

PALYNOLOGICAL INDICATORS OF PALAEOCLIMATE IN THE PENNSYLVANIAN IN THE INTRA-SUDETIC BASIN

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Abstract: On the basis of palynologic and palynofacies data from the Biały Kamień Formation in the Intra-Sudetic Basin (ISB), the composition of parent plant communities and the depositional environment during sedimentation of this unit were reconstructed. The results were then compared with earlier published palynological data from the stratigraphically older and younger lithostratigraphical units, the Wałbrzych and Żaclęż formations, allowing a general interpretation of floristic and environmental changes throughout the Serpukhovian to Moscovian interval. The floras in the Serpukhovian resemble the composition in the Moscovian. In both, their main feature is low lycopsid abundance, indicating relatively dry palaeoclimatic conditions. In contrast, the Bashkirian records a gradual increase in lycopsids and sphenopsids, peaking in the late Bashkirian during the maximum humid phase. This was followed in the Moscovian by a marked decline in lycopsids and a shift toward fern dominance, reflecting a transition to a drier climate associated with the First Dry Interval, proposed by Phillips and Peppers (1984). At the same time, the miospore record shows no evidence of abrupt floristic changes, contradicting the concept of a “floristic leap” at the Namurian A/B boundary.

Key words: Miospores, palynofacies, parent plant communities, Carboniferous, Intra-Sudetic Basin, palaeo-environment, palaeoclimate.

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INTRODUCTION

Dispersed palynological assemblages are the main objects of research, primarily for stratigraphic and palaeoecological interpretations. Palynostratigraphic studies of the Carboniferous in the ISB began in the 1960s, and their main achievements are discussed in the paper by Maćko and Górecka-Nowak (2024). Palynofacies studies, which constitute a valuable supplement to results obtained from palynomorph analysis, are not advanced in these rocks and this study is one of the first.

Carboniferous miospores, due to their widespread occurrence in terrestrial and marine rocks and their transport mainly by water, are found in a variety of geological environments, which increases their research value. They show significant mechanical resistance during sedimentation and chemical resistance in later geological processes, due to the presence of sporopollenin, a chemically complex biopolymer, forming part of their exine. This allows

them to survive under unfavorable geological conditions, making them exceptionally durable and valuable research materials.

Carboniferous miospores are a valuable group of microfossils, primarily used for stratigraphic purposes. In this application, the fact that they are found dispersed in sedimentary rocks without any association with the parent plant is not important. However, miospores can also be used in palaeoecological interpretations, providing important information about the depositional environment and its variability over time. For such interpretations, knowledge of the biological links between miospore taxa and their parent plants is essential. Thanks to advances in palaeobotanical research, especially studies of *in situ* spores, these relationships are now known for the several genera of Carboniferous miospores. This allows reconstruction of vegetation, consisting of parent plants, based on dispersed spore assemblages.

Palynological and palaeobotanical studies by U.S researchers allowed the determination of environmental preferences of plant groups during the Carboniferous (Phillips and Peppers, 1984; DiMichele and Phillips, 1985, 1994; Phillips *et al.*, 1985). These are the grounds for inferring the environmental conditions during the sedimentation of the studied rocks. Furthermore, the analysis of changes in the composition of plant communities over time can be used to interpret features of the Carboniferous palaeoclimate, as shown for North America by Phillips and Peppers (1984).

The results of palynological studies on Carboniferous rocks from the Intra-Sudetic Basin, including both coal and barren layers, provided a basis for a multidirectional interpretation. The primary objective of the palynological studies of the Wałbrzych, Biały Kamień and Żaclęř formations was the precise determination of their age (Górecka, 1969; Górecka-Nowak, 1988, 1995; Górecka-Nowak and Majewska, 2002, 2003; Górecka-Nowak *et al.*, 2021; Maćko and Górecka-Nowak, 2024). Additionally, the results of miospore studies and palynofacies observations from the rocks of the Wałbrzych Formation were interpreted from a palaeoenvironmental perspective (Górecka-Nowak and Majewska, 2003). Also, the results of miospore studies from the Żaclęř Formation, based on four deep boreholes located in the northwestern part of the Intra-Sudetic Basin, were used to interpret the composition of the parent plant communities. Changes in the composition of these communities during the sedimentation of the studied rocks were explained by probable climatic changes, involving fluctuations in humidity during the late Bashkirian and Moscovian (Westphalian A–C; Górecka-Nowak, 1996, 2002).

This paper presents the composition of miospore assemblages from the Biały Kamień Formation in terms of their palaeobotanical affinity and temporal changes, supplemented by palynofacies observations and their palaeoecological significance. The miospore data used for palynostratigraphical interpretation were published by Maćko and Górecka-Nowak (2024), whereas the results of palynofacies observations have not been published previously.

These information derived the Biały Kamień Formation complements the knowledge on changes in the vegetation and palaeoenvironmental features in the IBS over a relatively long time interval, from the Serpukhovian to the Moscovian (Namurian A–Westphalian C). These changes were certainly caused by many factors, including local environmental conditions and probably palaeoclimatic changes. The palynological data gathered from the ISB create a unique opportunity to reconstruct these changes in the Carboniferous during around 20 Ma.

GEOLOGICAL SETTING

The research area covers the northwestern part of the ISB, which is an extensive geological unit, located in the central part of the Sudetes (Fig. 1A). The ISB is filled with a succession of sedimentary rocks of the Carboniferous, Permian and Lower Triassic, with a significant presence of volcanic rocks. The rock layers dip towards the centre of this

structure, except for in the Wałbrzych Sub-Basin (WSB), located in the northern part of ISB, which is filled with Carboniferous rocks, dipping towards its centre and surrounded by young Palaeozoic volcanic rocks.

This article discusses the results of palynological studies of three lithostratigraphic units in the Upper Mississippian and Pennsylvanian: the Wałbrzych, Biały Kamień and Żaclęř formations, the ages of which are well-known, due to palynostratigraphic research. The thickness of each of these formations is several hundred metres, and two of them, namely the Wałbrzych and Żaclęř formations, contain coal seams that were of industrial importance and were exploited in the deep coal mines of the Lower Silesian Coal Basin. The Biały Kamień Formation, which separates the other two formations, is composed of coarse-grained clastic rocks, dominated by conglomerates, and contains negligible amounts of coal (Fig. 2).

MATERIAL AND METHODS

Samples for palynological analysis of rocks from the Wałbrzych and Biały Kamień formations were collected from surface outcrops within the WSB (Fig. 1B). The whole profiles of both formations were sampled, and the samples comprised mudstones, claystones, coaly shales and coal. In the case of the Żaclęř Formation, palynological data applied in this paper were obtained from the deep borehole Grzędy IG-1, located approximately 8 km west of Wałbrzych (Górecka-Nowak, 1988, 1995; Fig. 1B). This borehole provides the most nearly complete profile among the four profiles used for palaeoclimatic reconstructions by Górecka-Nowak (1996, 2002).

Palynological samples were processed, using standard procedures, as described by Bercovici and Vellekoop (2017) and Riding (2021). Palynofacies analysis of samples from the Biały Kamień Formation was conducted on non-oxidized palynologic material, whereas miospore analyses were carried out on slides, prepared from oxidized samples.

During the palynofacies analysis, three categories of palynological components were identified and counted: amorphous organic matter (AOM), palynoclasts and palynomorphs. Among the palynoclasts, the zoo- and various phytoclasts were distinguished and classified according to their shape, structure and size (Dybkiær, 1991; Tyson, 1995; Mendonça Filho *et al.*, 2011).

Slides from the Biały Kamień Formation were examined under transmitted light, using a Nikon Alphaphot-2 YS2 biological microscope. Palynofacies observations under UV radiation were conducted, using Zeiss Axioscope 5 fluorescence microscopes. Objectives of 20x and 40x magnification were used for transmitted light and 10x and 20x for UV. Photographs were taken with a DLT-Cam camera and particle measurements were carried out, using the ImageJ software.

