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High-resolution environmental changes recorded in ostracod and mollusc fauna from the Holsteinian palaeolake at Ortel Królewski II, eastern Poland

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To better understand the environmental variability during the Holsteinian interglacial, fauna of the palaeolake deposits at Ortel Królewski II, eastern Poland was investigated. The analysis covered the uppermost part of the profile, representing the so-called pre-optimal part of the Holsteinian interglacial (MIS 11c), namely the *Taxus* and *Pinus-Larix* pollen zones. Variability within the structure and composition of the faunal assemblage enabled a high-resolution palaeoecological reconstruction – lake level and temperature fluctuations, its trophy and energy of the environment. During the *Taxus* pollen zone the lake was relatively deep and characterized by medium trophy conditions, which is indicated by a low abundance of molluscs of temporary water bodies and low numbers of *Metacypris cordata* and *Scottia tumida*. The temperature was rather stable with only small fluctuations during the transition between the *Taxus* and *Pinus-Larix* zones. The occurrence of some cold-loving ostracod species within the beginning of the *Pinus-Larix* pollen zone indicates some deterioration of thermal conditions, which was additionally confirmed by using the mutual ostracod temperature range (MOTR) method. Lake level drop and expansion of reed zones within the *Pinus-Larix* pollen zone are inferred from the increased abundance of shallow water ostracod and mollusc species as well as from an increased Bithynia-index (BIN). The short cooling event documented early in the *Pinus-Larix* zone in the studied profile might be an equivalent to the mid-MIS 11c cooling, the so-called Older Holsteinian Oscillation. Thus, the improved knowledge about the climate dynamics recorded within the sediments from this site contributes to a better understanding of the spatial extent and pattern of the climatic changes within the Holsteinian interglacial across Europe.

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The evolution of lakes is closely linked to climatic forcing. Lake ecosystems respond to climate change in many ways, and their sediments contain a wide range of physical, chemical and biological proxies that can be used to reconstruct palaeoclimates (Last & Smol 2001). The resolution of climate records in sediment archives is related, among others, to the rate of deposition. Thus, lacustrine sediments usually have better resolution than marine ones, with 1 mm per year on average (Ruddiman 2014). Therefore, lake sediments are sensitive recorders of catchment and in-lake processes and they represent an excellent archive for high-resolution palaeoenvironmental studies (Björck *et al.* 2000; Lotter 2001).

By looking into lacustrine sediments, we can observe how the climate changed in the past. This is especially important these days when we want to find an analogue to the present situation and try to predict the direction of future climate changes. Considering the similarities of the orbital climate forcing, the Marine Isotope Stage (MIS) 11 seems to represent one of the closest climate analogues for the Holocene (Ruddiman 2005; Tzedakis 2010; Candy *et al.* 2014). Since the Holsteinian interglacial is widely accepted to be the terrestrial equivalent of MIS 11c in central Europe (Kukla 2003; Nitychoruk *et al.* 2005) the recognition of climatic changes within its records gains crucial relevance, especially since they occurred without human influence. Thus, the study of past interglacials can significantly contribute to improving the prediction of future climate change and its potential impact on the biotic and abiotic environment.

Past environmental conditions can be inferred from numerous proxies. Within lacustrine sediments it can be, for example, biological indicators such as ostracods, gastropods and bivalves. Because the distribution of these organisms is controlled by environmental factors, their presence in a sample allows inferences to be made about the ecological conditions during the sediment deposition (Holmes 1992; Wrozyna *et al.* 2012; Alexandrowicz *et al.* 2014). Ostracods and molluscs possess a number of attributes that make them an excellent archive of past environmental conditions: they are common in lacustrine environments, they typically have hard shells, are usually well preserved in sediments and they are relatively easy to detect in the environment. The shells of molluscs contain very detailed imprints of past climate change and they are among the most ubiquitous fossils present in Quaternary non-marine sediments. Ostracods also have an excellent potential in palaeolimnology; however, they have received less attention from Quaternary palaeoecologists than many other microfossil groups. This has arisen partly because of a perception that non-marine ostracods are difficult

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to identify to the species level (Holmes 2001). However, they have one important advantage – because of their small size (on average less than 1 mm) and high abundance within the sediment, it is possible to use them when only small samples are available. Both ostracods and molluscs constitute a valuable proxy for palaeoecological reconstructions. Their sensitivity to changes in water depth, temperature, salinity, oxygen level and nutrient availability are especially important (Miller & Tevesz 2001; Alexandrowicz 2007; Viehberg & Mesquita-Joanes 2012; Ruiz *et al.* 2013; Apolinarska *et al.* 2018).

Eastern Poland, as a transitional area between maritime and continental climates is well suited for palaeoenvironmental studies. There are around 30 well-documented MIS 11c sites with palaeolake deposits providing an excellent record of vegetation history and climate conditions in the Holsteinian (Mazovian) interglacial in the region (Bińka & Nitychoruk 1995, 1996; Krupiński 1995, 2000; Bińka *et al.* 1997; Nitychoruk 1997; Nitychoruk *et al.* 2005; Szymanek *et al.* 2016). These data offer a perspective for further studies focused on the recognition of short-term climate-environmental fluctuations with the use of multiproxy methods (Nitychoruk *et al.* 2018).

In this paper, highly resolved faunal analyses were conducted. The aim was to examine the natural environmental changes in the Holsteinian palaeolake at Ortel Królewski II based on ostracod and mollusc records. Particular focus was on the changes within the depth, temperature and trophy conditions in the pre-optimal part of the Holsteinian interglacial. The main assumption was that combining new ostracod and mollusc data will allow to decipher the influence of climate disturbances on the lake ecosystem.

Study site

Ortel Królewski II is located in eastern Poland ~160 km east of Warsaw and ~12 km southeast of Biała Podlaska (Fig. 1). The site is well known because of an extremely rich accumulation of mollusc shells, which often exceeds over 70% of the deposit volume (Albrycht *et al.* 1995). The palaeolake deposits of Holsteinian age are exposed in the eastern slope of the Zielawa River valley in a narrow belt ~50–100 m wide and 500 m long. They lie on

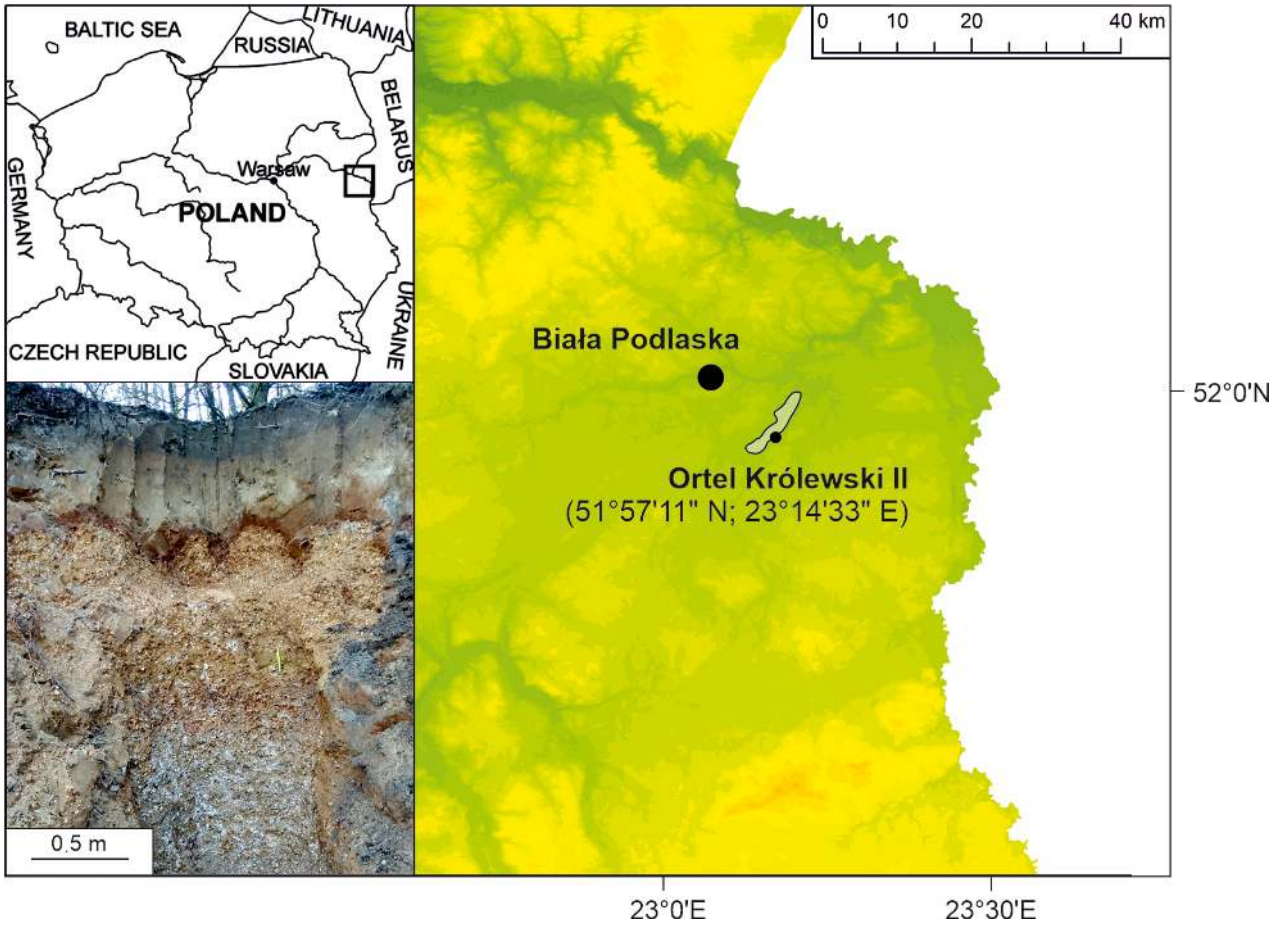

Fig. 1. Study site location with the hypothetical range of Ortel Królewski II palaeolake based on Szymanek (2017).

fluvio-periglacial sands of the Elsterian glaciation and are covered by fluvioglacial deposits of the Saalian glaciation or by up to 1-m-thick colluvial sands (Albrycht *et al.* 1995; Szymanek *et al.* 2005, 2016; Szymanek 2011). The total thickness of the palaeolake deposits reaches over 6 m, whereas in the studied outcrop 4 m of sediments are exposed. These are from the bottom fine-grained clayey sands with single molluscs, clayey silts, sandy silts and fine-grained sands with abundant malacofauna (Fig. 2).

