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New ^{14}C data of megafaunal remains from Lithuania – implications for the palaeoenvironmental interpretation of the Middle Weichselian

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Palaeobiological data, supplemented by new ^{14}C dates in conjunction with palaeobotanical and lithological information, have allowed reconstruction of Middle Weichselian (MIS 3) environmental fluctuations in the southern Eastern Baltic region. Palaeoenvironmental reconstructions implying non-glacial conditions during the Middle Weichselian (MIS 3) are supported by the spatial and temporal context of recently discovered remains of *Mammuthus primigenius* Blumenbach and *Rangifer tarandus* Linnaeus, 1758. Recording both cold and warm climatic reversals of MIS 3, representatives of the megafauna thrived in an environment characterized by a heterogeneity of vegetation and climate. ^{14}C dating shows that the majority of the megafaunal remains analysed represent the 38–45 cal kyr BP time-interval, which correlates with the Nemunas 2c cold interval (cryomer), and the 31–34 cal kyr BP or Mickūnai 3 thermomer. From pollen data, the palaeovegetation pattern varied from tree-less tundra to birch-predominating forest with an admixture of temporal tree species providing additional information about the diet and habitat preferences of these herbivores in the context of the MIS 3 climatic events.

Key words: *Mammuthus primigenius* Blumenbach, *Rangifer tarandus* Linnaeus, 1758, ^{14}C, environmental dynamics, Middle Weichselian, Lithuania.

INTRODUCTION

Many multi-proxy studies demonstrate that the Middle Weichselian may be described as a multifaceted time that included intervals of cold and warm climate characterized by changing palaeoenvironmental situations across extensive regions of the European continent (Ganopolski and Rahmstorf, 2001; Svendsen et al., 2004; Sánchez Goñi et al., 2008). In general, the transition from the Early to the Middle Weichselian and the Middle Weichselian itself (OIS 4–3) are the most problematic and disputed time intervals of the Late Pleistocene. So far, the most pronounced variations in the Middle Weichselian palaeoclimatic and palaeoenvironmental regime have been recorded in regions which were later influenced directly by the last Scandinavian Ice Sheet (SIS) (Bitinas, 2011; Lasberg, 2014). Thus, the southeastern Baltic territory, covered by SIS during the later stages of the Quaternary Period, demonstrates great potential for reconstructing the environmental dynamics of the Middle Weichselian in this part of Europe.

The spatial extent and chronology of the Middle Weichselian glacial advances (Lunkka et al., 2001; Mangerud, 2004; Marks, 2004, 2012; Kalm, 2006; Satkūnas et al., 2009), along with the character of palaeoenvironmental changes noted at the OIS 5–OIS 4 transition, are especially contentious in the Eastern Baltic and neighbouring territories. For instance, evidence of an early Middle Weichselian glacial event (OIS 4) was recorded in the central part of the Fennoscandian Ice Sheet (Hitura pit, Ostrobothnia) (Salonen et al., 2008). It is thought that the entirely ice-free Early Weichselian (79 cal kyr BP) was

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followed by a climatic deterioration during OIS 4 in the area. The subsequent deglaciation was dated to 55–62 cal kyr BP (Salonen et al., 2008). The sedimentary succession at Ruunaa indicates a Middle Weichselian glacial event before 52 cal kyr BP and an ice-free interval between 25–50 cal kyr BP in Eastern Finland (Lunkka et al., 2008). Zelčs and Markots (2004) proposed possible early Middle Weichselian glaciation in western Latvia (the so-called "Talsi Stadial") between 59 and 74 cal kyr BP Later, the "Talsi Stadial" was placed between 54–68 cal kyr BP (Zelčs et al., 2011). In west Lithuania, a till bed 5.5 m thick was recognized between two sandy successions of marine origin that were dated by the optically stimulated luminescence (OSL) method. The overlying sandy bed was dated between 43.7 ±4.0 and 48.8 ±6.2 cal kyr BP and the underlying one to 83.6 ±6.7–113.1 ±8.5 cal kyr BP (Damušytė et al., 2011). This till bed may be correlated with the Schalkholz (Nemunas 2a) stadial, geochronologically located between 59–74 cal kyr BP (Satkūnas and Grigienė, 2012). Estonia was ice-free at least between 26.8–43.2 cal kyr BP, according to ^{14}C and OSL data (Kalm, 2006). The inferred time interval of the early Middle Weichselian glaciation was placed between 44–68 cal kyr BP in Estonia (Kalm et al., 2011). In summary, glacial deposits attributed to the Middle Weichselian have been reported from southern Finland (Nenonen, 1995), Estonia (Liivrand, 1991), Poland (Marks, 2004, 2012), Denmark (Houmark-Nielsen, 2004, 2011) and west Lithuania (Damušytė et al., 2011).

However, these glacial episodes are challenged by data that suggest ice-free and warm conditions across the major part of eastern Fennoscandia in early MIS 3, i.e. around 53 cal kyr BP (Helmens and Engels, 2010). ^{14}C dates of biological material suggest that there was a large ice-free area in Fennoscandia during the Middle Weichselian, from ~44 to ~22.5 cal kyr BP (Ukkonen et al., 1999, 2007). Furthermore, there is an increasing number of palaeoclimatological, lithological, biostratigraphical, physical, and other datasets indicating ice-free conditions during the entire Middle Weichselian in the Eastern Baltic (Molodkov et al., 2007, 2010; Satkūnas et al., 2009; Rattas et al., 2010; Saks et al., 2012; Lasberg, 2014; Lamsters et al., 2017). Alongside the geological, lithological, isotopic and other data, the remains of terrestrial megafauna serve as a valuable proxy for both qualitative and quantitative reconstructions of the palaeoenvironmental situation, including the glaciation history, during the pre-LGM in this part of Europe (Stuart et al., 2002, 2004; Arppe and Karhu, 2010; Ukkonen et al., 2011; Arppe et al., 2011; Stuart and Lister, 2012). As none of the previous investigations conducted in Lithuania have provided integrated analysis of palaeobiological, sedimentological, palaeobotanical and isotopic (^{14}C) data required for palaeoenvironmental reconstruction of the Middle Weichselian, our publication encompasses:

- interpretation of new ^{14}C data of megafaunal remains in the palaeoenvironmental context of the Middle Weichselian;
- relating the changes identified to regional and global climate fluctuations.

