New data on bat fossils from Middle and Upper Pleistocene localities of France☆

Nouvelles données sur les chauves-souris fossiles de localités du Pléistocène moyen et supérieur de France

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Abstract

We describe the bat fossils preserved in four sites from the middle and upper Pleistocene, three of them being well-known French localities: the rock shelter of Les Valerots, the caves of l'Escale at Saint Estève Janson and "du Prince" at Grimaldi (Italy), and the filling of Combe-Grenal, all of them containing microvertebrate assemblages with yet undescribed bat fossils. All species represented in these four localities are still presently distributed in France and had been previously recorded in other Pleistocene localities of central and western Europe, including France. The four assemblages differ both in the abundance of bat fossils as in species composition. The characteristics of each assemblage are analysed under modern insights of bat taphonomy and ecology, and compared with those of other bat-bearing French localities of similar age. The relevance of these data concerning the use of the fossil bats to infer past environmental conditions is discussed.

Keywords: Chiroptera; Middle Pleistocene; Late Pleistocene; Western Europe; Paleoecology; Taphonomy

Résumé

Nous décrivons les restes fossiles de chauves-souris provenant de quatre sites du Pléistocène moyen et supérieur, dont trois localités françaises bien connues : l'abri sous roche des Valerots, les grottes de l'Escale à Saint Estève Janson et du Prince à Grimaldi (Italie), et le remplissage de Combe Grenal, toutes quatre contenant des assemblages de microvertébrés avec des fossiles de chauves-souris encore non-décrits. Toutes les espèces identifiées dans ces quatre localités sont toujours présentes en France et avaient déjà été identifiées dans d'autres localités pléistocènes d'Europe centrale et occidentale, dont la France. Les quatre assemblages diffèrent tant par l'abondance des fossiles de chauves-souris que par leur composition spécifique. Les caractéristiques de chaque assemblage sont analysées à la lumière des connaissances actuelles sur la taphonomie et l'écologie des chauves-souris, en comparaison avec celles d'autres localités françaises d'âge équivalent. La pertinence de ces données en ce qui concerne l'utilisation de chauves-souris fossiles à des fins de reconstruction paléoenvironnementale est discutée.

Mots clés : Chiroptera ; Pléistocène moyen ; Pléistocène supérieur ; Europe occidentale ; Paléoécologie ; Taphonomie

1. Introduction

The study of the Pleistocene has a long tradition in France. The important results obtained from the studies carried out in the large number of available localities of this age have been, and still are, a necessary reference for any archaeological and paleontological research in other European countries. The detailed study of the small mammals preserved in numerous localities enabled, for instance, to establish the characteristics of the evolution of many lineages of rodents that were useful as correlation tools. Some of the sites rich in small mammal remains frequently contained as well fossil bats; but their

☆ Invited editor: Jordi Agustí.

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limited use as biochronological indicators and the lack of clear criteria for their use as paleoecological indicators, led to comparatively limited results, even when compared to other small mammals other than rodents, such as insectivores or lagomorphs. Things have been changing though in the last years, thanks to intensive research leading to a better knowledge of the ecology of bats. Thus, detailed information on habitat and roost preferences, duration and preferred conditions for hibernation and other characteristics have become an additional source of information for palaeoenvironmental reconstructions in those localities where fossils of extant bats are found. As a result, the number of papers including data concerning these fossils in Quaternary small mammal assemblages has undergone an important increase in the recent years.

The origin of recent bat diversity in France must be looked for in the complex dynamics bat populations underwent during the Pleistocene and early Holocene. The southward shift of the timberline during the glacial phases left repeatedly a good part of France without forests, leading to a reduction in the abundance of bats and the withdrawal of strict forest-dependant species from areas previously covered by forests, as well as an increase in the use of caves as roosts by certain species. Sub-boreal and eastern continental species seem to have extended their distribution well into France, leaving relict populations in modern French faunas. Long and hard winters must have caused the disappearance or displacement of thermophilous species with short or intermittent hibernation. On the other side, during humid temperate cycles the extension of forests over large areas must have favoured an increase in the abundance and diversity of bat species. These important environmental changes that took place during the Pleistocene and Holocene are essential to understand today's diversity and patterns of distribution of bats in France. The aim of this paper is to make known the bats identified in four different Pleistocene localities as a contribution providing new data for the reconstruction of the history of bats in France and in Europe.

2. Material and methods

The material described in this paper comes from three French localities located in central and southern France, ranging in age from the latest Early Pleistocene to the early Late Pleistocene, and a fourth locality from north-western Italy, close to the French border, of Late Middle Pleistocene age (Fig. 1). Other French localities with fossil bats were considered in the discussion.

