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Diet and ecological niches of the Late Pleistocene hyenas *Crocuta spelaea* and *C. ultima ussurica* based on a study of tooth microwear

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ABSTRACT

Extinct hyenas of the genus *Crocuta* were typical representatives of the Late Pleistocene mammoth fauna of Eurasia. The geographical distribution of these animals was vast, stretching from the British Isles to the Pacific coast. In this paper, we studied the tooth microwear of *Crocuta spelaea* from the Prolom 2 grotto in Crimea and the Bukhtarminskaya Cave in eastern Kazakhstan, and *C. ultima ussurica* from the Geographical Society Cave in the Russian Far East, to provide a comparative analysis of the feeding habits of these two species and to test for ecological differences. We also tested for ontogenic differences in diet through a comparison of juvenile and adult individuals. Our findings show that the microwear patterns of these Late Pleistocene hyenas resemble those of extant spotted hyenas (*C. crocuta*) but differ from those of extant stripped (*Hyaena hyaena*) and brown hyenas (*Parahyaena brunnea*). However, we noted that the number of scratches in the *C. ultima ussurica* specimens exceeded the variability observed in extant spotted hyenas and instead more closely resembled the microwear signal of typical predators (e.g., lions). Adults and juveniles exhibited similar microwear patterns in terms of the quantity of pits and scratches; however, most juveniles lacked cross scratches, as also observed in most individuals from Prolom 2. This pattern could be related to a higher proportion of meat in the diet of juveniles, without excluding the consumption of bones. Our tooth microwear analysis improves the knowledge of the paleobiology of extinct representatives of the genus *Crocuta*.

1. Introduction

Extinct cave hyenas, frequently treated as the species *Crocuta spelaea* (Goldfuss, 1823), are known from numerous Pleistocene sites discovered across Eurasia from the British Isles to the Pacific coast. Its extant relative, the spotted hyena *Crocuta crocuta* (Erxleben, 1777), occurs in Africa, south of the Sahara. There is extensive literature on the relationship between both taxa. Several researchers have united them into a single species *C. crocuta* (e.g., Kurtén, 1957, 1968; Werdelin and Solounias, 1991), whereas others have treated them as separate species (e.g., Brugal et al., 1997; Baryshnikov, 1999).

A recent study of paleogenomes from Late Pleistocene Eurasian cave hyenas and genomes from extant African spotted hyenas revealed a deep temporal divergence (close to 2.5 Ma) between the two species. Evidence of bidirectional gene flow between African and Eurasian *Crocuta* following the split of the lineages is also available for this time (Westbury et al., 2020). These results show the intricate nature of the evolutionary history of the genus *Crocuta*, whose level of taxonomic diversity has not been fully determined. Notably, the most recent review of the genus *Crocuta* recognized seven fossil species, including *C. spelaea* and *C. ultima* (Lewis and Werdelin, 2022).

Mitochondrial phylogeny shows that Pleistocene hyenas in Eurasia were represented by two genetic lineages, one of which included extinct hyenas from eastern Asia (China and south of the Russian Far East) and the other cave hyenas from Europe and extant spotted hyenas from Africa. Both lineages diverged at around 1.85 Ma, providing an opportunity for the division of Late Pleistocene Eurasian hyenas into two taxa with specific ranks: *C. spelaea* from Europe and western to central Asia, and *C. ultima* (Matsumoto, 1915) from eastern Asia (Westbury et al., 2020; Rao et al., 2020; Hu et al., 2021; Lewis and Werdelin, 2022). The

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hyenas from eastern Asia are occasionally regarded as two distinct subspecies: the Middle Pleistocene *C. ultima ultima* and the Late Pleistocene *C. ultima ussurica* (Baryshnikov and Vereshchagin, 1996), which exhibit different tooth morphologies (Baryshnikov, 2014; Lewis and Werdelin, 2022). The latter taxon was described based on material from the Geographical Society Cave (GSC), which provided samples for phylogenetic analyses (Rohland et al., 2005; Westbury et al., 2020). Since no evidence of the genetic identity of hyenas from the Middle Pleistocene and the Late Pleistocene of eastern Asia is available, we consider it appropriate to also name the Late Pleistocene hyenas, *C. ultima ussurica*.

There is a distinctive morphological difference between the extant and extinct hyenas of the genus *Crocuta*. The cave hyenas show shorter distal limb elements than the spotted hyenas, which indicates their lower ability to run (Ehrenberg et al., 1938). Differences are also observed in the specialization of the dentition. The European *C. spelaea* has a metaconid developed in the lower carnassial tooth m1; although its occurrence varies, it is not characteristic of the extant spotted hyenas (Baryshnikov and Vereshchagin, 1996). The Chinese *C. ultima* is characterized by a pronounced increase in the height of P3 (Kurtén, 1957). These features point to the bone-crushing function of teeth in the extinct *Crocuta* populations, which is characteristic of scavenging hyenas. Other researchers, on the contrary, have noted the elongation of the metastylar blade of the upper carnassial tooth P4 in cave hyenas (Baryshnikov, 1999) and considered this feature as an indicator of the increased cutting ability of the dentition, which is more characteristic of hunters than scavengers. The study of the morphology and brain proportions in two Eurasian Pleistocene hyenas revealed them to closely resemble the recent *C. crocuta*, while having, however, a less developed anterior brain, suggesting less-developed social abilities (Vinuesa et al., 2016). The European *C. spelaea* cave hyenas accumulated large bone assemblages in their dens, including the bones of other hyenas, which was not typical for the extant spotted hyenas (Brugal et al., 1997). Thus, the available data suggest not only morphological but also behavioral differences between the Pleistocene and extant *Crocuta* hyenas. It should be mentioned that extinct Eurasian hyenas could have migrated from Africa to Eurasia before the behavioral adaptations of the spotted hyenas were developed (Lewis and Werdelin, 2022).

The extant spotted hyenas, *C. crocuta* are opportunistic predators, frequently living in large matriarchal clans and exhibiting complex social behaviors. For obtaining food, they use both active hunting and the consumption of carrion (Hayssen and Noonab, 2021). Cave hyenas are similar to spotted hyenas in many respects, but their distinctive features are determined by the former inhabiting ecosystems at temperate latitudes in Eurasia, while the latter inhabit ecosystems of equatorial Africa. No comparative data are known about the feeding and life habits of *C. spelaea* and *C. ultima ussurica*; however, ecological differences may exist between these taxa, whose distribution ranges are separated by several thousands of kilometers and located under different geographic conditions.

