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Quaternary Bat Diversity in the Dominican Republic

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ABSTRACT

The fossil record of bats is extensive in the Caribbean, but few fossils have previously been reported from the Dominican Republic. In this paper, we describe new collections of fossil bats from two flooded caves in the Dominican Republic, and summarize previous finds from the Island of Hispaniola. The new collections were evaluated in the context of extant and fossil faunas of the Greater Antilles to provide information on the evolution of the bat community of Hispaniola. Eleven species were identified within the new collections, including five mormoopids (*Mormoops blainvillei*, †*Mormoops magna*, *Pteronotus macleayii*, *P. parnellii*, and *P. quadridens*), five phyllostomids (*Brachyphylla nana*, *Monophyllus redmani*, *Phyllonycteris poeyi*, *Erophylla bombifrons*, and *Phyllops falcatus*), and one natalid (*Chilonatalus micropus*). All of these species today inhabitant Hispaniola with the exception of †*Mormoops magna*, an extinct species previously known only from the Quaternary of Cuba, and *Pteronotus macleayii*, which is currently known only from extant populations in Cuba and Jamaica, although Quaternary fossils have also been recovered in the Bahamas. Differences between the fossil faunas and those known from the island today suggest that dispersal and extirpation events, perhaps linked to climate change or stochastic events such as hurricanes, may have played roles in structuring the modern fauna of Hispaniola.

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FIGURE 1. Flooded floor of Oleg's Bat Cave in eastern Dominican Republic, where numerous bat cranial and postcranial remains can be observed. Photograph courtesy of the Dominican Republic Speleological Society and Phillip Lehman.

INTRODUCTION

The West Indies harbors a diverse fauna and flora with high levels of endemism (Myers et al., 2000; Hedges, 2001; Willig et al., 2009; Acevedo-Rodríguez and Strong, 2012; Dávalos and Turvey, 2012). Of the 53 extant bat species currently known from the West Indies, nearly half are endemic to the region (Dávalos and Turvey, 2012). There are 18 species of bats today living on the island of Hispaniola (Dávalos and Turvey, 2012; Nuñez Novas and León, 2011; Tejedor et al., 2005) and the sparse fossil record provides little evidence as to how this assemblage of species evolved (Griffiths and Klingener, 1988; McFarlane et al., 2000). Hispaniola has lost much of its mammalian diversity in the last 100,000 years, but the chronology of these extinctions is poorly documented (McFarlane et al., 2000). Understanding the timing of these extinctions is essential to understanding the evolution of the contemporary fauna of Hispaniola. Fossil bats have been recorded from superficial deposits and fossilized owl pellets from the Dominican Republic (Miller, 1929b, 1930; Morgan, 2001) and Haiti (Koopman, 1955; Miller, 1918, 1929a, 1930; Silva Taboada, 1952). New fossil faunas recovered from two sinkhole caves in the Dominican Republic represent the biggest chiropteran fossil collection recorded from

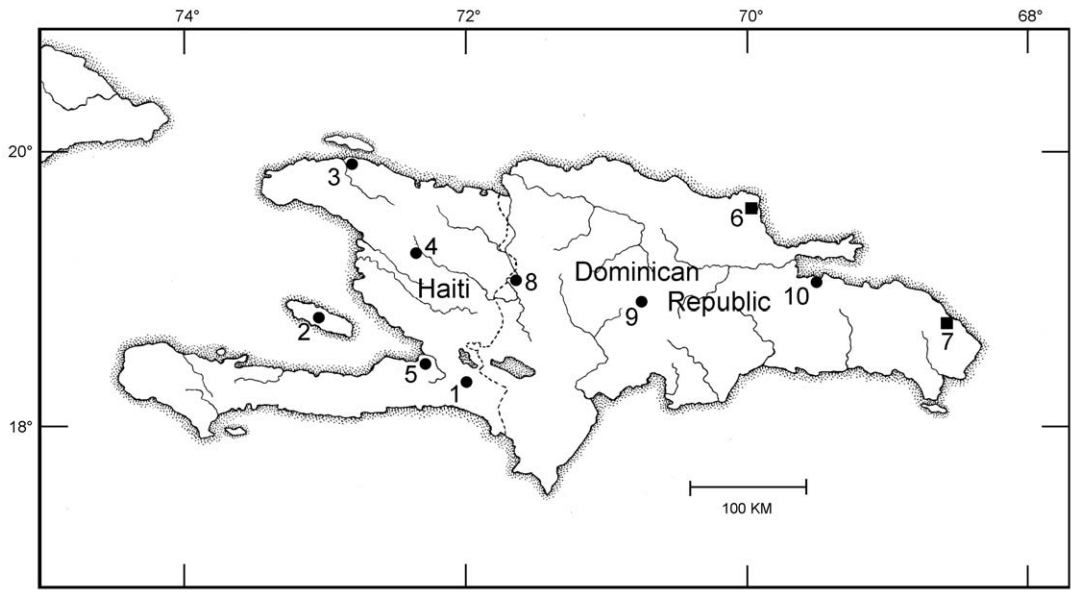

FIGURE 2. Map showing the localities where fossil bats have been recorded in Hispaniola. Circles indicate localities reported by other studies. Squares indicate localities presented by this study. **Haiti**: (**1**) Diquini, (**2**) Gonâve Island, (**3**) Port-de-Paix, (**4**) Saint-Michel-de-l'Atalaye, and (**5**) La Selle. **Dominican Republic**: (**6**) Cueva de Lily, (**7**) Oleg's Bat Cave, (**8**) Cerro de San Francisco, (**9**) Constanza, and (**10**) San Gabriel.

eastern Hispaniola (figs. 1–2). Here we describe these new collections in an effort to evaluate the taxonomic diversity of the fossil bat fauna of the island, and to provide context for understanding the bat diversity found in the Caribbean region today.

