Annales Societatis Geologorum Poloniae (2022), vol. 92: 201–218 doi: https://doi.org/10.14241/asgp.2022.07

PALAEOENVIRONMENT OF THE MIDDLE MIOCENE WETLANDS AT DRZEWCE, KONIN REGION, CENTRAL POLAND

Elżbieta WOROBIEC[1]*, Marek WIDERA[2] & Grzegorz WOROBIEC[1]

[1] *W. Szafer Institute of Botany, Polish Academy of Sciences, Lubicz 46, 31-512 Kraków, Poland, e-mails: e.worobiec@botany.pl, g.worobiec@botany.pl*

[2] *Institute of Geology, Adam Mickiewicz University, Krygowskiego 12, 61-680 Poznań, Poland, e-mail: widera@amu.edu.pl*

* *Corresponding author*

Worobiec, E., Widera, M. & Worobiec, G., 2022. Palaeoenvironment of the middle Miocene wetlands at Drzewce, Konin region, central Poland. *Annales Societatis Geologorum Poloniae*, 92: 201–218.

Abstract: Palynological analysis of the 1st mid-Polish lignite seam (MPLS-1) of the Drzewce deposit (Konin region, central Poland) was used as the data source for palaeoenvironmental and palaeoclimatic interpretations. Lignites of the 1st group developed in the middle Miocene, during and shortly after the last peak of the Mid-Miocene Climatic Optimum, over a large area of Poland, and they are the youngest of the main Neogene lignite seams in Poland. In the Konin region, these lignites have a relatively significant thickness (up to 20 m) and therefore they are (or were in the past) exploited in several open-pit mines. A total of 36 palynological samples from the 6.3-m-thick seam of the Drzewce opencast mine was studied in detail. Palynological analysis of the lignite seam indicates that the area was overgrown by palustrine wetland communities, similar in composition to modern pocosins. The most characteristic elements of them were shrubs in the Ericaceae family. The climate at that time was warm temperate and humid. The estimated mean annual temperature (MAT) for the lignite seam at Drzewce is 15.7–17.8 °C. Comparison with other palynofloras from the MPLS-1 shows that the climate during the formation of the group of seams was more or less homogenous across the entire Polish Lowlands. Sedimentological data and results of palynological studies (including NPPs) at Drzewce indicate that the palaeomires were relatively distant from the channels of the river system in the Konin Basin. The fossil fungal assemblage indicates dense vegetation on damp, swampy soils and the presence of small, shallow-water bodies, with a variable water level or even periodic reservoirs, existing only during the wet season or after floods. In small, flooded depressions, such as the pools in bogs, filamentous green algae occurred. The presence of zygospores of the desmids *Desmidiaceaesporites cosmarioformis* most probably indicates relatively nutrient-poor (ombrotrophic) conditions. Fluctuations in the frequency of individual plant taxa (including *Sequoia* and *Sciadopitys*) are likely to reflect changes in water level and trophic conditions.

Key words: lignite, palynology, non-pollen palynomorphs, palaeovegetation, palaeoclimate, fossil fungi, Neogene.

Manuscript received 6 March 2022, accepted 12 May 2022

INTRODUCTION

The 1st mid-Polish lignite seam group (MPLS-1) is the youngest among the main Neogene lignite seams in Poland. Lignites of this group of seams developed in the middle Miocene across a large area of Poland, excluding the Carpathian Mountains (Piwocki, 1998; Kasiński *et al.*, 2010; Kasiński and Słodkowska, 2016). The MPLS-1 lignites accumulated under continental conditions, mostly as low-lying mires under freshwater conditions, corresponding to the last peak of the Mid-Miocene Climatic Optimum and to the subsequent period, when the climate showed a cooling trend (Zachos *et al.*, 2001; Westerhold *et al.*, 2020; Widera *et al.*, 2021a). Recently, lignites of this group have been documented across an area of ca. 70,000 km^2 in western and central Poland. The lignite seam is also an important correlation horizon throughout much of the Polish Lowlands. In the vicinity of Konin and Turek, owing to the shallow depth of occurrence and considerable thickness (up to 20 m), these lignites are (or were in the past) exploited in several opencast mines (Kasiński *et al.*, 2010; Kasiński and Słodkowska, 2016; Widera, 2016).

The present contribution is the third in a series of new papers, dealing with the palynology of lignite seams of the MPLS-1 in the Konin-Adamów region. So far, lignite from the Adamów opencast in the Adamów deposit (Worobiec *et al.*, 2021, 2022b), and the Jóźwin IIB opencast in the Pątnów IV deposit (Słodkowska and Widera, 2021) has been studied in detail. The present study aims to reconstruct the plant communities and determine, which of them represent the sources of material for the formation of the Drzewce lignite deposit, using detailed palynological analysis. This research is a contribution to answering the question of whether palynological assemblages (and thus the plant communities) from different lignite lithotypes differ from each other. The authors also used spore-pollen analysis and non-pollen palynomorphs (NPPs; including freshwater algae and fungal microremains) as sources of data for palaeoenvironmental and palaeoclimatic interpretations.

GEOLOGICAL SETTING

The Drzewce lignite deposit is located 10–15 km east-northeast of the town of Konin in central Poland (Fig. 1). The studied section (52°16′13.2″N, 18°31′41.6″E) covers the easternmost part of a shallow, tectonic graben (up to 40 m deep), the fill of which includes the MPLS-1, mined for electricity production. The Cenozoic succession is underlain by marl and limy sandstones of Late Cretaceous age (Dadlez *et al.*, 2000; Widera, 2007).

Owing to the regional, tectonic uplift of central Poland during the Cenozoic, at least three main stratigraphic hiatuses can be identified in the study area. The result is that there are no deposits corresponding to the following time intervals: Paleocene–Eocene, late Oligocene and early Pliocene–early Pleistocene. Thus, the only Paleogene sediments are marine, glauconitic sands of early Oligocene age (Widera and Kita, 2007). In turn, the Neogene is entirely terrestrial and is divided into two lithostratigraphic formations, i.e., the lower Koźmin Formation and the upper Poznań Formation. The Koźmin Formation is composed of sands with coaly interbeds that were deposited during the early to middle Miocene. The Poznań Formation is divided lithologically into the lower Grey Clays Member and the upper Wielkopolska Member (Fig. 2).

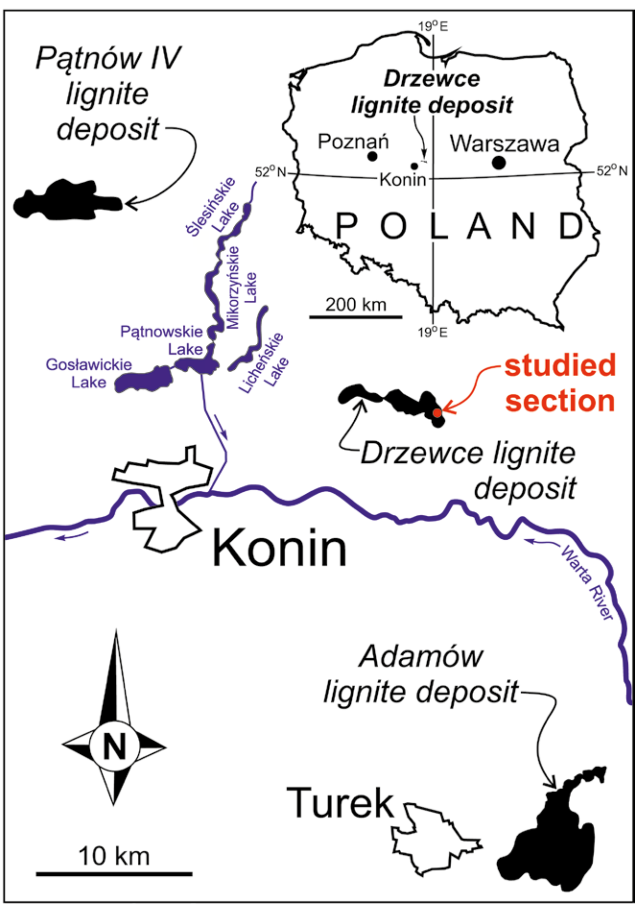

Fig. 1. Location of the studied section of the 1st mid-Polish lignite seam (MPLS-1) in the Drzewce deposit in central Poland.

In the study area, the Grey Clays Member consists almost entirely of the MPLS-1 (Piwocki and Ziembińska-Tworzydło, 1997). This lignite seam reaches a maximum thickness of 12.2 m (average 7.6 m) in the eastern part of the Drzewce deposit. However, the section examined in detail is only 6.3 m thick (in the altitude range of 66.4–72.7 m a.s.l.; Fig. 2). Most likely, the MPLS-1 accumulated during and shortly after the last peak of the Mid-Miocene Climatic Optimum (e.g., Słodkowska and Widera, 2021; Worobiec *et al.*, 2021), that is, in the time interval ~15–14.3 Ma (Widera *et al.*, 2021a, b). Moreover, lignite of this seam in the Drzewce deposit is characterized by an average ash yield of 12.6 wt.% (Chomiak, 2020), a low average sulphur content <1 wt.%, a low reflectance coefficient (*Ro*<0.3%) and carbon content (C^{daf}) in the range of 60–70% (Kwiecińska and Wagner, 2001). Hence, the studied MPLS-1 can be classified as humic and low-rank B or ortho-lignite (Widera, 2021).

The Wielkopolska Member of late mid-Miocene to early Pliocene age ends the Neogene succession in central Poland. It is composed mainly of clays and muds with palaeosol horizons, although sandy-muddy fillings of palaeochannels also occur among them. Therefore, these deposits are interpreted as representing an anastomosing (Widera *et al.*, 2017, 2019) or anastomosing-to-meandering river system of late Neogene age (Zieliński and Widera, 2020; Kędzior *et al.*, 2021). On top of the Neogene deposits are glaciogenic Quaternary sediments, which predominantly comprise fluvioglacial sands and gravels, locally interbedded with glacial tills (Fig. 2).

MATERIALS AND METHODS

A total of 36 palynological samples (Drz1–Drz36, numbered from bottom to top) was taken in the Drzewce opencast from the 6.3-m-thick lignite seam, belonging to the MPLS-1 (Fig. 2). All samples were taken from lignite, at 15–20 cm intervals. The lignite seam in the Drzewce deposit contains the following lignite lithotypes (Fig. 3): detritic (Drz1–Drz4), xylodetritic (Drz5–Drz22 and Drz25–Drz36) and weathered (Drz23–Drz24). The samples were processed in the Laboratory of the W. Szafer Institute of Botany, Polish Academy of Sciences, Kraków, using successively hydrochloric acid, potassium hydroxide and hydrofluoric acid to remove silicates (Moore *et al.*, 1991; details in Worobiec *et al.*, 2021). Additionally, the residuum was sieved at 5 μm on a nylon mesh. From each sample 2–4 microscope slides were made, using glycerine jelly as a mounting medium. In all of the slides, pollen grains, spores of plants and