In this study, we provide a comparative analysis of the two species by studying the tooth microwear patterns of *C. spelaea* from the Prolom 2 grotto in Crimea, Europe, and those of *C. ultima ussurica* from the GSC in the Russian Far East (Fig. 1). Both localities record signs of hyena dens, with numerous hyena tooth marks preserved on bones and other traces of hyena occupation (Enloe et al., 2000; Baryshnikov, 2014). The main objective of this study is to compare the paleodiets and ecological niches of the cave hyenas from different Pleistocene sites. In addition, we conduct a preliminary analysis of ontogenic differences in diets between juvenile and adult individuals. As suggested by Baryshnikov (2014), some of the hyena bites on bones were not left by adult animals, but by cubs. In order to test this hypothesis, we examined the microwear of deciduous teeth in the Pleistocene hyenas from both rock shelters and from the Bukhtarminskaya Cave in eastern Kazakhstan (Fig. 1).

Fig. 1. Map showing the location of the three examined sites. A – Prolom 2 grotto; B – Bukhtarminskaya Cave; C – Geographical Society Cave.

2. The study sites

The studied materials were obtained from three caves with similar geological ages, providing an opportunity to define the paleodiets of cave hyenas from eastern Europe (Crimea), Central Asia (Kazakhstan), and the Russian Far East during the Marine Isotope Stage 3 (MIS 3).

The Prolom 2 grotto (45°06′N, 34°43′E) is situated on the left bank of the Kuchuk-Karasu River in the eastern foothills of the Crimea mountains, near the city of Belogorsk (Fig. 1A). This rocky shelter has two chambers with a common entrance, which in ancient times constituted a single space (Kolossov et al., 1993).

Several ^{14}C dates have been obtained for the four layers of the sequence: layer I: 22,650 ± 100 (GrA-5445), 22,800 ± 600 (Ki-10,895), 24,550 ± 300 (Ki-10,745), and 22,900 ± 300 (Ki-10,746); layer II: 28,100 ± 350 (Ki-10,617); and layer III: 41,600 ± 800 (Ki-10,611) (Stepanchuk, 2006). Hyenas have not been dated directly, but their presence at Prolom 2 grotto during the isotopic stage MIS 3 may be inferred since no radiocarbon dates younger than 30,000 years are known for *C. spelaea* in Europe (Stuart and Lister, 2014).

Bone and tooth fragments of medium-sized and large mammals, numbering 6118 remains and belonging to 18 species, have been recovered from the Pleistocene layers (Stepanchuk, 1993; Enloe et al., 2000). Over half of the bones (54.4%, NISP = 3327) can be assigned to saiga antelopes (*Saiga tatarica*), although according to the minimum number of individuals, its portion is much smaller (26.4%, MNI = 89). Other herbivores are represented by two species of horses, *Equus latipes* and *E. hydruntinus* (14.7% combined) and by steppe bisons (*Bison priscus*) (2.9%). Woolly mammoths (*Mammuthus primigenius*) and woolly rhinoceros (*Coelodonta antiquitatis*) are predominantly represented by tooth fragments. Carnivores are diverse and include seven species: *Vulpes lagopus*, *V. corsac*, *V. vulpes* (11.9% combined), cave bears (*Ursus spelaeus*), wolves (*Canis lupus*) (1.9%), and cave lions (*Panthera spelaea*). Cave hyenas (*Crocuta spelaea*) constitute 6.4% of the total number of identified bones and 8.0% of the minimum number of individuals. Hyenas were recorded in all cave layers. The most common elements are teeth and tooth fragments, fragments of crania, maxilla, and mandibles, according to which 17 individuals were identified.

It was originally assumed that the species represented in the Prolom 2 grotto bone assemblage were the prey of Paleolithic hunters (Stepanchuk, 1993). However, the ratio of herbivores and carnivores exceeds the limits of typical archaeological sites (Klein, 1980). The diversity of carnivores, as well as a large portion of their remains, suggest that part of the assemblage (or even most of faunal material) was accumulated as a result of the action of non-human agents (Enloe et al., 2000).

This conclusion agrees with the type of bone preservation observed. Indeed, most bones are fragmented; percussion notches, scores and striations, crenulated diaphysis shafts, and other signs of hyena damage patterns are recorded. This damage is especially characteristic of the saiga antelope bones, including gnawed and punctured metapodials and phalanges. Bones with digestive corrosion are represented and the deciduous teeth of hyena cubs are also present in the assemblage. Thus, the bone destruction patterns are very consistent with carnivore and scavenger behavior (Brugal et al., 1997; Fosse, 1999; Fourvel et al., 2015) and allow the Prolom 2 grotto to be referred to as a hyena den. At the same time, several saiga antelope bones with cut marks point to the activity of hominins. Therefore, we deal here with the presence of a hyena den and a Paleolithic site in a single rocky shelter.

The Bukhtarminskaya Cave (49°37′N, 83°31′E) is situated on the right bank of the Burhtarma River, 12 km from the place of its confluence with the Irtysh River in the southern foothills of the Altai mountains, eastern Kazakhstan (Fig. 1B). This Upper Paleolithic site is known as “Peshchera” (“the cave”) (Beregovaya, 1960). Since this name is not geographically connected, we use the new one, the Bukhtarminskaya Cave, which has already been used in Panteleev (2015). In the area in front of the karst cave and in the second, small grotto, limestone blocks were found that had once collapsed from the ceiling. Paleolithic artefacts (coals, stone, and bone tools) were found below these blocks, at a depth of up to 1 m (Beregovaya, 1960).

The remains of large mammals, which are housed in the Zoological Institute RAS in Saint Petersburg, were identified by Vereshchagin and Mel'nikova (1958) and include material from Pleistocene and Holocene layers. The findings differ in the degree of bone fossilization, but the reliable differentiation of their geological ages is not always possible.

The Pleistocene collection incorporates nearly 152 remains of large and medium-sized mammals. The material is dominated by herbivores, such as steppe bisons (*Bison priscus*) (31% of the total number of remains), horses (*Equus ferus*) (30%), red deer (*Cervus elaphus*) (10%), and *Equus hemionus*, *Capreolus pygargus*, and *Camelus knoblochi.* Several bones were reported as belonging to *Mammuthus primigenius* and *Coelodonta antiquitatis*.

The fossil remains of carnivores are referred to as cave hyena *Crocuta spelaea* (10.5%). They are represented by cranium and mandible fragments, including the left mandible of a cub presenting deciduous teeth d3 and d4 and an erupting m1 (ZIN 34403–1, Fig. 2D) as well as by isolated teeth and tooth fragments. Altogether, 16 specimens were identified, which belong to at least two adults, two subadults, and one cub. A hyena coprolite was also recorded. The hyenas were radiocarbon dated to 38,130 ± 230 (MAMS-45709) (Dr. Radu Iovita, Tübingen, pers. comm., 2021). This date is similar to the >37,235 one (SOAN-2504) that was obtained for layer 11 containing hyena fossil remains in Denisova Cave on the northern slopes of Altai (Derevianko et al., 2003). These absolute dates testify to the occurrence of cave hyenas in this highland during MIS 3.

