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Browsers, grazers or mix-feeders? Study of the diet of extinct Pleistocene Eurasian forest rhinoceros Stephanorhinus kirchbergensis (Jäger, 1839) and woolly rhinoceros Coelodonta antiquitatis (Blumenbach, 1799)

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ABSTRACT

The wooly rhinoceros (*Coelodonta antiquitatis*) and forest rhinoceros (*Stephanorhinus kirchbergensis*) were prominent representatives of the Middle and Late Pleistocene glacial and interglacial faunas of Eurasia. Their diet has traditionally been inferred on functional morphology of the dentition and skull. In rare cases, food remains are preserved in the fossas of the teeth or as gut content. New approaches to infer diet include the study of isotopes and mesowear. Here we apply all four methods to infer the diet of these emblematic rhinoceros' species and compare the food actually taken with the food available, as indicated by independent botanical data from the localities where the rhinoceros' fossils were found: Gorzów Wielkopolski (Eemian) and Starunia (Middle Vistulian) as well as analysis of literature data. We also made inferences on the season of death of these individuals.

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Our results indicate that the woolly rhino in both Europe and Asia (Siberia) was mainly a grazer, although at different times of the year and depending on the region its diet was also supplemented by leaves of shrubs and trees. According to the results of isotope studies, there were important individual variations. The data show a clear seasonal variation in the isotope composition of this rhino's diet. In contrast, *Stephanorhinus kirchbergensis* was a browser, though its diet included low-growing vegetation. Its habitat consisted of various types of forests, from riparian to deciduous and mixed forests, and open areas. The diet of this species consisted of selected items of vegetation, also including plants growing near both flowing and standing waters. The food remains from the fossae of the teeth indicated flexible browsing, confirming the previous interpretations based on functional morphology and stable isotopes. Long-term data from mesowear and microwear across a wider range of *S. kirchbergensis* fossils indicate a more mixed diet with a browsing component. The different diets of both of rhinoceros reflect not only the different habitats, but also climate changes that occurred during the Late Pleistocene.

1. Introduction

The diet of extinct rhinos is usually inferred on the basis of functional morphology, dental wear, and isotopes (Zeuner, F. 1934; Fortelius et al., 1993; Bocherens et al., 1995; Rivals et al., 2007; Tafforeau et al., 2007; Tiunov and Kirillova, 2010; Bocherens, 2014; Pushkina et al., 2014; Van Asperen and Kahlke, 2015; Kirilova et al., 2017). In very particular cases, it is possible to study the gastro-intestinal content (e.g. Ukraintseva, 1993). Plant remains from the fossae of the teeth of herbivores are reported only in a few cases: the woolly rhinoceros *Coleodonta antiquitatis* from Siberia (Garutt et al., 1970; Boeskorov et al., 2011a, b; Boeskorov, 2012) and from inside of the rhinoceros from Starunia, Ukraine (Szafer, 1930), Quaternary herbivores from Alaska and NE Siberia (Guthrie, 1990, 2001), *Stephanorhinus kirchbergensis* from Neumark Nord, Germany (Grübe, 2003; Van der Made and Grübe, 2010) and the Chondon River (Kirillova et al., 2017) and the giant deer *Megaloceros giganteus* from the North Sea (Van Geel et al., 2019). Previously, the diet of *S. kirchbergensis* was also interpreted on the basis of tooth and skull morphology and mesowear (e.g. Zeuner, F. 1934; Fortelius et al., 1993; Van Asperen and Kahlke, 2015), also with carbon stable isotopes (Pushkina et al., 2014) and its habitat based on skeletal morphology and dietary adaptations (e.g. Fortelius et al., 1993). The three cases, where the last food of representatives of this species is known, are widely separated both geographically and temporally, cover different environments and seasons and thus provide a more complete idea of the diet of this species (Van der Made and Grübe, 2010; Kirillova et al., 2017; Van Geel et al., 2019).

The main research goals of the present study are to provide new data on the diet and food adaptations of extinct rhinos based on results obtained from two specimens representing *Stephanorhinus kirchbergensis* (Jäger, 1839) and *Coelodonta antiquitatis* (Blumenbach, 1799). The first one is originated from Gorzów Wielkopolski (Poland) from the Eemian Interglacial (Sobczyk et al., 2020) and the latter came from Starunia (Ukraine) from the Vistulian (Szafer, 1930). Previous findings of plant remains in fossas of the fossil teeth are uncommon, so the finding of a unique plant-rich assemblage of *S. kirchbergensis* from Gorzów Wielkopolski may significantly broaden our knowledge concerning food choices by this species. New studies include the identification of plant remains from fossas of teeth and surrounding sediments, accompanied by morphological and mesowear analysis, isotope studies, occurrence and palaecology of Cladocera remains, as well as a thorough analysis of literature sources. In addition, plant remains from the intestine of the most famous find of *C. antiquitatis* from Starunia are described here for the first time. These new data allow to reconstruct the diet of these species and the season of their supposed death. The obtained results were compared with similar finds from the Middle and Late Pleistocene of Eurasia.

2. Material and methods

2.1. The sites

2.1.1. Gorzów Wielkopolski

Plant remains found in the fossae of teeth and in the immediate vicinity of the *S. kirchbergensis* skeleton from Gorzów Wielkopolski (52°43′51″ N, 15°14′18″ E), NW Poland (Fig. 1) were studied. This specimen was buried in lacustrine sediments originating during the Eemian Interglacial (MIS 5e) (Sobczyk et al., 2020). The skeleton from Gorzów Wielkopolski was found in gyttja sandwiched between sediments dated with OSL between 123.6 ± 10.1 (lower horizon) and 98.8 ± 7.9 ka (upper horizon) (Sobczyk et al., 2020).

Rhino remains were retrieved from highly compacted lacustrine deposits represented by grey limnic chalk and calcareous gyttja. Numerous samples for studies were taken during detailed surveys of the profile. In the lake were plant debris, as well as mollusk shells, midge (Chironomidae) larvae, cladocerans, insects, and fish remains. Preliminary results of the study of the Gorzów profile include Badura et al. (2017) and results of geological research presented by Sobczyk et al. (2020). *S. kirchberensis* remains are deposited in the collection of the Department of Palaeozoology, Institute of Environmental Biology, Faculty of Biological Sciences of the University of Wrocław (Poland).

In addition to palaeobotanical studies (pollen and plant macroremains), mesowear and isotope analyses were also performed for a more complete reconstruction of the diet and paleoecology of this rhino. To get a comparative material, isotope analyses of the teeth of *S. kirchbergensis* were also carried out on specimens from Konin (Lorek, 1988) and Warsaw (Borsuk-Białynicka and Jakubowski, 1972), as well as the Palaeolithic site Wrocław-Hallera (Wiśniewski et al., 2009) (Table 1).

2.1.2. Starunia

The second analysed locality is Starunia (western Ukraine) (48°42′38″ N, 24°29′29″E) (Fig. 1), where more or less complete remains of four *C. antiquitatis* individuals were found, along with preserved soft parts, dated back to the end of the Last Glaciation. Plant remains from the most complete specimen were found in cheek tooth fossae, intestines of the rhinoceros, and from the sediments surrounding its mummified body. The present study includes the analysis of plant macroremains published by Szafer (1930), and a set of new data from materials deposited in the Palaeobotanical Museum of W. Szafer Institute of Botany, PAS (coll. no. Q236).

Starunia is famous for providing the first morphological data concerning the woolly rhino's diet from Europe, where an earth wax mine was established at the beginning of the 20th century. In 1929, almost complete remains of a 3-year-old female woolly rhinoceros were discovered there together with poorly preserved bones of two other individuals. They are in the collections of the Institute of Systematics and Evolution of Animals of the Polish Academy of Sciences in Kraków (Poland). In total, the remains of four rhinos and one mammoth were found there. In addition to large ungulates, the remains of insects, birds, mammals (rodents, lagomorphs, and carnivores), as well as accompanying plant remains were obtained (Bayger et al., 1914; Niezabitowski-Lubicz 1911a,b; Niezabitowski et al., 1914; Nowak et al., 1930; Stach, 1930; Lengersdorf, 1934; Zeuner F., 1934). Researchers have returned many times to Starunia, providing further geological, paleontological and geochemical research (Kubiak, 1971, 2003, 2008; Angus, 1973; Borsuk-Białynicka, 1973; Granoszewski, 2002; Pawłowski, 2003; Alexandrowicz, 2004; Kubiak and Drygant, 2005; Kotarba, 2005, 2009; Kotarba and Stachowicz-Rybka, 2008; Kotarba et al., 2008).

Several palaeobotanical studies were completed. In the sediments surrounding the rhino carcass, Szafer (1930) identified the taxa confirming the glacial type of the Starunia flora and determined that *Betula nana* was a dominant species. It gave a name for deposits ("clays with *Betula nana*") associated with beds from which the remains of large mammals were obtained. From the same context, branches of mosses (Gams, 1934; Szafran, 1934) and willow leaves (Kucowa, 1954) were studied. Due to recent palaeobotanical research of Starunia (Stachowicz-Rybka et al., 2009a, b), the history of the flora and environmental changes in that area during the Last Glacial Maximum (LGM) and Holocene were recreated in detail, providing a precise reconstruction of wetland ecosystem and its surroundings. The radiocarbon method allowed to estimate the exact age of the woolly rhinos from Starunia at

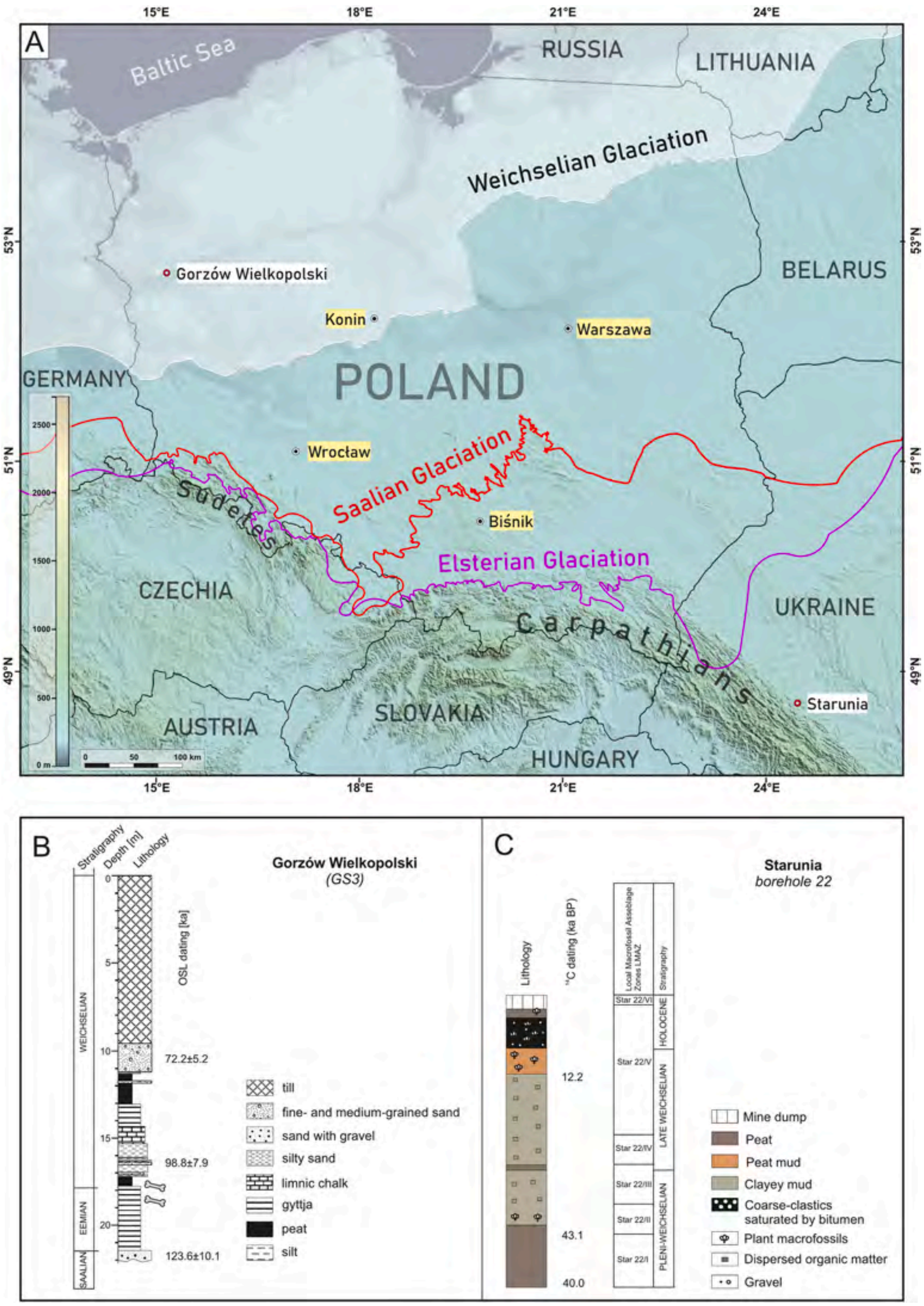

Fig. 1. Location map of Gorzów Wielkopolski and Starunia with findings of extinct rhinos. Digital elevation model is based on Shuttle Radar Topography Mission 3-arc-seconds data (Farr et al., 2007) with a marked maximum extent of the Pleistocene Scandinavian Ice Sheet during Elsterian, Saalian and Vistulian advances, respectively. A – SRTM-based (Farr et al., 2007) digital elevation model (DEM) for location of research sites with synthetisized lines of maximum Pleistocene Ice Sheet glaciations extent in Central Europe. Lower insets present simplified lithological sections for Gorzów Wielkopolski (B) and Starunia (C) reserach sites respectively. OSL dating results and 14C dating results are presented after Sobczyk et al. (2020) and (Kuc et al., 2012; Stachowicz-Rybka et al., 2009a, Sokołowski and Stachowicz-Rybka, 2009), respectively.

37.7 ± 1.7 ka (Kuc et al., 2009, 2012).