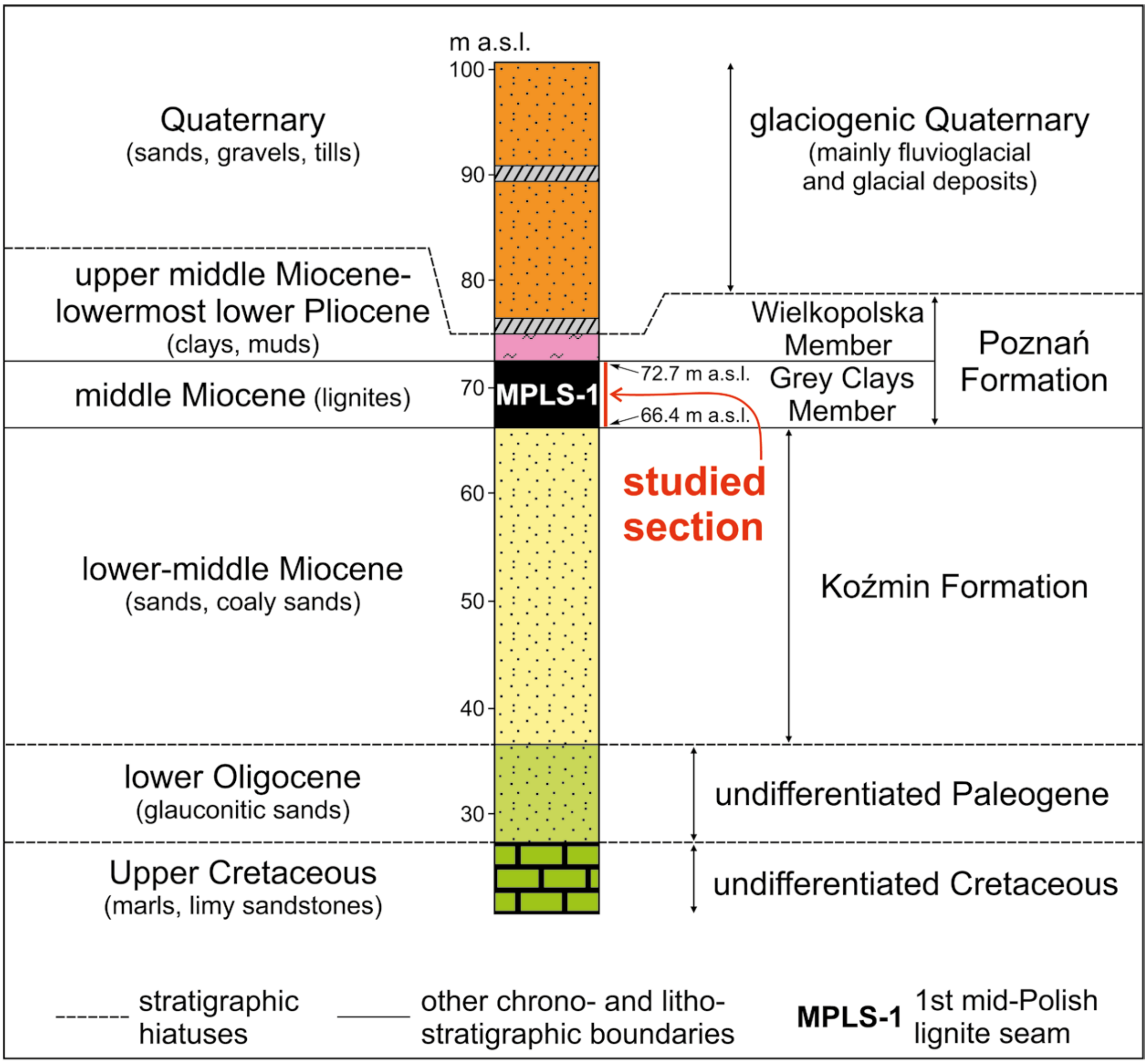

Fig. 2. Simplified lithostratigraphy of the Cenozoic succession in the area of the Drzewce lignite deposit with the exact, altitudinal position of the studied section of the 1st mid-Polish lignite seam (MPLS-1). For location of the studied section see Figure 1.

non-pollen palynomorphs (NPPs), such as algal remains and fungal remains, were studied. Microphotographs of selected palynomorphs (Figs 3, 4) were taken, using a Nikon Eclipse E400 microscope fitted with a Canon A640 digital camera.

The sporomorph taxa identified were classified on the basis of the *Atlas of Pollen and Spores of the Polish Neogene* (Stuchlik *et al.*, 2001, 2002, 2009, 2014). Data from the palynological spectra were used to construct a simplified, palynological diagram (Fig. 5). In the diagram, the percentage shares of the pollen and spore taxa were calculated from the total sum of pollen grains and spores; the proportion of non-pollen palynomorphs was computed separately in relation to the total sum using the POLPAL computer programme (Nalepka and Walanus, 2003). In the material studied, the following palaeofloristical 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); according to the classification used in Stuchlik *et al.* (2001, 2002, 2009, 2014).

The mean annual temperature (MAT) reconstruction in this work is based on the Coexistence Approach (CA) method (Utescher *et al.*, 2014; Prader *et al.*, 2017). For the CA method, the authors selected as many taxa as it was possible excluding fossil taxa with unknown botanical affinity, related to families, aquatic taxa, etc. The nearest living relatives and their MAT ranges follow *The Palaeoflora Database* (Utescher and Mosbrugger, 2015), supplemented by other available climatic data (Fang *et al.*, 2011). The fundamental background for the CA method is the nearest living relative (NLR) concept, which implies that a given fossil taxon lived under climatic conditions, similar to those of its living representative. The CA uses only the presence or absence of the taxa, without considering their relative frequency. The nearest living relatives (NLR) provide the information necessary to find a climatic distribution interval, where all plants could live (Coexistence Interval). Considering the limitations of the CA method (Grimm and Denk, 2012; Grimm *et al.*, 2016; Grimm and Potts, 2016), the present authors only estimated the MAT ranges for the whole palynoflora.

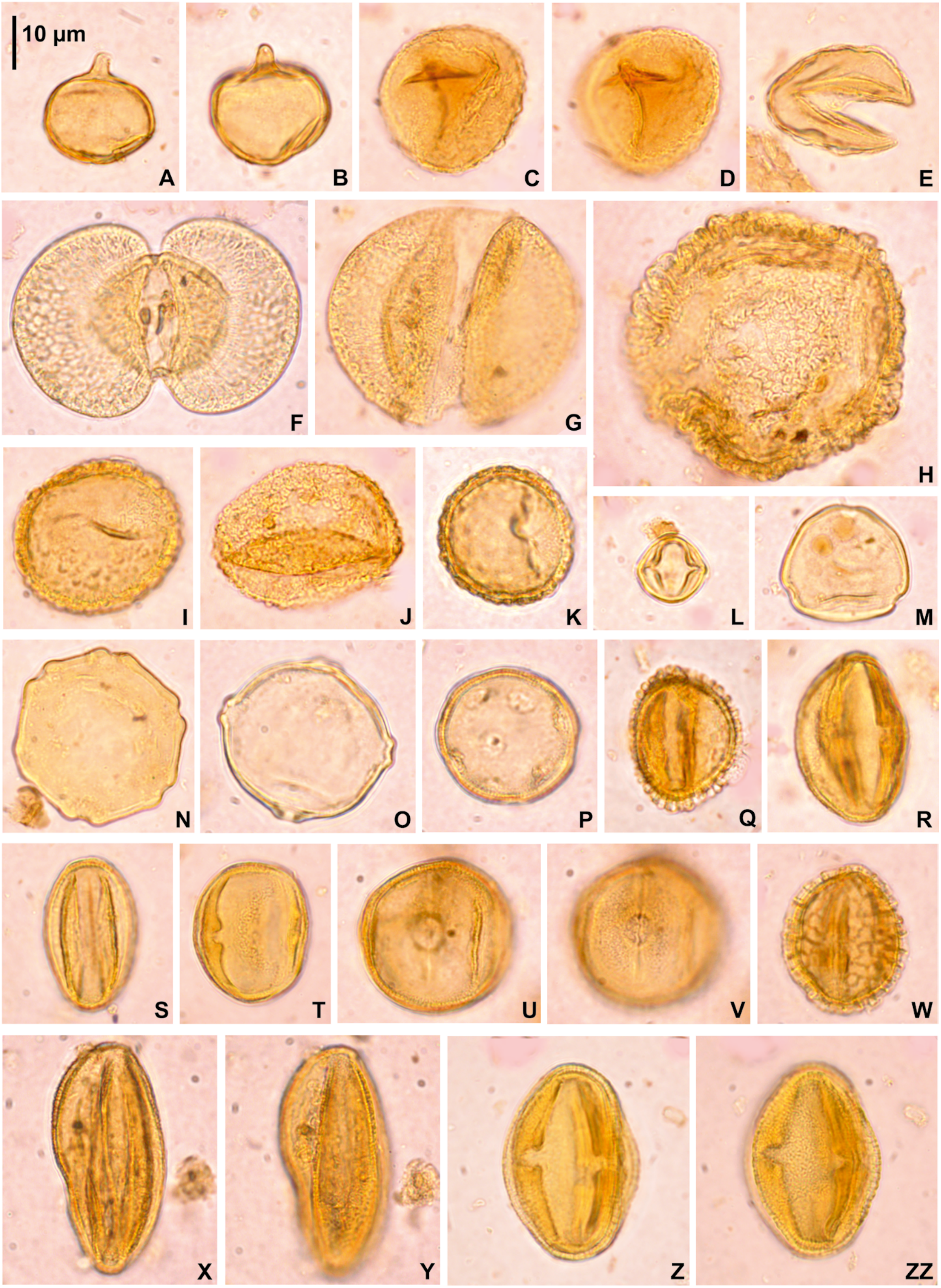

Fig. 3.

RESULTS OF THE PALYNOLOGICAL STUDIES

All studied samples yielded well-preserved pollen grains and spores, suitable for detailed palynological analysis (Figs 3, 4). In all samples, at least 500 pollen grains and spores as well as all co-occurring non-pollen palynomorphs were identified. A total of 114 fossil-species (including 12 species of plant spores, 25 species of gymnosperm pollen, and 77 species of angiosperm pollen) were identified (Tab. 1). Pollen grains of gymnosperms are most frequent in all samples and among them grains of Cupressaceae with distinct papillae (Fig. 3A–D; usually related to *Sequoia/Sequoiadendron/Metasequoia*), *Pinus* and *Sciadopitys* are the most common (Fig. 5). In addition, *Cathaya*, other Cupressaceae (Fig. 3E; usually related to *Taxodium/Glyptostrobus*), *Tsuga*, *Abies*, *Picea*, *Keteleeria*, and single pollen grains of *Cedrus* were present. Bouchal and Denk (2020) found that it is difficult, change to: or even impossible to distinguish the ecologically distinct genera of Taxodioideae and Sequoioideae on the basis of pollen morphology, because in the group of taxa with long papillae, *Cryptomeria*, *Metasequoia*, *Sequoia*, *Sequiodendron*, *Glyptostrobus*, and *Taxodium* are remarkably similar. Therefore, when interpreting them, the composition of the entire palynoflora should be taken into account (see discussion).

Table 1

Spores and pollen grains recorded in deposits at Drzewce. Taxonomy, botanical affinity and palaeofloristical elements according to Stuchlik *et al.* (2001, 2002, 2009, 2014). The following palaeofloristical elements have been distinguished: palaeotropical (P), including tropical (P1) and subtropical (P2), and "arctotertiary" (A), including warm-temperate (A1) and temperate (A2), as well as cosmopolitan (P/A).

Fossil taxa	Botanical affinity	Element
Spores of plants:		
Baculatisporites primarius (Wolff) Thomson et Pflug	Osmundaceae: *Osmunda*	P/A
Baculatisporites sp.	Osmundaceae: *Osmunda*	P/A
Distancoraesporis sp.	Sphagnaceae: *Sphagnum*	P/A
Laevigatosporites haardti (Potonié et Venitz) Thomson et Pflug	Polypodiaceae, Davalliaceae, and other ferns	P/A
Laevigatosporites sp.	Polypodiaceae, Davalliaceae, and other ferns	P/A
Leiotriletes sp.	Lygodiaceae and other ferns	P
Retitriletes sp.	Lycopodiaceae: *Lycopodium*	A
Stereisporites minor (Raatz) Krutzsch	Sphagnaceae: *Sphagnum*	P/A
Stereisporites stereoides (Potonié et Venitz) Thomson et Pflug	Sphagnaceae: *Sphagnum*	P/A
Stereisporites stictus (Wolff) Krutzsch	Sphagnaceae: *Sphagnum*	P/A
Stereisporites sp.	Sphagnaceae: *Sphagnum*	P/A
Verrucatosporites sp.	Davalliaceae, Polypodiaceae, and other ferns	P/A
Pollen of gymnosperms:		
Abiespollenites sp.	Pinaceae: *Abies*	A
Cathayapollis ponsii (Sivak) Ziembińska-Tworzydło	Pinaceae: *Cathaya*	A1
Cathayapollis pulaensis (Nagy) Ziembińska-Tworzydło	Pinaceae: *Cathaya*	A1
Cathayapollis vancampoae (Sivak) Ziembińska-Tworzydło	Pinaceae: *Cathaya*	A1
Cathayapollis sp.	Pinaceae: *Cathaya*	A1

Fig. 3. Pollen grains from Drzewce. Botanical affinity in brackets. One scale for all photographs. **A.** *Sequoiapollenites rotundus* (Cupressaceae), sample Drz33. **B.** *Sequoiapollenites rotundus* (Cupressaceae), sample Drz12. **C, D.** *Sequoiapollenites rugulus* (Cupressaceae), sample Drz14 – same specimen, various foci. **E.** *Inaperturopollenites* sp./*Cupressacites* sp. (Cupressaceae), sample Drz32. **F.** *Cathayapollis pulaensis* (*Cathaya*), sample Drz15. **G.** *Cathayapollis ponsii* (*Cathaya*), sample Drz31. **H.** *Zonalapollenites* sp. (*Tsuga*), sample Drz15. **I.** *Sciadopityspollenites* sp. (*Sciadopitys*), sample Drz17. **J.** *Sciadopityspollenites miniverrucatus* (*Sciadopitys*), sample Drz23. **K.** *Sciadopityspollenites crassus* (*Sciadopitys*), sample Drz14. **L.** *Cyrillaceaepollenites exactus* (Cyrillaceae, Clethraceae), sample Drz18. **M.** *Momipites punctatus* (*Engelhardia*, *Alfaroa*, *Oreomunnea*), sample Drz30. **N.** *Polyatriopollenites stellatus* (*Pterocarya*), sample Drz24. **O.** *Carpinipites carpinoides* (*Carpinus*), sample Drz15. **P.** *Periporopollenites stigmosus* (*Liquidambar*), sample Drz7. **Q.** *Ilexpollenites iliacus* (*Ilex*), sample Drz28. **R.** *Tricolporopollenites pseudocingulum* (Fagaceae?, Styracaceae?), sample Drz15. **S.** *Quercopollenites asper* (*Quercus*), sample Drz17. **T.** *Nyssapollenites accessorius* (*Nyssa*), sample Drz28. **U, V.** *Faguspollenites* sp. (*Fagus*), sample Drz5 – same specimen, various foci. **W.** *Caprifoliipites viburnoides* (*Viburnum*), sample Drz24. **X, Y.** *Aceripollenites reticulatus* (*Acer*), sample Drz15 – same specimen, various foci. **Z, ZZ.** *Edmundipollis vitiosus* (Araliaceae), sample Drz23 – same specimen, various foci.

