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Palynoflora and palaeoenvironment of the early Miocene palaeolake from the Bełchatów mine, central Poland

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The Bełchatów lignite deposits are a rich archive allowing palaeoenvironmental, palaeoecological and palaeoclimatic reconstructions from the Neogene and Quaternary periods. We describe the results of palynological studies (including non-pollen palynomorphs) of eight samples from the lower Miocene KRAM-P 211/214 collection of plant macroremains. The results of this palynological analysis are consistent with the results of previous studies of plant macroremains and significantly enrich our knowledge of vegetation and palaeoenvironment. Both studies indicate the presence of a freshwater body (a moderately large and deep lake) surrounded by wetland vegetation (including swamp forests with *Glyptostrobus*, *Taxodium*, *Nyssa* and *Osmunda*) and upland mesophytic forests. Evergreen or at least semi-evergreen forest communities grew along the ancient shores of the lake and on the slopes of the Mesozoic calcareus rocks surrounding the lake. In the lake, green algae (*Pediastrum*, *Tetraedron* and some *Botryococcus*) and freshwater peridinoid dinoflagellates were major components of the algal community. The same lake was the source of previously identified animal remains: freshwater fishes, molluscs, and mammals, including Megachiroptera bats. Our analysis shows that the climate was subtropical and humid, with an estimated mean annual temperature of 16.8–17.8°C.

Key words: palynology, palaeoclimate, palaeovegetation, Neogene, freshwater algae, central Europe.

INTRODUCTION

The Bełchatów lignite deposits (Fig. 1) were discovered in the 1960s, and since 1980s the Bełchatów Mine has yielded a diverse array of fossils, being a rich archive allowing palaeoenvironmental, palaeoecological, and palaeoclimatic reconstructions of central Poland during the Neogene and Quaternary. Moreover, fossils from this locality have considerably extended our understanding of past plant biodiversity (Stuchlik et al., 1990; Worobiec and Lesiak, 1998; Wójcicki and Zastawniak, 1998; Worobiec, G., 2003, 2007, 2014; Worobiec and Szynkiewicz, 2007, 2016; Worobiec et al., 2012; Worobiec and Worobiec, 2020), algae (Worobiec and Worobiec, 2008), fungi (Worobiec and Worobiec, 2017; Worobiec et al., 2020), cladocera (Dumont et al., 2020), insects (Wegierek, 1995), molluscs (Stworzewicz, 1993, 1995), freshwater fishes (Jerzmańska and Hałuszczak, 1986; Kovalchuk et al., 2020) and mammals (Kowalski, 1993; Rzebik-Kowalska and Kowalski, 2001; Garapich, 2002; Kowalski and Rzebik-Kowalska, 2002).

Most of the fossil plants (mainly macroremains) were found in mid-to upper Miocene deposits of slow-flowing rivers with swamps and oxbow lakes, while palaeobotanical data concerning lower Miocene deposits are rather limited (Worobiec, 1995, 2003). Plant macroremain assemblages KRAM-P 211 and KRAM-P 214 were collected in 1993 and 1994, respectively, in the open pit of the Bełchatów Lignite Mine. Both macrofloras came from grey clays overlaying paratonstein TS-3 (vel TS-4) and they were deposited in a large lake (Worobiec, 2003). The same lake was a source of animal remains of freshwater fishes (Jerzmańska and Hałuszczak, 1986; Kovalchuk et al., 2020), molluscs, and mammals, including Megachiroptera bats (Kowalski, 1995; Kowalski and Rzebik-Kowalska, 2002). Despite such interesting palaeontological findings, no palynological analysis of these gray clays was carried out.

This paper presents the results of palynological analysis of pollen, spore and non-pollen palynomorph (freshwater algae and fossil fungi) assemblages co-occurring with the Bełchatów KRAM-P 211/214 collection of plant macroremains (Worobiec, 2003). The relatively high taxonomic diversity of the well-preserved sporomorph association allowed reconstruction of the plant communities. Results of the palynological studies add also information about the age of the fossil flora. The palynological analysis significantly complements the data on palaeoflora and palaeovegetation obtained from previous studies of plant macroremains (Worobiec, 2003) and provides new information about the palaeoclimate and palaeoenvironment of the early Miocene.

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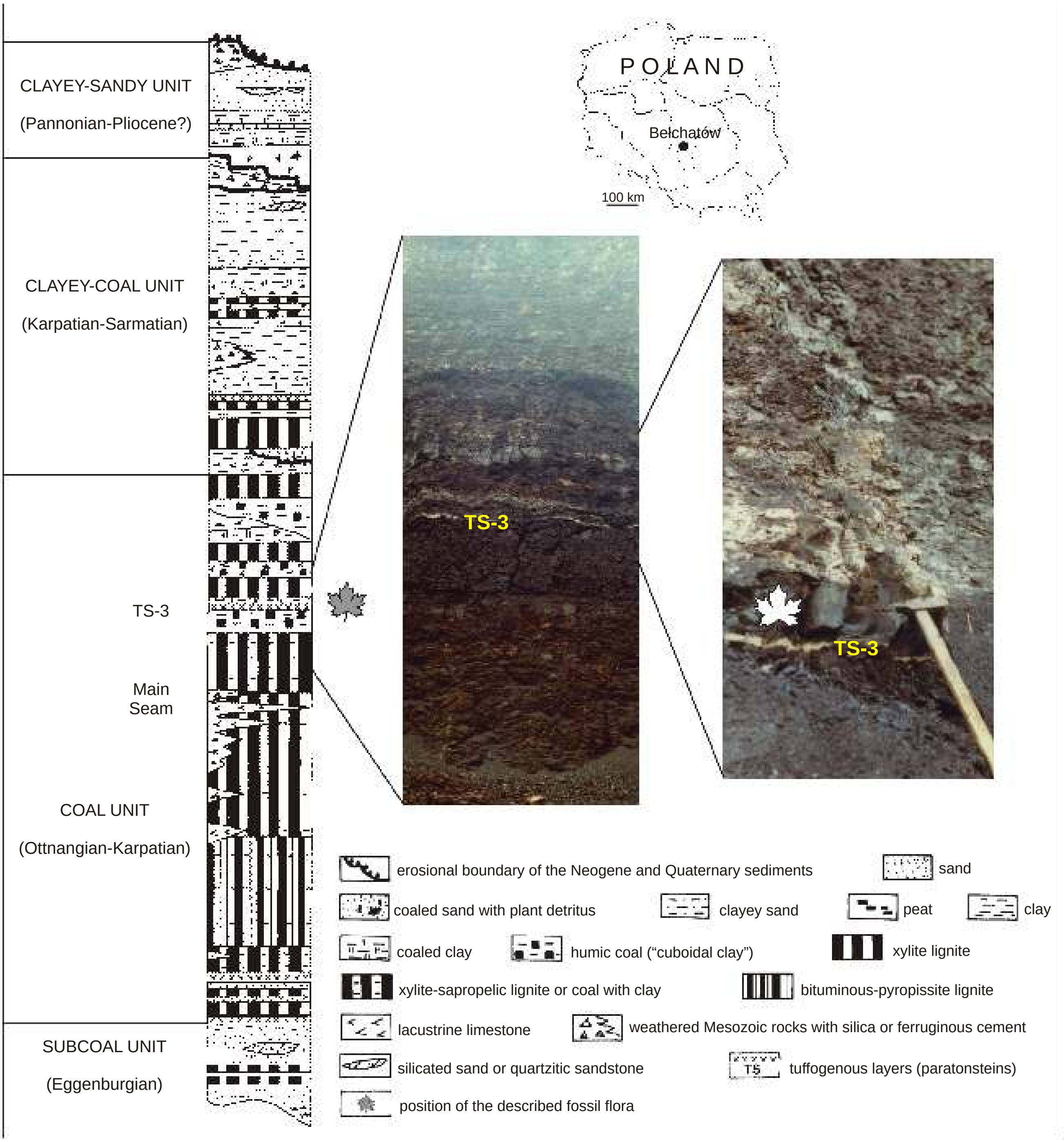

Fig. 1. Location of the Bełchatów Lignite Mine and the lithostratigraphic profile of the Neogene deposits in the Bełchatów Mine, modified from Stuchlik et al. (1990) and Worobiec (2003)

GEOLOGICAL SETTING

Bełchatów Lignite Mine is situated in central Poland (51°15'46.4"N 19°18'49.2"E), south of the town of Bełchatów (Fig. 1) in the southern part of the Central European Lowlands. Neogene deposits with lignite seams occur there within tectonic depressions of the Kleszczów Graben (Stuchlik et al., 1990). Four lithological units: subcoal unit (PW); coal unit (W) with the main seam (PG), seam B and seam C; clayey-coal unit (I–W) with seam A; and the youngest clayey-sandy unit (I–P) were distinguished in the Neogene sedimentary succession of the Kleszczów Graben (Czarnecki et al., 1992; Matl, 2000).

