

Late Neandertals and the intentional removal of feathers as evidenced from bird bone taphonomy at Fumane Cave 44 ky B.P., Italy

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A large and varied avifaunal bone assemblage from the final Mousterian levels of Grotta di Fumane, northern Italy, reveals unusual human modifications on species that are not clearly relatable to feeding or utilitarian uses (i.e., lammergeier, Eurasian black vulture, golden eagle, red-footed falcon, common wood pigeon, and Alpine chough). Cut, peeling, and scrape marks, as well as diagnostic fractures and a breakthrough, are observed exclusively on wings, indicating the intentional removal of large feathers by Neandertals. The species involved, the anatomical elements affected, and the unusual type and location of the human modifications indicate an activity linked to the symbolic sphere and the behavioral modernity of this European autochthonous population.

cut marks | raptors | symbolism | Middle Paleolithic

Archaeological evidence suggests that nonutilitarian human behaviors represented by coloring substances and ornamental objects made of animal bone and teeth, marine shells, and ostrich eggshells are associated with the Middle Stone Age and the Middle Paleolithic in Africa (1–4) and the Near East (5) and have been potentially ascribed to anatomically modern humans (6). In Europe, similar evidence regarding the symbolic use of teeth, marine shells, and pigments 50 ky B.P. (7–10) would seem to imply the independent emergence of behavioral modernity in autochthonous Neandertal populations, thus challenging the cognitive difference between Neandertals and anatomically modern populations as postulated in the human revolution model (11, 12). Anatomical elements extracted from hunted or scavenged animals are possible indicators of symbolic behavior when they preserve traces of unusual human intervention on their surfaces that cannot be linked to food or utilitarian purposes.

Avifaunal remains constitute a particular category of these materials, as they document a number of different utilizations according to the kind of element exploited. In Turkey, a terminal pedal phalanx of a very large raptor with a notch cut into its anterior proximal end has been found in layer B at Üçağizli Cave dated to ~29 ky¹⁴C B.P., approximately the end of the early Ahmari (13). In Europe, the use of long bones of large-sized birds (vultures, eagles, swans) to make ornamental objects or flutes appears ephemerally in the Castelperronian (7) and is well known in the archaeological record from the Aurignacian onward (14, 15). The exploitation of birds as a food resource during the Upper Paleolithic is also documented by taphonomic analyses and has been interpreted as a marker of the breadth of the human diet to support the notion that population pressure played a significant role in the evolution of Late Pleistocene human cultures (16, 17). The earliest evidence of this practice is often said to have been found in the Aurignacian of Grotta del Fossellone (18) and in the Aurignacian and Early Gravettian of Grotta Paglicci (19) in Italy, as well as in the Gravettian of Pavlov I in the Czech Republic (20). This revolution has been challenged by the discovery of a food exploitation of birds in the Middle Pleistocene at Bolomor Cave (21). A particular aspect of the use of bird bones or other elements by Neandertals has been inferred in France at Pech de l'Azé I (22, 23) and at Baume de Gigny (24), where some posterior phalanges of golden eagle (*Aquila chrysaetos*) and swan (*Cygnus cygnus*) bear striae produced by lithic

tools. A very similar find—an ungual phalanx of golden eagle with disarticulation striae, suggesting the removal of the claw (25)—was recovered in the Mousterian levels of Grotta di Fumane together with Levallois industries, sure evidence of Neandertal activity (26, 27). Specimens such as these, interpreted as ornaments, have an important symbolic value but require further confirmation based on extensive taphonomic analyses of larger assemblages. In response to this question, we submitted the avifaunal collection of some final Mousterian levels of Grotta di Fumane to a taphonomic analysis that resulted in the identification of striae produced by lithic tools on wing elements of raptors, chough, and pigeons. These findings support the hypothesis that the Neandertals had a particular interest in the feathers of these animals.

Results

Site. Grotta di Fumane is located on the southern edge of the Veneto Prealps in northern Italy and provided a dated sequence spanning from marine isotope stage (MIS) 5 to 2 (28–30) (*SI Text* and *Fig. S1*). Excavations have been carried out since 1988 in the cave entrance, where Mousterian, Uluzzian, and Aurignacian living floors have been identified within finely separated levels, yielding evidence of in situ human occupation with numerous lithic implements, faunal remains, hearths, and other structures (31–33).