Almost all bones of ungulates from the Bukhtarminskaya Cave are fragmented. Only the short limb bones (like the astragali) are well preserved. The bisons are mainly represented by distal parts of the humerus. Other findings exhibit the tooth marks of large carnivores as well as traces of digestive corrosion, but there are few perforated bones and bones with signs of chewing. Although the traces on the bones resulting from the activity of hyenas are less pronounced in the Bukhtarminskaya Cave than in the Prolom 2 grotto, a general taphonomic aspect of the paleontological material is quite characteristic of the hyena den. It cannot be ruled out that some of the ungulates were hunted and brought to the cave by Paleolithic hunters, however, no reliable cut marks from stone tools or traces of prey butchering were detected.

The Geographical Society Cave (GSC) (42°52′N, 133°00′E) is located on the right bank of the Partizanskaya River (former Suchan River), approximately 20 km from the city of Nakhodka (Primorsky Krai, Russia) (Fig. 1C). Six lithological layers were identified in the sequence. Pleistocene mammal remains were recovered predominantly from layer 4 (Ovodov, 1977). The remains were accompanied by occasional Paleolithic stone tools, suggesting short visits of hominins to the cave (Abramova, 1989).

The hyena bone fragments served as a basis for obtaining four AMS ^{14}C dates: >37,000 (AA-37072), >36,000 (AA-37073), >39,000 (AA-37074), and 34,510 ± 1800 (AA-38230) (Kuzmin et al., 2001). Two additional, earlier dates were subsequently defined: 46,000 ± 700 (OxA-17,046) and 48,650 ± 2380/1840 (KIA-25285) (Rohland et al., 2005; Stuart and Lister, 2014). These dates reveal that the dwelling of the hyenas in the southern part of the Russian Far East coincided with the MIS 3.

Ovodov (1977) identified 4848 remains in the collection from the GSC, which belong to 28 species of large and medium-sized mammals. Deer (*Cervus elaphus* and *C. nippon*) dominate the assemblage (46.0%), followed by horses *E. ferus* (4.7%) and bisons *B. priscus* (4.0%), and *Naemorhedus caudatus*, *Alces alces*, *Sus scrofa*, and *Moschus moschiferus*. Several fragments of bones and teeth of mammoths and woolly rhinoceros were recorded (1.6% combined). Carnivores constitute half of the species composition, but the number of their remains is lower than that of ungulates: wolves (8.0%), large felids (*Panthera spelaea*, *P. tigris*, *P. pardus*; 5.4% combined), brown bears (*Ursus arctos*) (3.6%), hyenas

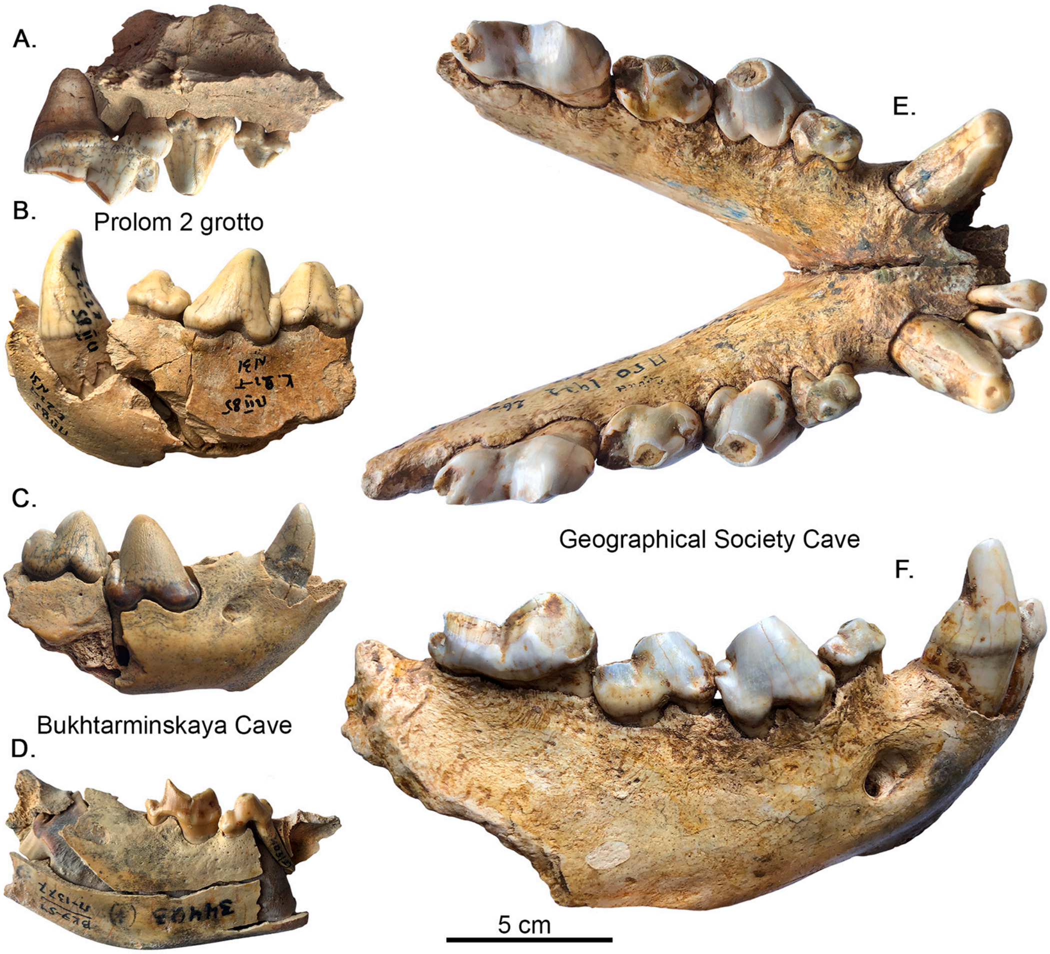

Fig. 2. Pleistocene *Crocuta* remains: *C. spelaea*, Prolom 2 grotto, fragment of left maxilla (P2-P4), lingual view (A), fragment of left mandible (c1-p4), labial view (B), Bukhtarminskaya Cave, fragment of right mandible of juvenile (c1-p4), labial view (C), fragment of right mandible of cub (d3-d4), labial view (D), *C. ultima ussurica,* Geographical Society Cave, mandible (c1-m1), occlusal view (E), right mandible (c1-m1), labial view (F).

(*C. ultima ussurica*) (3.5%), *Vulpes vulpes*, *Cuon alpinus*, and *Gulo gulo*. It is noteworthy that the number of identifiable remains of hyena is inferior to that of the wolves, brown bears, and large felids. Such a proportion may be explained if we assume that the GSC occasionally served as an overwintering place for bears and provided a refuge for hyenas and large felids that hunted ungulates and brought the carcasses into the cave. Wolves might have been the prey of big cats and hyenas.

The hyena collection includes one damaged skull (ZIN 34478), 15 cranium fragments, 23 mandible fragments, 32 isolated teeth, two immature mandible fragments, two deciduous teeth, 24 bone fragments, and 70 tooth fragments. One coprolite is also present (see Baryshnikov, 2014). This set of findings (adults and cubs, coprolite) is characteristic of hyena dens.

