Archaeozoological insights into avian exploitation in the Magdalenian of Belgium at the caves of Trou du Frontal and Trou des Nutons

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Abstract

Bird exploitation in the European Upper Palaeolithic remains poorly understood, particularly in northern regions. This study addresses that gap by presenting the archaeozoological analysis of bird remains from two Magdalenian sites in the Lesse valley (southern Belgium): Trou des Nutons and Trou du Frontal. Excavated in the 19th century, these sites are located near Trou de Chaleux—the most significant Magdalenian site in Belgium—and provide an opportunity to explore variability in human behaviour within a local microregion.

Our analysis reveals the first evidence of bird exploitation at Trou des Nutons and Trou du Frontal, with species including goose, merganser, ptarmigan, black grouse, and snowy owl. At Trou du Frontal, large bird bones also show evidence of use as raw material, consistent with patterns observed at Trou de Chaleux. Butchery marks linked to meat removal are present at both sites.

To refine the chronocultural attributions, new radiocarbon dates were obtained on four bird bones bearing anthropogenic marks. Given the small size of these remains, a tailored protocol was developed involving near-infrared screening, proteomic analysis to detect potential contaminants, and AMS dating using a gas ion source to maximize the chances of successful and reliable results. In addition, experiment to produce a reference collection of metal-tool scraping marks was conducted to aid interpretation.

These results not only highlight the complexity of Magdalenian subsistence and craft practices, but also demonstrate the research potential of historical collections for understanding past human–bird interactions.

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1. Introduction

In Belgium, the Magdalenian culture is associated with the recolonization of northwestern Europe following the Last Glacial Maximum, which ended around 19,000 BP (Cohen & Gibbard, 2019). Several Belgian sites, primarily cave sites, have yielded industries and artistic evidence attributed to this culture. The Lesse Valley, a tributary of the Meuse River, exhibits a high density of Magdalenian occupations, including the Trou de Chaleux, the most significant late Magdalenian site known in Belgium and one of the major sites of this period in northwestern Europe (Dewez, 1987 ; Dupont, 1872 ; Otte, 1994). Radiocarbon dates for the Belgian final Magdalenian are concentrated roughly between 16,000 and 14,000 cal BP, corresponding to the Bølling-Allerød interstadial, indicating that recolonization began during the Bølling phase (Charles, 1996 ; Stevens et al., 2009).

The sites in the Lesse Valley provide a valuable opportunity to document the lifeways of late Upper Palaeolithic hunter-gatherers in northwestern Europe on both regional and local scales. Lithic, osseous industries and large fauna have been the subject of extensive studies, whereas small fauna have received sporadic attention. However, understanding how humans interacted with small game, including birds, is essential for obtaining a comprehensive view of subsistence strategies, particularly because small, fast-moving prey required specific hunting techniques. In the 1970s, archaeologists proposed that human subsistence strategies diversified significantly toward the end of the Paleolithic, marked by an increased reliance on small game prior to the emergence of food-producing economies— a shift referred to as the ‘Broad Spectrum Revolution’ (Binford, 1968; Flannery, 1969). More recent evaluations of this diet breadth model have supported its core premise but suggest that the shift toward smaller prey occurred earlier than previously thought, beginning at the onset of the Upper Palaeolithic. This interpretation, based on faunal assemblages from the Mediterranean Basin, has been linked to human-driven depletion of high-ranked prey resources, potentially resulting from demographic growth, partial sedentarisation, or increased population density (e.g., Stiner, 2001 ; Stiner et al., 2000). In this context, it is important to analyse faunal assemblages from various periods of the Palaeolithic across Eurasia, including regions beyond the Mediterranean, in order to document how prehistoric populations interacted with small game, including birds. Recently, archaeozoological analysis of the avifauna from Trou de Chaleux has revealed a complex and intensive exploitation of birds (Goffette et al., 2020), yet comparative studies remain scarce in northwestern Europe and are even rarer at the local level. This study presents an analysis of bird remains from two caves occupied during the late Magdalenian in close proximity to Trou de Chaleux: the caves of Trou des Nutons and Trou du Frontal.

2. Presentation of the caves

Trou des Nutons and Trou du Frontal were excavated in 1864 under the supervision of É. Dupont (Charles, 1998). Both caves are small, only 200 m apart, and located approximately 6 km southeast of the modern town of Dinant, on the right bank of the Lesse River, about 2.5 km upstream from Trou de Chaleux. É. Dupont, a geologist, paid careful attention to stratigraphy for his time (Figures S1 and S2; additional information regarding the archaeological context of both caves is provided in Appendix S1 and Appendix S2, respectively). However, disturbances leading to layer mixing were not always recorded, rendering the stratigraphy of these sites imprecise. Previous radiocarbon dating has indicated mixing with more recent material (Table S1). To address this, new radiocarbon dating was conducted specifically on bird bones exhibiting anthropogenic modifications.

3. Material and Methods

The bird bones studied hereafter were recovered by hand during Dupont's excavations in the 'first ossiferous' layers from both caves. They are stored in the collections of Palaeontology of the Institute of Natural Sciences (Brussels) under the inventory number 2603, 2604 (Trou des Nutons), and 2188, 2897 to 2901, and 2530 (Trou du Frontal).

The zooarchaeological study includes detailed taphonomic and trace analyses. Anatomical identification and taxon determination were based on reference collections held at the Institute of Natural Sciences and specialized identification manuals (Table S2). When an identification is uncertain, we use 'cf.' in the scientific name in the tables. Taxonomy follows Gill et al. (2022), and anatomical features are described according to Baumel (1993). Measurements were taken following von den Driesch (1976) or other specialized manuals (Table S2). Quantification was based on the number of identified specimens (NISP) and the minimum number of individuals (MNI) (Lyman, 1994a). The MNI was calculated using the minimum number of skeletal elements (MNE), supplemented by laterality and age data. Age estimation was based on ossification stage following Serjeantson (2009). The sex of certain taxa was determined through measurements or the presence of medullary bone, the latter being a calcium-rich tissue deposited by female birds prior to egg-laying (Simkiss, 1961). Element side and completeness, preserved parts, and fracture edge morphology were recorded (Fernández-Jalvo & Andrews, 2016; Romero et al., 2016). Additionally, each bone was examined under a binocular microscope (magnification 6.5–50 ×) with oblique cold light to document surface alterations, such as color changes, root etching, erosion, thermal damage, weathering, pits, punctures and tool marks (Behrensmeyer, 1978; Lyman, 1994b; Behrensmeyer et al., 2003; López-González et al., 2006; Bocheński et al., 2009, 2018; Fernández-Jalvo and Andrews, 2016). The works of Barisic (2006) and Domínguez-Rodrigo et al. (2009) were used to assist in distinguishing between cut marks and trampling marks, acknowledging that it can be challenging to differentiate between intentional cut marks and trampling marks, especially when bones are mixed with lithic pieces in the sediment (Barisic, 2006).

To observe and illustrate some of the modifications in detail, a scanning electron microscope FEI Quanta 200 (23 kV; Mineralogical Laboratory of the Geological Survey of Belgium) was used and operated under low vacuum conditions. In addition, a digital microscope Hirox HRX-01 equipped with an H-2500E attachment and a LED ring light was used (acquisition mode multi-focus or 3D; TraceoLab of ULiège).

An experimental reference of marks left by modern metal tools was produced by scraping bones of contemporary feral rock pigeons (*Columba livia* f. domestica), collected devoid of meat and in a dry state, with a trowel (n = 1) and a scalpel (n = 1) (Figure S3). The cutting edge of each tool was held perpendicular to the long axis of the bone and moved back and forth five times along the surface, applying light pressure. All actions were performed by the first author (see results section).

To obtain new radiocarbon dates on bird bones bearing tool marks, a dedicated protocol was developed to maximize the likelihood of successful and reliable results. Selected bones first underwent non-destructive near-infrared analyses to prescreen for collagen preservation (Sponheimer et al., 2019 ; Vincke et al., 2014). This step enabled the selection of the most promising specimens and helped avoid unnecessary sampling of bones with poor collagen preservation (Appendix S3). Subsequently, the selected bones were sampled using a rotary cutting tool (Dremel). In parallel of collagen extraction, the samples underwent proteomic analysis (MALDI-FT-ICR) to screen for potential contaminants, such as collagen-based glues (Appendix S4). Only specimens without detectable contamination were subsequently radiocarbon dated using the AIX-MICADAS AMS system (Bard et al., 2015) (Appendix S5). Conventional radiocarbon ages (CRA) are expressed in years BP (before present) with 1 sigma errors

4. Results

4.1. Trou des Nutons

4.1.1. Biological information

The assemblage consists of 207 bird bones representing at least 58 individuals across 33 taxa (Table 1). The dominant orders are Galliformes, Passeriformes, Anseriformes, and Columbiformes (Figure S4). Galliformes are dominated by willow and rock ptarmigans, with notable representation of grey partridge and four remains of black grouse. Passeriformes are primarily corvids, but also include thrushes, white-throated dippers, and a few bones from smaller species. Anseriformes include diving and dabbling ducks, as well as geese, including barnacle goose. Columbiformes are well-represented, primarily by common wood pigeons, one of whose radii displays notable pathological exostoses (Figure 1F), along with a single stock dove. Other orders include less taxa, among which the identification of parasitic jaeger (Charadriiformes; Figure 1A), Eurasian green woodpecker (Piciformes; Figure 1B) and white-tailed eagle (Accipitriformes; Figure 1C) are noteworthy. Most of bird bones from Trou des Nutons originate from adult individuals (89.5%; Table S3). Sex determination was rarely possible based on measurements, while no medullary bone was observed in broken bones (Table S4).

Table 1. Trou des Nutons. Inventory of bird remains collected by Dupont in 1864 and analysed in the present study. The number of specimens exhibiting anthropogenic modifications, pits/punctures, and dissolution damage is also reported. Unid. = unidentified.

	Taxa	NISP		MNI		Human modification			Non-human modification	
		N	*%*	*N*	*%*	*NISP*	*%NISP*	*Proposed use*	*Pit/punct.*	*Dissolution*
	Anseriformes									
1	Barnacle goose (*Branta leucopsis*)	2	1.0	1	1.7	1	12.5	meat	-	-
2	Goose (*Anser* sp.)	12	5.8	2	3.4	3	37.5	meat. feather	2	-
	Goose (*Anser* sp. / *Branta* sp.)	1	0.5	-	-	1	12.5	meat	-	-
3	Mallard (*Anas platyrhynchos*)	2	1.0	1	1.7	-	-	-	1	-
4	Common teal (*Anas crecca*)	1	0.5	1	1.7	-	-	-	-	-
5	Common scoter (*Melanitta nigra*)	1	0.5	1	1.7	-	-	-	-	-
6	Tufted duck (*Aythya fuligula*)	1	0.5	1	1.7	-	-	-	-	-
7	Common goldeneye? (cf. *Bucephala clangula*)	1	0.5	1	1.7	-	-	-	-	-
8	Common merganser (*Mergus merganser*)	6	2.9	4	6.9	-	-	-	-	-
	Merganser (*Mergus* sp.)	1	0.5	-	-	-	-	-	-	-
	Anatinae size shoveler	2	1.0	-	-	-	-	-	-	-
	Anatinae size mallard (*Anas platyrhynchos*)	5	2.4	-	-	-	-	-	-	-
	Galliformes									
9	Grey partridge (*Perdix perdix*)	20	9.7	5	8.6	-	-	-	2	14
10	Willow ptarmigan (*Lagopus lagopus*)	2	1.0	2	3.4	-	-	-	-	-
11	Rock ptarmigan (*Lagopus muta*)	3	1.4	2	3.4	-	-	-	-	-
	Unid. ptarmigan (*Lagopus* sp.)	31	15.0	2	-	1	12.5	meat. feather?	2	4
12	Black grouse (*Lyrurus tetrix*)	4	1.9	1	1.7	1	12.5	meat	-	2
	Unid. Galliformes	3	1.4	-	-	-	-	-	1	-
	Accipitriformes									
13	White-tailed eagle (*Haliaeetus albicilla*)	1	0.5	1	1.7	-	-	-	1	-
	Falconiformes									
14	Peregrine falcon (*Falco peregrinus*)	3	1.4	2	3.8	-	-	-	-	-
15	Common kestrel? (*Falco* cf. *tinnunculus*)	2	1.0	2	3.8	-	-	-	-	1
	Falcon size peregrine	2	1.0	-	-	-	-	-	-	-
	Gruiformes									
16	Corn crake (*Crex crex*)	1	0.5	1	1.7	-	-	-	-	1
	Charadriiformes									
17	cf. whimbrel (cf. *Numenius phaeopus*)	1	0.5	1	1.7	-	-	-	-	-
18	Eurasian woodcock (*Scolopax rusticola*)	8	3.9	2	3.4	-	-	-	2	3