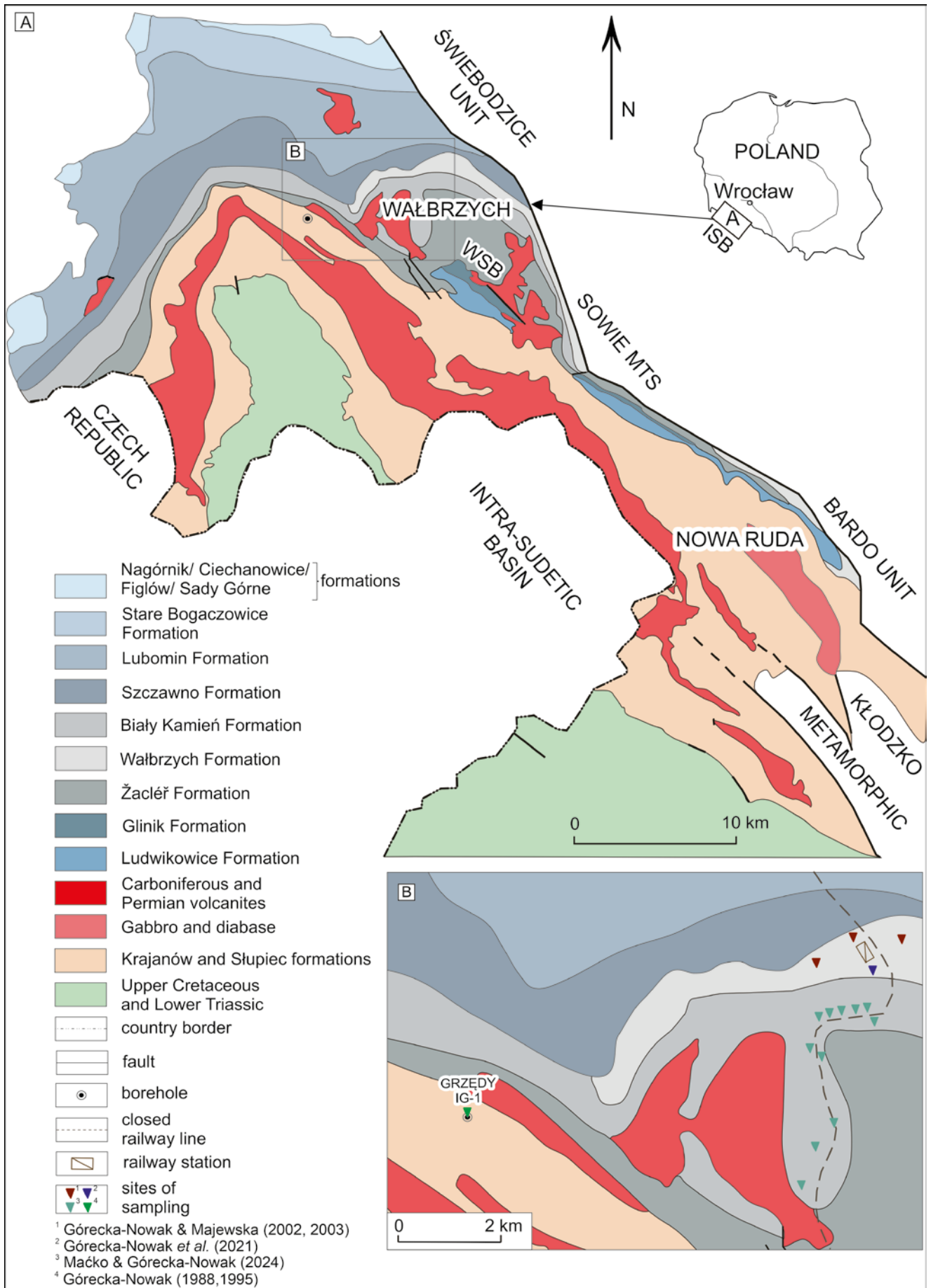


Fig. 1. Location maps. **A.** Simplified geological map of the Intra-Sudetic Basin (ISB). **B.** Fragment of the geological map, showing the Wałbrzych Sub-Basin (WSB) and the location of the Grzędy IG-1 borehole (based on Sawicki, 1967).

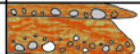
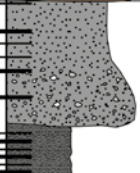

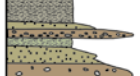
LITHO-STRATIGRAPHY (FORMATIONS)	THICKNESS (m)	COAL SEAM NUMBER	LITHOLOGY	PALYNOSTRATIGRAPHY		CHRONOSTRATIGRAPHY					
				(CLAYTON ET AL., 1977; OWENS ET AL., 2004)		BRITISH ISLES	CENTRAL EUROPE	GLOBAL DIVISION			
GLINIK	300 – 850			OT(?)	<i>T. obscura</i> – <i>T. thiesseii</i> (?)	ASTURIAN (?)	WESTPHALIAN	D	MOSKOVIAN	CARBONIFEROUS	
ŽACLÉŘ	500 – 900	301		SL	<i>T. securis</i> – <i>T. laevigata</i>	BOLSOVIAN		C			
		321		NJ	<i>M. nobilis</i> – <i>F. junior</i>	DUCKMANTIAN		B			
		423		RA	<i>R. aligerens</i>	LANGSETTIAN		A			
		448									
BIAŁY KAMIEŃ	150 – 380	549	SS	<i>C. saturni</i> – <i>T. sinani</i>	YEADONIAN MARSDENIAN KINDERSCHOUTIAN	NAMURIAN	C	BASHKIRIAN			
			FR	<i>R. fulva</i> – <i>R. reticulatus</i>			B				
			KV	<i>C. kosankei</i> – <i>G. varioreticulatus</i>							
WAŁBRZYCH	250	655		SO	SR		<i>L. subtriquetra</i> – <i>C. rarus</i>	ALPORTIAN CHOKERIAN	A		SERPU-KHOVIAN
		SV			<i>L. subtriquetra</i> – <i>A. variocorneus</i>						
				TK	<i>M. trigallerus</i> – <i>R. knoxi</i>		ARNSBERGIAN				
		SZCZAWNO		600 – 3000			CN	Vm	<i>C. capistratus</i> – <i>B. nitidus</i>	PENDLEIAN	
Cc	<i>C. capistratus</i>		BRIGANTIAN								
	VF		<i>T. vetustus</i> – <i>R. fracta</i>								

Fig. 2. Lithostratigraphy of the Carboniferous deposits in the Intra-Sudetic Basin, correlated with palynostratigraphy and chronostratigraphy. X – profile analyzed in this research.

MIOSPORE ASSEMBLAGES
AS INDICATORS OF VEGETATION
AND PALAEOENVIRONMENT

The progress of palaeobotanical research, mainly studies on *in situ* miospores, revealed the biological relationships between miospores, which are usually found dispersed in rocks and the parent plants that produced them. This information is particularly valuable, as it allows us to estimate the composition of vegetation that grew near the site of sediment deposition, on the basis of the composition of the miospore assemblages.

Botanical affinity of Carboniferous miospores

Thanks to the intensive research of spores *in situ*, most of the biological connections between Carboniferous miospores and their parent plants are already known. The information on these topics has been collected in several articles, including Balme (1995), Bek (2021) and Bek *et al.* (2021). On this basis, the taxonomic affiliations of miospore genera, identified in the rocks of the Biały Kamień Formation (Bashkirian) of the ISB, are summarized (Tab. 1). The identified miospore assemblage is dominated by spores, while pollen grains are scarce. These miospores were produced by the major groups of Carboniferous flora, including lycopsids, sphenopsids and ferns. Lycopsids are divided, on the basis of morphology and spore production, into arborescent and sub-arborescent/herbaceous plants (Phillips and Peppers, 1984; Balme, 1995). The most abundant group was the arborescent lycopsids. Genus *Lepidodendron* produced spores of *Lycopora*, the most common and widespread Carboniferous miospore, especially in Pennsylvanian strata

(Thomas, 2021). Another important miospore genus, *Craspispora*, was produced by *Sigillaria*, also belonging to arborescent lycopsids (Bek and Opluštil, 2021). Sub-arborescent lycopsids are represented by genera, such as *Densosporites*, *Cristatisporites* and *Endosporites*, while herbaceous lycopsids are represented by *Anapiculatisporites*, *Cingulizonates*, *Cirratriradites* and *Radiizonates*. These spores have been found *in situ* in various sporangiate structures, mainly in *Selaginella* and *Omphalophloios* (Chaloner, 1954; Bharadwaj and Venkatachala, 1968).