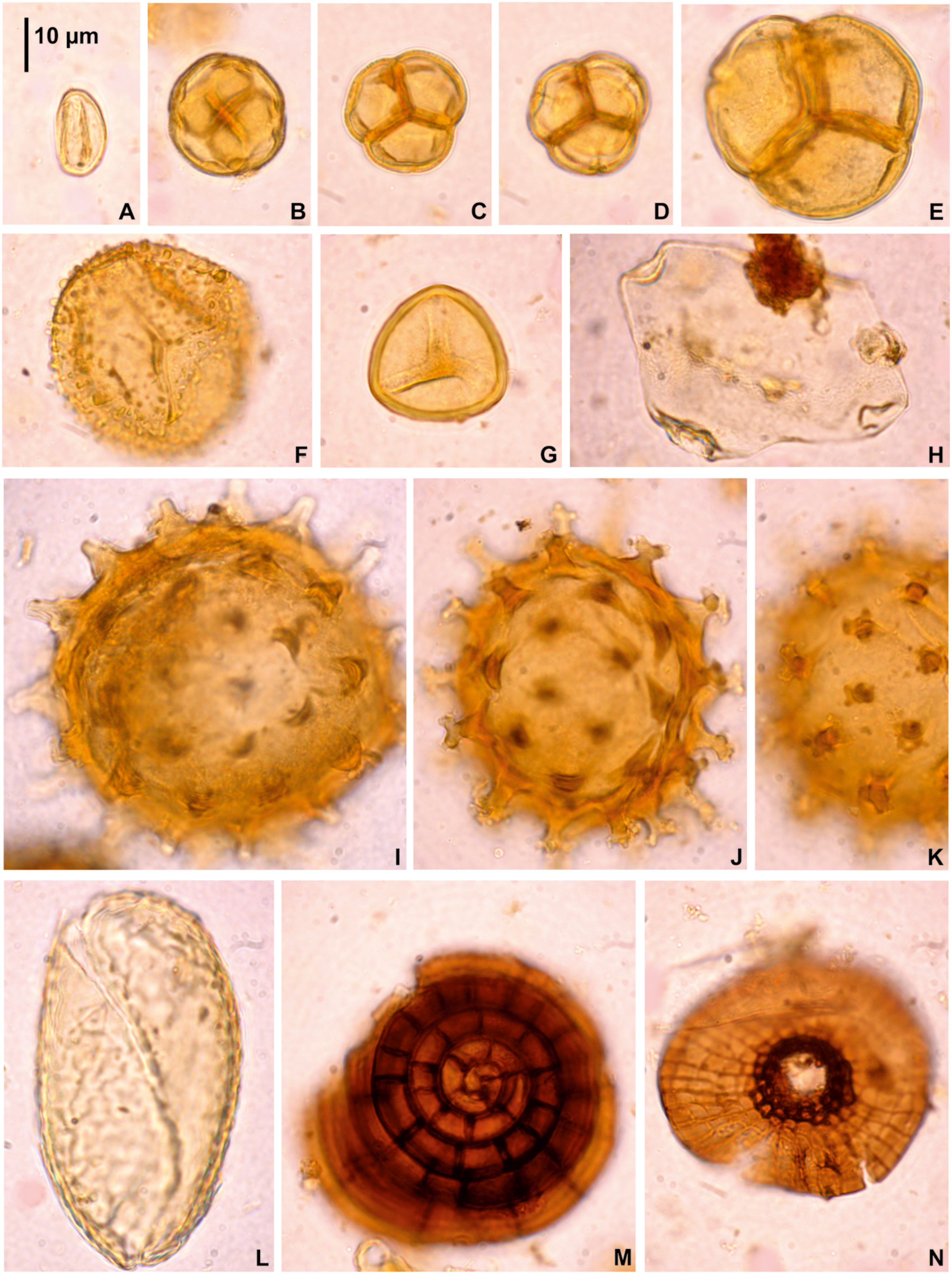

Fig. 4.

Fossil taxa	Botanical affinity	Element
Cedripites sp.	Pinaceae: *Cedrus*	A1
Cupressacites sp.	Cupressaceae	A1
Inaperturopollenites concedipites (Wodehouse) Krutzsch	Cupressaceae: *Taxodium*, *Glyptostrobus*	P2/A1
Inaperturopollenites dubius (Potonié et Venitz) Thomson et Pflug	Cupressaceae: *Taxodium*, *Glyptostrobus*	P2/A1
Keteleeriapollenites dubius (Khlonova) Słodkowska	Pinaceae: *Keteleeria*	A1
Piceapollis sp.	Pinaceae: *Picea*	A
Pinuspollenites labdacus (Potonié) Raatz	Pinaceae: *Pinus sylvestris* type	A
Pinuspollenites sp.	Pinaceae: *Pinus*	A
Sciadopityspollenites crassus Krutzsch	Sciadopityaceae: *Sciadopitys*	A1
Sciadopityspollenites miniverrucatus Kohlman-Adamska	Sciadopityaceae: *Sciadopitys*	A1
Sciadopityspollenites serratus (Potonié et Venitz) Raatz	Sciadopityaceae: *Sciadopitys*	A1
Sciadopityspollenites verticillatiformis (Zauer) Krutzsch	Sciadopityaceae: *Sciadopitys*	A1
Sciadopityspollenites sp.	Sciadopityaceae: *Sciadopitys*	A1
Sequoiapollenites gracilis Krutzsch	Cupressaceae: *Sequoia*, *Sequoiadendron*, *Metasequoia*, *Cryptomeria*	A1
Sequoiapollenites polyformosus Thiergart	Cupressaceae: *Sequoia*, *Sequoiadendron*, *Metasequoia*	A1
Sequoiapollenites rotundus Krutzsch	Cupressaceae: *Sequoia*, *Sequoiadendron*, *Metasequoia*	A1
Sequoiapollenites rugulus Krutzsch	Cupressaceae: *Sequoia*, *Sequoiadendron*, *Metasequoia*	A1
Sequoiapollenites sp.	Cupressaceae: *Sequoia*, *Sequoiadendron*, *Metasequoia*, *Cryptomeria*	A1
Zonalapollenites verrucatus Krutzsch	Pinaceae: *Tsuga*	A
Zonalapollenites sp.	Pinaceae: *Tsuga*	A
Pollen of angiosperms:		
Aceripollenites microrugulatus Thiele-Pfeiffer	Sapindaceae: *Acer*	A
Aceripollenites reticulatus Nagy	Sapindaceae: *Acer*	A
Aceripollenites sp.	Sapindaceae: *Acer*	A
Alnipollenites verus Potonié	Betulaceae: *Alnus*	P2/A
Araliaceoipollenites amplus Słodkowska	Araliaceae	P/A1
Araliaceoipollenites euphorii (Potonié) Potonié	Araliaceae	P/A1
Arecipites butomoides Krutzsch	Butomaceae, Araceae, Arecaceae	P/A
Arecipites sp.	Amaryllidaceae, Araceae, Arecaceae, Butomaceae	P/A
Caprifoliipites viburnoides (Gruas-Cavagnetto) Kohlman-Adamska	Adoxaceae: *Viburnum*	P/A1
Caprifoliipites sp.	Adoxaceae: *Sambucus*, *Viburnum*	P2/A1
Carpinipites carpinoides (Pflug) Nagy	Betulaceae: *Carpinus*	P2/A1
Caryapollenites simplex (Potonié) Raatz	Juglandaceae: *Carya*	A1
Celtipollenites sp.	Ulmaceae: *Celtis*	P/A1
Chenopodipollis sp.	Amaranthaceae (incl. Chenopodiaceae)	P/A
Cornaceaepollis satzveyensis (Pflug) Ziembińska-Tworzydło	Mastixiaceae: *Mastixia*	P1
Cornaceaepollis sp.	Cornaceae: *Cornus*	P/A
Corylopsispollenites microreticulatus E.Worobiec	Hamamelidaceae: *Corylopsis*	A1
Cupuliferoipollenites oviformis (Potonié) Potonié	Fagaceae: *Castanea*, *Castanopsis*, *Lithocarpus*	P2/A1
Cupuliferoipollenites pusillus (Potonié) Potonié	Fagaceae: *Castanea*, *Castanopsis*, *Lithocarpus*	P2/A1
Cyperaceaepollis neogenicus Krutzsch	Cyperaceae	P/A

Fig. 4. Pollen grains, spores, freshwater algae, and fungi from Drzewce. Botanical affinity in brackets. One scale for all photographs. **A.** *Tricolporopollenites fallax* (Fabaceae), sample Drz16. **B.** *Ericipites costatus* (Ericaceae), sample Drz24. **C, D.** *Ericipites callidus* (Ericaceae), sample Drz6 – same specimen, various foci. **E.** *Ericipites ericius* (Ericaceae), sample Drz5. **F.** *Baculatisporites primarius* (*Osmunda*), sample Drz34. **G.** *Stereisporites stictus* (*Sphagnum*), sample Drz5. **H.** *Tetrapidites* cf. *rhomboides* (*Mougeotia*), sample Drz15. **I.** *Desmidiaceaesporites cosmarioformis* (*Cosmarium*, *Euastrum*, *Staurastrum*, *Xanthidium*), sample Drz7. **J, K.** *Desmidiaceaesporites cosmarioformis* (*Cosmarium*, *Euastrum*, *Staurastrum*, *Xanthidium*), sample Drz12 – same specimen, various foci, K shows fragment of the surface. **L.** *Ovoidites ligneolus* (*Spirogyra*), sample Drz32. **M.** Helicosporous fungus (*Helicodendron*, *Helicoon*), sample Drz3. **N.** *Trichothyrites* sp., sample Drz36.

