

Response of Higher Plants to the Devonian Kačak Event (Czech Republic)

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Abstract—The Middle Devonian Kačak Event (Czech Republic), which was associated with anoxia in marine environments and accompanied by the extinction of many representatives of the marine biota, had no substantial influence on the development of terrestrial vegetation (higher plants and miospores).

Keywords: Middle Devonian, Kačak Event, higher plants, miospores.

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INTRODUCTION

The Kačak Event is one of the most significant anoxic episodes in the Middle Devonian history. It is widely debated among researchers, who consider it to be responsible for the extinction of many invertebrate taxa (House, 1985; Chlupač and Kukal, 1986; Chlupač, 1994; Budil, 1995a, 1995b; Walliser, 2000). Chlupač (1959) was the first to record the Kačak Event in the Barrandian sections of the central Czech Republic. He briefly described the lithology of the Kačak and Roblin members of the Middle Devonian Srbsko Formation and noted that the base of the Kačak Member is marked by the replacement of typical carbonate sediments by dark gray to black-gray shales. According to this author, a sharp change in rock coloration is observed at the boundary between the Kačak and Roblin members, which are composed of light gray shales and sandstones.

The influence of the Kačak Event on the Devonian terrestrial vegetation and miospores has never been investigated. Keeping this purpose in mind, we studied several Middle Devonian sections of the Czech Republic during field work in 2004–2007. The first of them was the Hlubočepy section located in the southwestern outskirts of Prague, which is frequently mentioned by researchers in the context of the Kačak Event. Our studies included the bed-by-bed description of the section with simultaneous tying of the sampled floral remains, as well as palynological and lithological samples (Jurina et al., 2009). In addition, several other sections were also visited (Raskatova and Jurina, 2007a, 2007b; Jurina, 2007; Jurina et al., 2009). Such studies have never been performed in the Czech Republic. The sampled collections of plants

and miospores were identified by Jurina and Raskatova, respectively; lithology was analyzed by E.V. Karpova (these results are to be published separately). The purpose of this work is to reveal the influence of the Kačak Event on higher plants. The study history of the Kačak Event, its causes, and influence on the invertebrate biota are considered elsewhere (Karpova et al., in press).

The Middle Devonian Kačak Event is documented in many world areas and may be classed with global phenomenon (Fig. 1). When interpreting changes associated with the Kačak Event, we accept the viewpoint of Hause and Chlupač, who correlate the base of the Kačak Member in sections with the upper part of the *kockelianus* Zone and that of the overlying Roblin Member, with the Givetian *hemiansatus* Zone (Chlupač, 1994; Weddige, 1996, 1998).

THE KAČAK EVENT AND HIGHER PLANTS

A. Macrofloral remains. Let us consider the influence of the Kačak Event on higher plants that lived on land surrounding sea basins. When analyzing the floral assemblages, we based our work on the analysis of the marine assemblages from these sediments performed by Hause and Chlupač, who particularly noted the extinction and appearance levels of floral taxa. Let us first analyze the data on the development of higher plants from the Kačak sediments. In the work by Marshall et al. (2007), where the influence of the Kačak Event on lacustrine environments of Scotland and Estonia is considered, these authors assumed that changes in the marine and lacustrine biotas were determined by the climatic factor in common. They presented a map with the sites in the Northern Hemis-

