

Record of environmental and climatic changes in middle Pleistocene sediments from Łuków (eastern Poland) on the basis of plant macroremains analysis

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ABSTRACT. Lacustrine sediments at the Łuków site bear a record of the Ferdynandovian interglacial, correlated with Marine Isotope Stage (MIS) 13–15, including two warm periods of interglacial rank (climatostratigraphic units Ferdynandovian 1 and 2) separated by cooling/glaciation (Ferdynandovian 1/2). On the basis of plant macroremains analysis, the type of local vegetation in the lake and its surroundings as well as changes in climate, trophic conditions and water level were reconstructed in detail. Ferdynandovian 1 was a time of development of tall sedge swamps. The presence of *Najas marina* and *N. minor* also suggests high levels of eutrophication, particularly in the younger part of the climatic optimum. The occurrence of *Zannichellia palustris* indicates habitats of variable water level and high salt content. In the terminocratic phase of Ferdynandovian 1, the communities showed the reoccurrence of *Betula nana*, *B. humilis* and *Larix* sp., the disappearance of thermophilous trees, and the intensification of succession processes linked to climate cooling. In the cool Ferdynandovian 1/2, *Betula nana* and *Cenococcum geophilum* increased their frequencies, most likely due to enhanced supply of mineral matter to the basin. During Ferdynandovian 2, the next climate warming of interglacial rank, communities of aquatic vegetation with the highest share of thermophilous taxa included the extinct *Aldrovanda borysthenica*, *Brasenia borysthenica*, and *Scirpus atroviroides*, as well as *Cyperus glomeratus*, a species not presently found in the flora of Poland. Another cooling in the Sanian 2 (Elsterian 2) glaciation is indicated by the development of peat communities, with numerous *Carex* sp., *Menyanthes trifoliata*, *Eriophorum vaginatum*, and *Andromeda polifolia*, accompanied by the extinct *Carex paucifloroides*, *Caulinia macrosperma*, and *Potamogeton praemaackianus*.

The provided description of the Ferdynandovian succession includes taxa which are extinct, not found in the Polish flora nowadays, or characteristic of a climatic context. The identified species included *Brasenia borysthenica*, *Aldrovanda borysthenica*, *Caulinia macrosperma*, *Potamogeton praemaackianus*, *Scirpus atroviroides*, *Cyperus glomeratus*, *Eleocharis praemaximoviczii*, *Nymphaea cinerea*, and *Ranunculus gailensis*. It has not yet been resolved whether the flora of Łuków includes *Euryale* sp., a particularly important taxon.

KEYWORDS: plant macroremains, climatic changes, Middle Pleistocene, MIS 13–15, eastern Poland

INTRODUCTION

Areas of eastern Poland, particularly the South Podlasie Lowland, are rich localities for palaeobotanical research, due to the presence of fossil lakelands of various age. Their sediments bear a record of climatic changes that proceeded in three interglacials, namely the Ferdynandovian, Mazovian, and Eemian, documented in palaeobotanical studies.

The Ferdynandów section is the stratotype for the Ferdynandovian succession (Janczyk-Kopikowa 1975, Janczyk-Kopikowa et al. 1980), dated to a period between the Sanian 1 and 2 glaciations and correlated with stages 13–15 on the oxygen isotope (O¹⁸) curve (Zagwijn 1996, Ber et al. 2007, Lindner & Marks 1994, 2008). Presently, following Mamakowa

(1996, 2003) and a division applied for the first time for section Podgórze B1 (drilled near the locality of Nowe Miasto nad Pilicą), it is accepted that the Ferdynandovian succession covers two warm units of interglacial rank separated by a cooling of glaciation/stadial rank.

Apart from the stratotype of Ferdynandów, several other sites with sediments of this age have been identified in Poland (Rzechowski 1996, Mamakowa 2003, Żarski et al. 2009). Drillings carried out as part of work on the 1:50 000-scale Detailed Geological Map of Poland provided material for studies of several new sites of the Ferdynandovian succession. At the sites for which the succession was already described, repeated drillings permitted a more detailed interpretation of the pollen diagrams. The most recently investigated sites with a complete record of the sequence include Zdany on the Siedlce Upland (Pidek 2000, 2003, Małek 2004) and Łuków on the Łuków Plain. Sediments from Łuków were initially interpreted as a unit separating two Middle Polish glaciations, namely the Odranian and Wartanian glaciations (Rühle 1969, Sobolewska 1969). As a new core was obtained at the site, its stratigraphy was reexamined and verified (Pidek & Małek 2010, Pidek 2013, Pidek & Poska 2013). Several other sites in the South Podlasie Lowland, such as Budziska, Kosiorki, Podlodów, and Stok, sediments of which were subjected to expert analysis, also include a record of the Ferdynandovian interglacial, but only its older optimum, Ferdynandovian 1 (Krupiński 2009, Żarski et al. 2009). Apart from Zdany, Łuków, Ferdynandów, and Podgórze, most likely only three other sections contain sediments with two warm units, referred to as two climatic optima, preserved.

The area covering the Ferdynandovian fossil lakeland in the surroundings of the Łuków site also includes a fossil lakeland of Mazovian age (MIS 11). In total, 42 sites of organogenic lacustrine sediments were documented in palaeobotanical and geological studies (Żarski et al. 2009). Recently the palaeobotanical record of the Eemian interglacial (MIS 5e) has been reported from 57 new sites. This large number of sites shows that after the retreat of the Odranian and Wartanian ice sheets the area was once again covered by a fossil lakeland, the extent of which overlaps the older Ferdynandovian and Mazovian lakelands (Żarski et al. 2009).

The first pollen analysis of the Łuków site was done by Sobolewska (1969) and later (as Łuków 3a) by Pidek (Pidek & Małek 2010, Pidek & Poska 2013, Pidek 2013). These examinations indicated the occurrence of two warm climatic periods of interglacial rank, an older and younger one, referred to as Ferdynandovian 1 and Ferdynandovian 2 respectively, separated by a cooling referred to as Ferdynandovian 1/2. In the present study I subjected the section to a detailed plant macroremains analysis. After Ferdynandów (Janczyk-Kopikowa 1975), Łuków 3a provides the second record of Ferdynandovian (Middle Pleistocene) macroflora in Poland.

The Ferdynandovian succession can be quite easily correlated with stratigraphic charts of Eastern Europe. Both the author of the stratotype profile (Janczyk-Kopikowa 1991) and Zagwijn (1996) correlate the Ferdynandów succession with sequences of the bioptimal Shklovian interglacial from Western Russia and Nizhninsky Rov in Belarus. Following Velichkevich et al. (1996), the succession includes two separate interglacials, the older Belovezhian and younger Mogilevian, corresponding to the lower and upper climatic optima of the Ferdynandovian succession respectively (Tab. 1). Presently, this bimodal sequence is correlated with the Belovezhian and Mogilevian/Borkhovian interglacials in Belarus and the Muchkapiian interglacial in Russia (Rylova & Savchenko 2005, Molodkov & Bolikhovskaya 2010, Yakubovskaya et al., 2014). In Eastern Europe, the first warm unit, Ferdynandovian 1, can be related to the Hareskovian interglacial in Denmark (Andersen 1965). A similar succession of vegetation was also recorded for Cromerian III (Tab. 1). The second warm unit, Ferdynandovian 2, is correlated with Cromerian IV (Zagwijn 1996).

The division into two interglacials within the Ferdynandovian succession is consistent with the interpretation of the diagram from Ferdynandów proposed by Zagwijn (1996), who concluded that most likely the two distinguished optima are separate interglacials even if the separating cold unit was not a period of extreme climatic conditions. The succession of Zdany (Pidek 2000, 2003) seems to be more complete than in the stratotype profile of Ferdynandów. However, as the samples were collected at low density, the rank of the cool unit between the two warm periods could not be identified.

STUDY AREA

Section Łuków 3a ($51^{\circ}55'58''$ N, $22^{\circ}26'09''$ E) was drilled from the Łuków Plain (Fig. 1) in the South Podlasie Lowland (Kondracki 2000). The thickness of Quaternary sediments in this area depends on the development of the pre-Quaternary basement and on average reaches several tens of metres, generally decreasing southwards and eastwards. The cover of Quaternary sediments is thickest (up to 170 m) in the northern part of the South Podlasie Lowland, in depressions, glacial channels and fossil river valleys near the town of Siedlce. The Quaternary deposits in the vicinity of Łuków are 50–70 m thick. These differences result from the fact that areas located to the south-east of Łuków were not covered by the Wartanian glaciation. Łuków itself is situated on sediments of the Odranian (Drenthe) glaciation, on a morainic upland in the upper Krzna Południowa river valley, within the southern foreland of the Wartanian (Warthe) glaciation

maximum (Terpiłowski 2001, Lisicki 2003, Harasimiuk et al. 2004, Marks 2004, Żarski 2004). The morainic upland comprises tills of the Odranian (Drenthe) and Sanian 2 (Wilgian, Elsterian 2) glaciations, locally separated by ice-dammed and glaciofluvial sediments. The surface of the upland, reaching 160–165 m a.s.l., is covered by weathering and aeolian sediments and cut by sandur plains formed by meltwaters originating from the front of the ice sheet of the Wartanian glaciation, and therefore oriented south-east and east. Most of these incisions are presently filled by waters of the Krzna Południowa, Bystrzyca, Samica, and other rivers.

STRATIGRAPHIC POSITION

The full-drillcore of Łuków 3a was obtained with the URB 2.5 drilling rig as part of work on the Łuków sheet of the 1:50 000-scale Detailed Geological Map of Poland (Małek & Buczek

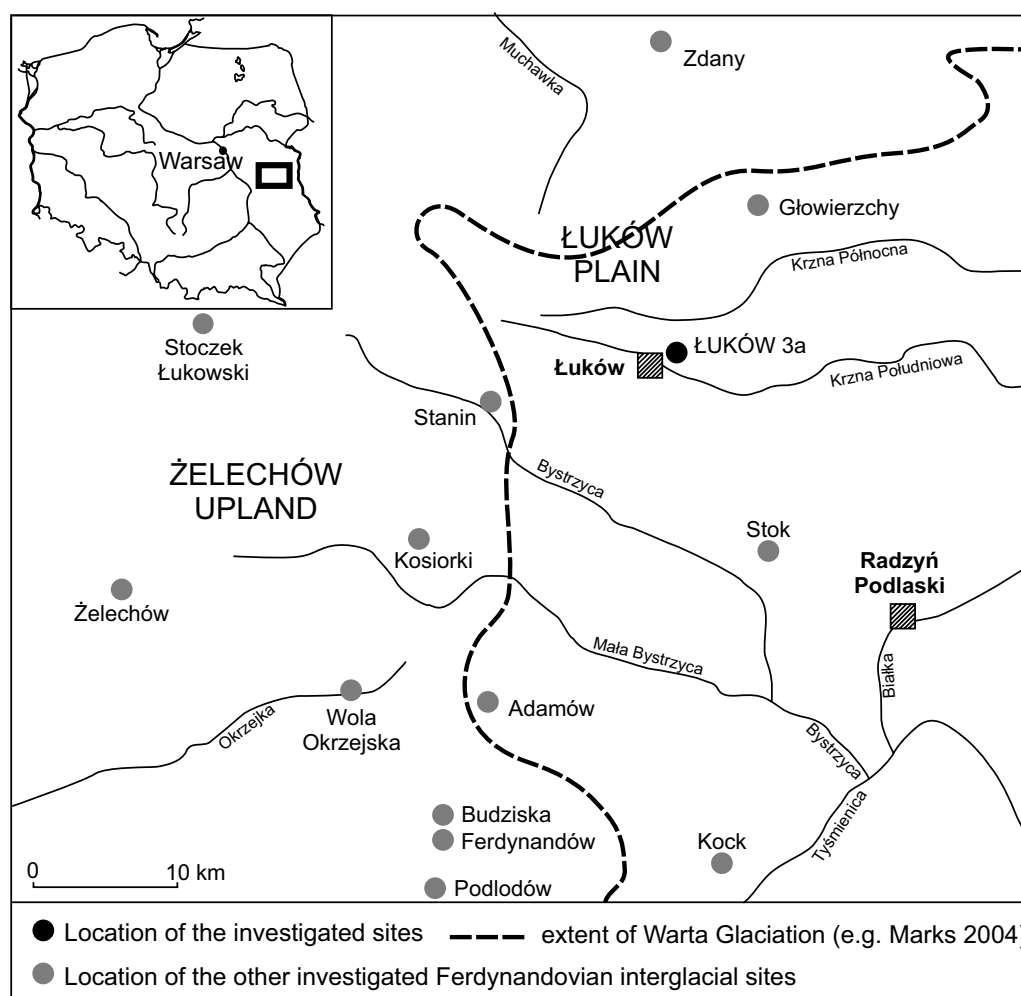


Fig. 1. Location of the investigated sites

2006). The interglacial lacustrine series was drilled at the 24.30–34.40 m depth interval (10.10 m of organic sediments in total). Compared to the archival drilling of Łuków 105 (Rühle 1969), in which the series including Ferdynandovian 1 was described for the first time (Sobolewska 1969), section Łuków 3a was drilled to the lower depth of 40 m, as the study was focused on interglacial sediments and a revised, detailed palaeobotanical examination of them. The new section appeared similar to the archival one but more complete.

