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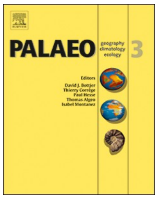

Dramatic change in the diet of a late Pleistocene *Elasmotherium* population during its last days of life: Implications for its catastrophic mortality in the Saratov region of Russia

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ABSTRACT

The late Pleistocene site of Irgiz 1 (Saratov Region, Russia) has yielded an accumulation of giant rhinoceros (*Elasmotherium sibiricum*) within the deposits of an oxbow lake. Irgiz 1 is one of the few sites in the world with a significant amount of elasmothere individuals of different age groups. Tooth mesowear and microwear are used to characterize the dietary traits of the giant rhinoceros on two temporal scales, the annual average diet and the diet at the time of death, respectively. Tooth mesowear, analyzed on 20 specimens, suggests a highly abrasive diet similar to that of extant grazers (similar to the extant white rhinoceros). Tooth microwear analyzed on 16 specimens, conversely, indicates that *E. sibiricum* was a browser (feeding on leaves from shrubs and trees) at the time of death. The strong discrepancy between the results from the two dietary proxies and the very low variability of the microwear signal suggest that these animals may have died in an event of short duration. The elasmotheres from the area around Irgiz 1 were grazers, but a catastrophic event, perhaps related to the significant accumulation of snow and/or ice coating (‘dzud’), limited the availability of grass and forced them to shift toward shrub/tree foliage that was still accessible. The combination of the two proxies, mesowear and microwear, allows the reconstruction of the dietary traits of *E. sibiricum*, but also to propose a hypothesis for death. This first study of tooth meso- and microwear on elasmotheres provided unique data which allows us to broaden our knowledge about the diet of these animals. The findings indicate that the Irgiz 1 population of elasmotheres died in a single catastrophic event and that the fossil assemblage is not time-averaged.

1. Introduction

Elasmotherium sibiricum is one of the largest representatives of the formerly widely diverse family Rhinocerotidae. The genus *Elasmotherium* was named by Gotthelf Fischer in 1808 (Fischer, 1808) and the name of the species *E. sibiricum* was published a year later (Fischer, 1809). This giant rhinoceros species weighed around 3500 kg (Kosintsev et al., 2019) and may reach up to 4000–5000 kg (Paul, 1998; Zhegallo et al., 2005). It was over two meters high at the withers, about 4–5 m long, and its skull was the second largest among rhinoceroses (around 0.85–0.9 m long) (Flerov, 1953; Schvyreva, 1995, 2016; Zhegallo et al., 2005). Besides their enormous size, the rhinoceroses of the genus *Elasmotherium* are known for their extraordinary anatomy, with the most famous anatomical feature being the dome-like protuberance on the frontal bones of the skull, which possibly played the role of a base for a giant horn (Flerov, 1953). The rhinoceros also had a large olfactory brain (Brandt, 1878), high-crowned (euhypsodont) teeth (Borissyak, 1914; Schvyreva, 1995, 2016; Koenigswald et al., 1999; Baygusheva et al., 2011), highly convoluted enamel plates, giant transverse processes of the atlas, and relatively slender limb bones with elongated metapodial bones (Teryaev, 1948; Schvyreva, 1995, 2016; Deng and Zheng, 2005).

The peculiar anatomy of *Elasmotherium* has generated two different hypotheses regarding their lifestyle and ecological niche. The first view represents these rhinoceroses as steppe-dwelling grazers feeding on grasses (Deng and Zheng, 2005). The most extravagant version of their habitat was proposed by Flerov (1953), who suggested *Elasmotherium* were “plough-beasts.” That is, the animals fed on both the aboveground

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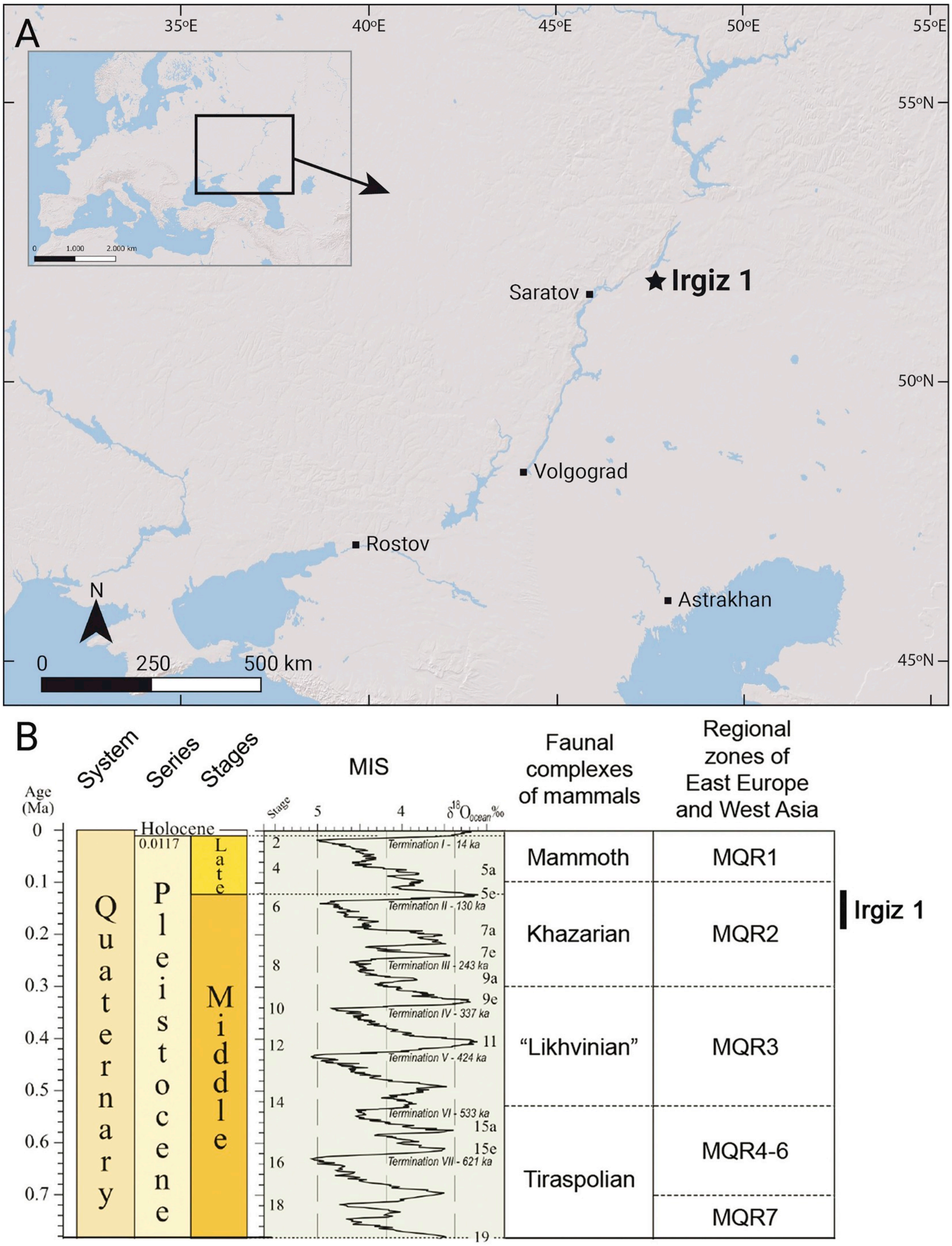

