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Original scientific paper

PERMO-CARBONIFEROUS FLORA OF THE MLAVA-PEK COAL BASIN (EASTERN SERBIA)

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Approximately 400 fossil plant remains from the Late Stephanian and Stephanian-Permian periods had been found in eastern Serbia, in the area between the rivers Mlava and Pek. They were classified into two collections: ‘Mlava-Pek *sensu lato*’ and ‘Borogin Potok, Ranovac village’. The fossil materials are remnants of a tropical Carboniferous forest that was dominated by seed ferns, primarily *Alethopteris, Linopteris, Odontopteris, Neuropteris, Autunia,* and tree ferns, mostly *Pecopteris / Asterotheca*, *Cordaites*, and to a much lesser extent by Lepidodendrales and Equisetidae. The ‘Mlava-Pek *sensu lato*’ collection contains Late Stephanian paleoflora and includes swamp plants Lepidodendrales and Equisetidae, while the ‘Borogin Potok, Ranovac village’ collection is composed of a slightly younger, Stephanian-Permian flora and does not include Lepidodendrales. It is dominated also by seed ferns, but there is no *Odontopteris* while *Autunia conferta*, as a species that is associated with the boundary layers of the Carboniferous-Permian, can be found in smaller quantities in both collections.

In addition to its scientific value, the ‘Mlava-Pek *sensu lato*’ collection also has an exceptional cultural and museological values because it contains the first paleobotanical fossils that were collected in Serbia in the course of the 19th century. In 2022, this collection was declared a Cultural Heritage of the Republic of Serbia.

Key words: seed ferns, *Alethopteris, Linopteris, Odontopteris*, Carboniferous, Stephanian, Permian

INTRODUCTION

The paper describes the Late Paleozoic flora that was found in the area of the coal basin located between the Mlava and Pek rivers in eastern Serbia (Figs. 1, 2). This paleoflora existed during the Stephanian and the transition into the Permian (Malešević *et al.* 1980, Kalenić *et al.* 1980). There were three main plant-geographic units on Earth in this period: the Euramerican tropical province, the Angaran north-temperate province, and the Gondwanan south-temperate province (Chaloner & Lacey 1973). The area of today's eastern Serbia, which is where the above described specimens were found, belonged to the Euramerican tropical province south of the Variscan Mountains (Figs. 3, 4).

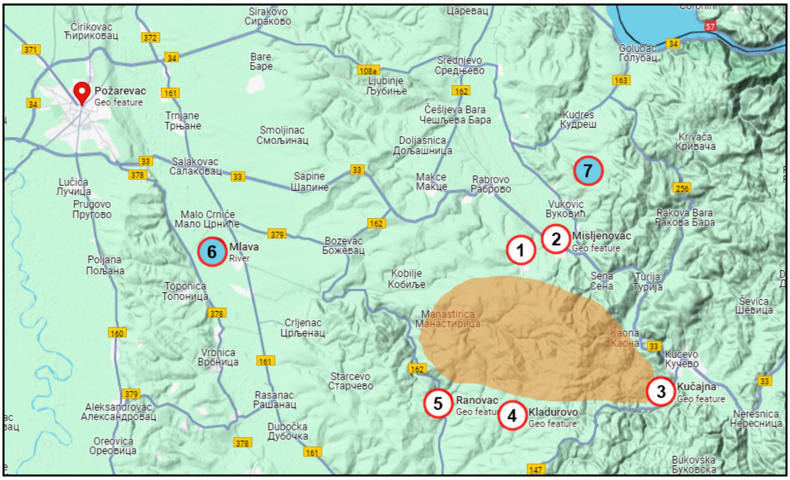

Fig. 1. – Mlava-Pek coal basin and the position of localities where paleoflora was found (Požarevac district): 1 Mustapić, 2. Mišljenovac, 3. Kučajna, 4. Kladurvo, 5. Ranovac (Borogin potok, Osipaonički potok, Slani potok), 6. Mlava river, 7. Pek river. Shaded area-central part of Mlava-Pek coalfield.

Fig. 2. – The geographic location of the Mlava-Pek coal basin, eastern Serbia (Google maps).

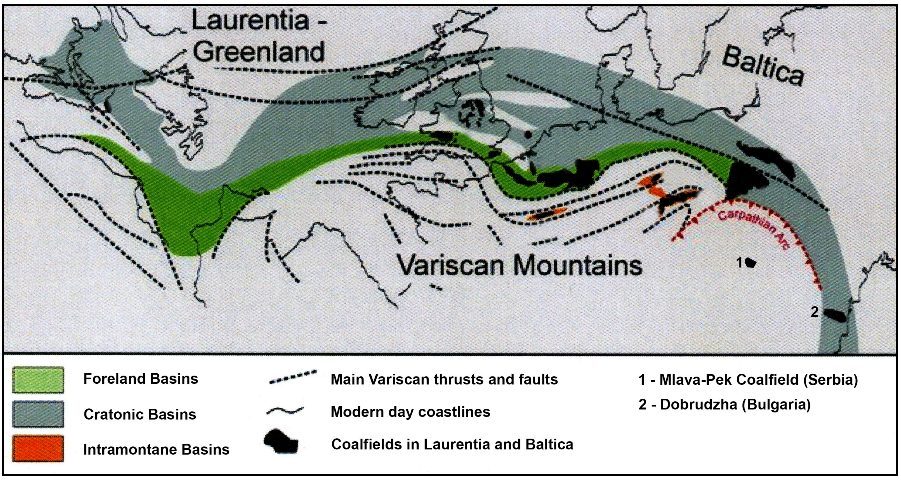

Fig. 3. – The position of the Mlava-Pek basin (1) in relation to the Variscan Mountains, and the relative position of this basin in relation to the Dobrudzha coal basin (2) in Bulgaria (slightly modified after Cleal *et al.* 2009).

Fig. 4. – Probable position of the Mlava-Pek coal basin (1) during the Late Carboniferous (slightly modified after C. R. Scoteze 2014 map57).

A bipolar cooling of the climate occurred during this period, within the Late Paleozoic Ice Age, reflected in the appearance of widespread ice sheets in the Southern Hemisphere (Gondwana) and the local glaciation of the Siberian land in the Northern Hemisphere (Fielding *et al.* 2008). The bipolar ice age phase led to the aridification of the climate on the equator, and the gradual disappearance of swamps and swamp vegetation of arborescent lycopods (Lepidodendrales). The endless Westphalian wetlands and swamps were gradually replaced by more arid areas dominated by tree ferns, seed ferns and *Cordaites*. The Late Paleozoic Ice Age began about 340 mya and gradually ended during the Permian, arond 290 mya; however, in some of the southern areas of Gondwana, it lasted until the middle of the Permian, cca 260 mya (Montanez & Poulsen 2013). This, as far as we know, was the longest ice age on our planet. There were several glaciations and interglaciations, of which the glaciation that occurred during the Stephanian and the beginning of the Permian was the last and strongest. After that, the Carboniferous icehouse climate was replaced by the Permian greenhouse climate (Fielding *et al.* 2008). The Late Carboniferous period was cold and very similar to the Pliocene and Pleistocene (DiMichele *et al.* 2001, Cleal & Thomas 2005).

The ice caps melted at the end of the Carboniferous and the beginning of the Permian; the greenhouse effect appeared as a consequence, fully manifesting in the second half of the Permian (Retallack 2013). The melting of the ice caused the level of the world sea to rise, so the wetlands - which are so characteristic of the Carboniferous period, slowly begin to disappear-turned into deeper water basins, causing in turn the disappearance of the typical wetland vegetation of the Westphalian and Lower Stephanian. The climate experienced a gradual aridification and arborescent lycopods were gradually replaced, to an ever-greater degree, by species from more arid habitats such as seed ferns and cordaites.

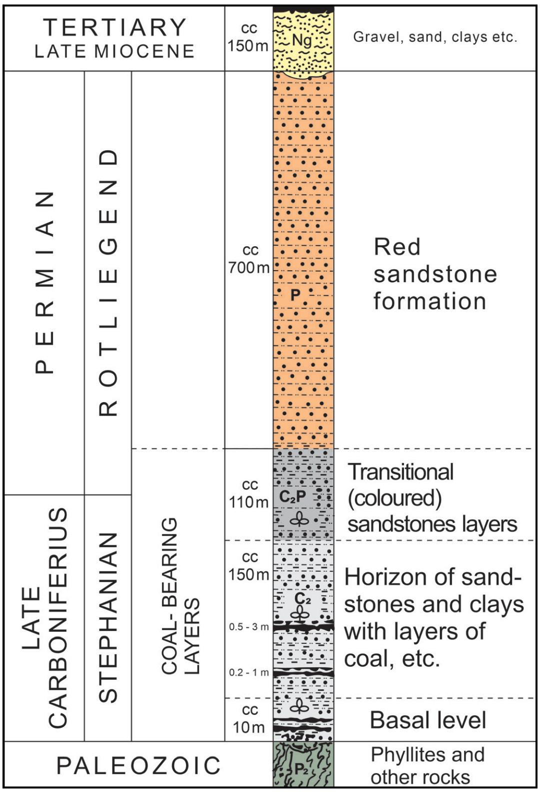

Fig. 5. – Geological column of the Mlava-Pek basin (after Pantić & Nikolić, 1973).

In Serbia, coal sediments of the Carboniferous age are rare and barely profitable. These are mainly deposits of limited surface, with poorly developed coal layers – rather interlayers - and significant admixtures of inorganic material. They are mainly part of the Carpatho-Balkanides of eastern Serbia (Getic nappe system): between Mlava and Pek rivers in the north, on Mt. Miroč, at the foot of Vrška Čuka, on Stara and Suva mountains, and southeast of Despotovac (Pantić & Nikolić 1973, Mladeno-vić *et al.* 2018). This entire area of eastern Serbia is known as the location where different Paleozoic and Mesozoic flora had been found. Namely, during the Paleozoic and Mesozoic, this area was part of the ocean coast, while central Serbia was mostly part of the ocean floor (Pantić 1960, Pantić & Nikolić 1962, Pantić 1969). Thus, it is possible to find Devonian, Carboniferous, Jurassic and Cretaceous floras along the border with Bulgaria and Romania (Djordjević Milutinović 2010), while various deep-sea fauna from the same periods can be found in central Serbia.

The coal-bearing series consists of three layers (Fig. 5). The first is the floor layer, which itself contains interlayers of coal layers. A coal-bearing horizon with two coal layers lies above it. These two layers are of variable and irregular thickness, and there is a large number of coal interlayers between them. The lower, older coal layer, with a thickness of approxima-tely 0.2 to 0.6 *m*, is not stable and does not occur in the entire basin, while the upper or main coal layer lies 15 *m* above it. Above the main coal layer there is a roof layer that is up to 100 *m* thick; it, too, contains interlayers of coal that transition into a layer of coloured sandstones, above which lies a series of red Permian sandstones. The red Permian sandstones continuously transition into coloured sandstones. Paleoflora was found in all three parts of the coal-bearing series, but mostly in the immediate roof of the main, i.e. younger coal layer.

MATERIAL AND METHODS

The fossil plants described in this paper can be found in the Paleobotanical Collection at the Natural History Museum in Belgrade. The material consists of approximately 400 specimens, of which inventory numbers PALBOT (Coll.No. 40 / I and 40 / II) 11, 12, 19, 25, 71–172, 222, 591, 616, 1028, 1929–1030, 1032, 1032–1034, 1036, 1504 and 1981 belong to the 'Mlava-Pek *sensu lato*' collection, while specimens bearing inventory numbers PALBOT (Coll.No. 40 / III) 1982–2094, belong to the collection entitled 'Borogin potok, Ranovac village'. Most of the specimens are adpressions of leaves without cuticles. But there are also seeds, as well as parts of stems fossilised in the form of adpressions, petrified parts or casts.

Fossil material is represented mainly by smaller fragments of fronds, such as pinnules, pinnae or parts of leaves, as is the case with *Cordaites*. Only in rare cases did the impressions preserve clearly visible secondary and especially tertiary veins. The identification was performed mainly based on pinnule morphology, venation (when it was possible), and the overall macro-anatomy (pinnule shape, i.e. whether robust or fragile, the appearance of the margin, and the overall impression). When counting the numbers of *Linopteris*, *Alethopteris* and *Odontopteris*, the pinnules of *Linopteris* were equated with the pinnae of *Alethopteris* and *Odontopteris*. The author was guided by the assumption that the pinnule of *Linopteris* is equal to the secondary pinna of *Alethopteris* and *Odontopteris* (Fig. 6).

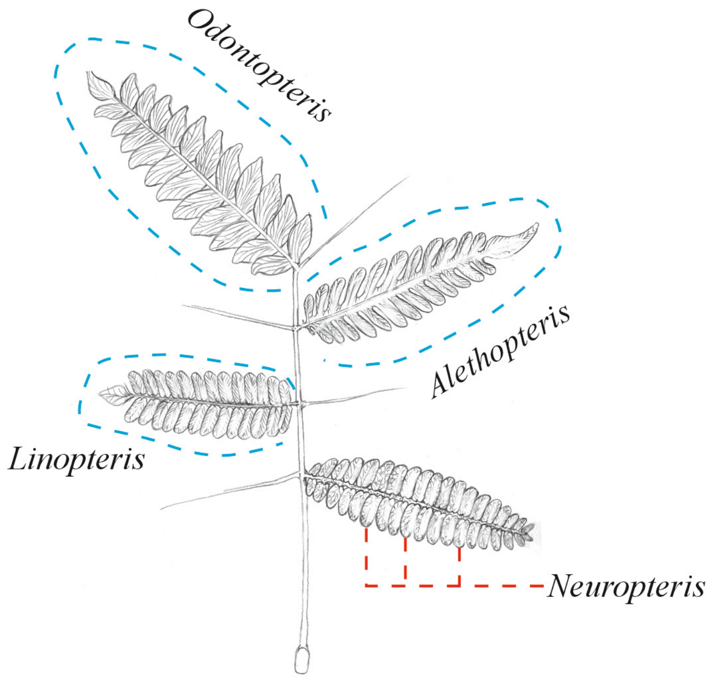

Fig. 6. – Hypothetical model of seed fern and explanation of which parts of the plant are most commonly found in fossil form in the Mlava-Pek region a. *Odontopteris*, parts of a pinna; b. *Alethopteris*, parts of a pinna; c. *Neuropteris*, parts of a pinna, d. *Linopteris*, individual pinnules.

The identification of plant fossils and the occasional revisions were made in different periods. The first identifications, in the 1880s, were made by Dionýz Štúr (Imperial Geological Institute in Vienna), and probably Josif Pančić (Grande école or "Velika škola" in Belgrade, Serbia).[1] It is

[1] Velika škola was the highest ranking educational institution in Serbia between 1808 and 1905.

possible that some were also made by Nikola Pantić (Faculty of Mining and Geology in Belgrade) around 1950; by Desa Djordjević Milutinović (Natural History Museum in Belgrade) in the period from 1995 to 2023; by Ivana Stevanović in 1996 (Faculty of Mining and Geology in Belgrade); and by Janaki Tenchov in 2010 (Geological Institute, Bulgarian Academy of Sciences), while some of the seed ferns were identified by Christopher Cleal in 2011–2012 (National Museum Wales, UK).

