Original article

Micromammals (rodents and insectivores) from the early Late Pleistocene cave site of Bois Roche (Charente, France): Systematics and paleoclimatology

Micromammifères (rongeurs et insectivores) du début du Pléistocène supérieur du gisement de la grotte de Bois Roche (Charente, France) : systématique et paléoclimatologie

Micromamíferos (Roedores e Insectívoros) del yacimiento del comienzo del Pleistoceno Superior de Bois Roche (Charente, Francia): sistemática y paleoclimatología

Carmen Sesé [a,*], Paola Villa [b]

[a] *Departamento de Paleobiología, Museo Nacional de Ciencias Naturales, C.S.I.C., C/ José Gutiérrez Abascal 2, 28006 Madrid, Spain*
[b] *University of Colorado Museum, UCB 265, Boulder, 80309-0265 Colorado, USA*

Abstract

We present the study of rodents and insectivores from the 1995 season of excavation at the early Late Pleistocene site of Bois Roche (Charente, France). The site is a small cave with a low ceiling, used as a den by hyenas. It contains a large herbivore assemblage (mainly bovids and equids) with a smaller representation of medium-size taxa (cervids), many microvertebrates, abundant coprolites and deciduous hyena teeth, and a few lithic artifacts (Middle Paleolithic) introduced into the cave by gravity and slope wash. The rodent fauna consists of *Eliomys quercinus* cf. *quercinus*, *Apodemus* sp., *Microtus gregalis*, *Microtus oeconomus*, *Arvicola terrestris* and *Dicrostonyx torquatus*. Insectivores are represented by *Neomys* cf. *fodiens*. The most common species is *M. gregalis* which forms 93.7% of the total MNI. The micromammal fauna suggests an open landscape, with some vegetation mainly of the steppe or tundra type, with areas of water and more wet vegetation and some areas with trees. The micromammal association of Bois Roche is characteristic of a cold or very cold dry climate.

© 2008 Elsevier Masson SAS. All rights reserved.

Résumé

Nous présentons l'étude des rongeurs et insectivores du gisement du début du Pléistocène supérieur de Bois Roche (Charente, France) à partir du matériel provenant de la campagne de fouille de 1995. Le gisement est situé dans une petite grotte à plafond bas, utilisée par des hyènes comme repère. Il renferme un grand ensemble d'herbivores (bovidés et suidés principalement), avec une mineure représentation de mammifères de taille moyenne (cervidés), plusieurs microvertébrés, abondants coprolithes et dents de lait d'hyènes, et quelques artefacts lithiques (Paléolithique moyen) introduits dans la grotte par gravité et ruissellement. La faune de rongeurs est composée de *Eliomys quercinus* cf. *quercinus*, *Apodemus* sp., *Microtus gregalis*, *Microtus oeconomus*, *Arvicola terrestris* et *Dicrostonyx torquatus*. Les insectivores sont représentés par *Neomys* cf. *fodiens*. L'espèce plus abondante est *M. gregalis* qui constitue 93,7 % du NMI total. La faune des micromammifères suggère un paysage ouvert, avec

---

* Corresponding author.

E-mail address: c.sese@mncn.csic.es (C. Sesé).

végétation principalement de steppe ou toundra, aires avec étangs et végétation plus humide et quelques zones avec des arbres. L'association des petits mammifères de Bois Roche est caractéristique d'un climat sec et froid ou très froid.

Resumen

Presentamos el estudio de los roedores e insectívoros del yacimiento del comienzo del Pleistoceno Superior de Bois Roche (Charente, Francia), procedentes de la campaña de excavación de 1995. El yacimiento está situado en una pequeña cueva de techo bajo, utilizada por las hienas como madriguera. Contiene gran abundancia de herbívoros (principalmente bóvidos y équidos) y una menor representación de mamíferos de talla media (cérvidos), muchos microvertebrados, abundantes coprolitos y dentición decidua de hienas, y algunos instrumentos líticos (Paleolítico Medio) introducidos en la cueva por gravedad y por el lavado de las pendientes. La fauna de roedores está formada por *Eliomys quercinus* cf. *quercinus*, *Apodemus* sp., *Microtus gregalis*, *Microtus oeconomus*, *Arvicola terrestris* y *Dicrostonyx torquatus*. Los insectívoros está representado por *Neomys* cf. *fodiens*. *Microtus gregalis* es la especie más abundante constituyendo el 93,7% del total de NMI. La fauna de micromamíferos sugiere un paisaje abierto con cierta vegetación esteparia o de tundra, con áreas de agua y vegetación más húmeda y algunas zonas arboladas. La asociación de micromamíferos de Bois Roche es característica de un clima seco y frío o muy frío.

© 2008 Elsevier Masson SAS. All rights reserved.

1. Introduction

1.1. The site

Bois Roche is a small cave located in the chateau of the same name in the Charente region, near the city of Cognac (France). The cave deposits were dated to late OIS 5 or early OIS 4 by preliminary ESR estimates by Liping Zhou, of Beijing University. Final dates, however, were never provided and new ESR work is now in progress by Rainer Grün of the Australian National University. The pollen (work in progress by Sánchez-Goñi, University of Bordeaux 1) and the macrofauna (analyses by Cedric Beauval and Valerie Bourdillat; Marra et al., 2004; Villa et al., 2004) conform to this age estimates. Evidence for a human presence is negligible consisting solely of a few Middle Paleolithic artifacts introduced into the cave by natural transport processes such as gravity and slope wash (Villa and Soressi, 2000). Various lines of evidence, described below, clearly show that the site was used as a den by hyenas.

Entrance to the cave is provided by a short, subvertical conduit which leads into a small vaulted area, called the Vestibule, about 5 m² in total. A larger chamber, 9 × 4 m in area, called Grande Salle, with sediments nearly filling it to the ceiling was discovered by the land owner, Jean-François Portet, and reported to the Service Archéologique of the Charente region in 1978. At the time of its discovery the surface was covered with bones, teeth and hyena coprolites; the paleosurface materials (including 1200 bones and teeth and 17 artifacts) were collected by the discoverer. Test excavations were conducted in 1979 and 1981 by Vandermeersch, then resumed by Laurence Bartram and Paola Villa in 1995, 1997–1998 and by Villa in 1999–2000. In total an area of about 18 m² (representing about half of the cave area at the existing surface level) has been opened down to a maximum depth of 60–80 cm (Figs. 1 and 2; Villa and Bartram, 1996; d'Errico and Villa, 1997; Bartram and Villa, 1998; Villa and Soressi, 2000; Villa

and d'Errico, 2001; Marra et al., 2004; Villa et al., 2004; Blain and Villa, 2006).

1.2. Stratigraphy and excavation methods

The deposits, which slope away from the entrance toward the rear of the inner chamber, consist of two major stratigraphic units along with four subdivisions of the upper unit (Goldberg, 2001) from top, as follows (Fig. 3):

- layer 1a (approximately 10–15 cm) is a stony silty clay, the paleosurface unit reworked at the top (layer 1ar) by the collecting activities of the land owner. Within 1a, layer 1am is a discontinuous layer that vary from 0 to 10 cm, whose main characteristic is to contain very abundant amphibian remains (Blain and Villa, 2006);
- layer 1b is a lens of finely laminated brown silty clay that varies from 0 to 6 cm, deposited by running water
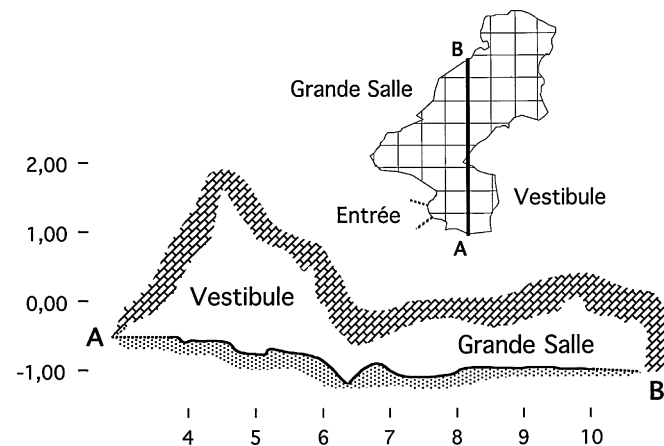

Fig. 1. Bois Roche. Plan and cross section of the cave at the level of the present-day surface.

Fig. 1. Bois Roche. Plan et coupe de la grotte au niveau de la surface actuelle.
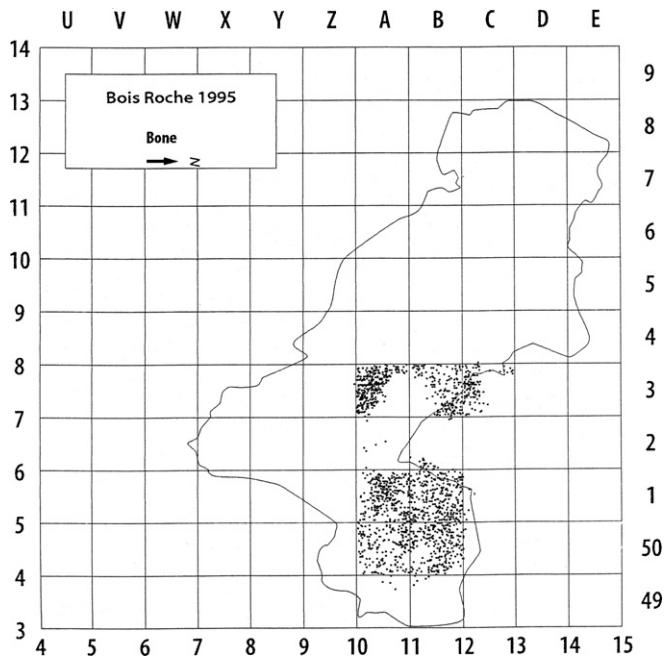
Fig. 2. Bois Roche, 1995 excavation. Distribution of plotted bones in the Vestibule (squares A50, A1, B50 and B1) and the Grande Salle (squares A3, B3 and C3). The grid system used at the site is double: the left and bottom numbers are the origin coordinates used by the laser theodolite for making horizontal and vertical plots, the line of numbers to the right and the letters at the top is the conventional system (corresponding to the grid system used in the 1979–1981 excavations by Bernard Vandermeersch) used to identify squares and to label objects and screen refuse.

Fig. 2. Bois Roche. Répartition horizontale des restes osseux de la fouille 1995 dans le Vestibule (carré A50, A1, B50 et B1) et dans la Grande Salle (carré A3, B3 et C3). Le carroyage utilisé dans le gisement est double : les numéros à gauche et en bas sont les coordonnées utilisées par la station totale pour produire des plans et des projections, les numéros de droite et les lettres en haut correspondent à l'ancien carroyage de Vandermeersch rétabli en 1995 et utilisé pour étiqueter chaque pièce et les refus de tamis.

(sheetflow). It is laterally discontinuous and was not present in the Vestibule;

- layer 1c, about 10 to 20 cm thick is composed of yellow-brown sandy clay silt with limestone rock fragments that range in size from granules to decimeter-size blocks;

- layer 1d is a grey-brown, sinter-like layer, 5–15 cm thick, with localized calcitic laminae, locally eroded by burrows. It was not present in the Vestibule;

- layer 2 is a massive (up to 30–40 cm) clast-supported accumulation of clayey silt with centimeter to decimeter size blocks of limestone roof fall and abundant remains of megafauna and microfauna. Lack of bedding is probably due to bioturbation by hyenas;

- layers 1c and 2 are rich in rounded millimeter sized coprolite fragments, evident in micromorphological slides, and very abundant in screen residues (Bartram and Villa, 1998: Fig. 2). The underlying layer 3 has been tested only.

Our excavations were done by 1-m grid system using the same datum level as Vandermeersch. Only brushes and small tools were used in the excavation, that is bamboo or wooden tools and dentist tools without a point (e.g. those used for mixing dental amalgam). All identifiable pieces of any size seen by the excavators and all pieces 2 cm or larger in maximum dimension were recorded with three cartesian coordinates in Excel files. The excavation was carried by one square meter units following the natural stratigraphy, established at the beginning of the excavation by the project geologist (P. Goldberg) from a standing section and checked in subsequent years; the maximum excavated thickness of an excavation unit (*décapage*) is 5 cm. All sediments were waters-creened with superimposed screens of 5 and 2 mm mesh; all identifiable or unidentifiable bone fragments, all the microfauna, coprolite fragments and small lithic debris from the screens were sorted and bagged by square and aggregate depth of the excavation units, that is 5 cm or less, depending on the natural stratigraphy.

