

FOSSIL CLADOCERA REMAINS IN THE EEMIAN SEDIMENTS – PRESERVATION, FREQUENCY AND DOMINANT SPECIES

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Abstract

This paper presents the results of fossil Cladocera analysis using material obtained from seven palaeolakes of the Eemian interglacial located in Poland. The main aim of this study was to investigate the state of preservation and diversity of species in the Eemian Cladocera. The studied Eemian lakes were formed at the end of the Wartanian Glaciation in tunnel and kettle holes. They had preserved a continuous record of environmental changes throughout the Eemian interglacial, until the Vistulian Glaciation. Cladocera fossils found in Eemian sediments were thinner and had a more damaged structure than fossils from the Holocene. Low degree of fossil preservation forced to develop an alternative method for preparation of the fossils for the microscopic analysis. Cladocera species found in the examined palaeolakes corresponded to the present-day species inhabiting Poland and Central and Northern Europe. The changes in species composition resulting from climate changes corresponded to the current geographic distribution of Cladocera. Despite the poor condition of the obtained fossil remains, the results showed that cladoceran fossils in sediments of palaeolakes may be used in the reconstruction of environmental conditions from the period preceding the last glaciation.

Key words: Cladocera analysis, palaeocology, Eemian Interglacial, Early Vistulian, Poland

INTRODUCTION

Fossil Cladocera have been studied in multiple institutes in the world for almost 90 years. In Poland, the first studies covering full profiles were conducted in the 1980s and 1990s. The studies presented a full reconstruction of lake development based on the development of Cladocera groups from the formation of the basins until present (Szeroczyńska 1985, 1991, 1998, Bińska *et al.* 1988, Polcyn 1994). Several of the studied lakes were deemed model sites and included in the studies conducted under the IGCP–158 and Global Change programmes. Furthermore, the condition of lakes influenced by human activity both in the Middle Ages (Polcyn 1997) and nowadays (Niewiadomski 1994) have attracted some attention.

Cladocera, thanks to their characteristics (small size, ability to produce ehippia which may be transported by birds to colonize new water bodies, and ability to reproduce by parthenogenesis), are much more expansive and mobile than the larger members of aquatic fauna. Therefore, their response to climatic and environmental changes may be quicker and more radical than in larger organisms (Frey 1962).

High usefulness of the analysis of Cladocera fossils in sediments for the reconstruction of environmental conditions led to a considerable interest in the method for its potential applicability also in the studies of older sediments from the period preceding the last glaciation. Analysing the Eemian interglacial, a warm period before the last glaciation, helps to estimate human influence on the environment and establish scenarios of future climatic and environmental changes (Cheddadi *et al.* 1998).

Sediments from the Eemian interglacial have been covered mainly by palynological analyses (more than 100 profiles were established for instance by Mamakowa 1989, Granoszewski 2000, Dobracka, Winter 2001, Kupryjano-wicz 2008). The studied sediments occur in different geological conditions, either covered with glacial sediments of the Vistula Glaciation periglacial layers, or aquatic accumulation products. The profile of Błonie (Karaszewski 1974) was the first, in which the age of organogeneus Eemian sediments was determined (by Prószyński 1981) using the TL (thermoluminescence) method. The estimated age was 125,000–108,000 years BP. In the light of the presented data, the Eemian interglacial period should be correlated with the last interglacial warming distinguished in deep sea cores as stage 5e of the ^{18}O to ^{16}O ratio, whose estimated age is 128,000–118,000 years BP (Shackleton, Opdyke 1976).

In general, the climate in Poland varied from subcontinental in the early Eemian to suboceanic at the optimum (Zagwijn 1996, Aalbersberg, Litt 1998). The oceanic influences were caused by the opening of the connection between the Baltic Sea and the White Sea (Zagwijn 1996, Aalbersberg, Litt 1998; Funder *et al.* 2002). The mean summer temperature increased from 10°C (Warta/Late Saalian Glaciation) to 16°C in the early Eemian and to 19–20°C during the *Corylus* zone (optimum), then decreased slightly to 17°C and finally to 10–11°C at the end of the Eemian. The mean winter temperature rose from –12°C at the beginning of the Eemian to –2 or to 0°C in the early Eemian, increased to 2–4°C during the optimum, and dropped to below 0°C (to –4°C) in the post-optimum period. During the *Carpinus* zone, a sudden

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Fig. 1. Eemian sites of lacustrine sediments, analysed for fossil Cladocera in Poland by the author: Besiekierz, Horoszki Duże, Solniki, KucówIIc, Studzieniec (Niska 2008), Ruszkówek, (Mirośław-Grabowska *et al.* 2009), and Kaliska (Mirośław-Grabowska, Niska 2007); and by others: Imbramowice (Mirośław-Grabowska, Gašiorowski 2010), Sławoszewem (Pawłowski 2011), and Władysławów (Tobolski 1991).

decrease to -5°C (Cheddadi *et al.* 1998) or a maximum of winter temperature of $+2^{\circ}\text{C}$ (Zagwijn 1996) has been suggested. During the early Eemian, annual precipitation increased to $700\text{--}800\text{ mm yr}^{-1}$, reached its maximum of ca. 1000 mm yr^{-1} in the optimum, and then gradually dropped to ca. 400 mm yr^{-1} (Cheddadi *et al.* 1998).

Analyses of Cladocera fossils in Poland have revealed detailed information of cladoceran species succession covering the last 13,000 years (Gašiorowski 2002, Szeroczyńska, Gašiorowski 2002, Szeroczyńska 2006). Cladocera fossils and ephippia have been sporadically found in sediments older than the last glaciation (Jessen, Milthers 1928, Dickinson 1959, and others). The first full analysis of fossil Cladocera from Eemian lakes in Europe was performed in Denmark (Frey 1962). Literature on Cladocera succession during the Eemian interglacial is scarce, as only a few Eemian locations in the world have been examined for the content of Cladocera fossils to date, many of them only preliminarily (Tsukada 1972, Kadota 1975, Hann, Karrow 1984, 1993).

The main aims of this study were to introduce a modified method for the sample preparation of the Eemian Cladocera remains developed by the author, to present the state of preservation of the remains of fossil Cladocera from Eemian lacustrine sediments and to compare them with the remains from the recent sediment (Holocene). An important part of this study was the presentation of the diversity and the dominant species of Cladocera in the Eemian interglacial, as well as the comparison of the results of Cladocera analysis in the Eemian palaeolakes with other Eemian positions from Poland and the world.

This paper presents the results of preparation and analysis of Cladocera remains from seven fossil bodies of fresh

water of the Eemian interglacial. A detailed description of the succession of Cladocera species and study area in each site has previously been published (Niska 2002, 2003, 2008, Mirośław-Grabowska, Niska 2005, 2007a b, Mirośław-Grabowska *et al.* 2009).

STUDY SITES AND LITHOLOGY

The study lakes were formed at the end of the Warta Stadial (Late Saalian Glaciation), Middle Polish Glaciation in the melt depression and glacial channel. Four of them are located to the south of the boundary of the last glaciation (Solniki, Besiekierz, KucówIIc, Horoszki Duże), and three of them, Studzieniec, Kaliska and Ruszkówek, are located to the north of the boundary (Fig. 1).

