Molecular, morphological and acoustic identification of *Eumops maurus* and *E. hansae* (Chiroptera: Molossidae) with new reports from Central Amazonia

ADRIÀ LÓPEZ-BAUCELLS[a,b,c,d]*, RICARDO ROCHA[a,c,d], VALÉRIA DA CUNHA TAVARES[e,f], LIGIANE MARTINS MORAS[e], SARA EMA SILVA[a], PAULO ESTEFANO DINELI BOBROWIEC[c], CHRISTOPH F.J. MEYER[a,c,g]

[a] Centre for Ecology, Evolution and Environmental Changes (cE3c). Faculty of Sciences, University of Lisbon, Building C2, Campo Grande, 1749-016 Lisboa (Portugal)

[b] Granollers Museum of Natural Science, Bat Research Group. c/Palaudàries, 102 - Jardins Antoni Jonch Cuspinera, 08402 Granollers, Catalonia (Spain)

[c] Biological Dynamics of Forest Fragments Project, Instituto Nacional de Pesquisas da Amazônia (INPA). Av. André Araujo, 2936, 69067-375 Manaus AM (Brazil)

[d] Metapopulation Research Group, University of Helsinki. Department of Biosciences, PO Box 65, Viikinkaari 1, FI-00014 Helsinki (Finland)

[e] Departamento de Zoologia, Universidade Federal de Minas Gerais (UFMG), Av. Antônio Carlos, 6627, MG-31270-901, Belo Horizonte, Minas Gerais MG (Brazil)

[f] Departamento de Biologia, Universidade Estadual de Minas Gerais (UEMG), Av. São Paulo, 3996, MG-32400-000 Ibirité MG (Brazil)

[g] School of Environment and Life Sciences, University of Salford, M5 4WT Salford (United Kingdom)

* Corresponding author: *adria.baucells@gmail.com // +4407843702369*

Orcid identifiers:

Adrià López-Baucells: orcid.org/0000-0001-8446-0108
Ricardo Rocha: orcid.org/0000-0003-2757-7347
Valéria da Cunha Tavares: orcid.org/0000-0003-0966-0139
Sara Ema Silva: orcid.org/0000-0001-8766-8131
Paulo Estefano Dineli Bobrowiec: orcid.org/0000-0002-8945-6105
Christoph Meyer: orcid.org/0000-0001-9958-8913

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Abstract

Eumops maurus and *E. hansae* are rarely captured Neotropical molossid bats for which information on taxonomy, natural history, and spatial distribution are scarce. This translates into a poor understanding of their ecology and limits the delimitation of useful characters for their identification. Here, we describe records of these two molossids from the Central Brazilian Amazon, providing data on their external and craniodental morphology, DNA barcode (COI) sequences complemented by acoustic data for the species. Morphological characters, DNA sequence data and phylogenetic relationships within the genus *Eumops* were consistent with those previously described for both species. Echolocation call characteristics did not differ significantly so as to be useful for separating *E. maurus* and *E. hansae* from other congeners. Our records are, respectively the first and the second for Central Amazonia as one individual previously attributed to *E. amazonicus* from Manaus may be considered a junior synonym for *E. hansae*. These new records increase the extent of the species' known ranges, partially filling in previous existing gaps in their distribution in central South America. Our data further suggest that these molossid bats forage in a wider range of habitats than previously thought.

Keywords: Amazonian rainforest, Barcoding, Bioacoustics, Brazil, Echolocation, Systematics, Taxonomy.

Introduction

The Molossidae are a diverse family of aerial insectivorous bats, with more than 100 extant species whose center of richness is in tropical and subtropical regions (Gregorin et al. 2016; Simmons 2005). Due to their high-flying habits of foraging above forest canopies and over open landscapes, molossids are usually hard to capture using ground level mist-nets, as a consequence of which knowledge of their ecology and distribution is still limited (Barataud et al. 2013; Gregorin, et al. 2016; Jung et al. 2014). Moreover, the relatively few records of molossids often come from colonies found within urban areas, leading to the biased perception that these bats may particularly be associated with anthropic environments (López-Baucells et al. 2017a; Sodré et al. 2008). Overall, data on molossid species from South America are scarce and despite the fact that multidisciplinary research on these bats is globally increasing (Gager et al. 2016) their natural history remains largely unknown, particularly for some of the more elusive species.

Bonneted bats of the genus *Eumops* Miller, 1906 are widely distributed throughout the New World, ranging from the southeastern United States to Patagonia, including some Antillean islands (Gardner 2008). *Eumops* is one of the most diverse molossid genera with 17 species currently recognized (Gregorin, et al. 2016). However, knowledge about the distributions of *Eumops* species is limited (Medina et al. 2012). Moreover, the taxonomy of the genus is in flux, as recently several previously unrecognized species have been described and the phylogeny of *Eumops* has been revised (Bartlett et al. 2013; Gregorin 2009; Gregorin, et al. 2016; Medina et al. 2014).

Both Sanborn's Bonneted Bat, *Eumops hansae* Sanborn, 1932, and the Guianan Bonneted Bat *E. maurus* (Thomas, 1901) are widely distributed throughout the Neotropics, but rarely captured. Their occurrence has been documented only through a handful of records across their

distributional ranges. While *E. hansae* has been recorded in 12 countries across Central and South America, *E. maurus* is only known from eight localities from Guiana, Brazil, Venezuela, Peru and Ecuador (Fig. 1). Not only are the ranges of these two species still poorly documented, but also basic natural history, ecological and genetic data are scarce and their echolocation calls remain undescribed (Best et al. 2001a, b). Here, we present data on the morphology, echolocation, and mitochondrial DNA of *E. hansae* and *E. maurus* from the Central Brazilian Amazon. We discuss the potential of each kind of information to aid in the reliable identification of the two species.

