Article

Who Killed the Small Mammals of Ittenheim (Northeastern France)? An Integrative Approach and New Taphonomic Data for Investigating Bone Assemblages Accumulated by Small Carnivores

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Abstract: Small carnivores are susceptible to regularly accumulating small- to medium-sized mammal remains in both natural and archaeological sites. However, compared to nocturnal birds of prey, these accumulations are still poorly documented and are generally based on a limited number of samples, including those of relatively small size. Here, we present an analysis of European hamster remains from a rescue excavation at Ittenheim (Bas-Rhin, Grand-Est, France), which were recovered from an infilled burrow, three meters below the current surface. The remains are well preserved and exhibit large proportions of tooth marks. Comparisons with a new and existing reference collection combined with an analysis of all recovered faunal remains suggest the accumulation reflects the action of young red foxes. This is supported by the fact that, although these young individuals leave teeth mark, they do not necessarily consume all parts of medium-sized prey species, including the European hamster. Conversely, the remains of smaller rodents, such as microtine, show distinct patterns of digestion and tooth marks. Carnivore bone accumulations from scats are generally poorly preserved; however, our results demonstrate prey size plays a major role, both qualitatively and quantitatively, in skeletal representation, bone preservation, and bone surface modifications. The present paper underlines the need for more diversified taphonomic reference collections based on an integrative approach designed to evaluate multi-taxa accumulations.

Keywords: burrow; fossil record; multi-taxa approach; small carnivore accumulations; small mammals; European hamster; taphonomy

1. Introduction

Small- and medium-sized mammal fossil remains are regularly preserved in both archaeological and palaeontological sites and can result from series of complex processes. Over the last 40 years, numerous taphonomic studies have investigated faunal assemblages and associated bone modifications in order to characterise each possible scenario responsible for these accumulations (e.g., [1–7], including bone collectors [8–10], human predation and consumption [11–19], and attritional or accidental-natural mortality [20]. Among these potential scenarios, while accumulations by mammalian carnivores are regularly cited [3,21–25], there is a paradoxical lack of detailed analyses, and studies are often limited to specific questions. In a recent synthesis, Denys and Cochard [24] listed a number of taphonomic studies based on reference collections; however, the comparative material for each predator is generally small and limited to few taxa. For instance, no reference collections are currently available for the least weasel (*Mustela nivalis*) or stoat (*Mustela erminea*),

despite these species being specialist predators who capture small prey in their tunnels, and store food in reserves [26]. Beyond the predators involved, reference collections do not routinely include sufficiently representative numbers of individuals or remains, often less than 10 individuals [27–30]. Furthermore, reference collections that intend to characterise accumulations of small-sized prey equally remain limited. For instance, among the eight listed by Denys and Cochard [24] for red foxes (*Vulpes vulpes*), only one concerns rodents [31], with the rest focusing on larger prey species, such as lagomorpha and/or birds [32–36]. This is important as prey size has a major influence on the traces left on bone remains [3,33,37–39]. Studies focusing on the taphonomy of small mammal remains are also rare [40–45], especially for European species [18,31,38,46], and often mix rodent species of different sizes [44]). Although the remains of small- and medium-sized mammals from archaeological sites do not necessarily result from the same processes, it is critical to develop multi-taxa approaches to decipher taphonomic issues [47].

Recent rescue excavation in Ittenheim (Alsace, France) recovered numerous small mammals from a burrow, including the European hamster, associated with small numbers of leporid and microtine (voles, wood mice) remains. Here, we explore whether this accumulation reflects attritional mortality or the action of carnivores based on data from three new reference collections of small mammal remains, two recovered from fox or badger dens (Bettant I and VIII, Ain, France) and one from a rabbit warren (Les Six Chemins, Charente, France).

2. Material and Methods

2.1. Description of Sites

Ittenheim is located in the Bas-Rhin region (Figure 1) and was the subject of rescue excavations carried out by the French National Institute for Preventive Archaeological Research (INRAP) in 2019 as part of a highway development project [48]. A deep sounding of 7 m was sunk in order to better contextualise fossil faunal remains recovered from the site's Pleistocene levels. Very few remains of large mammals were collected throughout the sequence, whereas no lithic material was identified [48]. Chronology of Ittenheim is still preliminary, mainly based on sedimentary correlations with local sequences. This loess sequence could have recorded discontinuously, due to many erosion processes, a time interval beginning from at least 350 ky (and possibly from 400 ky). The upper part of this loess deposit is attributed to the Weichselian glaciation (MIS 4-2), above a first paleosol correlated to the Eemian in-terglacial (MIS 5) [48]. Yet, no reliable OSL date have been obtained up to now. Approximately 3 m below the surface (172 m a.s.l.), in level 3, a burrow containing a large quantity of small mammal remains was identified in the loess deposits. No radiocarbon date on this bone material has been realized. The infill of the burrow was water sieved using two superimposed meshes (2.0 and 0.5 mm).

Bettant I and VIII are two morden spoil heaps from red fox (*Vulpes vulpes*) and badger (*Meles meles*) burrows, both of which yielded large faunal assemblages (approximately 5000 remains each). The remains of medium-sized mammals and *Talpa* sp. were studied as part of a previous taphonomic analysis [37,49]. For the present study, the remains of additional small mammals (rat, hedgehog, shrew, and vole) were collected following the water sieving of more than 500 litres of sediments from Bettant I and about 600 litres from Bettant VIII sediment using a 1.8 mm mesh, and analysed.

Les Six Chemins (LSC) is a morden rabbit warren in southwest France (Gensac-la-Pallue, France), which was excavated in 2015 using modern archaeological methods in order to provide taphonomic criteria for the identification of attritional death signatures in fossil accumulations [20,50] The remains of several small mammals demonstrate that the Les Six Chemins warren has supported trogloxene species. For this study, we recorded taphonomic data from small mammal bones recovered from all sedimentary units [20], totalling 2346 litres of sediments, wet-sieved with a 1.6 mm mesh. The warren lies approximately 100m from a fox den (*Vulpes vulpes*), where the remains of 15 rabbits were recovered, including seven with carnivore marks (tooth marks), in loose anatomical connection within

a 40 m radius of the den. While this association of warrens and fox dens is relatively common [51,52], no visible evidence of the presence of foxes or other predators was noted in the excavated area.
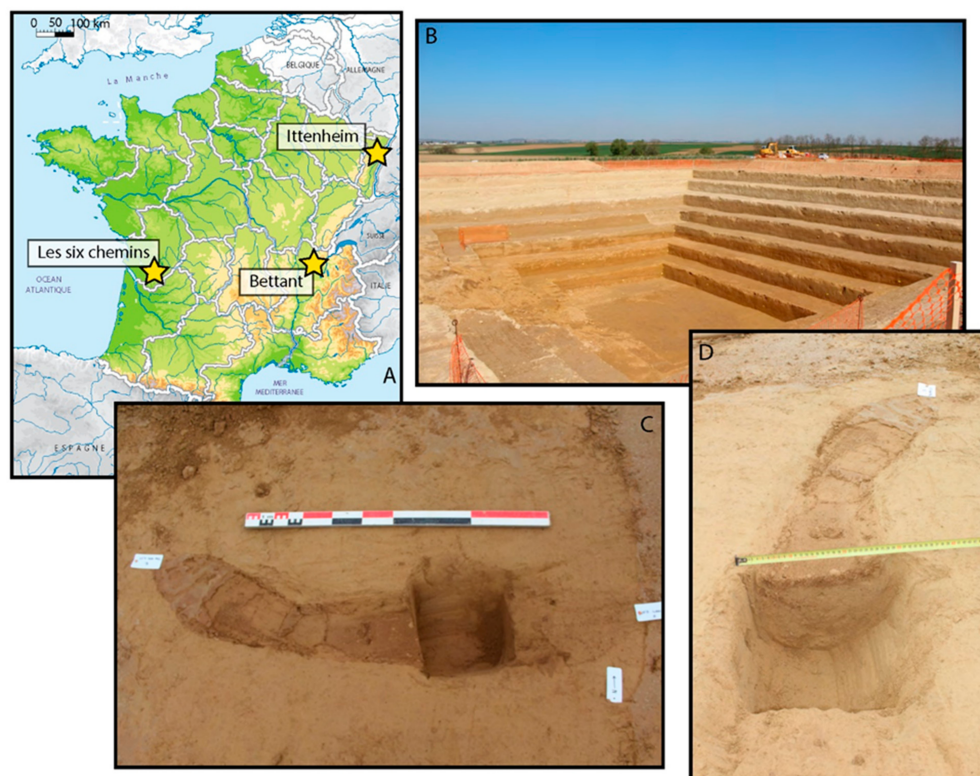
Figure 1. (**A**) Maps showing the locations of Ittenheim, Bettant, and Les Six Chemins; (**B**) excavations at Ittenheim; and (**C,D**) the Ittenheim burrow.

2.2. Taxonomic Identification

As recently demonstrated (e.g., [37–39]), prey size does matter, and is a key factor for interpreting the traces left on bones by predators. Accordingly, bone remains were assigned to four size categories: (1) leporids and fox; (2) hamster, rat, muskrat, and hedgehog; (3) larger voles (*Arvicola amphibius* and *A. sapidus*); and (4) smaller voles and mice, including *Microtus* sp., *Clethrionomys glareolus*, and *Apodemus* sp. Species were identified with reference to modern vertebrate collections curated at the Biogéosciences Laboratory of the Université Bourgogne Franche-Comté and at the PACEA Laboratory of the University of Bordeaux, France. The age-at-death of fox remains was estimated using the data previously published by Harris [53], which is based on tooth eruption and the closure of bone epiphysis. For hare, we used the same criteria as in Pelletier et al. [54], which are mainly based on long-bone epiphysis fusion.

2.3. Anatomical Representation, Bone Breakage, and Surface Modifications

Skeletal part representation was calculated primarily from the principal long bones: humerus (HUM), radius (RAD), and ulna (ULNA) for the forelimb; and the femur (FEM) and tibia (TIB) for the hindlimb; as well as the coxal bone (PELVIS), hemi-mandibles (MAND), maxillary (MAX), and vertebrae (VERT). Radial, carpal, metacarpal, tarsal, metatarsal, phalange, and rib fragments were excluded when calculating the number of identified skeletal elements (NISP) to simplify the approach and make the analysis more efficient (see [30] for more details). The relative abundance of skeletal elements [3,55] was calculated using the following formula:

$$Ri = MNEi/(MNI \times E) \times 100 \tag{1}$$

In which Ri is the relative abundance of element i, MNEi is the minimum number of skeletal elements i, MNI is the minimum number of individuals based on the greatest number of any single element in the assemblage, and E is the number of elements i in the prey skeleton.

