

## ANTHROPOLOGY

# The Châtelperronian Neanderthals of Cova Foradada (Calafell, Spain) used imperial eagle phalanges for symbolic purposes

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Evidence for the symbolic behavior of Neanderthals in the use of personal ornaments is relatively scarce. Among the few ornaments documented, eagle talons, which were presumably used as pendants, are the most frequently recorded. This phenomenon appears concentrated in a specific area of southern Europe during a span of 80 thousand years. Here, we present the analysis of one eagle pedal phalange recovered from the Châtelperronian layer of Foradada Cave (Spain). Our research broadens the known geographical and temporal range of this symbolic behavior, providing the first documentation of its use among the Iberian populations, as well as of its oldest use in the peninsula. The recurrent appearance of large raptor talons throughout the Middle Paleolithic time frame, including their presence among the last Neanderthal populations, raises the question of the survival of some cultural elements of the Middle Paleolithic into the transitional Middle to Upper Paleolithic assemblages and beyond.

## INTRODUCTION

Archeological personal ornaments such as beads and pendants have traditionally been recognized as direct evidence of symbolic behavior. Their confection and use have been further related to the emergence of “behavioral modernity” (1). Through analogies with recent societies, specialists interpret Paleolithic personal ornaments as encoding elements of nonverbal communications, most often carrying messages about the social identity of the bearer (2). This current paradigm indicates a long-lasting and widespread bead working tradition of marine shells, having emerged in Africa and the Levant among anatomically modern humans (AMHs) well before their arrival in Europe [100 to 75 thousand years (ka)] (3). Presumably in later times (50 to 37 ka), this expression appears among western European Neanderthals independently or by a process of acculturation, being particularly relevant for Châtelperronian (CP) assemblages found in archeological layers from Le Grotte du Renne (Arcy-sur-Cure) and La Grande Roche de la Plématricie (Quinçay) (4). From this point of view, recent investigations in Cueva de los Aviones (Spain) have proposed the use of marine shells by Iberian Neanderthals as beads and pigment containers as early as 115 ka, predating any expression of symbolism by AMH in Eurasia (5). These findings, together with new dates for some rock art motifs in three Spanish caves antedating the arrival of *Homo sapiens* in Europe (6), have generated a heated debate regarding the origin of symbolic behavior, cultural modernity, and the appearance of art in Europe.

Focusing on Neanderthal technocultural traditions, associated with the Middle Paleolithic (MP), Late MP (LMP), and transitional technocomplexes, other more controversial evidence of symbolism such as abstract engravings, body painting, use of feathers, funerary practices, and grave goods have been historically claimed as evidence for Neanderthal symbolic complexity (1, 7). The debate, however, does not stop at this. On the one hand, alternative explanations to this evidence of advanced symbolic thinking such as intervention of natural processes, purely functional character of symbolic items (e.g., pigments/ochre), stratigraphic mixtures, and even the lack of Neanderthal innate cognitive capacities have been proposed. On the other hand, the authorship of some of the European transitional industries, such as those of CP and Uluzzian, in which some of the most notable manifestations of modern behavior are inserted, is still a subject of debate (8). In the case of the CP, most of the studies show a clear cultural continuity of this transitional complex with the MP. Moreover, the CP is found with diagnostic fossils or biological traits typical of Neanderthals rather than those of modern humans (4, 9, 10). Notwithstanding, this statement is far from being universally accepted among researchers (11, 12).

Assuming that Neanderthals were responsible for the CP, the use of raptor talons as bead-like objects seems to be one of the most widespread evidence of symbolism among the MP and CP populations in Europe. At least 23 large raptor phalanges from 10 sites, dated between ~130 and 42 ka, present traces of anthropic manipulation in the form of cut marks (Table 1). The main arguments supporting the symbolic nature of these elements are (i) the anatomical distribution of cut marks, related with non-alimentary handling of animal resources, as contrasted through actualistic experiments; (ii) the scarcity or complete lack of nutritional value of a bird’s lower extremities; (iii) the rarity of large raptors in certain ecosystems (namely, their selective hunting/gathering); (iv) the established analogy with other cut-marked phalanges and talons from late Prehistoric contexts; and (v) their comparison with the ethnographic register (13–24). The lack of formal criticism of these interpretations indicates the plausibility of hypotheses regarding the anthropic modification of large raptor’s pedal phalanges by Neanderthals as their use for

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**Table 1. Sites and layers with cut-marked raptor phalanges interpreted as symbolic elements associated with Neanderthals or transitional MP/UP populations.** CP, Châtelperronian; CM, Classic Mousterian; L, Levallois; M, Mousterian; MTA, Mousterian of Acheulean Tradition; N, Neronian; N/A, not applicable/unknown.

Site	Layer	Age (ka)	Cultural attribution	Taxa CM	Common name	CM NISP	Bird NISP	Raptor NISP	Reference
Baume de Gigny*	XV	50	MP	<i>Cygnus cygnus</i>	Whooper swan	1	N/A	N/A	(13, 14)
Combe Grenal	52	90	MP-CM	<i>Aquila chrysaetos</i>	Golden eagle	1	7	1	(13)
Fumane	A12	MIS3	MP-L	<i>Aquila chrysaetos</i>	Golden eagle	1	N/A	1	(15, 16)
Fumane*	A9	38–42	MP-D	<i>Tetrao tetrix</i>	Black grouse	1	N/A	N/A	(17)
Grotte de L'Hyene	N/A	MIS3	MP	<i>Aquila chrysaetos</i>	Golden eagle	1	N/A	N/A	(13, 16)
Grotte du Renne	IX-X	44–42	CP	<i>Haliaeetus albicilla</i>	White-tailed eagle	1	N/A	N/A	(18)
Grotte du Renne	IX-X	44–42	CP	<i>Bubo bubo</i>	European eagle-owl	1	N/A	N/A	(18)
Krapina	N/A	100–130	MP-M	<i>Haliaeetus albicilla</i>	White-tailed eagle	5	29	12	(19)
Les Fieux	I/J	60–40	MP-DM	<i>Haliaeetus albicilla</i>	White-tailed eagle	1	81	3	(13, 20)
Les Fieux	Jbase	60–40	MP-MTA	<i>Haliaeetus albicilla</i>	White-tailed eagle	1	42	4	(13, 20)
Les Fieux	Ks	MIS3	MP-MTA	<i>Haliaeetus albicilla</i>	White-tailed eagle	2	97	8	(13, 20)
Les Fieux	Ks	MIS3	MP-MTA	<i>Aegypius monachus</i>	Cinereous vulture	1	97	8	(13, 20)
Les Fieux	Rec. clean	MIS3	MP-MTA	<i>Haliaeetus albicilla</i>	White-tailed eagle	2	>2	2	(13, 20)
Mandrin	E	52–56	MP-N	<i>Aquila chrysaetos</i>	Golden eagle	1	11	1	(15)
Pech de l'Azé I	4	44–48	MP-MTA	<i>Aquila chrysaetos</i>	Golden eagle	2	92	5	(14, 21)
Pech de l'Azé IV	8	100	MP-M	<i>Medium-sized raptor</i>	N/A	1	1	1	(22)
Rio Secco	7	48–49	MP-M	<i>Aquila chrysaetos</i>	Golden eagle	1	15	1	(15)
Cova Foradada	IV1	>39	CP	<i>Aquila [heliaca] adalberti</i>	(Iberian?) Imperial eagle	1	41	12	This work, (23)

\*The cases of Baume de Gigny and Fumane A9 correspond to other birds than raptors.

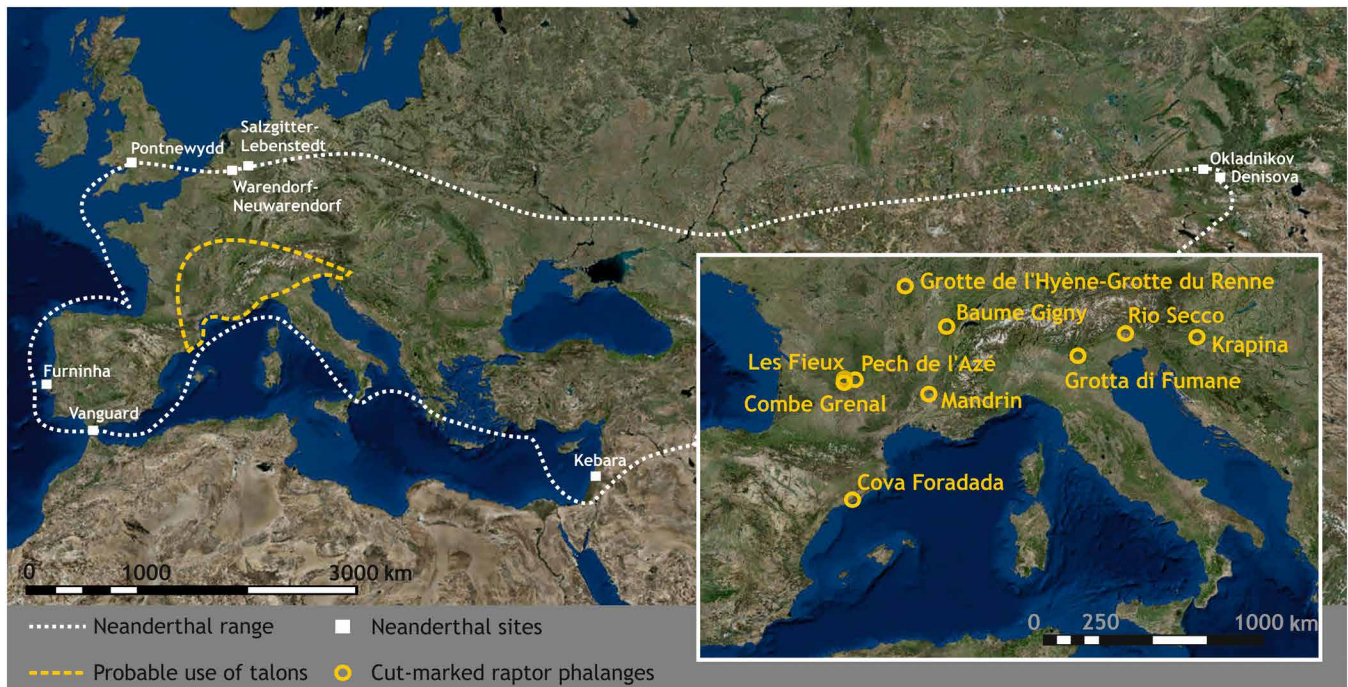
personal ornaments. Considering the large geographical distribution and temporal context of Neanderthals across Eurasia, this phenomenon seems to be concentrated in a very specific area of southern Europe (Fig. 1). Nevertheless, the relative novelty of these discoveries demands further investigation. Here, we present a new case of large raptor pedal phalanges associated with a CP context, thus expanding the geographical and chronological limits of this kind of evidence and providing new insights into the symbolic practices in pre-Upper Paleolithic (UP) European populations.

## RESULTS

### Site stratigraphy, chronology, and archeological record

Cova Foradada [Calafell, Catalonia, Spain; UTM (ETRS89) 381027.6–4562447.9] is a small karstic tunnel, 1.8 km far from the actual shoreline of the Mediterranean coastline of northeast Spain (Fig. 1

and fig. S1) (23). The morphology of the cave is defined by a circular entrance, yielding direct access to the “excavation hall” of ca. 14 m<sup>2</sup>. Stratigraphically, the excavated area consists of a 2.5-m section presenting four major lithostratigraphic units and 10 archeopaleontological layers, 8 with evidence of human occupation/use of the cave from the mid-Holocene to the Upper Pleistocene (Supplementary Materials) (23). Units I and II correspond to the Holocene epoch. The middle part of the sequence corresponds to the lithostratigraphic Unit III, formed by three different archeological layers. Layer III<sub>n</sub> has been associated with the Early Gravettian, followed by the almost sterile layer III<sub>g</sub> and layer III<sub>c</sub>, each corresponding to the Early Aurignacian. The basal part of the stratigraphic column corresponds to Unit IV, with layers IV, IV1, and IV2 being associated with the CP occupation. Found underneath these layers is an almost archeologically sterile unit (Unit V). Unit V has been further documented to be in contact with a thick basal flowstone (fig. S2).



**Fig. 1. Pre-UP symbolic use of raptor talons.** Geographical range of Neanderthal populations and sites with raptor cut-marked phalanges. The line of white dots roughly marks the probable range of Neanderthals in Eurasia, based on paleogenetic data and fossil remains. The yellow dotted line suggests the common cultural territory for the use of raptor talons before the arrival of the UP. The extended map indicates the location of all MP/CP sites, with raptor phalanges interpreted as symbolic elements, including Cova Foradada. Baume Gigny is included for the sake of clarity.

Archeological patterns shared by layers III<sub>n</sub> and III<sub>c</sub> and Unit IV suggest that the cave was only occasionally occupied by human groups, leaving a very scarce archeological record, formed mainly by shell ornaments in layer III<sub>n</sub> and hunting-related tools in both layers III<sub>c</sub> and IV. Fortunately, the lithic remains recovered from layers III<sub>c</sub> and IV are typologically diagnostic and, aside from the chronological context, are useful indicators attributing these occupations to their associated cultural technocomplexes (23).

Layer IV provided a small lithic assemblage highlighting the almost exclusive presence of CP points (fig. S1B). This represents the southernmost expression of this particular tool class in Europe, exclusively related with the CP culture and supposedly associated with the Neanderthals (4, 10).

The faunal assemblage of Unit IV is composed of 1289 remains [number of species (NSP)]; 1076 [number of identified species (NISP)] dominated by leporids (63.8% NISP), small bird remains (16.5% NISP), and Iberian lynx (9.4% NISP) (table S1). Twelve elements correspond to medium- and large-sized raptors, namely, that of the Iberian or Spanish imperial eagle (*Aquila adalberti*) (Table 2). Bone surface modification (BSM) analysis indicates scarce anthropogenic intervention, except for 31 burned bones (2.4% of NSP), 19 long bone shaft cylinders of leporids (11% of the total humerus, femur, and tibia NISP), and one fragment of a leporid tibia showing cut marks (fig. S4). The interpretation of the occupational dynamic in Unit IV suggests a very sporadic use of the cave by human groups, probably related to its use as a hunting shelter where they could rest, repair, and fine-tune certain hunting tools (23). Moreover, layer IV1 presents the remains of an imperial eagle with a cut-marked phalange. This find is horizontally and vertically associated with typical elements of the CP culture. Radiocarbon evidence currently places the occupations

of Unit IV >39 <sup>14</sup>C ka cal B.P. (calibrated years before the present) (fig. S3) (23).

### The FO15/IV1/E6/1339 specimen

The FO15/IV1/E6/1339 specimen (Fig. 2, STL S1, and movie S1) corresponds to the phalanx 1 of the first digit (the thumb or *Hallux*) from the left foot of a large eagle. The general morphology of the phalanx is stylized and svelte, as in the genus *Aquila*, thus different from the more robust morphology of *Aegypiiinae* (subfamily of vultures) and *Haliaeetus* (genus including white-tailed eagle). The palmar surface of the body is deeper than in vultures, presenting a well-marked attachment to fibrous sheaths of flexor tendons. The distal trochlea and the groove between them are well pronounced as in the genus *Aquila*. Studies regarding general morphology, dimensions, principal components analysis (PCA) results, as well as the distribution of past, extant, and Pleistocene large eagles in the Mediterranean Basin (25) all concur that *A. adalberti*, the Iberian imperial eagle, or an earlier ancestor, is the most plausible taxonomic match for the case of Foradada (Fig. 3).

