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New evidence for the greater noctule bat (*Nyctalus lasiopterus*) in the Late Pleistocene of western Europe

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Abstract

This article reports a new record of the greater noctule *Nyctalus lasiopterus* (Schreber, 1780) in the Late Pleistocene of Europe. A fragment of a left mandible from this species was collected in Layer O (around 55 ka) from the Abric Romaní rock shelter, providing evidence of the presence of the greater noctule in north-eastern Spain during the latest Late Pleistocene. The relevance of this new record, which is geographically not reported up to now in the area, is discussed in terms of environmental changes. ***To cite this article: J.M. López-García et al., C. R. Palevol 8 (2009).***

Résumé

Nouvelle mise en évidence de la noctule géante (*Nyctalus lasiopterus*) dans le Pléistocène supérieur de l'Ouest de l'Europe. Cet article rapporte une nouvelle mention fossile pour la noctule géante *Nyctalus lasiopterus* (Schreber, 1780) dans le Pléistocène supérieur d'Europe. Un fragment de mandibule gauche appartenant à cette espèce a été récolté dans le niveau O (environ 55 ka) de l'Abric Romaní apportant la preuve de la présence de la noctule géante dans le Nord-Est de l'Espagne pendant le Pléistocène supérieur final. L'importance de cette découverte, située en dehors de la distribution géographique actuelle connue pour l'espèce en Espagne, est commentée et mise en relation avec des changements environnementaux. ***Pour citer cet article : J.M. López-García et al., C. R. Palevol 8 (2009).***

Keywords: *Nyctalus lasiopterus*; Biogeography; Palaeoclimate; Abric Romaní; Spain

Mots clés : *Nyctalus lasiopterus* ; Biogéographie ; Paléoclimat ; Abric Romaní ; Espagne

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1. Introduction

Bats (*Chiroptera*) represent the second most diversified order of mammals, accounting for one fifth of the extant mammal species [28]. Even though the fossil record of the group extends over 50 million years, these mammals are extremely rare as fossils. During the Tertiary and Quaternary, the fossil record of bats usually consists of fragments of bones and isolated teeth [16,17,21,27,31], although, in some cases, they may form an important part of the mammal fauna on account of their remarkable diversity, especially in the early part of the Quaternary [34]. While not extensive, however, the fossil record of bats shows that several species once had a very different geographical distribution from that seen today, as is the case with the vespertilionid greater noctule, *Nyctalus lasiopterus*, in the Iberian Peninsula. Vespertilionid fossils are virtually non-existent prior to the Miocene, when the deterioration of the climate, which led to the disappearance of tropical species, seems to have favoured their expansion and diversification at the end of the Neogene [11].

The vespertilionids apparently profited from the disappearance of these bats by taking a wider range of habitats [11]. Since the Middle Pleistocene the Spanish chiropteran fauna is almost identical to the present; the main differences reside in their abundance and geographical distribution [27].

In the last few decades a considerable effort has been made in the study of small mammals from cave deposits. About three quarters of the extant European species are known as fossils, though a distinct bias towards cave bats is observed [29].

The extant vespertilionid genus *Nyctalus* Bowditch, 1825 is represented in Europe by three species, all of which occur in Spain. At present, the greater noctule, *N. lasiopterus* (Schreber, 1780), is the largest European bat. Its recent distribution extends over Europe, West Asia and North Africa. Its habitat is linked to deciduous forests, using cavities in trees as daytime shelters. It is the only species in Europe known to prey on small birds [10,12]. In turn, it is occasionally a prey for *Tyto alba* and *Bubo bubo*.

Though noctules are rare as fossils, two of the recent European species have a Middle and Late Pleistocene record in localities in south-eastern Europe [14,27,30]. The recently discovered fossil from the Late Pleistocene deposits of the Abric Romaní rock shelter (Barcelona), in north-eastern Spain [18,19] (Fig. 1), adds a new record for the genus in Europe and would be the second for this species in Spain.

