Annales Societatis Geologorum Poloniae (2025), vol. 95: 161–178 https://doi.org/10.14241/asgp.2025.11

POLLEN AND NON-POLLEN PALYNOMORPHS AS TOOLS FOR INTERPRETING PALAEOENVIRONMENTAL CHANGES IN THE MIOCENE LIGNITE IN THE CHŁAPOWO CLIFF (NORTHERN POLAND)

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

[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., Worobiec, G. & Widera, M., 2025. Pollen and non-pollen palynomorphs as tools for interpreting palaeoenvironmental changes in the Miocene lignite in the Chłapowo Cliff (northern Poland). *Annales Societatis Geologorum Poloniae*, 95: 161–178.

Abstract: Palynological analysis of samples taken from the lignite, exposed in the Chłapowo Cliff on the southern Baltic coast, allowed the reconstruction of the vegetation and palaeoclimate that predominated during the accumulation of the peat, from which the lignite was formed. In addition to pollen grains and spores, particular attention was given to non-pollen palynomorphs, such as algal, fungal and invertebrate micro-remains (Cladocera) that enabled a more accurate reconstruction of the palaeoenvironment. The lignite belongs to the 2nd Lusatian seam, which is an important correlation level in Central Europe, dated to the latest Early Miocene to the early Middle Miocene. The textural and structural features of the lignite seam indicate that the depositional environment of the peat is loosely combined with the overbank zone of an anastomosing or meandering river system. The results of the palynological study show the presence of wetland vegetation, including shrub bogs (most similar in their composition to modern pocosins, growing between river channels) and riparian forests, growing on periodically flooded areas and mesophilous vegetation, occurring in the vicinity. The composition of the palynoflora, including the thermophilic taxa, such as Sapotaceae and Meliaceae, indicates that the climate was warm, close to subtropical, with a mean annual temperature range of 15.7–17.8 °C.

Key words: Palynology, palaeovegetation, palaeoclimate, lignite seams, Neogene, Baltic coast, Central Europe.

Manuscript received 21 July 2025, accepted 25 September 2025

INTRODUCTION

Geological and palynological investigations on the Gdańsk coast (part of the Baltic Sea coast in northern Poland) have a long history, mainly due to the search for amber in this area (e.g., Piwocki *et al.*, 1985). Lignite-bearing deposits, exposed in the Chłapowo Cliff, also have been a matter of interest for a long time. The Miocene age of the lignite and co-occurring deposits was determined on the basis of studies of the fossil macroflora by Heer (1869). It was confirmed by other palaeobotanical (Zabłocki, 1935; Passendorfer and Zabłocki, 1946) and palynological (Grabowska, 1976) studies. In 1981, three full-core wells were drilled in the area (Chłapowo I, Chłapowo II and Chłapowo III), the main purpose of which was to identify amber-bearing deposits. Palynostratigraphic analysis of samples from those drill cores revealed palynological assemblages, characteristic of the Upper Cretaceous, Paleogene and Neogene, while Miocene sediments were analysed only in six samples from the Chłapowo I profile (Grabowska, 1987; Grabowska and Ważyńska, 1997). Therefore, palynological spectra from the cliff sediments so far have been the main source of data on these Miocene lignite-bearing sediments (Grabowska, 1976). Forty samples, taken from a 10-m-thick section, were analysed at that time, with lignite present in the form of several interbeds of different thicknesses in the middle part. However, most of the sediments were sand and silt with sand (Grabowska, 1976).

Lignite deposits are among the richest archives of data about the palaeovegetation and palaeoclimate of the Paleogene and Neogene. They are also important correlation horizons. This applies to the 2nd Lusatian lignite seam

(LLS-2), which includes lignite, exposed in the Chłapowo Cliff. LLS-2 occurs in an area of approximately 61,100 km^2, mainly in southwestern and central Poland, excluding the Carpathians (Piwocki, 1992, 1998; Kasiński *et al.*, 2010; Kasiński and Słodkowska, 2016). During the accumulation of the peat, from which this lignite was formed, conditions favouring the development of lush peat-forming vegetation existed across a large area of Central Europe (e.g., Zachos *et al.*, 2001; Mosbrugger *et al.*, 2005; Bruch *et al.*, 2007; Utescher *et al.*, 2012). Due to the fact that it reaches a thickness of several dozen to over 100 m (Kasiński and Słodkowska, 2016; Widera, 2021), LLS-2 is (or was in the past) exploited in several open-cast mines in the Konin-Adamów Region (i.e., Lubstów), the Western Region (e.g., Turów, Sieniawa), and the Łódź-Bełchatów Region (Bełchatów and Szczerców). This seam is also correlated with the 2nd Lusatian seam in the southeastern territory of Germany (Widera, 2016; Kus *et al.*, 2020), where in the Lusatia Region most of the lignite mining is concentrated in this seam (Holdgate *et al.*, 2016). The research area at Chłapowo is particularly interesting, because it is located in the northernmost part of Poland and therefore also the northernmost part of the range of this group of lignite seams. The Miocene lignite-bearing deposits, exposed in the Chłapowo Cliff, continue to attract research interest (e.g., Kramarska *et al.*, 2008; Kowalski and Worobiec, 2018; Widera, 2019). Half a century after Grabowska's (1976) research, detailed palynological studies were carried out, the results of which are included in this paper, focusing on a layer of lignite, over 2 m thick.

The main aim of the present study is to reconstruct plant communities and determine which represent the source of material for the formation of the Chłapowo lignite. Spore-pollen analysis and non-pollen palynomorphs (freshwater algae, fungal and invertebrate micro-remains) are also a source of data for palaeoclimatic and palaeoenvironmental interpretations to provide new insights into the latest Early Miocene to the early Middle Miocene evolution of vegetation and climate dynamics in Central Europe. That time is of particular interest, because the Miocene Climate Optimum (covering 16.9–14.7 Ma) took place then, which was the warmest period on Earth in the last ~25 myr (Böhme, 2003; Steinthorsdottir *et al.*, 2021).

GEOLOGICAL SETTING

The lignite section from the Chłapowo site examined palynologically is situated on the Baltic Sea coast, in northern Poland (Fig. 1). More precisely, it is located in the vicinity of the town of Władysławowo (54º48′58.6″N, 18º21′40.4″E), that is, ca. 0.7 km to the west of the Chłapowo Ravine (Fig. 1C).

The study area constitutes a fragment of the so-called Chłapowo Cliff, which is up to 10 m high, on both sides of the aforementioned Chłapowo Ravine. Thanks to coastal erosion, landslides are triggered, but also the sediments, from which the cliff is built, are exposed (Uścinowicz *et al.*, 2017). During fieldwork (September 2018), the cliff profile with Miocene and Quaternary sediments outcropped particularly well (Fig. 1C). The selected exposure was ca. 9.5 m high in relation to the sea level and ca. 8.5 m in relation to the beach level. In addition, it contained a 2.1-m-thick bed of lignite, which is the most important in the context of the present research (Figs 2, 3). The lower 7.4 m of the cliff walls are Miocene sediments, such as sands, coaly sands, coaly muds, and lignites. Above the erosional boundary lies a relatively thin bed of Quaternary sediments, mostly of glacial origin. They are represented by sands, gravels, muds, and tills (see Fig. 2). The described part of the Chłapowo Cliff is not glaciotectonically deformed, unlike the surroundings, where the traces of such deformations are clear (Wagner, 2007; Widera, 2019). This means that the studied lignite seam is preserved *in situ*.

The Miocene deposits represent two main lithostratigraphic units, that is, the Rawicz and Ścinawa formations (Fig. 2). The first predominantly consists of sands, in places carbonaceous, which are planar and trough cross-stratified on a large scale. Some researchers consider them typical of the Early Miocene depositional environment of a braided river system (Widera *et al.*, 2021b). However, in terms of the present research, much more important is the Ścinawa Formation (in northern Poland also called the Krajenka Formation) of Early–Middle Miocene age, as it contains lignites that usually were palynologically analysed. The above-mentioned lignites are considered to be the equivalent of the second Lusatian lignite seam (LLS-2) in other parts of Poland (Wagner, 2007). The age of its accumulation in the areas of tectonic grabens, where the LLS-2 thickness ranges from several dozen to >100 m, is estimated at the interval from the latest Early Miocene to the early Middle Miocene (Piwocki and Ziembińska-Tworzydło, 1997; Widera, 2021). The LLS-2, from which the samples were collected (see Fig. 2), is characterised by detritic and xylodetritic lignite lithotypes – without or occasionally with pieces of wood, respectively. The structure of these lithotypes is massive and horizontal, which is emphasised by thin (i.e., up to a few mm) layers of sand (Widera, 2019). Hence, the lignite from the Chłapowo Cliff, although it was exploited in 1859, has a lower calorific value than the lignites belonging to the LLS-2, mined in Poland on an industrial scale (cf. Wagner, 2007; Widera, 2021).

MATERIALS AND METHODS

Twenty-one samples were taken from the lignite layer at intervals of ca. 10 cm (Fig. 2). The samples were processed at the Laboratory of the W. Szafer Institute of Botany PAS, according to the following procedure: a portion of about 1 cm^3 of cleaned and 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). 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 samples, sporomorphs (pollen grains and spores of plants) and co-occurring non-pollen palynomorphs (NPPs), such as algal and fungal remains, were studied.

Fig. 1. Location maps of the Chłapowo site with the lignite bed analysed palynologically.