Nevertheless, the origin and evolution of this species are controversial. *A. adalberti* and *Aquila heliaca* (Eastern imperial eagle) are currently considered to be not only separate species but also subspecies, allospecies, or semispecies. On the basis of molecular data, some authors date the divergence between these two raptors to at least ca. 1 million years (Ma), while other authors propose the split to have occurred in the Holocene or terminal Pleistocene (<13 ka B.P.) (26, 27). Moreover, there seems to have been male-mediated gene flow after the divergence, complicating the scenario (26). Solving this problem is far from the objectives of this paper, although the Foradada specimens can contribute to our knowledge of the evolutionary

**Table 2. Raptor remains from Unit IV of Cova Foradada.** ID, unique identification number of each specimen; BSM, bone surface modifications; CM, cut marks; Dg, diagenetic breakage.

ID	Layer	Element	Side	Taxon	Common name	BSM
FO14/IV/ F8/2848 + 3453	IV	Tarsometatarsus	R	<i>Aquila [heliaca] adalberti</i>	(Iberian?) Imperial eagle	Broken-Dg
FO15/IV/G8/C1	IV	Phalange 2 toe II	L	<i>Aquila [heliaca] adalberti</i>	(Iberian?) Imperial eagle	–
FO14/IV/F9/1971	IV	Talon	–	Accipitridae sp.	–	–
FO14/IV/ F6/306 + 307	IV	Tibiotarsus	R	<i>Aquila [heliaca] adalberti</i>	(Iberian?) Imperial eagle	Broken-Dg
FO15/IV/D7/C1	IV	Humerus	L	Accipitridae cf. <i>Milvus milvus</i>	cf. Red kite	Broken-Dg
FO14/IV/D8/1018	IV	Phalange 2 toe III	R	<i>Gyps fulvus</i>	Griffon vulture	–
FO15/IV/E6/C1	IV	Phalange	–	Accipitridae cf. <i>Accipiter</i> sp.	–	–
FO14/IV1/F8/2864	IV1	Phalange 2 toe III	R	<i>Aquila [heliaca] adalberti</i>	(Iberian?) Imperial eagle	–
FO14/IV1/F8/2862	IV1	Phalange 2 toe III	L	<i>Aquila [heliaca] adalberti</i>	(Iberian?) Imperial eagle	–
FO14/IV1/F8/3129	IV1	Phalange 1 toe I	–	Accipitridae cf. <i>Aquila</i> sp.	–	Broken-indet.
FO15/IV1/E6/1339	IV1	Phalange 1 toe I	L	<i>Aquila [heliaca] adalberti</i>	(Iberian?) Imperial eagle	CM
FO15/IV2/D7/C1	IV2	Ulna	R	Accipitridae cf. <i>Milvus milvus</i>	cf. Red kite	Broken-indet.

history of imperial eagles. If the specimens presented in this paper belong to *A. adalberti* or their ancestor, then they would be the oldest recorded find of the species so far. If these remains belong to the species *A. heliaca*, then it would be the first occurrence of this species in the fossil record of Iberia (for the whole of the Quaternary, Pleistocene, or Holocene periods). Nonetheless, at this current point in time, this problem cannot be resolved for this case; therefore, the Foradada specimen will be referred to throughout the rest of this study following González's use of semispecies classification (27), expressed in brackets and trinomially as *A. [heliaca] adalberti* and as imperial eagle *sensu lato* when we refer to the vernacular name.

The phalange presents 12 cut marks on the dorsal side of the diaphysis, appearing along approximately two-thirds of the phalanx's total length (Fig. 2 and Supplementary Materials). Most of the cuts ( $n = 11$ ) are oriented obliquely to the principal axis of the bone, ranging from the proximal epiphysis to distal extremity of the bone. These striae are found oriented parallel among themselves. All these oblique cuts are deep and present both composed striae and associated shoulder effect as deep as the principal groove like those produced by retouched stone tools (28). An additional incision can be observed, presented obliquely oriented with a longitudinal tendency. This last mark is more superficial than the previous marks and superimposes all other incisions. The 12 incisions observed present an average length of 3.67 mm and width of 0.23 mm. As can be seen in table S2, a general increase in the opening angle of each groove can be observed, while a similar pattern is observed through a decrease in depth of each profile along the groove. This variation, however, is relatively subtle and gradual, most likely explained by the physical properties and pressure exerted when making an inci-

sion (29). The homogeneity of the groove's shape, however, is clearly represented by the cross-section morphology and its development along the course of the incision. Procrustes analysis indicates that all these marks present an asymmetrical V-shaped cross section (Fig. 4A and STL S2). This feature is one of the key characteristics described by multiple authors when diagnosing a taphonomic trace as a cut mark (28). Considering only the profile shape, these taphonomic traces are clearly comparable with cut mark samples studied by a great deal of taphonomists [e.g., (30)], as opposed to the morphology of other linear traces such as tooth scores (31).

Three-dimensional (3D) analysis (Fig. 4B and Supplementary Materials) indicates that the depth and shape of the linear marks are clearly more pronounced than what would be expected of a trampling mark. Combined with a clear lack of a rounded base, as well as other features, this also rules out the possibility that these marks can be confused as a product of other natural agents, carnivores, humans, or even herbivores (32). While these marks are associated with some other taphonomic alterations such as biochemical BSM, they do not prevent the morphological study of these traces to a degree where equifinality is overly present (33). Mark location and depth all agree with experimental works presented by Romandini *et al.* (15), associating these striae with the disarticulation of the claw and the entire digit from the tarsometatarsus. Other than FO15/IV1/E6/1339, no other specimen of eagle or raptor remains shows anthropic modifications. It should be noted, however, that all the remains of *A. [heliaca] adalberti* are from appendicular elements, of which only one talon has been recovered. This unusual skeletal element representation can be further considered important when comparing with the case of other abundant small bird remains in this site (tables S1 and S3 and fig. S5) (Supplementary Materials).



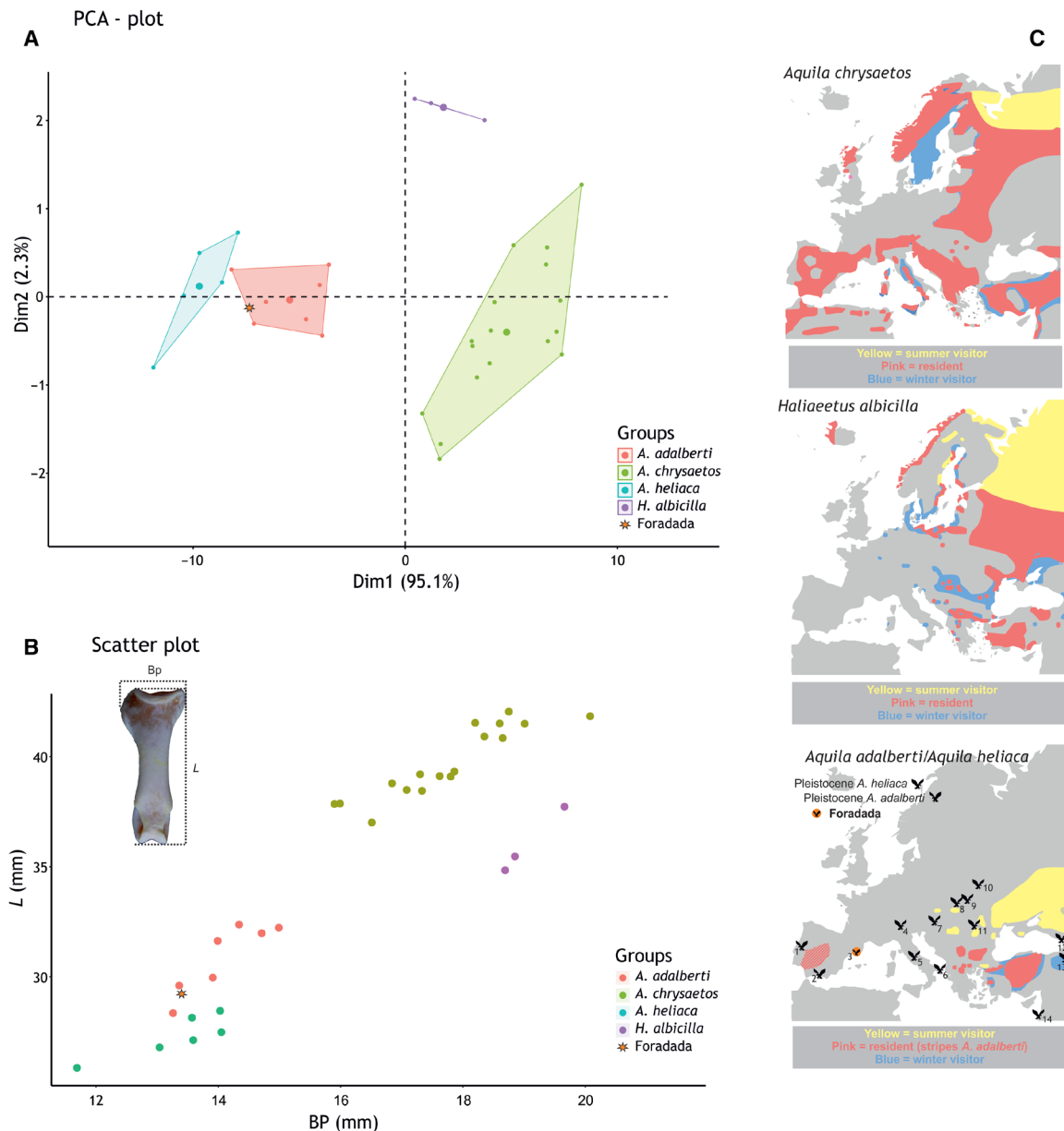
**Fig. 2.** FO15/IV1/E6/1339 specimen. (A) Dorsal, medial, plantar, and lateral views of the phalange (from left to right, respectively). (B) Detail of the cut marks in the dorsal view and dotted-line squares with the area amplified in photos (C) and (D). (E) Detailed photo of all the cut marks after cleaning and restoration. Photo credit: Antonio Rodríguez-Hidalgo, IDEA.

## DISCUSSION

The exploitation of birds as an alimentary and non-alimentary resource has been proven through several zooarchaeological investigations, suggesting that the trapping of birds formed a part of the behavioral variability of Neanderthal populations (7, 34, 35). While not being a frequent practice, the consumption of raptors among hunter-gatherers has further been confirmed through ethnographic data (36) and supported by the archeological record, including other Neanderthal sites (37, 38). Non-nutritional use of bird bones in Neanderthal sites is almost exclusively related to symbolic purposes (7), while their use as a raw material for creating domestic tools is extremely scarce (Supplementary Materials) (39).

In the case of talons, their non-nutritional value has been exhibited to support the claim of their symbolic use by Neanderthals, as opposed to their association with alimentary purposes (13, 15). Nevertheless, while the obvious consumption of talons can be considered a poor idea, according to current Spanish, Latin-American, and oriental recipes, the edibility of the raptor's feet may just be a question of cooking and taste to appreciate the skin and cartilaginous tissues present on these bones. Needless to say, cut marks are only indicators of anthropogenic manipulation. Their presence may simply indicate the butcher's removal of non-edible areas.

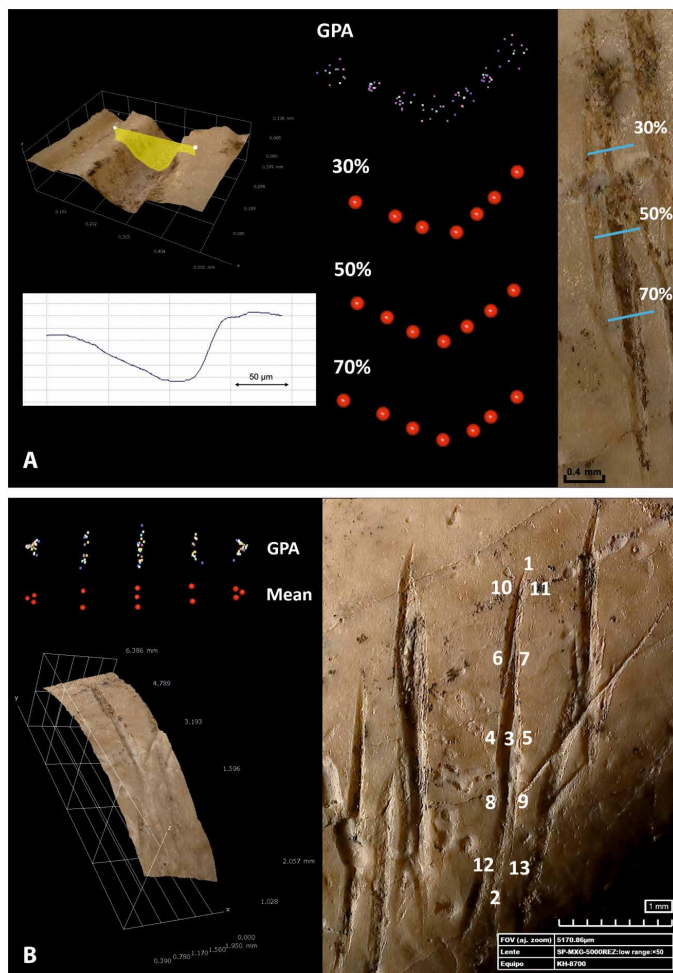
The present study demonstrates how a combination of traditional and newly developed methodological approaches in cut mark analysis can be a powerful tool when classifying BSMs. Our results lean strongly toward the classification of the marks on FO15/IV1/E6/1339 as cut marks. Their presence is a fundamental and unique find when constructing the hypothesis and reasoning behind the manipulation of these elements by ancient humans. For this reason, the combination of old and new methods and tools for BSM analysis is essential when the presence of cut marks may lead to relevant evolutionary hypotheses. Furthermore, we strongly agree with the interpretation of these cut marks as a product of talon extraction, or claw sheath removal, independent of the phalanx in which the traces are present (13–24). This observation is especially supported by neo-taphonomical experimentation, thus aiding in the construction of our interpretation (15). The additional arguments leading us to discard the alimentary nature of these remains are (i) the scarcity of raptor remains in the Foradada assemblage, namely, the selection of the species for anthropogenic handling; (ii) the high anatomical bias in favor of phalanges, thus presenting a selection of anatomical parts; and (iii) the absence of other BSMs related to anthropogenic consumption. This includes human chewing, green breakage, burning, and any traces of cooking BSMs on raptor bones or any other element in most of the faunal assemblage.



**Fig. 3. Data supporting species identification.** (A) PCA analysis of six measurements of the first phalanx of the toe I of different species of large eagles documented in the Iberian Pleistocene fossil record and *A. heliaca*. (B) Diagram with comparative measurements of the total length (L) and proximal breadth (Bp). (C) Current distribution of the three large eagles documented in the Iberian fossil record and European/Middle Eastern localities with the presence of imperial eagles (*A. adalberti/heliaca*) during the Pleistocene (references and dates of occurrences in the fossil record can be consulted in table S5).