Fig. 1. (A) Map of location of Irgiz 1 and (B) chronological position of the site among the faunal complexes of mammals and Regional zones of East Europe and West Asia after Tesakov et al. (2019). The chronological position of Irgiz 1 is indicated by a vertical bar.

as well as the underground parts of plants by ploughing the soil with their pointed rostrums and picking up rhizomes and other subterranean parts of the plants. The second view (Teryaev, 1930, 1948) suggests that *Elasmotherium* had a hippo-like, semiaquatic lifestyle in riparian biotopes in which the source of food was proposed to be river and marsh plants, bottom plants, and rhizomes. An intermediate hypothesis was suggested by Noscova and Zhegallo (Noskova, 2001; Zhegallo et al., 2005), who believed that food for such a large animal could not be provided by low-productivity biotopes with xerophilous plants. The authors considered the habitat of *Elasmotherium* as a steppe landscape where riparian plant associations were the preferred feeding grounds. The food of *Elasmotherium* was thought to be plants that reproduce with rhizomes; many monocotyledonous species such as sedge, cattail, and naiad; and some eudicots such as water-lilies (Zhegallo et al., 2005).

It is interesting to note that these reconstructions are based on the same anatomical features of *Elasmotherium*. First, there is the unique hypsodont teeth (Koenigswald et al. (1999) considered *Elasmotherium* as the only rhinoceros that developed euhypsodont molars), which, in combination with the highly convoluted enamel plates, whose pattern becomes more complex in the evolutionary line of elasmotheriins (Schvyreva, 1995, 2016). Second is the obtuse angle between the plane of the occiput and the palate. As noted by Zeuner (1934, 1936), who measured this angle in modern and fossil rhinoceros species, this angle indicates which layer of vegetation served as the main food source of the animal. Zeuner believed that browsers were characterized by a sharp or right angle, while grazers are characterized by an obtuse angle. However, the occipital angle and feeding habits of modern rhinoceroses indicate that for browsers (black, Sumatran, Javan rhinoceroses), the occipital angle actually is sharp or right, while for grazers it depends on the height of the feeding level. So, among modern grazers, the white rhinoceros (*Ceratotherium simum*) has an obtuse occipital angle, and the Indian rhinoceros (*Rhinoceros unicornis*) has a sharp occipital angle. This is consistent with the specific height of feeding level of these species; the white rhinoceros feeds at ground level (feeding height < 0.5 m), while the Indian rhinoceros has a significantly higher feeding level (feeding height > 1 m) (Hullot et al., 2019). Among other Quaternary rhinoceroses, *Elasmotherium* showed the most obtuse occipital angle (106–115°) (Schvyreva, 2016), close to that of the white rhinoceros (110.5°) (Zeuner, 1936). Tooth features indicate a high abrasive load on the teeth, and the obtuse occipital angle indicates adaptation to feeding close to the ground.

Proponents of a steppe-dwelling grazer habitat consider these features as arguments for a hyper-grazing adaptation for feeding on xerophilous plants. Proponents of the semiaquatic habitat (feeding on riparian and rhizomatous plants) consider these features as signs of the consumption of food with substantial quantities of dust or grit, such as highly abrasive sand soils. Another argument for the latter, hippo-like lifestyle of *Elasmotherium* is associated with the taphonomic observations of the burial site of *Elasmotherium* skeletons discovered in 1938 (Saratov region) and 1964 (Gaevskaya elasmothere, Stavropol region). The position of the skeleton of the Gaevskaya specimen was unusual, as the animal stood on a vertical plane, while the body was tilted forward, and the head was located below the pelvis, which may indicate that the animal had become bogged down (Schvyreva, 1995, 2016; Zhegallo et al., 2005). However, such a fact regarding the death of the animal does not itself provide any evidence of its lifestyle.

The objective of this paper is to provide quantitative data to reconstruct the paleodiet of *E. sibiricum*. According to its morphology, *E. sibiricum* is expected to be a true grazer. This hypothesis is tested using tooth mesowear and microwear analyses as proxies to reconstruct the diet in 28 specimens of *E. sibiricum* from Irgiz 1, a Late Pleistocene locality in Russia. The combination of the two proxies allows us to establish the average annual diet (mesowear) as well as the diet at the time of death (microwear).

2. Geological context

The material was found on the new site of Irgiz 1 (Fig. 1A), located in the Saratov region (Russia), and confined to the riverbed of the Bolshoy Irgiz (a tributary of the Volga River) (Prilepskaya et al., 2019). The study site is protected but exact location information will be shared with qualified researchers upon request. The occurrence of the bones of large mammals in the river basin of the Bolshoy Irgiz has been known since the 1920s and 1930s and is associated with the active work of K.I. Zhuravlev, the director of the Museum of Pugachev (Belyaeva, 1935).

