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Large mammals of Fouvent-Saint-Andoche (Haute-Saône, France): a glimpse into a Late Pleistocene hyena den

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ABSTRACT

The paleontological site of Fouvent-Saint-Andoche (Fouvent-le-Bas, Haute-Saône, France) is a large bone accumulation in a karstic context known since the early nineteenth century. This article focuses on the analysis of 14977 remains from both the historical collection (excavations in 1842) and the material of the recent excavations (1989-1992). A faunal list of 18/19 large mammal species has been established: 12 carnivores (*Crocota crocuta spelaea* (Goldfüss, 1832), *Panthera (Leo) spelaea* (Goldfüss, 1810), *Ursus spelaeus* Rosenmüller & Heinroth, 1794, *Canis lupus* Linnaeus, 1758, *Vulpes vulpes* Linnaeus, 1758, cf. *Alopex*, *Gulo gulo* Linnaeus, 1758, *Meles meles* Linnaeus, 1758, *Martes* sp., *Mustela eversmannii* Lesson, 1827, *Mustela* sp.) and seven/eight ungulates (*Mammuthus primigenius* Blumenbach, 1799, *Coelodonta antiquitatis* (Blumenbach, 1799), *Megaloceros giganteus* Blumenbach, 1799, *Cervus elaphus* Linnaeus, 1758, *Rangifer tarandus* (Linnaeus, 1758), *Equus germanicus* Nehring, 1884, *Bos primigenius* Bojanus, 1827 and/or *Bison priscus* Bojanus, 1827). The palaeontological analysis allows us to characterize the evolutionary stage related to each species and to comment their biochronological significance. The detailed study of particular species, such as *C. c. spelaea*, *E. germanicus*, or *C. antiquitatis* improves our knowledge on species associations and their implication in Late Pleistocene hyena dens.

KEY WORDS

Fouvent-Saint-Andoche,
hyena den,
OIS3,
palaeontology,
Carnivora,
Ungulata,
palaeoenvironmental
implications.

RÉSUMÉ

Les faunes de mammifère de Fouvent-Saint-Andoche (Haute-Saône, France) : aperçu d'un repaire d'hyène du Pléistocène supérieur.

Le gisement paléontologique de Fouvent-Saint-Andoche (Fouvent-le-bas, Haute-Saône, France), connu depuis le XIX^{ème} siècle, est composé d'un important assemblage osseux mis au jour en contexte karstique. Cet article se concentre sur l'analyse des 14977 vestiges issus des collections historiques (fouilles de 1842) et des travaux récents (1989-1992). Une liste faunique comprenant 18/19 espèces de grand mammifère a pu être établie: 12 carnivores (*Crocota crocuta spelaea* (Goldfuss, 1832), *Panthera (Leo) spelaea* (Goldfuss, 1810), *Ursus spelaeus* Rosenmüller & Heinroth, 1794, *Canis lupus* Linnaeus, 1758, *Vulpes vulpes* Linnaeus, 1758, cf. *Alopex*, *Gulo gulo* Linnaeus, 1758, *Meles meles* Linnaeus, 1758, *Martes* sp., *Mustela eversmannii* Lesson, 1827, *Mustela* sp.) et 7/8 ongulés (*Mammuthus primigenius* Blumenbach, 1799, *Coelodonta antiquitatis* (Blumenbach, 1799), *Megaloceros giganteus* Blumenbach, 1799, *Cervus elaphus* Linnaeus, 1758, *Rangifer tarandus* (Linnaeus, 1758), *Equus germanicus* Nehring, 1884, *Bos primigenius* Bojanus, 1827 et/ou *Bison priscus* Bojanus, 1827). L'analyse paléontologique nous permet ainsi de caractériser le degré évolutif des différentes espèces et de préciser leur apport biochronologique. L'examen détaillé de certain taxon dont *C. c. spelaea*, *E. germanicus*, ou *C. antiquitatis* améliore nos connaissances de ces associations fauniques ainsi que leur place au sein des repaires d'hyène pléistocène.

MOTS CLÉS

Fouvent-Saint-Andoche, repaire d'hyène, OIS3, paléontologie, Carnivore, Ongulé, implication paléoenvironnementale.

INTRODUCTION

The carnivores are part of bone accumulations in Pleistocene sites, even if they are often less abundant than large herbivores. By letting different traces and stigmata they may sometimes modify the bone assemblages (e.g., bioglyphes with coprolites, prints, polished, wallows, tooth marks). Their interactions with Palaeolithic human groups have frequently been attested since the nineteenth century (e.g., Nodot 1858-1859; Cartailhac 1881; Tournepiche 1994, 1996; Philippe & Fosse 2003; Garcia 2004; Hannus 2004; Münzel & Conard 2004; Rabinovitch *et al.* 2004; Sam & Moigne 2011; Daujeard *et al.* 2011).

Within these deposits with both lithic industries and faunal remains, the cave hyena drew particular attention. Its role in bone accumulations (e.g., den *sensu stricto*) as well as its impact on bone stock (e.g., aven, anthropic layers) had been discussed at length (see Fosse 1995 for a general review). First studies already showed that hyenas were bone collectors as well as consumers (e.g., Cuvier 1812; Buckland 1822; Bertrand de Doue 1828; Tournal 1833; Regnault 1885; Harlé 1892, 1899). The description of the bone accumulation at Kirkdale Cave (England) by Buckland (1822) is certainly the first characterization of hyena den. The diversity of carnivores, the overrepresentation of juvenile and senile ungulates (attritional mortality), the abundance of their antlers and acropods, the teeth marks, the number of individuals (many juveniles), and the presence of numerous coprolites permitted all together to give a precise definition of a den. Fouvent was also of paleontological interest (Cuvier 1825; Gervais 1870) and just after the work of Buckland at Kirkdale, this site allowed for precise determination of carnivore sites (Thirria 1828, 1833; Nodot 1858-1859).

More recently, the renewed attention in the predator habits and hyena dens was stimulated by the development of neotaphonomy (Binford 1981; Brain 1981) to understand hu-

man and carnivore interactions with their prey (Fosse 1994). In this context, new excavations were launched in Fouvent during the late 1980s and early 1990s. Thanks to this new material, we present here an up-to-date paleontological study of Fouvent, notably in a palaeoenvironmental perspective.

THE PALAEOANTHROPOLOGICAL SITE OF FOUVENT

LOCATION AND GEOLOGICAL CONTEXT

The palaeontological site of Fouvent, also named Abri Cuvier, is located in the karstic region of Fouvent-Saint-Andoche, in the Northwest of Haute-Saône department, precisely in the village of Fouvent-le-Bas, near Le Vannon River, at an estimated height of 200 meters above sea level (Fig. 1). The site is located in a karst area in Bathonian limestone diachlases (Detrey 1992). The cave has now disappeared and the limestone blocks were used to build a house. However, Fouvent has been described in previous publications by the time of its discovery. These descriptions indicated a cavity of moderate size: the cave stretched 10 m long, 4 m wide, and a height of about 2 m and it had two entrances. The main entrance was about 1 m² wide and the second was slightly smaller (Nodot 1858-1859). New excavations in the late 1980s revealed a passageway probably belonging to the original cave (Detrey 1992; Fosse 1997).

HISTORICAL CONTEXT: PREVIOUS RESEARCHES

The bone accumulations of Fouvent have a famous and long history starting from the beginning of the nineteenth century until recent excavations in 1992 (Fourvel 2012; Fourvel *et al.* 2014). The site highlighted changes in the way to study and to interpret bone layers through time (see synthesis in Fosse 1995). Since early works, Fouvent played a key role in Quaternary palaeontology: osteological distinction between

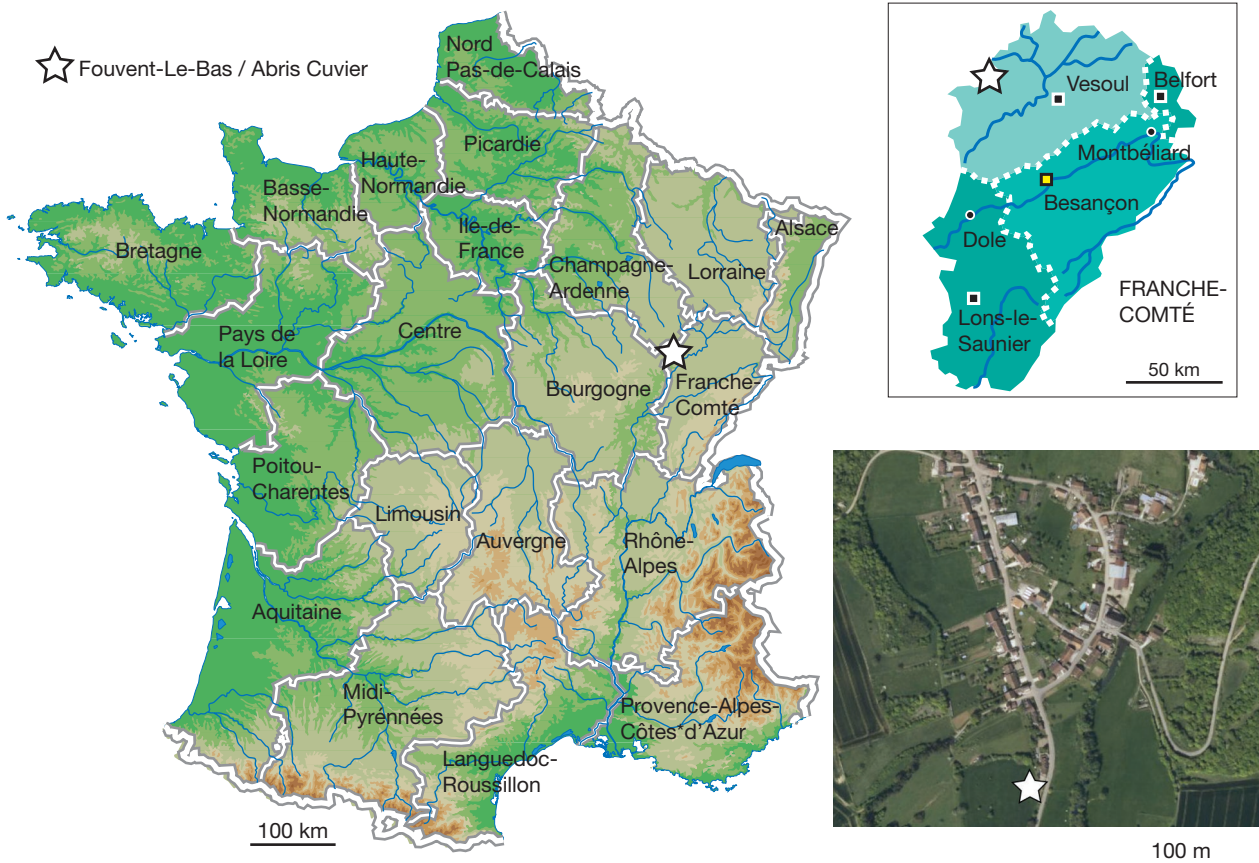


FIG. 1. — Geographical location of Fouvent-Saint-Andoche, NE France. Map realized using Geoatlas software and Geoportail open-access site.

current and fossil hyenas (Cuvier 1825), first reference of fossil wolverine in France (Gervais 1870) and first definition of a Pleistocene carnivore den (Thirria 1828, 1833; Nodot 1858-1859).

Nodot (1858-1859) advanced several arguments in favour of bone accumulation by cave hyenas. He highlighted the correlation between tooth marks, morphology of bone fractures and consumption of bones by carnivores. The first synthesis carried out on Fouvent was published by Bouillerot (1881). In comparison with observations and interpretations given at Kirkdale Cave (Buckland 1822), Bouillerot concluded that Fouvent was undoubtedly a hyena den cave.

The most recent excavations took place at the end of the 1990s. This area has been systematically excavated under the direction of J. Detrey between 1989 and 1992 (Detrey 1992; Fosse 1997). A very abundant faunal material and a small lithic assemblage composed of nearly 300 elements (cores, tools, and splinters) were reported to Châtelperronian or Mousterian facies (Fosse 1997). To date, only a small part of the “ancient” cavity has been excavated and studied.

STRATIGRAPHY

The recent excavations (dir. Detrey) have been focused on a 20 m² surface. These fieldworks allowed recovering an abundant and species-rich paleontological material, in-situ within a cryoclastic sedimentary matrix (typical for cold intervals).

Four main stratigraphic levels have been recognized, based on the observation and description of the sediment (Fig. 2).

The upper levels (E) are characterized by silty clay layers. The sedimentological analysis concludes to a deposit by run-off water and/or colluvial phenomenon (poor vegetal cover). Levels A and B are largely composed of rocks and cryoclastic gravels. The different grain sizes of the cryoclastic gravel as well as the collapsed blocks in the matrix permit to make a subdivision of the layer B into two levels: B1 and B2. The layer C is a silty clay horizon interbedded with fine cryoclastic gravel with angular elements. The major part of the sequence indicates relatively cold climatic conditions (Morin *in* Detrey 1992). A betterment of climatic conditions (temperature and humidity increase) throughout the documented sequence is suggested by the identification of silt levels which alternate with cryoclastic material and trace of gelifraction.

MATERIAL AND METHODS

Our study includes both the 1842 sample corresponding to Dubois' excavations during the 1800s, first published by Nodot (1858-1859) and revised by Lovis (1968), and the bone material unearthed during modern excavations, between 1989-1992 (dir. Detrey). We have observed a total amount of 14977 bone remains (both identifiable and

TABLE 1. — Faunal list of the late Pleistocene locality of Fouvent-Saint-Andoche, NE France (NISP, MNI, MNE, and frequencies) for each level (A-E), out of sequence (OS), and for historical excavations (1842).

Species	1842		E		E/A		A		A/B		B		B/C		C		OS		All layers				
	NISP	MNI	NISP	MNI	NISP	MNI	NISP	MNI	NISP	MNI	NISP	MNI	NISP	MNI	NISP	MNI	NISP	MNI	NISP	MNI	%NISP	MNE	MNI
<i>Crocota crocuta spelaea</i>	24	3	11	4	10	5	98	15	25	8	283	36	9	3	322	37	68	10	850	6	792	121	31
<i>Panthera (Leo) spelaea</i>	–	–	–	–	–	–	3	2	–	–	7	3	–	–	2	1	1	1	13	<1	13	7	2
<i>Panthera</i> sp.	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	1	–	–	1	<1	1	1	<1
<i>Ursus spelaeus</i>	4	3	–	–	–	–	4	2	–	–	1	1	–	–	7	2	1	1	17	<1	17	9	2
<i>Canis lupus</i>	–	–	1	1	1	1	4	3	–	–	17	2	1	1	8	2	5	2	37	<1	37	12	3
<i>Vulpes vulpes</i>	4	1	3	1	–	–	1	1	1	1	4	1	–	–	–	–	–	–	13	<1	12	5	1
cf. <i>Alopex</i>	–	–	–	–	–	–	–	–	–	–	1	1	–	–	–	–	–	–	1	<1	1	1	<1
<i>Vulpes/Alopex</i>	–	–	2	1	2	1	13	2	2	2	26	2	2	1	9	1	6	2	62	<1	55	12	3
<i>Gulo gulo</i>	1	1	1	1	2	1	1	1	–	–	2	1	–	–	–	–	2	1	9	<1	9	6	2
<i>Meles meles</i>	–	–	1	1	9	2	4	2	5	2	3	2	–	–	–	–	3	1	25	<1	24	10	3
<i>Martes</i> sp.	–	–	–	–	1	1	–	–	–	–	1	1	–	–	–	–	–	–	2	<1	2	2	1
<i>Mustela evermanni</i>	–	–	–	–	–	–	–	–	–	–	2	1	–	–	–	–	–	–	2	<1	2	1	1
<i>Mustela</i> sp.	–	–	–	–	3	1	1	1	–	–	3	1	–	–	–	–	1	1	8	<1	7	4	1
Carnivora (large)	–	–	5	–	6	–	7	–	4	–	17	–	1	–	5	–	12	–	57	<1	–	–	–
Carnivora (small)	–	–	–	–	5	–	2	–	–	–	5	–	–	–	–	–	1	–	13	<1	–	–	–
Total Carnivora	33	8	24	9	39	12	138	29	37	13	372	52	13	5	354	44	100	19	1110	7	972	191	49
<i>Mammuthus primigenius</i>	3	1	3	1	4	1	20	–	3	1	89	1	5	1	48	2	47	–	222	2	63	8	2
<i>Coelodonta antiquitatis</i>	11	2	1	1	2	1	15	4	3	1	80	10	6	3	72	10	35	7	225	2	178	39	10
<i>Megaloceros giganteus</i>	6	2	–	–	4	2	6	3	3	1	16	4	1	1	7	2	3	1	46	<1	45	16	4
<i>Cervus elaphus</i>	4	3	1	1	3	1	6	1	–	–	5	1	1	1	5	1	5	1	30	<1	29	10	2
<i>Rangifer tarandus</i>	5	1	–	–	3	2	16	1	3	1	38	3	3	2	27	3	18	3	113	1	94	16	4
<i>Capreolus capreolus</i>	–	–	2	1	–	–	–	–	–	–	6	1	–	–	–	–	3	1	11	<1	9	3	1
Cervidae	–	–	1	–	–	–	4	–	1	–	8	–	–	–	6	–	1	–	21	<1	–	–	–
<i>Equus caballus</i>	58	4	8	2	24	3	137	9	29	6	309	16	13	2	228	14	116	10	922	6	827	62	17
Equidae	3	–	1	–	–	–	2	–	–	–	7	–	–	–	2	–	2	–	17	<1	14	–	–
<i>Bos/Bison</i>	17	3	1	1	5	1	51	5	9	3	79	8	5	1	58	6	16	3	241	2	191	31	8
Ungulata	–	–	3	–	–	–	11	–	–	–	17	–	–	–	6	–	6	–	43	<1	–	–	–
Ungulata (small)	–	–	3	–	6	–	17	–	11	–	35	–	–	–	7	–	28	–	107	1	–	–	–
Ungulata (medium)	1	–	2	–	5	–	8	–	8	–	21	–	3	–	15	–	31	–	94	1	–	–	–
Ungulata (large)	3	–	3	–	5	–	15	–	7	–	39	–	1	–	36	–	18	–	127	1	–	–	–
Total Ungulata	111	17	29	7	61	11	308	24	77	13	749	44	38	11	517	39	329	26	2219	15	1457	192	49
<i>Lepus</i> sp.	1	1	1	1	–	–	–	–	–	–	–	–	–	–	1	1	–	–	3	<1	3	3	1
<i>Sciurus</i> sp.	–	–	–	–	1	1	–	–	–	–	–	–	–	–	–	–	–	–	1	<1	1	1	<1
<i>Marmota marmota</i>	–	–	1	1	2	1	7	–	1	1	1	1	–	–	2	1	–	–	14	<1	12	5	1
Mesomammals	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	1	<1	–	–	–
Undetermined	–	–	47	–	177	–	1544	–	242	–	4883	–	240	–	2348	–	2148	–	11629	78	–	–	–
Total	145	26	102	18	280	25	1997	53	357	27	6005	97	291	16	3222	85	2578	45	14977	100	2445	392	100

unidentifiable) distributed as follows: 145 specimens in the 1842 sample and 14832 specimens in the 1989-1992 sample. The identifiable specimens (3347 NISP) have been referred to 27 taxa, at species, genus or family level, including 12 carnivores and 7/8 ungulates (Table 1).