The bone collection of large and medium-sized mammals from the GSC reveals numerous and diverse traces of damage produced by large carnivores (Baryshnikov, 2014). The long limb bones of horses and bisons are broken and longitudinally cleft. The metacarpal bones of bisons are very robust, but even they were gnawed and chewed. Such damage could only have been caused by hyenas with their bone-crushing dentition. Many specimens exhibit signs of acidic corrosion and puncturing by canines. These details coincide with the hypothesis that the GSC served as a hyena den on regular basis. It cannot be excluded that some of the prey may have been hunted by large carnivores (cave lion, tiger). There are no signs of the utilization of prey by hominins.

3. Materials and methods

3.1. Materials

For tooth microwear analysis, the carnassial teeth (i.e., the upper P4 and lower m1) were sampled according to the protocol established by Bastl et al. (2012). All material available from the Prolom 2 grotto (N = 21), Bukhtarminskaya Cave (N = 2), and GSC (N = 23) was sampled (Fig. 2; Table 1). Additionally, we sampled five deciduous teeth (d4) to test whether juveniles had a similar diet to that of the adults; Prolom 2 grotto (N = 2), Bukhtarminskaya Cave (N = 1) and GSC (N = 2). Deciduous teeth are commonly discarded from microwear studies because juveniles may have a different diet than adults. However, in this study, one of the objectives was to test for differences in diets between juveniles and adults.

3.2. Methods

The microwear features of dental enamel were examined using a stereomicroscope on high-resolution epoxy casts of teeth following a standard cleaning, moulding, casting, and examination protocol (Solounias and Semprebon, 2002; Bastl et al., 2012). The surface of the teeth was cleaned using acetone followed by 96% ethanol. The surface was moulded using high-resolution silicone (vinylpolysiloxane), and casts were created using clear epoxy resin. All casts were carefully screened under the stereomicroscope. Those with poorly preserved enamel or

Table 1

Summary results of the microwear analysis on the hyaenas from Geographical Society Cave, Prolom 2 grotto, Bukhtarminskaya Cave from this study and the extant carnivores data from Bastl et al. (2012). Abbreviations: N = Number of specimens; M = Mean; SD = Standard deviation; NSP = Number of small pits; NLP = Number of large pits; NS = Number of scratches; %LP = Percentage of individuals with large pits; %G = Percentage of individuals with gouges; SWS = Scratch Width Score; %HC = Percentage of individuals with hypercoarse scratches; %PP = Percentage of individuals with puncture pits.

	N		NSP	NLP	NS	%LP	%G	SWS	%XS	%HC	%PP
Adults											
Geographical Society Cave	23	M	133.13	5.59	11.76	95.7	91.3	2.9	100	100	0
		SD	4.70	1.10	1.12						
Prolom 2 grotto	21	M	133.62	6.05	10.43	100	90.5	2.7	23.8	95.2	0
		SD	4.72	1.26	1.38						
Bukhtarminskaya cave	2	M	136.00	5.75	11.00	100	100	3	100	100	0
Juveniles											
Geographical Society Cave	2	M	136.75	6.00	11.50	100	100	3	0	100	0
Prolom 2 grotto	2	M	133.75	5.50	9.75	100	100	1.5	50	0	0
Bukhtarminskaya cave	1		136.50	6.00	8.50	100	100	2	0	0	0
Extant carnivores (from Bastl et al., 2012)											
Parahyaena brunnea	6		109.41	5.75	6.41	100	100	–	33.3	100	0
Hyaena hyaena	7		113.35	6.92	7.78	100	100	–	57.1	100	0
Crocuta crocuta	25		133.12	5.64	9	100	100	–	8.0	100	0
Acinonyx jubatus	19		92.15	13.23	5.23	100	21	–	52.6	84.2	0
Panthera leo	8		125.93	10.37	10.87	100	50	–	12.5	100	0
Lutra lutra	24		111.7	9.18	5.16	100	70	–	79.2	95.8	0
Vulpes vulpes	32		96.87	4.32	5.7	100	68	–	93.8	78.1	34.4
Nandinia binotata	6		148.91	11.08	10.58	100	0	–	100	83.3	100
Genetta genetta	12		107.08	7.83	5.75	100	0	–	91.7	75.0	91.7

taphonomic defects (features with an unusual morphology and size, or fresh features produced during the collecting process or during storage) were removed from the analysis, following King et al. (1999). The casts were examined under incident light with a Zeiss Stemi 2000C stereomicroscope at a 35 × magnification, using the refractive properties of the transparent cast to reveal microfeatures on the enamel. We used the classification of features defined by Solounias and Semprebon (2002) and Bastl et al. (2012), which distinguished pits and scratches. We identified and quantified the number of small and large pits (circular or sub-circular scars), scratches (elongated microfeatures with parallel sides), gouges (large scars with irregular borders), and puncture pits (deep and large circular pits). In addition, scratches were classified in terms of their texture as being either fine, coarse, or hypercoarse. The microwear features were quantified in a square area of 0.16 mm^2 using an ocular reticule. All data were collected by a single experienced observer (FR). The results were compared with a database constructed from ten extant carnivore taxa, including *Parahyaena brunnea*, *Hyaena hyaena*, and *Crocuta crocuta* (Bastl et al., 2012). The discrimination of the dietary traits among species was performed using bivariate plots and a principal component analysis (PCA) that considered all the microwear features. Because the microwear variables have different scale of values, the raw data were transformed with a square root transformation that reduced the data's range. Finally, we conducted a linear discriminant analysis (LDA) based on the microwear variables to classify the extant carnivorans. Using the R package MASS (Vernables and Ripley, 2002), we used the model derived from the LDA to classify the fossil species.

4. Results

The preservation of the enamel surfaces was excellent in the three localities. All teeth sampled were suitable for microwear analysis. The summary data are presented in Table 1 for the adults and the juveniles from the three sites.

The enamel surface of the fossil hyenas is characterized by a high number of scratches and pits, especially small pits (conversely, low numbers of large pits), and many coarse features such as gouges and coarse scratches (Fig. 3).

The comparison of the fossil hyenas with the extant carnivores, in terms of total numbers of pits and scratches (Fig. 4), shows that the population from the GSC overlaps with those of the lion (*Panthera leo*) and the African palm civet (*Nandinia binotata*). The samples from the Prolom 2 grotto and the Bukhtarminskaya Cave overlap with the spotted hyena (*C. crocuta*), the lion and the African palm civet. The large fossil samples, i.e., those from the Prolom 2 grotto and the GSC, differ significantly in the numbers of scratches but not in the numbers of pits. The graph in Fig. 4 provides an overall view of the similarities of our samples with the extant carnivores but it only reports the total numbers of features. There is a large overlap among the different species. Differences exist when the detailed features (e.g., small and large pits, gouges, fine, coarse, and hypercoarse scratches) are considered (Bastl et al., 2012).

