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Bats at the end of the world: new distributional data and fossil records from Patagonia, Argentina

Abstract: We report new recent and fossil records in Patagonia for six and three bat species, respectively. These findings significantly increase the previously known number of localities for these mammals in this entire region, filling gaps between previous references for some species (e.g., *Histiotus macrotus*) and/or extending by 140–350 km the range of others (e.g., *Myotis chiloensis*, *M. levis*, *Lasiurus varius*). In addition, we report for the second time the vespertilionid bat *Lasiurus blossevillii* in Patagonia. Fossils are mostly restricted to the Late Holocene period, and the recorded assemblages are similar to the recent ones. A preliminary analysis of richness indicates that bat diversity south of the Colorado River (around 39°S) decreases from five to six species in the northwestern to one species in the southeastern, changing abruptly around 43°S–46°S. Compared with similar latitudes of the Northern Hemisphere, bat diversity in the Neotropics follows a similar pattern, with <20 taxa occurring south of 35°S.

Keywords: biogeography; Chiroptera; *Histiotus*; Holocene; *Lasiurus*; *Myotis*; *Tadarida*.

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Introduction

Patagonia, located in southern South America, south of the Colorado River, is one of the few territories south of 40°S that maintain complex biotic communities (Soriano et al. 1983, Pardiñas et al. 2003, Lessa et al. 2012). Among mammals, 12 bat species have been recorded in this region (Barquez 2006, with modification according to Handley and Gardner 2007), clearly a reduced set compared with >60 species recognized for southern South America (Barquez et al. 1999, Barquez 2006, Díaz et al. 2011). Most of the available data about bat distribution in Patagonia are concentrated over a narrow band in the northern portion of the region, including forested and ecotonal areas of western Neuquén and Río Negro provinces (Figure 1) or along the northern river valley systems (e.g., Colorado, Negro). In contrast, the chiropteran assemblages in arid to semiarid steppes and basaltic plateaus of Central Patagonia, an area of ca. 700,000 square km, remain basically unknown (see Barquez et al. 1999).

The fossil history of bats in Patagonia, especially past distribution of current species, is also poorly studied, in consonance with the poor state of knowledge about fossil bats in the southernmost Neotropics (Iúdica et al. 2003). Paradoxically, the oldest bat fossil remains of South America were found in early Eocene beds (58.6–52 Myr) of Laguna fría, northwestern Chubut province, Central Patagonia (Tejedor et al. 2005, 2009). Later, Czaplewski (2010), see also Morgan and Czaplewsky 2012) mentioned the presence of the oldest known species of Phyllostomidae and two species of Molossidae, the extinct †*Mormopterus barrancae* and a second indeterminate species of *Mormopterus* from early Miocene deposits in the Gran Barranca, Chubut province. Despite having extensive sedimentary sequences with diverse mammal faunas (see reviews in Cione et al. 2007 and Tonni and Carlini 2008), no other Tertiary records of bats are known from Patagonia. Quaternary findings are restricted to a few mentions from Holocene deposits (Pardiñas et al. 2000, Iúdica et al. 2003).

This work had three main goals: 1) to document new localities of living bat species in the Argentinean Patagonia; 2) to provide new Holocene records and radiocarbon chronologies for bats in this region; and 3) to discuss several distributional and biogeographical aspects of the southernmost living bats of the world.

