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Elucidating the use of rhinoceros teeth by Neanderthals: Between experiments and the fossil record

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ABSTRACT

The use of faunal remains as tools by Neanderthals has long intrigued researchers. These remains include mammal teeth, which are particularly durable and resistant. Nevertheless, there is a significant gap in taphonomic analysis of dental remains, and archaeological experiments with tooth tools remain scarce. Recent studies suggest that Paleolithic groups may have used rhinoceros teeth as tools. This work seeks to elucidate this question by applying a multidisciplinary approach, including taphonomic and traceological analyses using various microscopic imaging techniques. We applied this approach to several rhinoceros teeth from key archaeological, paleontological, and contemporary collections. For the first time, we also set up controlled archaeological experiments on rhinoceros teeth. The results shed light on the potential role of rhinoceros teeth as versatile tools during the Middle Paleolithic in Western Europe and contribute to our understanding of Neanderthals' adaptive subsistence strategies and material culture.

1. Introduction

Sparse occurrences of bone tools have been recorded in the Lower Paleolithic in Eurasia (Stout et al., 2014; Rosell et al., 2015; Van Kolfschoten et al., 2015) and Africa (Pante et al., 2020; Sano et al., 2020; Hanon et al., 2021), consisting of various intentionally shaped artefact types, on the one hand, including bifaces or bone scrapers, and other elements used as expedient tools, on the other (Soressi et al., 2013; Boschian and Saccà, 2015; Julien et al., 2015; Moigne et al., 2016; Santucci et al., 2016; De La Torre et al., 2025; Parfitt and Bello, 2026). However, bone tools are much more widespread during the Middle Paleolithic, in particular with the expansion of the use of bone retouchers in various regions (Vincent, 1993; Patou-Mathis, 2002; d'Errico and Henshilwood, 2007; Mallye et al., 2012; Daujeard et al., 2014; Doyon et al., 2018; Hutson et al., 2018; Mateo-Lomba et al., 2019; Alonso-García et al., 2020; Baumann et al., 2020; Martellotta et al., 2020). Most of these tools are made on ungulate long bone shaft fragments, mainly selected from butchery remains. On rare occasions, Neanderthals made tools from other anatomical elements, such as antlers or teeth (Patou-Mathis, 1993, 1994, 2002, 2004; Patou-Mathis and Schwab, 2002; Abrams, 2018; Neruda and Lázničková-Galetová, 2018; Rendu et al., 2023), and from other species, such as carnivores, or even Neanderthal remains (Auguste,

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2002; Verna and d'Errico, 2011; Jéquier et al., 2012; Abrams et al., 2014; Serangeli et al., 2015; Rougier et al., 2016). However, only a few examples appear to derive from an intentional and specific *chaîne opératoire* (Patou-Mathis, 2002; Daujeard et al., 2014, 2018b; Abrams, 2018).

During the last two decades, the development of innovative technologies, including scanning electron microscopy (e.g., Mallye et al., 2012; Blasco et al., 2013; Van Kolfschoten et al., 2015), CT (e.g., Neruda and Lázničková-Galetová, 2018; Bello and Galway-Witham, 2019), confocal microscopy (e.g., Samper Carro, 2022; Ibáñez et al., 2019), focus variation microscopy (Bello and Galway-Witham, 2019), and geometric morphometrics (Kolobova et al., 2020), has enhanced our knowledge of the macromorphometric and micromorphometric characteristics of bone/teeth surface modifications. Analyses with these new techniques have brought to light the possible use of teeth as tools, which could be part of the *chaîne opératoire* of Paleolithic groups. However, one of the significant challenges the researchers are facing in this field is the lack of a standardized methodological protocol. Currently, as a result of the use of varying analytical techniques, magnifications, and trace descriptions, it is extremely difficult to compare data and replicate experimental works or analysis. Furthermore, taphonomic analyses of dental remains are scarce compared to postcranial bones, and little is known about how biological agents (such as humans with stone tools) or natural postdepositional processes alter tooth components (cementum, enamel, and dentine). Additionally, the identification of tooth tools in archaeological contexts is subject to debate as traces can be confused with marks generated by carnivores (Fisher, 1995; Blumenschine et al., 1996; Domínguez-Rodrigo and Piqueras, 2003; Fernández-Jalvo and Andrews, 2016; Bello and Parfitt, 2023; Parfitt and Bello, 2024), root vermiculation (Binford, 1981), and trampling (Blasco et al., 2008; Fernández-Jalvo and Andrews, 2016), which are common modifications in the archaeological and paleontological record.

In the Middle Paleolithic site of Payre (MIS 7-6) in Ardèche (France), a high proportion of isolated rhinoceros teeth (91% of the rhinoceros remains from the species *Stephanorhinus kirchbergensis* and *Stephanorhinus hemitoechus*) in relation to postcranial remains was observed. The recent revision of these elements revealed marks that have been associated with anthropogenic activity, suggesting an intentional transport and exploitation of rhinoceros teeth by Neanderthals (Daujeard et al., 2018a). In addition to Payre, only two other cases of the probable use of rhinoceros teeth by Paleolithic groups are known: at La Caune de l'Arago (in level F, ca. 400 ka), a cave with *S. hemitoechus* remains in south-western France (Chen and Moigne, 2018), and in Panxian Dadong (Guizhou province), a cave with *Rhinoceros sinensis* remains in Southern China (ca. 300–130 ka) (Miller-Antonio et al., 2000; Schepartz and Miller-Antonio, 2010a, 2010b). At La Caune de l'Arago, the teeth (40% of the rhinoceros remains) are highly fragmented. Chen and Moigne (2018) suggested that these fractures may have occurred nonintentionally during meat and grease extraction processes or that they may have been intentionally produced for secondary utilization for nonfood purposes. At Panxian Dadong, Miller-Antonio et al. (2000) suggest that the high number of isolated dental remains (74% of the rhinoceros remains) is due to the intensive and selective collection of these elements by hominins to obtain large enamel fragments to produce enamel flakes. These examples could attest to the specialized recovery of rhinoceros dental remains by Middle Pleistocene hominins for nonfood purposes and their use in percussive activities on hard and sharp materials. This behavior may also have occurred in other rhinoceros assemblages with a high ratio of isolated dental elements, where taphonomic studies have not yet been carried out from this perspective.

Although small- and medium-sized ungulates generally predominated in the Neanderthal diet, these humans also focused on megafauna, such as rhinoceros (e.g., Bocherens et al., 2005; Bocherens, 2011). Their presence and the evidence of their consumption and exploitation, including the production of bone tools, are documented at a considerable number of Middle Paleolithic contexts (such as Auguste et al., 1998; Bratlund, 1999; Smith, 2015; White et al., 2016; Wiβing et al., 2016; Daujeard et al., 2018a; Chen and Moigne, 2018; Luret et al., 2020; Martisius et al., 2020; Abrams et al., 2025). However, to date, no unequivocal evidence has been documented that directly links rhinoceros teeth to intentional anthropogenic modification or their systematic use as raw materials. Notably, the recurrent presence of rhinoceros remains, and specially isolated teeth, has raised questions regarding acquisition strategies: hunting with planned exploitation strategies vs. scavenging (Guérin, 1972, 1980; Guérin and Faure, 1983; Griggo, 1995; Auguste et al., 1998; Gaudzinski et al., 2005; Louguet-Lefebvre, 2005; Villa et al., 2005; Gaudzinski-Windheuser and Kindler, 2012; Santucci et al., 2016; White et al., 2016; Daujeard et al., 2018a; Baquedano et al., 2023; Gaudzinski-Windheuser et al., 2023; Villaescusa et al., 2026).

This work aims to elucidate these research questions and bridge the gap in the taphonomic analysis of dental remains by describing and identifying the origin of the diverse marks that can occur on rhinoceros teeth after the animal's death. For this purpose, rhinoceros dental remains from 16 archaeological and paleontological sites in Western Europe were revised and compared with 1) teeth used as tools by humans as part of controlled experiments, 2) teeth subject to experimental abrasion and sediment compaction tests to characterize these postdepositional alterations, and 3) contemporary rhinoceros teeth to distinguish between premortem and postmortem alterations.

This work is the first multidisciplinary in-depth research on this topic, carried out by different specialists in zooarchaeology, taphonomy, lithic industry, dental wear, and microscopic analysis in order to provide a complete taphonomic analysis of the rhinoceros teeth and a detailed description of the different marks, as well as illustrations with magnified images. Within this broader framework, the presence of rhinoceros teeth in archaeological assemblages could provide key insights into Neanderthal subsistence practices and site-use patterns.

