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Nelumbo protospeciosa Saporta 1891 from the Berane Basin (Lower Miocene)

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Abstract. Berane Basin in Montenegro has been known for rich paleoflora of diverse geological ages. The remains of paleovegetation of various ages were preserved by the lake occurring in this area from Late Oligocene to Early Pliocene. Therefore, the shifts in vegetation during the Miocene period may be easily followed by studying the paleofloras collected at the Berane Basin.

The first and only known remains of aquatic (floating) plants were collected in 1995 at the locality Rosulje (Berane Basin) in the Early Miocene sediments. According to the morphoanatomical characteristics of leaves such as shape of lamina, veins, venation, presence of central disk or position of petiola, the specimens were identified as *Nelumbo protospeciosa* Sap., a widely distributed form during the Tertiary of Eurasia.

No other plants or accompanying vegetation were recorded at the Rosulje site, so presence of *Nelumbo protospeciosa* was insufficient for determining the habitat, vegetation or climate during its existence. Therefore the paleoenvironmental reconstruction also included analysis of the already published Early Miocene flora from the locality Luge-Haremi (Berane Basin) and eco-climatic characteristics of recent *Nelumbo* species. At last was concluded that *Nelumbo*, which had leaves at least 30 cm in diameter, used to inhabit open, well-insolated sites, probably under the influence of the subtropical/Mediterranean-type climate.

Key words: Miocene, *Nelumbo protospeciosa*, *Nelumbium*, *Indricotherium*, Berane, paleoflora.

Апстракт. Берански басен у Црној Гори већ је од раније познат по наласку великог броја палеофлора различите старости. На овом подручју је од краја олигоцена до почетка плиоцена постојало језеро захваљујући коме су се сачували остаци палеовегетација различитих старости. Преко различитих палеофлора нађених у Беранском басену лако се може пратити смена вегетација током миоцена. Године 1995., на локалитету Росуље (Берански басен) у слојевим доњег миоцена, први пут су нађени остаци листова и коренова акватичних – флотантних, биљака. На основу морфоанатомских карактеристика нађених листова, као што су: облик лисне плоче, нерватура, присуство централног диска, дужина, број и гранање примарних нерава утврђено је да се ради о терцијарном лотосу, тачније морфоврсти *Nelumbo protospeciosa* Saporta 1891, који је од еоцена до плиоцена био широко распрострањен у Европи и једном делу Азије.

Поред *Nelumbo protospeciosa* на овом локалитету нису нађене друге биљке нити пратећа вегетација, тако да није било могуће само на основу фосилних остатака нађених лотоса закључити какво је било њихово станиште, нити каква је била вегетација или клима током њихове егзистенције. Зато је за реконструкцију станишта узета у обзир и анализа претходно већ публиковане доњомиоценске флоре са локалитета Луге-Хареми (Берански басен), као и разматрање еко-климатских карактеристика рецентних врста *Nelumbo* spp. На основу свега поменутог закључено је да је овде описани *Nelumbo protospeciosa,* чији су листови достизали најмање 30 cm у пречнику, насељавао отворена добро инсолирана места и да је вероватно живео у оквиру једне суптропске/медитеранске климе

Кључне речи: Миоцен, *Nelumbo protospeciosa*, *Nelumbium, Indricotherium*, Беране, палеофлора.

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Introduction

The Berane Basin in Montenegro is widely known for the large amount of fossil plants collected at the site. More than 700 specimens of fossil plants of various ages (Early Miocene to Pliocene) have been collected since mid-20th century (PANTIĆ, 1987; DJORDJEVIĆ MILUTINOVIĆ & ĆULAFIĆ 2008, 2010).

The first studies started in 1930, when Nikola Muravjov, a professor at the Berane Gymnasium, collected around 400 fossil plant specimens from the locality Luge (Lower Miocene) and sent them to the Natural History Museum in Belgrade, to the curator Pavle Ivanovič Černjavski. Middle Miocene flora at the locality Jasikovac was recorded in 1985 and published by PANTIĆ (1987), while the Upper Miocene and Pliocene floras were collected in 1994 and 1995. There are over 20 known sites with fossil plants, belonging to Lower (e.g. Luge, Haremi, Bunar T.J, Petnjk, Budimlja etc.), Middle (Jasikovac) and Upper Miocene and Pliocene (e.g. Popovići, Mašte).

As an addition to the existing collection of fossil plants, remains of aquatic *Nelumbo protospeciosa* were collected inside the lignite mine Rosulje at Budimlja (Berane Basin) in 1995 (Fig. 8; Pl. 1). This is the first record of genus *Nelumbo* in the Berane Basin and in contrast to other plant fossils, which were mostly preserved in marl, *Nelumbo protospeciosa* was represented by compressions and impressions of leaves and rhizomes in clay-based sediment.

Besides *Nelumbo*, no other plant remains were recorded at the site, although it must be noted that there was no targeted excavation, as the site was under mining works that could not be stopped or postponed. Therefore, these few *Nelumbo* leaves are all the record from that clay-based layer.

Fig. 1 *Nelumbo* remains were found at the locality of Rosulje coal mine in village Budimlja, the Berane Basin, Montenegro; N 42°51’40,70”, E 19°53’41,00”, Elev. 703 m.

Genus *Nelumbo* Adanson, commonly called lotus or sacred lotus, is an aquatic perennial plant that can often be found in fossil remains due to its solid bulky leaves. The leaf is very characteristic and easy to recognize in the fossil material. Its basic characteristics are: peltate shape and centrally placed petiole, actinodromous venation, 19 to 25 radially distributed primary veins that are dichotomously divided in their upper third, the presence of the unbranched midvein and the presence of the central disk at the point where the petiole enters the lamina (centrally peltate leaf). If the existence of one or more of these characteristics is determined in fossil remains, the leaf is usually classified as *Nelumbo*.

Today, only the *Nelumbo* genus belongs to the Nelumbonaceae family, with two species: *N. lutea,* native to North America, and *N. nucifera*, native to Asia. However, based on fossil findings, it has been established that from Cretaceous to this day, besides *Nelumbo*, there were also several other genera of the Nelumbonaceae: *Nelumbites, Exnelumbites, Paleonelumbo* and *Nelumbago*, which were present in Europe, Asia, North and South America (ESTRADA-RUIZ et al., 2011; GANDOLFO et al., 2005; LI et al., 2014b), which points to the fact that the former diversity of the Nelumbonaceae family was far greater.

Material and methods

The Berane basin is elongated in shape, about 8 km long and of variable width (maximum 5.5 km). The Tertiary sediments presently cover the area of 28 km^2 (Fig. 1). The southern and central parts of the basin are flattened, with an altitude of about 670 m, while toward east and northeast the terrain is slightly undulating and slowly rising to 750–830 m altitude. The town of Berane is situated almost in the central part of the Basin. The River Lim flows through the middle of the Basin (see DJORDJEVIĆ MILUTINOVIĆ & ĆULAFIĆ, 2010).

Geology and age

In 1995, as a result of an investigative section cut made for the purpose of determining the coal reserves and assessing the possibility of its surface exploitation, compression/impression of Lower Miocene *Nelumbo* leaves and rhizomes were found at the locality of Ro-

