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Bats from the classical site of Venta del Moro (Late Miocene, Eastern Spain)

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ABSTRACT
The presence of bat fossils in localities of fluvio-lacustrine origin is quite uncommon, and usually these remains are poorly preserved or not studied in detail. In the present work we study the bat association of the classical Late Miocene locality of Venta del Moro, which have yielded remains of five taxa of chiropterans. Two new bat species are described in this work: Pipistrellus rouresi sp. nov., a new form to the extremely scarce Neogene register of pipistrelle bats, and the horseshoe bat Rhinolophus antonioi sp. nov. Additionally, we describe the oldest and southernmost record of Myotis podlesicensis, a mouse-eared bat of African origin, as well as an undetermined taxon belonging to the noctule bats, Nyctalus sp., and a further taxon of Vespertilionidae indet. With the description of this new material, the record of Late Miocene bats from Europe is increased.

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Introduction
The site of Venta del Moro is well known since the 1970s, and it contains an abundant and diversified fossil assemblage including vertebrates, molluscs, arthropods, pollen and macro-flora, comprising more than one hundred taxa (Morales 1984; Montoya et al. 2006; Mansino et al. 2015). A preliminary faunal list was given by Montoya et al. (2006), not including any reference to bats.

The Iberian peninsula has an excellent continental Neogene record. Major basins such as the Duero, Tajo or Ebro basins are well known for their deposits with numerous localities rich in both macro- and microvertebrates, invertebrates and pollen record. The quality of the mammal assemblages found in these basins has enabled to establish several Western European mammal ages such as the Turolian, Vallesian, Aragonian or Ramblian. Geographically wide – spread taxa of large mammals and rodents found in the sites combined with the paleomagnetic data from the stratigraphic sequences of the exposures in which the sites were located, enabled in 1993 to build an overall correlation synthesis comprising the major Spanish basins and smaller iberian basins that contained a less extended record, and with Central and Eastern European reference localities (Calvo et al. 1993). New Neogene localities that have been described since then, and are still being discovered, to the point that the abundant available data has enabled to approach interesting issues such as the diachronical record of key taxa (Gómez-Canó et al. 2011), or speciation patterns of mammals (López-Martínez 2009).

In this scenario, the Neogene record of bats in the Iberian peninsula stands out as poorly characterised (Sevilla 1991). Because bats are rarely found in scats and pellets, their fossils are either rare or absent in assemblages originated in fluvial or lake deposits. Thus, most Spanish Neogene sites in which bats are reasonably well represented are karstic localities and provide a biased view of the diversity this mammal group had during the Miocene. Nevertheless, valuable information is usually obtained from the rare fluvio-lacustrine assemblages in which bats are present. Although specific determination is usually hampered because of the few available material and/or absence of diagnostic teeth, new undescribed species are usually identified in these sites, giving evidence of how much still remains to be discovered. The fossil bats found in Venta del Moro is a good example of this – the few bat fossils represent a relatively high number of species, most of them represented by a single or few elements with morphologies not found in known taxa and perforce belonging to new species.

In this work, we study the few and unique bat assemblage from Venta del Moro, that has enabled to describe the oldest record of a pipistrelle in Western Europe, a new species of horseshoe bat and the first mouse-eared bat with an African origin in Europe.

Material, methods and abbreviations
The studied fossils are kept at the Museum of Geology of the University of Valencia (MGUV) with the field labels VVmA-, VVmAB- and VVmB-. The nomenclature and measurement methods are those from Legendre (1984), Sevilla (1988) and Fracasso et al. (2011). The lower teeth are indicated as p4, m1, m2 and m3, and the upper teeth as M1, M2 and M3.
**Abbreviations** – MN, European Neogene land mammal units; MGUV, Museu de Geologia de la Universitat de València; L, length; W, width; Wtal, talonid width; Wtrig, trigonid width.

