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Paleoecological data on the distribution of Pinus peuce Griseb. in Southwestern Bulgaria for the last 30000 years

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Abstract. The paleoecological information on the distribution of the Tertiary relic and Balkan endemic *Pinus peuce* Griseb. (Macedonian pine) is summarized on the basis of the results from pollen analysis, plant macrofossil determination and radiocarbon dating of lake and peat bog sediments in the mountains of Southwestern Bulgaria. The oldest record is of Middle Pleniglacial age (30000-24000 cal. yrs. BP) when pollen of *P. peuce*, together with pollen of other coniferous and deciduous trees, was established from the West Rhodopes Mountain. During the Late Glacial (14500-11600 cal. yrs. BP) stands of pines, *P. peuce* included, thrived among cold-tolerant herb communities in the Rila, Pirin and the West Rhodopes mountains, confirmed by the first macrofossils (needles) determined. The minor participation of *P. peuce* in the early Holocene (11600-8800 cal. yrs. BP) *Betula* forests was succeeded by its wider distribution after 8200-7900 cal. yrs. BP when a coniferous belt composed by pines and *Abies* was shaped in the Rila and Pirin mountains. This vegetation reconstruction is supported by numerous macrofossils of *P. peuce* (needles, seeds, and partly stomata). Since 2600 cal. yrs. BP in the conditions of a more humid and cooler climate, the pulsating invasion of *Picea abies* restricted to some extent the distribution of *P. peuce*. Both species, together with *Pinus sylvestris*, shaped the timber-line at many places. The main conclusion from this survey is that populations of *P. peuce* survived the harsh glacial climatic conditions in montane refugia with subsequent gradual widespread during the Holocene.

Key words: *Pinus peuce*, paleoecology, pollen, macrofossils, radiocarbon dating, mountains, Southwestern Bulgaria.

Introduction

The basis of paleoecological research is to use the fossil remains preserved in sedimentary deposits to investigate the origin, history and long-term dynamics of individual taxa, populations, communities and ecosystems (Seppa, 2018). The geographical ranges of species are not static in time, showing expansions and contractions that depend on changes in climate variability and human influence, particularly after the dramatic climatic events of the Late Quaternary (Bennett & Provan, 2008; Svenning et al., 2015).

The species *Pinus peuce* Griseb., also known as Macedonian pine, is a Tertiary relic and Balkan endemic which natural area of occurrence consists of two parts separated by the valley of the River Vardar. The eastern part is in Southwestern Bulgaria and the western part is in North Macedonia, Southwestern Serbia, Kosovo, Southeastern Montenegro, Eastern Albania and Northwestern Greece (Fig. 1.). Though it occurs naturally from 800-900 m up to 2300-2400 m altitude, its optimum is most often at 1600-1900 m altitude. This tree prefers silicate terrains and less often carbonate ones, cold mountain climate and high air humidity. In our country *P. peuce* forms natural plantations in the Rila, Pirin, Slavyanka, partly in Stara Planina and West Rhodopes mountains between 1200 and 2200 m altitude and often shapes the timber-line together with *Picea abies* (L.) Karst. and *Pinus sylvestris* L. In the coniferous forests of Pirin and Rila mountains are the basic localities of Macedonian pine on the Balkans which determines its role as an important valuable forest-tree species (Aleksandrov & Andonovski, 2011).

The fossil history of *P. peuce* in Bulgaria is known from paleobotanical finds (needles, cones, cone scales) in Neogene basins from Middle Miocene to Early Pliocene (15–4.8 million years ago) (Palamarev et al., 2005; Bozukov et al., 2018). Of great interest are the fossil female cones and seeds of *P. peuce* established in the Pianico basin, Italian Pre-Alps. Their age was determined at about 780 000 years, deposited during one of the interglacials of the Middle Pleistocene. The subsequent alternating glacial/interglacial cycles caused the progressive disappearance of a number of species, *P. peuce* included, from the Italian peninsula (Pini et al., 2014).

This paper attempts to summarize the available palynological and paleoecological data on the distribution of *P. peuce* for the last 30000 years from sites in Southwestern Bulgaria. The survey does not discuss the evidence from Stara Planina Mountain as the few pollen records in which *P. peuce* is present are not supported by radiocarbon chronology (Filipovitch et al., 1997).

Fig. 1. Distribution map of *P. peuce* on the Balkans (modified after Aleksandrov & Andonovski, 2011).

