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Feeding on giants: Neotaphonomic evidence of hyena exploitation of megafaunal skulls and its implications for Pleistocene archaeology

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ABSTRACT

The role of hominins in the hunting and processing of megafauna is one of the most contentious topics in Pleistocene archaeology. Determining whether the remains of very large mammals (>800 kg) were shaped by human activity or carnivore modification requires robust neotaphonomic frameworks. Systematic patterns of carcass consumption by carnivores have been established, particularly for long bones. Yet research on megafauna, and especially on their cranial remains, are scarce despite their recurrent presence in archaeological contexts. This study investigates bone surface modification patterns on rhinoceros (*Ceratotherium simum*) and elephant (*Loxodonta africana*) cranial elements consumed by free-ranging spotted hyenas (*Crocuta crocuta*) in the Timbavati Private Nature Reserve, South Africa. The sample includes 20 cranial specimens (MNE = 20; 12 rhinoceros, 8 elephant) from individuals of different age groups that died naturally and were subsequently scavenged. Analyses using 40x hand lenses and Dino-Lite digital microscope to document bone surface modifications. Distinct patterns emerged: in rhinoceroses, near-complete destruction of mandibular condyles, coronoid processes, nuchal crest, and maxilla; in elephants, pronounced furrowing on mandibular condyles and the symphyseal region. Integrating these observations with published taphonomic analyses of Eurasian assemblages, a five-stage sequence of cranial exploitation is proposed, paralleling models established for long bone consumption. These results highlight prey species-specific differences in modification intensity linked to bone density, tissue distribution, and feeding strategies. More broadly, they provide comparative criteria for distinguishing hyena from hominin-induced modifications, and the paleoecological significance of megafauna in Pleistocene ecosystems.

1. Introduction

Archaeological and paleontological Pleistocene records consistently demonstrates that hominins, from the earliest representatives to *Homo sapiens* (Linnaeus, 1758), coexisted with hyenas and other carnivores across a variety of landscapes. Caves and rock-shelters often served as recurrent occupation sites for both groups, either in temporal succession or not (e.g., Straus, 1982; Brugal and Jaubert, 1991; Villa et al., 2004; Miracle, 2005; Brugal, 2010; Discamps et al., 2012; Morley et al., 2019). At many of these sites, the cumulative and overlapping modifications produced by both hominins and carnivores frequently result in complex palimpsests, making it difficult to identify the respective contributions of each agent to site formation processes.

Carnivore modifications on bones provide essential information for identifying the origins of fossil assemblages, offering valuable insights into both hominin and carnivore subsistence strategies. Spotted hyenas (*Crocuta crocuta,* Erxleben, 1777) have been responsible for many of the non-human bone accumulations during the Pleistocene in Africa and Eurasia (e.g., Mills and Mills, 1977; Fosse et al., 1998; Stiner, 2004; Villa et al., 2004; Diedrich and Žák, 2006; Kuhn et al., 2010; Diedrich, 2014b). Due to the considerable overlap in prey species and their bone-accumulating and modifying behaviours, hyena-generated

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assemblages can exhibit taphonomic signatures that closely mimic those produced by hominins, resulting in equifinality and complicating the differentiation between these agents. In this context, neotaphonomic and experimental studies of carnivore bone modifications have become increasingly important for the analysis and interpretation of fossil faunal assemblages.

Previous taphonomic research has mainly focused on reconstructing the timing of hominin and carnivore access to animal carcasses (e.g., Binford, 1981; Blumenschine, 1986; Selvaggio, 1994; Pante et al., 2012); documenting skeletal part representation and bone fragmentation (e.g., Blumenschine, 1986; Marean and Spencer, 1991); and characterizing bone surface modifications, including their anatomical distribution and frequency on long limb bones, to infer the carnivore taxa responsible for tooth-marking bone remains (e.g., Blumenschine, 1986; Haynes, 1983; Pickering et al., 2004; Coard, 2007; Young et al., 2015; Koungoulos et al., 2018). In addition, researchers are now employing a variety of advanced high-resolution imaging techniques (e.g., Pante et al., 2017; Arriaza et al., 2017; Courtenay et al., 2019), multivariate analyses (e.g., Domínguez-Rodrigo and Yravedra, 2009), and machine learning techniques (e.g., Harris et al., 2017; Domínguez-Rodrigo, 2019; Moclán et al., 2020; Abellán et al., 2022). However, the majority of these studies have concentrated on small, medium, and large-sized ungulates, while actualistic studies specifically addressing megafaunal remains are still rare.

In Eurasia, hominins and hyenas coexisted with different rhinoceros species during the Pleistocene, highlighting *Stephanorhinus hundsheimensis* (Toula, 1902), *Stephanorhinus kirchbergensis* (Jäger, 1939), *Stephanorhinus hemitoechus* (Falconer, 1868), and *Coelodonta antiquitatis* (Blumenbach, 1799a); and with several proboscidean species, like *Mammuthus meridionalis* (Nesti, 1825), *Mammuthus trogontherii* (Pohlig, 1885), *Mammuthus primigenius* (Blumenbach, 1799b), *Palaeoloxodon antiquus* (Falconer and Cautley, 1847). These megafaunal taxa represent a recurrent component of many Pleistocene faunal assemblages, presumably due to the substantial resources they provided, both for consumption (skin, meat, brain, viscera, fat and marrow; e.g. Fladerer, 2003; Mosquera et al., 2015; Daujeard et al., 2018) and for non-subsistence purposes, including tool production and shelter construction using hair, bones, and tusks (e.g. Germonpré et al., 2008; Pante et al., 2020; Demay et al., 2021).

The importance of improving our understanding of megafaunal bone assemblage formation processes has been recognized by Echassoux (2004), Moigne et al. (2006), Niven (2006) and Smith (2015), and specifically for proboscideans by Diedrich (2014a), Agam and Barkai (2018), and Haynes et al. (2020, 2021), and for rhinoceroses by Discamps (2011), Diedrich (2015), Daujeard et al. (2018), Daschek (2021), among others. However, neotaphonomic studies focused on bone modifications in megafaunal carcasses remain relatively scarce and focused on particular elements (i.e., long limb bones, scapula and pelvis in Haynes et al., 2020, 2021).

However, the recurrent presence of cranial and mandibular elements in sites of anthropic origin (e.g., Arago F (Chen and Moigne, 2018) and Gesher Benot Ya'aqov (Goren-Inbar et al., 1994; Rabinovich and Biton, 2011), carnivore origin (e.g., Bottrop (Diedrich, 2012b) and Vogelherd (Niven, 2006)) and mixed origin (e.g., Cotte de Saint Brelade (Scott, 1980, 1989; Smith, 2015) and Ambrona (Villa et al., 2005)) would confirm the transport and consumption of megaherbivores head's parts (including meat, brain, tongue, mandibular fat, etc.).

Discriminating between cultural and non-cultural patterns of bone modification is essential for the archaeological interpretation of megafaunal assemblages, particularly in assessing how hominins and carnivores, such as hyenas, interacted with these very large mammals. Although it is generally accepted that hominins exploited very large animals for food and raw materials, and that hyenas similarly utilized these carcasses, neotaphonomic studies providing detailed comparative data on the modification of cranial and mandibular remains are still largely lacking and represent an area of research that remains to be further explored.

This study presents the first neotaphonomic analysis of cranial remains from rhinoceros (*Ceratotherium simum,* Burchell, 1817) and modern African elephant (*Loxodonta africana,* Blumenbach, 1797) consumed by free-ranging spotted hyenas (*C. crocuta*) in the Timbavati Private Nature Reserve (South Africa). Here we document bone surface modifications, skeletal disturbances, and consumption patterns produced by hyenas, providing new data on carnivore modification of megafaunal cranial elements and their potential archaeological significance. These findings are further discussed in relation to similar modifications observed in Pleistocene archaeo-paleontological assemblages across Eurasia.

2. Materials and methods

The modern elephant's and rhinoceros' carcasses were recorded in the Timbavati Private Nature Reserve, located along the western boundary of Kruger National Park, spanning the Mpumalanga and Limpopo provinces in South Africa (Fig. 1A and B). The reserve covers over 53,000 ha, sharing open boundaries with Kruger National Park, which allows free wildlife movement between reserves. The landscape lies within the dry savanna biome, characterized by a mixed vegetation structure of grasslands, shrublands, and open woodland mosaics (Fig. 1C).

The sample comprises 3 crania and 5 mandibles from five elephants (*Loxodonta africana*; Supplementary Fig. 1), representing two adult and three senile individuals. Specimens E.C.01 and E.M.04 correspond to the same individual, while the rest specimens were found partially disarticulated. Additionally, 5 crania and 7 mandibles from seven white rhinoceroses (*Ceratotherium simum*; Supplementary Fig. 2) are included, representing two immature, four adult, and one late adult individual. Specimens R.C.05 and R.M.01 belong to the same rhinoceros.

Carcasses were located by the park's team of ecologists during their daily routine monitoring activities. The elephants died of starvation during drought events, while the cause of death for the rhinoceroses could not be determined, as it remains unclear whether they were predated by carnivores or died of natural causes, although active predation is considered unlikely. The bones derive from carcasses and skeletons that were neither skinned nor butchered by humans. However, in accordance with park management protocols, tusks and horns were collected by the Natural Reserve authorities 7–10 days after death, when the roots had sufficiently dried to allow safe removal without cutting the tusk or damaging the bone. Also, some mandibles were retrieved after natural skeletonization to assess the ontogenetic ages of deceased elephants and rhinoceroses, storing them in an open-air enclosure at the research centre inside the park.

The specimens analysed in this study include remains located and monitored during the end of the dry season of 2024 (September–October; Fig. 1C) between five days and two months after death, as well as specimens collected by park authorities over a five-year period (Fig. 1D). To minimize variability in gnawing intensity related to exposure time, only carcasses that had been systematically monitored and exposed to scavengers for approximately one to two months were included, matching the period park authorities usually wait before collecting remains. This timeframe is sufficient for bones in this area to be clean enough by carrion-eaters and environmental processes for analysis, leaving the bones found in situ mostly free of soft tissue but still greasy, whereas those previously collected were already dry and weathered after prolonged exposure. Importantly, the remains were not damaged during collection and only exhibit modifications resulting from scavenging by carnivores.

The anatomical identification of cranial and mandibular sections was conducted following the criteria outlined by Van der Merwe et al. (1995) and Todd (2010) for elephants, and Deng et al. (2021) for rhinoceroses.