**Geological setting**

The classical locality of Venta del Moro is situated in the Cabriel Basin, a middle-sized Neogene basin located between the Iberian platform to the north, and the Betic Cordillera to the south in East Iberia (Valencia, Spain; Figure 1). The watershed of this basin is mostly composed of Cenozoic limestones with detrital sediments, bearing several fossil mammal localities, which range from the Late Aragonian to Villanyian (MN7/8 to MN17) (see references in Ruiz-Sánchez et al. 2011). Venta del Moro section lies in the Los Isidros member of the Villatoya-Venta del Moro Formation (Robles 1970; Montoya et al. 2006). According to the nomenclature of levels of (Montoya et al. 2006), the fossil-bearing levels of Venta del Moro with bat remains are: VVm-A, -AB and -B. These fossiliferous sites are located in lacustrine sediments which first lacustrine cycle starts with grey mudstones, limestones and organic rich mudstones representing flood plains and shallow lakes interrupted by an erosive hiatus. The next cycle consists of clays, reddish sandstones and/or conglomerates, an overlying level of clays, and culminates, depending on the area, with a level of limestones or sandy limestones (Marín 2000).

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**Figure 1.** Location map of the locality Venta del Moro (VVm), and geological map of the continental sediments in the Venta del Moro area (Cabriel Basin) (modified after Mansino et al. 2014).
The bat association of this site (Morales 1984; Montoya et al. 2006) suggests a latest Miocene age (Late Turolian, or Ventian, sensu Morales et al. 2013), estimated by means of palaeomagnetic techniques at 6.23 Ma (Gibert et al. 2013). Because of its age, Venta del Moro is a key locality to understand the environmental and faunal changes that took place just before the Messinian Salinity Crisis (Montoya et al. 2006; Gibert et al. 2013).

**Systematic palaeontology**

**Order** Chiroptera Blumenbach, 1779  
**Suborder** Yinpterochiroptera van den Bussche and Hoofer, 2004  
**Family** Rhinolophidae Gray, 1825  
**Genus** Rhinolophus Lacépède, 1825  
**Type species:** Vespertilio ferrum-equinum Schreber, 1774; extant species.

*Rhinolophus antonioi* sp. nov. (Figure 2(A)–(C)) 2016 Rhinolophus sp. Crespo et al. 2016.

**Etymology** – Named after Antonio Crespo Bellés and his family, father of the first author.

**Holotype** – Left M3, VVmA-2814 (MGUV-32809).

**Type locality** – Venta del Moro A, Cabriel Basin, Eastern Spain.

**Type horizon** – Villatoya-Venta del Moro Formation, MN13, Late Turolian or Ventian (Late Miocene, 6.23 Ma).

**Material** – VVmA: 1 M1 (VVmA-2811, MGUV-32806), 1 M3 (VVmA-2814, MGUV-32809); VVmB: 1 m3 (VVmB-739, MGUV-33957).

**Diagnosis** – Rhinolophid of medium size with wide upper molars; the posterior cingulum of the M3 connected to the distal cingulum of the metaflex, surrounding the metacone.

**Differential diagnosis** – *Rhinolophus antonioi* sp. nov. differs from all the other European species of this genus by the labial cingulum of the metaflex surrounding the metacone in the M3, and by its narrower M3; it differs from *Rhinolophus ferrumequinum* (Schreber, 1774), by its smaller size and a less developed talon in the M1; it differs from *Rhinolophus lemanensis* Revilliod, 1920 from Petersbuch 28 and 62, by its smaller size, a less developed talon in the M1 and a narrow anterior cingulum.

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*Figure 2.* Fossil bats from Venta del Moro.  
Notes: (A–C) *Rhinolophus antonioi* sp. nov., (A), right M1, VVmA-2811. (B), left M3 (holotype), VVmA-2814. (C), left m3, VVmB-739. (D–G) *Pipistrellus roureii* sp. nov., (D), left M1 (holotype), VVmA-2813. (E), right M2, VVmA-2812. (F), right m1, VVmAB-129. (G), left m1, VVmB-740. (H–I) *Myotis podlesicensis*, (H), left M2, VVmB-894. (I), left m2, VVmB-893. (J) *Nyctalus sp.*, (J), right p4, VVmA-2840. (K) Vespertilionidae indet., (K), right m1.2, VVmA-2827. Scale: 1 mm.

Measurements – M1: (VVmA-2811) 1.71(L)x 1.97 (W); M3: (VVmA-2814) 1.18(L)x 1.38 (W); m2: (VVmB-739) -(L)x – (W)trag)x 1.04(Wtal).

Stratigraphic and geographic range – MN13, Late Miocene; Gabriel Basin of Eastern Spain.

