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Article

Foxes in Retrospect—Unraveling Human-Fox Relationships through Fox Tooth Ornaments in the Swabian Jura

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Abstract: Personal ornaments play an important role in our understanding of human cultural and behavioral change during the Upper Paleolithic, providing insights into intangible aspects of human cultural behavior. Some ornament forms are better studied than others, and fox tooth ornaments, despite their frequent occurrence and broad spatiotemporal span, are relatively under-addressed. Here we present the first comprehensive study of 40 perforated fox teeth recovered from four cave sites in southwestern Germany. This region's rich record of symbolic representations, as well as evidence of long-standing human–fox relationships, make the Swabian Jura an ideal case study for investigations of fox tooth ornaments. By applying a holistic approach, including geometric morphometrics and traceology coupled with experimental archaeology, we show that fox teeth were mostly perforated by bifacial scraping and grooving and were worn as ornaments. We discuss the role of foxes within human socio-symbolic and paleoenvironmental systems during the Upper Paleolithic of the Swabian Jura, and we contextualize our results within the broader context of sites across Europe during the Upper Paleolithic. The data we provide are in line with general trends observed across the continent and offer insight into the role of foxes during the Upper Paleolithic, especially regarding human subsistence, cultural expression, and ornament production.

Keywords: personal ornamentation; traceology; geometric morphometrics; Upper Paleolithic; Swabian Jura; foxes (*Vulpes vulpes* and *Vulpes lagopus*)

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1. Introduction

In the Swabian Jura (southwestern Germany), Upper Paleolithic symbolic culture is characterized by ivory figurines, musical instruments, and personal ornamentation [1–9]. Although small, ornaments are particularly informative, as they are numerous, well-preserved, diverse in form, and occur throughout the entirety of the Upper Paleolithic. Their hypothesized role as social and symbolic objects also lends insight onto intangible aspects of human cultural behavior, such as personal identity, group affiliation, language, movement, trade, and social status [8,10–17].

During the Upper Paleolithic, ornaments were produced from a variety of organic and inorganic raw materials, including ivory, tooth, bone, shell, fossil, and stone. Those made from ivory, shells, and cervid teeth are well studied [8,10,11,18–30], while fox tooth ornaments, primarily made from red (*Vulpes vulpes*) and arctic fox (*Vulpes lagopus*) canines, are comparatively under-addressed.

Fox tooth ornaments first appear during the Châtelperronian and persist throughout the entire Upper Paleolithic at sites spanning the Iberian Peninsula to the East European Plain (see Supplementary Materials) [13,17,31]. Most assemblages are small, usually less than twenty specimens (Table S1), although exceptional cases include sites like Pavlov I (Czechia) and Sunghir (Russia), each represented by over 200 fox tooth ornaments in association with Gravettian burials [10,32–34].

Despite their abundance and wide geographic span, detailed information on fox tooth ornaments is limited (e.g., on species and tooth selection, metric data, production methods, use-wear, taphonomy). This is especially disappointing, given their potential to illuminate not only the socio-symbolic aspects of ornamentation, but also the broader relationship between humans, foxes, and their shared environment. Unlike other ornament forms, animal teeth come from a living organism and are, therefore, directly related to local ecology and human subsistence practices. Fox tooth ornaments can thus be linked to the broader role of foxes on the landscape (e.g., paleoecology, human–animal relationships), in human diets (e.g., hunting methods, nutrition), and as a raw material (e.g., fur, bone tools, ornamentation).

This study presents an assemblage of Upper Paleolithic fox tooth ornaments (n = 40) from four sites in the Swabian Jura: Hohle Fels (n = 12), Geißenklösterle (n = 12), Brillenhöhle (n = 3), and Hohlenstein-Stadel (n = 13) (Supplementary Materials and Figures 1 and 2). This region's rich record of symbolic representation, as well as evidence of long-standing human–fox relationships [35–39], make the Swabian Jura the ideal location to explore the production and use of these ornaments and their relevance for broader human–fox relationships in the Upper Paleolithic.

In this study, we explore fox tooth ornaments from a diachronic and synchronic perspective by analyzing ornaments from the entire Upper Paleolithic sequence (Aurignacian to Magdalenian) and by considering intra- and inter-ornament variability and the influence of culture versus technological preferences. In particular, we aim to:

1. investigate diachronic changes in technology, production, and function and how these changes relate to the methods of the perforation and mode of use among the three cultures (Aurignacian, Gravettian, and Magdalenian) and within the four analyzed sites in the Swabian Jura,
2. explore the potential for species preferences between red fox and arctic fox within the analyzed sites and discuss the results in the framework of fox ecology and behavior, and
3. contextualize the results from the Swabian Jura within a broader context, drawing from an extensive literature review of fox tooth ornaments from sites across Europe during the Upper Paleolithic.

To do so, we apply three analytical methods to obtain a more holistic view of fox exploitation and ornament production, use, and discard. Geometric morphometrics facilitates the reliable differentiation of red versus arctic fox in isolated teeth, allowing us to investigate species selection and preference, fox paleoecology, and the interaction between humans and foxes in the Swabian Jura. This is complemented by traceological analysis coupled with experimental archaeology, in which microscopic observations of the perforations are used to identify manufacturing techniques and use-wear traces.

Foxes in the Swabian Jura

During the Late Pleistocene, climatic and environmental conditions influenced the distribution and composition of fox species on the landscape and their subsequent availability to hunter-gatherer populations [40,41]. At the start of the Upper Paleolithic, both red and arctic foxes were sympatric in Central Europe. Subsequent cooling associated with the Last Glacial Maximum forced red foxes to retreat into glacial refugia, such as the Iberian Peninsula [42,43]. Sympatric populations appeared again in Central Europe during the Late Glacial, but Allerød warming later pushed arctic foxes northward. A final period of sympatry is recorded during the Younger Dryas, followed by the northern retreat of arctic foxes in response to Holocene warming, after which both species attained their modern distributions [42].

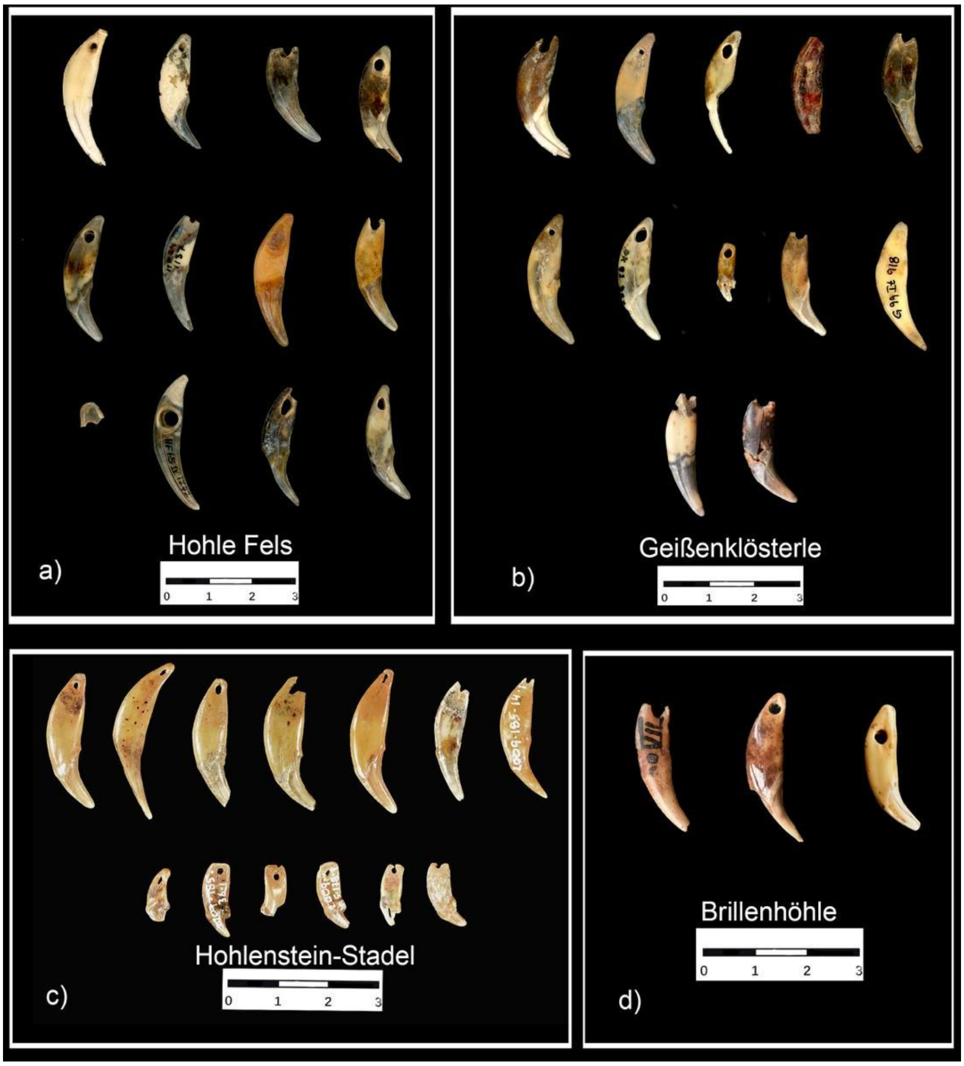


Figure 1. Perforated fox teeth analyzed in this study and their geographic location. Items from left to right. (**a**) Upper row: ID 461, ID 631.1, ID 1278.1, ID 1295; middle row: ID 1517.1, ID 1137, ID 1228.2, ID 964.1; lower row: ID 1227.1, ID 1742, ID 2099.1, ID 1713. (**b**) Upper row: ID 1B, ID 1A, ID 391, ID 89, ID 369; middle row: ID 286, ID 38F, ID 658.2, ID 226, ID 918; lower row: ID 487, ID 1511. (**c**) Upper row: ID 1.0380, ID 2.0380, ID 3.0380, ID 4.0380, ID. 5.0380, ID 141-1, ID 14-1; lower row: ID 33-1, ID 36-1, ID 167-1, ID 178-1, ID 9000-1, ID 9001-1. (**d**) ID 130, ID 131, ID 132.

In the Swabian Jura, both red and arctic foxes are found at numerous archaeological sites throughout the Paleolithic, generally accounting for 1–5% of NISP. Their abundance increased over time compared to other carnivores and large herbivores. A similar increase is recorded in hare, likely due to common acquisition methods, such as traps and snares, which elevated the catch rate of small game [44,45]. Juvenile foxes (<1 year) are rare, only accounting for ~2% of fox NISP. Most come from the Middle Paleolithic of Hohlenstein-Stadel (n = 17) [46], reflecting natural deaths from denning animals. The comparative dearth of juveniles from Upper Paleolithic contexts (Vogelherd Aurignacian, n = 1 [35]; Geißenklösterle Gravettian, n = 4 [39]; Vogelherd Magdalenian, n = 1 [35]; Langmahdalde Magdalenian, n = 6 [47]) may indicate issues with preservation or excavation techniques, that caves were not used as fox dens, or that humans did not intentionally hunt juveniles [44].

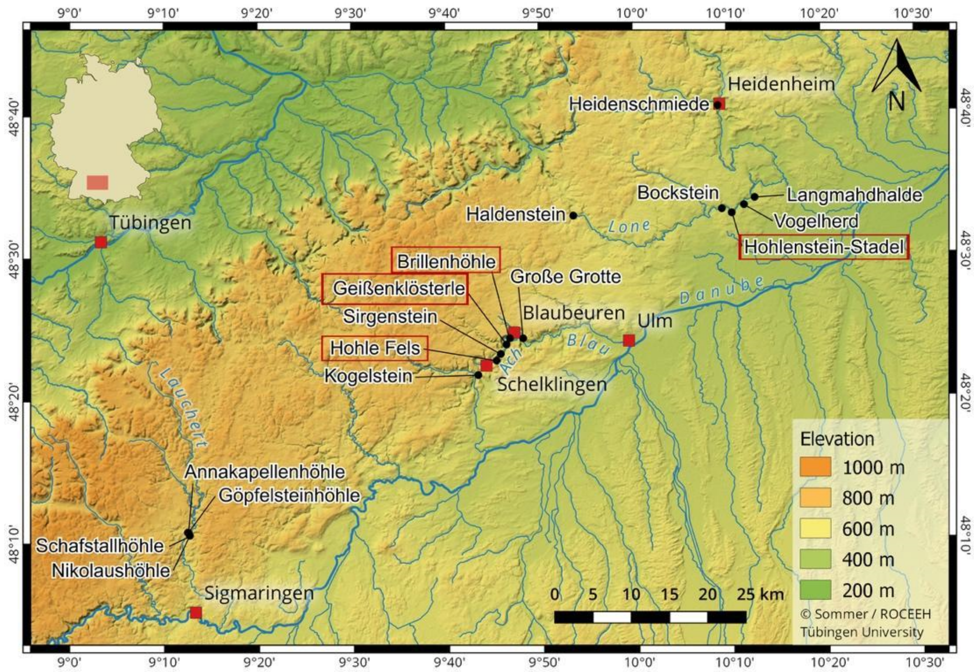


Figure 2. Map of the Swabian Jura with the location of important Paleolithic cave sites from the Ach, Lone, and Lauchert valleys. Four sites outlined in red provide Upper Paleolithic fox tooth pendants and are the focus of this study: Hohle Fels (1) Geißenklösterle (2), Brillenhöhle (3), Hohlenstein-Stadel (4). (Map provided by Christian Sommer/ROCEEH (2019): A map collection of the Paleolithic of the Swabian Jura (Version 1.0.0) (Data set). (modified by F.V.).