The bivariate plot of the total number of small pits versus large pits shows a strong similarity among the three fossil samples (Fig. 5). They overlap mainly with the spotted hyenas and only very slightly with the striped hyenas (*H. hyaena*).

The PCA considered all the microwear features, revealing a better discrimination among the extant species (Table 2; Fig. 6A). The first principal component (PC1) explains 41.3% of the variation in microwear features and is most strongly related to high numbers of small pits, gouges, and coarse scratches. The second principal component (PC2) explains 14.6% of the variation and is mostly related to high numbers of small puncture pits, small pits, cross scratches, and to low numbers of gouges. The specimens from the three localities are very similar and overlap mainly with the spotted hyenas and very slightly with the lions. The PCA separates most of the individuals from the GSC (above the axis) from those from Prolom 2 (below the axis) but some individuals do not follow this trend (Fig. 6B). The position of the specimens below the axis is due to a low percentage of cross-scratches. However, all the specimens fall within the variability known in the extant spotted hyenas. The few specimens from the Bukhtarminskaya Cave fall among the individuals from the last two sites. The microwear patterns recorded on the fossil samples are characterized by high numbers of small pits, gouges, and coarse scratches. The pattern resembles that of the extant spotted hyenas, but very different from that of the two other extant hyenas, the striped hyenas and the brown hyenas (*P. brunnea*). The linear discriminant analysis provided a very high discrimination among the nine extant carnivoran species with a correct classification rate of 96.5%. All the fossil specimens were classified with a diet resembling that of the extant

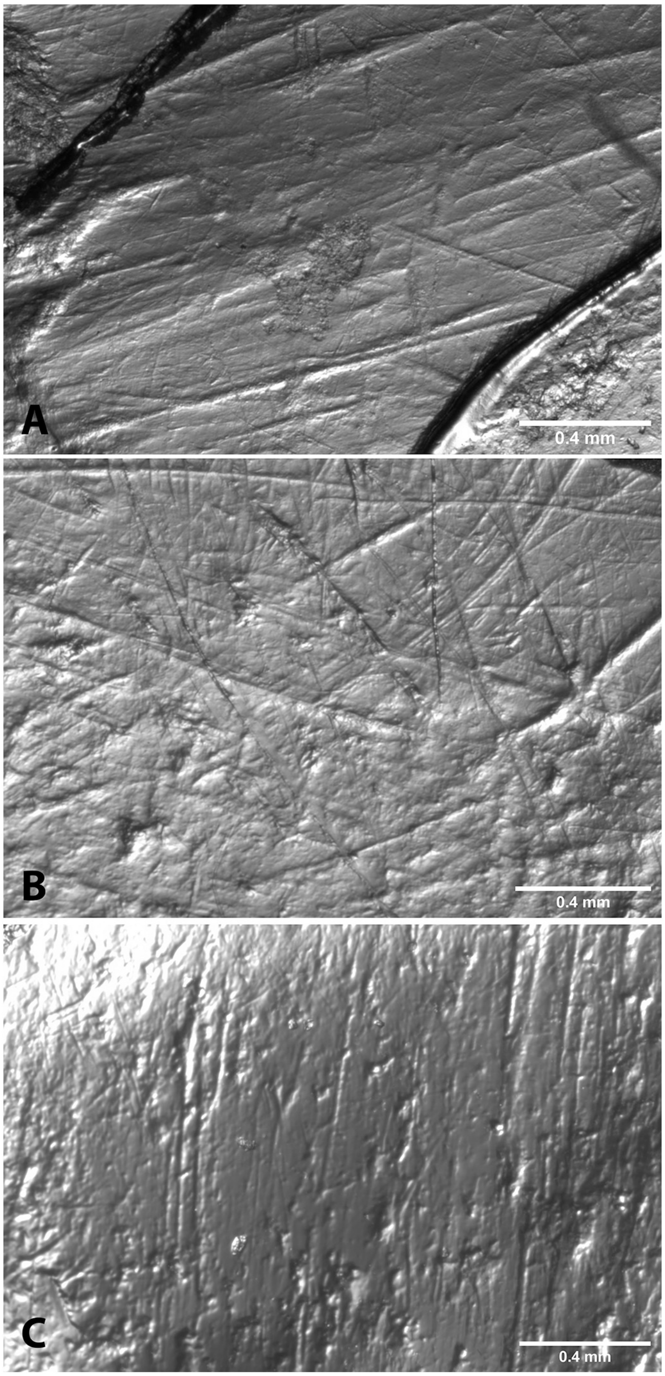

Fig. 3. Example of microwear patterns on adult (A, B) and juvenile (C) individuals. (A) Right P4 of an adult *Crocuta spelaea* from Prolom 2 grotto (sample # P5); (B) Right m1 of an adult *C. ultima ussurica* from Geographical Society Cave (ZIN-34490); (C) Right d4 of a cub *C. u. ussurica* from Geographical Society Cave (ZIN-34490(32)). Scale bar = 0.4 mm.

C. crocuta according to the microwear features (Table 3).

The adult ($N = 46$) and juvenile ($N = 5$) individuals (the latter indicated with a * on Fig. 6) occur together, suggesting a similar microwear pattern for the two age groups. Although all available teeth were sampled, the sample size for the juveniles is small and the results should thus be interpreted with caution. The similarity between the two ontogenic groups would suggests a dietary behavior based on similar food items. The juveniles (4 out of 5) plot below axis PC1 due to a low proportion of cross scratches.

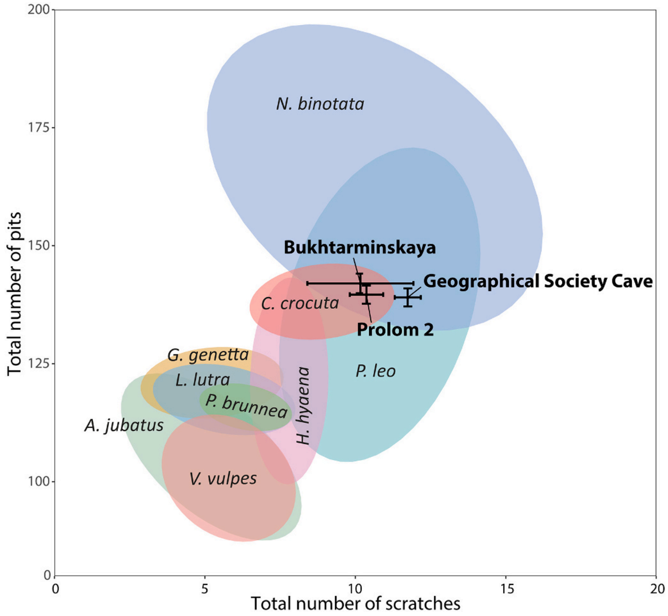

Fig. 4. Bivariate plot of the total number of pits and scratches. The ellipses correspond to the extant carnivores database from Bastl et al. (2012).