Ornamental objects and painted stones have been found exclusively in Aurignacian levels (33). During the MIS 3, humans occupied the cave in different climatic and environmental conditions, ranging from moist temperate at the base of the final Mousterian sequence (units A11 and A10), with alternating cooling in the final Mousterian and Uluzzian levels (units A9–A3) and a shift to cooler and drier conditions in the Aurignacian sequence (units A2–D3) (25). In the final Mousterian levels the most abundant faunal remains are red deer (*Cervus elaphus*), ibex (*Capra ibex*), and roe deer (*Capreolus capreolus*), whereas chamois (*Rupicapra rupicapra*), bison (*Bison priscus*), and giant deer (*Megaloceros giganteus*) are less frequent. Moose (*Alces alces*), horse (*Equus ferus*), and wild boar (*Sus scrofa*) are very rare. All ungulate species, with the exception of horse and wild boar, bear traces of human exploitation (34). In these same phases the cave was also used by carnivores, as evidenced by the presence of gnaw marks on ungulate bones and of numerous digested fragments. Wolf (*Canis lupus*), hyena (*Crocuta crocuta*), and fox (*Vulpes vulpes*) are common; both brown bear (*Ursus arctos*) and cave bear (*U. spelaeus*) are also present. Human traces, attributable exclusively to skinning, are present on both species of bear, as well as on fox and wolf.

A5–A6 and A9 Stratigraphic Complex. The stratigraphic complex of levels A5 and A6, dated to 44.8–42.2 ky calibrated B.P. (30),

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evidences accumulations of faunal remains and lithic artifacts referable to an occupation of the site shifting from intense and persistent (A6) to more ephemeral (A5). These two levels, excavated over the whole entrance area, provided evidence of a well-structured use of the living spaces (*SI Text*). Areas with combustion structures, close to dumps of combustion debris, are adjacent to areas used for Levallois flake manufacture; tool shaping and curation; butchering of ungulates; and treatment of hides and pelts. Below the sterile layer A7, level A9 has not yet provided secure radiocarbon dates. As with layers A5–A6, it records repeated site occupations over the whole entrance area, with combustion structures and zones used for flake manufacture and butchering mostly red deer and giant deer. Lithic industry in level A9 records an abrupt replacement by the discoid method.

Avifaunal Association. An analysis of the avifaunal assemblage from the final Mousterian levels A6–A5 resulted in the identification of 660 bones, belonging to 22 species of birds living in different biotopes (*Table S1*). Small- and medium-sized birds from open and rocky habitats (Alpine chough, *Pyrrhocorax graculus*, and corn crake, *Crex crex*) and from alpine forest habitat (black grouse, *Tetrao tetrix*) are prevalent. A large amount of specimens are Passeriformes, mainly Corvids and thrushes. Important ecological indicators, such as the water rail (*Rallus aquaticus*), the common moorhen (*Gallinula chloropus*), and the pied avocet (*Recurvirostra avosetta*), suggest the existence of humid zones close to the cave. The Galliformes are represented by the black grouse, together with the common quail (*Coturnix coturnix*), rock ptarmigan (*Lagopus muta*), and willow ptarmigan (*Lagopus cf. lagopus*), whereas the Columbiformes are represented only by the common wood pigeon (*Columba palumbus*).

The presence of several birds of prey should also be mentioned. The nocturnal raptors present are the long-eared owl (*Asio otus*) and the Tengmalm's owl (*Aegolius funereus*). The diurnal raptors are represented by three hawks, the most common being the Eurasian kestrel (*Falco tinnunculus*), followed by the red-footed falcon (*F. vesperinus*) and the common hobby (*F. subbuteo*). Of the large accipitiformes, there are only two specimens: one of Eurasian black vulture (*Aegypius monachus*) and one of lammergeier (*Gypaetus barbatus*).

Results of the Taphonomic Analyses. The taphonomic study of bird bones from the A5–A6 stratigraphic complex revealed a clear human interest in lammergeier, red-footed falcon, common wood pigeon, and Alpine chough, although the capture and consumption of other species cannot be excluded (*Table 1*). Nevertheless, several bones bear modifications made by raptors or small carnivores, as indicated by the presence of scores, pits, punctures, or traces of the action of digestive juices. A microscopic analysis of the surfaces led to the recognition of traces of human intervention on five wing elements, which, given their importance, will be described in detail below.