Material and Methods

Study area

Field work was carried out at the Biological Dynamics of Forest Fragmentation Project (BDFFP), located ca. 80 km north of Manaus in the Central Amazon, Brazil (2°25´S, 59°50´W; elevation 30-125 m a.s.l.) (Lovejoy and Bierregaard 1990). The predominant vegetation in this region is lowland primary *terra firme* forest (Bruna and Kress 2002), with minor areas of secondary forest (8,325ha). Mean annual temperature is 26 ºC (de Oliveira and Mori 1999) and annual rainfall ranges from 1,900-3,500 mm, with a rainy season from October to May. The primary forest canopy is 30-37 m tall, with emergent trees up to 55 m (Laurance et al. 2017).

[Figure 1 near here]

Bat sampling

Extensive standardized mist-netting was carried out across the BDFFP landscape between 2011 and 2014 as part of a comprehensive project on the effects of forest fragmentation on phyllostomid bats (Farneda et al. 2015; Rocha et al. 2017). Additionally, during the same period mist nets (12x2.5 m, 16 mm mesh, ECOTONE, Sopot, Poland) were also set opportunistically across streams and small lakes, both during the rainy and the dry season. Nets were left open for six hours after sunset and checked every 20-30 minutes. This opportunistic sampling resulted in captures of three adult males of *E. maurus* and three adult females of *E. hansae* over natural lakes, one in the Km 41 reserve (2°26'51.69"S, 59°45'2.05"W) and one in Colosso reserve (2°24'39.34"S, 59°52'8.55"W), between April and June 2014. All bats were captured in different nights. Lakes measured approximately 100x112 and 80x55 m respectively, and were up to 2 m deep. Both lakes underwent seasonal water level fluctuations, but carried water throughout the

year. However, they greatly differed regarding human use. The lake in Colosso was used as a water reservoir for cattle and horses, whereas the one in Km 41 is located far away from human settlements and surrounded by primary forest.

One individual per species was collected as voucher specimen. From all individuals, including the ones that were released, standard external measurements were taken in the field (see below). We also took wing tissue samples using commercial wing biopsy punches (2 mm, Stiefel Laboratories, Inc., Germany). Voucher specimens were deposited at the Mammal Collections of the Instituto Nacional de Pesquisas da Amazônia (INPA 6731 *Eumops maurus*; INPA 6732 *Eumops hansae*) in accordance with Brazilian conservation and animal welfare laws. Research was carried out under scientific license from the Instituto Chico Mendes de Conservação da Biodiversidade—ICMBio (permit number 26877-2).

Morphology

External and craniodental characters measured are based on Eger (1977) and Freeman (1981), and were recorded in millimeters (mm) using digital calipers accurate to 0.1 mm (Fig. 2). Body mass was recorded in grams (g) with a Pesola spring scale (accuracy of 0.5g). Measurements are defined as follows: total length (TL); tail (TAIL); thumb length (ThL); nail (Na); calcar length (Cal); antitragus width (AntW); antitragus height (AntH); hind foot length (HF); ear length (E); forearm length (FA); tibia length (TiL); fourth metacarpal length (MET-IV); first phalanx of the fourth digit (PHA1-IV); greatest length of the skull (GLS); condyloincisive length (CIL); zygomatic breadth (ZB); postorbital breadth (PB); braincase breadth (BB); maxillary toothrow length (MTRL); breadth across molars (BAM); breadth across canines (BAC); mandibular toothrow length (MANDL) and mandibular length (MANDLT).

[Figure 2 near here]

Echolocation recordings

Echolocation call recordings were obtained from captured individuals (two individuals per species were recorded) using a Pettersson D1000X detector (Pettersson Elektronik AB, Uppsala, Sweden) after each individual's release in forest clearings. To minimize bias in acoustic parameters, only those sequences recorded at least 5 seconds after the release (when the bats were normally flying at higher altitudes) were considered for analysis. Individual *Eumops hansae* were easily released from the hand as their small size allows them to take off even in quite cluttered environments from relatively low heights (they are more maneuverable than other molossid species), despite their narrow wings. With *Eumops maurus* the release process was slightly more complicated and we tried to facilitate their take-off by placing the bats high up on the trunks of dead trees or on poles. The detector was placed 15 m away from the animals. Recordings were made at a sampling frequency of 250 kHz, with 16 bits/sample. For sound analysis, we used a customized 512 point fast Fourier transform (FFT) with a Hanning window for both spectrograms and power spectrum. To characterize the echolocation calls, the following parameters were measured from 24 pulses for *E. hansae* and 49 pulses for *E. maurus*, using Kaleidoscope v.3.1.4b (Wildlife Acoustics, USA): peak frequency or frequency with maximum energy (FME), start frequency (St-freq) and end frequency (End-freq) (Jung, et al. 2014; López-Baucells et al. 2016a). Other common measurements such as bandwidth and pulse duration were not considered as they are particularly prone to be biased after hand release. To minimize measurement error and bias, we only measured those pulses from the recorded echolocation call sequences whose intensity was around 20 dB higher than the background noise.

DNA barcoding and phylogenetic analyses

DNA of the two *Eumops* species was extracted from muscle tissue of the collected individuals. For preserved tissue samples, PCR amplifications of COI were carried out in 15 µL reactions containing 60 ng of DNA, 1.5 U of Platinum Taq (Invitrogen®, Carlsbad, CA, USA), 1 x Platinum Taq PCR buffer, 1.5 mM $MgCl_2$, 200 µM dNTPs set (Invitrogen®) and 0.3 µM of each primer. The primers used for amplifications were modified from Folmer et al. (1994), available from the BOLD project (Ratnasingham & Hebert, 2007). We used the following cycling scheme for PCRs: 2 min at 94°C followed by 35 cycles of 30 s at 94°C, 40 s at 50°C for primer annealing and 1 min at 72°C for extension, and a final 10 min extension at 72°C after the last cycle. Sequencing of both strands was carried out on an ABI 3130 (Applied Biosystems®) automated sequencer using Big Dye Terminator Cycle Sequencing methodology (Applied Biosystems®). The sequences produced in this study were deposited in the BOLD database (http://www.boldsystems.org) under the process ID BRMAM620-15.