1.3. The assemblage

The assemblage so recovered is very large, consisting of about 12,500 three-dimensionally recorded objects with coordinates, 1200 items collected from the paleosurface by the discoverer of the site, more than 220,000 bone splinters recovered through fine-mesh water screening and the very abundant microfauna. The macrofaunal remains (bones and
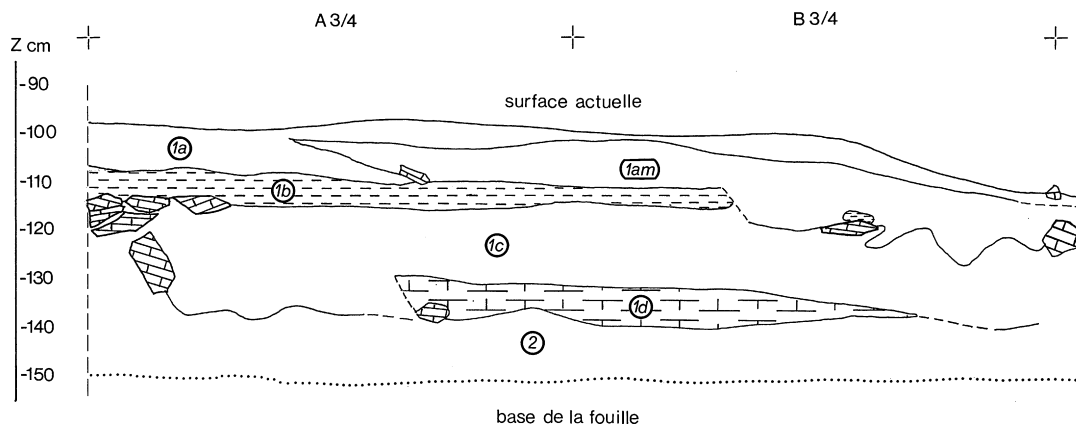

Fig. 3. Bois Roche, Grande Salle. Stratigraphic section, the dotted line indicates the base of the excavation in 1997.
Fig. 3. Bois Roche. Coupe stratigraphique dans la Grande Salle, la base de la fouille en 1997 est indiquée par la ligne en pointillée.

teeth) represent 89 to 96% of the plotted assemblage, depending on levels, with low proportions of plotted coprolites (2.8–13.7%) and flint artifacts (0–2.2%; Villa et al., 2004; Marra et al., 2004). More than 40,000 amphibian remains from all levels have been studied by Blain (Blain and Villa, 2006).

1.3.1. Macrofauna

The faunal assemblage shows high proportions of ungulates to carnivores. In layer 2 (the richest in faunal remains) hyenas are 7.4% and other carnivores are 1.4% of the total ungulate + carnivore number of individual specimens (NISP). If minimum number of individuals (MNI) are considered, the representation of hyenas is a bit higher, 10.5% and the other carnivores (canids) are 7.9% (Marra et al., 2004). According to Cruz-Uribe (1991) the representation of carnivores in various fossil hyena dens in southern Africa is always more than 20% of the total carnivore plus ungulate MNI. Modern spotted hyena dens, however, have very low proportions of carnivores, 10% or less. Bois Roche is clearly at the lower end of the range of values indicated in fossil hyena dens but has a better representation of carnivores compared to modern African examples. It has been shown by Fosse (1994: 132) that the relative proportion of carnivores and herbivores at European fossil dens is in fact quite variable. The representation of hyenas by NISP or MNI at Bois Roche falls in the interval between Camiac (7% NISP; MNI was not calculated at Camiac) to those of Lunel Viel lower levels (15% NISP; 26% MNI).

The taxonomic composition of the assemblage is not very diverse. The most common prey animals are bovids (*Bos* or *Bison*); whenever the specimens can be identified to genus, *Bison* absolutely predominates. The second most common prey taxon is the horse (*Equus caballus*) while cervids (*Cervus elaphus* and *Rangifer tarandus*) are very scarce.

1.3.2. Coprolites

The occurrence of coprolites in all layers and squares is an indication of occupation by hyenas. Note, however, that plotted coprolites at Bois Roche are but a small fraction of the original quantities. During excavation we plotted coprolites that were either intact or relatively well-preserved when uncovered. However, they are extremely fragile and difficult to extract and to conserve without damage, as they break easily in minute fragments. In contrast, rounded coprolite fragments are very common in micromorphological slides, some are broken in situ (Goldberg, 2001: Figs. 4–6). Millimeter-sized coprolite fragments represent the largest screen residue volume from all squares and all layers (Bartram and Villa, 1998: Fig. 2); their preservation is due to rapid drying of the wet-screen residue. In other words, proportions of plotted coprolites are relatively low as a result of a low degree of preservation, that is in situ destruction due to the humidity of the cave environment and intensive trampling by hyenas (suggested by the rounded fracture edges). The morphology of intact coprolites indicates hyenas: they have a near-circular cross section, sometimes pointed at one end, and a fairly small diameter (2–4 cm; size analysis is in progress; Horwitz and Goldberg, 1989; Larkin et al., 2000). In a few cases they contain tiny fragments of

digested bone; a digested rodent molar was observed by the pollen analyst (Sánchez-Goñi, pers. comm.).

1.3.3. Bone modifications

Surface preservation of the macrofaunal remains is generally excellent at Bois Roche, nevertheless some specimens can be difficult to observe due to partial exfoliation or friable, brittle surfaces or because they are too small (less than 3 cm) to be carrying distinctive gnaw marks. Evidence of human involvement with the bones is minimal. Modifications by carnivores of the total plotted assemblage in layer 2 (including NID, that is unidentified bone specimens and teeth, which may be digested, and excluding non observable, not well-preserved specimens) are very common (62.6%); bones without any marks are 36.8%. The proportions of carnivore marks are a bit higher if teeth are excluded from the sample.

The frequencies of carnivore gnaw marks are comparable to those reported by Cruz-Uribe (1991) for modern hyena dens (at least 50%). The frequencies of different kinds of gnaw marks indicate a very high proportion of tooth pits (about 46% in layer 2). It is possible that their high frequencies may have to do with the fact that Bois Roche appears to have functioned as a maternity den and that these tooth pits, often of small diameter, represent continued and intensive gnawing by juvenile hyenas that might be expected to leave lighter surficial marks than the those left by adult hyenas.

1.3.4. Digested bones

Partially digested and regurgitated bones from modern hyena dens have been described by Sutcliffe (1970); these pieces are also called acid-etched by Cruz-Uribe (1991). A sample of 431 small fragments showing single or multiple perforations and with a variety of surface modifications, studied by SEM and optical microscopy, has already been reported from Bois Roche (d'Errico and Villa, 1997). Because digested pieces are generally smaller than 9–10 cm and the majority is smaller than 3 cm, the frequency of digested bone fragments varies according to the method of recovery. At Bois Roche, due to wet-screening of all sediments and systematic sorting, their frequency is very high (about 87%) among the pieces recovered from the screens, that is bone fragments greater or equal to than 1 cm. We exclude pieces smaller than 1 cm from our counts because the class 0–10 mm is generally skewed, due to the fact that sorting of such large numbers of fragments cannot be efficiently done under a microscope. It is likely that the bulk of the very small "acid-etched" pieces at Bois Roche represent in fact not regurgitated pieces but bone fragments that have gone through the carnivore digestive system and were present in coprolites which were postdepositionally decomposed in the sediments (Brain, 1981: 63; Horwitz and Goldberg, 1989; Horwitz, 1990).

Teeth can be digested too although traces of digestion are less strongly expressed and digested teeth are generally a small portion of the total numbers.

1.3.5. Stone artifacts

Flint artifacts are very sparse in all layers. The stone artifact assemblage (made on local Senonian flint) includes a few

Levallois flakes, one Levallois core, many flake fragments, an abnormally large proportion of small debris and a few natural flint pieces. Processes of accumulation of the stone artifacts have been analyzed by Villa and Soressi (2000) and we refer to this paper for a general explanation of the presence of stone artifacts in what is clearly a hyena den as indicated in previous publications (Villa and Bartram, 1996; d'Errico and Villa, 1997, 1998; Bartram and Villa, 1998). The overall lithic assemblage composition by technological categories, metric attributes and studies of edge damage and abrasion, in addition to the bedding and geometry of deposits, show that lithics have been introduced by natural transport processes, such as gravity and slope wash. Bones and stones have accumulated independently and stone artifacts do not reflect human activities in situ. The original context of deposition of the artifacts must have been very close, on the limestone cliff near the entrance of the hyena den or on the slopes above the entrance, where a human occupation or human residues must have been present. However, their exact location will never be known since the limestone cliff has been heavily modified by the construction at the end of the last century of a wine-pressing building in which the cave now opens.

Another indication that the cave was not used by humans is the total absence of evidence for fire. Charcoal particles, which are very frequent in anthropogenic deposits of the Late Pleistocene, have never been found in the screen residues and are absent from micromorphological slides and from pollen slides (Sánchez-Goñi pers. comm.; Bartram and Villa, 1998). The cave ceiling is very low with respect to the preserved floor level (the paleosurface) and even at the base of the current excavation the cave could hardly have been used for human occupation.

In sum, demonstration that Bois Roche was a hyena den is provided by many lines of evidence: the carnivore to ungulate ratio, the high frequency of gnaw marks, the very high frequency of digested bones from the screens, the great abundance of coprolites in the micromorphological slides and in the screen refuse, the high proportions of deciduous hyena teeth (two thirds of total hyena teeth from screens), the chamber morphology with a very low ceiling and a narrow drop-down entrance, the absence of human occupation features such as fireplaces and the absence of charcoal particles in the sediments.

2. The micromammal sample

The micromammal remains studied in this paper come from the 1995 excavation season in squares A1, B1, A50 and B50 in the Vestibule, and A3 and C3 in the Grande Salle (Fig. 2). Most of square B2 had been removed by previous excavations by Vandermeersch and only a few pieces come from its remaining edges. In the Vestibule the upper part of layer 1c and all overlying layers had been removed by previous excavations by Vandermeersch and were only visible in the cleaned sections. In the Grande Salle the whole sequence is represented (Fig. 3) but had been partly affected by a test trench in squares A3–B3–C3 opened in the previous excavation.

3. Methodology

The nomenclature used in the description of the cheek teeth is according to López Martínez (1980). The teeth have been measured with a microscope with an ocular micrometer of 0.025 mm of precision. The measurements have been taken in the occlusal surface of the teeth oriented in their anatomical position and are given in millimeters. They correspond to the maximum length (L) and maximum width (W).

For *Arvicola* the measurements of the thickness of the enamel (SDQ = Enamel quotient derived from the German: "Schmelzband-Differenzierungs-Quotien") has been taken according to Heinrich (1990).

When the material is abundant the number of specimens (n) and the interval of variation of the measurements (minimum, mean and maximum) are provided. Other statistical measures are as follows: variance, standard deviation, skewness, kurtosis and the confidence interval. Drawings of teeth have been made with a camera lucida connected to a Nikon SZ 10 microscope.

In the Arvicolidae, only the M_1 has been taken into account for the taxonomical identification of the different taxa, morphological description, biometry and counting. *Microtus gregalis* is the predominant taxon that has provided a total of 6688 M_1. This is a very large number; it was not possible and in fact not necessary to make the morphobiometrical study of all M_1. Thus, we decided to choose one of the most abundant and complete subsamples for morphological and biometrical analysis. We have analyzed the sample from square B50 layer 2 with zed from 98 to 110 cm. This sample contained 1113 M_1 of *M. gregalis*. Most molars are complete, many of them still in the mandible. However, their degree of preservation is variable mainly due to the fact that many have been eroded so that morphology of the occlusal surface cannot be recognized. For this reason only 993 specimens could be identified to their anteroconid morphotype and we could only measure 634 out of 1113 specimens, that is to say a little more than the half of the specimens.

To compare the relative abundance of the different taxa we have taken into account the MNI of the M_1. All the material will be stored in the Museum of Angoulême (Charente).