Three age groups were established: immature (including perinatal and juvenile individuals), adult (including prime adult and late adult

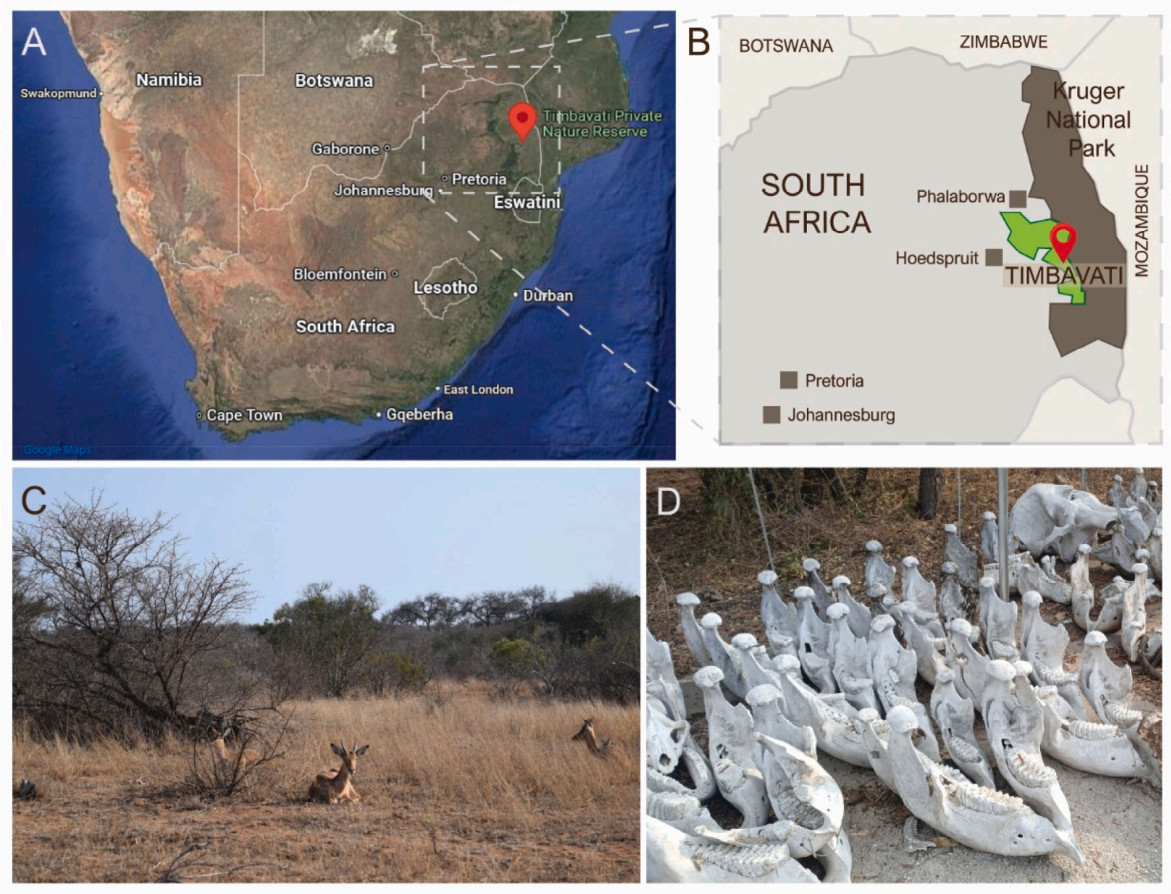

Fig. 1. A: Map of South Africa showing the general location of the study area. B: Detail of the Timbavati Private Nature Reserve in the northeastern part of the country. C: Typical landscape of the park at the end of the dry season, characterized by sparse vegetation and limited water availability. D: Accumulation of rhinoceros and elephant mandibles collected by park authorities during monitoring activities.

individuals), and senile. Given that the study focuses on cranial remains (crania and mandibles), age classification was based on the degree of dental crown development, the presence of deciduous or permanent teeth, and the degree of occlusal wear (e.g., Foster, 1965; Tong, 2001; Todd, 2010; Laws, 1966).

Specimen quantification was performed using the number of identified specimens (NISP), the minimum number of elements (MNE), and the minimum number of individuals (MNI), following the guidelines set out by Lyman (1994, 2008), Klein and Cruz-Uribe (1984), Brain (1969) and Pickering (2002). Bone surface modifications were examined in situ, using a 40x hand lens and natural light. When higher magnification was required, a Dino-Lite digital microscope with magnifications ranging from 10 to 70x up to 200x connected to a laptop were employed.

Individual bones were then examined and photographed to qualify and quantify bite marks and damages in detailed. Carnivore activity (Fig. 2) was determined by the presence of pits, punctures, scores, crenulated edges, gnawing and furrowing, following Haynes (1980, 1983), Binford (1981), Selvaggio (1994), and Pickering (2001).

3. Results: bone surface modification by carnivores

Owing to their large size and structural density, megafaunal bones display carnivore-induced modifications that often differ markedly from those observed in smaller-bodied species (White and Diedrich, 2012; Haynes and Klimowicz, 2015). In this study, we present new data on the modifications produced by free-ranged spotted hyenas (*Crocuta crocuta*) on megafaunal cranial remains, an anatomical region that remains underrepresented in neotaphonomic studies. The observations provided

Type of modification	Description/shape	Cause	Teeth used to make the modification
Score	Linear or sinuous marks, U section	Dragging over the surface	Incisors - Canines
Pit	Small, oval to round superficial marks	Press into the bone	Incisors - Canines
Puncture	Deep oval to round marks	Preassure that perforate the bone	Incisors - Canines
Gnawing	Polished/worn edge	Removal of bone	
Furrowing	Loss of bone tissue	Removal of bone and repeated scraping	Canines - Premolars - Molar
Crenulated edge	Irregular broken outline of the edge	Sawtoothed fracture outline	Premolars - Molar

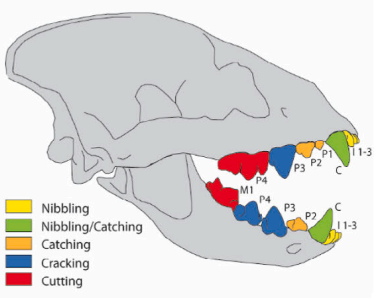

Fig. 2. Types of modifications made by spotted hyenas. Hyena skull modified from Diedrich (2013).

here aim to serve as a comparative reference for identifying hyena-related damage on proboscidean and rhinocerotid cranial elements. While the sample size is limited, these data contribute valuable insights for identifying the taphonomic signatures of hyena activity on megafaunal cranial remains within the fossil record.

3.1. *Spotted hyena modifications of proboscidean cranial specimens (Loxodonta africana)*

Specimen E.C.01 (Senile, Cranium): Scores, punctures, and furrowing were documented (Fig. 3A). Affected areas by scores include the processus alveolaris and palatinus (Fig. 3B), as well as the condylus occipitalis. Four pits were identified on the zygomatic bone (Fig. 3C), in contact with the fossa mandibularis. The pars tympanica, pars basalis, and pars lateralis were affected by furrowing.

Specimen E.C.02 (Senile, Cranium): This cranium showed scores on the corpus of the maxilla, the parietal bone, and the nasal bone. Furrowing was also observed on the processus frontalis and zygomatic region.

Specimen E.C.03 (Adult, Cranium): Clear evidence of scoring, pits, furrowing, and chewing was recorded (Fig. 3). There was advanced chewing of the zygomatic bones, processus zygomaticus of the temporal, and the incisive bone (Fig. 3D), extending through the processus alveolaris and palatinus of the maxilla. Scores were concentrated in the occipital region, both condyli occipitales and the zygomatic processes on both sides. The corpus of the maxilla also showed scores, along with furrowing on the ventral area of the temporal and occipital bones.

Specimen E.M.01 (Adult, Mandible): Scores were observed on both rami mandibulae and corpus mandibulae. Also, both coronoid processes were affected by continuous nibbling. Complete consumption of the processus condylaris and caput mandibulae was observed on both sides (Fig. 4A), leaving crenulated edges and scratches on the ramus (Supplementary Fig. 3A–B). The posterior part of the mandible was heavily modified, with the fossa pterygoidea heavily altered, nearly

Fig. 3. Spotted hyena modifications of proboscidean cranium specimens. A–C: Specimen E.C.01, D: Specimen E.C.03 (explanations for A-D see text).

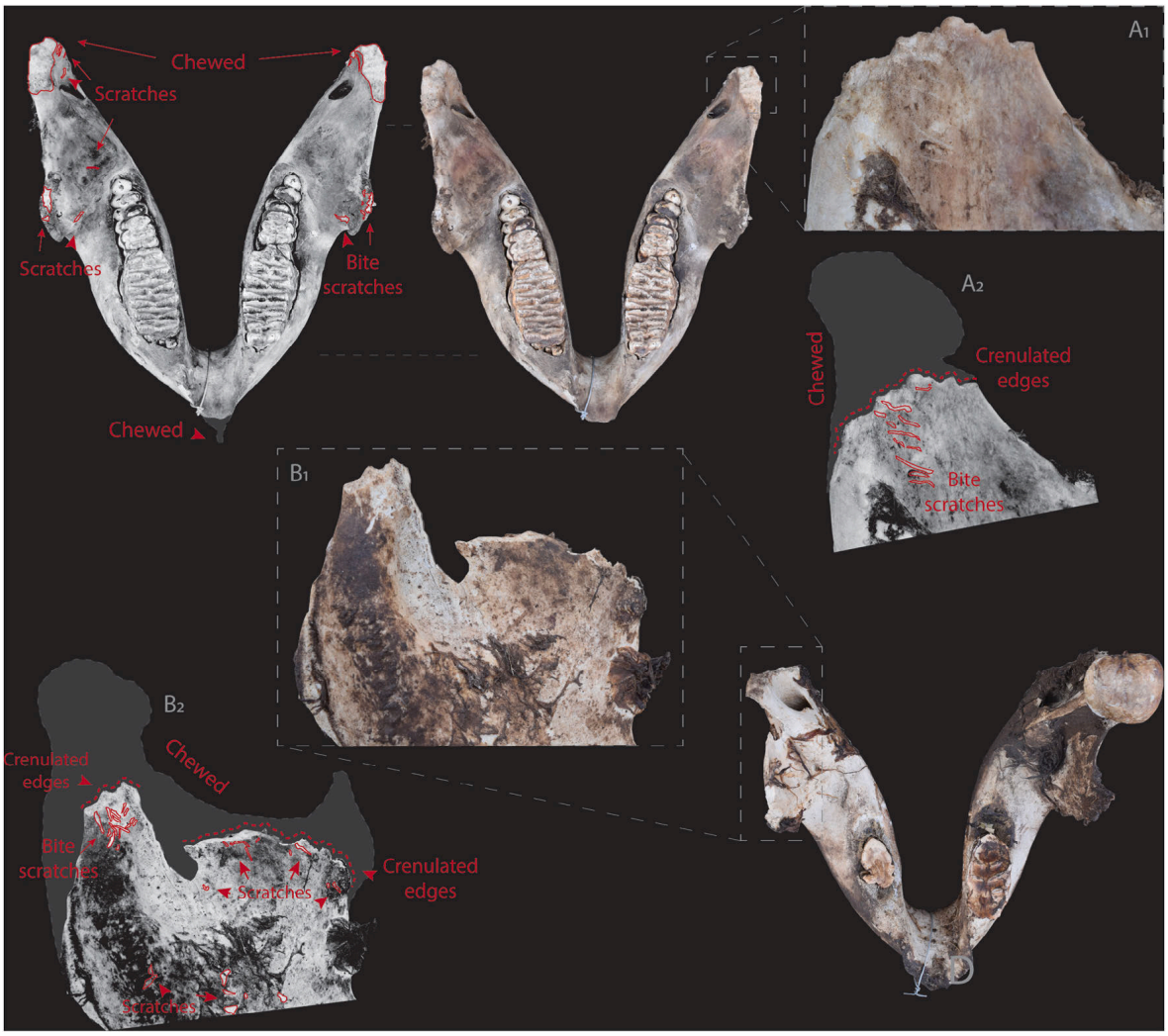

Fig. 4. Spotted hyena modifications of proboscidean mandible specimens. A: Specimen E.M.01, B: Specimen E.M.02 (explanations for A-B see text).

reaching the mandibular foramen, and the pars incisiva also consumed.