We retrieved sequence data available for six species of *Eumops* and also for *Tadarida brasiliensis* (outgroup) from BOLD and GenBank to perform phylogenetic analyses for the genus, and to infer the position of our specimens in the phylogeny. GenBank accession numbers are given in Table S1. We used MEGA 6 (Tamura et al. 2013) to align and edit the sequences, and to calculate genetic distances based on a Kimura 2-parameter (K2P) model (Kimura 1980). Partition Finder 1.0.1 (Lanfear et al. 2012) was used to select the best partitions and models of sequence evolution for phylogenetic inference, whereby fit was assessed by Akaike's information criterion (AIC) (Akaike 1974). Phylogenetic relationships were inferred using Maximum Likelihood (ML) and Bayesian analysis methods as implemented respectively in RAxML v8.2.0 (Stamatakis 2014) and MrBayes v3.2.4 (Ronquist et al. 2012). For the Bayesian

analysis, the three codon positions were analyzed separately under the following models: SYM+I for the first codon position, HKY for the second codon position and GTR+G for the third codon position. A run with 4 chains was conducted for 20,000,000 generations (sampled every 200 generations). The first 10% of trees were discarded as burn-in, and the remainder was used to estimate tree parameters and topology. Trees were visualized in FigTree v1.4.2 (http://tree.bio.ed.ac.uk/software/figtree/). Maximum Likelihood analyses were conducted using the GTRCAT substitution model with 1,000 bootstrap replicates.

Results

Morphology

We identified *Eumops hansae* based on a combination of characters, including its (i) small size (FA = 38.7 mm, Table 1), (ii) ears connected by a membranous stripe on the forehead, (iii) square-shaped tragus, and (iv) blackish brown dorsal pelage contrasting with the paler venter with three-colored banded fur. Our female specimen had a long skull with large and well-defined basisphenoid pits (Fig. 2D–F), and the third commissure of M3 nearly as well developed as the second (Fig. 2E). Individuals of *E. maurus* (all males) were readily identified based on external measurements (Table 2), the species' distinctive band of pure white hairs in the proximal ventral plagiopatagium (measuring approximately 5x20 mm), and the narrow band along the lateral body. The skull of our specimen had paired oval, and relatively shallow pits in its basisphenoid bone, and small anterior upper premolars (Fig. 2).

[Table 1 & 2 near here]

Echolocation calls

Echolocation calls of both *E. maurus* and *E. hansae* consisted of a quasi-constant frequency (QCF) component, and were almost constant at very low frequencies (Table 3, Fig. 3). As usual for molossids, the fundamental was the harmonic with the maximum energy in both cases. For *E. maurus,* peak frequency averaged 25.3 kHz, ranging between 19-30 kHz. *Eumops hansae* emitted low-frequency QCF pulses at a peak frequency of 21.9 kHz (range 18-24 kHz). For both species, the shape of the pulses was clearly concave and downward modulated, being the first part of the pulse highly modulated, and the terminal part almost constant. Based on our recordings there was no evidence of pulse alternation in either species.

[Table 3 near here] [Figure 3 near here]

DNA barcoding and phylogenetic analyses

Average pairwise COI distances between *Eumops* species ranged from 3.2% (*E. auripendulus* versus *E. maurus*) to 17.4% (*E. hansae* versus *E. perotis*) (Table 4 & 5), and intraspecific genetic distances ranged from 0% (*E. maurus* and *E. floridanus*) to 0.9% (*E. hansae*). Sequence similarity between the individuals of *E. hansae* from Guiana and our specimen from Brazil was high (99.3 - 99.8%). In contrast, similarity between our Brazilian specimen and the sequence from a single individual from Belize was considerably lower (96.3%). For *E. maurus*, the single published barcoding sequence comes from Guiana (Clare et al. 2011), and fully (100%) matched the sequence obtained for our Brazilian specimen.

Our specimen of *E. hansae* formed a clade with a specimen from Guiana, nested within a clade composed of representatives from Belize and several other individuals from Guiana, sister to all other *Eumops* species included in this analysis. The samples of *E. maurus* from Ecuador and Brazil formed a well-supported sister clade to *E. auripendulus* (Fig. 4).

[Table 4 & 5 near here] [Figure 4 near here]

Discussion

We used multiple methodological approaches in combination (external and craniodental morphology, DNA barcode and acoustic data) to confirm new occurrence records for 2 poorly known molossid species. Despite the clear advantages and improvements that multidisciplinary studies provide to scientists, they are still fairly rare within the literature, especially on tropical bat species (but see Gager, et al. 2016). Such integrative studies should be widely encouraged, as they can advance the further description and understanding of the diversity of bat species across the continent more efficiently than single-method studies.

Species distribution

Taxonomic uncertainties of *E. hansae* have led to knowledge on its natural history and current distribution lagging considerably behind that for other Neotropical molossids (Bartlett, et al. 2013). Although being one of the least known *Eumops* species, *E. hansae* had previously been captured in a wide range of habitats. These include forests off coastal areas (Álvarez-Castañeda and Álvarez 1991; Koopman 1982), tropical rainforests (Eisenberg 1989; Lee and Bradley 1992; Paglia et al. 2012; Simmons and Voss 1998), savannas (Ibáñez and Ochoa 1989), premontane humid forests (Ochoa et al. 1988), dry forests (Pineda et al. 2008), and tropical lowland forest in hilly terrains (Graham and Barkley 1984). However, despite the broad range of habitats where it has been found, captures were almost always over ponds, large clearings, rivers and large lagoons. The presence of this species in such a diverse range of environments suggests that *E. hansae* is not restricted to a particular habitat, and could in fact be widespread (Fig. 1). *Eumops maurus* inhabits a diverse array of habitats, including savannas, although it is often associated with swamps dominated by the palm *Mauritia flexuosa*, gallery forests, swampy evergreen forest

and urban spaces (Best, et al. 2001b; Sodré, et al. 2008). Overall, specimens from only seven localities are known for this poorly known bat (Fig. 1) comprising a total of six females and a single male from Guiana, the holotype. Our records from Manaus (3 males) fill a gap in the center of the previously known distribution (Fig. 1) representing a westward range expansion of 1900 km from Corumbá (Brazil) and 620 km southward from the Kanaku mountains (French Guiana: Sodré, et al. (2008)). Of the three individuals, one voucher was collected, which represents the second male specimen available in collections.