The taxonomic division for the higher taxonomy categories was based on PPG1 2016, for arborescent lycopods (Lycopodiopsida, Lepidodendrales), horsetails (Equisetidae, Polypodiopsida), tree ferns (Marattiidae and Polypodiidae), seed ferns (Pteridospermatopsida) and *Cordaites* (Gymnospermopsida). The division from DiMichele *et al.* (2006) was used to establish the seed ferns belonging to certain families: *Alethopteris* - Neuralethopteridaceae; Linopteris - Parispermaceae; *Odontopteris* and *Neuropteris* - Neurodontopteridaceae and *Autunia*, ordo Peltaspermales. Besides the literature listed in the text, the publication by Cleal & Thomas (1994) was also used to identify the fossil material.

It should be emphasized that the term “paleoflora” used in this paper does not correspond to and cannot be compared with the botanical term “flora”, just as “paleovegetation” cannot be compared to the term (recent) vegetation. Both paleoflora and paleovegetation, in addition to their spatial and taxonomic dimensions, also have a temporal dimension, encompassing taxa found in a nearby area that lived during the same or similar geological time period

The following cameras were used to take photographs that are shown on the panels: camera Nikon Z7 II, lens Nikon AF-S Micro NIKKOR 60mm f / 2.8G ED, flash Profoto D2 500 AirTTL Monolight; Nikon SB-5000 Speedlight; Nikon R1C1 Close-Up Speedlight System.

RESULTS

Initial Research

The paleoflora of the area of the Mlava-Pek coal basin has been known since the 19th century. Some of the oldest texts about the existence of Carboniferous paleoflora in this area can be found in the book “Geology of Serbia”, written by Jovan Žujović (1893). Žujović wrote that, in 1863, German geologist Bernhard von Cotta studied the Kučajna mine and the surrounding area, and that on the way to the village of Melinica he came upon layers of sandstone and alumina that contained fossilised *Stigmaria*. Later, at the end of the 19th century, plant fossils from this area were collected by geologist Jovan Žujović and botanist Josif Pančić, as well as by the mining engineer Felix Hofmann, who at one time was the owner of the Kučajna mine of lead and zinc and the coal-bearing fields near the villages of Kladurovo, Melnica, Mustapić, Ranovac and Mišljenovac (Fig. 1). A large part of the material - the current whereabouts of which is unknown - was collected by geologist Nikola Pantić (Pantić 1951a, 1952) in the middle of the 20th century. In the 1960s, some of the material was collected by "Geozavod", but the whereabouts of this material is not known either. The fossil material collected by Nikola Pantić and "Geozavod" is not the subject matter of this paper.

The Collection of the Natural History Museum in Belgrade

The collection described in this paper is kept in the Natural History Museum in Belgrade and is known by the name "Carboniferous Flora of Mlava and Pek". It includes approximately 400 specimens of Carboniferous plants originating from the Stephanian, as well as the Stephanian-Permian transitional layer. Generally speaking, it can be divided into two smaller collections:

1. 'Mlava-Pek *sensu lato*'

2. 'Borogin potok, village Ranovac'

Both collections consist of similar material and their biggest difference is that, in the case of the 'Borogin potok, village Ranovac' collection all relevant museological data is known, the most important being the exact locality from which the paleoflora was collected, while for the specimens from the 'Mlava-Pek *sensu lato*' collection we know only the wider area, but not the exact place they were discovered. For example, we know that it was "in the surroundings of Požarevac", or "in the village of Kladurovo", or "on the way to the village of Mustapić", etc. (Tab. 1).

Museological Description of the Two Collections:

1. The 'Mlava-Pek *sensu lato*' is a diverse collection that consists of approximately 300 plant taxa. It was found completely by accident in 1995, in the basement of the Museum. At the time of discovery there was no accompanying museum documentation for it, nor was a single specimen recorded in the inventory books. Up to this day, it is not known how and when the collection arrived at the Museum, and no information about it could be found anywhere, including the museum archives. The only available traces were the old labels that were placed on some of the specimens, marking the species and locality, or in many cases just the locality or a wider geographical area (Fig. 16, Tab. 1).

Today, after several years of searching, basic museum data have been found for most of the specimens that were marked by labels (who collected them and where, who identified them, and where they were located before they came to the Museum). The basic data regarding the specimens that did not have any labels were established indirectly, in terms of sediment, type of fossilisation or taxon, based on logical and obvious indicators such as similarity with the specimens that *were* marked by labels. It was determined that some of the specimens were once actually bigger pieces that were later broken into several parts (Fig. 7). There were also specimens that constituted compressions and impressions of the same plant. It is also worth mentioning the *Calamites* specimen, which had broken into two parts: one part was inventoried in 1995, as a specimen from an unknown locality, and the other part, which was actually marked by a label, was found only twenty years later, by complete chance (Fig. 8).

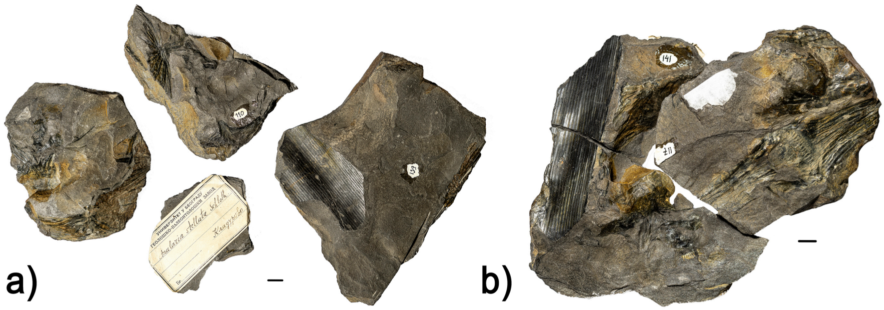

Fig. 7. – *Annularia stellata*, Kladurovo; four parts of the same fossil, disassembled (a) and assembled (b). Only one piece (inv. no. 141) had a label showing the species and locality. The pieces were found separately (inventory numbers: 110, 117, 139 and 141), scale bars = 10 *mm*.

From the cultural and museological point of view, some of the specimens from this collection have exceptional historical value because they are the first paleobotanical objects that were found in Serbia. We can include specimens with inventory numbers 115, 131, 132, 152 and 25 + 1030 in this group with complete certainty (Tab. 1). Although the date of collection is not written on any of the labels, based on subsequent research we now know that these specimens were collected prior to 1886, because they were mentioned in a publication that was published that year (Žujović 1886). Among other things, this material was collected for the world exhibition in Paris in 1889, but it is not known whether it was actually exhibited there. The specimens were collected by famous scientists, founders of natural sciences in Serbia, botanist Josif Pančić and geologist Jovan Žujović. The specimens collected by Jovan Žujović were identified by Professor Dionýz Štúr, Director of the Imperial Geological Institute in

Vienna. Žujović brought fossil material mainly from the area of Kladurovo and, most likely, Mišljenovac. On the other hand, unrelated to Žujović's explorations, Josif Pančić and Felix Hofmann collected material from Kladurovo and Mustapić. It is not known who identified those specimens; it is possible that they were identified by Pančić himself, but he was not the one who filled out the labels because the handwriting on them is not his (from private communication with Snežana Vukojčić, curator in the Botanical Garden "Jevremovac").

Fig. 8. – *Calamites varians*, Kladurovo. Two parts of the same specimen: inv. no. 25, inventoried in 1995, and inv. no. 1030, found in 2015, scale bar = 10 *mm*.

Based on the labels that were found next to certain specimens, we can conclude that they were collected from different localities within the Mlava-Pek coal basin (Tab. 2) i.e in Mustapić, Mišljenovac, Kladurovo, Kučajna, Požarevac, Slani Potok and Osipaonički Potok. Some labels are of a later date, such as those marked with the locality Osipaonički Potok or Slani Potok, which means that these specimens were collected later. It is not known when the specimens labeled *Locus ignotus* were collected, or by whom.

This is one of the rare museum collections for which there is no information as to how it got into the Museum. One of the initial assumptions, at the beginning of the research process, was that this plaeoflora was transferred to the Museum from the Grandes école at the beginning of the 20th century (because it was at that time that all the natural history collections from the Grande école were transferred to the Museum); however, there is no written data to prove that this was really the case. Another assumption was that the flora was brought to the Museum from the

University of Belgrade by geologist Nikola Pantić, who in 1950 was researching paleoflora from the area of Mlava and Pek for his graduation thesis (Pantić 1951a, 1952). However, it later turned out that not a single specimen Pantić described in his papers (Pantić 1951a, 1952) was in the Museum's collection. So, despite all the efforts, it remains unclear who, and when, brought this collection to the Museum. Based on the few existing labels it can be concluded that, before being brought to the museum, the collection was first stored at the Grande école, then at the Mining Department of the Ministry of Economy of the Kingdom of Yugoslavia, and finally at the Geological Institute of the University of Belgrade (Fig. 16).

2. The 'Borogin potok, Ranovac village' collection. This, second collection of Late Paleozoic flora plants, from the same basin and of the same age as the first one (Stephanian and Stephanian-Permian), has a clearly established origin and was sent to the museum in 1957 by Petar Pavlović, a teacher from Kladovo (Archives of the Natural History Museum). The collection was gathered in May 1957 and comes from the dump, i.e. the tailings pond of the Borogin Potok mine in the village of Ranovac. Borogin Potok was a small coal mine that was opened during the Second World War. The coal-bearing series in this mine belongs to the Upper Carboniferous and Carboniferous-Permian boundary layers (Kalenić *et al.* 1980, Malešević *et al.* 1980).

Comparative Analysis of the Two Paleofloras

The two collections are very similar in terms of sediment, composition and age, and the greatest difference between them is that there is no *Odontopteris* in the flora of 'Borogin Potok, Ranovac village' (Fig. 12), while they are quite numerous in the 'Mlava-Pek *sensu lato*' collection (Fig. 11). Also, the 'Borogin Potok' collection contains no arborescent lycopods, while Equisetidae are represented by only 4% (Fig. 10). The absence of Lepidodendrales and the small percentage of Equisetidae from Borogin Potok indicate a decrease in the number of shallow-water swamp basins in this locality, while the absence of *Odontopteris* cannot be easily explained. It may be that the layers in Borogin Potok are a bit younger and that, in that period, *Odontopteris* simply no longer existed in the area due to reduced humidity. Several specimens of *incertae sedis Linopteris* or *Neuropteris* from the reddish sandstone characteristic of the Permian (Pantić 1952, Kalenić *et al.* 1980, Malešević *et al.* 1980) were found also in this collection, and it is therefore possible that these specimens belong to slightly younger layers. It is possible that the reduced humidity at the beginning of the Permian caused the disappearance of *Odontopteris*, which perhaps was not able to withstand competition with other seed ferns - in this case, primarily *Alethopteris* and *Linopteris*.

The entire composition of the paleoflora of ‘Borogin Potok, Ranovac village’ indicates that it was more arid area compared to the Mlava-Pek *sensu lato* collection. Based on the percentage of dominant plant groups, we can conclude that the reduction of wetlands, and consequently of wetland plants such as arborescent lycopods and Equisetidae, led to the increase in the number of tree ferns (Marattiidae and Polypodiidae) and *Cordaites*, while the number of seed ferns (Pteridospermatopsida) remained more or less the same as in the ‘Mlava-Pek *sensu lato*’ collection.

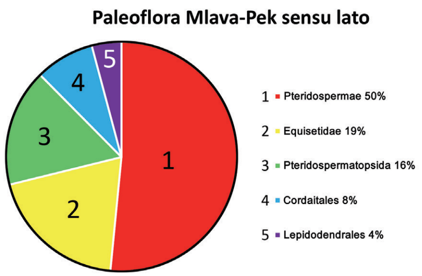

Fig. 9. – Representation of plants in the ‘Mlava-Pek *sensu lato*’ collection.

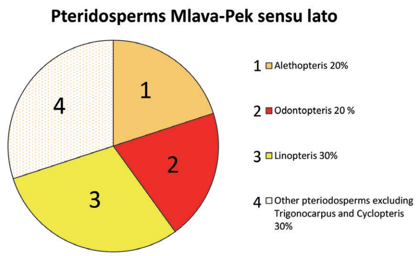

Fig. 11. – Representation of *Pteridospermae* seed ferns in the ‘Mlava-Pek *sensu lato*’ collection.

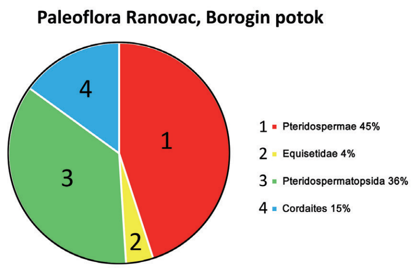

Fig. 10. – Representation of plants in the ‘Borogin Potok, Ranovac village’ collection.

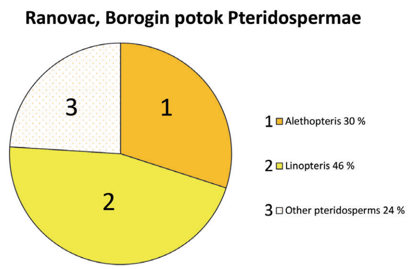

Fig. 12. – Representation of *Pteridospermae,* seed ferns, in the ‘Borogin Potok, Ranovac village’ collection.

Floristic Representation of the Examined Paleofloras

1. PALEOFLORA OF THE ‘MLAVA-PEK SENSU LATO’ COLLECTION

Based on the shown taxonomic composition (Fig. 9), where arborescent lycopods (Lycopodiophyta) as typical wetland plants of Westphalian make up only 4%, we can easily conclude that this is Late Carboniferous vegetation that was undoubtedly dominated by seed ferns, which constitute almost 50% of the found specimens. Seed ferns are dominant not only quantitatively, but also qualitatively, and the existence of 11 genera and a total of 30 different taxa (mostly species) has been established. This paleo-association includes all plant groups that existed at the time: Horsetails (Equisetidae, Polypodiopsida), arborescent lycopods (Lycopodiopsida, Lepidodendrales), tree ferns (Marattiidae and Polypodiidae), seed ferns (Pteridospermatopsida) and *Cordaites* (Gymnospermopsida). This was clearly, in terms of biodiversity, a diverse and long-lived association characterised by the presence of both primary zonal and azonal, and perhaps even relict, swamp vegetation.

PALEOFLORISTIC COMPOSITION:

ARBORESCENT LYCOPODS (LYCOPODIOPSIDA, LEPIDODENDRALES)

Cyperites bicarinatus Lindley & Hutton
Sigillaria cf. *euxina* Zeiller
Sigilllaria cf. *scholothemiana* Brongniart
Sigillaria sp.
Stigmaria ficoides (Sternberg) Brongniart
Ulodendron sp.

HORSETAILS (EQUISETIDAE)

Annularia sphenophylloides (Zenker) Gutbier
Annularia stellata (Schlotheim) Wood
Asterophyllites equisetiformis (Sternberg) Brongniart
Asterophyllites tenuifolia Brongniart
Asterophyllites sp.
Calamites carinatus Sternberg
Calamites cf. *carinatus* Sternberg
Calamites cistii Brongniart
Calamites cf. *cistii* Brongniart
Calamites ramosus Artis
Calamites varians Sternberg
Calamites spp.
Calamostachys tuberculata (Sternberg) Weiss
Equisetales aff. *Equisetites*
Equisetidae gen. et sp. indet.
Spenophyllum oblongifolium (Germar & Kaulfuss) Unger
Sphenophyllum costae Sterzel
Sphenophyllum emarginatum Brongniart
Sphenophyllum verticillatum Schlotheim
Sphenophyllum sp.