Among the sphenopsids, two subgroups are distinguished: the tree-like *Calamites* and shrubby to scrambling, now-extinct, *Sphenophyllales* (Taylor *et al.*, 2009). The most typical sphenopsid miospore is *Calamospora* found *in situ* in sporangia of *Calamostachys* and *Palaeostachya* and other related genera (Balme, 1995). *Sphenophyllales* produced spores, such as *Vestispora* and partly *Dictyotriletes* as well as *Laevigatosporites* (Bek and Libertin, 2010). Ferns were a taxonomically diverse and structurally complex group of plants, including columnar trees from the Marattialean group and small ground cover plants, belonging to *Zygopteridalean*, *Botryopteridalean* and *Schizaeceous* forms. The miospores of ferns were represented by various genera, mainly those possessing the trilete marks, for example, *Granulatisporites*, *Leiotriletes*, *Cyclogranisporites* and *Punctatisporites*. However, the smallest monolete spores belong to the Marattialean ferns, where also *Schulzospora* and *Wilsonites* belong. The larger monolete spores were produced by the sphenophylls. In the Carboniferous vegetation, gymnosperms formed an important group. Cordaitaleans could reach several metres in height and possessed a relatively shallow root system that extended almost horizontally from the trunk. In the miospore assemblage,

Table. 1.

Botanical affinities of miospore genera identified from the Biały Kamień Formation
(compiled after Balme, 1995; Bek, 2021; Bek *et al.*, 2021).

Plant groups		Spores
Lycopsids	<i>Arborescent</i>	<i>Crassispora, Lycospora</i>
	<i>Sub-arborescent /Herbaceous</i>	<i>Cristatisporites, Densosporites, Endosporites, Anapiculatisporites, Cingulizonates, Cirratiradites, Radiizonates</i>
Sphenopsids	<i>Calamitaceae</i>	<i>Calamospora</i>
	<i>Sphenophyllales</i>	<i>Dictyotrilites (muricatus), Punctatisporites (obesus), Reticulatasporites, Vestispora</i>
Ferns	<i>Marattiales</i>	<i>Verrucosisporites, Cyclogranisporite, Punctatisporites</i>
	<i>Zygopteridales</i>	<i>Convolutispora, Verrucosisporites, Apiculatasporites, Punctatisporites, Cyclogranisporites</i>
	<i>Botryopteridales</i>	<i>Verrucosisporites, Convolutispora, Microreticulatisporites, Raistrickia, Lophotrilites, Granulatisporites, Cyclogranisporites</i>
	<i>Gleicheniales</i>	<i>Triquitrites, Leiotrilites</i>
Gymnosperms	<i>Cordaitales</i>	<i>Florinites</i>
Unknown origin	<i>Acanthotrilites, Ahrensisporites, Anaplanisporites, Bellisporites, Converrucosisporites, Dictyotrilites, Foveosporites, Grumosporites, Knoxisporites, Kuhlensisporites, Lophozonotrilites, Mooreisporites, Murospora, Planisporites, Pustulatisporites, Savitrisporites, Simozonotrilites, Stenozonotrilites</i>	

cordaitaleans were represented exclusively by the genus *Florinites*, which has been found *in situ* within cordaitalean cones (*Cardiocarpus*; Balme, 1995). Other miospore genera of gymnosperms, mainly conifers, were *Potonieisporites*, *Pityosporites* and *Illinites* (Balme, 1995).

On the basis of palynological data, particularly the frequency of specific miospore genera and their known biological affiliations, an attempt was made to estimate the vegetation that once grew near the site of deposition of the studied rocks. Unfortunately, this reconstruction is complicated by several biological factors. One major challenge is that some miospore genera have not yet been definitively linked to specific parent plants. This necessitates designating a group of taxa with unknown botanical affiliation (Tab. 1), although their low frequency typically means they have little impact on the overall interpretation. Another difficulty stems from the ambiguous results of *in situ* spore studies. There are cases, where reproductive organs contain morphologically diverse miospores assigned to different taxa, or where a single miospore genus has been associated with reproductive structures of different plants (Taylor *et al.*, 2009; Tab. 1). Currently, such cases are considered rare, and it is hoped that future research will clarify these uncertainties. A more significant issue, potentially affecting reconstruction outcomes, is the variation in miospore productivity among different plant groups. Due to the limited understanding of this aspect, it has been omitted from further analysis, even though its impact may be substantial, unlike the two previously mentioned factors, which are likely to be of minor importance.

Possibility of environmental and palaeoclimatic reconstruction, based on miospore assemblages

In spite of all of the limitations mentioned above, the analysis of miospore data remains a key tool in reconstructing Carboniferous land ecosystems. Due to miospore resistance and their widespread occurrence, they continue to be an important source of information on Carboniferous palaeoenvironments. In the case of miospore assemblages derived from coal, these spores can be considered autochthonous or nearly autochthonous (Smith, 1961; Smith and Butterworth, 1967). They were undoubtedly produced by plants, inhabiting the mires, in which the accumulation of phytogenic material took place, ultimately giving rise to coal seams. In contrast, the miospores found in fine-grained clastic rocks, such as mudstones or siltstones, were probably subject to fluvial transport over distances that are difficult to estimate. Additionally, as a complicating factor, there was air transport of pollen grains with air sacs, although they were rare. Consequently, assemblages from these lithologies are regarded as allochthonous. However, their composition still reflects the character of plant communities in the vicinity of the depositional site. It can be assumed that the source area of these miospores corresponds to the boundaries of the sedimentary basin.

Identifying the botanical affinity of miospores is essential for reconstructing environments. The palaeoenvironmental analysis is based on the known ecological preferences of specific plant groups, which have been established through studies of miospore assemblages and anatomically

preserved plant remains in carbonate concretions from coal seams (so-called coal balls) from the Euramerican province (Phillips and Peppers, 1984). The data, used by Phillips and Peppers, originated from paralic coal basins of North America. Their climate change model corresponds well with the data from the ISB, partly because sedimentation during the Serpukhovian and Bashkirian stages also occurred near a marine shoreline, as indicated by recent findings (Górecka-Nowak *et al.*, 2025).

The distribution of major floristic groups shows that during the Bashkirian and Moscovian lycopsids occupied peat-forming wetlands and partly other wetland habitats, where they coexisted with sphenopsids. This latter group commonly appeared in various environments, where arborescent lycopsids and tree ferns also grew. Lowland regions were dominated by ferns, with a gradually increasing contribution of tree ferns throughout the Moscovian. Ferns also occurred in upland areas, where over time, they were replaced by cordaitaleans. For a relatively short period, in the late Bashkirian to early Moscovian, cordaitaleans became a quantitatively significant component of the vegetation in both uplands and lowlands and appeared also in peat-forming wetlands. After this period, the distribution of floristic groups returned to that of the early Bashkirian assemblages, with the only notable difference being an increased presence of tree ferns among the fern communities during the Moscovian. At the transition between the Moscovian and Kasimovian, significant shifts in the distribution of floristic groups across different biotopes occurred. Lycopsids ceased to dominate peatlands and were replaced by ferns, predominantly tree ferns. At the same time, lycopsids increasingly colonized other wetlands, where they displaced sphenopsids and became dominant. Lowlands continued to be dominated by ferns, with a considerable contribution of arborescent forms. Ferns were also present in higher parts, although uplands were increasingly populated by cordaitaleans and conifers. This vegetation is characteristic of the early Kasimovian. In the late Kasimovian, conifers and cordaitaleans partially expanded into lowlands, while seed ferns dominated wetlands, including peatlands. The floral preferences during the Gzhelian were similar to those at the beginning of the Kasimovian, with the main difference being the limited presence of cordaitaleans and conifers in lowland areas (Phillips and Peppers, 1984).

