

Multi-disciplinary study of a late Pleistocene woolly rhinoceros found in the Pannonian Basin and implications for the contemporaneous palaeoenvironment

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ABSTRACT: Excavation campaigns conducted at the Pécel-Kis hársas site (Hungary) between 2014 and 2017 yielded the remains of a mature female woolly rhinoceros (*Coelodonta antiquitatis*) and six lithic artefacts. Radiocarbon dating confirmed that the rhinoceros died ca. 20.4k cal a BP, at the very end of the Last Glacial Maximum and, considering the position of the artefacts when found, it was probably killed by Epigravettian hunters. Based on dental analyses of the specimen, a vigorous lichen- (and possibly moss-)consuming diet could be inferred for the end of the animal's lifetime. Based on Sr results, we can exclude the possibility of long-range migration. In accordance with the optimum environmental demands of the foraging lichen, the low $\delta^{18}\text{O}$ value of osseous material implies a relatively cold contemporaneous climate with a calculated mean annual air temperature of around 0.7 °C. Meanwhile, the extremely low $\delta^{15}\text{N}$ value may have resulted from the proximity of the discontinuous permafrost zone and some intensive soil dislocation. Consequently, poor vegetation and an open, tundra-like habitat can be assumed to have been dominant at the site at that time, which is also supported by palaeoenvironmental modeling experiments. © 2023 John Wiley & Sons, Ltd.

KEYWORDS: dental analysis; diet; LGM; palaeoenvironmental reconstruction; stable isotopes; woolly rhinoceros

Introduction

Woolly rhinoceros (*Coelodonta antiquitatis*) is one of the most emblematic members of the Pleistocene megafauna, an element of the Eurasian mammoth fauna also known as the *Mammuthus-Coelodonta* Faunal Complex (Kahlke, 2014; Kahlke and Lacombe, 2008). Until the Late Pleistocene, woolly rhinoceros was common in all cold stages of Europe, even under moderate temperatures, when the climate was sufficiently dry (Guérin, 1980; Kahlke and Lacombe, 2008). The first occurrence of the genus *Coelodonta* in Europe was discovered in deposits of a glacial meltwater delta of Marine Isotope Stage (MIS) 12 (about 460 ka) at the site of Bad Frankenhausen, Germany (Kahlke and Lacombe, 2008; Uzunidis et al., 2022). Hundreds of thousands of years later, the last examples of the species in the Western and Central European region (~16.7–17.0k cal a BP) were discovered in Switzerland, Germany and Poland. Meanwhile, its coexistence with human groups has long been known from numerous sites in Eurasia. Finally, woolly rhinoceros probably went extinct

close to the onset of the Allerød interstadial (GI-1c) ~13.9k cal a BP (Stuart and Lister, 2012; Rey-Iglesia et al., 2021) and the last occurrence worldwide was proposed to be near the Lena–Amga interfluvies, north-eastern Siberia, Russia. Despite long debate, recent investigations tend to suggest drastic environmental changes due to rapid climate changes as the main factor of extinction, although human impact also cannot be completely excluded (Cooper et al., 2015; Kuzmin, 2010; Stuart and Lister, 2007).

The Pannonian Basin has always been rich in Late Pleistocene vertebrate fossil sites. At least 150 of them, mainly cave sites, have additionally provided woolly rhinoceros remains. The most recent woolly rhinoceros remains found in stratigraphic sequence in Hungary (Vörös, 2000, and references therein) were associated with the Istállós-kő faunal phase (Middle Würm or the second half of MIS 3), using local biostratigraphy analyses. The presumed latest occurrence in Hungary comes from the mixed layer 11b in Remete Cave (Budapest), estimated to be ~17–18 ka, based on the composition of the faunal assemblage (Jánossy, 1986). Recently, the local presence of the species was estimated to be ~20 ka (Pazonyi, 2004). Nevertheless, despite thorough and detailed stratigraphic, archaeological and palaeontological

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elaboration of these assemblages, the lack of precise absolute dates and comprehensive natural science studies represent a serious issue. Consequently, the number of reliable data is still limited (Kovács, 2012; Kovács et al., 2012; Pazonyi, 2011, 2004).

In this study, in addition to classical palaeontological and archaeological observations, we present the results of a multi-disciplinary analysis applied on the remains of a female woolly rhinoceros and six associated lithic artefacts found side by side at the new Pécel-Kis hársas open-air site in Hungary. For the first time in the history of Hungarian palaeontological assemblages, we performed joint stable isotope ($\delta^{13}\text{C}$, $\delta^{15}\text{N}$, $\delta^{18}\text{O}$ against VPDB, AIR and SMOW respectively, in addition, Sr), dental mesowear and calculus/fossae analyses on osseous remains, aiming to reveal new palaeontological and palaeoenvironmental aspects related to the species and the finding locale at the very end of the Last Glacial Maximum (LGM). Wear analysis was also performed on the lithic artefacts to examine the association between the tools and the animal.

Materials and methods

Numerous bones of one woolly rhino specimen and six lithic artefacts (four made from chert and two from obsidian) were found at the Pécel-Kis hársas site (N47.49805, E19.37789, 192 m a.s.l.) between 2014 and 2017, which is located at the south-western edge of the Gödöllő Hills, 20 km east of Budapest, Hungary (Figure 1). During the campaigns, all the bone remains were recovered at a depth section between 50 and 100 cm but as this was a rescue excavation, detailed geological context of the fossil-bearing horizon was not recorded. However, the stratigraphic section of the site showed a finely laminated sequence of different layers (loessy

sand and slope loess). The dense bone accumulation and their position suggested that the pieces had been buried in *in situ* position on an ancient slope, close to the inclination point.

Palaeontological identification was based on a comparison with Pleistocene rhinoceros material collected from different European locations and stored in the Department of Palaeontology and Geology of the Hungarian Natural History Museum (HNHM) and the Hungarian Geological Institute (Mining and Geological Survey of Hungary) in Budapest, Hungary. The diagnostic morphological features were selected and listed by different authors (Guérin, 1980; Pandolfi and Tagliacozzo, 2015). The estimated age at death of the specimen was calculated using the stage of fusion of the long bone epiphysis, in addition to tooth eruption, replacement and wear stages suggested by Hillman-Smith et al. (1986) for white rhinoceros (*Ceratotherium simum*). Dental mesowear analysis was performed following the generalized individual dental age stage method (IDAS) (Anders et al., 2011), according to the suggestions of Mihlbachler et al. (2011) [Supporting Information Material 1 (SM1)]. Low-magnification dental microwear analysis was also attempted (for details see Solounias and Semprebon, 2002; Semprebon et al., 2004), but due to the poor preservation of the enamel surfaces this analysis was not successful.