**Description**

**M1** – Subquadrangular tooth. The parastyle is set at a right angle with the preparacrista. The precingulum is narrow and connected to the protocone; this cingulum has a small thickening near to the parastyle. A short precingulum is present on the anterior side of the protocone. The ectoloph is symmetric. On its labial side, both the paraflex and the metaflex display a narrow cingulum. The metacone is slightly higher than the paracone. The paraloph, metaloph, hypocone, paracristule and metaconule are absent. The talon is developed as a triangular projection directed posterior and lingually, with a small basin enclosed by a well developed cingulum. The postprotocrista connects the metacingulum, which ends at the base of the metastyle.

**M3** – Subtriangular tooth. The ectoloph is distally reduced, the postmetacrista practically absent, no metastyle present. The parastyle is on a right angle with the preprotocrista. The anterior cingulum is wide and connected to the preprotocrista; the postprotocrista connects the metacingulum. A precingulum and postcingulum are distinctly visible. The labial cingulum of the paraflex is small, whereas the metacone is surrounded by a distinct and well-developed cingulum on its lingual and distal side, connecting with the postprotocrista. A weak paraloph is present. The metaloph, hypocone, paracristule and metaconule are absent.

**m3** – a single distal fragment of this tooth has been recovered. It displays a nyctalodont pattern. The entoconid is slightly displaced lingually with respect to the hypoconulid. The valley between the entoconid and the hypoconulid is wide. The entocristid is concave on occlusal view. The labial cingulum is narrow and the connection with the posterior cingulum is very narrow.

**Discussion**

The genus *Rhinolophus* is a common bat in the Miocene karstic fissures of Europe. This, generally, is due to the distinctive preference of the species of this genus for karstic environments where they roost in caves, crevices, fissures, etc., only a few species as *Rhinolophus triglialis* Temminck, 1834 does not live in this kind of habitats, otherwise in the forests or other environments. They are very scarce in fluvio-lacustrine sites, probably because they are extremely uncommon in owl pellets (Kowalski 1995; Ziegler 2003; Hutson et al. 2008).

According to biometrical criteria, three groups of horse-shoe bats may be distinguished: a group of small sized species similar in size to extant *R. hipposideros*, a group that comprises intermediate size species represented by the recent *R. mehelyi-euryale* group and the last, consisting by larger sized species, in which recent *R. ferrumequinum* is the reference (Popov 2004). According to its size, *Rhinolophus antonioi* sp. nov. belongs to the *R. mehelyi-euryale* group. The width relation between M1 and M3 is variable, according to different species, while *R. antonioi* nov. sp. has 1.42, similar to *R. maghrebensis* (1.41), in other species, as *R. dehmi* from Wintershof West (1.26); *R. delphinensis* from Petersbuch 31 (1.18) or the actual *R. euryale/mehelyi* (1.06) is lower (Sevilla 1988; Ziegler 1993, 2003; Gunnell et al. 2011).

*Rhinolophus antonioi* sp. nov. is not belong to the species from the group of *R. ferrumequinum* by it has a small size. This fact discards the possible ascribe to the fossil species *R. delphinensis*, *R. lemanensis*, *R. csakvarensis* and *R. kowalskii* (Storch 1999). And, *R. antonioi* sp. nov. differs to *R. hipposideros* group and their fossil relative species by has a big size (Popov 2004).

Besides the recent *R. mehelyi* and *R. euryale*, this group includes another extant species, also distributed in the Mediterranean area, *Rhinolophus blasii* Peters, 1866 found in Southern Europe from Italy to the Eastern Mediterranean, reaching Ethiopia (Horáček et al. 2013). *Rhinolophus euryale* is known in the European fossil record since the Early Pliocene (Popov 2004), and supposedly is a descendant of the European Late Miocene *R. lissiensis* (or *grivensis*) (Ziegler 2003; Horáček et al. 2013). The earliest record of *R. euryale* is known from the Early Pliocene of Podlesice, in Poland (Woloszyn 1987). Another fossil form of this group, *R. neglectus*, is considered more closely related to *R. mehelyi*, known from the Late Pliocene and Early Pleistocene of the Mediterranean region (Sevilla et al. 1991; Popov 2004; Tata & Kotsakis 2005; Agustí et al. 2011). Also related to the group is the younger species *R. maghrebensis* described in the Pliocene of Aḥl al Oughlam (Morocco, MN16) (Gunnell et al. 2011; Horáček et al. 2013).