The analysis of floristic composition over time, combined with known environmental preferences and their variability, allows for interpretation of the causes behind these changes. The most likely cause was the variability of climatic parameters during the Pennsylvanian in the Euramerican province, which was characterized by a tropical climate, subject to periodic fluctuations. These fluctuations have been interpreted as changes in humidity levels, distinguished by Phillips and Peppers (1984), DiMichele and Phillips (2009), DiMichele *et al.*, (2010) and DiMichele (2014).

Five climatic phases have been identified, two of which represent relatively dry intervals. The Early Pennsylvanian (Bashkirian) climate was moderately humid. This was followed by the first dry phase in the late Bashkirian to middle Moscovian. At the end of the Moscovian, the humidity rapidly increased, reaching a peak that was much more humid

than at the onset of the Bashkirian. A rapid drying occurred in the early Late Pennsylvanian (Kasimovian), leading to an extended arid period known as the second dry phase. This drying was more pronounced than the earlier event and lasted throughout the Kasimovian, concluding with a return to a more humid climate in the Gzhelian (Phillips and Peppers, 1984).

The procedure applied in this study involved estimating the composition of parent floras, based on the identified miospore assemblages and known biological affinities. Using the inferred proportional composition of these communities, a detailed analysis of environmental conditions and their temporal variability was carried out. This interpretation was further supported by palynofacies observations, which enabled a more refined reconstruction of past ecosystems and their dynamics.

Record of the parent floras in the miospore assemblages from the Biały Kamień Formation

Samples for palynological studies of rocks of the Biały Kamień Formation were collected from the surface exposures within the WSB (Fig. 1B). They were taken from mudstones, siltstones and coal layers, occurring as intercalations within conglomerates and coarse-grained sandstones, exposed along the disused railway line between the former Biały Kamień station towards the south to the boundary with the Žacléř Formation (Fig. 1B).

All analyzed samples contained miospores, representing lycopsids, sphenopsids and ferns, although their relative abundances varied (Fig. 3). In the case of outcrop A', from which two samples were analyzed, a similar composition of the miospore assemblage was observed, but lycopsid miospores were more abundant, which made up an average of 50% of the total miospore assemblage.

Fern miospores were also a significant component, ranging from 16% to 19%, while sphenopsid miospores accounted for up to 14%. In sample A'₂, cordaitalean pollen grains were recorded, but their contribution did not exceed 1%, indicating only an accessory presence. In outcrop A, from which three samples were studied, lycopsid miospores were predominant, comprising an average of 42% of the total miospore assemblage. These samples also contained sphenopsid miospores, ranging from 14% to 37% and fern miospores, which accounted for 13% to 30%. No cordaitalean pollen grains were recorded there. Comparison of the miospore assemblages from three samples at outcrop B with those from previous sites shows that lycopsid and sphenopsid miospores still were abundant groups. Lycopsid miospores comprised 25% to 49% of the assemblages, while sphenopsid miospores ranged from 19% to 31%. Fern miospores accounted for 15% to 19%, indicating a significant but not predominant presence. Cordaitalean miospores were present in sample B₂, but again did not exceed 1%, suggesting a marginal role of these plants in the local vegetation. Two samples from outcrop C revealed miospore assemblages, indicating a floral composition similar to that of other sites. Lycopsid miospores predominated, constituting approximately 45% of the total miospore content, followed by sphenopsids (averaging 17%) and ferns (around 21%).

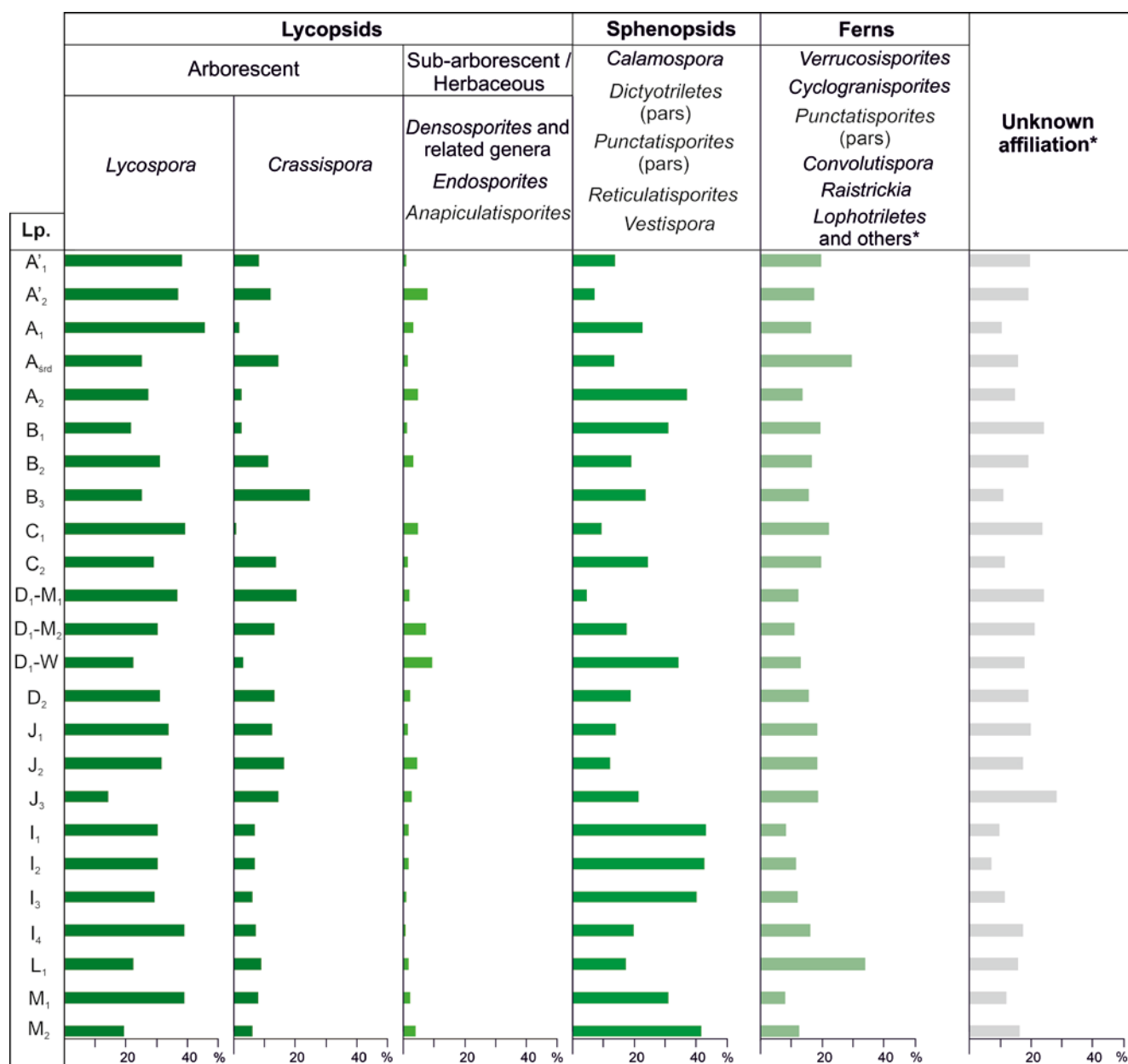


Fig. 3. Proportions of individual plant groups in the studied samples. * – taxa with a very minor contribution are grouped under “Others”; the grouping reflects botanical relationships, as presented in Table 1.

