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REVIEW in POLISH BOTANY CENTENNIAL

Polish Palaeobotany: 750 Million Years of Plant History as Revealed in a Century of Studies. Research on the Paleogene and Neogene (Tertiary)

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Abstract

On overview of over a hundred years of history of Polish palaeobotanical research on the Paleogene and Neogene (formerly Tertiary) is provided. Profiles of the researchers who laid the foundations for the development of paleofloristic research are presented. In particular, we describe individuals who have made significant research contributions, including M. Raciborski, J. Zabłocki, M. Kostyniuk, H. Czeczott, and W. Szafer. Research centers that were revived after World War II gathered scientists who continued and extended work in the field, including M. Łańucka-Środońowa, J. Oszast, A. Skirgiełło, J. Doktorowicz-Hrebnicka, J. Stachurska, and J. Mamczar. This tradition was maintained and developed by researchers of the next generation: L. Stuchlik, E. Zastawniak, A. Sadowska, M. Ziembińska-Tworzydło, I. Grabowska, H. Ważyńska, A. Hummel, Z. Baranowska-Zarzycka, and A. Kohlman-Adamska. Currently, the fourth generation of Polish palaeobotanists, including B. Słodkowska, E. Worobiec, G. Worobiec, P. Gedl, M. Garecka, E. Durska, and R. Kowalski, conduct multifaceted palaeobotanical research, with links to various fields of knowledge, including botany, geology, and palaeoclimatology. Studies of past changes in plant cover provide important insight current climate change.

Keywords

history; palaeobotany; macroflora; palynology; Paleogene; Neogene

1. Introduction

The Paleogene and Neogene (former Tertiary) is the period between 66.0 and 2.6 million years ago. At that time, the nature of the vegetation changed significantly and was dominated by angiosperms. The radiation of angiosperms occurred in the Late Cretaceous and Paleogene, with slower rates of evolution from the Eocene to the Pliocene. The nature of the vegetation gradually transformed from ancient taxa, which are now mainly extinct, to a composition resembling the modern vegetation. The Tertiary is therefore a key period in understanding the mechanisms leading to today's flora. After this period, plant communities similar to modern ones formed, and distributions of various taxa changed, shaping their current geographical ranges.

The history of the development and changes have been recorded in the sediments of the Paleogene and Neogene in the form of macro- and microremains. As a result of the processes of conservation and fossilization, these remains have survived to modern times. Macro-remains include fruits, seeds, leaves, wood, and rarely flowers and inflorescences. Among microremains, which are studied in a separate section of palaeobotany (palynology), spores, pollen grains, fungi, phytoplankton, including dinoflagellate cysts, acritarchs, green algae, diatoms, nanoplankton, other microscopic algae, and other plant meso-fossils (e.g., tissue fragments, phytoliths, and others) are most often preserved in the fossil state.

Fossil plant remains found in Paleogene and Neogene sediments are related to extant taxa of various ranks. Many plants of the early Paleogene (Paleocene and Eocene) are extinct, some of which can be classified to the order or family level and, in rare instances, to the genus level. In the younger Tertiary strata, from the Oligocene to the Miocene, there is a greater possibility of classifying fossils into modern families and genera. In the late Neogene (Pliocene), fossils can sometimes be compared to modern plant species (original lectures on palaeobotany for students of the Faculty of Geology, University of Warsaw – Ziembińska-Tworzydło, carried out in the years 1976–2003).

2. History of the Last Hundred Years of Polish Palaeobotanical Research on the Tertiary

Ewa Zastawniak and Piotr Köhler (2001) compiled an extensive history of Polish Tertiary research from the first works up to 2001. In addition to the research history, the authors included biographies of Polish palaeobotanists, both living and scientifically active as well as deceased, involved in the study of fossil remains of Tertiary plants. Observations of Tertiary plants in Poland began, like most palaeobotanical studies, with the works of Marian Raciborski in the 1920s. As Zastawniak and Köhler (2001) wrote, Raciborski himself did not publish descriptions of any of the Tertiary flora; however, based on his observations, he formulated a revealing statement at the time that "the Miocene vegetation of Europe was similar to modern vegetation of East Asia, Japan and North America" (Raciborski, 1927). The first Polish report on the remains of Tertiary plants was that of Kuźniar (1910), focused on the Eocene of the Tatra Mountains.

During the interwar period, palaeobotany was a field of no economic importance and intensive development was not possible; yet, some researchers at the time were fascinated by the fossil flora. One of these researchers was Jan Zabłocki, who in his doctoral thesis in 1926 described the Tertiary leaf flora from Chodzież (Zabłocki, 1924). He also investigated the flora from Chłapowo (Zabłocki, 1935). Zabłocki's greatest achievement was the description of Miocene seeds preserved in salt from Wieliczka (Zabłocki, 1930), which was one of the first palaeocarpology studies in Europe. Before the war, important on a European scale, the first attempt in Poland and one of the first few attempts in the world was made to extend pollen analyses to Tertiary formations. The study concerned pollen and wood of Tertiary plants from Mazowsze and Wołyń (Ukraine) by Mikołaj Kostyniuk (1938). During the interwar period, Hanna Czeczott (1934) also began observing fossils of Tertiary plants. An important achievement of this period was the summary by Jerzy Lilpop (1929) of the palaeobotanical knowledge at the time (also centered on the Tertiary), titled *Vegetation of Poland in the Past Epochs (Fossil Floras)*.

The war period was not conducive to scientific research, and even small achievements in the form of notes (for example, by Hanna Czeczott, Stefan Kownas, or Jan Zabłocki) were destroyed – oral records. In a great achievement at the time, Jerzy Lilpop saved the palaeobotanical collections at the Physiographic Museum of the Polish Academy of Arts and Sciences in Kraków from being transported to Germany.

Only Władysław Szafer was able to continue his work on the description of the Pliocene flora from Krościenko on the Dunajec, started before the war. Published shortly after the war (Szafer, 1946, 1947), it was the best documented of all palaeobotanical works by Szafer and is still cited in the world literature (Zastawniak & Köhler, 2001).

After the war, the laboratories that survived the occupation period were revived, and pre-war researchers studying the Tertiary flora very quickly launched new scientific institutions, which were largely of utility for geological research. The earliest research after the war was performed at the Botanical Institute of the Jagiellonian University in Kraków. Professor Władysław Szafer and a large team examined the flora from Tertiary and Quaternary sediments.

The Museum of the Earth was established in Warsaw in 1948. In 1949, Hanna Czeczott organized a palaeobotanical laboratory in the museum for the study of flora originating mainly from the lignite mine in Turoszów (Zastawniak & Köhler, 2001).

The Polish Geological Institute, resumed after the war in 1945, was originally located in Kraków. It was only in 1949 that the institute was moved back to Warsaw. The palaeobotanical laboratory was led by Jadwiga Raniecka-Bobrowska and the palynological laboratory was led by Julia Doktorowicz-Hrebnicka.

The most important scholars of the Tertiary flora from the interwar period established new university laboratories after the war. Mikołaj Kostyniuk established the Department of Palaeobotany at the University of Wrocław and, in 1954, the Division of Palaeobotany at the Department of Palaeontology at the Faculty of Geology of the University of Warsaw. In Wrocław, he was replaced by Anna Stachurska. Jan Zabłocki at the Nicolaus Copernicus University in Toruń and Stefan Kownas in Szczecin at the Department of Botany of the University of Agriculture also established palaeobotanical laboratories with a focus on Tertiary flora (Zastawniak & Köhler, 2001).

Researchers of the Tertiary flora of the pre-war generation achieved the organization of scientific activity at individual research centers after the war, the preparation of a cadre of young scientists as well as taxonomic studies of flora from new sites: Dobrzyń on the Vistula River (Kownas, 1956a, 1956b), Podhale, Stare Gliwice (Szafer, 1946, 1947, 1961), wood from Turów (Kostyniuk, 1967; Zalewska, 1961), a collection of seeds from Turów (Czeczott & Skirgiełło, 1961, 1967), plus seed floras from central, southern and south-western Poland: Rypin, Podhale, Orawa, Gozdnica (Łańcucka-Środoniowa, 1957, 1963), palynological studies of flora from Stare Gliwice, Piaseczno near Tarnobrzeg and Podhale (Oszast, 1960, 1967; Oszast & Stuchlik, 1977), and palynological characteristics of lignite from central Poland (Doktorowicz-Hrebnicka, 1961; Mamczar, 1960) should also be mentioned here.

