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Non-biting midges (*Chironomidae*) as a proxy for summer temperatures during the post-Holsteinian (MIS 11b) - a central European perspective

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Abstract. Climatic and environmental changes during past interglacial periods can be investigated to improve our understanding of mechanisms governing the changes which are currently observed. Numerous proxies might be utilised to reconstruct various environmental parameters. For instance, pollen analysis indicates changes in vegetation as well as winter temperature fluctuations, while *Chironomidae* larvae head capsules are widely used to recreate summer thermal conditions. Non-biting midges remains indicate trophy and pH of water bodies as well. Nevertheless, they have been used mostly in the studies of the Holocene with hardly any Chironomid-inferred temperature reconstructions conducted for MIS 11 period. In this study we present the first quantitative summer temperature reconstruction for the post-Holsteinian (Marine Isotope Stage - MIS 11b) in Central Europe based on the analysis of fossil chironomid remains preserved in palaeolake sediments recovered at Krępa, southeastern Poland. The stratigraphic context for the chironomid-based summer temperature reconstruction is provided by pollen data, together allowing to compare our results in the context of climate development at the end of the Holsteinian Interglacial. *Chironomidae* assemblages at the Krępa site consist mainly of oligotrophic and mesotrophic species (e.g *Corynocera ambigua-type, Chironomus anthracinus-type*) with lower abundance of eutrophic species (e.g. *Chironomus plumosus-type*). The chironomid-based summer temperature reconstruction indicates July temperature ranging between 15,3°C

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and 20,1°C during the early post-Holsteinian. Temperature changes during the first stadial after the Holstein Interglacial period are also reflected by the pollen data, which, however, show a certain delay compared to the chironomids. In any case, results from Krępa prove that conducting *Chironomidae* analysis is even feasible for periods as early as the mid-Pleistocene, enhancing our understanding of the mechanisms that control present-day climatic and environmental changes. The additional element of this research is indicating sites within the Polish borders that were investigated so far - mostly on the basis of pollen analysis, occasionally *Cladocera*, isotopes, etc. - and might be new objects of studies based on Chironomid-inferred temperature reconstructions. However, bringing Chironomid analysis with particular emphasis of challenges of conducting it with the use of sediments older than Holocene is the primary aim of this publication. Data from the MIS 11 complex are unique. There are only 4 sites with pre-Late Glacial chironomid-based summer temperature reconstructions in Europe.

1 Introduction

Climatic fluctuations occurred numerously throughout Earth's history and they were triggered by natural causes – without human participation. This situation creates the opportunity to compare those changes with the current ones, as the Holocene is the only interglacial during which human activity was considerable. The widely debated topic of the Anthropocene is presently taking place in the scientific community in various scientific disciplines from the establishment of the boundary of the unit through the scale of human influence on the functioning of the natural environment in the Holocene throughout all scales starting from micro, through regional to global (Brondizio et al., 2016).

Holocene stratigraphic units corresponding to marine isotope stages (MIS 1), whose time frame has from 11,500 years BP – present (Mayewski et al., 2017) is an abundant source of environmental archives, i.a. lakes, palaeolakes, ice cores, trees, oceans etc. which provide material for palaeoecological analyses. Taking advantage of the sensitivity of some groups of organisms to hydrological or climatic conditions change, we can use this knowledge to reconstruct past events that directly affected the abundance or species structure of these groups of organisms (Battarbee, 2000). Species, which are characterised by narrow ecological requirements, whether it be air temperature, water chemistry or water table depth, are used for certain palaeoenvironmental reconstructions (Juggins and Birks, 2012). Many ecological parameters can be reconstructed using different proxies. For example, foraminifera is a reconstruction tool for ocean pH (Foster and Rae, 2016; Roberts et al., 2018), pollen indicates changes in vegetation migration (Ralska-Jasiewiczowa et al., 2004; Kupryjanowicz et al., 2018) can be used as a proxy showing the activities of a human in the past (Chevalier et al., 2020) or serve as a palaeoclimatic proxy (e.g. Rylova and Savachenko, 2005; Hrynowiecka and Winter, 2016), whereas head capsules of Chironomids serve as the basis for summer air temperature reconstruction (Eggermont and Heiri, 2012). *Chironomidae* remnants analysis allows the assessment of the water reservoir trophy and pH as well (Płóciennik, 2005).

In general, palaeoecological and palaeoclimatological reconstructions indicate considerable human impact on the environment during the last 300 years (Zalasiewicz et al., 2010). However, these reconstructions are not capable of giving unequivocal information about exact air temperature changes nor whether these changes and their pace are induced by natural causes or

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human activity. To gain a deeper understanding of the present-day human impact on climate and environment, it is essential to investigate natural climate variability and environmental changes during past warm periods prior to any human activity. In this regard, one particularly suitable target is the Holsteinian Interglacial (or Mazovian Interglacial in Poland), which is commonly estimated to have lasted from 423 to 395 ka BP and is considered as corresponding to Marine Isotope Stage (MIS) 11c (Lauer and Weiss, 2018; Lauer et al., 2020; Fernández Arias et al., 2023). Climate conditions in Northern Europe were temperate at that time (Nitychoruk et al., 2018), but vegetation reconstructions suggest warmer and more humid conditions compared to climate during the Holocene (MIS 1) climatic optimum (Hrynowiecka and Winter, 2016). Two major climatic oscillations have so far been documented during the Holsteinian Interglacial - the Older Holsteinian Oscillation (OHO) and the Younger Holsteinian Oscillation (YHO). The OHO occurred around 418 BP (Koutsodendris et al., 2010, 2012; Górecki, 2023) and is clearly connected to a rapid cooling as indicated by the disappearance of temperate vegetation (mostly *Picea-Alnus* forests) and spread of pioneer tree taxa including *Betula*, *Pinus* and *Larix* (Koutsodendris et al., 2010, 2012; Candy et al., 2014; Hrynowiecka and Pidek, 2017; Górecki et al., 2022). Although the OHO has been described at multiple sites across northern Europe (Koutsodendris et al., 2012) it has so far not been identified in southern European (Kousis et al., 2018). In contrast to the OHO, the YHO occurred around 400 ka BP within the climatic optimum of the Holsteinian Interglacial (*Carpinus-Abies* phase) and was apparently not connected to a significant cooling (Górecki et al., 2022). Records from Germany and eastern Poland suggest a sudden regression of *Carpinus* from the forest communities (Koutsodendris et al., 2010; Hrynowiecka et al., 2019; Górecki et al., 2022) and particularly in Poland a rapid spread of *Abies* with an admixture of *Corylus* and at southern sites also *Taxus* is observed (Górecki et al., 2022), suggesting that temperature was not limiting the growth of *Carpinus*.

In this research we focus on the *Chironomidae* state of research in the Holstein Interglacial. Although non-biting midges remains are widely used in climate and palaeoenvironmental reconstructions (Eggermont and Heiri, 2012), there is still not much research considering using them to recreate ecological conditions during the Holsteinian Interglacial. In fact, quantitative reconstructions based on terrestrial archives for this period are rare, regardless of the proxy used. Exceptions from this rule include palynological reconstructions from Velay maar sites in southern France (Reille and de Beaulieu, 1995), Tenaghi Philippon in north-eastern Greece (Tzedakis et al., 2006; Ardenghi et al., 2019) and Lake Ohrid on the North Macedonian-Albanian border (Kousis et al., 2018). Pollen sequence from Ossówka palaeolake (eastern Poland) has also been conducted, nevertheless it covers only the last stage of the Holsteinian Interglacial (Bińka et al., 2023). Palynological data from MIS11 has been also studied based on material from Nowiny Żukowskie site (Hrynowiecka and Winter, 2016). Another site worth mentioning is Bilhausen in central Germany, which provides pollen record for Bilhausen Interglacial, however, it remains unclear whether this period is MIS 11 or MIS 13 analogue (Kühl and Gobet, 2010). There are even fewer northern-European Chironomid-inferred palaeoecological reconstructions covering MIS 11 period. One of the exceptions is Hoxne site in eastern England (Horne et al., 2023). Contemporary state of knowledge considering MIS11 has been reviewed by Candy et al. (2014). That is why extension of using *Chironomidae* proxy on other periods (i.a. Holsteinian Interglacial) is crucial to understand current climate changes.

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We tested temperature reconstruction using the Swiss-Norwegian-Polish Training Set and presented the first Chironomid-inferred temperature reconstruction from Poland before the Last Glacial Period and even for the post-Holsteinian. The literature contains data from pollen analysis for this period, but the temperature reconstruction will be one of the first for this time range. This work gives new light on the possibilities of analysing subfossil Chironomidae.

