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1 **Title: Los Batanes (Biescas, Spain), a roost site for horseshoe bats in the Pyrenees during**
2 **the late Pleistocene**

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13 **Abstract**

14 Los Batanes C4 is a cave-site in the Spanish Pyrenees, the minimum sediment calendar age was
15 determined to be $15,234 \pm 223$ cal BP by radiocarbon dating. The cave opens on the northern
16 bank of an eastern tributary of the River Gállego, at an altitude of 1,025 m. The small vertebrates
17 recorded are mainly bats, in order of abundance *Rhinolophus euryale*, *R. ferrumequinum*, *Myotis*
18 sp. and *Miniopterus schreibersii*. The association suggests that at the time of the accumulation the
19 climate was reasonably similar to the current climate; we situate it within a period of local retreat of
20 the ice-cover in the Gállego Valley during the Lateglacial. This is the highest record of these
21 species of *Rhinolophus* in the Iberian Quaternary, showing that the *R. euryale* altitudinal range was
22 similar to its extant range during the favourable periods of the Lateglacial. This could indicate that
23 this taxon was relatively quick in spreading into higher regions whenever climate conditions
24 allowed it.

25 **Key words**

26 *Rhinolophus euryale*, *Rhinolophus ferrumequinum*, Lateglacial, Pyrenean site, palaeoenvironment

1 1. INTRODUCTION

2 Los Batanes Cave C4 (Biescas, northern Spain, Fig. 1a) is a small karstic cavity (Fig. 1b) located
3 in the Tendeñera Range, on the southern side of the Pyrenees, at an altitude slightly above 1,000
4 m.a.s.l. (metres above sea level). This is one of the Pyrenean cave-localities with late Pleistocene
5 sedimentary fill that have been prospected by the Aragosaurus Group — a research group on
6 Mesozoic and Quaternary vertebrate palaeontology from the University of Zaragoza (UNIZAR) —
7 in recent years. The field-work at this locality forms part of an overall prospection plan whose main
8 goal is to expand what is known of the Pleistocene faunas on the Spanish side of the Pyrenees,
9 which is still very scarce when compared to the French side (Clot and Evin, 1986; Núñez-Lahuerta
10 et al., 2017; Sauqué et al., 2015; Sauqué et al., 2017; among others). The research is part of the
11 project 'Recovery of palaeontological remains, cataloguing and dating of the Pleistocene-Holocene
12 deposits of Huesca Pyrenees caves', which is headed by Dr. Raquel Rabal-Garcés and Dr. Victor
13 Sauqué-Latas (Sauqué et al., 2015) and focuses mainly on completing the Quaternary karst-filling
14 record.

15 A palaeontological excavation was performed at Los Batanes after the discovery of several large-
16 mammal fossil remains belonging to the extinct Pyrenean wild goat *Capra pyrenaica pyrenaica*
17 (commonly named “bucardo”) within the cave (Sauqué et al., 2017). A mixed team with participants
18 from the Aragosaurus Group together with the Speleological Centre of Aragón (CEA) and the
19 Pyrenean Institute of Ecology (IPE) took part in a field campaign at the site in August 2015
20 (Sauqué et al., 2015). When the sediment extracted had been adequately processed (washed and
21 sieved), a notable assemblage of small-vertebrate remains was found, with a predominance of
22 bats. Subsequently, the chiropteran assemblage from Los Batanes was studied in order to identify
23 the species recorded and to provide new data on the late Pleistocene bat distribution in the region
24 of the Spanish Pyrenees.

25 1.1. Horseshoe bats in the Aragonese Pyrenees and nearby areas. Background.

26 Horseshoe bats belong to the family Rhinolophidae, formed by a single genus, *Rhinolophus*, of
27 which four species currently inhabit the Iberian Peninsula: *Rhinolophus ferrumequinum*,

1 *Rhinolophus euryale*, *Rhinolophus mehelyi* and *Rhinolophus hipposideros*. These are small- to
2 medium-sized bats that feed mainly on insects, and the group is characterized by a complex
3 horseshoe-shaped nasal appendage which gives them their common name. This external structure
4 constitutes an adaptation to a very derived system of echolocation, which consists of the emission
5 of calls through the nose; these calls are directed and focused by the multiple skin folds forming
6 the nasal appendage (Dietz et al., 2009; Palomo et al., 2007; among others).
7 Despite the great variety of habitats and roosts available for bats in Aragonese territory, largely
8 consisting of Mesozoic and Tertiary limestone terrains, the studies of bats in this area are not very
9 abundant when compared to other regions in Spain (work on extant populations from the last two
10 decades: Alcalde et al., 2008; Bafaluy-Zoriguel, 1997, 1999, 2000; Garin et al., 2003; Woutersen
11 and Bafaluy-Zoriguel, 2001; among others). Three *Rhinolophus* species are currently present in
12 the Aragonese Pyrenees, with a discontinuous pattern of distribution: the greater horseshoe bat *R.*
13 *ferrumequinum*, the Mediterranean horseshoe bat *R. euryale* and the lesser horseshoe bat *R.*
14 *hipposideros* (Alcalde et al., 2008). The studied record of fossil and subfossil horseshoe bats in the
15 Iberian Pyrenees, the pre-Pyrenees and nearby areas is not very abundant either. In the upper
16 Pleistocene and prior to the LGM (Last Glacial Maximum), all three species are cited at Gabasa 1
17 Cave (Huesca, Mousterian period) (Blasco-Sancho, 1995), and *R. ferrumequinum* at Olopte Cave
18 (Girona, Mousterian period) (López-García, 2011). From the post-LGM record, *R. euryale-mehelyi*
19 and *R. ferrumequinum* are cited at Colomera Cave (Lleida, Holocene, 6-6.2 ka) (Oms et al., 2008);
20 *R. ferrumequinum* also appears at Marizulo (Guipuzkoa, Holocene, 5.2 ka) (Altuna, 1972), and
21 *Rhinolophus* sp. is recorded at Laminak II (Biscay, Holocene, 10.3 ka) (Pemán, 1994).

22 **1.2. Objectives**

23 The present work has the following objectives. The first aim is to characterize the fossil bat
24 assemblage in terms of its taxonomic composition and diversity, the relative abundance of bats in
25 comparison with other groups of small vertebrates in the cave, and the origin of the accumulation.
26 The second aim is to ascertain the palaeoenvironmental framework at the time of the accumulation
27 on the basis of the ecological data for the species of bats that form the assemblage. The final

1 objective is to provide new data on the ancient distribution of the bat species identified, which in
2 this case will also contribute to filling the gap in our knowledge about this group of mammals in the
3 palaeontological sites of the Iberian Pyrenees and pre-Pyrenees.

4 5 **2. KARSTIC FISSURE-FILL AND CAVE SEDIMENTS FROM LOS BATANES: GEOGRAPHICAL** 6 **AND GEOLOGICAL LOCATION AND CHRONOLOGICAL CORRELATION**

7 Los Batanes cave (X: 720.080; Y: 4726.585) is a karstic cavity that developed in late Cretaceous
8 (Maastrichtian) limestones (Ríos-Aragües et al., 1987; Gil-Peña et al., 1996) (Fig. 2). It is located
9 on the eastern side of the upper Gállego Valley, which drains a large part of the central-southern
10 Pyrenees and has a complex drainage area composed of various main and secondary valleys
11 (Palacios et al., 2015). The entrance to the cave opens at an altitude of 1,025 m.a.s.l., on the
12 northern bank of an eastern tributary to the River Gállego. It is a small-sized cave basically
13 consisting of a descending, narrow pressure tube of about 1-2 m width, which appears not to be
14 being used as a bat roost at present (personal observation).