4. Systematic paleontology

Order RODENTIA Bodwich, 1821
Family GLIRIDAE Thomas, 1897
Genus ***Eliomys*** Wagner, 1840
Eliomys quercinus cf. *quercinus* (Linnaeus, 1766)
Common name: garden dormouse
Fig. 4(1, 2)
Material: Layer 1C: 1 fragment of a left mandible with M_1 and M_3; MNI: 1.
Measurements: M_1: $L = 1.51$; $W = 1.75$; M_3: $L = 1.38$; $W = 1.49$.
Description and discussion: The M_1 simple morphology, without extra ridges between the principal ridges, is similar to that of *Eliomys quercinus quercinus* and different of that of *Eliomys quercinus helleri*. Its size fits well with that of the
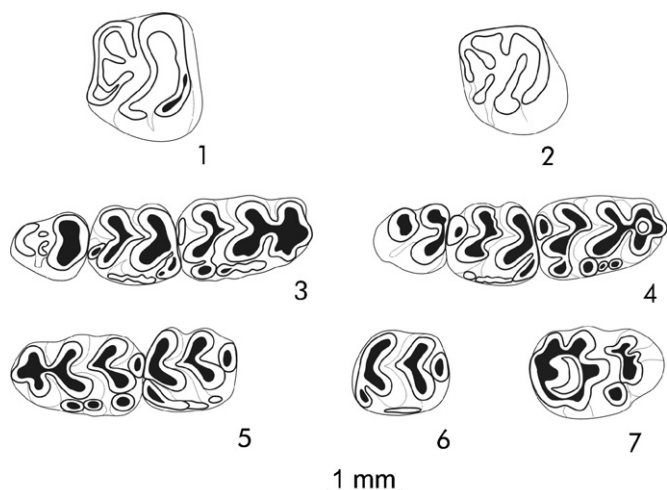
Fig. 4. *Eliomys quercinus* cf. *quercinus*: **1**: left M_1 (1C; C3: 120–124; 1); **2**: left M_3 (1C; C3: 120–124; 1); *Apodemus* sp.: **3**: right M_1–M_2–M_3 (1A; 116–120; 17); **4**: right M_1–M_2–M_3 (2; B1: 90–96; 1/2: 2); **5**: left M_1–M_2 (2; B1: 90–96; 1/2: 1); **6**: left M^2 (1A; C3: 5–116; 1); **7**: right M^1 (2; B1: 90–96; 1/2: 3).
Fig. 4. *Eliomys quercinus* cf. *quercinus* : **1** : M_1 gauche (1C ; C3 : 120–124 ; 1) ; **2** : M_3 gauche (1C ; C3 : 120–124 ; 1) ; *Apodemus* sp. : **3** : M_1–M_2–M_3 droite (1A ; 116–120 ; 17) ; **4** : M_1–M_2–M_3 droite (2 ; B1 : 90–96 ; 1/2 : 2) ; **5** : M_1–M_2 gauche (2 ; B1 : 90–96 ; 1/2 : 1) ; **6** : M^2 gauche (1A ; C3 : 5–116 ; 1) ; **7** : M^1 droite (2 ; B1 : 90–96 ; 1/2 : 3).

Table 1
Apodemus sp. material from Bois Roche
Tableau 1
Matériel de *Apodemus* sp. de Bois Roche

Layer	Material	MNI
1a	1 fr. of right man. with M_1–M_3; 1 fr. of left man. with M_2	1
2	1 fr. of right man. with M_1–M_3; 1 fr. of left man. with M_1–M_2; 1 fr. of right max. with M^1	1
Total		2

Table 2
Measurements of length and width of molars of the Bois Roche *Apodemus* sp.
Tableau 2
Mesures de la longueur et de la largeur des molaires de *Apodemus* sp. de Bois Roche

Tooth	n	Length			Width		
		Min.	Mean	Max.	Min.	Mean	Max.
M_1	3	1.74	1.77	1.81	1.10	1.12	1.12
M_2	4	1.23	1.24	1.26	1.09	1.13	1.17
M_3	2	0.95	0.96	0.98	0.85	0.89	0.94
M_1–M_3	2	3.90	3.95	4.0	—	—	—
M^1	1	—	1.78	—	—	1.22	—

different populations from the Late Pleistocene and is smaller than that of the present populations of *Eliomys quercinus quercinus* (Chaline, 1972; López Martínez, 1980).

The species *Eliomys quercinus* was widely distributed in Europe during practically all the Pleistocene. Chaline (1972) considers that its presence in the Pleistocene sites indicates some forest development in a temperate climate. The garden dormouse occurs nowadays in all of Europe from Spain to the Ural Mountains although is more abundant in the southern part. It occupies several habitats such as deciduous woods and open areas, stony or rocky but with some vegetation, from the sea level up to 2.000 m elevation in the Alps and Pyrenees (Blanco, 1998; Mitchell-Jones et al., 1999; Palomo and Gisbert, 2002). Kolfschoten (1995) points out that although this species is generally found in forests with deciduous and conifer trees of Central and Eastern Europe, authors like Storch (1978) indicate than the presence of woods is less important than the necessity of rocky subsoil.

Family MURIDAE Gray, 1821
   Genus ***Apodemus*** Kaup, 1829
   Apodemus sp.
   Common name of the genus: mouse
   Fig. 4(3–7); Tables 1 and 2
   Description and discussion: The material of Bois Roche has the characteristic morphology of the genus *Apodemus* and its size fits well with those of the species of middle size such as *Apodemus sylvaticus* and *Apodemus flavicollis* according to Michaux and Pasquier (1974). It is not possible to make species identification for lack of more characteristical material as M^2.

The cyclical variations of the populations of the species of middle size of the *Apodemus* genus during the Pleistocene could have a paleoclimatic significance according to Michaux and Pasquier (1974). They would be rare in the colder periods and more abundant in the relatively warmer ones in which they are associated to some forest taxa. Pemán (1985) also considers that this genus is forest and thermophile. *Apodemus flavicollis* and *Apodemus sylvaticus* have nowadays a wide distribution in Europe. They live in areas with a dense vegetation cover; the first one is typically a forest animal and the second one inhabits the edges of wooded areas (Kolfschoten, 1995; Mitchell-Jones et al., 1999; Palomo and Gisbert, 2002; Blanco, 1998).

Family ARVICOLIDAE Gray, 1821
   Genus ***Microtus*** Schrank, 1798
   Subgenus ***Stenocranius*** Kastschenko, 1901
   Microtus (Stenocranius) gregalis (Pallas, 1778)
   Common name: narrow-headed vole
   Fig 5(1–46); Tables 3–5
   Description and discussion: As it is common in the genus *Microtus*, the teeth are rootless and have crowns with cement in

Table 3
Microtus (Stenocranius) gregalis M_1 material from Bois Roche. Many of these M_1 are isolated but several are in their corresponding mandibles
Tableau 3
Matériel de M_1 de *Microtus (Stenocranius) gregalis* de Bois Roche. Plusieurs des M_1 sont isolées mais d'autres sont dans leurs mandibules

Layer	Right M_1 n	Left M_1 n	Total M_1 n	NMI
1a	18	19	37	19
1b	10	7	17	10
1c	727	758	1485	758
1d	3	1	4	3
2	2592	2553	5145	2592
Total	3350	3338	6688	3382

Table 4

Measurements of the length of the M_1 of *Microtus (Stenocranius) gregalis* from Bois Roche (BR) and of some populations of *Microtus (Stenocranius) gregalis* from the Pleistocene sites of La Fage (LF), La Quina (LQ) and Ightham (IG) according to Chaline (1972)

Tableau 4

Mesures de la longueur des M_1 de *Microtus (Stenocranius) gregalis* de Bois Roche (BR) et d'autres populations de *Microtus (Stenocranius) gregalis* des gisements du Pléistocène de La Fage (LF), La Quina (LQ) et Ightham (IG) d'après Chaline (1972)

M_1	BR	LF	LQ	IG
n	634	300	51	20
L M_1 Max.	3.25	3.1	3.18	3.73
L M_1 Mean	2.81	2.7	2.82	2.86
L M_1 Min.	2.37	2.21	2.56	2.66
Median	2.80	—	—	—
Variance	0.018	0.02	0.018	0.034
Standard deviation	0.134	0.17	0.137	0.18
Skewness	0.096	—	—	—
Kurtosis	0.610	—	—	—
Confidence interval	0.004	—	—	—

Table 5

Measurements of the length of the M_1 of *Microtus (Stenocranius) gregalis* from Bois Roche distributed by its corresponding morphotype

Tableau 5

Mesures de la longueur des M_1 de *Microtus (Stenocranius) gregalis* de Bois Roche distribuées par ses morphotypes respectifs

Tooth	n	Morphotype	Length		
			Min.	Mean	Max.
M_1	152	"Arvalid"	2.37	2.81	3.25
M_1	158	"Arvalid–gregalid"	2.49	2.81	3.16
M_1	324	"Gregalid"	2.40	2.81	3.22

the re-entrant angles and a differentiation of enamel thickness. The M_1, in which the enamel is thicker in the anterior part of the triangles, consists of a posterior lobe, five closed triangles and an anterior part or anteroconid complex of variable morphology. The M_1 of the population from Bois Roche, as it happens in other populations of *M. gregalis* from some Pleistocene sites (Chaline, 1972), has a great variability of the anteroconid complex that can be distributed in the following morphotypes: "arvalid" (Fig. 5(1–21)), "gregalid" (Fig. 5(34–46)) and an intermediate: "arvalid–gregalid" (Fig. 5(22–33)). In one of the samples of Bois Roche in which we study the frequency of these morphotypes (for further details see the methodology), we got the following results: from a total of 993 M_1 in which the morphology of its anteroconid complex is observable, 245 specimens (24.7%) have the morphotype "arvalid", another 245 specimens (24.7%) the morphotype "arvalid–gregalid" and 503 (50.6%) the morphotype "gregalid". This analysis shows that the great majority of the Bois Roche population has the morphotype "gregalid" and also that there is great morphological continuity between the extreme morphotypes ("arvalid" and "gregalid") with numerous intermediate cases ("arvalid–gregalid") which allow us to attribute it to only one species: *M. gregalis*.

The high morphological variability of the M_1 of *M. gregalis* has also been observed by other authors like Serdyuk (2001) in some populations of this species in northern Europe and Asia from the Middle Pleistocene until today. He concludes that there is a general tendency towards increasing complexity of the anteroconid complex of the M_1 during the Late Pleistocene. Our Bois Roche sample contains the seven morphotypes of the M_1 anteroconid complex of *M. gregalis* distinguished by Serdyuk (2001) in the Late Pleistocene populations of Denisova Cave.

In the population of *M. gregalis* of La Fage (Chaline, 1972), the specimens of the "gregalid" morphotype are generally smaller than those of the "arvalid" morphotype; the specimens of "arvalid–gregalid" morphotype have an intermediate size. This lead Chaline (1972) to conclude that there is continuity in the size between the extreme morphotypes that makes impossible to separate the two morphotypes in two species.

In the population of Bois Roche, the measurements of the length of the M_1 distributed between the corresponding morphotypes formerly described (Table 5) do not show significant differences between them; on the contrary, the means are the same and the interval of variation of the measurements are very similar. Moreover, the frequency distribution of the M_1 length (Fig. 6), is normal in one species. Therefore, this biometrical continuity of the Bois Roche population corroborates the existence of only one species.

Chaline (1972) considers that the species *Microtus anglicus* Hinton, 1910 is a subspecies of the species *M. gregalis* (Pallas, 1778) (*Microtus gregalis anglicus*) in which he includes the populations of the Late Pleistocene sites of La Quina and Ightam, and he creates the subspecies *Microtus gregalis martelensis* whose hypodigm is the population sample from the final Middle Pleistocene site of La Fage. The main difference between the two subspecies, according to Chaline (1972) is based on size: *M. gregalis martelensis* has a small size with a mean of the LM_1 of 2.67 mm, and *M. gregalis anglicus* has a larger size with a mean of the LM_1 that varies between 2.82 and 2.86 mm.

The size of the Bois Roche population (as can be observed in the Table 4), is larger than that of the Middle Pleistocene site of La Fage, similar to that of the Late Pleistocene (end of the "early Würm") site of La Quina, and smaller than that of the Late Pleistocene site of Ightham (Chaline, 1972). With regard to the populations of *M. gregalis* from Northern Europe, Belarus and Siberia (Serdyuk, 2001), the mean length of the M_1 of Bois Roche is also closer to those of the populations of the Late Pleistocene sites than to those of the Middle Pleistocene sites and recent ones.