This *Rhinolophus* material from Venta del Moro presents a unique combination of features, not found in any other species belonging to this genus. The presence of a well developed cingulum surrounding the M3, has only been described in *R. lemanensis* from the Early Miocene of Petersbuch 62, a species that belongs to *R. ferrumequinum* group (Storch 1999; Rosina & Rummel 2012), which, on the other hand, differs from the M3 from Venta del Moro by its smaller size, the presence of paraloph...
and less developed lingual cingulum. *R. delphinensis* from the Middle Miocene locality of Petersbuch 6 has a thin posterior cingulum (Ziegler 2003). Thus, this material must belong to a new species.

**Suborder** Yangochiroptera   
**Family** Vespertilionidae   
**Subfamily** Vespertilioninae s. str.  
**Tribe** Pipistrellini    
**Genus** Pipistrellus

**Type species** – *Vespertilio pipistrellus* Schreber, 1774; extant species.

**Pipistrellus rouresi** *sp. nov.* (Figure 2(D)–(G))  

**Etymology** – Named after Maria Isabel Roures Roures and her family, mother of the first author.

**Holotype** – Left M1, VVMa-2813 (MGUV-32808).

**Type locality** – Venta del Moro A, Cabriel Basin, Spain.

**Type horizon** – Villatoya-Venta del Moro Formation, MN13, Late Turolian or Ventian (Late Miocene, 6.23 Ma).

**Material** – VVMa: 1 M1 (VVMa-2813, MGUV-32808), 2 M2 (VVMa-2810, MGUV-32805; 2812, MGUV-32807), 1 m2 (VVMa-2826, MGUV-32821), 2 fragments of m12 (VVMa-2835, MGUV-32840; 2836, MGUV-32831); VVmAB: 1 m1 (VVmAB-129, MGUV-33112); VVMB: 1 m1 (VVM-B-740, MGUV-33958).

**Diagnosis** – Small *Pipistrellus* species with compressed upper molars; well-developed paralophs and metalophs; small metaconule and small paraconule in M1.

**Differential diagnosis** – *Pipistrellus rouresi* *sp. nov.* differs from *Pipistrellus semenovi* Rosina and Sinitsa, 2014 by having shorter upper molars, a less developed paraconule and a straight metaloph and a discontinuous posterior cingulum; it differs from *Pipistrellus kuhlii* (Kuhl, 1817) by having shorter upper molars and a small paraconule; it differs from *Pipistrellus* sp. from Egorovka 1, 2 and Palievo by having a narrower cingulum and the smaller size of the m1; it differs from *Pipistrellus pipistrellus* (Schreber, 1774), by the presence of a small paraconule in M1, a small hypocone, the absence of metaconule, and wider upper molars; it differs from *Pipistrellus nathusii* (Keyserling and Blasius, 1839), by the presence of a small paraconule in M1, a small hypocone and the absence of metaconule by having nyctalodont lower molars; it differs from *Pipistrellus rueppelli* (Fischer, 1829), by the presence of paraconule and shorter upper molars; it differs from *Hypsgo savii* (Bonaparte, 1837), by the presence of a small paraconule in M1, a small hypocone and the absence of metaconule by having nyctalodont lower molars; it differs from *Pipistrellus rueppelli* (Fischer, 1829), by the presence of paraconule and shorter upper molars; it differs from *Hypsgo savii* (Bonaparte, 1837), by the presence of a small paraconule in M1, a small hypocone, the presence of metaloph, the absence of metaconule, and nyctalodont lower molars (Sevilla 1986, 1988; Rosina & Sinitsa 2014).

**Measurements** – M1: (VVMa-2813) 1.14(L) x 1.44 (W); M2: (VVMa-2810) –(L)x 1.62 (W), (VVMa-2812) –(L)x 1.59 (W); m1 (VVmB-129) 1.13(L)x 0.69(Wtrig)x 0.82(Wtal); m2: (VVMa-2826) 1.09 (L)x –(Wtrig)x –(Wtal), (VVM-B-740) 1.17(L)x 0.76 (Wtrig)x 0.82(Wtal).

**Stratigraphic and geographic range** – MN13, Late Miocene; Cabriel Basin, Eastern Spain.

**Description**

*m1* – Nyctalodont tooth, with a U-shaped paralophid. The protoconid and the metaconid have a similar size. The entoconid and the hypoconulid are aligned in occlusal view. On occlusal view, the entoconid is distinctly concave. The talonid is wider than the trigonid. The lingual cingulum is only found in the trigonid basin and it is poorly developed. The labial cingulum is wide and runs from the mesio-lingual base of the paraconid to the base of the hypoconulid. This cingulum is of varying thickness, thin in the side of the talonid and thick in the trigonid side.