Our revision of the historical sample highlights several differences with the previous study realized by Lovis (1968). For instance, the cave bear *Ursus spelaeus* Rosenmüller & Heinroth, 1794 is the only ursid we have recognized (4NISP), whereas Lovis (1968) was considering the co-occurrence of the brown bear *Ursus arctos* and of the cave bear in Fouvent. On the other hand, several taxa within this assemblage are recognized for the first time, such as the red fox (*Vulpes vulpes* Linnaeus, 1758; four specimens), an unidentified lagomorph (1NISP), the wolverine (*Gulo gulo* Linnaeus, 1758, 1NISP) and the reindeer (*Rangifer tarandus* (Linnaeus, 1758), 5NISP). The material unearthed in 1989-1992 is much more numerous. Each

archeological level is characterized by the prominence of the horse *Equus germanicus* Nehring, 1884 (27.3%NISP, 16.8%MNI) and of the cave hyena *Crocota crocuta spelaea* (Goldfuss, 1832) (25.4%NISP, 30.8%MNI). Other taxa with a significant sample are a large bovid *Bos/Bison* (7.2%NISP, 7.5%MNI), the woolly rhinoceros *Coelodonta antiquitatis* (Blumenbach, 1799) (6.7%NISP, 9.9%MNI), the woolly mammoth *Mammuthus primigenius* Blumenbach, 1799 (6.6%NISP, 2%MNI), and the reindeer *R. tarandus* (3.4%NISP, 4.1%MNI).

The palaeontological analysis, focused on the identification of the faunal spectrum, aims at characterizing paleoenvironmental parameters, mostly based on osteometrical variables. The measurement protocol follows Von den Driesch (1976). However, the detailed analysis of peculiar species (e.g., hyena or horse) implies using specific measurements. Even if we could find a wide array of published data for these species, it appears that each author uses his

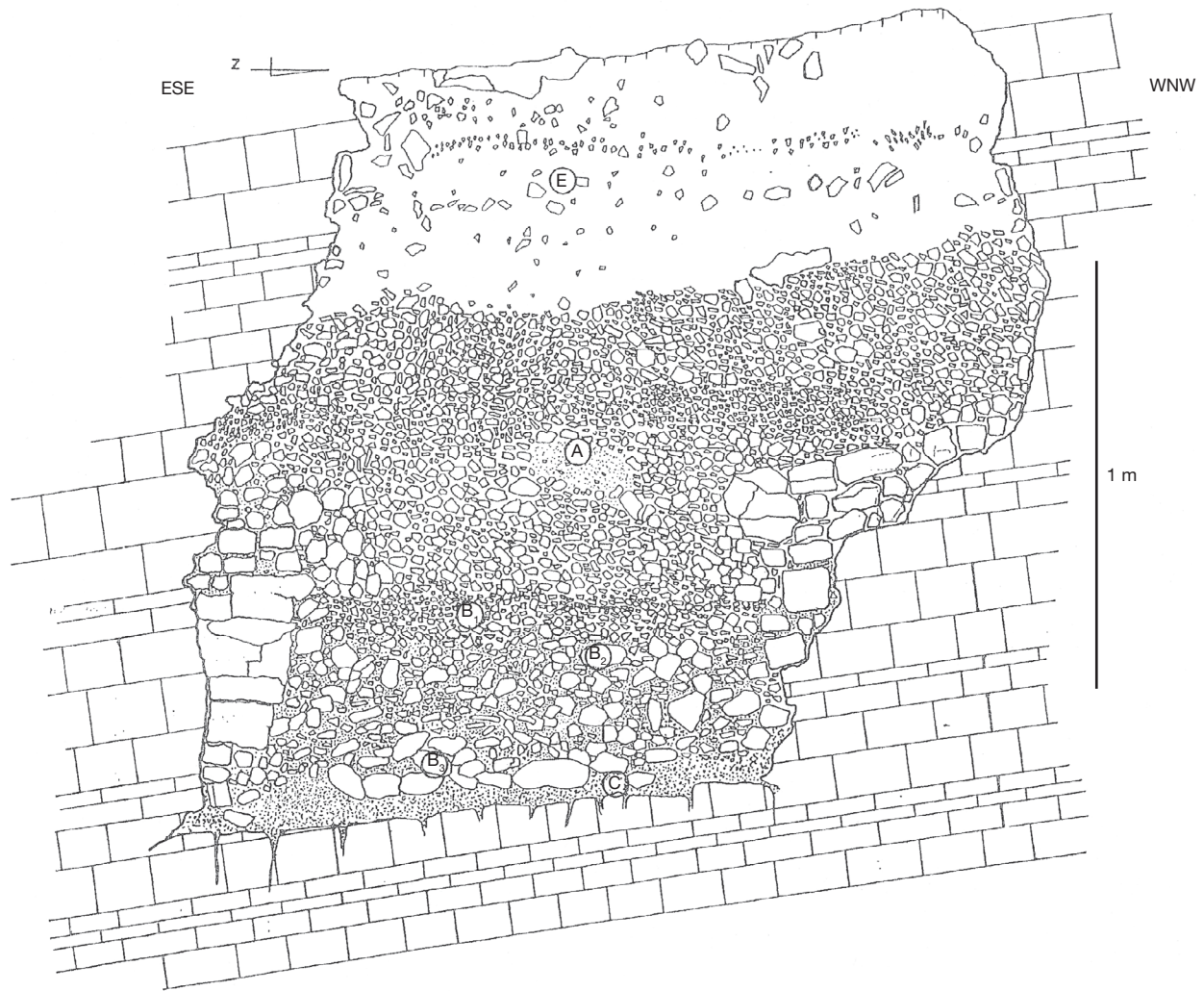


Fig. 2. — Stratigraphic sequence from Fouvent-Saint-Andoche (modified from Detrey 1992). Abbreviations: see text p. 239.

own measurement protocol, especially for hyenas (e.g., Ehrenberg 1938-1940; Clot 1980; Argant 1988; Dufour 1989; Cardoso 1994; Ambros 1998; Turner 2001; Baryshnikov & Tsoukala 2010). Accordingly, we selected several measurements that we considered as relevant for this study. The results are expressed in millimeters, in tables including the number (n) of measured specimen, the smallest (min) and largest (max) dimensions, the Mean and the standard-deviation (SD). Three main quantification units are used in this study: the number of identified specimens (NISP), the minimum number of elements (MNE) and the minimum number of individuals (MNI). For horses, confidence interval for the mean (95%) is also provided. Test and specific routines are calculated using both softwares *R*© (versions 2.13.2 and 2.14.0) and *XLStat*© (Version 11.4.07). We also used Kruskal-Wallis test of the one-way analysis of variance by rank (Kruskal & Wallis 1952). This method can be considered as the non-parametric equivalent of the ANOVA. It is used to compare more than two samples of different sizes and makes no assumptions about the shape of the distributions.

ABBREVIATIONS

B	breadth;
Bd	distal end transverse length;
Bp	proximal end transverse length;
B acet.	acetabulum breadth;
B incis.	breadth of the <i>incisura trochlearis</i> (ulna);
GL	greatest length;
H incis.	Height of the <i>incisura trochlearis</i> (ulna);
H int. mand.	height of <i>corpus mandibulae</i> (internal side);
L	length;
Ld	distal end, antero-posterior length;
Lp	proximal end, antero-posterior length;
L acet.	acetabulum length;
L metac.	metacone length, upper carnassial;
L para.	paraconid length, lower carnassial;
L proto.	protoconid length, lower carnassial;
L trig.	trigonid length, lower carnassial;
max	largest measured dimension;
min	smallest measured dimension;
MNE	minimum number of elements;
MNI	minimum number of individuals;
n	number of measured specimens;
NISP	number of identifiable specimens;
SD	standard-deviation;
W mand.	width of <i>corpus mandibulae</i> .

SYSTEMATIC PALAEOLOGY

Order CARNIVORA

Bowdich, 1821 [description JBF, PFos]

The observation of 1110 carnivore remains allows us to recognize 11 distinct taxa (either at species or genus level) related to Felidae, Hyaenidae, Canidae, Ursidae, and Mustelidae. The cave hyena is the main species, as it is represented by 850 bone and tooth remains (Fig. 3). Other carnivore species are quite rare: less than 50 elements have been observed for each species, excluding the small canids (Fig. 4).

Suborder CANIFORMIA Kretzoi, 1943

Family CANIDAE Fischer de Waldheim, 1817

Subfamily CANINAE Fischer de Waldheim, 1817

Genus *Canis* Linnaeus, 1758

Canis lupus Linnaeus, 1758

MATERIAL EXAMINED. — NISP=37; MNI=12.

1989-1992 sample: 1 left maxillary; 2 left I3; 1 right C; 1 left P4; 1 left M2; 3 right i1; 6 left i1; 1 i1?; 1 right i2; 1 left i2; 1 left i2-3; 1 right c; 1 left c; 1 left p3; 1 right p4; 1 right m1; 1 right m2; 1 left m3; 1 canine?; 1 right ulna; 1 left ulna; 1 left tibia; 1 left metatarsal II; 3 first phalanges; 3 second phalanges.

DESCRIPTION

In Europe, two medium-to-large-sized canids coexist during the Late Pleistocene: wolf *Canis lupus* and dhole *Cuon alpinus* Pallas, 1811. Their association in a same geochronological context suggests their potential identification in palaeontological samples (Perez-Ripoll *et al.* 2010; Pionnier-Capitan *et al.* 2011). Thirty seven bone remains recovered from the recent excavations have been related to large canids. The right lower carnassial (m1 – F9.C.264) has a large talonid with two cusps which is typical of wolves (Fig.4D, E). The general proportions of this carnassial (breadth=12.5 mm, length=27 mm) and of the left upper carnassial (P4 – H8.C.240) (breadth=13 mm, length=25 mm) match the range recorded for Late Pleistocene wolves (breadth and length variations in m1 11.1-13.2 by 26.5-33.4 mm and in P4 12.3-15.3 by 23.8-29.9 mm *in* Schütt 1969; Boudadi-Maligne 2010; Brugal & Boudadi-Maligne 2011). Yet, these carnassials are smaller than the ones referred to as *Canis lupus maximus* Boudadi-Maligne, 2012, described at Jaurens (OIS3; Boudadi-Maligne 2012).

Postcranial remains are also referable to *C. lupus*. In particular, the morphological features of the fragmentary left tibia G11.B.109 are diagnostic of *Canis*, as defined by Pionnier-Capitan *et al.* (2011): the border of the medial malleolus is salient and prominent, whereas the distal border of the cranial side is straight and regular; moreover, the proximo caudal tuberosity of the ulnar olecranon E11.B.112 is more prominent in *Canis* as observed by Pionnier-Capitan *et al.* (2011). To sum up, the large canid from Fouvent is unambiguously referable to *Canis* (morphological features) and more precisely to *Canis lupus* (dimensions).

Genus *Vulpes* Linnaeus, 1758

Vulpes vulpes Linnaeus, 1758

MATERIAL EXAMINED. — NISP=13; MNI=5.

1842 sample: 2 left humeri; 1 right tibia; 1 left tibia.

1989-1992 sample: 2 right c; 1 right mandible; 2 left mandibles; 1 left ulna; 1 left metacarpal II; 1 right calcaneus; 1 left metatarsal V.

DESCRIPTION

Among the small canids remains (n=76), some of them have been associated to the red fox *Vulpes vulpes* (n=13) corresponding to five adults. The low number of elements determined at species level is related both to the state of conservation of the material and to the difficulties to distinguish *Vulpes* and *Alopex* Kaup, 1829. The red fox is a small common carnivore in Pleistocene bone assemblages (e.g., Gönnersdorf *in* Poplin 1976; Gerde *in* Clot 1980). This predator is ubiquitous and well-represented during different Pleistocene glacial and interglacial climatic phases. In France, the red fox is found at Nauterie II (layer 11: Mindel-Riss), at Montmaurin-la-Niche, Nestier, and Gerde (Riss); it then cooccurs with the arctic fox *Alopex lagopus* (Linnaeus, 1758) throughout Würmian times, before it becomes a common carnivore during Holocene times (Clot & Duranthon 1990). Morphometrical similarities and potential co-occurrence of red and arctic foxes during the Oxygen Isotopic Stage 3 (OIS3; Cohen & Gibbard 2011) necessitate performing a careful analysis of the bone material. At Fouvent, cranial and dental elements are represented by a left mandibular branch with p2-m2, a fragment of left mandible with m1 and m2, and a broken right mandible with m1 and m2 with two canines. As regards the red fox, according to Poplin (1976), the lower canines are longer and thinner in comparison with *isatis*. At Gerde, Clot (1980) also pointed out the great difficulty to make the distinction between *Vulpes* and *Alopex* but determined the canines of fox based on their general proportions. We attributed the material of Fouvent to the red fox on the base of the concerned morphometrical data. Our three m1s (G8.B.509b, D11.E.3 and G8.B.507) leave no doubt for their specific assignment. Their large dimensions (respectively B = 6.4-6-6 with L = 16-16-16) match perfectly those of red foxes as provided at Gerde (Clot 1980: table 49) and at Gönnersdorf (Poplin 1976: 48 fig. 28). Postcranial elements of red fox include two humeri, one ulna, one metacarpal II, two tibiae, one calcaneus and one metatarsal V. The measurements are summarized in Table 2. According to Altuna (2004), the breadth of the distal humerus of the red fox ranges between 17.2 and 23.8 mm while Clot (1980) gives an interval comprised between 19.2 and 22 mm. According to these studies, the distal breadth of *isatis* is not greater than 19.5 mm, consequently the humerus of Fouvent (1842.118) is quite similar in size to the red fox. Published metric data available for the ulna are rare but the dimensions of the specimen of Fouvent suggest without no doubt an attribution to *Vulpes*.

The total length (47 mm) of the left metacarpal II (G8.A/B.165) of Fouvent is larger in comparison to the measurements of red fox (Altuna 2004). However, the left metacarpal falls into

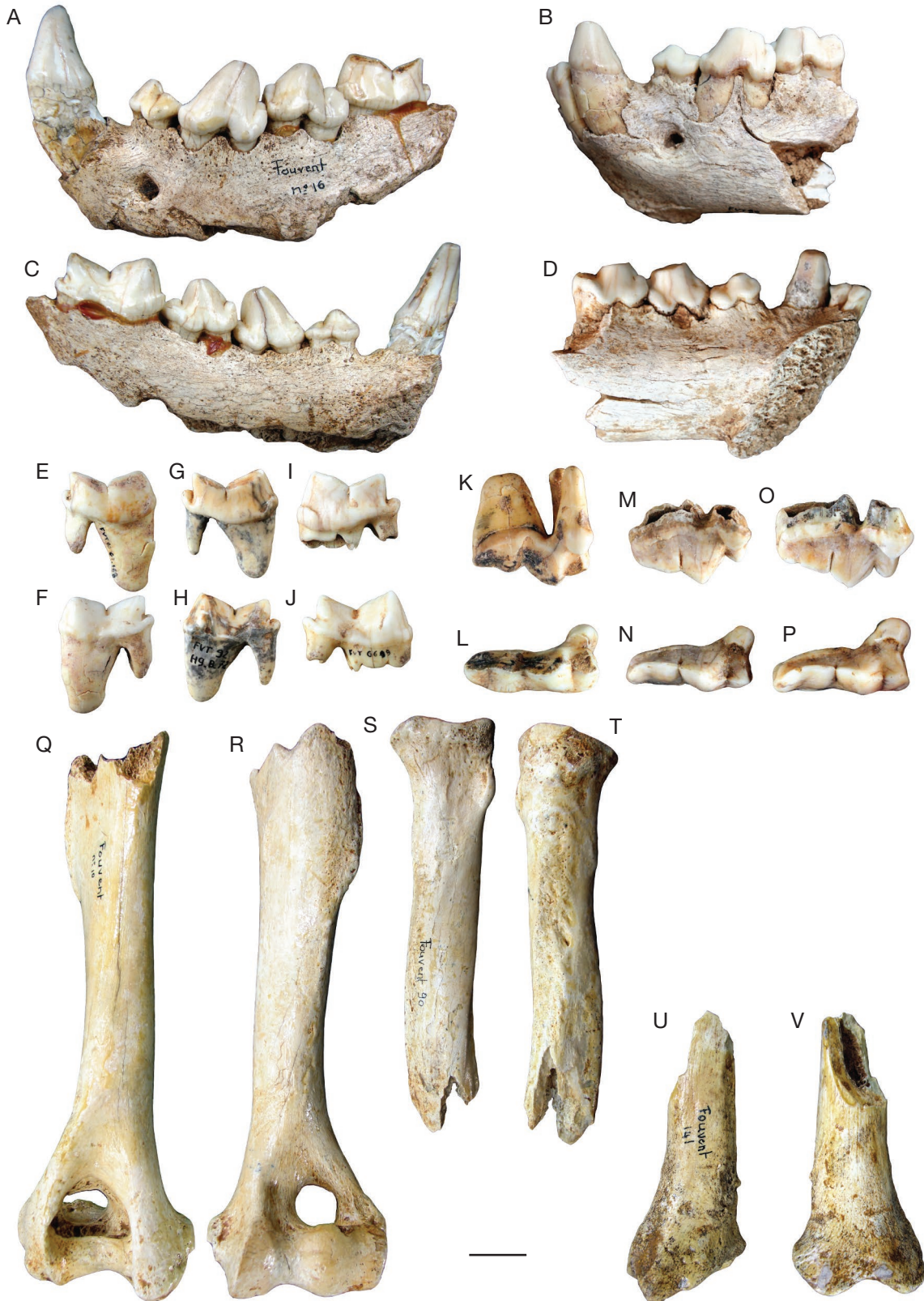


FIG. 3. — Cave hyena *Crocuta crocuta spelaea* (Goldfüss, 1832) remains from Fouvent-Saint-Andoche: **A-D**, left mandibles 1842.16 (**A, B**) and G6.82 (**C, D**); **E-J**, right G7.168 (**E, F**), H9.B.72 (**G, H**) and left G6.9 (**I, J**) lower carnassials; **K-P**, left upper carnassial F11.C.281 (**K, L**), no number (**M, N**) and G9.B.444 (**O, P**); **Q, R**, left humerus 1842.10; **S-T**, left radius 1842.90; **U-V**, right tibia 1842.141. Scale bar: 20 mm. Pictures by JBF.