Materials and Methods

The spatio-temporal changes in the distribution of *P. peuce* in the study area are traced with the application of several research approaches. The basic source of information is extracted from pollen diagrams of peat bogs, lakes and mires located in the Rila, Pirin and West Rhodopes mountains (Fig. 2). Pollen of *P. peuce* belongs to *Pinus haploxylon*-type group and could be morphologically differentiated from pollen of *Pinus diploxylon*-type group by its larger grains and sacci which are not sharply delimited from the main body, and also by a characteristic pattern on the ventral side. The pollen group of *P. diploxylon*-type in our country comprises the species *Pinus sylvestris, P. mugo* Turra, *P. nigra* Arn. and *P. heldreichii* H. Christ distributed in the mountains. The identification of separate species by pollen morphology within this group is not possible (Bozilova, 1963; Beug, 2004).

Simplified versions of three pollen diagrams, representative of the vegetation history in the relevant mountains, are constructed with the computer software *Tilia* ver. 3.0.1 (Grimm, 1991-2020). The diagrams are plotted against age and include the percentage values of *P. peuce* pollen and of several main tree and herb taxa through time (Figs. 3, 5-6).

Additional important information indicative of local presence is obtained from plant macrofossils (needles and seeds) of *P. peuce* found in the sediments studied (Table 2). As an example, a simplified macrofossil diagram from Lake Suho Ezero (Rila Mountain) is presented which plausibly illustrates the potential of macrofossil determination (Fig. 4). Fossil stomata of conifers also provide unambiguous evidence of past local presence but attempts to differentiate species within g. *Pinus* (*P. mugo, P. sylvestris* and *P. peuce*) with visual observations of stomata features were not successful, as the interspecific differences in stomata are too small for a separation (Trautmann, 1953; Tonkov et. al., 2018; Finsinger, Tinner, 2020). However, with some stipulation part of the fossil pine stomata could be attributed to *P. peuce* (Fig. 3).

The determination of the absolute age with radiocarbon dating in calibrated years BP or calendar years, i.e. before year 1950 (cited in the text as cal. yrs. BP) of sediment samples or plant macrofossils ensures the chronological framework of the changes in species abundance and vegetation development. In this study over 60 radiocarbon dates were used provided by foreign radiocarbon laboratories. A chronostratigraphical subdivision of the Last Glacial (Wùrm) and the Holocene is also presented (Table 1).

