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The usefulness of subfossil Cladocera remains in Younger Dryas climatic reconstructions in central Poland

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ABSTRACT:

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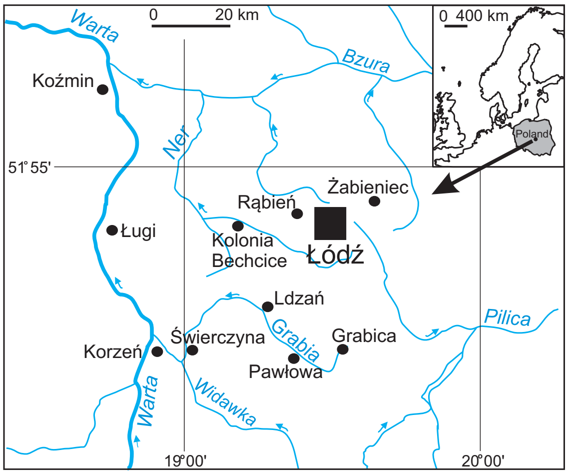
Cladoceran-based paleotemperature estimates for the Younger Dryas for ten sections of paleo-oxbow lakes, valley mires, and lacustrine sediments from central Poland are presented, and their potential usefulness to climatostratigraphy is described. Most of the changes observed in the cladoceran assemblages are responses to climate changes. The cladoceran-based temperature reconstructions reflect cold conditions during the Younger Dryas (YD) and allow a division of this period into two phases: an older colder phase, between 12,800 and 12,000 cal yrs BP, and a younger, warmer phase, between ca. 12,000 and 11,500 cal yrs BP. The geomorphological features of the study sites and local environmental forces are also taken into consideration. The cladoceran-inferred summer temperature estimates from all of the study sites correspond closely with the available climate reconstruction for the YD in central Europe.

Key words: Younger Dryas; Cladocera; Temperature; Oxbow lake; Climate.

INTRODUCTION

Since the later decades of the twentieth century, subfossil Cladocera analysis has been one of the most important methods in paleoecological studies (Frey 1986; Pawłowski 2011). The cladocerans (Branchiopoda, Cladocera) are the most abundant crustaceans preserved in lake sediments (Birks and Birks 1980). The group has been widely used as a proxy for reconstructing paleoclimates, as well as ecological and hydrological changes (Korhola and Rautio 2001; Mirosław-Grabowska *et al.* 2015), because their ecological preferences are relatively well understood. The response of cladocerans to changes in temperature and humidity is significantly more rapid than that of other proxies, e.g., pollen (Birks and Ammann 2000). Cladocerans can be used to quantitatively infer paleotemperature fluctuations and provide a reliable alternative method if a regional transfer function is not available (Nevalainen *et al.* 2012; Pawłowski *et al.* 2015a).

The Younger Dryas (YD), being a transition from the Last Glaciation to the Holocene, is characterized by a series of rapid climatic changes. This has had a strong influence on local ecosystems and the aquatic invertebrate fauna (Szeroczyńska 1985; Goslar *et al.* 1998; Isarin and Bohncke 1999; Isarin and Rensen 1999; Milecka *et al.* 2011; Feurdean *et al.* 2014; Mirosław-Grabowska and Zawisza 2013; Gandouin *et al.* 2016; Stivrins *et al.* 2016). The river valleys of central Europe underwent significant geological and hydrological transformation (Starkel 1990, 2002; Macklin *et al.* 2006; Starkel *et al.* 2007; Notebaert and Verstraeten 2010; Kaiser *et al.* 2012; Turner *et al.* 2013). In response to temperature fluctuations, this caused biotic changes and alterations in river environments (Pawłowski *et al.* 2015b, c). However, knowledge of European mires in river valleys is relatively lim-



Text-fig. 1. Locality map of the sections studied

ited, despite the fact that most mires (e.g., in central Poland) are located in river valleys (Żurek 1987). Oxbow lake and valley mire sediments provide comparable alternatives to lake and mire sedimentary deposits (Millet *et al.* 2012) for the study of past environmental change (Gandouin *et al.* 2007; Engels *et al.* 2008; Pawłowski *et al.* 2012).

Studies of cladoceran-inferred paleotemperature in the YD and Early Holocene valley mires of central Poland have already begun (Pawłowski *et al.* 2015a, 2016a). Although a few studies have used cladoceran-inferred paleotemperatures in the Late Glacial and Holocene, there have been no comparisons of Cladocera reconstructions in different geological and geomorphological situations in a region.

This study presents data from a number of sites situated in a range of geographical settings in a specific region with the aim of reconstructing climate variability during the YD. The aim of the study is thus to answer the question of how to compare the climate signal coming from lakes and mires located in river valleys with those on plateaus of glacial and aeolian origin in the same region, and thereby how to compare this climatic signal with that on a wider regional scale. This study thus also explores the reliability of cladoceran-inferred summer temperatures for reconstructing past climatic conditions.