TREE FERNS (MARATTIIDAE AND POLYPODIIDAE)

Asterotheca arborescens Schlotheim
Asterotheca candolleana Brongniart

Asterotheca hemitelioides Brongniart
Asterotheca sp.
Corynepteris sp.
Nemejcopteris feminaeformis (Schlotheim) Barthel
Pecopteris arborescens (Schlotheim) Sternberg
Pecopteris cf. *bourozii* Dalinval
Pecopteris cyathea (Schlotheim) Brongniart
Pecopteris sp.
Polymorphopteris polymorpha (Brongniart) Wagner
Sphenopteris cf. *schwerinii* (Štúr) Zeiller
Sphenopteris sp.

SEED FERNS (PTERIDOSPERMATOPSIDA)

Alethopteris cf. *grandinioides* Kessler
Alethopteris davreuxii (Brogniart) Zeiller
Alethopteris lesquereuxii Wagner
Alethopteris lonchitica Sernberg
Alethopteris pennsylvanica Lesquereux
Alethopteris robusta Lesquereux
Alethopteris subelegans (Potonié) Franke
Alethopteris valida Boulay
Alethopteris cf. *zeilleri* (Ragot) Wagner vel *A. valida* Boulay
Alethopteris zeilleri (Ragot) Wagner vel
A. grandini (Brongniart) Goeppert
Alethopteris sp.
Autunia conferta (Sternberg) Kerp
Callipteridium cf. *zeillerii* Wagner
Callipteridium sp.
Callipteris subauriculata (Weiss) Grand'Eury
Cyclopteris sp.
Laveineopteris tenuifolia (Sternberg) Cleal, Shute et Zodrow
Linopteris brongniarti (Gutbier) Potonié
Linopteris germari Giebel
Linopteris cf. *germari* Giebel
Linopteris cf. *neuropteroides* (Gutbier) Potonié
Linopteris neuropteroides (Gutbier) Potonié
Linopteris sp.
Linopteris vel *Neuropteris*
Mariopteris sp.
aff. *Neuralethopteris schlehanii* (Štur) Laveine
aff, *Neuralethopteris* sp.
Neuropteris flexuosa Sternberg
Neuropteris jongmasii Crookall
Neuropteris sp

Odontopteris brardi (Brongniart) Sternberg
Odontopteris minor Brongniart
Odontopteris minor f. *brongniarti* Potonié
Odontopteris minor f. *zeillerii* Potonié
Odontopteris osmundaeformis (Schlotheim) Zeiller
Odontopteris reichiana Gutbier
Odontopteris cf. *reichiana* Gutbier
Odontopteris sp.
Samaropsis sp.
Trigonocarpus sp.

CORDAITES (GYMNOSPERMOPSIDA)

Cordaites palmaeformis (Goeppert) Weiss
Cordaites principalis (Germar) Geinitz
Cordaites sp.

INCERTAE SEDIS

Calamites vel *Sigillaria*
Alethopteris zeilleri vel *Callipteris* sp.
Alethopteris sp. vel *Callipteridium* sp.

2. PALEOFLORA OF THE 'BOROGIN POTOK, RANOVAC VILLAGE' COLLECTION

As already mentioned, the taphocenosis of 'Borogin Potok, Ranovac village' differs from the taphocenosis of the 'Mlava-Pek *sensu lato*' by the complete absence of arborescent lycopods, seed ferns *Odontopteris*, and by significantly fewer horsetails.

PALEOFLORISTIC COMPOSITION:

HORSETAILS (EQUISETIDAE)

Annularia stellata (Schlotheim) Wood
Asterophyllites equisetiformis (Sternberg) Brongniart
Calamites sp.
Sphenophyllum sp.

TREE FERNS (MARATTIIDAE AND POLYPODIIDAE)

Asterotheca arborescens Schlotheim
Asterotheca cf. *arborescens* Schlotheim
Asterotheca candolleana Brongniart
Asterotheca hemitelioides Brongniart
Asterotheca sp.
Pecopteris arborescens (Schlotheim) Sternberg
Pecopteris bucklandi Brongniart
Pecopteris cyathea (Schlotheim) Brongniart
Pecopteris sp.

SEED FERNS (PTERIDOSPERMATOPSIDA)

Alethopteris grandini Goeppert
Alethopteris cf. *lancifolia* Wagner
Alethopteris pennsylvanica Lesquereux
Alethopteris serlii (Brogniart) Goppert
Alethopteris sp.
Autunia conferta (Sternberg) Kerp
Autunia conferta vel *Alethopteris*
Callipteridium striatum Wagner
Eusphenopteris obtusiloba (Brongniart) Novik
Neurocallipteris sp.
Neuropteris planchardi Doubinger vel *N. gallica* Zeiller
Linopteris florini Teixeira
Linopteris neuropteroides (Gutbier) Potonié
Linopteris obliqua (Bunbury) Zeiller
Linopteris sp.
Linopteris vel *Neuropteris*
Mariopteris muricata (Brongniart) Zeiller
Mariopteris sp.
Pachytesta sp. (petrified *Trigonocarpus* sp.)
Trigonocarpus sp.

CORDAITES (GYMNOSPERMOPSIDA)

Cordaites palmaeformis (Goppert) Weiss
Cordaites principalis (Germar) Geinitz
Cordaites sp.

INCERTAE SEDIS

semen indet.
trunkus indet.
strobus indet.

Comparative Overview of the Representation of Certain Taxa in Both Collections[1]

HORSETAILS (EQUISETIDAE)

1. 'Mlava-Pek *sensu lato*': If we take into account all the specimens of horsetail that were found, they make up a significant 19% of the total taphocenosis. A large number of taxa were found, as well as various forms of fossilisation, impressions, molds and permineralised remains. The diversity of taxa and types of fossilisation indicate that horsetails were quite well represented in this area. Fossil remains of sterile

[1] See Apendix (Tab 3).

(*Calamites*) and fertile (*Calamostachys*) parts of stems were found, as well as impressions of *Annularia*, *Asterophyllites* and *Sphneophyllum* leaves. Fossil remains of *Calamites* are numerous but poorly preserved; they are washed away, peeled off and difficult to identify. *C. cisti*, *C. carinatus*, *C. ramosus*, *C. varians* and a large number of *Calamites* sp. were found, and the remains most likely belong to a smaller number of biological species than there are morpho-species.

The genus *Sphenophyllum*, i.e. the species *S. oblongifolium,* is the most numerous of the horsetail foliar genera. Besides the above one, there are also *S. costae*, *S. thoni* and *S. emarginatum* (which is essentially very similar to *S. oblongifolium*). It is entirely possible that most of these *Sphenophyllum*-species belong to the same morpho-type, with a pronounced heterophylly (Galtier & Daviero 1999), as is the case with *Sphenophyllum costae*, where a high degree of heterophylly has been established thanks to some wonderfully preserved specimens (Bashforth & Zodrow 2007). The foliar genus *Annularia* appears in two clearly separated species: *A. stellata* and *A. sphenophylloides*. The genus *Asterophyllites,* with the species *A. equisetiformis*, is equally numerous as *Annularia stellata*, and it is possible that both taxa belong to the same biological genus, maybe even a single species with leaf dimorphism.

Looking at the fossil remains of Equisetidae realistically, we can conclude that there are at least three clearly defined horsetail morphotypes: first *Sphenophyllum,* second complex *Annularia stellata / Asterophyllites equisetiformis,* and the third one, with a clearly recognisable leaf shape - *Annularia sphenophylloides*. Consequently, we can probably define at least three biological species.

2. Borogin Potok, Ranovac village: There were visibly fewer Equisetidae here than in the previous location (Fig. 10). There are a total of 6 specimens, of which *Calamites* sp. and *Sphenophyllum* sp. are probably the stem and leaves of the same individual, given that they were located together, on the same specimen, one on top of the other.

ARBORESCENT LYCOPODS (LEPIDODENDRALES)

1. 'Mlava-Pek sensu lato': Arborescent lycopods are represented by only 4% (Fig. 9). The found fossils are not only rare, but also very poorly preserved. Leaf scars are barely visible, so the morpho-species were determined more or less subjectively, based on the overall morphological appearance. *Sigillaria* are represented the most, as the real biological genus in this association. The other morphogenera - *Stigmaria, Cyperites* and *Ulodendron* - may also belong to other arborescent lycopods, but it is still most likely that they are all parts of sigillarias.

Although they are few, these findings are quite important because they indicate the existence of Lepidodendrales, which in the Late Stephanian were already becoming extinct. It is important to note that the remains of *Sigillaria* were not found in only one locality, but in several (Tab. 2), as well as in different types of sediment, which indicates that their habitats – possibly swamps of a refugial type - were spread over a wider area.

2. 'Borogin Potok, Ranovac village': There are no Lepidodendrales.

SEED FERNS (PTERIDOSPERMATOPSIDA)

Since seed ferns dominate in both collections and were obviously the edificators of both associations, they will be given a bit more space here. The seed ferns were woody plants. They had monoaxial stems, sclerenchymatous cortical regions, and secondary xylem (DiMichele *et al.* 2006, Taylor & Taylor 2009). For the sake of comparison: neither common ferns nor palms (Arecaceae) have secondary xylem, but cycads do. They had fern-like leaves and radially symmetrical seeds. Ovules, microsporangia and seeds were found on the leaves, usually in two main positions: either instead of one or more pinnules, or attached to the main vein of the leaf (Fig. 15). Some had a stem similar to cycads, while in some they were similar to those of other gymnosperms, so some stems were highly branched out while others were not. Some were scrambling or vine / liana-like and some were upright trees. Medullosian seed ferns were uniformly rich in sclerenchyma and resin (DiMichele *et al.* 2006). Leaves of seed ferns were prone to di- or polymorphism, heteroblasty and different leaf architecture, depending on the degree of solar exposure (Schabilion & Reihman 1985).

1. 'Mlava-Pek sensu lato': Pteridospermatopsida, i.e. seed ferns are without any doubt the dominant group of plants in both examined collections, both quantitatively and taxonomically (Figs. 9, 10 and Tab. 3). An impression of a fern seed can be found on almost every specimen. They make up about 50% of all the found plants, and a total of 11 different morpho-genera were identified among them: *Alethopteris*, *Autunia, Callipteridium*, *Callipteris*, *Linopteris*, aff. *Neuralethopteris*, *Neuropteris*, *Odontopteris*, *Trigonocarpus*, *Cyclopteris* and *Laveniopteris*. Of all these taxa, which can sometimes be confused with each other in the process of identification (for example, due to poor preservation), we can without a doubt single out three clearly defined and distinct morpho-genera: *Alethopteris, Odonotpteris* and *Linopteris*. They also make up the largest number of seed ferns in this association

(Fig. 11) and are, practically, the associations' edificators. To this we can add *Neuropteris*, which is also morphologically clearly separated but represented by only 5%. Many specimens of seed ferns from this collection (i.e. inv. no. 114 and coll. no. bb. 2) were found - much like tree ferns - to be prone to pinnule or pinna polymorphism. This is especially characteristic of *Alethopteris* (Fig. 14). It is also known that heteroblastia, i.e. visible difference in the form of juvenile and adult fronds and pinnules, tends to occur in medullosan seed ferns (DiMichele *et al.* 2006), so it is quite possible that e.g. *Cyclopteris* which were found in the association belong to the juvenile forms of other species (i.e. *Neuropteris*).

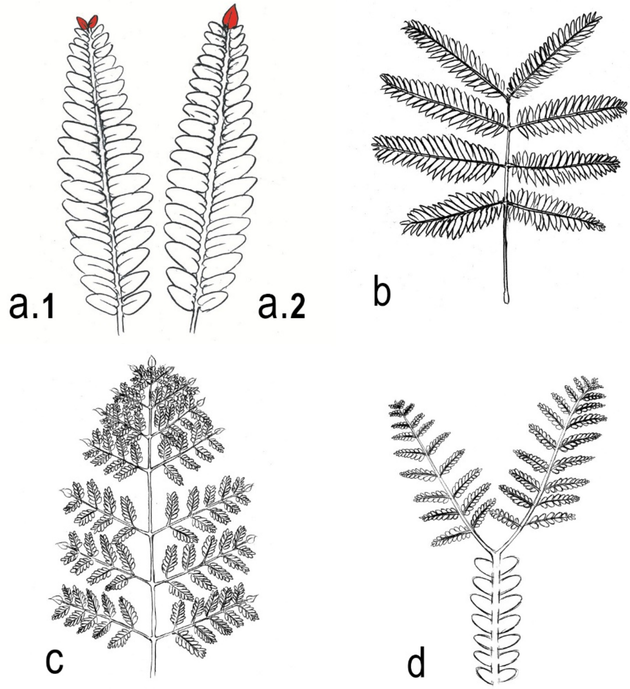

Fig 13. – The structure of seed fern fronds: a. monopinnate (1 paripinnate, 2. imparipinnate), b. bipinnate; c. tripinnate; d. bifurcate bipinnate.

Foliar genera *Alethopteris*, fam. Neuralethopteridaceae: *Alethopteris* is one of the dominant genera in both collections (Figs. 11, 12). It is represented by pinnae and parts of fronds. On some specimens one can also see apical pinnules, but in most cases only smaller central parts of pinnae were found. In some specimens, the veins are well preserved and the species can thus be identified with greater certainty, while other specimens were identified based on the shape of the pinnules and the probability that, if they are on the same specimen, they probably belong to the same species regardless of the fact that their veins are not preserved. A total of 12 morphospecies were identified: *A. grandides, A. grandini, A. davreuxii, A. lesquerci, A. lonchitica, A. pennsylvanica, A. robusta, A. serlii, A. subelegans, A. valida, A. zeilleri* and *A.* cf. *lancifolia*. Since the genus *Alethopteris* is prone to heterophylly (Fig. 14), especially depending on whether the central or apical part of the pinna has been preserved (Šimunek, 1989), we can assume that not 11 biological species of *Alethopteris* were represented (which is how many morpho-species have been identified), and that there were in fact fewer biological species.

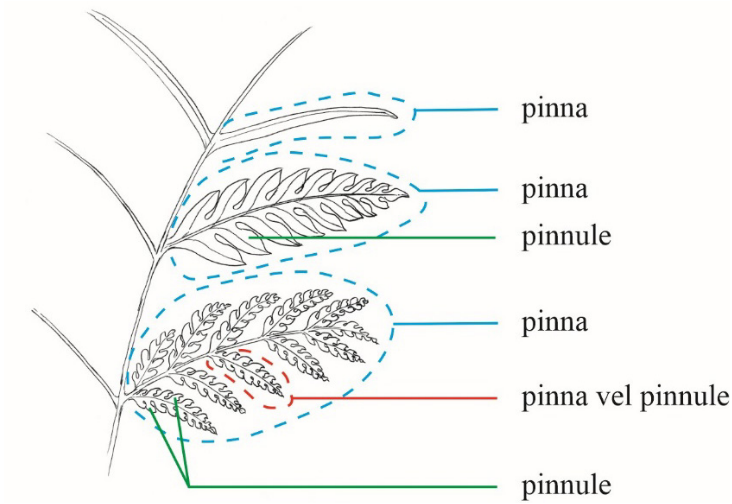

Fig. 14. – Leaf polymorphism in *Alethopteris* spp.

Morphological recongizable features of *Alethopteris*: The genus had enormous fronds that were up to 7–8 *m* long and 4 *m* wide (Laveine *et al.* 1992, DiMichele *et al.* 2006). The size of the fronds is quite disproportional to the height of the stem, which used to reach approximately 5m and had a diameter of about 20 *cm*. The fronds were bipinnate bifurcate (Álvarez-Vázquez 2020). In most species, the fronds would dry on the tree and not fall off; they would instead cover the stem, creating a protective “skirt” which protected it from parasites and fast-growing climbing plants (DiMichaele & Gastaldo 2008). So the stem of *Alethopteris* could have resembled the habitus of a recent tropical tree fern *Angiopteris evecta* (G. Forst.) Hoffm., whose gigantic fronds could reach the length of 8 m, and whose stem was up to 3 m high (pers.obs.). *Alethopteris* features are more xeromorphic than those of *Neuropteris,* and they usually occured in less rich soil, *A. zeilleri* in particular (Šimunek 1989, DiMichele *et al.* 2006).