19	Parasitic jaeger (*Stercorarius parasiticus*)	2	1.0	1	1.7	-	-	-	-	-
	Jaeger or gull (*Stercorarius* sp./*Larus* sp.)	1	0.5	-	-	-	-	-	1	-
	Columbiformes									
20	Stock dove (*Columba oenas*)	1	0.5	1	1.7	-	-	-	1	1
21	Common wood pigeon (*Columba palumbus*)	24	11.6	7	12.1	-	-	-	3	5
	Pigeon/dove (*Columba* sp.)	6	2.9	-	-	-	-	-	-	1
	Unid. Columbiformes	1	0.5	-	-	-	-	-	-	-
	Strigiformes									
22	Western barn owl (*Tyto alba*)	1	0.5	1	1.7	-	-	-	-	-
23	Tawny owl (*Strix aluco*)	6	2.9	2	3.4	-	-	-	-	2
	Tawny owl ? (cf. *Strix aluco*)	1	0.5	-	-	-	-	-	-	-
24	Eagle owl or snowy owl (*Bubo bubo*/*scandiacus*)	2	1.0	1	1.7	-	-	-	-	-
	Piciformes									
25	European green woodpecker (*Picus viridis*)	1	0.5	1	1.7	-	-	-	-	-
	Passeriformes									
26	Carrion crow (*Corvus corone*)	8	3.9	2	3.4	1	12.5	meat. feather?	-	1
	Carrion crow or rook (*Corvus corone*/*frugilegus*)	4	1.9	-	-	-	-	-	-	1
27	Northern raven (*Corvus corax*)	2	1.0	2	3.4	-	-	-	-	1
28	Eurasian jay (*Garrulus glandarius*)	3	1.4	1	1.7	-	-	-	-	-
29	Western Jackdaw (*Coloeus monedula*)	4	1.9	1	1.7	-	-	-	-	-
	Corvidae size of western jackdaw	5	2.4	-	-	-	-	-	3	1
30	Unid. thrush (*Turdus* sp.)	4	1.9	2	3.4	-	-	-	-	1
31	White-throated dipper (*Cinclus cinclus*)	1	0.5	1	1.7	-	-	-	-	-
32	Finch (*Fringilla* sp.)	1	0.5	1	1.7	-	-	-	-	-
33	Passeriformes size redpoll	2	1.0	1	1.7	-	-	-	-	-
	Passeriformes size thrush	7	3.4	-	-	-	-	-	1	-
	Total identified	**203**	**98.1**	**58**	**100**	8	100	-	**20**	**39**
	Unid. bird	**4**	**1.9**	**-**	-	**-**	**-**	-	-	-
	Total	**207**	**100**	**58**	**100**	**8**	100	-	**20**	**39**

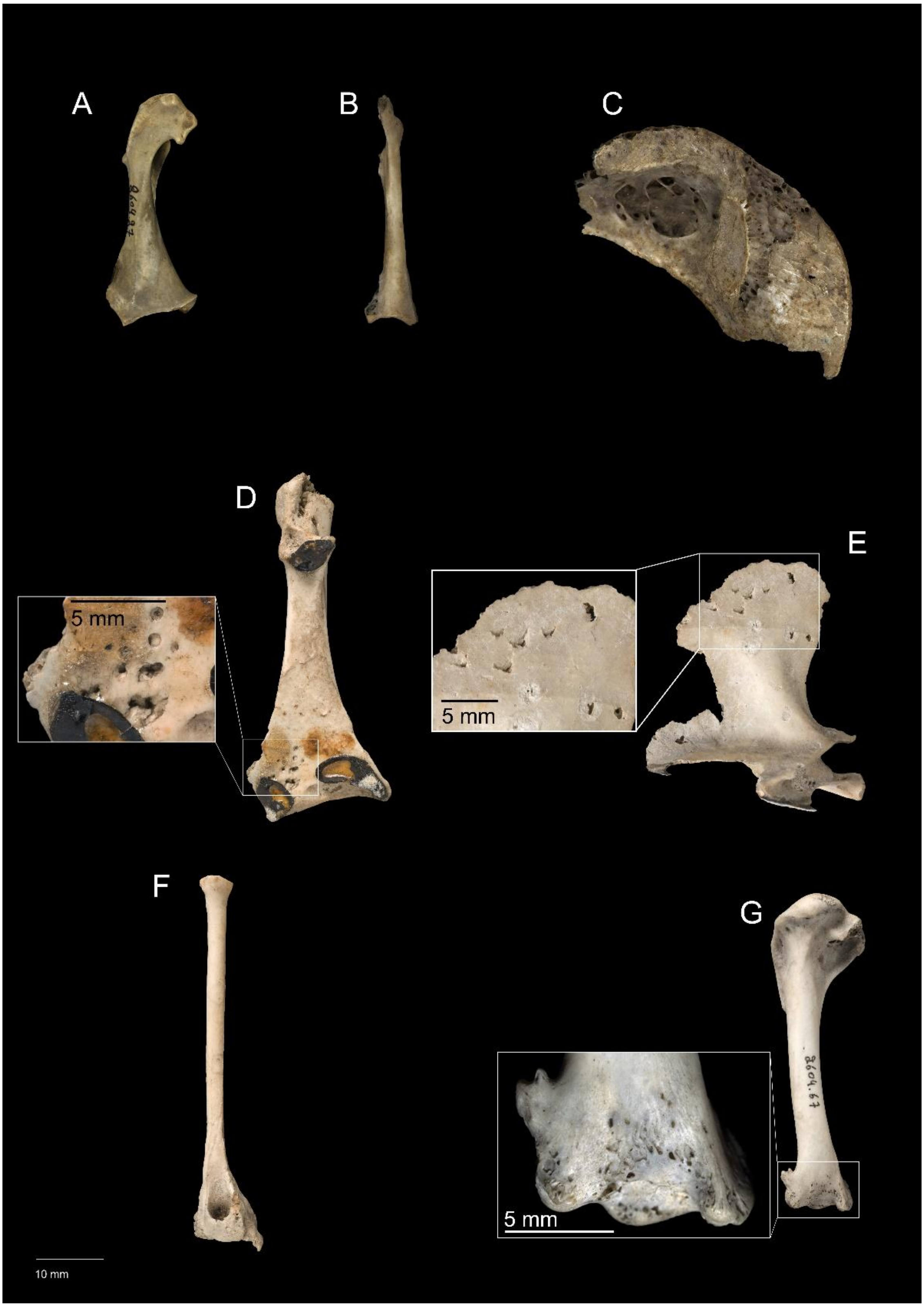

Figure 1. Trou des Nutons. **A.** Parasitic jaeger, right coracoid (IRSNB Av 0250). **B.** European green woodpecker, left coracoid (IRSNB Av 0249). **C.** White-tailed eagle, furcula, right part (IRSNB Av 0252). **D.** Duck size of mallard, left coracoid displaying small-diameter perforations attributed to a small carnivore (IRSNB Av 0251). **E.** Common wood pigeon, sternum with 'V'-shaped perforations attributed to a bird of prey (IRSNB Av 0248). **F.** Common wood pigeon, left radius with a pathological distal extremity exhibiting pronounced exostoses (IRSNB Av 0261). **G.** Jackdaw-sized corvid, left humerus showing digestive damage at the distal extremity (IRSNB Av 0254).

4.1.2. Taphonomic analysis

The bird bones from Trou des Nutons are generally well preserved. No coloured deposits or mineral crusts were observed. Six bones show faint marks of rootlets, and two specimens bear marks from rodent incisors. Longitudinal cracks are rare (3.4%) and faint.

4.1.2.1. Pits, punctures and dissolution damage

Perforations, likely caused by predators or scavengers, were identified on 20 bones (9.6%) from various species, primarily of small to medium size (Table 1). Larger species were also affected, including the furcula of a white-tailed eagle and a carpometacarpus of a goose. Some perforations and depressions exhibit a 'V'-shaped morphology typical of raptor beak strikes (Figure 1E). Conversely, small circular perforations suggest consumption by small carnivores such as a cat or fox cub (Figure 1D).

Dissolution damage is generally slight and affects 18.8% of the bones, which corresponds to Category 1 *sensu* Andrews (1990). It is more frequent on the bones of Galliformes, particularly the grey partridge, as well as on those of Columbiformes and Passeriformes (Figure 1G).

4.1.2.2. Fractures

Overall, 35.8% of the collected bones are complete. Long bones are frequently fractured, with only 63 being intact (39.6%) (Table S5). Among the taxa yielding more than 10 long bones, the highest fragmentation rates are observed in geese (7.7% of long bones intact) and ducks (22.2%). In contrast, ptarmigan (52.0%), grey partridge (44.4%), and small corvid bones (52.2%) are more frequently complete. All fractures observed on long bones (n = 81) have a curved contour, except for one bone, which exhibits a transverse fracture with a straight edge.

4.1.2.3. Skeletal representation

Certain skeletal elements are absent from the collection, such as posterior phalanges and ribs, or are significantly underrepresented, including vertebrae and anterior phalanges (Figure S5; Table S6). The number of remains per taxon is too low to reveal differences in skeletal representation. It is worth noting, however, that even in ptarmigan, which provided a greater number of remains, certain skeletal parts are missing. Only long bones are preserved, with humerus, carpometacarpus, and tarsometatarsus being the best-represented elements (Figure S6).

4.1.3. Anthropogenic modifications

4.1.3.1. Tool marks

Tool marks were identified on eight bones (3.9% of the assemblage; Table 1), all of which are wing bones.

Five of these belong to geese: three identified as from the genus *Anser*, one as a barnacle goose, and one as an indeterminate goose species. One ulna exhibits disarticulation marks on the proximal articular surface and longitudinal scraping marks on the distal portion of the bone's shaft on the anterior side (Figure 2A). Longitudinal incisions were observed on the posterior side of a second ulna, possibly from the same individual. These incisions are precisely located next to the papillae remigales caudales and suggest the extraction of secondary remiges (Figure 2B). One radius displays longitudinal scraping marks on the dorsal side of the bone shaft. Additionally, a carpometacarpus shows numerous fine longitudinal or oblique incisions on the antero-dorsal side (Figure 2C).

Tool marks were also observed on two Galliformes bones: a black grouse humerus and a ptarmigan ulna. The humerus exhibits numerous longitudinal and oblique incisions on its anterior face, just below the proximal joint (Figure 3A). A unilateral perforation on the same face may represent a human tooth mark left during bone gnawing. The ptarmigan ulna displays two wedge-shaped longitudinal incisions on the dorsal face (Figure 3C). Lastly, several groups of longitudinal or oblique incisions were identified on the ventral and anterior faces of a crow ulna (Figure 3B).

4.1.3.2. Polish

Rounded shape associated with pronounced polish was observed on the distal fractures of a goose ulna and radius (Figure 2B and 2D). A close examination of these polishes shows highly organized micro-striations affecting a mostly longitudinal orientation at the extremities, resulting from the use of these bones as tools in an undetermined activity.