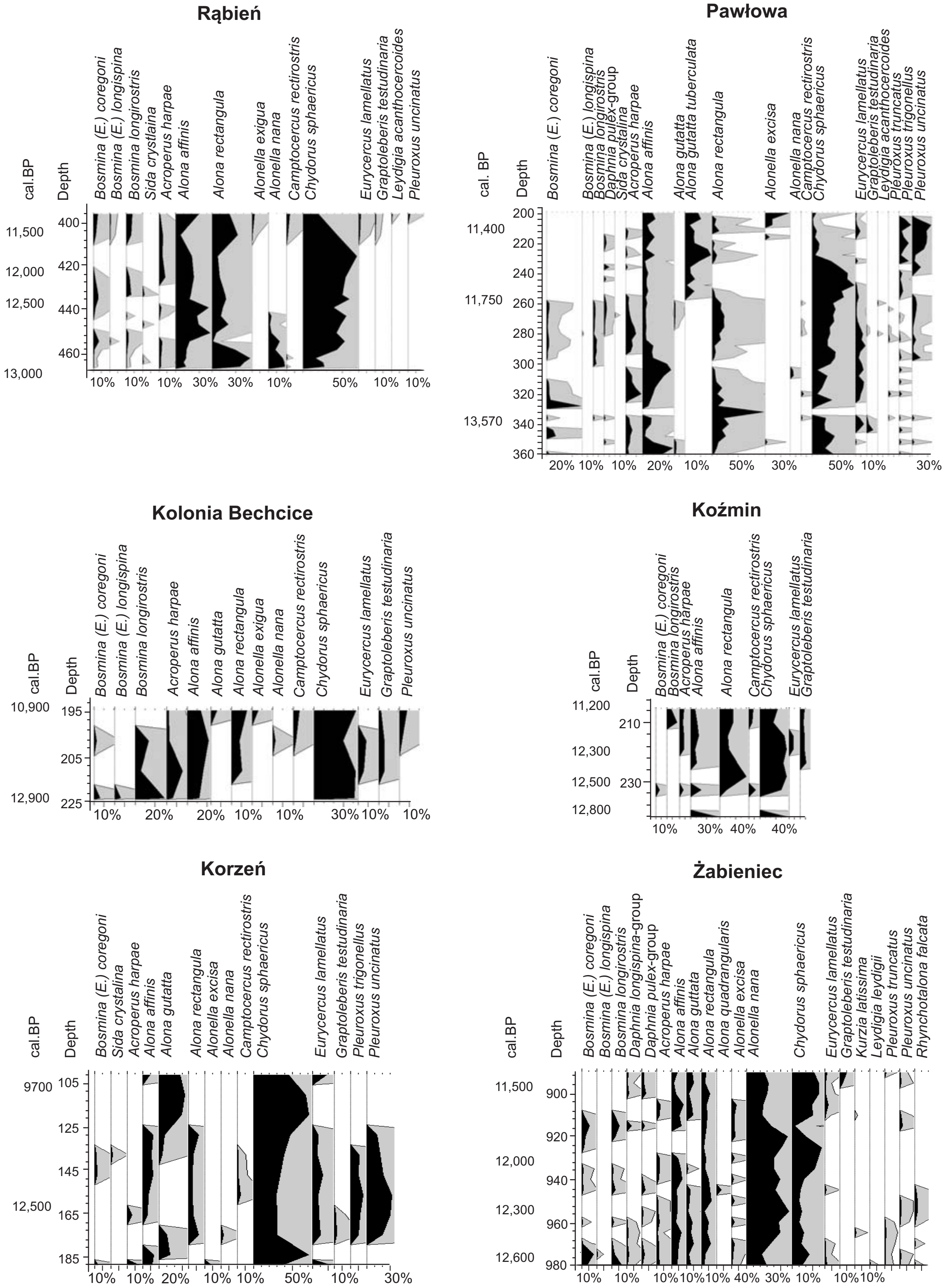
STUDY AREA

The investigated sites are located in the Łódź Region, central Poland (Text-fig. 1), which possesses a good record of the Saalian Glaciations, particularly the Wartanian Cold Stage of the Odranian Glaciation. All sites are located at approximately the same altitude (100–200 m a.s.l.; Table 1), but represent various geological and geomorphological situations (Forysiak 2012). There are lakes located (1) in river valleys – both active and in fossil valleys – and (2) on plateaus of both glacial and aeolian origin. Most of the lakes represent sites located in Polish river valleys: (1) Świerczyna, Pawłowa, Grabica, and Ldzań are on the valley floor of the Grabia River, (2) Korzeń is in the lower reaches of the Widawka River, (3) Kolonia Bechcice is in the middle reach of the Ner River, and (4) Koźmin is in the middle reach of the Warta River (Text-fig. 1). The Grabia, Ner, and Widawka Rivers are seminatural, partly unregulated tributaries of the Warta River (within the Odra River catchment). Most of the floodplains in these river valleys are occupied by a mire with peat pools and paleo-oxbow lakes, which are overgrown by riparian forests; they are located in cut-off paleochannels and also have different surface areas. Geologically, these river valleys are mostly filled with Late Glacial deposits and Holocene alluvium. The Saalian till is present on surrounding plains; locally it is overlain by glaciofluvial sands, and gravels surround the valley reaches (Forysiak 2012; Pawłowski *et al.* 2016a).

The two river valleys sites described here, Koźmin and Ługi, are unique. Koźmin represents a site with a fossil forest that persisted in the YD, in the potentially favourable growing conditions in the floodplain of the Warta River (Dzieduszyńska *et al.* 2014). The Ługi mire represents sites located in the fossil Jadwichna-Pichna River valley (part of the Warta River valley), which functioned as a proglacial water outflow during the Saalian Glaciation recession and as the main tract of the Warta River Valley in the Late Plenivistulian (Klatkowa and Załoba 1991; Forysiak 2012).

The two other sites, at Żabieniec and Rąbień, are located in the morainic uplands near Łódź (Text-fig. 1; Table 1). Żabieniec is on a plateau to the east of Łódź, in an oval depression surrounded by morainic hills (Forysiak 2012). This kettle hole was probably formed during the Late Saalian (Wartanian) and has a very irregular bottom configuration. The oldest sediments recorded were deposited at the end of the Upper Pleniweichselian. Rąbień, in turn, is located in the morainic Łask Upland to the west of Łódź (Text-fig. 1). This basin of aeolian origin is situated in an oval depression surrounded by dunes, which was formed during the Older Dryas (Forysiak 2012).

Detailed studies of the geology and relief of



Text-fig. 2. Percentages of Cladocera from the Rąbień, Pawłowa, Kolonia Bechcice, Koźmin, Korzeń, and Żabieniec sites

Site name	Latitude	Longitude	Altitude (m a.s.l.)	Location	Length of core (cm) / ca. length of studied period (cm)	Resolution of analysis (cm)
Grabica	51°29’11” N	19°32’12” E	215	active river valleys	200 / 80	4
Ldzań	51°35’31” N	19°13’58” E	173	active river valleys	100 / 44	4
Pawłowa	51°30’19” N	19°19’59” E	184	active river valleys	450 / 160	4
Świerczyna	51°28’02” N	18°59’89” E	146	active river valleys	336 / 176	4
Kolonia Bechcice	51°45’12” N	19°14’26” E	154	active river valleys	139 / 30	4
Korzeń	51°28’44” N	18°53’25” E	139	active river valleys	200 / 90	10
Koźmin	52°04’51” N	18°40’30” E	97	active river valleys	50 / 30	4
Ługi	51°43’52” N	18°42’46” E	123	fossil river valley	300 / 150	10
Rąbień	51°48’20” N	19°18’05” E	189	plateau of aeolian origin	620 / 65	4
Żabieniec	51°51’01” N	19°46’38” E	180	plateau of glacial origin	1600 / 80	4

Table 1. Sites location and basic sampling information

the area, with analysis of the sediments from these sites using the multiproxy approach and radiocarbon datings, have been presented by Forysiak (2012), Pawłowski (2012a, b), Dzieduszyńska *et al.* (2014), Pawłowski *et al.* (2014, 2015a, b, 2016a, b).

The sites are no more than about 80 km apart from each other. They are thus characterized by the same climate condition. The climate is transitional (Woś 1999) with more continental than oceanic influences. Mean annual rainfall ranges from 500 to 600 mm; the growth period lasts for 210 days. The mean monthly air temperature varies from -3°C in January to 17.9°C in July, while the mean annual temperature is 7.6–8.0°C (Kłysik 2001). Snow cover is present for an average of 50 to 70 days annually.

MATERIALS AND METHODS

The study sites have previously undergone Cladocera analysis (Pawłowski 2012a, 2012b; Dzieduszyńska *et al.* 2014; Pawłowski *et al.* 2015a, b, 2016a, b). However, the cladoceran-inferred paleotemperature estimates from most study sites – Żabieniec, Rąbień, Korzeń, Ługi, Kolonia Bechcice, and Koźmin – have not yet been presented. A new paleotemperature estimation from the YD was therefore constructed on the basis of the previous methods and is presented here. The results (Text-figs 2–4) concern only the YD periods, as the subfossil concentration was either too low or the remains were absent from the upper core section following peat accumulation (the low abundance of Cladocera made a cladoceran-inferred reconstruction impossible). The cladoceran-inferred temperature reconstructions are thus presented for this period.

