Genus *Quercus* in the Late Miocene flora of Baldevo Formation (Southwest Bulgaria): taxonomical composition and palaeoecology

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Abstract. The article presents the results of a study of the representatives of genus Quercus in the local paleoflora of the Gotse Delchev Basin. Twelve species of this genus were identified in the studied material. Three of them (*Q. licudensis*, *Q. abchasica* and *Q. lonchitis*) are new for the Bulgarian paleoflora. The taxonomical, palaeoecological, phytogeographical and biostratigraphic analysis give rise to certain conclusions about the paleoecological conditions in the region and the age of the studied paleoflora. Data on the epidermis structure of the species *Q. drymeja* and *Q. sosnowskyi* were obtained for the first time from Bulgarian fossil samples.

Key words: epidermis structure, Late Miocene, Quercus

Introduction

In the European Tertiary flora, the species of genus *Quercus* play an important floristic and coenotic role in the different in age and composition local paleofloras. The fossil finds reveal some important aspects of the general evolution of the genus on section and species level, contributing at the same time to the reconstruction of elements of the ecological conditions during different time intervals. That is why a detailed study of the genus in each local paleoflora shall contribute to obtaining a more integral regional and global pattern of its history.

The Gotse Delchev Neogene fresh-water Basin is situated in the southernmost part of Southwest Bulgaria, in the Valley of Mesta River. Morphologically, it coincides with the Gotse Delchev Kettle and is developed within the limits of the Gotse Delchev Graben, which is a Neogene extension of the Mesta Graben to the southeast. The Baldevo argillite-sandstone coal-bearing Formation (Vatzev 1980) surfaces as a broken strip in the northeastern part of the Gotse Delchev Graben, at Baldevo, Ognyanovo and Gurmen villages (Fig. 1). It is represented by an association of lake, delta and marsh terrigenous, clayey and biochemogenous rocks. The Formation varies in depth from 40–50 m to 100-120 m (Vatzev & Petkova 1996) (Table 1).

Materials and methods

The investigated material originated from surface excavations of the Baldevo Formation and was collected in the area of an open coal pit situated 1.5 km to the north of Ognyanovo village (Gotse Delchev district). The collected samples with imprints of leaves are deposited in the collection of the Paleobotany and Pollen Analysis Section of the Institute of Botany with the Bulgarian Academy of Sciences. One hundred and fifty-nine samples were studied. Distribution of the