Additionally, we have reviewed sites documenting lake sediments from the Holsteinian Interglacial period. Based on this we selected sites with a probable continuous sequence of interglacial sediments, which represent a potential archive for reconstructing the palaeotemperatures of the summer period on the basis of *Chironomidae*. In this paper we also discuss the potential that non-biting midges analysis brings to the wide range of proxies we use in the palaeoecology of quaternary sediments but also challenges such as those arising from evolution and interchanging adaptations to ecological requirements and the behaviour of fossil remains. In the presented article, we have collected all known sites of Holsteinian age from Poland. We have collected nearly 80 sites that were researched in Poland on the map. We also created an up-to-date set of sites. We hope that our list will be a handy syllabus for people interested in palaeoclimate research in Poland.

2 Data and methods

2.1 Data compilation

The research covered sites located in Poland. Holsteinian (Mazovian) Interglacial has been included. This analysis encompasses 80 sites. They are concentrated mainly in the eastern and central part of Poland (east of Warta valley), with only several sites located in western half of the country (Fig. 1). In general, they are focused in the area contained between Wartanian Glaciation and Odranian Glaciation maximum ranges (Krupiński, 2000). The sites' locations were presented in tabular form (Tab. 1). As the Holsteinian cores were often researched as early as in 1930-1960's, their exact location is not always known from scientific papers – it had to be estimated. In this case, location sketches and Google Earth were used as the location estimation tools.

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Figure 1: Holsteinian sites location in Poland with different glaciation ranges. The number of each location corresponds with Supplement Table 2. Sites from area in frame (A) are labelled in Supplement Figure 2. Krępa site is highlighted with a big red dot. Glaciation ranges based on Żarski et al. (2024), Pochocka-Szwarc et al. (2024), Marks (2023). Caption: map created with the use of EU 15s Digital Elevation Model; rivers downloaded from: https://www.naturalearthdata.com/. Map created in ArcMap programme.

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2.2 Holsteinian Interglacial

The climate during MIS 11c was characterised by relatively stable warm and moist conditions, with global temperatures approximately 1.5–2°C above the pre-industrial level (Masson-Delmotte et al., 2010). According to Raymo and Mitrovica (2012) and Muhs et al. (2012), the sea level was possibly 6–13 m higher than present. Part of it can be attributed to the melting of the Greenland Ice Sheet (Robinson et al., 2017), as pollen and palaeoDNA data suggest the existence of spruce forests in Greenland at this time (Willerslev et al., 2007; de Vernal and Hillaire-Marcel, 2008).

In Europe, warm and wet oceanic climate conditions extended far to the East as evidenced by the presence of *Taxus* and *Abies* pollen at sites in Lithuania (Kondratiene and Gudelis, 1983), Belarus (Mamakowa and Rylova, 2007), and the western Ukraine (Łanczont et al., 2003; Benham et al., 2016), while modern distribution limits of these taxa are located estimated further to the west (Benham et al., 2016). Evidence from several terrestrial records from Eurasia suggests that the MIS 11c climate was also highly complex, with pronounced climate variability occurring on both centennial and millennial timescales (Koutsodendris et al., 2010; Prokopenko et al., 2010; Tye et al., 2016; Oliveira et al., 2016; Tzedakis, 2010; Górecki et al., 2022).

The pollen succession of the Holsteinian Interglacial in Poland is characterised by the co-occurrence of pollen from *Picea-Alnus* and *Carpinus-Abies* trees, as well as a significant proportion of *Taxus* pollen, and a frequent occurrence of thermophilic taxa such as *Pterocarya*, *Celtis*, *Juglans*, *Ilex*, *Carya*, *Parrotia*, *Buxus*, *Vitis*, *Brasenia*, *Trapa*, and *Azolla* (Janczyk-Kopikowa, 1991). Temperature reconstructions based on the indicator-species method suggest for the warmest period, the *Carpinus-Abies* phase, temperatures of 0–3 °C in January and 21–26 °C in July, which along with high precipitation created a suitable environment for the spread of rare warmth-adapted taxa (Krupiński, 1995; Hrynowiecka and Winter, 2016). Palaeotemperatures reconstructions from Dethlingen (Koutsodendris et al., 2012) suggest, however, slightly lower temperatures in Western Europe for both January (-2.2 ± 3.1 °C) and July (17.8 ± 2.1 °C).

The warm character of the Holsteinian Interglacial was also confirmed by oxygen isotope studies based on endogenic lake carbonates (Nitychoruk et al., 2005) and snail shells (Szymanek, 2018). These showed significant changes in climatic conditions throughout the Holsteinian Interglacial, during which, continental and maritime influences intertwined in the northern part of Europe. Continental influences resulted in a shortened vegetation period with long winters, while the opposite situation occurred under maritime influence, i.e. the vegetation period was significantly longer and temperatures were milder and precipitation rates higher, reflected by the appearance of stenothermal species (Nitychoruk et al., 2005).

2.3 Study area

The Krępa site (51°37’53.2’’N, 22°18’38.1’’E, 146 m amsl.) is located in SE Poland, near Kock, approximately 120 km southeast of Warsaw. In a geomorphological sense it is situated in the central-eastern part of the North European Plain behind the maximum extent of the Saalian glaciation (Marks et al., 2018). The profile analysed in this paper is situated on a moraine plateau related to this ice sheet. Holsteinian Interglacial deposits in the area were first identified by Jesionkiewicz (1982) during cartographic work for the 1:50 000 Detailed Geological Map of Poland (DGMP; Sheet 676 - Kock) (Drozd and Trzepla,

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2007). On the moraine plateau, the interglacial deposits are found under a thin cover of moraine deposits, whereas at the slopes of the nearby Wieprz River valley, they are exposed directly at the surface. This study's material was obtained from a sediment core drilled in 2015 using a Geoprobe drilling device (Górecki, 2023).

2.4 Lithological description of the Krępa sediment succession and palaeoenvironmental interpretation

In the collected 23.8 m long sediment core, there is a 2 m thick layer of massive, light gray-brown sandy clays with a large number of Scandinavian rock fragments at the base (unit 1), which is interpreted as glacial till (Fig. 2). Directly above, a 0.6 m thick layer of rhythmically laminated sandy silts and sandy-clayey silts is found (unit 2), which gradually turns into a carbonate gyttja with small interlayers of carbonatic-minerogenic gyttja (unit 3). Between 11.87 and 7.6 m core depth, non-carbonatic organic-minerogenic gyttjas with a generally increasing mineral content towards the top are found (unit 4). This gyttja sequence is overlain by a 1.9 m thick layer of massive clays (unit 5), which is followed by a 1.1 m thick layer of fine- to medium-grained sands (unit 6) and a 3.1 m thick layer of rhythmically laminated sandy silts (unit 7). The profile is capped by a 1.5 m thick layer of sandy moraine clay with Scandinavian rock fragments (unit 8).

The position of the lower glacial till (unit 1) and its petrographic characteristics (Drozd and Trzepla, 2007) indicate that it was accumulated during the Elsterian glaciation (or Sanian 2 glaciation in Poland), which is considered to correspond to MIS 12. The sediments of unit 2 are interpreted as the result of glaciolimnic sedimentation in a relatively shallow water body between blocks of dead ice during the recession of the Elsterian glacier. The glaciolimnic sediments gradually pass into limnic sediments (unit 3), which are interpreted to be deposited in the profundal of an already relatively deep lake. The limnic sediments of unit 4 are related to the gradual shallowing of the lake, associated with its significant filling with sediments. At the same time, the change towards colder climate conditions led to increased denudation and erosion in the catchment and a systematic increase in mineral components in the lake sediments. The unit 5 sediments probably represent accumulation in a periglacial lake, which was subsequently covered by proglacial sediments (units 6 and 7) of the transgressing Early Saalian (MIS 10) ice sheet and finally covered by its moraine clays (unit 8).

The origin of the sedimentary basin at Krępa is difficult to interpret. Most sites with deposits from the Holsteinian (Mazovian) Interglacial in this region of Poland are associated with tunnel valleys formed during the Elsterian (Sanian 2) glaciation (Żarski et al., 2005; Nitychoruk et al., 2006). However, these sites are usually located beyond the maximum extent of the Late Saalian glaciation (Drenthe Stage in Germany; Odra glaciation in Poland; MIS 6) and are thus subtly visible in the current terrain morphology. In the case of Krępa, the covering of these deposits by the Late Saalian (Odra) glacial advance has resulted in the complete obliteration of the post-Elsterian landscape. Based on the geological cross section prepared by the authors of the Kock DGMP sheet (Drozd and Trzepla, 2007) and the distribution of interglacial deposits in the study area (Jesionkiewicz, 1982), it can only be inferred that this depression was a relatively extensive kettle hole, formed during the transgression and recession of the Elsterian (Sanian 2) ice sheet.

