quaternary

Supplementary Materials

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

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1. Upper Paleolithic of the Swabian Jura

The Swabian Jura, a low mountain range north of the Alps constrained by the Danube and Neckar rivers, hosts some of the richest Paleolithic sites in Central Europe. Early investigations began in the late 1800s with the first systematic excavations conducted by Fraas, followed by the earliest synthesis of the German Paleolithic by Schmidt [137–139]. Excavations and research are still ongoing, especially in the Ach and Lone valleys, which preserve a notable concentration of sites and material culture spanning the Middle to Upper Paleolithic.

Modern humans arrived in the Swabian Jura ~40,000 years ago, establishing an early Aurignacian occupation in Central Europe [140–143]. This industry exhibits abundant and diverse material culture, including some of the first forms of symbolic representation, such as ivory figurines of female and animal figures, bone and ivory flutes, and a wealth of personal ornamentation [3,4,4–8]. Upper Paleolithic ornament forms include beads made from ivory (e.g., double perforated beads, basket-shaped beads, teardrop pendants), animal teeth (cave bear, hyena, deer, fox, horse, ibex, wolf), bone, antler, soapstone, shell, fossil ammonite, and jet [5,26,140].

Our study focuses on four Paleolithic sites in the region that preserve fox tooth ornaments: three from the Ach Valley (Hohle Fels, Geißenklösterle, Brillenhöhle) and one from the Lone Valley (Hohlenstein-Stadel).

1.1. Hohle Fels

Hohle Fels is a large cave located seven meters above the Ach River [144]. Excavations began in the late 19th century with Oscar Fraas and Theodor Hartmann, followed by Robert Rudolf Schmidt, Gustav Riek, and Joachim Hahn in the early to mid-20th century [62,138,145]. In 1997, excavations were reinstated under the direction of Nicholas Conard in association with the University of Tübingen [146]. The Upper Paleolithic layers are attributed to the Aurignacian (Vb, Vaa, Va, IV, IIIb, and IIIa) dated to ~42–37 ka cal BP [147], the transitional Aurignacian-Gravettian (IIe and IId) and Gravettian (IIcf, IIc, and IIb) dated to ~35–31 ka cal BP [148], and the Magdalenian (IIa and I) dated to ~17–15 ka cal BP [149,150]. Significant findings include a diverse array of personal ornamentation [8], ivory figurines [3,4,151], the earliest known flute made from bird bone [7], and evidence of pigment processing alongside painted stones [152,153].

1.2. Geißenklösterle

Located a short distance northeast of Hohle Fels is Geißenklösterle, a partially collapsed cave situated 60 meters above the Ach River [144]. The site was discovered in 1958 and excavated in multiple campaigns by Eberhard Wagner (1973), Joachim Hahn (1974–1991), and Nicholas Conard (2001–2002) [60,142]. The Upper Paleolithic layers consist of the Lower Aurignacian (AH III) dated to ~43-41 ka cal BP, the Upper Aurignacian (AH II) dated to ~42-39 ka cal BP, the Gravettian (AH I) dated to ~37–30 ka cal BP [154], and a small Magdalenian component (AH Io) dated to ~16–14 ka cal BP [155] (calibrated with OxCal v4.4.4) [156,157]. Like Hohle Fels, Geißenklösterle contains abundant evidence of symbolic material culture including ivory figurines [151,158,159], bone and ivory flutes [7], personal ornamentation [8], and painted stones [153].

1.3. Brillenhöhle

The third study site from the Ach Valley, Brillenhöhle, is located a few hundred meters northeast of Geißenklösterle 80 meters above the Ach River [160]. The first excavations were conducted by Gustav Riek between 1955–1963 [161] and continue since 2021 under the direction of Yvonne Tafelmaier of the Landesamt für Denkmalpflege Baden-Württemberg [162]. Upper Paleolithic layers include a small Aurignacian assemblage (AH XIV) dated to ~30–33 uncal ka BP [161,163], the Gravettian (AH V–VII) dated to ~25–29 uncal ka BP [161,163], and the Magdalenian (AH IV). In addition to Gravettian personal ornamentation [161], Brillenhöhle is also well known for Magdalenian human remains evidencing secondary burial practices and/or cannibalism [164,165].

1.4. Hohlenstein-Stadel

The final study site is Hohlenstein-Stadel, one of three related sites from a limestone outcrop in the Lone Valley. Early excavations were conducted in the late 19th to mid-20th century by various scholars including Oscar Fraas, Robert Rudolf Schmidt, and Robert Wetzel [137,166,167]. More recently, excavations resumed led by Claus-Joachim Kind of the Landesamt für Denkmalpflege Baden-Württemberg [168,169]. Most Upper Paleolithic finds come from the Aurignacian (Kind AH 1 / Wetzel AH V-IV), which is dated to ~40–36 ka cal BP [65], but a Magdalenian component is also recorded from earlier excavations (Wetzel AH III) dated to ~17–15 ka cal BP [170] (calibrated with OxCal v4.4.4) [156,157]. In addition to numerous personal ornaments made from ivory and animal teeth [26,63,171], the most recognizable find is the therianthropic “lion man” figure made from a large piece of ivory [65,172].

2. Red and arctic fox ecology and behavior

Since their appearance during the Early-Middle Pleistocene [110,111,173,174], two fox species inhabited Europe: the red fox (*Vulpes vulpes*) and the arctic fox (*Vulpes lagopus*). Both the past and modern range of the former is expansive, including diverse environments across much of the Northern Hemisphere (e.g., semi-arid deserts, tundra, farmland, boreal forests) [91,175]. Arctic foxes, although broadly distributed throughout the Pleistocene [176], now inhabit a reduced range restricted to the Arctic tundra [89].

Red and arctic foxes are easily distinguished by their appearance. Red foxes are larger (3–14 kg) [91,177] and exhibit three color morphs: red, silver/black, and cross [91]. Arctic foxes are smaller (3-5 kg) and exhibit reduced features (limbs, snout, ears, body), both adaptations for cold environments [89,108,178]. They appear in two seasonally variable color morphs: white and blue [89,178].

Both taxa are omnivorous generalists who hunt and scavenge a variety of resources [89,91,179,180]. Diets vary, but most foxes rely heavily on rodents (e.g., lemmings, voles, mice, shrews) [89,108,110,181], which are supplemented by lagomorphs, birds, bird eggs, fish, shellfish, reptiles, and insects [180,182]. Foxes also access larger prey by scavenging from other carnivores, such as polar bears or wolves [183,184]. Other food sources include vegetation (e.g., fruits, berries, seaweed) and garbage from human activity [89,180,185,186].

The mobility and territoriality of foxes vary between species and populations [111,187–191]. Summer ranges are generally smaller, as foxes defend more restricted breeding territories. Winter ranges can be much larger, especially for arctic foxes, who may travel hundreds of kilometers over land and sea ice in search of food [184,189,190,192,193].

Both species breed in monogamous pairs during the late winter to early spring, birthing young after a 52-day gestation period [89,91,194,195]. Early life is localized to dens, where the young are protected and reared by parents and non-breeding adults [91,108,110,111,196,197]. Dens are used for numerous years, and competition for dens may occur between breeding pairs and other denning carnivores—for example, other fox species, badgers, and wolves [197].

Although foxes are predators, both red and arctic foxes fall prey to other animals. The most common are humans and larger carnivores (e.g., wolverine, lynx, wolf), but juveniles are also vulnerable to birds of prey (e.g., hawks, eagles, owls). Much of this predation is related to interspecific competition for similar resources, rather than habitual predation [89,108,110,111,198,199].

In sympatric contexts, red foxes are also known to predate arctic foxes. The former tends to suppress the latter, given their larger body size and more aggressive, opportunistic nature [89,91,109,111]. This is evidenced by observations of red foxes outcompeting arctic foxes for resources and occasionally hunting arctic fox juveniles [200,201]. Arctic foxes thus avoid competition by denning in higher altitudes and by occupying larger home ranges and more coastal habitats [89,109,111,181,200,201].

3. Differentiation of loose red and arctic fox canines

The archaeological record often contains loose fox canines, which are difficult to classify to species due to morphological similarities and size overlap between red and arctic foxes. Prior attempts at classification relied on the fact that red foxes are generally larger than their arctic counterparts and that this size difference is reflected in individual teeth. Poplin [101], for example, established size ranges for canine crown heights in both species at the Magdalenian site of Gönnersdorf (Germany). Combined with visual comparison, Poplin argued that this measurement provides a reliable indication of species, proposing size ranges for red fox upper canines (18–22 mm), red fox lower canines (16–20 mm), arctic fox upper canines (14–17 mm), and arctic fox lower canines (12–14 mm).