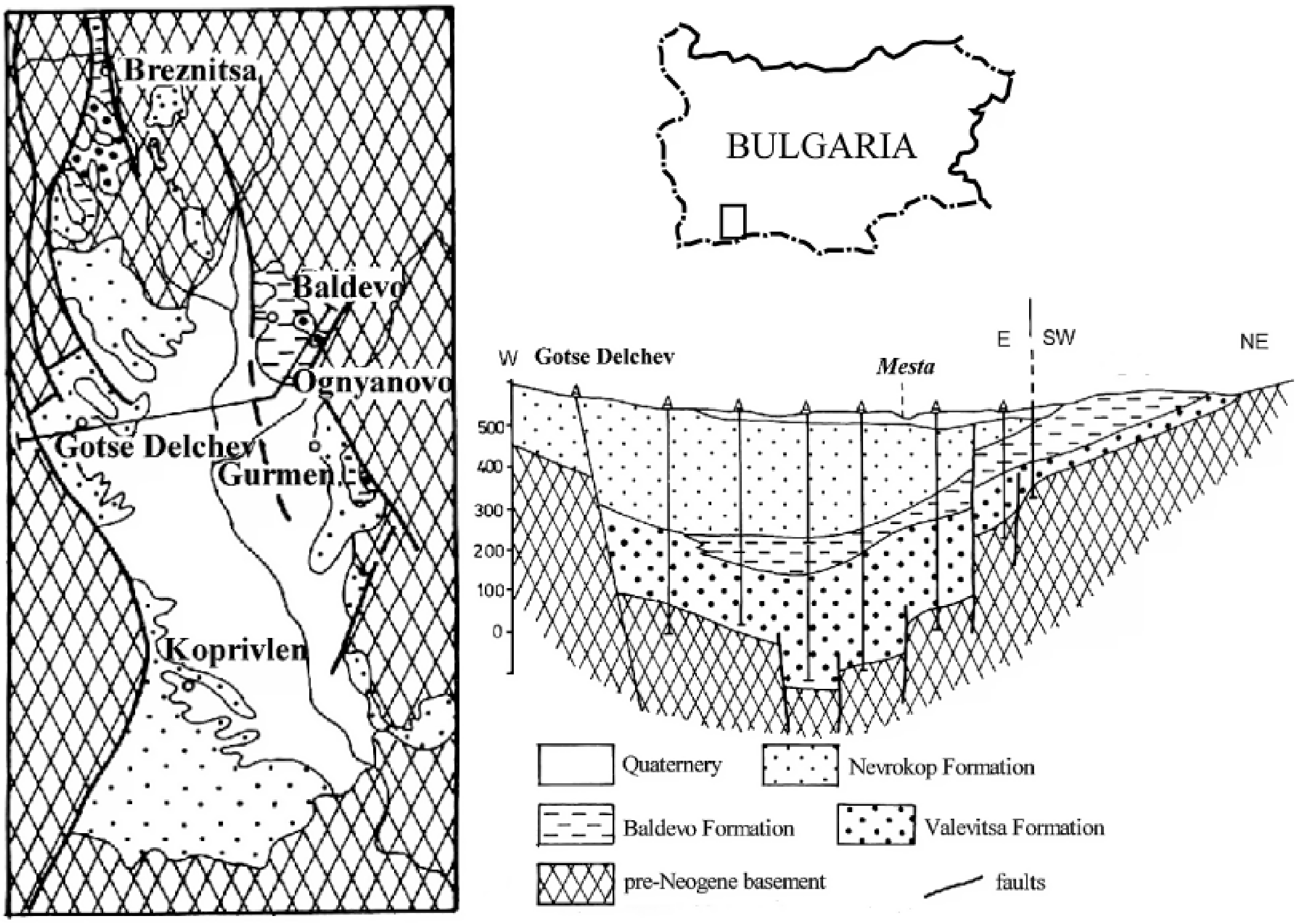

Fig. 1. Situation of the location and cross section of the Gotse Delchev valley according to Vatzev (1980), with supplement.

species by sections followed the taxonomical scheme of Menitski (1984). The morphological and anatomical characteristics of the leaf samples were analyzed with the help of the ichnophytological method and the methods of stomatographic (cuticular) analysis, after the scheme of Dilcher (1974). The characteristics were registered depending on the preservation of samples. In the process of work numerous comparisons were made with recent materials, on the basis of the rich collection of model samples of the Paleobotany and Pollen Analysis Section of the Institute of Botany.

Results

Genus *Quercus* L.
Subg. *Quercus*
Sect. *Quercus*
***Q. licudensis* Knobl. & Velitzelos**

1986. Knobloch & Velitzelos, p. 11, Pl. 3, Figs 6, 9; Pl. 4, Fig. 1.

Material: 15 leaf imprints (Plate I, Fig. 7).

Description: Shape elliptic; base broadly cuneate; top part acuminate, slightly elongate; margin of the leaf blade largely dentate; dents large, acuminate, with convex basal and concave apical part. Venation craspedodromous; median vein straight, almost evenly thickened: secondary veins in 21–23 pairs, straight and slightly curved at the ends, at an angle of 45–55° towards the median vein; tertiary veins undulate, parallel to each other, at an angle of 85–90° towards the secondary ones. Size: length 11–19 cm, width 3.7–7 cm.

The studied samples correspond to the type. The fossil species shows a considerable morphological similarity to another fossil species, *Q. gigas* Göpp. As they strongly resemble each other, their differentiation is not always possible. A more thorough analysis, however, shows certain differences, which could be probably entered in the variety circle of some of the two species. Thus, for instance, in *Q. licudensis* the leaf blade is relatively narrower than

Table 1. Phytogeographical table of the studied species:

Fossil species	Fossil species area	Recent analogues	Ecological type	Recent analogue area
Q. licudensis	Balcans	Q. aliena *Blume* *Q. griffithii* Hook. f. & Thomson	**m** **m**	SEA **SEA**
Q. mediterranea	Europe (without its Northern Parts)	*Q. ilex* L. *Q. coccifera* L. *Q. suber* L.	**mx** **mx** **mx**	**M & WA** **WA** **M**
Q. pontica-miocenica	East Europe & West Asia	*Q. aliena* Blume *Q. griffithii* Hook. f. & Thomson	**m** **m**	**SEA** **SEA**
Q. cf. *pliovariabilis*	West Georgia	*Q. variabilis* Blume	**hm**	**SEA**
Q. pseudocastanea	Europe (without its Northern Parts)	*Q.castaneifolia* C. A. Mey. *Q. vallonea* Kotschy *Q. hispanica* Lam.	**m** **mx** **mx**	**WA** **WA** **M**
Q. sosnowskyi	West Georgia	*Q. semecarpifolia* Sm. *Q. alnifolia* Poech *Q. suber* L.	**mx** **mx** **mx**	**SEA** **WA** **M**
Q. ilex foss.	Mediterranean lands & Caucasus	*Q. ilex* L.	**mx**	**M & WA**
Q. abchasica	West Georgia	*Q. semiserrata* Roxb. *Q. elmeri* Merr. *Q. edithae* Skan	**hm** **hm** **hm**	**SEA** **SEA** **SEA**
Q. drymeja	Europe (without its Northern Parts)	*Q. lancifolia* Schleich. & Cham. *Q. xalapensis* Bonpl.	**mx** **mx**	**CA** **CA**
Q. lonchitis	Europe (without its Northern Parts)	*Q. lancifolia* Schleich. & Cham.	**mx**	**CA**
Q. lyellii	Europe (without its Northern Parts)	*Q. imbricaria* Michx. *Q. laurifolia* Michx. *Q. flagelifera* Trel.	**hm** **hm** **hm**	**NA** **CA** **CA**
Q. neriifolia	Europe (without its Northern Parts)	*Q. phellos* L. *Q. imbricaria* Michx.	**hm** **hm**	**NA** **NA**

mx – mesoxerophytic; **m** – mesophytic; **hm** – hygromesophytic;
SEA – South East Asia; **M** – the Mediterranean; **WA** – West Asia; **CA** – Central America; **NA** – North America

in *Q. gigas*, while the secondary veins have a smaller divergency angle, as it was in our samples. That gives us grounds to refer our specimens to the species *Q. licudensis*.

The species was established for the first time for the fossil flora of Bulgaria.

Q. mediterranea **Ung.**

1847. Unger, p. 144, Pl. 32, Figs 5-9; 1929. Stojanoff & Stefanoff sub *Q. ilex* L. foss.; 1987. Palamarev & Petkova, rev. as *Q. mediterranea,* p. 70, Pl. 8, Fig. 5 a, b, p. 59, Pl. 6, Figs 7-9; text-fig. 15: 5.

Material: 9 leaf imprints (Plate I, Fig. 5).

Q. pontica-miocenica **Kubat**

1955. Kubat in Kubat & Bubik, p. 175, Pl. 10, Fig. 9; Pl. 11, Fig. 4; Pl. 12, Fig. 5; text-Fig. 16; 1987. Palamarev & Petkova, p. 68, Pl. 20, Fig. 1 a, b.

Material: 20 leaf imprints (Plate II, Figs 1, 6).

Sect. *Cerris* Dumort.

Q. **cf.** ***pliovariabilis*** **Kolak.**

1964. Kolakovsky, p. 88, Pl. 31, Fig. 1; 1980. *Castanopsis pliovariabilis* (Kolak.) Kolak. in Iljinskaja, p. 24; 1999. Bozukov, p. 4, Pl. I, Fig. 5.

Material: 1 leaf imprint (Plate II, Fig. 2).

Q. pseudocastanea **Göpp.**

1852. Göppert, p. 274, Pl. 25, Fig. 1-2; 1987. Palamarev & Petkova, p. 69, Pl. 20, Fig. 6; 1934. *Q. sp.* aff. *Q. castaneifolia* C. A. Mey., Stefanov & Jordanov, p. 18.

Material: 16 leaf imprints (Plate I, Fig. 1).

Subg. *Heterobalanus* (Oerst.) Menits.

Sect. *Heterobalanus*

Q. sosnowskyi **Kolak.**

1955. Kolakovsky, p. 247, Pl. 8, Fig. 4; 1984. Kitanov, p. 60, text-Fig. 12: 4.

Material: 64 leaf imprints (Plate I, Fig. 3; Plate II, Fig. 5; Plate III, Figs 1, 2).

Anatomy. Upper epidermis: areoles indistinct. Main epidermal cells polygonal, isodiametric, with straight thickened walls. Size: 25–30 µm. Lower epidermis: areoles distinct, quadrangular or pentagonal in shape. Cells above veins slightly elongated, with straight walls and the following size: length 20–30 µm and width 8–12 µm. The main epidermis cells polygonal, isodiametric, with straight or slightly curved walls. Size: 20–25 × 20-23 µm. Stomata regularly distributed in the areoles, widely elliptic to round. Size: 25–30 × 25–28 µm. A cyclocytic stomatal type. The ring of accompanying cells not always distinct. Accompanying cells 7–8 in number, slightly elongated. Average stomata density 600 mm^{-2}, and average value of the stomatal index I = 12.

Sect. *Ilex* Loud.

