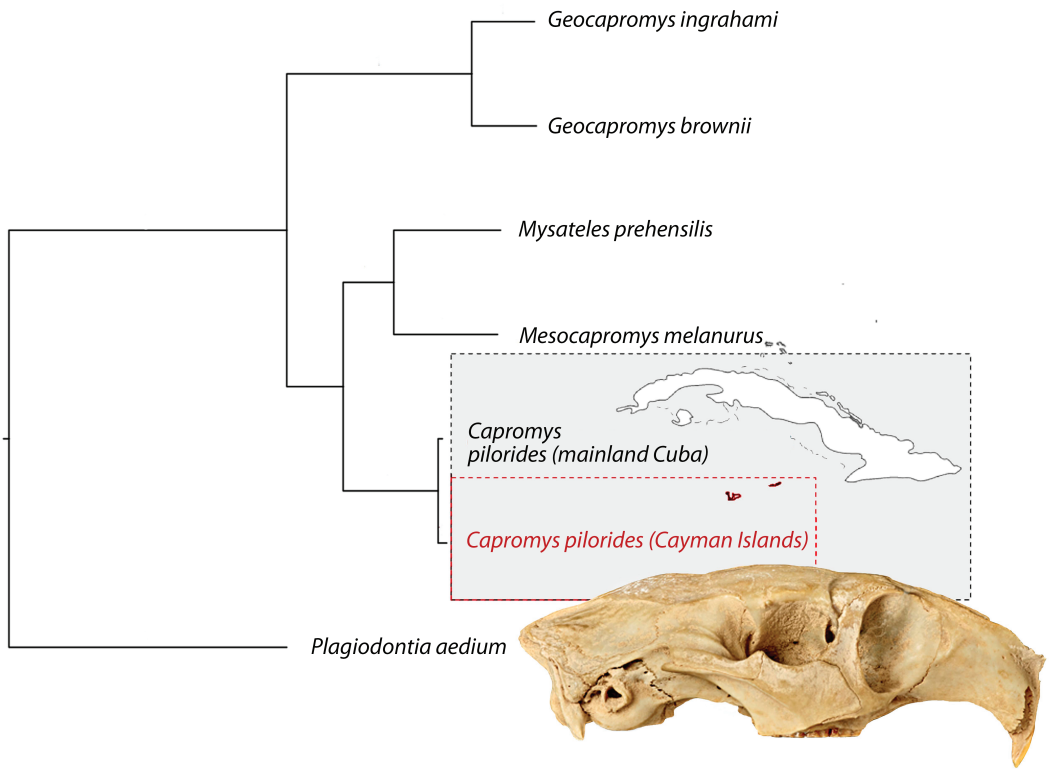
Late Quaternary Fossil Mammals from the Cayman Islands, West Indies

Gary S. Morgan, Ross D.E. MacPhee, Roseina Woods, and Samuel T. Turvey



Bulletin of the American Museum of Natural History

LATE QUATERNARY FOSSIL MAMMALS FROM THE CAYMAN ISLANDS, WEST INDIES

GARY S. MORGAN
New Mexico Museum of Natural History, Albuquerque, New Mexico

ROSS D.E. MacPHEE
Department of Mammalogy, American Museum of Natural History, New York

ROSEINA WOODS
School of Biological Sciences, Royal Holloway University of London
Department of Earth Sciences, Natural History Museum, London

SAMUEL T. TURVEY
Institute of Zoology, Zoological Society of London, London

BULLETIN OF THE AMERICAN MUSEUM OF NATURAL HISTORY
Number 428, 79 pp., 24 figures, 8 tables
Issued March 4, 2019

 ISSN 0003-0090

CONTENTS

ABSTRACT

Abundant fossils of nesophontid lipotyphlan insectivores and capromyid rodents have been collected from late Quaternary deposits on the Cayman Islands, an island group separated by a major marine barrier from other Caribbean landmasses and isolated from anthropogenic impacts until the arrival of Columbus in 1503 CE. These collections have not previously been formally described. Using morphological and ancient DNA approaches, we document three new taxa of extinct endemic terrestrial mammals from this island group: *Nesophontes hemicingulus* (Grand Cayman and Cayman Brac), *Capromys pilorides lewisi* (Grand Cayman, Little Cayman, and Cayman Brac), and *Geocapromys caymanensis* (Grand Cayman and Cayman Brac). Morphometric comparisons with other extinct and living West Indian mammals indicate that the biogeographic origins of all three new taxa are from source populations on Cuba. Ancient DNA data indicate very low sequence divergence of *Capromys pilorides lewisi* from mainland Cuban *C. pilorides* (only 0.5% across the entire mitogenome). Using probabilistic analysis of existing and new radiometric dates, we calculate an estimated extinction date of 1700 CE (95% confidence interval = 1632–1774 CE) for the Cayman Brac *Capromys* population. This result suggests that at least one endemic Cayman terrestrial mammal population survived for well over a century following first European arrival in the Cayman Islands. The West Indies lost nearly all its species-rich late Quaternary land mammal fauna during the late Holocene due to direct or indirect human impacts, and this study provides a new baseline to understand the magnitude of human-caused mammal extinctions during the recent past.

INTRODUCTION

It is often noted that oceanic-type island systems have rarely been colonized successfully by mammals other than bats. This generalization does not apply to the West Indies—the islands of the Caribbean Basin, comprising the Greater and Lesser Antilles and neighboring archipelagos—where land mammals once made up a considerable fraction of insular vertebrate faunas. Although some mammalian colonizations or vicariance events evidently occurred as early as the late Paleogene (Domning et al., 1997; Iturralde-Vinent and MacPhee, 1999; MacPhee and Iturralde-Vinent, 2005), for most of the Cenozoic the West Indian fossil record is either very poor or altogether lacking. The late Quaternary record is quite different: it is abundant, and reveals that the mammalian component of the region's terrestrial vertebrate fauna consisted of at least 130 species, comprising endemic radiations of sloths, lipotyphlan insectivores, platyrrhines, and several rodent and bat lineages (MacPhee, 2009; Dávalos and Turvey, 2012; Cooke et al., 2017a). During the Holocene, however, much of this diversity disappeared in the largest insular faunal collapse affecting mammals on record (MacPhee and Flemming, 1999; MacPhee, 2009; Turvey, 2009; Cooke et al., 2017a). Only 13 endemic nonvolant mammal species now survive in the West Indies, along with 60 bat species (Cooke et al., 2017a; Turvey et al., 2017).

Although direct and indirect human impacts are likely to be the main explanation for Caribbean mammal extinctions, the chronology, dynamics, and drivers of these uniquely severe extinctions are still incompletely understood (Morgan and Woods, 1986; MacPhee, 2009; Turvey, 2009; Cooke et al., 2017a). Taxonomic revision of species of questionable validity has led to ongoing instability in estimates of species richness in several Caribbean mammal groups (e.g., Díaz-Franco, 2001; Condis Fernández et al., 2005; Silva Taboada et al., 2007; Hansford et al., 2012). At the same time, fossils of extinct mammal populations likely to represent new species or subspecies have also been reported, but have yet to be formally described. New efforts to evaluate and describe such understudied collections of potentially distinct taxa are therefore essential (e.g., Brace et al., 2015) in order to strengthen

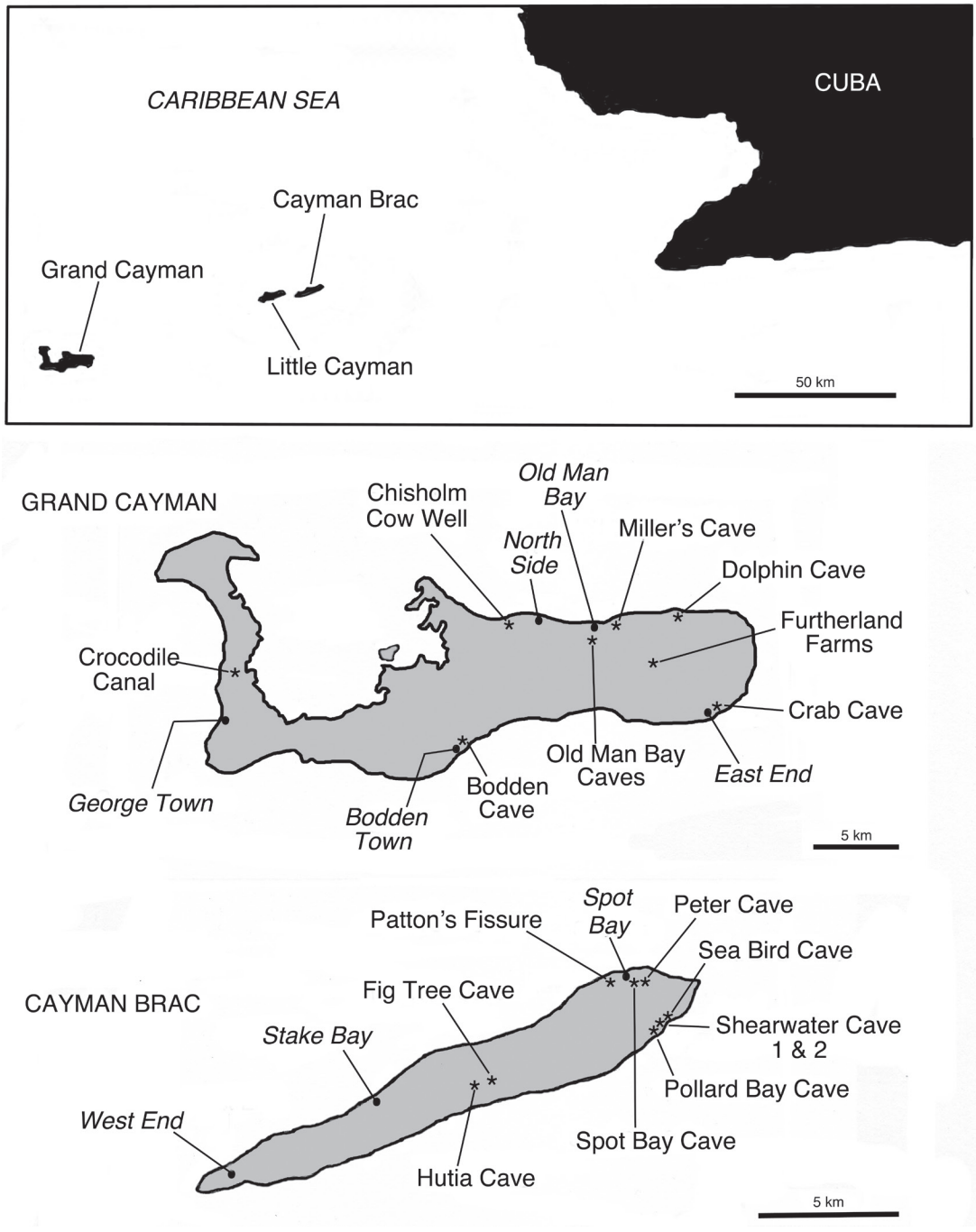
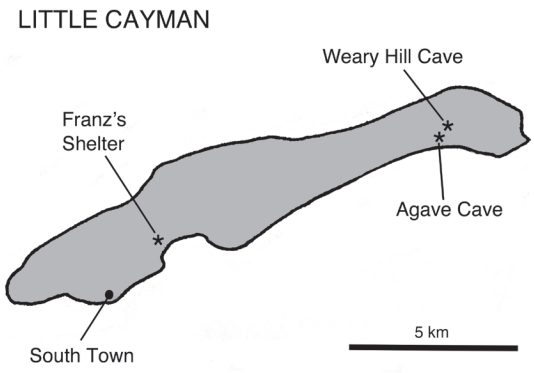


FIG. 1. Cayman Islands, showing geographical position and paleontological localities on Grand Cayman, Cayman Brac, and Little Cayman.



the evidence base for understanding the magnitude, patterns, and processes that transformed the world's biota during the human diaspora (Barnosky et al., 2017).

In this paper we undertake such an investigation into the extinct land mammal fauna of the Cayman Islands, a small archipelago consisting of three islands (Grand Cayman, Little Cayman, and Cayman Brac) distributed along a narrow arc (19°15′–19°45′ N, 79°42′–81°26′ W) in the northwestern Caribbean Sea (figs. 1, 2). Despite the existence of a major marine barrier separating these islands from other Caribbean landmasses, the extant vertebrate fauna of the Cayman Islands displays an overall close relationship to that of Cuba, with many conspecific taxa indicating recent gene flow (Brunt and Davies, 1994). As will be described in detail in this paper, Cayman representatives of three extinct nonvolant mammal genera—*Capromys*, *Geocapromys*, and *Nesophontes*—also have close counterparts in the late Quaternary vertebrate fauna of Cuba, providing further evidence of close biogeographic and evolutionary relationships between these islands.

GEOGRAPHIC AND GEOLOGIC SETTING

The largest member of the Cayman group, Grand Cayman, is 35 km long and up to 14 km wide, with an area of 197 km^2. The other two islands, Cayman Brac and Little Cayman, lie close together approximately 130 km northeast of Grand Cayman. Cayman Brac is nearly 20 km long and between 1–3 km wide, with an area of 38 km^2; of the three islands in the group, it lies closest to the larger islands of Cuba and Jamaica, and is approximately equidistant from both. Little Cayman is 16 km long, between 1–3 km wide, and 28 km^2 in area. The total land area of these islands amounts to 252 km^2.