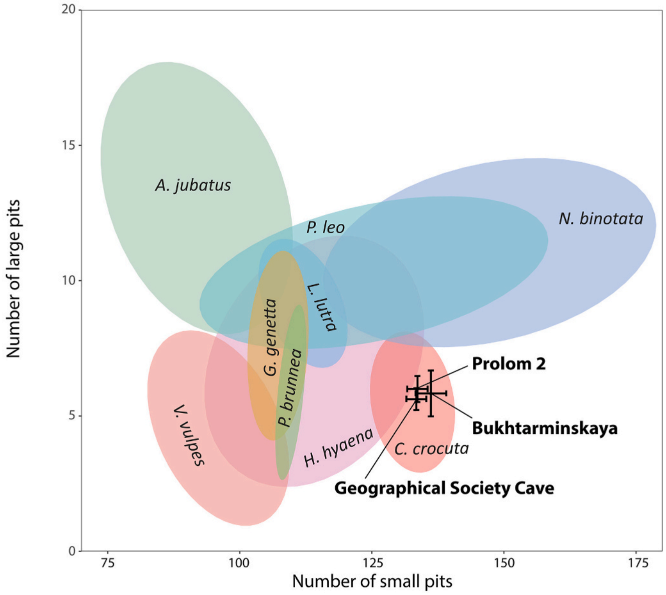

Fig. 5. Bivariate plot of the total number of small pits and large pits. The ellipses correspond to the extant carnivores database from Bastl et al. (2012).

Table 2
Eigenvalues and percentage of variance for the eleven axes of PCA.

PC	Eigenvalue	% variance
1	1.1639	41.29
2	0.4113	14.59
3	0.3689	13.09
4	0.2233	7.92
5	0.1724	6.12
6	0.1381	4.90
7	0.1256	4.46
8	0.0965	3.42
9	0.0651	2.31
10	0.0497	1.76
11	0.0044	0.15

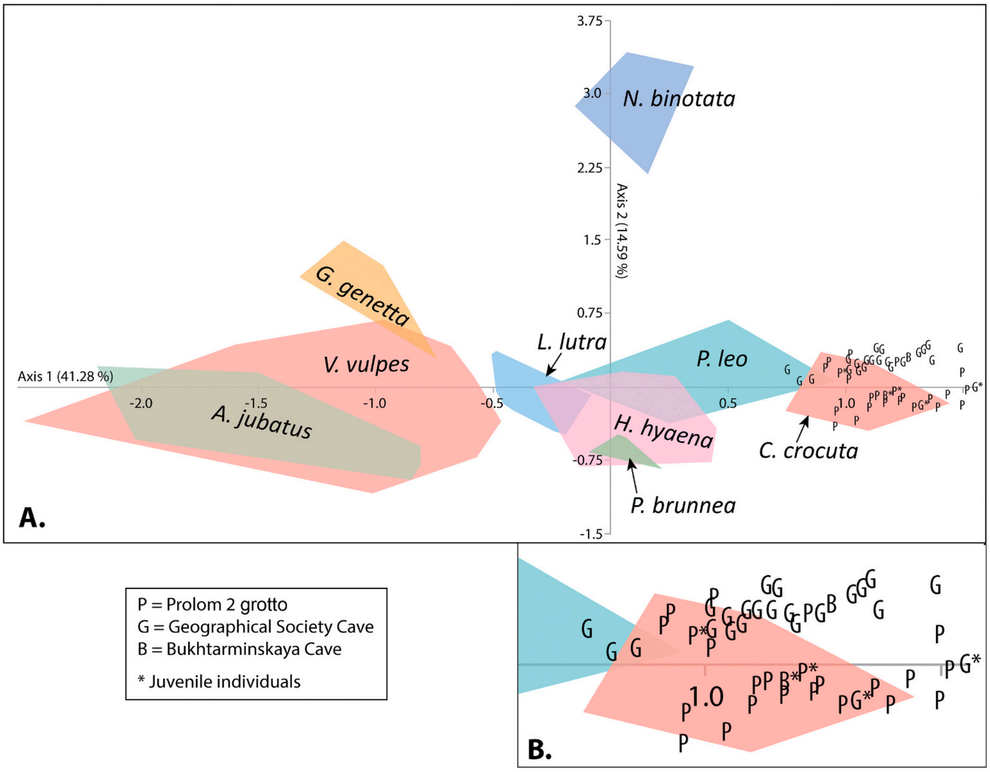

Fig. 6. PCA established on the 11 microwear variables: small pits, large pits, small puncture pits, medium puncture pits, large puncture pits, fine scratches, coarse scratches, hypercoarse scratches, wide hypercoarse scratches, cross scratches and gouges (A). The convex hulls correspond to the extant carnivores database from Bastl et al. (2012). Enlargement of the area where the fossil specimens are located (B).

Table 3
Summary of the linear discriminant analysis based on the microwear features.

Extant classification rate 96.53%			
	Fossil localities		
Extant species	Bukhtarminskaya Cave	GSC	Prolom 2 grotto
A. jubatus	0	0	0
C. crocuta	3	25	23
G. genetta	0	0	0
H. hyaena	0	0	0
L. lutra	0	0	0
N. binotata	0	0	0
P. brunnea	0	0	0
P. leo	0	0	0
V. vulpes	0	0	0

5. Discussion

5.1. *Dietary traits of the fossil hyenas from the Geographical Society Cave, Prolom 2 grotto, and Bukhtarminskaya Cave*

The species with high numbers of pits and scratches, like those we observed in the three fossil samples, are carnivores whose diets include a considerable amount of tough or hard items such as fruits, shells, or bones (Bastl et al., 2012). In herbivores, scratches allow for a distinction between grazers and browsers (Solounias and Semprebon, 2002), but among carnivores, pits appear to be the discriminating feature (Bastl et al., 2012). The higher numbers of small versus large pits allow us to distinguish the spotted hyenas from the two other hyenas (striped and brown hyenas) (Fig. 5). The microwear patterns on samples from the GSC and the Prolom 2 grotto, with high numbers of small pits, gouges, and coarse scratches, are comparable to those of extant spotted hyenas, i.e., the hyenas with the most extreme bone cracking behavior. The latter are very different from the striped hyenas (meat/bone diet with less bone intake) and the brown hyenas that also ingest fruits. The lower proportion of cross scratches in the individuals from Prolom 2 relative to the other two sites could be related to a lower proportion of bone in the diet. The results revealed some dietary inter-specific differences between *Crocuta spelaea* and *C. ultima ussurica*. In a more general approach, according to the classification of extant carnivorans into diet categories following the groups established by Wilman et al. (2014), the studied cave hyenas belong to the hypercarnivores, i.e., animals with a diet consisting of 80–100% of vertebrate flesh (muscle, organs, and bones). The results from the Bukhtarminskaya Cave should be omitted here due to the small sample size.