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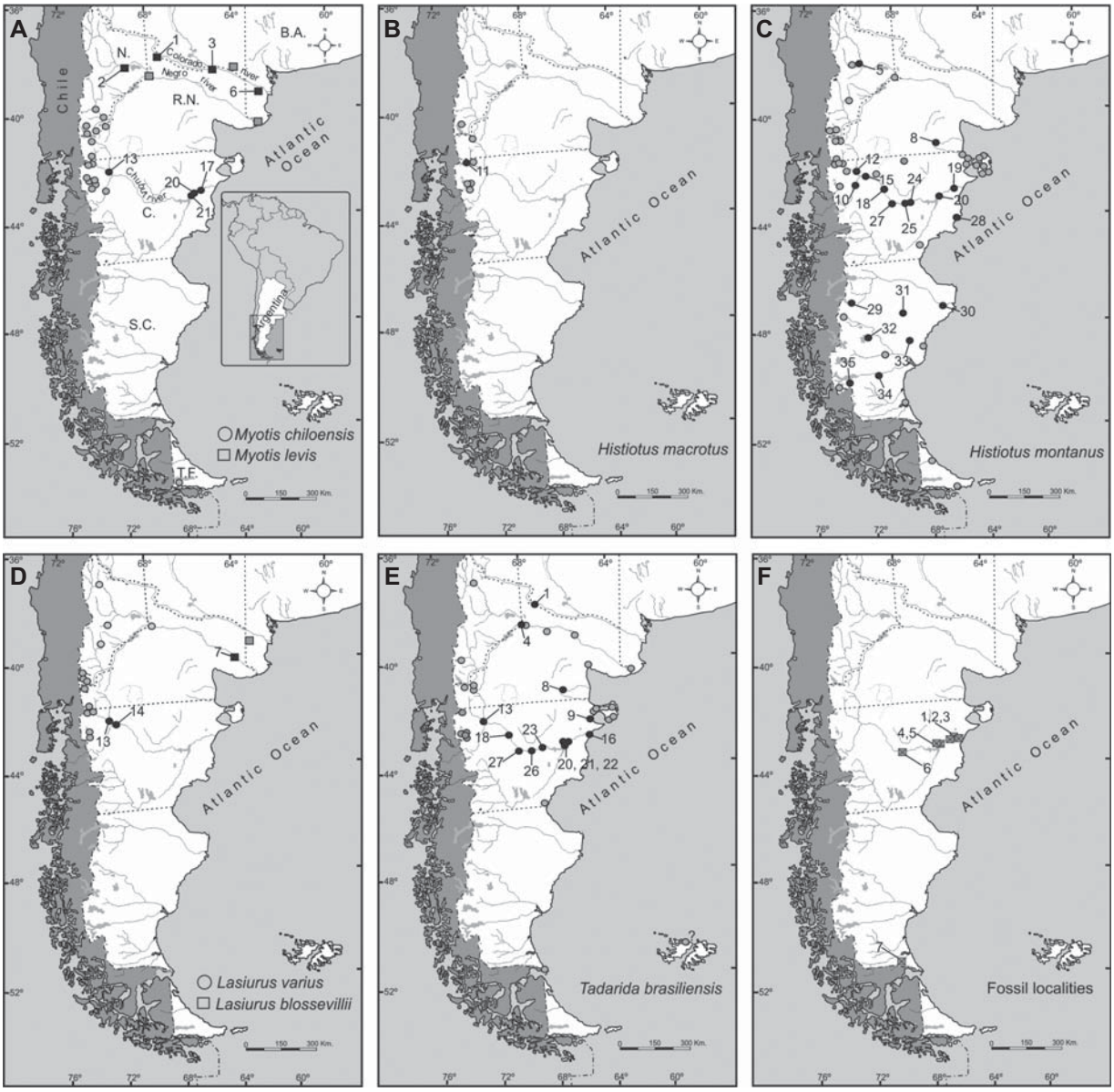

Figure 1. (A–E) New locality records (black circles and squares) for bat species in Patagonia, Argentina.
Locality numbers are those of Table 1. B.A., Buenos Aires province; N, Neuquén province; R.N., Río Negro province; C, Chubut province; S.C., Santa Cruz province; and T.F. Tierra del Fuego province. Previous records are shown in gray circles and squares and were compiled from several sources (e.g., Barquez et al. 1999, Petracci and Pérez 1999, Nabte 2010, Nabte et al. 2011, Giménez 2010, Teta and Andrade 2002). F, Fossil sites considered in this contribution: 1. Las Bardas Profile; 2. La Angostura Rockshelter; 3. Lle Cul (Pardiñas et al. 2000); 4. Caolinera Dique Ameghino Cave; 5. De la Virgen Cave; 6. Los Altares Profile; and 7. Oreja de Burro 1 Site (Pardiñas et al. 2011b).