Nearly 80% of Grand Cayman is <5 m in elevation, with a maximum elevation of 20 m. Small caves are abundant in the low bluffs along the southern coast and in the east-west trending ridges that parallel the north coast in the vicinity of Old Man Bay and North Side. Little Cayman has the least topographic relief, with only about 10% of the island >5 m, and with a maximum elevation of 12 m. Dry caves are much less common on Little Cayman compared with Grand Cayman and Cayman Brac. Cayman Brac has fewer mangrove swamps and brackish lagoons than the two other islands. This island is dominated by the Bluff, the interior plateau that rises from near sea level on the western end of the island to 43 m at its easternmost point, forming the highest elevation in the Cayman Islands (Brunt and Davies, 1994). Only a few hundred meters inland, steep cliffs paralleling the northern and southern coasts frame the plateau's margins, in which caves are abundant.

The Cayman Islands lack the lush tropical vegetation and habitat diversity characteristic of the Greater Antilles. This is a consequence of several factors, including lack of topographic relief, shallow soils, desiccating winds, occasional hurricanes, and limited freshwater availability due to the high permeability of the carbonate rocks that compose the islands. The vegetation of the Cayman Islands is classified as tropical dry forest in the Holdridge Life Zone System (Holdridge, 1967) or the dry evergreen formation series of Beard (1955) and Brunt (1994). Dry evergreen woodlands, also known as limestone forests, are found above 5 m in the interior regions of the islands, particularly on the Bluff on Cayman Brac and in the central and eastern regions of Grand Cayman. Mangrove, button-

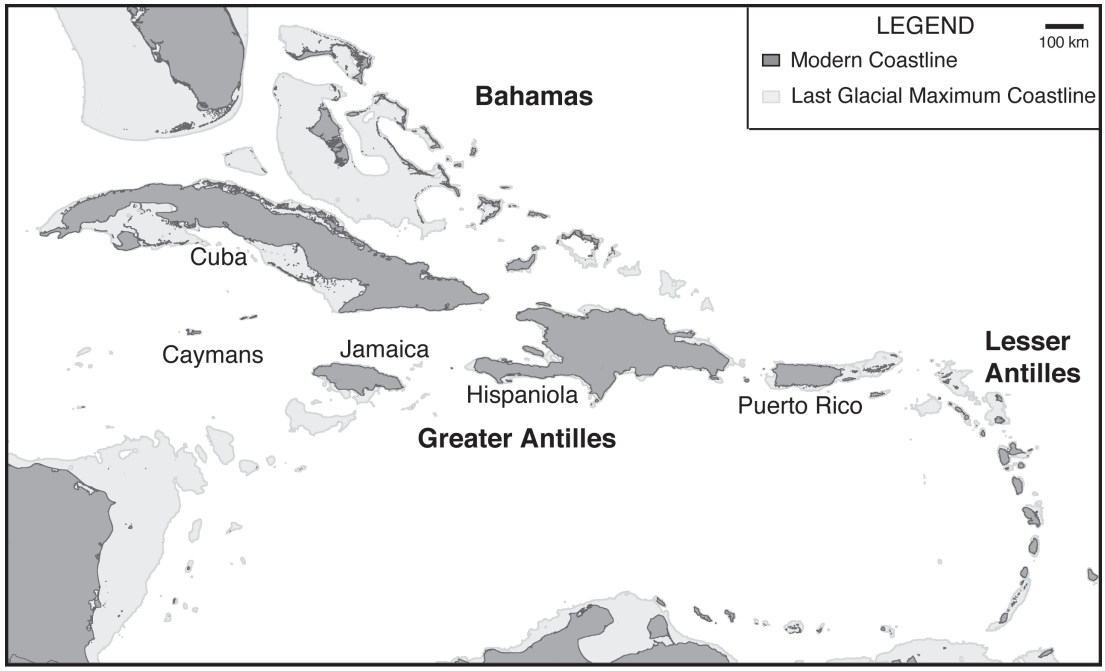


FIG. 2. Coastlines in the West Indies at height of Last Glacial Maximum, 26,500 yr BP (modified from Cooke et al., 2017a). Low sea level did not markedly increase the size of the Caymans at this time or place them in contact with other landmasses (Cayman, Misteriosa, and Rosario Banks are indicated but not identified WSW of the Cayman Islands).

wood swamps, and other wetlands (seasonal swamp and swamp formation series) predominate on Grand Cayman and Little Cayman at elevations below 5 m (Brunt, 1994).

The Cayman Islands are the subaerial manifestation of peaks projecting along the Cayman Ridge on the southern edge of the North American plate. The Cayman Ridge extends from the western terminus of the Sierra Maestra in southeastern Cuba west to the Gulf of Honduras, and is bordered to the south by the Cayman Trench. The trench is in turn bordered to the north and south by a series of transform faults that define the Gonâve microplate, the eastern portion of which includes the north coast of Jamaica and most of Hispaniola. The Cayman Islands are surrounded by deep water in all directions. Depths of 1000–2000 m or more occur between these islands and the northern Greater Antilles and Central America. The Cayman Trench, which in places exceeds depths of 7600 m, separates the Cayman Islands from Jamaica. The three islands are themselves separated from one another by significant deeps (2000 m between Grand Cayman and Little Cayman/Cayman Brac, and 900 m between these last two islands despite a sea-surface separation of only 7 km).

Although the three Cayman Islands are the only portion of the Cayman Ridge currently above water, several shallow submerged banks exist to the west of Grand Cayman, including the Cayman Bank and the Misteriosa and Rosario Banks (fig. 2). ODP hole 998 and dredge hauls along the Cayman Ridge indicate that the latter was covered by shallow water at least as far back as the Eocene-Oligocene transition, although the small size of outcrops and the difficulty of sampling the walls of the Cayman Trench by dredging preclude detailed analyses (Jones, 1994). It is likely that a shallow-water carbonate bank on the spine of the Ridge persisted through the early Miocene, when it began to subside in correlation

with the opening of the Cayman Trench (Perfit and Heezen, 1978; Iturralde-Vinent and MacPhee, 1999). Although the Cayman Islands and eastern Cuba lie along the same structural trend, there is no indication that subaerial lands existed along the Ridge earlier in the Neogene. However, late in the middle Miocene, strong volcanic activity with accompanying general uplift was initiated through much of the Caribbean region. Tectonic movements associated with this event subdivided the Cayman Ridge, creating isolated tectonic blocks separated by deepwater gaps (Dengo and Case, 1990; Iturralde-Vinent and MacPhee, 1999; Iturralde-Vinent, 2006). During this interval the Cayman Islands were raised above sea level, while the remainder of the Cayman Ridge continued to subside.

During the late Pliocene and Pleistocene, lowered sea levels correlated with major glaciations in the northern hemisphere had little geographical effect on the Cayman Islands. During the Last Glacial Maximum around 25,000 years ago, for example, the land areas of the individual islands would have increased to approximately 350 km^2, an increase of only 30% (Woodroffe et al., 1983; fig. 2). Because of the steep submarine slopes bounding each island, at no time would they have coalesced to form a single landmass, as occurred in the case of some of the northern Lesser Antilles (MacPhee et al., 1989) and islands on the Great Bahama and Little Bahama Banks (Morgan, 1989a).

Structurally, each of the three Cayman Islands is composed of a core of marine carbonate rock (limestone or dolostone) of the Bluff Group, which range in age from Oligocene to Pliocene (Jones, 1994). The Bluff Group is composed of the Brac, Cayman, and Pedro Castle formations (Fms) (Jones, 1994). The Cayman Fm, a dolostone of lower to middle Miocene age (Burdigalian to Serravallian, between 10 and 20 Ma), is the most widespread unit. Most of the caves in the Cayman Islands occur in the Cayman Fm. On Cayman Brac, the Cayman Fm is disconformably underlain by limestone and dolostone of the Brac Fm of lower Oligocene age (Rupelian, about 28 Ma), indicating a lengthy depositional hiatus between these units. The Brac Fm outcrops to a limited extent at the base of the Bluff on the north and south coasts at the northeastern end of Cayman Brac. A large number of caves occur in this region (Jones, 1994), some of which have produced vertebrate fossils (appendix 1). The Pedro Castle Fm, a dolostone of Pliocene age (Zanclian or Piacenzian, between 3 and 5 Ma), unconformably overlies the Cayman Fm in limited areas on the southern coast of Grand Cayman and near the southwestern tip of Cayman Brac (Jones, 1994). No caves are known from the Pedro Castle Fm. Pleistocene sediments of the Ironshore Fm overlie the Bluff Group on the periphery of each island (Matley, 1926; Jones, 1994). Woodroffe et al. (1983) obtained uranium-series radioisotopic dates averaging 124,000 ± 8000 yr BP on samples of unaltered aragonite from fossil corals from the reef facies of the Ironshore Fm on Grand Cayman and Cayman Brac. These dates indicate that the Ironshore Fm was deposited during the last interglacial high sea-level stand (Marine Isotope Stage 5e) when sea levels were about 6 m higher than present. Data on sea-level changes in the Late Neogene (Haq et al., 1987; Zachos et al., 2001; Miller et al., 2005) and the structural history of the Cayman Islands (Jones, 1994) suggest that at least some portion of the islands has been continuously above sea level since the late Pliocene (about 3 Ma), if not longer.

HISTORY OF PALEONTOLOGICAL COLLECTING IN THE CAYMAN ISLANDS

Remarkably, a report made during Sir Francis Drake's brief visit to Grand Cayman in April 1586 mentions the presence of "coneys" (Keeler, 1981: 113) and "little beasts like cattes" on this island (Keeler, 1981: 204). In Jamaica, "coney" is still the common term for *Geocapromys brownii*. The reference in the report is probably therefore to a capromyine hutia, which are cat sized, but the descriptions are not detailed enough to determine which particular animal the writer

observed. Whatever it was that Drake and his crew saw, there is no mention of land mammals in later travelers' accounts, nor in any of the early scientific papers on the Cayman Islands from the late 19th century (Morgan, 1994a). Evidently, the native land mammal fauna had disappeared before naturalists had an opportunity to record it (Morgan, 1994b).

The first reference to the presence of fossil vertebrates in the Cayman Islands occurs in a book by Lord Moyne (1938: 83), in which he noted "Bones found in caves on Cayman Brac show that capromys of at least one other species, now extinct, formerly existed on the Cayman Islands." According to specimen labels in the Vertebrate Palaeontology collection of the Natural History Museum, London (NHM), Moyne collected several *Capromys* skulls and long bones from a cave near Stake Bay, Cayman Brac, in 1937 (see figs. 1 and 2 for all toponyms and cave localities named in this section). Aware of Moyne's discovery, C. Bernard Lewis, a member of the Oxford University Cayman Islands Biological Expedition, collected several skulls and mandibles of *Capromys* in May 1938 from a cave located a quarter of a mile west of Stake Bay (C.B. Lewis, in litt., January 20, 1975). These fossils are now in the NHM's Mammalogy collections. In a brief summary of previous work on West Indian fossil vertebrates, Westermann (1953: 27), under the heading "*Capromys pilorides* subsp.," noted "Remains of this extinct sub-species of the common Hutia of Cuba (*C. pilorides*) occur in cave deposits at Cayman Brac. According to C.B. Lewis (personal commun., September 1953) this animal became extinct within the last 100 years, after the island was resettled with permanent inhabitants."

It bears mentioning that no Quaternary fossils of insectivores, bats, birds, or reptiles were recovered (or, at any rate, kept) by these early expeditions. Moyne and Lewis, for example, collected larger bones from surface deposits in caves, but apparently did not excavate underlying sediments. This is not surprising, since screenwashing for microvertebrate fossils did not become a common practice until the 1950s and 1960s (Hibbard, 1949; McKenna, 1962).

Nothing further concerning this otherwise unknown fauna came to light until Thomas H. Patton, then of the Florida State Museum (FSM; now the Florida Museum of Natural History, FLMNH), initiated a survey of cave fossil deposits on Cayman Brac in October 1964. In the summer of 1965, Patton and his field crew excavated two large cave deposits in the Bluff, a major landscape feature situated just inland from the north and south coasts of Cayman Brac (for additional information on this and other localities, see appendix 1). The first, called Cave 1 by Patton, was redesignated Pollard Bay Cave by Morgan (1994a) to underline its location near Pollard Bay on the southeastern tip of the island. Patton's second excavation took place in his Cave 2, since renamed Patton's Fissure, located on the north coast near Spot Bay (Steadman and Morgan, 1985; Morgan, 1994a). The only taxa specifically listed in Patton's brief review of the Cayman Brac fossil vertebrate fauna (Patton, 1966) were the small island-shrew *Nesophontes* and the capromyine rodent *Geocapromys*, although he did record the presence of reptiles and birds in these same deposits. Patton did not mention *Capromys* from Cayman Brac, even though his collections include numerous bones of that genus, and both Moyne (1938) and Westerman (1953) had noted its presence there. Patton's statement (1966: 181) that he had "recovered the first fossil vertebrate faunas reported from the Cayman Islands" indicates he was unaware of the earlier collections by Moyne and Lewis. Varona (1974) subsequently listed *Capromys* (*Capromys*) *pilorides* ssp. as an extinct taxon from Cayman Brac, based on Lewis' specimens as reported by Westermann (1953), and also noted the occurrence of *Nesophontes* sp. and *Capromys* (*Geocapromys*) sp. on Cayman Brac, following Patton (1966).