Due to the lack of absolute dating, the chronology of the lake is based on pollen analysis. The vegetation succession distinguishes four pollen zones of the Holsteinian interglacial within the whole profile of the lake: *Pinus-Betula*, *Picea-Alnus*, *Taxus* and *Pinus-Larix* (Albrycht *et al.* 1995; Szymanek *et al.* 2005, 2016; Szymanek 2011), which cover the pre-optimal part of the studied interglacial. Thanks to palynological chronology it is possible to corelate the studied profile with other well-known and palynologically documented sites within this region (Bińka & Nitychoruk 1995, 1996; Bińka *et al.* 1997; Krupiński 1995, 2000; Nitychoruk 2000; Nitychoruk *et al.* 2005). Additionally, using the pollen-based correlation with surrounding palaeolakes one can estimate that the deposition of the interglacial sediments in this region began ~430 ka ago as this is the thermoluminescence age of the nearby Ossówka palaeolake (Krupiński 1995; Nitychoruk 2000; Nitychoruk *et al.* 2005).

Former palynological, faunal, isotopic and geochemical studies have shown a great potential of this site for palaeoenvironmental studies of the Holsteinian interglacial (Albrycht *et al.* 1995; Skompski 1996; Szymanek *et al.* 2005, 2016; Szymanek 2011, 2016, 2017, 2018). However, only low-resolution malacological and ostracodological and pollen studies were conducted focused on the general changes of the faunal assemblage and its description through the whole sequence (Albrycht *et al.* 1995; Skompski 1996; Szymanek *et al.* 2005; Szymanek 2011; Wasążnik 2018). Thus, the lack of high-resolution data has as yet precluded deeper insights into the climate dynamics of these changes.

Therefore, the Holsteinian record of the Ortel Królewski palaeolake is one of the first case studies using a high-resolution approach. The present study focuses on the two top-most metres of the profile, which covers the end of the *Taxus* zone and the succeeding *Pinus-Larix* pollen zone (Szymanek *et al.* 2016). The *Taxus* zone is widely regarded as characteristic of the Holsteinian interglacial. Connected with the distinct influences of oceanic air masses this interglacial was dominated by temperate tree taxa such as yew, ash, oak and alder, whereas the *Pinus-Larix* zone is described as an intra-interglacial cooling and drying of the climate expressed by the regression in vegetation cover and dominance of pioneer tree species such as pine and birch (Krupiński 1995, 2000). This transformation is commonly identified in many European

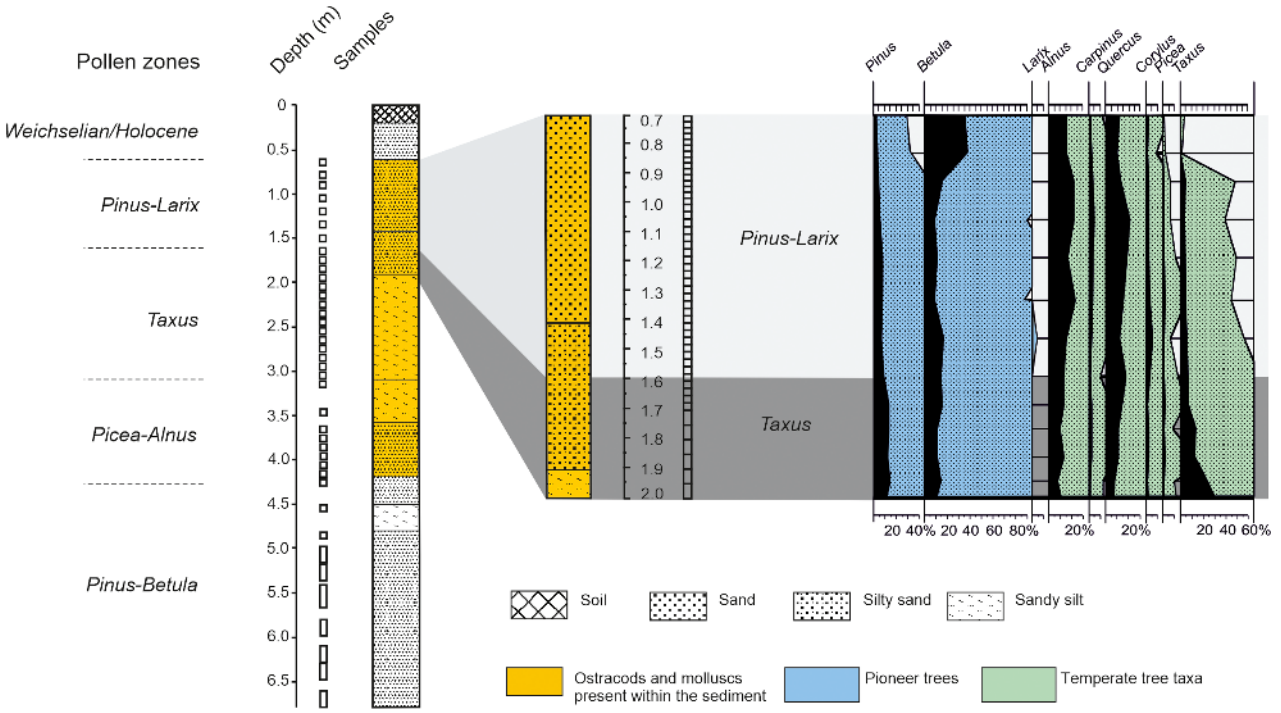

Fig. 2. Lithology and palynostratigraphy of the studied profile correlated with a previous ostracod study (Wasążnik 2018). Pollen zones of the Holsteinian interglacial and pollen diagram modified after Szymanek *et al.* (2016).

successions (Turner 1970; Müller 1974; Bińka & Nitychoruk 1995, 1996; Bińka *et al.* 1997; Hrynowiecka & Winter 2016).

The author has previously made a first complex characteristic of the ostracod fauna (Wasążnik 2018) after it was described by Skompski (1996). The same samples were previously examined by Szymanek *et al.* (2016) and were the subject of complex pollen analysis. Thus, by correlating these previous results with those of the present study it was possible to determine the limit between the two described pollen zones (Fig. 2).

Material and methods

Samples were collected from an excavation ~5 m long and 3 m deep from the 2.00–0.70 m depth interval. In total 49 samples were taken for analyses. The sampling interval varied from 2 to 5 cm. Samples with higher resolution covered the transition between the *Taxus* and *Pinus-Larix* pollen zones (1.70–0.70 m), whereas the final part of the *Taxus* (2.00–1.70 m) zone was sampled every 5 cm to obtain some comparative shell material. Approximately 0.2–0.5 L of sediment was taken per sample. Taking into account the previous studies on the site (Albrycht *et al.* 1995; Szymanek 2011; Szymanek *et al.* 2016; Wasążnik 2018) and the high abundance of fauna remains, this was enough to obtain shell material of sufficient quality and volume for palaeoecological studies.

Ostracods

For ostracods, every sample had a volume of 5 cm^3. The extraction of ostracods from sediment involved disaggregation of the sediment, size separation and picking. Disaggregation was based on the least aggressive treatment possible to avoid damage to the ostracod shells. In this case, samples were simply dispersed in water. Following disaggregation, the sediment was wet sieved through 500, 200 and 63 μm mesh to obtain the size fraction that contains most adult and later juvenile instars. Although earlier instars are usually found in the fine fraction, these are often not identifiable to species level and are disregarded in many studies (Holmes 2001). Due to this fact, the main interest was in the material from the 200-μm fraction. The valves were examined under a low-magnification stereoscopic microscope (with a magnification up to ×56). Species identification was performed based on the shape, size and the sculpture features of valves and carapaces according to Sywula (1974), Meisch (2000) and Fuhrmann (2012). In some cases, investigation using a scanning electron microscope (SEM) was needed and it was used additionally for species documentation. To ensure the statistical validity of the results a minimum of 300 valves of adult ostracods was counted in each sample, if possible (Holmes 2001). In samples with lower counts, all valves were picked. Additionally, a few samples were checked entirely to estimate the changes in ostracod productivity and the proportions between adults and juveniles. Additionally, to determine air temperature fluctuations the mutual ostracod temperature range (MOTR) method was applied (Horne 2007). For this method to be applied it is necessary to know the temperature ranges of the species involved; thus, the calculations were based on the ostracod list given in Horne *et al.* (2012). In order to reconstruct January and July temperature fluctuations the ranges for 13 ostracod species were compared: *Metacypris cordata*, *Darwinula stevensoni*, *Herpetocypris reptans*, *Cyclocypris laevis*, *Cypridopsis vidua*, *Candona neglecta*, *Candona candida*, *Pseudocandona compressa*, *Pseudocandona insculpta*, *Ilyocypris* cf. *decipiens*, *Limnocythere inopinata*, *Fabaeformiscandona protzi* and *Pseudocandona sucki*. Other species present in the studied profile were excluded from the analysis because either they are extinct (*Scottia tumida*, *Paralimnocythere bicornis*), no calibrations are available (*Pseudocandona lobipes*) or their identification is uncertain (*Cyclocypris* sp.). Finally, the ostracod diagrams were plotted by using 'PanPlot' software (Sieger & Grobe 2013).