Cladocera analysis

Sediment cores for the cladoceran studies were collected from all sites (Text-fig. 1) where the thickest organic deposits were found. In the laboratory, the cores were sampled at 4-cm; only two cores were taken at 10-cm resolution (Table 1). The sediment samples for Cladocera analysis were processed according to the standard procedure (Frey 1986); slides were prepared from 0.1 ml of each sample and examined with a microscope (100× magnification). The taxonomy of the cladoceran remains in this paper follows that presented by Szeroczyńska and Sarmaja-Korjonen (2007), and the ecological preferences of the cladoceran taxa were determined based on Bjerring *et al.* (2009). The results were plotted on a percentage diagram using POLPAL software (Walanus and Nalepka 1999).

Stratigraphy

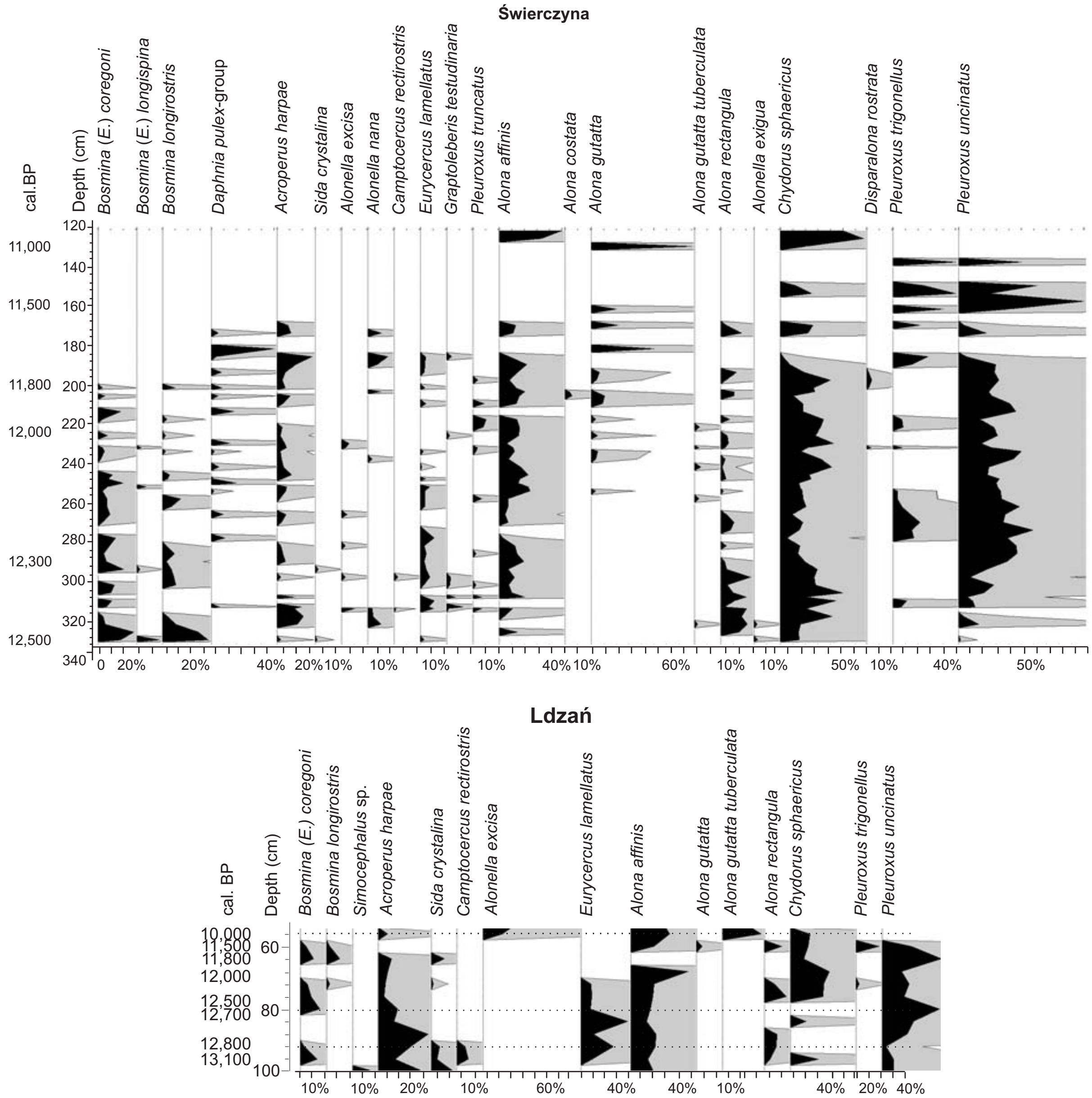
The chronology of the sediments from the study sites was determined on the basis of AMS ^{14}C dates (Table 2) and pollen biostratigraphy. Radiocarbon dates are limited to the YD period and are given in calibrated years BP; conventional radiocarbon dates were calibrated using the newest version of OxCal 4.2.3 (Bronk Ramsey 2009) and the IntCal13 calibration curve (Reimer *et al.* 2013). Although the YD period is presented here, the age-depth models for all studied sites were constructed based on all dates from the whole cores (for details, see the references in Table 2).

Cladoceran-inferred temperature reconstruction

A Finnish Cladocera-based mean July air temperature (T_{July}) transfer function was applied to

Site	Depth b.g.l. (cm)	^{14}C age (BP)	Calibrated age (95.40% probability) cal. BP	Source
GRAB	115	9150±50	10,486–10,225	Pawłowski *et al.* 2016a
	136	10,160±70	12,096–11,406	
	160	10,340±120	12,568–11,717	
	200	10,420±90	12,573–11,998	
LDZ	56	9930±50	11,605–11,234	Pawłowski *et al.* 2016a
	79	10,700±60	12,725–12,563	
	95	11,290±120	13,409–12,884	
PAW	208	9900±80	11,700–11,189	Pawłowski *et al.* 2016b
	264	10,140±80	12,079–11,395	
	336	11,690±120	13,759–13,292	
ŚWIERCZYNA	121	9500±50	11,080–10,931 (32.3%)	Pawłowski *et al.* 2015a, 2015b
			10,879 –10,646 (59.2%)	
			10,630–10,589 (3.9%)	
	148	10,010±70	11,799–11,785 (0.6%)	
			11,774–11,250 (94.8%)	
	176	10,150±90	12,124–11,389 (94.7)	
			11,377–11,353 (0.7%)	
	196	10,130±90	12,080–11,341	
	232	10,370±80	12,535–11,964	
	272	10,360±60	12,514–12,496 (0.9%)	
			12,423–11,984 (94.5%)	
	328	10,420±60	12,535–12,076	
KB	190–194	9520±90	11,149–10,581	Pawłowski 2012b; Płóciennik *et al.* 2016
	220	11,020±230	13,384–12,544	
KOŹMIN	200–204	10,000±80	11,821–11,240	Dzieduszyńska *et al.* 2014
	228–232	10,570±50	12,629–12,410	
	232–236	10,710±60	12,744–12,547	
	236–240	10,850±60	12,897–12,599	
KO	110	9710±110	11,323–10,715	Forysiak 2012; Pawłowski 2012b
ŁUGI	89–90	7430±90	8394–8043	Forysiak 2012
	140	10,110±130	12,225–11,244	
	279–281	13,820±130	17,130–16,302	
RAB	405	10,060±40	11,805–11,355	Forysiak 2012; Michczyńska *et al.* 2014
	475	11,180±45	13,150–12,962	
	505	11,625±45	13,569–13,353	
ŻAB	826	9130±50	10,479–10,468 (1.2%)	Forysiak 2012; Pawłowski 2012a
			10,423–10,204 (94.2%)	
	1036	11,860±60	13,858–13,479	