A total number of 85 bat fossils were identified in these four localities. As a whole, the material presents the usual characteristics of preservation observed in the fossil material of these small mammals when collected in karstic localities; fragmentation is important, the remains consisting mainly of broken maxillary bones or mandibles and isolated teeth. Fragments of mandibles or maxillae, frequently with the teeth in place, were found in the material from la Grotte de L'Escale and Combe-Grenal. In the Grotte du Prince and Les Valerots, the material consisted of isolated teeth, only canines and incisors assemblage in the latter.

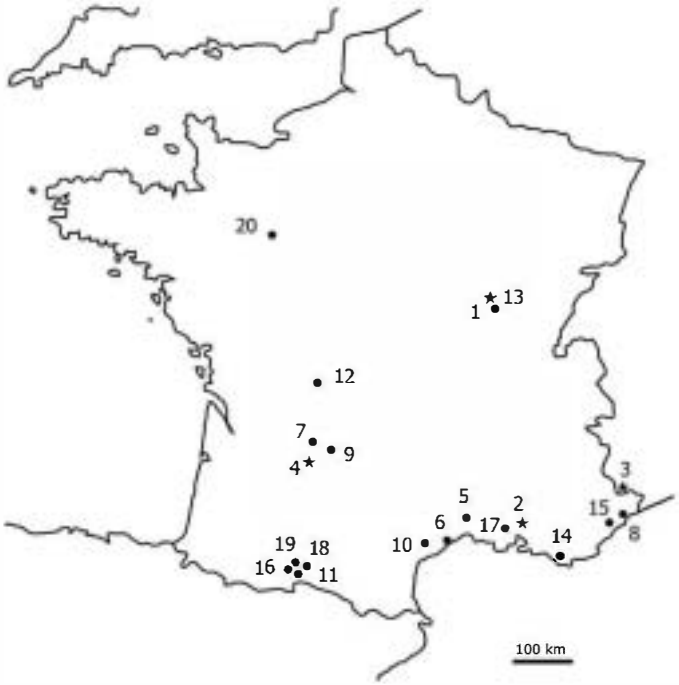

Fig. 1. Geographical position of the localities referred to in the text. Those studied in this paper are marked with an asterisk. **1**: Les Valerots; **2**: Saint-Estève Janson; **3**: Grotte du Prince; **4**: Combe-Grenal; **5**: Lunel Viel; **6**: Aldène; **7**: La Fage; **8**: Lazaret; **9**: Fontéchevade; **10**: L'Hortus; **11**: Gerde; **12**: Artenac; **13**: Santenay; **14**: Cimay; **15**: Pie Lombard; **16**: Peyreignes; **17**: Bisel; **18**: Grotte d'Espélugues; **19**: Grotte d'Espèche; **20**: Grotte Rochefort.

Species determination was carried out on mandibular fragments considering characters such as dental formula, shape of the symphysis, height of the body of the mandible and shape of the ramus. When the teeth remain attached to the mandible, their morphology provided additional criteria for species determination. Dental formula and the particular features observed on the teeth were the basis for species determination from maxillary remains. Isolated teeth needed of more detailed observations, such as the shape of the cusps and cristas, development of additional cusplets, shape of the cingulum and other characters (Menu and Sigé, 1971; Menu and Popelard, 1987; Sevilla, 1986). In most cases the canines, molars and fourth premolars have distinctive characters in each species, though measurements are needed to distinguish between closely taxa related. Measurements of the specimens are available in Appendix A. Among cryptic species, the lack of distinctive characters in the fossils and the overlap in the size makes species determination impossible.

The preference shown by some bat species for particular habitats was used as the basis for environmental interpretations, and refers mainly to temperatures and the development of different types of vegetation. We relied on the information provided by Dietz et al. (2009) and the IUCN (2010) Red List of Endangered Species for interpretations and discussion. Since the species number and identity in an assemblage differ depending whether it is a cave or a prey assemblage, signs of digestion were looked for in the material. Alteration patterns on bat bones and teeth are similar to those described by Andrews

(1990) for insectivores because of similarities in morphology and structure. The localities studied in this paper were compared to other French Pleistocene localities with bats in order to analyse the factors determining species composition.