Materials and methods

The new distributional data reported here came from trapped specimens, prepared as skin and skull (n=6) or fluid-preserved (n=25), and osseous remains (skulls and mandibles) recovered from owl pellet samples (n=108; Table 1). Living specimens were collected using mist nets (Avinet INC, 75/2 38 mm) placed in riparian forests of *Salix* sp. (Salicaceae) and outside caves, stables and other human buildings or directly by hand in their shelters. Owl pellets were collected mostly between 2003 and 2011 in raptors nest and roosting sites of *Tyto alba* (Tytonidae), *Athene cunicularia* (Strigidae), *Bubo magellanicus* (Strigidae) and indeterminate strigiforms (see Table 1).

Fossil remains studied in this contribution were recovered during the excavation of the following archaeological

Table 1 New locality records for bat species in Patagonia, Argentina (arranged by latitude).

Number	Locality	Latitude S	Longitude W	*H. montanus*	*H. macrotus*	*L. blossevillii*	*L. varius*	*M. chiloensis*	*M. levis*	*T. brasiliensis*	Province	Collection number	Source
1	Casa de Piedra	38°15′37″	67°15′51″						3	24	Río Negro	CNP-E 535	Owl pellets[a]
2	Paso de los Indios	38°33′01″	69°24′19″						5		Neuquén	CNP-E 627	Owl pellets[a]
3	Fortín Uno	38°51′23″	65°16′17″						2		Río Negro	CNP-E 578	Owl pellets[b]
4	Neuquén capital	38°55′31″	68°03′38″							1	Neuquén	CNP-E 558	Owl pellets[c]
5	Quili Malal	38°20′32″	69°54′44″	1							Neuquén	CNP-E 629	Owl pellets[d]
6	20 km S of Pedro Luro on Hwy 3	39°41′31″	62°40′23″						6		Buenos Aires	CNP 2462 CNP 2461	Captured specimens
7	20 km SE Gral. Conesa	40°11′11″	64°18′26″			1					Río Negro	CNP-E 600	Owl pellets[b]
8	Campana Mahuida	41°38′34″	66°26′45″	1						1	Río Negro	CNP-E 74	Owl pellets[a]
9	Puerto Madryn	42°47′10″	65°00′29″							1	Chubut	CNP 1756	Captured specimen
10	Puente RPN°25 sobre río Gualjaina	42°59′48″	70°46′51″	1							Chubut	CNP-E 244	Owl pellets[d]
11	El Hoyo	42°03′53″	71°31′11″		1						Chubut	CNP 2455	Captured specimen
12	Campo de Netchovitch	42°19′42″	70°33′40″	2							Chubut	CNP 1765, CNP 1770	Captured specimen
13	Fofo Cahuél	42°24′30″	70°31′46″				1	10		5	Chubut	CNP 1752, CNP 1759, CNP 1760, CNP 1762, CNP 1764, CNP 1766, CNP 1775, CNP 1767, CNP 1768, CNP 1772, CNP 1773, CNP 1779, CNP 1783, CNP 1778, CNP 1773	Captured specimen
14	Piedra Parada	42°38′51″	70°08′57″				1				Chubut	P. Wallace, field catalogue	Captured specimen
15	Campo de Cretón	42°41′46″	70°03′15″	1							Chubut	CNP 1751	Captured specimen
16	Rawson	43°17′57″	65°05′47″							1	Chubut	CNP 1777	Captured specimen
17	Piedra Grande 1	43°37′27″	66°22′43″					1			Chubut	CNP-E 114	Owl pellets[b]
18	Est. El Torito	43°16′46″	69°08′40″	1						1	Chubut	CNP-E 121	Owl pellets[b]
19	La Angostura	43°21′29″	65°33′49″	2							Chubut	CNP-E 148	Owl pellets[a]
20	Cueva Peligro	43°40′18″	66°24′51″	3				3		25	Chubut	CNP-E 236, CNP-E 308, CNP-E 63	Owl pellets[b]
21	Cueva Caolinera Dique Ameghino	43°40′48″	66°25′26″					1		2	Chubut	CNP-E 52	Owl pellets[a]
22	Cueva de la Virgen	43°42′10″	66°27′44″							1	Chubut	CNP-E 50	Owl pellets[b]