Regarding species and anatomical selection, to date, cut marks are yet to be found on the pedal phalanges of other birds, except for raptors, excluding the case of Baume Gigny and Fumane A9 (14, 17). This can be further extended to the case of large carnivore claws, which would be more common if they were to be used as tools. This exceptional find reinforces their interpretation as symbolic elements, supporting and further suggesting that Neanderthals transmitted similar symbolic connotations to large raptors as current traditional societies (35, 40). The symbolic meaning of majestic eagles as large predators could thus be transmitted to some parts of their bodies as talons and feathers. While most archeological cases have presented this use in large eagle's talons, other species, however, are also represented including vultures and eagle owls. Following the same logic, the talons of other species should also convey other meanings, considering that both traditional and current societies associate vultures and eagles with opposing concepts. The same can be said for the swan of Baume Gigny, where the modest claw of a duck can hardly express the same symbolic message as a white-tailed eagle talon. Similarly, the talon of the black grouse from Fumane A9 presents another interesting case. Our finds from Foradada increase the number of cases where large eagles have specifically been exploited for their talons. In this sense, the selection of the larger eagles available in the Palearctic ecosystems dominates during the Middle and Middle to Upper Paleolithic archaeological record, making up 91.3%

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**Fig. 4.** Analysis of cut mark morphology using the HIROX KH-8700 3D digital microscope. (A) 2D GPA and mean shape of cut mark cross-section profiles across 30, 50, and 70% of each incision. (B) 3D GPA and mean shape of the entire incision. Photo credit: Antonio Rodríguez-Hidalgo, IDEA.

of the total cases documented (21 cases of 23). This suggests a correlation between the chosen taxon and the processed object. Moreover, the example of Foradada also sees an increase in the number of represented species. Consequently, while some authors may have proposed a specific symbolic meaning behind the use of large eagle “ornamental talons” (13), as well as large diurnal raptors associated with scavenging habits (20, 35), at least in the case of talons, the increase in the variety of taxa documented in these sites, including imperial eagle in Cova Foradada and cinereous vulture and eagle-owl in other MP/CP sites (13, 18, 20), suggests a greater complexity in terms of the symbolic nature of these elements. Current inferences regarding talons interpreted as ornaments highlight them to be “surviving traces of ancient human communication” (2), and precisely because of this, talons of different birds with different appearances and behaviors could transmit different messages about the identity of the bearer. In contrast, these archaic populations might not have needed to taxonomically differentiate between large raptor species, regardless of whether they could or not.

Archeological parallels documented specifically among hunter-gatherers of the late Pleistocene and Holocene support the symbolic character of these types of elements (38, 41–44). Faced with the

same type of zooarcheological and taphonomic evidence, the interpretation of specimens as fully symbolic in contexts associated with AMH leaves little space for speculation. This is enforced when the same elements and evidence are found within MP/CP sites, such as the case of Foradada. Peculiarly, manipulated talons are not very abundant among UP assemblages, commonly found only in the Magdalenian (17/12 ka) (24). Furthermore, the cases documented during the early UP appear to be extremely rare. Only two have been published, a talon of *Bubo scandiacus* from La Quina Aval (associated with early Aurignacian) (42) and a talon of probable *Gyp fulvus* from Üçağizli (associated with Ahmarian) (41). Again, this can be applied to the case of Foradada, where no early or late UP layer has provided anthropogenically modified raptor phalanges. Seashell beads, on the other hand, are in abundance. Currently, UP sites in the Iberian Mediterranean region and the rest of the Iberian Peninsula also fail to present similar finds, except for the case of Santa Catalina, Biscay (Spain), where snowy owl (*Bubo scandiacus*) talons were recovered associated with Magdalenian archeological layers (24).

In addition to archeological parallels, the ethnographic data prove that different cultural groups of all continents have used raptor claws/talon for the elaboration of a great variety of elements associated with rituals, dances, personal adornments, grave goods, etc. (38, 44). Only the case of the National Eagle Repository (NER) in Colorado (United States) currently provides more than 600 eagle carcasses to American nations every year for religious and cultural purposes. The most used elements are feathers and the limbs of these animals (with between 1200 and 1500 eagle limbs delivered on a yearly basis). In all cases, carcasses belong to two species, the bald eagle (*Haliaeetus leucocephalus*) and the golden eagle (*Aquila chrysaetos*), because these species contain the highest symbolic meaning for most of the Native American people.

Once having ruled out a nutritional and utilitarian use of raptor talons and considering the interpretation of similar objects in contexts associated with modern humans, the final interpretation of their use as symbolic is both plausible and probable. Although researchers tend to agree on the symbolic nature of talons, their definition of these elements as personal ornaments has been explored with prudence. Most have advocated defining the talons as “supposed ornaments,” while others have opted to refer to these finds directly as an example of “Neanderthal jewelry” (19). In accepting the use of talons as personal ornaments, this can be considered a tradition that predates any other manifestation of symbolism among Neanderthals or AMH, especially those in which seashells play a central role (5). If not, this manifestation also entails important implications for the emergence of symbolism and behavioral modernity, although further investigation is necessary to establish the functionality behind these objects. Regardless of whether the talons were hanging “beads,” part of necklaces, earrings, or any other elements for which there are no current parallels, the case of Foradada indicates the symbolic use of talons to be a well-rooted tradition among the Neanderthals of southern Europe for more than 80 millennia. Furthermore, our research suggests the presence of a common cultural territory in which the meaning conveyed by these large-raptor talons could probably be recognized by individuals from different groups. To date, the total absence of raptor talon exploitation in the African Paleolithic record (35, 40) forces us to ask ourselves for the direction of cultural interactions between Neanderthals and modern humans.

Neanderthal origins are currently situated around the second half of the Middle Pleistocene, while classic forms of these populations appear somewhat later during the MIS 5/4. Moreover, the archeological record indicates that they were very close to modern humans in behavioral terms, especially considering their tools, use of fire technology, foraging/hunting strategies, organization of living areas, and mobility. Hybridization between Neanderthals and AMH has been recently proven, highlighting how close both species were (45). Encephalic evolution also supports that the fundamental components needed for symbolic and abstract thinking are likely to be present during the end of the Middle Pleistocene (46). Nevertheless, evidence of symbolic behavior among Neanderthals is still scarce, especially if we compare this with the subsequent inflation of symbolism of modern humans (2, 47). Even so, the claims for symbolism among Neanderthals are much more frequent than among any other human species (1, 4–7, 13–20).

The use of raptor talons in Foradada must be added to the scarce pieces of evidence of symbolism among premodern humans in Europe. The symbolic and non-utilitarian meaning of raptor talons implies that Neanderthals would have had the ability to create and understand fully abstract concepts. The standardization and recurrent use of this kind of element can be interpreted as a nonverbal code and could indicate part of a communicative technology (2). If we accept this interpretation, then Neanderthals would have had social and cultural structures complex enough to convey the use and meaning of these codes both in time, from generation to generation, and through space. This represents a remarkable advance with respect to our knowledge about the symbolic behavior of the Neanderthals because, in many occasions, such evidences are unique, sporadic, or little standardized facts.

The case presented in this paper is evidence of the last occurrence of the use of raptor talons among Neanderthals, immersed in a cultural movement in which other jewelry traditions, developed independently or not, are documented (1, 5, 39). This practice, which emerged in the early MP, appears from time to time but recurrently in the Neanderthal world surviving on one of the last expressions of their material culture, the CP, and probably extinguishing with them forever.

## MATERIALS AND METHODS

### Excavation methods

Cova Foradada was systematically excavated in extension according to an artificial subdivision of the site in 1 m × 1 m squares, following the natural inclination of the geological layers. Regarding faunal remains, all ≥2-cm and all identifiable specimens, regardless of size, were recovered and their coordinates were documented on a 3D plot. In addition, all the excavated sediment previously recovered by square, layer, and relative depth (5-cm ranges) were water-sieved using superimposed 1-, 0.5-, and 0.05-mm mesh screens. These finds were then bagged. Microfossils were then sorted and classified.

### Zooarcheological and taphonomical methods

Anatomical and taxonomic determination of mammalian and bird remains were carried out in the Zooarcheological and Taphonomical Laboratory of the Catalàn Institute of Human Paleoecology and Social Evolution (IPHES). Avian reference collections from the Nat-Museum de Ciències Naturals de Barcelona in Barcelona, Muséum National d'Histoire Naturelle in Paris, Laboratório de Arqueociências—LARC-

DGPC in Lisbon, Estación Biológica de Doñana in Seville, and Naturhistorisches Museum Wien were used for comparative purposes. The osteological measurements were taken using a digital caliper with a precision of two decimal places in six specified anatomical points: proximodistal length (L), proximal mediolateral width (BP), mediolateral width at midshaft (SD), distal mediolateral width (Bd1), distal mediolateral width at the beginning of the trochlea (Bd2), proximal dorsopalmar height (Bapp), and the distal dorsopalmar height at the beginning of the trochlea (Badp). The comparative data can be consulted in table S4. Bone surfaces of all faunal remains were inspected macroscopically and microscopically with a stereomicroscope (OPTHEC, 120 Hz model), using magnifications from ×15 to ×45.

Cut marks and their relationship with specific butchering activities were identified on the basis of the criteria of Domínguez-Rodrigo *et al.* (28) and Romandini *et al.* (15). In addition, 3D reconstructions of the marks were carried out following the methodological protocol established by Courtenay *et al.* (48). This approach digitalizes each trace using the HIROX KH-8700 3D Digital Microscope with an MXG-5000REZ triple objective revolving lens. First, cross sections of each mark were produced using the midrange lens at a ×600 magnification. A fixed high-intensity light-emitting diode light source was placed above each sample, combining the use of coaxial and ring illumination. 3D digital reconstructions were produced using a combination of quick auto focus and depth synthesis functions that are provided by the HIROX's system, generating a 3D display of each mark where measurements could be taken and cross-section profiles could be extracted. To construct each digital image, between 110 and 130 photos were taken for each profile. The capturing and assessment of the morphology of each mark's profile were carried out using a total of three cross sections, taken at 30, 50, and 70% of the total length of each mark. As described by Maté González *et al.* (30), this range along the groove is suggested to be the most representative for cut mark morphological analysis.

These profiles were then exported to the free tpsDig2 (v.2.1.7) software where the allocation of seven homologous landmarks was carried out following the geometric morphometric models described by Maté González *et al.* (30). The resulting files produced through landmark allocation were then edited and imported into the free software R [www.r-project.org; (49)], where a full Procrustes fit was performed using the Geomorph library (50). This package can be used to prepare the sample for multivariate statistical analysis and is commonly referred to as a generalized Procrustes analysis (GPA). Through GPA, each individual is standardized through a series of superimposition procedures involving the translation, rotation, and scaling of each shape. Any differences in structure can thus be studied through patterns of variation and covariation, which can then be statistically assessed (51). The library Shapes (52) was then used to calculate and plot the mean shape of each cross section. Additional measurements concerning the depth and opening angle of each of the profiles were later taken. To capture the entire shape of these incisions, further digital reconstruction was carried out on the entire mark using the low-range lens at ×100 or ×150 magnification, depending on the necessities of the analyst with regard to resolution (48). To capture the entire length of each mark, the HIROX's tiling function was used to create a mosaic and complete digital reconstruction of each groove. Thirty photos were taken for each tile, while any number between 15 and 32 tiles was used to create the final image. With the use of a high-pixel resolution and the consequential



stacking of photos produced by the microscope, the entire shape of the taphonomic trace could be reproduced digitally. A 13-landmark model, as developed by Courtenay *et al.* (53), was then used to capture the entire shape of the groove. The position of each landmark was recorded through a series of measurements. This was done first using the “xy-width” function to measure and plot the location of each landmark across a 2D graph, followed by the measurement of depth using the “point height” function to establish each landmark’s position along the z-axis of a 3D plot. Landmark coordinates were recorded and processed in the same manner as the 2D profiles.

## SUPPLEMENTARY MATERIALS

Supplementary material for this article is available at <http://advances.sciencemag.org/cgi/content/full/5/11/eaax1984/DC1>

Supplementary Text

Fig. S1. Different views of Cova Foradada and CP points.

Fig. S2. Stratigraphic column.

Fig. S3. Horizontal and vertical location of the phalange FO15/ IV1/E6/1339.

Fig. S4. Anthropogenic modifications on leporid bones in Unit IV of Cova Foradada.

Fig. S5. Anatomical representation of large raptors versus small birds.

Table S1. NISP, percentage and minimal number of individuals (MNI), and number of specimens for Unit IV and layer IV, IV1, and IV2 faunal assemblage at Cova Foradada.

Table S2. Average measurements of the opening angle and depth of incision profiles at 30, 50, and 70% of the groove’s total length.

Table S3. Skeletal representation of small birds from Unit IV of Cova Foradada.

Table S4. Measurements of the first phalanx of digit I used for comparative purposes and data from the specimen of Cova Foradada.

Table S5. Pleistocene/Early Holocene fossil remains of *A. adalberti* and *A. heliaca* in Europe and Near East.

Movie S1. Animation of the 3D model of eagle phalanx with cut marks recovered in Cova Foradada.

STL S1. [www.morphosource.org/Detail/MediaDetail/Show/media\\_id/44124](http://www.morphosource.org/Detail/MediaDetail/Show/media_id/44124)

STL S2. [www.morphosource.org/Detail/MediaDetail/Show/media\\_id/44124](http://www.morphosource.org/Detail/MediaDetail/Show/media_id/44124)

References (54–111)