The pre-war generation of palaeobotanists was surrounded by young researchers. In Kraków, Professor Władysław Szafer at Jagiellonian University and numerous young collaborators established the Department of Palaeobotany at the Institute of Botany of the Polish Academy of Sciences in 1956. Within a few years, the dynamic unit became a leading center for researchers of Tertiary and Quaternary floras not only from Poland but also from both Eastern and Western Europe (Zastawniak & Köhler, 2001).

In the palaeobotanical laboratory of the Polish Geological Institute, intensive palaeobotanical studies of both macro- and microremains were focused on newly discovered lignite deposits. A fairly large team of young researchers specialized in spore-pollen analysis. Palynological studies of Tertiary sediments dominated, as they yielded relatively quick results for biostratigraphy.

In the 1970s, the first attempts at the biogeographic synthesis of Miocene land sediments were made based on comprehensive palynological data. These analyses were performed by Jadwiga Raniecka-Bobrowska (1970) in south-western Poland and by Janina Oszast and Leon Stuchlik (1977) in southern Poland.

Researchers of the pre-war generation studying the Tertiary flora, apart from scientific research (Kostyniuk, 1951a, 1951b), were also engaged in popularizing and editorial activities, e.g., *Monographiae Botanicae* (Kostyniuk, 1958–1975) and members of the editorial board of *Wiadomości Botaniczne*. They wrote textbooks and scripts for students, e.g., *Outline of Palaeobotany* (Szafer & Kostyniuk, 1952, 1962), and *Handbook of Palynology* (Dyakowska, 1959).

From around 1970, a boom in Tertiary flora research began worldwide, and Polish researchers joined this trend. Junior researchers specialized in analyses of macro- and microflora. In addition to studies of many sites in Poland, studies of Tertiary flora involved extensive international cooperation and internships, especially in scientific centers of Eastern Europe (Zastawniak & Köhler, 2001).

In Kraków at the Department of Paleobotany (W. Szafer Institute of Botany, Polish Academy of Sciences), Maria Łańucka-Środoniowa studied the fruit and seed flora and created a catalogue of types of fossil species kept in the Museum of Institute of

Botany (Łańcucka-Środoniowa, 1985). Ewa Zastawniak studied fossil leaves from Bełchatów, Domański Wierch, Gozdnica, Holy Cross Mountains, Sośnica, Wieliczka, and several other sites (Zastawniak, 1972, 1980, 1992, 1996). She was also interested in the Tertiary leaves from Spitsbergen (Zastawniak, 1981) and was the first in the world to study the flora from early Tertiary sediments from Antarctica (King George Island) in 1985–1989 (Birkenmajer & Zastawniak, 1989). Pollen analyses of Tertiary sediments at the Kraków research center were carried out by Leon Stuchlik, who also studied the pollen flora from Antarctica (Stuchlik, 1981).

An important palynological study by Leon Stuchlik was the analysis of Miocene sediments from Rypin (Stuchlik, 1964). Later works were dominated by an interest in the Miocene palynofloras of southern Poland, e.g., Podhale, Nowy Sącz Basin, and other eastern parts of Paratethys, in cooperation with colleagues from the Czech Republic, Slovakia, Ukraine, Hungary, Georgia, and Bulgaria (Stuchlik, 1992). Moreover, he studied the pollen flora from Bełchatów (Stuchlik & Szynkiewicz, 1990). In the 1990s, Eva Planderová from Geological Institute Bratislava emphasized international cooperation among all palynologists studying the Neogene (Planderová et al., 1993). Leon Stuchlik in 1993–1994 became interested in the synthesis of vegetation and climate changes in the Miocene and Pliocene. In 1994, the Polish team led by L. Stuchlik introduced the concept of geofloristic elements, to which individual pollen taxa were assigned, to characterize the palynology of the Neogene (Ziembińska-Tworzydło et al., 1994). This was immediately picked up by European palynologists, not always citing the source.

In the 90s of the last century, Professor Maria Łańcucka-Środoniowa and Maria Lesiak studied the fruit and seed floras from Krościenko, Podhale, Orawa, Nowy Targ Basin, and Bełchatów (Zastawniak et al., 1996).

In Wrocław, Anna Sadowska dynamically headed the Department of Palaeobotany at the University of Wrocław, where palynological analyses of the Tertiary and Quaternary sediments were carried out. Her research interests were mainly the reconstruction of plant cover and palaeogeographic conditions in the late Miocene and Pliocene in south-western Poland, based on knowledge of the palynostratigraphy of deposits of the younger Tertiary (Sadowska, 1977, 1994).

At the Polish Geological Institute (PGI) in Warsaw, Irena Grabowska studied the main lignite seams from the Konin area (Grabowska, 1956). Other Tertiary palaeobotanical works carried out at the PGI were limited to palynology. Irena Grabowska studied mainly the palynoflora of the Paleogene and Neogene. Her first Paleogene work from 1965 on "Toruń clays" changed the stratigraphic position of this formation (Grabowska, 1965). In addition to pollen analysis, she also used dinocysts and other microorganisms in her research, which are very good stratigraphic tools for Paleogene marine sediments (Grabowska, 1983, 1996a, 1996b, 1996c). This led to the publication of *Atlas skamieniałości przewodnich i charakterystycznych* [Atlas of guide and characteristic fossils] (Malinowska & Piwocki, 1996b, 1996a) – in which the palynological features of the Neogene were described by Maria Ziembińska-Tworzydło (1996) and those of the Paleogene were described by Irena Grabowska (1996a, 1996b, 1996c).

There were two more centers of research on the Tertiary flora in Warsaw. The first was at the Museum of the Earth, Polish Academy of Sciences, where Professor Hanna Czeczott created a team to address this issue from various perspectives. Zofia Zalewska (1961) studied Tertiary woods, Krystyna Juchniewicz (1978) worked on dispersed leaf cuticules prepared from lignite, Zofia Baranowska-Zarzycka (1988) identified fruits and seeds, and Aleksandra Kohlman-Adamska (1993) conducted palynological research. Leaves preserved in Tertiary sediments were studied by Anna Hummel (1983, 1991), who developed an innovative method for the preparation of leaves with preserved cuticles, and Katarzyna Krajewska (1998, 2001), who studied the leaf floras from several localities in Lower Silesia.

The second center was at the University of Warsaw, Faculty of Geology. The head of the Department of Palaeobotany, Professor Mikołaj Kostyniuk, studied Tertiary fossil wood. His assistant Maria Ziembińska-Tworzydło was a palynologist studying Tertiary sediments in western Poland and in Turów (Ziembińska-Tworzydło, 1974, 1992). In addition, she analyzed the Paleogene Characeae from the Gobi Desert (Karczewska & Ziembińska-Tworzydło, 1972).

After years of scientific isolation, in the late 1980s and 1990s, intensive international cooperation began, involving research centers in Western Europe. In 1986, Polish palynologists (I. Grabowska, H. Ważyńska, and M. Ziembińska-Tworzydło) participated in the International Geological Correlation Programme (IGCP) project No. 124 concerning the Tertiary Basin of North-Western Europe. A summary of this collaboration was published in *Geologische Jahrbuch* (Grabowska et al., 1988a, 1988b).

In 1991, the International Palaeobotanical-Palynological Conference (IPPC) was held in Vienna, in which a large group of Polish palaeobotanists participated for the first time (Sadowska, 1992; Ziembińska-Tworzydło, 1992).

Polish researchers actively participated in the international symposium in Bratislava in 1992. The leading topics were paleofloristic and paleoclimatic changes during the Cretaceous and Tertiary. During this conference, the division of the Tertiary geoflora into two types was introduced: palaeotropical and arctotertiary (Planderova et al., 1993).

The 4th European Palaeobotanical-Palynological Conference (EPPC) was held in Kerkrade in the Netherlands in 1994, which was attended by a large group of Tertiary palaeobotanists. The 5th EPPC took place in 1998 at Kraków. It was organized mainly by the Institute of Botany in Kraków, with the participation of a number of Polish Tertiary palaeobotanists as well as researchers from Europe and elsewhere.

