


## Article

## A relict tropical forest bat assemblage from the early Miocene of the Ribesalbes-Alcora Basin (Castelló, Spain)

Vicente D. CRESPO<sup>1,2,3\*</sup> , Paloma SEVILLA<sup>4</sup>, Plini MONTOYA<sup>5</sup> and Francisco J. RUIZ-SÁNCHEZ<sup>3,5,6</sup><sup>1</sup> División de Paleontología de Vertebrados, Universidad Nacional de la Plata Facultad de Ciencias Naturales y Museo (CONICET), Paseo del Bosque s/n, B1900FWA La Plata, Argentina.<sup>2</sup> Museo Paleontológico de Alpuente, Avenida San Blas 17, 46178, Alpuente, Spain.<sup>3</sup> Museu Valencià d'Història Natural, L'Hort de Feliu, BOX 8460, 46018, Alginet, Spain.<sup>4</sup> Departamento de Paleontología, Universidad Complutense de Madrid, 28040, Madrid, Spain.<sup>5</sup> Departament de Botànica i Geologia, Universitat de València, 46100, Burjassot, Spain.<sup>6</sup> INCYT-UPSE, Universidad Peninsula de Santa Elena, EC240150, Santa Elena, Ecuador.\*Corresponding author Email: [vidacres@gmail.com](mailto:vidacres@gmail.com)

**ABSTRACT:** We present the bat assemblage from the early Miocene (MN4, 16.9–15.95 MY) basin of Ribesalbes-Alcora, which has yielded the remains of ten chiropteran taxa. Bat assemblages are rarely recovered in the fluvio-lacustrine fossil record. A bat species described in this work, *Cuvierimops penalveri* sp. nov., is a new form of a typically Oligocene free-tailed bat. In addition, the other molossids *Hydromops helveticus*, *Rhizomops* cf. *brasiliensis*, *Chaerephon* sp., *Tadarida* sp., and the vespertilionids *Myotis* cf. *intermedius* and *Miostrellus* aff. *petersbuchensis*, as well as undetermined fossils ascribed to the genera *Submyotodon*, *Plecotus*, and *Rhinolophus* are described. This is the first record of the genus *Rhizomops* in the early Miocene; the genus *Cuvierimops* is the first recording from the Neogene, while the 'Lazarus taxon' *Chaerephon* is the first fossil record of this genus, registered previously only in Holocene deposits. This bat assemblage with a high abundance of molossids is typical from the early Oligocene of western Europe, while in the early Miocene from Europe the molossids are scarce. The abundance of these bats is consistent with the presence of a tropical forest surrounding a paleolake. The fossils from the Ribesalbes-Alcora Basin represent the most complete bat assemblage of the Iberian Peninsula during this age, and significantly increase our knowledge about the early Miocene bats of Europe.

**KEY WORDS:** Chiroptera, *Cuvierimops penalveri* sp. nov., Lazarus taxa, palaeoecology, systematics.

Bats constitute one of the most diverse recent mammal groups; indeed, they represent over 20% of all extant species (Simmons 2005). In contrast, their fossil record is notably incomplete (Teeling *et al.* 2005; Eiting & Gunnell 2009; Brown *et al.* 2019). In the Mio–Pliocene of Spain (Table 1), their record mainly consists of indeterminate taxa presented as faunal lists (Sevilla 2002).

Despite their current abundance, fossil bats are one of the least common groups in fluvio-lacustrine sediments and typically only represent 0.01% or less of the small mammal assemblages (Sigé & Legendre 1983; Sevilla 2002; Crespo *et al.* 2018a). The scarcity of bats in the Neogene fluvio-lacustrine record enhances the importance of each discovery to improve the knowledge of this group and its biogeographic history. The relative abundance of chiropterans in the Ribesalbes-Alcora Basin (eastern Spain) provides an exceptional opportunity to understand bat assemblages in their ecological environment during the early Miocene in Europe.

### 1. Geological setting

The Ribesalbes-Alcora Basin is an intramontane basin (Fig. 1) located in the eastern Iberian Peninsula (Agustí *et al.* 1988).

The sections that yielded bat fossils include Mas dels Coixos, Mas de Torner, Barranc de Campisano, Foietta la Sarra, Mas d'Antolino B, and Corral de Brisca, all located in the Campisano ravine. They consist of nearly 120 m of grey mudstone, sandstone, and limestone belonging to the 'Unit Three' *sensu* Anadón (1983) (Crespo *et al.* 2019a).

Fossil mammals in the Ribesalbes-Alcora Basin were first described by Agustí *et al.* (1988). During the recent campaigns carried out between 2008 and 2011, up to 45 new mammal sites were found in this basin near the classic localities described by Agustí *et al.* (1988). It is important to note that we have not yet been able to find the original sites described by these authors (Crespo *et al.* 2019a). The recent campaigns have provided the southernmost occurrence of the herpetotheriid *Amphiperatherium frequens* (von Meyer, 1846) (Furió *et al.* 2012; Crespo *et al.* 2020), a new species of the dimydid *Plesiodimylylus ilercavonicus* Crespo, Furió, Ruiz-Sánchez & Montoya, 2018 (Crespo *et al.* 2018b), talpids (Crespo *et al.* 2019b), as well as sorcids and heterosoricids (Crespo *et al.* 2019c), erinaceids (Crespo *et al.* 2020), among other findings.

According to Crespo *et al.* (2019a), the study of the mammalian assemblages from these sections resulted in two biozones

**Table 1** Mio–Pliocene sites from Spain with remains of bats, excluding this work (Pons-Moyà *et al.* 1981; Sigé & Legendre 1983; Aguilar *et al.* 1984; Sesé 1986; Martínez-Salanova 1987; Alcalá *et al.* 1991; Robles *et al.* 1991; Sevilla 2002; Dam & Rubio 2003; Murelaga *et al.* 2004a, b, 2008; Álvarez-Sierra *et al.* 2006; Agustí *et al.* 2011; Mansino *et al.* 2016; Hoek Ostende *et al.* 2017; Crespo *et al.* 2018a).

Age	Sites
Early Miocene	Fuenmayor, Buñol, Rincón del Bu 1, Nasa 1, Barranco de Tudela, Barranco del Fraile, and Alto de Ballester 1
Middle Miocene	La Retama, Casetón 1A and 1B, Melero 20, and Escobosa de Calatañazor
Late Miocene	Puente Minero, Cal es Pou, and Venta del Moro
Pliocene	Layna, Salobreña, Maluenda 1B, Almenara-Casablanca 4, and Almenara Casablanca Mb

correlated with the local biozone C from Calatayud-Montalbán Basin (Meulen *et al.* 2012). The first local biozone is characterised by the association of *Ligerimys florancei* Stehlin & Schaub, 1951, together with *Megacricetodon primitivus* (Freudenthal, 1963) and *Democricetodon decipiens* (Freudenthal & Daams, 1988), in Mas dels Coixos, Mas de Torner, Barranc de Campisano, and the earlier part of Mas d'Antolino B. The other local biozone is characterised by the replacement of *L. florancei* by *Ligerimys ellipticus* Daams, 1976, in the later part of Mas d'Antolino B, Foietta la Sarra, and Corral de Brisca. Both biozones are indicative of an early Miocene age (lower Aragonian, MN4, ca.16.6–16 Ma, according to Meulen *et al.* 2012; Crespo *et al.* 2019a).

## 2. Materials, methods, and abbreviations

The fossils under study are currently held at the Museum of the University of Valencia of Natural History (MUVHN) with the field labels MCX-, MTR-, BC-, FS-, MAB-, and CBR-. We have followed the nomenclature (Fig. 2) and measurement methods of Sevilla (1988), Fracasso *et al.* (2011), and Gunnell *et al.* (2011). Biozonation follows the MN system described in Mein (1999, 2000). We follow Maitre's (2014) definition of myotodony, submyotodony, and nyctalodony.

**Abbreviations:** BC, Barranc de Campisano; CBR, Corral de Brisca; FS, Foietta la Sarra; L, length; MAB, Mas d'Antolino B; MCX, Mas dels Coixos; MGVU, Museu de Geologia de la Universitat de València; MN, European Neogene land mammal units; MTR, Mas de Torner; W, width. Lower teeth are indicated as i, c, p, and m, and upper teeth as I, C, P, and M.