Although readily applied in subsequent studies, this method is not without fault. Most problematic are the various factors, other than species, that may influence canine crown height. Natural variation is recorded between sexes and populations, and elements of life history (e.g., diet, abrasion) as well as taphonomic alterations may wear canines over time [102–105]. These factors were noted by Münzel [39], who applied Poplin's method to the Geißenklösterle faunal assemblage and revealed a potential bias towards arctic fox canines. As such, Poplin's ranges have limited applicability outside of the source material from Gönnersdorf and should be used with caution.

A geometric-morphometric approach based on multiple landmarks, rather than single measurements, is thus a more promising approach, one which may capture more nuanced differences in tooth morphology between red and arctic fox canines.

4. Experimental Program

The aim of the experimental program was to create a comprehensive reference collection of perforated fox tooth replicas to investigate: 1) variation in technological traces resulting from different perforation techniques, and 2) use-wear traces produced by various bindings and attachment modes over a long period of time.

The experimental protocol was built by F.V. on the basis of preliminary observations of the archeological material. The experiments were performed by graduate and undergraduate students as part of the Experimental Archeology class "From production to use. Exploring perforated Upper Paleolithic animal teeth" offered at the University of Tübingen in Winter 2022. The course also included the perforation of teeth from other animal species, but here we primarily report the results obtained from fox canines.

None of the students who designed and performed the experiments had previous experience in perforating teeth with lithic tools. Instructions on the perforation techniques and technical gestures were provided at the beginning of the experimentation and during the theoretical classes.

4.1. Technological Traces

The experimental sample for the investigation of the manufacturing traces included 28 modern fox canines. Based on the traces observed on the archeological fox teeth, we tested several ways to achieve a perforation, also combining different techniques with each other: (1) drilling (performed uni- and bifacially with a free hand drill, a hafted drill, and a bow drill), (2) scraping + grooving (performed uni- and bifacially), (3) scraping + grooving + widening of the hole; (4) scraping + free hand drilling, (5) abrasion + drilling (Table S4).

4.1.1. Drilling (without surface preparation):

Drilling was tested on seventeen fox canines using three different types of drills: a free hand flint drill (five bifacially, two unifacially), a hafted flint drill (one bifacially), and a bow drill equipped with a flint drill bit (six bifacially, three unifacially) (Figure S1a–c).

All perforations obtained by drilling resulted in very characteristic and diagnostic macro and micro traces.

Circular concentric striations developed in the inner walls of the perforation and are well visible at low and high magnification (Figure S1 d–h). In general, the morphology of the perforations is round in shape, but if the perforation was performed with a free hand drill, the walls are less even and smooth and the hole less symmetrical than those produced by a bow or hafted drill. (Figure S1d–f). This happens because the free hand drill bit only makes a partial rotation. Drilling with a bow or hafted drill makes a full rotation, regularizing the perforation. However, the final form of the perforation also depends on the morphology of the drill tip (narrow and pointed versus wide and rounded) and how deep it penetrates the root before achieving the perforation. As a result, there can be no difference between the inner and the external rim of the perforation (cylindrical hole in cross-section Figure S1f), or the inner and the outer circumference (conical or biconical hole in cross-section) (Figure S1d–e). The perforation is biconical when drilling is performed bifacially and conical when performed only on one face of the tooth.

We noticed that the bow drill allowed the user to achieve the perforation in a shorter time, but the high drilling speed can displace the drill from its original perpendicular position, resulting in holes shifted toward the right or the left (Figure S1h).

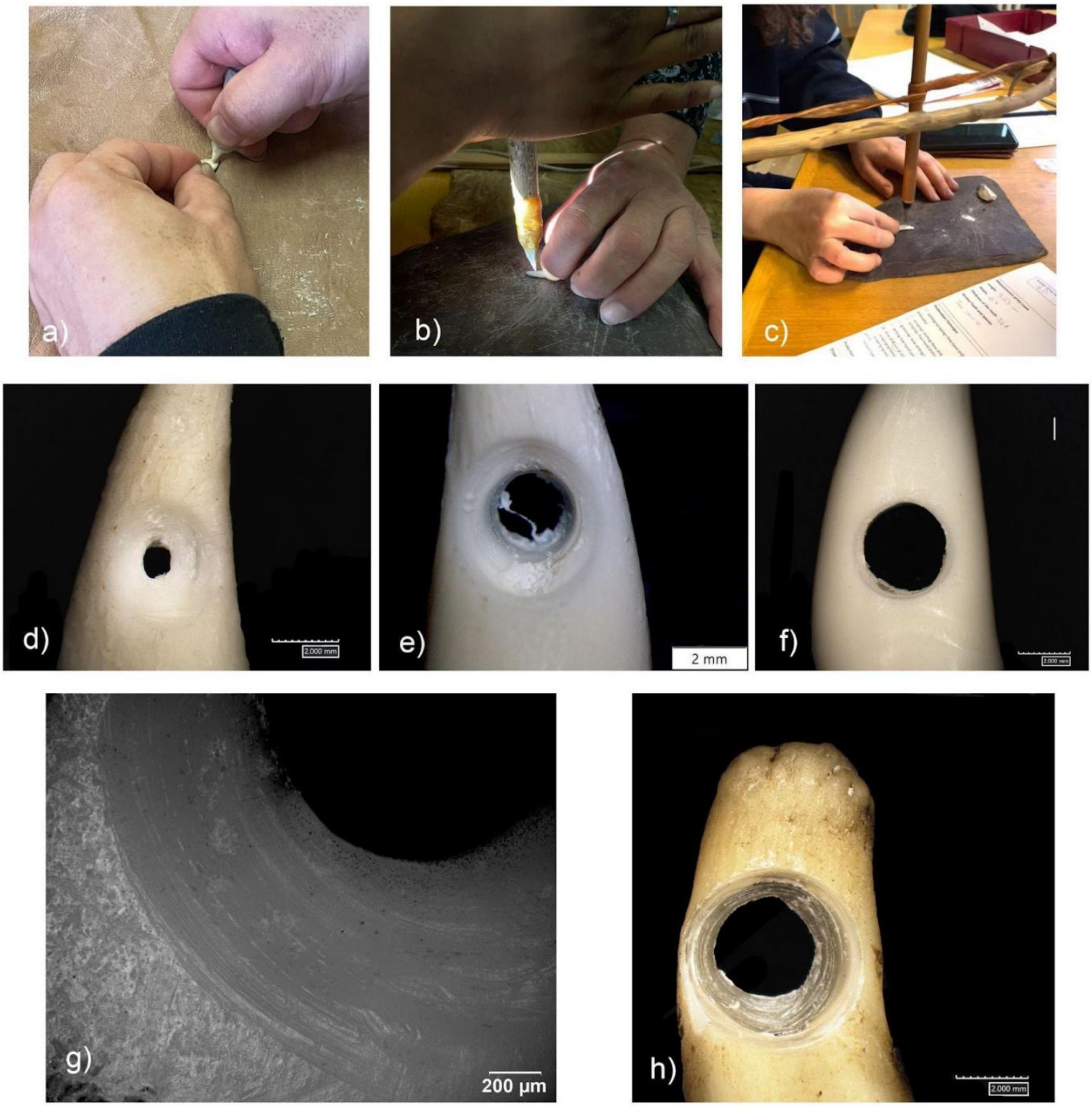

Figure S1. Overview of experimental technological traces by drilling. (a) Free hand drilling, (b) drilling with a hafted drill, (c) drilling with a bow drill, (d) macrograph of perforation achieved by free hand drilling, (e) macrograph of perforation achieved with a hafted drill, (f) macrograph of perforation achieved with a bow drill, (g) micrographs showing concentrical circular striations, (h) macrograph of perforation achieved with a bow drill and shifted toward the left.

4.1.2. Scraping + grooving + widening of the hole

Ten fox canines were perforated using scraping, grooving, and widening techniques. In particular, perforations were achieved on six teeth by scraping and grooving while, on an additional four teeth, the hole was later regularized and widened with a pointed lithic tool or drill (Figure S2a–c).