The sites of large mammals in the region are associated with lacustrine-alluvial (oxbow lake) sediments of the base of the coastal sections of the Bolshoy Irgiz River and its tributaries composing fragments of river terraces from the second half of the Middle Pleistocene (Prilepskaya et al., 2019). At the site, the fossil remains are confined to the upper part of a large erosive remnant, overlapped by gray-brown loams and clays from the Upper Pleistocene (Prilepskaya et al., 2019). Discovery of the bones of large mammals were made in dense blue-green clays in a scarp exposed by artificial structures - a dam and a descent to the pumping station. The length of the exposition of the productive horizon is up to 300–350 m, visible thickness varies from 1 to 1.5 m to 3–5 m, most of which is under the water of the river. Divers explored the underwater part of the site. The fauna of large mammals is represented by the remains of elasmothere (*E. sibiricum*), mammoth (*Mammuthus intermedius*), steppe bison (*Bison priscus*), as well as an isolated lower jaw of the river beaver (*Castor fiber*). In the association of small mammals, rodents associated with open steppe biotopes ($> 95\%$) dominate the assemblage. The presence of the yellow steppe lemming (*Eolagurus luteus*) and jerboa (*Allactaga* sp.) indicates dry steppe or semi-desert conditions (Prilepskaya et al., 2019).

Evolutionary level of the key taxa of micromammals (*Ellobius talpinus*, *Eolagurus luteus*, *Lagurus lagurus*) and mammoth (*Mammuthus intermedius*) suggests that the site belongs to the Khazar faunal complex (Prilepskaya et al., 2019) (see Fig. 1B). The composition of the micromammals complex of the site is close to other faunas of the Khazar fauna complex of the Lower Volga (Prilepskaya et al., 2019). The Khazar faunal complex corresponds to the regional zone MQR2 of East Europe and West Asia (Tesakov et al., 2019). The formation time of Khazar-Singil sediments corresponds to the end of the Middle Pleistocene and the beginning of the Upper Pleistocene and correlates with the MIS 7–5 of marine isotopic scale zones (Zastrozhnov et al., 2018). Thus, Irgiz 1 site represents one of the last known *Elasmotherium sibiricum* populations (Prilepskaya et al., 2019).

The dominant species among the large mammals at the site is *Elasmotherium sibiricum*, which represent 2/3 of the fossil remains (Fig. 2). Osteological data (fusion of the diaphysis and epiphyses) and the discovery of the jaw of a juvenile individual (with unerupted permanent teeth) suggest that *Elasmotherium sibiricum* remains represent all major age groups: juvenile, young, adult, and old animals; and represent at least seven different individuals (Prilepskaya et al., 2019). Irgiz 1 is one of the few sites in the world with a significant amount of elasmothere individuals of different age groups.

3. Materials and methods

3.1. Materials

The dental remains available were screened to select suitable materials for tooth mesowear and microwear analyses. The sample selected for analysis comprises a total of 28 specimens. These include a maxilla with P3 to M3, a complete jaw with p4 to m3, and 26 isolated upper and lower premolars and molars. All studied teeth belong to permanent teeth. Two upper teeth (RMZ 02/75 (see Fig. 2-I) and PR 6) belong to young individuals who have recently changed their deciduous teeth to permanent ones (a postfossette has not yet been closed on these teeth). The other teeth belong to adult animals. The number of the most represented teeth (Upper Right M1) suggests that at least 5 different individuals were studied here. Since most of the specimens are represented by isolated teeth ($N = 26$), we are not able to reliably determine the exact number of studied individuals. However, according to their morphology, size and wear stage, they could belong to different individuals. Therefore, we will consider each tooth as a separate individual.

The list of specimens sampled and analyzed, and the raw data for mesowear and microwear, are provided as Supplementary Material 1 (available at:https://doi.org/10.5281/zenodo.3903105). The material studied is currently stored in the collection of the Regional Museum of Earth Sciences, Saratov State University (SSU), Saratov, Russia.

3.2. Mesowear methodology

Mesowear analysis is a method of categorizing the gross dental wear of ungulate molars by evaluating the relief and sharpness of cusp apices in ways that are correlated with the relative amounts of attritive (tooth to tooth contact) and abrasive (tooth to food contact) dental wear (Fortelius and Solounias, 2000). Mesowear is scored macroscopically from the buccal side of molars. A diet with low levels of abrasion (such as dicotyledonous plants) maintains sharpened apices on the buccal cusps as the tooth wears. In contrast, high levels of abrasion, associated

Fig. 2. *Elasmotherium sibiricum* remains from Irgiz 1. Right maxilla RMZ 02/269, labial view (A), occlusal view (B); Left third upper molar PR 10, occlusal view (C), lingual view (D), labial view (E); Left first upper molar PR 8, occlusal view (F), lingual view (G), labial view (H); Left upper premolar (P3/P4) RMZ 02/75, occlusal view (I), lingual view (J), labial view (K); Left third lower molar PR 11, occlusal view (L), lingual view (M), labial view (N); Right second lower molar PR 12, occlusal view (O), lingual view (P), labial view (Q); Left mandible RMZ 02/11, labial view (R), occlusal view (S).

with a diet of siliceous grass, results in more rounded and blunted buccal cusp apices (Fortelius and Solounias, 2000). Unworn (and marginally worn) teeth, extremely worn teeth, and those with broken or damaged cusp apices, are omitted from mesowear analysis. Cusp sharpness is sensitive to ontogenetic age among young individuals (which have not yet developed substantial wear facets) and among dentally senescent individuals. However, for intermediate age groups, mesowear is found to be less sensitive to age and more strongly related to diet (Rivals et al., 2007) and therefore suitable for dietary reconstruction.