The palaeolake Ruszkówek is located near Konin (Kujawy Lakeland – central Poland) (Fig. 1). The 15-m thick sediments of Ruszkówek core has been palynologically analysed by Janczyk-Kopikowa (1997). On the bottom of the core sandy silts occur. Then the bright brown and greyish calcareous fine detritus gyttja appears (Fig. 2). The gyttja is interbedded with white homogenous lake marl. Next, dark brown detritus-rich peaty sands and peat occur. In the upper part of Ruszkówek core the light grey calcareous fine sands and silts appear again.

The Kaliska palaeolake is located near Lubień Kujawski (Central Poland) at 122 m a.s.l. (Fig. 1). The 5-m thick sediments of Kaliska core has been palynologically analysed by Janczyk-Kopikowa (1965). On the bottom of the core bright grey silty sands appear (Fig. 2). Sands are then replaced by bright grey and brownish gyttja, characterised by high CaCO_3 content, which increase up to above 80%. The gyttja is interbedded with lacustrine chalk. Next, organic silts and peat containing carbonate precipitations occur. In the upper part of Kaliska core carbonate sediments (gyttja, silts) appear again.

The palaeolake Besiekierz is located about 30 km in north from Łódź (Central Poland) at 130 m a.s.l. The sediments 4-m thick from Besiekierz core has been palynologically analysed by Z. Janczyk-Kopikowa (1991). The lowest part of the core is represented by silty sand and clayey silt, with low concentration of CaCO_3 . Then, calcareous gyttja in bright brown and grey colour appears. The upper part of this succession contains organic silts and peat (Fig. 2).

KucówIIc cross-section is located in open-cost mine Bełchatów. The thickness of the deposits filling the depression at Kuców IIc is 12,5 m. At the bottom there are alternating layers of slate and peat (2,5 m). It is overlain by 5-m thick series of organic silt, or peat silt, over which in turn lies a 5-m thick layer of organic silt (Fig. 3). The sediments from Kuców IIc core has been palynologically analysed by Balwierz (1998).

The palaeolake Studzieniec is located near Sierpc (central Poland) at 112-m a.s.l. The sediments of over 19-m thick Studzieniec core has been palynologically analysed by Krupiński (2005). On the bottom of the core (below 19.2 m) silty sand and clayey silt occur. Then bright brown and greyish gyttja appears. The gyttja is characterised by increasing content of CaCO_3 up to above 70%. The upper part of this succession contains organic silts and peat (Fig. 3).

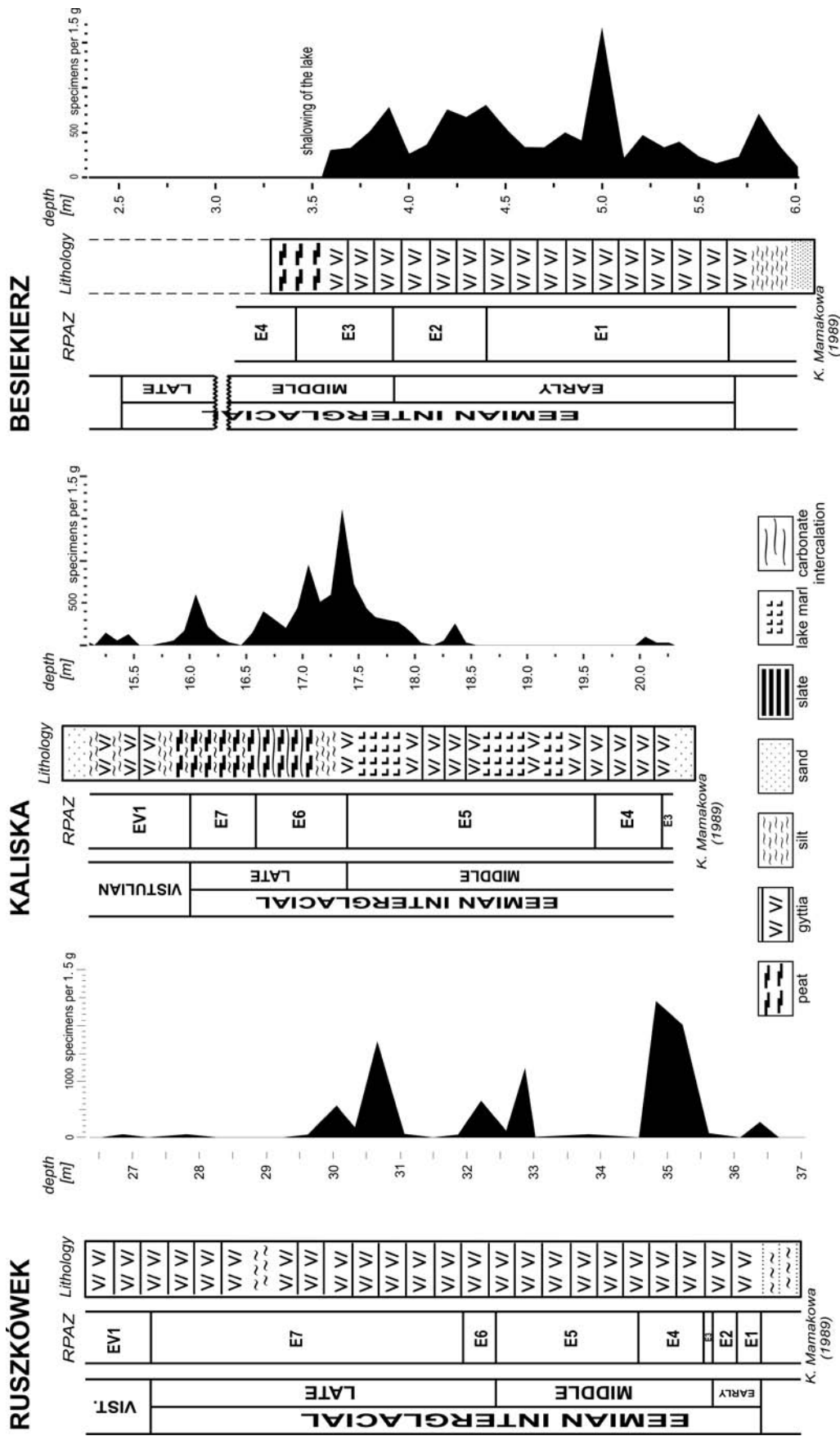


Fig. 2. Diagram of lithology and the total sum of Cladocera specimens in Ruszkówek, Kaliska, and Besiekierz.