No cordaitalean miospores were observed. Miospore assemblages from outcrop D₁, based on three samples, showed compositional diversity. Lycopsid miospores were predominant, comprising up to 48% of the assemblage. Sphenopsid miospores were also present, averaging 19%, while fern miospores accounted for approximately 12%. No cordaitalean pollen was detected. In outcrop D₂, lycopsid miospores were again predominant (47% of the total), while sphenopsid miospores accounted for 19% and fern miospores contributed approximately 16%. In the samples from this outcrop, miospores of unknown botanical affinity accounted for 13%. Cordaitalean pollen grains were absent. Outcrop J was also dominated by lycopsid miospores, averaging 44%. Fern miospores reached up to 18%, while sphenopsid miospores did not exceed 16%. In sample J₁, cordaitalean pollen grains were recorded but remained below 1%. In the samples from

outcrop I, the most abundant miospores were produced by lycopsid (up to 46%) and sphenopsid (up to 44%). Fern miospores did not exceed 16%. Cordaitalean pollen grains were found only in sample I₁, represented by a few grains. The miospore assemblage in sample L was dominated by fern and lycopsid miospores, each accounting for over 30% of the total. In contrast, assemblages from site M differed noticeably, with high proportions of sphenopsid and lycopsid miospores (36% each), while fern miospores comprised only 10%. Cordaitalean pollen grains were not recorded in any of the samples from site M.

Palynostratigraphic analysis of these rocks indicated that they belong to two miospore zones: *Crassispora kosankei* – *Grumosporites varioreticulatus* (KV) and *Raistrickia fulva* – *Reticulatisporites reticulatus* (FR), corresponding to the Bashkirian or interval from the upper part of the

Namurian A to the Namurian C (Owens *et al.*, 2004). According to the British subdivision, this interval covers the upper part of the Alportian, Kinderscoutian, Marsdenian and Yeadonian (Maćko and Górecka-Nowak, 2024)

Results of the palynofacies analysis of the Biały Kamień Formation and their palaeoecological significance

Palynofacies observations made for rocks of the Biały Kamień Formation from the WSB revealed that the palynological material in all examined samples was dominated by phytoclasts among which abundant miospores occurred, consisting of up to 10% of the material. The amorphous organic matter (AOM) was recorded in small amounts and zooclasts were absent. The phytoclasts were mostly opaque, less frequently transparent. Brown phytoclasts were wood fragments with a rectangular outline or had corroded outlines (Fig. 4).

Fluorescent cuticles were also observed, although in limited numbers. The use of fluorescence enabled a more precise assessment of the amount of amorphous organic matter (AOM), revealing that its rare and small clusters consisted of aggregates of fluorescent and non-fluorescent palynoclasts and palynomorphs with only minimal amounts of true AOM. The composition of the individual components of the palynological material indicates that the studied rocks of the Biały Kamień Formation belong to a single palynofacies type (Fig. 5), corresponding to a fluvial environment, according to Tyson's (1995) APP diagram. These results correlate well with the sedimentological characteristics of

the Biały Kamień Formation rocks, which were deposited in a complex fluvial system (Kurowski, 1998).

THE COMPOSITION OF VEGETATION BASED ON MIOspore ASSEMBLAGES FROM THE SERPUKHOVIAN TO THE MOSCOVIAN OF THE ISB

Serpukhovian and early Bashkirian (Namurian A)

The Serpukhovian (Namurian A) palynological data derived from the Wałbrzych Formation, outcropping in the WSB. Samples of mudstones, claystones and coal, probably seam number 678, were studied (Górecka-Nowak and Majewska, 2002; Górecka-Nowak *et al.*, 2021). This formation was included in two miospore zones: *Mooreisporites trigal-lerus* – *Rotaspora knoxi* (TK) and *Lycospora subtriquetra* – *Kraeuselisporites ornatus* (SO) according to Owens *et al.* (2004). The results of the palaeoenvironmental interpretation, based on miospore assemblages and palynofacies data, are presented in the paper by Górecka-Nowak and Majewska (2003). In this paper, the authors cited these data to analyse the composition of vegetation recorded in them, as well as its variability over time (Fig. 6).

Samples from the TK and SO zones show a diversified composition of miospore assemblages, reflecting complex interactions between environmental and climatic factors. The average content of lycopsids in the vegetation is relatively low and is barely a little over 30%. The more abundant group were arborescent lycopsids, mainly lepidodendrids, but also *Sigillaria*, constituting about 25% of the flora, suggesting that these plants formed a notable, yet variable, component of the vegetation, most likely responding to both local habitat changes and broader climatic shifts. The remaining lycopsids, sub-arborescent and/or herbaceous, were present in small numbers. Sphenopsids were a stable and quantitatively important part of the vegetation, occurring in an amount of about 20%. Ferns occur consistently and their cumulative abundance averages 26%, including about 5% from seed ferns. This composition suggests the presence of varied ecological niches and indicates that ferns were a major component of the regional flora, responding to both depositional setting and climate variability. A significant part of the vegetation, about 15%, has an undefined botanical affiliation. The fluctuating abundance of different floristic groups supports the interpretation of a dynamic environment, influenced by both sedimentary and climatic drivers.

Palynofacies observations by Górecka-Nowak and Majewska (2003) demonstrated that palynological material from the TK and SO zones is composed predominantly of phytoclasts and miospores with occasional zooclasts (showing spongy textures and spines) and no amorphous organic matter. This composition supports deposition in a fluvially dominated setting. Importantly, the analysis of coal seam 678 reveals a sedimentary succession from crevasse splay deposits, through floodplain environments to peatland, transitioning from a mixed to rheotrophic mire as the water table rose. These findings highlight a clear environmental

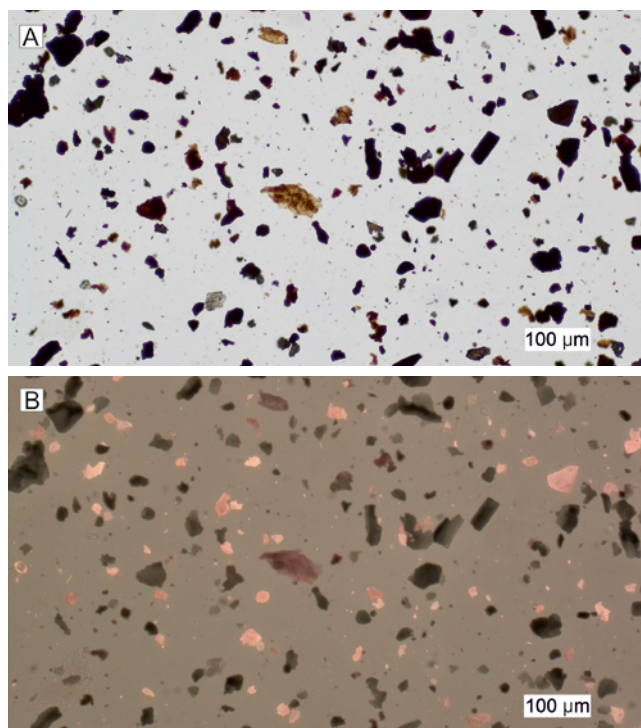


Fig. 4. General view of palynofacies. **A.** View under transmitted light. **B.** View under UV fluorescence light (10x, $\lambda = 380$ nm). The palynofacies is dominated by translucent and opaque phytoclasts with single palynomorphs or fragments of them and only a small amount of amorphous organic matter (AOM). Sample A₂ from exposure A in the Biały Kamień Formation profile along the abandoned railway line at Wałbrzych (Fig. 1B).