Research by Polish palynologists over 50 years was summarized in 1998 in a study edited by Hanna Ważyńska. This work summarizes palynological studies of the Neogene from palaeofloristic, palynostratigraphic, and palaeogeographic perspectives (Ważyńska, 1998).

The turn of the century was very fruitful for Polish palaeobotanical research of the Paleogene and Neogene.

The crowning achievement in palynological research at the turn of the twentieth and twenty-first centuries was the textbook *Palinologia* [Palynology] (Dybova-Jachowicz & Sadowska, 2003). The chapter on Miocene research, written by Sadowska and Ziembińska-Tworzydło (2003), contained recent palynology and palaeogeography data for this period in Poland. The Paleogene palynoflora was described by Grabowska and Słodkowska (2003).

Polish palynologists dealing with Tertiary sediments, including representatives of the older and younger generation (Ewa Durska, Irena Grabowska, Aleksandra Kohlman-Adamska, Anna Sadowska, Barbara Słodkowska, Leon Stuchlik, Hanna Ważyńska, Elżbieta Worobiec, and Maria Ziembińska-Tworzydło), worked together closely. The most important result of this cooperation was the development and publication of four volumes of the *Atlas of Pollen and Spores of the Polish Neogene* edited by Leon Stuchlik et al. (2001, 2002, 2009, 2014). This work has become a permanent fixture in the palynological literature, providing a basis for the identification of spores and pollen grains from Neogene sediments.

An important aspect of the research work was the storage of palaeobotanical collections, especially macroflora (Figure 1) – leaves (E. Zastawniak, A. Hummel, G. Worobiec, K. Krajewska), fruits, seeds, and flowers (H. Czeczott, A. Skirgiełło, J. Raniecka-Bobrowska, R. Kowalski), cuticles (K. Juchniewicz, G. Worobiec), and specimens embedded in amber (B. Kosmowska-Ceranowicz, A. Pielińska) – housed in the Paleobotanical Department, Institute of Botany, Polish Academy of Sciences and Museum of the Earth of the Polish Academy of Sciences. The basis of the palynological collection are photographs of holotypes of genera and species described in *Atlas of Pollen and Spores of the Polish Neogene*, deposited at the Museum of the Earth of the Polish Academy of Sciences. In addition, the second part of the palynological collection at the Museum of the Earth also contains original photographs of spores and pollen grains of uncertain systematic position for later identification by interested palynologists.

Figure 1 Miocene macroflora from the Polish Geological Institute Museum collection. Photo: K. Skurczyńska-Garwolińska.

3. Intensive Period of Research by the Next Generation of Polish Palaeobotanists Over the Last 20 Years

The current generation of palaeobotanists dealing with Tertiary flora work in Kraków and Warsaw. Their research interests range from classical macropalaeobotany and palynology to stratigraphic, environmental, and climatological studies.

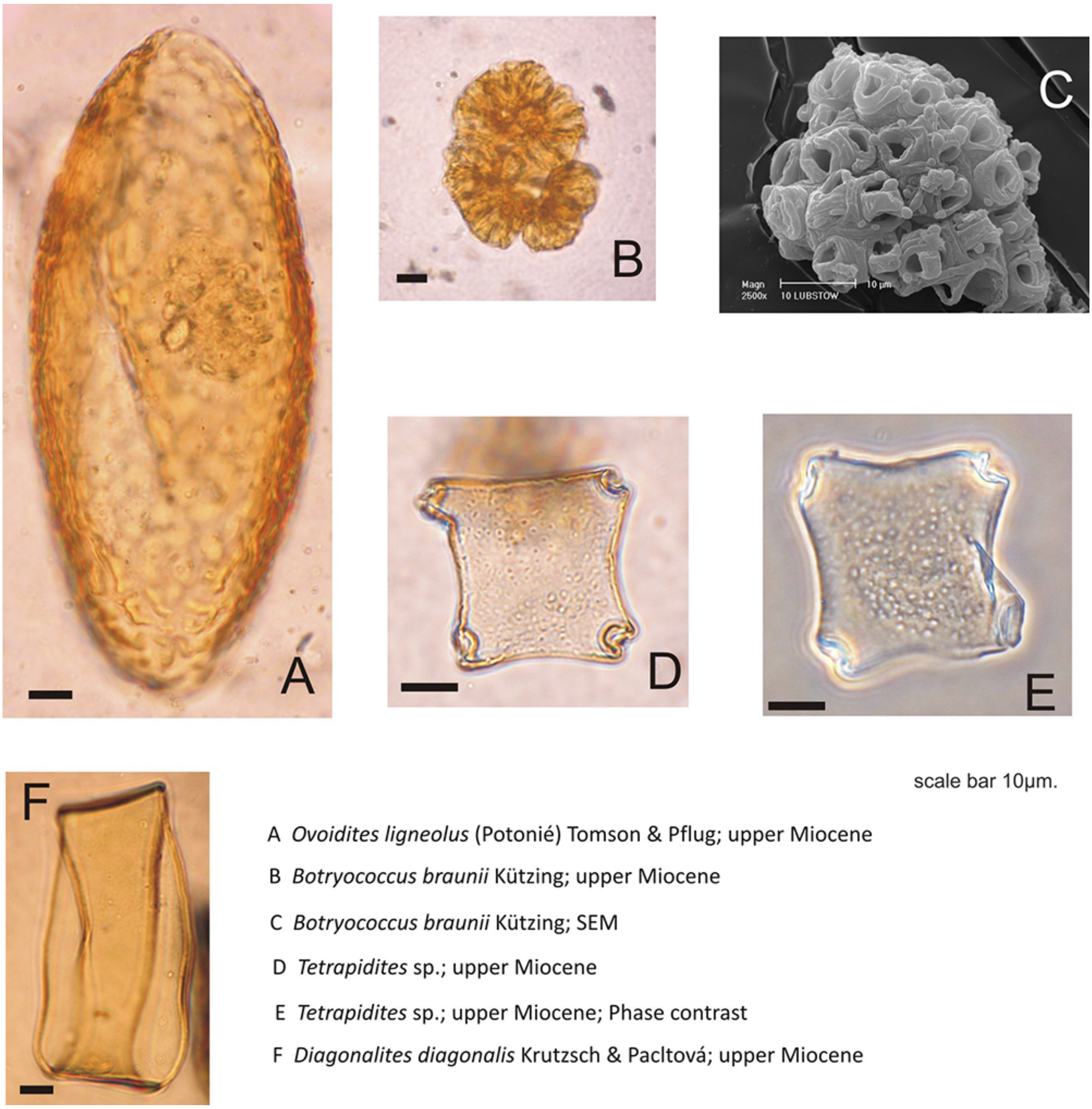


Figure 2 Freshwater microalgae (Chlorophyta) from Miocene deposits. Photo credits: Light microscopy (LM) – E. Worobiec; scanning electron microscopy (SEM) – M. Ziembińska-Tworzydło.

At the Kraków research center at the W. Szafer Institute of Botany, Polish Academy of Sciences, Elżbieta and Grzegorz Worobiec study various aspects of the development of the Tertiary flora.

Elżbieta Worobiec conducts research on the palynoflora from Neogene sediments using both pollen analysis and identification of non-pollen palynomorphs (mainly microremains of freshwater algae) (Figure 2). These are pioneering studies on a national scale and are mainly used in palaeoenvironmental and palaeoclimatic considerations (E. Worobiec, 2014a). Using non-pollen palynomorph methods, combined with a pollen and spore analysis, she studied the palynoflora from the lignite deposits in the Bełchatów, Konin and Legnica regions (Ivanov & Worobiec, 2017; E. Worobiec, 2009; E. Worobiec et al., 2021; E. Worobiec & Worobiec, 2016). In addition, she investigated Paleogene sediments from the Carpathian Foredeep (E. Worobiec & Gedl, 2018), Germany, Greenland, and Antarctica as well as Neogene of Bulgaria, Germany, Ukraine, and the United States (E. Worobiec et al., 2013). Her research contributed to the understanding of the palaeoflora, climate, and palaeogeography of these areas. The basic contributions of these studies are the reconstruction of the vegetation and sedimentation environment in Miocene mire communities as well as hydrological and trophic conditions. Palynostratigraphic studies have shown that sediments from karst sinkholes in Triassic limestones are of the Oligocene and Miocene age and indicate a multi-phase development of the palaeokarst in the Silesian-Cracow Upland (E. Worobiec & Szulc, 2010). The surrounding Oligocene and Miocene vegetation was reconstructed on the basis of the sediments filling the sinkholes (E. Worobiec & Szulc, 2020).