Q. ilex **L. foss.**

1984. Kitanov, p. 60, Fig. 12: 1; 1999. Bozukov, p. 5, Pl. I, Fig. 3.

Material: 3 leaf imprints (Plate I, Fig. 6).

Subg. *Cyclobalanoides* (Oerst.) Menits.

Sect. *Semiserrata* Menits.

Q. abchasica **Kolak.**

1980. Kolakovsky in Iljinskaja, p. 25; 1952. *Cyclobalanopsis kryshtofovichii* Kolak., p. 128, text-Fig. 2.

Material: 1 leaf imprint (Plate II, Fig. 4).

Description: Shape elliptic; base missing; top part narrowed, slightly elongated and rounded; margin of the leaf blade largely dentate, basal part entire; dents large, acuminate, with a convex basal and concave apical part; basal part 6 to 8 times longer than the apical. Venation craspedodromous, median vein straight, slightly thickened at the base; secondary veins in nine pairs, slightly arched, at an angle 45–50° towards the median vein; tertiary veins straight, parallel to each other, at an angle of 90° to the secondary ones, forming a loose network of rectangular areoles. Size: length 9.5 cm, width 3.6 cm. The investigated specimen corresponds to the type samples. The species was established for the first time for the fossil flora of Bulgaria.

Q. drymeja **Ung.**

1847. Unger, p. 113, Pl. 32, Figs 1-4; 1932. Konyaroff, p. 125, Table 32, Figs 3-5.

Material: 19 leaf imprints (Plate II, Fig. 3; Plate III, Figs 3, 4).

Anatomy: Upper epidermis: areoles indistinct, cells above the veins slightly elongated. Size: length 20–30 µm, width 5–10 µm. Main epidermal cells polygonal, isodiametric, with straight or slightly curved walls. Size: 20–22 × 23–25 µm. Lower epidermis: areoles indistinct; cells above the veins elongated, with straight walls. Size: length 45–50 µm, width 8–10 µm. The main epidermal cells polygonal, slightly rounded, isodiametric, with straight or slightly curved walls. Diameter 20–25 µm. Stomata evenly dispersed in the areoles, widely elliptic to round. Size 23–25 × 25–30 µm. Stomatal type cyclocytic. The subsidiary cells a little smaller than the main epidermal cells, rounded and slightly elongated. Mean stomatal density 346 mm^{-2}, and average value of the stomatal index I = 15.

Q. lonchitis **Ung.**

1850. Unger, p. 33, Pl. 9, Figs 3-8.

Material: 2 leaf imprints (Plate I, Fig. 4).

Description: shape lanceolate; base broadly cuneate or rounded; top part acuminate, slightly elongated; margin of the leaf blade dentate; dents small and sharp, with a straight or slightly concave basal and concave apical part; basal side 1.5–2 longer than the apical. Venation craspedodromous; median vein straight, slightly thickened at the base; secondary veins in 12–13 pairs, opposite, straight or slightly curved, unbranched, at an angle of 45-50° to the median vein; tertiary veins straight or slightly sinuously curved, often fork-like branched, almost perpendicular to the secondary veins, forming a loose network of triangular and rectangular areoles. Size: length 5.8–7 cm, width 1.5–1.8 cm. The studied specimens correspond to the type and fall in shape into the type range without deviations.

The species was established for the first time for the fossil flora of Bulgaria.

Subg. *Erithrobalanus* (Spach.) Oerst.

Sect. *Phellos* Oerst.

Q. lyellii **Heer**

1862. Heer, p. 40, Pl. 12, Figs 2-9; Pl. 13, Figs 1-4; Pl. 14, Fig. 12 b, Pl. 15, Figs 1, 2; Pl. 17, Figs 4-5; 1987. Palamarev & Petkova, p. 72, Table 20, Figs 4-5.

Material: 6 leaf imprints (Plate II, Fig. 2).

Q. neriifolia **(A. Braun) A. Braun**

1856. A. Braun in Heer, p. 45, Pl. 74, Figs 1-7; 1962. Hadžiev & Palamarev, p. 7; 1987. Palamarev & Petkova, p. 71, Table 20, Figs 2-3, 7; 1845; *Salix neriifolia* A. Braun, p. 170.

Material: 3 leaf imprints.

Results and discussion

In the late Miocene sediments of Baldevo Formation, genus *Quercus* was represented by 12 species: *Q. abchasica*, *Q. drymeja*, *Q. ilex*. foss., *Q. licudensis*, *Q. lonchitis*, *Q. lyellii*, *Q. mediterranea*, *Q. neriifolia*, *Q.* cf. *pliovariabilis*, *Q. pontica-miocenica*, *Q. pseudocastanea*, and *Q. sosnowskyi*.