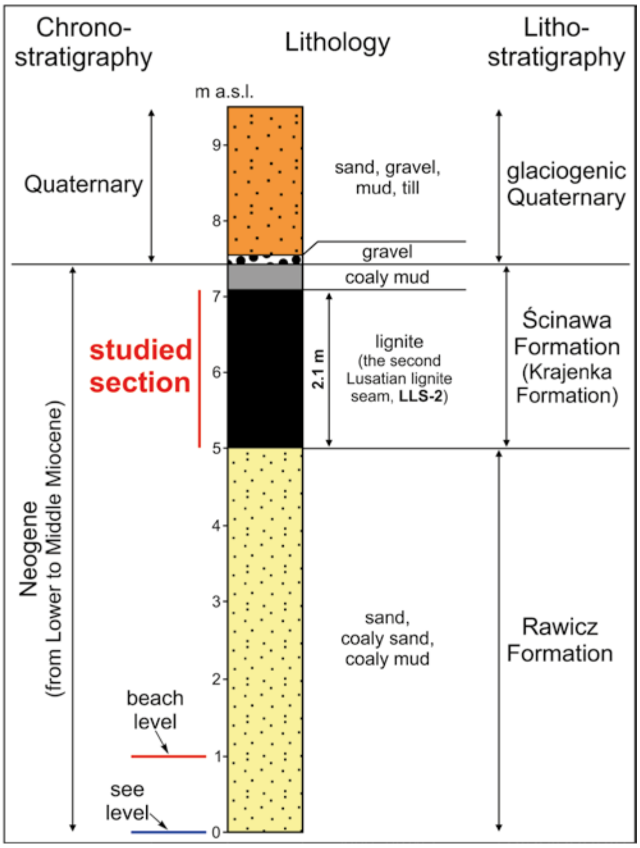

Fig. 2. Position of the studied section of the lignite seam in the Chłapowo site against a background of the chrono- and litho-stratigraphic subdivision of the Cenozoic. For the location of the Chłapowo site, see Figure 1.

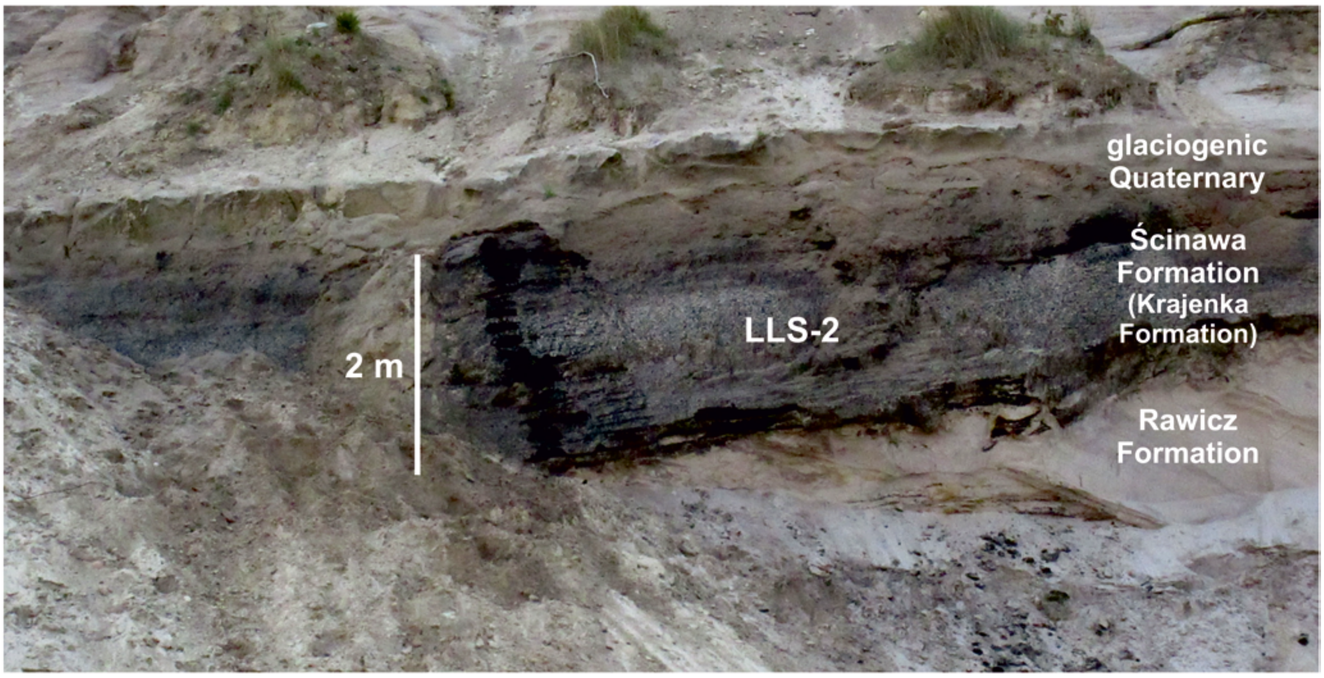

Fig. 3. Field photograph of the studied site.

Data from the palynological spectra were used to construct a simplified palynological diagram. In this diagram, the percentages of the pollen taxa were calculated from the total sum of the pollen grains; with the proportions of cryptogam spores and non-pollen palynomorphs, computed separately in relation to the total sum, using the POLPAL computer programme (Nalepka and Walanus, 2003). Microphotographs of selected palynomorphs 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). 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). The obtained spore-pollen spectra were correlated with the palynostratigraphic scheme for the Neogene of the Polish Lowlands area (Piwocki and Ziembińska-Tworzydło, 1997; Ziembińska-Tworzydło, 1998). The mean annual temperature (MAT) estimation in this study is based on the Coexistence Approach (CA) method (Utescher *et al.*, 2014). This method is based on the Nearest Living Relative (NLR) concept, which suggests that a given fossil taxon lived in conditions similar to those of its modern representative. The NLR provides the necessary information to determine the climatic distribution interval (coexistence interval), within which all the plants present in a fossil flora could have lived (Mosbrugger and Utescher, 1997; Utescher *et al.*, 2014). As many taxa as possible were selected for the CA method, excluding fossil taxa of unknown botanical affinity, taxa related to families, and aquatic taxa (e.g., according to Utescher *et al.*, 2014; Prader *et al.*, 2017). The nearest living relatives and their MAT ranges are taken from the Palaeoflora Database (Utescher and Mosbrugger, 2015; Utescher *et al.*, 2024), supplemented with other available climatic data (Fang *et al.*, 2011).

RESULTS

Palynofacies

Sedimentary organic matter, preserved in palynological samples from the lignite seam from the Chłapowo Cliff, consists of predominantly structured organic matter (SOM), both palynomorphs (plant sporomorphs, fungal spores and sporocarps, and phytoplankton) and palynomacerals, mostly structured phytoclasts (cuticles, wood and root tissues, fungal hyphae). Phytoclasts are represented by both opaque and translucent macerals. Amorphous organic matter (AOM) is represented, e.g., by resin particles. Some coalified or highly gelified structureless plant tissues are also present. No traces of marine palynomorphs and palynomacerals were found. Palynofacies from the lowermost samples, Ch1–Ch7, are dominated by small to large, opaque and translucent phytoclasts in varying proportions; opaque phytoclasts are usually strongly degraded. Palynomorphs are commonly found. In samples Ch8–Ch11, translucent phytoclasts predominate, mostly as fragments of usually well-preserved plant tissues. Sample Ch9 contains a significant amount of fungal material, in the form of fungal hyphae and spores. From sample Ch12, opaque, often strongly degraded phytoclasts again account for a significant proportion among palynomacerals. However, the content of translucent phytoclasts is still important in some of the samples. From sample Ch15 upwards, the proportion of plant sporomorphs decreases significantly, but fungal spores and sporocarps are in similar proportions, as in the previous samples. The uppermost Ch20–Ch21 samples are dominated by opaque, often highly degraded phytoclasts.

Pollen and spores of plants

All studied samples yielded well-preserved pollen grains and plant spores (Figs 4, 5), suitable for detailed palynological analysis (Tab. 1). In most samples, 300–500 pollen grains and plant spores were counted, except for sample Ch16, in which approximately 200 sporomorphs were counted, due to their lower frequency. A total of 114 fossil-species from 72 fossil-genera (including 13 species of plant spores, 25 species of gymnosperm pollen, and 76 species of angiosperm pollen) were identified (Tab. 1). In all samples, pollen from coniferous and deciduous trees and shrubs clearly predominate, while pollen grains of herbs and plant spores are rare (Fig. 6).

Among gymnosperms (Fig. 4C–H), the most common are *Pinus*, Cupressaceae (mainly pollen grains with distinct papillae usually related to *Sequoia/Sequoiadendron/Metasequoia/Cryptomeria*, but also others, including those related to *Taxodium/Glyptostrobus*) and *Sciadopitys*. In addition, several pollen grains from *Cathaya*, *Picea*, *Cedrus*, *Keteleeria* and *Tsuga* are present. Among angiosperms (Fig. 4I–GG), the most common are pollen grains of the fossil-species *Tricolporopollenites pseudocingulum* and those from *Myrica*, *Betula*, Cyrillaceae/Clethraceae (mainly the fossil-species *Cyrillaceaepollenites megaexactus*), Ericaceae and *Ilex*. Pollen grains of *Quercus* (*Quercoidites henricii* and *Quercopollenites*), *Fagus*, *Carpinus*, Mastixiaceae (*Cornaceaepollis satzveyensis*), fossil-genus *Edmundipollis*, Castaneoideae, Fabaceae (mainly *Tricolporopollenites fallax* and *T. liblarensis*), Engelhardioideae, Oleaceae, *Acer*, *Fraxinus*, *Nyssa* (mainly the fossil-genus *Nyssapollenites*), *Alnus*, *Cercidiphyllum*, *Salix* and *Ulmus* are recorded regularly, but in low percentages. In addition, several pollen grains of *Arceuthobium*, *Celtis*, *Cornus*, *Corylopsis*, *Diospyros*, *Eucommia*, *Itea*, *Liquidambar*, *Magnolia*, *Platanus*, *Vitis*, *Zelkova* and members of the families Araliaceae, Rhamnaceae and Tilioideae as well as the fossil-species *Parthenopollenites marcodurensis* are present. Pollen from *Carya*, *Platycarya*, *Pterocarya*, *Symplocos*, Meliaceae, Sapotaceae and the fossil-species *Tricolporopollenites mangiferoides* were found only in the lower part of the profile. Similarly, herbaceous plants, including Cyperaceae, Poaceae, Sparganiaceae/Typhaceae and a few *Utricularia* pollen grains, were mainly found in the lower part of the profile.