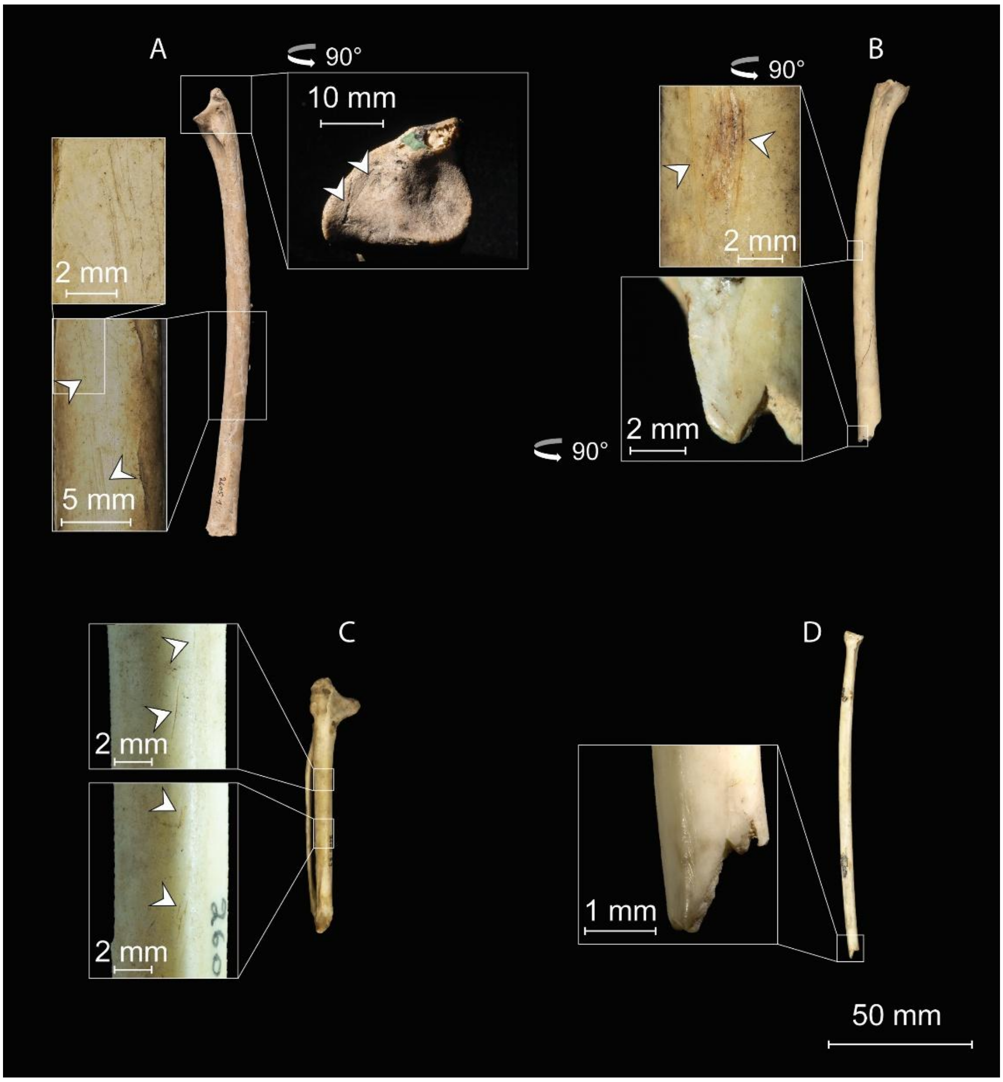

Figure 2. Trou des Nutons. Bones with anthropogenic marks. **A.** Goose, right ulna exhibiting disarticulation marks on the proximal articular side and scraping marks on the shaft of the bone (IRSNB Av 0255). **B.** Goose, left ulna showing tool marks near the papillae remigales caudales, suggesting feather extraction; a pronounced polish on the distal fracture indicates a use as a tool (IRSNB Av 0256). **C.** Goose, right carpometacarpus exhibiting fine oblique incisions on the shaft of the bone (IRSNB Av 0260). **D.** Barnacle goose, left radius with longitudinal scraping marks; a pronounced polish on the distal fracture indicates a use as a tool (IRSNB Av 0259).

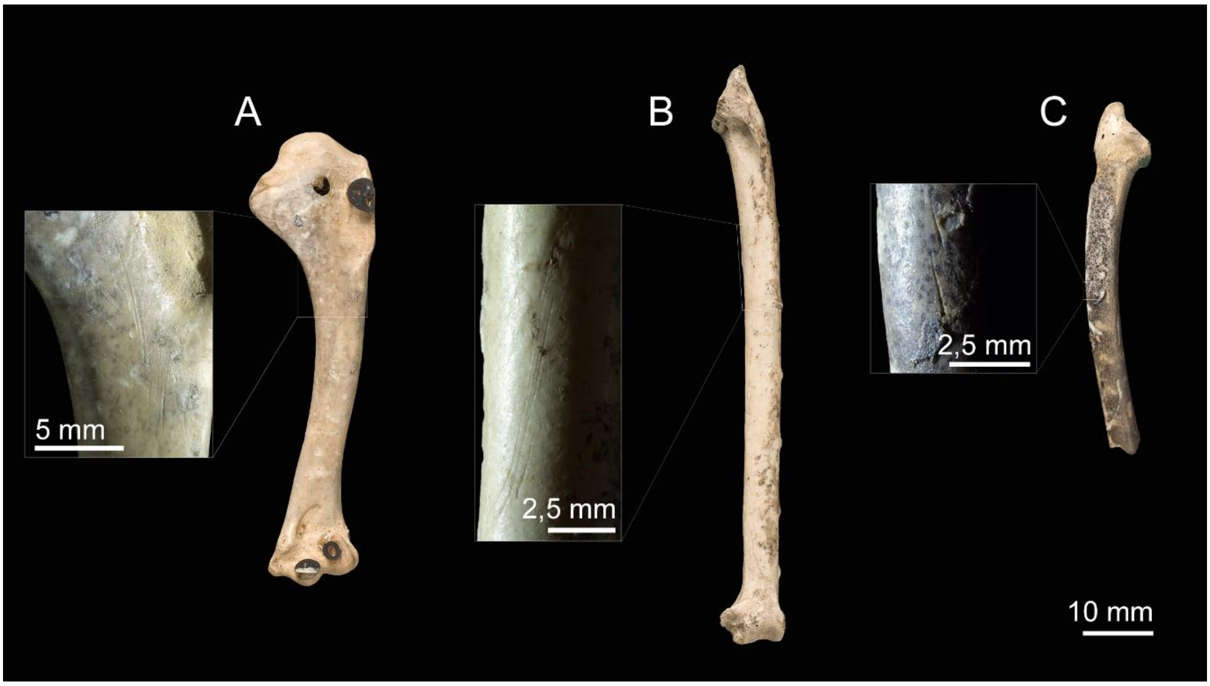

Figure 3. Trou des Nutons**.** Bones with anthropogenic marks. **A.** Black grouse, left humerus from a female displaying tool marks interpreted as associated with meat removal (IRSNB Av 0253). **B.** Carrion crow, right ulna showing oblique scraping marks (IRSNB Av 0258). **C.** Ptarmigan, right ulna exhibiting longitudinal incisions (IRSNB Av 0257).

4.2. Trou du Frontal

4.2.1. Biological information

Trou du Frontal totals 1,155 bone fragments, of which 1,023 (88.6%) have been identified. The bones were attributed to 132 individuals from 50 different taxa (Table 2). Galliformes and Passeriformes account for nearly two-thirds of the assemblage (Figure S4). The order Galliformes, by far the most represented, is overwhelmingly dominated by the domestic fowl (see discussion). Ptarmigans are the next most frequent, followed by the grey partridge. Second in importance, the order Passeriformes primarily includes large taxa, such as corvids like the northern raven or the Eurasian jay. Smaller species like the pine grosbeak are also present. The only taxon from the order Columbiformes identified is the common wood pigeon. The other bird orders are scarcer. The occurrence of four Piciformes taxa is noteworthy, including great spotted, middle spotted, black, and probably the green woodpecker (Figure 4D-F). Amongst Accipitriformes, a large taxon, possibly the imperial eagle, is present (Figure 4C). The Rallidae family is represented by the Eurasian coot, water rail, and corn crake. Finally, two bones from the little bustard, a very rare taxon in the Belgian paleontological record, are the only fragments attributed to the order Otidiformes (Figure 4A-B).

Table 2. Trou du Frontal. Inventory of bird remains collected by Dupont in 1864 and analysed in the present study. The number of specimens exhibiting anthropogenic modifications, pits/punctures, and dissolution damage is also reported. The specimens with scraping marks penecontemporaneous to the excavations are not counted in the 'Human modification' column. Unid. = unidentified.

	Taxa	NISP		MNI		Human modification			Non-human modification	
		N	*%*	*N*	*%*	*NISP*	*%NISP*	*Proposed use*	*Pit/punct.*	*Dissolution*
	Anseriformes									
1	Lesser white-fronted goose? (cf. *Anser erythropus*)	4	0.3	1	0.8	-	-	-	2	-
	Goose size lesser white-fronted	1	0.1	-	-	-	-	-	1	1
2	Goose size greater white-fronted	3	0.3	1	0.8	-	-	-	-	-
3	Goose size greylag	1	0.1	1	0.8	-	-	-	1	-
	Goose? (cf. *Anser* sp.)	1	0.1	-	-	1	3.4	Bone industry (needle?)	-	-
4	Barnacle goose? (*Branta* cf. *leucopsis*)	3	0.3	1	0.8	-	-	-	2	-
5	Tufted duck (*Aythya fuligula*)	3	0.3	1	0.8	-	-	-	1	-
6	Common merganser (*Mergus merganser*)	1	0.1	1	0.8	-	-	-	1	-
	Merganser (*Mergus merganser/serrator*)	6	0.5	-	-	1	3.4	Meat	1	-
7	Eurasian wigeon? (cf. *Mareca penelope*)	1	0.1	1	0.8	-	-	-	1	-
8	Common teal (*Anas crecca*)	1	0.1	1	0.8	-	-	-	-	-
	Anatinae size shoveler	8	0.7	-	-	-	-	-	1	2
	Anatinae size mallard	23	2.0	-	-	-	-	-	10	6
	Unid. Anseriformes	1	0.1	-	-	-	-	-	-	-
	Galliformes									
9	Common quail (*Coturnix coturnix*)	2	0.2	1	0.8	-	-	-	-	1
10	Grey partridge (*Perdix perdix*)	51	4.4	9	7.3	-	-	-	9	23
	Grey partridge? (cf. *Perdix perdix*)	11	1.0	-	-	-	-	-	2	5
11	*Domestic fowl (*Gallus gallus* f. domestica)	157	13.6	21	16.9	19	12.1	Meat. bone industry?	15	7
12	Hazel grouse (*Tetrastes bonasia*)	1	0.1	1	0.8	-	-	-	-	1
13	Willow ptarmigan (*Lagopus lagopus*)	4	0.3	2	1.6	-	-	-	-	2
14	Rock ptarmigan (*Lagopus muta*)	8	0.7	5	4.0	-	-	-	-	3
	Unid. ptarmigan (*Lagopus* sp.)	71	6.1	8	-	1	3.4	Meat	18	20
	Ptarmigan ? (cf. *Lagopus* sp.)	1	0.1	-	-	-	-	-	-	-
15	Black grouse (*Lyrurus tetrix*)	24	2.1	4	3.2	-	-	-	7	12
	Black grouse? (cf. *Lyrurus tetrix*)	1	0.1	-	-	-	-	-	-	-
16	Western capercaillie (*Tetrao urogallus*)	7	0.6	2	1.6	-	-	-	4	-
	Western capercaillie? (cf. *Tetrao urogallus*)	1	0.1	-	-	-	-	-	-	-