M. gregalis is the absolutely predominant species of the Bois Roche site: out of a total of a MNI of 3610 micromammals of Bois Roche, 3382 correspond to this species; that is to say the 93.7% of the total. Such a superabundance of a single taxon in a site so rich in micromammals remains is very unusual.

This species, which appeared in Europe in the Middle Pleistocene and was relatively abundant in many Late Pleistocene sites, even in southern areas, at present is found
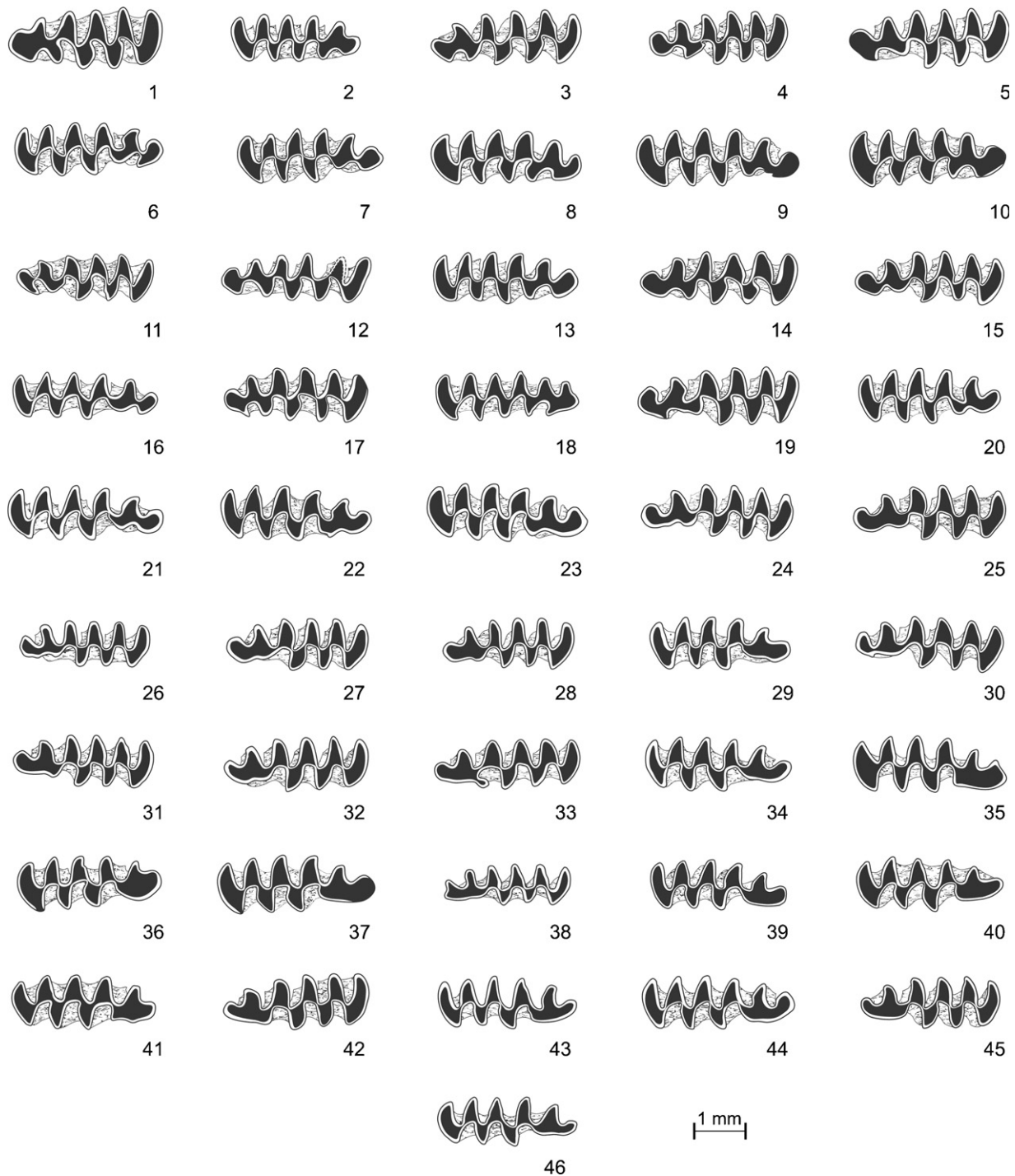
Fig. 5. *Microtus (Stenocranius) gregalis*: **arvalid morphotype**: **1**: left M₁ (1C; A3: 131–136; 37); **2**: right M₁ (2; B50: 105–110; 2/6: 152); **3**: left M₁ (2; B50: 105–110: 2/6: 124); **4**: left M₁ (2; A50: 105–110; 129); **5**: left M₁ (2; A50: 105–110; 163); **6**: right M₁ (2; A50: 105–110; 1/2; 54); **7**: right M₁ (2; A50: 105–110; 1/2; 64); **8**: right M₁ (1C; A50: 91–96; 3/3: 200); **9**: right M₁ (2; B1: 107–110; 5/7: 284); **10**: right M₁ (2; B1: 102–107; 1/4: 60); **11**: left M₁ (2; B50: 105–110; 2/4: 100); **12**: left M₁ (2; B50: 100–105; 1/3: 65); **13**: right M₁ (2; B50: 105–110; 5/6: 317); **14**: left M₁ (2; B50: 105–110; 5/6: 318); **15**: left M₁ (2; B50: 105–110; 5/6: 319); **16**: right M₁ (2; B50: 105–110; 5/6: 323); **17**: left M₁ (2; B50: 105–110; 5/6: 324); **18**: right M₁ (2; B50: 98–105: 3/3: 199); **19**: left M₁ (2; A50: 98–193: 1/4: 81); **20**: right M₁ (2; A50: 100–105: 2/2: 104); **21**: right M₁ (2; B50: 105–110; 1/6: 46); **arvalid–gregalid morphotype**: **22**: right M₁ (2; B50: 105–110; 2/6: 152); **23**: right M₁ (2; 105–110; 1/2: 27); **24**: left M₁ (2; B50: 105–110; 1/6: 29); **25**: left M₁ (2; B50: 105–110; 1/6: 33); **26**: left M₁ (2; B50: 105–110; 1/6: 35); **27**: left M₁ (2; B50: 105–110; 1/6: 42); **28**: left M₁ (2; 105–110; 3/6: 242); **29**: right M₁ (2; B50: 105–110; 1/6: 55); **30**: left M₁ (2; B50: 105–110; 3/4: 197); **31**: left M₁ (2; B50: 105–110; 1/6: 16); **32**: left M₁ (2; B50: 105–110; 2/6: 134); **33**: left M₁ (2; B50: 45–113: 16); **gregalid morphotype:** **34**: right M₁ (2; B50: 105–110; 1/6: 51); **35**: right M₁ (2; A1: 115–120; 39); **36**: right M₁ (2; B1: 102–107; 1/4: 18); **37**: right M₁ (2; B1: 102–107; 1/4: 25); **38**: left M₁ (2; B50: 105–110; 2/6: 111); **39**: right M₁ (2; B50: 105–110; 1/6: 7); **40**: right M₁ (2; B50: 11–118; 1/1: 44); **41**: right M₁ (2; 95–102; 1/1: 3); **42**: left M₁ (2; B50: 105–102; 2/6: 148); **43**: right M₁ (2; B50: 105–102; 2/6: 138); **44**: right M₁ (2; B50: 105–102; 2/6: 125); **45**: left M₁ (2; B50: 105–110; 1/6: 50); **46**: right M₁ (2; B50: 98–105; 3/3: 253).

Fig. 5. *Microtus (Stenocranius) gregalis* : **morphotype arvaloïde** : **1** : M₁ gauche (1C ; A3 : 131–136 ; 37) ; **2** : M₁ droite (2 ; B50 : 105–110 ; 2/6 : 152) ; **3** : M₁ gauche (2 ; B50 : 105–110 : 2/6 : 124) ; **4** : M₁ gauche (2 ; A50 : 105–110 ; 129) ; **5** : M₁ gauche (2 ; A50 : 105–110 ; 163) ; **6** : M₁ droite (2 ; A50 : 105–110 ; 1/2 : 54) ; **7** : M₁

Fig. 7. *Microtus (Pallasiinus) oeconomus*: **1**: right M_1 (2; A3: 136–141; 16); **2**: left M_1 (2: A50: 103–108; 2/3: 158); **3**: right M_1 (1C; A50: 96–98; 10); **4**: left M_1 (2; B1: 110–115; 2/4: 94); **5**: right M_1 (2; A50: 105–110; 2/3: 98); **6**: left M_1 (2; A50: 105–110; 3/3: 202); **7**: left M_1 (2; B1: 95–102; 1/1: 33); **8**: right M_1 (2; B50: 105–110; 3/4: 208); **9**: right M_1 (2; A50: 105–110; 2/2: 184).

Fig. 7. *Microtus (Pallasiinus) oeconomus*: **1**: M_1 droite (2 ; A3 : 136–141 ; 16) ; **2**: M_1 gauche (2 : A50 : 103–108 ; 2/3 : 158) ; **3**: M_1 droite (1C ; A50 : 96–98 ; 10) ; **4**: M_1 gauche (2 ; B1 : 110–115 ; 2/4 : 94) ; **5**: M_1 droite (2 ; A50 : 105–110 ; 2/3 : 98) ; **6**: M_1 gauche (2 ; A50 : 105–110 ; 3/3 : 202) ; **7**: M_1 gauche (2 ; B1 : 95–102 ; 1/1 : 33) ; **8**: M_1 droite (2 ; B50 : 105–110 ; 3/4 : 208) ; **9**: M_1 droite (2 ; A50 : 105–110 ; 2/2 : 184).
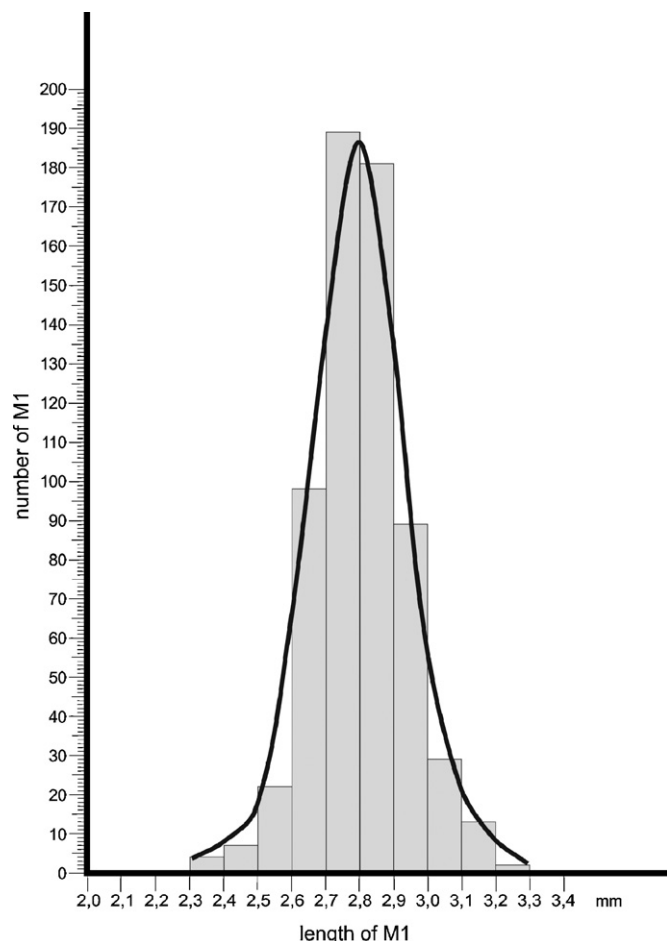

Fig. 6. Frequency distribution of the length of M_1 of *Microtus (Stenocranius) gregalis*.