MATERIALS AND METHODS

The fossil collections described in this paper were recovered from two sinkhole caves on the eastern coastline of Hispaniola: Cueva de Lily (19°33′51.19″ N, 69°54′27.32″ W) in the María Trinidad Sánchez province, and Oleg's Bat Cave (10 km West of Bavaro, precise locality information can be provided upon request) in the La Altagracia province (fig. 2). Specimens in both caves were collected as part of a joint project involving Brooklyn College and the Museo del Hombre Dominicano, focusing on the recovery of primate and other vertebrate remains from underwater caves. They were retrieved from the cave floors by a team of scuba divers. The Dominican Republic Speleological Society worked on behalf of the Museo del Hombre Dominicano.

Cueva de Lily is approximately a 900 m long system of fully freshwater-flooded passages and caverns, with a maximum depth of 21 m. The bat fossils were collected from two areas within the cave: one approximately 100 m from a secondary cave entrance, and the other further in at 180 m. The depth of the cave in both cases was between 3–8 m. The size of the tunnel at both collection sites was approximately 5 m wide by 5–6 m high, large enough to support a

Table 1. Diversity of extant, fossil, and subfossil remains of bats from Hispaniola reported by this study,[a] Morgan (2001),[b] Miller (1930),[c] Miller (1929b),[d] Miller (1929a),[e] Silva Taboada (1952),[f] Koopman (1955),[g] and Miller (1918).[h] The records presented here include extant records (e) and remains from three different sources: fossils (x), fossilized owl pellets (xx), and superficial deposits (yy).

Species	Extant on Hispaniola	Dominican Republic					Haiti				
		Cueva de Lily[a]	Oleg's Bat Cave[a]	Cerro de San Francisco[b]	Constanza[c]	San Gabriel[d]	Diquini[e, f]	Gonâve Island[g]	Port-de-Paix[h]	Saint-Michel-de-l'Atalaye[e]	La Selle[c]
Mormoops blainvillei	e	x	x	x				xx		yy	
†*Mormoops magna*			x								
Mormoops megalophylla[*]				x							
Pteronotus macleayii[*]		x	x								
Pteronotus parnellii	e	x	x	x			xx	xx			
Pteronotus quadridens	e	x	x	x							
†*Pteronotus* sp.				x							
Noctilio leporinus	e										
Brachyphylla nana	e		x	x					xx	yy	
Erophylla bombifrons	e	x	x	x					xx	yy	
Monophyllus redmani	e	x	x	x			xx	xx			
Phyllonycteris poeyi	e	x	x	x			xx			yy	
Macrotus waterhousei	e			x		xx	xx	xx		yy	

Species	Extant on Hispaniola	Dominican Republic					Haiti				
		Cueva de Lily[a]	Oleg's Bat Cave[a]	Cerro de San Francisco[b]	Constanza[c]	San Gabriel[d]	Diquini[e, f]	Gonâve Island[g]	Port-de-Paix[h]	Saint-Michel-de-l'Atalaye[e]	La Selle[c]
Artibeus jamaicensis	e			x		xx	xx	xx	xx	yy	
Phyllops falcatus	e		x	x	xx		xx		xx	yy	
Chilonatalus micropus	e	x		x							
Natalus major	e			x							
Eptesicus fuscus	e			x	xx	xx			xx	yy	xx
Lasiurus insularis[*, #]				x							
Lasiurus minor	e										
Molossus molossus	e										
Nyctinomops macrotis	e			x							
Tadarida brasiliensis	e			x						yy	
Tadarida sp.											xx

[*] Indicates extant species extirpated from Hispaniola.
[#] Referred to *Lasiurus intermedius* by Morgan (2001).

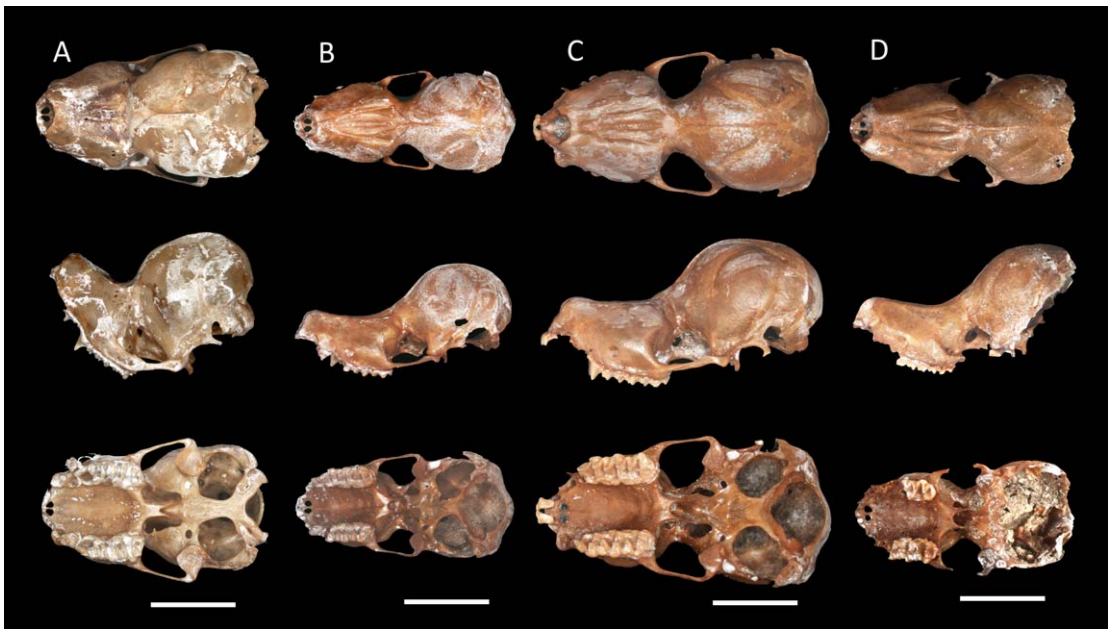

FIGURE 3. Mormoopidae skulls: dorsal, lateral, and ventral views. **A.** *Mormoops blainvillei*, **B.** *Pteronotus macleayii*, **C.** *Pteronotus parnellii*, **D.** *Pteronotus quadridens*. Scale bar = 5 mm.