## REFERENCES AND NOTES

- Z. Jilhão, The emergence of ornaments and Art: An archaeological perspective on the origins of “behavioral modernity”. *J. Archaeol. Res.* **15**, 1–54 (2007).
- S. L. Kuhn, Signaling theory and technologies of communication in the Paleolithic. *Biol. Theory* **9**, 42–50 (2014).
- M. Vanhaeren, F. d’Errico, C. Stringer, S. L. James, J. A. Todd, H. K. Mienis, Middle paleolithic shell beads in Israel and Algeria. *Science* **312**, 1785–1788 (2006).
- J.-J. Hublin, S. Talamo, M. Julien, F. David, N. Connet, P. Bodu, B. Vandermeersch, M. P. Richards, Radiocarbon dates from the Grotte du Renne and Saint-Césaire support a Neandertal origin for the Châtelperronian. *Proc. Natl. Acad. Sci. U.S.A.* **109**, 18743–18748 (2012).
- D. L. Hoffmann, D. E. Angelucci, V. Villaverde, J. Zapata, J. Zilhão, Symbolic use of marine shells and mineral pigments by Iberian Neandertals 115,000 years ago. *Sci. Adv.* **4**, eaar5255 (2018).
- D. L. Hoffmann, C. D. Standish, M. García-Díez, P. B. Pettitt, J. A. Milton, J. Zilhão, J. I. Alcolea-González, P. Cantalejo-Duarte, H. Collado, R. de Balbín, M. Lorblanchet, J. Ramos-Muñoz, G. -C. Weniger, A. W. G. Pike, U-Th dating of carbonate crusts reveals Neandertal origin of Iberian cave art. *Science* **359**, 912–915 (2018).
- M. Peresani, I. Fiore, M. Gala, M. Romandini, A. Tagliacozzo, Late Neandertals and the intentional removal of feathers as evidenced from bird bone taphonomy at Fumane cave 44 ky B.P., Italy. *Proc. Natl. Acad. Sci. U.S.A.* **108**, 3888–3893 (2011).
- P. Mellars, Neandertal symbolism and ornament manufacture: The bursting of a bubble? *Proc. Natl. Acad. Sci. U.S.A.* **107**, 20147–20148 (2010).
- J. Pelegrin, M. Soressi, Le Châtelperronien et ses rapports avec le Moustérien, in *Les Neandertaliens. Biologie et Cultures*, B. Vandermeersch, B. Maureille, Eds. (Éditions du CTHS, 2007) pp. 283–296.
- F. Welker, M. Hajdinjak, S. Talamo, K. Jaouen, M. Dannemann, F. David, M. Julien, M. Meyer, J. Kelso, I. Barnes, S. Brace, P. Kamminga, R. Fischer, B. M. Kessler, J. R. Stewart, S. Pääbo, M. J. Collins, J.-J. Hublin, Palaeoproteomic evidence identifies archaic hominins associated with the Châtelperronian at the Grotte du Renne. *Proc. Natl. Acad. Sci. U.S.A.* **113**, 11162–11167 (2016).
- O. Bar-Yosef, J.-G. B. Bordes, Who were the makers of the Châtelperronian culture? *Hum. Evol.* **59**, 586–593 (2010).
- B. Gravina, F. Bachelier, S. Caux, E. Discamps, J.-P. Faivre, A. Galland, A. Michel, N. Teyssandier, J.-G. Bordes, No reliable evidence for a Neandertal-Châtelperronian association at La Roche-à-Pierrot, Saint-Césaire. *Sci. Rep.* **8**, 15134 (2018).
- E. Morin, V. Laroulandie, Presumed symbolic use of diurnal raptors by Neandertals. *PLOS ONE* **7**, e32856 (2012).
- C. Mourer-Chauviré, Les oiseaux. La Baume de Gigny (Jura) sous la direction de M. Campy, J. Chaline, M. Vuilleme. *Gallia Préhistoire XXVII Supplément*, 122–129 (1989).
- M. Romandini, M. Peresani, V. Laroulandie, L. Metz, A. Pastors, M. Vaquero, L. Slimak, Convergent evidence of eagle talons used by late Neandertals in Europe: A further assessment on symbolism. *PLOS ONE* **9**, e101278 (2014).
- I. Fiore, M. Gala, A. Tagliacozzo, Ecology and subsistence strategies in the Eastern Italian Alps during the Middle Palaeolithic. *Int. J. Osteoarchaeol.* **14**, 273–286 (2004).
- I. Fiore, M. Gala, M. Romandini, E. Cocca, A. Tagliacozzo, M. Peresani, From feathers to food: Reconstructing the complete exploitation of avifaunal resources by Neandertals at Fumane cave, unit A9. *Quat. Int.* **421**, 134–153 (2016).
- A. Majkić, S. Evans, V. Stepanchuk, A. Tsvlykh, F. d’Errico, A decorated raven bone from the Zaskalnaya VI (Kolosovskaya) Neandertal site, Crimea. *PLOS ONE* **12**, e0173435 (2017).
- D. Radovčić, A. O. Sršen, J. Radovčić, D. W. Frayer, Evidence for Neandertal jewelry: Modified white-tailed eagle claws at Krapina. *PLOS ONE* **10**, e0119802 (2015).
- V. Laroulandie, J.-P. Faivre, M. Gerbe, V. Mourre, Who brought the bird remains to the Middle palaeolithic site of les Fieux (Southwestern, France)? Direct evidence of a complex taphonomic story. *Quat. Int.* **421**, 116–133 (2016).
- M. Soressi, W. Rendu, J. P. Texier, E. Claud, L. Daulny, F. d’Errico, V. Laroulandie, B. Maureille, M. Niclot, S. Schwartz, A. M. Tillier, Pech-de-l’Azé I (Dordogne, France): Nouveau regard sur un gisement moustérien de tradition acheuléenne connu depuis le XIXe siècle. *Les sociétés Paléolithiques dans un grand Sud-Ouest: Nouveaux gisements, nouveaux résultats, nouvelles méthodes*, Société Préhistorique Française, Talence, France, 24–25 Novembre 2006 (Société Préhistorique Française, 2008).
- H. Dibble, F. Berna, P. Goldberg, S. McPherron, S. Mentzer, L. Niven, D. Richter, D. Sandgathe, I. Théry-Parisot, A. Turq, A preliminary report on Pech de l’Azé IV, layer 8 (Middle Paleolithic, France). *PaleoAnthropology*, 182–219 (2009).
- J. I. Morales, A. Cebriá, A. Burguet-Coca, J. L. Fernández-Marchena, G. García-Argudo, A. Rodríguez-Hidalgo, M. Soto, S. Talamo, J.-M. Tejero, J. Valverdú, J. M. Fullola, The Middle-to-Upper Paleolithic transition occupations from Cova Foradada (Calafell, NE Iberia). *PLOS ONE* **14**, e0215832 (2019).
- V. Laroulandie, Hunting fast-moving, low-turnover small game: The status of the snowy owl (*Bubo scandiacus*) in the Magdalenian. *Quatern. Int.* **414**, 174–197 (2016).
- A. Sánchez-Marco, Avian zoogeographical patterns during the Quaternary in the Mediterranean Region and paleoclimatic interpretation. *Ardeola* **51**, 91–132 (2004).
- B. Martínez-Cruz, J. A. Godoy, Genetic evidence for a recent divergence and subsequent gene flow between Spanish and Eastern imperial eagles. *BMC Evol. Biol.* **7**, 170 (2007).
- L. M. González, Origin and formation of the Spanish Imperial Eagle (*Aquila adalberti*). *J. Ornithol.* **149**, 151–159 (2008).
- M. Domínguez-Rodrigo, S. de Juana, A. B. Galán, M. Rodríguez, A new protocol to differentiate trampling marks from butchery cut marks. *J. Archaeol. Sci.* **36**, 2643–2654 (2009).
- S. L. Potter, The physics of cutmarks. *J. Taphonomy* **3**, 91–106 (2005).
- M. Á. Maté González, J. Yravedra, D. González-Aguilera, J. F. Palomeque-González, M. Domínguez-Rodrigo, Micro-photogrammetric characterization of cut marks on bones. *J. Archaeol. Sci.* **62**, 128–142 (2015).
- M. C. Arriaza, J. Yravedra, M. Domínguez-Rodrigo, M. Á. Mate-González, E. García Vargas, J. F. Palomeque-González, J. Aramendi, D. González-Aguilera, E. Baquedano, On applications of micro-photogrammetry and geometric morphometrics to studies of tooth mark morphology: The modern Olduvai Carnivore Site (Tanzania). *Palaeoecol. Palaeoclimatol. Palaeoecol.* **488**, 103–112 (2017).
- Y. Fernández-Jalvo, P. Andrews, *Atlas of Taphonomic Identifications. 1001+ Images of Fossil and Recent Mammal Bone Modification*. *Vertebrate Paleobiology and Paleoanthropology* (Springer, 2016).
- A. Pineda, P. Saladié, J. M. Vergès, R. Huguet, I. Cáceres, J. Vallverdú, Trampling versus cut marks on chemically altered surfaces: An experimental approach and archaeological application at the Barranc de la Boella site (la Canonja, Tarragona, Spain). *J. Archaeol. Sci.* **50**, 84–93 (2014).
- R. Blasco, C. Finlayson, J. Rosell, A. S. Marco, S. Finlayson, G. Finlayson, J. J. Negro, F. G. Pacheco, J. R. Vidal, The earliest pigeon fanciers. *Sci. Rep.* **4**, (2014).
- C. Finlayson, K. Brown, R. Blasco, J. Rosell, J. J. Negro, G. R. Bortolotti, G. Finlayson, A. Sánchez Marco, F. Giles Pacheco, J. Rodríguez Vidal, J. S. Carrión, D. A. Fa, J. M. Rodríguez-Llanes, Birds of a feather: Neandertal exploitation of raptors and corvids. *PLOS ONE* **7**, e45927 (2012).
- J. Woodburn, An introduction to Hadza ecology, in *Man The Hunter*, R. B. Lee, I. DeVore, Eds. (Adeline Publishing Company, 1972) pp. 49–55.

37. A. Gómez-Olivencia, N. Sala, C. Núñez-Lahuerta, A. Sanchis, M. Arlegi, J. Rios-Garaizar, First data of Neandertal bird and carnivore exploitation in the Cantabrian region (Axlor; Barandiaran excavations; Dima, Biscay, Northern Iberian Peninsula). *Sci. Rep.* **8**, 10551 (2018).
38. D. Serjeantson, *Birds (Cambridge Manuals in Archeology)* (Cambridge Univ. Press, 2009).
39. M. Julien, M. Vanhaeren, F. d'Errico, Neanderthals of the Upper Paleolithic: Châtelperronian ornaments and bone industries, in *The Third Man. The Prehistory of the Altai*, J.-J. Cleyet-Merle, A. P. Derevianko, J.-M. Geneste, B. Gravina, A. Krivoshapkin, B. Maureille, A. Turq, M. V. Shunkov, L. Slimak, Eds. (Rèunion des musées nationaux-Grand Palais, 2017) pp. 111–121.
40. C. Finlayson, *The Smart Neanderthal: Bird Catching, Cave Art & the Cognitive Revolution* (Oxford Univ. Press, 2019).
41. S. L. Kuhn, M. C. Stiner, E. Güleç, I. Özer, H. Yılmaz, I. Baykara, A. Açıklol, P. Goldberg, K. M. Molina, E. Ünay, F. Suata-Alpaslan, The early upper paleolithic occupations at Uçağızlı cave (Hatay, Turkey). *J. Human Evol.* **56**, 87–113 (2009).
42. J.-B. Mallye, M.-C. Soulier, V. Laroulandie, Large carnivores and small games use from the Early Aurignacian of La Quina Aval (Charente, France) (V. Dujardin excavations). *Paleo* **24**, 235–248 (2013).
43. L. Gourichon, Bird remains from Jerf el Ahmar, a PPNA site northern Syria with special reference to Griffon Vulture (*Gyps fulvus*), in *Archaeozoology of the Near East V, Proceedings of the 5th conference of ASWA*, ICAZ, Irbid/Yarmouk University, Jordan, 2 to 5 April 2000 (ARC-Publicities, 2002).
44. P. W. Parmalee, Utilization of birds by the Archaic and Fremont cultural groups in Utah, in *Papers in Avian Paleontology Honoring Hildegarde Howard*, K. E. J. Campbell, Ed. (Natural History Museum of Los Angeles County, 1980), vol. 330, pp. 237–250.
45. S. Sankararaman, N. Patterson, H. Li, S. Pääbo, D. Reich, The date of interbreeding between Neandertals and modern humans. *PLoS Genet.* **8**, e1002947 (2012).
46. R. G. Klein, Language and human evolution. *J. Neurolinguistics* **43B**, 204–221 (2017).
47. E. Hovers, A. Belfer-Cohen, “Now you see it, now you don’t”–Modern human behavior in the Middle Paleolithic, in *Transitions before the Transition. Interdisciplinary Contributions to Archaeology*, E. Hovers, S. L. Kuhn, Eds. (Springer, 2006), vol. 332, pp. 295–304.
48. L. A. Courtenay, J. Yravedra, R. Huguet, A. Ollé, J. Aramendi, M. Á. Maté-González, D. González-Aguilera, New taphonomic advances in 3D digital microscopy: A morphological characterisation of trampling marks. *Quat. Int.* **517**, 55–66 (2019).
49. C. R. Team, *A Language and Environment for Statistical Computing* (R Foundation for Statistical Computing, 2014).
50. D. C. Adams, E. Otárola-Castillo, Geomorph: An R package for the collection and analysis of geometric morphometric shape data. *Methods Ecol. Evol.* **4**, 393–399 (2013).
51. P. Mitteroecker, P. Gunz, Advances in geometric morphometrics. *J. Evol. Biol.* **36**, 235–247 (2009).
52. I. L. Dryden, *Shapes Package. R Package Version 1.2.3* (R Foundation for Statistical Computing, 2017).
53. L. A. Courtenay, J. Yravedra, M. Á. Mate-González, J. Aramendi, D. González-Aguilera, 3D analysis of cut marks using a new geometric morphometric methodological approach. *Archaeol. Anthropol. Sci.* **11**, 651–665 (2019).
54. D. Gifford-Gonzalez, *An Introduction to Zooarchaeology* (Springer International Publishing, 2018), pp. XXIII, 604.
55. E. J. Reitz, E. Wing, *Zooarchaeology (Cambridge Manuals in Archaeology)* (Cambridge Univ. Press, 1999).
56. R. L. Lyman, *Quantitative Paleozoology (Cambridge Manuals in Archaeology)* (Cambridge Univ. Press, 2008).
57. P. Villa, E. Mahieu, Breakage patterns of human long bones. *J. Hum. Evol.* **21**, 27–48 (1991).
58. L. Lloveras, M. Moreno-García, J. Nadal, Taphonomic study of leporid remains accumulated by the Spanish Imperial Eagle (*Aquila adalberti*). *Geobios* **41**, 91–100 (2008).
59. D. Cochard, J.-P. Brugal, E. Morin, L. Meignen, Evidence of small fast game exploitation in the middle paleolithic of Les Canalettes, Aveyron, France. *Quat. Int.* **264**, 32–51 (2012).
60. R. J. Blumenschine, Percussion marks, tooth marks, and experimental determinations of the timing of hominid and carnivore access to long bones at FLK Zinjanthropus, Olduvai Gorge, Tanzania. *J. Hum. Evol.* **29**, 21–51 (1995).
61. R. J. Blumenschine, C. W. Marean, S. D. Capaldo, Blind tests of inter-analyst correspondence and accuracy in the identification of cut marks, percussion marks, and carnivore tooth marks on bone surfaces. *J. Archaeol. Sci.* **23**, 493–507 (1996).
62. R. J. Blumenschine, M. M. Selvaggio, Percussion marks on bone surfaces as a new diagnostic of hominid behaviour. *Nature* **333**, 763–765 (1988).
63. J. W. Fisher Jr., Bone surface modifications in zooarchaeology. *J. Archaeol. Meth. Theor.* **2**, 7–68 (1995).
64. P. Shipman, J. Rose, Early hominid hunting, butchering, and carcass-processing behaviours: Approaches to the fossil record. *J. Anthropol. Archaeol.* **2**, 57–98 (1983).
65. A. K. Blumensmeyer, Taphonomy and the fossil record. *Am. Scient.* **72**, 558–566 (1984).
66. L. R. Binford, *Bones. Ancient Men and Modern Myths* (Academic Press, 1981).
67. M. C. Stiner, S. L. Kuhn, S. Weiner, O. Bar-Yosef, Differential burning, recrystallization, and fragmentation of archaeological bone. *J. Archaeol. Sci.* **22**, 223–237 (1995).
68. E. Tchernov, Exploitation of birds during the Natufian and Early Neolithic of the Southern Levant. *Archaeofauna* **2**, 121–143 (1993).
69. L. Yeomans, T. Richter, Exploitation of a seasonal resource: Bird hunting during the late natufian at shubayqa 1. *Int. J. Osteoarchaeol.* **28**, 95–108 (2018).
70. A. Recchi, A. Gopher, Birds and humans in the Holocene: The case of Qumran Cave 24 (Dead Sea, Israel). *Acta Zool. (Cracoviensia)* **45**, 139–150 (2002).
71. S. Gaudzinski, Middle palaeolithic bone tools from the open-air site Salzgitter-Lebenstedt (Germany). *J. Archaeol. Sci.* **26**, 125–141 (1999).
72. F. Caron, F. d'Errico, P. Del Moral, F. Santos, J. Zilhão, The reality of Neandertal symbolic behavior at the Grotte du Renne, Arcy-sur-Cure, France. *PLOS ONE* **6**, e21545 (2011).
73. F. d'Errico, M. Julien, D. Liolios, M. Vanhaeren, D. Baffier, Many awls in our argument. Bone tool manufacture and use in the Châtelperronian and Aurignacian levels of the Grotte du Renne at Arcy-sur-Cure, in *The Chronology of the Aurignacian and of the Transitional Technocomplexes. Dating, Stratigraphies, Cultural Implications*, F. d'Errico, J. Zilhão, Eds. (Instituto Português de Arqueologia, 2003), pp. 247–270.
74. F. d'Errico, V. Borgia, A. Ronchitelli, Uluzzian bone technology and its implications for the origin of behavioural modernity. *Quat. Int.* **259**, 59–71 (2012).
75. M. Peresani, E. Cristiani, M. Romandini, The Uluzzian technology of Grotta di Fumane and its implication for reconstructing cultural dynamics in the Middle–Upper palaeolithic transition of Western Eurasia. *J. Hum. Evol.* **91**, 36–56 (2016).
76. F. Romagnoli, F. Martini, L. Sarti, Neandertal use of *Callista chione* shells as raw material for retouched tools in South-East Italy: Analysis of Grotta del Cavallo layer I assemblage with a new methodology. *J. Archaeol. Meth. Theor.* **22**, 1007–1037 (2015).
77. A. Markó, Leaf-shaped lithic and osseous tools from old excavated cave sites: Demonstrating associations, in *The Sound of Bones*, F. Lang, Ed. (Universität Salzburg, 2013) pp. 191–202.
78. I. Karvanić, F. H. Smith, Alternative interpretations of the Middle/Upper paleolithic interface at Vindija Cave (Northwestern Croatia) in the context of Central Europe and the Adriatic. *Archaeol. Ethnol. Anthropol. Eurasia* **41**, 11–20 (2013).
79. M. Soressi, S. P. McPherron, M. Lenoir, T. Dogandžić, P. Goldberg, Z. Jacobs, Y. Maigrot, N. L. Martisius, C. E. Miller, W. Rendu, M. Richards, M. M. Skinner, T. E. Steele, S. Talamo, J.-P. Texier, Neandertals made the first specialized bone tools in Europe. *Proc. Natl. Acad. Sci. U.S.A.* **110**, 14186–14190 (2013).
80. G. Abrams, S. M. Bello, K. Di Modica, S. Pirson, D. Bonjean, When Neandertals used Cave Bear (*Ursus spelaeus*) remains: Bone retouchers from unit 5 of Scladina cave (Belgium). *Quat. Int.* **326–327**, 274–287 (2014).
81. C. Daujeard, M.-H. Moncel, I. Fiore, A. Tagliacozzo, P. Bindon, J.-P. Raynal, Middle paleolithic bone retouchers in Southeastern France: Variability and functionality. *Quat. Int.* **326–327**, 492–518 (2014).
82. J.-B. Mallye, C. Thiébaud, V. Mourre, S. Costamagno, É. Claud, P. Weisbecker, The Mousterian bone retouchers of Noisetier Cave: Experimentation and identification of marks. *J. Archaeol. Sci.* **39**, 1131–1142 (2012).
83. M. Mozota, *El Hueso Como Materia Prima: El Utillaje Óseo del Final del Musteriense en el Sector Central del Norte de la Península Ibérica* (Universidad de Cantabria, 2012).
84. M. Romandini, E. Cristiani, M. Peresani, A retouched bone shaft from the late Mousterian at Fumane Cave (Italy). Technological, experimental and micro-wear analysis. *Comp. Rend. Palevol.* **14**, 63–72 (2015).
85. M. Turk, A. Košir, Mousterian osseous artefacts? The case of Divje babe I, Slovenia. *Quat. Int.* **450**, 103–115 (2017).
86. V. T. Dobosi, Ex Proboscideis-Proboscidean remains as raw material at four Palaeolithic sites, Hungary, in *The World of Elephants. Proceedings of the First International Congress*, G. Cavarretta, P. Gioia, M. Mussi, M. R. Palombo, Eds. (Consiglio Nazionale delle Ricerche, 2001) pp. 429–431.
87. M. Á. Maté-González, J. F. Palomeque-González, J. Yravedra, D. González-Aguilera, M. Domínguez-Rodrigo, Micro-photogrammetric and morphometric differentiation of cut marks on bones using metal knives, quartzite, and flint flakes. *Archaeol. Anthropol. Sci.* **10**, 805–816 (2018).
88. D. Adams, M. Collyer, A. Kaliontzopoulou, E. Sherratt, *Geomorph: Software for Geometric Morphometric Analyses. R Package Version 3.0.5* (2017).
89. D. E. Slice, Landmark coordinates aligned by procrustes analysis do not lie in Kendall's shape space. *Syst. Biol.* **50**, 141–149 (2001).
90. F. J. Rohlf, Shape statistics: Procrustes superimpositions and tangent spaces. *J. Classif.* **16**, 197–223 (1999).
91. P. L. Walker, J. C. Long, An experimental study of the morphological characteristics of tool marks. *Am. Antiq.* **42**, 605–616 (1977).
92. S. L. Olsen, Applications of scanning electron microscopy in archaeology, in *Advances in Electronics and Electron Physics*, W. H. Peter, Ed. (Academic Press, 1988), vol. 71, pp. 357–380.
93. S. M. Bello, C. Soligo, A new method for the quantitative analysis of cutmark micromorphology. *J. Archaeol. Sci.* **35**, 1542–1552 (2008).