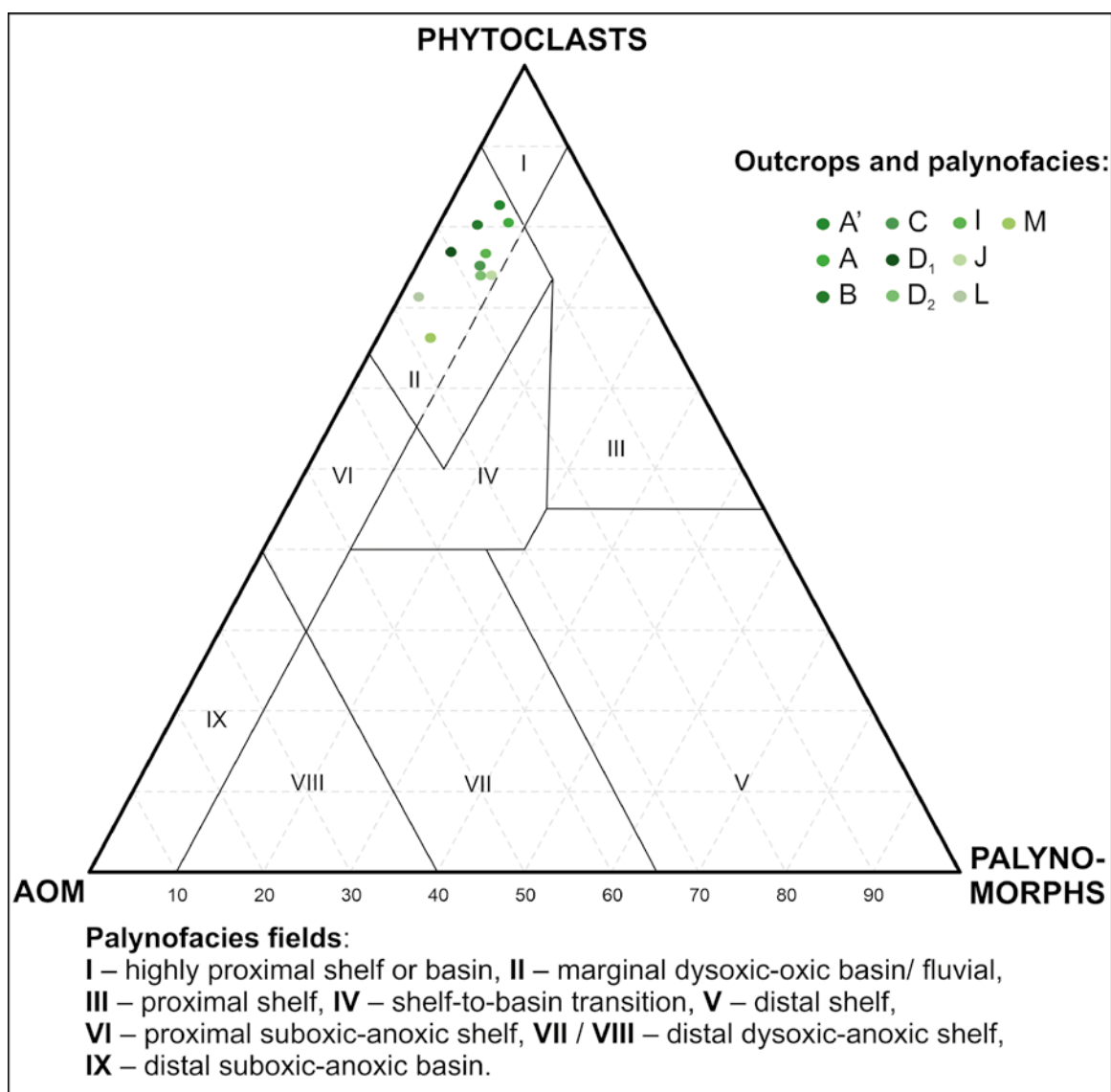


Fig. 5. Positions of the analyzed samples from the Biały Kamień Formation on Tyson's APP triangle (Tyson, 1995).

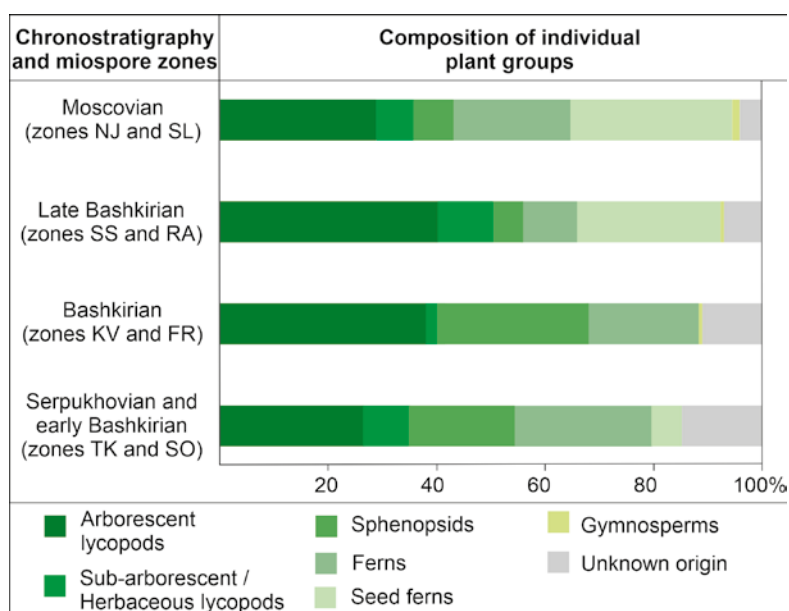


Fig. 6. Distribution of plant groups within the chronostratigraphic framework and corresponding miospore zones.

succession, but when interpreted alongside palynological changes, they also reveal that the evolution of floral assemblages was shaped by both local hydrological processes and broader climatic trends. The observed variability in vegetation thus results from the superposition of depositional setting dynamics and climatic fluctuations, underscoring the need to interpret miospore data in the context of both factors.

Bashkirian (latest Namurian A, Namurian B and Namurian C)

The majority of the Bashkirian palynological data, derived from the Biały Kamień Formation, belonged to two miospore zones: *Crassispora kosankei* – *Grumosporites varioreticulatus* (KV; samples from sites I, L, M described above) and *Raistrickia fulva* – *Reticulatisporites reticulatus* (FR; samples from sites A', A, B, C, D₁, D₂, J), distinguished by Mačko and Górecka-Nowak (2024). The combined miospore assemblage from the KV and FR zones shows a relatively stable composition, with only minor differences between the two. Arborescent lycopoid spores are the predominant group, with an average abundance of 38%, indicating their leading role in local vegetation throughout the deposition of both zones. Herbaceous and/or sub-arborescent lycopoid spores are rare, averaging around 3%. Sphenopsid spores are also common, accounting for 27% on average, suggesting their consistent presence in the palaeovegetation. Fern spores represent 20% of the assemblage and were an important component of the plant communities. Gymnosperm spores are nearly absent with a combined average of less than 1%. Miospores of unknown botanical affinity make up approximately 11% of the assemblage. This relatively uniform composition suggests that the structure of the vegetation remained broadly stable over time with only gradual shifts in dominance between major plant groups. The minor increase in fern and herbaceous lycopoid spores in the younger FR zone may reflect a subtle change in environmental conditions, possibly linked to a transition towards slightly drier habitats.

Late Bashkirian (Westphalian A)

The late Bashkirian (Westphalian A) palynologic data were obtained from the borehole section of Grzędy IG-1, where two miospore zones of this age were distinguished (Górecka-Nowak, 1995). The *Cirratiradites saturni* – *Triquitrites sinani* (SS) miospore zone was recorded in rocks referable to the Biały Kamień Formation at the depth interval 1,705.5–1,719.8 m, and miospore zone *Radiizonates aligerens* (RA) was distinguished in the lower part of the profile of the Żaclę Formation at depth interval 1,290.0–1,672.3 m.

The late Bashkirian rocks exhibited a higher abundance of the lepidodendrids in the original plant communities, although the genus *Sigillaria* occurred sporadically and in low quantities. Together, arborescent lycopoids constitute an average of 40% of the vegetation of this zone and this is significantly more, compared to older communities. The amount of lycopoids was enlarged by sub-arborescent and/or herbaceous lycopoids, which occurred by a dozen percent. The sphenopsids form a constant but minor component

of the flora with an average contribution of only 5%. The seed ferns are an important component, and its content reaches 27% and other groups of ferns account for about 10% of the community. Cordaites and conifers are very rare, and plants of unknown affinity constitute approximately 7% of the vegetation.

Moscovian (Westphalian B and Westphalian C)

The Moscovian palynologic data were obtained from the Grzędy IG-1 borehole section, where two miospore zones: *Microreticulatisporites nobilis* – *Florinites junior* (NJ) and *Torispora securis* – *Torispora laevigata* (SL) were documented at depths of 1,088.8–1,232.4 m and 803.1–1,063.0 m respectively.

