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Multi-proxy environmental reconstruction of the Eemian and Early Vistulian – Before, during and after the life of the forest rhino *Stephanorhinus kirchbergensis* (Jäger, 1839) from Gorzów Wielkopolski (NW Poland)

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ABSTRACT

The natural environment of the Eemian Interglacial (MIS 5e) and Early Vistulian (MIS 5 d-a) in many areas in Central Europe is still insufficiently and fragmentarily known. Therefore, after the discovery of an almost complete skeleton of the Eemian *Stephanorhinus kirchbergensis* (Jäger, 1839) in outcrop of palaeolake sediments near Gorzów Wielkopolski (GW site, GS3 profile), a multi-proxy analysis was conducted for a precise recognition of the environmental and climate changes taking place before, during and after the life of this individual. Comprehensive palaeobotanical investigations of sediments of two palaeolakes lying above each other were performed palynological analysis including NPPs and algal analysis, plant macroremains studies (including wood fragments), as well as palaeozoological analyses of the Cladocera, Chironomidae and Coleoptera. The picture of changes in the environment and climate obtained thanks to the performed analyzes presented in a short way looks as follows. The end of the Wartanian Glaciation (MIS 6) was characterised by the dominance of herbaceous vegetation. Along with the gradually changing climatic conditions, the landscape of the Eemian Interglacial was dominated in sequence by birch, pine, oak (the so-called First Thermal Optimum), hazel forests with linden, hornbeam (Second Thermal Optimum) with a rarely recorded dry oscillation, then spruce with fir and again pine forests. The “older Eemian lake” during this time changed from deep, cold, oligotrophic and carbonate to shallower, cold waters with higher trophy, then deeper with lower trophy, again shallower with peats and dystrophic conditions and finally became terrestrial. The age of the post-Eemian part of the GS3 profile was reinterpreted, recognizing OSL dating as more reliable than radiocarbon dating, determining the age as Early Vistulian. Subsequent stages of this part of profile were characterised by significant cooling and intense

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development of heaths and peatbogs (MIS 5d), double return of pine and birch forests separated by intra-interstadial cooling (MIS 5c), recooling with dominant herbaceous plants (MIS 5b) and last warming with birch forests (MIS 5a). The "younger Early Vistulian lake" was formed with the rising of the water level. It was shallow, cold, low-trophic, with the water heating up in the summer, which caused trophic increases. Water levels fluctuated. With the progressing terrestrialization, oligotrophy appeared. Each of used proxies reconstructs a fragment of palaeoenvironmental changes on land and/or in the reservoir, registering climatic events on both regional and local scales. However, only the combination of all results allows for a full picture of natural changes.

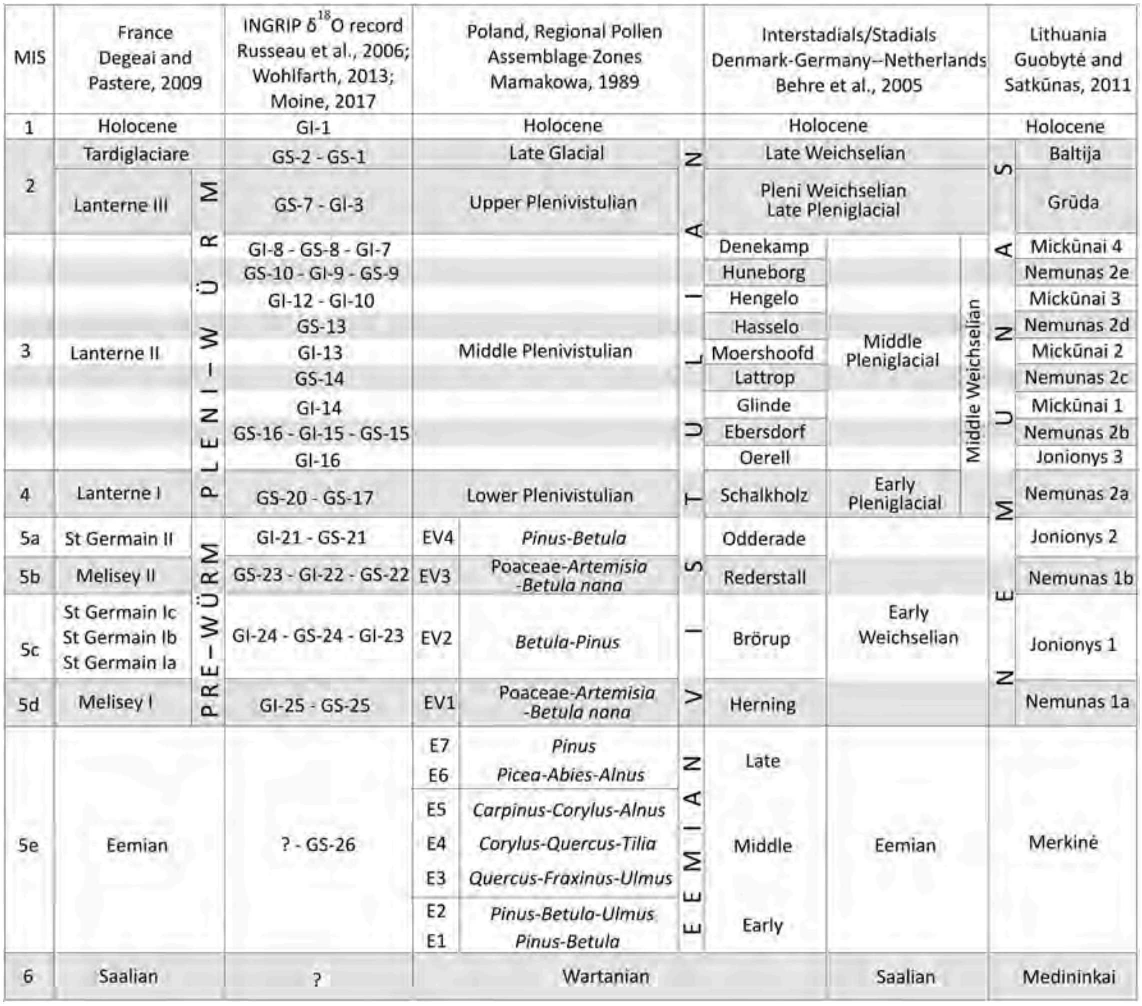
1. Introduction

Numerous studies have focused on the palaeoenvironmental and climate changes in the Eemian Interglacial and Early Vistulian in Europe (e.g. Rühberg et al., 1995; Litt et al., 1996) and Poland (Kupryjanowicz et al., 2018a). However, these palaeoenvironmental reconstructions are often unidimensional and fragmentary, because they often refer to only one environmental aspect, e.g. terrestrial vegetation. Combination of results obtained from a large spectrum of analyses allows for a multi-proxy reconstruction of the environment in the Eemian and Early Vistulian.

The skeleton of the extinct rhino *Stephanorhinus kirchbergensis* (Jäger, 1839) found in GS3 profile near Gorzów Wielkopolski (NW Poland) belonged to an over 30 years old female and is the largest and the best-preserved specimen of *S. kirchbergensis* found so far. This species had a wide geographic distribution, covering Europe and Asia, reaching northern Siberia (beyond the Arctic Circle) and tropical China (Tong and Wu, 2010; Billia, 2011; Billia and Zervanová, 2014; Kirillova et al., 2017; Shpansky and Boeskorov, 2018). The species range extends from the Middle to the Late Pleistocene (700–600 ka). In Europe it became extinct during the Last Glacial, probably in MIS 3 (ca. 40 ka; Table 1) (Lacombat, 2006; Van der Made, 2010; Billia, 2011; Billia and Zervanová, 2014; Pandolfi, 2018; Kirillova et al., 2017, 2021).

The discovery of this rhino specimen in an over 10 m exposure of Eemian palaeolake sediments (GS3 profile; Fig. 1; Sobczyk et al., 2020; Stefaniak et al., 2023) gave the opportunity to recognise changes taking place in the Eemian Interglacial, especially conditions during the life of the rhinoceros, and Early Vistulian palaeoenvironment based on a series of palaeobotanic and palaeozoological analyses. Such an outcrop is extremely rare, so researching this profile offered a very rare

Table 1
Chronostratigraphy of Late Pleistocene in Europe. The grey shading indicates glacials or stadials.



MIS	France Degeai and Pastere, 2009		INGRIP δ18O record Russeau et al., 2006; Wohlfarth, 2013; Moine, 2017	Poland, Regional Pollen Assemblage Zones Mamakowa, 1989			Interstadials/Stadials Denmark-Germany–Netherlands Behre et al., 2005			Lithuania Guobytė and Satkūnas, 2011	
1	Holocene		GI-1	Holocene			Holocene			Holocene	
2	Tardiglaciare		GS-2 - GS-1	Late Glacial		VISTULIAN	Late Weichselian			NEMUNAS	Baltija
	Lanterne III	PLENI – WÜRM	GS-7 - GI-3	Upper Plenivistulian			Pleni Weichselian Late Pleniglacial				Grūda
3	Lanterne II		GI-8 - GS-8 - GI-7	Middle Plenivistulian			Denekamp	Middle Pleniglacial	Middle Weichselian		Mickūnai 4
			GS-10 - GI-9 - GS-9				Huneborg				Nemunas 2e
			GI-12 - GI-10				Hengelo				Mickūnai 3
			GS-13				Hasselo				Nemunas 2d
			GI-13				Moershoofd				Mickūnai 2
			GS-14				Lattrop				Nemunas 2c
			GI-14				Glinde				Mickūnai 1
			GS-16 - GI-15 - GS-15				Ebersdorf				Nemunas 2b
			GI-16				Oerell				Jonionys 3
4	Lanterne I		GS-20 - GS-17	Lower Plenivistulian			Schalkholz	Early Pleniglacial			Nemunas 2a
5a	St Germain II	PRE – WÜRM	GI-21 - GS-21	EV4	*Pinus-Betula*		Odderade	Early Weichselian			Jonionys 2
5b	Melisey II		GS-23 - GI-22 - GS-22	EV3	Poaceae-*Artemisia* -*Betula nana*		Rederstall				Nemunas 1b
5c	St Germain Ic St Germain Ib St Germain Ia		GI-24 - GS-24 - GI-23	EV2	*Betula-Pinus*		Brörup				Jonionys 1
5d	Melisey I		GI-25 - GS-25	EV1	Poaceae-*Artemisia* -*Betula nana*		Herning				Nemunas 1a
5e	Eemian		? - GS-26	E7	*Pinus*	EEMIAN	Late	Eemian		Merkinė	
				E6	*Picea-Abies-Alnus*						
				E5	*Carpinus-Corylus-Alnus*		Middle				
				E4	*Corylus-Quercus-Tilia*						
				E3	*Quercus-Fraxinus-Ulmus*						
				E2	*Pinus-Betula-Ulmus*		Early				
				E1	*Pinus-Betula*						
6	Saalian		?	Wartanian				Saalian		Medininkai	

opportunity to obtain more data than from drilling. In addition, a series of further dating of the sediment (^{14}C and OSL) allowed the reinterpretation of the age of post-Eemian deposits from the GS3 profile, which resulted from earlier considerations (Mirosław-Grabowska et al., 2022).

Pollen analysis is most commonly used for palaeoenvironmental reconstructions in palaeobotanic studies, allowing to recognise the succession of terrestrial vegetation and climate changes with application of present-day plant indices. In NW Poland, studies based on pollen proxies

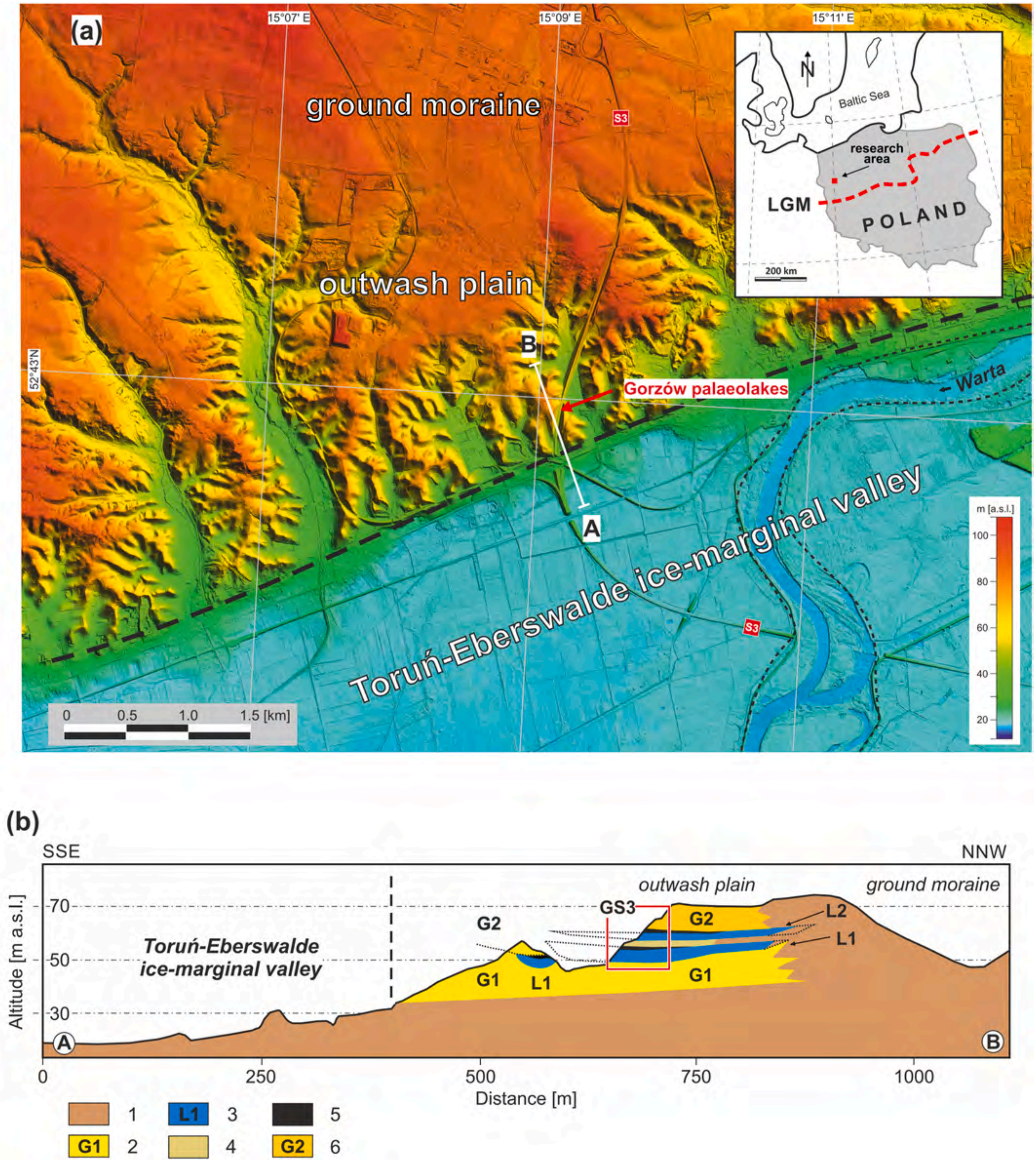


Fig. 1a. (a) LiDAR 1 × 1 m DEM location of research area in NW Poland with Gorzów Wielkopolski palaeolakes sediments excavated in a road cut. (b) Simplified geological cross-section A–B through GS3 (red box) Gorzów Wielkopolski palaeolakes sequence (modified after Stefaniak et al., 2023, in press). Explanations: 1 – mixed glaciofluvial sand and gravelly diamicton, 2 – Saalian glaciogenic deposits, 3 – lower palaeolake from which the mammal fossils have been excavated, 4 – lacustrine upper unit (sand, silt and calcareous gyttja), 5 – peat, 6 – Vistulian glaciogenic deposits, L2 – upper palaeolake, dotted lines – reconstructions of possible extension of the palaeolakes bodies. Profile vertical exaggeration × 3.

are rather few (Fig. 1b) in the analysed interval due to the deep burial of Eemian sediments (Urbański and Winter 2005). The Radówek (Urbański and Winter 2005), Laski Lubuskie (Janczyk-Kopikowa, 1972), Bytom Odrzański (Kuszell and Sadowska, 1994) and Zofiówka sites (Kuszell, 1997) were analysed only briefly. A too rare sampling in these few profiles allowed only the conclusion that the sediment originated from the Eemian Interglacial, without revealing any nuances that are discussed today. In central, eastern and north-eastern Poland (Kupryjanowicz et al., 2018a), characterised by the occurrence of Eemian Lakelands (Żarski et al., 2018; Roman et al., 2021), such studies are common. In NE Germany, pollen analyses of Eemian sediments were performed in Schonfeld (Erd, 1991; Hermsdorf and Strahl, 2008), Rathenow (Freund, 2000), Banzin (Börner et al., 2015), Hinterste Mühle (Börner et al., 2018), and in the remaining part of Germany: e.g. Bispingen (Field et al., 1994; Lauterbach et al., 2012), Klinge (Velichko et al., 2005), Gröbern (Litt, 1994; Kühl et al., 2007), Furamoos and Samerberg (Müller and Sánchez Goñi, 2007), and other sites (Fig. 1b). Another botanic marker used in palaeoenvironmetal reconstructions is plant macroremains analysis. It allows to reconstruct the succession of reed and water plants in the reservoir, and based on the knowledge of climatic and environmental requirements of particular species – also the depth, water pH and trophic levels. Only a few Eemian sites with such studies are located in western Poland, e.g. Sławno (Tołpa, 1961), Nakło (Noryśkiewicz, 1979), Jaworzyna Śląska, Wołów, Rusinów (Kuszell, 1980, 1998), and Imbramowice (Mamakowa, 1989); central Poland, including Ustków (Kołaczek et al., 2016) and Kozłów (Suchora et al., 2022), and northern Poland – Cierpięta (Marks et al., 2014) (Fig. 1b). Macroremains of terrestrial plants are also introduced into the lake bottom sediments, except seeds and fruits also wood fragments, and charcoals, which allow for the species determination of the encountered fragments, due to which the forest stands in the vicinity of the lake can be precisely recognised (Börner et al., 2015, 2018; Hrynowiecka et al., 2021).

Analysis of non-pollen palynomorphs (NPPs) supplements other palaeoecological analyses and helps in the reconstruction of local

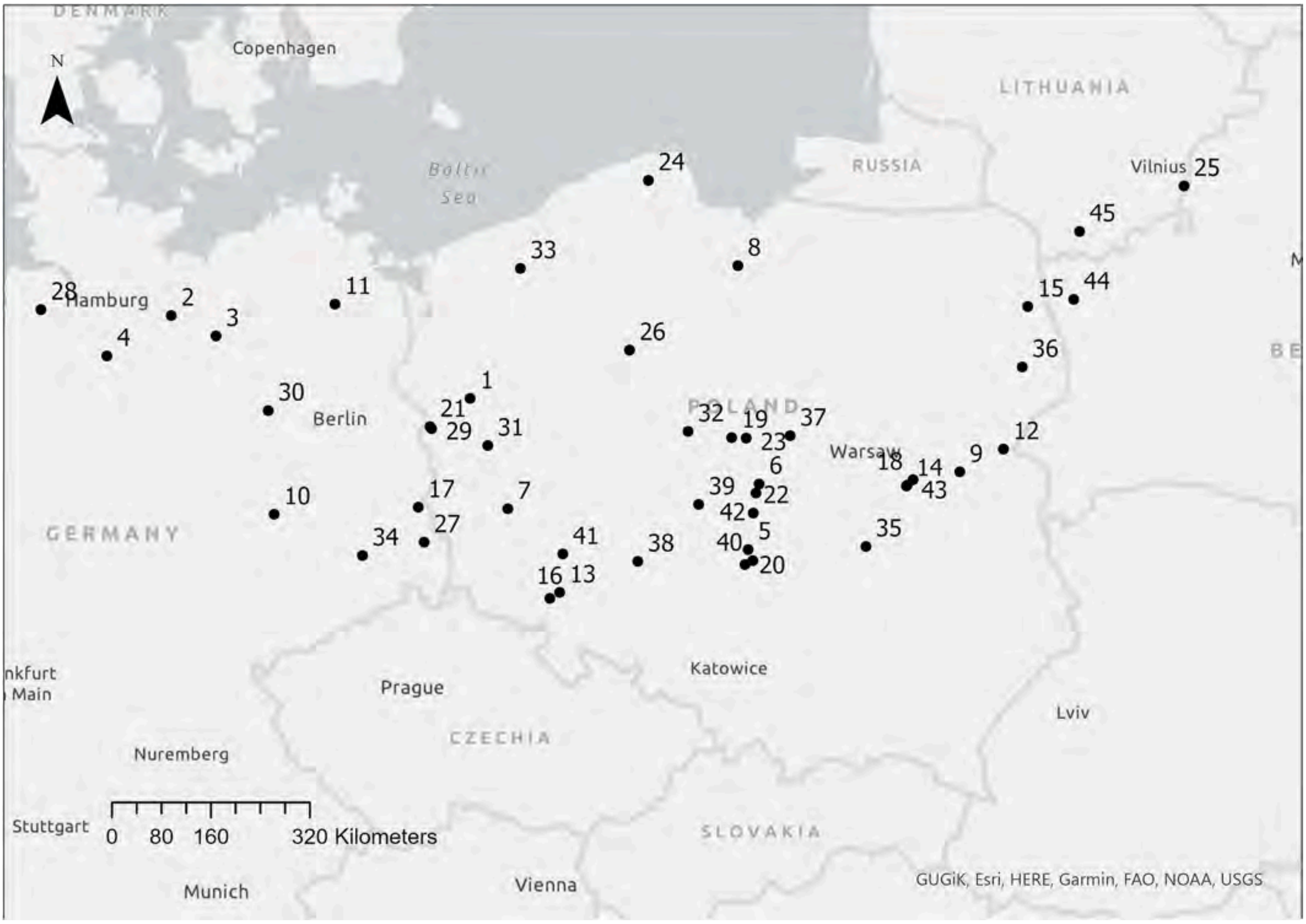


Fig. 1b. The locality of sites in Poland, Germany, and Lithuania (in alphabetical order except no 1) used in this paper for correlation of Eemian Interglacial and Early Vistulian. 1 – Gorzów Wielkopolski (GS3 profile, Sobczyk et al., 2020 and this paper), 2 – Banzin (Börner et al., 2015), 3 – Beckentin (Hrynowiecka et al., 2021), 4 – Bispingen (Field et al., 1994; Lauterbach et al., 2012), 5 – Bełchatów (Pawłowski, 1989; Balwierz, 1995), 6 – Besiekierz (Mirosław-Grabowska and Niska, 2005), 7 – Bytom Odrzański (Kuszell and Sadowska, 1994), 8 – Cierpieta (Marks et al., 2014), 9 – Dziewule (Bińka and Nitychoruk, 2001), 10 – Gröbern (Litt, 1994), 11 – Hinterste Mühle (Börner et al., 2018), 12 – Horoszki Duże (Granoszewski, 2003), 13 – Imbramowice (Mamakowa, 1989), 14 – Jagodne (Pidek et al., 2022), 15 – Jałówka (Kupryjanowicz et al., 2021), 16 – Jaworzyna Śląska (Kuszell, 1980), 17 – Klinge (Velichko et al., 2005), 18 – Kozłów (Suchora et al., 2022), 19 – Kubłowo (Mirosław-Grabowska et al., 2018), 20 – Kuców (Balwierz, 2003), 21 – Laski Lubuskie (Janczyk-Kopikowa, 1972), 22 – Lublinek (Balwierz, 1995), 23 – Łanięta (Balwierz, 2003), 24 – Łęczyce (Sokołowski et al., in press), 25 – Medininkai (Satkūnas et al., 2003), 26 – Nakło nad Notecią (Noryśkiewicz, 1979), 27 – Nochten (Bos et al., 2001), 28 – Oerel (Behre et al., 2005), 29 – Radówek (Urbański and Winter 2005), 30 – Rathenow (Freund, 2000), 31 – Rusinów (Kuszell, 1998), 32 – Ruszkówek (Mirosław-Grabowska et al., 2009), 33 – Rzecino (Winter et al., 2008; Niska and Mirosław-Grabowska, 2015), 34 – Schonfeld (Erd, 1991; Hermsdorf and Strahl, 2008), 35 – Sławno (Tołpa, 1961), 36 – Solniki (Kupryjanowicz, 2008), 37 – Studzieniec (Mirosław-Grabowska and Niska, 2007), 38 – Szklarka (Malkiewicz, 2018), 39 – Ustków (Kołaczek et al., 2016), 40 – Wola Grzymalina (Krzyszkowski et al., 1993), 41 – Wołów (Kuszell, 1980), 42 – Zgierz-Rudniki (Mamakowa, 1989), 43 – Żabieniec (Pidek et al., 2022); 44 – Komotowo (Rylowa et al., 2021), 45 – Jonionys (Rylowa et al., 2021).

environmental conditions (e.g. Kołaczek et al., 2020). It focuses on spores of fungi and cryptograms, plant and animal remains, algae and cyanobacterial cell walls, stomatocysts and other protists that can be identified. Their presence may provide information about surface run-off, herbivore activity, fire activity, conditions of local vegetation, hydrological conditions, and trophic conditions in lakes (see Miola, 2012). The NPPs are often used in multi-proxy research, still rarely, however, in investigations of older sediments, including the Upper Pleistocene (e.g. Kołaczek et al., 2016).