An exposure with fossil leaf assemblages KRAM-P 211 and KRAM-P 214 (Fig. 1) was located within the coal unit (W), on the coal escarpment no. 1, at an altitude of 61.3–75.0 m a.s.l., on the western slope of the Bełchatów open pit mine, between the boreholes 74.5/14.5 and 74/15 NS (Worobiec, 2003). In the lower part of the exposure, lacustrine limestone occurred interbedded with thin lignite intercalations, which graded into the main coal seam. The lacustrine limestone was overlain by black, humic coals, so-called "cuboidal clays", covered by a layer of 2–3 cm laminated pyroclastic deposits (paratonstein) referred to as TS-3 (Stuchlik et al., 1990) or TS-4 (Czarnecki et al., 1992; Wagner, 2000). The paratonstein was overlain by up to 1.5 m thick grey clays containing leaf macroremains. Clays with plant macroremains were overlain by lignites of the 3–9 m xylitic-clay seam C(III). The plant assemblages were deposited in a large lake as indicated by the presence of extensive lacustrine limestone deposits (Worobiec, 2003). The geological setting of the KRAM-P 211/214 fossil flora in clays overlaying paratonstein (tuffite, volcanic ash), dated using the fission-track (FT) method at 18.1 ±1.7 Ma (Burchart et al., 1988), and the composition of the leaf assemblage (Worobiec, 2003), suggest its early Miocene age.

MATERIALS AND METHODS

For this research, archival material from the collection of the W. Szafer Institute of Botany, Polish Academy of Sciences was used. The material was collected from the Bełchatów Lignite Mine opencast (Fig. 1). Forty eight specimens of the KRAM-P 211 fossil leaf assemblage from clays overlying paratonstein TS-3 were collected in 1993, while 193 specimens of the KRAM-P 214 leaf assemblage were collected in 1994. For palynological analysis eight samples from the KRAM-P 214 collection of plant macroremains, including four samples from specimens (rock samples with leaf macroremains numbers 129, 148, 149, 158) and four samples from rock fragments without numbers (A–D), were taken.

The palynological samples were processed in the Laboratory of the W. Szafer Institute of Botany, Polish Academy of Sciences, according to the following procedure: a portion of ~1 cm^3 of crushed rock was treated successively with 10% hydrochloric acid (HCl), 10% potassium hydroxide (KOH), 40% hydrofluoric acid (HF), and subsequently 10% hydrochloric acid (HCl) (Moore et al., 1991; Worobiec et al., 2021). Additionally, the residuum was sieved at 5 µm on a nylon mesh. From each sample 3–6 microscope slides were made, using glycerine jelly as a mounting medium. In all slides pollen grains, spores of plants and non-pollen palynomorphs (NPPs), such as algal remains and fungal remains, were studied. In each sample >600 pollen grains and spores (>5000 sporomorphs altogether) were identified and all co-occurring non-pollen palynomorphs were counted.

The sporomorph taxa identified were classified mainly on the basis of the "Atlas of pollen and spores of the Polish Neogene" (Stuchlik et al., 2001, 2002, 2009, 2014). In the material studied, the following palaeofloristical (and palaeoclimatic) elements were distinguished: "palaeotropical" (P), including: "tropical" (P1) and "subtropical" (P2), "arctotertiary" (A), including: "warm-temperate" (A1) and "temperate" (A2) as well as cosmopolitan (P/A). The mean annual temperature (MAT) estimation in this work is based on the Coexistence Approach (CA) method (Utescher et al., 2014). The basic assumption for the CA method is the concept that the nearest living relatives of fossil taxa provide the information necessary to find a climatic distribution interval, where all the plants could have lived (Coexistence Interval). The CA uses only the presence or absence of the taxa, without considering their relative frequency. The nearest living relatives and their MAT ranges follow The Palaeoflora Database (Utescher and Mosbrugger, 2015). For the CA method, the authors selected as many taxa as was possible excluding fossil taxa with unknown botanical affinity, related to families, aquatic taxa, etc. (Appendix 1). Microphotographs of selected sporomorphs and non-pollen palynomorphs (Figs. 2 and 3) were taken using a *Nikon Eclipse E400* microscope fitted with a *Canon A640* digital camera.

RESULTS OF THE PALYNOLOGICAL STUDIES

All samples studied yielded very well-preserved sporomorphs (Figs. 2 and 3) suitable for detailed palynological analysis. Pollen spectra from the samples are taxonomically diverse and they are very similar in composition. A total of 118 fossil-species of sporomorphs (including 11 species of plant spores, 25 species of gymnosperm pollen, and 82 species of angiosperm pollen) were identified (Table 1). In all samples, the pollen grains of conifers are slightly more numerous, but the angiosperms are more diverse. Among the conifers, bisaccate pollen grains are most frequent, including *Pinus* (mainly *Pinuspollenites labdacus*, mean 34.47% in the spore-pollen spectra for all samples), *Picea* (7.44%), *Cathaya* (4.14%), *Keteleeria* (1.71%), *Abies* (0.31%) and *Cedrus* (0.04%). Non-bisaccate pollen grains of gymnosperms are represented by Cupressaceae, including pollen grains with distinct papillae (Fig. 2F) usually related to *Sequoia/Sequoiadendron/Metasequoia/Cryptomeria* (3.04%) and other pollen (Fig. 2E) usually related to *Taxodium/Glyptostrobus* (15.43%), *Sciadopitys* (1.02%), and *Tsuga* (0.04%).

Angiosperms are represented mainly by trees and shrubs, whereas herbs are very rare. Most common are pollen grains of *Quercus* (including *Quercopollenites* – 2.20% and *Quercoidites henricii* + *Quercoidites microhenricii* – together 1.73%), Engelhardioideae (*Momipites*, 2.22%), Castaneoideae (*Cupuliferoipollenites oviformis* and *Cupuliferoipollenites pusillus*, together 2.00%), *Ulmus* (1.73%), *Carya* (1.65%), Myricaceae (1.43%), *Betula* (1.41%), *Acer* (mainly *Aceripollenites reticulatus*, 1.35%), Oleaceae (*Oleoidearumpollenites*, 1.33%), *Tricolporopollenites pseudocingulum* + *Tricolporopollenites leonensis* (1.18%), *Alnus* (1.00%), *Fagus* (0.84%), Tilioideae/Brownlowioideae (*Intratriporopollenites*, 0.84%), Mastixiaceae (*Cornaceaepollis satzveyensis*, 0.82%), Fabaceae (mainly *Tricolporopollenites fallax* and *Tricolporopollenites liblarensis*, together 0.70%), *Fraxinus* (0.70%), *Ilex* (0.53%) and *Cercidiphyllum* (0.51%). Pollen grains of *Carpinus*, Cyrillaceae/Clethraceae, Ericaceae, *Nyssa* (*Nyssapollenites* and *Nyssoidites rodderensis*), *Liquidambar*, *Platanus*, *Platycarya*, *Pterocarya*, *Salix*, Sapotaceae, *Arceuthobium*, Vitaceae (*Parthenopollenites marcodurensis* and *Vitispollenites tener*), and *Zelkova* were recorded regularly in quantities <0.50%. In addition, a few pollen grains of Arecaceae (e.g., *Dicolpopollis kockelii*), *Celtis*, *Corylopsis* and other Hamamelidaceae (*Tricolporopollenites staresedloensis*), *Liriodendron*, Meliaceae, *Symplocos*, as well as members of the fossil-genera *Edmundipollis*, *Fususpollenites* and *Subtriporopollenites* are present. Among herbs Cyperaceae (including *Cyperaceaepollis piriformis*, together 1.18%), *Potamogeton* (*Potamogetonacidites ovalis*, 0.43%), and Sparganiaceae/Typhaceae (0.12%) are most frequent.

