

## RESEARCH ARTICLE

# The first report of an 'evergreen *Castanopsis* type' wood (Fagaceae) for the Late Miocene–Early Pliocene of Europe (Bulgaria, Blagoevgrad Graben)

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In the present article, the establishment of the species *Castanopsis*: *C. bulgarica* Mantzouka, Ivanov, and Bozukov is proposed after the study of a new fagaceous fossil wood stem discovered in 2016 from a new Late Miocene to Early Pliocene plant fossiliferous locality east of Boboshevo town, south-west Bulgaria. A detailed palaeoxylotomical study of the fossil wood revealed characteristics of the 'evergreen *Quercus* type' (e.g. the gradual porosity of the vessels, the existence of two types of rays: uniseriate and multiseriate aggregate, the oval shape of the solitary vessels outline, the occurrence of tracheids) as well as heterocellular compound-aggregate rays, typical for *Castanopsis*. Similarities and differences of the anatomical characteristics/features of the studied specimen with the descriptions of the fossil representatives of Fagaceae (*Quercoxylon*, *Lithocarpoxyton*, and *Castanopsis*) along with its botanical affinities are discussed. A taxonomic list of the Bulgarian fossil fagaceous record of the same age and their nearest living relatives is provided. Emended xylotomical keys with the addition of *Castanopsis* have been created. Moreover, the presence of evergreen *Castanopsis* species with heterocellular rays of two distinct sizes in the fossil record of the 'evergreen oak woods' is supported.

## KEYWORDS

Blagoevgrad Graben, *Castanopsis*, Fagaceae, late Miocene–Early Pliocene, *Lithocarpoxyton*, palaeoxylotomy, *Quercoxylon*

## 1 | INTRODUCTION

The discovery of a new plant fossiliferous locality east of Boboshevo town, (Blagoevgrad Graben, south-west Bulgaria) during 2016 has increased the number of the Bulgarian localities containing Cenozoic flora to over 120 (Ivanov & Bozukov, 2017). Eleven taxa determined by fossil leaves, a cone scale, and a fossil wood stem are revealed and they represent the first evidence of a new Late Neogene (Messinian–Zanclean)

deciduous macroflora in Blagoevgrad Graben. The palaeofloristic macroremains of this area belong predominantly to Arcto-Tertiary species of conifers and angiosperms: *Abies garmensis*, *Alnus* aff. *viridis*, *Betula pendula* foss., *Fagus pliocenica*, *Ostrya* aff. *carpinifolia*, *Populus nigra*, *Salix* aff. *cinerea*, *Smilax hastata*, *Ulmus minor* foss., *Viscum morlotii*, and *Vitis silvestris* foss. as identified in Ivanov and Bozukov (2017).

The fossil wood stem from Blagoevgrad Graben represents a fossil oak wood. Fagaceae findings are principal components of the forest

palaeocoenoses (Palamarev & Mai, 1998) and of the biodiversity throughout the Middle-Late Cenozoic of Europe and Bulgaria (Palamarev & Ivanov, 2003).

Here we conduct a detailed xylotomical study on the fossil oak wood from south-west Bulgaria. Our new findings are discussed in the context of the fossil and extant evergreen fagaceous wood anatomical characteristics. Moreover, the application of the 'Whole Plant Concept' sensu Sakala (2004) including the examination of the relationship between our fossil wood with the nearest living relatives (NLRs) of the fossil Bulgarian fagaceous findings (macroremains) of the same age (Late Miocene–Early Pliocene) has been implemented.

## 2 | GEOLOGY

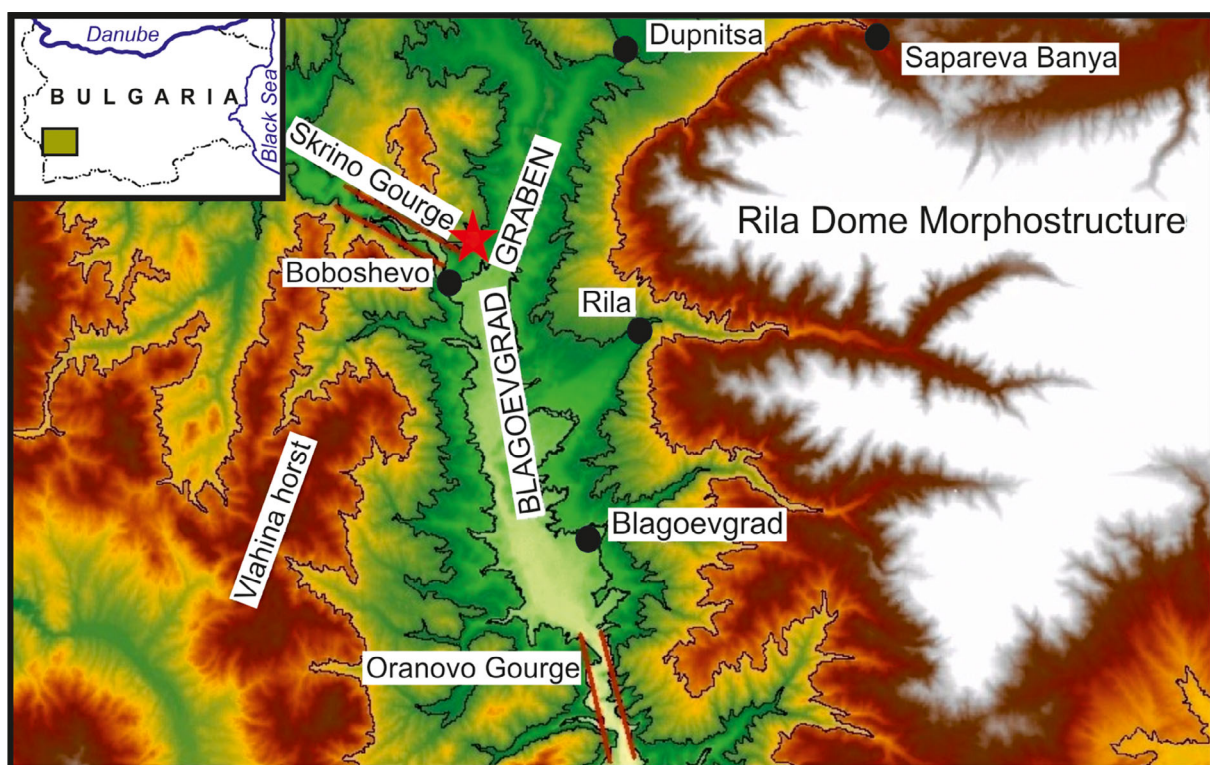
The genesis and evolution of Blagoevgrad Graben is linked to the Cenozoic back-arc extension of the Aegean (Burchfiel, Nakov, Tzankov, & Royden, 2000; Dinter & Royden, 1993; Kounov, Wüthrich, Seward, Burg, & Stockli, 2015; Zagorchev, 1992). It is a 40 km by 10 km depocentre filled with terrigenous Neogene sediments bounding the western and northwestern margins of the Rila Massif between Blagoevgrad and Sapareva Banya (Figure 1).

The basic lithostratigraphy of the Blagoevgrad Graben was introduced by Bakalov (1978) and revised by Ivanov (2016, 2018), Ivanov and Bozukov (2017, 2018), Marinova and Zagorchev (1991),

Nedjalkov, Kojumdjieva, Chermisin, and Nedjalkov (1990), and Zagorchev (1992).

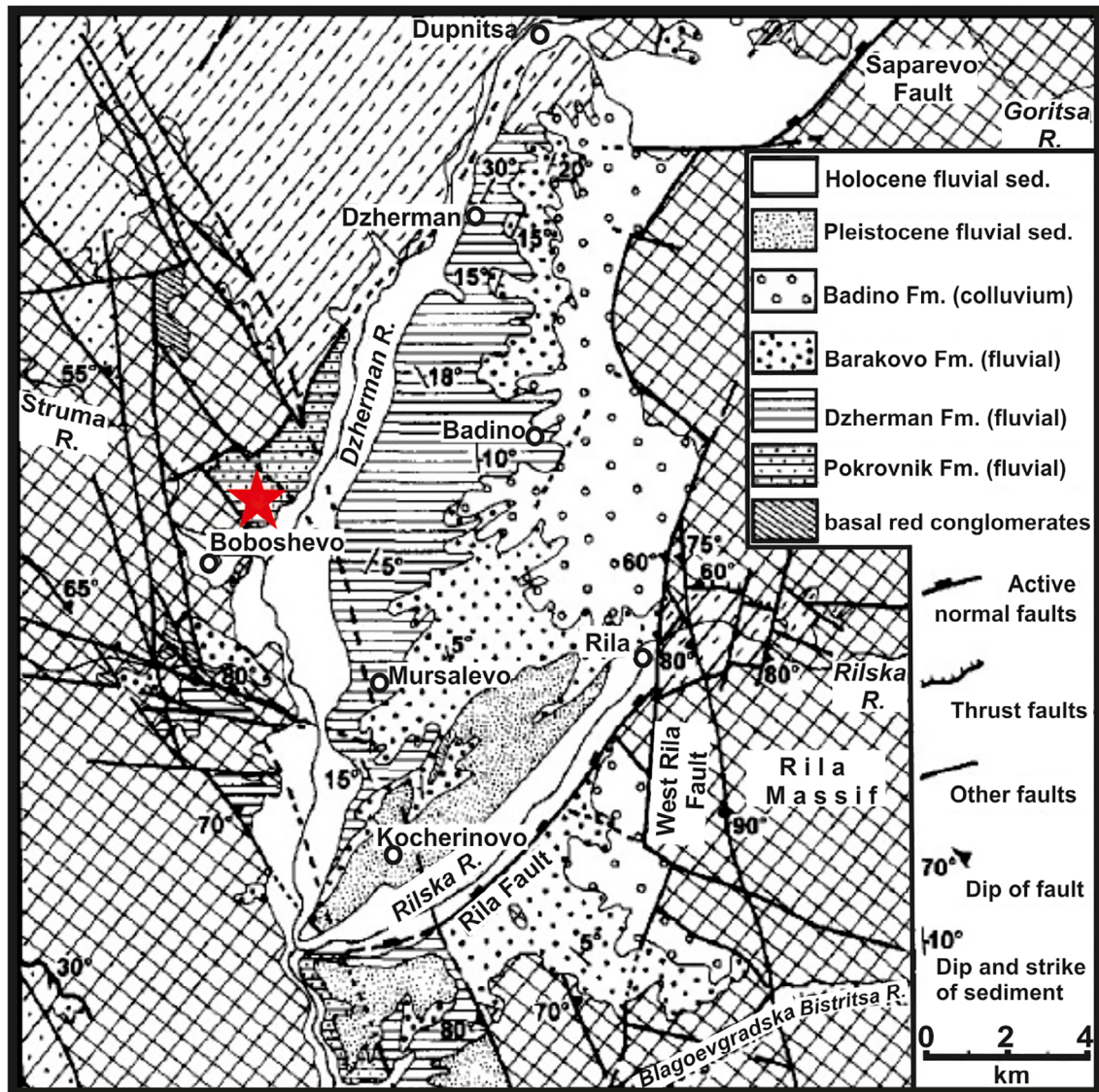
According to the geological map of Bulgaria, the Neogene sediments in Blagoevgrad Graben are separated in two main stratigraphic formations: Dzherman and Barakovo (Marinova & Zagorchev, 1991). The first consists of interbedded, parallel layers of white, yellow, and green fluvial sand and clay, interbedded with gravel lenses and is overlain by conglomerates of the Barakovo Formation consisting of well-rounded, but not well-sorted pebbles and cobbles. Near the villages of Kocherinovo, Mursalevo and Badino, inside the grey-green clays of the Dzherman Formation, a Late Vallesian–Early Turolian (MN11–MN12) mammalian fossil fauna has been found (Hristova, Geraads, Markov, & Spassov, 2013; Spassov, Tzankov, & Geraads, 2006; Tzankov, Spassov, & Stoyanov, 2005). There are no fossil findings inside the Barakovo Formation and the Pontian age of the last is determined based on the superposition of the Barakovo and Dzherman formations.

