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ORIGINAL PAPER

# Changes in the biota and sediments of glacial Lake Koźmin, Poland, during the late Saalian (Illinoian)

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**Abstract** Upper Saalian (Illinoian) glaciolacustrine deposits in central Poland, preserved in a tectonic graben, were exposed in an opencast lignite mine and investigated using sedimentological and micro-paleontological methods. The extraglacial lake sediments provide the first records of late Saalian cladoceran communities in central Europe, recovered from glaciolacustrine deposits. Sedimentation was dominated by a supply of clastics that fluctuated with the seasons, forming rhythmites. In addition to seasonal cyclicity, sedimentary and environmental conditions changed every several years to decades, with periods of increased inflow to the lake delivering sandy material, and periods of almost stagnant water dominated by suspension settling. The sediments contain Cladocera assemblages that indicate the lake was initially deep, oligotrophic, and filled with moderately cold water. Changes in Cladocera community composition and abundance were perhaps responses to climate seasonality. Zones without Cladocera were associated with seasons of higher inflow and sediment supply, and directly or indirectly, with tectonic activity in the graben. Earthquakes, documented by the presence of seismites, caused not only deformation of unconsolidated lake-bottom sediments, but possibly also changes in habitat characteristics. Combined sedimentological and biological data were used to infer the lake's history and show that deposits of glaciolacustrine lakes can be used as indicators of past ecological and climate changes.

**Keywords** Subfossil Cladocera · Sedimentary cycles · Glaciolacustrine deposits · Seismites · Climate changes · Late Saalian

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## Introduction

Multi-disciplinary paleolimnological studies of lakes of glacial origin are rare compared to the numerous studies of contemporary polar- and mountain-lake ecosystems because the latter provide records of environmental and climatic change. Polar and mountain lakes are highly sensitive to climate change and human impact. Modern high-mountain and Arctic glacial lakes have experienced considerable biotic and sedimentary changes in the past few centuries, which have accelerated in the past few decades (Lami et al. 2000; Battarbee et al. 2002). Multi-proxy studies of varved lake sediment on Svalbard, northern Norway, provided a record of such changes during the last 1,800 years (Guilizzoni et al. 2006). Similar studies of ecological changes in Holocene lakes of Greenland were carried out by Bennike (2000), who pointed out the potential of such lakes as paleoecological archives.

One faunal group that is useful for paleoecological reconstructions is the Cladocera, small crustaceans that live mostly in lakes, even at high latitudes and altitudes. Their ecological preferences are relatively well known, so cladoceran species are good indicators for inferring paleoenvironmental conditions in lakes, including trophic status, water-level fluctuations, and pH. The species diversity and biogeography of crustaceans in lakes all over the Arctic, including Arctic Canada, Nunavut, Greenland, Svalbard, eastern Siberia, the Beringian region, and Alaska have been described by Lauridsen et al. (2001), Samchyshyna et al. (2008), Sweetman et al. (2010) and others. Data on subfossil Cladocera community composition in Svalbard lakes were reported by Zawisza and Szeroczyńska (2011). Lakes in the Arctic are often inhabited by few species and accordingly, have simple pelagic food-web structures (Stross et al. 1980). The overall zooplankton community structure is also simple (Jeppesen et al. 2001). Environmental conditions for organisms in Arctic freshwater ecosystems are harsh, with short ice-free periods, low temperatures, high levels of ultraviolet radiation, and often low nutrient and food levels (Hebert and Hann 1986). Abiotic factors display temporal variations that are often large and unpredictable. This is another reason why the biodiversity of freshwater organisms is generally low in such environments (Stonehouse 1989). Most high-latitude organisms are adapted to withstand these harsh conditions (Morison et al. 2000) and have been found even in lakes with glacial varves (Merta 1986; Stewart et al. 2008).

Varved lake sediments have also been studied in Europe, where the focus was on seasonal variability of the late Weichselian and Holocene climate and corresponding changes in the flora and fauna (Goslar et al. 1998; Chapron et al. 2007; Voigt et al. 2008; Gedl 2011). Abundant studies have described trace fossils (arthropod and fish trackways) from varved lacustrine sediments (Benner et al. 2008; Uchman et al. 2009), but few reports deal with crustaceans, especially from the end of the Saalian glaciations to the beginning of the Eemian interglacial (Mirosław-Grabowska et al. 2009). There are no studies of Saalian cladocerans from glaciolacustrine, partly varved sediments as far as we are aware. Studies that combine sedimentological and biological evidence to reconstruct major changes in the paleolakes of Europe, especially during the Saalian, are rare. The present contribution is one of the first studies of this type in Poland.

Glacigenic lakes that receive glacial meltwater are, as a rule, oligotrophic and devoid of biota. Low water temperature and generally high dynamics make it nearly impossible for life to exist in glacial or glacially influenced lakes (Brodzikowski 1993). Additionally, water in such lakes is rich in oxygen. Nitrogen and phosphorus are present in small amounts and trophic state is low. Lakes fed by glacial meltwater are extreme habitats for life and they are commonly considered "deserts." Records of life in such lakes consequently provide important information about the ecological conditions that prevailed during glaciolacustrine sedimentation. Glacial Lake Koźmin is one of the rare sites in Europe where such a record has been preserved. This unique record is important because (1) Cladocera are present in the glacial lake sediments, which consist of mineral and organic deposits, (2) the lake possesses one of the longest (>10 m) and oldest records of late Saalian cladoceran communities in central Europe, (3) the combination of sedimentological and biological data can be used for inferring the lake's history and (4) graben tectonics influenced Cladocera development in the lake.

The present contribution provides the first data on Cladocera recovered from late Saalian, glaciolacustrine deposits from Poland. Data from the record were used to infer the paleoenvironmental changes that occurred during the late Saalian in central Europe.

## Site description

The studied glaciolacustrine deposits outcrop in Koźmin-South, which is part of an opencast lignite mine in central Poland (Koźmin-S—Fig. 1a). The mine is situated in the Adamów Graben (Fig. 2), a tectonic structure 13 km long in a NNE-SSW direction. It was active during the Paleogene and Neogene (Widera 1998, 2007), and ongoing subsidence during the Pleistocene led to the accumulation of a thick sedimentary succession.

The study site is situated within the area covered by ice during the Warthe (Saalian = Illinoian) Glacial