2. The locality

The Abric Romaní is a classical site with Neanderthal industries in a rock shelter. The site is near the town of Capellades, some 45 km to the northwest of Barcelona. Its geographical references are 1° 41′ 30″ east and 41° 32′ north, and it lies about 310 metres above the present sea level. Its situation, between the contact of the basin of the River Anoia and the Catalan pre-littoral mountain range, constitutes a good enclave in the route between the Mediterranean littoral and the River Ebro inner basin. The shelter is carved in Quaternary travertine, and the Mousterian lithics preserved in the succession of layers provide evidence that Neanderthals occupied the site at different moments within what is known as Marine Isotopic Stage 3 (MIS 3), about 70–40 ka [7]. The excavations at the site have been conducted in three different periods, the first of which extended from 1909 to 1929, the second from 1956 to 1961, while the present excavations, to which this paper refers, started in 1983 [8]. Sampling for pollen analysis at different levels of the succession shows changes in the structure and composition of the vegetation over time, leading to the differentiation of five distinct palaeoclimatic phases [1,6]. Level O, to which this paper refers, is placed in phase number three, dated between 56.8 and 49.5 ka, characterized by alternating temperate and cold events. The uranium series method, applied to the package of sediments that include level O, has given dates between 54.9 ± 1.7 kyr and 54.1 ± 1.6 kyr [3].

3. Description

The greater noctule bat material was obtained after sieve-washing the sediments excavated at level O during the 2004 to 2006 campaigns. The 2 mm mesh retained, together with other small mammal remains, the anterior half of a left mandible with a fourth premolar and two molars, which was recognised as belonging to a large bat species. To determine the genus, features such as the shape of the symphysis, the position of the mental foramen, the number of premolars, and the talonid pattern of the molars were considered. Differences in size and more detailed features of the dental morphology were used for determination at species level, as well as direct comparison with recent specimens loaned from different institutions. The terminology used to describe the teeth follows Van Valen [33], with modifications introduced by several authors [21,26] to describe specific dental features in bats. Measurements were taken following Sevilla [27], using an Olympus SZ-11 binocular