CHRONOSTRATIGRAPHIC SETTING

Geological records of Early-Middle Weichselian (OIS 5a-2) age, including fluvial, limnic, and biogenic deposits, have been discovered in the SE Baltic region (Table 1) (Gaigalas, 1997; Molodkov et al., 2007; Rattas et al., 2010; Saks et al., 2012; Lamsters et al., 2017), including in Lithuania (Fig. 1 and Table 2). Two sedimentary sequences, at Jonionys and Mickūnai (Fig. 1, Nos. 23 and 25) have been indicated as stratotypes for constructing the chronostratigraphic scheme of the Early-Middle Weichselian in Lithuania (Satkūnas and Grigienė, 2012). These sedimentary sequences, providing comprehensive palaeoenvironmental information, are interpreted as having formed in shallow palaeolakes or lacustrine systems. Based on lithological and palaeobotanical records as well as OSL and ^{14}C data, the sequences analysed have been tentatively subdivided into thermomers (periods with relatively warm climate) and cryomers (time intervals with a colder climatic regime) (Satkūnas and Grigienė, 2012). Altogether, six thermomers and six cryomers named after the Mickūnai and Jonionys stratotypes determine the chronostratigraphy of the Early-Middle Weichselian in the area (Table 2). Mickūnai 3, Jonionys 3, and Jonionys 2 have been correlated with biostratigraphic units identified in Central Europe (Behre, 1989) while others represent the Eastern Baltic region exclusively (Satkūnas and Grigienė, 2012).

PALAEOBOTANICAL AND PALAEOCLIMATIC INSIGHTS

Pollen and plant macrofossils are the principal sources for discussion of the palaeoenvironmental and palaeoclimatic dy-

Table 1

Early-Middle Weichselian sites revealing periods of ice-free conditions in the Baltic and adjacent areas

Site, region	Chronological interval [cal kyr BP]	Reference
Kileshino, Valdaj Upland, Russia	72–34	Lasberg (2014)
Ruunaa, E Finland	50–25	Lunkka et al. (2008)
Voka, NE Estonia	35–32	Molodkov et al. (2007)
Arumetsa, SW Estonia	44–37	Rattas et al. (2010)
Estonia	43–27	Kalm (2006)
W Latvia	52–25	Saks et al. (2012)
Central Latvia	117–24 (Early and Middle Weichselian)	Lamsters et al. (2017)
Šventoji, W Lithuania	49–44	Damušytė et al. (2011)
Rokai, C Lithuania	63–32	Gaigalas and Hütt (1996)
Svirkančiai, NW Lithuania	55–33	Satkūnas et al. (2013)

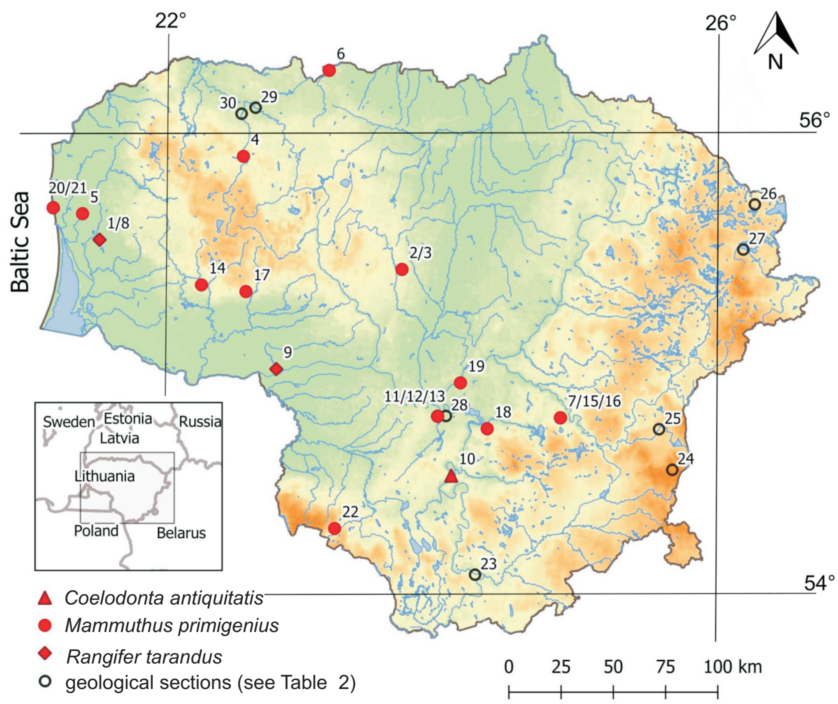

Fig. 1. Distribution of the dated megafaunal specimens and geological sites

Table 2

Geological type localities of MIS 3 age in Lithuania

No.	Locality	Coordinates (WGS)	Stratigraphic unit and chronological interval	References
23	Jonionys	54.158998; 24.117563	Early–Middle Weichselian 117–24 cal kyr BP	Kondratienė (1996), Satkūnas et al. (1998)
24	Medininkai	54.550405; 25.619771	Early–Middle Weichselian 117–24 cal kyr BP	Satkūnas et al. (2003)
25	Mickūnai	54.728446; 25.545516	Middle Weichselian 74–24 cal kyr BP	Satkūnas and Grigienė (2012)
26	Smalvos	55.654882; 26.406353	Middle Weichselian 74–24 cal kyr BP	Satkūnas et al. (1997)
27	Dysnai	55.466665; 26.287875	Middle Weichselian 74–24 cal kyr BP	Satkūnas et al. (1997)
28	Rokai	54.847241; 23.934653	Middle Weichselian 74–24 cal kyr BP	Gaigalas and Hütt (1996)
29	Purviai	56.204287; 22.63904	Middle Weichselian 74–24 cal kyr BP	Satkūnas et al. (2009)
30	Svirkančiai	56.180625; 22.529325	Early–Middle Weichselian 117–24 cal kyr BP	Satkūnas et al. (2013)

namics of the Late Pleistocene in the area (Kondratienė, 1996; Satkūnas et al., 1998, 2003, 2009, 2013; Satkūnas and Grigienė, 2012). The published data enable a brief overview (Table 3).

Existing biostratigraphical records (Kondratienė, 1996; Satkūnas et al., 2013) suggest the flourishing of sparse boreal forest with pine-spruce-birch during the Jonionys 2 Interstadial, and this has been tentatively correlated with Odderade Interstadial (74–85 cal kyr BP, *sensu* Behre, 1989), i.e. the time-interval preceding the Middle Weichselian (Table 3). The occurrence of *Larix* and deciduous taxa, including *Corylus* and *Carpinus*, alongside the broad-leaved species *Tilia* and *Quercus*, points to a mild and wet climatic regime.