Spores of bryophytes and pteridophytes are scarce and they are represented mainly by ferns, including *Osmunda* (*Baculatisporites*, 0.25%), fossil-genera *Laevigatosporites* (0.33%), *Leiotriletes* (0.08%), and *Triplanosporites*, fossil-species *Radialisporis radiatus* as well as *Sphagnum* (*Stereisporites*) and *Lycopodium* (*Retitriletes frankfurtensis*). Non-pollen palynomorphs are represented mainly by freshwater algae, including *Pediastrum boryanum* (mean 16.25% in the whole palynological spectra for all samples), peridinioid dinoflagellate cysts (1.23%), *Tetraedron minimum*, and *Botryococcus braunii*. Remains of freshwater Zygnemataceae algae

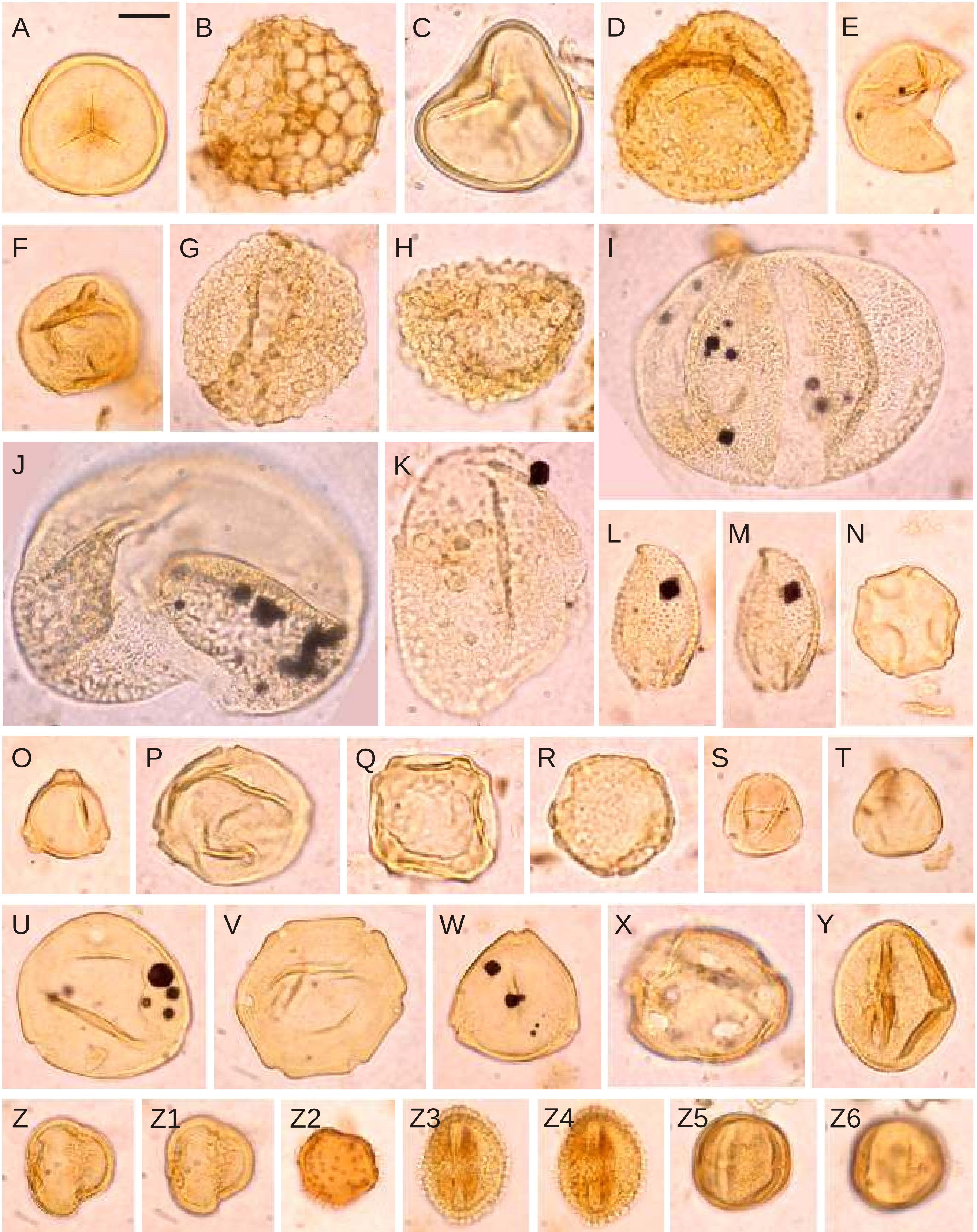

Fig. 2. Spores and pollen grains from the KRAM-P 214 collection

A – *Stereisporites* sp. (*Sphagnum*); **B** – *Retitriletes* sp. (*Lycopodium*); **C** – *Leiotriletes* sp. (Lygodiaceae); **D** – *Baculatisporites primarius* (*Osmunda*); **E** – *Inaperturopollenites concedipites* (Cupressaceae); **F** – *Sequoiapollenites rugulus* (Cupressaceae); **G** – *Sciadopityspollenites miniverrucatus* (*Sciadopitys*); **H** – *Sciadopityspollenites verticillatiformis* (*Sciadopitys*); **I** – *Cathayapollis* sp. (*Cathaya*); **J** – *Piceapollis praemarianus* (*Picea*); **K** – *Liriodendroipollis verrucatus* (*Liriodendron*); **L, M** – *Arecipites longicolpatus* (Amaryllidaceae, Araceae, Arecaceae), same specimen, various foci; **N** – *Alnipollenites verus* (*Alnus*); **O** – *Trivestibulopollenites betuloides* (*Betula*); **P** – *Carpinipites carpinoides* (*Carpinus*); **Q** – *Zelkovaepollenites potoniei* (*Zelkova*); **R** – *Ulmipollenites stillatus* (*Ulmus*); **S** – *Platycaryapollenites miocaenicus* (*Platycarya*); **T** – *Momipites quietus* (Engelhardioideae); **U** – *Caryapollenites simplex* (*Carya*); **V** – *Polyatriopollenites stellatus* (*Pterocarya*); **W** – *Myricipites pseudorurensis* (*Myrica*); **X** – *Periporopollenites* sp. (*Liquidambar*); **Y** – *Tricolporopollenites pseudocingulum* (Fagaceae?, Styracaceae?); **Z, Z1** – *Platanipollis ipelensis* (*Platanus*), same specimen, various foci; **Z2** – *Spinulaepollis arceuthobioides* (*Arceuthobium*); **Z3, Z4** – *Ilexpollenites margaritatus* (*Ilex*), same specimen, various foci; **Z5, Z6** – *Meliaceoidites angustiporatus* (Meliaceae), same specimen, various foci; scale bar in A is 10 µm and refers to all photographs; botanical affinity in brackets