Trigonocarpus is an adpression of large seeds of some *Pteridospermae* from the group of medullosian seed ferns such as *Alethopteris* or *Neuropteris*. *Pachistesta* is the same seed, but in petrified form. *Trigonocarpus / Pachitesta* was located either on the site of one pinnule, or on the rachis (Fig. 15). Since the pollen of seed ferns used to be large, it is assumed that pollination was not carried out by the wind but rather zoochorically, probably by arthropods. Pollination could also have been hydrophilous (DiMichele *et al.* 2006). Large seeds could have been a good source of nutrients for a variety of animals from the Carboniferous era.

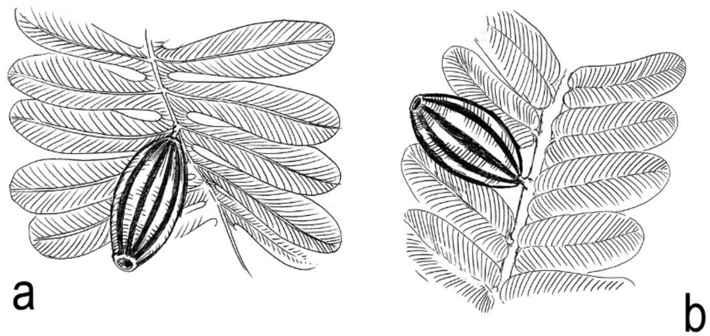

Fig. 15. – Position of *Trigonocarpus* on the pinna of a seed fern: a. on the rachis, b. instead of the pinnule.

Foliar genera *Linopteris*, fam. Parispermaceae: This genus is represented in both collections exclusively by individual pinnules, and not a single part of a frond, pinna or rachis was found with organically connected pinnules. In most specimens, the pinnules are large: they are 4–5 *cm* long and about 1–1.5 *cm* wide. The species *L. neuropteroides* and *L. obliqua* dominate, while *L. muensteri, L. brongniarti*, and *L. germari* appear in much smaller numbers. No significant pinnule polymorphism was found in *Linopteris* from this area, especially not in the two most common species, *L. neuropterioides* and *L. obliqua*. Pinnules are more or less uniform in appearance and size. Besides individual pinnules, parts of stems with remains of trichomes were found as well.

Much like other upright medullosian seed ferns, the fronds of *Linopteris* were also considerable in length. It is assumed that the fronds of *L. obliqua* (Zodrow *et al.* 2007) were about 7 m long. Most *Linopteris* species had pinnate compound fronds with two terminal pinnules on the rachis of each pinna (Fig. 13.a1). *Linopteris* seeds are known as *Hexagonocarpus* and had not been found in the Mlava-Pek area. Based on circumstantial evidence, Zodrow *et al.* (2007) considered the possibility that the reproductive period of *L. obliqua* was short-lived and probably conditioned by periods when pinnules were being shed (either seasonally or due to environmental stress), so that nutrient resources - now less needed by the photosynthetic tissue - were directed towards the formation of reproductive organs and seeds. The assumption that the shedding of pinnules in *Linopteris* was a common seasonal process corresponds with our findings, because it could serve as a logical explanation for finding in *Linopteris* only pinnules that had no organic **connection** to the rachis.

Foliar genera *Odontopteris*, fam. Neurodontopteridaceaea:

1. 'Mlava-Pek *sensu lato*': *Odontopteris* is represented equally as *Alethopteris* and *Linopteris* (Fig. 11). Each specimen that contains adpressions of *Odontopteris* also has adpressions of several pinnae. The pinnules of *Odontopteris* are small, thin and delicate, not exceeding the length of approximately 0.5 *cm*. Rachises are also thin and fragile. There are three species: *O. minor, O. reichiana* and *O. brardi*. The difference between the species is obvious on some of the specimens, but there are also others that appear more like transitional forms between species, so it is quite possible that some specimens that were identified as two species actually represent polymorphic leaves, perhaps even of the same individual.

<u>Physiognomy of habitus and fronds:</u> different species of *Odontopteris* probably had different types of stems; however, it was noticed that a certain number of *Odontopteris* (especially the small-pinned ones) can be associated with scrambling or climbing forms. The fronds can be bi- or tri-pinnate (Fig. 13.b and 13.c), while the pinnules of all species of *Odontopteris* are always sessile and do not have a one main vein, but several thinner ones (Krings *et al.* 2006). The fronds of small-pinned *Odontopteris* are only up to one metre long. In the Stephanian-Permian period, *Odontopteris reichiana* had resinous cells that may have played a role in repelling insects, while *Odontopteris brardi* did not have resinous cells, but did have hydathodes through which it expelled unnecessary water (DiMichele *et al.* 2006, Šimunek & Cleal 2011). The system of resinous canals was similar to that of conifers. Some scrambling or vine / liana-like forms of *Odontopteris* were covered with trichomes, which may also have provided defense against insects, as is the case with many recent plants.

2. Borogin Potok locality: There are no *Odontopteris*.

Foliar genera *Neuropteris* fam. Neurodontopteridaceae: is poorly represented in either collection. The 'Mlava-Pek *sensu lato;* collection includes only a few specimens of *N. flexuosa, N. jongmasii* and *Neuropteris* sp., while in 'Borogin Potok, Ranovac village' there are none that could be identified as *Neuropteris* with any kind of certainty. Although the appearance of *Neuropteris* is not that significant for the examined association due to the fact that its remains were found in negligible numbers, it is worth mentioning that one *Medullosa* found in France, probably *Neuropteris* (DiMichele *et al.* 2006), had a trunk with a diameter of 26 *cm* and petioles with a diameter of 16 *cm*. The stem had a very well-developed xylem. It is assumed that this genus preferred open habitats, where seeds could germinate under stronger insolation (*ibid.*).

Foliar genera *Autunia conferta* (syn. *Callipteris conferta*), ordo Peltaspermales: *Autunia* is a callipterid seed fern that was formerly known as *Callipteris conferta*. This is important to note because Pantić (1952) mentioned it by this name. *Autunia* is represented in both collections with just a small number of specimens, but it is significant that it was found at all. It was collected in coloured sandstones in the last layers of the Stephanian (Figs. 4, 5). The strata of the Stephanian-Permian boundary interval turn into red Permian sandstones. *Autunia* is a biostratigraphic indicator of the Carboniferous-Permian boundary (Meyen 1987, Taylor *et al.* 2008). It used to grow mainly in well-drained and more arid habitats. Its fronds are bi- or tri-pinnate (DiMichele *et al.* 2013), with pinnules that are similar to the alethopteris type, while megasporophyll is called *Peltaspermum*. This species was identified in the studied collection by its robust, strong alethopteroid pinnules and pronounced veins; however, intercalary pinnules, which are otherwise characteristic of this species, were not observed.

TREE FERNS (MARATTIIDAE AND POLYPODIIDAE)

Tree ferns are quite well represented in both collections. In the 'Mlava-Pek *sensu lato*', they make up 16% of the total paleoflora, while in the 'Borogin Potok' collection there are twice as many - as much as 36% of the total paleoflora (Figs. 9, 10). Foliar genus *Pecopteris* and its fertile counterpart *Asterotheca* dominate at both localities. Only these two genera – *Pecopteris* / *Asterotheca* – appear in the collection 'Borogin Potok, Ranovac village', while the 'Mlava-Pek *sensu lato*' collection is notable for its diversity in terms of ferns, because here, in addition to the *Pecopteris* / *Asterotheca* complex, there are also *Nemejcopteris feminaeformis*, *Polymorphopteris polymorpha, Scolecopteris* and *Sphenopteris*. Of the listed foliar genera, three are clearly morphologically different, indicating at least three biological taxa: the *Pecopteris* / *Asterotheca* complex, *Nemejcopteris* and *Sphenopteris*. Other genera may represent: **a.** leaf polymorphism of one of these three genera; **b.**

fertile parts of fronds; or **c**. separate biological species. In any case, their true nature cannot be determined with certainty based on morphological identification alone. Tree ferns reached their expansion during the Stephanian, in the then tropical belt of Euro-America.

Structure-wise, Carboniferous tree ferns were very similar to those of today. Their stem i.e. *Psaronius* used to reach the height of approximately 10 *m*. The fronds were several metres long, while pinnae and pinnules were characterised by marked polymorphism. Consequently, pinnules of various shapes and veins could have been found on the same pinna (Vieira *et al.* 2007).

CORDAITES (GYMNOSPERMOPSIDA, CORDAITALES)

Cordaites are represented in both collections. They constitute only 8% of the association (taphocenose) in the 'Mlava-Pek *sensu lato*' collection, while in the 'Borogin potok' collection there are twice as many, that is, 15%. The existence of two morpho-species, which differ when it comes to the types of veins, was established in both collections: *C. palmaeformis* (all the veins are of equal width) and *C. principalis* (weaker and stronger veins can be seen on the adpressions). However, it is most likely that these are not two species, but rather the abaxial and adaxial (front and back) sides of leaves of the same species. Namely, *Cordaites* leaves characteristically have both strong and weak veins. After several weak parallel veins, there is usually a strong one. Strong veins are sclerenchymal bundles, while weak veins are true conducting bundles (Darrah, 1969). In any case, at the level of morphological identification that was performed here, we cannot determine with certainty whether these are two different species of *Cordaites*, or leaf dimorphism of the same species, or the abaxial and adaxial sides of a leaf. The author believes that it is a single species, i.e. the front and back of the leaves, particularly because both species (*C. principalis* and *C. palmaeformis*) are represented equally on the same specimens. The leaves of both species partially overlap, which means that they inhabited the same ecological niche. It is more or less unlikely that two biological species of the same genus and with the same ecological requirements would exist in a single association, especially in the case of dendroflora. A similar case was described by Šimunek *et al.* (2009), where the authors concluded that *C. principalis* was the abaxial, and *C. palmaeformis* was the adaxial side of the same species of cordaite, *C. borasifolius*.

For these reasons, we tend to conclude that both species can be identified as the type species *Cordaites borasiflius* (Šimunek *et al.* 2009). As the mentioned authors described, this type of cordaite had a monopodial, or perhaps a sympodial stem, with a diameter of at least 50 *cm*, which reached a height of 20 to 30 *m*. The branching started a few metres above the ground, while the distance between the branches was about one metre. The crown was made up of palm-like arranged leaves. The leaves were whole and spirally arranged, ovate-lanceolate or rarely obovate, 35 to 90 *cm* wide and 40 to 70 *cm* long. The tip of the leaf was bluntly pointed. Our leaf samples are much smaller in size than those that were described by Šimunek *et al.* Their width does not exceed 5 *cm*, while the length is unknown because only fragments were found. There is only one entire leaf, but it is very small - about 6 *cm* long and 0.5 *cm* wide (at its widest point).

Reconstruction of the Vegetation – Comparative Overview

Based on the material at our disposal, we can conclude that, during the Stephanian and Stephanian-Permian, long-term tropical vegetation, dominated by seed ferns and tree ferns, existed in the wider area of the Mlava-Pek coal basin. During the Early Stephanian, the area had two main biomes that were common in the areas of the Late Carboniferous tropical belt: the wetland (swamp) biomes, and more arid areas whose vegetation was influenced by the seasonal change of dry and wet periods (Havlena 1971, DiMichele & Aronson 1992). In the wetlands (or swamps), there were numerous representatives of horsetails (Equisetidae), but there were also the last examples of arborescent lycopods, mostly *Sigillaria*, which were already on their way to extinction and probably had the character of a relict taxon. Seed ferns completely dominated this vegetation throughout the Staphanian and towards the Permian. They were the dominant group of plants in other Late Carboniferous associations as well. As DiMichele *et al.* (2001) noted, the dominance of pteridosperms in the history of the development of vegetation on Earth did not last long. It was relatively short-lived, but it is still extremely significant because its existence indicates the occurrence of some sort of global change - most likely a decrease in mean annual temperatures and seasonal precipitation.

Over time, as the Stephanian drew to an end, this zonal vegetation began to show signs of aridification: arborescent lycopods completely disappeared, and the swamp Equisetidae-vegetation was reduced by half. The change in the sediment, which slowly transformed from coal layers and carbonaceous clays rich in organic matter to layers of brown and red sandstones (Pantić 1951a, 1952), indicates increased aridification. The number of tree ferns increased and the number of typical swamp plants decreased; in other words, the reduction in the number of Equisetidae and the disappearance of arborescent lycopods led to a significant increase in the number of tree ferns. During the Late Carboniferous-Early Permian, a highly regular shift of vegetation that can be compared with today's studies of climate change, aridification and vegetation shifts took place in the area of the Mlava-Pek basin. At the time of transition from Carboniferous to Early Permian, seed ferns still dominated the zonal vegetation, but with a significant taxonomic change - there was no longer any *Odontopteris*, although the cause for its disappearance cannot be directly linked to the aridification of the climate at that time.

In addition to the above mentioned taxa, a significant percentage of *Cordaites* also existed in the studied area during the Stephanian and Stephanian-Permian periods. They, too, followed the aridification in a way, i.e. the climate change, as obvious from the rise of their percentage from 8% to 15%. Although *Cordaites* are generally described as having stems that were more than 20 *m* high (Opluštil *et al.* 2007, 2009, Šimunek *et al.* 2009), in the Mlava-Pek area they were probably significantly lower, maybe 10 to 15 *m*. This conclusion is self-evident based on the composition of the vegetation, which was dominated by seed ferns (approximately 5 m high) and tree ferns (up to 10 m high). As the most numerous, these two groups of plants determined the height of the the main canopy layer, so *Cordaites* had no need to be much higher than that. Their height probably did not exceed 15 *m*.

Based on all that was discussed above, we can reconstruct a picture of the vegetation that inhabited this part of the world during the Stephanian and the beginning of the Permian. The foundation of this Late Carboniferous forest was made up of Medullosales seed ferns: *Alethopteris, Odontopteris* and *Linopteris*, whose stems, as we have already mentioned, could have been upright or scrambling or vine / liana-like, depending on the taxa and environment. The upright ones were about 5 m high and had densely distributed fronds that did not fall off; instead, when they dried, they remained hanging on the stem, creating a covering made up of dry leaves which protected the main stem from liana-like plants and predators. The fronds were up to 7 m long. Due to this strange disproportion, where the height of the stem (5 m) was less than the length of the fronds (7 m), it is assumed that the fronds of different stems were intertwined, supporting each other and at the same time creating a thicket that caused the lowest floor to receive relatively little light. The other type of seed fern stem was scrambling or vine / liana-like. It was thin and longer than 5 *m*. The leaves on the stem were sparse and would fall off once they dried. The vine / liana-like plants wound themselves around the existing vegetation, probably more around *Cordaites* than around ferns and seed ferns, because tall cordaites stems made it possible for them to raise themselves above the the main canopy layer. Horsetails dominated the azonal swamp vegetation, with sigillaria - which were probably relict species - also appearing here and there.