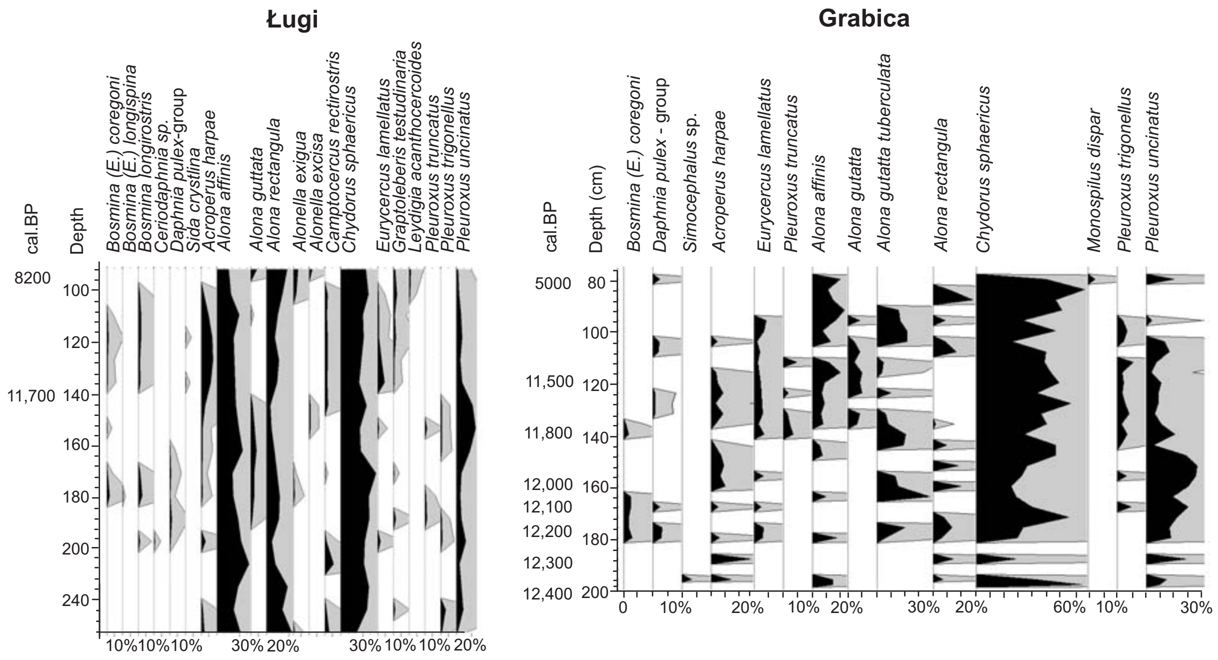
Table 2. Radiocarbon dating of samples from the studied sites (GRAB: Grabica; LDZ: Ldzań; PAW: Pawłowa KB: Kolonia Bechcice; KO: Korzeń; RAB: Rąbień; ŻAB: Żabieniec)



Text-fig. 3. Percentages of Cladocera from the Świerczyna and Ldzań sites

the Cladocera assemblages from all the study sites to create a quantitative estimate of past July air temperatures (Nevalainen *et al.* 2012). A weighted averaging-partial least squares regression (WA-PLS) technique model was used. The cladoceran-based T_{July} inference model had an rjack^2 of 0.67, RMSEP of 0.86°C, and mean and maximum biases of -0.017°C and 1.732°C, respectively (Luoto *et al.* 2011).

The reliability of the temperature reconstructions was tested by MAT (modern analogue analysis) and goodness-of-fit (GoF) analysis (Brooks *et al.* 2012) and evaluated by examining the squared residual distance of the modern and fossil passive samples in a canonical correspondence analysis (CCA), with the environmental variable of interest as the sole constraining variable (lack-of-fit *N* 10% of the extreme values in the modern calibration set). It was tested to see whether the samples have good modern analogs (threshold for good assemblage *N* 10% chord distance). CANOCO and C2 software, respectively, were used for these procedures (ter Braak and Šmilauer 2002; Juggins 2007).



Text-fig. 4. Percentages of Cladocera from the Ługi and Grabica sites

RESULTS

Cladoceran-inferred temperature reconstruction

The cladoceran-inferred mean July temperature (T_{July}) at the sites located in the river valleys (Koźmin, Ługi, Korzeń, Pawłowa, Ldzań and Grabica) reached a high of approximately 14.8°C (Text-fig. 5; Table 3) at the end of the Allerød. Similar values were reached at the upland hill sites (Rąbień and Żabieniec). In the YD, the mean summer temperature in the river valleys decreased to between 13.9°C to 14.7°C (Table 3). In turn, the upland hill sites had an average T_{July} of 14.3°C. The mean summer temperature at all studied sites decreased from ca. 12,800 cal yrs BP to ca. 12,500–12,000 cal yrs BP, when the lowest values were found (Text-fig. 5). From the mid-YD (ca. 12,000 cal yrs BP), all sites show an increasing trend for T_{July} and higher values in the late YD (ca. 11,500 cal yrs BP). In the Early Holocene, the cladoceran-based T_{July} showed higher temperatures than in the YD at all study sites. This indicates an increase of up to 15.7°C in the river valleys (Warta and Grabia valleys), and 15.3°C in the uplands (Żabieniec) (Table 3).

In the cladoceran-based mean July temperature reconstruction, only ca. 25% samples from the sites show a good fit to temperature (Text-fig. 6). For this reason, even though there are good modern analogs in the modern training set, most of the cladoceran-inferred temperatures must be treated with caution.