	Galliformes size domestic fowl	107	9.3	-	-	-	-	-	7	5
	Galliformes size ptarmigan	43	3.7	-	-	-	-	-	4	4
	Otidiformes									
17	Little bustard (*Tetrax tetrax*)	2	0.2	1	0.8	-	-	-	1	2
	Accipitriformes									
18	Buzzard (*Buteo* sp.)	4	0.3	2	1.6	-	-	-	1	1
19	Eurasian sparrowhawk (*Accipiter nisus*)	2	0.2	1	0.8	-	-	-	-	2
20	Northern Goshawk (*Accipiter gentilis*)	1	0.1	1	0.8	-	-	-	1	-
21	Eagle size imperial (*Aquila* sp.)	1	0.1	1	0.8	-	-	-	-	-
	Falconiformes									
22	Common kestrel (*Falco* cf. *tinnunculus*)	3	0.3	3	2.4	-	-	-	-	-
23	Peregrine falcon (*Falco peregrinus*)	3	0.3	2	1.6	-	-	-	1	-
	Falcon size kestrel	15	1.3	-	-	-	-	-	2	4
	Falcon size peregrine	11	1.0	-	-	-	-	-	-	1
	Falcon (*Falco* sp.)	1	0.1	-	-	-	-	-	-	1
	Gruiformes									
24	Eurasian coot (*Fulica atra*)	2	0.2	1	0.8	-	-	-	1	-
25	Water rail (*Rallus aquaticus*)	1	0.1	1	0.8	-	-	-	-	-
26	Corn crake (*Crex crex*)	2	0.2	1	0.8	-	-	-	1	-
	Rail (*Crex crex*/*Rallus aquaticus*)	2	0.2	-	-	-	-	-	-	-
	Charadriiformes									
27	European golden plover (*Pluvialis apricaria*)	1	0.1	1	0.8	-	-	-	-	1
28	Northern lapwing (*Vanellus vanellus*)	2	0.2	1	0.8	-	-	-	-	-
29	Whimbrel (*Numenius phaeopus*)	1	0.1	1	0.8	-	-	-	1	1
30	Godwit (*Limosa* sp.)	1	0.1	1	0.8	-	-	-	1	-
31	Eurasian woodcock (*Scolopax rusticola*)	54	4.7	9	7.3	-	-	-	14	16
	Charadriiformes size woodcock	5	0.4	-	-	-	-	-	-	1
	Columbiformes									
32	Common wood pigeon (*Columba palumbus*)	89	7.7	19	15.3	1	3.4	Meat	31	31
	Pigeon/dove (*Columba* sp.)	5	0.4	-	-	-	-	-	-	-
	Strigiformes									
33	Snowy owl (*Bubo scandiacus*)	1	0.1	1	0.8	1	3.4	Feathers. bone industry (tube?)	-	-
	Eagle owl or snowy owl (*Bubo bubo*/*scandiacus*)	3	0.3	-	-	-	-	-	1	-

34	Tawny owl (*Strix aluco*)	6	0.5	2	1.6	-	-	-	-	-
35	Long-eared owl (*Asio otus*)	1	0.1	1	0.8	-	-	-	-	-
36	Short-eared owl (*Asio flammeus*)	5	0.4	2	1.6	-	-	-	2	1
	Strigiformes size tawny owl (*Strix aluco*)	3	0.3	-		-	-	-	1	1
	Piciformes									
37	Greater spotted woodpecker (*Dendrocopos major*)	3	0.3	2	1.6	-	-	-	-	-
38	Middle spotted woodpecker (*Dendrocoptes medius*)	2	0.2	2	1.6	-	-	-	2	2
39	Black woodpecker (*Dryocopus martius*)	4	0.3	2	1.6	-	-	-	1	-
40	Europea green woodpecker? (cf. *Picus viridis*)	1	0.1	1	0.8	-	-	-	-	-
	Passeriformes									
41	Carrion crow (*Corvus corone*)	2	0.2	1	0.8	-	-	-	-	1
42	Rook (*Corvus frugilegus*)	1	0.1	1	0.8	-	-	-	-	1
	Carrion crow or rook (*Corvus corone/frugilegus*)	7	0.6	-	-	-	-	-	2	4
43	Northern raven (*Corvus corax*)	3	0.3	2	1.6	-	-	-	1	1
44	Western Jackdaw (*Coloeus monedula*)	2	0.2	1	0.8	-	-	-	1	-
45	Eurasian magpie (*Pica pica*)	1	0.1	1	0.8	-	-	-	-	1
	Eurasian magpie? (cf. *Pica pica*)	4	0.3	-	-	-	-	-	2	-
46	Eurasian jay (*Garrulus glandarius*)	5	0.4	2	1.6	-	-	-	3	1
	Eurasian jay? (cf. *Garrulus glandarius*)	1	0.1	-	-	-	-	-	-	-
47	Redwing? (cf. *Turdus iliacus*)	2	0.2	1	0.8	-	-	-	-	-
48	Barn swallow? (cf. *Hirundo rustica*)	2	0.2	1	0.8	-	-	-	-	1
49	Hawfinch (*Coccothraustes coccothraustes*)	1	0.1	1	0.8	-	-	-	-	-
50	Pine grosbeak (*Pinicola enucleator*)	2	0.2	1	0.8	-	-	-	1	-
	Passeriformes size warbler	6	0.5	-	-	-	-	-	-	-
	Passeriformes size finch	50	4.3	-	-	-	-	-	10	6
	Passeriformes size thrush	86	7.4	-	-	-	-	-	9	25
	Passeriformes size magpie	53	4.6	-	-	-	-	-	12	10
	Passeriformes size crow	13	1.1	-	-	-	-	-	-	-
	Total identified	**1023**	**88.6**	**132**	100	**28**	**96.6**	**-**	**190**	**208**
	Unid. bird	**132**	**11.4**	**-**	-	**1**	**3.4**	Feathers. bone industry	**12**	**-**
	Total	**1155**	**100**	**132**	100	**29**	**100**	**-**	**202**	**208**

Figure 4. Trou du Frontal. **A-B.** Little bustard, **A** left tibiotarsus (IRSNB Av 0241) and **B** left tarsometatarsus (IRSNB Av 0243), likely from the same individual. **C.** Imperial-sized eagle, carpometacarpus of a subadult individual (IRSNB Av 0238). **D.** Middle spotted woodpecker, left humerus (IRSNB Av 0233). **E.** Great spotted woodpecker, left humerus (IRSNB Av 0232). **F.** Black woodpecker, right humerus (IRSNB Av 0234).

4.2.2. Taphonomic analysis

The preservation of bird bones from Trou du Frontal is generally good. Mineral crusts are frequently observed (9.1% of the remains) but generally cover only a small part of the bone surface. Root etched (6.8%) and rodent gnaw marks (4.8%) are less frequent. Longitudinal fissures were observed fairly frequently (6.5%), consistent with a period of surface exposure prior to burial in sediment.

4.2.2.1. Pits, punctures and dissolution damage

Depressions and perforations indicative of predation or scavenging by non-human predators were observed on 201 specimens (17.4%). The most affected taxa include the common wood pigeon, ptarmigans, domestic fowl, and the Eurasian woodcock.

Five bones show depressions associated with gnawing marks (scoring) in two cases, whose morphology suggests the activity of small carnivores. One of these elements, a goose carpometacarpus, exhibits a deep depression transitioning into a scraped area (Figure 5A). Such scraped zones could easily be misinterpreted as tool marks.

Dissolution damage affects 18% of the material, and is characterized by a low intensity. These alterations were assigned to Category 1 *sensu* Andrews (1990). The common wood pigeon is heavily impacted, as are small Passeriformes, ptarmigans, the grey partridge, and the Eurasian woodcock.

4.2.2.2. Fractures

Overall, 25.5% of the specimens are complete. Long bone fragmentation is intense, with only 270 specimens remaining intact (31.2%) (Table S7). The lowest fragmentation rates were noted in corvids (61.9% of long bones complete) and small Passeriformes (38.2%), as well as various Galliformes such as ptarmigans (38.2%), the grey partridge (34.7%), and the domestic fowl (31.6%).

The morphology of fractures was evaluated for 326 long bones. Most fractures display curved outlines (67.5%), while transverse fractures are much rarer (14.1%). Intermediate patterns were observed in some cases (18.4%). The fracture edges are predominantly smooth (55.2%), which aligns with the dominance of curved fractures, as smooth edges are often associated with this morphology (Romero et al., 2016). However, some bones exhibit curved or intermediate fractures with rough edges (44.8%), resulting in a complex pattern likely linked to chewing by predators or scavengers (Blasco & Peris, 2009; Romero et al., 2016).

4.2.2.3. Skeletal representation

Almost all skeletal elements are represented. However, certain fragile elements, such as skulls, mandibles, or ribs, are scarce. Very small elements are few, such as anterior and posterior phalanges or vertebrae, or absent, such as quadrate or carpal bones (Table S8).

The survival rates of long bones were analysed for six taxa: ducks, grey partridge, domestic fowl, ptarmigans, Eurasian woodcock, and common wood pigeon (Figure S8). Differences are visible, but interpretation remains challenging. Generally, the ulna and scapula are underrepresented in most taxa, except for the domestic fowl. The grey partridge and ptarmigans show good preservation of the carpometacarpus and tarsometatarsus, and to a lesser extent, the humerus and radius. The Eurasian woodcock and common wood pigeon exhibit good preservation of the humerus, radius, and coracoid. The domestic fowl and ducks show more homogeneous preservation, despite deficits in the ulna and carpometacarpus for the former, and the scapula and ulna for the latter.