Comparison with Other Geographically Close Paleofloras of the Stephanian and the Stephanian-Permian

As regards Carboniferous floras in Serbia, they can be traced from the Westphalian, through the Stephanian, to the Stephanian-Permian (Djordjević Milutinović, 2010). We are relying on relatively small data from the Westphalian flora (Pantić 1955a, Pantić & Cvetičanin 1962, Milovanović 1995,) and there are only a few specimens that have not been studied in a systematic fashion. There are also several Stephanian floras in eastern Serbia (Pantić 1951b, 1952, 1955b, Pantić & Cvetičanin 1962, Djordjević Milutinović 2015), and one in western Serbia (Pantić 1951c), but they too were just noted as existing and have not been studied in detail. The only two Carboniferous floras worth mentioning are the Stephanian-Permian paleoflora from Vrška Čuka, which numbers about 300 specimens (Pantić 1951b, Djordjević Milutinović 2015) and the Stephanian-Permian paleoflora of the Mlava-Pek basin (Pantić 1952), which was studied in detail for the purpose of this paper and contains approximately 400 specimens. The paleoflora of Vrška Čuka (eastern Serbia, near the border with Bulgaria) has many similarities with the paleoflora of the Mlava-Pek basin. The main difference between these two paleofloras is that the taphocenosis of Vrška Čuka is dominated by *Cordaites*, which make up over 40% of the plant material. Seed ferns and tree ferns are represented equally, each group representing about 20% of the total vegetation. Paleoflora of Vrška Čuka and paleoflora of Mlava - Pek are certainly parts of the same zonal paleovegetation.

The Stephanian flora of Slovenia has been well known from the Jesenice area in the Southern Karavanke Mountains but it was studied only recently based on the museal collection (Kolar-Jurkovšek & Jurkovšek 2012, Pšenička *et al.* 2014). The composition of the Stephanian flora of the Jesenice area, although geographically relatively close, is completely different from that of the Mlava-Pek basin, and these two paleofloras have almost nothing in common. The Slovenian paleoflora is typical swamp vegetation dominated by Lepidodendrales and Equisetidae, almost completely devoid of seed ferns. On the other hand, Takšić (1947) mentions that in the Planina pod Golico locality from the same area he obtained fossil plant collection in which, in addition to numerous representatives of the Equisetidae and arborescent lycopsids, there was also a significant amount of *Alethopteris* spp.

The flora of Velebit in Croatia (Cleal *et al.* 2015) is more or less similar to the studied flora of the Mlava-Pek basin, especially to the ‘Mlava-Pek *sensu lato*' collection. The paleoflora from Velebit is dominated by seed ferns (*Alethopteris* and *Callipteridium*), but there are also Equisetidae, tree ferns, and a small percentage of arborescent lycopods. The biggest difference is the absence of *Cordaites* in the flora of Velebit, although authors state that Nemejc did record some from that site in 1936.

In Romania (Dragastan *et al.* 1997, Popa 2005), the Stephanian floras are similar to that of the Mlava-Pek basin. They, too, show a noticeable tendency towards aridification during the Stephanian, i.e. a decrease in the number of Lepidodendrales and Equisetidae and an increase in the number of *Cordaites* and tree ferns. They seem to also be dominated by seed ferns. The paleoflora of 'Borogin Potok', which by its composition seems more xerotmorphic than the paleoflora of 'Mlava-Pek *sensu lato*', has some taxonomic similarities with the Lower Peremian floras of Romania (Popa, 1999, 2005). However, there are conifers *Walchia piniformis* (Sternberg) Kerp in the Romanian paleoflora, while our collection contains none. Still, it should be noted that Pantić (1952) mentioned two findings of *Walchia* in Mlava-Pek regia. Some of the researched palaeoflora of the Resita basin in Romania (Popa 2009, Popa & Cleal 2012) also have a lot of similarities with Mlava-Pek paleoflora, with the fact that Resita-paleofloras have a much higher percentage of *Neuropteris*.

As regards Stephanian paleoflora of Bulgaria (Fig. 3), findings from the Dobrudzha basin are especially important because their study (Cleal *et al.* 2004) shows a similar representation of certain classes of plants, such as e.g. the percentage representation of seed ferns and tree ferns. However, we do not have complete insight into the composition of the Stephanian flora from Dobrudzha because mostly the studies of the Westphalian microflora have been published (among others: Dimitrova 2008, Dimitrova & Cleal 2007). So, in the light of current knowledge, a more precise comparison of these two basins cannot be made, although it is very likely that they were part of the same Upper Carboniferous biome.

CONCLUSION

Carboniferous paleoflora consists of two museum collections: 'Mlava-Pek *sensu lato*' and 'Borogin potok, Ranovac village'. The 'Mlava-Pek *sensu lato*' collection is composed of approximately 300 specimens from several sites, including about 50 specimens of fossil plants that were collected by Jovan Žujović and Josif Pančić at the end of the 19^{th} century. Most of the specimens were identified by Dionýz Štúr. The other collection from the same basin, 'Borogin Potok, Ranovac village', consists of about 100 specimens. It was collected in 1957 at the tailings pond of the Borogin Potok mine near the village of Ranovac. The specimens were collected and sent to the museum by Petar Pavlović, a local teacher.

Both paleofloras are dominated by seed ferns, which make up about 50% of the phytocenosis (the morphgenera *Alethopteris* and *Linopteris* occur in both associations in large numbers, while *Odontopteris* is represented only in Mlava-Pek sensu lato association). The percentage representation of other classes of plants is different and reflects the climatic conditions in which these floras existed. Specimens from the 'Mlava-Pek *sensu lato*' collection show that this flora is somewhat older. It contains a significant percentage of swamp floristic elements such as Equisetidae and relict representatives of *Sigillaria*. In the paleoflora of Borogin Potok, the percentage of Equisetidae is significantly smaller, while arborescent lycopods have completely disappeared. In parallel with the emerging aridification of the climate, they were replaced by *Cordaites* and tree ferns.

The studied paleoflora of the Mlava-Pek coal basin resembles the Stephanian or Stephanian-Permian flora of Vrška Čuka the most. It also shows certain similarities with the Stephanian floras of Croatia, Romania and Bulgaria, most certainly representing the western parts of the Stephanian vegetation of Romania and Bulgaria.

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SUPPORTING INFORMATION

Appendix: The oldest specimens from the 'Mlava-Pek sensu lato' collection that were found with apppropriate labels attached

Tab. 1 contains a list of specimens of special cultural and historical importance. In 2022, these specimens were declared Cultural Heritage of the Republic of Serbia. There is only one specimen from Mustapić, and it fully corresponds with the description of the fossils that were collected by

Josif Pančić and Felix Hofmann (Žujović 1886). All the written data presented in the table were copied from the old labels that were attached to these specimens. Almost all taxonomic determinations have been revised in the meantime; for that reason, wherever the paleofloristic list of plants is mentioned, these taxa are not listed in this paper (for example: *Lepidodendron* is not listed because it was changed to *Sigillaria* in 2010, while *Dictyopteris* was changed to *Alethopteris*). The table (Fig. 7) represents a historical and museological record of the first identifications of this collection, and shows where the collection was located prior to its arrival at the Museum. Since the Grande école (srb. Velika škola) transformed into the University of Belgrade in 1905, the specimens that were marked with Grande école labels are certainly those that were mentioned in Žujović's paper in 1886. Also, the specimens that bear glued labels written in ink in German are probably those that were collected by Žujević and identified by Štúr. In the case of specimens that only bear the label of the University of Belgrade, and no other, we cannot be certain who collected them and when, but it is most likely that these specimens also arrived from the Grande école or the Mining Department of the Ministry of Economy (because these are the two oldest types of labels, and it is obvious that the first collected specimens were deposited in one of these two institutions and only later moved to the University of Belgrade) (Fig. 16).

Fig 16. – Old labels found together with the specimens: a) Grande école, b) The Mining Department of the Royal Serbian Ministry of Economy, c) University of Belgrade.

Tab. 1. – Original list of specimens from the 'Mlava-Pek *sensu lato*' collection that were found with approriate labels. None of the labels included information about who had collected or identified the specimen; these data were obtained indirectly, based on the work of Žujović (1886).

Inventory number	Name of species written on the original museum labels (first identification)	Locality	Collected by	Identified by	Where it was located	Literature	Other notes contained on labels
11	*Pecopteris grandini* Bgt. *Dyctiopteris brongniarti*						
71	*Pecopteris grandini* *Dictyopteris brogniarti*						
77	*Dictyopteris brongniarti*	Kladurovo, Serbia					
78	*Annularia stellata* Schlo						
81	*Dictyopteris* cf. *brogniarti*				University of Belgrade		
93	Fruchtahn *Annularia*						3310
98	*Cyatheites* (*Pecopteris*) *arborescens* Schloth.	Kladurovo, Požarevac county			Mining Department of the Ministry of Economy		Number 16, Collection SFM
101	*Sigillaria* spec				University of Belgrade		
103	*Trigonocarpus* sp.				University of Belgrade		
105					University of Belgrade		
110, 117, 139, 141	*Annularia stellata*	Kladurovo			University of Belgrade		
111							1993
113	*Sphenophyllum scholotheimi*						
115	*Sphenophyllum scholotheimi* Germ	Kladurovo	Jovan Žujović, prior to 1886	Dionyz Štur, prior to 1886	1. Grande école 2. University of Belgrade		Žujović 1886
118		Mišljenovac			University of Belgrade		
122		Mišljenovac			University of Belgrade		
123	*Annularia sphenophylloides* *Scolecopteris* (*Pecopteris*) *arborescens* Schl. sp.						

Inventory number	Name of species written on the original museum labels (first identification)	Locality	Collected by	Identified by	Where it was located	Literature	Other notes contained on labels
124	*Dictyopteris brogniarti* Gutb	Kladurovo			University of Belgrade		
131	*Asterophyllites equisetiformis* Schl. sp.	Kladurovo	Jovan Žujović, prior to 1886	Dionyz Štur, prior to 1886	1. Grande école 2. University of Belgrade		Žujović 1886
132	a. *Dictyopteris neuropteroides* Gein b. *Alethopteris* cf, *pteroides* Brong c. *Pecopteris pluckeneti* Schloth	Mustapić, Požarevac county	Josif Pančić and Felix Hofman, prior to 1886	? Josif Pančić, prior zo 1886	Mining Department of the Ministry of Economy	Žujović 1886	Upper Carboniferous
133		Mišljenovac			University of Belgrade		
135	Steinkern[3] von *Sigillaria*						
136	*Stigmaria* sp.[4]						
138	Illegible						2817
140	*Pecopteris Grandini* *Dictyopteris Brogniarti*				University of Belgrade		
143	*D.....*[5]						
144	*Scolecopteris* (*Pecop.*) *arborescens* Schlot. spec.	Kučajna			University of Belgrade		3308
152	*Lepidodendron* cf. *rimosum* Sternb.	Kladurovo	Jovan Žujović, prior to 1886	Dionyz Štur, prior to 1886	Grande école	Žujović 1886	
222	*Annularia stellata* Schloth. sp.	Kučajna			University of Belgrade		
25, 1030	*Calamites varians* Stern.	Kladurovo	Jovan Žujović, prior to 1886	Dionyz Štur, prior to 1886	Grande école	Žujović 1886	
1033	*Odontopteris minor*						
1034	*Scolecopteris* (*Pecopteris*) *arborescens* Schl. sp.	Kučajna			University of Belgrade		3332
1036							3750

[3] *Sigillaria* mold

[4] There were no old labels on this specimen; however, this is the only *Stigmaria* in the entire collection and it is quite possible that it was collected by Cotta in 1863, since he had stated in his report that he had come across a layer containing Stigmaria (Žujović, 1886)

[5] Probably *Dictyopteris*. A remnant of an old label glued to the specimen

Tab. 2. – List of all specimens contained in the 'Mlava-Pek sensu lato' collection. 1. Kučajna; 2. Mišljenovac; 3. Kladurovo, 4. Mustapić; 5. Osipaonički Potok; 6. Slani Potok; 7. Petrovac; 8. Mlava-Pek locus ignotus. The fossils that *are* from the area of the Mlava-Pek coal basin but do not have a more precisely determined locality are listed under the name 'Mlava-Pek locus ignotus'.

TAXON	1	2	3	4	5	6	7	8
PTERIDOSPERMAE	**x**	**x**	**x**	**x**		**x**		**x**
ALETHOPTERIS	x	x	x	x				x
Alethopteris cf. *grandoides*								x
Alethopteris davreuxii								x
Alethopteris lesquerci			x					
Alethopteris lonchitica								x
Alethopteris pennsylvanica								x
Alethopteri srobusta			x					
Alethopteris subelegans		x						x
Alethopteris valida	x		x	x				x
Alethopteris zeilleri		x						
Alethopteris sp.			x					x
AUTUNIA		x						
Autunia conferta		x						
CALIPTERIDIUM		x				x		x
Callipteridium cf. *zeillerii*						x		
Callipteridium sp.		x						
? *Callipteridium crassinervum*								x
? *Callipteridium* sp.			x					
CALIPTERIS			x					x
Callipteris subauriculata			x					x
? *Callipteris* sp.								x
CORYNEPTERIS								x
Corynepteris sp.								x
CYCLOPTERIS								x
Cyclopteris sp.								x
LAVENIOPTERIS								x
Laveniopteris tenuifolia								x

TAXON	1	2	3	4	5	6	7	8
LINOPTERIS		x	x	x				x
Linopteris brogniarti								x
Linopteris cf. *germari*				x				
Linopteris neuropteroides		x	x	x				x
Linopteris cf. *neuropteroides*		x						x
Linopteris sp.			x					x
MARIOPTERIS			x					x
Mariopteris muricata			x					
Mariopteris sp.								x
AFF. NEURALETHOPTERIS		x						x
aff. *Neuralethopteris schlehanii*		x						x
aff. *Neuralethopteris* sp.								x
NEUROPTERIS		x						x
Neuropteris flexuosa,								x
Neuropteris jongmasii								x
Neuropteris sp.		x						x
ODONTOPTERIS	x	x	x			x		x
Odontopteris brardi,		x				x		x
Odontopteris minor		x	x					x
Odontopteris minor f. *brogniarti*								x
Odontopteris minor f. *zeillerii,*								x
Odontopteris reichiana	x	x	x					x
Odontopteris cf. *reichiana*								x
Odontopteris sp.			x					
TRIGONOCARPUS			x	x		x		x
Trigonocarpus sp.			x	x		x		x
PTERIDOSPERMAE inc.sed.			x					x
Alethopteris zeileri vel *Callipteris* sp.			x					
Alethopteris sp. vel *Callipteridium* sp.								x
Linopteris vel *Neuropteris*		x						x
EQUISETIDAE	**x**	**x**	**x**				**x**	**x**
ANNULARIA	x		x				x	x
Annularia stellata	x		x				x	x
Annularia sphenophylloides			x				x	x

TAXON	1	2	3	4	5	6	7	8
ASTEROPHYLLITES		x	x				x	x
Asterophyllites equisetiformis		x	x				x	
Asterophyllites tenuifolia								x
Asterophyllites sp.		x						x
CALAMITES		x	x				x	x
Calamites carinatus			x					
Calamites cf. *carinatus*								x
Calamites cf. *cistii*								x
Calamites ramosus							x	
Calamites varians			x					
Calamites sp.		x	x					x
CALAMOSTACHYS								x
Calamostachys tuberculata								x
EQUISETITES		x	x					
Equisetales aff. *Equisetites*		x	x					
SPHENOPHYLLUM		x	x					x
Sphenophyllum cf. *costae*			x					
Sphenophyllum emarginatum			x					
Sphenophyllum oblongifolium		x						x
Sphenophyllum thonii								x
Sphenophyllum verticillatum								x
Sphenophyllum sp.		x	x					x
Equisetophyta indet.			x					
TREE FERNS	**x**	**x**	**x**		**x**			**x**
ASTEROTHECA / PECOPTERIS	x	x	x					x
Asterotheca arborescens	x	x	x					x
Asterotheca candolleana		x	x					x
Asterotheca hemiptelidoides	x							
Asterotheca cf. *hemipteloides*								x
Asterotheca sp.								x
Pecopteris arborescens	x	x	x					x
Pecopteris cf. *bourozii*			x					
Pecopteris cadolleana								x
Pecopteris cyathea								x
Pecopteris sp.								x