The basal part of the lacustrine series comprises fine-grained sands interbedded with medium-grained sands and intercalated with clayey silts containing dispersed plant detritus. These sediments, attaining ca 30 m thickness (Ruszczynska-Szenajch 1976), represent the top part of fluvial sediments that filled the fossil valley at the end of the Sanian 1 (Elsterian 1) glaciation and at the beginning of the Ferdynandovian interglacial (Małek & Buczek 2006). The top part of the lacustrine series includes fluvial periglacial deposits 3.10 m thick, assigned to the early Sanian 2 (Elsterian 2) glaciation and developed as fine- and medium-grained sands intercalated with mixed-grained sands. The higher interval of 14.20–21.20 m is a layer of medium-grained sands and gravels with dropstones, forming the fluvioglacial sediment of the late Sanian 2 (Elsterian 2) glaciation. The sediments are overlain by deposits of the Odranian (Drenthe) glaciation.

DESCRIPTION OF SEDIMENT

24.00–24.30 m – dark brown, blackening towards the base, humic clayey silt; HCl^{+/–}

24.30–24.84 m – black, locally brown, strongly compressed highly peaty silt; thin intercalations of black peat, sandy silt and silty sand, mainly at the top; HCl[–]

24.84–25.75 m – dark brown, strongly compressed humic silt with a small admixture (becoming greater below 27.65 m) of sand and numerous intercalations of black and brown, strongly decomposed peat and beige-olive and grey-brown gyttja; HCl^{+/–}

25.75–28.90 m – reddish brown peat, blackening towards the base, at the top poorly decomposed and with abundant plant detritus; below 28.50 m black, strongly decomposed and compressed

28.90–30.70 m – brown silt with numerous intercalations of dark brown peat, mainly at the top, and reddish beige gyttja, as well as several laminas of fine-grained sand at the base; HCl⁺

30.70–33.80 m – brown silt with intercalations of olive-beige, compact gyttja, locally of low compactness, reddish beige and with a small admixture of sand; single intercalations of grey and brown, strongly compressed shales; the base comprises dark grey, compact silt, laminated with fine-grained sand, including dispersed humus, and with infrequent, thin intercalations of grey-beige gyttja; HCl⁺

33.80–34.40 m – grey, strongly clayed silt with intercalations of clayey silt and silty sand with humus

34.40–36.50 m – grey, clayed mixed-grained sand, locally horizontally stratified with silt and clayey silt; dispersed plant detritus; HCl^{+/–}

A detailed description of sediment in the interglacial series was given by Małek (Małek & Buczek 2006).

METHODS

From section Łuków 3a, 80 samples for plant macroremains analysis were collected from 24.40–34.50 m depth at average resolution of 10 cm (the same as in sampling for pollen analysis; Pidek 2013). Then the samples (150 ml of sediment each) were macerated with 10% KOH, boiled to pulp, and wet-sieved on a ϕ 0.2 mm sieve. Material remaining on the sieve was sorted under a stereoscopic microscope. Plant remains qualifying for identification were segregated and placed in a mixture of glycerine, water and ethyl alcohol (1:1:1) with addition of thymol. Macrofossils were identified with the use of keys, atlases (Berggren 1969, Cappers et al. 2006, Kats et al. 1965, Velichkevich & Zastawniak 2006, 2008), other studies and publications, as well as the reference collection of present-day seeds and fruits and collections of fossil floras housed in the Palaeobotanical Museum, W. Szafer Institute of Botany, Polish Academy of Sciences, Kraków.

Qualitative and quantitative results of examination are presented in a diagram (Fig. 2) plotted with POLPAL software for Windows (Nalepka & Walanus 2003).

STRATIGRAPHY OF MACROSCOPIC PLANT REMAINS

In the diagram of macroscopic plant remains plotted for section Łuków 3a, Local Macrofossil Assemblage Zones (L MAZ) were

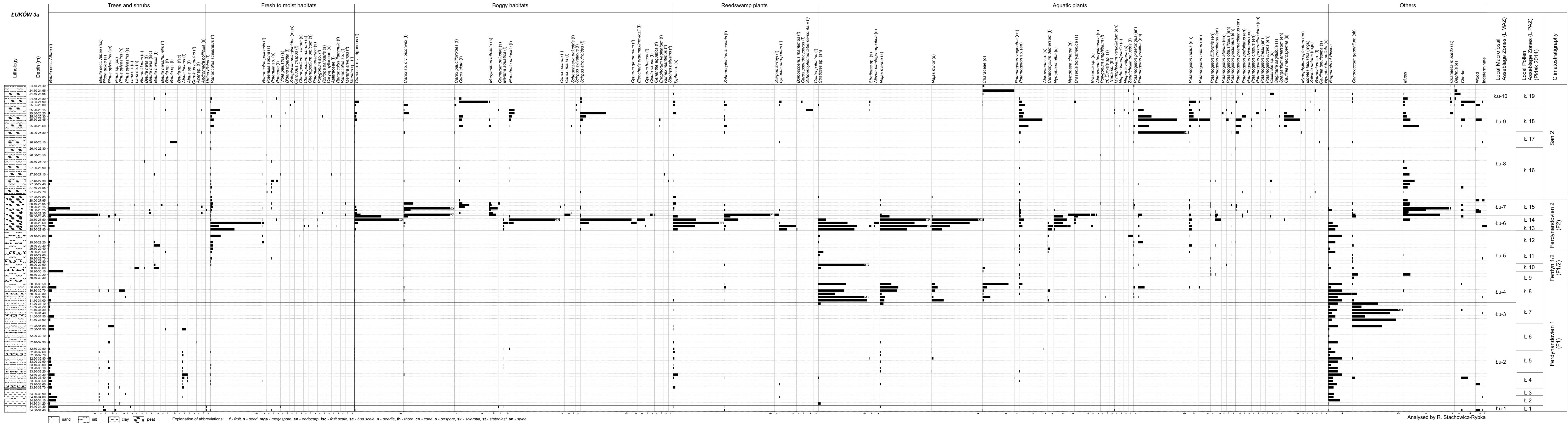


Fig. 2. Diagram plotted for plant macrofossils from section Łuków 3a

distinguished, numbered from base to top, and labelled from Łu-1 to Łu-10.

The division is based on the occurrence of one or several of the most abundant, characteristic or diagnostic taxa in the zone. The zone boundaries of the zones were determined on the basis of the appearance, disappearance, strong increase or decrease in the number of taxa of a significant quantitative or indicative value (Table 2).

FERDYNANDOVIAN 1 (F1)

Lake sedimentation in section Łuków 3a began with the start of the Ferdynandovian 1 interglacial. The sediment consists mainly of sands and clayey sands, with low content of organic matter and plant detritus. The low frequency of macroscopic plant remains hinders detailed reconstruction of the type and changes in the vegetation of the lake and its littoral zone during the initial phase of basin functioning.

The composition of tree vegetation in the first defined zone, **Łu-1 L MAZ**, including infrequent remains of *Betula* sect. *Albae*, *Larix* sp., *Picea abies*, *Pinus sylvestris*, and *Rubus idaeus*, indicates that during the protocratic phase of the interglacial the immediate surroundings of the lake were overgrown by boreal birch forest and birch-pine forest with spruce and larch. A similar pattern of tree vegetation has been shown in pollen analysis (Pidek 2013). Eutrophic, nitrogen-rich habitats in the littoral zone of the lake were sites of development of therophyte communities. They are

represented by species characteristic for various modern Bidentetea tripartiti units, such as *Bidens tripartita* and *Ranunculus sceleratus*. *Urtica dioica* most likely preferred nitrophilous habitats. *Potentilla supina*, *Potentilla* sp., and *Viola palustris* represented heliophilous species.

Peat habitats or communities similar to tall sedge swamps featured *Carex* sp. div. trigonous and *Comarum palustre*, as evidenced by the presence of their fruits. Swamp communities also played a significant role in the development of the landscape. Though the lake was in its initial phase, communities resembling present-day typical swamp with *Typha* sp., *Mentha aquatica*, *Schoenoplectus lacustris*, and *Alisma plantago-aquatica* probably were already present. Depending on the water depth, communities with *Schoenoplectus lacustris* may have interacted with open water communities inhabited by *Myriophyllum verticillatum* and *Najas marina*. Single fruits of *Myriophyllum verticillatum* may be indicators of initial communities including this species, subsequently replaced by other communities. Such a sequence is also observed in present-day basins (Podbielkowski & Tomaszewicz 1982). Remains of aquatic plants were accompanied by fish skeleton fragments. Near the bottom of the basin, also present were Characeae communities preferring clear water rich in calcium carbonate, which, extracted from the solution, encrusts their thalli (Piątkowski 1968) and consequently becomes a component of sediment.

Table 1. Correlation of the early Middle Pleistocene in Poland, Belarus, eastern Russia and western Europe

Palaeomagnetism	Stratigraphy	Western Europe (Zagwijn 1996)	Poland (Lindner & Marks 2008)	Belarus (Yakubovskaya, Litvinyuk, Motuzko 2014)	Eastern Russia (Molodkov & Bolikhovskaya 2010, Yakubovskaya et al. 2014)	MIS
Bruhnes	Pleistocene	Holsteinian	Mazovian	Alexandrian	Likhvinian	11
		Elsterian	Sanian 2	Berezinian	Oka	12
		Cromerian IV	Ferdynandovian 2	Mogilevian	Ikorets	13
		Glacial C	Ferdynandovian 1/2	Niznian	Navlya	14
		Cromerian III	Ferdynandovian 1	Borkovian	Muchkap	15
		Glacial B	Sanian 1	Yaseldinian	Don	16
		Cromerian II	Domutatovian	Korchevian	Semiluki	17–19
Matuyama		Glacial A	Nidanian	Narevian	Pokrovka	20–22
		Cromerian I	Augustovian 1	Rogachevian	Petropavlovka	21–23