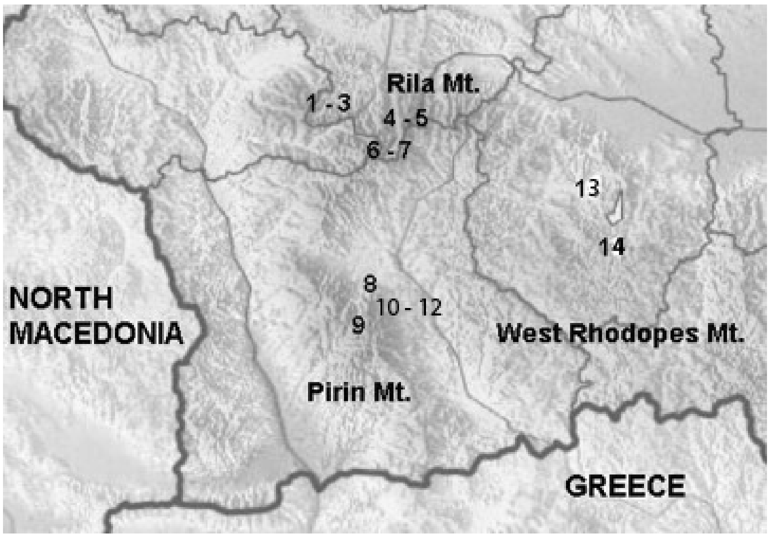

Fig. 2. Map of the sites in the study area with fossil data (pollen, plant macrofossils) of *P. peuce* and radiocarbon chronology mentioned in the text: Rila Mountain - 1 Lake Trilistnika, 2 Lake Ribno, 3 Lake Sedmo Rilsko (Tonkov, 2021); 4 Lake Ostrezko-2 (Tonkov & Marinova, 2005); 5 Peat bog Vodniza (Tonkov, 2021); 6 Lake Suho Ezero-2 (Bozilova et al., 1990; Tonkov, 2021); 7 Peat bog Vapsko-1 (Hoovers, 2017; Tonkov, 2021); Pirin Mountain - 8 Lake Ribno Banderishko (Tonkov, 2021; Tonkov & Possnert, 2021); 9 Peat bog Mozgovitsa (Marinova & Tonkov, 2012; Tonkov, 2021); 10 Lake Kremensko-5 (Stefanova et al., 2006a); 11 Lake Bezbog (Stefanova et al., 2006a, 2006b); 12 Lake Popovo Ezero-6 (Stefanova & Bozilova, 1995); West Rhodopes Mountain - 13 Mire Kupena (Tonkov et al., 2014), 14 Peat bog Shiroka Polyana (Stefanova et al., 2006b; Bozilova et al., 2011).

Table 1. Chronostratigraphical subdivision of the Last Glacial (Wùrm) and the Holocene.

Quaternary stage	Chronostratigraphic interval	Age in cal. yrs. BP
Holocene	Subatlantic (SA)	2600 - present
	Subboreal (SB)	5800 - 2600
	Atlantic (AT)	8800 - 5800
	Boreal (BO)	10000 - 8800
	Preboreal (PB)	11600 - 10000
Last Glacial (Wùrm)	Late Glacial (LGl)	14500 - 11600
	Late Pleniglacial (LPG)	24000 - 14500
	Middle Pleniglacial (MPG)	59000 - 24000
	Early Pleniglacial (EPG)	74000 - 59000
	Early Glacial (EGl)	114000 - 74000

Results

Rila Mountain

The oldest records of *P. peuce* pollen are of Late Pleniglacial age (c. 18000 cal. yrs. BP) observed in the sediments collected from the Seven Rila lakes (sites 1-3, Fig. 2). Subsequently, during the Late Glacial, pollen of *P. peuce* reaches 10-12%, accompanied by pollen of *P. diploxylon*-type (30-40%), minor quantities of deciduous tree pollen and dominance of *Artemisia* and Chenopodiaceae pollen (Fig. 3). In the early Holocene (11600-8800 cal. yrs. BP, Preboreal and Boreal) comparatively low pollen values are established. Afterwards begins an increase of *P. peuce* pollen with a maximum of 15-20% and stable presence between 7800 and 2000 cal. yrs. BP (Atlantic, Subboreal, partly in early Subatlantic). Macrofossils were not determined in the sediments of these subalpine lakes except for stomata of *Pinus* sp. after 10000 cal. yrs. BP (Fig. 3).

From the Peat bog Vodniza, central Rila Mountain (site 5, Fig. 2), pollen of *P. peuce* appears after 18000 cal. yrs. BP. Throughout the Late Glacial and the early Holocene (Preboreal, Boreal) its contribution is 5-10%. After 8500-8200 cal. yrs. BP an increase up to 25-30% is recorded, followed by 10% presence in the last 2000 years. Between 8200 and 3700 cal. yrs. BP a continuous presence of stomata of *Pinus* sp. is established and part of them could probably originate from *P. peuce*. In the macrofossil record from Lake Ostrezko-2 (site 4, Fig. 2) needles are continuously determined between 6500 and 3200 cal. yrs. BP, together with seeds (Table 2).

The plant macrofossil diagram from core Lake Suho Ezero-2 (site 6, Fig. 2), located in the coniferous belt of southwestern Rila Mountain, reveals interesting information about the presence of *P. peuce* since the Late Glacial (Fig. 4). The oldest remains of needles of *P. peuce* found so far in the Rila Mountain date back to 12350 cal. yrs. BP. An abundance of needles is recorded in the Holocene between 6000 and 2200 cal. yrs. BP, together with needles and bud-scales of *Pinus* sp. and seeds of *P. sylvestris*. Needles and seeds of *P. abies* appear rather late in the fossil assemblages after 2600 cal. yrs. BP.

The macrofossil record from Peat bog Vapsko-1 (site 7, Fig. 2) contains needles of *P. peuce* between 7500 and 5200 cal. yrs. BP (Table 2).