Alternations of vegetation structure indicating cold and warm climatic intervals were typical of the Middle Weichselian in this part of Europe (Helmens et al., 2000; Satkūnas et al., 2009; Helmens and Engels, 2010). In Lithuania, the palaeobotanical data point to the general thinning of vegetation i.e. increasing representation of non-arboreal (NAP) taxa (Asteraceae, Artemisia, Chenopodiaceae, Cyperaceae) at the onset of the Middle Weichselian. Chronologically, that coincides with the lower limit of the Nemunas 2a cryomer dated to 60–74 cal kyr BP (Table 3). Simultaneously, the number of arboreal (AP) taxa, both deciduous and coniferous, decreased, reflecting thinning of the

Table 3

Periodization of the Middle Weichselian (MIS 3) chronozones in Lithuania (Satkūnas and Grigienė, 2012) with a generalized overview of lithological and pollen data

Thermomer/ Cryomer	Time [kyr BP]	Type locality, section	Pollen data with indication of landscape structure
Mickūnai 4	26–28	Mickūnai 184 P Rokantai	The AP with 70% of the total pollen sum is characterized by predominance of *Betula* while participation of *Betula nana* increased considerably (up to 18%). NAP consists of Cyperaceae, Poaceae and *Artemisia*, predominantly. An open landscape with sparse birch.
Nemunas 2e	28–31	Mickūnai 184 P Rokantai	The pollen frequency is very low throughout the interval. Though *Betula* and *Alnus* predominate among AP (50% of the total pollen sum), Asteraceae, *Artemisia* and Chenopodiaceae are the best represent among NAP. Tundra landscape.
Mickūnai 3 (Denekamp Interstadial)	31–35	Purviai Medininkai 117P Mickūnai 184 P Rokantai Popierinė Gaidūnai	*Betula* plays the leading role among AP and the value of NAP (19%) is considerably low throughout the interval. A sparse birch forest.
Nemunas 2d	35–36	Purviai Medininkai 117P Mickūnai 184 P Rokantai Popierinė Gaidūnai	The pollen record is very scarce suggesting the NAP (53%) taxa as predominating. Poaceae is prevailing and Cyperaceae together with *Artemisia* presented in large numbers. Cold steppe landscape.
Mickūnai 2	36–38	Medininkai 117P Mickūnai 184 P Rokantai Popierinė Gaidūnai	The number of AP (66%) slightly increases with *Pinus* as predominating taxa while NAP is dominant by the Cyperaceae. An open landscape with sparse mixed pine – birch forest.
Nemunas 2c	38–44	Medininkai 117P Mickūnai 184 P Rokantai Popierinė Gaidūnai	Pollen record proves the flourishing of NAP taxa constituting up to 70%. Cyperaceae clearly predominates and percentage values of *Artemisia*, Ranunculaceae, Chenopodiaceae and *Helianthemum* increase indicating opening of the landscape structure.
Mickūnai 1	44–47	Mickūnai 184 P Rokantai Popierinė Gaidūnai	*Alnus* plays a leading role in the beginning of the interstadial while *Pinus* varies between 30 and 60% and the number of *Betula* is low. Cyperaceae and *Artemisia* are dominant among NAP (46%). North-boreal mesophytes are represent by *Selaginella selaginoides* and *Botrychium boreale*. The sparse northern boreal forest.
Nemunas 2b	47–49	Jonionys Gaidūnai	The tree pollen lowered to 60% and *Pinus* together with *Alnus* and *Betula* predominate. NAP group is represented by Cyperaceae and Poaceae predominantly. The light-demanding plants, e.g. Caryophyllaceae, *Artemisia*, *Armeria*, Plantaginaceae and *Botrychium* spores were noted. An open tree-less landscape.
Jonionys 3 (Oerel Interstadial)	49–60	Jonionys Gaidūnai Rokantai Svirkančiai	High representation of AP pollen (up to 90%) with *Betula* and *Alnus* as predominating taxa is typical for the Interstadial. While NAP pollen are represented by Cyperaceae, Poaceae, *Artemisia* and Chenopodiaceae mainly. Scarce boreal forest.
Nemunas 2a	60-74	Jonionys Medininkai 117P Mickūnai 184 P Gaidūnai	The number of AP varies around 60% and *Betula* together with *Pinus* playing the leading role. Cyperaceae flourishes among NAP. An open birch forest.
Jonionys 2 (Odderade)	74–85	Gaidūnai Jonionys Medininkai 117P	The value of AP pollen reaches up to 95% and *Pinus* is predominating. Also, *Alnus* is represented by high frequencies. The pollen of larch (*Larix*) and *Calluna* as well as spores of *Selaginella selaginoides* are noted. Boreal forest with pine, birch and admixture of spruce.

forest cover and the formation of open tree-less tundra or a sparse forest-tundra landscape.

The palaeobotanical records then suggest recovery of arboreal taxa including both deciduous (*Betula*, *Alnus*) and coniferous (*Picea*) species during the Jonionys 3 Interstadial (49–60 cal kyr BP). While some open habitats with *Betula nana* and other light-demanding taxa were present in the area, stabilisation of the soil layer started. Correlated with the Oerel Interstadial (Satkūnas et al., 1998) this time-interval indicates climatic amelioration in general.

Subsequently in the palaeoenvironmental history, a general thinning of the vegetation took place during the Nemunas 2b cold interval (47–49 cal kyr BP). At that time *Pinus* and *Betula* were present at the regional scale only. Moreover, the increasing representation of non-arboreal taxa, including Cyperaceae and Poaceae, was accompanied by many pioneer species in the area.

This climatic deterioration was followed by climatic warming that started after 47 cal kyr BP onward. Named the Mickūnai 1 thermomer and characterized by the flourishing of open northern boreal vegetation, it lasted until 44 cal kyr BP. At that time, thermophilous taxa disappeared, indicating general climatic deterioration and the predominance of a wet and relatively cold climatic regime. Only scattered stands of *Pinus*, *Betula* and *Alnus* survived in the area.

Ongoing opening of the vegetation characterized the cold Nemunas 2c interval (38–44 cal kyr BP) (Table 3). In the pollen spectra NAP taxa take over, reflecting a considerable increase in their variety, while the number of AP pollen decreased remarkably. Herbs and grasses predominated, forming a rich cover. Furthermore, up to 80% of NAP taxa consisted of pioneer species and light-demanding taxa suggesting a severe climatic regime with low humidity, unstable soils, and intense reworking processes.