In March and April of 1976, the lead author (G.S.M.) visited the Cayman Islands with Greg McDonald (now of the U.S. Bureau of Land Management) and archaeologist Nina Thanz-Borremans. On Grand Cayman they discovered

fossil deposits in eight caves and conducted extensive excavations in four of them: Bodden Cave (also called Pirate's Cave) in Bodden Town, Crab Cave in East End, and Old Man Cave and Barn Owl Cave located just south of Old Man Bay. They also collected a small sample of bones from the surface of Peter Cave located near the top of the Bluff on Cayman Brac. In July 1979, G.S.M. collected additional mammal fossils from Spot Bay Cave, located about 100 m west of Peter Cave on Cayman Brac. Shortly thereafter, in April 1980, Margaret Langworthy, Jacqueline Belwood, and G.S.M. collected fossil material from several cave deposits on Grand Cayman. They renewed excavations in Bodden Cave and Crab Cave, and discovered new deposits in Agouti Cave, Miller's Cave, and Tadarida Cave (all within the vicinity of Old Man Bay). They also excavated fossils from a dark organic peat deposit exposed in a mosquito control canal north of George Town, the Crocodile Canal Site (Morgan et al., 1993; Morgan, 1994a), so named because it yielded numerous fossils of the Cuban crocodile (*Crocodylus rhombifer*) as well as a few limb bones of capromyine rodents.

Sediments from the 1965 and 1976 expeditions were collected and shipped in bulk to Florida for screenwashing and sorting. During later expeditions, sediments were dry-screened or washed through 16 mesh (1.5 mm opening) window screen while in the field in order to concentrate the fossiliferous matrix and reduce weight. As a result, the vast majority of bones represented at these sites were recovered, including very small elements belonging to frogs, lizards, birds, and bats.

In January and February of 1986, at the invitation of the Mosquito Research and Control Unit and Natural Resources Study (MRCU) of the Cayman Islands government (now the Terrestrial Resources Unit of the Department of Environment), Richard Franz and G.S.M. visited all three of the Cayman Islands in an effort to locate additional productive localities. They excavated three new sites on Grand Cayman: Dolphin Cave near Anchors Point on the north coast, and two small, sediment-filled vertical caves or sinkholes (locally known as "cow wells") dubbed Chisholm Cow Well and Furtherland Farms Cow Well (Morgan, 1994a; see appendix 1). Chisholm Cow Well, located just inland from Grape Tree Point west of North Side, produced a large sample of bones of the Cuban crocodile, as well as a few fossils of capromyine rodents and the endemic Grand Cayman iguana (*Cyclura lewisi*). The cow well at Furtherland Farms was discovered when organic sediment was removed from a sinkhole to create a natural cistern for use in irrigating a nearby banana plantation. Furtherland Farms produced not only a large sample of *Crocodylus rhombifer*, but also a diverse avifauna and a few fossils of terrestrial mammals. During this same expedition several new test pits were dug in Peter Cave, Spot Bay Cave, and Pollard Bay Cave on Cayman Brac. Several small sea caves located in the Bluff east of Pollard Bay Cave were also explored and sampled. The richest of these were Shearwater Cave 1 and 2, both of which contained large samples of bones and feathers of Audubon's shearwater (*Puffinus lherminieri*), a species now locally extinct in the Cayman Islands (Morgan, 1994a). Also discovered were the first fossiliferous cave deposits on the top of the Bluff, Hutia Cave and Fig Tree Cave, both located along the north side of the road linking the Bluff Highway and the lighthouse. Richard and Shelley Franz carried out further excavations at Dolphin Cave and Furtherland Farms Cow Well on Grand Cayman in August 1987.

Disappointingly, and despite considerable effort, only two small fossil deposits were found on Little Cayman during the January-February 1986 expedition, both of which consisted of small overhangs or shelters rather than true caves. These two sites, Franz's Shelter in Mahogany Bay Estates and Agave Cave at Sandy Point, exclusively produced bones of *Capromys*, mostly edentulous mandibles, maxillae, and limb bones. A third small cave, Weary Hill Cave, located near Weary Hill on the eastern end of Little Cayman, was excavated by archaeologists from the Environmental Archaeology Program at FLMNH.

Like the two previous sites from Little Cayman, Weary Hill Cave yielded a small sample of *Capromys* remains. In recent years, fossils have been discovered in several additional caves on Little Cayman (Pat Shipman, Alan Walker, and William Verhoeven, personal commun.), including a nearly complete skull of *Capromys* from an unnamed cave on Little Cayman, although we have not had the opportunity to conduct a detailed study of these fossils.

The last expedition detailed here occurred in March and April 1993. Barbara Toomey, Reed Toomey, and G.S.M. conducted a controlled excavation just inside the entrance of Dolphin Cave on Grand Cayman. They also excavated several small test pits farther back in the cave that produced large samples of bats, as well as numerous elements of *Capromys* and *Geocapromys*. During this same trip, G.S.M. also recovered vertebrate fossils from a sinkhole deposit on the grounds of the newly established Queen Elizabeth II Botanic Park. Like most other sinkhole and cow well deposits on Grand Cayman, the Botanic Park site contained organic peaty sediments. Recovery predominantly consisted of bones of the Cuban crocodile, although small samples of rodents (*Capromys* and *Geocapromys*), birds, iguanas, and snakes were also found.

In summary, excavations on all three of the Cayman Islands over a span of almost 30 years by FLMNH parties led by Thomas Patton and G.S.M. have produced a wealth of fossils that comprehensively document the late Quaternary vertebrates of this island group (Morgan, 1994a). Overall, more than 30 vertebrate fossil deposits were discovered, ranging from tiny limestone crevices that have yielded only a few bones, to Patton's Fissure, which has produced thousands of fossils (appendix 1). Over a similar interval, many of these discoveries have been published and placed within the broader context of Caribbean vertebrate paleontology and extinction biology (e.g., Morgan and Patton, 1979; Morgan et al., 1980, 1993; Morgan, 1985, 2001; Steadman and Morgan, 1985; Morgan and Woods, 1986). Field research into the Quaternary fossil record of the Cayman Islands is also being continued by other groups. Harvey et al. (2016) recently announced the recovery of new mammalian fossils from a series of caves on Cayman Brac, but as this material has not yet been analyzed taxonomically it does not form part of this paper.

In a detailed examination of the results of the FLMNH expeditions to the Cayman Islands, Morgan (1994a) provided an overview of all of the mammalian fossil discoveries made until that time and documented the genus-level richness of extinct mammals formerly present on the islands, but provided no formal taxonomic descriptions or detailed assessment of the fauna's species diversity or affinities. It therefore remains to place the Cayman taxa of *Nesophontes*, *Capromys*, and *Geocapromys* in their proper systematic and biogeographic contexts.

PALEONTOLOGICAL MATERIALS AND METHODS

The systematic portion of this study is primarily based on fossils in the collections of the Florida Museum of Natural History, University of Florida (FLMNH, cataloged under the acronym UF) and the Natural History Museum, London (NHM). Comparative specimens of extant and/or fossil capromyines and nesophontids from Cuba, Hispaniola, Puerto Rico, Jamaica, Bahamas, and Little Swan Island were examined in collections of the aforementioned museums as well as the American Museum of Natural History, New York (AMNH); the Museum of Comparative Zoology, Harvard University, Cambridge (MCZ); and the U.S. National Museum of Natural History, Smithsonian Institution, Washington, D.C. (USNM). Dental descriptions of capromyine rodents follow Patterson and Wood (1982). Dental terminology for *Nesophontes* follows Szalay (1969; see also Ungar, 2010).

GENOMIC MATERIALS AND METHODS

DNA preservation in late Quaternary samples from tropical environments, such as those prevailing in the Caribbean region, is considerably

more limited in comparison to material from temperate or boreal environments due to rapid degradation of ancient biomolecules under hot humid conditions (e.g., Welker et al., 2015; Turvey et al., 2016). In recent years, however, attempts to extract and amplify ancient DNA from a range of late Quaternary Caribbean vertebrates have been increasingly successful, providing important new insights into the evolutionary history of several poorly understood extinct taxa (e.g., Brace et al., 2015, 2016; Kehlmaier et al., 2017). Genomic data could be very useful in testing whether, for example, Cayman land mammals were indeed closely related to taxa on Cuba. In the case of *Geocapromys* and *Nesophontes* such testing is not currently possible, because the Cuban species *G. columbianus* and *N. micrus* are both now extinct (Silva Taboada et al., 2007) and no DNA sequence data are available for either of these taxa. However, *Capromys pilorides* is still extant on Cuba, and sequence data from modern samples are available for all its living described subspecies. In addition to our morphological taxonomic assessment, we also report on DNA sequence data from material of the extinct Cayman *Capromys*, and use these data to evaluate its relationship to the extant Cuban *C. pilorides*.

Three *Capromys* specimens from Cayman Brac (UF 18588, 18671, 61292) were sampled for ancient DNA analysis, but only UF 18588 yielded sufficient endogenous DNA for sequencing and subsequent analysis. Bone specimens were sampled by drilling into the bone using a Dremel handheld drill with a 2–3 mm drill bit. The surface of the bone was first cleaned using the drill to minimize contamination, and surface bone powder was discarded. Drill bits were changed between specimens, and all equipment was sterilized with bleach and UV treated before and after use. In order to keep possible drill-induced heat damage of DNA to a minimum, drill speeds were kept low (below 1000 RPM) (Adler et al., 2011). Larger pieces of bone were powdered using a Mikro Dismembrator (Sartorius) prior to extraction. Extraction protocol was based on Dabney et al. (2013), and implemented as described in Brace et al. (2012). Single-index double-stranded DNA libraries were built following the protocol in Meyer and Kircher (2010). Extractions and post-PCR library builds took place in a dedicated ancient DNA laboratory in the NHM, physically removed from the post-PCR laboratories.

Samples underwent shotgun sequencing on the Illumina NextSeq 500 platform in order to assess endogenous content. After shotgun sequencing, samples were subjected to target capture enrichment in order to increase endogenous DNA yield. The latest version (v3) of the capture enrichment kits available from MYcroarray (www.mycroarray.com) was employed, using the target genes from *Capromys pilorides* available on GenBank (Benson et al., 2005) to produce the baits.

For postsequencing data analysis, data from Illumina Nextseq 500 runs were demultiplexed, and adapters were then removed from the paired-end Illumina reads, which were merged and then trimmed using quality scores, ambiguity criteria and read length.

In order to extract relevant genes from the Next Generation sequencing data, sequences were aligned or mapped to a *C. pilorides* mitochondrial genome reference sequence available on GenBank, from an individual from Villa Clara Province, central mainland Cuba (Fabre et al., 2017; GenBank accession number, KU892766). Basic Local Alignment Search Tool (Altschul et al., 1990) was used to confirm the identity of the consensus sequences. Consensus sequences and other available GenBank mitogenome sequences for other extant capromyine taxa published by Fabre et al. (2017; GenBank accession numbers: *Geocapromys brownii*, KU892767; *G. ingrahami*, KU892768; *Mesocapromys melanurus*, KU892769; *Mysateles prehensilis*, KU892770; *Plagiodontia aedium*, KU892771) were then aligned using the ClustalW (Larkin et al., 2007) alignment tool implemented in Geneious v.8.0.5 (Kearse et al., 2012). PartitionFinder (Lanfear et al., 2012) was used to access evolutionary models for partitioned genes.

Maximum-likelihood trees with bootstrap support values were generated in RAxML (randomized axelerated maximum likelihood) (Stamatakis et al., 2008) through the CIPRES Science Gateway V.3.3 (Miller et al., 2010). MrBayes v.3 (Ronquist and Huelsenbeck, 2003) was used to estimate phylogeny using Bayesian methods. The following parameters were utilized using a MrBayes block: the MCMCMC algorithm was incorporated in the MrBayes format using four chains (three heated, one cold) that were run for 1×10^6 generations; and sampling was initiated every 1×10^3 generations with a burn-in period of 250 trees. The Hispaniolan hutia *Plagiodontia aedium* was used as an outgroup for both analyses.

Pairwise genetic distances were also calculated to estimate the evolutionary distance between individual samples. Pairwise genetic distances were estimated in the program MEGA v.5 (Tamura et al., 2007). This technique provides a matrix of pairwise genetic distance values that can be compared with values from other species pairs, and uses a nucleotide substitution model also chosen in PartitionFinder (Lanfear et al., 2012).