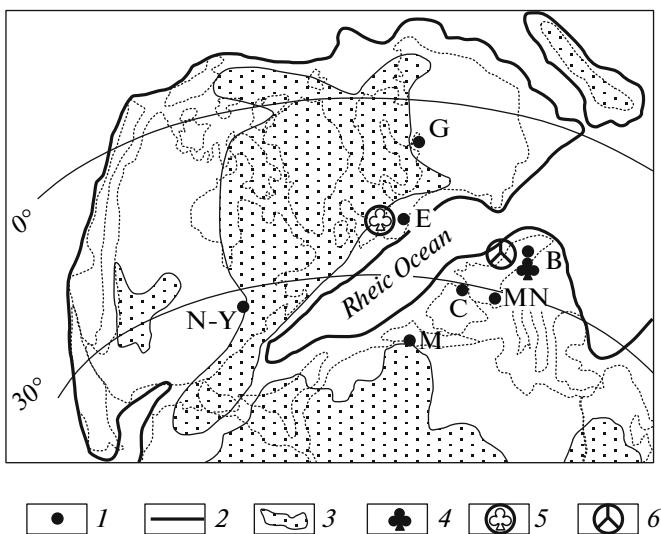


Fig. 1. Reconstruction of the Rheic Ocean with location of land blocks and sites with the documented Kačak Event (Marshall et al., 2007); flora localities are shown for the first time. (1) localities: (G) Gorodenka (western Ukraine), (E) Eifel, (B) Barrandian, (MN) Montagne Noire (southern France), (C) Cantabria (northern Spain), (M) Morocco (North Africa), (N-Y) State New York (North America); (2) continental shelf edge; (3) land; (4) Barrandian macroflora (original data); (5) Belgian macroflora (published data); (6) Barrandian miospores (original data).

sphere where the Kačak Event has been documented and the position of land blocks and the Rheic Ocean through the Middle Devonian. Most of these sites are largely confined to the southern shelf of the ocean and some of them, to the northern one (Fig. 1). These authors believe that the Rheic Ocean unfavorably affected the environments, comparing it with the present-day Nile system. They point to Eifel (without specifying particular localities) as an area located in the immediate vicinity to the northern slope of the Rheic Ocean, where the Kačak Event is reflected. In the Eifel region sensu lato, the sections with the Middle Devonian flora are known from Belgium and Germany. In our analysis, we use the Middle Devonian flora for the following reason: judging from the map, both the present-day Belgium and Eifel regions were located on the northern shelf of the Rheic Ocean at that time (Fig. 1). The Belgian sections demonstrate the complete succession of the *partitus* to *varcus* conodont zones corresponding to the interval with the Kačak Event in its upper part. This interval comprises four levels with floral remains.

The first attempts to correlate floral assemblages with conodont zones were undertaken elsewhere (Jurina, 1988). The floral assemblages from these stratigraphic units are usually dated within wide limits: from the epoch to age. Inasmuch as plant remains mostly occur in terrestrial sediments, correlation of beds enclosing certain floral assemblages with con-

odont zones is difficult. Therefore, the proposed correlation between beds with the flora and units with conodonts in Belgium needs further consideration. When analyzing below the Middle Devonian flora of Belgium, we use the data on the taxonomic composition of plants from the publications where they are described and information on their localities and distribution from Jurina (1988). Some additions concerning the taxonomic composition of Cladoxylaceae ferns are made after Meyen (1987).

The Eifelian flora known from the Ruyon greywacke (upper part of the *partitus* zone and largest part of the *costatus* zone) and preceding the Kačak Event is very impoverished, being represented by four species characterizing four genera (Fig. 2): one species belongs to Rhinophyta, two species to Polypodiophyta (Cladoxylaceae), and one species to Progymnospermopsida. The floral assemblage from the *australis* Zone is unknown from Belgium so far. The *kockelianus* Zone is correlated with the lithological member "H"-Co 2d, where the floral assemblage is substantially more diverse with respect of both generic and species compositions (seven genera and eight species). Only single plant genus (*Psilophyton*) became extinct from the pre-Kačak sediments, while three other genera (*Hyenia*, *Calamophyton*, and *Rellimia*) continued to exist and to become even more diverse. This interval is marked by the first appearance of several new genera: *Pseudosporochnus* (Cladoxylaceae ferns), *Aneurophyton* (Progymnospermopsida), *Ginkgophyton*, and *Platyphyllum* (plants of the unclear taxonomic position). No plant taxa extinction is registered at this level; to the contrary, the taxonomic composition of plants appears to be substantially renewed. As follows from the stratigraphic distribution of Middle Devonian plants, the Givetian *hemiansatus* Zone of Belgium shows no plant extinction. Its assemblage is characterized by both transient species and genera ranging from the *kockelianus* Zone to the *varcus* Zone, as well as by newly appeared forms. The floral assemblage from the *hemiansatus* Zone includes nine species belonging to nine genera from three higher taxa: Rhinophyta, Polypodiophyta, and Progymnospermopsida. The more abundant assemblage from the *varcus* Zone consists of 25 species belonging to 23 genera. Figure 2 presents for the *varcus* Zone only taxa originating from the underlying *hemiansatus* Zone.