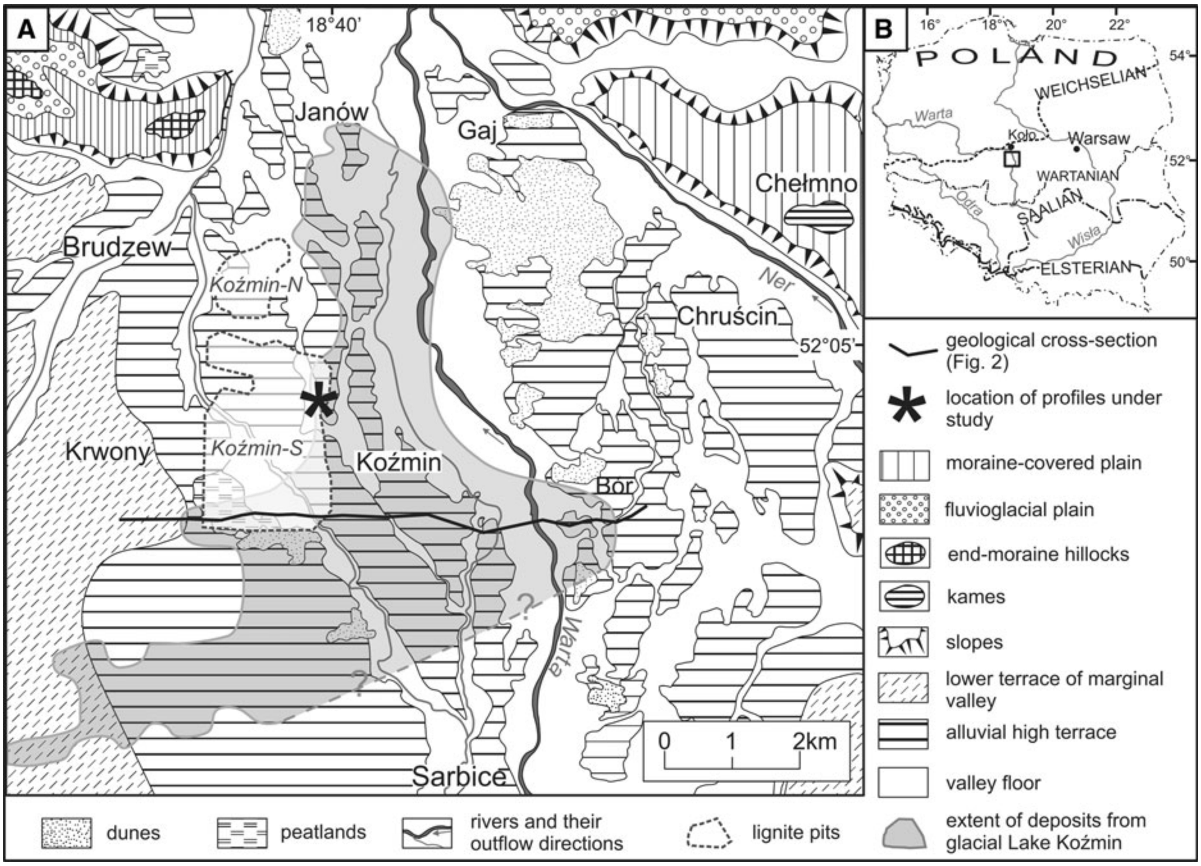


**Fig. 1** Location of the Koźmin site in Poland. **a** Geomorphological map of the area surrounding glacial Lake Koźmin. **b** Location of the site on the map of Poland with maximal extent lines of the four main glaciations

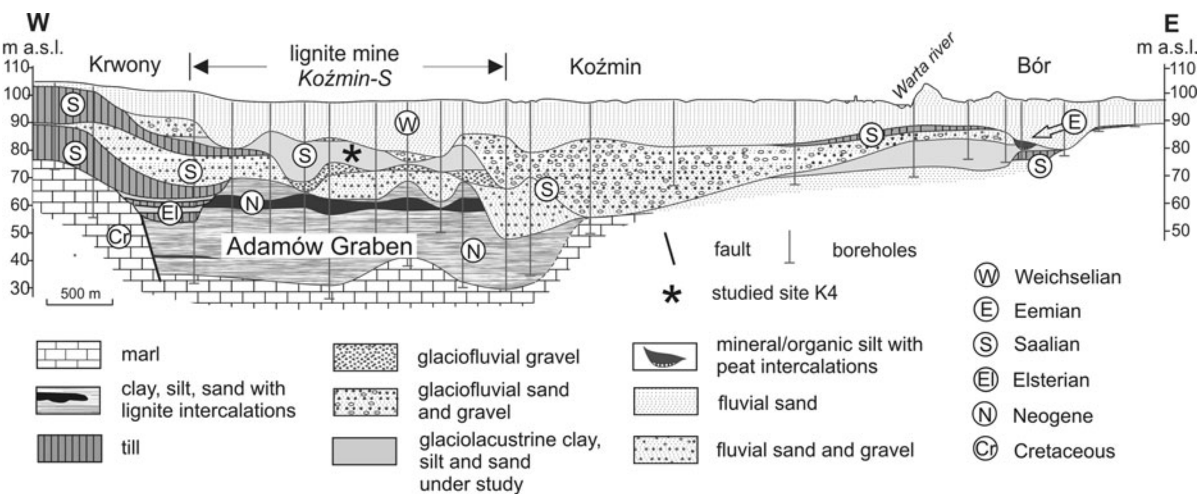


**Fig. 2** Geological cross-section through the Adamów Graben based on boreholes, complemented with observations in the mine walls. The location of cross-section is indicated in Fig. 1

Maximum (Fig. 1b). During the Last Glacial Maximum, the land-ice cap extended to about 20 km north of the study site (Petera and Forysiak 2003; Marks 2005).

Lake Koźmin, on which the present study focuses, was located in the middle reach of the contemporary Warta River (Fig. 1), which followed and eroded the valley that existed as a consequence of the graben lability during the successive glacials/interglacials of the Pleistocene and during the Holocene (Forysiak 2005). The lake was, according to field and borehole data, ~2 km wide in the north, and >8 km wide in the south, and was about 8 km long (Fig. 1a). The sections studied are near the central part of the graben (Fig. 2), which is filled with Neogene clay, silt, sand and lignite. The glaciolacustrine clastic sediments overlap the Saalian till from the west and east, and glaciofluvial sand and gravel in the central part. The contact with underlying series is sedimentary. This proves the glacial origin of the lake, although the main material supply was from past inflow of the Warta River, from the south. The glacial lake deposits are covered by the Saalian glaciofluvial sediments and till, which is largely eroded by sand of Weichselian age. The first information about glacial Lake Koźmin and its stratigraphic position was provided by Czarnik (1972), who placed it in the Warthe transgression. Glaciolacustrine and glacial deposits were dated using OSL and TL methods (Petera-Zganiacz et al. 2010). Results ranged from 175.4 ± 26.3 to 82.9 ± 12.4 ka BP (TL dates). Dates obtained with OSL are slightly younger, ranging from 106.9 ± 5.5 to 69.5 ± 4.8 ka BP. There are no visible hiatuses, i.e. large-scale erosional surfaces, in the sedimentary succession of the lake. It is likely, however, that the sediment record contains hiatuses because the investigated section is located in the marginal part of the waterbody and susceptible to erosion. This may, in part, explain the imprecise OSL and TL dates. Recent lithological and petrographic investigations of till underlying the glaciolacustrine deposit suggest the lake was formed at the end of the Warthe glaciation (Czubla et al. 2010).

## Materials and methods

### Lithology

The study focuses on sediments outcropping in the lignite mine. The four measured sections (K1:K4—Fig. 3) were sedimentologically analyzed. They are located from the margin to the central part of the glacial lake. The total thickness of the glaciolacustrine deposit was 11 m. The 10-m-thick K4 profile was sampled for grain-size and Cladocera analyses (Fig. 3).

The lithofacies and lithofacies associations were distinguished, described and interpreted (Figs. 3, 5). Soft-sediment deformations were identified and deformed layers were correlated along a cross-section through the lake deposits.

Samples were taken from the silty and clayey lithofacies for grain-size analysis by laser diffraction (Mastersizer 2000 particle size analyzer). The grain size is indicated following the Wenthword (1922) scale in which colloid clay is <1 μm, coarse clay is 1–3.9 μm, silt is 3.9–62.5 μm and sand is up to 2 mm.

### Cladocera

Cladocera analysis is based on samples from section K4, 32.50–23.50 m below ground surface. They were collected in 5-cm intervals. Samples of 1 $cm^3$ were processed according to Frey (1986), but without using a magnetic stirrer. All remains were counted, i.e. head shields, shells, postabdomens and postabdominal claws. The most abundant body part was chosen to represent the number of individuals for each taxon, and percentages were calculated from the sum of individuals. Because the frequency of Cladocera was low, 5–10 slides were counted per sediment sample. In most samples, 100 individuals were counted. The taxonomy of cladoceran remains follows Szeroczyńska and Sarmaja-Korjonen (2007). The presence of Cladocera species and their abundances were used to reconstruct the development of Lake Koźmin. Cladocera zones were distinguished using species composition and abundances (Figs. 5, 6). Ecological preferences of cladoceran taxa were determined following Whiteside (1970) and Szeroczyńska (1998).