2.2. *Palaeobotany*

2.2.1. *Palynological analysis*

During the preparation of the rhinoceros' skeleton from Gorzów Wielkopolski, plant debris was noticed in the fossae of its teeth. The collected material was prepared and analysed together with that surrounding the skeleton. The sediment filled the rhino's caverns teeth: P^2dex (sample 1), P^3dex (sample 2), P^4dex (sample 3), M^1dex (sample 4), M^2dex (sample 5), P^2sin (sample 6), P^3sin (sample 7), P^4sin (sample 8), M^1sin (sample 9), M^2sin (sample 10), M^3sin (sample 11). The sediment was extracted from the eleven tooth fossae, flooded with distilled water and left for 24 h. Then tissue fragments were rinsed in water on a 250 μm sieve. Larger fragments were separated and the water with the sediment was shaken in an ultrasonic washer on a 5 μm sieve. The material in the range of 5–250 μm was centrifuged during 3 min at 4900 rpm. The samples were then directly subjected to pollen analysis without further maceration. The sediment extracted from the tooth No. P^3sin is presented in Fig. S1.

Six samples of the lacustrine sediment directly adjacent to the rhino jaw ZPALUWr/GI/77 marked as M^1dex (6); P^1sin, P^3sin (10,11); M^2dex (5); P^4dex (7); P^3dex, P^2dex, P^2sin (4, 8, 9); M^1sin, M^2sin, M^3sin (1, 2, 3) were processed in laboratory using the acetolysis mixture by Erdtman's method (Erdtman, 1960) and heavy liquid method by Faegri and Iversen (1989).

The results of the analysis are presented on a diagram created with the POLPAL programm (Nalepka and Walanus, 2003).

2.2.2. *Analysis of plant macrofossils*

From Gorzów Wielkopolski for the identification of plant macrofossils, eleven samples extracted from tooth fossae and six samples of the lacustrine sediment directly adjacent to the rhino jaw ca. 4–40 mL were macerated in boiling water with the addition of 10% KOH to reduce the sediment and remove humic matter. The material was sorted under a stereoscopic microscope. Plant remains were preserved with a standard mixture of alcohol, water and glycerin in 1:1:1 proportion, with the addition of thymol. Fragments of plants were then dried with 50% ethyl alcohol.

From Starunia, the plant material associated to *C. antiquitatis* were deposited in the Museum of IB PAS (coll. no. Q236) in the form of plates, microscope slides, and cubicles. The samples contained vegetative parts of plants, seeds, fruits and seed scales extracted from the teeth, intestines of the rhinoceros and from the sediments surrounding the rhino's body. The only information about the origin of the material is contained in the original specifications placed on plates, cells or microscopic samples. These archival materials were described quite imprecisely. Most of these samples were signed only as "Starunia", some of the inscriptions have become unreadable, while other specimens have original labels comprising additional information about the exact collecting place (e.g. "from inside the rhinoceros", "from guts and teeth of the rhinoceros", "from intestines and teeth of the rhinoceros" and "near the rhinoceros". Only the 14 best-preserved samples (Q236/41, Q236/60, Q236/61, Q236/62a, Q236/63, Q236/108, Q236/110, Q236/112, Q236/124, Q236/125, Q236/126, Q236/127, Q236/128 and Q236/129) were chosen and analysed in our study. Unfortunately, there are no archival notes about the preparation, the method of collecting of this material or its exact location – especially in the case of sediment surrounding the rhino's body. These unusual materials have never been fully analysed, probably for two reasons. The work undertaken by Szafer was interrupted by World War II, and due to the lack of exact location and the method of preparation of plant remains, no attempt was ever made to process them. Due to the extraordinary value of these materials, we decided to present the content of preparations which are the most interesting in terms of diet and the living environment of *C. antiqiutatis*.

Macrofossils were identified using atlases (Kats et al., 1965; Berggren, 1969; Schweingruber, 1990; Cappers et al., 2006; Velichkevich and Zastawniak, 2006, 2008), a reference collection of extant plants and a collection of plant macrofossils from the Palaeobotanical Museum of W. Szafer Institute of Botany, Polish Academy of Sciences (IB PAS, Kraków, Poland). The majority of wood taxa were identified up to genus level since their species have similar anatomy (Schweingruber, 1990). Fruits and seeds were analysed under a stereomicroscope, while a reflected light microscope and Hitachi S-4700 scanning electron microscope (SEM) were used for the identification of wood remains in the Laboratory of Scanning Electron Microscopy and Microanalysis of the Institute of Geological Sciences, Jagiellonian University (Kraków, Poland). The results of the analysis are presented on a diagram created with the POLPAL programm (Nalepka and Walanus, 2003).

2.3. *Cladocera analysis*

Analysis of cladoceran remains was performed using six samples of sediment from the area in direct connection to the rhino's jaw from Gorzów Wielkopolski. Samples of 1 cm^3 were prepared according to a slightly modified standard procedure (Frey, 1986). After the removal of carbonates using HCl, each sample was boiled in 10% KOH for 20 min. After washing with distilled water, the residue was sieved through a 40-μm mesh sieve. The fine material was transferred into a polycarbon test tube. Prior to counting, the remains were coloured with safranine. The samples were analysed under a light microscope with a 100–400 × magnification. Firstly, all remains from each slide were counted (headshield, shell, postabdomen, postabdominal claws, exopods, antennules), and the most abundant remains of each taxon were chosen to represent the number of individuals. The identification and interpretation of the remains follow Frey (1958, 1962), Goulden (1964), Szeroczyńska (1985), Hofmann (1986, 2000), Korhola (1990), Duigan (1992), Flössner (2000), Szeroczyńska and Sarmaja-Korjonen (2007).

Table 1

Specimens studied by isotope analyses and infrared spectroscopy.

Species	Locality	Chronology	Inv. No.	Collection	Tooth	Lab code	Samples
S. kirchbergensis	Gorzów Wielkopolski	MIS 5e	ZPALUwr/GI/77	ZPALUWr	P_2 dex	StG	StG a–f
S. kirchbergensis	Wrocław-Hallera	MIS 4/3	B129/2016/Ha	IAUWr	M^1/M^2 dex	StH	StH a–f
S. kirchbergensis	Konin	MIS 5e	MOK/O/484/1	District Museum in Konin	P^4 sin	StK	StK a–j
S. kirchbergensis	Warszawa-Vistula River	?MIS 5e	MZ/VIII/Vm-450	ME	P^4 dex.	StW	StW a–r
C. antiquitatis	Biśnik Cave, l. 15	MIS 5/6 or MIS 7	B/06/W/5081	ZPALUWr	upper indet.	CoB15	CoB15 a–i
C. antiquitatis	Biśnik Cave, l. 16	MIS 6 or MIS 7	B/04/W/3249	ZPALUWr	P_2 dex	CoB16	CoB16 a–g
C. antiquitatis	Biśnik Cave, l. 18	MIS 6 or MIS 8	B/09/W/7190	ZPALUWr	Indet.	CoB18	CoB18 a–h
C. antiquitatis	Biśnik Cave, l. 19bc	MIS >7	W-8689	ZPALUWr	Indet.	CoB19	CoB19 a–i
C. antiquitatis	Skarszyn	MIS 2 or MIS 3	SKA/11/5	ZPALUWr	M^2 dex	CoS	CoS a–j

Collections: ZPALUWr – Department of Palaeozoology, University of Wrocław (Wrocław, Poland); IAWr – Institite of Archaeology, University of Wrocław (Wrocław, Poland), MK – The District Museum in Konin, (Konin, Poland), ME – Museum of Earth, Polish Academy of Sciences (Warsaw, Poland) (Niezabitowski et al., 1914; Niezabitowski-Lubicz, 1911a, 1911b; Lorek, 1988; Cyrek et al., 2010; Wiśniewski et al., 2009; Krajcarz et al., 2014a; Stefaniak, 2015; Marciszak et al., 2019).

2.4. Mesowear analysis

Measurements were taken and qualitative characteristics were recorded for the upper and lower teeth from Gorzów Wielkopolski following Lacombat (2009), who provided a system of measurements that was modified and expanded after Guérin (1980); Mazza (1988) and Fortelius et al. (1993).

Mesowear analysis is a well-validated method that indicates wear patterns over large part of the lifespan of an animal (Fortelius and Solounias, 2000; Rivals et al., 2007). Relatively small sample series (less than 10 specimens) give reliable and significant results (Fortelius and Solounias, 2000). Although in most cases, only M2 is used in mesowear analysis, here all three upper molars were scored for mesowear on the buccal side of the tooth to increase the sample size (Franz-Odendaal and Kaiser, 2003; see also Van Asperen and Kahlke, 2015). The occlusal relief was scored as either high or low. Cusp shape was scored on the sharpest cusp as sharp, round, or blunt. Tooth wear in browsers consuming mainly low-abrasive foodstuff, is dominated by sharp cusps and high relief. In contrast, grazers consume more grasses, often with a higher amount of grit, which contribute to an abrasion-dominated wear pattern with round or blunt cusps having low relief (Williams and Kay, 2001).

The diet of extant rhino species varies from grazing to browsing via mixed feeding (Owen-Smith, 1988). The diet of the Pleistocene rhinos was equally diverse (Kaiser and Kahlke, 2005; Hernesniemi et al., 2011; Kahlke and Kaiser, 2011; Van Asperen and Kahlke, 2015). Using the comparative dataset for 64 extant taxa of ungulates compiled by Fortelius and Solounias (2000) as a training set, a stepwise discriminant function analysis (DFA) using Wilk's lambda was carried out with the Pleistocene rhino samples and the Gorzów 1 specimen as an ungrouped specimen.

Specimens of *Stephanorhinus hundsheimensis* (Toula, 1902) from Voigtstedt and Süßenborn, *S. hemitoechus* (Falconer, 1859) from Bilzingsleben (Van der Made, 2000), Weimar-Ehringsdorf, British MIS 7 sites (Crayford, Ilford, Selsey) and British Ipswichian (MIS 5e) sites (Barrington, Joint Mitnor Cave, Kirkdale Cave, Raygill Fissure, Tornewton Cave and Victoria Cave), *S. kirchbergensis* from Bilzingsleben, Weimar-Ehringsdorf, Taubach and British MIS 7 sites (Crayford and Ilford) were also included as ungrouped specimens (data from Kaiser and Kahlke, 2005; Kahlke and Kaiser, 2011; Van Asperen and Kahlke, 2015).

Since the mesowear scores are not independent (teeth with blunt cusps have low relief), the analysed variables were % of the teeth with high relief, % of the teeth with sharp cusps, and % of the teeth with rounded cusps. Species with problematic dietary data ('mabra' species *sensu* Fortelius and Solounias, 2000) were left out of further analyses (cf. Kaiser and Solounias, 2003) and the conservative dietary classification of Fortelius and Solounias (2000).

2.5. Isotope analysis

The most informative tissues for paleoecology and diet reconstruction are bone collagen or dentine collagen. However, the analysed fossils of *S. kirchbergensis* are quite old (>100 000 years BP), and this reduces the chances for good preservation of the collagen and to obtain reliable results. Therefore, we focused on enamel, which is relatively resistant to diagenesis (Kendall et al., 2018). For comparative purposes, four *S. kirchbergensis* specimens and five *Coelodonta antiquitatis* specimens from Poland were studied and used for isotope analyses (Table 1), either isolated teeth or more complete skeletons with teeth.

2.5.1. Sampling

Prior to sampling, tooth surface was cleaned with acetone and then dried. The external enamel layer (ca. 0.3–0.5 mm in thickness) was removed with a Dremel diamond-coated bit, as this outer part was reported to be isotopically biased by late mineralisation (Trayler and Kohn, 2017). Enamel samples were collected by careful drilling about 10 mg of powder.

Different sectors of the enamel represent different periods of the animal's life and may therefore vary in isotope composition due to paleoenvironmental changes (Passey and Cerling, 2002; Blumenthal et al., 2014). To deal with this variability, we obtained several samples from each specimen (Table 1). The samples were taken in sequences along the vertical axis reflecting the direction of a tooth crown growth (Fig. S2). Due to this modification, we covered the entire time span of the given tooth formation. Apart of samples for isotope analyses, we took one additional sample per specimen for infrared spectroscopy.

2.5.2. Pretreatment

The chemical pretreatment method followed Koch et al. (1997) and Bocherens et al. (1996a, b). The powder was soaked in 1.5 mL of 30% H_2O_2 for 24 h to remove organic contamination, then centrifuged and rinsed with UHQ water several times. The powder was treated with 1.5 mL of 0.1 M acetic acid for 48 h to eliminate exogenous carbonates, and again centrifuged and rinsed with UHQ water. After pretreatment, the powder was dried at 60 °C for 48 h. The yield was determined as the ratio of dry sample weights before and after pretreatment. An aliquot of internal lab standard (powdered cattle enamel) was set between each 20 samples and treated with the same procedure to control the pretreatment. Such prepared samples were directed to the isotope measurement of the carbonate fraction.

In addition, around 5 mg spit taken from the largest sample from each specimen, was forwarded to phosphate extraction. The procedure followed Koch et al. (1997) and Tütken et al. (2006). The powder was dissolved in 0.8 mL of 2M HF for 24 h; then neutralized with 25% NH_4OH, with bromothymol blue used for pH control. Next, a 0.8 mL aliquot of 2M $AgNO_3$ was added to precipitate the phosphate. The precipitates were centrifuged and rinsed with UHQ water several times, and then dried at 50 °C by 72h.