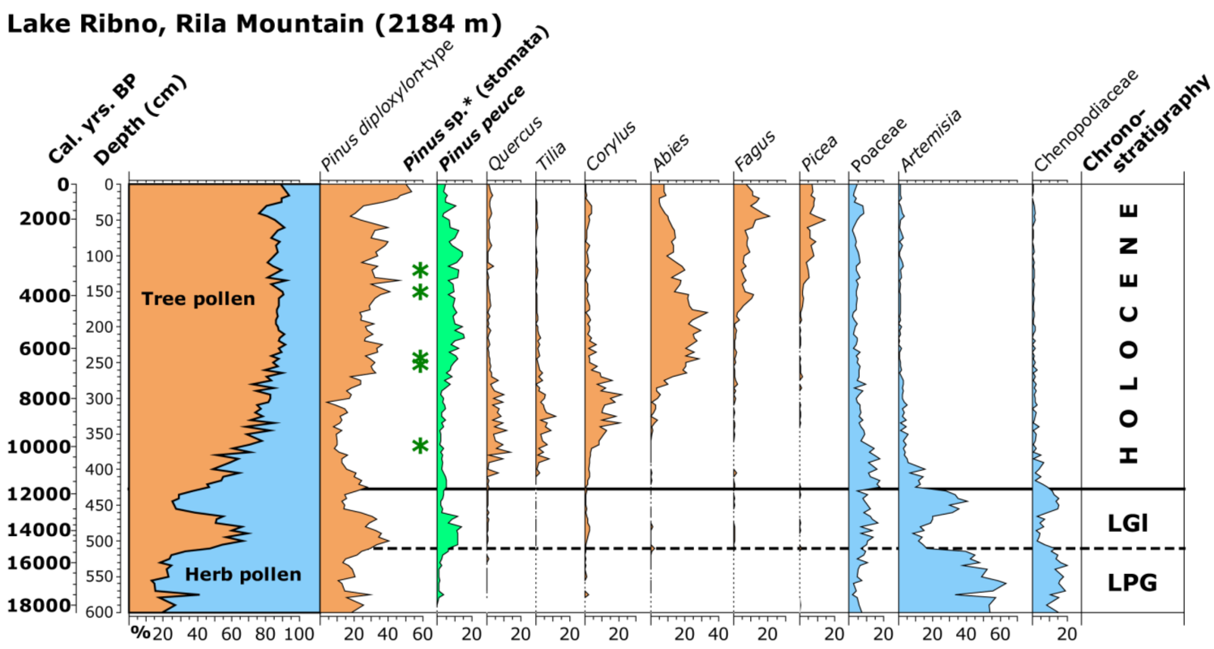

Fig. 3. Simplified percentage pollen diagram of Lake Ribno, Rila Mountain (modified after Tonkov, 2021).

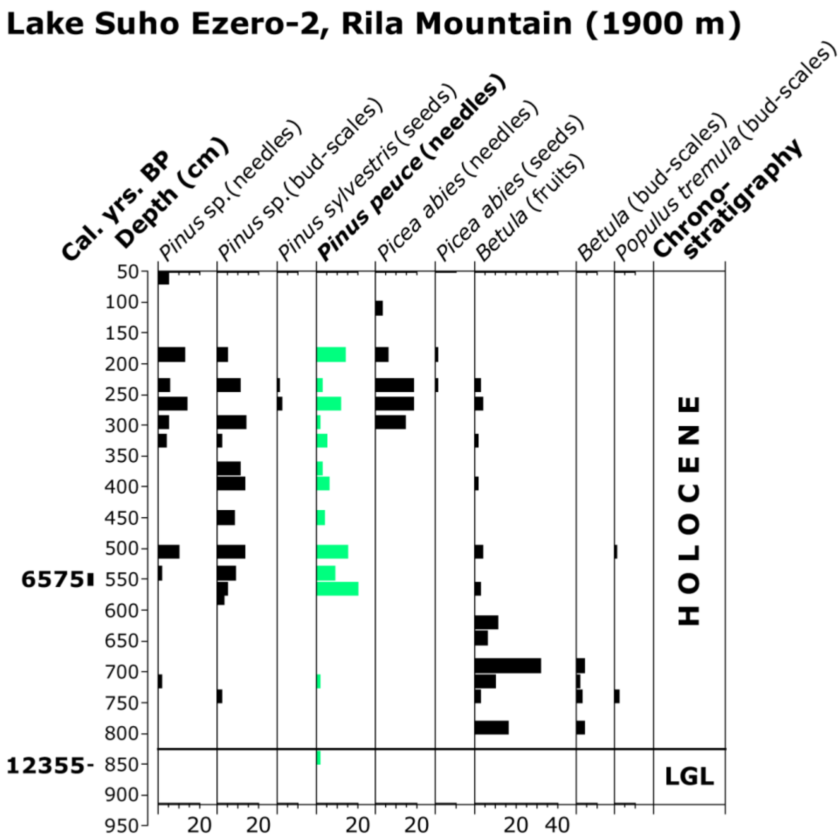

Fig. 4. Plant macrofossil diagram of Lake Suho Ezero-2, Rila Mountain (modified after Tonkov, 2021).