Molluscs

For molluscs, every second sample was analysed. Samples had at least a volume of 100 cm^3 and were dispersed in water and wet-sieved on 0.5-mm mesh to pick out all mollusc shells and their identifiable fragments. Specimens were determined under a magnifying glass and stereoscopic microscope at magnifications up to ×56 and counted following Ložek's (1964) method for broken individuals. Identification was performed according to Piechocki & Dyduch-Falniowska (1993) and Piechocki & Wawrzyniak-Wydrowska (2016). Additionally, the number of bivalves was halved in the calculation (1 individual = 2 valves) and some incomplete specimens, especially thin-walled *Pisidium* bivalves were determined only to genus level. Molluscs were then grouped in accordance with their ecological preferences. The latter attributions were based on Ložek (1964), Alexandrowicz (1987) and Alexandrowicz & Alexandrowicz (2011). In addition, for all samples, malacological spectra of species (MSS), malacological spectra of individuals (MSI) and a simplified malacological diagram were constructed. The Bithynia-index (BIN), representing the proportion of opercula and shells of *Bithynia tentaculata* was calculated in order to characterize the sedimentary environment. Based on the formula BIN = (opercula – shells)/(opercula + shells) (Steenberg 1917; Alexandrowicz 1999). Both the shells and opercula are often sorted in the littoral zone of water bodies. The opercula usually accumulate on the bottom in the reed zone and their domination is shown by the value of the index being close to +1, while associations

composed only of shells (BIN = −1) appear abundantly along the shores (Alexandrowicz & Alexandrowicz 2011).

In addition, an unconstrained cluster analysis (UPGMA similarity algorithm and the Morisita's index) was used to determine ostracod and mollusc species assemblages according to their community composition. This allowed the differentiation of the ostracod (OFZ) and mollusc (MFZ) faunal zones. Statistical analysis was performed using PAST (Paleontological Statistics), version 1.35 (Hammer *et al*. 2001).

Results

Taxonomic issues

Discussion on the changes within faunal assemblages should be preceded by an explanation of some taxonomic issues. Some uncertainties have arisen around *Scottia* species. Previous studies (Skompski 1996; Wasążnik 2018) identified two species of this genus, namely *S. tumida* and *S. browniana*. The main characteristic features allowing these two species to be distinguished are the shape of the valves and their dimensions. Usually, *S. tumida* is slightly smaller than *S. browniana*, with average length L = 0.64–0.73 mm and height H = 0.38–0.48 mm (Fuhrmann 2012). Additionally, there are also two other characteristic valve features: the knob present on the inner lamella of the left valve in its posterior part and the position of the inner list on inner calcareous lamella. Situated about in the middle of the lamella points to *S. browniana*, while in *S. tumida* it is placed closer to the external margin (Fig. 3). Difficulties in identifying these species have been described previously by de Deckker (1979), where the author compared the measurements of *S. browniana* and *S. tumida* made by a few other authors. Thus, based on the present information about the carapace features and the size of the single individual given by Kempf (1967) the species described from Ortel Królewski II should be classified as *S. tumida* and *Cyclocypris* sp.

Taxonomic uncertainties involve also the identification of specimens from the genus *Ilyocypris*. As the identification of living species from this genus relies mainly on appendages (Meisch 2000), in the fossil record where they are mostly not preserved the character of the valve is rather a characteristic trait. Its outline and ornamentation along with the presence of marginal ripplets play the key role (Sylvester-Bradley & Kemp 1973; Mazzini *et al*. 2014). Specimens from Ortel Królewski II (Fig. 3) are quite elongated and show some similarity to the species that Bridgland *et al*. (2013) identified as *Ilyocypris decipiens* in the MIS 9 assemblage at Purfleet, UK. Additionally, they have no marginal ripplets on the inner lamella of the left valve, which is typical of *Ilyocypris bradyi* (Fuhrmann 2012). However,

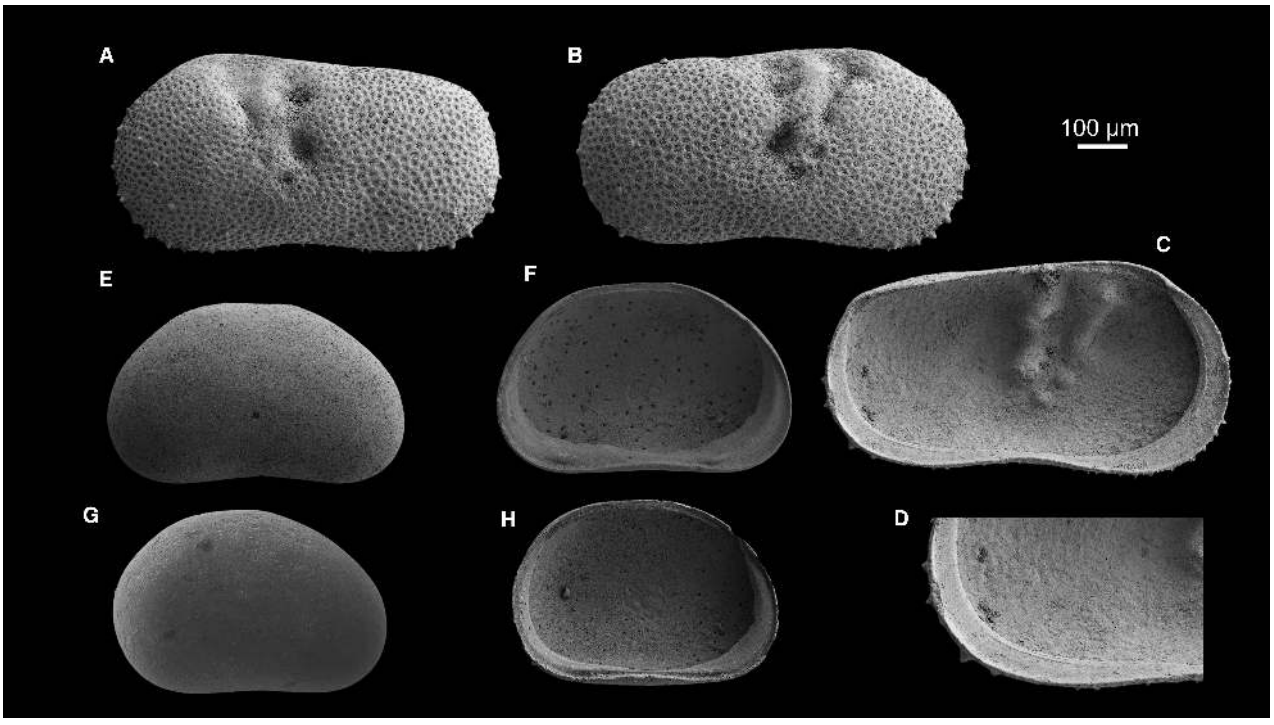

Fig. 3. Selected ostracod species from Ortel Królewski II. Part I. A–D: *Ilyocypris* cf. *decipiens*. A. Left valve (LV), external lateral view. B. Right valve (RV), external lateral view. C. LV, internal lateral view. D. Focus on the inner lamella of the posterior part of the LV. E–F: *Scottia tumida*. E. RV, external lateral view. F. LV, internal lateral view. G–H: *Cyclocypris* sp. G. RV, external lateral view. H. LV, internal lateral view.

the specimens identified as *I. decipiens* by Mazzini *et al.* (2014) are quite different – they do show the ripplets, but are also different from what they illustrated as *I. bradyi*. Despite the uncertainties discussed above, the studied species has been identified as *Ilyocypris* cf. *decipiens*.

Ostracods

In total 18 ostracod taxa (including 17 species) were recognized with a total of 6634 specimens. The number of taxa and specimens varied from 10 to 15 and from 99 to 447 per sample, respectively. It is worth noting that in the lower part of the profile (2.00–1.37 m) the whole sample had to be examined to provide a sufficient number of specimens, whereas in the upper part (1.37–0.70 m) the abundance of specimens increased considerably and the counting was stopped when reaching around 300 specimens. The abundance clearly exceeded 1000 individuals, without juveniles, as indicated by checking a few samples. Based on this assumption it can be estimated that the mean total number of ostracod valves in the bottom part of the profile was around 285 valves per 5 cm^3, while it exceeded 1000 valves per 5 cm^3 in the upper part. The ostracod fauna found in this core separates into two clearly different assemblages. At the bottom (2.00–1.37 m) high species diversity and low specimen abundance can be observed while in the upper part (1.37–0.70 m) the number of individuals per sample is increasing but with decreasing species diversity (Fig. 4).

The results of stratigraphically constrained cluster analysis allowed the differentiation of four ostracod faunal zones (OFZ I–IV; Fig. 4, Table 1):

- OFZ I (2.00–1.60 m) – *Candona* sp. juveniles dominate in the assemblage along with *Darwinula stevensoni* and *Scottia tumida*. The highest abundance of *Cyclocypris* sp. is also noted in this zone. It is worth noting that this may be a new species previously mistakenly identified as *S. tumida* (Skompski 1996; Wasążnik 2018).
- OFZ II (1.60–1.40 m) – this zone is characterized by the highest percentage of *D. stevensoni* and increasing abundance of *Metacypris cordata*. *Candona candida* occurs for the first time in this profile, being an accessory species together with *Fabeaformiscandona protzi*, *Candona neglecta*, *Pseudocandona lobipes* and *Pseudocandona insculpta*.
- OFZ III (1.40–1.10 m) – some species that occurred in the lower part of the sequence (e.g. *C. candida*, *C. neglecta*, *F. protzi*) disappear or their abundance distinctly decreases. At the same time an expansion of *S. tumida* is observed (up to 80%) along with increased percentages of *M. cordata* (around 12%) – a species characteristic for high abundance of water plants. The species diversity decreases in this zone, while the species abundance starts to increase (Fig. 4).
- OFZ IV (1.10–0.70 m) – the ostracod community is characterized by a low diversity and is dominated by