TABLE 2. — Postcranial measurements of *Vulpes vulpes* Linnaeus, 1758 from Fouvent-Saint-Andoche (in mm). Abbreviations: *, dimensions of the tuber calcanei; **sin**, left; **dext**, right. Other abbreviations: see text.

N°	Element	Side	GL	H incis	B incis	Bp	Lp	Bd	Ld
1842.118	Humerus	Sin	–	–	–	–	–	20.0	15.0
E10.B.10	Ulna	Sin	–	14.0	10.0	–	–	–	–
G8.A/B.165	2 nd Metacarpal	Sin	47.0	–	–	5.0	7.0	6.5	5.5
1842.119	Tibia	Sin	–	–	–	–	–	16.0	12.0
1842.92	Tibia	Dext	–	–	–	23.5	25.0	–	–
G8.E.26	Calcaneus	Dext	29.0	–	–	6.5*	9.8*	–	–
F9.B.135	5 th Metatarsal	Sin	56.0	–	–	4.0	8.0	6.0	6.0

TABLE 3. — Measurements of the Vth metatarsal of red and polar foxes, from Fouvent-Saint-Andoche (Fvt) and various localities (fossil and modern), in mm. Abbreviations see in text.

Taxon	Site	GL	Bp	Lp	Bd	Ld	Reference
	Fvt 90-92 G8.B.288	51.0	6.0	8.0	5.7	5.0	this study
<i>A. lagopus</i>	Aurensan inférieur	50.6	6.6	7.1	–	4.9	Clot 1980
	Predmost	46.0-48.0 (n=2)	5.0-5.7 (n=2)	6.5-6.4 (n=2)	5.2-5.7 (n=2)	5.0-5.0 (n=2)	Clot 1980
	Prolom 2 (OIS3)	42.7-47.5 (n=5)	4.5-6.6 (n=13)	–	4.7-5.8 (n=5)	4.1-4.7 (n=5)	Baryshnikov 2006
	Siuren 1 (OIS3)	44.9-50.0 (n=3)	5.0-6.1 (n=3)	–	5.6-5.8 (n=3)	4.4-4.9 (n=3)	Baryshnikov 2006
	Modern	42.0-51.0 (n=9)	–	–	–	–	Altuna 2004
<i>V. vulpes</i>	Coulet des Roches (OIS2)	56.8-66.5 (n=7)	6.7-8.0 (n=8)	7.6-9.0 (n=8)	5.7-7.3 (n=8)	5.5-6.2 (n=8)	Crégut-Bonnoure <i>et al.</i> 2010
	Gerde (OIS3)	56.5-65.2 (n=7)	6.0-7.8 (n=14)	6.3-8.3 (n=14)	5.9-6.8 (=8)	5.7-6.2 (n=8)	Clot 1980
	Modern	49.0-68.0 (n=26)	–	–	–	–	Altuna 2004

the variation range as provided by Clot (1980) for Pleistocene populations of *Vulpes*. The same is true for the measurements of both a proximal and a distal tibiae (respectively n°1842.119 and 1842.92) that we also assigned to the red fox.

In the Table 3, the maximum length (56 mm) of the left metatarsal V (F9.B.135) is roughly similar to the mean value observed in living foxes (Altuna 2004) corresponding to their smaller pleistocene representatives (Clot 1980). We observed the same thing with the maximum length of the calcaneus G8.E.26 (only 29 mm) that could be associated to a small red fox, while populations of *isatis* only reach a maximum of 28.4 mm.

cf. *Alopex* sp.

MATERIAL EXAMINED. — NISP=1; MNI=1.
1989-1992 sample: 1 right metatarsal V.

DESCRIPTION

A small right metatarsal V (Fvt 90-92 G8.B.288) could be related to the polar fox. Osteometrical comparison of this element with other modern or Würmian populations of both red and polar fox allows us to refer the concerned remain to as *Alopex* (Table 3). The metatarsal length (GL=51 mm) matches the larger specimens recorded in Pleistocene samples (Clot 1980; Baryshnikov 2006) and modern populations (Altuna 2004). However, the proximal breadth (Bp) is large (8 mm) and could coincide with measurements of the red fox. But, in contrast, metatarsals V of *Vulpes* with a length lower than 55 mm seems to be uncommon. This kind of small-sized red fox has been only recorded in extant populations (Altuna 2004). However, the recorded dimensions overlap those of both *Vulpes* and *Alopex*.

As such, the metatarsal V from Fouvent could either belong to a very small red fox or to a large polar fox. The geochronological context of Fouvent and the proportions/dimensions of the concerned bone are compatible with the presence of *A. lagopus*. Accordingly, we prefer to let this specimen in open nomenclature, referring it to as cf. *Alopex* sp.

Family MUSTELIDAE Fischer de Waldheim, 1817
Subfamily MUSTELINAE Fischer de Waldheim, 1817
Genus *Gulo* Linnaeus, 1758

Gulo gulo Linnaeus, 1758

MATERIAL EXAMINED. — NISP=9; MNI=6.

1842 sample: 1 left tibia.

1989-1992 sample: 1 left P3; 1 left humerus; 1 right ulna; 1 left ulna; 2 right innominates; 1 left innominate; 1 right femur.

The Pleistocene wolverine was recorded for the first time in France at Fouvent (Gervais 1870). This inhabitant of modern arctic areas (Pastichniak-Arts & Larivière 1995) was a conspicuous element of Last Glacial Maximum faunas in Europe (Kurtén 1968). Although it is found in many sites (review in Döppes 2001), detailed descriptions of both cranial and postcranial elements are quite rare (e.g., Villereversure *in* Martin 1968; Jaurens *in* Mallye & Guérin 2002). Nine remains from Fouvent (representing six individuals) have been attributed to the wolverine.

Seven remains brought to light some additional morphometrical features of the knowledge of this species (Table 4). For example the P3 (F11.B.223) shows a fairly massive crown which is made of a single antero-posterior cusp crossed by a protruding edge. Moreover, a cingulum is strongly developed



FIG. 4. — Carnivores (other than hyenas) remains from Fouvent-Saint-Andoche, exclusive of hyenas: **A, B**, *Panthera (Leo) spelaea* (Goldfuss, 1810) right upper canines E11.224 (**A**) and H8.C.241(**B**); **C**, *Panthera (Leo) spelaea* (Goldfuss, 1810) left lower carnassial F10.A.48; **D, E**, *Canis lupus* Linnaeus, 1758 right lower carnassial F9.C.264; **F**, *Vulpes vulpes* Linnaeus, 1758 left mandible E11.A.15; **G, H**, *Mustela (Putorius) eversmannii* left mandible F11.B.214; **I**, *Gulo gulo* Linnaeus, 1758 left innominate; **J, K**, *Ursus spelaeus* Rosenmüller & Heinroth, 1794 right M2 G9.B.558. Scale bar: 20 mm. Pictures by JBF.

at the base of the lingual side. The dimensions of this tooth compared to large recent and fossil mustelids (Wolverine and Badger) permit us to identify it as *G. gulo* (Fig. 5). Furthermore, morphometrical data allow us to exclude the Badger

Meles meles Linnaeus, 1758. Finally the specimen of Fouvent has relatively small dimensions compared to the Pleistocene gluttons but fits well among the greatest living representatives of *G. gulo*.

TABLE 4. — Measurements of *Gulo gulo* Linnaeus, 1758 remains from the Late Pleistocene hyena den of Fouvent-Saint-Andoche, NE France. Measurements in mm. *, juvenile; **sin**, left; **dext**, right. Other abbreviations: see text.

N°	Element	Side	B	L	GL	Bp	Lp	B incis	H incis	Bd	Ld	B acet	L acet
1842-144	Tibia	Sin	–	–	–	31.0	29.0	–	–	–	–	–	–
F10.B.129	Ulna	Dext	–	–	–	–	–	15.0	17.0	–	–	–	–
F9.E.14	Ulna	Sin	–	–	–	–	–	15.0	–	11.0	16.0	–	–
F11.B.223	P3	Sin	5.0	11.0	–	–	–	–	–	–	–	–	–
G9.A.24	Innominate	Sin	–	–	128.0	–	–	–	–	–	–	21.	20.0
G8.E/A.23	Humerus*	Sin	–	–	–	26.0	26.0	–	–	–	–	–	–
H9.9	Femur*	Dext	–	–	–	–	–	–	–	27.4	26.0	–	–

TABLE 5. — Mandibular measurements of *Mustela eversmanii* Lesson, 1827 from Fouvent-Saint-Andoche (F11.B.201 and F11.B.214). Measurements in mm. *, alveolar dimensions. Abbreviations: see text.

Taxon	Site	H. int. mand.	W. mand.	L m1	Reference
	F11.B.201	10.0	–	10.0	This study
	F11.B.214	11.0	4.8	9.3	This study
<i>Mustela eversmanii</i>	Romain-la-Roche RO.85.S16.2	12.3	5.2	9.0*	Fosse & Fourvel 2010
	Gigny	9.2	4.6	8.2	Delpech 1989
	Gigny	7.7	4.7	8.3	Delpech 1989
	La Fage	8.2	5.0	7.7	Huguency 1975
	Soyons	9.1	4.0	8.8	Koby 1964
	Trois-Frères	9.4	–	9.1	Koby 1964
	Kaltbrunnental	11.2	–	9.4	Koby 1964
	Mauer	11.0	–	–	Koby 1964
	Sirgenstein I	9.1	–	8.2	Koby 1964
	Sirgenstein II	9.8	–	9.1	Koby 1964
	Hohlefels	9.9	–	9.1	Koby 1964
<i>Mustela putorius</i>	Romain-la-Roche RO.86.Q15.33	7.2	–	7.6	Fosse & Fourvel 2010
	Sima de Los Huesos (n=5)	7.4 ± 0.4	–	7.9 ± 0.7	Garcia 2003
	Interlaken	7.0	–	8.1	Koby 1964
	Coll. Géol. Talence (n=3)	7.1 ± 0.3	4.1 ± 0.1	8.4 ± 0.3	Koby 1964
	Gerde (n=4)	8.2 ± 1.2	4.7 ± 0.3	8.1 ± 0.2	Clot 1980
	Pair-non-Pair (n=7)	9.1 ± 1.0	5.1 ± 0.5	9.1 ± 0.8	Clot 1980
	Coulet des Roches (n=3)	9.6-8.5-9.3	6.1-5.3-5.3	9.1-9.0-8.6	Crégut-Bonnoure <i>et al.</i> 2010
Aven des Planes	7.2	3.9	8.2	Crégut-Bonnoure <i>et al.</i> 2010	

Genus *Meles* Linnaeus, 1758

Meles meles Linnaeus, 1758

MATERIAL EXAMINED. — NISP=25; MNI=10.

1989-1992 sample: 1 left c; 1 canine; 2 thoracic vertebrae; 1 right scapula; 1 right radius; 1 left radius; 1 right ulna; 2 right metacarpals IV; 1 left metacarpal IV; 1 left metacarpal V; 1 right femur; 1 right innominate; 1 left femur; 1 femur; 1 patella; 2 right tibiae; 1 left tibia; 2 right metatarsals IV; 1 left metatarsal V; 1 first phalanx; 1 third phalanx.

DESCRIPTION

The badger *M. meles* is frequently found in Pleistocene samples. His role in bone assemblage disturbance and stratigraphic significance are regularly evoked (Clot & Duranthon 1990; Mallye 2007). It is clearly attested in Fouvent (NISP=25; MNI=10); the type of preservation/alteration of the concerned specimens supports their contemporaneity with the bulk of inventoried material. Their robustness and morphological features perfectly fit those of *M. meles*. In particular, the greatest lengths (GL) of all three metacarpals IV (36, 32.4, and 32.5 mm, respectively) fall within

the size range of Pleistocene badgers (between 28 and 32.5 mm; Ambros 2006) even if one of them appears larger than the compared data.

During the Late Pleistocene interval in Europe, *Meles* is only represented by *M. meles* (Kurtén 1968; Mallye & Guérin 2002). Accordingly, we have referred the concerned specimens to that species.

Genus *Mustela* Linnaeus, 1758

Mustela eversmanii Lesson, 1827

MATERIAL EXAMINED. — NISP=2; MNI=1.

1989-1992 sample: 1 right mandible; 1 left mandible.

DESCRIPTION

The bone sample from the recent excavations includes several remains attributed to small Mustelidae, among which a pine marten or a beech marten (NISP=2) and a smaller one related to genus *Mustela* (NISP=8). Two mandibles of greater size (related to a single individual) has been observed

in detail. Based on their general characters and size, the specific determination of these pieces could only be related to a polecat (European polecat *Mustela putorius* or steppe polecat *M. eversmanii*).

These species at Fouvent do not imply the same environmental conditions for the deposit. Morphologically, the mandible of steppe polecat is distinguished from the common polecat by a bulge of the horizontal branch under the m1 just below the paraconid (Hugueney 1975; Delpéch 1989). The mandible F11.B.214 (Fig. 4G, H) clearly shows this morphological feature. In addition, the dimensions of the two hemi-mandibles as well as the carnassials (L/B of m1 respectively 10/4 and 9.3/3.7 mm) suggest large-sized animals, similar to those of the steppe polecat (Table 5). Accordingly, everything concurs unambiguously to assign those remains to *Mustela eversmanii*.

Family URSIDAE
Fischer de Waldheim, 1817
Genus *Ursus* Linnaeus, 1758

Ursus spelaeus Rosenmüller & Heinroth, 1794

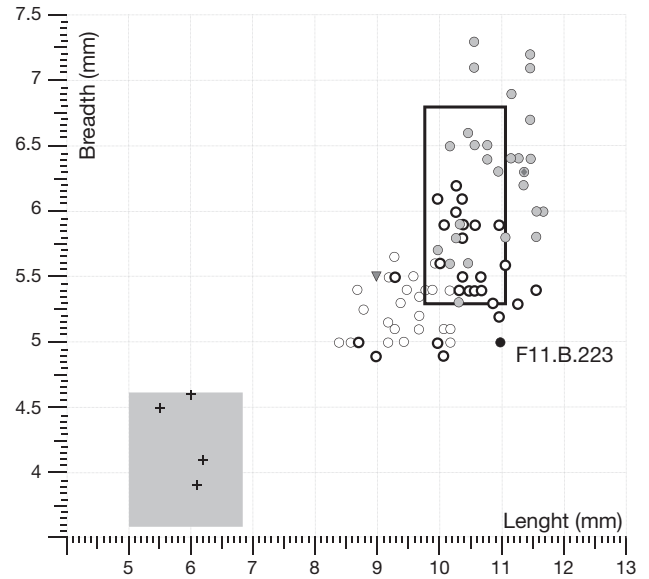
MATERIAL EXAMINED. — NISP=17; MNI=9.

1842 sample: 1 left maxilla; 1 right M1; 1 right mandible; 1 right m3.

1989-1992 sample: 1 right I2; 2 right I3; 1 left I3; 1 left C; 1 right M2; 1 right i1-3; 2 left c; 1 left m2; 1 left m3; 1 canine?; 1 lower molar?

DESCRIPTION

Bear remains are far from being well represented in the Fouvent assemblage. Seventeen elements, referred to nine individuals (adult and old bears) have been attributed to Ursidae. The original work of Lovis (1968), based on the 1842 sample, reports the presence of two different species: the brown bear *Ursus arctos* and the cave bear *U. spelaeus*. Re-examination of both this material and bone remains recovered from the 1989-1992 excavations allows identifying a single species, *U. spelaeus*. Morphometric data (Table 6) and morphological features (e.g., general shape and size of raw teeth, high development of numerous cusps) of unworn teeth (1842.66 left maxilla including M1 and M2; G9.B.558 right M2 (Fig. 4J, K); F10.C.263 left m3) relate unambiguously this material to the cave bear. The wide size range as recorded for a given dental locus (e.g., length ranging between 25.3 and 31 mm on M1 and between 40.5 and 48 mm on M2) might be due to either intraspecific variability or sexual dimorphism (marked in recent ursids). Such variability is often recorded for tooth length: Spahni (1954) recorded significant variations on M2 of bears from Austrian caves; a 38.5-48.7 mm range is observed on 18 teeth at Arcy-sur-Cure (Baryshnikov & David 2000); at Pestera cu Oase (Romania), the length of M2 ranges between 37.8 and 52.1 mm (Pacher & Quilès 2013). Be as it may, at Fouvent, the low number of teeth does not allow to test these variations in good statistical conditions.