In addition, the proportions of skeletal elements were evaluated using the two ratios originally proposed by Andrews [3] but slightly modified in order to ensure statistical rigor in calculating the confidence intervals [20,30,56] that take into account discarded bone elements:

$$-\textbf{AN}/\textbf{PO\%} = (\text{HUM} + \text{ULNA})/(\text{HUM} + \text{ULNA} + \text{FEM+TIB}) \times 100 \qquad (2)$$

where **AN** represents the number of bones from the anterior limbs, and **PO** is the number of bones of the posterior limbs:

$$-\textbf{CRA}/\textbf{POSTCRA\%} = \text{MAND} \times 2/(\text{MAND} \times 2 + \text{HUM} + \text{FEM}) \times 100 \qquad (3)$$

where **CRA** refers to the cranial elements and **POSTCRA** to the postcranial elements:

$$-\textbf{Z}/\textbf{E\%} = (\text{TIB} + \text{ULNA})/(\text{TIB} + \text{ULNA} + \text{FEM} + \text{HUM}) \times 100 \qquad (4)$$

where **Z** represents zygopodia (tibiae and ulnae) and **E** is stylopodia (femora and humeri).

All calculations produced values between 0 and 100. For instance, the absence of cranial or postcranial elements would produce a **CRA/POSTCRA%** value of 0 or 100, respectively, whereas the **CRA/POSTCRA%** would be around 50 when similar numbers of these different elements were recorded. These modifications allow a 95% confidence interval to be calculated from a binomial test.

The degree of bone breakage was calculated to assess overall assemblage fragmentation:

$$(\text{NISPi complete long bones})/(\text{total NISPi long bones}) \times 100 \qquad (5)$$

for each element (i).

Evidence for digestion was recorded on the lower and upper incisors; first lower molars of Arvicolinae; distal humerus; proximal femur, radius, ulna, and tibia; and the acetabulum. The degree of digestion evident on teeth were assessed based on the categories described by Andrews [3] and Fernández-Jalvo et al. [57]: null (0), light (1), moderate (2), heavy (3), and extreme (4). Isolated molars and incisors were not analysed separately from those still in situ in the mandible or maxillary, as the proportion of in situ teeth is highly dependent on the methods used to recover remains from archaeological contexts (i.e., water sieving with baths or continuous water flow). For all other skeletal elements, evidence for digestion was recorded as either present or absent.

Four types of tooth marks were recorded: (1) pitting, which corresponds to compressed oval areas without perforation; (2) punctures, which are areas of compression that pierced the cortical surface of the bone; (3) grooves/scoring in the form of channels associated with carnivore tooth marks; and (4) notches, which are semicircular to curved marks on a fracture edge. The location and character (multiple or bilateral) were also recorded for each bone. The proportion of tooth marks (Toothmark%) was calculated as:

$$(\text{NISPi long bones and coxal bone with tooth marks})/(\text{total NISPi long bones and coxal}) \times 100 \qquad (6)$$

2.4. Statistical Analyses

All statistical analyses were conducted in R v.3.6.3 [58] and are detailed in the Supplementary Materials. It includes the data of Ittenheim, and the three reference collections (Bettant I, VIII and Les Six Chemins) from this work, as well as many data as possible from previously published reference collections of dens and small carnivores consuming rodents and rabbits. Few data from pellets of diurnal and nocturnal birds of prey have been also included. Confidence intervals were generated using the probability of success from

the *binom.test* function in R. Correspondence analyses (CAs) were calculated using 'miss-MDA' [59] and 'FactomineR' [60] packages. Loss of basipods, scapula, and ribs results from numerous non-predator-related factors, including post-depositional alterations or recovery protocols. As such, these elements were removed from the CA analysis. As the assumptions of multivariate analysis of variance (MANOVA) were not fully met, we performed a non-parametric multivariate analysis of variance (NP-MANOVA) based on Bray–Curtis dissimilarity using the *adonis* function from the R 'vegan' package [61]. This was designed to test the null hypotheses of differences between modern carnivore reference collections according to prey species (rabbit vs. rodent) and origin (i.e., scat, no digested elements, den). A post-hoc multilevel pairwise analysis based on Bray–Curtis distances was also performed using the *pairwise.adonis* function in the pairwiseAdonis package [62]. The R script is available in the Supplementary Materials and at https://github.com/AurelienRoyer/Ittenheim (accessed on 16 July 2021).

3. Results

3.1. Ittenheim

A total of 2686 remains were determined from the Ittenheim burrow, representing at least nine distinct species (Table 1). The several hundred hare remains from Ittenheim were assigned to mountain hare or brown hare based on the size of the incisors and the morphology of the upper second premolars in order to differentiate this species from brown hare [63–67]). As only the remains of mountain hare (*Lepus timidus*) were identified, and taking into consideration the homogeneity of the assemblage, all hare remains were attributed to the mountain hare. Most hare remains were from juvenile individuals (i.e., less than four months; see [54,68]). Two red fox (*Vulpes vulpes*) individuals were identified, an approximately three and a four-month-old fox cub. The presence of a single baculum (length = 25 mm) indicates one of the two cubs was male. Compared to data published by Harris [53], its morphology and length are consistent with a 6-week-old fox cub. Based on the epiphysation of the metapods, the second individual could be less than 15 weeks old. Tooth marks, and to a lesser extent traces of digestion, were recorded on both leporid and canid remains (Table 2). Two elements exhibited evidence of digestion, one belonging to a hare, the other an unidentified medium-sized mammal (fox or hare). Tooth marks were recorded on nine hare remains and single fox mandible. Most tooth marks consisted of small depressions (pittings) on bone surfaces, primarily those of long bones. One element displayed scoring and another a fracture edge with a crenellated morphology.

Table 1. Number of remains (NISP), minimal number of individuals (MNI), and minimal number of elements (MNE) by taxa from Ittenheim.

Taxon	NISP	MNE	MNI
Lepus timidus	108	68	3
Vulpes vulpes	53	45	2
Lagomorpha/Vulpes	10	-	-
Cricetus cricetus	2358	2279	64
Apodemus cf. *sylvaticus*	4	4	2
Apodemus/mus	2	2	1
Muridae	25	25	1
Arvicola cf. *amphibius*	8	8	1
Microtus agrestis	4	4	3
Microtus arvalis/agrestis	5	5	3
Arvicolidae	87	85	-
Talpa europaea	7	7	1
Suinae	1	1	1
Bird	2	2	1
Indéterminés	12		-
Total	2686	2535	83

Table 2. Conservation of skeletal elements from Ittenheim by taxa (leporid and fox) and NISP bones showing digestion and tooth marks by anatomical element. %CB: Complete bones; %RA: Relative abundance; NISP CO: number of identified specimens complete.

Anatomy	Leporid (MNI = 3)							Fox (MNI = 2)						
	NISP	MNE	NISP CO	% CB	% RA	NISP Digested	NISP Bones with Tooth Marks	NISP	MNE	NISP CO	% CB	% RA	NISP Digested	NISP Bones with Tooth Marks
Mandible	-	-	-	-	-	-	-	3	3	2	66.7	75.0	0	1
Maxillary	2	2	0	0.0	33.3	-	0	0	0	-	-	0.0	-	-
Cranial	5	-	0	0.0	-	-	0	7	1	1	14.3	-	0	0
Incisors	1	1	1	100.0	5.6	-	0	2	2	1	50.0	8.3	0	0
Molars	9	8	4	44.4	12.1	1	0	1	1	0	0.0	5.0	0	0
Other teeth	-	-	-	-	-	-	-	2	2	2	100.0	50.0	0	0
Scapula	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Humerus	1	1	0	0.0	16.7	-	0	1	1	1	100.0	25.0	0	0
Radius	-	-	-	-	-	-	0	-	-	-	-	-	-	-
Ulna	1	1	0	0.0	16.7	-	1	3	2	2	66.7	50.0	0	0
Femur	8	3	2	25.0	50.0	-	4	1	1	0	0.0	25.0	0	0
Tibia	9	3	5	55.6	50.0	-	3	-	-	-	-	-	-	-
Pelvis	1	1	0	0.0	16.7	-	1	-	-	-	-	-	-	-
Calcaneum	5	5	5	100.0	83.3	-	0	-	-	-	-	-	-	-
Talus	3	3	3	100.0	50.0	-	0	1	1	1	100.0	25.0	-	0
Carpals/tarsals	7	7	7	100.0	9.7	-	0	1	1	1	100.0	25.0	0	0
Patella	1	1	1	100.0	16.7	-	-	-	-	-	-	-	-	-
Sesamoïd	-	-	-	-	-	-	0	1	1	1	100.0	-	-	0
Ribs	2	2	2	100.0	2.6	-	0	3	3	3	100.0	5.8	0	0
Vertebra	1	1	1	100.0	0.9	-	0	16	8	0	0.0	9.8	0	0
Sternum	-	-	-	-	-	-	0	1	1	1	100.0	50.0	-	0
Metapodial	34	22	23	67.6	40.7	-	0	7	7	3	42.9	19.4	0	0
Phalanx	21	20	20	95.2	19.6	-	0	10	10	6	60.0	9.6	0	0
Baculum	-	-	-	-	-	-	0	1	1	1	100.0	50.0	0	0
Total	111	81				1	9	61	46				0	1