*m2* – The m2 is similar to the m1, but the trigonid and the talonid have similar widths.

*M1* – Subquadrangular tooth. The parastyle is well developed and bent in a right angle with the preparacrista. The paracingulum is wide and connected to the protocone. A short precingulum is present. The labial cingulum of the paraflex is reduced to a spur, while the labial cingulum of the metaflex is better developed. The metacone is slightly higher than the paracone. The para and metacone are symmetric. The paraloph and the metaloph are well developed; the former is attached to a small paraconule and the latter is oblique and reaches the proprostocrista in a position anterior to the small metacone found at the end of the postprotocrista. There is no talon but the lingual cingulum thickens slightly in this position. The postcingulum and metastigulum are continuous.

*M2* – The M2 is similar to the M1, but narrower and with a more prominent distolingual region. The labial cingulum of the paraflex is small, while the labial cingulum of the metaflex is better developed. The paraloph reaches the protocone, and there is no paracone. The metaloph is attached to a shorter proprostocrista, and anteriorly to the small metacone.

**Discussion**

The absence of distinctly developed talons in upper molars indicates this material belongs to the family Verpertiolinidae. Within this family, we can discard the genera *Myotis*, *Eptesicus* and *Plecotus* because of their myodont lower molars (Menu 1985; Sevilla 1988). The genera *Barbastella*, *Eptesicus* and *Plecotus* do not have either paralophs or metalophs on the upper molars (Sevilla 1988). The genus *Nyctalus* resembles the studied remains, but the trigonid and the talonid are similar in width in the lower molars, and in the upper molars the cingulum is better developed (Rosina & Sinitsa 2014). *Miniopterus* differs from our specimens by the better development of the talon in the upper molars and the narrower cingulum in the talonids.

The genus *Pipistrellus* is exceptional in the Miocene fossil record (Mein 1999; Horáček & Jahelková 2005), the only fossil species described until now being *Pipistrellus semenovi* from Altestovo 5 (Ukraine). Some indeterminate species assigned to the genus are known from the French localities of Dionay and Bernardière and the Ukraine localities of Egorovka 1,2 and Palievo (Mein 1999; Rosina & Sinitsa 2014). In the Iberian Peninsula, the oldest record of a *Pipistrellus* species comes from the latest Pliocene site of Almenara Casablanca 4 (Agustí et al. 2011).
fall within the range of variability shown by recent *P. pipistrellus*, their widths are larger and closer to the values observed in *P. kuhlii* or *P. rueppelli*, giving them a ‘compressed’ appearance, especially in the M2.

Regarding morphological structures, the presence of well-developed paraloph and metaloph, with reduced metaconule and paraconule denotes that this is a primitive species, closer to *P. semenovi* or *P. kuhlii*, but differs from the latter taxa by having a more reduced paraconule (Menu 1985; Rosina & Smitsa 2014), similar to the primitive morphology A described by Menu (1985). Thus, *Pipistrellus rouesti* sp. nov. would be a primitive representative similar to the species *pipistrellus*-like group.

**Subfamily** Myotinae Tate, 1942  
**Genus** Myotis Kaup, 1829  
**Myotis podlesicensis** Kowalski, 1956 (Figure 2(H)–(I))

**Localities** – VVmA, VVmB  
**Material** – 2 m1 (VVmA-2838, MGUV-2838; VVmB-893, MGUV-34111), 2 M1 (VVmA-2819, MGUV-32814; VVmB-895, MGUV-34113), 1 M2 (VVmB-894, MGUV-34112).

**Measurements** – m1: VVmB-893: L: 1.57; Wtrig: 1.06; Wtal: 1.05

**Description**

*m1* – Myodont tooth, with a U-shaped paralophid on labial view. The protoconid is the highest cusp of the trigonid, the paraconid being slightly lower than the metaconid. Paraconid, metaconid and entoconid are aligned in occlusal view; the hypoconulid is slightly displaced labially. The entocristid is straight. The trigonid and the talonid are of similar width. The hypoconulid is well developed and stands alone but close to the entoconid. There is no lingual cingulum on the trigonid in one of the specimens (VVmA-2838) and a small and narrow one in the other (VVmB-893). The labial cingulum well developed, wide and uniform in thickness, and runs from the anterolateral base of the paraconid to the labial base of the hypoconulid.