A distal portion of a right ulna of lammergeier (*Gypaetus barbatus*; Fig. 1) has two long striae on the medioventral face, oblique to the main axis of the element, that pass through the distal epiphysis in correspondence to the depressio radialis (Fig. 1*B*). Other shorter striae, related and parallel to the previous ones, were observed: two are close to the tuberculum carpale and are interrupted by the natural depression of the incisura of the same tuberculum, and the other marginally invades the medial surface of the sulcus intercondylaris. On the lateral portion of the ventral face, at the top of the condylus dorsalis ulnae, there are three short and deep transversal marks (Fig. 1*C*). All of the traces are latero/medially oriented, reflecting the cut of the extensor carpi and flexor carpi ulnaris muscles for the ulna-carpometacarpus disarticulation.

Traces of a lithic tool are also present on a smaller raptor, the red-footed falcon (*Falco vesperinus*). A long and deep stria is located on the condylus dorsalis humeri of the distal epiphysis of a left humerus (Fig. 2*A* and *B*). This cut, situated on the inner side of the articulation surface, must have been made by stretching and opening the humerus-ulna articulation to separate the two bones.

Table 1. Modifications identified on the analyzed bird remains from the Mousterian levels A6–A5 of Fumane Cave

| Species | CTM | CTM? | PEE | ARR | BRK | FBFR | P/U | ST | DG | GW | TMOD | TNISPM |
|---------------------------------|-----|------|-----|-----|-----|------|-----|----|----|----|------|--------|
| <i>Gypaetus barbatus</i> | 1 | | | | | 1 | | | | | 2 | 1 |
| <i>Aegypius monachus*</i> | 1 | | | | | 1 | 1 | | 1 | 4 | 4 | 2 |
| <i>Falco tinnunculus</i> | | | | | | | | | 1 | 1 | 1 | 1 |
| <i>Falco vesperinus</i> | 1 | | | | | 1 | | | 1 | 3 | 3 | 2 |
| <i>Lagopus cf. lagopus</i> | | 1 | | | | | | | | | 1 | 1 |
| <i>Tetrao tetrix</i> | | | | 1 | | | | 3 | 2 | 6 | 6 | 6 |
| <i>cf. Tetrao tetrix</i> | | | | | | | | 1 | 4 | 5 | 5 | 5 |
| <i>Crex crex</i> | | | | | | | 1 | 4 | 2 | 4 | 11 | 9 |
| <i>cf. Vanellus vanellus</i> | | | | | | | 1 | | | 1 | 1 | 1 |
| <i>Scolopax rusticola</i> | | | | | | 2 | | | | 2 | 2 | 2 |
| <i>Columba palumbus</i> | 1 | | | | | 1 | | | | 2 | 1 | 1 |
| <i>Oriolus oriolus</i> | | | | | | 1 | | | | 1 | 1 | 1 |
| <i>Pyrrhocorax graculus</i> | 2 | 1 | 4 | | 1 | 8 | | 4 | 9 | 29 | 27 | 27 |
| <i>cf. Pyrrhocorax graculus</i> | | | | | | | 2 | 1 | 2 | 1 | 6 | 6 |
| Corvidae | | | | | | | 1 | | 1 | 2 | 2 | 2 |
| Passeriformes | | | | | | | | | 1 | 1 | 1 | 1 |
| Unidentified bird | | | 1 | | | 6 | | 3 | 2 | 12 | 12 | 12 |
| Total | 6 | 2 | 5 | 1 | 1 | 26 | 1 | 9 | 17 | 21 | 89 | 80 |

CTM, cut mark; CTM?, uncertain cut mark; PEE, peeling; ARR, *arrachement*; BRK, breakthrough; FBFR, fresh bone fracture; P/U, polish/use; ST, striae; DG, digested; GW, gnawed; TMOD, total modifications; TNISPM, total no. of identified specimens modified.

*Specimen from level A9.

A series of oblique cuts was detected on the medial edge of the mediiodistal diaphysis of an os metacarpale majus of a right carpometacarpus of common wood pigeon (*Columba palumbus*; Fig. 2*C* and *D*). Some of these cuts—short, repeated, and at different depths—are located only on the medial edge, whereas two other marks, longer and subparallel, also affect the ventral surface. On the whole, the striae can be referred to the cutting of the insertions of the extensor carpi and interosseus ventralis muscles and, as regards their localization, they can be related to the cutting and removal of the skin for collecting the remiges.