Radiocarbon dating, and stable carbon, nitrogen, oxygen and strontium analyses of the specimen were performed at the International Radiocarbon AMS Competence and Training Center (INTERACT), Debrecen, Hungary, following standard collagen extraction and bioapatite processing protocols in use at the laboratory (Gugora et al., 2022; Major et al., 2019; Molnár et al., 2012). Stable carbon, nitrogen and oxygen ratios were measured using a Thermo Finnigan Delta^{Plus} XP mass spectrometer. Mean $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values are presented against the VPDB and AIR references,

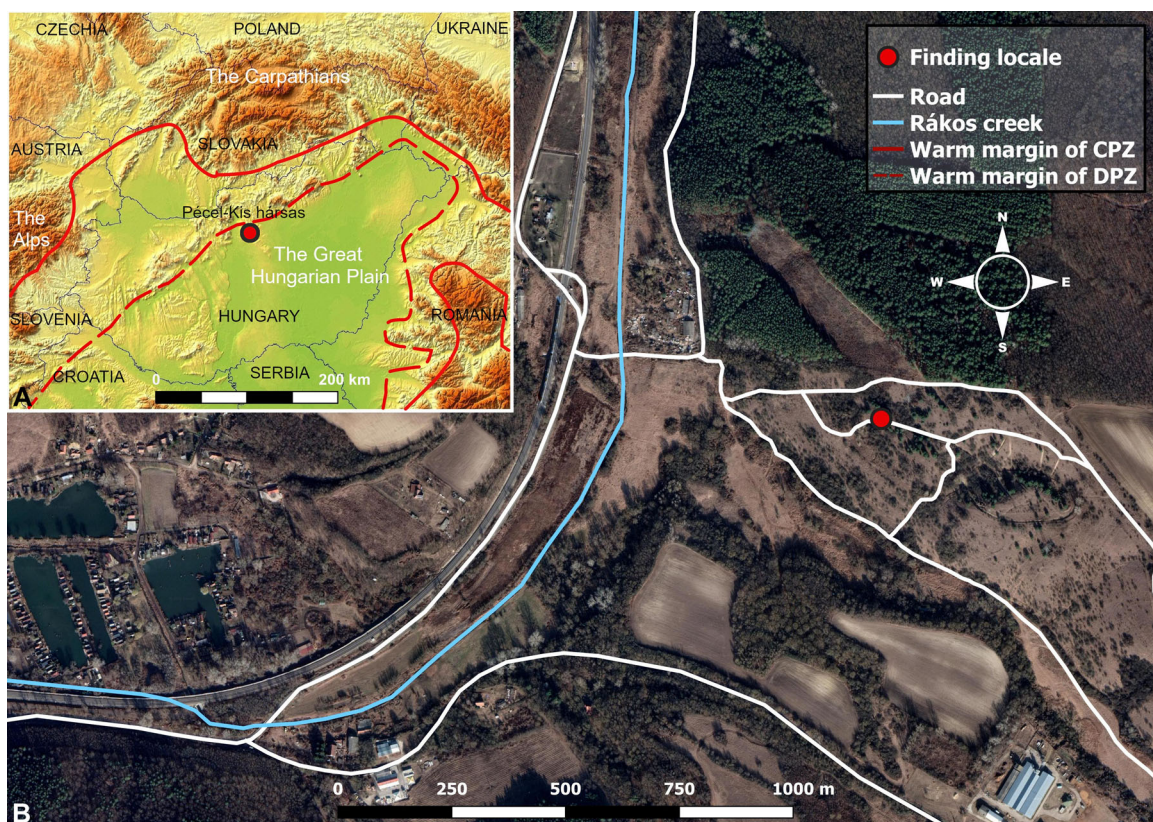


Figure 1. (A) Map of Central Europe showing the Pécel-Kis hársas locale of the rhinoceros skeleton in the Pannonian Basin. The southern margins of the continuous and discontinuous permafrost zones (CPZ and DPZ) are also indicated with reference to Ruszkiczay-Rüdiger and Kern (2016). (B) View from above of the Pécel-Kis hársas site (credit: Google maps). [Color figure can be viewed at wileyonlinelibrary.com]

respectively. For mean annual air temperature (MAAT) calculations, the measured stable oxygen results of the rhino bone phosphate ($\delta^{18}\text{O}_p$ against SMOW) and the calculated $\delta^{18}\text{O}_w$ values for water drunk by selected horse, bison and elephant specimens were included. The Pécel-Kis hársas site is located at similar distances from Krakow (~550 km to the north) and Zagreb (~650 km to south-west), and thus the MAAT value for the tooth and bone samples was calculated as the mean of temperatures related to Krakow (T_{airK}) and Zagreb (T_{airZ}). In addition, to verify our MAAT results, the respective noble gas temperatures (NGTs), using the same $\delta^{18}\text{O}_w$ values, were also calculated and compared to the respective air temperature values (Varsányi et al. 2011; SM2). To learn more about the diet of this specimen, micro-remains found in the dental calculus and fossae were also analysed at INTERACT, using an Alpha Euromex CMEX-5 polarizing light microscope. The surface morphology of these remains, for verification of their inorganic origin, were studied at the Laboratory of Material Science (Institute for Nuclear Research, Debrecen, Hungary), under an Hitachi S4300-CFE scanning electron microscope (SEM) equipped with energy dispersive X-ray spectroscopy (EDX) and operating at 15 kV with a detection threshold of 0.1 at%. More detailed descriptions concerning these analytical methods can be found in the SM1 and 2. Use-wear analysis of the obsidian tools was performed with a reflected light microscope (Zeiss AxioScope.A1, 50–500 \times) and a stereomicroscope (Zeiss Discovery V8, 6.3–80 \times) at the Institute of Archaeological Sciences of Eötvös Loránd University, Budapest, Hungary (see SM3 for details of sample preparation and observations).

Results

Results of the palaeontological and dental analyses of the rhinoceros

During the fieldwork, approximately one-third of the whole skeleton was documented within an area of 10 m² (78 skeletal elements in total). The main diagnostic features used to identify the species were based on the preserved cranial remains. Briefly, the excavated upper premolars are hypsodont with thick enamel; the medifossette is closed and circular and the ectoloph profile is wavy on P². The lower M₂ and M₃ have an angular trigonid, rough enamel and narrow V-shaped lingual valleys. The long bones and the metapodials are short and massive. All these characteristics fit well with the diagnostic features of *Coelodonta antiquitatis*. The two upper premolars are relatively worn. The left P² is less worn than P³ and still preserves the medifossette and postfossette. The lower teeth have different degrees of wear. The shape of the lingual valleys in the three premolars and M₁ cannot be observed and only the base of the posterior lingual valley on P₄ is evident. M₂ and M₃ are fully erupted in an advanced stage of wear, but the morphology of the lingual valleys can be still observed (Figure 2).

