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Acta Palaeobotanica 55(2): 233–251, 2015
DOI: 10.1515/acpa-2015-0011

Vegetation of the Ferdynandovian interglacial (MIS 13–15) based on plant macrofossils from a new profile of the stratotype site

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Received 23 September 2015; accepted for publication 19 October 2015

ABSTRACT. Early Middle Pleistocene palaeolacustrine sediments of the Ferdynandów site (E Poland), serving as a stratotype for the Ferdynandovian interglacial, were subjected to a new drilling in 2011. The obtained profile, covering the late Sanian 1 glaciation, two interglacial successions (Ferdynandovian 1 and 2), the cold Ferdynandovian 1/2 interval, and the early Sanian 2 glaciation, permitted a high-resolution plant macroremains analysis, correlated with the results of a palynological examination. In detailed studies of plant macroremains from the profile, new taxa were discovered for the Polish Pleistocene flora: specifically, species that are extinct or not found nowadays in Poland. On the basis of the taxonomic diversity and occurrence of bioindicators, the division into warm and cold units of the Ferdynandovian interglacial as well as units associated with the Sanian 1 and 2 glaciations, already applied in pollen studies, were confirmed, and the periods were described in terms of plant macroremains.

The Ferdynandovian succession is correlated with the Cromerian Complex (Cromerian III and IV) in the Early Middle Pleistocene of Western Europe, as well as with Marine Isotope Stages (MIS) 13–15. New geological and palaeobotanical data enabled a description of the palaeogeographic context and conditions of functioning, as well as the evolution of the interglacial lake at the stratotype site.

The outcome of plant macroremains analysis is presented and interpreted in comparison with corresponding results previously obtained for the Ferdynandów B profile, studied by Janczyk-Kopikowa (1975). Particular consideration is given to similarities between the succession of Ferdynandów 2011 and the profiles of Ferdynandów B and the nearby drilled Łuków 3A.

Study of the macrofossil flora of Ferdynandów 2011 revealed the presence of species absent in the archival Ferdynandów B. Taxa not formerly recorded in early Middle Pleistocene floras, such as *Brasenia borysthenica*, *Aldrovanda borysthenica*, *Pilularia borysthenica*, *Caulinia goretskyi*, and *Potamogeton saryanensis*, were identified. These species and other taxa of stratigraphic or climatic significance provided the basis for a more detailed description of the Ferdynandovian flora, afterwards compared with other stratigraphically corresponding Polish and European early Middle Pleistocene floras.

The composition of characteristic taxa also was used for comparisons between two bimodal interglacial sequences, namely the Ferdynandovian (correlated with MIS 13–15) and Augustovian (correlated with MIS 19–21), and the Domuratovian succession (correlated with MIS 17).

KEYWORDS: plant macroremains, environmental and climatic changes, Ferdynandovian interglacial, Middle Pleistocene, MIS 13–15, E Poland.

INTRODUCTION

In 2011 a core covering a complete sequence of glacial-interglacial lacustrine sediments was drilled at the Ferdynandów site, which serves as the stratotype for the Ferdynandovian pollen succession. The sediments were to be reexamined in new studies at much higher resolution. The collected material was used in plant macroremains analysis, presented in this paper, as well as in malacological, diatomological, sedimentological, palaeomagnetic, geochemical, and isotopic research, to be discussed in other publications. The first investigators of the sediments from Ferdynandów (Janczyk-Kopikowa 1975, 1991, Janczyk-Kopikowa et al. 1981, Rzechowski 1996) did not have the benefit of such a large range of analyses.

The profiles of Ferdynandów B (Janczyk-Kopikowa 1975, 1991, Janczyk-Kopikowa et al. 1981), Ferdynandów 2011 (Pidek 2015), and Łuków 3a (Pidek & Małek 2010, Pidek & Poska 2013, Pidek 2013) originate from sites close to each other; they include completely described successions covering two very well recognised warm periods of interglacial rank separated by a cooling of glaciation rank. The pollen diagrams from Łuków and Ferdynandów were divided into corresponding pollen assemblage zones and were correlated with the new division of the Ferdynandovian succession into two warm units of interglacial rank as proposed by Mamakowa (2003) in her studies of the Podgórze B1 profile drilled near the Nowe Miasto nad Pilicą locality.

Stratigraphically, the sequence is correlated with stages 13–15 in the oxygen isotope (O^{18}) curve and dated to a period between the Sanian 1 and 2 glaciations.

Both Janczyk-Kopikowa (1991) and Zagwijn (1996) correlated the Ferdynandovian succession with sequences of the bioptimal Shklovian interglacial from western Russia and of Nizhninsky Rov in Belarus. Following Velichkevich et al. (1996), the succession includes two separate interglacials, the older Belovezhian and the younger Mogilevian, corresponding to the lower and upper climatic optima of the Ferdynandovian succession, respectively. A different classification was presented by Lindner et al. (2004), who correlated the older warming (conformable with Ferdynandovian 1) with the Belovezhian 1 unit, the younger warming (conformable with Ferdynandovian 2) with the Belovezhian 2 unit, and the separating cooling of Ferdynandovian 1/2 with the Belovezhian 1/2 unit.

Similarly to the scheme proposed by Lindner & Marks (1994), Zagwijn (1996) related the Ferdynandovian sequence to oxygen isotope stages 13–15. In considering the West European stratigraphy, Zagwijn (1996) correlated the lower warm unit of Ferdynandów with Cromerian III and the upper unit with Cromerian IV.

Apart for the stratotype of Ferdynandów, several other sites with sediments of this age were identified in Poland (Rzechowski 1996, Mamakowa 2003, Żarski et al. 2009). Other sites with a complete record of the Ferdynandovian succession include Zdany on the Siedlce Upland (Pidek 2003) as well as several other sites subjected to expert analyses in the South Podlasie region (Żarski et al. 2009). Apart from Zdany, Łuków, Ferdynandów, and Podgórze, only three other profiles contain sediments in which the sequence was completely preserved. In this context, the Ferdynandów, Zdany, Łuków, and Podgórze sites, documenting a succession with two warm units separated by a cold one, seem particularly interesting.

Correlation of the results of a high-resolution palynological examination (Pidek 2015) and a plant macroremains analysis for the Ferdynandów 2011 profile allowed a more precise reconstruction of the development of the basin and the type of its vegetation.

Plant macrofossils from sediments corresponding to the Ferdynandovian interglacial in Poland have been widely studied in Eastern Europe, particularly in Belarus, at sites at Motol, Smolyarka (Velichkevich et al. 1993), and Nizhninsky Rov (Velichkevich et al. 1996), as well as in Russia at the Smolenskyi Brod site (Velichkevich 1978). The throrough survey carried out by Janczyk-Kopikowa (1975) at the Ferdynandów B site covered not only pollen but also plant macroremains, and for a very long time remained the only example of the Ferdynandovian macroflora described for Poland. The second site that appeared to document this fossil flora and provide important information on the development of the palaeolake itself was Łuków 3A (Stachowicz-Rybka 2015a). Species identified as characteristic for the Ferdynandovian interglacial included *Potamogeton praemaackianus*, *Nymphaea cinerea*, *Caulinia macrosperma*, *Brasenia borysthenica*, and *Aldrovanda borysthenica*.

Results of recent research at the Ferdynandów 2011 site are in accord with the scheme applied for the stratotype of Ferdynandów B (Janczyk-Kopikowa et al. 1981) and correspond to Belarusian profiles (Rylova & Savchenko 2005). All these classifications include corresponding climatostratigraphic units, confirming the wide, supraregional range of climatic changes proceeding in the interglacial periods of Ferdynandovian 1 and Ferdynandovian 2 and in the cooling of Ferdynandovian 1/2, typified by steppe-tundra communities and referred to as the X glaciation by Mamakowa (2003).

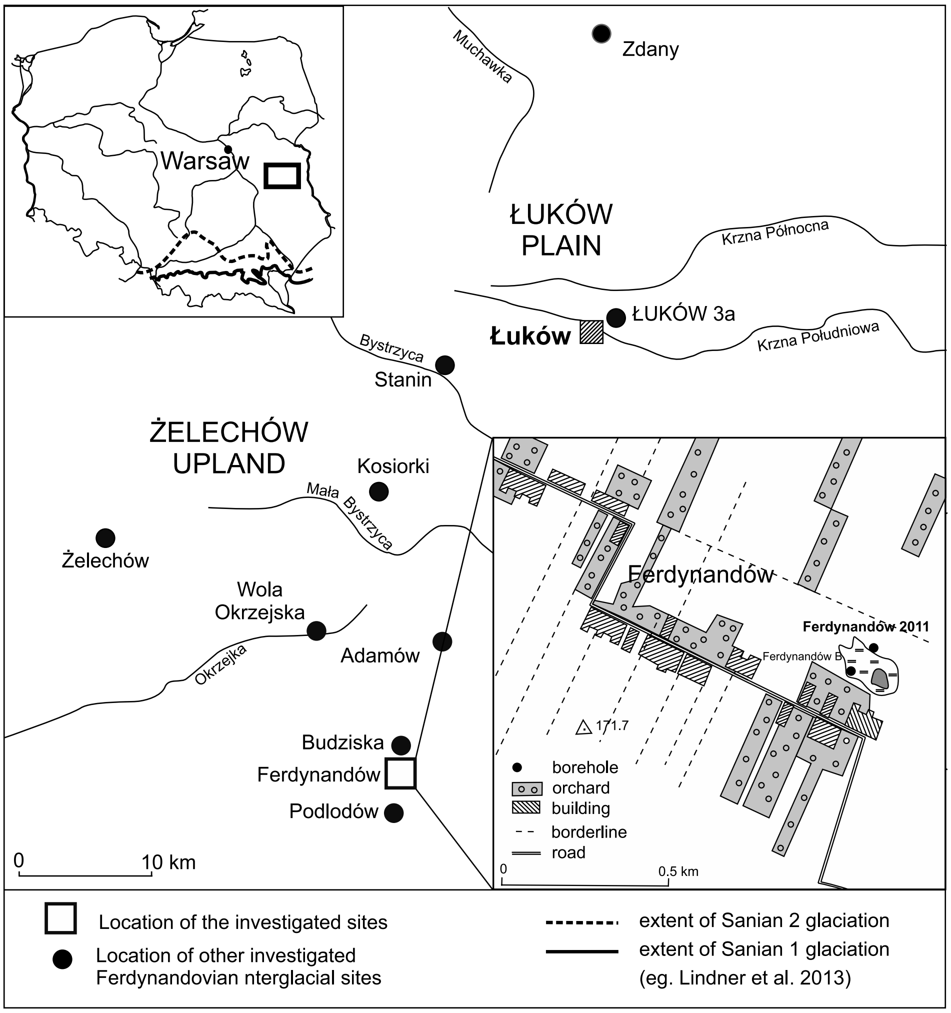

Fig. 1. Location of the investigated sites

In the old Ferdynandów B profile (Janczyk-Kopikowa 1975, 1991, Janczyk-Kopikowa et al. 1981, Rzechowski 1996), the cool period could not be easily recognised in the pollen diagram, as the sediment was compacted and the samples were collected at low density. New palynological data from the Ferdynandów 2011 profile support the strong compliance of the patterns of vegetation development and climate changes recorded for large areas of the European Lowland.