5.2. *Diets of juveniles vs. adults*

Spotted hyena cubs are born with their deciduous incisors and canines erupted (Werdelin and Solounias, 1991) or they erupt shortly after birth (Jaarsveld et al., 1987). Deciduous cheek teeth begin to erupt at 31 days, and permanent teeth appear by 10–18 months (Van Horn et al., 2003; Hayssen and Noonab, 2021). The first solid food appears in the diet of hyena cubs at three months of age, but only in rare cases do juveniles eat from kill before turning six months. Juveniles begin to hunt at 8–10 months of age (Kruuk, 1972) and weaning typically occurs between 12 and 18 months (Hayssen and Noonab, 2021). Furthermore, the development of the massive skull needed for bone cracking is not complete in spotted hyenas until 35 months (Hayssen and Noonab, 2021).

The behavior of spotted hyenas is characterized by the systematic transport and accumulation of carcasses to their dens. Spotted hyenas consume their prey or carrion in situ but also transport carcasses to their dens to feed young individuals of their groups (Kruuk, 1972; Sala and Arsuaga, 2018).

The adults and the juveniles have very similar microwear patterns in terms of the quantity of pits and scratches; however, most of the juveniles do not have cross scratches, like most of the individuals from Prolom 2. As suggested earlier, this pattern could be related to intraspecific differences due to a higher proportion of meat in the diet of the juveniles, without excluding the consumption of bones. This conclusion should be considered with caution due to the small number of juvenile individuals in the samples.

No samples of bones were available that could reliably be interpreted as having been gnawed by hyena deciduous teeth. However, it can be assumed that the cubs of Pleistocene hyenas ate the meat and gnawed the bones that were present in the den. Baryshnikov (2014) considered shallow marks from the teeth of a predator on the surface of the frontal part of the hyena's skull to represent such bites in the GSC (Fig. 7G–H). A specimen from the Bukhtarminskaya Cave represents the humerus of red deer (*Cervus elaphus*), whose distal part was probably gnawed by a predator (Fig. 7A–D). Notably, no other carnivores besides the cave hyenas have been detected in the Pleistocene fauna of the Bukhtarminskaya Cave. Hyena cubs could gnaw the bones not only while feeding, but also while playing with them or imitating adults. They could also gnaw the bones while they were teething and changing their deciduous teeth to permanent ones in the way of extant carnivore cubs.

Contrary to ursids and felids, adult hyenas typically modify bones of any size until the most advanced stages of consumption (Sala and Arsuaga, 2018). The limb bones of steppe bisons (*Bison priscus*) from the GSC bear strong evidence of furrowing marks related to carnivore gnawing (see Fig. 7E–F). Furthermore, spotted hyenas are capable of

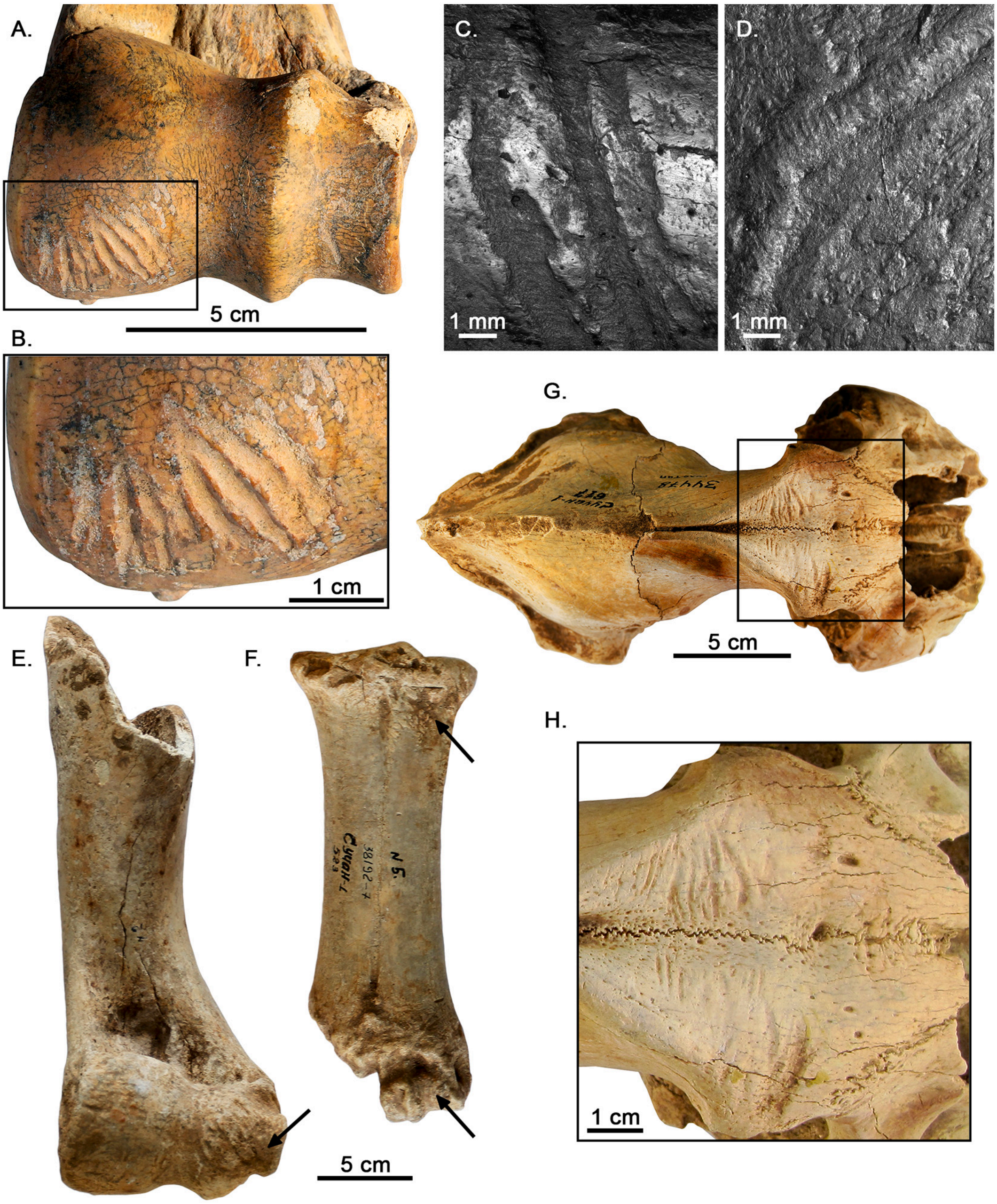

Fig. 7. Presumptive tooth mark of carnivore (A and B) and evidence of carnivore furrowing (E and F). A–B – distal part of right humerus of red deer, *Cervus elaphus*, Bukhtarminskaya Cave (ZIN 38263-1); C–D – Microphotographs of the marks of the humerus from Bukhtarminskaya Cave (ZIN 38263-1) at a magnification of 6.5x; E – Right humerus of bison, *Bison priscus* with evidence of incipient furrowing (ZIN 38192-18); F – Metacarpal of bison, *Bison priscus* with evidences of furrowing (ZIN 38192-7); G-H – Front part of skull of *C. c. ussurica*, Geographical Society Cave (ZIN 34478). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

swallowing bones and bone fragments that can be preserved with traces of dissolution by gastric acid (Sala and Arsuaga, 2018); an example of such bones digested by hyenas may include the remains of saiga antelope (*Saiga tatarica*) phalanges from the Prolom 2 grotto (see Fig. 8).