SYSTEMATIC PALEONTOLOGY

Class Mammalia Linnaeus, 1758

Order Lipotyphla Haeckel, 1866

Suborder Solenodonota Brace et al., 2016

Family Nesophontidae Anthony, 1916

Remarks: Nesophontidae is a family of solenodonotan lipotyphlans, the only known representatives of which are species of the late Quaternary Antillean genus *Nesophontes* (Whidden and Asher, 2001; Brace et al., 2016). The affinities of *Nesophontes* have been diversely treated in the century since the discovery of the first member of the genus (Anthony, 1916). Most authors have favored a close relationship to soricoids, usually on the basis of an apparently shared pattern of molar dilambdodonty (e.g., Saban, 1954; Van Valen, 1967), but others have discussed whether *Nesophontes* might instead be the sister taxon of *Solenodon*, another lipotyphlan restricted to the Caribbean but exhibiting molars that are morphologically zalambdodont (e.g., Gregory, 1920; McDowell, 1958; Asher and Sánchez-Villagra, 2005). This dispute was recently settled in favor of the latter hypothesis, on the basis of ancient DNA evidence collected from a 750 year old *N. paramicrus* specimen from Hispaniola (Brace et al., 2016). The closest known relatives of *Nesophontes* and *Solenodon* are probably Eocene and Oligocene insectivores in the family Geolabididae from North America (Simpson, 1956; McDowell, 1958; MacFadden, 1980; Lillegraven et al., 1981; Morgan and Woods, 1986). Molecular dating indicates that the split between Solenodontidae and Nesophontidae occurred around 40 Ma. In view of their distinctiveness and antiquity within Lipotyphla, these families were recently placed in their own suborder, Solenodonota, by Brace et al. (2016). Their mutual divergence may have occurred on the North American mainland, in which case two invasions of the Greater Antilles by solenodonotans must be inferred. Alternatively, divergence may have occurred after initial colonization of the island arc by a joint ancestor, requiring only a single invasion (Simpson, 1956; McDowell, 1958; MacFadden, 1980; Lillegraven et al., 1981; Morgan and Woods, 1986; Iturralde-Vinent and MacPhee, 1999). *Nesophontes* and *Solenodon* are the only two endemic genera of land mammals in the West Indies that are clearly of Nearctic origin. All other Antillean terrestrial mammals have explicitly South American or more general Neotropical affinities (Morgan and Woods, 1986).

The type species and largest member of the genus, *Nesophontes edithae*, was originally described from Puerto Rican cave deposits (Anthony, 1916). It is also known from Amerindian archaeological sites on Vieques and the Virgin Islands (Morgan and Woods, 1986; Quitmyer, 2003). Five species of *Nesophontes* have been described from Cuba: *N. micrus* Allen, 1917, *N. longirostris* Anthony, 1919, *N. major* Arredondo, 1970, *N. submicrus* Arredondo, 1970, and *N.*

superstes Fischer, 1977. Three species of *Nesophontes* have also been described from Hispaniola by Miller (1929): *N. hypomicrus*, *N. paramicrus*, and *N. zamicrus*. *Nesophontes* is unknown from Jamaica, Bahamas, or Lesser Antilles.

Considerable size variation exists within Puerto Rican samples of *N. edithae*, which was initially interpreted by Anthony (1916) as representing sexual dimorphism. As large-scale sexual dimorphism is unknown in other recent lipotyphlans, this variation was used as part of the original justification for erecting a new family to accommodate the species (Anthony, 1916). However, size variation in *N. edithae* has been subsequently interpreted as more likely to reflect allochronic plasticity, with specimens of varying sizes probably originating from different depositional horizons across the Late Quaternary (Choate and Birney, 1968; McFarlane, 1999). Condis Fernández et al. (2005) analyzed metrical and morphological variation in Cuban *Nesophontes*, and concluded that only two species could be supported, *N. major* and *N. micrus*, the latter incorporating all of the other nominal taxa. Importantly, these authors showed that size is a particularly labile character within Cuban *Nesophontes* and is therefore not a dependable basis for erecting species boundaries, especially when considered in isolation. Silva Taboada et al. (2007) went even further, suggesting that all previously diagnosed Cuban species of *Nesophontes* are in fact morphs of *N. micrus*. However, their subordination of all nominal taxa within a single species was made without any commentary, and they did not review the diagnostic value of the characters cited by Condis Fernández et al. (2005) for distinguishing *N. micrus* and *N. major*. The Hispaniolan species have not been subjected to revision in recent years, and the scale of intraspecific variation in Cuban *Nesophontes* raises the question whether these three species are truly distinct, or instead just size morphs of one or two variable species. Since this issue cannot be settled here, for the purposes of this study we retain Miller's taxa as valid.

The previous existence of *Nesophontes* on Cayman Brac and Grand Cayman has been repeatedly noted in the literature (e.g., Patton, 1966; Varona, 1974; Morgan et al., 1980; Steadman and Morgan, 1985; Morgan and Woods, 1986; Morgan, 1994a), but no formal systematic determination of its status has ever been undertaken. Regrettably, the Cayman material is too fragmentary or otherwise damaged to make a morphometric treatment worthwhile.

Nesophontes Anthony, 1916

***Nesophontes hemicingulus*,** new species

Figures 3–9

Holotype: UF 23295, partial skull lacking neurocranium (fig. 3); C1–M3 present on right side, C1–M2 on left side, with partial alveoli for I2–I3. Unfortunately, the skull broke along its long axis after collection, although little bone has been lost from complementary edges. All the cranial specimens from the Cayman Islands are damaged to a greater or lesser degree, and dentitions tend to be incomplete and much worn. UF 23295 was chosen as the holotype because its teeth are on average less worn than those in comparable specimens and all cheekteeth are preserved (albeit on one side only).

Type Locality: Patton's Fissure, near Spot Bay on the northern coast of Cayman Brac. The holotype was recovered from layer 5 (80–100 cm below the surface), which has been radiocarbon dated on the basis of land snail shell carbonate to 11,180 ± 105 ^{14}C yr BP (see Radiocarbon Dating).

Etymology: Frp, Latin *hemi-*, "half," and *cingulus*, "belt," in reference to absence of the precingulum on all upper molars.

Age: Late Pleistocene-Holocene (see Radiocarbon Dating).

Distribution: Known only from Cayman Brac and Grand Cayman. This species is the only member of the genus known outside the Greater Antilles and their satellite islands.

Referred Specimens: **Cayman Brac:** Patton's Fissure: partial skulls, UF 23258, 23264, 23277,

23279, 23293–23301, 23332–23337, 23360-23363, 23393, 23394, 23407; mandibles, UF 23241, 23242, 23245, 23251–23256, 23259, 23265–23269, 23280–23285, 23311–23313, 23324–23326, 23343, 23347–23359, 23364, 23365, 23367–23378, 23383, 23389, 23397, 23398, 23400, 23404, 23408–23417, 23421, 23426–23432, 23436, 23437, 23448–23450 (also includes a large sample of postcranial material not listed here). Pollard Bay Cave, Shearwater Cave 2. **Grand Cayman:** Dolphin Cave: UF 172845, right mandible with c1–m3; UF 172846, right mandible with c1–m3; UF 172863, right mandible with p2–m3; UF 172908, left mandible with p2, p4–m3; UF 172909, left mandible with c1, p2, m1–m3; UF 172910, left mandible with m1–m3; UF 172926, right mandible with m1–m2; UF 172939, partial skull lacking braincase, with right C1–M2 and left P2-M2; UF 172940, left mandible with p2, p4–m3; UF 172950, left mandible m1–m2. Barn Owl Cave: UF 23242, right mandible with p2–m3. Bodden Cave: UF 23241, right mandible with p4–m3. Furtherland Farms: UF 172803, left mandible with p2, p4–m3. Old Man Cave: UF 23245, right mandible with c1, p2, m1; UF 23246, right mandible with p2, p4–m3; UF 23247, edentulous right mandible; UF 23248, partial edentulous right mandible; UF 23249, right mandible with p2, p4m3; UF 23250, left mandible with p2, p4–m3; UF 23251, left mandible with p4–m3.

Diagnosis: Within *Nesophontes*, *N. hemicingulus* expresses unique reductions in cingulum/ectocingulid features on upper/lower molars. It can be distinguished in lacking precingula on all molars, attenuation of postcingula on M1 and M2, and uniform de-emphasis of ectocingulids on lower cheekteeth. Closest morphological similarities are to Cuban *N. micrus* in regard to tooth shape, dimensions, and discrete characters.

Description: In the absence of good cranial remains of Cayman nesophontids, teeth are the main source of characters (figs. 3–9). In the following set of differential diagnoses, we compare *N. hemicingulus* to species from the major islands on which *Nesophontes* formerly occurred: Puerto Rico (*N. edithae*), Cuba (*N. major*, *N. micrus*), and Hispaniola (*N. hypomicrus*, *N. paramicrus, N. zamicrus*). Hispaniolan *N. paramicrus* and Cuban *N. micrus* are very similar, and were in fact synonymized by Varona (1974) on the basis of his comparisons and those of Patterson (1962). However, these two species differ in some characters, such as the absence of a constricted infraorbital foramen in *N. micrus*, and for this reason are distinguished here. Cingulum/cingulid characters, the only reliably diagnostic characters for *N. hemicingulus* in the current hypodigm, are treated separately.

General Craniodental Features

Apart from size-related features, the cranial anatomy of *Nesophontes* varies little within the genus, with all species exhibiting a tubular skull featuring a low braincase, elongated rostrum, and incomplete zygomatic arch (Anthony, 1916, 1918). Compared to the plesiomorphic eutherian dental formula, the dentition of *Nesophontes* is complete except for the loss of P1/p1 (fig. 3–9). The upper canine is double-rooted, with deep grooves on anterior and lingual surfaces. P2 and P3 are simple, bladelike teeth, while P4 is trenchant and semimolariform. The tritubercular M1–M3 lack hypocones; M3 is significantly smaller than M1-M2 in most species. The sickle-shaped lower canines are the tallest teeth in the mandible. The p2 resembles the canine but is somewhat smaller; the p3 is bladelike, and the p4 is semimolariform. The three lower molars are similar in size and morphology, although m3 is usually smallest.

Nesophontes edithae is both the largest and the most distinctive of the nesophontids, and thus represents a standard against which conditions in the other species can be usefully compared and contrasted. Apart from cingulum/cingulid characters, treated below, when teeth are unworn *Nesophontes edithae* can be distinguished from *N. hemicingulus* (and all other species in the genus) by relative lack of reduc-

tion of P3/p3 compared with P2/p2 and also by the relatively larger size of m3 compared to m2 (Anthony, 1916; figs. 6, 8). Relative reduction of P3/p3 and of m3 in all other species of *Nesophontes* are considered to be derived conditions. Unfortunately, because of extreme wear these features are poorly represented in the material available for this study.

In addition to dental traits, the largest of the three nominal Hispaniolan species, *Nesophontes paramicrus*, exhibits a constricted infraorbital foramen. This character separates *N. paramicrus* from all other species of *Nesophontes*, including *N. hemicingulus*. The two smaller Hispaniolan species, *N. hypomicrus* and *N. zamicrus*, differ from *N. paramicrus* and *N. edithae* in the reduced relative size of the unworn p4, and from all other species of *Nesophontes* in having a reduced hypoconulid and thus a direct connection of the hypoconid and entoconid via the postcristid on m1 and m2. All other species of *Nesophontes*, including *N. hemicingulus*, have a relatively larger hypoconulid and a postcristid that connects the hypoconid and hypoconulid.

Although Condis Fernández et al. (2005) carried out a much-needed revision of Cuban *Nesophontes*, the two species retained (*N. major* and the smaller *N. micrus*) remain difficult to distinguish on grounds other than size-related features. These authors considered a large number of discrete and continuous characters, of which 18 were considered diagnostic (8 cranial and 10 mandibular). Continuous characters require intact landmarks for scoring; the few that could be taken on the present sample demonstrate that *N. hemicingulus* was similar in size to *N. micrus* (tables 1, 2). In their rediagnoses of *N. micrus* and *N. major*, Condis Fernández et al. (2005: 100) listed as distinguishing characters of *N. micrus* lesser development of mandibular molars and p3, greater supraoccipital inflation, and shorter length and width of rostrum. UF 23296 is the only specimen of *N. hemicingulus* with an intact rostrum (which is comparatively short and narrow). The caudal end of the skull is unknown in this species.

Cingulum/Cingulid Features

Nesophontids express very little cingulum/cingulid relief on their cheekteeth. Anthony (1916) stated that cingula were absent on cheekteeth of *N. edithae*, but this is clearly incorrect (figs. 6A, 7A). More accurately, in *Nesophontes edithae* the cingulum on maxillary posterior cheekteeth (as defined here, P4–M3) does not assume the form of a continuous, well-defined shelf ringing the entire lingual part of the tooth (as seen, by contrast, in *Solenodon*; McDowell, 1958), but instead consists of a series of semidiscrete low ridges (para- and metacingula, pre- and postcingula). This is also true of all other nesophontids, with *N. hemicingulus* having the most reduced cingulum of all (fig. 7C).

In *Nesophontes edithae* (figs. 6A, 7A) the mesiobucally positioned paracingulum is present and relatively large on all three molars but absent (or not separately distinguishable) on P4. Distobuccally, the metacingulum is present on all three molars and also on P4. The precingulum is present on all three molars. The postcingulum is likewise evident on all three molars as well as on P4. Infrequently (e.g., AMNH 17109, fig. 6A), M3 displays a tiny linguocingulum that bridges the gap that would otherwise exist between the termini of the pre- and postcingula. This feature is apparently never seen in other nesophontids (e.g., fig. 7B, C), nor is it evident in the illustration of the maxillary dentition of *N. edithae* by McDowell (1958).

In *Nesophontes micrus* (fig. 6B, 7B), as in *N. edithae*, the paracingulum is present and well defined on molars but absent on P4, while the metacingulum is present throughout the cheektooth series. With regard to pre- and postcingula, differences from *N. edithae* are notable. On M1 and M3 there is a poorly defined precingulum that continues the line of the paracingulum along the mesial flank of the protocone. By contrast, the precingulum is completely lacking on M2, and is present but tiny on M3. On M1 and M2 the postcingulum is present, whereas it is not distinguishable at all on M3.