The mesowear was analyzed on 3D models of the teeth. In total, 33 teeth, including 9 teeth from the maxilla and jaw, were scanned. The teeth were scanned with an Artec Space Spider 3D scanner and processed in Artec Studio 14 software. The resulting 3D models have a resolution of 0.15 mm and accuracy of up to 50 µm. For the 26 specimens that were scanned, six were discarded because the tooth cusps were taphonomically damaged. In this study, the standardized method (mesowear 'ruler') introduced by Mihlbachler et al. (2011) is employed. This method is based on seven cusp categories (numbered from 0 to 6), ranging in shape from high and sharp (stage 0) to completely blunt with no relief (stage 6). Using the mesowear ruler as a reference, cusps equal to or sharper and higher in relief than reference cusp 0 were assigned a value of 0. Cusps that were morphologically intermediate between reference cusp 0 and reference cusp 1, or equal to reference cusp 1, were

Table 1
Mesowear summary data for *Elasmotherium sibiricum* (this study) and the extant rhinoceroses, zebras and bison (Fortelius and Solounias, 2000). Abbreviations: N = number of specimens; MWS = Mesowear Score.

Species	N	MWS
Elasmotherium sibiricum	20	5.50
Ceratotherium simum (White rhinoceros)	24	4.67
Dicerorhinus sumatrensis (Sumatran rhinoceros)	5	0.40
Diceros bicornis (Black rhinoceros)	34	0.12
Rhinoceros sondaicus (Javan rhinoceros)	5	0.00
Rhinoceros unicornis (Indian rhinoceros)	5	0.40
Equus quagga (Plains zebra)	122	4.68
Equus grevyi (Grévy's zebra)	29	4.48
Bison bison bison (American bison)	15	5.47

assigned a value of 1, and so forth. The average value of the mesowear data from a single sample of fossil dentitions corresponds to the 'mesowear score' or MWS (Mihlbachler et al., 2011). To reduce inter-observer error, dental mesowear analysis was conducted by a single experienced researcher (FR).

3.3. Microwear methodology

Microwear features of dental enamel were examined using a stereomicroscope on high-resolution epoxy casts of teeth following the protocol developed by Solounias and Semprebon (2002) and Semprebon et al. (2004). In short, the occlusal surface of each specimen was cleaned using acetone and then 96% alcohol. The surface was molded using high-resolution silicone (Heraeus Kulzer, PROVIL novo Vinylpolysiloxane, Light C.D. 2 regular set) and casts were created using clear epoxy resin (C.T.S. Spain, EPO 150 + K151). All teeth molded were carefully screened under a stereomicroscope. Those with badly preserved enamel or taphonomic defects (features with unusual morphology and size, or fresh features made during the collection process or during storage) were removed from the analysis (King et al., 1999; El-Zaatari, 2010). From all the teeth, 19 were selected and molded. For the maxilla and jaw, all teeth were molded and analyzed, but only one tooth per specimen was considered in the analysis. After checking the teeth do not belong to the same individuals, according to Xafis et al. (2017) molars and premolars were selected for the analysis. After discarding four teeth with evidence of taphonomic alterations of the enamel surface, 15 teeth were suitable for microwear analysis. Casts were observed under incident light with a Zeiss Stemi 2000C stereomicroscope at 35 × magnification, using the refractive properties of the transparent cast to reveal microfeatures on the enamel. Microwear pictures of each specimen analyzed are provided in Supplementary Material 2 (available at:https://doi.org/10.5281/zenodo.3903105). To avoid inter-observer error, the scoring of microwear was done by a single observer (FR).

Microwear scars were quantified in two areas on the paracone of the upper teeth and the protoconid of the lower teeth in a square area of 0.16 mm^2 using an ocular reticule. We used the classification of features defined by Solounias and Semprebon (2002) and Semprebon et al. (2004) which distinguish pits and scratches. Pits are microwear scars that are circular or sub-circular in outline and thus have approximately similar widths and lengths, while scratches are elongated microfeatures that are not merely longer than they are wide, but have straight, parallel sides. These two categories are subdivided as follows. (1) Pits are classified as small pits (which appear bright and shiny), large pits (darker than small pits), or puncture pits (deep with regular margins). (2) Scratches are divided into fine (narrow), coarse (large and bright), and hypercoarse (very deep and dark). The presence of other features (cross scratches and gouges) is recorded qualitatively. In addition, scratch textures were assessed using the scratch width score (SWS), which is obtained by giving a score of '0' to teeth with predominantly fine scratches, '1' to those with a mixture of fine and coarse types of textures, and '2' to those with predominantly coarse scratches. Individual scores for a sample were then averaged to get the SWS. For a more precise categorization of the grazers, browsers, and mixed feeders, we used the percentage of individuals in a sample possessing scratch numbers that fall between 0 and 17 in the 0.16 mm^2 area (0–17%) (Semprebon, 2002; Semprebon and Rivals, 2007).

As seasonal changes in diet are recorded by microwear, the variability of the microwear signal was used to estimate the duration of the formation of the assemblages at the Irgiz 1. Following Rivals et al. (2015), we used two measurements of the variability of scratch density, namely the standard deviation (SD) and the coefficient of variation (CV). The combination of the two measurements of variability permits the classification of assemblages into one of the following categories: (A) seasonal events or shorter time windows, (B) events longer than a season (i.e. two or more contiguous seasons) and (C) separate events that occurred in different non-contiguous seasons.

4. Results

The mesowear pattern recorded on *Elasmotherium sibiricum* teeth is characterized by a very low relief and rounded or blunt cusps (Fig. 2). The individual mesowear scores (MWS) are between 4 and 6. The average MWS for the sample is 5.5 (Table 1). In comparison with the reference dataset on modern ungulates (Fortelius and Solounias, 2000), *Elasmotherium sibiricum* has mesowear values higher than the values reported for the extant white rhinoceros or the zebras and similar to that of the modern American bison (Table 1) suggesting a very abrasive diet.