Later Zagorchev (1992) revised the stratigraphy of Blagoevgrad Graben and proposed a new stratigraphic scheme of the Neogene sediments inside the Blagoevgrad Basin that consists of four stratigraphic units: Pokrovnik, Dzherman, Barakovo, and Badino formations (Figure 2). According to Zagorchev (1992) the Pokrovnik Formation is the oldest, with probable Tortonian–Messinian age, and consists mainly of proluvial, yellowish, polymictic conglomerates and interbeds of sands and sandy clays.



**FIGURE 1** Location of Blagoevgrad Graben. The red star indicates the new macrofossil site. The black circles show the towns and villages of the area [Colour figure can be viewed at [wileyonlinelibrary.com](http://wileyonlinelibrary.com)]





**FIGURE 2** Geological map of Blagoevgrad Graben (after Zagorchev, 1992). The red star indicates the new macrofossil site [Colour figure can be viewed at [wileyonlinelibrary.com](http://wileyonlinelibrary.com)]

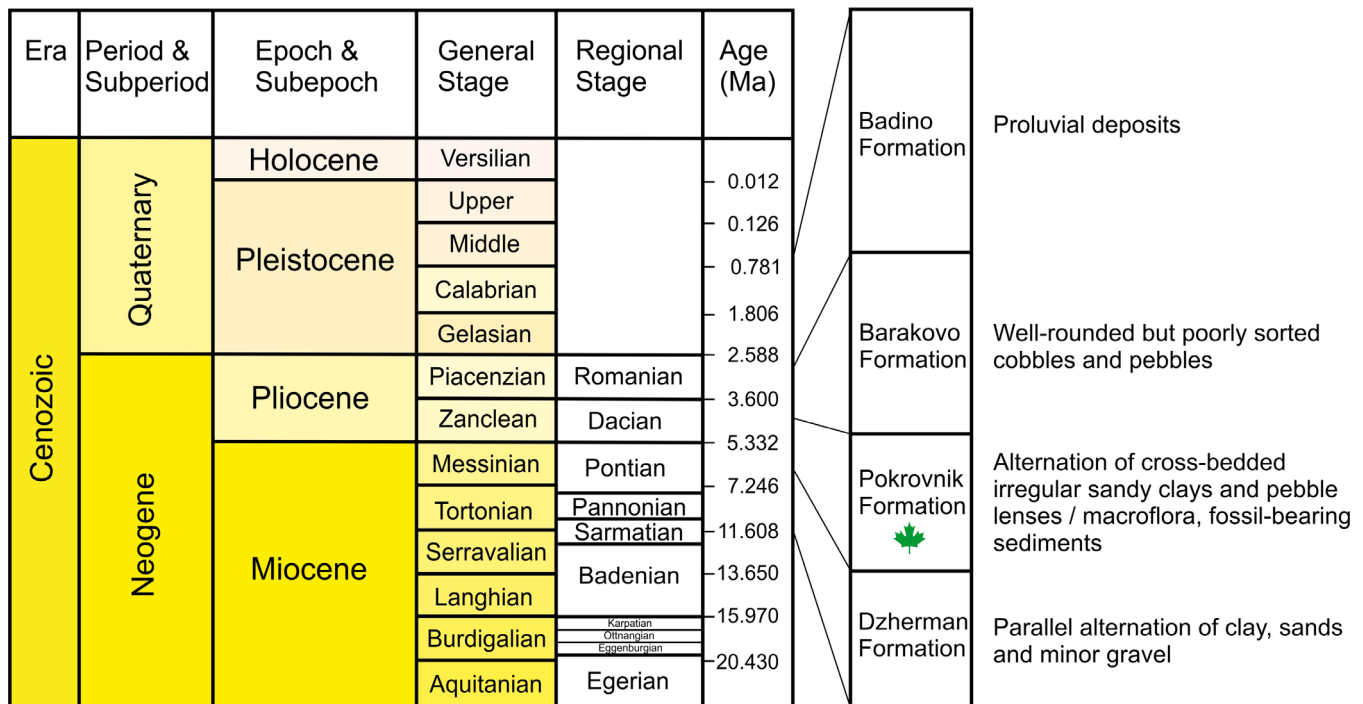
The Dzherman Formation interfingers with the Pokrovnik Formation and consists of predominantly alluvial deposits: greenish, whitish, or yellowish sands and clays interbedded with whitish or yellowish gravel (Zagorchev, 1992). The age of the Dzherman Formation is Tortonian probably continuing into the Messinian (Zagorchev, 1992).

The Barakovo Formation overlays the Dzherman and Pokrovnik formations and it is built of proluvial to alluvial deposits: polymictic to oligomictic conglomerates interbedded with sandstones and sandy clays (Zagorchev, 1992). The age of the Barakovo Formation is not proven and probably is Messinian–Pliocene (Zagorchev, 1992).

The sediments of the Badino Formation have a predominantly proluvial genesis and overlie the sediments of the Barakovo and Dzherman formations, thus representing the youngest strata of the aforementioned deposits. The age of the Badino Formation has been determined to be Pleistocene (Zagorchev, 1992).

Recent studies by Ivanov (2016, 2018) and Ivanov and Bozukov (2017) confirmed the presence of the four main lithostratigraphic units determined by Zagorchev (1992), but based on a newly discovered fossil site near the town of Boboshevo, the above mentioned authors corrected the stratigraphic position of the Pokrovnik and Dzherman formations (Figure 3).

The new fossil site provides the first data about the Late Neogene deciduous macroflora in Blagoevgrad Graben (Figure 2). It contains mainly Arcto-Tertiary species found in various habitats. Trees, bushes, lianas, and semi-parasitic bushes belonging to 12 taxa are represented. Of these 12 taxa, only one is representative of the gymnosperms, and the remaining 11 taxa belong to the angiosperms (Ivanov & Bozukov, 2017). The age of the Boboshevo flora is very likely to be Late Messinian–Early Zanclean. This fossil macrofloristic evidence has been found in situ inside the sediments of the Pokrovnik Formation, therefore the so far accepted Tortonian age of the Pokrovnik



**FIGURE 3** Main stratigraphic units of Blagoevgrad Graben (Dzherman Formation; Pokrovnik Formation; Barakovo Formation; Badino Formation) and their stratigraphic position after Ivanov and Bozukov (2017, 2018). The Late Miocene stratigraphy is according to Hilgen et al. (2012), Palcu, Tulbure, Bartol, Kouwenhoven, and Krijgsman (2015), Popov, Antipov, Zastrozhnov, Kurina, and Pinchuk (2010), and Steininger et al. (1996). The fossil wood, subject to this study, originates from the Pokrovnik Formation dated to the Late Messinian–Early Zanclean (Late Pontian–Early Dacian). The stratigraphic position of our fossil wood is indicated with a green leaf [Colour figure can be viewed at [wileyonlinelibrary.com](http://wileyonlinelibrary.com)]

Formation (Marinova & Zagorchev, 1991; Nedjalkov et al., 1990; Zagorchev, 1992) has to be corrected.

According to Ivanov and Bozukov (2017) the age of the Pokrovnik Formation, based on the new fossils, is Late Messinian–Early Zanclean, which means that it is younger than the Dzherman Formation (Figure 3). According to Ivanov and Bozukov (2018), the sediments of the Pokrovnik Formation are channel alluvium deposited by the braided system of the Paleo-Struma River. Because of the cut and fill function of the river channels, the Pokrovnik Formation has complex lateral relationships (interfingers) with the Dzherman Formation and also overlaps the last. The lack of fossils findings inside the Pokrovnik Formation until 2017 and the complex relationship with the Dzherman Formation are possible reasons for the mistaken stratigraphic position of the Pokrovnik Formation in previous research.