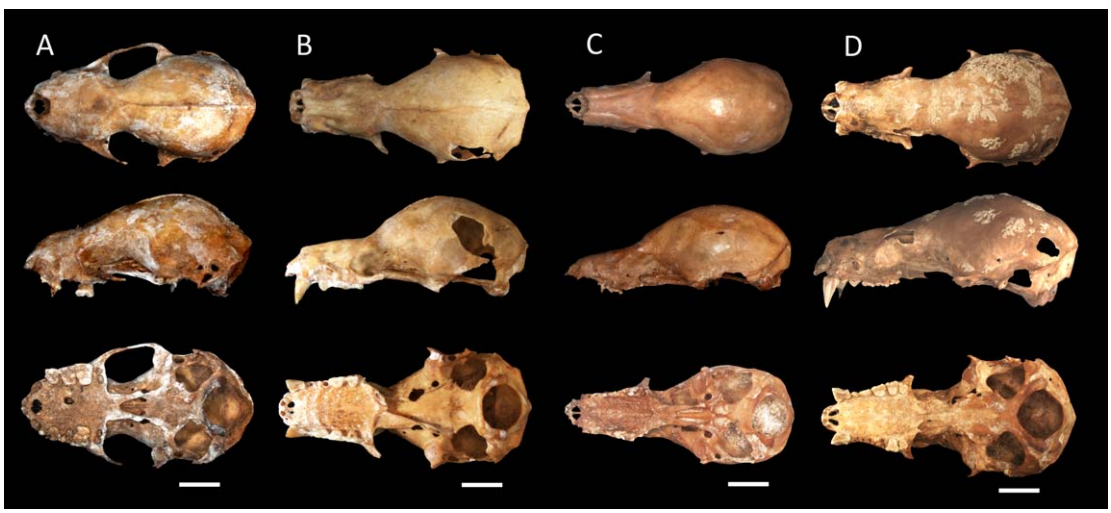

FIGURE 4. Phyllostomidae skulls: dorsal, lateral, and ventral views. **A.** *Brachyphylla nana*, **B.** *Erophylla bombifrons*, **C.** *Monophyllus redmani*, **D.** *Phyllonycteris poeyi*. Scale bar = 5 mm.

bat colony if dry. In the dry part at the second entrance of Cueva de Lily, there is currently a small bat colony.

Like Cueva de Lily, Oleg's Bat Cave is an approximately 900 m long system of fully freshwater-flooded passages and caverns, with a maximum depth of 11 m. The bat fossils were collected from the surface of a rocky area (fig. 1), located approximately 15 m away from the

