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Early Oligocene palaeoenvironment and palaeoclimate of the eastern periphery of the North Sea based on high-resolution palynological studies of the Grabówka PIG-1 borehole, northern Poland

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Early Oligocene palaeoenvironment and palaeoclimate of the eastern periphery of the North Sea based on high-resolution palynological studies of the Grabówka PIG-1 borehole, northern Poland

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ABSTRACT
High-resolution palynological studies of the lower Oligocene strata from the Grabówka PIG-1 borehole from the eastern peripheries of the North Sea (Polish Gulf) revealed the presence of 165 fossil-species of sporomorphs (pollen grains and spores), numerous marine palynomorphs (e.g. dinoflagellate cysts), freshwater and brackish algae, plus fungal remains (including microsclerotia of dark septate endophytes inhabiting roots of plants). The composition of the palynological assemblage, including the fossil-species *Boehlensipollis hohli* Krutzsch and *Aglaoreidia cyclops* Erdtman, confirms the early Oligocene age of the strata. The presence of numerous dinoflagellate cysts throughout the Grabówka PIG-1 succession clearly indicates its deposition in a shallow marine, near-shore environment. The results of the spore-pollen analysis indicate the presence of lush vegetation with numerous thermophilous elements (including members of the pantropical families Meliaceae Jussieu and Sapotaceae Jussieu as well as the subtropical-tropical families Arecaceae Berchtold & J.Presl, Schizaeaceae Kaulfman, Cyatheaceae Kaulfman and/or Gleicheniaceae C.Presl) in the neighbouring land area. Mixed mesophytic forests, wetland (swamp or riparian) forests, shrub bogs, and freshwater/marsh vegetation dominated there. The climate was subtropical and humid. The entire palynological succession corresponds to the 5th Czempiń group of lignite seams, correlated with the 5th Lusatian seam in south-eastern Germany, which is an important correlation horizon for the lower Oligocene in Central Europe. The results provide new insights into the vegetation and palaeoclimate changes in mid-latitudes during the early Oligocene greenhouse/icehouse transition.

KEY WORDS
Palynology,
pollen and spores,
non-pollen palynomorphs,
fossil algae,
fossil fungi,
palaeogeography,
Europe,
Paleogene.

RÉSUMÉ
Paléoenvironnement et paléoclimat de l'Oligocène inférieur de la périphérie orientale de la mer du Nord, d'après des études palynologiques à haute résolution du forage Grabówka PIG-1, Nord de la Pologne.
Les études palynologiques à haute résolution des strates de l'Oligocène inférieur du forage Grabówka PIG-1 des périphéries orientales de la mer du Nord (golfe polonais) ont révélé la présence de 165 espèces fossiles de sporomorphes (grains de pollen et spores), de nombreux palynomorphes marins (par exemple des kystes de dinoflagellés), des algues d'eaux douces et saumâtres, ainsi que des restes fongiques (y compris des microsclérotes endophytes bruns septés des racines des plantes). La composition de l'assemblage palynologique, comprenant les espèces fossiles *Boehlensipollis hohli* Krutzsch et *Aglaoreidia cyclops* Erdtman, confirme l'âge Oligocène inférieur des strates. La présence de nombreux kystes de dinoflagellés tout au long de la succession Grabówka PIG-1 indique clairement son dépôt dans un environnement marin peu profond, proche du rivage. Les résultats de l'analyse sporo-pollinique indiquent la présence d'une végétation luxuriante avec de nombreux éléments thermophiles (y compris des membres des familles pantropicales Meliaceae Jussieu et Sapotaceae Jussieu ainsi que les familles subtropicales-tropicales Arecaceae Berchtold & J.Presl, Schizaeaceae Kaulfman, Cyatheaceae Kaulfman et/ou Gleicheniaceae C.Presl) dans les terres voisines. Les forêts mésophytiques mixtes, les forêts de zones humides (marécageuses ou riveraines), les tourbières arbustives et la végétation d'eau douce/marais dominaient. Le climat était subtropical et humide. L'ensemble de la succession palynologique correspond à la 5e couche de lignite de Czempiń, corrélée à la 5e couche de Lusace dans le Sud-Est de l'Allemagne, qui constitue un horizon de corrélation important pour l'Oligocène inférieur en Europe centrale. Les résultats fournissent de nouvelles informations sur la végétation et les changements paléoclimatiques des latitudes moyennes au cours de la transition « greenhouse/icehouse » de l'Oligocène inférieur.

MOTS CLÉS
Palynologie,
pollen et spores,
palynomorphes non polliniques,
algues fossiles,
champignons fossiles,
paléogéographie,
Europe,
Paléogène.

INTRODUCTION

The Eocene-Oligocene transition was a period of dynamic changes in the Earth's climate and ecosystems presumed to be the most prominent one in the Cenozoic (e.g. Hutchinson *et al.* 2021). It is widely accepted that at that time (about 33.7 million years ago) an abrupt cooling occurred near that boundary (e.g. Shackleton & Kennett 1975; Kennett & Shackleton 1976; Kennett 1977; Pomerol & Premoli Silva 1986; Coxall & Pearson 2007; Liu *et al.* 2009). Climate change was very rapid and that shift lasted, depending on the author, from 500 000 years to some 790 000 years only (e.g. Coxall & Pearson 2007; Hutchinson *et al.* 2021). At that time, polar ice caps, absent during the Eocene and Paleocene (the time when ice sheets were missing is commonly known as the "greenhouse"), appeared (e.g. Coxall & Wilson 2011), and the early Oligocene is believed to represent the beginning of the modern "icehouse" world (i.e., time with polar glaciations present, starting from the Eocene-Oligocene transition till Recent), in which Earth's ecosystems adapted to cooling climatic conditions following the preceding late Eocene thermal maximum (Zachos *et al.* 2001, 2008; Li *et al.* 2018; Westerhold *et al.* 2020). Among the reasons cited as responsible for these climatic changes across the Eocene-Oligocene boundary, atmospheric CO_2 reduction seems to have the greatest impact, while the emergence of polar ice caps and changes in ocean current patterns induced by seafloor tectonics seem to have a lesser impact (e.g. Hutchinson *et al.* 2021). However, a precise scenario of climatic fluctuations and their extent during the transitional interval as well as in the subsequent times of the younger Oligocene times is still a matter of debate. Moreover, some data suggest less climatic cooling during the Oligocene than one might suppose from the word "icehouse" (e.g. O'Brien *et al.* 2020). To add some data to that issue we conducted a high-resolution palynological research on a lower Oligocene littoral section from the eastern periphery (Polish Gulf; Śliwińska *et al.* 2019) of the North Sea (northern Poland) that represents an age-counterpart of brackish-lacustrine sediments with lignite interlayers (the so-called Czempiń Formation) widespread in the Polish Lowland basin (Piwocki 2004). The mass accumulation of phytogenic deposits of that time, known as the 5th Czempiń group of lignite seams, reflected specific climatic and orographic conditions that have appeared in the Polish Lowland basin for the first time then. Subsequent periods of increased phytogenic accumulation, repeated regularly during the Miocene in the Polish Lowlands and adjacent areas, likely reflect optimal conditions for lush vegetation, which can be correlated with climatic fluctuations that occurred in the Miocene (see e.g. Kürschner *et al.* 2008).

The accumulation of phytogenic deposits of the 5th group of lignite seams reflected thus specific climatic conditions that had appeared for the first time during the early Oligocene, i.e., in the period traditionally regarded as "icehouse" cold time. To clarify these ambiguities, we conducted a palynological study of the 5.6-metre-thick succession from the Grabówka PIG-1 borehole. Although the lower Oligocene strata have been palynologically studied for years from relatively numerous sections in the Polish Lowlands (Grabowska & Piwocki 1975; Grabowska & Słodkowska 1993; Grabowska 1996b; Słodkowska 2004a, b, 2009; Kasiński & Słodkowska 2016), most of these studies are contributory only or are based on

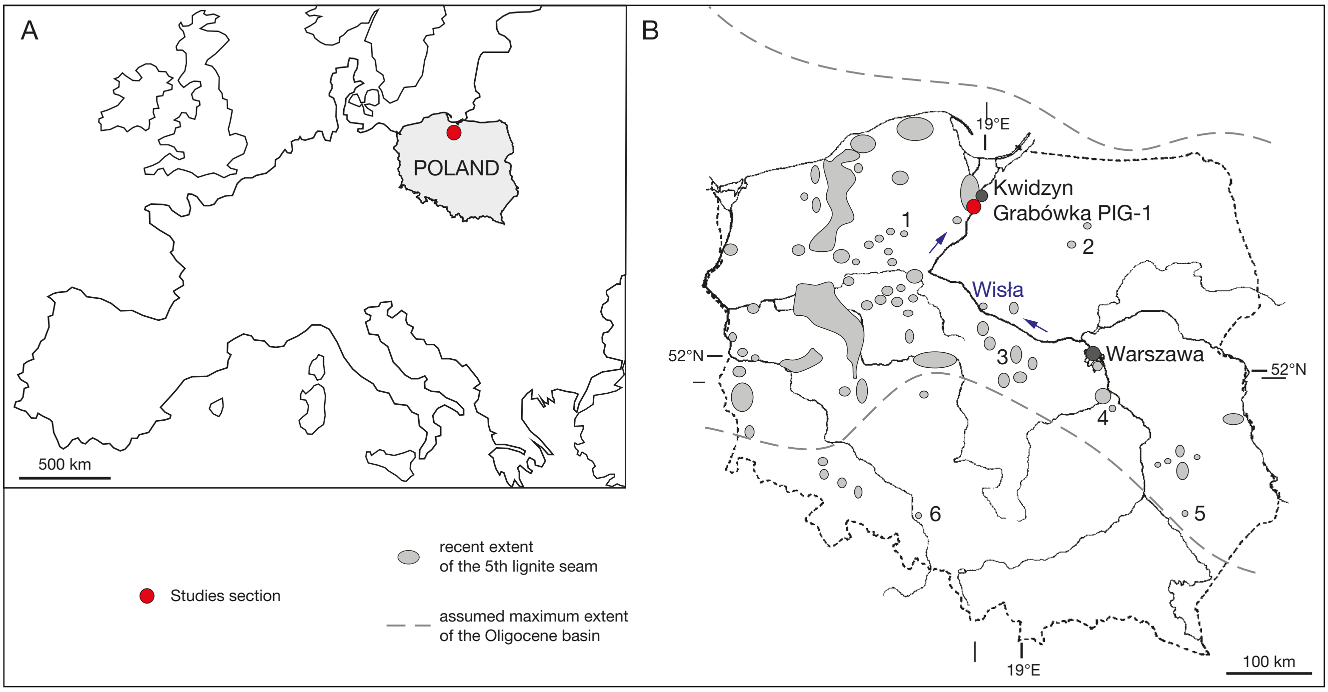

Fig. 1. — Location maps of the Grabówka PIG-1 borehole: **A**, general location; **B**, location of the Grabówka PIG-1 borehole in Poland and geographical extent of the Oligocene basin (according to Vinken 1988; Widera & Kita 2007) and the 5th Czempiń lignite seam group (simplified, after Kasiński & Słodkowska 2016; supplemented by Gedl *et al.* 2016; Worobiec & Szulc 2020). Lower Oligocene localities mentioned in the text: **1**, Pomeranian Lakeland area; **2**, Warmia and Mazury; **3**, Warszyce 19 borehole, Rogóźno deposit; **4**, Middle Vistula River valley; **5**, Łukowa-4 borehole; **6**, Górażdże.

very scarce material. The results and interpretations of our high-resolution (sampling every 10 cm) terrestrial palynological study (including spore-pollen, freshwater algae and fungal analysis) combined with the results of preliminary studies on marine dinoflagellate cysts provide new insights into climatic conditions during this interesting and dynamically changing period.

GEOLOGICAL SETTING

The study area is located in northern Poland (Fig. 1) in the Lower Vistula Valley. The riverbed of the Vistula (Wisła) river in this area is covered by Holocene river sands and gravel, which cut the upper parts of the plateau formed by the Pleistocene (Vistulian) moraines (Kozłowska & Kozłowski 1984). The Quaternary deposits in the study area are over 80 m thick and consist of glacial deposits of the Narew (MIS 22), San 2 (MIS 12), Odra (MIS 6), and Vistula glaciations (MIS 4-2) (Lisicki 2010). These strata rest directly upon Paleogene sediments (Neogene is missing in the study area), which start at the depth of 82.4 m in the Grabówka PIG-1 (Grabówka-2) well. The interval 82.4-88.0 m studied from the Grabówka PIG-1 well represents the so-called Czempiń Formation, a part of the Paleogene succession of the Polish Lowlands, which accumulated in the north-eastern peripheries of the NW European Tertiary Basin.