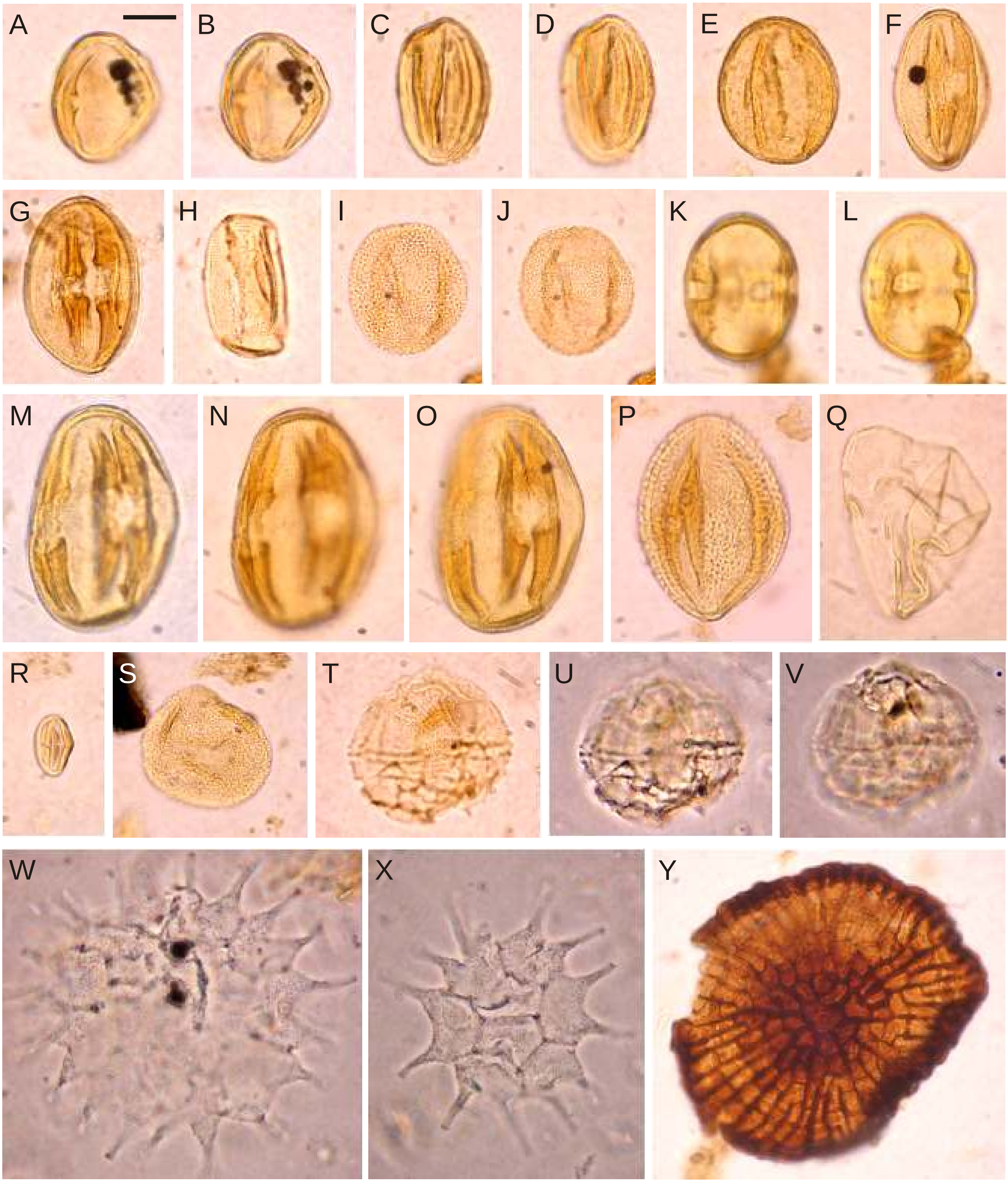

Fig. 3. Pollen grains and non-pollen palynomorphs from the KRAM-P 214 collection

A, B – *Nyssapollenites contortus* (*Nyssa*), same specimen, various foci; **C, D** – *Aceripollenites* sp. (*Acer*), same specimen, various foci; **E** – *Quercopollenites rubroides* (*Quercus*); **F** – *Quercopollenites* sp. (*Quercus*); **G, H** – *Cercidiphyllites minimireticulatus* (*Cercidiphyllum*); **I, J** – *Fraxinipollis oblatus* (*Fraxinus*), same specimen, various foci; **K, L** – *Sapotaceoidaepollenites* sp. (Sapotaceae), same specimen, various foci; **M–O** – *Tetracolporopollenites* cf. *sapotoides* (Sapotaceae?), same specimen, various foci; **P** – *Parthenopollenites marcodurensis* (Vitaceae); **Q** – *Cyperaceaepollis neogenicus* (Cyperaceae); **R** – *Cupuliferoipollenites oviformis* (Castaneoideae); **S** – *Potamogetonacidites paluster* (*Potamogeton*); **T–V** – peridinioid dinoflagellate cyst (Dinophyceae), same specimen, various foci; **U, V** – phase contrast; **W** – *Pediastrum boryanum*, phase contrast; **X** – *Pediastrum boryanum*, phase contrast; **Y** – sporocarp of epiphyllous fungus; scale bar in A is 10 µm and refers to all photographs; botanical affinity in brackets

Table 1

Results of palynological analysis (number of palynomorphs and their average percentages) of samples from the KRAM-P 214 collection of plant macroremains. Taxonomy, botanical affinity and palaeofloristical elements of pollen and spores according to Stuchlik et al. (2001, 2002, 2009, 2014)

Fossil taxa	Botanical affinity	Element	Sample								Mean [%]
			A	B	C	D	129	148	149	158	
SPORES OF BRYOPHYTES AND PTERIDOPHYTES:											
Baculatisporites major (Raatz) Krutzsch + *Baculatisporites primarius* (Wolff) Thompson et Pflug + *Baculatisporites* sp.	Osmundaceae: *Osmunda*	P/A	4	1	2	1	1	1	2	1	0.25
Laevigatosporites sp.	Polypodiaceae, Davalliaceae, and other ferns	P/A	1	3	5	2	4		2		0.33
Leiotriletes sp.	Lygodiaceae and other ferns	P	1	1			1			1	0.08
Radialisporis radiatus (Krutzsch) Jansonius et Hills	Lygodiaceae, Parkeriaceae	P		1		1			1		0.06
Retitriletes frankfurtensis Krutzsch + *Retitriletes* sp.	Lycopodiaceae: *Lycopodium*	A			2					1	0.06
Stereisporites sp.	Sphagnaceae: *Sphagnum*	P/A		1	1				1		0.06
Triplanosporites sp.	unknown	P			1						0.02
Verrucatosporites sp.	Davalliaceae, Polypodiaceae, and other ferns	P/A			1						0.02
POLLEN GRAINS OF GYMNOSPERMS:											
Abiespollenites sp.	Pinaceae: *Abies*	A	1	1	1	1	1	3	6	2	0.31
Cathayapollis potoniei (Sivak) Ziembińska-Tworzydło + *Cathayapollis pulaensis* (Nagy) Ziembińska-Tworzydło + Cathayapollis wilsonii (Sivak) Ziembińska-Tworzydło + *Cathayapollis* sp.	Pinaceae: *Cathaya*	A1	26	30	36	42	22	15	11	29	4.14
Cedripites sp.	Pinaceae: *Cedrus*	A1				1				1	0.04
Cupressacites sp.	Cupressaceae	A1	2	5	1		4	1	2		0.29
Inaperturopollenites concedipites (Wodehouse) Krutzsch + *I. dubius* (Potonié et Venitz) Thomson et Pflug + *Cupressacites bockwitzensis* Krutzsch	Cupressaceae: *Taxodium*, *Glyptostrobus*	P2/A1	133	108	109	41	115	149	94	37	15.43
Keteleeriapollenites dubius (Khlonova) Słodkowska	Pinaceae: *Keteleeria*	A1	8	10	8	18	5	8	13	17	1.71
Piceapollis praemarianus Krutzsch + *P. sacculiferoides* Krutzsch + *Piceapollis* sp.	Pinaceae: *Picea*	A	25	32	43	61	41	45	54	78	7.44
Pinuspollenites labdacus (Potonié) Raatz + *Pinuspollenites* sp.	Pinaceae: *Pinus*	A	210	225	161	251	221	163	202	323	34.47
Sciadopityspollenites miniverrucatus Kohlman-Adamska + *Sciadopityspollenites serratus* (Potonié et Venitz) Raatz et Potonié + *Sciadopityspollenites verticillatiformis* (Zauer) Krutzsch + *Sciadopityspollenites* sp.	Sciadopityaceae: *Sciadopitys*	A1	8	10	6	4	8	9	4	3	1.02
Sequoiapollenites rotundus Krutzsch + *Sequoiapollenites rugulus* Krutzsch + *Sequoiapollenites sculpturius* Krutzsch + *Sequoiapollenites* sp.	Cupressaceae: *Sequoia*, *Sequoiadendron*, *Metasequoia*, *Cryptomeria*	A1	19	12	21	8	28	33	28	6	3.04
Zonalapollenites sp.	Pinaceae: *Tsuga*	A1					1		1		0.04
POLLEN GRAINS OF ANGIOSPERMS:											
Aceripollenites reticulatus Nagy +Aceripollenites *striatus* (Pflug) Thiele-Pfeiffer + *Aceripollenites* sp.	Sapindaceae: *Acer*	A1	9	8	8	3	9	14	15	3	1.35
Alnipollenites metaplasmus (Potonié) Potonié + *Alnipollenites verus* Potonié	Betulaceae: *Alnus*	P2/A	4	3	18	4	3	10	6	3	1.00
Arecipites longicolpatus Krutzsch + *Arecipites* sp.	Amaryllidaceae, Araceae, Arecaceae, Butomaceae	P/A	1		2						0.06
Caprifoliipites sp.	Adoxaceae: *Sambucus*, *Viburnum*	P/A1				1					0.02
Carpinipites carpinoides (Pflug) Nagy	Betulaceae: *Carpinus*	P2/A1	1	1	1	1		1			0.10
Caryapollenites simplex (Potonié) Raatz	Juglandaceae: *Carya*	A1	15	6	11	3	13	11	19	6	1.65
Celtipollenites sp.	Ulmaceae: *Celtis*	P/A1	1				3		2		0.12
Cercidiphyllites minimireticulatus (Trevisan) Ziembińska-Tworzydło	Cercidiphyllaceae: *Cercidiphyllum*	A1	3	4	8	1	1	4	4	1	0.51
Chenopodipollis sp.	Amaranthaceae (incl. Chenopodiaceae)	P/A			1						0.02
Cornaceaepollis satzveyensis (Pflug) Ziembińska-Tworzydło	Mastixiaceae	P1	6	5	8	2	6	5	5	5	0.82
Corylopsispollenites microreticulatus E.Worobiec	Hamamelidaceae: *Corylopsis*	A1	1	2		1					0.08
Cupuliferoipollenites oviformis (Potonié) Potonié	Fagaceae: Castaneoideae	P2/A1	3	2	3	13	7	11	22	18	1.55
Cupuliferoipollenites pusillus (Potonié) Potonié	Fagaceae: Castaneoideae	P2/A1		1	4	8	3	2	3	2	0.45
Cyperaceaepollis neogenicus Krutzsch + *Cyperaceaepollis piriformis* Thiele-Pfeiffer	Cyperaceae	P/A	5	6	6	3	11	15	11	3	1.18

Tab. 1 cont.