2. Materials

2.1. Archaeological materials

Here, we examine 12 Middle Paleolithic sites spread across Spain and France. The criteria for site selection were well-known contexts and chronologies with faunal assemblages (preferably with abundant isolated rhinoceros teeth), produced primarily by human activity. These archaeological sites are (Fig. 1) El Castillo (number of identified specimens [NISP] analyzed = 202) (Castaños, 2018), Abric Romaní (NISP = 44) (Marín et al., 2017), Cueva Antón (NISP = 11) (Zilhão et al., 2016; Sanz et al., 2019), and level TD10 of the Gran Dolina in Atapuerca (NISP = 118) (Rodríguez-Hidalgo et al., 2015) in Spain and Pech-de-l'Azé II (NISP = 79) (Uzunidis-Boutillier, 2017), Le Moustier (NISP = 3) (Gravina et al., 2015), La Ferrassie (NISP = 4) (Bertran et al., 2008), Combe Grenal (NISP = 6) (Delpech and Prat, 1995), Rigabe (NISP = 5) (Uzunidis-Boutillier, 2017), Grotte Vaufrey (NISP = 1) (Delpech, 1989), Gatzarria (NISP = 1) (Ready, 2013), and La Pronquière (NISP = 1) (Coulonges and Lansac, 1954) in France.

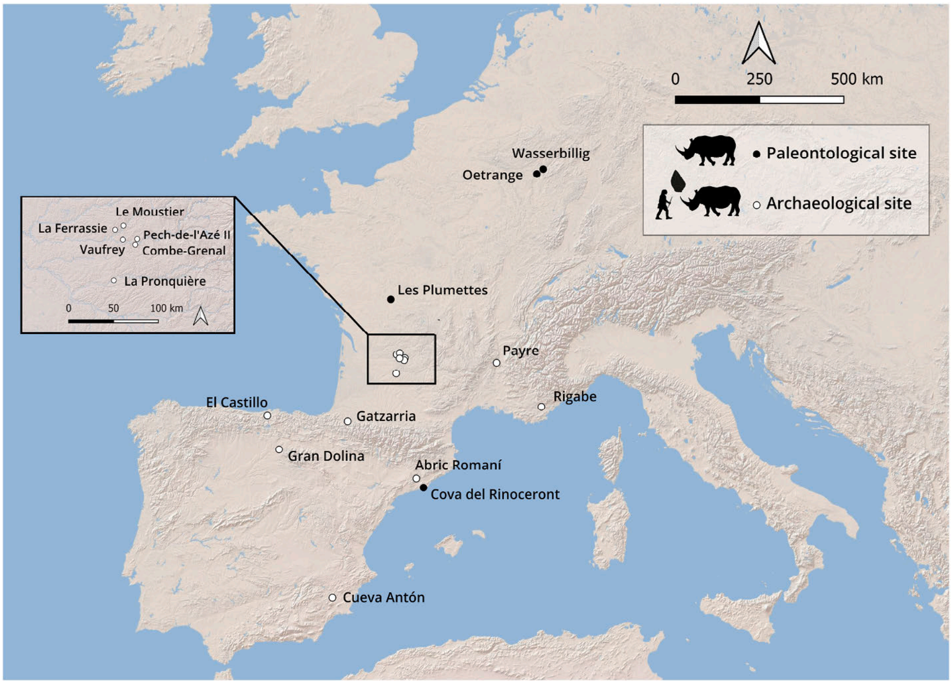


Figure 1. Location of the archaeological and paleontological sites studied in this work. Map created using QGIS 3.40.6, basemap data ESRI (Environmental Systems Research Institute). (For interpretation of the references to color in this figure, the reader is referred to the web version of this article.)

Of all these sites, only two—El Castillo and Pech-de-l'Azé II (detailed in the Supplementary Online Material [SOM] Information)—displayed particular fractures and recurrent enamel removal marks on rhinoceros tooth surfaces. Therefore, the taphonomic analysis focused on a total of 281 teeth from these two sites. In contrast, the other sites contained recurrent isolated rhinoceros tooth fragments, but without the specific aforementioned repeated marks. Therefore, they are not described in the results or discussion section. Table 1 shows the archaeological teeth analyzed in this work.

2.2. *Comparative materials*

Rhinoceros dental remains from several paleontological contexts (or with very little evidence of human presence), as well as contemporary osteological collections, were studied to provide a frame of reference for comparing our results. The selected paleontological sites span a diverse chronological range and comprise different geological and sedimentary contexts with various accumulation agents (from natural origin to carnivore accumulations) and therefore provide good references for

Table 1
Minimum Number of Individuals (MNI) and Number of Remains (NR) of rhinoceros teeth from the different collections analyzed in this work: archaeological sites, paleontological and contemporary comparative remains, and experimental materials.

Collection	Level	Sublevel	MNI	Upper teeth	Lower teeth	Total teeth
				NR	NR	NR
El Castillo (Spain)	Acheulean		7	3	16	19
	Mousterian	Alpha	25	62	81	143
		Beta	9	17	20	37
	Aurignacian	Delta	1	3		3
Subtotal			**42**	**85**	**117**	**202**
Pech-de-l'Azé II (France)	6		2	2	1	3
	7		6	13	17	30
	6–7	B	2	2	2	4
		C	2	4	1	5
	8		4	11	10	21
	9		2	7	9	16
Subtotal			**18**	**39**	**40**	**79**
Total archaeological materials			**60**	**124**	**157**	**281**
Wasserbillig (Luxembourg)	B		9	52	50	102
Oetrange (Luxembourg)	–		2	1	8	9
Cova del Rinoceront (Spain)	III		4	7	4	11
Plumettes (France)	II, IV		6	23	23	46
Total paleontological materials			**21**	**83**	**85**	**168**
Total Salle d'Anatomie Comparée (France)			**17**	**97**	**139**	**236**
Total experimental materials			**3**	**11**	**7**	**18**

postdepositional modifications and alterations on teeth. These materials include a total of 168 rhinoceros dental remains from four Western European Pleistocene paleontological sites (Fig. 1), briefly presented in the SOM Information: Wasserbillig (Luxembourg), Oetrange (Luxembourg), Cova del Rinoceront (Spain), and Plumettes (France). In order to establish a frame of reference of the alterations that can affect rhinoceros teeth throughout their lifetime, we also analyzed 236 teeth from the comparative collection of the Salle d'Anatomie Comparée from the Muséum National d'Histoire Naturelle (MNHN) in Paris (France). Table 1 shows the comparative teeth analyzed in this work.

2.3. *Materials from the experiments*

Obtaining rhinoceros teeth for the experiments proved to be an extremely difficult but indispensable exercise for this study. The use of other ungulates would not have been appropriate due to the unique structure and exceptional hardness of rhinoceros teeth (Fortelius, 1985; Teaford et al., 2000).

For the archaeological experiments developed in this work, we used 18 isolated contemporary white rhinoceros teeth (*Ceratotherium simum*) (11 upper/seven lower) (Table 1) provided by three French zoos: Safari de Peaugres, Réserve Africaine de Sigean, and the Montpellier Zoo. One knapper (D.P.) reproduced several gestures related to retouching, knapping, and the use of teeth as anvils with 19 Cretaceous quartz and flint lithic tools from France (for more details on the teeth and lithics used in the experiments, see the SOM Tables 1 and 2). The whole activity was recorded by three supervisors (A.S.-R., D.V., and C.D.). Additionally, a taphonomic experiment was conducted using three rhinoceros teeth (#RZM-002, #RZP-001, and #RZS-008) to simulate the effects of abrasion and compaction by sediment.

3. Methods

3.1. *Methodology applied to the analysis of rhinoceros teeth (archaeological, paleontological, and contemporary collections)*

Taxonomic identification was carried out according to Guérin (1980), Lacombat (2003), and Uzunidis-Boutillier (2017). For the nomenclature of the dental areas of the cheek rhinoceros teeth, we followed Antoine et al. (2010). Ontogenic age-at-death is based on dental eruption and replacement patterns, as well as tooth wear (Hitchins, 1978; Garutt, 1992, 1994; Forsten and Moigne, 1998; Tong, 2001). Length, breadth, and thickness were recorded with digital calipers.

We investigated dental microwear features associated with the mastication of phytoliths, as well as dust and grit contained in plants (Fox et al., 1994; Semprebon et al., 2004, 2011; Lucas et al., 2013; Ungar, 2015; Gallego-Valle et al., 2020) from the archaeological and paleontological collections, to rule out mastication as the cause of the observed marks. The presence or absence of these dietary marks in the traces confirms whether the removals were produced premortem or postmortem. For this purpose, the removal scars were cleaned with 96% ethanol and molded with high-resolution silicone (vinyl polysiloxane). Transparent casts were made using clear epoxy resin and analyzed using a stereomicroscope (Nikon SMZ 1500) at 35× magnification. The microtraces were classified into the following categories: pits (circular or subcircular scars), scratches (elongated microfeatures with straight and parallel sides), and gouges (larger than pits and with irregular edges), following Solounias and Semprebon (2002) and Semprebon et al. (2004). Microtraces related to trampling processes, sediment pressure, or chemical alterations were also identified morphologically according to the descriptions of Uzunidis et al. (2021) and Micó et al. (2024a, 2024b).