Well-recognizable bundles of narrow, long striations overlap wider and deeper grooves oriented parallel to the long axis of the tooth (Figure S2d). The shape of the perforation is always elongated (Figure S2d–e). Rounder and smoother perforations can be obtained by rotating a pointed tool inside the perforation. As a result of the widening, half-moon side notches are visible in sectors 3 and 9 on the inner and outer rims of the perforation (Figure S2g–i). Unlike drilling, widening the hole does not leave the typical drilling traces on the inner wall of the perforation, as the rotation is fast and only partial. The morphology of the hole tends to be oval with a defined enlargement to the right and left lateral sides (Figure S2h).

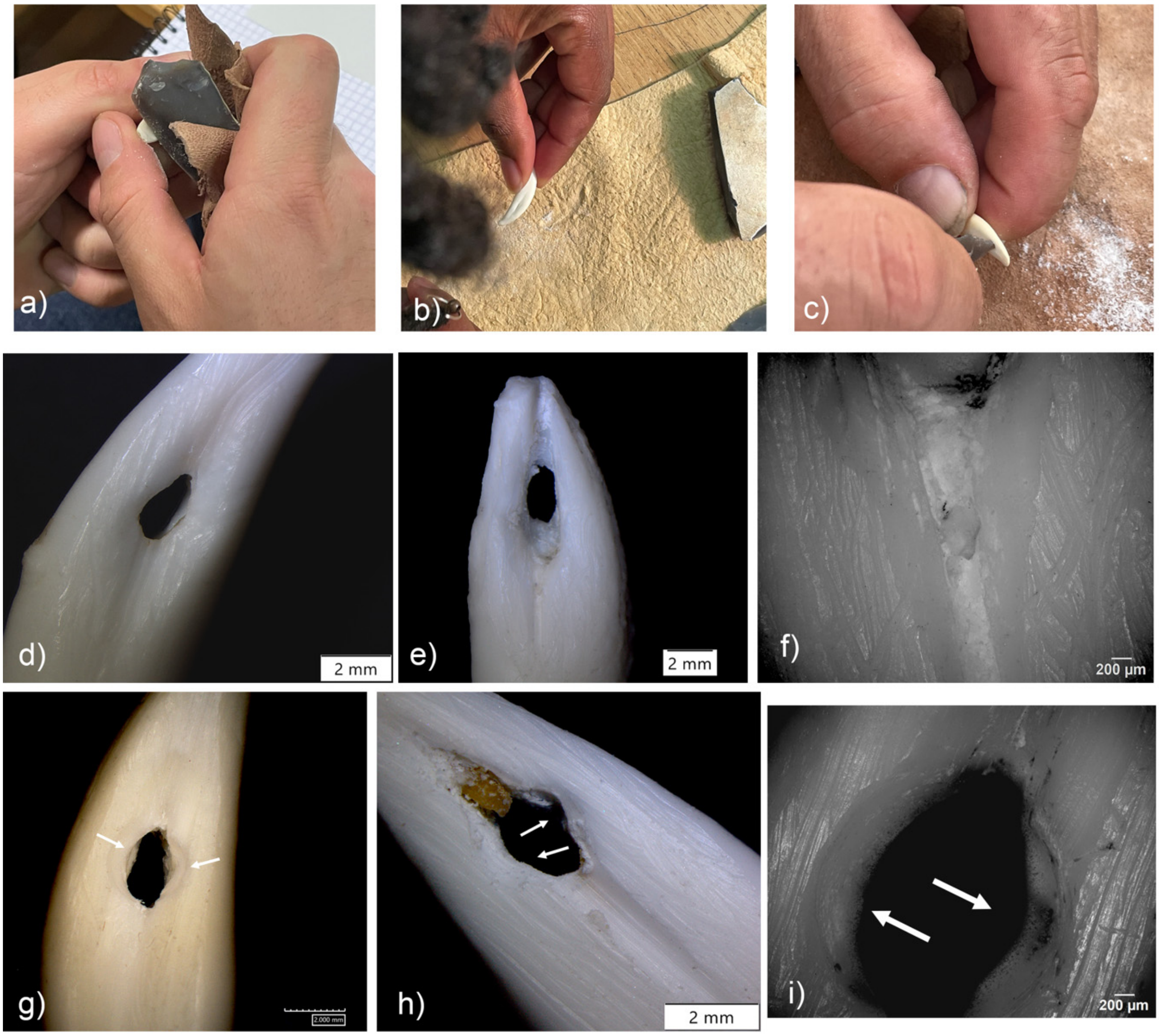

Figure S2. Overview of experimental technological traces by scraping/grooving. (a) Scraping the root for achieving the perforation, (b) resulting root after scraping and grooving, (c) widening of the hole with a drill, (d–e) macrograph of striations and grooves on the root, (f) micrograph of striations and grooves, (g–h) macrographs of the perforations after widening the hole, (i) close-up micrograph showing the enlargement of the hole with the half-moon side notches.

4.1.3. Scraping or abrasion (surface preparation) + drilling

Uni- or bifacially scraping or abrading the root was employed to flatten and thin the surface before making the perforation (Fig. S3 a-c). Although similar, the two motions produce slightly different traces at a macro and micro level. As shown in Figures S3d–e and g, abrading the root against a sandstone or coarse surface produces a flat facet with well-visible dense, parallel, and regular striations following the direction of abrasion. The striations can be narrow or wide according to the coarseness of the utilized stone. When the surface is instead scraped, the striations are uneven, long, large, deep, and usually organized in bundles. (Figure S3f–h). However, the morphology and the distribution of striations are also strictly dependent on the edge morphology of the tool used during the activity (retouched versus unretouched).