15 The excavation took place at the bottom of the tube, where it becomes slightly broader and where
16 there is a body of sediment of still unknown depth, sealed under a calcite crust (Fig. 1b). The
17 sedimentary deposits mainly consist of a clay matrix of mixed origin (both autochthonous
18 decalcification clays and allochthonous mud from outside), autochthonous carbonate clasts from
19 the walls of the cave, and allochthonous clasts that probably came from the erosion of a nearby
20 moraine, such as the granite clasts that ultimately originated in the Panticosa batholith (Fig. 2). The
21 fossil remains were recovered from the first 0.5 m of the sedimentary pack, beneath the calcite
22 crust. A bone belonging to *Capra pyrenaica pyrenaica* embedded in this crust was radiocarbon-
23 dated, giving an age of 13.507-13.061 years cal BC with the probability of 95.4% (2s) ($15.234 \pm$
24 223 cal BP). Analysis were made at Poznan Radiocarbon Laboratory (lab. ref. Poz-75800) and
25 calibrated with the OxCal v4.2.4 program (Bronk Ramsey and Lee, 2013).

26 The radiocarbon date allowed us to place the accumulation of our fossil assemblage
27 chronologically at the end of the upper Pleistocene, in the cold Marine Isotopic Stage (MIS) 2. It

1 was probably produced in a period of transition between the LGM (Last Glacial Maximum) and the
2 beginning of the Holocene (Hughes et al., 2013). At that time the climate underwent a warming
3 trend that was nonetheless interrupted by various cold, generally dry pulses (which in western
4 Mediterranean areas basically correspond to the Older Dryas, the intra-Allerød Cold Period and the
5 Younger Dryas; Fletcher et al., 2010; Palacios et al., 2015). These climatic and environmental
6 changes in the final part of the upper Pleistocene had consequences for faunal associations: in
7 many localities, the late Pleistocene-Holocene transition is marked by the substitution of some taxa
8 by others and by an increase in woodland habitats to the detriment of open landscapes (referring
9 to palynological studies: e.g. Carrión et al., 2010; Dorado et al., 2002; Fernández et al., 2007; Gil
10 García et al., 2002; referring to small-vertebrate associations: e.g. Cuenca-Bescós et al., 2009;
11 Cuenca-Bescós et al., 2010; López-García et al., 2015). As regards the palaeoclimatic framework
12 in the Spanish Pyrenees, specifically in the Gállego Valley, all the evidence points to a maximum
13 ice extent largely predating the global LGM (García-Ruiz et al., 2003). According to Palacios et al.
14 (2015), at least two episodes of glacial re-advance can be detected in the Gállego Valley during
15 the Lateglacial period (Guiter et al., 2003): before approximately 17 ka, and again at approximately
16 14-11.7 ka. Palacios et al. (2015) hypothesize that these can be related to the Oldest Dryas, and
17 the Older or Younger Dryas respectively (Fig. 2).

18

19 **3. MATERIAL AND METHODS**

20 **3.1. Fieldwork and fossil sorting**

21 The excavation area was located deep in the cave, at a distance of 40 m length and -12 m height
22 from the cave entrance (Fig. 1b). Access and digging at such a distance from the cave's opening
23 required speleological expertise. The extracted sediment was processed at the laboratories of the
24 IPE and UNIZAR. The clay matrix was removed by washing the sediment through two
25 superimposed sieves of 5 and 0.5 mm mesh-size respectively. Then, the bones of the small
26 vertebrates were picked out from the remaining sediment (consisting of clasts larger than 0.5 mm)
27 at the laboratory.

1 The fossil material studied here mainly consists of disarticulated bones from bats, both cranial and
2 postcranial. The recovered material is deposited at the Natural Science Museum of Zaragoza
3 (Canudo, 2018).

4 **3.2. Identification and description of the bat remains**

5 The bat remains were described and measured and determined to species level whenever
6 possible. The teeth were measured by taking photos of the specimens in occlusal view using an
7 Olympus SZ61 binocular stereo microscope with an attached camera (LC20 model); for larger
8 bones a caliper (Mitutoyo CD-8" CX Digimatic Caliper, Japan) with a theoretical precision of 0.01
9 mm was employed. We followed the taxonomic criteria established by Dupuis (1986), Felten et al.
10 (1973), Jenrich et al. (2012), Menu and Popelard (1987), Răduleț (2003) and Sevilla (1988) among
11 others. We undertook comparative anatomy with extant specimens of horseshoe bats from
12 Southwestern European populations belonging to the following institutions: the International Centre
13 for Water and Environment (CIAMA) at La Alfranca (Zaragoza), the National Museum of Natural
14 Sciences of Madrid (MNCN), the Archaeosciences Laboratory of Lisbon (LARC), the National
15 Museum of Natural History of Paris (MNHN), the Doñana Biological Station (EBD) and the
16 Smithsonian Institution, National Museum of Natural History, Division of Mammals. In
17 characterizing the fossil assemblage, we followed the taphonomic criteria established by Andrews
18 (1990), Bennàsar (2010), Fernandez-Jalvo (2016), Kowalski (1995) and López-García and Sevilla
19 (2012), among others. The classification according to age groups based on tooth wear follows the
20 same criteria as Popov and Ivanova (2002).

21 **3.3. Abbreviations**

22 Naming the teeth: i (incisor), c (canine), p (premolar), m (molar); teeth from the upper series are
23 named in capital letters while teeth from the lower series are named in lowercase letters (i.e. M1 is
24 the first upper molar; p3 is the third lower premolar). Measuring the teeth: L (anteroposterior
25 length), W (lateromesial width), L1 (greater length of upper molars, distance from the parastyle to
26 the metastyle), L2 (medium length of upper molars, measuring the constriction of the protoconal
27 basin), w1 (width of lower molars trigonid, distance from the metaconid to the protoconid) and w2

1 (width of lower molars talonid, distance from the entoconid to the hypoconid). Naming and
2 describing the cranial and postcranial skeleton: Cr (cranial), PCr (postcranial), mx (maxilla), md
3 (mandible), bu (tympanic bulla), at (atlas), vert (vertebra) sca (scapula), clav (clavicle), p ring
4 (pectoral ring), hu (humerus), ra (radius), metac (metacarpus), pelv (pelvic bone), fe (femur), ti
5 (tibia), R (right), L (left), fr (fragment), b (body), mr (mandibular ramus), pep (proximal epiphysis),
6 dep (distal epiphysis), diap (diaphysis). Other abbreviations: NR (number of remains, all the
7 recovered bone and dental fragments), NISP (number of identified specimens, all the remains
8 assigned to a certain skeletal element), MNI (minimum number of individuals), Ri (relative
9 abundance of the elements in the sample), Ni (minimum number of elements in the sample), Ei
10 (number of elements in an individual).

11

12 **4. RESULTS**

13 The fossil bat assemblage consists of 434 recovered bone and dental fragments: i.e. NR=434. Of
14 these, 164 specimens have been assigned to a certain skeletal element and taxon: i.e. NISP=164
15 (Table 1). It is mainly made up of bones from two species of horseshoe bats: the Mediterranean
16 horseshoe bat *R. euryale*, MNI=12, and the greater horseshoe bat *R. ferrumequinum*, MNI=2
17 (Table 1). Four more specimens have been assigned to the Vespertilionidae family (Table 1).