Lithostratigraphy of the Polish Lowlands' Paleogene succession has an informal character being composed of several units in the ranks of beds, series or formations; their definitions, correlations and age assessments changed throughout the years – in this paper we use the lithostratigraphic scheme (Fig. 2) proposed and discussed by Piwocki (2004). The oldest Oligocene unit in the Polish Lowlands is the Lower Mosina Formation which rest unconformably on the upper Eocene series. These are marine quartz-glauconite sands, usually fine-grained, locally loamy or with admixtures of quartz gravels, with phosphorite concretions in the basal intervals.

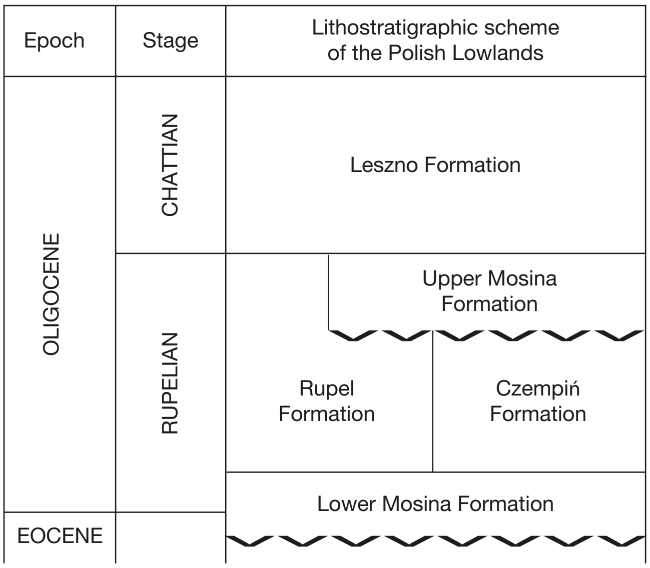

Fig. 2. — Lithostratigraphic scheme of the Oligocene in the Polish Lowlands (after Piwocki 2004).

The spatial distribution of this unit is the widest among the Oligocene ones in the Polish Lowlands; it covers an area similar to that of the entire Oligocene. Younger units show more local occurrence. The Lower Mosina Formation passes upwards in the north-western part of the Polish Lowlands into the Rupel Formation, which is also marine but finer-grained than the underlying strata; in the Rupel Formation mud and clay fractions predominate.

The Czempiń Formation, which is the subject of our study in the Grabówka PIG-1 well, is another Rupelian unit widespread in the Polish Lowlands. In contrast to the above-described units, these strata accumulated during the regressive phase of the early Oligocene in continental (swampy-lacustrine) and brackish (littoral, tidal, lagoonal, estuarine) sedimentary settings. This unit is composed mainly of dark-coloured mud and fine-grained sands with a high proportion of lignite, locally forming lignite seams (known as the 5th Czempiń group of lignite seams, see below). The youngest Rupelian unit in the Polish Lowlands is the Upper Mosina Formation, which transgressively overlies the older units. These are marine, mainly sandy deposits (quartz-glauconite, fine-grained sands with variable admixture of finer mud fraction) with characteristic gravel and phosphorite concretion layers at the base. The Upper Mosina Formation terminates the accumulation of Paleogene strata on an overwhelming part of the Polish Lowlands: during the latest Rupelian-earliest Chattian, the sea withdrew from these territories except for a small marine bay that existed during the Chattian in south-western Poland.

Transgression/regression oscillations from the North Sea during the early Oligocene caused vertical and lateral facies variations, which slightly obscure the simplified scheme given above (Piwocki 2004). The coastline of the basin cannot be precisely defined due to facies interfingering and subsequent erosion that removed large portions of the Paleogene cover. Nevertheless, the lithology and the thickness of these deposits suggest that the epicontinental sea connected to the North Sea extended further south than the present towns of Konin and Turek. The central-western Poland formed a southern marginal part of this basin (Widera & Kita 2007). The Rupelian marine and brackish deposits are most frequently synchronous with brackish-lacustrine sediments containing lignite interbeds of the 5th Czempiń lignite seam group (Piwocki 2004). The 5th lignite seam has a limited extent and it has been documented across an area of *c.* 7700 km^2, mainly in North-Western Poland (Fig. 1). Its thickness is usually small, not exceeding 1 m, although it reaches a considerable thickness in depressions in the salt dome caps. In extreme cases (e.g. in the Rogóźno and Wapno salt domes), its thickness may exceed 40 m (Kasiński & Słodkowska 2016). The Czempiń Formation corresponds to the so-called Septarian Clays of Germany (Piwocki 2004) and the Czempiń seam is correlated with the 5th Lusatian Seam in the south-eastern territory of Germany (Widera 2016). Palynological studies of the 5th group of lignite seams are used in a regional or interregional correlation of the lower Oligocene strata in a parastratigraphic sense (Vinken 1988; Widera & Kita 2007).

MATERIAL AND METHODS

Material

The Grabówka PIG-1 (Grabówka-2) borehole was drilled in July 2008 as a research well of the Middle Pleistocene strata. The borehole was located in the Kwidzyn Valley (Dolina Kwidzyńska) in the village of Grabówko (53°42'40"N, 18°50'30"E; Fig. 1), about 6 km south-east of the city of Kwidzyn, at an altitude of 14.5 m a.s.l., and reached a depth of 126 m (Lisicki 2010). The top 9.3 m of the well are Holocene fluvial deposits, below which almost 80 metres of Pleistocene glacial deposits occur. At the depth of 82.4-88.0 m a loamy to very fine-grained sandy interval with lignite occurs. This core fragment, thought to be a facies counterpart of the 5th group of lignite seams is the subject of the present study. Below, an unsampled interval composed of coarse-grained marine sands (88-95 m) and mudstones with chert concretions and fragments of mollusc shells (104.5-126.0 m) occurs. The results of petrographic and palynological studies of the Pleistocene from the Grabówka PIG-1 succession were compiled by Lisicki (2010), while the Paleogene part (based on material additionally collected during the Pleistocene studies) has not been investigated yet and is presented for the first time in this paper.

Preparation methods and palynological analysis

A total of 55 samples were collected from the Grabówka PIG-1 core interval of 87.8-82.4 m (with a sampling density of every 10 cm) for palynological studies including classical spore-pollen analysis and recognition of the presence of non-pollen palynomorphs (NPPs; such as freshwater algae, prasinophytes, acritarchs, dinoflagellate cysts, and fungal remains). The samples were processed in the Laboratory of the W. Szafer Institute of Botany, Polish Academy of Sciences, Kraków, using successively 10% hydrochloric acid (HCl), 10% potassium hydroxide (KOH), 40% hydrofluoric acid (HF) for four days to remove silicates (HF was heated at the beginning of the treatment), and subsequently 10% hydrochloric acid (HCl) (Moore *et al.* 1991; Worobiec *et al.* 2021). The residuum was then sieved at 5 µm on a nylon mesh. From each sample 1-2 (max. 8) microscope slides were made, using glycerine jelly or glycerine as a mounting medium.

Additionally, eleven samples from an interval of 87.80-82.80 m (sampling density every 50 cm, i.e., every fifth sample of these taken for spore-pollen analysis) were taken for organic-walled dinoflagellate cysts and processed separately. They were prepared at the Institute of Geological Sciences, Polish Academy of Sciences, Research Centre in Kraków. The samples were subjected to the processing procedure, which included 38% hydrochloric acid (HCl) treatment, 40% hydrofluoric acid (HF) treatment, heavy-liquid ($ZnCl_2$+HCl; density 2.0 g·cm^{-3}) separation, ultrasound for 10-15 s and sieving at 10 µm on a nylon mesh. No nitric acid (HNO_3) treatment was applied. The quantity of each rock sample processed was 20 g. Two slides from each sample were made using glycerine jelly as a mounting medium.

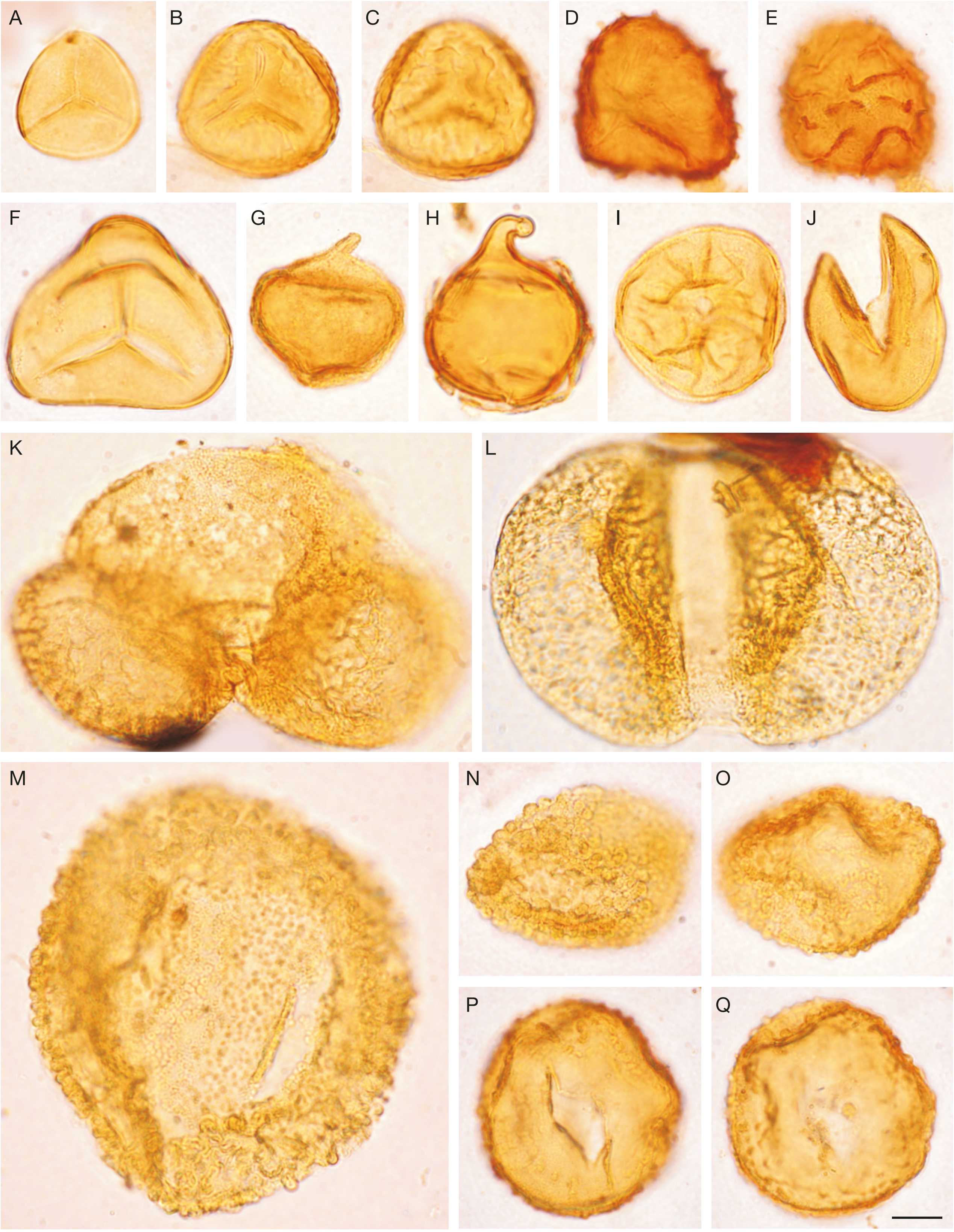

Fig. 3. — Spores of plants and pollen grains from Grabówka PIG-1: **A**, *Stereisporites stereoides* (Potonié & Venitz) Thomson & Pflug, 1953; **B**, **C**, *Camarozonosporites heskemensis* (Pflanzl) Krutzsch, 1959, same specimen, various foci; **D**, **E**, *Retitriletes annotinioides* Krutzsch, 1963, same specimen, various foci; **F**, *Leiotriletes* cf. *neddenioides* Krutzsch, 1962; **G**, *Sequoiapollenites rugulus* Krutzsch, 1971; **H**, *Sequoiapollenites megaligulus* Krutzsch, 1971; **I**, *Cupressacites* sp.; **J**, *Inaperturopollenites dubius* (Potonié & Venitz) Thomson & Pflug, 1953; **K**, *Pinuspollenites labdacus* (Potonié) Raatz ex Potonié, 1958; **L**, *Cathayapollis krutzschii* (Sivak) Ziembińska-Tworzydło, 2002; **M**, *Zonalapollenites* sp.; **N**, *Sciadopityspollenites serratus* (Potonié & Venitz) Raatz ex Potonié, 1958; **O**, *Sciadopityspollenites* sp.; **P**, **Q**, *Sciadopityspollenites quintus* Krutzsch ex Ziembińska-Tworzydło, 1974, same specimen, various foci. Scale bar: 10 µm.