Specimen E.M.02 (Senile, Mandible): In this mandible, scores were noted on the left caput mandibulae and both rami mandibulae, and furrowing was observed on both coronoid processes. The right processus condylaris and caput mandibulae were completely chewed by the hyenas (Fig. 4B). The fossa pterygoidea showed advanced consumption, nearly reaching the mandibular foramen, with similar damage on the left processus condylaris.

Specimen E.M.03 (Adult, Mandible): This mandible displayed consistent evidence of scoring across both rami mandibulae. The left coronoid process was particularly affected by furrowing. Complete loss of the processus condylaris and caput mandibulae on both sides was documented, along with deep chewing in the fovea pterygoidea, extending close to the foramen mandibulae.

Specimen E.M.04 (Senile, Mandible): Scores were observed on the right corpus mandibulae and around the pars incisiva of this specimen. Also, there were furrowing on the processus coronoideus.

Specimen E.M.05 (Old adult, Mandible): Scores and pits were present on both sides of the caput mandibulae and processus condylaris. Scores were also documented on both corpus mandibulae (Supplementary Fig. 3C). Additional damage was noted because of nibbling in the angulus mandibulae and both processus coronoideus.

3.2. *Spotted hyena modifications of rhinocerotid cranial specimens (Ceratotherium simum)*

Specimen R.C.01 (Adult, Cranium): Evidence of scoring and chewing was observed on this cranium (Fig. 5C). Scores were concentrated on the right zygomatic bone and the internal surfaces of both zygomatic processes. Additionally, extensive consumption was documented on the premaxilla, reaching the first premolars (Fig. 5D). The paraoccipital processes, nuchal crest, parietal crest, and nuchal tubercle, extending up to the occipital crest, were also chewed by the hyenas.

Specimen R.C.02 (Adult, Cranium): In this specimen, scores primarily affected both sides of the maxilla and the external face of the zygomatic bone, while furrowing was observed on the internal surface of the zygomatic bones. There was furrowing in the cornis/nasal horn boss derived from the consumption of part of the left side (Fig. 5A). The posterior part of the cranium was completely chewed (Fig. 5B), reaching the occipital crest. These areas showed evidence of advanced exploitation, with facial and occipital elements heavily altered, likely reflecting attempts to access soft tissue and/or cranial contents.

Specimen R.C.03 (Adult, Cranium): Furrowing was concentrated on the zygomatic bones and chewing of the nuchal crest in the occipital region (Supplementary Fig. 4A and B). Several scores can be observed on the corpus mandibulae (Supplementary Fig. 4C). The integrity of the facial skeleton was compromised by the consumption by the hyenas. There was evidence of chewing and advanced bone loss on the

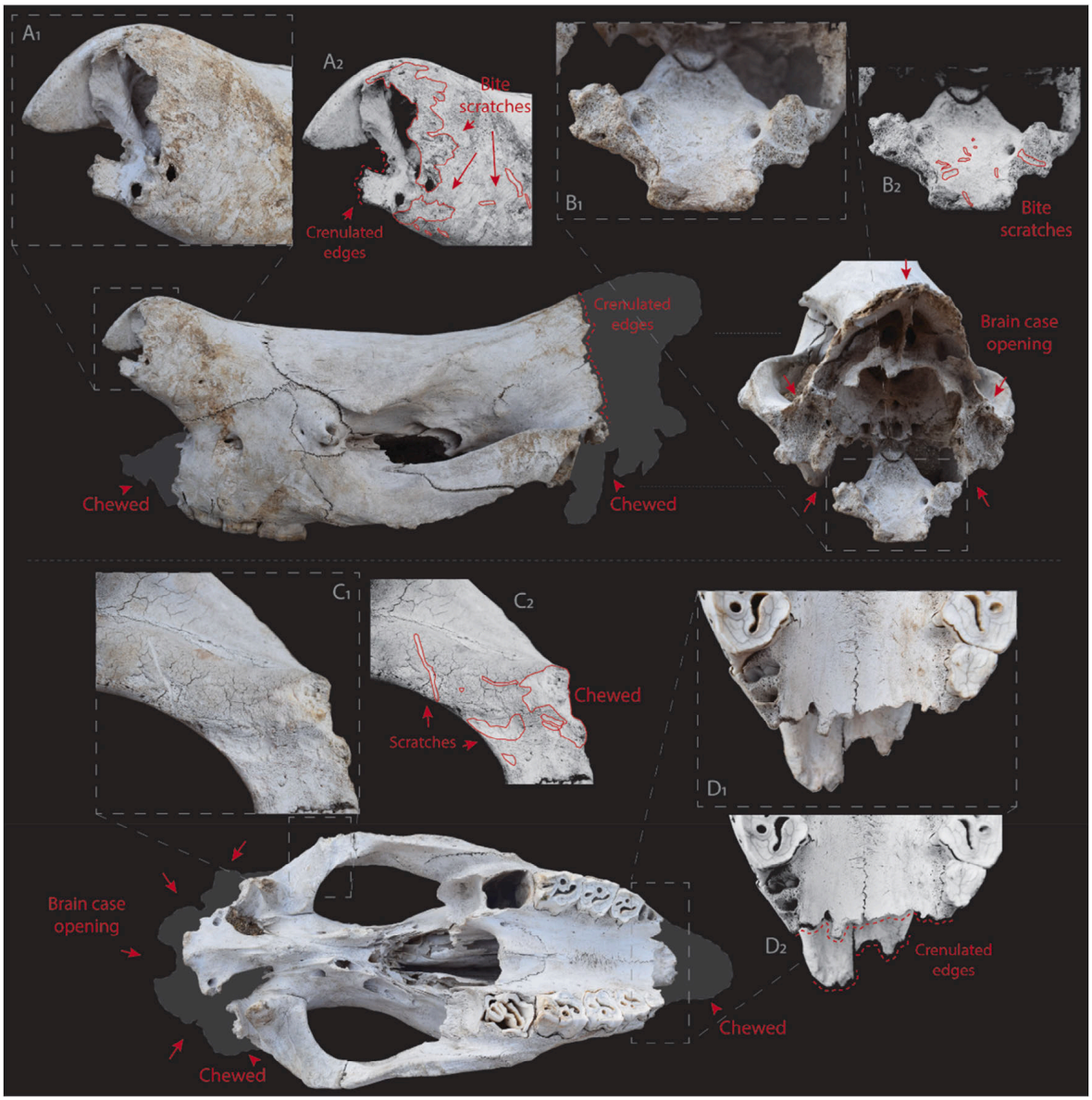

Fig. 5. Spotted hyena modifications of rhinocerotid cranial specimens. A–B: Specimen R.C.02, C–D: Specimen R.C.01.

premaxillae, extending up to the second premolars, and the end of the cornis.

Specimen R.C.04 (Adult, Cranium): This cranium presented scores on the nuchal crest, and furrowing on the cornis. The facial region was again heavily modified, notably the premaxillae, extending to the first premolars, creating the typical crenulated edges (Supplementary Fig. 5). The maxillae were also chewed up to the infraorbital foramen on the right side, and nearly to the same extent on the left.

Specimen R.C.05 (Old adult, Cranium): The specimen exhibited scores on the right maxilla and the premaxillae was chewed (Supplementary Fig. 6).

Specimen R.M.01 (Old adult, Mandible): Abundant scores were recorded on several parts of this mandible. The ramus and angulus mandibulae showed furrowing, scores and pits, indicative of prolonged nibbling and biting (Supplementary Fig. 10B). The coronoid process and postglenoid process groove were severely affected, with advanced consumption reaching up the molars. The symphysis mandibulae was destroyed, with damage extending to the premolars.

Specimen R.M.02 (Juvenile, Mandible): This specimen exhibited scores in both ramus mandibulae, along with furrowing in the left coronoid depression and posterior wall of groove. The right postglenoid process groove was consumed by hyenas (Fig. 6A), with bone removal extending to the coronoid depression, and the left show less consumption (Fig. 6B). Additionally, the symphysis mandibulae was heavily modified, with bone loss reaching nearly to the level of the premolars (Fig. 6C).

Specimen R.M.03 (Adult, Mandible): The postglenoid process grooves were chewed and the glenoid processes exhibited furrowing (Supplementary Fig. 7). The symphysis and the external surface of the ramus mandibulae presented scores (Supplementary Fig. 10A).

Specimen R.M.04 (Juvenile, Mandible): The symphysis mandibulae was chewed up to the level of the first premolars. Similarly, the coronoid and glenoid processes were completely removed on both sides (Supplementary Fig. 8A), with bone loss extending into the coronoid depression. Several scores were identified on the corpus and ramus mandibulae (Supplementary Fig. 8B), as well as near the mental foramina.