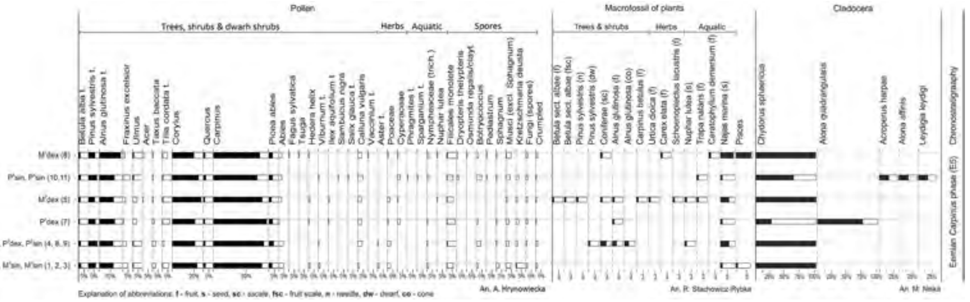

Fig. 2. Pollen, plant macrofossils and Cladocera analysis from the sediment adjaced directly to the jaw of *Stephanorhinus kirchbergensis* M^1dex (6); P^1sin, P^3sin (10,11); M^2dex (5); P^4dex (7); P^3dex, P^2dex, P^2sin (4, 8, 9); M^1sin, M^2sin, M^3sin (1, 2, 3).

Table 2

Description of palynological types of tooth content of the rhinoceros from Gorzów Wielkopolski.

Type	Name	Description
Type 1	*Betula-Corylus-*	*Betula* pollen was dominant in proportions of 50–55% (Table 3), accompanied by *Corylus*– 12–30%. *Carpinus* reached ca. 10%, and *Alnus* – 10–17%. *Quercus*, *Ulmus*, *Tilia* and *Pinus* reached more than 1% each. Other taxa occur in samples as isolated pollen grains. In total, 14–15 plant taxa were identified in samples 1 and 2.
Type 2	*Corylus-Betula*	The dominant was the pollen of *Corylus* (41%). *Betula* reached 33%, *Carpinus* – 14%, *Alnus* – 8%, and *Pinus* – 3%. Other taxa occurred as isolated pollen grains. In total, 8 plant taxa were identified in sample number 3.
Type 3	*Carpinus–Corylus*	The proportions of *Carpinus* pollen reached 37–51% (43% in average; Table 3). The accompanying pollen of *Corylus* was equal to 20–38% (26% in average). *Alnus* and *Pinus* appeared in proportions ca. 9%, *Picea* – ca. 7%, *Betula* – usually less than 2%. The proportion of *Quercus* and *Tilia* was less than 1%. Other taxa occurred as a single grain. In total, 17 plant taxa (average 10) were identified in samples 4–10.
Type 4	*Corylus*	*Corylus* pollen was dominant – 78%. Among other taxa, *Carpinus* reached 11%, *Betula* – 2.5%, *Alnus* – 3.5%, *Picea* – 2%. Other taxa occurred as isolated pollen grains. In total, 9 plant taxa were identified in sample number 11.

2.5.3. *Measurements*

Measurements of stable isotope ratios were conducted in the Stable Isotopes Lab of the Institute of Geological Sciences, Polish Academy of Sciences (Warsaw, Poland). Isotope analyses of the carbonate fraction ($\delta^{13}C_C$ and $\delta^{18}O_C$) were carried out in Finnigan Delta + mass spectrometer connected to KIEL IV, automatic CO_2 extraction device. The measurements were calibrated using the NBS18, NBS19, and LSVEC standards. Repeatability of the results is 0.2‰ for $\delta^{13}C_C$ and 0.25‰ for $\delta^{18}O_C$. The isotope ratios are expressed as delta (δ), deviation – in per mil from the standard value (which was VPDB).

Isotope analysis of the phosphate fraction ($\delta^{18}O_P$) was performed with Flash EA 1112HT elemental analyser (Thermo Scientific) coupled to Delta V Advantage IRMS (Thermo Scientific), with continuous flow of He. About 400 μg of Ag_3PO_4, wrapped in a silver foil, was decomposed at 1350 °C in presence of C. The obtained CO, separated from other gases on GC column, was then introduced into the mass spectrometer. The results of triplicate analysis were normalised to international standards UMCS 1, UMCS 2 and B2207 and reported relative to the VSMOW international standard. The measurement precision (1σ) was better than ± 0.3‰.

2.5.4. *Variance analysis*

To analyse the variance between isotope values of taxa, we used Kruskal-Wallis nonparametric test which can be adopted for non-equal sample sizes (Hammer, 2020). It was followed by Dunn's post hoc pairwise test to check differences between the studied specimens. Statistical analysis was performed with PAST software (Hammer et al., 2001).

2.5.5. *Infrared spectroscopy*

Infrared (IR) spectra were recorded using a Nicolet 6700 spectrometer with a DTGS KBr detector (Thermo Scientific, USA) in a transmission mode. The spectra were measured in 4000–400 cm^{-1} range at a resolution of 8 cm^{-1} as 100-scan averages. The samples were prepared in the form of pressed potassium bromide (KBr) pellets by mixing of 0.5 mg with 200 mg of KBr. Before analysis, samples and KBr dilutant were dried at 80 °C during 24 h.

Based on the assumption that IR bands absorption is proportional to the concentration of molecular species in the sample, the ratio of absorbances of CO_3 and PO_4 stretching bands (v_3) at 1415 cm^{-1} and 1040 cm^{-1}, respectively, was used to estimate the C/P ratio (CO_3/PO_4 absorbance ratio) for studying the diagenetic alteration of tooth enamel (Wright and Schwarcz, 1996; Beasley et al., 2014). Before calculations, the baseline was corrected in the region 1900–730 cm^{-1} for each spectrum based on linear model using OMNIC software (v. 8.3). The IR measurements were repeated two times on different portions of the sample to check the reproducibility of obtained results.

3. Results of the study

3.1. *Stephanorhinus kirchbergensis (Jäger, 1839) from Gorzów Wielkopolski*

3.1.1. *Palaeobotanical analysis*

3.1.1.1. Sediment adjacent to the upper jaw of Stephanorhinus kirchbergensis. All samples from the sediment adjacent to the jaw of

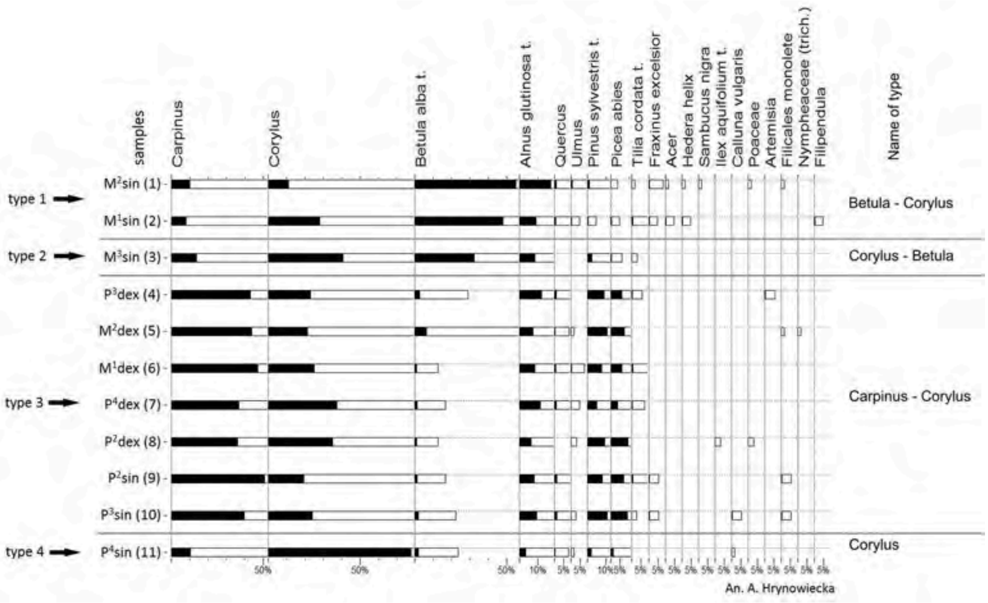

Fig. 3. Pollen analysis of the sediment from the tooth fossae of *S. kirchbergensis*.

Stephanorhinus kirchbergensis had high pollen frequency and presented a very similar pollen composition, which can be described as *Carpinus-Corylus* with *Alnus* admixture (Fig. 2). The percentages of the predominant *Carpinus* pollen were ca. 45% (Table 2) and the accompanying *Corylus* – ca. 23%. *Alnus* pollen reached approx. 14%, *Pinus* – 7.5%, *Picea* – 3.5%, *Betula* and *Quercus* – 2% each. *Fraxinus*, *Ulmus*, *Taxus baccata*, *Tilia cordata*, and *Abies* appeared in smaller proportions. *Acer*, *Fagus*, *Hedera helix*, *Viburnum*, *Ilex aquifolium*, *Sambucus nigra* and *Salix glauca* were recorded as single pollen grains. Herbs and dwarf shrubs were also represented by isolated pollen grains: *Calluna vulgaris*, *Vaccinium* t., *Aster* t., Poaceae, and Cyperaceae. The pollen of aquatic plants was present but scarce: *Phragmites* t., *Sparganium* t., *Nuphar lutea* and trichosclereids of Nympheaceae. In total, 38 plant taxa were identified.

Plant macroremains from the same six samples were relatively frequent and well-preserved. They were mostly represented by aquatic macrophytes such as *Trapa* sp., *Ceratophyllum demersum*, *Najas marina*, *Nuphar lutea*, and *Aldrovanda* sp. They also included shoots and wings of seeds of trees: the cone of *Alnus* sp., the fruit of *Carpinus betulus* and *Betula* sect. *albae*, and *Pinus sylvestris*. Besides trees, there was a vegetation typical for peat bogs, e.g. *Carex elata* and *Typha* sp., growing on the shores.

3.1.1.2. *Sediment from the tooth fossae of Stephanorhinus kirchbergensis.*

Pollen analysis of 11 sediment samples from rhino tooth fossae allowed to separate four types of pollen spectra (Fig. 3, Table 2). In all types, a much smaller number of taxa was found than that in the sediment. The pollen frequency was lower than usual (Table 2). Pollen was counted from at least three slides 20 × 20 mm, from 178 to 500 grains (ca. 350 grains in average).

Diaspores were almost entirely absent in the sediment from the tooth

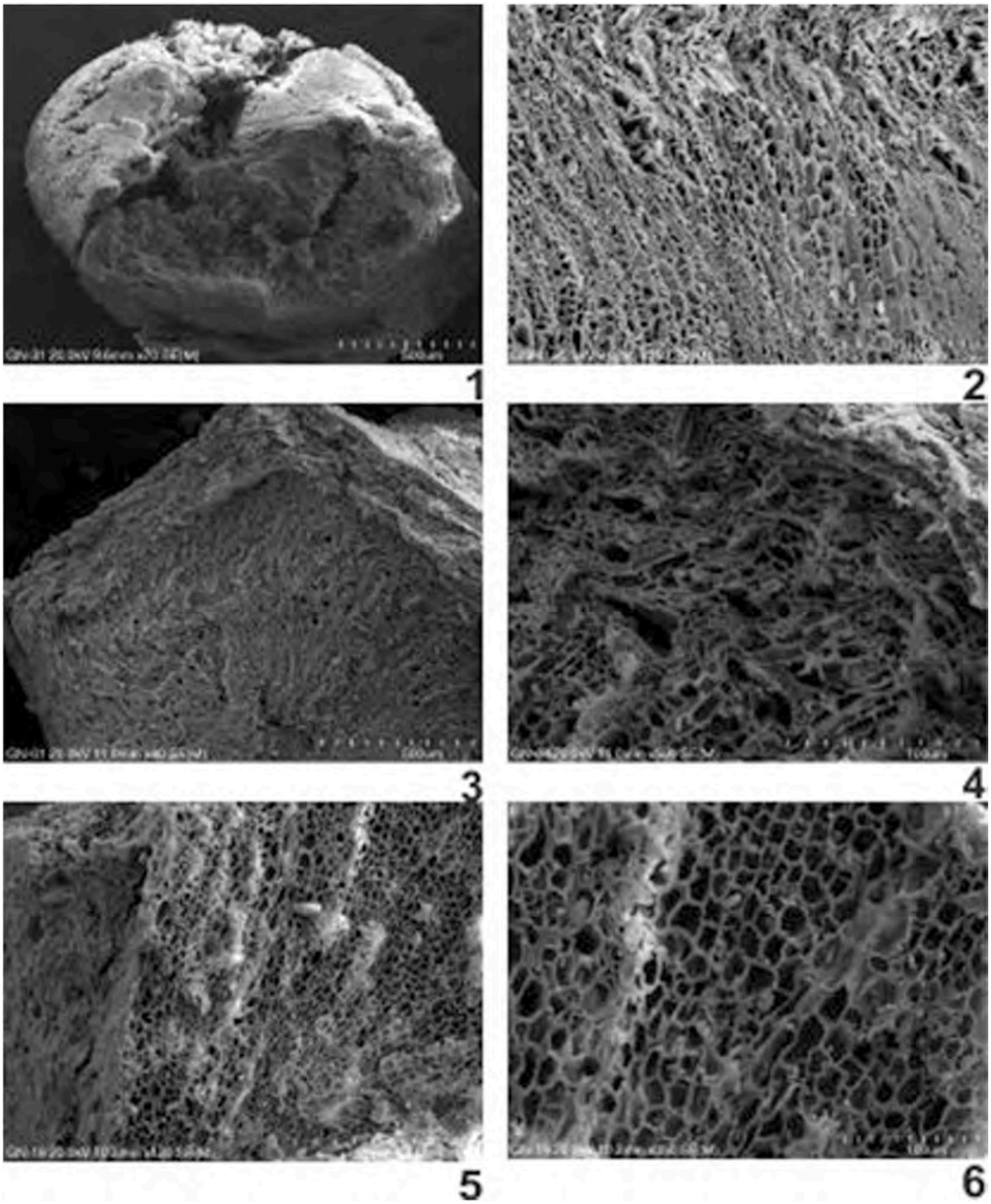

Fig. 4. 1, twig of *Corylus* sp. (P^2 dex), scale bar 500 μm; 2, twig of *Corylus* sp. (P^4 dex), scale bar 100 μm; 3–4, twig of *Carpinus* sp., scale bar 40 μm; 5–6, *Viscum* sp., Micrographs: M. Moskal-del Hoyo.

fossae. Only a single small and damaged fragment of a seed husk of *Betula* sp. was identified, although parts of small branches and other indistinguishable tissues were also found.

