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Colonization and defaunation on a small island: evidence from Quaternary fossils of Sombrero Island

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Abstract

The Caribbean islands represent some of the most biologically diverse places on Earth, but much of that diversity is now at risk due to human impact. Larger islands in the Caribbean host more native species, but small islands still hold together a significant portion of the regional biota. Although our knowledge of extinct and extirpated taxa continues to improve, there are hundreds of islands, each with their own unique faunal histories from where there is little information about their ancient diversity. Sombrero is a very small island (0.38 km^2) located within the limits between the Greater and Lesser Antilles and is largely barren of vegetation and freshwater. The island was extensively mined for bird guano in the 1800s, which profoundly altered its topography and fauna. Here, we describe a collection of microvertebrates recovered in 1964 from Sombrero, which documents an unexpectedly high number of colonization events and high extinction rate for this territory. The late Quaternary deposits from the island contain remains of five types of lizards, a snake, a tortoise, and an anuran that colonized the island once it became aerially exposed in the early Pleistocene. The ability for such a small, remote island to have eight colonizing taxa in < 2.5 Ma, provides support for the role that island hopping played in regional biodiversity in the Cenozoic (e.g., GAARlandia), even across small, barren islands. Furthermore, these fossils further show that large scale defaunation also affected vertebrate communities on very small islands in the Caribbean.

Non-technical Summary

The Caribbean contains thousands of islands, each containing a unique assemblage of animals. These islands combined host one of most diverse faunal assemblages on Earth but they have been put at risk with the arrival of humans to the region, a risk we cannot accurately assess without an understanding of animal diversity before human arrival. Such research requires studying the fossil record, especially those from the last few thousand years (i.e., Holocene). Although scientific studies on the diversity and fossil record of some Caribbean islands have been published, especially on larger islands like Cuba and Hispaniola, little is known or published on the many thousands of smaller islands throughout the region. For this study, we describe the Holocene fossils from the tiny island of Sombrero (0.38 km^2). Sombrero is one of the northernmost islands of the Lesser Antilles and is a barren limestone slab that was extensively mined for bird guano. Only four migratory bird species and three lizard species are presently found on Sombrero, and only one known extinction—a tortoise—has been reported. The fossils found on this island include fish, five lizards, a snake, a tortoise, an anuran, and two birds. Considering that this island is relatively young (less than 2.5 million years old) and small, it is surprising that it contained so many land vertebrates. The fossil record from Sombrero along with that from other islands in the Lesser Antilles provide evidence into the role that small islands played in the origin of diversity of life in the Caribbean.

Introduction

Of the 25 biodiversity hotspots identified by Myers et al. (2000), the Caribbean ranks sixth in the number of plant and animal species that it contains, while only representing 29,840 km² of land area. Much of that diversity is also unique to the Caribbean, with 100% of the amphibian species, 95% of the reptile species, and 74% of the mammal species being endemic (Myers et al., 2000). Because of this unique density, since the 19th century, the biodiversity of the Caribbean has been the focus of many zoological studies. Many of the early biodiversity studies were mostly accounts, intended to record the richness of the taxa represented in the region, but more recent work has expanded into conservation of Caribbean diversity, especially in the face of anthropogenic effects (e.g., Hedges et al., 2018; Kemp et al., 2020; Kemp, 2023). Those works have highlighted the deleterious impact of anthropogenically-induced forces, e.g., deforestation and the introduction of invasive species (e.g., cats, mongoose, and rodents; Kemp et al., 2020). Many of those impacts also happened at an alarming rate, with, e.g., a nearly 95% reduction of Haiti's original forest land cover from 1988 to 2016 (Hedges et al., 2018). Additionally, Caribbean mammalian extinction during the prehistoric Holocene is the highest in the world (MacPhee and Flemming, 1999; Woods and Sergile, 2001; Turvey, 2009). Unfortunately, for many Caribbean islands, much of our understanding of preanthropogenic populations is derived from 18th-century zoological reports, likely producing a significant underestimate of faunal and floral changes (Bochaton et al., 2015). However, the fossil record from the Quaternary of the Caribbean offers a more accurate window into prehuman diversity, with the karstic geology of many of the islands having excellent potential for fossil preservation. Indeed, recent reports over the past couple of decades utilized this record, demonstrating the severity of extinctions in the Caribbean (Biknevicius et al., 1993; Pregill et al., 1994; Steadman et al., 2019; Viñola-López and Almonte, 2022). An increasing understanding of the fossil record of the entire Caribbean not only creates a more complete record of diversity for the region, but it also can better demonstrate the deleterious effects that humans are having on these islands (Kemp et al., 2020; Orihuela et al., 2020; Bochaton et al., 2021b; Bochaton, 2022). Although our understanding of past diversity in the Caribbean is improving, there are > 700 islands in the region, from most of which there is little information available about their past biodiversity. The high rates of endemism and unique evolutionary history observed, even on the small islands and banks, make each of them meritorious of their own study (Leidy, 1868; Powell and Henderson, 2005; Bochaton et al., 2021b). Undescribed fossils collected in 1964 from Sombrero, currently housed in the Division of Vertebrate Paleontology of the Florida Museum of Natural History, offer new insights into the diversity and biogeographic history of the Lesser Antilles.

Located near the border between the Lesser Antilles and the Greater Antilles lies the small island of Sombrero, just northwest of the Anguilla Bank, 18°35’20”N, 63°25’33”W (Fig. 1) (Daltry, 1999; Cornée et al., 2023). The currently exposed surface on this island is only 0.38 km^2, and presently it hosts only three land vertebrates—*Pholidoscelis corvinus* (Cope, 1861); *Anolis gingivinus* Cope, 1864; and *Sphaerodactylus* sp. indet. (Lazell, 1964; Schwartz and Thomas, 1975; Daltry, 1999; Wright, 2011; Powell and Henderson, 2012). Even though it is relatively small, for many species of seabirds—*Sula leucogaster* (Boddaert, 1783), *Anous stolidus* (Linnaeus, 1758), *Onychoprion anaethetus* (Scopoli, 1786), *Onychoprion fuscatus*