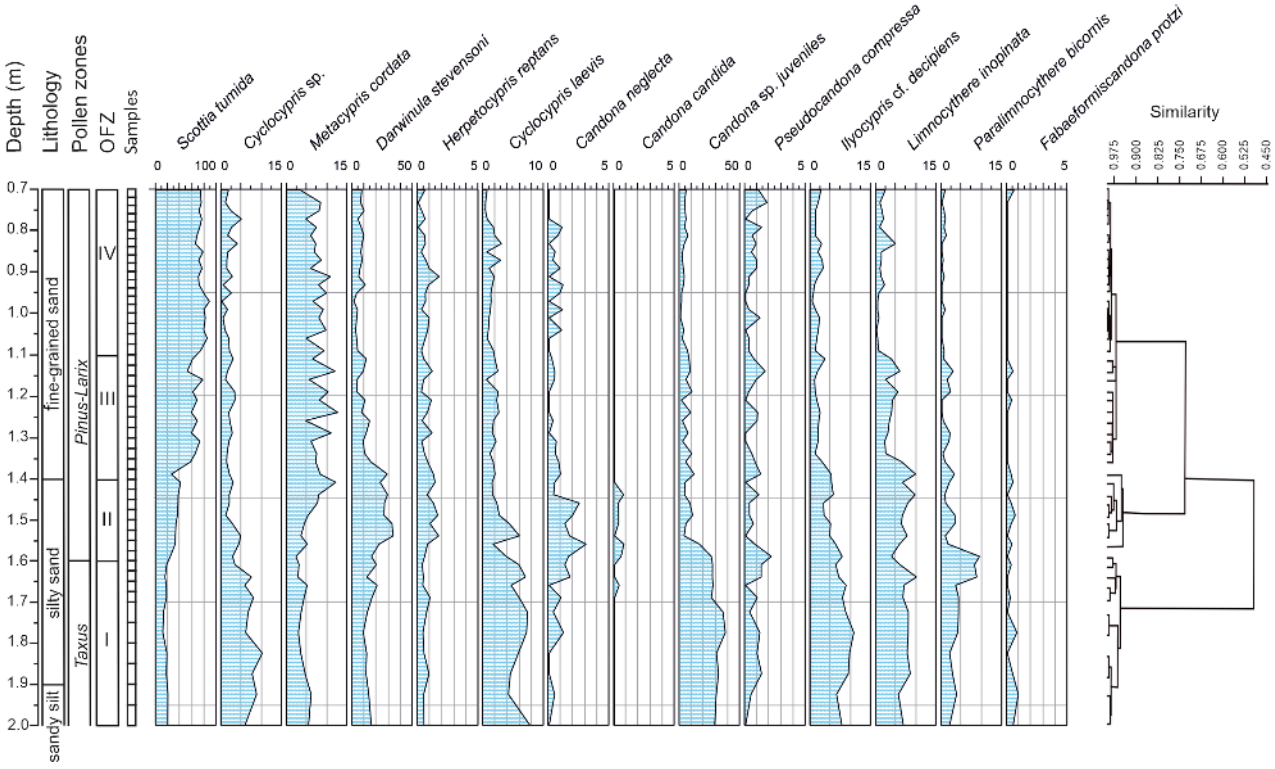

Fig. 4. Ostracod diagram of the Ortel Królewski II site, note different scales.

S. tumida reaching about 80% of the assemblage (Fig. 4). Of the accessory species, *M. cordata* and *D. stevensoni* are the most abundant. Cold-loving species *C. neglecta* and *F. protzi* almost completely disappear. Despite the low number of species, the abundance of fauna is flourishing here, reaching its highest numbers (Fig. 4).

Additionally, by using the MOTR method it was possible to reconstruct the mean January and July air temperature fluctuations. Despite the wide temperature ranges some observations can be made, especially when paying particular attention to the three-point running average signals. Firstly, the January and July maxima show a warming trend through the *Taxus* zone. Then a minor deflection toward lower temperatures, both winter (−7 to +2 °C) and summer (+15 to +21 °C), is observed at the beginning of the *Pinus-Larix* pollen zone (1.60–1.40 m depth). Then we observe a more prolonged warm period in the remainder of the *Pinus-Larix* zone with a cool fluctuation in mid-zone. Worth noting is that these trends are more obvious in the January maxima than in the July maxima.

Molluscs

The mollusc assemblage from Ortel Królewski II comprises 17 snail and 14 bivalve taxa represented altogether by 11 822 individuals. In general, the malacofauna from Ortel Królewski II is rich and diverse. The specimen abundance changes from 242 to 1034 per sample, which gives a concentration of 85 to 375 per 100 cm^3 of sediment. The number of taxa ranges from 15 to 23 and despite some fluctuations it gradually drops toward the upper part of the profile. Only at the depth of 1.05–0.90 m can a distinct increase in number of both species and specimens be observed.

All identified taxa are representative of freshwater environment. Based on molluscs' ecological preferences they can be classified into one of three groups: species of temporary water bodies (ecological group 10), species of permanent water bodies of stagnant waters (group 11) and species of flowing waters (group 12). Generally, the samples are dominated by group 11, which represents between 57 and 69% of all species and between 76 and 97% of specimens. Molluscs of temporary water bodies (group 10) are represented by only a few taxa and usually by single specimens. Only *Valvata cristata*, regarded as a plant-associated species (Piechocki 1979; Welter-Schultes 2012), reaches greater abundances (Fig. 5, Table 2). This is especially seen in the upper part of the profile, at the depth of 1.15–0.90 m. In contrast, molluscs preferring flowing waters (ecological group 12) such as *Pisidium supinum*, *Pisidium nitidum* and *Sphaerium rivicola* account for 23 to 31% of all taxa; however, only up to 9% of all individuals (Fig. 6).

The assemblage is dominated by four taxa – *Viviparus diluvianus*, *Lithoglyphus jahni*, *Bithynia tentaculata* and *Valvata piscinalis*. In the lowest part of the profile (depth 2.00–1.37 m) *Lithoglyphus jahni* prevails and is the main component of the fauna. Higher in the succession *L. jahni* is still a significant element of the community, but is gradually replaced by *Bithynia tentaculata* and *Valvata cristata*. Some other species of temporary water bodies (group 10) also occur within the upper part of the profile (*Segmentida nitida*, *Galba truncatula*); however, only as single specimens. Additionally, numerous *Valvata piscinalis*, *Gyraulus crista* f. *cristatus*, *Pisidium henslowanum*, *Acroloxus lacustris* and *Gyraulus albus* occur. The latter two species are typical of zones with rich immersed vegetation (Piechocki & Wawrzyniak-Wydrowska 2016). The community is clearly enriched by *Bithynia* opercula as indicated by the BIN ranging from 0 to +0.8 (Fig. 6).

Based on cluster analysis four clearly different mollusc assemblages (MFZ I–IV; Fig. 5) are distinguished at Ortel Królewski II. The lower ones (MFZ I, II) clearly differ from the upper part of the profile (MFZ III, IV):

- MFZ I (2.00–1.77 m) – represented by two samples with *L. jahni* predominating in the assemblage and reaching up to 61% of all individuals. Additionally numerous *V. diluvianus*, *B. tentaculata* and *V. piscinalis* occur. The mollusc concentration is moderately high, whereas the number of species is one of the lowest within the profile (Fig. 6).
- MFZ II (1.77–1.37 m) – *V. diluvianus* and *V. piscinalis* predominate in the mollusc assemblage along with a constant number of *B. tentaculata*. By the end of this zone, a slight increase of *L. jahni* is observed. Within the accessory species an increase of *P. henslowanum* and *P. supinum* is worth noting (Fig. 5).
- MFZ III (1.37–0.92 m) – *V. diluvianus* is still a significant component of the assemblage, being accompanied by an increasing number of *B. tentaculata*. Expansion of *V. cristata* is also noted. Among the accessory species, an increased abundance of *Sphaerium corneum* and *P. nitidum* is observed (Fig. 5).
- MFZ IV (0.92–0.70 m) – a decrease in abundance of *B. tentaculata*, *V. cristata* and *V. piscinalis* is characteristic for this zone. In general, a substantial decrease in number of specimens is noted with the lowest frequency within the whole profile. Species of temporary water bodies (quite abundant in MFZ III) are replaced by species of permanent water bodies of stagnant water (Fig. 6).

Besides ostracods and molluscs in many samples unidentifiable teeth and fragments of bones of small rodents and fishes were present through the studied profile, as well as some otoliths and glochidia of *Unio* bivalves.

Discussion

Biostratigraphy

The age of the sediment is confirmed by the faunal analysis. Two mollusc and two ostracod species identified at Ortel Królewski II have stratigraphical significance. These are *Viviparus diluvianus*, *Lithoglyphus jahni*, *Scottia tumida* and new to this site *Paralimnocythere bicornis* (Fig. 7). The first two are widely accepted as characteristic for the Holsteinian interglacial as they appeared for the last time during this time period (Albrycht *et al*. 1995). *S. tumida* used to be considered typical of the Holsteinian interglacial (Kempf 1971; Robinson 1980; Skompski 1991) until it was found in lacustrine deposits of Schöningen age (MIS 7) in Germany (Pietrzeniuk 1987) and was identified in the Eemian interglacial (MIS 5e) at Ruszkówek in central Poland (Kozydra & Skompski 1995). *Paralimnocythere bicornis* is an extinct species that disappeared at the end of the Holsteinian interglacial (Fuhrmann 2012). Until now it was unknown from the palaeolake deposits at Ortel Królewski II (Albrycht *et al*. 1995; Skompski 1996; Wasążnik 2018). All identified ostracod species are representative of freshwater environments and most of them have been described previously from this site (Skompski 1996; Szymanek *et al*. 2005; Wasążnik 2018). However, *Paralimnocythere bicornis*, *Pseudocandona lobipes* and *Pseudocandona insculpta* are completely new species to this site.

Structure and composition of the faunal assemblage

The presence of high numbers of ostracod and mollusc shells within the studied sediment sequence generally indicates favourable conditions for productivity and subsequent shell preservation, while the good preservation of shells and the structure of the ostracod assemblage with all development stages (from juveniles to adults) exclude significant transport of the material (see Holmes 2001).