The Moscovian communities of parent plants does not show a clear dominance of any single floristic group. The content of arborescent lycopoids is really low. They are mainly lepidodendrids, the amount of which does not exceed 30% and herbaceous and/or sub-arborescent lycopoids co-occur with them, reaching a content of approximately 10%, just like the sphenopsids. The most abundant group of plants were seed ferns, in content exceeding 30% and the amount of other groups of ferns was about a dozen percent. Cordaites and conifers occur in low amounts but are stable components of the vegetation, where only a couple of percent are plants of unknown affinity.

DISCUSSION

The analysis of the composition of parent vegetation, reconstructed from the miospore assemblages from the Biały Kamień Formation, taking account their ecological preferences and supplemented with literature-based data from the Wałbrzych and Żaclę formations, enabled the investigation of temporal changes in vegetation over a relatively long time interval, from the Serpukhovian to the Moscovian. These changes may be compared with the palaeoclimatic model, proposed by Phillips and Peppers (1984), which attributes floristic shifts in the Pennsylvanian to humidity fluctuations within a persistently tropical climate. Wetter intervals promoted the expansion of lycopoids and sphenopsids, whereas drier phases contributed to their decline and were accompanied by an increased presence of ferns and cordaitaleans. The vegetation changes in ISB can thus be interpreted in the context of palaeoclimatic trends. Although the Phillips and Peppers (1984) model was designed for the Bashkirian and younger intervals, the present authors have extended this approach to include the Serpukhovian communities, based on miospore data from the Wałbrzych Formation. This allows for a broader temporal framework for palaeoclimatic interpretation in the ISB.

In the diverse floras of the Serpukhovian and early Bashkirian, the relatively low lycopoid abundance and moderate presence of sphenopsids suggest lower humidity. The proportion of lycopoids during this interval is comparable to that observed in the Moscovian, a period identified by Phillips and Peppers (1984) as the First Dry Interval, implying that similarly dry climatic conditions prevailed in the

Serpukhovian of the ISB. The Bashkirian shows a trend toward increasing lycopsid and sphenopsid abundance. This trend, continuing through most of the Bashkirian, can be interpreted as evidence of gradually increasing humidity (Phillips and Peppers, 1984). These conditions reflect a humid setting with episodic hydrological changes, promoting mire development. The peak of this humid phase occurred in the late Bashkirian, when lycopsids reached their maximum abundance and largely displaced sphenopsids in wet habitats. At the same time, ferns (especially seed ferns) became increasingly significant, driven by both ecological and evolutionary factors. From the Bashkirian onward, gymnosperms are consistently present in the floras, and their abundance steadily increases over time. The observed floristic shifts suggest that the late Bashkirian marked a phase of maximum humidity, which corresponds to the wet interval, defined by Phillips and Peppers (1984) in that time.

Following this peak, the vegetation composition shifted, and in the Moscovian, lycopsid abundance declined substantially. This reflects a transformation of the ecosystems, with a reduction in mire taxa and increasing importance of plants adapted to variable water regimes, mainly ferns (~50% of the flora), sphenopsids, and low-abundance gymnosperms. These trends suggest a gradual lowering of the water table and a transition to drier conditions. Although cordaitaleans remained rare, the floristic changes indicate increasing aridity, consistent with the onset of the First Dry Interval. During the Moscovian, the decline in both arborescent and herbaceous lycopsids continued, along with an increasing dominance of ferns, indicating progressive drying of the environment and development of the dry interval. These floristic dynamics closely align with the Phillips and Peppers (1984) model, supporting the cyclic nature of Carboniferous palaeo-environmental changes and demonstrating that global climate fluctuations are reflected in the vegetation history of the ISB. The compositional similarity between the Serpukhovian and Moscovian assemblages is of particular interest, especially in terms of lycopsid abundance. This supports the interpretation of a similarly low-humidity climate in both intervals.

In addition, the floristic data from the Serpukhovian and Bashkirian in the ISB provide insight into the longstanding debate over the so-called “floristic leap”. This concept, widely discussed in older German and Polish palaeobotanical and stratigraphic literature after Gothan and Gropp (1933), refers to a hypothesized abrupt shift in vegetation composition at the early - late Namurian boundary, attributed to climatic change or a stratigraphic gap. To evaluate this hypothesis, the present authors analyzed both miospore records and the composition of parent vegetation communities. If a “floristic leap” had indeed occurred, it should be evident in the miospore record. However, all analyzed assemblages from the Wałbrzych and Biały Kamień formations consistently include the same floristic groups, though represented in different relative abundances. The observed compositional changes are progressive and continuous rather than sudden, challenging the notion of a discrete floristic turnover during the deposition of these lithostratigraphic units.

Although the data are strong, their interpretation should still take into account differences in how well the material is documented and some simplified methods, used in the

analysis. Górecka (1969) reached similar conclusions, finding no signs of a sudden change in vegetation within the Biały Kamień Formation. Instead, she observed a steady and gradual transformation. More recent palynostratigraphic studies of the Wałbrzych and Biały Kamień formations (Górecka-Nowak *et al.*, 2021; Maćko and Górecka-Nowak, 2024) confirm that there is no stratigraphic gap in the Namurian deposits. This supports the view that vegetation changed gradually over time and challenges the idea of a rapid, large-scale “floristic leap”. Similar observations apply to the Upper Silesian Coal Basin (USCB), where abrupt disappearances of macrofloral taxa at the transition from paralic to limnic facies were locally observed. These changes were interpreted as a “floral leap” and evidence for a depositional hiatus (Kotas, 1995). However, as in the ISB, the miospore records from the USCB (Oliwkiewicz-Miklasinska, 2001) do not support the hypothesis of a sudden floristic turnover or stratigraphic gap.

CONCLUSIONS

Vegetation changes in the ISB from the Serpukhovian to the Moscovian were closely correlated with humidity fluctuations within a persistently tropical climate. They may be correlated with the model of palaeoclimatic changes of Phillips and Peppers (1984), which covers the interval from the Bashkirian to Moscovian. The composition of vegetation in the Serpukhovian corresponds closely to that recorded in the Moscovian. In both of these communities, the main feature is low lycopsid abundance, indicating relatively dry palaeoclimatic conditions. In contrast, the Bashkirian records a gradual increase in lycopsids and sphenopsids, peaking in the late Bashkirian during the maximum humidity phase. This was followed in the Moscovian by a marked decline in lycopsids and a shift toward fern dominance, reflecting a transition to a drier climate, associated with the First Dry Interval distinguished by Phillips and Peppers (1984). Neither analysis of the composition of miospore assemblages nor parent plant communities confirm any sharp change in vegetation in the Serpukhovian and early Bashkirian that could correspond to a “floristic leap”. Recent palynostratigraphic studies also contradict the opinion on the stratigraphic gap, with which the “floristic leap” was supposed to be connected. Results of studies by the present authors confirm the cyclic nature of Carboniferous palaeoclimate changes, their global range and their distinct manifestation in the vegetation history of the ISB.