- Fouvent-Saint-Andoche
- ▼ *Gulo schlosseri* L'Escale (Bonifay 1971)
- *Gulo gulo* Late Pleistocene: Aufhäuserner, Baumannshöhle Grotta dell' Orso, Ludvikova jama, Drachenhöhle, Predmost
- Slouper Höhle, Salzöfen, Zoolithen (Döppes 2001) (Bonifay 1971)
- Trois-Frères, Bouxes (Mallye & Guérin 2002) (Bonifay 1971)
- *Gulo gulo* extant female (Döppes 2001)
- *Gulo gulo* extant male (Döppes 2001)
- *Gulo gulo* modern (Mallye & Guérin 2002)
- + *Meles thoralis* Saint-Valler, Lunel-Viel (Bonifay, 1971)
- *Meles meles* modern (Mallye & Guérin, 2002)

FIG. 5. — Wolverine *G. gulo* Linnaeus, 1758 P3 breadth and length ratio compared to extant and extinct wolverine and badger populations. Measurements in mm. The extant wolverines and badgers areas figure the range (minimal to maximum measurement) obtained for each variables (breadth and length).

Suborder FELIFORMIA
Kretzoi, 1945
Family FELIDAE
Fischer de Waldheim, 1817
Subfamily PANTHERINAE
Pocock, 1917
Genus *Panthera* Oken, 1816

Panthera sp.

MATERIAL EXAMINED. — NISP=1; MNI=1.

1989-1992 sample: 1 fragment of right C.

DESCRIPTION

A fragment of a right upper canine is reported to a Pantherine (F9.C.226). The general size of the fragment suggest a large size species like leopard *Panthera pardus* or cave lion *Panthera (Leo) spelaea* but the intense surface modification (dissolution) and the difficulty to take any measurements do not allow us to make precise attribution. Consequently this specimen is related to *Panthera* sp.

TABLE 6. — Dental measurements of *Ursus spelaeus* Rosenmüller & Heinroth, 1794 from Fouvent-Saint-Andoche. Measurements in mm. *, estimated measurements; **sin**, left; **dext**, right. Other abbreviations: see text.

N°	Teeth	Side	B	L
H8.C.194	I2	Dext	11.0	12.0
G8.C.610	I3	Sin	16.0	16.0
F10.C.379	I3	Dext	16.0	16.4
F11.A.67	I3	Dext	14.0	17.0
G9.C.580	C	Sin	14.0	20.5
1842.66	M1	Sin	18.0	25.3
1842.69	M1	Dext	22.0	31.0
G9.B.158	M2	Dext	24.0	48.0
1842.66	M2	Sin	21.0	40.5
G.A.40	c	Sin	14.5	20.0
G8.C.613	c	Sin	14.0	19.0
1842.70	m1	Dext	14.0*	30.0*
H8.C.258	m2	Sin	18.7	29.0
F10.C.263	m3	Sin	22.0	29.2
1842.65	m3	Dext	19.0	30.5

TABLE 7. — Dental measurements of *Panthera (Leo) spelaea* (Goldfuss, 1810) from Fouvent-Saint-Andoche. Measurements in mm. Abbreviations: see text.

N°	Teeth	Side	B	L	L			
					para	proto	trig	metac
E11.224	C	Dext	19.3	26.0	–	–	–	–
G9.B.460	C	Dext	15.0	22.0	–	–	–	–
H8.C.241	C	Dext	16.0	23.0	–	–	–	–
H8.B.36	P4	Dext	45.0	22.0	–	–	–	18.0
E10.B.59	P4	Sin	35.4	16.0	–	–	–	14.2
G9.C.287	p3	Dext	9.0	19.0	–	–	–	–
G9.B.216b	p4	Sin	11.0	24.8	–	–	–	–
G9.B.216a	p4	Sin	12.0	24.5	–	–	–	–
G9.B.207a	m1	Sin	14.0	28.0	14.0	14.0	25.0	–
G9.A.64a	m1	Dext	14.0	29.0	13.8	14.0	26.4	–
G9.A.64b	m1	Dext	14.0	29.0	14.0	15.0	27.0	–
G9.B.207b	m1	Sin	14.0	28.0	14.0	14.2	26.0	–
F10.A.48	m1	Sin	13.8	29.0	14.0	15.0	27.0	–

TABLE 8. — Dental measurements of the cave hyena *Crocota crocuta spelaea* (Goldfuss, 1832) (both permanent and deciduous). Measurements in mm.

Dental Rank	Breadth			Length		
	N	Min-Max	Mean	N	Min-Max	Mean
C	15	12.0-14.0	13.2	13	17.0-18.0	17.5
P1	20	6.0-9.0	7.6	21	7.0-9.0	7.7
P2	16	12.0-14.8	13.5	16	16.0-19.0	17.7
P3	22	15.0-19.0	17.5	20	23.0-26.0	24.5
P4	19	19.0-23.0	21.6	16	35.5-42.0	39.7
D2	8	7.0-9.0	7.6	8	11.6-14.0	12.5
D3	6	13.0-15.0	13.5	13	21.3-23.7	22.6
D4	7	12.0-15.0	12.6	6	9.0-11.0	10.2
c	41	12.0-16.0	13.7	40	14.4-19.0	16.3
p2	20	10.5-13.7	12.2	21	14.0-18.5	16.5
p3	41	15.0-17.3	16.4	44	21.0-24.0	22.5
p4	62	12.0-17.4	14.9	64	21.5-26.0	24.0
m1	46	12.0-14.5	13.4	42	27.5-34.0	31.7
d2	11	5.0-7.2	6.3	11	9.5-12.0	10.8
d3	16	5.4-8.0	7.1	15	12.7-15.0	13.9
d4	21	7.0-9.0	8.0	17	19.0-21.0	19.6

Panthera (Leo) spelaea (Goldfuss, 1810)

MATERIAL EXAMINED. — NISP=13; MNI=7.

1989-1992 sample: 3 right C; 1 right P4; 1 left P4; 1 right mandible (including p3); 2 left p4; 2 right m1; 3 left m1.

DESCRIPTION

Thirteen cranio-dental remains (upper and lower teeth, mandible) have been attributed to the cave lion. This material and its stratigraphical distribution within the locality suggest a minimum number of seven individuals. Teeth measurements reveal significant size variability (Table 7). Many palaeontological, phylogenetic, and biogeographical works have focused on the cave lion (e.g., Burger *et al.* 2004; Hemmer 2011; Sabol 2011; Stuart & Lister 2011). In Europe, Late Pleistocene lions are both represented by the subspecies *Panthera (Leo) spelaea* described at Gailenreuth (OIS3, Germany), and the smaller form, *P. (Leo) spelaea* var. *cloueti* (Filhol, 1891) (Filhol & Filhol 1871) of Jaurens (Ballesio 1980) (OIS3, France).

The taxonomic status of the small morph is a matter of debate, given that such size discrepancy may either reflect ecomorphotypy or sexual dimorphism. At Fouvent, the ratio B/L of the P4 and the m1 compared with fossil and living populations leads to some comments on the size of the different clines (Fig. 6). Thus, on the base of the m1 of Jaurens, a clear distinction appears between large-sized lions (Jaurens *in* Ballesio 1980) and a smaller form (Jaurens *in* Ballesio 1980; Espèche *in* Clot *et al.* 1984). In addition, many osteometrical datasets for Late Pleistocene cave lions confirm significant variability for the m1 (specimens smaller than *P. spelaea* var. *cloueti* and also larger than the biggest form of Jaurens). Moreover, current data confirm the presence of a strongly marked sexual dimorphism, increasing the probability of significant overlap between osteometrical dimensions. In our opinion, the different sizes observed at Jaurens seem to be more related to intraspecific sexual dimorphism than to any evolutionary stage or stratigraphical age-based discrepancy. Consequently, if we consider the small form of Jaurens as characteristic of females, the m1 of Fouvent which are very close in size could belong to females. The same thing is true concerning the two P4s of Fouvent, both presenting extreme values. The larger one could be associated to a large-sized male and the smaller to a female. However, it would be necessary to undertake a thorough revision of cave lion intraspecific variability in order to validate the concerned hypothesis.

Family HYAENIDAE Gray, 1821

Genus *Crocota* Erxleben, 1777

Crocota crocuta spelaea (Goldfuss, 1832)

MATERIAL EXAMINED. — NISP=850; MNI=121.

1842 sample: 2 left mandibles; 1 atlas; 3 cervical vertebrae; 3 thoracic vertebrae; 1 left humerus; 1 left radius; 1 left ulna; 1 left metacarpal II; 1 right metacarpal V; 1 right innominate; 1 left innominate; 1 left femur; 2 right tibiae; 1 right calcaneus; 1 left calcaneus; 1 left talus; 1 right metatarsal IV; 1 right metatarsal V.

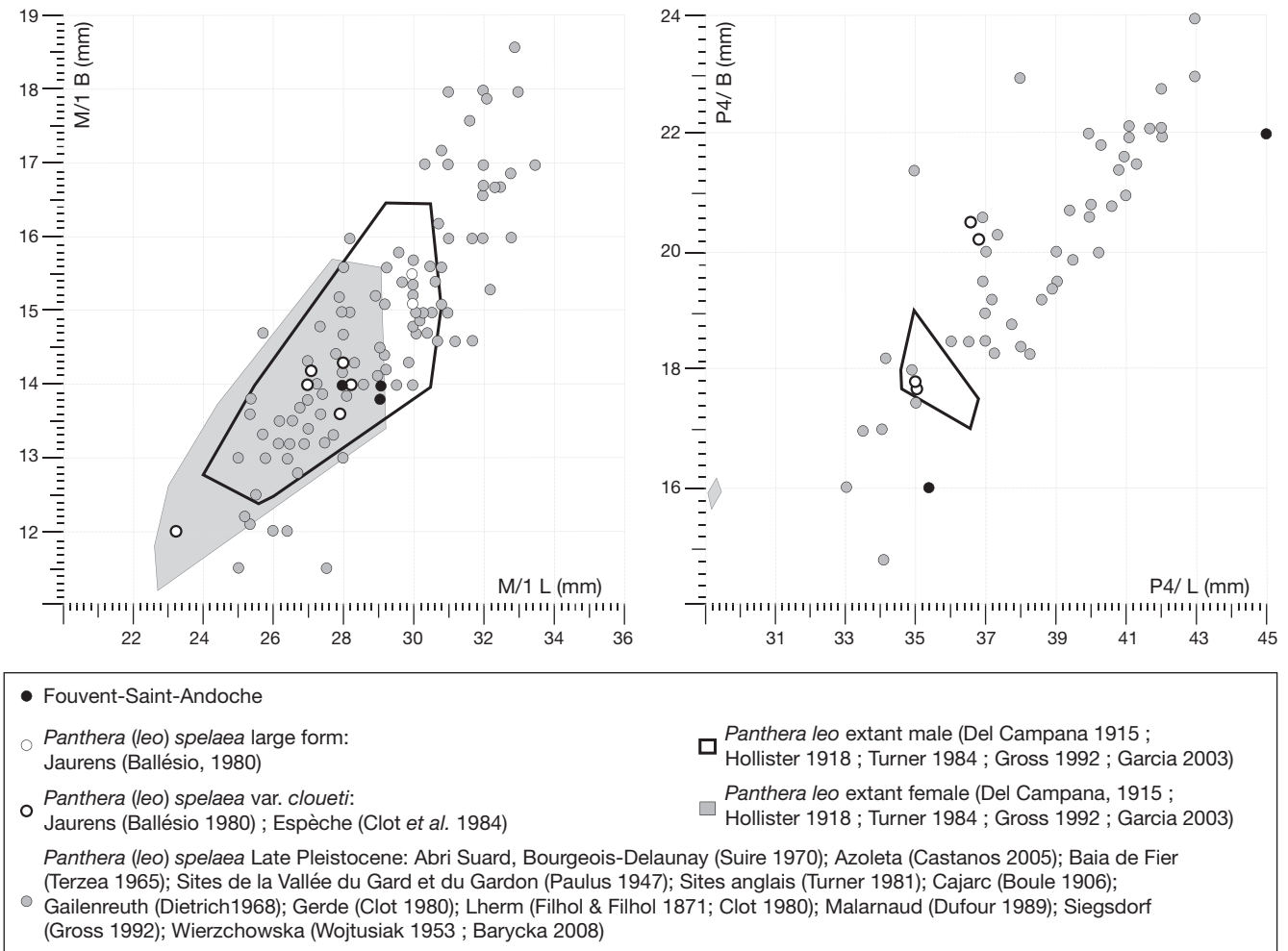


Fig. 6. — Cave lion *P. (leo) spelaea* upper (P4) and lower (M1) carnassial Breadth and Length ratio compared to extant and extinct populations. Measurements in mm. The male and female lions areas figure the maximum range obtained for each variables (breadth and length).

1989-1992 sample: 6 skull fragments (occipital); 2 right maxillae; 1 left maxilla; 4 right DI3; 6 left DI3; 8 right DC; 6 left DC; 5 right D2; 3 left D2; 4 right D3; 14 left D3; 3 right D4; 6 left D4; 1 right I1; 2 left I1; 2 right I1-2; 2 left I1-2; 15 right I2; 17 left I2; 16 right I3; 9 left I3; 8 right C; 8 left C; 7 right P1; 13 left P1; 8 right P2; 6 left P2; 9 right P3; 14 left P3; 14 right P4; 20 left P4; 11 right mandibles; 8 left mandibles; 5 mandibles?; 2 right dc; 7 left dc; 5 right d2; 9 left d2; 10 right d3; 11 left d3; 11 right d4; 20 left d4; 2 right d1; 5 left i1; 1 left i1-2; 5 right i2; 5 left i2; 1 right i2-3; 1 left i2-3; 20 right i3; 21 left i3; 22 right c; 21 left c; 7 left p2; 21 left p3; 20 right p3; 34 right p4; 35 left p4; 33 right m1; 23 left m1; 140 tooth fragments; 1 atlas; 1 cervical vertebra; 2 lumbar vertebrae; 4 caudal vertebrae; 3 right humeri; 4 left humeri; 2 left radius; 1 radius; 1 left ulna; 1 right scapholunar; 1 left scapholunar; 1 left pisiform; 1 pisiform; 2 right metacarpals II; 1 femur?; 1 patella?; 1 left tibia; 1 tibia?; 1 right fibula; 1 left fibula; 2 right tali; 1 left cuboid; 1 right metatarsal II; 1 left metatarsal II; 1 left metatarsal III; 1 left metatarsal V; 3 sesamoids?; 2 metapodials?; 9 first phalanges; 6 second phalanges; 6 third phalanges.

DESCRIPTION

Cave hyena is represented by 850 bone remains originating from both 1842 (NISP=24) and 1989-1992 (NISP=826) samples. This material represents about 6% of the complete collection,

about 25% of the NISP and 77% of the carnivores. Cave hyena remains are related to 121 individuals, ranging from juvenile to old adults (Fourvel *et al.* submitted); this series is among the largest ones for Late Pleistocene cave hyenas in Europe. Morphological characters (Fig. 3A, V) and measurements of both teeth and postcranial elements (Table 8) recovered in Fouvent closely match the descriptions of late Pleistocene *Crocota crocuta spelaea* published in the literature (Reynolds 1902; Clot 1980; Testu 2006; Barycka 2008). The extreme morphological variability of referred dental remains most probably coincides with ecomorphotypic variations, thus precluding any use of cave hyenas in a biochronological purpose (e.g., Kurtén 1963; Kurtén & Poulianos 1977; Klein & Scott 1989; Baryshnikov 1999). However, Würmian cave hyenas seem to differ from other representatives of *Crocota* in having a large size, especially as regards dentition. In Fouvent, upper and lower carnassials are at the same time large, robust, and highly metrically variable. Figure 7 shows breadth/length ratios for upper and lower carnassials (P4: Fig. 7A; m1: Fig. 7B) from Fouvent, compared to various Late Pleistocene and modern spotted hyena populations. Hyena teeth from Fouvent reveal strong size variability. However, this material has more large

dimensions (B/L) than Middle Pleistocene hyenas (*Crocota crocuta intermedia* from Lunel-Viel 1 *in* Bonifay 1971; *Crocota crocuta praespelaea* from Petralona *in* Kurtén & Poulianos 1977, 1981) and similar proportions than many OIS3 populations (Jaurens *in* Ballezio 1979; Cueva de las Hienas *in* Fosse 1997; Labeko Koba *in* Altuna & Mariezkurrena 2000; Conives *in* Fourvel 2008). Other teeth and postcranial elements are in perfect agreement with the observation as detailed here above. Morphological and metric features of the Fouvent cave hyena coincide with the large and robust hyenas as recorded in the OIS3 (between more or less 57 and 29 ky; Fourvel 2012).

Super-Order UNGULATA Linnaeus, 1766
[description by JBF, PFos, PFer, POA]

Eight ungulate species have been recognized (2219 NISP, 192 MNI). The collection is truly remarkable with a high frequency of mega-herbivores (8 mammoths and 39 woolly rhinoceroses) and large species (16 giant deers, 31 large bovids and 62 horses) (Figs 8, 9).

Order PROBOSCIDEA Illiger, 1811
Family ELEPHANTIDAE Gray, 1821
Subfamily ELEPHANTINAE Gray, 1821
Genus *Mammuthus* Brookes, 1828

Mammuthus primigenius Blumenbach, 1799

MATERIAL EXAMINED. — NISP=222; MNI=8.

1842 sample: 1 thoracic vertebra (apophysis); 1 humerus (portion of proximal end); 1 innominate (juvenile); 1 patella; 1 long bone fragment.

1989-1992 sample: 38 tusk fragments; 109 teeth and tooth fragments; 1 atlas; 2 vertebral apophyses; 2 ribs; 1 radius (shaft fragment); 1 ulna (fragment); 1 innominate (fragment); 4 femurs (shaft fragments); 1 right tibia (shaft cylinder); 3 tibiae (shaft cylinder); 1 right calcaneus fragment; 49 long bone fragments; 1 flat bone fragment (scapula or innominate); 3 compact bone portions (carpals or tarsals).