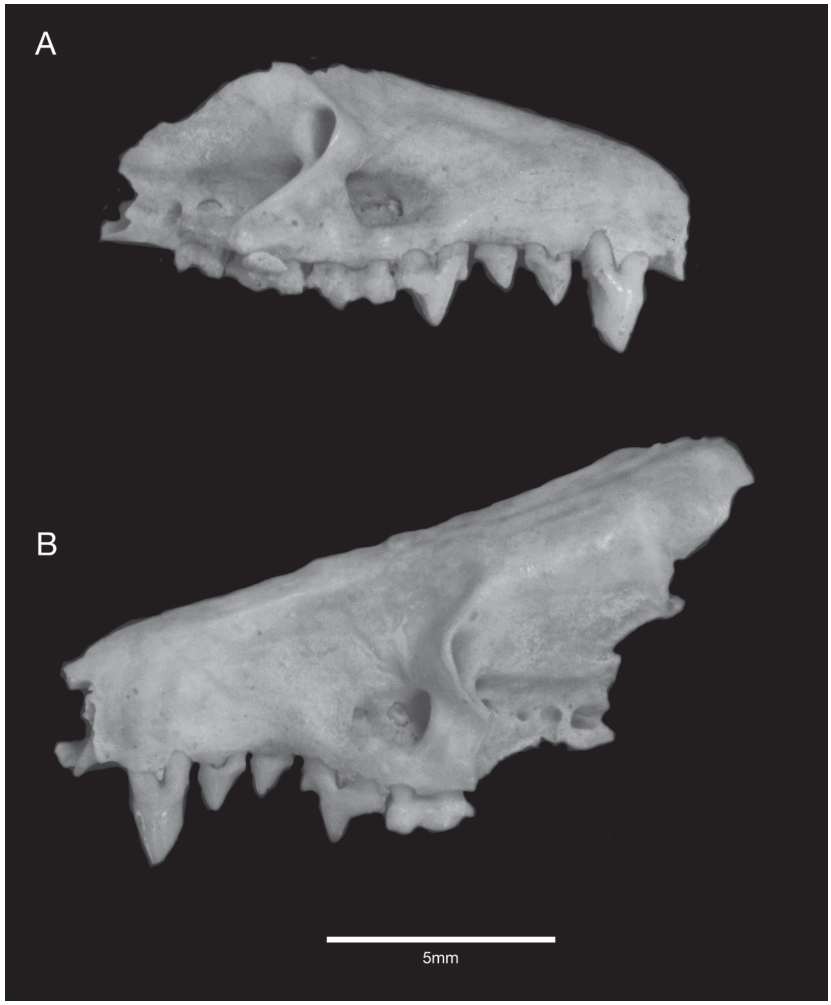
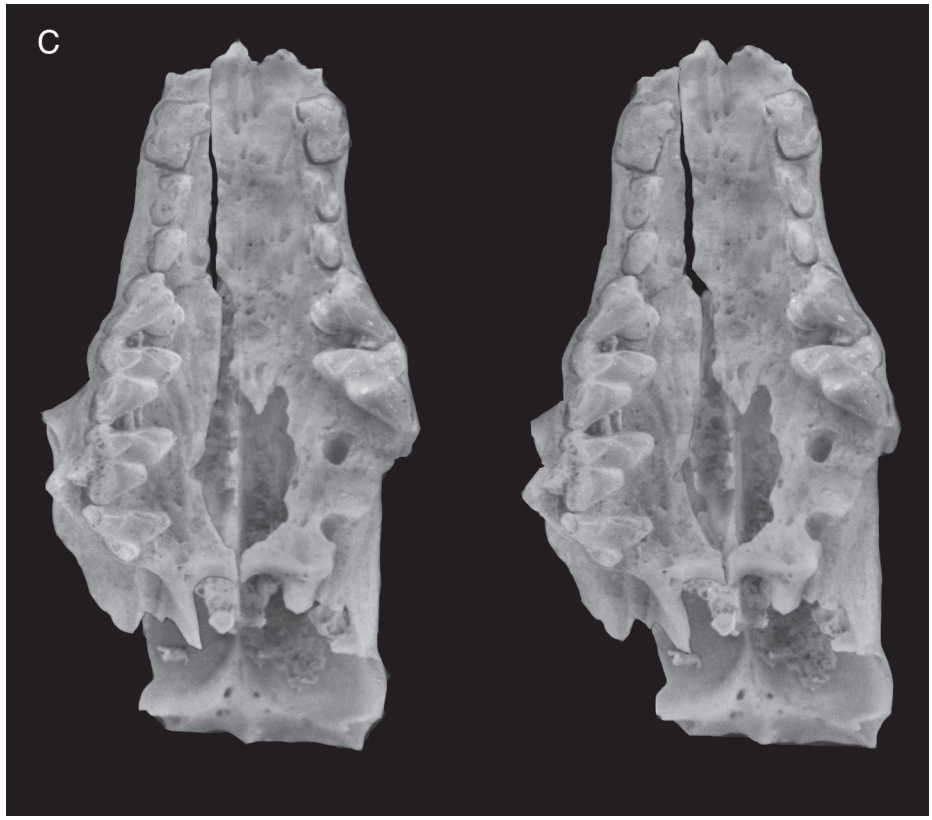


FIG. 3. Skull, *Nesophontes hemicingulus*, n. sp., UF 23295, holotype (Patton's Fissure, Cayman Brac): **A,** right lateral; **B,** left lateral; **C,** occlusal (stereopair). Teeth moderately worn.

In *Nesophontes hemicingulus* (figs. 3–5, 6C, 7C) the process of cingulum reduction is even more extreme. The precingulum is completely absent on P4–M3. Postcingula on M1 and M2 are present as amorphous swellings rather than shelves, and are reduced compared with their homologs in *N. micrus*. There is no trace of a postcingulum on M3, as in *N. micrus*.

As to cingulid architecture on mandibular cheekteeth, Condis Fernández et al. (2005) found that it was essentially invariant in all Cuban nesophontids and thus nondiagnostic of particular species. This is true of the family as a whole, although we found some minor differences in the definition of the ectocingulid. These may be summarized as follows (see figs. 8, 9). In all nesophontids, the ectocingulid is a minor subocclusal crest that runs along the mesiobuccal flanks of the paraconid and protoconid of the mandibular cheekteeth (p4–m3). It loses height distally and disappears completely below the position of the hypoconid. With regard to individual taxa, we found that in *N. edithae* (fig. 8A, 9A), in which the crest is best developed overall, the mesiobuc-



cal portion tends to be pronounced on p4–m3, but the distal portion is barely indicated and may be absent on p4 and m3. (See McDowell, 1958: fig. 13, in which the ectocingulid is portrayed in *N. edithae* in somewhat exaggerated form, evidently to enhance visibility.) In *N. micrus* AMNH 95708 (figs. 8B, 9B) the distal portion of the ectocingulid on m1 and m2 is less developed than in *N. edithae*, but once again reduced on p4 and m3. In *N. hemicingulus* (figs. 8C, 9C) ectocingulids are reduced still further, which is especially noticeable on m1 and m2. For example, although the mesiobuccal portion of the ectocingulid on these teeth is very similar to the condition in *N. micrus*, the tiny distal portion is barely discernible.

Cranial and mandibular measurements for most species of *Nesophontes* are presented in tables 1 and 2. Four nonoverlapping size groups are represented. As expected, the Hispaniolan species *N. zamicrus* is much smaller than any other nominal species in the genus, whereas *N. edithae* from Puerto Rico is substantially larger than any of its congeners. Other species fall between these extremes. Within *N. hemicingulus*, specimens from Cayman Brac are ~10% smaller than comparable fossils from Grand Cayman (table 1). The Cayman Brac population is slightly larger than *N. hypomicrus*, and closest in size to individuals formerly grouped as *N. submicrus*. The Grand Cayman sample is most similar in size to the original hypodigm of *N. micrus* (before the addition of synonymized taxa).

In summary, *N. hemicingulus* displays extremely close similarities to *N. micrus* in tooth shape and dimensions, but differs in its unique combination of cingulum/cingulid architecture (cf. Morgan, 1994a). These include the absence of the precingulum on all molars, attenuation of the M1 and M2 postcingula, and

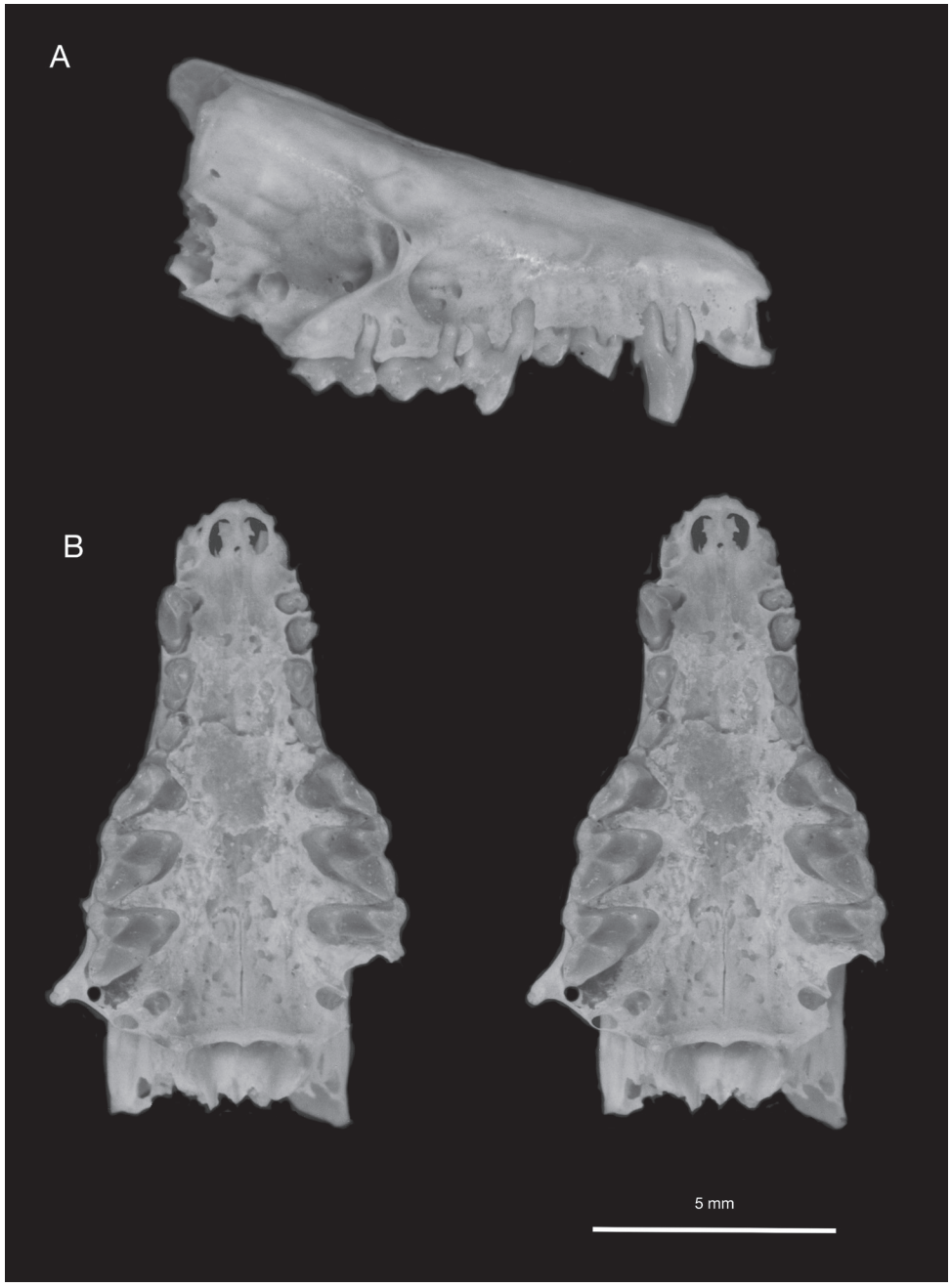


FIG. 4. Skull, *Nesophontes hemicingulus* UF 172939 (Dolphin Cave, Grand Cayman): **A,** right lateral; **B,** occlusal (stereopair). M3 missing on both sides; left M2 fractured.