Table 2. Description of Local Macrofossil Assemblage Zones in Łuków 3A section

Local Macrofossil Assemblage Zones L MAZ	Depth (m)	Description of zone
Lu-1 L MAZ	34.50–34.30 2 samples	Identified remains of trees and shrubs included nutlets of <i>Betula</i> sect. <i>Albae</i> , most frequent in the zone, seeds of <i>Larix</i> sp. and <i>Picea abies</i> , scales and a cone fragment of <i>Pinus sylvestris</i> , as well as <i>Rubus idaeus</i> . Within terrestrial vegetation, <i>Urtica dioica</i> most numerous, accompanied by <i>Ranunculus sceleratus</i> , <i>Potentilla supina</i> , <i>Viola palustris</i> , <i>Bidens tripartita</i> , and <i>Potentilla</i> sp. Peat and swamp vegetation represented by single fruits of <i>Carex</i> sp. div. trigonous, <i>Comarum palustre</i> , <i>Mentha aquatica</i> , <i>Typha</i> sp., and <i>Schoenoplectus lacustris</i> . Among aquatic plants, <i>Najas marina</i> , <i>Alisma plantago-aquatica</i> , <i>Myriophyllum verticillatum</i> and oospores of Characeae. Several fragments of charcoal and wood identified. Plant remains accompanied by fragments of fish skeletons. Upper boundary of zone marked by decrease in frequency of many taxa
Lu-2 L MAZ	34.30–31.90 21 samples	Numerous remains of trees and shrubs, including nutlets and scales of <i>Betula</i> sect. <i>Albae</i> , scales, seeds and needles of <i>Pinus sylvestris</i> , nutlets of <i>Alnus incana</i> and <i>Alnus</i> sp., and one fruit of <i>Acer</i> sp. Among terrestrial vegetation, <i>Ranunculus sceleratus</i> and <i>R. gailensis</i> most numerous. <i>Urtica dioica</i> also found. Infrequent remains of boggy and swamp plants included mainly species of <i>Carex</i> as well as <i>Mentha aquatica</i> and <i>Eleocharis palustris</i> . Within swamp vegetation, <i>Typha</i> sp., <i>Schoenoplectus lacustris</i> , <i>S. tabernaemontani</i> , and <i>Lycopus europaeus</i> also recorded. Aquatic plants represented by relatively frequent <i>Najas marina</i> and <i>N. minor</i> , single spines of <i>Stratiotes</i> sp., <i>Potamogeton vaginatus</i> and <i>Potamogeton</i> sp., and poorly preserved specimen of <i>Aldrovanda</i> sp. Upper boundary of zone marked by abundant appearance of sclerotia of <i>Cenococcum geophilum</i> and nearly complete disappearance of other plant macroremains
Lu-3 L MAZ	31.90–31.10 7 samples	No macroremains of herbaceous terrestrial plants, peat or aquatic plants recorded in zone. Remains of trees and shrubs showed lower frequency and diversity. Nutlets and seed scales of <i>Betula</i> sect. <i>Albae</i> and scales of <i>Pinus sylvestris</i> identified. Within swamp vegetation, infrequent occurrence of <i>Typha</i> sp. Zone clearly dominated by sclerotia of <i>Cenococcum</i> . Fragments of fish skeletons also present. Upper boundary of zone marked by decrease in amounts of <i>Cenococcum geophilum</i> sclerotia and reappearance of other plant macroremains
Lu-4 L MAZ	31.10–30.50 6 samples	Very abundant in remains. Among trees, nutlets and seed scales of <i>Betula</i> sect. <i>Albae</i> and scales of <i>Pinus sylvestris</i> identified. Needles and seeds of <i>Pinus sylvestris</i> and seeds of <i>Larix</i> sp. reappeared. No macroremains of herbaceous terrestrial plants recorded. Among peat vegetation, only single fruits of <i>Carex</i> sp. div. trigonous and <i>Carex</i> sp. div. biconvex determined. Swamp communities included <i>Typha</i> sp. and <i>Schoenoplectus lacustris</i> . Aquatic plants most frequent, represented by <i>Stratiotes</i> sp., <i>Najas marina</i> , <i>N. minor</i> , <i>Potamogeton praelongus</i> , <i>P. pusillus</i> , <i>P. rutilus</i> , <i>P. natans</i> , <i>P. sp.</i> , <i>Ceratophyllum demersum</i> , and fragment of <i>Euryale</i> sp. seed. Oospores of Characeae and fragments of fish skeletons found in high numbers. Upper boundary of zone marked by increase in amounts of diaspores, particularly of aquatic plants, and decrease in content of <i>Cenococcum geophilum</i>
Lu-5 L MAZ	30.40–29.00 13 samples	Reoccurrence of boreal elements. Among trees and shrubs, nutlets of <i>Betula humilis</i> and <i>B. nana</i> appeared; seeds and needles of <i>Larix</i> sp. and nutlets and scales of <i>Betula</i> sect. <i>Albae</i> continuously recorded. Fragment of <i>Pinus sylvestris</i> cone and single nutlet of <i>Carpinus betulus</i> . Terrestrial vegetation represented by fruits of <i>Ranunculus sceleratus</i> , <i>R. gailensis</i> , <i>Potentilla</i> sp., and <i>Chenopodium t. album</i> , and swamp vegetation by single remains of <i>Typha</i> sp. and <i>Schoenoplectus lacustris</i> . As in preceding zone, aquatic plants most abundant and include <i>Stratiotes</i> sp., <i>Najas marina</i> , <i>Callitriche autumnalis</i> , <i>Potamogeton praelongus</i> , <i>P. pusillus</i> , <i>P. rutilus</i> , <i>P. filiformis</i> , <i>P. gramineus</i> , <i>P. alpinus</i> , <i>P. obtusifolius</i> , <i>P. pectinatus</i> , <i>P. praemaackianus</i> , and <i>P. sp.</i> Frequent remains of <i>Ceratophyllum demersum</i> and, at top part, <i>Zannichellia palustris</i> . Oospores of Characeae and fragments of fish skeletons still recorded. Upper boundary of zone marked by renewed increase in amounts of diaspores, particularly of aquatic and swamp plants
Lu-6 L MAZ	28.90–28.40 6 samples	Tree stand surrounding basin still dominated by <i>Betula</i> sect. <i>Albae</i> , <i>B. humilis</i> , and <i>Pinus sylvestris</i> . Within terrestrial vegetation, <i>Ranunculus sceleratus</i> and <i>R. gailensis</i> dominant. Remains of <i>R. flammula</i> , <i>Urtica dioica</i> , <i>Chenopodium rubrum</i> , <i>Ch. urbicum</i> , <i>Polygonum</i> sp., Poaceae, and Caryophyllaceae recorded. Frequency of peat plants increased strongly versus preceding zones. Peat taxa include mainly <i>Carex</i> sp. div. trigonous, <i>Eleocharis palustris</i> and <i>Scirpus atroviroides</i> , accompanied by also frequent <i>Carex</i> sp. div. biconvex, <i>Cyperus glomeratus</i> , <i>Eleocharis praemaximoviczii</i> , and <i>Mentha aquatica</i> , and single <i>Cyperus fuscus</i> , <i>Cicuta virosa</i> , and <i>Menyanthes trifoliata</i> . Flora of swamp environments also abundant, represented mostly by <i>Typha</i> sp., <i>Schoenoplectus lacustris</i> , <i>Lycopus europaeus</i> , and <i>Bolboschenus maritimus</i> . Group of aquatic plants most diversified, with high shares of <i>Stratiotes</i> sp., <i>Najas marina</i> , <i>N. minor</i> , <i>Alisma plantago-aquatica</i> , <i>Brasenia borysthénica</i> , <i>B. sp.</i> , <i>Aldrovanda borysthénica</i> , <i>Ceratophyllum demersum</i> , <i>Nymphaea alba</i> , <i>N. cinerea</i> , <i>Potamogeton pusillus</i> , <i>P. rutilus</i> , <i>P. natans</i> , <i>P. gramineus</i> , <i>P. filiformis</i> , <i>P. pectinatus</i> , <i>P. perfoliatus</i> , and <i>P. sp.</i> Single remains of <i>Callitriche autumnalis</i> , <i>Sagittaria sagittifolia</i> , <i>Caulinia macrosperma</i> , and <i>Myriophyllum spicatum</i> found. Oospores of Characeae and fragments of fish skeletons numerous. Upper boundary of zone marked by decrease in amounts of diaspores, particularly of aquatic, swamp and peat plants

Table 2. Continued

Local Macrofossil Assemblage Zones L MAZ	Depth (m)	Description of zone
Lu-7 L MAZ	28.40–27.95 8 samples	Numerous tree remains, still dominated by nutlets of <i>Betula</i> sect. <i>Albae</i> , accompanied by seeds and needles of <i>Larix</i> sp. Nutlets of <i>Betula humilis</i> and <i>B. nana</i> recorded again. Fruits of <i>Andromeda polifolia</i> observed for the first time in the section. Terrestrial vegetation represented by still-frequent <i>Ranunculus sceleratus</i> and <i>R. gailensis</i> . Remains of <i>Urtica dioica</i> , <i>Potentilla</i> sp., <i>Rorippa palustris</i> , and <i>Mentha arvensis</i> present. Proportions of peat plants still high; group dominated by <i>Carex</i> sp. div. biconvex, <i>Carex</i> sp. div. trigonous, <i>C. elata</i> , <i>C. rostrata</i> , <i>C. riparia</i> , <i>Scheuchzeria palustris</i> , <i>Menyanthes trifoliata</i> , <i>Comarum palustre</i> , and <i>Scirpus atroviroides</i> . Swamp plants show composition strongly diminished versus preceding zone; <i>Typha</i> sp., <i>Schoenoplectus lacustris</i> , and <i>Lycopus europaeus</i> recorded. Aquatic plants much less abundant than in previous zone but still most diversified; taxa include <i>Najas marina</i> , <i>N. minor</i> , <i>Ceratophyllum demersum</i> , <i>Nymphaea alba</i> , <i>Brasenia</i> sp., <i>Polygonum amphibium</i> , <i>Hippuris vulgaris</i> , <i>Potamogeton praelongus</i> , <i>P. rutilus</i> , <i>P. filiformis</i> , <i>P. gramineus</i> , <i>P. pectinatus</i> , <i>P. praemaackianus</i> , <i>P. dvinensis</i> , and <i>P. friesii</i> . Stems of brown mosses recorded in large numbers. Upper boundary of zone marked by decrease in amounts of diaspores, particularly of aquatic, swamp, and peat plants
Lu-8 L MAZ	27.90–26.10 11 samples	Zone still included nutlets of <i>Betula</i> sect. <i>Albae</i> , <i>B. nana</i> and <i>B. humilis</i> , and numerous leaves of <i>Betula</i> sp. Terrestrial communities still composed of <i>Ranunculus sceleratus</i> , <i>R. gailensis</i> , <i>R. sp.</i> , <i>Urtica dioica</i> , <i>Potentilla supina</i> , <i>P. anserina</i> , <i>P. sp.</i> , <i>Viola palustris</i> , and <i>Mentha</i> sp., as well as Poaceae and Asteraceae. Composition of peat vegetation strongly diminished. Single fruits of <i>Carex</i> sp. div. trigonous, <i>C. sp. div. biconvex</i> , <i>C. elata</i> , <i>Eleocharis palustris</i> , <i>Scirpus atroviroides</i> , <i>Cicuta virosa</i> , <i>Rumex maritimus</i> , and <i>Stachys palustris</i> identified. <i>Typha</i> sp. and <i>Lycopus europaeus</i> the only components of swamp communities. Like the above groups, aquatic plants also less frequent, represented by single spines of <i>Stratiotes</i> sp. and seeds of <i>Alisma plantago-aquatica</i> , <i>Najas minor</i> , <i>Polygonum amphibium</i> , <i>Hippuris vulgaris</i> , <i>Potamogeton praelongus</i> , <i>P. pusillus</i> , <i>P. rutilus</i> , <i>P. filiformis</i> , <i>P. pectinatus</i> , <i>P. praemaackianus</i> , <i>P. perfoliatus</i> , and <i>Potamogeton</i> sp. Remains of <i>Callitriche autumnalis</i> , <i>Myriophyllum spicatum</i> , <i>Salvinia natans</i> , <i>Batrachium</i> sp., and <i>Caulinia tenuissima</i> also determined. Stems of brown mosses abundant. Upper boundary of zone marked by strong increase in content of remains of peat species of Cyperaceae family and aquatic species of Potamogetonaceae family
Lu-9 L MAZ	25.90–25.15 6 samples	Amounts of plant remains increased in nearly all ecological groups but trees and shrubs recorded at lower frequencies. Only single fruits of <i>Betula</i> sect. <i>Albae</i> and <i>B. nana</i> and seeds of <i>Andromeda polifolia</i> identified. Among remains of terrestrial plants, fruits of <i>Ranunculus sceleratus</i> showed increasing values; only single specimens of <i>Potentilla supina</i> , <i>P. sp.</i> , <i>Viola palustris</i> , <i>Bidens tripartita</i> , and <i>Rorippa palustris</i> . Content of peat plants of Cyperaceae family, such as <i>Carex</i> sp. div. biconvex, <i>Carex</i> sp. div. trigonous, <i>C. elata</i> , <i>C. paucifloroides</i> , <i>Scirpus atroviroides</i> , <i>S. sylvaticus</i> , and <i>Eleocharis palustris</i> , strongly increased. Remains of <i>Scheuchzeria palustris</i> , <i>Menyanthes trifoliata</i> , <i>Comarum palustre</i> , <i>Eriophorum vaginatum</i> , and <i>Rumex maritimus</i> also present. Swamp plants include the most numerous <i>Typha</i> sp., <i>Schoenoplectus lacustris</i> , and <i>S. tabernaemontani</i> , and single seed of <i>Caltha palustris</i> . Within aquatic vegetation, displaying the greatest diversity, remains of plants of Potamogetonaceae family very common. Most numerous <i>Potamogeton pusillus</i> , <i>P. rutilus</i> , <i>P. natans</i> , and <i>Potamogeton</i> sp., accompanied by less frequent <i>P. praelongus</i> , <i>P. alpinus</i> , <i>P. obtusifolius</i> , <i>P. pectinatus</i> , <i>P. praemaackianus</i> , <i>P. perfoliatus</i> , <i>P. crispus</i> , <i>P. panormitanus</i> , and <i>P. lucens</i> . Among macrophytes, <i>Caulinia macrosperma</i> abundant. Single seeds and fruits of <i>Myriophyllum spicatum</i> , <i>Najas tenuissima</i> , <i>Sparganium emersum</i> , <i>Isöetes lacustris</i> , <i>Nymphoides peltata</i> , <i>Zannichellia palustris</i> , <i>Hippuris vulgaris</i> , <i>Nuphar lutea/pumila</i> , and, at top part of zone, <i>Myriophyllum verticillatum</i> and <i>Stratiotes</i> sp. Upper boundary of zone marked by decrease in amounts of diaspores in all ecological groups
Lu-10 L MAZ	25.05–24.40 6 samples	Composition and frequency of plant remains in zone diminished. Numerous taxa disappeared completely. Nutlets of <i>Betula</i> sect. <i>Albae</i> , <i>B. humilis</i> , and <i>Betula</i> sp. still found. Herbaceous plants represented by single specimens of <i>Ranunculus sceleratus</i> and <i>R. gailensis</i> . Fruits of <i>Urtica dioica</i> and <i>Carduus crispus</i> and megaspores of <i>Selaginella selaginoides</i> . Frequency of peat plants slightly decreased versus preceding zones. <i>Carex</i> sp. div. trigonous, <i>C. sp. div. biconvex</i> , <i>C. paucifloroides</i> , <i>C. elata</i> , <i>Menyanthes trifoliata</i> , <i>Scirpus atroviroides</i> , and <i>S. sylvaticus</i> dominant. Swamp and aquatic plants numerous. Seeds of <i>Typha</i> sp., <i>Schoenoplectus lacustris</i> , <i>Lycopus europaeus</i> , and <i>Carex pseudocyperus</i> identified. Among aquatic vegetation, single spines and fragments of seeds of <i>Stratiotes</i> sp. and fruits of <i>Brasenia borysthénica</i> , <i>Potamogeton vaginatus</i> , <i>P. praelongus</i> , <i>P. pusillus</i> , <i>P. rutilus</i> , <i>P. natans</i> , <i>P. filiformis</i> , <i>P. pectinatus</i> , <i>P. praemaackianus</i> , <i>Potamogeton</i> sp., and <i>P. perfoliatus</i> recorded. Megaspore of <i>Salvinia natans</i> and fruits of <i>Batrachium</i> sp. and <i>Zannichellia palustris</i> also present. Oospores of Characeae frequent. Upper boundary of zone delimited by top organic sediments