An exhaustive taphonomic analysis of the teeth was carried out. The state of preservation of the dental surfaces is considered to be good when the entire surface is preserved, medium when at least half of the observable surface is preserved, and poor when less than half or none of the surface is observable. We consulted a specialized bibliography to help us identify, describe, and compare the traces (Binford, 1981; Vincent, 1993; Tartar, 2009; Mallye et al., 2012; Mozota, 2013; Daujeard et al., 2014; Fernández-Jalvo and Andrews, 2016; Vettese et al., 2020; Martellotta, 2023). We followed the proposal of Téllez et al. (2022) for thermoalterations, and the identification of fracture types (fresh, dry, or recent) was based on dental fracture shapes, features, and angles. Due to the absence of specialized literature on tooth fractures, we considered the work of Pittard (1935), as well as that of Villa and Mahieu (1991) for bone fractures. Regarding non-anthropogenic modifications, we also distinguished between alterations produced by carnivores, as well as natural postdepositional modifications including root vermiculation, bacterial activity, weathering, polish, abrasion, concretion, chemical corrosion, and manganese (Behrensmeyer, 1978; Potter and Rossman, 1979; Binford, 1981; Fisher, 1995; Blumenschine et al., 1996; Domínguez-Rodrigo and Piqueras, 2003; Fernández-Jalvo and Andrews, 2016, among others). All teeth were observed with the naked eye and with a 10× hand-lens under high incident light. When necessary, we used a portable digital microscope (Dino-Lite AM4515ZT, from 20× to 200×) and a stereomicroscope (Leica S8 APO).

3.2. *Methodology applied to the experiments*

Archaeological experiments The experiments took place at *L'archéosite de la Haute-Île* (Paris, France) with the main objective of reproducing the traces observed in the archaeological record. One knapper reproduced the gestures, and three supervisors, specialists in zooarchaeology and taphonomy, observed and documented the activity. The teeth and lithic tools were photographed before, during, and after experiments, and the whole activity was recorded by a camera. Particular attention was paid to the relationship between the characteristics of the traces produced during percussive activities and the raw materials involved, the position of the hands, the type of action (direct percussion, anvil techniques, etc.), and tool orientation (i.e., Castel et al., 2003; Mallye et al., 2012; Tartar, 2012; Mozota, 2013; Kolobova et al., 2022; Micó et al., 2024c; Parfitt and Bello, 2024a, among others). We used two different raw materials, quartz and flint (based on their presence in the archaeological record), and performed three main activities following different tooth orientations: retouching (tangential gesture), knapping (re-entrant gesture), and the use of teeth as anvils (Fig. 2). Gestures were mainly reproduced on the upper part of the crown and between the lingual and buccal sides to produce modifications on the occlusal surface while generating flakes or retouching flakes (continuous retouch). In total, 31 percussive activities on 15 rhinoceros teeth were carried out: Five teeth were used to retouch quartz, two to retouch flint, and four to knap flint; six teeth were knapped using a quartz percussor to obtain enamel flakes, as referenced in some works (Miller-Antonio et al., 2000); 10 teeth were used as anvils using quartz ($n = 8$) and flint ($n = 2$) tools against the occlusal surface to cut vegetal fibers and leather; and finally, three teeth were used to remove cementum and roots (a detailed description of the activities can be consulted in SOM Table 4). Given the limited knowledge of the use of rhinoceros teeth, we also explored the most comfortable and advantageous ways to use the teeth during these activities. The activity was stopped when traces developed, when the intended tool was produced, or when tooth breakage occurred.

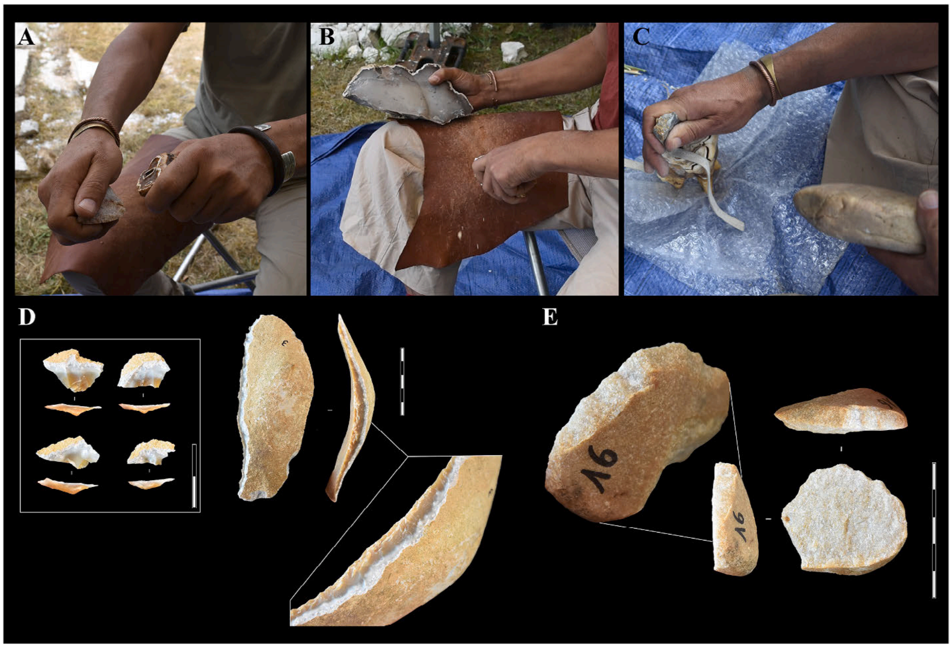


Figure 2. Example of the activities carried out in the archaeological experiments and the associated products. A–C: percussive activities reproduced in this work: A) retouching quartz; B) knapping flint; C) tooth as an anvil with quartz flake. D–E: Lithics used for this work: D) Flint flake retouched with a rhinoceros tooth and retouch flakes (Lithic n°3); E) quartz flake (Lithic n°16) retouched with a rhinoceros tooth. (For interpretation of the references to color in this figure, the reader is referred to the web version of this article.)

Taphonomic experiments The taphonomic experiments aimed to simulate the effects of abrasion and compaction on rhinoceros teeth and were carried out in the Laboratory of Environmental Analyses and Taphonomy of Madrid (Spain). The abrasion test was simulated using two rotors with the same sediment on three selected rhinoceros teeth (SOM Fig. 1). The sediment was provided by the Laboratory of Environmental Analyses and Taphonomy and collected from a semiarid area in Santaolalla (in Toledo, Spain) with nearby trees. It was composed of clay, silt, and sand and is similar to the sediment from numerous Paleolithic caves, such as El Castillo. The grain size distribution was 70 ml of sediment smaller than 1 mm, 20 ml between 1 and 2 mm, and 10 ml larger than 2 mm. In addition, 150 ml of distilled water was also added to the sample. All the teeth were separated from each other to avoid tooth-to-tooth contact. The aim was to continue the abrasion test until traces were produced on the teeth, for a maximum of seven days in continuous movement. Descriptions and measurements were noted throughout the process, as well as daily photographic documentation of the teeth using a photographic camera and a stereomicroscope Leica DFC450 camera. The compaction test was performed to reproduce natural vertical compaction by the same sediment surrounding the tooth. For this purpose, the Zwick/Roell Z2.5 machine applied a vertical force of 5 KN and a speed of 30 mm/min on a selected lower molar (#RZM002) (SOM Fig. 1) in order to deform 50% of the tooth.

Confocal microscope image acquisition The confocal microscope (Sensofar S Neox 3D optical profilometer) from the Institut Català de Paleoecologia Humana i Evolució Social (Tarragona, Spain) was used to characterize and differentiate the traces generated on the teeth, as well as to produce three-dimensional image reconstructions. The SensoSCAN software (Sensofar Tech, https://www.sensofar.com/metrology/industry-research/sneox/software/) scanned the tooth surfaces with magnifications ranging from 5× to 20× (numerical aperture from 0.15 to 0.45, working distance from 20 to 3 mm). The SensoVIEW analysis software was also applied during this process. Surface roughness measurements were carried out by S-L filtration by eliminating small- and large-wavelength components. Surface acquisitions were reviewed, and 'Restore' processing was applied to fill in empty spots when the measured data were <95%. The 'removal' shape made it possible to flatten the surface, and the aberrant points were corrected manually by a despiking filter.

4. Results

4.1. Analysis of rhinoceros teeth from the experiments

Archaeological experiments The reproduction of the 31 percussive activities detailed earlier clearly modified the rhinoceros tooth surfaces and produced significant traces in all but one of them (Exp. n° 12.1). The detailed description of the activities, as well as the modifications produced on each of them, can be consulted in SOM Tables 4 and 5. A total of 56 marks related to these activities were identified, 42 of which (75%) were macroscopically visible, while 14 (25%) were identified with the help of the confocal microscope.