Results were plotted in a percentage diagram (Fig. 6) using POLPAL software (Walanus and Nalepka 1999) and cluster analysis was done using MSVP version 3.1 software (Kovach 2007). Zonation was done by cluster analysis (Fig. 6), using Ward's method (the unweighted minimum-variance method) together with the squared Euclidean distance (Birks 1986). Ward's method tends to join clusters with a small number of observations, and it is strongly biased

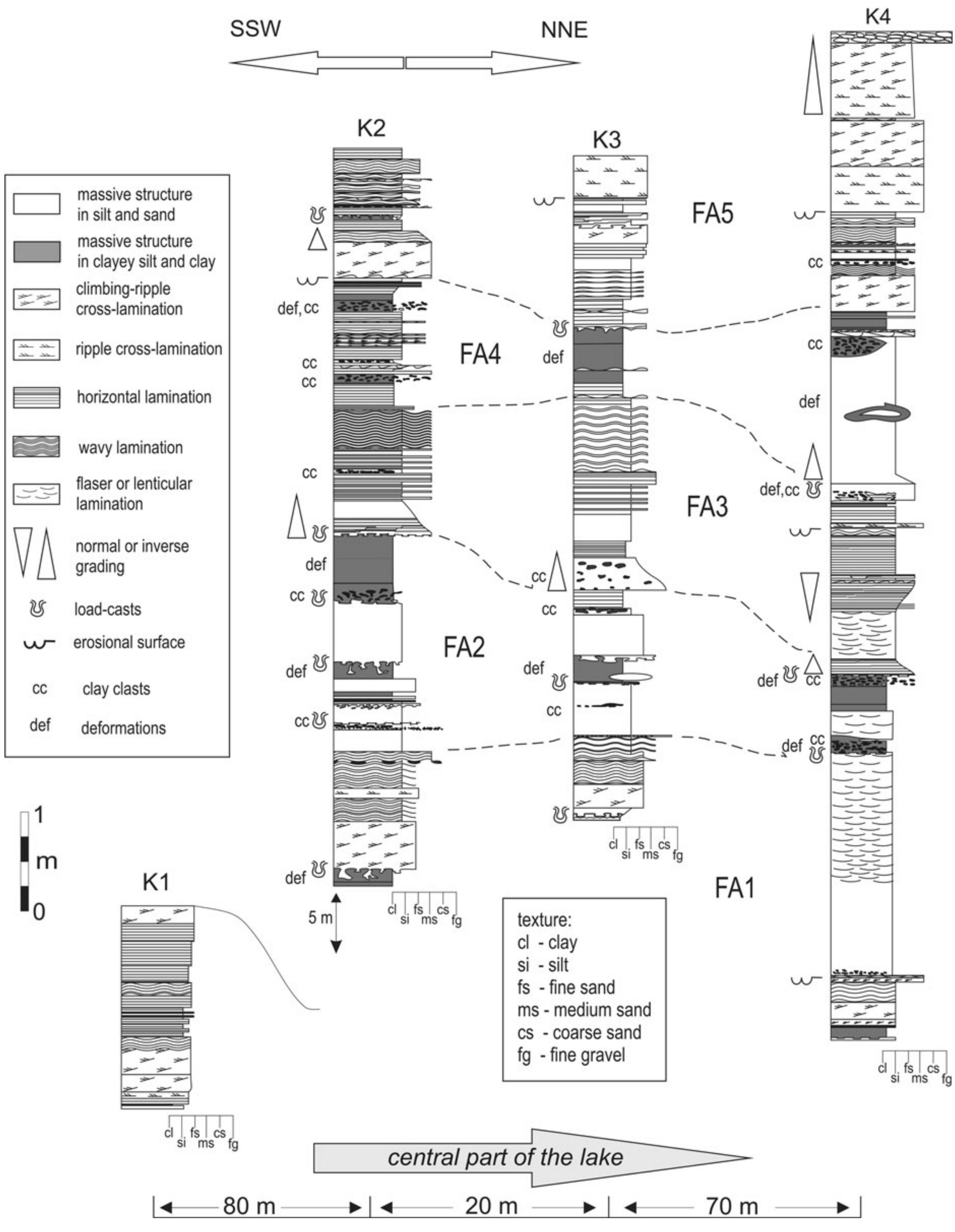


**Fig. 3** Sedimentological profiles from the Koźmin site covering more than 200 m of exposed deposits on the NW wall of the lignite mine. See the description of facies associations FA1–FA5 in the text

toward producing clusters with the same shape and with roughly the same number of observations. Only species with at least 5 % presence in each level were included in statistical calculations. Cladocera diversity is expressed by the Shannon-Wiener index (H′), which was calculated as $H' = -\sum(p_i)(\log2\ p_i)$, where the sum ($\Sigma$) is over the number of species and $p_i$ is the proportion of the total sample belonging to the *i*th species (Krebs 1994).

## Results

### Lithology and sedimentology

Clay and silt lithofacies predominate in all sections, commonly forming rhythmites. The clay units are massive and are ≤5 cm thick. The silt is massive or horizontally laminated, and forms layers up to 40 cm thick (Fig. 3).

The grain-size analysis shows that the macroscopically distinguished clay contains a relatively small amount of colloid clay, up to 20 %. Coarse clay makes up 27–54 %. The horizontally laminated silts usually contain up to 10 % colloid clay and up to 5 % fine sand.

The clays and silts are intercalated with laminae of fine sand in the form of thin films under the clay. Sand or sandy silt are also present as ripple cross-laminated layers with thicknesses up to 6 cm, or form cosets of climbing-ripple cross-lamination and wavy lamination, which are up to 1 m thick (Fig. 3). Some sandy/silty lithofacies show flaser or lenticular bedding (*sensu* Reineck and Wunderlich 1968). Horizontally laminated sandy layers are less common and can reach a maximum thickness of 40 cm.

In the studied sections, five facies associations (FA1–FA5) are distinguished (Fig. 3). Associations FA1, FA3 and FA5 are dominated by silt and sand, whereas associations FA2 and FA4 are dominated by clay and silt. The sediments show a distinct rhythmicity, which is present in all facies associations. Associations FA1, FA3 and FA5 contain cosets of ripple cross-laminated sand as well as wavy-laminated silt and sandy silt or silty sand of flaser lamination (Fig. 3). Some of them show normal grading, especially when ripple cross-laminated sand changes upward into climbing-ripple cross-lamination of the A, and then B type. The thickness of individual beds (up to 1 m) is larger than in associations FA2 and FA4. The latter units are dominated by clay and silt and all rhythmites finish with a clay layer (Fig. 4a). The thicknesses of the individual silt/clay couplets are <30 cm but thinner couplets of 2–3 cm are more common. The contact between silt and clay in the small-scale rhythmites is gradual rather than sharp.

Some deposits are strongly deformed. These deformations are present mainly in facies associations FA2 and FA4, where most of the clay layers are present (Fig. 3). They commonly comprise a few layers of clayey/silty or clayey/sandy rhythmites, constituting deformed beds that can be traced over all outcrops (Fig. 4d). The precise number of layers involved is usually not clear because the individual layers are strongly mixed (Fig. 4b). The deformed beds are 10–50 cm thick, have distinct, sharp upper boundaries, and commonly have deformed bases (Fig. 4c). Silty or silty-sandy load casts in the matrix of massive clay are the most common deformation, but different types of ball-and-pillow structures and small-scale sand and silt injections or plastic intrusions are also present. One of the deformed beds shows a breccia in the upper part. It consists of deformed clay clasts in a silty matrix. Some small faults occur as well (Fig. 4b). In the studied glaciolacustrine succession there are four such strongly deformed beds along the whole outcropped section (Figs. 3, 4).