On a complete right ulna of Alpine chough (*Pyrrhocorax graculus*), there are various types of striae (Fig. 3*A–D*). Two of these striae—short, isolated, and relatively deep—are located on the dorsal face of the olecranon on the proximal epiphysis, whereas the other is on the condylus dorsalis ulnae of the distal epiphysis. All of them can be referred to disarticulation. This activity is borne out by the presence of parallel grooves (peeling) on the ventral face of the olecranon.

On the medial face, at middiaphysis, there is a group of different types of striae. Some of these striae, located around one of the papillae remigiales ventrales, are short, oblique, curved, and referred to the same point, and are considered to be scrape marks (Fig. 3*B*). These are the origin of three other striae that are straight, long, and fine, longitudinal to the bone axis; one of them points toward the distal epiphysis, the other two to the proximal. A single short, oblique, and relatively deep stria is located close to the proximal papillae remigiales caudales dorsales (Fig. 3*C*). Further scraping traces are present in the same area on the lateral edge of the diaphysis (Fig. 3*D*). On the whole, the morphology of the striae indicates that the lithic tool was used both to cut the skin covering the ulna and for the removal of the remiges.

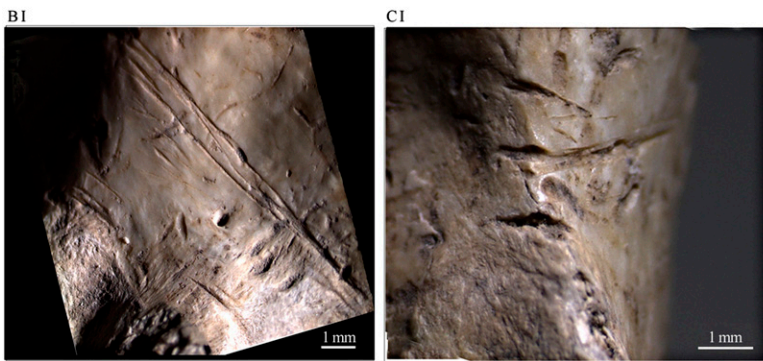
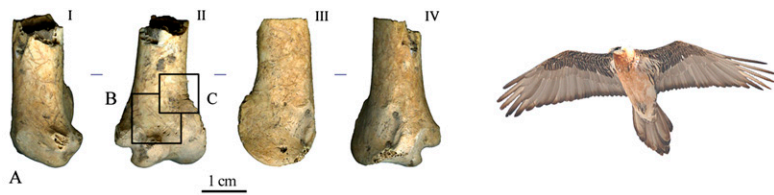


Fig. 1. Cut marks on the distal end of a right ulna of lammergeier (*Gypaetus barbatus*). (A) Different views of the ulna: (A, I) ventral view; (A, II) medioventral view; (A, III) dorsal view; (A, IV) laterodorsal view. (B and C) Localization of the cut marks; (B, I and C, I) details.

Other striae were identified on another complete left ulna of Alpine chough (Fig. 3E–G). Two were identified on the medial face of the distal extremity and are subparallel and longitudinal to the bone axis (Fig. 3F). One of the striae is deep and long, and the other is shorter and more superficial. These striae are interrupted by transversally oriented root marks. On the dorsal edge of the same face there is a series of at least three transversal marks, two limited to the edge, and another continuing on the diaphysis with a short interruption due to the concavity of the

bone (Fig. 3G). These striae can be related to the cutting of the flexor carpi ulnaris muscle. Finally, a short stria is present on the tuberculum carpale. On the whole, these traces may be interpreted as the result of the disarticulation of the ulna from the carpometacarpus.