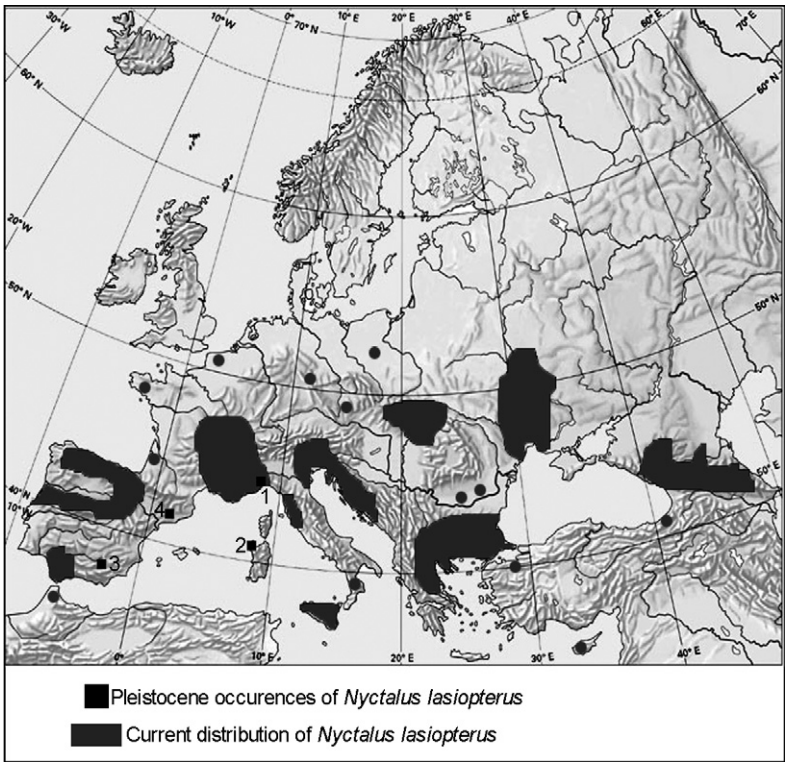

Fig. 1. Pleistocene occurrences of *Nyctalus lasiopterus* in western Europe (France, Italy, Spain) compared with their present distribution (modified from [4,13,15,32,]. (1) Le Lazaret [14]; (2) Punta Padre Bellu [30]; (3) Cueva del Agua [27]; (4) Abric Romaní (in this paper).
Fig. 1. Mentions fossiles de *Nyctalus lasiopterus* dans le Pléistocène d'Europe de l'Ouest (France, Italie, Espagne) comparées avec sa distribution actuelle (modifié [4,13,15,32,]). (1) Le Lazaret [14] ; (2) Punta Padre Bellu [27] ; (3) Cueva del Agua [30] ; (4) Abric Romaní (cet article).

microscope, and are given in millimetres both in Table 1 and Figs. 2 and 3.

The specimen described in this article is the anterior half of a relatively large and robust left mandible. The symphyseal area is elliptical, relatively narrow, slightly slanted mesially, and with a well-defined ventral projection (Fig. 2). Five anterior alveoli are clearly observed, followed by three teeth preserved in place. The first three alveoli correspond to the incisors, the third of which retains part of its root. The fourth alveolus is large, and would correspond to the canine; it is followed by a single fifth alveolus, indicating the presence of a single one-rooted premolar preceding the fourth premolar.

In lateral view, the mental foramen is observed to lie under the anterior margin of the missing premolar, and lies at mid-height of the mandible (Fig. 2).

The p4 presents a semicircular outline in occlusal view. The cusp is mesio-distally compressed and is surrounded by a well-developed cingulum that presents a thickening on its mesio-lingual part, developing a small but distinct basal cuspule (Fig. 2).

The two molars display a nyctalodont pattern [22]. The trigonid valley is relatively wide, and the entocristid is straight (Fig. 2). In buccal view, a well-developed cingulum is observed, somewhat irregular in its thickness, with a small inflection at the end of the trigonid (Fig. 2). The base of the talonid drops distally, so that the base of the hypoconid is conspicuously lower than the base of the protoconid (Fig. 2).

4. Results

Only two recent Spanish bat species are of a size that might fit with the specimen from the Abric Romaní. These belong to two different families, and both have nyctalodont molars and only two premolars in each mandible. One of these species is *N. lasiopterus*, commonly known as the greater noctule, and the other a molossid, *Tadarida teniotis*, the free-tailed bat. Though Fig. 3 shows that the molars and fourth premolar of *T. teniotis* seem to be closer in size to the specimen from the Abric Romaní, the morphology of the fossil specimen is closer to that of the greater noctule and differs from *T. teniotis* in several diagnostic features. Thus, in *T. teniotis* the mandible is relatively slender, without a ventral projection of the symphysis, and the mental

Table 1
Measurements (in millimetres) of the lower dentition in *Nyctalus lasiopterus, Nyctalus noctula, Nyctalus leisleri* and *Tadarida teniotis*.
Tableau 1
Mesures (en millimètres) de la dentition inférieure de *Nyctalus lasiopterus, Nyctalus noctula, Nyctalus leisleri* et *Tadarida teniotis*.

			n	Min	Max	Mean	S.D.
p4	*N. lasiopterus*	L	7	1.00	1.35	1.14	0.13
		W	7	1.27	1.61	1.44	0.11
	N. noctula	L	4	0.81	0.95	0.91	0.07
		W	4	1.01	1.14	1.09	0.06
	N. leisleri	L	7	0.56	0.84	0.71	0.09
		W	7	0.77	0.84	0.81	0.03
	T. teniotis	L	2	1.08	1.12	1.10	0.03
		W	2	1.15	1.25	1.20	0.07
m1	*N. lasiopterus*	L	7	2.15	2.51	2.29	0.15
		W	7	1.60	1.89	1.80	0.10
	N. noctula	L	4	1.65	1.80	1.74	0.60
		W	4	1.33	1.64	1.44	0.14
	N. leisleri	L	7	1.37	1.57	1.48	0.06
		W	7	0.90	1.33	1.18	0.13
	T. teniotis	L	2	2.08	2.13	2.11	0.04
		W	2	1.65	1.75	1.70	0.07
m2	*N. lasiopterus*	L	7	2.03	2.43	2.23	0.14
		W	7	1.55	1.89	1.76	0.11
	N. noctula	L	4	1.46	1.85	1.68	0.18
		W	4	1.38	1.59	1.45	0.10
	N. leisleri	L	6	1.40	1.61	1.47	0.08
		W	6	1.17	1.26	1.21	0.03
	T. teniotis	L	2	2.01	2.08	2.05	0.05
		W	2	1.61	1.75	1.68	0.10