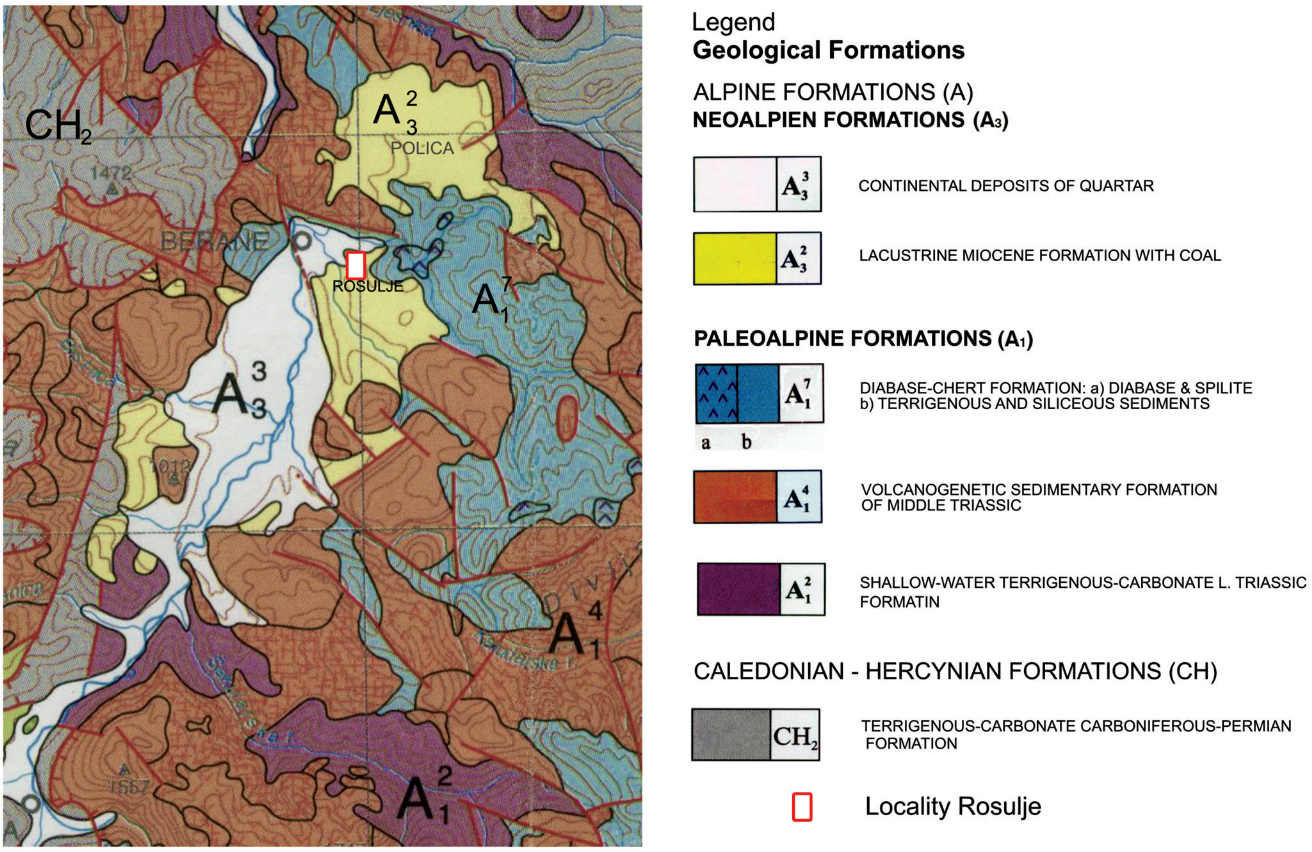

Fig. 2. Geological formations of the Berane coal basin area and the location of the Rosulje coal mine (modified according to PAJOVIĆ, 2000; DJORDJEVIĆ MILUTINOVIĆ & ĆULAFIĆ, 2008).

sulje Budimlja N 42°51'40,70"; E 19°53'41,00"; Elev. 703 m. (Berane Basin, Montenegro). The material was located in gray marly clay, about 2 meters above the coal seam (Fig. 3). In its upper part, this coal bed contains a thin layer of tuff corresponding to the second stage (cycle) of the formation of peat-mud sediments in the Berane coal basin, i.e. to the main coal seam (DROBNJAK et al., 1998). It is in this coal bed that the remains of *Indricotherium* sp. were discovered, on which grounds the bed was established to have been formed in Oligo–Miocene or Early Miocene (PETRONIJEVIĆ & THENIUS, 1958). The studied paleoflora of the Rosulje locality is closest to the reference coal seam and therefore also the oldest in comparison to the previously described flora of the whole Berane–Police coal basin.

In the Berane–Police Basin, the peat-mud sediments were formed during three cycles of sedimentation (Fig. 2). The first cycle included the northeastern part of Berane Basin (the area of Budimlje) and resulted in formation of so-called underlying coal layer (which most probably originated in late Oligocene). The second cycle of sedimentation included the whole area of Berane–Police Basin, resulting in formation of so-called main coal layer (formed during the Lower Miocene). The main coal layer has a complex structure as it includes several coal plates separated by barren sub-layers. The complete set of geological and geographic data on Berane basin relevant for records of paleoflora are presented in DJORDJEVIĆ MILUTINOVIĆ & ĆULAFIĆ (2010).

Fossil material

At the coal mine Rosulje there were about twenty recorded fragments of overlapping leaves (compression and impression). The central part of the lamina, with central plate typical for *Nelumbo* species, was preserved in some of the fragments, but the majority of the specimens include only the different peripheral parts of lamina with primary or secondary veins. Based on the comparison of different parts of fossil leaves, it was possible to establish the main characteristics of the leaf. Leaf cuticle was not preserved. In addition to the leaves, rhizome and roots were also found. This fossil material is deposited in the Natural History Museum in Belgrade, in the Paleobotanical collection NHMBEO 581: 957–967.

While the collected fossil material includes imprints (compressions and impressions) of leaves, rhizomes and roots, only the leaves were described as

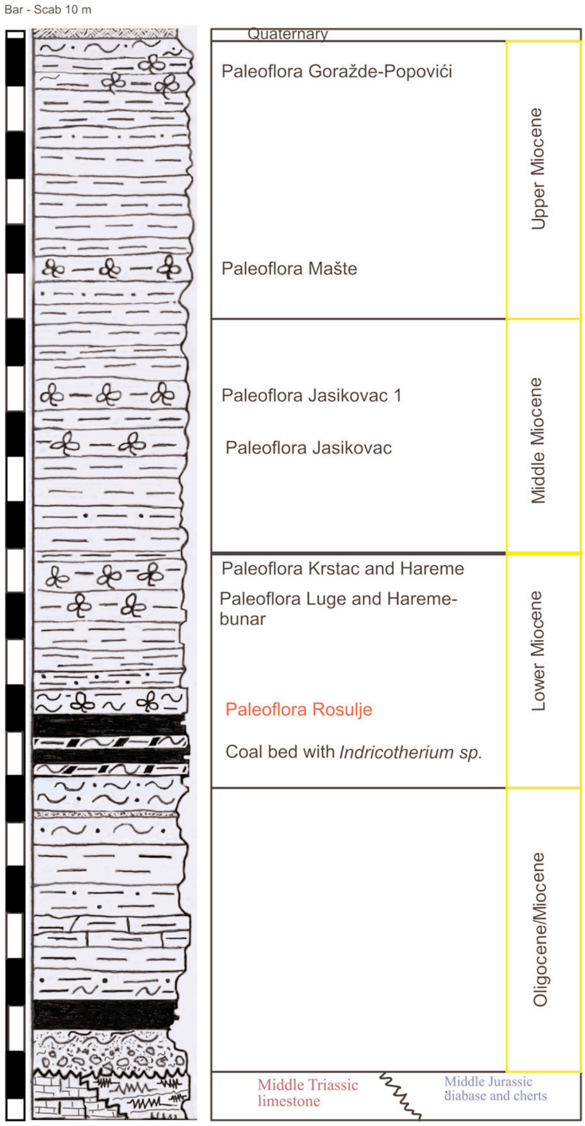

Fig. 3. Synthetic column of Miocene sediments of the Berane–Police Basin, with the position of the Rosulje paleoflora in relation to the main coal bed and the position of other paleofloras (modified according to Djordjević Milutinović & Ćulafić, 2010).

only they have *species specificus* characteristics necessary for the identification of fossil species.

Recent material

Extant leaves of *Nelumbo nucifera* and *Nelumbo lutea* were studied from herbarium materials and living specimens. The fresh, fully developed leaves were obtained from the ponds of Botanical Garden of the University of Zagreb (Croatia) and Szeged Botanical Garden (Hungary). The images of the lotus leaf for morphological analysis were taken by the image scanner including the whole lamina and some special parts to indicate the leaf venation pattern.

For the anatomical analysis of the leaves the samples were fixed in FAA (for-malin-acetic acid:ethanol, 10:5:85), dehydrated in graded ethanol series and embedded in paraffin wax at 58 °C. Sections (8 µm thick) were stained with haematoxylin and photographed under a Zeiss Axiovert microscope (Carl Zeiss GmbH, Göttingen, Germany).