The sporomorph taxa identified were classified based on the *Atlas of Pollen and Spores of the Polish Neogene* (Stuchlik *et al.* 2001, 2002, 2009, 2014). In the material studied, the following palaeofloristical (and palaeoclimatic) elements were distinguished: "palaeotropical" (P), including "tropical" (P1) and "subtropical" (P2), "arctotertiary" (A), including "warm-temperate" (A1) and "temperate" (A2), as well as cosmopolitan (P/A). Data from the palynological spectra were used to construct a simplified palynological diagram. In the diagram, the percentages of pollen and spore taxa were calculated from the total sum of pollen grains and spores; the proportions of non-pollen palynomorphs (NPPs) were computed separately from the total sum using the POLPAL computer programme (Nalepka & Walanus 2003). Photomicrographs of selected (the most important and characteristic) palynomorphs (Figs 3-5) were taken using a Nikon Eclipse E400 microscope, fitted with a Canon A640 digital camera.

Palaeoclimate reconstruction

The palaeoclimatic considerations presented in this paper are limited to general estimations, including the mean annual temperatures (MAT), as such data from marine sediments should be treated with caution. These MAT estimates are based on the Coexistence Approach (CA) method (Utescher *et al.* 2014), which basic assumption is that the nearest living relatives (NLR) of fossil taxa provide the information necessary to find a climatic distribution interval, where all plants could live (Coexistence Interval). The CA uses only the presence or absence of the taxa, without considering their relative frequency. The nearest living relatives and their MAT ranges follow The Palaeoflora Database (Utescher & Mosbrugger 2015; Utescher *et al.* 2024). For the CA method, the authors selected as many taxa as possible (Table 3) excluding fossil taxa with unknown botanical affinity, related to families, aquatic taxa, etc. Considering the limitations of the CA method (Utescher *et al.* 2014), e.g. the problem of determining the NLR of some fossil taxa (Kvaček 2007) and the fact that the difference between fossil and NLR increases with time distance, we only estimated the general MAT range for the palynoflora. We also excluded the species producing bisaccate pollen grains from this consideration, as they are exceptionally well adapted to long-distance transport.

Abbreviations

Institutional abbreviations

PIG	Polish Geological Institute, Warszawa.

Other abbreviations

A	"arctotertiary" palaeofloristical element;
A1	"warm-temperate" palaeofloristical element;
A2	"temperate" palaeofloristical element;
CA	Coexistence Approach;
DSE	dark septate endophytes;
MAT	mean annual temperature;
NLR	nearest living relatives;
NPP	non-pollen palynomorphs;
P	"palaeotropical" palaeofloristical element;
P1	"tropical" palaeofloristical element;
P2	"subtropical" palaeofloristical element;
P/A	cosmopolitan palaeofloristical element.

RESULTS OF THE PALYNOLOGICAL STUDIES

All samples processed yielded rich palynological organic matter, but the uppermost sample (depth 82.4 m) yielded material mixed with younger, probably Pleistocene palynomorphs (this sample was collected at the contact between the Paleogene and Pleistocene); therefore we excluded this sample from further consideration.

Spore-pollen analysis

The lowermost sample (depth 87.80 m) processed for pollen and spores yielded very few palynomorphs. The same sample treated with heavy liquid during processing (see chapter Material and methods) provided some dinoflagellate cysts. The remaining 53 samples (depth interval 87.7-82.5 m) gave well-preserved pollen grains and spores, suitable for detailed palynological analysis (Figs 3-5). In these samples, at least 500 pollen grains and spores of plants were identified as well as all co-occurring NPP were counted. The pollen grains of gymnosperms (Figs 3G-Q; 4A) are dominant in all samples, but angiosperms (Figs 4B-FF; 5A-M) are represented by many more taxa (mainly from trees and shrubs); plant spores (Fig. 3A-F) are few. A total of 165 fossil-species of sporomorphs (including 33 species of gymnosperm pollen, 108 species of angiosperm pollen, and 24 species of plant spores) were identified (Table 1). "Palaeotropical" (including "tropical" and "subtropical") and "palaeotropical/warm-temperate" palaeofloristical elements are common in the palynoflora (Table 1). The proportions of taxa representing various palaeofloristical elements are similar throughout the diagram (Fig. 6).

Among the gymnosperms, pollen grains of Pinaceae (mainly fossil-genus *Pinuspollenites* Raatz ex Potonié, 1958) and Cupressaceae (with distinct papillae and others) as well as some *Sciadopityspollenites* Raatz ex Potonié, 1958 are dominant. Pollen of *Distachyapites* (Krutzsch) Grabowska, 2002, related to the *Ephedra* genus, were encountered in five samples (depth 87.5 m, 87.0 m, 86.9 m. 84.3 m, 84.1 m). Angiosperms are represented mainly by small tricolporate pollen grains from the Fagaceae family (mainly fossil-species *Fususpollenites fusus* (Potonié) Kedves, 1978, *Cupuliferoipollenites pusillus* (Potonié) Potonié ex Potonié, 1960, and *Quercoidites microhenricii* (Potonié) Potonié, Thomson & Thiergart ex Potonié, 1960) as well as *Platanipollis ipelensis* (Pacltová) Grabowska, 1994, *Myricipites* Wodehouse emend. Grabowska & Ważyńska, 2009, *Cyrillaceaepollenites* (Mürriger & Pflug) Potonié, 1960, *Ericipites* Wodehouse, 1933, *Tricolporopollenites dolium* (Potonié) Thomson & Pflug, 1953, *Tricolporopollenites villensis* (Thomson) Thomson & Pflug, 1953, *Nyssapollenites* Thiergart, 1938, *Ilexpollenites* Thiergart ex Potonié, 1960, *Alnipollenites* Potonié emend. Grabowska & Ważyńska, 2009, members of the families Hamamelidaceae (fossil-species *Corylopsispollenites microreticulatus* E.Worobiec, 2014 and *Tricolporopollenites staresedloensis* Krutzsch & Pacltová, 1969), Sapotaceae, Juglandaceae (mainly members of the fossil-genera *Momipites* Wodehouse emend. Nichols, 1973, *Caryapollenites* Raatz

TABLE 1. — Spores and pollen taxa, recorded in samples from the Grabówka PIG-1 borehole. 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 & Pflug, 1953	Osmundaceae: *Osmunda* Linnaeus, 1753	P/A
Baculatisporites sp.	Osmundaceae: *Osmunda* Linnaeus, 1753	P/A
Camarozonosporites heskemensis (Pflanzl) Krutzsch, 1959	Lycopodiaceae: *Lycopodiella* Holub, 1964	P
Camarozonosporites sp.	Lycopodiaceae: *Lycopodiella* Holub, 1964	P
Cicatricosisporites dorogensis Potonié & Gelletich, 1933	Schizaeaceae	P
Corrugatisporites sp.	Lygodiaceae	P2
Distancoraesporis sp.	Sphagnaceae: *Sphagnum* Linnaeus, 1753	P/A
Laevigatosporites haardti (Potonié & Venitz) Thomson & Pflug, 1953	Polypodiaceae, Davalliaceae, and other ferns	P/A
Laevigatosporites sp.	Polypodiaceae, Davalliaceae, and other ferns	P/A
Leiotriletes maxoides Krutzsch, 1962	Lygodiaceae	P
Leiotriletes neddenioides Krutzsch, 1962	Lygodiaceae?, Cyatheaceae?	P
Leiotriletes wolffii Krutzsch, 1962	Lygodiaceae	P
Leiotriletes sp.	Lygodiaceae and other ferns	P
Monoleiotriletes sp.	ferns	unknown
Neogenisporis neogenicus Krutzsch, 1962	p.p. Gleicheniaceae	P1
Neogenisporis sp.	Gleicheniaceae, Cyatheaceae	P1
Polypodiaceoisporites sp.	Schizaeaceae?, Dicksoniaceae?, Pteridaceae?, Cyatheaceae?	P/A1
Retitriletes annotinioides Krutzsch, 1963	Lycopodiaceae: *Lycopodium* Linnaeus, 1753	A
Retitriletes lusaticus Krutzsch, 1963	Lycopodiaceae: *Lycopodium* Linnaeus, 1753	A
Retitriletes sp.	Lycopodiaceae: *Lycopodium* Linnaeus, 1753	A
Stereisporites stereoides (Potonié & Venitz) Thomson & Pflug, 1953	Sphagnaceae: *Sphagnum* Linnaeus, 1753	P/A
Stereisporites sp.	Sphagnaceae: *Sphagnum* Linnaeus, 1753	P/A
Triplanosporites sp.	unknown	P
Verrucatosporites sp.	Davalliaceae, Polypodiaceae, and other ferns	P/A
Pollen grains of gymnosperms:		
Abiespollenites sp.	Pinaceae: *Abies* Miller, 1768	A
Cathayapollis erdtmanii (Sivak) Ziembińska-Tworzydło *in* Stuchlik *et al.* 2002	Pinaceae: *Cathaya* Chun & Kuang, 1962	A1
Cathayapollis krutzschii (Sivak) Ziembińska-Tworzydło *in* Stuchlik *et al.*, 2002	Pinaceae: *Cathaya* Chun & Kuang, 1962	A1
Cathayapollis cf. *pulaensis* (Nagy) Ziembińska-Tworzydło *in* Stuchlik *et al.*, 2002	Pinaceae: *Cathaya* Chun & Kuang, 1962	A1
Cathayapollis sp.	Pinaceae: *Cathaya* Chun & Kuang, 1962	A1
Cedripites sp.	Pinaceae: *Cedrus* Trew, 1755	A1
Cunninghamiaepollenites sp.	Cupressaceae: *Cunninghamia* R. Brown *in* L. C. Richard, 1826	A1
Cupressacites sp.	Cupressaceae	A1
Distachyapites eocenicus (Wodehouse) Grabowska & Ważyńska *in* Stuchlik *et al.*, 2002	Ephedraceae: *Ephedra* Linnaeus, 1753	A
Distachyapites sp.	Ephedraceae: *Ephedra* Linnaeus, 1753	A
Inaperturopollenites concedipites (Wodehouse) Krutzsch, 1971	Cupressaceae: *Taxodium* Richard, 1810, *Glyptostrobus* Endlicher, 1847	P2/A1
Inaperturopollenites dubius (Potonié & Venitz) Thomson & Pflug, 1953	Cupressaceae: *Taxodium* Richard, 1810, *Glyptostrobus* Endlicher, 1847	P2/A1
Inaperturopollenites verrupapilatus Trevisan, 1967	Cupressaceae: *Taxodium* Richard, 1810, *Glyptostrobus* Endlicher, 1847	P2/A1
Keteleeriapollenites dubius (Khlonova) Słodkowska *in* Ziembińska-Tworzydło *et al.*, 1994	Pinaceae: *Keteleeria* Carrière, 1866	A1
Piceapollenites alatus Potonié ex Potonié, 1958	Pinaceae	P/A
Piceapollis planoides Krutzsch ex Hochuli, 1978	Pinaceae: *Picea* Dietrich, 1824	A
Piceapollis sp.	Pinaceae: *Picea* Dietrich, 1824	A
Pinuspollenites labdacus (Potonié) Raatz ex Potonié, 1958	Pinaceae: *Pinus sylvestris* Linnaeus, 1753 type	A
Pinuspollenites sp.	Pinaceae: *Pinus* Linnaeus, 1753	A
Sciadopityspollenites antiquus Krutzsch ex Planderová, 1990	Sciadopityaceae: *Sciadopitys* Siebold & Zuccarini, 1842	A1
Sciadopityspollenites miniverrucatus Kohlman-Adamska *in* Stuchlik *et al.*, 2002	Sciadopityaceae: *Sciadopitys* Siebold & Zuccarini, 1842	A1
Sciadopityspollenites quintus Krutzsch ex Ziembińska-Tworzydło, 1974	Sciadopityaceae: *Sciadopitys* Siebold & Zuccarini, 1842	A1
Sciadopityspollenites serratus (Potonié & Venitz) Raatz ex Potonié, 1958	Sciadopityaceae: *Sciadopitys* Siebold & Zuccarini, 1842	A1
Sciadopityspollenites varius Krutzsch ex Ziembińska-Tworzydło, 1974	Sciadopityaceae: *Sciadopitys* Siebold & Zuccarini, 1842	A1
Sciadopityspollenites verticillatiformis (Zauer) Krutzsch, 1971	Sciadopityaceae: *Sciadopitys* Siebold & Zuccarini, 1842	A1
Sciadopityspollenites sp.	Sciadopityaceae: *Sciadopitys* Siebold & Zuccarini, 1842	A1
Sequoiapollenites gracilis Krutzsch, 1971	Cupressaceae: *Sequoia* Endlicher, 1847, *Sequoiadendron* Buchholz, 1939, *Metasequoia* Hu & Cheng, 1948, *Cryptomeria* Don, 1838	A1

Table 1. — Continuation.