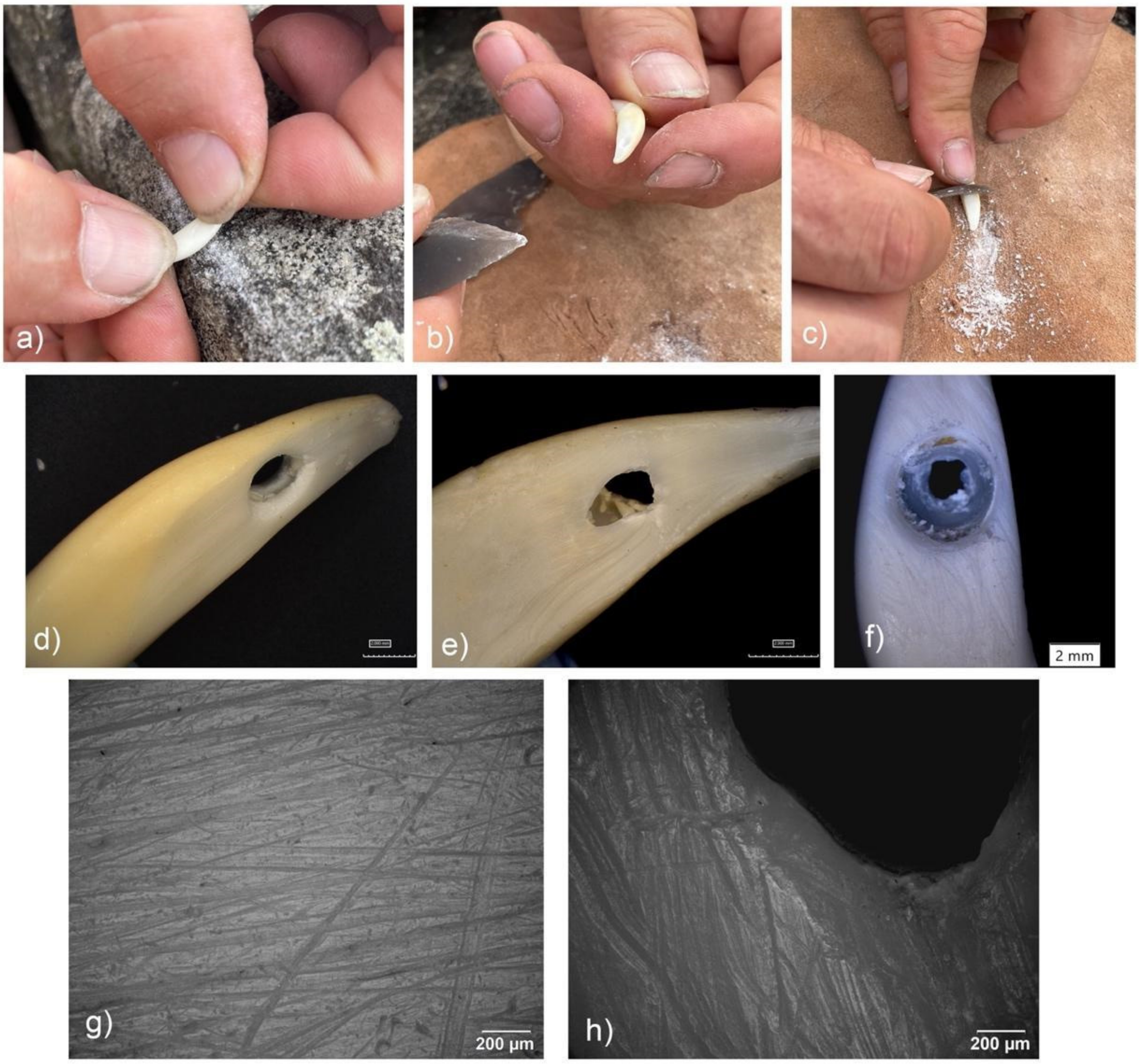

Figure S3. Overview of experimental technological traces by scraping or abrading and drilling. (a) Abrading the tooth root against a coarse surface, (b) drilling the root for achieving the perforation, (c) scraping the tooth root with a small blade, (d–e) flat facets on the roots and regular narrow striations produced by abrasion, (f) uneven, shallow, and dense striations produced by scraping, (g) micrograph of striations produced by abrasion, (h) micrograph of striations produced by scraping.

4.2. Use-wear traces

The second main objective of the experimentation focused on the investigation of traces developed after the teeth were worn as body ornaments. After production, the students were given the freedom to choose how to arrange and wear their teeth. Bindings were provided during the course and included strings made from sinew, intestine, nettle, and tanned leather. They could choose to use the bindings without any treatment, with the addition of a colorant (red ochre), or with animal fat (to simulate grease produced when sweating). Additional ornaments, such as various shells, fish vertebrae, and bones were also available to design necklaces, bracelets, anklets, and earrings. The teeth were worn as loose pendants or sewn onto pieces of tanned leather attached to different parts of the body. We paid particular attention to avoid any contact of the teeth with modern materials such as synthetic clothes. The teeth were worn by the students during their daily routine, recording the duration of wearing in minutes (Figure S4 and Table 5).

4.2.1 Results

Except for one tooth, regardless of wear time, we always recorded a certain degree of rounding and smoothing developed on the internal rim of the perforations. By comparing the pre- and post-use pictures, a common feature was the removal of bone splinters occurring inside the perforations after manufacture with subsequent rounding and widening (Figure S5c–f). On four perforations made by drilling, the smoothing also affected the internal walls of the perforations (Figure S6a). In most cases, the perforations maintained their original shape, but on seven teeth we noticed a widening of the hole resulting in a modified internal morphology of the rim. Two teeth reported a deformation of the internal rim on the area of contact with the bindings (Figure S5a–b).

At a microscopic level, polish developed on a total of 16 teeth. We recorded polished areas on the internal rims and, in a few cases, on the outer rims (Figure S6). Continuous polish never developed around the total circumference of the perforations but rather localized on the spots in contact with the bindings. We recorded short striations on the polish of a single ornament, but the micro rounding of the surface was still present (Figure S6e).

Finally, in five cases, polish was distributed on the root surface in the area around the perforations (on the lateral side or below). This was due to the abrasion of the tooth root against other adornments (shells, fish vertebras), while in three cases we attributed the polish to the tooth's contact against the leather upon which the ornaments were sewn.

Figure S4. Examples of various ornament replicas and modes of attachment during the experimentation. (a) necklace with loose fox teeth, (b) fox teeth sewn onto leather, (c) anklet with loose fox tooth as pendant, (d) earring and loose fox teeth, (e) anklet with fox teeth sewn onto leather, (f) necklace with fox teeth sewn onto leather, (g) anklet and fox teeth sewn onto leather.

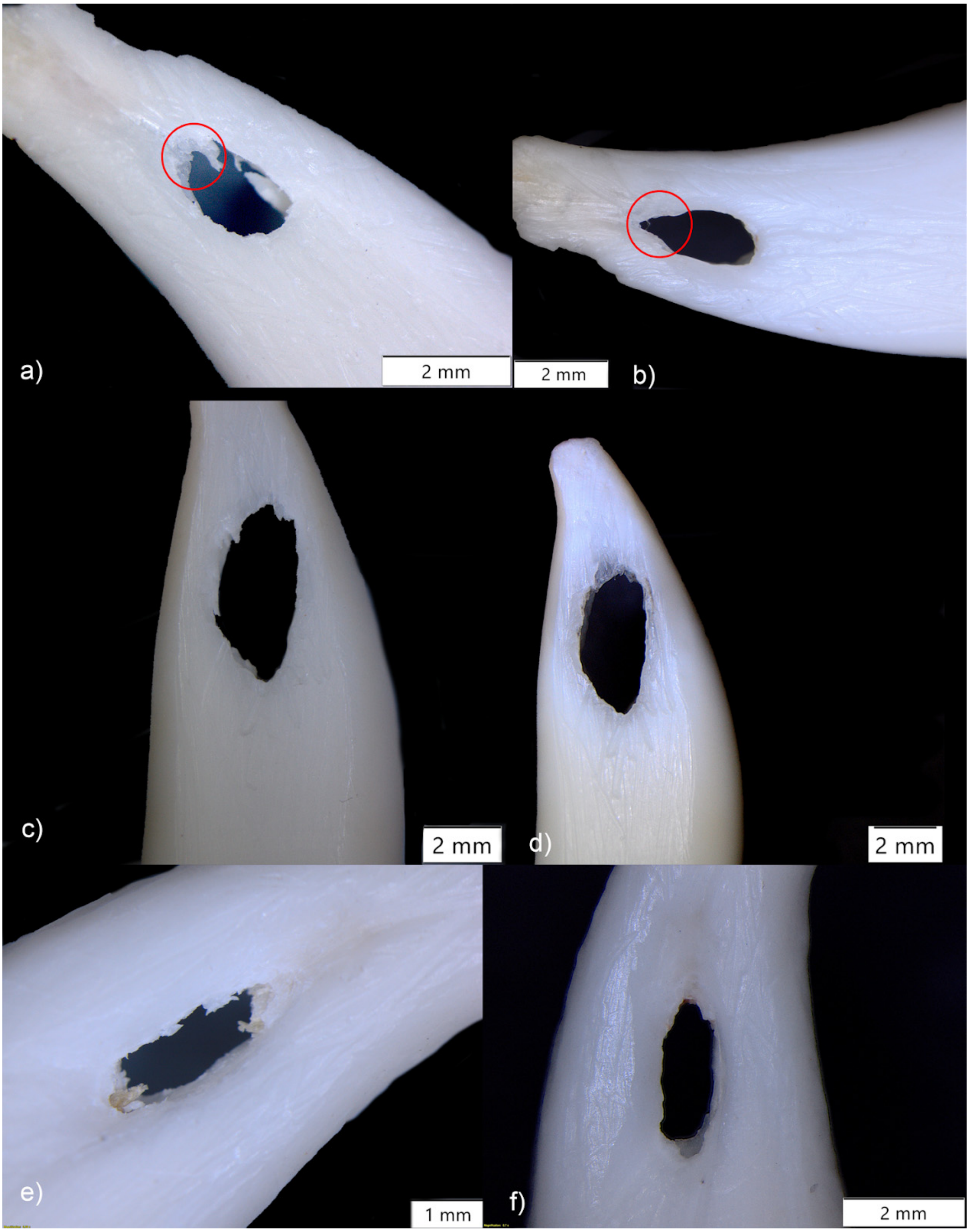

Figure S5. Pre- and post-use macrographs of the perforations. (a) pre-use; (b) post-use with deformations on the upper part of the hole and rounding of the internal rim; (c) pre-use; (d) post-use with a notable absence of splinters, rounding, smoothing of the rim, and widening of the hole; (e) pre-use; (f) post-use with absence of splinters and rounding and smoothing of the rim.