p4: fourth lower premolar; m1: first lower molar; m2: second lower molar; n: sample number; min: minimum; max: maximum; S.D.: standard deviation; L: length taken from the paraconid to hipoconulid; W: talonid width taken from the hipoconulid to the basal hypoconid.
p4 : quatrième prémolaire inférieure ; m1 : première molaire inférieure ; m2 : deuxième molaire inférieure ; n : numéro de l'échantillon ; min : minimum ; max : maximum ; S.D. : déviation standard ; L : longueur entre le paraconide et l'hipoconulide ; W : largueur du talonide prise entre l'hipoconulide et la base de l'hypoconide.

foramen lies between the two premolars and occupies a more ventral position. The p4 is relatively smaller, triangular in occlusal view, and presents two roots and no thickening of the cingulum; the molars are more slender, with narrower trigonid valleys, a lingually concave entocristid, and the base of the hypoconid is only slightly displaced ventrally (Fig. 3d). All these differences can be considered major ones and rule out the possibility that the specimen from the Abric Romaní might be a mandible of *T. teniotis*.

The features in which the specimen from the Abric Romaní differs from *Tadarida* are in fact traits observed in the three species of Iberian noctules. Accordingly, comparison with *Nyctalus noctula* was considered necessary since the fossil mandible shows a slight difference in size when compared to recent specimens of the greater noctule. However, the common noctule (*N. noctula*) is not only smaller but also differs from the specimen from the Abric Romaní in the shape of the p4, in which the lingual cusplet occupies a more mesial position; the absence of an inflexion in the cingulum dividing trigonid and talonid; and the slighter ventral drop in the talonid (Fig. 3d). On the basis of these differences, the mandible from the Abric Romaní cannot be ascribed to *N. noctula* and clearly belongs to *N. lasiopterus*.

5. Discussion

The specific habitat requirements of *N. lasiopterus*, which largely seem to depend on the development of mature forests, where hollow trees may provide for its day roosts, although occasionally it can use open areas for foraging and does not need large extensions of forest [25]. Its specific requirements are probably responsible for the low densities and patchy distribution that characterize this species recently, in spite of its relatively wide geographical range. Particularly in Spain, the greater noctule has been located at certain points in mountainous regions such as the western Pyrenees, the Iberian Range, the Cantabrian and central Range or in