*M1* – The two specimens are preserved uncomplete, VVmA-2819 only preserve the lingual side and VVmB-895 is the anterior side. One specimen (VVmB-895) the parastyle is even curved. The paracingulum is wide and connected to the protocone, but separated from the parastyle. A small paraconule is present in both specimens. A small precingulum is present on the anterior side of the protocone. On the paraflex there are no cingula. The preparacrista is shorter than postparacrista. Both the paraloph and metaloph are present, but weakly developed, and no paraconule is seen on the protocrista. The postprotocrista ends at a rounded, distinct metaconule of moderate height. The outline of the posterior lingual part of the tooth protrudes slightly at the place where the metaconule stands. The postcingulum and metacingulum are connected, and the protossoa is open distally.

*M2* – Subrectangular tooth. The parastyle is missing in the only available specimen. On the metaflex a labial cingulum is present on its distal part, extending from the metacone's labial valley to the metastyle. The paracingulum is strong and connected to the protocone. The paraconule is present but very weakly developed. A short precingulum is present on the anterior side of the protocone. The metacone is slightly higher than the paracone. Both paraloph and metaloph are present but weakly developed. The postprotocrista is connected to the metaconule, which is similar in morphology to the metaconule in the M1. The postcingulum and metacingulum have the same characteristics as described for the M1.

**Discussion**

The presence in the material from Venta del Moro of a myodont bat characterized by the presence of a paraloph and metaloph in the upper molars, without talon and hypocone, may be referred to the genus *Myotis* (Sevilla 1988). These features enable to discard other myodont genera such as *Plecotus*, *Eptesicus*, *Miostrellus* and *Paleptesicus*, present in the European fossil record (Sevilla 1988; Horáček 2001). In addition, this material from Venta del Moro differs from other morphologically similar genera (or subgenera) such as *Leuconoe* or *Stehlinia* by lacking a well-developed paraconule (Godawa Stormark 1998; Ziegler 2000, 2003). Although most *Myotis* species the metalophs, paralophs, metaconules and paraconules are usually absent, some less derived species retain these structures (Godawa Stormark 1998).

The genus *Myotis* is highly diverse; but size groups in which certain morphological features are shared can be distinguished (Rosina & Kruskop 2011). Thus, the smaller sized species have delicate molars in which paraloph and metaloph are present, whereas the larger sized species have robust molars without paraloph or metaloph. The material from Venta del Moro of this genus belongs to middle size group, with a size similar to *M. podlesicensis* (Rosina & Kruskop 2011).

The presence of both metaloph and paraloph in this material from Venta del Moro makes it distinct from the extant species *Myotis myotis* (Borkhausen, 1797), *Myotis blythi* (Tomes, 1857), which are larger, or from *Myotis nattereri* (Kuhl, 1818), a middle-sized species. It also differs in this sense from fossil species such as *Myotis intermedius* Ziegler, 2000, *Myotis reductus* Ziegler, 2003 and *Myotis darebellidensis* Gunnell et al., 2011 (Ziegler 2000; Gunnell et al. 2011). From *Myotis boyeri* Mein, 1964 it also differs in the morphology of the postprotocrista, which is continuous with the distal cingulum (Ziegler 2003), a rare feature in *Myotis* but found in other vespertilionids such as *Plecotus*. In *Myotis bavaricus* Ziegler, 2003 and in recent *Myotis emarginatus* (Geoffroy, 1806), weak paralophs and metalophs are present (Ziegler 2003). However, in *M. bavaricus* the lingual cingulum of the upper molars is continuous and the protocone is more rounded than in our material.

From all known species, this material coincides with the size and morphology seen in the Early Pliocene species *M. podlesicensis*, described from the Polish locality of Podlesicze, which has both paraloph and metaloph in the upper molars in similar position and similar development (Rosina & Kruskop 2011). These authors propose an African origin for this clade, characterized by primitive features such as the presence of paralophs and metalophs. According to them, the expansion of the group must have happened at the end of the Miocene or earliest Pliocene, which makes Venta del Moro the site containing one of the oldest representatives of this clade in Europe.