Zone **Łu-2 L MAZ** corresponds to several pollen assemblage zones, namely Ł 2 to Ł 6 L PAZ (Pidek 2013). The composition of their pollen spectra indicates that open boreal birch and birch-pine forests were still present during the protocratic interglacial phase (zone Ł 2 L PAZ). In subsequent pollen assemblage zones (Ł 3–Ł 6 L PAZ), pollen of plants with higher temperature requirements becomes dominant, indicating the development of multispecies deciduous forests in the F1 interglacial climatic optimum, after which, in the younger part of the optimum, spruce, fir and maple appeared in forest communities. The presence of several tree species growing close to the shores of the basin was confirmed by fruits and scales of *Betula* sect. *Albae* and remains of *Pinus sylvestris*. These probably grew in depressions or in humid and sandy habitats, since such conditions are preferred by birch-pine communities. Peaty areas and depressions at the lake shores attracted *Alnus glutinosa*. The potential proximity of *Ribes nigri-Alnetum* Sol.-Górń. (1975) 1987 communities was confirmed by the presence of sparse vegetative remains of *Alnus glutinosa* and seeds of *Rubus idaeus* and *Urtica dioica*. A single fruit of *Acer* sp. was also identified, the occurrence of which correlates with the maximum of its pollen curve in zone Ł 6 L PAZ (Pidek 2013). The most highly eutrophic habitats probably supported a community resembling the present-day *Rumicetum maritimi*, with *Ranunculus sceleratus* and *R. gailensis*. The presence of remains of *Typha* sp., *Schoenoplectus lacustris*, *S. tabernaemontani*, *Lycopus europaeus*, *Eleocharis palustris*, and *Mentha aquatica* probably is associated with communities similar to modern typical swamp. Shallow, calm coves were inhabited by *Stratiotes* sp., found in the sediment in the form of spines and seed fragments. At that time the lake water must have already been quite rich in organic compounds. Species known for their preference for meso- and eutrophic water, such as *Najas marina* and *N. minor*, were recorded, but accompanied by *Aldrovanda* sp., characteristic for shallow coves with rapidly heated waters. The taxon grows at peaty shores of shallow lakes with bottoms covered with a thick layer of mineral-organic mud (Każmierczakowa et al. 2014) and acidic waters having pH 4.5–5.5 (Zarzycki 1984).

Basal sediments of zone **Łu-2 L MAZ**, in the period preceding the climatic optimum,

included *Potamogeton vaginatus*, not found in the Polish flora nowadays and characteristic for boreal climate. Infrequent sclerotia of *Cenococcum geophilum* do not indicate intensive solifluction processes, contrary to what was observed in the next zone, **Łu-3 L MAZ**. In this period, *Cenococcum geophilum*, a ubiquitous ectomycorrhizal fungus living on, in, or just below the litter horizon (Thormann et al. 1999, Wurzbürger et al. 2004), was detected in great numbers. The record of its sclerotia could indicate that organic matter in surface soil eroded and was deposited in the lake (Wick et al. 2003, Tinner et al. 2008). Hardly any plant remains were recorded, particularly in the groups of terrestrial, peat, and aquatic plants. Zone **Łu-3 L MAZ** corresponds to pollen assemblage zone Ł 7 L PAZ, which represents the beginning of the terminocratic phase of the interglacial. The values of *Pinus*, *Betula*, and NAP increase, while *Larix* and *Betula nana* t. appear in the pollen spectra, confirming that the disappearance of thermophilous trees and the succession processes proceeding in the forest communities were related to climate cooling (Pidek 2013). Among the plant macroremains, nutlets and seed scales of *Betula* sect. *Albae* and scales of *Pinus sylvestris* were determined. Numerous fragments of fish skeletons, including bones, vertebrae and scales, may indicate that the lake was a vast and relatively deep basin. The frequency of macroremains identified in this zone shows that only trace amounts of plant fragments from the lake shores and shallow swamp zone were incorporated into this part of the sediment. Further development of the lake in Łuków is recorded in zone **Łu-4 L MAZ**, marked by the increasing shares of both aquatic vegetation and plants of the swamp zone. The changes in their composition are greater than those observed for terrestrial vegetation. Once again, in comparison to the previous zone, the share of macrophyte flora grows.

The swamp zone was inhabited by *Typha* sp. and *Schoenoplectus lacustris*, while shallow coves with muddy bottoms were overgrown by *Stratiotes* sp., as indicated by very numerous but uncharacteristic spines that could have originated from *Hydrocharietum morsus-ranae* communities. These types of communities are most common in quiet and calm stagnant waters, and grow mainly in lake coves, oxbow lakes, and ponds. The expansion

of *Najas marina* also indicates the occurrence of strongly insolated and wind-sheltered areas in the lake (Matuszkiewicz 2008, Tomaszewicz 1979). The species was accompanied by the nearly as numerous *Najas minor*, known to prefer eutrophic, alkaline water in the pH range of 6.0–9.3 (optimum of 6.6–7.2) and to show optimum occurrence at ca 0.5–2 m depth. It is resistant to turbidity and often forms dense monocultures (Wentz & Stuckey 1971). The eutrophic nature of the basin is also confirmed by the presence of *Pediastrum boryanum*. Similar significance may be attributed to *Salvinia*, recorded as microsporangium tissue (Pidek 2013). Very numerous Characeae oospores present in this zone reflect the intensive development of stonewort meadows, which are much less likely to occur in shallow basins and generally appear in stagnant waters of high transparency, with usually neutral to slightly alkaline pH and increased calcium carbonate content. Patches of communities dominated by *Najas marina*, *Najas minor*, and Characeae were accompanied by an admixture of *Potamogeton praelongus* (Pl. 1, Fig. 17), *P. pusillus*, *P. rutilus*, *P. natans*, *Potamogeton* sp., and *Ceratophyllum demersum* (Pl. 1, Fig. 12). A fragment of a *Euryale* sp. seed (Pl. 1, Figs 13, 14) seems to be an important finding. Regrettably, due to the lack of a whole seed or even a fragment including the operculum and hilum in the investigated material, it is not possible to determine the species. The modern species *Euryale ferox* may be found in tropical and subtropical zones of Southeast Asia (India, China, Japan, Korea, south-eastern Siberia). Mean July temperature required for the growth of this taxon is estimated at 21°C but in extreme conditions it tolerates temperatures as low as –18°C. It also withstands very large temperature amplitudes, especially very hot summers and frosty winters (Sobolewska 1977). In Poland the species is known from sediments of the Mazovian interglacial (Stanowice site; Sobolewska 1970, 1977) and the Augustovian interglacial (Czarnucha and Żarnowo sites; Stachowicz-Rybka 2011). In the Pleistocene of Europe, fossil remains of *Euryale ferox* are so far known from the Mazovian (Holsteinian) interglacial in Germany (Gripp & Beyle 1937), the Lower Pleistocene in south-eastern England (Aalto et al. 1996), and the Belovezhian (= Ferdynandovian 1) interglacial (floras of Kosteshi and Smolenskiy Brod; Velichkevich

1978, 1979). *Euryale* was also identified in sediments of the Tegelen in the Netherlands (Reid & Reid 1907, 1915) as *E. europea* and *E. limburgensis*, and sediments of the Likhvinian interglacial in Russia as *Euryale* sp. (Sukat-scheff 1908). The terrestrial flora was continuously dominated by pine, birch and larch. Among peat plants, only single fruits of *Carex* sp. div. trigonous and *Carex* sp. div. biconvex were determined. The basin was most likely surrounded by a bulrush swamp with *Typha latifolia* (Pidek 2013).

FERDYNANDOVIAN 1/2 (F1/2)

The base of zone **Łu-5 L MAZ** corresponds to three pollen assemblage zones (Ł 9–Ł 11 L PAZ) distinguished by Pidek (2013). Rapidly increasing NAP values and the rising content of *Betula nana* t., *Juniperus*, *Salix* undiff., and *Sphagnum* spores, all recorded already from zone Ł 9 L PAZ, evidence great changes in the plant communities, particularly the expansion of vegetation typical of open areas, including tundra, steppe-tundra, and peat bogs. The next change in zone Ł 10 L PAZ, dominated by *Pinus* and *Betula*, reflects an interstadial fluctuation within F1/2, being a glacial or stadial period separating the two warm units (F1 and F2) in the Ferdynandovian sequence. The fluctuation was followed by another cooling of climate, resulting in the return of open communities (Ł 11 L PAZ). Considering plant macroremains, zone Łu-5 L MAZ also features the reappearance of boreal elements, such as *Betula humilis*, *B. nana*, and *Larix* sp. The frequency of macroscopic plant remains is lower than in the previous zone, but they still include sparse amounts of nutlets of *Betula* sect. *Albae* and remains of *Pinus sylvestris*. This composition of trees and shrubs, accompanied by herbaceous species such as *Chenopodium* t. *album* and *Potentilla* sp., indicates cool climate as well as the important role of patches of dwarf shrub tundra-type vegetation and the simultaneously growing proportion of heliophyte communities in the landscape of lake surroundings. Communities with *Ranunculus sceleratus* and *R. gailensis* were gradually gaining greater shares in eutrophic habitats of periodically emerging shores. There appeared single specimens of *Schoenoplectus lacustris* and *Typha* sp., which presently form *Scirpo-Phragmitetum*-type communities

(Podbielkowski & Tomaszewicz 1982) but in this case may have been of little significance in the landscape of lake surroundings. Among the aquatic plants often determined in late glacial periods characterised by cool climate, species such as *Potamogeton praelongus*, *P. pusillus*, *P. filiformis*, *P. gramineus*, *P. alpinus* (Pl. 1, Fig. 15), and *P. obtusifolius* were found. The depth interval attributable to pollen assemblage zone Ł 10 L PAZ, marked by interstadial fluctuation, did not include any taxa indicating climate improvement but showed a significantly increased number of specimens, particularly spines of *Stratiotes* sp. and remains of *Betula humilis*, *Betula* sect. *Albae*, and *Larix* sp. The presence of a single nutlet of *Carpinus betulus* (Pl. 1, Fig. 1), recorded in the zone correlated with Ł 11 L PAZ, assigned to the glacial period of Ferdynandovian 1/2, seems somewhat surprising. It may be an artefact of drilling.