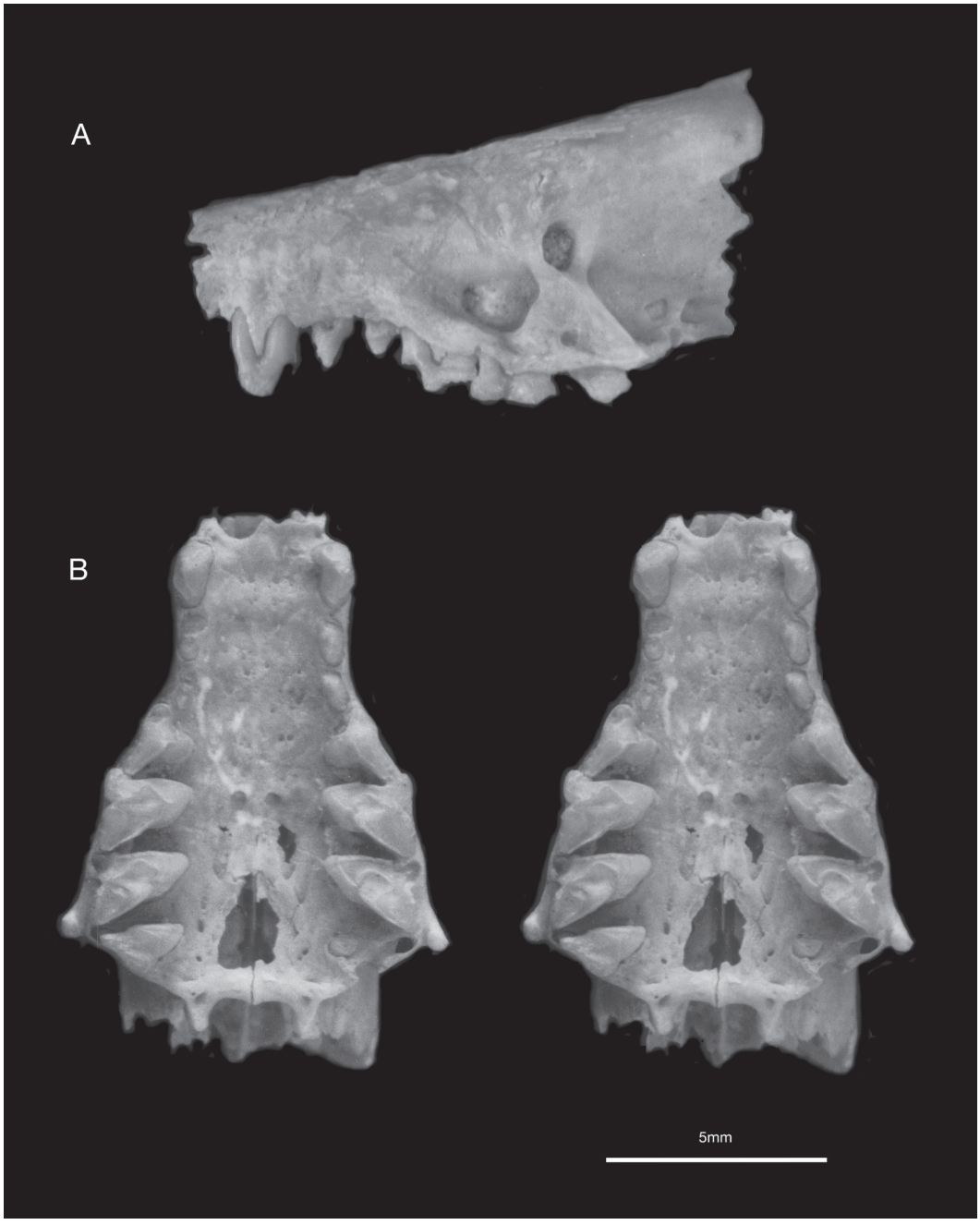


FIG. 5. Skull, *Nesophontes hemicingulus* UF 23296 (Patton's Fissure, Cayman Brac): **A,** left lateral; **B,** occlusal (stereopair). Teeth heavily worn; left M3 missing.

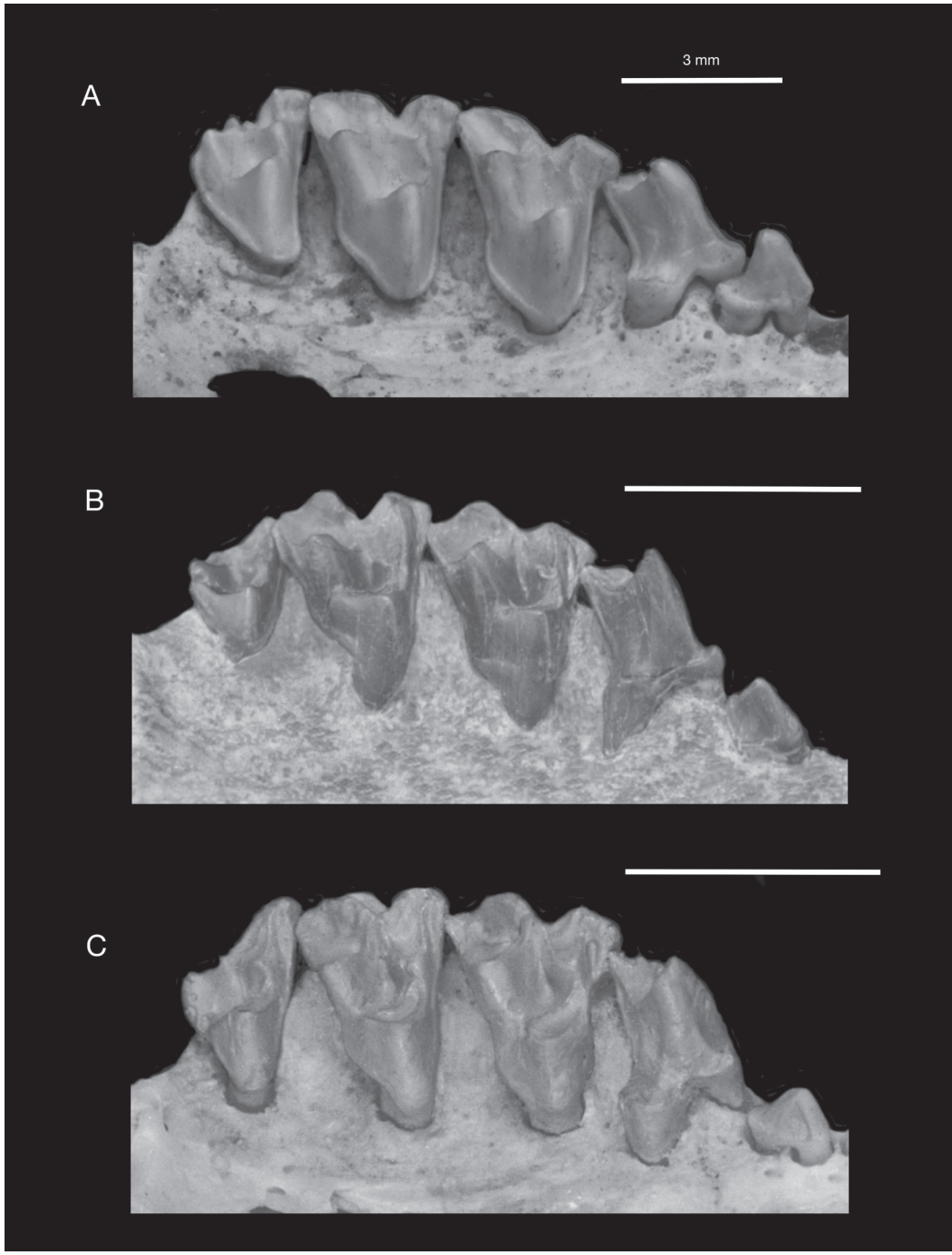


FIG. 6. Maxillary cheekteeth comparison, oblique lingual view: **A,** *Nesophontes edithae* AMNH 17109 (Cueva Catedral, Morovis, Puerto Rico); **B,** *N. micrus* (= *N. longirostris*) AMNH 17626 (Cave near Daiquiri, Cuba); **C,** *N. hemicingulus* UF 23295, holotype (Patton's Fissure, Cayman Brac).

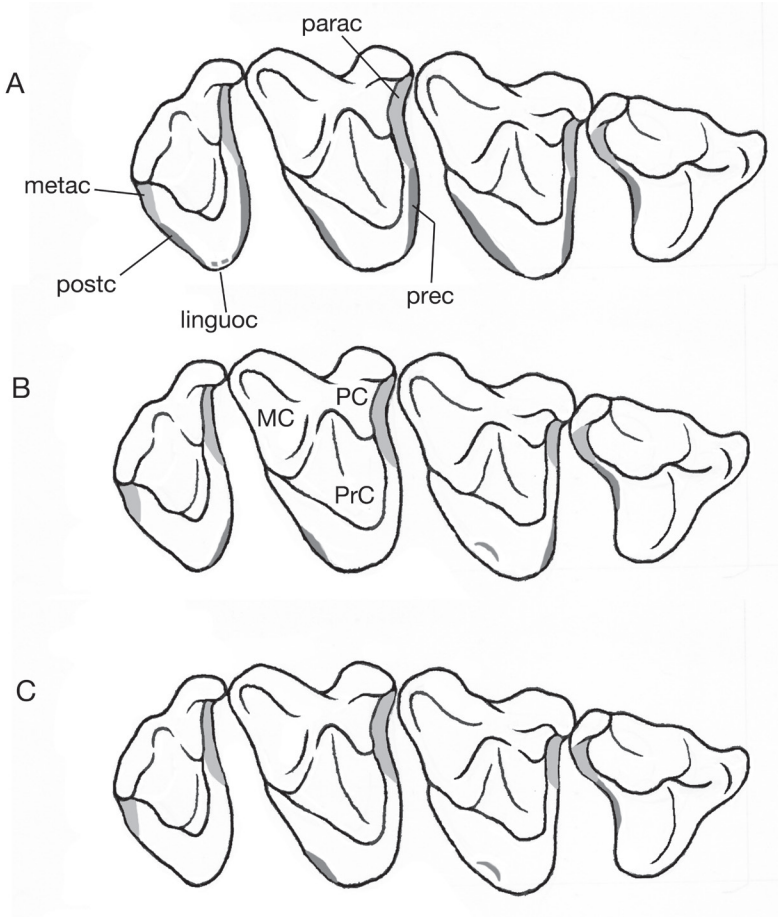


FIG. 7. Diagrammatic presentation of species variation in pre- and postcingula, based on various specimens: **A,** *Nesophontes edithae*; **B,** *N. micrus*; **C,** *N. hemicingulus*. In A, pre- and postcingula are developed on all molars; third molar occasionally expresses a lingual cingulum. In B, precingulum is absent on M2, postcingulum strongly reduced on M2 and absent on M3. In C, precingulum absent on all molars, postcingulum strongly reduced on M2 and absent on M3.

a somewhat greater reduction of ectocingulids on the lower cheekteeth. Because the Cayman and Cuban species are so similar in terms of overall craniodental measurements, such differences as do exist are unlikely to be size related. Sexual dimorphism in the expression of cingulum/cingulid features cannot be rejected, given the small sample sizes available for study, although this too seems unlikely, and supposed sex-related differences have been discounted in other species of *Nesophontes* (McFarlane, 1999).

Remarks: In his previous published assessment of the Cayman Quaternary fossil mammal fauna, Morgan (1994a) proposed that nesophontid populations on Cayman Brac and Grand Cayman should be interpreted as two distinct species on the basis of slight size variation (cf. palatal width difference, figs. 4B and 5B). While biogeographically this makes sense, given the distance between islands, the populations appear to be essentially identical morphologically for features such as molar dimensions. Furthermore, the size range seen within the revised species hypodigm of

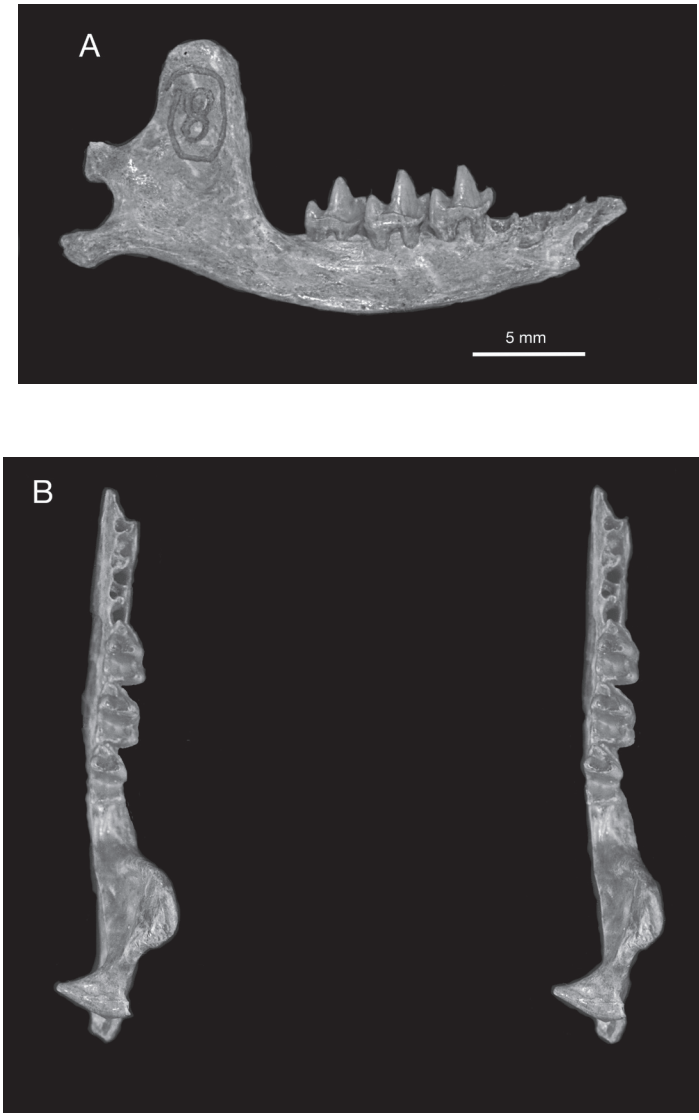
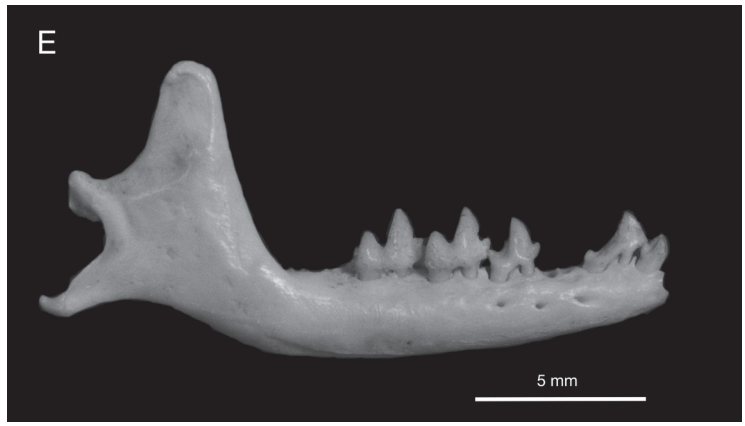


FIG. 8. Mandibular cheekteeth comparison, buccal and occlusal views (above and on successive pages): **A, B,** *Nesophontes edithae* AMNH 55005 (Cueva Catedral, Morovis, Puerto Rico); **C, D,** *N. micrus* AMNH 95708 (Cueva de los Macha [sic], Soledad, Cuba); **E, F,** *N. hemicingulus* UF 23252 (Patton's Fissure, Cayman Brac).