Fossil taxa	Botanical affinity	Element
Cyrillaceaepollenites brühlensis (Thomson) Durska	Cyrillaceae, Clethraceae	P
Cyrillaceaepollenites exactus (Potonié) Potonié	Cyrillaceae, Clethraceae	P
Cyrillaceaepollenites megaexactus (Potonié) Potonié	Cyrillaceae, Clethraceae	P
Edmundipollis vitiosus (Mamczar) Słodkowska et Ziembińska-Tworzydło	Araliaceae	P/A1
Edmundipollis sp.	Cornaceae, Mastixiaceae, Araliaceae	P/A
Ericipites callidus (Potonié) Krutzsch	Ericaceae	A
Ericipites costatus Grabowska	Ericaceae	A
Ericipites ericius (Potonié) Potonié	Ericaceae	A
Ericipites sp.	Ericaceae	A
Eucommiapollis minor Menke	Eucommiaceae: *Eucommia*	A1
Faguspollenites verus Raatz	Fagaceae: *Fagus*	A
Faguspollenites sp.	Fagaceae: *Fagus*	A
Fraxinipollis oblatus Słodkowska	Oleaceae: *Fraxinus*	A
Fraxinipollis sinuosimuratus (Trevisan) Słodkowska	Oleaceae: *Fraxinus*	A
Graminidites sp.	Poaceae: Pooideae	P/A
Ilexpollenites iliacus (Potonié) Thiergart	Aquifoliaceae: *Ilex*	P/A1
Ilexpollenites margaritatus (Potonié) Thiergart	Aquifoliaceae: *Ilex*	P2
Intratriporopollenites sp.	Malvaceae: Brownlowioideae, Tilioideae	P/A
Iteapollis angustiporatus (Schneider) Ziembińska-Tworzydło	Iteaceae: *Itea*	P
Juglanspollenites verus Raatz	Juglandaceae: *Juglans*	A1
Magnoliaepollenites sp.	Magnoliaceae: *Magnolia*	P/A1
Momipites punctatus (Potonié) Nagy	Juglandaceae: *Engelhardia*, *Alfaroa*, *Oreomunnea*	P2
Myricipites coryphaeus (Potonié) Potonié	Myricaceae	P2/A1
Myricipites sp.	Myricaceae	P2/A
Nymphaeacidites typicus Sah	Nymphaeaceae: *Nymphaea*	P/A
Nyssapollenites accessorius (Potonié) Potonié	Nyssaceae: *Nyssa*	A1
Nyssapollenites analepticus (Potonié et Venitz) Planderová	Nyssaceae: *Nyssa*	P/A1
Nyssapollenites contortus (Pflug et Thomson) Nagy	Nyssaceae: *Nyssa*	P2/A1
Nyssapollenites pseudocruciatus (Potonié) Thiergart	Nyssaceae: *Nyssa*	P/A1
Nyssapollenites sp.	Nyssaceae: *Nyssa*	P/A1
Nyssoidites rodderensis Thiergart	Nyssaceae: *Nyssa*	P/A1
Oleoidearumpollenites sp.	Oleaceae	P2/A1
Ostryoipollenites rhenanus (Thomson) Potonié	Betulaceae: *Ostrya*	A1
Parthenopollenites marcodurensis (Pflug et Thomson) Traverse	Vitaceae	P/A1
Periporopollenites stigmosus (Potonié) Thomson et Pflug	Altingiaceae: *Liquidambar*	A1
Polyatriopollenites stellatus (Potonié) Pflug	Juglandaceae: *Pterocarya*	A1
Quercoidites henricii (Potonié) Potonié, Thomson et Thiergart	Fagaceae: *Quercus*	P2/A1
Quercopollenites asper (Pflug et Thomson) Kohlman-Adamska et Ziembińska-Tworzydło	Fagaceae: *Quercus*	A1
Quercopollenites rubroides Kohlman-Adamska et Ziembińska-Tworzydło	Fagaceae: *Quercus*	A1
Quercopollenites sculptus Kohlman-Adamska et Ziembińska-Tworzydło	Fagaceae: *Quercus*	A1
Quercopollenites sp.	Fagaceae: *Quercus*	A1
Rhamnaceaepollenites triquetrus Thiele-Pfeiffer	Rhamnaceae	P2/A
Salixipollenites densibaculatus Nagy	Salicaceae: *Salix*	A
Salixipollenites sp.	Salicaceae: *Salix*	A
Sparganiaceaepollenites sp.	Sparganiaceae, Typhaceae	P/A
Spinulaepollis arceuthobioides Krutzsch	Santalaceae: *Arceuthobium*	P2/A1
Symplocoipollenites vestibulum (Potonié) Potonié	Symplocaceae: *Symplocos*	P

Fossil taxa	Botanical affinity	Element
Tricolporopollenites fallax (Potonié) Krutzsch	Fabaceae	P/A
Tricolporopollenites liblarensis (Thomson) Hochuli	Fabaceae	P/A
Tricolporopollenites pseudocingulum (Potonié) Thomson et Pflug	Fagaceae?, Styracaceae?	P/A1
Tricolporopollenitws rosacearum Durska	Rosaceae	A
Trivestibulopollenites betuloides Pflug	Betulaceae: *Betula*	A
Ulmipollenites undulosus Wolff	Ulmaceae: *Ulmus*	A2
Ulmipollenites sp.	Ulmaceae: *Ulmus*	A2
Vitispollenites tener Thiele-Pfeiffer	Vitaceae: *Vitis*	P2/A1
Zelkovaepollenites potoniei Nagy	Ulmaceae: *Zelkova*	A1
Zelkovaepollenites sp.	Ulmaceae: *Zelkova*	A1

Among the pollen grains of angiosperms, the most common are Ericaceae, *Nyssa* (mainly fossil-genus *Nyssapollenites*), *Fagus*, *Quercus* (*Quercoidites henricii* and *Quercopollenites*), fossil-species *Tricolporopollenites pseudocingulum*, Cyrillaceae/Clethraceae, *Alnus*, and *Ilex*. Pollen grains of *Acer*, *Arceuthobium*, *Betula*, *Carpinus*, *Carya*, *Castanea/Castanopsis/Lithocarpus*, *Celtis*, *Myrica*, Fabaceae (*Tricolporopollenites fallax* and *T. liblarensis*), *Fraxinus*, *Liquidambar*, Mastixiaceae (*Cornaceaepollis satzveyensis*), Oleaceae, *Pterocarya*, *Salix*, *Ulmus*, and *Vitis*, are recorded regularly. In addition, single pollen grains of Adoxaceae, Araliaceae, *Cercidiphyllum*, *Cornus*, *Diospyros*, fossil-genus *Edmundipollis*, *Eucommia*, Hamamelidaceae, Rhamnaceae, Tilioideae, *Zelkova*, and a few others are encountered. Herbs are represented only by the pollen of Cyperaceae and Sparganiaceae/Typhaceae as well as single specimens of Chenopodiaceae, *Nymphaea*, Poaceae, and most probably *Butomus*.

Spores of ferns, including fossil-genera *Laevigatosporites*, *Leiotriletes*, and *Verrucatosporites* as well as *Osmunda* (fossil-genus *Baculatisporites*), were encountered regularly, but in low quantities. Similarly, the spores of *Sphagnum* occur in most samples. Among non-pollen palynomorphs are 14 fossil-species of freshwater algae (Tab. 2) and the micro-remains of fungi. The fossil-species *Desmidiaceaesporites cosmarioformis*, most probably related to desmids, is the most common and is present in almost all samples (Fig. 5). Single zygospores of Zygnemataceae, related to the modern genera *Mougeotia* (fossil-genus *Tetrapidites*), *Spirogyra* (*Ovoidites*), and *Zygnema* (*Stigmozygodites*) were also encountered regularly. Fungal spores occur in all samples, reaching up to 15% of the total sum of palynomorphs. In most samples, other fungal microfossils, including sporocarps of epiphyllous fungi with the fossil-genera *Plochmopeltinites* and *Trichothyrites*, plus remains of helicosporous and rhizosphere fungi, were found as well.

Pollen grains and spores representing warm-temperate and temperate taxa predominate (Tab. 1). Palaeotropical elements are represented by *Cyrillaceaepollenites* spp., *Ilexpollenites margaritatus* as well as single specimens of *Leiotriletes* sp., *Cornaceaepollis satzveyensis*, *Iteapollis angustiporatus*, *Momipites punctatus*, and *Symplocoipollenites vestibulum*, whereas the representation of the palaeotropical/warm-temperate taxa is more significant. Proportions of taxa representing various palaeofloristical elements are similar in the whole diagram.

DISCUSSION

Plant communities and palaeoenvironment deduced from pollen, spores and algae

The composition of the palynoassemblage from Drzewce shows the presence of wetland and mesophytic vegetation at the time of sedimentation. Many of the taxa recorded, for example members of the Ericaceae, Cyrillaceae and Clethraceae families as well as *Ilex* and *Myrica*, most probably were components of shrub bog communities, most similar to modern pocosins. Nowadays, these palustrine wetland ecosystems occur on the southeastern Coastal Plain of the USA (Richardson, 2003) and the most characteristic elements of them are Ericaceae (members of the *Chamaedaphne*, *Gaylussacia*, *Kalmia*, *Lyonia*, *Vaccinium*, and *Zenobia* genera), *Clethra alnifolia*, *Cyrilla racemiflora*, *llex coriacea*, *llex glabra*, plus *Aronia arbutifolia*, *Arundinaria tecta*, *Chamaecyparis thyoides*, *Gordonia lasianthus*, *Magnolia virginiana*, *Persea palustris*, *Smilax laurifolia*, *Toxicodendron vernix*, and others. Modern pocosins consist of a dense shrub layer, usually less than 1.5 m tall (up to 4–6 m). In openings, *Carex striata*, ferns *Woodwardia virginica*, *Sphagnum* and others occur. Small, flooded depressions, such as pools in bogs, could be a habitat for algae from the Zygnemataceae family, including the *Spirogyra*, *Mougeotia*, and *Zygnema* genera. These filamentous green algae are common in stagnant or slowly flowing waters. They may also occur near the margins of lakes and in moist soils or bogs (Kadłubowska, 1984). Zygnemataceae produce resting cells (zygospores) that enable them to survive through unfavorable growth conditions (e.g., desiccation) without damage to the living content of the dormant spores. In these algae, zygospore formation occurs mostly in shallow water, exposed to direct solar radiation, at least during the warm season (van Geel, 1976; van Geel and Grenfell, 1996; Worobiec, 2011, 2014a). The presence of the fossil-species *Desmidiaceaesporites cosmarioformis* (Fig. 4I–K), most probably related to the zygospores of desmids, such as *Cosmarium*, *Euastrum*, *Staurastrum* or *Xanthidium*

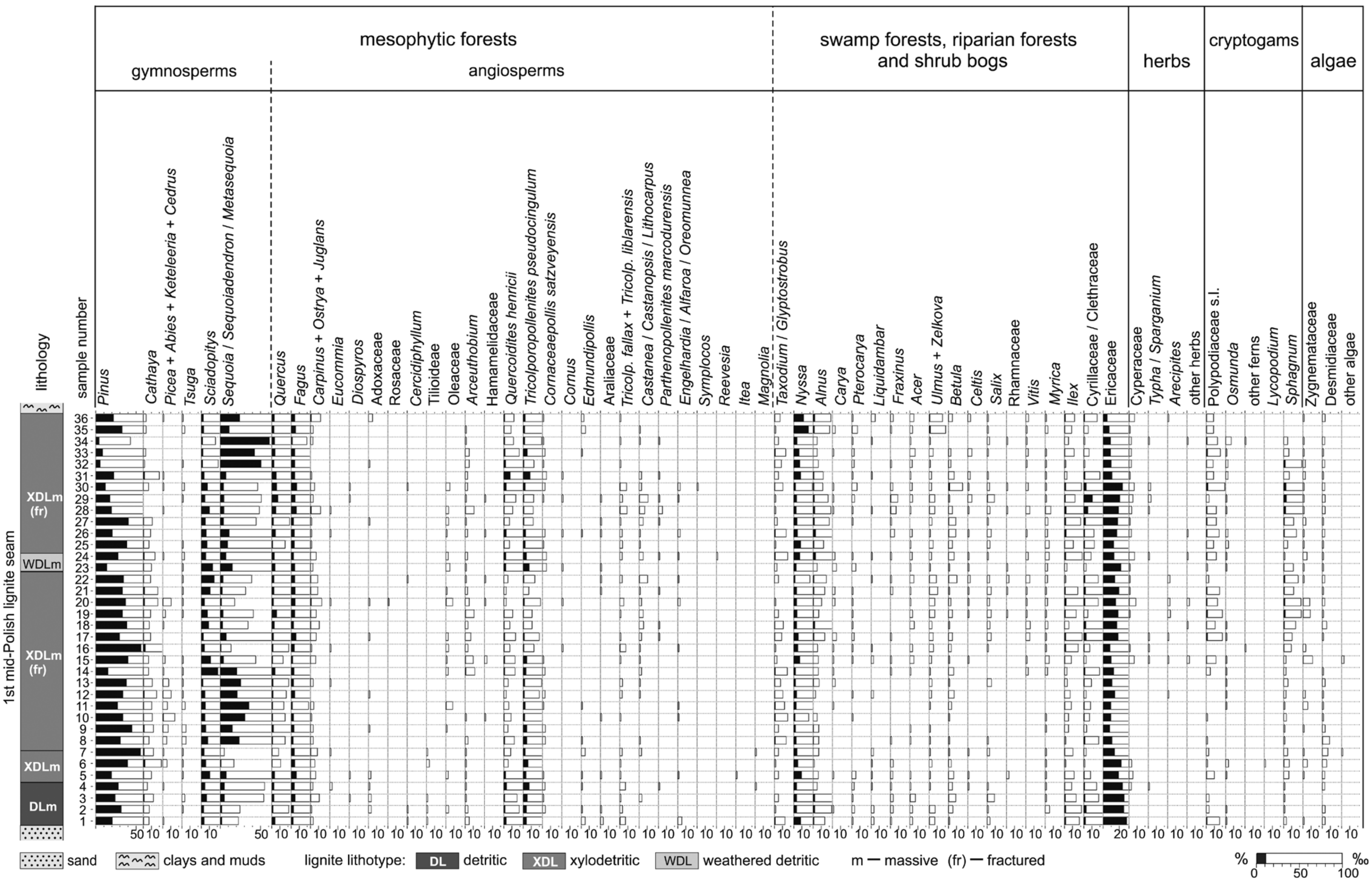

Fig. 5. Simplified percentage diagram of pollen and spores of plants as well as freshwater algae from Drzewce. Numbers in the bottom of the diagram show ranges of percentages for each taxon separately. Black bars show percentages (%), white bars show percentages ×10 (‰).