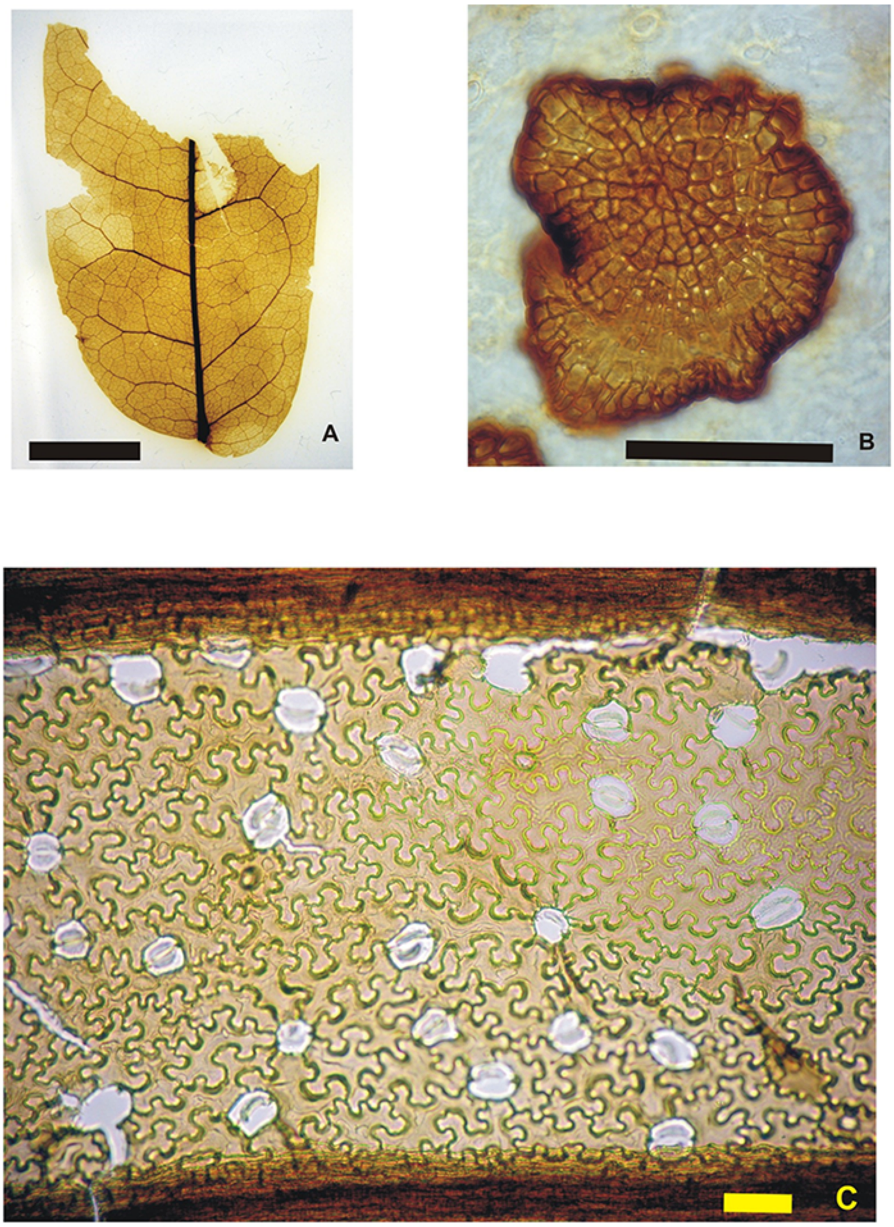
Grzegorz Worobiec is a specialist in the area of plant macroremains and fungal microremains from Cenozoic deposits (Figure 3). He performs comprehensive taxonomic and palaeoecological studies of fossil leaf assemblages and dispersed leaf cuticles, especially from lignite deposits, e.g., the Bełchatów Lignite mine (G. Worobiec, 2014) and the Ruja lignite deposit in the Legnica region (G. Worobiec et al., 2008). He conducts comprehensive research aimed at taxonomy and palaeoecology of leaf assemblages and microfungi found in palynological samples (G. Worobiec et al., 2015). He described several new taxa based on leaf, fungal, and dispersed cuticle samples. G. Worobiec developed a new technique for the isolation and mounting of fossil leaves from clay deposits. This technique enabled the preparation of permanent preparations of whole leaves and the analysis of the leaf venation architecture (G. Worobiec, 2003). Research on plant macroremains from most sites was supplemented with data from pollen analyses performed by E. Worobiec. This collaboration led to the reclassification of separate taxa based on organ morpho-fossils (leaves, fruits, and pollen grains) to a single plant in the genus *Reevesia* (G. Worobiec & Worobiec, 2020). Moreover, based on microremains of fossil fungi (e.g., sporocarps of epiphyllous fungi, ascospores, and conidia), G. Worobiec describes new taxa and revises taxonomic assignments of existing fossil species from Poland as well as Germany, Greenland, Hungary, and the United States (G. Worobiec et al., 2017, 2018, 2020). In collaboration with Sławomir Florjan from the Institute of Botany of the Jagiellonian University, he published the first monograph in Poland on the taphonomy of fossil plants (Florjan & Worobiec, 2016).

Two researchers working at the Kraków branch of the Polish Geological Institute – National Research Institute evaluate the plant characteristics of Tertiary sediments.

The main area of research by Wojciech Granoszewski is the palynoflora of the Pleistocene; however, he also devoted several works to the study of Neogene sediments. He examined the palynological profile of the Złoczew lignite deposit and dated the sediments to the middle Miocene (second and third seams); he also palynologically examined organic sediments from the Nowy Targ profile, dating them to the late Pliocene.

At the same research center, Małgorzata Garecka investigates other plant microremains, i.e., calcareous nanoplankton. Her work emphasizes the usefulness of single-celled marine algae belonging to Coccolithophorales for biostratigraphy, palaeoenvironmental, and palaeoclimatic analysis of Miocene marine sediments of the Carpathians and the Carpathian Foredeep (Peryt et al., 2021) (Figure 4). Their widespread occurrence in surface exposures and shallow drillings makes these algae useful in the implementation of the tasks of the Polish Geological Survey.

At the Institute of Geological Sciences of the Polish Academy of Sciences (Research Center in Kraków), Przemysław Gedl studies fossil dinoflagellate cysts from Mesozoic and Cenozoic sediments in the Carpathian Mountains and the Carpathian Foredeep (Figure 5). He described the dinocyst record of the Cretaceous/Paleogene boundary and conducted studies of Palaeogene dinocysts in the Inner Carpathians, southeast (SE) Poland, and Ukraine (Gedl, 2014, 2015; Gedl & Garecka, 2008; Gedl & Worobiec, 2020). On the basis of dinocyst assemblages, he also described the Eocene/Oligocene boundary in the Carpathian flysch (Gedl & Leszczyński, 2005). Miocene sediments from the Carpathian Foredeep are another subject of his studies. His work on dinocyst assemblages is related to biostratigraphy and the palaeoenvironmental record. For example, he recorded significant changes in assemblages caused by changes in the sedimentation environment of evaporetic formations in the Carpathian Foredeep (Peryt et al., 2020).



Scale bar: A - 1cm; B, C - 100 µm.