3. Results

3.1. Les Valerots (Côte d'Or, France)

This karstic filling was discovered in a limestone quarry close to the locality of Nuits-Saint-Georges in Burgundy, France (Chaline and Delingette, 1965). The filling, 30 m in height and narrowing towards the base, consisted of six different levels. The three upper levels contain microfauna with rodents that indicated a late lower Pleistocene age (Chaline, 1985). According to differences in the nature of the deposits, each level was related to a series of distinct climatic cycles. Remains of eight different bat species were found in level 4, which, according to the remaining fauna, was formed during a cold and dry cycle. All the bat fossils consisted of isolated teeth (NISP = 16), mainly canines (Fig. 2(1–5); Table S1). The best represented species are *Miniopterus schreibersii* (NISP = 5, MNI = 2) and *Plecotus auritus* (NISP = 4, MNI = 3), followed by *Rhinolophus ferrumequinum* (NISP = 2, MNI = 1). The remaining species, *Myotis bechsteinii*, *M. daubentonii*, *M. emarginatus*, *M. nattereri* and *Eptesicus serotinus* are represented in the assemblage by a single remain. Clear signs of digestion are observed on at least two specimens, pointing towards a probable prey assemblage. This is supported by the spectra of species, since several of them are frequent owl preys and are rare in caves. The absence of strict thermophilous bats together with the presence of several species linked to forest habitats such as *P. auritus*, *M. bechsteinii*, *M. emarginatus* and *E. serotinus*, agree with the landscape inferred from the rodent assemblage (Chaline, 1985), according to which open steppes with occasional small isolated groves prevailed in the region, though a more important development of wooded areas is indicated from the bat assemblage.

3.2. Grotte de L'Escale at Saint-Estève Janson (Bouches-du-Rhône, Southern France)

The early middle Pleistocene deposits preserved in the cave known as L'Escale in Saint-Estève Janson, discovered in 1960 and excavated during the following years (Bonifay and Bonifay, 1963), yielded abundant fossil fauna. Small mammals were found at several levels, but were particularly abundant at beds G and H, where a wide representation of different rodent species was found associated to several insectivores, a lagomorph, as well as to some reptiles and amphibians (Chaline, 1972). Bat remains were located in four of the five layers recognised in Bed G, and represent six different species with a total number of 58 remains. The material consists mainly of large fragments of mandibles with teeth, a few fragments of maxillae and an odd number of isolated teeth (Fig. 2(6–12); Table S2). *Miniopterus schreibersii* dominates the assemblage, with 79% of the MNI (NISP = 46, MNI = 19), and since most part of the material of this species presents unworn or only slightly worn teeth, the assemblage was most likely originated under a breeding colony. Together with *M. schreibersii*, another five bat species were identified in Bed G: *Rhinolophus ferrumequinum* (NISP = 4, MNI = 1), *Myotis nattereri* (NISP = 2, MNI = 1), *M. bechsteinii* (NISP = 3, MNI = 1), *M. blythii* (NISP = 1) and *Plecotus austriacus* (NISP = 1). No evidence of digestion is observed in any of the remains, and considering the characteristics of the assemblage, with a dominating colonial species, accompanied by a lower number of other species common in caves, the bat fossils collected at L'Escale are most certainly a thanatocoenosis built within the cave from bats roosting in it.

Bed G at the bottom of the cave contains cinders which were interpreted as either remains of hearths, or of summer fires resulting from thunderstorms (Bonifay and Bonifay, 1963). *M. schreibersii* is a species especially sensible to human presence and usually abandons roosts frequented by humans; summer colonies would not be present in the cave at the same time as humans. Thus, if the cinders are evidence of hearths, a seasonal use of the cave may be inferred. Breeding colonies of these bats occupied the cave during the summer while it was free of human occupation. The absence of bats in the remaining beds might indicate periods of more permanent presence of humans in the cave, or a reduction of the preferred foraging habitats in the neighbouring areas. The bat assemblage of Bed G includes species with preference for warmer conditions (*M. schreibersii* and *M. blythii*) or for humid and wooded landscapes (*M. bechsteinii*). This agrees with the environmental conditions inferred from the rodent assemblage, according to which Bed G was formed during a temperate phase in which open landscapes and forest areas were found in the neighbourhood of the site.

3.3. Grotte du Prince (Grimaldi, Vintimille, Italy)

The material described from this locality comes from the excavations conducted in two breccias of the cave, which yielded a few rodent remains characteristic enough to determine a late middle Pleistocene age and warm climatic conditions (Chaline, 1970). Four bat remains of three different species were found among the fossil material excavated in these breccias (Fig. 3(6–8); Table S3): *M. bechsteinii* (NISP = 1), *R. hipposideros* (NISP = 1), and an isolated canine and a mandible broken in two fragments assigned to *Plecotus austriacus* (MNI = 1). Slight digestion observed on the material of *R. hipposideros* suggests a prey assemblage. The three species of bats represented in the assemblage are more common in areas with forests and fit with the environment indicated by the few rodents found in the same assemblage, which are linked to Mediterranean landscapes.