After 38 cal kyr BP, i.e. at the onset of the Mickūnai 2 thermomer (36–38 cal kyr BP), a brief recovery of the vegetation started. First of all, the recorded number of *Pinus* pollen (up to 30%), indicates the sparse presence of this taxon, suggesting formation of open forest-tundra vegetation in the area. At the same time, participation of the deciduous taxa in the pollen spectra points to some climatic amelioration, while the high participation of Cyperaceae suggests the formation of wet terrain.

A climatic climatic deterioration, named the Nemunas 2d cryomer (35–36 cal kyr BP), was recorded between the Mickūnai 2 and 3 thermomers. The pollen spectra show a predominance of Poaceae, Cyperaceae, Asteraceae, Artemisia and other NAP reflecting the formation of open wet habitats and nitrogen-rich soil in the area. As the number of AP pollen are negligible in spectra, a harsh climatic regime and predominance of open poor landscape with tundra vegetation can be deduced.

This was followed by amelioration indicated by the palaeobotanical data. Flourishing of birch-predominating light forest with a few non-arboreal taxa, a lack of open habitats and the formation of a stable soil layer was typical of the Mickūnai 3 thermomer, correlated with the Denekamp Interstadial and dated to 31–35 cal kyr BP. Furthermore, the occurrence of alder suggests increasing wetness. Thus, a cool boreal environment was typical of the region at that time.

The episodic appearance of palaeobotanical data indicating one more negative climatic reversal – the Nemunas 2e cryomer (28–31 cal kyr BP) – suggests the probable local scale of this event. However, low pollen frequency makes characterisation of the vegetation pattern of this interval difficult (Table 3). Nevertheless, based on the available date, we may infer a brief and sudden decay of the boreal forest and the formation of open tundra vegetation.

Recovery of the open birch-predominating forest with high participation of *Betula nana* points out to a prevalence of boreal conditions during the Mickūnai 4 thermomer (26–28 cal kyr BP) in the area that experienced the Nemunas 2e cryomer.

MATERIALS AND METHODS

MEGAFAUNAL MATERIAL

During this project, six new macrofossils were analysed by the ^{14}C (AMS) technique.

In the village of Šnaukštai in western Lithuania (Fig. 1 and Table 4, No. 1), an antler of *Rangifer tarandus* was found at the bottom of a gravel quarry, at a depth of ~4.5–5.5 m. Accumulation of the gravelly beds, overlain by fine and very fined-grained or even clayey sand, took place by reworking of the Late Weichselian (Nemunas) Glaciation deposits, with subsequent transportation of the terrigenous matter and its deposition on a glaciofluvial delta. Today this territory is part of the southwestern Samogitian Plain, a part of the Samogitian Insular Upland (SIU) (Guobytė, 2002). The *Rangifer tarandus* antler from Šnaukštai has been dated twice by the ^{14}C analysis, in different laboratories, in order to acquire the best possible radiocarbon age (Girininkas and Daugnora, 2015; Girininkas et al., 2017).

In the similar geological-geomorphological situation associated with Žemgrindžiai Quarry, situated ~14 km north-west of Šnaukštai, a *Mammuthus primigenius* bone was discovered (Fig. 1 and Table 4, No. 5). Situated very close to the limit of the glaciofluvial-glaciolacustrine deposits of the southwestern Samogitian Plain (Guobytė, 2002), this sedimentary basin contains gravel and coarse-grained sand. The location might represent the coastal zone of the large sedimentary basin that existed during the retreat of the Late Weichselian ice cover in the area (Guobytė and Satkūnas, 2011). This specimen, overlain by glaciofluvial deposits of the Late Weichselian age, was discovered at a depth of ~4.5 m.

One more fragment of *Mammuthus primigenius* was discovered in the Sviraičiai Quarry, Telšiai district, NW Lithuania (Fig. 1 and Table 4, No. 4; Butrimas, 2020), at a depth of ~5 m and overlain by a glaciolacustrine bed consisting of clayey and fine-grained sand. Geomorphologically, this territory is considered to be part of the Northern Samogitian Plateau (Guobytė, 2002).

Two *Mammuthus primigenius* fragments were discovered in glaciofluvial coarse-grained sand and gravel near Ariogala village, Central Lithuania (Fig. 1 and Table 4, No. 2 and 3). Geomorphologically, this area belongs to the Middle Lithuanian Plain (Guobytė, 2002). Here, meltwater stream deposits of the Late Weichselian Glaciation have been discovered overlying the basal till. These fossils were collected at depths of ~5–8 m, located ~80 m apart.

So far, a single fragment of *Mammuthus primigenius* is known from the northern part of Lithuanian territory. It was discovered in the Žagarė Esker, Joniškis district, northern Lithuania (Fig. 1 and Table 4, No. 6), a classical ice-marginal geomorphological structure formed during the retreat phase of the Late Weichselian Glaciation. During the exploitation of the gravel quarry, this fossil was found at a depth of ~8 m.

All these newly discovered macrofossils have been investigated by osteological analysis including visual inspection and measurement, and evaluation of the state of preservation and of reworking during transport. The specimens are stored in the Lithuanian National Museum in Vilnius, Tadas Ivanauskas Zoological Museum in Kaunas, Samogitia Museum "Alka" in Telšiai, local museums, and private collections.