FERDYNANDOVIAN 2 (F2)

The beginning of the next warm period of interglacial rank, Ferdynandovian (F2), is indicated by zone Ł 12 L PAZ, showing reexpansion of boreal birch forests followed by the appearance of thermophilous deciduous trees and shrubs such as *Quercus*, *Ulmus*, and *Corylus* (Pidek 2013). This pollen assemblage zone corresponds to the top part of zone **Łu-5 L MAZ**. Although there was no strong increase in the frequency of plant macroremains, the appearance of single remains of *Najas marina*, *Potamogeton praemaackianus* (Pl. 1, Fig. 16), and *Ceratophyllum demersum* indicates improved temperature conditions. *Zannichellia palustris* and Characeae oospores were also numerous. The climatic optimum of this warm period is best observed in zones Ł 13 and Ł 14 L PAZ (Pidek 2013) in the overwhelming dominance of *Carpinus*. Again, the Łuków area was overgrown by multispecies deciduous oak-hornbeam forests with numerous hazel and admixtures of lime and maple. In the diagram of plant macroremains (Fig. 2), climatic optimum F2 is displayed in zone **Łu-6 L MAZ**, including the record of the most extremely thermophilous communities of aquatic vegetation in the Łuków basin. In addition to having the highest number of identified species, the zone also has the highest specimen frequency within the distinguished

ecological groups. The type of tree vegetation, at least in the composition of plant macroremains, did not change significantly versus the previous zone. Domination of *Betula* sect. *Albae*, *B. humilis*, and *Pinus sylvestris* was still observed. The composition of herbaceous vegetation changed conspicuously and was dominated by *Ranunculus sceleratus* and *R. gailensis*, which occur in highly eutrophic habitats of periodically emerging shores. *Ranunculus sceleratus* is most frequently found in communities similar to the present-day *Rumicetum maritimi*. Communities of wet, humid and nitrogen-rich habitats were occupied by *Urtica dioica* and *R. flammula*. Vegetation of fresh and humid areas included taxa such as *Chenopodium rubrum*, *Ch. urbicum*, *Polygonum* sp., Poaceae, and Caryophyllaceae. The very significant increase in the proportion of peat vegetation versus the preceding zones most likely results from gradual shallowing of the basin and intensive overgrowth of its shores. Habitats bordering the shores of the lake in Łuków were dominated by abundant *Carex* sp. div. trigonous, *Elocharis palustris* and *Scirpus atroviroides* (Pl. 1, Fig. 4; Pl. 2, Figs 3, 4). At the level of 128.60–128.50 m, extremely numerous fruits of *Elocharis palustris* (appearing suddenly in very large quantities and as rapidly disappearing) may indicate the formation of monospecific assemblages of this taxon. Presently these types of communities represent the outer belt of swamp vegetation. Very numerous fruits of *Elocharis palustris* indicate soil rich in calcium carbonate, as also confirmed by the presence of Characeae oospores in the sediment. It also includes infrequent fruits of *Cyperus glomeratus* (Pl. 1, Fig. 3), not found in the Polish flora nowadays and inhabiting Southern Europe and across to the Caucasus, Iran, Uzbekistan, northern China, Japan and Siberia (Stankov & Taliev 1949). The taxon was exceptionally abundant in Augustovian interglacial II and slightly less frequent in Augustovian interglacial I (Stachowicz-Rybka 2011). It grows on riverbanks and presently also often in rice paddies. *Scirpus atroviroides*, occurring in floras of interglacial periods since the Late Pliocene, was found in much greater abundance in the zone. In Poland the species is also known from the Augustovian interglacial, recorded at the Czarnucha and Żarnowo sites (Stachowicz-Rybka 2011) and in the Mazovian flora of Konieczki (Nita 1999). In Europe it

has been found in the Eopleistocene flora of Daumantai-1 in Lithuania (Velichkevich et al. 1998) and in many floras of different age, from the Late Pliocene to Middle Pleistocene, in the western part of the East European Plain (Velichkevich & Zastawniak 2003). Both *Cyperus glomeratus* and *Scirpus atroviroides* are indicators of moderately warm climate.

The zone also comprises *Carex* sp. div. biconvex, *Mentha aquatica*, and single specimens of *Cyperus fuscus*, *Cicuta virosa*, and *Menyanthes trifoliata*, indicating that the lake surroundings were covered by fens and tall sedge swamps. The optimum period was also the time of occurrence of the extinct *Eleocharis praemaximoviczii* (Pl. 1, Fig. 2).

The typical swamp belt was formed by *Typha* sp., *Lycopus europaeus*, *Alisma plantago-aquatica*, and *Bolboschenus maritimus*, as evidenced by the great number of their remains, particularly at the base of the zone. Fruits of *Schoenoplectus lacustris*, especially in the younger part of the zone, may indicate the existence of communities similar to the modern *Scirpetum lacustris*. These communities usually cover large areas of sandy, loamy, or sandy-gravelly ground by eutrophic and mesotrophic basins, and form the first swamp belt bordering aquatic communities. At that time, aquatic vegetation was most luxuriant. Shallow, insolated coves in the littoral were inhabited by *Stratiotes* sp. Such conditions may have also been preferred by the extinct *Aldrovanda borysthenica* (Pl. 1, Fig. 7; Pl. 2, Figs 5, 6), found as a component of the *Brasenia* complex, characteristic for the climatic optima of the Belovezhian and Mogilevian interglacials of Belarus and analogous interglacials of other European countries (Velichkevich & Zastawniak 2008).

In the composition of aquatic plants, seeds of *Najas marina* and *N. mainor* reappeared in remarkably high numbers. Together with remains of *Myriophyllum spicatum*, *Potamogeton perfoliatus*, and *P. pusillus*, the finding of those species suggests that the littoral belt of the basin included habitats with variable water level, which could be an area of the spread of a community resembling the *Potamo-Najadetum marinae* association (Matuszkiewicz 2008). Communities of macrohydrophytes, usually rooted and dominated by forms with surface-floating leaves, were composed mainly of *Nymphaea alba*, *N. cinerea* (Pl. 1, Fig. 6; Pl. 2, Figs

10–12), *Brasenia borysthenica* (Pl. 1, Fig. 8), *Brasenia* sp., *Ceratophyllum demersum*, and *Myriophyllum spicatum*. Seeds of *Brasenia borysthenica* were found mostly in sediments of the optimum of the Mazovian (Alexandrian) interglacial and the second optimum of the Ferdynandovian (Mogilevian) interglacial.

Macrophytes, found in various communities, included *P. rutilus*, *P. natans*, *P. gramineus*, *P. filiformis*, *P. pectinatus*, *P. sp.*, *Callitriche autumnalis* (Pl. 1, Fig. 5), and *Sagittaria sagittifolia*. Single Characeae oospores indicate that the waters of the basin were heavily shaded by the numerous macrophytes. Strong eutrophication additionally decreased water clarity. The end of the optimum of the Ferdynandovian 2 interglacial is marked by a decrease in the abundance of diaspores, particularly in the groups of aquatic and swamp plants.

Zone Łu-7 L MAZ is correlated with a period of a strong rise in the *Pinus* pollen curve and an increase in NAP values, both pointing to another cooling of climate, within zone Ł 15 L PAZ. This zone is associated with the terminocratic phase of the Ferdynandovian 2 interglacial, during which thermophilous trees disappeared and were replaced by pine forests or, in areas of higher humidity, by spruce communities (Pidek 2013).

Zone Łu-7 L MAZ still includes numerous remains of trees, dominated by nutlets of *Betula* sect. *Albae* and accompanied by seeds and needles of *Larix* sp. The reappearance of vegetation characteristic for cool climate, in this case *Betula humilis* and *B. nana*, components of dwarf shrub tundra communities, indicates a decrease in mean July temperature to 7.5–10°C (Dahl 1986).

For the first time, vegetation surrounding the basin includes *Andromeda polifolia*, typical of oligotrophic, strongly acidic habitats such as raised and transition bogs as well as bog forest. A decline in the frequency of tree vegetation enabled the intensive development of dwarf shrub communities and the expansion of unshaded habitats preferred by *Potentilla* sp., *Rorippa palustris*, and *Mentha arvensis*. Similarly to *Andromeda polifolia*, acidic habitats of transition bogs or fringes of raised bogs were often favoured by *Scheuchzeria palustris*, *Menyanthes trifoliata*, and *Comarum palustre*, frequently found in the zone as fruits. In addition to acidic habitats, the basin in Łuków was surrounded by boggy, strongly eutrophicated

shores overgrown by *Ranunculus sceleratus* and *R. gailensis*. Humid, nitrogen-rich habitats were occupied by *Urtica dioica*. The littoral part of the basin was covered by a swamp belt with *Typha* sp., *Schoenoplectus lacustris*, *Scirpus atroviroides*, *Polygonum amphibium*, and *Lycopus europaeus*. The zone was characterised by the dominance of *Carex* sp. div. biconvex, *Carex* sp. div. trigonous, *C. elata*, *C. rostrat*, and *C. riparia*, which, together with *Menyanthes trifoliata*, *Comarum palustre*, and mosses, could form communities having a composition similar to the present-day *Caricetum elatae* Koch. association (Matuszkiewicz 2008), indicating conditions of strong vertical water flow (Nowiński 1967).

The clearly decreasing abundance of aquatic vegetation, combined with the dynamic development of peat vegetation, suggests that the lake basin became shallower as it was filled with gyttja and peat deposits. *Najas marina*, *N. minor*, and *Nymphaea alba* continued to grow in the lake but left very few remains as compared to the preceding zone. *Stratiotes* sp., in the previous zone inhabiting shallow, warm coves, disappeared completely. *Ceratophyllum demersum* and *Brasenia* sp. were infrequent as well. *Hippuris vulgaris* appeared in the zone; it occurs at minimum July temperature of +10°C and in the United Kingdom and Scandinavia was recorded as one of the first plants to inhabit lakes at the beginning of the late glacial (Kolstrup 1980, Wasylikowa 1964). It has also been found at numerous sites in Poland in late glacial and Early Holocene sediments (Gałka et al. 2014, Środoń 1989), and in non-optimal periods of the Augustovian (Stachowicz-Rybka 2011), Ferdynandovian (Janczyk-Kopikowa 1975) and Mazovian (Hrynowiecka & Szymczyk 2011) interglacials. The increasing abundance of *Cenococcum geophilum* and *Pediastrum kawraiskyi* (Pidek 2013) may be associated with supply of mineral matter to the basin.

Macrophyte communities were dominated by numerous Potamogeton species, including *Potamogeton praelongus*, *P. rutilus*, *P. filiformis*, *P. gramineus*, *P. pectinatus*, and *P. friesii*, which prefer cool climate with minimum July temperatures ranging between +8°C (*P. filiformis*, *P. gramineus*, *P. praelongus*) and +10°C accepted for *Potamogeton pectinatus* (Gaillard 1984, Kolstrup 1980). The presence of the extinct *Potamogeton dvinensis* and

P. praemaackianus is also worthy of note. The latter was described from the Late Pliocene flora of Belarus (Velichkevich 1975) and the Cromerian flora of Germany (Mai 2003). Fossil endocarps are characteristic for the Eopleistocene and the first half of the Glaciopleistocene. The species was not recorded in Neopleistocene floras (Velichkevich & Zastawniak 2006).