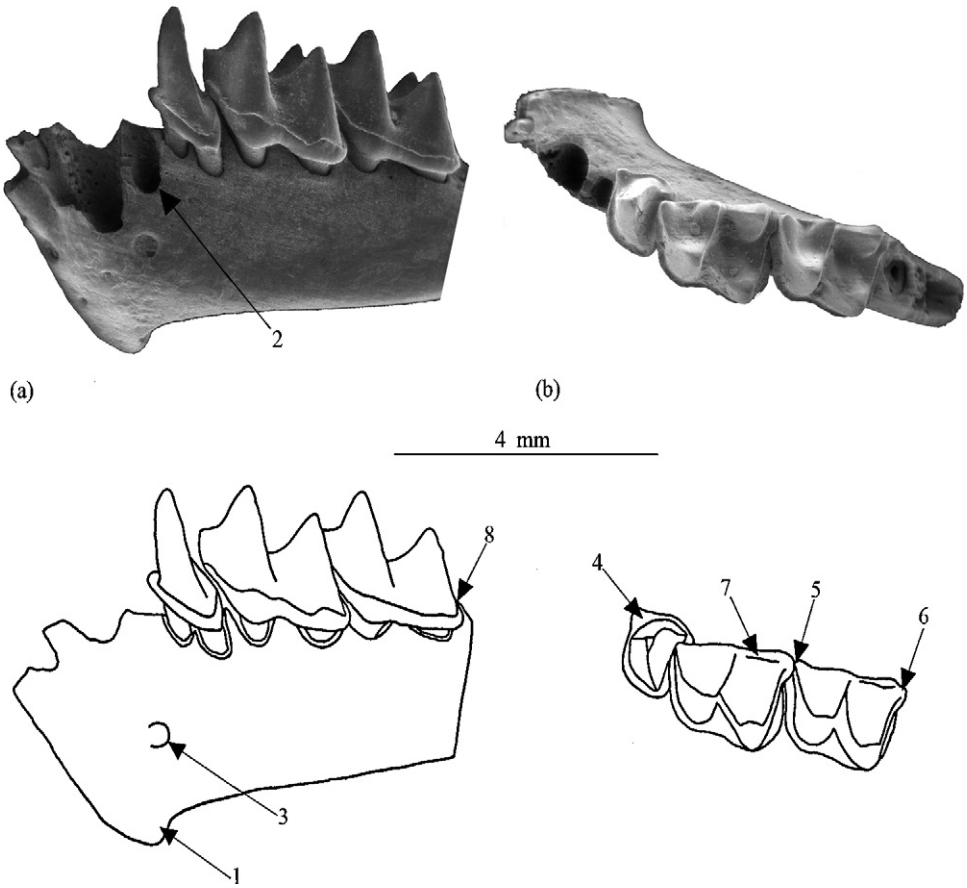

Fig. 2. Left lower mandible of the greater noctule bat *Nyctalus lasiopterus* from the Abric Romaní, level O: buccal view (a), occlusal view (b). The diagnostic traits of the former include (1) elliptical symphysis with a well-defined ventral projection, (2) one-rooted p3, (3) mental foramen under the anterior margin of p3, (4) antero-lingual cuspule in p4, (5,6) nyctalodont molars, (7) straight entocristid, (8) ventral drop in talonid.
Fig. 2. Mandibule inférieure gauche de noctule géante *Nyctalus lasiopterus* du niveau O de l'Abric Romaní : vue buccale (a), vue occlusale (b). Les caractères diagnostiques de la forme incluent (1) une symphyse elliptique avec une projection ventrale bien définie, (2) une p3 avec une seule racine, (3) un foramen mentonnier en dessous du bord antérieur de la p3, (4) une cuspule antéro-linguale sur la p4, (5,6) des molaires nyctalodontes, (7) un entocrestide rectiligne, (8) le talonide plus bas ventralement.

more open Mediterranean landscapes in the south [24]. Its shelters are mainly found in deciduous forests with *Quercus* or *Fagus*, but also in pine forests. The size of specimens might follow a cline variation, with smaller southern specimens.

As a forest species, noctules are hardly expected to be found in small mammal fossil assemblages. Small mammal fossil assemblages in caves and rock shelters are usually caused by predation, and are most commonly the result of the accumulation of owl pellets [2,9]. Occasional predation on bats by nocturnal birds of prey might account for the mandible of *N. lasiopterus* in the Abric Romaní, though *in situ* death might also account for it, since this species has occasionally been observed to occupy rock crevices.

In either case, the mandible of the greater noctule in the Abric Romaní provides evidence of changes in species distribution during the Late Pleistocene and Holocene, though not easy to link to specific environmental changes. Thus, no evidence of well-developed forests is given by the pollen analysis conducted by Burjachs and Julià [6], which includes level O in phase 3; this analysis indicates an important predominance of *Artemisia* and *Poaceae*, typical steppe vegetation, currently considered in the Pleistocene to be indicative of arid and cold climate conditions during which forest cover was scarce or absent. However, these authors also point out that during this cold and arid climatic phase, major oscillations in the pollen curves are observed, indicating short warming periods with a small increase in the proportions of pollen from deciduous trees in addition to that of *Pinus*.