DESCRIPTION

We could not get access to the complete mammoth collection from Fouvent. However, the palaeontological analysis of the proboscideans was already realized by the late P. Paupe during the 1989-1992 excavations. The present study is largely inspired from his unpublished report. Our own analysis was focused on highly fragmented deciduous teeth (ridges of enamel) and long bone fragments which were not identified anatomically in spite of their large proportions. We have observed directly 222 remains attributed to *M. primigenius* but were not able to describe thirty-three isolated teeth and two tusk fragments. Based on P. Paupe's observations and our own analysis, eight up to ten individuals are represented in Fouvent. Juveniles are dominant: four individuals died between two and seven years old. Four teeth are referred to prime adults (between 10-20 and 30 years old). Two molars point to the presence of two old individuals, aged of 45 and 50 years, respectively. In our analysis, dental remains are mostly represented by fragments

of lamella mostly belonging to very young animals (n=81). This did not allow us to deduce neither their rank, nor their laterality and even less the MNI. Although the preliminary study of P. Paupe is based on a small dental sample (n=11), our observations confirm his taxonomic assignment with certainty. Thus, both the morphological description of teeth as well as the morphometrical indices (e.g., lamellar frequency between 10 to 16, length/height ratio) demonstrate a high evolved degree of the mammoths that are associated without no doubt to *M. primigenius* (Paupe *in* Detrey 1992).

Order PERISSODACTYLA Owen, 1848
Suborder HIPPOMORPHA Wood, 1937
Family EQUIDAE Gray, 1821
Subfamily EQUINAE Gray, 1821
Genus *Equus* Linnaeus, 1758

Equus germanicus Nehring, 1884

MATERIAL EXAMINED — NISP=922; MNI=62

1842 sample. — 1 palate; 1 right I1; 1 left I1; 1 right I2; 1 left I2; 1 right I3; 1 left I3; 1 right P2; 1 left P2; 2 right P3-4; 2 right M1-2; 2 left M1-2; 1 right M2; 1 left M3; 1 left d2; 2 right p2; 1 left p2; 3 left p3-4; 1 left p4; 1 right m1-2; 2 left m1-2; 1 left m3; 3 tooth fragments; 1 cervical vertebra; 1 right scapula; 1 left radio-ulna; 1 right metacarpal; 1 left metacarpal; 1 left innominate; 1 right tibia; 1 left pathological cuneiform and scaphoid; 1 right talus; 2 left tali; 2 left calcanei; 1 right metatarsal; 1 metatarsal; 1 vestigial metapodial; 2 first phalanges; 2 second phalanges.

1989-1992 sample: 3 left D1; 8 right D2; 8 left D2; 1 right D3; 13 right D3-4; 16 left D3-4; 1 right I1; 1 left I1; 1 I1; 1 right I1-2; 1 right I2; 1 I3; 9 upper canines; 33 upper tooth fragments; 25 right P2; 23 left P2; 53 right P3-4; 60 left P3-4; 1 left M1; 94 right M1-2; 84 left M1-2; 3 M1-2; 34 right M3; 30 left M3; 1 mandible; 4 right di; 1 left di; 2 di; 6 right d2; 5 left d2; 2 left d3; 10 right d3-4; 4 left d3-4; 3 right d4; 5 left d4; 1 left lower deciduous tooth; 5 right i1; 5 left i1; 2 right i1-2; 2 left i1-2; 1 left i2; 1 right i2-3; 1 right i3; 16 right p2; 18 left p2; 28 right p3-4; 37 left p3-4; 1 left p3; 1 left p4; 1 right m1; 25 right m1-2; 46 left m1-2; 4 right m2; 4 left m2; 22 right m3; 21 left m3; 11 lower tooth fragments; 1 pisiform; 1 right scaphoid; 1 left scaphoid; 1 right metacarpal; 1 right tibia; 1 tibia; 2 fibulae; 4 vestigial metapodials; 4 third phalanges; 3 sesamoids; 41 cheek tooth fragments; 14 incisor fragments.

DESCRIPTION

Because *Equus caballus* Linnaeus, 1758 includes wild and domestic caballine forms that may belong to several distinct lineages, we will not use here sub-specific rank but the binomen *Equus germanicus*. Morphometric data of the horse of Fouvent have not been described so far. Only an archaeozoological-taphonomical study was recently undertaken (Fourvel *et al.* 2014) as well as horse population dynamics study analysis on the basis of dental crown heights (Fernandez *et al.* 2006). A part of this dental material is presented here.

E. germanicus was recognized for the first time at Remagen (Germany) and in many European sites (Guadelli 1987; Fernandez 2006). The phylogeny of this species is not yet conclusively established and among different scenarios it could have derived from *Equus taubachensis* (Eisenmann 1991;

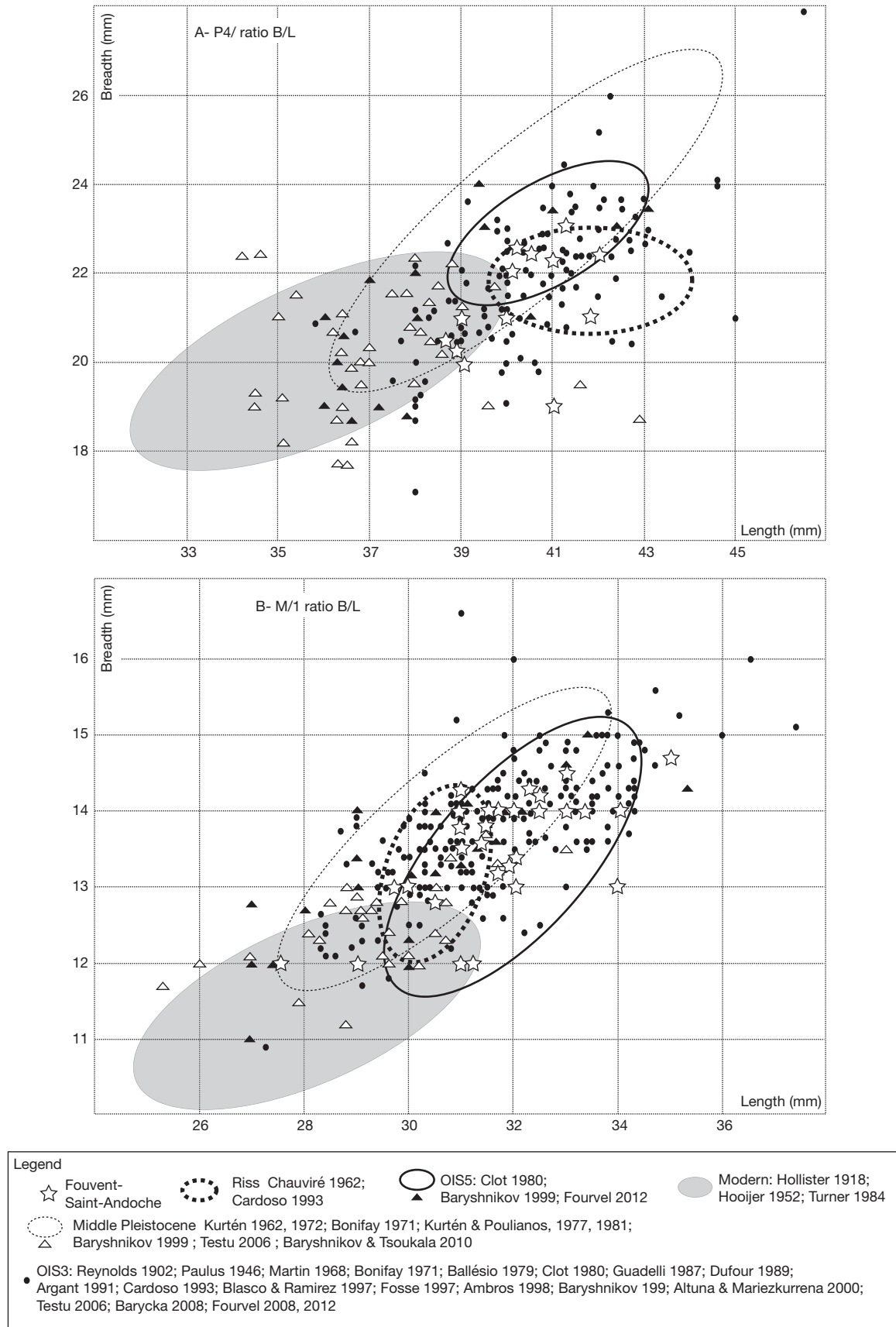


FIG. 7. — Cave hyena *C. c. spe/aea* (Goldfuss, 1832): Upper (P4) and lower (M1) carnassial Breadth and Length ratios compared to extant and extinct populations. Measurements in mm. Confidence ellipses with confidence interval (0.95) are figured.

TABLE 9. — Upper cheek teeth measurements of European horse species. *, measurements at P point; **O-md-l**, occlusal mesio-distal length; **O-vl-w**, occlusal vestibulo-lingual width; **O-lp**, occlusal length of protocone; **O-pi**, occlusal protocone index. For each measurement: **n**, min.-max. values; mean eventually followed by +/- interval of confidence of the mean; standard deviation.

Measurements	Fouvent	Bau Aubesier Fernandez 2006	Blache-Saint- Vaast Auguste 1995	Mosbach Eisenmann 1980	Taubach Musil 1977	Prolom 2 Eisenmann & Baryshnikov 1994	Combe- Grenal Guadelli 1987	La Quina (4b) Armand 1998	Camiac Guadelli 1987	Solutré Guadelli 1987	
	<i>Equus germanicus</i>	<i>Equus mosbachensis</i>			<i>Equus taubachensis</i>	<i>Equus cf. taubachensis</i>	<i>Equus germanicus</i>	<i>Equus gallicus</i>			
P2	O-md-l	43 32.7-41.5 37.26+/-0.52 1.75	13 34.8-42.6 39.75+/-1.12 2.06	6 35.2-41.3 38.85 2.44	11 38-47 41.6 2.67	10 36-43.9 40.54 2.44	10 38-42.5 40.4 1.64	25 36-41.5 39.08+/-0.68 1.64	17 34-40.7 37.58+/-0.72 1.69	10 36-40 37.59 1.57	8 35-38.7 36.82+/-0.96 1.15
	O-vl-w	43 20.5-28.3 25.45+/-0.44 1.46	15 24-28 25.76+/-0.66 1.3	6 25.3-29.2 27.1 1.36	12 27-29.5 27.9 0.76	10 26-29.3 26.69+/-1.48 2.39	10 24.6-29.2 26.5 1.43	33 24-29 26.48+/-0.37 1.05	19 22.7-27.9 25.19+/-0.58 1.47	10 24.4-27 25.46+/-0.74 1.04	8 23.2-26 24.86+/-0.75 0.9
	O-lp	43 7.5-11 9.48+/-0.25 0.84	15 8.1-12 9.53+/-0.52 1.02	6 8.8-10.7 9.75 0.63	12 9.5-12 10.4 0.82	10 8.5-13 9.82 1.26	10 8.6-11.1 9.9 0.84	36 8-12 9.75+/-0.27 0.8		10 9-10.5 9.76+/-0.39 0.54	8 8.5-10.6 9.31+/-0.55 0.66
	O-pi	43 21.91-28.20 25.4+/-0.52 1.75	13 20.57-28.17 24.07+/-1.26 2.32	6 23.24-26.78 25.14 1.48	10 23.25-26.13 24.43 0.82	10 23.13-29.62 24.18+/-1.34 2.16	10 20.4-27.1 24.6 1.95	24 22.5-30.6 25.17+/-1.02 2.42	15* 32.2-38.7 35.76+/-0.75 1.64	10 22.5-28.38 25.82+/-1.18 1.66	8 23.78-28.42 25.28+/-1.22 1.46
P3 P4	O-md-l	72 25-32.3 29.26+/-0.35 1.53	21 27.3-34.7 31.42+/-0.86 2.01	11 29.5-35.4 31.31 1.86	30 29-36 32.3 1.64	10 29-33.8 31.15 1.36	41 25.7-33.3 29.9 1.94	73 27-33.5 30.28+/-0.39 1.7		22 27-30 28.79+/-0.45 1.02	20 26.5-31 28.6+/-0.59 1.27
	O-vl-w	72 25-30.5 27.74+/-0.25 1.07	22 27.5-31.2 28.96+/-0.43 1.03	10 27.1-32.1 28.42 1.29	29 28-32.5 30.5 1.12	10 28.2-31.9 29.53 1.29	40 26.5-31.9 29.5 1.38	67 26-31 28.33+/-0.31 1.29		22 26-30 27.87+/-0.53 1.19	19 23.2-30 27.4+/-0.89 1.84
	O-lp	72 9-16 12.85+/-0.36 1.57	22 11.7-16.9 14.18+/-0.61 1.45	9 12.2-16.8 14.06 1.54	29 12-18.5 15.1 1.59	10 13.4-17 14.37 1.00	40 10.8-17.4 14.5 1.39	72 11-18 13.79+/-0.33 1.43		22 11.5-15 13.07+/-0.4 0.92	20 12-15.7 13.54+/-0.52 1.12
	O-pi	72 30-54 44.01+/-1.28 5.53	21 35.29-57.51 45.46+/-2.73 6.39	9 40.67-50.15 44.61 2.78	29 37.68-56.06 46.91 5.13	10 42.4-50.29 46.13 2.5	40 35.1-60 48.8 5.71	71 36.1-62.1 45.74+/-1.28 5.4		22 40.26-55.26 45.48+/-1.69 3.82	20 40.65-56.07 47.41+/-1.89 4.05
M1 M2	O-md-l	120 22.8+/-31.5 26.11+/-0.27 1.51	51 25.2-34.6 28.27+/-0.53 1.92	12 27-30.8 28.18 1.14	27 26.5-32.5 28.5 1.39	15 26.8-32.8 29.51+/-0.85 1.69	32 25-30.8 27.6 1.32	71 23-30 26.82+/-0.41 1.73		33 23.7-30.6 25.76+/-0.45 1.28	23 24.5-29 25.99+/-0.61 1.42
	O-vl-w	119 22-29 26.28+/-0.22 1.27	47 21.8-30 27.19+/-30.8 1.47	12 25.5-31.2 27.74 1.41	26 26.5-31 28.6 1.06	14 23.4-29.7 26.26+/-0.8 1.52	32 15.1-31.3 27.3 2.69	60 24.5-29.5 26.93+/-0.33 1.26		33 24.2-28.2 26.46+/-0.35 0.99	20 24-27.6 26.15+/-0.51 1.09
	O-lp	118 10.3-17 13.58+/-0.21 1.19	55 11-16.9 14.19+/-0.4 1.52	12 13-16.6 14.15 1.09	27 11.5-18.5 14.5 1.64	14 13-16.7 14.71+/-0.49 0.94	32 11.1-16.8 14.3 1.38	72 11-17 14.13+/-0.31 1.32		33 12-16 13.76+/-0.37 1.04	22 13-16.9 14.39+/-0.48 1.08
	O-pi	118 35.51-65.62 52.17+/-0.88 4.91	51 37.67-59.21 50.3+/-2.08 5.31	12 45.42-55.52 50.19 2.87	27 41.81-58.18 50.84 4.78	14 46.26-55.67 50.14+/-1.44 2.76	32 40.4-60 51.9 5.00	70 40.7-68 52.73+/-1.19 4.97		33 45.42-60.76 53.59+/-1.29 3.63	22 48.19-66.02 55.68 4.72
M3	O-md-l	48 24.1-32.5 28.13+/-0.58 2.03	22 25.6-31.5 28.59+/-0.63 1.51	7 26.9-36 29.01 2.93	7 29.5-33 30.9 1.36	8 26.5-32.6 28.79+/-1.28 1.85	14 26.7-33 30.3 1.88	46 23-32.5 26.69+/-0.7 2.35	20 24-30 27.14 +/-0.58 1.49	14 25-32.2 27.76+/-1.05 1.82	4 26-28.3 27.07+/-1 1.02
	O-vl-w	47 20.4-27.2 23.54+/-0.42 1.48	21 20-25.7 23.58+/-0.56 1.31	7 21.8-27 23.64 1.69	6 22.5-25 24.2 1.08	8 20.7-23.7 22.06+/-0.82 1.18	14 22-27 24.8 1.45	49 18-29 23.82+/-0.54 1.87	20 21.2-25.4 23.36+/-0.41 1.07	13 20.7-25.2 22.65+/-0.75 1.25	3 22.5-23 22.8

TABLE 9. — Continuation.

Measurements	Fouvent	Bau Aubesier Fernandez 2006	Blache-Saint- Vaast Auguste 1995	Mosbach Eisenmann 1980	Taubach Musil 1977	Prolom 2 Eisenmann & Baryshnikov 1994	Combe- Grenal Guadelli 1987	La Quina (4b) Armand 1998	Camiac Guadelli 1987	Solutré Guadelli 1987
	<i>Equus germanicus</i>	<i>Equus mosbachensis</i>			<i>Equus taubachensis</i>	<i>Equus cf. taubachensis</i>	<i>Equus germanicus</i>	<i>Equus gallicus</i>		
M3	47	22	7	7	8	14	55		14	3
	12-17.7	12.1-18	12.3-15.5	14-18	12-16.4	11.5-18.8	11.5-19		11.7-15.4	14.4-15.5
	14.72+/-0.34 1.19	14.80+/-0.58 1.39	14.26 1.1	15.7 1.34	14.43+/-0.85 1.22	15.7 1.88	14.59+/-0.39 1.43		13.7+/-0.06 1.05	14.8
O _{1p}	47	22	7	7	8	14	46	15*	14	2
	43.10-61.03	42.31-59.71	43.06-52.98	46.77-54.54	45.28-54.04	24.9-58.8	42.1-63.5	44.52-58.10	41.92-54.8	52.73-54.34
	52.44+/-1.16 4.06	51.79+/-1.86 4.45	49.35 3.67	50.75 2.71	50.08+/-1.69 2.44	50.3 8.64	52.13+/-1.6 5.37	52.76 +/-1.92 4.21	49.47+/-2.45 4.24	53.53

Eisenmann & David 1994), in spite of strong affinities with *Equus steinheimensis* von Reichenau, 1915 (Prat 1968). *Equus germanicus* is mainly represented in the early Late Pleistocene (Prat 1968; Mourer-Chauviré 1980; Guadelli 1987; Eisenmann 1991; Armand 1998). It was replaced during the OIS3 by *Equus gallicus* Prat, 1968, a robust but rather small-sized horse determined at Solutré (Saône-et-Loire), with longer protocones (Prat 1968). Radiocarbon dates for *E. c. gallicus* were recently provided in southeastern France in Coulet des Roches and in the aven des Planes (Vaucluse). They are still present in these two sites at respectively 13.090±70 BP and 13.360±80 BP (Crégut-Bonnouire *et al.* 2014). According to Eisenmann (1991), *E. gallicus* reported in many French localities, could be a small form of *E. germanicus*. At Bize (Aude, France), a period of transition between *E. germanicus* and *E. gallicus* could be placed around *c.* 33 ka BP (Patou-Mathis 1994). A radiocarbon age of *c.* 35 ka is cautiously given at Camiac (Gironde, France; Guadelli 1987), while an age by thermoluminescence around 43 ka could be retained in the layer 6a of the Station Amont of La Quina (Charente, France; Armand 1998). The species *E. caballus* aff. *germanicus* was also recognized in Provence at the end of the OIS2 in the Aven des Fourches II (Vaucluse, France; Brugal *et al.* 2001).