STUDY AREA

The Ferdynandów site is located on the Łuków Plain, part of the South Podlasie Lowland (Kondracki 2000), beyond the limits of the Vistulian glaciation. The drilling at Ferdynandów 2011 (51°39′46.0″N, 22°12′49.5″E) was carried out in an area presently forming an endorheic depression, ca 150 m north of the drilling of Ferdynandów B from 1963 (Fig. 1). The plant succession of this archival drilling was initially assigned to the Mazovian (Janczyk-Kopikowa 1975), but after reexamination it was for the first time described as a new interglacial sequence, referred to as the Ferdynandovian succession (Janczyk-Kopikowa 1991, Rzechowski 1996).

In the new drilling of Ferdynandów 2011, the lacustrine series of sediments of the Ferdynandovian interglacial, subjected to detailed studies of plant macroremains, reaches 6.75 m thickness and comprises mainly silts, non-calcareous gyttjas, silts with calcium carbonate precipitates, shaly silts, and strongly compressed peats. The lacustrine series is underlain by 7.6 m thick tills passing into 3.15 m thick laminated basin silts. These sediments are correlated with the Sanian 1 glaciation. Peats ending the lacustrine series are overlain by organic silts and laminated silts. On the basis of palynological analysis, these 3.5 m thick basin sediments are dated to the Sanian 2 glaciation. This series, ending at

13.8 m depth, is covered by 1.2 m thick ice-dammed silty sands of the Odranian glaciation. The Ferdynandów 2011 drilling confirmed the stratigraphic position of the Ferdynandovian interglacial, assigned to a period between the Sanian 1 and 2 glaciations (Pidek et al. 2015).

Description of sediment:

Depth (m)	Lithology
32.10–34.10	grey fine-grained sand with admixture of silty sand interbedded with silt and clay
34.10–34.76	dark brown laminated organic silt
34.76–37.60	dark brown-grey silt
37.60–37.80	strongly compressed peat
37.80–38.00	grey-black shaly silt
38.00–38.20	dark grey silt laminated with brown strongly compressed peat
38.20–38.90	olive-grey gyttja
38.90–39.20	dark grey shale
39.20–39.45	dark grey silt
39.45–39.65	dark grey silt with pale intercalations
39.65–39.77	grey silt with pale precipitates of calcium carbonate
39.20–39.77	dark grey silt with precipitates of calcium carbonate at basal part
39.77–40.55	olive-grey strongly compressed gyttja
40.55–41.00	olive strongly compressed shale
41.75–41.00	olive, hard and brittle shaly gyttja
43.30–41.75	grey, hard and brittle shaly gyttja
43.30–44.00	olive slightly clayed gyttja
44.00–44.35	brown-black slightly clayey silt with pale laminas
44.00–44.90	navy blue-black silt
44.90–47.15	grey silt laminated with organic matter
47.15–47.50	blue-grey laminated clayey silt
47.50–47.90	blue-grey fine-grained sand

METHODS

From the Ferdynandów profile (depth interval 34.15–47.95 m) 99 samples were analysed. Down to 36.40 m depth they correlate with samples examined palynologically by Pidek (2015). The samples (120–150 cm^3 sediment each) were macerated with 10% KOH, boiled to pulp, and wet-sieved on a ø 0.2 mm sieve. Material remaining on the sieve was sorted under a stereoscopic microscope. Conservation of plant remains was done with a standard 1:1:1 mixture of alcohol, water, and glycerin, with thymol added. Fragments of plants were then dried with 50% ethyl alcohol. Macrofossils were identified with the use of plant keys, atlases (Berggren 1969, Cappers et al. 2006, Kats et al. 1965, Velichkevich & Zastawniak 2006, 2008), other scientific descriptions and publications, as well as the reference collection of modern seeds, fruits, and wood, and a collection of fossil floras housed in the Palaeobotanical Museum of the W. Szafer Institute of Botany, Polish Academy of Sciences, Cracow. Qualitative and quantitative results were presented in diagrams plotted with POLPAL software (Nalepka & Walanus 2003).

STRATIGRAPHY OF MACROSCOPIC PLANT REMAINS

In the diagram of macroscopic plant remains from the Ferdynandów 2011 profile, particular taxa were assigned to habitat groups in order of appearance. Local macrofossil assemblage zones (L MAZs) were distinguished, numbered from base to top, and labelled from Fe-1 to Fe-11 (Fig. 2; see also Fig. 3).

The division was based on the occurrence of the one or more most abundant characteristic or diagnostic taxa in the zone. Zone boundaries were determined on the basis of the appearance, disappearance, strong increase, or strong decrease in the number of taxa having a significant quantitative or indicative value (Table 1).

DEVELOPMENT OF LOCAL VEGETATION AGAINST CLIMATE CHANGES

The results of plant macroremains analysis correspond to the record of all climatostratigraphic units distinguished by Pidek (2015), namely the Ferdynandovian interglacial and the late Sanian 1 and early Sanian 2 glaciations. The units were correlated with Marine Isotope Stages (MIS).

Late Sanian 1 (MIS 16)

In Ferdynandów, the beginning of accumulation of lacustrine sediments, falling within the late Sanian 1 glaciation and recorded in the **Fe-1–Fe-2 L MAZs**, is typified by low frequency of diaspores, similar to the low content of sporomorphs in the pollen spectra (Fig. 2) of the corresponding Fe-1 L PAZ (Pidek 2015). Only single remains of taxa characteristic of boreal climate, such as *Betula nana*, *Selaginella selaginoides* (Fig. 4: 1,2), *Potamogeton vaginatus*, and the heliophilous *Rorippa palustris*, were observed. Their presence indicates conditions of open landscape and cool climate. The surroundings of the basin supported the development of plant communities in which peat vegetation, represented by remains of *Carex* sp., *Menyanthes trifoliata*, *Comarum palustre*, *Viola palustris*, and numerous stems of brown mosses, was accompanied by *Betula nana* and *B. humilis*, typical of dwarf shrub tundra. Macroremains recorded in the **Fe-2 L MAZ** also evidence the local presence of trees, mainly birch, as documented by macroscopic remains (fruits and fruit scales) of *Betula* sect. *Albae* and by

