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

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

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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.

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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

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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.

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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 representados 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.

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Keywords: Rodents; Insectivores; France; Early Late Pleistocene; Systematics; Paleoclimate

Mots clés : Rongeurs ; Insectivores ; France ; Début du Pléistocène supérieur ; Systématique ; Paléoclimatologie

Palabras clave : Roedores; Insectívoros; Francia; Comienzo del Pleistoceno Superior; Sistemática; Paleoclimatología

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.
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, sintere-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 waterscreened 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
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 (carnivores) 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-Góñi 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 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 M₁ 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 M₁. This is a very large number; it was not possible and in fact not necessary to make the morphobiometrical study of all M₁. 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 M₁ 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 M₁. 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 M₁ and M₃; MNI: 1.

Measurements: M₁: L = 1.51; W = 1.75; M₃: L = 1.38; W = 1.49.

Description and discussion: The M₁ 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
different populations from the Late Pleistocene and is smaller than that of the present populations of *Eliomys 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 it 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).

It 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

**Description and discussion:** As it is common in the genus *Microtus*, the teeth are rootless and have crowns with cement in them.

---

**Table 1**

<table>
<thead>
<tr>
<th>Material</th>
<th>MNI</th>
</tr>
</thead>
<tbody>
<tr>
<td>1a</td>
<td>1</td>
</tr>
<tr>
<td>2</td>
<td>1</td>
</tr>
<tr>
<td>1 fr. of right man. with M1–M3; 1 fr. of left man. with M2</td>
<td>1</td>
</tr>
<tr>
<td>1 fr. of right man. with M1–M2; 1 fr. of left man. with M2</td>
<td>1</td>
</tr>
<tr>
<td>1 fr. of right max. with M1</td>
<td>2</td>
</tr>
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</table>

**Table 2**

<table>
<thead>
<tr>
<th>Layer</th>
<th>MNI</th>
</tr>
</thead>
<tbody>
<tr>
<td>M1</td>
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<tr>
<td>M2</td>
<td>4</td>
</tr>
<tr>
<td>M3</td>
<td>2</td>
</tr>
<tr>
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<td>2</td>
</tr>
<tr>
<td>M1</td>
<td>1</td>
</tr>
</tbody>
</table>

**Table 3**

<table>
<thead>
<tr>
<th>Right M1 n</th>
<th>Left M1 n</th>
<th>Total M1 n</th>
<th>NMI</th>
</tr>
</thead>
<tbody>
<tr>
<td>1a</td>
<td>18</td>
<td>19</td>
<td>37</td>
</tr>
<tr>
<td>1b</td>
<td>10</td>
<td>7</td>
<td>17</td>
</tr>
<tr>
<td>1c</td>
<td>727</td>
<td>758</td>
<td>1485</td>
</tr>
<tr>
<td>1d</td>
<td>3</td>
<td>1</td>
<td>4</td>
</tr>
<tr>
<td>2</td>
<td>2592</td>
<td>2553</td>
<td>5145</td>
</tr>
<tr>
<td>Total</td>
<td>3350</td>
<td>3338</td>
<td>6688</td>
</tr>
</tbody>
</table>

---
The high morphological variability of the M1 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 M1 during the Late Pleistocene. Our Bois Roche sample contains the seven morphotypes of the M1 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 M1 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 M1 length (Fig. 6), is normal in one species. Therefore, this biommetrical 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 Ightham, 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 LM1 of 2.67 mm, and *M. gregalis anglicus* has a larger size with a mean of the LM1 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 M1 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

### Table 4

Measurements of the length of the M1 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)