Fossil taxon	**Botanical affinity**	**Element**
Sequoiapollenites major Krutzsch, 1971	Cupressaceae: *Sequoia* Endlicher, 1847, *Sequoiadendron* Buchholz, 1939, *Metasequoia* Hu & Cheng, 1948, *Cryptomeria* Don, 1838	A1
Sequoiapollenites megaligulus Krutzsch, 1971	Cupressaceae, incl. *Sequoiadendron* Buchholz, 1939	A1
Sequoiapollenites rugulus Krutzsch, 1971	Cupressaceae: *Sequoia* Endlicher, 1847, *Sequoiadendron* Buchholz, 1939, *Metasequoia* Hu & Cheng, 1948	A1
Sequoiapollenites sp.	Cupressaceae: *Sequoia* Endlicher, 1847, *Sequoiadendron* Buchholz, 1939, *Metasequoia* Hu & Cheng, 1948, *Cryptomeria* Don, 1838	A1
Zonalapollenites verrucatus Krutzsch ex Ziembińska-Tworzydło, 1974	Pinaceae: *Tsuga* (Endlicher) Carrière, 1855	A
Zonalapollenites sp.	Pinaceae: *Tsuga* (Endlicher) Carrière, 1855	A
Pollen grains of angiosperms:		
Aceripollenites striatus (Pflug) Thiele-Pfeiffer, 1980	Sapindaceae: *Acer* Linnaeus, 1753	A1
Aceripollenites sp.	Sapindaceae: *Acer* Linnaeus, 1753	A
Aglaoreidia cyclops Erdtman, 1960	Sparganiaceae?, Potamogetonaceae?, Ruppiaceae?	P
Alnipollenites metaplasmus (Potonié) Potonié, 1960	Betulaceae: *Alnus* Miller, 1754	A
Alnipollenites verus Potonié, 1931	Betulaceae: *Alnus* Miller, 1754	P2/A
Araliaceoipollenites euphorii (Potonié) Potonié ex Potonié, 1960	Araliaceae	P/A1
Araliaceoipollenites sp.	Araliaceae	P/A1
Arecipites convexus (Thiergart) Krutzsch, 1970	Arecaceae	P/A1
Arecipites minireticulatus Kohlman-Adamska & Ziembińska-Tworzydło *in* Stuchlik *et al.*, 2014	Arecaceae	P/A1
Arecipites pseudoconvexus Krutzsch, 1970	Amaryllidaceae, Araceae, Arecaceae	P2/A1
Arecipites sp.	Araceae, Arecaceae, Butomaceae	P/A
Boehlensipollis hohli Krutzsch, 1962	Elaeagnaceae?, Lythraceae?	P2/A1
Caprifoliipites viburnoides (Gruas-Cavagnetto) Kohlman-Adamska *in* Ziembińska-Tworzydło *et al.*, 1994	Adoxaceae: *Viburnum* Linnaeus, 1753	P/A1
Caprifoliipites sp.	Adoxaceae: *Sambucus* Linnaeus, 1753, *Viburnum* Linnaeus, 1753	P2/A1
Carpinipites carpinoides (Pflug) Nagy, 1985	Betulaceae: *Carpinus* Linnaeus, 1753	P2/A1
Caryapollenites simplex (Potonié) Raatz ex Potonié, 1960	Juglandaceae: *Carya* Nuttall, 1818	A1
Caryapollenites triangulus (Pflug) Krutzsch, 1961	Juglandaceae: *Carya* Nuttall, 1818	P
Celtipollenites sp.	Ulmaceae: *Celtis* Linnaeus, 1753	P/A1
Cercidiphyllites minimireticulatus (Trevisan) Ziembińska-Tworzydło *in* Ziembińska-Tworzydło *et al.*, 1994	Cercidiphyllaceae: *Cercidiphyllum* Siebold & Zuccarini, 1846	A1
Chenopodipollis sp.	Amaranthaceae (incl. Chenopodiaceae)	P/A
Cornaceaepollis major (Stuchlik) Stuchlik ex Jansonius *et al.*, 1998	Cornaceae: *Cornus* Linnaeus, 1753	P/A
Cornaceaepollis satzveyensis (Pflug) Ziembińska-Tworzydło ex Jansonius *et al.*, 1998	Mastixiaceae: *Mastixia* Blume, 1826	P1
Cornaceaepollis sp.	Cornaceae: *Cornus* Linnaeus, 1753	P/A
Corsinipollenites sp.	Onagraceae	P/A
Corylopsispollenites microreticulatus E. Worobiec *in* Stuchlik *et al.*, 2014	Hamamelidaceae: *Corylopsis* Siebold & Zuccarini, 1835	A1
Cupanieidites eucalyptoides Krutzsch, 1962	Myrtaceae?, Sapindaceae?	P/A1
Cupuliferoipollenites oviformis (Potonié) Potonié ex Potonié, 1960	Fagaceae: Castaneoideae: *Castanea* Miller, 1754, *Castanopsis* (Don) Spach, 1841, *Lithocarpus* Blume, 1826	P2/A1
Cupuliferoipollenites pusillus (Potonié) Potonié ex Potonié, 1960	Fagaceae: Castaneoideae: *Castanea* Miller, 1754, *Castanopsis* (Don) Spach, 1841, *Lithocarpus* Blume, 1826	P2/A1
Cyperaceaepollis neogenicus Krutzsch, 1970	Cyperaceae	P/A
Cyrillaceaepollenites brühlensis (Thomson) Durska *in* Stuchlik *et al.*, 2014	Cyrillaceae, Clethraceae	P
Cyrillaceaepollenites exactus (Potonié) Potonié, 1960	Cyrillaceae, Clethraceae	P
Cyrillaceaepollenites megaexactus (Potonié) Potonié, 1960	Cyrillaceae, Clethraceae	P
Dicolpopollis sp.	Arecaceae	P
Dicolporopollis middendorfii (Potonié) Krutzsch, 1961	unknown	unknown
Edmundipollis sp.	Cornaceae, Mastixiaceae, Araliaceae	P/A
Ericipites callidus (Potonié) Krutzsch, 1970	Ericaceae	A
Ericipites ericius (Potonié) Potonié, 1960	Ericaceae	A
Ericipites triangulus Grabowska *in* Stuchlik *et al.*, 2014	Ericaceae	A
Ericipites sp.	Ericaceae	A
Faguspollenites sp.	Fagaceae: *Fagus* Linnaeus, 1753	A
Fraxinipollis sp.	Oleaceae: *Fraxinus* Linnaeus, 1753	A
Fususpollenites fusus (Potonié) Kedves, 1978	Fagaceae: *Trigonobalanus* Forman, 1962 s.l. (incl. *Colombobalanus* Nixon & Crepet, 1989)	P1
Graminidites sp.	Poaceae: Pooideae	P/A
Ilexpollenites iliacus (Potonié) Thiergart ex Potonié, 1960	Aquifoliaceae: *Ilex* Linnaeus, 1753	P/A1
Ilexpollenites margaritatus (Potonié) Thiergart, 1938	Aquifoliaceae: *Ilex* Linnaeus, 1753	P2
Intratriporopollenites insculptus Mai, 1961	Malvaceae: Brownlowioideae, Tilioideae	P/A1

Table 1. — Continuation.

Fossil taxon	**Botanical affinity**	**Element**
Intratriporopollenites sp.	Malvaceae: Brownlowioideae, Tilioideae	P/A
Juglanspollenites sp.	Juglandaceae: *Juglans* Linnaeus, 1753	A1
Magnoliaepollenites sp.	Magnoliaceae: *Magnolia* Linnaeus, 1753	P/A1
Meliaceoidites sp.	Meliaceae	P
Milfordia hypolaenoides Erdtman, 1960	Restionaceae, Centrolepidaceae	P
Milfordia miocaenica Grabowska & Słodkowska *in* Stuchlik *et al.*, 2009	Restionaceae, Centrolepidaceae	P
Momipites punctatus (Potonié) Nagy, 1969	Juglandaceae: Engelhardioideae: *Engelhardia* Leschenault & Blume, 1826, *Alfaroa* Standley, 1927, *Oreomunnea* Oersted, 1856	P2
Momipites quietus (Potonié) Nichols, 1973	Juglandaceae: Engelhardioideae: *Engelhardia* Leschenault & Blume, 1826, *Alfaroa* Standley, 1927, *Oreomunnea* Oersted, 1856	P
Myricipites bituitus (Potonié) Nagy, 1969	Myricaceae: *Myrica* Linnaeus, 1753	P2/A1
Myricipites megabituitus (Pflug) Grabowska & Ważyńska *in* Stuchlik *et al.*, 2009	Myricaceae: *Myrica* Linnaeus, 1753	P2/A1
Myricipites myricoides (Kremp) Nagy, 1969	Myricaceae	P2/A1
Myricipites sp.	Myricaceae	P2/A
Myrtaceidites myrtiformis Simoncsics, 1964	Myrtaceae	P/A1
Nyssapollenites analepticus (Potonié) Potonié ex Planderová, 1990	Nyssaceae: *Nyssa* Linnaeus, 1753	P/A1
Nyssapollenites contortus (Pflug & Thomson) Nagy, 1985	Nyssaceae: *Nyssa* Linnaeus, 1753	P2/A1
Nyssapollenites sp.	Nyssaceae: *Nyssa* Linnaeus, 1753	P/A1
Nyssoidites rodderensis Thiergart ex Potonié, 1960	Nyssaceae: *Nyssa* Linnaeus, 1753	P/A1
Oleoidearumpollenites microreticulatus (Pflug & Thomson) Ziembińska-Tworzydło *in* Ziembińska-Tworzydło *et al.*, 1994	Oleaceae	P2/A1
Oleoidearumpollenites reticulatus Nagy, 1969	Oleaceae	P2/A1
Oleoidearumpollenites sp.	Oleaceae	P2/A1
Oligopollis andreanus (Bruch) Durska *in* Stuchlik *et al.*, 2014	unknown	unknown
Parthenopollenites marcodurensis (Pflug & Thomson) Traverse, 1994	Vitaceae	P/A1
Periporopollenites orientaliformis (Nagy) Kohlman-Adamska & Ziembińska-Tworzydło *in* Stuchlik *et al.*, 2009	Altingiaceae: *Liquidambar* Linnaeus, 1753	A1
Periporopollenites stigmosus (Potonié) Thomson & Pflug, 1953	Altingiaceae: *Liquidambar* Linnaeus, 1753	A1
Platanipollis ipelensis (Pacltová) Grabowska *in* Ziembińska-Tworzydło *et al.*, 1994	Platanaceae: *Platanus* Linnaeus, 1753	P/A1
Platycaryapollenites sp.	Juglandaceae: *Platycarya* Siebold & Zuccarini, 1843	P2/A1
Polyatriopollenites stellatus (Potonié) Pflug, 1953	Juglandaceae: *Pterocarya* Kunth, 1824	A1
Polyatriopollenites sp.	Juglandaceae: *Pterocarya* Kunth, 1824	A1
Quercoidites henricii (Potonié) Potonié, Thomson & Thiergart ex Potonié, 1960	Fagaceae: *Quercus* Linnaeus, 1753	P2/A1
Quercoidites microhenricii (Potonié) Potonié, Thomson & Thiergart ex Potonié, 1960	Fagaceae: Quercoideae	P2/A1
Quercopollenites sp.	Fagaceae: *Quercus* Linnaeus, 1753	A1
Reevesiapollis microreticulatus Krutzsch, 2004	Malvaceae: *Reevesia* Lindley, 1827	P
Reevesiapollis sp.	Malvaceae: *Reevesia* Lindley, 1827	P
Restioniidites minimus (Krutzsch) Kedves, 1974	Restionaceae, Centrolepidaceae, Flagellariaceae	P
Rutacearumpollenites rutaceoides Kohlman-Adamska & Ziembińska-Tworzydło *in* Stuchlik *et al.*, 2014	Rutaceae	P/A1
Salixipollenites gracilis Durska *in* Stuchlik *et al.*, 2014	Salicaceae: *Salix* Linnaeus, 1753	A1
Salixipollenites sp.	Salicaceae: *Salix* Linnaeus, 1753	A
Sapotaceoidaepollenites manifestus (Potonié) Potonié, Thomson & Thiergart ex Potonié, 1960	Sapotaceae	P
Sapotaceoidaepollenites obscurus (Pflug & Thomson) Nagy, 1969	Sapotaceae	P
Sapotaceoidaepollenites sp.	Sapotaceae	P
Sparganiaceaepollenites sp.	Sparganiaceae, Typhaceae	P/A
Spinulaepollis arceuthobioides Krutzsch, 1962	Santalaceae: *Arceuthobium* M. Bieb., 1819	P2/A1
Subtriporopollenites sp.	Juglandaceae?	P
Symplocoipollenites calauensis (Krutzsch) Grabowska *in* Stuchlik *et al.*, 2014	Symplocaceae: *Symplocos* Jacquin, 1760	P
Symplocoipollenites sp.	Symplocaceae: *Symplocos* Jacquin, 1760	P
Tetracolporopollenites sapotoides Pflug & Thomson *in* Thomson & Pflug, 1953	Sapotaceae	P
Tetracolporopollenites sp.	Meliaceae?, Sapotaceae?	P
Tricolporopollenites dolium (Potonié) Thomson & Pflug, 1953	Fagaceae?	unknown
Tricolporopollenites fallax (Potonié) Krutzsch *in* Krutzsch *et al.*, 1960	Fabaceae	P/A
Tricolporopollenites liblarensis (Thomson) Hochuli, 1978	Fabaceae	P/A
Tricolporopollenites quisqualis (Potonié) Krutzsch, 1954	Fabaceae	P/A
Tricolporopollenites pseudocingulum (Potonié) Thomson & Pflug, 1953	Fagaceae?, Styracaceae?	P/A1
Tricolporopollenites staresedloensis Krutzsch & Pacltová *in* Krutzsch, 1969	Hamamelidaceae	P2
Tricolporopollenites villensis (Thomson) Thomson & Pflug, 1953	Fagaceae?	unknown