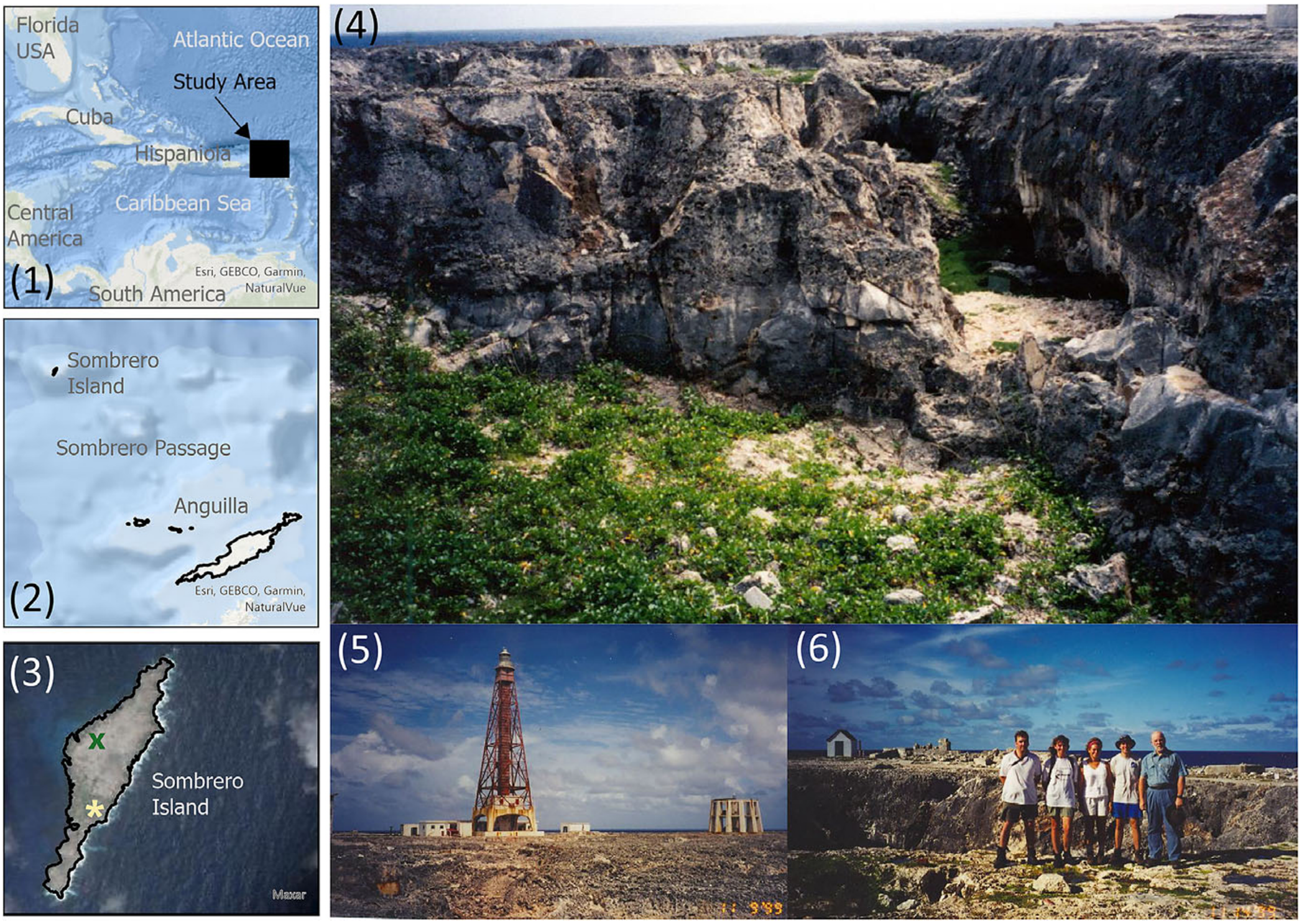

Figure 1. Maps and photographs of Sombrero with insert illustrating Sombrero's location in relation to surrounding islands: (**1**) the Caribbean region, with the study area indicated; (**2**) the northern Lesser Antilles; (**3**) satellite image of Sombrero island showing locations of the lighthouse (*) and the old mines (x); (**4**) remnants of a guano quarry; (**5**) lighthouse and supporting infrastructure; (**6**) Michael Ivie and his research team standing near a quarry. Photo credit to Justin Runyon.

(Linnaeus, 1766)—it is considered one of the most important islands for breeding in the eastern Caribbean (Pierce, 1998). There is no evidence of Amerindians occupying Sombrero and it was not populated permanently until the middle of the 19th century (Lawrence, 1867). Economically valuable reserves of guano were identified in the mid-1800s, having been long deposited by seabird populations. Dynamite was used to extract the guano, scouring the surface, and creating a flat, no-longer sombrero-like surface that is barren and heavily pitted. The guano reserves were depleted by 1890 and until 2001, the only human occupants on the island were lighthouse keepers (Fig. 1) (Lazell, 1964; Daltry, 1999; Powell and Henderson, 2012). Now automated, the lighthouse is unmanned and the island uninhabited since 2001 (Anguilla Archaeological and Historical Society, 2017).

A geologically young island, Sombrero has only had terrestrial exposure since the Pleistocene, and currently has only one known reported extinction, the tortoise *Chelonoidis sombrerensis* (Leidy, 1868) (Auffenberg, 1967; Ogden et al., 1985; Kemp, 2023). Here, we report on the microfossils collected by Walter Auffenberg and J.C. Dickinson from fissure fills along the northern part of Sombrero, which were unstudied until now and currently represent the best fossil collection from the island. These fossils document the presence of multiple groups of reptiles and an amphibian that are absent in the modern fauna of Sombrero.

Materials and methods

The fossils described here come from a bag of sediment with matrix and fossils collected by Walter Auffenberg and J.C. Dickinson in 1964 from a breccia in boulder near the old dynamite tower, northeast of the lighthouse on Sombrero (Auffenberg, 1964). In his fieldnotes, Auffenberg (1964) indicated that the breccia contained remains of birds, tortoises, and lizards. Therefore, it is very likely that the microvertebrates described here come from a single locality. Specimens of *Chelonoidis sombrerensis* (a humerus and shell elements) recovered during this expedition and described in detail by Auffenberg (1967), come from a consolidated breccia-filled fissure near the windward cliff, northwest of Point Elliott, but no other vertebrate taxa were found there (Auffenberg, 1964). The tortoise specimens were considered Pleistocene in age by Auffenberg (1967) but no detail for the age determination was provided. The specimens collected by Auffenberg and Dickinson are well mineralized and often covered by a carbonated layer mixed with red clay, similar to that observed on Quaternary fossils elsewhere in the Caribbean (unpublished field data, L.W. Viñola-López, 2022). Some specimens of *Chelonoidis sombrerensis* described by Auffenberg (1967) were completely encased within hard, consolidated sediment composed of a clay matrix (Auffenberg, 1964).