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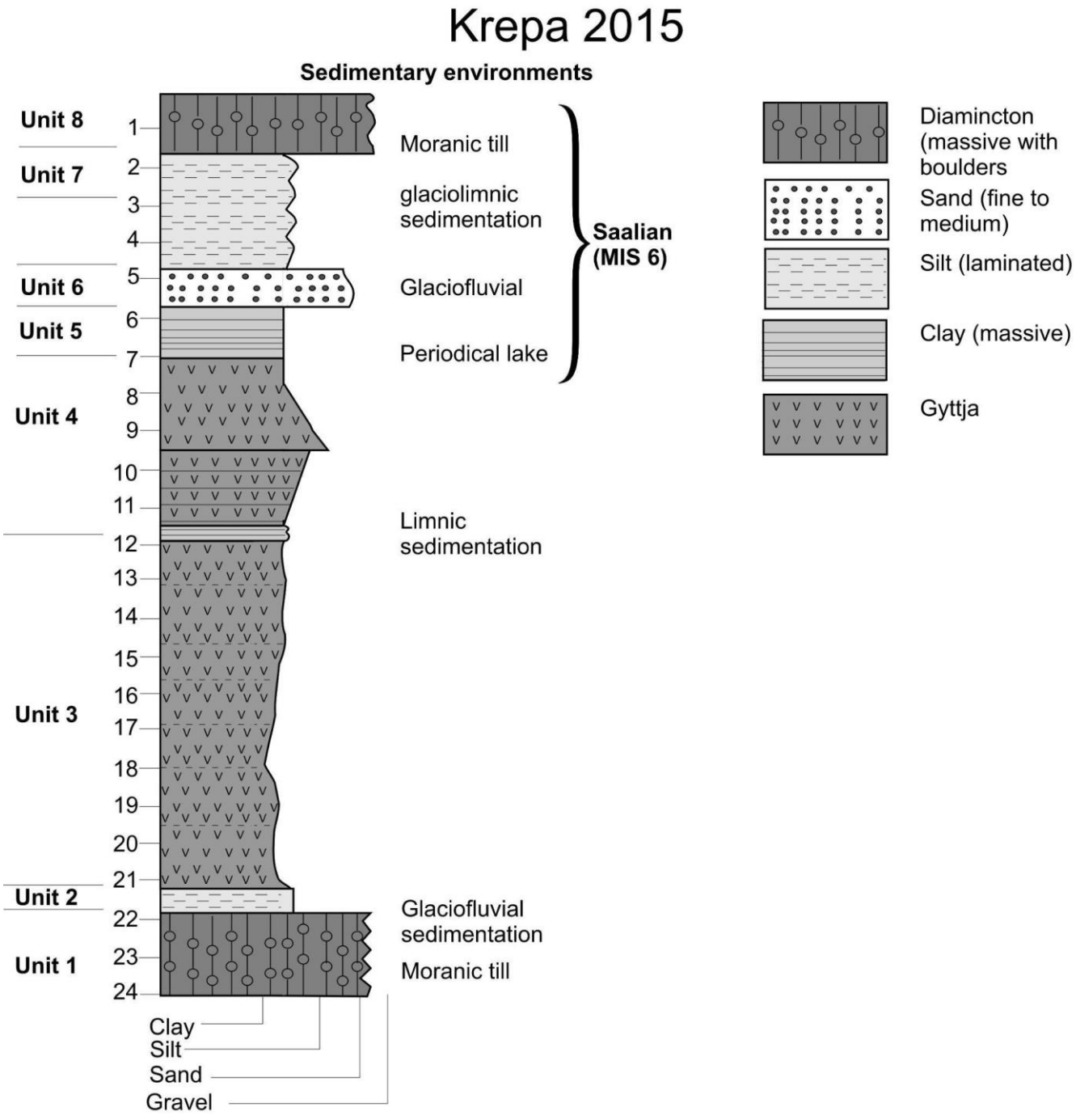

Figure 2: Krępa site lithological profile.

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2.5 Pollen analysis

Palynological samples were prepared following the standard methodology outlined by Erdtman (1960), with modifications involving the use of HF acid (Berglund and Ralska-Jasiewiczowa, 1986). Prior to laboratory processing, a *Lycopodium* indicator tablet was added to each sample to determine the absolute sporomorph concentration (Stockmarr, 1971). Pollen grains were counted using a ZEISS Axio Imager A2 light microscope. For most samples, counts were conducted up to 500 grains, including both arboreal (AP) and non-arboreal (NAP) plants. However, samples from glacial-age sediments, which were low in palynomorphs concentrations, were counted up to 300 grains. Percentages were calculated based on the sum of pollen grains from trees, shrubs (AP), herbaceous plants, and dwarf shrubs (NAP).

The outcomes of the palynological analysis are depicted in a shortened pollen diagram (Fig. 3), divided into 14 Local Pollen Assemblage Zones (LPAZ). The formation of the lake can be traced back to the end of the Elsterian (Sanian 2) glaciation, although a hiatus in the pollen record is evident at 21.10–21.15 m, possibly encompassing the entirety of Pollen Period I (*Betula* and *Betula-Pinus* phases). The Holsteinian (Mazovian) commences with the *Picea-Alnus* phase of Pollen Period II. The upper segment of the succession, starting at 13.10 m, indicates multiple cold/warm oscillations, usually connected to the Early Saalian (Liviecian) Glaciation. More elaborate descriptions regarding pollen analysis results are provided in Górecki (2023).

2.6 Chironomidae analysis

Sediment samples for chironomid analysis were taken at 5–40 cm intervals (sample volume approximately 1 cm^3). Chemical preparation methods followed Brooks et al. (2007). The precipitate was initially heated with KOH. The wet sediment was passed through 212 and 100 µm mesh sieves and subsequent residues were treated in an ultrasonic bath for 3 sec. The processed sediment were examined under a stereo binocular microscope at 25× magnification. Chironomid head capsules from each sample were picked and mounted in Euparal. Identification of chironomid head capsules followed by Wiederholm (1983), Schmid (1993), Klink and Pillot (2003), Brooks et al. (2007) and Andersen et al. (2013). Ecological preferences of identified taxa are based mainly on Brooks et al. (2007).

2.7 Mean July air temperature reconstruction

In order to reconstruct mean July air temperatures (T_{jul}) from the Krępa chironomid assemblage, the Swiss-Norwegian-Polish training set (SNP TS, Kotrys et al., 2020) was used. The training set includes 357 lakes, 134 taxa, covers a temperature range between 3.5 and 20.1 °C. and uses the weighted averaging-partial least squares transfer function (WA-PLS). The RMSEP for this combined training set is 1.39°C, and the R^2 is 0.91 (Kotrys et al., 2020). The temperature reconstruction was carried out using the C2 software (Juggins, 2007).

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222 **3. Results and interpretation**

223 **3.1 Regional and local vegetation changes during the end of Holsteinian interglacial and Early Saalian at Krępa site**

224 **Table 1: Description of local pollen assemblage zones (LPAZ) and distinguished in the sediments from the Krępa site**

225

LPAZ	Depth	Main features of Local Pollen Assemblage Zones (LPAZ)	Main features of significant in the chironomid record
KR-1	**2120-2180**	NAP values peak at >40 % (mostly Poaceae, but also *Artemisia* and *Betula nana*). Open communities are dominant. Tree pollen primarily comprises *Pinus* and *Betula* with both taxa potentially existing locally as small trees. Pollen of temperate species is sourced from redeposition.	No *Chironomidae*.
KR-2	**2027.5-2110**	Initially, a conspicuous dominance of pollen originating from pioneering arboreal species, notably *Pinus* (up to 61 %) and *Betula* (up to 38%), coupled with a negligible representation of herbaceous plant pollen, signifies the prevalence of dense birch and pine forests. Subsequently, *Picea* (up to 24%) becomes established and *Alnus* (up to 35 %) colonises areas with higher soil moisture, probably adjacent to the lake. Rising pollen values of riparian species, e.g. *Fraxinus* (3,5 %), *Ulmus* (2,5 %), and *Quercus* (4 %), suggest local presence.	No *Chironomidae*.

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KR-3	**1957.5-2027.5**	At the beginning, the percentage of *Taxus* increases sharply (<40 %), suggesting a key role in the formation of forest communities. Continued presence of riparian forests. *Corylus*, *Viburnum*, *Sambucus nigra* and thermophilic species such as *Pterocarya fraxinifolia*, *Vitis*, *Hedera helix*, *Ligustrum* and *Buxus sempervirens* appeared in the forest understorey. Despite favourable climatic conditions, high *Pinus* percentages (>40 %) persisted, suggesting that this taxon was still important in the formation of forest communities.	No *Chironomidae*.
KR-4	**1892.5-2027.5**	Rapid decline of *Taxus* forests (<5 %). *Alnus* (<25 %) and *Picea* (<30 %) regain significance in the forest communities. Contribution of riparian taxa remains low (*Fraxinus* and *Ulmus* <1,5 %). Appearance of *Carpinus*, reaching up to 7 %. Continued presence of thermophilic taxa (*Viscum*, *Pterocarya fraxinifolia*, *Vitis*, *Hedera helix*, *Ligustrum*, *Buxus sempervirens*) indicates favourable climate conditions.	One specimen of *Chironomus anthracinus-type*.