## 3. Systematic palaeontology

Order Chiroptera Blumenbach, 1779

Suborder Yangochiroptera Koopman, 1984

Superfamily Vespertilionoidea Gray, 1821

Family Molossidae Gervais, in de Castelnau, 1855

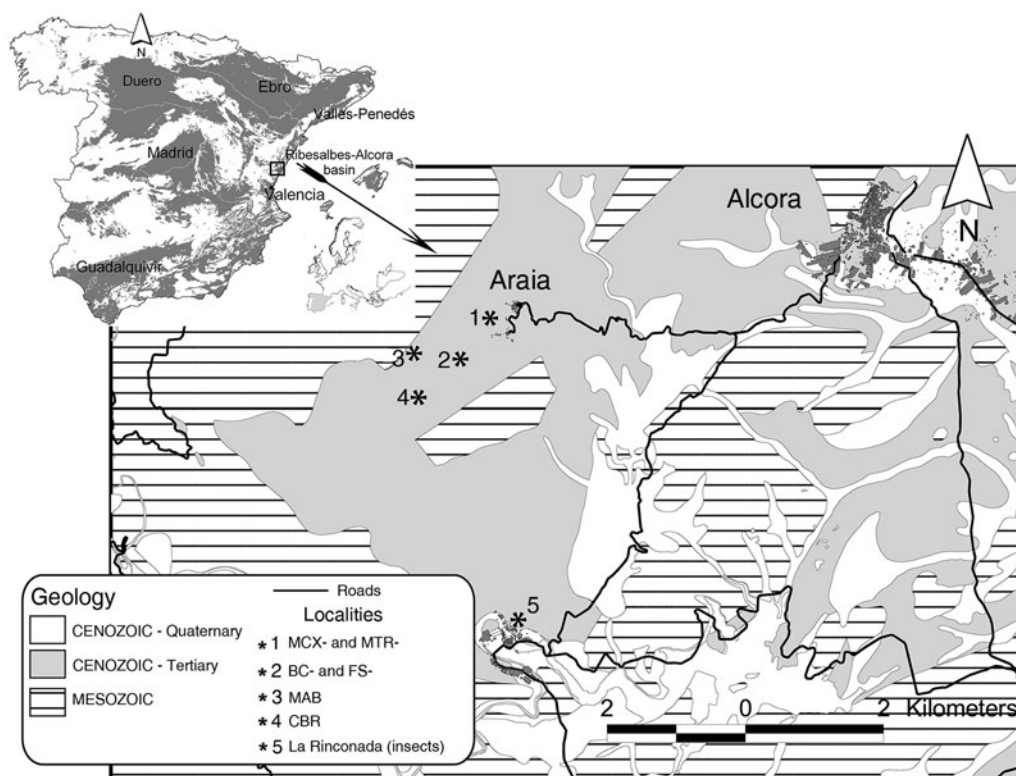
Genus *Cuvierimops* Legendre & Sigé, 1982

*Cuvierimops penalveri* sp. nov.

(Fig. 3a, b)

**Type species.** *Cuvierimops parisiensis* Cuvier in Pictet, 1844 2017 *Tadarida (Rhizomops) cf. brasiliensis* (in part) Crespo, 2017.

**Etymology.** Named after Enrique Peñalver, our colleague, friend, and one of the scientists who studied insects from the classical sites of Ribesalbes-Alcora Basin.



**Figure 1** Cenozoic basins from Spain, with location of the Ribesalbes-Alcora Basin and the schematic distribution of sediments. Abbreviations: MCX = Mas dels Coixos; MTR = Mas de Torner; BC = Barranc de Campisano; FS = Foietta la Sarra; MAB = Mas d'Antolino B; CBR = Corral de Brisca. La Rinconada is the classical fossil-lagerstätte site with remains of insects, plants, and amphibians. Modified from Crespo *et al.* (2019a). Scale bar = 2 km.

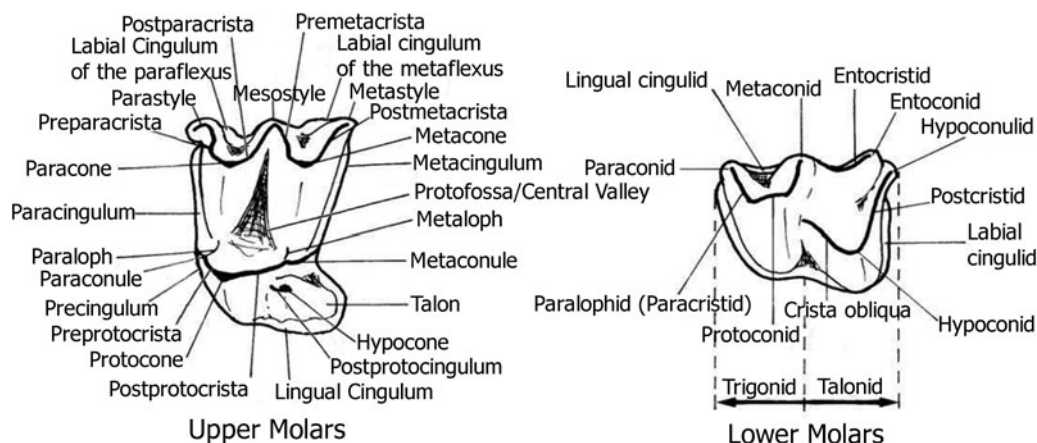


Figure 2 Terminology of the Chiroptera teeth after Sevilla (1988), Fracasso *et al.* (2011), and Gunnell *et al.* (2011).

**Holotype.** Right M2, MAB11-99 (MGUV-38486;  $1.37 \times 1.87$ ).

**Type locality.** Mas d'Antolino B 11, Ribesalbes-Alcora Basin, Spain, MN4, early Miocene.

**Material and measurements.** 1 M2 (MAB11-103; MGUV-38490); 2 M3 (MAB11-98 (MGUV-38485); MAB11-100 (MGUV-38487)). Doubtful remains: 1 c (MAB11-140 (MGUV-38527);  $0.86 \times 0.81$ ); 1 p3 (MAB11-138 (MGUV-38525);  $0.74 \times 0.52$ ).

**Diagnosis.** The youngest and smallest species of *Cuvierimops*, upper molars with less developed lingual cingula.

**Differential diagnosis.** Differs from all other species of *Cuvierimops* in terms of its smaller-sized upper molars and less developed lingual cingula from *Rhizomops* in its M1/2 conical hypocone.

**Stratigraphic and geographic range.** MN4, early Miocene; Ribesalbes-Alcora Basin, eastern Spain.

### 3.1. Description

**M2.** Tooth with a subquadrate outline in occlusal view. The parastyle is curved. The paracingulum starts close to the parastyle. It connects lingually to the protocone and continues with the postprotocrista and the metacingulum. A well-developed talon is present; the hypocone is a tall cusp and the postprotocrista is a small crest between the protocone and metaconule. The hypocone has a small precingulum, while the lingual cingulum is poorly developed in one specimen and divided into two

cingula in the other. The metaloph and the paraloph are developed. The metastyle shows a right-angle shape with the postmetacrista.

**M3.** The teeth are broken and the parastyle is not preserved; their posterior part is reduced regarding the upper molars of the other. The metastyle is absent and the premetacrista and metacone are well developed and similar in length to the postparacrista. The paracone and the metacone are of similar height. The paraloph is developed. An independent paracingulum is present and ends at the upper part of the protocone. A short labial cingulum on the posterior part of the protocone is present.

### 3.2. Description of the tentatively referred material

**c.** A broken tooth without the main cusp. It presents a triangular outline in occlusal view. The cingulid is continuous, surrounding most of the base of the tooth; it is briefly interrupted on its posterior margin where the cingulid has thickened and forms a small triangular cusplule. The root is wider than it is elongated.

**p3.** An elongated tooth with only one root preserved; a single main cusp and a well-developed cingulid. In the posterior part of the tooth, a small basin divided by a crest is present between the cusp and the cingulid.