Morphology

Morphological variation within molossids makes reliable species identification sometimes difficult and may lead to inconsistent results among studies (Gregorin 2009), particularly if based mostly on continuous characters. That is, for instance, the case for the use of forearm length to separate *E. maurus* from other *Eumops* species. In these cases, sometimes consistent discrete characters, such as the presence of the large lateral stripe of white ventral fur alongside its body, and the oval shaped, relatively shallow pit in its basisphenoid bone (Best, et al. 2001b; Gregorin 2009), make *E. maurus* easy to identify. As reported previously for specimens from Surinam, there was a small anterior upper premolar present in our voucher, which Eger (1977) reported to be absent in the holotype, and therefore this character may be considered a variable condition for the species. Our specimen of *E. maurus* has a somewhat smaller forearm compared to the range of forearm lengths of specimens from other localities, including the holotype (male) collected in Guiana (Table 2). Cranial measurements of our specimen did not differ much from those of the holotype. Unfortunately, no additional *E. maurus* male skull measurements are available for comparison. Based on the sparse cranial measurements available for male and female *E. maurus* we tentatively posit that males have somewhat longer skulls than females, but are otherwise

similar in size. All measurements from *E. hansae* fell within the expected range for the species, and the few measurements available for males were larger than those for females (Table 1).

Echolocation calls

In contrast to other families, most molossid species are known to forage in open spaces adapting their echolocation to long-range prey detection. Like their congeners, quasi-constant frequency pulses characterize the echolocation calls of *E. maurus* and *E. hansae* and reflect their adaptation to flying in open spaces (Aldridge and Rautenbach 1987; Russo and Jones 2002). There is a considerable overlap in peak frequency between *E. maurus* and other *Eumops* species, including *E. hansae*, *E. auripendulus, E. glaucinus*, and *E. dabbenei* (Table 3, Fig. 3) thus rendering this parameter useless for species identification. Some Neotropical molossids such as *Molossus molossus*, *M. rufus* and *Promops centralis* can be easily identified acoustically based on the alternation of pulses, call shape (concave vs convex or upward- versus downward-modulated for instance), and peak frequencies (Barataud, et al. 2013; Jung, et al. 2014; López-Baucells, et al. 2016a). Unfortunately, based on our recordings, no parameter was found to be diagnostic so as to allow reliable discrimination between either of the two *Eumops* species. Until more acoustic data become available, allowing for a comprehensive genus-wide analysis, we recommend grouping all species from the genus *Eumops* into a single phonic group. The fact that we could not find any pulse alternation could result from the stress caused by the handling and the proximity of cluttered forest where they were released. More calls recorded under natural conditions would be essential to complement the description of the echolocation call characteristics of the species. The fact that other poorly studied species of *Eumops* have similar calls stresses the need for further studies to evaluate additional criteria for their acoustic discrimination.

DNA barcoding and phylogenetic analyses

Cytochrome c Oxidase subunit I (COI) has been proposed as a global scale barcode for animal species identification (Kress et al. 2015; Ratnasingham and Hebert 2007) and has already been successfully used to aid in the identification and discovery of Neotropical bats (Clare et al. 2013; Lim and Arcila Hernandez 2015). Our sequences from *E. hansae* and *E. maurus* were properly classified at species level using the DNA barcode database. This corroborates, as suggested by Clare, et al. (2011), that DNA barcoding is a powerful auxiliary tool to identify specimens. While COI sequences available in GenBank are still scarce for *E. maurus*, for *E. hansae* several sequences can be found. Nevertheless, for both of these *Eumops* species and congeners there are large sampling gaps throughout their distribution range. The position of *E. hansae* within the *Eumops* tree has shifted historically to either basal to all species of *Eumops*, or nested with small *Eumops* (Bartlett, et al. 2013; Gregorin, et al. 2016). Our phylogenetic analyses recovered *E. hansae* as sister to all other *Eumops*, as did the concatenated data of Bartlett, et al. (2013) and Gregorin, et al. (2016). Alternatively, *E. hansae* has been previously hypothesized to be sister to all small-sized *Eumops* (*bonariensis*, *patagonicus*, *nanus*) based on molecular (Medina, et al. 2014) and morphological evidence (including *delticus*) (Gregorin 2009, Medina, et al. 2014). On the other hand, the position of *E. maurus* within *Eumops* seems more stable as this taxon is frequently recovered as the sister of *auripendulus* based both on molecular (Bartlett, et al. 2013; Gregorin, et al. 2016; Medina, et al. 2014) and morphological data (Gregorin 2009).

DNA barcoding is still not always employed in studies that report new species occurrences or distribution range expansions in many taxa (Bezerra et al. 2005; Khedkar et al. 2016; López-Baucells et al. 2013, 2014; Moras et al. 2015; Tavares et al. 2014; but see Khedkar, et al. 2016; López-Baucells et al. 2016b, 2017b; Nagy, et al. 2012; Seyhan and Turan 2016). Its increasingly

common use as a supporting tool for inventories will certainly accelerate the study and description of Neotropical bat diversity.

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Tables

Table 1. External and craniodental measurements (mm) of *Eumops hansae.* Mean ± SE, observed range (in parentheses), and sample size are provided. See text for an explanation of variable acronyms.