Specimen R.M.05 (Juvenile, Mandible): This mandible was heavily modified. Both rami were chewed (Supplementary Fig. 9A), as well as the symphyseal region (Supplementary Fig. 9B) and the coronoid and

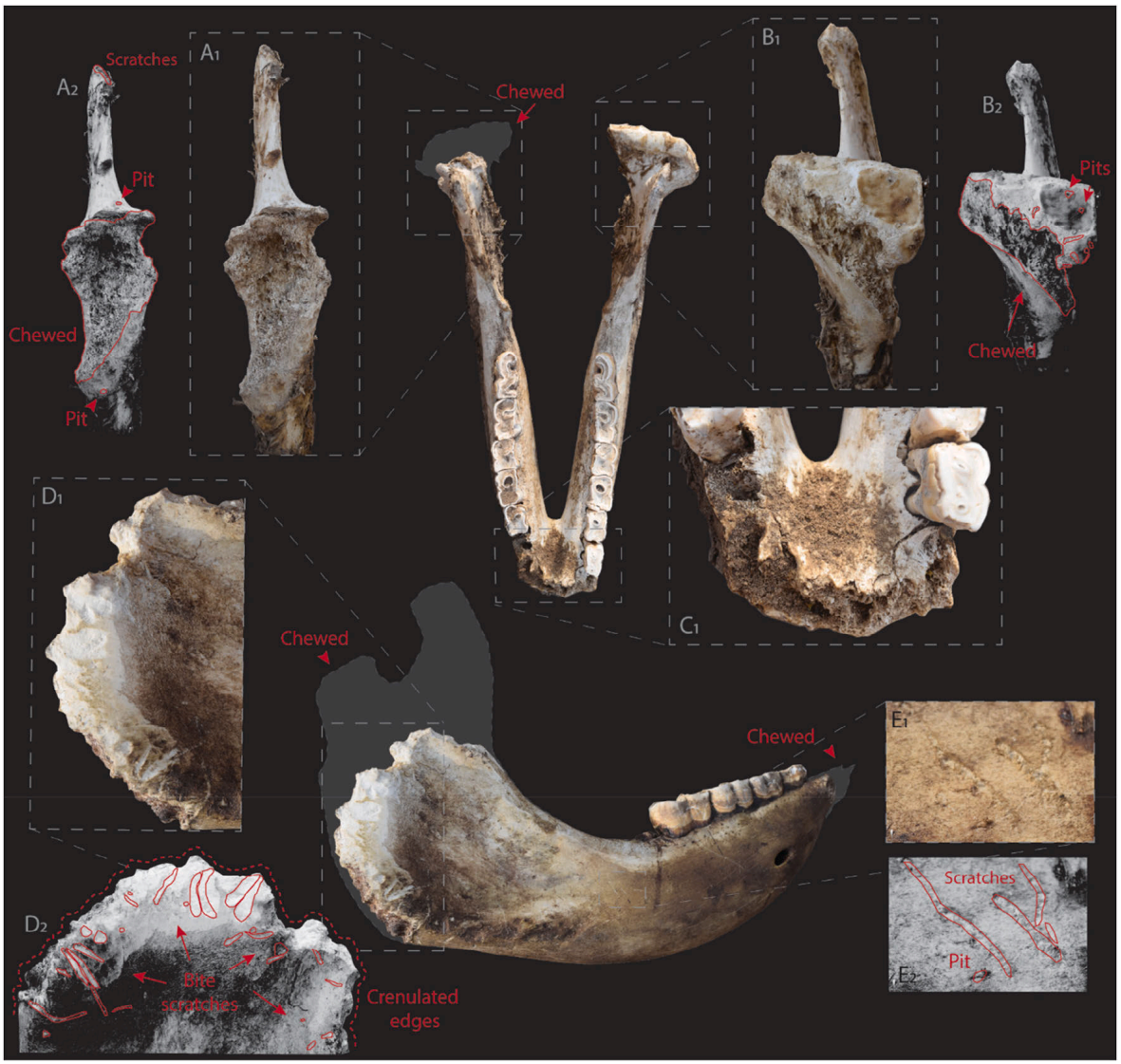

Fig. 6. Spotted hyena modifications of rhinocerotid cranial specimens. A–C: Specimen R.M.02, D–E: Specimen R.M.05.

condylar areas (Fig. 6D). On the right side, bone loss extends below the coronoid depression, while on the left it is slightly less pronounced. The mandible presented scores and pits on the ramus mandibulae (Fig. 6E; Supplementary Fig. 9C and F; Supplementary Fig. 10C), as well as furrowing on the edges of these areas (Supplementary Fig. 9D).

Specimen R.M.06 (Adult, Mandible): The symphysis mandibulae was chewed by the hyenas, and on the right side, bone loss along the mandibular corpus extended to the level of the first molar, with the P2 absent. The ramus exhibited clear evidence of furrowing and scoring in several areas.

Specimen R.M.07 (Adult, Mandible): In the anterior portion, the symphysis mandibulae was slightly consumed. On the posterior portion, the coronoid and condylar areas are also slightly chewed (Supplementary Fig. 11). Furrowing and scores were observed on both sides of the corpus and ramus mandibulae.

3.3. Patterns of cranial and mandibular consumption

Based on the bone surface modifications recorded in the analysed sample, several categories of cranial and mandibular consumption can be distinguished. These categories reflect increasing degrees of destruction and differ slightly between elephants and rhinoceroses.

Low-intensity consumption: Specimens show only minimal hyaena modification, limited to light tooth scores on the most prominent surfaces. Overall bone loss does not exceed ~5 % in either taxon. Examples include specimens E.C.02, E.M.04, and R.M.07.

Moderate consumption of protruding elements: Remains exhibit more advanced damage affecting prominent structures such as the zygomatic arch, mandibular symphysis, and mandibular condyles. Estimated bone loss ranges between 5 and 15 %. Examples include Specimens E.C.01, R.C.05, R.M.02, and R.M.03.

Intermediate consumption: Specimens display substantial destruction, with 15–30 % of the bone missing accompanied by abundant tooth marks and crenulated edges, like rhinoceros specimens R.C.04, R.M.04, R.M.05, and R.M.06. Elephant specimen E.M.05 shows comparable levels of modification, though slightly lower than that observed in rhinoceroses (15–20 %). The left hemimandible of E.M.02 also fits within this range.

Advanced consumption: Specimens present advanced destruction of the posterior portions and other prominent areas. Rhinoceros remains show 30–50 % bone loss, whereas elephants typically present 20–30 %, particularly in mandibular elements. The right hemimandible of E.M.02 and specimens E.M.01, E.M.03, R.C.01, R.C.02, and R.M.01 are examples of this category.

Atypical cases: Elephant cranium E.C.03 exhibits the most advanced consumption observed for this taxon, with destruction affecting the

posterior cranium, zygomatic arches, and incisive bones. Even so, overall bone loss does not exceed ~30–35 %. Also, specimen R.C.03 represents an intermediate pattern that does not fully align with the categories above: while the entire posterior portion of the cranium is missing, other raised structures, such as the zygomatic arches or the nasal/cornis boss, remain largely unmodified.

4. Discussion

4.1. Evaluating hyena-modified cranial remains of elephant and rhinoceros

The results reveal a consistent pattern of selective bone modification by spotted hyenas, with clear distinctions between cranial and mandibular elements, as well as between the two megafaunal taxa analysed. Overall, mandibles exhibit more frequent and severe alterations than crania in both elephants (*Loxodonta africana*) and rhinoceroses (*Ceratotherium simum*), suggesting that hyenas prioritize these elements, likely due to their easier accessibility and greater association with soft tissue.

In elephant crania (n = 3), the occipital region, including the condylus occipitalis, displayed furrowing in the 33 % of the cases, while scores were present in all specimens. These patterns suggest focused feeding on the posterior cranium, potentially reflecting attempts to access musculature near the neck and foramen magnum. The zygomatic bones and processus zygomaticus were modified in all specimens to varying degrees, with furrowing likely due to their fragility and proximity to meat-rich areas. Additional modifications were noted on the nasal and frontal processes, reinforcing the idea of progressive exploitation of the facial region tissue.

In comparison, rhinoceros' crania (n = 5) showed more intense damage to structurally robust areas. In the facial area, consumption of the maxillae and premaxillae reached the premolars in most specimens (80 %), accompanied by scores. Complete or near-complete bone loss of the zygomatic bones and advanced furrowing on the cornis were also recorded. Posteriorly, the nuchal and parietal crests showed advanced chewing and, in one case, complete consumption of this area. These modifications would likely be associated with attempts to access the brain, a nutrient-rich target despite the resistance of cranial bone.

Mandibular elements, particularly the symphysis, condyles, and coronoid processes, were systematically targeted in both taxa. In elephants (n = 5), the symphysis mandibulae was damaged in 60 % of the sample. The processus condylaris and caput mandibulae were either heavily altered or chewed, reflecting continued access to the temporomandibular joint. Notably, all specimens exhibited furrowing on the coronoid process, and 100 % presented scores along the ramus and corpus, reflecting repeated tooth contact during skull manipulation and/or muscle removal during carcass processing.

Similarly, rhinoceros mandibles (n = 7) showed extensive alteration. The symphysis was completely or extensively consumed in all cases, sometimes reaching the premolars. Scores and pits were frequently observed on the ramus, corpus, and angulus mandibulae, with the latter showing bone loss in some cases, suggesting muscle detachment as a feeding strategy. The coronoid process and postglenoid groove were heavily modified, often displaying deep furrowing in the coronoid depression, pointing to systematic targeting of posterior and prominent mandibular regions.

Despite their robustness, structurally dense areas such as the nuchal crest, condyles, and coronoid processes were also damaged. On the contrary, they often showed the most intensive damage, underscoring a feeding strategy aimed at maximizing nutritional return, even at the cost of increased processing effort. The presence of crenulated edges, along with furrowing and scores, suggests repeated chewing rather than biting and nibbling, reflecting both the resistance of these skeletal elements and potential constraints in hyena feeding behaviour when processing megafaunal carcasses.

Species-specific differences were also observed. In elephants, damage was more concentrated in the condyles and symphysis, while in rhinoceroses, greater damage occurred on the posterior skull, with emphasis on the coronoid and condylar processes, nuchal crest, and occipital area. These contrasts likely reflect variations in bone density, anatomy projection, and tissue distribution, influencing carcass accessibility and processing.

Collectively, these findings enhance our understanding of hyena-mediated bone modification in large-bodied taxa and offer comparative data for interpreting similar patterns in the fossil record. They highlight the importance of considering anatomical structure, bone density, and feeding behaviour when reconstructing taphonomic histories in archaeological and paleontological contexts. Further research should explore how these variables influence selective consumption across different carnivore species and ecological settings.

4.2. Megafaunal accumulation and skull exploitation across Eurasia in cultural and non-cultural assemblages

Rhinoceroses and proboscideans can represent between 20 and 77 % of hyena's prey choice in non-cultural accumulations (Table 1), as documented in Koneprusy Cave (Diedrich, 2011), Nad Kacakem Cave (Diedrich, 2017), Vallonnet Cave (Echassoux, 2004), Bad Widlungen-Biedensteg (Diedrich, 2006a, 2013), Bottrop (Diedrich, 2011, 2012b), Hohle Stein Cave (Diedrich, 2011), Hyaena Den (Currant and Jacobi, 2004) and Perick Caves (Diedrich, 2008), among others (Table 1). In contrast, in anthropogenic accumulations (Table 1), assemblages containing only rhinoceros remains, or both rhinoceros and proboscidean remains, exhibit lower values in the percentage of megafaunal specimens relative to the total NISP (%NISP), ranging from 0.2 % at Covalejos (Yravedra et al., 2016, 2019) to 25 % at Terra Amata (Valensi, 2001). However, assemblages exclusively composed by proboscidean remains may show substantially higher %NISP values, such as the 77.7 % recorded at EDAR Culebro 1 (Yravedra et al., 2014) or the 99 % recorded at Pit site in La Boella (Mosquera et al., 2015).

A different pattern emerges in mixed accumulations, with megafaunal %NISP tending to be higher in assemblages where humans acted as the primary accumulating agent and carnivores played a secondary role. This is observed at sites such as Castel di Guido, where megafauna represent 42.6 % of the NISP (Saccà, 2012), Ambrona with 61.9 % (Villa et al., 2005), Molodova I with 84.2 % (Demay et al., 2012) and Áridos 2, where megafauna account for 100 % of the assemblage (Yravedra et al., 2010), among others (Table 1). Conversely, in assemblages where carnivores had primary access to rhinoceros and proboscidean carcasses (or where their role remains unclear), megafaunal representation is considerably lower, with values not exceeding 7.18 % at Balver Höhle (Kindler, 2012), 11.2 % in the upper levels (UAL) of Fuente Nueva 3 (Espigares et al., 2013; Yravedra et al., 2021; Palmqvist et al., 2024), and 3.1 % and 0.2 % at El Forn and La Mina respectively at Barranc de la Boella (Pineda et al., 2017).