Spores of ferns (Fig. 4B) from the families Lygodiaceae, Osmundaceae and probably Davalliaceae, Polypodiaceae and Gleicheniaceae, including the fossil-genera *Baculatisporites*, *Laevigatosporites*, *Leiotriletes*, *Neogenisporis* and *Verrucatosporites*, are encountered regularly, but in low quantities. Spores of Lycopodiaceae (fossil-genera *Camarozonosporites* and *Retitriletes*) and *Sphagnum* (fossil-genera *Distancoraesporis* and *Stereisporites*; Fig. 4A) are very rare.

Table 1

Spores and pollen grains, recorded in samples from Chłapowo. 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 taxon	Botanical affinity	Element
Spores of plants		
Baculatisporites primarius (Wolff) Thomson et Pflug	Osmundaceae: *Osmunda*	P/A
Baculatisporites sp.	Osmundaceae: *Osmunda*	P/A
Camarozonosporites decorus (Wolff) Krutzsch	Lycopodiaceae: *Lycopodiella*	P
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 maxoides Krutzsch	Lygodiaceae	P
Leiotriletes sp.	Lygodiaceae and other ferns	P
Neogenisporis crassicus Krutzsch	p.p. Gleicheniaceae	P1
Neogenisporis neogenicus Krutzsch	p.p. Gleicheniaceae	P1
Retitriletes sp.	Lycopodiaceae: *Lycopodium*	A
Stereisporites sp.	Sphagnaceae: *Sphagnum*	P/A
Verrucatosporites sp.	Davalliaceae, Polypodiaceae, and other ferns	P/A
Pollen grains of gymnosperms		
Cathayapollis erdtmanii (Sivak) Ziembińska-Tworzydło	Pinaceae: *Cathaya*	A1
Cathayapollis potoniei (Sivak) Ziembińska-Tworzydło	Pinaceae: *Cathaya*	A1
Cathayapollis sp.	Pinaceae: *Cathaya*	A1
Cedripites sp.	Pinaceae: *Cedrus*	A1
Cupressacites bockwitzensis Krutzsch	Cupressaceae	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
Inaperturopollenites verrupapilatus Trevisan	Cupressaceae: *Taxodium*, *Glyptostrobus*	P2/A1
Keteleeriapollenites dubius (Khlonova) Słodkowska	Pinaceae: *Keteleeria*	A1
Piceapollis planoides Krutzsch	Pinaceae: *Picea*	A
Piceapollis sp.	Pinaceae: *Picea*	A
Pinuspollenites labdacus (Potonié) Raatz	Pinaceae: *Pinus sylvestris* type	A
Pinuspollenites sp.	Pinaceae: *Pinus*	A
Sciadopityspollenites quintus Krutzsch et Ziembińska-Tworzydło	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 megaligulus Krutzsch	Cupressaceae: *Sequoiadendron*	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 sp.	Pinaceae: *Tsuga*	A

Fossil taxon	**Botanical affinity**	**Element**
Pollen grains of angiosperms		
Aceripollenites sp.	Sapindaceae: *Acer*	A
Alnipollenites verus Potonié	Betulaceae: *Alnus*	P2/A
Araliaceoipollenites euphorii (Potonié) Potonié	Araliaceae	P/A1
Arecipites sp.	Araceae, Arecaceae, Butomaceae	P/A
Carpinipites carpinoides (Pflug) Nagy	Betulaceae: *Carpinus*	P2/A1
Caryapollenites simplex (Potonié) Raatz	Juglandaceae: *Carya*	A1
Celtipollenites sp.	Ulmaceae: *Celtis*	P/A1
Cercidiphyllites minimireticulatus (Trevisan) Ziembińska-Tworzydło	Cercidiphyllaceae: *Cercidiphyllum*	A1
Cornaceaepollis major (Stuchlik) Stuchlik	Cornaceae: *Cornus*	P/A
Cornaceaepollis satzveyensis (Pflug) Ziembińska-Tworzydło	Mastixiaceae: *Mastixia*	P1
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
Cyrillaceaepollenites brühlensis (Thomson) Durska	Cyrillaceae, Clethraceae	P
Cyrillaceaepollenites exactus (Potonié) Potonié	Cyrillaceae, Clethraceae	P
Cyrillaceaepollenites megaexactus (Potonié) Potonié	Cyrillaceae, Clethraceae	P
Edmundipollis edmundii (Potonié) Konzalová, Słodkowska et Ziembińska-Tworzydło	Cornaceae, Mastixiaceae	P1
Edmundipollis sp.	Cornaceae, Mastixiaceae, Araliaceae	P/A
Diospyrospollenites ovalis (Tarasevich) Skawińska	Ebenaceae: *Diospyros*	P
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 parainstructus Krutzsch	Malvaceae: Tilioideae	P2/A
Intratriporopollenites sp.	Malvaceae: Brownlowioideae, Tilioideae	P/A
Iteapollis angustiporatus (Schneider) Ziembińska-Tworzydło	Iteaceae: *Itea*	P
Lentibulariaceaepollenites miocaenicus Thiele-Pfeiffer	Lentibulariaceae: *Utricularia*	P/A
Magnoliaepollenites magnolioides (Krutzsch) Planderová	Magnoliaceae: *Magnolia*	P/A1
Meliaceoidites sp.	Meliaceae	P
Momipites punctatus (Potonié) Nagy	Juglandaceae: *Engelhardia*, *Alfaroa*, *Oreomunnea*	P2
Myricipites coryphaeus (Potonié) Potonié	Myricaceae	P2/A1
Myricipites pseudorurensis (Pflug) Grabowska et Ważyńska	Myricaceae: *Myrica*	A
Myricipites sp.	Myricaceae	P2/A
Nyssapollenites analepticus (Potonié et Venitz) Planderová	Nyssaceae: *Nyssa*	P/A1

Fossil taxon	Botanical affinity	Element
Nyssapollenites pseudocruciatus (Potonié) Thiergart ex Potonié	Nyssaceae: *Nyssa*	P/A1
Nyssapollenites sp.	Nyssaceae: *Nyssa*	P/A1
Nyssoidites rodderensis Thiergart	Nyssaceae: *Nyssa*	P/A1
Oleoidearumpollenites microreticulatus (Pflug et Thomson) Ziembińska-Tworzydło	Oleaceae	P2/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
Platanipollis ipelensis (Pacltová) Grabowska	Platanaceae: *Platanus*	P/A1
Platycaryapollenites sp.	Juglandaceae: *Platycarya*	P2/A1
Polyatriopollenites stellatus (Potonié) Pflug	Juglandaceae: *Pterocarya*	A1
Quercoidites henricii (Potonié) Potonié, Thomson et Thiergart	Fagaceae: *Quercus*	P2/A1
Quercopollenites rubroides Kohlman-Adamska et Ziembińska-Tworzydło	Fagaceae: *Quercus*	A1
Quercopollenites sp.	Fagaceae: *Quercus*	A1
Rhamnaceaepollenites triquetrus Thiele-Pfeiffer	Rhamnaceae	P2/A
Rhuspollenites ornatus Thiele-Pfeiffer	Anacardiaceae: *Rhus*	P/A1
Salixipollenites sp.	Salicaceae: *Salix*	A
Sapotaceoidaepollenites sp.	Sapotaceae	P
Sparganiaceaepollenites sp.	Sparganiaceae, Typhaceae	P/A
Spinulaepollis arceuthobioides Krutzsch	Santalaceae: *Arceuthobium*	P2/A1
Subtriporopollenites sp.	Juglandaceae?	P
Symplocoipollenites vestibulum (Potonié) Potonié	Symplocaceae: *Symplocos*	P
Tricolporopollenites fallax (Potonié) Krutzsch	Fabaceae	P/A
Tricolporopollenites leonensis Kohlman-Adamska et Ziembińska-Tworzydło	Styracaceae?, Fagoideae?	P/A
Tricolporopollenites liblarensis (Thomson) Hochuli	Fabaceae	P/A
Tricolporopollenites mangiferoides Słodkowska	Anacardiaceae: *Mangifera*	P1
Tricolporopollenites pseudocingulum (Potonié) Thomson et Pflug	Fagaceae?, Styracaceae?	P/A1
Tricolporopollenites quisqualis (Potonié) Krutzsch	Fabaceae	P/A
Trivestibulopollenites betuloides Pflug	Betulaceae: *Betula*	A
Ulmipollenites stillatus Nagy	Ulmaceae: *Ulmus*	A
Ulmipollenites undulosus Wolff	Ulmaceae: *Ulmus*	A2
Vitispollenites tener Thiele-Pfeiffer	Vitaceae: *Vitis*	P2/A1
Zelkovaepollenites sp.	Ulmaceae: *Zelkova*	A1

Non-pollen palynomorphs

Among freshwater algae, the most common are colonies of *Botryococcus braunii*, and several of them were found in the slides from samples Ch3, Ch5, Ch6, Ch9, Ch11, Ch12 and Ch15. Several resting zygotes of green algae from the Zygnemataceae family were encountered (Tab. 2), most likely including *Spirogyra* (single specimens of the fossil-species *Ovoidites ligneolus* in samples Ch2 and Ch3 and *Ovoidites elongatus* in sample Ch10) and *Mougeotia* (single specimens of the fossil-species *Tetrapidites* sp. in samples Ch18 and Ch19; Fig. 5A). One resting zygote from Closteriaceae (fossil-genus *Closteritetrapidites* in sample Ch3) was recorded. In the upper part (samples Ch17–Ch19), resting zygotes of desmids from the fossil-species *Desmidiaceaesporites cosmarioformis* are present (Fig. 5B, C). In addition, one specimen of *Sigmopollis pseudosetarius* was encountered in the uppermost sample (Ch21).