Fragments of wood appeared in all samples. The majority of them were represented by unidentified tissues, but twigs of *Corylus* sp. 1–4 mm in diameter (Fig. 4.1-4.2), *Carpinus* sp. (Fig. 4.3-4.4), and *Viscum* sp. (Fig. 4.5-4.6) were also documented. Some fragments were preserved with bark and this enables the observation of terminal annual rings that were formed just before the end of the growth of plants. Fig. 4.4 shows that the last annual ring is characterised by the presence of earlywood vessels which were developed at the beginning of the growing season (during spring) and latewood vessels. The observation of latewood zone of the previous ring may indicate that it was probably not completely formed (Fig. 4.4). This may suggest that the twig was cut and consumed by the rhino during summer or early autumn.

3.1.2. *Cladocera analysis*

Analysis of the subfossil remains of Cladocera was carried out for six samples marked as M^1dex (6); P^1sin, P^3sin (10, 11); M^2dex (5); P^4dex (7); P^3dex, P^2dex, P^2sin (4, 8, 9); M^1sin, M^2sin, M^3sin (1, 2, 3), from the sediment surrounding the jaw of *Stephanorhinus kirchbergensis* (Fig. 2). The analysis proved the presence of cladocerans, which indicates lacustrine sediment. The remains identified in the material were poorly preserved and characterised by poorly marked taxonomic features hindering their identification. Such condition of the remains was caused by the age and sediment in which they were found (high carbonate gyttja). The frequency of remains was low.

Five Cladocera species were identified in the samples. All of them belong to the littoral group, living among submerged plants and near the bottom of shallow water bodies. Remains of the species living in open waters are absent. The most common taxon was *Chydorus sphaericus* (represented in all samples). It was the only species in three samples (Fig. 2). It is eurytopic, resistant to environmental stress, and able to migrate between different lake parts. The number of identified species varied in different samples. The richest species composition is in the samples P^1sin and P^3sin (10, 11), where four Cladocera species were identified: *Chydorus sphaericus* (62.5%), *Acroperus harpae* (12.5%), *Leydigia leydigi* (12.5%), and *Alona affinis* (12.5%).

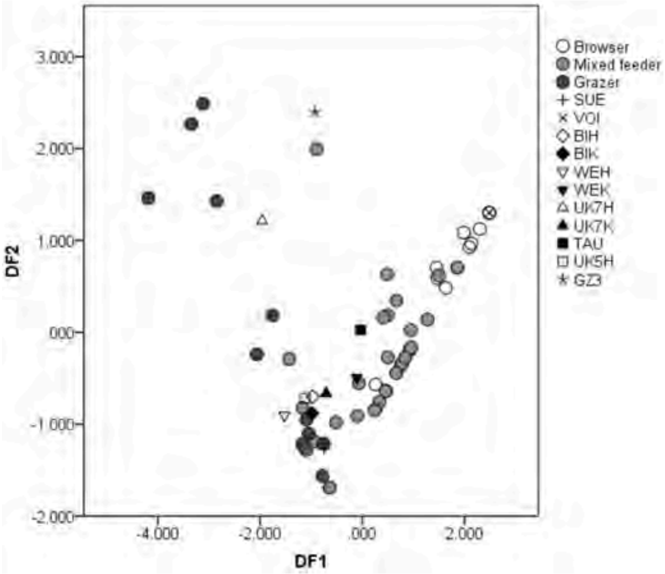

Fig. 5. Plot of scores on DF2 vs. DF1 for a range of extant herbivore species and Pleistocene rhino assemblages; SUE = Süssenborn; VOI = Voigtstedt; BI = Bilzingsleben; WE = Weimar-Ehringsdorf; UK7 = British MIS 7 sites; TAU = Taubach; UK5 = British Ipswichian sites; GZ3 = Gorzów Wielkopolski; H = *S. hemitoechus*; K = *S. kirchbergensis*.

3.1.3. *Mesowear analysis*

The Gorzów individual was classified as a grazer in the DFA (Fig. 5). It ploted closer to extreme grazers *Bison bison*, *Equus burchelli*, *Equus grevyi*, and *Ceratotherium simum*.

Species clustering with the Gorzów individual are mostly grazers in grassland, savannah and open woodland in Africa, as well as the North American bison *Bison bison* whose diet consists of grass.

In contrast to other Middle and Late Pleistocene populations of *S. kirchbergensis* which tended to be mix-feeders, the Gorzów rhinoceros possibly had a mostly grazing diet over the later part of its life. It should be remembered that individuals can vary in their feeding behaviour and range habitats over lifetime, and that the mesowear signature of the Gorzów individual is not uncommon within the variation in other *S. kirchbergensis* populations (data from Van Asperen and Kahlke, 2015). Furthermore, the Gorzów individual was an old individual. Mesowear tends to be somewhat lower in relief and rounder than in younger adults (Fortelius and Solounias, 2000; Rivals et al., 2007), and thus more grazer-like. Therefore, this individual's mesowear signature cannot be extrapolated to the entire population.

3.2. *Coelodonta antiquitatis (Blumenbach, 1799) from Starunia*

3.2.1. *Palaeobotanical analysis*

Among the new plant remains extracted from the teeth, intestines of the rhinoceros and from the sediments surrounding the rhino body from Starunia, 36 taxa were identified (Table S1; Figs. 6 and 7). The samples "from intestine and teeth of the rhino" and "from guts and teeth of the rhino" contained mainly fruits of Cyperaceae, including *Carex dioica*, *C. pulicaris*, *C. cannescens* (Fig. 7.15–7.16), *C. divulsa*, *C. pseudocyperus*, *C. rostrata* and *C. nigra* (Fig. 7.7), among which *C. nigra* and *C. divulsa* were the most numerous. *Plantago lanceolata*, *Potentilla alba*, and *Linum* cf. *extraaxillare* were also present. Unfortunately, the presence of the fruit of *Brasenia schreberi* is not clear, which is a species that last appeared in Europe during the Eemian Interglacial (Drzymulska, 2018). In the samples "from intestine and teeth of the rhinoceros", there are remains of aquatic plants such as *Potamogeton filiformis*, *Nuphar pumila*, and *Comarum palustre*.

The samples described "from inside of the rhinoceros" and "near the rhinoceros" comprise several hundred fruits of the genus *Carex*, mainly *C. nigra*, *C. gracilis*, and *C. cannescens*. The sediment was also filled with seeds, leaves and seed scales of *Betula nana* (Fig. 7.1–7.3). The seeds of *Plantago lanceolata* were also extremely numerous and well-preserved. Herbaceous species such as *Plantago media*, *Allium* sp., *Armeria maritima* (Fig. 7.5), *Dianthus arenarius*, *Fragaria vesca* (Fig. 7.18), *Medicago lupina* (Fig. 7.13) and *Lychnis flos-cuculi* predominated in the assemblage. It should be noted that, according to Stach (1930), the stomach was absent, and the internal cavity was filled with the surrounding sediments. The species composition of plants "from guts and teeth of the rhino" and those "from inside of the rhinoceros" was similar, including the presence of *Betula nana* and *Plantago lanceolata*.

3.2.2. *Isotope analysis*

3.2.2.1. *Reliability of isotope results.* An important factor which could bias the isotope composition of the fossil enamel is geochemical alteration due to weathering and diagenesis. We used three independent proxies to evaluate the isotope preservation state of our material: 1) comparison of oxygen isotope composition in CO_3 and PO_4 fractions; 2) CO_3/PO_4 (C/P) ratio; and 3) theoretical evaluation of isotope signal among taxa. The C/P ratio represents the amount of CO_3^{2-} in enamel phosphate which might change during weathering or diagenesis. Unaltered *in vivo* amount varies between taxonomic groups (Wright and Schwarcz, 1996) and is unknown for the studied fossil rhino species. However, the ratio between C/P and isotope composition may be regarded as a proxy of alteration (Wright and Schwarcz, 1996; Beasley

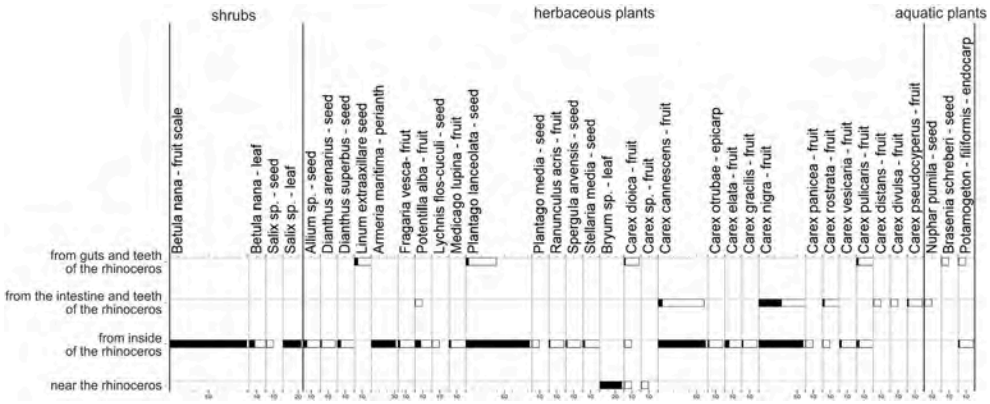

Fig. 6. Plant remains identified from the woolly rhino remains found in Starunia. Detailed information in Table S1.

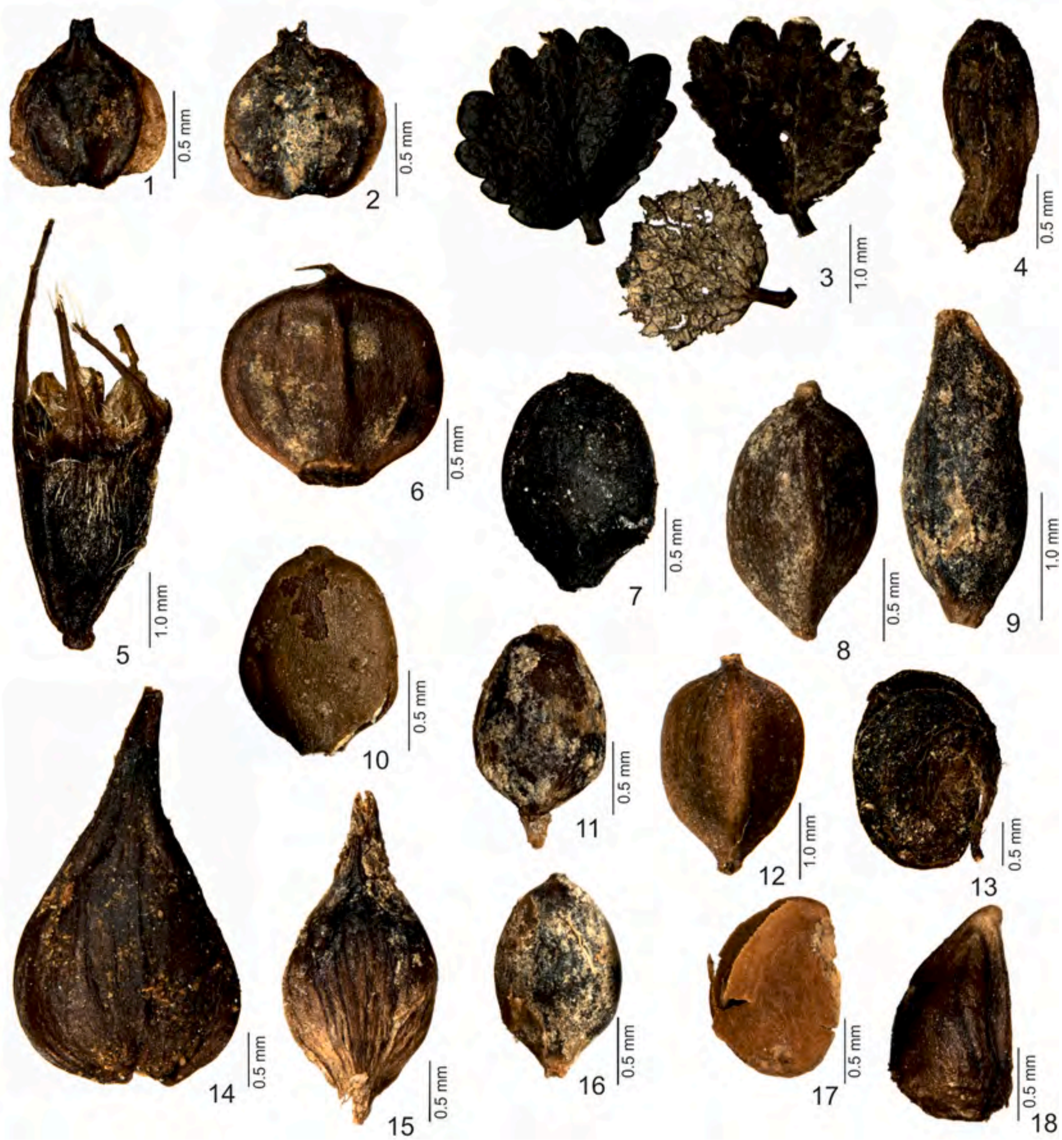

Fig. 7. Plant macroremains from Starunia. 1–2, *Betula nana*, fruit (Q236/62a); 3, *B. nana*, leaves (Q236/62a); 4, *Salix* sp., fruit (Q236/108); 5, *Armeria maritima*, perianth (Q236/63); 6, *Carex elata*, fruit (Q236/108); 7, *Carex nigra*, fruit (Q236/108); 8, *Carex pseudocyperus*, fruit (Q236/112); 9, *Carex distans*, fruit (Q236/112); 10, *Carex vulpina*, fruit (Q236/112); 11, *Carex divulsa*, fruit (Q236/112); 12, *Carex rostrata*, fruit (Q236/112); 13, *Medicago lupina*, seed (Q236/109); 14, *Carex otrubae*, epicarp (Q236/108); 15, *Carex cannescens*, epicarp (Q236/112); 16, *Carex cannescens*, epicarp (Q236/112); 17, *Potentilla alba*, seed (Q236/112); 18, *Fragaria vesca/viridis*, seed (Q236/108). Photo: K. Stachowicz.

et al., 2014).