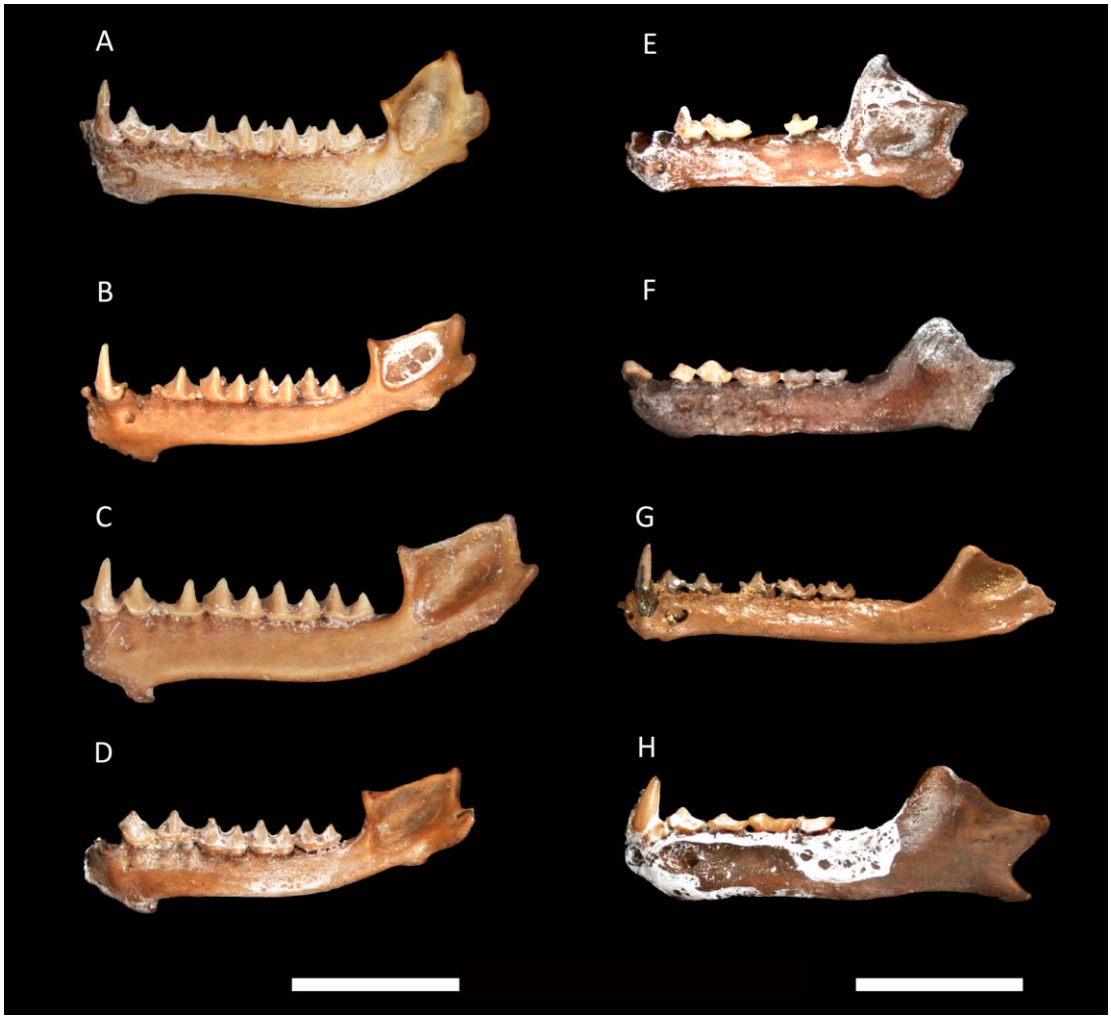

FIGURE 5. Chiropteran mandibles. **A.** *Mormoops blainvillei*, **B.** *Pteronotus macleayii*, **C.** *Pteronotus parnellii*, **D.** *Pteronotus quadridens*, **E.** *Brachyphylla nana*, **F.** *Erophylla bombifrons*, **G.** *Monophyllus redmani*, **H.** *Phyllonycteris poeyi*. Scale bar = 5 mm.

nearest entrance/exit. Although there was some silt present, the collecting process did not involve any excavation, only picking specimens off the substrate surface. The rocky plateau was at a depth of 8 m (fig. 1).

All specimens were hand collected and removed from the caves in water-filled plastic containers. Specimens were placed on screens to dry and many were sprayed lightly with White Rain® hairspray as a means of hardening them. After collection and drying, all specimens were subsequently processed and identified at Duke University and the American Museum of Natural History. Specimens were identified based on comparisons with skeletal material of the 18 extant chiropteran species of Hispaniola as well as closely related species from elsewhere in the Caribbean region, Central America, and South America. Extant specimens utilized in the comparative

Table 2. Measurements (mm) of the humeri of the three species of *Mormoops*.

	Mormoops blainvillei[a]	†*Mormoops magna*					*Mormoops megalophylla*[c]
		IZAC 344.1 Holotype	IZAC 344.2 Paratype	Cuevas Blancas[b]	Oleg's Bat Cave	Oleg's Bat Cave	
Length of the humeri	27.6 (25.0–27.4)	32.6	32.8	(33.0–33.2)	33.6	–	31.6; 31.7 (27.8–30.5)
Lateral diameter at middle of shaft	1.4	1.8	1.8	(1.6–1.8)	1.75	1.78	1.5; 1.5 (1.5–1.6)
Width of proximal epiphysis	3.2	4.2	4.1	(3.9–4.0)	4.09	4.01	3.7; 3.8 (3.5–3.7)

[a] Measurement of ROM 89973 followed by an observed range in parentheses from Silva Taboada (1974).
[b] Observed range of four humeri from Jiménez Vázquez et al. (2005).
[c] Measurements of AMNH 25589, 25602 followed by an observed range in parentheses from Silva Taboada (1974).

analysis (see appendix) were taken from the collections of the American Museum of Natural History, New York (AMNH), the Royal Ontario Museum, Toronto, Canada (ROM), and the National Museum of Natural History, Smithsonian Institution, Washington, DC (USNM). The fossil specimens described in this paper are housed in the AMNH Mammalogy collections and the Museo del Hombre Dominicano, Santo Domingo, Dominican Republic (MHD).

RESULTS

A total of 497 skeletal elements were identified, 165 from Oleg's bat cave and 332 from Cueva de Lily. Eleven species from three families were identified from these collections (figs. 3–6). Many of these species inhabit Hispaniola today, including all five phyllostomids, the single natalid, and three of the five identified mormoopid species.

Species Accounts

FAMILY MORMOOPIDAE SAUSSURE, 1860

Mormoops blainvillei Leach, 1821

Figures 3, 5

Material examined: **Cueva de Lily:** 2 complete skulls, 1 skull fragment, 1 femur, 2 radii. **Oleg's Bat Cave:** 6 complete skulls, 1 skull fragment, 4 dentaries, 1 scapula.

Extant distribution: Cuba, Jamaica, Hispaniola, and Puerto Rico (Dávalos and Turvey, 2012).

Fossil record: In Hispaniola *Mormoops blainvillei* has been recovered from superficial deposits (Saint-Michel-de-l'Atalaye) and fossilized owl pellets (Gonâve Island) in Haiti, and from cave fossils (Cerro de San Francisco) from the Dominican Republic (fig. 2; table 1). Additionally, *M. blainvillei* has been found in Pleistocene or Holocene cave deposits in Anguilla, Antigua and Barbuda, the Bahamas, Cuba, Jamaica, and Puerto Rico (Gundlach, 1878; Anthony, 1918; Koopman, 1951; Koopman and Williams, 1951; Koopman et al., 1957; Choate and Birney, 1968; Silva Taboada, 1974; Olson and Pregill, 1982; Steadman et al., 1984; Morgan and Woods, 1986; Morgan, 2001).

Remarks: No consistent differences in cranial or postcranial morphology or size were found between our sample and the comparative material of modern bats examined (appendix).

†*Mormoops magna* Silva Taboada, 1974

Figure 6

Material examined: **Oleg's Bat Cave:** 2 humeri.

Distribution: Cuba and Hispaniola (Silva Taboada, 1974; Jiménez Vázquez et al., 2005; this report).

Remarks: †*Mormoops magna* is a large-bodied *Mormoops* known only from humeral fragments and diagnosed only on the basis of size (Silva Taboada, 1974; Jiménez Vázquez et al., 2005). The two humeri recovered in this study correspond well with the measurements of †*Mormoops magna* provided by Silva Taboada (1974) and Jiménez Vázquez et al. (2005) (table

2). Previous to this study, †*M. magna* was known only from two cave deposits in Cuba (Silva Taboada, 1974; Jiménez Vázquez et al., 2005). Our record represents a range extension of over 1200 km from the localities in Cuba.