<table>
<thead>
<tr>
<th>Tooth</th>
<th>n</th>
<th>LF</th>
<th>LQ</th>
<th>IG</th>
</tr>
</thead>
<tbody>
<tr>
<td>M1</td>
<td>634</td>
<td>300</td>
<td>51</td>
<td>20</td>
</tr>
<tr>
<td>L M1 Max.</td>
<td>3.25</td>
<td>3.1</td>
<td>3.18</td>
<td>3.73</td>
</tr>
<tr>
<td>L M1 Mean</td>
<td>2.81</td>
<td>2.7</td>
<td>2.82</td>
<td>2.86</td>
</tr>
<tr>
<td>L M1 Min.</td>
<td>2.37</td>
<td>2.21</td>
<td>2.56</td>
<td>2.66</td>
</tr>
<tr>
<td>Median</td>
<td>2.80</td>
<td>—</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td>Kurtosis</td>
<td>0.018</td>
<td>0.02</td>
<td>0.018</td>
<td>0.034</td>
</tr>
<tr>
<td>Standard deviation</td>
<td>0.134</td>
<td>0.17</td>
<td>0.137</td>
<td>0.18</td>
</tr>
<tr>
<td>Variance</td>
<td>0.018</td>
<td>0.02</td>
<td>0.018</td>
<td>0.034</td>
</tr>
<tr>
<td>Median</td>
<td>2.80</td>
<td>—</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td>Kurtosis</td>
<td>0.018</td>
<td>0.02</td>
<td>0.018</td>
<td>0.034</td>
</tr>
<tr>
<td>Standard deviation</td>
<td>0.134</td>
<td>0.17</td>
<td>0.137</td>
<td>0.18</td>
</tr>
<tr>
<td>Variance</td>
<td>0.018</td>
<td>0.02</td>
<td>0.018</td>
<td>0.034</td>
</tr>
</tbody>
</table>

### Table 5

Measurements of the length of the M1 of *Microtus (Stenocranius) gregalis* from Bois Roche distributed by its corresponding morphotype

<table>
<thead>
<tr>
<th>Tooth</th>
<th>n</th>
<th>Morphotype</th>
<th>Length</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td>Min.</td>
</tr>
<tr>
<td>M1</td>
<td>152</td>
<td>“Arvalid”</td>
<td>2.37</td>
</tr>
<tr>
<td>M1</td>
<td>158</td>
<td>“Arvalid–gregalid”</td>
<td>2.49</td>
</tr>
<tr>
<td>M1</td>
<td>324</td>
<td>“Gregalid”</td>
<td>2.40</td>
</tr>
</tbody>
</table>

The high morphological variability of the M1 of *M. gregalis*
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; 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: 319); 16: right M1 (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; B50: 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; B50: 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: 33); 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
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 *Pallasiius* Kretzoi, 1964

*Microtus (Pallasiius) oeconomicus* Pallas, 1776

Common name: root vole

**Fig. 7.** *Microtus (Pallasiius) oeconomicus:* 1: right M1 (2; A3: 136–141; 16); 2: left M1 (2; A50: 103–108; 2/3: 158); 3: right M1 (1C; A50: 96–98; 10); 4: left M1 (2; B1: 110–115; 2/4: 94); 5: right M1 (2; A50: 105–110; 2/3: 98); 6: left M1 (2; A50: 105–110; 3/3: 202); 7: left M1 (2; B1: 95–102; 1/1: 33); 8: right M1 (2; B50: 105–110; 3/4: 208); 9: right M1 (2; A50: 105–110; 2/2: 184).

**Description and discussion:** The M1 are rootless and have crowns with cement in the re-entrant angles, the labial and
Table 6
Microtus (Pallastinus) oeconomus M1 material from Bois Roche

<table>
<thead>
<tr>
<th>Layer</th>
<th>Right M1 n</th>
<th>Left M1 n</th>
<th>Total M1 n</th>
<th>MNI</th>
</tr>
</thead>
<tbody>
<tr>
<td>1a</td>
<td>12</td>
<td>9</td>
<td>21</td>
<td>12</td>
</tr>
<tr>
<td>1b</td>
<td>0</td>
<td>5</td>
<td>5</td>
<td></td>
</tr>
<tr>
<td>1c</td>
<td>59</td>
<td>66</td>
<td>125</td>
<td>66</td>
</tr>
<tr>
<td>1d</td>
<td>1</td>
<td>1</td>
<td>2</td>
<td></td>
</tr>
<tr>
<td>2</td>
<td>121</td>
<td>110</td>
<td>231</td>
<td>121</td>
</tr>
<tr>
<td>Total</td>
<td>193</td>
<td>191</td>
<td>384</td>
<td>205</td>
</tr>
</tbody>
</table>

Some of these M1 are isolated and others are in their corresponding mandibles. Quelques M1 sont isolées et d’autres sont dans leur mandible.