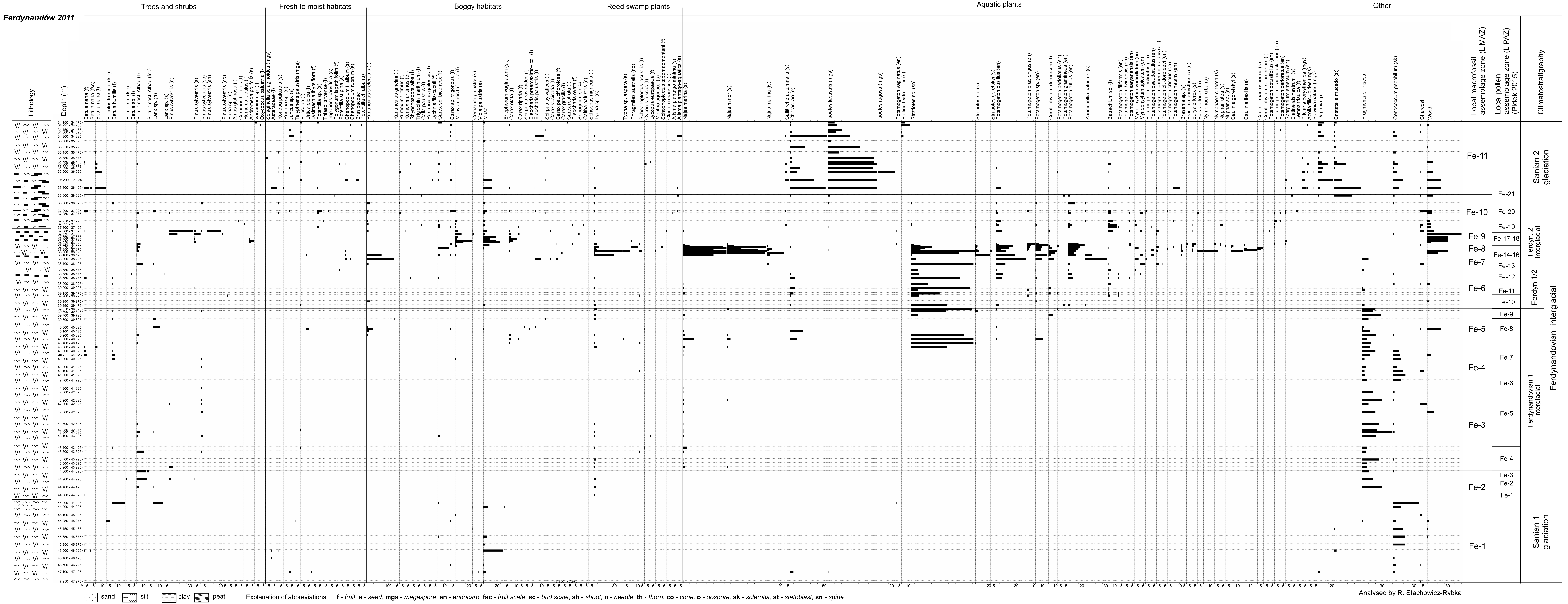

Fig. 2. Diagram plotted for plant macrofossils from the Ferdynandów 2011 profile

Ferdynandów B

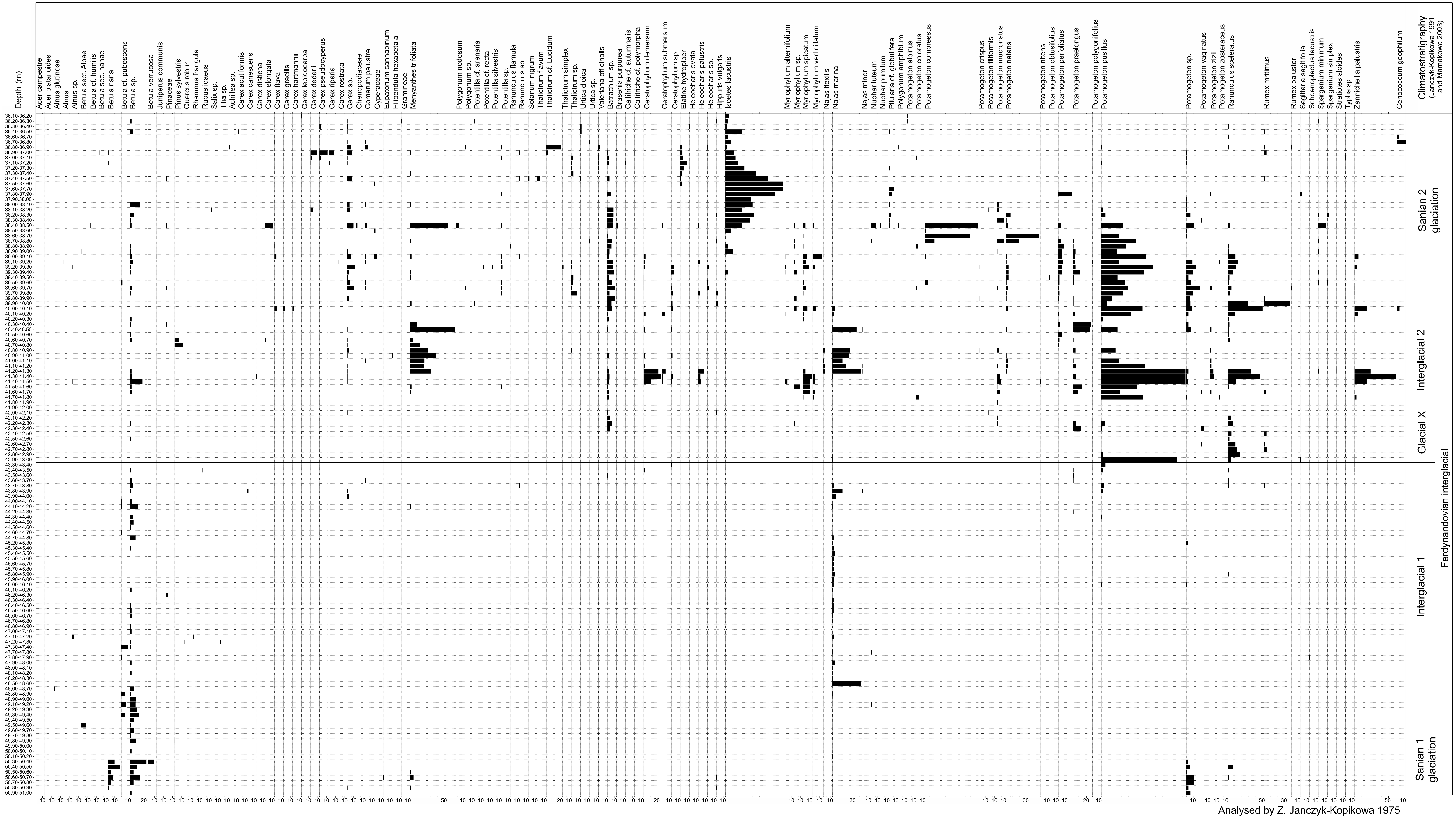

Fig. 3. Diagram plotted for plant macrofossils from the Ferdynandów B profile (Janczyk-Kopikowa 1975)

high proportions of *Betula* undiff pollen. Seeds and needles of *Pinus sylvestris* and *Larix* sp. confirm the at least occasional appearance of pine and larch in the communities. Another component of initial forests was most likely poplar, *Populus tremula*. Several catkin scales were also identified in sediment. Subsequent samples still provide a record of a vegetation succession typical of tundra communities. The close of the late glacial was still marked by the

Table 1. Description of Local Macrofossil Assemblage Zones in profile Ferdynandów 2011

Local macrofossil assemblage zones L MAZ	Depth (m)	Description of zone
Fe-1 L MAZ	47.975–44.900 11 samples	Trees and shrubs include nutlets and scales of *Betula nana* and scales of *Populus tremula*. Terrestrial herbaceous vegetation represented by abundant megaspores of *Selaginella selaginoides*, *Rorippa palustris*, *Thelyptheris palustris*, *Lysimachia thyrsiflora*, *Juncus* sp., and Asteraceae. Among peat plants, fruits of *Carex* sp. div. trigonous and *Carex* sp. div. biconvex, single fruits of *Menyanthes trifoliata*, *Comarum palustre*, and *Viola palustris*, and numerous stems of brown mosses. Remains of swamp plants not recorded. Aquatic vegetation comprises infrequent fruits of *Najas marina*, megaspores of *Isoëtes lacustris*, seeds of *Callitriche autumnalis*, and oospores of Characeae. Several fragments of charcoal and wood, abundant sclerotia of *Cenococcum geophilum*, statoblasts of *Cristatella mucedo*, ephippia of *Daphnia*, and fish skeleton fragments. Upper boundary of zone marked by an increase in the frequency of remains of trees and shrubs
Fe-2 L MAZ	44.825–44.000 5 samples	Numerous remains of trees and shrubs, including nutlets of *Betula nana* and *B. humilis*, nutlets and scales of *Betula* sect. *Albae*, needles of *Larix* sp., and seeds and needles of *Pinus sylvestris*. Terrestrial herbaceous vegetation represented by occasionally recorded megaspores of *Selaginella selaginoides* and fruits of *Ranunculus sceleratus* and *Juncus* sp. Remains of peat plants (e.g. *Carex* sp. div. biconvex) in minor amounts. Among swamp and aquatic vegetation, single remains of *Typha* sp. and *Potamogeton vaginatus*. Sclerotia of *Cenococcum geophilum* and fragments of fish skeletons. Upper boundary of zone marked by the beginning of the constant presence of *Najas marina* in sediment and a decrease in the frequency of remains of trees and shrubs
Fe-3 L MAZ	43.925–41.900 14 samples	Macroremains of trees and shrubs, such as nutlets of *Betula* sect. *Albae* and *B. humilis*, needles of *Larix* sp., and needles and bud scales of *Pinus sylvestris*. Among terrestrial herbaceous vegetation, fruits of *Urtica dioica* and Poaceae. Peat plants represented by single specimens of *Carex* sp. div. biconvex, and swamp plants by seeds of *Typha* sp. and fruits of *Schoenoplectus lacustris*, *Cyperus fuscus*, *Lycopus europaeus*, and *Phragmites australis.* Among aquatic vegetation, remains of *Najas marina*, recorded constantly throughout the zone, accompanied by single remains of *Najas minor* and, in basal part of zone, megaspores of *Salvinia natans.* Fragments of fish skeletons clearly dominant. Sclerotia of *Cenococcum geophilum* and fragments of charcoal and wood also present. Upper boundary of zone marked by a decrease in the amounts of plant macroremains in all ecological groups
Fe-4 L MAZ	41.725–40.600 7 samples	Remains of trees, such as nutlets of *Betula* sect. *Albae* and *B. humilis*, and bud scales of *Pinus sylvestris* and *B. nana*, in top part of zone. No macroremains of terrestrial herbaceous plants recorded. Peat vegetation represented by only single fruits of *Menyanthes trifoliata.* Among swamp vegetation, fruits of *Schoenoplectus lacustris* and *Phragmites australis*. Among aquatic plants, minor amounts of *Najas marina* fruits. As in previous zone, fragments of fish skeletons and sclerotia of *Cenococcum geophilum* dominant. Fragments of charcoal and wood also present. Upper boundary of zone marked by an increase in the amounts of diaspores, particularly of aquatic plants, and a decrease in the content of *Cenococcum geophilum*
Fe-5 L MAZ	40.525–39.550 11 samples	Zone typified by high frequency of boreal elements. Remains of trees and shrubs include nutlets of *Betula humilis* and *Betula* sect. *Albae*, nutlets and leaves of *B. nana*, needles of *Larix* sp., and bud scales of *Pinus sylvestris*. Terrestrial herbaceous vegetation represented by fruits of *Ranunculus sceleratus* and *R. gmelini*. Frequency of peat plants strongly increased versus preceding zones. Remains of *Carex* sp. div. biconvex, *Carex* sp. div. trigonous, *C. elata*, *C. riparia*, *Eleocharis praemaximoviczii*, *E. palustris*, *Scirpus atroviroides*, and *S. sylvaticus*, and stems of brown mosses. Among swamp vegetation, numerous remains of *Typha* sp. and *Typha* sp.1, and single remains of *Schoenoplectus lacustris* and *Cyperus fuscus*. Aquatic plants reach greatest abundance in this zone; their most frequent remains include spines and seeds of *Stratiotes* sp., seeds of *Najas marina* and *N. minor*, oospores of Characeae, and endocarps of *Potamogeton praelongus*, *P. pusillus*, *P. perfoliatus*, and *Potamogeton* sp. Fruits of *Ceratophyllum demersum* also numerous. Abundant fragments of fish skeletons, single sclerotia of *Cenococcum geophilum*, and fragments of charcoal and wood still recorded. Upper boundary of zone marked by a strong decrease in the amounts of fish skeleton fragments and an increase in the frequency of aquatic plants