Pteronotus macleayii (Gray, 1839)
Figures 3, 5, 6

Material examined: **Cueva de Lily:** 4 radii. **Oleg's Bat Cave:** 6 complete skulls, 2 skull fragments, 2 dentaries, 1 humerus, 3 femora.

Extant distribution: Cuba and Jamaica (Dávalos and Turvey, 2012).

Fossil record: Fossil and subfossil remains are known from Pleistocene and Holocene deposits in Cuba and the Bahamas (Silva Taboada, 1974; Morgan, 1989).

Remarks: No consistent differences in cranial or postcranial morphology or size were found between our sample and the comparative material (appendix). This is the first record of *P. macleayii* for Hispaniola. Absence of this species from the modern fauna despite years of extensive collecting suggests that it has been extirpated from the island.

Pteronotus parnellii (Gray, 1843)
Figures 3, 5

Material examined: **Cueva de Lily:** 4 complete skulls, 1 skull fragment. **Oleg's Bat Cave:** 19 complete skulls, 6 dentaries.

Extant distribution: Cuba, Jamaica, Puerto Rico, Hispaniola, Saint Vincent, and possibly Trinidad and Tobago (Dávalos and Turvey, 2012; Clare et al., 2013).

Fossil record: In Hispaniola *Pteronotus parnellii* has been recovered from fossilized owl pellets (Diquini and Gonâve Island) in Haiti and from a Quaternary deposit (Cerro de San Francisco) in the Dominican Republic (fig. 2; table 1). Additionally, *P. parnellii* sensu stricto (see below) has been found in Pleistocene or Holocene cave deposits in Antigua, the Bahamas (New Providence), Cuba, Grand Cayman, Jamaica, Puerto Rico, and Tobago (Martin, 1972; Morgan, 1989, 2001).

Remarks: No consistent differences in cranial morphology or size were found between our sample and comparative material from the modern fauna of Hispaniola (appendix). The taxonomy and biogeography of bats of the *Pteronotus parnellii* complex is currently in a state of flux. Although traditionally recognized as a single species ranging through the Greater Antilles and from Mexico south to Peru and Brazil (e.g., Simmons, 2005), recent authors have found multiple diagnosable species within what was once called *Pteronotus parnellii*. Morphological and molecular studies have demonstrated that this complex includes at least five species and perhaps more, only some of which seem to correspond to previously delimited subspecies (Gutiérrez and Molinari, 2008; Clare et al., 2013). Because the holotype *P. parnellii* is from Jamaica and Antillean populations are typically much smaller than mainland forms, it seems likely that the name *P. parnellii* properly applies to all these bats including those from Hispaniola.

Pteronotus quadridens (Gundlach, 1840)

Figures 3, 5

Material examined: **Cueva de Lily:** 1 complete skull, 2 skull fragments, 1 dentary, 2 radii. **Oleg's Bat Cave:** 1 complete skull, 1 dentary.

Extant distribution: Cuba, Hispaniola, Jamaica, and Puerto Rico (Dávalos and Turvey, 2012; Simmons, 2005).

Fossil record: *Pteronotus quadridens* has previously been recovered from a Quaternary cave deposit (Cerro de San Francisco) in the Dominican Republic (fig. 2; table 1). Additionally, *P. quadridens* has been found in Pleistocene or Holocene cave deposits in Cuba (Silva Taboada, 1974, 1979; Woloszyn and Silva Taboada, 1977) and the Bahamas (Andros, Great Abaco, and New Providence; Morgan, 2001).

Remarks: No consistent differences in cranial or postcranial morphology or size were found between our sample and the comparative material (appendix).

FAMILY PHYLLOSTOMIDAE GRAY, 1825

SUBFAMILY GLOSSOPHAGINAE BONAPARTE, 1845

Brachyphylla nana Miller, 1902

Figures 4–6

Material examined: **Oleg's Bat Cave:** 25 complete skulls, 8 mandibles, 5 dentaries, 7 scapula, 11 pelvises, 16 humeri, 4 femora.

Extant distribution: Cayman Islands (Grand Cayman), Cuba, Hispaniola, and Turks and Caicos Islands (Middle Caicos) (Simmons, 2005).

Fossil record: *Brachyphylla nana* has been recovered from fossilized owl pellets (Port-de-Paix) and superficial deposit material (Saint-Michel-de-l'Atalaye) in Haiti and from a Quaternary cave deposit (Cerro de San Francisco) in the Dominican Republic (fig. 2; table 1). Additionally, *B. nana* has been found in Pleistocene or Holocene cave deposits in the Bahamas (Andros and New Providence), Cayman Islands (Cayman Brac), Cuba, and Jamaica (Peterson, 1917; Anthony, 1919; Miller, 1929a; Koopman and Williams, 1951; Williams, 1952; Koopman and Ruibal, 1955; Arredondo, 1970; Mayo, 1970; Silva Taboada, 1974; Woloszyn and Silva Taboada, 1977; Swanepoel and Genoways, 1978; Morgan, 2001).

Remarks: No consistent differences in cranial or postcranial morphology or size were found between our sample and the comparative material (appendix).

Erophylla bombifrons (Miller, 1899)

Figures 4–6

Material examined: **Cueva de Lily:** 1 complete skull, 2 skull fragments, 3 dentaries, 16 humeri, 2 femora, 19 radii. **Oleg's Bat Cave:** 12 complete skulls, 6 mandibles, 2 dentaries, 1 scapula, 2 humeri, 2 femora.

Extant distribution: Hispaniola and Puerto Rico (Dávalos and Turvey, 2012; Simmons, 2005).