Evidence of fox butchery is rare compared to other taxa in the Swabian Jura [44]. During the Middle Paleolithic, a single phalanx from Bockstein exhibits a circular cut mark associated with skinning [48]. During the Aurignacian, cut marks on two mandibles at Vogelherd [49,50] and a fifth metacarpal at Geißenklösterle [39] also indicate skinning, while cut marks on a rib and ulna at Hohle Fels are from defleshing [37]. During the Gravettian, only two cut marks are present on fox remains at Hohle Fels, one on a pelvis and the other on a femur, both related to defleshing [37]. Lastly, during the Magdalenian, one cut-marked ulna is recorded from Hohle Fels [51] and one cut-marked mandible is present at Langmahdhalde [52], indicating defleshing and skinning, respectively. In addition to cut marks, human tooth marks are also recorded on three Aurignacian and Gravettian fox elements from Hohle Fels [53]. Combined, these traces clearly establish foxes were used for both fur and food, as well as a raw material for the 40 fox tooth ornaments discussed in this study.

Human–fox relationships also extended beyond human predation, as evidenced by isotopic studies of fox paleoecology, which suggest some foxes were commensal to humans [38,44,54,55]. Prior to the Upper Paleolithic, foxes inhabited expected niches as either rodent specialists or commensals to large carnivores (for an overview on fox ecology and behavior, see the Supplementary Materials). However, during the Aurignacian, a new fox niche emerged, characterized by a diet of primarily reindeer with a smaller proportion of rodents and other large game. The likely explanation is that some foxes became commensal to humans to take advantage of food waste, perhaps in response to increasing human population density [38,55]. By engaging in this synanthropic commensal behavior, foxes were able to access new, more reliable food resources as well as protection from large carnivores who were deterred by humans. Humans also benefited, gaining more frequent access to foxes for food, fur, and raw materials, as well as a means of food disposal, which indirectly protected humans from large carnivores [54]. This relationship lasted throughout the Aurignacian and Gravettian before dogs and wolves largely took over the niche during the Magdalenian, although some foxes remained commensal [38,55].

2. Materials and Methods

2.1. Archaeological and Comparative Materials

The complete assemblage includes 40 perforated fox tooth ornaments from the Aurignacian, Gravettian, and Magdalenian horizons of four sites in the Swabian Jura: Hohle Fels, Geißenklösterle, Brillenhöhle, and Hohlenstein-Stadel (Table 1). Most are canines (n = 32), although incisors (n = 4) and premolars (n = 2) are also present as well as some indeterminate root fragments (n = 2).

Table 1. List of studied perforated fox tooth ornaments from the Swabian Jura. QU = quadrant, ID = find ID, GH = geological horizon, AH = archaeological horizon, Morph = morphological species identification, GM = geometric-morphometric species identification from this study, [1] = Kölbl and Conard [5].

Culture	QU	ID	GH	AH	Species ID (Morph)	Species ID (GM)	Tooth
Hohle Fels:							
NA (Upper Paleolithic)	28	964.1	1ka-7	0/I-IV	*Vulpes* sp.	*Vulpes vulpes*	Canine
Gravettian	58	1295	3c	IIc	*Vulpes lagopus* [1]	*Vulpes lagopus*	Canine
Gravettian	79	1228.29	3c-3d	IIc-IId	*Vulpes* sp.	*Vulpes lagopus*	Canine
Gravettian	66d	461	3bl	IIb	*Vulpes* sp. [1]	*Vulpes vulpes*	Canine
Aurignacian-Gravettian	76	1227.1	5	IIe	*Vulpes* sp. ?	NA	Root fragment
Aurignacian-Gravettian	59	2099.1	5-7	IIe-IV	*Vulpes lagopus* [1]	NA	Canine
Aurignacian	24	1137	7	IV	*Vulpes* sp.	Indeterminate	Canine
Aurignacian	26	631.1	7a	Va	*Vulpes* sp.	*Vulpes lagopus*	Canine
Aurignacian	69	1713	7	IV	*Vulpes lagopus* [1]	*Vulpes vulpes*?	Canine
Aurignacian	89	1517.1	7	IV	*Vulpes* sp.	*Vulpes lagopus*	Canine
Aurignacian	24	1278.1	7	IV	*Vulpes* sp.	*Vulpes lagopus*	Canine
Aurignacian	65	1742	7	IV	*Vulpes* sp.	NA	Canine
Geißenklösterle:							
NA (likely Gravettian)	22	1A	disturbed	disturbed	*Vulpes* sp.	*Vulpes vulpes* ?	Canine
NA (likely Gravettian)	22	1B	disturbed	disturbed	*Vulpes* sp.	*Vulpes lagopus*	Canine
Gravettian	67	658.2	7	It	*Vulpes* sp.	NA	Incisor
Gravettian	98	391	7	It	*Vulpes* sp.	*Vulpes vulpes*	Canine
Gravettian	99	918	7	It	*Vulpes* sp.	*Vulpes lagopus* ?	Canine
Gravettian	100	89	5b	Ir	*Vulpes* sp. [1]	*Vulpes* sp.	Canine
Gravettian	140	226	7	It	*Vulpes* sp.	*Vulpes lagopus*	Canine
Gravettian	98	286	7	It	*Vulpes* sp.	NA	Canine
Gravettian	98	387	7	It	*Vulpes lagopus* [1]	NA	Canine
Aurignacian	59	369	16	IIIb	*Vulpes* sp. [1]	*Vulpes vulpes*	Canine
Aurignacian	58	487	15	III	*Vulpes* sp.	NA	Canine
Aurignacian	67	1511	15	IIIa	*Vulpes* sp.	NA	Canine
Hohlenstein-Stadel:							
Aurignacian	NA	1.0380	19./20. Meter, 6. Hieb	NA	*Vulpes* sp.	*Vulpes lagopus*	Canine
Aurignacian	NA	2.0380	19./20. Meter, 6. Hieb	NA	*Vulpes* sp.	*Vulpes vulpes*	Canine
Aurignacian	NA	3.0380	19./20. Meter, 6. Hieb	NA	*Vulpes* sp.	*Vulpes vulpes*	Canine
Aurignacian	NA	4.0380	19./20. Meter, 6. Hieb	NA	*Vulpes* sp.	*Vulpes lagopus*	Canine
Aurignacian	NA	5.0380	19./20. Meter, 6. Hieb	NA	*Vulpes* sp.	*Vulpes lagopus*	Canine
Aurignacian or Magdalenian	NA	36-1	backdirt	NA	*Vulpes* sp.	NA	Incisor
Aurignacian or Magdalenian	NA	90001-1	backdirt	NA	*Vulpes* sp.	NA	Incisor
Aurignacian or Magdalenian	NA	9000-1	backdirt	NA	*Vulpes* sp.	NA	Incisor
Aurignacian or Magdalenian	NA	14-1	backdirt	NA	*Vulpes* sp.	*Vulpes* sp.	Canine
Aurignacian or Magdalenian	NA	141-1	backdirt	NA	*Vulpes* sp.	*Vulpes* sp.	Canine
Aurignacian or Magdalenian	NA	178-1	backdirt	NA	*Vulpes* sp.	NA	Premolar
Aurignacian or Magdalenian	NA	33-1	backdirt	NA	*Vulpes* sp.	NA	Premolar
Aurignacian or Magdalenian	NA	167-1	backdirt	NA	*Vulpes* sp. ?	NA	Root fragment
Brillenhöhle:							
Gravettian	NA	132	NA	VII	*Vulpes* sp.	NA	Canine
Gravettian	P7	131	NA	VII	*Vulpes* sp.	NA	Canine
Gravettian	NA	130	NA	VII	*Vulpes* sp.	NA	Canine

The ornaments from Hohle Fels are stored at the University of Tübingen as part of a larger study of the faunal assemblage. Most of the ornaments from Geißenklösterle are also stored at the University of Tübingen, while two others are on display at the Landesmuseum Württemberg Stuttgart alongside the ornaments from Brillenhöhle. The Hohlenstein-Stadel ornaments are stored and curated at the Museum Ulm, some of which are on display.

The Hohle Fels assemblage includes 12 total ornaments, which come from the Aurignacian layers Vb-IId (n = 8), the Gravettian layers IIe-IIb (n = 3), and a profile collapse spanning multiple Upper Paleolithic horizons (n = 1) [3,5,53,56–59].

Geißenklösterle hosts 12 total ornaments, which come from the Aurignacian layers IIIb-III (n = 3), the Gravettian layers It-Ir (n = 7), and from disturbed contexts that are likely Gravettian (n = 2) [60,61]. Here, we publish one of the Aurignacian ornaments (ID 1511) for the first time. Two additional Gravettian ornaments are known from Kölbl and Conard [5] (Kat. 75, ID 359) and the Geißenklösterle database (ID 786); however, these two objects could not be located for this study and are not included in the total count.

For Brillenhöhle, the assemblage includes three Gravettian ornaments from layer VII (Riek, 1973).

Lastly, the Hohlenstein-Stadel assemblage includes 13 total ornaments. Those excavated in association with the lion man figurine (n = 5) are considered Aurignacian [61–64], while those excavated from the backdirt (n = 8) cannot be assigned to a specific cultural period [63,65]. The latter likely belong to the Aurignacian, although the Magdalenian cannot be excluded.

The assemblage we present here is likely incomplete. It is likely that excavators in the early 20th century overlooked smaller finds due to their coarser excavation methods. Excavations are also ongoing at Brillenhöhle and Hohle Fels, and we can expect to discover more animal tooth pendants from these sites in the future.

For the geometric morphometric analysis, our sample includes a total of 24 Aurignacian and Gravettian ornaments from Hohle Fels (n = 10), Geißenklösterle (n = 7), and Hohlenstein-Stadel (n = 7) (Table S2). To establish a comparative baseline, we also curated 42 modern, unmodified, adult fox canines (Table S3) from the comparative zooarchaeological collection of the University of Tübingen alongside two canines from the private collection of Chris Baumann (University of Tübingen). The comparative sample includes 13 upper and 9 lower arctic fox canines (Banks Island, Canada) as well as 9 upper and 11 lower red fox canines (southwestern Germany).

2.2. Geometric Morphometric Methods

Micro-computed tomography (μCT) scanning of the archaeological sample was carried out with a Nikon XT H 320 μCT scanner at isotopic voxel length between 20 and 61 μ from the Terrestrial Palaeoclimatology working group at the University of Tübingen. For the comparative sample, 16 arctic and 16 red fox canines were scanned with the same machine, while 6 arctic and 4 red fox canines were scanned with a GE Phoenix v | tome | x s240 μCT scanner at an isotopic voxel length between 15 and 55 μ from the Paleoanthropology High Resolution CT Laboratory at the University of Tübingen.

Our geometric morphometric analysis follows protocols established by Benazzi et al. [66] and Röding et al. [67] for the cervical outline of hominin molars with some modifications for fox canines. As the cervical outline lacks homologous fixed points and a clear start or end point, landmark collection does not fall into the usual concept of fixed or semi-landmarks, thus necessitating additional steps during data collection for the removal of orientation, location, and absolute size from the landmark coordinates.

After scanning, we post-processed and sectioned the μCT images in Avizo 9.2 (Visualization Sciences Group), orienting each tooth to establish a best-fit plane along the cervical outline. We then virtually sectioned the images along this outline, removing the portion below the cervical plane, so that only the crown remained. Next, in Rhinoceros 6 (Robert McNeel and Associates), we translated the best-fit plane into an x-y coordinate system for landmark selection. To ensure consistent positioning, each tooth was rotated so that the lingual surface was parallel to the right side of the z-axis. Additionally, the area centroid of the cervical outline was calculated, upon which the outline was centered and translated to the Cartesian coordinate position (10,10,0). After positioning, sixteen landmark positions along the cervical outline were generated through equiangular spaced radial vectors from the centroid. The coordinates at the intersection of the vector with the cervical outline served as pseudo-landmarks and were recorded clockwise starting from the middle-upper landmark. Following established methods [68,69], all left canines were mirrored and treated as right canines. However, it should be noted that fluctuating asymmetry in dentition may increase noise when left and right teeth are combined [67].