(Hunger, 1953), indicates relatively nutrient-poor waters (cf. Coesel and Meesters, 2007). This confirms the interpretation of the results of the spore-pollen studies. The hydrology of modern pocosins is palustrine, seasonally flooded or saturated. As they are primarily watered by rainfall, they are nutrient-poor (ombrotrophic) and in pocosins phosphorus is the main limiting nutrient (Weakley and Schafale, 1991; Richardson, 2003).

In some cases, *Pinus serotina* (pond pine) is the most characteristic tree of modern pocosins (Sharitz and Gibbons, 1982; Weakley and Schafale, 1991), therefore it can be assumed that a significant proportion of the *Pinus* pollen found in the samples comes from trees growing on-site. The parasitic *Arceuthobium* probably grew on *Pinus* trees (cf. Ohngemach and Straka, 1982). *Sequoia* and *Sciadopitys* presumably also could have grown in wet places (Schneider, 1992; Mosbrugger *et al.*, 1994; Figueiral *et al.*, 1999; Kovar-Eder *et al.*, 2001; Worobiec *et al.*, 2021).

Riparian and swamp forests with *Nyssa*, *Alnus* as well as *Acer*, *Carya*, *Celtis*, *Fraxinus*, *Liquidambar*, *Pterocarya*, *Salix*, *Ulmus*, Vitaceae, *Zelkova*, plus *Taxodium* and/or *Glyptostrobus*, probably grew in places with intermediate to long hydroperiods. Modern bay forests, composed of *Acer rubrum*, *Nyssa sylvatica* var. *biflora*, *Taxodium ascendens*, *Cyrilla racemiflora*, *Lyonia lucida*, and *Woodwardia virginica*, grow in the south Atlantic Coastal Plain of the USA (Sharitz and Gibbons, 1982; Christensen, 2000). In the vicinity, mesophytic forests composed of *Fagus*, *Quercus* (also thermophilous trees, producing pollen of fossil-species *Quercoidites henricii*), *Carpinus* as well as Adoxaceae, Araliaceae, Castaneoideae, *Cercidiphyllum*, Cornaceae, Engelhardioideae, *Eucommia*, Fabaceae, Hamamelidaceae, Mastixiaceae, and conifers occurred.

Fluctuations in the frequency of individual taxa, most pronounced for *Pinus*, *Sequoia/Sequoiadendron/Metasequoia* and *Sciadopitys*, are likely to reflect changes in water level and trophic conditions, not climate variability (see the chapter below). The frequency of the palaeotropical and palaeotropical/warm-temperate taxa is similar in the whole diagram. The estimated mean annual temperature (MAT) for the MPLS-1 at Drzewce is 15.7–17.8 °C; with the bordering taxa *Cornaceaepollis satzveyensis*, related to the *Mastixia* genus (15.7–27.8 °C), and *Cercidiphyllites minimireticulatus*, related to the *Cercidiphyllum* genus (2.2–17.8 °C). This is presented in the Appendix. The results indicate that at the time of sedimentation, the climate was warm temperate (to 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).

Fossil fungi and their palaeoenvironmental implications

Among the palynomorphs found in palynological samples from Drzewce are numerous remains of fungi. These are various fungal spores, sporocarps and remains of fungi associated with the rhizosphere microbiome, including mycorrhizal fungi. They represent three ecological groups: terrestrial epiphyllous fungi, rhizosphere fungi, and aero-aquatic mitosporic fungi. Epiphyllous fungi from

Table 2

Freshwater algae, recorded in deposits at Drzewce (number of specimens). Botanical affinity and indication according to Krutzsch and Pacltová (1990), Scott (1992), Coesel and Meesters (2007), and Worobiec (2010, 2014a, and literature cited therein).

Fossil taxa	Botanical affinity	Indication	Number of specimens
Circulisporites circulus (Wolf) Krutzsch et Pacltová	unknown	springs, swamps, and alluvial areas, damp soil	2
Closteritetrapidites sp.	Closteriaceae: *Closterium*	oligo- to eutrophic, fresh waters	1
Cycloovoidites cyclus (Krutzsch) Krutzsch et Pacltová	Zygnemataceae: *Spirogyra*	shallow, stagnant, oxygen-rich, fresh waters, lake margins	2
Desmidiaceaesporites cosmarioformis Hunger	Desmidiaceae: *Cosmarium*, *Euastrum*, *Staurastrum*, *Xanthidium*	clear, relatively nutrient-poor waters with low abundance of algae	58
Ovoidites elongatus (Hunger) Krutzsch + *O. minoris* Krutzsch et Pacltová	Zygnemataceae: *Spirogyra*	shallow, stagnant, oxygen-rich, fresh waters, lake margins	9
Ovoidites ligneolus (Potonié) Tomson et Pflug	Zygnemataceae: *Spirogyra*	shallow, stagnant, oxygen-rich, fresh waters, lake margins	18
Stigmozygodites mediostigmosus Krutzsch et Pacltová + *S. multistigmosus* (Potonié) Krutzsch et Pacltová + *Stigmozygodites* sp.	Zygnemataceae: *Zygnema*	shallow, meso- to eutrophic, open, fresh waters	6
Tetrapidites foveolatoides Krutzsch et Pacltová + *T. laevigatus* Krutzsch et Vanhoorne + *T. rhomboides* Krutzsch et Pacltová + *Tetrapidites* sp.	Zygnemataceae: *Mougeotia*	shallow, stagnant, oxygen-rich, fresh waters, lake margins	14

Drzewce are represented by the sporocarps of fossil-genera *Plochmopeltinites* and *Trichothyrites* (Fig. 4N). They inhabited surfaces of leaves (phylloplane), probably those decaying as leaf litter (Worobiec and Worobiec, 2017; Worobiec *et al.*, 2018, 2022b). Therefore, their presence indicates a humid climate and the accumulation of leaf litter (Bannister *et al.*, 2016). Rhizosphere fungi are represented by various forms and among them are the remains of a *Cenococcum*-like, mycorrhizal mantle. The numerous remains of these fungi confirm the presence of dense vegetation during the time of deposition (Worobiec *et al.*, 2018).

The remains of helicosporous conidia of mitosporic aero-aquatic fungi (Fig. 4M) are of particular importance for the reconstruction of the palaeoenvironment at Drzewce. These fungi are saprophytes, mainly on decaying leaves, wood, and bark, accumulated in small, shallow, freshwater bodies, like stagnant woodland or swampy pools, ditches or slowly running streams (Dix and Webster, 1995; Goh and Hyde, 1996; Webster and Weber, 2007; Markovskaja, 2012). Some helicosporous taxa were also reported from raised bogs or tropical peat swamps (Voglmayr, 1997; Sri-Indrasutdhi *et al.*, 2015). Aero-aquatic fungi grow on submerged substrates, often in semi-anaerobic conditions, but sporulate only when the substrate is exposed to air. Aero-aquatic fungi, including helicosporous taxa, form buoyant conidia that are dispersed by water, when the substrate is submerged again (Dix and Webster, 1995; Goh and Hyde, 1996; Webster and Weber, 2007; Zhao *et al.*, 2007). The helicosporous conidia at Drzewce, similar to the modern genera *Helicoon* and *Helicodendron*, are barrel-shaped, enclosing the air that allowed buoyancy and the dispersal of the conidia (Zhao *et al.*, 2007). Fossil helicosporous fungi from swampy environments previously were reported from Eocene to Holocene deposits (van Geel, 1978; Kalgutkar and McIntyre, 1991; Kalgutkar and Sigler, 1995; Shumilovskikh *et al.*, 2015; Romero *et al.*, 2021; Saxena *et al.*, 2021).

In the fungal association at Drzewce, helicosporous, aero-aquatic fungi were found together with terrestrial epiphyllous and mycorrhizal taxa. The same could be observed in modern communities of aquatic and aero-aquatic mitosporic fungi. Leaves that were shed in autumn could be transported by rain or wind into the depositional environment and with them the terrestrial fungi from forest litter and leaf phylloplane (Markovskaya, 2009). In summary, the fossil fungal association at Drzewce indicates dense vegetation on damp, swampy soils and the presence of small, shallow water bodies with variable water levels or even periodic reservoirs, existing only in the wet season or after floods.

Comparison of the palynoflora from Drzewce with other palynoassemblages from the MPLS-1

Numerous palynofloras from the MPLS-1 have been studied so far (Ziembińska and Niklewski, 1966; Ziembińska-Tworzydło, 1974; Dyjor and Sadowska, 1977; Grabowska and Słodkowska, 1993; Kohlman-Adamska, 1993; Worobiec, 2009, 2011; Worobiec and Szulc, 2010; Worobiec *et al.*, 2022a) and they generally are correlated with the VIII *Celtipollenites verus* zone in the scheme of the spore-pollen zones of the Neogene in the Polish Lowlands (Piwocki and Ziembińska-Tworzydło, 1997). In the area of Konin, the MPLS-1 was examined palynologically by Kremp (1949), Mamczar (1960), Sadowska and Giża (1991), Słodkowska and Widera (2021) as well as Worobiec *et al.* (2021). The spore-pollen assemblage at Drzewce is most similar in composition to the palynoflora of the neighboring Adamów deposit (Fig. 1; Worobiec *et al.*, 2021), which also is located in the Konin Basin (Fig. 1). Both areas were overgrown by palustrine wetland communities, similar in composition to the modern pocosins, dominated by members of the Ericaceae family. In both profiles, *Desmidiaceaesporites cosmarioformis* occurs in most samples. Another similarity is the presence of numerous *Sequoia* and *Nyssa* pollen grains, simultaneously with a low amount of *Taxodium/Glyptostrobus* type pollen. A difference is the relatively high content of *Sciadopitys* pollen and the lower content of *Tricolporopollenites pseudocingulum*, *Edmundipollis* and other thermophilous elements in the Drzewce profile.

Similarly, in the MPLS-1 at the Jóźwin IIB lignite opencast (Pątnów IV deposit) in the Konin region (Fig. 1; Słodkowska and Widera, 2021), the most abundant were pollen grains of *Pinus*, *Nyssa*, Ericaceae, *Fagus*, and *Sequoia/Sequoiadendron/Metasequoia*. Important elements in the development of mires were shrubs, including the Clethraceae, Cyrillaceae, Ericaceae, Myricaeae, Oleaceae, and Salicaceae. Nevertheless, in the Jóźwin IIB profile, a cyclicity in the percentage of pollen of thermophilous plants, including *Tricolporopollenites pseudocingulum*, *Quercoidites henricii*, *Edmundipollis*, and *Araliaceoipollenites euphorii*, was observed.

The thoroughly examined palynoflora from the Jóźwin I opencast (Kasiński *et al.*, 2010), belonging to the Konin Lignite Mine, was dominated by conifers: *Taxodium/Glyptostrobus* (up to 40%), Pinaceae (mainly *Pinus*) and *Sciadopitys*. Angiosperms were represented by *Nyssa*, *Alnus*, Cyrillaceae/Clethraceae, Ericaceae, *Castanea/Castanopsis/Lithocarpus*, *Quercoidites henricii*, and *Tricolporopollenites pseudocingulum*. The area was covered with swamp forests of *Taxodium*, *Glyptostrobus*, *Nyssa*, and *Alnus*. In addition, there were bush swamps (shrub bogs or swamps), riparian forests, and mesophytic forests. The main difference between the Drzewce and Jóźwin I palynoassemblages is the high content of *Taxodium/Glyptostrobus* pollen in the latter.

The Jóźwin I palynoflora is similar to the assemblages from the MPLS-1 of the Legnica-Ścinawa complex in the Fore-Sudetic region, SW Poland, so-called "Henryk seam". For example, in many profiles from this region, such as the Legnica and Ruja deposits (Wacnik and Worobiec, 2001; Worobiec *et al.*, 2008; Worobiec, 2009; Ivanov and Worobiec, 2017; Worobiec *et al.*, 2022a), the pollen of *Taxodium/Glyptostrobus* (max. 60%), *Sequoia*, *Pinus*, *Nyssa*, *Alnus*, *Quercus*, *Tricolporopollenites pseudocingulum*, *Fagus*, and *Celtis* were the most frequent. Such *Taxodium/Glyptostrobus-Nyssa* swamp forests, probably enriched in *Alnus*, were widespread in Europe during the Oligocene to Pliocene as one type of Neogene peat-bog vegetation and they evolved in slowly subsiding, tectonic basins or along the coast during some phases of sea level change (Mai, 1981; Schneider, 1992; Holdgate *et al.*, 2016; Kasiński and Słodkowska, 2016). Nowadays, similar *Taxodium-Nyssa* swamp forests occur in swampy lowlands: along the lower Atlantic Coastal Plain from southern Delaware to southern Florida and along the lower Gulf Coast Plain to southeastern Texas, including the Mississippi River delta (Wilhite and Toliver, 1990; Barnes, 1991). The Legnica-Ścinawa lignite resource complex is a platform-type deposit that extends over a large area in the Legnica Depression. The *Taxodium/Glyptostrobus-Nyssa-Alnus* forests were sources for thin horizons or lenses of lignites of the MPLS-1 in the Legnica (Worobiec, 2009) and Ruja (Worobiec *et al.*, 2022a) deposits.