Fossil record: The only previous fossil record for this species is from Hispaniola, consisting of specimens recovered from fossilized owl pellets (Port-de-Paix) and superficial deposit material (Saint-Michel-de-l'Atalaye) from Haiti, and from a Quaternary cave deposit (Cerro de San Francisco) from the Dominican Republic (fig. 2; table 1).

Remarks: No consistent differences in cranial or postcranial morphology or size were found between our sample and the comparative material (appendix).

Monophyllus redmani Leach, 1821

Figures 4–6

Material examined: **Cueva de Lily:** 14 complete skulls, 14 skull fragments, 2 dentaries, 7 humeri, 9 radii. **Oleg's Bat Cave:** 20 complete skulls, 9 dentaries, 8 humeri, 2 femora.

Extant distribution: The Bahamas (Acklins, Crooked Island), Cuba, Hispaniola, Jamaica, Puerto Rico, Turks and Caicos Islands (Middle Caicos, North Caicos, and Providenciales) (Dávalos and Turvey, 2012).

Fossil record: *Monophyllus redmani* has previously been recovered from fossilized owl pellets (Diquini and Gonâve Island) from Haiti as well as from Quaternary cave deposits (Cerro de San Francisco) from the Dominican Republic (fig. 2; table 1). Additionally, *M. redmani* has been found in Pleistocene or Holocene cave deposits in the Bahamas, Cayman Islands, Cuba, Jamaica, Puerto Rico, and Middle Caicos in the Turks and Caicos Islands (Anthony, 1925; Koopman and Willliams, 1951; Williams, 1952; Koopman, 1955; Koopman and Ruibal, 1955; Choate and Birney, 1968; Silva Taboada 1974; Morgan, 2001).

Remarks: No consistent differences in cranial or postcranial morphology or size were found between our sample and the comparative material (appendix).

Phyllonycteris poeyi Gundlach, 1861

Figures 4–6

Material examined: **Cueva de Lily:** 151 complete skulls, 84 skull fragments, 4 mandibles, 17 dentaries, 2 scapulae, 3 femora, 32 humeri, 29 radii. **Oleg's Bat Cave:** 6 complete skulls, 2 mandibles, 2 scapulae, 1 femur.

Extant distribution: Cuba and Hispaniola (Dávalos and Turvey, 2012; Simmons, 2005).

Fossil record: *Phyllonycteris poeyi* has previously been recovered from fossilized owl pellets (Diquini) and superficial deposit material (Saint-Michel-de-l'Atalaye) in Haiti and from a Quaternary cave deposit (Cerro de San Francisco) in the Dominican Republic (fig. 2; table 1). Additionally, *P. poeyi* has been found in late Quaternary cave deposits in the Bahamas (Abaco and New Providence), Cuba, and Cayman Islands (Cayman Brac) (Anthony, 1919; Koopman and Ruibal, 1955; Silva Taboada 1974; Morgan, 2001).

Remarks: No consistent differences in cranial or postcranial morphology or size were found between our sample and the comparative material (appendix).

SUBFAMILY STENODERMATINAE GERVAIS, 1856

Phyllops falcatus (Gray, 1839)

Material examined: **Oleg's Bat Cave:** 2 left scapulae.

Extant distribution: Cayman Islands (Grand Cayman and Cayman Brac), Cuba, and Hispaniola (Morgan, 2001; Tavares and Mancina, 2008; Dávalos and Turvey, 2012).

Fossil record: *Phyllops falcatus* has previously been recovered from fossilized owl pellets (Diquini and Port-de-Paix) and superficial deposit material (Saint-Michel-de-l'Atalaye) in Haiti and from fossilized owl pellets (Constanza) and Quaternary cave deposits (Cerro de San Francisco) in the Dominican Republic (fig. 2; table 1). Additionally, *P. falcatus* has been found in late Quaternary cave deposits in Cuba (Anthony, 1919; Koopman and Ruibal, 1955; Arredondo, 1970; Torres and Rivero de la Calle, 1970; Silva Taboada and Woloszyn, 1975; Suárez and Díaz-Franco, 2003).

Remarks: No consistent differences in scapula shape or size were found between the Oleg's Bat Cave samples and the comparative material (appendix).

FAMILY NATALIDAE GRAY, 1866

Chilonatalus micropus (Dobson, 1880)

Material examined: **Cueva de Lily:** 1 radius.

Distribution: Colombia (San Andrés and Providencia islands), Hispaniola, and Jamaica (Tejedor, 2011).

Fossil record: *Chilonatalus micropus* has previously been recovered from a late Quaternary deposit (Cerro de San Francisco) in the Dominican Republic (fig. 2; table 1; Morgan, 1994, 2001). The fossil records of *C. micropus* from Cuba and Grand Cayman Island reported by Morgan (2001) correspond to *C. macer* (Tejedor, 2011).

Remarks: No differences in radius shape or size were found between the Cueva de Lily sample and the comparative material (appendix).

DISCUSSION

The flooded nature of both cave localities makes it impossible to determine the age of the fossils or the time span in which they were deposited. However, the presence of extinct (†*Mormoops magna*) and extirpated (*Pteronotus macleayii*) species along with other vertebrate taxa recovered from these caves that are currently under study (final identifications not yet available) suggests that these fossils may be from the Late Pleistocene. Extinct sloth remains have been recovered from Cueva de Lily. Among the more interesting remains from Oleg's Bat Cave, which is more complex geologically and may be more heterogeneous taphonomically, are sloths, extinct rodents, a solenodon, an extinct bird with Cuban affinities, and the extirpated Cuban crocodile, *Crocodylus rhombifer*.