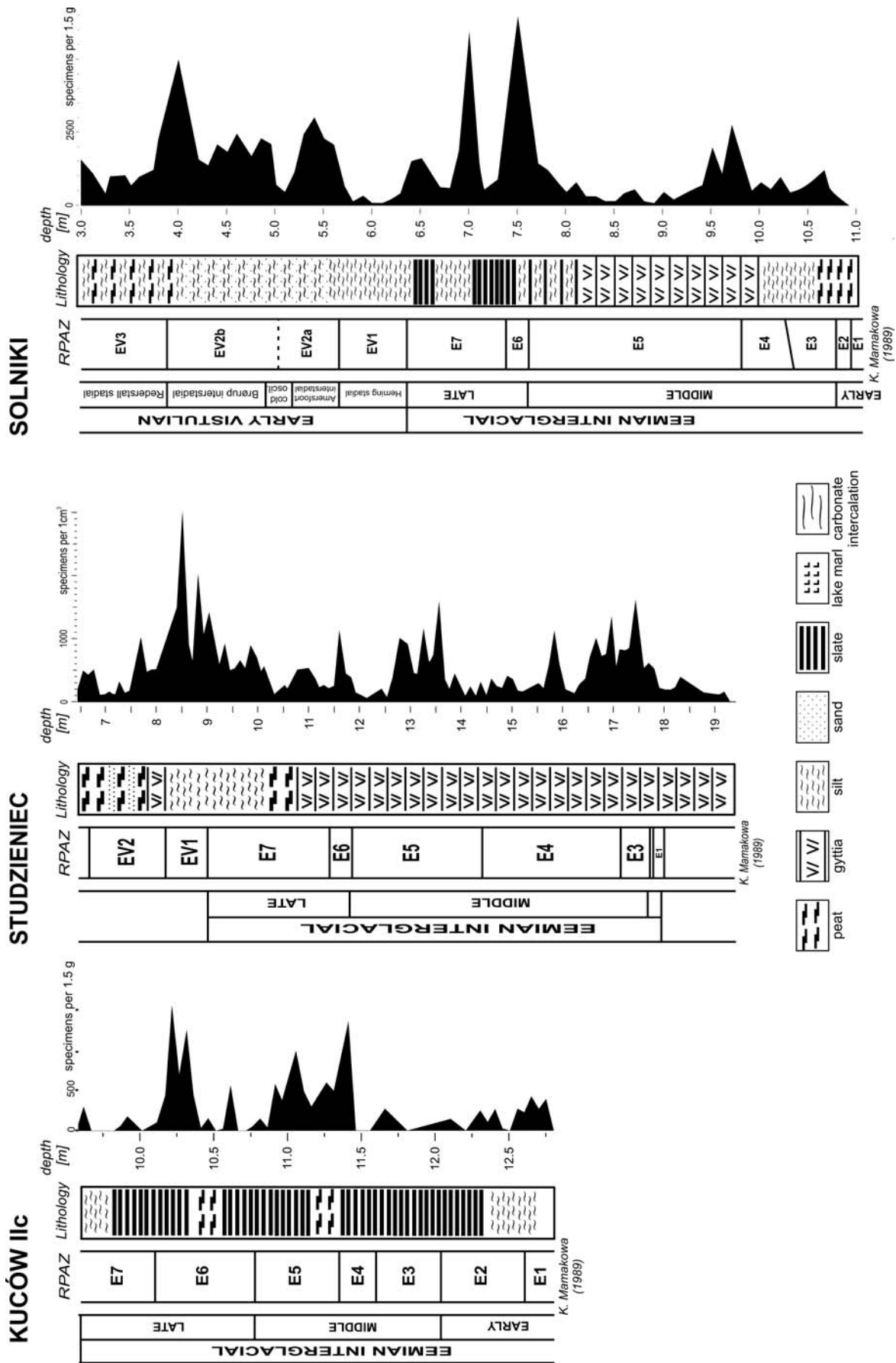


Fig. 3. Diagram of lithology and the total sum of Cladocera specimens in Kuców IIc, Studzieniec, and Solniki.

A 10-m thick lake series at Solniki (Fig. 3) was discovered during cartographic works at Trześcianka sheet of Detailed Geological Map of Poland 1:50000 (Kurek, Preidl 2001). It is covered by 3-m layer of sands and sandy clays. Till is not present in the covering layer. Lake deposits fill a relatively large melt depression. The Eemian deposits (ca. 5 m thick) are represented in the lower part by slightly clayey peat (ca. 0.40 m thick), followed by organic silts. The Eemian part of the section is followed by 3.3 m of Early Vistulian (Weichselian) clayey and peaty silts.

The palaeolake Horoszki Duże is located in southern Podlasie (Fig. 1). An attempt to analyse the remains of Cladocera from the Horoszki profile failed. They were too damaged, preventing the identification of species.

The cores from the studied palaeolakes are only "palynologically dated". There are no radiometric dates because the entire Eemian Interglacial falls outside the range of the radiocarbon dating and the carbonate lacustrine sediments are very problematic subject to other absolute chronometric dating methods e.g. the uranium-thorium dating. Therefore, only the results of palynological analysis confirm the Eemian age of the studied palaeolake deposits. The samples were collected at intervals of 5 to 10 cm, based on lithological changes in the succession.

METHODS – MODIFIED SAMPLE PREPARATION FOR CLADOCERA ANALYSIS

Sediments for palaeolimnological studies collected from existing and fossil lakes of the Holocene are usually poorly consolidated, which significantly facilitates obtaining sediment samples of appropriate volume. The Eemian material was highly consolidated, which impeded a precise collection of 1 cm³ of sediment for the analyses. With highly consolidated material, the samples were weighed. Subsequently, the sediment sample was immersed in distilled water (100 ml) and left to disintegrate (macerate) for 24 hours. The samples of Cladocera were preliminarily prepared according to the method required by IGCP project 158 (Frey 1986). However, that method was proposed for significantly younger sediments, in which chitinous remains of Cladocera are far thicker and harder, and thus much more resistant to the preparation procedures. Modification was required in the use of a magnetic stirrer, due to the poor condition of the remains. Stirring combined with mineral particles led to excessive grinding of the sediments containing the Cladocera remains. The stirrer was only used for samples composed largely of organic matter, for which there was no risk of sample destruction.

Once 1 cm³ or 1.5 g sediment was prepared, depending on the profile, 100 ml of 10% potassium hydroxide (KOH) were added to the sample and then heated with gentle stirring using a rod. The mixture was maintained near the boiling point for approx. 20–30 minutes. Subsequently, the sample was cooled down and supplemented with 100 ml distilled water. After 24 hours, the sample was filtered on two sieves of different mesh size 0.05mm and 0.5 mm to separate fractions of containing the Cladocera remains. The sample was prepared for microscopic analysis by staining with glycerine solution of safranin.

RESULTS AND DISCUSSION

State of preservation

Cladocera fossils deposited during the Eemian interglacial, compared to those from the Holocene sediments, were thinner, had a more damaged structure and often lacked characteristic features enabling species determination (Fig. 4). Those fossils were particularly difficult to handle in qualitative and quantitative analyses and did not stain efficiently with safranin, which additionally complicated their differentiation from the surrounding mass of decomposed organic matter.

Relatively well-conserved were the remains of species endowed with the thickest armour. The "postabdomens" (water flea appendages) were also numerous. Once preliminary microscopic Cladocera assessment was carried out, it was clear that the remains derived from the gyttja sediments were the most difficult to analyse (Fig. 5), as the mass of highly decomposed plant tissues filled the Cladocera remains completely and prevented their examination. A series of methodical experiments was conducted to obtain "pure" material for the studies. The samples were treated with cool and hot KOH solutions at various concentrations. The sediments were also boiled in H₂O only, but no effect was observed. The problem was partially solved by adding several drops of a detergent (dish soap) to the last wash. The detergent separated the residues, which made the remains more visible.