Specimens of reference. For comparison and taxonomic placement, we used skeletons from extant taxa housed at the Division of Zooarchaeology of the Florida Museum of Natural History (*Haemulon* sp. indet., UF-Z-4491), the Division of Herpetology of the Florida Museum of Natural History—*Eleutherodactylus leoncei* Shreve and Williams, 1963, UF-Herp-99358; *Ctenosaura similis* (Gray, 1831), UF-Herp-48750; *Cyclura carinata* Harlan, 1825, UF-Herp-32675; *Cyclura cornuta* (Bonnaterre, 1789), UF-Herp-51408; *Iguana delicatissima* Laurenti, 1768, UF-Herp-15778; *Iguana iguana* (Linnaeus, 1758), UF-Herp-49243, 149744; *Anolis richardii* Duméril and Bibron, 1837, UF-Herp-144546; *Leiocephalus carinatus* Gray, 1827, UF-Herp-175478; *Sphaerodactylus argus* Gosse, 1850, UF-Herp-11955; *Pholidoscelis taeniurus* Cope, 1862, UF-Herp-99572; *Ameiva ameiva* (Linnaeus, 1758), UF-Herp-144537—and the Division of Ornithology of the Florida Museum of Natural History—*Geranoaetus melanoleucus* (Viellot, 1819), UF-O-38062; and *Buteo jamaicensis* (Gmelin, 1788), UF-O-41079. Characters used for preliminary taxonomic assignment were taken from Berkovitz and Shellis (2016) and Bochaton et al. (2015).

Photography. Images of the microfossils were captured using a Hayear 34MP digital microscope camera with uniform top-lighting provided by a lens-mounted LED (light emitting diode) ring light. Depth of field was increased by taking a series of images at different focal distances and blending them together (image stacking) using Helicon Focus software v. 8.2.18 (https://www.heliconsoft.com/heliconsoft-products/helicon-focus/). Digital noise was smoothed and features sharpened with Topaz Photo AI software v. 1.5.0. (https://www.techspot.com/downloads/7551-topaz-photo-ai.html).

Geographic considerations. For much of the late 20th century, the Herpetofaunal Stability Hypothesis was utilized by many Quaternary herpetological studies for assigning taxonomic placement to fossils. As demonstrated by a series of studies, North American paleoherpetofaunal communities appeared to change little over the last million years when compared to modern faunas (Brewer, 1985; Holman, 1989, 1995). As such, with minimal morphological comparison, authors assigned fossils to modern taxa simply based on shared geographic ranges between the fossil locality and modern species ranges (Gibbons et al., 2000; Lannoo, 2005). More recently, studies on comparative herpetofaunal anatomy and fossil biogeography have provided evidence against the Herpetofaunal Stability Hypothesis, casting doubt on the ability to assign fossils to modern contiguous taxa (Norell, 1989; Kennedy and Bhullar, 2008; Bell et al., 2010). Although more work is required to support or refute this hypothesis, because this island is geographically and temporally restricted, we have chosen to utilize the assumptions on which the Herpetofaunal Stability Hypothesis is based in instances where the fossils potentially match taxa known from the area today. Such assumptions will only be used for species assignments and will be clearly indicated in the Remarks sections.

Sombrero island size reconstruction throughout time. The exposed extent of Sombrero and Anguilla islands during the late Pleistocene into the early Holocene was assessed using bathymetry contours surrounding Sombrero and Aguilla. Bathymetry was derived from the General Bathymetric Chart of the Oceans (GEBCO) 2024 Grid (https://www.gebco.net/data_and_products/gridded_bathymetry_data/, accessed 7 September 2024). A geographically-referenced TIF image file of bathymetry values surrounding Sombrero and Anguilla was downloaded from GEBCO (https://www.gebco.net/data-products-gridded-bathymetry-data/gebco2024-grid). The TIF data cell values were based on a 450 m × 450 m grid. The spatially-enabled TIF was ingested into ESRI's ArcGIS Pro v. 3.5 (Environmental Systems Research Institute, https://www.esri.com/en-us/arcgis/products/arcgis-pro/overview). Next, the spatial image was projected from WGS84 geographic coordinates to UTM Complex Zone 20 North, units in meters. ArcGIS's spatial analysis tool Contour was used to convert the bathymetry from cell values to bathymetry polygons at 30 m intervals (-30 m, -60 m, -90 m, and -120 m), and from there to reconstruct island size during the Last Glacial Maximum, the terminal Pleistocene, early Holocene, and middle Holocene (Peltier and Fairbanks, 2006; Peros et al., 2023). The perimeter for each bathymetric depth and the area encompassed between these contours was calculated. Total combined area at each depth was also calculated. The present shoreline of Sombrero was digitized using ESRI's ArcGIS World Imagery Basemap (https://services.arcgisonline.com/ArcGIS/rest/services/World_Imagery/MapServer) and its area calculated. Present-day Anguilla's spatial outline was obtained from the Humanitarian Data Exchange (https://data.humdata.org/dataset/cod-ab-aia, accessed 7 September 2024).

Repositories and institutional abbreviations. All of the specimens of living and fossil vertebrates examined during this study are housed at the Florida Museum of Natural History (FLMNH), Gainesville (UF). Other institutional abbreviations used throughout the text are: Academy of Natural Sciences of Drexel University, Philadelphia (ANSP), Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts (MCZ), and The Natural History Museum, London (BMNH).

Systematic paleontology

Clade **Osteichthyes** Huxley, 1880
Class **Actinopteri** Cope, 1871
Family **Haemulidae** Gill, 1885
Haemulidae gen. indet. sp. indet.
Figure 2.1

Materials. Four vertebrae (UF 545892–545895).

Remarks. Each vertebra contains an amphicoelous centrum and attachments for hemal and neural arches, with the presence of a notochordal pit allowing for assignment to Osteichthyes. UF 545894 bears paired lateral processes that allow for placement to the anteriormost vertebrae, and are morphologically similar to either the family Centrarchidae or Haemulidae. However, considering the marine and Caribbean origin for these vertebrae, the assignment to Haemulidae is more likely.

Class **Amphibia** Gray, 1825
Order **Anura** Fischer von Waldheim, 1813
Anura indet.
Figure 2.2

Materials. A partial tibiofibula (UF 545891).