Fig. 6. Distribution des fréquences de longueur de M_1 de *Microtus (Stenocranius) gregalis*.

only in the Eurasian tundra and in the Asiatic steppe. Thus, it is considered an indicator of a cold and arid climate in a tundra or steppe environment (Chaline, 1972; Kowalski, 2001). This last author points out that although during the Pleistocene this species is usually associated to the lemmings, it also was present in arid but less cold environments. Many authors, for example, Sutcliffe and Kowalski (1976), Jánossy (1986), Kordos (1990), Terzea (1995), Montuire et al. (1997) and Kowalski (2001) indicate that *M. gregalis* was very abundant in Europe in the colder periods of the Pleistocene, especially during the Late Pleistocene, reaching Southern France, and,
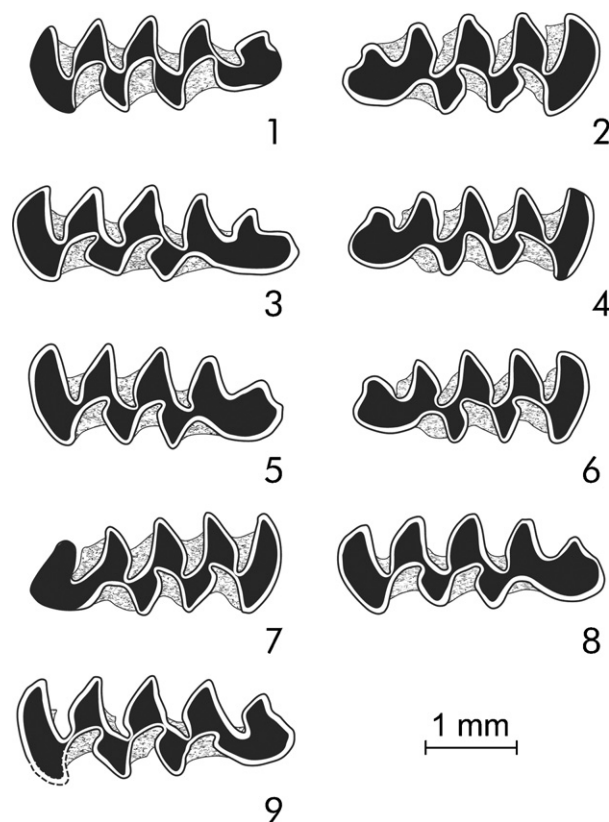
during the last part of the Late Pleistocene, eastern Cantabria in northern Spain, although in this area it is recorded only in few sites and it is rare (Pemán, 1985, 1994; Sesé, 2005).

Subgenus ***Pallasiinus*** Kretzoi, 1964

Microtus (Pallasiinus) oeconomus Pallas, 1776

Common name: root vole

Fig. 7(1–9); Tables 6 and 7

Description and discussion: The M_1 are rootless and have crowns with cement in the re-entrant angles, the labial and

droite (2 ; A50 : 105–110 ; 1/2 ; 64) ; **8**: M_1 droite (1C ; A50 : 91–96 ; 3/3 : 200) ; **9**: M_1 droite (2 ; B1 : 107–110 ; 5/7 : 284) ; **10**: M_1 droite (2 ; B1 : 102–107 ; 1/4 : 60) ; **11**: M_1 gauche (2 ; B50 : 105–110 ; 2/4 : 100) ; **12**: M_1 gauche (2 ; B50 : 100–105 ; 1/3 : 65) ; **13**: M_1 droite (2 ; B50 : 105–110 ; 5/6 : 317) ; **14**: M_1 gauche (2 ; B50 : 105–110 ; 5/6 : 318) ; **15**: M_1 gauche (2 ; B50 : 105–110 ; 5/6 : 319) ; **16**: M_1 droite (2 ; B50 : 105–110 ; 5/6 : 323) ; **17**: M_1 gauche (2 ; B50 : 105–110 ; 5/6 : 324) ; **18**: M_1 droite (2 ; B50 : 98–105 : 3/3 : 199) ; **19**: M_1 gauche (2 ; A50 : 98–193 : 1/4 : 81) ; **20**: M_1 droite (2 ; A50 : 100–105 : 2/2 : 104) ; **21**: M_1 droite (2 ; B50 : 105–110 ; 1/6 : 46) ; **morphotype arvaloïde–gregaloïde**: **22**: M_1 droite (2 ; B50 : 105–110 ; 2/6 : 152) ; **23**: M_1 droite (2 ; 105–110 ; 1/2 : 27) ; **24**: M_1 gauche (2 ; B50 : 105–110 ; 1/6 : 29) ; **25**: M_1 gauche (2 ; B50 : 105–110 ; 1/6 : 33) ; **26**: M_1 gauche (2 ; B50 : 105–110 ; 1/6 : 35) ; **27**: M_1 gauche (2 ; B50 : 105–110 ; 1/6 : 42) ; **28**: M_1 gauche (2 ; 105–110 ; 3/6 : 242) ; **29**: M_1 droite (2 ; B50 : 105–110 ; 1/6 : 55) ; **30**: M_1 gauche (2 ; B50 : 105–110 ; 3/4 : 197) ; **31**: M_1 gauche (2 ; B50 : 105–110 ; 1/6 : 16) ; **32**: M_1 gauche (2 ; B50 : 105–110 ; 2/6 : 134) ; **33**: M_1 gauche (2 ; B50 : 45–113 ; 16) ; **morphotype gregaloïde**: **34**: M_1 droite (2 ; B50 : 105–110 ; 1/6 : 51) ; **35**: M_1 droite (2 ; A1 : 115–120 ; 39) ; **36**: M_1 droite (2 ; B1 : 102–107 ; 1/4 : 18) ; **37**: M_1 droite (2 ; B1 : 102–107 ; 1/4 : 25) ; **38**: M_1 gauche (2 ; B50 : 105–110 ; 2/6 : 111) ; **39**: M_1 droite (2 ; B50 : 105–110 ; 1/6 : 7) ; **40**: M_1 droite (2 ; B50 : 11–118 ; 1/1 : 44) ; **41**: M_1 droite (2 ; 95–102 ; 1/1 : 3) ; **42**: M_1 gauche (2 ; B50 : 105–102 ; 2/6 : 148) ; **43**: M_1 droite (2 ; B50 : 105–102 ; 2/6 : 138) ; **44**: M_1 droite (2 ; B50 : 105–102 ; 2/6 : 125) ; **45**: M_1 gauche (2 ; B50 : 105–110 ; 1/6 : 50) ; **46**: M_1 droite (2 ; B50 : 98–105 ; 3/3 : 253).

Table 6

Microtus (Pallasiinus) oeconomus M_1 material from Bois Roche

Tableau 6

Matériel des M_1 de *Microtus (Pallasiinus) oeconomus* de Bois Roche

Layer	Right M_1 n	Left M_1 n	Total M_1 n	MNI
1c	2	3	5	3
2	8	6	14	8
Total	10	9	19	11

Some of these M_1 are isolated and others are in their corresponding mandibles.
Quelques M_1 sont isolées et d'autres sont dans leur mandibule.

Table 7

Measurements of the length and width of *Microtus (Pallasiinus) oeconomus* M_1 from Bois Roche

Tableau 7

Mesures de la longueur et de la largeur des M_1 de *Microtus (Pallasiinus) oeconomus* de Bois Roche

Tooth	n	Length			Width		
		Min.	Mean	Max.	Min.	Mean	Max.
M_1	11	2.62	2.87	3.17	1.02	1.09	1.17

lingual triangles are asymmetrical, and the enamel is slightly differentiated, thicker in the anterior than in the posterior part of the triangles. The M_1 consists of a posterior lobe, four closed triangles and an anterior part or anteroconid complex with a very constant morphology corresponding to the "ratticepid" morphotype that is very characteristical of the species *Microtus oeconomus* (= *Microtus ratticeps* Keyserling and Blasius, 1841) according to Chaline (1972). The morphology of the "ratticepid" morphotype is as follows: there is no T6 triangle, the T5 triangle connects more or less widely with the anterior cusp and the T7 triangle, that is the smallest triangle, connects widely with the anterior cusp.

The root vole appeared in Europe in the Middle Pleistocene and was very common in the Late Pleistocene extending towards the South until the North of Spain (Sesé, 1994, 2005; Sesé and Sevilla, 1996; Kowalski, 2001). At present *M. oeconomus* does not occur in Spain nor in France but in northern areas of Eurasia: the Netherlands, northern and eastern Germany, Poland, Scandinavia, Austria, Slovakia, Hungary, Belarus, central and northern European Russia, Siberia, China, Mongolia, and Alaska (Mitchell-Jones et al., 1999). Its modern distribution shows that it is broadly distributed in the colder

Table 8

Arvicola terrestris M_1 material from Bois Roche

Tableau 8 Matériel de M_1 de *Arvicola terrestris* de Bois Roche

Layer	Right M_1 n	Left M_1 n	Total M_1 n	NMI
1a	12	9	21	12
1b	0	5	5	5
1c	59	66	125	66
1d	1	1	2	1
2	121	110	231	121
Total	193	191	384	205

Some of these M_1 are isolated and others are in their corresponding mandibles.
Quelques M_1 sont isolées et d'autres sont dans leur mandibule.

Table 9

Measurements of *Arvicola terrestris* M_1 from Bois Roche

Tableau 9

Mesures des M_1 de *Arvicola terrestris* de Bois Roche

M_1	n	Min.	Mean	Max.
L	25	3.12	3.79	4.15
W	22	1.41	1.60	1.84
W/L	22	0.38	0.42	0.46
SDQ	22	63.24	79.25	96.23
SDQ3	22	70.80	88.06	127.8

parts of Eurasia and that it prefers environments with moist to wet vegetation inhabiting humid meadows and marshy or flooded areas in the artic tundra, in the steppe zone and in the boreal forests (Mitchell-Jones et al., 1999; Kowalski, 2001). Because of its artic distribution some authors like Chaline (1972), Pemán (1985) and Chaline et al. (1995) confer a paleoclimatic significance to the fluctuations of their populations during the Late Pleistocene, thus being more abundant in colder periods.

Genus *Arvicola* Lacépède, 1799
  Arvicola terrestris (Linnaeus, 1758)
  Common name: water vole
  Fig. 8(1–21); Tables 8 and 9

Description and discussion: The teeth are rootless and have crown cement in the re-entrant angles. The M_1 consists of a posterior lobe, three closed triangles, and the triangles T4 and T5 connect with the anterior cusp, which has a more or less ovoid shape. In the M_1 the enamel is differentiated and it is thicker in the anterior than in the posterior part of the triangles. This is a distinctive feature of the *Arvicola terrestris* species that distinguishes it from *Arvicola sapidus* where the opposite is true.

The SDQ index which quantifies the degree of differentiation of the enamel, has always a value larger than 100 in the *A. terrestris* species (Heinrich, 1990). In the Bois Roche population, the value of SDQ (Table 10) corresponds to those of *A. terrestris* and its interval of variation is comparable to those of some populations of this species of many Late Pleistocene European sites (Heinrich, 1990; Kolfschoten, 1990; Rekovets, 1990; Maul et al., 1998). The size of the Bois Roche population is also similar to other populations of that species of other Pleistocene sites of France (Chaline, 1972) and a little smaller than some populations from some Late Pleistocene sites from northern Spain (Altuna, 1972).