### 3.3. Discussion

*Cuvierimops* is a typical genus from the early Oligocene of Europe. Until now, it was considered to have disappeared at the end

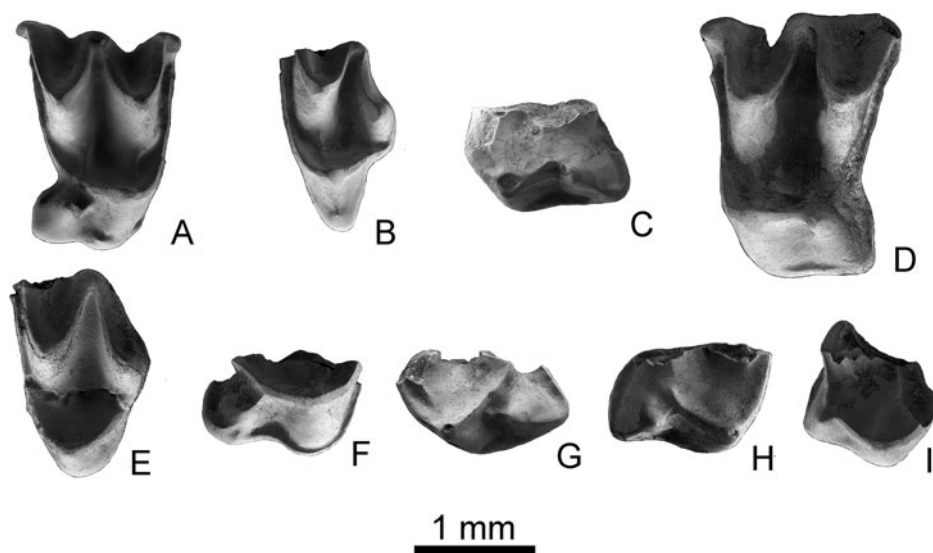


Figure 3 Molossid teeth from the Ribesalbes-Alcora Basin. *Cuvierimops penalveri* sp. nov.: (A) right M2 (MAB11-99; holotype); (B) left M3 (MAB11-100). *Hydromops helveticus*: (C) left M1 (MAB0A-85); (D) left M2 (MAB5-386); (E) left M3 (MAB5-397). *Rhizomops cf. brasiliensis*: (F) right M2 (MAB5-443). *Chaerephon* sp.: (G) left M1 (MAB11-104); (H) right M2 (MAB5-437). *Tadarida* sp.: (I) right M2 (MTR2-37). Scale bar = 1 mm.



of the Oligocene (MP26, Saint-Privat-des-Vieux, France; Maitre 2014; Vianey-Liaud *et al.* 2014). It is characterised by a strong hypocone on the M1 and M2, isolated from the posprotocrista.

*Cuvierimops* differs from *Tadarida* in the presence of a metaloph and a strong paraloph, although both genera share a cusped hypocone (Legendre 1985). On the other hand, the extant *Rhizomops* differs from its ancestor *Cuvierimops* with better development of the talon and the presence of a crestiform hypocone on the upper molars, which has only been detected in some specimens of *Cuvierimops legendrei* Maitre, 2014. This species is likely the ancestor of *Rhizomops* (Legendre 1985; Maitre 2014).

Maitre (2014) describes one lineage of this genus characterised by the simplification of the anterior part of the jaw through anteroposterior compression of the premolars, the appearance and the increasing proportion of submyotodonty, and, subsequently, myotodonty on the lower molars, as well as an increase in size (Table 2). This lineage includes the species *C. parisiensis* and *C. legendrei*. The small size of *Cuvierimops penalveri* sp. nov. enables us to discard the possibility that it might pertain to this lineage. Nevertheless, Maitre (2014) remarks on the existence of a small undetermined species described by Sigé (1995) from Le Garouillas (29.1–27.6, MP25, France), which has been considered to be one of the last representatives of the genus. Due to its small size, we suggest that *C. penalveri* sp. nov. belongs to a new second lineage together with *Cuvierimops* indet. A from Le Garouillas, and that this lineage was the only one to survive the end of the Oligocene.

Genus *Hydromops* Legendre, 1984

*Hydromops helveticus* (Revilliod, 1920)

(Fig. 3c–f)

2017 *Miniopterus* sp. nov. Crespo, 2017.

2017 *Mormopterus* (*Hydromops*) cf. *helveticus* (in part) Crespo, 2017.

**Localities.** MAB0A, MAB5.

**Table 2** Measurements of the M2 of the different species, subspecies, and populations of the genus *Cuvierimops* (Maitre 2014; this publication). Abbreviations: L = length; W = width.

Site	Measurement	<i>n</i>	Min.	Med.	Max.
<i>Cuvierimops parisiensis intermedius</i> (MP17b-18)					
Coyrou 3	L	2	1.54	1.57	1.61
	W	2	2.04	2.1	2.17
Les Sorcières	L	2	1.53	1.67	1.81
	W	2	2.14	2.24	2.34
Perrière <sup>1</sup>	L	93	1.07	1.59	1.84
	W	93	1.87	2.2	2.49
Malpérié	L	14	1.51	1.69	1.78
	W	14	1.99	2.18	2.31
Théron	L	3	1.71	1.75	1.79
	W	3	2.16	2.19	2.21
Crégols	L	1		1.76	
	W	1		2.32	
<i>Cuvierimops parisiensis</i> (MP19)					
Rosières 2	L	13	1.67	1.72	1.841.27
	W	13	2.13	2.25	2.420.80
Escamps	L	3	1.59	1.62	1.64
	W	3	1.98	2.06	2.2
<i>Cuvierimops legendrei</i> (MP22)					
Baraval	L	16	1.6	1.73	1.83
	W	16	2.25	2.35	2.49
<i>Cuvierimops penalveri</i> sp. nov. (MN4)					
Mas d'Antolino B 11	L	1		1.37	
	W	1		1.87	

<sup>1</sup>In this population, in specimens with the same length/width as Ribesalbes-Alcora Basin material, the width/length is considerably larger.

**Material and measurements.** 3 m1 or m2 (MAB0A-13 (MGUV-36900); MAB5-428 (MGUV-25218); -x1.40; MAB5-746 (MGUV-38169); -x1.24); 1 M1 (MAB0A-85; MGUV-36972); 1 M2 (MAB5-386 (MGUV-25176); 1.71 × 2.20); 1 M3 (MAB5-397 (MGUV-25187); 1.19x-). Doubtful remains: 1 mandible (MAB0A-17; MGUV-36904), 1 c (MAB5-434 (MGUV-25224); 1.01x-); 1 P2/P3 (MAB5-903 (MGUV-38326); 0.68 × 0.78).

### 3.4. Description

**m1 or m2.** Only the medium-sized trigonid is preserved. The paralophid is curved. The trigonid basin is open lingually. The metaconid and the paraconid are of similar size and are aligned. The protoconid is the highest cusp. The labial cingulid is well developed and straight in lateral view. The crista obliqua meets the trigonid near the centre of the crown.

**M1.** A broken tooth with complex protocone and hypocone. The precingulum is absent. A very weak metaloph is present; the paraloph is better developed. The postprotocrista links the protocone with the hypocone, the second cusp being lower. The lingual cingulum is well developed. The posterior crest of the hypocone joins the metacingulum.

**M2.** Tooth with a subrectangular outline in occlusal view. The parastyle is straight. The paracone and the metacone are similar in size and connected by a well-developed mesostyle. Only the valley of the paracone (paraflexus) shows a notch in the labial side of the tooth. The paracingulum almost joins the parastyle; lingually, it connects to the protocone. The paraloph is poorly developed. A well-developed talon is present. The hypocone is a poorly developed cusp; the postprotocrista is reduced to a small crest between the protocone and hypocone. The protocone has a narrow lingual and posterior cingulum linked to the metastyle. The metaloph is not present. The metastyle is broken.

**M3.** The tooth is broken and shows a reduced posteriorly, with no metastyle present. The parastyle is broken. The premetacrista and the metacone are well developed; the former is as long as the postparacrista. The paracone and the metacone are of similar height. The paraloph is well developed. An independent paracingulum is present, ending at the top of the protocone.

### 3.5. Description of the tentatively referred material

**Mandible.** Fragment of mandible with a large mental foramen, situated between the canine and the p2, near the alveolar margin.

**c.** Fragment of tooth with a principal cusp and a broken well-developed cingulid.

**P2/P3.** Subtriangular medium tooth; its principal cusp shows three sides, with a well-developed cingulum and a small cusp in the posterolingual part of the cingulum.