Fossil taxa	Botanical affinity	Element	Sample								Mean [%]
			A	B	C	D	129	148	149	158	
Cyrillaceaepollenites brühlensis (Thomson) Durska + *Cyrillaceaepollenites exactus* (Potonié) Potonié + *Cyrillaceaepollenites megaexactus* (Potonié) Potonié	Cyrillaceae, Clethraceae	P	2	2	4	5	1	3			0.33
Dicolpopollis kockelii Pflanzl	Arecaceae: Calamoideae	P	1								0.02
Edmundipollis edmundi (Potonié) Konzalová, Słodkowska et Ziembińska-Tworzydło + *Edmundipollis* sp.	Cornaceae, Mastixiaceae, Araliaceae	P1, P/A1		1	2	2					0.10
Ericipites callidus (Potonié) Krutzsch + *Ericipites* sp.	Ericaceae	P/A	1	2	2	3		1	1		0.19
Faguspollenites bockwitzensis (Walter et Zetter) Kohlman-Adamska et Ziembińska-Tworzydło + *Faguspollenites* sp.	Fagaceae: *Fagus*	A	3	7	5	3	8	7	8	2	0.84
Fraxinipollis oblatus Słodkowska	Oleaceae: *Fraxinus*	A	2	4	2	1	7	10	7	3	0.70
Fususpollenites sp.	Fagaceae (incl. *Colombobalanus*)	P1		1			1				0.04
Graminidites sp.	Poaceae: Pooideae	P/A		1							0.02
Ilexpollenites iliacus (Potonié) Thiergart + *Ilexpollenites margaritatus* (Potonié) Thiergart + *Ilexpollenites propinquus* (Potonié) Potonié	Aquifoliaceae: *Ilex*	P/A1, P2	2	7	5	3	4	4	1	1	0.53
Intratriporopollenites instructus (Potonié) Thomson et Pflug + *Intratriporopollenites* sp.	Malvaceae: Brownlowioideae, Tilioideae	P/A1	9	7	10	6	6	3	1	1	0.84
Juglanspollenites sp.	Juglandaceae: *Juglans*	P2/A1					1				0.02
Liriodendroipollis verrucatus Krutzsch	Magnoliaceae: *Liriodendron*	P2/A1				1					0.02
Meliaceoidites angustiporatus Durska	Meliaceae	P	1					1			0.04
Momipites quietus (Potonié) Nichols + *Momipites punctatus* (Potonié) Nagy	Juglandaceae: Engelhardioideae	P, P2	11	7	17	15	11	23	20	9	2.22
Myricipites pseudorurensis (Pflug) Grabowska et Ważyńska + *Myricipites* sp.	Myricaceae	P2/A	11	9	14	15	6	8	6	4	1.43
Nyssapollenites contortus (Pflug et Thomson) Nagy + *Nyssapollenites* sp. + *Nyssoidites rodderensis* Thiergart	Nyssaceae: *Nyssa*	P2/A1	5	2	3	2	1	2	1	2	0.35
Oleoidearumpollenites microreticulatus (Pflug et Thomson) Ziembińska-Tworzydło + *Oleoidearumpollenites reticulatus* Nagy	Oleaceae	P2/A1	5	4	12	11	5	13	13	5	1.33
Parthenopollenites marcodurensis (Pflug et Thomson) Traverse	Vitaceae	P/A1	1		1		1	1	1		0.10
Periporopollenites stigmosus (Potonié) Pflug et Thomson	Altingiaceae: *Liquidambar*	A1	3		3	3	1	1	3	2	0.31
Platanipollis ipelensis (Pacltová) Grabowska	Platanaceae: *Platanus*	P/A1	2	2	3	4	1	3	2	1	0.35
Platycaryapollenites miocaenicus Nagy + *Platycaryapollenites* sp.	Juglandaceae: *Platycarya*	P2/A1	3	1	3	2	1	4	3	1	0.35
Polyatriopollenites stellatus (Potonié) Pflug	Juglandaceae: *Pterocarya*	A1	2	1	2	1		1	1	1	0.17
Potamogetonacidites paluster (Manten) Mohr	Potamogetonaceae: *Potamogeton*	P/A	1	3	2	1	3	6	4	2	0.43
Quercoidites henricii (Potonié) Potonié, Thomson et Thiergart + *Q. microhenricii* (Potonié) Potonié, Thomson et Thiergart	Fagaceae: Quercoideae	P2/A1	11	12	20	5	12	13	11	4	1.73
Quercopollenites rubroides Kohlman-Adamska et Ziembińska-Tworzydło + *Quercopollenites* sp.	Fagaceae: *Quercus*	P2/A1	16	22	7	7	16	17	19	8	2.20
Salixipollenites sp.	Salicaceae: *Salix*	A	1	1	3	2	1		1	1	0.19
Sapotaceoidaepollenites obscurus (Pflug et Thompson) Nagy + *Sapotaceoidaepollenites* sp. + *Tetracolporopollenites* cf. *sapotoides* Pflug et Thomson	Sapotaceae	P	2	1	2			1	1		0.14
Sparganiaceaepollenites sp.	Sparganiaceae, Typhaceae	P/A	2		2	1	1				0.12
Spinulaepollis arceuthobioides Krutzsch	Santalaceae: *Arceuthobium*	P2/A1	3	1	2	3	7	2	1	1	0.39
Subtriporopollenites sp.	Juglandaceae?	P	1		2	1			1		0.10
Symplocoipollenites vestibulum (Potonié) Potonié	Symplocaceae: *Symplocos*	P						1			0.02
Tricolporopollenites dolium (Potonié) Pflug et Thomson	Fagaceae?	un-known	1		1						0.04
Tricolporopollenites cf. *euryoides* Kohlman-Adamska et Ziembińska-Tworzydło	Pentaphylacaceae: *Eurya*	P		2	3				1		0.12
Tricolporopollenites fallax (Potonié) Krutzsch + *Tricolporopollenites liblarensis* (Thomson) Hochuli + *Tricolporopollenites quisqualis* (Potonié) Krutzsch	Fabaceae	P/A	1	4	4	9	4	3	8	3	0.70
Tricolporopollenites leonensis Kohlman-Adamska et Ziembińska-Tworzydło + *Tricolporopollenites pseudocingulum* (Potonié) Thomson et Pflug	Fagaceae?, Styracaceae?	P/A1	10	8	7	4	5	10	8	8	1.18
Tricolporopollenites staresedloensis Krutzsch et Pacltová	Hamamelidaceae	P2	1								0.02

Tab. 1 cont.