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REFERENCES

- Balme, B. E., 1995. Fossil in situ spores and pollen grains: an annotated catalogue. *Review of Palaeobotany and Palynology*, 87: 81–323.
- Bek, J., 2021. Paleozoic *in situ* spores and pollen. Sphenopsida. *Palaeontographica. Abteilung B. Paläophytologie, Palaeobotany, Palaeophytology*, 301: 141–201.
- Bek, J. & Libertin, M., 2010. In situ reticulate sphenophyllalean spores. *Review of Palaeobotany and Palynology*, 159: 56–61.
- Bek, J. & Opluštil, S., 2021. Early Pennsylvanian to early Permian (Bashkirian-Asselian) miospore and pollen assemblages of the Czech part of the Intra-Sudetic Basin. *Bulletin of Geosciences*, 96: 341–360.
- Bek, J., Opluštil, S., Pšenicka, J. & Votočková-Frojdová, J., 2021. Quantitative relationship of spore and plant assemblages from the Radnice Basin, Middle Pennsylvanian of the Czech Republic: preliminary results. *Geological Quarterly*, 65: 1–12.
- Bercovici, A. & Vellekoop, J., 2017. Methods in Paleopalynology and Palynostratigraphy: An Application to the K-Pg Boundary. In: Zeigler, K. E. & Parker, W. G. (eds.), *Terrestrial Depositional Systems. Deciphering Complexities through Multiple Stratigraphic Methods*. Elsevier, pp. 127–164.
- Bharadwaj, D. C. & Venkatachala, B. S., 1968. Suggestions for a morphological classification of spores dispersae. *Review of Palaeobotany and Palynology*, 6: 41–59.
- Chaloner, W. G., 1954. Notes on the spores of two British Carboniferous lycopods. *Annals and Magazine of Natural History*, 12: 81–91.
- Clayton, G., Coquel, R., Doubinger, J., Gucinn, K. J., Loboziak, S., Owens, B. & Streel, M., 1977. Carboniferous miospores of Western Europe: illustration and zonation. *Mededelingen Rijks Geologische Dienst*, 29: 3–5.
- DiMichele, W. A., 2014. Wetland-dryland vegetational dynamics in the Pennsylvanian ice age tropics. *International Journal of Plant Sciences*, 175: 123–164.
- DiMichele, W. A., Cecil, C. B., Montanez, I. P. & Falcon-Lang, H. J. F., 2010. Cyclic changes in Pennsylvanian paleoclimate and effects on floristic dynamics in tropical Pangaea. *International Journal of Coal Geology*, 83: 329–344.
- DiMichele, W. A. & Phillips, T. L., 1985. Arborecent Lycopod reproduction and paleoecology in a coal-swamp environment of late middle Pennsylvanian ge (Herrin Coal, Illinois, Usa). *Review of Palaeobotany and Palynology*, 44: 1–26.
- DiMichele, W. A. & Phillips, T. L., 1994. Paleobotanical and paleoecological constraints on models of peat formation in the Late Carboniferous of Euramerica. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 106: 39–90.
- DiMichele, W. A. & Phillips, T. L., 2009. Clades, ecological amplitudes, and ecomorphs: phylogenetic effects and persistence of primitive plant communities in the Pennsylvanian-age tropical wetlands. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 127: 83–105.
- Dybckjær, K., 1991. *Palynological zonation and palynofacies investigation of the Fjerritslev Formation (Lower Jurassic–basal Middle Jurassic) in the Danish Subbasin*. *Danmarks Geologiske Undersøgelse, Serie A*, 30: 1–142.
- Górecka, T., 1969. Stratigraphy of the Biały Kamień Formation in the northwestern part of the Intra-Sudetic Basin based on palynological studies. *Biuletyn Instytutu Geologicznego*, 230: 167–291. [In Polish, with English summary.]
- Górecka-Nowak, A., 1988. Palynostratigraphy of Upper Carboniferous deposits from the Grzędy IG-1 borehole. *Geologia Sudetica*, 23: 103–119. [In Polish, with English summary.]
- Górecka-Nowak, A., 1995. Palynostratigraphy of the Westphalian deposits in the north-western part of the Intrasudetic Basin. *Acta Universitatis Wratislaviensis*, 1583. *Prace Geologiczno-Mineralogiczne*, 40: 1–156. [In Polish, with English summary.]
- Górecka-Nowak, A., 1996. The succession of Westphalian miospore assemblages from the Intra-Sudetic Depression as an indicator of paleoclimate and paleoenvironmental changes. *Acta Universitatis Wratislaviensis*, 1795: 95–100. [In Polish, with English summary.]
- Górecka-Nowak, A., 2002. Palynological record of paleoclimatic changes in Late Carboniferous - an example from the Intrasudetic Basin (SW Poland). *Review of Paleobotany and Palynology*, 118: 101–114.
- Górecka-Nowak, A., Jankowska, A. & Muszer, J., 2021. Age revision of Carboniferous rocks in the northern part of the Intra-Sudetic Basin (SW Poland) based on miospore data. *Geological Quarterly*, 65: 1–14.
- Górecka-Nowak, A. & Majewska, M., 2002. Remarks on palynostratigraphy of the Namurian Wałbrzych formation in the northern part of the Intra-Sudetic Basin (SW Poland). *Geological Quarterly*, 46: 101–115.
- Górecka-Nowak, A. & Majewska, M., 2003. The palynostratigraphy and palynofacies of the Namurian Wałbrzych formation in the northern part of the Intrasudetic Basin (SW Poland). In: Wong, T. E. (ed.), *Proceedings of the XVth International Congress on Carboniferous and Permian Stratigraphy*. Royal Netherlands Academy of Arts and Sciences, Amsterdam, pp. 333–342.
- Górecka-Nowak, A., Muszer, J. & Mačko, A., 2025. The Carboniferous of the Sudetes in the light of new biostratigraphic studies. *Przegląd Geologiczny*, 73: 776–783. [In Polish, with English abstract.]
- Gothan, W. & Gropp, W., 1933. Paläobotanisch-Stratigraphische Untersuchungen im niederschlesischen Karbon. *Zeitschrift Berg Hütten und Salinwesen im Preussischen Staate*, 81: 88–98.
- Kotas, A., 1995. Upper Silesian Coal Basin. The Carboniferous system in Poland. *Prace Państwowego Instytutu Geologicznego*, 148: 124–134.
- Kurowski, L., 1998. Fluvial sedimentology of the Biały Kamień Formation (Upper Carboniferous, Sudetes, Poland). *Geologia Sudetica*, 31: 69–77.
- Mačko, A. & Górecka-Nowak, A., 2024. New palynostratigraphic data from the Namurian Biały Kamień Formation in the northern part of the Intra-Sudetic Basin (SW Poland). *Geological Quarterly*, 68: 1–9.
- Mendonça-Filho, J. G., Menezes, T. R. & Mendonça, J. O., 2011. Organic composition (palynofacies analysis). *ICCP Training Course on Dispersed Organic Matter*, 5: 33–81.
- Oliwkiewicz-Mikłasińska, M., 2001. New distinctive miospore species from the Namurian of the Upper Silesia Coal Basin, Poland. *Journal of Micropalaeontology*, 20: 169–177.

- Owens, B., McLean, D. & Bodman, D., 2004. A revised palynozonation of British Namurian deposits and comparison with eastern Europe. *Micropaleontology*, 50: 89–100.
- Phillips, T. L. & Peppers, R. A., 1984. Changing patterns of Pennsylvanian coal-swamp vegetation and implications of climatic control on coal occurrence. *International Journal of Coal Geology*, 3: 205–255.
- Phillips, T. L., Peppers, R. A. & DiMichele, W. A., 1985. Stratigraphic and interregional changes in pennsylvanian coal-swamp vegetation: environmental inferences. *International Journal of Coal Geology*, 5: 43–109.
- Riding, J. B., 2021. A guide to preparation protocols in palynology. *Palynology*, 45, S1: 1–110.
- Sawicki, L., 1967. *Mapa geologiczna regionu dolnośląskiego (bez utworów czwartorzędowych) 1: 200 000*. Państwowy Instytut Geologiczny, Warszawa. [In Polish.]
- Smith, A. H. V., 1961. The palaeoecology of Carboniferous peats based on the miospores and petrography of bituminous coals. *Proceedings of the Yorkshire Geological Society*, 33: 423–474.
- Smith, A. H. V. & Butterworth, M. A., 1967. Miospores in the coal seams of the Carboniferous of Great Britain. *Special Papers in Palaeontology*, 1: 1–324.
- Taylor, T. N., Taylor, E. L. & Krings, M., 2009. Sphenophytes. In: Taylor, T. N., Taylor, E. L. & Kring, M. (eds), *Paleobotany: The Biology and Evolution of Fossil Plants*. Elsevier, London, pp. 360–363.
- Thomas, B. A., 2021. Why lycospora dominated many Pennsylvanian spore assemblages. *Fossil Imprint*, 77: 11–16.
- Tyson, R. V., 1995. *Sedimentary Organic Matter Organic Facies and Palynofacies*. Chapman Hall, London, 455 pp.