Table 2. Macrofossils of *P. peuce* in sediments from sites in Southwestern Bulgaria (* - radiocarbon dated macrofossils).

Site	Macrofossils	Age (cal. yrs. BP)	Publication
Rila Mountain			
Lake Ostrezko-2 (2320 m)	needles seeds	6500-3200 3400-2250	Tonkov & Marinova (2005); Tonkov (2021)
Lake Suho Ezero-2 (1900 m)	needles	12350; 8200; 6000-2200	Bozilova et al. (1990); Tonkov (2021)
Peat bog Vapsko-1(2143 m)	needles	7500-5200	Hoevers (2017)
Pirin Mountain			
Lake Ribno Banderishko (2190 m)	needles	11000*; 6600*; 4200*	Tonkov (2021)
Peat bog Mozgovitsa (1800 m)	needles and seeds	9300; 7300; 4800	Marinova & Tonkov (2012); Tonkov (2021)
Lake Kremensko-5 (2124 m)	needles seeds	14600-11600; 10000-9500; 8000-5500 7000-4800	Stefanova et al. (2006a)
Lake Bezbog (2240 m)	needles	12600; 10470*; 8000-4200; 5620*; since 2800 onwards	Stefanova et al. (2006a, 2006b)
Lake Popovo Ezero-6 (2185 m)	needles seeds	7580-2530 4670	Stefanova & Bozilova (1995)

Pirin Mountain

Traces of *P. peuce* pollen are recorded during the Late Glacial in the pollen diagram (Fig. 5) from Lake Ribno Banderishko, northern Pirin Mountain (site 8, Fig. 2), but it is absent in the first half of the Holocene until 6600-6500 cal. yrs. BP. Later on, its participation hardly exceeds 5%. Against the background of the low pollen frequencies, needles were radiocarbon dated at several sample levels (Table 2). These finds serve as evidence of local presence of individual groups. From the Peat bog Mozgovitsa (site 9, Fig. 2) the initial presence of pollen grains averages 8% between 9300 and 7300 cal. yrs. BP followed by a steep increase to 15-20% until the beginning of the Subatlantic. The growth of *P. peuce* is confirmed also by the establishment of macroremains (needles and seeds) (Table 2).

Investigations from other lakes in the northern Pirin Mountain (sites 10-12, Fig. 2) expand the picture of *P. peuce* distribution in postglacial time. In the Late Glacial (14500-11600 cal. yrs. BP) and early Holocene (10000-9500 cal. yrs. BP, Boreal) sediments of Lake Kremensko-5 were found needles. Seeds were established for the Atlantic and early Subboreal (7000-4800 cal. yrs. BP). Needles of *P. peuce* were determined at 12600 cal. yrs. BP (Late Glacial) in the sediments of Lake Bezbog and others were radiocarbon dated (Table 2). The maximum presence of *P. peuce* macrofossils (8000-4200 cal. yrs. BP) coincides with the maximum of pollen in the interval 6000-5000 cal. yrs. BP. Studies from Lake Popovo Ezero-6 showed abundance of needles between 7580 and 2530 cal. yrs. BP and seeds at 4670 cal. yrs. BP as well (Table 2).