Table 1. — Continuation.

Fossil taxon	Botanical affinity	Element
Tricolporopollenites sp.	Fagaceae?	unknown
Triporopollenites megagranifer (Potonié) Thomson & Pflug, 1953	Betulaceae?, Ulmaceae?	P2/A1
Triporopollenites undulatus Pflug *in* Thomson & Pflug, 1953	unknown	P1
Trivestibulopollenites betuloides Pflug *in* Thomson & Pflug, 1953	Betulaceae: *Betula* Linnaeus, 1753	A
Ulmipollenites stillatus Nagy, 1969	Ulmaceae: *Ulmus* Linnaeus, 1753	A
Ulmipollenites undulosus Wolff, 1934	Ulmaceae: *Ulmus* Linnaeus, 1753	A2
Vitispollenites tener Thiele-Pfeiffer, 1980	Vitaceae: *Vitis* Linnaeus, 1753	P2/A1
Zelkovaepollenites sp.	Ulmaceae: *Zelkova* Spach, 1841	A1

ex Potonié emend. Krutzsch, 1961, *Platycaryapollenites* Nagy emend. Frederiksen & Christopher, 1978, and *Polyatriopollenites* Pflug, 1953), Fabaceae, and Ulmaceae (members of the fossil-genera *Celtipollenites* Nagy emend. Kohlman-Adamska & Ziembińska-Tworzydło, 2009, *Ulmipollenites* Wolff, 1934, and *Zelkovaepollenites* Nagy, 1969). Pollen grains of *Aceripollenites* Nagy, 1969, *Arecipites* Wodehouse emend. Krutzsch, 1970, *Boehlensipollis hohli* Krutzsch, 1962, *Caprifoliipites* Wodehouse emend. Słodkowska, 2014, *Carpinipites carpinoides* (Pflug) Nagy, 1985, *Cercidiphyllites minimireticulatus* (Trevisan) Ziembińska-Tworzydło, 1994, *Fraxinipollis* Słodkowska, 2014, *Intratriporopollenites* Pflug & Thomson, 1953, *Milfordia* Erdtman, 1960, *Oleoidearumpollenites* Nagy, 1969, *Periporopollenites* Pflug & Thomson, 1953, *Reevesiapollis* Krutzsch, 1970, *Salixipollenites* Srivastava, 1967, *Sparganiaceaepollenites* Thiergart emend. Krutzsch, 1970, *Subtriporopollenites* Pflug & Thomson emend. Krutzsch, 1961, *Symplocoipollenites* Potonié ex Potonié, 1960, *Trivestibulopollenites betuloides* Pflug, 1953, and *Vitispollenites tener* Thiele-Pfeiffer, 1980, occur regularly. Pollen grains of *Cornaceaepollis satzveyensis* (Pflug) Ziembińska-Tworzydło ex Jansonius *et al.*, 1998, *Faguspollenies* Raatz, 1937, and *Quercopollenites* Nagy, 1969 are more abundant in the upper part of the profile, while *Tricolporopollenites pseudocingulum* (Potonié) Thomson & Pflug, 1953 occurs only in the upper part. *Aglaoreidia cyclops* Erdtman, 1960, *Araliaceoipollenites* Potonié ex Potonié, 1960, *Cupanieidites eucalyptoides* Krutzsch, 1962, *Dicolpopollis* Pflanzl ex Potonié, 1966, *Dicolporopollis middendorfii* (Potonié) Krutzsch, 1961, *Edmundipollis* Konzalová, Słodkowska & Ziembińska-Tworzydło, 2014, *Meliaceoidites* Wang ex Jansonius & Hills, 1992, *Rutacearumpollenites rutaceoides* Kohlman-Adamska & Ziembińska-Tworzydło, 2014, *Triporopollenites megagranifer* (Potonié) Thomson & Pflug, 1953, and several others are also recorded.

Spores of ferns, mainly from the fossil-genera *Baculatisporites* Pflug & Thomson, 1953, *Laevigatosporites* Ibrahim, 1933, *Leiotriletes* (Naumova) Potonié & Kremp, 1954, and *Neogenisporis* Krutzsch, 1962, plus fossil-species *Cicatricosisporites dorogensis* Potonié & Gelletich, 1933, were regularly encountered. Similarly, spores of Lycopodiaceae (*Camarozonosporites heskemensis* (Pflanzl) Krutzsch, 1959 and *Retitriletes* Pierce emend. Döring, Krutzsch, Mai & Schulz, 1963) and *Sphagnum*-related spores (members of the fossil-genera *Distancoraesporis* (Krutzsch) S.K.Srivastava, 1973 and *Stereisporites* Pflug, 1953) occur in most samples.

AQUATIC PALYNOMORPHS

Aquatic palynomorphs are present in all samples. Twenty fossil-species of freshwater and brackish algae other than dinoflagellate cysts were identified (Table 2). Colonies of *Botryococcus* Kützing, 1849 are present in most samples, but their abundance exceeds 1% only in the upper part of the profile. Single specimens of zygospores from Zygnemataceae (mainly members of the fossil-genus *Ovoidites* Potonié emend. Krutzsch, 1959), as well as prasinophycean algae (*Cymatiosphaera eupeplos* (Valesi) Deflandre, 1954), *Sigmopollis pseudosetarius* (Weyland & Pflug) Krutzsch & Pacltová, 1990, and acritarchs, occur. Several cenobia of *Pediastrum* Meyen, 1829 were encountered in the upper part of the profile.

Among the aquatic palynomorphs, dinoflagellate cysts dominate, the majority of which are thought to be of marine origin. The preliminary study of eleven samples (see chapter Material and methods) shows that they are present throughout the entire succession studied. Their high frequencies, the general homogeneity of the assemblages, and a very good state of preservation indicate that most of them are *in situ*, and their motile stages inhabited the photic zone of the basin during the accumulation of the strata in question. All samples studied for dinoflagellate cysts yielded gonyaulacacean-dominated assemblages composed mainly of representatives of *Glaphyrocysta* Stover & Evitt, 1978 and *Homotryblium* Davey & Williams, 1966, to a lesser extent of *Enneadocysta* Stover & Williams, 1995 and *Lingulodinium* D.Wall, 1967, which are less common, showing an increase in frequency only in some samples. Noteworthy is the rare occurrence of *Spiniferites* Mantell, 1850. Peridinioids are subordinate in most samples being almost exclusively represented by *Wetzeliella* Eisenack, 1938.

FUNGAL REMAINS

Fungal microremains are rare in all samples and do not exceed 1% of the palynological spectrum. They consist mainly of spores, including dictyospores. In addition, some microsclerotia of terrestrial fungi were found in the samples from a depth of 86.9-87.3 m. These microsclerotia were intracellularly formed by fungi called dark septate endophytes (DSE) in the cortical cells of the plant roots. Microsclerotia consist of compact, darkly pigmented, thick-walled hyphae which previously filled usually the entire interior of the cortical cells tightly. They have various shapes depending on the shapes of the cells in which they were formed (Fig. 5N, O). Nowadays dark septate endophytes are darkly pigmented (melanised) fungi, mainly ascomycetes that colonise living plant

Fig. 4. — Pollen grains from Grabówka PIG-1: **A**, *Distachyapites* sp.; **B**, *Milfordia miocaenica* Grabowska & Słodkowska, 2009; **C**, **D**, *Restioniidites minimus* (Krutzsch) Kedves, 1974, same specimen, various foci; **E**, *Myricipites* sp.; **F**, *Aglaoreidia cyclops* Erdtman, 1960; **G**, *Ulmipollenites undulosus* Wolff, 1934; **H**, *Caryapollenites simplex* (Potonié) Raatz ex Potonié, 1960; **I**, *Momipites* cf. *punctatus* (Potonié) Nagy, 1969; **J**, *Platycaryapollenites* sp.; **K**, **L**, *Periporopollenites orientaliformis* (Nagy) Kohlman-Adamska & Ziembińska-Tworzydło, 2009, same specimen, various foci; **M**, *Nyssapollenites* sp.; **N**, **O**, *Aceripollenites striatus* (Pflug) Thiele-Pfeiffer, 1980, same specimen, various foci; **P**, **Q**, *Ilexpollenites margaritatus* (Potonié) Thiergart, 1938, same specimen, various foci; **R**, *Tricolporopollenites staresedloensis* Krutzsch & Pacltová, 1969; **S**, *Faguspollenites* sp.; **T**, *Quercoidites microhenricii* (Potonié) Potonié, Thomson & Thiergart ex Potonié, 1960; **U**, *Tricolporopollenites pseudocingulum* (Potonié) Thomson & Pflug, 1953; **V**, *Tricolporopollenites villensis* (Thomson) Thomson & Pflug, 1953; **W**, *Fususpollenites fusus* (Potonié) Kedves, 1978; **X**, *Fususpollenites fusus* (Potonié) Kedves, 1978; **Y**, **Z**, *Fususpollenites fusus* (Potonié) Kedves, 1978, same specimen, various foci; **AA**, **BB**, *Caprifoliipites viburnoides* (Gruas-Cavagnetto) Kohlman-Adamska, 1994, same specimen, various foci; **CC**-**EE**, *Platanipollis ipelensis* (Pacltová) Grabowska, 1994, same specimen, various foci; **FF**, *Platanipollis ipelensis* (Pacltová) Grabowska, 1994. Scale bar: 10 µm.