Location	Manaus (Brazil) [1]	Santa Catarina (Brazil)	São Paulo (Brazil)	Several[2]
n	3	1 (Holotype)	1	5 (skull: 4)
Collection number	INPA 6732	USNM 2009	MZUSP 15442	
Age / Sex	Adult ♀	Adult ♂	Adult ♂	Adult ♀
EXTERNAL MEASUREMENTS				
TL	55.5 ± 4.3 (50.5-58.1)			
TAIL	27.5 ± 1.6 (25.8-29)			
ThL	4.7 ± 0.5 (4.1-5)			
Na	1.03 ± 0.2 (0.9-1.3)			
Cal	12.9 ± 1.6 (11.3-14.4)			
AntW	5.4 ± 0.3 (5.1-5.7)			
AntH	4.3 ± 0.3 (3.9-4.5)			
HF	8.1 ± 1.2 (6.8-9.1)			
E	17.7 ± 2.5 (15.1-20.1)		14.28	
FA	37.9 ± 0.6 (37.2-38.4)	41.57	41.1	37.8 ± 0.34
TiL	13 ± 0.9 (12-13.5)			
MET-IV		41.01	41.44	
PHA1-IV		13.55	14.7	
CRANIODENTAL MEASUREMENTS				
GLS	20.16	21.5		18.86 ± 0.20
CIL	18.73	20.56		17.90 ± 0.12
ZB	11.95	12.75		10.83
PB	4.26	4.19		4.0 ± 0.04
BB	9.09	9.13		
MTRL	7.32	7.87		6.89 ± 0.08
BAM	8.34	8.8		
BAC	4.94	5.17		
MANDL	14.44	15.85		
MANDTL	7.62	7.88		

[1] Only 1 specimen collected. [2] Five females reported in Eger (1977) collected from localities in Costa Rica (n = 1), Guiana (n = 2), Panama (n = 1), Venezuela (n = 1). Abbreviations are as follows: INPA (National Institute of Amazonian Research, Manaus, Brazil); USNM (National Museum of Natural History, Washington, USA); MZUSP (Museum of Zoology of the University of São Paulo, São Paulo, Brazil).

Table 2: External and craniodental measurements (mm) of *Eumops maurus*. Mean ± SE, observed range (in parentheses), and sample size are provided. See text for an explanation of variable acronyms. All measurements except for our specimens were taken from literature.

Location	Manaus (Brazil) [1]	Tocantins and Goiás (Brazil) [2]		Guiana	Venezuela	Ecuador	Suriname	Peru	São Paulo (Brazil)
n	3	5	7	1	1	1	1	1	1
Collection number	INPA 6731			BMNH 1.6.434	EBRG 16124	ROM 106326	RNH 12943**	CML 7559	CCZ 761
Age	Adult ♂	Adult ♂	Adult ♀	Adult ♂	Adult ♀	Adult ♀	Adult ♀	Adult?	Adult ♀
EXTERNAL CHARACTERS									
TL	65.4 ± 3.4 (62.5-69.2)	73 ± 7.2 (62.8–81) 5	69.6 ± 2.6 (67.7–76.4)	63				49	
TAIL	42.6 ± 3.6 (39.7-46.6)	47 ± 3.5 (43.3–52.1) 5	47.4 ± 2.3 (44–51.4)	50.5					
ThL	7.1 ± 0.4 (6.7-7.5)								
Na	1.1 ± 0.3 (0.8-1.3)								
Cal	22.5 ± 0.9 (21.5-23.2)								
AntW	5.4 ± 0.4 (5-5.7)								
AntH	4.6 ± 0.3 (4.4-5)								
HF	10.8 ± 1.2 (9.7-12.1)			9.5				12	
E	21.1 ± 0.8 (20.2-21.7)	21.4 ± 3.1 (17.8–25.1) 5	22.4 ± 1.2 (20.1–24.3)	19	22	21	30.7	22	
FA	53.2 ± 1.1 (52.5-54.5)	57.6 ± 2.1 (54.9–60.8) 5	55.3 ± 2.2 (52.7–59.1)	53.1	53.8	52		55.5	56.1
TiL	18.1 ± 0.5 (17.7-18.6)			16.7					
MET-IV				51.9		51.7	51.9		
PHA1-IV				20.3		19.4	20.3		
CRANIODENTAL CHARACTERS									
GLS	21.5		22.6, 22.7	20.6	21.3	20.8	21.4	20	22.8
CIL	20.3		21.6, 21.7	20.1	19.9	19.2	19.4	18.9	21.8
ZB	-		13.2	12.3	12.1	12	12.5	12.4	13.1
PB	4.2		4, 4.1	4.9	4	4	4.1	4.3	3.9
BB	9.9			9.7		9.9	10.2	10.5	
MTRL	8.4		9	8.2	8.2	8.1	8.4	7.6	9
BAM	9.3		9.2	8.9	8.7	8.3	8.9	8.3	9.1
BAC	5.4			5.2		4.9	5.1	5	
MANDL	15.9		17.1, 17.2	15		14.9		15.2	16.9
MANDTL	9.05			8.6		8.4	9	8.3	

[1] Only 1 specimen collected. [2]. Abbreviations are as follows: INPA (National Institute of Amazonian Research, Manaus, Brazil); BMNH (British Museum of Natural History, London, United Kingdom); EBRG (Estación Biológica de Rancho Grande, Maracay, Venezuela); ROM (Royal Ontario Museum, Toronto, Canada); RNH (Rijksmuseum van Natuurlijke Historie, Leiden, Netherlands); CML (Colección Mamíferos Lillo, Tucumán, Argentina); CCZ (Centro de Controle de Zoonoses).

Table 3: Search flight call parameters for *Eumops maurus*, *E. hansae* and other *Eumops* species. Mean ± SE, observed range (in parentheses).