The interesting micro-remains of a freshwater Crustacea were found in sample Ch6, namely the shell of the cladoceran (water flea) genus *Chydorus* from the Chydoridae family (Fig. 5I, J). It is worth noting that the pre-Quaternary fossil record of Cladocera is very scarce (Van Damme and Kotov, 2016) and this is only the second site after Bełchatów

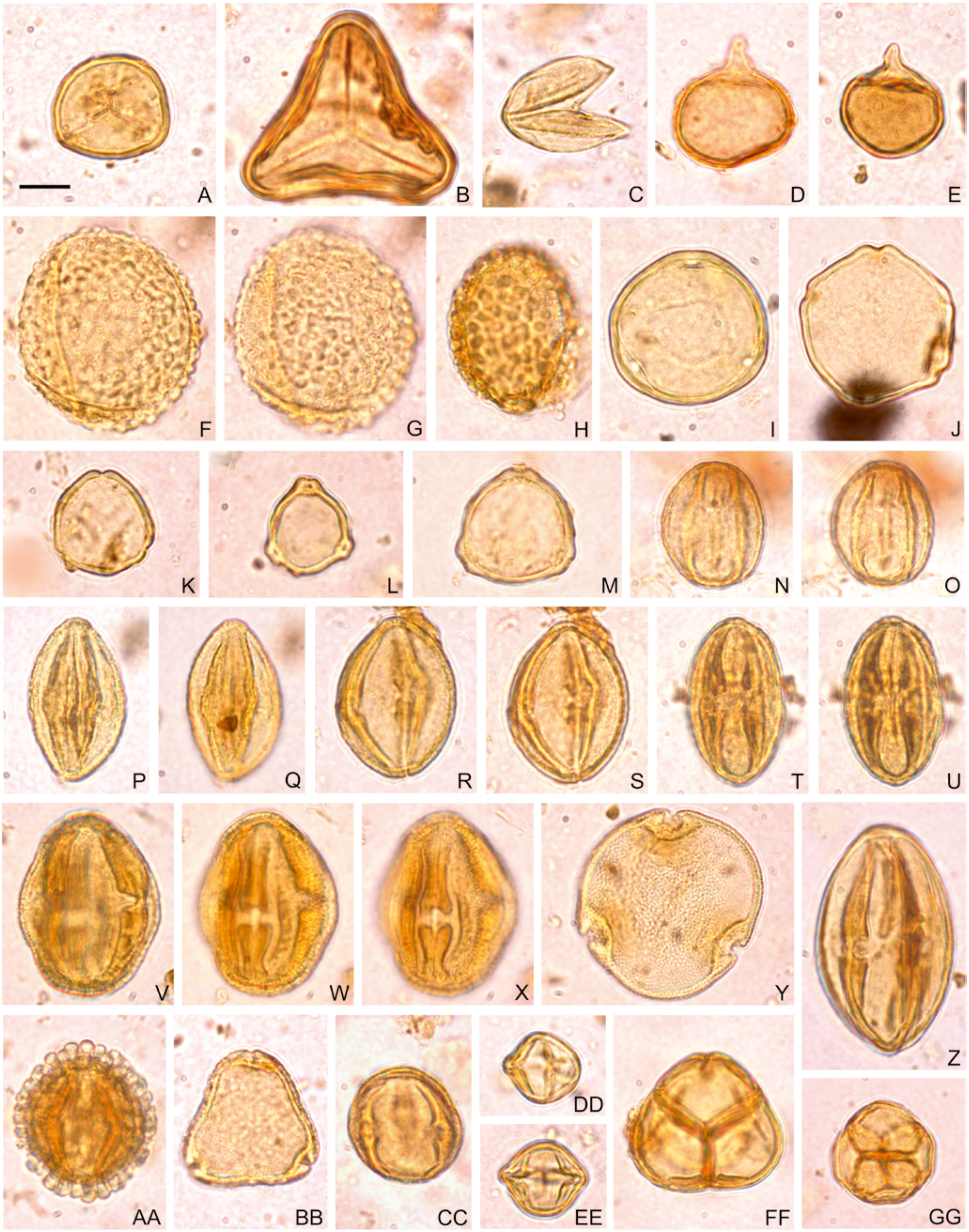

Fig. 4. Spores and pollen grains from Chłapowo. **A.** *Stereisporites* sp., sample Ch4. **B.** *Neogenisporis crassicus* Krutzsch, sample Ch10. **C.** *Inaperturopollenites concedipites* (Wodehouse) Krutzsch, sample Ch9. **D.** *Sequoiapollenites megaligulus* Krutzsch, sample Ch2. **E.** *Sequoiapollenites rotundus* Krutzsch, sample Ch8. **F, G.** *Sciadopityspollenites verticillatiformis* (Zauer) Krutzsch, same specimen, various foci, sample Ch10. **H.** *Sciadopityspollenites serratus* (Potonié et Venitz) Raatz, sample Ch10. **I.** *Caryapollenites simplex* (Potonié) Raatz, sample Ch2. **J.** *Polyatriopollenites stellatus* (Potonié) Pflug, Ch11. **K.** *Momipites punctatus* (Potonié) Nagy, sample Ch3. **L.** *Trivestibulopollenites betuloides* Pflug, sample Ch3. **M.** *Myricipites* sp., sample Ch14. **N, O.** *Quercopollenites rubroides* Kohlman-Adamska et Ziembińska-Tworzydło, same specimen, various foci, sample Ch9. **P, Q.** *Quercoidites henricii* (Potonié) Potonié, Thomson

Table 2

Non-pollen palynomorphs, recorded in deposits at Chłapowo. Biological affinity and indication according to Coesel and Meesters (2007), Worobiec (2014, and literature cited herein), Worobiec *et al.* (2022a), as well as Szeroczyńska and Sarmaja-Korjonen (2007).

Taxa	Biological affinity	Indication
Algae		
Botryococcus braunii Kützing	Dictyosphaeriaceae: *Botryococcus braunii*	open water, fresh and probably brackish waters
Closteritetrapidites sp.	Closteriaceae: *Closterium*	oligo- to eutrophic fresh waters
Desmidiaceaesporites cosmarioformis Hunger	Desmidiaceae: *Cosmarium*, *Euastrum*, *Staurastrum*, *Xanthidium*	clear, relatively nutrient-poor waters with low abundance of algae
Ovoidites elongatus (Hunger) Krutzsch	Zygnemataceae: *Spirogyra*	shallow, stagnant, oxygen-rich fresh waters, lake margins
Ovoidites ligneolus (Potonié) Thomson et Pflug	Zygnemataceae: *Spirogyra*	shallow, stagnant, oxygen-rich fresh waters, lake margins
Sigmopollis pseudosetarius (Weyland et Pflug) Krutzsch et Pacltová	Chlorophyta?, other algae?	eutrophic to mesotrophic open fresh waters
Tetrapidites sp.	Zygnemataceae: *Mougeotia*	shallow, stagnant, oxygen-rich fresh waters, lake margins
Fungi		
Helicoma sp.	*Helicoma* sp.	small, shallow freshwater bodies
Phragmothyrites sp.	Fungi	dense vegetation with a high proportion of trees and shrubs
cf. *Plochmopeltinites* sp.	Fungi	dense vegetation with a high proportion of trees and shrubs
Trichothyrites sp.	Fungi	dense vegetation with a high proportion of trees and shrubs
Invertebrates:		
Chydorus sp.	Chydoridae: *Chydorus*	freshwater habitats, including water bodies of various sizes and depths, from oligotrophic to eutrophic

(Dumont *et al.*, 2020), where such organic micro-remains of Cladocera have been found in the Neogene sediments.

Fungal spores, sporocarps and indeterminable fungal hyphae were found in all palynological samples from Chłapowo. Three ecological groups of fungi, mitosporic aero-aquatic fungi, epiphyllous fungi, and root-inhabiting endophytic fungi, can be distinguished. Epiphyllous fungi from Chłapowo were represented by sporocarps of the fossil-genera *Phragmothyrites*, cf. *Plochmopeltinites*, and *Trichothyrites* (Fig. 5G, H). The remains of root endophytic fungi were found as isolated microsclerotia of dark septate endophytes (DSE). Mitosporic aero-aquatic fungi were represented by helicosporous conidia, similar to representatives of the modern *Helicoma* genus (Fig. 5D–F). Fungal spores usually constitute less than 10% of the entire palynological spectrum, with a maximum of approximately 15% in sample Ch9.