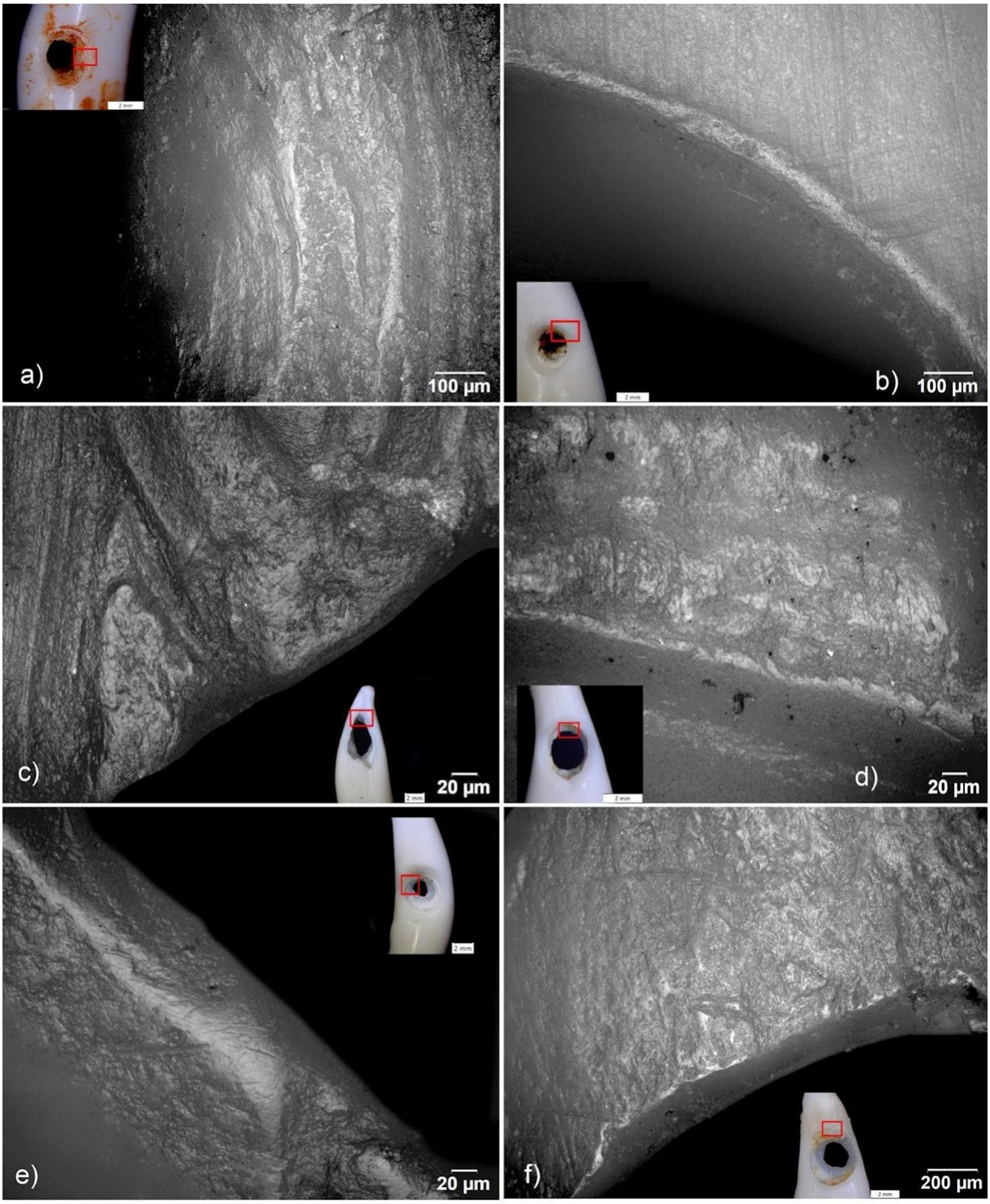

Figure S6. Micrographs of polish recorded on the perforations and corresponding location. (a) Developed rounded and smooth polish on the inner walls in sector 3, (b) developed smooth and domed polish along the rim in sector 2, (c) polish developed on the outer rim in sector 12, (d) polish developed on the outer rim in sector 12, (e) smooth and domed polish with short oblique striations developed in sector 9, (f) smooth discontinuous polish developed on the outer rim in sector 1.

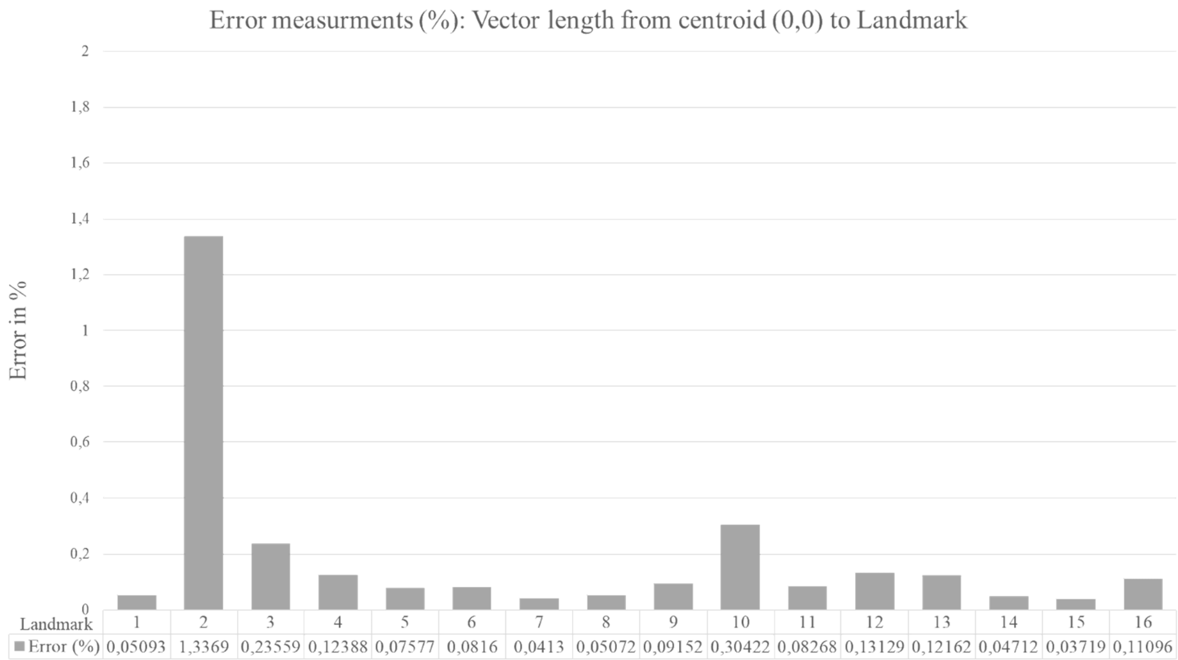

Figure S7. Error margins for the 16 landmarks placed along the cervical outline.

Country	Site	Culture	Red Fox	Arctic Fox	Indet. Fox	Tooth Type	Total	Source
FR	Grotte du Renne	Châtelperronian	0	0	8+	canines (8+)	8+	[20,202]
FR	Quinçay	Châtelperronian	0	0	3	canines (3)	3	[118]
FR	Châtelperron	Châtelperronian (mixed?)	0	0	1	canines (1)	1	[20]
FR	Gatzarria	Aurignacian (early) or Châtelperronian	0	0	9	incisors (1), canines (8)	9	[118,203,204]
FR	La Quina	Aurignacian (early) or Châtelperronian	0	0	28	canines (28)	28	[118]
BU	Kozarnika	Aurignacian (IUP)	-	-	present	NA	present	[205]
RU	Denisova	Aurignacian (IUP)	0	0	4	canines (4)	4	[206]
RU	Kostenki	Aurignacian (IUP and EUP)	0	0	37+	canines (37+)	37+	[13,119,120,207–209]
AT	Willendorf II	Aurignacian	-	-	present	NA	present	[210]
BE	Goyet	Aurignacian	-	-	present	NA	present	[13]
BE	Spy	Aurignacian	-	-	present	NA	present	[13]