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KR-5 OHO	**1855-1892.5**	Clear change in the composition of forest communities Rapidly disappearing temperate vegetation was replaced by pioneer trees such as *Betula* (25 %) and *Pinus* (45 %). Forest communities remain a dominant element of the landscape, as suggested by the lack of an increase in NAP. Temperate species survived but at a much lower share. The clear shift in species composition suggests a much colder and drier climate compared to the previous zones.	No individuals of *Chironomidae*.
KR-6	**1697.5-1855**	This zone is associated with the dominance of *Abies* and *Carpinus* (both up to 27 %). Mixed *Abies* forests most likely occupied poorer soils, while more fertile soils were covered by deciduous forests consisting of *Carpinus*, *Quercus* (<15 %) and *Corylus* (<15 %) in the understorey. *Taxus* persists but only as an admixture (<2 %). The entire phase is characterized by the undisturbed occurrence of *Alnus*, which proves the persistence of this taxon near the lake. Similarly, no significant changes in forest density are recorded as evidenced by low NAP percentages. Abundant thermophilic taxa, including *Viscum*, *Pterocarya fraxinifolia*, *Vitis*, *Hedera helix*, *Ligustrum*, *Buxus sempervirens*, *Parrotia persica*, *Celtis*, *Carya* and *Juglans* indicate favourable climate conditions.	No *Chironomidae*.

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KR-7 YHO	**1647.5-1697.5**	This zone encompasses an apparent change in forest communities, reflected by a breakdown of *Carpinus* (to 3 %) and an increase of *Abies* (up to 34 %), *Corylus* (22 %) and *Taxus* (5 %). Mixed fir forests replaced deciduous forests at that time, while *Corylus* could be both an admixture in mixed forests and create its communities in bright places on more fertile soils. The *Carpinus* crisis probably did not last long, and it soon began to rebuild its presence. A continuous occurrence of thermophilic taxa is observed throughout the zone.	One specimen of *Glyptotendipes pallens-type*.
KR-8	**1497,5-1647.5**	As in KR-6 the two key taxa were *Abies* and *Carpinus*. Although percentages of the latter were rising to 36 %, *Abies* (up to 26 %) remained important and, in some parts, dominated over *Carpinus*. *Buxus* deserves special attention among abundant thermophilic taxa since it occurs at a greater frequency than in the previous zone. The end of the zone is associated with a decline in the percentage of *Abies*.	No *Chironomidae*.

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KR-9	**1362.5-1497.5**	A characteristic feature of this zone is the dominance of *Carpinus* (up to 44 %) and a significant decrease in the importance of *Abies* (<10 %). Mixed forests with a significant share of *Quercus* (up to 33 %) could develop in poor soils instead of *Abies* forests. Thermophilic species were the most abundant in the entire profile, especially *Pterocarya fraxinifolia* (1 %) and *Buxus sempervirens* (<2 %). Slow overgrowth of the lake is reflected by the slow decline in the proportion of aquatic plants and the decline in *Alnus* percentages. The phase ends with the decline of *Carpinus* and *Corylus* and the reappearance of *Picea*.	No *Chironomidae*.
KR-10	**1312.5-1362.5**	The beginning of the zone is marked by the slow disappearance of temperate deciduous species, including *Alnus*, *Quercus*, *Corylus*, and *Carpinus*. *Abies* gains importance again (up to 32 %), creating conifer forests together with *Picea* (up to 13 %) and *Pinus*. Thermophilic taxa are still present. The end of the zone is associated with the disappearance of *Abies*, the dominance of *Pinus* (67 %), and the appearance of *Larix* <1,5 %).	No *Chironomidae*.

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KR-11a	**1257,5-1312.5**	From this zone, the dominance of pioneer trees and herbs begins. The palynological record suggests the development of sparse *Betula* and *Pinus* forests with an admixture of *Larix* (12 %) and possibly locally occurring *Alnus* (3 %) and *Picea* (5 %). Pollen of other temperate trees originate from redeposition or long-distance transport and are not indicative of local occurrence. The high share of NAP pollen also proves the openness of forest communities in this period. A rapid change in vegetation is observed in the middle part of the phase. Open communities began to dominate the landscape (NAP <40 %), and woody vegetation was reduced to loose birch-larch tree stands that occured locally under favourable conditions. *Juniperus* (33 %) and Poaceae (23 %) had the highest share among the herbaceous plants, suggesting the presence of shrub tundra. Vast areas of open ground favour soil erosion and redeposition of older material, which in the palynological record is visible as a sudden increase in the proportion of pollen from temperate taxa. Following the dominance of herbaceous vegetation, the *Betula-Larix* forests reentered the area. The zone ends with a sudden increase in the percentage of *Pinus* pollen.	No *Chironomidae*.
KR-11b	**1222.5-1257.5**	*Pinus-Betula* forests spread within this zone with an admixture of *Larix* and *Picea*. Although forest communities dominated most of the landscape, there were still patches of herbaceous plant communities, as indicated by high NAP percentages. The zone ends with a sudden decrease in *Pinus* percentagesand an increase in the *Betula* share.	No *Chironomidae*.

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KR-11c	**1187.5-1222.5**	Initially, loose birch forests with an admixture of *Larix* and *Pinus* spread. In the middle of the zone, the landscape was further opened and likely dominated by *Juniperus* shrub tundra. The zone ends with a sharp increase in the percentage of *Pinus* and a decrease in *Betula* and NAP.	Single specimens of *Chironomus plumosus-type*.
KR-12a	**1122.5-1187.5**	At the beginning of the zone, the development of *Pinus* forests with an admixture of *Picea* (up to 6 %) is observed. Trace amounts of NAP suggest a very dense vegetation. However, percentages of *Pinus* and other tree species gradually decrease, and open herbaceous communities appear. The end of the zone is associated with a decrease in the percentage of *Pinus* pollen.	Low amounts of *Chironomidae* (approximately 15 head capsules per sample). Dominance of *Chironomus anthracinus-type* (25 %) and *Corynocera ambigua-type* (16 %).
KR-12b	**1072.5-1122.5**	A further decrease in *Pinus* pollen is observed. At the end of the zone, the landscape was likely already dominated by open communities (NAP up to 40 %) and sparse *Pinus* forests.	Dominance of *Corynocera ambigua - type* (24 %) and high contents of *Chironomus anthracinus-type*. The number of *Glyptotendipes pallens-type* and *Glyptotendipes severini-type*.
KR-12c	**1022.5-1072.5**	Initially, dense *Betula* forests with *Larix* as an admixture dominated the landscape. Subsequently, a rapid development of *Pinus* forests is observed. The end of the zone is associated with a sudden drop in the percentage of *Pinus* pollen.	The number of *Chironomidae* declines. Dominant species are *Chironomus anthracinus-type* (17 %), *Corynocera ambigua-type* (15 %) and *Glyptotendipes pallens-type* (13 %).

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KR-13a	**967.5-1022.5**	Initially, there was a significant opening in the vegetation, and herbaceous plants and shrubs dominated the landscape. In the middle section of the zone, there was a temporary return of very sparse *Pinus* and *Betula* forests, followed by another expansion of herbaceous vegetation. The end of the zone is associated with an increase in *Betula* pollen.	Significant increase in the number of *Chironomidae* (on average 450 individuals per sample). Dominant species are *Corynocera ambigua-type* (approx. 29 %) and *Chironomus anthracinus-type* (18 %).
KR-13b	**877.5-967.5**	Relatively high percentages of *Pinus* (15-48 %) and *Betula* (29-49 %) suggest the existence of sparse *Pinus-Betula* forests in the vicinity of the lake. The presence of *Betula nana* (<5 %) indicates patches of shrub tundra in the area. The end of the zone is associated with the further spread of open communities.	Unidentifiable individuals. At the end of the zone, the number increases slightly. The dominant species is *Propsilocerus lacustris*-type and single *Chironomus plumosus-type* and *Dicrotendipes nervosus-type occur. Corynocera ambigua-type* is also abundant.

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KR-14	**765-877.5**	Within this zone, open communities further expanded, likely steppes dominated by Poaceae and *Artemisia*. The vegetation also featured shrubs, such as *Juniperus* and *Betula nana*. Tree species of the *Betula* genus were present throughout the zone, and percentage variations for this taxon were low. Conversely, *Pinus* percentages considerably fluctuated. Both pioneer tree species might have formed sparse patches of forest vegetation in favourable environmental conditions.	This zone is characterized by a low abundance of *Chironomidae*. Only two individuals of *Chironomus plumosus-type* were recorded in the sediment.