Fossil taxa	Botanical affinity	Element	Sample								Mean [%]
			A	B	C	D	129	148	149	158	
Tricolporopollenites villensis (Thomson) Thomson et Pflug	Fagaceae?	un-known			1		2		1		0.08
Trivestibulopollenites betuloides Pflug	Betulaceae: *Betula*	A	7	5	9	20	11	12	5	3	1.41
Ulmipollenites stillatus Nagy + *Ulmipollenites undulatus* Wolff	Ulmaceae: *Ulmus*	A	14	9	15	9	17	10	11	3	1.73
Vitispollenites tener Thiele-Pfeiffer	Vitaceae: *Vitis*	P2/A1	1		1			1	1	1	0.10
Zelkovaepollenites potoniei Nagy + *Zelkovaepollenites* sp.	Ulmaceae: *Zelkova*	A1			4	3	4	2	1	1	0.29
Other pollen grains	unknown	un-known	5	9	3	5	7	8	4	5	0.90
SUM	628	613	644	618	653	671	654	612	100.00		
SELECTED NON-POLLEN PALYNOMORPHS AND PALYNOCLASTS:											
Botryococcus braunii Kützing	Dictyosphaeriaceae: *Botryococcus braunii*	X			2	4	1			2	0.14
Pediastrum boryanum (Turp.) Menegh. + *Pediastrum* sp.	Chlorophyta: *Pediastrum*	X	72	49	229	76	83	274	198	39	16.25
Tetraedron minimum (A. Braun) Hansgirg	Chlorophyta: Chlorococcaceae: *Tetraedron*	X			5	6					0.17
Peridinioid dinoflagellate cysts	Dinophyceae	X	1		3			26	46	1	1.23
Leaf-spines	Hydrocharitaceae, Ceratophyllaceae: *Ceratophyllum*	X	1		1	1		2	1		0.09
Spores of fungi	Fungi	X	5	3	8	4	6	8	13	9	0.89
Sporocarps and conidia of fungi (incl. *Phragmothyrites*)	Fungi	X	0	0	1	0	0	1	1		0.05
TOTAL SUM			707	665	893	709	743	982	913	663	100

Palaeofloristical elements: A – "arctotertiary" (A1 – "warm-temperate", A2 – "temperate"); P – "palaeotropical" (P1 – "tropical", P2 – "subtropical"); P/A – cosmopolitan; X – undetermined

are absent. Fungal remains are scarce. In addition, in most samples leaf-spines of *Ceratophyllum*/Hydrocharitaceae type were encountered. The palynological analysis revealed numerous euhedral and framboidal pyrite (up to 25 μm in diameter), noted in all samples.

The composition of the palynoflora shows a high abundance of "warm-temperate" and "palaeotropical/warm-temperate" palaeofloristical elements (Table 1 and Fig. 4). "Palaeotropical" elements are represented by spores of *Leiotriletes* sp., *Radialisporis radiatus*, and *Triplanosporites* sp. as well as pollen grains of *Cornaceaepollis satzveyensis*, *Cyrillaceaepollenites brühlensis*, *Cyrillaceaepollenites exactus*, *Cyrillaceaepollenites C. megaexactus*, *Dicolpopollis kockelii*, *Edmundipollis edmundi*, *Fususpollenites* sp., *Ilexpollenites margaritatus*, *Meliaceoidites* sp., *Momipites quietus*, *Momipites punctatus*, *Sapotaceoidaepollenites obscurus*, *Sapotaceoidaepollenites* sp., *Subtriporopollenites* sp., *Symplocoipollenites vestibulum*, *Tricolporopollenites staresedloensis* and probably *Tricolporopollenites euryoides* (Table 1).

DISCUSSION

PLANT COMMUNITIES AND PALAEOENVIRONMENT BASED ON THE RESULTS OF THE PALYNOLOGICAL ANALYSIS AND THE KRAM-P 211/214 MACROFLORA

Twenty-eight fossil-species from the genera *Glyptostrobus*, *Pinus*, *Taxodium*, *Tetraclinis*, *Acer*, *Alnus*, *Carya*, *"Castanea"*, *Daphnogene*, *Dicotylophyllum*, *Laurophyllum*, *Liquidambar*, *Myrica*, *Nyssa*, *Populus*, *Quercus*, *Smilax*, *Stratiotes*, *Symplociphyllum*, *Ulmus* and *Osmunda* were identified among the plant macroremains from the Bełchatów KRAM-P 211/214 collection (Worobiec, 2003). The results of the palynological analysis are consistent with the results of studies of plant macroremains and most of the macroremain genera are also represented by pollen and spores (Table 1), except for *Populus* and Lauraceae producing pollen grains that do not preserve in fossil state. As in the case of the upper Miocene assemblages from Bełchatów (Worobiec and Worobiec, 2016), the main difference is in the taxonomic richness between micro- and macroflora. The fossil assemblage was formed in lake deposits and thus, among macroremains, plants from the vicinity of the lake dominate, whereas among sporomorphs many taxa from places located farther from the lake are present (Ferguson et al., 1998). Therefore, the results of pollen analysis considerably enrich our knowledge about the vegetation and palaeoenvironment.

The results of both studies indicate the presence of a freshwater body (lake), surrounded by wetland vegetation (including swamp forests) and upland mesophytic forests, at the time of sedimentation. In the water body, green algae (Chlorophyta), such as *Pediastrum*, *Tetraedron*, and some *Botryococcus* colonies, as well as freshwater peridinioid dinoflagellates were major components of the algal community. Among the algae *Pediastrum boryanum* is the most frequent. *Pediastrum* algae are common phytoplankton of lakes and ponds and therefore are of significance in palaeoenvironmental reconstruction (Zamaloa and Tell, 2005; Worobiec, E., 2011, 2014). Fossil *Pediastrum* in pollen slides has been widely used as a biological

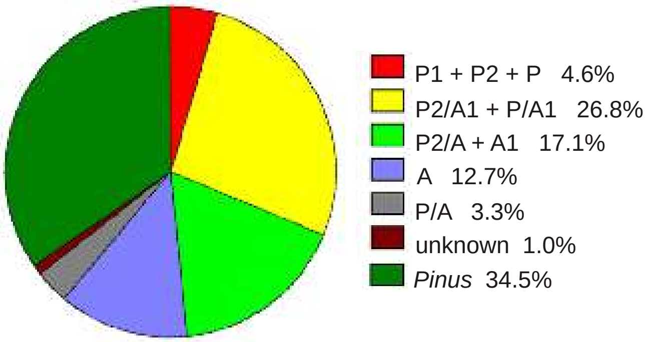

Fig. 4. Diagram showing proportions of sporomorphs of particular palaeofloristical elements in the samples from the KRAM-P 214 collection

P1 – "tropical", P2 – "subtropical", P – generally "palaeotropical", A1 – "warm-temperate", A – generally "arctotertiary", P/A – cosmopolitan; elements according to Stuchlik et al. (2001, 2002, 2009, 2014)

indicator for freshwater environments (open water surface) and a temperate or warm climate (Jankovská and Komárek, 2000). The extant *Pediastrum boryanum* generally occurs in mesotrophic to eutrophic waters. These algae typically are planktonic organisms, drifting and floating in ponds, marshes, pools and lakes (Komárek and Jankovská, 2001). Similarly, *Tetraedron* is a cosmopolitan planktonic alga occurring in fresh waters. *Botryococcus* is one of the most common palynomorphs of coccal algae in lagoonal and lacustrine sediments. Generally, these algae live in freshwater bogs, temporary pools, ponds and lakes as well as in brackish habitats (Batten and Grenfell, 1996).

Freshwater dinoflagellates can also be valuable in determining water conditions (Herrmann, 2010; Worobiec et al., 2013). The sparse presence of *Botryococcus* algae and the simultaneous abundance of freshwater dinoflagellates presumably indicate a depositional environment of alkaline water conditions (Herrmann, 2010). These alkaline conditions facilitated preservation of mollusc shells as well as bones and teeth of fishes and mammals. Alkaline waters are also indicated by the presence of lacustrine limestone deposits (Worobiec, 2003). The abundance of pyrite in the deposits studied suggests that organic matter degradation most probably occurred under predominantly anaerobic conditions (Casagrande, 1987). All this indicates that sedimentation took place in a fairly large and rather deep lake, that was the habitat of various fishes, including cyprinids (*Tinca* sp.) and esocids (*Esox sibiricus* and *Esox* sp.) (Kovalchuk et al., 2020).

The floating and rooted macrophytes included *Potamogeton* and *Stratiotes*. Numerous fossil seeds of *Stratiotes kaltennordheimensis* were found in the KRAM-P 211/214 flora (Worobiec, 2003). The presence of leaf-spines of plants with submerged leaves also points to the occurrence of such aquatic plants as Hydrocharitaceae or *Ceratophyllum*, commonly found in fresh waters. Along the margin of the lake *Typha* and/or *Sparganium*, as well as members of the Cyperaceae family grew. *Glyptostrobus*, *Taxodium*, *Nyssa*, *Osmunda* and presumably *Alnus* were components of swamp forests that may have overgrown the shoreline with a high groundwater level. In the KRAM-P 211/214 flora *Glyptostrobus europeus*, *Taxodium dubium*, *Nyssa ornithobroma* and *Osmunda parschlugiana* were noted (Worobiec, 2003). *Acer*, *Alnus*, *Carya*, *Fraxinus*, *Ulmus* as well as *Celtis*, *Liquidambar*, *Pterocarya*, *Salix*, *Zelkova* and Vitaceae may have grown in wet areas surrounding the lake. Fossil leaves of members of the above-noted genera (including *Acer integrilobum*, *Acer tricuspidatum*, *Acer* sp. div., cf. *Carya serrifolia*, *Liquidambar* sp. and *Ulmus* sp.) plus *Populus* sp. were found in the macroflora. Lianas were represented by *Smilax sagittifera* (Worobiec, 2003). Members of the families Cyrillaceae, Clethraceae, Ericaceae, Myricaceae (including *Myrica lignitum*) and possibly *Ilex* may be components of both swamp forests and shrub bogs.