Significantly better results were obtained with peat sediments, reasonably good results were obtained with silt sediments, whereas slate usually lacked Cladocera fossils. It was initially thought that the main cause of poor material condition was its drying after the collection (archival samples obtained for analysis were often highly desiccated). Nonetheless, analyses performed with fresh material did not bring better results. The material for qualitative analyses was collected from the humid walls of fossil water bodies in Bełchatów Faustynów and Chabielice near position KucówIIc. The samples were prepared for analysis immediately after delivery to the laboratory, but the obtained remains were equally damaged. It may therefore be suspected that the most deteriorative factors were time and chemical reaction in the sediment.

Number of species and their frequency

Fossil Cladocera remains examined in the Eemian sediments did not exhibit substantial differences in appearance and size compared to the present-day remains. Cladocera species analysed in the Eemian sediments in Poland and in other parts of the world (Frey 1962, Hann, Karrow 1993) correspond to the species currently found worldwide. Sometimes differences in size and the thickness of chitin armour etc. are reported, but they mainly stem from different edaphic and chemical conditions in water bodies, as well as the time that has passed since the deposition of the remains, which marks the length of the exposure to damaging factors (Niska 2002). Changes occurring in Cladocera species composition, as an effect of climatic changes in the studied water bodies in the Eemian interglacial, correspond to the current geographic distribution of the species (Frey 1962).

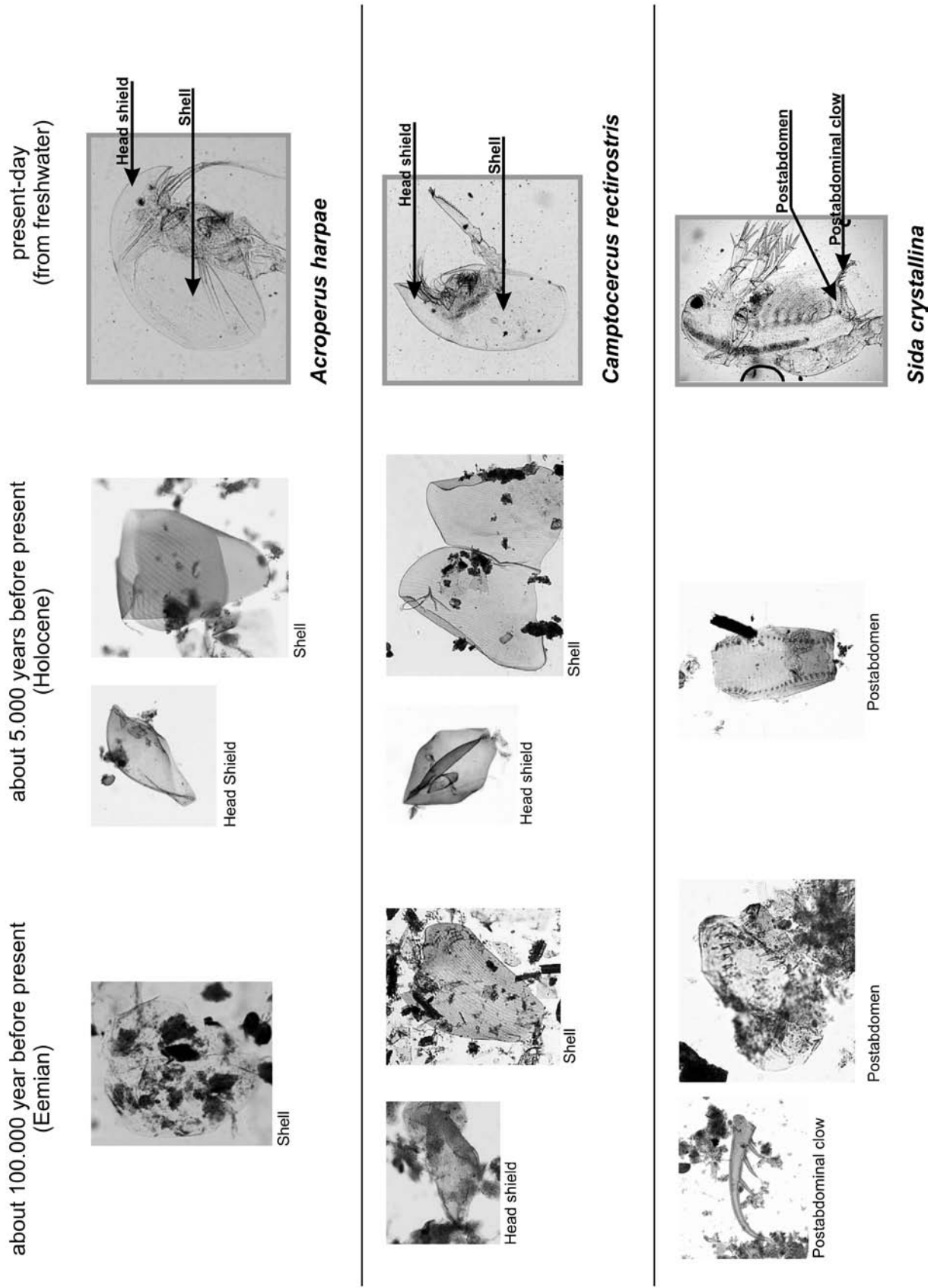


Fig. 4. Comparison of the preservation of Cladocera remains from different age of organic deposits. Photographs: Intact animals – I. Rybak, ca. 5000 years old remains – K. Szeroczyńska, Eemian remains – M. Niska.

