

NEW QUATERNARY FOSSILS FROM HIGH ELEVATION
CAVE DEPOSITS IN CUBANuevos fósiles del Cuaternario colectados en depósitos
cavernarios a alta elevación en CubaLázaro W. Viñola-López^{1,2*}, Osvaldo Jiménez-Vázquez³, Abel Hernández Muñoz⁴,
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ABSTRACT

High elevation fossil deposits in Cuba have been poorly studied, and there is a limited understanding of how altitudinal changes could have affected the composition of faunal communities in the past. Here, we report fossils of 13 vertebrate species and an invertebrate from 11 late Quaternary cave deposits at elevations ranging from 532 to 1123 meters above sea level, located in the Guamuhaya Masiff in central Cuba. The composition of the vertebrate fauna assemblages recovered from these localities resembles that known from other lowland deposits and includes eight extinct, one extirpated, and four extant species. Furthermore, the specimens reported here record the highest elevation known for nine species recovered.

Keywords: extinct vertebrates, Pico San Juan, Guamuhaya Massif, mammal, Caribbean.

RESUMEN

Los depósitos paleontológicos de cuevas a gran elevación en Cuba han sido poco estudiados y existe una comprensión limitada de cómo los cambios altitudinales pudieron afectar la composición de comunidades terrestres durante el pasado. Aquí reportamos fósiles de 13 especies de vertebrados y un invertebrado colectado en 11 depósitos paleontológicos cavernarios del Cuaternario tardío a una altura que oscila entre 532 y 1123 metros sobre el nivel del mar, ubicadas en el macizo Guamuhaya, en el centro de Cuba. La composición de la fauna



de vertebrados recuperados en estas localidades se asemeja a la conocida de otros depósitos en las tierras bajas, e incluye ocho especies extintas, una extirpada y cuatro que aun habitan la región. Los especímenes reportados aquí registran la elevación más alta conocida para nueve de las especies recuperadas.

Palabras clave: vertebrados extintos, Pico San Juan, Macizo Guamuhaya, mamífero, Caribe.

Quaternary fossil-bearing deposits with vertebrate remains are relatively abundant throughout the Cuban archipelago, especially in areas of elevated karstification. In Cuba, fossils are often found in cave deposits, sinkholes, and fissures but have also been reported less often from springs and tarpits (Silva et al., 2007; Woloszyn & Silva, 1977). Most of these localities lie at low elevations above the current sea level, as most of the karst development in Cuba is located in the lowlands. Therefore, there is a limited understanding of the fauna that inhabited some of the highest mountains in Cuba during the Quaternary and how they may relate to what has been described elsewhere (Nuñez Jimenez, 1998; Silva et al., 2007). Today, these high-elevation areas are biodiversity hotspots within the island and provide habitat to many local endemic and endangered species (Gonzalez Alonso et al., 2012).

Similarly, mountain ranges on other islands in the Caribbean region are refugia for a high diversity of endemic vertebrates, some of which are local endemics and others that have a broader historical distribution but, because of habitat fragmentation, are restricted to remaining high elevation primary forest (Anadón-Irizarry et al., 2012; Hedges et al., 2018). Fossils collected in caves in the mountains of the Tiburon Peninsula in Hispaniola have preserved the co-occurrence of extinct locally endemic mammals in association with species that once had a wider distribution throughout the island in the late Quaternary and are either extinct today or have suffered from significant habitat reduction (Cooke et al., 2011; Viñola-López et al., 2022; Woods, 1989).



Figure 1. Localities in the Guamuhaya Massif in central Cuba. **A)** forest in the region of Pico San Juan and general areas from where several of the caves with fossils reported here are found. **B)** entrance of Cueva El Sedro Seco, one of the richest localities collected. **C)** interior of Cueva 92 Aniversario de Antonio Nuñez Jimenez with secondary formations.