Nearly 92% of the remains (*n* = 2019) from Ittenheim can be attributed to hamsters (*Cricetus cricetus*), corresponding to a minimum of 64 individuals. All individuals show teeth wear with young adults, adults, and old ones. While all elements of the skeleton are represented, cranial and dental remains are by far the most abundant (MNI was based on hemi-maxillae, Table 3). Only one complete skull was recorded, with the other 45 being broken at the level of the occipital. Conversely, long bones and pelvis are underrepresented, with an average survival rate of 61%. Despite this, the remains are generally well preserved, with completeness values ranging from 38 to 65%. Only the pelvis bones are more heavily fragmented, which is primarily due to the fragility of the pubic symphysis.
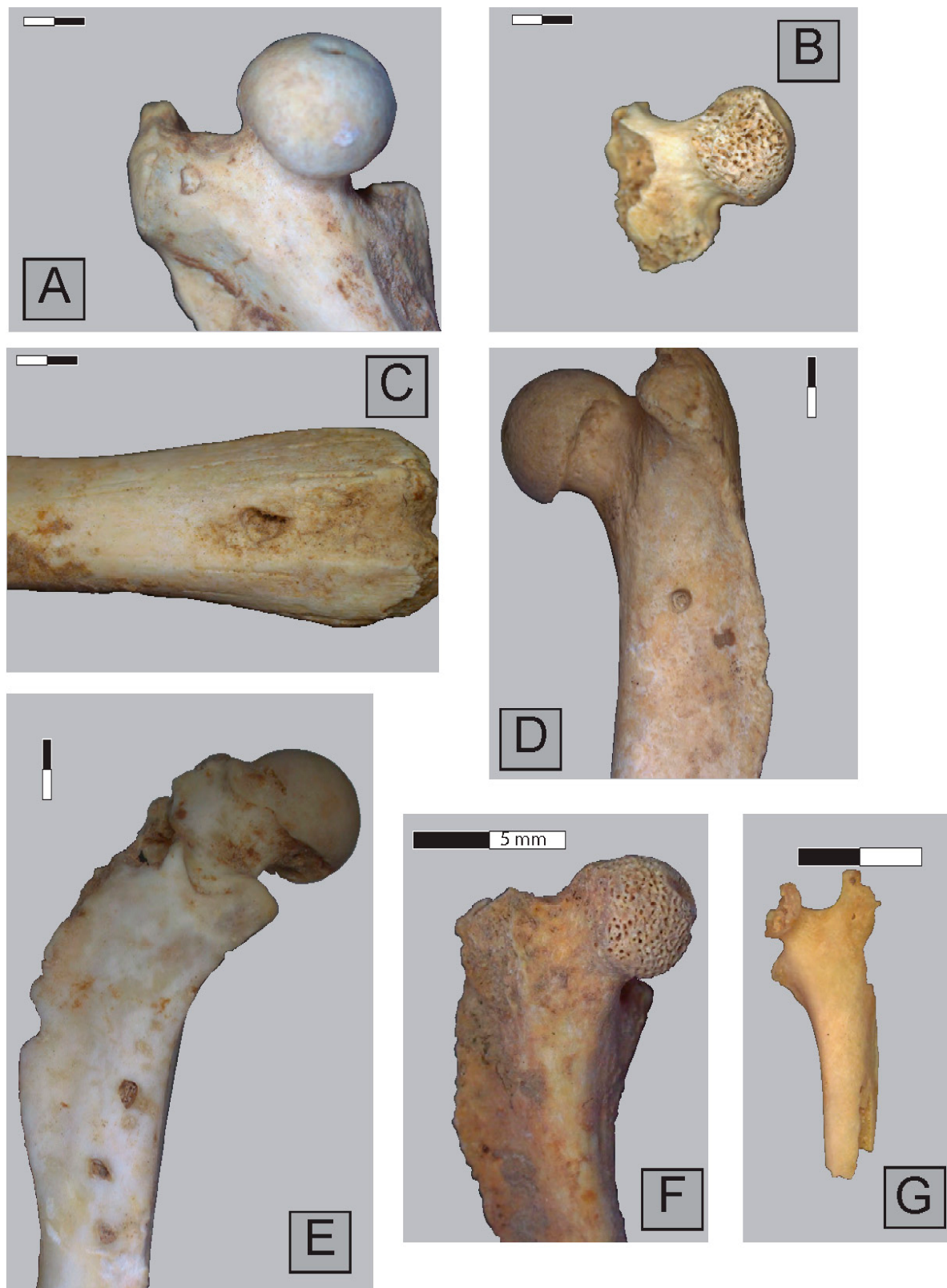
No traces of digestion were observed on hamster incisors, radius, ulna, tibia, or coxal, and only 2.0 and 5.7% of femur and humerus, respectively, bear evidence of digestion (Figures 2 and 3). In contrast, on average, 24% of the hamster remains bear tooth marks (Table 3), primarily the humerus and pelvis (40% of all remains). Among the various carnivore traces observed on long bones, grooves are rare, observed on only two bones (Figure 2C). Notches are evident on more than 50% of bones, while puncture and pitting were observed on 44 and 32%, respectively, of bones. Approximately 65% of bones with carnivore traces exhibit only one form of alteration (Figure 4); bilateral marks are evident in more than 10% of cases, with the majority occurring on the pelvis and humerus (Figures 5 and 6). Trends in the location of the marks are also evident; for example, all pits observed on the ulna are located in the proximal portion of the diaphysis, while punctures are concentrated on the head (Figure 4). In six cases, osteal tissue was removed from the olecranon (Figure 4).

Small mammals from Ittenheim include at least one European mole (*Talpa europaea*) individual and seven voles, the water vole (*Arvicola amphibius*) and field vole (*Microtus agrestis*); and four individuals of muridae, including the wood mouse (*Apodemus sylvaticus*) and possibly *Mus* sp., although the two teeth potentially belonging to this species are heavily altered by digestion, precluding a definitive species attribution. Although small mammal remains are limited, they show distinct patterns, unlike the hamster remains. Skeletal profiles differ as a function of poorer bone preservation and a high degree of fragmentation. On average, more than 65% of small mammal bones and more than 70% of teeth exhibit traces of digestion, some reaching degrees 3 and 4 (Tables 3 and 4, Figures 2G and 3C,D). Again, contrary to the hamster remains, tooth marks are rare and primarily occur on the acetabulum (Figure 5F). However, not all small mammal remains depict the same tendencies; for example, mole remains, which exhibit neither traces of digestion nor tooth marks. Finally, four passerine bird bones were recorded, all bearing digestion damage.

Table 3. Conservation of skeletal elements from Ittenheim by taxa (hamster, *Arvicola* sp., and small rodents) and percentages of digestion and tooth marks by anatomical element. %CB: Complete bones; %RA: Relative abundance; x: observation of digestion recorded but not quantified; *: observations based only on first lower molars.

Anatomy	Hamster (MNI = 64)					Small Voles and Mice (MNI = 7)					*Talpa europaea* (NMI = 1)				
	MNE	%CB	%RA	%Digestion	%Bones with Tooth Marks	MNE	%CB	%RA	%Digestion	%Bones with Tooth Marks	MNE	%CB	%RA	NISP Digested	NISP Bones with Tooth Marks
Mandible	119	47	93.0	-	13.1	5	20	35.7	-	0	0	-	-	-	-
Maxillary	125	-	97.7	-	-	2	0	14.3	-	-	0	-	-	-	-
Incisors	219	-	85.5	0	-	26	-	92.9	72.7	-	-	-	-	-	-
Molars	544	-	70.8	-	-	64	-	76.2	85.7 *	-	-	-	-	-	-
Scapula	28	0	21.9	-	-	-	-	-	-	-	1	100	50	0	0
Humerus	74	32	57.8	5.7	40.2	5	0	35.7	60	0	1	100	50	0	0
Radius	72	52	56.3	1.2	10.7	1	0	7.1	100	0	-	-	-	-	-
Ulna	67	40	52.3	0	17.0	5	20	35.7	60	0	1	100	50	0	0
Femur	93	56	72.7	2.9	23.1	7	43	50.0	28.6	14.3	2	100	100	0	0
Tibia	78	53	60.9	0	21.6	2	0	14.3	100	0	1	0	50	0	0
Pelvis	85	8	66.4	0	39.8	7	0	50.0	57.1	57.1	1	100	50	0	0
Calcaneum	62	-	48.4	x	-	-	-	-	-	-	-	-	-	-	-
Talus	56	-	43.8	-	-	-	-	-	-	-	-	-	-	-	-
Carpals/tarsals	-	-	-	-	-	-	-	-	-	-	0	-	-	-	-
Vertebra	397	-	20.7	x	x	22	-	-	x	-	-	-	-	-	-
Metapodial	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Phalanx	-	-	-	x	-	-	-	-	-	-	-	-	-	-	-
Total	2019					146					7				