The microwear pattern observed on the *Elasmotherium sibiricum* teeth is characterized by low numbers of scratches and pits (Table 2; Fig. 3). In comparison to the modern rhinoceroses (from Rivals et al., 2010), its pattern is very different from the extant black rhinoceros *Diceros bicornis* and the white rhinoceros *Ceratotherium simum* (Fig. 4). In terms of scratches, which is the variable that mostly separate browsers from grazers (Solounias and Semprebon, 2002), *E. sibiricum* is not significantly different from *Diceros bicornis* (Table 3). In term of pits, *E. sibiricum* has significantly lower numbers of pits than the two extant rhinoceroses (Table 3). In *E. sibiricum*, the higher scratch width score, together with the presence of hypercoarse scratches, suggests that the diet, besides leaves from dicots or ligneous plants, also included some bark, maybe from the branches of bushes or low parts of trees. The absence of puncture pits, as in extant rhinoceroses, allows discarding the consumption of fruits and seeds.

The variability of the numbers of scratches in the Irgiz 1 sample is low (SD = 1.52; CV = 0.13). The sample plots in area [A] of the bivariate graph (Fig. 5) which is the area corresponding to a short term event of the formation of an assemblage that lasted less than 3 months. It could correspond either to a single and unique event, or to a repeated accumulation events at the same season each year.

Table 2
Microwear summary data for *Elasmotherium sibiricum* (this study) and the extant black rhinoceros and white rhinoceros (Rivals et al., 2010). Abbreviations: N = number of specimens; NP = average number of pits; NS = average number of scratches; %LP = percentage of specimens with large pits; %XS = percentage of specimens with cross scratches; %G = percentage of specimens with gouges; SWS = scratches width score (from 0 = fine scratches only to 2 = coarse scratches only); %HC = percentage of specimens with hypercoarse scratches; %PP = percentage of specimens with puncture pits; %0–17 = percentage of specimens with between 0 and 17 scratches.

Species	N	NP	NS	%LP	%G	SWS	%XS	%HC	%PP	%0–17
E. sibiricum	16	14.7	11.8	75	50	1.3	100	37.5	0	100
D. bicornis	10	88.6	11.5	90	40	0.2	50	-	0	90
C. simum	10	95.9	18.6	40	30	0.3	40	-	0	30

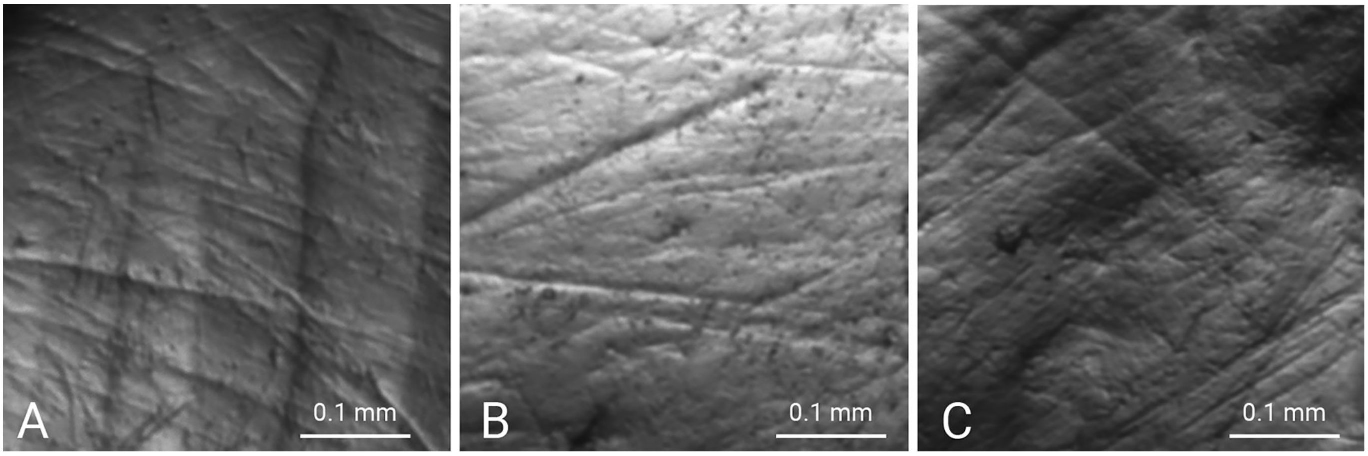

Fig. 3. Selected microphotographs at 35× magnification of microwear features on enamel surfaces of *Elasmotherium sibiricum* teeth from Irgiz 1. A. Specimen PR4; B. Specimen RMZ 02/74; C. Specimen RMZ 02/84.

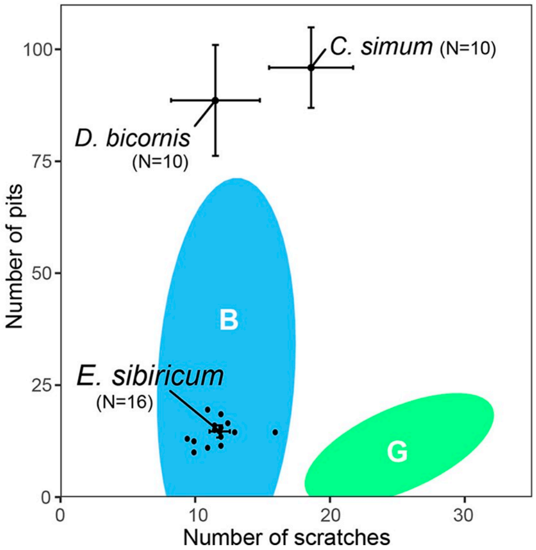

Fig. 4. Bivariate plot of the average numbers of pits and scratches for *Elasmotherium sibiricum* from Irgiz 1. Error bars correspond to standard error of the mean (± 1 SEM) for each sample. Plain ellipses correspond to the Gaussian confidence ellipses ($p = .95$) on the centroid for extant leaf browsers and grazers based on the reference database from Solounias and Semprebon (2002).