3.2 Ecological reconstruction based on *Chironomidae* assemblages from the Krępa site

The description of *Chironomidae* assemblages was prepared following the Local Pollen Assemblages Zones (LPAZ) as these reflect climate change better than the chironomid assemblages. However, the low number of head capsules as well as the small species diversity made it impossible to statistically determine a good modern analogue reconstruction of *Chironomidae* zones. At the base of the sediment sequence (2120-2027.5 cm), there are no remains of *Chironomidae* preserved. The first individuals occur in LPAZ KR-4 (1892.5-2027.5 cm) and KR-7 (1647.5-1697.5 cm). In these zones, eurytopic *Chironomus anthracinus-type* in a poor state of preservation is observed (Fig. 4). There are no remains of *Chironomidae* in the following LPAZ belonging to the Holsteinian and the first single remains of head capsules of *Chironomus plumosus-type* are recorded again in LPAZ KR-11c (1187.5-1222,5 cm), which is already considered as post-Holsteinian. This species occurs in a wide range of habitats and is particularly resistant to anoxia (Brooks et al., 2007). The following LPAZ KR-12a (1122.5-1187.5 cm) is characterised by eurytopic conditions with low amounts of *Chironomidae*. Assemblages could indicate a deterioration of environmental conditions (*Chironomus anthracinus-type* and *Corynocera ambigua-type*). KR-12b (1072.5-1122.5 cm) contains mainly cold-adapted and freeze-resistant species like *Corynocera ambigua-type*, *Glyptotendipes pallens-type* and *Glyptotendipes severini-type*, which are often associated with algae and diatoms or mine leaves (Tarkowska-Kukuryk, 2014). LPAZ KR-12c (1022.5-1072.5 cm) is characterized by species highly resistant to difficult environmental conditions, i.a. *Chironomus anthracinus-type*, *Corynocera ambigua-type* and *Glyptotendipes pallens-type*. The next LPAZ KR-13a (967.5-

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1022.,5 cm) is a phase with mainly cold-adapted species such as *Corynocera ambigua-type*. During LPAZ KR-13b (877.5-967.5 cm) the number of *Chironomidae* gradually increased with indicators of progressive eutrophication (e.g. *Chironomus plumosus-type* and *Dicrotendipes nervosus-type* (Iwakuma and Yasuno, 1981)) and cold oligotrophic but post-eutrophic environments (*Corynocera ambigua-type*)(Brooks et al., 2007) occurring more frequently. During LPAZ KR-14 (765-877.5 cm) the amount of *Chironomidae* is low. Only eurytopic, warm species, which are resistant to anoxia such as *Chironomus plumosus-type* appear (Brooks et al., 2007). The disappearance of *Corynocera ambigua-type* could also be the result of large changes in oxygen concentration, reduced production of benthic algae or changes in the structure of the sediment (Brodersen and Lindegaard, 1999b).

In general, the chironomid assemblages preserved in the Krępa sediments are dominated by the two species *Corynocera ambigua-type* and *Chironomus anthracinus-type*. *Corynocera ambigua-type* is a species often described as cold-adapted oligotrophic (Fjellberg, 1972; Pinder and Reiss, 1983; Walker and Mathewes, 1988; Brooks et al., 2007; Luoto et al., 2008; van Asch et al., 2012), inhabiting shallow Arctic and subarctic regions. Adults do not fly and breed on the water surface when the temperature reaches approximately 7-8°C (optimum 13.7°C). Mothes (1968) concluded that *Corynocera* has a growth period in autumn and winter, while the eggs do not develop but only survive during summer. The decline in their numbers may be due to the growth of filamentous algae in summer. This taxon is also found in eutrophic lakes (Halkiewicz, 2008; Kotrys et al., 2020). Among others, larvae of *Corynocera ambigua-type* are eurythermic, while the pupae are cold-stenothermic (Brundin, 1949). They only reproduce at low temperatures and inhabit reservoirs with a maximum depth of approximately 25 m. The number of *Corynocera ambigua-type* has shown to correlate with the content of charophytes (Brodersen and Lindegaard, 1999b). Although charophytes are not food for this species, their presence may increase the number of diatoms and stabilize the trophic status and water clarity (Forsberg, 1965; Blindow, 1992). *Corynocera ambigua-type* species lives in dendritic tubes. Its food is diatom/algal detritus and fining of mineral grains (Fjellberg, 1972; Boubee, 1983).

The occurrence of this species has been recorded during cold episodes or glacial periods, at sites in England (Bedford et al., 2004), Norway (Velle et al., 2005), Poland (Płóciennik et al., 2015), and the Baltic region (Hofmann and Winn, 2000). However, *Corynocera ambigua-type*, cannot be considered a merely cold species. Some authors believe that it's occurrence depends on high oxygen contents in the water (Brodersen and Lindegaard, 1999a) and for some authors, it is a pioneer species that appears first after glacier retreats, just like *Chironomus anthracinus-type* (e.g. Heiri and Millet, 2005; Ilyashuk et al., 2005, 2013; Gandouin et al., 2016; Ilyashuk et al., 2022). Luoto and Sarmaja-Korjonen (2011) claim that this is how the species adapts to existing climatic conditions. The decline in *Corynocera ambigua-type* numbers could also be attributed to changes in lake productivity related to changes in the environment. For example, when the production of soil and trees increased, the number of this species has been found to decrease (Magny et al., 2006; Larocque-Tobler et al., 2009).

Since these are the only species that appear there, let us take a closer look at their occurrence and the habitat conditions in which they were recorded in modern times. *Chironomus anthracinus-type* occurs in various zones of the lake. This species is capable of surviving approximately 2-4 months of oxygen deficiency in the water (Hamburger et al., 1994). It is a species that easily inhabits niches inaccessible to other species due to difficult conditions. According to some authors, it is a eutrophic

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(Kansanen, 1985; Brodersen and Lindegaard, 1999b) or cold-adapted species (Rohrig et al., 2004; Brooks et al., 2007; Płóciennik et al., 2011). It prefers softer and more organic sediments (McGarrigle, 1980). The appearance of *Chironomus anthracinus-type* and *Glyptotendipes pallens-type* may indicate the onset of eutrophication. Both *Chironomus anthracinus-type* and *Corynocera ambigua-type* are species found in stratified lakes (e.g., Saether, 1979; Heiri, 2004). As we can see, both species can be called resistant to unfavorable environmental conditions. They have a fairly wide range of conditions in which they occur today and can even withstand long periods of anaerobic conditions in lake reservoirs.

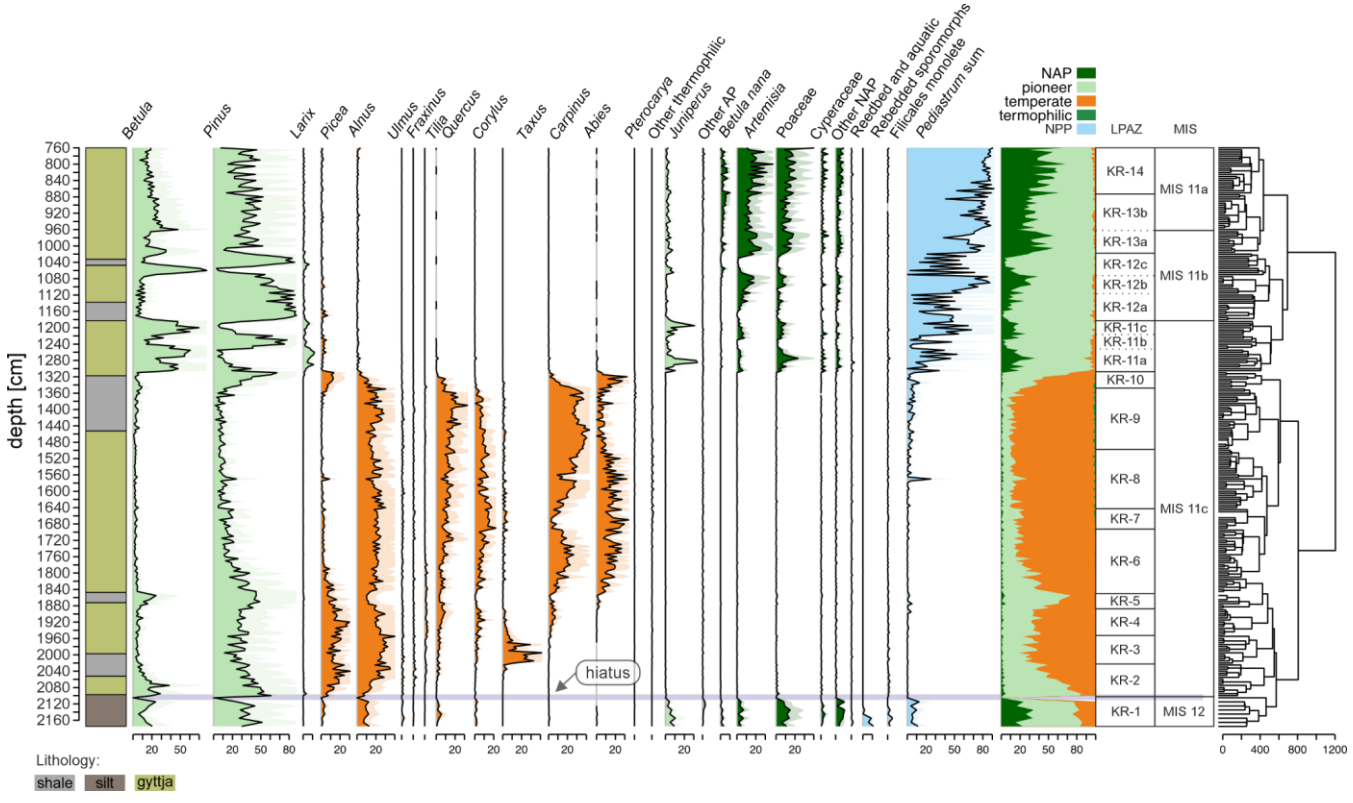

Figure 3: Percentage diagram of selected pollen, spore, and algal taxa form the Krępa site core on depth scale (cm) with zonation of the diagram.