18 **4.1. Taxon assignation**

19 4.1.1. Rhinolophidae

20 The assignation of most of the specimens from Los Batanes to the genus *Rhinolophus* is
21 unequivocal. Regarding the cranial skeleton, as the premaxilla is only attached to the maxilla via a
22 restricted caudal joint, this bone is detached in fossil specimens (Fig. 3a) and usually absent, so
23 the most anterior alveolus shown by the upper jaw is the canine one. P4 and M1 have well-
24 developed heels, as has M2 to a lesser extent (Fig. 3a), and C is robust, trapezoidal and presents
25 a concave lingual side of the crown (Fig. 3b) (Sevilla, 1988). The mandibular ramus is rectangular
26 in external view with an almost horizontal mandibular notch (Fig. 3a); the lower molars are
27 nyctalodont (Menu and Sige, 1971) and present a narrow, regular cingulum (Fig. 3c), which is also

1 characteristic of this genus. The dental formula of *Rhinolophus* is 1.1.2.3/2.1.3.3 (Sevilla, 1988;
2 Palomo et al., 2007). The tympanic bulla has a characteristic conical spiral shape.

3 As regards the postcranial skeleton, a distinctive structure of horseshoe bats is the pectoral ring
4 (Fig. 3d) consisting of various fused bones: the sternal body, the first pair of ribs, and the first
5 pectoral vertebra (Fomin and Lovachev, 2000). The scapula is leaf-shaped with a pointed inferior
6 angle (Fig. 3f). The proximal epiphysis of the humerus is diagnostic in having a trochin almost as
7 big as the trochiter with a humeral head that is small and round (Dupuis, 1986) (Fig. 3e); the distal
8 epiphysis is diagnostic in having a pen-shaped styloid process, a broad epitrochlea (Dupuis, 1986;
9 Felten et al., 1973), and dorsally projected condyles (Fig. 4b). The radius is strong, and by contrast
10 with most vespertilionid bats (except *Miniopterus*) the ulna insertion is in the middle zone of the
11 diaphysis instead of close to the proximal epiphysis. The proximal epiphysis of the radius of
12 horseshoe bats differs from that of *Miniopterus* in having an open flexor fossa and a rounded
13 proximal tip (Dodelin, 2002). The pelvis presents a characteristic oval, anteroposteriorly elongated
14 small obturator foramen and a wide ischiopubic ramus. The femur has a flattened head and a
15 pronounced, curved medial ridge, well differentiated from the lesser trochanter; the distal condyles
16 are tiny and a broad groove separates them from one another (Fig. 3g).

17 ***Rhinolophus euryale*** (Mediterranean horseshoe bat, Table 1, Table 2, Fig. 3). The remains
18 belong to a medium-sized form of horseshoe bat, of which two species inhabit the Iberian
19 Peninsula: *R. mehelyi* and *R. euryale*, the former slightly larger than the latter (Dietz et al., 2009;
20 Palomo et al., 2007). We compared the molar measurements of our assemblage (Table 3) with
21 those of extant horseshoe bats from Southwestern European populations (Fig. 5), which allowed
22 us to assign the cranial remains to the species *R. euryale* (Fig. 3a,b,c). The distal epiphyses of the
23 humeri present a straight styloid process with convex edges by contrast with that of *R. mehelyi*,
24 which is quadrangular; both morphology and size of the distal epiphysis (Fig. 3e, Table 3) supports
25 the assignation to *R. euryale* (Dupuis, 1986; Felten et al., 1973).

26 *R. euryale* currently inhabits the Mediterranean region of Europe, as well as some parts of northern
27 Africa and the near East (Dietz et al., 2009). Given its preference for roosting in caves, this species

1 is linked to karstic areas; for nursery colonies it generally chooses roosts at an altitude of less than
2 800 m.a.s.l. and therefore with a milder, more favourable climate (Dietz et al., 2009). It has been
3 recorded in present-day Spain at a maximum altitude of 1,360 m.a.s.l. (Palomo et al., 2007), but in
4 the Pyrenees the altitudinal range for nursery roosts of this species is 509-792 m.a.s.l. (Alcalde et
5 al., 2008). Although the species has been associated with forests, recent studies have indicated
6 that the significant factor in the choice of foraging areas by these bats is the existence of edge
7 habitats (Goiti et al., 2003; Goiti et al., 2008).

8 ***Rhinolophus ferrumequinum*** (Greater horseshoe bat, Table 1, Table 2, Fig. 4a,b).

9 This taxon is only rarely represented in the association. The large size of the remains (Table 3)
10 allows them to be assigned unequivocally to this species, as it is the largest extant horseshoe bat
11 in Europe (Dietz et al., 2009; Palomo et al., 2007; Sevilla, 1988); the molar measurements confirm
12 the assignation of the cranial remains to *R. ferrumequinum* (Fig. 4a and 5). This taxon presents the
13 dental formula of the genus, although p3 is very tiny and appears labially displaced outside the
14 tooth row (Sevilla, 1988; Topal, 1979) (Fig. 4a).

15 *R. ferrumequinum* has a broader distribution throughout Europe and Asia than *R. euryale*, although
16 the epicentre of its distribution is also the Mediterranean basin; in central Europe it only occupies
17 environments with a mild climate (Dietz et al., 2009). The greater horseshoe bat generally inhabits
18 temperate plains and Mediterranean mountains (Dietz et al., 2009); its altitudinal range in Aragon
19 has been recorded as 149-1,597 m.a.s.l. (Alcalde et al., 2008). It chooses its roosts in places with
20 a presence of mixed habitats for foraging: deciduous forest alternating with meadows and
21 shrubberies (Dietz et al., 2009). In the south of Europe, it is generally associated with medium-
22 sized horseshoe bats, together with *M. schreibersii*, *M. emarginatus* and *M. capaccinii* (Dietz et al.,
23 2009).

24 ***Rhinolophus sp.*** (Horseshoe bat specimens, Table 1, Table 2).

25 Some recovered material is too fragmented or deteriorated to be assigned unequivocally to either
26 of the two horseshoe bats identified in the association, or it comprises bones which could not be

1 compared to previous descriptions in the literature or to extant specimens for comparative
2 anatomy.

3 4.1.2. Vespertilionidae

4 ***Miniopterus schreibersii*** (Schreibers' bent-winged bat, Table 1, Table 2, Fig. 4e).

5 The size of the scapula corresponds to a medium-sized bat. The general morphology is different
6 from that of horseshoe bats, having a long straight lateral border which forms an angle of
7 approximately 60° with the spine. The coracoid process projects medially (unlike in *Myotis* and
8 *Plecotus*); the external edge of the supraspinal fossa at the junction of the spine and the superior
9 scapular border is rounded (instead of angulated as in other vespertilionids); and the superior
10 border shows a wide, triangular lamella projecting ventrally. For all these reasons we assign the
11 remnant to *Miniopterus*; there is no other species of this genus currently living in Iberia.

12 *M. schreibersii* today inhabits the Mediterranean region of Europe, as well as some parts of
13 northern Africa and the near East (Dietz et al., 2009). Its habitat preferences include all the
14 Mediterranean landscapes, and it shows a strong preference for roosting in caves (Dietz et al.,
15 2009; Palomo et al., 2007). Its altitudinal range is quite wide in Spain at present; it has been
16 recorded at heights as great as 1,599 m.a.s.l. (Alcalde et al., 2008).

17 ***Myotis* sp.** (Small mouse-eared bat specimens, Table 1, Table 2, Fig. 4d).

18 The size of the distal epiphyses of both humeri (Table 3) matches with the smallest forms of
19 Vespertilionidae. The morphology of the proximal edge between the trochlea and the condyle (Fig.
20 4d) is straight or slightly concave as in *Myotis* spp. by contrast with *Plecotus* spp., which presents a
21 convex edge (Dupuis, 1986; Felten et al., 1973). Possible taxa to which the remains might be
22 assigned are *M. nattereri*, *M. capaccinii*, *M. emarginatus*, *M. daubentonii* (although data in the
23 previous literature indicate slightly larger distal epiphyses for this species), *M. mystacinus* (data in
24 the literature indicate slightly smaller distal epiphyses) (Dupuis, 1986; Felten et al., 1973) and *M.*
25 *alcaethoe* (Dietz et al., 2009).