Based on the methodology developed in this work (an evaluation of the applied methodology is available in the SOM Information), we have identified and classified the following marks as modifications related to percussive activities:

- **Scaled areas:** These are the superposition of small irregular fractures or the detachment of enamel/dentine plaques of the tooth surface at the top of the crown or the occlusal surface produced by the concentrated accumulation of blows on the same area (Fig. 3A–D, F). Similar modifications have also been observed on bone retouchers (Mallye et al., 2012; Mozota, 2013). Sometimes, these fractures are more marked, with a 'stepped' morphology (Fig. 3B, C), and can also be surrounded by associated enamel/dentine fissures (tooth weaknesses that run through the different tooth layers and stop before breakage).

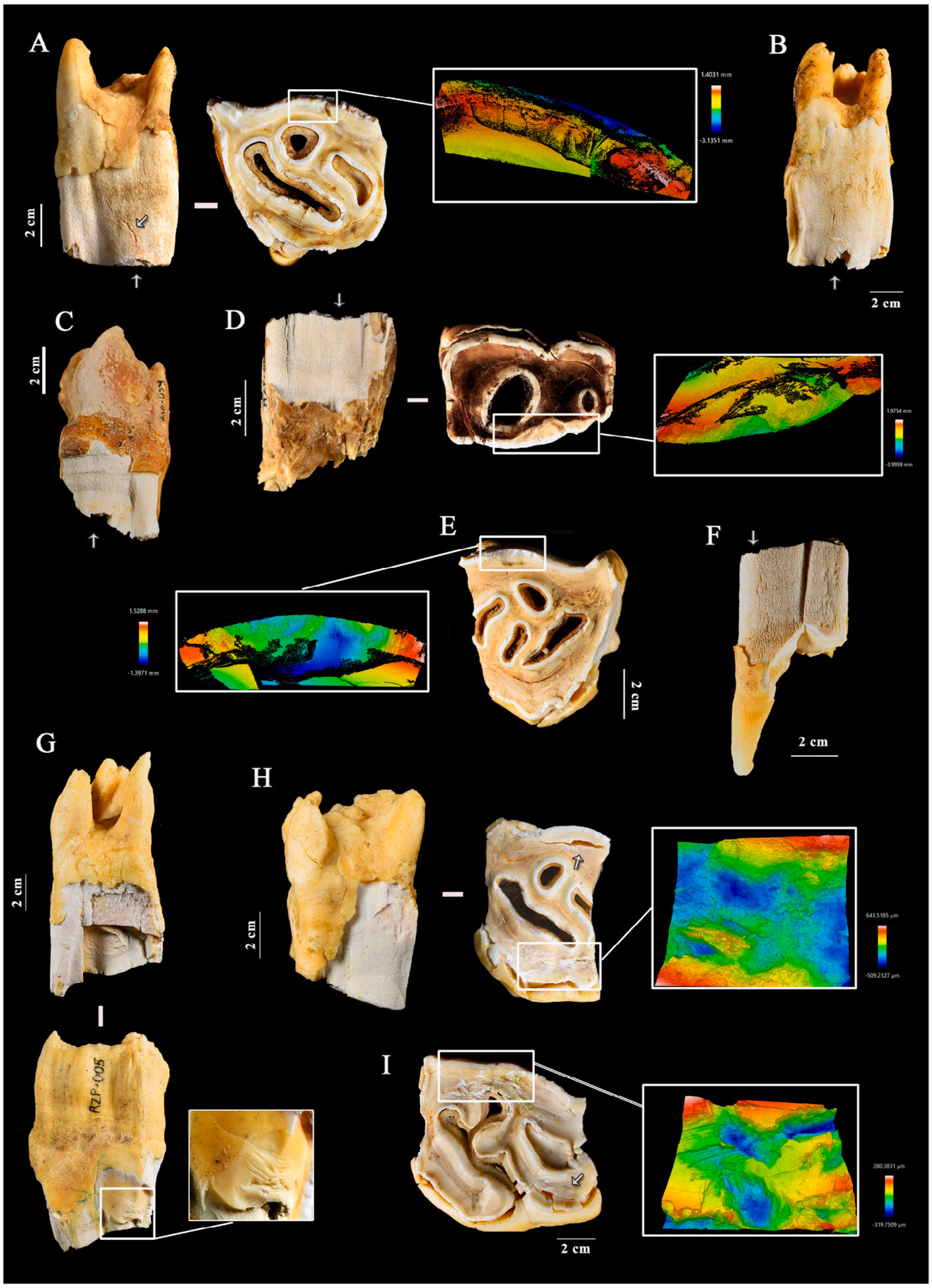


Figure 3. Modifications documented on rhinoceros teeth during the archaeological experiments and 3D reproductions with confocal microscope (3D = three dimensional). A) P^3 (#RZS002) used for quartz retouching: buccal side with groove and scaled area, occlusal view with notches and micronotches, and 3D reproduction. B) P^4 (#RZS006) used for knapping flint: buccal side with scaled area. C) Upper premolar (#RZM001): buccal side with cementum removal and scaled areas produced during flint retouching. D) P$_3$ (#RZP008) used for quartz retouching: buccal side with cementum removal and scaled area, occlusal view with notches and micronotches, and 3D reproduction. E) P^3 (#RP004) used for quartz retouching: occlusal view with notches and micronotches and 3D reproduction. F) P$_4$ (#RZS005): buccal side with fracture produced during the removal of the root and scaled area produced during flint knapping. G) P^4 (#RZP005): buccal side with fracture produced by knapping teeth with quartz percussor and sliding marks. H) P^3 (#RZP003) used as anvil with quartz: buccal side, occlusal view with pitting areas, and 3D reproduction. I) M^1 (#RZS003): occlusal view with pitting areas on the hypocone, produced by the use of tooth as an anvil with flint, and pitting areas in the paracone and metacone, produced by quartz, as well as and 3D reproduction of the pitting areas and microstriations produced with quartz. (For interpretation of the references to color in this figure, the reader is referred to the web version of this article.)

- **Pitting areas:** These are depressions located in the dentine of the occlusal area, sometimes also in the enamel, produced by the accumulation of blows in the same zone (Fig. 3H, I). They are generally shallow and grouped, similar to those observed on bone retouchers (Mallye et al., 2012), which may bear microstriations inside. The observation of these striations has been possible with the confocal microscope. They are superficial, short, and parallel, with a 'V-shaped' profile, and form when the roughness of a hammer or percussor scrubs the tooth surface. Pitting areas can also be associated with fissures or adhering enamel/dentine flakes. Sometimes, the dentine may collapse or a tooth fracture can appear.
- **Notch:** It is the enamel/dentine flake scar, normally located at the occlusal level on the buccal or lingual sides, close to scaled

areas or tooth fractures, and associated with small fissures (Fig. 3A, D, and E). Generally, a notch comprises small micronotches inside it, with different lengths and depths, grouped and lined up on the same notch orientation and separated by an angular fracture line. This mark could be comparable to percussion notch identified in long bones (i.e., Blumenschine, 1988; Vettese et al., 2020).

- **Adhering flake:** It is an enamel or dentine flake with an incomplete fracture line and is thus still attached to the tooth (i.e., Vettese et al., 2020).
- **Tooth fractures:** Fractures can be a consequence of percussive activities affecting the enamel or both the enamel and dentine (Fig. 3G, F). Unlike in bones, it is difficult to identify the angle, profile, and edge of tooth fractures since dentine and enamel behave differently when they break: The enamel shows a more irregular fracture, while dentine fractures are more similar to green bone fractures, with a smoother edge, sometimes accompanied by fissures and ripple marks (Vettese et al., 2020). When tooth fractures occur in the crown, they extend toward the roots following the morphology of the tooth and previous cracks or fissures, sometimes showing a V-shaped morphology.
- **Sliding marks:** These are shallow and thin striations, with oblique orientations and internal microstriations, resulting when the irregular edge of a lithic tool slides across the tooth surface during percussive activities (Fig. 3G). Similar traces have also been identified in bone retouchers (Daujeard et al., 2014, 2018b; Costamagno et al., 2018; Bello et al., 2021). They are observed in both enamel and dentine and are at times only clearly perceptible when viewed through the confocal microscope.
- **Grooves:** These are superficial and sinuous impressions produced by the impact of the lithic edge during blows (Fig. 3A) (Mallye et al., 2012; Daujeard et al., 2014, 2018b). They are short and isolated with an oblique orientation.
- **Cementum removal:** It is the removal of the outermost layer of the tooth covering the enamel. Removal is clean when the cementum layer is completely separated from the underlying enamel layer (Fig. 3G). This is observed in poorly preserved teeth since fissures can appear in the cementum, facilitating its natural separation. On the contrary, removal is not clean when the outermost part of the underlying enamel layer is also partially removed. For the latter, better tooth preservation impedes the separation of the cementum and enamel layers easily.