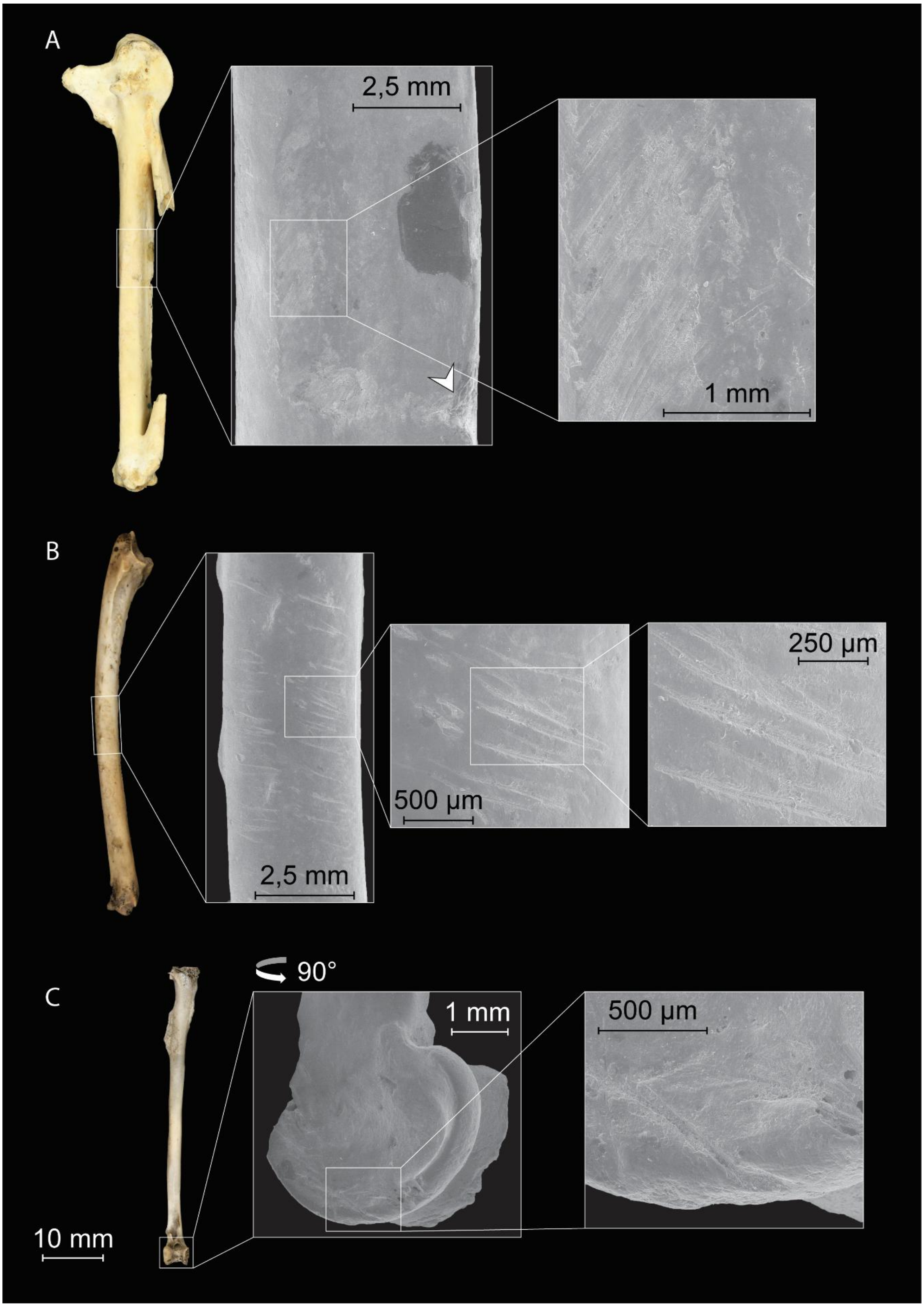

Figure 5. Trou du Frontal. **A.** Likely lesser white-fronted goose, right carpometacarpus displaying a depression interpreted as a carnivore tooth mark, associated with a scraping zone (IRSNB Av 0239). **B.** Eurasian woodcock, left ulna showing several rows of incisions interpreted as raptor beak marks (IRSNB Av 0237). **C.** Passeriformes of thrush size, right tibiotarsus with sharp but shallow incisions on the distal end, interpreted as raptor beak marks (IRSNB Av 0242).

4.2.3. Anthropogenic modifications

4.2.3.1. Burn marks

Burn marks were observed on five domestic fowl bones: one humerus, one ulna, two femurs, and one tarsometatarsus.

4.2.3.2. Tool marks

The assemblage from the Trou du Frontal contains several bones bearing marks from tools or similar-looking marks, the interpretation of which proved complex. Indeed, some morphologically similar marks likely stem from actions or periods that are sometimes very distant from each other. A critical analysis of each piece was therefore necessary to isolate bones attributable to human activities during the Palaeolithic.

4.2.3.2.1. Scraping marks contemporary with excavations

Longitudinal scraping marks were observed on the shafts of 54 bones, some covering extensive areas (Figure 6A-B). Due to their regular, linear morphology, these marks were interpreted as tool-related. However, several peculiarities were noted —for instance, the presence of such marks on bones also showing evidence of non-human predation (e.g. raptors). Some tool marks were covered by 19^{th}-century glue, definitively ruling out their creation during our study. Other marks, which cut through adhering sediment or appeared particularly ‘fresh’, clearly resulted from scraping activities during excavation or in the post-excavation phase, prior to display preparation. These should therefore not be considered archaeological in origin.

Experimental marks produced using metal tools (a trowel and a scalpel; Figure 6C–D) show strong similarities to those observed on the archaeological bones (Figure 6A-B), supporting the interpretation that the latter were made with metal instruments. Although our experimental series is limited—comprising only one bone scraped with a trowel and one with a scalpel—the morphological resemblance between the experimental and archaeological marks is consistent with our hypothesis that these traces were produced by metal excavation tools. Given the intensity of scraping on some specimens, it is unlikely that all such marks occurred during excavation; rather, some were likely created post-excavation, during cleaning of the specimens. This type of scraping mark was not observed on material from Trou des Nutons or Trou de Chaleux. Based on the evidence presented, we conclude that the marks observed on the 54 bones from Trou du Frontal were most likely produced during the 19^{th}-century excavation, as a result of cleaning with metal tools.

4.2.3.2.2. Archaeological marks from metal tools

Fine and deep incisions observed on 18 domestic fowl bones correspond to metal tools (Fernández-Jalvo & Andrews, 2016 ; Greenfield, 2013): four humeri, one ulna, one pelvis, four femurs, seven tibiotarsi (Figure 7A-B), and one tarsometatarsus. Since the introduction of domestic fowl in Belgium dates back at the earliest to the Iron Age (800–57 BC), these marks must be considered post-prehistoric (Goffette et al., 2019), which is further supported by the use of metal tools. One femur specimen shows pronounced scraping marks on the cranial, medial, and caudal faces (Figure 7C). It was roughly sawed through the middle of the bone, primarily from the cranial face. These actions were likely aimed at exploiting the bone as raw material.

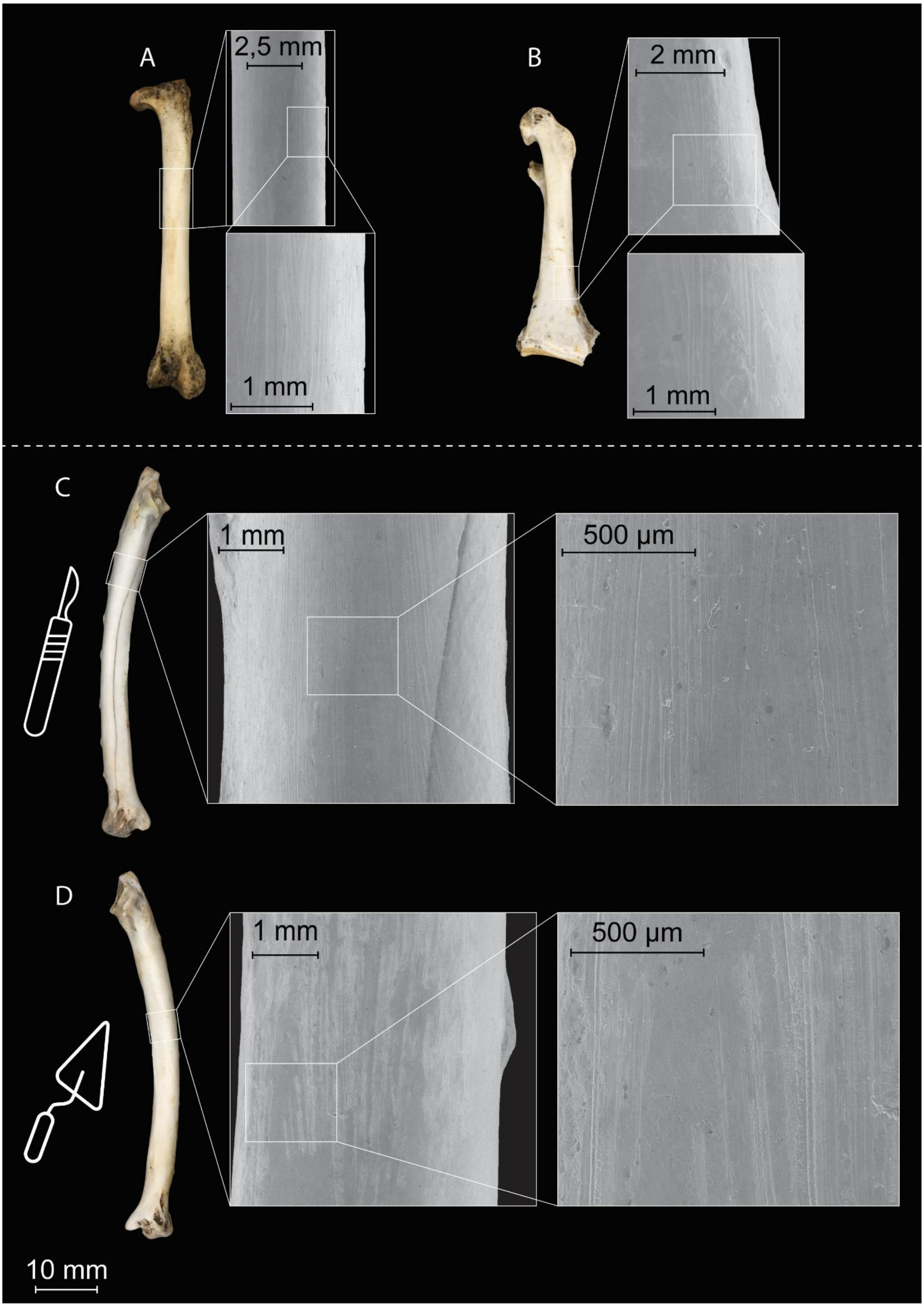

Figure 6. Above (**A-B**). Archaeological specimens from Trou du Frontal. Bones with scraping marks interpreted as having been made with metal tools around the time of the excavation. **A.** Rook, left femur (IRSNB Av 0240). **B.** Common wood pigeon, left coracoid (IRSNB Av 0231). Below (**C-D**).

Scraping marks produced during the experiment. Modern ulnae of feral rock pigeon scraped with metal scalpel (**C**) and trowel (**D**).

4.2.3.2.3. Archaeological marks from stone tool

Six specimens show tool marks compatible with exploitation during the Magdalenian, based on the morphology of the observed marks and/or the taxa involved (Table 2).

The distal part of a snowy owl ulna shows four groups of incisions next to the papillae remigales caudales, suggesting feather extraction (Figure 7C). This element also exhibits scraping marks, likely resulting from bone working. The complex and unusual (semi-lunar) shape of the fracture at the distal end may have been produced during the use of the object and could have extended from a perforation initially present on the distal articular surface, although this cannot be stated with certainty. A fragment of an ulna from a goose-sized bird (Figure 7D) shows deep scraping marks, particularly near the papillae remigales caudales, suggesting remiges removal and/or smoothing of the papillae. A fragment of the tibiotarsus from a large bird, possibly a goose, shows intense scraping (Figure 7E). Two deep longitudinal grooves, one on the cranial face and the other on the caudal face, were likely made to split the bone for splinters. In our view, the intensity of the scraping observed on these three bones is better explained by bone working than by meat removal alone, as demonstrated in previous experiments (Goffette et al., 2023). Therefore, these marks should not be interpreted as solely indicative of butchery activities.

Three specimens show marks consistent with butchery activities related to meat removal, made with lithic tools. A merganser coracoid displays scraping marks on the medial face below the proximal joint (Figure 8A). A ptarmigan coracoid shows short, superficial, oblique scraping marks below the proximal joint on the caudal face (Figure 8B). While trampling cannot be entirely ruled out due to the superficial nature of these marks, their orientation and location align with butchery marks observed on ptarmigan bones from La Vache cave (Laroulandie, 2000), suggesting anthropogenic activity.

The third specimen is a common wood pigeon ulna, with deep incisions on the distal part of the medial face (Figure 8C). These marks resemble experimentally produced marks by V. Laroulandie (2001) and similar archaeological marks from Fumane cave, where a yellow-billed chough shows a comparable longitudinal incision at the same location (Figure 3 in Peresani et al., 2011).