Genus *Nelumbo* includes two species: *N. nucifera* and *N. lutea.* As morphoanatomical structure of leaves of both species is very similar, instead of repeated listing of both species the expression *species plurimae* - *Nelumbo* spp. was used throughout this paper as needed.

Results and discussion

Several species of *Nelumbo/Nelumbium* leaves from Tertiary period were recorded in Europe: *Nelumbium buchii* Ett.; *Nelumbium nymphaeoides* Ett.; *Nelumbium casparianum* Heer; *Nelumbium provinciale* Sap.; *Nelumbium protospeciosum* Sap.; *Nelumbo hungarica* Tuzson; *Nelumbium weylandii* Dotzler. Two species we were not taken into consideration: *Nelumbium ettingshausenii* Sieber 1890, which was subsequently found to be pseudofossil (Nemejc, 1975), and *Nelumbium lignitum* Schaff, mentioned by Heer (1859), for which the authors were unable to find any other data.

Of the above-mentioned species, *Nelumbo* from Berane are most similar to *N. protospeciosa* Sap. (Saporta, 1891) and *N. hungarica* Tuzson (Tuzson, 1911)*,* especially on the basis of the similar leaf shape, number of veins and type of venation. All of these characteristics are more or less common for both species, but as Tuzson specifically stated that existence of midvein is a species-specific characteristic of *Nelumbo hungarica*, the authors decided to determine the fossil records from Rosulje as *N. protospeciosa*, as presence of midvein was not definitively determined in material from Berane.

The other species of fossil *Nelumbo* do not match the imprints from Berane, as they have certain characteristics not recorded in our material: *Nelumbium buchii* Ett. had a pinnate midvein and primary veins that were not clearly dichotomously branched (Ettingshausen, 1855); *Nelumbium nymphaeoides* Ett. had a deeply indented lamina similar to *Nyphaeaceae* (Ettingshausen, 1855); *Nelumbium caspiarianum* Heer lacked clearly defined characteristics that could be used for identification (Heer, 1859); *Nelumbium provinciale* Sap. lacked the pronounced dichotomy of primary veins (Saporta, 1890a); *Nelumbium weylandii* Dotzler was defined according to veins that formed loops near the edge of the leaf margin (Dotzler, 1938) – the material from Berane does not include the part of leaf with margins.

Regarding all above criteria during the identification process it was not difficult to establish that fossil

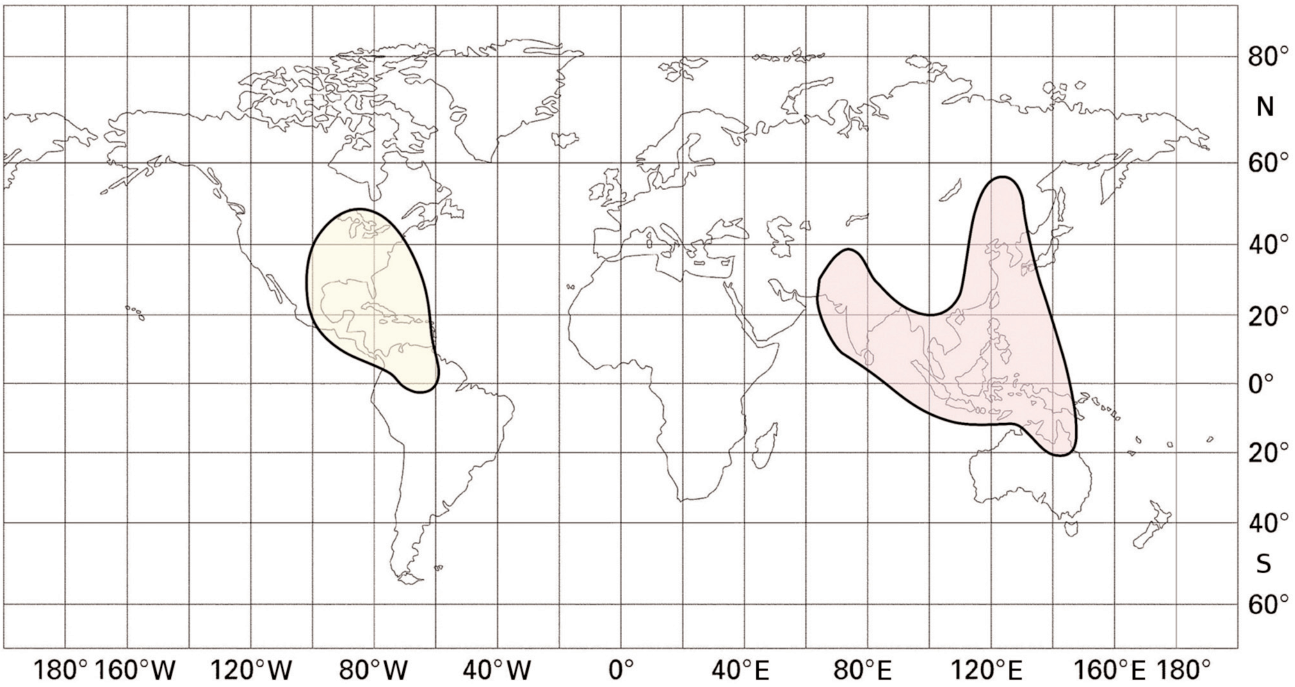

Fig. 4. Distribution of *Nelumbo lutea* and *Nelumbo nucifera* (modified according to Snigirevskaya, 1964).

material belonged to *Nelumbo protospeciosa* Sap., due to the typical characteristics of this species: centrally peltate leaf, completely orbicular lamina, radial (actinodromous) venation and approximately 20 dichotomously branched veins (Saporta, 1891).

Extant genus *Nelumbo* Adans 1763

Taxonomy

Genus *Nelumbo* belongs to the monogeneric family Nelumbonaceae, which, according to the modern phylogenetic classification of angiosperm (APG III 2009), belongs to the clade of eudicots, order Proteales.

Ordo: Proteales Jussieu ex Berchtold & J. Presl 1820
Familia: Nelumbonaceae Dumortier 1828
Genus: *Nelumbo* Adanson 1763 syn. *Nelumbium* Jussieu 1789

Nelumbo nucifera Gaertner 1788
Nelumbo lutea Willdenow 1799

Genus Nelumbo includes two species: *N. nucifera* Gaertner, which is naturally distributed in moderately warm to tropical regions of Asia and northeastern Australia, and *N. lutea* Willdenow, native to North America, all the way to Mexico and the Caribbean. In addition to these well-known scientific names, numerous synonyms have been used for both species. For example, synonyms for *N. lutea* are: *Nelumbium luteum* Willd., *Nelumbium pentapetalum* Walt. and *Nelumbo pentapetalum*, while *N. nucifera* is also referred to as *N. speciosum* Willd. or *Nymphaea nelumbo*.

Recent species *N. lutea* and *N. nucifera* are very similar to each other and there are no major differences between them. The main difference is observed in the colour of the flowers: in *N. lutea* the flowers are yellowish-creamy, while in *N. nucifera* they can be white, pale, pinkish to pale or distinctly pink. Some authors believe that they should not be divided into two species, and that they are actually two sub-species: *Nelumbo nucifera* ssp. *nucifera* and *Nelumbo nucifera* ssp. *lutea* (Guo et al., 2007).

Description of the leaves of recent *Nelumbo* spp.

Extant species of the *Nelumbo* have floating and emergent leaves (Fig. 5). Both develop from rhizomes. The lamina of the young leaves is small, incomplete and laterally rolled up (Fig. 5A). Young leaves are shaped this way to allow easier penetration from the rhizomes to the surface, regardless of whether they grow in deeper waters or muddy shallows. It is believed that it takes about two weeks for a rolled up leaf to fully develop (Tsuchiya & Nohara, 1989).

Emergent leaves (Fig. 5C) are usually more or less concave, depressed, funnel-shaped, and most often have a larger and thicker lamina than those that are floating (Fig. 5B). They are stouter, of stronger structure, and probably also have more sclerenchyma, as is the case with emergent leaves of other aquatic plants (Janković et al., 1980.). Also, the petioles of emergent leaves are more voluminous than those of flotant leaves. The length of the petiole depends on the depth of the water basin, ranging from 10 cm in shallow waters to 50 cm and longer in the deep.