DISCUSSION

Vegetation, palaeoenvironment and palaeoclimate

The results of the palynological study show the occurrence of bottomland wetland vegetation, including the plant communities, from which the lignite was formed (i.e., shrub bogs, riparian forests and swamp forests) and upland mesophilous communities, occurring in the vicinity. Many of the recorded taxa (e.g., *Acer*, *Betula*, *Celtis*, *Eucommia*,

---

et Thiergart, same specimen, various foci, sample Ch7. **R, S.** *Tricolporopollenites pseudocingulum* (Potonié) Thomson et Pflug, same specimen, various foci, sample Ch8. **T, U.** *Cornaceaepollis satzveyensis* (Pflug) Ziembińska-Tworzydło, same specimen, various foci, sample Ch20. **V-X.** *Edmundipollis edmundii* (Potonié) Konzalová, Słodkowska et Ziembińska-Tworzydło, same specimen, various foci, sample Ch10. **Y.** *Intratriporopollenites parainstructus* Krutzsch, sample Ch3. **Z.** *Diospyrospollenites ovalis* (Tarasevich) Skawińska, sample Ch10. **AA.** *Ilexpollenites iliacus* (Potonié) Thiergart, sample Ch10. **BB.** *Symplocoipollenites vestibulum* (Potonié) Potonié, sample Ch8. **CC.** *Nyssapollenites analepticus* (Potonié et Venitz) Planderová, sample Ch9. **DD.** *Cyrillaceaepollenites exactus* (Potonié) Potonié, sample Ch20. **EE.** *Cyrillaceaepollenites brühlensis* (Thomson) Durska, sample Ch2. **FF.** *Ericipites callidus* (Potonié) Krutzsch, sample Ch21. **GG.** *Ericipites costatus* Grabowska, sample Ch12. Scale bar in A: 10 µm, refers to all photographs.

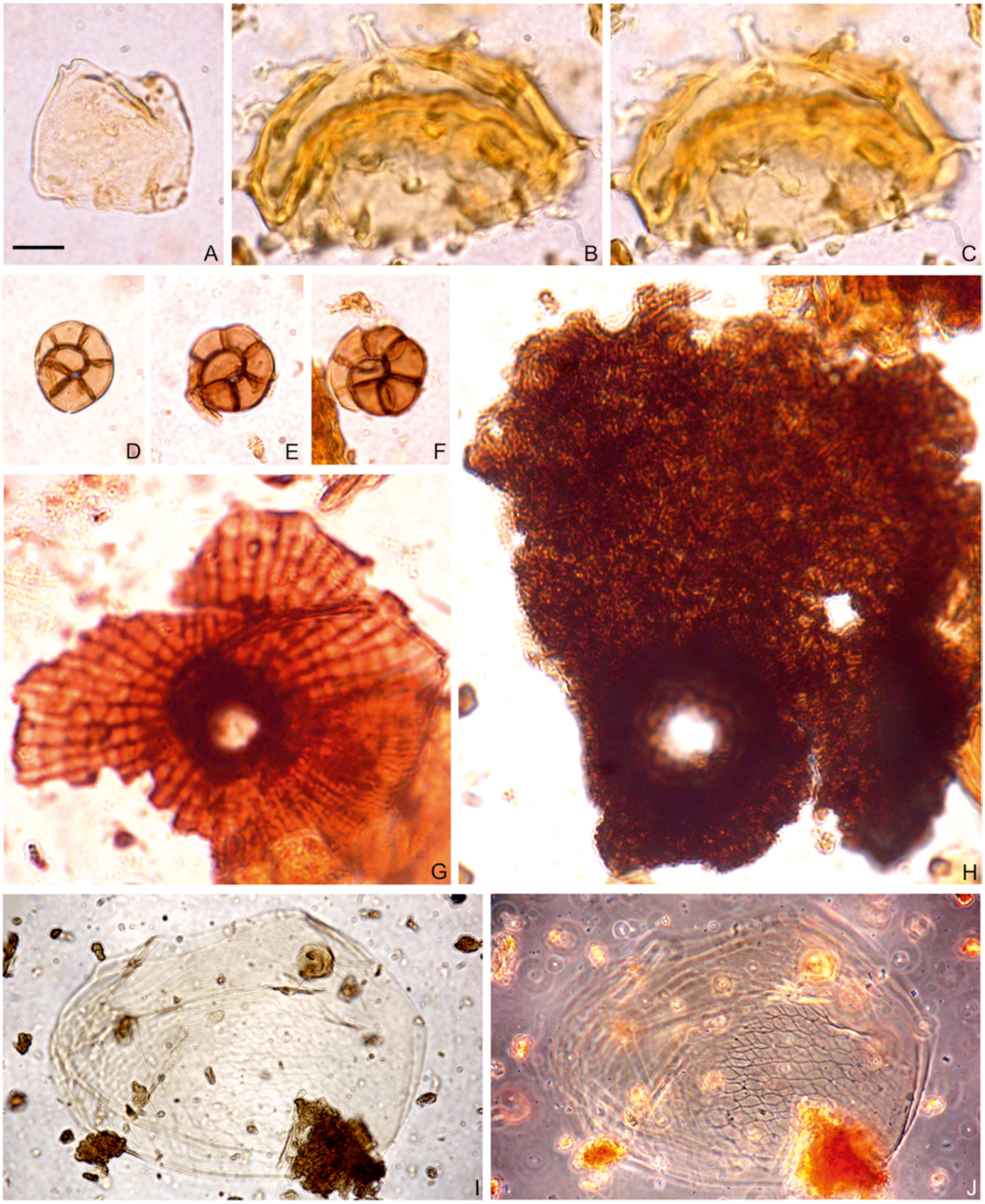

Fig. 5. Non-pollen palynomorphs from Chłapowo. **A.** *Tetrapidites* sp., sample Ch18. **B, C.** *Desmidiaceaesporites cosmarioformis* Hunger, same specimen, various foci, sample Ch18. **D.** *Helicoma* sp., sample Ch7. **E.** *Helicoma* sp., sample Ch5. **F.** *Helicoma* sp., sample Ch4. **G.** *Trichothyrites* sp., sample Ch10. **H.** cf. *Plochmopeltinites* sp., sample Ch14. **I, J.** *Chydorus* sp., same specimen; J – phase contrast, sample Ch6. Scale bar in A: 10 μm, refers to all photographs.

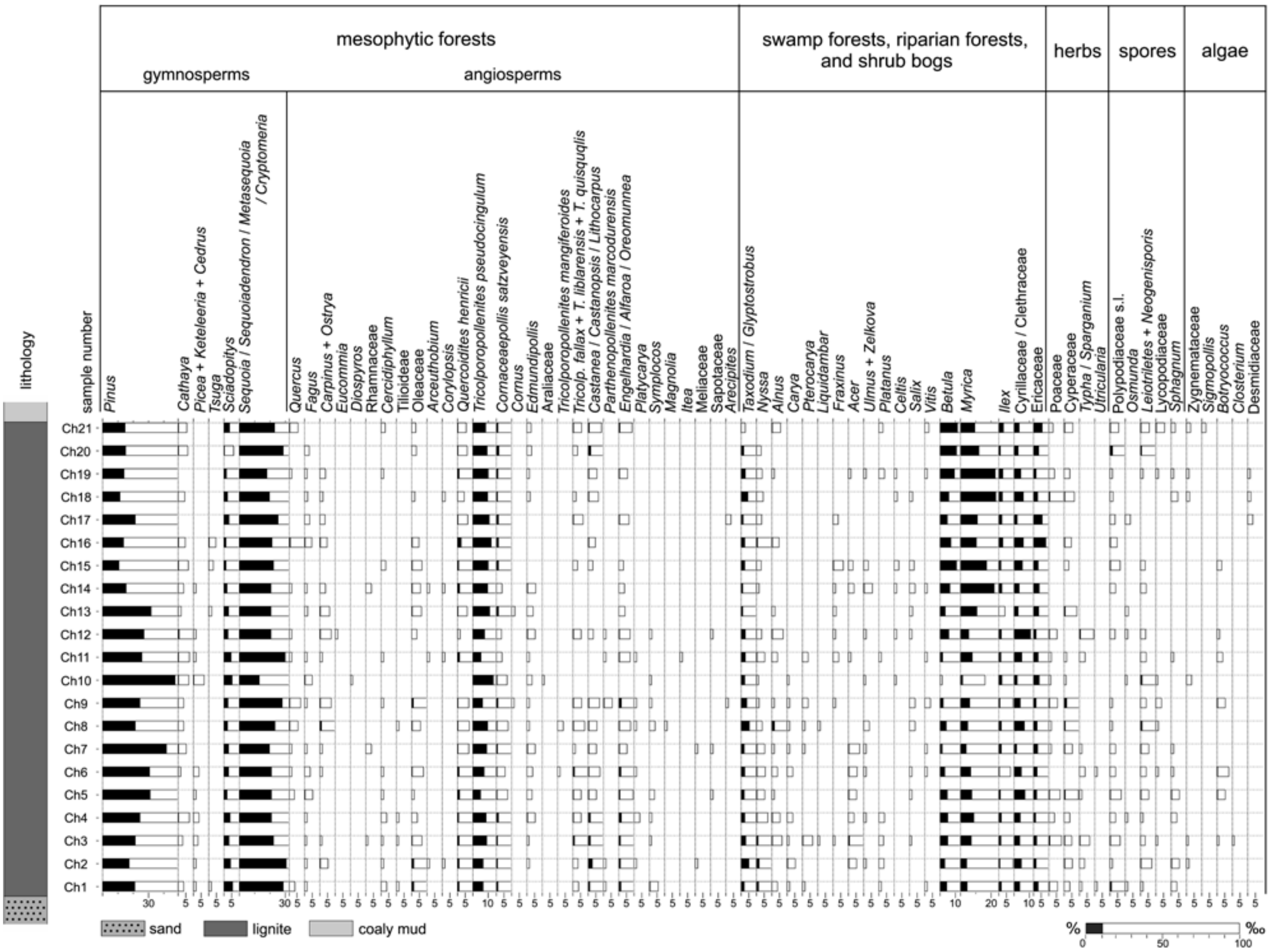

Fig. 6. Simplified percentage diagram of pollen and spores of plants as well as freshwater algae from the Chłapowo profile. Numbers in the bottom of the diagram show ranges of percentages for each taxon separately.