Before analyzing the landmark data, we tested for intra-observer error to evaluate the alignment, reliability of landmark positions, and the relative reproducibility of individual landmarks. This was calculated as the percent error of the Euclidean distance between the configuration centroid and repeated landmark measurements. To accomplish this, we performed each step in Aviso and Rhinoceros five times for a random sample with a time gap of five hours, one day, one week, and one month after the first analysis. The randomization was performed by assigning a number to each used sample, and a random number generator was then used to select a sample for error measurements. Afterward, for each repeated landmark set, the centroid and the 16 Euclidean distances between the centroid and each landmark were calculated using unscaled landmark data. We then calculated the percent error for each landmark as well as the average and standard deviation.

After data collection, we performed multivariate statistical analyses in the program R (R Development Core Team 2011, version 4.1.2, © 2021) using multiple packages: Geomorph [70,71], ggplot2 [72], ggpubr [73], and ggrepel [74]. Analyses were conducted separately for upper and lower canines. For some teeth, the cervical outline was absent or unclear due to surface modifications or poor preservation. We considered five ornaments too incomplete for further analysis (ID 391, ID 89, ID 1227.1, ID 14-1, ID 141-1). However, for teeth with less severe damage, we attempted to reconstruct the cervical outline with the function estimate.missing in geomorph (method = "TPS"). The method was successful for a CN45 upper canine, ID 1A, ID 226, and ID 2.0380 but unsuccessful in the case of the CN99 upper canine. The former were included in subsequent analyses, while the latter was removed from the statistical sample.

We analyzed the landmark sets with two Principal Component Analyses (PCA)—a Shape PCA (gm.prcomp function) and a Form PCA (prcom function) [70]. The Shape PCA only utilizes the scaled and superimposed landmark coordinates, whereas the Form PCA, defined as shape considered with size, uses the logarithmized centroid size added as a variable. To satisfy the assumptions of our PCAs, we estimated Cook's distance for each individual to ensure our dataset did not include outliers or influential specimens, and no canines fell over the recommended cut-off value [75]. Shape changes along the PCs were visualized as landmark configurations at ±2 standard deviations [67].

2.3. Traceological Methods

Traceological analyses were carried out on the complete ornament assemblage in the Material Culture Laboratory (hereafter MCL) at the University of Tübingen. We performed the analysis using three microscopes to identify manufacture traces, perforation techniques, and use-wear traces. While we analyzed the manufacturing traces on broken and complete perforations, observations at higher magnification in search of use-wear traces were only carried out on teeth with intact and well-preserved perforations.

Following well-established protocols for microwear analyses of material culture [76–78], we combined observations at low and high magnification. Macroscopic traces were observed with an Olympus SZX7 stereomicroscope with magnification ranging from 8× to 56× and equipped with an LED ring light source in combination with a Hirox HRX-01, a 3D digital microscope covering a magnification range of 20×–2500×. Observations at higher magnification were performed with an Olympus BX53M metallographic microscope in transmitted light with magnification up to 500×, alongside the aforementioned 3D digital microscope.

Before analysis, the perforations of the best-preserved teeth were cleaned with a cotton swab immersed in demineralized water. For the description of macro and micro traces, we used established nomenclature [78–81]. When describing the location of traces, we used the dial plate system [82], in which specific "hours" on the dial plate correspond to a sector, i.e., sector 1 corresponds to hours 12 to 1, sector 2 to hours 1 to 2, and so on.

We compared the technological and use-wear traces observed on the archeological specimens with a reference collection of 28 perforated fox teeth, which were produced for this study (see Supplementary Materials). Additionally, comparisons were made with previous microwear studies of animal tooth ornaments from other prehistoric and ethnographic contexts [25,82,83,83–88].

3. Results

3.1. Geometric-Morphometric Results

Our novel approach to differentiate red versus arctic fox individuals from loose canines was ultimately very successful. Of the total assemblage, we identified 17 (71%) ornaments as either red (n = 10) or arctic fox (n = 7) individuals. Two ornaments (8%) were classified as indeterminate, and five (21%) were excluded due to damage affecting the visibility of the cervical outline (Table 2). Of the arctic foxes, six correspond to the Aurignacian and four to the Gravettian. Of the red foxes, five correspond to the Aurignacian and two to the Gravettian.

Table 2. Species classification of the archaeological ornaments after geometric-morphometric analyses.

Site	Red Fox	Arctic Fox	Indeterminate	Unsuitable for Analysis
Geißenklösterle (n = 7)	2	3	0	2
Hohle Fels (n = 10)	3	4	2	1
Hohlenstein-Stadel (n = 7)	2	3	0	2
Total (n = 24)	7	10	2	5

The statistical analyses revealed that, while both the Shape and Form PCAs exhibited significant distinction and little overlap between species, the Shape PCA is best suited for this analysis. The Form PCA, which considers the size of the cervical outline, reveals more variability between the archaeological ornaments than the comparative sample.

Error measurements fall under the acceptable 5% deviation between the five repeated measurements (Figure S7). Landmark 2 exhibited the greatest error (1.3%), where the error measurements fell under 0.4%. This may indicate landmark 2 was more susceptible to variations in outline placement in Avizo or in subsequent orientation in Rhinoceros. However, the overall low deviation between samples indicates our method is suitable for fox canines.

3.1.1. Upper Canines

The upper canine assemblage includes the archaeological specimens ID 369, ID 226, ID 1137, ID 964.1, ID 461, ID 1228, and ID 2.0380 alongside the modern comparative upper canines (n = 21).

The Shape PCA (Figure 3a) cumulatively explains 84% of variance in the first two PCs, with PC1 and PC2 explaining 64% and 20% of variance, respectively. Red and arctic fox canines mainly differ across PC1, where arctic foxes plot more positively and red foxes plot more negatively, although a small overlap occurs between 0.00 and 0.01. On PC2, red foxes exhibit a narrower range than arctic foxes and fall mostly within the arctic fox range.

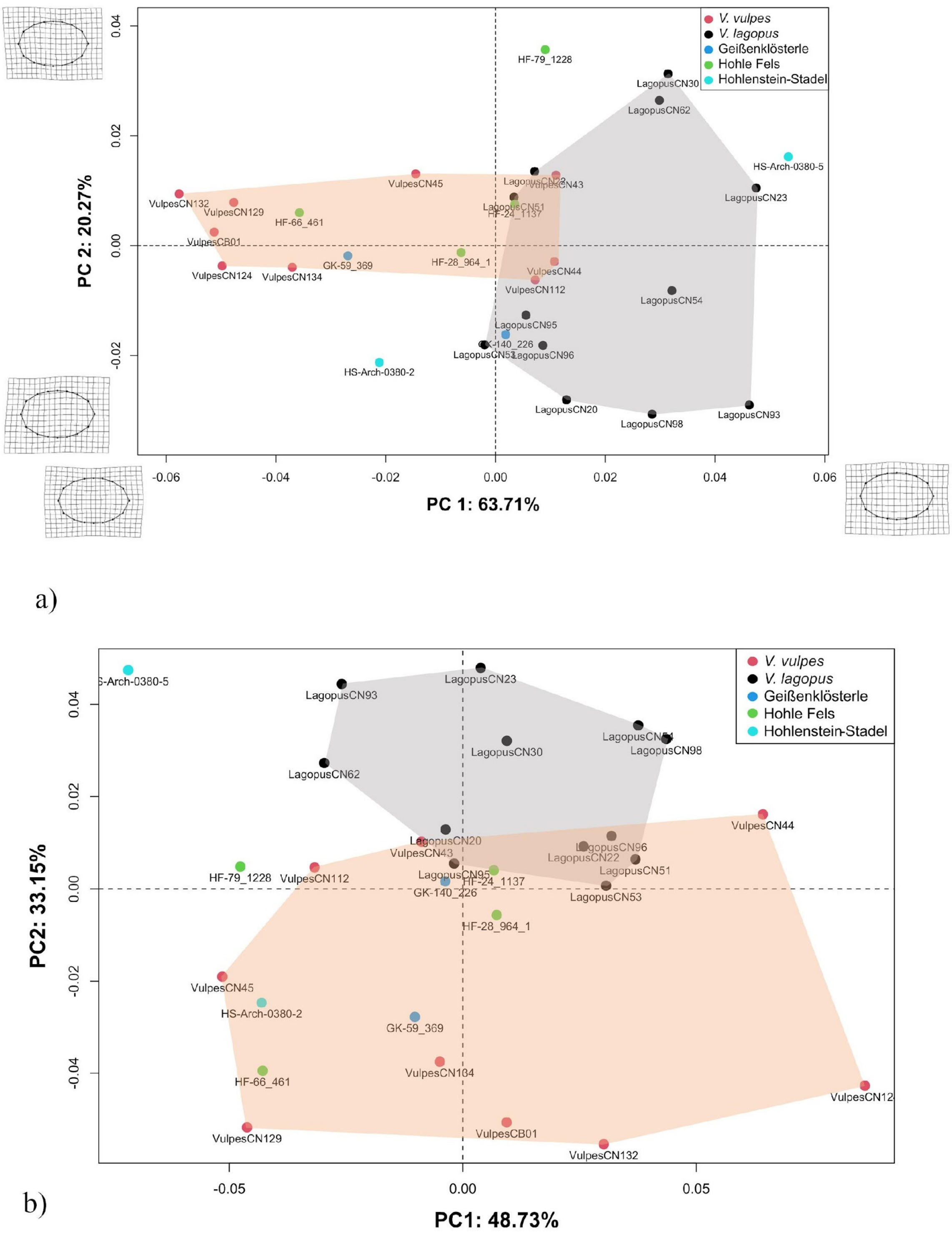


Figure 3. GM: Shape (**a**) and Form (**b**) PCA of upper canines and pendants.

Although most ornaments plot clearly within the arctic or red fox groups, some require further consideration. ID 1137 plots in an area of overlap along both PC1 and PC2, so a clear species assignment was not possible. Three pendants plot outside the distribution of the recent upper canines for both species: ID 1228, ID 2.0380, and ID 5.0380. Although clear species classifications were not possible, ID 1228 is likely an arctic fox, given the more positive PC2 value, and ID 5.0380 is likely also an arctic fox, given the more positive PC1 value.

The Form PCA (Figure 3b) cumulatively explains 9% of variance in the first two PCs, with PC1 and PC2 explaining 49% and 33% of variance, respectively. Similar to the Shape PCA, a distinction between red and arctic foxes is apparent. While red fox presents a broader range than arctic fox in PC1, the primary separation is visible in PC2, where arctic fox plots more positively and red fox plots more negatively. Areas of overlap occur between −0.04 and 0.04 in PC1 and between 0.00 and 0.01 in PC2.

Although size is considered in the Form PCA, species classifications do not fundamentally change from the Shape PCA; however, some specimens require further consideration: Ornament ID 226 plots within the arctic fox range in the Shape PCA but plots slightly outside of the arctic fox and within the red fox range on PC2 in the Form PCA. This indicates that ID 226 can be viewed as a larger arctic fox canine. As in the Shape PCA, ID 1137 plots in an area of overlap between species, inhibiting a clear species assignment. ID 1228 still plots outside of both groups, but within the red fox range on PC1 and in an overlapping area on PC2; however, a clear assignment was not possible. ID 2.380 plots within the red fox distribution on both PC1 and PC2; considering the Shape PCA, this tooth was tentatively identified as a red fox canine. Lastly, ID 5.0380 plots outside of the red and arctic fox values on PC1 and within the arctic fox values on PC2, indicating that the size of this tooth falls outside of the range of recent arctic foxes.

3.1.2. Lower Canines

The lower canine assemblage includes the archaeological specimens ID 1A, ID 1B, ID 918, ID 1278.1, ID 631, ID 1295, ID 1713, ID 1517, ID 1.0380, ID 3.0380, and ID 4.0380 alongside the modern comparative lower canines (n = 22).

The Shape PCA (Figure 4a) cumulatively explains 76% of variance in the first two PCs, with PC1 and PC2 explaining 60% and 16% of variance, respectively. The species are primarily distinguished on PC1, where arctic foxes plot more positively and red foxes more negatively with an area of overlap between −0.01 and 0.01. PC2 exhibits similar ranges between groups and is thus a poor indicator of species.