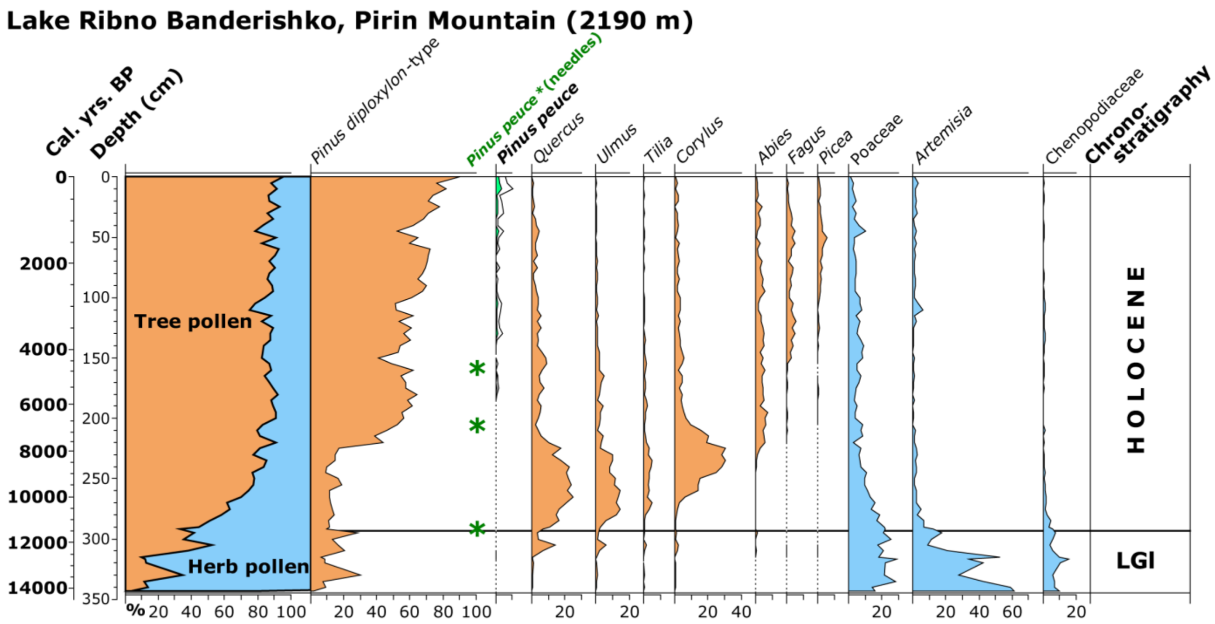

Fig. 5. Simplified percentage pollen diagram of Lake Ribno Banderishko, Pirin Mountain (modified after Tonkov, 2021).

West Rhodopes Mountain

Pollen of *P. peuce* was found in the sediments from Mire Kupena (site 13, Fig. 2) around 30000 cal. yrs. BP, being well represented during the Middle and Late Pleniglacial with 5-10%, and partly during the Late Glacial. It is accompanied by pollen of *P. diploxylon*-type (30-40%), *Artemisia* (25-50%), Chenopodiaceae up to 30%, and minor quantities of deciduous (*Quercus*, *Tilia*, *Fagus*, *Corylus*) and coniferous (*Abies*, *Picea*) tree pollen. In the Holocene two distinct periods of increase are recorded around 8500 and 2000 cal. yrs BP (Fig. 6).

In the interior of the mountain at Peat bog Shiroka Polyana (site 14, Fig. 2) pollen of *P. peuce* is present with minimal values throughout the Late Glacial. Since the onset of the Holocene, it gradually increases to 2-3% and a short-term maximum of 20% is recorded around 6200 cal. yrs. BP.