(Table 1 Continued)

Number	Locality	Latitude S	Longitude W	*H. montanus*	*H. macrotus*	*L. blossevillii*	*L. varius*	*M. chiloensis*	*M. levis*	*T. brasiliensis*	Province	Collection number	Source
23	9.5 km W Las Plumas	43°43′17″	67°22′45″							5	Chubut	CNP-E 300	Owl pellets[a]
24	Cañadón Carbón	43°49′32″	67°51′28″	1							Chubut	CNP-E 136	Owl pellets[a]
25	20 km E Los Altares	43°50′47″	68°11′48″	1							Chubut	CNP-E 252	Owl pellets[a]
26	Cueva Pardiñas-Gomes	43°51′26″	67°56′56″							1	Chubut	CNP-E 297	Owl pellets[a]
27	36 km W Los Altares	43°51′44″	68°49′36″	1						1	Chubut	CNP 1754, CNP-E 70	Owl pellets[a]
28	Pto El Palenque, Ea. La Maciega	44°25′55″	65°24′07″	1							Chubut	CNP-E 316	Owl pellets[a]
29	18 km E Lago Posadas	47°34′28″	71°36′43″	2							Santa Cruz	CNP-E 499	Owl pellets[a]
30	Cañadón Paso Marsicano	47°51′43″	66°26′00″	1							Santa Cruz	CNP-E 354	Owl pellets[b]
31	Ea. La María	48°24′36″	68°52′11″	1							Santa Cruz	CNP-E 469	Owl pellets[a]
32	Extremo N Lago Cardiel y RNN°40	48°54′00″	71°01′00″	1							Santa Cruz	CNP-E 96	Owl pellets[a]
33	Ea. Julia	49°35′26″	69°35′32″	3							Santa Cruz	CNP-E 489	Owl pellets[b]
34	Cerro Fortaleza	50°14′10″	70°53′17″	6							Santa Cruz	CNP-E 420, CNP-E 500	Owl pellets[b]
35	Cerro Comisión	50°20′23″	72°28′16″	3							Santa Cruz	CNP-E 428, CNP-E 413	Owl pellets[a]

[a]Strigiform indeterminate; [b]*Tyto alba*; [c]*Athene cunicularia*; [d]*Bubo magellanicus*.

or paleontological sites (see Figure 1F): 1) Las Bardas profile (43°21′24″S, 65°37′36″W, Chubut); 2) Lle cul (43°20′S, 65°35′W, Chubut; Pardiñas et al. 2000); 3) La Angostura rockshelter (43°21′31″S, 65°38′21″W, Chubut); 4) Caolinera Dique Ameghino Cave (43°40′48″S, 66°25′26″W, Chubut); 5) de la Virgen Cave (43°42′10″S, 66°27′44″W, Chubut); and 6) Los Altares profile (43°53′35″S, 68°23′21″W, Chubut) and Oreja de Burro 1 site (52°07′46″S, 69°33′9″W, Santa Cruz; Pardiñas et al. 2011b). Bat remains were recovered mixed with bones and teeth of small rodents and marsupials by sieving the sediment. Radiocarbon dates for these sites were performed on small mammal bones, charcoal and/or rodent feces in the Laboratorio de Tritio y Radiocarbono of the Museo de La Plata [LP], Argentina. Studied samples indicated middle to late Holocene ages (Table 2). Detailed descriptions of collecting techniques, stratigraphy and chronologies for these sites are fully discussed by Udrizar Sauthier (2009) and Pardiñas et al. (2011b).