3.4. Combe-Grenal (Dordogne, France)

This shelter, a well-known Quaternary locality, yielded an interesting collection of fauna and lithics dating from the late Middle Pleistocene to the Late Pleistocene (Bordes and de Sonneville-Bordes, 1970). The main part of the fauna was collected at level Sα, dated as early Late Pleistocene, which

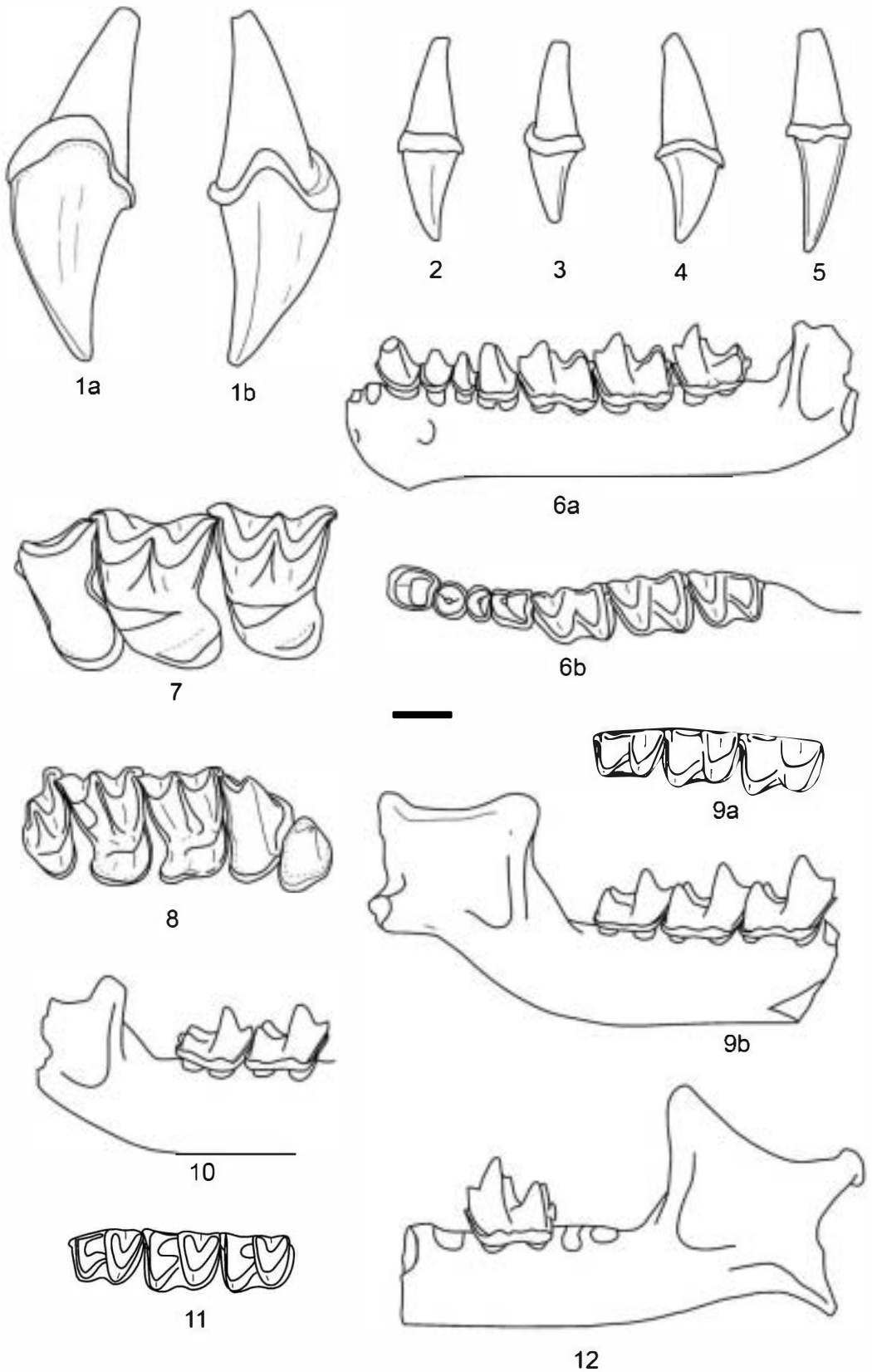

Fig. 2. **1–5**: Les Valerots. **1a, b**: left upper canine of *Rhinolophus ferrumequinum*. **2**: left upper canine of *Plecotus auritus*. **3**: left upper canine of *Myotis daubentonii*. **4**: right upper canine of *Myotis bechsteinii*. **5**: left upper canine of *Miniopterus schreibersii*. **6–12**: Grotte de l'Escale. **6a, b**: *Myotis nattereri*: left hemimandible with canine to M_3. **7**: *Rhinolophus ferrumequinum*, left maxillary series with P^4 to M^2. **8**: *Miniopterus schreibersii*, right maxillary series with P^3 to M^3. **9**: *M. schreibersii*, fragment of right hemimandible with M_1 to M_3. **10**: *Myotis bechsteinii,* right mandible with M_2-M_3. **11**: *Myotis nattereri*, right mandible with M_1 to M_3. **12**: *Plecotus austriacus*, fragment of left mandible with M_2. Scale bar: 1 mm.