Table 3
Kruskal-Wallis test results for differences in microwear features among fossil and extant rhinos. H values below the diagonal, p values above the diagonal, significant comparisons are in bold.

	E. sibiricum	*D. bicornis*	*C. simum*
Number of pits.			
E. sibiricum	-	< **0.0001**	< **0.0001**
D. bicornis	17.78	-	0.3636
C. simum	17.78	0.8229	-
Number of scratches.			
E. sibiricum	-	0.5958	< **0.0001**
D. bicornis	0.2778	-	**0.0063**
C. simum	15.63	7.406	-

5. Discussion

5.1. Dietary traits of the elasmotheres from Irgiz 1 and other sites

The mesowear pattern observed on the teeth of *E. sibiricum* indicates a pure grazing diet, as would be expected from the morphological characteristics for that species. The cranial morphology (obtuse angle between the plane of the occiput and the palate) and the euhypsodont molars with a highly convoluted enamel ridge suggest an adaptation to grazing. The mesowear score is similar to that of the extant white rhinoceros (*Ceratotherium simum*), a grazer that feeds on very short grasses (Groves, 1972; Kleynhans et al., 2011). Because the white rhinoceros feeds on plants at close proximity to the ground, the ingestion of high proportions of exogenous particles (such as soil, dust and grit) also contributes to the presence of high abrasion on the teeth (Mihlbachler et al., 2018).

The microwear pattern observed on the enamel surfaces of *E. sibiricum*, which suggest leaf browsing dietary traits with some amounts of bark, contrasts with the morphological characteristics and the results from the mesowear analysis. Our findings do not question the diet of the *E. sibiricum* as a grazer but suggest alternative hypotheses to explain the discrepancy observed between the results. Considering the different temporal scales recorded by mesowear (i.e., the "annual" average diet) and microwear (i.e., the diet of the last days or weeks before death), our results indicate that *E. sibiricum* experienced a change in diet. All the individuals recovered from Irgiz 1 shifted from grazing to leaf browsing during the last days or weeks before they died. The results suggest that *E. sibiricum* was able to use other types of resources than grass, depending on the context. It is difficult to identify the reason for this discrepancy, because it could be an occasional and limited change in its diet related to the availability of resources or to competition with other species, among other reasons. Even if *E. sibiricum* had euhypsodont teeth adapted to grazing, our results provide some evidence of the existence of a certain degree of flexibility in its diet. Because there is only very little evidence about the dietary traits of *E. sibiricum* available in the literature, it is difficult to establish whether or not the pattern observed at Irgiz 1 is only a punctual and limited case for that particular population. The only reliable data can be found in a recent study of stable isotopes (Kosintsev et al., 2019), which notes that high δ^{13}C and δ^{15}N values found in *E. sibiricum* enamel are typical for inhabitants of dry steppe and desert biotopes and are the closest, among modern mammals, to the saiga antelope. The δ^{13}C values may be influenced by the consumption of C_4 plants (*Chenopodiaceae*). Other reliable data are provided by a short note (Baygusheva et al., 2011) about the microwear of an early *Elasmotherium* representative, *E. caucasicum*. While the authors did not supply quantitative data of the microwear features (numbers of scratches and pits), they did however argue that the M2 enamel of the Taman *Elasmotherium* had a high number of scratches and a relatively high number of pits. The pattern of microwear is reported to fall into the upper limits of variability for extant grazers (i.e. animals feeding principally on grass). The average number of scratches on *E.*

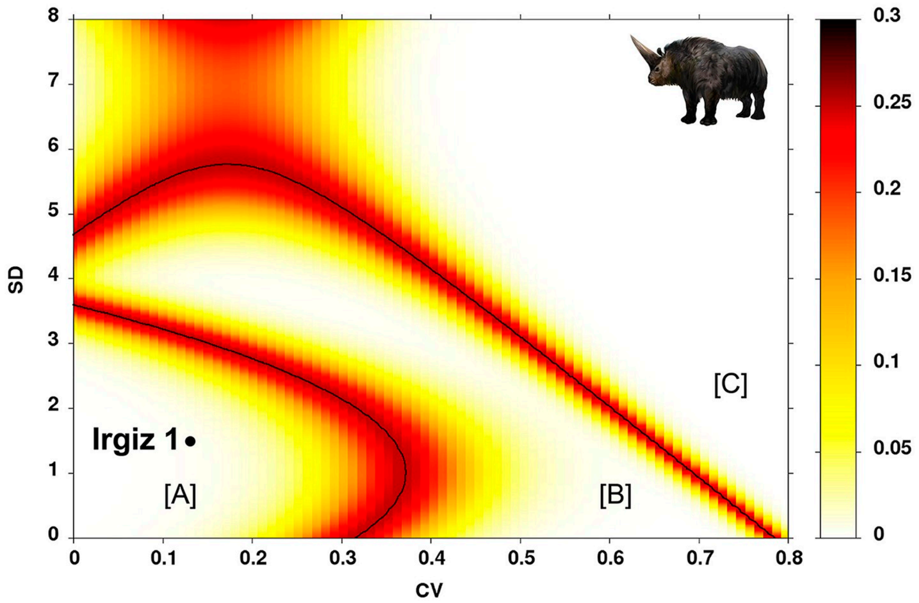

Fig. 5. Boundary lines with the error probability (heat map) based on standard deviations and coefficient of variation values of microwear data used for the classification of samples into short events (region A), long-term events (region B), or two separate short events (region C). The black dot corresponds to the sample of *Elasmotherium sibiricum* from Irgiz 1.

caucasicum enamel is also described as higher than for other rhinoceroses (Baygusheva et al., 2011). In that case, tooth microwear is in agreement with the expected diet for this species.