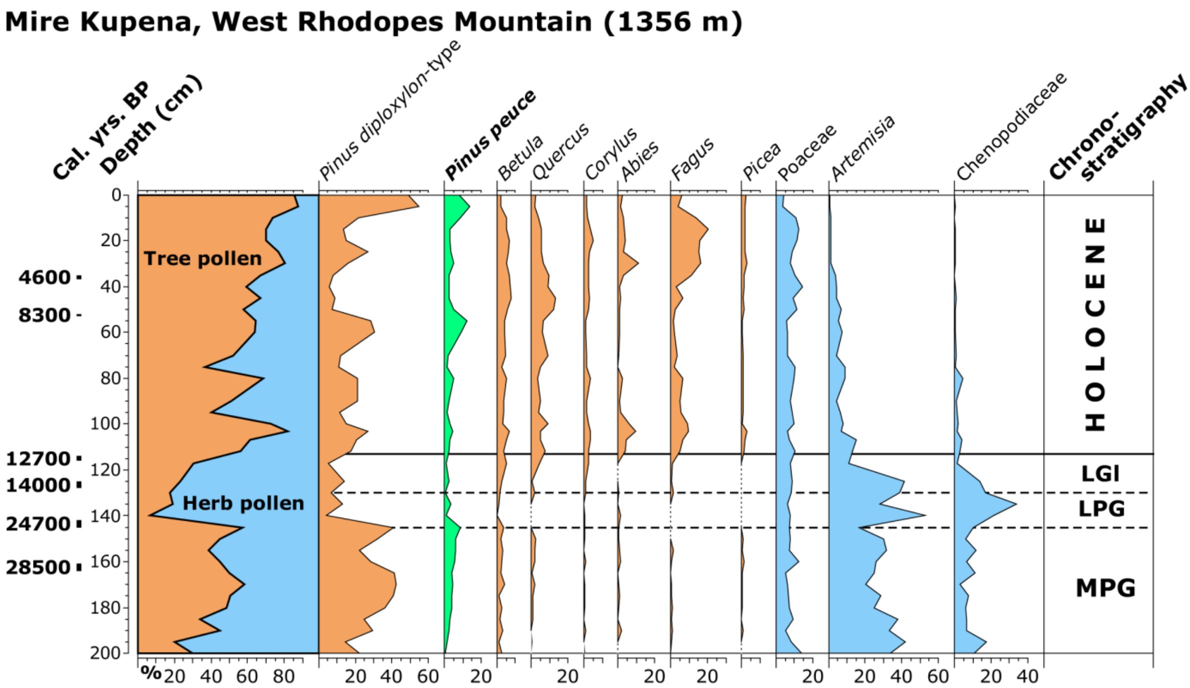

Fig. 6. Simplified percentage pollen diagram of Mire Kupena, West Rhodopes Mountain (modified after Tonkov et al., 2014).

Discussion

The earliest record of *P. peuce* in the area under discussion originates from Mire Kupena, the West Rhodopes Mountain (Fig. 6). In accordance with the radiocarbon chronology the reconstruction of the vegetation cover for the time window 30000-24000 cal. yrs. BP reveals that the mountain slopes were covered by sparse forests of *Pinus* (most probably *P. sylvestris/nigra* and *P. peuce*) with stands of *Betula*, among cold-tolerant herb communities dominated by *Artemisia*, Chenopodiaceae and Poaceae species. At lower altitudes, under more favorable microclimatic and edaphic conditions, groups of deciduous (*Quercus*, *Corylus*, *Fagus*, etc.) and coniferous (*Abies*, *Picea*) trees thrived. The regional presence of various trees and shrubs, including *P. peuce*, confirms that this area has served as one of the Middle Pleniglacial refugial places in the Rhodopes Mountain and the Balkans during the Last Glacial (Tonkov et al., 2014).

The information about the distribution of *P. peuce* for the Late Pleniglacial and Late Glacial (24000-11600 cal. yrs. BP) becomes more diverse as not only pollen (Figs. 3, 5-6) but also macrofossils were identified. Despite that the montane herb communities retained their dominant role, the tree pollen percentages indicate an initial stage of afforestation in the Rila and Pirin mountains with stands of pines (*P. mugo*, *P. sylvestris*, *P. peuce*) and some *Betula* after around 15000 cal. yrs. BP as a response to the general tendency to warmer climate which started after 16000 cal. yrs. BP (de Klerk, 2004). The needles of *P. peuce* in the sediments of Lake Kremensko-5, Lake Bezbog and Lake Suho Ezero-2 since 14600 cal. yrs. BP (Table 2) support this vegetation reconstruction and confirm that *P. peuce* was an important constituent of the sparse coniferous tree cover. Alongside with the distribution of pines during the Bölling/Allerød interstadial (14500-12800 cal. yrs. BP) of the Late Glacial, the deciduous trees also migrated along the mountain slopes from their refugial places at lower altitudes. The final stage of the Late Glacial, the Younger Dryas stadial (12800-11600 cal. yrs. BP), was characterized by a reversal to glacial conditions which triggered the re-advance of the herb communities and the partial retreat of arboreal vegetation, mostly deciduous trees. The presence of pollen and needles of *P. peuce* from nearly all sites studied in the Rila and Pirin mountains serves as evidence that this tree has survived the last climate deterioration of the Late Glacial (Stefanova, 2006a; Tonkov, 2021).

The onset of the Holocene featured a quick amelioration of the climate which resulted in a decline of the mountain herb vegetation and the initiation of the re-forestation processes in the Rila and Pirin mountains. For nearly 3000 years pioneer forests of *Betula* occupied the mountain slopes at mid-high altitudes on barren soil, accompanied by stands of *P. mugo*, *P. sylvestris* and *P. peuce*. The local presence of the last species at the timber-line is confirmed by the macrofossils (needles, seeds and probably stomata) in the sediments of the lakes and peat bogs studied (Table 2). It should be pointed out that the pollen percentages of *P. peuce* during the Preboreal and Boreal were even a bit lower compared to the situation during the Late Glacial. Also, mixed oak forests expanded up to mid-elevations. The reason was that relatively dry conditions in the early Holocene are implied, perhaps a result of higher summer insolation, which may have been the cause for the elevational increase in temperate deciduous trees and the restriction of conifers (Stefanova et al., 2006b).