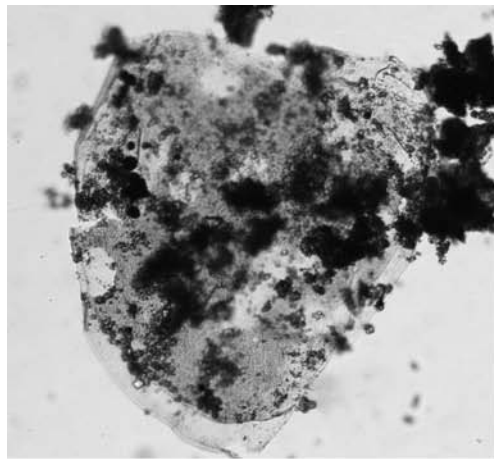
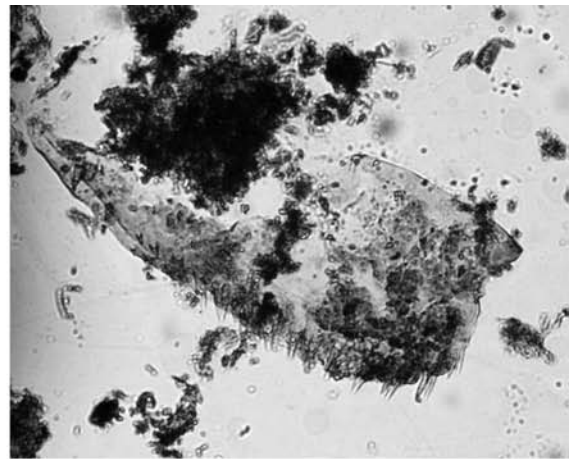
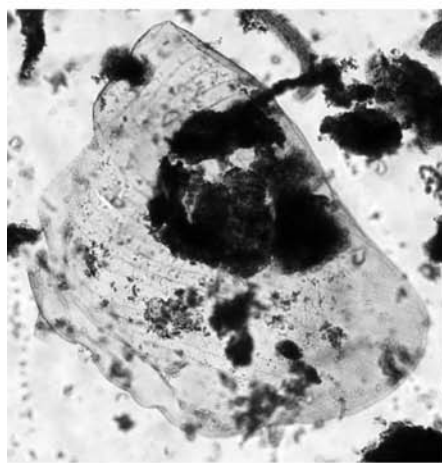
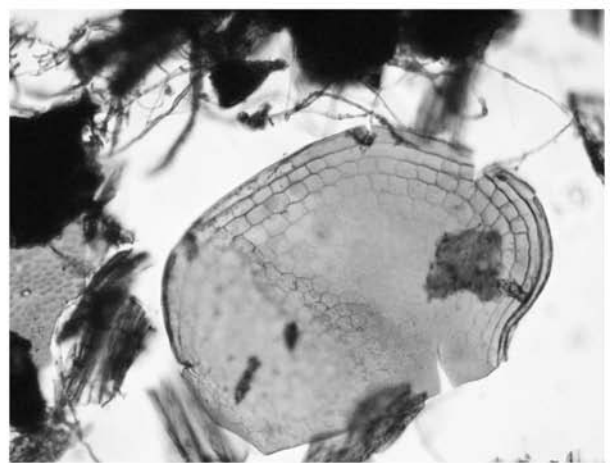
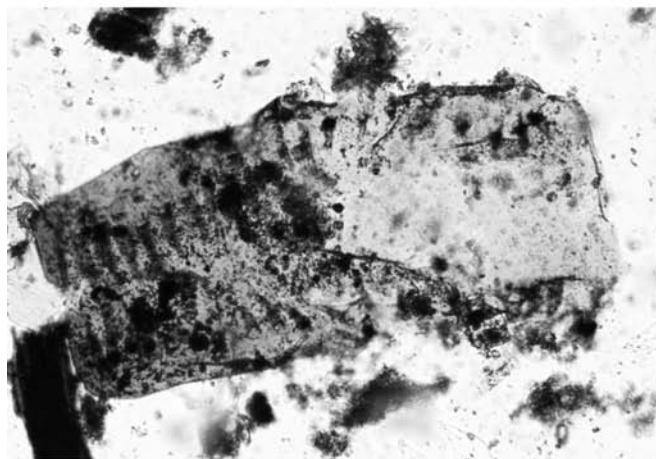
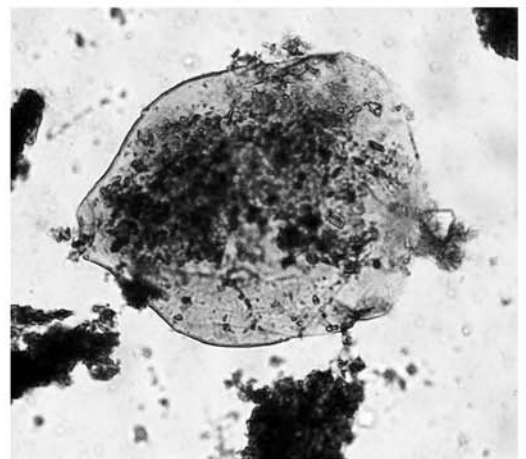
*Acroperus harpae* (gyttja)*Alona* sp. (gyttja)*Acroperus harpae* (peat)*Chydorus sphaericus* (peat)*Sida crystallina* (silt)*Monospilus dispar* (silt)

Fig. 5. Subfossil Cladocera remains from the Eemian gyttja, peat, and silt sediments.

In the Eemian palaeolakes of this study, the author found 26 Cladocera species (Table 1). These 26 species of Cladocera has also been found in other Eemian palaeolakes in Poland. In comparison, in the Late Glacial sediments in Poland the occurrence of a few to several Cladocera species has been recorded, and in the Holocene lacustrine sediments about 30 species (Szeroczyńska, Zawisza 2007).

The total number of Cladocera individuals identified in each sample (in 1 cm³ or 1.5 g) did not exceed 6000 (Figs 2, 3). The total concentration of remains was lower than in Holocene sediments. The smaller number of remains is probably due to the destruction of remains as a result of chemical and physical processes in sediments, i.e. "time effect", as well as the inability to recognize some of the remains.

Table 1

Identified species of Cladocera in the sediments of the Eemian lakes

	M. Niska						K.	D.	M.
	Ruszkó- wek	Kaliska	Biesie- kierz	Kuców Ile	Studzie- niec	Solniki	Szeroczyńska Władysła- wów	Pawłowski Sławosze- wek	Gasiorowski Imbramo- wice
1. <i>Acroperus harpae</i> (Baird, 1835)	+	+	+	+	+	+	+	+	+
2. <i>Alona affinis</i> (Leydig, 1860)	+	+	+	+	+	+	+	+	+
3. <i>Alona guttata</i> (Sars, 1861)	+	+	+	+	+	+		+	+
4. <i>Alona quadrangularis</i> (Muller, 1785)	+	+		+	+	+	+	+	+
5. <i>Alonella excisa</i> (Fischer, 1854)					+			+	+
6. <i>Alonella exigua</i> (Lillieborg, 1853)		+			+	+	+	+	+
7. <i>Alonella nana</i> (Baird, 1843)		+	+	+	+	+		+	+
8. <i>Anchistropus emarginatus</i> (Sars, 1861)				+			+	+	+
9. <i>Bosmina longirostris</i> (O. F. Muller, 1776)	+	+		+	+	+	+	+	+
10. <i>Bosmina longispina</i> (Leydig, 1860)						+			+
11. <i>Camptocercus rectirostris</i> (Schodler, 1862)	+	+	+	+	+	+	+	+	+
12. <i>Ceriodaphnia</i> sp. (Dana, 1853)			+		+	+	+	+	+
13. <i>Chydorus sphaericus</i> (O. F. Muller 1776)	+	+	+	+	+	+	+	+	+
14. <i>Disparalona rostrata</i> (Koch, 1841)					+		+		+
15. <i>Eurycercus lamellatus</i> (O. F. Muller, 1776)	+	+	+	+	+	+	+	+	+
16. <i>Graptoleberis testudinaria</i> (Fischer, 1848)	+	+		+	+	+	+	+	+
17. <i>Leydigia acanthocercoides</i> (Fischer, 1854)	+				+			+	
18. <i>Leydigia leydigi</i> (Schodler, 1863)		+		+	+	+		+	+
19. <i>Monospilus dispar</i> (Sars, 1861)	+	+		+	+	+		+	+
20. <i>Oxyurella tenuicaudis</i> (Sars, 1862)					+		+	+	+
21. <i>Peracantha truncata</i> (O. F. Muller, 1785)			+		+			+	+
22. <i>Pleuroxus trigonellus</i> (O. F. Muller, 1776)	+			+	+		+	+	
23. <i>Pleuroxus uncinatus</i> (Baird, 1850)	+	+	+	+	+	+		+	
24. <i>Sida crystallina</i> (O. F. Muller, 1785)	+	+	+	+	+	+	+	+	+
25. <i>Daphnia longispina</i> group (O. F. Muller, 1776)					+		+	+	
26. <i>Daphnia pulex</i> group (Straus, 1820)	+							+	
27. <i>Leptodora kindti</i> (Focke, 1844)							+	+	
28. <i>Bosmina coregoni</i> (Austin, 1942)							+	+	+
29. <i>Chydorus globosus</i> (Baird, 1850)							+	+	