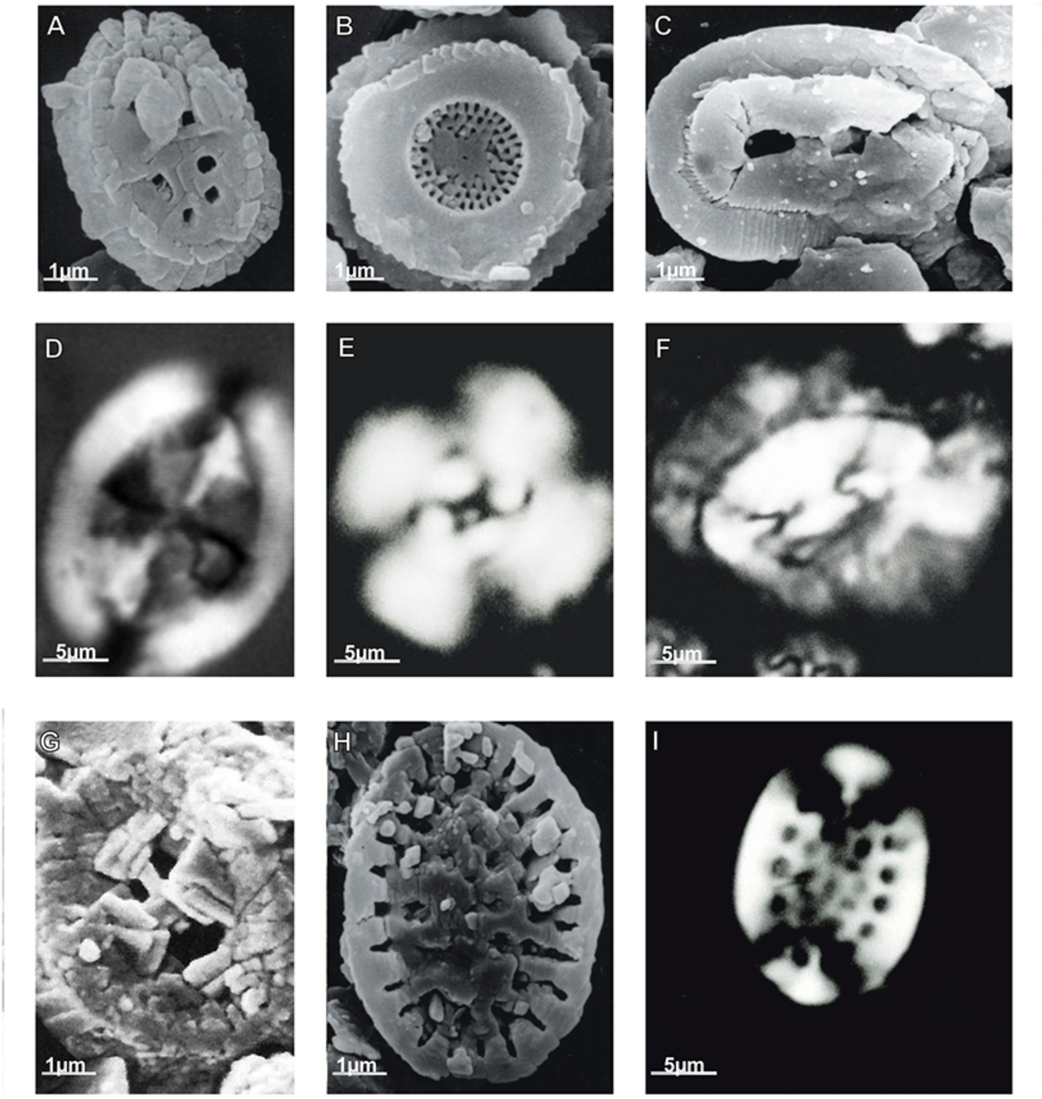
A. *Leguminophyllum kvacekii* G. Worobiec, leaflet, middle/late Miocene

B. *Neomycoleptodiscus pertusus* (Dilcher) G. Worobiec, sporodoichium (sporocarp) of mitosporic epiphyllous fungus, early Miocene

C. *Osmunda parschlugiana* (Unger) Andreánszky, abaxial epidermis of fern leaflet, middle Miocene

Figure 3 Macro and microremains of plants and fungi from the Polish Miocene. Photo: G. Worobiec.

Three research centers deal with the Tertiary flora in Warsaw. At the University of Warsaw, Faculty of Geology, Department of Paleontology, Ewa Durska studied the biostratigraphy of Miocene land sediments from several sites in Poland. Her greatest and extremely interesting discovery was the observation and documentation of the phenomenon of plasmolysis occurring in pollen grains of various types of plants in



A.Arkhangelskiella cymbiformis Vekshina
B.Cyclicargolithus floridanus (Roth et Hay) Bukry
C.Helicosphaera compacta Bramlette et Wilcoxon
D.Arkhangelskiella cymbiformis Vekshina
E.Cyclicargolithus floridanus (Roth et Hay) Bukry
F.Helicosphaera compacta Bramlette et Wilcoxon
G.Coccolithus pelagicus (Wallich) Schiller
H.Pontosphaera multipora (Kamptner) Roth
I.Pontosphaera multipora (Kamptner) Roth

Figure 4 Calcareous nannofossils of the Polish Carpathians and Carpathian Foredeep. Photo: M. Garecka.

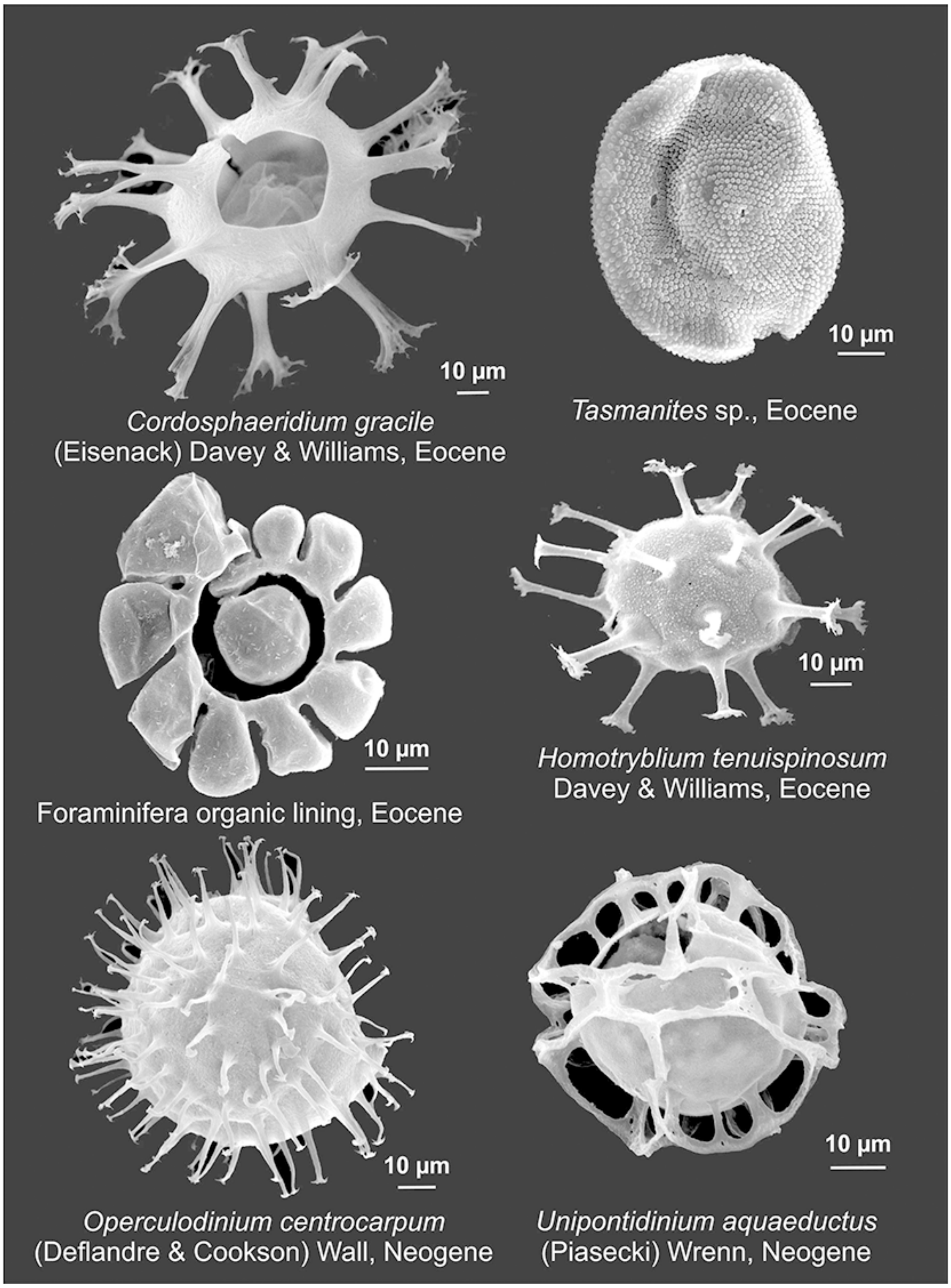


Figure 5 Dinocysts, Chlorophyta algae, and foraminifera organic lining from Paleogene and Neogene deposits. Photo: P. Gedl.

the Miocene evaporite sediments of the Carpathian Foredeep (Durska, 2016, 2017) (Figure 6). This represented a unique observation of the state of pollen conservation under stressful conditions in salt sediments.