Table 7
Measurements of the length and width of Microtus (Pallastinus) oeconomus M1 from Bois Roche

<table>
<thead>
<tr>
<th>Tooth</th>
<th>n</th>
<th>Length</th>
<th>Width</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>Min.</td>
<td>Mean</td>
</tr>
<tr>
<td>M1</td>
<td>11</td>
<td>2.62</td>
<td>2.87</td>
</tr>
<tr>
<td></td>
<td></td>
<td>1.02</td>
<td>1.09</td>
</tr>
</tbody>
</table>

lingual triangles are asymmetrical, and the enamel is slightly differentiated, thicker in the anterior than in the posterior part of the triangles. The M1 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 characteristic 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 Microtus 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 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 M1 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 M1 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 8
Arvicola terrestris M1 material from Bois Roche

<table>
<thead>
<tr>
<th>Layer</th>
<th>Right M1 n</th>
<th>Left M1 n</th>
<th>Total M1 n</th>
<th>NMI</th>
</tr>
</thead>
<tbody>
<tr>
<td>1a</td>
<td>12</td>
<td>9</td>
<td>21</td>
<td>12</td>
</tr>
<tr>
<td>1b</td>
<td>0</td>
<td>5</td>
<td>5</td>
<td></td>
</tr>
<tr>
<td>1c</td>
<td>59</td>
<td>66</td>
<td>125</td>
<td>66</td>
</tr>
<tr>
<td>1d</td>
<td>1</td>
<td>1</td>
<td>2</td>
<td></td>
</tr>
<tr>
<td>2</td>
<td>121</td>
<td>110</td>
<td>231</td>
<td>121</td>
</tr>
<tr>
<td>Total</td>
<td>193</td>
<td>191</td>
<td>384</td>
<td>205</td>
</tr>
</tbody>
</table>

Some of these M1 are isolated and others are in their corresponding mandibles. Quelques M1 sont isolées et d’autres sont dans leur mandible.

Table 9
Measurements of Arvicola terrestris M1 from Bois Roche

<table>
<thead>
<tr>
<th>M1</th>
<th>n</th>
<th>Min.</th>
<th>Mean</th>
<th>Max.</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>L</td>
<td>W</td>
<td>W/L</td>
</tr>
<tr>
<td>L</td>
<td>25</td>
<td>3.12</td>
<td>3.79</td>
<td>4.15</td>
</tr>
<tr>
<td>W</td>
<td>22</td>
<td>1.41</td>
<td>1.60</td>
<td>1.84</td>
</tr>
<tr>
<td>W/L</td>
<td>22</td>
<td>0.38</td>
<td>0.42</td>
<td>0.46</td>
</tr>
<tr>
<td>SDQ</td>
<td>22</td>
<td>63.24</td>
<td>79.25</td>
<td>96.23</td>
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<tr>
<td>SDQ3</td>
<td>22</td>
<td>70.80</td>
<td>88.06</td>
<td>127.8</td>
</tr>
</tbody>
</table>

Table 10
Dicrostonyx torquatus M1 material from Bois Roche

<table>
<thead>
<tr>
<th>Layer</th>
<th>Right M1 n</th>
<th>Left M1 n</th>
<th>Total M1 n</th>
<th>NMI</th>
</tr>
</thead>
<tbody>
<tr>
<td>1a</td>
<td>1</td>
<td>3</td>
<td>4</td>
<td>3</td>
</tr>
<tr>
<td>1c</td>
<td>3</td>
<td>2</td>
<td>5</td>
<td>3</td>
</tr>
<tr>
<td>2</td>
<td>1</td>
<td>—</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>Total</td>
<td>5</td>
<td>5</td>
<td>10</td>
<td>7</td>
</tr>
</tbody>
</table>
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

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

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
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 Carigua 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

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

---

**Table 11**

<table>
<thead>
<tr>
<th>Tooth</th>
<th>Length</th>
<th>Width</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Min.</td>
<td>Mean</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>M₁ 7</td>
<td>3.17</td>
<td>3.55</td>
</tr>
<tr>
<td></td>
<td>1.18</td>
<td>1.34</td>
</tr>
</tbody>
</table>

---

**Fig. 9. Dicrostonyx torquatus:** 1: left M₁ (IC: A3: 116–121; 24); 2: left M₁ (IB: A3: 111–116; 6); 3: left M₁ (IB: A3: 111–116; 8); 4: right M₁ (IC: A3: 126–131; 9); 5: right M₁ (IC: B2: 87–96; 1/1; 23); 6: right M₁ (IC: A3: 131–136; 1).