Palynofloras from Drzewce, Adamów (Worobiec *et al.*, 2021), Pątnów (Sadowska and Giża, 1991) and several other palynoassemblages from central and western Poland (Ziembińska and Niklewski, 1966; Ziembińska-Tworzydło, 1974; Dyjor and Sadowska, 1977; Sadowska, 1977) are characterized by a high proportion of pollen from the Ericaceae, Cyrillaceae/Clethraceae, *Ilex*, *Myrica*, Rosaceae and other shrubs, and a low frequency of swamp taxa (including *Taxodium/Glyptostrobus*). A common feature of most of the palynoassemblages in the MPLS-1 is also the high content of *Sequoia* pollen (Raniecka-Bobrowska, 1970; Ziembińska-Tworzydło and Ważyńska, 1981). For example, a relatively high frequency of *Sequoia* pollen (max. 30%) was recorded in the palynofloras from the Konin region (Kremp, 1949; Mamczar, 1960; Doktorowicz-Hrebnicka, 1960; Sadowska and Giża, 1991; Worobiec *et al.*, 2021) as well as from other localities in central and western Poland (Mamczar, 1961; Ziembińska and Niklewski, 1966; Ziembińska-Tworzydło, 1974; Dyjor and Sadowska, 1977; Ciuk and Grabowska, 1991; Worobiec, 2009). This relatively high frequency of *Sequoia* pollen sometimes was considered to be a characteristic feature of the MPLS-1, which found its expression in distinguishing a *Sequoia* phase (Raniecka-Bobrowska, 1970) or a *Sequoia-Nyssa-Quercus* phase (Ziembińska-Tworzydło and Ważyńska, 1981). Lignite lithotypes with abundant *Sequoia* probably were formed under conditions that were slightly drier than those produced by reed marsh or the *Glyptostrobus-Taxodium-Nyssa* swamp forests (cf. Holdgate *et al.*, 2016; Worobiec *et al.*, 2021). Similarly, a high frequency of *Sequoia* pollen (*Sequoiapollenites polyformosus*) has been observed in the Upper Seam in the Lower Rhine Basin in northwestern Germany. In addition, in this lignite seam, recurring trends in the carbon isotope record were detected, which correlate with the variability in abundance of *Sequoiapollenites polyformosus* in the pollen record. According to those reports, these changes indicate fluctuactions in groundwater levels and changes in precipitation (Jones *et al.*, 1997; Utescher *et al.*, 2012, 2021). A similar environment with *Sequoia* and *Sciadopitys*, with changing groundwater tables, was presented by Dolezych and Schneider (2006, 2007) from the middle Miocene lignite seams of the Lower Lusatian region in Germany.

The relatively high frequency of *Sciadopitys* pollen most likely also reflects trophic conditions. Kus *et al.* (2020) analyzed Miocene wood of fossil-species belonging to the families Sciadopityaceae, Pinaceae, and Cupressaceae *sensu lato* from the Piskowitz open-cast mine, Lusatia region, Germany. Those authors distinguished, among others, the MSc-facies ("*Sciadopitys* bog facies"), representing a nutrient-poor and acid environment. This statement is in agreement with results of the palynological analysis of the present authors. The continuous presence of the fossil-species *Desmidiaceaesporites cosmarioformis* in the Drzewce profile indicates relatively nutrient-poor (ombrotrophic) conditions (cf. Coesel and Meesters, 2007; Worobiec and Worobiec, 2016).

Lignite deposition depended on both climatic and tectonic changes (Kasiński and Słodkowska, 2016; Widera *et al.*, 2021b). The tectonic subsidence of the Polish part of the Carpathian foreland resulted in an increase in accumulation, and under favorable climatic conditions, peat bogs (later transformed into the MPLS-1) began to develop intensively in central Poland. Widera *et al.* (2021a) proposed a depositional model, depicting the differences between the areas of the Konin Basin during the accumulation of the MPLS-1. In this model the areas of the Jóźwin IIB (Pątnów IV deposit) and Tomisławice were located close to the mid-Miocene river channels (a meandering and/or anastomosing river system), while the Adamów area was relatively far away from them (Widera *et al.*, 2021a). The palaeomires from the Jóźwin IIB and Tomisławice were flooded periodically, as evidenced by the presence of several layers of sediments from crevasse splays and lakes within the MPLS-1. In contrast, such siliciclastic interbeds are not seen in the Adamów opencast mine (Widera *et al.*, 2021a, b). Similarly, sedimentological data and the results of palynological studies of the present authors (including NPPs) from Drzewce indicate that these palaeomires were relatively distant from the river channels.

According to Kasiński and Słodkowska (2016), the temperature range for the MPLS-1 was 15.7–19.7 °C. Data from Drzewce (MAT between 15.7–17.8 °C), Adamów (15.7–18.0 °C; Worobiec *et al.*, 2021), Jóźwin I (15.0–18.5 °C; Kasiński *et al.*, 2010), Jóźwin IIB (15.7–20.5 °C; Słodkowska and Widera, 2021), Legnica (15.6–16.6 °C; Ivanov and Worobiec, 2017) and Ruja (15.7–17.8 °C; Worobiec *et al.*, 2022a) do not demonstrate differences in the mean annual temperature between the sites. These results confirm that the climate was more or less homogenous across the entire Polish Lowlands during the formation of the MPLS-1. The results from Poland are also similar to other middle Miocene MAT ranges from Central Europe and they correspond to globally observed Mid-Miocene Climatic Optimum. The temperature increased in the late Burdigalian and a warm period persisted to the earlier part of the Serravallian. In Germany, the MAT at that time, based on the microfloras (when averaging means obtained from all samples), was 18.3 °C, and the mean temperature, based on macroflora, ranged between 17.8–19.6 °C (Mosbrugger *et al.*, 2005; Bruch *et al.*, 2007; Utescher *et al.*, 2009, 2012, 2021). During this time span, the annual precipitation in Bulgaria and SW Poland was estimated to be ca. 800 to over 1300 mm (Ivanov and Worobiec, 2017). The climate at the time of the formation of the MPLS-1 was warm temperate and humid, similar to the climate that currently prevails in the southern and south-eastern USA, where the MAT is in the range of 16.0–19.8 °C, and annual precipitation is up to 1200–1500 mm (e.g., Barnes, 1991). For comparison, the present-day climate of the Konin area, adjacent to the Drzewce lignite deposit, is characterized as “generally warm and temperate”. The mean annual temperature in Konin averages 9.6 °C and the annual precipitation is 635 mm (Climate-Data, 2022).

During the last peak of the Mid-Miocene Climatic Optimum, large areas in Central Europe were covered by swamps, peat bogs, and slowly flowing waters. As a result, the lignites of the MPLS-1 were formed across a large area. The differences between palynofloras dominated by swamp forests (e.g., from Józwin I and Legnica) and palynofloras dominated by shrub bogs (e.g., from Drzewce and Adamów), are most probably a reflection of various plant communities, developing in different hydrological and trophic conditions (cf. Worobiec *et al.*, 2022a). Later on, mean temperatures decreased and the next warmer period occurred towards the end of the Tortonian (Mosbrugger *et al.*, 2005; Bruch *et al.*, 2006). However, the conditions were no longer favourable for the formation of thick lignite seams. Therefore, in the Polish Lowlands after the MPLS-1, only small lenses of lignites, late Tortonian in age, are recorded (Słodkowska, 1998; Szulc and Worobiec, 2012; Worobiec, 2014b).

CONCLUSIONS

Palynological analysis of the MPLS-1 at Drzewce indicates that the area was overgrown by palustrine, wetland communities, similar in composition to the modern pocosins. Most characteristic elements of them were shrubs from the Ericaceae, Cyrillaceae and Clethraceae families as well as *Ilex* and *Myrica*. *Pinus*, *Sequoia* and *Sciadopitys* presumably also could have grown in wet places. Fluctuations in the frequency of these trees are likely to reflect changes in water level and trophic conditions, rather than climate. The fossil fungal assemblage from Drzewce, including helicosporous, aero-aquatic fungi, found together with terrestrial epiphyllous and mycorrhizal taxa, indicates dense vegetation on damp, swampy soils and the presence of small, shallow-water bodies with variable water level or even periodic reservoirs, existing only during wet seasons or after floods. In small, flooded depressions, such as pools in bogs, filamentous green algae from the Zygnemataceae family occurred. The presence of their resting cells (zygospores) also indicates that the peat-forming environment periodically might have dried out or was subjected to seasonal warming. The presence of the zygospores of desmids *Desmidiaceaesporites cosmarioformis* most probably indicates relatively nutrient-poor (ombrotrophic) conditions. Sedimentological data and the results of palynological studies (including NPPs) at Drzewce indicate that these wetlands were rather distant from the river channels of the meandering and/or anastomosing river system in the Konin Basin. The climate was warm temperate and humid, and the estimated mean annual temperature (MAT) for the lignite seam at Drzewce is 15.7–17.8 °C. Most likely, the MPLS-1 accumulated during the last peak of the Mid-Miocene Climatic Optimum. Comparison with other palynofloras from the MPLS-1 shows that the climate during formation of the group of seams was more or less homogenous across the entire Polish Lowlands.

Acknowledgements

The authors would like to express special thanks to the authority of the Konin Lignite Mine for granting permission for the fieldwork in the mine opencast. We also thank Angela A. Bruch and Johannes Martin Bouchal for their valuable comments on this article. This work was supported by the W. Szafer Institute of Botany, Polish Academy of Sciences, through its statutory funds and National Science Centre, Poland, under Grant 2017/27/B/ST10/00001.

REFERENCES

Bannister, J. M., Conran, J. G. & Lee, D. E., 2016. Life on the phylloplane: Eocene epiphyllous fungi from Pikopiko Fossil Forest, Southland, New Zealand. *New Zealand Journal of Botany*, 54: 412–432.

Barnes, B. V., 1991. Deciduous forests of North America. In: Röhrig, E. & Ulrich, B. (eds), *Ecosystems of the World. 7. Temperate Deciduous Forests.* Elsevier, Amsterdam London-New York-Tokyo, pp. 219–344.

Bouchal, J. M. & Denk, T., 2020. Low taxonomic resolution of papillate Cupressaceae pollen (former Taxodiaceae) impairs their applicability for palaeo-habitat reconstruction. *Grana*, 59: 71–93.

Bruch, A. A., Uhl, D. & Mosbrugger, V., 2007. Miocene climate in Europe – Patterns and evolution. A first synthesis of NECLIME. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 253: 1–7.

Bruch, A. A., Utescher, T., Mosbrugger, V., Gabrielyan, I. & Ivanov, D. A., 2006. Late Miocene climate in the circum-Alpine realm – a quantitative analysis of terrestrial paleofloras. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 238: 270–280.

Chomiak, L., 2020. Variation of lignite ash in vertical and horizontal sections of mining walls in the Konin Lignite Mine, central Poland. *Geology, Geophysics and Environment*, 46: 17–28.

Christensen, N. L., 2000. Vegetation of the southeastern Coastal Plain. In: Barbour, M. G. & Billings, W. D. (eds), *North American Terrestrial Vegetation, 2nd Edition*. Cambridge University Press, Cambridge, pp. 397–448.

Ciuk, E. & Grabowska, I., 1991. Synthetic stratigraphic section of the Tertiary in the Lubstów brown coal deposit at Lubstów, Konin district. *Biuletyn Państwowego Instytutu Geologicznego*, 365: 47–72. [In Polish, with English summary.]

Climate-Data., 2022. *Climate: Konin*. https://en.climate-data.org/europe/poland/greater-poland-voivodeship/konin-3071/ [February, 2022].

Coesel, P. F. M. & Meesters, K. (J.), 2007. *Desmids of the Lowlands: Mesotaeniaceae and Desmidiaceae of the European Lowlands*. KNNV Publishing, Zeist, the Netherlands, 351 pp.

Dadlez, R., Marek, S. & Pokorski, J. (eds), 2000. *Mapa geologiczna Polski bez utworów kenozoiku w skali 1:1000000*. Państwowy Instytut Geologiczny, Warszawa [In Polish.]

Dix, N. J. & Webster, J., 1995. *Fungal Ecology*. Springer-Science + Business Media, B.V., 549 pp.