Quercus (also evergreen oaks producing pollen of the fossil-species *Quercoidites henricii* and *Quercoidites microhenricii*), Engelhardioideae, Castaneoideae, *Betula*, Oleaceae, *Fagus*, Tilioideae and/or Brownlowioideae, Mastixiaceae, Fabaceae, *Ilex*, *Cercidiphyllum*, various conifers as well as *Corylopsis* and other Hamamelidaceae, *Alnus*, *Liriodendron*, Meliaceae, *Symplocos*, *Carpinus*, *Platanus*, *Platycarya*, Sapotaceae, as well as some Arecaceae and plants producing pollen of the fossil-species *Tricolporopollenites pseudocingulum*, *Tricolporopollenites leonensis*, and fossil-genera *Edmundipollis*, *Fususpollenites* and *Subtriporopollenites* were probably components of mesophytic forests located on elevated places, probably away from the lake. *Alnus julianiformis*, *Quercus rhenana*, *Quercus* sp. sect. *Cerris* vel sect. *Dentata* and *Tetraclinis salicornioides* were found among the macroremains (Worobiec, 2003). Some thermophilous taxa (such as members of the families Arecaceae, Mastixiaceae, Meliaceae, Sapotaceae, plus *Symplocos*) grew in these plant communities. The KRAM-P 211/214 flora is also distinguished by a high proportion of thermophilous evergreen taxa, including the representatives of the Lauraceae family, such as *Daphnogene polymorpha* and *Laurophyllum pseudoprinceps* (Worobiec, 2003).

Various species of the *Acer*, *Betula*, *Celtis*, *Fagus*, *Fraxinus*, *Quercus*, *Ulmus* and other genera could grow both in wetland and mesophytic plant communities (Worobiec and Worobiec, 2016). Similarly, *"Castanea" kubinyii*, a species dominating this fossil macroflora in terms of the number of specimens (118 specimens), may have grown in wetland forest or in mesophytic forest (Worobiec, 2003). Some pollen grains of Pinaceae (*Pinus*, *Picea*, *Abies*, and *Tsuga*) possibly come from plant communities growing on elevated terrains, farther from the water body. The most common bisaccate pollen grains (*Pinus* and *Picea*) come from trees producing pollen in large quantities that are well equipped for long-distance dispersal (Szczepanek et al., 2017). Therefore they are most probably over-represented in the palynoflora studied. Nevertheless, some pollen grains of Pinaceae and *Sciadopitys* could have originated from trees growing as an admixture in both mixed mesophytic or wetland forests close to the water body (Mosbrugger et al., 1994). For example, in the KRAM-P 211/214 flora two completely preserved fossil cones of *Pinus hampeana* as well as several needle fragments and seed wings of *Pinus* sp. div. were found (Worobiec, 2003). The parasitic *Arceuthobium* lived on conifers (probably *Pinus*) (cf. Ohngemach and Straka, 1982).

PALAEOCLIMATE

The macro- and microflora studied from the KRAM-P 211/214 collection are dominated by "palaeotropical/warm-temperate" taxa and contain thermophilous elements, such as fossil leaf taxa of conifers (*Glyptostrobus* and *Tetraclinis*) and angiosperms (*Daphnogene*, *Laurophyllum*, and *Smilax*) or pollen grains of Arecaceae, Mastixiaceae, Meliaceae and Sapotaceae. For example, in the palynoflora, sporomorphs of "palaeotropical" elements (P + P1 + P2) comprise 4.6% and "palaeotropical/warm-temperate" elements (P2/A1 + P/A1) make up 26.8% (Fig. 4). The composition of both leaf and spore-pollen floras indicate that at the time of sedimentation the climate was subtropical and humid, comparable to the Cfa climate type (warm temperate, fully humid with hot summer) in the Köppen-Geiger climate classification (Kottek et al., 2006). The estimated mean annual temperature (MAT) was 16.8–17.8°C (Appendix 1).

On a cuticle of fossil leaf of *Daphnogene polymorpha* (Lauraceae) from the KRAM-P 214 assemblage numerous sporodochia of the epiphyllous anamorphic fungus *Neomycoleptodiscus pertusus* (Dilcher) G. Worobiec (earlier known as *Callimothallus pertusus* Dilcher) were found (Worobiec, 2003; Worobiec et al., 2020: pl. 1, figs. 4–7). Besides *Neomycoleptodiscus pertusus*, another epiphyllous fungus, from the *Phragmothyrites* genus, was found. These phylloplane inhabitants are considered as a good proxy for past climate as extant relatives of these taxa show the highest abundance and taxonomic diversity in warm and humid subtropical and tropical regions (Worobiec and Worobiec, 2017). The thermophillous *Neomycoleptodiscus pertusus* corroborates the warm (subtropical) and probably humid climatic conditions of the early Miocene of Bełchatów (Worobiec et al., 2020).

Besides plant and fungal remains, in the lower Miocene deposits of the Bełchatów Mine, numerous animal fossils including molluscs, fish skeletons, and mammal bones and teeth (mammalian horizon "Bełchatów C", biozone MN 4) were found. In the lacustrine limestone horizon, lying below the leaf assemblage KRAM-P 211/214, numerous aquatic and terrestrial molluscs were found. Among them, with respect to palaeoecology, shells of the terrestrial snail *Pomatias bisulcatum* Zieten (Stworzewicz, 1995) are of specific interest. Modern representatives of the genus *Pomatias* (family Pomatiasidae) usually live in warmer parts of Europe (especially in the Mediterranean Basin), Turkey, Caucasus and the Canary Islands (Stworzewicz, 1993; Sümegi et al., 2018). The modern xerothermophilic species *Pomatias elegans* occurs from Western Europe to Turkey and North Africa, usually in woods, shrublands, rock rubble, maritime grasslands, but also along rivers and lake sides (Kerney et al., 1979; Crispino and Esu, 1995; AnimalBase Project Group, 2021). Like all modern Pomatiasidae, *Pomatias elegans* is restricted to calcareous soils (Rumsey, 1972) and the northern limit of its occurrence is connected with the 2°C January isotherm (AnimalBase Project Group, 2021). Considering this, it can be assumed that the fossil *Pomatias bisulcatum* from the Bełchatów Mine indicates the presence of Mesozoic calcareous rock slopes surrounding the ancient lake and corroborates the mild climatic conditions of the coldest season in the Bełchatów region in the early Miocene. This is in line with the results of research on mammalian remains found in the lower Miocene mammalian horizon "Bełchatów C", indicating a subtropical climate (Kowalski and Rzebik-Kowalska, 2002).

In deposits with the leaf assemblage KRAM-P 211/214, the remains of a fossil fruit-eating bat (Rzebik-Kowalska and Kowalski, 2001) and skeletons of freshwater fishes (Jerzmańska and Hałuszczak, 1986; Kovalchuk et al., 2020) were found. The fossil bat, found within deposits containing the lower Miocene plant macroremains from Bełchatów, represents the palaeotropical family Pteropodidae (Megachiroptera) and presumably is related to the recent species *Rousettus aegyptiacus* (Rzebik-Kowalska and Kowalski, 2001). This is the only member of the Pteropodidae family that has a large part of its distribution in the Palaearctic region (along the sea coasts of the Mediterranean, from Egypt to Lebanon, and the Middle East, from SW Turkey and Cyprus up to Pakistan and India; Benda et al., 2011) and the only member of Megachiroptera found in Europe (island of Kastellorizo, Dodecanese, Greece; Strachinis et al., 2018). The presence of this representative of the Pteropodidae in the lower Miocene of Bełchatów (the world's northernmost fossil site of Megachiroptera) indicates a warm, subtropical climate and the presence of forest (arboreal) vegetation, as *Rousettus aegyptiacus* completely depends on the availability of fresh parts of plants (mainly fruits, also leaves and pollen are eaten) during the entire year (Korine et al., 1996; Rzebik-Kowalska and Kowalski, 2001). Together with the remains of the Pteropodidae bat, skeletons of the freshwater fish *Esox sibiricus* Sytchevskaya were found (Kovalchuk et al., 2020). This species of fossil pike is considered thermophilic (Kovalchuk et al., 2020). From the above data it can be concluded that the early Miocene vegetation reflected in the KRAM-P 211/214 plant assemblage of the Bełchatów Mine developed in a subtropical and humid climate with mild winters. Evergreen or at least semi-evergreen forest communities grew along the ancient shores of the lake and on the slopes of the Mesozoic calcareus rocks surrounding the lake.