Here, we report the faunal assemblage from eleven caves between 532 and 1123 meters above sea level (m) located near Pico San Juan in the Guamuhaya Massif, Municipality Cumanayagua, Cienfuegos Province in south-central Cuba (Fig. 1). The specimens from Cueva de Maguayara (532 m), Cueva de Carmen y Lito (671 m), Cueva El Almiqui (1037 m), Cueva El Cedro Seco (1023 m), Cueva de la Lechuza (763 m), Cueva Julio

Cesar (1053 m), and Cueva Cimarrones 16 (991 m), Cueva 92 Aniversario de Antonio Nuñez Jimenez (1021 m), and Cueva A6 (1123 m) were collected by members of the spelunking group Samá from the Sociedad Espeleológica de Cuba between 2014 and 2018 (Hernández Muñoz et al., 2015). Fossils from Cueva de Doña Rosa (900 m) were likewise collected by members of Samá in August 2001. Fossils from Cueva de la Campana (1010 m) were collected by Roberto Castellón from the Sociedad Espeleológica de Cuba in Agosto de 1979.

The specimens are housed at the Gabinete de Arqueología, Oficina del Historiador de La Habana, the facility of the spelunking group Samá in the city of Sancti Spiritus, and the Museo Municipal de Cumanayagua, in Cienfuegos. The vertebrates identified from these localities are well-known from the late Quaternary fossil record of Cuba, and their identification was based on characters described in the literature (Aranda et al., 2015; Jiménez-Vázquez et al., 2005; Olson, 1974; Silva et al., 2007) and comparison with specimens available in the collections at the Instituto de Ecología y Sistemática, and the Gabinete de Arqueología de la Oficina del Historiador de la Habana in Havana, Cuba. Radiometric dates are not available for any of the localities reported here, but considering the faunal association,