Table 4

^{14}C data of megafaunal remains from Lithuania

No.	Locality	Coordinates (WGS)	Dated object	Lab. No.	C^{14} BP	cal BP 1 (68.2%)	cal BP 2 (95.4%)	References
NEW DATA								
1	Šnaukštai, Klaipėda district	55.656763; 21.415358	*R. tarandus* Antler	GrA-65623	37690 ±280	42290–42045	42395–41902	
2	Ariogala Quarry, Raseiniai district	55.483353; 23.699984	*M. primigenius* Incisivi	FTMC-FR-48-2	28633 ±95	33235–32840	33330–32220	
3	Ariogala Quarry, Raseiniai district	55.483353; 23.699984	*M. primigenius* Incisivi	FTMC-FR-48-1	25159 ±86	29565–29205	29790–29165	
4	Sviraičiai, Telšiai district	55.997408; 22.531575	*M. primigenius* Humerus fragment?	RICH-22970	35415 ±231	40910–40360	41070–40000	
5	Žemgrindžiai Quarry, Klaipėda district	55.770005; 21.290009	*M. primigenius* Tibia	FTMC-OZ78-1	26579 ±50	31000–30855	31065–30785	
6	Žagarė esker, Joniškis district	56.351188; 23.219142	*M. primigenius* Incisivi	KIA-55701	27960 ±230	32220–31550	32880–31360	
7	Kazokiškiai Quarry, Elektrėnai municipality	54.807648; 24.819865	*M. primigenius* Incisivi	OxA-10874	46300 ±1100	50235–47310	52415–46160	Ukkonen et al. (2011)
8	Šnaukštai, Klaipėda district	55.656763; 21.415358	*R. tarandus* Antler	BETA-407751	41460 ±560	44880–43920	45240–43230	Girininkas and Daugnora (2015)
9	Kalnėnai, Jurbarkas district	55.080504; 22.719889	*R. tarandus* Antler	Tua-7686	28685 ±356	33590–32735	34020–31915	Girininkas and Daugnor (2015)
10	Naravai, Prienai district	54.589252; 23.984141	*C. antiquitatis* Cranium	OxA-12017	44950 ±650	48010–46540	48710–45960	Daugnora (2004)
				GrA 65622	38950 ±310	42750–42465	42905–42355	
11	Jiesia River, Kaunas town	54.858016; 23.928227	*M. primigenius* Molar	LuS-7531	42300 ±1000	45920–44310	47090–43235	Arppe et al. (2011)
12	Jiesia River, Kaunas town	54.858016; 23.928227	*M. primigenius* Molar	LuS-7532	41350 ±800	44805–43405	45555–42980	Arppe et al. (2011)
13	Jiesia River, Kaunas town	54.858016; 23.928227	*M. primigenius* Incisivi	OxA-10872	40900 ±650	44395–43315	44850–42915	Ukkonen et al. (2011)
14	Jucaičiai, Šilalė district	55.452251; 22.179107	*M. primigenius* Molar	OxA-10870	40600 ±800	44280–43090	44910–42680	Ukkonen et al. (2011)
15	Kazokiškiai Quarry, Elektrėnai municipality	54.807648; 24.819894	*M. primigenius* Incisivi	OxA-10875	38050 ±700	42605–41985	42980–41470	Ukkonen et al. (2011)
16	Kazokiđkiai Quarry, Elektrėnai municipality	54.807648; 24.819894	*M. primigenius* Incisivi	OxA-10873	33740 ±380	39320–38075	39650–37470	Ukkonen et al. (2011)
17	Pilsūdai, Tauragė district	55.417344; 22.513392	*M. primigenius* Molar	LuS-7533	33650 ±300	39205–38100	39395–37545	Arppe et al. (2011)
18	Kruonis, Kaišiadorys district	54.780597; 24.270912	*M. primigenius* Incisivi	OxA-10810	30350 ±250	35070–34505	35290–34350	Ukkonen et al. (2011)
19	Turžėnai Quarry, Jonava district	54.983857; 24.092497	*M. primigenius* Molar	LuS-7528	21400 ±120	25875–25675	25960–25350	Arppe et al. (2011)
20	Olando kepurė (Dutchman's cap), Klaipėda city	55.79779; 21.067516	*M. primigenius* Molar	Hela-3320	27490 ±250	31635–31200	31895–31110	Girininkas and Daugnora (2015)
21	Klaipėda Duchman cap, 2008	55.79779; 21.067516	*M. primigenius* Molar	LuS 7918	>43000	infinite	–	Ukkonen et al. (2011)
22	Juodelių Quarry, Kalvarija region	54.386867; 23.104404	*M. primigenius* Tusk	OxA-10844	>31400	infinite	–	Ukkonen et al. (2011)

^{14}C ANALYSIS

The vertebrate macrofossils were subject to ^{14}C dating using the AMS technique. Measurements on six samples were performed in four different laboratories: the Centre for Isotope Research University of Groningen Nijenborgh, the Netherlands (Laboratory code – GrA); the Center for Physical Sciences and Technology, Laboratory of Mass Spectrometry (Vilnius Radiocarbon), Lithuania (Laboratory code – FTMC); and the Royal Institute for Cultural Heritage, Belgium (Laboratory code – RICH) and Leibniz-Labor fur Altersbestimmung und Isotopenforscung, Kiel AMS, Germany (Laboratory code – KIA).

The reliability of ^{14}C dates decreases beyond 30 cal kyr BP Nevertheless, all results, except those noted as "infinite", were calibrated by applying *OxCal v4.4* software (Bronk Ramsey et al., 2009) with the IntCal2020 calibration curve (Reimer et al., 2020). All dates are reported at both 1d (68.27%) and 2d (95.45%) confidence levels and the calibrated age is referred to as cal kyr BP in text.

RESULTS

OSTEOLOGICAL DATA

The fossils were interpreted as representing the tusk, molars, tibia, and a fragment of humerus of mammoths, together with the antler of a reindeer (Table 4).

The antler of *R. tarandus* from Šnaukštai Quarry (Table 4, No. 1) is 30.8 cm long and ~2.7 cm in diameter, dark brown and well-preserved with no noticeable secondary bone injury.

The *M. primigenius* remains from Ariogala Quarry are more poorly preserved. Sample 1 (Table 4, No 2), described as part of a tusk, is ~35.5 cm long along the external curve. It represents just a part of the external tusk so its original diameter cannot be measured. Another specimen from the Ariogala Quarry (Table 4, No. 3), described as a tusk fragment, is ~12 cm long though again of unknown original diameter.

The humerus fragment from Sviraičiai is well-preserved and light brown (Table 4, No. 4), ~50 cm long though of unknown original diameter.

The tibia of a young animal discovered in the Žemgrindžiai Quarry (Table 4, No. 5) is also well-preserved. Its length reaches 43 cm, the width varying from 10.7 to 7.3 cm in the middle part and ~11.4 cm across the articular surface.

The most poorly preserved of these fossils is from Žagarė (Table 4, No. 6): a tusk originally ~50 cm long was left in a dry room for a few years and broke into ~35 small light brown fragments ~5–8 cm long.

DATING

In total twenty-two dated bone samples, including the six analysed in the context of the present study, provide the chronological background for discussion. The general information describing these samples, including radiocarbon ages, is outlined in Table 4.