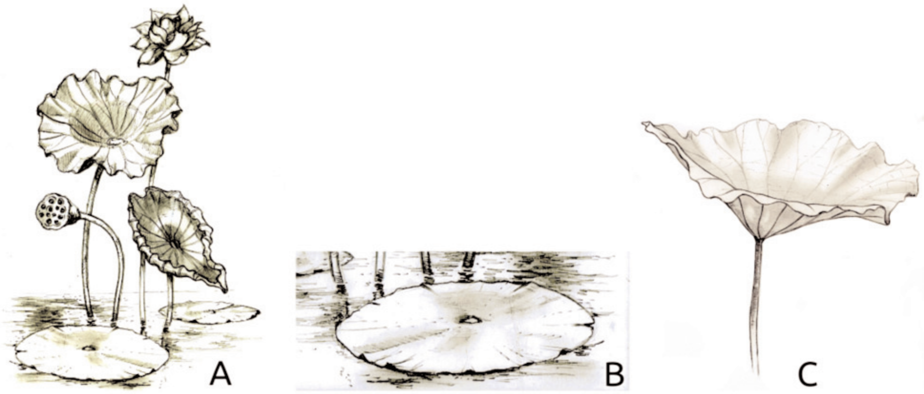

Fig. 5. *Nelumbo* spp. **A.** Floating and emergent leaves, young rolled up leaf that began to unfold, flower and fruit in natural habitat. **B**. Flotant leaf detail. **C.** Emergent leaf detail.

Both the emergent and floating leaves have the same macromorphological characteristics (Fig. 6): primary veins, clearly visible and slightly raised above the surface of the lamina, are radially distributed from the central disc located exactly above the spot where the petiole is inserted in the leaf. The diameter of the leaves ranges from 50 cm to 1 m. The leaf is centrally peltate with actinodromous venation, i.e. 20–25 strong primary veins are extending radially from the central disc to the margins. Primary veins branch dichotomously two to three times, usually in the upper third portion of the lamina. A similar number of primary veins was reported in *N. lutea* (Hall & Penfound, 1944). The midvein does not branch in either species of *Nelumbo*, extending instead in a straight line from the central disk to the margin of the leaf. As the bifurcation of the primary vein starts roughly from its upper third portion, reticulate-like venation of 3° and 4° veins is noticeable in this part of the leaf, almost at the edge.

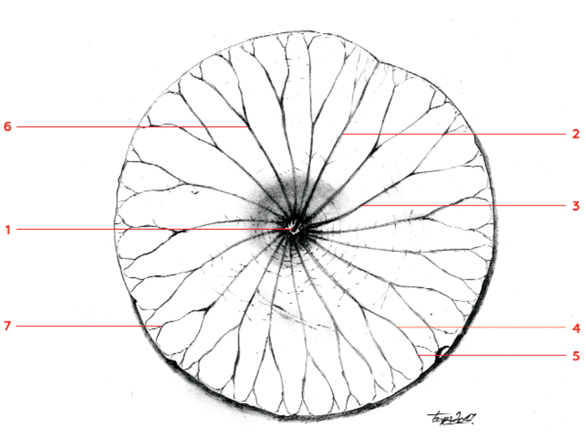

Fig. 6 Main leaf characteristics of *Nelumbo* spp. **1.** central plate; **2.** midvein; **3.** radial (actinodromous) venation; **4–5.** secondary veins; **6.** first dichotomous branching; **7.** second dichotomous branching.

In the epidermis of the central disk there are very large stomata (twice the size of those in the epidermis of the lamina), which are somewhat indrawn into the epidermis below which no palisade tissue exists (that is why the central disc is lighter in colour than the remaining part of the leaf) and where aerenchyma tissue and a number of air ducts developed instead. Such a central disc is an occurrence that is unique to *Nelumbo*, and its composition was described back in 1949. by Vouk & Njegovan who, at the time, named it “special pneumatoid organ”. With the help of today’s modern methods, it was however established that it is actually a special system of “pressurised ventilation” which provides aeration that is necessary in almost anaerobic, hypoxic muddy environment of swampy areas. According to various data from the literature (Matthew & Seymour, 2006), the air tubes in the leaf petiole occupy approximately 25 to 40% of the space.

The lamina is otherwise covered with papillae, which provides it with the so-called ultra (super) hydrophobicuty (Ensikat et al., 2011); in this way, the plate of the leaf does not become wet or dirty (“lotus effect”). As is the case with the majority of aquatic plants, stomata are located only on the upper side of the leaf, while collenchyma (mechanical tissue) is developed on the both side.

Description of the fossil leaves from Berane Basin

Nelumbo protospeciosa Saporta 1891

1890 *Nelumbium proto-speciosum* nomen nudum – Saporta, p. 192.
1891 *Nelumbium proto-speciosum* sp.n. – Saporta, p. 17, pl. 1, figs. 2–3, pl. 4, fig. 1.
1903 *Nelumbium protospeciosum* Saporta – Fritel, p. 269, fig. 335.
1961 *Nelumbo protospeciosa* Saporta – Vasilev, p. 140, pl. 15, figs. 1–3

The leaf is centrally peltate, lamina is orbicular, and venation is radial, actinodromous. The diameter of the leaf cannot be precisely determined since no leaves were preserved in their entirety, but it can be estimated that it was greater than 30 cm because the length of the longest preserved vein is 13 cm (Fig. 7B, B1; Pl. 1, fig. 5) before the point of the second bifurcation which is not preserved. Approximately 20 radially distributed primary veins extend from the central plate (Fig. 7A, A1; B, B1; Pl. 1, figs. 4–5). Primary veins are robust, straight, with dichotomous branching (bifurcations). The angle of first bifurcation is 30°–40° (Fig. 7C, C1; Pl. 1, fig. 1). Two specimens, compression and impression of the same leaf, (Pl. 1, figs. 4–5) contain a complete central part of lamina. Thanks to those specimens it can be seen that all primary veins, except unbranched one, made first bifurcation on the distance of 7–8 cm away the central plate. The unbranched vein is 9 cm long and it could possible be the midvein. Primary veins are robust and can reach a width of 4.5 mm (Pl. 1, fig. 3); longitudinal stripes, quite possibly air tubes or gas canals (Matthews & Seymour, 2006), can be noticed on the surface of some primary veins (Pl. 1, fig. 2). Secondary veins, created by the dichotomous branching (first bifurcation) of the primary veins, can be longer than 5 cm (Pl. 1, fig. 1). Primary and secondary veins are interconnected by opposite percurrent tertiary veins that are very similar to those found in recent *Nelumbo*. No second bifurcation point nor secondary veins are preserved in our material.

