic structure of the family took place at the end of the Meotian and during the Pontian, when the numbers of alienoid and cerroid oaks increased. The Late Pontian floras evidenced a new change in Fagaceae evolution, probably as a result of the increased climate aridity. It led to proliferation of semixerophyte and xerophyte oaks and emergence of forest or shrub formations of the palaeomediterranean type, dominated by *Quercus sosnowskyi* Kolak., *Q. mediterranea* Ung., *Q. ilex* L. foss., and *Q. coccifera* L. foss.

During the Pliocene, this palaeomediterranean type of vegetation gave way to mesophytic thermophilic oak forests, dominated by *Q. cardanii* Massal., *Q. cerris* L. foss. and *Q. gigas* Goepp., and with an insignificant participation of some relicts of Lauraceae (e.g. *Ocotea* and *Sassafras*) (Stojanoff & Stefanoff 1929, Kitanov B. 1956). Consequently, alienoid and cerroid oaks acquired major importance.

CONCLUSIONS

The hitherto existing palaeobotanical studies reveal 28 species in the Balkan history of Fagaceae, belonging to the following genera: *Fagus*, *Castanea*, *Castanopsis*, *Lthocarpus*, *Pasaniopsis*, *Quercus*, *Cyclobalanopsis*, and. *Trigonobalanopsis* (Tab. 9). *Quercus* (16 species) showed the highest biodiversity, while *Castanea* and *Castanopsis* were represented by single species each. Many important transformations took place during the Miocene, both from the taxonomic and from the ecological point of view. They reveal significant changes in the family evolution, namely, gradual replacement of the earlier evergreen and semi-evergreen species with deciduous oaks of the sections *Quercus* and *Cerris*.

In the Middle Miocene (Badenian and Volhynian) the representatives of Fagaceae grew as components of hygromesophytic and mesophytic forests of the subtropical, moderate hygrophilous type and in laurophyllous coenoses. At the end of the Sarmatian (Bessarabian and Chersonian) these forests transformed into deciduous or semi-evergreen mixed forest formations, of a meso- to xerophytic character.

Table 9. Composition of the Fagaceae in the Bulgarian Neogene flora. Legend: **m** – mesophyte; **hm** – hygromesophyte; **mx** – mesoxerophyte; **x** – xnnerophyte.

Fossil species	Recent relative	Ecol.	Section, subgenus or tribe
Fagus decurrens E.M. Reid	*F. sieboldii* Endl.	m	*Fagus*
F. pliocaenica Sap.	*F. orientalis* Lip.	m	*Fagus*
F. pristina Sap.	*F. grandifolia* Ehrh.	m	*Fagus*
F. silesiaca Walther & Zastawn.	*F. longipetiolata* Seem., *F. hayata* Palib.	m	*Fagus*
Castanea sativa Mill.foss.	*C. sativa* Mill.	m	Castaneae Prantl
Castanopsis elisabethae Kolak.	*C. fabri* Hance, *C. ounbiensis* Hickel. & Camus	hm-m	?
Castanopsis pliovariabilis (Kolak.) Kolak.	*C. chinensis* Hance	hm-m	?
Cyclobalanopsis stojanovii Palam. & Kitan.	*C. glaucoides* Schottky, *C. myrsinifolia* (Bl.) Oerst.	hm-m	*Cyclobalanopsis* Oerst.
Lithocarpus palaeobalcanicus Palam. & Petkova	*L. conocarpa* (Oudem.) Rehd., *L. hui* Camus	hm-m	*Pasania* (Miq.) Barnett
Pasaniopsis decurrens (Andr.) Palam. & Mai	*Lithocarpus* spp. vel *Quercus* ex sect. *Acuta* Menits.	hm	*Pasania* (Miq.) Barnett
Quercus bulgarica Kitan.fill.	*Q. cerris* L., *Q. castaneifolia* C.A. Mey.	mx	*Cerris* Dumort.
Q. cardanii Massal.	*Q. hartwissiana* Stev., *Q. canariensis* Willd.	m	*Quercus*
Q. cerris L. foss.	*Q. cerris* L.	mx	*Cerris* Dumort.
Q. coccifera L. foss.	*Q. coccifera* L.	x	*Ilex* Loud.
Q. glaucifolia Andr.	*Q. glauca* Thunb.	hm	*Glauca* Menits.
Q. ilex L. foss.	*Q. ilex* L.	mx	*Ilex* Loud.
Q. kubinyii (Ett.) Czeczott	*Q. libani* Oliv., *Q. acutissima* Carr.	mx	*Cerris* Dumort.
Q. lonchitis Ung. s. l.	*Q. serrata* Thunb., *Q. gilva* Bl. *Q. setulosa* Hickel. & Camus		*Semiserrata* Menits. vel *Gilva* Menits.
Q. lyellii Heer compl.	*Q. flagellifera* Trel., *Q. laurifolia* Michx.	hm	*Phellos* Michx.
Q. mediterranea Ung.	*Q. infectoria* Oliv., *Q. brantii* Lindl.	mx	*Quercus*
Q. neriifolia A. Br.	*Q. imbricaria* Michx., *Q. phellos* L.	hm-m	*Phellos* Michx.
Q. gigas Goepp.	*Q. griffithii* Hook. & Thoms., *Q. aliena* Bl.	m	*Quercus*
Q. pseudocastanea Goepp.	*Q. castaneifolia* C.A. Mey., *Q. aegielops* L.	mx	*Cerris* Dumort.
Q. sosnowskyi Kolak.	*Q. suber* L., *Q. alnifolia* Poech.	mx	*Heterobalanus* (Oerst.) Menits.
Q. trojana Webb. foss.	*Q. trojana* Webb.	mx	*Cerris* Dumort.
Q. cruciata A. Br.	*Q. falcata* Michx., *Q. triloba* Michx., *Q. macrocarpa* Michx., *Q. rubra* L.	m-mx	*Rubrae* Michx. and *Albae* Michx.
Trigonobalanopsis rhamnoides (Rossm.) Kvaček & Walther	*Trigonobalanus* (=*Colombobalanus*) *excelsa* Lozano & al. vel *Castanopsis wallichii* King., *C. tribuloides* DC	m	Trigonobalaneae (Lozano & Henao) Menits.
T. exacantha (Mai) Kvaček & Walther	*Trigonobalanus verticillata* Forman vel *Trigonobalanus* (=*Formanodendron*) *doichangensis* (Camus) Forman	hm-m	Trigonobalaneae (Lozano & Henao) Menits.

Apparently the Pontian resembled the Badenian-Volhynian time period in respect to oak-laurophyllous forests, but with definite changes in the species composition. Moreover, during that time the mesoxerophyte lineage in oak evolution became more distinct and evergreen communities of the palaeomediterranean type appeared, with the participation of oaks of section *Ilex*, as well as of mixed oak-pine coenoses.

A profound change occurred during the Pliocene (Dacian-Romanian) related to disappearance and strong reduction in diversity of the oak-laurophyllous forests and evergreen palaeomediterranean communities, dominated by species of the *Ilex* section. Communities of deciduous species of the genera of *Quercus* (ex. sect. *Cerris* and *Quercus*), *Castanea* and *Fagus* replaced the above-mentioned mesophytic deciduous forests.

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