94. S. M. Bello, S. A. Parfitt, C. Stringer, Quantitative micromorphological analyses of cut marks produced by ancient and modern handaxes. *J. Archaeol. Sci.* **36**, 1869–1880 (2009).
95. S. M. Bello, *New Results from the Examination of Cut-Marks Using Three-Dimensional Imaging in Developments in Quaternary Sciences*, S. G. L. Nick Ashton, S. Chris, Eds. (Elsevier, 2011), vol. 14, pp. 249–262.
96. M. Á. Maté-González, J. Aramendi, D. González-Aguilera, J. Yravedra, Statistical comparison between low-cost methods for 3D characterization of cut-marks on bones. *Remote Sens. (Basel)* **9**, 873 (2017).
97. M. Á. Maté-González, J. Aramendi, J. Yravedra, R. Blasco, J. Rosell, D. González-Aguilera, M. Domínguez-Rodrigo, Assessment of statistical agreement of three techniques for the study of cut marks: 3D digital microscope, laser scanning confocal microscopy and micro-photogrammetry. *J. Microsc.* **267**, 356–370 (2017).
98. M. Á. Maté-González, J. Yravedra, D. M. Martín-Perea, J. Palomeque-González, M. San-Juan-Blazquez, V. Estaca-Gómez, D. Uribelarrea, D. Álvarez-Alonso, F. Cuartero, D. González-Aguilera, M. Domínguez-Rodrigo, Flint and quartzite: Distinguishing raw material through bone cut marks. *Archaeometry* **60**, 437–452 (2018).
99. A. K. Behrensmeyer, K. D. Gordon, G. T. Yanagi, Trampling as a cause of bone surface damage and pseudo-cutmarks. *Nature* **319**, 768–771 (1986).
100. P. Andrews, J. Cook, Natural modifications to bones in a temperate setting. *Man* **20**, 674–691 (1985).
101. P. Saladié, R. Huguet, C. Díez, A. Rodríguez-Hidalgo, E. Carbonell, Taphonomic modifications produced by modern brown bears (*Ursus arctos*). *Int. J. Osteoarchaeol.* **23**, 13–33 (2013).
102. M. Andrés, A. O. Gidna, J. Yravedra, M. Domínguez-Rodrigo, A study of dimensional differences of tooth marks (pits and scores) on bones modified by small and large carnivores. *Archaeol. Anthropol. Sci.* **4**, 209–219 (2012).
103. Y. Fernández-Jalvo, P. Andrews, When humans chew bones. *J. Hum. Evol.* **60**, 117–123 (2011).
104. P. Saladié, A. Rodríguez-Hidalgo, C. Díez, P. Martín-Rodríguez, E. Carbonell, Range of bone modifications by human chewing. *J. Archaeol. Sci.* **40**, 380–397 (2013).
105. M. Domínguez-Rodrigo, P. Saladié, I. Cáceres, R. Huguet, J. Yravedra, A. Rodríguez-Hidalgo, P. Martín, A. Pineda, J. Marín, C. Gené, J. Aramendi, L. Cobo-Sánchez, Use and abuse of cut mark analyses: The Rorschach effect. *J. Archaeol. Sci.* **86**, 14–23 (2017).
106. S. M. Domingues-Figueiredo, *A Avifauna Pliocénica de Portugal. Especificidades Evolutivas, Anatômicas e o Seu Contexto Paleontológico, Geológico e Arqueológico* (Departamento de Prehistória, História Antigua y Aqueología, USAL, 2010).
107. F. Hernández, Catálogo provisional de los yacimientos con aves del cuaternario de la Península Ibérica. *Archeofauna* **2**, 231–275 (1993).
108. T. Tyrberg, Arctic, montane and steppe birds as glacial relicts in the West Palearctic. *Ornith. Verh.* **25**, 29–49 (1991).
109. T. Tyrberg, *Pleistocene Birds of the Palearctic: A Catalogue. Publications of the Nuttall Ornithological Club* **27** (Nuttall Ornithological Club, 1998).
110. T. Tyrberg, *Pleistocene Birds of the Palearctic. Supplement of Pleistocene Birds of the Palearctic: A Catalogue. Publications of the Nuttall Ornithological Club* **27** (Nuttall Ornithological Club, 2005).
111. T. Tomek, Z. M. Bocheński, P. Socha, K. Stefaniak, Continuous 300,000-year fossil record: Changes in the ornithofauna of Bisnik Cave, Poland. *Palaeo. Electronica* **15**, 20 (2010).
- C. Lefevre, E. Maldonado, C. Núñez-Lahuerta, Ó. Pérez-Parque, J. Quesada, Y. Quintino, A. J. Romero, R. Sáez, G. A. Tsoukalos, P. Vallverdú, and D. Wiist for providing different data, references, comments, and help that have improved this work. We thank E. Moreno for restoring of the Foradada specimens. We thank our colleagues at the NeanderArt conference (celebrated in August 2018 in Torino, Italy) for their feedback. L.A.C. would like to thank the team, especially J. Yravedra, for their support and help with the studies. We thank D. Wiist for providing information about the National Eagle Repository and A. Majkic and F. d'Errico for the information about the talons of Grotte du Renne unpublished yet by Julien *et al.* [L'industrie osseuse Chatelperronienne de la Grotte du Renne, (Arcy-sur-Cure). Supplément a Paléo]. Last, we thank the editor, associate editor, and two anonymous reviewers for their constructive comments, which helped us to improve the manuscript. **Funding:** This research was financed by the Spanish Ministry of Science, Innovation and Universities (HAR2017-86509-P) (MICINN-FEDER PGC2018-093925-B-C32) and Generalitat de Catalunya through 2017 SGR 1040 supported within the framework of CERCA Programme/Generalitat de Catalunya, and 2017 SGR 00011 and CLT009/18/00024 projects (the last two directed by J.-M.F. as the principal investigator). The research work of A.R.-H. was financed by the Spanish Ministry of Science, Innovation and Universities (FJCI-2015-24144, Subprograma Juan de la Cierva) and CGL2015-65387-C3-1-P (MINECO/FEDER). The research of J.I.M. was financed by the Juan de la Cierva-Incorporación (JCI-2017-31445) MICINN fellowship. The research of G.G.-A. was financed by the Universitat de Barcelona APiF 2018 fellowship. The research work of J.L.F.-M. was financed by FPI program of the Spanish Ministry of Economy and Competitiveness MINECO/FSE (BES-2015-074931). The research work of J.-M.T. was funded by CNRS UMR 7041 ArScAn équipe Ethnologie préhistorique (P. Bodu). J.M. is the beneficiary of an Erasmus Mundus Doctorate scholarship for an International Doctorate in Quaternary and Prehistory (IDQP). **Author contributions:** A.R.-H., J.I.M., G.G.-A., L.A.C., J.L.F.-M., and J.-M.T. wrote the paper. A.R.-H., J.I.M., L.A.C., P.S., and J.M. analyzed data. A.R.-H. designed and performed research. J.I.M. and A.C. directed the field works. A.R.-H., J.L.F.-M., and M.S. performed graphics, and L.A.C. edited the English text as a native speaker. J.-M.F. directed the project. All authors have read, corrected, and approved the manuscript. **Competing interests:** The authors declare that they have no competing interests. **Data and materials availability:** All necessary permits were obtained from the Departament de Cultura of the Generalitat de Catalunya and local authorities for the excavation of the Cova Foradada under the direction of A.C., J.-H.M., and J.-M.F. and for the described study, which complied with all relevant regulations. The unique identification numbers (IDs) of the specimens analyzed in this paper are in Table 2. The Cova Foradada specimens are temporary housed at the Institut Català de Paleoeologia Human i Evolució Social, in the Collections Room (Tarragona, Spain), with the permission of the Departament de Cultura of the Generalitat de Catalunya. The specimens are available to any researcher to be inspected. The micro-CT scan models are available under request. Virtual 3D models of the complete specimen and the cut-marked area of interest from the FO15/IV1/E6/1339 specimen are provided as SOM Files STL S1 and S2, respectively, available from MorphoSource ([www.morphosource.org](http://www.morphosource.org)) [www.morphosource.org/Detail/SpecimenDetail/Show/specimen\\_id/23751](http://www.morphosource.org/Detail/SpecimenDetail/Show/specimen_id/23751).

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## Supplementary Materials for

### The Châtelperronian Neanderthals of Cova Foradada (Calafell, Spain) used imperial eagle phalanges for symbolic purposes

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#### The PDF file includes:

Supplementary Text

Fig. S1. Different views of Cova Foradada and CP points.

Fig. S2. Stratigraphic column.

Fig. S3. Horizontal and vertical location of the phalange FO15/ IV1/E6/1339.

Fig. S4. Anthropogenic modifications on leporid bones in Unit IV of Cova Foradada.

Fig. S5. Anatomical representation of large raptors versus small birds.

Table S1. NISP, percentage and minimal number of individuals (MNI), and number of specimens for Unit IV and layer IV, IV1, and IV2 faunal assemblage at Cova Foradada.

Table S2. Average measurements of the opening angle and depth of incision profiles at 30, 50, and 70% of the groove's total length.

Table S3. Skeletal representation of small birds from Unit IV of Cova Foradada.

Table S4. Measurements of the first phalanx of digit I used for comparative purposes and data from the specimen of Cova Foradada.

Table S5. Pleistocene/Early Holocene fossil remains of *A. adalberti* and *A. heliaca* in Europe and Near East.

STL S1. [www.morphosource.org/Detail/MediaDetail/Show/media\\_id/44124](http://www.morphosource.org/Detail/MediaDetail/Show/media_id/44124)

STL S2. [www.morphosource.org/Detail/MediaDetail/Show/media\\_id/44124](http://www.morphosource.org/Detail/MediaDetail/Show/media_id/44124)

References (54–111)

#### Other Supplementary Material for this manuscript includes the following:

(available at [advances.sciencemag.org/cgi/content/full/5/11/eaax1984/DC1](http://advances.sciencemag.org/cgi/content/full/5/11/eaax1984/DC1))

Movie S1 (.mp4 format). Animation of the 3D model of eagle phalanx with cut marks recovered in Cova Foradada.