26 The above-mentioned species of small-sized *Myotis* present a notable variety of extant distribution
27 and habitat preferences. Although most of them inhabit all of Europe, the species *M. capaccinii* and

1 *M. emarginatus* are mainly restricted to the Mediterranean area of influence (Dietz et al., 2009), the
2 former being a markedly thermophilic taxon (Palomo et al., 2007). As regards their foraging areas,
3 they mostly prefer more or less closed forests (*M. daubentonii*, *M. mystacinus*, *M. alcahoe*, *M.*
4 *emarginatus*), although some also employ open landscapes (*M. nattereri*) or are conditioned by
5 other factors such as the presence of water bodies (*M. daubentonii*, *M. capaccinii*) (Palomo et al.,
6 2007; Dietz et al., 2009).

7 **4.2. Characterization of the taphocenosis**

8 The composition of the whole small-vertebrate assemblage is mainly dominated by bats, but other
9 groups of animals are also represented here (NR=49): rodents (*Apodemus* sp. MNI=1; *Eliomys*
10 *quercinus*, MNI=1), shrews (*Crocidura russula*, MNI=1) and birds (MNI=8).

11 The majority of the small bone remains have a fair coloration from white to beige, but just under a
12 fifth of the total specimens have darker, orange-brown tones or present small areas with black
13 staining (Fig. 6a,b,c). Almost half of the sample shows strong surface weathering, generally linked
14 to a fairer surface colour, whereas a small amount of the remains (15 %) shows dissolution marks
15 on the surface, and some specimens show both types of alteration (Fig. 6d,e,f). The *Rhinolophus*
16 sample presents a notable differential loss of skeletal elements. Considering the relative
17 abundance of elements ($R_i = N_i / (MNI \times E_i) \times 100$; Andrews, 1990; Bennàsar, 2010), the best-
18 preserved elements are the humeri and radii, the only bones with a survival percentage above 50%
19 (Table 4). The composition of the sample in terms of age groups based on tooth wear is as follows:
20 a minimum of five individuals of *R. euryale* were subadults (the teeth show no wear), whereas at
21 least two individuals were adults whose teeth show rounded cusps in one case, and dentine fields
22 in the other; the only mandible of *R. ferrumequinum* preserved belonged to an old adult individual
23 as dentine fields are observed in the molar (Fig. 6g,h,i). No teeth are preserved for the remaining
24 seven individuals, but all the limb bones preserved are completely fused, suggesting that they
25 belonged to individuals old enough to fly (Adams, 2008; Dietz et al., 2007, 2009).

26

27 **5. DISCUSSION**

1 **5.1. Origin of the accumulation**

2 Two hypotheses are considered here: (1) that the accumulation of the bat remains was due to the
3 action of predators and the subsequent transport of their discards deep into the cave by a water
4 flow, or (2) that the accumulation was produced by bats roosting in the cave followed by an *in situ*
5 death.

6 The varying degrees of coloration and weathering shown by the fossil bones point to different time-
7 spans of subaerial exposure and burial, which is a common phenomenon even among the bones
8 of a single skeleton once it is accumulated (Fernandez-Jalvo, 2016). The dissolution marks
9 observed in some specimens may be caused either by digestion or by the environmental moisture
10 of a water flow. The elements with the highest survival percentage in the assemblage are humeri
11 and radii, the two largest and strongest bones in the bat skeleton. The differential lack of skeletal
12 elements in the recovered assemblage may be explained as the effect of transport within the cave-
13 system or of predation. However, bats are rarely hunted by birds, carnivorous mammals or lizards
14 and cases of predation on horseshoe bats are even scarcer as this group is apparently more
15 efficient at eluding predators (Dietz et al., 2009; Kowalsky, 1995). The global composition expected
16 for a small-vertebrate assemblage produced by predatory accumulation is a small number of bats
17 represented in comparison with other small mammals such as rodents or with small birds, which is
18 contrary to the small-vertebrate assemblage from Los Batanes. If the bats died in the cave, the
19 dominance of bats in the assemblage could be explained by the continuous roosting of *R. euryale*
20 in the site, and the occasional presence of the other taxa. In the light of the great predominance of
21 bats within the assemblage, the most probable origin of the accumulation is the death of the
22 animals that formed a colony within the cave. Most of the Mediterranean horseshoe bats recorded
23 were subadult specimens, but with no obvious infants within the association it cannot be
24 determined whether it was a nursery colony. The relatively high location of the cave points instead
25 to a hibernating colony, which in these species of horseshoe bats usually involves a small cluster
26 of individuals (Alcalde et al., 2008; Palomo et al., 2007).

27 **5.2. Palaeoenvironmental framework**

1 The two species of horseshoe bats recorded in Los Batanes currently inhabit the Pyrenees of
2 Aragon although they have a discontinuous distribution (Alcalde et al., 2008). The bat species that
3 constitute the fossil assemblage studied here are typically associated with each other when
4 forming colonies in caves nowadays (Dietz et al., 2009; Palomo et al., 2007).

5 The bat association from Los Batanes Cave consists of a majority of Mediterranean-related
6 species with foraging strategies generally linked to the presence of forest habitat or at least patchy
7 arboreal cover. The other small mammals recorded in the site are today widespread throughout the
8 Iberian Peninsula with relatively wide altitudinal ranges, and they currently show habitat
9 preferences for both arboreal cover (*Apodemus* sp. and *E. quercinus*) and open landscapes (*C.*
10 *russula*) (López-García, 2011; Palomo et al., 2007). Based on the association, and having the
11 altitude of the site into account, the most plausible scenario for the period of accumulation was a
12 temperate, mild climate and a landscape with a notable presence of forest but a generally mixed
13 structure, where hedge habitats were prominent. In the light of the radiocarbon date obtained for
14 Los Batanes assemblage (an age of about 15.5-15 ka BP) and according to the two ice re-
15 advances detected in the Gállego Valley during the Lateglacial (one at about 17 ka BP, the other at
16 14-11.7 ka BP, Palacios et al., 2015), it is reasonable to conclude that at the time the accumulation
17 took place, the Gállego Valley was in a period of local ice-cover retreat soon after the first local re-
18 advance of the Lateglacial. Finally, the recorded bat association suggests that the climate
19 conditions in the area by that time were at least as mild as they are today.

20 **5.3. Palaeobiogeography**

21 The two *Rhinolophus* species found in Los Batanes were already present in Spain in the late
22 Pliocene (Agustí et al., 2011) and have a regular but scanty record throughout the Iberian
23 Quaternary (e.g. Sevilla, 1988; Galán et al., 2016a; Galán et al., 2016b), including some localities
24 in the Pyrenees and the pre-Pyrenees (Altuna, 1972; Blanco-Sancho, 1995; López-García, 2011;
25 Oms et al., 2008; Pemán, 1994). However, none of the localities in the literature with a record of
26 the two *Rhinolophus* species in the Pyrenees and the pre-Pyrenees is at such a great altitude as
27 Los Batanes Cave. This new record provides reliable evidence that the distribution of *R. euryale*

1 and *R. ferrumequinum* reached altitudes as high as 1,025 m in the Iberian Pyrenees during the
2 Lateglacial. In the case of the former species this is quite close to its extant altitudinal maximum in
3 Spain (1,360 m.a.s.l. according to Palomo et al., 2007). The fact that the altitudinal range of *R.*
4 *euryle* was at least as great then as it is today can be interpreted as an indicator of the relative
5 speed of this taxon in spreading into higher regions whenever climate conditions allowed it, even
6 during a period of time such as the Lateglacial which was mainly characterized by climate
7 instability and alternations of local ice-cover retreats and re-advances (García-Ruiz et al., 2003;
8 Palacios et al., 2015).