During the quartz/flint retouching activities, the most common modifications produced were scaled areas on the lingual/buccal edge (Fig. 3A, C, and D). For quartz, we also produced notches and micronotches on the occlusal surface (Fig. 3A, D, and E) and, sometimes, also grooves (Fig. 3A) and an adhering dentine flake. The number of blows required to produce these modifications varied from 10 (in less than 10 seconds) to 260 (during more than two minutes of activity). On the contrary, retouching flint did not produce notches and more blows were performed until visible modifications occurred or until the lithic tool was completed (between 250 and 460 blows per tooth with an average of 2.14 min. per experiment). The experimenter's feedback was that rhinoceros premolars were too small to grip comfortably for retouching quartz, whereas they were suitable for retouching the flint tools used. The use of lower teeth in transverse orientation (use of the mesial face) was felt to be the most comfortable.

The knapping activities produced enamel and dentine fractures in the use area, generating scaled areas (Fig. 3B, F) or larger fractures in the crown, sometimes with a 'V-shaped' morphology. These exercises did not exceed 27 blows (with an average of 40 seconds per exercise) since the activity was stopped several times because the tooth was not effective or the tooth broke during the process, causing the dispersion of numerous small enamel and dentine fragments during the activity. In addition to knapping flint, we used a quartz percussor to knap two rhinoceros premolars (one upper and one lower) to obtain enamel flakes. Six attempts were performed for this purpose, which did not produce relevant modifications on the teeth, except for some enamel and dentine fractures and sliding marks on the dentine when preparing the blow (Fig. 3G).

Ten attempts were made using upper rhinoceros teeth as anvils. Quartz and flint tools were used against the occlusal surface of the tooth to cut vegetal fibers and leather, producing similar traces in all of them, mainly pitting areas (Fig. 3H, I). However, in the case of quartz, confocal microscope analysis identified microstriations inside these depressions, whereas flint produced more circular depressions without microstriations. The teeth resisted the blows quite well (even with more than 100 blows), and the marks appeared very quickly on the dentine (once after only two blows). In general, all the exercises were considered to be effective by the experimenter, successfully cutting plant fibers and leather, although in some cases, not without discomfort, and another experimenter stepped in to facilitate the task.

In sum, the most common modifications produced were scaled areas, pitting areas, and tooth fractures (generated in 9/31 tests), followed by sliding marks (8/31) and notches (5/31) (Table 2). It is interesting to note that the experiments involving the use of quartz produced more modifications and sooner than experiments with flint. Similar but fewer marks were produced with flint, and we needed more blows to produce them. Surprisingly, the dentine resisted the blows better than the enamel, probably because it is more elastic, despite being less hard. However, we cannot rule out the possibility that this may be related to tooth preservation (some teeth showed previous fissures produced by cleaning processes, as indicated in SOM Table 1). Despite the large size of rhinoceros teeth and their considerable weight (see SOM Table 1), the experimenters' feedback maintained that in general, the teeth were suitable for achieving the stated objectives, although they noted that larger teeth and flatter areas were more comfortable, in keeping with previous works on bone and tooth retouchers (i.e., Maylle et al., 2012; Micó et al., 2024c).

Taphonomic experiments The abrasion test lasted for a total of seven full days. During the first hours of the experiment, no visible changes could be observed, either to the naked eye or with the stereomicroscope. The first visible modifications appeared after the second day of abrasion, especially rounding of the enamel on the occlusal area. After the seventh day, we decided to stop the experiment since the modifications produced were totally different to those obtained during the archaeological experiments developed in this work. The main alterations were abrasion and polishing of the more protruding parts of the teeth, but there were no enamel or dentine fractures and no notches, striations, or pitting areas, as observed after percussive activities. The modifications from the first day of abrasion to the seventh day are presented in Figure 4.

The compaction test did not produce traces similar to those obtained during the archaeological experiments or to the abrasion test. On the contrary, the lower rhinoceros tooth (#RZM-002) supported a maximum force of 1170 N before being 50% deformed, resisting vertical compaction with only a few fissures but no fractures. The sediment probably contributed in some way to protecting the teeth from fractures. However, these results must be interpreted with caution as the sample is very small.

Table 2
Modifications identified in the different collections of rhinoceros teeth analyzed in this work.

Collection	% Anthropogenic modifications								Fractures	% Nonanthropogenic modifications						
	Thermoalterations	Scaled areas	Pitting areas	Notch	Adhering flake	Sliding marks	Grooves	Cement removal		Roots	Weathering/ exfoliation	Polish/ abrasion	Concretion	Corrosion	Manganese	Trampling
El Castillo (Spain)	2	12.4		12.4					3% fresh, 1% vertical, dry		48.6–29.4			59.5–31.6	33.3–15.8	
Pech-de-l'Azé II (France)				5.6		1.4		Dry	Dry						100–90	75–70
Wasserbillig (Luxembourg)									Dry		52.1/40.8	11.3/47.9		23.9	21.1	
Oetrange (Luxembourg)									Dry						100	
Cova del Rinoceront (Spain)									Dry		75		49			
Plumettes (France)									Dry	23.9		32.6	39.1	56.5		
Salle d'Anatomie Comparée (MNHN)	–								Dry							
Archaeological experiments	–	29	29	16.1	3.2	25.8	6.5	12.9	29 % fresh							
Taphonomic experiments	–											100				

MNHN = Muséum National d'Histoire Naturelle.

4.2. *Analysis of the archaeological assemblages*

The rhinoceros teeth from El Castillo Cave (Spain) Most of the 202 *S. hemitoechus* teeth analyzed from the Obermaier collection are from the Mousterian Alpha level, followed by the Mousterian Beta, Acheulean, and Aurignacian Delta levels. Based on the NISP, the most abundant elements are permanent upper premolars and lower molars (SOM Table 3). In general, the tooth surface is well preserved. Seventeen upper and eight lower isolated teeth (12.4% of the total dental remains) revealed traces on the occlusal surface and roots that were assumed to be related to anthropogenic activity. Most of them (NISP = 22: 15 upper/7 lower) are from the Mousterian Alpha level, followed by the Acheulean level (NISP = 2: 1 upper/1 lower), and Mousterian Beta (NISP = 1: upper tooth), while no such traces were observed in the Aurignacian Delta level. In all cases, the upper teeth are more intensely modified than the lower ones. The most abundant marks are notches, observed on all the modified teeth ($n = 25$). The impact points of the notches are mainly located not only in the dentine of the occlusal area but also on the crown enamel and, more rarely, on the roots. These conchoidal marks occur between one and five times per tooth, are mainly isolated, and are only occasionally consecutive or superimposed. Sometimes, there are also scaled areas (i.e., specimens #2754 and #8557 of Figs. 5 and 6), which may be related to the accumulation of notches or deep impacts in the same area. Large dentine extractions were also identified on some teeth (as in #2587 in Fig. 5). Regarding fractures, two teeth (#2582 and #2490 in Fig. 5) show a vertical fracture on the occlusal plane and, in six cases, fresh fractures were observed on the roots (such as #2611 in Fig. 5). In addition, four teeth show thermoalterations, all with brown rubefaction (three in the Mousterian Alpha level and one in the Mousterian Beta level). No cut marks were observed.

Alterations related to postdepositional processes were also observed on the teeth, with variations according to the sedimentary levels (Table 2). In the Acheulean level, fissures and weathering are the most abundant, followed by chemical corrosion, bacterial activity, and manganese, while in the Mousterian Alpha and Beta levels, chemical corrosion is the most widespread alteration. These modifications indicate constant humid conditions and sediment flooding. Abrasion and polishing are marginal, affecting less than 1% of the assemblage. There are no elements with carnivore or rodent tooth marks.

The rhinoceros teeth from Pech-de-l'Azé II (France) The Pech-de-l'Azé II collection comprises a total of 79 rhinoceros teeth (*S. kirchbergensis* in levels 9, 8, 7, 6-7b, and 6-7c and *Coelodonta antiquitatis* in level 6). Level 7 is the richest archaeological level, followed by levels 8, 9, 6, and finally, 6-7b and 6-7c with only seven dental remains. Based on the NISP, the most numerous elements are permanent lower teeth, followed by upper teeth (SOM Table 3). Most of the teeth (84%) show good surface preservation. Four upper teeth (5.6% of the total dental remains) from adult and senile individuals revealed marks possibly related to anthropogenic activity, consisting of notches on the occlusal surface with angular scars and associated with fissures. These are (see Fig. 5) an M^2 (#P.A.II-9-31) from level 9 with a notch affecting the enamel of the buccal side in the occlusal area and with an associated sliding mark; another M^2 (#P.A.II-7-D11-482) from level 7 with three notches on the buccal side of the occlusal surface; a fragment of the buccal side of a P_3 (#P.A.II-7-E10-458) with three notches; and finally, a fragment of the buccal side of an upper tooth (#P.A.II-6-7c-G13-455) from level 6-7c with three notches, with one of them located on the occlusal surface, while the other two bear a possible pseudo notch on the posterior face. No fresh fractures or cut marks have been identified.