5.3. *Ecological niche of Pleistocene Crocuta*

The spotted hyenas (*Crocuta crocuta*) and other representatives of the genus are characterized by a peculiar bidirectionality in the evolution of the dentition, which is expressed, on the one hand, by an increase in the cutting ability of their carnassial teeth (P4/m1), and on the other hand, by an increase in the bone-cracking specialization of cone-shaped premolars (P3/p3). This feature characterizes the spotted hyenas as predators capable of actively hunting for fresh meat, as well as feeding on the carcasses of large animals and gnawing through thick-walled tubular bones. Such an ecological niche has proven to be very successful. Therefore, hyenas of the genus *Crocuta* show a pronounced taxonomic diversity and a more extensive range of distribution compared to hyenas of the genera *Hyaena* and *Parahyaena*. The latter do not extend beyond the tropical and subtropical zones; at the same time, two species of *Crocuta* (*C. spelaea*, *C. ultima*) were distributed in the southern regions of moderate latitudes of Eurasia during the Late Pleistocene, forming part of the *Mammuthus-Coelodonta* complex.

Unlike other extant hyenas, spotted hyenas are active predators that hunt as much as lions do (Kruuk, 1972). They directly kill 60–95% of the food they eat (Smith and Holekamp, 2019). The dietary niche of spotted hyenas resembles that of lions and the two species have a 58.6% overlap of actual prey species (Hayward, 2006). However, unlike the rest of Africa's large predators, spotted hyenas do not preferentially prey on any species. Depending on the parts of its range and season, *C. crocuta* prefers to hunt a variety of small, medium, and large-sized ungulates (Holekamp et al., 1997; Hayward, 2006). The diet of spotted hyenas is very flexible; in some parts of its range hyenas primarily prey on birds and reptiles while in other parts carrion constitutes a substantial part of their food (Mills and Hofer, 1998). Indeed, in the Serengeti, the proportion of carrion in the diet of *C. crocuta* reaches one third. The spotted hyenas can eat and digest tendons, cartilages, and tubular bones very efficiently (Kruuk, 1972). Thus, on the one hand, the diet of spotted hyenas shows a large degree of dietary overlap with that of *Panthera leo*, and on the other, is very flexible and unselective.

Our results (Figs. 5 and 6) show that the microwear patterns of Pleistocene cave hyenas' teeth from three caves in Europe and Asia generally resemble those of extant spotted hyenas and differ significantly from those of extant stripped and brown hyenas. This indicates a

Fig. 8. Limb bones of *Saiga tatarica* from Prolom 2 grotto; phalanges with traces of dissolution by gastric acid (A–E) and distal fragments: right humerus (F), right tibia (G) and metapodials (H, I).

similarity of the ecological niche and dietary patterns of the extant and extinct representatives of *Crocuta*. However, the number of scratches (see Fig. 4) in hyenas from the GSC exceeds the variability of the extant spotted hyenas and share similarities with typical predators (e.g., lions). This corresponds well with the increase in the length of the upper carnassial tooth P4 (and elongation of its metastylar blade) in the sample from the GSC (Baryshnikov, 1999).

As already noted, the Prolom 2 grotto and part of the Bukhtarminskaya Cave contain stone tools, indicating the possible contribution of human groups to the formation of the bone assemblages, while no tools were detected in the GSC. Bone assemblages from Prolom 2 and GSC reveal a high species diversity which is low in the Bukhtarminskaya Cave. Carnivores constitute a significant percentage of the fossil assemblages in the GSC (48.5%) and Prolom 2 (23.5%), but this is substantially lower in the Bukhtarminskaya Cave (10.5%).

The percentage of carnivores in fossil bone assemblages from southern Africa fluctuates from 13% to 31%, whereas it constitutes 9% in extant hyena bone assemblages (Hill, 1989). Bones were more fragmented in Prolom 2 relative to the two other examined caves (Fig. 8F–I). Large fragments of bison humerus bones were not recorded in Prolom 2 but are present in the Bukhtarminskaya Cave and the GSC (Fig. 7). In the GSC, eight intact metacarpal bones of bison were found, but only one large fragment of this bone was found in Prolom 2. The disproportion between the numerous fragments of limb bones and the scarcity of vertebrae fragments is also for the bone assemblages accumulated by hyenas (Hill, 1989). In Prolom 2, numerous saiga phalanges exhibit bites from canines and others have traces of hyena gastric acid (Fig. 8A–E). Some of the small bones were presumably entirely digested. Thus, in general, all the examined caves show signs of hyena dens, although the assemblage from Prolom 2 (see sites description) was found to be somewhat peculiar, which is probably due to the involvement of Neanderthal hunters in its accumulation.

There is a great deal of discussion regarding the relationship between Neanderthals and cave hyenas, from co-existence to conflict (see Dusseldorp, 2013). Our study showed that on the one hand, the ecological niche of the cave hyenas shares many similarities with that of extant spotted hyenas, and on the other hand, exhibits some plasticity in different parts of its ancient range. The cave hyenas were characterized by eating both the fresh meat and carcasses of large animals and gnawing at their bones. Although Neanderthals were skilled hunters, they remained omnivorous. Consequently, the ecological niches of both top predators differed.

Our study of tooth microwear shows a similar diet of the hyenas in the three dens, although in the GSC, the animals' diets somewhat shifted towards those of predators such as lions. Notably, the genetic differences between *Crocuta spelaea* and *C. ultima* suggest that both species may have occupied the predator niche simultaneously and independently.

6. Conclusions

The first application of tooth microwear analysis to study the paleodiets of cave hyenas revealed the ecological niche and dietary patterns of the extinct representatives of the genus *Crocuta*. The high resolution offered by tooth microwear allowed for the identification of similar diets in the Prolom 2 grotto and the GSC and an overall similarity with the known diets of extant spotted hyenas. The sample from the Bukhtarminskaya Cave shows a similar pattern but the sample size is too small to yield robust results. The microwear patterns also allowed for the identification of some ontogenic differences between the adults exhibiting a bone crushing behavior, and the juveniles, that besides bones, may have included a larger proportion of meat in their diet. This interpretation should be confirmed with larger samples. In general, there are similarities between the dietary traits of cave hyenas and those of extant *C. crocuta*, but the microwear patterns reveal some relevant interspecific and intra-specific differences.

Data availability

Datasets related to this article can be found at https://doi.org/10.5281/zenodo.6466217, hosted at Zenodo (open repository developed under the European OpenAIRE program and operated by CERN).

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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