### 3.6. Discussion

The genus *Hydromops*, originally a subgenus of *Mormopterus*, is represented in the European record by two species, *Hydromops stehlini* (Revilliod, 1920) and *M. helveticus* (Storch 1999). The first one was recorded from the nearby locality of Buñol (Robles *et al.* 1991). Here we align with the common opinion (Legendre 1985; Sigé *et al.* 1991; Storch 1999; among others) that considers these species as likely belonging to the same lineage, the first of which is found in MN1-2, while the second is distributed from MN3 to MN7/8 (Storch 1999).

This genus is characterised by an open protofossa, the absence of the metaloph, a weak paraloph, and the hypocone included in the postprotocrista (Legendre 1984a). The crestiform hypocone differs from those shown by *Mormopterus* (*Neomops*) *faustoi* ('*Tadarida*' *faustoi* after Paula Couto, 1956) (Legendre 1985) and *Cuvierimops* (Maitre 2014). *Hydromops helveticus* differs from the recent *Hydromops* species in the absence of metaloph, the posterior opening of the protofossa, and the connection

between the hypocone and the protocone (Legendre 1985). In general, the material from the Ribesalbes-Alcora Basin is similar in morphology and size to the material described from Anwil (Switzerland, MN7/8; Engesser 1972).

Genus *Rhizomops* Legendre, 1984

*Rhizomops brasiliensis* (Geoffroy, 1824)

*Rhizomops cf. brasiliensis*

(Fig. 3g)

2017 *Chaerephon* sp. Crespo, 2017.

**Locality.** MAB5.

**Material.** 1 M2 (MAB5-443; MGUV-25233).

### 3.7. Description

**M2.** Only a complex hypocone–protocone is preserved. The protofossa is closed. The paraloph and the metaloph are present. The hypocone is included in the postprotocingulum, which makes contact with the postprotocrista. The talon is well developed. The lingual cingulum is also well developed and has contact with the precingulum.

### 3.8. Discussion

*Rhizomops* species are characterised by M1/2 with a closed protofossa and the presence of a metaloph and a paraloph. Overall, these species are very similar to those of the stratigraphically older genus *Cuvierimops*. They differ from the latter in having a crestiform hypocone, which is included in the postprotocingulum; the talon is better developed, whereas the lingual cingulum is less developed in comparison (Legendre 1985; Maitre 2014). Accordingly, the material from MAB5 cannot be assigned to *Cuvierimops*, nor to the genus *Tadarida*, because of the presence of a paraloph and a metaloph in the Ribesalbes-Alcora tooth – two features that are absent in *Tadarida* upper molars (Legendre 1984a). Other similar genera can be discarded: *Sauromys* has no lingual cingulum and *Otomops* by its different morphology of the talon, being more similar to the first of the genera (Legendre 1984a; Hand 1990). For discussion about whether European fossils belong to a *Rhizomops* or a different but convergently evolved taxon, see Owen *et al.* (1990).

The record of *Rhizomops cf. brasiliensis* is scarce in the Paleogene and Neogene fossil record of Europe, with the only two records originating from Venelles (latest Oligocene, MP30, France) and Collet Redon (middle Miocene, MN7/8, France) (Storch 1999; Maitre 2014). On the other hand, morphological studies involving more character systems of the cranium, mandible, and molecular genetic studies suggested that *R. brasiliensis*, although found today only in America, is a member of an Old World *Tadarida* clade closely related to *Tadarida aegyptiaca*, *Sauromys*, and *Otomops*, and separated from the New World *Tadarida*'s clade (Freeman 1981a; Ammerman *et al.* 2012). Therefore, we have provisionally assigned this tooth to *R. cf. brasiliensis*, awaiting new material collected in the Ribesalbes-Alcora Basin that might enable a more precise description and characterisation of this taxon.

Genus *Chaerephon* Dobson, 1874

*Chaerephon* sp.

(Fig. 3h–i)

2017 *Tadarida (Rhizomops) cf. brasiliensis* (in part) Crespo, 2017.

2017 *Mormopterus (Hydromops) cf. helveticus* (in part) Crespo, 2017.

**Localities.** MAB5 and MAB11.

**Material and measurements.** 1 M1 (MAB11-104; MGUV-38491). 1 M2 (MAB5-437; MGUV-25227). Doubtful remains: 1 c (MAB5-427 (MGUV-25217); 1.15 × 1.18), 2 p3 (MAB5-158 (MGUV-

24948); 0.57 × 0.71; MAB5-907 (MGUV-38330): 0.5 × 0.82), 3 p4 (MAB5-431 (MGUV-25221): 0.86 × 0.91; MAB5-764 (MGUV-38187): 0.89 × 0.7; MAB5-903 (MGUV-38326)), 1 I (MAB5-772 (MGUV-38195): 0.68 × 0.48), 1 C (MAB5-426 (MGUV-25216): 1.18 × 1.56; MAB5-912 (MGUV-38335): 1.18 × 1.58).

### 3.9. Description

**M1.** Only a complex hypocone–protocone is preserved. The protofossa is almost closed. The paraloph is well developed, while the metaloph is less apparent. The hypocone is included in the postprotocingulum that makes contact with the metacingulum. The talon is well developed. The lingual cingulum is also well developed and the precingulum is short in length.

**M2.** Incomplete tooth with well-developed protocone and hypocone. The posterior opening of the protofossa is wider than in the M1. The hypocone is included in the postprotocingulum, which is connected to the postprotocrista. The paraloph and the metaloph are small in size. The talon is well developed. The lingual cingulum is present but more poorly developed than in the M1; a short precingulum is present.

### 3.10. Description of the tentatively referred material

**c.** Subrectangular outline in occlusal view. The cingulid is continuous around the tooth, although less developed on the lingual side and protruding on the anterolabial part of the tooth. The cusp is straight and displays a distinct crest on its anterior side. A strong triangular root is preserved.

**p3.** A large subtriangular tooth, whose main cusp has three sides with a well-developed cingulum that bears a cuspule on its posterolingual margin.

**p4.** A subtriangular tooth with a well-developed cingulid, elevated anteriorly with the lingual side being wider than the labial side. As for the p3, the cingulid protrudes on the posterolingual side, forming a small cusp.

**I.** Tooth elongated with two cusps; the anterior cusp is better developed than the posterior cusp; the cingulum is well developed, except on the anterolingual side where it is absent.

**C.** A large tooth, subtriangular in occlusal view. A well-developed continuous cingulum is present around the tooth; the mesio-lingual part of the cingulum thickens and protrudes. A single cusp is present, in which a postero-lingual crest that runs from the tip to the base of the crown is clearly observable.

### 3.11. Discussion

The genus *Chaerephon* is the only molossid in which the protofossa may be either closed or open in the M1–2, depending on whether or not the postprotocrista reaches the metacingulum (Legendre 1984a). In contrast, in *Mops* and *Hydromops*, the postprotocrista is always in contact with the hypocone (Legendre 1984a, b). In our material, the two morphotypes are observed: the M1 has a closed protofossa and the paraloph is better developed, while the M2 has an open protofossa and the paraloph is less apparent. In both molars, the metaloph is absent.

*Chaerephon* is currently distributed in Asia, Africa, and Australia (Hand 1990), and, according to Eiting & Gunnell (2009), no fossil specimen exceeding 12,000 years has yet been found. As a result, the teeth excavated at Mas d'Antolino B 5 and 11 are the first pre-Quaternary remains of *Chaerephon* described in the fossil record. For this reason, the genus can be considered thus far to be a stratigraphic 'Lazarus taxon' (Fara 2001) due to the absence of records from the early Miocene to the early Holocene.

Genus *Tadarida* Rafinesque, 1814

*Tadarida* sp.

(Fig. 3j)

2017 *Mormopterus (Hydromops) cf. helveticus* (in part) Crespo, 2017.

**Locality.** MTR2.

**Material.** 1 M2 (MTR2-34 (MGUV-38781) and MTR2-37 (MGUV-38784)).

### 3.12. Description

**M2.** Two fragments of a tooth; one of them has a right-angled parastyle and a tall paracone. The other fragment shows a well-developed protocone and a small hypocone joined by a short postprotocingulum. The postprotocrista connects to the meta-cingulum and closes the protofossa. The paraloph is small. The hypocone has a small posterolingual cingulum that is unconnected to the metacingulum.

### 3.13. Discussion

The species of this genus are characterised by a closed protofossa and a well-developed hypocone isolated from the protocone, as well as by a short postprotocingulum with a well-developed talon (Legendre 1984a).