TABLE 2. — Freshwater and brackish algae, recorded in samples from the Grabówka PIG-1 borehole. Botanical affinity and indication according to Kadłubowska (1984), Krutzsch & Pacltová (1990), Grabowska (1996a), van Geel & Grenfell (1996), and Worobiec (2010, 2011, 2014, and literature cited herein).

Taxon	**Botanical affinity**	**Indication**
Acritarcha indiff.	unknown	brackish waters?
Botryococcus braunii Kützing, 1849	Dictyosphaeriaceae: *Botryococcus braunii* Kützing, 1849	open water, fresh and brackish waters
Closteritetrapidites sp.	Closteriaceae: *Closterium* Nitzsch ex Ralfs, 1848	oligo- to eutrophic fresh waters
Crassosphaera sp.	Chlorophyta?, Prasinophyta?	brackish waters?
Cymatiosphaera eupeplos (Valesi) Deflandre, 1954	Prasinophyceae	brackish waters
Diagonalites diagonalis Krutzsch & Pacltová, 1990	Zygnemataceae: *Mougeotia laetevirens* (Braun) Wittrock, 1877 type	shallow, stagnant, oxygen-rich fresh waters, lake margins
Megatetrapidites megatetroides Krutzsch & Pacltová, 1990	Zygnemataceae: *Mougeotia* Agardh, 1824	shallow, stagnant, oxygen-rich fresh waters, lake margins
Ovoidites elongatus (Hunger) Krutzsch, 1959	Zygnemataceae: *Spirogyra* Link *in* Nees, 1820	shallow, stagnant, oxygen-rich fresh waters, lake margins
Ovoidites gracilis Krutzsch & Pacltová, 1990	Zygnemataceae: *Spirogyra* Link *in* Nees, 1820	shallow, stagnant, oxygen-rich fresh waters, lake margins
Ovoidites grandis (Pocock) Zippi, 1998	Zygnemataceae: *Spirogyra* Link *in* Nees, 1820	shallow, stagnant, oxygen-rich fresh waters, lake margins
Ovoidites ligneolus (Potonié) Tomson & Pflug, 1953	Zygnemataceae: *Spirogyra* Link *in* Nees, 1820	shallow, stagnant, oxygen-rich fresh waters, lake margins
Ovoidites minoris Krutzsch & Pacltová, 1990	Zygnemataceae: *Spirogyra* Link *in* Nees, 1820	shallow, stagnant, oxygen-rich fresh waters, lake margins
Pediastrum boryanum (Turpin) Meneghini, 1840	Hydrodictyaceae: *Pediastrum boryanum* (Turpin) Meneghini, 1840	eutrophic fresh waters, open water surface
Pediastrum simplex Meyen, 1829	Hydrodictyaceae: *Pediastrum simplex* Meyen, 1829	eutrophic to mesotrophic fresh waters, open water surface
Pediastrum sp.	Hydrodictyaceae: *Pediastrum* Meyen, 1829	eutrophic to mesotrophic fresh waters, open water surface
Planctonites stellarius (Potonié) Krutzsch *in* Krutsch *et al.*, 1960	Zygnematales: desmids	fresh and probably brackish waters
Sigmopollis laevigatoides Krutzsch & Pacltová, 1990	Chlorophyta?, other algae?	eutrophic to mesotrophic open fresh waters
Sigmopollis pseudosetarius (Weyland & Pflug) Krutzsch & Pacltová, 1990	Chlorophyta?, other algae?	eutrophic to mesotrophic open fresh waters
Stigmozygodites sp.	Zygnemataceae: *Zygnema* Agardh, 1824	shallow, meso- to eutrophic, open fresh waters
Tetrapidites foveolatoides Krutzsch & Pacltová, 1990	Zygnemataceae: *Mougeotia* Agardh, 1824	shallow, stagnant, oxygen-rich fresh waters, lake margins
Tetrapidites sp.	Zygnemataceae: *Mougeotia* Agardh, 1824	shallow, stagnant, oxygen-rich fresh waters, lake margins

roots by forming both superficial and intraradical hyphae (Ruotsalainen *et al.* 2022). The ability to form intracellular microsclerotia is a unique feature of DSE among fungal plant root endophytes (Kariman *et al.* 2018: table 1). Dark septate endophytes colonize the roots of almost 600 modern plant species within 144 families (Jumpponen & Trappe 1998) in all major biomes of the world (Ruotsalainen *et al.* 2022). Similarly to mycorrhizal fungi, dark septate endophytes form close associations with plants both negative (parasitic) and symbiotic ones (Jumpponen 2001). The taxonomy of these fungi is rather complicated due to the lack of their sporulation and their morphological variability (Sieber 2002).

INTERPRETATION AND DISCUSSION

Age of the palynoflora

The composition of the palynological assemblage from the Grabówka PIG-1 clearly indicates its early Oligocene age. The stratigraphically most important pollen fossil-species are *Boehlensipollis hohli* and *Cupanieidites eucalyptoides*. The ranges of these taxa are confined to the Rupelian-early Chattian (Grabowska 1996b) and they occur (usually in small numbers) in almost all Rupelian palynofloras from Poland. *Cicatricosisporites dorogensis* and *Aglaoreidia cyclops* are also stratigraphically important as their ranges end in the lower Oligocene (Grabowska 1974, 1996b; Krutzsch *et al.* 1992). The Rupelian spore-pollen spectra from various localities of the Polish Lowlands are taxonomically uniform. Gymnosperms are usually most abundant and, depending on whether the spectra come from brackish/marine or freshwater sediments, they are dominated by Pinaceae (*Pinuspollenites*) or Cupressaceae (*Inaperturopollenites* and *Sequoiapollenites*) pollen, respectively. Small tricolporate pollen grains from Fagaceae (mainly *Fususpollenites fusus*, but also *Cupuliferoipollenites pusillus* and *Quercoidites microhenricii*) almost always dominate among angiosperms. Palm and *Ephedra* pollen is more common in terrestrial sediments (Grabowska 1996b). For example, the Grabówka palynoflora studied here is very similar to spore-pollen assemblages from the 5th Lignite Seam of

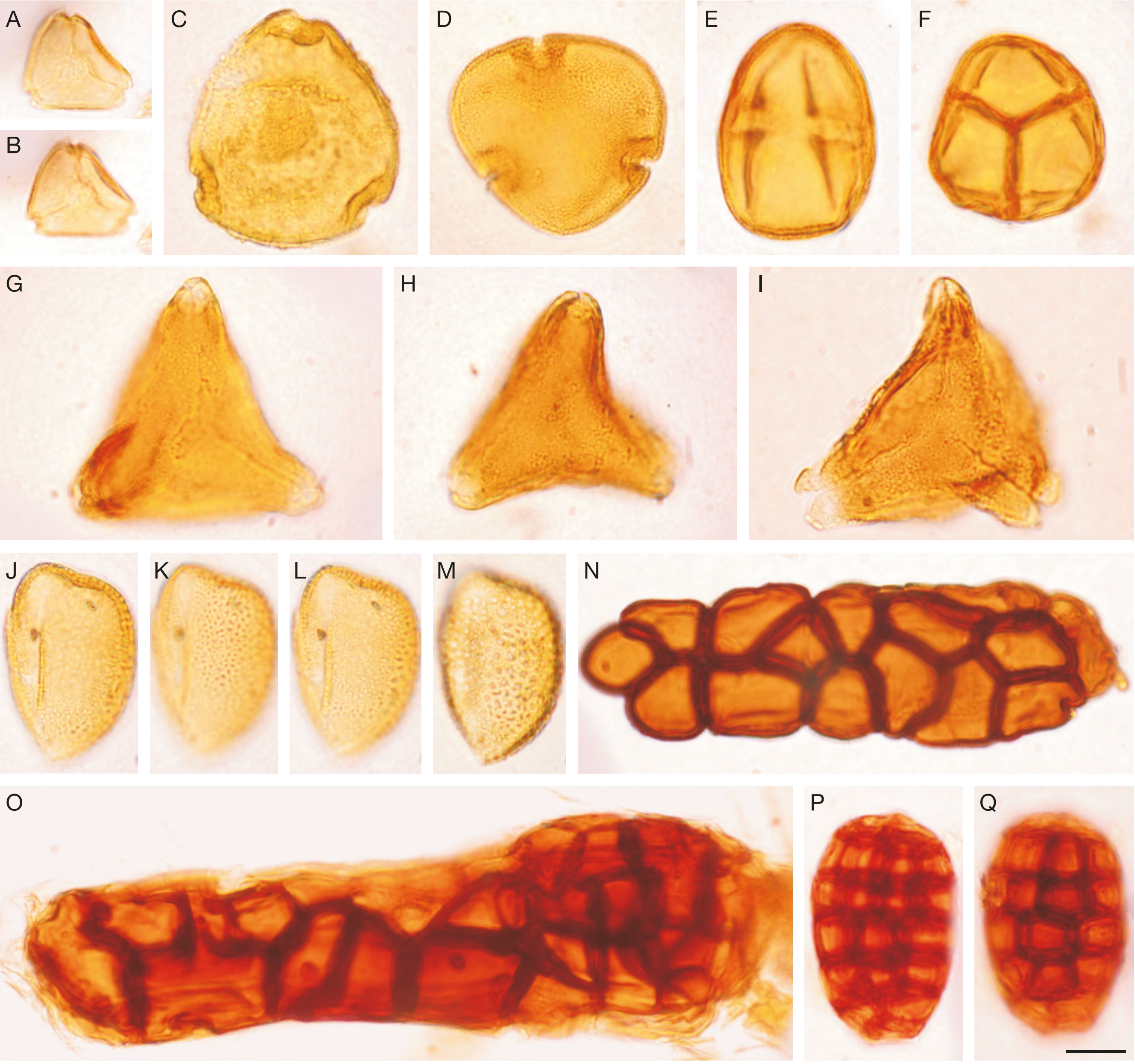

FIG. 5. — Pollen grains and fungi from Grabówka PIG-1: **A**, **B**, *Myrtaceidites myrtiformis* (Kremp) Nagy, 1969, same specimen, various foci; **C**, *Symplocoipollenites calauensis* (Krutzsch) Grabowska, 2014; **D**, *Intratriporopollenites insculptus* Mai, 1961; **E**, *Tetracolporopollenites sapotoides* Pflug & Thomson, 1953; **F**, *Ericipites triangulus* Grabowska, 2014; **G**, *Boehlensipollis hohli* Krutzsch, 1962; **H**, *Boehlensipollis hohli* Krutzsch, 1962; **I**, *Boehlensipollis hohli* Krutzsch, 1962; **J**-**M**, *Arecipites pseudoconvexus* Krutzsch, 1970, same specimen, various foci; **N**, microsclerotium of DSE fungus; **O**, microsclerotium of DSE fungus; **P**, **Q**, dictyosporous fungus, same specimen, various foci. Scale bar: 10 µm.

the Warszyce 19 borehole, central Poland (Grabowska 1969 *fide in* Kasiński & Słodkowska 2016) as well as it resembles very closely palynofloras from the lower Oligocene of the Pomeranian Lakeland (Słodkowska 2004a), Warmia and Mazury (Słodkowska 2009), and the Middle Vistula Valley (Słodkowska 2004b). The most important taxa in those palynofloras were: *Fususpollenites fusus*, *Quercoidites microhenricii*, *Cupuliferoipollenites pusillus*, *Inaperturopollenites* sp. (Cupressaceae), *Sequoiapollenites*, *Cyrillaceaepollenites*, *Myricipites*, *Tricolporopollenites liblarensis*, *T. quisqualis*, *Pinuspollenites*, *Tricolporopollenites dolium*, *T. villensis*, *Platanipollis ipelensis*, *Momipites*, *Boehlensipollis hohli*, *Dicolporopollenites middendorfi*, *Milfordia incerta*, *Triporopollenites megagranifer*, *Camarozonosporites heskemensis*, *Cicatricosisporites dorogensis*, and *Cupanieidites eucalyptoides*.