### Interpretation of the facies and facies associations

Facies associations FA1, FA3 and FA5 (Figs. 3, 5), dominated by silt and sand lithofacies, were apparently formed by the action of bottom currents. The supply of sand and silty sand must have been constant for long periods, considering the accumulation of layers >1 m thick. The climbing-ripple cross-stratified units, finishing with wavy lamination, originated during waning currents and are typical of proximal deltaic bottomsets (Brodzikowski and Van Loon 1991). Both the sandy nature and the presence of structures formed by bottom currents point to deposition in a proximal part of the lake, relatively close to the source; a delta is consequently plausible. The rhythmic patterns, finishing with finer-grained sediments, reflect distinct seasonal changes in material supply.

Facies associations FA2 and FA4 (Figs. 3, 5) represent a more distal environment. The rhythmites

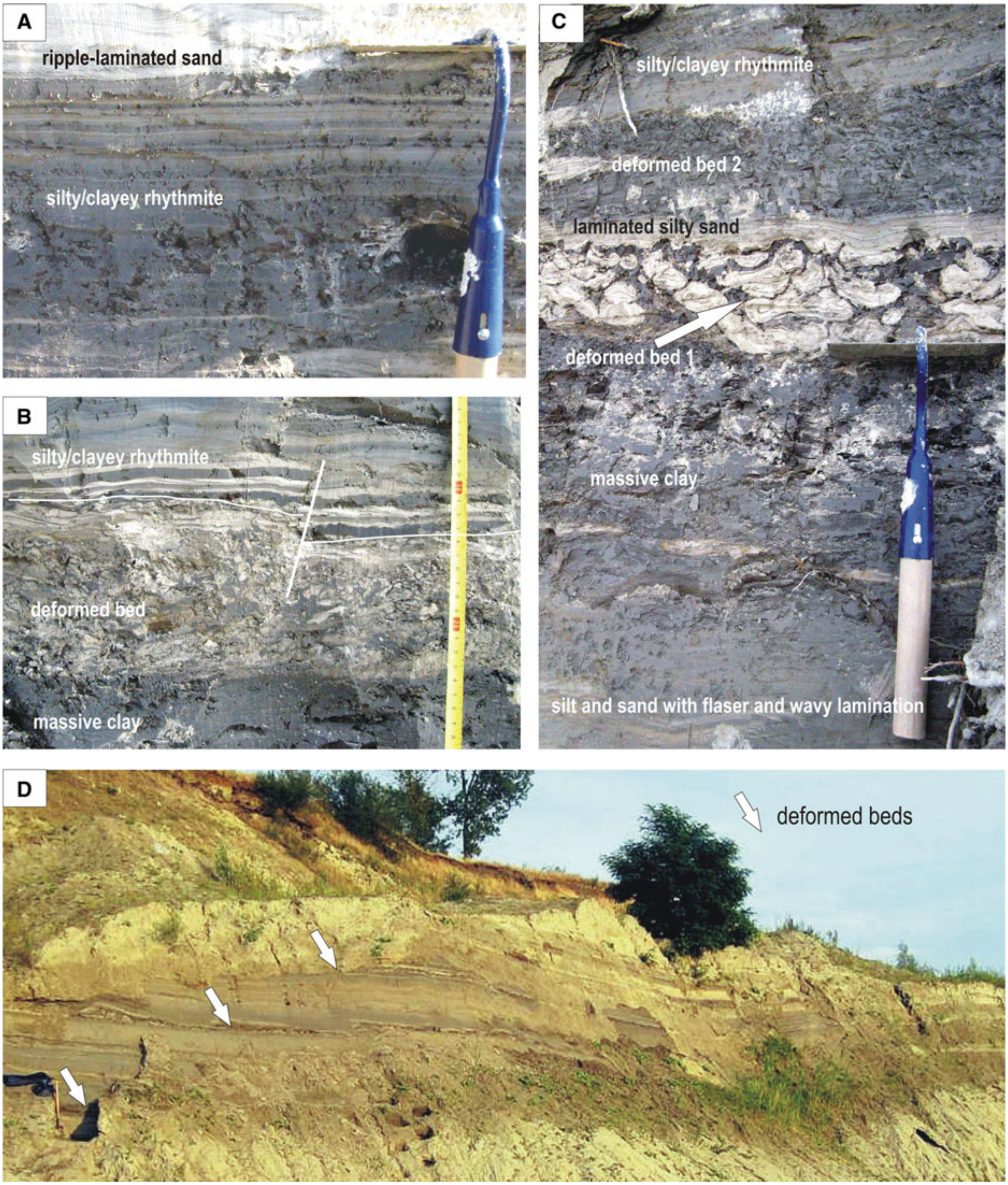


**Fig. 4** Glaciolacustrine deposits of Lake Koźmin. **a** Silty/clayey rhythmites dominated facies associations FA2 and FA4. **b** Deformed bed (seismite) cut by syndeposition fault. **c** Two deformed beds (seismites) intercalated by horizontally laminated silty sand. The lower deformed bed 1 contains sandy silty load casts in a clayey matrix. The upper deformed bed 2 contains smaller-scale deformations made by mixing of silty and sandy layers. **d** Position of seismites in part of the studied section