Remarks. Partially preserved, the single specimen includes the diaphysis with the tibiofibular foramen well preserved on both sides. The epiphyses are not preserved, and the sulcus intermedius is only preserved on one end of the fossil that, considering the position of the tibiofibular foramen, is probably the proximal epiphysis. By comparison with other anuran taxa, the foramen is medially located on one side and proximal on the other. The sulcus intermedius that is preserved is deeper and wider on the ventral than on the dorsal side. Laterally, there are subtle crests that run along the diaphysis. The small fragment of tibiofibula is not assigned to any specific anuran taxa due to lack of diagnostic features in the preserved portion of the fossil. It is similar to *Eleutherodactylus* Duméril and Bibron, 1841 in size and *Eleutherodactylus* is the only native taxon of this size in the region. However, the fossil is robust and has the lateral crests in the diaphyses that are seen in toads of the genus *Peltophryne* Fitzinger, 1843. Because of the uncertainty, we refer this specimen to Anura indet.

Class **Reptilia** Laurenti, 1768
Order **Squamata** Oppel, 1811
Family **Anolidae** Cocteau, 1836
Genus ***Anolis*** Daudin, 1802

Type species. Anolis punctatus Daudin, 1802.

***Anolis* sp. indet**.
Figure 2.3–2.5

Lectotype. Adult male, BMNH 1946.8.29.15, designated by Lazell (1980).

Materials. A partial frontal (UF 545876), a partial right dentary (UF 545877), a partial left dentary (UF 545878), and a left maxilla (UF 545899).

Remarks. This is the most commonly found taxon in the sample, and the dentaries and maxilla can be assigned to *Anolis* based on the presence of medial and posterior tricuspid teeth with very reduced lateral cusps, whereas the anterior teeth are monocuspid. Living anoles collected on Sombrero have been referred to *Anolis gingivinus* (Lazell, 1964; Powell and Henderson, 2012), a species described originally from the Anguilla Bank. However, Daltry (1999) noticed some morphological differences between the populations from Sombrero and Anguilla that suggest that they could represent different species. In the first report of this anole in Sombrero, Lazell (1964) also noticed marked ecological differences between the Sombrero and Anguilla populations but considered the possibility that *Anolis gingivinus* might have recently been introduced in Sombrero. These fossils suggest that *Anolis* was present on the island likely before the arrival of humans, but direct comparison with skeletal remains of the extant populations on Sombrero is necessary to determine if they are conspecific.

Family **Iguanidae** Oppel, 1811
Iguanidae gen. indet. sp. indet.
Figure 2.6–2.8

Materials. An edentulous dentary (UF 545869), a partial vertebra (UF 545870), two maxillae fragments (UF 545871, 545872), and three isolated teeth (UF 545873–545875).

Remarks. The largest lizards found in the Caribbean all belong to the group Iguanidae (sensu Conrad, 2008). The distal teeth of *Iguana* Laurenti, 1768 are pleurodont and flared distally, containing three to eight cusps. There is marked heterodonty within dentigerous elements of Iguania, with mesial teeth being more unicuspid and recurved. Two genera of Iguanidae can be found in the Caribbean; *Iguana* Laurenti, 1768 with a natural distribution across the Lesser Antilles, *Cyclura* Harlan, 1825 occurring in the Greater Antilles and Bahamas (Censky et al., 1998). The teeth on UF 545871 and UF 545872 are large, spatulate-shaped, and have multiple cusps (more than three) like the teeth of *Cyclura* and *Iguana.* However, these specimens are highly eroded, the cusps poorly visible, and without additional material, it is not possible to assign them to genus. However, the three additional isolated teeth (UF 545873–545875) are large and tricuspid, outside of the dental variation found within *Cyclura* and *Iguana* species. UF 545874 has a marked curvature, suggesting a more mesial placement, whereas UF 545873 is straight and likely distal. The genus *Ctenosaura* Wiegmann, 1828 includes tricuspid teeth resembling