BE	Trou Magrite	Aurignacian	-	-	present	NA	present	[13]
BU	Bacho Kiro	Aurignacian	0	0	1	canines (1)	1	[210]
BU	Bacho Kiro	Aurignacian	-	-	present	NA	present	[211]
DE	Breitenbach	Aurignacian	0	0	3+	canines (3+)	3+	[212]
DE	Hohle Fels	Aurignacian	1?	3	6	canines (6)	6	this study [5,6,56,57]
DE	Geißenklösterle	Aurignacian	1	0	4	canines (5)	5	this study [5,60]
DE	Hohlenstein-Stadel	Aurignacian	2	3	0	canines (5)	5	this study [61,62]
FR	Grotte de Castaigne	Aurignacian	0	0	1	canines (1)	1	[213]
FR	Saint-Jean-de-Verges	Aurignacian	0	0	14	canines (14)	14	[117]
FR	Isturitz	Aurignacian	0	0	13	canines (13)	13	[25,85]
FR	Les Cottés	Aurignacian	0	0	3	canines (3)	3	[214]
FR	Rois	Aurignacian	-	-	1+	NA	1+	[13,215]
FR	Abri Peyrony	Aurignacian	-	-	present	NA	present	[13]
FR	Castanet	Aurignacian	-	-	present	NA	present	[13]
FR	Flageolet I	Aurignacian	-	-	present	NA	present	[13]
FR	Grotte des Hyenes	Aurignacian	-	-	present	NA	present	[216]
FR	La Piage	Aurignacian	-	-	present	NA	present	[13]
FR	Pages	Aurignacian	-	-	present	NA	present	[13]
FR	Abri Pataud	Aurignacian	-	-	present	NA	present	[13]
FR	Roc de Combe	Aurignacian	-	-	present	NA	present	[13]
FR	Rochette	Aurignacian	-	-	present	NA	present	[13]
FR	Souquette	Aurignacian	-	-	present	NA	present	[13]
FR	Sous-les-vignes	Aurignacian	-	-	present	NA	present	[13]
FR	Tuto de Camalhot	Aurignacian	-	-	present	NA	present	[216]
FR	Vachons	Aurignacian	-	-	present	NA	present	[13]
FR	Trou Renard	Aurignacian	-	-	present	NA	present	[210]
FR	Aurignac	Aurignacian	-	-	present	NA	present	[216]
FR	Grotte Tournal	Aurignacian	-	-	present	NA	present	[216]
FR	Tarté	Aurignacian	-	-	present	NA	present	[216]
IT	Fossellone	Aurignacian	-	-	present	NA	present	[13]
PO	Mamutowa Cave	Aurignacian	0	0	3	NA	3	[217]
RO	Ohaba-Ponor / Bordu Mare	Aurignacian	-	-	present	NA	present	[217]
RO	Cioclovina	Aurignacian	-	-	present	NA	present	[217]
RU	Muralovka	Aurignacian	0	0	2+	canines (2+)	2+	Hahn, 1972
SP	El Ruso I	Aurignacian	0	0	1	canines (1)	1	[31]

SP	El Otero	Aurignacian	0	0	1	canines (1)	1	[31]
SP	Cobalejos	Aurignacian	-	-	present	NA	present	[13]
UA	Siuren I	Aurignacian (late)	0	0	1	canines (1)	1	[218]
DE	Hohle Fels	Aurignacian - Gravettian	0	1	0	canines (1)	1	this study [5]
DE	Hohlenstein-Stadel	Aurignacian or Magdalenian	0	0	8	canines (8)	8	this study [63,168,171]
FR	Abri Pataud	Gravettian (early)	0	0	11	canines (11)	11	[219]
AT	Krems-Wachtberg	Gravettian	0	0	4+	incisors (3+), premolars (1)	4+	[220–222]
CZ	Pavlov I	Gravettian	0	0	284	incisors (146), canines (105), premolars (33)	284	[34,94]
CZ	Pavlov IV	Gravettian	0	1	0	NA	1	[223]
CZ	Dolni Vestonice I	Gravettian	present	42	31	canines (42)	73	[106,107]
CZ	Milovice IV	Gravettian	0	0	2	incisors (1), canines (1)	2	[224]
CZ	Predmosti I	Gravettian	-	-	present	NA	present	[225]
DE	Hohle Fels	Gravettian	1	2	1	canines (4)	4	this study [5]
DE	Brillenhöhle	Gravettian	0	0	3	canines (3)	3	this study [161]
DE	Geißenklösterle	Gravettian	2?	4?	3	incisors (1), canines (8)	9	this study [5]
FR	Isturitz	Gravettian	0	0	4+	canines (4+)	4+	[85]
FR	Tarté	Gravettian	-	-	present	NA	present	[226]
FR	Rideaux	Gravettian	-	-	present	NA	present	[226]
RO	Râsnov	Gravettian	0	0	1	canines (1)	1	[227]
RO	Gura Cheii Cave / Rasnov	Gravettian	0	0	1	canines (1)	1	[227,228]
RO	Poiana Ciresului - Piatra Neamt	Gravettian	0	0	2	canines (2)	2	[228]
RU	Sungir	Gravettian	0	0	305+	canines (305+)	305+	[17]
RU	Zaraysk	Gravettian	0	41	0	incisors (32), premolars (9)	41	[99]
SP	La Garma A	Gravettian	0	0	1	canines (1)	1	[31]
SP	Aitzbitarte III	Gravettian	0	0	2	canines (2)	2	[31]
UK	Buran-Kaya III	Gravettian	0	1	0	canines (1)	1	[229]
RO	Climente II Cave	Epigravettian	0	0	1	canines (1)	1	[228]
FR	Les Jamblancs	Solutrean	0	0	3+	canines (3+)	3+	[230]
FR	Pech de la Boissiere	Solutrean	0	0	3+	canines (3+)	3+	[230,231]
FR	Combe Saunière	Solutrean	0	0	6	canines (6)	6	[84]
FR	La grotte des Harpons	Solutrean	-	-	present	NA	present	[226]

SP	Cueto de la Mina	Solutrean	0	0	1	canines (1)	1	[31]
SP	Altamira	Solutrean	0	0	1	canines (1)	1	[31]
AT	Gudenushöhle	Magdalenian	-	-	present	NA	present	[31,122]
BE	Goyet	Magdalenian	-	-	present	NA	present	[31,122]
BE	Trou du Frontal	Magdalenian	-	-	present	NA	present	[31,122]
CH	Schweizersbild	Magdalenian	-	-	present	NA	present	[31,122]
CH	Kesslerloch	Magdalenian	-	-	present	NA	present	[31,122]
DE	Petersfels	Magdalenian	0	16	25	incisors (14), canines (20), premolars (7)	41	[95–97]
DE	Kniegrotte	Magdalenian	0	5+	0	canines (5+)	5+	[232]
DE	Hollenberg-Höhle 3 BL	Magdalenian	0	0	3	canines (3)	3	[233]
DE	Gönnersdorf	Magdalenian	0	0	45	NA	45	[31,121,122]
DE	Andernach-Martinsberg-2	Magdalenian	-	-	present	NA	present	[122]
FR	Isturitz	Magdalenian	0	0	35+	canines (35+)	35+	[85]
FR	Les Jamblancs	Magdalenian	0	0	3+	canines (3+)	3+	[230]
FR	Gourdan	Magdalenian	0	0	3	canines (3)	3	[85]
FR	d'Arudy	Magdalenian	0	0	4	canines (4)	4	[85]
FR	Mais d' Azil	Magdalenian	0	0	3	canines (3)	3	[85]
FR	la Vache	Magdalenian	0	0	35	canines (35)	35	[85]
FR	Fontales	Magdalenian	0	0	2	canines (2)	2	[126]
FR	Bruniquel	Magdalenian	0	0	13	canines (13)	13	[126,234]
FR	Courbet	Magdalenian	0	0	2	canines (2)	2	[234]
FR	Angles-sur-l'Anglin	Magdalenian	0	0	1+	canines (1+)	1+	[235]
FR	la Madeleine	Magdalenian	0	0	12	canines (12)	12	[124]
SP	Abauntz	Magdalenian	0	0	1	incisors (1)	1	[31]
SP	Cueto de la Mina	Magdalenian	0	0	3	canines (3)	3	[31]
SP	El Pendo	Magdalenian	0	0	2	canines (2)	2	[31]
SP	Urtiaga	Magdalenian	0	0	1	canines (1)	1	[31]
PO	Wilczyce	Magdalenian (late)	0	162	0	incisors (149), canines (13)	162	[86]
FR	la Crouzade	Azillian/Epimagdalenain	0	0	2	canines (2)	2	[226]
SP	Morín	Azilian	0	0	2	canines (2)	2	[31]

Table S1. Summary of the literature review on Upper Paleolithic fox tooth ornaments.