Many well-known paleobotanists have studied the Middle Devonian flora of the Czech Republic. Obrhel (1959, 1960, 1961), whose works served as our basis for the thorough study of the type floral assemblages from the Czech Republic, contributed much to the knowledge of its flora in the middle of the last century. We became acquainted with the collection stored at the Czech National Museum and also carried out field works in the Czech Republic in 2004–2007 sampling floral remains from sections known from publications. These data yielded a more complete knowledge of the Middle Devonian flora from Czechia and allowed

	Higher plant taxa	Rhyniophyta	Polypodophyta					Progymnospermopsida	Incertae sedis							
	Species		Henia spheno-phylloides	Henia elegans	Calamophyton primaevum	Calamophyton renieri	Honseleria verticillata	Pseudosporochnus verticillatus	Pseudosporochnus nodosus	Relimia sp.	Rellinia thomsonii	Aneurophyton germanicum	Dicroidoxylon sp.	Dicroidoxylon goensis	Cinkgophyton glikinetti	Platyphyllum williamsenii
Eifelian	Standard conodont zones	Psilophyton sp.	Serulacaulis furcatus													
	Varcus															
	Hemiansatus															
	Kockelianus															
	Australis															
	Costatus															
	Partitus															

Fig. 2. Stratigraphic ranges of higher plants in the Middle Devonian (Kačak interval) section of Belgium.

some considerations to be proposed on this topic (Jurina, 1988, 2005). It is primarily noteworthy that no exact stratigraphic position of plant remains was provided in works by Czech paleobotanists and geologists; labels accompanying the floral collection in the National Museum are lacking such information as well. Only the presence of plants is indicated for each lithological member or bed without specifying its particular position in the section (basal, middle, or upper parts) let alone their bed tying. This prevented analysis of changes in the flora composition through the section. The acquaintance with the collection brought doubt upon the validity of some taxa (Jurina et al., 2009).

It is established that the Hlubočepy section described in the bed-by-bed manner encloses several levels with plant remains: one in the upper part of the Kačak Member and five in the Roblin Member, where they are more or less regularly distributed through the section. No plant remains are found in the Hotech Member underlying the Kačak one. Figure 3 illustrates changes of the plant composition through the section. We show the stratigraphic ranges of plant taxa with consideration of the data by Obrhel, who has studied the flora from this section, revised in Jurina et al. (2009). As was mentioned, the stratigraphic position of each species in works by previous researchers is unclear; therefore, their stratigraphic ranges appear to be slightly generalized. The Hotech Member corresponding to the *kockelianus* Zone (Klapper, 1977) is known to enclose the only plant taxon (Lycopodiales *Protolepidodendron scharianum*) found also in the overlying Kačak and Roblin members. The floral assemblage of the Kačak Member is represented by

seven species belonging to five genera and four higher taxa: Rhyniophyta, Lycopodiales, Polypodiophyta (Cladoxylaceae ferns), and Progymnospermopsida. It should be noted that no extinctions are recorded for the Kačak time; on the contrary, the taxonomic composition of plants appeared to be renewed at both the genera and higher levels at that time. By its composition, the floral assemblage from the Roblin Member is very close to its counterpart from the Kačak Member, being almost identical to the latter. It is conceivable that development of terrestrial higher plants was uniform both during the Kačak Event and later.