TAXON	1	2	3	4	5	6	7	8
NEMEJCOPTERIS					x			x
Nemejcopteris feminaeformis		x			x			
? *Nemejcopteris feminaeformis*								x
POLIMORPHOPTERIS								x
Polymorphopteris polymorpha								x
SCOLECOPTERIS		x						
Scolecopteris sp.		x						
SPHENOPTERIS								x
Sphenopteris cf. *schwerinii*								x
Sphenopteris sp.								x
Polipodiophyta indet.		x						
CORDAITES	**x**	**x**	**x**					**x**
Cordaites palmaeformis	x	x	x					x
Cordaites principalis	x		x					x
Cordaites sp.	x							x
SAMAROPSIS								x
Samaropsis sp.								x
LEPIDODENDRALES	**x**		**x**			**x**		**x**
CYPERITES								x
Cyperites bicarinatus								x
SIGILLARIA	x		x			x		x
Sigillaria cf. *euxina*	x							
Sigilllaria cf. *scholothemiana*						x		
Sigillaria sp.			x					x
STIGMARIA								x
Stigmaria sp.								x
ULODENDRON			x					
Ulodendron sp.			x					
INCERTE SEDIS								
Calamites vel *Sigillaria*	?x							
Strobus indet.								x
Semen								x

Tab. 3. – Comparative overview of taxa from both collections. The figures show the number of specimens in which a certain genus was found, in relation to the total number of specimens (for example: *Alethopteris* 26 / 120 means that out of 120 specimens found in the collection, the genus *Alethopteris* was found in 26 specimens). An additional explanation may be needed here to avoid confusion: In the 'Mlava-Pek *sensu lato*' collection, there are a total of 120 pieces of rock containing approximately 300 taxa. In the 'Borogin Potok' collection, there are about 100 pieces containing around 130 taxa (identified plant remains).

TAXON	Mlava-Pek *sensu lato*	Borogin Potok, Ranovac village
PTERIDOSPERMAE		
ALETHOPTERIS	26/120	12/100
Alethopteris cf. *grandoides*	x	
Alethopteris cf. *lancifolia*		x
Alethopteris davreuxii	x	
Alethopteris grandini		x
Alethopteris lesquerci	x	
Alethopteris lonchitica	x	
Alethopteris pennsylvanica	x	x
Alethopteris robusta	x	
Alethopteris serlii		x
Alethopteris subelegans	x	
Alethopteris valida	x	
Alethopteris zeilleri	x	
Alethopteris sp.	x	x
AUTUNIA	5/120	1/100
Autunia conferta	x	x
CALLIPTERIDIUM	6/120	2/100
Callipteridium striatum		x
Callipteridium cf. *zeillerii*	x	
Callipteridium sp.	x	
? *Callipteridium crassinervum*	x	
? *Callipteridium* sp.	x	
CALLIPTERIS	3/120	0
Callipteris subauriculata	x	
? *Callipteris* sp.	x	
CORYNEPTERIS	x	
Corynepteris sp.	x	
CYCLOPTERIS	x	
Cyclopteris sp.	x	
EUSPHENOPTERIS	0	1/100
Eusphenopteris obtusiloba		x
LAVENIOPTERIS	1/ 120	0
Laveniopteris tenuifolia	x	

TAXON	Mlava-Pek *sensu lato*	Borogin Potok, Ranovac village
LINOPTERIS	38/120	24/100
Linopteris brogniarti	x	
Linopteris florini		x
Linopteris cf. *germari*	x	
Linopteris neuropteroides	x	x
Linopteris cf. *neuropteroides*	x	
Linopteris obliqua		x
Linopteris cf. *obliqua*		x
Linopteris sp.	x	x
MARIOPTERIS	2/120	4/100
Mariopteris muricata	x	x
Mariopteris sp.	x	x
AFF. NEURALE THOPTERIS	2/120	0
aff. *Neuralethopteris schlehanii*	x	
aff. *Neuralethopteris* sp.	x	
NEUROPTERIS	7/120	0
Neuropteris flexuosa	x	
Neuropteris jongmasii	x	
Neuropteris sp.	x	
ODONTOPTERIS	37/120	0
Odontopteris brardi	x	
Odontopteris minor	x	
Odontopteris minor f. *brogniarti*	x	
Odontopteris minor f. *zeillerii*	x	
Odontopteris reichiana	x	
Odontopteris cf. *reichiana*	x	
Odontopteris sp.	x	
TRIGONOCARPUS	11/120	3/100
Trigonocarpus sp.	x	x
PTERIDOSPERMAE inc.sed.	3/120	3/100
Alethopteris zeileri vel *Callipteris* sp.	x	
Alethopteris vel *Callipteridium*	x	
Linopteris vel *Neuropteris*	x	
Autunia conferta vel *Alethopteris*		x
Linopteris vel Neuropteris		x
EQUISETIDAE		
ANNULARIA	12/120	3/100
Annularia stellata	x	x
Annularia sphenophylloides	x	
ASTEROPHYLLIT ES	7/120	0
Asterophyllites equisetiformis	x	
Asterophyllites tenuifolia	x	
Asterophyllites sp.	x	

TAXON	Mlava-Pek *sensu lato*	Borogin Potok, Ranovac village
CALAMITES	16/120	1/100
Calamites carinatus	x	
Calamites cf. *carinatus*	x	
Calamites cf. *cistii*	x	
Calamites ramosus		
Calamites varians		
Calamites sp.	x	x
CALAMOSTACHYS	3/120	0
Calamostachys tuberculata	x	
EQUISETITES	3/120	0
Equisetales aff. *Equisetites*	x	
SPHENOPHYLLUM	15/120	1
Sphenophyllum cf. *costae*	x	
Sphenophyllum emarginatum	x	
Sphenophyllum oblongifolium	x	
Sphenophyllum thonii	x	
Sphenophyllum verticillatum	x	
Sphenophyllum sp.	x	x
Equisetophyta in det.	x	
TREE FERNS		
ASTEROTHECA / PECOPTERIS complex	37/120	43/100
Asterotheca arborescens	x	x
Asterotheca cf. *arborescens*		x
Asterotheca candolleana	x	x
Asterotheca hemiptelidoides	x	
Asterotheca cf. *hemipteloides*	x	
Asterotheca sp.	x	x
Pecopteris arborescens	x	x
Pecopteris cf. *bourozii*	x	
Pecopteris bucklandi		x
Pecopteris cadolleana	x	
Pecopteris cyathea	x	
Pecopteris sp.	x	x
NEMEJCOPTERIS	2/120	0
Nemejcopteris feminaeformis	x	
? *Nemejcopteris feminiformis*	x	
POLIMORPHOPTERIS	2/120	0
Polymorphopteris polymorpha	x	
SCOLECOPTERIS	1/120	0
Scolecopteris sp. sporangium	x	
SPHENOPTERIS	2/120	0
Sphenopteris cf. *schwerinii* sporangium	x	
Sphenopteris sp.	x	

TAXON	Mlava-Pek *sensu lato*	Borogin Potok, Ranovac village
Polipodiophyta indet	x	
CORDAITES		
CORDAITES	25/120	12/100
Cordaites palmaeformis	x	x
Cordaites principalis	x	x
Cordaites sp.	x	x
SAMAROPSIS	1/120	0
Samaropsis sp. seed	x	
LEPIDODENDRALES		
CYPERITES	1/120	0
Cyperites bicarinatus	x	
SIGILLARIA	5/120	0
Sigillaria cf. *euxina*	x	
Sigilllaria cf. *scholothemiana*	x	
Sigillaria sp.	x	
STIGMARIA	1/120	0
Stigmaria sp.	x	
ULODENDRON	2	0
Ulodendron sp.	x	
INCERTAE SEDIS		
Calamites / Sigillaria	x	
Strobus indet.	x	x
Seed	x	

СТЕФАНСКО-ПЕРМСКА ПАЛЕОФЛОРА СА ПОДРУЧЈА МЛАВСКО-ПЕЧКОГ БАСЕНА, ИСТОЧНА СРБИЈА

ДЕСА ЂОРЂЕВИЋ МИЛУТИНОВИЋ

РЕЗИМЕ

У раду су приказане две збирке стефанских и стефанско-пермских фосилних биљака нађених на подручју између река Млава и Пек (Млавско-печки угљени басен). У зависности од расположивих података фосилни налази су раздвојени у две колекције:

1. Колекција Млава-Пек *sensu lato*: обухвата примерке нађене углавном крајем 19. века на различитим локалитетима у оквиру Млавско-печког басена (Мишљеновац, Рановац, Кладурово, Мустапић, Слани поток. Осипаонички поток и Кучајна).

2. Колекција Борогин поток, село Рановац: обухвата примерке који потичу само са једног локалитета - халде рудника Борогин поток. Они су сакупљени 1957. године.

У збирци Млава-Пек *sensu lato* заступљене су све основне класе биљака карактеристичне за горњекарбонски период: дрволике пречице Lepidodendrales, различити ратавићи и каламити Equisetidae, дрволике папрати Marattiidae и Polypodiidae, семене папрати Pteridospermatopsida (*Alethopteris*, *Linopteris*, *Odontopteris*) и кордаити (Cordaites). Семене папарти доминирају заједницом и чине преко 50% укупне асоцијације. Друге доминантне групе су раставићи и дрвенасте папрати. Кордаити су заступљени у релативно малом броју, међутим могуће је да су они живели на просушенијим местима даље од депозиционе средине тако да је, сходно томе, и могућност њихове фосилизације била смањена. Пречице се такође јављају у малом броју, највише су заступљене сигиларије (*Sigillaria*) које су у овој асоцијацији највероватније представљале реликтне таксоне.

Колекција Борогин поток, село Рановац има нешто другачији таксономски састав, овде такође доминирају семене папрати (45%) *Alethopteris* и *Linopteris*, али нема *Odontopteris*-а. Такође нису нађени представници дрволиких пречица, а представници раставића и каламита су видно смањени. Ова палеофлора показује аридниji карактер и вероватно је нешто млађа од претходне. У њој је нађено и неколико примерака биљака фосилизованих у млађим слојевима тј. у црвеним пермским пешчарима.

У збирци се налази велики број примерака (преко 400 појединачних фосила) чиме је омогућена сасвим добра и тачна реконструкција некадашњег екосистема и фитоценолошке заступљености појединих таксона. Управо захваљујући тако великом броју примерака било је могуће закључити да *Sigillaria* представља реликтни таксон преостао из некадашњег вестфалског периода.

Приказана палеофлора највише сличности показује са стефанско-пермском флором Вршке Чуке у Србији (Pantić 1951b, Djordjević Milutinović, 2015), затим са горњекарбонском флором Велебита у Хрватској (Cleal *et al.* 2015), са румунским флорама пермско-карбонске старости (Dragastan *et al.* 1997, Popa 1999, 2005, 2009, Popa & Cleal 2012) и са бугарским горњекарбонским флорама (Cleal *et al.* 2004).

Описане палеофлоре чувају се у Природњачком музеју у Београду: колекција Млава-Пек *sensu lato* PALBOT 40 / I и 40 / II: 11, 12, 19, 25, 71–172, 222, 591, 616, 1028, 1929–1030, 1032, 1032–1034, 1036, 1504, 1981 и колекција Борогин поток, село Рановац PALBOT 40 / III: 1982–2094.

PLATE 1

1. *Sigillaria* cf. *euxina* Zeiller, ?Kučajna, inv.no. 135.
2. *Sigillaria* sp., Mlava-Pek *locus ignotus,* inv.no. 101.
3. *Sigillaria* sp. vel *Lepidodendron* cf. *rimosum*, Kladurovo, inv.no. 152.
4. *Stigmaria* sp., Mlava-Pek *locus ignotus*, inv.no. 136.
   All scale bars = 10 *mm*.

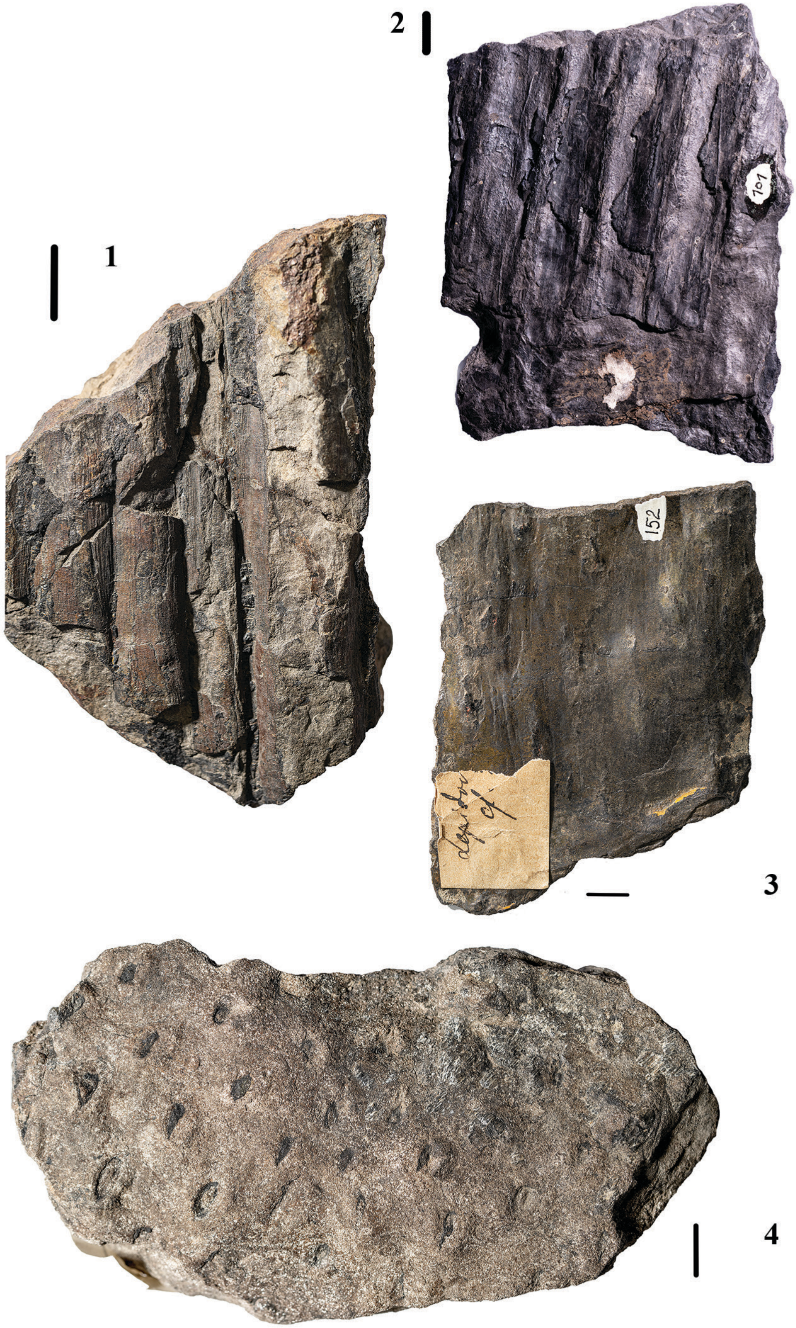

1
2
3
4

PLATE 2

1. *Sphenophyllum* cf *coste* Sterzel, Kladurova, inv.no. 158.
2. *Annularia stellata* (Schlotheim) Wood, Kladurovo, inv.no. 131a.
3. *Annularia sphenophylloides* (Zenker) Gutbier, Mlava-Pek *locus ignotus*, inv.no. 163.
4. *Calamostachys tuberculata* (Sternberg) Weiss, Mlava-Pek *locus ignotus*, inv.no. 116.
5. *Calamostachys tuberculata* (Sternberg) Weiss, Mlava-Pek locus *ignotus*, inv.no. 93.
6. *Annularia stellata* (Schlotheim) Wood, Kučajna, inv.no. 222.
   All scale bars = 10 *mm*.