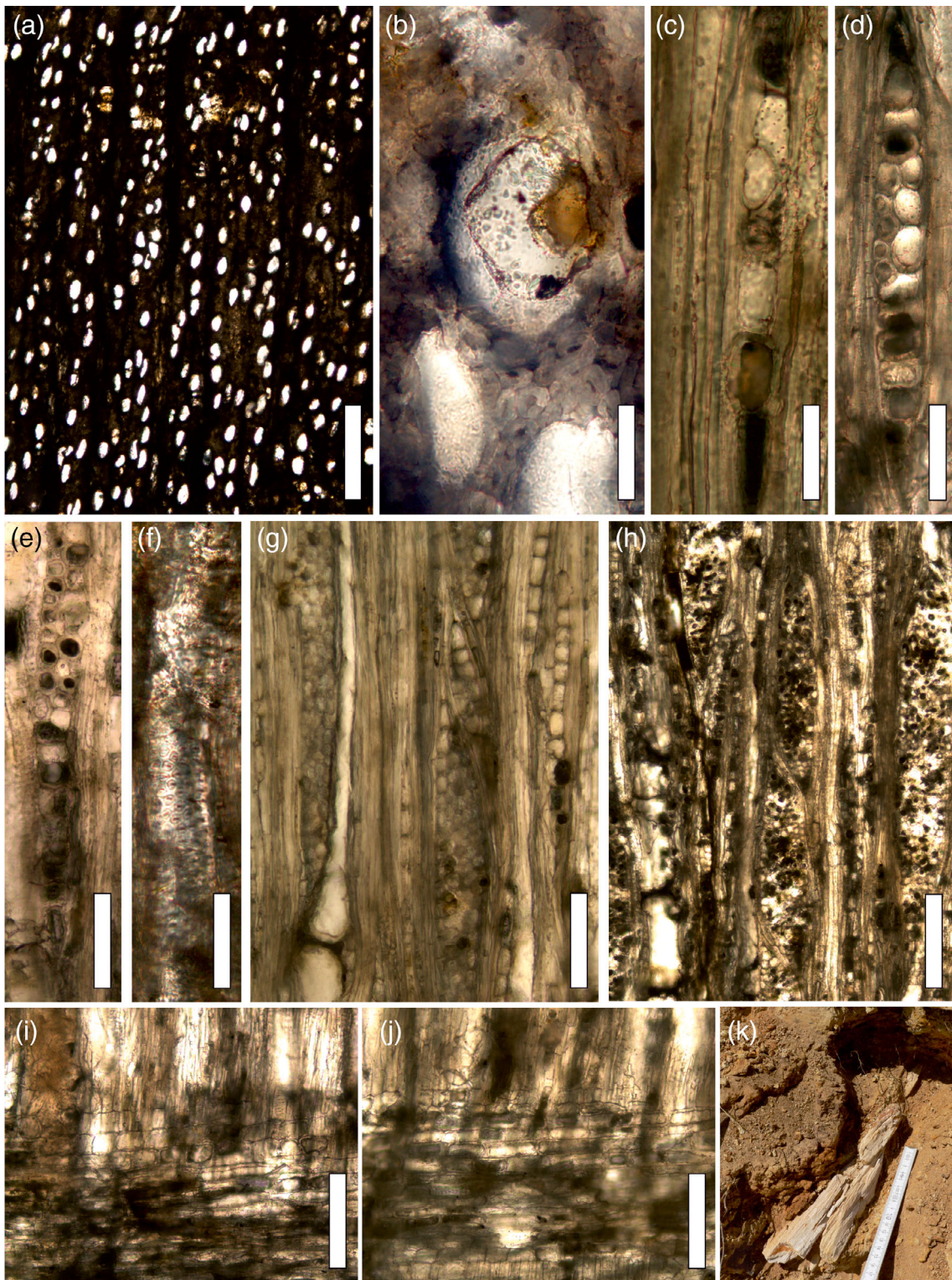
### 3 | MATERIALS AND METHODS

Our material was found in situ in the Pokrovnik Formation, Blagoevgrad Graben (south-west Bulgaria), in a plant fossiliferous locality which was discovered in 2016. The Pokrovnik Formation consists of alluvial channels created by the Palaeo-Struma River (Ivanov & Bozukov, 2018) and is of Late Messinian–Early Zanclean (Late Pontian–Early Dacian) age (Ivanov & Bozukov, 2017).

The specimens are stored in the geological collection of the department of 'Geography Ecology and Natural Preservation' of South-West University 'Neofit Rilski' Blagoevgrad, Bulgaria. After their collection, the dimensions of the fossil woods from Blagoevgrad Graben were measured, photographed (with a Panasonic lumix), and then catalogued. The wood remnant (38 cm long with 7 cm diameter at the thick end) belongs either to a stem or represents a piece of a bigger trunk, enclosed inside a clay lens which is incorporated in cross-bedded alluvial sediments. Thin slides (transversal, radial, and tangential) were prepared at the microscopic preparation laboratory of the Geological Institute of the Bulgarian Academy of Sciences (BAS) following the standard techniques. The thin slides are stored at the Institute of Biodiversity and Ecosystem Research, Bulgarian Academy of Sciences.

The thin sections were examined with a Leica DMEP light microscope equipped with an Olympus UC30 camera and Olympus cell 'A' image analysis software, in the facilities of the Department of Historical Geology and Paleontology, Faculty of Geology and Geo-environment, NKUA and with a Leica DM5500 microscope equipped with a Leica QWIN camera and image analysis software in the facilities of the Palaeobotanical Section of the Senckenberg Institute, Dresden. Data tables were subsequently created using the Microsoft Office Excel. The anatomical descriptions of the recently found fossil wood samples are in accordance with the IAWA Hardwood List (Wheeler, Baas, & Gasson, 1989) and InsideWood Web site





**FIGURE 4** (a) Distinct growth rings, gradual porosity (semi-ring to diffuse-porous wood), exclusively solitary (medium to large) vessels rounded to oval (in early wood) turning to more angular (in latewood) with a dendritic pattern. (b) Tylosis, rounded to oval solitary vessels, scanty vascentric paratracheal parenchyma. (c) Narrow heterocellular short uniseriate ray. Vascentric tracheids in fibres present with simple to minutely/distinctly bordered pits of 2.5–5  $\mu\text{m}$  diameter. (d) Narrow short uni- to biseriate ray. (e) Narrow partly triseriate ray. (f) Intervessel pits alternate minute to small about 2.5–6  $\mu\text{m}$  across. (g,h) Rays of two distinct sizes (i) uni/bi/triseriate and (ii) multiseriate: aggregate and compound, up to 180  $\mu\text{m}$  wide and even more than 1.2 mm high; the multiseriate rays are splitted in oblique. Vascentric tracheids in fibres present with simple to minutely/distinctly bordered pits of 2.5–5  $\mu\text{m}$  diameter. (i,j) Rays heterocellular, body of multiseriate rays composed of procumbent with mostly 2–4 rows of upright and square marginal cells. Vessel-ray pits similar to intervessel pits. (k) *Castanopsis bulgarica* Mantzouka, Ivanov, and Bozukov sp. nov. as found in situ. The specimen is of whitish colour and considered as a piece of 38 cm length and 7 cm diameter thickness. (a,b) TS; (c–h) RLS; (i,j) TLS. TS, RLS, and TLS denote transversal, radial, and tangential longitudinal sections, respectively. Scale bars = 30  $\mu\text{m}$  (b–d,f); 80  $\mu\text{m}$  (e,i,j); 100  $\mu\text{m}$  (g); 200  $\mu\text{m}$  (h); 250  $\mu\text{m}$  (a) [Colour figure can be viewed at [wileyonlinelibrary.com](http://wileyonlinelibrary.com)]

**TABLE 1** The Bulgarian fagaceous fossil findings of Messinian–Zanclean age

Taxa	Bulgarian plant macrofossil localities (Late Pontian–Early Dacian)			
	Gaber	Novi Iskar	Podgumer	Gurmen
<i>Castanea sativa</i> Mill. foss.		Lf		Lf
<i>Fagus decurrens</i> C. and E. Reid	Cp			
<i>F. longipetiolata</i> Seem. foss.			Lf	Lf
<i>F. pliocenica</i> Saporta		Lf	Lf	Lf
<i>F. silesiaca</i> H. Walth. and Zast.		Lf		
<i>Cyclobalanopsis stajanovii</i> Palam. and Kitan. fil. <sup>E</sup>	Cu, Lf			
<i>Pasaniopsis</i> sp. 2 and 3 <sup>E</sup>		Lf		
<i>Quercus</i> aff. <i>acrodonta</i> Seem. <sup>E</sup>	Lf			
<i>Q. bulgarica</i> Kitan. fil.				Cp, Lf
<i>Q. cardanii</i> A. Massal.	Lf		Lf	Lf
<i>Q. cerris</i> L.		Lf	Lf	
<i>Q. coccifera</i> L. foss. <sup>E</sup>		Lf		
<i>Q. gigas</i> Göpp.	Lf			
<i>Q. glaucifolia</i> Andr. <sup>E</sup>	Lf			
<i>Q. ilex</i> L. foss. <sup>E</sup>				Lf
<i>Q. kubinyi</i> (Kováts) Czecczott	Lf	Lf		
<i>Q. mediterranea</i> Unger <sup>E</sup>		Lf		
<i>Q. neriifolia</i> A. Braun				Lf
<i>Q. pontica</i> C. Koch foss.				Lf
<i>Q. sosnowskyi</i> Kolak.	Lf			Lf
<i>Q. trojana</i> Webb foss.	Lf	Lf		

Note: The abbreviations follow the terminology by Bozukov and Tsenov (2012) and Palamarev et al. (2005): 'Lf' for leaf imprints; 'Cp' denotes 'cupules'; and 'Cu' is used for cuticles (epidermal structure), including phytoleims, as well as dispersed cuticles; 'E' denotes 'the fagaceous evergreen macrofloristic findings (especially leaves) from the Bulgarian localities of the same age as our specimen'. Source: Modified after Bozukov and Tsenov (2012).

(InsideWood, 2004–onwards; Wheeler, 2011). Moreover, each vessel was counted separately, both for density and vessel grouping percentage, as proposed by Wheeler (1986).

The following abbreviations were used throughout the manuscript: Bulgarian Academy of Sciences (BAS), National and Kapodistrian University of Athens (NKUA).

## 4 | RESULTS

### 4.1 | Systematics

Fagaceae Dumortier

*Castanopsis* (D. Don) Spach

*Castanopsis bulgarica* Mantzouka, Ivanov, and Bozukov sp. nov.

*Holotype*: Designated here.

*Material*: BAS-BGQ1 (Repository: 'Geography Ecology and Natural Preservation Department' in South-West University 'Neofit Rilski' Blagoevgrad, Bulgaria), three slides (Repository: Institute of Biodiversity and Ecosystem Research, Bulgarian Academy of Sciences).

*Plant Fossil Names Registry Number*: PFN000968 (for new species).

*Etymology*: The epithet, bulgarica, is related to the origin of the described material (south-west Bulgaria).

*Locality*: Blagoevgrad Graben (south-west Bulgaria).

*Stratigraphic type horizon*: Pokrovnik Formation.

*Age*: Late Messinian–Early Zanclean (Late Pontian–Early Dacian).

#### 4.1.1 | Diagnosis

Heteroxylous wood, growth rings present, diffuse to semi-ring porosity, numerous vessels per sq. mm; vessels medium to large, characteristically arranged in 2–3 regularly interrupted tangential rows and in dendritic pattern (flame-like), exclusively solitary, circular to oval in outline in early wood and more angular in late-wood, tyloses present; exclusively simple perforation plates; opposite to alternate intervessel pits; fibres: present; vasicentric tracheids present; paratracheal axial parenchyma, scanty, vasicentric; apotracheal axial parenchyma diffuse in aggregates; heterocellular rays of two distinct sizes: (a) narrow (uni-, bi- and triseriate) and (b) multiseriate compound and aggregate rays present; no crystals present.