Of the totally studied 159 leaf imprints, the greatest number was claimed by *Q. sosnowskyi* (64 imprints), and the lowest by *Q. abchasica* and *Q.* cf. *pliovariabilis* (one imprint each). The investigated species belong to six sections: *Quercus* (3 species), *Cerris* (2 species), *Heterobalanus* (1 species), *Ilex* (1 species), *Phellos* (2 species), and *Semiserrata* (3 species). All species of the studied genus were tree species and five of them (judging by their recent analogues) were probably deciduous (the species belonging to the sections *Quercus* and *Cerris*), while the remaining seven were evergreen.

From the evolutionary viewpoint it should be pointed out that two groups stand out within the composition of the genus:

a) *ancient Paleogene relicts*: *Q. lonchitis, Q. lyellii, Q. mediterranea,* and *Q. neriifolia.*

b) *typical Neogene* species: *Q. abchasica, Q. drymeja, Q. ilex* foss., *Q. licudensis, Q.* cf. *pliovariabilis, Q. pontica-miocenica, Q. pseudocastanea,* and *Q. sosnowskyi.*

Mention also deserves another fact that the studied flora provided the second location for two of the species: *Q. licudensis* and *Q. abchasica.* The first species was established for the first time in the Late Miocene of Thessaly (Knobloch & Velitzelos 1986), and the second in the Pontian flora of the Caucasus (Kolakovsky 1952).

In ecological terms, the investigated species could be divided into three groups:

1. *Hygromesophytic* to *mesophytic* (4 species): *Q.* cf. *pliovariabilis*, *Q. lyellii, Q. neriifolia,* and *Q. abchasica*;

2. *Mesophytic* (2 species): *Q. licudensis* and *Q. pontica-miocenica*;

3. *Xeromesophytic* to *xerophytic* (6 species): *Q. pseudocastanea, Q. sosnowskyi, Q. ilex* foss, *Q. mediterranea, Q. drymeja,* and *Q. lonchitis*.

This division probably corresponds to the spatial distribution of these species around the then existing lake basin. The hygromesophytic species probably inhabited the coastal zone of the water basin, the xeromesophytic species occupied the drier mountain slopes around the basin, while the mesophytic species were situated in the median transitional section.

As it could be seen from the above-stated, the evergreens and xerophytic species, characteristic of the plant communities of maqui type, prevailed in the studied group. The presence of typically mesophytic, deciduous species characteristic of the temperate latitudes, however, gives rise to the assumption that a transition from subtropical to warm temperate climate took place, permitting the development of such a combination of species. As in order to obtain more precise data it will be necessary to study the entire flora of the region, so this is just an initial assumption.

The fossil species can be divided into three groups according to their areas:

1. *East European – West Asian* (species whose area used to cover the territories around the recent Black Sea): *Q.* cf. *pliovariabilis, Q. sosnowskyi, Q. pontica-miocenica,* and *Q. abchasica.*

2. *Mediterranean* (species, whose area used to cover the southernmost parts of Europe and the northern parts of Africa, around the recent Mediterranean Sea): *Q. ilex* foss. and *Q. licudensis.*

3. *European* (the area of the species covered Europe almost entirely, without its northern parts): *Q. pseudocastanea, Q. lyellii, Q. neriifolia, Q. mediterranea, Q. drymeja* and *Q. lonchitis.*

The process of comparison of these areas with the areas of recent analogues brought to the fore an interesting dependence. The areas of recent analogues of the first group of fossil species are mainly in Southeast Asia; the areas of recent analogues of the Mediterranean fossil species are mainly in Asia Minor and the Mediterranean; and the areas of recent analogues of the European fossil species are in the Mediterranean, North and Central America (Table 1).

Biostratigraphic analysis of the studied fossil species

Data in Table 2 show that the studied species can be divided into two groups:

1. The group of *transit Paleogene-Neogene* species: *Q. mediterranea, Q. neriifolia, Q. lonchitis,* and *Q. lyellii*.

2. The group of *indicatory Neogene* species: *Q. abchasica, Q. licudensis, Q.* cf. *pliovariabilis, Q. pseudocastanea, Q. drymeja, Q. sosnowskyi, Q. pontica-miocenica,* and *Q. ilex* foss.

From a stratigraphic viewpoint, the second group is more important and can be divided into two groops:

1. *Typically Miocene* species: *Q. abchasica, Q. licudensis, Q.* cf. *pliovariabilis*, *Q. drymeja* and *Q. sosnowskyi*.

2. *Late Miocene-Pliocene*: *Q. pseudocastanea, Q. ilex* foss. and *Q. pontica-miocenica* (the latter two species with even narrower stratigraphic range extending only to the Late Miocene).