*Tadarida* is represented by two lineages: among the New World species, the paraloph and the metaloph converge at the lingual side, while the species of the Old World are characterised by a weak paraloph and the absence of a metaloph (Legendre 1984a). Additionally, Legendre (1984a) and Arroyo-Cabrales

*et al.* (2002) indicated that in certain African species, such as *Tadarida lobata* (Thomas, 1891) and particularly in *Tadarida fulminans* (Thomas, 1903) and *Tadarida ventralis* (Heuglin, 1861), the hypocone is smaller than in the other species of the genus.

Some features of the hypocone complex observed in our material, such as a small, low hypocone with a short postprotocingulum and a poorly developed talon, are also characteristic of the African species of *Tadarida*. For this reason, we suggest that this material belongs to an indeterminate species of the African lineage of the genus *Tadarida*. However, the near-contemporary African species *Tadarida rusingae* Arroyo-Cabrales, Gregorin, Schlitter & Walker, 2002 shows a more developed hypocone and postprotocrista (Arroyo-Cabrales *et al.* 2002).

Family Vespertilionidae Gray, 1821

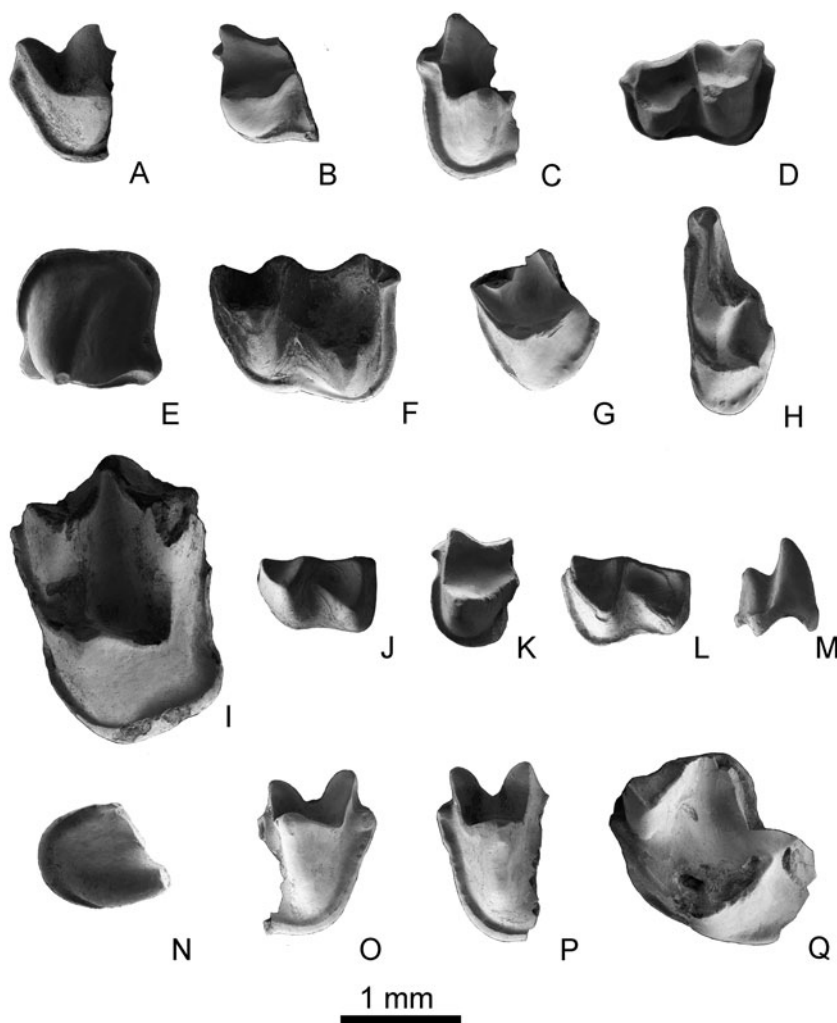
Genus *Submyotodon* Ziegler, 2003

*Submyotodon* sp.

(Fig. 4a–d)

**Localities.** BC1, MAB3, MAB5, and MAB11.

**Material and measurements.** 5 m1 or m2 (MAB3-737 (MGUV-37745): -x 1.26, MAB3-750 (MGUV-37758), MAB3-754 (MGUV-37762): -x1.22, MAB5-747 (MGUV-38170): -x1.32, MAB11-117(MGUV-38504)); 1 m3 (MAB3-725 (MGUV-37733): 1.33 × 1.02). Doubtful remains: 1 c (BC1-169 (MGUV-



**Figure 4** Non-molossid teeth from the Ribesalbes-Alcora Basin. *Submyotodon* sp.: (A) left m1/2 (MAB3-737); (B) right m1/2 (MAB3-750); (C) right m1/2 (MAB11-117); (D) right m3 (MAB3-725). *Myotis cf. intermedius*: (E) left p4 (MAB3-817); (F) left m1/2 (MAB3-752); (G) left M1/2 (MAB3-719); (H) left M3 (MAB3-712). *Miostrellus* aff. *Petersbuchensis*: (I) left M1 (CBR1-38). *Plecotus* sp.: (J) left m1/2 (MAB5-891); (K) right m1/2 (MAB5-381); (L) right m1/2 (MAB5-438); (M) I (MAB5-774); (N) C (MAB5-149). *Rhinolophus* sp.: (O) right m1/2 (MTR2-196); (P) left m1/2 (MAB3-741); (Q) left M1 (MAB3-708). Scale bar = 1 mm.



26249);  $0.85 \times 1.03$ ); 2 p2 (MAB5-430 (MGUV-25220):  $0.84 \times 0.91$ ; MAB5-773 (MGUV-38196):  $0.82 \times 0.84$ ); 1 P2/P3 (MAB5-908 (MGUV-38331):  $0.59 \times 0.60$ ).

### 3.14. Description

**m1 or m2.** Submyotodont, medium-sized teeth. The paralophid is not sharp (it has a U-shape in labial view). The trigonid valley is wide and open lingually. The paraconid and the metaconid are similar in size and both are arranged in line with the dental axis. The protoconid is straight and constitutes the tallest cusp. The labial cingulum is well developed. In both the m1 and m2, the cristid obliqua ends in the middle of the tooth. The entocristid is concave and well developed. The labial valley of the talonid, entoconid, and hypoconid are well developed, the latter cusp being the highest on the talonid. The hypoconulid is poorly developed and the labial cingulid is wide in occlusal view and straight in lateral view.

**m3.** Submyotodont and medium-sized tooth. In occlusal view, the paraconid and the metaconid are parallel with the dental axis. The trigonid basin is large and open, and the paraconid stands wide apart from the metaconid. The paralophid is not sharp (it is a U-shape in labial view). The protoconid is the highest cusp of the trigonid. The metaconid and the paraconid are of similar height. Due to the reduction of the entoconid, the talonid is as narrow as the trigonid. The entocristid is well developed and straight. The hypoconulid, hypoconid, and entoconid are also well developed. The anterior end of the cristid obliqua terminates at the middle of the tooth. The labial valley of the talonid is well developed. The labial cingulum is wide and straight in lateral view and thickened anteriorly.

### 3.15. Description of the tentatively referred material

**c.** A broken tooth lacking the top of the cusp, sub-triangular in occlusal view. The cingulid is well developed and surrounds the tooth. The main cusp has two sections of thickening in the posterior part of the tooth that confer a subtriangular appearance. The root is longer than it is wide, and is laterally flattened.

**p2.** Tooth of subquadrangular outline with one main cusp that shows three faces. The cingulum is present and wide posteriorly, but absent anteriorly. Lingually, the cingulid is well developed. It is elevated anterolingually and displays a protrusion posterolingually.

**P2/P3.** A round small tooth with a rounded cusp and a well-developed cingulum with a small posterior expansion.

### 3.16. Discussion

Among the bat remains recovered in the Ribesalbes-Alcora Basin, the submyotodont lower molars are of particular interest. Vespertilionidae typically have nyctalodont lower molars, except for some species of the genera *Pipistrellus* and *Lasiurus* and all species of the genera *Myotis*, *Miostrellus*, *Paleptesicus*, *Plecotus*, and *Submyotodon*; the condition of the postcristid is unknown in *Samonycteris* (Ziegler 2003). Other Miocene bats with submyotodont teeth are the molossids *Cheiromeles* and *Mormopterus* (Legendre 1984a). In contrast to the Spanish fossils, *Cheiromeles* is characterised by a small paraconid (Legendre 1984a), while the Miocene *Mormopterus* species from Europe had lower molars showing myotodonty (Hand 1990). On the other hand, to date, no submyotodont molossid bats have been reported in the Miocene of Europe. In terms of size, the material studied in the Ribesalbes-Alcora Basin is larger than *Submyotodon petersbuchensis* Ziegler, 2003, the only species of this genus recognised during the Miocene (Ziegler 2003; Rosina & Rummel 2012).