Fraxinus, *Pinus*, *Quercus*, and *Ulmus*) should not be associated with one specific type of vegetation, because their contemporary closest relatives occur in various habitats (cf. Worobiec and Szynkiewicz, 2016). The textural and structural features of the lignite seam, exposed in the Chłapowo Cliff, indicate that the depositional environment of the peat is loosely combined with the overbank zone of an anastomosing or meandering river system (see Widera, 2019). The results of the palynological research presented are consistent with those findings, as they showed the existence of plant communities, developing in such conditions. This applies in particular to the shrub bogs, most similar in their composition to modern pocosins, growing between river channels, and riparian forests, growing on periodically flooded areas.

Various members of the Cyrillaceae, Clethraceae and Ericaceae families as well as *Myrica* and *Ilex* probably were components of the shrub bogs. Modern pocosins occur on the south-eastern coastal plain of the USA from Virginia to north Florida and these communities produce thick peat deposits (Richardson, 2003). Their hydrology is palustrine, seasonally flooded or saturated. As they are watered mainly by rainfall (ombrotrophic), they are acidic and low-nutrient. The peat in modern pocosins is deep, so that plant roots never reach the mineral soil (Weakley and Schafale, 1991; Richardson, 2003). The presence of freshwater algae (including *Botryococcus*, *Closterium* and Zygnemataceae) and herbaceous plants (Cyperaceae, *Utricularia*, *Typha* and/or *Sparganium*), mainly in the lower part of the profile, indicates that there may have been small, temporary water bodies in the peat bog or that these plants and algae inhabited the banks of the river and its water. Additionally, a shell of the cladoceran *Chydorus* genus was found in sample Ch6. Extant members of this genus occur in various freshwater habitats, including water bodies of various sizes and depths, from oligotrophic to eutrophic (Szeroczyńska and Sarmaja-Korjonen, 2007).

The occurrence in the upper part of the profile of the fossil-species *Desmidiaceaesporites cosmarioformis*, most likely related to the resting zygotes of desmids, such as *Cosmarium*, *Euastrum*, *Staurastrum* or *Xanthidium* (Hunger, 1953), also indicates a freshwater, but rather nutrient-poor environment. Extant Desmidiaceae usually occur in clear, relatively nutrient-poor waters, with a low abundance of algae, often in small reservoirs, like pits in bogs (cf. Coesel and Meesters, 2007; Worobiec *et al.*, 2021). Their presence in the upper part of the profile may indicate the depletion of nutrients in the peat bog and the appearance of dystrophic conditions.

Some *Pinus* species may also have grown in peat bogs, just as modern *Pinus serotina* (pond pine) grows in modern pocosins (Sharitz and Gibbons, 1982; Weakley and Schafale, 1991). Similarly, *Sciadopitys* and *Sequoia* could grow in wet settings (Schneider, 1992; Mosbrugger *et al.*, 1994; Figueiral *et al.*, 1999; Kovar-Eder *et al.*, 2001; Worobiec *et al.*, 2021). In permanently or temporarily flooded places, *Taxodium* and/or *Glyptostrobus*, *Nyssa*, *Alnus*, *Acer*, *Betula*, *Fraxinus*, *Salix*, *Ulmus*, *Celtis*, *Liquidambar*, *Platanus*, *Vitis*, *Zelkova*, *Carya*, *Pterocarya*, *Osmunda* and others also grew. Nowadays, swamp forests with *Taxodium* and *Nyssa* occur 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).

Less humid places in the area, such as river terraces and upland localities, may have been overgrown with mesophilous communities. They were floristically rich and were characterised by a fairly significant share of plants of the "palaeotropical" element (both "tropical" and "subtropical"), with a significant share of "warm-temperate/palaeotropical" and "warm-temperate" taxa. Plants producing pollen of the fossil-species *Tricolporopollenites pseudocingulum*, *Quercus* (including thermophilous trees producing pollen of the fossil-species *Quercoidites henricii*), *Fagus*, Engelhardioideae, Castaneoideae, *Carpinus*, *Cercidiphyllum*, *Symplocos*, *Platycarya*, Araliaceae, Cornaceae, Mastixiaceae, Fabaceae, Tilioideae, Sapotaceae, *Corylopsis*, Meliaceae, Vitaceae, plus conifers and ferns, could have been components of these plant communities. The parasitic *Arceuthobium* lived on the branches of conifers (probably pine). Presently, similar mesophytic forests occur in warm temperate and subtropical climatic zones, mainly in China, Japan, Korea, Vietnam, and part of North America (Mai, 1981; Ching, 1991; Christensen, 2000).

The composition of the studied spore-pollen assemblages, including the occurrence of thermophilic taxa, such as Sapotaceae and Meliaceae, which currently have a pantropical distribution, indicates that the climate was warm, close to subtropical. The mean annual temperature (MAT), based on the coexistence approach (CA) method (Utescher *et al.*, 2014, 2024), was estimated in the range of 15.7–17.8 °C, with the bordering taxa: *Cercidiphyllites minimireticulatus* and *Cornaceaepollis satzveyensis* (Tab. 3).

Fossil fungi from Chłapowo most probably represent the remains of the indigenous fungal taxa of Miocene peat-forming communities. They could grow on dead plant debris, such as leaves, branches and trunks, and probably on living leaves and as endophytes in roots during the formation of peat, from which the lignite seam discussed was formed. Helicosporous aero-aquatic fungi, present in samples Ch1–Ch16 along with root endophytes (DSE), can suggest the presence of small, shallow-water bodies with variable water levels on peat bogs, and numerous plant roots in the peat layer indicate the dense vegetation cover, including trees and shrubs, during the time of peat deposition (Worobiec *et al.*, 2022a). Modern helicosporous aero-aquatic fungi are saprophytes, usually on decaying plant remains, such as leaves and wood, accumulated in small, shallow freshwater bodies, also located on raised bogs or tropical peat swamps. Aero-aquatic fungi sporulate only when their substrate is exposed to air and their conidia are dispersed by water (Dix and Webster, 1995; Goh and Hyde, 1996; Voglmayr, 1997; Webster and Weber, 2007; Zhao *et al.*, 2007; Markovskaja, 2012; Sri-Indrasutdhi *et al.*, 2015). The decline in the abundance of helicosporous aero-aquatic fungi and microsclerotia of root fungal endophytes, starting with sample Ch17, was probably caused by significant habitat changes, which were also manifested by the appearance of desmids and changes in palynofacies. The continuous presence of epiphyllous fungi in samples Ch10–Ch21 indicates the occurrence of dense vegetation with a high proportion of trees and shrubs at that time. These fungi inhabited the phyllosphere of leaves, both living and decaying as leaf litter, and may indicate the accumulation of leaf litter (Worobiec and Worobiec, 2017; Worobiec *et al.*, 2018, 2022a). Their presence may suggest a humid climate (Bannister *et al.*, 2016; Worobiec *et al.*, 2022a). The poorer state of preservation of palynomorphs (including sporomorphs and fungal remains) in the upper part of the profile may result from better access to oxygen. This, in turn, was probably the result of drying out of the overgrown pocosin peat bog.

Palynoflora from the Chłapowo Cliff in comparison with plant communities from other sites of the LLS-2 seam

The 2nd Lusatian seam (LLS-2) is relatively well-studied palynologically (Grabowska and Słodkowska, 1993; Worobiec *et al.*, 2022b and literature cited herein), due to its occurrence in a large area of the Polish Lowlands (Kasiński *et al.*, 2010; Kasiński and Słodkowska, 2016). The sites studied so far occur mainly in western and southwestern Poland (Sadowska, 1977; Wacnik and Worobiec, 2001; Worobiec, 2009; Kasiński *et al.*, 2010; Worobiec *et al.*, 2022b and unpublished reports by Sadowska cited herein), northwestern and central Poland (Stuchlik *et al.*, 1990; Ciuk and Grabowska, 1991; Kohlman-Adamska, 1993; Durska, 2008), northern Poland (Grabowska, 1987; Grabowska and Ważyńska, 1997; Słodkowska, 2004; Kramarska *et al.*, 2015) and Lusatia in eastern Germany (e.g., Thiergart, 1937; Krutzsch, 1970; Schneider, 1992; Dolezych and Schneider, 2006, 2007). The results of the present palynological investigations at Chłapowo are generally similar to other spectra from the 2nd lignite seam, correlated with the V spore-pollen zone – *Quercoidites henrici* phase and partly to the VI spore-pollen zone – *Tricolporopollenites megaexactus* phase (Piwocki and Ziembińska-Tworzydło 1997; Ziembińska-Tworzydło 1998), two zones from the beginning of the Middle Miocene. A recent palynological analysis of six samples of the lignite, containing fossil fruits from the Chłapowo Cliff, revealed that they could be correlated with the VI climatic phase (Kowalski and Worobiec, 2018).