Figure 2. Hamster femur with a single tooth impact (**A**,**C**,**D**), multiple impacts (**E**), and digestion marks (**B**,**F**). Digested *Microtus* sp. femur (**G**). Scale bar represents 2 mm, unless another value is indicated.
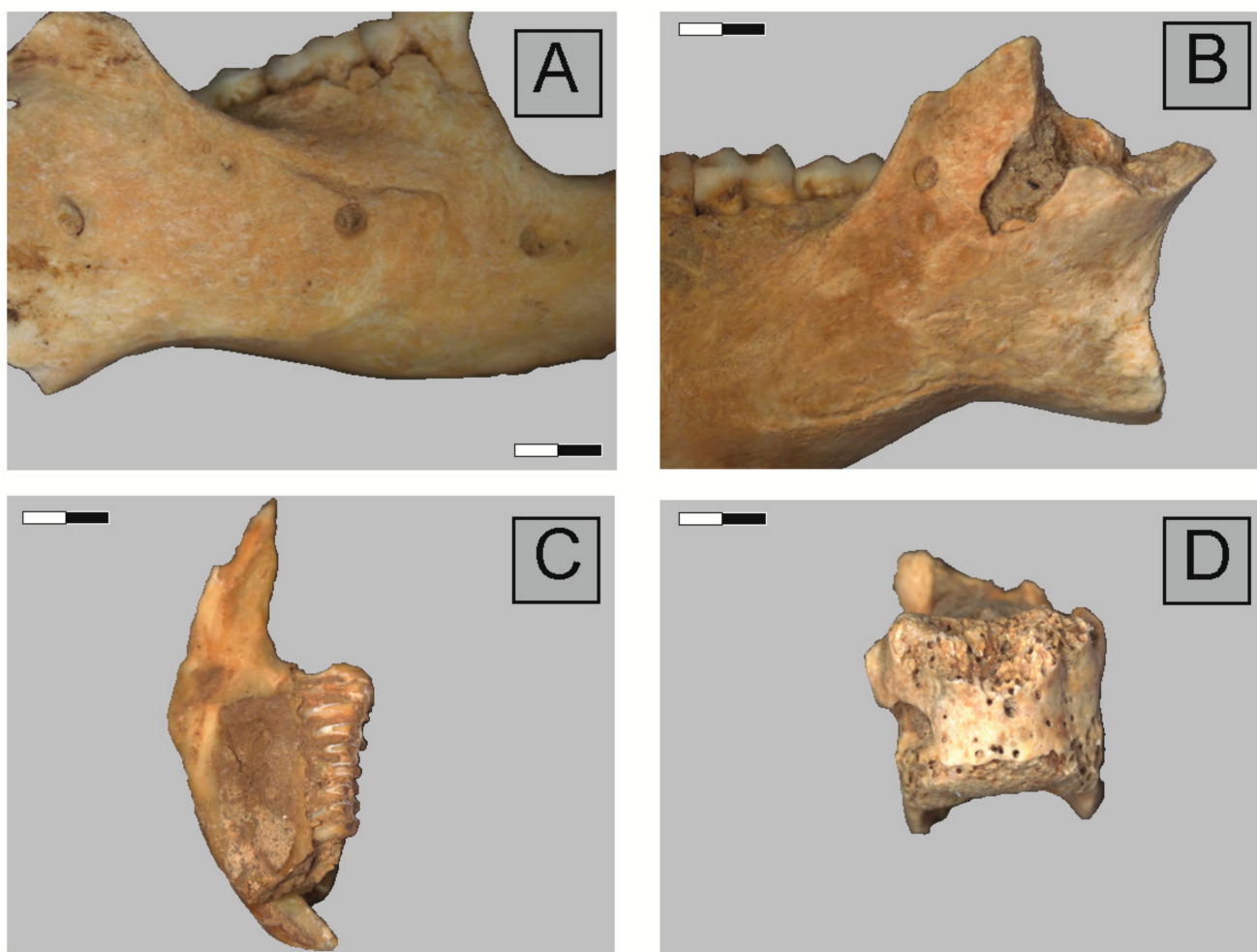
Figure 3. Hamster mandibles from Ittenheim with punctures (**A**,**B**), notch (**B**), and multiple pits (**A**). Digested *Microtus arvalis/agrestis* mandible (**C**) and vertebrae of a small rodent (**D**). Scale bar represents 2 mm.
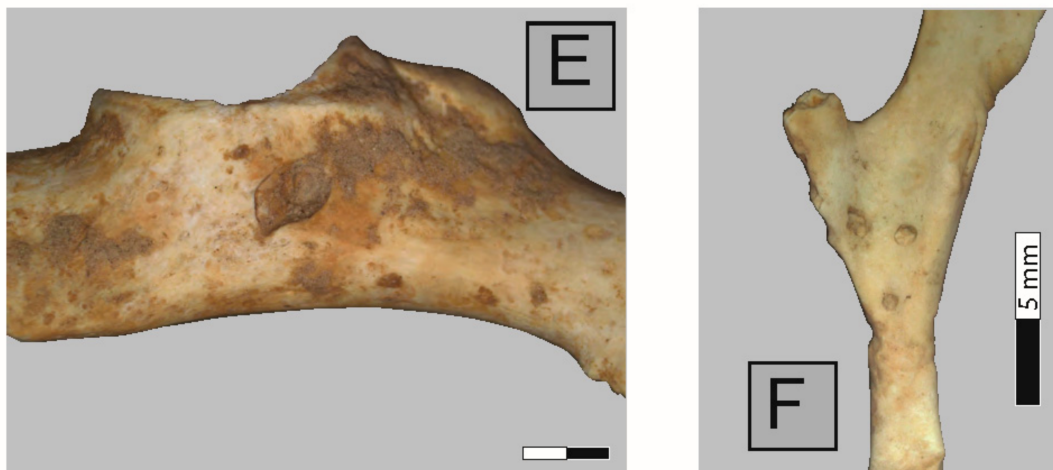

Figure 4. *Cont.*

Figure 4. Ittenheim hamster ulna with osteal tissues removed from the olecranon (**A,D,E,F**), pits (**A**), and punctures (**B,C**). Ittenheim hamster tibia with punctures (**G**) or pits (**H**). Digested tibia of *Arvicola* sp. (**I**). Scale bar represents 2 mm, unless another value is indicated.
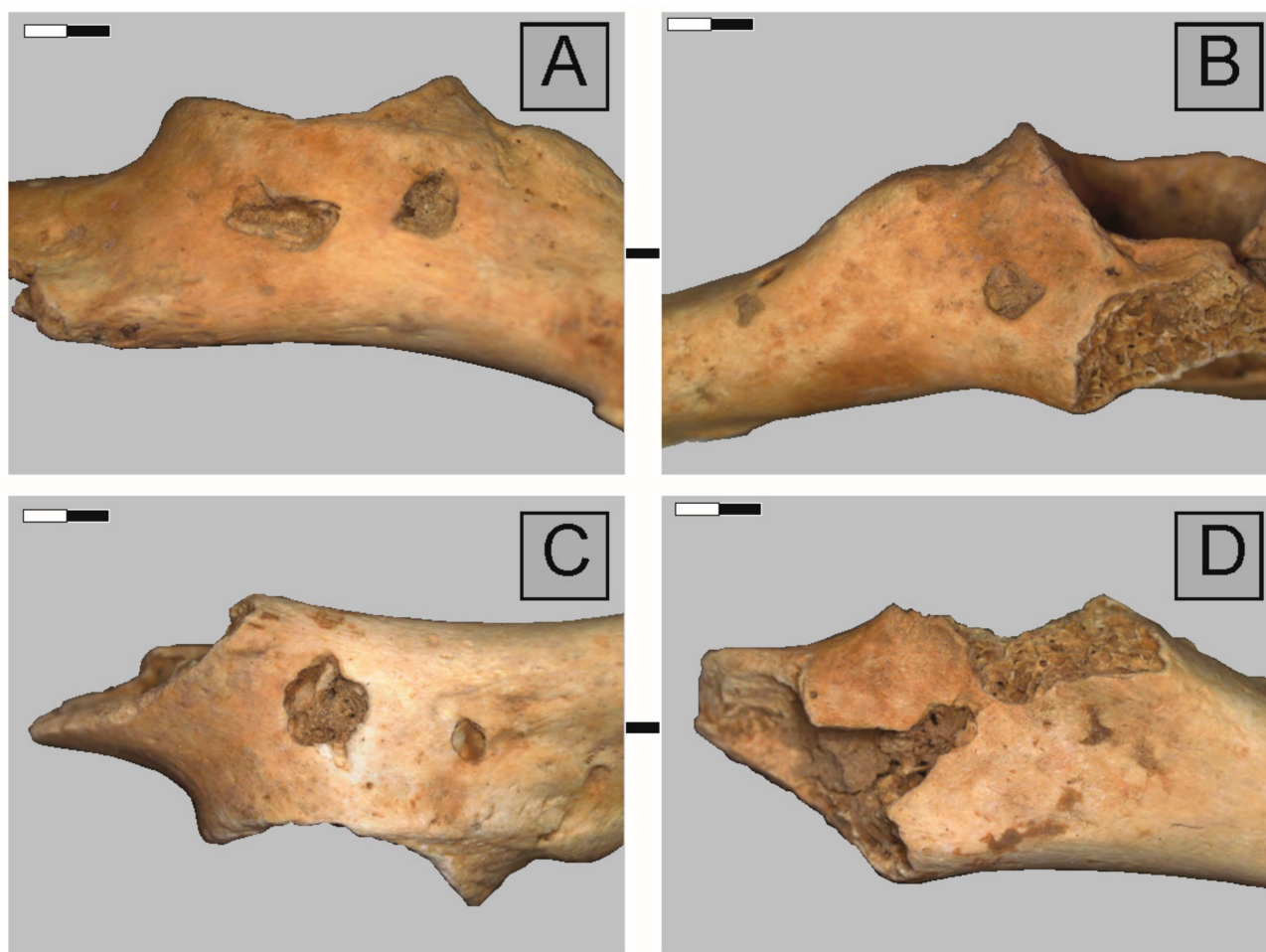

Figure 5. *Cont.*

Figure 5. Ittenheim hamster coxal bones exhibiting bilateral and multiple tooth marks (**A–E**). Pelvis bones of *Arvicola* sp. (**F**) from Ittenheim with tooth marks. Scale bar represents 2 mm, unless another value is indicated.

Table 4. Degree of digestion by elements, sites, and prey sizes. Counts are expressed in NISP. I inf: lower incisors, I sup: upper incisors, m1 inf: lower first molars, FEM = femur heads.

Site	Size	Element	Digestion					Total
			0	**1**	**2**	**3**	**4**	
Bettant I	*Ondatra, Rattus* and *Erinaceus*	I inf	4	1	0	0	0	5
		I sup	2	2	0	0	0	4
		m1 inf	3	1	1	0	0	5
		FEM	4	-	-	-	-	4
	Arvicola sp.	I inf	4	1	0	0	0	5
		I sup	2	0	0	0	0	2
		m1 inf	4	3	1	0	0	8
		FEM	0	2	0	0	0	2
	Small voles and mice	I inf	58	34	8	7	0	107
		I sup	43	26	6	3	1	79
		m1 inf	64	37	23	5	4	133
		FEM	10	3	0	0	0	13
Bettant VIII	*Rattus* and *Erinaceus*	I inf	3	-	-	-	-	3
		I sup	6	-	-	-	-	6
		m1 inf	1	-	-	-	-	1
		FEM	1	-	-	-	-	1
	Arvicola sp.	I inf	2	0	0	1	0	3
		I sup	3	1	0	0	0	4
		m1 inf	2	2	4	3	1	12
		FEM	1	-	-	-	-	1
	Small voles and mice	I inf	29	16	6	3	3	57
		I sup	20	17	2	3	0	42
		m1 inf	36	20	18	12	3	89
		FEM	3	2	2	1	0	8
Les Six chemins	*Rattus rattus*	I inf	1	-	-	-	-	1
		I sup	0	-	-	-	-	0
		m1 inf	2	-	-	-	-	2
		FEM	2	-	-	-	-	2
	Small voles and mice	I inf	32	3	1	2	1	39
		I sup	28	0	0	1	0	29
		m1 inf	18	6	4	0	0	28
		FEM	6	1	0	0	0	7