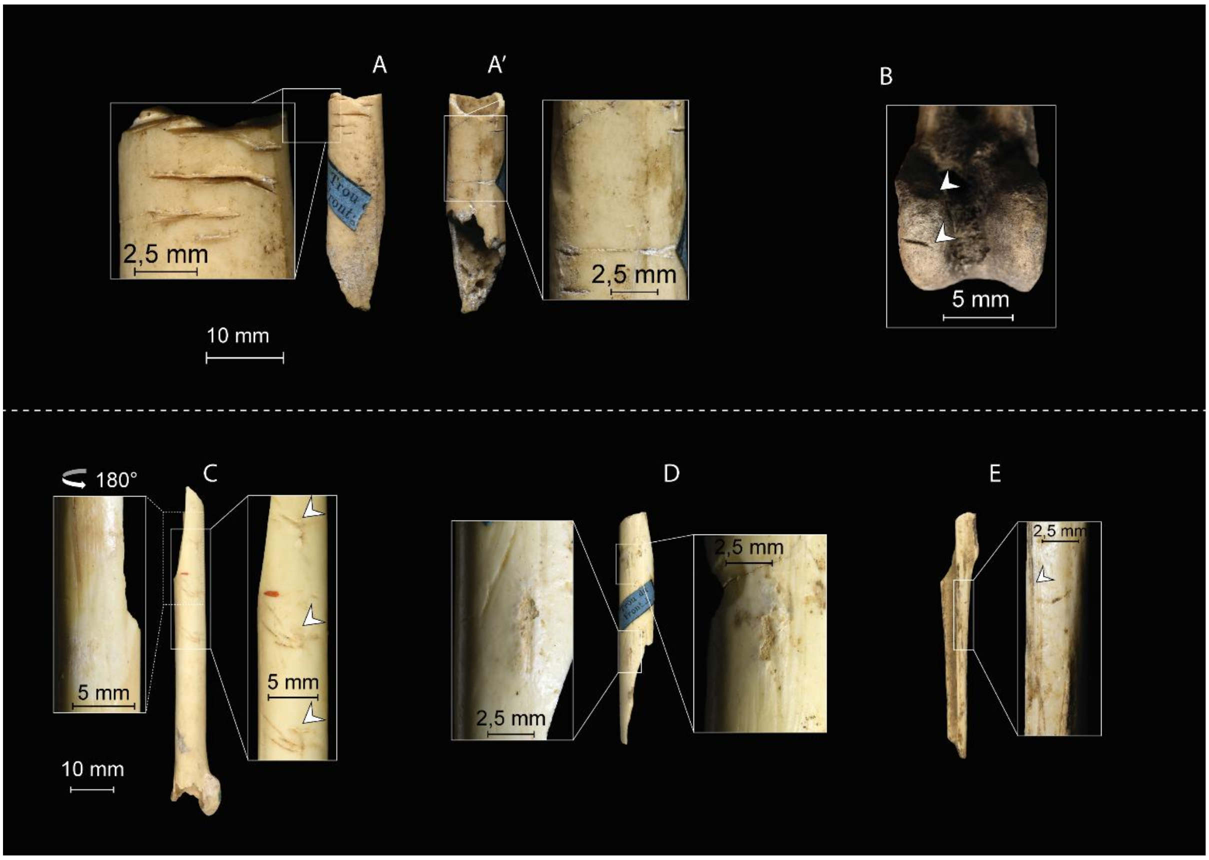

Figure 7. Trou du Frontal. Bones with anthropogenic marks. **A.** Domestic fowl, right femur showing longitudinal scraping marks and transversal sawing, roman period (IRSNB Av 0244). **B**. Domestic fowl, left tibiotarsus with tool marks made with metal tool (IRSNB Av 0246). **C.** Snowy owl, right ulna (IRSNB Av 0235). **D**. Bird of goose size, ulna (IRSNB Av 0245). **C** and **D** show incisions indicating feather extraction and intense scraping marks, interpreted as evidence of bone working. **E**. Goose?, right tibiotarsus showing scraping and longitudinal grooving marks, interpreted as intended for the production of bone rods (IRSNB Av 0247).

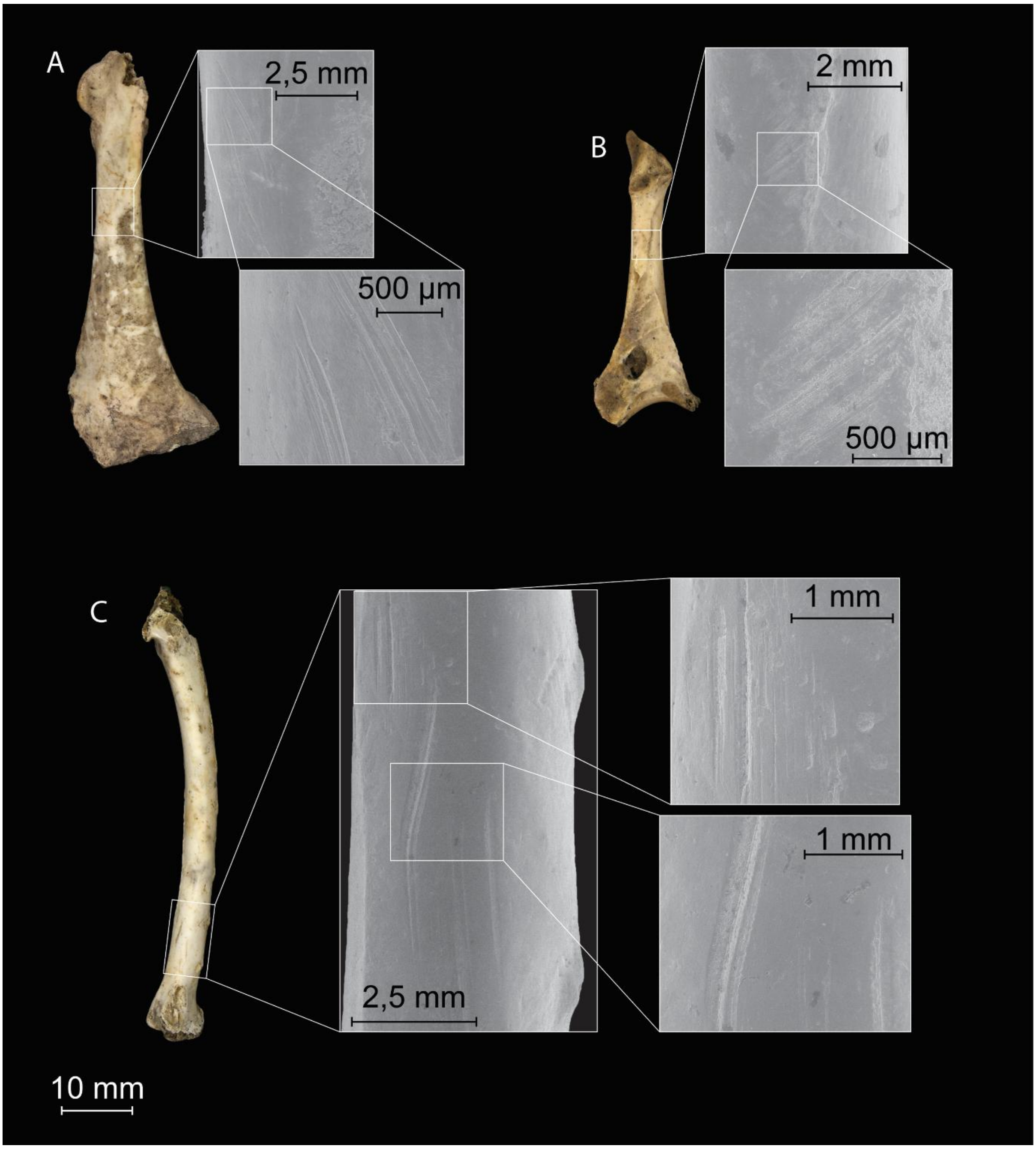

Figure 8. Trou du Frontal. Bones with anthropogenic scraping marks and incisions related to meat removal. **A.** Merganser, right coracoid (IRSNB Av 0229); **B.** Ptarmigan, left coracoid (IRSNB Av 0230); **C.** Common wood pigeon, left ulna (IRSNB Av 0236).

4.2.3.3. Polish

Three pieces bearing anthropogenic marks attributable to the Magdalenian display a polished appearance, likely linked to their handling by humans (Figure 7C-E).

4.2.3.4. Ambiguous marks

Seven (nearly) complete elements show ambiguous marks, making it difficult to attribute them to either human activities or non-human predators. The marks are sharp but shallow incisions, resembling cuts made by lithic tools. However, several factors complicate this attribution: a) these elements come from taxa whose bones frequently display non-human predators marks at the site; b) three show depressions and/or digestive damage, consistent with predator activity; c) on four specimens, the marks are symmetrically arranged on opposite surfaces (bilateral).

Some marks are puzzling in their location and frequency. For example, a woodcock ulna displays groups of transverse or slightly oblique incisions, sometimes arranged symmetrically (Figure 5B). High magnification reveals longitudinal micro-striae inside some incisions, suggesting lithic tool use, though the 'U'-shaped striae are more typical of dull metal tools. Digestion marks are visible at both ends of the bone. Similarly, a tibiotarsus from a blackbird-sized passerine (Figure 5C) shows clear incisions on the distal lateral surface, suggesting disarticulation. While the location aligns with human disarticulation, the marks on the lateral face are unusual for such a small taxon, where disarticulation would typically be straightforward for humans. Again, the incisions are clean but shallow, with a narrow 'U' section.

4.3. Paleoproteomic analysis

We suspected that collagen-based animal glue may have been used to consolidate some of the bone specimens included in this study, as has previously been documented for other collections preserved at the Institute of Natural Sciences (Devièse et al., 2021). This conservation technique was commonly employed for bones in the 19th century (Masschelein-Kleiner, 1995; Schellmann, 2007). Unfortunately, conservation records for many historical collections are incomplete or entirely absent. Because the chemical composition of animal glue is identical to that of endogenous collagen, its presence would go undetected during radiocarbon dating and could result in artificially young dates. In consequence, molecular techniques such as proteomics or ancient DNA analysis are required to detect past conservation treatments and evaluate the suitability of samples for radiocarbon dating.

In this study, we performed paleoproteomic analyses (ZooMS) on all samples to screen for collagen-based glue and verify the taxonomic attribution of the bones (Method in Appendix S5). The results revealed the presence of mammalian collagen in 4 out of 5 samples from Trou des Nutons and in 2 out of 5 from Trou de Chaleux, suggesting that glue derived from mammalian tissues had likely been applied (Table S9). Since it is not possible to separate exogenous collagen-based glue and endogenous collagen, these samples were excluded from AMS dating, and the extracted collagen was archived for potential future research. On a more encouraging note, ZooMS analysis successfully identified a previously indeterminate Galliformes bone as domestic fowl (Figures 7A). Conversely, a ptarmigan bone and a goose-sized bird bone yielded proteomic profiles consistent with the morphological identifications, but their taxonomic resolution could not be refined to the genus or species level (Table S9).

4.4. Radiocarbon dating

New radiocarbon dates have been obtained for the Magdalenian sites in the Lesse Valley.

At Trou de Chaleux, five samples yielded sufficient collagen for radiocarbon dating. Two produced more than 25 mg of collagen and have been archived for future compound-specific dating (Devièse et al., 2018). Of the remaining three other samples, two were identified as containing animal glue and were therefore excluded from dating. Consequently, only one sample was radiocarbon dated at this stage. This sample (Chaleux-12) yielded an age of 12,860 ± 200 BP (Aix-12142.1.1), calibrated to 16,025–14,500 cal BP (95.4% probability) using OxCal v. 4.5 (Bronk Ramsey, 2009) and the IntCal20 calibration curve (Reimer et al., 2020). This result is consistent with previously reported dates for the site (Table S1 and Table S10).

At Trou du Frontal, none of the five samples showed evidence of animal glue contamination, and all yielded sufficient collagen for radiocarbon dating. Two samples (Frontal-2 and Frontal-23) yielded over 25 mg of collagen and were reserved for future compound-specific dating. Samples Frontal-18 and Frontal-19 were each dated twice using the gas ion source of the AMS. Frontal-19 yielded ages of 12,930 ± 180 BP (Aix-12147.1.1) and 12,975 ± 185 BP (Aix-12147.1.2). Because both measurements were obtained from the same collagen extract, they were combined in OxCal using the R-Combine function, resulting in a calibrated age of 16,040–14,945 cal BP (95.4% probability). This age is consistent with previously reported dates for the site (Table S1) and with the date obtained from Trou de Chaleux (Aix-12142.1-1). A domestic fowl femur (Frontal-18; Figure 7A) was also dated twice using the gas ion source of the AMS, producing ages of 1,805 ± 70 BP (Aix-12143.1.1) and 1,790 ± 70 BP (Aix-12143.1.2). As these measurements were obtained from the same collagen extract, they were combined in OxCal to yield a calibrated age of 1,870–1,540 cal BP (95.4% probability), corresponding to the Roman period. Sample Frontal-4, coming from a common wood pigeon ulna, yielded an age of 5,343 ± 27 BP (Aix-12167.1.1), calibrated to 6,270–6,000 cal BP (95.4% probability), corresponding to the Middle Neolithic period (Table S1 and Table S10).