These facts confirm the conclusion of Palamarev (1970), Pirumova & Vatzev (1979) and Temniskova-Topalova (1994), based on the studies of macro- and diatom flora, that the age of Baldevo Formation is Late Miocene (most probably Pontian). Therefore, the composition of genus *Quercus* from this Formation reflects a Late Miocene stage in the evolution of the genus in the Balkan Peninsula.

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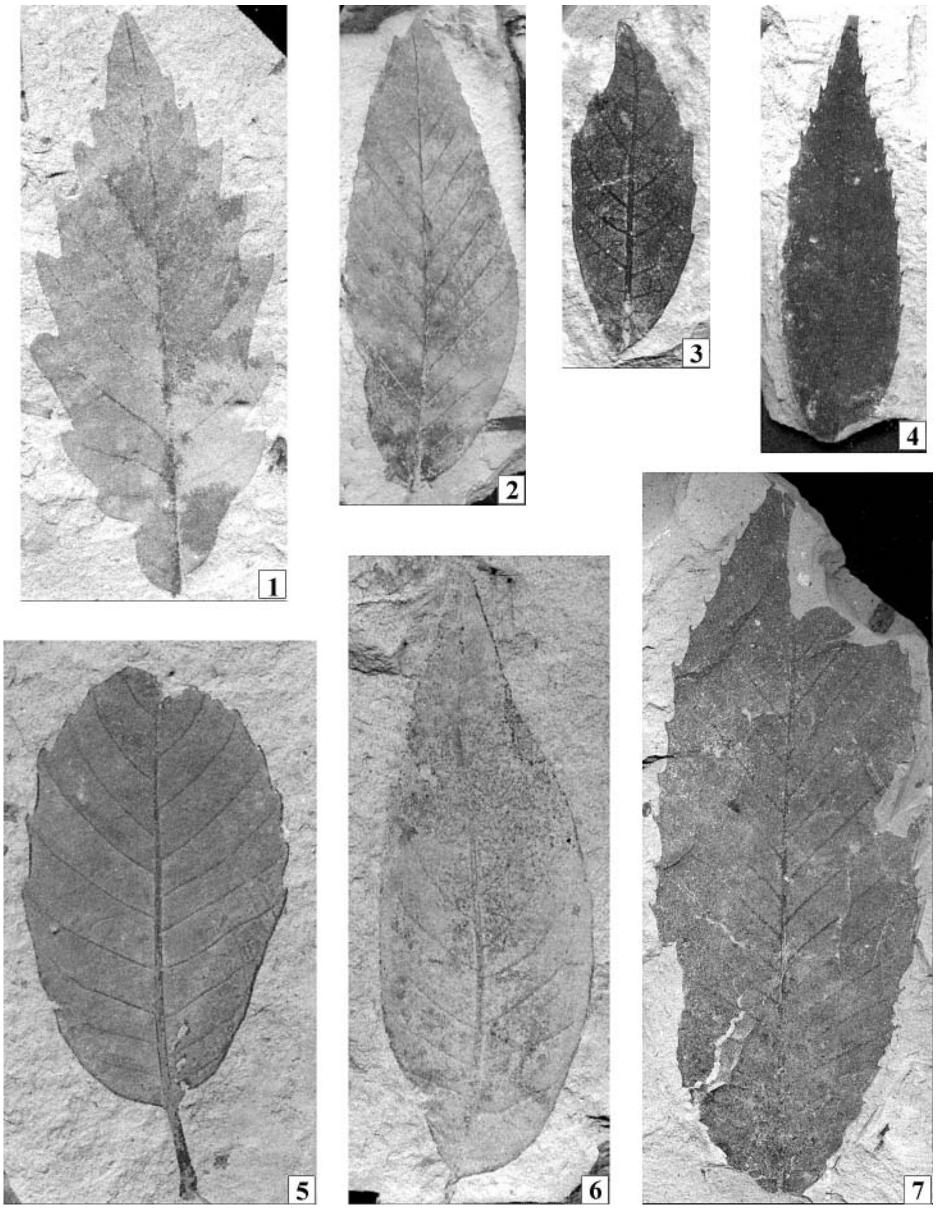
Table 2. Biostratigraphic table of the studied species.