9

10 **6. CONCLUSIONS**

11 The late Pleistocene bat assemblage from the site of Los Batanes provides the highest Quaternary
12 record of *R. euryale* and *R. ferrumequinum* in the Spanish Pyrenees and pre-Pyrenees, which is
13 very close to present altitudinal limit of the first species. The clear Mediterranean affinity presented
14 by the bat association together with the altitude of the site suggests that even in a period
15 characterized by climatic instability as it was the Lateglacial, local climate conditions could be as
16 mild as they are nowadays during the moments of ice-cover retreat. Finally, the presence of *R.*
17 *euryle* in a site with this location and chronology could be an indicator of the relatively high speed
18 of this taxon in spreading into higher regions whenever climate conditions allowed it.

19 Further investigations into Quaternary mountain localities will improve the resolution of the bat
20 fossil record and increase our understanding of the effect of climate fluctuations on the distribution
21 of these horseshoe bat species.

22

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1 Figure 1. Los Batanes site; a: geographical location of the cave; b: scheme of the morphology of
2 Los Batanes Cave (elevation view), with the location of the fossil bone remains (topographical map
3 provided by the CEA member M. Gisbert).

4 Figure 2. Geological map of the Gállego Valley; 1: granites; 2: Devonian; 3: Cretaceous; 4:
5 Palaeogene; 5: Quaternary; MIE: local Maximum Ice Extent (predating global LGM); star: Los
6 Batanes Cave. Modified from Ríos-Aragües et al., 1987; Gil-Peña et al., 1996; Palacios et al.,
7 2015.

8 Figure 3. *Rhinolophus euryale* fossil specimens from Los Batanes Cave; a: mx with P4-M3 (L)
9 2017/1144 in occlusal (top) and labial (bottom) view; b: C (L) 2017/1145 in labial (top left), lingual
10 (top right) and occlusal (bottom) view, c: md with p4-m3 (L) 2017/1146 in occlusal (left) and labial
11 (right) view; d: p ring 2017/1147 in anterior (top) and posterior (bottom) view; e: hu (L) 2017/1149
12 in external (top) and internal (bottom) view; f: sca (L) 2017/1148 in external (top), dorsal (second
13 top), internal (second bottom) and ventral (bottom) view; g: fe (R) 2017/1150 in posterior (top) and
14 anterior (bottom) view.

15 Figure 4. *Rhinolophus ferrumequinum* fossil specimens from Los Batanes Cave; a: md with m2 (R)
16 2017/1151 in occlusal (left) and labial (right) view; b: dep hu (L) 2017/1152 in external (left) and
17 internal (right) view. cf. *Miniopterus schreibersii* fossil specimen from Los Batanes Cave; c: sca (L)
18 2017/1153 in ventral (left), internal (second left), in dorsal (second right), and in external (right)
19 view. *Myotis* sp. fossil specimens from Los Batanes Cave; d: dep hu (R) 2017/1154 in external
20 (left) and internal (right) view.

21 Figure 5. Dot plots comparing the anteroposterior lengths (L) of upper and lower molars of the
22 *Rhinolophus* specimens from Los Batanes and the extant specimens in the collections (see
23 paragraph 3.2.). The circles and squares represent the mean value for each group, the lines
24 represent the standard deviation, in mm. Anatomical abbreviations in paragraph 3.3.

25 Figure 6. Main taphonomic remarks. Bone coloration; a: orange-brown mandible of *R. euryale*; b:
26 beige mandible of *R. euryale*; c: white mandible of *R. euryale*. Bone surface alterations; d: non-
27 altered bone and enamel in a *R. euryale* mandible; e: bone surface affected by weathering, but not

1 the enamel, in a *R. euryale* mandible; f: surface weathering and dissolution marks in a distal
2 epiphysis of *R. euryale* humerus. Tooth-wearing; g: subadult specimen of *R. euryale*, the m2
3 shows no wear; h: adult specimen of *R. euryale*, the m2 shows notable wear on the occlusal
4 surface; i: adult specimen of *R. ferrumequinum*, the m2 shows notable wear on the occlusal
5 surface.

6 Table 1. Presence in terms of NISP (number of identified specimens) and MNI (minimum number
7 of individuals) of each identified bat taxon.

8 Table 2. List of the recovered material for each bat taxon; Elem: element; Lat (laterality), n: number
9 of assigned specimens. Anatomical abbreviations in paragraph 3.3.

10 Table 3. Biometric characterization of the teeth and humeri of Los Batanes fossil bat assemblage,
11 Elem: element, Meas: measurement, n: number of measured specimens; Min: minimum value of
12 the sample (mm); Max: maximum value of the sample (mm); M: mean value (mm); SE: standard
13 error (mm); SD: standard deviation (mm). Anatomical abbreviations in paragraph 3.3.

14 Table 4. Relative abundance of the main skeletal elements recovered at Los Batanes and
15 assigned to genus *Rhinolophus*; Elem: element; Ri: relative abundance of the elements in the
16 sample; Ni: minimum number of elements in the sample; Ei: number of elements in an individual.
17 Anatomical abbreviations in paragraph 3.3.