3.3 July air temperature reconstruction based on *Chironomidae* assemblages from the Krępa site

Chironomidae subfossil larvae were obtained from a total of 30 samples from the lacustrine sediments. Samples that contained significantly fewer than 50 head capsules were merged except for a solitary sample at 1000 cm core depth. For 5 samples the required number of 50 head capsules was obtained and the remaining 24 samples were merged into seven clusters. After

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merging, sample clusters at 975 cm, 1080 cm, 1120 cm and 1125 cm core depth still did not reach 50 head capsules, but nonetheless, these samples and the one from 1000 cm core depth were included in the reconstruction because the test of the reconstruction showed acceptable results. The lowest number of head capsules used for the T_{jul} reconstruction was 5 individuals at 1070 cm core depth whereas the highest number was 78 at 985 cm core depth. After merging, the total number of samples used for the T_{jul} reconstruction was 15.

Due to the low number of chironomid head capsules preserved in the Krępa sediments, a chironomid-based summer temperature reconstruction was only possible for the uppermost part of the sediment core, encompassing the post-Holsteinian MIS 11b stadial (Tab. 2). In LPAZ KR-12a (1122.5-1187.5 cm), which marks the onset of MIS 11b that directly follows the Holsteinian Interglacial, average summer temperatures still ranged between 17 and 19 °C before shortly dropping to about 16 °C and increasing again to 18-20 °C in LPAZ KR-12b (1072.5-1122.5 cm). Summer temperatures remained at this level in LPAZ KR-12c (1022.5-1072.5 cm) before significantly dropping to 15-17 °C in the middle of LPAZ KR-13a (967.5-1022.5 cm). Only at the end of LPAZ KR-13a (967.5-1022,5 cm), which is equivalent to the transition to the MIS 11a interstadial, summer temperatures markedly increased again to about 20 °C.

Table 2: Chironomid-based summer air temperature reconstruction from the Krępa site with reconstructed mean July air temperature (Tjul), error of the estimated Tjul, minimum dissimilarity between core and training set samples (MinDC) and corresponding LPAZ

Core depth (cm)	T_{jul}	error of est. (T_{jul})	MinDC	LPAZ
969	20.09	1.59	9.8283	KR-13a
975	15.26	1.62	6.08105	
980	16.82	1.55	7.89471	
985	17.23	1.57	8.37351	
990	15.93	1.68	7.35685	
995	15.83	1.71	6.77137	
1000	18.76	1.50	8.2743	
1011	18.09	1.60	7.90763	
1022	19.24	1.49	7.06444	KR-12c
1080	18.76	1.48	6.7485	KR-12b
1102	19.24	1.54	9.04927	
1120	18.80	1.53	5.99662	
1125	16.05	1.59	7.31879	
1122	17.08	1.50	8.29472	KR-12a
1148	19.13	1.54	7.16015	

According to the SNP TS reconstruction, 13 samples with good modern analogues remain below the 5% percentile threshold (minDC), while 2 samples with average modern analogues have values above the 5% percentile threshold (8.5053 < minDC > 9.7531).

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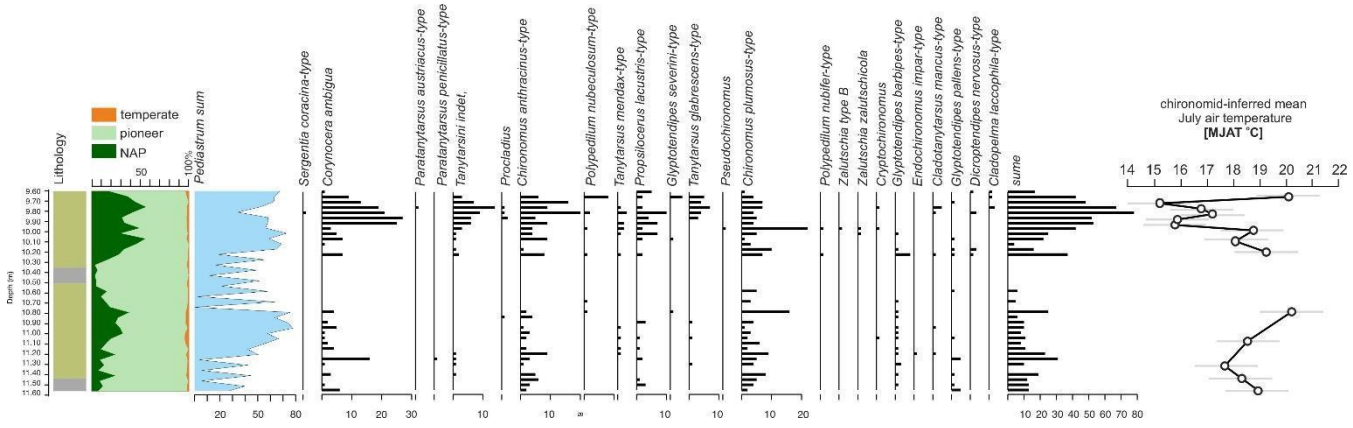

Figure 4: Chironomid-inferred mean July temperature reconstruction from Krępa site.

4. Discussion

4.1 *Chironomidae* analysis as a method of palaeoclimate reconstruction

The analysis of subfossil *Chironomidae* is part of the palaeoecological analysis and an important element of geological, geomorphological, and archaeological research. *Chironomidae* are insects belonging to the order of Nematocera. They are common and inhabit aquatic environments, from moist soil to lakes. Their development cycle can last from 20 days to several years, because they can extend the duration of the larval stage depending on environmental conditions (Butler, 1982). Thanks to the ability of the head capsule to preserve in the lake and peat bog sediment for several hundred thousand years, it is possible to reconstruct the diversity of the environment in the past centuries. On the basis of *Chironomidae*, it is possible to reconstruct the average July palaeotemperature quantitatively, the trophy of the reservoir, and qualitatively the type and dynamics of the reservoir, water pH, and microhabitats. Training sets were also created to reconstruct the water level, salinity or oxygen content (Lotter et al., 1997).

4.1.1 Possible difficulties in climate reconstruction based on *Chironomidae* analysis during past interglacials

The basic principle of palaeoecological reconstructions is geological actuality (Krzeminski and Jarzembowski, 1999). The processes taking place on Earth in the past had the same course as today. This makes it possible to reconstruct the temperature based on the *Chironomidae*. In palaeoreconstructions, we assume that a given species from the *Chironomidae* family still has the same habitat requirements as thousands or hundred thousands of years ago. The oldest recorded Chironomid remains date back to the Late Triassic, i.e. 202 ± 1 Ma BP (Krzeminski and Jarzembowski, 1999). Data from Krępa and preliminary observations from the Holstein Interglacial site of Ossówka (Fig. 1), indicate a big difference in the number and state of preservation of the remains compared to Holocene sites. The worst condition of the remains was in the sediments from the

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Ossówka site. A number of 50 individuals is required to create a reconstruction of the average July temperature. With a smaller amount, the error range is larger, therefore the higher the number of counts, the more stable the result. With a small number of head capsules, it is recommended to smooth the reconstruction of temperatures down the core, i.e. to combine adjacent samples (Heiri and Lotter, 2001). In order to be able to select subsequent sites that have the potential to reconstruct the palaeoenvironment, it is worth analysing the factors that could limit the degree of preservation of the remains or cause the disappearance or decrease in the number of individuals. Paleolake Krępa is a site that provides us with reliable and credible reconstructions in the late Vistulian. However, the question remains why the older sediment does not allow us to obtain quantitative and qualitative results from the analysis of subfossil Chironomidae. In order to get closer to the answer, we analyze situations that are rarely discussed in the literature, i.e. the absence, disappearance or sudden decline of Chironomidae in the sediment. We also analyze the most difficult conditions in which various species of Chironomidae occur. We look for conditions that could differ from those still accepted today by the Chironomidae community.