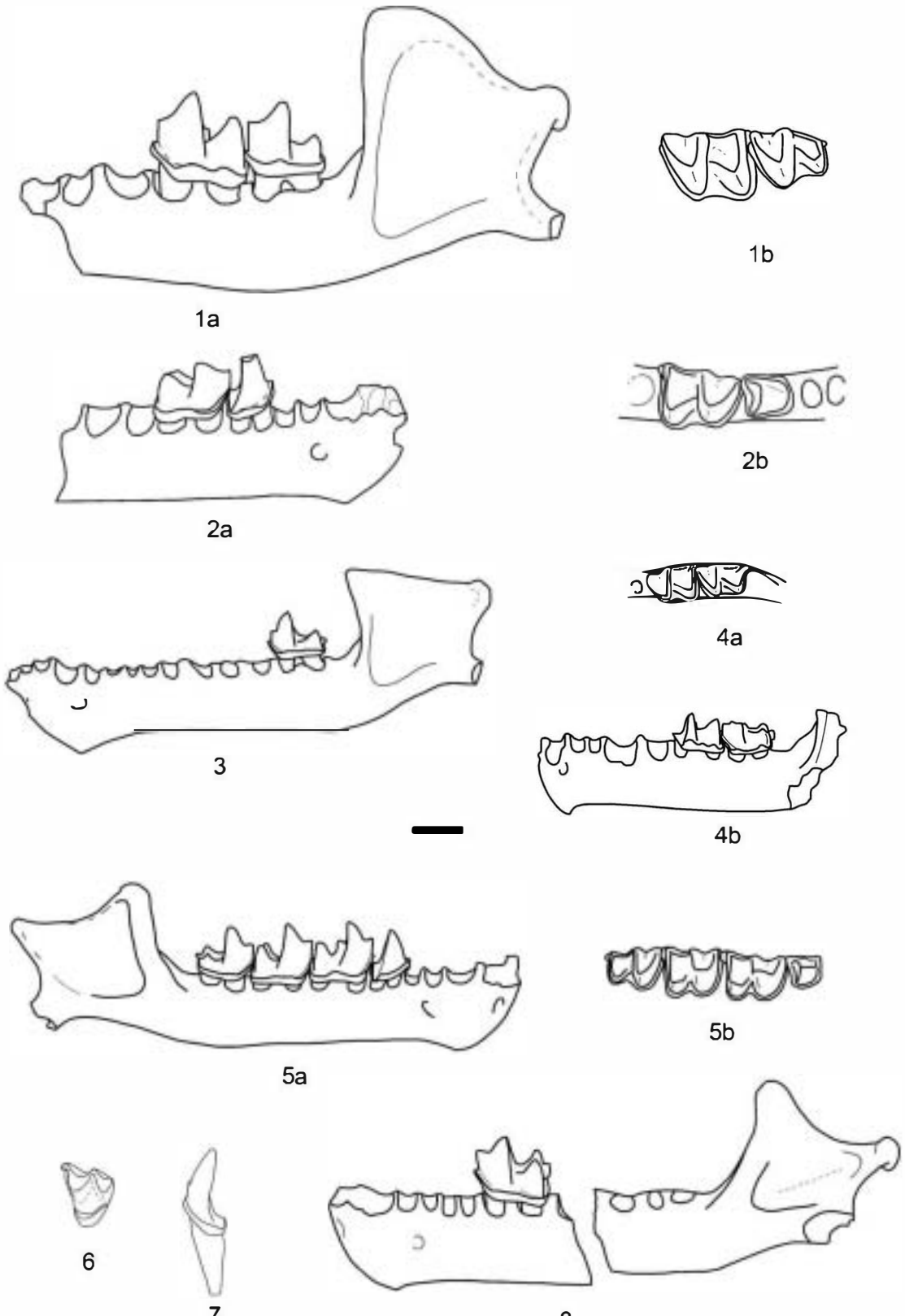

Fig. 3. **1–5**: Combe Grenal. **1a, b**: *Myotis blythii*, fragment of left hemimandible with M_2-M_3. **2a, b**: *Myotis nattereri*, fragment of right hemimandible with P_4-M_1. **3**: *Myotis daubentonii*, left mandible with M_3. **4a, b**: *Pipistrellus pipistrellus/pygmaeus*, left hemimandible with M_1-M_2. **5**: *Plecotus auritus*, right hemimandible with P_4 to M_3. **6–8**: Grotte du Prince. **6**: *Rhinolophus hipposideros*, left M^3. **7**: *Plecotus austriacus*, left lower canine. **8**: *Plecotus austriacus*, broken left hemimandible with M_1. Scale bar: 1 mm.

contained a diversified assemblage of vertebrates including carnivores, insectivores, rodents, bats and amphibians. According to the rodent and insectivore species, a temperate dry environment with forests was interpreted for this level (Chaline, 1972). Bats are represented by only seven remains assigned to five different species (Fig. 3(1–5); Table S3), some of them already referred to in Chaline (1972). *M. blythii*, with 3 remains (MNI = 2) is a species relatively common in the Pleistocene assemblages of eastern and central Europe, but rare until the Late Pleistocene in western Europe; it is usually linked to warm and open enviromnents. The remaining four bat species found in Combe-Grenal, *Pipistrellus pipistrellus/pygmaeus*, *P. auritus*, *M. daubentonii* and *M. nattereri*, are represented in the assemblage with a single remain each. Though no evidence of digestion was observed in the material, a prey assemblage cannot be completely discarded considering the low number of remains and relative high species richness, involving two taxa mainly (*P. auritus*, *M. daubentonii*) found in forest habitats and rarely roosting in caves.

4. Discussion

4.1. Species representation

Current data indicate the presence of a total number of 34 different bat species in French territory (Dietz et al., 2009). Most of these are found throughout France, but a few are restricted to particular regions due to climatic preferences or to historical reasons. The material identified in the four localities studied in this paper belong to species that are still present in France and all of them had been previously recorded in other French Pleistocene localities. Though examples are known of species recorded out of their recent range of distribution during the