**TABLE 2** Messinian–Zanclean evergreen oak leaf species from nearby Bulgarian localities with their nearest living relatives and their synonyms (Bozukov et al., 2011; Bozukov & Tsenov, 2012; Kitanov, 1984; Palamarev & Kitanov, 1988; Palamarev & Petkova, 1987; Stefanoff & Jordanoff, 1934; Stojanoff & Stefanoff, 1929)

Bulgarian evergreen fagaceous fossil species (leaves) of the same age of our fossil wood	Nearest living relatives
<i>Cyclobalanopsis stojanovii</i> Palam. and Kitan. fil.	<i>Cyclobalanopsis glaucoides</i> Schottky [syn. <i>Quercus schottkyana</i> Rehder and E. H. Wilson or <i>Quercus glauca</i> Thunb., or <i>Quercus glaucoides</i> (Schottky) Koidz., or <i>Quercus glauca</i> subsp. <i>schottkyana</i> (Rehder and E. H. Wilson) Menitsky]
<i>Pasaniopsis</i> sp. 2	<i>Castanopsis cuspidata</i> (Thunb.) Schottky
<i>Pasaniopsis</i> sp. 3	<i>Lithocarpus glaber</i> (Thunb.) Nakai
<i>Quercus</i> aff. <i>acrodonta</i> Seem.	<i>Q. ilex</i> L. var. <i>acrodonta</i> (Seemen) Skan (synonym of <i>Quercus acrodonta</i> Seemen)
<i>Q. coccifera</i> L. foss.	<i>Q. coccifera</i> L.
<i>Q. glaucifolia</i> Andr.	<i>Q. glauca</i> Thunb.
<i>Q. ilex</i> L. foss.	<i>Q. ilex</i> L.
<i>Q. mediterranea</i> Unger	<i>Q. ilex</i> L., <i>Q. coccifera</i> L.

## 4.2 | Description

### 4.2.1 | Macroscopic description

Due to the relative curvature of the growth rings, the specimen is considered a piece of a rather small stem 38 cm in length and 7 cm in diameter. It is of whitish colour (Figure 4k).

### 4.2.2 | Microscopic description

Growth rings: distinct (Figure 4a). (a) Wood: Diffuse-porous to semi-ring porous (gradual porosity) (Figure 4a). (b) Vessels: exclusively solitary with more than 90% solitary vessels/sq. mm (Figure 4a), 10–20 vessels/sq. mm in early wood (mean 15) and 15–30 vessels/sq. mm in latewood (mean 22); tangential diameter 50–130 µm, mean: 80 µm; radial diameter of the solitary vessels 50–150 µm, mean: 100 µm (early wood); tangential diameter 10–40 µm, mean: 20 µm; radial diameter of the solitary vessels 30–50 µm, mean: 40 µm (latewood); outline of solitary vessels round to oval (Figure 4a); vessels' arrangement: in dendritic pattern (flame-like) in 2–3 seriate rows (Figure 4a); perforation plates exclusively simple; tyloses common (Figure 4b); intervessel pits opposite to alternate, minute to small about 2.5–6 µm across (Figure 4f). (c) Rays: of two distinct sizes (i) uni/bi/triseriate (Figure 4c–e) and (ii) multiseriate: aggregate, compound (Figure 4g,h)

up to 10 seriate/180 µm wide (Figure 4g,h) and in some cases more than 1.2 mm high (Figure 4g,h). Uni/biseriate ray cells' size (in tangential section): tangential diameter: 15–25 µm, radial diameter: 15–35 µm. Multiseriate ray cells' size (in tangential section): tangential diameter: 7–20 µm, radial diameter: 7–40 µm. Rays heterocellular, body of multiseriate rays composed of procumbent with mostly 2–4 rows of upright and square marginal cells (Figure 4i,j); no crystals observed. (d) Vessel-ray pits similar to intervessel pits (Figure 4i,j). (e) Axial parenchyma: apotracheal diffuse in aggregates (Figure 4a), vasicentric, scanty paratracheal (Figure 4b). (f) Fibres: vasicentric tracheids present with simple to minutely/distinctly bordered pits of 2.5–5 µm diameter (Figure 4c,e,h–j).

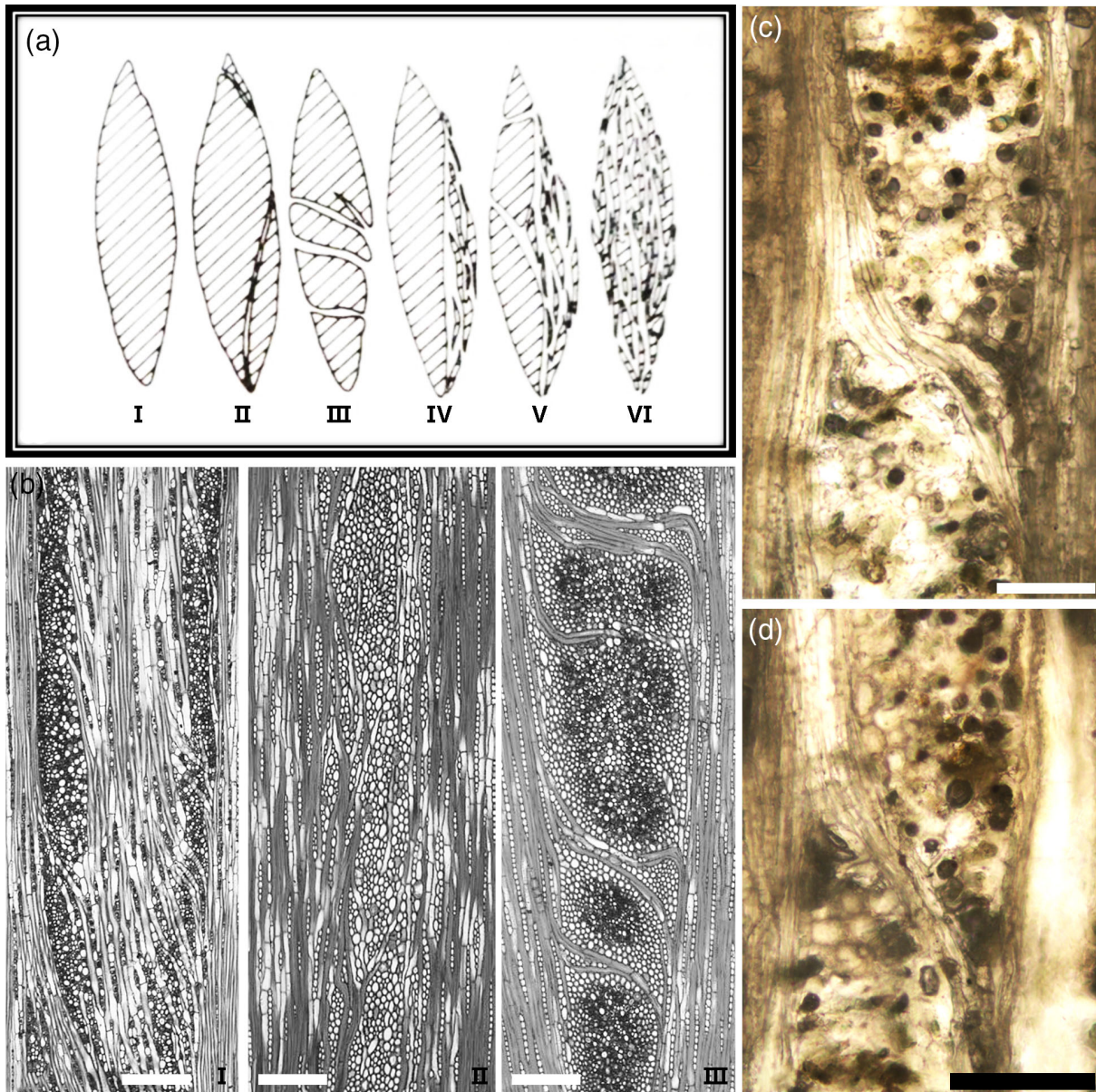
## 5 | DISCUSSION

### 5.1 | Comparison with other fossil fagaceous wood

The gradual (semi-ring/diffuse) porosity of the vessels and the existence of two types of rays (uniseriate and multiseriate aggregate), along with the oval shape of the solitary vessels outline, suggest that the sample belongs to an evergreen oak tree.

Suzuki and Ohba (1991), following the work of Shimaji (1962), have noticed that the term 'evergreen oaks' includes the evergreen species of '*Quercus*' (represented by subgenus *Cerris*: sections *Cyclobalanopsis* and *Ilex* and some species of subgenus *Quercus*: section *Lobatae* sensu Denk, Grimm, Manos, Deng, & Hipp, 2017), *Lithocarpus* and the tropical species of *Castanopsis*. According to our research on the wood anatomical characteristics of Fagaceae, presented in the key on the xylotomical identification of modern Fagaceae (Section 5.3) the previously mentioned 'evergreen oaks' share similar xylotomical characteristics with *Notholithocarpus* Manos, Cannon, and Oh, *Trigonobalanus* Forman and possibly with *Quercus* subgenus *Quercus* sections *Protobalanus* and *Virentes*. Unfortunately, the wood anatomical descriptions of the latter are scarce and they are not found in the fossil wood record yet. In conclusion, the fossil 'evergreen oaks' are represented by various species of *Quercoxylon* (I), *Lithocarpoxyton* (II), and *Castanopsis* (III).

(I) Müller-Stoll and Mädler (1957) provided an emended diagnosis of the genus based on the work by Kräusel (1939) and also on the revisions and reidentifications they made in selected Unger's and Felix's material, including ring (e.g. *Q. densum*, *Q. staubii*, *Q. böckhianum*), diffuse-porous wood (*Q. helictoxyloides*), and root specimens (*Q. viticulosum*), as follows: "ring or diffuse porous secondary wood, with distinct or indistinct growth rings, always single vessels, simple perforation, large alternate intervessel pits, pits enlarged to the parenchyma and medullary ray cells, irregularly oval to polygonal, mostly upright, cross-field pits enlarged, wood matrix made from libriform fibers, tracheids around the vessels, parenchyma in an alternating arrangement, mostly scattered and in short, uniseriate tangential bands, medullary rays of two sizes: single-row in addition to very wide and high, in the latter sometimes inclined to form false medullary rays". This diagnosis does not inform us about the cellular composition of the rays (homocellular



**FIGURE 5** (a) Types of multiseriate rays in Quercineae in tangential section (after Petrescu, 1976): I, Compact; II, Compact-Compound; III, Compound; IV, Compact-Aggregate; V, Compound-Aggregate; VI, Aggregate rays. (b) Types of different 'splitting' of broad rays (from Noshiro & Sasaki, 2011): I, *Lithocarpus* semi-compound ray (vertical split); II, *Quercus* subg. *Sclerophyllodrys*, aggregate to semi-compound rays (vertical to oblique split); III, *Q.* subg. *Cyclobalanopsis*, large aggregate to compound rays (oblique split). I, II, and III represent tangential sections (TLS), scale bar: 200  $\mu\text{m}$ . (c) *Castanopsis bulgarica* Mantzouka, Ivanov, and Bozukov sp. nov. (BAS-BGQ1b) broad ray (oblique split), tangential section (TLS), scale bar: 100  $\mu\text{m}$ . (d) *Castanopsis bulgarica* Mantzouka, Ivanov, and Bozukov sp. nov. (BAS-BGQ1b) broad ray (vertical to oblique split), tangential section (TLS), scale bar: 50  $\mu\text{m}$ . Following the classification by Denk et al. (2017) *Q.* subg. *Sclerophyllodrys* is replaced by subgenus *Quercus*, sections *Protobalanus* and *Lobatae* and *Q.* subg. *Cyclobalanopsis* is replaced by subgenus *Cerris* section *Cyclobalanopsis* [Colour figure can be viewed at [wileyonlinelibrary.com](http://wileyonlinelibrary.com)]

or heterocellular sensu Kribs, 1935 or sensu Wheeler et al., 1989) and make us think that it follows the cellular composition of the modern analogues discussed in the same paper (Müller-Stoll & Mädler, 1957, p. 123, "*Quercus* species are homocellular, some *Lithocarpus* species are weakly heterocellular and *Castanopsis* species are heterocellular"), and also in Metcalfe and Chalk [Metcalfe & Chalk, 1965: "...homocellular (Kribs's Types I and III), except in *Nothofagus* and some species of *Castanopsis* and *Lithocarpus*, in which there are commonly 1 to 2

marginal rows of square cells"]. Since the rays are of diagnostic value for this genus, the cellular composition of the rays is regarded by the authors of the present article as a key factor for the identification of the samples and perhaps also for the evolutionary traits of the fagaceous genera.