Species	Source	N (n)*	Call type	Call shape	FME	Start frequency	End frequency
E. maurus	Current study	49 (2)	mono	QCFd	25.29 ± 2.613 (19.2 - 30.8)	33.45 ± 2.86 (25.6 - 39.1)	19.80 ± 2.72 (14.3 - 24.3)
E. hansae	Current study	24 (2)	mono	QCFd	21.86 ± 1.79 (17.9 - 23.9)	34.77 ± 3.83 (25.6 - 40.1)	13.78 ± 1.96 (11 - 16.8)
E. auripendulus	Personal recordings	6	low	QCFd	23.13 ± 1.76 (16.4 - 27.5)	34.35 ± 3.13 (23.8 - 42.2)	19.97 ± 2.63 (12 - 26.7)
	Barataud (2013)	2	low	QCFd	26.70 (26.3 - 27)		
	Jung et al. (2014)	41 (9)	low	FMu/QCFd		32.4 ± 4.3	18.2 ± 1.6
	Barataud (2013)	16	middle	FMd/QCF	23.30 (20.1 - 25.7)		
	Current study	6	high	QCFd	25.77 ± 2.01 (23.1 - 28.7)	28.59 ± 2.32 (25.9 - 33.7)	24.73 ± 2.20 (21.2 - 27.7)
	Barataud (2013)	22	high	QCF	18.70 (17.3 - 21.8)		
	Jung (2014)	27 (9)	high	FMu/QCFd		35.8 ± 4.1	21.9 ± 1.6
E. dabbenei	Jung et al. (2014)	22 (6)	low	FMu/QCFd		21.3 ± 1.2	13.7 ± 0.5
	Jung et al. (2014)	23 (6)	high	FMu/QCFd		24.6 ± 2.3	15.8 ± 0.8
E. glaucinus	Jung et al. (2014)	37 (10)	low	FMu/QCFd		27.4 ± 3.4	19 ± 0.4
	Jung et al. (2014)	16 (10)	high	FMu/QCFd		29.3 ± 4.2	20.3 ± 0.3
E. nanus	Jung et al. (2014)	8 (4)	low	FM/QCFd		27.9 ± 0.1	25.2 ± 0.2
	Jung et al. (2014)	9 (4)	high	FM/QCFd		30.5 ± 2.5	26.8 ± 0.8
E. underwoodi	Miller (2003)	1046 (150)	mono	QCFd	16.25 ± 4.2 (12.43 - 20.75)	15.4 ± 2.88 (12.43 - 18.18)	18.09 ± 2.7 (15.76 - 21.05)

* N (n) = number of pulses (number of individuals); Call type: mono = no frequency alternation; low/middle/high = echolocation that alternates frequency on subsequent pulses; Call shape: QCF = Quasi Constant Frequency; FM = Frequency Modulated; u = upward-modulated; d = downward-modulated; FME: Frequency of maximum energy.

Table 4: Average pairwise Kimura 2-parameter percentage sequence divergence among *Eumops* species based on 657 base pairs of the COI gene for 26 individuals. Intraspecific divergence is on the diagonal.

	n	*E. auripendulus*	*E. floridanus*	*E. hansae*	*E. maurus*	*E. perotis*	*E. underwoodi*
E. auripendulus	8	0.3					
E. floridanus	2	12.4	0.0				
E. hansae	12	16.3	13.4	0.9			
E. maurus	2	3.2	12.9	16.5	0.0		
E. perotis	1	12.1	10.0	17.4	11.8	-	
E. underwoodi	1	14.0	10.4	17.1	13.2	10.3	-

Table 5. List of taxa used in the present study and BOLD and GenBank accession numbers.

Species	**Accession numbers (GenBank)**
Eumops auripendulus	EF080345 - EF080349; JF448843; JF454657; KR608253
Eumops hansae	EF080350 - EF080357; JF435947; JF44884, BOLDAAC7539
Eumops maurus	JF448845; BOLDAAY3575
Eumops perotis	KP4219
Eumops underwoodi	KP734223
Eumops floridanus	KR337728, KR337729
Tadarida brasiliensis	JF446884

Figures

Fig. 1 Distribution of *Eumops maurus* and *E. hansae* in South America. [1] Pompeya Sur, Napo Province, Ecuador (Reid et al., 2000); [2] Uverito, State of Monagas, Venezuela (Sánchez et al., 1992); [3] Kanaku mountains, Guiana (holotype) (Thomas, 1901); [4] Peixe/Angical Hydroelectric Plant, State of Tocantins (Sodré et al., 2008); [5] Corumbá Hydroelectric Plant IV, State of Goiás (Sodré et al., 2008); [6] São Paulo, State of São Paulo (Sodré et al., 2008); [7] Santuario Nacional Pampas, Peru (Luna et al., 2002); [8] San Juan: Asociación de Viviendas 15 de Mayo, Peru (Diaz et al., 2011); [9] Chiapas, Mexico (Álvarez and Álvarez-Castañeda, 1990); [10] Lancetilla Atlantida, Honduras (Lee and Bradley, 1992) [11] Several locations, Costa Rica (Eger, 1977; Gardner, 2008; Hall, 1981); [12] Peru (Graham and Barkley, 1984); [13] Venezuela (Eisenberg, 1989); [14] Venezuela (Handley, 1976); [15] French Guiana (Simmons and Voss, 1998); [16] Manaus, State of Amazonas (Handley, 1955); [17] Bolivia (Ibáñez and Ochoa, 1989); [18] Uberlândia, Minas Gerais (Stutz et al., 2004); [19] São Paulo (Novais unpublished); [20] Colônia Hansa, Joinville, Santa Catarina (holotype) (Sanborn 1932). According to Eger (1977), in Suriname and Brazil there are two *E. hansae* with imprecise location. Map downloaded and adapted from the map of National Aggregates of Geospatial Data Collection (NAGDC): *Population, Landscape and Climate Estimates, v3: Biomes South America*; from the NASA Socioeconomic Data and Applications Center (SEDAC) at http://sedac.ciesin.columbia.edu/data/collection/groads/maps/gallery/search. Accessed on 20/08/2015.