Analysis of algae makes it possible to reconstruct the conditions that prevailed in the water reservoir in the past. Green algae representing *Pediastrum* (Meyen, 1829) *sensu lato* (Chlorophyceae, Sphaeropleales, Hydrodictyaceae), forming microscopic flat star-shaped colonies called coenobia, are considered indicators in palaeoecological studies. Jankovská and Komárek (1995, 2000) and Whitney and Mayle (2012) listed their abundance in freshwater lakes and wetlands, global distribution, survival of harsh chemical treatment of pollen preparations, and easy recognition in pollen slides. Trends in *Pediastrum* occurrence in fossil material are connected with changes in water level, trophic level, content of matter of mineralogical origin, salinity or temperature, but they can also result from anthropogenic pressure (Mensing, 1999; Jankovská and Komárek, 2000; Makohonienko, 2000; Lenarczyk et al., 2015).

Diatom analysis (Baccillariophyta) reconstructs the reservoir depth, shoreline changes, climate conditions and many other environmental proxies, such as water salinity, pH, or trophic level (Bennion et al., 2010; Hall and Smol, 2010; Wolin and Stone, 2010). Having thecae composed of silica (biogenic silica frustule), diatoms are usually well-preserved in sediments (Smol and Stoermer, 2010). The history of diatom application in environmental reconstructions interlaces with the recognition of the ecological requirements of particular species and their application as bioindicators, as diatom floras from the Pleistocene do not differ much from the present-day ones (Rioual et al., 2007; Mirosław-Grabowska et al., 2009; Hoff et al., 2019).

Zoological markers that assist in palaeoenvironmental reconstruction include the Cladocera, Chironomidae, and Coleoptera. Cladocera are crustaceans that are a component of lake zooplankton and have remained virtually unchanged for hundreds of thousands of years, which allows the use of ecological and climatic requirements of existing species in the interpretation of changes that have occurred in the past (Korhola, 1999). Analysis of biodiversity changes and abundance of cladocerans allows to indicate climatostratigraphic boundaries, changes in the presence of plankton-eating fish (Korosi et al., 2013) and macrophytes (Davidson et al., 2011), lake trophy (lake type) (Manca et al., 2007), thermal and hydrological conditions (Nevalainen, 2011), and water pH (Krause-Dellin and Steinberg, 1986), which took place during the sedimentation of a given sediment layer. Cladocera were analysed in some sites with Eemian lake sediments in Poland (e.g. Solniki, Studzieniec, Kubłowo, Besiekierz, Ruszkówek, Rzecino: Niska, 2012; Niska and Mirosław-Grabowska, 2015; Mirosław-Grabowska et al., 2018, Fig. 1b) and northern Germany (Hinterste Mühle: Börner et al., 2018, Fig. 1b).

Remains of chironomid larvae (non-biting flies) are used to reconstruct past summer temperatures (Walker and Mathews, 1989). Their strong relationship with air and water temperature has been reported from different regions of Europe and North America (e.g. Brooks and Birks, 2001; Larocque et al., 2001; Heiri et al., 2011; Self et al., 2011). Chironomidae are fast reproducing insects and their assemblages respond much faster to environmental and climatic changes than e.g. plant communities. Midge head capsules accumulate in large quantities in small volumes of sediments (Brooks et al., 2007). Approximately 50 (Kotrys et al., 2014) head capsules are enough for obtaining significant results (Quinlan and Smol, 2001). The combined Swiss-Norwegian-Polish training set model is used to reconstruct the temperature in Central Europe (Kotrys et al., 2020). Because of poorly preserved material, studies of Chironomidae for older periods are rarely recorded.

Analysis of the Coleoptera (beetles), organisms whose adult life takes place on land, is most rarely used to reconstruct palaeoenvironmental changes. It follows from extremely rare preservation of insect remains (usually single fragments of wing-cases) in the sediment. However, abundant insect remains may point to or confirm specific climate trends, such as more humid environmental conditions, and a milder and warmer climate. With regard to data from Poland, comparative material is limited to data from several studies (Galewski and Głazek, 1978; Kuśka, 1985; Pawłowski and Kuśka, 1987). According to Pawłowski (1989), probably the oldest known Quaternary site in Poland is the brown coal succession in Bełchatów (Fig. 1b), where Scarabaeidae and Carabidae remains were found. Eemian sediments are very rarely analysed for beetles. Oerel (NW Germany; Behre et al., 2005, Fig. 1b) turned out to be one of the richest sites in this respect, with beetle species from various families being found.

The presented work is focused on: (i) reconstruction of changing palaeoenvironment and climate in the vicinity of Gorzów Wielkopolski (NW Poland) as accurately as possible, using available palaeobotanical and palaeozoological factors, (ii) determining in which periods of the studied succession *Stephanorhinus kirchbergensis* could have lived, and (iii) revision the GS3 profile stratigraphy in its post-Eemian part.

2. Regional setting

The analysed sediments were originally excavated in a road cut located to the west from Gorzów Wielkopolski municipality, in NW Poland (52°43′00″, 15°9′33″; Fig. 1a). Palaeolake horizons crop out at the junction of the Gorzów Plain morainic-outwash sequence to the north and the Toruń-Eberswalde ice marginal valley to the south (Fig. 1). Results reported here were derived for profile GS3 samples, which represent two palaeolake horizons sandwiched by glaciofluvial (bottom) and glacial (top) material of Saalian (Wartanian) and Vistulian (Weichselian) age, respectively (Sobczyk et al., 2020). The lower GS3 lacustrine sequence (Fig. 1a) contains calcareous gyttja, peat and silty sand (bottom-up), whereas the upper lake (Fig. 1a) consists of calcareous gyttja and peat, topped with fine and medium-grained glaciofluvial sand (Fig. 2). Geochronological investigations (OSL ages) constrain the timing of the quartz-rich clastic sedimentation between 123 and 72 ka, hence during the Eemian (lower palaeolake) and Early Vistulian (upper palaeolake) stages (Tables 1 and 2).

3. Material and methods

3.1. Pollen, NPP and algae (Pediastrum) method

Each of the 342 samples was collected between 0 and 1026 cm of the GS3 profile. Regardless the sediment type (silt, sand, gyttja and peat), samples were taken every 3 cm. Laboratory processing was performed on 171 samples, every 6 cm, 1 cm^3 each. All samples were prepared according to standard procedures for Pleistocene deposits and one *Lycopodium* tablet was added per 1 cm^3 of each sample (Stockmar, 1971; Berglund and Ralska-Jasiewiczowa, 1986). Sporomorph extraction was achieved by gravitation separation using a $ZnCl_2$ with a density of ~2.0 g/cm^3, and an acetolysis mixture following Erdtman's method (Erdtman, 1960). Pollen spectra were analysed under × 400 magnification with a Nikon Eclipse light microscope (LM). Pollen was counted on two cover slides with a surface area of 20 × 20 mm. Counting was carried out above 500 pollen grains (AP and NAP sum) identified on the basis of Fægri and Iversen (1989), Moor et al. (1991), Reille (1992), Beug (2004) and Stuchlik et al. (2001).

NPPs, except for algae (*Pediastrum*, and diatoms), were analysed under × 400 magnification with a Zeiss AxioScope LM and counted until the number of *Lycopodium* spores reached the number of indicators in a parallel palynological sample. The NPPs were identified based on e.g. Van Geel (1972), Van Geel and Aptroot (2006) and the Non-Pollen Palynomorphs Image Database (http://non-pollen-palynomorphs.uni-goettingen.de/).

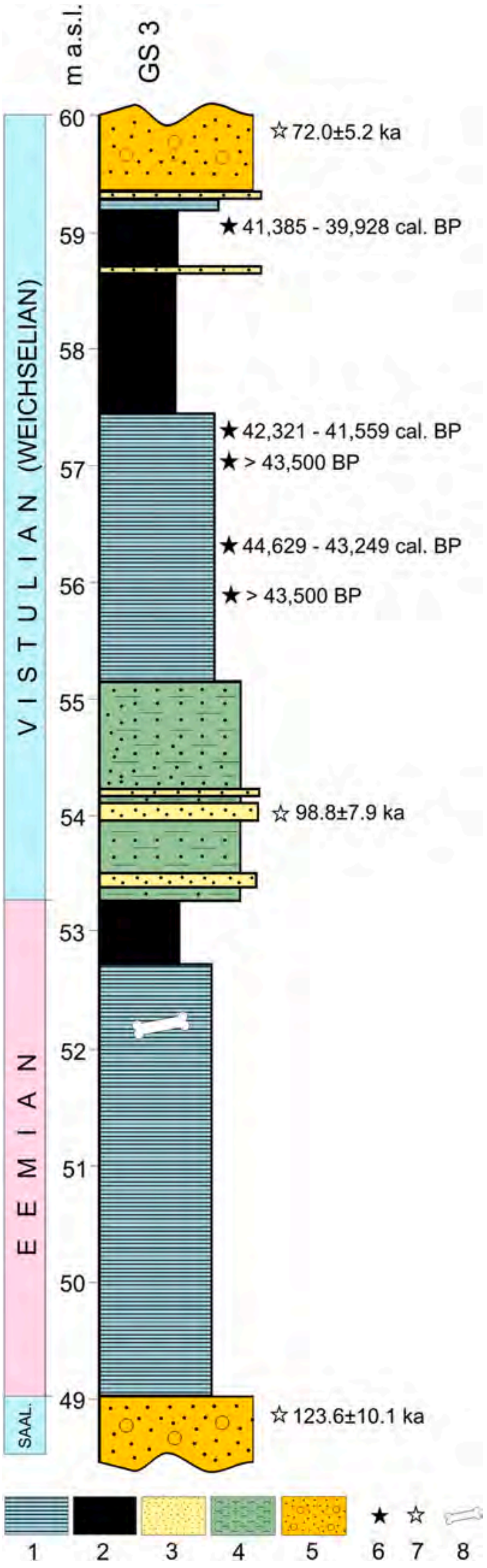


Fig. 2. Lithostratigraphic sequence at the GS3 outcrop with two palaeolakes horizons. Legend: 1 – calcareous gyttja; 2 – peat; 3 – fine and medium grain sand; 4 – silty sand; 5 – unsorted sand mixed with gravel; 6–^{14}C age ka BP (after Sobczyk et al., 2020); 7 – OSL age ka BP (after Sobczyk et al., 2020); 8 – bones of *Stephanorhinus kirchbergensis*. SAAL. – Saalian.

A total of 88 samples spaced every 12 cm along the GS3 profile were tested for the algae representing *Pediastrum sensu lato* (Chlorophyceae). The number of *Pediastrum* colonies was counted in relation to the number of *Lycopodium* spores (in parallel palynological samples) in 20 equidistant rows on the area of a 20 × 20 mm cover slide were analysed under × 400 magnification with a Nikon Eclipse Ni LM. *Pediastrum* specimens were identified on the basis of e.g. Komárek and Jankovská (2001), Lenarczyk (2014) and the taxonomic system of Komárek and Jankovská (2001). Two taxa were distinguished within *Pediastrum boryanum* (Turpin) Meneghini 1840: the variety *longicorne* and taxon comprising the remaining varieties ('var. div.') (Lenarczyk et al., 2020). Unidentified specimens, damaged or without characteristic taxonomic features, were classified as '*Pediastrum* undiff.'.

Pollen, NPP and algae data are presented on diagrams as the percentage proportions of taxa found in the analysed spectra. Percentage calculations were based on the basic sum AP (Arboreal Pollen – trees and shrubs) and NAP (Non-Arboreal Pollen – terrestrial herbaceous plants and dwarf shrubs). The percentage proportion of reed and aquatic plants, spores of Pteridophyta, Bryales and fungi, colonies of algae, NPPs and other microfossils were calculated in relation to the basic sum.

3.2. Macroremains, wood fragments and Coleoptera

Plant macroremains were analysed in 171 samples. Samples with a volume of ca. 150 ml, collected at 6 cm intervals were macerated The samples were macerated according to a standard procedure (adopted by e.g., Stachowicz-Rybka, 2011). Macrofossils were identified with the use of plant keys, atlases (Kats et al., 1965; Berggren, 1969; Cappers et al., 2006; Velichkevich and Zastawniak, 2006, 2008), and a reference collection of modern and fossil floras from the National Biodiversity Collection of Recent and Fossil Organisms stored at W. Szafer Institute of Botany, Polish Academy of Sciences, in Krakow (herbarium KRAM).

Wood fragments from 56 samples were identified with a metallographic microscope using × 100–500 magnifications and compared with anatomical atlases and specimens from the comparative collection housed in the Department of Palaeobotany at the W. Szafer Institute of Botany, Polish Academy of Sciences, Kraków. Identification of individual fractions of woods based on the observation of fresh fractures in three anatomical sections: transverse, longitudinal radial and longitudinal tangential. In order to observe all anatomical details characteristic of the respective species, it is recommended to examine fragments larger than 4 mm^3; however, smaller specimens are usually also identifiable.

Coleoptera remains were collected additionally during analysis of plant macroremains.

3.3. Diatom analysis

Diatom analysis was performed on 171 samples. Dried sediment samples (ca. 0.5 g) were etched with 10% HCl in order to remove carbonates and then boiled in hydrogen peroxide (~37%) for 2–12 h. Each stage was preceded by a fourfold rinsing with demineralized water every 12 h. The suspension was installed on glass slides with 10% NH_4Cl and left to dry in air temperature; later NH_4Cl was calcined for ca. 3 min. In 351 °C. Solid preparates were made with application of Naphrax® resin. The glued preparates were subject to short-term, strong heating to remove air bubbles and humidity.

At least two microscopic preparates with different density of the material were made out of each sample, which were analysed by Zeiss Axio Scope A1 and Nikon Eclipse E600 LMs, under magnification × 1000, with an immerse PlanApo lens. If present, up to 400 diatom frustules were identified in each preparate. The identification was based on Krammer (2000, 2002, 2003), Lange-Bertalot (2001), Levkov (2009), Lange-Bertalot et al. (2011, 2017), Hofmann et al. (2011), Bąk et al. (2012), and Levkov et al. (2013, 2016).

Table 2
Results of new and reported (1) Sobczyk et al. (2020);2) Mirosław-Grabowska et al. (2022) geochronological analyses available for the Gorzów Wielkopolski GS3 profile using radiocarbon dating (^{14}C) and Optically Stimulated Luminescence (OSL) methods. N/A – data not available due to not enough material suitable for AMS measurements.

Sample code	Sampling altitude (m a.s.l.)	Dated material and deposits	Conventional^{14}C age years BP	Cal 1 sigma^{14}C years BP (95%)	OSL central age (ka)
GdTL-2831$^{1)}$	59.8	Glaciofluvial sands and gravels	–	–	72.0 ± 5.2
GS3-1$^{1)}$	58.7	Peat/Macrofossils	36,010 ± 330	41,385–39,928	–
GS3-141,015$^{2)}$	57.7	Peat/Macrofossils	>43,500	N/A	–
GS3-139,095$^{2)}$	57.6	Peat/Macrofossils	37,380 ± 320	42,321–41,559	–
GS3-GOR4$^{2)}$	56.3	Gyttja/Macrofossils	41,120 ± 370	44,629–43,249	–
GS3-GOR5	56.0	Gyttja/Macrofossils	>43,500	N/A	–
GdTL-2830$^{1)}$	53.8	Fine and medium grained sand	–	–	98.8 ± 7.9
GdTL-2829$^{1)}$	48.5	Glaciofluvial sands and gravels	–	–	123.6 ± 10.1

3.4. Cladocera analysis

For Cladocera analysis, 171 samples of 1 cm^3 each were prepared according to the standard procedure (Frey, 1986; Korhola and Rautio, 2001) using a lower temperature of maceration of max. 60 °C. Olympus BX53 (magnifications × 10, × 20, × 40) was used to identify the remains. Identification and ecological interpretation of the Cladocera remains were carried out following Korhola (1990), Duigan (1992), Hofmann (2000), Flössner (2000), Szeroczyńska and Sarmaja-Korjonen (2007), and Błędzki and Rybak (2016). Results of quantitative and qualitative analyses were presented in a diagram of the absolute number of Cladocera individuals and the total number of Cladocera in 1 cm^3 of sediment.

3.5. Chironomidae analysis

Chironomidae preparation methods followed Brooks et al. (2007). The wet sediment was sieved through a 212 and 100 μm mesh sieves and subsequent residues were treated in an ultrasonic bath for 3 s. The resulting sediment was observed under a stereo-binocular microscope at × 25 magnification. Where applicable, a minimum of 50 chironomid head capsules from each sample were picked and mounted in Euparal® medium. Chironomid head capsules were identified by keys Wiederholm (1983), Schmid (1993), Klink and Moller Pillot (2003), and Andersen et al. (2013). Nomenclature for chironomid morphotypes and ecological preferences of identified taxa are based mainly on Brooks et al. (2007).

The Chironomidae-inferred mean July air temperature was reconstructed using Swiss-Norwegian-Polish training set (SNP TS).

3.6. Drawing of diagrams

Diagrams showing qualitative and quantitative results of palynological (including NPP), algological, plant macroremains (including wood), Coleoptera, Cladocera and Chironomidae analyses were plotted with POLPAL software (Nalepka and Walanus, 2003).

3.7. Dating analysis

In this study, we utilized geochronological data sourced from Sobczyk et al. (2020) and Mirosław-Grabowska et al. (2022). All optically stimulated luminescence (OSL) ages, subsequent to Sobczyk et al. (2020), were meticulously acquired within the Department of Radioisotopes at the Silesian University of Technology in Poland. The sophisticated automated Risø TL/OSL DA-20 reader, coupled with the procedures outlined in the aforementioned studies, was employed for the OSL age determinations.

For the 14C dating component, we provided results obtained within the Beta Analytic Radiocarbon Dating Laboratory in Miami, USA. The samples – designated as [Beta-493,676] GS3-1, [Beta-582,624] GS3-141,015, [Beta-596,601] GS3-GOR4, and [Beta-596,602] GS3-GOR5 – underwent acceleratory mass spectrometry (AMS) on plant remains following the established techniques endorsed by this laboratory (Bronk Ramsey, 2009; Reimer et al., 2020).

To ensure the accuracy and reliability of our 14C data, calibration was executed using the OxCal IntCal13 (sample GS3-1) approach (Reimer et al., 2013) and IntCal20 (GS3-141,015, GS3-GOR4, GS3-GOR5) sample calibration method (Reimer et al. (2020). The comprehensive dataset derived from these analyses is presented in Table 1 for reference and further examination.

4. Results

4.1. Pollen, NPPs, and algae (Pediastrum and Bacillariophyta)

A total of 137 taxa, including 39 taxa of trees, shrubs and dwarf shrubs, 45 – herbaceous plants, 21 – reed and water plants, 8 – Pteridophyta (Fig. 3a, b, 3c) and 24 – others, e.g.: Crumpled, Rebedded, various fungi spores, *Sphagnum* spores and other microfossils were identified (Fig. 3d). Among higher plants, 48 taxa were determined to species, 22 – to genus, 10 – to family, and 24 – to phylum. Profile GS3 was subdivided into 27 LPAZs (Local Pollen Assemblage Zones), including the part corresponding to the Eemian Interglacial at 7 RPAZ (Regional Pollen Assemblage Zones) according to Mamakowa (1989) (Fig. 4). Sporomorph abundance was usually high; in depth intervals 588–582, 528–510, 492 and 258 cm, however, the samples did not contain pollen.