Historically, 23 species of bats have been recorded from Hispaniola of which only 18 species are currently extant on the island (table 1). Of the five species that no longer occur on Hispaniola, two are extinct mormoopid species (†*Mormoops magna* and †*Pteronotus* sp.) and

FIGURE 6. Chiropteran humeri. **A.** *Mormoops blainvillei* (extant, ROM 89973), **B.** *Mormoops megalophylla* (extant, AMNH 25589), **C.** †*Mormoops magna*, **D.** †*Mormoops magna* (mirror image), **E.** *Pteronotus macleayii* (mirror image), **F.** *Brachyphylla nana* (mirror image), **G.** *Erophylla bombifrons* (mirror image), **H.** *Monophyllus redmani* (mirror image), **I.** *Phyllonycteris poeyi*. Scale bar = 10 mm.

three are extant species that occur elsewhere in the Caribbean (*Mormoops megalophylla*, *Pteronotus macleayii*, and *Lasiurus insularis*). †*Mormoops magna*, apparently endemic to the islands of Cuba and Hispaniola, is known only from humeri remains from three localites. Similarly, †*Pteronotus* sp. is known only from a single mandible collected at Cerro de San Francisco (Morgan, 2001). The abundance of fossil bat remains in Oleg's Bat Cave and Cueva de Lily opens the possibility that future collecting expeditions may be able to collect additional material for these two species. Little is known about these extinct taxa other than that they occurred sympatrically with congeners, suggesting that diversity of sympatric mormoopid communities may have been even greater in the Pleistocene than it is today. A recently discovered correlation between loss of species and loss of island area due to rising sea levels since the last glacial maximum (LGM) suggests that climate change may have been one of the major drivers of extinction of Caribbean bats since the Pleistocene (Dávalos and Russell, 2012).

Mormoops megalophylla, *Pteronotus macleayii*, and *Lasiurus insularis* are species that have been recorded in Hispaniola only as fossils. Extant populations of *Pteronotus macleayii* are currently found on the adjacent islands of Cuba and Jamaica, with Pleistocene records from Cuba, Hispaniola, and the Bahamas (New Providence). *P. macleayii* is considered an obligate cave-dwelling species (Silva Taboada, 1979; McFarlane, 1986; Rodríguez-Durán and Kunz, 2001; Genoways et al., 2005). The slightly larger Pleistocene range of this taxon suggests that it was extirpated relatively recently from the more northern and eastern parts of its range, perhaps as a result of flooding of roost caves due to rising sea levels and climate change (Morgan, 2001).

Extant populations of *Mormoops megalophylla* have a wide range in mainland Central and South America but a very restricted distribution in the Caribbean, apparently limited to Aruba,

Curaçao, and Bonaire (Netherlands Antilles), Trinidad, and Margarita Island (Simmons, 2005). In the West Indies, Pleistocene remains of *M. megalophylla* had been found in the Bahamas (Andros, Great Abaco), Cuba, Hispaniola, Jamaica, and Tobago, indicating that this taxon was once widespread in the Caribbean (Morgan, 2001; Rojas Martín, 2006). In the case of *Lasiurus insularis*, extant populations occur today only in Cuba, but fossils of this species are known from both Cuba and Hispaniola (Morales and Bickham, 1995; Morgan, 2001; Simmons, 2005; Dávalos and Turvey, 2012; Nuñez Novas and León, 2011). Reasons for the local or regional extinctions of these taxa could have included a variety of factors including competition with other bat species (Koopman and Williams, 1951; Williams, 1952), natural habitat changes (e.g., increased xerification; Pregill and Olson, 1981), deforestation (Gannon et al., 2005), flooding of roost caves due to sea-level changes (Morgan, 2001; Dávalos and Turvey, 2012), or more complex ecological factors associated with reduced island areas after the LGM (Dávalos and Russell, 2012). In the case of *Lasiurus insularis*, a tree-roosting species (Silva Taboada, 1979), anthropogenic deforestation and stochastic events such as hurricanes might have played a significant role; in the case of *Mormoops* and *Pteronotus* species, which rely on caves for roosts, rising sea levels and cave flooding seem more likely.

Only two of the extant species currently distributed in Hispaniola are thus far completely absent from the fossil record of the Island—*Noctilio leporinus* and *Molossus molossus*. Both species share a widespread distribution that extends from Mexico southward to Argentina and the West Indies. In the Caribbean region their fossil record is sparse, with the former species reported as fossils only from Barbuda, Cuba, and Puerto Rico, while the latter is known from fossils only from Antigua and possibly Jamaica[7] (Morgan, 2001; Olson and Nieves-Rivera, 2010). This may at least in part reflect the roosting habits of these taxa, both of which in natural situations prefer roosts in hollow trees to those in caves (Hood and Jones, 1984; Morgan, 2001; Genoways et al., 2005). Caves, which offer many opportunities for fossilization of vertebrates trapped or deposited within them, are by far the greatest source of fossil bats in the Caribbean region (Morgan, 1989, 1994, 2001). It is perhaps ironic that the flooding of these caves as a result of postglacial climate change may have significantly contributed to the extirpation and extinction of multiple populations of bats on Hispaniola and other Caribbean islands (Morgan, 2001; Dávalos and Turvey, 2012; Dávalos and Russell, 2012). However, in the case of Oleg's Bat Cave and Cueva de Lily, flooding has helped to preserve ancient records of bat diversity that provide new insights into the fauna of Hispaniola.

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[7] According to Morgan (2001) it is unclear whether this record based on Koopman and Williams (1951) corresponds to fossil deposits or recent owl pellet deposits.

ing curators and collection staff graciously provided access to specimens under their care: Eileen Westwig (AMNH), Burton Lim (ROM), and Alfred Gardner and Suzanne Peurach (USGS Patuxent Wildlife Research Center/United States National Museum). Gary Morgan and an anonymous reviewer read early drafts of this report and made helpful suggestions for its improvement, for which we are grateful. Patricia J. Wynne drew figure 2. This research was supported by the National Science Foundation Research Experience for Undergraduates (REU) program at the AMNH, and NSF grant DEB 0949859 to N.B.S. Support was also provided by grants from the Leakey Foundation and Waitt Foundation/National Geographic Society to A.L.R. and the Explorers Fund Grant to S.B.C.