Gros (1981) had revised *Quercoxylon* by replacing the term 'intervessel pits large' with 'intervessel pits of variable dimensions, mostly small and medium'.



Selmeier (1992b) had described *Quercoxylon* types from Southern Germany grouping them in three categories according to their porosity: (a) evergreen (diffuse-porous woods) of Late Pliocene age, (b) white oaks (ring porous) of Late Miocene age, and (c) red oaks (semi-ring porous). What is interesting is that Selmeier noticed that the extant fagaceous evergreen representatives have homocellular (and only weak heterocellular) rays, while the white oaks have heterocellular rays and the red oaks only homocellular rays.

Our fossil could be identified as an evergreen *Quercus* type but according to Selmeier (1992b) it should have homocellular rays. On the contrary, our fossil has heterocellular rays.

Selmeier (1997) also noticed that a characteristic of *Lithocarpus* is that the broad rays of this wood are clearly heterocellular compared to *Quercus* species, as also mentioned in Gros (1981, 1983). Noshiro and Sasaki (2011) have found that subgenus *Cerris*, section *Cyclobalanopsis* sensu Denk et al. (2017) (former: *Quercus* subg. *Cyclobalanopsis*) has species with semi-compound rays divided by oblique files of fibres, as in our fossil wood.

(II) Petrescu (1978) described *Lithocarpoxyton* as a genus with “growth rings distinct or scarcely distinct. Radial or diffuse porous wood. Vessels exclusively solitary, oval to circular with tyloses. Transition from early to late wood gradually or indistinct. Perforation plates exclusively simple. Vasicentric tracheid and parenchyma present. Fibres abundant. Two types of rays: a) narrow rays (1-seriate), very numerous, homocellular, and b) broad rays, heterocellular, aggregate; crystal present”. Petrescu (1978) included the cellular composition of the rays in his description, stating also that this is the big difference between *Quercoxylon* and *Lithocarpoxyton*: the existence of heterocellular (exclusively) aggregate rays in the second one. The similarity of the anatomical characteristics between *Lithocarpus* and *Q.* section *Cyclobalanopsis* (subgenus *Cerris*, section *Cyclobalanopsis*: Denk et al., 2017) was discussed in several papers (e.g. Selmeier, 1986, 1992b, 1997). Noshiro and Sasaki (2011) have found a characteristic of a probable phylogenetic base occurring only in *Lithocarpus* species (‘to the major clade of subgenus *Pasania*’): the vertical splitting of compound rays (or the ‘very steep angle of the inserted axial elements’ sensu Shimaji, 1962) into nearly equal halves. In the same paper they stated that *Quercus* subg. *Cyclobalanopsis* (subgenus *Cerris*, section *Cyclobalanopsis* sensu Denk et al., 2017) has species with semi-compound rays divided by oblique files of fibres.

(III) Evergreen oak findings from India led Navale (1962) to create the genus *Castanoxyton* with anatomical details of *Castanea*, *Castanopsis*, *Lithocarpus*, and *Quercus*. Navale’s work (1962) follows the anatomical key of Fagaceae proposed by Müller-Stoll and Mädler (1957) and therefore the tropical *Castanopsis* species sensu Suzuki and Ohba (1991) with aggregate rays are not included. Moreover, *Castanoxyton* (Navale, 1962) was published before the work by Petrescu (1978) so, the genus *Lithocarpoxyton* was not created yet. This fossil genus described by Navale (1962) as *Castanoxyton* includes fossil Fagaceae members of ring and diffuse porosity with 1–2-seriate rays (but without aggregate rays) and therefore cannot be used in our case.

Recently, Huang, Jin, Quan, and Oskolski (2018) have used the genus *Castanopsis* (D. Don) Spach to describe two upper Oligocene fossil species of *Castanopsis* with distinct anatomical characteristics from south China: *Castanopsis nanningensis* Huang, Jin, Quan et Oskolski and *C. guangxiensis* Huang, Jin, Quan et Oskolski. *C. nanningensis* is a ring porous wood with uniseriate–partly biseriate homocellular rays and occasionally (no broad) rays with aggregate parts composed of closely associated uni- and biseriate rays and with crystals in chambered axial parenchyma. *C. guangxiensis* is a diffuse-porous wood with uniseriate–partly biseriate homocellular and (no broad) aggregate rays and with crystals in chambered axial parenchyma.

Regarding the extant *Castanopsis* wood, according to Shimaji (1959, 1962), it can be separated in two groups based on anatomical characteristics as follows: A types with ring to radial-porous wood (or ring to semi-ring sensu Wheeler et al., 1989) and (A1) two types of rays: broad (compound and aggregate broad aggregate rays) and narrow rays or (A2) with only narrow rays, and B types with radial-porous wood and (B1) narrow (uni/biseriate rays) and of broad aggregate rays or (B2) of only narrow (uni/biseriate rays) sensu Shimaji (1962) combined with the results of Phromprasit, Vajrodya, and Kermanee (2016). Moreover “*Lithocarpus* has exclusively uni-seriate and broad rays while *Castanopsis* has exclusively fine rays (uni-biseriate) and broad rays” (Rao, Sharma, Dayal, & Raturi, 1991; Shimaji, 1962) and “rhombohedral crystals are absent in the broad rays of *Castanopsis* and present in *Lithocarpus* and *Q. semiserrata*” (Rao et al., 1991).

We think that *Castanopsis zonatum* (Selmeier) Suzuki and Terada represents the *Castanopsis* A2 group sensu Shimaji (1962) with ring porous wood and uniseriate rays with a tendency to be heterocellular. *Castanopsis uchiuraensis* Suzuki and Terada (1996) from the Early Miocene of Yanagida Formation (Japan) should belong to the same category. On the other hand, the diffuse-porous woods with uniseriate rays of *Castanoxyton indicum* Navale (Navale, 1962), *C. tertiarum* Navale (Navale, 1962), and *C. eschweileri* Burgh (van der Burgh, 1973) may represent the *Castanopsis* B2 group sensu Shimaji (1962).

Although Metcalfe and Chalk (1965) treated *Castanopsis* as a mostly ring porous genus with uni- up to biseriate heterocellular rays, several authors over the last 60 years (e.g. Hwang, 1962; Lee, 1968; Pande, Chauhan, & Singh, 2005; Phromprasit et al., 2016; Rao et al., 1991; Shimaji, 1959, 1962) have noticed the significance also of the *Castanopsis* semi-ring/diffuse-porous species with two kinds of rays: fine and broad (compound and/or aggregate) rays and (in some species also the occurrence of) crystals in axial parenchyma [e.g. *C. hystrix* A.DC., *C. lanceifolia* (Oerst.) Hickel and A. Camus, *C. longicaudata* (Hayata) Nakai, *C. acuminatissima* (Blume) A.DC., *C. armata* (Roxb.) Spach., *C. echidnocarpa* (Hook.f. and Thomson ex A. DC.) A.DC., *C. indica* (Roxb.) A.DC., *C. stipitata* (Hayata ex Koidz.) Nakai, *C. tribuloides* (Sm.) A.DC., *C. sieboldii* (Makino) Hatus].

Taking into account the work by Müller-Stoll and Mädler (1957) we compared our fossil with several *Quercoxylon* species and found out that the Blagoevgrad fossil is different from *Q. densum* Müller-Stoll and Mädler, *Q. staubii* (Felix) Müller-Stoll and Mädler and *Q.*

*böckhiannum* (Felix) Müller-Stoll and Mädél since it is diffuse up to semi-ring porous and not ring porous as the above mentioned species. It differs from *Q. viticulosum* (Unger) Müller-Stoll and Mädél in the dimensions of the vessels and other characteristics and it is close to *Quercoxylon helictoxyloides* (Felix) Müller-Stoll and Mädél from the Pontian (Late Miocene) of Austria ('*Quercus* root wood' according to Suzuki & Ohba, 1991), which unfortunately is not described in detail (e.g. rays' cellular composition, occurrence of tracheids, crystals).

Our fossil was also compared with the fossil oak woods from the Massif Central of France identified by Privé (1975), namely: *Quercoxylon bavaricum* Selmeier, *Q. angustannulatum* Privé, *Q. pelletieri* Privé, *Q. courpierense* Privé. From the above mentioned fossils only the last one is an evergreen oak wood which has great differences (e.g. the kind of the broad rays and of the vessel-ray pits) from ours.

Among the Greek species of *Quercoxylon* and *Lithocarpoxyylon* (Petrescu & Velitzelos, 1981; Suzuki & Ohba, 1991) our specimen seems to be close to *Quercoxylon praehelictoxyloides* Petrescu [= *Lithocarpoxyylon praehelictoxyloides* (Petrescu) Suzuki and Ohba] and *Q. intermedium* but not identical because of the small width of its multi-seriate rays. *Quercoxylon praehelictoxyloides* Petrescu [= *Lithocarpoxyylon praehelictoxyloides* (Petrescu) Suzuki and Ohba], *Lithocarpoxyylon justiniani*, along with *L. mixtum* were found in north-western Transylvania and *Q. intermedium* was identified from the fossil forest of Thrace, northeastern Greece. Our fossil differs also from the three fossil 'evergreen' oaks from Japan (*Lithocarpoxyylon hobashiraishi*, *L. radiporosum*, *L. simarense*) described by Suzuki and Ohba (1991) as having distinct growth ring boundaries, semi-ring to diffuse porosity, and no crystalliferous content observed.

Our fossil has been compared also with *Q. intermedium* which was identified recently (Iamandei, Iamandei, Bozukov, & Tsenov, 2012) from the Oligocene of the Nanovitsa Depression (Rhodopes, Bulgaria), but the Blagoevgrad wood has multiseriate rays of up to 180 µm width and no crystalliferous content. It has been also compared to *Quercoxylon* sp. cf. *Quercus frainetto* Ten. as described in Iamandei, Iamandei, and Diaconu (2011) but it differs from it because the latter is a ring porous wood.