Therefore, *Submyotodon* is thus far the only Miocene genus of Vespertilionidae with submyotodont lower molars. Although the m3 is always submyotodont, the m1 and m2 may be either submyotodont, nyctalodont, or myotodont (Ziegler 2003; Rosina &

Rummel 2012). For this reason, it has been previously misplaced within the genera *Myotis* or *Vespertilio*. Recently, it has been identified among the extant faunas from Asia, represented by the extant species *Submyotodon latirostris* (Kishida, 1932) and *Submyotodon caliginosus* (Tomes, 1859), in which m1 and m2 have a nyctalodont pattern and a submyotodont m3 (Benda & Gaisler 2015; Ruedi *et al.* 2015). According to molecular clocks, the appearance of this genus is dated between 23 and 18 Ma (Lack *et al.* 2010; Ruedi *et al.* 2013). This date is in agreement with the age proposed for the material of the Ribesalbes-Alcora Basin. For these reasons, this material has been assigned to an indeterminate species of *Submyotodon*.

Subfamily Vespertilioninae Gray, 1821

Tribe Myotini Tate, 1942

Genus *Myotis* Kaup, 1829

*Myotis intermedius* Ziegler, 2000

*Myotis cf. intermedius*

(Fig. 4e–h)

2017 *Myotis cf. intermedius* Crespo, 2017.

2017 *Miniopterus* sp. nov. (in part) Crespo, 2017.

**Locality.** MAB3

**Material and measurements.** 1 p4 (MAB3-817 (MGUV-37825):  $1.21 \times 1.24$ ); 5 m1 or m2 (MAB3-733 (MGUV-37741), MAB3-747 (MGUV-37755), MAB3-752 (MGUV-37760):  $1.59 \times 1.22$ , MAB3-755 (MGUV-37763), MAB3-798 (MGUV-37806)); 4 M1 or M2 (MAB3-719 (MGUV-37727), MAB3-723 (MGUV-37731), MAB3-776 (MGUV-37784), MAB3-789 (MGUV-37797)); 1 M3 (MAB3-712 (MGUV-37720):  $0.73 \times 1.74$ ). Doubtful remains: 1 c (MAB3-816 (MGUV-37824):  $0.80 \times 1.05$ ); 2 p2/p3 (MAB3-782 (MGUV-37790):  $0.79 \times 0.89$ , MAB3-790 (MGUV-37798)).

### 3.17. Description

**p4.** Tooth with a quadrate outline and one main cusp located at the centre-lingual side of the crown. The cusp shows four faces; a crest runs down towards the postero-lingual side of the cusp. The postero- and anterolingual margin of the cingulid present a swelling at the base. The cingulid is well developed around the tooth. Two roots are preserved.

**m1 or m2.** Myotodont teeth with a trigonid narrower than the talonid. The paralophid is rounded. Although both the paraconid and the metaconid are low, the former is lower while the latter protrudes lingually. The trigonid valley is open lingually. The entocristid is straight. The entoconid and the hypoconid are relatively large but the latter is better developed. The hypoconulid is developed, and a cingulid start at its base. The labial cingulid is wide in the talonid, narrow in the trigonid, and straight and wide in lateral view.

**M1 and M2.** The teeth are fragmented. The parastyle is short and angular, the precingulum starts in the parastyle. The paraloph and the metaloph are present, but are low and short. The precingulum and the postcingulum are well developed. The preprotocrista is connected to the paracingulum. The postprotocrista is short and does not join the metacingulum. The hypocone is absent.

**M3.** The tooth is short and wide with a reduced posterior part. The parastyle is extended and ends with a curve. The paracingulum is narrow; it starts near the end of the parastyle and is connected to the protocone, which exhibits a small precingulum. The paracone is the largest cusp and is connected to a small metacone by the mesostyle. A small paraloph is present. The protocone is well developed, and shows a distinct labial cingulum. The postmetacrista is absent.

### 3.18. Description of the tentatively referred material

c. Subtriangular tooth in occlusal view with a rounded anterior part and is somewhat flattened posteriorly. The cingulid is absent on the labial side but well-developed towards the posterior. A distinct labial crest runs all along the main cusp.

**p2/p3.** Tooth with a C-shape outline and a single main cusp with three faces located in the centre of the crown. The cingulid is present and wide except on the anteriormost part of the tooth, where it is absent. On the posterolingual side, the cingulid has a cuspule. The main cusp has a crest directed towards the anterior part of the tooth.

### 3.19. Discussion

*Myotis* is one of the most common bat genera in the fossil record and has a wide stratigraphic range (Gunnell *et al.* 2017). It is characterised by myotodont lower molars that have a medium to wide cingulid. The upper molars typically have no basined talon nor hypocone. The paraloph and the metaloph are occasionally present and the M3 is always distally reduced with only three lingual crests, without postmetacrista (Sevilla 1988). All of these features appear in the studied material.

Both *Myotis* and the similar genus *Leuconoe* are highly diverse. The comparison with *Myotis* species enables us to assign the material described here to *Myotis* (aff.) *murinoides* since this species is characterised by a cusplated cristid obliqua, a small crest between the hypoconulid and the entoconid, well-developed paraloph and metaloph, and the presence of a hypocone in the M1 (Ziegler 1994; Sevilla 2002). *Myotis elegans* Hall, 1962 differs by its well developed and advanced protocone (Sevilla 2002). In *Myotis boyeri* Mein, 1964, the postprotocrista is connected to the distal cingulum (Sevilla 2002). The fossils of *Myotis* aff. *minor* from Casetón are smaller than our material and show a less reduced M3 (Sevilla 2002). *Myotis minor* Ziegler, 2000 is smaller and the paraloph and metaloph are better developed. *Myotis major* Ziegler, 2000 is slightly larger and the protocone is more rounded (Ziegler 2000). *Myotis korotkevichae* Rosina & Semenov, 2012 is characterised by a more developed metaloph and paraloph, and a less reduced M3 (Rosina & Semenov 2012). *Myotis bavaricus* Ziegler, 2003 shows an angular paraloph on the upper molars; the M3 is only moderately reduced and the upper molars lack both the paraloph and metaloph (Ziegler 2003). *Leuconoe antiquus* (Gaillard 1899) shows a protolophid and a metalophid with a very low notch, and a premetacrista that is shorter than the postparacrista (Sevilla 2002). *Leuconoe sanctialbani* (Viret, 1951) reveals conules in the lingual cingulum of the upper teeth (Baudelot 1972; Ziegler 2000).

The species closest to our material is *Myotis intermedius* from the upper Oligocene of Herrlingen 8 and 9, although these populations display a slightly smaller size. Although the diagnosis of this species indicates the absence of the paraloph and the metaloph, the presence of both small crests can be seen in the photographic images given by Ziegler (2000; pl. 6, figs 65, 66). Due to these reasons and the scarcity of the studied material, we have left it to allow open nomenclature and assign the material to *Myotis cf. intermedius*.

Tribe Vespertilionini Gray, 1821

Genus *Miostrellus* Rachl, 1983

*Miostrellus petersbuchensis* Rosina & Rummel, 2012

*Miostrellus* aff. *Petersbuchensis*

(Fig. 4i)

2017 *Miostrellus cf. petersbuchensis* Crespo, 2017.

**Locality.** CBR1.

**Material.** 1 M1 (CBR1-38; MGUV-36794).

### 3.20. Description

**M1.** Broken tooth without parastyle and metastyle. The postparacrista and premetacrista are connected by a well-developed mesostyle. The paracingulum is directly connected to the preprotocrista without a paraconule. The paraloph and metaloph are absent. The precingulum starts at the anterolabial side of the protocone, joins the postcingulum, and reaches the metacingulum; the posterior side of the lingual cingulum is slightly wider than the anterior. The postprotocrista is connected to the metacone, thus forming a V-shape in lateral view. The protofossa is closed and deep.