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The taxonomy follows Barquez (2006), with modifications for *Histiotus* and *Myotis* according to Handley and Gardner (2007) and Wilson (2007), respectively. According to these authors, we included *Histiotus magellanicus* (Philippi, 1866) under the synonymy of *montanus* and provisionally considered *Myotis dinelli* Thomas, 1902 as a subspecies of *M. levis*. Captured specimens and osseous remains were identified by examination of external coloration, skull and dentaries, following the literature (e.g., Barquez et al. 1999, Handley and Gardner 2007, Wilson 2007) and by comparisons with specimens housed at the Colección de Mamíferos del Centro Nacional Patagónico (CNP), Puerto Madryn, Chubut, Argentina. Studied specimens are deposited in the CNP collection (Table 1) and also in the Colección de Material de Egagrópilas y Afines "Elio Massoia" (CNP-E; Table 1), and Centro Nacional Patagónico. Dental formulas were especially useful for genus determination, as each taxon has a distinctive combination (*Histiotus*=2/3, 1/1, 1/2, 3/3; *Lasiurus*=1/3, 1/1, 2/2, 3/3; *Myotis*=2/3, 1/1, 3/3, 3/3; and *Tadarida*=1/3, 1/1, 2/2, 3/3). Additional characters used for taxonomic identification of the studied specimens are as follow. *H. macrotus*: length of ear from notch >30 mm (Handley and Gardner 2007); greatest length of skull >18.4 mm; postpalatal length >7 mm; *H. montanus*: length of ear from notch <30 mm; greatest length of skull <18.4 mm; postpalatal length <7.2 mm (Handley and Gardner 2007); *L. blosevilli*: dentary robust; p4 double-rooted; lower toothrow 4.5–4.8 mm (Barquez et al. 1999); *L. varius*: dorsal fur chestnut, venter orange-buff; forearm 38.7–43.4 mm; lower toothrow 5.3–5.4 mm (Barquez et al. 1999, Gardner and Handley 2007); *M. chiloensis*: fur bicolored; forearm averaging 36 mm; distance between canines 3.7–4 mm

Table 2 Bat species found in Holocene fossil sites of Patagonia, Argentina.

Sites	*Histiotus montanus*		
	NISP	**MNI**	**Dating**
Las Bardas profile	4	3	>200 year BP to Modern
La Angostura rockshelter	2	2	>150 year BP to Modern
Lle Cul	6	–	1830±70 year BP
Caolinera Dique Ameghino	5	5	<3050±70–570±70 year BP
De la Virgen Cave	6	5	Modern
Oreja de Burro 1 site	1	1	1760±70–>620±200 year BP
Los Altares profile	4	3	2210±70–650±60 year BP
	Myotis chiloensis		
Las Bardas profile	2	2	~150 year BP
Los Altares profile	1	1	1280±90 year BP
	Tadarida brasiliensis		
Las Bardas profile	30	17	>200 year BP to Modern
La Angostura rockshelter	3	2	Modern
Lle Cul	11	–	1830±70 year BP
Caolinera Dique Ameghino	15	10	3050±70–570±70 year BP
De la Virgen Cave	10	10	5470±110 year BP to Modern
Los Altares profile	4	3	<2210±70–650±60 year BP

NISP, number of identified specimens; MNI, minimum number of individuals.

(Barquez et al. 1999, Wilson 2007); *M. l. dinelli*: postorbital constriction <3.8 mm; distance between canines 3.3–3.7 mm (Barquez et al. 1999); and *T. brasiliensis*: upper lip with deep vertical grooves or wrinkles; inner edges of ears not joined; anterior border of hard palate emarginated; upper incisors separated by distinct gap; nyctalodont molars (Barquez et al. 1999).