Meat, viscera, and fat represent the most immediately attractive resources provided by megafaunal carcasses for both hominins and carnivores. Consumption of these tissues by carnivores, particularly hyenas, has been documented in most macrofaunal assemblages (Table 1). Rhinoceros remains bearing cut marks are relatively abundant in the archaeological record, as observed at sites such as Caours (Antoine et al., 2006), Abric Romaní (Rosell et al., 2012), Boxgrove (Parfitt and Roberts, 1998), and La Biache Sant Vast (Auguste, 1995), among others (see also references on Tong, 2000, 2001; Daujeard et al., 2018; Chen and Moigne, 2018, Table 1). In contrast, proboscidean remains with cut marks are comparatively rare (Table 1), largely due to the substantial thickness of cartilage and periosteal tissues that complicate defleshing activities (Haynes and Klimowicz, 2015). Nevertheless, such modifications have been recorded at several sites, including Fuente Nueva 3 (Espigares et al., 2013; Yravedra et al., 2021; Palmqvist et al., 2024), Barranc de la Boella (Mosquera et al., 2015; Pineda et al., 2017), Gesher

Table 1
Summary of archaeological and paleontological sites with megafaunal remains.

Country	Site	Level	Chronology	NISP	MF	%NISP MF	TM	CM	Others	Origin	References
Austria	Krems-Wachtberg (!)		~27 ka	350	MA	53	yes	yes	AS, LI, FI	H	Fladerer (2003)
Belgium	Scladina Cave	5		1871	MA, C.a	3.3	no	yes			Abrams et al., 2013
Belgium	Spy			10000	MA, C.a	11.8	no	no	AS	H**	Germonpré et al., 2014
China	Dadong Cave		MIS 6-7	7045	RH (R.s)	24	yes	no	AS, LI, PP	H/C	Miller-Antonio, et al., 1999; Schepartz and Miller-Antonio (2010)
China	Guanyindong Cave				RH		no	no	AS	H**	Li and Wen, 1986; Tong (2000)
China	Nanjing Man Cave		500 ka		RH		yes	no	AS	H/C	Tong (2001)
China	Shanshenmiaozui		1.2 Ma		RH (C.n)		yes		LI		Tong et al., 2011; Liu et al., 2016
China	Zhoukoudian				RH		no	no	FI		Chow, 1978; Tong (2000)
Czech Republic	Prošek Dome		Early Pleistocene		C.a		yes	no		C	Diedrich (2006b)
Czech Republic	Koneprusy Cave		Middle Pleistocene	126	C.a	25	yes	no		C	Diedrich (2011), 2017
Czech Republic	Nad Kacakem Cave			40	C.a	30	yes	no		C	Diedrich (2017)
Czech Republic	Sloup Cave			63	MA, C.a	17	yes	no		C	Diedrich, 2012c
Czech Republic	Srbsko Chlum–Komın Cave		Upper Pleistocene	3569	C.a	4	yes	no		C	Diedrich (2006b), 2017
Czech Republic	Axamitova Brána Cave (!)		Middle-Upper Paleolithic		C.a		yes	yes		H/C	Diedrich (2006b)
Djibuti	Borogali				EL				LI		Berthelet and Chavaillon, 2001
France	Biache St Vaast	IIa & IIb	MIS 7	20000	PAL, RH	7.5	yes	yes		H	Louguet-Lefebvre, 2005; Auguste (1995); Bahain et al., 2015
France	Camiac (!)		MIS 3	2526	RH	20	yes	yes	LI	C/H	Guadelli (1989); Discamps (2011)
France	Caours	4a & 6b	MIS 5e	892	PAL, RH	1	no	yes			Antoine et al. (2006)
France	Caune de l'Arago	F	MIS 12	7404	RH (S.h.)	5.71	yes	yes		H	Moigne et al. (2006); Chen and Moigne (2018)
France	Caune de l'Arago	C	MIS 11		RH (S.h.), EL	6.13					Moigne et al. (2006)
France	Caune de l'Arago	J	MIS 13		RH (S.h.)	7.63					Moigne et al. (2006)
France	Caune de l'Arago	Q	MIS 14		RH (S.h.)	2.12					Moigne et al. (2006)
France	Clèon (!)	1, 2, 3, 5, 6	MIS 10-7		PAL, D.h.						Patrick et al., 2003;
France	Mont Dol	6 & 8	MIS 5b	4159	MA, C.a	37.9	yes	yes			Louguet-Lefebvre, 2005
France	Payre	G	MIS 8-7	815	RH (S.k., S.h.)	17.3	yes	yes		C	Daujeard et al. (2018)
France	Payre	F	MIS 8-7	3027	RH (S.k., S.h.)	8.77	yes	yes		C	Daujeard et al. (2018)
France	Payre	D	MIS 6-5	963	RH	8.93	yes	yes		C	Daujeard et al. (2018)
France	Plumettes	Upper (II)	MIS 3	2537	MA, C.a	1.64	yes	no	LI	C	Beauval and Morin, 2010
France	Plumettes	Lower (IV, VI, VIII)	MIS 3	3328	C.a	0.61	yes	no	LI	C	Beauval and Morin, 2010
France	Ranville			698	PAL, RH	17.9		yes			Auguste, 2008
France	Rochers de Villeneuve	J	MIS 3	5282	C.a	0.58	yes	no	LI	C	Beauval and Morin, 2010
France	Rochers de Villeneuve	N	MIS 3	1242	MA, C.a	2.64	yes	no	LI	C	Beauval and Morin, 2010
France	Saint Cesaire	10, 11, 12	MIS 3	1682	MA, C.a	2	yes	yes			Morin, 2012
France	Terra Amata	C1	~380 ka	~2400	EL, RH (S.h)	25		no	AS, BPR, PP	H	Valensi (2001)
France	Vallonnet Cave		1.2–1.1 Ma	7204	MA, RH (S.hu., C.s)	20.07	yes	yes		C	Echassoux (2004)
Georgia	Dmanisi		1.8 Ma		MA, RH (S.e)	159				H	Gabunia et al., 2000; Ros-Montoya et al., 2025
Germany	Ariendorf 2	Bed I & II	MIS 8	336	MA, C.a	60.1		yes			Turner, 1998; Turner et al., 1997
Germany	Bad Widlungen-Biedensteg		MIS 5	260	MA, C.a	34	yes	no		C	Diedrich (2006a), 2013
Germany	Balver Höhle		MIS 5	5796	MA, C.a	7.18	yes	yes	LI	C/H	Kindler (2012)
Germany	Bollschweil			22093	MA, C.a	57.4	no	no			Conard and Niven, 2001

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Table 1 (*continued*)

Country	Site	Level	Chronology	NISP	MF	%NISP MF	TM	CM	Others	Origin	References
Germany	Bottrop		63.3–101.5 ka	3820	MA, C.a	61	yes	no		C	Diedrich (2011), 2012b
Germany	Gröben		MIS 6		PAL, RH		yes	yes	LI	H	Gaudzinski (2004); Gaudzinski-Windheuser et al. (2023)
Germany	Hohle Stein Cave			151	MA, C.a	52	yes	no		C	Diedrich (2011)
Germany	Koneprusy Cave	Main Dome area	Upper Pleistocene	711	C.a		yes	no		C	Diedrich and Žák (2006); Diedrich (2011)
Germany	Krölpa (!)		Late Pleistocene	43	C.a	77	yes	no		C	Diedrich (2015)
Germany	Lehringen		Middle Pleistocene		PAL, RH		yes	no		C	Thieme and Veil, 1985; Gaudzinski (2004)
Germany	Neumark-Nord Lake 1		MIS 5e		PAL, RH		yes	no		C	Mania et al., 1990; Mania, 2010; Gaudzinski (2004); Diedrich (2013)
Germany	Perick Caves			2275	MA, C.a	20	yes	no		C	Diedrich (2008)
Germany	Salzgitter-Lebenstedt			2860	MA, C.a	14.3	yes	yes		H/C-C/H	Gaudzinski and Roebroeks, 2000
Germany	Selm-Ternsche				C.a		yes	no		C	Diedrich (2012b), 2013
Germany	Selm-Ternsche		Late Pleistocene		C.a		yes	no		C	Diedrich (2012b)
Germany	Srbsko-Chlum-Komín			260	C.a	4	yes	no		C	Diedrich (2012a)
Germany	Taubach (!)	bone sand	MIS 5e	4864	PAL, RH	36.2	yes	yes	LI	H	Bratlund (2000); Gaudzinski (2004); Gaudzinski-Windheuser et al. (2023)
Germany	Teufelskammer Cave (!)		Lower Weichselian	199	MA, C.a	29	yes	no		C	Diedrich (2011)
Germany	Tönchesberg	2B		921	RH	1	yes	yes		H/C-C/H	Conard, 1992
Germany	Untermassfeld		Early Pleistocene		S.hu	*n = 1065	yes	no		C	Kotowski et al. (2020)
Germany	Vogelherd Cave	Layers IV-V	29-36 ka	17000	C.a	4.7	yes	no	AS	H**	Niven (2006)
Germany	Vogelherd Cave	Layer VII	Middle Paleolithic	518	C.a	13.3	yes	no		C	Niven (2006)
Germany	Weinberg Caves				MA		yes	no		C	Diedrich (2011)
Hungary	Erd	EnsL	MIS 5b		MA, C.a	*n = 7			LI	H	Daschek (2021)
Hungary	Erd	EnsU	MIS 3		MA, C.a	*n = 251	yes	yes	LI, AS, BPR	H/C-C/H	Daschek (2021)
Israel	Gesher Benot Ya'aqov	1			EL	100		yes	LI	H/C	Goren-Inbar et al., 1994; Rabinovich and Biton (2011)
Italy	Asolo	all	MIS 4	50	MA	100	no	no			Mussi and Villa, 2008
Italy	Castel di Guido		MIS 9	3245	PAL	42.6	yes	yes	LI, PP,	H/C	Saccà, 2012
Italy	Notarchirico	A	675-610 ka	85	PAL	44.7	no	no	LI	Natural?	Pineda et al., 2024
Russia	Kostënki 21 (!)	layer III, complexes 3-6	21-23 ka	758	MA	66.7	yes		LI	H	Reynolds et al., 2019; Demay et al. (2021)
Russia	Kostënki 21 (!)	layer III, complexes 1-3	21-23 ka	655	MA, C.a	71.87	no	yes	LI	H	Reynolds et al., 2019; Demay et al. (2021)
Russia	Yudinovo	complexes 3-4	~14.5 ka		MA	*n = 517	yes	yes	AS, ST, LI	H/C	Germonpré et al. (2008)
Spain	Abric Romaní	J	MIS 3	1265	RH (S.h.)	4.74	no	yes	LI, FI	H	Rosell et al. (2012)
Spain	Ambrona	AS1, AS2, AS3	400-350 ka	611	EL	61.9	yes	yes	LI	H/C	Villa et al. (2005)
Spain	Arenero Pedro Jaro		Middle Pleistocene		RH			yes	LI	H	Yravedra et al. (2019)
Spain	Áridos 1		MIS 9		EL		no		LI		Villa, 1990; Soto et al., 2001
Spain	Áridos 2		MIS 11		EL	100	yes	yes	LI	H/C	Yravedra et al. (2010)
Spain	Bolomor Cave		~350 ka-100 ka		EL			yes	LI, FI	H	Blasco and Fernandez Peris (2012); Blasco et al. (2013)
Spain	Covalejos	J	MIS 3-5	3990	RH	0.2		yes	LI	H	Yravedra et al. (2016), 2019
Spain	Cueva Des-Cubierta	3	MIS 5/4	333	RH (S.h)	25.8	yes	yes	LI, FI	H/C	Baquedano et al., 2023
Spain	EDAR Culebro 1	2 & 3		45	MA	77.7	no	yes		H	Yravedra et al. (2014)
Spain	ETB-H02		MIS 6/7	947	EL, RH (S.sp.)	2.1	no	no	LI		Yravedra et al. (2019)
Spain	Fuente Nueva 3	lower (LAL)	Early Pleistocene	1400	EL	5.8	yes	yes	LI	H/C	Espigares et al. (2013); Yravedra et al. (2021); Palmqvist et al. (2024)
Spain	Fuente Nueva 3	5	1.2 Ma		MA, RH (S.e)		yes	yes	LI	C/H	Yravedra et al., 2024
Spain	Fuente Nueva 3	upper (UAL)	Early Pleistocene	7692	EL	11.2	yes	yes	LI	C/H	Espigares et al. (2013); Yravedra et al. (2021); Palmqvist et al. (2024)
Spain	La Boella (El Forn)	1–4	0.96–0.781 Ma	736	MA, RH (S.hu)	3.1	yes	no	LI, PP	C/H	Pineda et al. (2017)
Spain	La Boella (La Mina)	Unit II level 2	0.96–0.781 Ma	578	MA	0.2	yes	no	LI, PP	C/H	Pineda et al. (2017)
Spain	La Boella (Pit)	2	1.07–0.87 Ma	164	MA	99	no	yes	LI	H	Mosquera et al. (2015)