Based on the ^{14}C data obtained (Fig. 2), the dates generally cluster within the Middle Weichselian climatostratigraphic intervals of the continental and regional scales. Dated to ~25–26 cal kyr BP the youngest specimen of *Mammuthus primigenius* representing the Nemunas 3 cold interval (cryomer) of the Middle Weichselian was discovered in Turžėnai quarry, Jonava district (Fig. 1 and Table 4, No. 19). The oldest dated specimen (Fig. 1 and Table 4, No. 7) relates to the Jonionys 3 warm interval (thermomer) which is correlated with the Oerel interval (Behre, 1989). However, some of the dates, i.e., the *Coelodonta antiquitatis* cranium (Fig. 1 and Table 4, No. 10), have to be taken with some caution as different dates were obtained from different laboratories.

DISCUSSION

PALAEOENVIRONMENTAL DYNAMICS

Despite the many investigations conducted across Europe, including in Fennoscandia and the Baltic region (Wohlfarth, 2010; Lasberg, 2014), both the climatostratigraphic subdivision and palaeogeographic interpretation of the Middle Weichselian timespan remain unclear in some areas (Behre, 1989; Helmens et al., 2000; Houmark-Nielsen, 2011; Svendsen et al., 2004). Preceding the Late Weichselian Glaciation, this interval plays a particular role in the spatio-temporal reconstruction of the climatic and environmental situation prior to the advance of the youngest glaciation. Furthermore, Middle Weichselian palaeoenvironmental and chronostratigraphic investigations are essential for determining the onset of the Late Weichselian Glaciation while, along with data representing the Late Weichselian, may aid in improving the understanding of the climatic evolution and the environmental reactions throughout the full glaciation macrocycle event. However, the number of well-preserved geological records of Middle Weichselian age is very limited or are missing in the territories later influenced by the Last Scandinavian Glaciation. As the available information can be insufficient for detailed analysis, additional data sources are required. Biotic turnovers, particularly those noted in the faunal records, have "implications for reconstructing the history of SIS" (Ukkonen et al., 2011) and such data has helped reconstruct the Middle Weichselian palaeoenvironmental history of this part of the SE Baltic. In general, remains of woolly mammoth (Fig. 3) and reindeer are widely distributed in this part of Europe (Ukkonen et al., 2006, 2011; Stefaniak and Marciszak, 2009; Piskorska and Stefaniak, 2014; Stefaniak et al., 2020) while these of woolly rhinoceros (Fig. 4) are more scarce, with only one dated specimen recognised from the Eastern Baltic (Stuart and Lister, 2012). In recent years new specimens, i.e. *Mammuthus primigenius* and *Rangifer tarandus*, have been discovered and investigated in Lithuania.

In continental-scale records of the MIS 3 interval the climatic instability has been emphasised (Johnsen et al.,1992; Grootes et al., 1993; Allen et al., 1999; Genty et al., 2003; Svedsen et al., 2004; Lasberg, 2014) with a series of cold stadials and warmer interstadials being identified. Alongside this, glacial deposits of Middle Weichselian age have been recognized extensively across northern and northeastern Europe (Liivrand, 1991; Nenonen, 1995; Marks, 2004, 2012; Zelčs and Markots, 2004; Houmark-Nielsen, 2011; Damušytė et al., 2011). However, recent investigations have shown a predominance of ice-free conditions in the larger part of eastern Fennoscandia throughout the Middle Weichselian (Ukkonen et al., 1999, 2007; Molodkov et al., 2007; Satkūnas et al., 2009; Helmens and Engels, 2010; Wohlfarth, 2010; Rattas et al., 2010; Saks et al., 2012; Lasberg, 2014; Lamsters et al., 2017). An increasing number of palaeoclimatological, lithological, biostratigraphical and physical investigations conducted in the eastern Baltic suggests that non-glacial (periglacial and interstadial) palaeoenvironments also predominated in this part of Europe during the Middle Weichselian (Table 1). In Lithuania, 5 intervals of climatic amelioration (thermomers) and at least 5 cold intervals (cryomers) have been described based on lithological and palaeobotanical