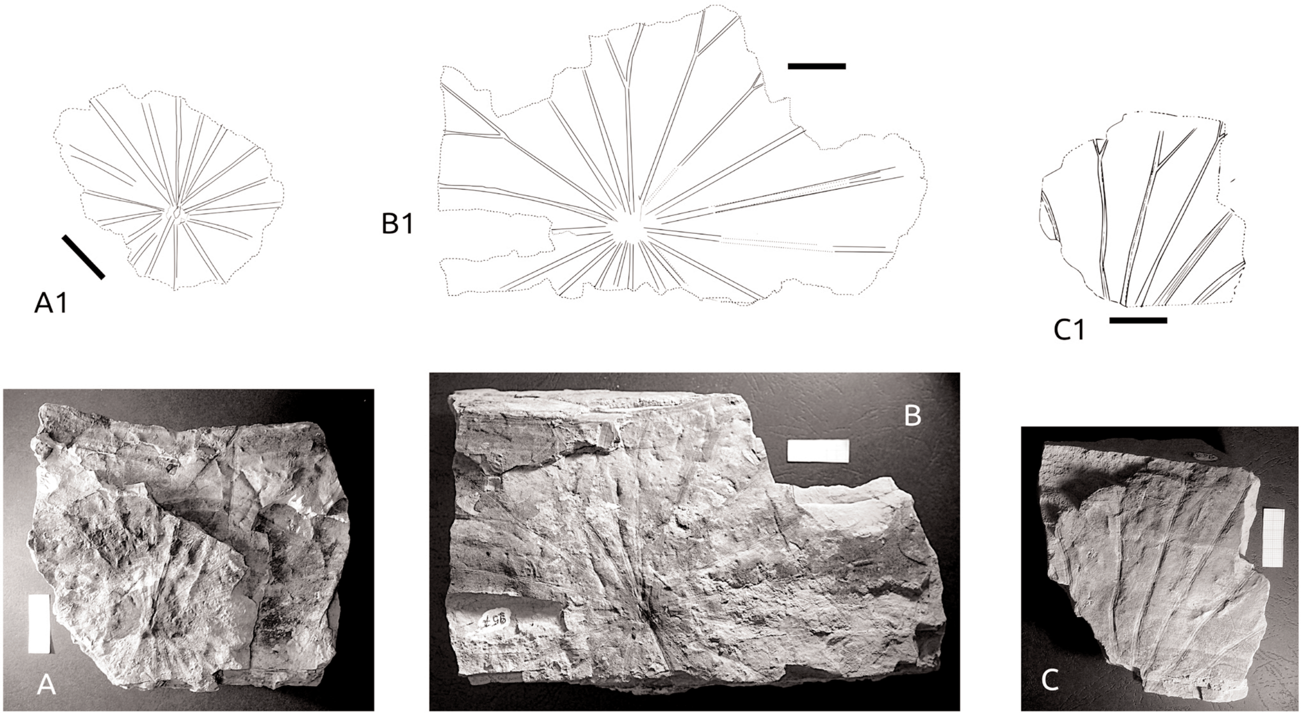

Fig. 7. *Nelumbo protospeciosa* Saporta from Berane basen, photograph and interpretative outline drawing. **A.** NHMBEO 581: 957; **B.** NHMBEO 581: 966; **C.** NHMBEO 581:963. Scale bar = 3 cm.

Nelumbo protospeciosa was recorded in several localities in Europe and Asia, dated from Eocene to Pliocene. It was first described by Saporta (1890b, 1891) from the locality Manosque, France (Oligocene/Early Miocene). According to the morphoanatomical structure of leaves and especially the number of primary veins (20–24), dichotomous vein branching and leaf size of about 40 cm, Saporta (1891) assumed that *Nelumbo* recorded at Manosque was a direct ancestor of modern *Nelumbo nucifera* Gaertn 1788 (syn. *Nelumbium speciosum* Willd. 1799). Therefore he named it *Nelumbium proto-speciosum*. According to shape and structure of leaves, Berry (1917) also assumed that *N. protospeciosa* was a direct ancestor of *N. nucifera*.

In addition to Mansoque (Saporta, 1891; Steur, 1993), fossil leaves of *N. protospeciosa* were also recorded in other localities of Eurasia (Fig. 9): Bulgaria, ?Eocene (Palamarev et al., 1998); China, Eocene (Guo, 1979) - later it was consider as new species *N. changchangensis* (He et al., 2010, Li et al., 2016); Iran, Miocene (Gabrielyan at al., 2012); Kazahstan Eocene, Oligocene and Miocene (Vasilev, 1961; Snigirevskaya, 1974); Poland, Miocene, only receptacles (Kowalski, 2016); Russia, Eocene and Miocene (Snigirevskaya, 1974: Budantsev, 1997 in Li et al., 2014a); Slovakia, Miocene (Kučerova, 2010); Romania, Pliocene (Ţicleanu & Diaconiţa, 1997; Ticleanu, 2006; Diaconu & Ticleanu, 2006); Ukraina, Pliocene, (Snigirevskaya, 1974).

Paleoenviroment

Except *Nelumbo*, no other plant remains were recorded at locality Rosulje. The imprints of rhizomes and roots (Fig. 8), indicate that *Nelumbo* was recorded *in situ* at the littoral zone of a Miocene lake. It is not possible to determine any more precise or more concrete characteristics of either climate or habitat just only on presence of *Nelumbo* fossils. Therefore, it was necessary to use the actualistic principle and examine the characteristics of modern lotus species, simultaneously with an analysis of the Lower Miocene vegetation of Luge-Haremi (Djordjević Milutinović & Ćulafić, 2010) recorded in the layer above the *Nelumbo* (Fig. 3). Finally, it is also necessary to consider the record of *Indricotherium* in the layer immediately below the layer with *Nelumbo*.

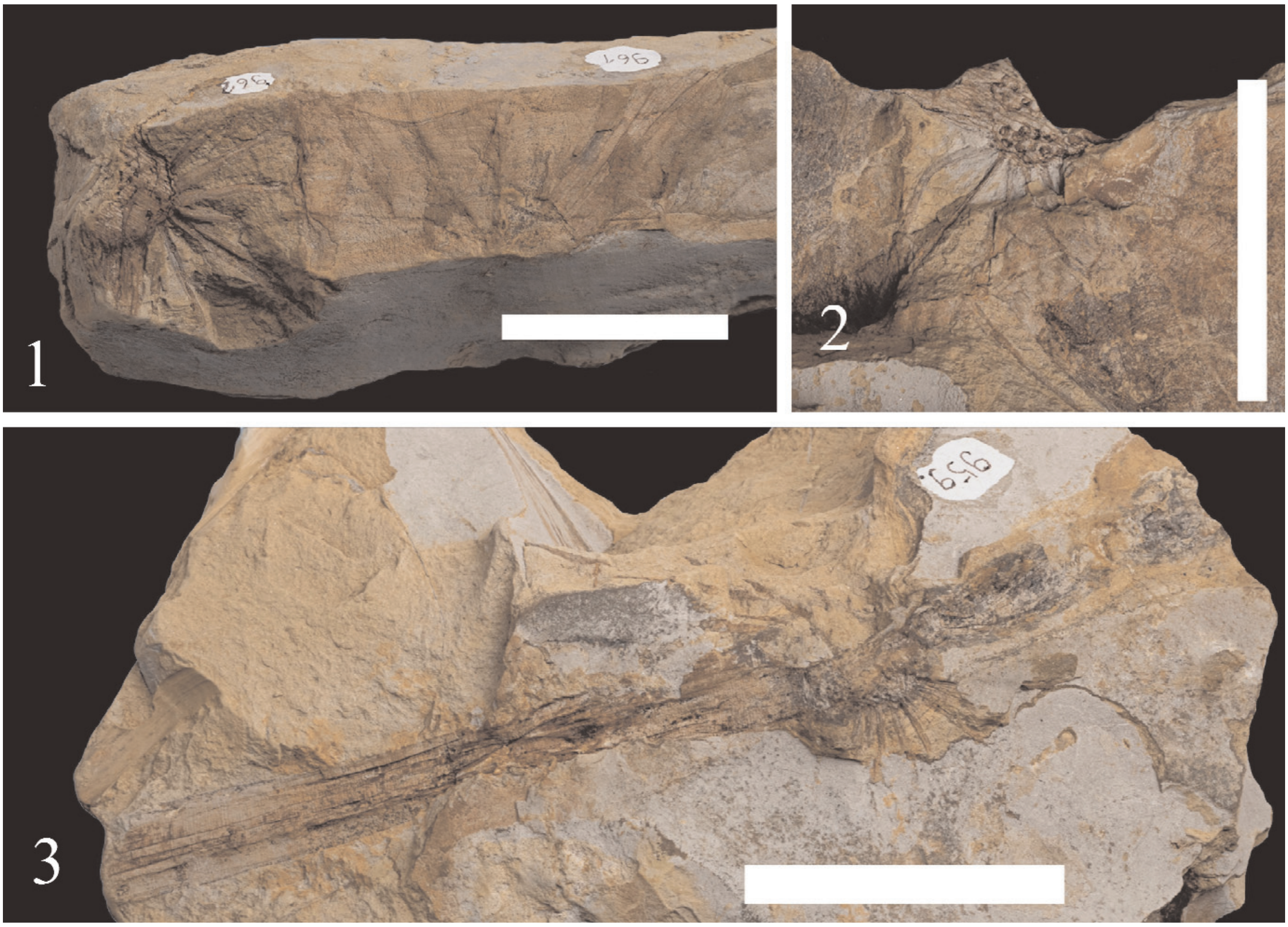

Fig. 8. Roots and rhizomes of *Nelumbo protospeciosa* Sap. found in Rosulje. **1.** NHMBEO 581:962; **2.** NHMBEO 581: 962a. **3.** NHMBEO 581:959. Scale bar = 5 cm.