Dominant species

The species of Cladocera have not undergone major evolutionary changes for hundreds of thousand years, therefore, it is presumed that the knowledge of ecological and climatic requirements of the present-day species may be used to interpret the changes occurring in lakes in the past (Szeroczyńska in: Toboloski 1991). Identification and ecological interpretation of the studied Cladocera remains from lake sediments was conducted following the studies by Duigan (1992), Frey (1958, 1962), Goulden (1964), Hofmann (1986), Korhola (1990) Szeroczyńska (1985) and Szeroczyńska, Sarmaja-Korjonen (2007).

In the Eemian water bodies, the prevalent and the most varied group of species were the littoral forms of the Chydoridae family. Species belonging to this family are the most interesting study material, providing information on the shore

line status and the climate. Members of this family are the best indicators of thermal and environmental factors (Frey 1958, Goulden 1964, Poulsen 1928). The family Bosminidae was represented by *Bosmina longirostris*, *Bosmina (Eubosmina) longispina*, and *Bosmina (Eubosmina) coregoni*, while the family Daphniidae was represented by *Ceriodaphnia* sp., the *Daphnia pulex* group, and the *Daphnia longispina* group. The members of those families live mainly in the open water zone and constitute an element of the pelagic environment (Lampert, Sommer 2001). Some of them, especially the members of the family Daphniidae, are rarely encountered in sediment material due to the poor conservation of their chitin armour. What was found in sediments, were mainly their ephippia and postabdominal claws. The species (Bosminidae, Daphniidae) are important indicators of water level changes and trophic status of the water body (Alhonen 1970). *Sida crystallina* was the only found species of the family Sididae.

Table 2

The list of dominant species of Cladocera occurring at different phases of the studied Eemian sediments

Stratigraphy (Mamakova 1089)		Solniki	Besiekierz	Studzieniec	Kuców IIc	Kaliska	Ruszkówek
Early Vistulian/ Weichselian	EV3	<i>Chydorus sphaericus</i> <i>Alona quadrangularis</i> <i>Bosmina longirostris</i>	-	-	-	-	-
	EV2b	<i>Chydorus sphaericus</i> <i>Bosmina longispina</i> <i>Camptocercus</i> <i>rectirostris</i> <i>Alona affinis</i>	-	-	-	-	-
	EV2a	<i>Bosmina longispina</i> <i>Sida cristallina</i> <i>Alona affinis</i> <i>Alona rectangula</i>	-	<i>Chydorus sphaericus</i> <i>Acroperus harpae</i> <i>Disparalona rostrata</i>	-	-	-
	EV1	<i>Chydorus sphaericus</i> <i>Alona guttata</i> <i>Bosmina</i> <i>longispina</i>	-	<i>Chydorus sphaericus</i> <i>Pleuroxus uncinatus</i> <i>Bosmina longirostris</i>	-	<i>Alona affinis</i> <i>Chydorus</i> <i>sphaericus</i> <i>Eurycercus</i> <i>lamellatus</i>	<i>Alona guttata</i>
Eemian Interglacial	E7	<i>Bosmina longispina</i> <i>Bosmina longirostris</i> <i>Acroperus harpae</i>	-	<i>Chydorus sphaericus</i> <i>Alona quadrangularis</i> <i>Alona guttata</i> <i>Bosmina longirostris</i>	-	<i>Alona affinis</i> <i>Chydorus</i> <i>sphaericus</i> <i>Eurycercus</i> <i>lamellatus</i>	<i>Chydorus</i> <i>sphaericus</i> <i>Alona</i> <i>quadrangularis</i> <i>Alona guttata</i> <i>Bosmina</i> <i>longirostris</i> <i>Pleuroxus</i> <i>uncinatus</i>
	E6	<i>Bosmina longispina</i> <i>Bosmina longirostris</i> <i>Alona affinis</i> <i>Monispilus dispar</i>	-	<i>Alonella nana</i> <i>Alona guttata</i> <i>Alona affinis</i> <i>Eurycercus lamellatus</i>	<i>Graptoleberis</i> <i>testudinaria</i> <i>Camptocercus</i> <i>rectirostris</i> <i>Acroperus harpae</i>	<i>Acroperus harpae</i> <i>Graptoleberis</i> <i>testudinaria</i> <i>Camptocercus</i> <i>rectirostris</i>	<i>Eurycercus</i> <i>lamellatus</i> <i>Alona</i> <i>quadrangularis</i> <i>Alona guttata</i>
	E5	<i>Alona guttata</i> <i>Alona affinis</i> <i>Bosmina longispina</i> <i>Camptocercus</i> <i>rectirostris</i>	-	<i>Acroperus harpae</i> <i>Alona guttata</i> <i>Bosmina longirostris</i> <i>Eurycercus lamellatus</i>	<i>Alona guttata</i> <i>Alona affinis</i>	<i>Chydorus</i> <i>sphaericus</i> <i>Eurycercus</i> <i>lamellatus</i> <i>Alona affinis</i> <i>Acroperus harpae</i>	<i>Alona</i> <i>quadrangularis</i> <i>Camptocercus</i> <i>rectirostris</i> <i>Alona</i> <i>guttata</i> <i>Pleuroxus</i> <i>uncinatus</i>
	E4	<i>Alona affinis</i> <i>Bosmina</i> <i>longispina</i>	-	<i>Alona guttata</i> <i>Alonella nana</i> <i>Bosmina</i> <i>longirostris</i>	<i>Eurycercus</i> <i>lamellatus</i>	<i>Alona guttata</i> <i>Alona affinis</i> <i>Eurycercus</i> <i>lamellatus</i>	<i>Alona</i> <i>quadrangularis</i> <i>Alona guttata</i> <i>Camptocercus</i> <i>rectirostris</i> <i>Alona affinis</i>
	E3	<i>Alona affinis</i> <i>Bosmina longispina</i> <i>Acroperus harpae</i> <i>Chydorus sphaericus</i> <i>Eurycercus lamellatus</i>	<i>Chydorus</i> <i>sphaericus</i> <i>Camptocercus</i> <i>rectirostris</i>	<i>Alona guttata</i> <i>Alonella nana</i> <i>Bosmina</i> <i>longirostris</i>	<i>Alona affinis</i>	-	<i>Eurycercus</i> <i>lamellatus</i> <i>Acroperus harpae</i> <i>Pleuroxus</i> <i>uncinatus</i>
	E2	<i>Alona affinis</i> <i>Chydorus sphaericus</i> <i>Eurycercus lamellatus</i>	<i>Camptocercus</i> <i>rectirostris</i> <i>Alona affinis</i> <i>Sida cristallina</i>	<i>Alona guttata</i> <i>Camptocercus</i> <i>rectirostris</i> <i>Eurycercus lamellatus</i>	<i>Acroperus harpae</i> <i>Alona guttata</i> <i>Alona affinis</i>	-	<i>Chydorus</i> <i>sphaericus</i>
	E1	-	<i>Camptocercus</i> <i>rectirostris</i> <i>Acroperus harpae</i>	<i>Eurycercus lamellatus</i> <i>Camptocercus</i> <i>rectirostris</i> <i>Chydorus sphaericus</i>	<i>Alona</i> <i>quadrangularis</i> <i>Bosmina</i> <i>longirostris</i>	-	<i>Eurycercus</i> <i>lamellatus</i> <i>Alona affinis</i> <i>Sida cristallina</i>
	Wartanian/Late Saalian	-	<i>Alona affinis</i> <i>Alona guttata</i> <i>Chydorus</i> <i>sphaericus</i>	<i>Alona affinis</i> <i>Alona quadrangularis</i>	-	-	-