Also to be noted is the recovery of another wing element of particular interest from the Mousterian level A9. This is a distal portion of the left carpometacarpus of a Eurasian black vulture (*Aegypius monachus*; Fig. 4A) where there is a clearly identifiable

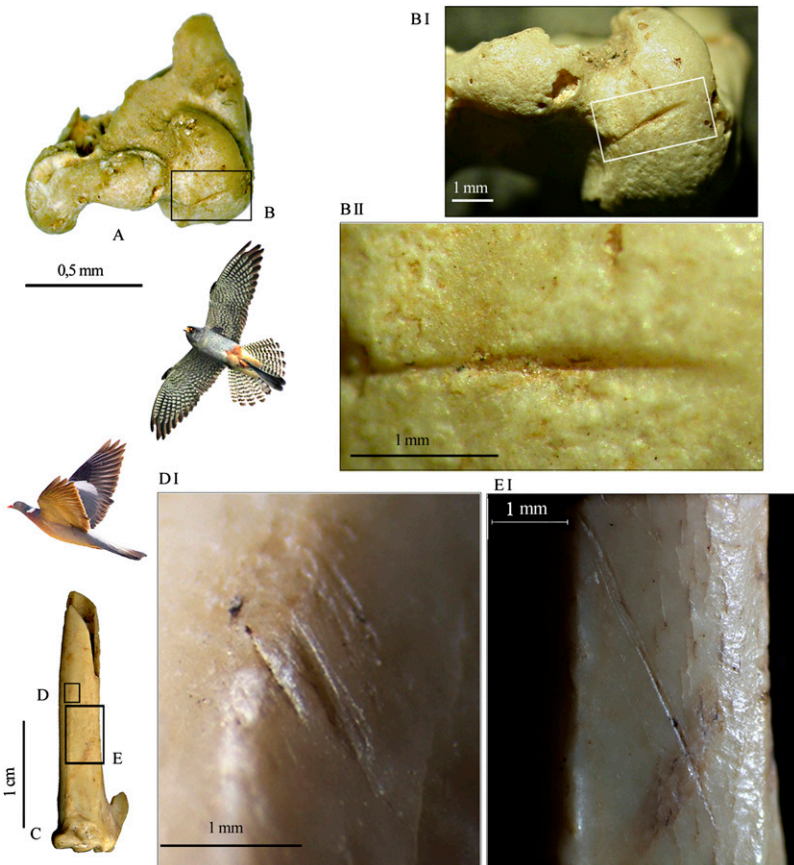


Fig. 2. Cut marks on the left distal humerus of red-footed falcon (*Falco vespertinus*) and on the right distal carpometacarpus of common wood pigeon (*Columba palumbus*). (A) Cranial view of the *Falco vespertinus* humerus. (B) Localization of the cut marks; (B, I and B, II) details. (C) Ventral view of the *Columba palumbus* carpometacarpus. (D and E) Localization of the cut marks; (D, I and E, I) details.