General ecology of recent *Nelumbo* spp.

As typical aquatic plants that grow in slurry, shallow (mainly 2 m deep) water habitats, *Nelumbo* are characterised by heterophylly (polymorphism) i.e. developed floating and emergent leaves, flowers elevated highly above the water, strong rhizomes and weak roots (Stevanović & Janković, 2014).

Species of genus *Nelumbo* predominantly inhabit tropical-subtropical wetland zones, both in eastern Asia and Australia (*N. nucifera*) and in North America (*N. lutea*). Habitats of *Nelumbo* species include lakes, swamps, marshes, ponds, riverbanks, floodplains, where these perennial plants grow as floating/emergent hydro/hygrophytes. Both extant species of genus *Nelumbo* grow in shallow, calm waters with muddy bottom and in full sunlight. They also appear in wetland environments of temperate zone, at different altitudes, while *N. nucifera* may even be recorded in lakes at 1400 m above sea level in the Himalayan mountain range (Mukherjee et al., 2009). Generally these plant species are not cold resistant, therefore low temperature and short day length in the temperate zone induces their dormancy. There they survive the unfavorable winter period in form of tuber as dormant organs (Masuda et al., 2006; Li et al., 2014b). As mentioned previously, both *Nelumbo* species have two type of leaves, floating and emergent or aerial ones. In the beginning of vegetation period, primarily developed the floating leaves, flat in shape, followed by the emergent ones funnel-shaped and rising above the water surface. The floating leaves have shorter life span than that of emergent leaves. In disturbed habitat conditions *Nelumbo* spp. does not form abundant populations but floating leaves generally develop and their position ensures good photosynthetic activity and survival of the plant (Tsuchiya & Nohara, 1989). *Nelumbo* spp. are invasive species that often form mats and their wide floating leaves may cover a large part of the lake. Due to their extraordinary decorative appeal, *Nelumbo* plants are now distributed throughout the world, not only due to human cultivation and consumption, but also because of the very aggressive spreading from their natural habitats.

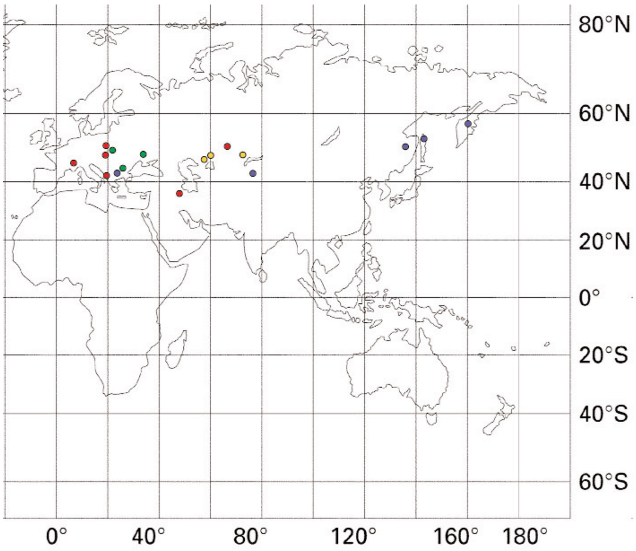

Fig. 9. Distribution of *Nelumbo protospeciosa*: Eocene (blue); Oligocene (yellow); Miocene (red) and Pliocene (green).

Lower Miocene flora of Berane Basin (Luge, Haremi)

Some very abundant paleoflora from Lower Miocene (Fig. 11) was recorded in at about a dozen synchronous localities listed under the shared name Luge–Haremi (Djordjević Milutinović & Ćulafić, 2010). This flora-bearing marl layer is situated above the *Nelumbo* layer but as they are both of Lower Miocene age (Fig. 3), it should be included during the reconstruction of climatic conditions and environment in which *Nelumbo* specimens once lived. As Djordjević Milutinović & Ćulafić assumed, the paleoflora Luge–Haremi (Fig. 11) indicates existence of a mixed deciduous-evergreen subtropical association which probably developed under Mediterranean climate. Presence of typical swamp dendroflora such as *Taxodium, Nyssa* or *Glyptostrobus* is minimal cc 2%, indicating that the banks were not overgrown with thick swamp forests and instead were mostly penetrable and well-insulated. Such open habitat also favors the heliophilous *Nelumbo*. Broad leaf deciduous (BLD) species were slightly more 40% abundant than the broad leaf evergreen species (BLE) 30% and the diversity of BLD was much greater. On the other hand, the broadleaf evergreen species were represented only with a few morphotypes, indicating displacement of evergreen floristic element by the deciduous one. Such composition of paleoflora indicates seasonal changes during the year (a colder or drier period alternating with a warmer or more humid period).

As the described flora also belonged to Lower Miocene it may be assumed that *Nelumbo protospeciosa* also lived under influence of more or less similar Mediterranean climate. Therefore its habitats were probably closest to habitats of modern *Nelumbo* spp. inhabiting regions around 40° N (Fig. 4).

The occurrence of *Indricotherium*

The third factor that may contribute to determining the habitat of Miocene lotus at Berane was appearance of *Indricotherium* (Petronijević & Thenius). Its remains were recorded in the main coal layer immediately below the layer with *Nelumbo*. *Indricotherium* (syn. *Paraceratherium*) was hornless rhinoceros and the largest known land mammal, up to 7 m tall. Those animals were herbivorous and lived in herds. As they inhabited steppe-savanna areas (Prothero, 2013),

Fig. 10. Supposed appearance of the lake shore habitat of *Nelumbo protospeciosa*.

Broad-leaved evergreen (BLE) component 30%	Broad-leaved deciduous (BLD) component 40%	Conifer component 13%	Sclerophyllous and legume-type component 20%:
Aristolochia sp.	*Acer palaeosacharinum*	*Cunninghamia miocenica*	*Berberis bursukensis*
Daphnogene sp.	*Acer tricuspidatum*	*Glyptostrobus europaeus*	*Fabales*
Dicotylophyllum sp. 1.	*Acer* sp.	*Juniperus* sp.,	*Ilex sphenophylla*
Lauraceae	*Acer* sp. fructus	*Pinus hepios*	*Mahonia* sp.
Magnolia sp.	? *Alnus ducalis*	*Pinus* sp. conus	*Quercus alexevii*
Ocotea herii	*Alnus gaudinii*	*Pinus tadaeformis*	*Quercus mediterranea*
Persea sp.	*Alnus kefersteinii* fructus	*Sequoia abietina*	*Sapotacites minor*
Quercus apocinophyllum	*Betulaceae* gen. et sp. indet.	*Taxodium dubium*	
Quercus neriifolia	*Castanea atavia*	*Taxodiaceae* leaves	
Rhodomyrtophyllum sinuatum	*Cercidiphyllum crenatum*	*Taxodiaceae* conus	
	Cyclocarya cyclocarpa		
	Engelhardtia orsbergensis		
	Fagus attenuata		
	Fagus pristina		
	Fagus saxonica		
	Fraxinus sp. fructus		
	Juglans acuminata		
	Populus germanica		
	Pterocarya paradisiaca		
	Ulmus carpinoides		
	Zelkova zelkovifolia		

Fig. 11. Paleofloristic composition of the Lower Miocene marly beds in Luge-Hareme locality in Berane basen (Djordjevic Milutinović & Ćulafić, 2010).

their presence indicates that the wider region around the Berane Basin included lowland grasslands suitable for movement of such large animals (Fig. 10).

All three presented factors: Lower Miocene paleoflora Luge–Haremi; heliophilous characteristics of recent *Nelumbo* spp. and presence of large hornless indricotherids, could indicate that the coastal part of the lake, inhabited by the population of *Nelumbo protospeciosa*, was under influence of subtropical/Mediterranean climate and well-insulated, with noticeable absence of typical swamp forests of *Taxodium* and *Glyptostrobus*. Due to low percentage of swamp trees and their aerial-roots (pneumatophores) protruding from ground, the lake shore was probably accessible as a drinking area for large herbivores.