The small mammal assemblage at level O (Table 2) includes an important proportion of species linked

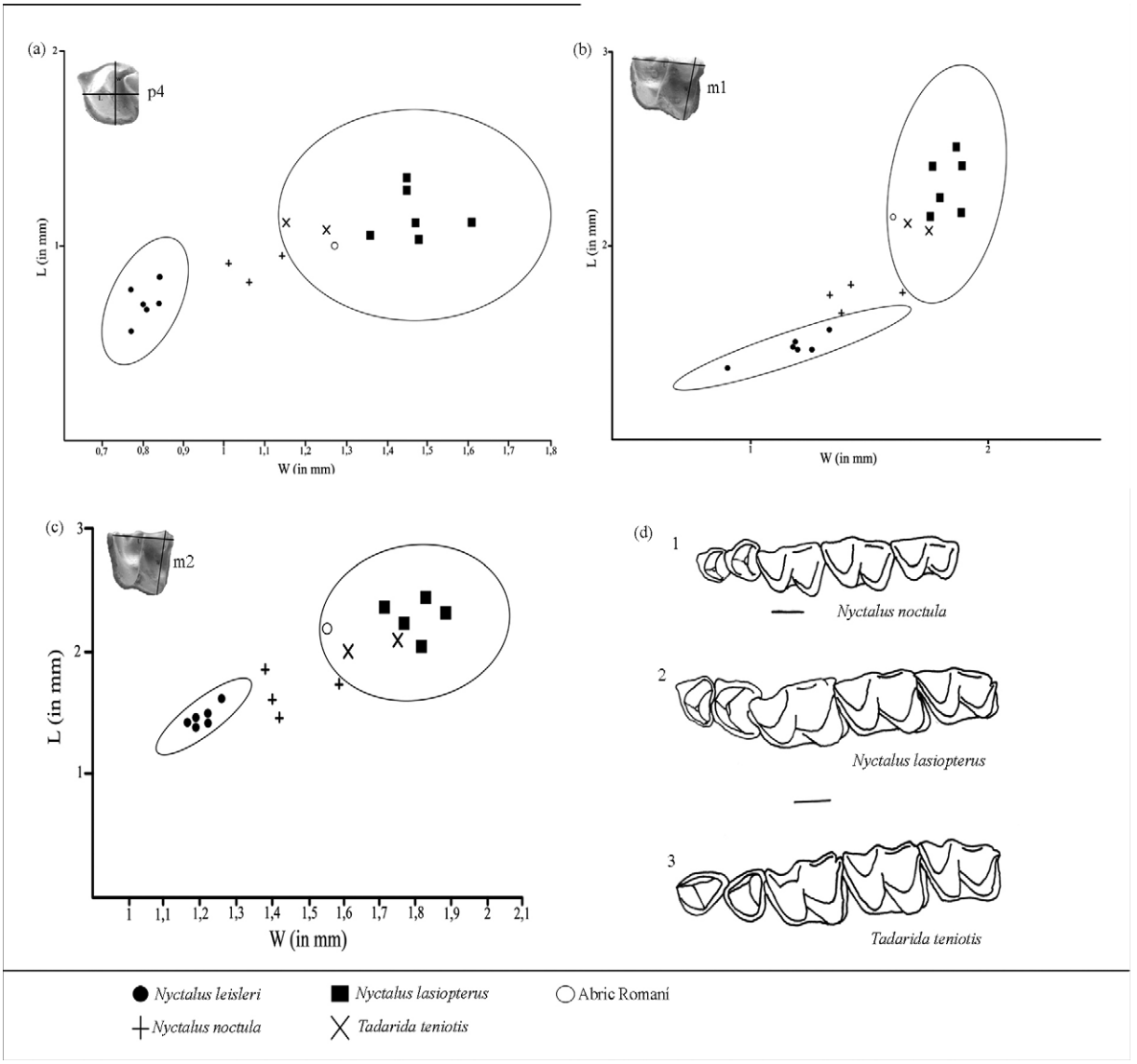

Fig. 3. Scatter diagram comparing the length (L) and width (W) in (a): the fourth lower premolar (p4), (b): the first lower molar (m1) and (c): the second lower molar (m2). *Nyctalus leisleri* ($n = 7$), *Nyctalus noctula* ($n = 4$), *Nyctalus lasiopterus* ($n = 6$), *Tadarida teniotis* ($n = 2$), Abric Romaní specimen ($n = 1$). Measurements are given in millimetres. The ellipse indicates the 95% confidence. (d) Left mandible (p3–m3) of *Nyctalus noctula* (1), *Nyctalus lasiopterus* (2) and *Tadarida teniotis* (3). Scale 1 mm.

Fig. 3. Diagramme de dispersion comparant la longueur (L) et la largeur (W) en (a) : la quatrième prémolaire inférieure (p4), (b) : la première molaire inférieure (m1) et (c) : la deuxième molaire inférieure (m2). *Nyctalus leisleri* ($n = 7$), *Nyctalus noctula* ($n = 4$), *Nyctalus lasiopterus* ($n = 6$), *Tadarida teniotis* ($n = 2$), spécimen de l'Abric Romaní ($n = 1$). L'ellipse montre l'intervalle de confiance 95%. (d) Mandibule gauche (p3–m3) de *Nyctalus noctula* (1), *Nyctalus lasiopterus* (2) et *Tadarida teniotis* (3). Échelle 1 mm.

to aquatic environments (southern water vole *Arvicola sapidus*), humid grassland (Iberian vole *Iberomys cabrerae;* common mole *Talpa europaea*), shrubland (field mouse *Apodemus sylvaticus*), or even forests (garden dormouse *Eliomys quercinus*), placing the assemblage in one of these short periods within the major arid phase, which would account for its relatively high species richness and for the presence of the noctule.

When the mutual climatic range method, which infers climatic conditions at a given time on the basis of the habitat coincidence of the species represented at the site (e.g. [5]), is applied to the small mammal assemblage, lower mean annual temperature (−7.5 °C) and higher mean annual precipitation (+ 299 mm) are given for level O as compared to the present-day climate in this area of Catalonia [18,20].