C
5 mm


D


E
5 mm


F

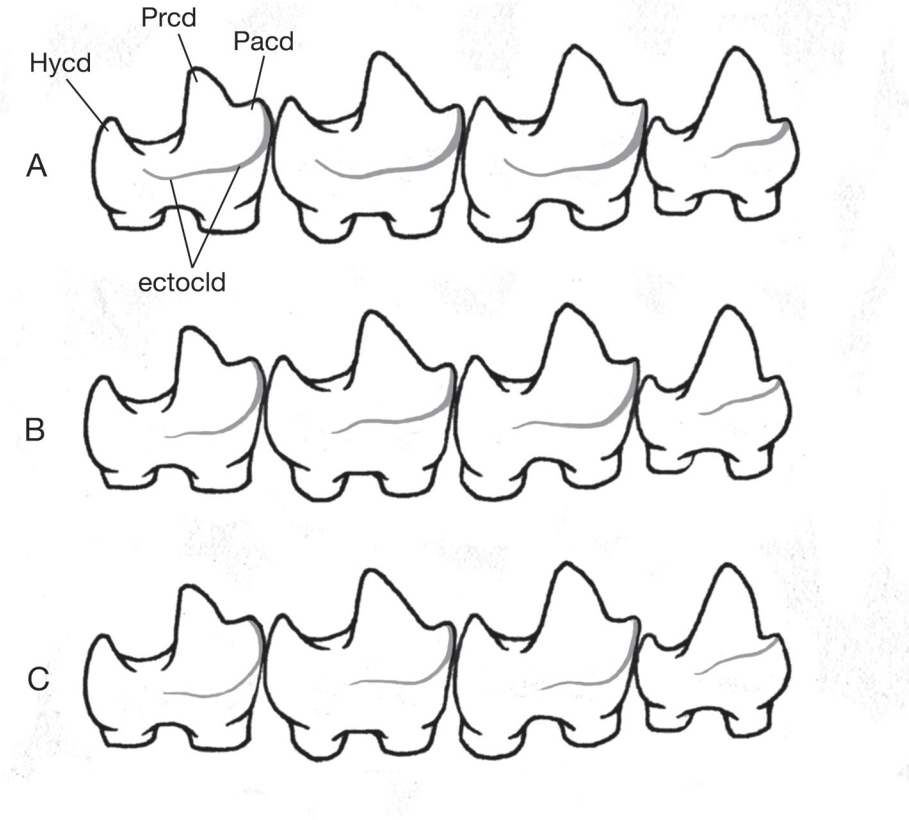


FIG. 9. Diagrammatic presentation of species variation in ectocingulid definition, based on various specimens: **A,** *Nesophontes edithae*; **B,** *N. micrus*; **C,** *N. hemicingulus*.

N. micrus (based on the revision of Condis Fernández et al., 2005) incorporates the range of variation seen in the individual island samples of *N. hemicingulus*. Assuming that Condis Fernández et al. (2005) were correct in subsuming *N. submicrus* within *N. micrus* and interpreting the small-to-medium size cluster of Cuban *Nesophontes* as a single species, recognition of intraspecific size variation within Cuban *Nesophontes* therefore challenges the idea that, based on slight size differences alone, populations on Cayman Brac and Grand Cayman represent distinct species.

Although biogeographical considerations are certainly relevant in this case, we hesitate to formally name subspecies for populations that cannot be distinguished by reference to any synapomorphies. Slight size differences are unhelpful in this regard, because size has no bearing on how to recognize evolutionary relationships among species of *Nesophontes*, in which body size was probably closely tied to variable ecological parameters, such as availability of food, competition, habitat diversity, and island size (cf. McFarlane, 1999). For example, the sympatric presence of *Solenodon* on Cuba and Hispaniola may have controlled the maximum size attainable by nesophontids (Morgan et al., 1980; Morgan and Ottenwalder, 1993), and it is probably no coincidence that the largest species of *Nesophontes*, *N. edithae*, lived on *Solenodon*-free Puerto Rico. Further assessment of the taxonomic status of the two allopatric Cayman *Nesophontes* popula-

TABLE 1
Comparative measurements (in mm) of skull and upper dentition of *Nesophontes hemicingulus* from Cayman Brac and selected species of *Nesophontes* from Cuba, Hispaniola, and Puerto Rico. Abbreviations: **M,** mean; **R,** range; and ***N*,** sample size.

Species		Upper toothrow length	Crown length of M1–M3	Palate length	Palate breadth at P4	Palate breadth at M3	Rostrum breadth at canines	Minimum interorbital breadth
N. hemicingulus (Cayman Brac)	M	10.7	4.9	11.7	6.8	9.4	4.2	6.4
	R	10.4–11.1	4.8–5.0	11.4–12.1	6.3–7.1	8.6–10.0	3.7–4.6	6.0–6.5
	N	16	6	8	17	12	18	9
N. micrus (Cuba)	M	11.4	5.3	12.1	7.6	10.9	4.9	7.2
	R	10.7–12.4	5.2–5.6	11.4–13.4	7.2–8.3	9.9–11.8	4.3–5.7	6.3–7.8
	N	10	5	4	12	11	10	11
N. paramicrus (Hispaniola)	M	12.1	5.7	13.0	7.5	11.0	4.5	7.4
	R	11.9–12.5	5.4–6.0	12.8–13.4	7.1–8.1	10.6–11.6	4.2–4.8	7.1–7.7
	N	6	4	4	5	5	5	4
N. hypomicrus (Hispaniola)	M	9.9	4.5	10.7	6.1	8.9	3.9	6.0
	R	9.6–11.0	4.3–4.7	10.3–11.5	5.8–6.5	8.8–9.1	3.5–4.1	5.6–.6.2
	N	13	8	7	8	5	10	7
N. edithae (Puerto Rico)	M	—	—	17.1	—	—	6.8	9.4
	R	—	—	15.4–18.9	—	—	5.7–8.1	8.5–10.3
	N	—	—	10	—	—	17	17

tions requires additional data, ideally derived from analysis of ancient DNA or other ancient biomolecules if Quaternary material can be found that is sufficiently well preserved. For the present, we interpret the two allopatric Cayman *Nesophontes* populations as conspecific.

Order Rodentia Bowdich, 1821

Family Capromyidae Smith, 1842

Subfamily Capromyinae Smith, 1842

Remarks: The Capromyidae is a diverse group of rodents of fairly large body size (~0.5–4 kg) endemic to the West Indies. Capromyids are most closely related to the Echimyidae (spiny rats) and Myocastoridae (coypu) among mainland Neotropical hystricognath rodents. These three families have been referred to the hystricognath superfamily Octodontoidea, which also includes the southern South American families Abrocomidae, Ctenomyidae, and Octodontidae (Woods and Kilpatrick, 2005). Molecular analysis by Leite and Patton (2002) suggested placement of the Capromyidae as a subfamily (Capromyinae) within the Echimyidae, although these authors sampled only a single species of capromyid, *Capromys pilorides*. More recent molecular phylogenies, which have included all extant genera of capromyids, have reached different conclusions over whether the Capromyidae could be distinguished as a family separate from the Echimyidae and Myocastoridae (Kilpatrick et al., 2012; Fabre et al., 2014, 2017). Pending further molecular analyses, we tentatively recognize the Capromyidae as an endemic West Indian family, with close phylogenetic relationships to both the Echimyidae and Myocastoridae.

Current taxonomy recognizes five extant genera in the Capromyidae, separated into two subfamilies: *Plagiodontia* (Hispaniola) in the subfamily Plagiodontinae; and *Capromys*, *Mesocapromys*, and *Mysateles* (Cuba) and *Geo-*

TABLE 2
Comparative measurements (in mm) of the mandible and lower dentition of *Nesophontes hemicingulus* from Cayman Brac and Grand Cayman, and selected species of *Nesophontes* from Cuba, Hispaniola, and Puerto Rico. Abbreviations: **M,** mean; **R,** range; and ***N*,** sample size.

Species		Mandible length	Mandibular toothrow length	Crown length of m1–m3	Depth of horizontal ramus	Height of coronoid process
N. hemicingulus (Cayman Brac)	M	18.3	10.6	5.7	2.6	6.8
	R	17.2–19.7	9.9–11.3	5.5–5.9	2.3–2.9	6.3–7.4
	N	16	48	44	87	64
N. hemicingulus (Grand Cayman)	M	—	11.9	6.4	2.9	7.5
	R	—	11.5–12.4	6.1–6.8	2.6–3.3	7.0–8.4
	N	—	3	5	8	4
N. micrus (Pinar del Rio, Cuba)	M	20.6	11.7	6.2	3.2	7.8
	R	19.6–21.8	11.2–12.5	6.0–6.5	2.8–4.0	7.0–8.8
	N	5	5	7	15	13
N. micrus (Oriente, Cuba)	M	20.7	—	—	3.1	8.0
	R	19.6–22.2	—	—	2.6–3.6	7.3–8.9
	N	35	—	—	35	34
N. paramicrus (Hispaniola)	M	20.4	11.9	6.5	3.0	7.8
	R	19.6–21.9	11.3–12.4	6.1–6.9	2.4–3.6	6.8–8.7
	N	10	21	25	37	33
N. hypomicrus (Hispaniola)	M	17.0	9.8	5.3	2.3	6.3
	R	16.1–18.4	9.0–10.4	4.8–5.6	2.0–2.7	5.5–6.9
	N	23	42	47	58	52
N. zamicrus (Hispaniola)	M	13.8	7.9	4.4	1.6	4.5
	R	13.6–14.0	7.6–8.0	4.3–4.5	1.5–1.8	4.2–4.7
	N	2	5	3	5	5
N. edithae (Puerto Rico)	M	27.4	—	—	4.0	10.6
	R	24.5–33.8	—	—	3.0–5.2	9.1–13.3
	N	15	—	—	15	15

capromys (Jamaica, Bahamas) in the subfamily Capromyinae (Morgan, 1985; Woods and Kilpatrick, 2005; Silva Taboada et al., 2007; Borroto-Páez et al., 2012; Dávalos and Turvey, 2012). A recently extinct species of *Geocapromys* is known from Little Swan Island in the western Caribbean, and the Capromyidae also has an extensive late Quaternary history in the Greater Antilles and Bahamas as well as the Cayman Islands. In addition to material from the Cayman Islands described here, the capromyine Quaternary fossil record includes *Capromys*, *Geocapromys*, *Mesocapromys*, and *Mysateles* from Cuba, and *Geocapromys* from Jamaica and many Bahamian islands where this genus no longer occurs (Morgan, 1985, 1989b, 1994a; Silva Taboada et al., 2007; Borroto-Páez et al., 2012; Dávalos and Turvey, 2012). The Quaternary record also documents several extinct capromyids from Hispaniola, divided among three subfamilies: two additional species in the extant genus *Plagiodontia*, and additional

species in the extinct genera *Hyperplagiodontia* and *Rhizoplagiodontia* in the Plagiodontinae; and two other extinct genera, each referred to an extinct subfamily, *Hexolobodon* (Hexolobodontinae) and *Isolobodon* (Isolobodontinae) (Woods and Kilpatrick, 2005; Borroto-Páez et al., 2012; Dávalos and Turvey, 2012; Hansford et al., 2012). *Isolobodon* was originally described from Puerto Rico (*I. portoricensis*) but occurs there and on Vieques and the Virgin Islands only in archaeological sites, apparently because it was translocated from Hispaniola by Amerindian peoples. Quaternary fossil sites from Puerto Rico lack native capromyids but instead contain the large hystricognath *Elasmodontomys*, which has been referred to the Heptaxodontidae ("giant hutias"). Other heptaxodontids are also known in the Greater Antilles from Hispaniola and Jamaica, where they cooccurred with capromyids (Woods and Kilpatrick, 2005; MacPhee, 2011). The presence of an early Miocene capromyid from Cuba, the extinct genus *Zazamys* from the Domo de Zaza fauna, establishes a long history of this family in the Greater Antilles (MacPhee and Iturralde-Vinent, 1995).