27 LPAZs were distinguished (i.a. Fig. 3a). The low content of tree pollen (AP – Arboreal Plant), including the complete lack of thermophilic trees pollen, and the high content of herbaceous plants pollen (NAP – Non Arboreal Plant) allowed to distinguish 1 LPAZ belonging to the cold unit corresponding to the late Wartanian Glaciation (MIS 6). The strict order of appearance of the main taxa: *Betula*, *Pinus*, *Ulmus*, *Quercus*, *Corylus* and *Tilia*, *Carpinus*, *Picea*, *Abies*, *Pinus* allowed to distinguish 16 LPAZs and assign them to the warm unit corresponding to the Eemian Interglacial. The next 10 LPAZs were distinguished thanks to the variable participation of *Betula* and *Pinus* pollen and the appearing high content of NAP pollen – characteristic for Early Vistulian climatic fluctuations.

NPPs analysis revealed the presence of 71 taxa belonging to various taxonomic groups: fungi (20), algae (16), microremains of macrophytes (water plants; 5), cyanobacteria (4), numerous spicules of sponges, dinoflagellates (2), flatworms (2), one testate amoeba, one rotifer, one crustacean, one cladoceran, and fragments of insect eyes (Fig. 3d). The remaining 16 taxa could not be assigned to any of the mentioned groups.

Seven *Pediastrum* species were found: *P. alternans* (Nygaard, 1950), *P. boryanum* (identified as var. Longicorne or other varieties, ‘var. div.‘), *P. duplex* (Meyen, 1829) [represented by *var. Rugulosum* (Raciborski, 1890)], *P. integrum* (Naegeli, 1849), *P. kawraiskyi* (Schmidle, 1897), *P. orientale* [(Skuja) Jankovská and Komárek, 1995] and *P. privum* [(Printz) Hegewald, 1979]. *Pediastrum boryanum* was the most abundant among other species and particularly abundant relative to pollen at depth intervals 348–420, 270–294, and 198–228 cm. It occurred in 33 samples, especially those collected from the upper part of the profile (Fig. 3c). *Pediastrum alternans* and *P. privum* were observed only in single

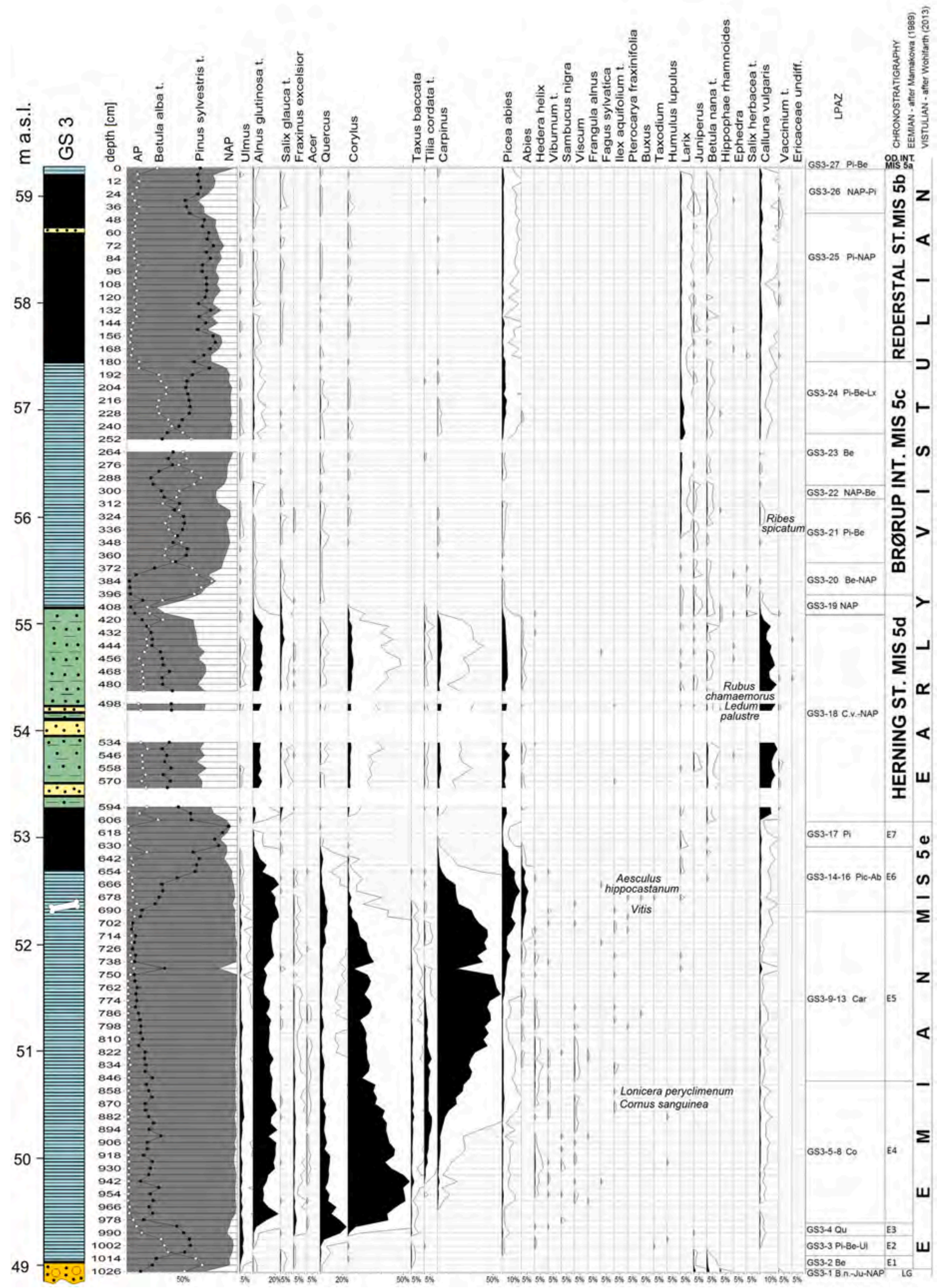


Fig. 3a. Percentage pollen diagram presenting all the curves of trees, shrubs, and dwarf shrubs in the GS3 profile. Abbreviations: AP – Arboreal Pollen; NAP – Non-Arboreal Pollen; LPAZ – Local Pollen Assemblage Zones; LG – Late Glacial; OD. INT – Odderade Interstadial. Extension of LPAZs names in the text. Lithology like in Fig. 2. Analysed by A. Hrynowiecka.

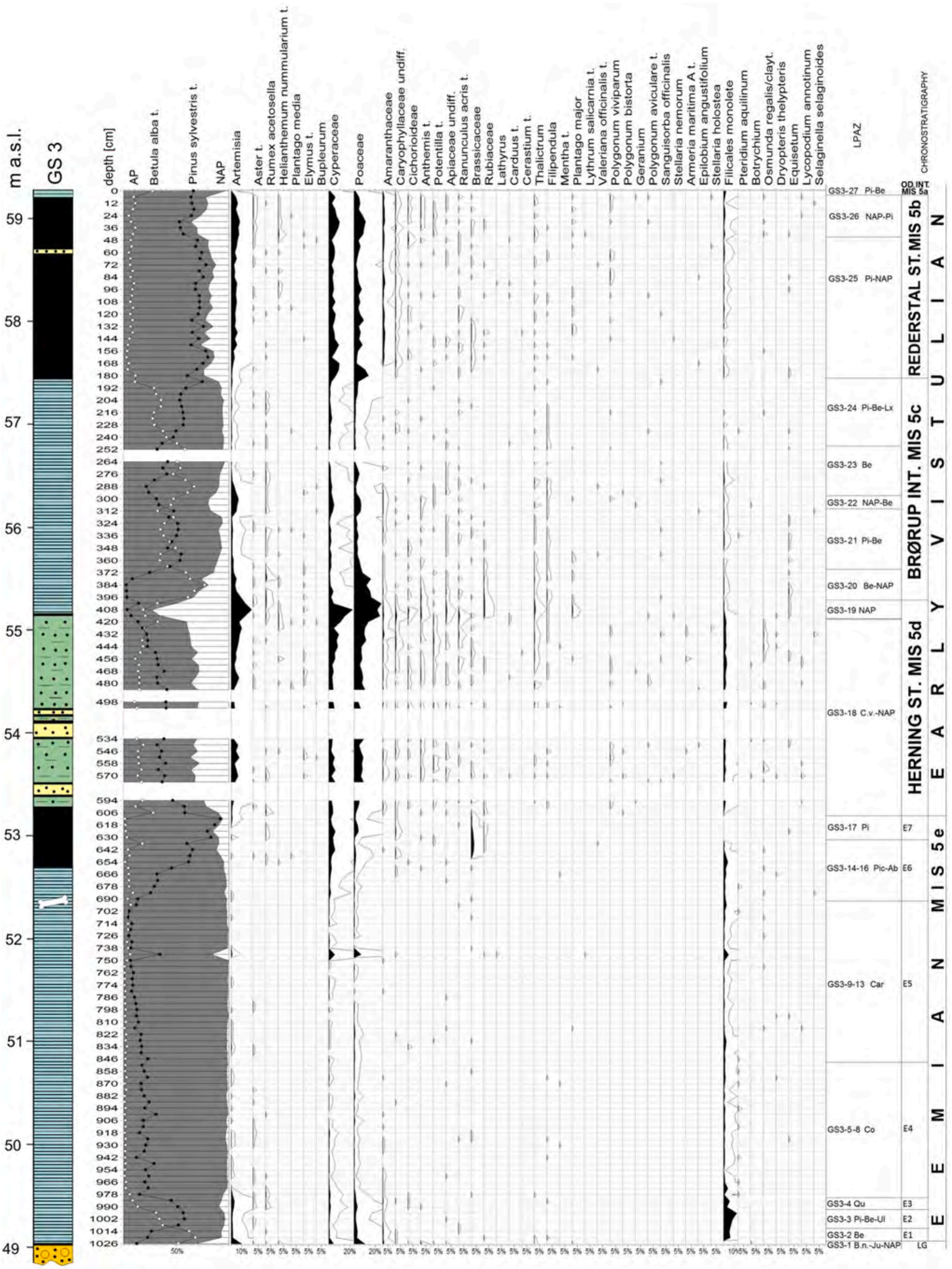


Fig. 3b. Percentage pollen diagram presenting all the curves of herbs pollen and Pteridophyta spores in the GS3 profile. Abbreviations like in Fig. 3a. Lithology like in Fig. 2. Analysed by A. Hrynowiecka.

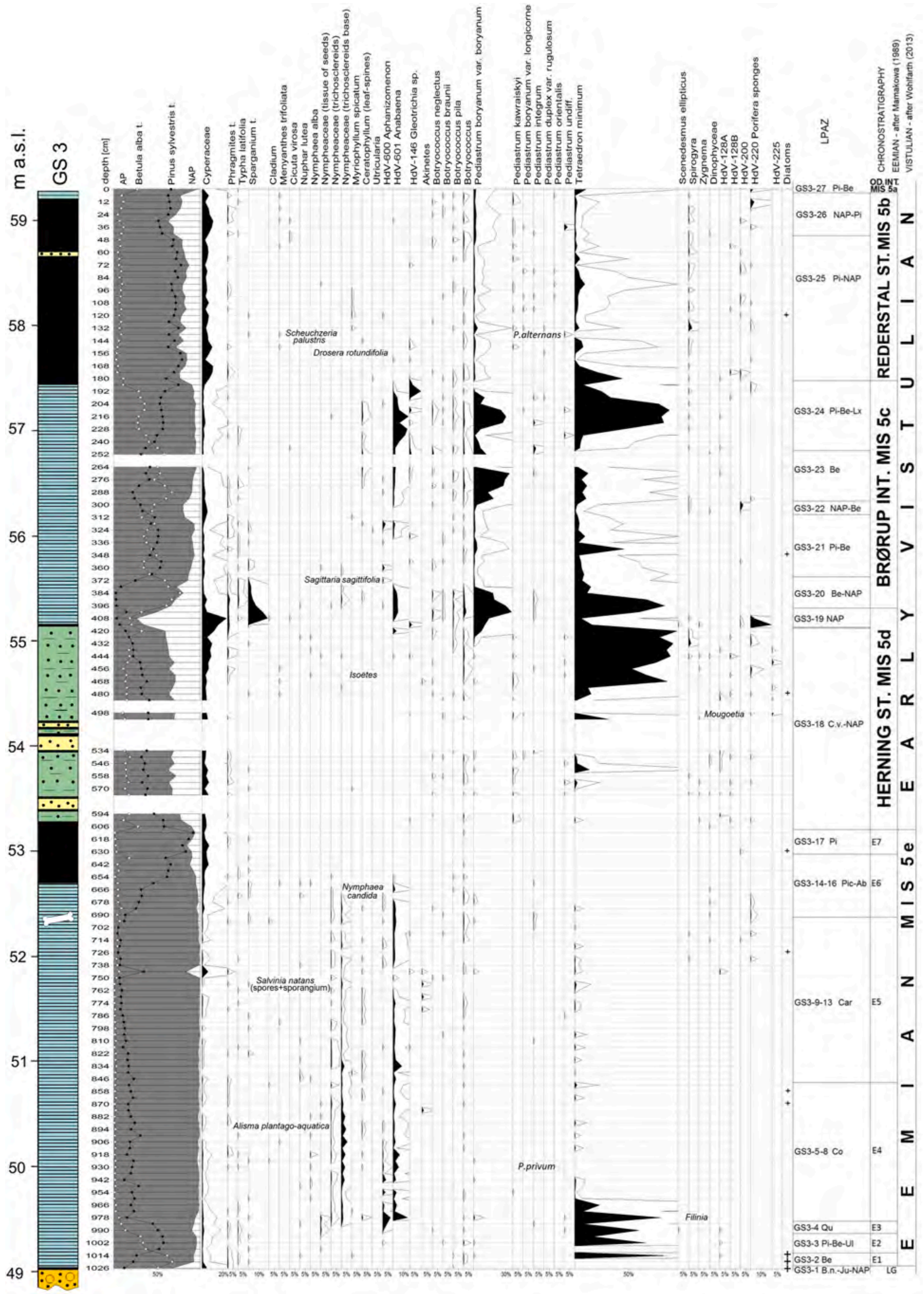


Fig. 3c. Percentage pollen diagram presenting all the curves of reed swamp and aquatic plants pollen, colonies and various indicators of Algae, including Diatoms, in the GS3 profile. Abbreviations like in Fig. 3a. Lithology like in Fig. 2. Analysed by A. Hrynowiecka, J. Kowalska, J. Piątek and M. Bąk.

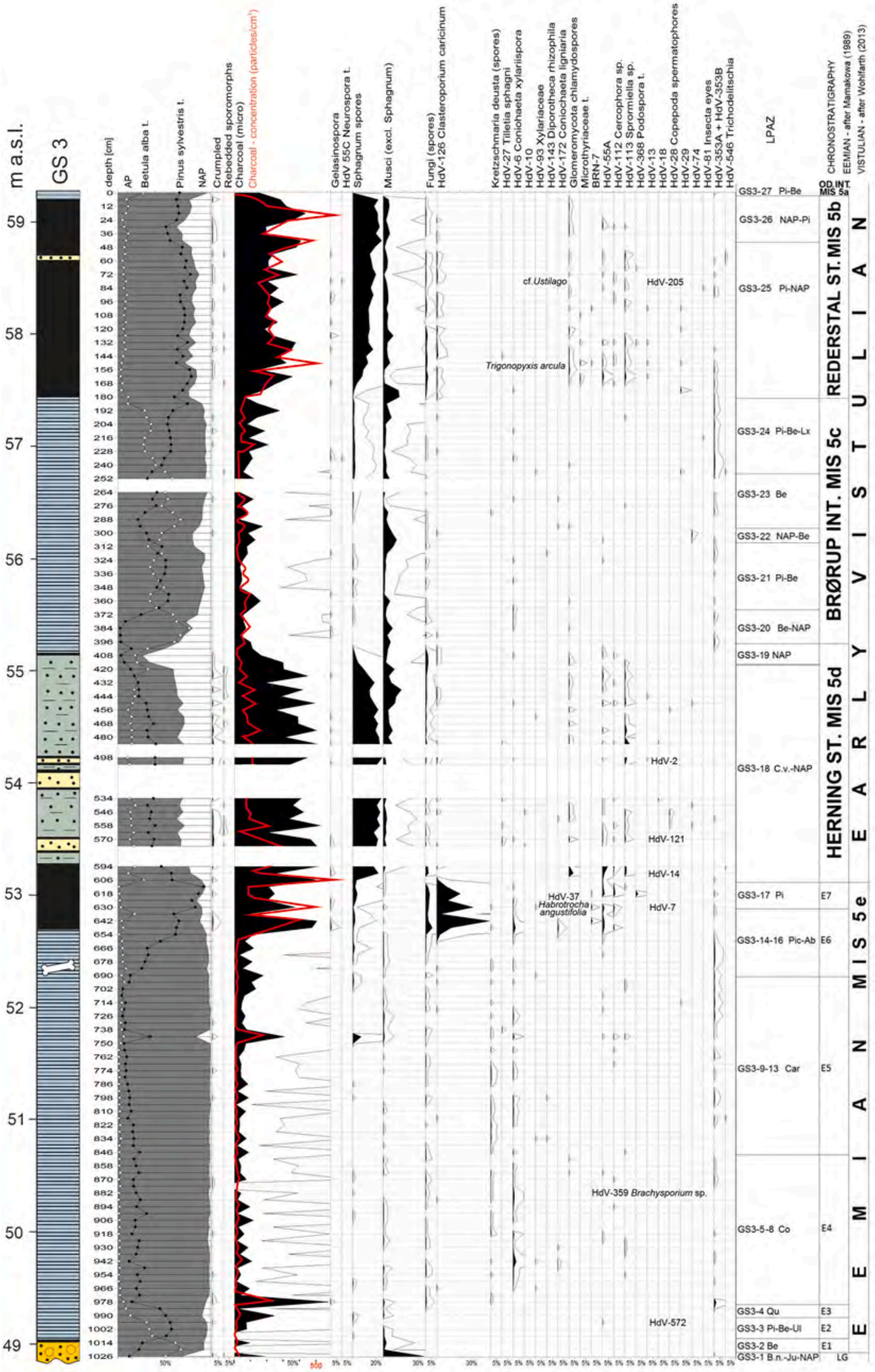


Fig. 3d. Percentage pollen diagram presenting all the curves of other taxa, including crumpled and rebedded sporomorphs, Musci and Fungi spores and various Non-Pollen Palynomorphs indicators in the GS3 profile. Abbreviations like in Fig. 3a. Lithology like in Fig. 2. Extension of names in text. Analysed by A. Hrynowiecka, M. Karpińska-Kołaczek and P. Kołaczek.

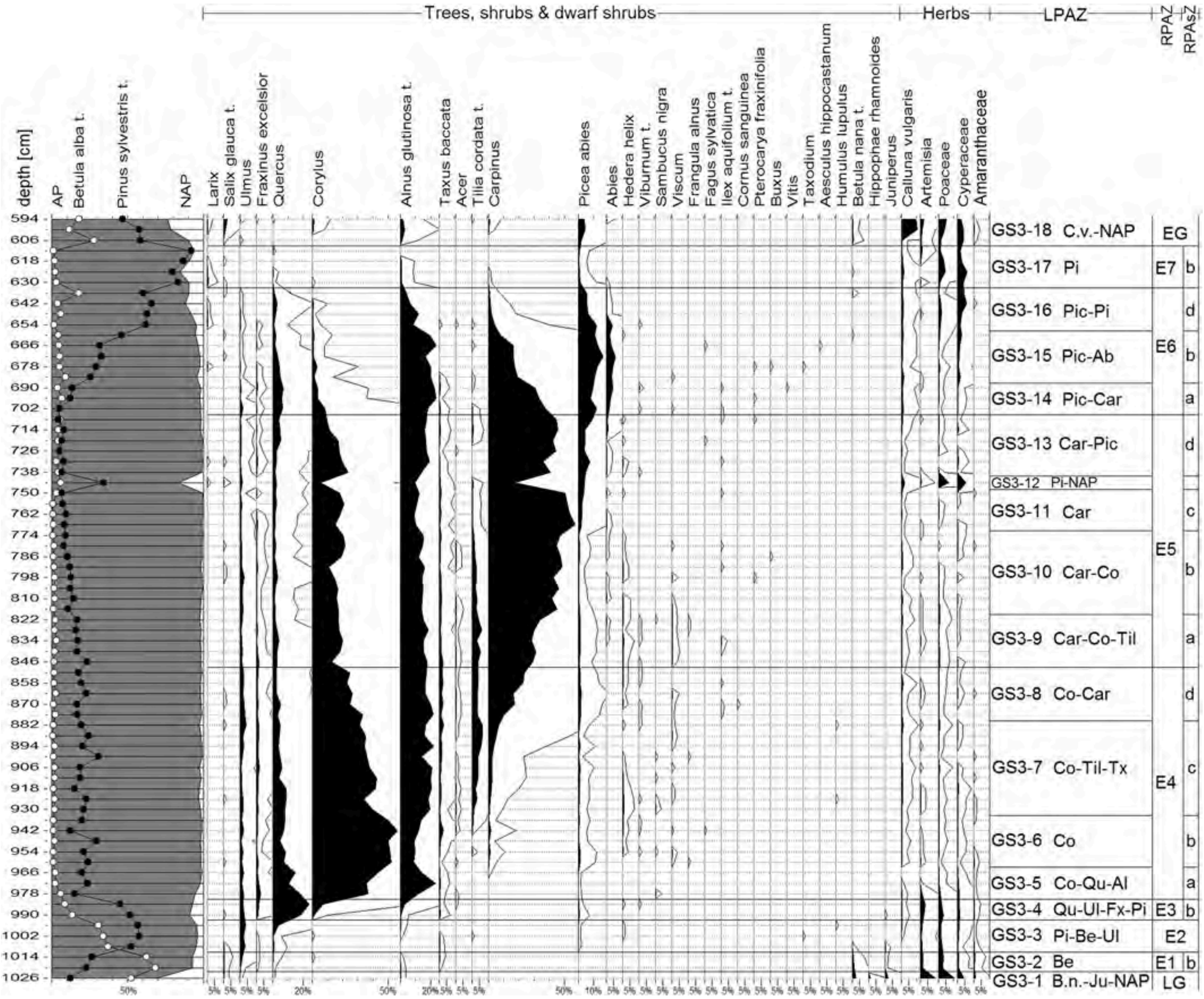


Fig. 4. A detailed division of GS3 profile in Eemian Interglacial part including Regional Pollen Assemblage Zones (RPAZ) after Mamakowa (1989) and Regional Pollen Assemblage Subzones (RPAsZ) after Kupryjanowicz and Granoszewski (2018). Abbreviations like in Fig. 3a. Analysed by A. Hrynowiecka.

samples (at 138 and 930 cm, respectively), and other taxa were sporadically found in a few samples, especially in the middle and upper part of the profile.