The comparison of the Belgian and Czech floras known from pre-Kačak, Kačak, and post-Kačak sediments reveals that they have many features in common. In both of them, the genus *Psilophyton* is known only in pre-Kačak sediments. In both regions, the Kačak time was marked by wide development of Cladoxylaceae ferns: in Belgium, their generic composition is more diverse as compared with that in Czechia (four genera vs. a single genus). There is a single genus in common (*Pseudosporochnus*), although it is characterized by different diversities (single species in Belgium and two species (endemic so far) in Czechia). Both floras are marked by the first appearance of Progymnospermopsida with almost similar generic and species composition. Some difference between the Belgian and Czech floras consists in the lack of Lycopodiales representatives in the first of them and the presence of the *Protolepidodendron* and *Barrandeina* genera in the second. It should be emphasized that the Middle Devonian flora of Belgium is generally more diverse as compared with its Czech counterpart. In our opinion, these differences are not of principal signifi-

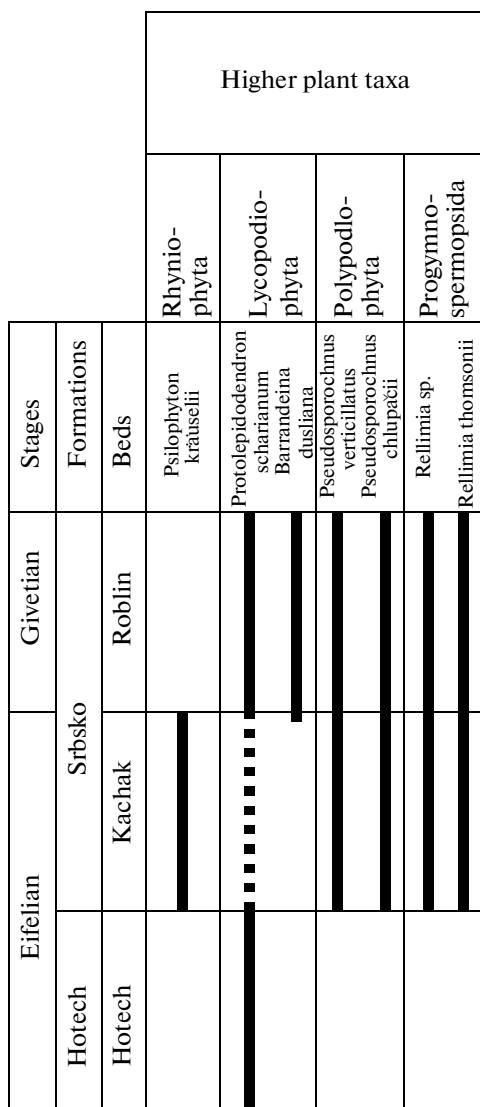


Fig. 3. Stratigraphic ranges of higher plants in the Middle Devonian (Kačak interval) Hlubočepy section of the Czech Republic.

cance. It is conceivable that they are explained by slightly different habitat conditions in biotopes of these floras. Judging from the distribution of the Kačak transgression (Fig. 1), land areas for plant occupation in the northern part of the Rheic Ocean corresponding to the present-day Belgian territory were substantially larger than in its southern part. We assume that the Middle Devonian vegetation of Czechia was of the island type, which explains its taxonomic impoverishment. The same factor is likely responsible for the lower diversity of the post Kačak Czech flora as compared with that of Belgium.

B. Miospores. The taxonomic composition of dispersed and in situ Devonian miospores from the Srbsko Formation of the Czech Republic has never been investigated. Only some researchers just briefly note their occurrence.

Obrhel (1959, 1961) was the first to define and briefly describe spores from isolated sporangia of the genus *Rellimia* found in the Kačak Member of the Hostim section, although without substantiation of their generic belonging. Judging from the size of spores mentioned by Obrhel, one can conclude that they are attributable to megaspores. The taxonomic affinity of spores remains unknown. Based on the analysis of described and illustrated in situ megaspores, we think that they most likely belong to the dispersed species *Rhabdosporites langii* (Eisenack) Richardson, 1960. This taxon was established in sporangia of the Middle Devonian form *Rellimia thomsonii* (Dawson) Leclercq et Bonamo from the sections of Belgium, Germany, and North America (State New York) (Leclercq and Bonamo, 1971; Bonamo, 1977; Gensel and Andrews, 1984).

Obrhel (1959, 1961) also described miospores from isolated sporangia belonging, in his opinion, to the species *Barrandeina dusliana* (Krejčí) Štúr. He attributed them to the form genus *Lycospora* Schopf, Wilson et Bentall., 1944. In our opinion this is somewhat doubtful, since, according to Y. Sommers (1972), who revised the latter genus, it is lacking characteristic features of the genera.