Table 1. Continued

Local macrofossil assemblage zones L MAZ	Depth (m)	Description of zone
Fe-6 L MAZ	39.475–38.550 10 samples	Among trees and shrubs, nutlets of *Betula* sect. *Albae*, *B. nana* and *B. humilis*, and seeds of *Pinus sylvestris*, *Picea* sp. and *Larix* sp. Terrestrial herbaceous vegetation represented by fruits of *Potentilla supina* and Poaceae, and remains of *Ranunculus sceleratus* and *Rhynchospora alba*, both typical for habitats of higher humidity. Remains of peat plants less frequent than in previous zone and include fruits of *Carex* sp. div. biconvex and stems of brown mosses. Flora of swamp environments not very diverse, comprising seeds of *Typha* sp. and *Schoenoplectus lacustris*. Aquatic vegetation displays highest abundance and diversity in zone; frequent remains still include spines and seeds of *Stratiotes* sp., fruits of *Najas marina* and *Ceratophyllum demersum*, oospores of Characeae, and endocarps of *Potamogeton praelongus*, *P. pusillus*, *P. perfoliatus*, and *Potamogeton* sp., accompanied by fruits of *Batrachium* sp. and *Zannichellia palustris* and endocarps of *Potamogeton gramineus*, *P. rutilus*, *P. filiformis*, *P. dvinensis*, and *P. saryanensis*. In top part of zone, endocarps of *Myriophyllum spicatum* and *M. verticillatum* also present. Upper boundary of zone marked by an increase in the amounts of diaspores of terrestrial herbaceous and aquatic plants
Fe-7 L MAZ	38.425–38.100 3 samples	Infrequent remains of trees, such as nutlets of *Betula* sect. *Albae* and needles of *Larix* sp. Nutlets of *Alnus glutinosa* observed for the first time in the profile. Among terrestrial vegetation, remains of *Urtica dioica*, *Juncus* sp., *Chenopodium* t. *album*, and *Ch. rubrum*. Fruits of *Ranunculus sceleratus* exceptionally numerous. Again, high amounts of peat plants such as *Carex* sp. div. biconvex, *Carex* sp. div. trigonous, *C. vesicaria*, *C. paucifloroides*, *Menyanthes trifoliata*, and *Eleocharis palustris*. Composition of swamp vegetation diminished; only *Typha* sp. identified at top of zone. Aquatic plants most diversified, represented by frequent spines and seeds of *Stratiotes* sp., *Najas marina*, *Zannichellia palustris*, and *Ceratophyllum demersum*, endocarps of *Potamogeton praelongus*, *P. pusillus*, *P. rutilus*, *P. pseudorutilus*, *P. perfoliatus*, *P. pectinatus*, *P. panorminatoides*, *P.* cf. *dorofeevi*, *Potamogeton* sp., *Myriophyllum spicatum*, and *M. verticillatum*, and seeds of *Brasenia* sp. Fish skeleton fragments and charcoal abundant. Upper boundary of zone marked by the highest frequency of diaspores of aquatic plants
Fe-8 L MAZ	38.075–37.825 9 samples	Among trees and shrubs, only nutlets of *Betula* sect. *Albae*. Terrestrial herbaceous plants represented by single diaspores of *Chenopodium* t. *album*, *Potentilla* sp., and *Ranunculus sceleratus*. Remains of peat vegetation still include fruits of *Carex* sp. div. biconvex, *Carex* sp. div. trigonous, *C. paucifloroides*, and *Menyanthes trifoliata*; additionally, *Carex elata*, *C. gracilis*, *C. rostrata*, and *Eleocharis ovata*, and stems of brown mosses. Among swamp plants, *Typha* sp. still present and accompanied by *Typha* sp.1, *Schoenoplectus lacustris*, *S. tabernaemontani*, and *Phragmites australis.* Aquatic plants dominant in the zone. Fruits of *Najas marina* and *N. minor* as well as spines and seeds of *Stratiotes* sp. and *S. goretskyi* exceptionally abundant. Also numerous are endocarps of Potamogetonaceae species such as *Potamogeton praelongus*, *P. pusillus*, *P. rutilus*, *P. pseudorutilus*, *P. perfoliatus*, *P. pectinatus*, *P. panorminatoides*, and *Potamogeton* sp., megaspores of *Isöetes lacustris*, and oospores of Characeae. *Potamogeton saryanensis*, *P. praemaackianus*, *P. natans*, *P. crispus*, and *P. vaginatus* appear at top of zone. Taxa such as *Ceratophyllum demersum*, *Batrachium* sp., *Myriophyllum verticillatum*, and *Brasenia* sp. also identified. Some specimens observed for the first time in the profile: for example, seeds of *Brasenia borysthenica*, seed fragments and spines of *Euryale ferox*, and remains of *Nymphaea alba*, *N. cinerea*, *Nuphar lutea*, *Nuphar* sp., *Caulinia flexilis*, *C. goretskyi*, *C. macrosperma*, and *Sparganium emersum.* Upper boundary of zone marked by a strong decrease in the frequency of aquatic plant remains
Fe-9 L MAZ	37.800–37.500 6 samples	Amounts of plant remains decrease in nearly all ecological groups, particularly aquatic plants. Proportion of trees and shrubs slightly increases, particularly at top of zone, where fruits of *Betula nana* and *B. humilis*, seeds, needles, cones, and bud scales of *Pinus sylvestris*, seeds of *Andromeda polifolia*, and leaves of *Vaccinum* sp. appear. Terrestrial herbaceous plant remains include fruits of *Urtica dioica*, *Ranunculus sceleratus*, and *Triglochin maritimum*, and perianths of *Rumex maritimus.* Strongly increased frequency of peat plants, represented by remains of *Menyanthes trifoliata*, *Comarum palustre*, *Carex elata*, *C. riparia*, and *C. vesicaria*, stems of brown mosses and remains of *Sphagnum* sp. Swamp vegetation includes *Typha* sp., *Phragmites australis* and *Cladium mariscus*. Aquatic plants most diminished versus previous zone. Taxa such as *Najas marina*, *Potamogeton vaginatus*, *P. pusillus*, *P. saryanensis*, *P. panorminatoides*, and *P. obtusifolius*, mainly at top of zone. *Callitriche autumnalis*, *Ceratophyllum demersum*, *C. submersum*, and *Sparganium emersum* also present. Abundant fragments of charcoal and wood, and single sclerotia of *Cenococcum geophilum* still observed. Upper boundary of zone marked by an increase in the amounts of diaspores of most ecological groups

Table 1. Continued

Local macrofossil assemblage zones L MAZ	Depth (m)	Description of zone
Fe-10 L MAZ	37.425–36.600 8 samples	Increased diversity and frequency of plant remains. Nutlets and leaves of *Betula nana*, nutlets of *Betula* sect. *Albae*, *B. humilis* and *Betula* sp., needles of *Larix* sp., seeds and bud scales of *Pinus sylvestris*, and fruits of *Carpinus betulus* and *Humulus lupulus* still recorded. Terrestrial herbaceous vegetation represented by specimens of *Rorippa palustris*, *Juncus* sp., *Potentilla* sp., *Thlaspi arvense*, *Polygonum lapathifolium*, and *Impatiens parviflora*. Numerous fruits of *Ranunculus sceleratus* and occasional remains of *R. gailensis*, *Rumex maritimus* and *Calla palustris*. Peat plants include *Carex* sp. div. biconvex, *Carex* sp. div. trigonous, *C. elata*, *C. rostrata*, *Menyanthes trifoliata*, *Scirpus atroviroides*, *S. sylvaticus*, *Eleocharis palustris*, *E. ovata*, *Caltha palustris*, and stems of brown mosses. Among swamp vegetation, seeds of *Typha* sp., *Alisma plantago-aquatica*, and *A. plantago-minima*. Aquatic plants abundant and represented by fruits of *Najas marina*, spines and seeds of *Stratiotes* sp., and frequent endocarps of Potamogetonaceae species such as *Potamogeton praelongus*, *P. pusillus*, *P. rutilus*, *P. pseudorutilus*, *P. gramineus*, *P. filiformis*, *P. saryanensis*, *P. pectinatus*, *P. crispus*, *P. natans*, *P. praemaackianus*, *P. perforatus*, and *Potamogeton* sp., accompanied by seeds of *Callitriche autumnalis*, numerous fruits of *Batrachium* sp., single megaspores of *Isöetes lacustris*, and oospores of Characeae. Remains of *Ceratophyllum demersum*, *Batrachium* sp., *Myriophyllum verticillatum*, *M. spicatum*, seed fragments and spines of *Euryale ferox*, as well as remains of *Nuphar lutea* and *Sparganium emersum*. *Elatine alsinastrum* and *Lemna trisulca* also appear. Upper boundary of zone marked by a strong increase in the frequency of *Isöetes lacustris* megaspores
Fe-11 L MAZ	36.425–34.150 15 samples	Exceptionally abundant megaspores of *Isöetes lacustris*. Remains of trees and shrubs still comprise nutlets, seed scales and leaves of *Betula nana*, nutlets of *Betula* sect. *Albae*, *B. humilis*, and *Andromeda polifolia*, and leaves of *Oxycoccus palustris* and *Vaccinum* sp. Among terrestrial herbaceous vegetation, frequent megaspores of *Selaginella selaginoides* and fruits of *Rorippa palustris*, *Rorippa* sp., *Juncus* sp., Poaceae, Asteraceae, *Potentilla supina*, *P. alba*, *Potentilla* sp., and *Chenopodium* t. *album*. Wetter habitats inhabited by *Ranunculus sceleratus*, *Rumex maritimus*, *Rhynchospora alba*, and *Lychnis flos-cuculi*. Peat plants represented by *Carex* sp. div. trigonous, *Carex* sp. div. biconvex, *C. elata*, *C. rostrata*, *Eleocharis palustris*, *Scirpus atroviroides*, *S. sylvaticus*, *Schoenus nigricans*, and numerous stems of brown mosses. Among swamp vegetation, seeds of *Typha* sp., *Cyperus fuscus*, *Lycopus europaeus*, and *Alisma plantago-aquatica*. Very numerous remains of aquatic plants, dominated by megaspores of *Isoëtes lacustris* and *I. rugosa* and oospores of Characeae, accompanied by seeds of *Callitriche autumnalis*, *Elatine hydropiper*, *E. alsinastrum*, *Potamogeton praelongus*, *P. pusillus*, *P. perfoliatus*, *P. saryanensis*, *P. pectinatus*, *P. pseudorutilus*, *P. panormitanoides*, *P. natans*, *P. perforatus*, and *Potamogeton* sp. Fruits of *Batrachium*, seeds of *Nuphar* sp., endocarps of *Sparganium emersum*, as well as megaspores of *Pilularia borysthenica*, *Azolla filiculoides*, and *Salvinia natans* also present. Also numerous statoblasts of *Cristatella mucedo*, ephippia of *Dapnia*, fragments of charcoal and wood, and sclerotia of *Cenococcum geophilum*. Upper boundary of zone delimited by top organic sediments

presence of *Betula humilis* and *B. nana*. The lack of dense plant cover triggered solifluction processes, as indicated by the numerous sclerotia of *Cenococcum geophilum*. The composition of aquatic vegetation also suggests its initial stage of development. Fruits of *Potamogeton vaginatus* and *Potamogeton natans*, presently found within depauperate aquatic communities (Matuszkiewicz 2008), were determined. Taxa such as *Callitriche autumnalis*, *Najas marina*, and *Isoëtes lacustris* (Fig. 4: 5,6) were also recorded, though infrequently. The occurrence of bryozoans (*Cristatella mucedo*) and daphnias (*Daphnia*) confirms the presence of water in the sedimentary basin.