In theory, C/P is expected to be constant in a given species, while isotope values should be variable among specimens depending on paleoenvironmental conditions. Therefore, if any correlation can be observed between these values in the fossil specimen, this suggests a post-depositional process which had altered the chemical and isotope composition of the enamel (Wright and Schwarcz, 1998). In our samples, there is only a weak correlation between C/P and $\delta^{13}C_C$ ($R^2 = 0.4604$) and no systematic correlation between C/P and $\delta^{18}O_C$ ($R^2 = 0.1402$) (Fig. S3). This suggests a well preservation of the enamel and supports the reliability of our results. We also calculated $\Delta^{18}O_P$, i.e., the difference between $\delta^{18}O_P$ directly measured in phosphate fraction and theoretically calculated from the $\delta^{18}O_C$ in carbonate fraction. With the $\delta^{18}O_C$ into $\delta^{18}O_P$ values convertion according to Lehn et al. (2020) (i.e., $\delta^{18}O_P = 1.0322 \cdot \delta^{18}O_C - 9.6849$), the difference is expected to be around 0 for well preserved specimens, with accepted deviation up to +2‰ or −2‰ (Skrzypek et al., 2011). Of our specimens, only two (wolly rhinos CoB15 and CoB19 from Biśnik Cave) gave $\Delta^{18}O_P$ slightly outside of this range (Fig. S4). The isotope signatures of the studied taxa reflect the general pattern observed at Pleistocene sites, i.e. relatively low $\delta^{13}C$ values in *S. kirchbergensis* (e.g., Kuitems et al., 2015; Szabó et al., 2017) and high in *C. antiquitatis* (Biasatti, 2009; Krajcarz and Krajcarz, 2014a; Bocherens et al., 2015). The repeatability observed for internal lab standard (a modern cattle) was 0.12‰ for $\delta^{13}C_C$, and 0.30‰ for $\delta^{18}O_C$ (standard deviations for N = 4).

3.2.2.2. Isotope composition of the enamel. The results of isotope and IR analyses are presented in Table S2. All studied enamel samples exhibit $\delta^{13}C_C$ values below −10.5‰ VPDB, which indicates a pure C_3 plant-based diet (Bocherens and Drucker, 2013). The $\delta^{13}C_C$ values for *S. kirchbergensis* are lower by 1.83‰ in average than for *C. antiquitatis*, while the $\delta^{18}O_C$ values are higher by 3.28‰ in average. Kruskal-Wallis test reveals that differences in medians among *S. kirchbergensis* and *C. antiquitatis* are highly significant for both $\delta^{13}C_C$ ($p < 10^{-13}$) and $\delta^{18}O_C$ ($p < 10^{-11}$).

Post hoc comparison (Dunn's post hoc, Table S3) shows that for $\delta^{13}C_C$, specimen from Warsaw (MIS 5e) (StW) significantly differs from other *S. kirchbergensis* specimens within Poland ($p < 0.001$ for each pair) and *S. kirchbergensis* from Wrocław-Hallera street (MIS 4/3) (StH) differs from Konin (MIS 5e) (StK) (however, $p = 0.0468$ is slightly below the accepted significance level $\alpha = 0.05$). No remarkable differences were found in pairs *S. kirchbergensis* from Gorzów (MIS 5e) and Konin (StG-StK), Gorzów and Wrocław-Hallera street (StG-StH). In the case of *C. antiquitatis*, post hoc comparison (Table S4) shows that for $\delta^{13}C_C$, the specimen from Biśnik Cave layer 15 (MIS 5/6 or 7) (CoB15) significantly differs from those of Biśnik Cave layer 16 (CoB16), layer 18 (CoB18) (MIS 6 or 7) and layer 19 (MIS >7) (CoB19) ($p < 10^{-4}$ for each pair). *C. antiquitatis* from Skarszyn (MIS 2 or 3) (CoS) differs from that of Biśnik Cave CoB16, CoB18 and CoB19 ($p = 0.0037$, $p = 0.0125$ and $p = 0.0019$, respectively). Differences were found neither in pairs from Biśnik Cave CoB16-CoB18, CoB16-CoB19, CoB18-CoB19 nor for *C. antiquitatis* from Biśnik Cave layer 15 – Skarszyn (CoB15-CoS) (Borsuk-Białynicka and Jakubowski, 1972; Lorek, 1988; Wiśniewski et al., 2009; Cyrek et al., 2010; Krajcarz et al., 2014a; Marciszak et al., 2019) (Tables S2 and S3).

We also applied the analysis of variance (Dunn's post hoc tests) to the sets of isotopic data for *Coelodonta* and *Stephanorhinus* species known from the literature (Bocherens et al., 1995; Ecker et al., 2013; Bocherens, 2014; Krajcarz and Krajcarz, 2014b; Pushkina et al., 2014; Szabó et al., 2017 with further references there; Biasatti et al., 2018; Pandolfi et al., 2018). Comparisons revealed that two genera significantly differ both in terms of $\delta^{13}C_C$ and $\delta^{18}O_C$ values ($p < 10^{-26}$ and $p < 10^{-5}$, respectively). Comparisons made separately for both taxa (Tables S5–S8), revealed that *Stephanorhinus* and *Coelodonta* show almost no significant differences in $\delta^{13}C_C$ with respect to chronology and to geographic regions (the only exception is statistically significant difference between late Middle Pleistocene and late Late Pleistocene *Coelodonta*). This observation suggests low dietary flexibility of these rhinoceroses. In the case of $\delta^{18}O_C$ values, analysis of variance revealed much greater variability, with statistically significant differences observed for *Stephanorhinus*, both in terms of chronology and geography (Tables S5–S6). On the other hand, chronological and geographic groups of *Coelodonta* revealed only few statistically significant differences (Tables S7–S8). As $\delta^{18}O_C$ values are connected to climate, this suggests that *Stephanorhinus* inhabited variable climatic zones, while *Coelodonta* was ecologically attached to the narrow climatic interval.

4. Discussion

4.1. Diet of Stephanorhinus kirchbergensis based on plant micro- and macro-remains

The genus *Stephanorhinus* (Kretzoi, 1942) was widespread in Europe and Asia during the Quaternary. In the Late Pleistocene, two species of *Stephanorhinus* were distinguished: *S. hemitoechus* (the steppe rhino) and *S. kirchbergensis* known as Merck's or the forest rhinoceros. Both species were adapted to a various climate. Although they were found together in a number of localities, *S. kirchbergensis* probably preferred wooded areas, while *S. hemitoechus* lived in open grasslands (Lacombat, 2009). In Europe, remains of *Stephanorhinus* were found in many sites, but in most cases, there are only few bones or teeth (Billa and Zervanová, 2015). For this reason, the discovery of an almost complete skeleton with well-defined stratigraphic context in Gorzów Wielkopolski is of keen interest.

4.1.1. Local environment

The rhino skeleton was deposited in part of the sediment formed in the final phase of E5 of the Eemian Interglacial. (Sobczyk et al., 2020). At that time the communities of macrophytes spread in the palaeoreservoir when the new lake was still relatively deep, reaching approximately 10m. In addition, plant macrofossils, such as fruits of *Carpinus betulus*, nuts of *Trapa* sp., *Aldrovanda vesiculosa* and *Brasenia* sp. indicate the warm phase of the Eemian interglacial. This species composition allows to determine the time when the rhinoceros lived as the end of the middle Eemian Interglacial (E5, see Mamakowa, 1989) defined for Poland as *Carpinus-Corylus-Alnus* R PAZ (Mamakowa, 1989; Litt et al., 1996; Sobczyk et al., 2020).

Macrofossils and pollen associated with the skeleton indicate that *Carpinus*, *Corylus*, *Alnus* and *Taxus* could have been dominant plants in the environment. This indicates a warm climate and an environment of luxuriant broad-leaved deciduous forests. The results of pollen analysis (Fig. 2) show the dominance of *Carpinus* and *Corylus* communities as a rhinoceros' living environment.

The lacustrine genesis of the sediment taken from the part located near the teeth is also confirmed by the results of subfossil Cladocera analysis. In addition, based on the species identified in the lacustrine

Table 3

Similarity of pollen values of selected taxa from type 3 rhinoceros' teeth sediment (Fig. 3; 11 samples) and the sediment near the teeth (Fig. 2; 6 samples).

Taxa	Sediment	Min. %	Max. %	Average %
Betula	adjacent to the teeth	1.3	2.4	2
	from tooth fossae	1.3	7	2
Carpinus	adjacent to the teeth	40.5	49	45
	from tooth fossae	37	51	43
Corylus	adjacent to the teeth	20	26.5	23
	from tooth fossae	20	38	26
Alnus	adjacent to the teeth	12.5	19.5	14
	from tooth fossae	8	12.5	9
Picea	adjacent to the teeth	2.5	4.6	3.5
	from tooth fossae	4	9.5	7.3
Pinus	adjacent to the teeth	6	8	7.5
	from tooth fossae	5.5	11	9

sediments, it can be concluded that the zone, from which the material was collected, was relatively shallow with well-developed macrophytes providing shelter for Cladocera species (Fig. 2). Among them, *A. harpae* and *A. affinis* are closely related to the macrophyte zone, living in clear calm waters (Flössner, 1972). Both species are tolerant to high water alkalinity and prefer oligo-, β-mesosuppressive sites and higher electrolyte concentrations (Rybak and Błędzki, 2010) being occurred most frequently at the depth of 0.7–3 m (Adamczuk, 2014). *Leydigia leydigi* lives at the bottom; it is an indicator for mesotrophic water bodies and preferred a pH range of 6.5–7.5. In addition, *Alona quadrangularis* was found in the P^3dex, P^2dex, P^2sin (4, 8, 9) sample (75%). This species also exists among bottom sediments and is characteristic for β-mesosaprobic waters (Rybak and Błędzki, 2010). It shows a tolerance to high pH, but the highest frequency of this species is achieved at pH 6.0 and 7.9. Based on indicator species, the water body can be defined as oligo-mesotrophic, oligo-, β-mesosuppressive with pH 7. Identified species do not show strong preferences for water temperature. Probably the depth of the lake, in the part where the rhinoceros' skeleton buried, was about 3 m.

4.1.2. *Diet*

Plant remains were found in deep fossae of the occlusal surface of molars from Gorzów Wielkopolski, which is common for rhinos (Van der Made and Grübe, 2010). Pollen values derived from the sediment inside the teeth, type 3 (samples No. 4–10; Fig. 3) are similar to those in the surrounding sediments (Fig. 2, Table 3). It allows to conclude that sediments from the teeth in samples No. 4–10, (type 3) are of lacustrine origin and placed into teeth of the rhino *post mortem*. The clearest differences can be observed in the values of the *Alnus* pollen – in sample 1 (M^1dex tooth) from the sediment lying near the jaw it equals maximally 19.5%, and only 9% on average in the samples from the sediment at tooth fossae. A further difference is visible in the proportions of *Picea* pollen. The average percentage of *Picea* pollen is 3.5% in adjacent to the teeth and 7.3% in tooth fossae (Fig. 2; Tables 2 and 3).

Samples Nos. 7 and 8 from the teeth contain nearly 40% of *Corylus* pollen, while the remaining samples representing this type – ca. 25% (Fig. 3; Table 2), which may indicate a partial mixing of the original content of tooth fossae with lacustrine sediments.

Four sediment samples from teeth fossae of the rhinoceros from Gorzów Wielkopolski were definitely different. They contain less *Carpinus* pollen (approx. 10%) and almost no pollen of *Pinus* and *Picea*. Type 1 (samples No. 1–2, Fig. 3) indicates that the rhino could have fed mainly on birches, hazel and alder, probably on a short distance from the reservoir, in riparian communities. This is evidenced by the presence, apart from *Betula* and *Alnus* pollen, of *Ulmus*, *Fraxinus*, *Acer*, *Hedera*, and *Sambucus*. Type 2 (sample No. 3, Fig. 3) confirms that the *Corylus* and *Betula* communities might have been selected by an extinct rhino. Similarly, Type 4 (sample No. 11) also indicates communities with *Corylus*.

These results indicate that, due to the availability, the food of the studied rhino individual could be young and low-growing shoots of *Corylus* and *Betula*. The low proportions of *Carpinus* pollen in the sediment fom the teeth suggest that, despite the predominance of this taxon in the surrounding environment, it was less frequently chosen since trees contain leaves and twigs that could be out of reach of the rhinoceros, but they could be available from young individuals of *Carpinus* found in the undergrowth and from its seedlings and offshoots. These pollen data are confirmed by macrofossil plant remains from these fossae of the rhino from Gorzów Wielkopolski, which included twigs of *Carpinus* and *Corylus* along with fruit scales of *Betula*. Among the remains found in tooth fossae, the twigs of *Viscum* were also identified, either eaten together with the other branches. The pollen samples indicated that *Betula* and *Corylus* were primary food items for *S. kirchbergensis*.

The abundance of fruit remains associated with the skull and skeleton suggested that the time of death could be summer or early autumn. However, the material found in the tooth fossae provided a better indication for this period: among the twigs of *Carpinus*, few specimens contained terminal annual rings with vessels of earlywood and the beginning of latewood. It indicates that the last food consumption could take place in the end of summer or in early autumn. In addition, the almost complete absence of pollen of herbaceous plants should be noted, which confirms the forest environment and determines the season when this rhino died.

4.1.3. *Comparison with other sites*

Plant remains from teeth fossae of *S. kirchbergensis* were also found in three European sites and one site from north-eastern Asia (Table S9), but such findings are extremely rare and cannot be representative for such a large area of various bio-climatic regions.