Dental mesowear analyses revealed that both M₂ of the specimen were characterized by blunt cusps of low elevation; these dental elements had a mesowear score of 6. Dental micro-remain studies showed that the material prepared for microscopy was rich in sand/mineral and calcium phosphate grains. From analyses of the dental calculus and tooth fossae, 2024 particles of isotropic plant micro-fragments were counted and classified, although 4.2% of the plant remains could not be identified with total certainty. Approximately 80% of the plant remains came from the deep fossae and just a smaller fraction from the dental calculus. Plant micro-remains

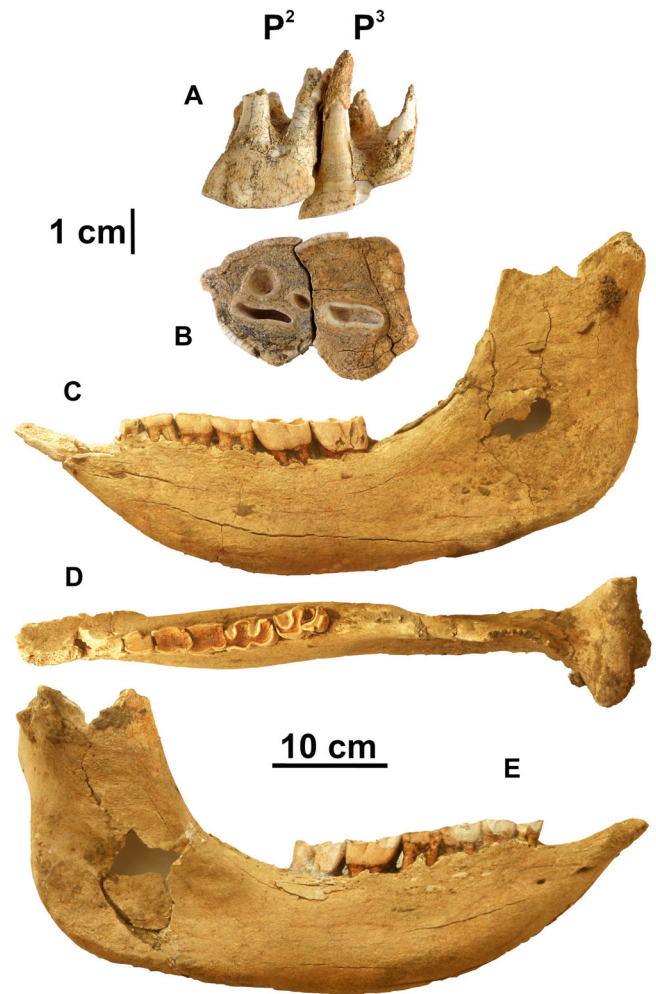


Figure 2. Photos of the P² and P³ teeth (A: labial, B: occlusal view), the left mandible (C: buccal, D: occlusal view) and the right mandible (E: buccal view) of the Pécel woolly rhinoceros. [Color figure can be viewed at wileyonlinelibrary.com]

consisted of lichen fragments, fungal remains, plant tissues, phytoliths, vessels and starch grains. Most of the microfossils were derived from lichen fragments; that is, 87% of the total identified were fungal, generative and vegetative, filamentous structures with distinctive septate texture and characteristic birefringence (Cao, 1990). Furthermore, the conformations revealed characteristics of lichen thalli in many instances with recognizable parts of the lichen cortex, photobiont layer with fungal sheaths of the photobiont cells, soredia, conidia, skeletal elements or asci (Fig. 3; Supporting Information Figs S1 and S2).

The smaller part of the dental micro-remains (13%) consisted of lignified vascular tissues from dicotyledons, plant fibres, fragments of moss epidermis, blocky phytoliths presumably from conifer or dicot bark, stone cells and starch grains. However, the different microfossil particles were not found in great quantity. Propagules of higher plants, such as seeds and pollens, were absent from the fossae. The water used for rinsing and cleaning the teeth was also desiccated and examined to compare with the micro-remains of the samples. As a result, there was no appreciable microfossil content in this dried sample, except for a few unidentified plant fibres. EDX analysis of five pieces of lichen-like fragments showed that the sum of the carbon and oxygen element content of the studied microfossils was 60–68 at.%, indicating the organic origin of the particles.