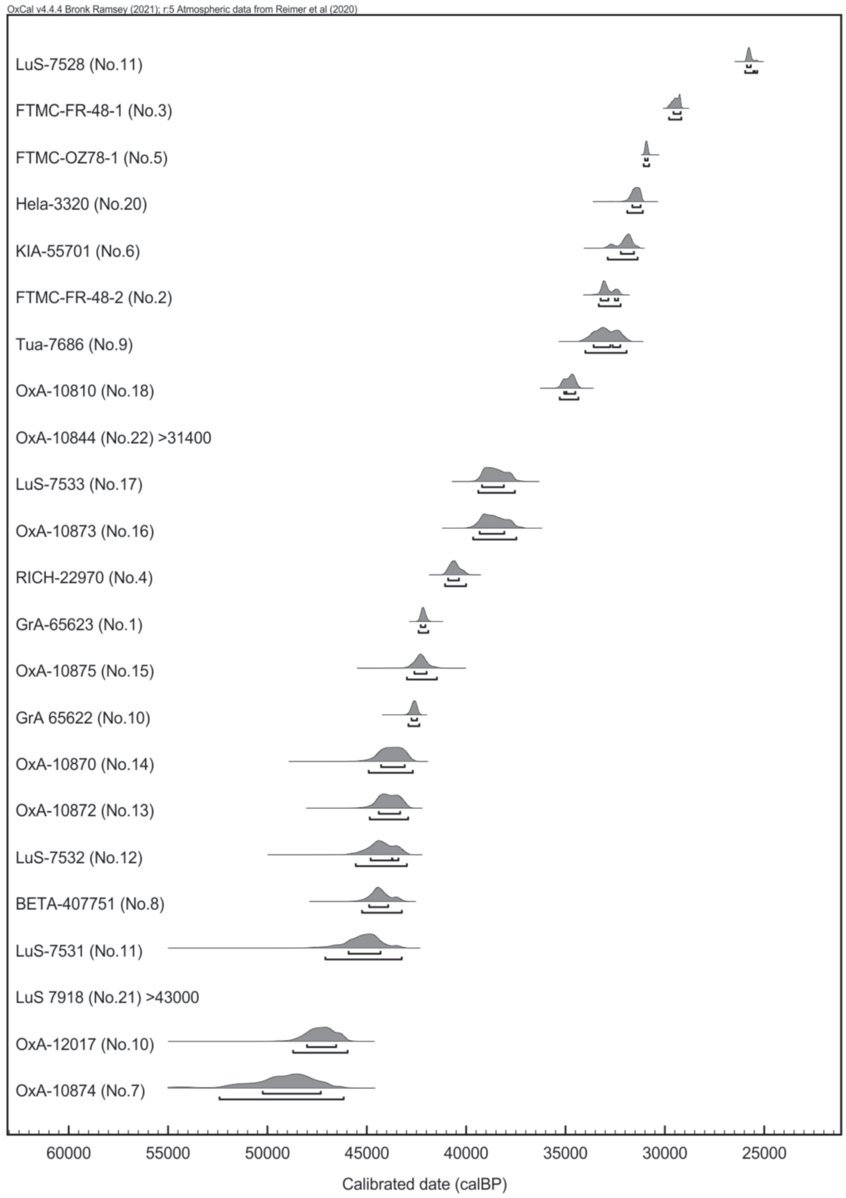

Fig. 2. Calibrated ^{14}C data of the megafaunal remains

evidence (Satknas and Grigienė, 2012). Nevertheless, the restricted availability of the data, including chronological data, hinders the analysis and subsequent correlation of the identified turnovers as well as reliable reconstruction of palaeoclimatic and palaeoenvironmental fluctuations. In such circumstances, the lack of lithostratigraphic constraints on ice cover i.e. coincident with the climatic deteriorations, increases the significance of the biostratigraphic records. Thus, fossil data are important to recovering information on the past climatic and environmental dynamics in the area.

In eastern Lithuania, the oldest record of *Mammuthus primigenius* (Fig. 1 and Table 4, No. 7, OxA-10874, 46160–52415 cal kyr BP), points to the presence of this mammal at the transition from the final stages of the Jonionys 3 thermomer (49–61 cal kyr BP) to the Nemunas 2b cryomer (47–49 cal kyr BP) here (Fig. 5). A characteristic negative shift of the δ^{18}O curve indicate the pronounced climatic cooling that started simultaneously across this area. Furthermore, the pollen record points to the formation of an open landscape encompassing wide grass-predominating habitats with some pine and birch. Alder was also present, suggesting sufficient humidity and correlating with data from Sokli, NE Finland, where relatively moist climatic conditions have been indicated at ~40–50 cal kyr BP (Helmens et al., 2007). Traditionally the habitat of the woolly mammoth, the so-called “steppe mammoth”, originally described as a cold-steppe biome (Guthrie, 1968), may have consisted of a mosaic of diverse landscapes (Guthrie, 2001). In general, distinct vegetational and climatic heterogeneity has been noted in analysing the ecology of this megaherbivore in different parts of Europe (Arppe et al., 2011). Here, in the Baltic region, mammoths “subsisted in a colder and wetter environment” *sensu* Arppe et al. (2011). Another date, from the cranium of *Coelodonta antiquitatis*, also represents the Nemunas 2b interval (Fig. 1 and Table 4, No. 10, OxA-12017,

Fig. 3. Tibia of *Mammuthus primigenius*, Žemgrindžiai (Fig. 1 and Table 1, No. 5)

Fig. 4. Cranium of *Coelodonta antiquitatis*, Naravai (Fig. 1 and Table 1, No. 10)

48710–45960 cal kyr BP). But, it must be discarded due to a discrepancy identified during re-dating of the specimen.

*Mammuthus primigeniu*s and *Rangifer tarandus* remains are present between 44–47 cal kyr BP, roughly correlating with Mickūnai 1 thermomer (Table 3). Remains of reindeer represent the second half of the interval (Fig. 1 and Table 4, No. 8, BETA-407751, 43230–45240 cal kyr BP) while mammoth settled earlier (Fig. 1 and Table 4, No. 11, LuS-7531, 43235–47090 cal kyr BP) in area. This is the oldest dated reindeer specimen in Lithuania (Girininkas and Daugnora, 2015) and one of the rare finds representing the MIS 3 interval in this part of Europe. Though it is assumed that the reindeer was typical for the Eurasian periglacial fauna during the Weichselian, most previously dated remains represent Late Weichselian and postglacial times (Ukkonen et al., 2006). The new data are crucial for analysing the distribution of this species before the formation of the last glacial cover. In general, the eastern Baltic region could be of particular importance in discussing the spatial and temporal distribution of the tundra and forest reindeer populations during the Pleistocene (Piskorska and and Stefaniak, 2014). Meanwhile, pollen data demonstrate the existence of an open boreal forest with the presence of deciduous taxa, *Alnus* in particular, in the area. Thus, the increasing vegetational density is corroborated by the stabilisation of the NAP curve, that is especially pronounced during the first half of the interval. Later, pine established in the region as the recorded *Pinus* value (30–35%) shows the local origin of the deposited pollen grains (Huntley and Birks, 1983). Noted variations of the vegetation structure are contemporaneous with those seen in the isotope record, i.e., a pronounced peak in the $\delta^{18}O$ curve was followed by a remarkable drop (Fig. 5). As pine prefers increasing continentality (Walker, 1995), such a climatic regime most probably predominated in the area. Moreover, the contemporaneous appearance of north-boreal mesophytes, i.e., *Selaginella*