Chironomidae inhabit all moist or aquatic habitats from moist wood to the ocean, ranging from the tropic climate zone to the Arctic climate zone. The high specialisation of individual species of *Chironomidae* decided about such a common occurrence and the ability to survive difficult conditions. Among the features that allowed the family to succeed are: a short life cycle (in some cases only 8 days) (Reyes-Maldonado et al., 2021), osmoregulation enabling survival of high salinity of the reservoir (Kokkinn, 1986) or parthenogenesis giving high efficiency of population reproduction, faster colonisation rate and high fertility (Lencioni, 2004; Nondula et al., 2004; Donato and Paggi, 2008; Orel and Semenchenko, 2019; Lackmann et al., 2020), as well as a short DNA chain and the ability to repair the genome, which reduces the accumulation of harmful mutations (Gusev et al., 2010; Cornette et al., 2015). Some species of *Chironomidae* are able to change the food resources they use depending on their availability in the habitat (Tokeshi, 1995; Davis et al., 2003). Large reservoirs have a greater variety of habitats and thus more diverse communities of *Chironomidae* (Allen et al., 1999; Heino, 2000; Tarr et al., 2005), attract a more migratory population (J. Baber et al., 2004; Tarr et al., 2005) and they are more resilient to extreme droughts and other extreme events. Isolated, highly remote habitats reduce species diversity and dispersal (Roberts, 2003).

Despite the specialisation of *Chironomidae*, there are many conditions in the environment that limit the number of communities. One of the main factors limiting and determining the life processes of *Chironomidae* is temperature. Each life stage of the *Chironomidae* is dependent on this factor. The development of eggs, larvae and pupae, nutrition and growth, the emergence of individuals or the ability to fly have their temperature maxima and minima, beyond which the given processes no longer take place. In sub-zero temperatures, when the tank freezes, most groups can tolerate low sub-zero temperatures. The temperature below which the development of most species does not occur is -15°C (Walker and Mathewes, 1989; Płóciennik, 2005). Frost tolerance is the highest in the Orthocladinae family and the lowest in the Tanypodinae (Danks, 1971). Some species stop eating and empty their intestines for the winter. There are larvae in which feeding continues, and the temperature only affects the occurrence of pupation. There are species (e.g. *Einfeldia synchrona-type*) that burrow deeper in winter, penetrating deeper layers of silt. Early developmental stages of larvae often do not occur in winter. Another protective mechanism against freezing is the production of cocoons or sealing the tube (Danks, 1971).

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Another factor strongly limiting the number of *Chironomidae* is low - acidic pH. Below 6.0, most *Chironomidae* taxa are eliminated and replaced by *Chaboridae* and *Ceratpogonidae* (Henrikson et al., 1982; Walker et al., 1985; Walker, 2001; Brooks et al., 2007). Only a few species can withstand pH as low as 1.4, such as *Chironomus sulfurosus-type*, *Chironomus acerbiphilus-type* or *Polypedilum tamanigrum-type* (Takagi et al., 2005; Doi et al., 2007).

The factor causing the decline of the population is the lack of oxygen in the water. However, it is not possible to see this in palaeoreconstruction. The only thing that can indicate in the palaeo-record are remains and a large accumulation of organic matter. An increase in organic matter can increase the amount of bacterial respiration, causing oxygen deficiency in the deep zone (Charlton, 1980; Matzinger et al., 2010; Müller et al., 2012). One of the species resistant to oxygen deficiency is, for example, *Sergentia coracina-type*, which disappears after the concentration decreases to the level of 2.7 mg L-1 (Quinlan and Smol, 2001) and <4 mg L-1 (Luoto and Salonen, 2010). Oxygen deficiency can also be caused by freezing of the lake, as a result of which it is cut off from atmospheric oxygen (Pechlaner, 1966; Welch, 1991). Also, freezing can reduce the amount of calcite and the manganese to iron ratio, which may indicate an increase in decomposition processes at the bottom of the reservoir (Koinig et al., 2003). These changes may be caused by morphological factors (Aeschbach-Hertig et al., 1999) and thermal stratification (Jankowski et al., 2006) or the supply of biogenic elements: nitrogen and phosphorus (Rabalais et al., 2010; Frossard et al., 2013; Belle et al., 2016).

The abundance of *Chironomidae* and their dispersal is limited by the poor ability to select a flight site and lay eggs. The *Chironomidae* larvae only has the ability to disperse around the reservoir and select the substrate for life. This dispersal is often done passively by water currents, by phototaxis or by the ability to feed on plankton. *Chironomidae* larvae have the ability to rheotaxis, which allows for quick and effective colonisation of environments (Davies, 1976).

Another factor limiting the behaviour of *Chironomidae* in the sediment are mechanical factors that cause damage to the head capsule. Tanypodinae remains, due to their large size, are not very resistant to disintegration and the number of preserved capsules may be smaller (Walker et al., 1984). It is also debated how resistant the head capsule arising from the periodic shedding of the *Chironomidae* exoskeleton produced by ecdysis and the larvae that are buried and tanning in the sediment (Walker, 1987). Only remains from the 3rd and 4th larval stages are preserved in the sediments. This is most likely due to the increased amount of chitin in these developmental stages, which makes the remains more resistant to further disintegration. The capsules preserved in the sediment come from the habitats of living larvae (Iovino, 1975). The remains of *Chironomidae* may not be preserved in the sediment because there was a low accumulation rate, while those from the shore habitats could be poorly preserved. However, most studies confirm the positive relationship between biocenosis and thanatocoenosis (Iovino, 1975; Walker et al., 1984). The number of generations per year may also affect the abundance of *Chironomidae*, multivoltine species being overrepresented to bivoltine.

The physicochemical properties of water are also a factor causing changes in chironomid communities. For example, a reduction in the number of chironomids may be caused by floods and heavy rainfall. Floods cause for example pollution, surface runoff, lowering of pH and/or instability and rolling of the substrate (Teristiandi, 2021). A decrease in the water level also leads to the disappearance of chironomid larvae with a subsequent changes in the groupings from lacustrine to semi-

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terrestrial and terrestrial communities (Płóciennik et al., 2015, 2020) and droughts may cause the extinction of larvae (Buck, 1965; Berglund and Digerfeldt, 1970; Delettre, 1988; Jackson and Mclachlan, 1991; Rohrig et al., 2004). The chemical properties of water, such as increased concentrations of aluminium and other metals (Bitusik and Kubovcik, 2000), or Fe, NH4+ compounds also have an impact on chironomid communities (De Haas et al., 2006). A less significant impact is also reported for interspecific and intraspecific competition and predation (Davis et al., 2003; Roberts, 2003) or fish predation (Goyke and Hershey, 1992; Rieradevall and Roca, 1995; Mousavi et al., 2003; Milardi et al., 2016; Sayer et al., 2016).

The main factor influencing the preservation of the remains is the content of CaCO3 in the soil and the bottom of the reservoir, especially in medium and strongly acidified reservoirs. This factor is often more important than pH, depth or time deposition of remains (Bailey et al., 2005). The microenvironment and the presence of organic matter are of great importance for the preservation of remains (Briggs and Kear, 1993; Sageman and Hollander, 1999). The faster mineralization occurs, the better the preservation of the remains (Briggs and Kear, 1993; Park, 1995). Moist and anaerobic environments such as ditches, peat bogs or cold or desert conditions are more favourable (Speight, 1974; Huchet, 2014). Clay is a better environment for preserving remains than water. Clay has tanning properties, catalyses the cross-linking of proteins. It also protects the remains from bacterial degradation. Kaolinites are a component conducive to the preservation of remains, they can facilitate preservation and accelerate mineralization. Mineralization is also favoured by the fine grain size of the sludge, the solubility of its components in organic acids with hypoxia or low dissolved oxygen, and the content of minerals: Fe, Al or Cr (Naimark et al., 2016). The main factors of decay are physical factors (such as pressure) or biological factors including bacteria and fungi (Speight, 1974; Huchet, 2014).

In our preliminary tests, we did not use chemicals and we soaked the samples for a long time to eliminate as much mechanical damage to the head capsules as possible during the sieving of the samples. Nevertheless, from some sites, whole head capsules have not been preserved, which could have been caused by high pressure and compression of the sediment. A small number of head capsules may be a difficulty at the stage of material. This necessitates summing up the samples and increasing the volume of the analyzed samples (some of the samples were even 20 cm3 in volume). Difficulties arising at the preparation stage also include the lack of continuity in the occurrence of *Chironomidae* and their low frequency in the sediment.

The factors reducing the abundance are: extreme temperatures, low nutrient levels, adverse geomorphology, or following large storm events, acidic water pH, or high Se concentration (Mousavi, 2002; Gresens et al., 2007; Del Wayne et al., 2018). The content of hydrogen sulphide during holomixis, above 0.3 ppm, may also contribute to the death of *Chironomidae*. *Chironomidae* do not occur, as well as during paludification in the lake (Takagi et al., 2005; Płóciennik et al., 2020).