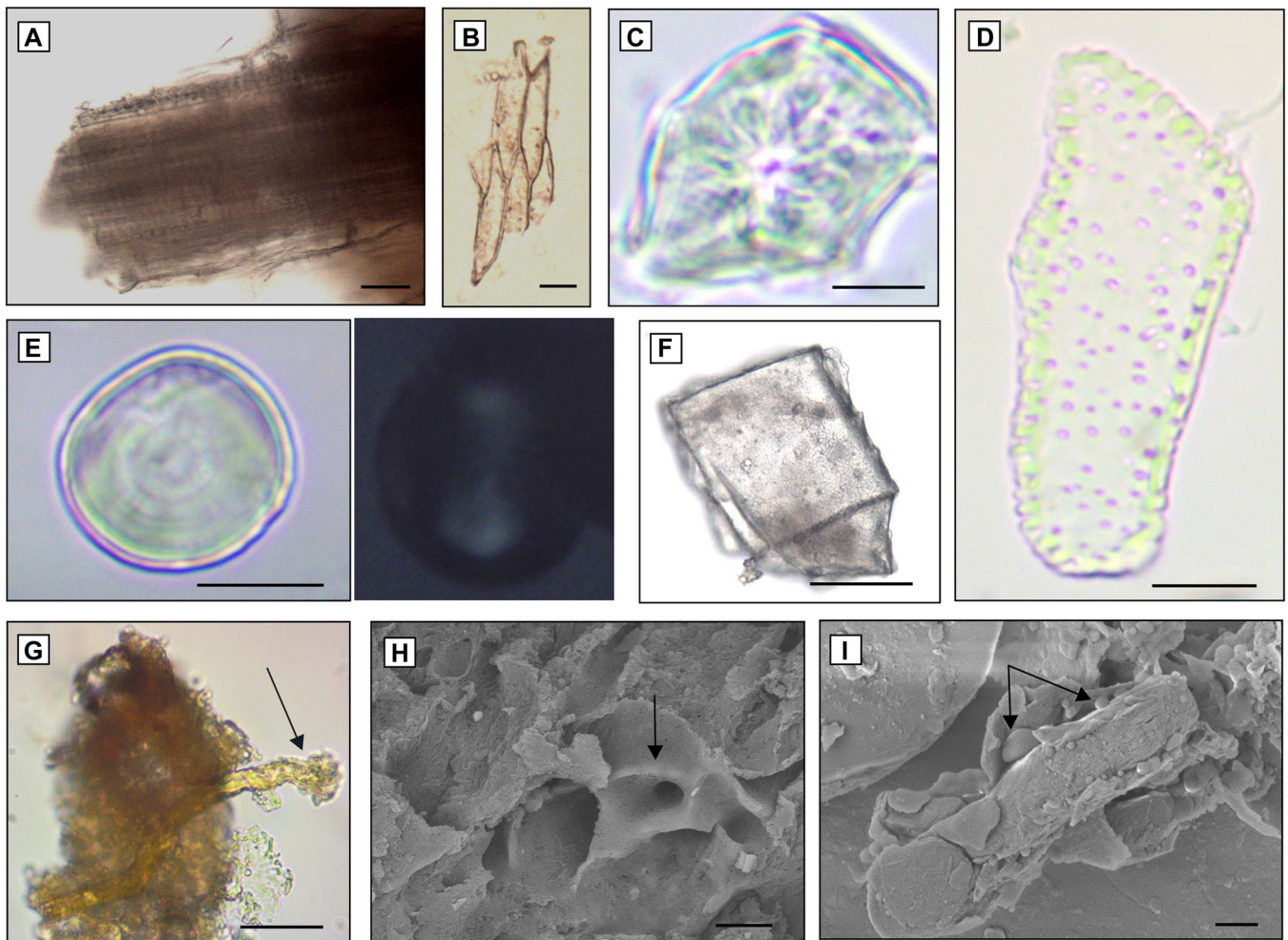


Figure 3. Light and scanning electron micrographs of the plant remains found in the rhinoceros dental calculus and fossae. (A) lignified vascular tissue from dicotyledons. (B) fragment of moss epidermis. (C) stone cell. (D) porous stone cell from bark or xylem. (E) starch grain with its polarized light image showing birefringence. (F) blocky phytolith. (G) lichen fragment with a skeletal binding hypha (arrow). (H) scanning electron micrograph of lichen thallus fragments with hyphae forming photobiont sheaths (arrow). (I) scanning electron micrograph of conidiophore with different stages of microconidium formation (arrows). Scale bars: A, B, E, H, I = 10 µm; C, D, F, G = 20 µm. (Additional photos are provided in SM1). [Color figure can be viewed at wileyonlinelibrary.com]

Table 1. Summary of the results of dating and stable isotope analyses performed on the Pécel rhino

Analysis performed on the Pécel woolly rhino specimen	Sesamoid bone	P ³ tooth
Ultrafiltered collagen content (%)	2.1	4.9
Atomic C/N ratio of collagen	3.4	3.3
Laboratory code of AMS measurements	DeA-18899	DeA-28935
Radiocarbon date (¹⁴ C a BP)	16 940 ± 110	16 900 ± 110
Combined calibrated date range (cal a BP)	20 670–20 220 (median of 20 440)	
δ ¹³ C of collagen (‰, vs. VPDB)	-20.2 ± 0.1	-19.9 ± 0.1
δ ¹⁵ N of collagen (‰, vs. AIR)	1.2 ± 0.1	3.5 ± 0.1
δ ¹⁸ O _p of apatite (‰, vs. SMOW)	10.3 ± 0.4	10.0 ± 0.4
Calculated δ ¹⁸ O _w (‰, vs. SMOW) (calibration Eqs 1–3)	-14.8 ± 0.7	-15.2 ± 0.7
Calculated δ ¹⁸ O _w (‰, SMOW) (calibration Eq. 3)	-14.1	-14.4
Calculated MAAT ranges (°C) (for European city calibration equations)	-0.4 to 2.5	-1.1 to 1.9
Most probable MAAT (°C) (Krakow–Zagreb calibration Eq. 6)	1.0	0.4
Calculated NGT-temperature (°C) (Eq. 7)	0.8	0.0
Smallest difference between MAAT and NGT temperatures (°C)	0.2	0.4
⁸⁷ Sr/ ⁸⁶ Sr isotope ratio of apatite*	0.709132 ± 0.000040	0.709047 ± 0.000021

*The average of the values is 0.709089, within the range determined by the local background samples (0.708788 and 0.709272).

Results of radiocarbon and stable isotope analyses of the osseous samples

Based on visual inspection and sufficient collagen contents, the selected sesamoid bone and the P³ tooth were in good preservation. The carbon and nitrogen contents (45.2 and

15.5%, and 43.8 and 15.6%, respectively), in addition atomic C/N ratios of 3.4 and 3.3 of the ultrafiltered collagen also supported their good condition for isotopic measurements. For the bone and the tooth, radiocarbon measurements yielded blank-corrected radiocarbon dates of 16 940 ± 110 and 16 900 ± 110 ¹⁴C a BP, respectively, providing an average of 16

920 ± 80 ^{14}C a BP (Table 1). Using the 'combine' function in the OxCal program, the mean radiocarbon age corresponds to a calibrated age range of 20 670–20 220 cal a BP (median 20 440 cal a BP) at a 95.4% confidence level (Bronk Ramsey, 2009; Reimer et al., 2020).

The stable carbon and nitrogen isotope measurements of the bone provided a mean $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ value ($\pm\text{SD}$) of -20.2 ± 0.1 and $+1.2 \pm 0.1\text{‰}$, respectively. The $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values ($\pm\text{SD}$) of the P³ tooth were higher, -19.8 ± 0.1 and $+3.5 \pm 0.1\text{‰}$, respectively, and this nitrogen value is significantly different from that of the bone. The $\delta^{18}\text{O}_\text{P}$ values obtained for the indigenous phosphate of the sesamoid bone and P³ enamel samples were $+10.3 \pm 0.4$ and $+10.0 \pm 0.4\text{‰}$, respectively. Regarding the $\delta^{18}\text{O}_\text{w}$ values, the means and standard deviations obtained by the three selected calibration equations specific for horse, bovine and elephant (SM2 Eqs 1, 2 and 3, respectively) ranged from -14.8 ± 1.6 to $-15.1 \pm 1.7\text{‰}$ (Skrzypek et al., 2011). In the MAAT calculations (SM2, Eq. 6), various linear regression equations for more European cities were tested, offering a wider possible temperature interval ranging from -5.2 to $+3.1$ °C. Due to the location of the Pécel site, an average of the Krakow and Zagreb calibration curves (SM2, Eqs 4 and 5) was used in the final MAAT calculations. Other cities are either situated at a too large distance from the site or other geographical effects might influence the $\delta^{18}\text{O}_\text{w}$ values. In addition, applying the $\delta^{18}\text{O}_\text{w}$ values obtained by the three equations, the smallest difference between the MAAT values and the respective NGT-related temperatures (namely -0.2 – 0.4 °C, SM2, Eq. 7) was found in the case of the elephant-related equation ($\delta^{18}\text{O}_\text{w}$ values for the bone and the tooth enamel are -14.1 and -14.4‰). The combination of these two equations gave final MAAT values of 1.0 and 0.4 °C for the bone and enamel (mean of 0.7 °C), which are regarded for our assumptions to be the most likely air temperatures for the studied period. In the frame of the last isotopic analysis, the strontium measurements also yielded consistent results; that is, the values of the local background samples (pine cone, shell) ranged between 0.708788 and 0.709272, constituting one cluster with the rhino's average value of 0.709089.