## Supplementary Text

### 1. Stratigraphic description

The stratigraphic sequence of Cova Foradada consists of ca 2.5 m of sediments divided into four major litho-stratigraphic units (fig. S2). From top to bottom these are:

-Unit I. The uppermost unit of the sedimentary infill, comprising breccias of calcarenite cobbles and boulders with dusty organic sand and pebbles, and including an important presence of charcoal and ashes in a tabular, massive stratum. Unit I was intensively affected by bioturbation, mainly burrowing and root growth, but also, until recently, by anthropic activities. Subdivided into two archaeological sublayers (Ia and Ib) based on its integrity, the layer was dated as mid-Holocene.

-Unit II. A small lenticular stratum of brownish sandy clays containing abundant calcarenite cobbles and boulders from the collapse of the cave roof. Severely affected by trampling, bioturbation, and sediment removal during the latest funerary activities. The original deposition was associated with the Late Glacial-Early Holocene.

-Travertine Platform 1 (TP-1). TP-1 is a small relic of a larger, soft (tufa-like) travertine deposit. Identified only in the NE area of the excavation. Stratigraphically, TP-1 overlies Unit III and probably sealed it. During the excavation, only some remnants of TP-1 were identified on the northern and eastern walls of the cave.

-Unit III. Formed by the archeological layers III<sub>n</sub>, III<sub>g</sub>, and III<sub>c</sub>, this is the most complex unit documented. It is unevenly distributed throughout the excavation hall because of erosive processes affecting the upper sub-units. At its top, it contains the archaeological layer III<sub>n</sub>, a breccia comprising calcarenite slabs infilled by yellowish calcareous sands and charcoals. It is truncated in the south and only preserved in a small sector at the northern end of the excavation hall, close to the cave walls. It represents the sedimentary infilling of a scoured surface with cryptokarstic structures (23). The excavated area is less than 2 m<sup>2</sup>. Layer III<sub>g</sub> is composed of weakly cemented and massive yellow calcareous sands and is only preserved close to the cave walls. Archeological remains are almost absent. Layer III<sub>g</sub> presents a scoured surface in the middle of the excavation hall, most likely related to the truncation of layer III<sub>n</sub>. Layer III<sub>c</sub> is the first continuous archeological layer within the Pleistocene sequence. It is a tabular stratum 0.3-0.4 m thick; comprising massive lithochromic calcareous sands of a very pale brown (10 YR 7/3) color with a few calcarenite slabs of cobble and boulder size. Layer III<sub>c</sub> contains abundant charcoal, combustion structures and reddened stones (23).

-Travertine Platform 2 (TP-2). This is a poorly bedded breccia of calcarenite boulders infilled with yellow (10YR 8/1), weathered calcite precipitates, and has a 0.5 m-thick dome shape. TP-2 is stratified between Unit III and Unit IV, extending across almost half the excavation hall (lines B, C and D). Layer III<sub>n</sub> rests on TP-2 in squares B-C/6-7. Layers III<sub>g</sub> and III<sub>c</sub> have a lateral contact with TP-2, indicating that it had already formed at the time Unit III was laid down. Unit IV underlies TP-2 across its entire extent.

-Unit IV. Stratified breccia of boulder-sized travertine (calc-sinter) slabs, with massive calcareous muddy sands of reddish-yellow color (7.5 YR 6/8), partially or totally infilling between the boulders, with a thickness of 0.6 m. Two continuous tabular strata of travertine boulders form pavements separating sublayers IV, IV1, and IV2. Unit IV is homogeneously distributed across the entire excavated area. It appears directly below layer III<sub>c</sub> in the central and southern areas of the excavation. In the north it is well stratified below layers III<sub>n</sub>, III<sub>c</sub>, and TP-2.

-Unit V. This is the basal unit of the excavation and is characterized by a breccia made up of yellow (10 YR7/8) cobbles and boulders of travertine (calc-sinter) slabs, infilled with reddish-yellow (7.5 YR 6/8) calcareous muddy sands. Unit V contains cryptokarstic structures. The breccia overlies marls and calcilutite deposits with black cryptocrystalline impregnations (23).

## 2. Zooarchaeological and taphonomic analysis

The study of faunal remains was carried out following standardized methods and techniques frequented in Zooarchaeological studies (54, 55). Four measurements were used to quantify faunal abundance: The Number of Specimens (NSP), the Number of Identified Specimens (NISP), Minimum Number of Elements (MNE), Minimum Number of Individuals (MNI) and % of Relative Abundance (%RA) (56). In order to assess the nature of fragmentation, an analysis of fracture planes following the criteria of Villa and Mahieu (57) was performed. In the case of leporids and small birds we assessed fragmentation and breakage patterns according to the relative proportions among different anatomical elements as described in (58) and (59). Bone surface modifications were identified through a binocular lens using between 10x to 40x magnification, as proposed by Blumenschine (60, 61). Additionally, the specific diagnostic criteria proposed by Blumenschine and Selvaggio (62), Fisher (63), Domínguez-Rodrigo et al. (28), Shipman and Rose (64), Behrensmeier (65), Binford (66) and Fernández-Jalvo and Andrews (32) was used. We follow the criteria described by Stiner et al. (67) to record degrees of burning damage. The frequencies of these modifications were calculated in association with NSP counts.

A total of 2397 faunal remains originating from the Pleistocene sediments of Cova Foradada were analyzed. These remains are unevenly distributed throughout the different layers and units. Layer IIIc presents the highest frequency of faunal remains (NSP = 934) while Layer V represents the contrary (NSP = 14). Unit IV yields 1289 faunal remains unequally distributed throughout the layers (table S1). The taxonomic representation, skeletal profiles and mortality profiles are similar in all layers with small variations among them. The presence of abundant species and specimens of carnivores and large raptors, young individuals, tooth marks, digested bones and coprolites suggest an important contribution of different non-human predators to this assemblage. Nevertheless, all layers except for layer V present different degrees of anthropogenic contribution.

Remains of meso-vertebrates (small birds of the families of Corvidae, Phasianidae and other small passerines, and leporids of the genus *Lepus* and *Oryctolagus*) are the most abundant taxonomic group, representing between 50 and 87% of the identified remains in every layer (Foradada NISP = 1696, Unit IV NISP = 865). Although preliminary, the anatomical representation of said mesofauna suggests that all skeletal parts are represented in the assemblage, including small bones such as phalanges and isolated teeth belonging to many individuals of all ages. In the case of leporids, postcranial elements are better represented than cranial, with the posterior limbs, especially tibia, being more abundant than any of the anterior limbs. In the case of small birds in Unit IV, the limbs are much more represented than the bones of the core (CO/LB=8.9%), while long bones those from wings are better represented than legs (W/L =69%). The phalanges of small birds are represented by 11.8% NISP, and talons are 48% of the pedal phalanges. Bone breakage is low in leporids and small birds, however the majority of leporid long bones are strongly fractured both by post-depositional/excavation breakage and by green breakage. Among small birds most long bones are complete in 54.6% of the cases. Breakage is mainly post-depositional, although there are some green fractures of an indeterminate origin. The preliminary MNI for small birds from Unit IV is 17 (table S1).

Carnivorous mammals are abundant in the number of specimens (NISP = 209) and species (n = 7). Some of them show recurrent cave behaviour such as the Iberian lynx (*Lynx pardinus*), brown

bear (*Ursus arctos*), leopard (*Panthera pardus*) and hyena (*Crocuta crocuta*). In other cases, such as the fox (*Vulpes vulpes*), wolf/dhole (*Canis/Cuon*) and lion (*Panthera leo*), these animals visit caves sporadically. The Iberian lynx is the most represented carnivore in Cova Foradada (175 specimens), being the only carnivore in layer IIIIn. Usually, most of the carnivores are represented by isolated remains of single prime adult individuals, however lynxes show a good representation of all anatomical elements belonging to a minimum of 15 individuals (50% of the carnivore MNI) of all ages, including perinatal. The integrity of the carnivore elements is high. Usually, they are complete, or near complete, although some limb bones of lynx show green and dry fractures.

Ungulate remains (NISP = 126) correspond to red deer (*Cervus elaphus*), large bovids (*Bos/Bison*) and equids (*Equus* sp.). All these taxa are represented by few specimens (less than 10% of the NISP in every layer) and individuals (maximum 3). However, their role in the assemblage is higher possibly due to most of the indeterminate remains corresponding to medium and large sized ungulates. A minimum of 18 individuals has been estimated for the ungulates, five in the case of large bovids and equids with eight in the case of red deer. Young individuals are dominant (n = 11), and old individuals are only represented by one red deer. Breakage is high in this taxonomic group and none of the elements have been recovered complete, except for small bones such as phalanges or articular elements.

Analysis of bone surfaces indicate a predominance of post-depositional modifications related with the environment of the cave. These include manganese coatings, chemical corrosion, cementations and some other taphonomic agents related to the presence of varied organic activities such as root etching and microbial bio-erosion. Apart from this, a small proportion of the specimens show modifications related with carnivore and human activity (table S1). Regarding carnivores as taphonomic agents, tooth marks in the form of pits and scores (especially in Unit IV), furrowing, digested bones and macro-mammal limb bone shaft cylinders have been documented. In the case of leporids, we noted the presence of tooth marks and digested bones; however, the frequency of this type of alteration is relatively, with layer IV being the only exception.

Finally, some anthropogenic modifications in the form of cut marks, burned bones and bone breakage have been observed. Cut marks have been located on three bones; one vertebra of red deer from layer IIIc, one tibia of rabbit from layer IV and the pedal phalange of an eagle from layer IV1. Burned bones (n = 95) are found in all layers, except for layer V, varying between 14% of layer IIIIn to 0.4% of layer IV (table S1). Changes in color can be observed to varied degrees in macro-mammal remains (ungulates and carnivores), leporids and the fragment of Testudinae plaque from layer IIIc.

Anthropogenic bone breakage is exclusively found over limbs of leporids in the form of mid-shaft cylinders (NISP = 45) (fig. S4). Some large notches in limb shaft fragments of macro-mammals could be indicative of anthropogenic breakage, however the absence of percussion marks and the scarcity of cut marks demands for a more reserved interpretation.

### **3. Puncturing elements in the Middle Paleolithic and Transitional Middle to Upper Paleolithic**

In most studies, the use of raptor talons as tools (both in Neandertal and AMH contexts) have been ruled out, imposing the interpretation of these items as decorative in nature. Only occasionally has their use as tools has been proposed, without any specification for their functionality (68-70). Nevertheless, it is evident that the talons of large raptors have the potential to be used as a perforating implement, hook or awl. Some authors have argued that the fragility of sharp claws and their composition, based on keratin, are characteristics that would indicate their low efficiency and durability (18). This contrasts with the great variety of expeditious



technologies that we find throughout the Paleolithic. In our opinion, only a detailed experimental program based on function and use-wear can shed light on this issue.

Although evidence is scarce in Mousterian sites, especially those that have been duly contrasted by taphonomic analysis (71), the truth remains that bone technologies are evidence of the technological innovations of the Neanderthals. These evidences begin to multiply, especially when the so-called transition complexes begin to appear (Châtelperronian, Uluzzian, Szeletian, etc.), in which the pointed tools fabricated on bone begin to appear more frequently. This type of material appears on a large scale in several Châtelperronian sites in France such as the Grotte du Renne, with 183 tools on bone (72), of which 48 are awls (73) or in Italian Uluzzian sites of Grotta della Cala, Grotta del Cavallo, Grotta di Castelcivita (74) and Fumane (75). It is noteworthy that the Uluzzian sites have other evidence of technological change of the last Neanderthals as is the use of bivalve shells for the manufacture of tools (76). The evidence located in sites assigned to the Szeletian present many more problems of context than the rest of transition cultures. On the one hand, most of the recovered bone tools have been located in old collections, found in stratigraphically complex deposits with notably problematic interpretations. Additionally, several of the recovered tools correspond to osseous projectile points, directly implicating these deposits in recent debates regarding the appearance of such artifacts, currently considered fossil directors of the Aurignacian technocomplex in Western Europe (77, 78).

In Europe there are several sites in which the first bone tools presenting a pointed morphology appear precisely during the final Mousterian or in transitional technocomplexes, some of them with obvious marks of having been polished. These bone industries are of increasing complexity and are sometimes manufactured from anatomical elements such as the ribs (71, 79), since they do not require the preparation of the entire cortical surface. In these cases, as shown by the analysis of the materials of Grotta du Renne –both in the case of the two Mousterian as well as the Châtelperronian awls – these tools differ from awls that appear in the Aurignacian in that they are always manufactured on expeditious formats, obtained through breaking the bone in order to gain access to the medullary cavity (73).

Nevertheless, rough tools on bone are still manufactured throughout, with Neandertals still producing retouching implements (among others: 80-83) and sidescrapers (84). Alongside these different technologies, however, pointed elements begin to appear with all their surface transformed (85). Needless to say, the unfortunate preservation of some of these implements are compromised with obvious signs of corrosion that do not allow an optimal observation of their technological marks and use-wear patterns. Other Mousterian utensils produced on hard raw materials of animal origin are seen in the case of the completely polished and pigment stained lamella tooth of a mammoth from Tata (86).

The location of bone pointed tools in various European sites related to Neanderthals shows the existence of an expeditious technology for the manufacture of awls and other bone industries. The appearance of these artifacts with little anthropic alterations helps discard, to a certain extent, a utilitarian use of the claws of different birds of prey (73), not only for the ease of the manufacture when making bone awls, but also for the ease of grip that these supports have in relation to the claws.

#### **4. Taphonomic and Microscopic Morphological Characterization of Cut Marks**

##### *Methods*

Each of the marks were digitalized using a HIROX KH-8700 3D Digital Microscope with a MXG-5000REZ triple objective revolving lens, following the protocol established by Courtenay

et al. (48). Firstly, cross-sections of each mark were produced using the mid-range lens at a 600x magnification. A fixed high intensity LED light source was placed above each sample, combining the use of coaxial and ring illumination. 3D digital reconstructions were produced using a combination of quick auto focus and depth synthesis functions that are provided by the HIROX's system, generating a 3D display of each mark where measurements could be taken, and cross-section profiles extracted. To construct each digital image, between 110 and 130 photos were taken for each profile. The assessment of each cut mark profile's morphology was carried out using a total of three cross section, taken at 30, 50 and 70 percent of the total length of each mark. As described by Maté-González et al. (87), this range along the groove is suggested to be the most representative for cut mark morphological analysis.

These profiles were then exported to the free tpsDig2 (v.2.1.7) software where the allocation of seven homologous landmarks was carried out following the geometric morphometric models described by Maté-González et al. (87). The resulting files produced through landmark allocation were then edited and imported into the free software R ([www.rproject.org](http://www.rproject.org), 49) where a full Procrustes fit was performed using the Geomorph library (50, 88). This package can be used to prepare the sample for multivariate statistical analysis and is commonly referred to as a generalized Procrustes analysis (GPA). Through GPA each individual is standardized through a series of superimposition procedures involving the translation, rotation and scaling of each shape. Any differences in structure can thus be studied through patterns of variation and covariation which can then be statistically assessed (89, 90). The library shapes (52) as then used to calculate and plot the mean shape of each cross section.

Additional measurements concerning the depth and opening angle of each of the profiles were later taken.

In order to capture the entire shape of these incisions, a further digital reconstruction was carried out on the entire mark using the low-range lens at 100x or 150x magnification, depending on the necessities of the analyst with regards to resolution. To capture the entire length of each mark, the HIROX's tiling function was used to create a mosaic and complete digital reconstruction of each groove. 30 photos were taken for each tile while any number between 15 and 32 tiles were used to create the final image. With the use of a high pixel resolution as well as the consequential stacking of photos produced by the microscope, the entire shape of the taphonomic trace could be reproduced digitally.