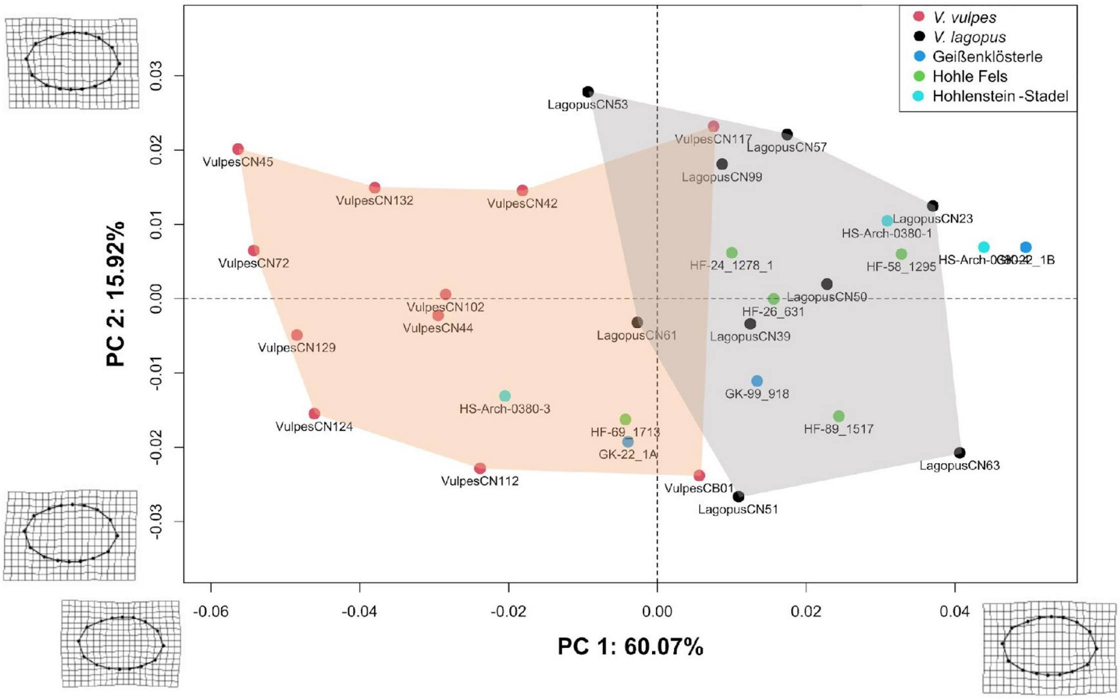
Most ornaments exhibit clear adherence to either red or arctic fox, although some specimens are more ambiguous. ID 1A and ID 1713 both plot within the red fox group, although overlap with the arctic fox group along PC1 makes this identification tentative. ID 1B and ID 4.0380 both plot outside the distribution of recent fox canines, but their more positive PC1 values indicate these individuals correspond to arctic foxes.

The Form PCA (Figure 4b) mostly confirms the identifications presented in the Shape PCA and explains 84% of variance in the first two PCs, with PC1 and PC2 explaining 59% and 25% of variance, respectively. The greatest species separation occurs along PC2 with arctic fox plotting more positively and red fox more negatively with some overlap between −0.01 and 0.01.

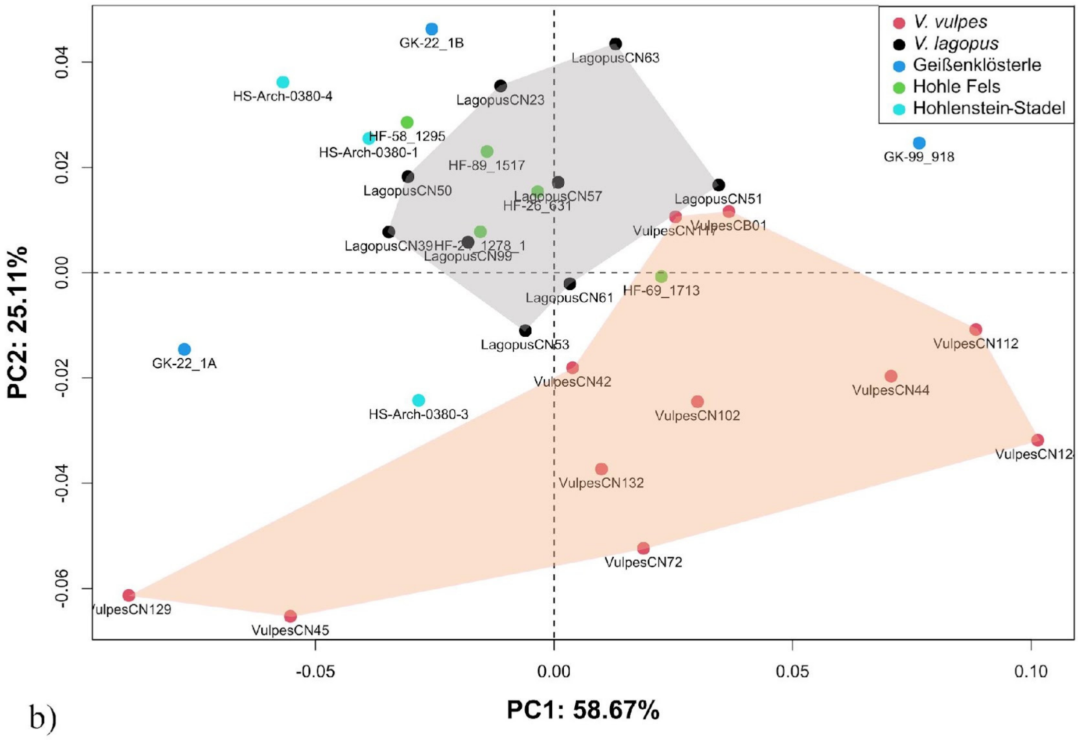
Several ornaments plot outside the defined species groups, indicating the size of cervical outlines varied more in the archaeological sample than the modern sample. In the Shape PCA, ID 1A is tentatively classified as a red fox given its more negative PC2 value, which is supported by the Form PCA's PC1 value. Although ID 1713 plots within the red fox group, the potential for overlap is high, making the classification as red fox tentative. ID 981 overlaps with the red fox range along PC1; however, the location within the arctic fox group of the Shape PCA combined with the more positive PC2 values of the Form PCA suggests a tentative identification as arctic fox. For ID 1B, ID 1295, ID 1.0380, and ID 4.0380, more positive PC2 values indicate they belong to arctic foxes. Lastly, the more negative PC2 values of ID 3.0380 indicates this individual is a red fox.

3.2. Traceological Results

We present the traceological results by site, focusing on root modifications to determine perforation techniques. Additionally, we pay special attention to the identification of potential macro and microwear traces related to the use of the teeth as pendants or as ornaments sewn onto clothes or other goods.



a)



b)

Figure 4. GM: Shape (**a**) and Form (**b**) PCA of lower canines and pendants.

3.2.1. Hohle Fels

Among the 12 fox canines analyzed at Hohle Fels, seven exhibit complete perforations, while three are broken at the tip of the root and one fragment only represents the upper part of the eyelet. The twelfth tooth is incompletely perforated. Overall, 11 teeth were suitable for the macro and microscopic analysis (Table 3).

Table 3. List of archeological fox teeth analyzed in this study from Hohle Fels.

Site	Culture	Find Number (ID)	Tooth	Integrity of Perforation	Technique of Perforation	Use Traces
Hohle Fels	Aurignacian	1517.1	Canine	Complete	Scraping + grooving + drilling	Used: rounding/ smoothing
Hohle Fels	Aurignacian	1137	Canine	Fragmentary	Scraping	Not diagnostic
Hohle Fels	Aurignacian	631.1	Canine	Complete	Probably scraping + widening	Not diagnostic
Hohle Fels	Aurignacian	1713	Canine	Complete	Scraping + grooving + widening	Used: rounding/smoothing/Polish and striae
Hohle Fels	Aurignacian	1278.1	Canine	Complete (broke during analysis)	Scraping + grooving	Used: rounding/ smoothing
Hohle Fels	Aurignacian	1742	Canine	Complete	Drilling	Used: rounding/ smoothing
Hohle Fels	Aurignacian-Gravettian	2099.1	Canine	Complete	Scraping + grooving	Possibly used
Hohle Fels	Gravettian	1295	Canine	Complete	Scraping + grooving+ possibly widening	Used: rounding/smoothing/Polished
Hohle Fels	Gravettian	1228.29	Canine	Perforation unaccomplished	Carving + Scraping + grooving	Not Used
Hohle Fels	Aurignacian-Gravettian	1227.1	Root fragment	Fragmentary	NA	NA
Hohle Fels	Gravettian	461	Canine	Complete	Scraping + drilling	Used: rounding/ smoothing
Hohle Fels	NA	964.1	Canine	Fragmentary	Scraping + grooving	Not diagnostic

Under the microscopes, the assemblage shows different degrees of preservation: most teeth have shiny, damaged surfaces and two exhibit "very poor" preservation. Only two teeth are considered "well preserved".

Manufacturing Traces

At Hohle Fels, we identified two manufacturing techniques: (1) scraping/grooving and (2) drilling.

1. Scraping/grooving: nine teeth show traces of scraping or grooving, which we define as isolated groups of close, narrow striations, and/or deep grooves (Figure 5a–c). Technological deformations in sectors 1 and 6 of five teeth indicate deep gouging for the purpose of creating an opening in the root (Figure 5a). In three cases, we observed specular lateral deformations in sectors 3 and 9, which we interpret as the result of the widening and smoothing of the perforations through a semi-circular motion with a borer or pointed lithic tool (Figure 5c,d and comparison in the Supplementary Materials and Figure S2g–i). This scraping/grooving technique was always performed bifacially and resulted in elongated perforations on the vertical axis of the root (Figure 5a,c). Interestingly, tooth ID 1228 exhibits bilateral whittling/carving traces complemented by scraping, but it was abandoned during early manufacture before achieving a complete perforation, providing some insight into the order of operations (Figure 5e).

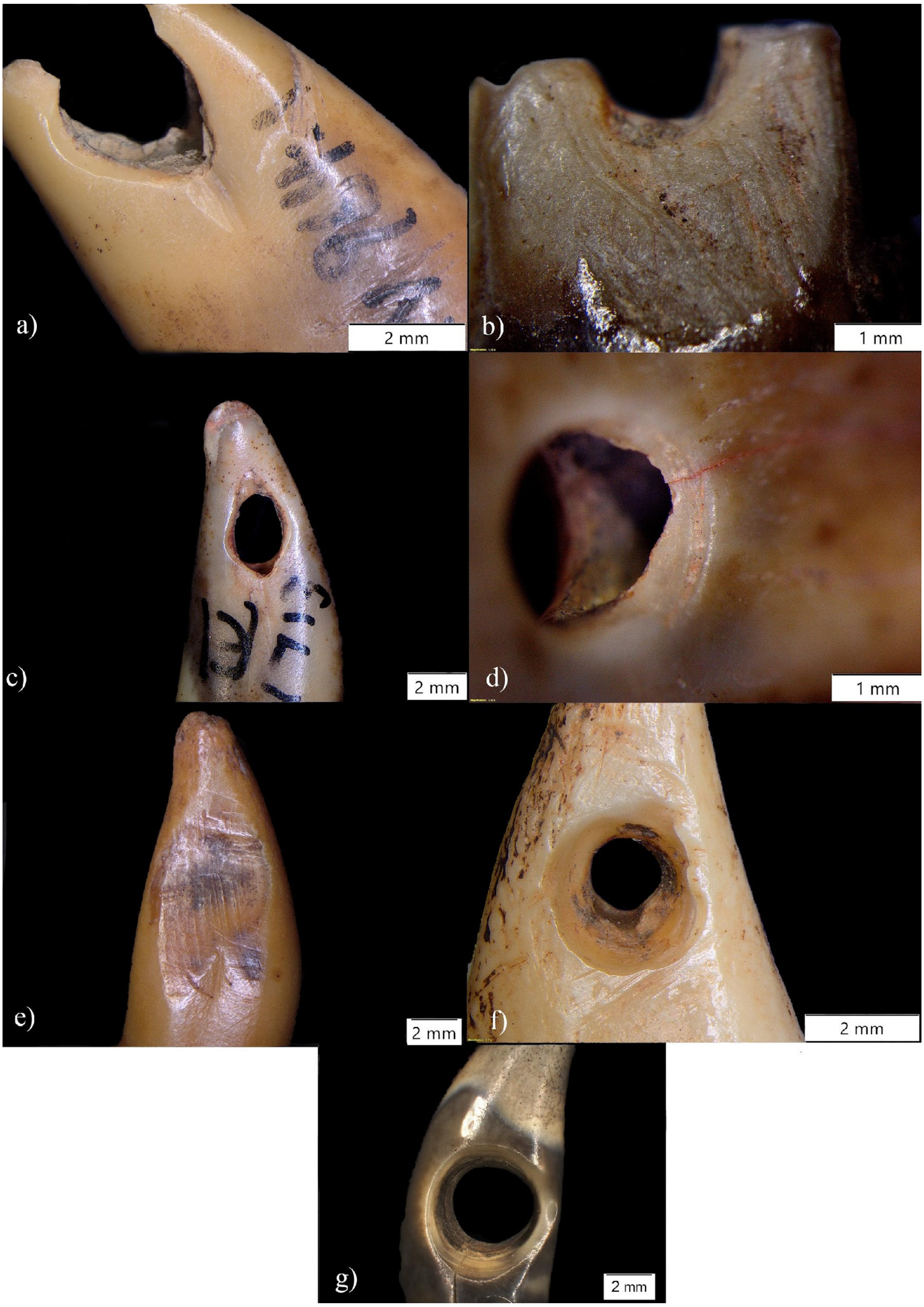


Figure 5. Overview of technological traces recorded on fox teeth from Hohle Fels. (**a**) ID 964, grooving marks; (**b**) ID 1137, scraping and grooving marks; (**c**) ID 1713, scraping and grooving marks and evidence of inner widening of the hole (notice the lateral half-moon enlargement); (**d**) ID 1517.1, circular striations by semi-rotational drilling; (**e**) ID 1228.2, whittling/carving marks and scraping traces; (**f**) ID 461, drilling traces; (**g**) ID 1742, drilling traces.