Discussion

Palaeontological implications for the specimen based on the dental and stable isotope results

The Pécel woolly rhino specimen is one of the most complete, well-documented and age-constrained *Coelodonta* findings from Central Europe, which makes its scientific study exceptionally important. Regarding its biological age, compared with the data reported by Hillman-Smith et al. (1986) for white rhinoceros, the studied specimen resembles those of age class XIV, with an estimated age between 25 and 32 years. This is also supported by analyses of dental wear, based on teeth eruption, facet development and the wear stage of the different teeth positions (IDAS 4 – late adult – stage) (Anders et al., 2011). This late adult stage is characterized by a completely eroded M₁ and P₄. Furthermore, all other lower teeth were in wear, but are not worn down completely. This means that, even though the examined specimen was relatively old, its teeth still retained their functionality well, enabling further analyses of the wear of the molars. At the same time, the P² preserved several features that suggest a younger age. The IDAS 4 relative age stage could be characteristic not only for the older adult specimens of rhinoceroses but also for much younger specimens).

Hillman-Smith et al. (1986) found that the IDAS 4 age stage in the case of *Diceros bicornis* covered almost 40% (beginning at around 20% and spanning until ~60%) of its potential lifespan. Nevertheless, the stage of wear of the lower teeth of the Pécel specimen suggests an age >25 years old.

Based on dental mesowear analyses, both M₂ teeth were characterized by low cusp elevation and blunt cusps. This may be the result of two factors. One possibility is that it was caused by the old age of the specimen. As previously seen, the specimen was possibly in a late adult stage of its life. Mesowear scoring is most reliable when applied to worn teeth that have not yet lost their functionality. Thus, its use on a possibly old specimen with highly abraded molars raises some concerns related to the reliability of the results. As an another possibility, low and blunt cusps can form due to environmental factors. Such low and blunt cusps are implied to be characteristic for specimens consuming almost exclusively abrasive plant materials, as a primarily grazer or due to the increased involuntary intake of grit (dirt, sand, loess particles), which is also supported by the analyses of dental fossae rich in sand/mineral. Similarly, highly abraded molars were recorded for woolly rhinoceros by Pushkina et al. (2020) from the Late Pleistocene Villa Seckendorff location (south-western Germany) and by Rivals et al. (2010) from Late Pleistocene sediments from Brown Bank (North Sea). It must be emphasized that these mesowear results are based on a possibly older specimen, and thus they should be treated with caution. In previous studies, analyses of plant remains from rhino fossae and palynological analysis of the stomach contents of a mummified rhino carcass have revealed that woolly rhinoceros had a diet dominated mainly by grasses, sagebrush and other forbs (Boeskorov et al., 2011; Garutt et al. 1970; Lazarev and Tirskaia 1975; Schreve et al., 2013). In contrast, a single study by Rivals et al. (2010) recorded (using low-magnification micro-wear of woolly rhino specimens from Brown Bank, North Sea) and showed that woolly rhinoceros had a more mixed diet, plotting closer to the browser dietary morphospace. Recently, a seasonally mixed diet was shown by Stefaniak et al. (2021), but the species itself was still tagged as a grazer.

Stable isotopic and dental calculus/fossae analyses allowed us to explore more the details of this specimen's diet. For rhinos older than 31.1k cal a BP, the most comprehensive $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ data set ($n = 32$), ranging from -20.8 to -19.2‰ and from $+0.7$ to $+8.3\text{‰}$, respectively, was published by Jacobi et al. (2009). For younger specimens ($n = 5$), mean $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of $-21.0 \pm 0.8\text{‰}$ and $+5.8 \pm 1.7\text{‰}$ were obtained, but no suggestion was given in either study towards an accurate diet reconstruction of the species (Bocherens, Drucker., 2003). Recently, Rey-Iglesia et al. (2021) collected and reviewed the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of 268 specimen from all over Eurasia and our $\delta^{13}\text{C}$ values around -20‰ fit well into the dataset, reflecting a preferably C3 plant-based diet (Figure 4).

In their publication, Bocherens et al. (1997) assumed some physiological reasons behind the higher $\delta^{15}\text{N}$ values in tooth dentin relative to bones, and thus the $\delta^{15}\text{N}$ value of 3.5‰ for the P³ tooth (erupted at juvenile age) is excluded from our evaluation. As shown in Fig. 4, the $\delta^{15}\text{N}$ value of the sesamoid bone of the Pécel specimen is located in the lower section of the compiled data, so water or nutritional stress (which generally increases the $\delta^{15}\text{N}$ value) can be excluded. Studying the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values along the nasal horn of a woolly rhino, Tiunov and Kirillova (2010) suggested that more positive $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values indicated a summer diet, consuming more graminoids, while lower values possibly represent a larger proportion of woody and shrub-derived forage in the winter diet. Thus, for the Pécel specimen, some minor