The structure of the prevalent Cladocera species in the sediments of the strata correlated with palynological levels depended on age, developmental phase, the rate of change, and the morphometry of the lake (Table 2). Lake depth significantly affected the response of Cladocera to changes in the sedimentation rate and climate. In the middle Eemian interglacial, the temperature was relatively high and the climate was drier (Kupryjanowicz 2003). This led to a decrease in water level in the large palaeolakes, whereas the shallowest palaeolake, Besiekierz, underwent terrestrialization.

Throughout the existence of the water bodies in the Eemian interglacial, the prevalent species were those endowed with broad thermal and edaphic tolerance: *Acroperus harpae*, *Alona affinis*, *Alona guttata*, *Alona quadrangularis*, *Alonella nana*, *Bosmina longirostris*, *Bosmina (E.) longispina*, *Chydorus sphaericus*, *Eurycerus lamellatus*, *Graptoleberis testudinaria*, *Monospilus dispar*, *Pleuroxus uncinatus*, *Sida crystallina* and thermophilic *Camptocercus rectirostris*.

In the initial phase of the studied water bodies, i.e. at the last stage of the Warta Glaciation (Saalian), mainly pioneer species prevailed: *Alona affinis*, *Alona guttata*, *Chydorus sphaericus* and *Alona quadrangularis*. At the beginning of the Eemian interglacial, apart from species tolerant of cool water (*Eurycerus lamellatus*, *Chydorus sphaericus*, *Acroperus harpae*), a species preferring warmer water, *Camptocercus rectirostris*, was sporadically present (Poulsen 1944). In the following period, the fossil population was mainly represented by species residing among aquatic plants: *Acroperus harpae*, *Alona guttata*, *Alona affinis*, *Chydorus sphaericus*, *Eurycerus lamellatus*, *Camptocercus rectirostris*, and *Sida crystallina*. At the end of the early Eemian interglacial, the dominant species were enriched by pelagic species *Bosmina longirostris* and *Bosmina (E.) longispina*.

In the middle phase of interglacial, a putative lowering of water level occurred in the studied water bodies, which was reflected as a decreasing occurrence of Cladocera. This led to the final terrestrialization of the Besiekierz lake, whereas other water bodies were dominated by the following species: *Alona affinis*, *Bosmina (E.) longispina*, *Alona guttata*, *Alonella nana*, *Bosmina longirostris*, and *Eurycerus lamellatus*. These species are characterized by high thermal tolerance; they tolerate well both cooler and warmer water. Especially in mesotrophic lakes (the Solniki lake), the period corresponding to the onset of the late Eemian interglacial was marked by the appearance of *Monospilus dispar*, a species inhabiting sands. In the palaeolake Kuców IIc, *Graptoleberis testudinaria* appeared, which is often found in water containing humic substances (this lake underwent temporary terrestrialization). The end of the Eemian interglacial was the ending point for most of the studied water bodies (Kuców IIc, Ruskówek, Kaliska). The other two lakes (Solniki, Studzieniec) were dominated mainly by species tolerant of low-temperature conditions. In the former lakes, the species were: *Bosmina (E.) longispina*, *Bosmina longirostris*, *Alona affinis*, and *Acroperus harpae*, while in the latter: *Bosmina longirostris*, *Alona guttata*, *Alona quadrangularis*, and *Chydorus sphaericus*.

Lake Studzieniec was still present at the beginning of the Early Vistulian (Weichselian). In that period, the most preva-

lent species were *Acroperus harpae* and *Chydorus sphaericus*, while other significant species were *Bosmina longirostris*, *Pleuroxus uncinatus*, *Alona quadrangularis*, and *Disparalona rostrata*. Lake Solniki existed throughout the Early Vistulian and was dominated by *Chydorus sphaericus* and *Bosmina (E.) longispina*.

Other studies of Eemian Cladocera

To date, the attempts to reconstruct the development of lakes in Poland based on Cladocera succession in the Eemian interglacial sediments have been made for two locations in the region of Konin, namely Władysławów, studied by K. Szeroczyńska (in: Tobolski 1991), and Sławoszewek, studied by Pawłowski (2004, 2011), and one location of Imbramowice, studied by M. Gąsiorowski (Mirosław-Grabowska, Gąsiorowski 2010).

Upon the comparison of the fossil Cladocera results, it was deduced that the studied Cladocera groups determined by the author are similar to those found in other profiles established for other regions of Poland.

In the Władysławów profile, K. Szeroczyńska examined 24 samples, in which 21 species of Cladocera were detected, belonging to four families: Bosminidae, Chydoridae, Sidiidae, and Leptodoridae (in: Tobolski 1991). The study encompassed Eemian and Early Vistulian (Weichselian) sediments. The condition of the fossils was unsatisfactory, which made their proper analysis impossible in several attempts. The initial period of water body development was related mainly to the appearance of such species as: *Chydorus sphaericus*, *Bosmina (Eubosmina) coregoni*, *Alona* sp., *Alona quadrangularis*, and *Alona affinis*. This list of species from the initial phase of water body development was similar to the lakes studied by the author, except for *Bosmina (E.) coregoni*.

In the Imbramowice profile, M. Gąsiorowski analysed 26 sediment samples and found 26 Cladocera species from four families. Four of the species, *Acroperus elongatus*, *Alona intermedia*, *Chydorus piger* and *Ophyroxus gracillis*, have not been found in other palaeolakes (Table 1). The highest reported frequency of individuals reached 1700 per 1 g of sediment. M. Gąsiorowski determined 7 Cladocera development phases covering the early and middle Eemian interglacial (Mirosław-Grabowska, Gąsiorowski 2010).