Ferdynandovian 1 (MIS 15)

Trees and shrubs grew in the area, as indicated by macroremains of *Betula* sect. *Albae* and *B. humilis*, identified in the **Fe-3 L MAZ**. Needles and bud scales of *Pinus sylvestris* and *Larix* sp. were frequent as well. The pollen composition recorded in the diagrams for the Fe-2–Fe-3 L PAZ (Pidek 2015) indicates the beginning of forest formation. Remains of aquatic plants were not numerous, but the ecological requirements of the determined taxa suggest warm climate. The continuous though infrequent presence of seeds of *Najas marina* and minor amounts of remains of *Najas minor* was observed. These species are most commonly found in highly insolated, sheltered spots (Matuszkiewicz 2008, Tomaszewicz 1979) and are the most thermophilous taxa identified within Ferdynandovian 1. Following Aalbersberg & Litt (1998), *Najas minor* serves as an indicator of T_{mjul} +18°C, and *Najas marina* an indicator of T_{mjul} +15°C. Similar temperature and trophic conditions are preferred by the floating fern *Salvinia natans*, recorded at the basal part of the zone and typical for warm areas of suboceanic and moderate climate as well as tropical climate (Holm et al. 1979). The species inhabits mainly eutrophic waters of large or shallow and slow-flowing rivers, oxbow lakes, ditches, and channels (Casper & Krausch 1980). For the development of its megaspores it requires winter-month temperatures not falling below 0°C (Święta-Musznicka et al. 2011).

Further development of the Ferdynandów basin is recorded in the **Fe-4 L MAZ**, where the amounts of macroremains are the lowest for the entire profile. Apart from nutlets of *Betula* sect. *Albae* and *B. humilis*, as well as remains of *Pinus sylvestris* and *B. nana*, observed at the top of the zone, only single fruits of *Menyanthes trifoliata*, *Schoenoplectus lacustris*, and *Phragmites australis*, likely to have originated from lakeside peat bogs and the swamp zone, were identified. *Najas marina* was found only occasionally.

The warming of climate at the beginning of the Ferdynandovian 1 interglacial and the resulting development of organisms in the basin should be reflected in a great increase in the content of organic matter and plant remains in the sediment. However, throughout nearly the entire optimum, the frequency of diaspores is very low, though fragments of fish skeletons (fishbones, vertebrae and scale fragments) appear abundantly. It is very likely that in this period the lake was vast and deep, so that only sparse fragments of plants reached its central part from the lakeshore and shallow swamp zone. The corresponding zone of the Ferdynandów B profile includes very numerous planktonic diatoms, characteristic for deep basins (Przybyłowska-Lange 1990). Plant macroremains analysis of the above-mentioned profile (Janczyk-Kopikowa 1975) also revealed that apart from minor amounts of fruits of birches and naiads the sediment was nearly devoid of diaspores.

Such a feature of the lacustrine succession in Ferdynandovian 1 was also recorded in the Łuków 3A profile (Stachowicz-Rybka 2015). The results of pollen analysis suggest that the climatic conditions of this period were similar to Augustovian 1 of the Czarnucha profile (Stachowicz-Rybka 2011), where a similar pattern of basin evolution and aquatic vegetation development was observed.

Another stage in the formation of the Ferdynandów basin is recorded in the basal part of the **Fe-5 L MAZ**. In this period the lake became shallower and the role of swamp and aquatic vegetation as well as macrophyte flora increased. Numerous endocarps of *Potamogeton* species, such as *P. praelongus*, *P. pusillus*, *P. perfoliatus*, and *Potamogeton* sp., as well as *Najas marina* and *N. minor*, suggesting water eutrophication, were identified. The functioning of a shallow eutrophic basin was also recorded in the pollen diagram for the Fe-8 L PAZ, marked by an increase in the frequency of *Pediastrum* green algae, particularly *P. boryanum* var. *boryanum* (Pidek 2015). The swamp zone was inhabited by *Typha* sp., *Lycopus europaeus* and *Schoenoplectus lacustris*, while shallow coves with muddy bottoms were colonised by *Stratiotes* sp., identified from abundant though not very specific spines. In the younger part of the zone, the terrestrial flora dominated by birch and larch, observed in the Fe-8–Fe-9 L PAZ (Pidek 2015), was accompanied by *Carex gracilis*, *C. elata*, *C. paucifloroides*, *Carex* sp. div. trigonous, and brown mosses, which appeared on lakeshores and formed low peat bogs and tall sedge swamps. Fens and most eutrophic habitats were covered by *Ranunculus sceleratus* and *Urtica* sp. and also likely supported *Scirpus atroviroides* (Fig. 5: 16,17) and *Eleocharis praemaximoviczii*, extinct species often coexisting in interglacial floras since the Late Pliocene. In Poland they are also known from the Ferdynandovian flora of Łuków 3A (Stachowicz-Rybka 2015a), Augustovian floras of Czarnucha and Żarnowo (Stachowicz-Rybka 2011), and the Mazovian flora of Konieczki (Nita 1999).

The end of Ferdynandovian 1 was characterised by the reappearance of taxa of cool boreal climate, such as *Betula humilis* and *B. nana*, growing in dwarf shrub tundra; the frequency of *Larix* sp. rose as well. Such communities most likely also included *Ranunculus gmelini*, an arctic-boreal species observed in tundra- and woody tundra-type interstadial floras and

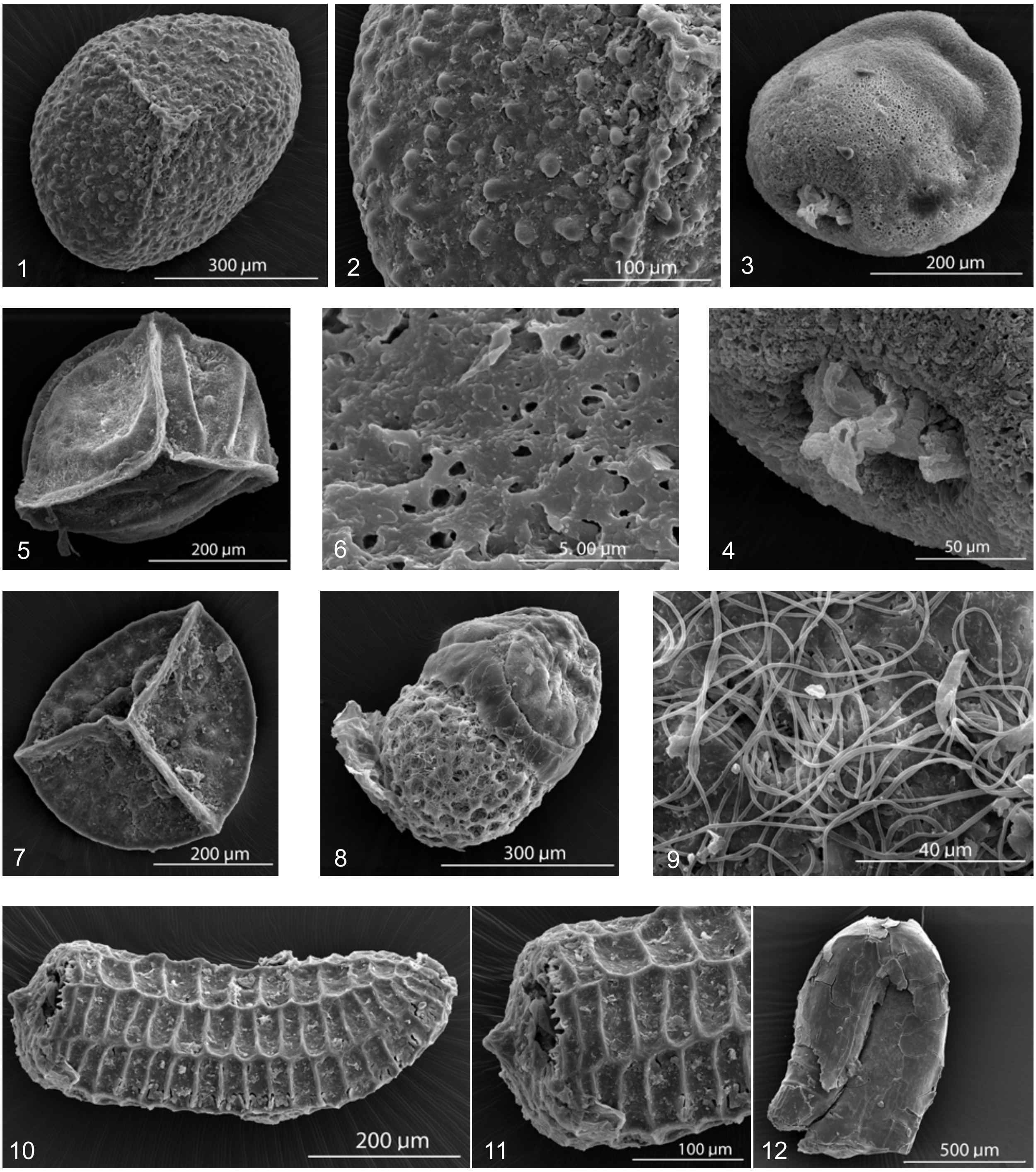

Fig. 4. **1**. *Selaginella selaginoides* L., megaspore; **2**. *Selaginella selaginoides* L., megaspore, details of surface; **3**. *Pilularia borysthenica* Wieliczk., megaspore; **4**. *Pilularia borysthenica* Wieliczk., megaspore, details of surface; **5**. *Isoëtes lacustris* L., megaspore; **6**. *Isoëtes lacustris* L., megaspore, details of surface; **7**. *Isoëtes rugosa* L., megaspore; **8**. *Azolla filiculoides* Lam., megaspore; **9**. *Azolla filiculoides* Lam., megaspore, details of surface; **10**. *Elatine alsinastrum* L., seed; **11**. *Elatine alsinastrum* L., seed, details of surface; **12**. *Alisma plantago-minima* Wieliczk.

usually overgrowing boggy areas and shores of rivers and lakes. In Eastern Europe it was identified in the Middle and Upper Pleistocene at Minichi, Krukenichi, Panfilovo (Velichkievich 1982), and Verkhov'e-1 (Velichkievich 1977). It is also known from Vistulian sites at Ściejowice, Brzeziny, and Białka Tatrzańska (Velichkievich & Mamakowa 1999).