2. Drilling: Two teeth (ID 1742 and 461) exhibit clear concentric striations on the inner walls of their perforations, characteristic of the rotating action of a borer or a pointed

lithic tool. According to our reference collection, the perforation of tooth ID 461 was created by bifacial free hand drilling (Figure 5f). Tooth ID 1742 was probably bifacially perforated with the use of a bow drill or a hafted hand drill (Figure 5g). The difference between the two techniques is indicated by the high regularity of the drilling traces and the asymmetrical shape of the perforation, which indicates bow drilling. These features may result from the difficulty of controlling a bow drill at high speeds (see for comparison Figure S1h). Only the root surface of ID 461 appears to be prepared by scraping prior to drilling.

Use-Wear Related Traces

All seven teeth with complete perforations showed very round and smooth perforations, specimens ID 1742 and ID 1713 in particular. We found clear microwear traces associated with use on two specimens. On tooth ID 1295 and ID 1713, we recorded smooth and polished areas in sectors 1, 2, and 12 with linear traces in the form of long, shallow, and straight striations running parallel to the longitudinal axis of the root (Figure 6a–d, see Figure S6e for comparison).

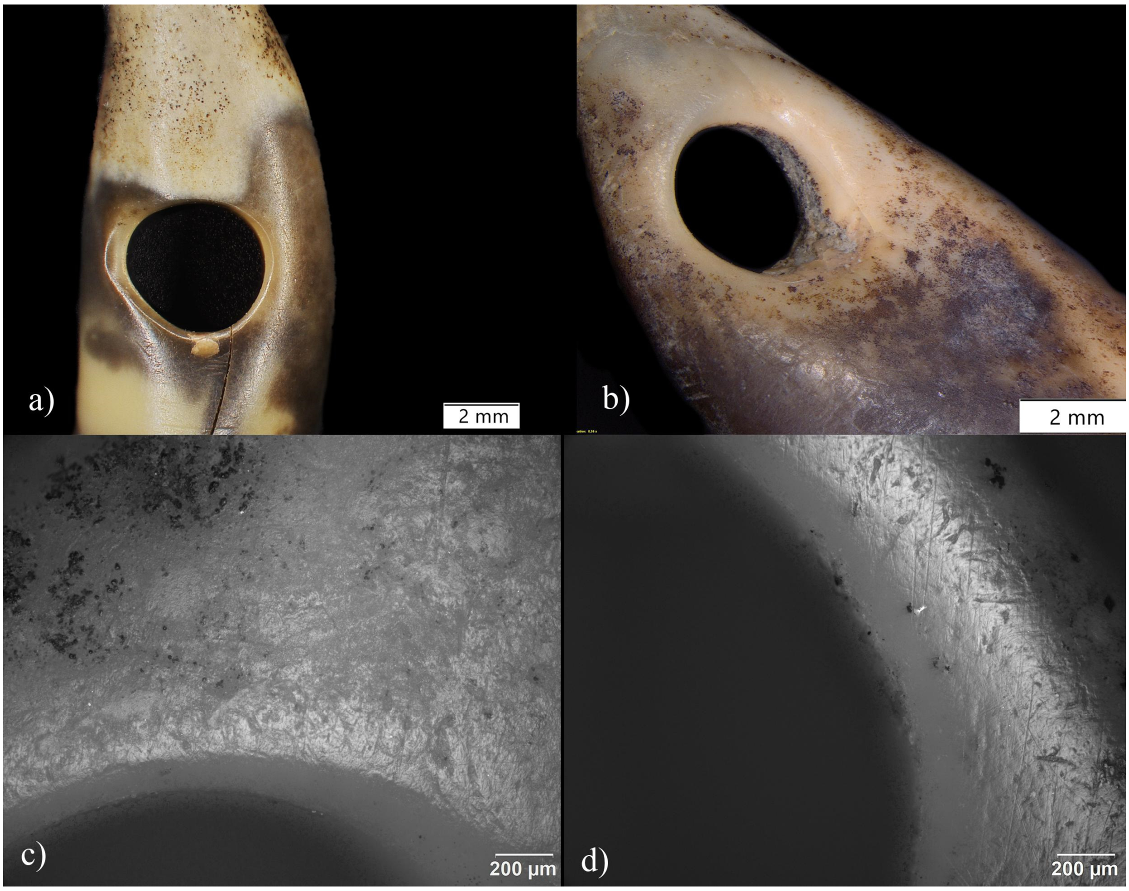


Figure 6. Overview of use-related traces recorded on fox teeth from Hohle Fels. (**a**) ID 1742, high rounding and smoothing; (**b**) ID 1295, rounding and smoothing; (**c**) ID 1295, rough polish developed in sector 12; (**d**) ID 1713, smooth polish with parallel long and narrow striations developed in sector 3.

3.2.2. Geißenklösterle

At Geißenklösterle, fox canines are represented by 12 total specimens divided as follows: five teeth with complete perforations, five with broken perforations, one non-human modified tooth, and another modified tooth with a broken root displaying no perforation (Table 4). The state of preservation is variable: two specimens exhibit very shiny surfaces, one is affected by patina, and three have calcite encrustation around the holes, while the remainder are in medium-good state of preservation.

Table 4. List of archeological fox teeth analyzed in this study from Geißenklösterle.

Site	Culture	Find Number (ID)	Tooth	Integrity of Perforation	Technique of Perforation	Use Traces
Geißenklösterle	Aurignacian	487	Canine	Fragmentary	Scraping + drilling/ lateral carving	Not eligible
Geißenklösterle	Aurignacian	1511	Canine	Fragmentary	Possibly scraped + widening	Not eligible
Geißenklösterle	Aurignacian	369	Canine	Fragmentary	Grooving	Not diagnostic
Geißenklösterle	most likely Gravettian	1A	Canine	Fragmentary	Gouging + widening	Not diagnostic
Geißenklösterle	most likely Gravettian	1B	Canine	Complete	Scraping + drilling	Not diagnostic
Geißenklösterle	Gravettian	391	Canine	Complete	Grooving + Carving	Used: rounding/polish/striae (lateral sides)
Geißenklösterle	Gravettian	918	Canine		Non-human modified	/
Geißenklösterle	Gravettian	658.2	Incisor (?)	Complete	Light scraping + possibly widening	Used: rounding/smoothing/ Polish (apex)
Geißenklösterle	Gravettian	89	Canine	Not preserved	NA	NA
Geißenklösterle	Gravettian	226	Canine	Fragmentary	Scraping + grooving	Not diagnostic
Geißenklösterle	Gravettian	387	Canine	Complete	Possibly scraping + widening	Used: rounding/polish/striae (lateral sides)
Geißenklösterle	Gravettian	286	Canine	Complete	Scraping/grooving + widening	Not diagnostic

Manufacturing Traces

As in Hohle Fels, at Geißenklösterle we identified two main production techniques: (1) scraping/grooving/gouging and (2) drilling.

1. Scraping/grooving/gouging. Scraping and grooving appeared in eight cases, sometimes combined with gouging. In all cases, this technique was performed bifacially. Scraping is represented by a bundle of close and narrow, long and short striations, while grooving is attested by deep isolated long grooves (Figure 7a–c). In the case of ID 391, the perforation was opened by bifacial gouging and superficial carving of the root, whose traces are evident in sectors 12 and 6 (Figure 7d). The perforations associated with this technique are elongated or sub-oval.
2. Drilling. Drilling is attested at Geißenklösterle from only two teeth, both showing traces of scraping to prepare the surface of the root. Clear circular and concentric drilling traces are visible at low and high magnification. The irregularity of the perforations suggests the use of free hand drills (Figure 7e,f). Interestingly, the root of ID 487 is worked in two ways, suggesting two different attachment methods. The root was previously scraped and subsequently drilled in order to obtain a circular hole, which later broke (Figure 7f,g). Underneath the perforation, the root is carved on both lateral sides to create two deep incisions, which might have served to secure a thread (Figure 7f,g). Unfortunately, we could not establish whether the perforation broke ab antiquo or was a result of post-depositional events. Moreover, we were unable to perform observations at higher magnification in search of use-related traces on the carved lateral sides, as the piece could not leave the museum. We thus cannot establish whether the root was carved after the perforation broke to re-facilitate attachment or if it was a stylistic choice.

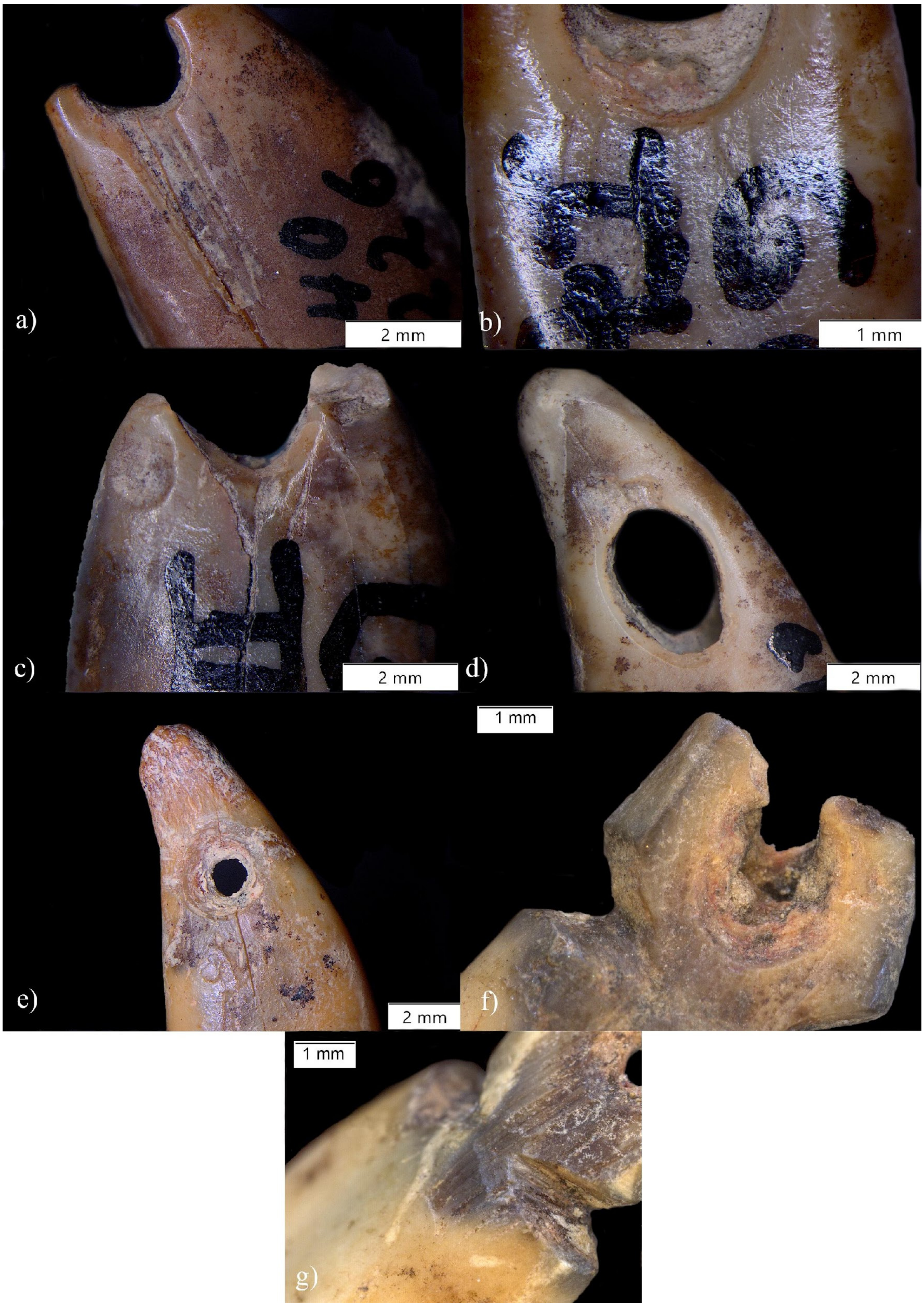


Figure 7. Overview of technological traces recorded on fox teeth from Geißenklösterle. (**a**) ID 226, grooving marks; (**b**) ID 658.2 scraping marks; (**c**) ID 360, grooving mark; (**d**) ID 391, carving traces in sector 12; (**e**) ID 1b, drilling traces; (**f**) ID 487, drilling traces and lateral carved notches; (**g**) ID 487, close up of scraping marks.