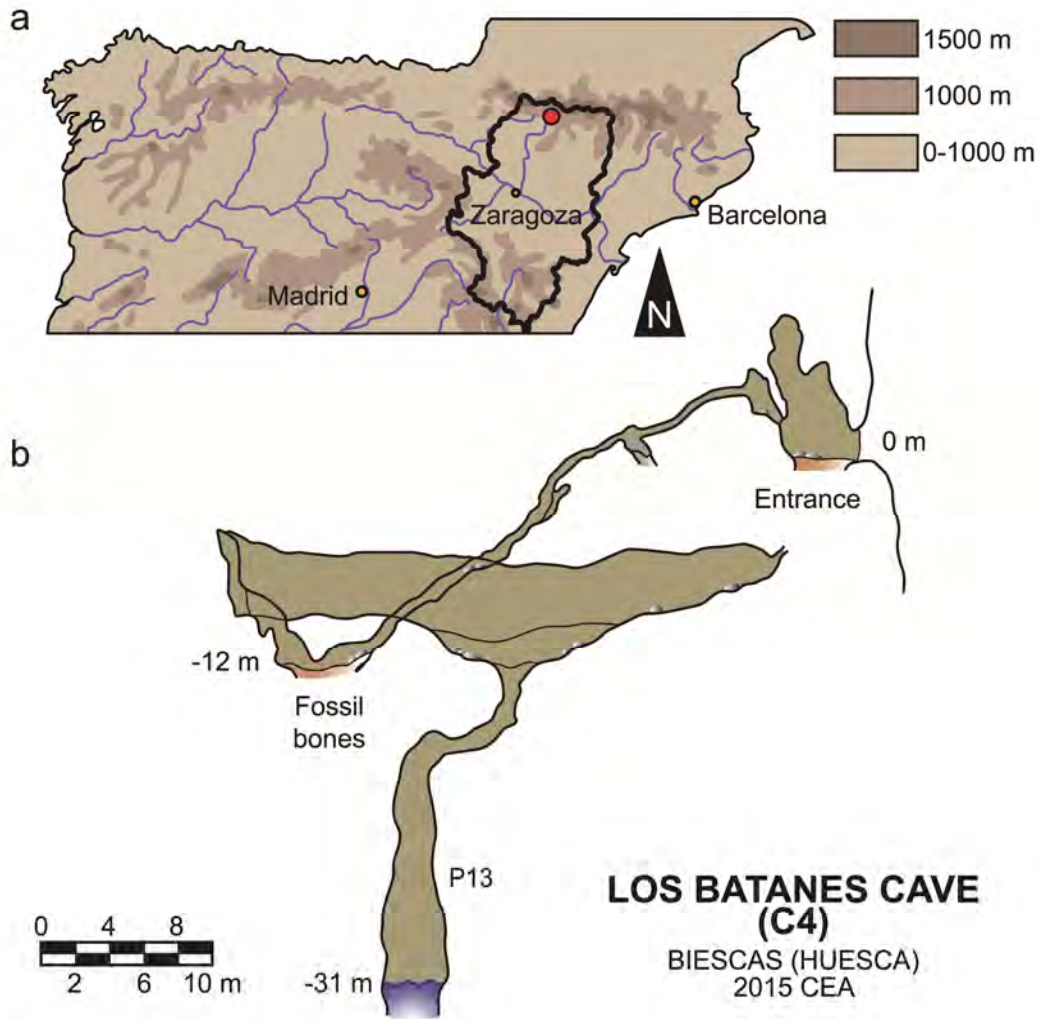
18

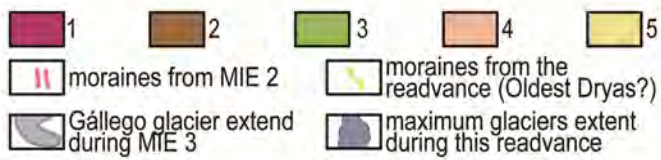
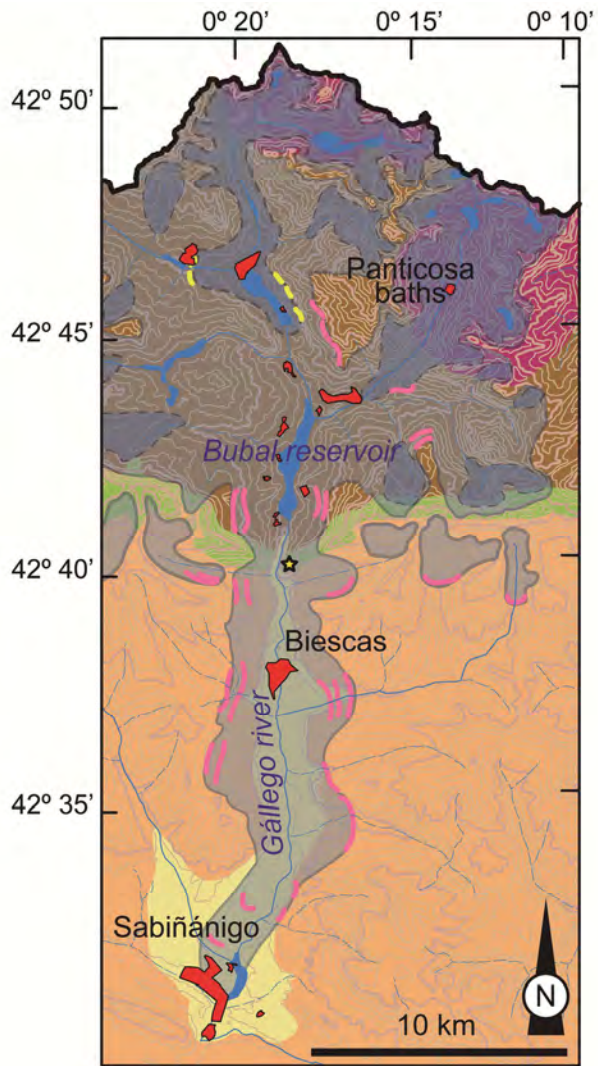
Element (Cr)	Ni	Ei	Ri (%)	Element (PCr)	Ni	Ei	Ri (%)
bu	9	2	32.1	clav	9	2	32.1
mx	2	2	7.1	p ring	3	1	25.0
md	9	2	32.1	esc	5	2	17.9
teeth	9	16	4.0	pelv	1	2	3.6
				metcp (ii-v)	26	8	23.2
				hu	17	2	60.7
				ra	20	2	71.4
				fe	10	2	35.7
				ti	5	2	17.9

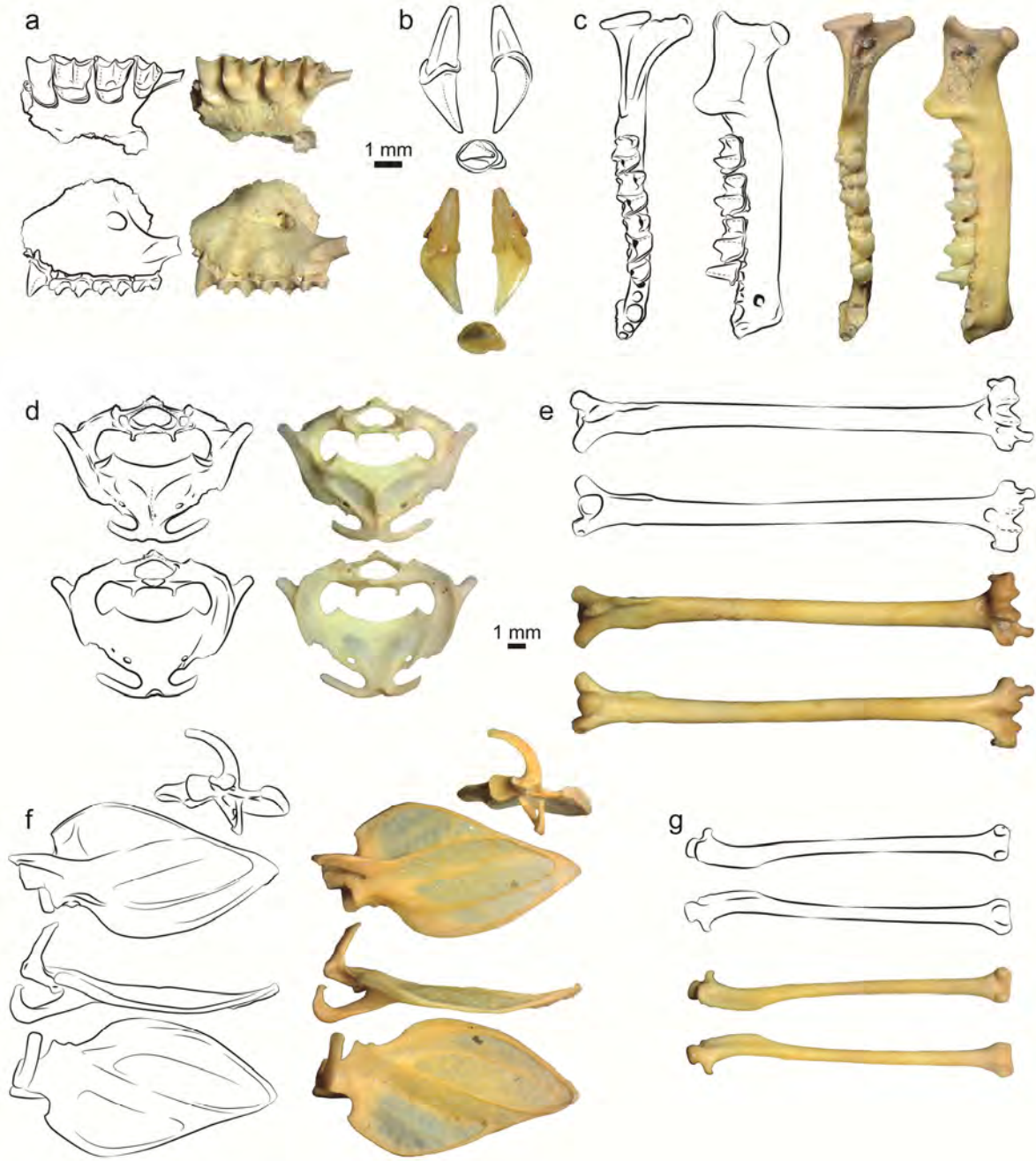
Taxa	Elem	Lat	n	Taxa	Elem	Lat	n
<i>R. euryale</i>	bu	R	7	<i>R. euryale</i>	dep ra	R	4
		L	2			L	2
	mx	R	1		pep ra	L	6
		L	1		diap ra	-	3
	C	R	1		ti	R	3
		L	1		pep ti	L	1
	M1	R	1		fe	R	5
		L	2		pep fe	R	3
	P4	L	1			L	2
	md	R	3		dep fe	R	1
		L	4	md	R	1	
	md b	R	1	m1	R	1	
		L	2	hu	R	1	
	fr md	R	2	dep hu	R	1	
		L	1		L	2	
	c	R	1	pep hu	L	1	
		L	2	pep ra	R	2	
	p4	R	1		L	1	
	at	-	1	diap ra		2	
	p ring	-	3	ti	L	1	
esc	R	2	fr pelv		1		
	L	3	fr pep ra	L	1		
hu	R	3	pep	R	6		
	L	4	metcp II	L	1		
pep hu	L	2	pep	R	4		
dep hu	L	5	metcp IV	L	5		
dep + diap hu	L	1	pep	R	7		
diap hu	-	1	metcp V	L	3		
ra	L	1	<i>M. schreibersii</i>	sca	L	1	
	R	1	<i>Myotis sp.</i>	hu	R	2	
pep + diap ra	R	3	Chiroptera indet.	fr clav		9	
	L	5		vert		12	