Lower teeth are under study and will be included later in a more complete analysis with post-cranial elements. For now, 283 upper cheek teeth have been studied (Table 9). In this table, teeth are compared to a reference dataset of Pleistocene equids. For each measurement the number of teeth, minimum and maximum values, mean and confidence interval at 95% and standard deviation are given. The morphometrical distinction between ranks of premolars and molars (e.g., P3-P4 and M1-M2) is usually difficult or impossible with isolated teeth. Accordingly, we have chosen not to distinguish P3 from P4 and M1 from M2 in order to compare the sample of Fouvent to a larger number of cheek teeth from literature.

As a first step, we wanted to know if the cohorts of horses from the different levels of Fouvent could be considered as coming from the same species. Thus, we grouped the stratigraphic units (e.g., Ab, Ba, C2...) in three levels namely A, B

TABLE 10. — Kruskal-Wallis test ($\alpha=0.05$) comparing protocone index (Pi) for each dental rank in layers A, B and C from Fouvent-Saint-Andoche (see details of the Kruskal-Wallis test in text).

	Layer	Significant differences according to Dunn (1964)			p-value (bilateral)
		A	B	C	
Pi of P2	5 A	–	No diff.	No diff.	0.51
	21 B	No diff.	–	No diff.	
	12 C	No diff.	No diff.	–	
Pi of P3P4	6 A	–	No diff.	No diff.	0.40
	30 B	No diff.	–	No diff.	
	24 C	No diff.	No diff.	–	
Pi of M1M2	12 A	–	No diff.	No diff.	0.69
	51 B	No diff.	–	No diff.	
	39 C	No diff.	No diff.	–	
Pi of M3	4 A	–	No diff.	No diff.	0.48
	17 B	No diff.	–	No diff.	
	12 C	No diff.	No diff.	–	

and C. Dental remains without stratigraphic location were excluded, as well as few teeth from the levels E and E9. We compared the Protocone Index using the Kruskal-Wallis test of one-way analysis of variance by ranks detailed previously. The analysis clearly indicates that there was no statistically significant difference between levels A, B, and C ($\alpha=0.05$). Thus, dental material from those levels can be considered as originating from the same demographic/evolutionary unit, which is confirmed by the lack of differences in pairs of Dunn (1964) (Table 10). The method of Dunn (1964) compares the mean of the ranks, the latter being those used in the calculation of *k* according a normal asymptotic distribution for the standardized difference of the average of the ranks.

The dimensions of most upper teeth of Fouvent match the variation range of both *E. germanicus* and *E. gallicus* (Table 9). This is also the case in the upper part of the sequence of La Quina (Charente, France) which hosted the two species and made impossible their distinction based on their dimensions (Armand 1998). Here, we propose a new quantitative approach using biometric

TABLE 11. — Average upper cheek teeth measurements of middle and late Pleistocene European horse species (data from Eisenmann 1991, table 2. Biache-Saint-Vaast and Bau de l'Aubesier, from Auguste (1995) and Fernandez (2006), respectively. P-ol= Occlusal length of P3P4; M-ol= Occlusal length of M1M2; P-pl= Protocone length of P3P4; M-pl= Protocone length of M1M2; PM-ol = Average occlusal length of P3P4-M1M2; PM-pl= Average length of protocone of P3P4-M1M2; Theoretical median Confidence Interval (CI) with $\alpha=0.05$ calculated with *R software Version 2.14.0*. * Using wilcox.test function; **Using t.test function (see details in text).

	Species	Localities	P3P4				M1M2			P3P4-M1M2		
			n	P-ol	n	P-pl	n	M-ol	M-pl	n	PM-ol	PM-pl
Antewürmian horse species and localities	<i>Equus mosbachensis</i>	Mosbach (Graues)	30	32.3	29	15.1	27	28.5	14.5	27	30.4	14.8
	<i>Equus chosaricus</i>	Arago	37	32.8	37	15.9	42	28.8	15.1	42	30.8	15.5
	<i>Equus achenheimensis</i>	Angletterre (Hoxnien)	12	32.7	12	15	15	29.6	15.1	13	31.2	15.1
	<i>Equus palustris</i>	Lunel Veil	9	30.4	9	13.5	8	26.8	13.8	8	28.6	13.7
	<i>Equus achenheimensis</i>	Achenheim (LAI)	18	32.1	18	14.9	19	28.7	13.7	19	30.4	14.3
	<i>Equus achenheimensis</i>	La Fage 1	1	32.7	1	15	1	29.5	14	1	31.1	14.5
	<i>Equus taubachensis</i>	Achenheim (LAM)	6	31.7	6	13.3	5	27.8	14.1	5	29.8	13.7
	<i>Equus chosaricus</i>	Ehringsd. Tr. inf.	20	32.9	19	16.1	27	29	15.1	28	31	15.6
	<i>Equus taubachensis</i>	Angleterre (antelpsw)	8	31.5	7	14.1	10	28.5	14.5	9	30	14.3
	<i>Equus steinheimensis</i>	Unknown	6	31	6	13.3	3	27.2	12	3	29.1	12.7
	<i>Equus steinheimensis</i>	Châtillon-Saint-Jean	3	30.3	3	12.5	2	29	12.5	2	29.7	12.5
	<i>Equus chosaricus</i>	La Fage 2	5	29.5	5	14.3	5	25.7	13.4	6	27.6	13.9
	<i>Equus chosaricus</i>	Unknown	6	30.8	6	15.3	6	27.3	14.8	6	29.1	15.1
	<i>Equus missi</i>	Unknown	9	25.8	9	11.7	10	22.9	12	10	24.4	11.9
	<i>Equus germanicus</i>	Fontéchevade	7	29.1	7	13.1	11	26.2	13.4	12	27.7	13.3
	<i>Equus taubachensis</i>	Suard	26	30.8	26	14.7	26	27.9	15.3	26	29.4	15
	<i>Equus taubachensis</i>	Taubach	26	30.2	26	14.3	23	27.4	14.7	22	28.8	14.5
	<i>Equus taubachensis</i>	Weimar	22	31.2	22	14.3	15	27.2	14.9	13	29.2	14.6
<i>Equus achenheimensis</i>	Paglicci-Riparo	1	32.4	1	15.5	2	29.7	14.8	2	31.1	15.2	
<i>Equus mosbachensis</i>	Bau de l'Aubesier (IJ)	21	31.42	22	14.18	51	28.27	14.19	55	29.84	14.18	
<i>Equus mosbachensis</i>	Biache-Saint-Vaast	11	31.31	9	14.06	12	28.18	14.15	12	29.74	14.1	
CI with $\alpha=0.05$			[30.60; 31.85]*		[13.78; 14.79]**		[27.30; 28.54]*		[13.64; 14.62]*		[29.04; 30.19]*	[13.76; 14.66]**
Würmian horse species and localities	<i>Equus sp.</i>	C.Grenal (22-25)	22	30.8	22	14.4	26	27.6	14.1	26	29.2	14.3
	<i>Equus sp.</i>	Monteagudo	9	30.3	7	13.7	11	27	13.6	10	28.7	13.7
	<i>Equus sp.</i>	Gigny	9	31.2	8	13.8	7	27	13.9	6	29.1	13.9
	<i>Equus germanicus</i>	La Quina B3-C3	18	29.6	18	13.8	28	25.8	14.1	28	27.7	14
	<i>Equus germanicus</i>	Pair-non-Pair	15	28.8	15	12.4	30	25.9	13.9	30	27.4	13.2
	<i>Equus germanicus</i>	Remagen	4	28	4	10.8	4	25.8	13.5	4	26.9	12.1
	<i>Equus germanicus</i>	C. Grenal 12-15	40	30.1	40	13.6	40	26.1	14	41	28.1	13.8
	<i>Equus germanicus</i>	Arcy (RGS)	80	28.7	76	13.6	88	25.9	14	88	27.3	13.8
	<i>Equus gallicus</i>	Camiac	22	28.8	22	13.1	33	25.8	13.8	33	27.3	13.5
	<i>Equus gallicus</i>	Jaurens	38	28.3	38	12.5	37	25.1	13.5	37	26.7	13
	<i>Equus antunesi</i>	Salemas	5	27.8	5	13.2	8	24.6	12.4	7	26.2	12.8
	<i>Equus antunesi</i>	Fontainhas	2	28.6	2	13.6	2	25.6	12.5	2	27.1	13
	<i>Equus chosaricus</i>	San Sidero 6	2	32.5	2	18	2	28	16.5	2	30.3	17.3
	<i>Equus sp.</i>	Kostenki (sup)	18	31.1	18	13.9	24	28	15.1	24	29.5	14.5
	<i>Equus arcelini</i>	Mézine	23	30.3	23	14.8	30	26.1	14.9	30	28.2	14.8
	<i>Equus arcelini</i>	Chasse	8	28.1	7	14.4	8	25.4	13.6	8	26.8	14
	<i>Equus arcelini</i>	Le Quéroy	4	28.9	4	14.1	4	25	14.3	4	26.9	14.2
	<i>Equus sp.</i>	Joao Ramos	2	28.3	2	13	2	25	14	2	26.6	13.5
	<i>Equus sp.</i>	Weimar (sup)	3	26.8	3	11.9	4	25.1	13.2	4	26	12.5
<i>Equus germanicus</i>	Fouvent	64	29.27	64	12.76	76	25.98	13.54	76	27.62	13.15	
<i>Equus przewalskii</i>	Unknown	36	27.4	36	13.1	38	24.5	13.2	38	26	13.2	
<i>Equus ferus</i>	Unknown	2	28.8	2	11.3	2	23.8	10.8	2	26	11	
CI with $\alpha=0.05$			[28.54 ; 29.85]**		[12.84 ; 13.90]*		[25.34 ; 26.37]**		[13.25 ; 14.25]**		[26.95 ; 28.09]**	[13.15 ; 13.99]*

data, sourced from Eisenmann's (1991) overview. Despite the phylogenetic uncertainties highlighted by her, all the caballine equids from Europe during the middle and late Pleistocene are carefully and methodically described in her analysis. The only difference with Eisenmann (1991) that we made here is that we consider as valid the well known species *E. gallicus* represented in France at Solutré (Prat 1968), Jaurens (Mourer-Chauviré 1980), Camiac (Guadelli 1987), or La Quina (Armand 1998). The dataset of Eisenmann (1991) allowed us to calculate confidence intervals for lengths of upper teeth (except for P2 and

M3, unavailable) and their protocone (CI with $\alpha=0.05$). From a methodological point of view, the normality was tested using the Shapiro-Wilk test. For each measurement following a normal distribution, the confidence interval on the mean was given using the basic t-test of Student with the software R (2.14.0; t.test function). For the measurements which did not satisfy the conditions of normality, the confidence interval we derived was estimated from the theoretical median (wilcox.test function in R). Results indicate that intervals associated to Würmian species are well individualized from those related to ante-Würmian

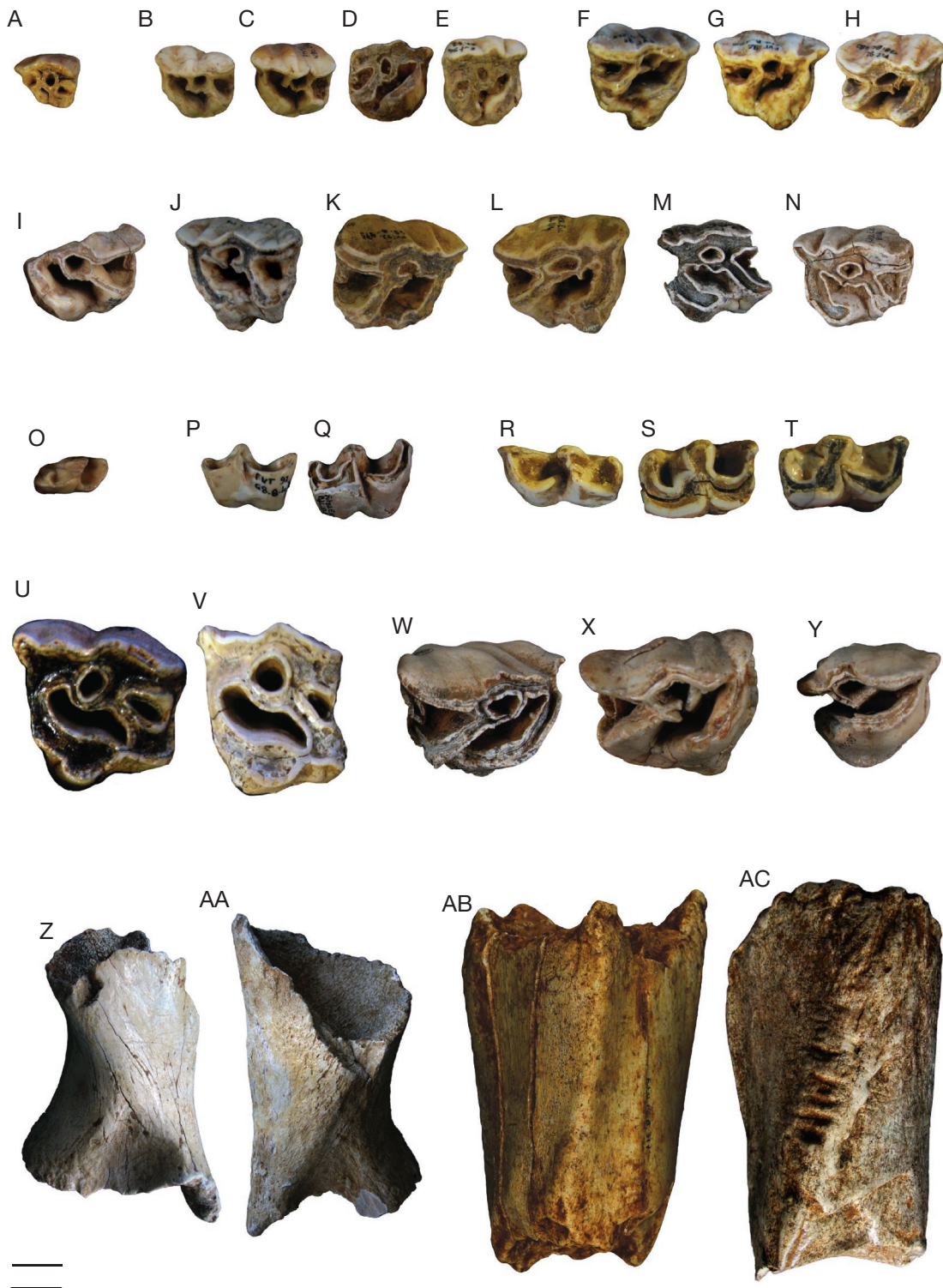


FIG. 8. — Woolly rhinoceros *Coelodonta antiquitatis* (Blumenbach, 1799) remains from Fouvent-Saint-Andoche (*Coelodonta antiquitatis*): A, D1; B-E, D2; F-H, D3; I-N, D4; O, d2; P, Q, d3; R-T, d4; U, V, M1; W, X, M2; Y, M3; Z, AA, humerus shaft cylinders; AB, AC, tibia shaft cylinders. Scale bar: 20 mm. Pictures by JBF.

equids. They only overlap on measurements which include the protocone length. Table 11 also shows that dimensions of the upper teeth of Fouvent are systematically associated to Würmian horses. This is confirmed by the occlusal protocone index of molars and premolars, which is always comprised between 114 and 126 for Würmian species (119.6 in Fouvent) and always

lower than 114 for older equids, with the exception of *Equus chosaricus* Gromova, 1949 (114.1; Table 12).

To identify the horse of Fouvent at species level through dental measurements, we used the routine package *knn.cv* from *R* software (version 2.13.2). The program corresponds to one of the more efficient non-parametric methods for

TABLE 12. — Ratio of protocone index of middle and late Pleistocene European horse species. Data from Eisenmann (1980: tables 20, 21), except for Bau de l'Aubesier (Fernandez 2006) and Biache-Saint-Vaast (Auguste 1995).