Use-Wear Related Traces

Out of four complete perforations, three showed polish and shallow long striations on the internal rim. In particular, ID 658.2 showed a small, polished area in sector 12 with a developed rounding of the internal rim (Figure 8a) while ID 391 and ID 76 exhibited a smooth polish on sectors 3 and 9 associated with striations (Figure 8b,c).

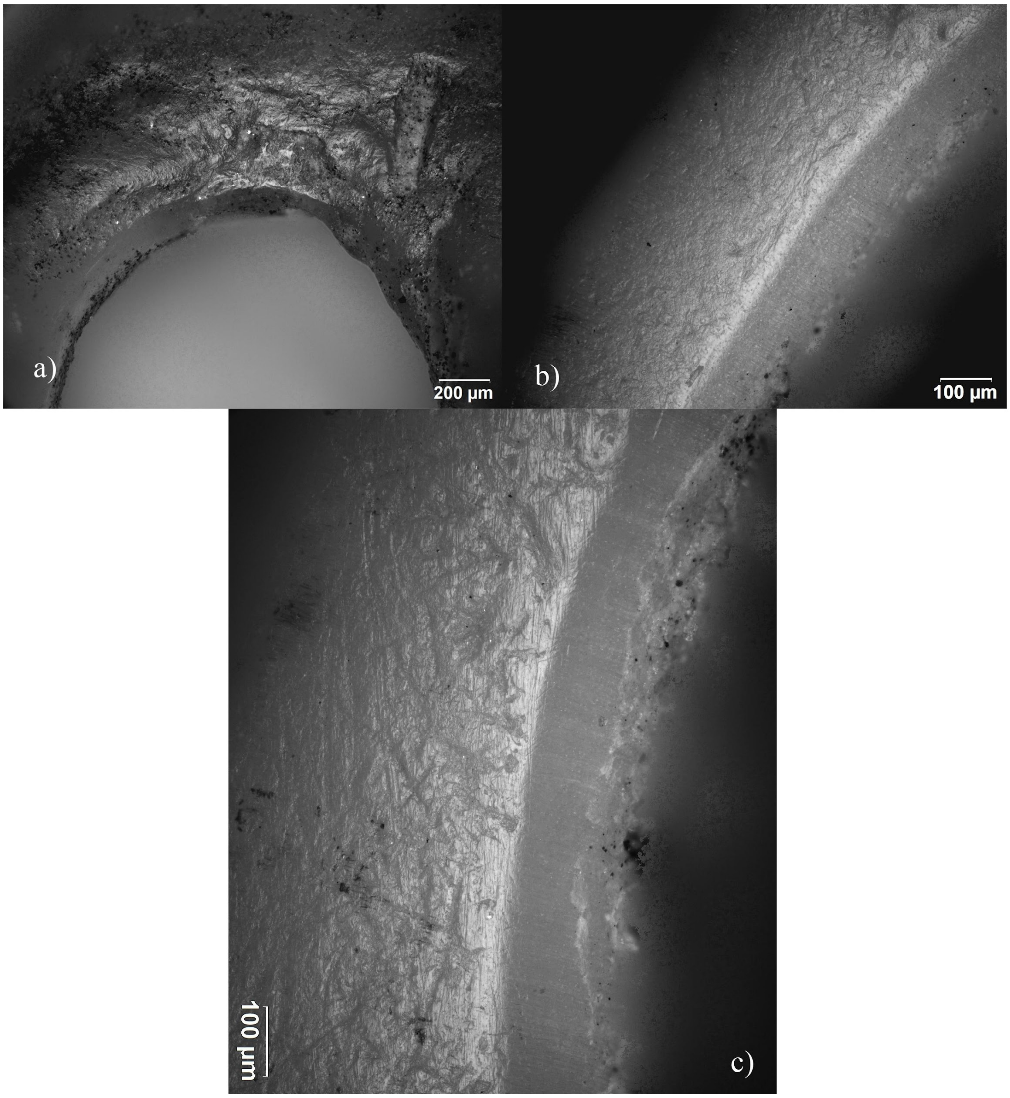


Figure 8. Overview of use-related traces recorded on fox teeth from Geißenklösterle. (**a**) ID 658.2, polish developed in sector 12; (**b**) ID 38F, smooth polish developed in sector 9; (**c**) ID 391, smooth polish with short shallow striations developed in sector 9.

3.2.3. Hohlenstein-Stadel

Perforated fox teeth are represented at Hohlenstein-Stadel by 13 specimens including seven canines, three incisors, and two premolars. A root fragment showing a complete perforation could not be assigned to a specific tooth type (Table 5). The state of preservation of the entire sample is good. Most teeth displayed complete perforations, and only four were broken in the upper part of the eyelet. Unfortunately, 10 teeth showed varnish around the perforations, and some had traces of glue inside the holes, which hampered observation at high magnification.

Table 5. List of archeological fox teeth analyzed in this study from Hohlenstein-Stadel.

Site	Culture	Find Number (ID)	Tooth	Integrity of Perforation	Technique of Perforation	Use Traces
Hohlenstein-Stadel	Aurignacian	1.0380	Canine	Complete	Scraping + widening	Most likely used: rounding
Hohlenstein-Stadel	Aurignacian	2.0380	Canine	Complete	Scraping + carving	Most likely used: rounding
Hohlenstein-Stadel	Aurignacian	3.0380	Canine	Complete	Scraping	Most likely used: rounding
Hohlenstein-Stadel	Aurignacian	4.0380	Canine	Fragmentary	Scraping + grooving	Not diagnostic
Hohlenstein-Stadel	Aurignacian	5.0380	Canine	Complete	Scraping	Not diagnostic
Hohlenstein-Stadel	Aurignacian or Magdalenian	14.1	Canine	Fragmentary	Grooving	Not diagnostic
Hohlenstein-Stadel	Aurignacian or Magdalenian	141.1	Canine	Fragmentary	Scraping + possibly widening	Not diagnostic
Hohlenstein-Stadel	Aurignacian or Magdalenian	167.1	Root fragment	Complete	Possibly abrasion/ scraping + widening	Most likely used: rounding
Hohlenstein-Stadel	Aurignacian or Magdalenian	178.1	Premolar	Complete	Possibly abrasion/ scraping + widening	Most likely used: rounding
Hohlenstein-Stadel	Aurignacian or Magdalenian	33.1	Premolar	Complete	Carving + widening	Most likely used: rounding
Hohlenstein-Stadel	Aurignacian or Magdalenian	36.1	Incisor (?)	Complete	Possibly abrasion/ scraping + widening	Used: rounding/ smoothing
Hohlenstein-Stadel	Aurignacian or Magdalenian	9000.1	Incisor (?)	Complete	Possibly abrasion/ scraping + possibly widening	Most likely used: rounding
Hohlenstein-Stadel	Aurignacian or Magdalenian	9001.1	Incisor (?)	Fragmentary	Possibly abrasion/ scraping + possibly widening	Not diagnostic

Manufacturing Traces

Only one technique was attested at Hohlenstein-Stadel for perforating fox teeth: scraping. All 13 teeth were longitudinally scraped to flatten and thin the root, the marks of this preparation being visible as long and irregular striations (Figure 9a,b,d,e). In several cases, the extension of the striations exceeded the area of the hole, reaching the enamel. Bifacial longitudinal scraping was performed until perforations were achieved, resulting in perforations with an elongated form (Figure 9b,d,e). However, we recognized traces corresponding to the widening of the hole, likely to achieve a more rounded and regular shape (Figure 9c).

It is interesting to notice that the five canines likely associated with the Aurignacian horizon show a common singular technological trait: the upper part of the root is strongly bent, almost to form a step between the end of the perforation and the apex of the root (Figure 9d–f). This was due to the deep and strong scraping resulting in an almost carved surface on the apical side of the perforation, well visible in tooth ID 2.380 (Figure 9e).

Hohlenstein-Stadel is the only site in the Swabian Jura to report perforated fox premolars. Interestingly, two premolars and three incisors show flat facets around the perforation in association with striations, which differ from those on the canines in being wider, more regular, deeper, and in an oblique direction (Figure 9g,h). In those cases, abrasion against a coarse surface might better explain these traces than scraping with a lithic tool. However, they are subsequently worked following the same scheme, namely by flattening the surface until achieving the perforation and later widening the hole with bifacial semi-rotation.

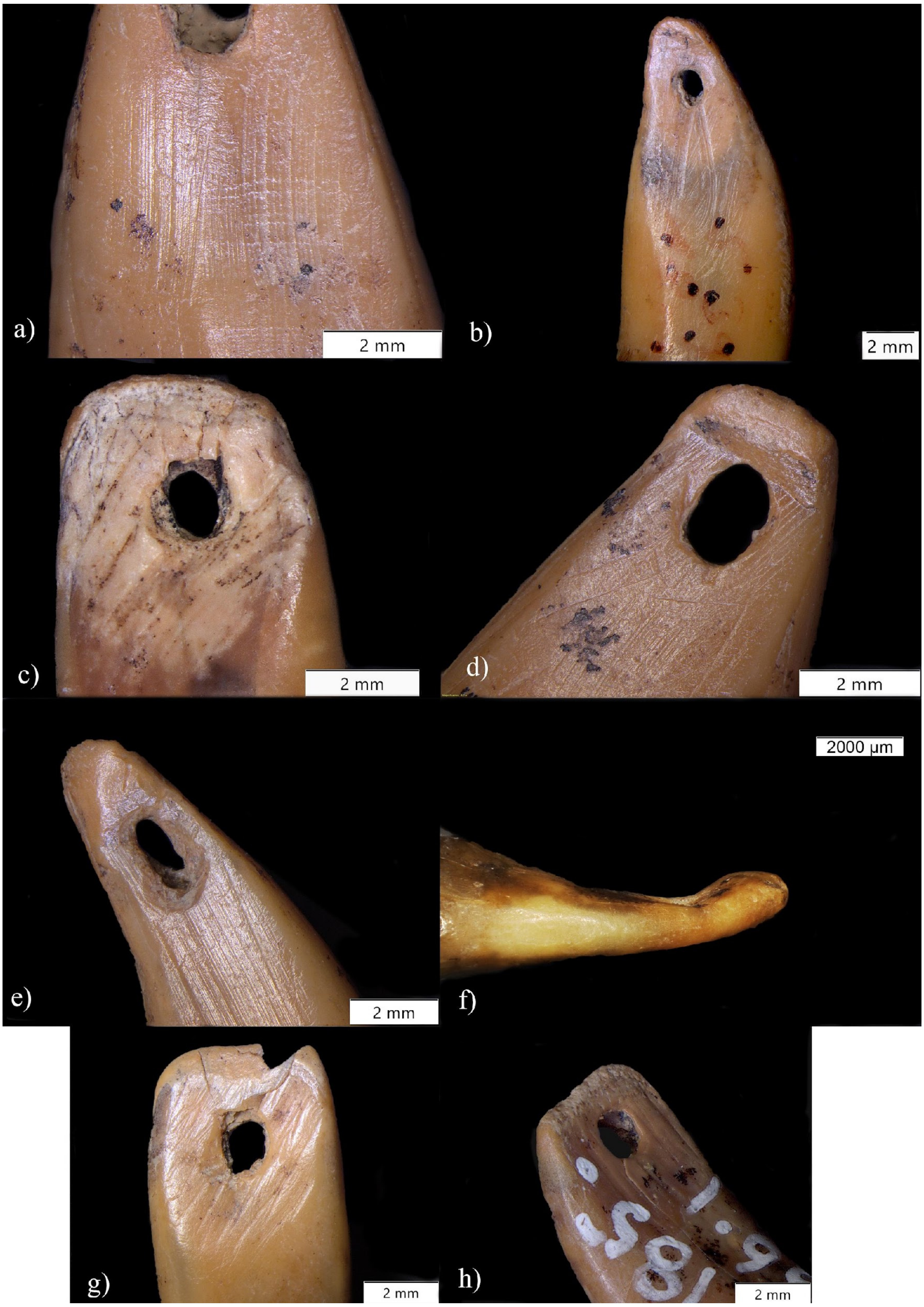


Figure 9. Overview of technological traces recorded on fox teeth from Hohlenstein-Stadel. (**a**) ID 3.380, scraping marks; (**b**) ID 1.380, scraping and grooving marks; (**c**) ID 178.1, widening by semi-rotational drilling; (**d**) ID 3.380, deep scraping marks resulting in a bent upper root; (**e**) ID 2.380, striations and carving marks; (**f**) ID 33.1, deep carving resulting in a bent upper root; (**g**) ID 167.1, abrasive/scraping marks; (**h**) ID 36.1, flat facet and abrasive/scraping marks.