Pleistocene, such as the occurrence of *E. nilssonii* in La Fage (Mein, 1975) and La Grotte de Rochefort (Noel et al., 2008), or of *M. dasycneme* in La Fage (Mein, 1975) and La Grotte de Espèche (Clot and Duranthon, 1990), all the species described in this paper are within their present-day distribution areas, though certain records such as that of *Miniopterus schreibersii* in Les Valerots or *M. blythii* in Combe-Grenal are located at their northernmost limits of distribution in France.

Species representation of bats in the Middle and Late Pleistocene of France is very varied (Fig. 4). The most common taxa in fossil localities of this age are the Greater and Lesser Mouse-eared bats (*Myotis myotis* and *M. blythii*, respectively) and the Long-eared bats *P. auritus* and *P. austriacus*. The morphology and size of the Greater Mouse-eared bat is very close to that of the Lesser Mouse-eared bat, and difficulties arise when trying to distinguish between both species in a fossil assemblage when material is scarce. *M. blythii*, slightly smaller than *M. myotis,* is of a more Mediterranean character, and its recent distribution in France extends only through its southern half. A few remains of this species were found in the localities of la Grotte de L'Escale and Combe-Grenal, both related to warm periods.

Remains of two of the four species of Long-eared bats (genus *Plecotus*) found in continental Europe are also relatively common in the French Pleistocene. Fossils assigned to *P. auritus* were found in Les Valerots and Combe-Grenal, and of *P. austriacus* in the Grotte de L'Escale and Grotte du Prince. Both species are currently distributed throughout the whole of France, mainly linked to forest habitats. However, *P. auritus* prefers dense humid woodland and temperate habitats whereas *P. austriacus* is more tolerant to warmer, open and arid landscapes where trees are disperse.

Another relatively common species in the French Quaternary is the Greater Horse-shoe bat *(R. ferrumequinum).* The French border with the Netherlands practically marks the northern limits of this species in western Europe. It is mainly distributed in areas with woodland, and is a common component of cave communities, though usually represented in low numbers and frequently mixed with other species. A few remains of this species were found in Les Valerots and the Grotte de L'Escale.