I inf: lower incisors, I sup: upper incisors, m1 inf: lower first molars, FEM = femur heads.
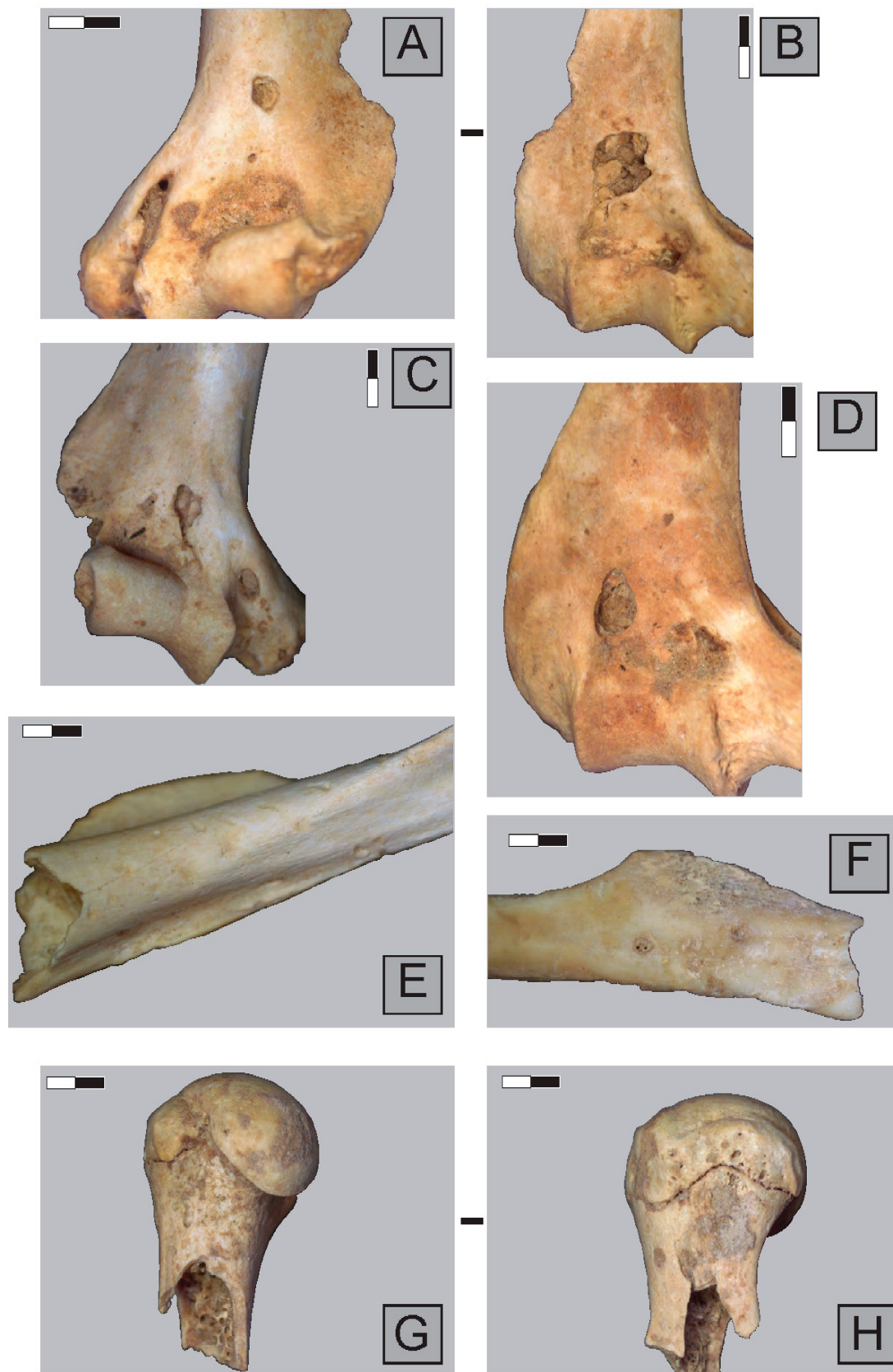
Figure 6. Punctures (**A**–**D**,**F**), pits (**E**,**F**), and bilateral impact marks (**A**,**B**) with notches (**G**,**H**) on hamster humerus. Scale bar represents 2 mm.

3.2. Bettant I, a Meles/Vulpes den

Bettant I produced a total of 1091 identifiable bone elements, representing *Rattus rattus, Ondatra zibethicus, Erinaceus europaeus, Arvicola amphibius, Microtus arvalis, Microtus agrestis, Clethrionomys glareolus*, and *Apodemus sylvaticus*. The first three species correspond to larger rodents, which are well preserved, represented by more than 40% complete bones, including a complete rat skull (Table 5). While digestion marks are only present in the form of a slightly altered first lower molar of *Ondatra zibethicus* (Tables 4 and 5), tooth marks are frequent on all long bones, affecting more than 40% of the remains. These marks are primarily pits observable across the bone surface, and are accompanied by two long bones with punctures and one with a single notch.

Of the 113 bone and teeth remains, five individuals of *Arvicola amphibius* were identified at Bettant I. These remains are both poorly preserved and highly fragmentary. Digestion marks are frequent on bones and teeth, and only four bones show tooth marks (pits and punctures).

A total of 895 remains of smaller rodents from Bettant I were identified, representing at least 73 individuals. Less than 10% of bones bear tooth marks, primarily pits followed by punctures and a few notches, although the latter are difficult to reliably determine due to the small size of the remains. More than half of all long bones exhibit traces of digestion. Interestingly, Bettant I also yielded teeth from at least 16 newborn *Microtus arvalis/agrestis* individuals, without tooth wear, but of which half show signs of digestion.

3.3. Bettant VIII, a Meles/Vulpes den

At least five *Rattus rattus* or *Erinaceus europaeus* were identified from Bettant VII. Slight traces of digestion were observed on the humerus and femur. Multiple pits and punctures are frequent on long bones (Table 6), with the pelvis the most affected by tooth marks, particularly around the acetabulum, sometimes in the form of opposed marks. Half of all identified notches also concern this bone.

Numerous individuals of *Arvicola amphibius* and *Arvicola sapidus* were recognized at Bettant VIII, comprising 145 bones and teeth. Although no complete innominate was recovered, this bone is the most abundant element. All *Arvicola* sp. remains are highly fragmented, showing a low level of completeness, and are poorly preserved, as is the case with the radius, ulna, and mandibles. Less than half of the long bones show no carnivore traces (i.e., digestion, teeth marks). The proportions of digested bones or those with tooth marks are relatively high, varying from 20 to 75% for the most abundant long bones, with several exhibiting both forms of modification. More than 20% of long bones bear notches, and tooth marks are primarily represented by pits, occasionally associated with notches.

A total of 768 remains of Arvicolidae and Muridae were identified from Bettant VIII, including *Apodemus flavicollis, Apodemus sylvaticus, Clethrionomys glareolus, Eliomys quercinus, Microtus agrestis, Microtus arvalis*, and *Microtus (Terricola) subterraneus*. These bones are slightly more complete compared to those from *Arvicola* sp. Like the *Arvicola* sp. remains, these bones bear both evidence of digestion and tooth marks, affecting 34 and 14% of long bones, respectively. Most tooth marks are pits, and punctures are rare (<15% of tooth marks). Clear notches are observed in less than 10% of remains, although several are somewhat uncertain. Numerous teeth show evidence of rounding and corrosion due to digestion, with a non-negligible proportion exhibiting second and third degree traces of digestion (Table 4).

3.4. Les Six Chemins, a Rabbit Warren

The small number of *Rattus rattus* (*n* = 26) remains from Les Six Chemins come from three individuals, including bones of a very young individual with un-erupted molars. Remains are moderately well preserved, fairly complete, and bear no evidence of digestion or tooth marks (Table 7).

Table 5. Conservation of skeletal elements from Bettant I by taxa (*Ondatra*, *Rattus* and *Erinaceus*, *Arvicola* sp., and small rodents) and percentage of digestion and tooth marks by anatomical element. %CB: Complete bones; %RA: Relative abundance; *: observations based only on first lower molars; **: observations based only on first lower molars of *Ondatra zibethicus*.

Anatomy	*Ondatra, Rattus,* and *Erinaceus* (MNI = 5)					*Arvicola* sp. (MNI = 5)					Small Voles and Mice (MNI = 73)				
	MNE	%CB	%RA	%Digestion	%Bones with Tooth Marks	MNE	%CB	%RA	%Digestion	%Bones with Tooth Marks	MNE	%CB	%RA	%Digestion	%Bones with Tooth Marks
Mandible	5	50.0	50.0	-	16.7	0	-	0.0	-	-	50	21.2	54.3	-	8.0
Maxillary	6	-	60.0	-	-	1	-	6.3	-	-	18	-	19.6	-	-
Incisors	7	-	35.0	33.3	-	7	-	21.9	11.1	-	186	-	101.1	45.7	-
Molars	16	-	26.7	33.3 **	-	29	-	30.2	50.0 *	-	225	-	40.8	52.2*	-
Scapula	3	0.0	30.0	-	x	1	-	6.3	-	-	22	-	23.9	-	-
Humerus	5	100.0	50.0	0.0	40.0	2	0.0	12.5	0.0	50	49	24.3	53.3	65.3	1.4
Radius	2	50.0	20.0	0.0	100.0	2	0.0	12.5	100.0	0.0	14	64.3	15.2	7.1	14.3
Ulna	3	66.7	30.0	-	33.3	0	-	0.0	-	-	42	44.2	45.7	42.9	2.4
Femur	4	100.0	40.0	0.0	25.0	6	25.0	37.5	100.0	12.5	46	23.2	50.0	51.1	8.9
Tibia	5	80.0	50.0	0.0	25.0	6	28.6	37.5	50.0	25.6	37	30.4	40.2	52.9	14.8
Pelvis	5	16.7	50.0	0.0	50.0	3	0.0	18.8	50.0	0.0	35	2.6	38.0	53.8	10.3
Calcaneum	1	-	10.0	-	-	-	-	-	-	-	-	-	-	-	-
Talus	0	-	0.0	-	-	-	-	-	-	-	-	-	-	-	-
Carpals/tarsals	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Vertebra	21	-	14.0	-	-	56	-	37.3	-	-	171	-	12.4	-	-
Metapodial	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Phalanx	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Total	83					113					895				

Table 6. Conservation of skeletal elements from Bettant VIII by taxa (*Rattus* and *Erinaceus*, *Arvicola* sp., and small rodents) and percentage of digestion and tooth marks by anatomical element. %CB: Complete bones %RA: Relative abundance; x: observation of digestion was recorded but not quantified; *: observations based only on first lower molars.