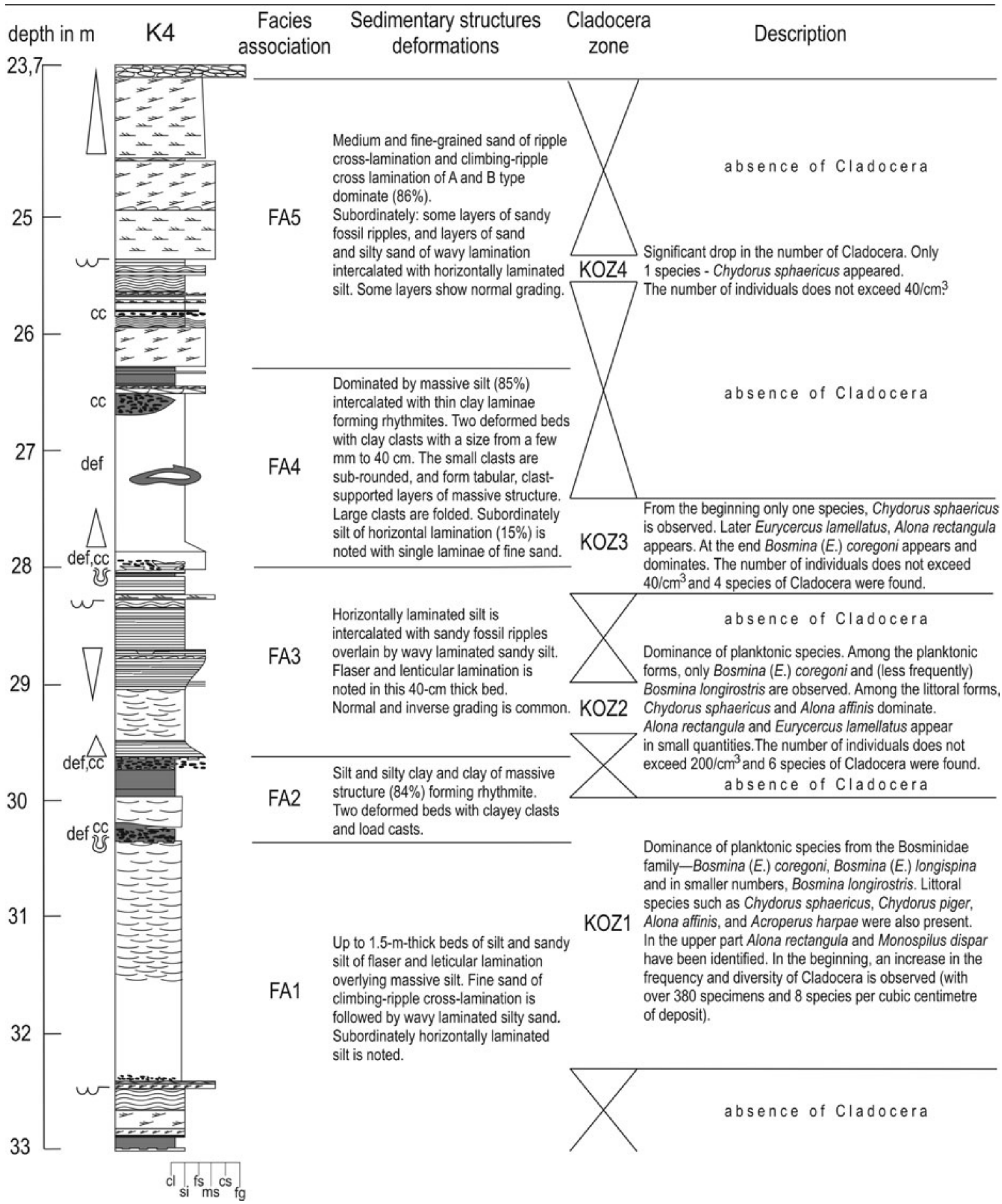


**Fig. 5** Characteristics of facies associations versus Cladocera zones distinguished for the K4 sediment log. See Fig. 3 for the log details

are thinner and sand is restricted to thin layers between silt. All couplets finish with clay (Fig. 4a). The small thickness of the rhythmites indicates that the supply of material to the lake was much less than for associations FA1, FA3 and FA5, during both warmer and colder seasons. The amount of colloidal clay is, however, relatively low for the heavy clay (Ringberg and Erlström 1999) that is typical of glaciolacustrine varves. Yet most such varve successions in Poland that occur in tectonic grabens have a relatively low content of colloidal clay, both in their proximal and distal parts (Gruszka 2001, 2007). Gradual transitions between silt and clay layers indicate distal turbidity currents as the depositional process. Such deposits used to be interpreted as turbidite varves (Sturm and Matter 1978), being equivalent to varves, but deposited in the proximal part of the lake, close to the inflow or on a delta foreslope. Even if we assume that the rhythmites are varves, it is still difficult to estimate the number of years in which associations FA2 and FA4 were deposited, as there was strong deformation of the beds.

We emphasize that the facies associations dominated by sand and silt (FA1, FA3 and FA5) are followed by associations dominated by silt and clay (FA2, FA4). This allows us to divide the glacial lake development into five cycles of higher rank than the simple rhythmic deposits. It seems that sedimentary and environmental conditions distinctly changed every few years to decades, with periods of increased inflow to the lake that delivered sandy material, and periods of almost stagnant water during which suspension settling and distal turbidity currents predominated.

The deformed beds are relatively thick and are comprised of an unknown number of varves. Their number may range from a few to tens of individual silty/clayey couplets. They lie between non-deformed sediments, show sharp upper boundaries, broad extent (traceable over the entire glaciolacustrine outcropping unit, i.e. a few hundred meters), and no major change in thickness. The deformed beds display all the characteristics of seismites (Bowman et al. 2004; Moretti and Ronchi 2011), which are in situ deformed beds that formed as a consequence of earthquakes in the basement. An important additional argument for the interpretation of these deposits as seismites, is that structures such as loadcasts of different scale, ball and pillow structures and flame structures, resulted from liquefaction inside the beds (Fig. 4b, c). The small faults, which cut the upper surface of the seismite layers, must have resulted from secondary shocks. To identify a seismite, it is important to prove not only that an earthquake was the trigger mechanism (detailed regional context is necessary), but also to exclude gravity as the cause (Bowman et. al. 2004). Although the first seismites were described >30 years ago (Seilacher 1969), there is still debate about their identification in the sedimentary succession (Greb and Dever 2002) as well as the trigger mechanism for sediment liquefaction in different lithologies (Chunga et al. 2007; Owen and Moretti 2011).

The location of the lake in a tectonic graben supports the possible occurrence of earthquakes in the study area during the Pleistocene. Although there is no proof that the Adamów Graben was still active during the Pleistocene, it is very well possible, if not likely. During the Pleistocene, the area was covered several times by an ice sheet, which must have favoured renewed subsidence as a consequence of ice weight and glacioisostasy, as was proven for the Kleszczów Graben (Brodzikowski 1985), about 150 km southeast of the site.

## Cladocera

The sediments of glacial Lake Koźmin contain 10 Cladocera species (Fig. 6), belonging to two families. The number of Cladocera remains is low and ranges from 10 to 380 individuals per $cm^3$ (Fig. 6). The most abundant are littoral species of the Chydoridae family. Among the chydorids, *Chydorus sphaericus* is dominant. *Paralona pigra* and *Alona affinis* are quite abundant. The relative abundance of pelagic individuals from the Bosminidae family locally exceeds 80 % (Fig. 6). Planktonic Cladocera are represented by three species, *Bosmina (Eubosmina) longispina*, *Bosmina (Eubosmina) coregoni* and *Bosmina longirostris*.

On the basis of the Cladocera abundances and changes in the frequency of species, four Cladocera zones were distinguished: KOZ1–KOZ4 (Figs. 5, 6). Zone KOZ1 is characterized by a low abundance of Cladocera specimens, but compared to the rest of the section, the number of taxa (7) is high (Fig. 6). The second zone (KOZ2) is characterized by a lower abundance of Cladocera specimens. In the third zone (KOZ3), >80 % of the Cladocera assemblage is *C. sphaericus*, and *B. coregoni* only dominates in the