The terminocratic phase of the interglacial, represented by the Fe-9 L PAZ (Pidek 2015), is marked by an increase in the content of *Pinus*, *Betula*, and NAP, the appearance of *Larix*, and the presence of *Betula nana* t. in the pollen spectra, which is evidence of the disappearance of thermophilous trees and succession processes in forest communities, resulting from climate

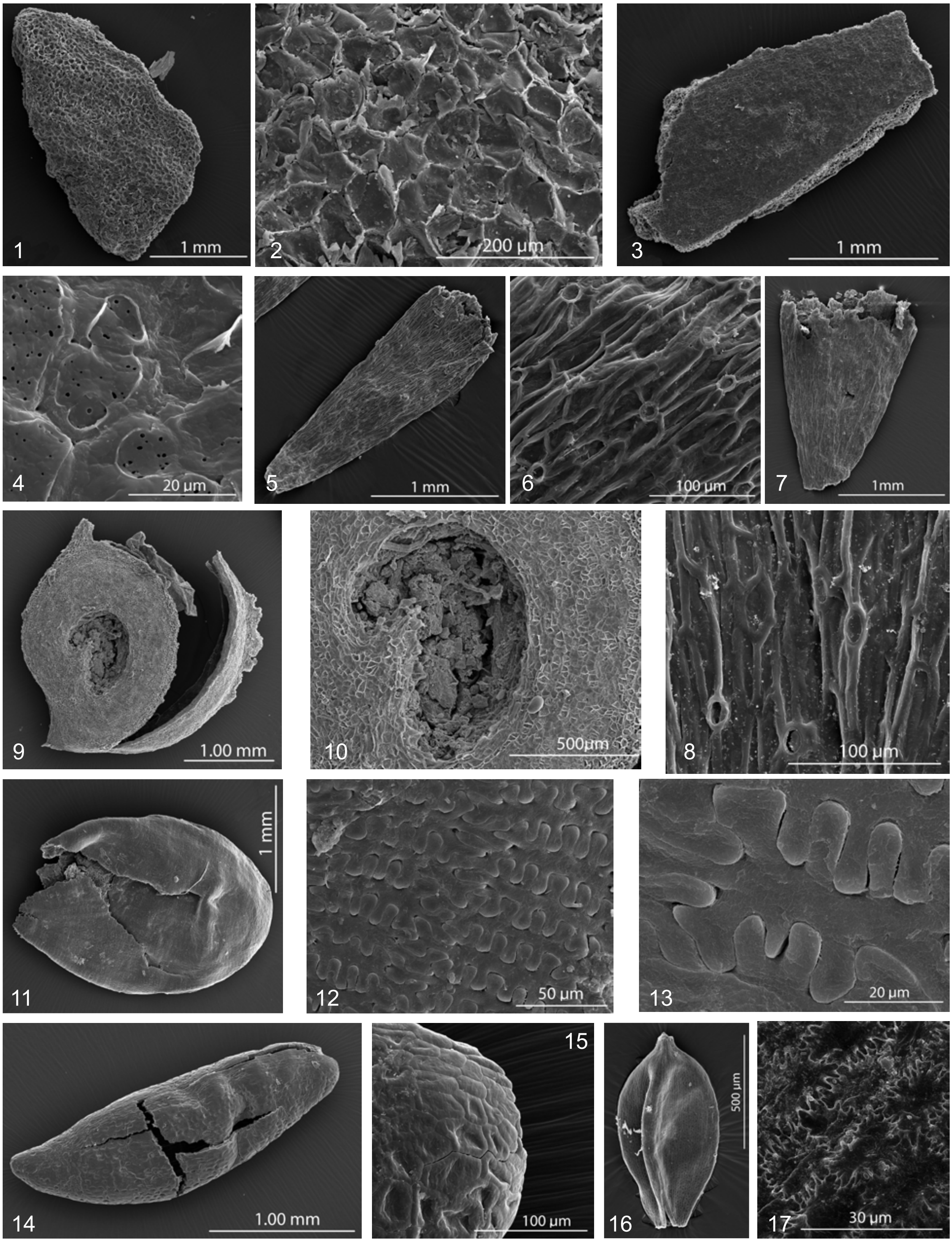

Fig. 5. **1**. *Euryale ferox* Salisb., fragment of seed from the Ferdynandów 2011 profile; **2**. *Euryale ferox* Salisb., details of surface of seed; **3**. *Euryale ferox* Salisb., fragment of present-day seed; **4**. *Euryale ferox* Salisb., details of surface of present-day seed; **5.** *Euryale ferox* Salisb., spine from Ferdynandów 2011 profile; **6**. *Euryale ferox* Salisb., details of surface of spine; **7**. *Euryale ferox* Salisb., present-day spine; **8**. *Euryale ferox* Salisb., details of surface of present-day spine; **9**. *Potamogeton perforatus* Wieliczk., endocarp; **10**. *Potamogeton perforatus* Wieliczk., details of surface; **11**. *Nymphaea cinerea* Wieliczk., seed; **12**, **13**. *Nymphaea cinerea* Wieliczk., details of surface; 14. *Caulinia goretskyi* Wieliczk., fruit; 15. *Caulinia goretskyi* Wieliczk., details of surface; **16**. *Scirpus atroviroides* Dorof., fruit; **17**. *Scirpus atroviroides* Dorof., details of surface

cooling. However, this part of the diagram also displays features of short-term warming, demonstrated by increasing amounts of *Quercus* and *Ulmus*, probably indicating the episodic spread of communities including these trees, which afterwards disappeared due to cooling. The top part of the Fe-5 L MAZ, similarly to the corresponding pollen assemblage zone documenting an interstadial fluctuation, and to the Łuków 3A profile Stachowicz-Rybka 2015a), does not contain taxa suggesting an obvious improvement in climate but shows an increase in the number of specimens, particularly spines and seed fragments, of *Stratiotes* sp. as well as *Najas minor*, *N. marina*, and *Scirpus atroviroides*.

Ferdynandovian 1/2 (MIS 14)

The cool period separating the two interglacial units, referred to as F 1/2, is represented by the **Fe-6 L MAZ** and the basal part of the **Fe-7 L MAZ**. It still includes taxa identified at the cool end of Ferdynandovian 1, such as *Betula nana*, *B. humilis*, and *Larix* sp. Such a composition of trees and shrubs, as well as the appearance of herbaceous plants such as *Ranunculus gmelini*, evidences cool climatic conditions and the important role of patches of dwarf shrub tundra-type vegetation in the landscape of the lake surroundings. Increased eutrophication, reflected in the greater diversity of taxa with higher trophic requirements in all ecological groups, indicates that the basin gradually became shallower and overgrown. In eutrophic habitats of periodically exposed lakeshores, communities with *Ranunculus sceleratus* gained importance. In humid areas with lower trophy there also appeared *Rhynchospora alba*, found mainly in transition bogs and humid depressions of raised bogs. Single fruits of *Schoenoplectus lacustris* and *Typha* sp. may have originated from communities resembling present-day Scirpo-Phragmitetum swamps (Podbielkowski & Tomaszewicz 1982) but not an important component of the landscape in this case. Aquatic plants also included species typical for late glacial periods and their cool climate. *Potamogeton praelongus* and *P. gramineus*, requiring a minimum July temperature of +8°C (Gaillard 1984, Kolstrup 1980), as well as *Potamogeton pusillus* and *P. rutilus*, were identified.

Cool, clear, calcium carbonate-rich lake water was inhabited by Characeae, which indicates the presence of stonewort meadows, typical for waters up to 10 m in depth (Hannon & Gaillard 1997). Such a water level, as well as pH of ca 7.8, is also supported by the occurrence of *Ceratophyllum demersum* (Gaillard & Birks 2007). *Zannichellia palustris*, known to prefer habitats of variable water level and high salt content, appeared as well.

The first sample of the Fe-7 L MAZ contained endocarps of two extinct species, *Potamogeton panormitanoides* and *P.* cf. *dorofeevii.*

Ferdynandovian 2 (MIS 13)

The younger interglacial period, Ferdynandovian 2, is documented in sediments of the Fe-7 L MAZ, Fe-8 L MAZ, and Fe-9 L MAZ. Both plant macroremains and palynological analyses (Pidek 2015) point to this unit as the warmest one in the Ferdynandovian succession. In contrast to Ferdynandovian 1, the tree vegetation of this period included high numbers of *Carpinus* pollen grains. The **Fe-8 L MAZ** bears a record of the final phase of overgrowing of the eutrophic basin, additionally affected by advantageous climatic conditions and therefore marked by remarkably intensive development of aquatic, swamp, and peat vegetation. Sediment of this period is exceptionally abundant in diaspores, displaying the greatest taxonomic diversity. Shallow warm waters were inhabited by *Brasenia borysthenica*, a component of the *Brasenia* complex, characteristic for the optimal climatic phases of the Belovezhian and Mogilevian interglacials of Belarus and analogous interglacials of other European countries (Velichkevich & Zastawniak 2008). Remains of *Euryale ferox*, represented by large fragments of thick-walled seeds, with easily recognised, characteristic pitted surface sculpture (Fig. 5: 1,2), and several spines with a sculpture visible in SEM images (Fig. 5: 5,6), were also identified. Seed fragments and spines from the Ferdynandów 2011 profile were compared with seeds and spines found at the Czarnucha and Żarnowo sites (Stachowicz-Rybka 2011) and at Stanowice (Sobolewska 1970), as well as with modern specimens of *Euryale ferox* (Fig. 5: 3,4 and Fig. 5: 7,8). All *Euryale* spines from modern seeds and from the Czarnucha and Ferdynandów 2011 profiles showed the same shape, size and sculpture. In the Ferdynandovian flora described for the nearby Łuków 3A site (Stachowicz-Rybka 2015a), the presence of *Euryale* sp. was uncertain, as its seed fragments were poorly preserved and spines were not observed at all. The modern *Euryale ferox* may be found in tropical and subtropical zones of Southeast Asia, where mean July temperatures reach 21°C. In Poland the species is known from sediments of the Mazovian interglacial (Sobolewska 1970, 1977) and the Augustovian interglacial (Stachowicz-Rybka 2011). In the Pleistocene of Europe, fossil remains of *Euryale ferox* have previously been described for the Mazovian (Holsteinian) interglacial in Germany (Gripp & Beyle 1937), the Lower Pleistocene in south-eastern England (Aalto et al. 1996), and the Tegelen in the Netherlands (Reid & Reid 1907, 1915), where they were classified as *E. europea* and *E. limburgensis*, and the Likhvinian interglacial in Russia (Sukatscheff 1908).