Anatomy	*Rattus* and *Erinaceus* (MNI = 5)					*Arvicola* sp. (MNI = 8)					Small Voles and Mice (MNI = 46)				
	MNE	%CB	%RA	%Digestion	%Bones with Tooth Marks	MNE	%CB	%RA	%Digestion	%Bones with Tooth Marks	MNE	%CB	%RA	%Digestion	%Bones with Tooth Marks
Mandible	2	50.0	20.0	-	0.0	2	50	12.5	-	0.0	50	14.8	54.3	-	13.0
Maxillary	1	-	10.0	-	-	0	-	0.0	-	-	13	-	14.1	-	-
Incisors	9	-	45.0	0.0	-	7	-	21.9	33.3	-	100	-	54.3	50.5	-
Molars	5	-	8.3	-	-	45	-	46.9	83.3 *	-	170	-	30.8	59.6 *	-
Scapula	3	0.0	30.0	-	-	3	-	18.8	-	-	14	-	15.2	-	-
Humerus	2	0.0	20.0	50.0	0.0	7	9.1	43.8	57.1	45.5	38	19.2	41.3	60.5	5.7
Radius	2	100.0	20.0	0.0	50.0	2	100.0	12.5	0.0	0.0	7	57.1	7.6	28.6	0.0
Ulna	0	-	0.0	-	-	3	33.3	18.8	33.3	0.0	19	21.1	20.7	50.0	10.5
Femur	3	20.0	30.0	33.3	40.0	7	8.3	43.8	42.9	75.0	38	18.2	41.3	59.5	31.8
Tibia	1	0.0	10.0	0.0	100.0	7	8.3	43.8	100.0	41.7	30	13.9	32.6	70.0	22.2

Table 6. *Cont.*

Anatomy	*Rattus* and *Erinaceus* (MNI = 5)					*Arvicola* sp. (MNI = 8)					Small Voles and Mice (MNI = 46)				
	MNE	%CB	%RA	%Digestion	%Bones with Tooth Marks	MNE	%CB	%RA	%Digestion	%Bones with Tooth Marks	MNE	%CB	%RA	%Digestion	%Bones with Tooth Marks
Pelvis	8	12.5	80.0	0.0	87.5	13	0.0	81.3	28.6	26.7	19	0.0	20.7	43.5	30.4
Calcaneum	0	-	0.0	-	-	-	-	-	-	-	-	-	-	-	-
Talus	0	-	0.0	-	-	-	-	-	-	-	-	-	-	-	-
Carpals/tarsals	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Vertebra	7	-	4.7	-	x	33	-	13.8	-	-	236	-	17.1	-	-
Metapodial	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Phalanx	-	-	-	-	x	-	-	-	-	-	-	-	-	-	-
Total	43					129					734				

Table 7. Conservation of skeletal elements from Les Six Chemins by taxa (*Rattus rattus* and small rodents) and percentage of digestion and tooth marks by anatomical element. %CB: Complete bones; %RA: Relative abundance; *: observations based only on first lower molars.

| Anatomy	*Rattus rattus* (MNI = 3)					Small Voles and Mice (MNI = 21)				
	MNE	%CB	%RA	NISP Digested	NISP Bones with Tooth Marks	MNE	%CB	%RA	%Digestion	%Bones with Tooth Marks
Mandible	3	33.3	50.0	-	0	29	60.0	69.0	-	0.0
Maxillary	1	-	16.7	-	-	13	-	31.0	-	-
Incisors	1	-	8.3	0	-	69	-	82.1	12.5	-
Molars	7	-	19.4	-	-	65	-	25.8	35.7 *	-
Scapula	0	-	0.0	-	-	2	-	-	-	-
Humerus	1	0.0	16.7	-	0	10	28.6	23.8	16.7	0.0
Radius	2	50.0	33.3	0	0	11	72.7	26.2	0.0	0.0
Ulna	1	100.0	16.7	0	0	3	100.0	7.1	0.0	0.0
Femur	4	50.0	66.7	0	0	14	36.8	33.3	20.0	0.0
Tibia	0	-	0.0	-	-	19	54.2	45.2	0.0	0.0
Pelvis	1	0.0	16.7	0	0	11	9.1	26.2	44.4	18.2
Calcaneum	0	-	0.0	-	-	-	-	-	-	-
Talus	0	-	0.0	-	-	-	-	-	-	-
Carpals/tarsals	-	-	-	-	-	-	-	-	-	-
Vertebra	5	-	5.6	-	-	16	-	-	-	-
Metapodial	-	-	-	-	-	-	-	-	-	-
Phalanx	-	-	-	-	-	-	-	-	-	-
Total	26					275				

Small rodents from the Les Six Chemins warren include at least 15 individuals of trogloxene species, including the common vole (*Microtus arvalis*), field vole (*Microtus agrestis*), bank vole (*Clethrionomys glareolus*), and muridae (*Apodemus* sp. and *Mus* sp.). Unlike the rats from Les Six Chemins, the remains of these small rodents are fragmented or generally lack most skeletal elements, particularly the ulna. Tooth marks are rare and are only evident on the acetabulum. Digestion marks affect up to 45 and 36% of the pelvis and molars, respectively, and to a lesser extent, incisors, femur, and humerus (Table 7), suggesting a proportion were introduced to the warren by carnivores. Finally, two fragmented passeriform vertebrae were identified.

3.5. Comparison with Other Carnivore Reference Collections

We performed correspondence analyses that included as many reference collections as possible for small carnivores that consume rodents and rabbits, as well as several from dens and pellets from rapacious birds (Figure 7A,B, see Supplementary Table S1 for more details). This correspondence analysis is based on anatomical representation. The first two axes explain more than 65% of the total inertia, the third 15.7%. The first axis is characterized by a major contribution of the mandibles (50.9%), tibia (21.7%), and radius (12.4%) and is relatively well correlated with **CRA/POSTCRA%** (Pearson's correlation: r = −0.36, t = −3.16, df = 65, *p*-value = 0.002). The second axis opposes posterior limb bones, the femur (19.3%) and pelvis (19.0%), and anterior limb bones, the scapula (16.5%) and ulna (24.2%), and is highly correlated with **AN/PO%** (r = 0.77; t = 9.91, df = 67, *p*-value < 0.00001), while the third is highly negatively correlated with **Z/E%** (r = −0.73; t = −8.71, df = 67, *p*-value < 0.00001). Reference collections are distributed over a large area of the factorial space of the first two axes, reflecting significant variation in skeletal profiles, particularly those of canidae predators. Nonetheless, the ordination space appears strongly influenced by prey categories, with minimal overlap between rabbits and rodents, which are primarily associated with smaller carnivore reference collections. This separation is likely connected to distinct proportions of mandibles and zigopodia between rodents and leporids. Rodent scats and reference collections comprising non-ingested leporids reference collections occupy opposite ends of axis 1. Reference collections of nocturnal rapacious by prey size tend to cluster together and are distinct from leporids and rodents, while diurnal birds of prey are separate. The Ittenheim hamsters fall in the middle of the factorial space defined by first two axes, relatively close to both the Ittenheim small rodents and the Bettant I rats. Bettant VIII small rodents overlap with scats as well as the Les Six Chemins small rodents and rats. Rats and *Arvicola* sp. from Bettant VIII are closer to rabbit assemblages accumulated by *Bubo* sp. and to the cache of Iron Age small mustelids described by Vigne et al. [26] and characterized by high proportions of femur and tibia. These reference collections occupy opposite ends of the second axes of *Talpa europaea* remains.

The **CRA/POSTCRA%, AN/PO%**, and **Z/E%** values (Figure 7C,D) show similar trends to those obtained from CA analyses, including considerable variability amongst scats. The same separation according to prey size (rabbits vs. rodents) and the origin of the material (i.e., scat, den, non-ingested) is also evident; for example, rabbits tend to display **CRA/POSTCRA%** values lower than 50, reflecting an over-representation of postcranial elements, or scats tend to have a **Z/E%** values lower than 50 and an overabundance of stylopodia elements. Hamsters and rodents from Ittenheim fall both within the variability of carnivore scats with rodent prey, as well as small rodents and rats from Bettant I and small rodents from Bettant VIII (Figure 7C,D). Only rats and *Arvicola* sp. from Bettant VIII tend to be associated with rabbit prey reference collections. An NP-MANOVA test returned low not statically significant *p*-values, except for the interaction (NP-MANOVA interaction term *p* ≈ 0.01) between the prey (rodents and leporids) and their origins (den, scat, non-ingested, natural death). While these results depict some general trends, in particular for non-ingested elements according to pairwise comparisons, the high degree of variability prevents any clear separation with the other categories.
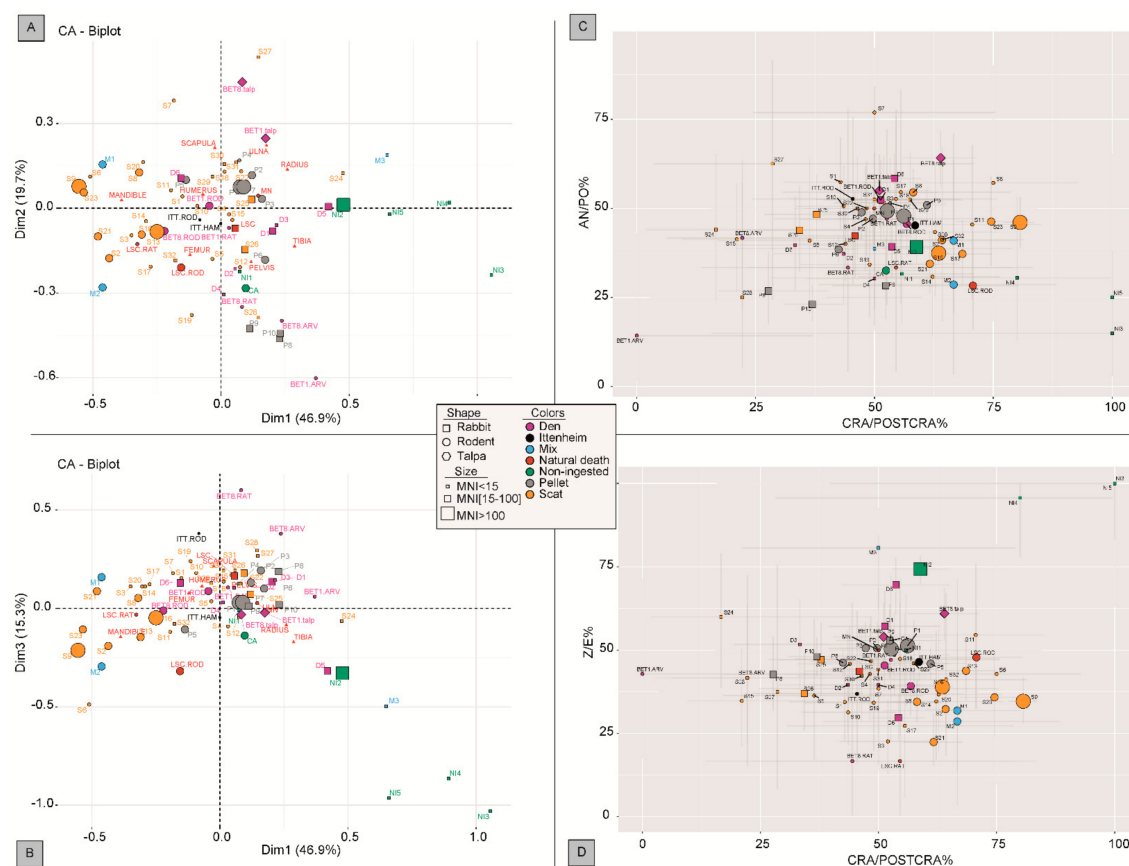
Figure 7. Correspondence analysis biplot of carnivore bone accumulations and reference collections from this study (**A**) dimensions 1 and 2, and (**B**) 1 and 3. In red, coordinates of each bone used in the analysis. Scatter plots of AN/PO% and CRA/POSTCRA% (**C**) and Z/E% and CRA/POSTCRA% (**D**) from the carnivore reference collections. The light grey in scatter plots represents the calculated 95% confidence intervals. For biplots and scatter plots, reference codes are listed in the supplementary data and correspond to: this study = ITT.HAM−Hamster of Ittenheim; ITT−ROD−small rodents; LSC.ROD−small rodents of Les Six Chemins; LSC.RAT−rat, BET1.RAT−rats, muskrats and hedgehogs from Bettant I, BET1.*ARV*−*Arvicola* sp., BET1.ROD−small rodents, BET8.RAT−rats and hedgehogs from Bettant VIII, BET8.ARV−Arvicola sp., BET8.ROD−small rodents; from the literature = BET1.talp−[37], BET8.talp−[37], LSC−rabbit warren [20], P = pellets, P1−[3], P2−[69], P3−[69], P4−[69], P5−[3], P6−[70], P7−[30], S = scats, S1−[3], S2−[3], S3−[3], S4−[3], S5−[3], S6−[3], S7−[3], S8−[44], S9−[46], S10−[40], S11−[40], S12−[40], S13−[43], S14−[71], S15−[41], S16−[42], S17−[72], S18−[38], S19−[73], S20−[73], S21−[74], S22−[17], S23−[75], S24−[45], S25−[34], S26−[34], S27−[35], S28−[35], S29−[76], S30−[73], M = Mix, M1−[38], M2−[38], CA = Cache, CA−[26], MN = Natural death, MN−[77], D = Den, D1−[33], D2−[37], D3−[37], D4−[78], D5−[79], D6−[80], NI = Non−ingested, NI1−[81], NI2−[82], NI3−[82], NI4−[35], M3−[35], NI5−[17], S31−[17], S32−[83], P8−[84], P9−[84], P10−[70]. Shapes represents different prey (squares for rabbits, circles for rodents, and hexagons for talpa), size varies according to the number of prey according to three size groups ([1–15[, [15–100[, ≥100), and colours illustrate the different origins (Den−purple, Ittenheim−black, Mix−blue, Natural Death−red, Non−ingested elements−green, Pellets−grey and Scat−orange).