Medium-sized *Myotis* species (*M. bechsteinii*, *M. nattereri* and *M. emarginatus*) are also relatively common in the French Pleistocene, usually represented by low numbers of individuals. They can be found in a variety of roosts that include caves, rock crevices and tree holes. Generally, breeding and winter colonies of these species comprise few individuals, rarely over a hundred, but examples of larger colonies have been reported in northern parts of Europe, where their fossils are also more numerous. *M. bechsteinii* fossils were identified in three of the four localities described in this paper (it is absent in Combe-Grenal), *M. nattereri* in all but the Grotte du Prince, whereas *M. emarginatus* was only recorded in Les Valerots.

Less common species in the French Quaternary have been identified in the assemblages studied in this paper. For instance, *Pipistrellus pipistrellus*, or its recently described cryptic species, *P. pygmaeus*, recorded in Combe-Grenal, is a relatively rare component of Pleistocene cave assemblages, even though caves are included among the variety of roosts it uses and is rarely found roosting alone. *M. schreibersii*, a typically cave-dwelling bat, is less common in Pleistocene French localities than in Italy or Spain, probably due to its Mediterranean character. Where it occurs, it is usually found forming large colonies, frequently reaching thousands of individuals. At the Grotte de L'Escale, it was found to be the dominating species in the bat assemblage; at Les Valerots this species is represented by a few isolated canines. *R. hipposideros* was recorded only at the Grotte du Prince, by a single digested upper canine. Rare in northern France, this species roosts almost exclusively in caves, but forages in a wide variety of habitats including landscapes where trees are scarce.

Among the least common species in the French fossil record, but identified in the described assemblages, are *M. daubentonii* and *E. serotinus*. The first of this species, identified in the assemblage from Les Valerots, had only been previously recorded in Santenay (Sevilla, 1990). It is a species rarely found roosting in caves and strongly linked to riparian forests. The single remain in Les Valerots assigned to *E. serotinus* adds a new record to this species in the French Pleistocene, until now only recorded in L'Hortus (Jullien, 1972). *E. serotinus* is nowadays a widespread anthropophilous species found in a

		Rhinolophus ferrumequinum	*Rhinolophus hipposideros*	*Rhinolophus euryale / mehelyi*	*Myotis myotis / blythii*	*Myotis daubentonii*	*Myotis dasycneme*	*Myotis brandti*	*Myotis emarginatus*	*Myotis nattereri*	*Myotis bechsteinii*	*Vespertilio murinus*	*Eptesicus serotinus*	*Eptesicus nilssonii*	*Nyctalus lasiopterus*	*Pipistrellus pipistrellus / pygmaeus*	*Pipistrellus kuhlii*	*Barbastella barbastellus*	*Plecotus auritus / austriacus*	*Miniopterus schreibersii*	**SPECIES RICHNESS**
LATE PLEISTOCENE	**Grotte Rochefort**													x				x	x		3
	Grotte de Espélugues				x																1
	Grotte d'Espèche				x		x				x					x			x		5
	Bise1				x																1
	Peyreignes	x																			1
	L'Hortus	x		x	x								x			x		x	x	x	8
	Santenay		x			x		x	x	x	x							x	x		8
	Pie Lombard	x	x	x	x																4
	Combe Grenal				x	x				x						x			x		5
	Artenac	cf			x				x	x	x	x									6
	Gerde		x																		1
	Fontéchevade	x	x		x													x	x		5
	Cimay			x																x	2
MIDDLE PLEISTOCENE	**Lazaret**														x						1
	Grotte du Prince		x								x								x		3
	La Fage (V)			x	x		cf		x	x	x			x					x		8
	Aldène	x		x	x											x	x	x		x	7
	Lunel Viel			x	x																2
	L'Escale	x			x					x	x								x	x	6
E.P.	**Les Valerots**	x				x			x	x	x		x						x	x	8

Fig. 4. Bat species recorded in the localities described in this paper and other Middle and Late Pleistocene localities in France, arranged according to their age. Localities with cold climate assemblages are shaded in gray (E.P., Early Pleistocene).

variety of habitats and roosts, occasionally in caves and rock fissures; it is usually found in groups of few individuals. As a fossil, it is not particularly abundant in central and western Europe.

4.2. *Taphonomy and paleoecology*

Recent patterns of distribution and abundance of bats depend on several environmental factors such as temperatures, availability of roosts and the presence of adequate foraging grounds in the area. These specific requirements should provide tools for the reconstruction of past environmental conditions comparable to that of other small mammals. However, when we consider the French Pleistocene record of bats (Fig. 4), species richness is very heterogeneous and does not show any distinct pattern that can be linked directly to climatic phases, the geographic situation of the locality or its age. Thus, the interpretation of climate, or of the presence of particular environments from bat assemblages must rely on the presence of indicator species (strictly Mediterranean, with restricted foraging grounds, etc.), and less in diversity patterns.