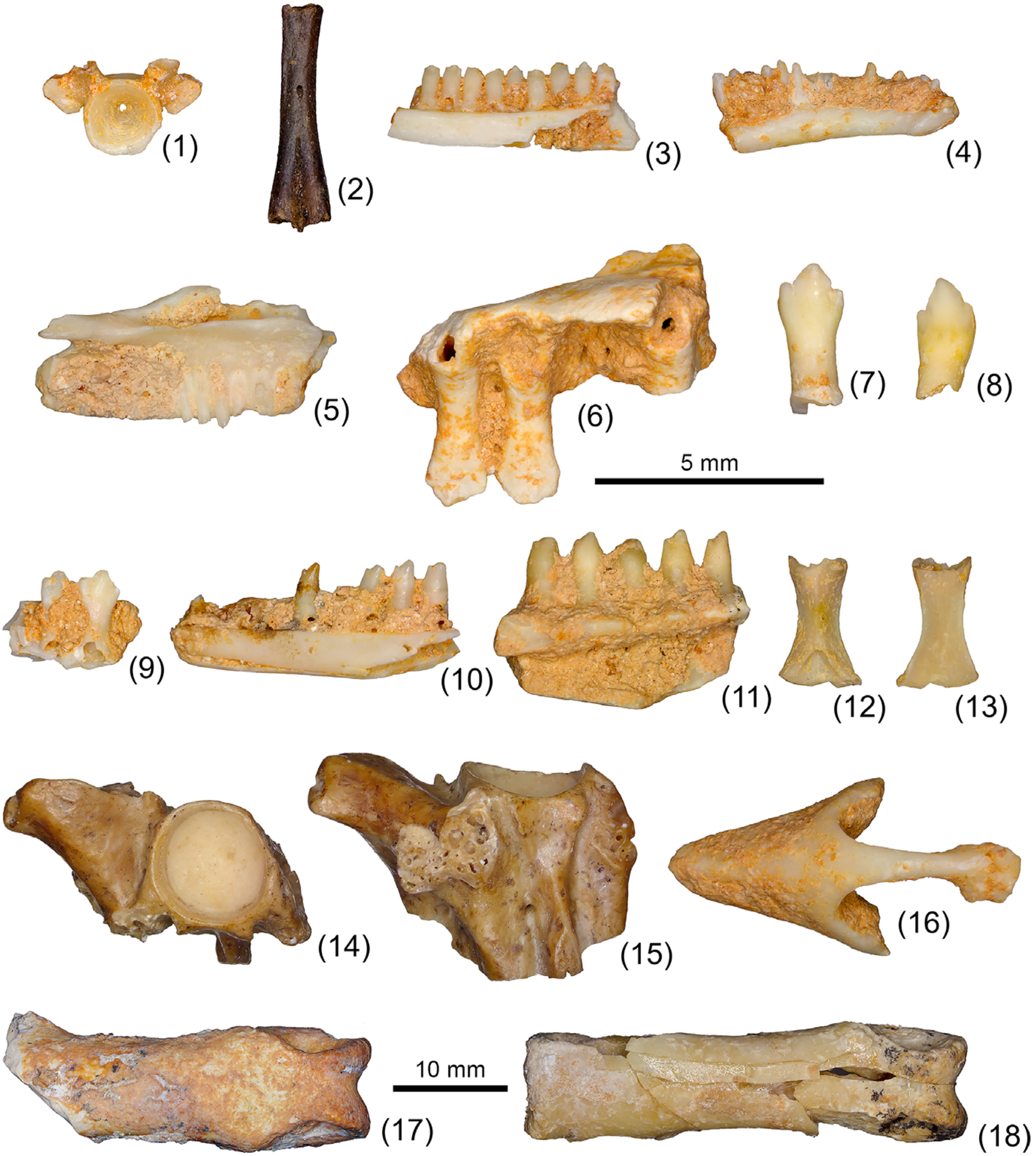

Figure 2. Fossils from the Pleistocene deposits of Sombrero: (**1**) UF 545894, Haemulidae gen. indet. sp. indet., vertebra in anterior view; (**2**) UF 545891, Anura indet., diaphysis of tibiofibula in medial view; (**3**–**5**) *Anolis* sp. indet.: (**3**) UF 545877, partial right dentary in lingual view; (**4**) UF 545878, partial left dentary in lingual view; (**5**) UF 545899, left maxilla in lingual view; (**6**–**8**) Iguanidae gen. indet. sp. indet.: (**6**) UF 545871, partial maxilla; (**7**) UF 545873, tooth; (**8**) UF 545874, teeth in lingual view; (**9**) UF 545880, *Leiocephalus* sp. indet., dentary fragment in lingual view; (**10**) UF 545885, *Pholidoscelis corvinus* right partial dentary in lingual view; (**11**) UF 545886, *Pholidoscelis corvinus* (Cope, 1861), partial right dentary in lingual view; (**12, 13**) UF 545882, *Sphaerodactylus* sp. indet., frontal, in ventral (**12**) and dorsal (**13**) views; (**14, 15**) UF 545889, Colubridae gen. indet. sp. indet., partial presacral vertebra, in anterior (**14**) and ventral (**15**) views; (**16**) UF 545890, *Melanospiza bicolor* (Linnaeus, 1766), rostrum in dorsal view; (**17, 18**) Accipitridae gen. indet. sp indet., phalanges in dorsal view: (**17**) UF 545897; (**18**) UF 545898,. Scale bars = 5 mm (**1**–**16**); 10 mm (**17, 18**).

morphologically the specimens described here, however, that taxon is only found today on the Caribbean islands nearest the Colombian coast, with no record in the Caribbean Archipelago (Malone et al., 2017). Although the specimens could belong to a giant form of *Leiocephalus* Gray, 1827, they partially preserve a cusplet between the central and lateral cusps, which is present in *Ctenosaura* but not in *Leiocephalus*. Furthermore, the more mesial curved tooth is tricuspid like those of *Ctenosaura* whereas the anterior curved teeth of *Leiocephalus* are monocuspid. Because of the size of Sombrero, it seems unlikely that two large-bodied iguanids would co-occur and, given the morphological ambiguity seen within these iguanid materials, our ability to assign them to any lower-order classification is limited (Berkovitz and Shellis, 2016).

Family **Leiocephalidae** Frost and Etheridge, 1989
Genus ***Leiocephalus*** Gray, 1827

Type species. Leiocephalus carinatus Gray, 1827.

***Leiocephalus* sp. indet**.
Figure 2.9

Materials. Three dentary fragments (UF 545879—545881).

Remarks. The teeth of *Leiocephalus* are tricuspid and can be separated from those of *Anolis* and other tricuspid lizards in the region because they are flared distally. In *Leiocephalus*, the central cusp is clearly delimited from the lateral cusps, which are large and well separated from the midline, whereas in *Anolis*, the secondary ones are considerably smaller and closer to the central cusp. *Leiocephalus* can be separated from other iguanids in the region because its teeth are significantly smaller than those of *Cyclura* and *Iguana* and are spatulate-shaped, usually with more than three cusps. *Leiocephalus* has not been reported before from Sombrero Island, but historical specimens and fossil remains of at least three different species are known from elsewhere in the Lesser Antilles, including the nearby Anguilla Bank (Etheridge, 1964; Pregill et al., 1988; Kemp and Hadly, 2016, Bochaton et al., 2021a) and two other extinct species of *Leiocephalus* also were described from Puerto Rico. However, given the fragmentary nature of the specimens described here, it is not possible to assess specific affinity.

Family **Teiidae** Gray, 1827
Genus ***Pholidoscelis*** Fitzinger, 1843

Type species. Ameiva major Duméril and Bibron, 1839.

Pholidoscelis corvinus (Cope, 1861)
Figure 2.10, 2.11

Syntypes. The type series of this species includes the specimens ANSP 9115-30 and MCZ 10525, 5531, 3613, and 52215-16.

Materials. A frontal (UF 545883), three dentary fragments (UF 545884—545886), and two partial maxillae (UF 545887, 545888).

Remarks. The specimens are assigned to the genus *Pholidoscelis* because the dentary has an open Meckelian canal, bicuspid middle teeth, and monocuspid distal teeth with rounded apices. Also, from ventral view, the dentary curves laterally. The maxilla fragments lack ornamentation and also possess comparably large, rounded posterior teeth. These diagnostic characters are shared with other members of the family Teiidae (Gauthier et al., 2012), but taking into account that the only known genus of this family present in the region is *Pholidoscelis*, we refer the fossils to this genus. Similarly, the fossils are referred to *Pholidoscelis corvinus* because it is the only species present there today and is endemic to Sombrero, where it seems to be relatively abundant (Tucker et al., 2017; Richardson, 2023). Phylogenetic analysis indicates that *Pholidoscelis corvinus* is nested in the *Pholidoscelis plei* group that includes other species from the Lesser Antilles and is more closely related to *Pholidoscelis corax* (Censky and Paulson, 1992) from Little Scrub Island on the Anguilla Bank (Tucker et al., 2017).

Family **Sphaerodactylidae** Underwood, 1954
Genus ***Sphaerodactylus*** Wagler, 1830

Type species. Lacerta sputator Sparrman, 1784.

***Sphaerodactylus* sp. indet**.
Figure 2.12, 2.13

Materials. A frontal (UF 545882).