The lists of taxa from various lignite deposits, belonging to LLS-2, are very similar and include such characteristic taxa as the fossil-species *Tricolporopollenites pseudocingulum*, *Quercoidites henricii*, *Cornaceaepollis satzveyensis*, *Cyrillaceaepollenites megaexactus*, *Caryapollenites simplex*, *Polyatriopollenites stellatus*, *Parthenopollenites marcodurensis*, *Cercidiphyllites minimireticulatus*, *Spinulaepollis arceuthobioides*, *Tricolporopollenites fallax* and/or *T. liblarensis*, *Symplocoipollenites vestibulum*, *Momipites*

Table 3

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; Utescher *et al.*, 2024). 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
Aceripollenites spp.	*Acer*	-1.1–24.0
Alnipollenites verus	*Alnus*	-13.3–27.4
Carpinipites carpinoides	*Carpinus*	0.0–25.8
Celtipollenites sp.	*Celtis*	2.5–25.8
Cercidiphyllites minimireticulatus	*Cercidiphyllum*	2.2–17.8*
Cornaceaepollis satzveyensis	*Mastixia*	15.7–27.8
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
Myricipites sp.	*Myrica*	-8.9–28.1
Nyssapollenites sp.	*Nyssa*	4.4–23.9
Nyssoidites rodderensis	*Nyssa*	4.4–23.9
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
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.

punctatus, members of the fossil-genera *Sciadopityspollenites*, *Nyssapollenites*, *Edmundipollis*, *Cupuliferoipollenites*, *Araliaceoipollenites*, *Arecipites*, *Myricipites*, *Ilexpollenites*, *Periporopollenites*, and members of the families Cupressaceae (pollen grains with distinct papillae and others), Magnoliaceae, and Sapotaceae (e.g., Słodkowska, 1998; Kasiński and Słodkowska, 2016). Differences are visible, mainly in the frequencies of taxa, belonging to various plant communities (e.g., Worobiec *et al.*, 2022b). This is most evident in the profiles, from which many samples were examined palynologically, which allowed a more detailed understanding of the composition of plant communities and their succession. For example, the *Taxodium/Glyptostrobus-Nyssa* swamp forests were widespread in Europe during the Oligocene to Pliocene. Their role was significant in the formation of Oligocene–Miocene lignites in Germany, including the Rhenish and Lusatian deposits (Mai, 1981; Schneider, 1992; Holdgate *et al.*, 2016), and in Poland (e.g., Kasiński *et al.*, 2010). In the Polish Lowlands, the most favourable conditions for them occurred in the Early and Middle Miocene (Kasiński and Słodkowska, 2016), which can be observed, among others, in pollen spectra from LLS-2 in the Lubstów lignite deposit, central Poland (Durska, 2008), Legnica, SW Poland (e.g., Worobiec, 2009), and Turów, SW Poland (Kasiński *et al.*, 2010). In contrast, in the palynoflora from the lower part of the LLS-2 profile in the Ruja deposit, adjacent to the above-mentioned Legnica deposit, a high frequency of pollen from riparian species (mainly *Liquidambar*) was observed. This was accompanied by a low proportion of pollen grains, typical of swamp forests (e.g., *Taxodium/Glyptostrobus*). Such a difference may result from different topographic and hydrological conditions (Worobiec *et al.*, 2022b).

Another type of Miocene peat-forming plant community is the shrub bog. The results of the current research show that this type of vegetation was the main source of peat, from which the examined lignite from Chłapowo was formed. This type of plant community, with Ericaceae, Cyrillaceae and/or Clethraceae (producing mainly pollen from the fossil-species *Cyrillaceaepollenites megaexactus*), is commonly recognised in the upper part of LLS-2, reflected in the identification of the VI spore-pollen zone – *Tricolporopollenites megaexactus* phase, which is a synonym for *C. megaexactus* (Piwocki and Ziembińska-Tworzydło, 1997; Ziembińska-Tworzydło, 1998). The VI phase was previously confirmed in northwestern Poland (Raniecka-Bobrowska, 1970; Kohlman-Adamska, 1993) and southwestern Poland (Worobiec 2009; Worobiec *et al.*, 2022b). The composition of the presently examined palynoflora from Chłapowo indicates that this lignite may be equivalent to the upper part of LLS-2.

A similar type of vegetation also occurred during the formation of the peat bogs, from which the slightly younger (also Middle Miocene) 1st mid-Polish seam (MPLS-1) group were formed, with the difference, however, that in MPLS-1, there are almost no such highly thermophilic taxa as Meliaceae and Sapotaceae (cf. Worobiec *et al.*, 2022b). For example, similar pollen assemblages, characteristic of peat bogs, were observed in lignites belonging to MPLS-1 in the southern part of the Konin–Adamów Region, i.e., in the Adamów (Widera *et al.*, 2021a; Worobiec *et al.*, 2021) and Drzewce (Worobiec *et al.*, 2022a) deposits.

The origin of LLS-2 is associated with the formation of extensive wetlands on the coastal plains, surrounding a bay of the former North Sea, extending far to the east (Piwocki, 1992, 1998). The results of previous studies indicate that climatic conditions were quite stable at that time and comparable to climate type Cfa (warm temperate, fully humid with hot summer) in the Köppen-Geiger climate classification (Kottek *et al.*, 2006). Humid and warm conditions favoured the development of extensive peat-forming vegetation (Kasiński and Słodkowska, 2016), which produced large amounts of peat. The mean annual temperature (MAT) for the Chłapowo site was estimated to be in the range of 15.7–17.8 °C. The same MAT range was estimated for LLS-2 in the Ruja deposit (Worobiec *et al.*, 2022b). At Legnica, the MAT ranged mainly between 15.6–18.6 °C, with some intervals between 17.2–18.6 °C. The mean temperature of the warmest month (TWM) coexistence intervals registered for the Legnica palynofloras were constantly 24.7–27.8 °C, with some small fluctuations; the most common CA-intervals for the mean annual precipitation (MAP) were 823–1,308 mm (Ivanov and Worobiec, 2017). For the Turów deposit MAT was estimated in the range of 16–19 °C, TWM was 24–27 °C, and the MAP was 1,000–1,250 mm (Durska, 2008; Kasiński *et al.*, 2010).

The current research fits well into existing knowledge on the Miocene Climatic Optimum (MCO). At that time, Eurasia was dominated by subtropical evergreen and mixed mesophytic forests with many thermophilic elements (Kovar-Eder *et al.*, 2008; Utescher *et al.*, 2011; Steinthorsdottir *et al.*, 2021). In a large area of Central Europe, the climate was warm and humid and quite even, which is reflected also in the extent of the lignite deposits. Climatic data from Poland and Bulgaria suggest a small latitudinal temperature gradient in Europe during the MCO (Ivanov and Worobiec, 2017). Finally, the present study demonstrates similar climatic conditions during the formation of the peat that gave rise to LLS-2, occurring in various areas of Miocene peat deposition in Central Europe (also as distant as the Legnica-Ruja complex, in southwestern Poland and Chłapowo).

CONCLUSIONS

Although lignite and associated sediments from the Chłapowo Cliff had already been examined palynologically (also from boreholes), usually a small number of Miocene samples were examined at that time, and non-pollen palynomorphs have not been studied at all, except for a few freshwater algal taxa. The present palynological analysis confirmed that the lignite bed belongs to the 2nd Lusatian seam (LLS-2). LLS-2 is an important correlation horizon in Central Europe, dated to the latest Early Miocene to the early Middle Miocene. Thus, the large distribution of lignites of this seam and numerous sites examined palynologically enable a broader view of the vegetation and palaeoclimate that prevailed during the accumulation of the peat, from which the lignites were formed. So far, the thick lignite seams of LLS-2, which were formed over large areas and in deep tectonic grabens, most often have been studied. However, palynological studies of the Chłapowo profile show that examining also the thinner lignite beds allows a more detailed understanding of the complexity of past palaeoenvironments.

The results of the current palynological study reveal the presence of shrub bogs, similar to the present pocosins, growing between river beds, composed of Cyrillaceae, Clethraceae and Ericaceae. The depositional environment of the peat is loosely combined with the overbank zone of an anastomosing or meandering river system. Wetland vegetation with *Taxodium* and/or *Glyptostrobus*, *Nyssa*, *Alnus*, *Acer*, *Betula*, *Fraxinus*, *Salix*, *Ulmus*, *Celtis*, *Liquidambar*, *Platanus*, *Vitis*, *Zelkova*, *Carya*, *Pterocarya*, *Sciadopitys*, *Sequoia*, *Pinus* and *Osmunda* occurred in permanently or temporarily flooded areas. Nearby mesophilous communities included plants, producing pollen of the fossil-species *Tricolporopollenites pseudocingulum*, *Quercus* (including thermophilous trees producing pollen of the fossil-species *Quercoidites henricii*), *Fagus*, Engelhardioideae, Castaneoideae, and such thermophilic taxa as Sapotaceae and Meliaceae, which currently have a pantropical distribution. The climate was warm, close to subtropical, and the mean annual temperature was estimated to have been in the range of 15.7–17.8 °C. Although Chłapowo is located at the northern margin of the LLS-2 range, the deduced palaeoclimate is not significantly different from previously studied sites in Central Europe. This is consistent with other studies that suggested a more uniform climate in Central Europe at that time.

Non-pollen palynomorphs, including algal and fungal remains, and the presence of the cladoceran genus *Chydorus*, allowed a better reconstruction of the palaeoenvironment. The occurrence of various ecological groups of fungi (mitosporic aero-aquatic fungi, epiphyllous fungi, and root-inhabiting endophytic fungi) indicate dense woody vegetation in lignite-forming peat bogs and the presence of small, shallow and perennial water bodies with variable water levels or periodic reservoirs, occurring only during a wet season or after floods. Changes in the abundance of individual groups of fungi correlated with the variability of other palynomorphs, and palynofacies indicate significant habitat modification, including trophic changes and drainage.