SANIAN 2 GLACIATION

The next cooling starts with the beginning of zone **Łu-8 L MAZ**, corresponding to pollen assemblage zones Ł 16 and Ł 17 L PAZ (Pidek 2013), and is correlated with a glacial sequence related to the early Sanian 2 glaciation. Both palynological and plant macroremains analyses showed that the Sanian 2 glaciation definitely is marked by stadial-interstadial fluctuations, represented by four pollen assemblage zones (Ł 16–Ł 19 L PAZ) and three macrofossil assemblage zones (Łu-8–Łu-10 L MAZ). The presence of trees and shrubs near the basin is documented in zone Łu-8 L MAZ by sparse remains of tree and shrub birches, *B. nana* and *B. humilis*. Numerous fragments of leaves of *Betula* sp. seem to belong to *B. nana* but their state of preservation does not allow precise identification. Habitats covering periodically emerging shores still included communities similar to the modern *Rumicetum maritimi* association, with *Rumex maritimus*, *Ranunculus sceleratus*, *R. gailensis*, and *Ranunculus* sp. This community indicates periodic water level fluctuations and occurs at shores of the most eutrophic lakes and ponds. Numerous herbaceous taxa from various types of communities and wet habitats were determined in the zone and, though recorded only as occasional specimens, showed the great diversity of shore communities. They comprised, for example, *Urtica dioica*, *Potentilla supina*, *P. anserina*, *Potentilla* sp., *Viola palustris*, *Mentha* sp., and remains of plants from the Poaceae and Asteraceae families. The composition of remains of peat vegetation was clearly diminished. Only single fruits of *Carex* sp. div. trigonous, *Carex* sp. div. biconvex, and *C. elata*, as well as *Eleocharis palustris*, *Scirpus atroviroides*, *Cicuta virosa*, and *Stachys palustris* were observed. *Typha* sp. and *Lycopus europaeus* were still components of swamp communities. The development of peat bogs on basin shores is more clearly recorded in the pollen

data, indicating high values of *Sphagnum* sp. spores and Cyperaceae as well as maximum frequencies of *Pediastrum* algae (Pidek 2013), very good indicators of both increased trophic and increased depth of the lake. Similar conditions are indicated by remains of aquatic plants such as *Myriophyllum spicatum* and *Batrachium* sp., which, though few in number, have ecological significance, indicating a rise in the water level.

The group of aquatic plants shows the disappearance of taxa typical for warmer periods. Single spines of *Stratiotes* sp. and the first appearance of megaspores of *Salvinia natans* (most likely rebedded) are recorded. Taxa that continued to grow in the Łuków basin included *Alisma plantago-aquatica*, *Najas minor*, *Polygonum amphibium*, *Hippuris vulgaris*, and numerous Potamogeton species such as *Potamogeton praelongus*, *P. pusillus*, *P. rutilus*, *P. filiformis*, *P. pectinatus*, *P. praemaackianus*, *P. perfoliatus*, and *Potamogeton* sp., as well as *Callitriche autumnalis* and *Caulinia tenuissima* (Pl. 1, Fig. 11). *C. tenuissima* is not found in the Polish flora nowadays but is known from Pleistocene sediments at the sites of Ciechanki Krzesimowskie (Brem 1953), Styków (Wąs 1956), and Czarnucha (Stachowicz-Rybka 2011). It was also recorded in Russia in the Nowochopersk region (Nikitin & Dorofeev 1953) and Jaroslavsk (Gorlova 1960). Seeds of *Najas tenuissima* were also identified in the Cromerian zone of an unspecified chronostratigraphic position (Godwin 1975). Palaeobotanical studies indicated the presence of the species in various interglacials, and a former wide distribution (Tralau 1962).

The next distinguished zone, **Łu-9 L MAZ**, corresponds to the Ł 18 L PAZ (Pidek 2013) and is correlated with an interstadial sequence. Dwarf shrub tundra with dwarf birch, *Betula nana*, and *Andromeda polifolia*, typical of humid, open habitats, was continuously present in the landscape of the lake surroundings. Tree birch, *Betula* sect. *Albae*, was observed as well. A slight increase in the amounts of *Ranunculus scleratus* and *Rumex maritimus* fruits points to periodic water level fluctuations and the occurrence of areas with higher trophic. Single remains of *Potentilla supina*, *P.* sp., *Viola palustris*, *Bidens tripartita*, and *Rorippa palustris* indicate that communities of open and insolated habitats were an important part of the landscape. There is also an increase in

the frequency of remains of peat plants from the Cyperaceae family, including *Carex* sp. div. biconvex and *Carex* sp. div. trigonous. *Eriophorum vaginatum* was spreading as well; it is typical mainly of raised and transition bogs, is known to prefer humid, acidic habitats with trophic conditions from extremely poor to oligotrophic, and can be dominant in the humid margins of peat bogs or can grow in their shallow depressions. *Andromeda polifolia*, which appears together with *E. vaginatum*, most commonly inhabits low clumps within raised bogs or humid hollows between the clumps, but does not tolerate very high humidity (Jacquemart 1998). Similarly to *E. vaginatum*, it grows in extremely oligotrophic habitats and acidic raised and transition bogs (Witkowska-Żuk 2008). The also observed *Scheuchzeria palustris*, *Menyanthes trifoliata*, and *Comarum palustre* may have been associated with more humid areas in the peat bog. *Carex paucifloroides*, an extinct species most closely related to the present-day *Carex pauciflora*, which occurs on raised bogs and peaty meadows, was determined for the first time in this zone. In Poland the extinct taxon has been identified at several sites of the Mazovian (Mamakowa & Velichkevich 1993) and Augustovian (Stachowicz-Rybka 2011) interglacials. It has also been found at numerous sites of the Korchevian, Belovezhian, and Alexandrian interglacials in Belarus (Velichkevich 1975, 1979, 1982, 1990) and in the Snajgupele flora of Lithuania (Velichkevich 1974), and is known from the Upper Pliocene of Germany (Mai & Walther 1988, Gumbel & Mai 2004). Remains of *Carex elata*, *Scirpus atroviroides*, *S. sylvaticus*, and *Eleocharis palustris* were also identified. The group of swamp plants was dominated by *Typha* sp., *Schoenoplectus lacustris*, *S. tabernaemontani*, and *Caltha palustris*. Also noteworthy is the presence of *Isoetes lacustris* (Pl. 2, Figs 1, 2), patches of which develop in deeper parts of cool lakes at ca 2 m water depth with small amounts of nutrients. This sciophyte presently grows in waterbodies surrounded by pine forest or acidophilous deciduous forest. Among macrophytes, the extinct *Caulinia macrosperma* (Pl. 1, Fig. 9.10; Pl. 2, Figs 7–9), characteristic for the Belovezhian interglacial of Belarus and other floras of similar age (Velichkevich & Zastawniak 2008), was numerous. This species is most closely related to the modern *Caulinia tenuissima* and, considering the composition

of vegetation, shows similar climatic requirements. Remains of *P. natans*, *P. obtusifolius*, *P. praemaackianus*, *P. perfoliatus*, *P. crispus*, and *P. panormitanus* were less frequent. They were accompanied by single seeds and fruits of *Myriophyllum spicatum*, *Nuphar lutea/pumila*, *Stratiotes* sp., *Sparganium emersum*, and at the top of zone, remains of *Nymphoides peltata* and *Zannichellia palustris*, which occur in eutrophic stagnant or slow-flowing waters and tolerate only low salinity. The presence of *Betula nana* and plants associated with an aquatic environment and serving as climate indicators, such as *Hippuris vulgaris*, *Potamogeton alpinus*, *Potamogeton pusillus*, *P. rutilus*, and *Najas tenuissima*, points to conditions of boreal climate. In contrast, the occurrence of *P. lucens*, *P. pectinatus*, *P. praelongus*, and *Myriophyllum verticillatum* indicates optimum mean July temperature above 13°C.

The last zone of the Łuków section, **Łu-10 LMAZ**, is equivalent to pollen assemblage zone Ł 19 L PAZ distinguished by Pidek (2013), and is correlated with a stadial sequence. At that time the lake shores were still covered by tundra with *Betula humilis*. Terrestrial communities included tree birch. The finding of only single specimens of *Ranunculus sceleratus* and *R. gailensis* suggests that conditions in eutrophic habitats were not favourable for those species. Impoverishment of the composition and frequency of the trees and shrubs, as well as the return of communities typical of open habitats, with *Urtica dioica*, *Carduus crispus*, and *Selaginella selaginoides*, indicate an obvious cooling of climate. This change was intensive enough to have a strong negative impact on aquatic vegetation. The lack of dense plant cover triggered solifluction processes, reflected in the presence of *Cenococcum geophilum* in sediment. The occurrence of such taxa as *Salvinia natans* or *Brasenia borysthénica* seems to be due to rebedding of older sediments into the basin. The waters of the lake in Łuków still included *Stratiotes* sp., *Potamogeton vaginatus*, *P. praelongus*, *P. pusillus*, *P. rutilus*, *P. natans*, *P. filiformis*, *P. pectinatus*, and *P. praemaackianus*; *P. perfoliatus*, *Batrachium* sp. and *Zannichellia palustris* were recorded as well. Characeae oospores appeared in the basin once again, indicating intensive development of stonewort meadows, which occur in quite deep (even up to 10 m; Hannon & Gaillard 1997), clear,

calcium carbonate-rich waters. The frequency of peat vegetation was lower than in the previous zone, but areas bordering the basin shores were still dominated by numerous species typical of peat habitats, such as *Carex* sp. div. trigonous, *C. sp. div. biconvex*, *C. paucifloroides*, *C. elata*, *Menyanthes trifoliata*, *Scirpus atroviroides*, and *S. sylvaticus*, while the swamp zone was overgrown by *Typha* sp., *Schoenoplectus lacustris*, *Lycopus europaeus*, and *Carex pseudocyperus*.

DISCUSSION

To date, two bimodal interglacial sequences have been documented in Poland: the Ferdynandovian interglacial, correlated with MIS 13–15 (Ber et al. 2007, Lindner & Marks 2008, Janczyk-Kopikowa 1975, 1991, 1996, Pidek 2000, 2003, 2013, Winter 2006, Zagwijn, 1996), and the Augustovian interglacial, correlated with MIS 19–21 (Ber 1996, Ber et al. 1998, Janczyk-Kopikowa 1996, Stachowicz-Rybka 2007, 2009, 2011, Winter 2001, 2008, 2009).

For both interglacials, the record of a bimodal sequence containing two warm periods separated by a cool unit has been analysed in terms of cyclic changes in vegetation and climate. High-resolution pollen analyses of material from several sites in Poland have provided the basis for a detailed reconstruction of both successions. The results of palynological studies characterising these sequences were confirmed by examinations of plant macroremains at sites of the Augustovian interglacial (Stachowicz-Rybka 2005, 2009, 2011), but a full comparison of the successions was not possible without recent data on the Ferdynandovian interglacial. The only site of Ferdynandovian age previously investigated by plant macroremains analysis was the stratotype of Ferdynandów (Janczyk-Kopikowa 1975). The Łuków 3a site presented here, with a complete record of the Ferdynandovian sequence, yielded the data needed to carry out such a comparison, as presented in Table 3. To describe the two successions, extinct taxa and those characteristic for a climatic context were selected in both floras. Their composition was then compared for the two climatic optima and the separating cool periods, as well as for stadial and interstadial phases of the Nidanian and Sanian 2 glaciations.

Table 3. Comparison of taxa characteristic for the Augustovian and Ferdynandovian interglacials