Remarks. The isolated frontal is assigned to the genus *Sphaerodactylus* based on its small size and closed olfactory canal on the ventral side. Only one species of *Sphaerodactylus* has been reported from Sombrero, which was considered conspecific with *Sphaerodactylus sputator* (Sparrman, 1784) from the Anguilla Bank (Powell and Bauer, 2012). Although most authors recognized a close relationship of the Sombrero gecko with *Sphaerodactylus sputator*, they also considered it a distinct undescribed species (Lazell, 1964; Daltry, 1999; Hodge et al., 2011; Powell and Henderson, 2012). Surveys have found this *Sphaerodactylus* in several areas of Sombrero, usually under stones (Daltry, 1999). Daltry (1999) also reported that one of the *Anolis gingivinus* collected by them regurgitated the torso of a *Sphaerodactylus.*

Family **Colubridae** Oppel, 1811
Colubridae gen. indet. sp. indet.
Figure 2.14, 2.15

Materials. A cervical vertebra fragment (UF 545889).

Remarks. A partial anterior trunk (cervical) vertebra is preserved ventrally and anteriorly. It includes the centrum and anterior part of the right prezygapophysis, which are dorsally worn but do show evidence of the presence of an auxiliary process. The centrum cotyle is rounded and well preserved. Ventrally, the hemal keel is well developed and of increasing depth posteriorly, developing into a hypapophysis. Because the posterior end of the vertebra is broken, it is not possible to determine the complete length of the hypapophysis. There are two ventral foramina, one on each side of the hypapophysis, along the well-developed subcentral ridges. Laterally, the parapophyses and diapophyses are preserved, with the parapophyses being wider and more anteroventrally oriented than the diapophyses. This cervical vertebra is assigned to Colubridae based on the presence of a combination of characters including the clear presence of a broken auxiliary process of the prezygapophysis (weakly developed and of different appearance than in viperids), the overall elongated shape of the centrum, which is short and stout as seen in other families, and a well-developed hypapophysis (Auffenberg, 1963; Holman, 2000).

Class **Aves** Linnaeus, 1758
Order **Passeriformes** Linnaeus, 1758
Family **Thraupidae** Cabanis, 1847
Genus ***Melanospiza*** Ridgway, 1897

Type species. Loxigilla richardsoni Cory, 1886.

Melanospiza bicolor (Linnaeus, 1766)
Figure 2.16

Type Specimens. Described by Linnaeus (1766) as *Fringilla bicolor* based on Catesby's (1729–1732, pl. 37) illustration and descriptions but no physical type specimen exists.

Materials. A rostrum (UF 545890).

Remarks. The specimen is referred to *Melanospiza* because of its small size and because it has a wide rostrum with straight sides. The specimen also lacks a bulge anterior to the contact between the nasal and maxilla, which is present on *Tiaris olivaceus* Swainson, 1827. Of the two species within *Melanospiza—Melanospiza bicolor*, *Melanospiza richardsoni* (Cory, 1886)—only the former is widely distributed across the Caribbean region and has been reported from fossil deposits in Hispaniola and Anguilla, whereas *Melanospiza richardsoni* has only been reported from Saint Lucia (Bernstein, 1965; Pregill et al., 1994; Burns et al., 2014).

Order **Accipitriformes** Vieillot, 1816
Family **Accipitridae** Vieillot, 1816
Accipitridae gen. indet. sp indet.
Figure 2.17, 2.18

Materials. Two pedal phalanges; a digit I, phalanx I (UF 545897), and a digit III, phalanx I (UF 545898).

Remarks. The specimens belong to an accipitri with robust phalanges resembling those of *Geranoaetus melanoleucus.* The distal width of digit I (11.2 mm) and total length of digit III (37.37 mm) are ~10% and 24.9% larger than previously reported values for *G. melanoleucus* (see Steadman et al., 2019) and significantly larger than those of *Buteo jamaicensis*, the largest extant accipitrid in the region. Although digit I might still be within the size range of *G. melanoleucus*, these fossil phalanges likely represent different accipitrids. The phalanges each have a pit for the flexor on the distal region like in other accipitrids. Based on the differences in proportion between the two phalanges, they belonged to different individuals and likely to different taxa. Several extinct large accipitrids have been described from upper Quaternary deposits from the Greater Antilles and the Bahamas but have not been recorded yet from the Lesser Antilles (Suárez and Olson, 2021; Suárez, 2022).

Discussion

Fossil fauna from Sombrero and its affinities. As a small island deprived of vegetative cover, Sombrero today has a low diversity of vertebrates composed of three lizards (*Pholidoscelis corvinus*, *Anolis gingivinus*, *Sphaerodactylus* sp. indet.) found permanently on the island and 36 species of birds (Lawrence, 1867; Lazell, 1964; Schwartz and Thomas, 1975; Daltry, 1999; Powell and Henderson, 2012). Most of the birds are sporadic visitors from the larger nearby islands but at least six seabird species nest in large numbers on Sombrero—*Sula dactylatra* Lesson, 1831, *Sula leucogaster*, *Sterna dougallii* Montagu, 1813, *Thalasseus maximus* (Boddaert, 1783), *Anous stolidus*, *Phaethon aethereus* Linnaeus, 1758 (Townsend, 1998). Sombrero has been considered the most important nesting ground of seabirds in the eastern Caribbean (Pierce, 1998). Based on the large volumes of guano extracted from the mines between 1856 and 1890 (3,000 tons every year by 1876; Christian, 1998), the island was likely an important nesting site for seabirds for thousands of years. Therefore, it is surprising that in our sample, there were no fossils of any of the bird species known commonly to nest on Sombrero. Nonetheless, Julien (1878) reported that among the samples collected from Sombrero, Jeffries Wyman identified remains of seabirds from the more superficial deposits. At the same time, the vertebral fragments of small fishes in our sample probably were part of the food brought to the nesting grounds by the birds. In our small collection of fossils, there are at least 11 vertebrate species, including an indeterminate bony fish, five lizard taxa, a snake, a tortoise, an anuran, and two birds.