Conclusion

During the Lower Miocene, the lake in Berane basin was inhabited by populations of Miocene lotus *Nelumbo protospeciosa* Sap., with leaf diameter of at least 30 cm. The main morphoanatomical characteristics of leaves were very similar to those in recent *Nelumbo* spp. The leaf was orbicular in shape, with a centrally placed petiole. Venation was actinodromous with about 20 larger veins, each branching dichotomously about 8 cm from the central disk. The existence of midrib (main vein) could not be determined with any certainty, although one of the recorded veins, about 9 cm long, did not show dichotomous branching and may represent the remains of the midrib.

As collected leaves were accompanied by rhizomes and roots, it may be concluded that material was *in situ*, at the same place where the plants lived. The lake shore was probably not inhabited by swamp dendroflora but open and well-insulated, matching the habitat of modern, heliophilous lotus species. According to the previous studies on Lower Miocene flora of Luge–Haremi it is believed that lotus plants at Berane Basin probably lived under conditions of subtropical/Mediterranean climate.

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Резиме

Nelumbo protospeciosa Saporta 1891. из Беранског басена у Црној Гори (доњи миоцен)

Током истражних радова 1995. године у руднику угља Росуље у Беранском басену у Црној Гори (Figs. 1, 2) нађени су у глиновитим лапорцима доњомиоценске старости (Fig. 3) фосилни остаци лотоса *Nelumbo protospeciosa* Sap. (Fig. 8; Pl. 1).

Фосилни материјал се састоји од двадесетак отисака, компресија и импресија, листова, коренова и ризома и налази се депонован у Природњачком музеју у Београду у Палеоботаничкој колекцији NHMBEO 581: 957–967.

Савремени представници рода *Nelumbo*

Nelumbo Adanson 1763
syn. *Nelumbium* Jussieu 1789

Савремени род *Nelumbo* обухвата две врсте: индијски лотос *Nelumbo nucifera* Gaertner 1788 који расте у Азији и жути лотос *Nelumbo lutea* Willdenow 1799 који насељава Северну Америку (Fig. 4). Обе врсте су веома сличне и разлика међу њима је углавном у боји цвета и географском распрострањењу. Основне карактеристике листа (Fig. 6) заједничке за обе врсте су: а) округла, орбикуларна, лисна плоча; б) централно постављена лисна дршка; в) присуство централног диска, структуре која се формира на месту где лисна дршка улази у лисну плочу; г) актинодромна нерватура коју гради око двадестеак примарних нерава; д) прва бифуркација или дихотомо гранање примарне нерватуре – сваки нерв, осим једног, се дихтомо грана на горњој трећини лиске дајући два секундарна нерва. ђ) друга бифуркација – сваки секундарни нерв се грана у близини маргине; ж) постојање главног нерва: један примарни нерв се не дели дихотомо већ као негранат иде до маргине и улази у њу. Овај негранати нерв се назива главни нерв и он је оса око које је са леве и десне стране „уролан“ млади лист лотоса градећи копљасту структуру којом се пробија кроз воду (Тек када стигне до површине копљасто уролана листа се отвара и формира препознатљив орбикуларни облик).

У случају када се код фосилног материјала установи постојање две или више описаних карактеристика лист се углавном идентификује као *Nelumbo*. Од свих наведених карактеристика најређа је и најтеже се уочава присутност главног нерва, јер је он нежнији и тањи од осталих и ретко када се очува у фосилном материјалу.

Опис фосилног материјала

Nelumbo protospeciosa Saporta 1891

Приликом прегледа фосилног материјала на основу отисака коренова и ризома од самог почетка је било јасно да се ради о акватичним биљкама, али је тек на основу листова закључено да је у питању род *Nelumbo*. Даљом провером морфоанатомије листа, утврђене су карактеристике које недвосмислено говоре да се ради о врсти *Nelumbo protospeciosa* Sap.

Лист је орбикуларан, лисна дршка је централно постављена. Примарни нерви су радијално распоређени, нерватура је актинодромна. Пречник листа не може бити прецизно утврђен јер се ни један лист није сачувао у целости од центра до маргине, али може се оценити да је пречник био већи од 30 cm, јер се на једном примерку налази нерв који је дугачак 13 cm (Fig. 7B, B1) пре места друге бифуркције. Од централног диска полази око двадесетак јаких примарних нерава који се на 7–8 cm дужине дихотомо деле на два секундарна нерва (Fig. 7. B, B1). Угао рачвања (дихотомог гранања) је код већине око 30°–40° (Pl. 1, fig. 1). На примерцима NHMBEO 581: 957 и 966, који представљају позитив и негатив истог листа сачуван је и један негранати примарни нерв дугачак 9 cm. Он нема рачвање на два секундарна нерва па се може претпоставити да би то могао бити главни нерв. Сви примарни нерви су крупни и неки од њих достижу ширину до 4.5 mm (Pl. 1, fig. 3). Дуж неких нерава, нарочито крупнијих, могу се запазити уздужне линије које вероватно представљају остатке аеренхимског ткива или канала за вентилацију (Fig. 7C, C1; Pl.1, fig. 2).

Станиште *Nelumbo protospeciosa* Sap.

Глиновото-лапоровити слој у коме су нађени остаци *Nelumbo protospeciosa* налази се између лапоровитог слоја у коме је нађена веома богата доњемиоценска флора Луге–Хареми (Djordjević Milutinović & Ćulafić, 2010) и главног угљеног слоја у коме су нађени остаци безрогог носорога *Indricotherium* sp. (Petronijević & Thenius, 1958). Овакав положај слојева са *Nelumbo protospeciosa* (Fig. 3) указује да су остаци лотоса доњемиоценске старости и треба напоменути да они за сада представљају најстарију флору нађену у Беранском басену.

Поред отисака *Nelumbo* нису нађени остаци других биљака. Тако да на основу само овог налаза не можемо рећи ништа ближе о станишту, вегетацији или клими овог миоценског предела. Остаци ризома и коренова (Fig. 8) указују да је *Nelumbo* нађен *in situ* и да је управо ту била литорална зона миоценског језера. Због недостатка других фосилних налаза за реконструкцију станишта и климата миоценског лотоса примењен је актуелистички принцип и разматрање станишта у односу на станиште данашњег *Nelumbo* spp. као и анализа доњемиоценске флоре Луге–Хареми (Fig. 11) која је нађена у слоју изнад *Nelumbo*. На крају треба узети у обзир и налазак *Indrocotherium*-а у слоју непосредно испод слоја са *Nelumbo*.

На основу остатака акватичних биљака *Nelumbo protospeciosa,* анализе палеофлоре Луге–Хареми, примене актуелистичког принципа поређења са рецентним *Nelumbo* spp. као и претходних истраживања Беранско-Поличког басена (Drobnjak et al., 1996; 1998;) можемо закључити да је током миоцена на подручју Беранског басена, који је био под утицајем суптропске /медитеранске климе, постојало језеро чије су обале и плићаке почетком миоцена, а вероватно и касније, насељавале популације *Nelumbo protospeciosa* Sap. Ова врста миоценског лотоса била је веома слична рецентним врстама, нарочито у погледу морфоанатомије листова који су достизали ширину од око 30 cm. Услед недостатка типичне мочварне дендрофлоре (*Taxodium, Nyssa* и *Glyptorstrobus* чине свега 2% палеофлоре) станиште миоценских лотоса у Беранском басену било је отворено, добро инсолирано, и вероватно приступачно животињама и као појило. С обзиром да је за род *Nelumbo* каратеристично да гради изузетно велике и густе популације, стварајући при том значајну количину хранљиве биомасе, можемо претпоставити да су га миоценске хербиворе често користиле и као извор хране. Да ли је *Nelumbo protospeciosa* Sap. наставио своју егзистенцију и током средњег и горњег миоцена или плиоцена за сада није познато, јер у млађим беранским слојевима нису нађени остаци *Nelumbo* или других акватичних и семиакватичних биљака.