DISCUSSION

Cladoceran-inferred temperature reconstitution and regional comparison

The YD cooling is visible in the cladoceran-based temperature reconstructions at all the central Poland study sites (Table 3). The temperature reconstructions from lakes located on active river valley beds show a drop in the July temperature (starting from 12,800 cal yrs BP) and reflect the beginning of the YD cooling (Text-fig. 5). Between ca. 12,500 and 12,300 cal yrs BP, the record from the river valleys is characterized by decreases in summer temperatures from 14°C to 12°C. After that, summer temperatures show a pattern fluctuating between 12.2°C and 16.5°C (with an average of 14.3°C). Finally, the summer temperature increases to 15°C at the end of the YD. The estimates from lakes located on (both active and fossil) river valley beds correlate well with the estimates from plateaus, whether of glacial (Żabieniec) or aeolian origin (Rąbień) (Table 3; Text-fig. 5). This confirms that the temperature estimates from study sites are consistent. These reconstructions are also similar to

	Upland Hills		River Valleys							
	Rąbień this study	Żabieniec this study	Koźmin this study	Ługi this study	Korzeń this study	Kolonia Bechcice this study	Świerczyna (Pawłowski *et al.*, 2015a)	Grabica (Pawłowski *et al.*, 2016a)	Ldzań (Pawłowski *et al.*, 2016a)	Pawłowa (Pawłowski *et al.*, 2016b)
EH	15.1°C	15.3°C	15.7°C	15.1°C	14.9°C	15.3°C	14.7°C	14.8°C	14.7°C	15.5°C
YD	14.3°C	14.3°C	14.6°C	14.4°C	14.0°C	14.5°C	14.2°C	14.7°C	13.9°C	14.0°C
LA	14.5°C	14.6°C	14.8°C	14.3°C	14.5°C				14.5°C	14.3°C

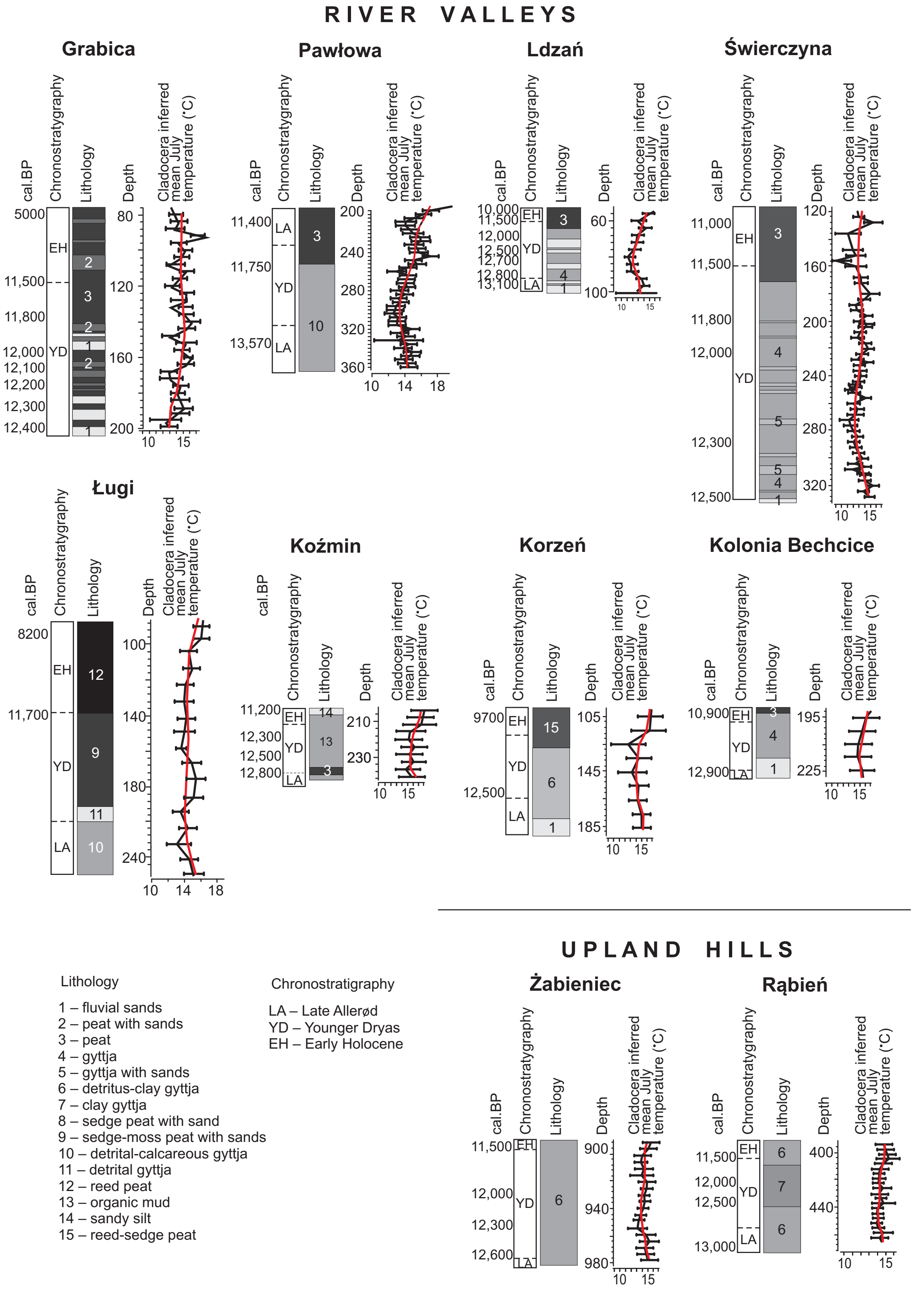
Table 3. Mean T_{July} estimation for the YD (gray field) from central Poland based on cladoceran-inferred model. EH: Early Holocene; YD: Younger Dryas; LA: Late Allerød

most YD paleotemperatures reconstructed for the YD for central Poland, based on chironomid models that show the YD mean average July air temperature to have been ca. 14°C (Żabieniec, Płóciennik *et al.* 2011; Koźmin, Dzieduszyńska *et al.* 2014). However, at sites like Rąbień and Świerczyna, which are dominated by the chironomid *Corynocera ambigua* (80–90%), the reconstructed summer temperatures are much lower (at ca. 8°C) than at nearby localities. This is because they are closely associated with the local environmental conditions (i.e., high levels of mineral matter, flooding, and weakly developed plant communities) that affected the chironomid assemblages (Pawłowski *et al.* 2015a).

The cladoceran-inferred summer temperature reconstruction from paleo-oxbow lakes in central Poland seems to be reliable and comparable to the record from plateau sites that are not exposed to the direct activity of rivers. There is insufficient radiocarbon data from all the study sites to allow plausible discussion of the correlation of annual or near-annual resolution records; however, it can be suggested that most study sites reflect fluctuating conditions during the YD. This period can thus be divided into a first phase, associated with lower temperature (to 12,000 cal yrs BP), and a second warmer YD phase (ca. 12,000–11,500 cal yrs BP). These observations confirm previous investigations from the region, which show similar patterns of temperature and precipitation (Płóciennik *et al.* 2011; Pawłowski *et al.* 2015a). Additionally, this trend is consistent with the bipartite climate division of the period (a cold first part followed by a warmer second part) detected by Peyron *et al.* (2005) in records from central and northwestern Europe. This situation also has been linked with changes in atmospheric circulation regimes (Bakke *et al.* 2009; Lane *et al.* 2013).