Use-Wear Related Traces

Among the teeth with complete perforations, five showed a well-developed rounding of their internal and external rim, especially localized in sectors 12, 3, and 9 (Figure 10a–d). On five better-preserved teeth subjected to observation at higher magnification, we did not identify any diagnostic use-related microwear. The rest of the assemblage exhibited traces of varnish and glue and, consequently, it was not possible to perform more detailed microscopic observations.

Figure 10. Overview of use-related traces recorded on fox teeth from Hohlenstein-Stadel. (**a**) ID 178.1, rounding and smoothing of the inner and outer rim; (**b**) ID 36.1, rounding and smoothing of the rim; (**c**) ID 9001.1 rounding of the rim; (**d**) ID 178.1, rounding of the inner wall of the perforation.

3.2.4. Brillenhöhle

At Brillenhöhle, three perforated canines come from the Gravettian. Two show complete perforations and good preservation of the surfaces, while one is broken on the apical side of the root (Table 6). We could only make macroscopic observations of these teeth and were unable to perform observations at higher magnification because the specimens could not leave the museum.

Manufacturing Traces

The perforations of all three ornaments were achieved by scraping/grooving. However, scraping was not performed as a preliminary thinning treatment, but rather to directly achieve the perforation. On ID 130, the remaining lower part of the perforation in sector 6 is V-shaped, suggesting an original elongated hole made by grooving/carving (Figure 11a). Specimen ID 132 exhibited unifacial short grooves and a depression on the upper part of the hole produced by deeply grooving the root. On the other face, the perforation showed traces of widening for regularizing the shape of the hole (Figure 11b). Tooth ID 131 carries a few technological traces and exhibits a round and smooth perforation. Due to the presence of encrusted soil particles on the inner wall, it was not possible to ascertain if the perforation was made by drilling or by semi-rotation for widening the hole. No clear rotational traces are visible even if the roundness of the hole suggests a complete rotational movement. A depression in the upper part of the root might suggest a scraping/grooving activity (Figure 11c).

Table 6. List of archeological fox teeth analyzed in this study from Brillenhöhle.

Site	Culture	Find Number (ID)	Tooth	Integrity of Perforation	Technique of Perforation	Use Traces on Perforation
Brillenhöhle	Gravettian	132	Canine	Complete	Grooving/carving + widening	Most likely used: rounding/smoothing
Brillenhöhle	Gravettian	131	Canine	Complete	Scraping/grooving + widening or drilling	Most likely used: rounding/smoothing
Brillenhöhle	Gravettian	130	Canine	Fragmentary	Scraping + grooving	Not diagnostic

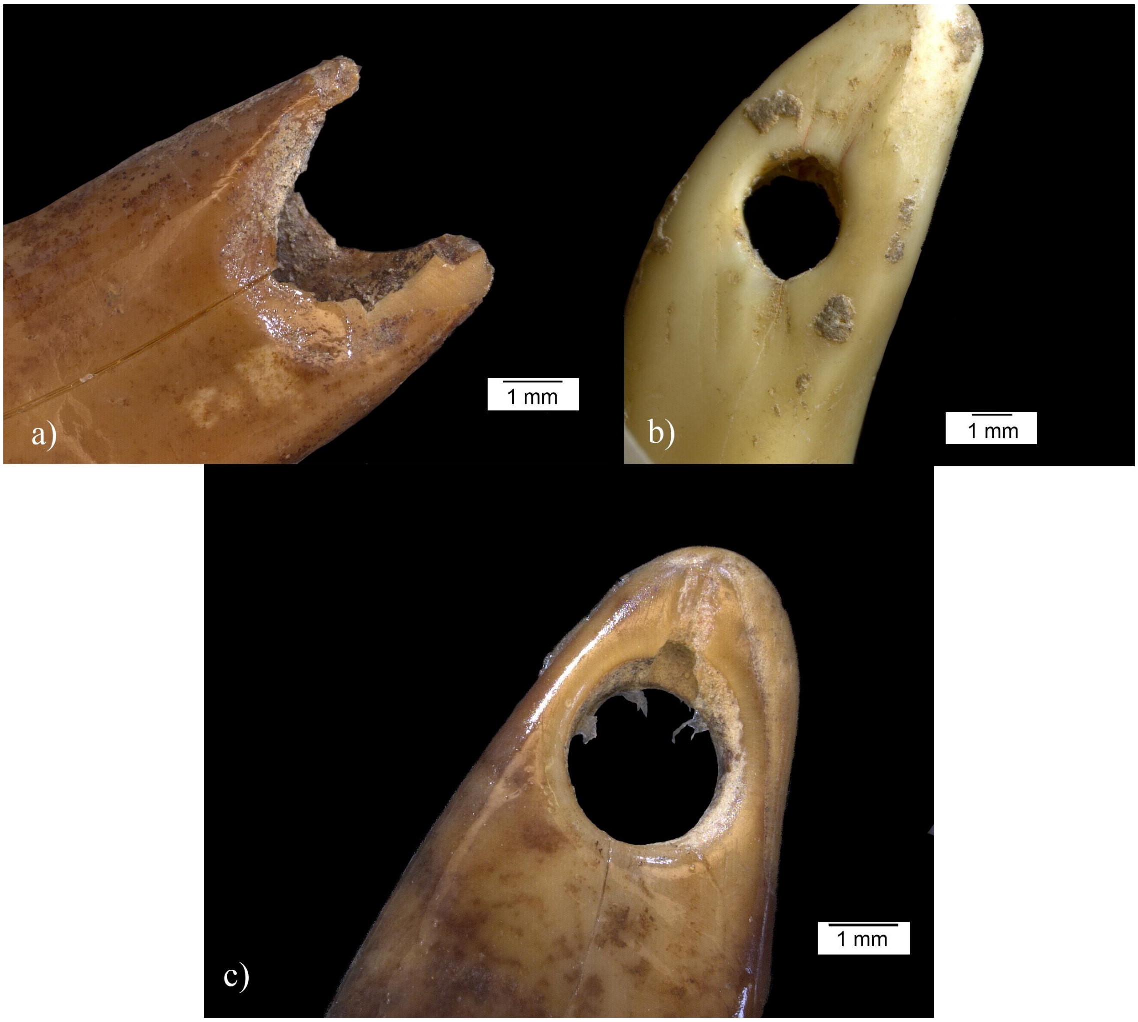


Figure 11. Overview of technological traces recorded on fox teeth from Brillenhöhle. (**a**) ID 130, carving marks, (**b**) ID 132, grooving marks; (**c**) ID 131, grooving mark in the upper perforation.

4. Discussion

The use of animal teeth as ornaments during the Upper Paleolithic provides valuable insights into the creativity, symbolism, and cultural practices of our ancestors, giving us a glimpse into their way of life and how they interacted with the natural and animal world. Indeed, the use of animal remains as a source of food, as well as a raw material (e.g., teeth for ornaments, fur for clothes, bones for tools), evidences an intimate relationship between humans and animals. This is particularly true for animals like foxes, which exhibit behaviors showing their charisma, adaptiveness, and ability to influence their surroundings and shape human communities. The human–fox relationship—today, as in the past—is often characterized by the commensal behavior of foxes and their coexistence with humans and their ability to thrive in human-constructed environments [38,44,54,55,89–91]. The result of this relationship is still observed in urban and suburban environments today, where foxes often live in close proximity to humans [92,93].

This human–fox relationship also existed in prehistory, as evidenced by the frequent occurrence of fox bones and teeth in the archaeological record, many of which were used to produce ornaments [55,94]. Although foxes are not the most common taxa in the archeological record of the Swabian Jura [55], their perforated teeth are a particularly informative class of artifacts with the potential to shed light on the role foxes played in past human societies.

4.1. Production of Fox Tooth Ornaments in the Swabian Jura

The results presented in this study show that canines were the preferred tooth type for ornamentation made from foxes in the Swabian Jura. In our assemblage, Hohlenstein-Stadel exhibits ornaments made from other teeth, namely incisors (one of which is also present at Geißenklösterle) and premolars, albeit in lesser quantities than canines. Based on the available published data, only a handful of other sites share this variability in tooth choice, one of which is the Magdalenian site of Petersfels (Germany), a few hundred kilometers south of the Ach and Lone valleys in the Swabian Jura (see Table S1) [95–97]. Given the uncertain context of some of the Hohlenstein-Stadel ornaments as either Aurignacian or Magdalenian, it is possible that the use of premolars and incisors indicates a Magdalenian origin for these five ornaments, like those represented at Petersfels.

From a traceological point of view, we noticed that five Hohlenstein-Stadel canines (Aurignacian) were processed by scraping with a lithic tool, while the two premolars and three incisors (Aurignacian or Magdalenian) were possibly abraded to achieve the perforations. This difference might suggest a deliberate cultural choice in technique. However, the other two canines from the uncertain context also show traces in line with the five Aurignacian canines, suggesting the chosen technique was more dependent on tooth type and likely morphology rather than a cultural or individual preference. Tooth morphology also influences the practical aspects of perforation. Canines, for example, are larger with a greater root surface area than other teeth, making ornament production easier and perhaps providing a specific aesthetic function regarding their shape, size, and luster.

Despite the likely morphological influence on production technique, some of the Hohlenstein-Stadel ornaments may still belong to the Magdalenian, given their uncertain stratigraphic context. However, a cultural explanation for tooth preference is complicated by the broader record of fox tooth ornaments throughout the Upper Paleolithic. Ornaments made from fox incisors and premolars are found at numerous sites across Europe in the Magdalenian but also the Gravettian [34,86,94–96,98,99] (Table S1). Retracing the context of the Hohlenstein-Stadel ornaments, as well as traceological comparison with other ornament assemblages, may thus illuminate the potential hunter-gatherer networks that influenced tooth choice in the Swabian Jura.

Regarding the perforation techniques, our four sites show a common trend: the preferred technique was bifacial scraping and grooving combined with the widening of the hole to regularize the perforation. In most of the analyzed teeth, the scraping and grooving technique was not performed to thin the root as a surface preparation, but rather to make the perforation itself. Only two specimens (one from Hohle Fels and one from Geißenklösterle) were instead scraped before being rotationally drilled. In one case, we recorded deep gouging around the perforation (ID 2.0380), while in a few others, the root was scraped and carved producing a hollowed facet around the hole (ID 1228, ID 33-1).

According to our experimental reproductions, scraping and grooving was an efficient method of perforation that did not require any prior surface treatment. For teeth from larger animals with thicker roots, this might not be the case. By analyzing perforated teeth from other animal species at Hohle Fels and Geißenklösterle, we noticed that horse incisors always exhibit a scraped surface before the perforation is achieved by drilling (F.V., personal communication). This reflects the need to adjust perforation techniques according to the constraints of the raw material.

In our assemblage, we did not notice any correlation between a specific technique with a particular cultural horizon or site. This might reflect our singular focus on fox teeth. Comparing the perforated teeth from different animal species at these sites (for an overview of numbers and percentages see Table S6) may highlight variations in techniques revealing a tooth functional-dependent choice, rather than cultural or individual preferences. However, it is worth noting that the five canines assigned to the Aurignacian at Hohlenstein-Stadel show the same technological trait of bent upper roots (Figure 9d,f). This signature is a distinct marker for the site and strengthens the attribution of the teeth to the same Aurignacian horizon. Moreover, we suggest here the possibility that these five teeth were worked by the same person using a distinctive and repetitive technical gesture, which was not recorded at the other sites.

Another aspect to discuss is if and how the teeth were worn. Microtraces on teeth are always very ambiguous because of their naturally shiny surfaces and animal life history, especially considering the various post-depositional processes that can also impact preservation. However, macro traces such as rounding and smoothing localized on the inner and outer rim of perforations are a clear marker of use. More difficult is to reconstruct when teeth served as hanging pendants or when they were sewn to clothes or other objects. In our assemblage, we considered all well-preserved teeth with complete perforations to be most likely used, based on the presence of developed and localized rounding and smoothing of the perforations (Tables 3–6). For the teeth exhibiting use-related polishes and striations, we do not feel confident in assigning a specific attachment mode or binding method. However, the presence of striations recorded on some specimens may be related to the use of abrasive strings like nettle or other rough vegetal/animal materials. Strings treated with colorant such as ochre can also develop smoother polish and bundles of striations. Indeed, we recorded traces of red pigment in seven teeth from Hohle Fels and one from Geißenklösterle. Other than ID 1713 (Figure 5c), which shows reddish traces inside the inner rim in association with rounding, polish, and striations likely from ochred strings, we interpreted most red coloration as post-depositional, given its presence within recent fractures, in the cavity of the root, and/or mixed with the adhering sediment.