ID	Species ID (GM)	Position	Layer	Culture	Description	Collection	µCT scanner	Voxel length
Geißenklösterle:								
GK 22/1A	*Vulpes vulpes?*	lower left	AH I	Gravettian?	pendant, root with broken perforation	UFG	Nikon XT H 320	55.1
GK 22/1B	*Vulpes lagopus*	lower right	AH I	Gravettian?	pendant, root with perforation	UFG	Nikon XT H 320	55.1
GK 59/369	*Vulpes vulpes*	upper right	AH IIIb	Aurignacian	pendant, root with broken perforation	UFG	Nikon XT H 320	55.8
GK 99/918	*Vulpes lagopus?*	lower left	AH It	Gravettian	fabricate	UFG	Nikon XT H 320	55.7
GK 98/391	*Vulpes sp.*	upper right	AH It	Gravettian	pendant, root with perforation, damaged cervical outline	UFG	-	-
GK 100/89	*Vulpes sp.*	upper left	AH Ir	Gravettian	fabricate, root flattened, no visible outline	UFG	Nikon XT H 320	55.1
GK 140/226	*Vulpes lagopus*	upper right	AH It	Gravettian	pendant, root with broken perforation	UFG	Nikon XT H 320	55.8
Hohle Fels:								
HF 24/1137	*Vulpes sp.*	upper right	AH IV	Aurignacian	pendant, root with broken perforation	UFG	Nikon XT H 320	55.7
HF 24/1278.1	*Vulpes lagopus*	lower right	AH IIc	Aurignacian	pendant, root with perforation	UFG	Nikon XT H 320	55.7
HF 26/631.1	*Vulpes lagopus*	lower left	AHVa	Aurignacian	pendant, root with perforation	UFG	Nikon XT H 320	55.8
HF 28/964.1	*Vulpes vulpes*	upper right	AH IV	Aurignacian	pendant, root with broken perforation	UFG	Nikon XT H 320	55.7
HF 58/1295	*Vulpes lagopus*	lower left	AH IIc	Gravettian	pendant, root with perforation	UFG	Nikon XT H 320	55.7
HF 66d/461	*Vulpes vulpes*	upper left	AH IIb	Gravettian	pendant, root with perforation	UFG	Nikon XT H 320	55.7
HF 69/1713	*Vulpes vulpes?*	lower left	AH IV	Aurignacian	pendant, root with perforation	UFG	Nikon XT H 320	55.7
HF 76/122.1	*Vulpes sp.*	upper left	AH IIe	Gravettian	pendant, root with broken perforation	UFG	-	-
HF 79/1228.29	*Vulpes sp.*	upper left	AH IIc-IId	Gravettian	fabricate, root flattened	UFG	Nikon XT H 320	55.7
HF 89/1517.1	*Vulpes lagopus*	lower left	AH IV	Aurignacian	pendant, root with perforation	UFG	Nikon XT H 320	55.7
Hohlenstein-Stadel:								
HS Arch-0380-1	*Vulpes lagopus*	lower left	NA	Aurignacian?	pendant, root with perforation	Ulm	Nikon XT H 320	25.6
HS Arch-0380-2	*Vulpes vulpes*	upper right	NA	Aurignacian?	pendant, root with perforation, damaged crown + cervical outline	Ulm	Nikon XT H 320	25.6
HS Arch-0380-3	*Vulpes vulpes*	lower left	NA	Aurignacian?	pendant, root with perforation, damaged crown	Ulm	Nikon XT H 320	25.6
HS Arch-0380-4	*Vulpes lagopus*	lower left	NA	Aurignacian?	pendant, root with broken perforation	Ulm	Nikon XT H 320	25.6
HS Arch-0380-5	*Vulpes lagopus*	upper right	NA	Aurignacian?	pendant, root with perforation	Ulm	Nikon XT H 320	25.6
HS 2009-185-14-1	*Vulpes sp.*	indeterminate	NA	Aurignacian / Magdalenian	pendant, root with broken perforation, no visible cervical outline	Ulm	Nikon XT H 320	20.3
HS 2009-185-141-1	*Vulpes sp.*	indeterminate	NA	Aurignacian / Magdalenian	pendant, root with broken perforation, no visible cervical outline	Ulm	Nikon XT H 320	20.3

Table S2. List of archaeological fox canines included in the geometric-morphometric analysis. UFG = Ur- und Frühgeschichte collection at the University of Tübingen, ULM = Ulmer Museum.

ID	Position	Age and Sex	Origin	Collection	µCT scanner	Voxel length (in µm)
Vulpes lagopus:						
CN20	upper right	adult m/f	Banks Island, Canada	Tübingen	Nikon XT H 320	55.1

CN22	upper right	adult m/f	Banks Island, Canada	Tübingen	Nikon XT H 320	55.1
CN23	upper left	adult m/f	Banks Island, Canada	Tübingen	Nikon XT H 320	54.9
CN23	lower left	adult m/f	Banks Island, Canada	Tübingen	Nikon XT H 320	54.9
CN30	upper left	adult m/f	Banks Island, Canada	Tübingen	Nikon XT H 320	54.9
CN39	lower right	adult m/f	Banks Island, Canada	Tübingen	Nikon XT H 320	55.1
CN50	lower right	adult m/f	Banks Island, Canada	Tübingen	Nikon XT H 320	54.9
CN51	upper right	adult m/f	Banks Island, Canada	Tübingen	Nikon XT H 320	54.9
CN51	lower right	adult m/f	Banks Island, Canada	Tübingen	Nikon XT H 320	54.9
CN53	lower right	adult m/f	Banks Island, Canada	Tübingen	Nikon XT H 320	54.9
CN53	upper right	adult m/f	Banks Island, Canada	Tübingen	GE Phoenix v|tome|x s230	15-55
CN54	upper right	adult m/f	Banks Island, Canada	Tübingen	GE Phoenix v|tome|x s230	15-55
CN57	lower left	adult m/f	Banks Island, Canada	Tübingen	Nikon XT H 320	54.9
CN61	lower left	adult m/f	Banks Island, Canada	Tübingen	Nikon XT H 320	55.1
CN62	upper right	adult m/f	Banks Island, Canada	Tübingen	Nikon XT H 320	54.9
CN63	lower left	adult m/f	Banks Island, Canada	Tübingen	Nikon XT H 320	54.9
CN93	upper right	adult m/f	Banks Island, Canada	Tübingen	GE Phoenix v|tome|x s230	15-55
CN95	upper right	adult m/f	Banks Island, Canada	Tübingen	GE Phoenix v|tome|x s230	15-55
CN96	upper right	adult m/f	Banks Island, Canada	Tübingen	GE Phoenix v|tome|x s230	15-55
CN98	upper right	adult m/f	Banks Island, Canada	Tübingen	GE Phoenix v|tome|x s230	15-55
CN99	upper right	adult m/f	Banks Island, Canada	Tübingen	Nikon XT H 320	55.1
CN99	lower left	adult m/f	Banks Island, Canada	Tübingen	Nikon XT H 320	54.9
Vulpes vulpes:						
CB01	upper left	adult m/f	Southwestern Germany	Chris Baumann	Nikon XT H 320	55.7
CB01	lower right	adult m/f	Southwestern Germany	Chris Baumann	Nikon XT H 320	55.7
CN42	lower right	adult m/f	Southwestern Germany	Tübingen	Nikon XT H 320	61.3
CN43	upper right	adult m/f	Southwestern Germany	Tübingen	Nikon XT H 320	55.1
CN44	lower right	adult m/f	Southwestern Germany	Tübingen	Nikon XT H 320	55.1
CN44	upper right	adult m/f	Southwestern Germany	Tübingen	Nikon XT H 320	55.1
CN45	lower right	adult m	Southwestern Germany	Tübingen	Nikon XT H 320	55.1
CN45	upper right	adult m	Southwestern Germany	Tübingen	Nikon XT H 320	61.3
CN72	lower left	adult m	Southwestern Germany	Tübingen	Nikon XT H 320	55.1
CN102	lower left	adult m/f	Southwestern Germany	Tübingen	Nikon XT H 320	55.7
CN112	upper right	adult m/f	Southwestern Germany	Tübingen	Nikon XT H 320	55.1
CN112	lower right	adult m/f	Southwestern Germany	Tübingen	Nikon XT H 320	55.1
CN117	lower right	adult m/f	Southwestern Germany	Tübingen	Nikon XT H 320	55.1
CN124	upper right	adult m/f	Southwestern Germany	Tübingen	Nikon XT H 320	55.1
CN124	lower right	adult m/f	Southwestern Germany	Tübingen	Nikon XT H 320	55.1
CN129	upper right	adult m/f	Southwestern Germany	Tübingen	GE Phoenix v|tome|x s230	15-55
CN129	lower left	adult m/f	Southwestern Germany	Tübingen	Nikon XT H 320	55.1
CN132	upper right	adult m/f	Southwestern Germany	Tübingen	GE Phoenix v|tome|x s230	15-55
CN132	lower left	adult m/f	Southwestern Germany	Tübingen	Nikon XT H 320	55.1
CN134	upper left	adult m/f	Southwestern Germany	Tübingen	GE Phoenix v|tome|x s230	15-55

Table S3. List of modern fox canines included in the geometric-morphometric analysis. m = male, f = female, Tübingen = Comparative zooarchaeological collection of the University of Tübingen; Chris Baumann = Property of Dr. Chris Baumann (University of Tübingen).