The first description of fossils from Sombrero was provided by Leidy (1868) who named *Chelonoidis* (*Emys* Duméril, 1805) *sombrerensis* based on the posterior lobe of a plastron, today deposited at ANSP. That publication was followed by that of Julien (1878) who reported on a collection of some seabird, tortoise, and iguanid remains collected from the northern excavation on the island but he was seemingly unaware of Leidy's work. Auffenberg (1967) was the last one to report on newly collected fossils from Sombrero but focused only on the tortoises. *Chelonoidis* Fitzinger, 1835 is more commonly found in late Pleistocene and Holocene deposits across the Greater Antilles and the Bahamas but are scarce in the Lesser Antilles (Ray, 1964; Lazell, 1993; Kehlmaier et al., 2021; Viñola-López and Almonte, 2022). It is unclear whether *Chelonoidis sombrerensis* is more closely related to tortoises in the radiations from the western or the eastern Caribbean, but until more fossils from the Lesser Antilles are collected, this will be difficult to evaluate. Sombrero lies near the contact between the Greater and the Lesser Antilles, and both island groups could have been contributing sources for the species there. Similarly, *Leiocephalus* had and has a wide distribution across the Antilles but the poor preservation of the specimens from Sombrero do not allow us to evaluate their relationship with other Caribbean taxa. This is also the case of the fossil colubrid snake and anuran reported here. The three extant genera of lizards that are today found on the island, *Anolis*, *Pholidoscelis*, and *Sphaerodactylus* are also found in the fossil assemblage. If these fossils are conspecific with the species on Sombrero today, it indicates that they were not introduced by humans, as Lazell (1964) tentatively suggested for the anole and gecko. These three species have a closer relationship with other lizards from the nearby Anguilla Bank (Lazell, 1964; Tucker et al., 2017). Although we lack direct radiometric dates of the fossils, the preservation and degree of mineralization of these specimens suggest that they are likely subfossil and precede the very recent human settlement in the mid-19th century.

Some of the most puzzling fossils from the island are those of at least one large iguanid of unclear relationships. To the west of Sombrero, *Cyclura* is distributed across the Greater Antilles whereas native populations of *Iguana* are located in numerous islands in the Lesser Antilles (Breuil et al., 2020; Reynolds et al., 2022). Some of the isolated tricuspid fossil teeth differ from the multicuspid distally-flared teeth of *Cyclura* and *Iguana* but resemble those of *Ctenosaura.* However, the last genus is found in Mexico, Central America, and a few islands on the Caribbean coast off of the mainland (Malone et al., 2017). Fossils of large accipitrids like those reported here are reported from late Quaternary deposits in the Greater Antilles and Bahamas but have not been found so far in the Lesser Antilles (Steadman et al., 2019; Suárez, 2022). The fossils from the Greater Antilles document several radiations of large diurnal raptors that specialized on feeding on native vertebrates. Although native mammals are unknown from Sombrero, the large amount of guano extracted indicates that the island was likely an important nesting ground for bird for long periods of time. Therefore, it is possible that the large accipitrid preyed on seabird colonies as well as some of the larger reptiles on the island like *Chelonoidis sombrerensis* and the iguana. The considerable size reduction of

Sombrero associated with changes in sea level, reduction of bird nesting size, and extinction of *Chelonoidis sombrerensis* and the iguana could have been associated with the loss of the accipitrid.

Faunal colonization and extinction on a small island. The fossils from Sombrero offer good insight into how faunal assemblages come together on small islands and evolve over time. Because Sombrero is on its own carbonate platform separated from other island banks, its fauna must have arrived by overwater dispersion either from the Greater or the Lesser Antilles. Furthermore, the limestone on which the island is built is Pleistocene in age, constraining the subaerial exposure of the Sombrero to < 2.5 Mya (Ogden et al., 1985). The island today has an area of 0.38 km^2; during the Last Glacial Maximum (20 ka) in the late Pleistocene with a sea level 120 m below current one, Sombrero had an exposed area of 36 km^2 (Fig. 3). The leading edge of this paleoisland was still separated by 31–34 km from the edge of the fully exposed Anguilla Bank. In the Sombrero Passage, which separates Anguilla and Sombrero, there were another two islands exposed that are currently submerged. In the latest Pleistocene (12 ka), sea level increases caused an area reduction to ~29 km^2. With rapid sea level increase in the early Holocene (10 ka), its area further decreased to 16 km^2 and by the middle Holocene (6 ka), when sea level reached values similar to current ones, Sombrero was likely close to its current size. In < 14 ka, Sombrero island lost nearly 99% of its area, which more than likely had a profound impact on its biota.

Eight of the fossils and living vertebrates found (*Chelonoidis sombrerensis*, *Anolis gingivinus*, *Pholidoscelis corvinus*, *Sphaerodactylus* sp. indet., *Leiocephalus* sp. indet, large iguanid, colubrid snake, and anuran) are completely terrestrial and do not disperse actively through marine barriers, but reached Sombrero in the last 2.5 Ma. If these colonization events were independent from each other, it would result in an average rate of one successful passive dispersal every 312,500 yr. However, given that the exact moment in the Pleistocene when the island became aerially exposed is unknown and that other groups of vertebrates from the nearby islands could also have reached Sombrero (e.g., boids, Oryzomyini rodents), it is possible that the actual dispersal rate was higher.

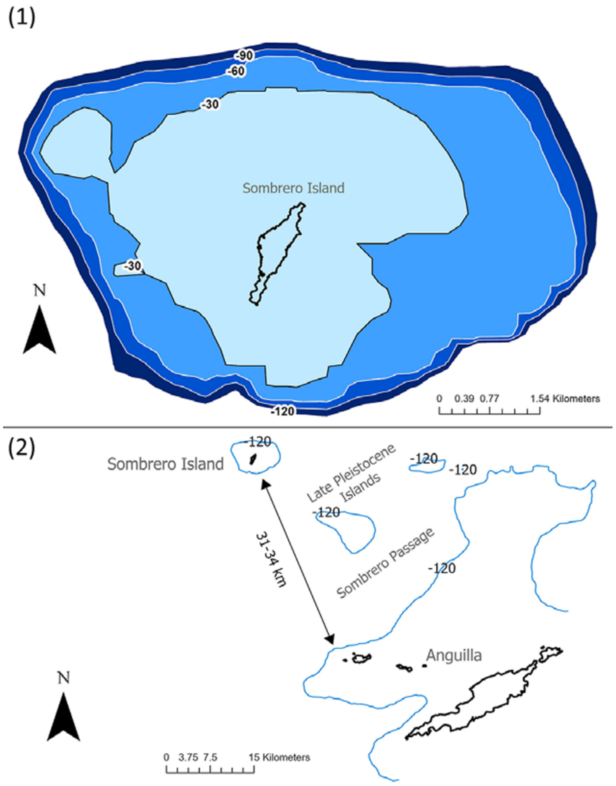

Figure 3. (**1**) Reconstruction of Sombrero size at 120 m, 90 m, 60 m, and 30 m below current sea level, based on bathymetric data. (**2**) Coastal outline of Sombrero, the lost Sombrero Passage islands, and northern Anguilla Bank during the Last Glacial Maximum in the late Pleistocene.