Figure 8A shows the percentage of digested femur alongside the percentage of digested incisors according to the different predator categories defined by Andrews [3]. Whether for rabbits or rodents, clear differences are evident for carnivore prey recovered from scats, with high proportions of digested and non-ingested remains or those from natural death assemblages. The hamsters from Ittenheim fall squarely in this latter category. The other reference collections fall between these two extremes and correspond to category 2, 3, and 4 predators. Small rodent assemblages from Ittenheim, Bettant I, and Bettant VIII are similar to those produced by category 3 and 4 predators, whereas rats from Bettant I and VIII are closer to predators from categories 1 and 2. Conversely, *Arvicola* sp. from Bettant I stand out from the others, given a high proportion of digested femur and low numbers of

digested incisors, which may be partially due to the small number of individuals. Small rodents from Ittenheim are characterized by slightly more digested incisors compared to femurs. When the percentage of digested incisors is compared to the percentages of tooth marks, an inverse correlation can be seen between these two taphonomic signatures (Figure 8B). A first group comprises scat and is characterized by high proportions of digestion teeth and low (or no) numbers of tooth marks. Den, non-ingested reference collection, and Ittenheim are all characterized by higher proportions of tooth marks and lower proposition of bone with signs of digestion. Smaller rodents have intermediate values for both tooth and digestion marks. European hamsters from Ittenheim show a distinct pattern characterized by the absence of signs of digestion on all incisors and relatively high proportions of tooth marks.
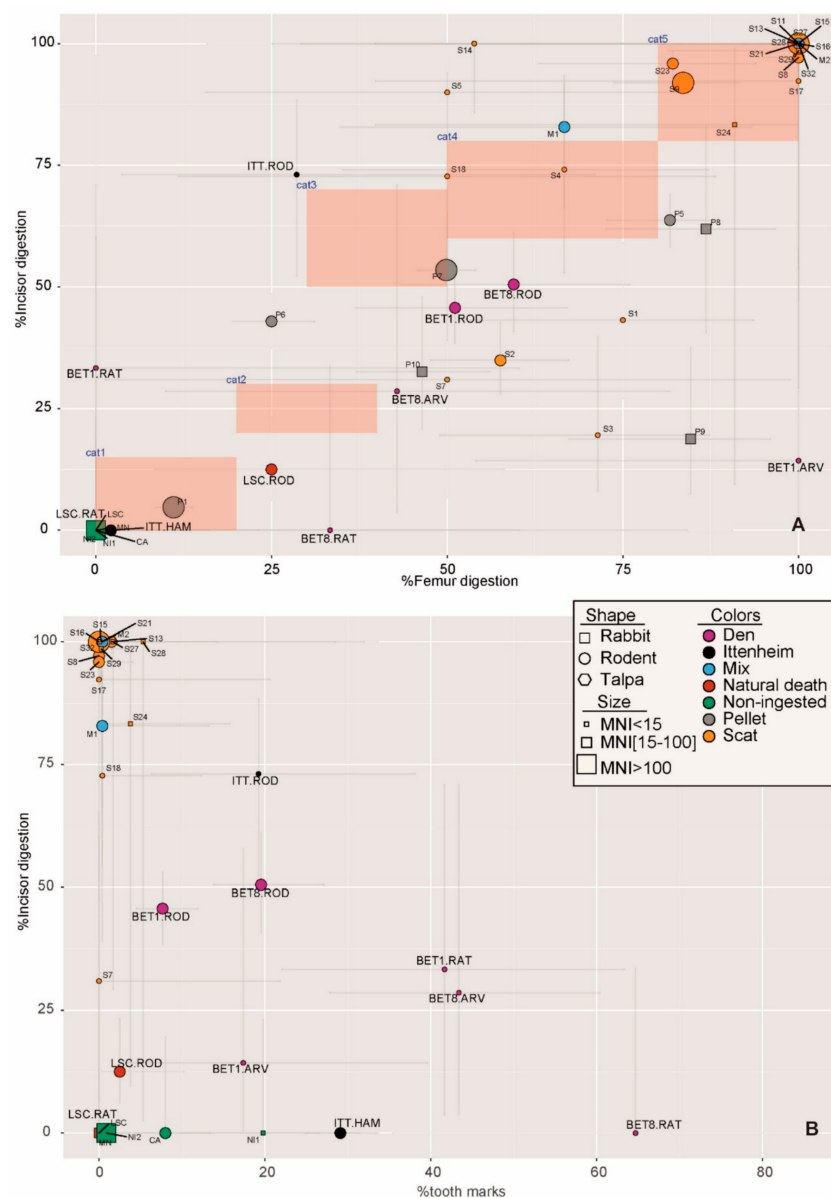
Figure 8. Scatter plot of percentages of digested incisors (**A**) and femur heads, (**B**) and tooth marks, from carnivore reference collections and those built for this study. Corresponding codes are listed in Figure 7 and in the supplementary data. As in Figure 7, shapes represent different prey (squares for rabbits, circles for rodents, and hexagons for Talpa), size varies according to the number of prey according to three size groups ([1–15[, [15–100[, ≥100), and colours illustrate the different origins (Den−purple, Ittenheim−black, Mix−blue, Natural Death−red, Non ingested elements−green, Pellets−grey and Scat−orange). The light grey lines represent the 95% confidence interval.

4. Discussion

4.1. An Integrative Approach for Reconstructing the Taphonomic History of the Ittenheim Accumulation

The small and medium mammal bone accumulations from Ittenheim depict limited species diversity comprising less than 10 species. While no radiocarbon dates are currently available, the presence of interglacial fauna suggests a Holocene age, which would be consistent with the possible presence of *Mus* sp. [85]. However, the identification of *Lepus timidus*, which is no longer present in the region, but whose date of last occurrence is still unknown, also attests to a non-modern accumulation. The Ittenheim accumulation is remarkable due to the high number of hamster (*Cricetus cricetus*) remains, representing at least 64 individuals, associated with the remains of young leporids, fox cubs, and numerous small rodents. Given the context of the site, a faunal assemblage accumulated by rapacious birds can safely be ruled out, leaving only two other possibilities: a catastrophic death related to the collapse of a burrow that was also occupied by trogloxene species or a carnivore accumulation

The hypothesis of catastrophic death related to the collapse of the burrow would be consistent with the fact that hamsters are burrowing mammals. However, this moderately sized rodent (weighing between 150 and 600 g according to the season) is a solitary mammal [86], with each individual occupying a unique burrow, the one exception being nursing females [87,88]. A female can give birth to more than 10 young, which leave the burrow following weaning. Hamsters dig one small burrow during the summer and a deeper, more complex one during the winter, which can reach depths of up to two meters and can include, for example, several food storage and waste disposal areas [86]. The diameter of the burrow's tunnels varies between approximately 5 and 10 cm. Although they have distinct behavioural characteristics compared to rabbits, hamster burrows are likely to display some traits that overlap with rabbit warrens [20]. A similar accumulation for denning hamsters would be characterized by numerous juvenile and immature individuals, an under-representation of postcranial remains, no digestion or tooth marks, and a low proportion of fragmented bones. However, apart from the excellent preservation of the remains, none of these criteria were encountered for the Ittenheim assemblage. The important numbers of tooth marks, reaching almost 30%, amongst the highest observed for the rodent and rabbit carnivore accumulations, undoubtedly attests to a trogloxene carnivore contribution to the accumulation. Furthermore, no young hamster individuals were recorded. As hamsters are solitary mammals, the high number of adult hamster individuals argues against a natural death assemblage, which should theoretically concern only a single individual, as in the case of Combe-Cullier [77]. While the Ittenheim hamsters being accumulated by carnivores seems the most parsimonious hypothesis, the question remains of which of its main predators is responsible: a small predator, such as *Mustela erminea*, *Mustela nivalis*, *Martres foina*, or *Martres martres*; or a larger one, such as *Meles meles* or *Vulpes vulpes*.