**Genus** Nyctalus Bowdich, 1825  
**Nyctalus** sp. (Figure 2(J))

**Locality** – VVmA  
**Material** – 1 p4 (VVmA-2840, MGUV-32835)  
**Measurements** – L: 1.39 x W: 1.52
Description

p4 – Subtriangular outline on occlusal view. The cingulum is thick and encloses the molar. There is a cusp on the anterolingual side, and a less developed posterolingual cusp. The cingulum bears a small valley on its posterolabial side.

Discussion

A very compressed p4 is a typical feature of both the genera Nyctalus and Vespertilio, but the well-developed mesiocingual cusps are typical of Nyctalus (Rosina & Sinitza 2014; Rosina 2015). Thus, this single remain is referred to the genus Nyctalus. Its size is close to that of extant N. lasiopterus, the largest of the three species currently found in continental Europe. The fossil record of this genus is extremely rare, mostly described in Quaternary localities and belonging to smaller taxa (Tata & Kotsakis 2005; López-García et al. 2009; Boston et al. 2015) being the first Miocene record of a noctule reported in Spain.

Vespertilionidae indet. (Figure 2(K))
Locality – VVMa
Material – 1 m1,2 (VVMa-2827, MGUV-32822)

Description

m1,2 – Fragment of myodont tooth, the trigonid is absent. The entocristid is straight. The hypoconulid is independent and well developed. The labial cingulum is wide.

Discussion

The myodonty is a distinctive feature of the lower molars of some insectivorous bats, useful to distinguish between different vespertilionid genera (Menu & Sigé 1971; Sevilla 1988). Although M. podlesicensis found in the same site also has myotodont lower molars, specimen VVMa-2827 cannot be assigned to it because of its considerably larger size. Thus, this specimen must belong to a further bat species represented in Venta del Moro A by this single remain.

Palaeoecological and palaeobiogeographical considerations

Fossil bats are less common in fluviolacustrine sediments than other small mammals such as rodents or insectivores. In Venta del Moro they represent approximately 0.005% of the small mammal remains. The bat record in fluviolacustrine and karstic sites does not differ only in abundance of remains, but also in taxonomical content (Sigé & Legendre 1983), hampering the comparison of the content coming from different sites. As a general rule, karstic sites are dominated by Rhinolophidae and cave-dwelling forms of Vespertilionidae (Rosina & Sinitza 2014). However, the assemblage from Venta del Moro is a mixture of non-cave dwellers (Pipistrellus and Nyctalus) and cave dwellers (Myotis and Rhinolophus), and represents more clearly an assemblage of scatological origin (Kowalski 1995).

Turolian and Ruscinian bats are poorly known, when compared to the available data from other small mammals. Their record in Spain remains very scarce making these new findings from Venta del Moro an interesting contribution. Karstic sites of Turolian age in Spain where fossil bats have been found are rare. For instance, in Cala Es Pous, a single m1 was found, ascribed to R. cf. grivensis (Pons-Moyà et al. 1981); in Salobreña, a more diverse assemblage has been indicated in its faunal list, with the taxa Rhinolophus sp., Myotis cf. boyeri, Myotis sp., Miniopterus cf. fossilis and Tadarida sp. (Aguiar et al. 1984), but which are still to be described in detail. Pliocene karstic localities with bats comprise the Early Pliocene site of Almenara Mb, with Myotis sp. and Miniopterus fossilis (Mansino et al., forthcoming 2015), Layna, with R. delphinensis and Vespertilionidarium div. sp. (Sigé & Legendre 1983), and the Late Pliocene site of Almenara Casablanca 4, until now the most diverse bat record of the Spanish Pliocene, with twelve different bat species belonging to the genera Rhinolophus, Myotis, Miniopterus, Plecotus, Eptesicus and Pipistrellus, with a clear dominance of the rhinolophids (Agustí et al. 2011). Even more rare are the fluviolacustrine sites that have yielded bat remains. Such is the case of Puente Minero, of Turolian age (Alcalá et al. 1991) with a single bat remain, an M2 assigned to R. delphinensis, an undescribed tooth from Maluenda 1B of Pliocene age (MN14; van Dam & Rubio 2003). More distant in age are some karstic and fluviolacustrine localities of Early and Middle Miocene age of Fuenmayor (Martínez-Salanova 1987), Rincón del Bu, Nasa 1, Barranco de Tudela and Barranco del Fraile (Murelaga et al. 2004), Casaetón 1A y 2B (Sevilla 2002), Melero-20 (Murelaga et al. 2008), La Retama (Álvarez Sierra et al. 2006) and Escobosa de Calatanañor (Sesé 1986). This scanty record makes impossible to compare the different assemblages and to interpret the assemblage of Venta del Moro within the chiropteran fauna of Spain during the Turolian.