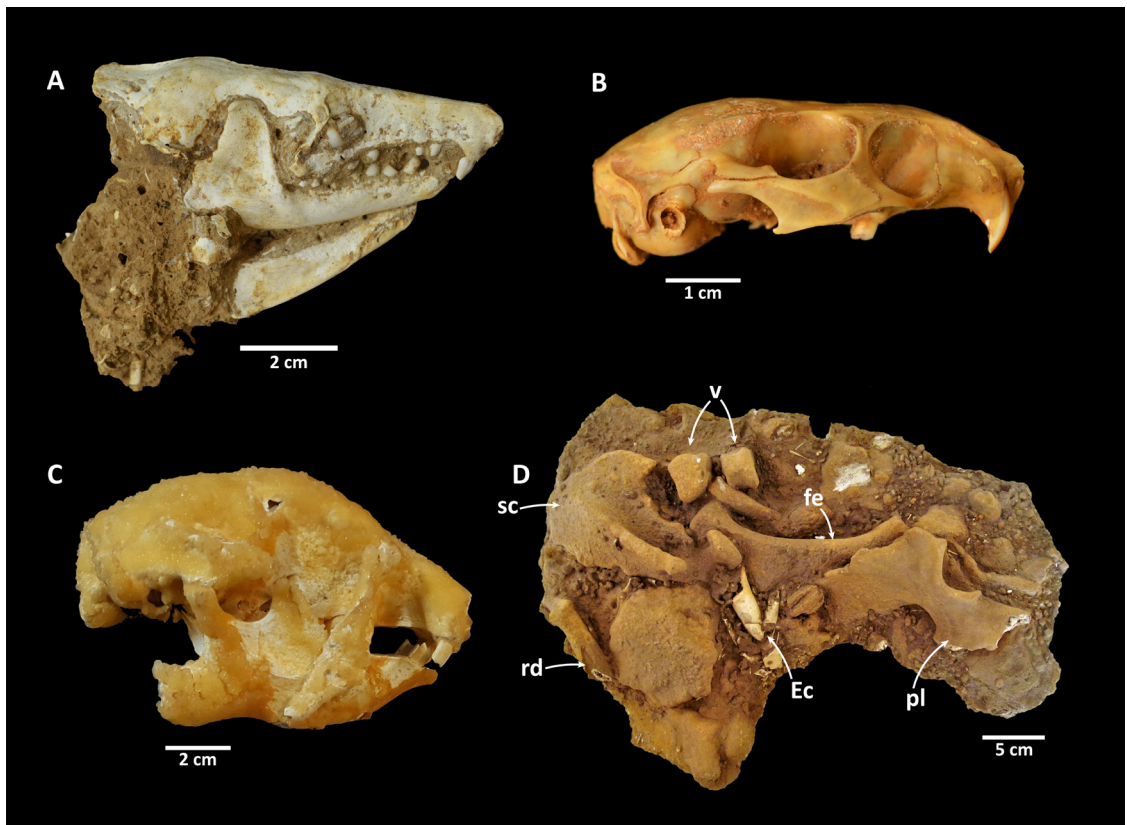


Figure 2. Selection of fossils recovered from several caves in the Guamuhaia Massif. **A)** Skull and associated mandibles of *Atopogale cubana* collected in Cueva El Almiqui; **B)** skull of subadult specimens of *Boromys offella* collected in Cueva El Sedro Seco; **C)** skull with associated mandible of *Neocnus glirisformis* collected in Cueva 92 Aniversario de Antonio Nuñez Jimenez; **D)** partial skeleton of juvenile specimen of *Megalocnus rodens* recovered from Cueva de la Campana. Abbreviations: Ec, chela cf. *Epiloboceras*; fe, femur; pl, pelvis; rd, radius; sc, scapula; v, vertebrae.



Figure 3. Skeleton of *Neocnus gliriformis* partially covered by carbonates in Cueva 92 Aniversario de Antonio Nuñez Jimenez in association with a specimen of *cf. Epiloboceras* (see arrow).

which includes extant and recently extinct species (Table I), the fossils are likely from the late Quaternary (Orihuela et al., 2020b). The differential preservation of the specimens from different cave deposits suggests that they are likely allochronic (Fig. 2). Direct and indirect dates of the extinct species recovered from these cave deposits are available from elsewhere in Cuba and fall in the late Pleistocene-Holocene (Orihuela et al., 2020b).

Most of the species found in these caves were widespread in Cuba during the late Quaternary, and their remains have been collected from other paleontological deposits at low elevations (Jiménez-Vázquez et al., 2005; Silva et al., 2007; Suarez, 2022). Among mammals, only two of the ten species are still present in the region, and the fossils reported here represent the highest elevation on record for the extinct and extirpated species. Fossils of rodents are the most

abundant in the cave deposits, and four species are identified. Two of the species (*Geocapromys columbianus* and *Boromys offella*) are extinct, but the other two (*Capromys pilorides* and *Mysateles prehensilis*) are still present in the area of Pico San Juan (Fig. 2) (Silva et al., 2007).

The four sloth species known from the late Quaternary of Cuba are present in the collection, including the more terrestrial species *Mesocnus browni* and *Megalocnus rodens* (Figs. 2 and 3). Besides the more terrestrial habits of *Megalocnus rodens* and *Mesocnus browni* and their abundance in localities with open habitats (Arredondo Antunez, 2012; Silva et al., 2007), the fossils from Cueva El Amiquí, Cueva Cedro Seco, and Cueva de la Campana show that they additionally inhabited mountain forests and likely used a wide range of ecosystems through the altitudinal gradient. This is further supported by the discovery of remains of *Mesocnus browni* and *Megalocnus rodens* inside caves and sinkholes in mogotes and hills at intermediate elevations near the 200 m in western and central Cuba (Condis Fernandez, 2010; Nuñez Jimenez, 1998; Silva et al., 2007). Three partial skeletons of sloth corresponding to two species were found in Guamuhaia Massif, but most of the fossils reported correspond to isolated bones. A partial skeleton of *Megalocnus rodens* was collected from Cueva de la Campana (1010 m), (Fig. 2), and two skeletons of *Neocnus gliriformis* (a subadult and an adult) were found in Cueva 92 Aniversario de Antonio Nuñez Jimenez (1021 m) (Figs. 2 and 3). Explanations for how these specimens were deposited into the cave include that they could have been transported during a storm, may have fallen inside the cave and become trapped, or perhaps utilized the cave as a refugium typical of some mainland species (e.g., Hunt & Lucas, 2018; Thompson et al., 1980). Partial and complete skeletons of sloths have been found in multiple cave and sinkhole deposits in Cuba, but taphonomy studies about the origin of those specimens are lacking.