Diatom frustules were not observed in most samples, whereas single frustules characterised by high dissolution occurred in a few samples spanning the whole profile (depths 126, 348, 480, 630, 726, 858, 870 cm). Samples from 1014, 1020 and 1026 cm (lowermost part of the GS3 profile, Fig. 3c) contained numerous strongly dissolved diatom frustules.

4.2. Macroremains, woods, and Coleoptera

The analysed sediments were exceptionally rich in plant macroremains. The presence of 122 taxa was noted, including higher plants (92), lower plants (2), fungi (1), and 19 taxa determined to genus, 5 taxa – to family, 1 – to section, 3 – to phylum, and 3 to genera of animal remains. Among wood fragments, 9 taxa of various rank belonging to trees and shrubs were determined.

Plant macroremains and wood fragments are presented on the joint diagrams (Fig. 5a, b, 5c) and assembled in 23 LMAZs (Local Macrofossil Assemblage Zones). The subdivision was based on the presence of one or several most abundant or characteristic and diagnostic taxa for a given level. The zonal boundaries were distinguished on the basis of the presence, increase or decrease in the abundance of abundant or index taxa. The taxa were assembled in groups according to similar morphology into trees and shrubs (23), and the most commonly inhabited sites, i.e. wet and moist habitats (34), peatbog plants (21), reed swamp plants (6), and water plants (33).

The presence of bioindicators and species diversity within the ecological groups of selected local assemblages of plant macroremains have allowed to distinguish 13 LMAZs belonging to a warm unit corresponding to the Eemian Interglacial (MIS 5e). Taxa characteristics of the Eemian Interglacial were determined: *Salvinia natans* [(Linnaeus) All., 1785], *Dulichium* sp., *Trapa natans* (Linnaeus, 1753), and *Brasenia holsatica* [(Web.) Weber.]. Species characteristic of glacial periods, i.e.: *Betula nana* (Linnaeus, 1753), *Selaginella selaginoides* [(Linnaeus) P. Beauv. ex Schrank and Mart., 1892], *Najas tenuissima* [(A. Braun ex Magnus) Magnus, 1870], *Potamogeton alpinus* (Balb., 1804), *Potamogeton filiformis* [(Pers.) Börner, 1912], and *Hippuris vulgaris* (Linnaeus, 1753) occurred in 10 LMAZs related with the cold unit of the Early Vistulian Glaciation (MIS 5 d-a).

Very fine remains of beetles (Coleoptera) from 11 families have been encountered in 75 samples. The most common were representatives of

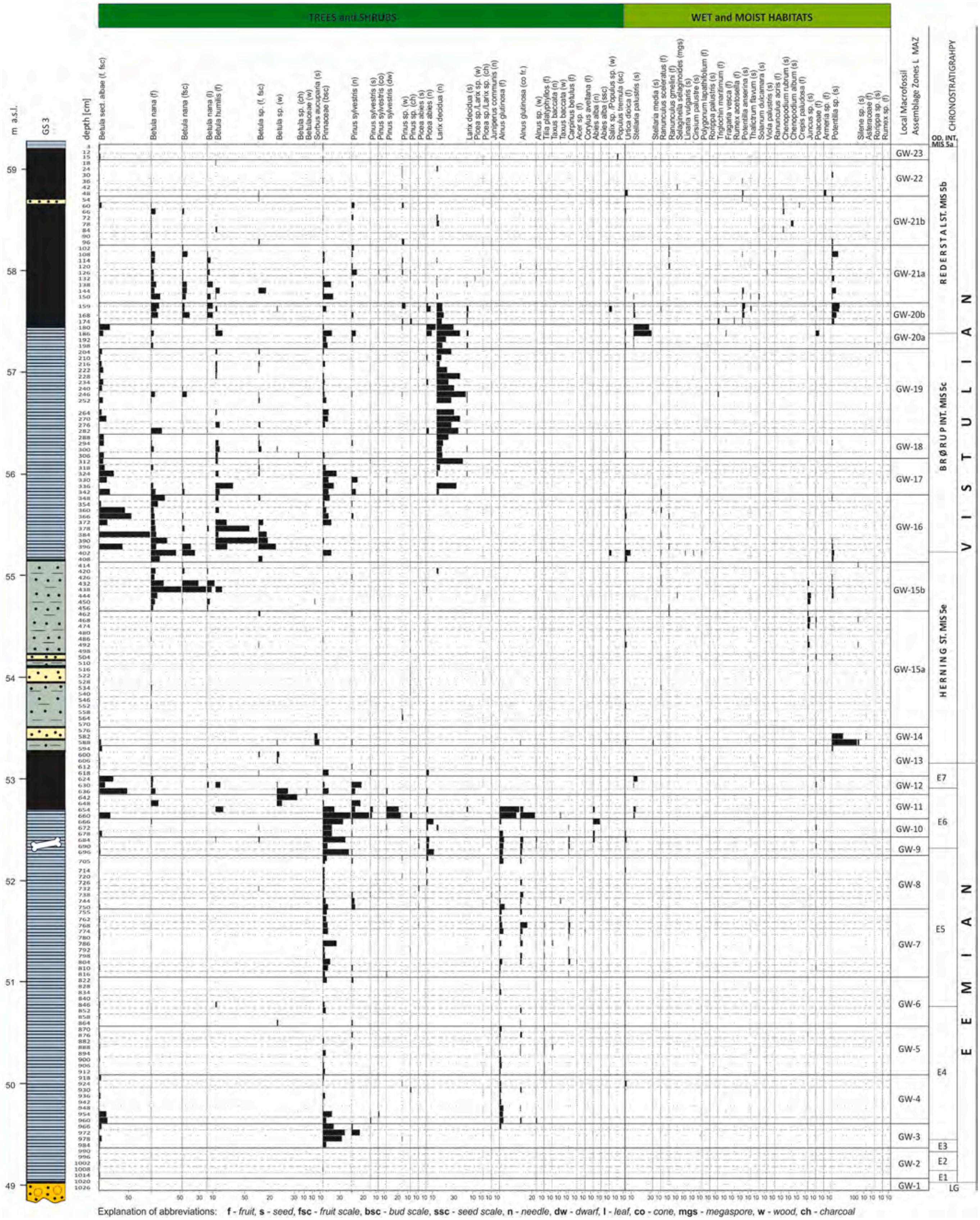


Fig. 5a. Qualitative and quantitative results of macroremains and wood fragments in the GS3 profile – trees and shrubs. Analysed by R. Stachowicz-Rybka, K. Stachowicz and M. Moskal-del-Hoyo.

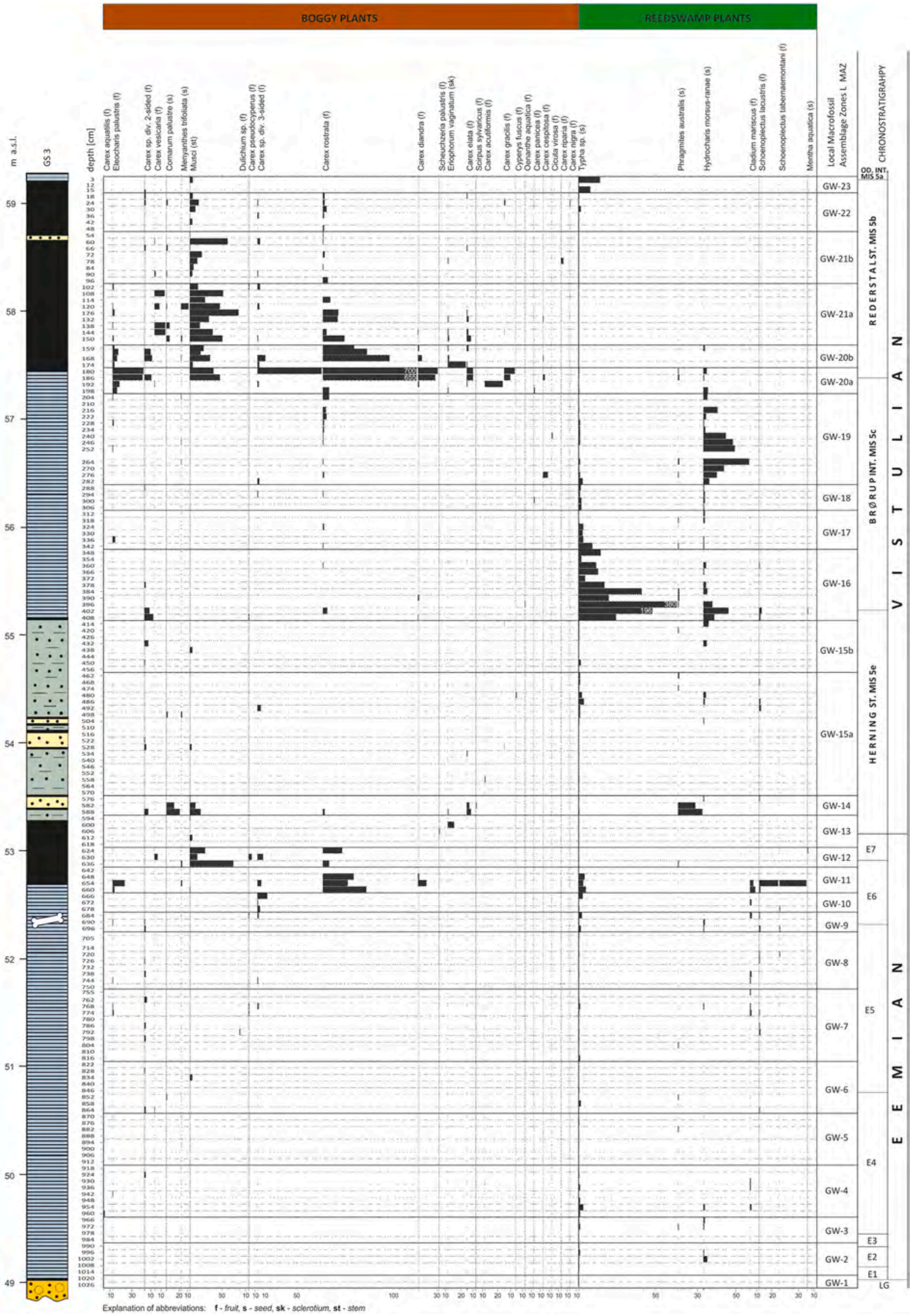


Fig. 5b. Qualitative and quantitative results of macroremains in the GS3 profile – boggy and reedswamp. Analysed by R. Stachowicz-Rybka and K. Stachowicz.

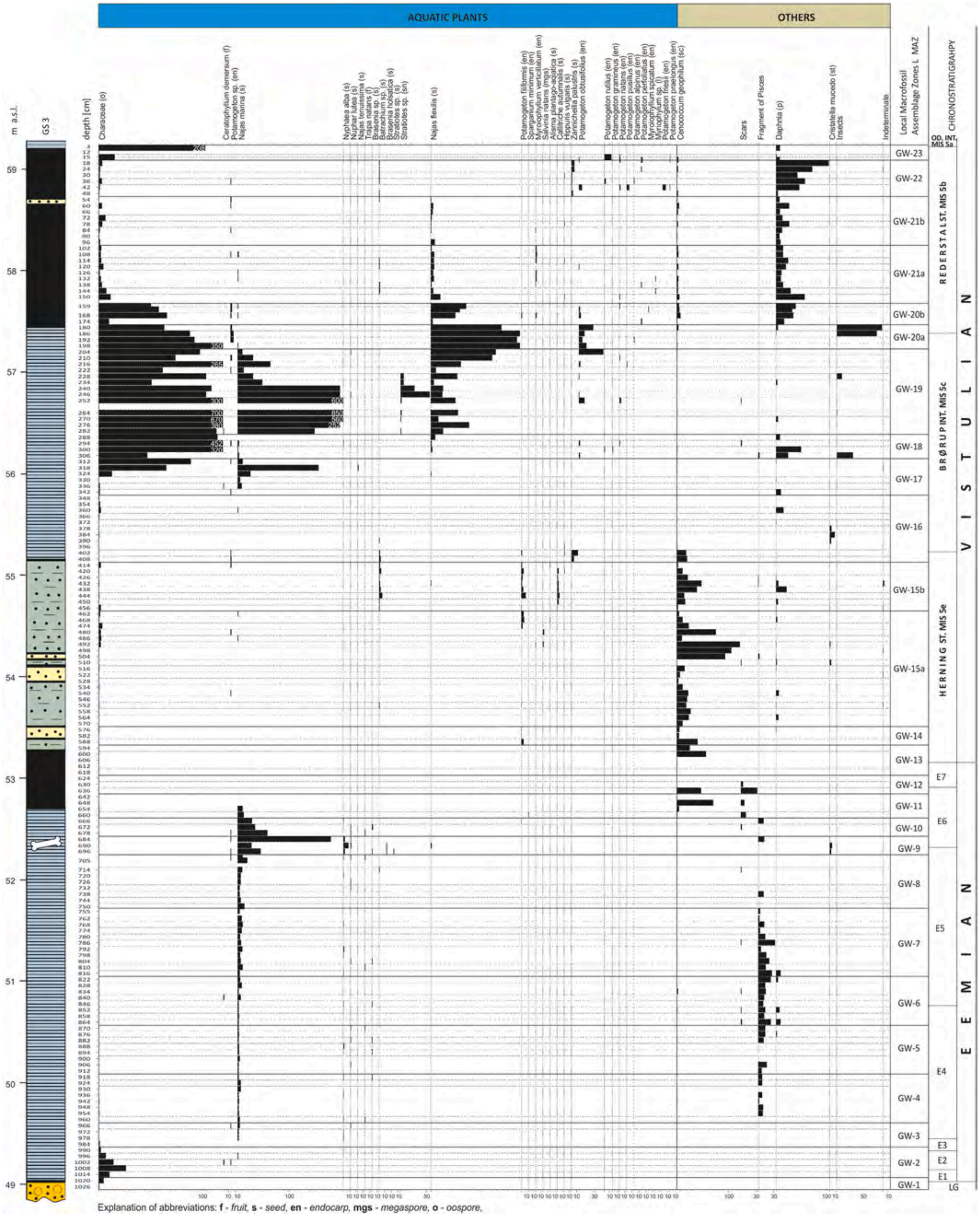


Fig. 5c. Qualitative and quantitative results of macroremains in the GS3 profile – aquatic and others. Analysed by R. Stachowicz-Rybka and K. Stachowicz.

the Carabidae (27 samples), Scarabaeidae (7 samples) and Chrysomelidae (7 samples; Fig. 8). The remaining families were represented in only a few samples: Staphylinidae (in 2 samples), Elateridae (1), Anobiidae (3), Ptinidae (2), Cucujidae (2), Cryptophagidae (1), Lagridae (2) and Curculionidae (3) (Fig. 8). Some beetle fragments were so fine that they could not be assigned even to family. None of the encountered fragments could be assigned to genus or species. A complete individual of Stegobium paniceum (Ptinidae) was noted at 834 cm, but with high probability it represents a much younger (present-day?) form compared to the other coleopterid fragments.

4.3. *Cladocera*

The analysed sediments contain 19 species of Cladocera belonging to the families: Chydoridae (14 species), Eurycercidae (1), Sididae (1), Daphnidae (1), and Bosminidae (2). They were classified into three littoral habitat preference groups: bottom-dwelling, associated with vegetation, and restricted to vegetation species (Whiteside, 1970; Hofmann, 1986; Whiteside and Swindoll, 1988; Korhola, 1990); open water species were also categorised. The Chydoridae include littoral species. Planktonic species belong to the Bosminidae and Daphnidae. Compared to other Eemian profiles, the Eemian part of GS3 profile contains a relatively low number of species and remains of Cladocera, with diagnostic features difficult to identify. Their remains in the Early Vistulian were much better preserved and more abundant. Cladocera species were identified in the entire profile except depth intervals 984–1026 cm (Cladocera Assemblage Zone I – CAZ I) and 606–654 cm (CAZ III). Two species had an exceptional dominance in the reservoir: *Chydrous sphaericus* (O.F. Müller, 1776), a eurytopic species with a wide environmental tolerance that could occur in diverse settings, and *Alona affinis* (Leydig, 1860) related to the macrophyte zone, living in clean calm waters (Flössner, 1972).

Based on the absolute and percentage content of the Cladocera individuals in 1 cm^3 of sediment, and total number of individuals and species, 6 main phases and 6 sub-phases of Cladocera assemblages – CAZs (Cladocera Assemblage Zones) were distinguished (Fig. 6a and b). The first three zones (CAZ I-III) are related to the Eemian Interglacial – they are characterised by greater species diversity and the presence of thermophilic species (Camptocercus, Pleuroxus). Zones IV-VI correlate with the glacial period, characterised by a smaller amount of remains (sometimes complete absence), lower biodiversity, dominance of species resistant to adverse conditions, including cold. The exception is CAZ V – correlated with the Brørup Interstadial (MIS 5c) period in which the species composition reflects interglacial conditions more.

4.4. *Chironomidae*

54 morphotypes of the Chironomidae were identified in 45 samples of lake sediments collected from depth interval 600−210 cm. The most commonly occurring taxa include: *Chironomus* (Meigen, 1803), *Corynocera* (Zetterstedt, 1838), *Microtendipes* (Kieffer, 1922), *Paratanytarsus* (Thienemann and Bause, 1913), *Tanytarsus* (Van der Wulp, 1874) and *Sergentia* (Kieffer, 1922). The most abundant taxa were represented by *Chironomus*, *Corynocera* and *Tanytarsus.* The most abundant Chironomidae were noted in depth interval 417−477 cm (51 to a maximum of 82 fragments, Fig. 7). In depth interval 555−579 cm the number of identified individuals varied from 46 to 51, and at 309 and 501 cm–52 and 54 individuals, respectively. In the remaining samples the accumulation of Chironomidae was between 1 and 40 specimens. Averagely, 30 subfossil Chironomidae have been counted in each sample.

Samples collected from below 6 m were removed from palaeoenvironmental interpretation due to the very low Chironomidae abundance averagely reaching 4 fragments, and the selective preservation of head capsules.

5. Interpretation and discussion

5.1. *Environmental evolution*

5.1.1. *Before the life of the forest rhino*

5.1.1.1. Late Wartanian Glaciation (MIS 6). Sedimentation in the palaeobasin began when tundra-moss communities with *Betula nana*, Cyperaceae and numerous mosses (Musci), and steppe communities with Poaceae, *Artemisia* and rich herbaceous vegetation prevailed in its vicinity (GS3-1 LPAZ, *Betula nana-Juniperus*-NAP LPAZ, Fig. 3a). Single *Pinus* trees, *Juniperus* and *Hippophäe rhamnoides* (Linnaeus, 1753) shrubs grew occasionally (Fig. 3a). Such communities indicate cold climate conditions of the Late Glacial, which should be correlated with the Late Saalian (Wartanian) Glaciation, and are comparable to Late Glacial successions from other sites. They are similar particularly with regard to *Juniperus* occurrence. However, among sites located close to the range of the Wartanian Glaciation, the sites located to the west of GW had a higher content of *Hippophäe rhamnoides* (e.g. Hinterste Mühle site: Menke and Tynni, 1984; Börner et al., 2018), while to the east this shrub had a minor significance in the landscape (e.g. Dziewule site: Bińka and Nitychoruk, 2001; Horoszki Duże site: Granoszewski, 2003, Fig. 1b). Both taxa preferred sandy substrates, exposed habitats, were resistant to drought and did not tolerate shade (Stewart et al., 1994; Li and Beveridge, 2003).

Analysis of macroremains in two basal samples from GS3-1 LMAZ, encompassing the terminal part of the Saalian Glaciation, does not allow for a wider interpretation. Rare charcoals and Characeae oospores are present. The presence of charcoals is very common and characteristic of terminal glacial periods. Such phenomena are often observed in Younger Dryas sediments (Van der Hammen and Van Geel, 2008) and interpreted as accumulations of large volumes of undecomposed biomass during climate transition from interstadial to cold. The undecomposed biomass became a perfect fuel for vast fires. Charcoals were later transported with eolian sand over a sparsely vegetated area even for large distances. In the GW site they were accumulated in a relatively deep reservoir (Fig. 9) dominated by the Characeae (Fig. 5c). A similar case is observed in Nakło (Noryśkiewicz, 1979) and Hinterste Mühle (Börner et al., 2018), where Characeae oospores were noted in Late Wartanian and early interglacial sediments.

The forest rhino could not have lived in the vicinity of the analysed lake in the Late Glacial (MIS 6) due to cold climate and the limited availability of vegetation that it could have fed on (Grübe, 2003; Kahlke and Kaiser, 2011; Van Asperen and Kahlke, 2015; Stefaniak et al., 2020a).

5.1.1.2. Early Eemian (MIS 5e)

5.1.1.2.1. Betula phase (E1 RPAZ after Mamakowa, 1989). Slight climate warming resulted in conditions typical of pioneer birch forests (GS3-2 LPAZ, *Betula* LPAZ, Fig. 3a) in the beginning of the Eemian Interglacial in the present-day European Lowlands (e.g. La Grande Pile site: Helmens, 2013; Jammertal: Müller et al., 2005; Ustków: Kołaczek et al., 2012; Horoszki Duże: Granoszewski, 2003; Medininkai: Satkūnas et al., 2003, Fig. 1b). Very high contents of *Betula* pollen point to the dominance of birch in sunlit and sparse forests, in which herbaceous plants densely overgrew the forest floor.