5.2. Comparison with other Pleistocene rhinoceros species

The various species of the Pleistocene genus *Stephanorhinus* show a wide diversity of dietary traits. Cranial morphology (occipital angle) suggests that *S. etruscus*, *S. hundsheimensis*, and *S. kirchbergensis* were browsers, and *S. hemitoechus* had the characteristics of a grazer (Zeuner, 1945; van der Made and Grube, 2010). However, analyses based on stable isotopes, mesowear and microwear, indicate a more complex situation. Except for the more primitive brachydont taxa *S. etruscus,* which is a dedicated browser (Rivals and Lister, 2016; Ballatore, 2016; Ballatore et al., 2017), *S. hundsheimensis*, *S. kirchbergensis*, and *S. hemitoechus* show diets ranging from browsing to grazing, including browse- or grass-dominated mixed feeders. It appears that *S. kirchbergensis* and *S. hemitoechus*, in particular, display a strong dietary flexibility, but show interspecific niche partitioning (Rivals and Lister, 2016).

For *S. kirchbergensis*, mesowear data and the plant remains identified in the teeth indicate that the species was a mixed feeder that tended to browse on leaves from trees or shrubs, but also included grasses and dicots in its diet (van der Made and Grube, 2010; van Asperen and Kahlke, 2015; Saarinen et al., 2016; Kirillova et al., 2017; van Geel et al., 2019). Stable isotope analysis (Pushkina et al., 2014) suggests that *S. kirchbergensis* lived in shrubland and woodland compared to *C. antiquitatis,* which inhabited more open spaces. Tooth wear (mesowear and microwear) analyses indicate browsing and browse-dominated mixed feeding diets (Rivals and Lister, 2016).

For *S. hemitoechus,* mesowear and microwear indicate a generalized and flexible mixed-feeding diet (van Asperen and Kahlke, 2015; Rivals and Lister, 2016). Stable isotope analysis (Pushkina et al., 2014) suggests that *S. hemitoechus* lived in similar environments to *S. kirchbergensis* (i.e., shrubland and woodland). Mesowear and microwear further indicate habitat diversity and variation in feeding behavior over that fit within the grass-dominated mixed feeder populations (van Asperen and Kahlke, 2015; Rivals and Lister, 2016).

Different strategies are evidenced among the rhinoceroses during the Pleistocene, from the more eurytopic species, such as *S. kirchbergensis* and *S. hemitoechus,* to the more stenotopic species, like *S. etruscus* or *C. antiquitatis*. The giant rhinoceros, *E. sibiricum*, would belong to the latter group. It would normally have a grazing diet, but it would have been able to use other vegetal resources, such as leaves from trees or shrubs when needed. The following discussion (section 5.4) will touch upon the reason(s) for this punctual shift in diet, which in this case occurred just before these animals died.

5.3. Dietary flexibility in rhinoceros and other ungulates

In other Quaternary rhinoceros species, there are significant amounts of data about dietary traits as well as solid and convincing evidence of dietary flexibility. A similar example to what was observed for *E. sibiricum* was reported for the wooly rhinoceros, *Coelodonta antiquitatis*. For that species, fossil remains were found not only as individual bones and full skeletons, but also as complete frozen, mummified carcasses. Most of the dietary proxies are in agreement and identify *C. antiquitatis* as a true grazer. Spore-pollen analysis of food remains in the teeth of a complete rhinoceros from the Khalbui River revealed the dominance of grasses (Poaceae; 68.2%) and sagebrush (*Artemisia*; 17.1%) over woody-shrubby vegetation (~4.5%) (Garutt et al., 1970). The stomach content analysis of a Kolyma River rhinoceros confirmed the dominance of herbaceous plants (Poaceae 46.07%, Compositae 41.46%) (Boeskorov et al., 2011). Morphology (Zeuner, 1945; Stuart and Lister, 2012) as well as dietary proxies like pollen in the teeth or stomach contents, stable isotopes, mesowear, and microwear (Bocherens, 2003; Boeskorov et al., 2011; Pushkina et al., 2014; Saarinen et al., 2016; Rivals and Lister, 2016; van Geel et al., 2019) indicate that *C. antiquitatis* was a pure grazer. However, microwear analysis of samples from the North Sea and adjacent areas suggests that wooly rhinoceroses included woody components in their diet (Rivals et al., 2010). Other proxies such as stable isotopes or ancient DNA also suggest a forb-dominated diet in the Arctic region (Tiunov and Kirillova, 2010; Willerslev et al., 2014). As previously observed for *E. sibiricum*, on some occasions, *C. antiquitatis* shifted its grazing diet toward increased browsing.

The phenomenon of inter-seasonal and interpopulation shifts in diet among true grazers has been well studied for modern equids (see Ransom and Kaczensky, 2016), which are primarily grazers and typically select graminoids over other species, when available. However, shrubs can play an important role in the diet of feral horses, especially in winter. For example, the proportion of shrubs and forbs in the diet of feral horses on the Whiskey Peak Allotment in Wyoming increases from less than 1% in the spring-summer seasons to ~20% during the winter season (Crane et al., 1997). In some regions, the proportion of grass in a horse's diet is significantly reduced throughout the year; for example, the diet of feral horses in New Mexico contains only 50% grass (Hansen, 1976). Moreover, the variability of the diet for these horses is very high and depends on the season, so the proportion of Mesquite (*Prosopis juliflora*) pods and leaves makes up 53% of their diet in September and decreases to only 2% (leaves) in March (Hansen, 1976). Shrubs become a major component in the diet of feral burros (*Equus asinus*) in North America. In Death Valley National Park, California, shrubs account for more than half (50–81%) of their diet from September to October (Ginnett and Douglas, 1982), and shrubs dominate the diet (58–83.8%) of burros in the Chemehuevi Mountains of California from June to January (Woodward and Ohmart, 1976). At the same time, feral burros in the arid Trans-Himalayan region of India eat shrubs only in summer, and shrubs make up only a small part of their overall diet (< 10%) (Mishra et al., 2004). In the Pleistocene record, most of the tooth meso- and microwear studies on horses reveal grazing traits. However in few cases, browsing populations of horses have been reported, such as at Schöningen 13 II-4 (MIS 9; Kuitems et al., 2015), Igue des Rameaux amont (MIS 9; Uzunidis et al., 2017), and Taubach (MIS 5e; Rivals et al., 2009). The data on extant species and the fossil record provide evidence that true grazers can, in some occasions, shift their diet to include a significant proportion of browse.