Table 2
Small mammal assemblage in Minimum Number of Individuals (MNI) from the Abric Romaní level O, taken from López-García [19].
Tableau 2
Association des micromammifères du niveau O de l'Abric Romaní en Numéro Minimum d'Individus, d'après López-García [19].

Taxa	MNI
Crocidura russula	5
Sorex gr. *coronataus-araneus*	1
Talpa europaea	3
Nyctalus lasiopterus	1
Microtus arvalis	13
Microtus agrestis	5
Iberomys cabrerae	20
Terricola duodecimcostatus	11
Arvicola sapidus	29
Apodemus sylvaticus	20
Eliomys quercinus	1
Total MNI	109

The absence of adequate shelters does not in itself explain the present distribution of *N. lasiopterus* in Spain, and more particularly its absence in the area near the Abric Romaní, since the present vegetation is typically Mediterranean oak forest and shrubland with *Quercus ilex* and *Quercus coccifera*, though strongly modified by human activities favouring the development of pine forests of *Pinus halepensis,* with wide extensions of *Erica arborea* and *Rosmarinus officinalis* [23].

As such, the mandible of the greater noctule found at the Abric Romaní level O reinforces the evidence that this species was widely distributed during the Pleistocene in Spain, particularly during the temperate phases in which the pollen record puts in evidence the development of extensive forest areas. The reduction in the extension of mature forests providing roosts for the species during the Holocene, together with other environmental factors, more difficult to interpret, may have determined the recent low densities and patchy distribution observed in recent *N. lasiopterus* today.

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