The eulipotyphlans *Nesophontes micrus* and *Atopogale cubana* were widely distributed throughout Cuba until the late Holocene. The former survived until the arrival of Europeans to Cuba and is abundant in paleontological deposits, particularly in ancient owl roosts (MacPhee et al., 1999; Orihuela, 2023). Historical accounts indicate that *A. cubana* may have survived in the Guamuhaia Massif until the second half of the 19th century. However, today it is found only in the mountain forests of Pico Cristal and Alejandro de Humboldt national parks in eastern Cuba at an elevation between 400 and 800 m (Kennerley et al., 2018; Silva et al., 2007) but fossil and archaeological specimens from elsewhere on the island show that this species occupied a broader spectrum of habitats (Silva et al., 2007). The Cuban Solenodon builds tunnel systems used by family groups and is primarily nocturnal (Silva et al., 2007). In Cueva El Almiquí, a partial skeleton comprised of several vertebrae, ribs, a scapula, two mandibles, and a complete skull was collected (Fig. 2), and an additional partial skeleton was recovered in Cueva Julio Cesar. The discovery of these two individuals of *A. cubana*, as well as partial skeletons of the extinct *A. arredondoi* inside other caverns in western Cuba, suggest that the species *Atopogale* may have frequented inside caves or were accidentally trapped inside them (Condis Fernandez, 2011).

The frog *Osteopilus septentrionalis* is widespread throughout the island today and is found in a broad range of habitats. Fossils referred to this species have been collected primarily in central and western Cuba (Aranda et al., 2017; Jiménez-Vázquez et al., 2005; Orihuela, 2010). On the other hand, 58 species of *Eleutherodactylus* are known in Cuba today.

Fossils of *Eleutherodactylus* have been reported from other quaternary deposits in central and western Cuba, and Isla de la Juventud (Aranda et al., 2020; Jiménez-Vázquez et al., 2005; Orihuela et al., 2020a), but identification beyond the generic level is difficult due to a lack of comparative anatomical studies.

One of the more interesting findings from the caves in Pico San Juan are remains of the extinct bird *Nesotrochis picapicensis*, which survived until the late Holocene and is common in paleontological and cultural deposits in western Cuba. Remains of this species collected in Cueva Julio César represent the easternmost and highest fossil record to date. However, there is a pendant made from a tarsometatarsus of *N. picapicensis* that was found in the archaic archaeological site Cueva de los Chivos, localized on the Valle Jibacoa, Guamuaya Massif Sancti Spiritus Province, which is further east (Cordoba Medina, 2014). *Nesotrochis picapicensis* was initially considered to be a rail (Fischer & Stephan, 1971) but mitochondrial genome analysis of a congeneric species from Hispaniola (*N. steganinos*) showed that *Nesotrochis* is sister to Sarothruridae and Aptornithidae from the old world (Oswald et al., 2021). The humerus of *Nesotrochis* shows that these birds were flightless like other endemic birds from the Caribbean islands (Olson, 1974). Remains of *N. picapicensis* are often found in association with other vertebrates that preferred wetlands and open habitats, like *Crocodylus rhombifer*, *Mesocapromys nanus*, *M. sanfelipensis*, *Mustelirallus cerverai*, *Ferminia cerverai* (Jiménez-Vázquez et al., 2005; Rojas-Consuegra et al., 2012; Suarez, 2022; Viñola-López et al., 2018). However, the presence of *N. picapicensis* and *N. steganinos* in cave deposits at high elevations in Cuba (Cueva 92 Aniversario de ANJ, 1021 m; Cueva Julio Cesar, 1053 m) and Hispaniola (Trouing Jeremie # 5, 1275 m; Touring Marassa, 1875 m; Touring Pas Konnen, 1980 m) (Oswald et al., 2021; Viñola-López et al., 2023) may suggest that these species were also forest dwellers and inhabited montane habitats. Some extant members of the family Sarothruridae, sister taxa of *Nesotrochis*, are found in a wide range of habitats from sea level to montane forests at 2000 m (Colyn et al., 2019; Goodman et al., 2011). The specimens of *N. picapicensis* from Cueva 92 Aniversario de ANJ correspond to a partially associated skeleton collected 50 meters inside the cave in association with partial skeletons of a *Mysateles prehensilis* and two *Neocnus gliriformis*. No evidence of an owl or raptor roost was found in this locality, suggesting that a predator did not transport the specimens from lower elevations.