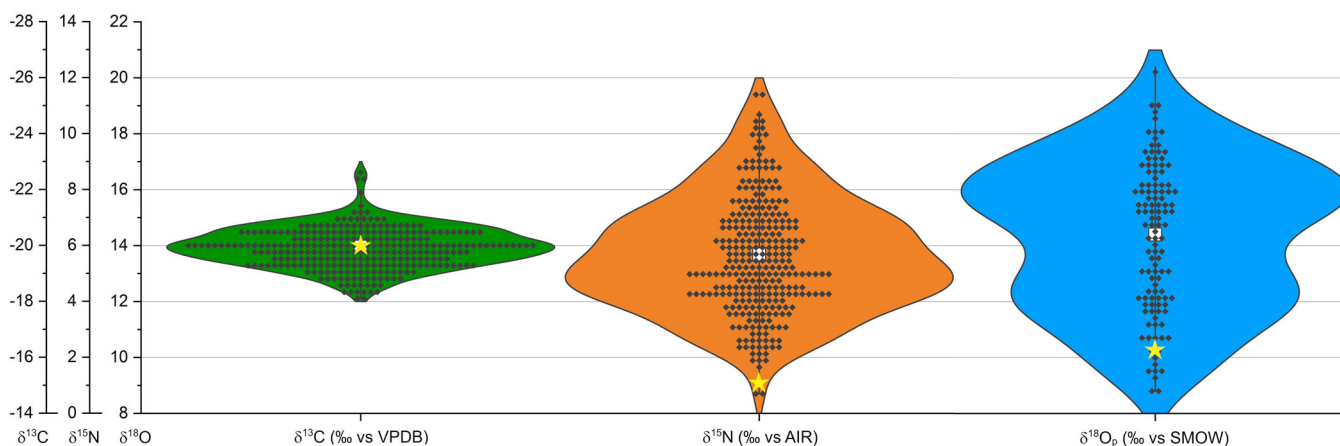


Figure 4. $\delta^{13}\text{C}$, $\delta^{15}\text{N}$ and $\delta^{18}\text{O}_p$ results of the Pécel woolly rhinoceros bone (indicated by yellow star) in a Eurasian context. White squares represent the means of the respective measures. The carbon and nitrogen data set containing 286 results was published by Rey-Iglesia et al. (2021) while the phosphate oxygen data derive from other studies related to Pleistocene large herbivores such as mammoth and horse in Europe (Arppe and Karhu, 2010; Drucker et al., 2015; Kovács et al., 2012; Tütken et al., 2006). [Color figure can be viewed at wileyonlinelibrary.com]

influences deriving from consumption of shrubs, woody or other low-nutrition plants should also be considered, consistent with the suggestions for grazers by Stefaniak et al. (2021). This assumption was partly supported by our dental plant microfossil analyses, in which 87% of the microfossils derived from lichen fragments. Nevertheless, plant remains in the fossae can frequently be exchanged during feeding and drinking, representing only the food in the last months of the animal's life (Grube, 2003; Stefaniak et al., 2021; van der Made and Grube, 2010). Based on previous dental calculus analyses from various locations and species [e.g. Gobetz and Bozarth (2001) for *Mammuthus americanus*; Scott-Cummings and Albert (2007) for *Mammuthus columbi*], a large number of grass phytoliths would have been expected for this woolly rhinoceros, but only two phytoliths, presumably originating from conifer or dicot bark, were found in the calculus (ICPT, 2019). In addition, the microfossils in the fossae showed that the last food of the Pécel specimen consisted mostly of lichens. Although the relatively depleted $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values may suggest the consumption of mosses as well, the preservation of those remains usually is poor (Fox-Dobbs et al., 2008). The lignified vascular tissues, fibres and stone cells, presumably of bark origin, are also indicative of feeding on shrub shoots. The absence of herbaceous plants, pollen and other diaspores remains in the fossae suggests that the animal's death occurred during a cold period (Grube, 2003; van der Made and Grube, 2010; Stefaniak et al., 2021). Consequently, this specimen was most probably primarily a grazer, with some seasonal changes to its diet. During cold periods with an absence of grass and herbs, presumably it might have eaten soft shoots of trees and shrubs (Stefaniak et al., 2021), or according to our results, a larger amount lichen or moss. Thus, the more depleted $\delta^{15}\text{N}$ values during the winter diet, observed by Tiunov and Kirillova (2010), can also be refined, indicating the possibility of consuming lichen and moss.

Environmental implications for the Pécel site based on the dental and stable isotope results

The Pécel-Kis hársas woolly rhinoceros is partial, but there is no evidence to suggest an influence of carnivores or scavengers in the formation of the assemblage. The surface of the bones and teeth have been largely destroyed by root etching, and consequently no cut-marks could be recognized on them. Nevertheless, based on the spatial association of four chert points to the scapula and a rib (Figure 5), we assume that

the specimen was hunted and/or butchered onsite by Epigravettian people (15.0–26.5 ka) (Markó, 2018). Wear analysis revealed traces on the stones which may correspond to hunting and/or butchering activities, but not exclusively, and thus failed to clearly identify such activities (SM3).

In addition to revealing any human presence in the area, our final goal was to at least partly reconstruct some ambient environmental characteristics that prevailed in the region at the time. Bone stable isotope ($\delta^{13}\text{C}$, $\delta^{15}\text{N}$, $\delta^{18}\text{O}$, $^{87}\text{Sr}/^{86}\text{Sr}$), combined dental mesowear and plant microremnant results were jointly evaluated to gain more information about the environmental and climatic conditions. Since the $^{87}\text{Sr}/^{86}\text{Sr}$ results of the left P³ tooth and the sesamoid bone showed the same strontium isotope ratio value within a 95.4% confidence level, and are within the range determined from the local background samples, any significant long-distant migration of the specimen can be excluded. Hence, biogeochemical analyses of the remains can be used to for palaeoenvironmental reconstruction of the Pécel-Kis hársas site.

The calculated MAAT values of 0.4 °C (for tooth enamel) and 1.0 °C (for the bone) suggest a relatively low ambient temperature. Similar MAAT prevails today in the boreal forest and forest tundra biomes of Eurasia (Walter and Box, 1976). Considering that the P² tooth erupts at the age of 7–9 years (Hillman-Smith et al., 1986) and the specimen died after the age of 25 years, the ambient MAAT might not have varied significantly over these 15–20 years. These MAAT values are in good agreement with the NGT temperatures of 0.0 and 0.8 °C calculated from the $\delta^{18}\text{O}_w$ values for the enamel and bone samples, respectively. Earlier noble gas measurements have shown that in the southern part of the Great Hungarian Plain (southern Pannonian Basin), the average infiltration temperature of surface water was 3.3 ± 0.4 °C at the end of the LGM (Varsányi et al., 2011). Pécel is, however, situated farther north relative to the Plain. This loessy-sandy area has a relatively cold mesoclimate still today, with cold continental forest steppe vegetation (Fekete et al., 2010), so the lower values are unambiguously plausible. Assuming that the lower/higher $\delta^{18}\text{O}_p$ values of the osseous material are directly proportional to lower/higher MAAT temperatures, placing our value of 10.0‰ for the bone into continental and regional contexts can help us to establish an average stable oxygen and an indirect MAAT scale over Europe (Figure 4). For example, for the northern European region spanning from Denmark to Estonia, Arppe et al. (2010) showed new quantitative oxygen isotopic records regarding the middle