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Table 1 (*continued*)

Country	Site	Level	Chronology	NISP	MF	%NISP MF	TM	CM	Others	Origin	References
Spain	PRERESA		MIS 5		EL		yes	yes	LI	H/C	Yravedra et al., 2012
UK	Cotte de Saint Brelade (1)	C to 6.1	MIS 6-7	1395	MA, C.a	46.2	yes	yes	LI, FI	H/C	Scott (1980), 1986; Smith (2015)
UK	Hyaena Den			1586	MA, C.a	30	yes	no		C	Currant and Jacobi (2004)
UK	Kent's Cavern			853	MA, C.a	17.4	yes			C	Campbell and Sampson, 1971 (from Smith (2015); Wragg-Sykes, 2010
UK	Little Paxton				MA, C.a					C	Wragg-Sykes, 2010
UK	Lynford		MIS 3	3498	MA, C.a	66.1	yes	no	LI	C/H?	Schreve, 2006, 2012; Smith, 2012
UK	Pin Hole	lower cave			MA, C.a		yes			C	Jenkinson, 1984; Wragg-Sykes, 2010
UK	Robin Hood Cave				MA, C.a		yes			C	Jenkinson, 1984; Wragg-Sykes, 2010
Ukraine	Halich 1		Upper Paleolithic		MA	*n = 151		no	LI, FI	H	Wojtal et al., 2001
Ukraine	Ketrosy		~100 ka	~500	MA, C.a			yes	LI, ST	H	David (1980); Demay et al. (2021)
Ukraine	Molodova I	4	MIS 3	2438	MA, C.a	84.2	yes	yes	LI, FI	H/C	Demay et al. (2012)

Column headings: Country, Site, Level, Chronology, NISP (number of identified specimens), MF (megafaunal taxa identified: EL: Elephantidae; MA: mammoth; PAL: *Palaeoloxodon antiquus*; RH: rhinoceros; C.a: *Coelodonta antiquitatis*; C.n: *Coelodonta nihowanensis*; S.h: *Stephanorhinus hemitoechus*; S.e: *Stephanorhinus etruscus*; S.hu: *Stephanorhinus hundsheimensis*; R.n: *Rhinoceros sinensis*; C.s: *Ceratotherium simum*), %NISP MF (percentage of megafaunal specimens relative to total NISP), TM (tooth marks), CM (cut marks), Others (BPR: body part representation; AS: age structure; LT: lithic industry; ST: structure; FI: fire; PR: projectile; PP: percussion pits), Origin (interpretation of accumulation origin as reported by the original authors; H: hominin, C: carnivore, H/C: hominin first and carnivore later, C/H: carnivore first and hominin later), References. (!) Indicates sites with specimens recovered during early, unsystematic excavations, with limited stratigraphic control and/or potential vertical displacement; *NISP of megafauna (MF), not to the %NISP; **accumulation's origin established based on additional contextual factors. Full bibliographic references are provided in the supplementary material.

Benot Ya'Akov (Goren Inbar et al., 1994), Ambrona (Shipman and Rose, 1983; Villa et al., 2005), Áridos 2 (Yravedra et al., 2010), La Cotte de St. Brelade (Scott, 1980, 1986; Smith, 2015), Castel di Guido (Mussi, 2005), Taubach and Gröbern (Gaudzinski-Windheuser et al., 2023).

Hyenas are capable of gnawing and consuming the fat stored within megafaunal long bones after the death of the animal. In the case of elephants across African environments, from semi-arid savannas to tropical woodlands, this process may occur one to three years post-mortem, or even longer when sheltered by vegetation or shade (Haynes and Klimowicz, 2015). Although the feasibility of hominins accessing marrow in proboscidean bones remains a subject of debate (Haynes et al., 2021), bones could be used as fuel (Perlès, 1977; Théry-Parisot et al., 2005; Glazewski, 2006), as documented in Krems-Wachtberg (Fladerer et al., 2014); as material for the construction of shelters and dwelling structures, as seen at Yudinovo (Germonpré et al., 2008) or Ketrosy and Molodova I/4 (David, 1980; Demay et al., 2012, 2021); and as tools, at several Olduvai localities, includying BK (Leakey, 1971), Beds I-IV at Olduvai (Pante et al., 2020), and The T69 Complex (De la Torre et al., 2025); or other sites such as La Polledrara (Villa et al., 1999).

Although the attention has been given mainly to the exploitation of meat, viscera, fat, and marrow from postcranial elements, skull provided access to nutrient-rich tissues during carcass exploitation by both hominins and carnivores. Thus, cranial remains of rhinoceroses and proboscideans have been identified at least at 43 archaeological and paleontological sites (Supplementary Table 1), both in cave contexts and open-air deposits, excluding assemblages where only isolated teeth are present.

When megafaunal skulls are considered in cultural contexts, their presence is typically interpreted as evidence of processing for the extraction and consumption of brain tissue and tongue. For instance, at Bolomor Cave, a *Palaeoloxodon antiquus* mandible bearing cut marks was recovered (Blasco and Fernandez Peris, 2012; Blasco et al., 2013). At Yudinovo, 37 megafaunal skulls have been found, and their fracturing patterns suggest that humans exploited them for the extraction of fresh fatty brain tissue (Germonpré et al., 2008). Similar interpretations have been proposed for other sites such as Gesher Benot Ya'Aqov (Goren-Inbar et al., 1994), Erd (Daschek, 2021), and Arago F (Chen and Moigne, 2018).

However, as noted by Haynes et al. (2020), fracturing of modern megafaunal cranial elements may also result from other non-anthropogenic factors, such as being kicked or trampled by large mammals. In addition, Diedrich (2006a, b, 2012a, b, 2013, 2015) has documented hyena consumption of megafaunal remains in non-cultural fossil accumulations, including several crania and mandibles of rhinoceros.

Given that many Pleistocene assemblages in Eurasia were accumulated by cave hyenas (*C. crocuta spelaea*), it is important to consider the morphological and behavioural distinctions between these extinct populations and modern spotted hyenas. Over the years, cave hyenas have been considered distinct from the extant spotted hyenas. Morphologically, *C. spelaea* shows shorter distal limb elements (Sauqué et al., 2017) and a less trenchant cheek tooth morphology, possibly linked to a greater reliance on scavenging rather than active hunting (Ehrenberg et al., 1938). However, as illustrated in Sauqué et al. (2017), these traits often overlap or are reversed. Nevertheless, genetic studies based on mtDNA have demonstrated that both cave and modern spotted hyenas belong to the same species (*Crocuta crocuta*), with differences reflecting regional adaptations rather than taxonomic separation (Rohland et al., 2005; Westbury et al., 2020).

In terms of behavioural ecology, direct inferences are necessarily limited. Still, Vinuesa et al. (2016) documented reduced anterior brain volumes in *C. spelaea* and *C. ultima* compared to *C. crocuta*, which may indicate less complex social structures that should be considered when assessing the bone accumulations they produced.

Having these considerations in mind, and by documenting the full

range of taphonomic modifications produced by modern *Crocuta crocuta*, the neotaphonomic data obtained in this study provides a useful comparative framework to assess the modifications observed on megafaunal cranial remains in Pleistocene Eurasian assemblages. The patterns documented in the experimental sample are consistent with many of the damage types described in fossil contexts (e.g., Diedrich, 2006a,b, 2012a,b, 2013, 2015; Schepartz and Miller-Antonio, 2010; Kotowski et al., 2020), supporting the interpretive value of the current neotaphonomic observations for evaluating carnivore involvement in the formation of archaeological and paleontological megafaunal bone accumulations.

The experimental sample reveals clear parallels with fossil assemblages in the anatomical regions most frequently targeted by hyenas during cranial exploitation. In Pleistocene assemblages where rhinoceros crania display extensive damage in the occipital and parietal regions (Fig. 7A–E, F, G), the modifications are comparable to the damage observed on Specimen R.C.01 and Specimen R.C.02. The zygomatic area is commonly consumed (Fig. 7B, C, D, E, G) and the premaxilla frequently show bone loss (Fig. 7A–G F), similarly to the five cases presented in this study.

Mandibular elements display consistent damage patterns across both modern and fossil samples (Figs. 6 and 8), with severe bone loss and edge rounding at the symphyseal region, especially in Fig. 8A1, B, and D, which are similar to specimens R.M.01, R.M.02, R.M.04, R.M.05, R.M.06 and R.M.07, reaching up the premolars. The condyles and rami appear to be more extensively consumed in the fossil record, with modification sometimes extending into the mandibular corpus (Fig. 8A1, A2, B, C) as observed in specimens such as R.M.01 or R.M.05.