The diatom frustules dissolved as a result of the high content of carbonates in the sediment (Newberry and Schelske, 1986; Ryves et al., 2006) are numerous in both the birch (E1 phase) and Late Glacial phases (Fig. 3c). Although the diatoms cannot be taxonomically assigned, they probably represent *Pinnularia* (Ehrenberg, 1843), as shown by frustule size, their massive character and characteristically bent terminations of the fracture in most specimens. Commonly, *Pinnularia* species occur in oligo- and dystrophic, often acidic waters, in springs, peat waters, on marshes and bogs. Therefore, oligotrophic conditions are thus

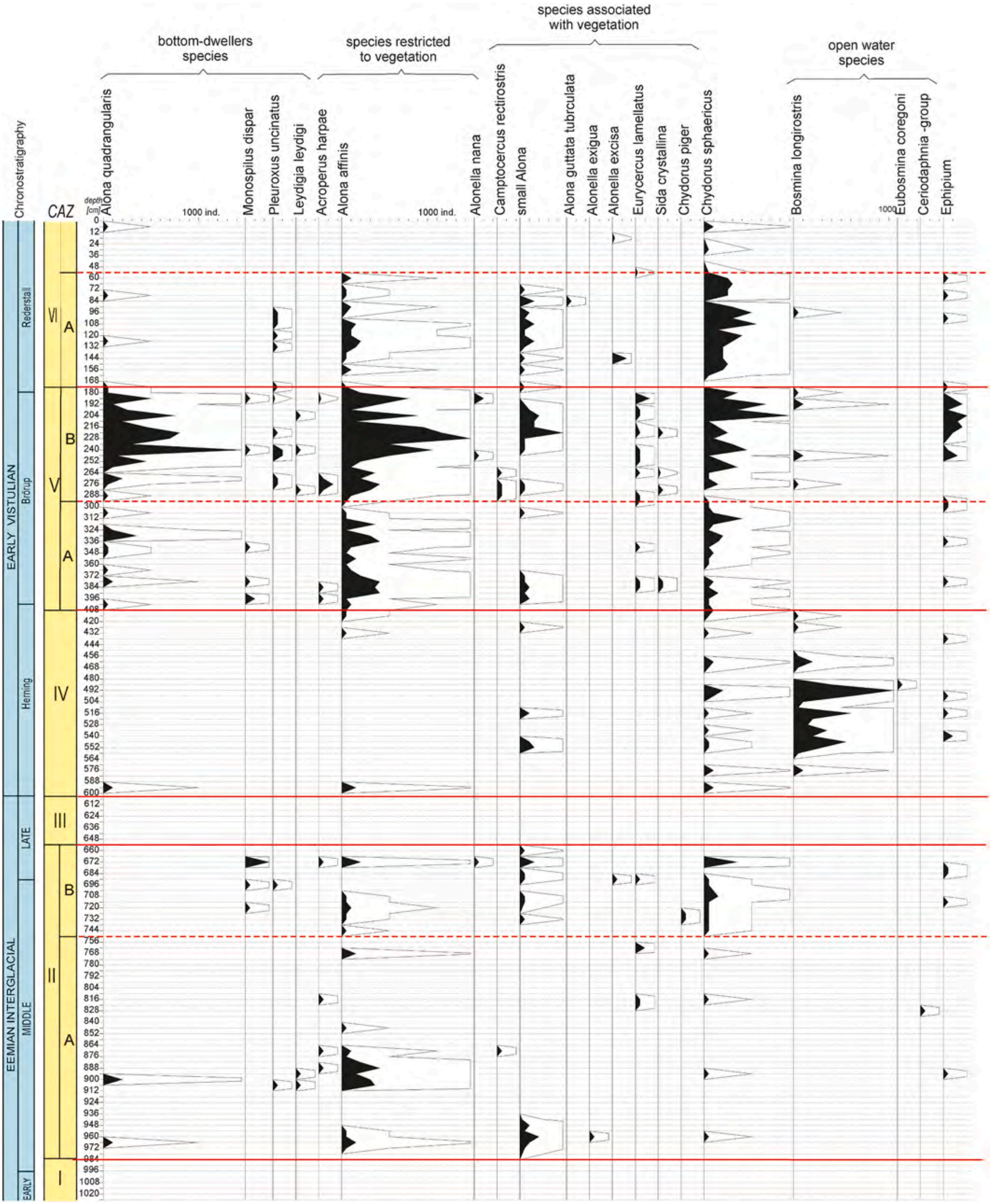


Fig. 6a. Relative abundance diagram of subfossil cladoceran taxa in the sediments of the GS3 profile. CAZ – Cladocera Assemblage Zones; LPAZ – Local Pollen Assemblage Zones (like in Fig. 3a); ind. - individuals. Analysed by M. Niska.

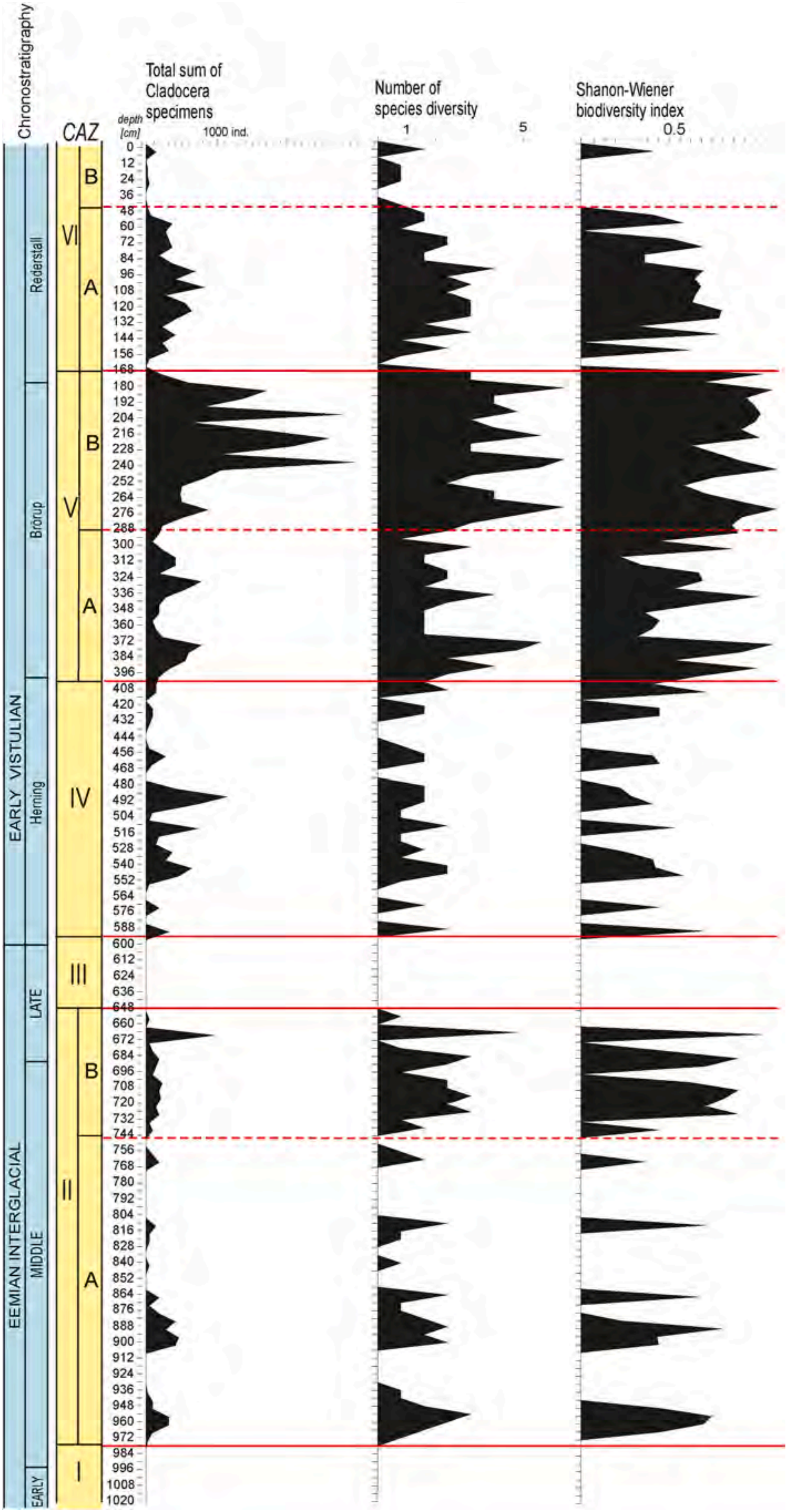


Fig. 6b. Diagram of Cladocera specimens' total number and number of species diversity in the GS3 profile. Abbreviations like in Fig. 6a. Analysed by M. Niska.

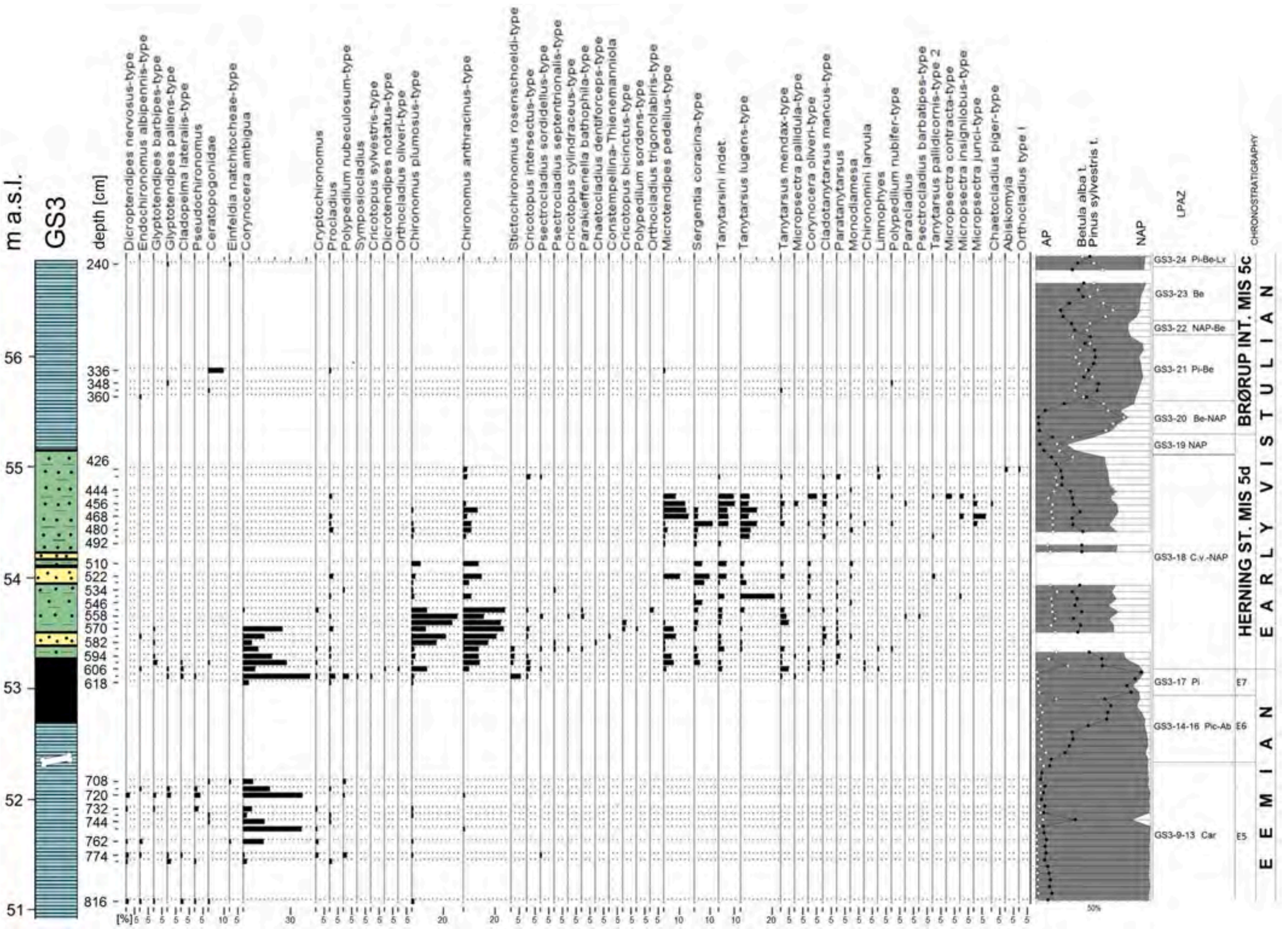


Fig. 7. A quantitative diagram presenting occurring all the Chironomidae taxa in the GS3 profile in correlation to the palyno-, and chronostratigrapy. Abbreviations like in Fig. 3a. Analysed by B. Kotrys.

postulated for the analysed lake. However, the degree of frustule destruction clearly indicates that diatoms with frustules less saturated with silica, i.e. less resistant to dissolution, could not be preserved. Thus, environmental conditions cannot be determined in this case.

5.1.1.2.2. Pinus-Betula phase (E2 RPAZ after Mamakowa, 1989). Further improvement of climate conditions (both thermal and humidity) caused that birch trees began to be accompanied and later dominated by *Pinus* (GS3-3 *Pinus-Betula-Ulmus* LPAZ; Table 2), which led to the formation and dispersal of boreal pine forests (Fig. 3a, high values of *Pinus* pollen). In more humid areas, forest stands comprised *Ulmus* with ferns and sedges (Fig. 3b). At a strongly developed water network, the proportions of *Ulmus* could azonally reach very high values in this phase of the Eemian (like in e.g. Jammertal site: Müller et al., 2005; Solniki site: Kupryjanowicz, 2008, Fig. 1b), whereas typically, as in the case of profile GW, they remained on a low, however not negligible, level. Birch dominance is evidenced in the results of plant macroremains analysis for GS3-2 LMAZ (Fig. 5a). Beside Pinaceae bud scales, these are the only tree remains observed in this interval. A reed zone with *Typha* sp. and *Hydrocharis morsus-ranae* (Linnaeus, 1753) began to develop along the lake margins. Abundant Characeae oospores evidence intense development of charophyte meadows on the deep lake bottom (Fig. 5c). Generally they occur in standing waters, usually with a neutral to slightly alkaline reaction and increased calcium carbonate content. A few examples of *Ceratophyllum demersum* (Linnaeus, 1753), *Najas marina* (Linnaeus, 1753) and *Potamogeton* sp. have also been noted pointing to gradual increase in water temperature, and thus also in the environment gradual increase of climate conditions. *Tetraedron minimum* [(A. Braun) Hansgirg, 1889] (Fig. 3c) characterising eutrophic reservoirs (Messyasz, 2006) also appeared regularly, as well as single taxa related with larger biogen availability, e.g. *Aphanizomenon* and *Pediastrum boryanum* var. *boryanum* (Komárek and Jankovská, 2001; Paerl and Paul, 2012, Fig. 5c).

Cladoceran remains have not been observed, most probably due to low water temperature and/or frosty winters. A similar case was observed in Rzecino (Niska and Mirosław-Grabowska, 2015) and Łęczyce (Sokołowski et al., in press) in northern Poland, where Cladocerans were not noted in the Early Eemian. In Hinterste Mühle (Börner et al., 2018), their lower abundance was observed in comparison to the late Saalian, suggesting a possible cooling in the beginning of the Eemian Interglacial (E1 and E2 phases) in reservoirs located in the northern part of Central European countries (southern coast of the PreBaltic Sea).

In the beginning (E1 and E2 phases), malacological data showed numerous *Bithynia tentaculata* (Linnaeus, 1758) indicating the shallow, nearshore part of the littoral zone. This species was gradually being replaced by *Valvata piscinalis* (O.F. Müller, 1774), suggesting a slight deepening of the lake (Alexandrowicz et al., 2021) which can be correlated with begin of *Quercus* phase (E3).

5.1.1.2.3. Quercus phase (E3 RPAZ phase after Mamakowa, 1989). Further climate warming and rising humidity, and water network development resulted in the dispersion of riparian forests with *Ulmus*, *Fraxinus* and rare *Alnus*. A significant role of these communities in the landscape is confirmed by the percentage pollen content of *Ulmus* and

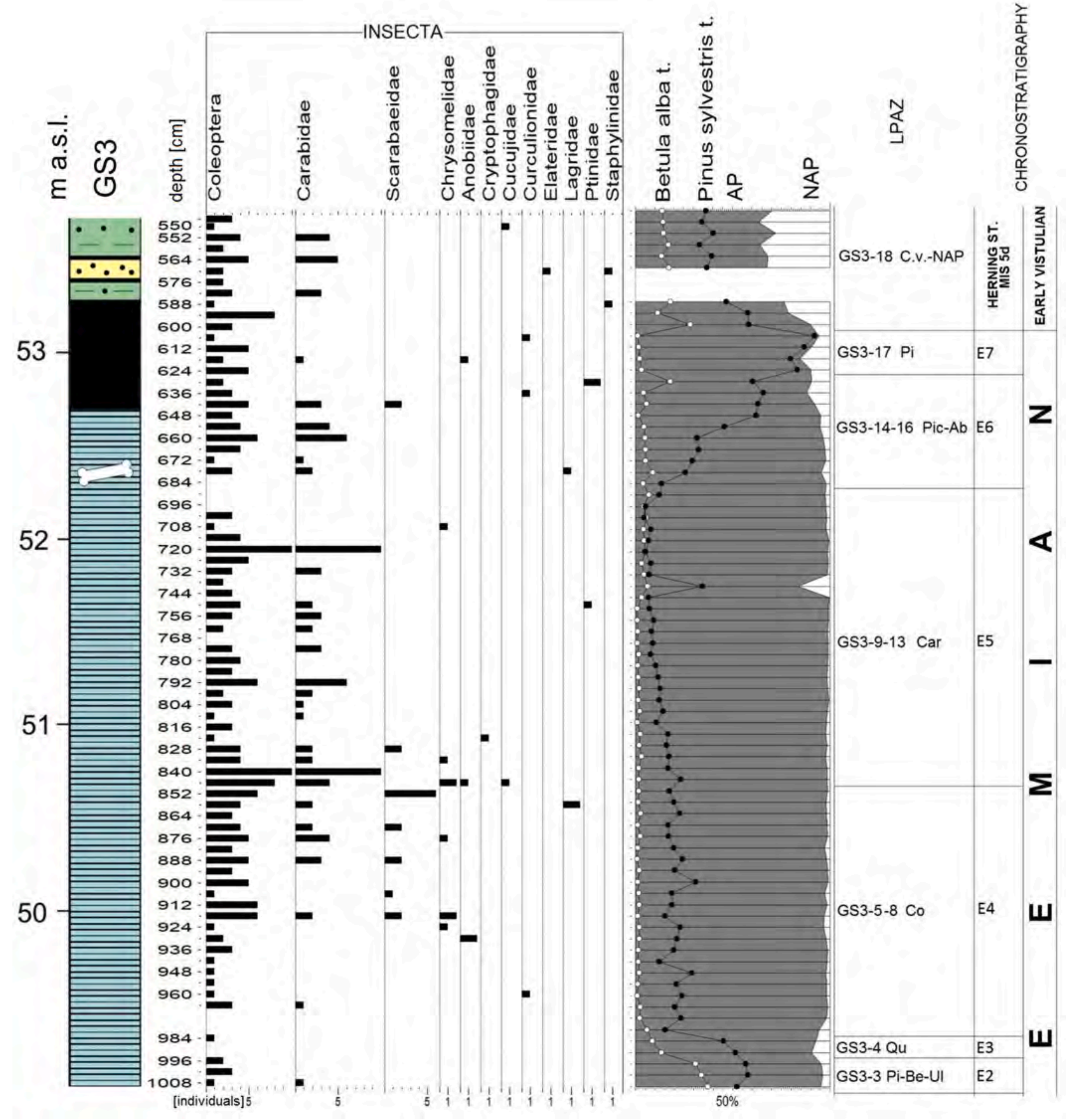


Fig. 8. A quantitative diagram presenting occurring all the Coleoptera taxa in the GS3 profile in correlation to the palino-, and chronostratigrapy. Abbreviations like in Fig. 3a. Analysed by D. Tarnawski and M. Kadej.

Fraxinus after recalculation in accordance with Andresen indexes (Fig. 10). In turn, dryer habitats were covered by sunlit oak woods with *Quercus* and *Pinus* (GS3-4 *Quercus-Ulmus-Fraxinus-Pinus* LPAZ, E3a subzonee after Kupryjanowicz and Granoszewski, 2018, Table 2). Development of forests with *Quercus* was favoured by increased January and July temperatures to the first thermal maximum (Pidek et al., 2022). The maximum content of *Quercus*, described by Kupryjanowicz and Granoszewski (2018) as E3b *Quercus*, is observed in the analysed profile in GS3-4 LPAZ (Fig. 4, Table 2).