The closest site to the finding of the rhino from Gorzów Wielkopolski is Neumark-Nord in Germany, which is a well-documentated site yielding the remains of *S. kirchbergensis*, *S. hemitoechus* and *C. antiquitatis*. However, its age is under discussion, representing the MIS 7 interglacial (e.g. Heinrich, 2010; Van der Made, 2010) or the Eemian interglacial (MIS 5e, e.g. Litt, 1994). Plant remains were found in tooth fossae of several individuals of *S. kirchbergensis* from this site (Grübe, 2003; Van der Made and Grübe, 2010), including cuticle remains belonging to plants of the Poaceae family, fruits and seeds of herbaceous plants and trees and shrubs. The last group was also represented by buds. Remains of aquatic plants were also found (see Table S9 for details). This rhino browsed primarily *Populus*, *Quercus*, *Crataegus*, *Pyracantha*, *Urtica*, and *Nymphaea* (Grübe, 2003; Van der Made and Grübe, 2010), indicating a clear selection of plants, many of which were not the most abundant ones in that environment. Buds and thorns with fruits and seeds may suggest that the time of death (shortly after the last feeding) could be the end of winter or the beginning of the growing season (Grübe, 2003; Van der Made and Grübe, 2010) (Table S9).

Another European site providing evidence for a rhino's diet is Zwolle-Haerst from the North Sea and the Netherlands. The pollen spectrum from the tooth of *S. kirchbergensis* from Eemian Interglacial or early Vistulian interstadial (Van Geel et al., 2019) showed the dominance of tree pollen, mainly of *Alnus* and *Corylus*. Also, *Viscum album*, *Hedera helix*, ferns and *Kretzschmaria deusta*, parasitic fungus living on dead and live wood, were detected (Table S5). This confirms the browsing behaviour of this rhino (Van Geel et al., 2019).

The latest data on the *S. kirchbergensis* diet come from the previously known Spinadesco specimen found in northern Italy (Persico et al., 2015). According to E. Burkanova et al. (2020), pollen of deciduous and coniferous trees and shrubs were found in the dental fossae of this specimen, among which *Alnus* and *Salix* were the most numerous (Table S9). Also, herbaceous plants and aquatic plants were documented. According to Burkanova et al. (2020), the habitat of the rhino specimen from Spinadesco was a flood plain, with forests dominated by *Alnus* and *Fagus* nearby. A large amount of *Hippophaë rhamnoides* pollen and other shrubs indicate that the leaves of trees and shrubs played a significant role in the diet of this rhino. It also fed on herbaceous vegetation and soft aquatic plants *Potamogeton* sp. and *Myryophillum* sp. All these data confirm the browsing behaviour of this species. The authors also identified the probable period of the rhino's death as spring or summer (Table S9).

An interesting find of a skull of *S. kirchbergensis* was documented in northern Siberia in the Chondon River (Arctic Yakutia, Russia), but in contrast to previously commented rhinos this finding represents different chronology as it is dated to MIS 3 (Kirillova et al., 2017). However, according to Shpansky and Boeskorov (2018) tundra landscapes that dominated on the north of Yakutia during MIS 3 were unsuitable for *S. kirchbergensis* and for this reason they suggest the Middle Pleistocene age (MIS 9 – MIS 11) of this specimen. Among plant remais (Table S9), bryophytes of the genera *Aulacomnium* and *Polytrichium* as well as Ericaceae, Poaceae and diatoms were identified. Inside the skull and between the teeth, the most abundant plant remains were barks of *Salix* sp. and *Betula* sp. as well as shoots of *Larix* sp., *Larix* sp./*Picea* sp.

and *Vaccinium* sprouts. According to the authors, these rhinoceros died during the cold season, and the last food it consumed were shoots of *Larix*.

Of similar chronology is the finding of Mus-Khaya locality. The spore-pollen spectrum corresponded to a warming, forest-tundra and tundra-steppe types of vegetation in northern Yakutia at that time (Shpansky and Boeskorov, 2018).

Based on palaeobotanical studies of materials found in the teeth of the rhinos from the European sites, and on the basis of the structure of the species' teeth, it can be concluded that *S. kirchbergensis* fed on branches of trees and shrubs – hard deciduous tree and shrub vegetation (e.g. Neumark-Nord, Van der Made and Grübe, 2010) and that the leaves of trees and shrubs were most often consumed by this species. However, available data clearly indicate that the rhino also fed on herbaceous plants and grasses. *S. kirchbergensis*, when it had the opportunity, eagerly fed on soft aquatic or riparian vegetation as evidenced by the presence of such taxa in the diet of specimens from Neumark Nord, Spinadesco and Gorzów Wielkopolski (Table S9). The specimen from Chondon, living probably in more severe conditions of MIS3, used the low-growing vegetation to a greater extent than specimens from European sites, due to the vegetation available there (Kirillova et al., 2017), which showed that this species had a mixed diet depending on the climate zone and the growing season. These data together with other plant remains found in teeth fossae (Table S9) from the Middle and Upper Pleistocene of Eurasia clearly show that *S. kirchbergensis* was a browser, although a variability of its diet depended on food availability and the environment. The differences between the European localities are also visible. Specimens from Gorzów Wielkopolski and the North Sea, originating from the Eemian Interglacial or the beginning of the last glacial, lived in a densely forested environment than rhinos from Spinadesco and Neumark-Nord.

4.2. *Diet of Coelodonta antiquitatis based on plant micro- and macro-remains*

The woolly rhinoceros, together with the mammoth, steppe bison and horse, is well-known and thoroughly studied species of the *Mammuthus-Coelodonta* Complex (Kahlke, 1999). This species was widespread in Eurasia during the Pleistocene, although, unlike other representatives of this complex, it did not occur in North America. It was a large animal, massively built and reached over two tons of body weight (Vereshchagin and Baryshnikov, 1982; Kahlke, 1999, 2014; Stewart and Lister, 2012; Shpansky, 2014). The woolly rhinoceros is also known because of the finds of whole bodies and their fragments. Most of these specimens come from Siberia, but remains of three individuals were found in the modern territory of Ukraine in Starunia (Bayger et al., 1914; Nowak et al., 1930; Gams, 1934; Kormos, 1934; Lengersdorf, 1934; Zeuner F.E., 1934, 1939). The first specimens from Siberia were described already in the 19th century (Brandt, 1849; Schmalhausen, 1876; Chersky, 1879, 1891; Schrenk, 1880a, 1880b; Fortelius, 1983; Garutt, 1998; Boeskorov, 2001, 2012; Boeskorov et al., 2011a).

4.2.1. *Local environment*

A unique feature of Starunia clays is the strong saturation of sediments with salt and oil that has already appeared in the Pleistocene and has continued uninterrupted to this day. The reason for this is the Vorotyshcha Beds – salt-bearing deposits lying under the Quaternary beds (Koltun et al., 2005). Nowadays, it results in the occurrence of plants typical for salt flats such as *Puccinellia distans* (Mościcki et al., 2009). At the beginning of the Middle Pleniglacial, species tolerant to increased salinity such as *Triglochin maritimum*, *Schoenoplectus tabernemontani*, and *Phragmites australis* occurred there. *Puccinellia distans* and *Triglochin maritimum* prefer eutrophic or saline environment. These taxa are now present in Starunia, forming dense stands in boggy areas (Mościcki et al., 2009), but they were there also during the Middle Pleniglacial (Stachowicz-Rybka et al., 2009a). The swamp area was dominated by *Eleocharis palustris* and *Typha* sp. which were found together in *Phragmition* communities. *Potamogeton filiformis* was present there (Stachowicz-Rybka et al., 2009a, b).

In the sediments surrounding the rhino carcass, Szafer (1930) identified 14 plant taxa, among which *Betula nana* was a dominant species. From the clays surrounding the rhino body, remains of mosses were also extracted (Szafran, 1934; Gams, 1934) (Table S10). The composition of herbaceous plants, especially numerous *Carex* species suggests that low-moor habitats predominated at that time. In the Middle Pleniglacial, there were no tree remains found in Starunia, with the exception of *Betula humilis*, dwarf shrubs *B. nana* and *Salix* spp. represented by twelve species (Szafer, 1930; Kucowa, 1954, Table S10). *Betula nana* was an important component of peat bogs and wet meadows. In addition to mosses, Poaceae, Cyperaceae and other herbaceous vegetation, *Dryas octopetala* and *Arctostaphylos uwa-ursi* had a significant share. These data indicate a predominance of open landscapes and woodless plant communities. The major plant communities were tundra and steppe, the presence of which was marked by the occurrence of various grasses, sedges and dwarf shrub species.

4.2.2. *Diet*

The new study of the plant materials from Starunia demonstrated a number of plant species that were not reported by Szafer (1930), focused mainly on leaf analysis in the initial note. The most interesting was the content of samples labelled as "from intestine and teeth of the rhino" and "from guts and teeth of the rhino", which contained mainly fruits of Cyperaceae, including mostly various *Carex* species and other herbaceous plants (Fig. 7.5–7.18). In the samples "from intestine and teeth of the rhinoceros", there are remains of aquatic plants, which indicated at least a temporary functioning of the water body with a constant surface (Fig. 6, Table S1). In the remaining samples, a dominance of the genus *Carex* was observed, followed by seeds, leaves and seed scales of *Betula nana* (Fig. 7.1–7.3) as well as *Plantago lanceolata* accompanied by various herbaceous species (Table S1)

These data suggest that the rhinos from Starunia fed mostly on herbaceous plants and low-growing shrubby vegetation developed on the tundra and steppe. This is in accordance with a reconstruction of the Pleni-Vistulian plant communities, both during stadials and interstadials, which showed that the so-called mammoth steppe dominated at that time in the Starunia region and, to a broader extent, within the Ukrainian Carpathians (Stachowicz-Rybka et al., 2009b). This formation was characteristic for localities where large Pleistocene mammals were found to be present in both Eurasia and North America (Guthrie, 1990).

4.2.3. *Comparison with other sites*

The evidence of plant diet of *C. antiquitatis* came mostly form the region of Yakutia as well as from the North Sea and the Netherlands, all of them dated to MIS 3 and 2. Historically, the first reports about the woolly rhino diet dated back to the nineteenth century. These data were based on plant remains obtained from tooth fossae of the rhino from the Vilyui River. Brandt (1849) reported the remains of conifers. Fruit fragments of the genus *Ephedra* and *Salix* branches were also described (Table S10). From another woolly rhino specimen deposited in the Irkutsk Museum, Schmalhausen (1876) described Poaceae leaves and other herbaceous plants, along with branches of *Picea*, *Larix*, *Salix*, and *Ephedra* (Garutt et al., 1970). In 1970, the skull, which was found in 1877 in Khalbuy River, Yakutia near Verkhoyansk, was examined again. This find was originally described by Chersky (1879, 1891) and Schrenk (1880a,b). Palaeobotanical analysis showed the dominance of Poaceae, *Artemisia* and herbaceous plants, while a few pollen grains of *Betula* and *Alnus* were also found (Garutt et al., 1970). These studies confirmed the hypothesis that the woolly rhinoceros ate mainly herbaceous plants including grasses, perennials and probably shrubs, although its diet in some cases also included branches of trees and shrubs (Table S10).

A skeleton of the woolly rhinoceros with horns and soft tissue remains was found at the Churapcha site in central Yakutia. Lumps found in the gastrointestinal tract were interpreted as the remains of chewed (maybe digested) food. Excrements contained Poaceae, *Eriophorum* and Cyperaceae, while fecal pollen belonged to various herbaceous plants. Plant communities were restored based on palaeobotanical analysis of sediments surrounding the rhino's skeleton. Meadow and steppe communities with grasses and small forests with *Larix* and other conifers and *Betula* dominated there, as demonstrated by the pollen diagram (Table S10) (Lazarev and Tirskaya, 1975). The woolly rhino was mainly a grazer. During the Interplenivistulian, it lived in meadow-steppe with forests comprising *Larix*, other conifers and *Betula*, and with the cool and dry climate (Lazarev, 1977; Vereshchagin and Baryshnikov, 1982; Lazarev et al., 1998).

The dominance of herbaceous plants over forest-shrub vegetation was previously noted in the analysis of food remains from the teeth of the woolly rhinoceros from the Khalbui River (Poaceae constituted 68.2%, *Artemisia* – 17.1%) (Garutt et al., 1970) as well as based on those extracted from the gastrointestinal tract of the specimen from Churapcha site: Poaceae comprised 89%, *Artemisia* – 2.5% (Lazarev and Tirskaya, 1975) (Table S6).

Another important discovery occurred in 2007 in Yakutia near the Malaya Filippova River, 8 km east of Chersky village. Parts of an adult female mummy were found, including fragments of the trunk, head, skull, and limbs. Most internal organs were destroyed, but the stomach and its content were still present. The age of these specimens was determined as Interplenivistulian (MIS 3, Karginian interstadial) (Boeskorov et al., 2011a, b; Boeskorov, 2012), while a rib of this individual was dated using the AMS radiocarbon method (39,140 ± 390 BP, OxA-18755; Sher et al., 2009), which is consistent with other dates for this species of this area (Sulerzhitsky and Romanenko, 1997) (Table S10). In the stomach of the woolly rhinoceros from Kolyma, herbaceous plants clearly predominated (98.9%) showing typical for steppe and steppe-meadow taxa, with a relatively high content of Poaceae, abundant Asteraceae, including *Artemisia*, and numerous and diverse herbaceous plants. Pollen grains of trees and shrubs were also identified. Only few spores were preserved as well as remains of *Pediastrum* algae colonies and various fungal spores (Table S6). The pollen spectrum obtained from the soil surrounding the rhino mummy (Table S10) was characterised by a high content of pollen grains, dominated by Poaceae and other herbaceous plants and indicated plant communities of dry continental climate associated with the warmer phases of the Karginian interstadial (Boeskorov et al., 2009).

Similar pollen spectra were identified based on samples taken from the Ice Complex exposures in the Yakutia coastal lowlands (Giterman, 1963; Sher et al., 1979; Vasilchuk, 2003), e.g. in the upper part of the Ice Complex stratotype (Yedoma Suite), Duvanny Yar section on the right bank of the Kolyma River (130–140 km upstream of Chersky village). The pollen spectrum reflected the taxonomic diversity of herbaceous plants associated with mosaic-like plant communities. The predominance of herbaceous vegetation contained both in the teeth and intestine as well as in the sediment surrounding the rhino body from Starunia seems to correspond to the composition of the diet and the environment that was typical for the woolly rhino from Churapcha (Lazarev, 1977; Vereshchagin and Baryshnikov, 1982) and Verkhoyansk in Yakutia (Schrenk, 1880b; Chersky, 1879, 1891; Garutt et al., 1970).