Doktorowicz-Hrebnicka, J., 1960. Correlation of brown coal seams from the provinces of Poznań and Bydgoszcz. *Biuletyn Instytutu Geologicznego*, 157: 69–138. [In Polish, with English summary.]

Dolezych, M. & Schneider, W., 2006. Inkohlte Hölzer und Cuticulae dispersae aus dem 2. Miozänen Flözhorizont im Tagebau Welzow (Lausitz) – Taxonomie und vergleichende feinstratigraphisch-fazielle Zuordnung. *Zeitschrift für Geologische Wissenschaften*, 34: 165–259.

Dolezych, M. & Schneider, W., 2007. Taxonomie und Taphonomie von Koniferenhölzern und Cuticulae dispersae im 2. Lausitzer Flözhorizont (Miozän) des Senftenberger Reviers. *Palaeontographica Abteilung B*, 276: 1–95.

Dyjor, S. & Sadowska, A., 1977. Problem of the age and correlation of Upper Miocene brown coal seams in the Western Poland. *Geologia Sudetica*, 12: 121–134. [In Polish, with English summary.]

Fang, J., Wang, Z. & Tang, Z., 2011. *Atlas of Woody Plants in China: Distribution and Climate*. Higher Education Press, Beijing, 2000 pp.

Figueiral, I., Mosbrugger, V., Rowe, N. P., Ashraf, A. R., Utescher, T. & Jones, T. P., 1999. The Miocene peat-forming vegetation of northwestern Germany: an analysis of wood remains and comparison with previous palynological interpretations. *Review of Palaeobotany and Palynology*, 104: 239–266.

Goh, T. K. & Hyde, K. D., 1996. Biodiversity of freshwater fungi. *Journal of Industrial Microbiology and Biotechnology*, 17: 328–345.

Grabowska, I. & Słodkowska, B., 1993. *Katalog profili osadów trzeciorzędowych opracowanych palinologicznie*. PIG, Warszawa, 80 pp. [In Polish.]

Grimm, G. W., Bouchal, J. M., Denk, T. & Potts, A., 2016. Fables and foibles: a critical analysis of the Palaeoflora database and the Coexistence Approach for palaeoclimate reconstruction. *Review of Palaeobotany and Palynology*, 233: 611–622.

Grimm, G. W. & Denk, T., 2012. Reliability and resolution of the coexistence approach – A revalidation using modern-day data. *Review of Palaeobotany and Palynology*, 172: 33–47.

Grimm, G. W. & Potts, A., 2016. Fallacies and fantasies: the theoretical underpinnings of the coexistence approach for palaeoclimate reconstruction. *Climate of the Past*, 12: 611–622.

Holdgate, G., Wallace, M., O'Connor, M., Korasidis, V. & Lieven, U., 2016. The origin of lithotype cycles in Oligo–Miocene brown coals from Australia and Germany. *International Journal of Coal Geology*, 12: 327–347.

Hunger, R., 1953. Mikrobotanisch-stratigraphische Untersuchungen der Braunkohlen der südlichen Oberlausitz und die Pollenanalyse als Mittel zur Deutung der Flözgenese. *Freiderberg Forschungshefte, Reihe* C, H. 8: 1–38.

Ivanov, D. & Worobiec, E., 2017. Middle Miocene (Badenian) vegetation and climate dynamics in Bulgaria and Poland based on pollen data. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 467: 83–94.

Jones, T. P., Fortier, S. M., Mosbrugger, V., Roessler, J., Utescher, T. & Ashraf, A. R., 1997. $^{13}C/^{12}C$ ratio double cyclicity in a Miocene browncoal: Isotopic signals and orbital forcing. *Terra Nova*, 9: 19–23.

Kadłubowska, J. Z., 1984. *Süßwasserflora von Mitteleuropa. Band 16: Chlorophyta VIII-Conjugatophyceae I (Zygnemales)*. Gustav Fischer Verlag, Stuttgart, 532 pp.

Kalgutkar, R. M. & McIntyre, D. J., 1991. Helicosporous fungi and Early Eocene pollen, Eureka Sound Group, Axel Heiberg Island, Northwest Territories. *Canadian Journal of Earth Sciences*, 28: 364–371.

Kalgutkar, R. M. & Sigler, L., 1995. Some fossil fungal form-taxa from the Maastrichtian and Palaeogene ages. *Mycological Research*, 99: 513–522.

Kasiński, J. R., Piwocki, M., Swadowska, E. & Ziembińska-Tworzydło, M., 2010. Lignite of the Polish Lowlands Miocene: Characteristics on a base of selected profiles. *Biuletyn Państwowego Instytutu Geologicznego*, 439: 99–153. [In Polish, with English summary.]

Kasiński, J. R. & Słodkowska, B., 2016. Factors controlling Cenozoic anthracogenesis in the Polish Lowlands. *Geological Quarterly*, 60: 959–974.

Kędzior, A., Widera, M. & Zieliński, T., 2021. Ancient and modern anastomosing rivers: insights from sedimentological and geomorphological case studies of the Triassic, Neogene and Holocene of Poland. *Geological Quarterly*, 65: 54.

Kohlman-Adamska, A., 1993. Pollen analysis of the Neogene deposits from the Wyrzysk region, North-Western Poland. *Acta Palaeobotanica*, 33: 91–298.

Kottek, M., Grieser, J., Beck, C., Rudolf, B. & Rubel, F., 2006. World Map of Köppen Geiger Climate Classification updated. *Meteorologische Zeitschrift*, 15: 259–263.

Kovar-Eder, J., Kvaček, Z. & Meller, B., 2001. Comparing Early to Middle Miocene floras and probable vegetation types of Oberdorf N Voitsberg (Austria), Bohemia (Czech Republic), and Wackersdorf (Germany). *Review of Palaeobotany and Palynology*, 114: 83–125.

Kremp, G., 1949. Pollenanalitische Untersuchungen des miozanen Braunkohlenlagers von Konin an der Warthe. *Palaeontographica B*, 90: 53–93.

Krutzsch, W. & Pacltová, B., 1990. Die Phytoplankton – Mikroflora aus den Pliozänen Süsswasserablagerungen des Cheb-Beckens (Westböhmen, ČSFR). *Acta Universitatis Carolinae – Geologica*, 4: 345–420.

Kus, J., Dolezych, M., Schneider, W., Hofmann, T. & Visiné Rajczi, E., 2020. Coal petrological and xylotomical characterization of Miocene lignites and *in-situ* fossil tree stumps and trunks from Lusatia region, Germany: palaeoenvironment and taphonomy assessment. *International Journal of Coal Geology*, 217, 103283.

Kwiecińska, B. & Wagner, M., 2001. *Application of Reflectance in Natural and Technological Classification of Brown Coal (Lignite)*. Wydawnictwo Akademii Górniczo-Hutniczej, Kraków, 53 pp. [In Polish, with English summary.]

Mai, D. H., 1981. Entwicklung und klimatische Differenzierung der Laubwaldflora Mitteleuropas im Tertiär. *Flora*, 171: 525–582.

Mamczar, J., 1960. Standard section of the Middle Miocene of Central Poland. *Biuletyn Instytutu Geologicznego*, 157: 13–68. [In Polish, with English summary.]

Mamczar, J., 1961. Standard spore-pollen section of the Upper Miocene brown coal in Central Poland – Rogóźno brown coal deposit. *Biuletyn Instytutu Geologicznego*, 158: 305–323. [In Polish, with English summary.]

Markovskaja, S., 2009. Fungi inhabiting submerged forest litter in a temperate stream (South Eastern Lithuania). *Botanica Lithuanica*, 15: 105–116.

Markovskaja, S., 2012. Aero-aquatic fungi colonizing decaying leaves in woodland swampy pools of Aukštadvaris Regional Park (Lithuania). *Botanica Lithuanica*, 18: 123–132.

Moore, P. D., Webb, J. A. & Collinson, M. E., 1991. *Pollen Analysis.* Blackwell, Oxford, 216 pp.

Mosbrugger, V., Gee, C. T., Belz, G. & Ashraf, A. R., 1994. Three-dimensional reconstruction of an in-situ Miocene peat forest from the Lower Rhine Embayment, northwestern Germany – new methods in palaeovegetation analysis. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 110: 295–317.

Mosbrugger, V., Utescher, T. & Dilcher, D. L., 2005. Cenozoic continental climatic evolution of Central Europe. *Proceedings of the National Academy of Sciences of the United States of America*, 102: 14964–14969.

Nalepka, D. & Walanus, A., 2003. Data processing in pollen analysis. *Acta Palaeobotanica*, 43: 125–134.

Ohngemach, D. & Straka, H., 1982. Pollenanalytischer Nachweis einer mexikanischen *Pinus*-Art mit Hilfe ihres Parasiten. *Abhandlungen des Naturwissenschaftlichen Vereins zu Bremen*, 39: 397–403.

Piwocki, M., 1998. An outline of the palaeogeographic and palaeoclimatic developments. In: Ważyńska, H. (ed.), *Palynology and Palaeogeography of the Neogene in the Polish Lowlands*. *Prace Państwowego Instytutu Geologicznego*, 160: 8–12.

Piwocki, M. & Ziembińska-Tworzydło, M., 1997. Neogene of the Polish Lowlands – lithostratigraphy and pollen-spore zones. *Geological Quarterly*, 41: 21–40.

Prader, S., Kotthoff, U., McCarthy, F. M. G., Schmiedl, G., Donders, T. H. & Greenwood, D. R., 2017. Vegetation and climate development of the New Jersey hinterland during the late Middle Miocene (IODP Expedition 313 Site M0027). *Palaeogeography, Palaeoclimatology, Palaeoecology*, 485: 854–868.

Raniecka-Bobrowska, J., 1970. Stratigraphy of Late Tertiary in Poland on the basis of palaeobotanical research. *Kwartalnik Geologiczny*, 14: 728–753. [In Polish, with English summary.]

Richardson, C. J., 2003. Pocosins: hydrologically isolated or integrated wetlands on the landscape? *Wetlands*, 23: 563–576.

Romero, I. C., Nuñez Otaño, N. B., Gibson, M. E., Spears, T. M., Fairchild, C. J., Tarlton, L., Jones, S., Belkin, H. E., Warny, S., Pound, M. J. & O'Keefe, J. M. K., 2021. First record of fungal diversity in the tropical and warm-temperate Middle Miocene Climate Optimum forests of Eurasia. *Frontiers in Forests and Global Change*, 4: 768405.

Sadowska, A., 1977. Vegetation and stratigraphy of Upper Miocene coal seam of the South-Western Poland. *Acta Palaeobotanica*, 18: 87–122. [In Polish, with English summary.]

Sadowska, A. & Giża, B., 1991. The flora and age of the brown coal from Pątnów. *Acta Palaeobotanica*, 31: 201–214. [In Polish, with English summary.]

Saxena, R. K., Wijayawardene, N. N., Dai, D. Q., Hyde, K. D. & Kirk, P. M., 2021. Diversity in fossil fungal spores. *Mycosphere*, 12: 670–874.

Schneider, W., 1992. Floral successions in Miocene swamps and bogs of Central Europe. *Zeitschrift für Geologische Wissenschaften*, 20: 555–570.

Scott, L., 1992. Environmental implications and origin of microscopic *Pseudoschizaea* Thiergart and Frantz ex R. Potonié emend. in sediments. *Journal of Biogeography*, 19: 349–354.

Sharitz, R. R. & Gibbons, J. W., 1982. *The Ecology of Southeastern Shrub Bogs (Pocosins) and Carolina Bays: a Community Profile*. U.S. Fish and Wildlife Service, Division of Biological Services, Washington, D.C., 93 pp.

Shumilovskikh, L. S., Schlütz, F., Achterberg, I., Bauerochse, A. & Leuschner, H. H., 2015. Non-pollen palynomorphs from mid-Holocene peat of the raised bog Borsteler Moor (Lower Saxony, Germany). *Studia Quaternaria*, 32: 5–18.

Słodkowska, B., 1998. Palynological characteristics of the Neogene brown coal seams. In: Ważyńska, H. (ed.), *Palynology and Palaeogeography of the Neogene in the Polish Lowlands*. *Prace Państwowego Instytutu Geologicznego*, 160: 28–33.

Słodkowska, B. & Widera, M., 2021. Vegetation response to environmental changes based on palynological research on the Middle Miocene lignite at the Jóźwin IIB open-cast mine (Konin region, central Poland). *Annales Societatis Geologorum Poloniae*, 91: 149–166.

Sri-Indrasutdhi, V., Tsui, C. K., Chuaseeharonnachai, C., Yamaguchi, K., Suetrong, S., Okane, I., Nakagiri, A. & Boonyuen, N., 2015. *Helicocentralis hyalina* gen. et sp. nov., an aero-aquatic helicosporous fungus (Leotiomycetes, Ascomycota) in Thailand. *Mycological Progress*, 14: 1–12.