Acknowledgements

This study was supported by the W. Szafer Institute of Botany, Polish Academy of Sciences, through its statutory funds. Nela Doláková (Masaryk University) and Barbara Słodkowska (Polish Geological Institute – National Research Institute) are acknowledged for their careful reviews. This study contributes to NECLIME – the research NEtwork on Cenozoic CLIMate and Ecosystems.

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.

Böhme, M., 2003. The Miocene Climatic Optimum: evidence from ectothermic vertebrates of Central Europe. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 195: 389–401.

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.

Ching, K. K., 1991. Temperate deciduous forests in East Asia. In: Röhrig, E. & Ulrich, B. (eds), *Ecosystems of the World. 7. Temperate Deciduous Forests.* Elsevier, Amsterdam London-New York-Tokyo, pp. 539–555.

Christensen, N. L., 2000. Vegetation of the Southeastern Coastal Plain. In: Barbour, M. G. & Billings, W. D. (eds), *North American Terrestrial Vegetation*. Cambridge University Press, 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.]

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.

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

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.

Dumont, H. J., Pociecha, A., Zawisza, E., Szeroczyńska, K., Worobiec, E. & Worobiec, G., 2020. Miocene cladocera from Poland. *Scientific Reports*, 10: 12107.

Durska, E., 2008. A 90 m-thick coal seam in the Lubstów lignite deposit (Central Poland): palynological analysis and sedimentary environment. *Geological Quarterly*, 52: 281–290.

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., 1976. Palinologiczna charakterystyka osadów mioceńskich w klifie nadbałtyckim w okolicach Chłapowa. *Kwartalnik Geologiczny*, 20: 406–407. [In Polish.]

Grabowska, I., 1987. Palynofloristic and microplanktonic characteristic of the Tertiary sediments in northern Poland based on the sections Chłapowo I and Chłapowo III. *Biuletyn Państwowego Instytutu Geologicznego*, 356: 65–87. [In Polish, with English summary.]

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

Grabowska, I. & Ważyńska, H., 1997. Spore-pollen and phytoplankton investigations of the Tertiary deposits from the Gdańsk sea-coast and the Baltic floor. *Biuletyn Państwowego Instytutu Geologicznego*, 375: 5–32. [In Polish, with English summary.]

Heer, O., 1869. Miocene baltische Flora. *Beiträge zur Naturkunde Preussens, Königsberg*, 2: 1–104.

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.

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.

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 the Köppen-Geiger climate classification updated. *Meteorologische Zeitschrift*, 15: 259–263.

Kovar-Eder, J., Jechorek, H., Kvaček, Z. & Parashiv, V., 2008. The integrated plant record: An essential tool for reconstructing Neogene zonal vegetation in Europe. *PALAIOS*, 23: 97–111.

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.

Kowalski, R. & Worobiec, E., 2018. Revision of *Comarostaphylis globula* (Ericaceae) from Cenozoic of Central Europe. *Review of Palaeobotany and Palynology*, 254: 20–32.

Kramarska, R., Kasiński, J. R. & Czapowski, G., 2008. Węgle brunatne w profilu klifu chłapowskiego. Sesja terenowa punkt 2. In: Kramarska, R. & Jurys, L. (eds), *XI Seminarium z cyklu Metodyka rozpoznawania i dokumentowania złóż kopalin oraz geologicznej obsługi kopalń pt. Dokumentowanie i ochrona złóż kopalin. Gdańsk-Sobieszewo. 4-6.06.2008*, pp. 9–14. [In Polish.]

Kramarska, R., Kasiński, J. R., Czapowski, G., Piwocki, M. & Słodkowska, B., 2015. The standard section of Neogene deposits from Eastern Pomerania at Łęczyce near Lębork (northern Poland). *Biuletyn Państwowego Instytutu Geologicznego*, 461: 193–250. [In Polish, with English summary.]

Krutzsch, W., 1970. *Atlas der mittel- und jungtertiären dispersen Sporen und Pollen- sowie der Mikroplanktonformen des nördlichen Mitteleuropas. Liferung VII: Monoporate, Monocolpate, Longicolpate, Dicolpate und Ephedrioide (Polyplicate) Pollenformen*. VEB Gustav Fischer Verlag, Jena, Germany, 175 pp.

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.

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

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., 1997. The coexistence approach – a method for quantitative reconstructions of Tertiary terrestrial palaeoclimate data using plant fossils. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 134: 61–86.

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.

Passendorfer, E. & Zabłocki, J., 1946. O trzeciorzędowych i czwartorzędowych utworach brzegu Bałtyku, pomiędzy Wielką Wsią a Jastrzębią Górą. *Rocznik Polskiego Towarzystwa Geologicznego*, 16: 169–176. [In Polish.]

Piwocki, M., 1992. Extent and correlations of main groups of the Tertiary lignite seams on Polish platform area. *Przegląd Geologiczny*, 40: 281–286. [In Polish, with English summary.]

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., Olkowicz-Paprocka, I., Kosmowska-Ceranowicz, B., Grabowska, I. & Odrzywolska-Bieńkowa, E., 1985. Stratygrafia trzeciorzędowych osadów bursztynonośnych okolic Chłapowa koło Pucka. *Prace Muzeum Ziemi*, 37: 61–77. [In Polish.]

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.

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.]

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

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.

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., 2004. Palynological studies of the Paleogene and Neogene deposits from the Pomeranian Lakeland area (NW Poland). *Polish Geological Institute Special Papers*, 14: 1–116.

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.

Steinthorsdottir, M., Coxall, H. K., de Boer, A. M., Huber, M., Barbolini, N., Bradshaw, C. D., Burls, N. J., Feakins, S. J., Gasson, E., Henderiks, J., Holbourn, A. E., Kiel, S., Kohn, M. J., Knorr, G., Kürschner, W. M., Lear, C. H. Liebrand, D., Lunt, D. J., Mörs, T., Pearson, P. N., Pound, M. J., Stoll, H. & Strömberg, C. A. E., 2021. The Miocene: The future of the past. *Paleoceanography and Paleoclimatology*, 36: e2020PA004037.

Stuchlik, L., Szynkiewicz, A., Łańcucka-Środoniowa, M. & Zastawniak, E., 1990. Results of the hitherto palaeobotanical investigations of the Tertiary brown coal bed "Bełchatów", Central Poland. *Acta Palaeobotanica*, 30: 259–305. [In Polish, with English summary.]

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.

Szeroczyńska, K. & Sarmaja-Korjonen, K., 2007. *Atlas of Subfossil Cladocera from Central and Northern Europe.* Towarzystwo Przyjaciół Dolnej Wisły, Świecie, 84 pp.

Thiergart, F., 1937. Die Pollenflora der Niederlausitzer Braunkohle, besonders im Profil der Grube Marga bei Senftenberg. *Jahrbuch der Königlich Preussischen Geologischen Landesanstalt und Bergakademie zu Berlin*, 58: 282–351.

Uścinowicz, G., Jurys, L. & Szarafin, T., 2017. The development of unconsolidated sedimentary coastal cliffs (Pobrzeże Kaszubskie, Northern Poland). *Geological Quarterly*, 61: 491–501.

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., 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., Bruch, A. A., Micheels, A., Mosbrugger, V. & Popova, S., 2011. Cenozoic climate gradients in Eurasia – a palaeo-perspective on future climate change? *Palaeogeography, Palaeoclimatology, Palaeoecology*, 304: 351–358.

Utescher, T., Bruch, A. A. & Mosbrugger, V., 2024. T*he Palaeoflora Database - Documentation and Data (Version 2024)* [Data set]. Zenodo. https://doi.org/10.5281/zenodo.10881069

Utescher, T. & Mosbrugger, V., 2015. *The Palaeoflora Database*. http://www.palaeoflora.de/ [July, 2023].

Van Damme, K. & Kotov, A. A., 2016. The fossil record of the Cladocera (Crustacea: Branchiopoda): Evidence and hypotheses. *Earth-Science Reviews*, 163: 162–189.

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.

Wagner, M., 2007. The Miocene coal deposits from the Kępa Swarzewska at the Baltic Seaside. *Geologia*, 33: 69–90.

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.

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

Widera, M., 2019. What can be learned about the deposition and compaction of peat from the Miocene lignite seam exposed in the Chłapowo Cliff on the Polish coast of the Baltic Sea? *Geology, Geophysics and Environment*, 45: 111–119.

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., 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., 2014. 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., Widera, M. & Worobiec, G., 2022a. Palaeoenvironment of the middle Miocene wetlands at Drzewce, Konin region, central Poland. *Annales Societatis Geologorum Poloniae*, 92: 201–218.

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. & Kasiński J. R. 2022b. 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. & Szynkiewicz, A., 2016. Neogene wetland vegetation based on a leaf assemblage from the Bełchatów

Lignite Mine (Central Poland). *Acta Palaeobotanica*, 56: 441–497.

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

Zabłocki, J., 1935. Dotychczasowe wyniki badań nad trzeciorzędową florą Chłapowa na Pomorzu. In: *Streszczenie referatów wygłoszonych na Zjeździe Polskiego Towarzystwa Botanicznego w Krakowie w dniach 29 i 30 czerwca 1935 r.* Polskie Towarzystwo Botaniczne, Kraków, pp. 14–16. [In Polish.]

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.

Ziembińska-Tworzydło, M., 1998. Climatic phases and spore-pollen zones. In: Ważyńska, H. (ed.), *Palynology and Palaeogeography of the Neogene in the Polish Lowlands*. *Prace Państwowego Instytutu Geologicznego*, 160: 12–16.