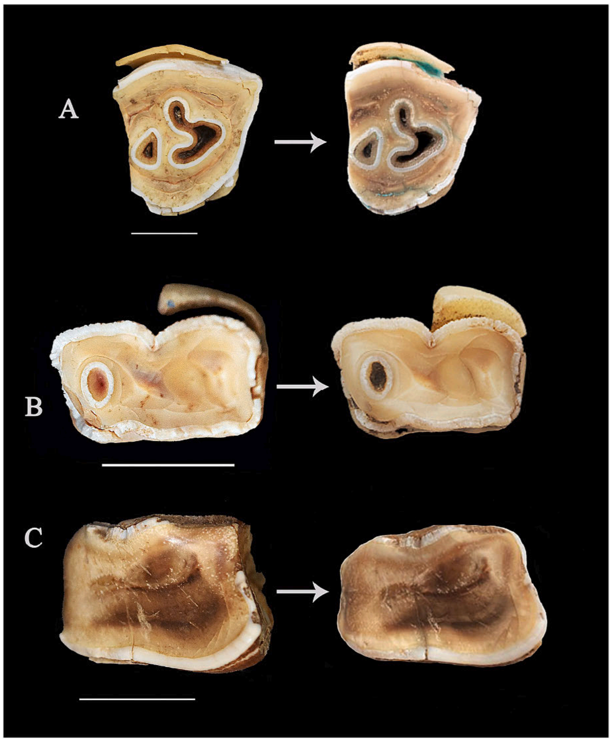


Figure 4. Modifications on rhinoceros teeth (occlusal views) before abrasion (left) and after abrasion (right) test after seven days: A) P^2 (#RZP001); B) P_2 (#RZS008); C) lower molar (#RZM002). (For interpretation of the references to color in this figure, the reader is referred to the web version of this article.)

Postdepositional alterations are similar in all levels (Table 2). The presence of manganese oxide dendrites is the most common alteration, affecting 100% of the dental remains in all levels, except in level 8, where the percentage drops to 90%. The second most common alteration consists of fissures caused by sediment pressure, except in level 6, where there are no such fissures. Finally, trampling affects 75–70% of teeth in all levels.

4.3. Analysis of the comparative collections of extinct and extant rhinoceroses

The rhinoceros teeth from Wasserbillig (Luxembourg) The surface preservation of the dental remains recovered from this site can be considered to be good to medium. Nine teeth bear dry fractures located on the enamel and the roots, mostly with a straight plane and associated with fissures (Fig. 7B). However, some fracture planes are polished and abraded and cannot be accurately described. No traces on the dentine or enamel similar to those produced during the archaeological experiments were identified. Some small and rounded impacts on the enamel and dentine were observed, especially on the buccal face of the tooth, in all the teeth of the skull #2055-1942, and in seven isolated teeth (Fig. 7A). These particular marks differ from the pitting areas produced during archaeological experiments, and we believe they could be related to the animal's diet. The most common postdepositional alteration is the presence of fissures, which affects 64.8% of the total dental remains, followed by weathering and exfoliation in 52.1–40.8%. Abrasion and polishing (47.9–11.3%) (Fig. 7C), chemical corrosion (23.9%) (Fig. 7D), and manganese (21.1%) are also present (Table 2). However, varnish had been applied to all the tooth surfaces for conservation purposes, and it is consequently difficult to observe some modifications satisfactorily.

The rhinoceros teeth from Oetrange (Luxembourg) In general, the preservation of tooth surfaces is good. No modifications similar to those produced during the archaeological experiments or fresh fractures were observed in the dentine or the enamel. Only an upper deciduous premolar displays dry fractures in the enamel of the protocone and a fissure in the anteroposterior root. The main postdepositional alteration is the presence of manganese in the form of dendrites and fissures along all the teeth, with some small dry fractures (Fig. 7E, F) (Table 2).

The rhinoceros teeth from Cova del Rinoceront (Spain) Tooth surface preservation can be considered good to medium, with the presence of several postdepositional alterations, such as fissures and exfoliation (Fig. 7G, H). Some dry tooth fractures were identified in the assemblage, with regular planes delineated by fissures. In some cases, the cracks are filled with sediment, producing minor deformations in tooth morphology. These alterations may, in part, be related to the effects of quarrying activity at the site and the subsequent exposure of some materials (Daura et al., 2015). Percussion marks or cut marks were not observed in this collection. However, the abundance of concretions limited the observation of the tooth surfaces (Table 2).

The rhinoceros teeth from Plumettes (France) Dental surface preservation is good, although some postdepositional modifications are visible in the assemblage, mainly postdepositional dentine fractures with regular planes following the delineation of fissures (in most cases, only observed on the cementum) (Fig. 7I, J). The fractures in the roots also show planes typical of dry bone fractures (Fig. 7K). As in Wasserbillig, modifications in the junction of the dentine and enamel on the buccal side were observed, showing a reduction of the enamel through small domes on the surface, probably as a result of small impacts related to chewing activity. Chemical corrosion is also widespread, affecting 56.5% of the assemblage. Concretions (39.1%), manganese (34.8%), abrasion (32.6%), and root vermiculations (23.9%) were also identified (Table 2). No notches or fresh fractures in the enamel or dentine were observed.

The contemporary rhinoceros teeth from the Salle d'Anatomie Comparée (Muséum National d'Histoire Naturelle) After the detailed analysis of the 201 contemporary rhinoceros teeth from the MNHN collection, we did not observe fresh fractures, notches, or other modifications similar to those observed in the archaeological assemblages of El Castillo and Pech-de-l'Azé II. The most common alteration is the presence of very abundant fissures on the cementum covering the lingual and buccal surfaces of the molars, especially on the upper teeth. These fissures seem to be related to the laboratory cleaning processes of the skulls and mandibles and to natural tooth degradation due to the loss of organic matter. This is probably also the cause of the dry fractures identified on the occlusal surface of the teeth, which follow the vertical structure of the enamel or the delineation of the previous fissures in all cases. In several lower teeth from the same individual (#1928-310), some depressions in the enamel were identified on the buccal and lingual sides, similar to those observed in Wasserbillig and Plumettes. These depressions do not extend beyond the enamel and do not affect the dentine.

4.4. Dental microwear analysis

Dental microwear analysis carried out on the rhinoceros teeth from the archaeological collections of El Castillo and Pech de l'Aze revealed no dietary marks associated with the mastication of phytoliths in the notches identified in the taphonomic analysis. The tooth surface is rough and very irregular in these areas, with no signs of abrasion or fracturing that could have been produced during chewing or the consumption of dust particles contained in plants (SOM Fig. 3).