*Quercoxylon marbasianum* Hadžiev and Mädél from East Maritsa Basin-Troyanovo West (Maritsa Formation, lower Pontian-upper Dacian) and *Q. stojanovii* Hadžiev and Mädél from Sofia Basin-Kutina (Gnilyane Formation, lower Pontian) are quite different from our fossil, as well. *Q. marbasianum* has very high (2–5.3 mm) and wide (1–3 mm) multiseriate rays as also *Q. stojanovii* (1.5–4.7 mm height and 1–1.4 mm width). Both of them have crystalliferous parenchyma.

#### *Special characteristics of our specimen*

Great emphasis must be given at specific characteristics defining our specimen: (a) the porosity (diffuse to semi-ring, or 'radial' sensu Shimaji, 1962), (b) the vessels' dimensions (medium and not large), frequency and arrangement in 2–3 rows and in non-continuous vessel zone, (c) the existence of two kinds of rays (uni-bi-triseriate and broad), (d) the type of the broad rays (compound and aggregate mostly divided in oblique), (e) the cellular composition of the broad rays

(strongly heterocellular), and (f) the absence of crystals. These points are discussed below:

(a–b) The definition of porosity is an important issue which could be related to phylogenetic trends (Shimaji, 1959) or even to the climatic conditions, vegetation type (concerning the connection between evergreen or deciduous trees and ring, semi-ring or diffuse-porous wood), and plant hydraulics of the species and still requires more research (e.g. Boura & De Franceschi, 2007). According to Wheeler et al. (1989) three main types of angiosperm wood porosity are recognized: (1) ring, (2) semi-ring, and (3) diffuse porosity. Semi-ring porosity is an intergrading pattern occurring between ring and diffuse porosity reflecting an intermediate condition (Esau in Evert 2006). The term 'radial' in Shimaji's work (1954b, 1959, 1962) is related to the porosity—equal to the semi-ring porosity—and not to vessel arrangement. Shimaji (1962) examined fagaceous vessels' porosity phylogenetically and found evolutionary trends from diffuse to radial (or semi-ring) to ring porosity. He found also another intermediate condition between radial and ring porosity when examining the temperate *Castanopsis* species: the radial-ring porosity (Shimaji, 1959, 1962). The radial/semi-ring to diffuse porosity which is described in our wood has been noticed by Shimaji (1962) who observed this type of porosity for the adult wood of temperate *Castanopsis* species and found that it occurs also in the root wood of specific *Quercus* species (e.g. *Q. crispula*).

According to Müller-Stoll and Mädél (1957) the evergreen representatives of *Quercus* and *Lithocarpus* have a vessel diameter (VD) of 100–200 µm. The smaller vessel size of our sample in correlation with the high numbers of vessels per sq. mm, along with the fact that many narrow growth rings of close distance occur, are either typical of some palaeoenvironments or extreme hydrological changes in the soil (e.g. 'flooded woods' or 'exposure of a large part of the root system' sensu Schweingruber, 2007, pp. 93–100).

Sharma, Sharma, Carter, and Kharkongor (2011) have investigated the inter-species wood variation of some *Castanopsis* species of Meghalaya (India) showing that specific anatomical characteristics such as the vessel and fibre length and diameter show significant differences among the *Castanopsis* species.

On the other hand, Selmeier (1970a, 1972, 1992a) had found fossil *Castanopsis* wood sensu Navale (1962) with homocellular, uniseriate rays from the Tortonian of Bavaria (Southern Germany). The NLR of those *Castanopsis* woods is *Castanopsis chrysophylla* (Dougl.) A.Dc. from North America (Selmeier, 1992a) which now belongs to *Chrysolepis* Hielmquist. The fossil *Castanopsis* woods from Southern Germany are of similar age as our wood and could be attributed to *Castanopsis* A2 group sensu Shimaji (1962), with ring porosity and only uniseriate rays (or to *Chrysolepis*). What has to be mentioned is also the fact that the numbers of the latewood vessels (concerning their dimensions and quantity) are similar to ours.

Another point that should be mentioned is the existence of 2–3 interrupted tangential (=non continuous) rows of vessels in our specimen as described in Shimaji (1962). Moreover, the latewood vessels are mostly angular (and thin-walled) in our wood. The latter



characteristics are found in *Castanopsis* A group species according to Shimaji (1962, p. 9).

The importance of the continuity of the vessels zones was also reported by Suzuki and Terada (1996) who renamed several *Castanoxylon* species proposing new combinations of *Castanea* or *Castanopsis*, based on the occurrence of the previously mentioned characteristics.

(c–d) The occurrence of aggregate broad rays is another characteristic of Fagaceae. Carlquist (2001) reports that the fagaceous species “differ in the degree to which aggregate rays become converted into homocellular masses lacking intercalated libriform fibers”. Concerning the evergreen fagaceous wood findings with two kinds of rays, narrow, and broad rays, our research in literature revealed that they include the following genera: *Notholithocarpus* Manos, Cannon, and Oh, *Quercus* L. subgenus *Cerris* section *Ilex* and section *Cyclobalanopsis*, *Lithocarpus* Bl., *Trigonobalanus* Forman, the tropical species of *Castanopsis* Spach, and possibly also *Quercus* L. subgenus *Quercus* section *Protobalanus* and section *Virentes* (presented in the key on the xylotomical identification of modern Fagaceae, Section 5.3). Rao et al. (1991) described the existence of uni-, bi-, triseriate and broad rays in *Castanopsis* species while only uniseriate and broad rays are observed in *Lithocarpus* and *Trigonobalanus*. Moreover, in the tangential section one can observe the occurrence of ‘orderly in oblique line’ imperforate tracheary elements once to three times each in each multiseriate ray. This ‘separation’ of the aggregate rays is discussed in Carlquist (2001) but the ‘oblique splitting’ follows the observations by Noshiro and Sasaki (2011) and is further discussed in Section 5.4.

(e–f) The degree of heterogeneity in rays reveals a crucial characteristic of the differentiation of genera and species but also is related to evolution (Kribs, 1935). On the other hand, two kinds of rays with homocellular to slightly heterocellular rays were observed in *Lithocarpus* species and heterocellular rays were observed in *Castanopsis* species (Shimaji, 1962). Selmeier (1997) had noticed also that the rays of *Lithocarpus* are heterocellular, in difference to many *Quercus* species.

## 5.2 | Comparison with other fossil fagaceous findings from Bulgaria

Fagaceous leaf imprints and macroremains of the same age as our sample (Late Miocene–Early Pliocene: ~6–4.5 Ma) have been reported from several localities in Bulgaria (Bozukov & Tsenov, 2012; Palamarev, Bozukov, Uzunova, Petkova, & Kitanov, 2005). The Bulgarian Fagaceous macroremains of Messinian–Zanclean age are shown in Table 1.

The only fagaceous finding from Blagoevgrad Graben is *Quercus cardanii* Massalongo, the NRLs of which are the deciduous species *Q. hartwissiana* Stev. (Bulgarian endemic species), *Q. macranthera* F. et M. (Caucasian oak, or the Persian oak), and the deciduous to semi-evergreen *Q. canariensis* Willd. (native to southern Portugal, Spain, Tunisia, Algeria, and Morocco). Our wood sample represents an evergreen oak wood. If a future research on plant remnants of this area does not

reveal other evergreen oak remains then one should apply the ‘Whole Plant Concept’ correlating our wood with the evergreen oak leaves of the same age from nearby Bulgarian locations: *Cyclobalanopsis stojanovii* Palam. and Kitan. fil., *Pasaniopsis* sp. 2, *Pasaniopsis* sp. 3, *Quercus* aff. *acrodonta* Seem., *Q. coccifera* L. foss., *Q. glaucifolia* Andr., *Q. ilex* L. foss., *Q. mediterranea* Unger (Table 2).

The above-mentioned species belong to the hygromesophyte–mesophyte lineage of oaks representing remnants of the subtropical evergreen communities of the past (Palamarev & Ivanov, 2003).

Applying the ‘Whole Plant Concept’ sensu Sakala (2004) we correlate the NRLs of the evergreen oak leaves of the same age (Messinian–Zanclean) from the Bulgarian fossiliferous sites (presented in Table 2) with their wood anatomical characteristics in order to find a possible relation with our fossil wood. Synonyms from The Plant List (2013) were also taken into account. The results are shown below:

*Cyclobalanopsis stojanovii* Palam. and Kitan. fil. has as its NLR *Cyclobalanopsis glaucooides* Schottky which is a diffuse-porous wood (Robert, Mencuccini, & Martínez-Vilalta, 2017), with compound rays (Noshiro & Sasaki, 2011), two types of tracheids (vasicentric and terminal) (Shimaji, 1962) and crystals in axial parenchyma and in broad rays (Shimaji, 1954b). The occurrence of crystals and the fact that its rays are homocellular (Shimaji, 1962) are the differences from our wood.

*Pasaniopsis* sp. 2 has as its NLR *Castanopsis cuspidata* (Thunb.) Schottky. This species belongs to *Castanopsis* A Group sensu Shimaji (1962) and has been described as a ring porous wood with a tendency to radial porosity, with vasicentric tracheids and two kinds of rays (broad compound-aggregate and narrow), the broad ones being heterocellular. Takahashi and Takahashi (2016) have recently described it as a diffuse-porous (evergreen) wood. This wood is closer to our fossil sample.

*Pasaniopsis* sp. 3 has as its NLR *Lithocarpus glaber* (Thunb.) Nakai which is a diffuse-porous wood with semi-compound rays which are splitted vertically, banded axial parenchyma, and uniseriate rays in outer growth rings (Noshiro & Sasaki, 2011). As is discussed in Noshiro and Sasaki (2011), this kind of vertical splitting characterizes the broad rays of *Lithocarpus*. This characteristic is not in accordance with observations made from our specimen.

*Quercus* aff. *acrodonta* Seem. has *Q. ilex* L. var. *acrodonta* (Seemen) Skan as NLR. According to Lee (1968) this species is synonymous to *Quercus phillyraeoides* A. Gray which is a diffuse-porous wood with two kinds of rays, the broad rays of which are homocellular, a characteristic which differs from our wood.

*Q. coccifera* L. foss. has as its NLR *Q. coccifera* L. This species has palisade vessel-ray pits, (Crivellaro & Schweingruber, 2015) and, according to Shimaji (1962), has the same wood anatomical features as *Q. ilex*, for example, homocellular rays, and therefore is not similar to our wood.

*Q. glaucifolia* Andr. has as its NLR *Q. glauca* Thunb. which is a diffuse-porous wood, with small-medium vessels (TVD: 53–117 μm) (Noshiro & Sasaki, 2011) and homocellular rays (Shimaji, 1962). The cellular composition of its rays is not in accordance with our specimen.