Results and discussion

New recent and fossil records

We report 35 new locality records for six living species of bats in Patagonia (Table 1). This number increases by 43.2% the previously known records for this entire region (n=81; see Massoia and Chébez 1993, Barquez et al. 1999 Barquez et al. 2012, Petracci and Pérez 1999, Teta and Andrade 2002, Merino et al. 2003, Nabte 2010, Giménez 2010, Nabte et al. 2011, Giménez et al. in press) encompassing significant range extensions for some species. At least three of these taxa were also found in middle to late Holocene stratified deposits.

Histiotus macrotus (Poeppig, 1835) was previously known for Neuquén and Río Negro provinces (Barquez et al. 1999, Handley and Gardner 2007; Figure 1B). More recently, Giménez (2010) and Giménez et al. (2012) reported this bat for four localities in northwestern Chubut province. Our findings and those of Giménez et al. (2012) contribute to fill the gap between the localities reported by these authors, showing that this species has a nearly continuous distribution along the Andean foothills in northern Patagonia. *Histiotus montanus* (Philippi and Landbeck 1861) is the most widely distributed bat in Patagonia (Figure 1C), reaching the southern border of Tierra del Fuego island (Handley and Gardner 2007). Its documented records are mostly concentrated in the northwestern portion of Patagonia, with only a few recording localities for the interior plains and coastal areas (Barquez et al. 1999, 2012, Teta and Andrade 2002, Nabte 2010). Here we report 19 new localities, filling the gap between the eastern and western populations, especially across the northern portion of Chubut province and southern Santa Cruz province (Figure 1C). This species was found in the seven studied paleontological and archeological sites (Table 2). Its chronological range is extended from ca. 3000 years BP to the present, being the second best represented bat in Patagonian Holocene sequences.

Three species of *Lasiurus* occur south of the Colorado River (Barquez et al. 1999, Gardner and Handley 2007). We present the southernmost record for *Lasiurus blossevillii* (Lesson, 1826) and the second documented reference for Patagonia (first mention was made by Merino et al. 2003), enlarging the distribution of this bat ca. 115 km to the southwest (Figure 1D). *Lasiurus varius* (Poeppig 1835) is endemic to forest and ecotonal areas of Patagonia, reaching southward the north side of the Magellan Strait (there

is an unconfirmed record for Tierra del Fuego, see Massoia and Chébez 1993). In Argentina, it is known from twelve localities in Neuquén, Río Negro and Chubut provinces (Barquez et al. 1999, 2012, Giménez et al. 2012). Two new specimens are reported here from northwestern Chubut province, which extend its distribution ca. 113 km to the east and represent the first documented record for this bat in open steppe areas (Figure 1D).

The known distribution of *Myotis chiloensis* (Waterhouse, 1840) is a narrow band along the western margin of Patagonia, from Neuquén to Tierra del Fuego provinces (Massoia and Chébez 1993, Wilson 2007). Here, we document this species in four localities, all located in the Chubut river basin (Figure 1A). These occurrences are from steppe environments quite different from the humid, forested to ecotonal habitats that this species occupies in western Patagonia. In addition, these records imply a range extension of ca. 350 km to the east from the previous nearest references. This species is also recorded in two paleontological sites (Table 2). A second species of this genus, *Myotis levis* (I. Geoffroy, 1824) is mostly marginal in Patagonia, and it is represented by only two previous references (Barquez et al. 1999). Here, we add two records, primarily referred to *M. l. dinelli*, that suggest that this species has more continuous populations along the Colorado River (Figure 1A). We also enlarge its distribution ca. 125 km westward through its finding in central-eastern Neuquén province (Figure 1A).