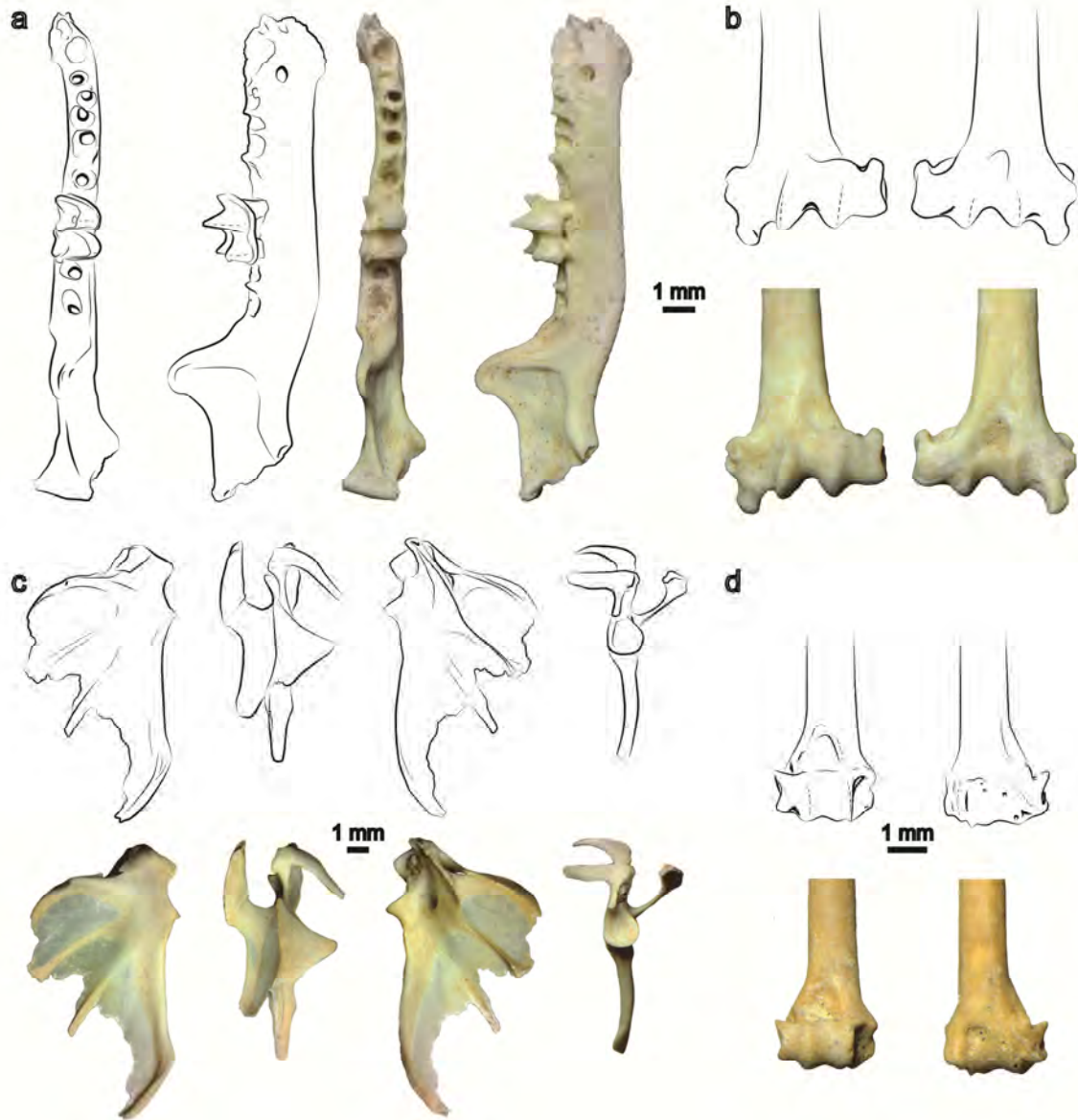
Taxon	NIPS	MNI
<i>Rhinolophus euryale</i>	99	12
<i>Rhinolophus ferrumequinum</i>	13	2
<i>Rhinolophus</i> sp.	28	-
cf. <i>Miniopterus schreibersii</i>	1	1
<i>Myotis</i> sp.	2	2
Chiroptera indet.	21	-
TOTAL	164	17

Taxon	Elem	Meas	n	Min	Max	M	SE	SD
<i>R. euryale</i>	P4	W	3	1.13	1.19	1.16	0.02	0.03
		L	3	1.20	1.67	1.37	0.15	0.27
	C	W	2	1.02	1.08	1.05	0.03	0.04
		L	2	1.44	1.49	1.46	0.02	0.03
	M1	W	1			1.83		
		L1	1			1.63		
		L2	1			1.17		
	M2	W	4	1.64	1.75	1.71	0.02	0.05
		L1	4	1.45	1.48	1.46	0.01	0.01
		L2	4	1.01	1.12	1.06	0.02	0.05
	M3	W	2	0.17	1.50	0.84	0.67	0.94
		L1	2	1.11	1.15	1.13	0.02	0.03
		L2	2	0.74	0.81	0.78	0.04	0.05
	m1	w1	8	0.77	1.06	0.92	0.03	0.09
		w2	8	0.85	1.08	0.95	0.02	0.07
l		8	1.50	1.68	1.64	0.02	0.06	
m2	w1	9	0.84	1.12	0.98	0.03	0.09	
	w2	9	0.90	1.11	1.00	0.02	0.07	
	l	9	1.53	1.59	1.55	0.01	0.02	
m3	w1	6	0.82	1.01	0.93	0.03	0.08	
	w2	6	0.67	0.83	0.76	0.03	0.06	
	l	6	1.24	1.44	1.37	0.03	0.07	
hu	dep W	10	4.35	4.61	4.44	0.03	0.09	
<i>R. ferrumequinum</i>	m1	w1	1			1.47		
		w2	1			1.56		
		l	1			2.02		
	m2	w1	1			1.49		
		w2	1			1.62		
		l	1			2.02		
hu	dep W	3	4.94	5.11	5.04	0.05	0.09	
<i>Myotis sp.</i>	hu	dep W	2	2.36	2.44			