The fossil record also exhibits evidence of more advanced stages of cranial destruction, often resulting in the near-complete consumption or disintegration of cranial bones. This may be related to morphological differences between modern and fossil hyena species, or to extended or

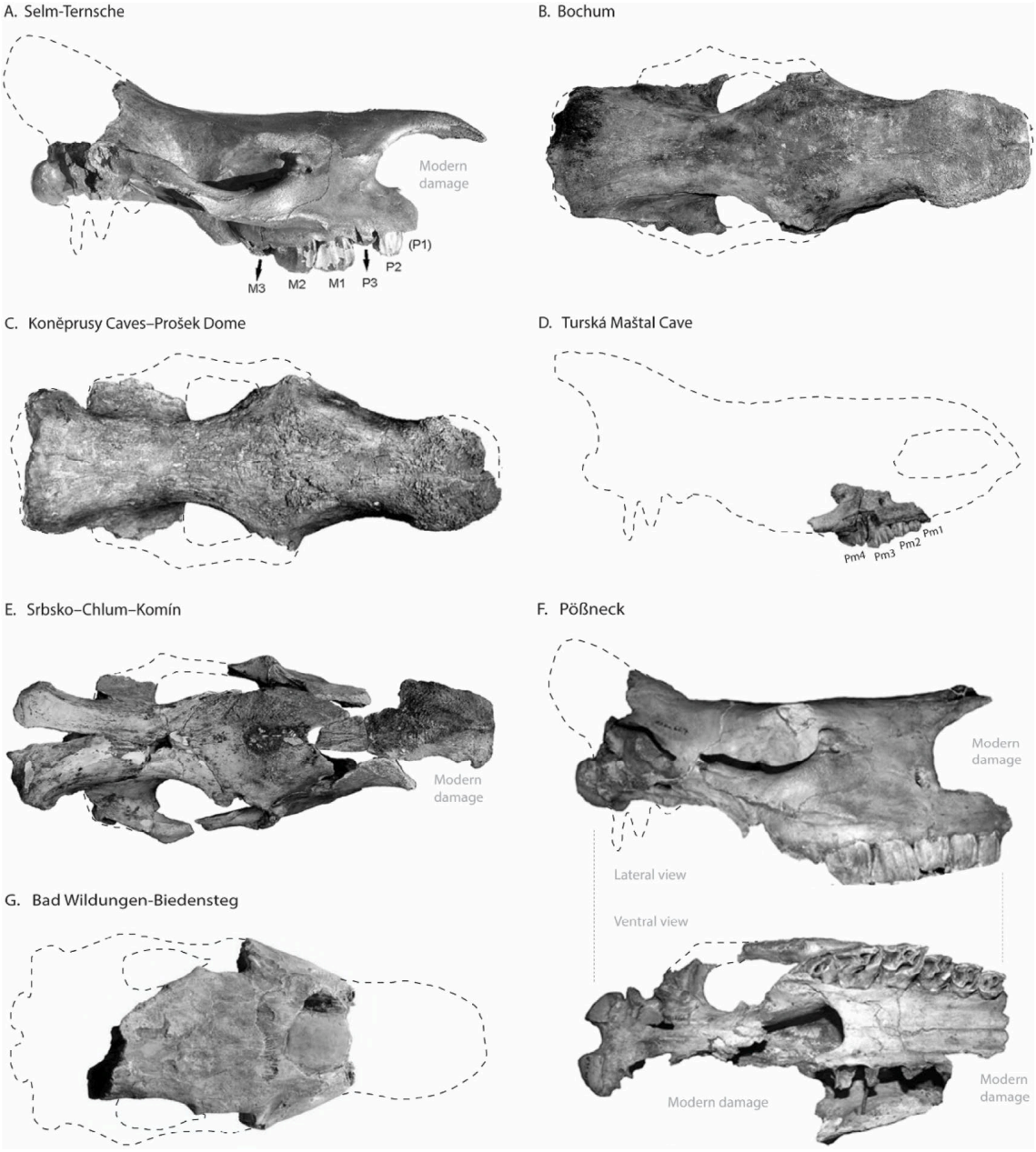

Fig. 7. Hyena-induced modifications on rhinoceros cranial remains from non-cultural assemblages extracted from Diedrich (2006a),b, 2011, 2012a,b, 2013, 2015 and 2017.

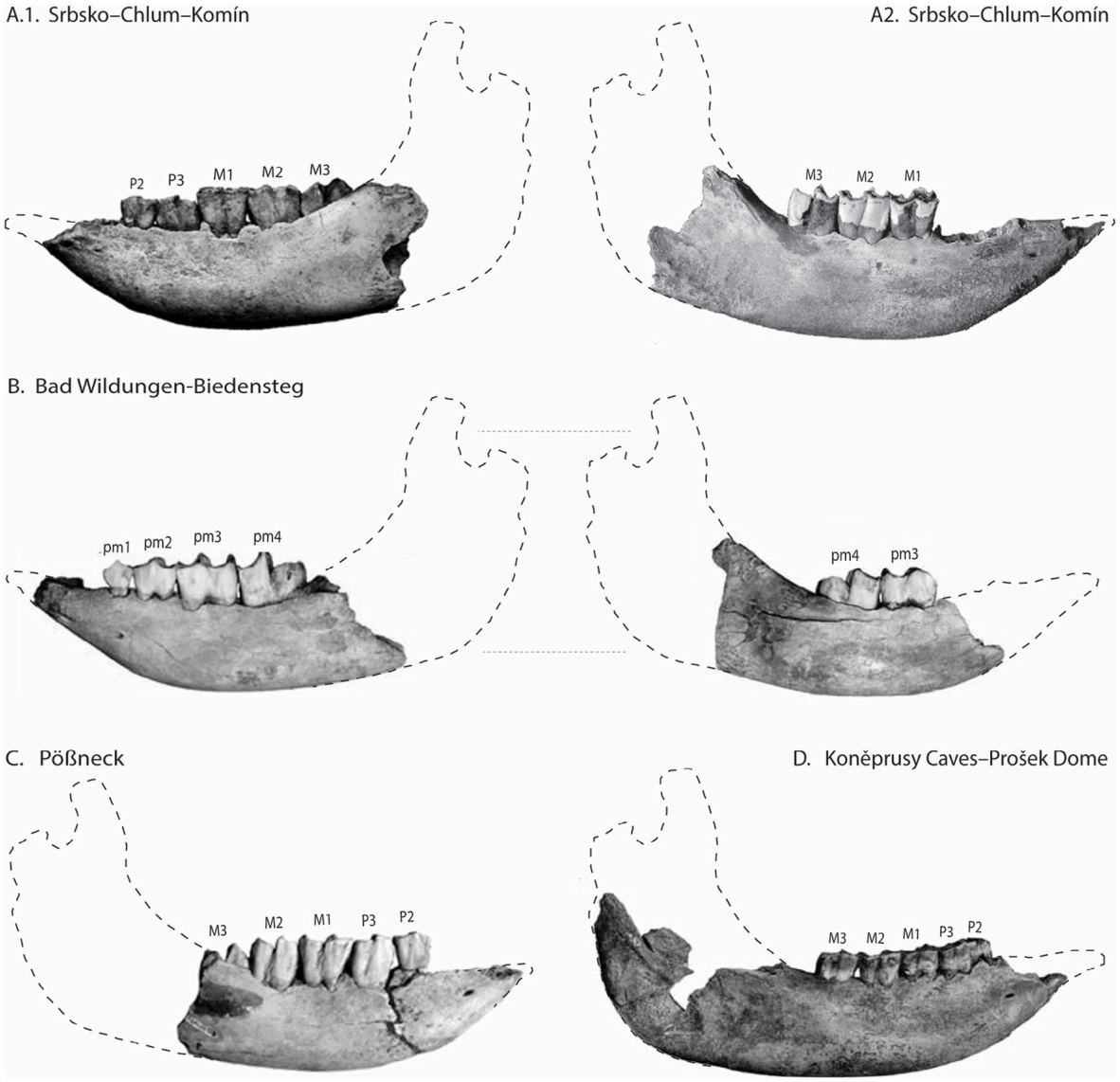

Fig. 8. Hyena-induced modifications on rhinoceros mandibles remains from non-cultural assemblages extracted from Diedrich (2006a),b, 2011, 2013, 2015 and 2017.

repeated access to megafaunal carcasses, producing in some cases, almost total fragmentation of crania and mandibular elements (Fig. 7D–G, and Fig. 8B). In contrast, the neotaphonomic sample analysed here, while showing substantial modification of specific cranial regions, does not reach the extreme levels of bone destruction documented in some fossil contexts, likely due to shorter exposure periods and more limited access by hyenas to the remains.

The present neotaphonomic study provides new reference data for understanding the modification of megafaunal cranial remains by hyenas. The observed damage modifications closely mirror many of the modifications documented in Pleistocene assemblages. Importantly, these neotaphonomic observations allow for a more precise characterization of hyena-induced modification patterns, offering a comparative framework to distinguish carnivore-generated damage from hominin processing in fossil contexts. This distinction is particularly relevant given the equifinality that often arises when both hominins and carnivores exploit similar cranial resources, such as brain tissue, sinusal fat, and mandibular marrow (Smith, 2015; Agam and Barkai, 2016; Gaudzinski-Windheuser et al., 2023). By incorporating neotaphonomic data into archaeological and paleontological analyses, this study contributes to a more accurate identification of bone-modifying agents and offers new perspectives for reconstructing hominin and carnivore subsistence behaviours, as well as the broader ecological dynamics that characterized Pleistocene ecosystems.

4.3. Feeding sequence and stages of hyena-induced cranial modification in megafaunal carcasses

The degree of modification observed on very large mammal bones often reflects the extent and duration of carnivore feeding, which can vary spatially and temporally depending on prey availability and interspecific competition (Haynes, 1980, 1982, 1991; White and Diedrich, 2012; Haynes and Klimowicz, 2015). Spotted hyenas follow a consistent feeding sequence, as described Haynes and Hutson (2020: Table 2) for selected elephant bones (i.e., scapula, humerus, radius, ulna, femur, tibia, and pelvis). In Stage 1, initial gnawing produces tooth marks and ragged edges. Stage 2 involves moderate gnawing, with epiphyses exhibiting increasing crenulation. During Stage 3, feeding intensifies, resulting in deep furrowing, diaphyseal breakage, and near-destruction of major joints. Finally, Stage 4 represents the advanced consumption and fragmentation phase, leaving only scattered, heavily tooth-marked fragments of bone.

Table 2
Proboscidean and rhinoceros bone damage types which can be divided in five stages for cranial bones.