At the Museum of the Earth of the Polish Academy of Sciences in Warsaw, Rafał Kowalski conducts research on fruit, seeds, and inflorescences from Cenozoic sediments, mainly from the Neogene (Figure 7). He described fruit and seed floras from many localities, such as Turów, Konin, Lubstów (Konin Lignite Basin), Dobrzyń nad Wisłą, Chłapowo, and Rozewie (Kowalski, 2017). Recently, he has examined the Oligocene flora from Lower Silesia (Kowalski et al., 2020) and the Paleocene from the vicinity of Szczecin (Kowalski, 2018).

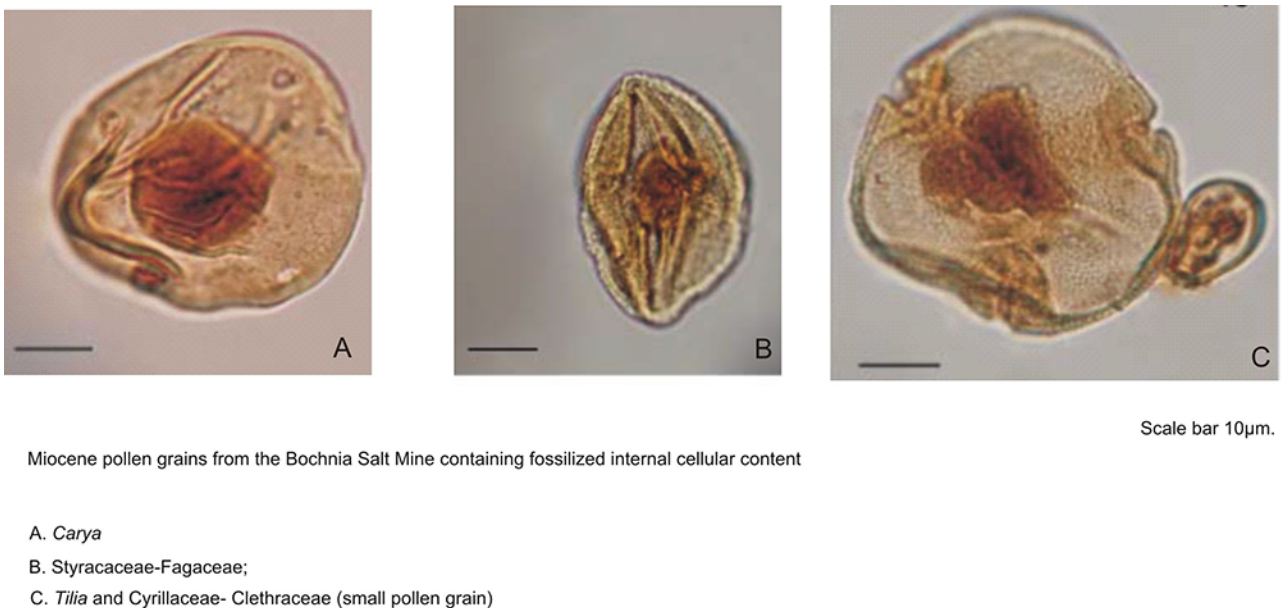


Figure 6 Miocene pollen grains from the Bochnia Salt Mine containing fossilized internal cellular contents. Photo: E. Durska.

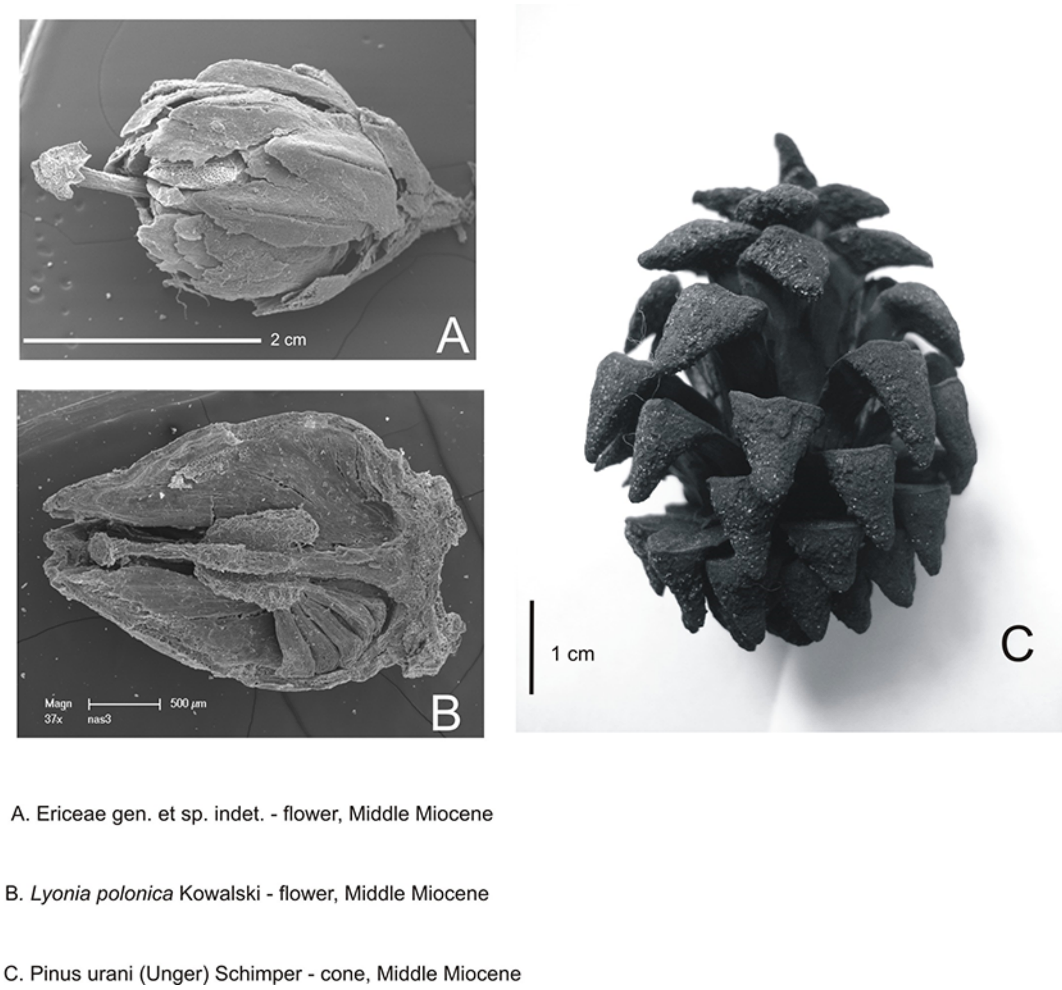
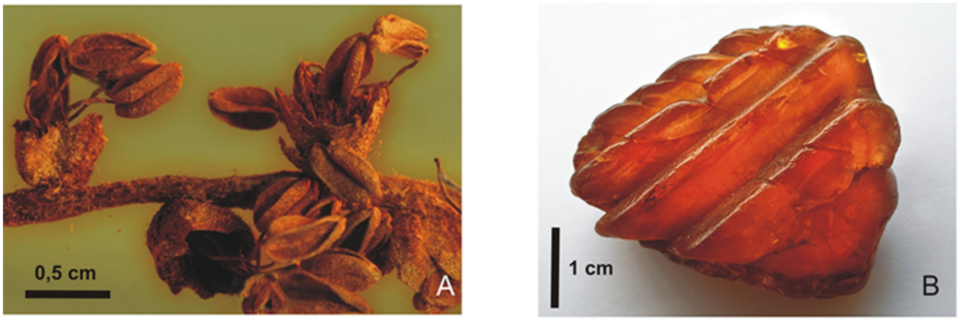


Figure 7 Middle Miocene flowers and cone. Photo: R. Kowalski.