Within the whole profile four ostracod taxa dominate within the assemblage at Ortel Królewski II: *Scottia tumida*, *Candona* sp. juveniles, *Darwinula stevensoni* and *Metacypris cordata*. At the bottom part of the profile (OFZ I), correlated with the *Taxus* pollen zone, the dominance of *Candona* sp. juveniles was noted, whereas the abundance of adults is relatively low. These findings may reflect some unfavourable conditions, which prevailed in the lake and caused extinction of juveniles from this genus and/or valve segregation associated with wave action (Holmes 2001; Keatings *et al*. 2010). However, the low abundance and diversity of ostracods during OFZ I seem to support the first interpretation. On the other hand, similar proportions of *Candona* sp. juveniles have been reported from other Middle Pleistocene sites such as Tönnisberg (Kempf 1967) or West Runton (de Deckker 1979), being correlated with colder climate. This assumption contradicts the pollen data from the Ortel Królewski II site. This is because this part of the profile represents the moderately warm *Taxus* pollen zone, where mixed forests with high abundance of yew and hazel were prevailing among the forest community (Krupiński 1995, 2000). Probably other factors had an influence on the composition of the ostracod development stages of *Candona* species. Additionally, the presence of both adults and instars of other species excludes the possible redeposition of the material. Only at the beginning of the *Pinus-Larix* zone (at the depth of 1.6–1.4 m – OFZ II), an increase of *Candona* fauna can be observed. This is the only time when *C. candida* is present in the profile, suggesting a seasonal (especially winter) drop in temperatures. According to pollen analyses (Szymanek *et al*. 2016) in relation to *Taxus* zone, the climate was more continental in character, and the oceanic influence in eastern Poland had gradually disappeared at that time.

Noticeable changes within the ostracod assemblage are noted in the upper part of the studied profile. Within OFZ III and OFZ IV some species that occurred in the lower part of the sequence (e.g. *C. candida*, *C. neglecta*, *F. protzi*) disappear or their abundance distinctly decreases. Simultaneously increased numbers of *M. cordata* and *S. tumida* as well as a higher abundance of ostracods were noted, which suggests the creation of a broad range of ecological niches that can be inhabited in the lake (Cooke *et al*. 2001; Iglikowska & Namiotko 2012).

The lack of good, quantitative data precludes detailed comparison of the ostracod succession from Ortel Królewski II with other sites in this region. However, a few species such as *Scottia browniana* and *Darwinula stevensoni* have been noted, for example in Szymanowo (Szymanek 2014). On the other hand, a similar structure of ostracod assemblages has been noted in several European Middle Pleistocene sites. Abundant *Scottia* fauna was noted among others at Sugworth (Great Britain), where *S. browniana* was a dominating species, accounting for up to 97% of the total ostracod count (Robinson 1980). It is worth noting that most localities with *S. browniana* were connected with small, overgrowing water bodies (Kempf 1971; Robinson 1998). At Syrniki in eastern Poland (Diebel 1961) and Tönnisberg (Germany) (Kempf 1967) *S. tumida* was the most abundant species reaching about 50% of the fauna assemblage. At Wildschütz (eastern Germany), as documented by Fuhrmann (1991), the ostracod fauna strongly resembles that of the Ortel Królewski site where *Paralimnocythere bicornis* was identified for the first time. At Szymanowo *S. browniana* and *Darwinula stevensoni* were reported, but the lack of quantitative data precludes detailed regional comparisons (Szymanek 2014).

The mollusc assemblage at Ortel Królewski II shares many similarities with many neighbouring sites

Table 1. Ostracods from the Ortel Królewski II site.

Depth (m)	Sample number	*Scottia tumida* (Jones, 1850)	*Cyclocypris* sp.	*Metacypris cordata* (Brady and Robertson 1870)	*Darwinula stevensoni* (Brady and Robertson, 1870)	*Herpetocypris reptans* (Baird, 1835)	*Cyclocypris laevis* (O.F. Müller, 1776)	*Cypridopsis vidua* (O.F. Müller, 1776)	*Candona neglecta* (Sars, 1887)	*Candona candida* (O.F. Müller, 1776)	*Candona* sp. juveniles	*Pseudocandona compressa* (Koch, 1838)	*Pseudocandona lobipes* (Hartwig, 1900)	*Pseudocandona insculpta* (Müller, 1900)	*Pseudocandona sucki* (Hartwig, 1901)	*Ilyocypris cf. decipiens* (Masi, 1905)	*Limnocythere inopinata* (Baird, 1843)	*Paralimnocythere bicornis* (Fuhrmann, 1991)	*Fabaeformiscandona protzi* (Hartwig, 1898)	Total sum of specimens	Total sum of taxa
0.70–0.72	1	267	6	12	27	2	2	1			18	4				9	8	3	2	361	13
0.72–0.74	2	251	3	28	22		1				13	6				6	3			333	9
0.74–0.76	3	250	8	28	33	1	1				15	2				4	5	2		349	11
0.76–0.78	4	262	17	16	15	2	2	1			17					4	6	3		345	11
0.78–0.80	5	268	9	27	26		6		4		14	5				4	3	2		368	11
0.80–0.82	6	370	8	32	50	3	10		4		36	3				6	15	6		543	12
0.82–0.84	7	220	13	24	26	2	10				12	3				9	16			335	10
0.84–0.86	8	310	6	27	27	1	2		2		8	2				7	5			397	11
0.86–0.88	9	225	4	27	25	2	9		1		6	3				9	4	1		316	12
0.88–0.90	10	250	4	19	20	3	3		3		9	3				10	3			327	11
0.90–0.92	11	240	9	37	17	6	6				12	1				6	4	2		340	11
0.92–0.94	12	247	1	27	36	3	5		4		10	1				3	7			344	11
0.94–0.96	13	266	8	33	11	2	4		3		4					2	2			335	10
0.96–0.98	14	289		21	3	2	4				4					1	1			325	8
0.98–1.00	15	282	5	32	14	1	4		4		2	1				4	1	3		353	12
1.00–102.5	16	269	1	26	11	3	3				1	4				7	2			327	10
1.025–1.05	17	302	3	37	9	3	3		4		12					7				380	9
1.05–1.075	18	290	6	16	11	2	2				6	1				5	1			340	10
1.075–1.10	19	271	7	34	15	1	6				23	1				4	2	2		366	11
1.10–1.125	20	259	12	27	48	2	8		1		32	3			2	15	16	2		427	13
1.125–1.15	21	219	6	51	37	5	10		2		36	7	4			7	25	12	2	423	14
1.15–1.175	22	171	2	12	8	1	1	1	1		11	2				2	5	3		220	13
1.175–1.20	23	226	12	38	13	1	9				37	1				4	20	8		369	11
1.20–1.225	24	186	9	22	28	3	6				3					4	11		1	273	10
1.225–1.25	25	232	7	50	29	3	10				35	4				9	15			394	10
1.25–1.275	26	209	6	14	43	1	5		1		6	3				6	10	1		305	12
1.275–1.30	27	203	9	38	39	4	5				23					6	10	7		344	10
1.30–1.325	28	245	6	20	29	1	7		2		7					6	7	6		336	11
1.325–1.35	29	247	5	28	38	2	4		2		37	2				4	9	1		379	12
1.35–1.375	30	145	3	18	38	2	4	1	2		12	2				7	16	2		252	13
1.375–1.40	31	79	6	26	91	4	6		3		37	4				16	31	10	1	314	13
1.40–1.425	32	86	6	26	49	3	3		1		9					11	14	4	1	213	12
1.425–1.45	33	98	5	21	78	2	4		1	2	10	3			1	15	26	2		268	14
1.45–1.475	34	115	6	24	84	4	7		8	1	26	1		1		10	25	3	1	316	15
1.475–1.50	35	108	3	16	80	5	8	2	6	1	32	1	1			10	20	10	2	305	16
1.50–1.525	36	100	8	13	100	3	13		4	1	15	2				15	19	10	1	304	14
1.525–1.55	37	74	11	8	79	4	14		4		8	1				11	18	2		234	12
1.55–1.575	38	81	11	13	57	2	4		8	2	42	2				16	15	4	1	258	14
1.575–1.60	39	86	10	8	58	2	14		6	2	97	8			2	29	14	35		371	14
1.60–1.625	40	52	10	9	60	1	18		4		83	4				19	18	25	1	304	13
1.625–1.65	41	33	17	6	27	1	16		4		62	3				16	23	20		228	12
1.65–1.675	42	43	15	13	53	1	12			1	72					23	18	9		260	11
1.675–1.70	43	68	32	17	65	4	24	1	4		106	4	1			32	27	17	1	403	15
1.70–1.75	44	34	19	10	35	2	21		1		103	1				25	23	12		286	12
1.75–1.80	45	27	15	7	22	1	18		3		95	3				27	20	10	2	250	13
1.80–1.85	46	36	21	7	24	1	12				63	2				20	16	4		206	11
1.85–1.90	47	37	17	10	25	2	10				72	3				21	19	6	1	223	12
1.90–1.95	48	42	19	13	29	1	9		1		66	1				14	12	8	2	217	13
1.95–2.00	49	39	12	11	32	1	16				60					16	14	4	1	206	11

(Szymanek 2012, 2013, 2014). Generally, it is dominated by four species: *Viviparus diluvianus*, *Lithoglyphus jahni*, *Bithynia tentaculata* and *Valvata piscinalis*. In the lowermost part of the profile (MFZ I), correlated with the *Taxus* pollen zone, *L. jahni* predominates. Unfortunately, environmental interpretation is hindered here by the scarce ecological data about this extinct species. According to Urbański (1975) and Skompski & Makowska (1989) *L. jahni* inhabited lakes and rivers; however, no bathymetric data are available. Higher in