		Stage 1	Stage 2	Stage 3	Stage 4	Stage 5
Rhinoceros	**Cranium**	Superficial scores and pits in premaxillae and maxillae	Maxillae and cornis furrowed, protruded surfaces tooth marked	Furrowing and partial bone loss of zygomatic bones, nuchal, and parietal crests. Crenulated edges	Crests and posterior cranium chewed, zygomatic bones and maxilla consumed. Crenulated edges	Near-total breakdown of facial/posterior cranium
	Mandible	Initial modification of symphysis mandibulae. Condyle/process and angulus mandibulae with tooth marks	Chewing of the symphysis and initial furrowing of the projected structures	Intense furrowing in postglenoid grooves and coronoid processes and corpus tooth marked	Symphysis and condylar area absent. Ramus completely chewed. Crenulated edges	Near-total breakdown of ramus and corpus
Proboscidea	**Cranium**	Light scoring in maxilla and processus nasalis	Tooth marks and initial furrowing in zygomatic bones and processus zygomaticus and occipital areas.	Furrowing and bone loss in occipital condyles, fossa pterygoidea, maxilla and incisive bone	Advanced furrowing in condilus occipitalis, maxilla, and incisive bone	Structural breakdown of the posterior cranium, furrowing in structurally prominent regions
	Mandible	Pars incisiva and joint areas tooth marked	Increased numbers of scores and pits in ramus and corpus mandibulae. Initial furrowing	Chewing of caput mandibulae and condylar processes. Crenulated edges	Symphysis and ramus mandibulae near-total chewed. Crenulated edges	Advanced furrowing, only the horizontal ramus remains

Similar occurred for rhinoceroses' same skeletal elements, with a simpler three-stage framework proposed by Diedrich (2012b: fig. 20B): Stage 1 shows limited gnawing at proximal or distal epiphyses, in Stage 2 one epiphysis is lost through heavy chewing, and in Stage 3 only the diaphysis with jagged and irregularly broken ends remains.

The cranial and mandibular modifications documented in this study, together with the taphonomic analyses available for those archaeological and paleontological sites with studied cranial remains included in this work, reveal a structured sequence of skull exploitation by spotted hyenas, progressing through five stages of increasing intensity (Table 2; Fig. 9). Building upon previous models that defined consumption stages for long bones, scapula, and pelvis, this study extends the framework to skull remains by integrating neotaphonomic observations from free-ranging hyenas with published fossil evidence, filling a gap in current taphonomic research. Elements assigned to advanced modification stages often retain traces of the alterations characteristic of preceding stages.

In Stage 1, comparable to the low-intensity consumption category, alterations affect accessible and fragile regions such as the pars incisiva and symphysis mandibulae, typically displaying superficial scores and isolated pits, indicating superficial interaction. Specimens E.C.02, E. M.04, and R.M.07 from the neotaphonomic study would fall within

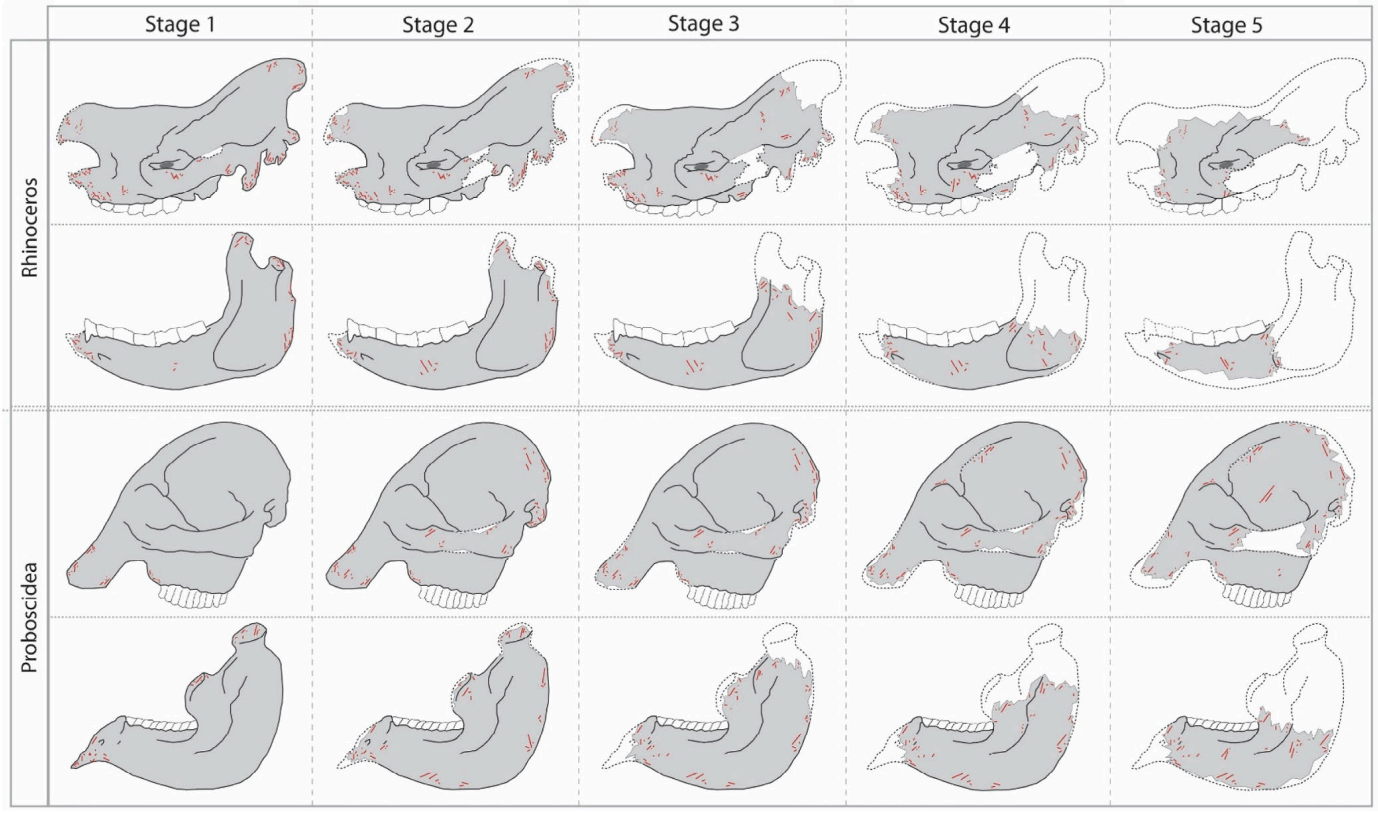

Fig. 9. Proboscidean and rhinoceros bone damage types which can be divided in five stages for cranial bones. Red lines represent the most probable location of tooth marks, reconstructed from the observations in this study and from the comparative literature reviewed herein. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

stage 1. Stage 2, comparable to the moderate consumption category, is characterized by tooth marking and initial furrowing focused on muscle-rich or structurally weaker zones, such as the zygomatic bones, symphysis, and condyles (Fig. 9). Examples of stage 2 include specimens E.C.01, R.C.05, R.M.02, and R.M.03 from this study.

Stage 3, comparable to the intermediate consumption category, reflects intensified processing, with cranial modifications extending to more robust zones and, in mandibles, involving destruction of joints and fracturing of protruding portions to access marrow, grease, or soft tissues (Table 2). Specimens E.M.05, R.C.04, and R.M.06 from the Neotaphonomic sample would be representative examples of stage 3, as well as the cranium from Selm-Ternsche and Srbsko-Chlum-Komín (Fig. 7A–E). The cranium from PöBneck shows characteristics from stage 2 and 3 (Fig. 7F).

Stage 4, comparable to the advanced consumption category, involves loss of cranial robustness due to near-complete structural breakdown of the facial and posterior cranium in rhinoceroses (Fig. 9). In mandibles, severe chewing with loss of mandibular projected structures is observed. From this study, specimens E.M.02, R.C.03, R.M.04, and R.M.05 illustrate how a single sample may display features corresponding to more than one stage, showing characteristics of both stage 3 and stage 4. This also occurred in the craniums from Bochum and Koněprusy Caves-Prošek Dome (Fig. 7B and C). In contrast, E.M.01, E.M.03, R.C.01, R.C.02, and R.M.01 and all the mandibles shown in Fig. 8 are best classified as stage 4.

Finally, Stage 5 encompasses advanced consumption stages, marked by pronounced nibbling and furrowing on elephant crania, and near or complete destruction of rhinoceros cranial bones (Table 2, Fig. 9), together with almost total consumption of the ramus and corpus mandibulae. The only specimen from the neotaphonomic sample exhibiting characteristics of both stage 4 and stage 5 is E.C.03. Stage 5 stage was not directly observed in the present study but is inferred from comparative analyses of damage modifications described in non-cultural assemblages, particularly in relation to rhinoceros cranial remains as previously documented (e.g., Tong, 2001; Moigne et al., 2006; Goren-Inbar et al., 1994; Diedrich, 2006a,b, 2012b, 2013, 2014; Schepartz and Miller-Antonio, 2010; Agam and Barkai, 2016). The crania from Turská Maštal Cave and Bad Wildungen-Biedensteg are two such examples documented in the literature (Fig. 7D–G).

The anatomical location and severity of modifications vary between taxa, particularly in Stages 3–5. Elephant remains exhibit more frequent damage in the temporomandibular and pterygoid regions, whereas rhinoceros crania show greater alteration of the nuchal and facial crests. These differences may reflect contrasts in cranial robustness and soft tissue distribution, influencing hyena feeding behaviour and carcass processing strategies. Altogether, the progressive modification patterns observed emphasize both the dietary specialization of hyenas and their ability to exploit highly resistant skeletal elements.

5. Conclusion

This study provides new neotaphonomic data on cranial modification patterns produced by free-ranging spotted hyenas (*Crocuta crocuta*) on modern elephant (*Loxodonta africana*) and rhinoceros (*Ceratotherium simum*) remains from Timbavati Private Nature Reserve, South Africa. The observed sequences of damage, which complements and builds on previous similar studies, reveal a pattern of carcass exploitation, with preferential targeting of anatomical regions based on their exposure and structural properties. Progressive chewing, furrowing, cortical removal, and advanced fracturing were documented across both cranial and mandibular elements, demonstrating the capacity of hyenas to modify even highly resistant skeletal tissues when carcasses remain accessible over prolonged periods.

Prey species-specific differences in modification intensity may result from hyena feeding behaviour, as well as from contrasts in cranial bone density, tissue distribution, and body size, with rhinoceros exhibiting greater destruction than those of elephants possibly due to lower structural resistance. Expanding neotaphonomic research to include megafauna and cranial elements, particularly under natural conditions with free-ranging animals, provides a valuable comparative framework for distinguishing carnivore and hominin modifications in fossil assemblages, ultimately improving our ability to reconstruct the taphonomic histories of Pleistocene megafaunal bone accumulations.

CRediT authorship contribution statement

Clara Mielgo: Writing – original draft, Project administration, Methodology, Investigation, Funding acquisition, Data curation, Conceptualization. **Sorina Venter:** Writing – review & editing, Resources, Investigation. **Almero Bosch:** Writing – review & editing, Supervision, Resources. **Rosa Huguet:** Writing – review & editing, Validation, Supervision, Resources. **Jan A. Venter:** Writing – review & editing, Supervision, Resources, Project administration.

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.jas.2025.106458.

Data availability

All data are contained within the submission.

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