The lack of oxygen in the sediment could have limited not only the number of *Chironomidae* but also the number of preserved head capsules in the sediment. Chitin usually does not accumulate in anaerobic sediments because it is more easily broken down by Fibrobacteria. Chitin was effectively mineralized into CH4 and CO2 (Wörner and Pester, 2019).

In the researched core, we have interruptions in the preservation of the head capsules. The sediment indicates that the lake was functional, but Chironomidae head capsules are not recorded. Based on the literature and our results, we are currently only able to exclude factors that do not affect the degree of preservation of the Chironomidae heads. In fact, in some periods, no

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parts of *Chironomidae* or chitinous insect parts or macroremains were visible in the samples, suggesting a lack of preservation of the remains. One of the hypotheses could be that chitin was mineralized from the head capsule and changed the contain of carbon in the sediment. It is especially possible with the lack of cellulose remains of plants too. However, further extended research on Pleistocene sediments is needed to discover which environmental factor caused the lack of capsules.

4.1.2 Summer temperature and ecological reconstructions based on Chironomids from the Krępa site in relation to environmental change

A chironomid-based summer temperature reconstruction was only possible for the part of the Krępa sediment core that corresponds to LPAZ KR-12 and early KR-13, which most probably correspond to MIS 11b. July temperatures during the early part of this interval (LPAZ KR-12a and KR-12b), i.e. directly after the Holsteinian Interglacial, were most probably still relatively high and stable, ranging from 19 to 21 °C, but dropping rapidly in LPAZ KR-12c and KR-13a to 15-17 °C before increasing again to about 20 °C at the top of LPAZ KR-13a, possibly reflecting the transition into the post-Holsteinian interstadial that corresponds to MIS 11a. These data indicate that summer temperature maximum during the post-Holsteinian period was even slightly higher than indicated in the Polish training set (17-20°C)(Kotrys et al., 2020). On the other hand, there were periods with colder summers than today (15°C). Comparing MIS 11 to the Holocene, it is crucial to mention that insolation patterns for those periods differ - MIS 11 is characterised by two insolation maxima, whereas there is one (but more distinct) during the latter period (Rohling et al., 2010). In fact, summer temperature increase during MIS 11b might be explained by increasing insolation rate at the time.

In general, *Chironomidae* remains in the Krępa sediment core occur mostly during cool periods. For example, in the interglacial part of the profile isolated remains can only be found in LPAZ KR-4 that precedes the OHO and in LPAZ KR-7 that corresponds to the YHO. The most abundant *Chironomidae* record is present in the part relating to LPAZ KR-12. This zone is thought to roughly correspond to MIS 11b, which is considered the first colder phase of MIS 11 (Imbrie et al., 1984; Fawcett et al., 2011) encompassing the transition into the glacial period that corresponds to MIS 10. The pollen record during LPAZ KR-12a suggests the presence of a *Pinus*-dominated forest, possibly still with a small admixture of *Picea*, which might indicate more humid conditions, but not necessarily a warmer climate (Caudullo et al., 2016). In the pollen record, cold periods like LPAZ KR-12b and KR-13a are characterized by rapid increases in NAP, which suggests the decline of forests. The *Pediastrum* remains, especially abundant during these phases, were identified as *P. kawraiskyi*, a species which, according to Jankovská and Komárek (2000), usually dominates the algal communities found in the cool phases of the Pleistocene, Late Glacial, and Early Holocene in Europe. The Krępa palaeolake during LPAZ KR-12b was possibly an oligotrophic lake surrounded by open vegetation. Considering the dominance of herbs and dwarf shrubs in the pollen spectrum, the limiting factor for the development of forest communities was more likely connected to low winter temperatures as summer temperatures were still relatively high.

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LPAZ KR-12c begins with the formation of pioneer *Betula-Larix* forests. Initially, the forests were sparse and shrub tundra communities were still present in the area as indicated by *Juniperus* and *Betula nana* pollen. In the following, vegetation gradually changed into dense *Pinus*-dominated forests. *Chironomidae* are absent during this interval, in agreement with our observation that their presence is rather restricted to colder periods. They only re-appear during the final stage of MIS 11b, which is represented by LPAZ KR-13a. The apparently rather gradual cooling during LPAZ KR-13a possibly still enabled the presence of sparse *Betula* forests at the beginning of the phase. This is in agreement with reconstructed summer temperatures of about 19°C, similar to the end of LPAZ KR-12b. The following rapid cooling is reflected by the dominance of NAP in LPAZ KR-13a after the decline of *Betula*. Summer temperatures during this period reached only 15°C, but the limiting factor for vegetation development still remained the winter temperatures. At the end of LPAZ KR-13a, another increase in temperature is observed, which might be connected to the warming at the onset of the following interstadial, being equivalent to MIS 11a. As the pollen record during stadials is mostly controlled by wind-pollinated overproducers such as Poaceae and the long-distance transport of tree pollen (mostly *Pinus*), it is unfortunately not possible to directly connect temperature changes to the occurrence of specific plant taxa.

In general, the results from Krępa are really difficult to compare because chironomid-based temperature reconstructions from Europe are so far mostly restricted to the Weichselian Late Glacial and the Holocene (Gandouin et al., 2016; Nazarova et al., 2018; Druzhinina et al., 2020). In contrast, there are only very few chironomid-based summer temperature reconstructions for the Late and Middle Pleistocene prior to 20 ka BP available (Gandouin et al., 2007; Samartin et al., 2016; Plikk et al., 2019; Ilyashuk et al., 2020; Bolland et al., 2021; Rigterink et al., 2024), but so far none for MIS 11 complex. However, these records are characterised by higher abundance and species diversity of *Chironomidae*, while at Krępa *Chironomidae* occur only during the early glacial period following the Holsteinian Interglacial. A similar phenomenon has so far only been observed in the Laptev Sea region (Arctic Siberia), where *Chironomidae* also appear only in the cold period of the Eemian Interglacial, when the site was surrounded by wet grass-sedge shrub tundra, while *Chironomidae* were absent during the warm period (Andreev et al., 2004). The lack of accurate absolute dating for terrestrial sediment sequences from the Holsteinian Interglacial makes it difficult to compare the results from Krępa to other MIS 11 sites. However, as there are a few quantitative temperature reconstructions based on pollen and biomarkers from other sites in Europe available for the post-Holsteinian, a general comparison of temperature levels during this interval seems feasible. It is worth mentioning that a few palaeotemperature reconstructions based on proxies has been conducted, e.g. in SW Europe - Iberian margin (Oliveira et al., 2016). Pollen analysis from this site shows similar climatic and ecological patterns for MIS 11b as observed in Krępa site - forest decline events and relatively high temperature levels. This also seems to be confirmed by palynological data from the SE Europe site - Lake Ohrid (Kousis et al., 2018). Convergence of data from different parts of the continent increases potential plausibility of palaereconstruction from Krępa.

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Conclusion

The reconstruction from the available section has mainly good modern analogues, which means that *Chironomidae* are a good proxy for temperature reconstruction also for the Pleistocene epoch. They are an environmental indicator. There is a great need for further research to better understand the factors limiting the functioning and preservation of *Chironomidae* in the Pleistocene. Up to date, the vast majority of palaeoenvironmental studies relies on pollen analysis. Nevertheless, this does not prejudge the lack or low abundance of Chironomid-inferred reconstruction in sites other than Holocenian. More than that, they might prove to be a priceless source of knowledge, considering potential differences between pollen and Chironomid-inferred records. By comparing the results from different sites, it will be possible to find the factor that influenced the preservation of subfossil remains of *Chironomidae*.

Further study of *Chironomidae* from the Pleistocene will allow us to trace climate changes without human influence. This will enable us to learn about the natural processes of global warming, the factors causing them, and the variability and specialisation of species.

To summarize our results, the subfossil remains occur abundantly only in non-calcareous gyttja - while investigating Holocene sites, it can be found in most lake sediment types. In contrast to Holocene sediment records, which are usually characterised by a high abundance and diversity of *Chironomidae* (Engels et al., 2020), the Holsteinian Interglacial sediments from Krępa reveal only a low number of *Chironomidae*, while they are more abundant/better preserved during the transition into the following glacial period.

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Authors contribution

TP analyzed the Chironomid data, proposed the idea of the main text, constructed the manuscript, and contributed to the figures. TP and AGr wrote the original draft version of the manuscript. BK performed the Chironomid-inferred summer temperature reconstruction. MŻ collected the core in the field. TP, AGr, AG, SL, and MS analyzed the pollen and chironomid data. TP, AGr, AG, MB, MS did the visualizations (graphs and maps). AG, AH, MŻ, MB, JN, MC, SL, MS reviewed the paper. All authors have made substantial contributions to the submission of this manuscript.

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Competing interests

The authors declare that they have no conflict of interest.

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