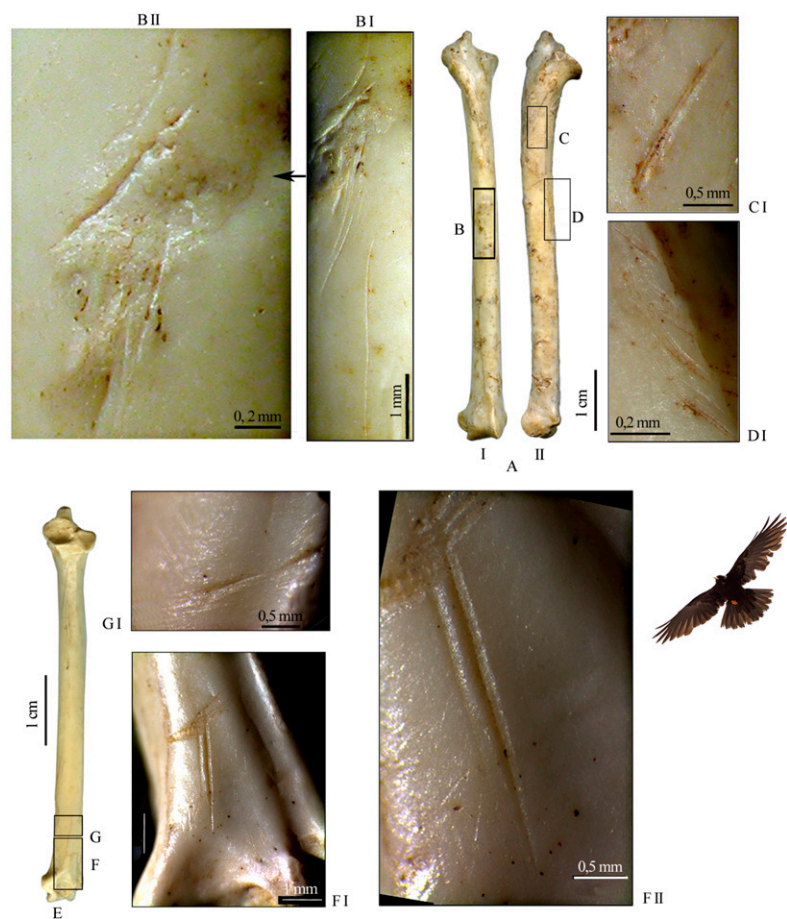


Fig. 3. Cut marks on two ulnae of Alpine chough (*Pyrrhoroax graculus*). (A) Different views of the right ulna; (A, I) medioventral view; (A, II) dorsolateral view. (B and D) Localization of the cut marks; (B, I; B, II; C, I; and D, I) details. (E) Lateral view of the left ulna. (F and G) Localization of the cut marks; (F, I; F, II; and G, I) details.

series of eight short striae on the ventral face, oblique to the main axis of the anatomical element, located on the neck of the epiphysis close to the synostosis metacarpalis distalis (Fig. 4B). Two other striae, less marked and deep, but related to the previous ones, are visible on the distal epiphysis on the facies articularis digiti minoris. All of these have a latero/medial orientation. Finally, on the dorsal face, longitudinal to the main axis of the bone and close to the sulcus interosseus, there is a proximal/distally oriented cut mark. On the whole, these striae reflect an action of disarticulation of the carpometacarpus from the phalanges involving the separation of the interosseus ventralis, interosseus dorsalis, and flexor digiti minoris muscles. The fracture edge of the dorsal face shows signs of polishing associated with microstriae and small marks (*SI Text*).

Over 20 wing bones display features characteristic of fresh fracturing, and four remains bear traces typical of peeling (mainly on Alpine chough) (35, 36) and, in a single case, a breakthrough, i.e., a perforation resulting from the pressure of the olecranon of the ulna on the humerus during manual disarticulation (37). These modifications may provide a broader and better definition of human actions on bird carcasses (*SI Text* and Figs. S2–S6). Other typologies of pre- and postdepositional modifications can be related mainly to root etching, trampling, corrosion, and small carnivore gnawing (38) (Figs. S4D and E and S7). On very few of the other bones, traces have been observed that are morphologically comparable with those made by a lithic implement, but uncertainties have arisen because of their small size (Figs. S2 B and B1 and S3 A and B1 and Table 1).

Discussion

This taphonomic study of the avifaunal assemblage from Mousterian levels of Fumane provides evidence that humans focused

only on some of the species. There is no doubt that the human modifications (striae, peeling, and breakthrough) indicate an unusual significance, as they are present on rare species with no particular food utility. These are mainly birds living in open areas close to rock cliffs and caves (lammergeier, Eurasian black vulture, and Alpine chough) as well as in clearings on the edges of woods and forests (red-footed falcon and common wood pigeon). It cannot be excluded that the presence of some individuals of Alpine chough may have been due to natural causes, whereas other elements must surely have been introduced by humans, who collected them from wounded or dead animals or intentionally captured individuals.

As well as an interest in leg phalanges (25), already evident from other sites (22–24), the Neandertals from Fumane show a particular interest in wings. Their goal could have been the appropriation of the whole wing, or just the remiges—as indicated by the ulna of Alpine chough (Fig. 3B)—or just the bone, as the signs of polishing on the left carpometacarpus of the Eurasian black vulture from level A9 (Fig. S6) would seem to indicate. However, the use of long bones from large birds for making tools, flutes, and other products has been documented in Europe only in more recent periods (7, 12, 13, 20). The interest in wings seems to be linked neither to the size of the bird nor to a specific plumage color, in that there are several different colors, including the gray of the red-footed falcon, the blue-gray of the common wood pigeon, the orange-shaded slate gray of the lammergeier, and the uniform black of the Alpine chough. In fact, the few remains of lammergeier and red-footed falcon (besides the common wood pigeon) are represented by front limb bones, and even in the more abundant Alpine chough, there is an overrepresentation of humeri and ulnae. This interest in wings is confirmed not only by the high percentage of bones from this portion (about 43%) in the