4.2. Selection of Red versus Arctic Fox

The relationship between humans and a specific fox species—red or arctic—is often impossible to determine in the archaeological record, given the nondiagnostic nature of isolated faunal elements. Differentiation in loose teeth is particularly tricky (see Supplementary Materials). Although some teeth are distinguishable based on size, canines are more ambiguous [100], and prior attempts at metric differentiation [101] exhibit notable flaws that decrease the reliability of species determinations [39,102–105]. For this reason, a geometric morphometric approach is advantageous and a potential improvement on existing morphological and metric methods.

With the help of our modern comparative sample, we successfully determined the species of 17 (71%) ornaments from our archaeological sample. Although some ornaments plotted outside the recent fox ranges, their position within the PCAs still shows tendencies toward a specific classification. The larger range of the archaeological sample may indicate noise in landmark placements, which is expected in archaeological specimens due to post-depositional damage resulting in alterations to the cervical outline. Other factors, such as variation between individuals, sexes, and populations also impact crown heights.

Our results show that both red and arctic foxes were used to produce ornaments in the Swabian Jura. On a site level, there is no clear preference for species; however, the total assemblage includes slightly more arctic than red foxes. Between cultural periods, there is also no strong preference for species—the Aurignacian is represented by five red foxes and six arctic foxes, while the Gravettian includes two red foxes and four arctic foxes.

Concerning the broader Upper Paleolithic record of fox tooth ornaments, few studies provide species-specific identifications. Our literature review revealed limited information from Aurignacian assemblages, but more from the Gravettian and the Magdalenian. In the Gravettian, two notable sites report high numbers of perforated arctic fox teeth: 42 at the Czech site of Dolní Věstonice I (alongside 31 indeterminate) and 41 at the Russian site of Zaraysk (Table S1) [99,106,107]. For the Magdalenian, 16 perforated arctic fox teeth are reported from Petersfels (alongside 25 indeterminate), at least 5 come from Kniegrotte [95–97], and 162 were recovered from Wilczyce in Poland (Table S1) [86]. Few sites report perforated red fox canines, with Dolni Věstonice I being the only clear example from our literature review [99,106,107].

Despite the overwhelming abundance of perforated arctic fox canines, both arctic and red foxes were available to hunter-gatherers across Europe. In the Swabian Jura, red and arctic foxes were even found within the same layers at sites like Geißenklösterle [39]. Although both species were likely sympatric during the Upper Paleolithic (see Supplementary Materials), their abundance may have varied. In modern sympatric contexts, arctic foxes are observed in smaller numbers [108–111]; if the same were true for the Paleolithic, hunter-gatherers would have encountered red foxes more frequently. As acquisition methods like traps and snares were non-selective, the ratio of captured animals would thus reflect this natural abundance. However, setting traps at known fox dens, perhaps dens used by a single species, may have enabled selective acquisition (see Supplementary Materials).

It is thus possible that the relative scarcity of arctic foxes on the landscape increased their value as a motif for ornamentation and influenced their preferential exploitation across Europe. However, local paleoenvironments and faunal assemblages should be considered. Although foxes were likely sympatric in a broad sense, our modern understanding of interspecific fox relationships may be a poor analog for the Paleolithic. Additionally, climate and environmental conditions varied significantly throughout this period, sometimes within a short timeframe, potentially influencing the degree of species overlap. The resolution of the archaeological record may also limit our ability to parse moments in time when conditions were more or less hospitable to a particular species. A closer look at the ratio of red and arctic foxes in the broader faunal assemblages would further illuminate their nuanced relationship within the local paleoenvironment. Biomolecular techniques, such as aDNA and ZooMS [112,113], would also increase the reliability of these distinctions.

In the Swabian Jura, some information on the ratio of foxes in the broader faunal assemblages is available [39,46,51,55]. As with the ornaments, there is no overwhelming preference for arctic versus red fox. This near-equal distribution suggests the ornament ratio likely reflects the hunted ratio and perhaps the ratio of animals on the landscape. Butchery traces indicate foxes were used as food and for their fur. Concerning the former, other species, namely ungulates, provided a far greater contribution to hunter-gatherer diet. However, fox fur may have served a unique purpose. Arctic foxes are uniquely valued amongst modern arctic hunter-gatherer populations for their small size and bright, white color [114,115]. This then may be a convincing argument for the relative overabundance of arctic fox canines elsewhere in Europe—an aesthetic or functional preference for their fur.

A final consideration is the method of identification. Arctic fox canines, due to their small size, are far more recognizable with simple morphological and metric characteristics. Those in the area of overlap may go unidentified, or are identified as arctic fox by default, and few specimens are large enough to be confidently identified as red fox. Unfortunately, few studies report their methods of species determination and the commonly applied metric method [101] may be biased towards arctic foxes [39]. Future application of geometric-morphometric methods, like those applied in this study, would help to clarify this point and allow further investigation of the other factors influencing red versus arctic fox abundance in the Upper Paleolithic.

4.3. Fox Tooth Ornaments in the Broader European Context

We report the data from our literature review of fox tooth ornaments across the European Upper Paleolithic in Table S1. These ornaments first appear in small numbers during the Châtelperronian at sites such as La Grotte du Renne [20,116]. Increasing in the Aurignacian, fox tooth ornaments dominate various German, French, and Russian sites [10]. The richest French sites are those of Isturitz, Saint-Jean-de-Verges, and La Quina, showing 13, 14, and 28 perforated canines, respectively [25,117,118]. In Russia, Kostenki hosts at least 37 pierced fox teeth from the Initial and Early Upper Paleolithic layers, the richest for the Aurignacian [119]. Comprehensive studies on the investigation of perforation techniques are generally rare, but at Isturitz fox canines were first thinned by fine abrasion and then bifacially scraped to open a perforation. Deep carving of the root followed by scraping and bifacial semi-rotational perforation is also attested [25].

Foxes continued to be an important ornament resource during the Gravettian, especially in Central and Eastern Europe. Hunter-gatherers also began to exploit a greater variety of tooth types, including incisors and premolars in addition to canines. In Czechia, two sites in Moravia recorded a high number of fox teeth used as pendants. At Pavlov I, a total of 284 perforated fox teeth were discovered, among which 146 are incisors, 105 are canines, and 33 are premolars [94]. The nearby site of Dolní Věstonice I reports 73 perforated teeth, of which 42 are canines [106,107]. Moving eastward, in Russia, the site of Zaraysk exhibits only 32 incisors and 9 premolars for a total of 41 teeth, all assigned to arctic fox and found together as a "necklace" [99]. The funerary site of Sunghir in Russia offers the best glimpse into the complex worldview of some of the first anatomically modern humans in Europe. Within the several burials, a large number of fox tooth ornaments (>300) were discovered in situ and in close association with human remains, offering a snapshot of how personal ornaments were worn by this group of hunter-gatherers [17,120]. Numerous perforated fox teeth were found on the forehead of an adult male (Sunghir 1), >40 on the cranial vault and >250 on the belt of another individual (Sunghir 2), one in association with an isolated cranium (Sunghir 5), and at least two found in association with a final individual (Sunghir 10). In addition to heavy adornment, the individuals were also covered with a large quantity of red ochre and other grave goods [17].

Foxes are also well-represented in Magdalenian ornament assemblages from Germany and France with 41 perforated teeth from Petersfels [95–97] and 45 from Gönnersdorf in Germany [31,121,122] as well as at least 35 from the Magdalenian layers of Isturitz [85] and La Vache [123], 12 from La Madeleine [124], and 13 from Bruniquel [125,126] in France. Although canines were the preferred tooth type, Petersfels also exhibits several incisors and premolars. With 162 fox teeth, the Polish site of Wilczyce is the richest with 149 pierced incisors alongside 13 canines. These were all acquired from the upper jaws of a minimum of 31 arctic foxes and may represent the remains of a necklace associated with a neonatal burial [86].

These data show that the Upper Paleolithic sites of the Swabian Jura are in line with the general trends observed across Europe concerning the use of fox teeth as ornaments. Their exploitation does not represent a unique signature or a key cultural marker for the region, but a shared and well-established behavior amongst European Upper Paleolithic groups. Canines are the preferred tooth type in both the Swabian Jura and the whole of Europe, while incisors and premolars are less frequently used, although their presence might represent a cultural preference or individual choice within certain groups of hunter-gatherers. The techniques of perforation used in the analyzed sites compare well with other European sites; although, scraping seems more common to achieve the perforation itself rather than as a surface preparation method. The ubiquitous presence of perforated fox teeth throughout the Upper Paleolithic in Central Europe attests to the important role and intimate relationship this animal established with prehistoric human communities. Although rare, evidence of fox butchery in the Swabian Jura suggests they were hunted for food, for their furs, and as a raw material for ornamentation. The diversity of resources provided by foxes along with their commensal behavior likely granted them a special significance in the ecological, dietary, functional, and symbolic realms of Upper Paleolithic hunter-gatherers.

5. Conclusions

Our results provide insight into the role of foxes during the Upper Paleolithic, especially regarding human subsistence, cultural expression, and ornament production.

Focusing on the latter, we cannot overlook the fact that foxes were one of many species exploited for ornamentation in the Swabian Jura. Other taxa whose teeth were used as ornaments include various herbivores like horses, reindeer and red deer, as well as carnivores such as wolves, bears, and lions (Table S6). However, like the other species, foxes had their own unique relationship with humans. As previously discussed, their opportunistic nature likely drew foxes to human food waste, bringing both species closer together in commensal relationships, which are attested to throughout the Upper Paleolithic. Once connected, foxes played at least three key roles: as a resource, as a symbol, and as a companion animal [127]. The latter two are less tangible in the archaeological record, while study of material culture derived from foxes allows us to illuminate the economic and symbolic significance of foxes in the Upper Paleolithic.

Although butchery traces on fox remains are rare, cut marks suggest foxes were likely consumed as food in the Swabian Jura. Other marks indicate their use as a raw material, particularly for their fur, a valuable resource for clothing and other sewn goods [53,55]. The striking color and waterproof quality of their pelts likely played a role in the selection and use of foxes for this resource [121]. While direct evidence is lacking, fox bones may have also been used for tools (e.g., awls). Otherwise, fox tooth ornaments are the best example of the use of foxes as a raw material.

The study of fox tooth ornaments helps us to unravel the symbolic importance of foxes among Upper Paleolithic hunter-gatherers. This is because ornaments are social objects, capable of reflecting otherwise unsaid aspects of the wearer, conveying messages on ethnic, gender, social, and/or personal identity [14,15,128,129]. We can thus assume foxes, both as a raw material and as a species, had a symbolic value in the lives of the hunter-gatherers who wore their teeth.

Despite their clear symbolic importance, it is surprising that foxes are rarely depicted in parietal or figurative art, other than a cave engraving at the Aurignacian site of Altxerri B Cave in Spain [130]. In comparison, ungulates and larger predators, such as lions or bears, are regularly depicted. This appears to change, however, during the Pre-Pottery Neolithic and Natufian, when foxes increase in abundance, are commonly depicted in relief (e.g., at Göbekli Tepe, Turkey) [131], and are buried alongside humans (e.g., at Uyun al-Hammam, Jordan) [132]. A continued strengthening of the human–fox relationship is also evidenced in the Neolithic [131,133], with the first possible evidence of fox domestication in the Early-Middle Bronze Age [134].

To conclude, there is no doubt that the relationship between humans and foxes was significant and started as early as the Initial Upper Paleolithic. The effect of this long-lasting link still persists today in the folklore and mythology of many cultures, which depict foxes as beautiful, clever, cunning, and magical beings [135,136].

Supplementary Materials: The following supporting information can be downloaded at: https://www.mdpi.com/article/10.3390/quat6030050/s1, Figure S1: Overview of experimental technological traces by drilling, Figure S2: Overview of experimental technological traces by scraping/grooving, Figure S3: Overview of experimental technological traces by scraping or abrading and drilling, Figure S4: Example of various ornament replicas and modes of attachment during the experimentation, Figure S5: Pre- and post-use macrographs of perforations, Figure S6: Micrographs of polish recorded on the perforations and corresponding location, Figure S7: Error margins for the 16 landmarks placed along the cervical outline, Table S1: Summary of the literature review on Upper Paleolithic fox tooth ornaments, Table S2: List of archaeological fox canines included in the geometric-morphometric analysis, Table S3: List of modern fox canines included in the geometric-morphometric analysis, Table S4: Experimental fox canine replicas and related technological results, Table S5: Experimental fox canine replicas with wear information and related recorded traces, Table S6: Perforated animal teeth from the Swabian Jura (Hohle Fels, Geißenklösterle, Brillenhöhle, Bockstein, Hohlenstein-Stadel, and Vogelherd). Ornaments unidentifiable to species and ornaments from uncertain stratigraphic contexts are not included [137–248].

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