At that time (GS3-2 and GS3-3 LMAZs), conditions in the lake changed. Characeae meadows were replaced by increasing vegetation preferring shallower waters with a higher trophy, e.g. *Najas marina*, *Nymphaea alba* (Linnaeus, 1753) and *Nuphar lutea* [(Linnaeus) Sibth. and Sm., 1809] (Fig. 5c). Larger availability of nutrients influenced the arrival of new species among *Pediastrum* and *Botryococcus*, and the abundant *Tetraedron minimum* (Komárek and Jankovská, 2001; Messyasz, 2006, Fig. 3c). Climate conditions improved sufficiently for the thermophilic *Trapa natans* to appear among floating macrophytes at the end of E3 phase, whereas increased biogen availability resulted in the entrance of *Aphanizomenon* cyanobacteria (Paerl and Paul, 2012, Fig. 3c

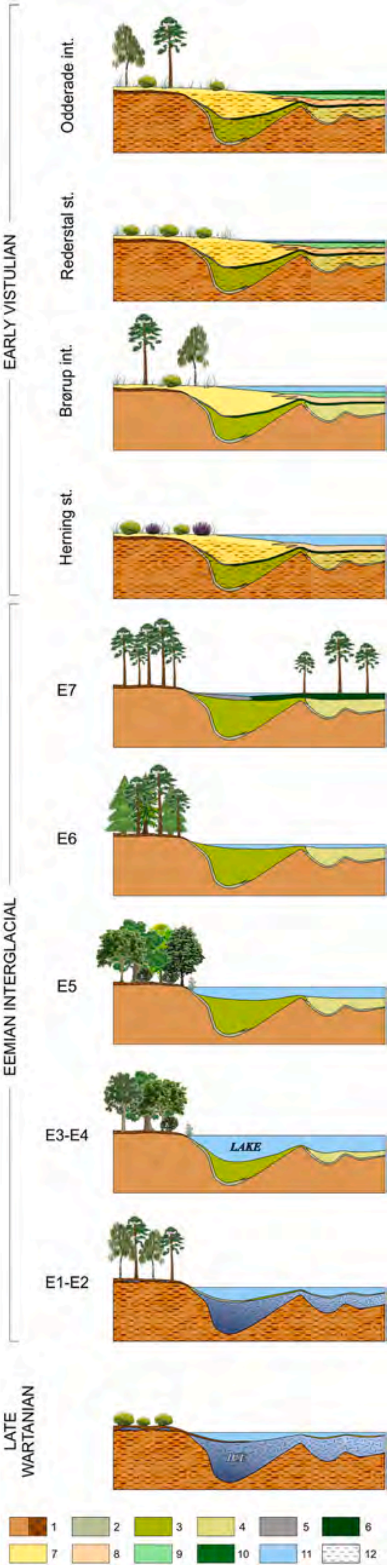


Fig. 9. Model of the evolution of the Gorzów Wielkopolski palaeolake based on the paleoenvironmental analyses. E1–E7 – Eemian phases after Mamakowa (1989); st. – stadial; int. – interstadial. Prepared by K. Łabęcka.

and 5c). A similar macrophyte succession is observed in Imbramowice site (Mamakowa, 1989, Fig. 1b), although the remains of *Trapa natans* and *Trapa* sp. are noted there in the more optimal phases of E4 and E5. Worth attention in profile GS3 is the high participation of tree fragments, particularly woody birches and pines, at the complete lack of terrestrial herbaceous plants. This indicates dense pine-birch forests overgrowing the nearest vicinity of the analysed lake (Fig. 5a).

Lack of Cladocera points to conditions unfavourable for microfauna development. Nutrients such as algae were available, therefore it is rather assumed that Cladocera occurrence was limited by low water temperatures and/or frosty winters.

At the end of this phase, the climate may have dried, as indicated by the high concentration of microcharcoal (Fig. 3d) and the lake became shallower (Fig. 9), which is confirmed by malacological data (Alexandrowicz et al., 2021). At this point, the malacological profile indicates the presence of terrestrial *Succinea putris* (Linnaeus, 1758), *Pseudotrichia rubiginosa* (Rossmässler, 1838)) and temporary water bodies species (*Valvata cristata* (O.F. Müller, 1774)*, V. macrostoma* (Mörch, 1864). This fauna assemblage is typical of flat lake shores and is characterised by wet, swampy, periodically flooded terrestrial biotopes. The periodic appearance of intercalations with terrestrial fauna within successions containing lake mollusc assemblages has been widely described throughout the Holocene European Lowland (e.g., Alexandrowicz, 2013; Meng et al., 2009).

The forest rhino could have lived in the Early Eemian Interglacial, particularly in its terminal phase with *Quercus* dominance. This thermophilic species dwelled in forests and forest-steppes, and was a browser feeding on leaves, tree sprouts and soft vegetation growing on lower stands (Van der Made and Grübe, 2010; Kahlke and Kaiser, 2011; Van Asperen and Kahlke, 2015; Kirillova et al., 2017; Burkanova et al., 2020; Stefaniak et al., 2020a).

5.1.1.3. Middle Eemian

5.1.1.3.1. Corylus phase (E4 RPAZ after Mamakowa, 1989). Corylus intensely encroaching fertile and humid habitats partly superseded *Quercus* (GS3-5 *Corylus-Quercus-Alnus* LPAZ, E4a subzone after Kupryjanowicz and Granoszewski, 2018, Fig. 4; Table 3). A similar phenomenon took place in riparian habitats in the reservoir margins, in places partly flooded by water where alder forests with *Alnus glutinosa* [(Linnaeus) Gaertn., 1791] dominated, and with a small admixture of *Ulmus* and *Fraxinus* (Fig. 3a). Such intense development of communities with *Corylus* and *Alnus* was favoured by precipitation increase at slight decrease of average January and July temperatures (Pidek et al., 2022). Dominating deciduous forests became dense, thus less sunlight reached their floors, influencing the presence of herbaceous plants both in abundance and diversity (slight pollen proportion of herbaceous plants, see Fig. 3b). The steadily rising annual precipitation led to *Corylus* dominance (GS3-6 *Corylus* LPAZ, E4b subphase after Kupryjanowicz and Granoszewski, 2018, Fig. 4; Table 3). At later decrease of annual precipitation, deciduous forests transformed into forests with a larger stand variety. Besides *Corylus*, *Tilia* became abundant, mainly *T. cordata* (Mill., 1768) but also *T. platyphyllos* (Linnaeus, 1771) (GS3-7 *Corylus-Tilia-Taxus* LPAZ, E4c subzone after Kupryjanowicz and Granoszewski, 2018, Fig. 4, Table 3); its actual abundance could have even exceeded that of *Corylus* (Fig. 10). In Eastern Lithuania, *Tilia* pollen participations at that time amounted to even 70% (Šeirienė et al., 2014). *Carpinus* became progressively frequent in riparian forests and *Taxus baccata* (Linnaeus, 1753) started to spread out under the canopy composed of *Alnus*, *Fraxinus* and *Ulmus* (Fig. 3a). The end of the *Corylus* phase was characterised by the gradual distribution of *Carpinus* in deciduous forests (GS3-8 *Corylus-Carpinus* LPAZ, E4d subzone after Kupryjanowicz and Granoszewski, 2018, Fig. 4; Table 3). The poor health of trees are testified by the larger abundance of Xylariaceae (HdV-44 *Kretzschmaria deusta* [(Hoffm.) P.M.D. Martin, 1970] and HdV-93 Xylariaceae) and Coniochaetaceae (HdV-6 *Coniochaeta*

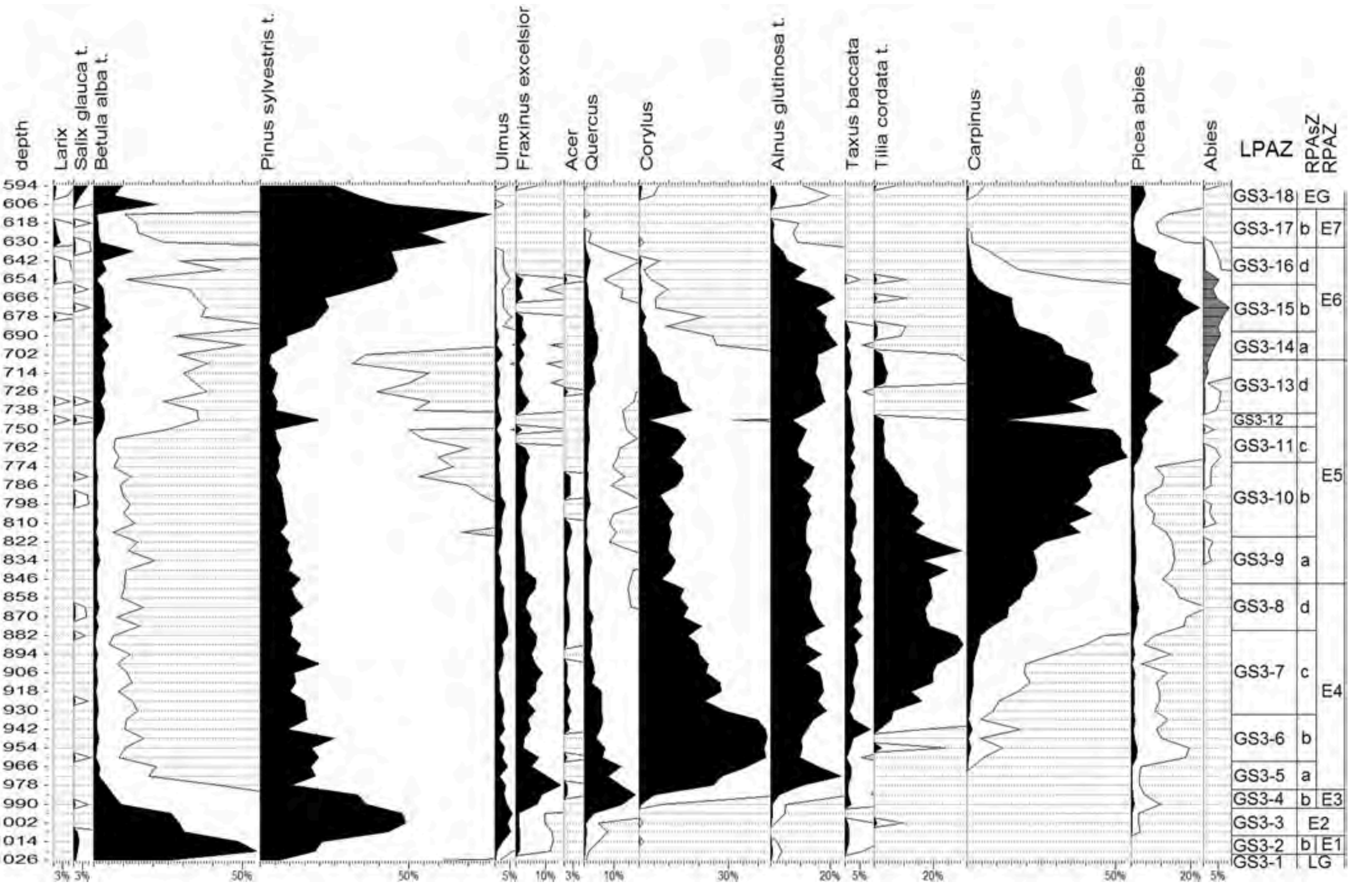


Fig. 10. Selected tree taxa from profile GS3 counted with correction index after Andersen (1973); black – tree taxa count with correction index (Andersen, 1973); grey – tree taxa count like *Picea*, taxa uncounted: *Larix*, *Salix glauca* t., *Taxus baccata*. Analysed by A. Hrynowiecka.

xylariispora [(Cook and Ellis) Sacc., 1882] and HdV-172 *Coniochaeta ligniaria* [(Grev.) Cooke 1887) (Fig. 3d), among which occur saprophytes and plant pathogens, including endophytes (Dennis, 1981; Harrington et al., 2019). *Kretzschmaria deusta*, which is not only a saprophyte species, but also a parasite on various species of deciduous trees, could have occurred in riparian forests (Prager et al., 2012).

E4 RPAZ is recorded in four zones with plant macroremains. GS3-3 to GS3-6 LMAZs, characterised by rather stable conditions of the lake waters. *Najas marina*, *Nymphaea alba*, *Nuphar lutea* and *Trapa natans* dominated among macrophytes, which is confirmed by the presence of trichosclereides of Nymphaeceae among the NPPs (Fig. 3c). The reed zone slightly expanded and contained *Typha* sp., *Phragmites australis* [(Cav.) Trin. ex Steud., 1841] and *Schoenoplectus lacustris* [(Linnaeus) Palla, 1888] (Fig. 5b). *Brasenia* sp. seeds were noted at the end of this phase, in GS3-5 and GS3-6 LMAZs (Fig. 5c). The extant *Brasenia schreberi* (J.F. Gmel., 1791) is a water plant growing in oligo- or mesotrophic environments, in shallow lakes and ponds, and streams with gently flowing waters in eastern Asia, Australia, Oceania, Africa, West Indies, and South, Central and North America. Despite the fact that the taxon has a wide climatic tolerance, from tropical habitats to almost boreal ones, presently this genus does not occur in Europe (Drzymulska, 2018). The appearance of *Brasenia* sp. In the lake may indicate decrease of water trophy probably related with increased humidity and water level rise. This is in accordance with changes in algal composition, i.e. decreased content of *Tetraedron minimum*, a proxy of eutrophic conditions (Messyasz, 2006), and the appearance of *Pediastrum privum*, which occurs in reservoirs with lower trophy and dystrophic conditions (Komárek and Jankovská, 2001; Hindák and Hindáková, 2004, 2008; Pełechaty et al., 2007; Kowalska and Wołowski, 2010, Fig. 3c). This is also testified by the presence of fish skeleton fragments beginning from GS3-4 LMAZ (Fig. 5c). Numerous fish species were described from the Eemian Interglacial in GW by Stefaniak et al. (2020b). Oscillations in the trophic level are evidenced by the abundant cyanobacteria *Aphanizomenon* and *Anabaena* (respectively HdV-600 and HdV-601, Fig. 3d). It is possible that close to the lake animals had access to water, because spores of coprophilous fungi (HdV-55 A *Sordaria*, HdV-112 *Cercophora*, HdV-113 *Sporormiella*; Lee et al., 2022) were recognised (Fig. 3d).

With the beginning of the Middle Eemian, correlated with E4 RPAZ, Cladocera began to occur in the sediment (Fig. 6a and b). In the entire Middle Eemian, however, Cladocera had a low abundance and diversity. The phase was dominated by littoral species, with practically no deep-water species, pointing to relatively small lake depths (Fig. 9). Small *Alona* [including two species A. guttata and A. rectangula (Sars, 1862)] and *Alona affinis*, *Alonella exigua* (Lilljeborg, 1853), *Camptocercus rectirostris* (Schödler, 1862) and *Acroperus harpae* dominated, i.e. species linked with shallow, clean (low productivity) and rather calm waters with a water plants zone (Korhola, 1999), and reaching the highest abundance in reservoirs with the depth of 3 m (Adamczuk, 2014). Two bottom dwelling species suggesting a higher trophic level appeared: *Pleuroxus uncinatus* (Baird, 1850) (with higher thermal requirements) and *Leydigia leydigi* (Schödler, 1863). In turn, the bottom dwelling *Alona quadrangularis* (O.F. Müller, 1776) prefers sites rich in plant substrate among the rocky and muddy substrate, at a slightly higher water level and larger basin size, and is characteristic of β-mesosaprobic waters (Błędzki and Rybak, 2016). Rhabdocoela cocoons which feed on cladocerans (see Schwartz and Hebert, 1982) also appeared (Fig. 3d).

In the central part of E4 phase, an increase in the number of ground beetles (Carabidae) is observed (Fig. 8). Due to the fact that Carabidae are predators mainly active at night, penetrating moist habitats in the soil (litter), microhabitats under stones, under dead wood, their

Table 3

Correlation between LPAZs identified on pollen diagram GS3 profile with reference to RPAZs after Mamakowa (1989, LG – Late Glacial; E – Eemian; EV – Early Vistulian), to subzones after stratigraphy by Kupryjanowicz and Granoszewski (2018; LW – Late Wartanian) and Kupryjanowicz (2008), to Central Germany after Litt et al. (1996, changed; WE – Early Weichselian = Early Vistulian) and Menke and Tynni (1984; SSC – Saale Late Glacial zone C) and for Lithuania after Šeirienė et al. (2014; Md2 – Medininkai (Wartanian) Late Glaciation, M1–M5 – Merkinė (Eemian) phases, Nm_{1a}–Nm_{1b} and J_1–J_2 – Nemunas Stadials and Jonionys Interstadials – stages of Vistulian in Lithuania).

Chronostratigraphy (MIS)	LPAZs from Gorzów Wielkopolski GS3 profile		RPAZ		Subzones of Eemian and of Early Vistulian		Stratigraphic subzones in Central Germany		Lithuanian phases of Merkinė, Nemunas and Jonionys		Phases of vegetation dominance
Odderade Interstadial (MIS 5a)	GS3-27	*Pinus-Betula*	EV4	*Pinus-Betula*	EV4	*Pinus-Betula*	WE IV	*Pinus-Betula*	J_2	*Pinus-Betula*	*Pinus-Betula*
Rederstal Stadial (MIS 5 b)	GS3-26	NAP-*Pinus*	EV3	Poaceae-*Artemisia-Betula nana*	EV3	*Artemisia*-Poaceae	WE III	NAP	Nm_{1b}	NAP-*Betula*	NAP
	GS3-25	*Pinus*-NAP									
Brörup Interstadial (MIS 5c)	GS3-24	*Pinus-Betula-Larix*	EV2	*Pinus-Betula*	EV2	*Betula*	WE IID	*Pinus-Betula*	J_1	*Pinus-Betula*	*Pinus-Betula*
	GS3-23	*Betula*									
	GS3-22	NAP-*Betula*					WE IIC	NAP-*Betula*			
	GS3-21	*Pinus-Betula*					WE IIB	*Pinus-Betula*			
	GS3-20	*Betula*-NAP					WE IIA	*Betula*-NAP			
Herning Stadial (MIS 5 d)	GS3-19	NAP	EV1	Poaceae-*Artemisia-Betula nana*	EV1	*Artemisia*-Cyperaceae-Amaranthaceae	WE IIC WE IB	NAP-Ericaceae *Betula-Pinus*-NAP	Nm_{1a}	NAP-Ericaceae	NAP
	GS3-18	*Calluna vulgaris*-NAP					WE IA	NAP			
Late Eemian Interglacial (MIS 5e)		–	E7	*Pinus*	E7e	*Pinus-Betula*	VII	*Pinus*	M_5	*Pinus*	*Pinus*
		–			E7d	NAP					
		–			E7c	*Betula*					
	GS3-17	*Pinus*			E7b	*Pinus*					
		–			E7a	*Pinus-Picea*					
	GS3-16	*Picea-Pinus*	E6	*Picea-Abies-Alnus*	E6d	*Picea-Pinus*	VIb	*Pinus-Picea-Abies*	M_4	*Picea*	*Picea-Abies*
		–			E6c	*Picea*					
	GS3-15	*Picea-Abies*			E6b	*Picea-Abies*	VIa	*Carpinus-Abies*			
	GS3-14	*Picea-Carpinus*			E6a	*Picea-Carpinus*					
Middle Eemian Interglacial (MIS 5e)	GS3-13	*Carpinus-Picea*	E5	*Carpinus-Corylus-Alnus*	E5d	*Carpinus-Picea*	V	*Carpinus*	M_{3c}	*Carpinus*	*Carpinus*
	GS3-12	*Pinus*-NAP				–					
	GS3-11	*Carpinus*			E5c	*Carpinus*					
	GS3-10	*Carpinus-Corylus*			E5b	*Carpinus-Corylus*					
	GS3-9	*Carpinus-Corylus-Tilia*			E5a	*Carpinus-Corylus-Tilia*					
	GS3-8	*Corylus-Carpinus*	E4	*Corylus-Quercus-Tilia*	E4d	*Corylus-Carpinus*	IVb	*Corylus-Taxus-Tilia*	M_{3b}	*Corylus-Tilia*	*Corylus*
	GS3-7	*Corylus-Tilia-Taxus*			E4c	*Corylus-Tilia-Taxus*					
	GS3-6	*Corylus*			E4b	*Corylus*	IVa	*Quercetum mixtum-Corylus*			
	GS3-5	*Corylus-Quercus-Alnus*			E4a	*Corylus-Quercus*					
Early Eemian Interglacial (MIS 5e)		–	E3	*Quercus-Fraxinus-Ulmus*	E3b	*Quercus*	III	*Pinus-Quercetum mixtum*	M_{3a},	*Quercus-Ulmus*	*Quercus*
	GS3-4	*Quecrus-Ulmus-Fraxinus-Pinus*			E3a	*Quecrus-Fraxinus-Ulmus-Pinus*					
	GS3-3	*Pinus-Betula-Ulmus*	E2	*Pinus-Betula-Ulmus*	E2	*Pinus-Betula-Ulmus*	II	*Pinus-Betula*	M_2	*Pinus-Betula-Ulmus*	*Pinus-Betula*
	GS3-2	*Betula*	E1	*Pinus-Betula*	E1b	*Betula-Pinus*	I	*Betula*	M_1	*Pinus-Betula*	*Betula*
		–			E1a	*Pinus*-NAP					
Late Saalian Gl. (MIS 6)	GS3-1	*Betula nana-Juniperus*-NAP	LG	Cyperaceae-*Artemisia-Betula nana*	LW	NAP	SSC	*Hippophaë-Juniperus*	Md2	NAP-*Pinus-Picea obovata*	NAP

increasing number can be explained by the improvement of humidity conditions (increase in humidity) and the availability of a rich food base (other invertebrates including insects).

5.1.2. During the life of the forest rhino

5.1.2.1. Middle Eemian (continued)

5.1.2.1.1. Carpinus phase (E5 RPAZ after Mamakowa, 1989). The beginning of this phase is marked by the gradual retreat of *Corylus* forest habitats (GS3-9 *Carpinus-Corylus-Tilia* LPAZ, E5a subzone after Kupryjanowicz and Granoszewski, 2018, Fig. 4, Table 3). Increasing dominance of *Carpinus* rose from the significant decrease of annual precipitation as a result of the second thermal optimum (Pidek et al., 2022). Following the appearance of better adapted habitats with *Carpinus*, *Tilia cordata* began to retreat (GS3-10 *Carpinus-Corylus*, E5b after Kupryjanowicz and Granoszewski, 2018), which led to the domination of *Carpinus* in tree stands (GS3-11 *Carpinus*, E5c after Kupryjanowicz and Granoszewski, 2018, Fig. 4, Table 3).

A disturbance in the evolution of deciduous forests is noted in the analysed pollen curves. Stepping of *Pinus* into forest habitats at increased significance of herbaceous plants (Fig. 3a) points to possible local changes of environmental conditions and weakening of deciduous forest stands (GS3-12 *Pinus*-NAP LPAZ, Fig. 4, no correlative in the subzonal subdivision after Kupryjanowicz and Granoszewski, 2018). At that time, a high concentration of microcharcoals was also observed (Fig. 3d), which, with the increase in the proportions of *Pinus*, indicates of influence of a dry continental climate. Weakness of deciduous forest stands was related to the occurrence of tree parasites *Kretzschmaria deusta* and *Coniochaeta xylariispora* (Fig. 3d). A similar change was observed in Beckentin, NE Germany (Hrynowiecka et al., 2021, Fig. 1b). Its lack in other profiles of this part of Europe may be caused by too rare sampling of profiles. The disturbance seems to be short-term and return to *Carpinus* domination was rapid. However, this crysis (especially the appearance of *Pinus*) may have caused soil acidification, resulting in an increasing admixture of *Picea* and *Abies* (GS3-13 *Carpinus-Picea* LPAZ, E5d subzone after Kupryjanowicz and Granoszewski, 2018). Alder forests with *Alnus glutinosa* still dominated on the reservoir margins by the end of E5 RPAZ, although *Picea abies* [(Linnaeus) H. Karst, 1881] appeared in forest stands around the lake.