A. Fragment of oak inflorescence in baltic amber. PAS Musem of the Earth collection. Photo J. Kupryjanowicz

B. Imprint of a palm leaf piece in baltic amber. PAS Musem of the Earth collection. Photo B. Gronuś-Dutko

Figure 8 Flora in Baltic amber from the Museum of the Earth of the Polish Academy of Sciences collection.

Alicja Pielińska also works at the Museum of the Earth as a curator in the Amber Department. She deals with the taxonomy and documentation of the Paleogene macroflora embedded in Baltic amber (Figure 8). She spreads knowledge about amber-bearing forests as well as amber museum collections and researchers in the field (Pielińska, 1997, 2001).

At the Polish Geological Institute – National Research Institute (PGI-NRI), Barbara Słodkowska performs palynological studies of Paleogene and Neogene sediments using pollen (Figure 9), phytoplankton, and palynofacies (Słodkowska, 2003). She focuses on palynostratigraphy, the reconstruction of plant communities, and palaeoclimatic and palaeogeographic changes (Słodkowska & Kasiński, 2016a). She documented, using palynological methods, mega-scale glacitectonic structures in sediments from the vicinity of the Dylewskie Hills and confirmed such disturbances in the Muskau Arch (Kasiński & Słodkowska, 2017; Słodkowska & Gałązka, 2015). She demonstrated the importance of the *Pollenites edmundi* pollen morphotypes for palaeoclimatic considerations (Słodkowska & Ziembińska-Tworzydło, 2017). Barbara Słodkowska also conducted palynostratigraphic analyses of the Złoczew lignite deposit and in the Milicz region. She reconstructed the climatic conditions during the formation of the main lignite deposits in the Polish Lowlands (Kasiński & Słodkowska, 2016). In lignite mine opencasts in the Konin region, she observed the palaeoflora response to changing climatic conditions, linking them to global climatic events in the Miocene (Słodkowska & Widera, 2021). She developed a new litho- and palynostratigraphic division scheme for the Late Neogene. B. Słodkowska also contributes to research on phytoplankton (dinocysts, acritarchs, prasinopytes, green algae, and others) in Paleogene marine sediments (Słodkowska, 2004, 2009). In the Eocene deposits, she identified palynologically amber-bearing strata. She also distinguished characteristic dinocyst communities in prospective amber-bearing sediments in the northern Lublin region (Słodkowska & Kasiński, 2016b; Słodkowska et al., 2022).

Marzena Kłusek, currently employed at the Silesian University of Technology, studies the anatomy of fossil angiosperm wood (Kłusek, 2012) as well as wood of some coniferous taxa (Kłusek, 2014).

Palaeobotanical studies of the Paleogene and Neogene flora continue to progress, with active research internationally. This activity is especially visible in the exchange of interns, joint grants, publications, research programs, and wide participation in numerous scientific conferences, particularly the European Palaeobotanical-Palynology Conference (EPPC), International Palynological Congress (IPC), and International Organisation of Palaeobotany Conference (IOPC). Tertiary palaeobotanists are involved in scientific consortia and research networks. An example is the active participation of palaeobotanists (L. Stuchlik, M. Ziembińska-Tworzydło, B. Słodkowska, E. Worobiec, and G. Worobiec) in the international research network NECLIME (https://www.neclime.de/), aimed at the

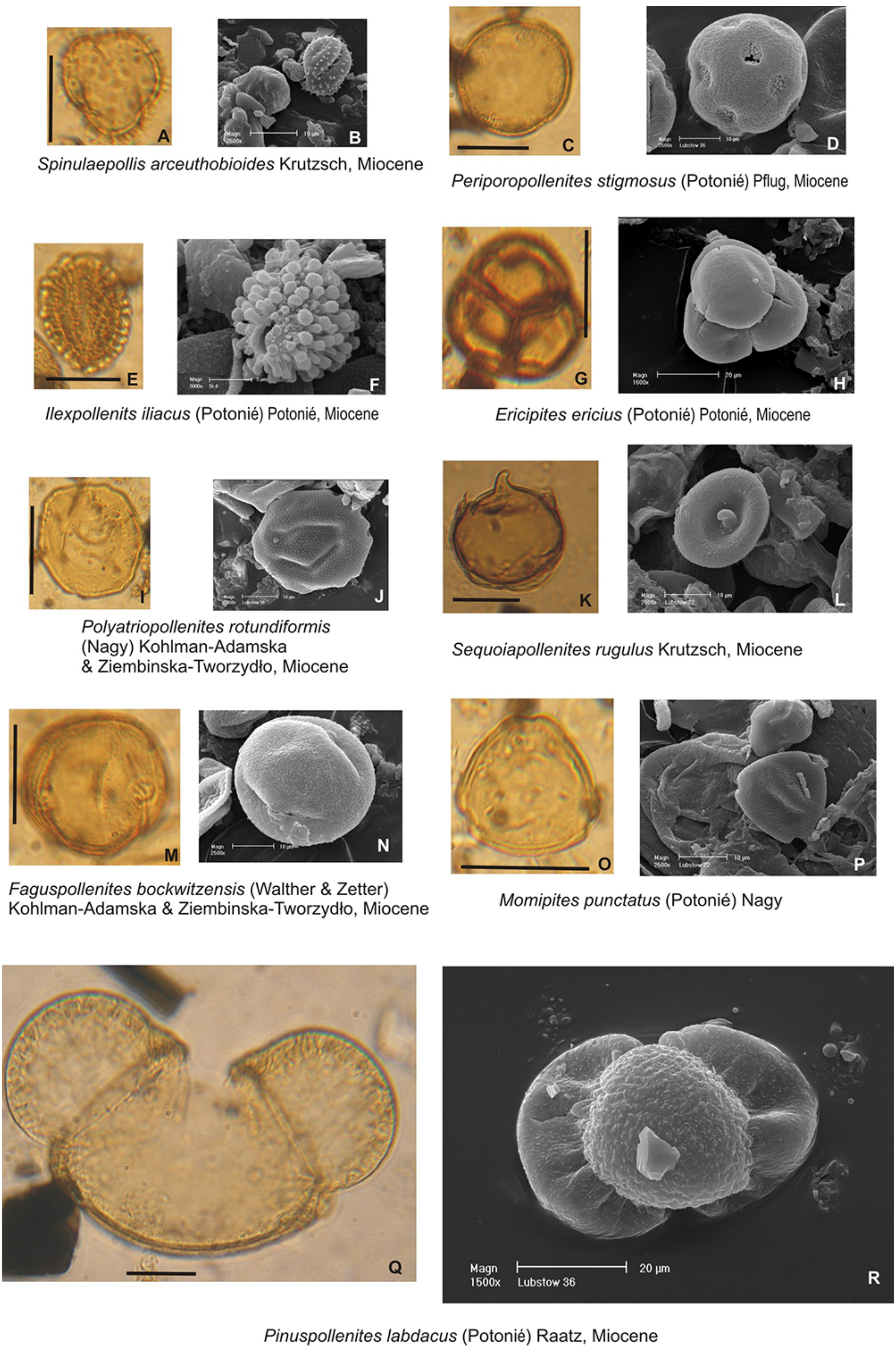


Figure 9 Pollen grains from the Tertiary sediments. (**A,C,E,G,I,K,M,O,Q**) Photo: B. Słodkowska. Scale bar 20 µm. (**B,D,F,H,J,L,N,P,R**) Scanning electron microscopy (SEM) images. Photo: M. Ziembińska-Tworzydło. Scale bars in the photos.

observation of climate changes in the Neogene, recorded in land sediments. In this program, palaeofloristic data make it possible to accurately reconstruct palaeoclimatic and palaeovegetation changes in the Neogene of Eurasia (since the late Oligocene to the late Pliocene) and relate these changes to the present day. Another example of scientific collaboration is the participation of E. Worobiec in the National Science Foundation – CAREER: "Exploring the Neogene Plant Record of Global Vegetational and Climatic Changes in eastern North America – Research and Education Program." Polish palaeobotanists have various roles in international societies and scientific organizations. They serve as members of editorial boards of scientific journals, conduct didactic activities, and organize national and international scientific conferences (B. Słodkowska, E. Worobiec, and G. Worobiec).