Fossil species	PALEOGENE					NEOGENE				
	EOCENE			OLIGOCENE		MIOCENE			PLIOCENE	
	lower	middle	upper	lower	upper	lower	middle	upper	lower	upper
Q. licudensis								■		
Q. mediterranea					■	■	■	■	■	
Q. pontica-miocenica								■	■	
Q. pliovariabilis								■		
Q. pseudocastanea							■	■	■	■
Q. sosnowskyi							■	■		
Q. ilex foss.							■	■	■	■
Q. abchasica						■	■	■		
Q. drymeja						■	■	■		
Q. lonchitis					■	■	■	■		
Q. lyellii					■	■	■	■		
Q. neriifolia	■	■	■	■	■	■	■	■	■	

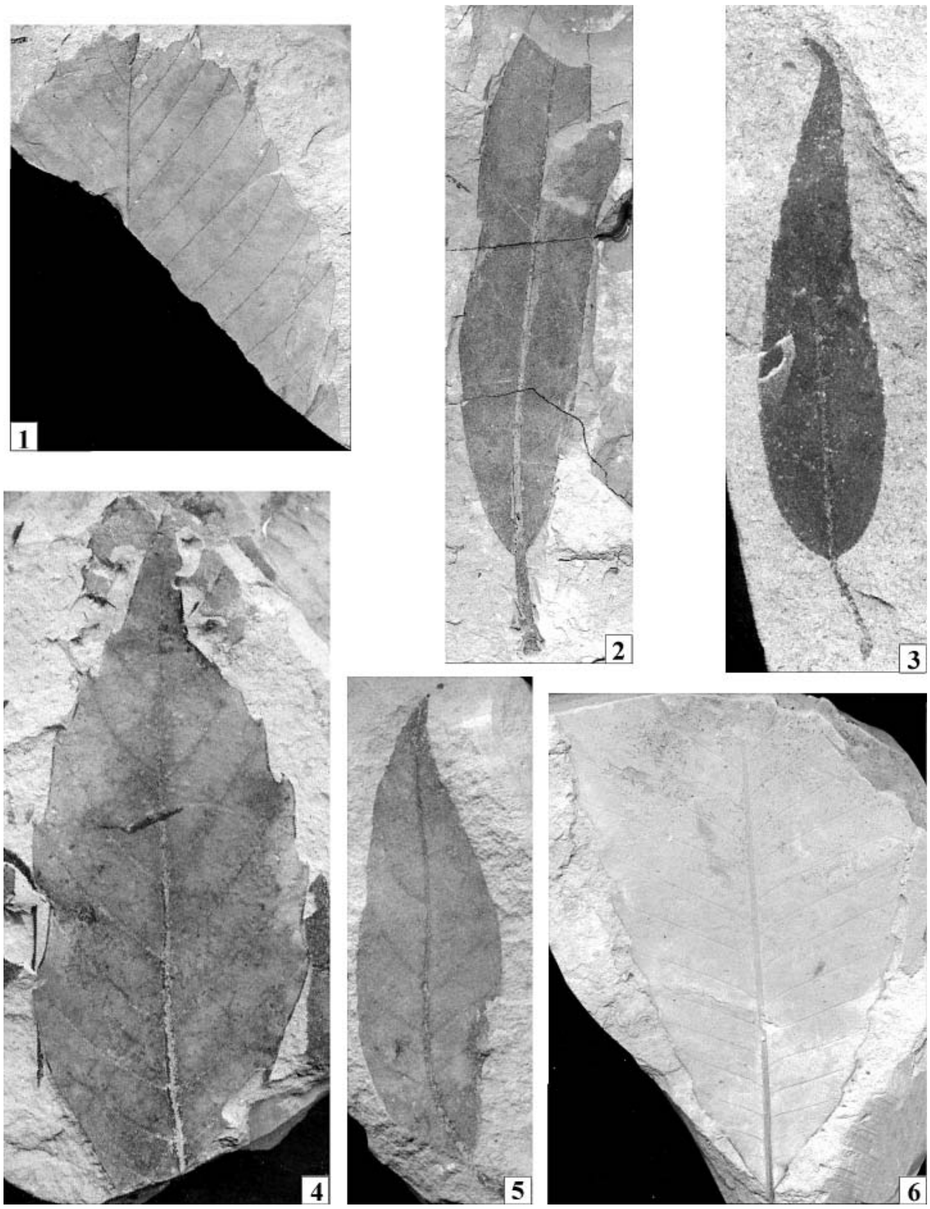
Plate I



Figs 1-7. Pictures of the investigated fossil species:

1, *Q. pseudocastanea* (× 1); **2**, *Q.* cf. *pliovariabilis* (× 1); **3**, *Q. sosnowskyi* (× 1); **4**, *Q. lonchitis* (× 1); **5**, *Q. mediterranea* (× 1); **6**, *Q. ilex* foss. (× 1); **7**, *Q. licudensis* (× 0.5).