*Q. ilex* L. foss. has as its NLR *Q. ilex* L. This species is a semi-ring to diffuse-porous wood (Schweingruber, 1990). The main differences from our wood are the occurrence of prismatic crystals in ray cells (Crivellaro & Schweingruber, 2013) and of homocellular rays (Crivellaro & Schweingruber, 2013; Shimaji, 1962).

*Q. mediterranea* Unger has as its NLR *Q. ilex* L. and *Q. coccifera* L., both of which have been analysed above.

As shown above, our fossil wood is closer to *Pasaniopsis* sp. 2 and its NLR *Castanopsis cuspidata* (Thunb.) Schottky. This species was earlier regarded as a ring porous wood with tendency to radial porosity (Shimaji, 1962), but recent studies have shown that it is a semi-ring/diffuse (evergreen) porous wood (Takahashi & Takahashi, 2016).

### 5.3 | *Castanopsis* and xylotomical keys

In several works there are comparisons between the fossil evergreen *Quercoxylon* and/or *Lithocarpoxyton* species with *Quercus ilex* – subgenus *Lepidobalanus* (e.g. Akkemik, Akkılıç, & Güngör, 2019; Mädél-Angeliewa, 1968; Privé-Gill, Cao, & Legrand, 2007) or subgenus *Quercus* section *Quercus* sensu Denk et al. (2017). These comparisons are mainly based on the oaks' categorization in three types according to their wood anatomical characteristics, based on the work by Müller-Stoll and Mädél (1957) and followed by Hadziev and Mädél (1962), Privé (1975), Gros (1983, 1988), and Selmeier (1986, 1992b):

1. 'White oak-type': with ring porous, closely spaced latewood vessels with thin walls, usually angular in cross-section, numerous between two rays, with abrupt transition from early to latewood (logs of the mostly deciduous species of subgenus *Quercus* section *Quercus* sensu Denk et al., 2017; former *Lepidobalanus* and *Macrobalanus* sections of the genus *Quercus*),
2. 'Red oak type': with ring porous, latewood vessels relatively large, rounded, and thick-walled (woods from the deciduous subgenus *Quercus* section *Lobatae* and some species of subgenus *Quercus* section *Quercus* sensu Denk et al., 2017; former sections of *Erythrobalanus* and *Lepidobalanus*, respectively),
3. 'Evergreen oaks' of the genera *Quercus* and *Lithocarpus*, species of 'sempervirent type' with diffuse or semi-ring porous, scanty, and relatively closely spaced vessels with radial pattern (radially oriented) with tendency to form aggregate rays (false rays). A similar character can be seen in root wood with diffuse porosity, numerous large vessels, indistinct growth rings and tendency to form false rays (aggregate rays).

Taking into account the fact that modern *Castanopsis* is a genus which includes also diffuse-porous/semi-ring porous species of two kinds of rays [narrow (1–2–3seriate) and broad heterocellular rays] we think that also the 'tropical' *Castanopsis* species should belong to the previously mentioned '3—evergreen oaks' category.

The fossil fagaceous wood anatomical studies of the previous years (e.g. Greguss, 1969; Gros, 1981, 1983, 1988;

Petrescu, 1976; Petrescu, Velitzelos, & Stavropodis, 1980; Privé, 1975; Selmeier, 1970a,b,c, 1972, 1986, 1992a,b, 1997) were based on the work by Müller-Stoll and Mädél (1957), which did not include the work by Shimaji (1954b, 1959, 1962) about *Castanopsis* with two kinds of rays. Therefore, we suppose, that numerous specimens already described as *Quercoxylon* or *Lithocarpoxyton* could belong to *Castanopsis* type A1 or B1 sensu Shimaji (1959) and that several *Castanoxyton* species sensu Navale (1962) represent *Castanea* fossil species or *Castanopsis* A2 or B2 species sensu Shimaji (1959). The occurrence of extant *Castanopsis* species with two kinds of rays (fine narrow and broad) should be finally investigated in the fossil record. Therefore, the authors of the present article have also surveyed several reports concerning anatomical details of identification such as the difference in the splitting of broad rays and the cellular composition of the rays along with the decrease in vessel diameter and increase of the number of vessels.

In the present article, the key on the xylotomical identification of modern Fagaceae by Müller-Stoll and Mädél (1957) has been revised, excluding genera which do not belong in this family anymore (e.g. *Nothofagus*; for further information see: Patel, 1986 and Poole, 2002), following the most recently accepted classification of oaks (Denk et al., 2017), including also the work of Carlquist (2001), other literature resources (Carlquist and Hoekman (1985); Cutler (1964); Forman (1964); Forman and Cutler (1967); Gupta and Gupta (2020); Kubitzki, Rohwer, and Bittrich (1993); Lee (1968); Lemmens, Soerianegara, and Wong (1995); Pearson and Brown (1932); Serdar and Mazlum (2014); Sharma et al. (2011); Sharma, Sharma, Kharkongor, and Carter (2011); Sharma, Shylla, and Sharma (2017); Shimaji (1952, 1954a,b, 1959, 1962); Sudworth and Mell (1911); Manos, Cannon, and Oh (2008); Melville (1982); Mennega (1980); Metcalfe and Chalk (1965); Nixon (2007); Pande et al. (2005); Phromprasit et al. (2016); Tillson and Muller (1942), observations from atlases (e.g. Akkemik & Yaman, 2012; Grosser, 1977; Ilic, 1991; Ilvessalo-Pfäffli, 1995; Ruffinatto & Crivellaro, 2019; Schweingruber, 1990) and InsideWood Web site (InsideWood, 2004–onwards), and corrections regarding the validity of the species (concluding to their position in the new classification) from The Plant List (2013):

(1)Wood ring porous (in species of the temperate zone), vessels moderately large to very large (100–200 µm), always solitary (rarely sporadically forming groups), vessel pits alternate, cross-fields with enlarged, vertical pits, perforations plates simple, *vasicentric tracheids present*, wood fibres with or without distinctly bordered pits.....2i, 2ii

(2i)Rays only uniseriate (rarely biseriate) .....3

(3)Vessels partially forming radial multiples, latewood vessels thin-walled and angular, homocellular rays.....*Castanea* Mill.

(3')Latewood vessels thin-walled and angular, perforation plates simple and in some species also scalariform rays partially heterocellular, with square edge cells .....*Castanopsis* Spach. temperate species and *Chrysolepis Hjelmski*



(2ii) Rays of two sizes, uniseriate and multiseriate.....  
.....4

(4) only homocellular rays and latewood vessels thick-walled and rounded (rarely with tyloses).....4i, 4ii

(4i) with compound broad rays .....*Quercus* L. subgenus *Cerris* section *Cerris*

(4ii) with few, large latewood vessels, transition from early to late-wood gradual, height of broad rays rarely >3.8 cm ..... *Q.* subgenus *Quercus* section *Lobatae* (red oaks)

(4') only homocellular compound rays and latewood vessels small, numerous thin-walled and angular (usually with tyloses), transition from early to latewood abrupt, height of broad rays commonly >3.8 cm .....*Q.* subgenus *Quercus* section *Quercus* (white oaks)

(1') Wood semi-ring/diffuse-porous, vessels moderately large to very large (100–200 µm), always solitary (rarely sporadically forming groups), vessel pits alternate, cross-fields with enlarged, vertical pits, perforations plates simple, rays of two sizes: uniseriate and multiseriate, vasicentric tracheids present, wood fibres with or without distinctly bordered pits .....5a, 5b, 5c

(5a) Latewood vessels thick-walled and rounded, rays of two sizes, uniseriate and multiseriate (the latter in some species tending to form false pith rays), only homocellular rays.....  
.....5a.i, 5a.ii

(5a.i) with vessels uniformly distributed throughout the annual layers of growth .....*Notholithocarpus* Manos, Cannon, and Oh

(5a.ii) with aggregate rays or semi-compound rays  
.....

.....*Q.* subgenus *Cerris* section *Ilex* and *Q.* subgenus *Cerris* section *Cyclobalanopsis*

(5b) Latewood vessels thick-walled and rounded, rays uniseriate and multiseriate, slightly heterocellular .....  
.....5b.i, 5b.ii

(5b.i).....

*Lithocarpus* Bl.

(5b.ii) with relatively small number of vessels per mm<sup>2</sup>.....  
*Trigonobalanus* Forman

(5c) Latewood vessels thin-walled and angular, rays uni-bi-(tri)seriate and multiseriate aggregate (heterocellular), perforation plates simple and in some species also scalariform ..... *Castanopsis* Spach. tropical species

(1'') Wood diffuse-porous, closely spaced vessels of 50 up to 100 µm in diameter, often forming groups, vessel pits opposite, occasionally also scalariform, perforations plates simple and scalariform, cross-fields with enlarged, mostly horizontal pits, rays of two sizes, uniseriate and multiseriate, homocellular, vasicentric tracheids missing, fibres with bordered pits .....*Fagus* L.

Unfortunately, the information on wood anatomy of *Q.* subgenus *Quercus* sections *Protobalanus*, *Ponticae*, and *Virentes* is rather scarce. Most possibly *Q.* subgenus *Quercus* section *Ponticae* is placed in 2ii (ring porous wood with simple perforation plates and rays of two sizes, uniseriate and multiseriate) and *Q.* subgenus *Quercus* section *Protobalanus* and section *Virentes* belongs to 5a (semi-ring/diffuse-

porous wood with simple perforation plates and homocellular rays of two sizes and with thick-walled and rounded latewood vessels and no tyloses). Regarding the distinction between *Q.* subgenus *Cerris* section *Ilex* and *Q.* subgenus *Cerris* section *Cyclobalanopsis*, some authors report the existence of only aggregate rays in species of the section *Ilex* and of aggregate or semi-compound in species of the section *Cyclobalanopsis*. The cellular composition of *Castanopsis* rays (homocellular or heterocellular) is also under investigation regarding the ontogenetic and inter-species wood variation (Sharma et al. 2011; Shimaji, 1959, 1962).