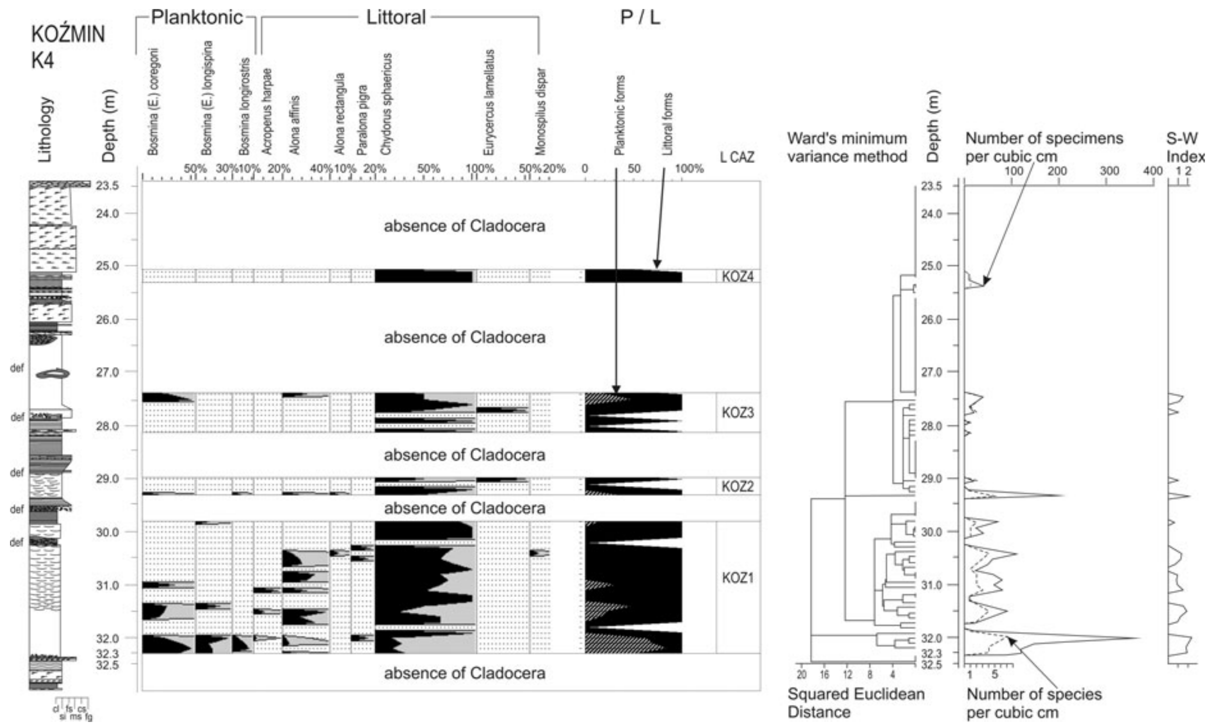


**Fig. 6** Percentage diagram of the Cladocera assemblages, ratio of planktonic (P) to littoral (L) forms and proposed Cladocera zones (CAZ), simple numerical analyses of cladoceran data (cluster-analysis diagram), total number of species and specimens in 1 $cm^3$ of sediment, and Shannon-Wiener diversity index (S-W index) in the Koźmin K4 section. For lithology and other details, see Fig. 3

upper part of the zone. In the fourth zone (KOZ4), the only species present is *C. sphaericus*. These zones are separated by intervals with no Cladocera remains. At depth intervals of 29.80–29.30, 29.00–28.10, and 27.40–25.30 m, no cladoceran remains occur (Fig. 6). The first occurrence of Cladocera remains was noted at 32.3 m depth. The last occurrence of the crustaceans is at a depth 25.30 m below the ground surface.

According to changes in the abundance of Cladocera, two main phases were distinguished. The first phase, represented by zone KOZ1, is characterized by a relatively high concentration and biodiversity of remains, whereas the later, second phase, zones KOZ2–KOZ4, shows a much lower concentration and diversity of remains (Fig. 6).

## Interpretation of Cladocera

The Cladocera assemblages display low species diversity in the whole section, which is ascribed in large part to the extreme climate conditions. Zone KOZ1 represents the initial period of lake colonization. Initially, the lake was probably deep, but with time it became shallower. This is confirmed by the abundance of planktonic species, as high as 80 % during early stages of basin development. The low frequency and occasional total lack of planktonic forms can be explained by the littoral location of the section under study.

Cladocera zones KOZ2–KOZ4 represent a time when Cladocera re-colonized the basin (Figs. 5, 6). Pioneer species, representing immigrant taxa, dominated zone KOZ2, but habitat conditions were probably good enough for further Cladocera development. Presence of planktonic species, which live in the open-water zone of the lake, suggests a relatively deep basin. The dominance of *B. coregoni,* which prefers somewhat warmer environments (Megard 1964), and the presence of *B. longirostris*, suggest only moderately cold water and probably, improving habitat conditions (Sweetman et al. 2010). Additionally, presence of littoral species such as *A. affinis* and *Eurycercus lamellatus*, suggests the lake supported littoral vegetation.

The third zone (KOZ3) represents worse conditions. Replacement of dominant *C. sphaericus* by *B. coregoni* in the upper part of the zone probably reflects a rise in water level (Fig. 6).

Zone KOZ4 was apparently a suboptimal period for Cladocera because of the dominance of a single taxon, *C. sphaericus,* which is a cosmopolitan species that occurs over a wide range of latitudes and altitudes. The decrease in abundance and diversity of the Cladocera toward the upper part of the section is ascribed to the increased supply of sediment particles to the lake, resulting in gradual shallowing and infilling. This increasing sediment supply prevented the development of Cladocera populations. Eventually, Lake Koźmin ceased to exist, having filled with sediment.

## Discussion

### Past environmental conditions

Late Saalian deposits that contain cladoceran remains are very rare compared to organic lake deposits of the Eemian interglacial (Mirosław-Grabowska and Niska 2005, 2007; Pawłowski 2011). Sediments from late Saalian sites (Mirosław-Grabowska and Niska 2005, 2007; Mirosław-Grabowska et al. 2009) represent only a short phase when lakes formed just before the Eemian interglacial. Unfortunately, sediments from Eemian lakes have not been analyzed sedimentologically. Hence, environmental conditions of the Eemian lakes are difficult to compare with the Koźmin data.

The geomorphology of the area and borehole data suggest the study site is at the former margin of a large glacial lake (Fig. 1a). The presence of structures formed by bottom currents that supplied sand and sandy silt to the lake indicate a position close to the lake margin and additionally imply a lack of “true” varves. Abundant littoral cladoceran remains provide additional evidence for a shallow-water setting. Absence of debris left by ice rafting, i.e. dropstones in the lake sediments, suggests an extraglacial position of the lake, at great distance from the active ice front (Brodzikowski and Van Loon 1991). The location of the glacial lake within the Warta valley implies supply of material from the south. Most likely, glacial Lake Koźmin was an extraglacially-fed basin with a relatively stable hydrodynamic system, which explains the presence of crustaceans. Because of the distance from the ice sheet, the climate must have been only moderately cold, not as extreme as temperatures in terminoglacial lakes (i.e. in direct contact with the ice sheet). The presence of rhythmites in the entire glaciolacustrine section proves the seasonal dependence of material supply, characteristic of glacigenic settings (Brodzikowski and Van Loon, 1991; Ringberg 1991).

Temperature largely determines the growth, reproduction, life history, as well as altitudinal and latitudinal distribution of Cladocera species. Most cladoceran species in Lake Koźmin are known from widespread sites in both Arctic and temperate regions. Among the planktonic forms, two species, *Bosmina coregoni* and *B. longispina*, dominated the cladoceran community in the basin. These taxa co-occur in most European, oligotrophic mountain lakes (Korhola 1999) and even in sub-Arctic environments (Hann and Karrow 1993). A similar community composition has been found at other late Saalian sites in Poland (Mirosław-Grabowska and Niska 2005, 2007; Mirosław-Grabowska et al. 2009). In all these paleolakes, pioneer species of Cladocera that tolerate cool water occurred, including, among others, *A. affinis* and *C. sphaericus*. The presence of *P. pigra* also suggests clear, oligotrophic and cold water, although the ecology of *P. pigra* is not yet fully understood (Whiteside 1970; Korhola 1999; Kattel et al. 2008) because this species is also common in lakes with warmer water temperature.

In addition to the cosmopolitan taxa and species that are characteristic of Arctic regions, the Koźmin basin also possessed species that prefer water of moderate temperature (Røen 1995). The community composition, in particular the presence of *Monospilus dispar*, indicates improving habitat conditions. This species lives in relatively warm environments under mesotrophic conditions (Røen 1995), but this may mainly reflect summer water temperature (Kattel et al. 2008). Also, the presence of species such as *Alona rectangula* and *B. longirostris* suggests moderate water temperature and more nutrients, but the trophic state of the lake evidently remained oligotrophic. On the other hand, *M. dispar* depends on the bottom sediment and is a sand-preferring or sediment-dwelling species (Frey 1986). Shoreline habitats dominated by sandy and silty substrates, particularly areas where streams enter the lake, can be inhabited by *M. dispar* (Kattel et al. 2008). Occurrence of this species thus points to the proximal part of the sedimentary basin and suggests the inflow of streams to the basin.