A 13-landmark model, as developed by Courtenay et al. (53), was then used to capture the entire shape of the groove. The position of each landmark was recorded through a series of measurements. This was done firstly using the 'XY-width' function to measure and plot the location of each landmark across a 2-Dimensional graph, followed by the measurement of depth using the 'point height' function in order to establish each landmarks position along the Z-axis of a 3-Dimensional plot (48). Landmark coordinates were recorded and processed in the same manner as the 2D profiles.

## *Results*

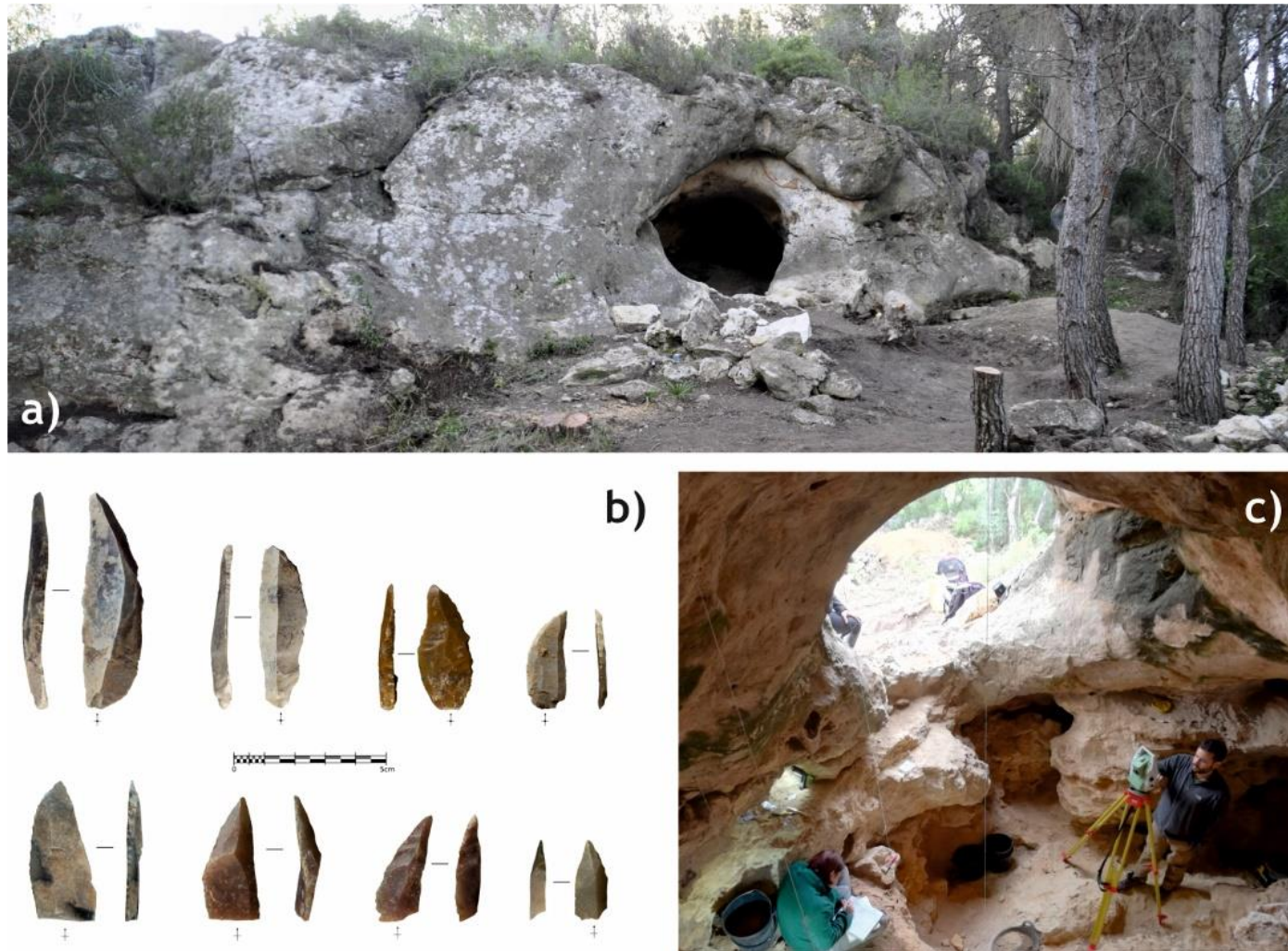
The 12 incisions observed present an average length of 3.678mm and width of 0.234mm. As can be seen in Table 1, a general increase in the opening angle of each groove can be observed while a similar pattern is observed through a decrease in depth of each profile along the groove. This variation, however, is relatively subtle and gradual, most likely explained by the physical properties and pressure exerted when making an incision (29). When producing a cut mark, the

initial act of creating the incision would produce a deeper mark while the act of drawing the tool away leaves a shallower and wider groove. The observations made here indicate a gradual change in pressure, rather than the irregular groove which would be expected in other taphonomic traces such as trampling marks. The homogeneity of the groove's shape, however, is clearly represented by the cross-section morphology and development of said morphology along the course of the incision. Through Procrustes analysis we can clearly observe that all of these marks present an asymmetrical  $\nabla$  shaped cross section (Fig. 1). This particular feature is one of the key characteristics described by multiple authors when diagnosing a taphonomic trace as a cut mark (28, 91, 92). Considering their profile shape alone, these taphonomic traces are clearly comparable with cut mark samples studied by a great deal of taphonomists (87, 93-98) as opposed to the morphology of other linear traces such as tooth scores (31).

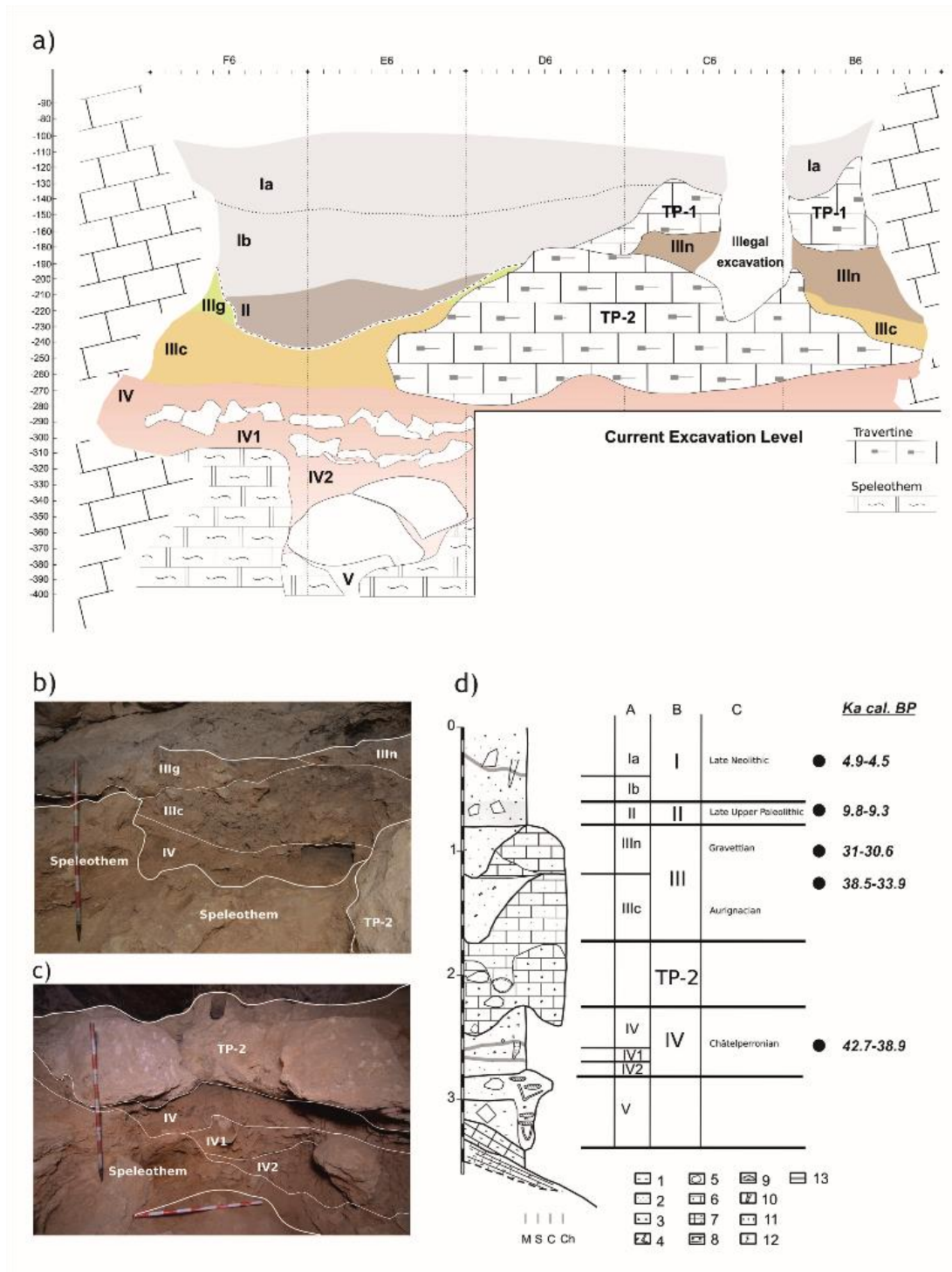
With regards to 3-Dimensional reconstructions and analysis (Fig. 2), the depth and shape of these linear marks are clearly more pronounced than what would be expected of a trampling mark, for example. Trampling marks in general are more likely to be appearing with a curvy or sinuous shape (48) whereas these marks present a straight incision across the bone's surface (28, 99). Combined with a clear lack of a rounded base, as well as other features, this also rules out the possibility that these marks can be confused as a product of other natural agents (100), carnivores (66, 101, 102), humans (103, 104). While these marks are associated to a great deal of other taphonomic alterations such as biochemical bone surface modifications, fortunately they do not impede the morphological study of these traces to a degree where equifinality is overly present (33).

While the use of the HIROX KH-8700 3D Digital Microscope has already been used for geometric morphometric studies of cut mark profiles (104, 105), as well as for more generic characterization of cut marks (104), this article presents a powerful application of this microscope to the study of linear mark morphology. Here we provide an objective approximation to cut mark morphological studies using high resolution technological equipment to provide a quantitative classification. Through statistical models of calculating and evaluating morphology and shape, provided through an advanced series of measurements on bidimensional as well as tridimensional models derived from 3D reconstructed data, we have been able to objectively classify and quantify the shape of these grooves. Recent advances in the field of taphonomy, as well as the application of new methodologies to bone surface modification analysis, highlight the high level of subjectivity present when carrying out simple descriptive classifications of marks (105). In this study qualitative observations have been constructed through quantitative models, reducing the subjectivity in simple qualitative analysis that may provide erroneous classifications. The present study demonstrates how a combination of statistical tools as well as the use of sophisticated microscopy can be a powerful approach to classifying bone surface modifications.

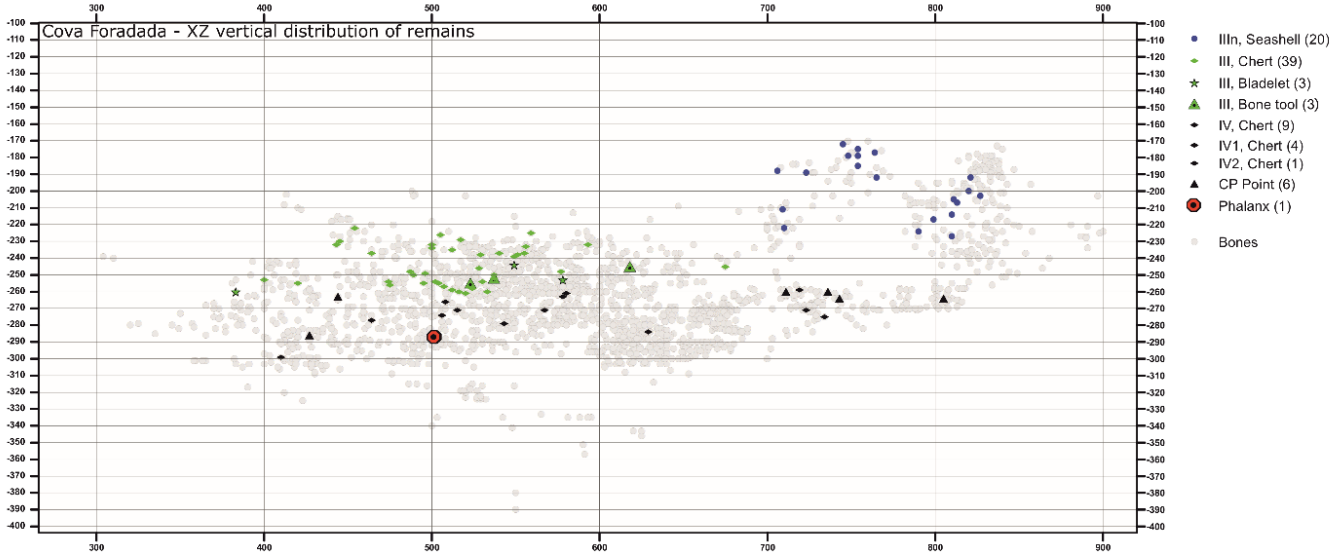
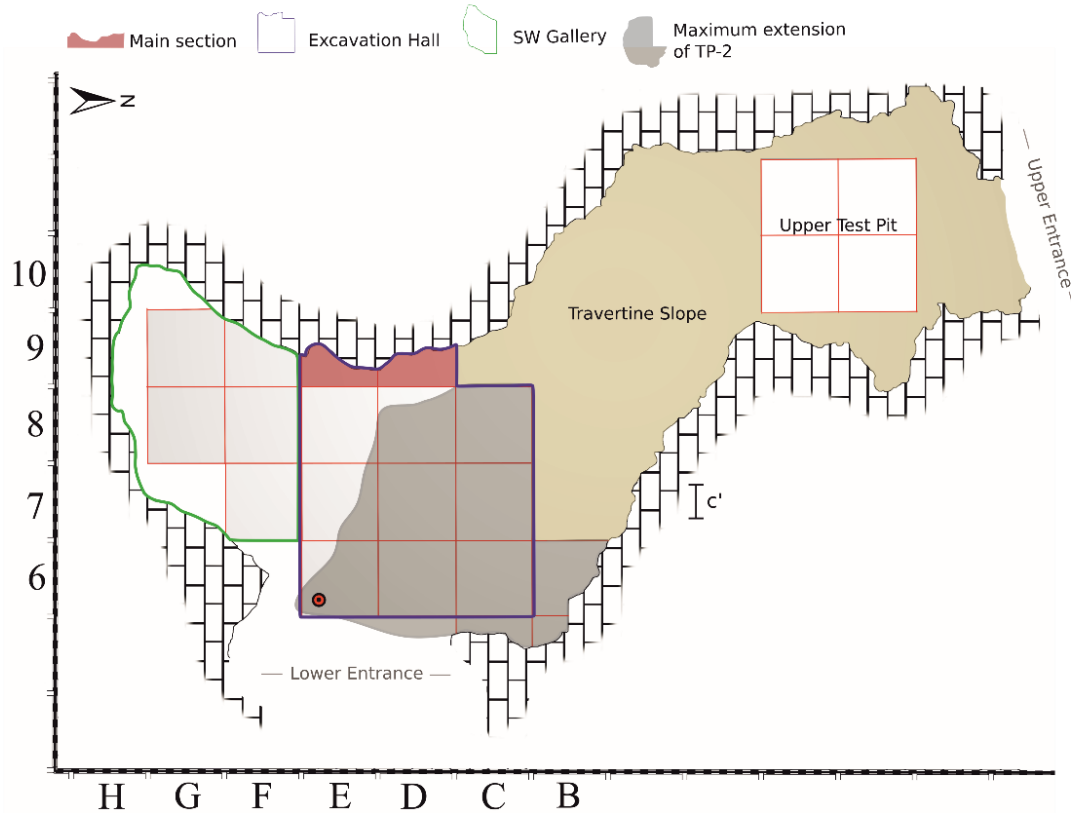
**SUPPLEMENTARY FIGURES, TABLES AND LINKS TO STL**



**Fig. S1. Different views of Cova Foradada and CP points.** (a) View from the outside of the cave and lower entrance. (b) Châtelperronian point recovered in the Unit IV (c) View of the interior of the cave in the excavation hall, during the excavation of Unit IV. Photo Credit: Juan Ignacio Morales, Universitat de Barcelona (UB).