### 3.21. Discussion

*Miostrellus* is characterised with respect to upper molars without paraloph and metaloph, and an almost complete postprotocrista (Horáček 2001). These features appear in the specimen described here, although the postprotocrista is complete and is connected to the metacone.

Regarding the specific ascription, we can discard: (1) *Miostrellus risgoviensis* Rachl, 1983, which shows a more extended posterior part of the protocone; (2) *Miostrellus egerensis* Horáček, 2001, which has a postprotocrista that does not reach the metacone; and (3) *Miostrellus noctuloides* (Lartet, 1851), which presents conules and lophes (Rosina & Rummel 2012). The most similar species is *Miostrellus petersbuchensis*, although the junction of the postprotocrista and metacone is weaker than in the tooth described here.

Tribe Plecotini Gray, 1866

Genus *Plecotus* Geoffroy Saint-Hilaire, 1813

*Plecotus* sp.

(Fig. 4j–n)

**Localities.** BC1, MAB3, and MAB5.

**Material and measurements.** 11 m1 or m2 (BC1-19 (MGUV-25334): -x1.23, MAB3-738 (MGUV-37746): -x1.37, MAB3-749 (MGUV-37757), MAB3-753 (MGUV-37761), MAB3-754 (MGUV-37762); -x1.22, MAB5-381 (MGUV-25171), MAB5-417 (MGUV-25207), MAB5-420 (MGUV-25210), MAB5-438 (MGUV-25228), MAB5-745 (MGUV-38168), MAB5-748 (MGUV-38171), MAB5-891 (MGUV-38314)); 1 m3 (MAB5-438 (MGUV-25228): 1.17 × 0.83), 1I (MAB5-774 (MGUV-38197): 0.73 × 0.41), 2 C (MAB5-149 (MGUV-24939): 0.87 × 0.94; MAB5-432 (MGUV-25222): 0.91 × 0.87). Doubtful remains: 1 p2/p3 (MAB5-771; MGUV-38194).

### 3.22. Description

**m1 or m2.** Broken small-sized teeth with a curved paralophid. The paraconid is similar in size to the metaconid and both are aligned with the entoconid. The protoconid is the highest cusp. The labial cingulid is narrow and well developed. The obliqua cristid starts mid-width of the tooth. The lingual cingulid is well developed with regular thickness in lateral view. The talonid is myotodont and the entocristid is concave lingually. The talonid basin, entoconid, and hypoconid are large and distinct, whereas the hypoconulid is poorly developed.

**m3.** The tooth is myotodont and small in size. The line formed by the paraconid and the metaconid is parallel to the dental axis and similarly sized. The paralophid is curved. The protoconid is the tallest cusp of the trigonid. The talonid is narrower than the trigonid, although the entoconid is reduced. The entocristid is well developed and straight. The obliqua cristid joins the trigonid at the middle of the metalophid. The hypoconid and the lingual valley of the talonid are well developed. The labial cingulid is wide and straight in lateral view.



**I.** Teeth with an elliptical outline, with the main cuspid divided into two subcuspid, one of which is distinctly less developed. The cingulum is complete on the labial side and absent on the lingual side; posteriorly, there is a small cuspule.

**C.** A long tooth with two well-developed cusps and a distinct cingulum on the labial side; there is a small basin on the lingual side.

### 3.23. Description of the tentatively referred material

**p2/p3.** A fragment of tooth with a well-developed cingulid, wider posteriorly, and protruding posterolingually.

### 3.24. Discussion

Species of the *Plecotus* are characterised by myotodont lower molars with a wide cingulid and reduced m3 (Sevilla 1988), as well as bicuspid upper incisors and small canines (Menu & Popelard 1987). The material from the Ribesalbes-Alcora Basin fits with this description; however, the diagnostic material is insufficient for a specific attribution. The Miocene fossil record of *Plecotus* is limited, the oldest species being *Plecotus schoepfelii* Rosina & Rummel, 2012 from the early Miocene of Petersbuch 28 (Rosina & Rummel 2012). The late Miocene record has yielded *Plecotus atavus* Topál, 1989 in Polgárdi 4 (Topál 1989) and Kohfidish (Storch 1999), and a similar taxon, *Plecotus* aff. *atavus*, from the middle Miocene of Petersbuch 6 and upper Miocene of Gritsev (Ziegler 2003; Rosina *et al.* 2019). The indeterminate species of *Plecotus* from Ribesalbes-Alcora Basin is likely an ancestral form pre-dating the first major split of the lineage that took place in the middle Miocene according to genetic studies (Spitzenberger *et al.* 2006) and made way for to the different extant species currently distributed through Europe.

Suborder Yinpterochiroptera Koopman, 1984

Family Rhinolophidae Gray, 1825

Genus *Rhinolophus* Lacépède, 1799

*Rhinolophus* sp.

(Fig. 4a–q)

**Localities.** MTR2 and MAB3

**Material and measurements.** 7 m1 or m2 (MTR2-192 (MGUV-38939), MTR2-196 (MGUV-38943), MTR2-201 (MGUV-38948), MAB3-741 (MGUV-37749): -x1.50, MAB3-743 (MGUV-37751): -x1.64; MAB3-744 (MGUV-37752): -x1.60; MAB3-760 (MGUV-37768)), 1 M1 (MAB3-708; MGUV-37716), 1 M1/2 (MTR2-202; MGUV-38949) Doubtful remains: 1 i3 (MAB3-800 (MGUV-37808):  $0.77 \times 0.59$ ), 1 c (MAB3-25 (MGUV-25281):  $0.59 \times 0.74$ ), 1 P4 (MAB3-793; MGUV-37801).

### 3.25. Description

**m1 or m2.** The teeth are broken. The parolophid is curved and the trigonid basin is open. The paraconid is lower than the metaconid and slightly protruding. The protoconid is the most developed cusp. The lingual cingulid is wide and well developed; on its anterior, there is a small cusp that is most developed in specimen MTR2.

**M1.** A fragment of a large tooth. It has a wide paracingulum without paraconule, which is connected to the protocone. The precingulum is small. The postprotocrista is well developed. The talon is broken and the protofossa is wide and deep.

### 3.26. Description of the tentatively referred material

**i3.** A single tooth with a subtrapezoidal occlusal outline. It has four cusps, three of which are in line, the central one being larger than the other two. The valleys between cusps are wide and deep.

There is an additional shallow valley between the cingulid and the cusps.

**c.** A single tooth with a subtriangular occlusal outline. The cingulid is continuous, but poorly developed on both the lingual and labial sides. The main cusp is straight and has a crest on the anterior face that runs from the tip of the crown to the base. The root is triangular in section, flattened posteriorly.

**P4.** A fragmented tooth; the talon and anterior side are missing. The paracone is well developed and cone-shaped; the post-paraconule is directed towards the cusp and ends in a curved metastyle. The preserved anterior part of the lingual cingulum is wide and is directed towards the talon.

### 3.27. Discussion

*Rhinolophus* material is common in Neogene fossil assemblages and easily identified due to its characteristic morphology. Although the fossil material in Ribesalbes-Alcora Basin is scarce, *Rhinolophus* material has been reported at a nearby locality of Buñol (Robles *et al.* 1991). The morphology of the upper molars with an expanded talon and without hypocone is present in two common genera of the Neogene in Europe, *Rhinolophus* and *Hipposideros* (Sevilla 1988). Although similar at first sight, there are differences that enable us to distinguish both genera in fossil material. For instance, whereas in *Hipposideros collongensis* (Depéret, 1892) the postprotocrista runs towards the metacone in the upper molars, in *Rhinolophus*, including the material described here, it runs posteriorly (Sevilla 1988; Ziegler 2003; Rosina & Rummel 2012) and lacks a precingulum (Sevilla 1990; Álvarez-Sierra *et al.* 2006). Although in modern *Rhinolophus* species the cingulid in the lower molars tend to be straight and narrow (Sevilla 1988), some Miocene species display a thicker cingulid, such as in *Rhinolophus grivensis* (Depéret 1892) from Petersbuch 6 or *Rhinolophus lemanensis* Revilliod, 1920 from Petersbuch 62 (Ziegler 2003; Rosina & Rummel 2012), a feature that is also observed in the material described here.