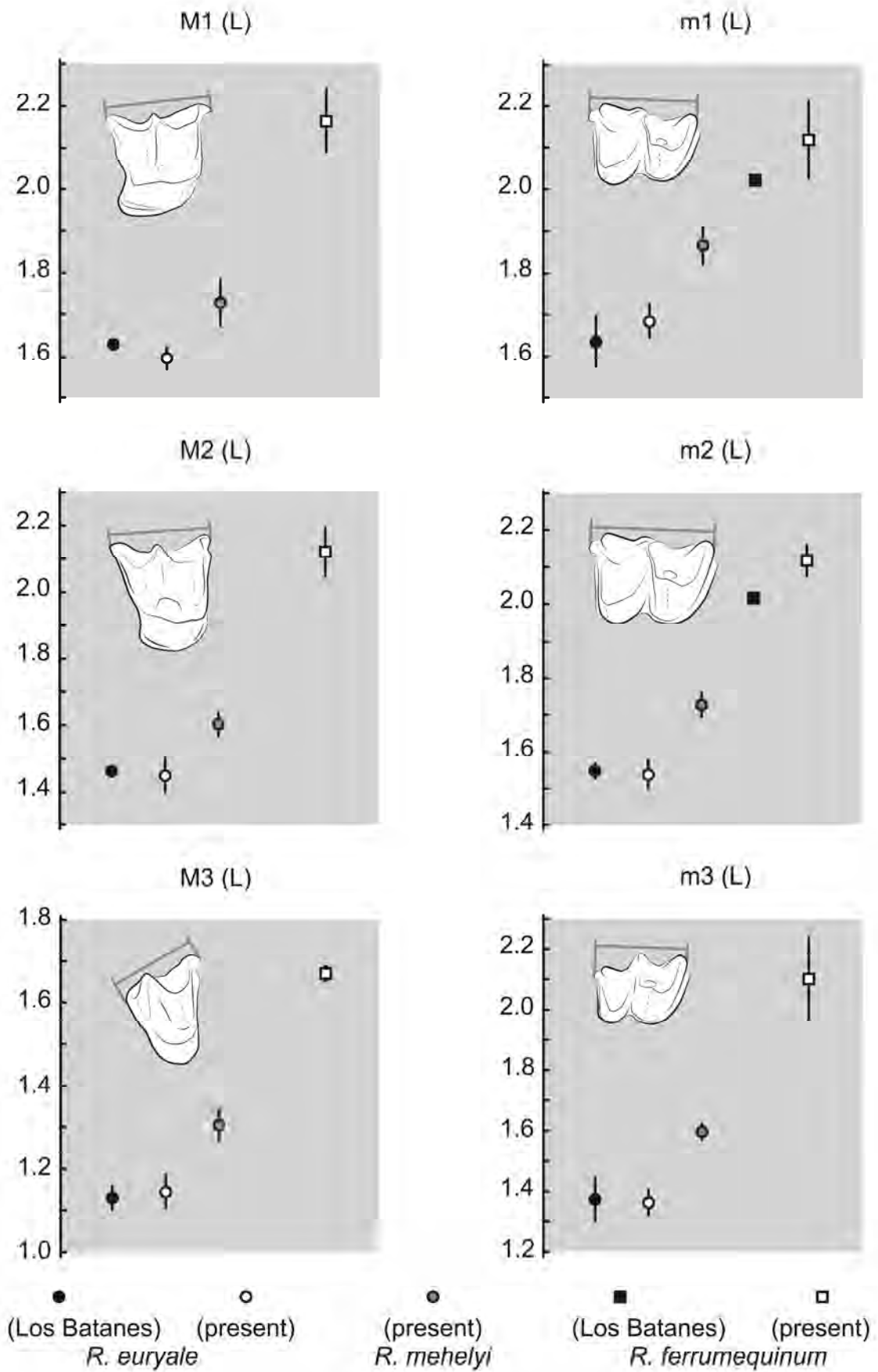


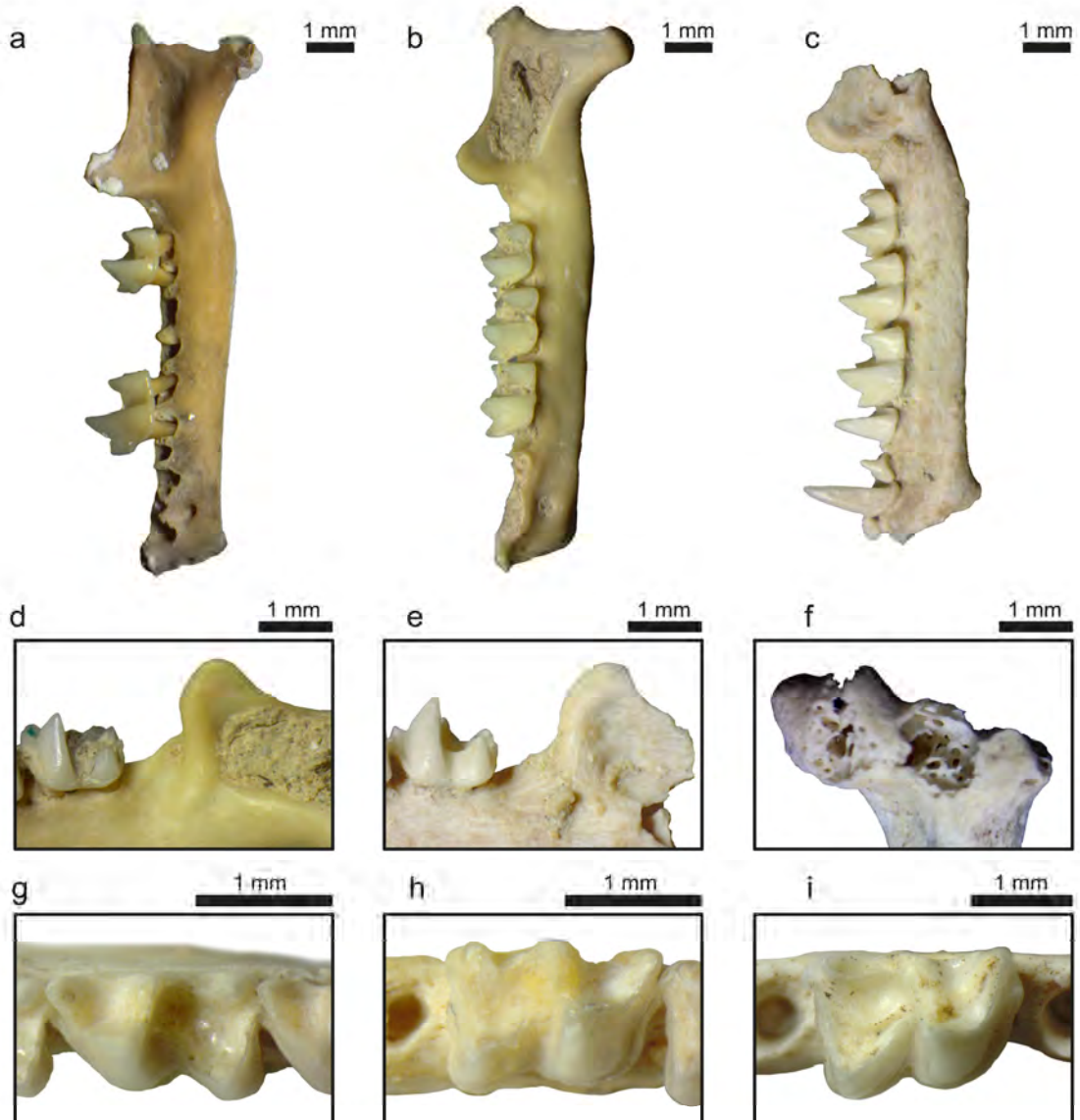






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