Concerning the taxonomic representation found in the assemblage from Venta del Moro, it is interesting to see that although bat remains are very scarce in abundance compared to other mammals, they represent a relatively high species richness that provide interesting information. Thus, although some modern pipistrelles are clearly opportunistic taxa in terms of their roosting ecology, and for this reason can be found in a wide variety of environments (Rosina & Sinitza 2014), other pipistrelles as well as other taxa found in Venta del Moro such as Nyctalus or Rhinolophus are more restrictive concerning their roosts (rock crevices, caves, trees) and hunting areas (Rosina & Sinitza 2014; Woloszyn 1987) providing environmental information. A predominantly open environment under warm climatic conditions is in accordance to the presence of the middle-sized Rhinolophus, reinforced by the presence of Myotis podlesicensis. Smaller forested patches, however, are inferred from the presence of Nyctalus and, perhaps Pipistrellus.

The presence of Myotis podlesicensis in the Venta del Moro assemblage is also of interest. Besides being the first record of this species in Spain, it provides additional evidence of African influence in the Late Miocene fauna of Spain. M. podlesicensis was first described in the Polish site of Podlesice (Early Pliocene, MN13/14), a karstic locality for which a Mediterranean climate was inferred (Woloszyn 1987; Rosina & Kruskop 2011). This taxon has been related to the myotid Ethiop clade (sensu Stadelmann et al. (2004)), and consequently considered of African origin. Thus, M. podlesicensis represents a new addition to the diverse vertebrate assemblage (fishes, reptiles and mammals) of African ancestry present in Venta del Moro. Regarding
the faunal interchanges between the Iberian Peninsula and Africa, the different authors agree that it was previous to the Messinian Salinity Crisis, although there are different hypothesis proposing one or various migration events (Agustí et al. 2006; Van der Made et al. 2006; Minwer-Barakat et al. 2009; Gibert et al. 2013; García-Alix et al. 2016). The record of *M. podlesicensis* in Venta del Moro at an earlier age than that of Podlesice fits well with this African origin and subsequent expansion of the species through Europe.

Further evidence supports these interpretations. The palynological data from Venta del Moro, indicates predominance of steppe-like landscapes dominated by herbaceous plants, developed within a dry climate that eventually became slightly more humid. The record of diversified hygrophyte elements also indicates the local presence of wetland areas with tree trenches (Casas-Gallego et al. 2015). This landscape fits well with the type of bats found in the assemblage; a variety of hunting grounds would be available for taxa with different foraging preferences, with predominance of open landscapes. These bats became the prey of the predator or predators that gave place to the fossil assemblage.

**Conclusions**

Although bats are one of the less abundant mammal orders groups represented in Venta del Moro, this mammal order is represented in the site by a relatively high number of species, as five different taxa have been identified. This assemblage provides the largest collection of Turolian bats from an Iberian fluvo-lacustrine site described to the moment, comprising four species belonging to the families Vespertilionidae and Rinolophidae, two of which are new. With the description of this material, the preliminary faunal list of these localities is completed by adding to it the Chiroptera, which had not been included in the previous papers dealing with the fauna from Venta del Moro.

The list of species comprises the following taxa: *Rhinolophus antoni* sp. nov., *Pipistrellus rouresi* sp. nov., *Myotis podlesicensis*, *Nyctalus* sp. and Vespertilionidae indet.

The bat assemblage of Venta del Moro shows the low abundance in bat remains expected in a fluvo-lacustrine locality as well as the taxonomical disparity resulting from a scatological origin.

Venta del Moro is the first Spanish locality where *M. podlesicensis* has been identified. Accordingly, this record becomes the southernmost and oldest record of this species in Europe, providing support for an African origin of this taxon.

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**References**


Gómez-Canero AR, Hernández-Fernández M, Alzheimer-Sierra MA. 2011. Biogeographic provincialism in rodent faunas from the Iberocccitanian Region (southwestern Europe) generates severe diachrony within the Mammalian Neogene (MN) biocloronologic scale during the Late Miocene. Palaeogeogr Palaeoclimatol Palaeoecol. 307:193–204.

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