Most of the angiosperm taxa mentioned above also occur in the lower Oligocene palynofloras from southern Poland (upland area separating the Polish Lowlands in the north and Carpathians in the south), but in those palynological assemblages, the lack of marine palynomorphs and the low frequency of bisaccate pollen grains are characteristic. Those strata, with lignites correlated with the 5th lignite seam group, were deposited in isolated basins and the phytogenic terrestrial accumulation took place under continental, freshwater conditions, most likely in a swampy-lacustrine environment, as indicated by the presence of *Botryococcus* in spectra from the Łukowa-4 borehole, SE Poland (Gedl *et al.* 2016), or in karst sinkholes in south-western Poland (Worobiec & Szulc 2020).

Such a homogeneous composition of spore-pollen spectra makes the deposits of the lower Oligocene (including the 5th group of lignite seams) a good correlation horizon throughout the Polish Lowlands. Moreover, the 5th lignite seam is correlated with the 5th Lusatian (Lausitz) Lignite Seam in the eastern territory of Germany (Widera 2016). For example, the Calau Beds in Brandenburg, Germany, which represent estuarine to continental, lignite-bearing deposits (the 5th Lusatian Lignite Seam), yielded e.g. stratigraphically significant elements like: *Aglaoreidia cyclops*, *Boehlensipollis hohli*, *Dicolpopollis middendorfi*, *Camarozonosporites heskemensis*, *Cicatricosisporites paradorogensis*, *Plicapollis pseudoexcelsus* group, *Pentapollenites* sp., *Porocolpopollenites calauensis* as well as the group of smooth pollen grains of palms (Krutzsch *et al.* 1992; Mai 1998, and the literature cited therein).

Diversified early Oligocene plant assemblages known from marine deposits occur in the Upper Rhine Graben (Bodenheim Formation) and in the Paratethys region (Kvaček 2004; Hably & Erdei 2015; Kovar-Eder 2016). In contrast, the early Oligocene floras from the Czech Republic (northern Bohemia) and adjacent parts of Germany (mainly Saxony) originate mainly from lacustrine deposits in the adjacent volcanic hinterland (volcanic floras *sensu* Kvaček & Walther 2001 and Walther & Kvaček 2007) or were deposited in coastal lowlands (Leipzig Embayment; Mai & Walther 1978). Despite the differences in the composition of individual spore-pollen assemblages, *Boehlensipollis hohlii* is among the early Oligocene index sporomorphs found in those floras (Mai & Walther 1978; Konzalová 1981; Pross *et al.* 2001; Walther & Kvaček 2007).

Sedimentary setting

The presence of numerous dinoflagellate cysts throughout the whole Grabówka PIG-1 succession clearly indicates that these deposits accumulated in the marine environment. The composition of their assemblages shows a proximal, littoral setting as most species present, such as *Glaphyrocysta*, *Homotryblium*, *Membranophoridium*, *Lingulodinium*, are commonly found in rocks deposited in proximal marine environments (e.g. Köthe 1991; Brinkhuis 1994). Simultaneously, dinoflagellate cyst assemblages from Grabówka PIG-1 lack offshore species such as *Impagidinium* (e.g. Harland 1983; Brinkhuis 1994; Zonneveld *et al.* 2013). The near-shore environment can also be inferred from the presence of fungal microsclerotia of terrestrial DSE. Fungal remains represent palynological traces of terrestrial fluxes into the marine settings washed away from the adjacent lands (de Vernal 2009) and tend to accumulate in most proximal sites, decreasing basinward (Farr 1989; van Waveren 1989; Oboh 1992; Tyson 1995). The presence of algae, such as *Botryococcus*, Zygnemataceae, *Pediastrum*, and *Sigmopollis*, which are restricted to freshwater environments (Kadłubowska 1984; Guy-Ohlson 1992; Batten & Grenfell 1996; van Geel & Grenfell 1996; Zippi 1998), also suggests proximity to land.

All the sporomorphs found must have been transported from their vegetation areas into the marine basin where they were deposited. Fortunately, several studies show that the composition of the palynological assemblages from neritic marine sediments correlates well with the main types of contemporary terrestrial plant communities. Moreover, the percentage of pollen in marine sediments generally reflects the vegetation of the surrounding area and can roughly be used for palaeoclimatic considerations (e.g. Mudie 1982; Heusser 1983; Hooghiemstra & Agwu 1986; Van der Kaars 2001; Luo *et al.* 2014; Prader *et al.* 2017). Due to the fact that terrestrial elements are transported over different distances by water and air, these marine spore-pollen spectra may be used for the reconstruction of past environments only with great caution. For example, in marine sediments, bisaccate pollen (mainly *Pinus*) is usually over-represented, while other elements (for example pollen of insect-pollinated plants) are reduced (the so-called Neves Effect; e.g. Traverse 2007). Nevertheless, the large number of samples we analysed also allowed us to encounter some of these rarer pollen grains and spores (see chapters above).

Terrestrial vegetation

The results of the palynological analysis indicate the presence of lush vegetation on the nearby land. Mixed mesophytic forests that grew there were composed of members of the Fagaceae family (*Colombobalanus*/*Trigonobalanus*, Castaneoideae, evergreen *Quercus* and others), *Platanus*, Engelhardioideae, *Platycarya* as well as *Carpinus*, *Cercidiphyllum*, *Reevesia*, *Symplocos*, members of the Adoxaceae, Araliaceae, Arecaceae, Cornaceae, Fabaceae, Hamamelidaceae, Mastixiaceae, Meliaceae, Oleaceae and Sapotaceae families, conifers, and others. Many of them are thermophilous taxa. *Acer*, *Alnus*, *Carya*, *Celtis*, *Fraxinus*, *Liquidambar*, *Nyssa*, *Pterocarya*, *Salix*, *Ulmus*, and Vitaceae were most likely elements of wetland (swamp or riparian) forests. Shrubs from the Clethraceae and/or Cyrillaceae, Ericaceae and Myricaceae families, *Ilex* and some palms were probably components of shrub bog communities. Some pollen grains of conifers, e.g. *Pinus* and *Sciadopitys* could also have grown in wet places and/or in the margins of peat-bogs (Mosbrugger *et al.* 1994; Figueiral *et al.* 1999; Richardson 2003; Kus *et al.* 2020). Among the Cupressaceae are members of the Taxodioideae and Sequoioideae subfamilies, producing pollen of various morphologies (Fig. 3G-J), including the group of taxa with long papillae (Bouchal & Denk 2020). *Cryptomeria*, *Glyptostrobus*, *Metasequoia*, *Sequoia*, *Sequoiadendron*, and *Taxodium* were most likely components of different plant communities. For example, *Glyptostrobus* and *Taxodium*, together with *Nyssa*, could have grown in swamp forests in permanently flooded areas. The *Taxodium–Nyssa* swamp forests, often with *Glyptostrobus* and *Alnus*, were widespread in Europe during the Oligocene to Pliocene period as a type of Neogene peat bog vegetation (Mai 1981, 1995). *Sequoia* presumably has grown in wet places as well (Schneider 1992; Holdgate *et al.* 2016; Worobiec *et al.* 2021); some authors consider it as a riparian element (Kovar-Eder *et al.* 2001). Pollen of *Milfordia* and *Aglaoreidia cyclops* can probably be

TABLE 3. — Fossil taxa used for the estimation of the mean annual temperature (**MAT**) based on the Coexistence Approach (**CA**) method (Utescher *et al.* 2014). The nearest living relatives and their MAT ranges follow The Palaeoflora Database (Utescher & Mosbrugger 2015; Utescher *et al.* 2024).

Fossil taxa	**Nearest living relatives**	**MAT range [°C]**
Aceripollenites spp.	*Acer*	–1.1-24.0
Alnipollenites spp.	*Alnus*	–13.3-27.4
Carpinipites carpinoides (Pflug) Nagy, 1985	*Carpinus*	0.0-25.8
Caryapollenites spp.	*Carya*	4.4-26.6
Celtipollenites sp.	*Celtis*	2.5-25.8
Cercidiphyllites minimireticulatus (Trevisan) Ziembińska-Tworzydło, 1994	*Cercidiphyllum*	2.2-17.8
Cornaceaepollis satzveyensis (Pflug) Ziembińska-Tworzydło ex Jansonius *et al.*, 1998	*Mastixia*	15.7-27.8
Cornaceaepollis sp.	*Cornus*	–12-23.1
Corylopsispollenites microreticulatus E.Worobiec, 2014	*Corylopsis*	9.1-25.5
Faguspollenites spp.	*Fagus*	4.4-23.1
Fraxinipollis spp.	*Fraxinus*	0.0-24.0
Fususpollenites fusus (Potonié) Kedves, 1978	*Trigonobalanus* s.l. (incl. *Colombobalanus*)	17.2-27.7
Ilexpollenites spp.	*Ilex*	–0.4-27.7
Juglanspollenites sp.	*Juglans*	0.0-27.5
Magnoliaepollenites sp.	*Magnolia*	4.1-27.0
Myricipites spp.	*Myrica*	–8.9-28.1
Nyssapollenites spp.	*Nyssa*	4.4-23.9
Nyssoidites rodderensis Thiergart ex Potonié, 1960	*Nyssa*	4.4-23.9
Periporopollenites spp.	*Liquidambar*	11.5-25.5
Platanipollis ipelensis (Pacltová) Grabowska, 1994	*Platanus*	6.6-27.4
Platycaryapollenites sp.	*Platycarya*	6.9-23.1
Polyatriopollenites spp.	*Pterocarya*	3.9-24.2
Quercoidites henricii (Potonié) Potonié, Thomson & Thiergart ex Potonié, 1960	*Quercus* (evergreen)	8.7-22.1
Quercopollenites spp.	*Quercus* (deciduous)	–1.4-27.0
Reevesiapollis spp.	*Reevesia*	13.5-25.5
Salixipollenites sp.	*Salix*	–17.0-27.7
Spinulaepollis arceuthobioides Krutzsch, 1962	*Arceuthobium*	–5.5-27.7
Symplocoipollenites spp.	*Symplocos*	4.5-27.7
Trivestibulopollenites betuloides Pflug, 1953	*Betula*	–15.0-25.8
Ulmipollenites spp.	*Ulmus*	–4.9-26.6
Vitispollenites tener Thiele-Pfeiffer, 1980	*Vitis*	0.0-27.4
Zelkovaepollenites sp.	*Zelkova*	6.2-21.9

considered as representatives of the freshwater/marsh vegetation (e.g. Akkiraz *et al.* 2006). Similarly, Sparganiaceae and/or Typhaceae, and Cyperaceae grew in wet places. Among the ferns and lycopods several thermophilous taxa, including members of the Lygodiaceae, Schizaeaceae, Cyatheaceae and/or Gleicheniaceae families, were present.

Fossil pollen of *Ephedra* is known to be an indicator of a dry palaeoclimate (Bolinder *et al.* 2016) because modern members of this genus are xeromorphic. However, *Ephedra* species today also grow under more humid climate conditions on dry soils such as seashores with direct sun exposure. Moreover, according to Frink & Szabó (2009), the current relict sites of *Ephedra distachya* in Romania mark the seashore level of the Pannonian Sea before its regression at the end of the Neogene.

PALAEOCLIMATE

Pollen and spore taxa of thermophilic plants, including "warm-temperate" and "palaeotropical/warm-temperate" (Table 1), play a significant role or even dominate in the palynoflora studied. The presence of plant genera, growing now under tropical and subtropical climatic conditions, is clearly visible throughout the palynological diagram. Among them are members of the pantropical families Meliaceae and Sapotaceae as well as the subtropical-tropical families Arecaceae, Schizaeaceae, Cyatheaceae and/or Gleicheniaceae. This observation indicates that the climate during the sedimentation of the deposits studied was very warm (subtropical) and humid. It cannot be ruled out that fluctuations in the frequency of individual plant taxa are caused by climatic fluctuations, but the changes in the abundance of dinoflagellate cysts show that these are mainly caused by changes in the sea level and the distance of the sedimentation site from land.