Three environmental variables, lake-water temperature, nutrients, and dissolved organic carbon, could explain a significant part of the variation in the structure of the cladoceran community, as suggested by Sweetman et al. (2010) for central Canadian Arctic lakes. The most important environmental factor in Lake Koźmin was probably temperature, which influenced not only the diversity, abundance, and fecundity of the zooplankton species, but also the periodic development of macrophytes. Similar observations were described from modern Arctic lakes (Sweetman et al. 2010), alpine lakes in Europe (Lotter et al. 1997) and fossil lake successions (Lotter et al. 2000; Duigan and Birks 2000; Sarmaja-Korjonen et al. 2006).

To understand why Cladocera appeared and disappeared in the sediment record of this basin, we compared the Cladocera zones with sedimentological data (Fig. 5). Generally, Cladocera remains occur in silt layers with a massive structure or with flaser lamination, and less so in silt with horizontal lamination. A complete absence of cladoceran remains is recorded in sand and sandy silt layers with ripple and climbing-ripple cross-lamination. This indicates that the intervals in which Cladocera were present were, as a rule, related to time intervals without or with extremely limited inflow, which means stagnant water and settling of suspended matter or distal turbidity currents, represented by facies associations FA2 and FA4. This suggests that inflow of sediment-laden water occurred far from the study site, during phases when Cladocera became more frequent. Vice versa, the absence of Cladocera represents phases of increased inflow and increased supply of sediment particles (Figs. 5, 7). Fluctuations in the distance from the sediment source to the deposition site of the section under study are explained by changes in the locations where streams entered the lake. This means that the lake area fluctuated, which implies changes in lake water level. These may have been caused by glacigenic or tectonic activity (subsidence or tectonic stability) and partly explain the appearance and disappearance of planktonic Cladocera species over time.

The Upper Saalian sediments of glacial Lake Koźmin show a cyclicity that was caused not only by seasonal changes in material supply, but also by a factor that changed the sediment supply over periods of several years to decades. This is documented by changes in the facies associations, from those dominated by sand to those dominated by silt and clay. The reasons behind these changes are still not clear. They might be the consequence of climate changes or changes in the amplitude of the lake-level fluctuations. Unfortunately, we have no data to plausibly infer the climate context. Nevertheless it is possible that these higher-rank cycles (equivalent to lithofacies associations) are related to sun-spot cycles. Lundqvist (1997, 1999) showed that esker deposits and accompanying varves followed the slower or faster ice-sheet retreat, corresponding to the 11-year sun-spot cycle.

Changes in the supply of material to Pleistocene glacial lakes are typical and can be related to, for instance, movements of the ice-sheet margin, proximity of entering glacial rivers, seasonality of the ice sheet melting and climate changes (Ashley and Warren 1997; Błaszkiewicz and Gruszka 2005). It seems that Cladocera colonized Lake Koźmin and took advantage of periods with relatively low material supply (Figs. 6, 7). Their ecological plasticity allowed them to inhabit a wide range of freshwater conditions, even after tectonic shocks. The time intervals with high sediment supply to the lake might be connected with climate warming (fast ice-sheet retreat), whereas climate cooling (ice-sheet stagnation) was associated with a dominance of suspended silt and clay (FA2, FA4—Figs. 3, 5). We estimated the relative durations of the deposition of sand-dominated and silt/clay-dominated facies associations, and it seems the latter were relatively longer and interrupted by tectonic activity.

## Preservation of crustaceans and seismic activity

Low cladoceran concentrations in glacial lakes may be a consequence of low food and nutrient availability, low water temperatures, unfavorable sediment types, high sedimentation rates, etc. Understanding the development of Lake Koźmin requires consideration of these factors as well as more general processes, including taphonomy, in their geological context.

The small number of species and Cladocera individuals is consistent with the observation that littoral taxa shed their exoskeletons in the littoral habitat, but they are subsequently transported to the lake center. Transport of such remains in the lake basin can occur

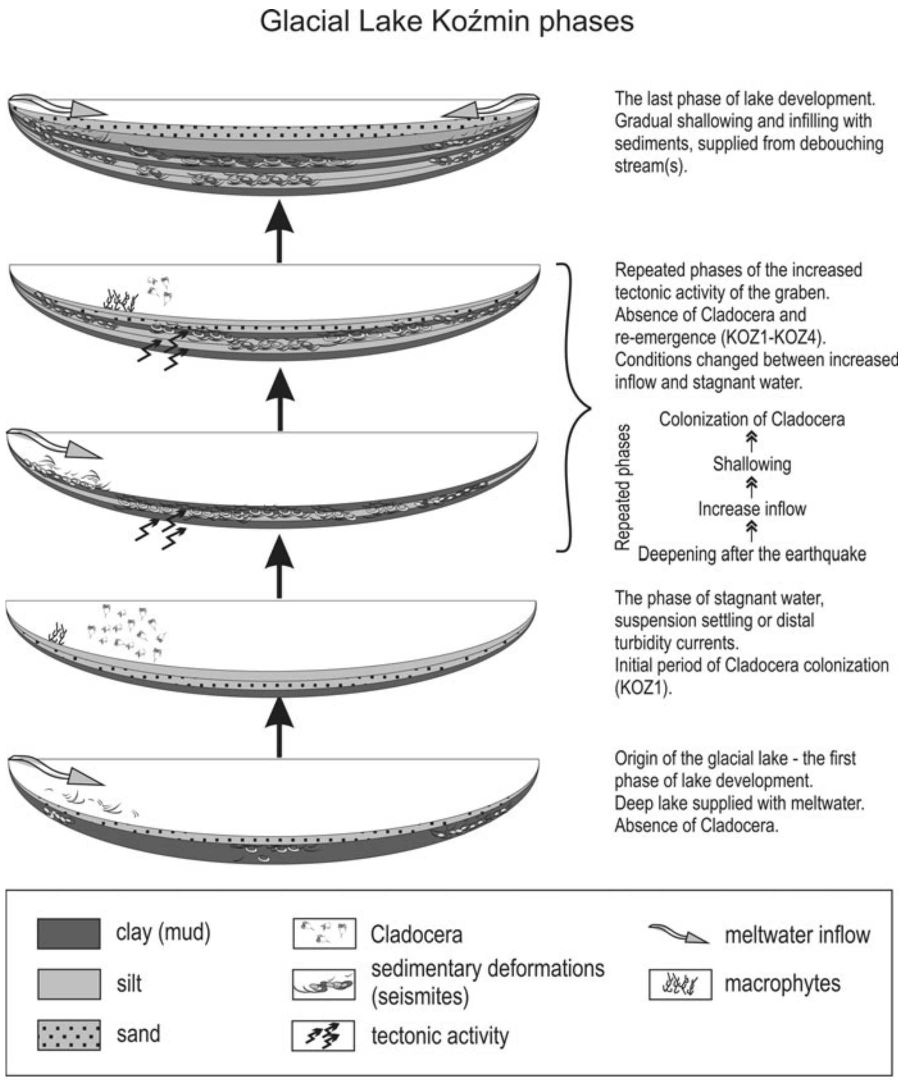


**Fig. 7** Summary diagram and scheme illustrating the phases of development of Saalian glacial Lake Koźmin

through several processes such as wind-induced wave action and currents (Whiteside and Harmsworth 1967). A taphonomic study by Kattel et al. (2007) suggested that remains of littoral taxa (particularly chydorids), after death or molting, show relative enrichment in their original habitat. Planktonic remains are relatively enriched towards the deeper, center of the lake.

It is interesting that we did not find ephippia, especially because viable diapausing eggs are often extremely abundant and can survive in aquatic sediments for decades or longer (Hairston 1996; Brendock and De Meester 2003). Ecologically, this seems strange, because diapausing eggs enable Cladoceran populations to survive in water bodies during stressful periods (Meijering 2003).