One defining feature of the Ittenheim hamster assemblage is its overall good preservation and low proportion of digested elements, indicating a large part of the assemblage did not pass through a predator's digestive tract. Independent of the carnivore, all scats clearly contain a large proportion of digested remains, whereas non-ingested elements generally bear only tooth marks (Figure 8). Although there is an under-representation of limb bones compared to cranial bones, which would be in agreement with a carnivore accumulation, the skeletal profile is not entirely consistent with the non-ingested assemblages, falling more within the large variability of scats and dens.

Small mustelids are known to cache excess prey for later consumption (e.g., [89,90]). Generally, these predators tend to dispatch their prey by targeting the occipital and brain, eating the latter promptly. Consequently, these caches can be characterized by large numbers of prey, including numerous skulls with occipital breaks. In the case of the Ittenheim hamster accumulation, numerous fragmented skulls lack their occipital region. Impacts evident on the bones are also similar to those described by Vigne et al. [26] for *Mus/Apodemus*,

Eliomys, and *Arvicola* remains, characterized by numerous small perforations in, for example, the olecranon area. However, the proportions of remains at Ittenheim with these types of marks are much greater, affecting more than 20% of the long bones. Tooth marks observed on hamster remains are relatively similar to the ones observed on rodent remains from Bettant I and VIII. Their distribution also follows a similar pattern as those observed for rabbits from the fox den of Les Rochers-de-Villeneuve [33], with tooth marks preferentially located on mandibles, girdles, and long bones with partially removed bony eminences, such as the olecranon. Vigne et al. [26] interpret these small perforations to reflect predation by small carnivores, such as weasels or stoats, which would be consistent with the small quantity of associated weasel remains. Such perforations can also be produced by fox or badger cubs, as demonstrated, for example, by Mallye et al. [37] for the bird and mole remains from the Bettant dens. Though similar, tooth marks were nevertheless relatively rare amongst mole remains, being evident on about 5% of remains compared to 20–30% for larger vertebrate remains. Similar patterns were observed for both small and large birds, demonstrating the clear impact of prey size on patterns of bone modification [37]. Campmas et al. [38] showed that larger rodents (*Ctenodactylus gundi* weighing between 200 and 300 g) exhibit similar patterns (digestion and fragmentation) to hyraxes and leporids from scats of small and medium carnivores, leading them to propose a weight limit of prey between small and medium mammal preys of around 300 g. Our analysis of the Bettant remains is in good agreement with these observations as well as a clear relation between proportions of tooth marks and prey size. The larger rodents (rats, muskrats) and hedgehogs are characterised by good bone preservation, as reflected in the presence of a complete rat skull, low proportions of digested bones, and large proportions of bones with tooth marks. On the contrary, smaller rodents are represented by only a few complete bones, small quantities of tooth marks (mainly pits), and numerous traces of digestion on incisors, molars, and bones. Intermediate rodents from *Arvicola* sp. present an intermediate pattern, with both high proportions of digestion and tooth marks. Prey size therefore has a direct impact on the proportions of bone surface modifications that varies according to predator size; for example, young foxes cannot swallow larger prey, such as hamsters. The distinct patterns between these two prey sizes reflect different ways in which predators consume prey, shredding the larger ones and swallowing the smaller.

Finally, the Ittenheim accumulation shows similar patterns to those from Bettant. Both are characterised by a faunal spectrum comprising small and medium mammals, as well as other vertebrates, such as birds. Leporid remains, including young individuals, bear limited traces of carnivore damage, primarily traces of gnawing. Larger rodents and hedgehogs exhibit high proportions of tooth marks and low proportions of digestion damage, whereas smaller ones show an opposite pattern. This being the case, the accumulation of small- and medium-sized mammals at Ittenheim could be interpreted as reflecting a red fox (*Vulpes vulpes*) den, an interpretation consistent with the presence of a small quantity of fox cub remains, as recovered from the Bettant den. The only exception is *Talpa europaea*, which, given the absence of carnivore modification, could represent a natural death. In summary, the Ittenheim bone accumulation could be the result of foxes occupying a burrow. Ethological data show that female foxes occupy the den during denning and the weaning period of juveniles, from March to the end of summer. After the lactation period, foxes bring whole prey to the cubs in the den before they are strong enough to follow their mother during hunting episodes [91,92]. The accumulation of hamsters, other rodents, and hares could reflects these hunting episodes. Furthermore, given the age at death of the fox cubs, Ittenheim could have been occupied during the late spring and early summer. During this period, rodent populations experience a jump in birth rate and a significant increase in population size. Considering that the density of some hamster populations during the summer vary between 300 and 500 individuals per hectare [86], the Ittenheim accumulation resulting from a single occupation of the burrow by a fox family cannot be ruled out.

4.2. Implications for New Reference Collections and Fossil Material

Small carnivores constitute a potential accumulation agent of small and medium mammal bones [3,24,25,31,32,35,37,38,73,75,76,78,81,93–95]. Identifying the role played by small carnivores in fossil-bearing contexts remains challenging. While numerous taphonomic studies have focused on establishing reference collections for each of these mammal accumulators in order to identify taphonomic criteria susceptible to differentiating them, several studies have highlighted difficulties in identifying predators to species, suggesting identifications should remain at the genus level [96,97]. While statistically, the Ittenheim accumulation does not overlap with any particular reference collection, the results of our integrated systemic approach are most consistent with a fox den. The results of our study suggest two major avenues for future research: (1) the importance of contextual data and the integration of all types of remains, and (2) the need for more diversified reference collections that reflect the complexity of fossil accumulations.

We emphasise the importance of the discovery context and the integration of all recovered remains when analysing fossil materials. Our interpretation of the Ittenheim hamster remains was only possible by the identification of the burrow during excavations and the presence of leporid and fox remains, and to a lesser extent those of passeriform birds. The presence of young fox remains, which are regularly found in carnivore dens [37,49,78] supports the hypothesis of the Ittenheim burrow being a fox den. However, predator remains in fossil accumulation do not necessarily indicate the predator responsible for its formation [3], as they also could be the prey or just visiting roommates. Moreover, other trogloxene vertebrates take advantage of pre-existing burrows, such as the wood mouse [78] or muskrat, leading to difficulties in interpreting their presence in faunal assemblages. For instance, the partly digested juvenile remains of *Microtus arvalis/agrestis* from Bettant I pose questions as to their origin. In the case of the Les Six Chemins warren, the presence of neonate rats clearly indicates this rodent used the burrow alongside an additional small predator that introduced the remains of other vertebrate species, as demonstrated by the presence of bird bones and digested small rodent remains. This once again underlines the importance of including multiple multi-spectrum reference collections when reconstructing the formation history of bone accumulations [80,98].

Mammalian carnivores are the most taphonomically destructive predators, compared to diurnal raptors and owls [3,96,97]. Digestion marks and high proportions of fragmented bones are frequently considered as one of the main elements identifying carnivore bone accumulations [3], especially as tooth marks were mainly recorded on bones from canid scats. However, this paradigm has primarily been derived from currently available reference collections. Most taphonomic reference collections concern carnivore scats and clearly demonstrate how bones are modified as they pass through the digestive tracts of carnivores, sometimes becoming heavily altered and fragmented [3]. Non-ingested elements exhibit higher proportions of tooth marks, including those consumed by felids [33,35,45,81], which could be slightly more important during the denning season due to the presence of infants [79]. As mentioned above, beyond issues related to the reliance on modern references to evaluate taphocoenosis [99], without taking into the account the complexity of fossilization processes and attendant post-depositional changes, carnivore bone accumulations could be more complex than just remains coming from a defecation area, particularly in burrows. Burrows are complex structures that can fulfil multiple functions: temporary refuge, long term shelters, or food storage areas [100]. Remains recovered in burrows can therefore reflect natural deaths, stored or discarded food storage, or a mix of all these different origins. The Ittenheim and Bettant carnivore accumulations show clear taphonomical patterns distinct from those of scats. Furthermore, given the complexity of living, burrows can be used differently by multiple animals, as was the case for the Les Six Chemins warrens. Relying only on data from scat to understand fossil accumulation may run the risk of producing erroneous interpretations, especially when variability in carnivore bone accumulations is not incorporated. For example, most neotaphonomic experiments and reference collections did not take into account the

variability [29,100–107] that can be observed between individuals [3,27,99,108] or reflect population-level variability [3,75,105,109]). Moreover, several experimental studies have involved captive animals [17,35,76,79,81,93,110], leading Gidna et al. [111] and Comay and Dayan [97] to caution against the inappropriate use of actualistic data derived from inadequate contexts, which can lead to erroneous analogies and, subsequently, unreliable interpretations of prehistoric faunal assemblages. More diverse statistically representative reference collections in terms of the number of individuals or types of remains are necessary to reliably incorporate both the natural diversity and taphonomic implications of distinct contexts in analyses [26,37,78,112,113]. Furthermore, these new reference collections should be based on an integrative approach designed to evaluate multi-taxa accumulations [30,47,70,98].

5. Conclusions

Small carnivores constitute potential accumulation agents of both small- and medium-sized mammal bones. Our analysis of taphonomic modifications on bones from three modern and one fossil accumulation demonstrates three important aspects that need to be taken into account when evaluating fossil accumulations: (1) prey size, as tooth marks are more frequent on larger prey while traces of digestion occur in larger proportions on smaller ones; (2) the discovery context and the need to include all elements of the faunal spectrum in order to reconstruct the full history of bone accumulations; and (3) the fact that den and burrow reference collections clearly differ from those built from carnivore scat. Our data illustrate the need for more taphonomic reference collections and not only ones based on scats or from feeding carnivores in zoos. Finally, further efforts are needed to multiply modern reference collections of carnivore scats to include larger samples reflecting prey sizes and origins in order to better characterise the variability of these different types of accumulations.

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