The latest data on the woolly rhino's diet were provided by observations of Van Geel et al. (2019) from the North Sea and the Netherlands. Plant remains obtained from the teeth of *C. antiquitatis* demonstrated that the quantities of tree pollen were low, while Poaceae, Cyperaceae, *Plantago*, *Galium*, *Gentianella campestris*, *Scabiosa*, *Helianthemum*, *Artemisia* and other representatives of Asteraceae dominated. Poaceae pollen aggregates in three samples indicate the consumption of flowering grasses, which is why, according to the authors, Poaceae were probably over-represented in pollen spectra. These observations confirmed that this species was a grazer. The material also contained spores of fungi indicating more humid environments and those found only in the interstadial sediments of the last glaciation (Van Geel et al., 2019) (Table S10).

The palaeobotanical data from the Arctic zone of the Yakutia and from regions of the North Sea indicating that this species was mainly a grazer and herbaceous plants, mostly Poaceae and *Artemisia*, played a dominant role in the diet of *C. antiquitatis*. This specialisation is indicated by the shape of the occiput, favouring feeding near the ground, and the high teeth with cement (Table S10).

4.3. Diets and environments of rhinoceros based on multi-proxy analysis

Zeuner F. (1934) interpreted the diet of mammals based on the shape of their occipitals. Species with occipitals extending more caudally than the occipital condyles tend to hold their heads low and are grazers. Species with the occipitals positioned anterior to the occipital condyles tend to hold their heads high and browse on shrubs. The biomechanical reason for such interpretation is that the complex muscle inserts on the occiput and different occiput shapes maximise the momentum of this muscle according to habitual orientation of the skull.

Stephanorhinus kirchbergensis has the occipital morphology of a browser, as do *S. hundsheimensis* and *S. etruscus*, while *S. hemitoechus* and *Coelodonta* had the occiput like those in living grazing rhinoceroses. The extant white rhinoceros is a grazer and is called the square-lipped rhino because of the shape of its lips adapted to cropping grass. The black or hook-lipped rhino is a browser and has a narrow snout and lips. It has a narrower mandibular symphysis. The narrow and elongate mandibular symphysis of *S. kirchbergensis* was interpreted as indicative of browsing (Gromova, 1935; Shpansky and Boeskorov, 2018).

The three cases documenting the last food taken by individuals of *S. kirchbergensis* (Van der Made and Grübe, 2010; Niezabitowski et al., 1914; Niezabitowski-Lubicz, 1911a, 1911b) as well as that from Gorzów Wielkopolski cover a wide geographical range, and a considerable geological time, different seasons and local environments. In each of these cases, the food taken was different, which was probably due to differences in the seasons, local environments and possibly also to individual preferences. In any case, this shows the feeding flexibility of *Stephanorhinus kirchbergensis*. Common is that the individuals ate a great variety of food items, and there is an evidence that specific food items were preferred over others, some of which were more abundant in the environment. Each of the individuals was very selective. Though in case of the Chondon rhinoceros the diet was mainly browsing, there is an evidence that some grass was taken. This contrasts with the findings of Van Asperen and Kahlke (2015), who, based on mesowear, classified different samples of the species as "mixed feeder and browsers – open environments" and "mixed feeders and grazers", but none as "mainly browsers" or "mixed feeder and browsers – closed/cold environments".

According to the 'you are what you eat' principle of isotope ecology, the isotope composition of animal tissues reflects their diet (Bocherens et al., 1996a; Bocherens and Drucker, 2013; Krajcarz et al., 2018). Using these data, we can apply the isotope analysis of animal remains to reconstruct the dietary habits and ecology of the animals. In the case of herbivores, the most informative are stable isotopes of carbon, because the $^{13}C/^{12}C$ ratio is highly variable in plants and is related to the ecological types of plant communities, such as C_3 and C_4 physiological types and the density of vegetation (Smith and Epstein, 1971; DeNiro and Epstein, 1978; Broadmeadow and Griffiths, 1993; Marshall et al., 2007). Geographic and climatic factors, such as water availability, temperature, latitude and altitude, and the concentration of CO_2 in the atmosphere, are also important (DeNiro and Epstein, 1978; Körner et al., 1991; Zhu et al., 2010; Agurla et al., 2018).

The C_3 and C_4 types of plants reflect different physiological adaptations to the environment (Smith and Epstein, 1971). The $\delta^{13}C$ values in herbivore enamel collagen ranging from −16‰ to −8‰ indicate a pure C_3 diet, whereas values that are > −2‰ indicate a pure C_4 diet (Smith and Epstein, 1971; Sponheimer and Lee-Thorp, 1999; Bocherens and Drucker, 2013). This is a universal rule in herbivores, so we may assume

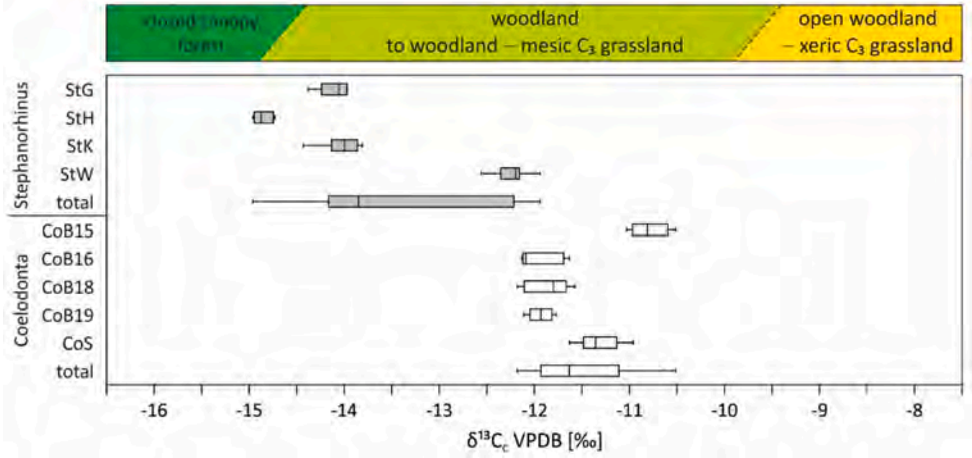

Fig. 8. Isotope values in rhino enamel samples from the Pleistocene of Poland: mean and standard deviation (box plots), minimum and maximum values (whiskers). Boundaries between vegetation types calculated according to Domingo et al. (2013), using the −6.4‰ and −6.9‰ end values of air CO_2 $\delta^{13}C$ during the Late Pleistocene after Eggleston et al. (2016).

that this also concerns the extinct rhinoceroses (Koch, 2007; Biasatti et al., 2018).

All rhino enamel samples, both *Stephanorhinus* and *Coelodonta*, studied by us exhibit $\delta^{13}C_C$ values below −10.5‰ VPDB (Table S2), which indicates a pure C_3 plant-based diet. This is in accordance with modern distribution of physiological types of plants, as C_3 type clearly prevails in Central Europe and only around 2% of modern vegetation here are C_4 plants (Pyankov et al., 2010). We may expect that the distribution of C_3 and C_4 plants in the Pleistocene of Central Europe was similar to the recent one. This was supported by studies of isotope composition of other Central European Pleistocene animals, whose $\delta^{13}C$ signals stay in the range of C_3-dominated ecosystems (e.g., Krajcarz and Krajcarz, 2014a, 2014b; Krajcarz et al., 2014b; Piskorska et al., 2015; Krajcarz et al., 2016).

An additional factor responsible for the $^{13}C/^{12}C$ ratio in plants is vegetation density, the so-called ‘canopy effect’. Under a dense forest canopy, the atmospheric and plant-incorporated carbon becomes ^{12}C-enriched due to low air exchange and low intensity of sunlight (Broadmeadow and Griffiths, 1993; Buchmann et al., 1997; Heaton, 1999; Hiyama et al., 2017). In boreal forests, vascular plants exhibit $\delta^{13}C$ values between −27‰ and −32‰, while in open environments this signal ranges between −24‰ and −28‰ (Brooks et al., 1997; Marshall et al., 2007), being reflected by herbivore tissues (Drucker et al., 2008; Bocherens and Drucker, 2013; Hofman-Kamińska et al., 2018). In C_3-dominated European Pleistocene ecosystems, the $\delta^{13}C_C$ values in enamel of herbivores inhabiting dense forests is expected to be below −14.5‰ (Domingo et al., 2013). Higher values indicate more open environments.

In our dataset, there was a clear discrepancy in $\delta^{13}C_C$ values between *S. kirchbergensis* and *C. antiquitatis* (Fig. 8). Three *S. kirchbergensis* specimens (i.e. Wrocław-Hallera StH, Gorzów Wielkopolski StG and Konin StK) exhibit $\delta^{13}C_C$ values significantly lower from all *C. antiquitatis* specimens and from another *S. kirchbergenis* specimen from Warszawa (StW). This difference, supported by statistics, indicates different diets. The three mentioned *S. kirchbergensis* specimens used to forage in more forested environment compared to the others.

In the case of Wrocław-Hallera (StH) the specimen, which records the lowest $\delta^{13}C_C$ values in our dataset, there certainly was a closed canopy forest. Two other specimens (Gorzów Wielkopolski StG and Konin StK) inhabited slightly more open woodland (Fig. 8). Specimens were found in lacustrine sediments, the reconstructed environment of their occurrence based on paleobotanical data was quite similar (Gorzów in this work; Malkiewicz, 2002 from Konin). The specimen from Wrocław-Hallera according to Wiśniewski et al. (2009) came from the end of the MIS 4 period or Interplenivistulian MIS 3. Isotope analysis of this specimen as given above showed surprising results, according to which this rhino lived in a closed canopy forest. The fragments of *Alnus* and *Ulmus* wood were marked from the sediment surrounding the rhino, although the samples containing the wood come from sediments of a riverine environment. Therefore, it can be assumed that these remains were transported (Pyszyński and Wiśniewski, 2005). At that time, there were no such environments in Poland. It is possible that this specimen was redeposited from other interglacial layers (Niezabitowski et al., 1914; Niezabitowski-Lubicz, 1911a, 1911b; Mamakowa, 1976, 1988; Lorek, 1988; Malkiewicz, 2002, 2010; Cyrek et al., 2010; Wiśniewski et al., 2009; Krajcarz et al., 2014a; Stefaniak, 2015; Marciszak et al., 2019).

All studied *C. antiquitatis* specimens differ from *S. kirchbergensis*, as they record ^{13}C-enriched diet, reflecting open woodland or grassland landscapes (Fig. 8). All specimens of *C. antiquitatis* from the Biśnik Cave come from the Middle Pleistocene layers. The specimen from the layer No. 15 could come from the Saalian glacial (MIS 6), which explains more open environment and resemblance to the specimen from Skarszyn which came from the Vistulian glacial (MIS 2 or 3). The specimens from layers Nos. 16, 18 and 19bc came from the warmer periods, the end of the interglacial or interstadial, which was reflected by the isotope signal. There were areas with dense forests and open areas in the vicinity of the Biśnik Cave (Cyrek et al., 2010; Krajcarz et al., 2014a; Stefaniak, 2015; Marciszak et al., 2019).

A single *S. kirchbergensis* specimen from Warszawa (StW) is more similar to *C. antiquitatis* than to other *S. kirchbergensis* rhinos (Fig. 8). This animal foraged in open woodland or grassland. This different diet might be interpreted as the result of a taxonomic difference of the fossils from Wrocław-Hallera street (StH), Gorzów Wielkoplski (StG) and Konin (StK) belonging to *S. kirchbergensis* and that from Warszawa (StW) to another species.

The age of the *S. kirchbergensis* skull from Warszawa was not clearly defined by Borsuk-Białynicka and Jakubowski (1972). It was generally assumed based on other finds of the forest elephant *Palaeoloxodon antiquus* (Falconer and Cautley, 1847) from this area, that this specimen originated from the last interglacial (Jakubowski, 1996). It is possible that the remains of *Stephanorhinus* skull from Warszawa, however, come from the beginning of the last glacial, i.e. a cooler period, when there was a significant rebuilding of plant communities and the share of grasses and herbaceous plants increased, and hence the difference in diet reflected by the isotope signal (Mamakowa, 1976, 1988; Malkiewicz, 2002, 2010).