	Localities and/or species	Protocone index of M1M2 / Protocone index of P3P4
Antwürmian horse species and localities	Montoussé (<i>Equus mosbachensis</i>)	103.4
	Pech-de-l'azé (niveau 9)	104.8
	Caune de l'Arago (<i>Equus chosaricus</i>)	108.3
	<i>Equus mosbachensis</i>	108.4
	Tilloux	109
	<i>Equus missi</i>	109.5
	<i>Equus taubachensis</i>	109.6
	Ehringsdorf	109.7
	<i>Equus achenheimensis</i>	109.8
	Bau de l'Aubesier (IJ)	110.6
	<i>Equus piveteaui</i>	111.6
	Biache-Saint-Vaast	112.5
	La Micoque	111.8
	Bau de l'Aubesier (H)	113.8
<i>Equus chosaricus</i>	114.1	
Würmian horse species and localities	Kniegrotte	114
	<i>Equus gallicus</i>	114.9
	Bourgeois-Delaunay (niveau 4)	116.7
	La Chaise (Aurignacien 1)	116.9
	St-Germain-la-Rivière	117.3
	Grotte des fées	117.5
	Bourgeois-Delaunay (niveau 9)	118.2
	Combe-Grenal	118.4
	Fouvent	119.6
	Gavaudin	121.5
Pair-non-Pair	121.8	
<i>Equus germanicus</i>	126.3	

data classification in data mining: the so-called *k*-Nearest Neighbors (or *k*-NN for short; see details of the method in Mathieu-Dupas 2010). When there is little or no prior knowledge about the distribution of the original data, the rationale consists of finding among the predefined training samples (e.g., measurements of well known species) the closest distances of the new points that may be assigned to the original data. In this study, we applied the Euclidean distance, which is most commonly used. As an example, for a data point *x* of Fouvent, we computed the distance between *x* and all the data points from the training samples, in order to attribute the species determined by the nearest points of *x* according to *k*. This number *k*, usually an odd number, ranks the nearest neighbors from the training data. It determines the species to be assigned on the base of the majority vote using cross validation. When *k* is small (e.g., *k*=1), it improves the power of association even if noise may somewhat affect the results. However, when *k* increases it is less sensitive to noise and makes the borders of the classes less distinct but necessarily requires large training samples (Mathieu-Dupas 2010). Table 13 shows unambiguously and whatever *k* is, that the nearest species for the ratio of protocone length to occlusal length of M1M2 [M-pl/M-ol] is always *E. germanicus*. The same is true for the ratio of the length of protocone to the occlusal average length of P3P4M1M2 [PM-pl/PM-ol], except for an isolated case (*k*=7) which is associated to

Equus antunesi Cardoso & Eisenmann, 1989. Nevertheless, *E. steinheimensis* appears for the ratio of the length of the protocone to the occlusal length of P3P4 [P-pl/P-ol], as the closest species except for *k*=9, *k*=13 and *k*=14 which are attributed once again with *E. germanicus*. However, the dental morphology of *E. steinheimensis* allows undoubtedly excluding such an assignment because caballoid and stenoid characters are not observed at Fouvent, contrary to what occurs at Châtillon-Saint-Jean (Drôme, France; Mourer-Chauviré 1972). At Fouvent, dentition shows styles with splits on the premolars, molars with simple parastyle and mesostyle, concave interstylar surfaces, and bilobed protocones. Even so, the proximity between *E. steinheimensis* and *E. germanicus* is not trivial and refers to the hypothesis of a possible phylogenetic relationship, as mentioned by Prat (1968: 520). Finally, our analysis does not either reveal a possible association between the horse of Fouvent and the more evolved *E. gallicus*.

At the end of this study, it appears that dental morphometry, coupled with high resolution analytical tools can account for evolutionary stages of Pleistocene horses. We have shown that the horse of Fouvent was associated to the typical species *E. germanicus* but did not yet reach the evolutionary stage as observed in *E. gallicus*. In conclusion, in an anagenetic perspective, it is quite reasonable to consider that the deposition *E. germanicus* of Fouvent is probably associated to the time interval from the very end of OIS 4 to the end of OIS 3.

Suborder CERATOMORPHA Wood, 1937
 Family RHINOCEROTIDAE Gray, 1821
 Subfamily RHINOCEROTINAE Gray, 1821
 Genus *Coelodonta* Bronn, 1758

Coelodonta antiquitatis (Blumenbach, 1799)

MATERIEL EXAMINED. — NISP=225; MNI=39.

1842 sample: 1 right M2; 3 tooth fragments; 1 right humerus; 1 left humerus; 1 left ulna; 1 right innominate; 1 innominate; 1 right tibia; 1 right talus.

1989-1992 sample: 2 petrosal bones; 4 left D1; 4 right D2; 4 left D2; 12 right D3; 8 left D3; 5 right D4; 7 left D4; 1 upper deciduous tooth fragment; 1 right P2; 3 left P2; 2 right P3; 1 left P3; 2 right P4; 1 left P4; 1 right M1; 4 left M1; 1 right M2; 4 left M2; 3 right M3; 2 left M3; 2 upper molar fragments; 2 right d1; 1 left d1; 4 left d2; 3 right d3; 9 left d3; 6 right d4; 1 left d4; 1 d4; 2 lower deciduous tooth fragments; 1 left p2; 1 p2-3; 2 right p3; 1 right p3-4; 3 left p3-4; 4 lower premolar fragments; 4 right m1; 1 left m1; 1 left m2-3; 1 right m3; 2 left m3; 2 lower molar fragments; 55 tooth fragments; 1 left scapula; 2 right humeri; 2 left humeri; 2 radii; 1 left metacarpal IV; 2 left innominates; 1 right femur; 1 femur; 4 right tibiae; 4 left tibiae; 6 tibiae; 1 right talus; 1 first phalanx; 3 long bone fragments; 1 flat bone fragment (scapula or innominate); 1 metapodial.

DESCRIPTION

More than 90 isolated teeth (mainly deciduous teeth), and several postcranial elements have been attributed to the woolly rhinoceros *C. antiquitatis* (Blumenbach, 1799) (Fig.8). The



FIG. 9. — Ungulates (other than rhinoceros) remains from Fouvent: **A, B**, giant deer *Megaloceros giganteus* Blumenbach, 1799: right 1842.14 (**A**) and left 1842.13 (**B**) mandibles; **C-E**, red deer *Cervus elaphus* Linnaeus, 1758: basal part of right antler 1842.109 (**C**) and ingested left talus 1842.97 (**D**, palmar view; **E**, dorsal view); **F-H**, horse *Equus germanicus* Nehring, 1884: right metacarpal 1842.2 (**F**), first 1842.6 (**G**) and third H9.A.1 (**H**) phalanges; **I-L**, large bovid Bovidae: right calcaneum 1842.78 (**I**), first phalange G10.E/A.9 (**J**, dorsal view; **K**, lateral view) and metapodial distal portion F11.A.50 (**L**); **M-O** reindeer *Rangifer tarandus* (Linnaeus, 1758): basal part of left antler 1842.106 (**M**), portion of right antler F10.B.329 (**N**) and right metatarsal G9.24 (**O**). Scale bar: 20 mm. Pictures by JBF.

TABLE 13. — Results of *k*-Nearest Neighbors cross-validators classification from training set of Table 11 (package *knn.cv* from R, version 2.13.2). Abbreviations: [1], *k*=Number of neighbors considered; [2], tested measurements (nomenclature of measurements in Table 11); [3], code number of the closest species returned by *k*-NN with: 1, *E. mosbachensis* von Reichenau, 1915; 2, *E. chosaricus* Gromova, 1949; 3, *E. achenheimensis* Nobis, 1971; 4, *E. palustris* Bonifay, 1980; 5, *E. taubachensis* Freudenberg, 1911; 6, *E. steinheimensis* von Reichenau, 1915; 7, *E. missi* Gromova, 1949; 8, *E. germanicus* Nehring, 1884; 9, *Equus* sp.; 10, *E. gallicus* Prat, 1968; 11, *E. antunesi* Cardoso & Eisenmann, 1989; 12, *E. arcelini* Guadelli, 1986; 13, *E. przewalskii* Poliakov, 1881; 14, *E. ferus* Boddaert, 1785. [4], proportion of the votes for the winning class returned as % according to *k*. See details of *k*-NN method in text.

	<i>k</i> =1		[1]
P-pl/P-ol	M-pl/M-ol	PM-pl/PM-ol	[2]
6	8	8	[3]
1.00	1.00	1.00	[4]
<hr/>			
	<i>k</i> =2		
P-pl/P-ol	M-pl/M-ol	PM-pl/PM-ol	
6	8	8	
1.00	1.00	0.50	
<hr/>			
	<i>k</i> =3		
P-pl/P-ol	M-pl/M-ol	PM-pl/PM-ol	
6	8	8	
0.66	0.66	0.50	
<hr/>			
	<i>k</i> =4		
P-pl/P-ol	M-pl/M-ol	PM-pl/PM-ol	
6	8	8	
0.75	0.50	0.50	
<hr/>			
	<i>k</i> =5		
P-pl/P-ol	M-pl/M-ol	PM-pl/PM-ol	
6	8	8	
0.60	0.40	0.40	
<hr/>			
	<i>k</i> =6		
P-pl/P-ol	M-pl/M-ol	PM-pl/PM-ol	
6	8	8	
0.50	0.50	0.33	
<hr/>			
	<i>k</i> =7		
P-pl/P-ol	M-pl/M-ol	PM-pl/PM-ol	
6	8	11	
0.42	0.57	0.28	
<hr/>			
	<i>k</i> =8		
P-pl/P-ol	M-pl/M-ol	PM-pl/PM-ol	
6	8	8	
0.37	0.62	0.37	
<hr/>			
	<i>k</i> =9		
P-pl/P-ol	M-pl/M-ol	PM-pl/PM-ol	
8	8	8	
0.33	0.55	0.33	
<hr/>			
	<i>k</i> =10		
P-pl/P-ol	M-pl/M-ol	PM-pl/PM-ol	
6	8	8	
0.40	0.60	0.30	
<hr/>			
	<i>k</i> =11		
P-pl/P-ol	M-pl/M-ol	PM-pl/PM-ol	
6	8	8	
0.36	0.54	0.36	
<hr/>			
	<i>k</i> =12		
P-pl/P-ol	M-pl/M-ol	PM-pl/PM-ol	
6	8	8	
0.33	0.50	0.41	
<hr/>			
	<i>k</i> =13		
P-pl/P-ol	M-pl/M-ol	PM-pl/PM-ol	
8	8	8	
0.30	0.46	0.38	
<hr/>			
	<i>k</i> =14		
P-pl/P-ol	M-pl/M-ol	PM-pl/PM-ol	
8	8	8	
0.26	0.42	0.35	

morphology of this Eurasian Pleistocene species is well-known (for review, see Guérin 1980). The Fouvent sample presents all the morphological features of this species (large size, high crowned teeth, quadrangular M3s with distinct ectoloph and metaloph).

We have used the tooth wear stage-based protocol developed by one of us (POA) for reconstructing mortality curves in both extant and extinct rhinoceroses, based on isolated teeth (Bacon *et al.* 2008). The age classes as characterized on the white rhinoceros by Hillman-Smith *et al.* (1986) are used in this study because of the phylogenetic, chronological and ecological close relationships between this extant species and the woolly species (Antoine 2002). We have restricted this analysis to upper teeth, more abundant in Fouvent (69 specimens), as they display a much more homogenous eruption and wear pattern than the lower teeth, both in the white rhino and in the woolly rhino. The mortality curve obtained for *C. antiquitatis* is trimodal, with a majority of individuals ranging from classes I to IX (1.5 months up to 9 years) (Fig. 10); the first mode is comprised between 1.5 and 4 years (classes V-VI), which coincides with a period encompassing weaning and abandonment of juvenile individuals by the mother (Groves 1972). The second mode includes specimens the individual age of which ranges from 4 and 9 years, e.g., more or less the subadult-adult transition (classes VIII-IX; Hillman-Smith *et al.* 1986). The third and last mode, with less specimens, includes adult individuals (14-28 years; classes XII-XIII). Based on upper teeth, juveniles (61%) are far overrepresented with respect to subadults (23%) and adults (16%). Such a structure is significantly distinct from that of natural populations of recent Indian rhinos (*Rhinoceros unicornis* Linnaeus, 1758), consisting of 27% juveniles, of 21% subadults, and of 52% adults (Laurie 1982; Laurie *et al.* 1983). On the other hand, the Fouvent mortality profile is much similar to what is observed for the late Pleistocene rhino tooth sample of Duoi U’Oi, in Vietnam and other Southeast Asian cave localities, for which the accumulating factor is also of biological origin (porcupines; Bacon *et al.* 2008; Antoine 2012). Nevertheless, 14 woolly rhino teeth from the 1989-1992 excavation sample in Fouvent are eroded, which attests to a by-pass and a hydrodynamical erosion, both post-mortem and pre-accumulation (n°32, 42, 78, 87, 107, 124, 158, 192, 225, 269, 293, 330, 337, and 480). A lower tooth was split into two pieces then eroded, before both halves were recovered from two distinct excavation units (FVT 92 G9B-525 and FVT 92 F9B-165).

Several teeth from Fouvent show environmental enamel hypoplasia, which expresses a severe physiological stress during odontogenesis (but does not imply any genetic origin). On deciduous teeth, this pathology is due to a starving episode for the mother during pregnancy or nursing, whereas enamel hypoplasia on permanent teeth expresses denutrition coinciding with either weaning or abandonment of the calf by a newly pregnant mother (Mead 1999). In Fouvent, the specimens showing the most spectacular pathologies are the M1 G9D 607, the M2 E11B 218, and the d4 F11 C243 (Fig. 11).

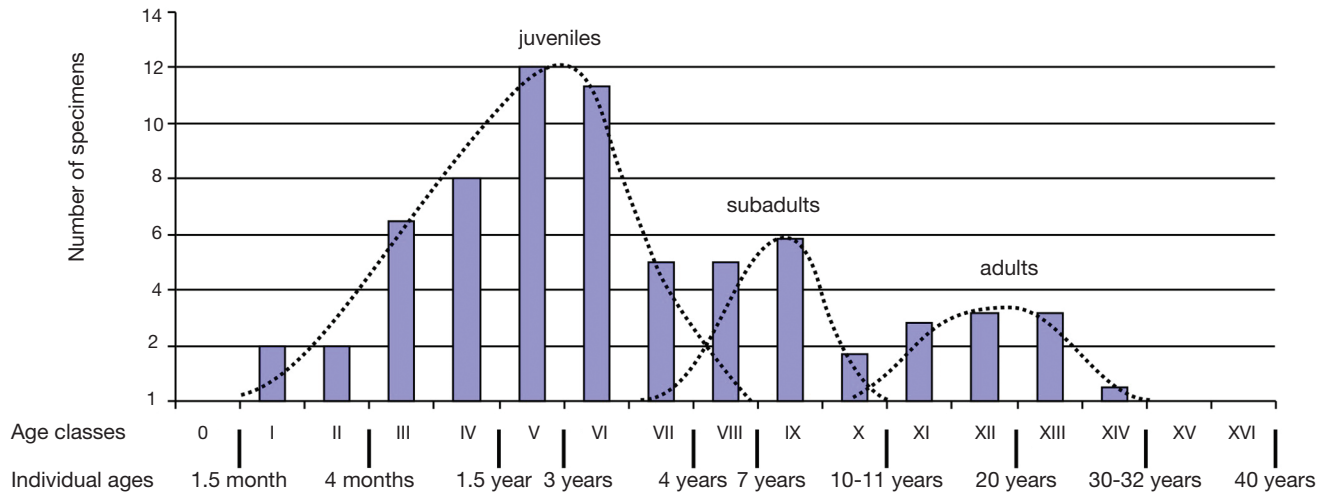


FIG. 10. — Mortality curve of the woolly rhino (*Coelodonta antiquitatis* (Blumenbach, 1799)) from the late Pleistocene of Fouvent, based on dental eruption and wear stages. Modified from the protocol of Hillman-Smith *et al.* (1986), as detailed in Bacon *et al.* (2008).

Order ARTIODACTYLA Owen, 1848
 Suborder RUMINANTIA Scopoli, 1777
 Family BOVIDAE Gray, 1821
 Subfamily BOVINAE Gray, 1821
 Genus *Bison* Smith, 1827

Bison priscus Bojanus, 1827

MATERIAL EXAMINED. — NISP=241; MNI=31.

1842 sample: 1 skull (parietal fragment); 1 left horn core; 1 horn core; 1 left M1-2; 2 right M1-2; 2 left m3; 1 right radius; 2 left metacarpals; 1 right innominate; 1 right tibia; 1 left talus; 1 left calcaneus; 2 right calcanei.

1989-1992 sample: 10 petrosal bones; 1 skull (frontal fragment); 2 right D2; 3 left D3; 2 right D3; 2 right D4; 2 left P2; 2 left P3-4; 2 right P3-4; 3 left P4; 1 left M1; 4 right M1-2; 3 left M1-2; 3 right M2; 1 left M2; 1 right M3; 1 left mandible including m and m2; 1 right d2; 2 left d4; 1 right d4; 1 right i1-2; 1 right i2; 1 left p2; 2 right p3; 5 left p3; 3 right p4; 2 left p4; 4 right m1; 8 left m1; 3 right m1-2; 5 left m1-2; 2 m1-2; 5 right m3; 6 left m3; 1 m3; 1 upper premolar fragment; 6 upper molar fragments; 10 lower molar fragments; 1 incisor fragment; 2 premolar fragments; 1 molar fragment; 18 tooth fragments; 2 cervical vertebrae; 1 sacral fragment; 5 right humeri; 4 left humeri; 3 humeri; 1 right radius; 2 right radii; 6 radius; 3 ulnae; 1 scaphoid; 1 metacarpal; 1 right femur; 1 left femur; 11 femorae; 5 right tibiae; 3 left tibiae; 14 tibiae; 1 right malleolus; 1 right talus; 3 right calcanei; 2 left cuneiforms; 1 right metatarsal; 3 left metatarsals; 4 metatarsals; 2 first phalanges; 2 sesamoids; 4 metapodials.