One question that arises is "what was the mechanism of Cladocera re-emergence?" The absence of eggs suggests that re-colonization of cladocerans resulted from dispersal. Some taxa, e.g. planktonic species, lack a dormant stage and may have an enhanced ability to disperse, thus avoiding locally harsh conditions (Hairston 1996). A regional climate change, however, may decrease the efficacy of such dispersal if all habitats within the region are similarly affected.

Changes in Cladocera reproduction can also explain the absence of eggs in Koźmin Lake. In northern boreal and subarctic lakes, members of the Chydoridae family reproduce asexually during a large part of the season when the lake is free from ice cover (Sarmaja-Korjonen 2003). This favors rapid population growth and maintenance. On the other hand, it is possible that some species were so tolerant of severe climate conditions that they were primarily acyclic (Røen 1995) and reproduced mainly asexually.

It is possible that tectonic activity and water currents temporarily led to deterioration of the lake ecosystem and that egg banks were destroyed or brought to the sediment surface and transported to the deepest areas of the lake. These processes may also have led to poor recruitment, and may thus have caused the elimination of some species, including ephippia (Hairston 1996). Supply of coarser material to the basin may also have suppressed the development of Cladocera in the lake, at least in the part of the lake under study, or resulted in the physical destruction of the Cladocera exoskeletons within the sediments.

The depositional environment may have been unfavorable for Cladocera preservation. The water in such lakes is rich in oxygen (Brodzikowski 1993) and life depends on the dynamics and temperature of the water. The occurrence of benthic infauna (e.g. *M. dispar*) indicates that near-bottom oxygen deficiency did not occur. The benthos, however, underwent occasional changes, which does not preclude bottom anoxia, especially during the winter season. Changes in the water chemistry were probably not sufficient to have influenced Cladocera preservation.

The most probable explanation for the lack of ephippia is gradual shallowing of the lake caused by the inflow of sediment-laden water. It led to progressive widening of the shallow littoral zone and to expansion of aquatic vegetation during summer. Presence of littoral species, such as *A. affinis*, *A. harpae* and *E. lamellatus*, suggests that the lake was colonized by littoral vegetation when the environment was favorable. Longer growing seasons and increased temperatures could have yielded higher habitat diversity. Increased macrophyte abundance has a large impact on cladoceran communities (Sweetman et al. (2010).

It might have been, however, that Cladocera populations declined or disappeared completely because of predation by fish (Jeppesen et al. 2001). Also, changes in predator/prey relationships might have caused changes in reproductive strategies (Sarmaja-Korjonen 2003). The absence of large *Daphnia* and presence of small *Bosmina* is compatible with the presence of zooplanktivorous fish (Gliwicz et al. 2001; Guilizzoni et al. 2006), but no fish or invertebrate predator species are known from Lake Koźmin during these times. Moreover, the absence of *Daphnia* might be explained by the fact that this group prefers open water, whereas the section under study was near the lake's littoral zone. We cannot, however, exclude the possibility of fish predation. It is possible that Cladocera were not an important prey item for fish, as suggested by the presence of some large cladocerans (*E. lamellatus*), indicating a decrease in fish-predation pressure and/or low fish-predation pressure in this part of the lake. Fluctuations in sedimentation rate may have made the habitat unfavorable for visual predators.

The lack of cladoceran remains in the seismites and just above them is particularly intriguing. The earthquakes caused not only deformation of unconsolidated lake-bottom sediments, but possibly also changes in some habitat characteristics, e.g. water depth, transparency, food and nutrient availability.

Seismites are beds that contain *in situ* soft-sediment deformations, triggered by earthquakes. Many of these deformation structures also occur in layers of reworked sediments that moved downwards over the lake-basin slope. Faulting, even if occurring several km below the lake bottom, may induce earthquakes (Van Loon 2009), and may result in seismites if the surface sediments have the appropriate granulometry, or in subaqueous slides and other types of mass flows. Because the Koźmin Basin is situated in a graben, it is possible that graben tectonics were still active during deposition of the Saalian glaciolacustrine deposits. The same reworking process is known to have acted in the best studied graben of Poland (the Kleszczów Graben), in which not only seismites (Gruszka and Van Loon 2007), but numerous other tectonic structures in the Quaternary overburden are well documented (Brodzikowski et al. 1987; Goździk and Van Loon 2007). The advancing ice sheet caused increasing loading of the basement, which accelerated subsidence and reactivated the older Neogene faults. The same mechanism must have occurred in the Adamów Graben (Fig. 2), where the deepest part of Lake Koźmin was situated.

The presence of seismites in glacial Lake Koźmin indicates shocks of high magnitude. Similar structures have commonly been interpreted as being the result of earthquakes of magnitudes between M5.5 and M8 (Rodríguez-Pascua et al. 2000, 2003; Berra and Felletti 2011). Such shocks must have also induced a large instability on the lake margins, probably resulting in mass flows and sediment resuspension (Van Loon et al. 1995). Earthquakes may also have changed the position of the lake bottom, i.e. shallowing or deepening of the basin, which in turn influenced the distance to the inflowing streams. Avsar et al. (2010) showed that earthquakes of magnitude >7 can change the depth of a lake by as much as 1/3. Uplift in the area of a lake outlet of a few meters can result in considerable water-level rise (Ambraseys 1989). This can explain the absence of Cladocera remains in the layers with seismically induced deformations and in the layer just above them. The shocks may have destroyed the living organisms, which are highly susceptible to many factors, and it may have taken some time to renew the Cladocera populations. Another possibility is that after these shocks, the water was highly turbid, so that little or no light could penetrate, leading to poor living conditions, especially limited food, for Cladocera. If the water level rose, anoxic conditions may also have prevailed and suppressed life.

## Conclusions

- Glacial Lake Koźmin developed in a river valley that was eroded during the Saalian (Warthe) glaciations along the tectonic graben, and existed at the end of this glaciation. The lake was fed by extraglacial streams that displayed seasonal discharge. It is likely that Lake Koźmin was a vast basin, deep in the center, but with an extensive littoral zone. Sediments accumulated until the basin filled completely.
- The sedimentary succession shows cycles of at least two orders. Higher-order cycles, represented by facies associations, formed during long phases of increased sediment supply to the lake and bottom-current activity. These phases had durations of a few years to several decades and were probably associated with changes in water level. The relation of these cycles to climate changes or sun-spot cycles is unclear. Lower-order cycles represent seasonal changes in sediment supply as a consequence of changing flows or suspension settling in standing water, and are recorded in the form of rhythmites.
- The Cladocera data represent one of the oldest records of this kind from Europe. In the cold climate, with slightly fluctuating temperatures, environmental conditions in the lake were sufficiently favorable for Cladocera, which are represented mainly by species that live under oligotrophic conditions.
- The presence of Cladocera was also dependent on the inflow of water to the basin and on the lake's hydrologic regime. Periods of increased inflow increased the sediment supply and made the habitat unsuitable for Cladocera.
- The occurrence of seismites within the Koźmin succession proves seismic activity of the Adamów graben when this basin existed. Tectonic activity may also explain, in part, the absence of Cladocera remains in some intervals of the succession. The absence of Cladocera immediately above the seismite layers suggests that earthquakes not only deformed the lake-bottom sediments, but also changed habitat characteristics.
- The presence of cladocerans, including species requiring milder climate conditions, provide ecological and climate information on Saalian glacial-lake ecosystems, which were generally poor in biota. The described response of cladocerans to environmental/climate changes was probably influenced by the marginal position of the study section, supply of clastics, as well as tectonic activity. The data do not allow more detailed interpretation, but suggest that such glacial lakes can be used for exploring past climate changes.

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