The composition of aquatic vegetation changed much and became dominated by *Najas marina* (over 450 specimens per sample), preferring highly insolated, sheltered spots in lakes (Matuszkiewicz 2008, Tomaszewicz 1979). The species most likely formed underwater fields with the also abundant *Najas minor*, presently often growing in dense monocultures in highly eutrophic habitats having pH 6.0–9.3 (optimally 6.6–7.2) on muddy or muddy-sandy bottoms at ca 0.5–2 m depth (Wentz & Stuckey 1971). In areas of moderately warm climate, *Najas marina* and *N. minor* occur as characteristic species of the *Potamo-Najadetum marinae* association (Matuszkiewicz 2008). In communities of macrohydrophytes, usually rooted, the dominant *Najas marina* and *N. minor* were most likely accompanied by the extinct *Caulinia macrosperma*, *Caulinia goretskyi* (Fig. 5: 14–15), and *Brasenia borysthenica*, as well as by *Nuphar lutea*, *Ceratophyllum demersum*, *Myriophyllum spicatum*, and *M. verticillatum.* In other communities, the macrophytes also included *Potamogeton praelongus*, *P. pusillus*, *P. rutilus*, *P. perfoliatus*, *P. pectinatus*, *P. natans*, *P. crispus*, *P. vaginatus*, and *Potamogeton* sp., as well as the extinct *P. pseudorutilus*, *P. panorminatoides*, *P. saryanensis*, and *P. praemaackianus*. Those species, known, for example, from Late Pleistocene floras of Belarus (Velichkevich 1975) and Cromerian floras of Germany (Mai 2003), possibly formed communities resembling the modern *Parvopotamo-Zannichellietum* (Matuszkiewicz 2008). Remains of *Nymphaea cinerea* (Fig. 5: 11–13), typical of the Middle Pleistocene (Velichkevich & Zastawniak 2008), and seeds of the extinct *Stratiotes goretskyi*, of stratigraphic significance, were observed as well. The latter was also recorded at the Czarnucha site in Poland (Augustovian interglacial II), as well as at Korchevo (Velichkevich 1982) and Dvorec (Velichkevich 1990) in Belarus.

The **Fe-9 L MAZ** bears a record of the end of the warm Ferdynandovian 2, when the lake-to-peat bog transition entered its final phase. Taxa typical of transition bogs became more abundant and are represented mainly by remains of *Menyanthes trifoliata*, *Comarum palustre*, *Carex elata*, *C. riparia*, and *C. vesicaria*, stems of brown mosses, remains of *Sphagnum* sp., seeds of *Andromeda polifolia*, and leaves of *Vaccinum sp.* Tall sedge communities most likely formed a belt adjacent to the basin shore. The occurrence of *Carex elata*, *C. riparia*, and *C. vesicaria* was also characteristic. Present-day sedge patches may be dominated by one of those species. *Carex elata*, most tolerant of water table fluctuations and to deep water conditions, is often a pioneer species. At initial succession stages it forms single, dispersed, spaced tufts which become larger and denser with time. The water between tufts reaches depth up to 0.5 m and pH 4.5–8.

In the terminocratic phase of Ferdynandovian 2, features of terrestrial vegetation already indicated the incipient cooling, as manifested by the reappearance of nutlets of *Betula nana* and *B. humilis* in sediment as well as by the high content of pollen of *Pinus sylvestris* and *Betula* undiff. in the Fe-17–Fe-18 L PAZ (Pidek 2015). However, aquatic vegetation was still abundant among the thermophilous taxa. The swamp zone and deep waters were inhabited by *Cladium mariscus* and macrophytes such as *Najas marina*, *Ceratophyllum demersum*, *C. submersum*, and *Nuphar* sp. Such an observation is typical for the end of an interglacial, when lake water cools down at a slower rate than the surrounding land, serving as a warm habitat for plant development for a longer time. Nevertheless, the number of diaspores, particularly those of aquatic and swamp plants, generally decreased.

Early Sanian 2 (MIS 12)

The early Sanian 2 glaciation is recorded in the top part of the Fe-9 L MAZ as well as in the Fe-10–Fe-11 L MAZs. The zones comprise sediments of acidic peats and coarse detritus gyttjas developed in a cool, oligotrophic lake. Deterioration of climatic conditions resulted in the reappearance of species typical for tundra landscape, such as *Betula nana*, *Selaginella selaginoides* (Fig. 4: 1,2), and *Rorippa palustris*, in the lake surroundings. However, in the **Fe-10 L MAZ** the remains of *Larix* sp. and *Pinus sylvestris* were accompanied by fruits of taxa with higher temperature requirements, such as *Carpinus betulus* and *Humulus lupulus*, the presence of which should be linked to stadial-interstadial fluctuations. In the Fe-19–Fe-21 L PAZ, representing stadials, the pollen values for taxa associated with tundra and steppe-tundra communities also fluctuated (Pidek 2015). The Fe-10 L MAZ records the disappearance of aquatic vegetation and the arrival of peat plant associations in the area of the palaeolake, indicating terrestrialisation of the basin, no longer filled with open water. In this period of the early Sanian 2 glaciation, the discussed depression was covered with a peat bog including numerous *Carex* sp. div. biconvex, *Carex* sp. div. trigonous, *C. elata*, *C. rostrata*, *Menyanthes trifoliata*, *Scirpus atroviroides*, *S. sylvaricus*, *Eleocharis palustris*, *E. ovata*, and *Caltha palustris.* The upper part of the zone yielded a single seed of *Alisma palntago-minima* (Fig. 4: 12) megaspores of *Isoëtes lacustris*, and oospores of Characeae.

Remains of aquatic plants reappeared abundantly only in the last sediment sample of the zone. They included mainly endocarps of Potamogetonaceae species, such as *Potamogeton praelongus*, *P. pusillus*, *P. rutilus*, *P. pseudorutilus*, *P. gramineus*, *P. filiformis*, *P. saryanensis*, *P. pectinatus*, *P. crispus*, *P. natans*, *P. praemaackianus*, *P. perforatus* (Fig. 5: 9,10), and *Potamogeton* sp., accompanied by seeds of *Callitriche autumnalis*, fruits of *Batrachium* sp., *Ceratophyllum demersum*, *Myriophyllum verticillatum*, and *M. spicatum*, seed fragments and spines of *Euryale ferox*, as well as remains of *Nuphar lutea* and *Sparganium emersum. Elatine alsinastrum* (Fig. 4: 10,11) and *Lemna trisulca* were also identified. Such a taxonomic composition suggests a strong rise in the water level of the peat bog and the reoccurrence of a water basin, initially inhabited by taxa similar to the ones recorded in the Fe-9 L MAZ.

Macroremains found in the **Fe-11 L MAZ** show that the water basin of Ferdynandów was surrounded by rather thin pine-birch forests, as evidenced by seed scales and leaves of *Betula nana* and nutlets of *Betula* sect. *Albae* and *B. humilis* determined in the zone, as well as by the high curve of *Pinus sylvestris* in the Fe-21 L PAZ (Pidek 2015). The waters of the basin were colonised by taxa from an association likely to have resembled the modern *Isoëto-Lobelietum*, with *Isoëtes lacustris* (Fig. 4: 5,6) as a characteristic species. At Ferdynandów its megaspores were very numerous and accompanied by infrequent megaspores of *Isoëtes rugosa* (Fig. 4: 7). Both are sciophytes, presently growing in oligotrophic waterbodies in pine forests and acidophilous mixed coniferous forests. The *Isoëto-Lobelietum* association usually develops in oligo- and mesotrophic lakes with sandy or sandy-rocky bottoms. Patches of *Isoëtes lacustris* cover deeper (ca 2 m deep) parts of lakes. The species serves as an indicator of rather cool and nutrient-poor waters. Presently, *Isoëto-Lobelietum* includes companion species such as *Carex rostrata* and *Eleocharis palustris* (Podbielkowski & Tomaszewicz 1982). The presence of both *Isoëtes lacustris* and numerous oospores of Characeae in the basin suggests a noticeable rise in its water level. These results were confirmed by the spore-pollen spectra for the Fe- 20–Fe-21 L PAZ (Pidek 2015), where spores of *Isoëtes* were recorded abundantly. Megaspores of aquatic ferns such as *Pilularia borysthenica* (Fig. 4: 3,4), an extinct species characteristic for Mogilevian floras in Belarus, as well as *Azolla filiculoides* (Fig. 4: 8,9) and *Salvinia natans*, both found on a large scale in Augustovian floras, were also identified.

Changes in climatic conditions and the proceeding acidification of soils altered the structure of vegetation in the surroundings of the basin. A transition bog began to function. The diversity of local taxa increased, as recorded in the Fe-11 L MAZ. The remains of several sedge species and *Andromeda polifolia*, leaves of *Oxycoccus palustris*, *Rhynchospora alba*, and *Vaccinum* sp., as well as seeds and nodes of *Eriophorum vaginatum* and *Comarum palustre*, were identified. However, the hydrological conditions of the peat bog were still unstable, as indicated by the variable proportions of pine and birch, capable of expanding to the peat bog area, on the one hand, as well as by the appearance of species requiring greater humidity, such as *Oenanthe aquatica*, *Carex* *pseudocyperus*, *Lycopus europaeus*, and *Lysimachia thyrsiflora*, on the other. This pattern suggests a change in hydrogeological conditions and the transition of the Sphagnum bog to a raised bog.

DISCUSSION

The development of local vegetation and the accompanying climatic and environmental changes described for the Ferdynandów 2011 profile correspond closely to its pollen succession proposed by Pidek (2015). Similarly, such a correspondence has been observed for two other sites representing the Ferdynandovian interglacial in the area and subjected to both plant macroremains and palynological analyses, namely Ferdynandów B (Janczyk-Kopikowa 1975, 1981) and Łuków 3A (Pidek 2010, 2013, Pidek & Poska 2013, Stachowicz-Rybka 2015a).

Other sites of this age bearing a record of a complete Ferdynandovian succession, such as Podgórze B1 (Mamakowa 1996) and Zdany (Pidek 2000), were not analysed palaeocarpologically. Analogous climatostratigraphic units distinguished at the sites confirm the wide range of climatic changes proceeding in the F1 and F2 interglacial periods and in the F1/2 cool period. The characteristic succession of local vegetation was common to the Ferdynandów B and Ferdynandów 2011 profiles. The same stages of basin development in particular climatostratigraphic units were described for the Łuków 3A site, located ca 40 km distant (Stachowicz-Rybka 2015a). The basins of Ferdynandów and Łuków 3A were formed at nearly the same time and most likely functioned among other numerous lakes of the Ferdynandovian palaeolakeland, covering the Łuków Plain after the retreat of the Sanian 1 glaciation (Żarski et al. 2009).

The macrofloras of the Ferdynandów B (Janczyk-Kopikowa 1975) and Ferdynandów 2011 profiles, obtained from two different parts of the same basin (Fig. 1), appeared to be similar in many aspects. For Ferdynandów B (Fig. 3), Janczyk-Kopikowa reported similar phases of vegetation development in warm and cold periods, and a taxonomic composition like that described for Ferdynandów 2011 (Fig. 2), but many species, particularly the extinct ones, could not be found, could not be determined, or were classified as extant taxa. Moreover, as the sediment was compacted and was sampled at low density, the cool unit of F1/2, separating two warm periods, could not be easily recognised and consequently its rank could not be identified. The new drilling and reexamination of the Ferdynandów profile at much higher resolution provided enough evidence to resolve the question of the occurrence of an interstadial fluctuation within the F1/2 cooling. Such fluctuations are typical for glacial periods separating two warm units, and have been observed not only for the Ferdynandovian interglacial, particularly in the Łuków 3A profile (Pidek 2013, Stachowicz-Rybka 2015a), but also for the Augustovian interglacial (Winter 2001, 2008, 2009).