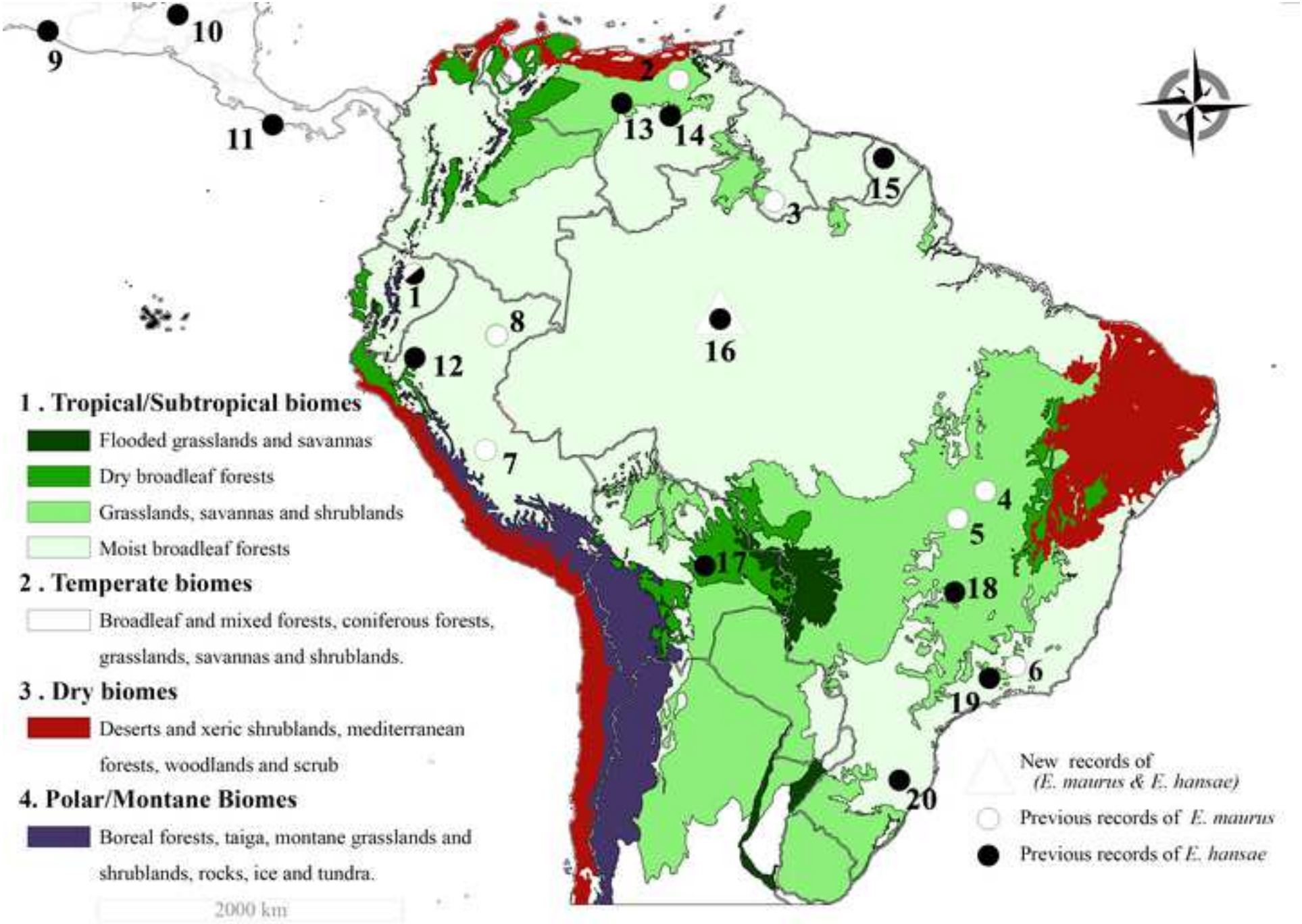
Fig 2. *Eumops maurus* (INPA 6731; male). – A. Dorsal view. – B. Ventral view. – C. Lateral view. *E. hansae* (INPA 6732; female). – D. Dorsal view. – E. Ventral view. – F. Lateral view. Note the large and well-defined basisphenoid pits and the third commissure of M3 developed in *E. hansae* (E). Scale bar: 5mm.

Fig. 3 Echolocation calls of *Eumops maurus* (A: spectrogram of single pulse; B power spectrum; C commuting flight sequence) and *E. hansae* (D: spectrogram of single pulse; E power spectrum; F commuting flight sequence).

Fig. 4 Tree resulting from the Bayesian analysis of COI showing the evolutionary relationships among *Eumops* species. Values above branches represent Bayesian posterior probabilities (BPP) and below branches, the maximum likelihood (ML) bootstrap. Our specimens are represented by asterisks. Abbreviations are as follows: BEL: Belize; BRA: Brazil; ECU: Ecuador; GUA: Guatemala; GUY: Guyana; PER: Peru; USA: United States of America.