Lele (1972) was the first to study dispersed miospores from Middle Devonian sediments of the Barrandian. This researcher defined two miospore assemblages: from the Eifelian Dalei Shales and Srbsko Formation; following Obrhel (1961), he attributed the latter assemblage to the Givetian. No differences in the composition of miospore assemblages from the Kačak and Roblin members, which constitute the Srbsko Formation, were emphasized. This work is also lacking indications of the exact stratigraphic position for palynological samples; only their closeness to the outcrop in the Srbsko area is mentioned. The author also omitted from consideration differences in the compositions of miospore assemblages from Eifelian (14 genera without indications of species) and Givetian (18 species belonging to 15 genera) sections. In all, nine miospore genera (*Leiotriletes*, *Punctatisporites*, *Biornatispora*, *Convolutispora*, *Apiculiretusipora*, *Dibolisporites*, *Aneurospora*, *Samarisporites*, and *Ancyrospora*) appeared to be in common for different-age assemblages. Lele indicated four genera dominant in this assemblage from the Srbsko Formation: *Samarisporites*, *Spinozonotriletes*, *Calyptosporites*, and *Auroraspora*. No images of miospores are presented in his work. The author does not mention the Kačak Event and ignores changes in the taxonomic composition of miospores at the Kačak–Roblin boundary.

When studying Devonian miospore assemblages from the Barrandian of Czechia, McGregor (1979) mentions five samples from the Hotech, Kačak, and Roblin beds, which he received from Obrhel in 1961. Only two of these samples (from the Kačak and Roblin

members) contained moderately preserved spores, although data on their composition have never been published.

Using the stratigraphic model from (Chlupač, 1993), Daškova and Vacek (2009) collected eight samples from the Hlubočepy section for palynological analysis: three of them from the Hotech Member, two from the middle and upper parts of the Kačak Member, and three from the upper part of the Roblin Member. These authors mention several miospore and Chitinozoa genera from these sediments. The Hotech Member contains only Chitinozoa and Scolecodondten. No miospores are found in the middle part of the Kačak Member, and two miospore genera (aff. *Apiculiretusispora* sp., aff. *Grandispora* sp.) are indicated for its upper part. The upper part of the Roblin Member contains miospores identified as aff. *Geminispora* sp., aff. *Grandispora* sp., and aff. *Samarisporites* sp. No images are given for all these taxa. Due to the impoverished composition of the miospores, their biostratigraphic significance has never been estimated.

Thus, prior to our analysis, it was established that Middle Devonian sediments of the Czech Republic contain diverse miospores represented by many genera and species. It was also known that dispersed assemblages from the Kačak Member under consideration include *Rhabdosporites langii* previously indicated for isolated sporangia from these beds. However, miospores have never been investigated from the standpoint of either their belonging to taxa of the recent artificial taxonomy, or distinguishing assemblages from different stratigraphic units, or defining biostratigraphic zones. The problem of the influence of the Kačak Event on the taxonomic composition of miospores has never attracted the attention of researchers as well.

We have thoroughly studied two sections: Hlubočepy and Hostim-classic. In total, 15 palynological samples were taken from the Eifelian–Givetian succession constituting the Hlubočepy section: two, six, and seven samples from the Hotech, Kačak, and Roblin members, respectively. The Hostim-classic section represented only by the Roblin Member yielded five samples. The samples for the miospore analysis were collected in a bed-by-bed manner from different genetic rock types with their connection to particular lithological samples. Some of them were collected from beds with diverse plant remains and others immediately from the Kačak–Roblin boundary layers (Jurina et al., 2009). Dispersed miospores were macerated from host rocks by applying advanced physico-chemical treatment methods.