DESCRIPTION

Among the ungulate remains from Fouvent, 241 specimens could be associated to large bovines (*Bos* or *Bison*). Tooth wear, as well as the bones dispersal within the different layers, suggest a minimum of 31 individuals from different age classes: adult, juvenile and senile. Their precise taxonomic identification (at genus or specific level) in association with other species provides usually a valuable asset to reconstruct palaeo-environments. *B. priscus* is commonly associated to an open/steppic land, while *B. primigenius* Bojanus, 1827 is more adapted to open spaces and open woodland. Some morpho-

metrical discriminating criteria for bovines during Pleistocene were widely detailed in the last decades (Olsen 1960; Brugal 1983; Slott-Moller 1990; Auguste 1995; Fernandez 2006). Unfortunately, fragmentation of dental and postcranial material with numerous surface alterations (dissolution, bone desquamation, etc...) have strongly restricted our observations and measurements as regards Fouvent. The dental material is abundant with 91 teeth isolated or within jaws, i.e. 37% of the total sample. The distinction between *Bos* and *Bison* was mainly conducted on a small part of the sample starting from dental morphological criteria of Slott-Moller (1990). We observed on ten M3 that the height of the ectostylid, as well as the mesial vestibular convexity of the crown, were consistent with the typical morphological features of *Bison*. Among postcranial elements, a complete astragalus (1842.7) and a complete calcaneus (1842.78; Fig.9I) were ascribed to *B. priscus*. The upper trochlea shows in both cases the typical "U" profile of bison as described by Slott-Moller (1990). The medial tubercle appears isolated above the proximal margin line of the distal trochlea, which is characteristic of *Bison* (Olsen 1960). Similarly, the calcaneus meets the criteria mentioned for the bison (Brugal 1983; Magniez 2010). If some remains are associated to *B. priscus*, however it is not possible to assign by extension all the material to this species. On the one hand, the sample size with morphological evidence of bison is too small, on the other hand it is quite possible that other bones (coxal, metapods, carpals, and tarsals still under study) could either correspond to *B. primigenius* as it is often the case.

Family CERVIDAE Goldfuss, 1820
 Subfamily CERVINAE Goldfuss, 1820
 Genus *Megaloceros* Brooks, 1828

Megaloceros giganteus Blumenbach, 1799

MATERIAL EXAMINED. — NISP=46; MNI=16.

TABLE 14. — Dental measurements of *Megaloceros giganteus* Blumenbach, 1799 from Fouvent. Measurements in mm.

Dental Rank	Breadth			Length		
	N	Min-Max	Mean	N	Min-Max	Mean
P2	4	19.0-23.5	21.2	6	17.0-21.6	19.8
M1	1	33.0	-	1	28.0	-
M2	4	27.0-32.0	29.4	4	26.0-31.0	28.0
M3	2	25.0-29.5	27.3	2	33.0-35.0	34.0
p3	3	12.0-14.2	13.4	2	17.0-22.0	19.5
p4	5	14.0-17.5	16.1	4	22.0-31.0	25.5
m1	4	15.0-19.5	18.1	3	22.0-24.0	23.0
m2	6	20.0-21.5	20.8	6	26.0-31.0	28.7
m3	7	17.5-22.0	19.8	6	39.0-44.0	41.3

1842 sample: 2 right mandibles; 1 left mandible; 2 right tali; 1 naviculo-cuboid.

1989-1992 sample: 1 left maxilla; 1 right mandible; 3 left mandibles; 6 left P2; 1 left M1; 3 left M2; 1 left M3; 1 left d4; 2 right p3; 2 right p4; 1 left p4; 1 right m1; 1 left m1; 2 right m2; 1 left m2; 3 left m3; 8 tooth fragments; 1 right humerus; 2 left humeri.

DESCRIPTION

The giant deer *M. giganteus* is represented by 46 remains (mainly cranial elements including teeth). Sixteen individuals (mainly adults and olds) have been counted based on the dispersion within the stratigraphy. The giant deer is quite common in the Late Pleistocene interval, even if the samples are generally small (Kurtén 1968; Delpech & Guérin *in* Guérin & Patou-Mathis 1996; Magniez 2010). Dental morphology of the Fouvent sample closely matches that of published material (e.g., Thenius 1966; Croitor 2008; Magniez 2010). Upper premolars and molars are robust with a strong cingulum. On the lingual face, they have a well developed and individualized interlobar column. The mandibular fragments of Fouvent with m1, m2 and/or m3 also show individualized interlobar column (Fig.9A, B). Measurements are summarized in Table 14 and their comparison with published data confirms our attribution to the Megaceros. The basal length and the width of six left P2 are quite similar of the ones recorded at Tournal (23-23 mm for the length and 22-23 for the width *in* Magniez 2010) and at Conives (22 mm for the length and 21.4 mm for the width *in* Fourvel 2008). The comparison dataset concerning lower cheek teeth are rarer but the measurements recorded at Fouvent are close to the values of Tournal. Nonetheless the first lower molars are smaller; the length for example is comprised between 15 and 19.5 mm whereas the only m1 from Tournal is 28.1 mm long (Magniez 2010). In addition, if the measurements of the m2 are similar at Fouvent and Tournal they are much smaller than the only m2 of the megaceros of Labeko Koba, Spain (L=34 mm; B=22.2 mm). Six postcranial elements have been attributed to the giant deer based on their morphology and general proportions. Three humeral shaft fragments (G8.A/B.215, E11.B.71, F10.B.416) have been determined as a giant deer because of their size and morphology excluding each other large species (equids, bovids

or rhinoceros). Two right tali (1842.103 and 1842.79) and one naviculo-cuboid (1842.80) present the same characters as described in Breda (2005) and Magniez (2010).

Genus *Cervus* Linnaeus, 1758

Cervus elaphus Linnaeus, 1758

MATERIAL EXAMINED. — NISP=30; MNI=10.

1842 sample: 3 right antlers; 1 left talus.

1989-1992 sample: 1 left M1-2; 1 right i1; 1 left i2-3; 1 right p2; 3 left p3; 1 right p4; 1 left m2; 2 left m3; 1 lower tooth fragment; 1 right humerus; 2 left humeri; 2 radii; 1 left femur; 2 femorae; 1 right tibia; 1 left tibia; 2 tibiae; 1 right metatarsal III-IV; 1 first phalanx.

DESCRIPTION

The red deer *C. elaphus* is represented by 30 cranial and postcranial remains which are related to 10 individuals. The dental material is attributed undoubtedly to *C. elaphus*. Premolar and molar size, proportion, and morphology are consistent with the descriptions of Bouchud (*in* Lavocat 1966) and easily distinguishable from the reindeer. In addition, their size clearly does not correspond to the roe-deer and there is no interlobar column on molars as for the giant-deer. The morphometrical features, in particular on M3, do not match the descriptions of the small form *Cervus simplicidens* (Guadelli 1996). Unfortunately, with the exception of a left talus (1842.97; Fig. 9D, E), bones are too much fragmented for any biometric analysis. However, diagnostic criteria for the red deer as described by Bouchud (*in* Lavocat 1966) were observed at Fouvent (e.g., the well-developed median gutter of the metapods). The occurrence of a red deer at Fouvent is not surprising, as this ubiquitous species has been recognized in Europe from the Middle Pleistocene (e.g., Mosbach, Mauer) until recent times. It is commonly found in Late Pleistocene samples (Delpech & Guérin *in* Guérin & Patou-Mathis 1996; Magniez 2010).

Subfamily ODOCOILEINAE Pocock, 1923

Genus *Rangifer* Smith, 1827

Rangifer tarandus (Linnaeus, 1758)

MATERIAL EXAMINED. — NISP=113; MNI=16.

1842 sample: 1 left antler; 3 antler fragments; 1 left talus.

1989-1992 sample: 2 right antlers; 1 left antler; 3 antler fragments; 3 petrosal bones; 1 left P2; 1 left P2-3; 2 right P3-4; 1 right M1-2; 3 left M1-2; 1 right M2; 1 right M3; 1 right i1; 1 left i1; 4 left p4; 1 left m1; 2 left m2; 1 right m3; 4 left m3; 2 right m1-2; 1 left m1-2; 4 tooth fragments; 5 right humeri; 2 left humeri; 4 humeri; 2 left radii; 4 radii; 1 ulna; 2 left magnum; 1 right lunate; 1 left scaphoid; 1 left metacarpal III-IV; 1 left femur; 4 femorae; 1 patella; 4 right tibiae; 1 left tibia; 4 tibiae; 2 naviculo-cuboids; 3 right metatarsals III-IV; 1 left metatarsal III-IV; 2 metatarsals; 1 sesamoid; 2 vestigial metapodials; 1 long bone fragment; 4 metapodials; 7 first phalanges; 5 second phalanges; 4 third phalanges.

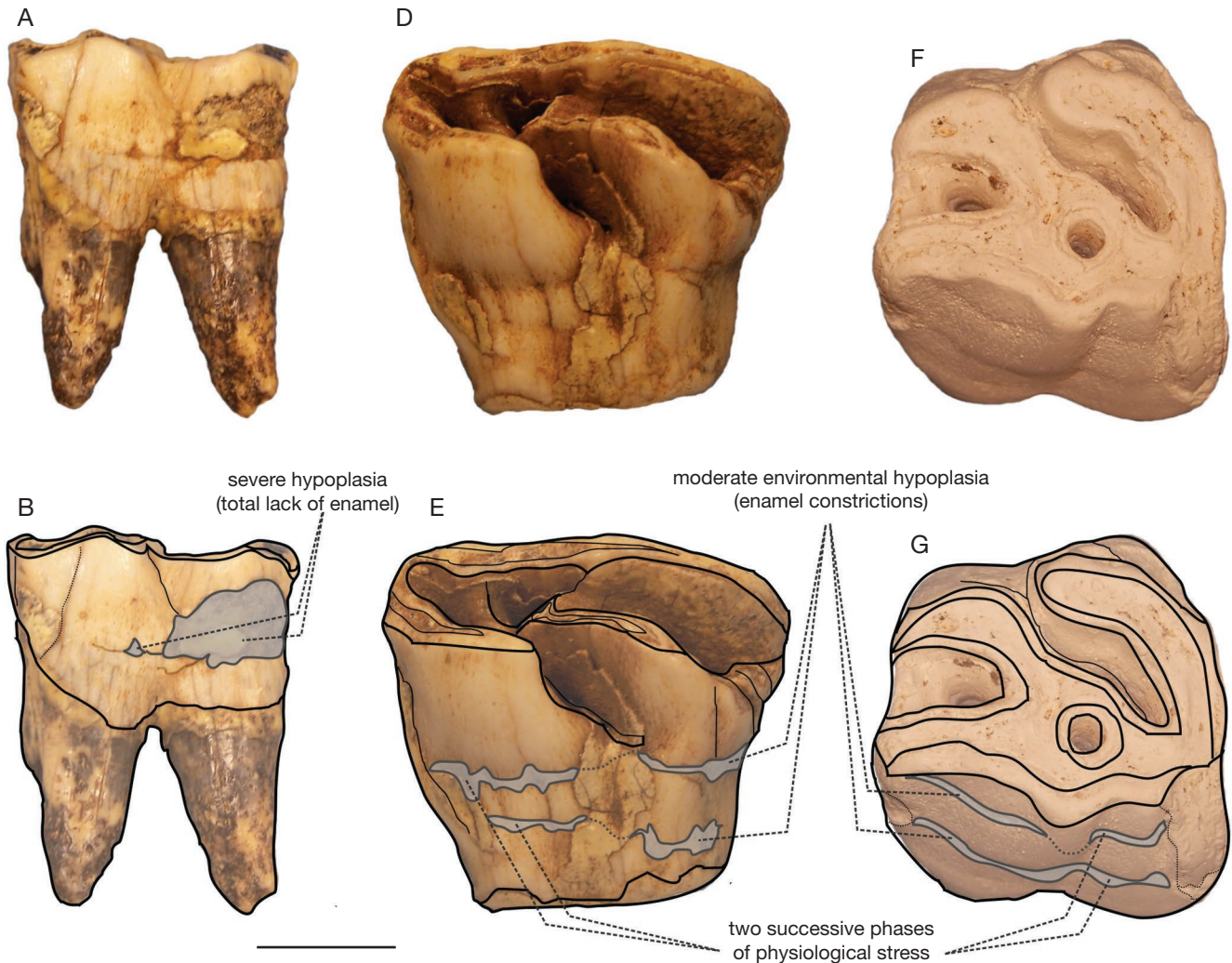


FIG. 11. — Enamel hypoplasia on the tooth sample of *Coelodonta antiquitatis* (Blumenbach, 1799) (woolly rhino) from Fouvent: **A, B**, left d4 F11 C342, with a severe hypoplasia, characterized by the total lack of enamel on a part of the ectolophid (grey area). **C, D**, left M1 G9 D607; **E, F**, left M2 E11 B218. The last two teeth show less severe hypoplasia, visible through enamel constrictions on the lingual side (G9D607) and the ectoloph (F1 C243). These constrictions, parallel and remote, indicate the occurrence of two distinct episodes of physiological stress on each tooth. A, C, E, photographs. B, D, F, interpretative drawings (POA).

DESCRIPTION

One hundred and thirteen bone remains (both cranial and postcranial elements) have been referred to as the reindeer, *R. tarandus*. Their stratigraphical location at Fouvent suggests a minimal number of 16 individuals. All the typical reindeer morphological features (see Magniez 2010 for a review) could be observed on the material (including teeth, antler and postcranial elements). Unfortunately, this material is too much altered and the sample is not sufficiently abundant to meet the conditions for any population structure analysis (age-structure, sex-ratio...). Be as it may, a left basilar fragment of shed antler (FVT.1842.106) can be associated to a male adult (Fig. 9M). Another small fragment (FVT.1992.F10.B.329) could match a female or a young male (Averbouh pers. comm.; Fig. 9N). Finally, distinct tooth wear stages as observed on isolated teeth suggest various age classes (young adults, adults, old adults, and seniles).

Genus *Capreolus* Frisch, 1775

Capreolus capreolus (Linnaeus, 1758)

MATERIAL EXAMINED. — NISP=11; MNI=3.

1989-1992 sample: 1 left i3; 1 left humerus; 1 radius; 1 left ulna; 1 right femur; 1 femur; 1 right tibia; 1 right talus; 3 metatarsals III-IV.

DESCRIPTION

Roe deer is represented by 11 remains (including one isolated tooth), which correspond to three adult individuals. Appendicular skeleton is not sufficiently abundant and well preserved to allow any taxonomic identification. However, the size and the general morphology of metatarsals are typical of *Capreolus* (i.e. presence of a narrow longitudinal dorsal gutter; proximal epiphysis distinct from other comparable small ungulate species). The roe deer *C. c. suessenbornensis* has been attested in Europe (e.g., Süßenborn) since the Middle Pleistocene, and

it became abundant with *C. c. capreolus* during the Cromerian stage. This latter subspecies has been widespread in Europe from the late Pleistocene until today (Kurtén 1968; Delpech & Guérin *in* Guérin & Patou-Mathis 1996).

DISCUSSION

The bone collection coming from previous excavations of Fouvent led to famous works in the field of palaeontology. As an example, taking into account the material of Gaylenreuth and Fouvent, Georges Cuvier was the first to make the distinction between fossil hyenas and their current representatives, starting from morphological cranial comparisons (Cuvier 1812). In this study, Cuvier made a synthesis of the previous works (six studies involving three collections from the different campaigns of excavations) and described the faunal association. The first species association, based on the material collected by Mr. Le Febvre de Morey and transmitted to Cuvier, reported at least three species: the horse, the elephant and a hyena. The successive works suggested an open steppic environment under a cold climate, with an assemblage encompassing horses, mammoths, woolly rhinoceroses, reindeers, and a wolverine.

The faunal association of Fouvent reflects a steppe-tundra-like open landscape under a severe cold climate as reported in the preliminary study of Fosse (1997). The association of *Dicrostonyx* Gloger, 1841 and *Lemmus* Link, 1795 (lemmings) as well as the presence of marmots is also characteristic of cold climates (Roger unpublished). From a strict biochronological point of view, the species of Fouvent are quite similar to OIS3 faunal assemblages integrating gregarious species (*B. priscus*, *E. germanicus*, *R. tarandus*) in a steppic environment (*C. antiquitatis* and *M. primigenius*). The evolutionary stage of ungulates of Fouvent points to the Würmian period and more probably OIS3. Most carnivores of Fouvent are ubiquitous species (*P. (Leo) spelaea*, *U. spelaeus*, *C. lupus*, *C. c. spelaea*, *M. meles* and *V. vulpes*). The hyena of Fouvent is robust and quite similar to the large hyenas of OIS3 the body size of which increased during recent phases of the Pleistocene (Kurtén 1963; Klein & Scott 1989). The recognition of the wolverine (*G. gulo*) and the steppic polecat (*M. eversmannii*), as well as the probable presence of *Isatis*, are clear indications of a cool phase.

The mammalian fauna of Fouvent is quite similar to those of many coeval dens. Such carnivore (hyena, lion, wolf, bear, and fox)/medium-sized ungulate (roe deer, deer and reindeer)/large ungulate (horses, bison, giant deer)/mega-herbivore (rhinoceros, mammoth) assemblages are conspicuous in hyena dens during Würmian OIS3. The bone accumulations of Camiac (Guadelli 1987), Bourdette (Discamps *et al.* 2012), Plumettes (Beauval 1997; Beauval & Morin 2010), Conives (Fourvel 2008; 2012), and Unikoté (Michel 2005) in France, as well as those of Redaka II in Bulgaria (Fernandez & Guadelli 2008), Labeko Koba in Spain (Altuna & Mariezkurrena 2000) or Teufelslucken (Ehrenberg 1966) and Villa Seckendorf (Ziegler 1996) in Germany are perfectly comparable to that of Fouvent.

CONCLUSION

The palaeontological site of Fouvent could be considered as an original example of a Late Pleistocene hyena den (Fourvel 2012; Fourvel *et al.* 2014). The association of various criteria such as predator abundance, in particular the cave hyena (850NISP, 121MNI), the diversity of ungulate prey-species (ranging from small-sized species such as the roe deer to mega-herbivores, like woolly rhinos and mammoths) and the general context of the bone accumulation (horizontal karstic cavity) suggests a long-termed occupation of the site by the predator, which in turns defines a cave hyena den. The bone accumulation is particularly species-rich in terms of large mammals, encompassing seven or eight ungulate species and eleven carnivore species. These faunal elements point to the latest phase of the Late Pleistocene (Würmian stage). The evolutionary stage of equids (referred to *E. germanicus*), the abundance of woolly rhinoceroses and reindeers, and the large dimensions of the cave hyena allow us to refer this faunal assemblage to the Isotopic Stage 3. Palaeoenvironmental conditions as inferred by the co-occurrence of horses, mammoths, woolly rhinoceroses, reindeers, and wolverines, coincide with a steppe/tundra-like open landscape under a cold climate, which are perfectly compatible with the Oxygen Isotopic Stage 3 (OIS3; 57-29 ka BP; Fourvel 2012).

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