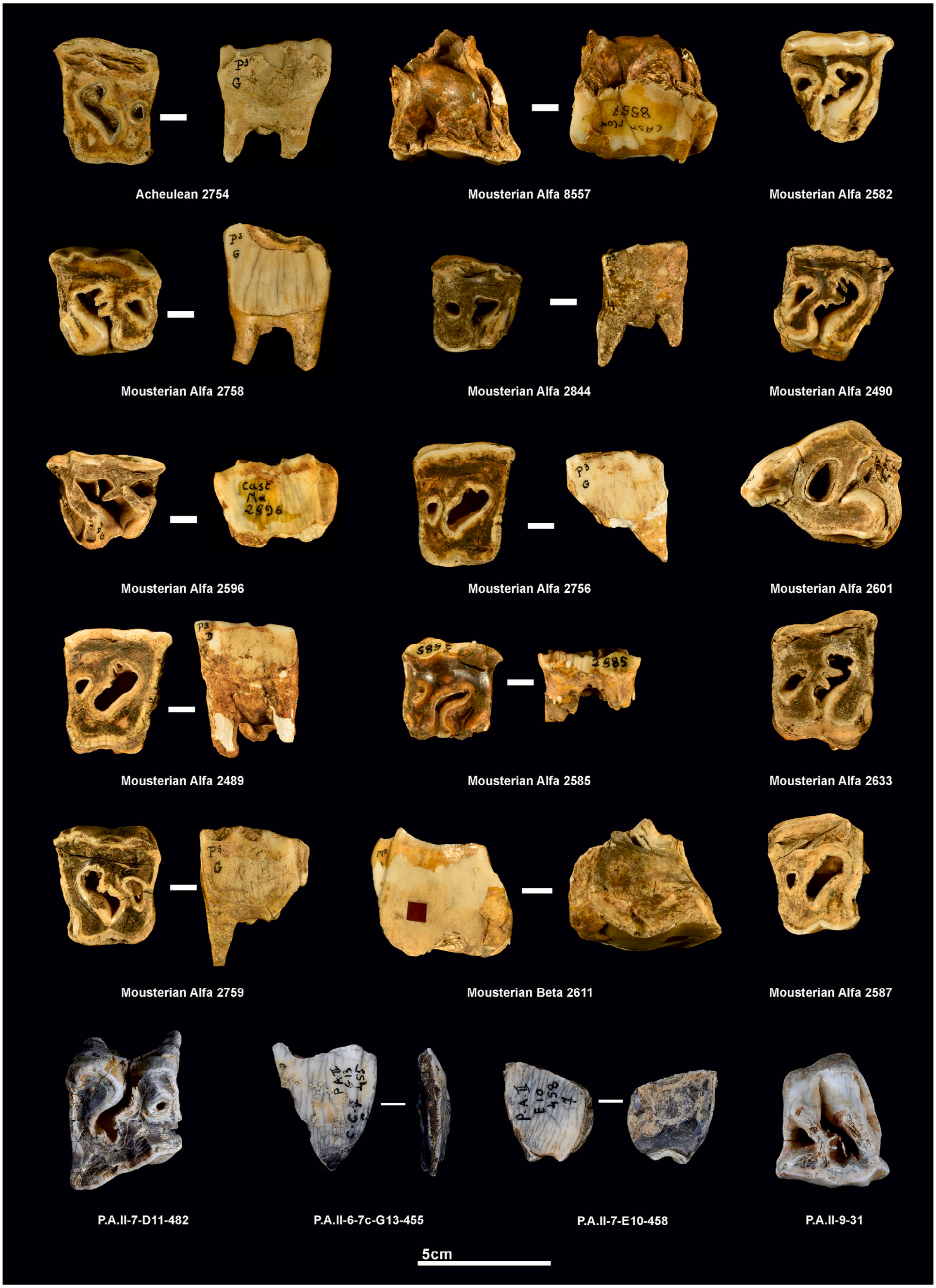
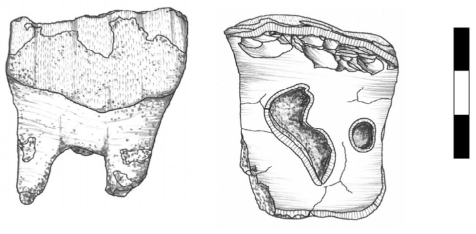


Figure 5. Rhinoceros teeth of El Castillo and Pech de l'Azé II with traces related to anthropogenic origin. (For interpretation of the references to color in this figure, the reader is referred to the web version of this article.)

5. Discussion

5.1. *What is the cause of the marks observed on rhinoceros teeth?*

The rhinoceros teeth analyzed from the Middle Paleolithic sites of El Castillo and Pech-de-l'Azé II show similar traces, mainly recurrent notches and scaled areas, as well as some fresh fractures and sliding marks (Table 2). In these sites, the alteration of the faunal assemblage by Neanderthals has been proved mainly by bone fractures and cut marks, although modifications produced by carnivore activity and natural postdepositional processes were also documented (Texier, 2006; Luret et al., 2020; Sanz-Royo et al., *El Castillo - n°2754*



El Castillo - n°8557

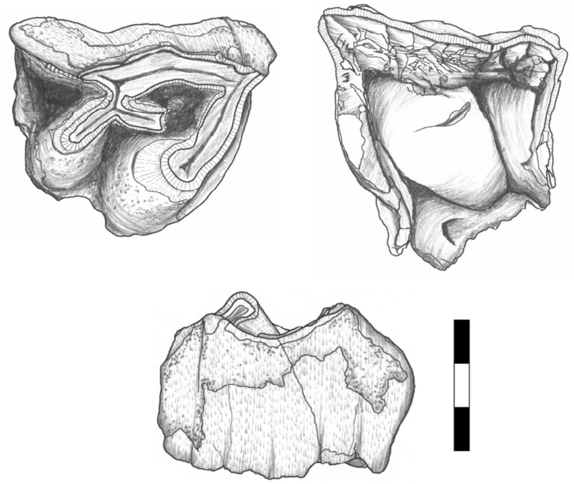


Figure 6. Drawing of the traces observed on #2754 and #8557 teeth from El Castillo (drawings by Sophie Guégan).

2024). The taphonomic analysis of rhinoceros teeth shows no carnivore marks or relevant postdepositional alterations (such as abrasion/polishing), suggesting a different accumulation origin of these remains inside the caves.

The traces identified in these archaeological sites differ from those observed in the paleontological collections analyzed in this work (Table 2). The taphonomic analysis of the teeth recovered in Wasserbillig, Oetrange, Cova del Rinoceront, and Les Plumettes brought to light the alteration of rhinoceros dental remains in different sedimentary contexts and accumulation agents (natural or carnivore accumulations). Dry fractures and other postdepositional alterations, such as root vermiculation and abrasion/polishing, were identified, but there were no recurrent scaled areas, notches, or sliding marks as observed in teeth from El Castillo and Pech-de-l'Azé II. Besides, the alterations produced by the taphonomic experiments were completely different from those observed in the archaeological record. Only abrasion/polishing and fissures generated by sediment abrasion and compaction were identified, which are common natural postdepositional alterations in the fossil record. On the contrary, the archaeological experiments carried out in this work produced relevant modifications in the teeth (Table 2), mainly scaled areas, pitting areas, and tooth fractures, followed by sliding marks and notches. The morphology, recurrence, and location of these marks (mainly in the occlusal area or at the top of the crown) are similar to those documented in the archaeological assemblages. Unlike in the paleontological sites and taphonomic experiments, these activities did not produce polishing or dry fractures. Furthermore, dental microwear analysis on the teeth from El Castillo and Pech-de-l'Azé II rules out the possibility that the observed modifications were produced during the animal's lifetime and confirms that they occurred postmortem since no microwear signals were observed inside the traces. The taphonomic analysis of contemporary rhinoceros teeth from the MNHN collection also shows that natural alterations during the lifetime of the animals do not produce marks similar to those mentioned in the archaeological sites.

Therefore, this research demonstrates that percussive activities can produce similar modifications of rhinoceros teeth to those observed in the archaeological record, while natural postdepositional processes (including abrasion and compaction) and activities occurred during the animal's lifetime do not. To date, apart from this work, no experiments have been carried out on rhinoceros teeth, and most of the mentions of the use of rhinoceros bones and teeth as artefacts are old publications, now considered unreliable (Guérin, 1980), except for two bone tools identified by ZooMS in Scladina Cave (Belgium) (Abrams et al., 2025) and Abri Peyrony (France) (Martisius et al., 2020).

In the Early Middle Paleolithic site of Payre, similar notches, grooves, and pitting areas were also observed on the occlusal surface of 38 rhinoceros teeth, mainly on very worn teeth from senile individuals (Daujeard et al., 2018a). These marks appear to be related to anthropogenic percussion activities. In unit F of La Caune de l'Arago (France, MIS 11), fractures on rhinoceros teeth have been interpreted as intentional, attributed to the extraction of consumable cranial and mandibular elements or to the secondary utilization of tooth fragments (Chen and Moigne, 2018). At Panxian Dadong (China, MIS 8-6) (Miller-Antonio et al., 2000; Schepartz and Miller-Antonio, 2010a, 2010b), the accumulation of many isolated rhinoceros teeth suggests that hominins could have amassed them for use as possible tools, perhaps due to the poor quality of the lithic raw materials available in the immediate environment (limestone and basalt) and to difficult access (forested environments). According to the aforementioned authors, the large enamel surfaces on rhinoceros teeth (especially upper ones), unlike those of other ungulates, can be easily fractured following natural fault lines to obtain sharp-edged enamel and dentine, similar to lithic flakes to use as tools. Enamel is the hardest mammal component, with a chemical composition of 97% hydroxyapatite, 1% collagen, and around 2% water. The structure of enamel presents good mechanical properties and resistance to fracture, capable of supporting large forces (Bajaj and Arola, 2009; Darnell et al., 2010; Winkler and Kaiser, 2015; Renteria et al., 2021) and, therefore, strong percussive activities. Specifically, the structure of rhinoceros tooth enamel is particularly resistant to shocks (Fortelius, 1985; Teaford et al., 2000), which may have been an incentive for human groups to use it as raw material. We noted that most of the teeth with traces had a flat occlusal surface due to tooth wear. Thus, rhinoceros teeth may present auspicious morphological characteristics in terms of size, weight, morphology, flat occlusal surface, and resistance to breakage, which could have made them suitable for use as tools.