Figure

Click here to download Figure Figure_1v02.jpg



Figure

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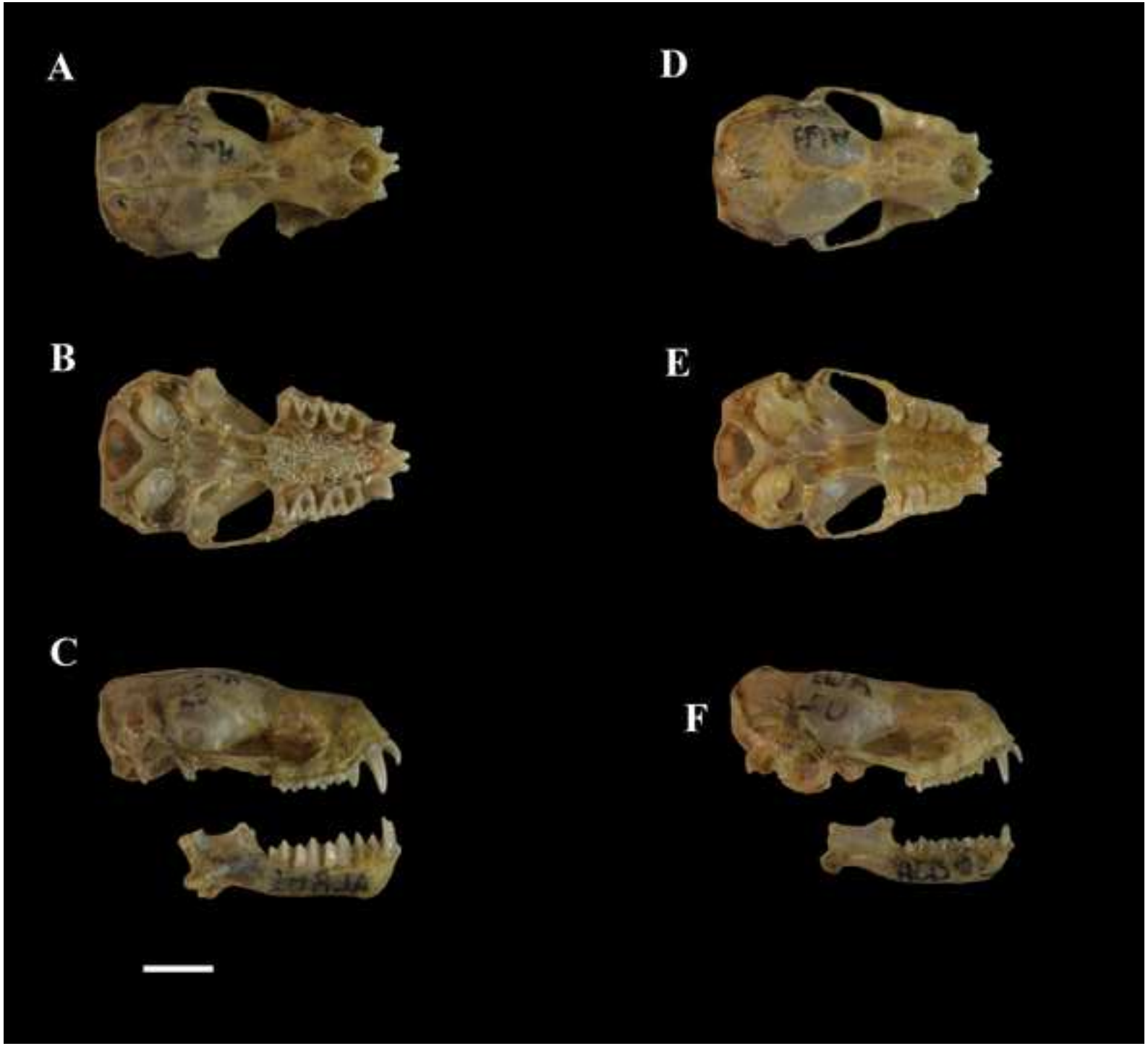

Figure

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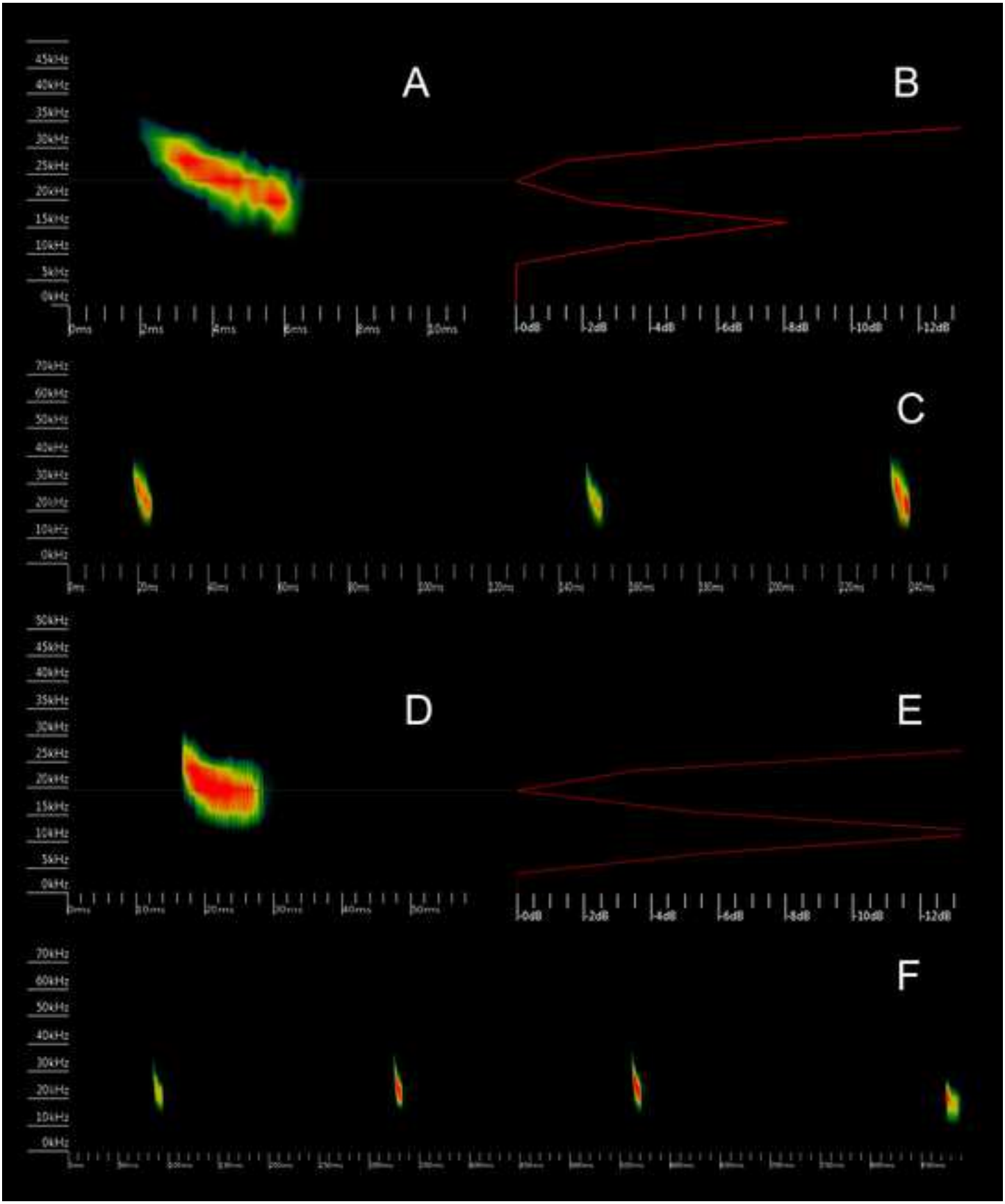

Figure

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