Table 10

Dicrostonyx torquatus M_1 material from Bois Roche

Tableau 10

Matériel des M_1 de *Dicrostonyx torquatus* de Bois Roche

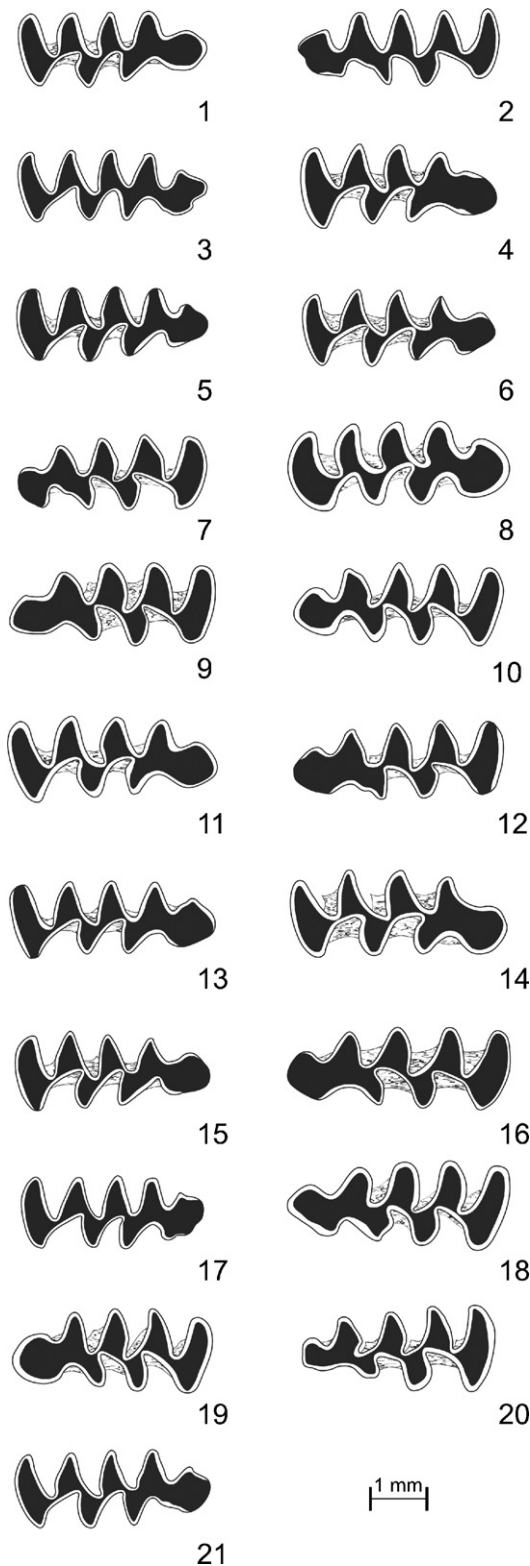| Layer	Right M_1 n	Left M_1 n	Total M_1 n	NMI
1a	1	3	4	3
1c	3	2	5	3
2	1	—	1	1
Total	5	5	10	7

Fig. 8. *Arvicola terrestris*: **1**: right M₁ (2; A1: 115–120; 8); **2**: left M₁ (1B; A3: 111–116; 11); **3**: right M₁ (1C; A3: 116–121; 19); **4**: right M₁ (1C; A3:116–121; 10); **5**: right M₁ (1C; A3: 116–121; 12); **6**: right M₁ (1C; A3: 116–121; 14); **7**: left M₁ (1C; A50: 96–98; 3); **8**: right M₁ (2; B50: 108–113; 2/3: 86); **9**: left M₁ (2; B50: 108–113; 2/3: 88); **10**: left M₁ (2; B50: 98–105; 2/3: 107); **11**: right M₁ (2; B50: 98–105; 2/3: 106); **12**: left M₁ (2; B1: 107–110; 1/7: 27); **13**: right M₁ (2; B1: 107–110; 1/7: 34); **14**: right M₁ (2; B50: 100–105; 1/3: 84); **15**: right M₁ (2; A3: 150–155; 6); **16**: left M₁ (2; A3: 150–155; 7); **17**: right M₁ (2; A3: 150–155; 8); **18**: left M₁ (2; B50: 105–110; 3/6: 267); **19**: left M₁ (2; B50: 105–110;

A. terrestris appeared in Europe at the end of the Middle Pleistocene or at the beginning of the Late Pleistocene according to different authors (Heinrich, 1990; Kolfschoten, 1990; Rekovets, 1990; Maul et al., 1998); it was at that time already completely differentiated from the Middle Pleistocene *Arvicola cantiana*.

At present this vole has a wide distribution in Europe but it does not occur in the central and southern parts of the Iberian Peninsula, nor in southern and western France, the highest elevations in the Alps, Ireland, southern Greece and the Mediterranean islands. It extends to northern Asia, to Lake Baikal and the Lena basin in Siberia, northwestern China, north of the Aral Sea, northern Iran and the Near East (Mitchell-Jones et al., 1999; Kowalski, 2001). Because of its fossorial habits, the water vole needs wet, deep and rich soils (Blanco, 1998). Except in the north of Spain where it inhabits in meadows, in the rest of Eurasia is an almost aquatic rodent that lives in wet areas with good vegetation cover, near rivers, streams, lakes, marshes and woods, but it can also inhabit drier areas as meadows. It lives from lowlands to the mountains, in areas with different types of vegetation including the tundra and the steppe (Kolfschoten, 1995; Mitchell-Jones et al., 1999; Kowalski, 2001; Palomo and Gisbert, 2002).

Genus ***Dicrostonyx*** Gloger, 1851
    Dicrostonyx torquatus (Pallas, 1778)
    Common name: artic lemming
    Fig. 9(1–6); Tables 10 and 11

Description and discussion: The teeth are rootless and very hypsodont, without any cementum in the re-entrant angles and with the re-entrant angles as deep buccally as labially. The M₁ has the characteristic morphology of *D. torquatus*: it is formed by a posterior lobe, seven closed triangles (from T1 to T7), and an eight buccal triangle (T8) that joins with the anterior cusp which has either a round or lanceolate shape due to the development of a ninth triangle (T9) in its labial side. The enamel is very differentiated: in the M₁ it is thicker in the anterior than in the posterior side of the triangles, and is generally interrupted at the apex of the triangles and in the anterior edge of the anterior cusp.

The size of the Bois Roche population is similar to that of some Middle and Late Pleistocene populations of the *D. torquatus* species (Chaline, 1972): the size of the single M₁ of the La Fage site coincides with the maximum

3/6: 268); **20**: left M₁ (2; A50; 105–110; 28); **21**: right M₁ (1A; C3: 116–120; 13).

Fig. 8. *Arvicola terrestris* : **1** : M₁ droite (2 ; A1 : 115–120 ; 8) ; **2** : M₁ gauche (1B ; A3 : 111–116 ; 11) ; **3** : M₁ droite (1C ; A3 : 116–121 ; 19) ; **4** : M₁ droite (1C ; A3 :116–121 ; 10) ; **5** : M₁ droite (1C ; A3 : 116–121 ; 12) ; **6** : M₁ droite (1C ; A3 : 116–121 ; 14) ; **7** : M₁ gauche (1C ; A50 : 96–98 ; 3) ; **8** : M₁ droite (2 ; B50 : 108–113 ; 2/3 : 86) ; **9** : M₁ gauche (2 ; B50 : 108–113 ; 2/3 : 88) ; **10** : M₁ gauche (2 ; B50 : 98–105 ; 2/3 : 107) ; **11** : M₁ droite (2 ; B50 : 98–105 ; 2/3 : 106) ; **12** : M₁ gauche (2 ; B1 : 107–110 ; 1/7 : 27) ; **13** : M₁ droite (2 ; B1 : 107–110 ; 1/7 : 34) ; **14** : M₁ droite (2 ; B50 : 100–105 ; 1/3 : 84) ; **15** : M₁ droite (2 ; A3 : 150–155 ; 6) ; **16** : M₁ gauche (2 ; A3 : 150–155 ; 7) ; **17** : M₁ droite (2 ; A3 : 150–155 ; 8) ; **18** : M₁ gauche (2 ; B50 : 105–110 ; 3/6 : 267) ; **19** : M₁ gauche (2 ; B50 : 105–110 ; 3/6 : 268) ; **20** : M₁ gauche (2 ; A50 ; 105–110 ; 28) ; **21** : M₁ droite (1A ; C3 ; 116–120 ; 13).
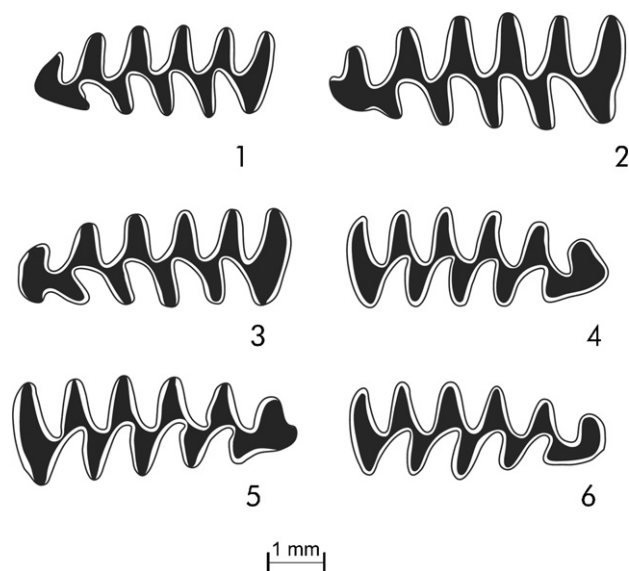
Fig. 9. *Dicrostonyx torquatus*: **1**: left M$_1$ (1C; A3: 116–121; 24); **2**: left M$_1$ (1B; A3: 111–116; 6); **3**: left M$_1$ (1B; A3: 111–116; 8); **4**: right M$_1$ (1C; A3: 126–131; 9); **5**: right M$_1$ (1C; B2: 87–96; 1/1: 23); **6**: right M$_1$ (1C; A3: 131–136; 1).
Fig. 9. *Dicrostonyx torquatus*: **1** : M$_1$ gauche (1C ; A3 : 116–121 ; 24) ; **2** : M$_1$ gauche (1B ; A3 : 111–116 ; 6) ; **3** : M$_1$ gauche (1B ; A3 : 111–116 ; 8) ; **4** : M$_1$ droite (1C ; A3 : 126–131 ; 9) ; **5** : M$_1$ droite (1C ; B2 : 87–96 ; 1/1 : 23) ; **6** : M$_1$ droite (1C ; A3 : 131–136 ; 1).

measurement of the Bois Roche population; the La Quina, La Garenne and Saint-Mihiel I samples fit in the interval of variation.

The population of Bois Roche shows some morphological and biometrical differences with the material of *Dicrostonyx antiquitatis* Chaline, 1972 (species later included in the genus *Predicrostonyx* and made synonymous of *Predicrostonyx compitalis* Zazhigin, 1976 according to Kowalski, 1995, 2001) described in the Lower Pleistocene site of Les Valerots by Chaline (1972). In the M$_1$ of this last species there are only five, not seven closed triangles, and there is no indication of the T8 and T9 triangles. Moreover, although the size of the single specimen of Les Valerots (LM1 = 3.26) fits in the interval of variation of the population of Bois Roche, it is near its minimal value. Kowalski (1995, 2001) suggests that the genus *Predicrostonyx* is probably the direct ancestor of the genus *Dicrostonyx* and points out that in the lineage of the latter there is an evolution towards a more complicated structure of the molars during the Pleistocene.

Table 11
Measurements of the length and width of *Dicrostonyx torquatus* M$_1$ from Bois Roche
Tableau 11
Mesures de la longueur et de la largeur des M$_1$ de *Dicrostonyx torquatus* de Bois Roche

Tooth	n	Length			Width		
		Min.	Mean	Max.	Min.	Mean	Max.
M$_1$	7	3.17	3.55	3.83	1.18	1.34	1.52

The genus *Dicrostonyx* was widely distributed during the Middle and Late Pleistocene in all Europe including southern areas like France (Kowalski, 2001), but not reaching the Iberian Peninsula (Sesé, 2005). In Spain the only reference of this genus, with the new species *Dicrostonyx andaluciensis*, is in the Late Pleistocene site of Cariguela in the province of Granada (Ruiz Bustos and García Sánchez, 1977). But this identification was later rejected by Ruiz Bustos (2000) who attributed the material to *Chionomys nivalis*. The genus *Dicrostonyx* disappeared from most of Europe at the end of the last glaciation (Kowalski, 2001).

The several species of the *Dicrostonyx* genus live at present in dry tundra and polar deserts (Kowalski, 2001; Duff and Lawson, 2004), in very cold areas of the Northern Hemisphere even (as *D. torquatus*) beyond the 75° of north latitude. *D. torquatus* inhabits the artic tundra region of northeastern Europe and Siberia, mainly in treeless and dry areas with some plant cover (Nowak and Paradiso, 1983).

According to Kowalski (1995) the genus *Dicrostonyx* since its appearance in Pleistocene Europe was associated to cold climates; its extension several times to the south-west of Europe was always associated with other faunal taxa indicative of cold and dry climates. The fluctuations in the abundance of *Dicrostonyx* during the Pleistocene are, therefore, associated to climatic and vegetation changes: this taxon would be more abundant in the colder and drier periods and more scarce in the more temperate ones (Chaline, 1972; Nadachowski, 1989; Chaline et al., 1995; Kowalski, 1995).