Between 12,500 and 12,300 cal yrs BP, the pollen-based reconstructions from central Polish river valleys are characterized by decreases in winter temperatures from -11 to -22°C (Pawłowski *et al.* 2015a). These estimates are very close to the results of the climate stimulations of Isarin and Bohncke (1999), who reported a decrease in the YD winter temperatures to -25°C in northwestern and central Europe. This confirms the general trend toward cold and dry conditions over central and eastern Europe during the YD, driven by enhanced continentality. The decline in temperatures in the YD was found to be more pronounced in winter than in summer (Feurdean *et al.* 2014); the winter temperature estimates seem to be similar throughout Europe (Pawłowski *et al.* 2015a).

The cladoceran-based summer temperature reconstructions from central Poland (12.2–16.5°C) are similar to the cladoceran-based estimates for eastern Poland (11.5–14.5°C; Łukie Lake; Zawiska *et al.* 2014) and to the chironomid-inferred summer temperature estimates for the mid-latitudes (50–55°N) of east and central-southern Europe (Heiri *et al.* 2014). Additionally, the YD temperature values from central Poland studied here are very similar to the estimates from lowlands and mid-elevation (up to 700 m a.s.l.), central European and southern European lakes (Table 4), whose temperatures ranged between 12°C and 16°C (Steregoiu, Romania; Feurdean *et al.* 2008), 13.5°C and 16°C (Kraków-Wieluń Upland, Poland; Lorenc 2008), 12.1°C and 14.4°C (15.7–17.3°C, Żabieniec, Poland; Płóciennik *et al.* 2011), 14.8°C and 15.8°C (Koźmin, Poland; Dzieduszyńska *et al.* 2014), 13.5°C and 14.5°C (Hijkermeer, Netherlands; Heiri *et al.* 2007), 13°C and 16°C (Friedländer Große Wiese, Germany; van Asch *et al.* 2012), 14°C and 15°C (Lautrey, France; Heiri and Millet 2005), 15°C and 15.5°C (Ech, France; Millet *et al.* 2012), and ca. 16°C (Lago di Piccolo, Italy; Larocque and Finsinger 2008). In turn, the summer estimates in northern and eastern Europe were significantly lower (Table 4): 8–10°C (England; Lang *et al.* 2010); 7.5–10°C (Lough Nadourcan, Ireland; Watson *et al.* 2010); 10–12°C (Sergeevskoe, Belarus; Veski *et al.* 2015); 11–14°C (Kurjanovas, Latvia; Veski *et al.* 2015); and 9.5–13°C (Nakri, Estonia; Veski *et al.* 2015).



Text-fig. 5. Summary diagram demonstrating the cladoceran-inferred summer temperature reconstructions from central Poland. Records are plotted versus the age-depth model. Black lines: cladoceran-inferred models; red lines: smoothed trend of reconstruction; error bar estimates are shown as black horizontal spans

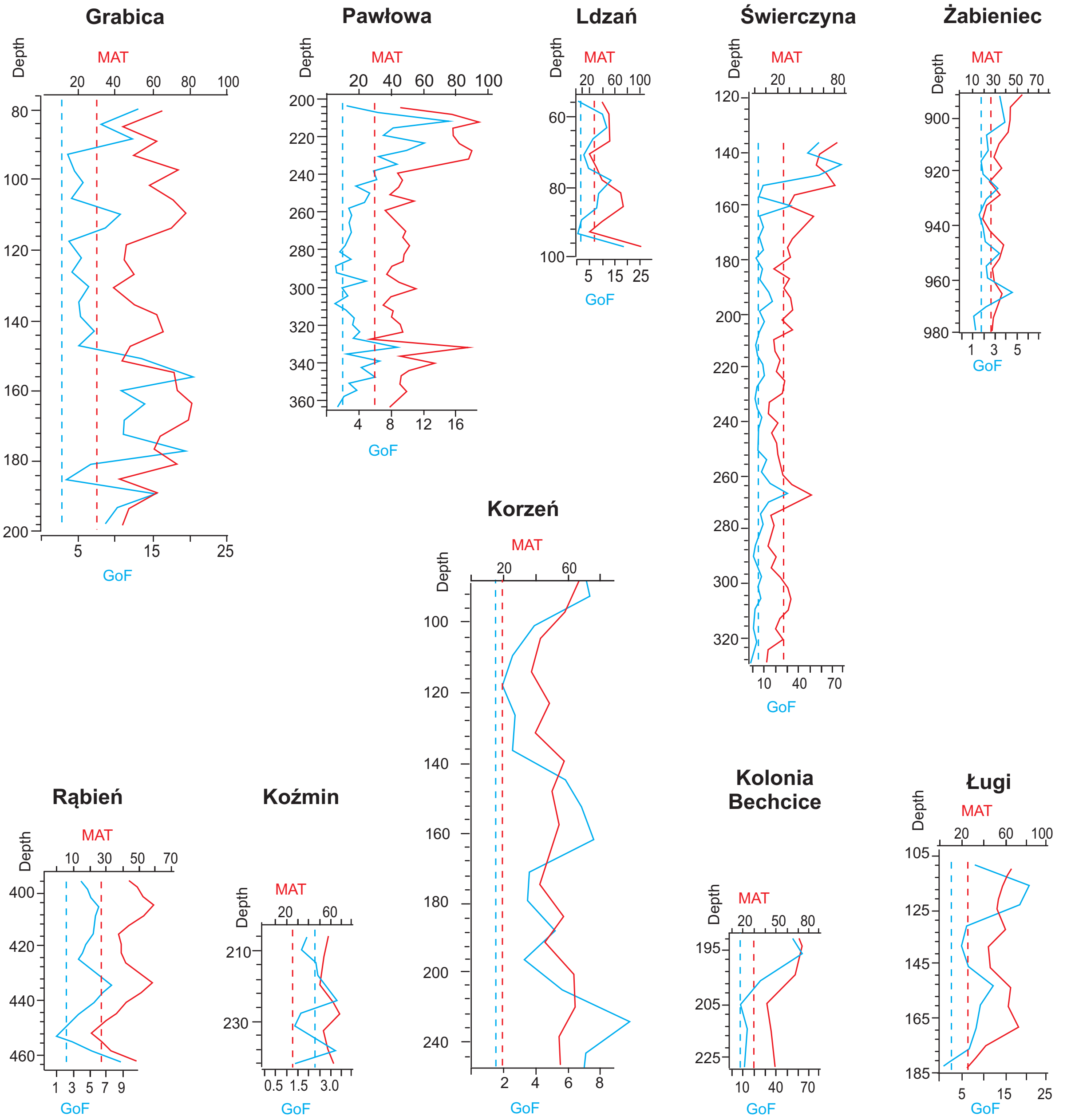
	Central and southern Europe								
	Koźmin ** Poland	Żabieniec ** Poland Norwegian TS Swiss TS	Krakowsko-Wieluńska Upland *** Poland	Łukie Lake * Poland	Hijkermeer ** Netherlands	Friedländer Grobe Wiese ** Germany	Ech ** France	Lautrey ** France	Lago di Piccolo ** Italy
YD	14.8–15.8°C	12.1–14.4°C 15.7–17.3°C	13.5–16°C	11.5–14.5°C	13.5–14.5°C	13–16°C	15–15.5°C	14–15°C	16°C