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Plate I

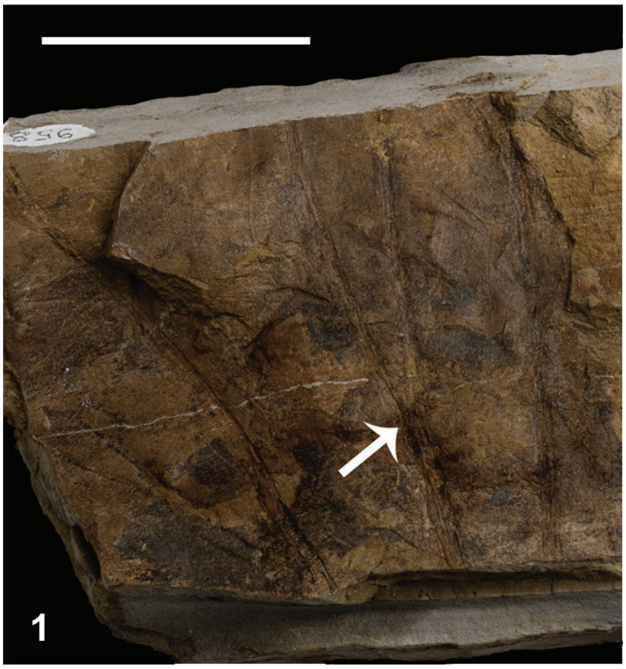
The selected fossils leaves of *Nelumbo protospeciosa*
Scale bar = 5 cm

Fig. 1. Bifurcation of primary veins, NHMBEO 581:958.

Fig. 2. Longitudinal lines originating from the air tubes are noticeable on the primary veins, NHMBEO 581:563.

Fig. 3. Part of the leaf near the central plate. The largest width of the secondary veins – 4.5 mm, was recorded in this specimen, also noticeable is a 3° venation. NHMBEO 581:964;

Figs. 4,5. Impression and compression of the same leaf, with a very well preserved central plate. Based on this two specimens fossils material are identified as *Nelumbo* genera. NHMBEO 581:966 and 957.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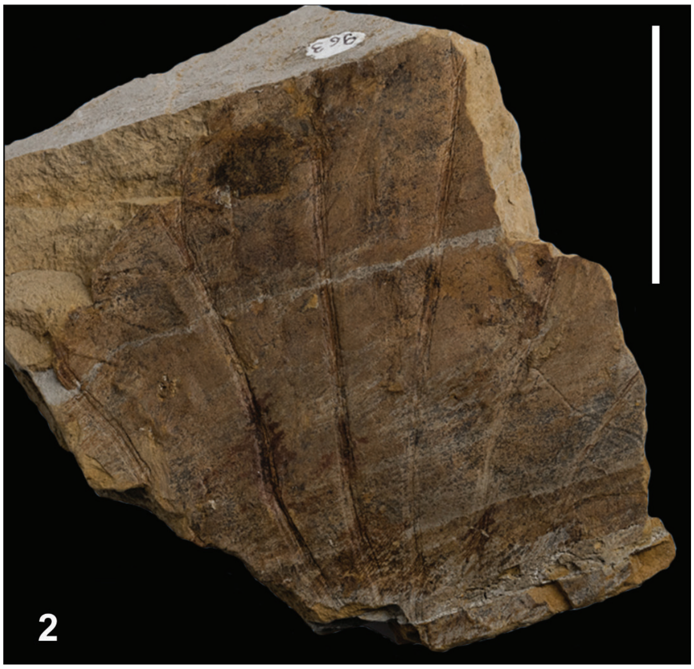

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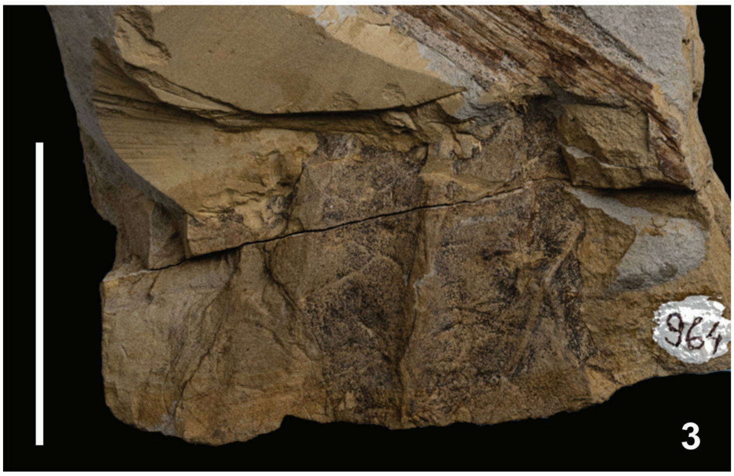

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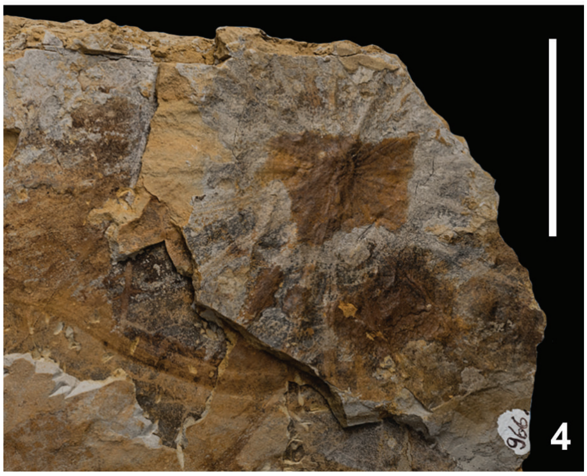

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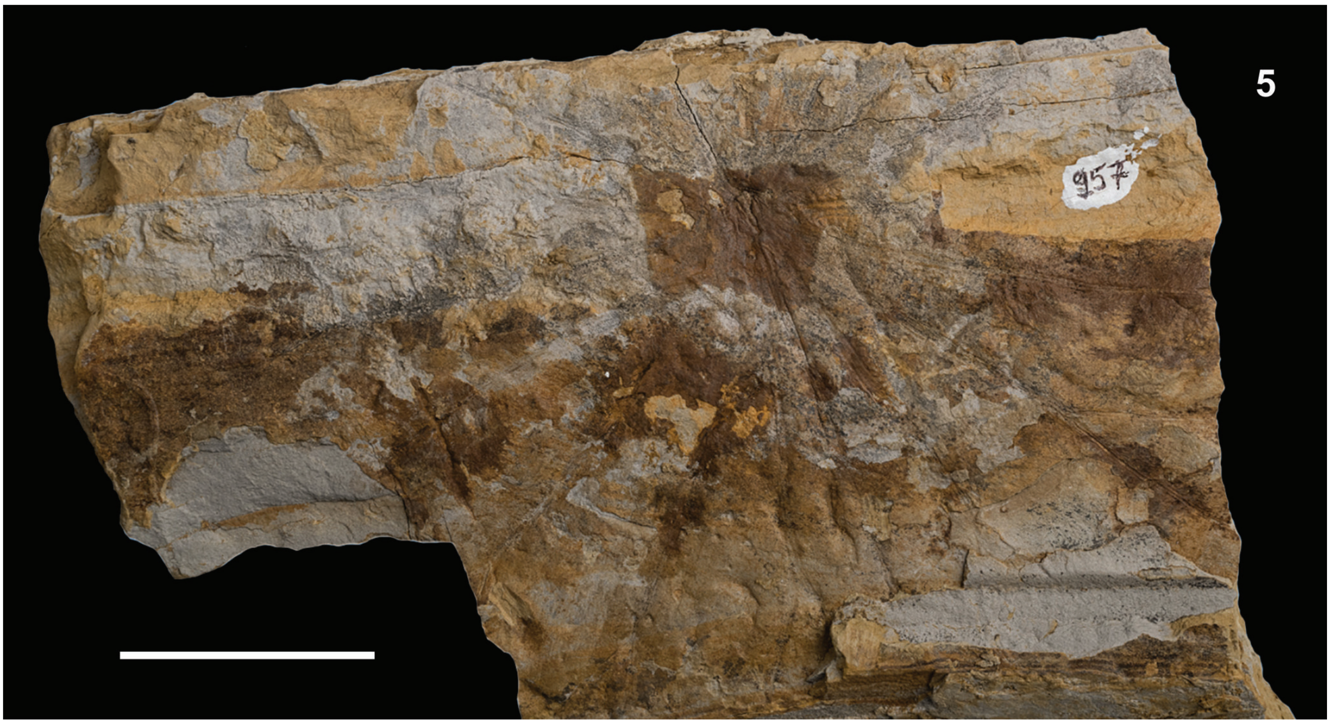

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