In the West Rhodopes Mountain *P. peuce* did not play an important role in the forest cover during the early Holocene which is evident by its low pollen values until about 8500 cal. yrs. BP (Fig. 6).

An important change in the forest composition and its altitudinal zonation in the Rila and Pirin mountains occurred after 8200-7900 cal. yrs. BP (Atlantic). In the course of nearly 2000 years the ecological conditions favored the formation of a coniferous belt dominated by *Pinus* sp., *P. peuce* and *Abies*, replacing at many places the birch and oak forests. This transformation presumes a climatic shift towards cooler summers and warmer winters in southeastern Europe with increase in air and soil humidity (Davis et al., 2003; Tonkov, 2021). The share of *P. peuce* in the composition of the coniferous forests significantly enlarged as demonstrated by its higher pollen values (Fig. 3) and the regular presence of macrofossils (needles and seeds) (Table 2). The latter indicated that by that time the timber-line with *P. peuce* as an important constituent was running 150-200 m higher compared to nowadays, particularly in the Pirin Mountain (Stefanova & Ammann, 2003).

In the West Rhodopes Mountain after 8500 cal. yrs. BP the role of *P. peuce* in the composition of the coniferous or mixed coniferous-deciduous forests was not so important, although periods of enlargement according to pollen data and radiocarbon chronology were established at 8300, 6200 and 2000 cal. yrs. BP. This result correlates in broad lines with the data from the Rila and Pirin mountains.

The Subboreal interval (5800-2600 cal. yrs. BP) featured a maximal distribution of *P. peuce* together with *P. sylvestris* in the coniferous woods and the commencement of *Abies* decline in the Rila and Pirin mountains. Later on, since 2600 cal. yrs. BP (Subatlantic) in the conditions of a more humid and cooler climate, the pulsating invasion of *P. abies* in the coniferous forest belt restricted to some extent the distribution of *P. peuce*. Both species, together with *P. sylvestris*, shaped the timber-line at many places. However, needles of *P. peuce* found in the sediments of Lake Panichishte (1357 m) and assigned to 1400-1100 cal. yrs. BP indicated its presence also in the lower part of the coniferous forests in the northwestern Rila Mountain (Tonkov, 2021). In historical times the destructive changes in the coniferous forest belt were intensified which led to opening of new terrains for pasture land and the use of coniferous wood for various purposes.

Conclusions

The paleoecological evidence for the spatial and temporal changes of *P. peuce* distribution in Southwestern Bulgaria for the last 30000 years based on pollen, macrofossils and radiocarbon chronology, allows to present the following main conclusions:

1. Macedonian pine was preserved in isolated refugial places with sufficient soil and air humidity during the Last Glacial in the high mountains of Southwestern Bulgaria. For the time interval 30000-24000 cal. yrs. BP (Middle Pleniglacial) this tree was a component of the sparse coniferous woods in the West Rhodopes Mountain.

2. During the Late Pleniglacial (18000-14500 cal. yrs. BP) and Late Glacial (14500-11600 cal. yrs. BP) stands of *P. peuce* and other pine species thrived among cold-tolerant herb communities in the Rila, Pirin and the West Rhodopes mountains. Since that time, alongside fossil pollen, the first macrofossil remains (needles) were determined.

3. In the early Holocene (11600-8800 cal. yrs. BP) conifers, *P. peuce* included, displayed a limited occurrence in the forest cover which was domina-

ted by *Betula* communities in the upper montane zone.

4. The development of a coniferous forest belt in the Rila and Pirin mountains with considerable participation of *P. peuce* started after 8200-7900 cal. yrs. BP, proved by abundant pollen and plant macrofossils (needles and seeds). This transformation in the vegetation cover was a response to climatic shift towards cooler summers and warmer winters.

5. The partial reduction of *P. peuce* after 2600 cal. yrs. BP was a result of the expansion of *P. abies*, the spread of *P. mugo* and *P. sylvestris* in the conditions of an increasing anthropogenic impact including deforestation and fires to obtain new pasture land.

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