In the northern Lesser Antilles, there are no large rivers that could produce large vegetation mats and rafts as in the Greater Antilles (Silva-Taboada et al., 2007), suggesting that 'island-hopping' must have been driven primarily by large storms and oceanic surface currents moving northwest (Hedges, 1996; 2006).The groups found in the fossil record of the island are examples of good dispersers, meaning that they achieved wide distributions across the Caribbean and are found on islands and island banks that were not connected in the recent geological past. Some of them possess physiological traits and behaviors (e.g., direct development, survival for long periods without food or freshwater) that have been tied with their ability to overcome marine barriers and there is molecular evidence that supports numerous instances of dispersal between islands that were never connected (e.g., de Queiroz, 2005; Gerlach et al., 2006; Heinicke et al., 2007; Tucker et al., 2017). This dispersal capacity and their ability to survive even on small relict islands is consistent with molecular and paleontological studies suggesting that ancestors of *Leiocephalus*, *Anolis*, and *Sphaerodactylus* might have dispersed into the Caribbean region before or soon after the islands became permanently exposed in the late Eocene (Heinicke et al., 2007; Kumar et al., 2017; Ali and Hedges, 2021). After the formation of the first Caribbean islands in the late Cretaceous and until the region became more stable in the Eocene, islands (and their biota) had at best an ephemeral life of several million years (Iturralde-Vinent, 2006). Therefore, island hopping is one of the mechanisms used to explain the presence of several of those groups (e.g., *Leiocephalus*, *Anolis*) with divergent ages that date back to the Cretaceous and Paleogene. At the same time, the existence of a short-lived landspan or closely spaced group of islands involving the Greater Antilles and the Aves Ridge in the Eocene-Oligocene transition, known as the Greater Antilles Aves Ridge Land Bridge (GAARlandia), has been proposed to explain the origin of numerous extant and extinct South American lineages found in the Caribbean. The degree of exposure and contribution of the Aves Ridge to GAARlandia is a topic of debate (e.g., Iturralde-Vinent and MacPhee, 1999, 2023; Iturralde-Vinent, 2006; Ali, 2012; Philippon et al., 2020; Ali and Hedges, 2021; Garrocq et al., 2021), but the presence of a continuous land connection seems to have been highly unlikely (Ali and Hedges, 2021). Furthermore, Ali and Hedges (2021) argued that the islands exposed on the Aves Ridge would have been too shallow and small to sustain a high diversity of taxa and allow them to disperse. However, the fossils from Sombrero show that small islands can be colonized rapidly by reptiles and amphibians from nearby islands after becoming subaerially exposed. This is also consistent with paleontological studies on other small islands like Marie-Galante that emerged in the middle Pleistocene (Cornée et al., 2023) and also had a high diversity of terrestrial vertebrates (Bochaton et al., 2015). Although the geology of the Aves Ridge is still poorly understood, recent work in the northern Lesser Antilles demonstrated the existence of a large land mass (Greater Antilles–northern Lesser Antilles, GrANoLA) exposed in the late Eocene–early Oligocene consistent with GAARlandia (Philippon et al., 2020). Paleomagnetic studies further indicate that the northern Lesser Antilles and the Puerto Rico-Virgin Islands Bank could have been significantly closer to South America and played a significant role in faunal dispersion from South America in the late Eocene (Montheil et al., 2023).

Fossils from Sombrero not only provide some insight into the colonization of small islands in the Caribbean and elsewhere but also allow us to assess extinction events in these settings. The insular Caribbean is recognized worldwide as one of the island systems most affected by extinction in the late Pleistocene—early Holocene (Turvey et al., 2021; Rozzi et al., 2023). Nearly 90% of the native land mammals that inhabited the region are extinct today and most of the remaining species are threatened with extinction or extirpation (Silva-Taboada et al., 2007). Species loss also affected several groups of birds and reptiles across the region, and recent chronological studies showed that those community collapses occurred in multiple waves, the last one following the arrival of Europeans (Orihuela et al., 2020; Bochaton et al., 2021a, b; Viñola-Lopez et al., 2022). The introduction of invasive species further contributed to the collapse of the native fauna and reshaped the Caribbean biota as we know it today (Kemp et al., 2020; Kemp, 2023).

The understanding of these extinction events varies across regions and taxa in the Caribbean. The Greater Antilles have been more intensively sampled and studied than the Lesser Antilles although in recent years, numerous articles describing the fossil and archaeological fauna of the Lesser Antilles have come to light (e.g., Boudadi-Maligne et al., 2016; Kemp and Hadly, 2016; Bochaton et al., 2021a, b). Similarly, several comprehensive studies started addressing larger scale extinction and functional-loss patterns across the Caribbean, including some of the smallest islands like Sombrero (Cooke et al., 2017; Kemp et al., 2020; Kemp, 2023). However, even with these few studies, the fossil fauna from small islands of the Caribbean remains poorly understood due to a lack of collecting and published data. The use of the limited and biased available data from the paleontological and archaeological record can create misconceptions (Bochaton, 2022), as is the case with Sombrero. More recent articles that discuss Lesser Antillian biodiversity cite *Chelonoidis sombrerensis* as the only extinct vertebrate from the island, although Julien (1878) reported the presence of a large iguanid. Because of the lack of evidence in the significant loss of functional diversity on Sombrero compared with larger islands, Kemp (2023) argued that Sombrero and three other small islands are examples of how long-term human impact can create different biodiversity outcomes. However, based on the evidence presented here, there are at least five groups of land vertebrates (four of them reptiles) that disappeared from the island. Whether losses were related to changes of the island's exposed area through time or human influence is currently unknown without a chronology of extinction. It is worth noting that Julien (1878) did not mention any living reptiles on the island in his mid-19th century study, which suggests that at least the large iguanian and the tortoise were already absent. Furthermore, Julien (1878) reported on the significant impact that humans had on the nesting birds of the island, greatly reducing their populations, and mentioned that feral cats were also on the island at the time. The fossils described here are a good example of how the absence of data is not an indication of the absence of species loss and how small islands are also prone to significant species loss. Similarly, Bochaton et al. (2020) reported on the loss of six species of land vertebrates on another very small island located nearby on the Anguilla Bank. Given that all of the taxa described here (*Anolis*, *Pholidoscelis*, *Leiocephalus*, *Sphaerodactylus*, *Chelonoidis*, Anura, Iguanidae, Colubridae) are often found across the Caribbean (Powell and Henderson, 2012), our results could be used as a guide for paleontologists to search for and potentially document other examples of extinction/extirpation, even in the apparent absence of these species in the recorded fossil records of small islands.

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