Inasmuch as miospores in macerates are characterized by their sporadic occurrence and their ground-mass is represented by different-size fragments of plant tissues, we used a special technique for the enrichment of such samples based on the difference of the specific weight characteristic of organic matter constituting miospore envelopes (Teteryuk and Filip-

pov, 1989). A repeated (3–6 times) high-velocity (1000 rpm) centrifugation in water allows the macerate to be cleansed of small fragments of vascular tissue and epidermis. The first centrifugation of suspended organic matter obtained by maceration is conducted for 60 s. Suspended particles of organic matter are removed, if they are barren of miospores. Then, sediment is again mixed with water, shaken, and centrifuged for 50 s. The centrifugation is reduced every time until miospores appear in the suspended state. The sediments are examined under the microscope only after they sink during centrifugation.

The samples from the Hotech Member of the Hlubočepy section contained single miospores that were insufficient for an adequate analysis. The two samples from the lower and upper parts of the Kačak Member, respectively, were practically barren of miospores and two samples from different layers of its middle part yielded variably preserved miospores. In the Roblin Member of the Hlubočepy section, moderately preserved miospores are found at six levels: in its lower (four levels), middle (single level) and upper (single level) parts. All six samples contained a single assemblage of miospores and the remains of the sporangial tissue. In the Hostim-classic section, miospores are established in the lower and upper parts of the Roblin Member.

The miospore assemblage from the Kačak Member is represented by 19 species belonging to 12 genera: *Calamospora atava* (Naumova) McGregor, *C. microrugosa* (Ibrahim) Schopf, Wilson et Bentall, *Calyptosporites proteus* (Naumova) Allen, *Apiculiretusispora aculeoata* (Tchibrikova) Arkhangelskaya, *A. gaspiensis* McGregor, *A. plicata* (Allen) Strel, *A. minor* McGregor, *Retusotriletes rotundus* (Strel) Strel, *R. rugulatus* Riegel, *Geminispora lemurata* Balme, *Dibolispores capitellatus* (Tchibrikova) Arkhangelskaya, *D. antiquus* (Kedo) Arkhangelskaya, *D. echinaceus* (Eisenack) Richardson, *Rhabdosporites langii* (Eisenack) Richardson, *R. sp.*, *Retispora archaelepidophyta* (Kedo) MacGregor et Camfield, *Grandispora naumovae* (Kedo) McGregor, *G. macrotuberculata* (Arkhangelskaya) McGregor, *Hystricosporites corystus* Owens, and *Densosporites devonicus* Richardson, *Camarozonotriletes* sp.

Densosporites devonicus, the index species of the synonymous zone appears in the middle part of the Kačak Member (20%). Another index species (*Grandispora naumovae*) is also established in its middle part, where it occurs as single specimens. The miospore assemblage is dominated (20–25%) by species belonging to the genera *Apiculiretusispora* and *Dibolispores*. The percentage of small miospores from the genera *Retusotriletes* and *Camarozonotriletes* is also relatively high (up to 10–15%), although their poor preservation prevents one from identifying some of them at the species level. The shares of *Rhabdosporites langii* and *Geminispora lemurata* are up to 5 and 1–3% respectively. The Kačak miospore assem-

blage includes patinate miospores with destroyed patina (up to 5%) and dark large miospores of an unknown taxonomic affinity with a destroyed exine layer. Images of the miospores from the Kačak sediments are presented elsewhere (Raskatova and Jurina, 2007b, 2008; Jurina et al., 2009).

Initially (Jurina and Raskatova, 2006) miospores from the Srbsko Formation (Kačak and Roblin members) outcropping in the Hlubočepy section were referred to the *Rhabdosporites langii* and *Geminispora extensa* zones defined in the upper Eifelian–Givetian interval of East Europe (Avkhimovich et al., 1993). Subsequently (Jurina et al., 2009), this section yielded additional information on the miospore assemblage contained in the Kačak sediments. This allowed the upper Eifelian *Densosporites devonicus*-*Grandispora naumovae* Zone by (Richardson and McGregor, 1986) to be defined for this interval of the section.