---

**Fig. 10. Neomys cf. fodiens:** 1: left mandibular condyle and coronoid process in posterior view (2; B1: 110–115; 1); 2: left P₄–M₁ (2; B1: 110–115; 1); 3: right M₁–M₂ (C: A1: 105–110; 1).
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 Neomys fodiens and about 4.2 mm in Neomys 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 Neomys fodiens and 3.9–4.4 mm in Neomys 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 Neomys fodiens (Chaline et al., 1974; Reumer, 1996). Moreover, in a direct comparison with the material of the MNHN collections, the size of the mandible and the teeth of Neomys fodiens de Bois Roche are similar to those of the present-day populations of the Neomys 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
      - 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 M1 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 characteristic corrosion produced by digestion.

To quantify the number of teeth that present some type of corrosion we have chosen the complete sample of M1 of M. gregalis from the B50 square (see Methodology). On a total

<table>
<thead>
<tr>
<th>Table 12</th>
<th>Neomys cf. fodiens material from Bois Roche</th>
</tr>
</thead>
<tbody>
<tr>
<td>Layer</td>
<td>Material</td>
</tr>
<tr>
<td>1c</td>
<td>1 fr. man right with M1–M2; 1 fr. man left. with M1–M2</td>
</tr>
<tr>
<td>2</td>
<td>1 fr. man right with M1–M2; 1 fr. man left. with P2–M1 that preserves the condyle and the coronoid process</td>
</tr>
<tr>
<td>Total</td>
<td></td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Table 13</th>
<th>Measurements of the length and width of Neomys cf. fodiens teeth from Bois Roche</th>
</tr>
</thead>
<tbody>
<tr>
<td>Tooth</td>
<td>n</td>
</tr>
<tr>
<td></td>
<td></td>
</tr>
<tr>
<td>P2</td>
<td>1</td>
</tr>
<tr>
<td>M1</td>
<td>4</td>
</tr>
<tr>
<td>M2</td>
<td>3</td>
</tr>
</tbody>
</table>
of 1113 specimens of M1, 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 M1 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

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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

<table>
<thead>
<tr>
<th>Layers</th>
<th>1a</th>
<th>1b</th>
<th>1c</th>
<th>1d</th>
<th>2</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td>Taxa</td>
<td>MNI</td>
<td>%</td>
<td>MNI</td>
<td>%</td>
<td>MNI</td>
<td>%</td>
</tr>
<tr>
<td>Eliomys quercinus</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>1</td>
<td>0.12</td>
</tr>
<tr>
<td>Apodemus sp.</td>
<td>1</td>
<td>2.86</td>
<td>—</td>
<td>—</td>
<td>10</td>
<td>66.67</td>
</tr>
<tr>
<td>Microtus gregalis</td>
<td>19</td>
<td>54.29</td>
<td>10</td>
<td>66.67</td>
<td>758</td>
<td>91.11</td>
</tr>
<tr>
<td>Microtus oeconomus</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>3</td>
<td>0.36</td>
</tr>
<tr>
<td>Arvicola terrestris</td>
<td>12</td>
<td>34.29</td>
<td>5</td>
<td>33.33</td>
<td>66</td>
<td>7.93</td>
</tr>
<tr>
<td>Dicrostonyx torquatus</td>
<td>3</td>
<td>8.57</td>
<td>—</td>
<td>—</td>
<td>3</td>
<td>0.36</td>
</tr>
<tr>
<td>Neomys cf. fodiens</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>1</td>
<td>0.12</td>
</tr>
<tr>
<td>Total</td>
<td>35</td>
<td>100</td>
<td>15</td>
<td>100</td>
<td>832</td>
<td>100</td>
</tr>
</tbody>
</table>

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Fig. 11. Frequency distribution of rodents of Bois Roche by taxon and layer
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 *Apopodemus* 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. Nevertheless, this extraordinarily rich micromammal association gives many indications about the environment.

We wish to thank Peter Robinson (University of Colorado) for sorting and preliminary identification of several tens of thousands of microvertebrate remains. The Bois Roche excavations have been funded by the French Ministry of Culture, the Leakey Foundation, the National Science Foundation, the General Council of the Charente Region, the Association of Archeologists of the Poitou–Charente Region and Franklin and Marshall College. Carmen Sesé is grateful to Enrique Soto who digitized the teeth drawings, set up the figures of micromammals, and revised the French translation of the abstract and the figure captions. Paola Villa is grateful to Laurence Bartram, co-director of excavations in 1995–1998, to MM. George and Jean-François Portet who provided warm hospitality at Bois Roche and to Jean-François Baratin and Véronique Dujardin of the Service Régional de l’Archéologie de Poitou–Charentes who made work at Bois Roche possible.

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