If we compare the marks observed on rhinoceros teeth with those identified on bone tools, and especially bone retouchers, flake scars, fractures and crushing of the working edges, percussion notches, pitting/hatched/scaled areas, and cut marks or sliding marks are frequent (Mallye et al., 2012; Daujeard et al., 2014; Costamagno et al., 2018; Doyon et al., 2021; Abrams, 2023). Some of these modifications are similar to those observed in this work. However, in accordance with the experiments carried out by Micó et al. (2024c) on horse teeth, dental elements showed a relatively higher frequency of traces than bones, especially scaled areas. This

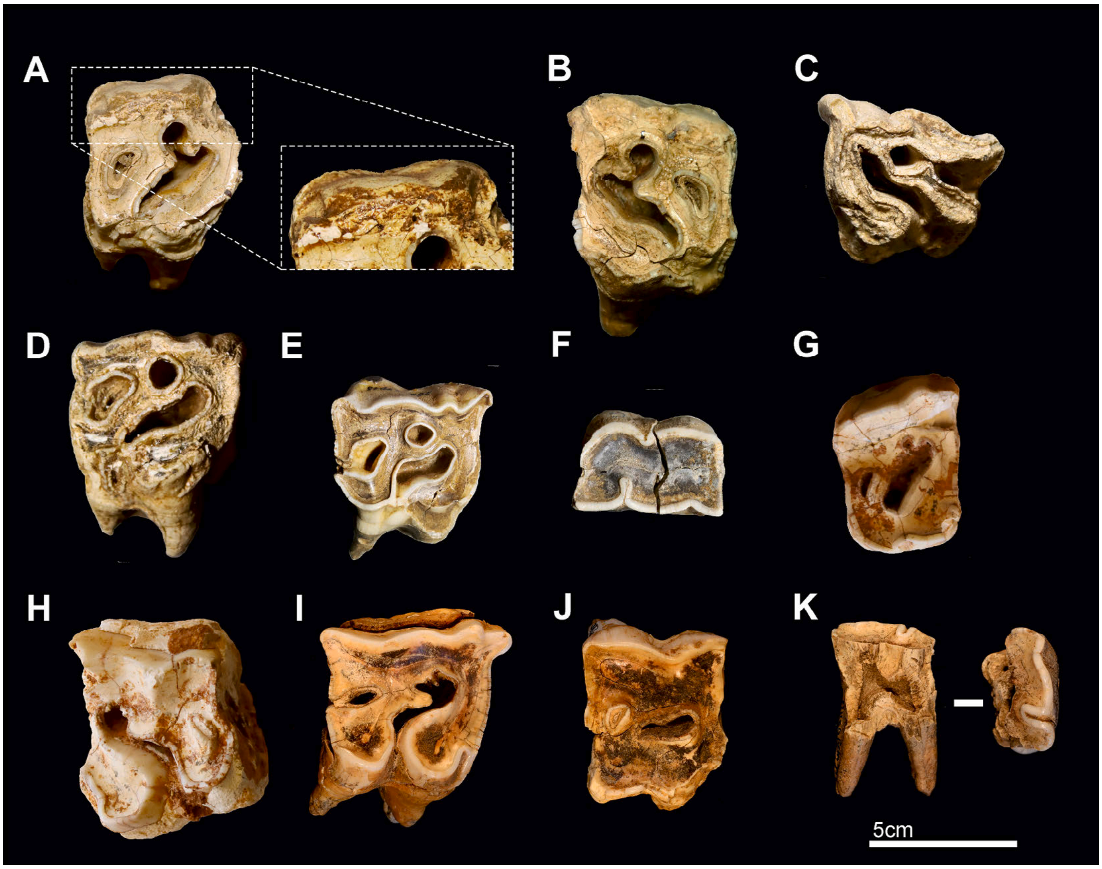


Figure 7. Main modifications observed on rhinoceros teeth (occlusal views) from the paleontological comparative collections: A) Rounded impacts on the enamel and dentine of a tooth from the Wasserbillig site; B) dry fractures on the enamel and dentine from the Wasserbillig site; C) abrasion and polishing from the Wasserbillig site; D) chemical corrosion from the Wasserbillig site; E, F) manganese dendrites and fissures along the teeth from the Oetrange site; G, H) fissures and desquamation from the Cova del Rinoceront site; I, J) dentine fractures with regular planes following the delineation of fissures from the Plumettes site; K) root fractures showing planes typical of dry bone breakage from the Plumettes site. (For interpretation of the references to color in this figure, the reader is referred to the web version of this article.)

is probably due to their chemical structure and composition (cementum, enamel, and dentine layers). On the contrary, unlike bone artefacts, we did not observe cut marks, intentional polish, or associated scraping marks on rhinoceros teeth.

5.2. How did Neanderthals produce these marks?

Our results suggest that the traces observed on the rhinoceros teeth recovered at El Castillo and Pech-de-l'Azé II were caused by percussive-related activities. This result is in keeping with the information provided by previous taphonomic and zooarchaeological studies carried out in the faunal assemblages, which proposed that the main accumulators of the faunal remains (including rhinoceros) were Middle Paleolithic groups (Landry, 2005; Texier, 2006; Luret et al., 2020; Sanz-Royo et al., 2024). But how did Neanderthals produce these traces on rhinoceros teeth and for what purpose?

Given the type of identified traces and their predominant location, the most likely hypothesis is the use of teeth as active tools in direct percussion, possibly as retouchers or percussors, or even as anvils, against hard materials like lithic tools. We cannot exclude the possibility that some rhinoceros tooth fragments were used as raw materials for producing large enamel flakes, as proposed by Miller Antonio et al. (2000), especially for specimen #P.A.II-6-7c-G13-455 of Pech-de-l'Aze II. However, difficulties encountered when attempting to produce enamel and dentine flakes during our experiments show that rhinoceros teeth are not conducive to flake production. Although we do not rule out the possibility that this could be due to the state of preservation of the teeth. The fact that these modifications are mainly found on teeth with advanced wear may suggest an intentional selection of older individuals by Neanderthals, either due to a more suitable dental morphology associated with flatter surfaces or because they were easier prey.

The specialized recovery of rhinoceros teeth points to megafaunal exploitation by Middle Paleolithic populations, not only for consumption but also for nondietary purposes, in a planned framework (Auguste et al., 1998; Parfitt and Roberts, 1999; Costamagno et al., 2006; Gaudzinski, 2006; Gaudzinski-Windheuser and Kindler, 2012; Rendu et al., 2012; White et al., 2016; Daujeard et al., 2018a). Similar behaviors have been observed among Neanderthals from layer 4 in Molodova I (Ukraine) (Demay et al., 2012), where mammoths were used as food and as building resources. Many other herbivores, of all sizes, were also used concomitantly as food resources and raw materials during the Middle Paleolithic (e.g., Patou-Mathis and Schwab, 2002; Daujeard et al., 2012; Abrams, 2018; Neruda and Lázničková-Galetová, 2018; Hutson et al., 2018; Moclán et al., 2023). Percussive Neanderthal tool kit is quite diverse, and both mineral and organic raw materials were used for different purposes (Roussel et al., 2009; Cuartero Monteagudo, 2014; Daujeard et al., 2014; Arrighi et al., 2020; Mathias et al., 2021; Cuartero and Bourguignon, 2022). The use of rhinoceros teeth as potential tools, therefore, extends the range of tools in hard animal materials used by Neanderthals, in addition to antlers and bone retouchers (i.e., Mallye et al., 2012; Daujeard et al., 2014; Hutson et al., 2018; Baumann et al., 2020; Martellotta et al., 2020). This proposal, although it is the first one made on rhinoceros, aligns with other studies on the use of teeth as tools, mainly with horse teeth (which are also hypsodont with a similar morphology) (Bello et al., 2021; Rendu et al., 2023; Micó et al., 2024c).

6. Conclusions

This work presents, for the first time, archaeological and taphonomic experiments on present-day rhinoceros teeth and proposes that human activities, rather than natural compaction and abrasion processes, can cause similar traces to those observed in the archaeological record. According to our results, the traces identified on the rhinoceros teeth recovered at El Castillo (Spain) and Pech-de-l'Azé II (France) are potentially attributable to the use of teeth as soft hammers and anvils, suggesting that these elements could be part of the Neanderthal tool kit and participate in the *chaîne opératoire* during the Middle Paleolithic. These human groups might have focused on older rhinoceros individuals, either because they were easier prey, because the advanced wear of their teeth made them more useful and comfortable tools, or both. Our results contribute to the knowledge of Neanderthal behavior, technical choices, and capabilities, providing insights into the human exploitation of animal resources, as well as expanding the diversity of raw materials collected and used by Neanderthals.

This multidisciplinary work contributes to the development of new methodologies and analytical techniques in the study of mammal dental remains, such as confocal microscopy, providing qualitative and quantitative data. With this study, we also emphasize the relevance of multidisciplinary research and the importance of the taphonomic analysis of dental remains from archaeological contexts. We aim to encourage the replication of archaeological experiments and to stimulate debate on the interpretation of such experiments.

Declaration of competing interest

The authors declare no competing interests.

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Supplementary Online Material

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