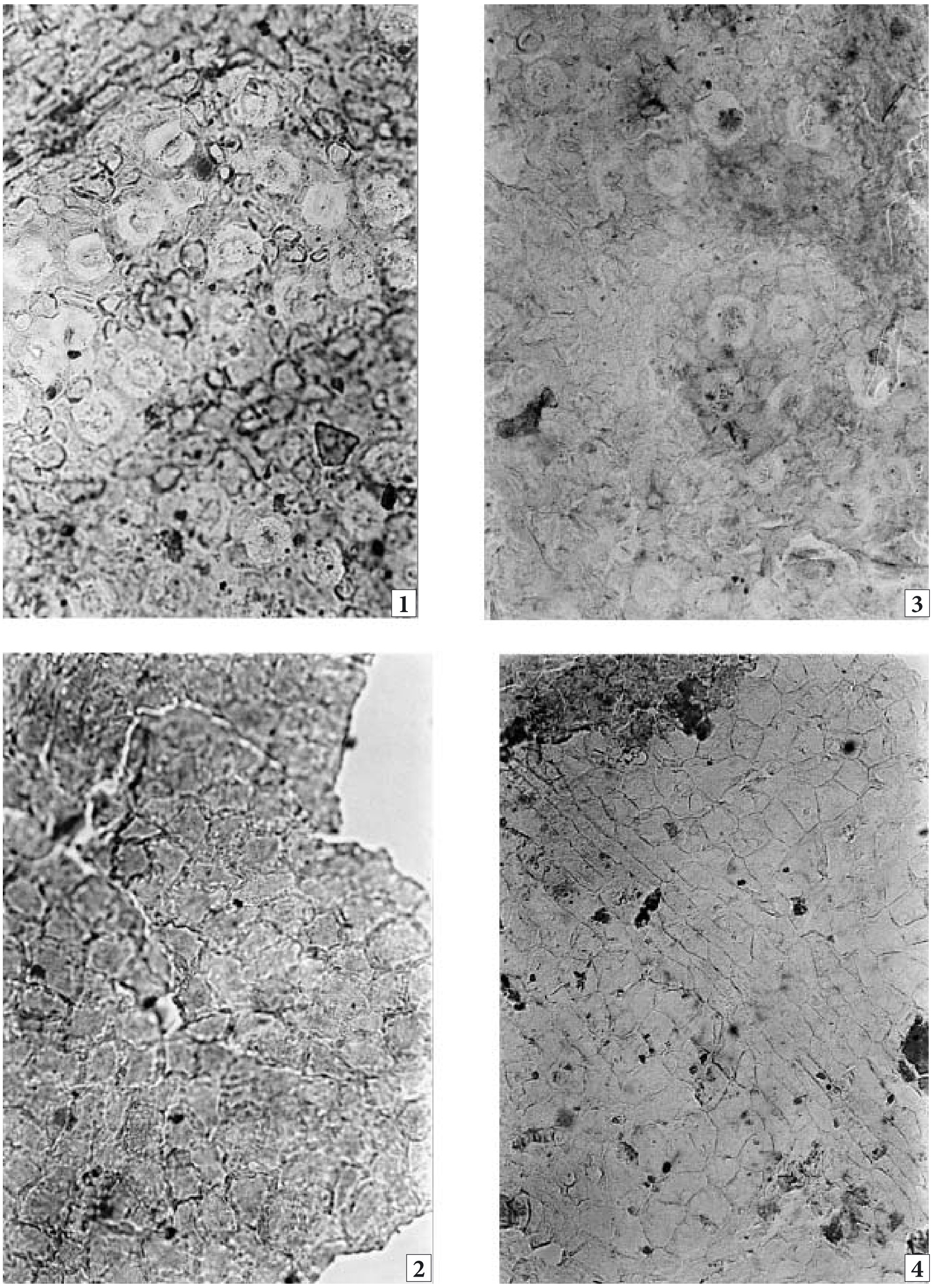
Plate II



Figs 1-6. Pictures of the investigated fossil species:

1, *Q. pontica-miocenica* (× 0.5); **2**, *Q. lyellii* (× 0.5); **3**, *Q. drymeja* (× 1); **4,** *Q. abchasica* (× 1); **5**, *Q. sosnowskyi* (× 1); **6**, *Q. pontica-miocenica* (× 0.5).

Plate III



Figs 1-4. Pictures of the cuticular structure of:

Q. sosnowskyi – **1**, lower epidermis (× 250); **2**, upper epidermis (× 250); *Q. drymeja* – **3**, lower epidermis (× 250); **4**, upper epidermis (× 250);

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