Figure 5. Position of chert artefact no. 1 relative to the left scapula (a and b) and artefact no. 2 relative to a rib (c) of the rhinoceros specimen. [Color figure can be viewed at wileyonlinelibrary.com]

and late Weichselian period (24–52k cal a BP), using 28 mammoth enamel samples. In their study, $\delta^{18}\text{O}$ values of enamel phosphate spanned the range 8.8–16.1‰, corresponding to air temperatures between $-5.6/ -3.8$ and 6.3 °C. For Western Europe, Drucker et al. (2015) showed that phosphate $\delta^{18}\text{O}$ results of woolly mammoth, reindeer and horse specimens of 20–35k cal a BP found in Germany and France ranged from 14.0‰ to 20.4‰, but these isotope results were not converted into MAAT values. The average $\delta^{18}\text{O}_p$ value for mammoths, steppe bisons and one woolly rhinoceros that lived between 45 and 50k cal a BP near Zurich, Switzerland was 11.7 ± 0.9 ‰, corresponding to a MAAT of 4.3 ± 2.1 °C. This low temperature was then associated with a C3 plant-dominated ‘open tundra-like’ environment (Tütken et al., 2006). The situation in East Central Europe, including Hungary, was studied by Kovács et al. (2012), revealing that the $\delta^{18}\text{O}_p$ of woolly mammoths, horses and one woolly rhino around 16–30 ka varied from 13.1‰ to 19.2‰, pointing to a minimum MAAT of 8.1 °C. Thus, considering the 124 published results above, an approximate $\delta^{18}\text{O}$ scale can be drawn for Europe, where 8.8 and 20.4‰ represent the cool and warm endpoints. The value of 10‰ is still situated in the ‘cold climate’ segment of the data, and thus we may assume that the site was dominated by a rather low ambient temperature and cold climate at the end of the LGM.

The harsh conditions, mainly through habitat and diet, might have also played a role in developing a significantly low bone $\delta^{15}\text{N}$ value at the end of the lifetime of the specimen. The value of 1.2‰ of the bone was probably due to environmental factors such as temperature or moisture (Richards and Hedges, 2003). Similar to previous studies involving other species, Rey-Iglesia et al. (2021) revealed a significant and gradual decline in $\delta^{15}\text{N}$ of woolly rhinos inhabiting the Western/Central European and the Eastern European/Urals regions from the pre-LGM to the end of the post-LGM periods (~ 59 –12k cal a BP). Uniformly, the post-LGM decrease of $\delta^{15}\text{N}$ was attributed to increasing moisture due to higher precipitation and degrading permafrost (Drucker and Billiou, 2003; Stevens and Hedges, 2004; Stevens et al., 2008; Rabanus-Wallace et al., 2017). Moreover, temperature and moisture are closely associated with the open or closed nature of the soil’s nitrogen cycle (nitrogen re-cycling against the inputs and outputs in the ecosystem) in some regions (Stevens and Hedges, 2004; Stevens et al., 2008), where the interactions between plants and symbiotic fungi (mycorrhizae) might have also been a significant mechanism influencing the soil and plant $\delta^{15}\text{N}$ values (Rey-Iglesia et al., 2021). Even today, plants in cold and nutrient-poor environments (taiga and tundra belts) rely on ecto- or ericoid mycorrhizal associations to aid their uptake of accumulated organic nitrogen, which often induces especially depleted plant $\delta^{15}\text{N}$ values due to the retention of

enriched N forms by fungi (Hobbie and Ho, 2012). As the MAAT values indicate, effective warming or higher moisture is not likely to have occurred in the lifetime of this rhinoceros, and thus we assume that the depleted $\delta^{15}\text{N}$ value resulted from the degraded nitrogen cycle of the local soil. Although the continuous ice sheet did not cross the Carpathian Mountains, sporadic and temporary permafrost, inducing cryoturbation structures and sand-wedge polygons, have been shown to have penetrated into the northern part of the Pannonian Basin during the Late Pleistocene (Kovács et al., 2007; Fábián et al., 2014; Ruszkiczay-Rüdiger and Kern, 2016). The margin of continuous permafrost, which was modeled for the contemporaneous region by Ruszkiczay-Rüdiger and Kern

(2016), was situated close to the southern border of the Carpathians, and the Pécel-Kis hársas site is also located directly next to the contemporaneous margin of the discontinuous permafrost zone (Figure 1a). Thus, a very harsh and cold climate should have occasionally dominated the region, which can explain the reduction in soil productivity (Drucker et al., 2003, Stevens et al., 2008). Nevertheless, probably due to the cold climate, some soil dislocation or formation of new loessy sand layers also cannot be excluded, resulting in a significant change in the soil-derived forms of nitrogen available for plants and plant–fungi associations. Our dental calculus analyses, inferring a mostly lichen/moss diet, also suggest nutrient-poor and basic soil conditions with bare surfaces in

Table 2. Summary of our results and conclusions

	Results	Conclusions	Highlight
Palaeontological observations	78 skeletal elements at the Pécel-Kis hársas locality	The bones belonged to a woolly rhinoceros (<i>Coelodonta antiquitatis</i>) that lived at the end of the Last Glacial Maximum (LGM)	At the time of the rhino's death, the climatic conditions corresponded to a cold, tundra-like environment, associated with a basic and open vegetation. Archaeological data suggest (but this could not be demonstrated strongly) that this rhino specimen was killed by Epigravettian people living contemporaneously in the Pannonian Basin
	The combined radiocarbon age range for a sesamoid bone and P3 tooth is 20 670–20 220 cal a BP		
	The upper premolar teeth are hypsodont with thick enamel. The lower M ₂ and M ₃ have an angular trigonid, rough enamel and narrow V-shaped lingual valleys. The long bones and the metapodials are short and massive		
	The enamel surface of the specimen was mostly covered by fine scratches with a negligible number of coarse and no hypercoarse scratches	This specimen was a primarily grazer that altered its diet seasonally. A strong influence deriving from lichen and moss consumption can be observed, related to the last period of the specimen's life. At this time, the specimen did not obtain a sufficient amount of appropriate forage of grasses	
	87% of the total identified plant remains in the teeth derived from fungal, generative and vegetative, filamentous structures with distinctive septate texture and characteristic birefringence		
	Only 13% of the dental micro-remains composed of lignified vascular tissues from dicotyledons, plant fibres, fragments of moss epidermis, blocky phytoliths presumably from a conifer or dicot bark, stone cells and starch grains		
Archaeological observations	Six artefacts were found next to the bone assemblage. The distribution and/or types of fractures, scars and striations found on two obsidian flakes led to the conclusion that the artefact was used before being fractured	These traces show that the artefacts were involved in longitudinal motion (i.e. cutting or sawing) to process soft to medium hardness material. Striations (including chatter marks) on the artefacts are likely to be related to hafting	
	The edges of Pécel 005 are heavily altered by striations		
Environmental implications	The stable strontium isotopic ratio ($^{87}\text{Sr}/^{86}\text{Sr}$) of a sesamoid bone of the rhino specimen was 0.709132 ± 0.000040 , constituting one cluster with the local background values	The ambient temperature might be low enough to hinder the productivity of the soil. Some upper ground dislocation could also promote the basic character of the soil. The vegetation is suggested to have been pioneering and open due to the immature soil	
	The stable carbon isotopic ratio ($\delta^{13}\text{C}$ VPDB) of the same sesamoid bone was $-20.2 \pm 0.1\text{‰}$		
	The stable nitrogen isotopic ratio ($\delta^{15}\text{N}$ AIR) of the same sesamoid bone was $1.2 \pm 0.1\text{‰}$		
	The stable oxygen isotopic ratio ($\delta^{18}\text{O}$ SMOW) of the same sesamoid bone was $10.3 \pm 0.4\text{‰}$		
	The calculated mean annual air temperature is suggested to have been around 1 °C		