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APPENDIX

Specimens Examined

The following list includes all the specimens used in the comparative analysis of this study. Specimens examined belong to the collections of the American Museum of Natural History, New York (AMNH), the Royal Ontario Museum, Toronto (ROM), or the United Stated National Museum, Smithsonian Institution, Washington, D.C. (USNM).

FAMILY MORMOOPIDAE

Mormoops blainvillei: **Dominican Republic:** San Rafael, Rancho La Guardia (AMNH 213897); Barahano, Pedernales, Cabo Rio (AMNH 238144). **Jamaica:** Saint Catherine, Saint Clair Cave (ROM 89973).

Mormoops megalophylla: **Mexico:** Nayarit, Amatlán de Cañas, Rancho Palo Amarillo (AMNH 25589, 25602).

Pteronotus macleayii: **Jamaica:** Saint James, Montego Bay (AMNH 45256, 45258, 45260, 45261, 45266, 60917); Saint Elizabeth, Balaclava, Oxford Cave (AMNH 45268).

Pteronotus parnellii: **Dominican Republic:** Santiago Rodríguez, Moncion, Cueva Duran (AMNH 212996). **French Guiana:** Paracou, near Sinnamary (AMNH 267284). **Jamaica:** Saint James Parish, Montego Bay, Sewell Cave (AMNH 271546, 271547); Saint Mary Parish, Lucky Hill, Mount Plenty Cave (AMNH 271542, 271543); Manchester Parish, Auchtembeddie, Oxford Cave (AMNH 271544).

Pteronotus quadridens: **Dominican Republic:** Santiago Rodríguez, Moncion, Cueva Duran (AMNH 212995). **Haiti:** Sud, Sapoti (AMNH 236654). **Jamaica:** Saint Catharine Parish, Ewarton, Saint Clair Cave (AMNH 271545, 271554, 271555); Saint Elizabeth, Balaclava, Oxford Cave (AMNH 45248). **Puerto Rico:** San Juan, Pueblo Viejo, Cueva de Fari (AMNH 39359); Trujillo Alto (AMNH 39397, 39405, 39417).

FAMILY PHYLLOSTOMIDAE

Artibeus jamaicensis: **French Guiana:** Paracou, near Sinnamary (AMNH 266345).
Haiti: Sud, Paillant (AMNH 236678, 236679).

Brachyphylla cavernarum: **U.S. Virgin Islands:** Saint John, Lameshur (AMNH 188237); Saint John, Cruz Bay (AMNH 208181).

Brachyphylla nana: **Dominican Republic:** San Cristóbal, Los Haitises (AMNH 244909, 244910, 244912, 244914); Barahona, Los Patos (AMNH 97597). **Cayman Islands:** Grand Cayman, Prospect (USNM 538177).

Erophylla bombifrons: **Dominican Republic:** La Vega, Bonao (USNM 538347). **Puerto Rico:** Pueblo Viejo (AMNH 39339, 39341).

Macrotus waterhousii: **Cuba:** Guantanamo Bay, Kittery Beach Road (USNM 598957). **Dominican Republic:** Samana, San Juan River (AMNH 91343).

Monophyllus redmani: **Haiti:** Sud, Paillant (AMNH 236663, 236669). **Jamaica:** Trelawny, Quick Step (USNM 546355). **Puerto Rico**: Trujillo Alto, La Cueva de Mollfulleda (USNM 178028).

Phyllonycteris poeyi: **Cuba:** Habana, Aguacate, Cueva de la Numancia (AMNH 176027); Habana, Guanajay (AMNH 23758; USNM 103445).

Phyllops falcatus: **Dominican Republic:** Elias Pina, Río Limpio (USNM 542273). **Haiti:** Sud, Paillant (AMNH 236696).

FAMILY NATALIDAE

Chilonatalus macer: **Cuba:** Isla de la Juventud, Cueva de Punta Brava (AMNH 186978).

Chilonatalus micropus: **Dominican Republic:** Samana, Samana, Vicenti cove (AMNH 216128).

Natalus jamaicensis: **Jamaica:** Saint Catharine Parish, Ewarton, Saint Clair Cave (AMNH 246127).

Natalus major: **Dominican Republic:** Barahona, Maniel Viejo (AMNH 97589).

FAMILY NOCTILIONIDAE

Noctilio Leporinus: **Bolivia:** Beni, Mamore, Mamore River (AMNH 210667); Beni, Yacuma, Apere River (AMNH 210666). **Dominican Republic:** Pedernales, Oviedo, La Poza (AMNH 244903, 244904).

FAMILY MOLOSSIDAE

Molossus molossus: **Dominican Republic:** Distrito Nacional, Santo Domingo, La Bracita (AMNH 62469); Santiago Rodríguez, Moncion, Cueva Duran (AMNH 213000). **French Guiana:** Paracou, near Sinnamary (AMNH 267250). **British Virgin Islands:** Guana Island (AMNH 256412). **U.S. Virgin Islands:** Saint John, Cruz Bay (AMNH 206704).

Nyctinomops macrotis: **Dominican Republic:** Distrito Nacional, Domingo, Santo Domingo (AMNH 244932, 244936). **Jamaica:** (USNM 210546).

Tadarida brasiliensis: **Bolivia:** Cochabamba, Tablas Monte (AMNH 268655). **Haiti:** Sud, Sapoti (AMNH 236705).

FAMILY VESPERTILIONIDAE

Eptesicus fuscus: **Dominican Republic:** San Cristobal, Cueva Santa Maria (AMNH 244927). **United States of America:** Arizona, Cochise, south fork of Cave Creek (AMNH 207699).

Lasiurus borealis: **United States of America:** New York, New York City, American Museum of Natural History Building (AMNH 238155); New York, New York City, 138 Convent Avenue, City College (AMNH 203072).