The results of palaeoecological studies of the lower Miocene plant association from Bełchatów are consistent with the data on the vegetation of the early Miocene of Central Europe. In the later Burdigalian, temperature increased and the succeeding warm time span persisted through the earlier part of the Serravallian and corresponds to the Mid-Miocene Climatic Optimum (MMCO, ~17–15 My), that is globally observed (Zachos et al., 2001; Mosbrugger et al., 2005). A similar trend is also observed in central and northwestern Europe (Bruch et al., 2007; Utescher et al., 2021). In northwest Germany, from the latest Burdigalian to the Serravallian, a MAT of 18.3°C was obtained from microfloras when averaging means obtained from all samples (Utescher et al., 2012). This value is close to the macroflora-based temperature ranges (17.8–19.6°C) from Germany (Utescher et al., 2012). Deposits of this warm phase, with a near-subtropical climate, are also known from the Polish Lowlands, particularly from its western part (Piwocki and Ziembińska-Tworzydło, 1997).

For comparison, in the late Serravalian or Tortonian (latest middle Miocene and late Miocene) leaf assemblages from the Bełchatów Lignite Mine (KRAM-P 218 and KRAM-P 225) yielded a MAT range estimated at 13.5–16.5°C (Worobiec and Szynkiewicz, 2016; Worobiec and Worobiec, 2019). Thermophillous plant macroremain taxa (such as *Daphnogene*, *Laurophyllum*, and *Tetraclinis*) in the Bełchatów deposits from this period mostly disappeared. The present-day climate of the Łódź and Piotrków Trybunalski area, adjacent to the Bełchatów lignite deposit, is characterized as "warm and temperate" (Cfb) and the mean annual temperature averages 9.0–9.1°C (Climate-Data, 2021).

CONCLUSIONS

In the palynological analysis of eight samples from the lower Miocene Bełchatów KRAM-P 211/214 collection of plant macroremains 118 fossil-species of sporomorphs (including 11 species of plant spores, 25 species of gymnosperm pollen, and 82 species of angiosperm pollen) were identified. Non-pollen palynomorphs (NPP) are represented mainly by freshwater algae and some fungal palynomorphs (spores and sporocarps). The palynological (spore-pollen and NPP) analysis indicates the presence of a moderately large and deep lake. Green algae (*Pediastrum*, *Tetraedron* and some *Botryococcus*) and freshwater peridinoid dinoflagellates were major components of the algal community. *Potamogeton*, *Stratiotes* and possibly Hydrocharitaceae or *Ceratophyllum* were among the macrophytes. Along the margin of the lake *Typha* and/or *Sparganium* as well as members of the Cyperaceae family grew.

The presence of lacustrine limestone deposits and the composition of the algal association indicate a deposition environment in alkaline water conditions. The abundance of pyrite in the deposits studied suggests that organic matter degradation most probably occurred under predominantly anaerobic conditions. Those conditions favoured the preservation of faunal remains (bones, teeth). The same lake was the source of previously identified freshwater fishes, molluscs, and mammals, including a Megachiroptera bat.

The lake was surrounded by wetland vegetation (including swamp forests with *Glyptostrobus*, *Taxodium*, *Nyssa* and *Osmunda*) and upland mesophytic forests, with a significant share of thermophilous plants (*Glyptostrobus*, *Tetraclinis*, *Daphnogene*, *Laurophyllum*, *Smilax* as well as members of the Arecaceae, Mastixiaceae, Meliaceae and Sapotaceae families). Evergreen or at least semi-evergreen forest communities grew along the ancient shores of the lake and on the slopes of the calcareus rocks surrounding the lake.

The results of the palynological analysis and previous studies of plant macroremains indicate that the climate was subtropical and humid. Similar conclusions about the climate can be drawn from the previously found epiphyllous anamorphic fungus *Neomycoleptodiscus pertusus*, the fossil pike *Esox sibiricus*, the terrestrial snail *Pomatias bisulcatum* and the Megachiroptera bat. The mean annual temperature (MAT), estimated from plant taxa, based on the Coexistence Approach (CA) method, was 16.8–17.8°C.

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APPENDIX 1

The mean annual temperature (MAT) reconstruction for the KRAM-P 214 flora, based on the Coexistence Approach (CA) method (Utescher et al., 2014). The nearest living relatives and their MAT ranges follow The Palaeoflora Database (Utescher and Mosbrugger, 2015)

Fossil taxa	Nearest Living Relatives	MAT range [°C]
Cathayapollis spp.	*Cathaya*	13.4–18.0
Keteleeriapollenites dubius	*Keteleeria*	12.8–23.2
Piceapollis sp.	*Picea*	–8.9–21.7
Aceripollenites spp.	*Acer*	–1.1–24.0
Alnipollenites spp.	*Alnus*	–13.3–27.4
Carpinipites carpinoides	*Carpinus*	0.0–25.8
Caryapollenites simplex	*Carya*	4.4–26.6
Celtipollenites sp.	*Celtis*	2.5–25.8
Cercidiphyllites minimireticulatus	*Cercidiphyllum*	2.2–**17.8**
Cornaceaepollis satzveyensis	*Mastixia*	15.7–27.8
Corylopsispollenites microreticulatus	*Corylopsis*	9.1–25.5
Cyrillaceaepollenites spp.	*Cyrilla*	13.6–23.9
	Clethra	7.4–27.7
Edmundipollis edmundi	*Diplopanax*	**16.8**–22.2
Faguspollenites spp.	*Fagus*	4.4–23.1
Fraxinipollis spp.	*Fraxinus*	0.0–24.0
Ilexpollenites spp.	*Ilex*	–0.4–27.7
Nyssapollenites sp.	*Nyssa*	4.4–23.9
Nyssoidites rodderensis	*Nyssa*	4.4–23.9
Periporopollenites stigmosus	*Liquidambar*	11.5–25.5
Platanipollis ipelensis	*Platanus*	6.6–27.4
Platycaryapollenites sp.	*Platycarya*	6.9–23.1
Polyatriopollenites stellatus	*Pterocarya*	3.9–24.2
Quercoidites henricii	*Quercus (evergreen)*	8.7–22.1
Quercopollenites spp.	*Quercus (deciduous)*	–1.4–27.0
Salixipollenites sp.	*Salix*	–17.0–27.7
Spinulaepollis arceuthobioides	*Arceuthobium*	–5.5–27.7
Symplocoipollenites spp.	*Symplocos*	4.5–27.7
Trivestibulopollenites betuloides	*Betula*	–15.0–25.8
Ulmipollenites spp.	*Ulmus*	–4.9–26.6
Vitispollenites tener	*Vitis*	0.0–27.4
Zelkovaepollenites sp.	*Zelkova*	6.2–21.9
*Osmunda parschlugiana**	*Osmunda regalis*	6.2–25.8
*Glyptostrobus europeus**	*Glyptostrobus lineatus*	9.1–25.0
*Taxodium dubium**	*Taxodium* sp.	13.3–25.0
*Tetraclinis salicornoides**	*Tetraclinis articulata*	15.6–19.9
*Acer tricuspidatum**	*Acer Sectio Rubra*	3.4–23.9
Acer sp.*	*Acer*	–1.1–24.0
*Alnus julianiformis**	*Alnus trabeculosa, Alnus japonica*	6.2–22.1
Liquidambar sp.*	*Liquidambar*	11.5–25.5
*Myrica lignitum**	*Myrica*	–8.9–28.1
*Nyssa ornithobroma**	*Nyssa sinensis*	15.3–23.9
Populus sp.*	*Populus*	–16–21.3
*Quercus rhenana**	*Quercus imbricaria, Quercus laurifolia*	3.3–25.0
*Pterocarya paradisiaca**	*Pterocarya fraxinifolia*	8.1–18.1
Ulmus sp.*	*Ulmus*	–4.9–26.6

* – macroremains; coexistence interval: 16.8–17.8°C; bordering taxa: 16.8–22.2°C – *Edmundipollis edmundi*; 2.2–17.8°C – *Cercidiphyllites minimireticulatus*; no outliers