Regarding the occurrence of crystals in Fagaceae we found that:

- Some *Fagus* species can have crystals of calcium oxalate in rays [e.g. *F. crenata* Blume, *F. japonica* var. *multinervis* (Nakai) Y.N.Lee] and also in axial parenchyma (e.g. *F. grandifolia* Ehrh.) while others have no crystalliferous content (*F. japonica* Maxim., *F. sylvatica* L., *F. hayatae* Palib. ex Hayata).
- Genus *Quercus* subgenus *Cerris* (a. section *Cerris*, b. section *Ilex*, c. section *Cyclobalanopsis*) can have rhomboidal crystals of calcium oxalate in rays and axial parenchyma (e.g. *Q. acutissima* Carruth., *Q. variabilis* Blume, *Q. phillyreoides* A.Gray, *Q. acuta* Thunb., *Q. delavayi* Franch., *Q. gilva* Blume, *Q. lineata* Blume, *Q. myrsinifolia* Blume, *Q. sessilifolia* Blume, *Q. salicina* Blume., *Q. glauca* Thunb., *Q. hondae* Makino, *Q. gemelliflora* Blume, *Q. lineata* Blume, *Q. oidocarpa* Korth.).
- Genus *Quercus* subgenus *Quercus* section *Quercus* (white oaks) species usually do not have crystalliferous content [at least the majority of the species, e.g. *Q. mongolica* subsp. *crispula* (Blume) Menitsky., *Q. aliena* Blume, *Q. mongolica* Fisch. ex Ledeb., because some species like *Q. dentata* Thunb. or *Q. serrata* Murray may have crystals in rays and/or axial parenchyma].
- *Lithocarpus* species can have crystals in rays and in chambered axial parenchyma cells [e.g. *L. edulis* (Makino) Nakai, *L. glaber* (Thunb.) Nakai, *L. celebicus* (Miq.) Rehder, *L. neorobinsonii* A.Camus, *L. sundaicus* (Blume) Rehder].
- *Notholithocarpus* has crystals in axial parenchyma and in rays.
- *Trigonobalanus* has crystals in rays [*T. verticillata* Forman, *T. doichangensis* (A.Camus) Forman] or in axial parenchyma (*T. excelsa* Lozano, Hern. Cam. and Henao).

## 5.4 | General aspects

The fossil fagaceous evergreen species with two kinds of rays (narrow and multiseriate) included *Quercoxylon* and *Lithocarpoxyton* with botanical affinities of *Quercus* and *Lithocarpus* species of Indo-Malayan, Sino-Japanese, and Californian floras (Selmeier, 1986), or of the temperate regions of the North Hemisphere and of East Indies (=south-east Asia including India and the Islands) sensu Privé (1975).

After careful studies we come to the conclusion that the category of the evergreen fossil oaks should include also some types of *Castanopsis*. According to Tang (2015), *Castanopsis* represents a genus

with almost 130 species, mainly restricted to south-east and east Asia (Yunnan, China, Indochina to Indonesia, Malaysia, Japan, southern Korea, and eastern Himalayas). Yunnan (38 spp.) has the highest *Castanopsis* species diversity in China, with 11 species endemic to Yunnan, and Indochina has 82 species.

Regarding the evergreen fossil oaks, the authors would like to draw attention to the relationship between wood porosity and leaf habit as discussed in Boura and De Franceschi (2007) because ring porous woods are always deciduous while the occurrence of diffuse (or radial/semi-ring) porous wood may not always represent evergreen species (e.g. *Fagus sylvatica*). The correlation with the plant organs from the same locality ('whole plant concept' sensu Sakala, 2004) can be very useful in order to overcome this scientific obstacle.

Compound broad rays (Figure 5a-III) sensu Petrescu (1976) are equal to the obliquely splitted broad rays (Figure 5b-III) of *Quercus* subg. *Cyclobalanopsis* reported in Noshiro and Sasaki (2011). Compact-aggregate, compound-aggregate and aggregate (Figure 5a-IV-VI) sensu Petrescu (1976) are equal to the vertically (and vertically to obliquely) splitted broad rays (Figure 5b-I,II) of *Lithocarpus* and *Q.* subg. *Sclerophylloids* reported in Noshiro and Sasaki (2011). Our fossil wood has broad rays with oblique split (and also vertical to oblique) which could lead to the result that our wood is close to *Q.* subg. *Cyclobalanopsis* and not close to *Lithocarpus*. The broad rays of our wood show also vertical to oblique splitting and moreover, their cellular composition is heterocellular. *Quercus* (according to Müller-Stoll and Mädler (1957) has homocellular rays and *Lithocarpus* has slightly heterocellular rays (maybe of type 'heterocellular II-III' sensu Kribs, 1935 or 'body ray cells procumbent with one row of upright and/or square marginal cells' sensu Wheeler et al., 1989). As shown in Figure 4i,j our wood has strongly heterocellular rays. As reported by Shimaji (1959, 1962) homocellular and heterocellular broad compound and aggregate rays are observed in *Castanopsis cuspidata* Schottky (Kojii). This is another proof that our fossil can be related to *Castanopsis* and, more precisely, to *Castanopsis cuspidata*.

As a conclusion, our fossil wood has the following specific characteristics: growth rings present, semi-ring porosity, vessels exclusively solitary in 2–3 rows of interrupted tangential zones, circular to oval in outline in early wood and more angular in latewood, tyloses; simple perforation plates; vasicentric tracheids; heterocellular rays of two distinct sizes: (a) narrow and short (uni-, bi-, and triseriate) and (b) multiseriate (not very wide) compound and aggregate rays present; no crystals present. The combination of the latter is found only in *Castanopsis* species.

The specimen from the south-west part of Bulgaria is identified as *Castanopsis bulgarica* because its wood anatomy significantly differs from other fossil fagaceous wood species described so far. *C. bulgarica* is very close to modern *Castanopsis cuspidata* (as described in Shimaji, 1959, 1962). However, wood anatomical descriptions of modern *Castanopsis* species are rather scattered in the literature, and their intraspecific variation quite complicated (Sharma et al. 2011). Consequently, also other NLRs might come into consideration in the course of future research.

*Castanopsis* species can inhabit a wide range of tropical to subtropical locations, extending to temperate habitats, and are often keystone species in their ecosystems. They are plentiful in ecotones as diverse as Borneo montane rain forests and Chinese subtropical evergreen broad-leaved forests (Tang, 2015).

Although *Castanopsis* is common in lauro-fagaceous-dominated subtropical/warm-temperate evergreen broad-leaved forests, dominant element in upper montane forests and even keystone genus in its ecosystem (Tang, 2015), the possible assignment of the plant fossiliferous locality of Blagoevgrad Graben to the East-Asian laurophyll warm-temperate lauro-fagaceous forest sensu Box, Chou, and Fujiwara (1998) is under consideration for now but requires more findings in order to be strongly supported.

According to Hristova, Ivanov, and Bozukov (2015); Ivanov et al. (2012); Kovar-Eder, Kvaček, Martinetto, and Roiron (2006); Palamarev, Bozukov, and Ivanov (2002), the climatic character of the Late Miocene (Pontian/Messinian)–Early Pliocene (Dacian/Zanclean) plant assemblages of Bulgaria corresponds to a humid warm-temperate regime with only a short period of precipitation deficiency (MAT: 12–13°C, CMT: 3–5°C, WMT: 20–22°C, MAP: 800–1,200 mm). The presently described materials, found in the context of the newly detected Boboshevo flora is of Messinian (Pontian)–Zanclean (Dacian) age (Ivanov & Bozukov, 2017) represents an evergreen fossil *Castanopsis* species identified as *Castanopsis bulgarica*. The Nearest Living Relative (and possibly the 'ecologically analogous plant' sensu Kvaček, 2007) of our fossil, is *Castanopsis cuspidata* (Thunb.) Schottky. Although the fossil plant could have differed in autecology from its Nearest Living Relative it can be stated that its climatic requirements are in broad agreement with the above mentioned palaeoclimatic characteristics and largely coincide with the geographical and climatic range (tropical-subtropical-temperate habitats and ecotones) of the modern genus (Tang, 2015).

The occurrence of *Castanopsis* (based mostly on leaves and fruits findings) during the Cenozoic, along with its importance in the fossil flora, has been discussed in classic works (Kvaček & Walther, 1988; Mai, 1989, 1995). Recently, there is increasing scientific evidence for the occurrence of fossil *Castanopsis* macro- and microfossils (Gee, Sander, & Petzelberger, 2003; Huang et al., 2018; Wilf, Nixon, Gandolfo, & Cúneo, 2019). Moreover, it can be assumed that numerous fossil wood specimens of evergreen oaks with rays of two distinct sizes belonging to fossil *Castanopsis* have been identified as *Quercoxylon* (e.g. *Q. courpierense* Privé which has heterocellular rays), due to the lack of evidence regarding the wood anatomy of extant *Castanopsis* species.

The preparation of the revised key on the xylotomical identification of Fagaceae enables us to (a) observe that some anatomical characteristics of different genera or sections are overlapping and, consequently, that some characteristics used in the past as indicators for fossil species identifications could belong also to different genera, keeping in mind addressed difficulties regarding its use for the fossil wood record, such as ontogenetic and inter-species wood variation (discussed for example in Sharma et al. 2011; and in Shimaji, 1959, 1962) and intra-tree variability (Falcon-Lang, 2005), and to



(b) understand the necessity of more xylotomical works on specific genera (e.g. *Chrysolepis*, *Trigonobalanus*, *Castanopsis*), sections (e.g. *Q.* subgenus *Quercus* sections *Protobalanus*, *Ponticae* and *Virentes*) and species.

The previously mentioned observations (c), in combination with publications on fossil Fagaceae (e.g. Kvaček & Walther, 1989) lead to a legitimate requirement regarding the systematic reassessment of the megafossil records of Fagaceae both in terms of the reappraisal of species identifications (focused on their anatomical characteristics) and of the correlation of different parts of the fossil record (whole plant concept). After all, 'the fossil wood anatomy could play a very important role for the classification of Fagaceae' (Denk et al., 2017) and also in the biogeographic history of the Fagaceae family on a trans-continental scale.

## 6 | CONCLUSIONS

- The fossil wood stem from south-west Bulgaria (Blagoevgrad Graben) is of Late Miocene–Early Pliocene (Pontian-Dacian) age and is first described here as *Castanopsis bulgarica* Mantzouka, Ivanov and Bozukov.
- The detailed xylotomical study of the fossil revealed characteristics of 'the evergreen oaks' and some special features which belong to (sub/tropical) *Castanopsis*.
- The careful study of the literature provided important information on the division (oblique or vertical 'splitting') and the cellular composition (homocellular or heterocellular) of the aggregate rays characterizing the *Castanopsis* genus.
- The broad rays of our fossil are semi-compound divided by oblique files of fibres, as in subgenus *Cerris*, section *Cyclobalanopsis*, but they are heterocellular as in *Lithocarpus*. Both the pre-mentioned characteristics are found in *Castanopsis*.
- Fagaceous xylotomical keys (for fossil and extant specimens) have been reappraised and revised with the inclusion of *Castanopsis*.
- The application of the 'Whole Plant Concept', after the comparison of our wood with the Bulgarian fagaceous findings of the same age and their Nearest Living Relatives, has revealed *Castanopsis cuspidata* (Thunb.) Schottky as botanical affinity of the new fossil species.
- Although xylotomical studies on *Castanopsis* species are rare in the literature and the intraspecific variation complicated, the authors of the present study strongly support the necessity of further research on the occurrence of evergreen *Castanopsis* species in the fossil record.

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