Order INSECTIVORA Bodwich, 1821
    Family SORICIDAE Gray, 1821
    Genus *Neomys* Kaup, 1829
    Neomys cf. *fodiens* (Pennant, 1771)
    Common name: water shrew
    Fig. 10(1–3); Tables 12 and 13

Description and discussion: The tooth cusps are colored in red as is usual in the Soricinae and shows the most
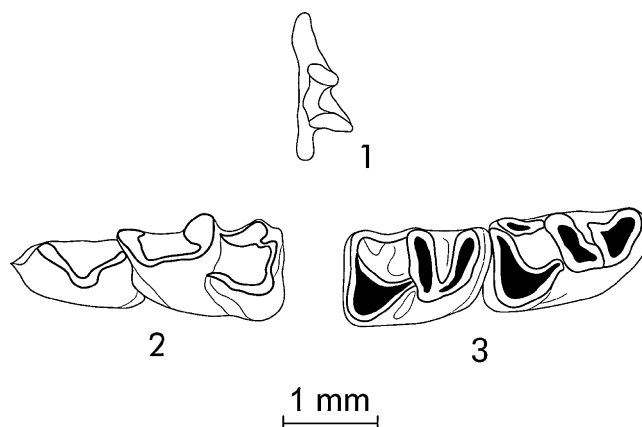

Fig. 10. *Neomys* cf. *fodiens*: **1**: left mandibular condyle and coronoid process in posterior view (2; B1: 110–115; 1); **2**: left P$_4$–M$_1$ (2; B1: 110–115; 1); **3**: right M$_1$–M$_2$ (C: A1: 105–110; 1).
Fig. 10. *Neomys* cf. *fodiens* : **1** : apophyse angulaire du corps mandibulaire gauche en vue postérieure (2 ; B1 : 110–115 ; 1) ; **2** : P$_4$–M$_1$ gauche (2 ; B1 : 110–115 ; 1) ; **3**. M$_1$–M$_2$ droite (C : A1 : 105–110 ; 1).

Table 12
Neomys cf. *fodiens* material from Bois Roche
Tableau 12
Matériel de *Neomys* cf. *fodiens* de Bois Roche

Layer	Material	MNI
1c	1 fr. man right with M_1–M_2; 1 fr. man left. with M_1–M_2	1
2	1 fr. man right with M_1–M_2; 1 fr. man left with P_4–M_1 that preserves the condyle and the coronoid process	1
Total		2

Table 13
Measurements of the length and width of *Neomys* cf. *fodiens* teeth from Bois Roche
Tableau 13
Mesures de la longueur et de la largeur des dents de *Neomys* cf. *fodiens* de Bois Roche

Tooth	n	Length			Width		
		Min.	Mean	Max.	Min.	Mean	Max.
P_4	1	—	1.36	—	—	0.75	—
M_1	4	1.70	1.74	1.82	1.02	1.06	1.09
M_2	3	1.51	1.59	1.65	1.02	1	1.06

characteristic feature of the *Neomys* genus: the mandibular condyle has an "L" shape with two well differentiated articular facets (Chaline et al., 1974). According to these authors, one of the most important features that differentiate the species *Neomys anomalus* from *Neomys fodiens*, is the larger size of this latter species, especially the mandible height at the coronoid process. This height is about 5 mm in *N. fodiens* and about 4.2 mm in *N. anomalus* (Chaline et al., 1974). Reumer (1996) agrees with this method of distinguishing the two species giving values for the coronoid height of 4.4–5.3 mm in *N. fodiens* and 3.9–4.4 mm in *N. anomalus*. The value of this coronoid height in the material on Bois Roche is of 4.64 mm, which fits well with the values of the present, Middle and Late Pleistocene and Holocene populations of *N. fodiens* (Chaline et al., 1974; Reumer, 1996). Moreover, in a direct comparison with the material of the MNCN collections, the size of the mandible and the teeth of Bois Roche are similar to those of the present-day populations of the *N. fodiens* species.

The *N. fodiens* species has been reported by Reumer (1996) in many Middle and Late Pleistocene and Holocene sites in southwest France. At present this water shrew has a wide distribution in Eurasia from northern Spain (Cantabrian and Pyrenean regions) to the Lake Baikal in Siberia. It is an almost aquatic species associated to riparian and littoral habitats of lakes, rivers and seasides, humid woods and meadows; in southern Europe it inhabits in mountainous areas near the streams, riverine forests and reedbeds of lakes (Mitchell-Jones et al., 1999).

5. Conclusions

5.1. Systematics and biostratigraphy

The faunal list of the micromammals in the Bois Roche site is the following:
Order RODENTIA Bodwich, 1821
Family GLIRIDAE Thomas, 1897
Eliomys quercinus cf. *quercinus* (Linnaeus, 1766)
Family MURIDAE Gray, 1821
Apodemus sp.
Family ARVICOLIDAE Gray, 1821
Microtus (Stenocranius) gregalis (Pallas, 1778)
Microtus (Pallasiinus) oeconomus Pallas, 1776
Arvicola terrestris (Linnaeus, 1758)
Dicrostonyx torquatus (Pallas, 1778)
Order INSECTIVORA Bodwich, 1821
Family SORICIDAE Gray, 1821
Neomys cf. *fodiens* (Pennant, 1771)
Of the two orders of micromammals identified in this paper, that is Rodentia and Insectivora, Rodentia is the most abundant and best represented with six different taxa, and Insectivora with only one species. Lagomorphs (including *Oryctolagus* and *Lepus*) and bats are also present at the site, in samples excavated in later seasons, but are rare.

This micromammal association, by its composition and the evolutionary stage of some species, is typical of the Late Pleistocene and conforms with the estimated age of the cave deposits to late OIS 5 or early OIS 4. Of this fauna, at present, four taxa still live in France (*E. quercinus*, *Apodemus*, *A. terrestris* and *N. fodiens*) and three of them (*M. gregalis*, *M. oeconomus* and *D. torquatus*) no longer live in France but occur in northern areas.

5.2. Taphonomy

With regard to the possible source of the micromammal accumulation at Bois Roche, many observations support the hypothesis that they are prey remains:

- the extraordinary abundance of cranial and postcranial remains;
- the fact that the skeletal elements were not found in anatomical connection;
- the teeth are in general in good stage of preservation (complete, without signs of rolling), and, although many of them are isolated, there are a lot that are in their corresponding mandibles;
- the number of right and left M_1 is quite similar in each taxa, as can be observed in the list of material, even in the most abundant species;
- many teeth show the various stages of the characteristical corrosion produced by digestion.

To quantify the number of teeth that present some type of corrosion we have chosen the complete sample of M_1 of *M. gregalis* from the B50 square (see Methodology). On a total

Table 14

Frequencies of rodents and insectivores of Bois Roche by taxon and layer

Tableau 14

Fréquences des rongeurs et insectivores de Bois Roche par taxon et par couche

Layers	1a		1b		1c		1d		2		Total	
Taxa	MNI	%	MNI	%	MNI	%	MNI	%	MNI	%	NMI	%
Eliomys quercinus	—	—	—	—	1	0.12	—	—	—	—	1	0.03
Apodemus sp.	1	2.86	—	—	—	—	—	—	1	0.04	2	0.06
Microtus gregalis	19	54.29	10	66.67	758	91.11	3	75	2592	95.15	3382	93.68
Microtus oeconomus	—	—	—	—	3	0.36	—	—	8	0.29	11	0.30
Arvicola terrestris	12	34.29	5	33.33	66	7.93	1	25	121	4.44	205	5.68
Dicrostonyx torquatus	3	8.57	—	—	3	0.36	—	—	1	0.04	7	0.19
Neomys cf. *fodiens*	—	—	—	—	1	0.12	—	—	1	0.04	2	0.06
Total	35	100	15	100	832	100	4	100	2724	100	3610	100

of 1113 specimens of M_1, at least 564 of them (the 50.7% i.e. half of the population) show corrosion of the enamel. Of these 564 eroded specimens, 53% have a low or moderate wear and the 47% have a wear so high that the occlusal surface is completely modified.

The absolute predominance of a single taxon, in this case of *M. gregalis*, is striking. Of a total of 3610 MNI of M_1 of micromammals identified at a taxonomical level, there are 3382 specimens that correspond to such species, that is to say the 93.7% of the total (Table 14; Fig. 11). Although it is common to observe an abundance of one or just a few taxa in the accumulations produced by birds of prey, in modern and Pleistocene cases (Chaline et al., 1974; Andrews, 1990) we see at Bois Roche an extremely high representation of a single taxon while the remaining taxa are very scarce: only one species – that is *A. terrestris* – is represented by 5.7% and all the other five taxa (*E. quercinus*, *Apodemus* sp., *M. oeconomus*, *D. torquatus* and *Neomys* cf. *fodiens*) are represented by 0.6%.

None of the identified micromammals in Bois Roche inhabits a cave; they must have been transported from outside by some kind of predator. The role of raptors in micromammal accumulation is well known. As noted on the introduction of this paper, a digested microtine molar was observed inside a hyena coprolite by Sánchez-Goñi, the pollen analyst (Villa and Bartram, 1998: Fig. 3). To what extent hyenas have played a role in the accumulation of micromammals at Bois Roche is as yet unknown; this is a line of research pursued by Yolanda Fernández-Jalvo and Jim Williams whose detailed taphonomic analysis of all the microvertebrate of the 1995 season is in progress.

5.3. Paleoenvironment

When inferring the paleoenvironmental conditions from the micromammal fauna we must take into account that we do not know yet which predator is the origin of the micromammal
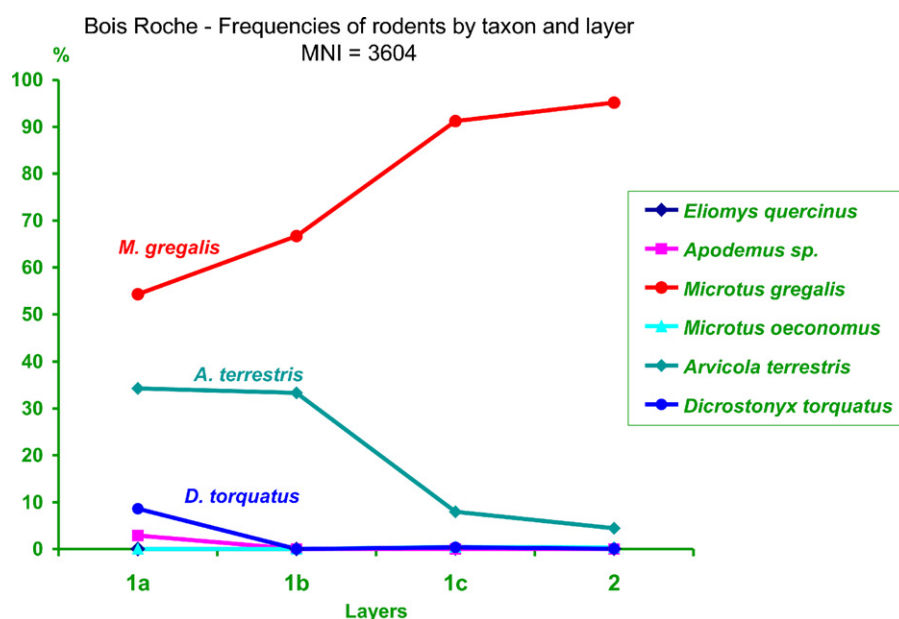

Fig. 11. Frequency distribution of rodents of Bois Roche by taxon and layers except layer 1d.

Fig. 11. Diagramme de fréquences des rongeurs de Bois Roche par taxon et niveaux, excepté le niveau 1d.

accumulation. We do not know if that predator was a generalist and if the micromammal association is a good representation of all the habitats around the site. The screen size (2 mm) may have been the cause of loss of some smaller remains such as isolated shrew premolars and isolated incisors of bats but not of teeth implanted in mandibles. Nevertheless, this extraordinarily rich micromammal association gives many indications about the environment.

The majority of the taxa, like *M. gregalis*, live in open habitats, although with a certain development of the vegetation. *M. gregalis* and *D. torquatus* are species of tundra and steppe; *M. oeconomus* inhabits in areas with wet soil and vegetation, and *A. terrestris* and *Neomys* cf. *fodiens* are almost aquatic species inhabiting areas with some vegetation. Some of the scarcest taxa like *Eliomys quercinus* and *Apodemus* sp. require a good development of the vegetation cover and they are the only species that would indicate the presence of some trees. In sum, the fauna suggests an open landscape, with some vegetation mainly of the steppe or tundra type, with areas of water and wet vegetation and some areas with trees.