Deciduous forests rich in shrubs growing around the lake, plants overgrowing the lake margins and soft water plants comprised the optimal biotope for the forest rhino, as confirmed by palaeobotanic studies of food from tooth sinuses of the specimen from GW (Stefaniak et al., 2020a) and other sites with this species. These conclusions are confirmed by the cranium and teeth morphology. Sediments with the rhino skeleton, representing E5 phase of the Eemian and older phases of the Middle Eemian, seem to have been the perfect habitat for the species (Zeuner, 1934; Loose, 1975; Fortelius, 1982; Grübe, 2003; Kaiser and Kahlke, 2005; Van der Made, 2010; Van der Made and Grübe, 2010; Kahlke and Kaiser, 2011; Van Asperen and Kahlke, 2015; Kirillova et al., 2017; Van Geel et al., 2019; Burkanova et al., 2020).

No significant changes took place in the lake with regard to water plants. Conditions were stable through most of E5 RPAZ, and the NPP content including coprophilous fungi was not subject to significant changes (Fig. 3d). The sediment, i.e. fine-detrital calcareous gyttia also did not change much. *Najas marina*, *Nymphaea alba*, *Brasenia* sp. and *Nuphar lutea* still dominated among the macrophytes (Fig. 5c). *Trapa natans* was also present, which suggests that the minimal warmest month temperatures could have reached +21 °C. *Cladium mariscus*.

[(Linnaeus) Pohl, 1809] appeared in the reed zone, suggesting both improvement in climatic conditions and calcium carbonate presence. The reed zone comprised also *Typha* sp., *Phragmites australis*, *Carex pseudocyperus* (Linnaeus, 1753), *Schoenoplectus lacustris* and *S. tabernaemontani* [(C.C. Gmel.) Palla, 1888] (Fig. 5b), which is common for interglacial optima (Stachowicz-Rybka, 2011, 2015). In GS3-8 LMAZ at the end of E5 RPAZ, fish remains were less common, whereas water macrophytes included only *Nuphar lutea*, *Nymphaea alba* and *Najas marina* (Fig. 5c). New taxa, i.e. *Gleotrichia* (HdV-146), *Spirogyra* and Porifera representatives (HdV-220) appeared (Fig. 3d). Sponges (HdV-220) have diverse ecological requirements, however their appearance as late as by the end of this phase points to change of habitat conditions towards more dystrophic (Økland and Økland, 1996). This lies in accordance with local vegetation changes, because higher contents of peatbog plants suggests the expansion of peatbog areas as fens with *Carex* sp. and *Rumex* sp., and reeds with *Typha* sp., *Phragmites australis*, *Carex pseudocyperus* and *Cladium mariscus* (Fig. 5b). This resulted from humidity decrease observed also in the pollen analysis, manifested by a breakdown in the *Carpinus* curve i. a. at the Żabieniec and Jagodne sites (Pidek et al., 2022, Fig. 1b).

The last period of the Middle Eemian (E5 phase after Mamakowa, 1989) was unfavourable for cladocerans but did not influence Rhabdocoela occurrence. Cladocera abundance and diversity decreased (CAZ IIA/B, Fig. 6a and b). At first *Pleuroxus uncinatus* and *Leydigia leydigi* related with the basin bottom and higher trophy disappear from the lake (in result of trophy decrease). *A. quadrangularis* and *Ceriodaphnia* (Dana, 1853) (the latter characterising open waters) also retreated, suggesting a lower water level (Fig. 9). By the end of this interval, *Monospilus dispar* (Sars, 1862) appeared among the bottom-dwelling species, which is linked with sandy substrates, mesotrophic conditions and higher water temperatures. Species linked with macrophytes were also rare. By the end of this phase the frequency of small *Alona* and *Chydorus sphaericus* increases, while *Chydorus piger* (synonym *Paralona pigra*; Sars, 1862) and *Pleuroxus uncinatus* appear, suggesting trophy and temperature increase by the end of E5 RPAZ.

5.1.3. After the life of the forest rhino

5.1.3.1. Late Eemian

5.1.3.1.1. Picea-Abies phase (E6 RPAZ after Mamakowa, 1989). Gradual disappearance of *Carpinus* from deciduous forests with the dominating *Picea* and *Abies*, and the increasing content of *Pinus* (GS3-14 *Picea-Carpinus* LPAZ, E6a after Kupryjanowicz and Granoszewski, 2018, Fig. 4, Table 3) was probably caused by precipitation rise and fall of average January and July temperatures (Pidek et al., 2022). This resulted in the dominance of coniferous forests (GS3-15 *Picea-Abies* LPAZ, E6b subzone, Fig. 4, Table 3). The low proportions of *Abies* in GS3 profile in relation to sites located in south-western Poland (Malkiewicz et al., 2018) are caused by the range of occurrence of this tree in the Eemian Interglacial. The sites in Central Germany are characterised by high shares of *Abies* (like Gröbern: Litt, 1994), in the northern and north-eastern parts of Poland they are very small (i.a. Łęczyce: Sokołowski et al., 2023, in press; Horoszki Duże: Granoszewski, 2003; Solniki: Kupryjanowicz, 2008) and in Lithuania and Belarus this tree did not occur (Medininkai: Satkūnas et al., 2003; Komotowo and Jonionys: Rylowa et al., 2021). Maximum *Picea* abundance (E6c *Picea* subzone after Kupryjanowicz and Granoszewski, 2018) was observed in E6b in profile GS3 (Fig. 4). In turn, the highest values of *Picea* were recorded in Lithuania and Belarus (Rylowa et al., 2021), in central, eastern and north-eastern Poland (Jagodne and Żabieniec: Pidek et al., 2022; Horoszki Duże: Granoszewski, 2003; Solniki: Kupryjanowicz, 2008), while in the west and in Germany its proportions clearly decrease (Imbramowice: Mamakowa, 1989; Grobern: Litt, 1994). Later withdrawal of *Picea* took place with the fall of annual precipitation and temperature increase (Pidek et al., 2022). Such conditions favourable for the better adapted *Pinus* (GS3-16 *Picea-Pinus*, E6d after Kupryjanowicz and Granoszewski, 2018, Fig. 4; Table 3).

Progressive lake shallowing (Fig. 9) resulted in a much richer development of water plants during GS3-9 and GS3-10 LMAZs. *Najas marina*, *Nymphaea alba, Nuphar lutea*, *Trapa natans*, *Stratiotes* sp. and *Brasenia* sp. absolutely dominated among the macrophytes. *Najas flexilis*

[(Willd.) Rostk. and W.L.E. Schmidt] appeared also after the maximal occurrence of *Najas marina* (Fig. 5c). The lake dried up in GS3-11 LMAZ, when plants of the reed zone started to dominate after open water vegetation retreat, as reflected in the NPPs composition (Fig. 3d). Trichosclereids of Nymphaeaceae, cyanobacteria, algae and sponges disappeared (Fig. 3c). Macroremains of *Schoenoplectus lacustris*, *S. tabernaemontani* and *Cladium mariscus* became very abundant (Fig. 5b); presently these plants often form monospecific assemblages. Along with *Typha* sp. they could form assemblages similar to the present-day *Scirpo-Phragmitetum* (Podbielkowski and Tomaszewicz, 1982). The landscape of the lake margins also underwent radical changes. Fruits of *Eleocharis palustris* [(Linnaeus) Roem. and Schult., 1817], *Carex rostrata* (Stokes, 1787), *C. diandra* (Schrank, 1781), and numerous fruits of bi- and tricolpate *Carex* and *Menyanthes trifoliata* (Linnaeus, 1753) (Fig. 5b) indicate that various assemblages of sedge meadows occurred in the vicinity, as confirmed by high contents of HdV-126 *Gaeumanomyces* cf. *caricis* (Pals et al., 1980, Fig. 3d). These areas were most probably willingly visited by animals, as evidenced by the common occurrence of coprophilous fungi in comparison to previous zones. Coniferous forests with *Picea abies* and *Abies alba* (Mill., 1768) are evidenced by their numerous remains, e.g. needles, seeds and seed scales (Fig. 5a). However, *Alnus glutinosa* played the dominating role in humid habitats and at the boundary with the reed zone.

At first in E6 RPAZ (CAZ IIB/III, Fig. 6a and b) the Cladocera diversity remained at the level from E5 RPAZ. The frequency of species with a higher resistance to environmental stress and wider tolerance, e. g. small *Alona* and *Chydorus sphaericus* slightly, increased. Water plants were supplemented by *Alonella nana* (Baird, 1843) and *A. excisa* (Fischer, 1854), which live in smaller and shallower reservoirs with a lower water pH (Krause-Dellin and Steinberg, 1986), and in bogs (Korhola, 1999). Increase of ephippia abundance suggests gradual deterioration of living conditions (environmental stress). By the end of this phase the abundance of all species, including also the Rhabdocoela, distinctly decreased (Fig. 3d), suggesting deterioration of the conditions – water level fall due to drying up.

5.1.3.1.2. Pinus phase (E7 RPAZ after Mamakowa, 1989). Low precipitation and decrease of average temperatures resulted in *Pinus* dominance. Only one subzone of this phase was noted in the profile: GS3-17 *Pinus* LPAZ (E7b after Kupryjanowicz and Granoszewski, 2018, Fig. 4; Table 3), which corresponds to the maximal proportions of *Pinus* in the terminal part of the Eemian. Subzones: E7a *Pinus-Picea* (partly included in GS3-16 *Picea-Pinus*), E7c *Betula* and E7d NAP related to the deterioration of climatic conditions, and E7e *Pinus-Betula* (Table 3) linked with the return to boreal pine forests with *Betula* admixture were not observed. They are particularly characteristic for NE and SE Poland (Kupryjanowicz and Granoszewski, 2018). The top peat layers in which these zones were recorded may have been destroyed by surface runoff in the next stage.

A significant abundance of microcharcoals was observed during this phase, confirming that the climate has become significantly dry and continental (Fig. 3d), which may have intensified fires.

The end of the Eemian Interglacial in GS3-12 and GS3-13 LMAZs is recorded in a peat level, whose topmost part dried up and then was erosionally sheared by the overlying fine clay sands (Fig. 2). The peats are almost devoid of determinable plant macroremains, which unequivocally points to drying up and degradation of this layer. *Carex pseudocyperus*, *C. rostrata*, *Menyanthes trifoliata* fruits and numerous branches of brown mosses from various bog habitats, and large-sedge reeds are preserved in GS3-12 LMAZ (Fig. 5b). HdV-126 *Gaeumanomyces carici* [(Sacc.) Arx and D.L. Olivier, 1952], linked with *C. pseudocyperus in situ* (Van der Wiel, 1982), occurs in large abundance. High contribution of coprophilous fungi points to frequent animal visits (Fig. 3d). Changes in peatbog recharge by oligotrophic rainwater and simultaneous trophy decrease began in GS3-13 LMAZ. *Scheuchzeria palustris* [(Linnaeus) Dulac., 1753] and *Eriophorum vaginatum* (Linnaeus, 1753) appeared at that time. Similar trophy decrease by the end of the Eemian is marked e.g. in Ustków (Kołaczek et al., 2016), where *Sphagnum* sp. was noted. With trophy decrease coupled with temperature fall, the lake margins became dominated by assemblages with *Betula nana* (Linnaeus, 1753), and relatively abundant woody birches and pine.

Sediments from the top of the Eemian Interglacial (CAZ III, Fig. 6a and b) do not contain Cladocera remains, resulting from gradual cooling, further water level decrease, oligotrophisation and drying up of the reservoir (Fig. 9). Similar decrease in the frequency of cladocerans in sediments correlated with E7 RPAZ was also noted in Łęczyce (N Poland, Sokołowski et al., in press), and Hinterste Mühle and Beckentin (Hrynowiecka et al., 2021; NE Germany).

The disappearance of the lake caused by complete shallowing is also confirmed by malacological analysis pointing to relatively numerous terrestrial species (*Succinea putris* (Linnaeus, 1758), *Pseudotrichia rubiginosa* (Rossmässler, 1838) and *Vertigo antivertigo* (Draparnaud, 1801) and periodic water bodies taxa, eg. *Valvata macrostoma* (Mörch, 1864; Alexandrowicz et al., 2021).

The forest rhino probably could not have lived in the vicinity of the lake in E6 and E7 because the area was then overgrown by coniferous forests, not favoured by this species (Van der Made and Grübe, 2010; Kahlke and Kaiser, 2011; Van Asperen and Kahlke, 2015; Kirillova et al., 2017; Burkanova et al., 2020). It would rather browse in the neighbouring areas with a shallowing lake, where plants with soft sprouts grew (Stefaniak et al., 2020a).

The Late Eemian to Early Vistulian transition in the subfossil Chironomidae record points to relatively cool climate with a tendency to temperate, as indicated by Chironomidae preferring habitats of cold and temperately warm waters of oligo-/mesotrophic lakes with mineral and organic-mineral sediments (*Chironomus anthracinus*-type, *Sergentia coracina*-type, *Corynocera ambigua*-type, *Micropsectra pallidula*-type, *Microtendipes pedellus*-type, Fig. 7) (Brooks et al., 2007).

5.1.3.2. Early Vistulian (MIS 5 d-5a)

5.1.3.2.1. Herning stadial (MIS 5 d, GI25-GS25 after Wohlfarth, 2013). Strong climate cooling resulted in the retreat of tree communities and domination of herbaceous plant and moor communities (GS3-18 *Calluna vulgaris*-NAP LPAZ, Fig. 3a and b) with *Sphagnum* patches. *Calluna vulgaris* [(Linnaeus) Hull, 1808] presence is confirmed by the occurrence of its parasite *Meliola ellisii* (Roum., 1880) (HdV-14), while the parasite of *Sphagnum* was *Tilletia sphagni* [(Navashin) Cif., 1953] (HdV-27; Shumilowski et al., 2015, Fig. 3d). Numerous resedimented taxa of thermofilous trees (Fig. 3a) and curve uniformity suggests surface flow; it resulted from precipitation increase and disappearance of vegetation maintaining a compact soil structure. Erosional processes are testified by the presence of Glomeromycota chlamydospores (Kołaczek et al., 2013, Fig. 3d). The long record of this subzone points to fast sedimentation rates. Moor communities grew at the Vistulian ice-sheet range margin, in Lithuania (Medininkai: Šeirienė et al., 2014; Rylowa et al., 2021) northern Poland (Radówek: Urbański and Winter 2005; Rzecino: Winter et al., 2008; Łęczyce: Sokołowski et al., in press), and Germany (Gröbern: Litt, 1994; Hinterste Mühle: Börner et al., 2018, Fig. 1b). Communities with *Juniperus* appeared further to the south (e.g. Ustków: Kołaczek et al., 2016; Zgierz-Rudniki: Mamakowa, 1989; Szklarka: Malkiewicz, 2018, Fig. 1b). Additional cooling and probably further decrease of annual precipitation, i.e. expanding continental climate influence, resulted in the domination of herbaceous vegetation (GS3-19 NAP LPAZ; Fig. 3b). Reservoir margins were regularly visited by animals as indicated by coprophilous fungi (Fig. 3d). The Herning stadial is distinctly bipartite, which is typical for this part of Europe (Malkiewicz, 2002; Urbański and Winter 2005; Kołaczek et al., 2012; Wohlfarth, 2013) and evidenced also in the NPPs record. A significant but short-term change took place at the end of the stadial (GS3-19 NAP LPAZ), when *Tetraedron minimum* was replaced by the widely spreading *Pediastrum boryanum* and Porifera (HdV-220)

(Fig. 3c).

The highest contribution of *Cenococcum geophilum* (Fr., 1829) sclerotia indicates significant redeposition. Sclerocia of this fungus often accompany solifluction processes or erosion of soils devoid of vegetation cover. In GS3-15a LMAZ (Fig. 5a and c) numerous macroremains of herbaceous terrestrial plants, e.g. *Stellaria media* [(Linnaeus) Vill., 1789], *Urtica dioica* (Linnaeus, 1753), and *Ranunculus sceleratus* (Linnaeus, 1753), indicators of cold climate, e.g. *Betula nana*, and water plants, e.g. *Potamogeton filiformis*, *Batrachium* sp. and *Myriophyllum verticillatum* (Linnaeus, 1753) were determined. Among algae dominated *Botryococcus* and *Pediastrum*, with a regular contribution of *Pediastrum kawraiskyi*, linked with low-trophy cooler waters (Komárek and Jankovská, 2001, Fig. 5c). That species is also known from brackish and saline waters (Mensing, 1999; Lenarczyk, 2015) suggesting a higher salinity of the palaeolake, which is in accordance with the high content of lithophilous elements and the highest contributions of elements pointing to erosion (Na + K + Mg/Ca). They reflect more intense mechanical processes of denudation and suggest a sparse vegetation cover in the catchment (Mirosław-Grabowska et al., 2022). A higher sedimentation rate caused by the supply of terrigenous material is evidenced by fine-grained sediments, i.e. muddy sands and muds (Fig. 2). Worth noting is the presence of the megaspore *Salvinia natans*, which is a thermophilous species and thus more obvious for the interglacial optimum. In Imbramowice (Mamakowa, 1989), Ustków (Kołaczek et al., 2016), and Beckentin (Hrynowiecka et al., 2021, Fig. 1b) it dominates in E4-6 RPAZ. In this level its presence is probably also related with redeposition. Despite the fact that in the subsequent GS3-15 b MAZ the content of *Cenococcum geophilum* is still high, other redeposition traces are much fewer. There is a stable presence of taxa pointing to cold climate, i.e. *Betula nana*, and rise of water level, i.e. *Potamogeton filiformis*, *Hippuris vulgaris*, *Callitriche autumnalis* (Linnaeus, 1753) or *Batrachium* sp. (Fig. 5c). Additionally, single occurrences of Nymphaeaceae (trichosclereids and plates, Fig. 3c) indicate lake renovation (Fig. 9). Among water microorganisms more abundant are Cyanophyta, whereas *Tetraedron minimum* is regular and very abundant (Fig. 3c). Its occurrence in this relatively cool interval points to the presence of shallow places in the lake, which rapidly warmed up during the summer allowing for proliferation, and to progressive eutrophication (Messyasz, 2006) resulting from climate change towards more continental as in the younger part of the Herning stadial in western Europe (Germany and Netherlands; Caspers and Freund, 2001). A similar scenario was registered in Ustków located more to the east (Kołaczek et al., 2016). Cold climate and restricted supply of terrigenous material to the lake are confirmed by geochemical data which point to restricted production of organic matter and only sporadic supply of terrigenous organic matter to the lake (Mirosław-Grabowska et al., 2022).

Cladocerans appear again in the lake in this interval (CAZ IV; Fig. 6a and b). The dominating species are more resistant to environmental stress and with a higher tolerance to lower temperatures (cold-tolerant species; Hofmann, 2000): *Chydorus sphaericus*, *Bosmina longirostris* (O.F. Müller, 1776) and small *Alona*. These species may indicate a higher trophy. *B. longirostris* is a deep-water taxon; in unfavourable conditions (higher trophy, lack of nutrients), however, it could migrate to shallower zones. Beside the three dominating species in the initial stage of this phase, in small numbers occurred *Alona affinis* and *A. quadrangularis* (Fig. 6a). Their appearance could correspond to water level rise.

The Chironomidae composition (Fig. 7) supplies data on the relatively stable conditions of the water environment and a temperate cold climate. It shows a higher diversity with taxa preferring both cold and warm waters, and the presence of species characteristic of water reservoirs with an organic or mineral-organic bottom (*Tanytarsus lugens*-type, *Sergentia coracina* (Zetterstedt, 1850), *Microtendipes pedellus*-type, *Tanytarsus mendax* (Kieffer, 1925), *Chironomus anthracinus*-type) (Brooks et al., 2007).

The forest rhino could not have lived in the vicinity of the lake in the Early Vistulian stadial due to cold climate and dominance of dwarf shrub, shrub, and dwarf shrub/steppe vegetation. The region was devoid of trees, which probably prevented the species from inhabiting the area (Van der Made and Grübe, 2010; Kahlke and Kaiser, 2011; Van Asperen and Kahlke, 2015; Kirillova et al., 2017; Burkanova et al., 2020; Stefaniak et al., 2020a).

5.1.3.2.2. Brørup interstadial (MIS 5c, GI24-GS24-GI23 after Wohlfarth, 2013). Improvement of climate conditions enabled the development of sparse pioneer birch forests with strongly dispersed herbaceous vegetation (GS3-20 *Betula*-NAP LPAZ, Fig. 3a and b). Boreal sparse pine-birch forests developed later (GS3-21 *Pinus-Betula* LPAZ). This was the first warmer stage of this interstadial. The mid-interstadial cooling resulted in the retreat of *Pinus* and largely also *Betula*, at a distinct rise of herbaceous plants (GS3-22 NAP-*Betula* LPAZ, Fig. 3a). After the cooling, yet again developed sparse pioneer birch forests (GS3-23 *Betula*) followed by denser pine forests with *Betula*, *Larix* and *Picea*; this was the second warmer stage in this interstadial (GS3-24 *Pinus-Betula-Larix* LPAZ, Fig. 3a). Thus, a tripartite view of this Early Vistulian stage emerges, which is also confirmed by other studies (Wohlfarth, 2013). The similar course of *Betula* and *Pinus* curves are observed in Horoszki Duże and Jałówka located more to the east (Helmens, 2013; Kupryjanowicz et al., 2021), the nearer Kubłowo, Zgierz-Rudniki, and Ustków (Mamakowa, 1989; Kołaczek et al., 2016; Mirosław-Grabowska et al., 2018), and Gröbern and Nochten lying to the west (Litt, 1994; Bos et al., 2001, Fig. 1b). The warmest interstadials intervals (GS3-21 and 24) are also recorded as an increase in proportions of aquatic microorganisms preferring warm/eutrophic waters, i.e. *Anabaena*, *Pediastrum boryanum* var. div. and *Tetraedron minimum* (A.Braun) Hansgirg 1889; Komárek and Jankovská, 2001; Messyasz, 2006; Paerl and Paul, 2012; Fig. 3c). Micoorganisms reacted earlier to improving climate conditions, which is linked with their faster reaction in comparison to higher plants, particularly trees.