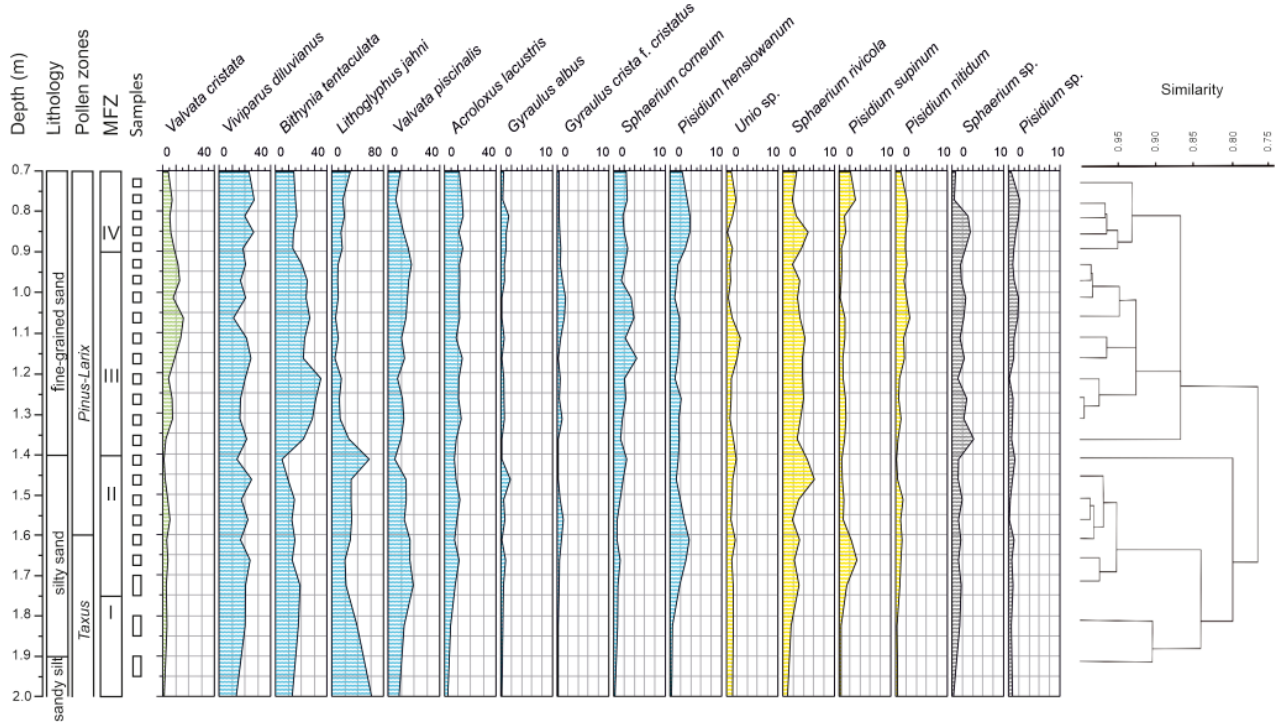

Fig. 5. Malacological diagram of the Ortel Królewski II site, note different scales. For colour explanation see Fig. 6.

the succession *L. jahni* is replaced by *B. tentaculata* and *V. cristata* together with high numbers of *Gyraulus albus*, *Gyraulus cristata* f. *cristatus* and *Acroloxus lacustris*, which suggests distinct palaeoenvironmental changes in the lake.

Palaeoenvironmental reconstruction

The reconstruction of palaeoenvironmental changes within the Ortel Królewski II palaeolake based on ostracod and mollusc assemblages includes information on depth, trophy and temperature fluctuations. As no absolute dating is available, when discussing the changes, we will use the palynological zonation. The faunal assemblage from the analysed part of the profile represents the pre-optimal part of the Holsteinian interglacial (~MIS 11c). As mentioned previously, pollen-based studies allow the studied section to be assigned to the *Taxus* and *Pinus-Larix* pollen zones (Szymanek *et al.* 2016). The *Taxus* pollen zone is recorded at the depth of 2.00–1.60 m and by OFZ I and MFZ I, while *Pinus-Larix* covers the 1.60–0.70 m depth interval with OFZ II, III, IV and MFZ II, III, IV (Figs 4, 5).

Lake level change. – The water level changes may be inferred from the structure and composition of the faunal assemblage through the studied sequence. At the lower part of the profile (2.00–1.40 m) representing the *Taxus* and the beginning of the *Pinus-Larix* pollen zone, the water level was relatively high, which is indicated by the relative proportions of the different mollusc ecological groups (Fig. 6). In this part of the profile group 11 (species of permanent water bodies of stagnant water) definitely dominates within the assemblage. Additionally, the relative proportions of *B. tentaculata* and *V. piscinalis* point to a somewhat deeper environment (Fig. 5). While *B. tentaculata* prefers shallow water bodies and usually occurs in shallow waters (0.7–1.8 m), *V. piscinalis* is commonly found at depths of around 3–10 m (Piechocki & Wawrzyniak-Wydrowska 2016).

The depth of the lake started to gradually decrease during the *Pinus-Larix* pollen zone. This change is represented on the diagram by two faunal zones OFZ III, IV and MFZ III, IV. It is indicated by the increasing numbers of ostracod species preferring shallow littoral zones, e.g. *M. cordata*, *D. stevensoni* and *S. tumida* and molluscs of temporary water bodies (group 10) associated with rich aquatic vegetation such as *A. lacustris*, *G. albus*, *G. cristata* f. *cristatus* and *V. cristata* (Figs 4, 5). The lake shallowing is especially noticeable in the upper part of this zone (1.10–0.70 m) where the abundance of *S. tumida* reaches almost 90% of the assemblage (Fig. 4). According to Iglikowska & Namiotko (2012) the presence of immersed vegetation creates suitable conditions for ostracod development, which is reflected in the increasing number of specimens at Ortel Królewski II.

The lake level drop is also indicated by isotopic records of *V. diluvianus* and *V. piscinalis* shells from Ortel

Table 2. Molluscs from the Ortel Królewski II site.

Depth (m)	Sample number	Sample volume (cm³)	*Valvata cristata* (Müller)	*Galba truncatula* (Müller)	*Anisus vorticulus* (Troschel)	*Segmentina nitida* (Müller)	*Viviparus diluvianus* (Kunth)	Bithynia tentaculata (Linnaeus)	*Lithoglyphus jahni* (Urbański)	*Valvata piscinalis* (Müller)	*Acroloxus lacustris* (Linnaeus)	*Lymnea stagnalis* (Linnaeus)	*Gyraulus albus* (Müller)	*Gyraulus crista* f. *cristatus* (Linnaeus)	*Gyraulus crista* f. *nautileus* (Linnaeus)	*Sphaerium corneum* (Linnaeus)	*Pisidium ponderosum* (Stelfox, 1918)	*Pisidium henslowanum* (Sheppard)	*Pisidium hibernicum* (Westerlund)	*Pisidium moitessierianum* (Paladilhe)	*Unio* sp.	*Sphaerium rivicola* (Lamarck)	*Sphaerium solidum* (Normand)	*Pisidium amnicum* (Müller)	*Pisidium supinum* (A. Schmidt)	*Pisidium nitidum* (Jenyns)	*Pisidium subtruncatum* (Malm)	*Radix* sp.	*Lymnaea* sp.	*Gyraulus* sp.	*Anisus* sp.	*Sphaerium* sp.	*Pisidium* sp.	Total sum of specimens	Total sum of taxa	Concentration per 1 cm³
			10				11														12															
0.72–0.74	2	700	22				135	81	163	52	64		2	1		14	1	13		3	5	15			12	5	2				3	2	594	19	84.8
0.76–0.78	4	600	38			1	152	85	89	30	74		1	1		14		18	1	4	10	10			17	12					2	12	568	19	94.7
0.80–0.82	6	500	29				115	95	109	50	82		8	1		10		22		3	6	15			5	13					18	11	590	17	118.0
0.84–0.86	8	500	39	2			183	93	90	78	73		6	2	2	13		26		4	0	33			8	13		1			24	9	697	20	139.3
0.88–0.90	10	500	50			1	109	78	91	91	82		5	3	2	16		17		4	6	21	1		2	11		1		3	1	15	6	614	23	122.8
0.92–0.94	12	500	117				207	207	86	181	113		5	4		21	1	14		2	5	18	1		4	21		1		4	16	7	1034	21	206.7
0.96–0.98	14	250	119				152	229	74	145	106		5	8		13		11		1	6	30			2	14					16	9	938	17	375.0
1.00–102.5	16	250	21				56	65	24	40	30			4	1	9		2			1	8				6					7	5	278	16	111.0
1.05–1.075	18	150	66				45	111	19	56	47			5	1	16		7		3	4	14			4	11					9	7	425	17	283.0
1.10–1.125	20	100	29				45	48	19	21	18		1	1	1	5		4			6	9			2	3					3	2	216	17	215.5
1.15–1.175	22	200	25			1	70	61	10	35	38					13		4		3	6	11			2	5					7	3	290	16	145.0
1.20–1.225	24	150	10				51	90	35	17	27		1	1		5		2		1	2	10			2	2					3		257	16	171.0
1.25–1.275	26	200	32				77	148	50	50	49		2	1		11		10		2	4	19		1	5	2		1			13	4	478	19	239.0
1.30–1.325	28	200	28				62	112	46	46	49		2	3	1	6		6		2	2	13			5	4					9	3	397	18	198.5
1.35–1.375	30	200	6				72	73	87	32	29					4		6		3	4	9			3	1					14	2	344	15	171.8
1.40–1.425	32	200	1				42	14	181	14	22	1				8		5		1	6	15			1	0		1			4	4	317	17	158.5
1.45–1.475	34	200	3				60	22	70	32	20		4		1	4		3		1	3	15			1	1					3	2	242	17	120.8
1.50–1.525	36	200	9				46	39	79	37	31		1	1		3		5		3	3	8			2	4		1			5	1	276	18	138.0
1.55–1.575	38	200	25				110	61	149	60	45		3	5	3	3		13		3	4	9			3	4					6		504	17	251.8
1.60–1.625	40	150	8			1	52	47	89	53	23			2	2	2		12		3	5	10			7	4		1			5	3	328	19	218.3
1.65–1.675	42	250	14				97	51	79	67	44	1	3	1		5		12		2	4	9			14	4		2			5	2	413	19	165.2
1.70–1.75	44	250	13		1		124	115	129	117	47		2	1		4		11		4	7	19			8	4		4			10	5	623	19	249.2
1.80–1.85	46	300	14				104	91	201	62	21	1	1			3		2		1	6	8			1	1					7	2	525	17	174.8
1.90–1.95	48	250	4				113	110	538	69	16					1		1		3	9	7			2	2					1	6	880	15	352.0