Tadarida brasiliensis (I. Geoffroy, 1824) is a widely distributed molossid bat restricted in continental Patagonia to a few localities (Barquez et al. 1999, 2012, Nabte 2010, Nabte et al. 2011, Giménez et al. 2012). Here, we present 10 new localities for the species, most of them found along the Chubut river basin (Figure 1E). These new records fill the gap between northern and southern previous references and confirm the presence of this bat in open, shrubby steppe areas of central Patagonia. This species is the most common bat in Patagonian Holocene sequences, with a chronological range extending between 5500 years BP to the present (Table 2).

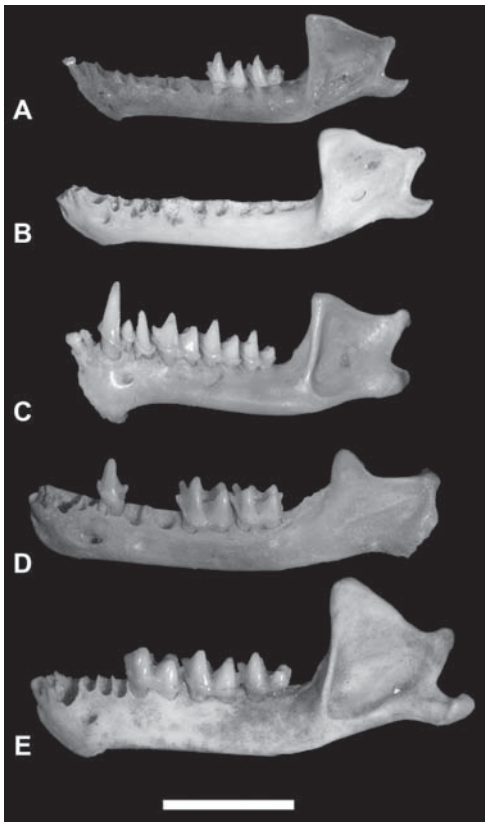

Figure 2 Specimens recovered in owl pellets (B, D) and fossil sites (A, C, D) from Patagonia, Argentina.
(A) *Myotis levis* (Paso de los Indios; locality 2); (B) *Myotis chiloensis* (Las Bardas Profile; ~150 year BP); (C) *Lasiurus blossevillii* (20 km SE Gral. Conesa; locality 7); (D) *Tadarida brasiliensis* (De la Virgen Cave; 5470±110 year BP); (E) *Histiotus montanus* (Caolinera Dique Ameghino Cave; <3050±70 year BP). Scale, 5 mm.

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Bat biogeography in southernmost South America

Twelve species of bats are cited for Patagonia (Barquez 2006, with modifications according to Handley and Gardner 2007). However, several species included in this list are still under discussion. The molossid *Molossops temminckii* (Burmeister, 1854) and the phyllostomid *Sturnira lilium* (É. Geoffroy, 1810; Phyllostomidae) could be considered as accidental or even erroneous as both species typically occur north of 34°S; in fact, both taxa were recorded once each, and their precise collection localities are unknown, being referred to as "Chubut" and "Río Negro", respectively (see Barquez et al. 1999, Barquez 2006). *Eumops patagonicus* Thomas, 1924 was also cited for "Chubut," although its typical distribution is mostly restricted to subtropical latitudes north of 35°S (Barquez et al. 1999). Monjeau et al. (1994) mentioned a second Patagonian specimen for *E. patagonicus* for the locality of Dolavon, Chubut, although this record was not properly documented. Questionable records also include the presence of the phyllostomid *Desmodus rotundus* (É. Geoffroy, 1810) in central-eastern Chubut (Barquez 2006). However, the vespertilionids *Lasiurus blossevillii* and *L. cinereus* are marginal elements reaching the northern border of Patagonia, a geographic range also shared by *Myotis levis*. Taking into account this evidence, only five species, four vespertilionids (*Histiotus montanus*,

Histiotus macrotus, *Lasiurus varius*, and *Myotis chiloensis*) and one molossid (*Tadarida brasiliensis*), constitute the Patagonian bat assemblage (see Figure 1A–E). A sixth species, *Myotis aelleni* Baud, 1979, tentatively considered as valid, is restricted to a small area of western Patagonia; however, this form perhaps represents a synonym of the broadly distributed *M. chiloensis* (Pearson and Pearson 1993, Barquez et al. 1999).