Ferdynandovian interglacial	Augustovian interglacial
<p>Sanian 2 glaciation Stadial – <i>Betula humilis</i>, <i>Selaginella selaginoides</i>, <i>Carex paucifloroides</i>, <i>Potamogeton vaginatus</i>, <i>P. praemaackianus</i> Interstadial – <i>Betula nana</i>, <i>Rorippa palustris</i>, <i>Carex paucifloroides</i>, <i>Scirpus atroviroides</i>, <i>Potamogeton alpinus</i>, <i>P. obtusifolius</i>, <i>P. praemaackianus</i>, <i>Caulinia macrosperma</i>, <i>Najas tenuissima</i>, Stadial – <i>Betula nana</i>, <i>B. humilis</i>, <i>Potentilla anserina</i>, <i>Scirpus atroviroides</i>, <i>Hippuris vulgaris</i>, <i>Potamogeton praemaackianus</i>, <i>Caulinia tenuissima</i></p>	<p>Nidanian glaciation Stadial – <i>Salix</i> sp., <i>Pinus sylvestris</i>, <i>Chenopodium</i> sp., <i>Ranunculus sceleratus</i>, <i>Plantago media</i>, <i>Typha</i> sp. Interstadial – <i>Betula nana</i>, <i>B. humilis</i>, <i>Azolla filiculoides</i>, <i>Salvinia natans</i>, <i>Carex paucifloroides</i>, <i>Selaginella</i> cf. <i>tetraedra</i>, <i>Lemna trisulca</i>, <i>Callitriche</i> sp., <i>Stratiotes</i> sp. Stadial – <i>Betula nana</i>, <i>Larix</i> sp., <i>Selaginella selaginoides</i>, <i>Rorippa palustris</i>, <i>Elatine hydropteroides</i>, <i>Plantago media</i>, <i>Eupatorium cannabinum</i>, <i>Potentilla anserina</i></p>
<p>Ferdynandovian interglacial (F2) <i>Betula</i> sect. <i>Albae</i>, <i>B. humilis</i>, <i>Pinus sylvestris</i>, <i>Ranunculus sceleratus</i>, <i>R. gailensis</i>, <i>Urtica dioica</i>, <i>Chenopodium rubrum</i>, <i>Scirpus atroviroides</i>, <i>Cyperus glomeratus</i>, <i>Eleocharis praemaximoviczii</i>, <i>Bolboschenus maritimus</i>, <i>Stratiotes</i> sp., <i>Najas marina</i>, <i>N. minor</i>, <i>Brasenia borysthenica</i>, <i>Aldrovanda borysthenica</i>, <i>Ceratophyllum demersum</i>, <i>Nymphaea alba</i>, <i>N. cinerea</i>, <i>Potamogeton praemaackianus</i>, <i>P. dvinensis</i>, <i>Callitriche</i> sp., <i>Sagittaria sagittifolia</i>, <i>Caulinia macrosperma</i>, <i>Myriophyllum spicatum</i></p>	<p>Augustovian interglacial (A2) <i>Azolla filiculoides</i>, <i>Salvinia natans</i>, <i>Euryale</i> cf. <i>ferox</i>, <i>Selaginella</i> cf. <i>tetraedra</i>, <i>Stratiotes</i> cf. <i>goretskyi</i>, <i>Carpinus betulus</i>, <i>Potamogeton dvinensis</i>, <i>P. perforatus</i>, <i>P. nodosus</i>, <i>Carex paucifloroides</i>, <i>Nymphaea cinerea</i>, <i>Scirpus atroviroides</i>, <i>Scirpus kreczetoviczii</i>, <i>Schoenoplectus tabernaemontani</i>, <i>Cyperus glomeratus</i>, <i>Ranunculus gailensis</i>, <i>Eleocharis praemaximoviczii</i>, <i>Trapa natans</i>, <i>Elatine hydropteroides</i>, <i>Najas marina</i>, <i>N. minor</i>, <i>Alisma plantago-minima</i>, <i>Typha aspera</i>, <i>Selaginella</i> cf. <i>tetraedra</i>, <i>Urtica</i> cf. <i>laethevi-rens</i>, <i>Urtica</i> cf. <i>thunbergiana</i></p>
<p>Ferdynandovian interglacial (F1/2) <i>Betula humilis</i>, <i>B. nana</i>, <i>Larix</i> sp., <i>Chenopodium t. album</i>, <i>Potentilla</i> sp., <i>Ranunculus gailensis</i>, <i>Schoenoplectus lacustris</i>, <i>Potamogeton alpinus</i>, <i>P. pusillus</i>, <i>P. filiformis</i>, <i>P. gramineus</i>, <i>P. praelongus</i>, <i>P. obtusifolius</i>, <i>Stratiotes</i> sp.</p>	<p>Augustovian interglacial (A1/2) <i>Betula nana</i>, <i>B. humilis</i>, <i>Larix</i> sp., <i>Thalictrum minus</i>, <i>Rorippa palustris</i>, <i>Ranunculus gmelinii</i>, <i>Selaginella selaginoides</i>, <i>S. helvetica</i>, <i>Potentilla anserina</i>, <i>Azolla filiculoides</i> foss., <i>Salvinia natans</i>, <i>Carex paucifloroides</i></p>
<p>Ferdynandovian interglacial (F1) <i>Larix</i> sp., <i>Picea abies</i>, <i>Urtica dioica</i>, <i>Potentilla supina</i>, <i>Viola palustris</i>, <i>Bidens tripartita</i>, <i>Potentilla</i> sp., <i>Comarum palustre</i>, <i>Mentha aquatica</i>, <i>Typha</i> sp., <i>Schoenoplectus lacustris</i>, <i>Alisma plantago-aquatica</i>, <i>Myriophyllum verticillatum</i>, <i>Schoenoplectus tabernaemontani</i>, <i>Najas marina</i>, <i>N. minor</i>, <i>Ceratophyllum demersum</i>, <i>Scirpus atroviroides</i>, <i>Stratiotes</i> sp., <i>Potamogeton praelongus</i>, <i>Aldrovanda</i> sp., <i>Euryale</i> sp.</p>	<p>Augustovian interglacial (A1) <i>Betula humilis</i>, <i>Larix</i> sp., <i>Pinus sylvestris</i>, <i>Juniperus communis</i>, <i>Urtica</i> cf. <i>laethevi-rens</i>, <i>U.</i> cf. <i>thunbergiana</i>, <i>Scirpus atroviroides</i>, <i>Cyperus glomeratus</i>, <i>Lemna trisulca</i>, <i>Carex paucifloroides</i>, <i>Euryale</i> sp., <i>Stratiotes aloides</i>, <i>S. cf. brevispermus</i>, <i>Ceratophyllum demersum</i>, <i>Potamogeton dvinensis</i>, <i>P. panormitanoides</i>, <i>Caulinia tenuissima</i>, <i>Azolla filiculoides</i> foss., <i>Salvinia natans</i>, <i>Lemna trisulca</i>, <i>Zannichellia palustris</i></p>
	<p>Narevian glaciation <i>Betula nana</i>, <i>Larix</i> sp., <i>Ranunculus gailensis</i>, <i>Zannichellia palustris</i>, Characeae</p>

The presence of *Azolla filiculoides*, *Salvinia natans*, *Selaginella* cf. *tetraedra*, *Scirpus kreczetoviczii*, *Stratiotes* cf. *goretskyi*, *Stratiotes* cf. *brevispermus*, and *Typha aspera* in Augustovian floras makes them significantly different from the Ferdynandovian floras, which, on the other hand, include taxa such as *Brasenia borysthenica*, *Aldrovanda borysthenica*, *Caulinia macrosperma*, and *Potamogeton praemaackianus*, as observed in Łuków. The two types of floras have certain extinct species in common, such as *Scirpus atroviroides*, *Cyperus glomeratus*, *Eleocharis praemaximoviczii*, *Nymphaea cinerea*, and *Ranunculus gailensis*. It has not yet been fully resolved whether the flora of Łuków includes *Euryale* sp. (Pl. 1, Figs 13, 14; Pl. 2, Figs 13, 15), a particularly important taxon. The two fragments of its seed found were too small to enable estimation of the size of the whole seed and did not include diagnostic structural elements. However, their surface was similar to that of the modern *Euryale*

ferox (Pl. 2, Fig. 14). This is significant, since *Euryale* sp. seed fragments were preserved in a similar way in Augustovian floras (Stachowicz-Rybka 2011); in this case, however, the occurrence of the species was also confirmed by remains of characteristic spines. For the Ferdynandovian flora of Łuków, the presence of *Euryale* sp. is not entirely certain.

The succession of plant macroremains and the corresponding climatic and environmental changes described for section Łuków 3a are consistent with the pollen succession proposed by Pidek (Pidek & Małek 2010, Pidek 2013, Pidek & Poska 2013) and may also be related to other sites investigated in the area, such as Ferdynandów (Janczyk-Kopikowa 1975, Janczyk-Kopikowa et al. 1981), Podgórze B1 (Mamakowa 1996), and Zdany (Pidek 2000). In particular, the macroflora from Łuków can be compared to the succession of plant macroremains from Ferdynandów (Janczyk-Kopikowa 1975), the only sequence of Ferdynandovian

age previously documented in Poland. The floras of the two basins are similar in many aspects: not only in the occurrence or lack of characteristic taxa, but, most important, in the phases of vegetation development during warm and cold periods.

For the first optimum (F1), at both sites the record of local vegetation overgrowing the basins was sparse in comparison to terrestrial vegetation, which in both cases most likely resulted from the great depth of the lakes, rapid supply of allochthonous material, and very intensive growth of diatoms and other lower plants. Among the higher plants only *Najas marina* and *N. minor* were numerous, while other taxa, such as *Potamogeton pusillus* and *P. praelongus*, appeared rather infrequently and discontinuously.

Aquatic and boggy vegetation did not develop more intensively until the end of the optimum. High water levels in optimum F1 presumably resulted from changes towards a more oceanic climate, as also confirmed by pollen data from Łuków and Zdany which was analysed by the modern pollen analogue approach (Pidek & Poska 2013).

In both Łuków and Ferdynandów the vegetation of the cool period (F1/2) was strongly diminished and was marked by the appearance of species characteristic for boreal climate.

For the second optimum (F2), both sections showed the greatest species diversity and abundance of specimens. Undoubtedly the temperature conditions were advantageous for luxuriant development of vegetation. As the basins gradually filled with sediments they became shallow eutrophic lakes overgrown by *Brasenia borysthena* (Łuków) or *B. purpurea* (Ferdynandów), *Ceratophyllum demersum* and *Najas marina*, and at the end of this period became peat bogs with numerous mosses, Cyperaceae, *Menyanthes trifoliata*, and *Eleocharis palustris*. The similar record of an interstadial unit within the early Sanian 2 glaciation is also worthy of note. At both sites the water level obviously increased at the beginning of the glaciation, and the peat bogs were replaced by quite deep lakes with cool and most likely oligotrophic waters, inhabited by *Isoëtes lacustris*, *Pilularia globulifera*, *Elatine hydropiper*, and *Hippuris vulgaris*. The trophic status of these waters, covered by both strongly eutrophic and oligotrophic plants, seemed uncertain as early as in the work of

Janczyk-Kopikowa (1975). In the Łuków section the decrease in trophy is also indicated by the presence of *Isoëtes lacustris*, *Hippuris vulgaris*, *Najas tenuissima*, and *Andromeda polifolia*. The development phases and vegetation of the palaeolakes at the two sites, spaced ca 40 km apart, make a very coherent sequence that appears to be valid for a larger area and corresponds to cyclic climatic changes recorded in deep marine cores (MIS 13–15). The modern pollen analogues approach applied to pollen data from Łuków and Zdany (Pidek & Poska 2013) gave precise estimations of temperature ranges and total precipitation in successive periods of the Ferdynandovian interglacial.

As indicated by the presence of the most extremely thermophilous taxa, identified in plant macroremains analysis, during optimum F1 the temperature ranged from +18°C $T_{m\text{jul}}$ (*Najas minor*) to +15°C $T_{m\text{jul}}$ (*Najas marina*) (Aalbersberg & Litt 1998). Palaeotemperature reconstruction based on the modern pollen analogues method showed temperatures varying between +16°C $T_{m\text{jul}}$ and -14°C $T_{m\text{jan}}$ at the beginning of interglacial F1, afterwards rapidly increasing by 8–9°C as evidenced by the appearance of *Ulmus* (Pidek & Poska 2013).

Period F2 was the time of development of aquatic communities including many more thermophilous plants, such as *Cyperus glomeratus* (+20°C $T_{m\text{jul}}$; Aalbersberg & Litt 1998) and two extinct species: *Brasenia borysthena* (+20–21°C $T_{m\text{jul}}$ estimated for *B. schreberi*; Tobolski 1991) and *Aldrovanda borysthena* (+18°C $T_{m\text{jul}}$ estimated for *A. vesiculosa*; Aalbersberg & Litt 1998). Following the modern pollen analogues approach (Pidek, Poska 2013), the temperature of the warmest month ($T_{m\text{jul}}$) reached ca +19°C in this period.

The early Sanian 2 glaciation covered an interstadial period of higher temperatures, enabling boreal forests to dominate. Mean July temperature ($T_{m\text{jul}}$) in this period reached ca +12°C, as indicated by modern pollen analogues or, slightly lower, to +10°C, as indicated by plant macroremains of *Myriophyllum spicatum*, *M. verticillatum*, and *Eleocharis palustris* (Aalbersberg & Litt 1998). $T_{m\text{jul}}$ of +10°C is supported by the occurrence of *Hippuris vulgaris* (Wasylikowa 1964), while the presence of *Potamogeton praelongus* points to $T_{m\text{jul}}$ even down to +8°C (Kolstrup 1980).

Further studies of plant macroremains from sediments of Ferdynandovian age, including

material from repeated drilling of the Ferdynandów section carried out in 2011, should greatly contribute to more detailed analyses of changes in the climate, environment and occurrence of characteristic plant taxa in this period.