In both the "old" and "new" profiles from Ferdynandów, the pattern of local vegetation in the Ferdynandovian 1 unit is not obvious, most likely because of the great depth of the lake, the rapid supply of allochthonous material, and the very intensive growth of the flora of diatoms and other lower plants. The constantly high water level could also be an effect of stronger climate oceanisation, as confirmed by the modern pollen analogues approach applied to pollen data from Łuków 3A and Zdany (Pidek & Poska 2013). Among macrophytes, only a few taxa, including *Najas marina* and *N. minor*, were abundant, while other species such as *Salvinia natans*, *Schoenoplectus lacustris*, *Lycopus europaeus*, and *Cyperus fuscus* appeared rather occasionally and discontinuously. At the end of the climatic optimum, as the lake basin was gradually filled with sediment and became shallower while the shallow littoral zone became broader, the swamp belt, inhabited by numerous species, developed intensively. Similarly, strong growth of vegetation was recorded in boggy habitats and in shallow waters close to lakeshores. The interstadial fluctuation at the close of Ferdynandovian 1 was marked mostly by an increase in the number of specimens of several taxa, including spines and, in particular, seed fragments of *Stratiotes sp.* Seeds of the modern *Stratiotes aloides* are extremely rare, as the species reproduces mainly vegetatively because many waterbodies contain either males or females of the species (Cook & Urmi-König 1983, Gałka 2007, Mowszowicz 1973, Smolders et al. 1995). However, loss of an ability to produce seeds may result primarily from the climate cooling and borealisation. In older interglacials, warmer than the Holocene, seeds of *Stratiotes aloides* have been recorded frequently (Velichkevich & Zastawniak 2008). Seed fragments of *Stratiotes* sp. and remains of *Najas minor*, *N. marina*, and *Scirpus atroviroides* suggest an improvement of climatic conditions.

Ferdynandovian 1/2 was characterised by the presence of species typical for boreal climate, such as *Betula nana*, *B. humilis*, and *Ranunculus gmelini*. Terrestrial vegetation was slightly diminished, but aquatic plants did not show a noticeable response to the deterioration of temperature conditions. Various pondweed species and *Najas marina* were dominant.

In Ferdynandovian 2, both the "old" and "new" profiles of Ferdynandów showed the most luxuriant vegetation, in terms of both the diversity and abundance of species inhabiting the basin. Considering the entire Ferdynandovian succession, the temperature conditions of this particular period were definitely the most advantageous for the development of vegetation. The much shallower eutrophic lake was covered by the most thermophilous aquatic communities, including *Brasenia borysthenica*, *Euryale ferox*, and *Najas minor* in Ferdynandów 2011, *Brasenia purpurea* in Ferdynandów B, as well as *Ceratophyllum demersum* and *Najas marina*. At the close of this period, the Ferdynandów basin transitioned to a peat bog with abundant mosses, Cyperaceae, *Andromeda polifolia*, and *Vaccinum* sp. Numerous remains of pine, indicating its appearance in the peat bog area, were identified as well.

For the early Sanian 2 glaciation, the plant macroremains analyses for both Ferdynandów profiles point to a strong rise in the water level and the transition of the peat bog to a relatively deep, cool, oligotrophic lake. A similar pattern was reported for Łuków 3A, where oligotrophic environmental conditions were indicated by the presence of *Isoëtes lacustris*, *Hippuris vulgaris*, *Najas tenuissima*, and *Andromeda polifolia* (Stachowicz-Rybka 2015a). The trophic status of the Ferdynandów palaeolake, in this period covered by both eutrophic and definitely oligotrophic plants, seemed uncertain for Janczyk-Kopikowa (1975). Similarly, in Nierybno Lake of Holocene age (Milecka & Bogaczewicz-Adamczak 2006), a palaeoecological reconstruction of the development of trophic conditions showed that at the initial stages of its functioning the basin was eutrophic and filled with alkaline waters, while at the beginning of the Atlantic it became oligotrophic and had lower water pH.

The floras of Łuków 3A and Ferdynandów 2011 included taxa not now found in Poland, such as *Azolla filiculoides*, *Cyperus glomeratus*, and *Euryale ferox*, as well as extinct species such as *Pilularia borysthenica*, *Aldrovanda borysthenica*, *Alisma plantago-minima*, *Brasenia borysthenica*, *Carex paucifloroides*, *Caulinia goretskyi*, *C. macrosperma*, *Eleocharis praemaximowiczii*, *Nymphaea cinerea*, *Potamogeton dvinensis*, *P. dorofeevii*, *P. panormitanoides*, *P. perforatus*, *P. pseudorutilus*, *P. praemaackianus*, *P. saryanensis*, *Ranunculus gailensis*, *Scirpus atroviroides*, *Scirpus kreczetoviczii*, and *Stratiotes goretskyi*. The presence of these taxa, characteristic for floras of Ferdynandovian age, allowed their correlation with other stratigraphically corresponding floras in Eastern Europe, particularly in Belarus at Motol (Velichkevich et al. 1993), Smolyarka (Velichkevich et al. 1993) and Nizhninsky Rov (Velichkevich et al. 1996), as well as in Russia at Smolenskyi Brod (Velichkevich 1978).

The composition of characteristic taxa also allowed comparisons between two bimodal interglacial sequences, namely the Ferdynandovian, 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, correlated with MIS 19–21 (Ber 1996; Ber et al. 1998, Janczyk-Kopikowa 1996, Stachowicz-Rybka 2005, 2007, 2009, 2011, Winter 2001, 2008, 2009), as well as the Domuratovian succession (Winter & Lisicki 2005, Stachowicz-Rybka 2015b, Winter et al. in press).

The Ferdynandovian, Domuratovian and Augustovian successions were compared with respect to extinct species or those not found in the present-day flora of Poland but which occurred in a flora of a particular age, as presented in Table 2. The Ferdynandovian floras of Ferdynandów 2011 and Łuków 3A contained taxa such as *Brasenia borysthenica*, *Aldrovanda borysthenica*, *Pilularia borysthenica*, *Caulinia goretskyi*, and *Potamogeton saryanensis*, not recorded in the older Domuratovian and Augustovian successions; this is an important difference between the floras.

CONCLUSIONS

The sediments of the Ferdynandów 2011 profile bear a record of vegetational and climatic changes that affected the investigated basin. The changes described here, most of which proceeded gradually, reflect particular stages in the development of the depression from a lake to a peat bog. At the end of Ferdynandovian 2 the eutrophic lake changed to a peat bog which at the beginning of the Sanian 2 glaciation turned into a lake again, but one filled with cool oligotrophic waters dominated by *Isoëtes lacustris*, presently typical of lobelia lakes. The phases of development of palaeolakes and their vegetation on the Łuków Plain make a very coherent sequence which appears to be valid for a greater area and corresponds to cyclic climatic changes recorded in deep marine cores (MIS 13–15).

The zones distinguished for Ferdynandów 2011 in plant macroremains analysis were correlated with those determined for the profile in palynological studies, and were compared with results obtained for Ferdynandów B and Łuków 3A. Some of the macrofossil taxa discovered in Ferdynandów 2011 apparently are new for the Ferdynandovian flora. Apart from species observed in the flora of Łuków, *Euryale ferox* was unequivocally identified; *Pilularia borysthenica*, *Potamogeton trichoides*, *Caulinia goretskyi*, *Potamogeton* cf. *dorofeevii*, *P. saryanensis*, *P. pseudorutilus*, and *Stratiotes goretskyi* were determined as well. The presence of these taxa provided the basis for correlating

Table 2. Comparison of extinct taxa and taxa characteristic for the Ferdynandovian interglacial of Łuków 3A (Stachowicz-Rybka 2015a) and Ferdynandów 2011 (this paper), the Augustovian interglacial of Czarnucha and Żarnowo (Stachowicz-Rybka 2011), and the Domuratovian interglacial of Domuraty 2 (Stachowicz-Rybka 2015b)

Taxon	Augustovian interglacial MIS 19–21	Domuratovian interglacial MIS 17	Ferdynandovian interglacial MIS 13–15
Azolla filiculoides foss.	+	+	+
Pilularia borysthenica			+
Salvinia natans	+	+	+
Selaginella tetraedra	cf.+		
Aldrovanda borysthenica			+
Alisma plantago-minima	+	+	+
Brasenia borysthenica			+
Carex paucifloroides	+	+	+
Caulinia goretskyi			+
Caulinia macrosperma		+	+
Cyperus glomeratus	+	+	+
Dulichium arundinaceum		+	
Elatine hydropiperoides	+		
Eleocharis praemaximowiczii	+	+	+
Euryale ferox	cf.+		+
Nymphaea cinerea	cf.+	+	+
Potamogeton dvinensis	+	+	+
Potamogeton dorofeevii			cf.+
Potamogeton panormitanoides	+		+
Potamogeton perforatus	+	+	+
Potamogeton pseudorutilus			+
Potamogeton praemaackianus		+	+
Potamogeton saryanensis			+
Potamogeton trichoides	+		
Ranunculus gailensis (=*R. sceleratoides*)	+		+
Scirpus atroviroides	+	+	+
Scirpus kreczetoviczii	+	+	
Stratiotes brevispermus	cf.+		
Stratiotes goretskyi	cf.+	cf.+	+
Trapa natans	+		
Typha aspera	+	+	
Urtica cf. *laetevirens*	+		
Urtica cf. *thunbergiana*	+		
Zannichellia palustris	+	+	+

the Ferdynandovian flora with other Polish and European early Middle Pleistocene floras.

ACKNOWLEDGEMENTS

The research was financed by the Ministry of Science and Higher Education (grant No. N N307 039940) and by the W. Szafer Institute of Botany, Polish Academy of Sciences from its statutory funds. I warmly thank Krzysztof Stachowicz, MSc, for valuable assistance in the laboratory during sample collection and preparation, and Wojciech Granoszewski, PhD, (Polish Geological Institute – National Research Institute, Cracow), and Judit Bajzath, PhD, (Hungarian Natural History Museum, Budapest) for very helpful review comments and suggestions. Sincere thanks to Dorota Salata, PhD, for SEM work performed in the Laboratory of Field Emission Scanning Electron Microscopy and Microanalysis at the Institute of Geological Sciences of the Jagiellonian University.

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