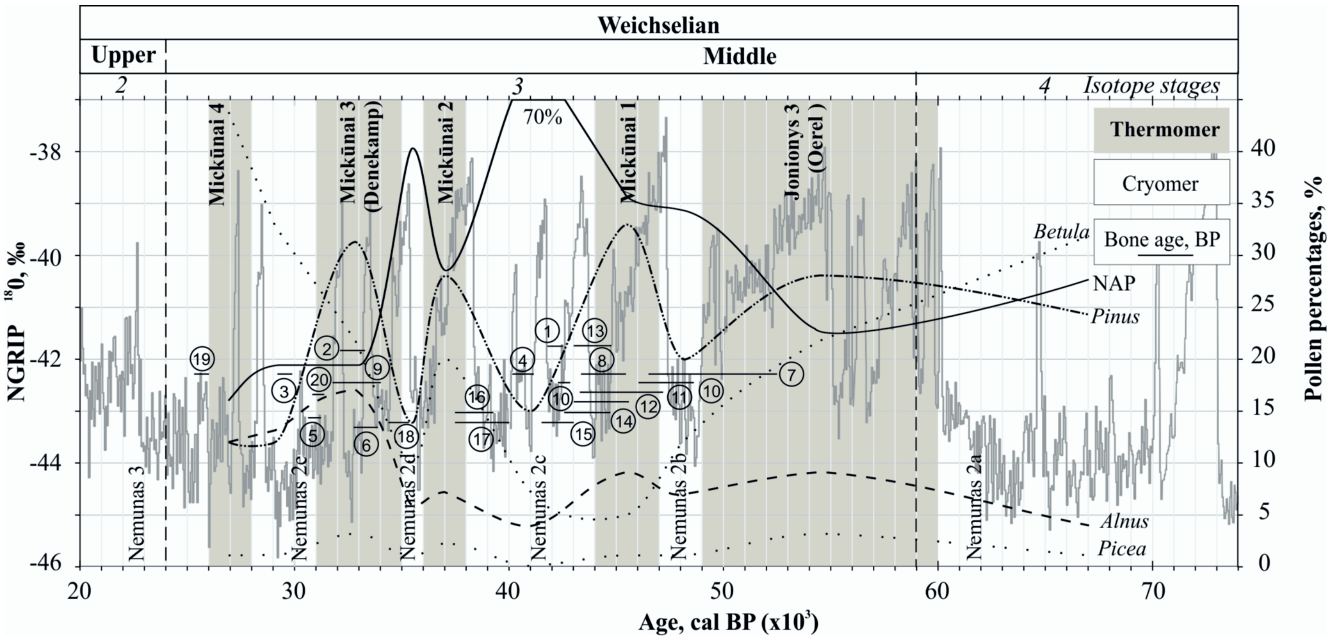

Fig. 5. Chronological distribution of the fossils dated *versus* NGRIP δ^{18}O (‰) (Rasmussen et al., 2006) and pollen data

selaginoides and *Botrychium boreale*, points to drastic climatic and environmental shifts. Being adapted to different types of habitat, varying from steppe-tundra to forests (Piskorska and Stefaniak, 2014), reindeer might have migrated into the area when an open boreal forest flourished here. Analysis of reindeer molars suggests that individuals did "feed on hard food, such as shrub twigs or tree bark, possibly in forest-tundra" during the MIS 3 (Piskorska and and Stefaniak, 2014). Furthermore, as was hypothesised by Arppe et al. (2011) the relative proportion of woody plant material in the mammoths' diet was higher in the north-east part of Europe. In such a way the spread of these megaherbivores through the sparse northern boreal forest seems realistic.

Almost continuous faunal ^{14}C evidence is demonstrated between 38–45 cal kyr BP, i.e., the time-interval comparable to the Nemunas 2c cryomer (Fig. 5). Reindeer were present in the territory while *Mammuthus primigenius* predominated with an increasing population density. An expansion of these species may have been triggered by the changing landscape structure, i.e., formation of open tree-less herb tundra with especially high primary productivity, that would be consistent with the pollen data. A high participation of NAP taxa, including light-demanding and pioneer species, suggests thorough reorganization of the terrain, which might have been influenced by the prominent climatic shifts noted after 45 cal kyr BP. Multiple oscillations of the isotopic record support this presumption, and available palaeoclimatic reconstructions suggest brief temperature drops to –25°C in winter (Luoto et al., 2004) in eastern Poland during the middle Pleniglacial (Marks et al., 2019).

There is a further temporal concentration of dated faunal remains between 31–34 cal kyr BP (Fig. 5). That time-interval is coincident with the Mickūnai 3 thermomer, correlated with the Denekamp Interstadial in Lithuania (Satkūnas et al., 2009). Though described as a time of warming climate with July temperatures averaging ~0°C in Laarhuis near Denekamp (Kolstrup and Wijmstra, 1977) this interval overlaps with negative shifts of the δ^{18}O curve pointing to some brief climatic cooling's (Fig. 5), and dates of *Mammuthus primigenius* and *Rangifer tarandus* material correlate positively with those negative reversals of the δ^{18}O curve. Meantime, palaeobotanical data suggest the flourishing then of birch-predominating light forest with scattered stands of pine and alder and low representation of non-arboreal taxa in Lithuania (Satkūnas and Grigienė, 2012). Habitats favourable for the spread of megafauna predominated in the area even during the colder intervals. In regional palaeobotanical records "an open tree-less environment with sparse birch forests" predominated during MIS 3 in central Sweden (Robertsson, 1988; Wohlfarth, 2009). In principle, MIS 3 is characterized "by a more continental climate for much of the glaciated region of northern Europe from ~50–25 ka" (Arppe and Karhu, 2010) and surface air temperatures in the territories of the present Czech and Slovak republics and Hungary were 2–9°C colder than present between 12–33 ka cal BP (Kovács et al., 2012). Nevertheless, remarkable discrepancies occurred in the climatic regime within MIS 3 shown by the interpretation of periglacial landforms (e.g., van Huissteden et al., 2003), coleopteran remains (Coope, 2002), and mammoth enamel temperature estimates (Arppe and Karhu, 2010; Ukkonen et al., 2011) across different parts of Europe. Thus, the newly provided palaeobiological and ^{14}C data is of particular importance for the reconstruction of the environmental history during the Denekamp Interstadial in the SE Baltic.

The other two *Mammuthus primigenius* samples represent the Nemunas 2e and Nemunas 3 cryomers. According to the pollen data (Fig. 5), open tundra vegetation flourished, pointing to the existence of traditional mammoth habitats at that time in the area.

Subsequently, the biological and ^{14}C data obtained reflect both cryomers and thermomers being suitable for the establishment of the megafauna during MIS 3 in the SE Baltic. This is of particular importance for the further analysis of both biotic turnovers and environmental patterns during the pre-LGM in this part of Europe.

CONCLUSIONS

The temporal distribution of the megafaunal remains analysed [woolly mammoth (*Mammuthus primigenius* Blum.) and reindeer (*Rangifer tarandus* Linnaeus, 1758)] implies the existence of non-glacial conditions during the Middle Weichselian (MIS 3) in the investigated part of the eastern Baltic region. According to ^{14}C (AMS) data, most of the discovered megafaunal remains represent two intervals: 38–45 cal kyr BP (Nemunas 2c cryomer) and 31–34 cal kyr BP (Mickūnai 3 thermomer (Denekamp Interstadial). The temporal distribution of the ^{14}C dates is consistent with intervals reporting both cold and warm climatic phases of MIS 3. Based on pollen data, the vegetation pattern of these intervals varied from the tree-less tundra to birch-predominating forest with an admixture of temporal tree species, i.e. *Pinus* or *Alnus*, providing additional information about the diet and habitat preferences of the large herbivores. The environmental situation, including the vegetation pattern, was conducive to the existence of different species of megafauna there at that time.

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