ID	Exp N.	Species and position	Technique of perforation	Technological Traces
#1	8A	Fox canine	Scraping+grooving+widening	Bundle of striations and grooves
#2	12A	Fox canine	Bow drilling bifacial	Concentric striations
#3	13A	Fox canine	Free hand drilling bifacial	Concentric striations
#4	8A	Fox canine	Scraping+grooving	Striations and grooves
#5	5A	Fox canine	Free hand drilling bifacial	Concentric striations
#6	2A	Fox canine	Bow drilling bifacial	Concentric striations
#7	2FB	Fox canine	Grooving+scraping	Grooves, striations
#8	3FB	Fox canine	Grooving+scraping	Grooves, striations
#9	6FB	Fox canine	Grooving+scraping	Striations
#10	1FB	Fox canine	free hand drilling	Concentric striations
#11	4FB	Fox canine	Bow drilling bifacial	Concentric striations
#12	7FB	Fox canine	Grooving (bifacially)+scraping	Grooves, striations
#13	14D	Fox canine	Grooving+scraping+widening	Grooves, striations
#14	15D	Fox canine	Grooving+scraping	Grooves, striations
#15	16D	Fox canine	Grooving+scraping+widening	Grooves, striations
#16	6D	Fox canine	Bow drilling unifacial	Concentric striations
#17	7D	Fox canine	Bow drilling bifacial	Concentric striations
#18	9D	Fox canine	Drilling free hand bifacial	Concentric striations
#19	8D	Fox canine	Drilling free hand unifacial	Concentric striations
#20	12D	Fox canine	Bow drilling unifacial	Concentric striations
#21	13D	Fox canine	Bow drilling bifacial	Concentric striations
#22	23C	Fox canine	Scraping+free hand drilling unifacial	Concentric striations
#23	22C	Fox canine	Scraping+grooving unifacial and widening bifacial	Striations, deep grooves, conical perforation
#24	14C	Fox canine	Bow drilling bifacial	Concentric striations
#25	9C	Fox canine	Bow drill unifacial	Concentric striations
#26	6C	Fox canine	Free hand drilling bifacial	Concentric striations
#27	18C	Fox canine	Free hand drilling unifacial	Concentric striations
#28	13C	Fox canine	Bow drilling bifacial	Concentric striations

Table S4. Experimental fox canine replicas and related technological results.

ID	Exp. #	Species and position	Bindings / Wearing Mode / Wearing Time	Use-related Traces on Perforation
#1	8A	fox canine	Intestine string (fat treated)/sewn onto leather treated with ochre (as Anklet)/7680 min	Smoothing+rounding internal rim, polished area around the hole (rubbing against leather)
#2	12A	fox canine	Intestine string (fat treated)/sewn onto leather treated with ochre (as Anklet)/7680 min	Smoothing+rounding internal walls, widening of the hole, no significant microwear
#3	13A	fox canine	Nettle string (ochre treated)/loose on leather (as Anklet)/12600 min	Smoothing+rounding internal walls, widening of the hole, developed polish internal walls
#4	6A	fox canine	Sinew string (fat treated)/sewn onto leather (as Anklet)/105 min	Smoothing+rounding and widening of the hole, polished area around the hole (rubbing against leather)
#5	5A	fox canine	Sinew (fat treated)/ sewn onto leather (as Anklet)/6660 min	Smoothing, rounding of the hole, developed polish outer rim, well developed polish outer rim (possible rubbing against shell)
#6	2A	fox canine	Sinew string/ sewn onto leather (as Anklet)/105 min	Smoothing internal rim, polished area around the hole (rubbing against leather)
#7	2FB	fox canine	Nettle string/ sewn onto linen/3060 min	Smoothing+rounding /Polish internal rim
#8	3FB	fox canine	Leather strand/sewn onto leather/3060 min	Smoothin+rounding, slightly polished rim
#9	6FB	fox canine	Nettle string/sewn onto linen/3060 min	Smoothing+rounding, developed polish on the rim
#10	1FB	fox canine	Intestine string/ loose as pendant (Bracelet)/1680 min	Smoothing+rounding, no significant microwear
#11	4FB	fox canine	Nettle string/sewn onto leather (as Bracelet)/ 1680 min	Smoothing+rounding internal rim, polish on the rim
#12	7FB	fox canine	Leather strand/ sewn onto leather/3060	Smoothing+rounding, deformation and widening of the hole, polish on contact with leather binding
#13	14D	fox canine	Leather strand/loose as pendant (Bracelet)/ 105 min	Smoothing+rounding, polish around perforation (rubbing against bone)
#14	15D	fox canine	Sinew string/sewn onto leather (as Necklace)/ 66 min	Smoothing rim, no significant microwear
#15	16D	fox canine	Sinew string/sewn onto leather (as Necklace)/ 66 min	Smoothing rim, no significant microwear
#16	6D	fox canine	Leather strand/loose as earring/78 min	Rounding, No significant microwear
#17	7D	fox canine	Nettle string/loose as earring/148 min	No significant modifications
#18	9D	fox canine	Leather strand/loose as pendant (Bracelet)/105 min	Rounding, No significant microwear

#19	8D	fox canine	Intestine strand/loose as earring/167 min	Smoothing+rounding internal rim, polish outer rim
#20	12D	fox canine	Intestine strand/loose as earring/167 min	Rounding, No significant microwear
#21	13D	fox canine	Sinew/loose as pendant (Hair tie) / 97 min	Rounding, No significant microwear
#22	23C	fox canine	Intestine strand/ loose on leather (as Anklet)/7200 min	Smoothing+rounding internal rim, deformation and widening of the hole, highly developed polish+striae
#23	22C	fox canine	Intestine strand/ loose on leather (as Anklet)/7200 min	Rounding of the hole, no significant microwear
#24	14C	fox canine	Sinew string/loose on leather (as Necklace)/4800 min	Smoothing+rounding internal walls, widening of the hole, polish internal rim
#25	9C	fox canine	Sinew string/loose on leather (as Necklace)/4800 min	Light rounding, Polish internal rim
#26	6C	fox canine	Leather strand/loose as pendant (Necklace)/4800 min	Smoothing+rounding internal walls, widening of the hole, polish internal rim
#27	18C	fox canine	Leather strand/Loose as pendant (Necklace)/1200 min	Smoothing+rounding of the hole,
#28	13C	fox canine	Sinew string/sewn onto leather (as Necklace)/1200 min	Rounding, No significant microwear

Table S5. Experimental fox canine replicas with wear information and related recorded traces.

Species	**Aurignacian**	**Gravettian**	**Magdalenian**	**Total**
Fox (*Vulpes* sp.)	15	14	0	29
Ibex (*Capra ibex*)	2	1	0	3
Cave Bear (*Ursus spelaeus*)	2	8	0	9
Horse (*Equus ferus*)	7	4	0	11
Hyena (*Crocuta crocuta*)	1	1	0	2
Red deer (*Cervus elaphus*)	9	2	3	14
Reindeer (*Rangifer tarandus*)	0	4	21	25
Wolf (*Canis lupus*)	0	4	0	4
Total	36	38	24	98
Proportion of Foxes				
% Fox	42%	37%	0%	30%
% Others	58%	63%	100%	70%

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. References: [56,58,59,236–248]