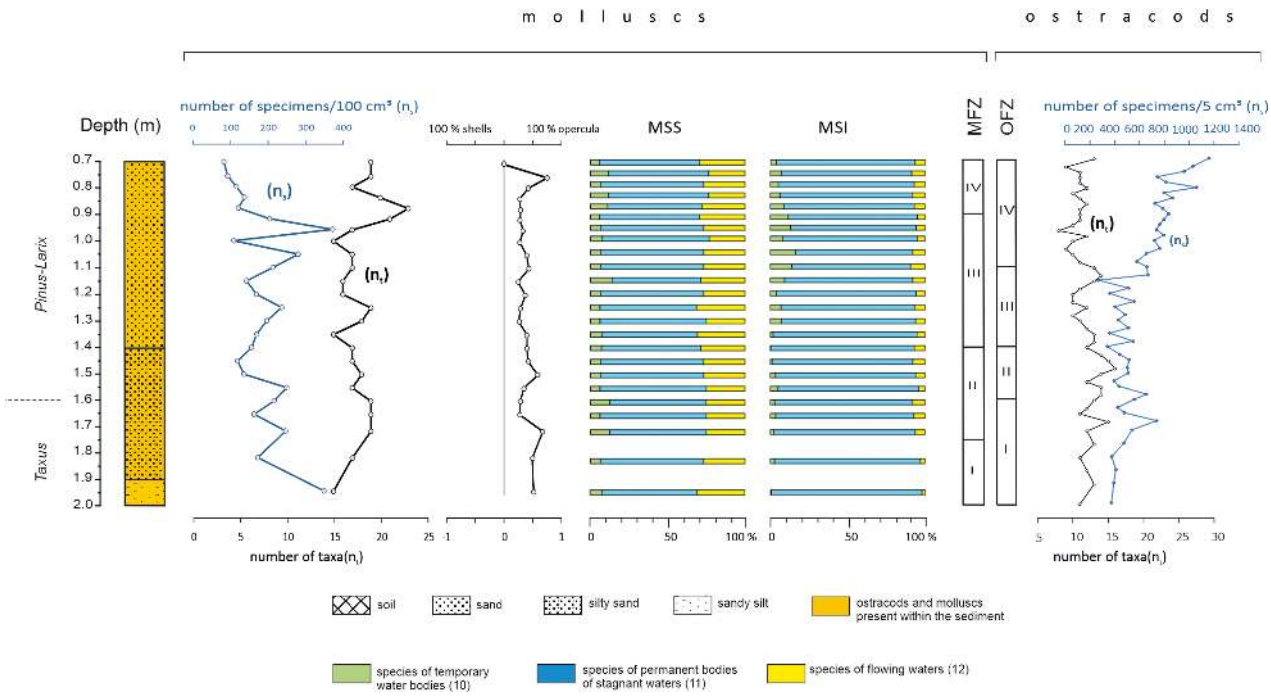

Fig. 6. Lithology of the studied profile along with malacological composition, the Bithynia-index (BIN) of the Ortel Królewski II site and changes in number of species (n_s) and number of specimens (n_t) of both ostracods and molluscs.

Królewski II and was connected with the increased aridity associated with the increase of continental influences in eastern Poland (Szymanek 2016; Szymanek *et al.* 2016). This episode is well known in the region as lowering of the water level in the *Pinus-Larix* zone affected many palaeolakes, including Kaliłów, Woskrzenice, Lipnica and Ossówka among others (Lindner *et al.* 1991; Albrycht *et al.* 1995; Bińka & Nitychoruk 1995, 1996; Bińka *et al.* 1997; Nitychoruk *et al.* 2005; Szymanek 2012, 2013, 2014). The low lake level was expressed by sedimentary hiatuses and/or lithological changes, thus its recognition has been incomplete or based mostly on pollen record. The deterioration of the climatic conditions connected with the increased continentality favoured development of pine at the expense of more demanding species (Bińka & Nitychoruk 1995, 1996; Bińka *et al.* 1997; Nitychoruk *et al.* 2005). Krupiński (1995, 2000) postulated a drop in the humidity and decrease in winter temperatures at that time.

Aquatic vegetation and lake trophy. – During the *Taxus* pollen zone and the transition between the *Taxus* and *Pinus-Larix* pollen zones the lake productivity was rather low. Sparse vegetation in the lake may be inferred from the low number of plant-associated mollusc species such as *A. lacustris* and *V. cristata* (Fig. 5), whereas the low faunal abundance at the depth of 1.60–1.40 m (Figs 4, 6) points to somewhat less favourable conditions for fauna to thrive.

Expansion of aquatic plants occurred within the *Pinus-Larix* pollen zone and is evidenced by a high abundance of *V. cristata* and *A. lacustris*. Vegetation changes can be also inferred from high values of the Bithynia-index (BIN), reaching 0.8 in the uppermost part of the succession (Fig. 6). This may indicate progressive overgrowing of the lake by reed and bulrush, presumably connected with the lake shallowing and amelioration of trophic conditions.

At the same time, the higher trophic status is indicated by the high abundance of *Metacypris cordata* within OFZ III and IV (Fig. 4), which is characteristic of eutrophic lakes (Danielopol *et al.* 1996; Viehberg 2004; Sohar & Meidla 2010). Absolon (1973) correlates the occurrence of the so-called cordata-fauna with the transition from oligotrophic to eutrophic conditions and thus an early stage of lake extinction. Enhanced productivity at that time is also reflected in decreased abundance of *F. protzi* (Fig. 4), which appears to have a limited tolerance for eutrophication (Danielopol *et al.* 1993). Additionally, the increasing abundance of *S. tumida* from 20% at the bottom of the profile to over 80% at its top is consistent with this hypothesis. Overall, the lake level decrease led to increased occurrence of water plants, and of molluscs and ostracods preferring rich vegetation. This process is especially distinct in the upper part of the studied profile correlated with both OFZ (III, IV) and MFZ (III, IV).

The faunal record is in agreement with isotope geochemical studies from Ortel Królewski II (Szymanek

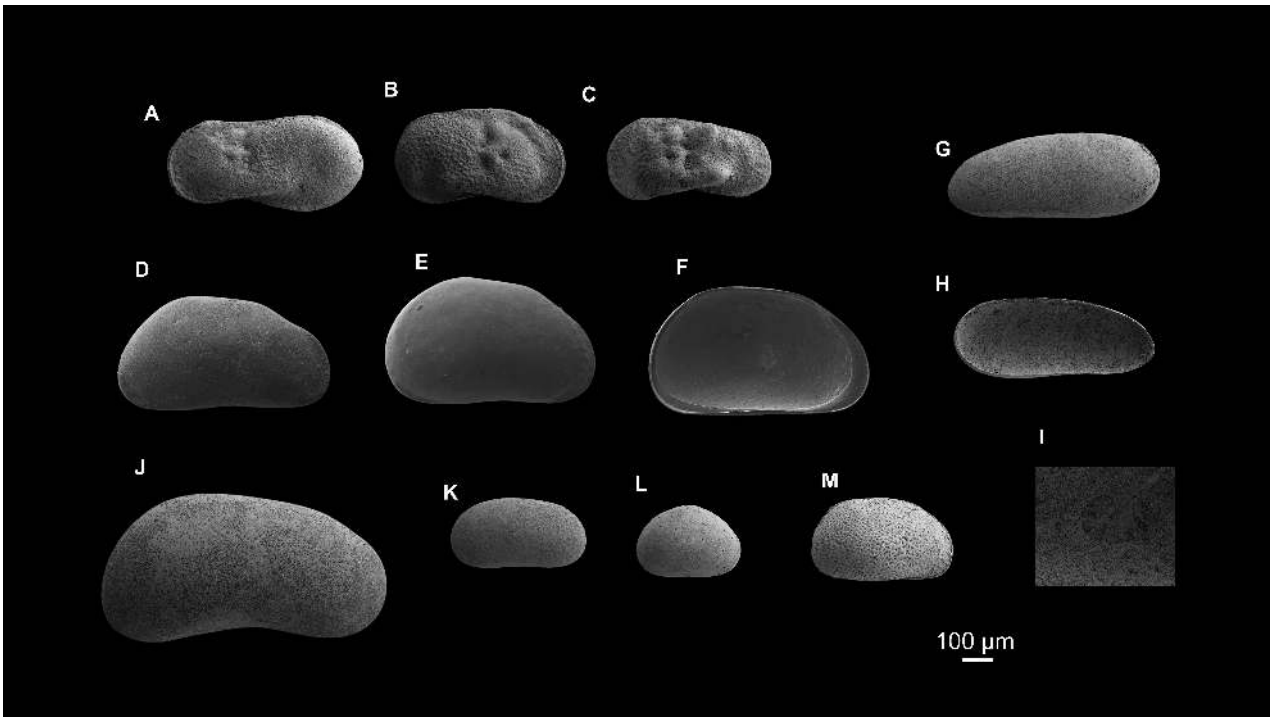

Fig. 7. Selected ostracod species from Ortel Królewski II. Part II. A–B: *Limnocythere inopinata*. A. RV, male, external lateral view. B. LV, female, external lateral view. C. *Paralimnocythere bicornis*, LV, external lateral view. D. *Pseudocandona compressa*, RV, external lateral view. E. *Pseudocandona insculpta*, RV, external lateral view. F. *Pseudocandona lobipes*, LV, internal lateral view. G–I: *Darwinula stevensoni*. G. LV, external lateral view. H. LV, internal lateral view. I. Focus on the muscle scars. J. *Candona neglecta*, RV, external lateral view, adult. K. *Candona* sp., juvenile. L. *Cyclocypris ovum*, LV, external lateral view. M. *Metacypris cordata*, RV, external lateral view.

2016, 2018; Szymanek *et al*. 2016). Increasing values of both Fe and Fe/Mn of mollusc shells representing the *Pinus-Larix* pollen zone point to some bottom-water anoxia caused by lake eutrophication, higher productivity and enhanced oxygen consumption during decay of organic matter (Szymanek 2018). These changes correspond with a distinct rise in $\delta^{13}C$ connected with rich aquatic vegetation and more intensive photosynthesis (Szymanek *et al*. 2016).

Temperature. – The *Pinus-Larix* zone in eastern Poland is characterized by a regressive phase of vegetation that could be connected with increased aridity and decreased winter temperatures, which caused shallowing of the surrounding lakes (Krupiński 1995, 2000; Bińka *et al*. 1997; Nitychoruk 2000). In the pollen record at Ortel Królewski II this is indicated by the sharp decline of *Taxus* in forest communities, decreased contribution of *Picea* and the expansion of boreal forests with *Pinus* and *Betula* and admixture of *Larix* (Szymanek *et al*. 2016).