Five species of the genus *Epiloboceras* are found in freshwater habitats on the island. The species *E. capolongoi* is known exclusively from mountain rivers and streams in the Guamuaya Massif and was recently reported from several localities at an elevation near the 1000 m in the surroundings of Pico San Juan (Rodríguez-Cabrera et al., 2023). The two fossils of crustaceans from Cueva de la Campana and Cueva A6 morphologically resemble *E. capolongoi*, which is the only large freshwater crustacean found in the area. Its direct association with fossils of the extinct sloths *Megalocnus rodens* and *Neocnus gliriformis* indicate that this species has been present in the Guamuaya Massif at least since the late Quaternary. However, until the specimens are studied and described in more detail, we refer the specimens to genus level

The specimens described here extend the altitudinal distribution of extinct rodents, sloths, the eulipotyphlans *Nesophontes micrus* and *Atopogale cubana*, and the flightless bird *Nesotrochis picapicensis*. Although these species are also known from Quaternary deposits elsewhere

in Cuba, their fossils discussed here provide necessary insight regarding the fauna that once inhabited the highlands. Further exploration of these and other high elevation paleontological deposits in Cuba will help us better understand changes in faunal composition related to habitat and altitude gradients.

Table I. Fossil vertebrates found in cave deposits at high elevation near Pico San Juan in the Guamuhaia Massif in south-central Cuba. † = extinct; * = extirpated; 1 = reported by Silva et al. (2007). CEA, Cueva El Almiquí; CCS, Cueva El Cedro Seco; CJC, Cueva Julio Cesar; CL, Cueva de la Lechuza; CC16, Cueva Cimarrones 16; CC, Cueva de la Campana; CM, Cueva Mayaguara; CCL, Cueva Carmen y Lito; CANJ, Cueva 92 Aniversario de ANJ; CA6, Cueva A6; CDR, Cueva Doña Rosa.

Taxa	CEA	CCS	CJC	CL	CC16	CC	CM	CCL	CANJ	CA6	CDR
Mammalia											
<i>Atopogale cubana</i> *	X		X		X					X	
<i>Nesophontes micrus</i> †		X								X	
<i>Mysateles prehensilis</i>		X	X	X	X				X		X
<i>Capromys pilorides</i>		X			X						
<i>Geocapromys columbianus</i> †		X					X	X	X		X
<i>Boromys offella</i> †		X									X
<i>Megalocnus rodens</i> †		X				X	X			X	X
<i>Mesocnus browni</i> †	X		X			X					
<i>Acratocnus antillensis</i> †			X								X ¹
<i>Neocnus gliriformis</i> †			X						X		
Amphibia											
<i>Osteopilus septentrionalis</i>			X								
<i>Eleutherodactylus</i> sp.						X					
Aves											
<i>Nesotrochis picapicensis</i> †			X						X		
Crustacea											
cf. <i>Epiloboceras</i> sp.						X				X	

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