The narrowest range of mean annual temperature (MAT) that can be estimated for the Grabówka PIG-1 palynoflora is 17.2-17.8°C (Table 3); with the bordering taxa *Fususpollenites fusus*, related to the genus *Trigonobalanus s.l.* (incl. *Colombobalanus*) (17.2-27.7°C), and *Cercidiphyllites minimireticulatus*, related to the *Cercidiphyllum* genus (2.2-17.8°C). It should be mentioned that *Cercidiphyllites minimireticulatus* was found in eight samples from different parts of the profile (Fig. 6). *Fususpollenites fusus* is present in all samples, but its botanical affinity is not entirely certain (Kohlman-Adamska & Ziembińska-Tworzydło 2001; Stuchlik *et al.* 2014). *Quercoidites microhenricii* and *Q. henricii*, common in all studied samples, could indicate that the MAT ranged up to 22.1°C (8.7-22.1°C); they are related to evergreen oaks from several different sections of the *Quercus* genus (MAT range and botanical affinity based on Utescher & Mosbrugger 2015). Therefore, the wider, but probably less error-prone, MAT range for the studied palynoflora is 15.7-23.1°C; with the bordering taxa *Cornaceaepollis satzveyensis*, related to the

Mastixia genus (15.7-27.8°C), and *Platycaryapollenites* sp., related to the *Platycarya* genus (6.9-23.1°C) or *Faguspollenites* sp., related to the *Fagus* genus (4.4-23.1°C).

Previous studies indicate a typical humid subtropical climate with distinct seasonality in central Europe during the Oligocene (Zachos *et al.* 2001, 2008; Mosbrugger *et al.* 2005; Li *et al.* 2018; Westerhold *et al.* 2020). Indeed, not all paratropical taxa found in the Eocene Climatic Optimum disappeared immediately, but some persisted into the early Oligocene (Collinson & Hooker 2003). Moreover, the timing and scale of this floral transition were not uniform in various regions of central and southeastern Europe (Kvaček & Walther 2001; Utescher *et al.* 2021). For example, in the Calau flora the following families were represented: Adiantaceae (C.Presl) R.M.Tryon, Altingiaceae Horaninow, Arecaceae Martius ex Dumortier, Betulaceae Gray, Cornaceae Berchtold & J.Presl, Dennstaedtiaceae Lotsy, Elaeagnaceae Jussieu, Ephedraceae Dumortier, Eucommiaceae Engler, Fagaceae Dumortier, Gleicheniaceae C.Presl, Juglandaceae Perleb, Loranthaceae s.l., Lycopodiaceae P.Beauvois, Mastixiaceae Calestani, Myricaceae Kunth, Nepenthaceae Dumortier, Onagraceae Jussieu, Osmundaceae Martinov, Pinaceae F.Rudolphi, Polypodiaceae J.Presl & C.Presl, Restionaceae R.Brown, Sapotaceae Jussieu, Schizaeaceae Kaulfman, Sciadopityaceae Luersson, Sparganiaceae Hanin, Sterculioideae Beilschmied, Symplocaceae Desfontaines, Taxodiaceae Saporta = Cupressaceae Bartlink, Tilioideae Arnott, and Ulmaceae Mirbel. Those included plants there were many taxa with high thermal requirements, but also plants whose living relatives grow in temperate climates. The composition of the fossil flora from Calau suggests a mixed mesophytic forest vegetation growing under humid temperate (subtropical) climatic conditions (Mai 1998). Similarly, the lignites of the 5th group of seams in the Polish Lowlands originated within isolated wetland basins, surrounded by very lush and mostly mesophilous vegetation with numerous highly thermophilous plants (Grabowska 1996b; Słodkowska 2004a, 2004b). The climate at that time was warm and humid, with the MAT in the range of 17.2-23.9°C and mean annual precipitation between 1 217 and 1 520 mm, when *Trigonobalanus* was used in the CA analysis (Kasiński & Słodkowska 2016). The palaeoclimate corresponded to a subtropical climate (Cfa type) in the sub-division of Köppen (Kottek *et al.* 2006), characterised by hot, usually humid, summers and mild winters (Kasiński & Słodkowska 2016). Palaeoclimatic conditions during the sedimentation of the middle Rupel Clay in the Mainz Basin, estimated based on the CA, also revealed a warm and humid palaeoclimate. MAT ranged from 16 to 18°C, the mean coldest month temperature 6-10°C, the mean warmest month temperature 25-28°C, and the mean annual precipitation 1 000-1 300 mm (Pross *et al.* 1998, 2001; Kvaček 2004). Other examples are from sites in Saxony, Germany, where MAT was estimated for the lowermost Oligocene Beucha site at 15.6-16.1°C, upper lower Oligocene Haselbach site at 15.7-18.3°C, and lower Oligocene Regis III site at 16.5-23.9°C; with hot summers and mild winters, and mean annual precipitation in the range of 897-1 281 mm (Roth-Nebelsick *et al.* 2004).

Sea water temperature

Aquatic palynomorphs from the Grabówka PIG-1 succession do not allow a direct reconstruction of seawater temperature; none of the species found has precisely known water temperature preferences that could suggest their value. The only suggestions excluding cold-water conditions can be based on the absence of high-latitude dinoflagellate cyst species, like *Svalbardella cooksoniae* or *Impagidinium velorum*, which are considered indicators of cold-water northward migrations during the early Oligocene (e.g. Gedl 2004; Van Simaeys *et al.* 2005; Śliwińska & Heilmann-Clausen 2011). This somehow contrasts with the palaeotemperature data obtained for the early Oligocene sea water from the north-western Polish Lowlands based on foraminifera analysis. Odrzywolska-Bieńkowa *et al.* (1978) suggested cool water conditions, though without precise values. That interpretation was based on foraminifera associations (mainly benthic) from marine strata occurring in the north-western Polish Lowlands. The bottom waters (and hence the benthic foraminifera) in this area were likely intensively influenced by the cold and dense waters exchanged from the North Sea basin, where isotopic evidence suggests a significant temperature drop (e.g. Buchardt 1978). These changes were not necessarily associated with climatic changes and the near-shore embayment, where the investigated Czempiń Formation was probably accumulated, may lie beyond the reach of cold bottom waters of the main part of the basin.

However, the absence of cold-water dinoflagellate cysts does not necessarily solve the problem of water temperature conditions. Firstly, the investigated Czempiń Formation is a near-shore facies without offshore species such as *Impagidinium velorum*. Although palaeoenvironmental preferences of *Svalbardella cooksoniae* are not precisely known (except for its cold-water preferences), Śliwińska & Head (2020) suggested that its sister species *Svalbardella kareniae* favoured offshore waters. Moreover, the lack of peridinioid *S. cooksoniae* in the present material can be explained by generally hostile conditions for peridinioids, which are scarce (mainly Wetzeliellaceae). Secondly, the strata in question are presumably slightly younger than the earliest Oligocene cooling event responsible for the appearance of cool-water species as far south as the Carpathian basins (see e.g. Gedl 2004). The studied strata are also slightly older than another cooling event that, according to Van Simaeys *et al.* (2005), occurred close to or at the boundary between the Rupelian and the Chattian and was also manifested by the appearance of *Svalbardella* at lower latitudes.

CONCLUSIONS

The samples from the Grabówka PIG-1 borehole yielded rich palynological material consisting of terrestrial and marine palynomorphs. The composition of the palynoflora, including such stratigraphically important fossil-species as *Boehlensipollis hohli*, *Cupanieidites eucalyptoides*, *Cicatricosisporites dorogensis*, and *Aglaoreidia cyclops*, clearly indicates its early Oligocene age.

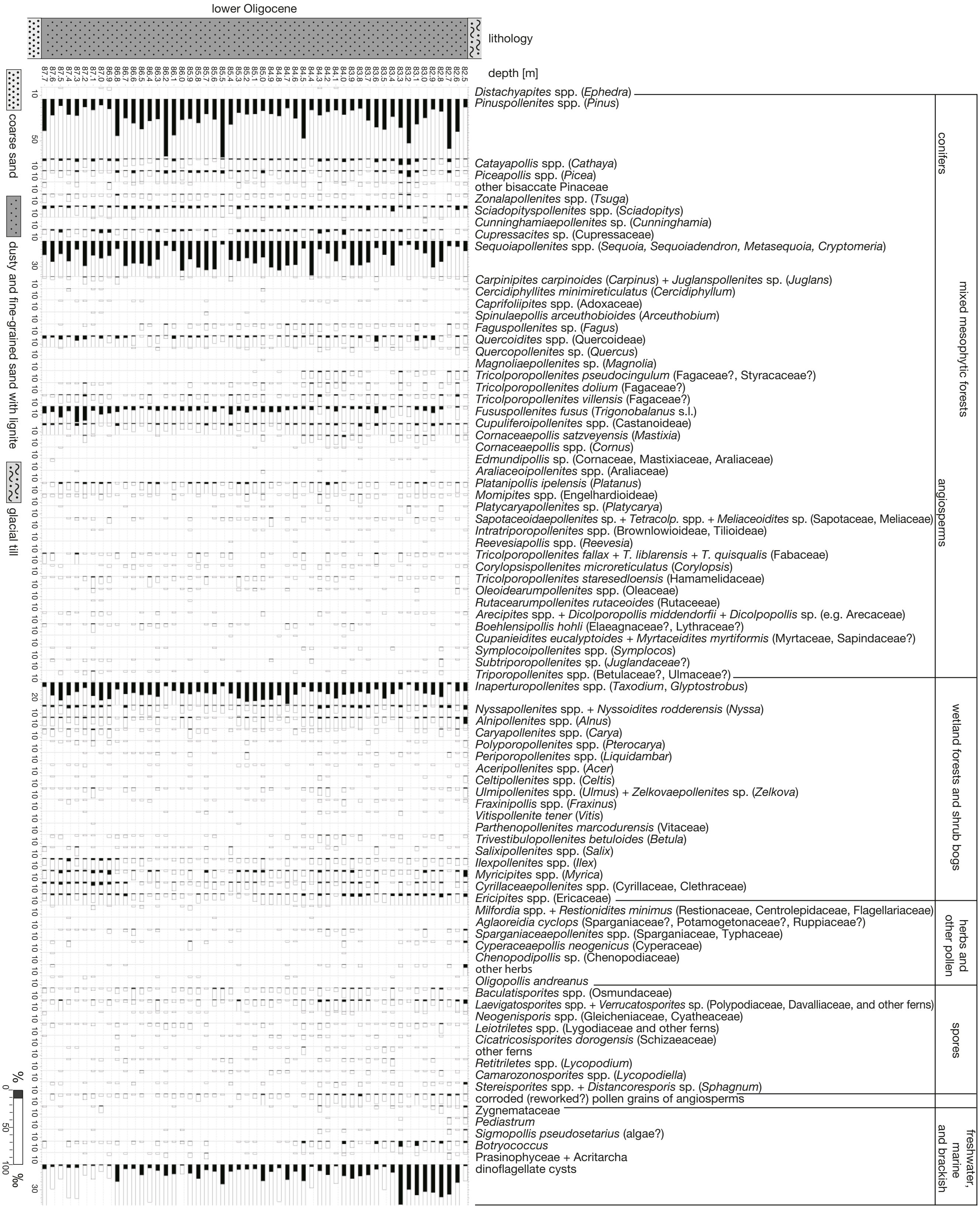

Fig. 6. — Simplified percentage diagram of pollen and spores of plants, and non-pollen palynomorphs from the Grabówka PIG-1 borehole. **Black bars** show percentages (%), **white bars** show percentages ×10 (‰).

The composition of the spore-pollen assemblage corresponds to the 5th Czempiń lignite seam group. The presence of dinoflagellate cysts throughout the succession studied clearly indicates that it was deposited under marine conditions. The whole sequence was deposited in a near-shore environment of the epicontinental sea connected with the North Sea. The proximity to land is indicated by large amounts of terrestrial plant remains and freshwater algae. The presence of fungal microsclerotia (dark septate endophytes) in the lower part of the profile may also suggest proximity to the coastline.

The results of the spore-pollen analysis indicate the presence of lush vegetation with numerous thermophilous elements (including members of the pantropical families Meliaceae and Sapotaceae as well as the subtropical-tropical families Arecaceae, Schizaeaceae, Cyatheaceae and/or Gleicheniaceae, plus many "warm-temperate" taxa) in the adjacent land area. Mixed mesophytic forests were composed mainly of members of the Fagaceae and Juglandaceae families as well as *Platanus*, *Carpinus*, *Cercidiphyllum*, *Reevesia*, *Symplocos*, members of the Adoxaceae, Araliaceae, Arecaceae, Cornaceae, Fabaceae, Hamamelidaceae, Mastixiaceae, Meliaceae, Oleaceae and Sapotaceae families. There were also wetland (swamp or riparian) forests, shrub bogs, and freshwater/marsh vegetation. *Ephedra* grew on seashores. The climate during the sedimentation of the deposits was subtropical and humid, with the estimated MAT range of 15.7-23.1°C.

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