some places. In a study conducted in the recent Arctic tundra region, the most depleted $\delta^{15}\text{N}$ values (from -5 to -2.5%) for plants were found primarily in association with lichens and mosses, reflecting the $\delta^{15}\text{N}$ signals of atmospheric N deposition on the surface or primary N fixation (Skrzypek et al., 2015). Thus, based on the isotopic and dental microfossil remains, we assume that the late life and the death of this rhinoceros occurred during harsh and cold climatic conditions in a tundra-like environment with open vegetation.

Although our environmental assumptions are based solely on analytical results from one specimen, they are also supported by other studies performed for the whole Pannonian Basin. So far, quantitative large-scale climate reconstructions for the LGM and last glacial termination have been based on pollen, loess, mollusc and stable isotope analyses and climate models (Sümegei et al., 2018, 2011; Bradák et al., 2011; Újvári et al., 2017; Magyari et al., 2019, 2014). Based on the most relevant quantitative comparison of modern and fossil pollen spectra (e.g. at Nagymohos Peat Bog in Northern Hungary and Kokad Mire in Eastern Hungary), it has been inferred that the landscape of the Pannonian Basin was dominated by cold steppe or steppe–tundra outside the river floodplains. In contrast, wet and mesic grasslands and boreal forest steppe occurred in floodplains and locations with sufficient water supply. Aiming to assess the vegetation of the Pécel–Kis hársas site, biome reconstructions were performed on the nearest pollen records (Danube–Tisza Interfluvium) covering the last glacial termination. The deposits of inter-dune hollow lakes (Bócsa and Kolon lakes, ~ 80 – 90 km south of Pécel; Járai–Kömlödi, 1985; Borsy et al., 1991; Lóki et al., 1995) indicate pine–birch forest steppe and cold continental steppe vegetation around 21–20 ka. Summer mean temperatures (June–August) here might have fluctuated around 12 – 14 °C (Magyari et al., 2022). In another reconstruction study from the Debrecen–Brickyard sequence in the Hajdúság loess region (East Hungary), Sümegei (2005) showed that the species-poor mollusc fauna was dominated by cold-adapted xeromontane and arctic-alpine species during the LGM, pointing to a mosaic-structured, cold treeless steppe or steppe–tundra landscape influenced by edaphic factors around 21k cal a BP. Unfortunately, the time resolution of these sediment-based pollen and plant-remain records is still too low to be suitable for accurate estimation of the climatic conditions during such a short period as the lifespan of this rhinoceros. In contrast, sequential isotope analysis on bones and teeth of large herbivores and carnivorous found at a site, the time resolution of any environmental reconstruction may be reduced to a couple of years or decades (Table 2).

Conclusions

Palaeontological and combined multi-disciplinary analyses were performed on the remains of a mature female woolly rhinoceros (*Coelodonta antiquitatis*) found at the Pécel–Kis hársas site, in order to reconstruct the diet and palaeoenvironment of the specimen. No cutmarks were recognized on the etched surface of the osseous material, but we assume that the rhino was killed by Epigravettian hunters ~ 20.4 k cal a BP. The hypothesis of human influence was inferred by the four chert tools and two obsidian blades, which were found directly near the bone assemblage. However, apart from the position of the finds, no evidence has been found to unequivocally support this hypothesis. Regarding the specimen, based on the isotopic and dental plant microfossil results, a specialized lichen- (and possibly moss-) consuming diet could be identified regarding the last period of its life. Such diet preference has

not been highlighted in the literature previously with regard to woolly rhinoceros. Strontium and $\delta^{18}\text{O}$ results of bone bioapatite suggest a cold climate with a MAAT of ~ 0.7 °C for the contemporaneous site. Meanwhile, the $\delta^{15}\text{N}$ value is extremely low, even in a Eurasian context, and may have resulted from the proximity of the discontinuous permafrost zone and some intensive upper soil dislocation. Based on the environmental conditions implied by the low ambient temperature and open, lichen-dominated vegetation, the specimen may have died in a harsh tundra-like (steppe tundra) habitat. These conclusions are also supported by palaeoenvironmental reconstruction modeling experiments related to the Debrecen–Brickyard sequence in the Hajdúság loess region, resulting in an adjacent mosaic-structured, cold treeless steppe or steppe–tundra landscape around 21 ka.

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Data availability statement

All relevant data are provided in the text and the Supporting Information.

Supporting information

Additional supporting information can be found in the online version of this article.

SM1. Dental mesowear and calculus/fossae analyses.

SM2. Radiocarbon dating and stable isotope analyses.

SM3. Use-wear analysis of the stone artefacts from the Pécel–Kis hársas site.

Abbreviations. LGM, Last Glacial Maximum; MAAT, mean annual air temperature; HNHM, Hungarian Natural History Museum; IDAS, individual dental age stage; INTERACT, International Radiocarbon AMS Competence and Training Center; T_{airK} , mean of temperatures related to Krakow; T_{airZ} , mean of temperatures related to Zagreb; NGT, noble gas temperature; SEM, scanning electron microscope; EDX, energy dispersive X-ray spectroscopy; C/N, atomic carbon/nitrogen ratio; MIS, Marine Isotope Stage.

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