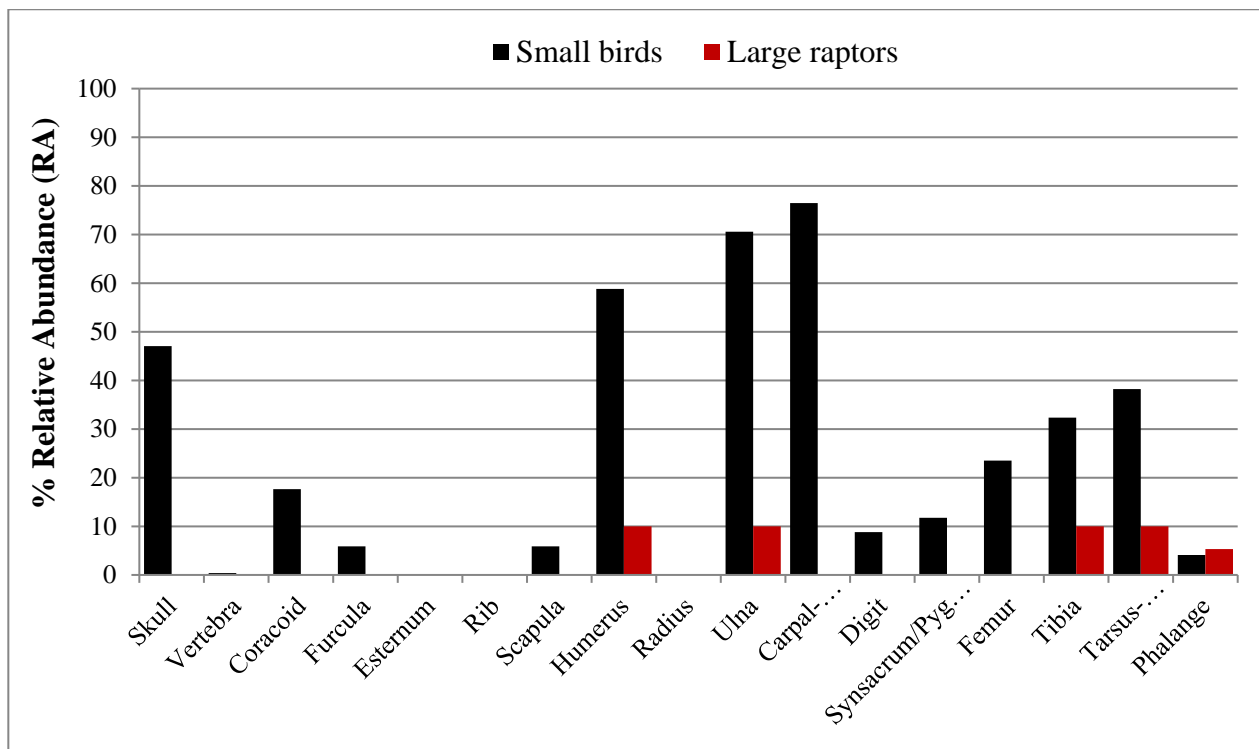
**Fig. S2. Stratigraphic column.** a) Reconstruction of the site's stratigraphy succession based on field maps and material distribution from the line y=6. Black dashed line between layers II, IIIg and IIIc indicates the basal part of the erosive process affecting the top of the Unit III; b) and c) D6-7 section where TP-2 separates Unit III and Unit IV; d) composed lithostratigraphic column from de E6-D6 E-W section. Lithology: M = muds; S = sands; C = cobbles and boulders; Ch = chemical deposits. Symbology: 1, mud; 2, sand; 3, pebbles; 4, cobble and boulder slabs; 5, boulder; 6, calcarenite; 7, calcilutite and marls; 8, black impregnations; 9, cryptokarst; 10, root casts; 11, black cryptocrystalline impregnations; 12, massive; 13, archeological sublayers. Columns: A, archaeological layers; B, lithostratigraphic units; C, cultural attribution, dates calibrated dates BP (23). Photo Credit: Juan Ignacio Morales, Universitat de Barcelona (UB).



**Fig. S3. Horizontal and vertical location of the phalange FO15/ IV1/E6/1339.** Cova Foradada plant in which the different parts of the cave are appreciated (up). Projection of the 3D plotted archaeological materials in vertical section N-S (down).



**Fig. S4. Anthropogenic modifications on leporid bones in Unit IV of Cova Foradada.** Midshaft bone cylinders and fragments of limb bones showing notches (white arrows) produced by human breakage to consume to the interior marrow documented in the different layers in the Unit IV (up). © Detail of a cut-marked fragment of leporid tibia in form of scraping (down). Y Burned bones. Photo Credit: Antonio Rodríguez-Hidalgo, IDEA.



**Fig. S5. Anatomical representation of large raptors versus small birds.** Percentage of relative abundance (%RA) of the skeletal elements of small birds, represented by 17 individuals and large raptors of the Unit IV of Cova Foradada, represented by 5 individuals.



**Table S1. NISP, percentage and minimal number of individuals (MNI), and number of specimens for Unit IV and layer IV, IV1, and IV2 faunal assemblage at Cova Foradada.**

Taxa	IV			IV1			IV2			Total Unit IV		
	NISP	%	MNI	NISP	%	MNI	NISP	%	MNI	NISP	%	MNI
Bovinae cf. <i>Bos/Bison</i>	10	2.5	2	4	0.8	1	0	0	0	14	1.3	3
<i>Equus</i> sp.	16	4.0	2	3	0.6	1	0	0	0	19	1.8	3
<i>Cervus elaphus</i>	18	4.4	2	12	2.4	2	2	1.1	1	32	3.0	5
Ungulate	8	2.0	0	7	1.4	0	2	1.1	0	17	1.6	0
<i>Ursus</i> cf. <i>arctos</i>	1	0.2	2	2	0.4	1	1	0.6	1	4	0.4	4
<i>Canidae</i> cf. <i>Canis/Cuon</i>	1	0.2	1	0	0	0	0	-	0	1	0.1	1
<i>Panthera pardus</i>	1	0.2	1	0	0	0	0	-	0	1	0.1	1
<i>Lynx pardinus</i>	35	8.6	3	38	7.6	4	28	16.1	3	101	9.4	10
Carnivore	5	1.2	0	4	0.8	0	1	0.6	0	10	0.9	0
Leporidae	191	47.2	9	369	74.2	18	127	73.0	10	687	63.8	37
Large Raptor	7	1.7	3	3	0.6	1	2	1.1	1	12	1.1	5
Small Bird	112	27.7	7	55	11	8	11	6.3	2	178	16.5	17
Indeterminate	147	-	0	43	-	0	23	-	0	213	-	0
Total	405	100	32	497	100	36	174	100	18	1076	100	3
Total NSP	552	-	-	540	-	-	197	-	-	1289	-	-
Cut Mark	1	-	-	1	-	-	0	-	-	2	-	-
Burned	23	-	-	2	-	-	6	-	-	31	-	-
Tooth Mark	36	-	-	12	-	-	12	-	-	60	-	-
Coprolites	7	-	-	0	-	-	0	-	-	7	-	-

**Table S2. Average measurements of the opening angle and depth of incision profiles at 30, 50, and 70% of the groove's total length.**

	30%	50%	70%
Opening Angle (°)	109.45	114.92	121.26
Depth (mm)	0.21	0.15	0.09

**Table S3. Skeletal representation of small birds from Unit IV of Cova Foradada.** For abbreviations see the zooarcheological methods in Supplementary Material.

Small birds (MNI 17)					
	NISP	%NISP	MNE	%MNE	%RA
Skull	9	5.1	8	5.5	47.1
Vertebra	1	0.6	1	0.7	0.4
Coracoid	6	3.4	6	4.1	17.6
Furcula	0	-	1	0.7	5.9
Sternum	0	-	0	-	-
Rib	0	-	0	-	-
Scapula	1	0.6	2	1.4	5.9
Humerus	26	14.6	20	13.7	58.8
Radius	0	-	0	-	-
Ulna	37	20.8	24	16.4	70.6
Carpal-Metacarpal	32	18.0	26	17.8	76
Digit	3	1.7	3	2.1	8.8
Synsacrum/Pygostyle	2	1.1	2	1.4	11.8
Femur	8	4.5	8	5.5	24
Tibia	15	8.4	11	7.5	32.4
Tarsus-Metatarsus	17	9.6	13	8.9	38
Phalange	21	11.8	21	14.4	4.1
Total	178	100	146	100	-

**Table S4. Measurements of the first phalanx of digit I used for comparative purposes and data from the specimen of Cova Foradada.**

Species	Specimens	L	Bp	Bapp	Bd1	Bd2	Bapd	SD
<i>A_chrysaetos</i>	1	40.92	18.35	11.5	11.19	11.33	5.48	8.55
<i>A_chrysaetos</i>	2	40.85	18.65	12.43	10.52	11.12	5.76	8.01
<i>A_chrysaetos</i>	3	39.33	17.86	12.29	9.88	10.83	6.46	8.81
<i>A_chrysaetos</i>	4	38.49	17.08	10.08	9.44	10.11	5.63	7.9
<i>A_chrysaetos</i>	5	38.45	17.33	9.53	9.42	10.11	5.72	8.04
<i>A_chrysaetos</i>	6	42.05	18.75	10.2	10.42	11.03	6.8	8.45
<i>A_chrysaetos</i>	7	41.5	19.01	9.57	10.06	10.87	6.49	8.31
<i>A_chrysaetos</i>	8	37.87	15.99	9.12	9.07	9.3	5.29	7.19
<i>A_chrysaetos</i>	9	37.85	15.9	9.19	8.48	9.37	5.69	7.36
<i>A_chrysaetos</i>	10	37.01	16.51	8.24	8.5	9.16	5.48	7.07
<i>A_chrysaetos</i>	11	41.84	20.08	11.98	10.57	11.78	6.32	9.21
<i>A_chrysaetos</i>	12	41.51	18.6	10.02	10.8	12.26	6.82	9.22
<i>A_chrysaetos</i>	13	41.54	18.2	10.21	10.8	11.94	6.87	9.02
<i>A_chrysaetos</i>	14	39.2	17.3	9.62	9.71	10.48	6.29	8.04
<i>A_chrysaetos</i>	15	39.1	17.8	9.96	9.86	10.75	5.67	8.37
<i>A_chrysaetos</i>	16	38.79	16.84	9.73	9.45	10.28	5.96	8.19
<i>A_chrysaetos</i>	17	39.12	17.62	9.77	9.76	10.47	5.86	8.19
<i>H_albicilla</i>	1	35.47	18.85	9.22	9.83	10.31	5.59	8.22
<i>H_albicilla</i>	2	34.84	18.69	9.55	9.05	10.07	5.18	8.11
<i>H_albicilla</i>	3	37.73	19.66	9.79	10.74	10.76	5.89	7.54
<i>A_adalberti</i>	1	28.35	13.26	7.69	8.11	8.34	4.4	6.7
<i>A_adalberti</i>	2	32.37	14.34	8.74	8.03	8.89	4.82	7.58
<i>A_adalberti</i>	3	32.23	14.99	9.31	8.07	9.22	4.65	7.64
<i>A_adalberti</i>	4	31.63	13.99	8.56	8.3	8.96	4.46	7.61
<i>A_adalberti</i>	5	31.98	14.71	8.79	8.42	8.98	4.82	7.42
<i>A_adalberti</i>	6	29.6	13.36	7.88	7.91	8.29	4.46	6.46
<i>A_adalberti</i>	7	29.96	13.91	7.98	7.92	8.31	4.71	6.54
<i>A_heliaca</i>	1	25.86	11.69	6.38	7.15	6.12	4.83	6.03
<i>A_heliaca</i>	2	28.14	13.57	7.43	7.79	7.33	4.76	6.26
<i>A_heliaca</i>	3	27.12	13.59	6.67	7.88	6.9	4.55	6.76
<i>A_heliaca</i>	4	28.45	14.03	7.74	8.33	7.65	4.84	6.86
<i>A_heliaca</i>	5	27.48	14.05	-	-	-	-	-
Foradada	1	29.21	13.4	7.42	7.28	9.06	4.83	7.07

**Table S5. Pleistocene/Early Holocene fossil remains of *A. adalberti* and *A. heliaca* in Europe and Near East.**

The code referred to the figure 3 in the main text.

Code	Site	Country	Chronology	Species	Reference
1	Lapa da Rainha	Portugal	25,580-20,300 BP	<i>Aquila adalberti</i>	106
2	Cueva de Nerja	Spain	13,300-8,770 BP	<i>Aquila adalberti</i>	107
3	Cova Foradada	Spain	39,000 BP	<i>Aquila [heliaca] adalberti</i>	This work
4	Grotte de Cotencher	Switzerland	70,000-40,000 BP	<i>Aquila heliaca</i>	108
5	Saccopastore	Italy	115,000-60,000 BP	<i>Aquila heliaca</i>	109
6	Grotta Romanelli	Italy	11,800-9,050 BP	<i>Aquila heliaca</i>	110
7	Hundsheim	Austria	Early Middle Pleistocene	<i>Aquila heliaca</i>	110
8	Somssichhégy	Hungary	Early Pleistocene	<i>Aquila cf. heliaca</i>	110
9	Kalman Lambrecht Cave	Hungary	115,000–60,000 BP	<i>Aquila heliaca</i>	109
10	Biśnik Cave layer 2/4	Poland	57,000-29,000 BP	<i>Aquila heliaca</i>	111
11	Rîpa	Romania	70,000–60,000 BP	<i>Aquila heliaca</i>	108
12	Kudaro 3	Georgia	70,000–35,000 BP	<i>Aquila heliaca</i>	108
13	Binagady	Azerbaijan	120,000-95,000 BP	<i>Aquila heliaca</i>	110
14	Saaidé II	Lebanon	Late Glacial	<i>Aquila cf. heliaca</i>	110

STL S1. [www.morphosource.org/Detail/MediaDetail/Show/media\\_id/44124](http://www.morphosource.org/Detail/MediaDetail/Show/media_id/44124)STL S2. [www.morphosource.org/Detail/MediaDetail/Show/media\\_id/44124](http://www.morphosource.org/Detail/MediaDetail/Show/media_id/44124)