Taphonomic processes may be behind the important heterogeneity observed among different localities. Thus, identifying prey assemblages and cave assemblages may be important because of the influence on species representation in the assemblage and the environments that might be consequently interpreted. Bat fossils found in cave assemblages are primarily taken for thanatocoenosis, their occurrence together with other non cave-dwelling vertebrates being usually interpreted as the result of mixing processes. Predation, however, might be a more common source of bat fossils than generally assumed, especially when found together with those of other small vertebrates.

Digestion and particular breakage patterns, as direct evidence of predation, are usually overlooked in fossil bats. Moreover, in the absence of these signs, predation cannot be

completely discarded. Most bats are potentially subject to opportunistic predation by a variety of predators such as snakes, birds and mammals. Breakage and digestion inflicted by most of these predators lead to the destruction of the delicate bat bones; this leaves owls as the most probable predators responsible for bat fossils in a prey assemblage (Kowalski, 1995). Bats appear regularly but usually in negligible numbers in owl pellets. However, a variety of favourable conditions have been described in the literature under which bats become an important part of the diet of individual predators. Not all species are equally preyed on. Thus, most common in owl pellets are *M. myotis*, *M. nattereri*, *E. serotinus*, *Nyctalus noctula*, *P. auritus* and *P. austriacus*; less common prey are other species such as *M. daubentonii*, *E. nilssonii* and *Pipistrellus pipistrellus*, and least of all are the species of the genus *Rhinolophus*, almost always absent in pellets with bat bones (Krzanowski, 1973; Ruprecht, 1979; Kowalski, 1995; Sommer et al., 2009).

In cave or karstic assemblages with small mammals, where bats are represented by few remains and a relatively high number of species common in owl pellets, the possibility that the bat fossils were originally part of a prey assemblage must be considered, even if no signs of digestion are evident. This was the basis for considering three of the four assemblages studied in this paper as prey assemblages. In both Les Valerots and the Grotte du Prince the digestion observed in some of the bat fossils supports predation. In Combe-Grenal, though no evidence of digestion was observed in the material, the structure of the fossil assemblage does not agree with what might be expected for a cave assemblage, neither in species composition nor in their relative abundances. Thus, it is interpreted as a probable prey assemblage.

Cave assemblages are usually characterised by an important representation of typical cave-dwellers, frequently with a dominant species represented by a high number of remains, together with lower numbers of accompanying species. In France, the dominant species in cave communities are usually the Large Mouse-eared bat (*M. myotis*) or Schreiber's Long-fingered bat (*M. schreibersii*); the accompanying species are usually Rhinolophids and middle-sized *Myotis* species (*M. bechsteinii*, *M. emarginatus* and *M. nattereri*). The assemblage in the Grotte de L'Escale agrees with this pattern and, supported by the absence of digestion, was considered as evidence of a cave assemblage. Moreover, the high proportion of juvenile *M. schreibersii* individuals points towards a community occupying the cave during the summer.

Similarly to the differences outlined by Sigé and Legendre (1983) between fluvio-lacustrine and karstic assemblages, cave assemblages picture drier and warmer conditions due to the higher representation of Rhinolophids than in prey assemblages, where Vespertilionids are better represented and which include species rarely found in caves. Though the environmental conditions inferred from the fossil bats represented in the assemblages described in this paper mainly agree with those inferred from the other small mammals from the same localities, the slight differences that are observed coincide with what might be expected considering the origin of each assemblage. For instance, the bat species found in Combe-Grenal indicate more humid conditions than those inferred from rodents; a higher density of trees is inferred from the bats from Les Valerots, or a more Mediterranean character from the bat assemblage in the Grotte de L'Escale.

Acknowledgements

This paper is dedicated to our well-appreciated colleague, Dr. P. Mein, in acknowledgement of his important contributions to the study of fossil mammals, including bats. We are also grateful to Dr. J. Agustì for giving us the opportunity to take part in this volume. Dr. J.M. López-García, Dr. B.W. Woloszyn and Dr. G. Escarguel helped to improve the first manuscript with useful comments and criticisms. Dr. P. Sevilla receives research funds from projects CGL2009-7896/BTE from the Spanish Ministry of Science and Innovation and the UCM-BSCH Research Group GR58/08-910607.

Appendix A. Supplementary data

Supplementary data (Tables S1–S3) associated with this article can be found, in the online version, at doi:10.1016/j.geobios.2011.01.002.

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