As such, the material under study clearly belongs to a large species of the genus. These remains are larger than *R. lemanensis*, which is the largest species in Petersbuch (Ziegler 2003; Rosina & Rummel 2012), or *R. grivensis* and *Rhinolophus delphinensis* Gaillard, 1899 from Escobosa de Calatañazor (Spain; Sesé 1986). Our material is similar in size to the extant species *Rhinolophus ferrumequinum* (Schreber, 1774) and *Rhinolophus macrorhinus* Topál, 1967, and even to the Plio–Pleistocene species *Rhinolophus postdelphinensis* Topál, 1979 (Sevilla 1988).

Therefore, we can assume that this material comes from perhaps one of the largest *Rhinolophus* species of the Miocene; however, the scarcity of the material precludes any specific classification.

## 4. Discussion

### 4.1. Palaeoecological and palaeobiogeographic considerations

Considering the fact that bat remains are uncommon in fluvio-lacustrine fossil sites, it can be said that they are extraordinarily frequent in the Ribesalbes-Alcora Basin. They constitute 6% of the small mammal assemblages in MAB11 and around 2–4% of the other sites (all sites with more than 100 specimens of small mammals recovered), whereas they usually account for only 0.01% of the small mammal fossils in fluvio-lacustrine sites (Sigé & Legendre 1983; Sevilla 2002). The discovery of fluvio-lacustrine sites containing fossil bats is interesting because the assemblages in this type of site typically contain taxa that are either absent or uncommon in karstic localities, thus providing

important data to obtain a clearer picture of the past diversity of Chiroptera (Sigé & Legendre 1983; Maitre 2014).

One of the particularities of the *Araia* assemblage is the high abundance and diversity of typically rare molossids. The combination of a high number of species and a low number of individuals is common in present day Neotropical, Ethiopian, and Indo-Australian molossid faunas (Freeman 1981b). This family includes high, fast, and direct fliers, which likely have few competitors (Freeman 1981b; Fenton 1983). The ability for similar and related species to live in syntopy is probably favoured by their different habitat preferences, and feeding and roosting strategies; however, generally this family tends to avoid thickly forested habitats or subcanopy areas since they are fast flyers specialised in insect hawking (Freeman 1981b; Hill & Smith 1984; Norberg & Rayner 1987; Hand 1990). The highly diverse molossid assemblages consisting of five species suggests tropical climatic conditions (Freeman 1981b) for the Ribesalbes-Alcora paleolake and the surrounding area. The diversity is higher in sites starting from the end of the local biozone C (end of early Miocene), with four species, than in those from the lower part of the local biozone C, with two species. The relatively cool climatic event Mi-2, which was likely recorded in site MAB5 (Rios 2013; Crespo 2017), does not seem to affect the diversity of molossids.

The genus *Myotis* currently shows a widespread distribution, which suggests that its fossil species might have lived in many different habitats (Norberg & Rayner 1987; Ziegler 2000). The genus *Plecotus* can roost both in caves and trees, always in small groups; it is a slow surface hunter in thick woods (Norberg & Rayner 1987; Sevilla 1988). The genus *Submyotodon* occurs nowadays in southeastern Asia and is commonly misidentified as *Myotis*. Both genera might share similar modes of life, hunting small flying insects, drinking directly from the surface of the waters where insects tend to trawl (Richardson 1993; Bonaccorso 1998; Benda & Gaisler 2015). The extant rhinolophids are more diverse in tropical to subtropical regions, but are also found in temperate areas of Europe; they can roost in caves or forests (Sevilla 1988, 1990) and are specialised in hunting flying insects and occasionally stationary prey on foliage or the ground (Norberg & Rayner 1987). *Myotis*, *Plecotus*, and *Rhinolophus* are common taxa in the European fossil record and are consistent with the ecological interpretation inferred for the sites being studied, since all are either generalised in their ecological requirements or are dependent on the presence of tree cover or bodies of water. According to Crespo (2017), these were the conditions in the area at the time during the sites were formed.

Studies of habitat use demonstrate that bats spend significant time near water bodies (Walsh & Harris 1996; Vaughan *et al.* 1997). It is likely that bats benefit from shallow warm waters with macrophytes since these environments provide abundant insects (Zimmer *et al.* 2000). The fossil record of bats associated with lacustrine sites where a high diversity of species is observed may be related to the favourable conditions provided by these water bodies, in which different ecological niches sustained a high level of diversity and abundant resources. As such, for bats, these environments ensured a variety of prey consisting of both insects and fish, water to drink, and places to roost. The remains of the animals that died either due to predation or natural causes and had ended up in the lake were preserved with other vertebrate remains as a result of the fast burial that ensured the preservation of their delicate bones and teeth. Therefore, the presence of a paleolake in the Ribesalbes-Alcora Basin may have played an important role in the presence of bats in its fossil assemblages.

Compared to other sites of similar age from central and southern Europe, the bats from the Ribesalbes-Alcora Basin show interesting and unusual differences, for instance, with those from Petersbuch 28 and 62, Wintershof-West, Cremat,

Bouzigues, Vieux-Collonges, and Merkur-North, among others (Sigé & Legendre 1983; Sigé *et al.* 1991; Ziegler 1993; Horáček 2001; Rosina & Rummel 2012; Fortelius 2016). The main differences are found in the relatively high abundance of molossids, while non-molossid families appear to be less common in the material described here than in central and other southern European localities. The fossil record of molossids in Africa, which starts in the early Miocene, is also rather scarce (Arroyo-Cabrales *et al.* 2002). This particular feature of the Ribesalbes-Alcora Basin assemblages cannot be a consequence of the type of sedimentary environment, since non-molossids in the Miocene are predominant both in karstic and fluvio-lacustrine sites. Furthermore, certain molossids are cave dwellers (Freeman 1981b) and might be expected to be better represented in karstic sites. However, molossids are not rare in the early Oligocene sites of western Europe (Maitre 2014), but seem to have undergone a regression in central and western Europe from the late Oligocene onwards (Sevilla 1990; Ziegler 2000), thus becoming increasingly less common. Other fossil assemblages with bats from the middle Miocene of the Iberian Peninsula differ from the material described here in their proximity to modern faunas in taxonomic representation with a predominance of rhinolophids and vespertilionids (Sesé 1986; Sevilla 2002). The particularity of the assemblages in the Ribesalbes-Alcora Basin could be explained by the presence of tropical forests in the area, which would favour a higher proportion of molossids in the assemblages compared to the dominance of taxa linked to more arid environments represented in other localities. Highly diverse molossid communities are seen today in tropical Neotropical regions (Freeman 1981b). This interpretation is supported by the fact that in the Ribesalbes-Alcora Basin, molossids are most abundant and diverse in sites known to correspond to densely forested areas according to the associated fauna, such as eomyids, beavers, and some kinds of dormouse and insectivores, although they are scarce elsewhere (Crespo 2017; Crespo *et al.* 2019a). The development of open forests and grassland habitats during the late early Miocene and the middle Miocene at the expense of pre-existing dense forest areas (Barrón *et al.* 2010) provoked a dramatic change in these early Miocene bat assemblages, in which molossids were well represented, resulting in faunas more similar to recent ones where they are practically non-existent.

## 5. Conclusions

The order Chiroptera is one of the least abundant mammal groups in the Ribesalbes-Alcora Basin in the early Miocene record. Nevertheless, ten different taxa – one of which is a new species – have been identified in the localities studied. This constitutes, thus far, the first and largest collection of fossil bats from the early Miocene of the Iberian Peninsula.

The ten taxa identified in the sites from the Ribesalbes-Alcora Basin are *Cuvierimops penalveri* sp. nov., *Hydromops helveticus*, *Rhizomops cf. brasiliensis*, *Chaerephon* sp., *Tadarida* sp., *Submyotodon* sp., *Myotis cf. intermedius*, *Miostrellus* aff. *petersbuchensis*, *Plecotus* sp., and *Rhinolophus* sp. The genera *Cuvierimops*, *Rhizomops*, and the Lazarus genus *Chaerephon* are reported globally for the first time in the early Miocene.

The richness of molossids recorded in this material reveals the high diversity attained by this group in the Miocene of Europe, which had been largely unrecognised as a result of such fossils being typically underrepresented in the Neogene fluvio-lacustrine fossil record. The abundance of these bats in the Ribesalbes-Alcora Basin is consistent with the presence of a tropical forest surrounding a paleolake, as suggested also by the presence of other mammal taxa such as eomyids, certain types of dormouse, and insectivores.

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