In the interstadial beginning, the content of *Cenococcum geophilum* falls quite distinctly (Fig. 5c), which is linked with improving climate conditions and development of a compact vegetation cover, followed by decrease in the intensity of solifluction processes. It is recorded in the lower number of Glomeromycota chlamydospores (Kołaczek et al., 2013) (Fig. 3d). The development of the reed zone as a barrier may also have reduced the influx of remains from the catchment area (Szymczyk, 2015). Significant increase in the contribution of *Typha* sp., *Phragmites australis*, *Schoenoplectus lacustris*, and *Hydrocharis morsus-ranae* (Fig. 5b) preferring shallow eutrophic waters, is observed in GS3-16 LMAZ. Water shallowing (Fig. 9) and eutrophication is marked by *Anabaeana*, high contents of *Pediastrum boryanum* var. div. and *Tetraedron minimum* (Komárek and Jankovská, 2001; Messyasz, 2006; Paerl and Paul, 2012, Fig. 3c), and increased contribution of e.g. *Carex* sp. div, *Urtica dioica*, *Potentilla* sp. and other terrestrial herbaceous plant species (Fig. 5a). Significant water level rise in GS3-17 LMAZ is reflected in increased contents of Characeae and *Najas marina*. The mid-interstadial cooling in GS3-18 LMAZ is recorded in the increased content of ephippia of *Daphnia*, lower content of *Najas marina* and the presence of *Potamogeton gramineus* (Linnaeus, 1753), *P. obtusifolius* (Mert. and Koch, 1823) and *P. rutilus* (Wolfg., 1827) (Fig. 5c). Similarly as in the pollen analysis, *Pinus sylvestris* decreases, being replaced by *Larix decidua* (Mill., 1768), *Betula humilis* (Schrank, 1789) and *B. nana*.

In the Brørup Interstadial, the lake was dominated by the Najadaceae; according to the common succession of this family, at first two species co-occurred with the prevalence of *Najas marina*, to be later dominated by *N. flexilis* (Fig. 5c), which dispersed in the lake as late as in GS3-24 *Pinus-Betula-Larix* LPAZ (Fig. 3a). The expansion of *Najas flexilis* was linked with climate deterioration and increasing dominance of pine and larch, which caused oligotrophy and habitat acidification (Kupryjanowicz et al., 2018b; Bishop et al., 2019). The level with abundant *Najas flexilis* is also rich in *Potamogeton obtusifolius*, which like *Najas flexilis* is an endangered species today.

In the Brørup Interstadial occurred the best conditions for the development of water macrophytes and zooplankton (CAZ V, Fig. 6a), resulting in the highest biodiversity and abundance of Cladocera (max. 3200 individuals/1 cm^3, Fig. 6b). All Cladocera species appeared at that time in the reservoir. Species linked with the lake bottom included *A. quadrangularis* and *M. dispar*, which suggests higher water temperatures and higher trophy (mesotrophy). Lack of open water species in the first part of this interval (CAZ VA) points to low water levels (Fig. 9). Common species dwelling in the water plant zone i.e. *A. affinis*, *A. harpae*, *A. nana*, *C. rectirostris*, small *Alona* and *Eurycercus lamellatus* (O.F. Müller, 1776), i.e. those linked with clean calm waters, suggest that it was wide and rich in nutrients. In turn, *Sida crystallina* (O.F. Müller, 1776), similarly as *Eurycercus*, occurs more readily in larger basins among plants and in electrolyte-rich waters. Due to its size, *Eurycercus* is an important component of fish food. In the second part of this interval (CAZ VB), species occurring earlier became more abundant; moreover, new species pointing to higher trophic levels, e.g. *Pleuroxus uncinatus*, *Leydigia leydigi*, *B. longirostris*, small *Alona* and *Chydorus sphaericus* also appeared. *C. rectirostris* and *P. uncinatus* likewise suggest higher water temperatures. By the end of this interval the abundance of ephippia rose significantly, indicating environmental stress inducing intense sclerotia production. Moreover, the abundance of all species dropped, thus the dwelling conditions must have deteriorated.

The forest rhino could not have lived in the lake vicinity during the interstadial intervals of the Early Vistulian due to unfavourable cold climate and dominance of sparse birch-pine forests. Probably unfavourable climate was the factor restricting its occurrence in the area rather than vegetation, because it could find food in the birch tree patches and the well-developed reed zone. However, in this interval the species did not occur in Europe (Tong and Wu, 2010; Deng et al., 2011; Tong, 2012; Kirillova et al., 2017, 2021; Pandolfi et al., 2017; Shpansky, 2017; Shpansky and Boeskorov, 2018; Pandolfi, 2018; Van Geel et al., 2019; Stefaniak et al., 2020a).

5.1.3.2.3. Rederstal stadial (MIS 5 b, GS23-GI22-GS22 after Wohlfarth, 2013).

Subsequent cooling is evidenced by the more common occurrence of herbaceous plants (GS3-25 *Pinus*-NAP LPAZ, Fig. 3a and b). The climate was also strongly dried, as evidenced by a significant concentration of microcharcoals in sediments (Fig. 3d). Apparently numerous destroyed *Pinus* pollen is from far transport, whereas *Betula* is so rare that it probably did not occur at all in the vicinity of the site. Advancing cooling led to a much higher NAP content in the park tundra (GS3-26 NAP-*Pinus* LPAZ; Fig. 3a and b). At that time, much higher proportions of *Betula* pollen and much lower proportions of *Pinus* pollen at a larger content of NAP pollen are observed in Kubłowo and Zgierz-Rudniki in central Poland (Mamakowa, 1989; Mirosław-Grabowska et al., 2018, Fig. 1b). However, in the nearby Ustków (Kołaczek et al., 2016) these proportions are similar as in profile GS3, pointing to a local character of these relationships. Szklarka and Gröbern located more to the south of the Vistulian ice-sheet range (Litt, 1994; Kühl et al., 2007; Malkiewicz, 2018, Fig. 1b) show rather even values of *Betula* and *Pinus* pollen.

Advancing cooling had an impact on microorganism and water plant composition in the lake and its direct vicinity, restricting green algae occurrence, and reducing and removal of the Najadaceae. They were replaced by boreal vegetation, e.g. *Potamogeton alpinus*, *Hippuris vulgaris*, *Myriophyllum verticillatum*, *Callitriche autumnalis* and *Batrachuim* sp. (Fig. 5c). The rising content of *Daphnia* ephippia suggests deterioration of thermal conditions (Fig. 5c and 6a). With advancing cooling began groundwater level fall and reservoir overgrowing (Fig. 9). In shallow, nearshore waters at first dominated *Eleocharis palustris*, followed by vegetation of humid and peatbog habitats with *Stellaria palustris* (Ehrh. ex Hoffm., 1791), mosses and Cyperaceae, causing more intense reservoir shallowing and overgrowing. *Menyanthes trifoliata* and *Eriophorum vaginatum* indicate periodical oligotrophization in GS3-20 b LMAZ (Fig. 5b and c). The area was willingly visited by animals as testified by abundant coprophilous fungi (Fig. 3d). A higher contribution of *Spirogyra* zygospores was also noted (Fig. 3c). These green algae prefer shallow, well-oxygenated, well-insolated parts of reservoirs and meso-to eutrophic waters (Ulikowski et al., 2015). *Spirogyra* filaments were observed in waters of Central Europe at pH of ca. 6–9 and in a broad conductivity range.

During the Rederstal Stadial cladocerans had a lower diversity and abundance (CAZ VI, Fig. 6a and b). The dominating species was *Chydorus sphaericus*, a species indicating high resistance to unfavourable conditions, often remaining as the only one in the lake at very adverse settings. Eight species dwelled in the lake in the first part of this interval (CAZ VIA). Among those related with the lake bottom remained *Pleuroxus uncinatus*, characterised by higher trophic and thermal requirements, and *Alona quadrangularis* – both species dwell in electrolyte-rich waters with various types of substrates (muddy and sandy). The water plant zone was inhabited by *A. affinis* and small *Alona*. The appearance of *Alona guttata* var. *tuberculata* (Stark, 1930) and *Alonella excisa* may suggest periodical pH decrease (Korhola, 1990). Among deep water species periodically appeared *B. longirostris*, but in small numbers, which may suggest slight water level rise. The second part of this interval (CAZ VIB) was characterised by advancing unfavourable conditions. The number of species fell to only 3 and their abundance decreased to max. 150. Only *Chydorus sphaericus* remained in the lake, and periodically also *A. quadrangularis* and *A. excise*. This was probably the effect of advancing cooling.

5.1.3.2.4. Odderade interstadial (MIS 5a, GI21-GS21 after Wohlfarth, 2013).

The appearance of more numerous *Betula* and lower content of herbaceous plants in the topmost part of the profile suggests slight improvement of conditions (GS3-27 *Pinus*-*Betula* LPAZ; Fig. 3a and b). The decrease in ephippia of *Daphnia*, increase in Characeae and subsequent increase in the reed plants content also confirm slight improvement of climate conditions, and a rise in water level and transparency (Fig. 5c). Among the Cladocera, only remains of *Chydorus sphaericus*, a species resistant to unfavourable conditions, and *Alona quadrangularis*, a bottom-dwelling species, were noted in the lake (Fig. 6a).

5.2. Problematic chronostatigraphy of the Early Vistulian

The first chronological interpretation (Mirosław-Grabowska et al., 2022, Fig. 11) assuming the Pleniglacial age of the post-Eemian sediments in profile GS3, was based on 3 radiocarbon dates, of which one is open (Table 2). Additional OSL dating performed at 59.8 m pointed to an older age of sediments overlying the peats (Table 2, Fig. 2) than the radiocarbon age of the peats. Supplementary radiocarbon analyses of two samples from 56 m to 58.7 m (Table 2, Fig. 2) indicate a similar age for the shallower samples as from earlier datings, and an open date for the deeper samples. This result confirms the trend indicating an older age of post-Eemian sediment than in earlier age determinations (Mirosław-Grabowska et al., 2022). According to palynological analysis performed for sites located close to the ice-sheet range in the Vistulian Pleniglacial period (MIS 4–3; Table 1), AP values do not exceed 10% (e.g. Wola Grzymalina site: Krzyszkowski et al., 1993: Bełchatów and Lublinek sites: Balwierz, 1995; Kuców and Łanięta sites: Balwierz, 2003, Fig. 1b). In profile GS3 lying in the Vistulian ice-sheet range, AP values oscillate from 30% in the coolest interval to even 95% (Fig. 11). Moreover, particular stadial and interstadial intervals distinguished according to the new stratigraphy for profile GS3 show a similar course of pollen curves as in other profiles spanning the Early Vistulian Glaciation. The *Calluna vulgaris* curve in the Herning stadial has a similar course in e.g. Radówek in E Poland (Urbański and Winter 2005), Ustków in Central Poland (Kołaczek et al., 2012), and Hinterste Mühle and Rathenow in NE Germany (Freund, 2000; Börner et al., 2018, Fig. 1b). The Herning stadial, with an older phase loaded with significant redeposition and common moors, and a younger phase dominated by Poaceae, *Artemisia* and Cyperaceae, is distinctly bipartite, which is a typical phenomenon for this cold interval (e.g. Wohlfarth, 2013; Majecka, 2014; Kołaczek et al., 2016). The development of the Brørup interstadial with a mid-interstadial cooling is almost identical in Gröbern (Litt, 1994), Kubłowo (Mirosław-Grabowska et al., 2018), and Jałówka

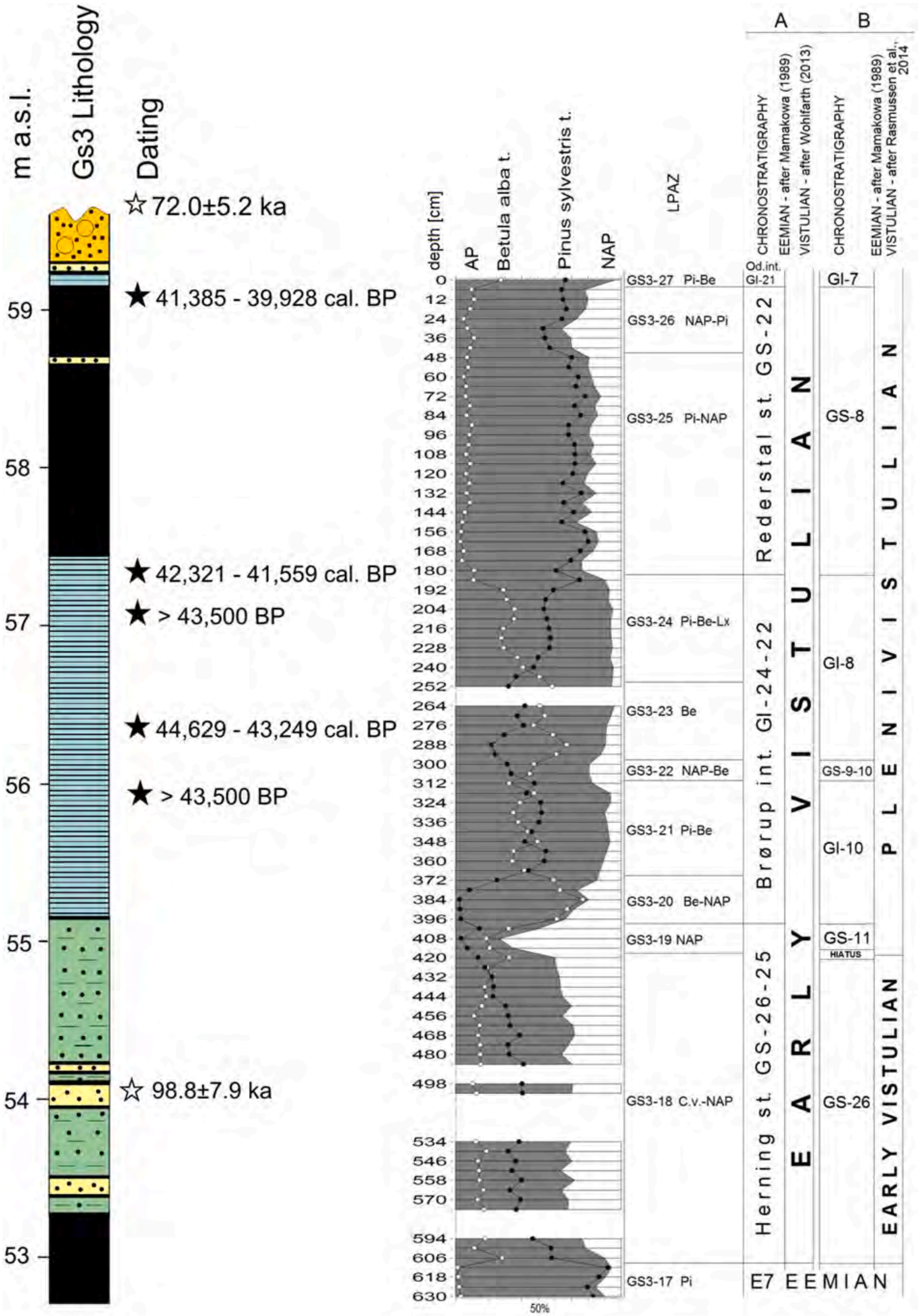


Fig. 11. Comparison of Vistulian Glaciation stratigraphy proposed in this paper (A) and by Mirosław-Grabowska et al. (2022) (B). Abbreviations like in Fig. 3a.

(Kupryjanowicz et al., 2021, Fig. 1b), which is also confirmed by the record of curve $\delta^{18}O$ in NGRIP (Wohlfarth, 2013, Table 2). Tree pollen curves in the Rederstal stadial seem more variable compared to other sites of this age and dependent on local conditions. However, the sum of tree pollen in this phase in profile GS3 is much higher compared to profiles spanning the Pleniglacial. Therefore, according to the revised stratigraphy for profile GS3, its post-Eemian sequence is assumed as the Early Vistulian.

6. Conclusions

Palaeoenvironmental conditions taking place in NW Poland in the Eemian Interglacial (MIS 5e) and Early Vistulian Glaciation (MIS 5 d-a) have been precisely recognised based on multiproxy analysis in profile GS3 from Gorzów Wielkopolski. Palynological analysis was used to reconstruct the humidity and terrestrial vegetation cover, including tree stands (supplemented by analysis of macroremains and wood fragments), and the changing climate conditions. Macroremains, cladocerans and algae were applied to recognise the lake conditions, including the changing depth, trophy, temperature, water chemistry and pH. The study was supplemented with NPPs, Chironomidae and Coleoptera analysis, which confirmed and/or specified the obtained results. The results comprise a huge database, which allows us to draw the following conclusions.

1. In the Late Glacial, an almost treeless landscape dominated cool-climate tundra-moss and steppe habitats. The beginning of the Eemian was marked by the gradual improvement of climate conditions, as indicated by the dominance of pioneer forests with Betula (E1) and then Pinus (E2). Evident temperature rise occurred in the Quercus-dominated interval (E3), which should be considered the First Thermal Optimum of the Eemian. An increase of precipitation at only a slight temperature fall corresponds to Corylus phase (E4). In Carpinus phase (E5) temperature rose and humidity fell (decrease of precipitation), which led to the crisis in deciduous forests, that were attacked by parasitic fungi. This interval correspond to the Second Thermal Optimum. An episode of short-term climate drying led to Pinus invasion and the rising significance of herbaceous plants. This oscillation is observed very rarely in Eemian records. When Carpinus returned after this oscillation, increasing proportions of Picea accompanied. Then the precipitation rise and temperature fall occurred causing the development of coniferous forests with Picea, Abies, and Pinus (E6) and subsequently Pinus domination (E7).
2. The reservoir in the Late Glacial and E1 phase filled the deep, cold, oligotrophic carbonate lake was overgrown by Characeae meadows. In E2 reed zones on margins appeared. In E3 plants preferring shallower, cold waters with higher trophy dominated in the lake. In E4 increase of precipitation and humidity caused water level rise and trophy fall (oscillations) in the lake, around which a reed zone started to expand. In E5 and E6 the lake became shallower, the reed zone began to expand, peats and dystrophic conditions appeared. In E7 complete terrestrialization of the Eemian lake (“older”) took place, with the dominating role of reed and peatbog habitats, followed by drying up and degradation of subsurface peat layers. Change of recharge into precipitation waters and trophy decrease was observed in the peatbog.
3. The correspondence of the obtained paleaeoenvironmental reconstructions with the well-known stadials and interstadials of the Early Vistulian was established. In the first stadial – Herning Stadial (MIS 5 d) significant cooling and decrease of precipitation resulted in retreat of trees and intense development of herbaceous plants, dwarf shrubs, moors, and peatbogs occurred. In the Brørup Interstadial (MIS 5c) two warm intervals with a similar scenario were observed – with an initial dominance of birch and later birch-pine forests, separated by distinct cooling (increasing role of herbaceous plants). Subsequent cooling and drying – Rederstal Stadial (MIS 5 b) – caused the retreat of forest habitats and development of park tundra with single Pinus trees, and rich tundra and steppe vegetation. During the last warming in the Early Vistulian – the Odderade Interstadial (MIS 5a) – sparse birch forests dominated the landscape.
4. The reservoir in the Early Vistulian became the lake again (“younger "). In the shallow, cold, low-trophy Herning Stadial lake water occasionally warmed up in the summer, causing trophy increase. In Brørup Interstadial in the lake developed a reed zone and water plants indicate was at first shallow, relatively warm, and meso/eutrophic; later the water level rose and trophy decreased. In Rederstal Stadial the lake became shallower again, resulting in warmer waters during summer and terrestrialization, while the trophy changed from eu-to oligotrophic. In Odderade Interstadial Characeae spread and the reed zone expanded in the deeper carbonate lake with a lower trophy.
5. Conditions recognised for the Eemian and Early Vistulian allowed to determine that the browser *Stephanorhinus kirchbergensis* had the optimal life conditions in the study area during the Middle Eemian (E4-*Corylus* and E5-*Carpinus* phases), when humid deciduous forests and warm climate prevailed. Less favourable conditions existed during phases with coniferous forests – Early (E1-*Betula*, E2-*Pinus-Betyla* and E3-*Quercus* phases) and Late Eemian (E6-*Picea-Abie* and E7-*Pinus* phases). The least favourable conditions were in the Late Wartanian Glaciation and in the Early Vistulian, when it was too cold and most importantly there were no soft tree sprouts that served as food for the species.
6. It was noticed that the application of palaeobotanical and palaeozoological analyses as separate proxies result in a fragmentary picture of the palaeoenvironment. Each proxy depends on the preservation state of the analysed remains or even on their presence in the sediment; there is also no single proxy allowing for a precise recognition of the environment. Therefore, only the combination of available analyses, describing the largest possible number of macro- and microremains recorded in the sediment allows to understand all environmental changes. As a result, the precise causes of the vegetation succession, climate and humidity changes in a given geological interval can be precisely determined and connected in a cause and effect entity.
7. Revision of the post-Eemian sequence in profile GS3, based on reinterpretation of 6 knows and 1 new age determinations (radiocarbon age) and a detailed comparison of the pollen succession with other sites of the Early and PleniVistulian, points to the Early Vistulian age of the analysed sediments.

Author contributions

Conceptualization and Writing (Original draft preparation): Anna Hrynowiecka. All authors contributed to Methodology, Investigation, Visualisation, and Interpretation. Supervision: Anna Hrynowiecka and Ryszard K. Borówka. Funding acquisition and Project administration: Anna Hrynowiecka and Krzysztof Stefaniak. All the Co-authors contributed to the Discussion and Conclusions.

Data availability

The dataset related to this article is stored at the Marine Geology Branch, Polish Geological Institute-National Research Institute, Gdańsk, Poland.

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