Barquez et al. (1999) discussed the Argentinean bat fauna considering phytogeographical regions (sensu Cabrera and Willink 1973) as units of analysis. These authors found that Subantarctic and Patagonian regions shared most of their fauna, which suggests that bats do not reflect habitat differences between these regions. However, changes in species richness or impoverishment patterns within regions remain unexplored.

Bat diversity in Patagonia decreases from northwestern to southeastern, changing abruptly around 43°S–46°S (Figure 3). North of this latitude, nine to eleven species were documented (Figure 1A–E), whereas south of this latitude, only three species were found and two of these were only recorded on the western side of the Andes. Higher numbers of bat species occur in *Nothofagus* forest and adjoining ecotonal areas of southern Neuquén, western Río Negro and northwestern Chubut provinces, between 40°S–43°S, where five to six species were documented (Figure 3). In turn, the lowest bat diversity corresponds to the open steppe areas of southeastern Patagonia, where only one to two bat species were documented (Figure 3). This is not an unexpected situation, considering the physiological limitations imposed by cold environments on insectivorous bats, such as vespertilionids and molossids (McNab 1982). The overall pattern described above is in accordance with global patterns of species richness, which show a strong latitudinal gradient, decreasing toward poles and responding to the interaction of different causes (Gaston 2000). This same pattern was not only observed in bats, but also in other groups of Patagonian mammals (Lessa et al. 2012). For example, sigmodontine rodent (Cricetidae: Sigmodontinae) richness decreases towards the south, with 25 species northwards of 47°S, 16 species below this latitude and only 6 in Tierra del Fuego island (Pardiñas et al. 2011a).

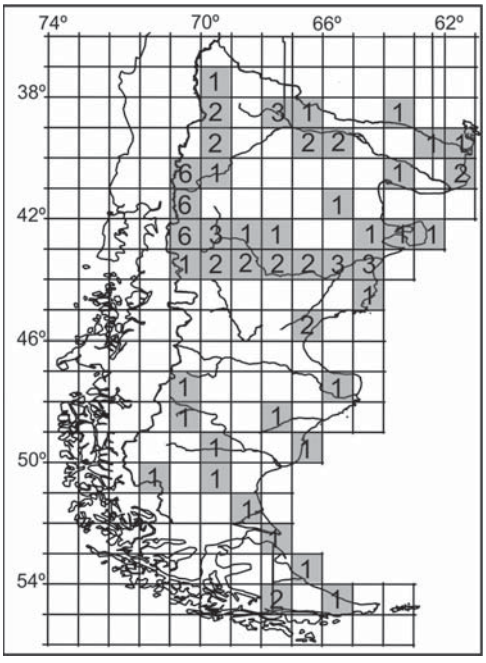

Figure 3. Bat species richness in Argentinean Patagonia. A square equals 1 degree.

Bats reach their highest diversity, both ecologically and in number of species, in tropical ecosystems (Kalko 1997). This pattern is especially evident in South America, where bat diversity drops from ca. 100–120 species in the Equator to two species in Tierra del Fuego. Compared with similar latitudes of the Northern Hemisphere, bat diversity in the Neotropics follows a similar pattern, with <20 taxa occurring south of 35°S (Findley 1993).

This contribution suggests that bat biogeography in Patagonia is a more complex issue than previously envisioned. Despite the hostility of southernmost South American environments, chiropterans must be considered important elements in the understanding of biotic evolution of this area. Clearly, much work must be done, field research in particular, to obtain a better picture of bats diversity and distribution in higher latitudes of the Southern Hemisphere.

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