At Trou des Nutons, four out of the five samples unfortunately showed evidence of animal glue contamination. The fifth sample, however, yielded over 100 mg of collagen and will be dated in the future using the compound-specific approach.

5. Discussion

5.1. Taxa and environments

The avian remains from both Trou des Nutons and Trou du Frontal exhibit considerable taxonomic diversity, though their compositions differ. Compared to mammal remains, bird remains at Trou des Nutons are significantly less numerous, representing only 25.2% of the total identified mammal and bird individuals.. In contrast, Trou du Frontal produced a much richer assemblage, surpassing mammals (67.0%).

In both sites, Galliformes (dominated by ptarmigans), Passeriformes, and Anseriformes constitute the majority of the remains. The common wood pigeon is the most represented Columbiformes. Some rarer species, such as the parasitic jaeger and the white-tailed eagle at Trou des Nutons, and the hazel grouse, at least three species of woodpeckers, a large eagle (imperial-sized), the little bustard, and the pine grosbeak at Trou du Frontal, were also identified.

A significant proportion of the avian taxa at both sites are forest-dwelling species, which seem incompatible with the open environments characterising the end of the older Dryas (Heinrich 1 event), suggesting that a substantial part of the assemblages is intrusive and postdates the Magdalenian occupation. At Trou du Frontal, this is particularly evident in the presence of domestic fowl, which alone accounts for more than 13% of the total assemblage. This taxon was introduced during the Iron Age in the region of modern-day Belgium and is therefore not associated with human activities during the Palaeolithic (Goffette et al., 2019). By contrast, open-habitat taxa such as grey partridge, corn crake, common quail, and little bustard are present and correspond well to the open environmental conditions prevailing at the end of the Older Dryas. At the same time, the presence of cold-adapted species such as the rock ptarmigan (both sites), snowy owl, and pine grosbeak (Trou du Frontal) supports the notion that at least part of the assemblages is contemporaneous with the Magdalenian occupation.

5.2. Taphonomic processes and accumulating agents

The accumulation of bird remains at both sites results from multiple processes. A significant portion appears to have been deposited by non-human predators, primarily raptors, but also small carnivores. The scarcity of fragile elements, such as skulls and ribs, could be attributed to differential preservation in the sediment or the activity of certain non-human predators. Indeed, the skull and mandible are often underrepresented in assemblages associated with various raptors, such as the Eurasian eagle-owl (Bocheński, 2005). Similarly, the underrepresentation of the scapula in wild taxa at Trou du Frontal aligns with patterns commonly observed in accumulations resulting from avian predators (Bocheński, 2005). The dissolution damage observed on the material from both caves is interpreted as digestive damage caused by predators. The frequency and low intensity of the observed alterations exclude carnivores and correspond well to the damage produced by owls (Category 1 *sensu* Andrews, 1990), supporting the above-mentioned hypothesis. At Trou du Frontal, shallow, sharp incisions of ambiguous origin with a 'U'-shaped cross-section and micro-striations (Figure 5B-C) are interpreted as raptor beak marks due to their bilateral arrangement and frequent association with digestion marks. They could have been produced by raptors consuming meat or plucking feathers (Figure 5B) or while cutting through joints to ingest portions of prey carcasses (Figure 5C). Similar marks found at the Sima del Elefante site in Spain have been interpreted in the same way (Marqueta et al., 2023).

Additionally, archaeological excavation biases may have influenced the composition of the assemblages, as some bird bones may not have been collected during excavation or were subsequently lost or discarded, particularly at Trou des Nutons. The underrepresentation of very small elements (e. g. phalanges, carpal bones) at both sites could be attributed to collection methods or a selective sorting process favouring the preservation of more diagnostic elements. At Trou du Frontal, approximately 5% of bird bones exhibit scraping marks likely caused by metal tools during or shortly after excavation, complicating the identification of prehistoric anthropogenic modifications due to their morphological similarity. Furthermore, metal-cutting tool marks and burning traces on domestic fowl bones relate to human activity during historical periods. Radiocarbon dating proved that at least one domestic fowl femur (Figure 7A) has been exploited during the Roman period (Table S1).

5.3. Evidence of Magdalenian exploitation of birds

The absence of sieving during the excavation of these two sites represents a clear limitation in reconstructing the role of birds in Magdalenian food procurement, as small bird bones were likely missed during fieldwork. However, the hand collection appears to have been conducted with considerable care, at least at Trou du Frontal. When excluding intrusive and historically modified specimens, the number of bones bearing traces of Magdalenian human activity is low at both sites, with eight specimens at Trou des Nutons and five at Trou du Frontal.

At Trou des Nutons, flight feathers were extracted from an ulna and possibly from a carpometacarpus of goose. Additionally, an ulna and a radius of goose, both bearing scraping marks, display significant polish on fracture edges, which result from their use as tools for as yet unidentified purposes. Cut marks indicative of butchery were identified on geese, ptarmigan, black grouse, and crow bones in this site.

At Trou du Frontal, bird bones have been used as raw material for manufacturing artifacts. A snowy owl ulna was exploited for the production of a tubular object, while rods were extracted from a goose-sized bird tibiotarsus, possibly intended for making needles, several specimens of which were recovered from the site. It is likely that bones from these large species were selectively chosen for crafting and transported to the cave specifically for processing, as indicated by the strongly uneven skeletal representation. Remains of merganser and ptarmigan show evidence of consumption. These species were likely introduced to the site as (sub-) complete carcasses. Although a common wood pigeon ulna bearing cut marks produced by stone tools was found in the assemblage, the exploitation of this taxon during the Magdalenian remained uncertain. While this species has already been identified—alongside other taxa with present-day temperate affinities—in a cold-stage assemblage from Pin Hole Cave, England (MIS 3; Stewart & Jacobi, 2015), its occurrence in a periglacial context appeared questionable. A radiocarbon date was therefore obtained on this specimen. The result confirms that it is not associated with Magdalenian occupation, as it yielded a calibrated age of 6,270–6,000 cal BP, corresponding to the Middle Neolithic period.

In summary, while both sites exhibit clear evidence of bird exploitation during the Magdalenian, the anthropogenic traces are proportionally scarce, mainly due to significant post-Magdalenian intrusions. The main activities involving birds in the Prehistory included feather extraction, bone modification for tool production, and butchery and meat consumption.

5.4. Bird exploitation in the Magdalenian at local and regional scales

The exploitation of birds during the Magdalenian exhibits significant similarities across both sites presented here and the close-by Trou de Chaleux, which presents the richest and most homogeneous assemblage. At Trou de Chaleux, large anatids—geese and swans—were the primary birds exploited, represented mainly by wing bones (Goffette et al., 2020). Geese were processed for the extraction of remiges, and the humeri, radii, and ulnae were used as raw materials in bone industry to produce tubes, which were sometimes used as tool or as matrix for preparing bone rods, likely intended for needle production. This interest in goose wing bones is also evident in the assemblages from Trou des Nutons, where remiges and possibly meat were extracted. Duck was consumed at Trou de Chaleux and Trou du Frontal, and ptarmigan at all three sites. Snowy owl meat was consumed at Trou de Chaleux, whereas at Trou du Frontal, this species was exploited for feather extraction, and an ulna was worked to produce a tube, likely similar to those crafted from goose ulnae at Trou de Chaleux (figure 5 in Goffette et al., 2020). This site also yielded an additional fragment of a goose-sized bird worked to produce bone rods, as at Trou de Chaleux.

These three sites in the Lesse Valley, which are geographically and chronologically close, provide evidence of diverse avian-related activities. Reflecting the scale of the occupation, Trou de Chaleux, which served as a base camp for long-term occupation or repeated stays (Charles, 1998 ; Otte, 1994), yielded evidence of varied bird exploitation: food, feathers, bone craft, and symbolic activities. In contrast, bird exploitation appears to have been much more limited at the other two sites, though still diverse. At Trou des Nutons, birds were consumed, their feathers extracted, and some specimens have been used as tools. Trou du Frontal also provides evidence of bird consumption, feather extraction, and bone modification for craft activities. Ultimately, only the symbolic use of birds appears unique to Trou de Chaleux.

Trou du Frontal and Trou des Nutons also share common traits with contemporaneous Magdalenian assemblage outside the Lesse Valley, such as Bois Laiterie cave, Belgium (~15,000 cal BP), located about 20 km to the northwest (Straus, 1997), and Pincevent, France (15,500–13,000 cal BP; Debout et al., 2014), where large birds have been exploited as raw material to produce bone tubes and rods (David et al., 2014). At Verberie, France (15,900 and 13,900 cal BP; Enloe & Audouze, 2010), birds were exploited solely for food (Mignard, 2015). Further east, the Magdalenian sites of Gönnersdorf and Andernach-Martinsberg, Germany (ca. 15,600 cal BP; Street & Turner, 2016), exhibit numerous similarities in bird exploitation, especially the interest in long wing bones of large Anseriformes.

6. Conclusion

The new data obtained from Trou des Nutons and Trou du Frontal provide valuable insights into avian exploitation and, more broadly, human activities during the Magdalenian in the Lesse Valley. The evidence attest to the multifaceted use of birds for their meat and feathers, and as raw material for crafting tubular objects, some of which served as tools or were transformed into bone rods. These findings both confirm and extend previous results from Trou de Chaleux, the primary Magdalenian site in the region.

This study also underscores the limitations inherent to historical collections. The assemblages present a chronological mix resulting from accumulations by various agents over different periods of time, including small carnivores, birds of prey, and humans and are further affected by 19th century excavation techniques and curatorial practices (e.g., no sieving performed, selective recovery, post-excavation modifications, and contamination with modern conservation materials). Consequently, the proportion of bird remains that can be confidently attributed to Magdalenian human activity remains limited.

Future research could focus on analysing the polish observed on several specimens to improve interpretations of their use. In addition, the currently limited experimental dataset on scraping marks produced with metal tools should be expanded to better understand the variability of these marks and to confirm—or challenge—our current interpretation that they were produced during or shortly after excavation.

Despite several challenges, these old collections hold irreplaceable value. Beyond their archaeological relevance, they offer substantial potential for advancing our understanding of past avian diversity and human-bird interactions.

Bibliography

Andrews, P. (1990). *Owls, caves and fossils: predation, preservation and accumulation of small mammal bones in caves, with an analysis of the Pleistocene cave faunas from Westbury-Mendip, Somerset, UK*. London: Natural History Museum.

Bard, E., Tuna, T., Fagault, Y., Bonvalot, L., Wacker, L., Fahrni, S., & Synal, H.-A. (2015). AixMICADAS, the accelerator mass spectrometer dedicated to 14C recently installed in Aix-en-Provence, France. *Nuclear Instruments and Methods in Physics Research Section B: Beam Interactions with Materials and Atoms*, 361, 80-86.

Barisic, M. (2006). *Étude de l'effet du piétinement humain sur des ossements de faune mélangés à un amas de taille*. Master thesis, Université Bordeaux 1, UMR PACEA 5199, Sciences et Technologies: Anthropologie Biologique, Paléoanthropologie et Préhistoire.

Baumel, J. J. (1993). *Handbook of avian anatomy: nomina anatomica avium* (Vol. 23) (Publications of the Nuttall Ornithological Club). Cambridge.

Behrensmeyer, A. K. (1978). Taphonomic and Ecologic Information from Bone Weathering. *Paleobiology*, 4 (2), 150-162.