	Central and southern Europe			Northern and eastern Europe				
	Gościąż *** Poland	Witów *** Poland	Steregoiu *** Romania	5 sites in England **	Lough Nadourcan ** Ireland	Sergeevskoe *** Belarus	Kurjanovas ** / *** Latvia	Nakri ** / *** Estonia
YD	10–14°C	12°C	12–16°C	8–10°C	7.5–10°C	10–12°C	11–14°C 9–10.5°C	9.5–13°C 9.5–11.5°C

Table 4. Temperature estimation for the YD (gray field) from Europe (without the Alpine and Norway regions) based on the cladoceran-inferred model (*), the chironomid-inferred model (**), and other indicators: pollen-inferred models, selected plant indicators, bird bones (***). References to temperature estimates sources are cited in the text

Similarly, Isarin and Bohncke (1999) suggested summer temperatures of about 10–14°C in north and central Europe during the YD. In turn, Ralska-Jasiewiczowa *et al*. (1998) suggest 10°C for Poland in the first part of the YD and about 12–14°C in the second part (Wasylikowa 1964) (Table 4). However, this estimate was based on the thermal requirements of selected climate indicator plant species, and should thus be treated with caution when compared with other results or reconstructions (Pawłowski *et al*. 2015a). Overall, the central and southern Europe climate trend during the YD differs from those in the northern and eastern part of Europe. This thermal offset is probably due to latitudinal shifts and the restructuring in the oceanic surface current circulation over the North Atlantic area (Ganduoin *et al*. 2016). The estimates from central Poland, which are slightly higher than the reconstructions for northern and eastern Europe, could also be explained by the influence of more continental than oceanic air masses affecting the weather conditions in the eastern and northern parts of Europe. Further, the enhanced continentality could have resulted in a temporary increase in summer temperatures and lower winter temperatures, resulting in a more rapid reaction of aquatic invertebrates to this event, but a complete lack of reaction from vegetation. According to the results from central Poland, the cladoceran-based model infers a rise in the YD summer temperature slightly earlier than does the pollen-based model (Pawłowski *et al*. 2015a). It is probable that this is related to the high sensitivity of cladocerans to changing conditions and to their short life cycle, which allows them to respond more quickly to climate change. Finally, it is possible that discrepancies have arisen from the different methods of estimation used in cladoceran, chironomid, and pollen/plant reconstructions; a model which is constructed to infer summer mean temperatures reflects a true mean and not individual measurements; otherwise, chance factors may strongly influence the resulting model. Additionally, the new findings of temperate-adapted species, such as *Quercus* and *Fagus* from central Europe in the YD (Robin *et al*. 2016), may suggest higher temperature estimates than the reconstructions known to us at present. The Cladocera-based temperature scenario thus seems to be realistic and appears to be the most plausible.

During ca. 12,000–11,500 cal yrs BP, a gradual warming occurred (Text-fig. 5). This warming likely resulted in strongly contrasting seasonal hydrological conditions: summer temperatures increased (13.5–16°C), corresponding to a gradual rise in winter temperatures and in annual precipitation (which was, however, variable in spring and summer) in the Grabia River valley (Pawłowski *et al*. 2015a). A similar shift in the mid-YD as a climatic amelioration associated with changes driven by the large-scale reorganizations of atmospheric and oceanic circulation patterns has been noted in Kråkenes (Norway; Bakke *et al*. 2009) and Meerfelder Maar (Germany; Lane *et al*. 2013). Although these atmospheric reorganizations, which resulted in rapid alternations between glacial growth and melting during the later YD, were



Text-fig. 6. Modern analogue analysis (MAT; red line) and goodness-of-fit (GoF; blue line) of the fossil assemblages to temperature. The vertical red dotted line indicates 10% of the squared chord distances of the fossil sample to the samples in the modern calibration dataset. The vertical blue dotted line indicates 10% of the squared residual distances of the modern samples to the first axis in a CCA. The samples to the right of the lines have no good modern analogue and have respectively a poor or very poor fit-to-temperature. The units for GoF are 'squared residual distance'; for MAT, 'squared chord distance

expressed most clearly on the margins of the polar and Atlantic air masses, it is possible that these climate shifts could also have influenced periodicity in central Poland during the YD. In addition, this situation confirms that the mid-YD transition was locally abrupt but time-transgressive across Europe. A similar warming trend at the end of the YD has been widely observed in other lakes throughout Europe (Bohncke *et al.* 1993; Goslar *et al.* 1993; Ralska-Jasiewiczowa *et al.* 1998; Lotter *et al.* 2000; Velichko *et al.* 2002; Birks and Ammann 2000; Birks *et al.* 2010; Neugebauer *et al.* 2012; Brooks and Langdon 2014; Ganduoin *et al.* 2016). Most authors have suggested a probable strong warming (ca. +2–3°C) in the second and terminal parts of the YD. The sites investigated here are located within a transition zone between the influences of the North Atlantic and the continental climatic regimes, resulting in variable weather conditions. Some of the results thus reflect the climate dynamics of western, northwestern, and southern European sites (Magny *et al.* 2006; Neugebauer *et al.* 2012; Hošek *et al.* 2014). These results suggest that Atlantic air masses may have penetrated to the east during the second part of the YD and led to oceanic influence on terrestrial ecosystems, causing changes in seasonality (i.e., relatively warm and wet winters, and an increase in spring precipitation).

The beginning of the Holocene at the study sites was characterized by an increase in summer temperatures and precipitation, as well as by prolonged growing seasons. This could indicate a decrease in the influence of the continental climate and may imply a temporary climatic connection of the study area with the circum-North Atlantic air masses (Pawłowski *et al.* 2015a).

Reliability of the cladoceran-based temperature reconstruction

The GoF and MAT analyses suggest that temperature may be one of the major drivers of change in the cladoceran assemblages. However, most subfossil samples had no 'close' analogue in the modern calibration data set (Text-fig. 6). These lack-of-fit measures indicate that the fossil cladoceran assemblages in those samples may be responding to changes in an environmental variable other than temperature. Temperature reconstructions from samples where goodness-of-fit values are particularly extreme may thus be less reliable; they should be considered tentative and interpreted with caution. It is however possible that, in samples lacking a close modern analogue in the training set, the dominant taxa in the fossil sample are less well-represented in the modern training set. Rather than suggesting that temperature is not a strong driver of these samples, it may be that the temperature optima of these taxa has not been well-estimated; the temperature estimate of these samples would therefore be less reliable. For this reason, it is necessary to exclude drivers associated with local changes or climate conditions. The local factors (e.g., water level changes and influence of the rivers, habitat modification, macrophyte abundance, eutrophication, acidity, predation of fish, and presence of $CaCO_3$) may also be crucial in determining cladoceran assemblages, and therefore the Cladocera-based temperature estimation could be dubious.