D. Pawłowski, in the Sławoszewek location, analysed fossils of 30 Cladocera species belonging to 5 families: Bosminidae, Chydoridae, Daphniidae, Leptodoridae, and Sidiidae. Two of the identified species has not been found in the other palaeolakes: *Simocephalus* sp. and *Ilyocryptus* sp. (Table 1). The first development stage of the lakes in the region of Konin proposed by D. Pawłowski was related to the beginning of the studied palaeolake Sławoszewek. Environmental conditions in initial period were adverse, and Cladocera community consisted of few individuals. This stage may be noticed in all water bodies studied by the author and in the Imbramowice profile, in which it is well marked by the presence of pioneer Cladocera species.

The early Eemian interglacial involved a gradual climate warming. In the lake of the region of Konin (Sławoszewek), Cladocera groups were joined by: *Camptocercus rectiro-*

stris, *Graptoleberis testudinaria*, and *Pleuroxus* sp. The number of individuals and the variability of Cladocera species increased as well. Improved conditions and, especially, increased water temperature were also marked in the water bodies examined by the author and in the Imbramowice profile. However, due to relatively long distances between the lakes, it may be noticed that the period of improvement in each studied water body occurred at different times.

In the middle stage of the Eemian interglacial, the number of individuals in the water bodies near Konin decreased and the only survivors were the species tolerant of low temperatures and environmental stress: *Chydorus sphaericus*, *Alona rectangula*, and *Alona affinis*. The reason for this situation was the lowering water level. In the sediments of that stage a peat layer may be found. A similar stage with a decreasing number of Cladocera species and individuals was found in the palaeolakes of this study, Besiekierz, Kuców IIc, Solniki, and Studzieniec. At the end of the middle Eemian interglacial, Cladocera in the Imbramowice profile were missing, which stemmed from terrestrialization of the water body.

According to Pawłowski (2004, 2011), the late Eemian interglacial involved improvement in habitat conditions. In the Sławoszewek lake, species structure was rich and diversified. This was also noted in the palaeolakes of this study, Solniki and Studzieniec, for which that period was the most beneficial in the history of those water bodies. The end of the interglacial ceased the existence of the palaeolake Sławoszewek, similarly to Kuców IIc, Kaliska, and Ruszkówek. The palaeolake Władysławów, as well as Solniki, and Studzieniec, were still present at the beginning of the Early Vistula glaciation.

The Danish location, which was the first location in the world to receive a full profile of Cladocera succession in Eemian sediments, presents a good comparison with the studied Eemian locations in Poland. Frey (1962) analysed fossil Cladocera remains in 13 Eemian sediment samples from Herning. Palynological analysis was also performed for those sediments (Andersen 1961).

Of the approx. 34 Cladocera species of the Chydoridae family currently known in Denmark, 25 were found in the Eemian sediments from Herning (Frey 1962). The prevalent species were *Chydorus sphaericus*, *Acroperus harpae*, *Eurycercus lamellatus*, and *Peracantha truncata*. The first three species are equally common in Polish lakes, both in the past and current days, whereas *Peracantha truncata* is rather rare. The remains of *Monospilus dispar* and *Chydorus piger* were more frequent in the Danish Eemian sediments than they are nowadays, however, as was reported by Frey, their armour is quite thick, which may result in their better conservation in the sediments. Lower frequency in the examined Eemian sediments than currently was observed for *Peracantha truncata*, whose armour is very thin and thus prone to damage (Frey 1962). The analysed remains from Herning were characterized by a high degree of damage (crushed and ground), which prevented the identification of over 1000 corpus arms in the sediment (Frey 1962).

Cladocera species which occurred in the initial phase of the Danish Eemian water body development (Frey 1962) corresponded with those found in Poland. In the pre-Eemian pe-

riod, the prevalent species were *Bosmina* sp. and *Chydorus sphaericus*, which were joined by the group of large *Alona* at the beginning of the interglacial. Periods of decreased water level were also found in the phase of middle interglacial. In that period, a decrease in the percentage of deep-water forms of *Bosmina* sp. was noticed, while an increased prevalence was reported for shallow-water species, such as *Chydorus sphaericus*, *Monospilus dispar*, *Camptocercus rectirostris*, *Alona* sp. (small *Alona*), *Pleuroxus* sp., *Alonella nana*, and *Graptoleberis testudinaria*. Moreover, the reported species structure indicates a relatively high water temperature, as among the prevailing species there were none which tolerate cool water, except *Chydorus sphaericus*. The water body existed even in the post-Eemian period, when littoral fauna tolerant of cool water prevailed (Frey 1962).

In North America, the Eemian interglacial which occurred in Europe, should be correlated with the Sangamon interglacial. The results of Cladocera analysis from the Sangamon interglacial (the Don Formation) have been presented by Hann, Karrow (1984, 1993). They analysed Cladocera fossils from three water bodies in the region of Toronto, Canada, and found thirty species of Chydoridae, two species of Bosminidae, and one species of both Daphniidae and Sidiidae. The prevailing species was *Bosmina (E.) longispina*. The species found in the interglacial lakes of Canada were identical to those currently inhabiting the lakes. The species of the Don Formation were typical of present-day lakes characterized by moderate water temperature, mesotrophy and a vast littoral zone with macrophytes. Changes in the species composition of Cladocera in the interglacial sediments also brought information on water level changes, lake trophy and the types of macrophytes present (Hann, Karrow 1984, 1993).

SUMMARY

The studied Eemian lakes in Poland arose at the end of the Warta Glaciation (Saalian) in tunnel and kettle holes. They were relatively shallow, had a well-developed littoral zone and no proper pelagic zone. The studied sediments constituted an almost continuous record of environmental changes since the end of the Warta Glaciation, through the Eemian interglacial, until the Vistula Glaciation. Cladocera species found in the studied Eemian sediments corresponded to the present-day species inhabiting Poland and other parts of Europe, while the changes of species structure corresponded to the currently observed geographic distribution of Cladocera. In the Eemian sediments, the author determined 26 Cladocera species, which is comparable to the number of species occurring in the Holocene. The total number of individuals identified in each Cladocera sample was up to 6,000 individuals. The examined remains did not exhibit substantial differences in appearance and size compared to the present-day remains. Cladocera fossils deposited during the Eemian interglacial, compared to those from the Holocene sediments, were thinner, had a more damaged structure and they often lacked characteristic features enabling species determination. Those fossils were particularly difficult to handle in qualitative and quantitative analyses and did not stain efficiently with safranin, which forced the use of a modified sample preparation. The prevalent species in each of lake de-

velopment stages, correlated with palynological phases, were those characterized by very modest habitat requirements and a high resistance to environmental stress, residing in the water bodies throughout the Eemian interglacial. In each of the studied water bodies, several developmental stages were distinguished, which were reflected in the changes within Cladocera species composition. The nature of development was related to morphometric properties of the water bodies, as well as local and global climatic conditions encountered in the Eemian interglacial. Despite a more laborious method of sample preparation, the obtained results are fully credible and may be used in the reconstruction of environmental conditions from the period preceding the last glaciation.

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