Signs of possible intra-interglacial cooling can be found within the studied profile at the depth of 1.60–1.40 m, which represents the beginning of the *Pinus-Larix* pollen zone. A cooler interval is particularly indicated by the changes in ostracod assemblages. During the beginning of the *Pinus-Larix* pollen zone one can observe a distinct zone (OFZ II) characterized by an increased abundance of the cold-tolerant ostracods *Candona neglecta*, *Fabaeformiscandona protzi* and *Candona candida* (1.60–1.40 m; Fig. 4). While *C. neglecta* and *C. candida* have a calibrated mean January air temperature range of −10 to +13 °C and −40 to +9 °C, respectively, *F. protzi* tolerates temperatures from −40 to +3 °C (Horne *et al*. 2012). Furthermore, single valves of *Pseudocandona sucki* in this interval point to a possibly lower winter temperature as the winter temperature range of this species is about 1 °C lower than the rest of ostracod species within the assemblage. Some deterioration of thermal conditions may be also inferred from the mollusc fauna. Despite the continuous change within the faunal assemblage, this period is characterized by a decreased species richness (Fig. 6). Low numbers of molluscs within MFZ II may be a reaction of the fauna to cooling and drying of the climate. The latter is confirmed by isotope studies (Szymanek 2016; Szymanek *et al*. 2016) where the decrease in $\delta^{18}O$ seen within the *Pinus-Larix* pollen zone points to somewhat lower temperatures (Fig. 8).

Additionally, by using the MOTR method (Horne *et al*. 2012) it was possible to reconstruct the temperature ranges, represented by maximum and minimum values, of

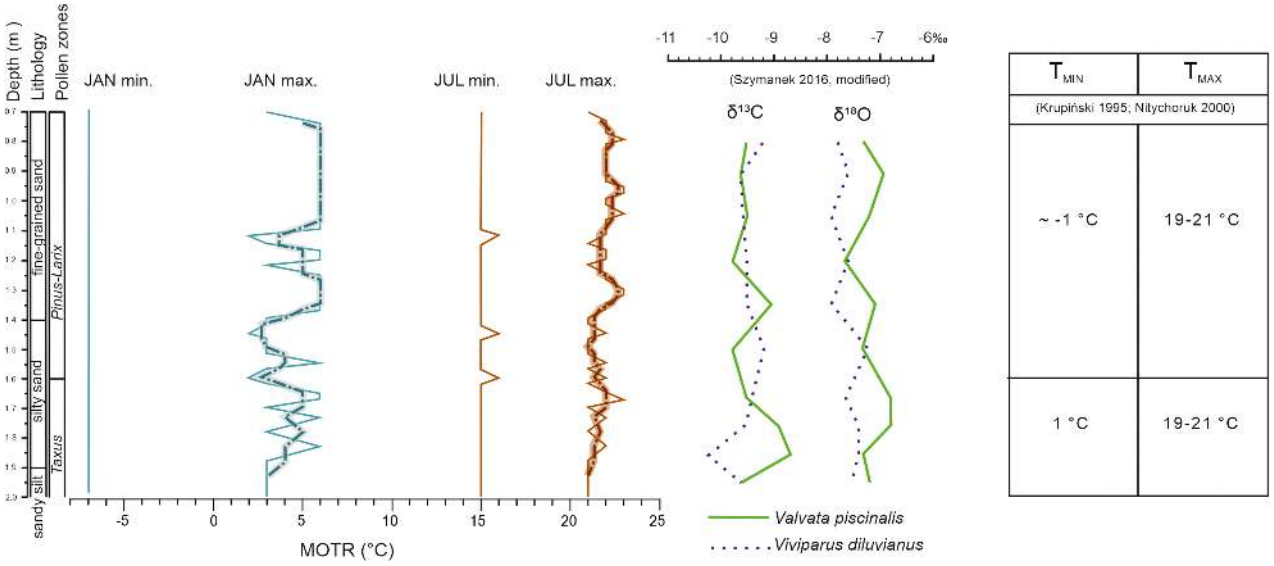

Fig. 8. Estimated January and July air temperature ranges using the MOTR method compared with isotopic data (Szymanek 2016) and mean temperature of coldest month (T_{MIN}) and mean air temperature of the warmest month (T_{MAX}) based on Krupiński (1995) and Nitychoruk (2000). The three-point running averages were added onto the figure to smooth out the January and July maxima signal (January – blue, July – brown).

mean January and mean July air temperature. While it is impossible to determine precisely the actual temperatures within the reconstructed ranges, some constraints may be discussed. For example, the January maxima can be used to represent a coldness threshold (Marchegiano *et al.* 2020). With this approach, the beginning of the *Pinus-Larix* pollen zone is characterized by mean temperatures a few degrees colder (Fig. 8). However, this period is mainly determined by the occurrence of *P. sucki* and *F. protzi*, which are only accessory species within the studied assemblage. Thus, these results should be discussed with caution and confirmed with further research.

The comparison of the MOTR results with the pollen-based palaeotemperature reconstructions of Krupiński (1995) shows some interesting results. During the *Taxus* pollen zone the mean temperature of the warmest month ranged between 19 and 21 °C and average January temperature ranged around 1 °C (Fig. 8). During the *Pinus-Larix* pollen zone the average January temperature dropped probably by a few degrees centigrade, whereas the July temperature could have been close to that of the *Taxus* zone (Krupiński 1995). Overall, the pollen reconstructions are consistent with the MOTR ranges (Fig. 8). However, the cooling of pollen-based winter temperature from +1 °C in the *Taxus* zone to −1 °C in the overlying *Pinus-Larix* zone appears to contradict the MOTR January maximum curve, which suggests a comparative warming overall. Details of the MOTR signals (particularly the three-point running average maxima for January) suggest an early cool phase at the start of the *Pinus-Larix* zone (1.60–1.40 m), followed by a warming phase in the upper part. A possible explanation for this data disagreement is that the pollen-based temperatures (Krupiński 1995) represent the combined assemblage of the whole zone, whereas the MOTR reconstructions are done sample by sample. Thus, the disagreement reflects a limitation of the low stratigraphical resolution of the pollen-based reconstructions.

The cooling event documented early in the *Pinus-Larix* zone in the studied profile might be an equivalent to the mid-MIS 11c cooling seen at many sites in central and northwestern Europe. The so-called Older Holsteinian Oscillation was documented mostly in England (West 1956; Turner 1970; Coxon 1985; Thomas 2001), Germany (Müller 1974; Diehl & Sirocko 2007), and Poland (Bińka & Nitychoruk 1995, 1996; Krupiński 1995; Bińka *et al.* 1997; Nitychoruk *et al.* 2005; Hrynowiecka & Pidek 2017). However, most of these studies were based on pollen records only and lacked temporal resolution. Therefore, the lack of high-resolution data has yet precluded deeper insights into the climate dynamics of this phase. Despite many unknowns, recent years have brought new multiproxy information concerning the OHO event. Studies from Dethlingen and Marks Tey shed a light on the climate conditions during this abrupt cooling event (Koutsodendris *et al.* 2010, 2011, 2013; Tye *et al.* 2016). While the summer temperatures were rather stable, with increased aridity, which is also in agreement with the MOTR results from the studied profile (Fig. 8), a significant decrease of the temperature was observed in the coldest months. According to Koutsodendris *et al.* (2012), the mean temperature declined at that time by ~1.5 °C, whereas in Ortel Królewski II the temperature dropped probably around 2–3 °C (Fig. 8). However, previous studies from this site based on the oxygen isotopes of aquatic gastropods (Szymanek 2017) did not indicate significant differences between average water temperatures

estimated for the *Taxus* and *Pinus-Larix* zones. This data disagreement might be caused by the fact that molluscs' isotopic record reflects the growth-season period, which rather points to stable conditions in the summer season. Thus, further isotopic studies based especially on ostracod carapaces might provide some valuable insight into this discussion. Compilation of available evidence from other sites across Europe would also definitely help to determine the dynamics of the climatic fluctuations during this part of the Holsteinian interglacial.

Conclusions

The analysed record provides insight into the influence of Holsteinian climatic changes on the structure of ostracod and mollusc communities. Faunal analysis from Ortel Królewski II reveals detailed palaeoenvironmental changes during the pre-optimal part of the Holsteinian interglacial. Climate fluctuations are reflected in the faunal assemblages as well as by the presence of individual species. The improved knowledge about the climate dynamics recorded within the sediments from this site contributes to a better understanding of the spatial extent and pattern of the climatic changes within the Holsteinian interglacial across Europe. Thanks to the increased resolution of the samples compared to previous studies it was possible to record in detail the changes in the lake level, its trophy and temperature fluctuations. The evolution of the lake within the studied part of the Holsteinian interglacial starts from the relatively deeper water body with medium trophy conditions within the *Taxus* pollen zone followed by a shallow lake with dense vegetation and increased trophy within the *Pinus-Larix* pollen zone. The temperature was rather stable, with only a minor fluctuation towards lower winter temperatures at the beginning of the *Pinus-Larix* pollen zone.

The major conclusions are as follows:

- Significant lake shallowing is noted in the second part of the *Pinus-Larix* pollen zone (1.40–0.70 m), which is associated with changing moisture conditions. More arid, continental climate prevailed at that time. Both the ostracod and mollusc data show increasing numbers of species preferring the shallow littoral zone.
- The ostracod record covering the initial part of the *Pinus-Larix* pollen zone provides information about the seasonal temperature fluctuations. The presence of the *Candona* fauna indicated that the temperature, especially in winter, might have dropped. Single valves of *Pseudocandona sucki* in the 1.6–1.4 m interval indicate that the winter temperature might have declined by a few degrees.
- The identification of the ostracod *Paralimnocythere bicornis* allowed further confirmation of the age of the site as this species, along with the molluscs *V. dilu-vianus* and *L. jahni*, does not occur in deposits younger than MIS 11.
- Additionally, the identification of the *Scottia* species present in the study site was revised, with the dominant species classified as *S. tumida*.

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Data availability statement. – The data that support the findings of this study are available from the corresponding author upon reasonable request.

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