The miospore assemblage from the Roblin Member is characterized by a higher abundance and diversity as compared with that in the Kačak sediments. Of seven examined samples from the Hlubočepy section, six samples appeared to contain from 100 to 150 miospore grains; two samples were taken from beds with plant remains. Two samples with miospores from the Hostim-classic were collected from beds that were barren of floral remains. We analyzed the miospores assemblage from the Hlubočepy and Hostim-classic sections together. Their assemblage from the Roblin member consists of 20 species belonging to 13 genera: *Calamospora atava* (Naumova) McGregor, *Calyptosporites velatus* (Eisenack) Richardson, *Acinosporites lindlarensis* Riegel, *A. acanthomammillatus* Richardson, *Apiculiretusispora brandtii* Streel, *A. plicata* (Allen) Streel, *A. minor* McGregor, *A. gaspiensis* McGregor, *Geminispora lemurata* Balme, *G. tuberculata* (Kedo) Allen, *Cymbosporites magnificus* (McGregor) McGregor et Camfield, *Chelinospora concinna* Allen, *Archaeozonotrites variabilis* Naumova, *Rhabdosporites langii* (Eisenack) Richardson, *Grandispora inculta* Allen, *G. macrotuberculata* (Arkhangelskaya) McGregor, *Verrucosporites scurrus* (Naumova) McGregor et Camfield, *Hysricosporites gravis* Owens, *H. reflexus* Owens, *Densosporites devonicus* Richardson.

In the Roblin assemblage, *Geminispora lemurata* is a common element, which constitutes up to 15% of the total miospore abundance. The appearance of *Chelinospora concinna* in the upper part of the Roblin Member section indicates that these sediments are Givetian in age (Turnau, 1996). As a whole, the assemblage is dominated by species belonging to the genus *Geminispora* represented by forms with sharply tubercular exine ornamentation (*G. tuberculata*), the share of which is insignificant (3–5%) and species with its rounded tubercular ornamentation (*G. lemurata*, *G. aff. lemurata*), which are abundant at this stratigraphic level. Miospores belonging to the genus *Archaeozonotrites* are frequently characterized by a

destroyed (corroded) patina, which prevented identifying some of them at the species level and, correspondingly, determining their abundances. It is noteworthy that *Rhabdosporites langii*, which was established in the Kačak Member, is also recorded in Roblin sediments. This species shows variations in the size of miospores proper, as well as in the size and density of exine ornamentation.

The knowledge of the taxonomic composition of miospores from the Roblin Member and their preservation degree is better than in previous works (Jurina and Raskatova, 2006; Raskatova and Jurina, 2007a, 2008). This provided grounds for defining the Givetian *Geminispora lemurata*–*Cymbosporites magnificus* Zone by (Richardson and McGregor, 1986) in Roblin sediments. The first index species is common in the Roblin Member. Another zonal species occurs as single specimens frequently of poor preservation.

The comparison between miospore assemblages from the Kačak and Roblin members reveals that they are characterized by a similar taxonomic composition, with the last assemblage being slightly more diverse. In addition, the latter includes dominant typical Givetian species, such as *Geminispora lemurata*, *Chelinospora concinna*, and *Grandispora inculta*. It should be noted that miospores from both Kačak and Roblin sediments are frequently characterized by poor preservation, which is explained, in our opinion, by sedimentation environments at their burial stage rather than by the production character of miospores.

CONCLUSIONS

The Kačak Event, which was accompanied by anoxia in the sea basin, had no substantial influence on higher plants. Their taxonomic compositions demonstrate no reduction; to the contrary, they became more diverse or, at least, remained unchanged. The transgression corresponding to the Kačak time undoubtedly reduced the distribution area of higher plants, which could affect their biomass and generic or species diversity, although these changes were, in our opinion, insignificant: plants continued to populate islands and bay coasts. Chlupač (1994) notes that the Kačak Event spared the inner shelf and platforms behind advancing cold oceanic waters; in these areas, trilobites developed without any changes through the Eifelian to the Givetian. It is conceivable that higher plants also were spared any negative consequences. No extinctions are documented in the Belgian and Czech floras during the Kačak Event. It is unclear so far, what the influence of insolation was on the Middle Devonian flora, the consequences of which are noted in the coeval Scottish and Estonian floras (Marshall et al., 2007).

The Kačak Event accompanied by anoxia in the sea basin had no substantial influence on the development of higher plants and miospores. It undoubtedly only affected their preservation negatively.

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