5.4. Possible causes of death of elasmotheres at Irgiz 1 and the formation of bone accumulation

The causes of death of most animals in Pleistocene fossil assemblages are either related to natural phenomena (paleontological sites) or to anthropic activities (scavenging or hunting) in archaeological sites. At Irgiz 1, the elasmothere bones do not present any evidence of human activity. Irgiz 1 is a paleontological site, and the elasmotheres there certainly died from natural causes (Prilepskaya et al., 2019). Mass mortality events in large mammals are numerous and well-documented through many studies, such as in extant wild horses (Berger, 1983), cervids (Takatsuki et al., 1994), and saiga antelopes (Kock et al., 2018), among many others. In the fossil record, examples are known in many ungulate taxa (e.g., Kahlke and Gaudzinski, 2005; Mihlbachler et al., 2018). Mortality is often associated with ecological stress due to seasonality and other stochastic events, such as droughts, thick snow cover, ice coating or *dzud*, storms, floods, volcanoes, or infectious diseases. Such events may have caused shifts in feeding the ecology preceding death. Seasonal changes in diet before death are evidenced in the discrepancies found between mesowear and microwear; assemblages that show greater microwear–mesowear incongruence may have been due to mortality events of short duration (Sánchez-Hernández et al., 2016; Mihlbachler et al., 2018).

At Irgiz 1, we report two points of evidence for a seasonal shift in diet prior to death (Fig. 6). First, the strong discrepancy found between the diet reconstructed from mesowear (grazing) and from microwear (browsing) suggests a dietary shift in the last days or weeks before these animals died. Second, the low variability of the microwear pattern is indicative of a short duration for the formation of the elasmothere assemblage. Our results are supported by observations of geological sections of the site, which are composed of homogeneous dense clays that indicate a low dynamic of water in the waterbody. In the structure of the clays, there was no evidence, either visually or during sampling for microfauna, of any levels, lenses, or interlayers of condensation or redeposition of terrigenous (psammitic or psephitic dimension [sand or pebbles]) or osteological material (Kuznetsova et al., 2015; Prilepskaya et al., 2019). The bones of the mammals do not show any marks of redeposition or traces of significant movement. The *E. sibiricum* remains represent all major age groups, and the Irgiz 1 paleontological site is considered autochthonous (Prilepskaya et al., 2019). The above evidence, combining geology and tooth microwear, may indicate a relatively short-term accumulation of materials. According to Mihlbachler et al. (2018), we can assume that the Irgiz 1 fossil assemblage that provided incongruous microwear and mesowear data could be the result of a mortality event related to ecological disturbances that occurred just before death (Fig. 6).

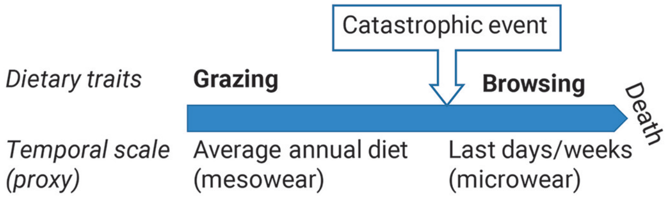

Fig. 6. Change in the dietary traits of *Elasmotherium sibiricum* from Irgiz 1 at different timescales as interpreted from tooth mesowear and microwear.

The climatic and environmental context of Irgiz 1 that was reconstructed from the small mammals' assemblage indicates dry steppe or semi-desert conditions, and the climate was continental (Prilepskaya et al., 2019), as it is today in the semi-desert steppes of Kazakhstan and Mongolia. Common causes of ungulate mortality in cold climates are strong winds and snowstorms, increase in snow cover thickness, and ice coating or *dzud* that prevent animals from foraging food under the snow (Berger, 1983; Formozov, 1990; Bouman and Bouman, 1994; Rindel and Belardi, 2006; Sternberg, 2010; Spasskaya and Paklina, 2012). *Dzud* is one of the greatest hazards during winter for many ungulates. It can form due to a thaw and subsequent frost, as well as during strong winds. In such severe winter conditions, ice coating prevents ungulates from getting access to food (Formozov, 1990; Bouman and Bouman, 1994). In addition, animals often injure the soft tissues of their legs while breaking through the ice coating and can die from infections (Formozov, 1990). With some ungulates, snow cover may limit the access to certain plants and force them to feed on other plants above the snow cover (Warchałowski et al., 2015). In many cases, such strong changes in the resources available for the ungulates may lead to starvation and death (Martinka, 1967; Dau, 2005). In the case of Irgiz 1, if the short grasses that were the usual food of the elasmotheres were not available due to the thick snow cover and/or ice coating, these animals may have shifted to different resources and foraged on the leaves from shrubs or small trees that were available above the ice coating as well as those reachable in the upper layer of the thick snow cover. A similar shift to leaf browsing was evidenced though mesowear and microwear analyses in the extant guanaco (*Lama guanicoe*) from the Lake Cardiel area in Southern Patagonia that died from a catastrophic mortality event in the winter of 2000 (Rivals et al., 2013). The thick snow cover and ice coating modified the availability of resources and forced the animals to shift their diet toward browsing. At Irgiz 1, the elasmotheres may have survived for a certain time following this change, yet if the poor conditions persisted and food became limited, they likely died, and their carcasses accumulated by the river in the oxbow lake.

6. Conclusions

The Irgiz 1 fossil assemblage results from a seasonal mortality that likely occurred during winter. The elasmotheres show a microwear pattern that suggests an altered diet near the time of death. As the habitual grass resources (evidenced through mesowear) were not available, the animals shifted their diet toward browse (identified through microwear) and probably died from a lack of resource availability. This work puts in evidence the relevance of combining different proxies to reconstruct dietary behavior during different timeframes.

Declaration of Competing Interest

None.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.palaeo.2020.109898.

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