During the past century of palaeobotanical research, knowledge of the Paleogene and Neogene palaeoflora and appreciation for the field have expanded substantially. These features have been passed down from generation to generation. The fourth generation of scientists continues to study Tertiary plants, using modern research methods and tools, while establishing new research directions.

4. Directions of Contemporary Palaeobotanical Studies of the Palaeogene and Neogene Flora

Palaeobotanical studies of the Paleogene and Neogene are multifaceted. They broaden and improve knowledge in seemingly distant fields, making a substantive contribution to the development of other branches of science, including botany, geology, and climatic and palaeoecological research.

4.1. Botany

Observations of fossil plants, especially their spores and pollen grains, are of interest to biologists, including the analysis of the ultrastructure of the cell membrane (Bińka, 2005) and the comparative anatomy of fossil and contemporary taxa (Kohlman-Adamska & Ziembińska-Tworzydło, 1999). Recently, the first observation of the phenomenon of fossil plasmolysis in Miocene pollen grains preserved in salt sediments was reported (Durska, 2016, 2017).

In botany, a lot of information comes from taxonomic studies of fossil plants, making it possible to trace evolutionary trends of individual systematic groups. Additionally, for botanists, the *whole plant concept* (i.e., the reconstruction of a whole fossil plant from separate organs) is important to understand past biodiversity (G. Worobiec & Worobiec, 2020; G. Worobiec et al., 2010). Determining the systematic position of a fossil plant makes it possible to link it with a contemporary taxon. Establishing botanical affinities for both macro- and microremains is the basis for the description of fossil plant communities. In addition, research in systematics provides an overview of changes in the flora. In this way, the evolutionary history of the plant cover in a selected research area is studied, enabling palaeoecological reconstructions. Comparative studies have shown that contemporary plant communities in Georgia (Stuchlik, 1993), SE China, and SE United States (Florida, Louisiana, and South Carolina) may constitute refuges of Tertiary vegetation (E. Worobiec et al., 2021).

4.2. Geology

Palaeobotanical research is widely used in geology. Findings of both fossil macro- and microflora in Paleogene and Neogene deposits are frequent. The occurrence of the Tertiary fossil flora is related to the type of sediment, e.g., lignite, amber, and diatomite (Kowalski et al., 2020; Słodkowska & Kasiński, 2016b; E. Worobiec, 2009; Ziembińska-Tworzydło, 1992). Moreover, it is found in evaporites (Durska, 2016, 2017), river sediments, lake sediments, mires (Słodkowska & Widera, 2021; E. Worobiec et al., 2021), marine sediments (Słodkowska, 2004), caves (E. Worobiec, 2014b), etc. Palaeobotanical studies of fossil remains and, in particular, the microflora of these sediments, allow for fairly quick biostratigraphic inferences (Piwocki & Ziembińska-Tworzydło, 1997). It is also important to link changes in plant communities with geological events, especially geotectonics and glaciotectonics (Kasiński & Słodkowska, 2017; Słodkowska & Gałązka, 2015). Plant remains also play an important role in the correlation of sediments and are helpful in facies and palaeogeographic reconstructions.

Palynological research frequently involves palynofacies analyses, consisting of inventories of all components of organic matter contained in sediments. This provides an overview of the palaeoenvironment of sedimentation and the underlying processes (Gedl, 1999, 2016; Kasiński et al., 2010).

Palynofacies analyses are also used in the search for hydrocarbon occurrences (especially in Carpathian areas). A method of determining the degree of thermal maturity by the TAI (Thermal Alteration Index) is used for this purpose (Staplin, 1969).

In marine environments, in addition to microflora derived from terrestrial plants, phytoplankton are also abundant, including dinocysts, acritarchs, prasinophytes, green algae, and other algae. These microfossils are sensitive indicators of changes in basin bathymetry, salinity, water temperature, trophicity, and other parameters (Gedl, 2013; Słodkowska, 2004, 2009). Phytoplankton is often found in the Paleogene sediments in the Polish Lowlands and the Paleogene and Neogene in the Carpathians and their foreland (Gedl, 2016).

Palaeobotanical research is used in various tasks of the Polish Geological Survey, particularly to resolve issues related to geological structure, hydrocarbon geology (Dziadzio et al., 2016), and the occurrence of thermal and healing waters. This research also has implications for protection against landslides, railway and road investments, and the identification of areas of geological structures useful for waste storage and other purposes (archival studies stored in the National Geological Archive, PGI-NRI and archives of external companies).

5. Palaeoclimatic and Palaeoenvironmental Research

Both fossil and modern plants are sensitive indicators of climate change.
To determine the causes of contemporary changes, it is important to observe past changes and look for records in the fossil state analogous to modern ones.
The Tertiary is a period of dynamic climate change, the effects of which have been recorded in the sediments of this age (Słodkowska & Kasiński, 2016a). The Paleogene and Neogene mark the beginning of the modern world in terms of the collocation of lands and seas as well as the flora and fauna. Changes in the composition of the flora indicate climatic oscillations most often caused by global factors. Various palaeobotanical research methods are used to reconstruct past climate change.
To record past vegetation of the Paleogene and Neogene, the P/A method is used, which involves assigning fossil pollen taxa to modern botanical counterparts (nearest living relatives) and classifying them to the appropriate palaeofloristic element (i.e., palaeotropical or arctotertiary), divided into tropical and subtropical as well as warm and cool temperate classes (Ziembińska-Tworzydło et al., 1994). Another method for palaeoclimate reconstruction is the CA (coexistence approach) (Mosbrugger & Utescher, 1997), in the climatic requirements for fossil plants are determined by establishing the climatic requirements of the nearest living relatives. By analyzing the assemblage of fossil flora, the extent of coexistence of vegetation tolerating specific climatic parameters (temperature and precipitation) can be determined. This method can be applied to both micro- and macroflora. The key to both methods presented above is the correct determination of the botanical affinity of fossil taxa.
The IPR (integrated plant record) method integrates data obtained from all parts of fossil plants (leaves, seeds, pollen, etc.) for the reconstruction of zonal plant cover and the paleoenvironment (Kovar-Eder et al., 2008). PTFs (plant functional types) are used for the reconstruction of biomes based on fossil plant assemblages, making it possible to determine climatic requirements (Smith et al., 1993).

When discussing the role of palaeoflora in palaeoclimatic reconstructions, it is necessary to identify the global factors influencing climate change in the Tertiary. The Paleogene is a period of very warm subtropical climate with two significant climatic events: the Paleocene-Eocene Thermal Maximum (PETM) at the

Paleocene-Eocene boundary and the Early Eocene Climatic Optimum (EECO). This event was followed by a progressive cooling trend, and the Eocene-Oligocene Transition (EOT) climatic collapse took place on the boundary of the Eocene and Oligocene around 33 million years ago. This is an important event due to the end of the *greenhouse* age, with no ice sheets, and the transition to *icehouse* conditions, when ice sheets developed at both poles (Słodkowska & Kasiński, 2016a). These events are associated with the transformation from the ancient to modern flora, recorded in many sites containing macro- and microflora. In the Neogene, on the other hand, conditions that favor the accumulation of lignite-forming biomass are cyclical. Such conditions prevailed in the early and middle Miocene. The last warm peak, defined as the Middle Miocene Climatic Optimum (MMCO), is recorded about 15 million years ago, and it is followed by a cooling down during the Middle Miocene Climatic Transition (MMCT), after which the conditions for the development of thermophilic flora in Central Europe no longer existed (Słodkowska & Widera, 2021). In the youngest layer of the Neogene–Pliocene, the vegetation was similar to the modern vegetation, with greater richness and more thermophilic taxa than the current flora. The composition of the modern flora reflects the destructive effect of Pleistocene glaciations.

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