The greatest differences in the estimated YD temperature occurs between the sites located in the river valleys – Ldzań (13.9°C), Grabica, and Koźmin (at approximately 14.7°C). There are a few possible explanations. The first may be related to the geomorphological position of the sites, changes in the riverbeds, or large individual floods. An increase in fluvial activity during the YD has been widely reported from Polish and European valleys (e.g. Huisink 2000; Andres *et al.* 2001; Starkel 2002, 2011; Borisova *et al.* 2006; Gao *et al.* 2007; Starkel *et al.* 2007, 2015; Pawłowski *et al.* 2015b; Petera-Zganiacz *et al.* 2015). The floodwaters may significantly decrease the water temperature in the oxbow lake, as at the Ldzań site. In contrast to other sites investigated here, which are located much further from active river channels (from 600 m to 2000 m), Ldzań is situated very close (100 m) to the present-day Grabia River channel (Pawłowski *et al.* 2014). The impact of the river could thus have been more significant on the water temperature of this oxbow lake than at the other sites. The second possible explanation is associated with the density and composition of vegetation, which affects the duration of snow cover and seasonal snowmelt. In the YD, the Koźmin site was a very shallow periodic flood basin with the riparian forest, which persisted through the YD under potentially good growing conditions in the floodplain of the Warta River, despite the generally open landscape of central Poland (Dzieduszyńska *et al.* 2014). It is therefore possible that places such as Koźmin, which offer vegetation associations some protection and refuge from climate extremes, could affect the T_{July} estimations, which could be slightly higher than in other paleo-oxbow lakes in floodplains. The peak in cladoceran density could also be associated with periods when the water was relatively warm; an increase in water temperature generally results in rich macrovegetation covering the littoral zone, allowing an increase in the number of macrophyte-associated species. This situation does not support the idea that the slightly higher frequency of Cladocera at sites on plateaus or isolated from fluvial influences (Żabieniec and Rąbień) constitutes the only reason for higher temperature estimates; similar T_{July} estimations are, after all, present at paleo-oxbow lakes. The third possible explanation for the higher T_{July} estimate at Koźmin and Grabica is connected with fact that these sites were very shallow pools during the YD. Water level changes seem to be a very important factor affecting the cladoceran community (Pawłowski *et al.* 2016a). In extremely shallow water, the inferred values and residuals in the

Cladocera-based calibration set most likely cause an overestimation of temperature. In such water pools, Cladocera are represented mainly by taxa such as *A. affinis*, *Ch. sphaericus*, *Al. excisa*, and *A. guttata* var. *tuberculata*. These benthic taxa are abundant in temperate lakes and mires, and their T_{July} optima are similar (ca. 14.5–15.2°C). Their presence in such shallow sites could lead to overestimations in temperature, as their high frequency is presumably related to nonclimatic limnological factors (such as macrophyte density and low pH); however, these changes may also result from climate-related variables (such as T_{July}). Similar situations have been observed in the Cladocera-inferred water depth models (Luoto *et al.* 2011; Nevalainen 2011; Pawłowski *et al.* 2016a) as "edge effects". Such effects suggest that the Cladocera-based inference model can most reliably quantify past water level changes at intermediate depths relative to the training set depth gradient (because they lead to overestimation at shallow sites and an underestimation at deeper sites). It is possible that this could be applied to temperature estimations. However, such "edge effects" in the nonlinear distortions at the ends of the gradients constitute a problem inherent to all unimodal-based calibration methods (Lotter *et al.* 1997).

It is very interesting that the presence of zooplanktivorous fish seems not to be the main influence on the cladoceran-based temperature model. Fish generally affect zooplankton communities and have major cascading effects on food webs (Jeppesen *et al.* 2001; Davidson *et al.* 2007). Although fish predator species are known only at Pawłowa (Pawłowski *et al.* 2016b), it cannot be excluded that there was at least temporary fish predation at other sites. Size-selective predation on larger cladoceran species could increase the relative abundance of some planktonic species. For example, the rise of *Bosmina longirostris* in concert with the density of zooplanktivorous fish could also result in an absence of *Daphnia pulex* (Davidson *et al.* 2010). However, changes associated with size-selective predation of larger species (e.g., *Daphnia* spp.) and increases in small-bodied Bosminidae, as described at Pawłowa (Pawłowski *et al.* 2016b), are likely to have affected the T_{July} reconstruction only to a small extent, because these planktonic taxa have similar T_{July} optima of around 14.9–15.9°C. These remarks also apply to a number of larger benthic chydorid taxa, in particular *A. harpae*, *E. lamellatus*, *Pleuroxus* spp., and *Ch. sphaericus*; a slight increase in zooplanktivorous fish density may have resulted in the absence of these taxa. These cladocerans are abundant in temperate lakes and mires and are strongly associated with the presence of aquatic macrophytes at lower fish densities (Davidson *et al.* 2010). However, their T_{July} optima are similar to those of small-bodied Bosminidae, ca. 14.5–15.7°C. Similarly, there is no link between low *Daphnia* incidences and the very low calcium content in the water of the studied lakes (Jeziorski *et al.* 2008) in the YD, which could have influenced the Cladocera-based temperature estimation.

The high $CaCO_3$ content at the Ługi and Pawłowa sites (the presence of detrital-calcareous gyttja) is also unlikely to have affected the T_{July} reconstruction in the YD (Text-fig. 5). The $CaCO_3$ enrichment of sediments at Pawłowa can be attributed to biochemical calcite precipitation due to the activity of autotrophic organisms in the lake (e.g., *Chara*), inputs of detrital carbonates, and leaching of carbonate-rich raw soils in the lake's catchment (Pawłowski *et al.* 2016b). In contrast to Pawłowa, there is no insight into the direct mechanism involved in calcium carbonate precipitation in Ługi. It is thus possible, though less plausible, that these changes refer to a change in the temperatures in spring and summer when most autochthonous carbonates are precipitated within the lake; however, in the sites studied, this problem applies only to the Allerød period (Text-fig. 5).

CONCLUSIONS

This study concludes that the distribution of cladoceran species from different lakes located on active river valley beds, in fossil valleys, and on plateaus of glacial and aeolian origin is mainly associated with changes in temperature. Although other environmental changes in physical, chemical, and biological lake dynamics could have affected the cladoceran assemblages, temperature remains the most important control variable in the system of interest. These aquatic organisms thus have potential as quantitative climate indicators in the YD. The cladoceran-inferred summer temperature estimates show two phases during the YD: a first colder phase between 12,800 and 12,000 cal yrs BP, and a second warmer phase between ca. 12,000 and 11,500 cal yrs BP. In the YD, the cladoceran-based summer temperature reconstructions in central Poland show a decreasing trend and had an average estimate of ca. 14°C. The lowermost estimates, at ca. 12°C, are between 12,500 and 12,300 cal yrs BP. In turn, the highest estimates, at ca. 15°C, are at the end of the YD.

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