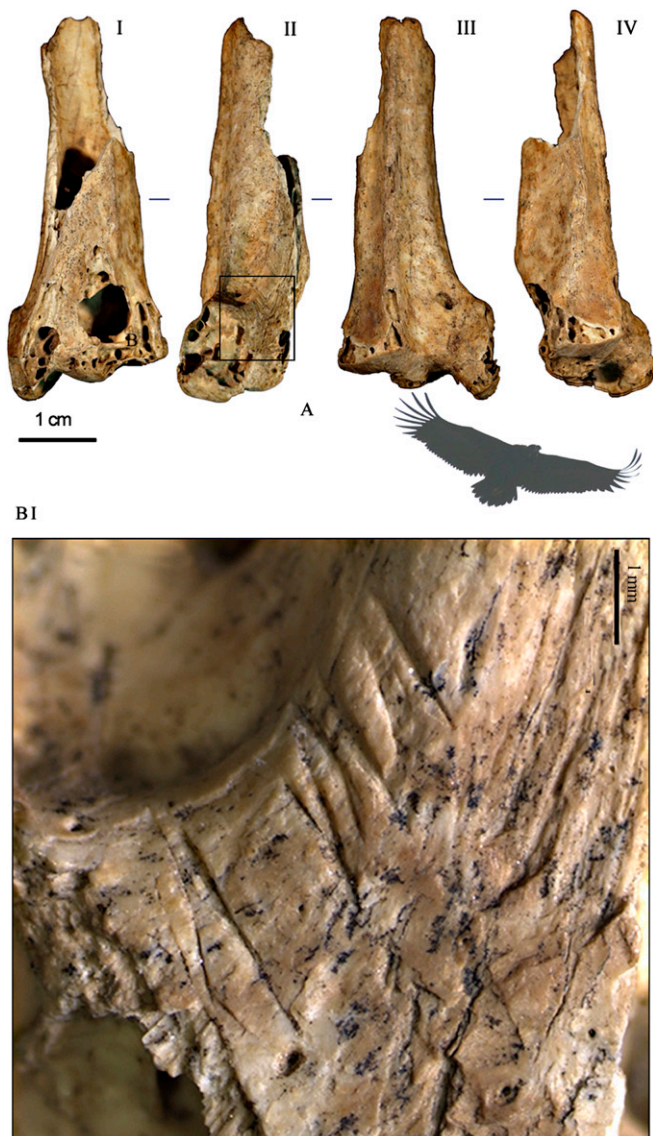


Fig. 4. Cut marks on the distal end of the left carpometacarpus of Eurasian black vulture (*Aegypius monachus*) from the Mousterian level A9. (A) Different views of the carpometacarpus: (A, I) ventral view; (A, II) medioventral view; (A, III) dorsal view; (A, IV) lateral view. (B) Localization of the cut marks; (B, I) detail.

osteological sample as a whole, but also by the fact that there is a high percentage of anthropic modifications (about 7%) only on these skeletal portions (*SI Text*).

Striae produced by lithic artifacts are mainly related to the action of disarticulation—of the humerus from the ulna in the case of the red-footed falcon; of the ulna from the carpometacarpus in the case of the lammergeier and the Alpine chough; and of the carpometacarpus from the phalanges in the case of the Eurasian black vulture. In the wood pigeon and Alpine chough, there is also the suggestion of the cutting and removal of the skin for the collection of the remiges. Usually, striae located on the proximal humerus, the coracoid, and the scapula in the meat-rich pectoral portion, together with those on the pelvis and femur in the thigh portion, indicate a use of the birds for food. Furthermore, it should be taken into account that the overrepresentation of wing elements in archaeological sites has also been interpreted as a consequence of capture, butchery, and food use by humans, as well as of postdepositional natural causes and of differential preservation of the bones (39).

Despite the presence of species at Fumane that were clearly of interest as food (*Lagopus*, *Coturnix*, *Rallus*, etc.), some of these being particularly numerous (*Crex* and *Tetrao*), there is only sporadic evidence of them actually being eaten, such as the *arrachement* on the ulna of *Tetrao* and the striae, albeit doubtful, on the carpometacarpus of *Lagopus*. There is also evidence of their exploitation by other predators (carnivores or birds of prey), as indicated by the traces of digestion and bites on numerous bones (Table 1). Though the traces that are definitely anthropic, referable to disarticulation, skinning, and plucking, could be related to processing for consumption as food, especially those on the carpometacarpus of pigeon, it should be underlined that they are present above all on bones from portions of the anatomy with a low meat content and from birds considered as nonedible, such as birds of prey and chough. Thus, the species involved, the anatomical elements affected, and the uniqueness of the human modifications indicate a specific Neandertal interest in the wings, and especially the feathers, of some particular birds.