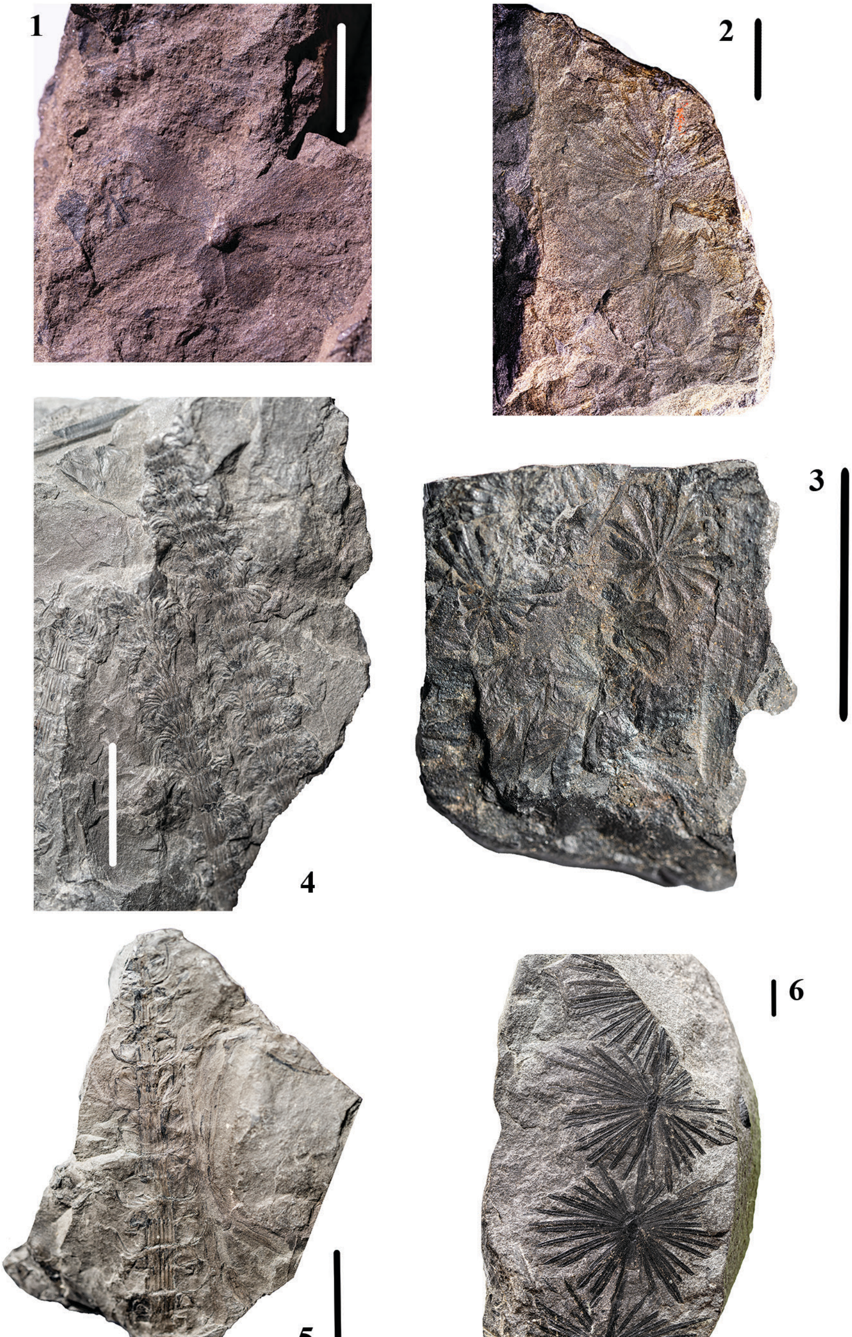

1
2
3
4
5
6

PLATE 3

1. *Asterotheca arborescens* Schlotheim, Borogin potok, Ranovac village, inv.no. 2081.
2. *Pecopteris cyathea* (Schlotheim) Brongniart, Borogin potok, Ranovac village, inv.no. 2080.
3. *Pecopteris arborescens* (Schlotheim) Sternberg, Kladurovo or Kučajna, inv.no. 19.
4. *Pecopteris cyathea* (Schlotheim) Brongniart, Mlava-Pek *locus ignotus*, inv.no. 84.
5. *Nauralethopteris scholehanii*, (Štur) Laveine, Mišljenovac, inv.no. 72.

All scale bars = 10 *mm*.

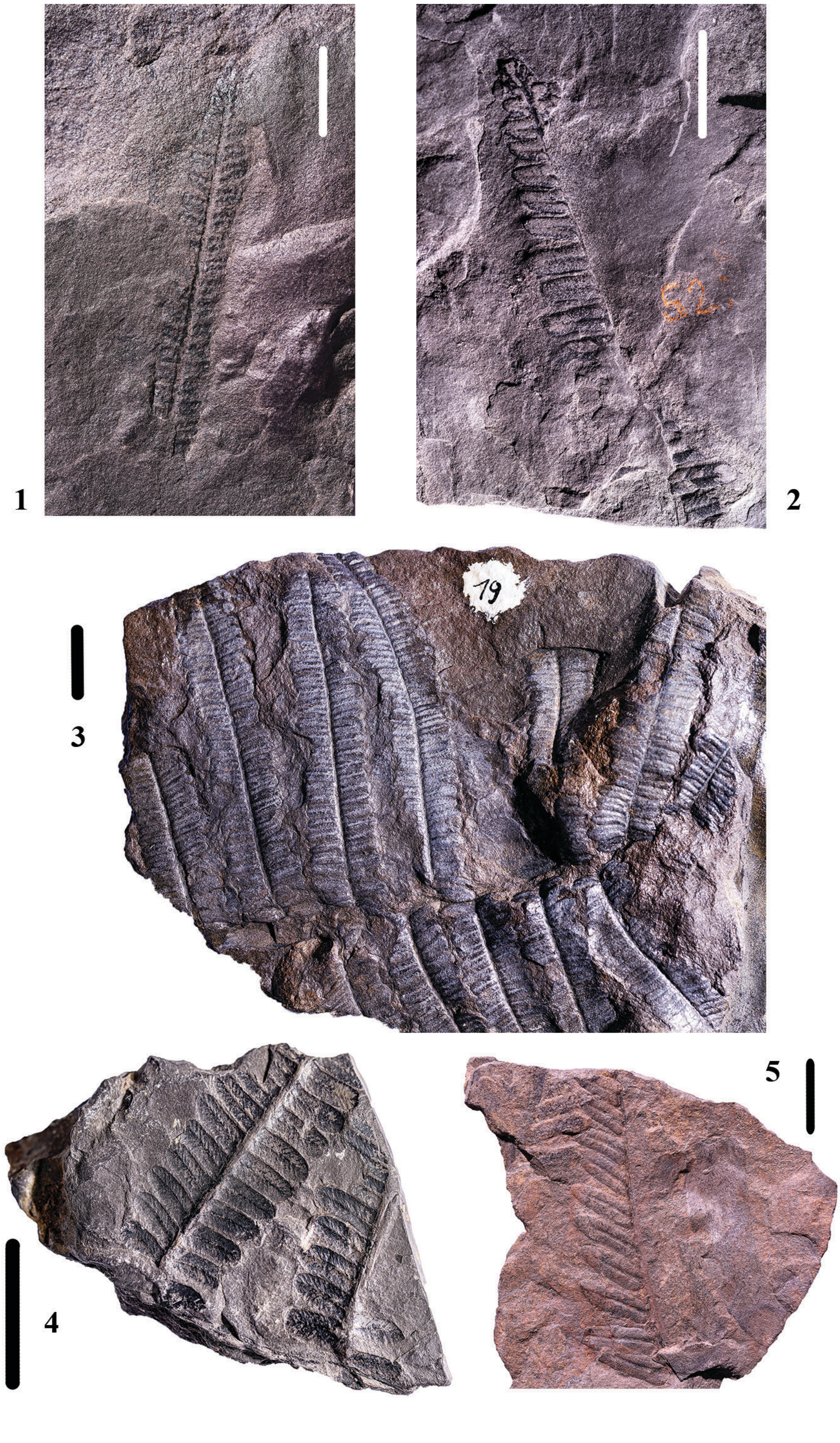

1
2
52
19
3
4
5

PLATE 4

1. *Odontopteris* cf. *brardi* (Brongniart) Sternberg, Mlava-Pek *locus ignotus*, inv.no. 170.
2. *Odontopteris reichiana* Gutbier, Mišljenovac, inv.no. 104, apical part.

3a. *Odontopteris minor* Brongniart, Mlava-Pek *locus ignotus,* inv.no. 122a.

3b. *Alethopteris* sp., Mišljenovac, Mlava-Pek *locus ignotus,* inv.no. 122b.

4. *Odontopteris brardi* (Brongniart) Sternberg, Mlava-Pek *locus ignotus*, inv.no. 107.
5. *Odontopteris minor* Brongniart, Mlava-Pek *locus ignotus*, inv.no. 1033.
6. *Odontopteris* cf. *osmundaeformis* (Schlotheim) Zeiller, Mlava-Pek *locus ignotus*, inv.no. 130.

All scale bars = 10 *mm*.

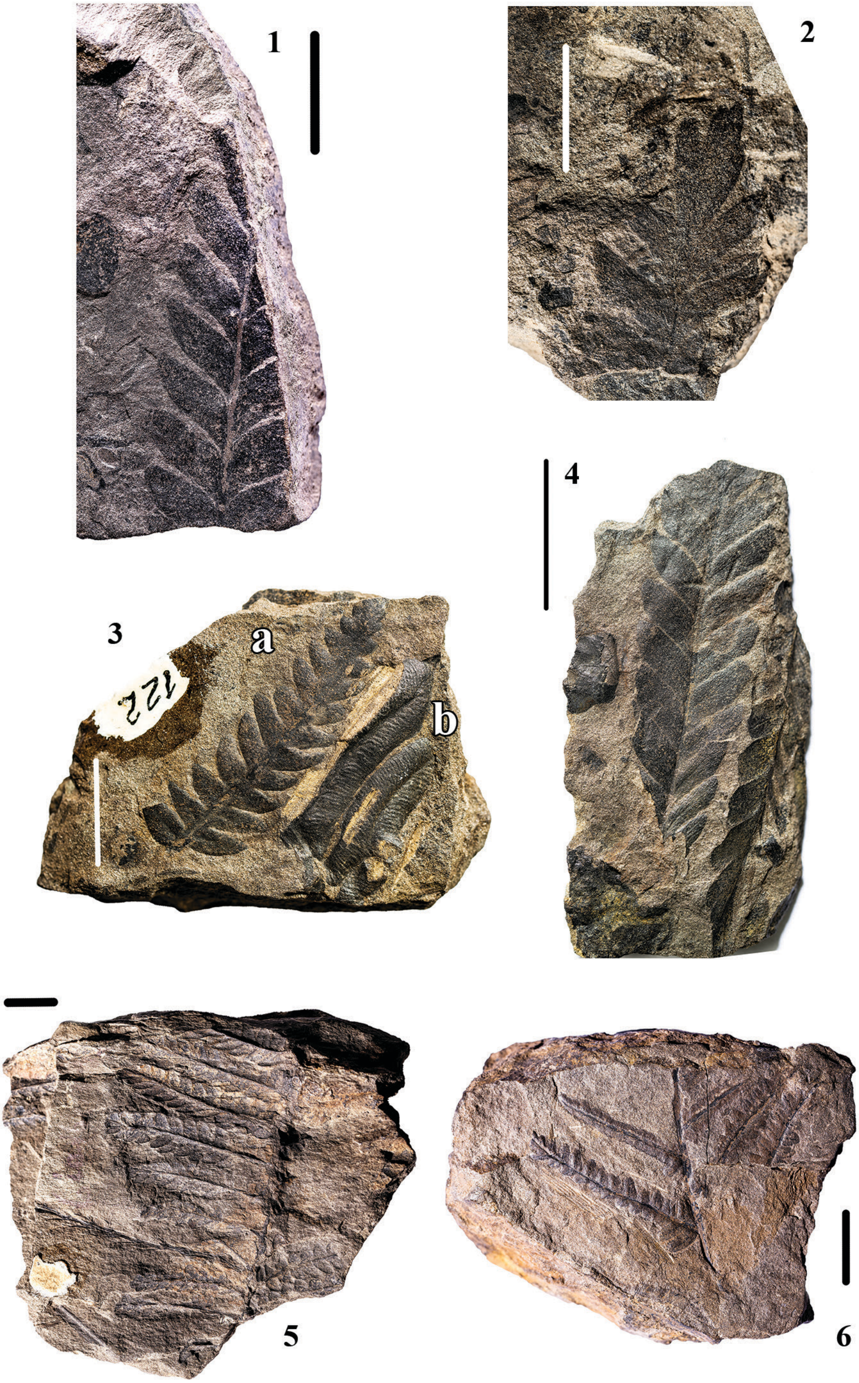

1
2
3
a
122
b
4
5
6

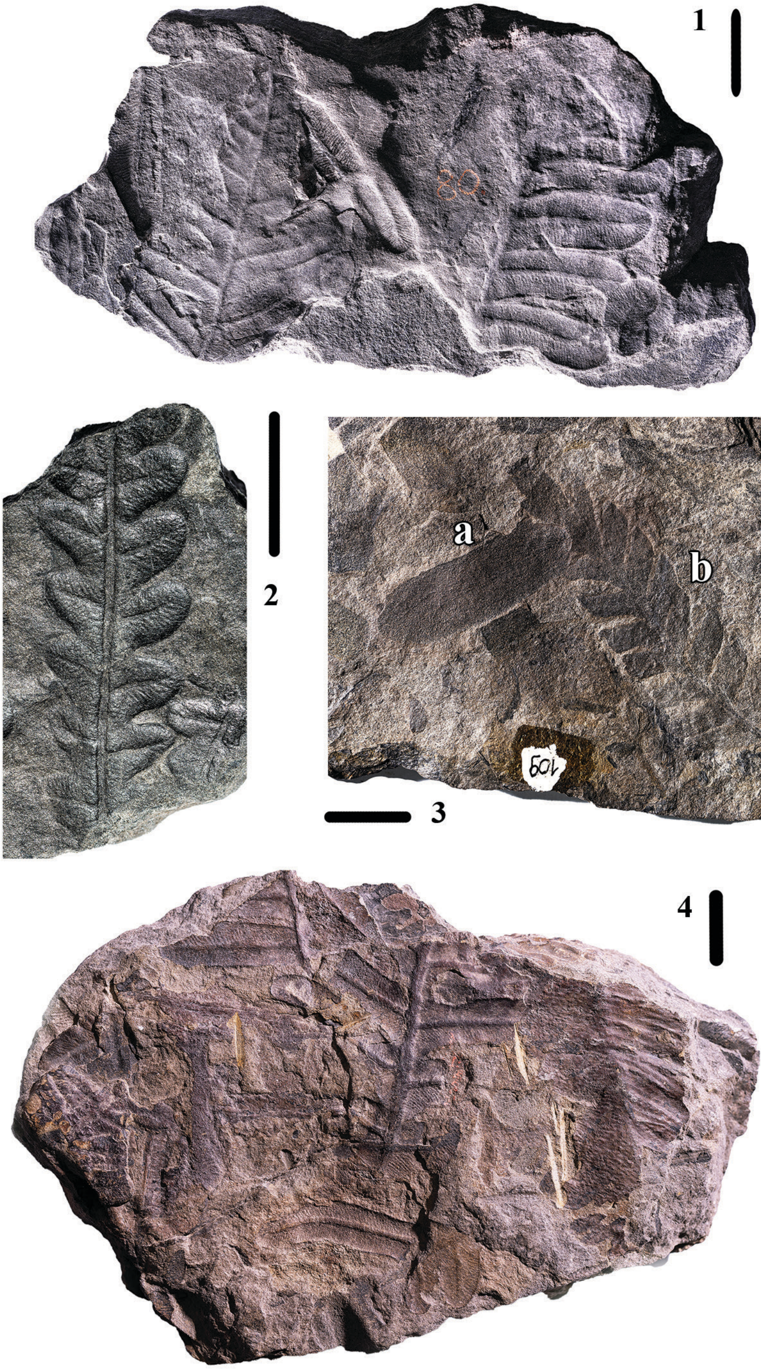
PLATE 5

1. *Alethopteris serlii* (Brogniart) Goppert, Borogin potok, Ranovac village, inv.no. 2083.
2. *Alethopteris grandini* Goeppert, Borogin potok, Ranovac village, coll.no. 40 / III: 77.