Behrensmeyer, A. K., Stayton, C. T., & Chapman, R. E. (2003). Taphonomy and Ecology of Modern Avifaunal Remains from Amboseli Park, Kenya. *Paleobiology*, 29 (1), 52-70.

Binford, L. R. (1968). Post-Pleistocene adaptations. In L. R. Binford & S. R. Binford (Eds.), *New Perspectives in Archaeology*. Chicago.

Blasco, R., & Peris, J. F. (2009). Middle Pleistocene bird consumption at Level XI of Bolomor Cave (Valencia, Spain). *Journal of Archaeological Science*, 36 (10), 2213-2223.

Bocheński, Z. M. (2005). Owls, diurnal raptors and humans: signatures on avian bones. In T. O'Connor (Ed.), *Biosphere to Lithosphere. New studies in vertebrate taphonomy*. Oxford: Oxbow Books, pp. 31–45.

Bocheński, Z. M., Tomek, T., & Wertz, K. (2009). The State of Preservation of Bird Remains in a Cave Environment: A Case Study from Ciemna Cave (Poland). *Acta zoologica cracoviensia*, 52 (1-2), 1-16.

Bocheński, Z. M., Wertz, K., & Tomek, T. (2018). What happens to dead birds left in a cave and its vicinity for a quarter of a century? A taphonomic experiment. *Historical Biology*, 30 (6), 855-867.

Bronk Ramsey, C. (2009). Bayesian Analysis of Radiocarbon Dates. *Radiocarbon*, 51 (1), 337-360.

Charles, R. (1996). Back into the north: the radiocarbon evidence for the human recolonisation of the north-western Ardennes after the last glacial Maximum. *Proceedings of the Prehistoric Society*, 62, 1-17.

Charles, R. (1998). *Late Magdalenian chronology and faunal exploitation in the North-Western Ardennes* (BAR International Series, 737). Oxford: Archeopress.Cohen, K. M., & Gibbard, P. L. (2019). Global chronostratigraphical correlation table for the last 2.7 million years, version 2019 QI-500. *Quaternary International*, 500, 20-31.

David, F., Enloe, J., Mourer-Chauviré, C., & Bignon-Lau, O. (2014). La faune : espèces chassées, consommées ou utilisées. In M. Julien & C. Karlin (Eds.), *Un automne à Pincevent. Le campement magdalénien du niveau IV20*. Paris: Société préhistorique française, pp. 77-80.

Debout, G., Valentin, B., Leesch, D., Bodu, P., Dumarçay, G., Schoch, W., & Thiébault, S. (2014). Pincevent et la chronologie du Magdalénien septentrional. Nouveaux éléments au débat. In M. Julien & C. Karlin (Eds.), *Un automne à Pincevent. Le campement magdalénien du niveau IV20*. Paris: Société préhistorique française, pp. 49-60.

Devièse, T., Abrams, G., Hajdinjak, M., Pirson, S., De Groote, I., Di Modica, K., Toussaint, M., Fischer, V., Comeskey, D., Spindler, L., Meyer, M., Semal, P., & Higham, T. (2021). Reevaluating the timing of Neanderthal disappearance in Northwest Europe. *Proceedings of the National Academy of Sciences*, 118 (12), e2022466118.

Devièse, T., Comeskey, D., McCullagh, J., Bronk Ramsey, C., & Higham, T. (2018). New protocol for compound-specific radiocarbon analysis of archaeological bones. *Rapid Communications in Mass Spectrometry*, 32 (5), 373-379.

Dewez, M. (1987). *Le Paléolithique supérieur récent dans les grottes de Belgique* (Publication d'Histoire de l'Art et d'Archéologie de l'Université Catholique de Louvain, 57). Louvain-la-Neuve.

Domínguez-Rodrigo, M., de Juana, S., Galán, A. B., & Rodríguez, M. (2009). A new protocol to differentiate trampling marks from butchery cut marks. *Journal of Archaeological Science*, 36 (12), 2643-2654

Dupont, E. (1872). *L'Homme pendant les âges de la pierre dans les environs de Dinant-sur-Meuse*. Bruxelles: Muquardt.

Enloe, J. G., & Audouze, F. (2010). The Magdalenian site of Verberie (Le Buisson Campin): An overview. In E. Zubrowe, F. Audouze, & J. G. Enloe (Eds.), *The Magdalenian Household. Unraveling Domesticity*. New-York: State University of New-York, pp. 15-21.

Fernández-Jalvo, Y., & Andrews, P. (2016). *Atlas of Taphonomic Identifications* (Vertebrate Paleobiology and Paleoanthropology): Springer.

Flannery, K. (1969). Origins and ecological effects of early domestication in Iran and the Near East. In P. J. Ucko & G. W. Dimbleby (Eds.), *The domestication and exploitation of plants and animals*. Chicago: Aldine, pp. 73-100.

Gill, F., Donsker, D., & Rasmussen, P. (2022). IOC World bird list (v 12.1).

Goffette, Q., Ervynck, A., & Van Neer, W. (2019). Have birds ever mattered? An evaluation of the contribution of avian species to the archaeozoological record of Belgium (Iron Age to recent times). *Archaeological and Anthropological Sciences*, 11, 6353–6369.

Goffette, Q., Germonpré, M., Lefèvre, C., Brecko, J., Goemaere, E., & Rots, V. (2020). Bird bones from Trou de Chaleux and the human exploitation of birds during the late Magdalenian in Belgium. *Journal of Archaeological Science: Reports*, 29, 102096.

Goffette, Q., Lepers, C., Jadin, I., & Rots, V. (2023). A handful of duck radiuses: Peculiarities of the avifaunal exploitation at the Gravettian site of Maisières-Canal (Belgium). *International Journal of Osteoarchaeology*, 33 (4), 668-682.

Greenfield, H. J. (2013). “The Fall of the House of Flint”: A Zooarchaeological Perspective on the Decline of Chipped Stone Tools for Butchering Animals in the Bronze and Iron Ages of the Southern Levant. *Lithic Technology*, 38 (3), 161-178.

Laroulandie, V. (2001). Les traces liées à la boucherie, à la cuisson et à la consommation d'oiseaux. Apport de l'expérimentation. In L. Bourguignon, I. Ortega, & M.-C. Frère-Sautot (Eds.), *Préhistoire et approche expérimentale*. Montagnac: Editions Monique Mergoil, pp. 97-108.

López-González, F., Grandal-d'Anglade, A., & Vidal-Romaní, J. R. (2006). Deciphering bone depositional sequences in caves through the study of manganese coatings. *Journal of Archaeological Science*, 33 (5), 707-717.

Lyman, R. L. (1994a). Quantitative units and terminology in zooarchaeology. *American Antiquity*, 59 (1), 36-71.

Lyman, R. L. (1994b). *Vertebrate taphonomy* (Cambridge manuals in archaeology). Cambridge: Cambridge University Press.

Marqueta, M., Huguet, R., & Núñez-Lahuerta, C. (2023). Accumulation agents and bird assemblages: the case of the TE9d level at Sima del Elefante (Sierra de Atapuerca, Spain). *International Journal of Osteoarchaeology*, 33, 652-667.

Masschelein-Kleiner, L. (1995). *Ancient Binding Media, Varnishes and Adhesives*. Rome: A & J Servizi Grafici Editoriali.

Mignard, M. (2015). *L'exploitation des oiseaux à Verberie. Quelle place pour l’avifaune dans les stratégies de subsistance magdaléniennes ?* Mémoire de master, Université de Paris I - Panthéon Sorbonne, Histoire de l'art et Archéologie.

Otte, M. (1994). *Le Magdalénien du Trou de Chaleux (Hulsonniaux, Belgique)* (ERAUL, 60). Liège.

Peresani, M., Fiore, I., Gala, M., Romandini, M., & Tagliacozzo, A. (2011). Late Neandertals and the intentional removal of feathers as evidenced from bird bone taphonomy at Fumane Cave 44 ky B.P., Italy. *Proceedings of the National Academy of Sciences*, 108 (10), 3888-3893.

Reimer, P. J., Austin, W. E. N., Bard, E., Bayliss, A., Blackwell, P. G., Bronk Ramsey, C., Butzin, M., Cheng, H., Edwards, R. L., Friedrich, M., Grootes, P. M., Guilderson, T. P., Hajdas, I., Heaton, T. J., Hogg, A. G., Hughen, K. A., Kromer, B., Manning, S. W., Muscheler, R., Palmer, J. G., Pearson, C., van der Plicht, J., Reimer, R. W., Richards, D. A., Scott, E. M., Southon, J. R., Turney, C. S. M., Wacker, L., Adolphi, F., Büntgen, U., Capano, M., Fahrni, S. M., Fogtmann-Schulz, A., Friedrich, R., Köhler, P., Kudsk, S., Miyake, F., Olsen, J., Reinig, F., Sakamoto, M., Sookdeo, A., & Talamo, S. (2020). The IntCal20 Northern Hemisphere Radiocarbon Age Calibration Curve (0–55 cal kBP). *Radiocarbon*, 62 (4), 725-757.

Romero, A. J., Díez, J. C., Rodríguez, L., & Arceredillo, D. (2016). Anthropic fractures and human tooth marks: An experimental approach to non-technological human action on avian long bones. *Quaternary International*, 421, 219-227.

Schellmann, N. C. (2007). Animal glues: a review of their key properties relevant to conservation. *Studies in Conservation*, 52 (sup1), 55-66.

Serjeantson, D. (2009). *Birds* (Cambridge Manuals in Archaeology). Cambridge: Cambridge University Press.

Simkiss, K. (1961). Calcium metabolism and avian reproduction. *Biological Reviews*, 36 (3), 321-359.

Sponheimer, M., Ryder, C. M., Fewlass, H., Smith, E. K., Pestle, W. J., & Talamo, S. (2019). Saving Old Bones: a non-destructive method for bone collagen prescreening. *Scientific Reports*, 9 (1), 13928.

Stevens, R. E., Germonpré, M., Petrie, C. A., & O'Connell, T. C. (2009). Palaeoenvironmental and chronological investigations of the Magdalenian sites of Goyet Cave and Trou de Chaleux (Belgium), via stable isotope and radiocarbon analyses of horse skeletal remains. *Journal of Archaeological Science*, 36 (3), 653-662.

Stewart, J. R., & Jacobi, R. M. (2015). The long term tesponse of birds to climate change: new results from a cold dtage avifauna in Northern England. *PLoS ONE*, 10 (5), e0122617.

Stiner, M. C. (2001). Thirty years on the "Broad Spectrum Revolution" and paleolithic demography. *Proceedings of the National Academy of Sciences*, 98 (13), 6993-6996.

Stiner, Mary C., Munro, Natalie D., & Surovell, Todd A. (2000). The tortoise and the hare: small-game use, the Broad-Spectrum Revolution, and Paleolithic demography. *Current Anthropology*, 41 (1), 39-79.

Straus, L. G. (1997). La grotte du Bois Laiterie: the site, stratigraphy, chronology and excavations. In M. Otte & L. G. Straus (Eds.), *La grotte du Bois Laiterie* (ERAUL, 80). Liège, pp. 25-64.

Street, M., & Turner, E. (2016). Eating crow or a feather in one's cap: the avifauna from the Magdalenian sites of Gönnersdorf and Andernach-Martinsberg (Germany). *Quaternary International*, 421, 201-218.

Vincke, D., Miller, R., Stassart, É., Otte, M., Dardenne, P., Collins, M., Wilkinson, K., Stewart, J., Baeten, V., & Fernández Pierna, J. A. (2014). Analysis of collagen preservation in bones recovered in archaeological contexts using NIR Hyperspectral Imaging. *Talanta*, 125, 181-188.

von den Driesch, A. (1976). *A guide to the measurement of animal bones from archaeological sites* (Peabody Museum Bulletin, 1). Harvard.