This fact suggests various hypotheses on the use of the anatomical portions of birds analyzed in the study. The use of at least the longer remiges of Eurasian black vulture, lammergeier, and red-footed falcon as stabilizing elements for hunting spears, even after their reduction and preparation for fletching, does not seem possible. As well as there being uncertainties in the interpretation of the ballistic evidence on lithic tips used as armaments on the thrusting or throwing spears of Neandertals in Europe (40), the utilitarian hypothesis regarding the use of feathers for the stabilization of throwing spears does not concur with the ballistic criteria, as this stabilization is not necessary (41). A further possible use of stiff, strong feathers, including those extracted from smaller birds like Alpine chough and common wood pigeon, could have been in fletching spears launched with the aid of a spear thrower and arrows fired from a bow, as could be inferred on the basis of the earliest evidence on the invention and use of the atlatl, which, however, dates to not earlier than the Upper Solutrean, and of the bow, whose earliest remains date to the end of the Upper Paleolithic (42). Moreover, the support for the fletching hypothesis is no more than that given by ethnographic comparisons, which also attest to the use of feathers, or parts of them (e.g., the rachis), as tools or colorant containers (43).

The possibilities for the use of these anatomical elements in the social and symbolic sphere, however, are extremely abundant. Limiting the field to the recent and better-documented ethnographic contexts, it can be inferred that the use of bird feathers was very widespread and that humans have always attributed a broad and complex value to this practice, ranging from social significance and games to the production of ornamental and ceremonial objects. These objects consisted of single feathers, wings, or compositions of feathers or rachises applied on or in the body (head, ears, or nose), and also inserted in supporting material by means of elaborate feathering techniques to give form to headdresses, skirts, and hunting or war masks, or to adorn parade spears, calumets, and dancing drums (43–48).

Conclusions

The debate over the cognitive and behavioral capabilities of Neandertals, especially in the period around the first appearance of anatomically modern humans in Europe, is extensive and often based on archaeological records from a handful of pivotal sites. One of these, the Grotte du Renne site at Arcy-sur-Cure, France, provides a range of ornaments and tools usually associated with modern human industries from Châtelperronian levels, along with Neandertal teeth. Another is St. Césaire, where the relation of the Châtelperronian with Neandertals was reinforced by the discovery of a burial.

Nevertheless, a new radiocarbon dataset (49) and a reinvestigation of the available data (50) from the first and the second sites, respectively, have challenged the association between human remains and cultural assemblages. These studies, however, provide no direct evidence to invalidate the association and can, at most, be taken as implying that a minority of the symbolic

objects from the Grotte du Renne's Châtelperronian may be intrusive. The Fumane evidence on the ornamental exploitation of the feathers of large raptors and other birds strengthens the contention that the Grotte du Renne's associations are genuine and adds to the growing body of data that demonstrates the appearance of modern behavior in extinct autochthonous populations of Europe well before the immigration of modern humans (9). Moreover, the absence of evidence of this kind in the earliest Aurignacian levels at Grotta di Fumane (51) proves that, even before the Uluzzian, Neandertals achieved this level of behavioral complexity independently, and that it was not culturally transmitted or mimicked via incoming modern humans. Last, at least in southern Europe, the backdating of the acquisition of valuable elements of bird plumage opens the door to further perspectives in the exploration of the interactions that led to our extinct relatives manifesting an interest in a form of symbolic behavior.

Materials and Methods

The taxonomic determination has been based on comparison with the zoological collection of the Quaternary Paleontology and Archaeozoology Section of the Pigorini National Ethnographic Museum and Italian Institute of Human Paleontology of Rome. Microscopic analyses of the bone surfaces were carried out using Nikon 1000 stereomicroscope with 20–220 magnification range. Descriptive terms of the anatomical elements are in agreement with Livezey and Zusi (52).

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