Stuchlik, L., Ziembińska-Tworzydło, M., Kohlman-Adamska, A., Grabowska, I., Słodkowska, B., Ważyńska, H. & Sadowska, A., 2009. *Atlas of Pollen and Spores of the Polish Neogene. Volume 3 – Angiosperms* (*1*). W. Szafer Institute of Botany, Polish Academy of Sciences, Kraków, 233 pp.

Stuchlik, L., Ziembińska-Tworzydło, M., Kohlman-Adamska, A., Grabowska, I., Słodkowska, B., Worobiec, E. & Durska, E., 2014. *Atlas of Pollen and Spores of the Polish Neogene. Volume 4 – Angiosperms* (*2*). W. Szafer Institute of Botany, Polish Academy of Sciences, Kraków, 466 pp.

Stuchlik, L., Ziembińska-Tworzydło, M., Kohlman-Adamska, A., Grabowska, I., Ważyńska, H. & Sadowska, A., 2002. *Atlas of Pollen and Spores of the Polish Neogene. Volume 2 – Gymnosperms*. W. Szafer Institute of Botany, Polish Academy of Sciences, Kraków, 237 pp.

Stuchlik, L., Ziembińska-Tworzydło, M., Kohlman-Adamska, A., Grabowska, I., Ważyńska, H., Słodkowska, B. & Sadowska, A., 2001. *Atlas of Pollen and Spores of the Polish Neogene. Volume 1 – Spores*. W. Szafer Institute of Botany, Polish Academy of Sciences, Kraków, 158 pp.

Szulc, J. & Worobiec, E., 2012. Neogene karst sinkhole and its deposits from Górażdże Quarry, Upper Silesia – archive for palaeoenvironmental reconstructions. *Annales Societatis Geologorum Poloniae*, 82: 371–385.

Utescher, T., Ashraf, A. R., Dreist, A., Dybkjær, K., Mosbrugger, V., Pross, J. & Wilde, V., 2012. Variability of Neogene continental climates in Northwest Europe – a detailed study based on microfloras. *Turkish Journal of Earth Sciences*, 21: 289–314.

Utescher, T., Ashraf, A. R., Kern, A. K. & Mosbrugger, V., 2021. Diversity patterns in microfloras recovered from Miocene brown coals of the lower Rhine Basin reveal distinct coupling of the structure of the peat-forming vegetation and continental climate variability. *Geological Journal*, 56: 768–785.

Utescher, T., Bruch, A. A., Erdei, B., François, L., Ivanov, D., Jacques, F. M. B., Kern, A. K., Liu, Y-S. (C.), Mosbrugger, V. & Spicer, R. A., 2014. The coexistence approach – theoretical background and practical considerations of using plant fossils for climate quantification. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 410: 58–73.

Utescher, T. & Mosbrugger, V., 2015. *The Palaeoflora Database*. http://www.palaeoflora.de/ [December, 2021].

Utescher, T., Mosbrugger, V., Ivanov, D. & Dilcher, D. L., 2009. Present-day climatic equivalents of European Cenozoic climates. *Earth and Planetary Science Letters*, 284: 544–552.

van Geel, B., 1976. Fossil spores of Zygnemataceae in ditches of a pre-historic settlement in Hoogkarspel (The Netherlands). *Review of Palaeobotany and Palynology*, 22: 337–344.

van Geel, B., 1978. A palaeoecological study of Holocene peat bog sections in Germany and the Netherlands, based on the analysis of pollen, spores and macro-and microscopic remains of fungi, algae, cormophytes and animals. *Review of Palaeobotany and Palynology*, 25: 1–120.

van Geel, B. & Grenfell, H. R., 1996. Spores of Zygnemataceae. In: Jansonius, J. & McGregor, D. C. (eds), *Palynology: Principles and Applications. 1*. American Association of Stratigraphic Palynologists Foundation, pp. 173–179.

Voglmayr, H., 1997. Two new aero-aquatic species of the hyphomycete genus *Helicodendron* from Austria. *Plant Systematics and Evolution*, 205: 185–193.

Wacnik, A. & Worobiec, E., 2001. Pollen analysis of the Middle Miocene profile from Legnica, southwestern Poland. *Acta Palaeobotanica*, 41: 3–13.

Weakley, A. S. & Schafale, M. P., 1991. Classification of pocosins of the Carolina Coastal Plain. *Wetlands*, 11, *Special Issue*: 355–375.

Webster, J. & Weber, R. W. S., 2007. *Introduction to Fungi. Third edition*. Cambridge University Press, 841 pp.

Westerhold, T., Marwan, N., Drury, A. J., Liebrand, D., Agnini, C., Anagnostou, E., Barnet, J. S. K., *et al*., 2020. An astronomically dated record of Earth's climate and its predictability over the last 66 million years. *Science*, 369: 1383–1387.

Widera, M., 2007. *Lithostratigraphy and Palaeotectonics of the sub-Pleistocene Cenozoic of Wielkopolska*. Adam Mickiewicz University Press, Poznań, 224 pp. [In Polish, with English summary.]

Widera, M., 2016. Genetic classification of Polish lignite deposits: A review. *International Journal of Coal Geology*, 158: 107–118.

Widera, M., 2021. *Geologia polskich złóż węgla brunatnego*. Wydawnictwo Naukowe Bogucki, Poznań, 180 pp. [In Polish.]

Widera, M., Bechtel, A., Chomiak, L., Maciaszek, P., Słodkowska, B., Wachocki, R., Worobiec, E., Worobiec, G. & Zieliński, T., 2021a. Palaeoenvironmental reconstruction of the Konin Basin (central Poland) during lignite accumulation linked to the mid-Miocene climate optimum. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 568: 110307.

Widera, M., Chomiak, L. & Zieliński, T., 2019. Sedimentary facies, processes and paleochannel pattern of an anastomosing river system: an example from the Upper Neogene of Central Poland. *Journal of Sedimentary Research*, 89: 487–507.

Widera, M. & Kita, A., 2007. Paleogene marginal marine sedimentation in central-western Poland. *Geological Quarterly*, 51: 79–90.

Widera, M., Kowalska, E. & Fortuna, M., 2017. A Miocene anastomosing river system in the area of Konin Lignite Mine, central Poland. *Annales Societatis Geologorum Poloniae*, 87: 157–168.

Widera, M., Zieliński, T., Chomiak, L., Maciaszek, P., Wachocki, R., Bechtel, A., Słodkowska, B., Worobiec, E. & Worobiec, G., 2021b. Tectonic-climatic interactions during changes of depositional environments in the Carpathian foreland: An example from the Neogene of central Poland. *Acta Geologica Polonica*, 71: 519–542.

Wilhite, L. P. & Toliver, J. R., 1990. *Taxodium distichum* (L.) Rich., Baldcypress. In: Burns, R. M. & Honkala, B. H. (technical coordinators), *Silvics of North America: 1. Conifers. Agriculture Handbook 654*. U.S. Department of Agriculture, Forest Service, Washington, DC, USA, pp. 563–572.

Worobiec, E., 2009. Middle Miocene palynoflora of the Legnica lignite deposit complex, Lower Silesia, Poland. *Acta Palaeobotanica*, 49: 5–133.

Worobiec, E., 2010. Late Miocene freshwater phytoplankton from Józefina (Poland). *Micropaleontology*, 56: 517–537.

Worobiec, E., 2011. Middle Miocene aquatic and wetland vegetation of the paleosinkhole at Tarnów Opolski, SW Poland. *Journal of Paleolimnology*, 45: 311–322.

Worobiec, E., 2014a. Fossil zygospores of Zygnemataceae and other microremains of freshwater algae from two Miocene palaeosinkholes in the Opole region, SW Poland. *Acta Palaeobotanica*, 54: 113–157.

Worobiec, E., 2014b. The palynology of late Miocene sinkhole deposits from Upper Silesia, Poland. *Review of Palaeobotany and Palynology*, 211: 66–77.

Worobiec, E. & Szulc, J., 2010. A Middle Miocene palynoflora from sinkhole deposits from Upper Silesia, Poland and its palaeoenvironmental context. *Review of Palaeobotany and Palynology*, 163: 1–10.

Worobiec, E., Widera, M., Worobiec, G. & Kurdziel, B., 2021. Middle Miocene palynoflora from the Adamów lignite deposit, central Poland. *Palynology*, 45: 59–71.

Worobiec, E. & Worobiec, G., 2016. Miocene palynoflora from the KRAM-P 218 leaf assemblage from the Bełchatów Lignite Mine (Central Poland). *Acta Palaeobotanica*, 56: 499–517.

Worobiec, E., Worobiec, G. & Kasiński, J. R., 2022a. Decline of Neogene lignite formation as a result of vegetation and climate changes reflected in the middle Miocene palynoflora from the Ruja lignite deposit, SW Poland. *Review of Palaeobotany and Palynology*, 298, 104593.

Worobiec, G. & Worobiec, E., 2017. Epiphyllous fungi from Miocene deposits of the Bełchatów Lignite Mine (Central Poland). *Mycosphere*, 8: 1003–1013.

Worobiec, G., Worobiec, E. & Kasiński, J., 2008. Plant assemblages of the drill cores from the Neogene Ruja lignite deposit near Legnica (Lower Silesia, Poland). *Acta Palaeobotanica*, 48: 191–275.

Worobiec, G., Worobiec, E. & Liu, Y. C., 2018. Fungal remains from late Neogene deposits at the Gray Fossil Site, Tennessee, USA. *Mycosphere*, 9: 1014–1024.

Worobiec, G., Worobiec, E. & Widera, M., 2022b. Middle Miocene wetland fungi from the Adamów Lignite Mine, central Poland. *Historical Biology*, 34: 841-856.

Zachos, J., Pagani, M., Sloan, L., Thomas, E. & Billups, K., 2001. Trends, rhythms, and aberrations in global climate 65 Ma to present. *Science*, 292: 686–693.

Zhao, G. Z., Liu, X. Z. & Wu, W. P., 2007. *Helicosporous hyphomycetes* from China. *Fungal Diversity*, 26: 313–524.

Zieliński, T. & Widera, M., 2020. Anastomosing-to-meandering transitional river in sedimentary record: A case study from the Neogene of central Poland. *Sedimentary Geology*, 404: 105677.

Ziembińska, M. & Niklewski, J., 1966. Stratigraphy and correlation of brown coal beds in the Ścinawa deposits on the basis of spore-pollen analysis. *Biuletyn Instytutu Geologicznego*, 202: 27–48. [In Polish, with English summary.]

Ziembińska-Tworzydło, M., 1974. Palynological characteristics of the Neogene of Western Poland. *Acta Palaeontologica Polonica*, 19: 309–467.

Ziembińska-Tworzydło, M. & Ważyńska, H., 1981. A palynological subdivision of the Neogene in Western Poland. *Bulletin of the Polish Academy of Sciences. Earth Sciences*, 29: 29–43.

Appendix

The mean annual temperature (MAT) reconstruction, 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). The MAT ranges refer to entire genera, not individual species.

Fossil taxa	Nearest Living Relatives	MAT range [°C]
Cathayapollis spp.	*Cathaya*	13.4–18.0
Piceapollis sp.	*Picea*	-8.9–21.7
Zonalapollenites spp.	*Tsuga*	-5.0–21.9
Aceripollenites spp.	*Acer*	-1.1–24.0
Alnipollenites verus	*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
Cornaceaepollis sp.	*Cornus*	-12–23.1
Corylopsispollenites microreticulatus	*Corylopsis*	9.1–25.5
Cyrillaceaepollenites spp.	*Cyrilla racemiflora* *Clethra*	13.6–23.9 7.4–27.7
Faguspollenites spp.	*Fagus*	4.4–23.1
Fraxinipollis spp.	*Fraxinus*	0.0–24.0
Ilexpollenites spp.	*Ilex*	-0.4–27.7
Iteapollis angustiporatus	*Itea*	7.7–27.7
Juglanspollenites verus	*Juglans*	0.0–27.5
Myricipites sp.	*Myrica*	-8.9–28.1
Nyssapollenites sp.	*Nyssa*	4.4–23.9
Nyssoidites rodderensis	*Nyssa*	4.4–23.9
Periporopollenites stigmosus	*Liquidambar*	11.5–25.5
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 vestibulum	*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 spp.	*Zelkova*	6.2–21.9

Coexistence interval: 15.7–17.8 °C
Bordering taxa: 15.7–27.8 °C – *Cornaceaepollis satzveyensis*
2.2–17.8 °C – *Cercidiphyllites minimireticulatus*
no outliers

*According to Fang *et al*. (2011) MAT for modern *Cercidiphyllum japonicum* is 2.0–18.2 °C.