All studied specimens show relatively low amplitudes of the

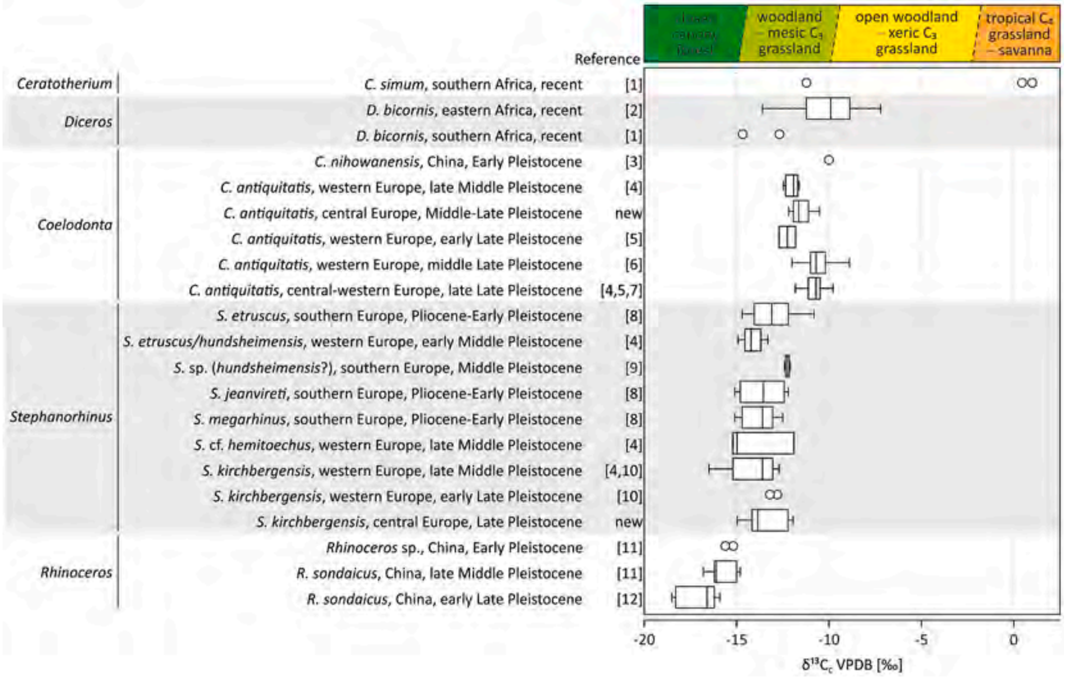

Fig. 9. Isotope values in the enamel of Pleistocene and extant rhinos (the symbols follow Fig. 8). Data after: [1] Codron et al. (2018); [2] Niezabitowski et al. (1914); Niezabitowski-Lubicz (1911a, 1911b); [3] Biasatti et al. (2018); [4] Pushkina et al. (2014); [5] Bocherens (2014); [6] Bocherens et al. (1995); [7] Krajcarz and Krajcarz (2014b); [8] Szabó et al. (2017) with further references there; [9] Pandolfi et al. (2018); [10] Ecker et al. (2013); [11] Qu et al. (2014); [12] Sun et al. (2019); and new data.

measured $\delta^{13}C_C$ values (Fig. 9), reaching 0.23‰ in case of *C. antiquitatis* from Wrocław-Hallera Street (StH), up to 0.67‰ in case of Skarszyn (CoS) specimen. It is noteworthy that the samples were taken in sequences, and in each case they represented the entire period of a given enamel formation, which is expected in rhinos to be around 2 years (Tafforeau et al., 2007).

A study of the Eastern Siberian *Coelodonta* by Tiunov and Kirillova (2010) revealed much greater inter-specimen variability of δ^{13}C, reaching almost 3‰. Although that study concerned another tissue (horn keratin), it presents well the seasonal variability of the isotope composition of a rhino's diet. Lower amplitudes in specimens from Poland are probably a result of the dampening effect in the enamel, related to mineralisation processes (Bernard et al., 2009), and/or can be related to more uniform diet of these rhinos than case of Eastern Siberia, and consequently less important shift between winter and summer ecology.

Our results are in accordance with literature data. Fig. 9 shows a comparison between enamel δ^{13}C signatures of rhinoceroses from Poland and other Quaternary rhinoceroses from Eurasia and Africa, both fossil and recent ones. *S. kirchbergensis* specimens from Poland are in the range of the isotope signal of this genus in western and southern Europe (Ecker et al., 2013; Bocherens, 2014; Pushkina et al., 2014; Codron et al., 2018). It is apparent that *Stephanorhinus* species did not change their diet, and possibly habitats, since Early to Late Pleistocene. These rhinos lived in intermediate habitats between dense forests inhabited by south-east Asian *Rhinoceros* (see Qu et al., 2014; Sun et al., 2019) and modern African grasslands and bushlands inhabited by black rhino (see: Bocherens et al., 1996a; Codron et al., 2018). Isotope data from bone collagen *S. kirchbergensis* from MIS 7 of Germany, although difficult to be directly compared with enamel data, also indicate woodland habitat (Kuitems et al., 2015).

The results of palaeobotanical analysis were partly confirmed by the isotope data. Samples taken from the horns of this species from Siberia were examined (Tiunov and Kirillova, 2010). The authors found light and dark areas on the horns from the Panteleikha River valley near Chersky (Kolyma). Isotope data indicated that the dark areas were formed during the summer until the beginning of autumn, when the amount of food was sufficient. At that time, the woolly rhino fed on a diet mainly composed of Poaceae. In cold periods (late autumn, winter, up to the beginning of spring) bright zones were formed. During this period, the rhinoceros probably fed on shrub vegetation and tree leaves. Its diet at that time was similar to that of the elk. Tiunov and Kirillova (2010) suggested diet similarity in the woolly rhinoceros and the woolly mammoth. According to them, the palaeobotanical data and morphology of the preserved skulls of the woolly rhinoceros do not contradict their inference. Data from isotope analysis of the bone of this species from two localities near Baikal indicated that the woolly rhino's diet was dominated by C_3 plants. Woolly rhinos in this area inhabited rather different communities than those from the north of Siberia. These were mainly semi-arid areas or dry cool steppe, as well as river valleys with water bodies (Khubanova et al., 2016). Although the woolly rhino is regarded as a component of *Mammuthus-Coelodonta* faunal assemblage and its remains are commonly found in the same strata as mammoth remains (Kahlke, 1999), rhino and mammoth did not rely on the same diet. The isotopic data from multiple sites compared by Bocherens (2015; and further references there) indicated that the isotopic δ^{13}C and δ^{5}N signal of the woolly rhinoceros was different from that of the woolly mammoth in the entire Eurasia. In Western Europe the woolly rhino's diet was similar to that of Equidae and large Bovidae, while in Yakutia the rhino occupied a separate and isolated niche.

Collagen stable isotope data for the Eurasian Pleistocene woolly rhino show that this species had relatively uniformed diet throughout its range (e.g. Bocherens et al., 1994, 1996b; 2005, 2015; Bocherens, 2014; Pushkina et al., 2014; Khubanova et al., 2016; Krajcarz et al., 2016) despite the fact that it was widespread from western Europe to Beringia. This indicates its narrow ecological adaptation. According to collagen data, woolly rhino usually occupied an isotope niche similar to those of horse, bison, and muskox, but dissimilar with mammoth. Our enamel isotope data are similar to those known for the Early Pleistocene *Coelodonta nihowanensis* (Chow, 1978) from China (Biasatti et al., 2018) and the Middle and Late Pleistocene *C. antiquitatis* from Western and Central Europe (Bocherens et al., 1995; Bocherens, 2014; Pushkina et al., 2014;

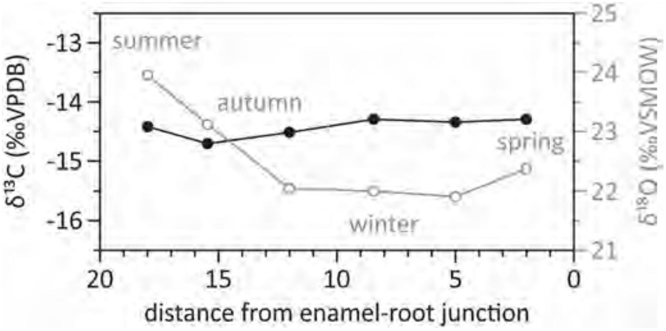

Fig. 10. Intra-tooth $\delta^{13}C$ and $\delta^{18}O$ variability in *Stephanorhinus kirchbergensis* from Gorzów Wielkopolski, along the crown growth axis.

Krajcarz and Krajcarz, 2014b) (Fig. 9). This observation indicates limited adaptative dietary changes in *Coelodonta* during the Quaternary.

In terms of enamel stable isotopes, the woolly rhino's diet and habitat could be compared to those of modern African white rhino, except for the different climate. Its $\delta^{13}C$ values overlap also the range of modern black rhino. Due to high $\delta^{13}C$ values, we can interpret its habitat as one of the most open environments inhabited by rhinoceroses studied by enamel stable isotopes. Clearly higher $\delta^{13}C$ values are exhibited only by African white rhino (Codron et al., 2018) and some pre-Quaternary Asian species (Biasatti et al., 2018), but this can be an effect of C_4 plant-based diet of those rhinoceroses (Fig. 9).

There are discrepancies between the palaeobotanical data, isotope signal and mesowear signature of the Gorzów Wielkopolski rhino. The isotope signal reflected the foraging environment during the time in animal's life when the teeth enamel was formed. In large ungulates, the premolar enamel starts to form already during intra-uterine life, but continues during further months or even years (Fricke and O'Neil, 1996; Martin et al., 2008). The enamel formation is finished when premolar started to erupt, which in modern Sumatran and Javan rhinos happens when the animal almost reached its adult size (Groves, 1967). In the case of the studied specimen from Gorzów Wielkopolski, the examined premolar was heavily worn and only the lower part of the enamel was preserved, i.e. the enamel from the late stage of formation. This suggests that only the post-weaning signal was recorded for this specimen, and it reflects well the isotope composition of both the diet and drunk water.

The sequencial sampling allowed to track the temporal change of isotope signal in the Gorzów Wielkopolski specimen (Fig. 10). The shape of $\delta^{18}O$ curve along the enamel growth axis reflected the change of $\delta^{18}O$ signal of ingested water during the following seasons, and indirectly – the seasonal climate change (Fricke and O'Neil, 1996). This allowed to recognise summer (the highest $\delta^{18}O$ value), winter (the lowest $\delta^{18}O$ value) and transitional seasons (Fig. 10), and indicate that more than half of a year was recorded in the preserved enamel.

Because $\delta^{13}C$ values were measured in the same samples as $\delta^{18}O$, we can detect the change of $\delta^{13}C$ signal for this specimen, and indirectly its diet, during the year (Fig. 10). Surprisingly, high $\delta^{13}C$ values are recorded both for the warmest and the coldest parts of a year. The lowest $\delta^{13}C$ value is connected with the transition from warm to cold season. This indicates that the individual shifted its diet during a year, and used to forage in forested areas during autumn, while it spent summers and winters in more open landscapes. This may reflect the seasonal availability of food types, or individual foraging preferences. This isotope record also explains the discrepancy between the observations based on mesowear and plant macrofossil analyses. The presence of plant macroremains indicative of autumn could be connected with seasonal migration of this rhino to woodlands; while the grass-impacted mesowear characteristics may reflect the foraging in grasslands for the greater part of the year. However, the overall variability of $\delta^{13}C$ values in the Gorzów Wielkopolski specimen is low (with amplitude = 0.41‰ and sd = 0.15). Therefore, the observed isotopic differences may be of minor relevance or may reflect only minor seasonal changes in diet.

Whilst the isotope signal indicates that the animal fed in woodland landscape with an admixture of wooded and more open areas, this does not preclude a grazing-dominated diet. Grazers in such environments can find sufficient food in the undergrowth, forest edges and open areas, possibly playing a role in maintaining such open spaces. In contrast, the mesowear signature reflects diet over a longer period of time (months to years), and a grazing mesowear signature does not preclude occasional browsing, especially at the end of an individual's life, when environmental conditions or illness may prevent the animal from procuring its usual food. Furthermore, the Gorzów Wielkopolski rhino was an old individual, and mesowear in older individuals tends to be skewed towards a blunter signature even in animals that have a mixed or browsing diet. The palaeobotanical data show that the animal selected plants which were less common in the environment where it lived, indicating a browsing diet. However, this represents the last few meals of the individual and cannot be extrapolated to its entire lifetime. This individual might be ill before it died and for that reason may not have eaten its normal food.

Many animals also have fall-back foods that they eat when other food is scarce, often including browse in grazers (e.g. modern wood bison diet can include up to 95% of browse in summer, but the animals still have a mix-feeder mesowear signature; Reynolds et al., 1978; Campbell and Hinkes, 1983; Waggoner and Hinkes, 1986; Larter and Gates, 1991). In short, the apparent contradictions between these different dietary proxies are largely due to the different timescales represented as well as the old age at which this individual died.

5. Conclusions

Stephanorhinus kirchbergesis was mostly a mix-feeder incorporating both of browse and grass in its diet. Its habitat included various types of forests, from riparian communities, deciduous and mixed forests to more open areas (forest-steppe), and its selection of foraging areas depended on a season. It occurred in the Middle and Late Pleistocene in localities ranging from warm to moderate climate, during both interglacial and interstadial periods. This rhino ate terrestrial vegetation, including that occurring near both flowing and standing waters. The obtained data are from different growing seasons from winter or spring (Chondon), through spring (Neumark-Nord), summer (Spinadesco) and end of summer – beginning of autumn (Gorzów). The diet of different individuals may varied with the local environments and its record may be biased by the season of death, but in all cases some plant species were selected that were not the most abundant in the local environment. The food remains from the fossae of the teeth indicated flexible browsing, confirming the previous interpretations based on functional morphology and stable isotopes.

Coelodonta antiquitatis was a grazer in localities from glacial, interglacial and interstadial periods, although according to our results this species adjusted its diet to the local vegetation and season. During periods of shortage of grass and herbaceous vegetation, this rhino could also eat leaves of trees and shrubs. Its diet slightly differed in individuals from Europe and Asia as shown by the results of isotope studies. These data show a clear seasonal variation in the isotope composition of this rhino's diet. Much lower amplitudes of $\delta^{13}C$ in specimens from Poland, both *S. kirchbergensis* and *C. antiquitatis*, indicated a more uniform diet of these rhinos than those in Eastern Siberia, both during winter and summer.

Isotope analyses are important and useful for studying the paleoecology of extinct rhino species. In the case of the rhino from Gorzów Wielkopolski this analysis helped in explaining the discrepancy between the observations based on mesowear and plant macrofossil analyses concerning the type of diet. The former showed foraging in grasslands, while the latter indicated the use of woody plants originated from forests. Thanks to the analysis of intra-specimen stable isotope variation, it is clear that such a discrepancy may be connected with seasonal migrations of the individual.

Plant remains obtained from fossas of the teeth provide important information on the diet of extinct rhino species as they offer a direct evidence of plant species consumed by the rhinos. However, since these only represent the food consumed at the very end of the animal's life, these data need to be supplemented by dietary indicators that reflect diet over a larger part of the lifetime. Longer-term data from mesowear and microwear from a wider range of *S. kirchbergensis* fossils indicate a more mixed diet with a browsing component (e.g. Van Asperen and Kahlke, 2015; Rivals and Lister, 2016).

In the case of the Gorzów Wielkopolski rhino, which was very old when it died with heavily worn teeth, the isotope signal and palaeobotanical remains likely give a more accurate picture of the animal's diet than the mesowear signature.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.quaint.2020.08.039.

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