The micromammal association of Bois Roche is characteristic of a cold or very cold dry climate as indicates the great abundance of *M. gregalis* accompanied by *D. torquatus* and *M. oeconomus* which as a whole represent the 94.2% of the total MNI (3400/3610). In effect, these three species do not live in France now; they occur in the northern and boreal regions according to Chaline et al. (1995). Species that are abundant in temperate climates such as *Eliomys quercinus* and *Apodemus* sp. (3/3610 i.e. 0.09%) or that indicate the presence of water, like *A. terrestris* and *Neomys* cf. *fodiens* (207/3610 i.e. 5.74% of the total MNI) are very rare at Bois Roche.

The climatic conditions of southern France during the Late Pleistocene period need not have been as cold as the climate in the artic areas where *M. gregalis* and *D. torquatus* live at present because in the colder periods of the glaciations during the Pleistocene these species expanded in the southern regions pushed by the extension of the ice in northern areas of Eurasia.

Acknowledgements

References

Altuna, J., 1972. Fauna de mamíferos de los yacimientos prehistóricos de Guipúzcoa. Con catálogo de los Mamíferos Cuaternarios del Cantábrico y del Pirineo Occidental. Munibe 24, 1–464.

Andrews, P., 1990. Owls, Caves and Fossils. The University of Chicago Press, Chicago.

Bartram, L., Villa, P., 1998. The archaeological excavation of prehistoric hyena dens: why bother? In: Brugal, J.P., Meignen, L., Patou-Mathis, M. (Eds.), Économie préhistorique : les comportements de subsistence au Paléolithique. Éditions APDCA, Sophia Antipolis, pp. 15–30.

Blain, H.A., Villa, P., 2006. Amphibians and squamate reptiles from the early Upper Pleistocene of Bois Roche Cave (Charente, Southwestern France). Acta Zoologica Cracoviensia 49A, 1–32.

Blanco, J.C., 1998. Mamíferos de España. 2: Cetáceos, Artiodáctilos, Roedores y Lagomorfos de las Península Ibérica, Baleares y Canarias. GeoPlaneta, Barcelona.

Brain, C.K., 1981. The Hunters or the Hunted? University of Chicago Press, Chicago and London.

Chaline, J., 1972. Les Rongeurs du Pléistocène Moyen et Supérieur de France (Systématique, Biostratigraphie, Paléoclimatologie). Cahiers de Paléontologie, 1–410.

Chaline, J., Baudvin, H., Jammot, D., Saint Girons, M.C., 1974. Les proies des rapaces. Petits Mammifères et leur environnement. Éditions Doin, Paris.

Chaline, J., Brunet-Lecomte, P., Campy, M., 1995. The last glacial/interglacial record of rodent remains from the Gigny karst sequence in the French Jura used for palaeoclimatic and palaeoecological reconstructions. Palaeogeography, Palaeoclimatology, Palaeoecology 117, 229–252.

Cruz-Uribe, K., 1991. Distinguishing hyena from hominid bone accumulations. Journal of Field Archaeology 18, 467–486.

Duff, A., Lawson, A., 2004. Mammals of the World. A Checklist. A and C Black, London.

d'Errico, F., Villa, P., 1997. Holes and Grooves. The contribution of microscopy and taphonomy to the problem of art origins. Journal of Human Evolution 33, 1–31.

d'Errico, F., Villa, P., 1998. Nouvelle analyse des os gravés et perforés du Paléolithique inférieur et moyen. Implications pour l'origine de la pensée symbolique. Paléo 10, 265–290.

Fosse, P., 1994. Taphonomie paléolithique : les grands mammifères de Soleihac (Haute-Loire) et de Lunel Viel 1 (Hérault). Thèse de Doctorat, Université de Provence (inédit).

Goldberg, P., 2001. Some micromorphological aspects of prehistoric cave deposits. Cahiers d'Archéologie du CELAT, Série Archéométrie 1, Québec 10, 161–175.

Heinrich, W.D., 1990. Some aspects of evolution and biostratigraphy of *Arvicola* (Mammalia, Rodentia) in the central european Pleistocene. In: Fejfar, O., Heinrich, D. (Eds.), International Symposium Evolution, Phylogeny and Biostratigraphy of Arvicolids (Rodentia, Mammalia), Rohanov (Czechoslovakia), 1987. Geological Survey, Praha, pp. 165–182.

Horwitz, L.K., 1990. The origin of partially digested bones recovered from archaeological contexts in Israel. Paléorient 16, 97–106.

Horwitz, L.K., Goldberg, P., 1989. A study of Pleistocene and Holocene hyaena coprolites. Journal of Archaeological Science 16, 71–94.

Jánossy, D., 1986. Pleistocene vertebrate faunas of Hungary. Developments in Paleontology and Stratigraphy 8, 1–208.

Kolfschoten, T. van, 1990. Review of the Pleistocene arvicolid faunas from the Netherlands. In: Fejfar, O., Heinrich, D. (Eds.), International Symposium Evolution, Phylogeny and Biostratigraphy of Arvicolids (Rodentia, Mammalia), Rohanov (Czechoslovakia), 1987. Geological Survey, Praha, pp. 255–274.

Kolfschoten, T. van, 1995. On the application of fossil mammals to the reconstruction of the paleoenvironment of northwestern Europe. Acta zoologica cracoviensia 38, 3–84.

Kordos, L., 1990. The evolution of Upper Pleistocene voles in Central Europe. In: Fejfar, O., Heinrich, D. (Eds.), International Symposium Evolution, Phylogeny and Biostratigraphy of Arvicolids (Rodentia, Mammalia), Rohanov (Czechoslovakia), 1987. Geological Survey, Praha, pp. 275–284.

Kowalski, K., 1995. Lemmings (Mammalia, Rodentia) as indicator of temperature and humidity in the European Quaternary. Acta zoologica cracoviensia 38, 85–94.

Kowalski, K., 2001. Pleistocene Rodents of Europe. Folia Cuaternaria 72, 1–389.

Larkin, N.R., Alexander, J., Lewis, M.D., 2000. Using experimental studies of recent faecal material to examine hyaena coprolites from the West Runton Freshwater Bed, Norfolk, U.K. Journal of Archaeological Science 27, 19–31.

López Martínez, N., 1980. Los Micromamíferos (Rodentia, Insectivora, Lagomorpha y Chiroptera) del sitio de ocupación Achelense de Aridos-1 (Arganda, Madrid). In: Santonja, M., López Martínez, N., Pérez-González, A. (Eds.), Ocupaciones Achelenses el Valle del Jarama (Arganda, Madrid). Diputación Provincial de Madrid, pp. 161–202.

Marra, A.C., Villa, P., Beauval, C., Bonfiglio, L., Goldberg, P., 2004. Same predator, variable prey: taphonomy of two Upper Pleistocene hyena dens in Sicily and SW France. In: Brugal, J.P., Fosse, P. (Eds.), Humans and Carnivores, special issue. Revue de Paléobiologie 23, pp. 787–801.

Maul, L., Masini, F., Abbazzi, L., Turner, A., 1998. The use of different morphometric data for absolute age calibration of some South- and Middle European arvicolid populations. Palaeontographica Italica 85, 11–151.

Michaux, J., Pasquier, L., 1974. Dynamique des populations de Mulots (Rodentia, *Apodemus*) en Europe durant le Quaternaire. Premières données. Bulletin de la Société géologique de France (7) 16, 4, 431–439.

Mitchell-Jones, A.J., Amori, G., Bogdanowicz, W., Krystufek, B., Reijnders, P.J.H., Spitzenberger, F., Stubbe, M., Thissen, J.B.M., Vohralík, V., Zima, J., 1999. The Atlas of European Mammals. The Academic Press, London, 1-484.

Montuire, S., Michaux, J., Legendre, S., Aguilar, J.-P., 1997. Rodents and climate. 1. A model for estimating past temperatures using arvicolids (Mammalia: Rodentia). Palaeogeography, Palaeoclimatology, Palaeoecology 128, 187–206.

Nadachowski, A., 1989. Origin and History of the Present Rodent Fauna in Poland Based on Fossil Evidence. Acta Theriologica 34, 37–53.

Nowak, R.M., Paradiso, J.L., 1983. Walker's Mammals of the World, Vol.2. The Johns Hopkins University Press, Baltimore and London, pp. 568–1307.

Palomo, J., Gisbert, J. (Eds.), 2002. Atlas de los Mamíferos Terrestres de España. Organismo Autónomo de Parques Nacionales. DGCNA- MIMAM, Madrid, 1–564.

Pemán, E., 1985. Aspectos climáticos y ecológicos de los Micromamíferos del yacimiento de Erralla. Munibe 37, 49–57.

Pemán, E., 1994. Los micromamíferos de Laminak II (Berriatua, Bizcaia). Kobie. Serie Paleoantropología 21, 225–233.

Rekovets, L.I., 1990. Principal development stages of the water-vole genus *Arvicola* (Rodentia, Mammalia) from the East European Pleistocene. In: Fejfar, O., Heinrich, D., (Eds.), International Symposium Evolution, Phylogeny and Biostratigraphy of Arvicolids (Rodentia, Mammalia), Rohanov (Czechoslovakia), 1987. Geological Survey, Praha, pp. 369–384.

Reumer, J.W.F., 1996. Quaternary Insectivora (Mammalia) from southwestern France. Acta zoologica cracoviensia 39, 413–426.

Ruiz Bustos, A., 2000. Estudio paleoecológico de los sedimentos con presencia del hombre Neandertal en la cueva de la Carihuela (Piñar, Granada). Síntesis ambiental del Würm mediterráneo en la Cordillera Bética. Ayuntamiento de Piñar, Granada, 1-91.

Ruiz Bustos, A., García Sánchez, M., 1977. Las condiciones ecológicas del Musteriense en las depresiones granadinas. La fauna de micromamíferos en la Cueva de la Carigüela. Cuadernos de Prehistoria de la Universidad de Granada 2, 7–17.

Serdyuk, N.V., 2001. Morphotypic variability in the dentition of *Stenocranius gregalis* Pallas (Rodentia, Mammalia) from the Pleistocene of Denisova Cave. Paleontological Journal 35, 433–441.

Sesé, C., 1994. Paleoclimatical interpretation of the Quaternary small mammals of Spain. Geobios 27, 753–767.

Sesé, C., 2005. Aportación de los micromamíferos al conocimiento paleoambiental del Pleistoceno Superior en la región cantábrica. In: Montes Barquín, R., Lasheras Corruchaga, J.A. (Eds.), Actas de la Reunión Científica: Neandertales Cantábricos: Estado de la Cuestión, Monografías del Museo Nacional y Centro de Investigación de Altamira 20, pp. 167–200.

Sesé, C., Sevilla, P., 1996. Los micromamíferos del Cuaternario peninsular español l: Cronoestratigrafía e implicaciones bioestratigráficas. Revista Española de Paleontología, 278–287.

Storch, G., 1978. *Eliomys quercinus* (Linnaeus, 1766) – Gartenschläfer. In: Niethamme, J., Krapp, F. (Eds.), Handbusch der Säugertiere Europas. Nagetiere I. Akademische Verlagsgesellschaft, Wiesbaden, Bd. 1, pp. 208–226.

Sutcliffe, A.J., 1970. Spotted hyena: crusher, gnawer, digestor and collector of bones. Nature 227, 1110–1113.

Sutcliffe, A.J., Kowalski, K., 1976. Pleistocene rodents of the British Isles. Bulletin of the British Museum (Natural History) Geology 27, 31–147.

Terzea, E., 1995. Mammalian events in the Quaternary of Romania and correlations with the climatic chronology of Western Europe. Acta zoologica cracoviensia 38, 109–120.

Villa, P., Bartram, L., 1996. Flaked bone from a hyena den. Paléo 8, 1–22.

Villa, P., Bartram, L., 1998. La grotte de Bois Roche (Cherves-Richemont, Charente). Rapport de fouille programmé, SRA Poitou-Charentes (inédit).

Villa, P., Castel, J.-C., Beauval, C., Bourdillat, V., Goldberg, P., 2004. Human and carnivores sites in the European Middle and Upper Paleolithic: Similarities and differences in bone modification and fragmentation. In: Brugal, J.P., Fosse, P. (Eds.), Humans and Carnivores, special issue. Revue de Paléobiologie 23, pp. 705–730.

Villa, P., d'Errico, F., 2001. Bone and ivory points of the Lower and Middle Paleolithic of Europe. Journal of Human Evolution 41, 69–112.

Villa, P., Soressi, M., 2000. Stone tools in carnivore sites: the case of Bois Roche. Journal of Anthropological Research 56, 187–215.