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PLATES

Plate 1

1. *Carpinus betulus* L. seed
2. *Eleocharis praemaximiviczii* Dorof., fruit
3. *Cyperus glomeratus* L., fruit
4. *Scirpus atroviroides* Wieliczk., fruit
5. *Callitriche autumnalis* L., seed
6. *Nymphaea cinerea* Wieliczk., seed
7. *Aldrovanda borysthenica* Wieliczk., seed
8. *Brasenia borysthenica* Wieliczk., seed
9. *Caulinia macrosperma* (Wieliczk.) Wieliczk., seed
10. *Caulinia macrosperma* (Wieliczk.) Wieliczk., seed
11. *Caulinia tenuissima* (A. Br.) Tzvel., seed
12. *Ceratophyllum demersum* L., fruit
13. *Euryale* sp., fragment of seed
14. *Euryale* sp., fragment of seed
15. *Potamogeton alpinus* Balb., fruit
16. *Potamogeton praemaackianus* Wieliczk., fruit
17. *Potamogeton praelongus* Wulfen, fruit

Phot. R. Stachowicz-Rybka

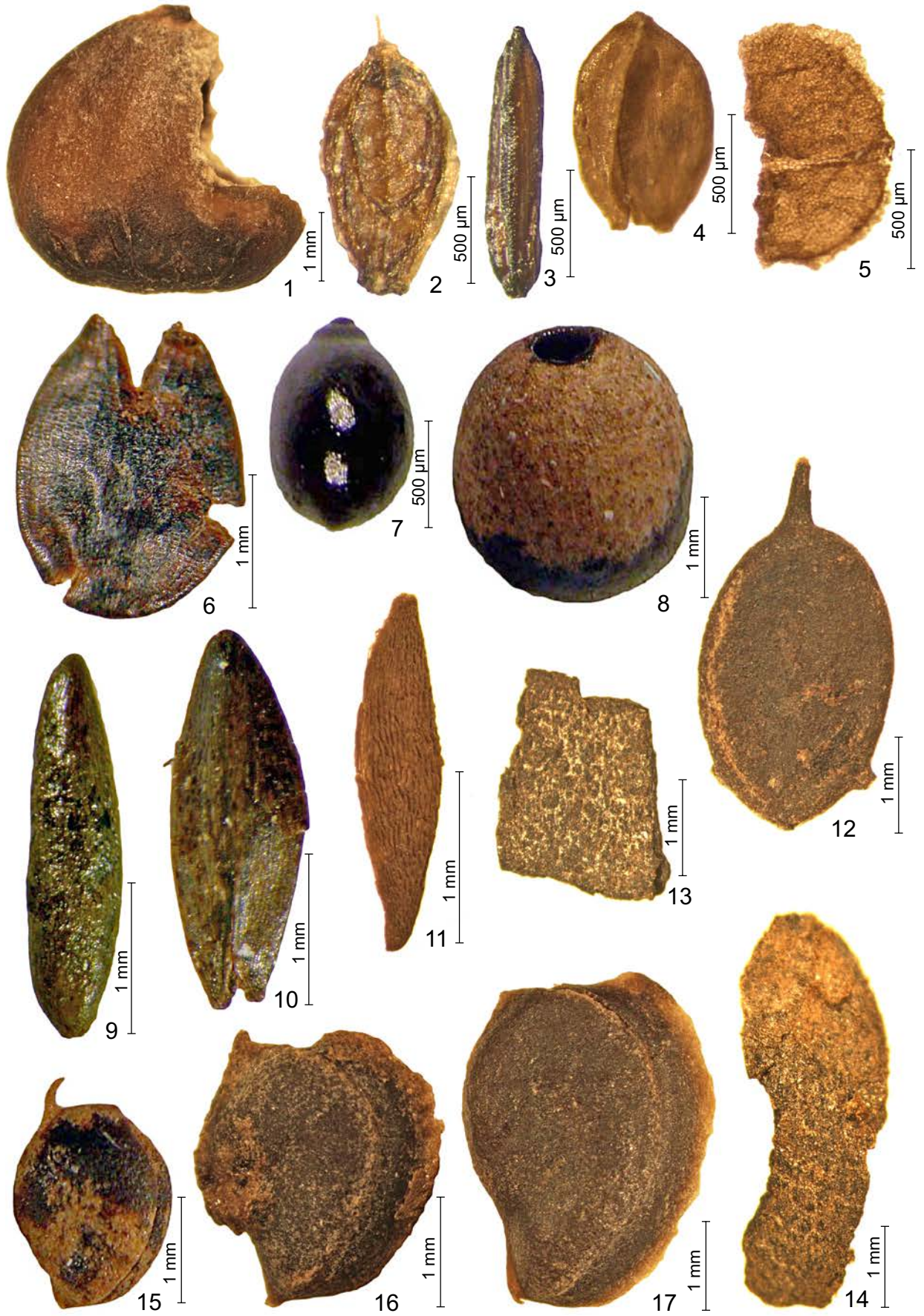
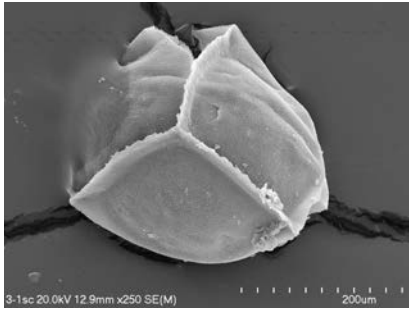


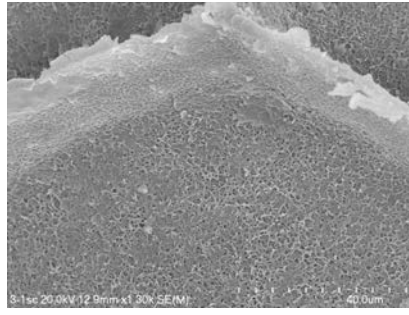
Plate 2

1. *Isoëtes lacustris* L. megaspore
2. *Isoëtes lacustris* L. megaspore, detail of surface
3. *Scirpus atroviroides* Wielicz., fruit
4. *Scirpus atroviroides* Wielicz., fruit, detail of surface
5. *Aldrovanda borysthenica* Wielicz., seed
6. *Aldrovanda borysthenica* Wielicz., seed, detail of surface
7. *Caulinia macrosperma* (Wielicz.) Wielicz., seed
- 8,9. *Caulinia macrosperma* (Wielicz.) Wielicz., seed, detail of surface
10. *Nymphaea cinerea* Wielicz., seed
11. *Nymphaea cinerea* Wielicz., seed, detail of surface
12. *Ceratophyllum demersum* L., fruit
13. *Euryale* sp., fragment of seed
14. *Euryale* sp., details of surface of a present-day seed,
15. *Euryale* sp., fragment of seed, detail of surface

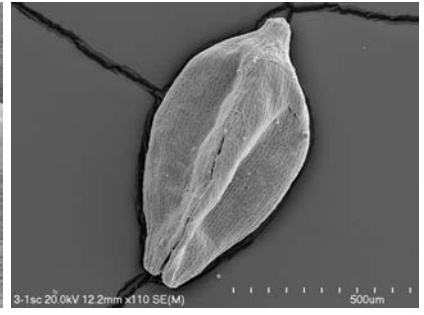
Phot. R. Stachowicz-Rybka



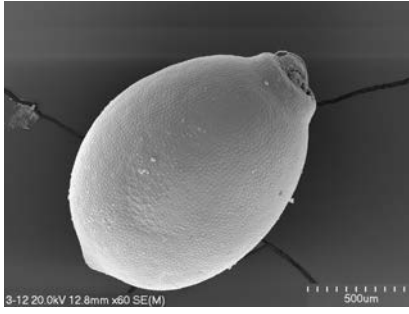
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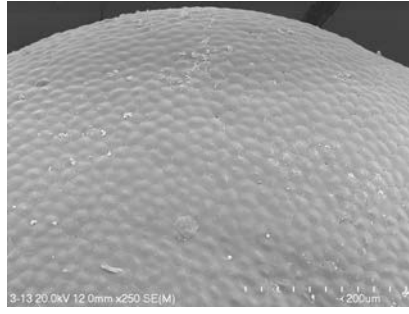
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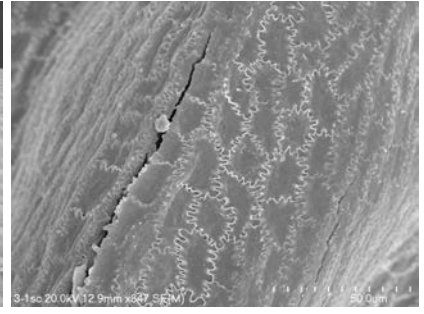
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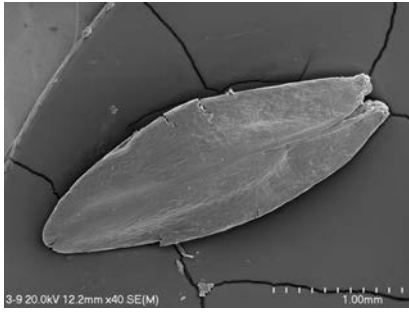
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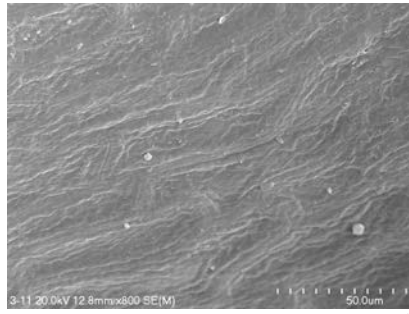
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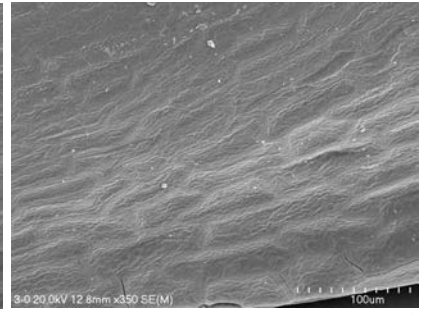
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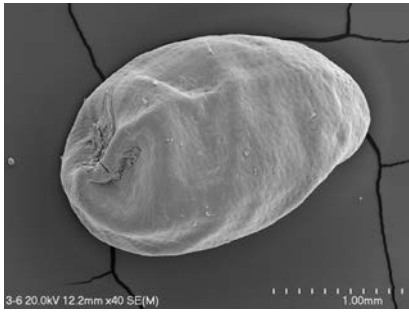
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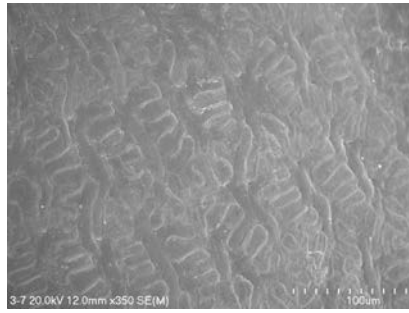
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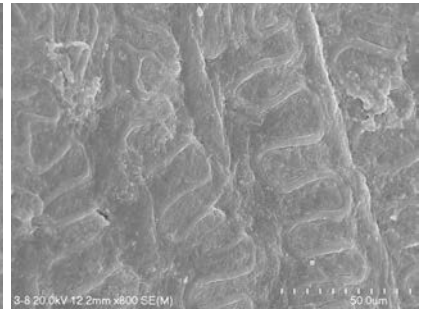
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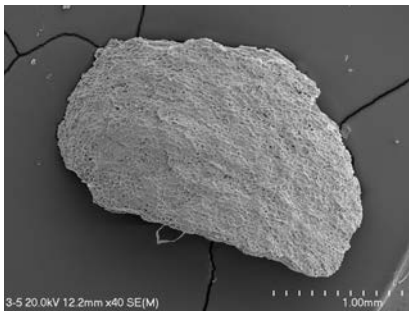
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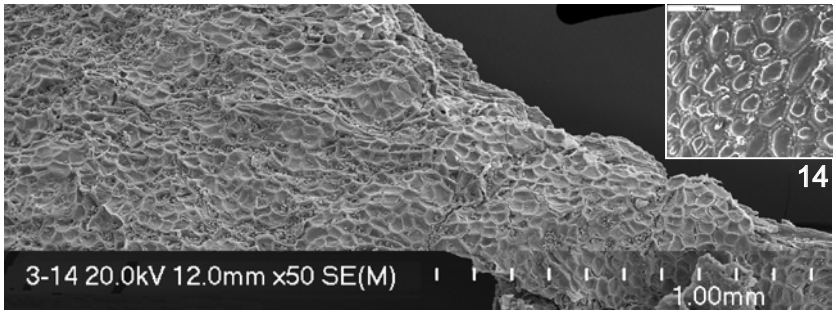
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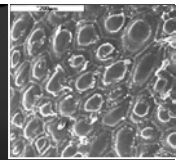
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13



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