3a. *Linopteris* cf. *germari* Giebel, Mlava-Pek *locus ignotus*, inv.no. 109a.

3b. *Odontopteris* cf. *reichiana*, Gutbier, Mlava-Pek *locus ignotus*, inv.no. 109b.

4. *Alethopteris valida* Boulay, ?Kučajna, inv.no. 86.
   All scale bars = 10 *mm*.



1
2
a
b
3
4

PLATE 6

1. *Alethopteris lonchitica* Sternberg, Kladurovo, inv.no. 77.
2. *Alethopteris pensylvanica* Lesquereux, Borogin potok, Ranovac village, inv.no. 2089.
3. *Alethopteris zeilerii* vel *Callipteris* sp., Borogin potok, Ranovac village, inv.no. 2082.
4. *Neurocallipteris* sp., Borogin potok, Ranovac village, inv.no. 2088.
   All scale bars = 10 *mm*.

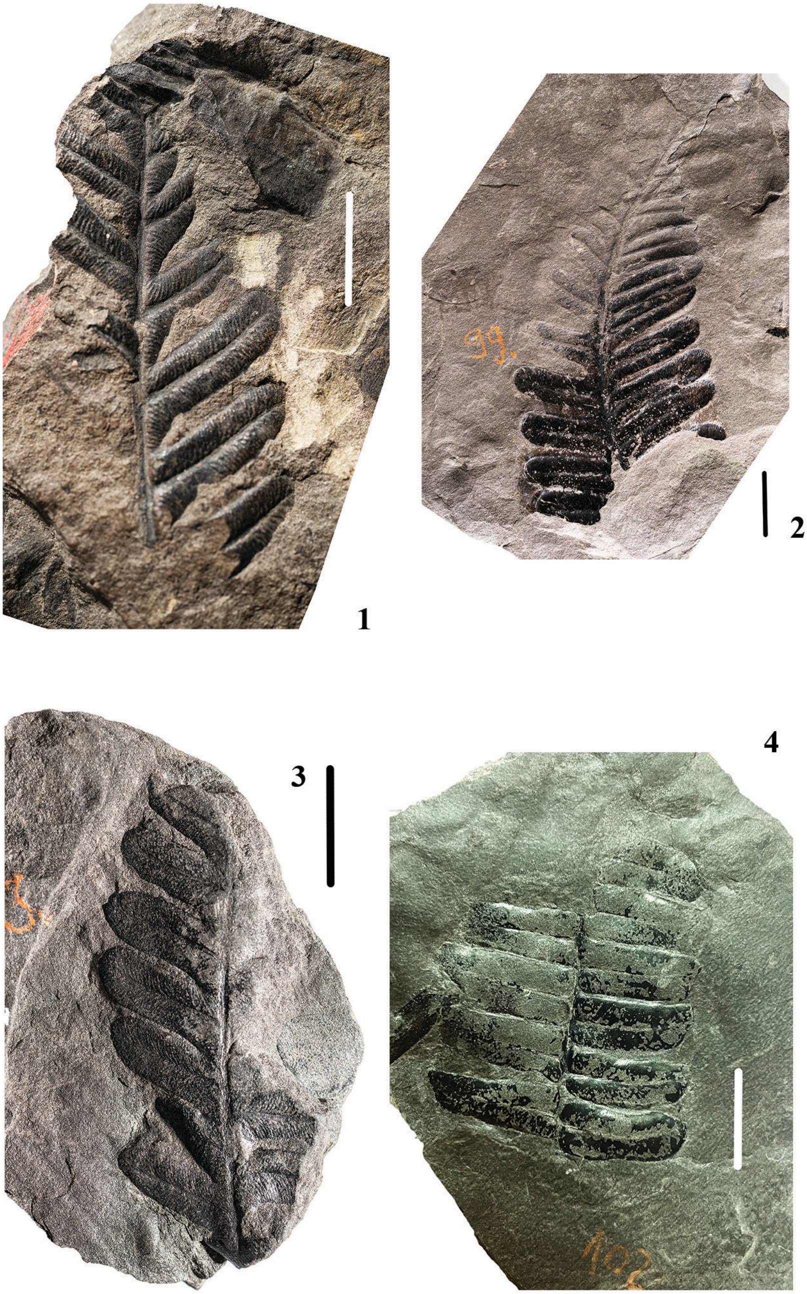

1
2
3
4

PLATE 7

1. *Alethopteris* sp., Borogin potok, Ranovac village, inv. no. 2090, leaf dimorphism.
2. *Callipteris subauriculata* (Weiss) Grand'Eury, Mlava-Pek *locus ignotus*, inv.no. 1029.
3. *Autunia conferta* (Sternberg) Kerp, ?Mišljenovac, inv.no. 1028.
4. *Autunia conferta* (Sternberg) Kerp, ?Mišljenovac, inv.no. 616.

   All scale bars = 10 *mm*.


1
2
3
4
1029

PLATE 8

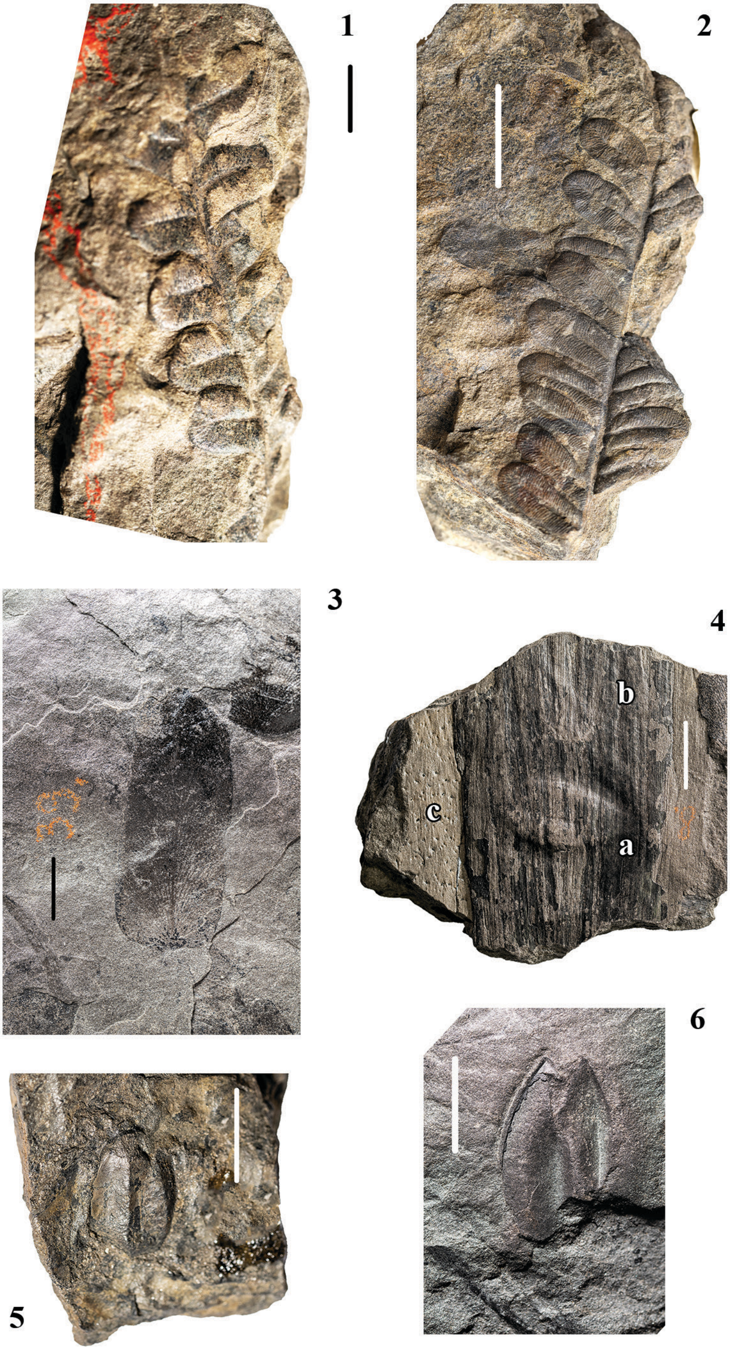
1. *Callipteris subauriculata* (Weiss) Grand'Eury, Kladurova, inv. no. 75.
2. *Autunia conferta* (Sternberg) Kerp, Misljenovac, inv.no. 89.
3. *Linopteris neuropteroides* (Gutbier) Potonié, Borogin potok, Ranovac village, inv. no. 2091.

4a. *Trigonocarpus* sp., Borogin potok, Ranovac village, inv. no. 2092a.

4b. *Cordaites principalis* (Germar) Geinitz, Borogin potok, Ranovac village, inv. no. 2092b.

4c. Trichome-scarred stem, Borogin potok, Ranovac village inv. no. 2092c.

5. *Pachytesta* sp. (petrified *Trigonocarpus* sp.), Mlava-Pek *locus ignotus*, inv.no. 103.
6. *Trigonocarpus* sp., Borogin potok, Ranovac village, inv.no. 2079.
   All scale bars = 10 *mm*.

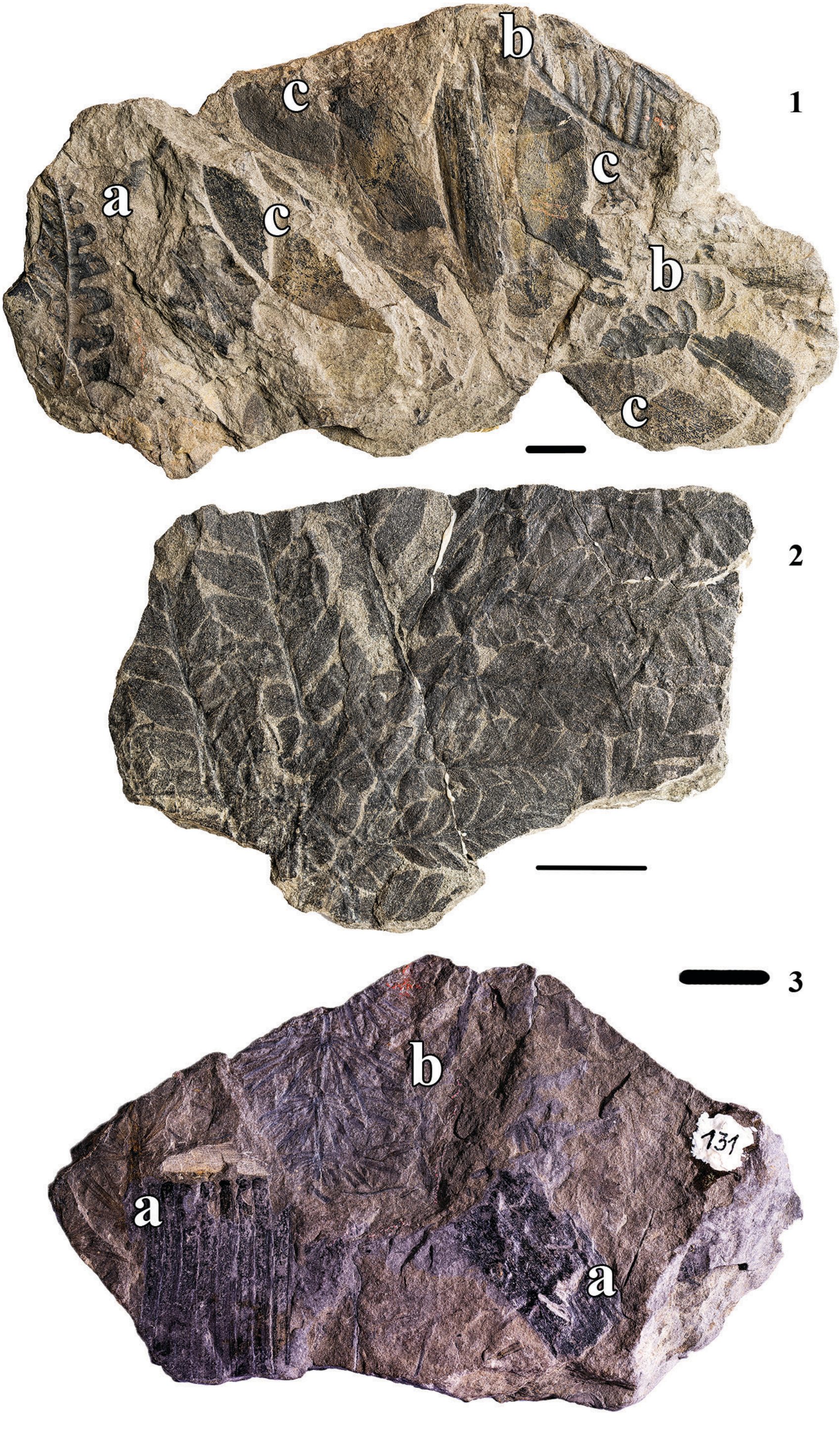


1
2
3
4
b
c
a
5
6

PLATE 9

1. Different parts of seed ferns, Mlava-Pek *locus ignotus*, inv. no. 124.
1a. *Callipteris* sp. inv. no. 124a.
1b. *Alethopteris* spp. inv. no. 124b.
1c. *Linopteris* sp, inv. no. 124c.
2. Part of the frond with several pinnae. *Odontopteris minor* Brongniart, Mlava-Pek *locus ignotus*, inv. no. 127.
3. Different parts of the horsetails, possibly from the same individual, Kladurovo, inv.no. 131.
3a. *Calamites* sp. inv.no. 131a.
3b. *Asterophyllites* sp. inv.no. 131b.

All scale bars = 10 *mm*.


1
a
b
c
c
c
b
c
2
3
b
131
a
a