The genus *Capromys* has received considerable attention in the past few decades, much of which has focused on the description of new species, both living and extinct. Until the mid 1970s, almost all Cuban species in the family Capromyidae were referred to *Capromys* (Varona, 1974). During the 1970s, a proliferation of new generic and subgeneric names was proposed for Cuban capromyids formerly included in *Capromys* (e.g., Kratochvil et al., 1978; Varona and Arredondo, 1979). The systematic review by Silva Taboada et al. (2007) synonymized many of the previously described genera, subgenera, and species of Cuban capromyids, and recognized five genera of Capromyidae in Cuba, *Capromys*, *Geocapromys*, *Macrocapromys*, *Mesocapromys*, and *Mysateles*, one of which (the extinct genus *Macrocapromys*) has since been synonymized with *Capromys* (Borroto-Páez et al., 2012). The Quaternary and extant Cuban Capromyidae includes four genera and 11 described species (although see further discussion below): three species of *Capromys* (one living, *C. pilorides*, and two extinct, *C. acevedo* and *C. latus*); one extinct species of *Geocapromys* (*G. columbianus*); six species of *Mesocapromys* (five living, *M. angelcabrerai*, *M. auritus*, *M. melanurus*, *M. nanus*, and *M. sanfelipensis*, and one extinct, *M. kraglievichi*); and one living species of *Mysateles* (*M. prehensilis*).

Capromys Desmarest, 1822

Capromys pilorides (Say, 1822)

***Capromys pilorides lewisi*,** new subspecies

Figures 10–12, 14–17

Holotype: NHM (Mammalogy) 71.1558/M15705, complete skull with left M1 and right PM4–M3 (figs. 10A, 12A).

Type Locality: Stake Bay Cave, 0.25 miles west of Stake Bay, Cayman Brac.

Etymology: Named in honor of the late C. Bernard Lewis, former curator and director of the Institute of Jamaica and a member of the 1938 Oxford University Cayman Islands Biological Expedition, who collected the holotype skull of this new subspecies.

Age: Late Pleistocene-Holocene (see Radiocarbon Dating).

Distribution: Known only from Cayman Brac, Little Cayman, and Grand Cayman. The only representative of the genus *Capromys* known outside Cuba and its satellite islands.

Referred Specimens: **Cayman Brac:** Stake Bay Cave: NHM (Mammalogy) 71.1558/M15704, NHM (Palaeontology) M15733, M15734, M42027, M42028, skulls; UF 61291, nearly complete skull lacking nasals and right jugal, with left M1 and right M1–M2, and associated mandibles; NHM (Mammalogy) 71.1558/M15706, 71.1558/M15707, 71.1558/unnumbered, NHM (Palaeontology) M15735, M15736, M15737, M15738, M15739, M15740, M42029, mandibles. Blackie's Cave: UF 172782, partial skull. Fig Tree Cave: UF 172759, 172760, edentulous mandibles. Hutia Cave: UF 172751,

nearly complete edentulous skull lacking jugals, with associated edentulous mandibles, innominates, and tibia; UF 172752, 172753, 172758, partial skulls; UF 172755, 172763, edentulous mandibles. Patton's Fissure: UF 18763, 21406, partial skulls; UF 21405, palate; UF 18647, 18650, 21385, mandibles with p4–m3; UF 18557, 18617, mandibles with p4–m2; UF 21395, mandible with p4; UF 21385, 22850, mandibles with m1–m3; UF 18542, 18588, 18597, 18618, 18619, 18670, 18671, 21351, 21355, 21395, 22853, edentulous mandibles. Peter Cave: UF 22855, partial skull; UF 61291, nearly complete skull with right M1–M2 and left M1; UF 22854, edentulous mandible. Pollard Bay Cave: UF 22886, palate; UF 18557, mandible with i, p4–m2. Shearwater Cave 2: UF 172792, 2 cervical vertebrae. Spot Bay Cave: UF 172764, skull; UF 172767, mandible with p4–m3; UF 172766, mandible with m2. **Grand Cayman:** Agouti Cave: UF 172870, partial skull; UF 172871, mandible with p4–m3; UF 172872, mandible with p4–m2; UF 172875, mandible with i, m2–m3; UF 172873, 172874, 172876–172882, edentulous mandibles. Barn Owl Cave: UF 22875, 22877, 22878, palates; UF 22872, mandible with p4–m3; UF 22871, mandible with p4–m2; UF 22876, mandible with p4–m1; UF 22873, 22874, 22879, edentulous mandibles. Big Ear Cave: UF 162850, mandible with i1, m1. Chisholm Cow Well: UF 172821, premaxilla with I1; 172820, mandible with p4; UF 172836, edentulous mandible. Crab Cave: UF 22865, maxilla with P4; UF 22858, mandible with p4–m3; UF 22857, 22860, 22862, 22863, edentulous mandibles. Crocodile Canal: UF 61147, i1; UF 61149, 61150, 61154, femora. Dolphin Cave: UF 172920, nearly complete skull with left and right M1; UF 172921, edentulous partial skull; UF 172911, 172912, 172848, 172862, 172927–172929, 411275–411277, edentulous mandibles. Furtherland Farms Cow Well: UF 172798, 172799, humeri; UF 172801, 172802, 172814, innominates; UF 172800, 172815, tibia. Miller's Cave: UF 172089, partial skull; UF 172890, maxilla with P4–M1; UF 172896, mandible with i1, p4, m3; UF 172897, mandible with p4–m2; UF 172898, mandible with p4–m1; UF 172891, mandible with m1–m2; UF 172892–172895, 172899–172902, edentulous mandibles. Old Man Cave: UF 22880, nearly complete skull lacking left premaxilla, portion of left maxilla, both jugals, and all teeth; UF 22881, mandible with p4, m2. Queen Elizabeth II Botanic Park: UF 172947, mandible with p4–m3. Tadarida Cave: UF 61293, partial skull; UF 172837, mandible with m2; UF 172840, mandible with i1. **Little Cayman**: Agave Cave: UF 172794, humerus; UF 172793, femur. Franz's Shelter: UF 172795, edentulous maxilla; UF 172796, 172797, edentulous mandibles. Weary Hill Cave: UF Environmental Archaeology Collection (uncat.), edentulous mandible. [This list of Referred Material does not include all *Capromys* fossils from the Cayman Islands, only the most complete cranial and mandibular specimens. Postcranial specimens are listed if they represent the only records of *Capromys* from a particular site. There is also a large sample of isolated teeth and postcranial elements not listed here.]

Diagnosis: Differs from all described Cuban subspecies of *Capromys pilorides* in: smaller overall size; shorter maxillary and mandibular toothrows, resulting from smaller, lower-crowned cheekteeth with reduced amount of cement on anterior and posterior edges; maxillary toothrows strongly convergent anteriorly and nearly parallel from the anterior margin of P4 to the border between M1 and M2; narrow, anteriorly directed dorsal maxillary process; smaller orbit (about half the height of infraorbital foramen), owing to strong inflation of frontals posteriorly between orbits and parietal suture (frontals greater in height than parietals), and deeper zygomatic arch ventral to orbit; more constricted internal narial opening, which is rounded rather than triangular in ventral outline; shorter and less inflated auditory bullae; and shorter mandibular symphysis with reduced posterior margin.

Description: One of the most characteristic features of the Cayman *Capromys* is the com-

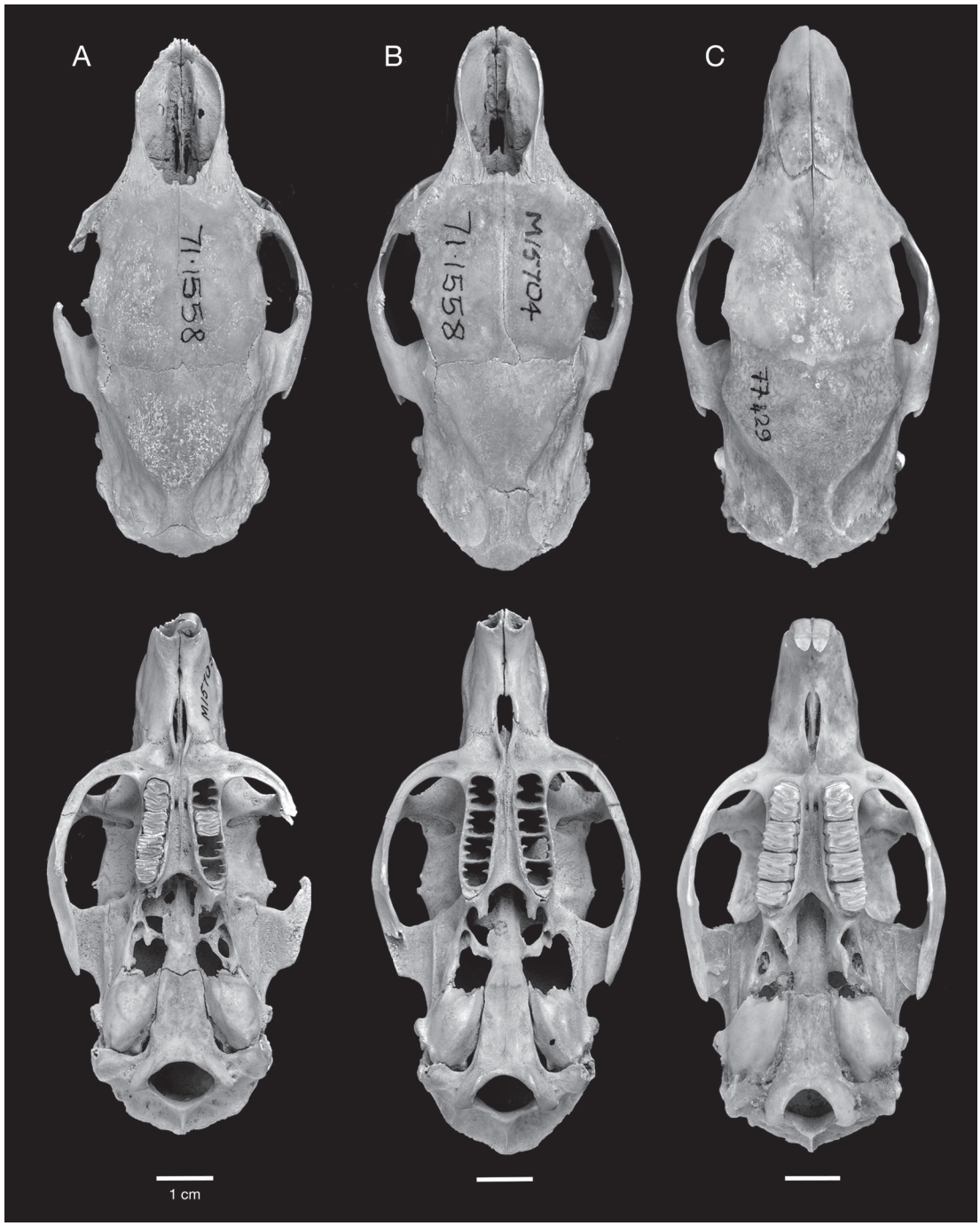


FIG. 10. *Capromys pilorides* skulls in dorsal and ventral view. **A,** *Capromys pilorides lewisi*, n. subsp., holotype, NHM (Mammalogy) 71.1558/M15705 (Stake Bay Cave, Cayman Brac); **B,** *Capromys pilorides lewisi* NHM (Mammalogy) 71.1558/M15704 (Stake Bay Cave, Cayman Brac); **C,** *Capromys pilorides pilorides* NHM (Mammalogy) 77.429 (Cuba).

FIG. 11. *Capromys pilorides lewisi* skulls in dorsal and ventral view. **A,** UF 172920 (Dolphin Cave, Grand Cayman); **B,** UF 22880 (Old Man Cave, Grand Cayman).

FIG. 12. *Capromys pilorides lewisi* skulls in lateral view. **A,** holotype, NHM (Mammalogy) 71.1558/M15705 (Stake Bay Cave, Cayman Brac); **B,** NHM (Mammalogy) 71.1558/M15704 (Stake Bay Cave, Cayman Brac); **C,** UF 22880 (Old Man Cave, Grand Cayman); **D,** UF 172920 (Dolphin Cave, Grand Cayman).

FIG. 13. *Capromys pilorides pilorides* skulls from Cuba in lateral view, showing variation in inflation of posterior frontals. **A,** NHM (Mammalogy) 742.a/555.4.286; **B,** NHM (Mammalogy) 77.429.

paratively short maxillary toothrows relative to the total length of the skull. The mandibular toothrows are also correspondingly short. The mean alveolar lengths of the upper toothrows and lower toothrows are very similar (tables 3, 4). Although the majority of partial skulls, isolated maxillae, and mandibles are edentulous, there are specimens that preserve partial or complete upper and lower dentitions (figs. 10–11, 16–17). In these specimens, the teeth are somewhat compressed anteroposteriorly, and they have a comparatively thin layer of cement on the anterior and posterior margins of the individual teeth. We were only able to take dental measurements of the upper cheekteeth (P4 and M1–M3) on a few specimens, including the holotype, but were able to measure a larger sample of lower cheekteeth (tables 3, 4).

The upper toothrows are strongly convergent anteriorly, with an average palatal width of only 3.3 mm opposite P4 (table 3). The convergence of the upper toothrows continues posteriorly to approximately the level of the border between M1 and M2, with the toothrows essentially parallel between P4 and M1. Posterior to M1, the toothrows begin to diverge laterally, reaching their greatest width at the posterior palatal margin. The convergence of the upper toothrows is also evident dorsal to the toothrows, as the internal narial opening is constricted both vertically and transversely, and is rounded rather than triangular in ventral outline. The root capsule for the incisor is barely visible on the external surface of the premaxilla and maxilla. The origin for the incisor root capsule is located immediately anterior to P4 and just dorsal to the maxillary

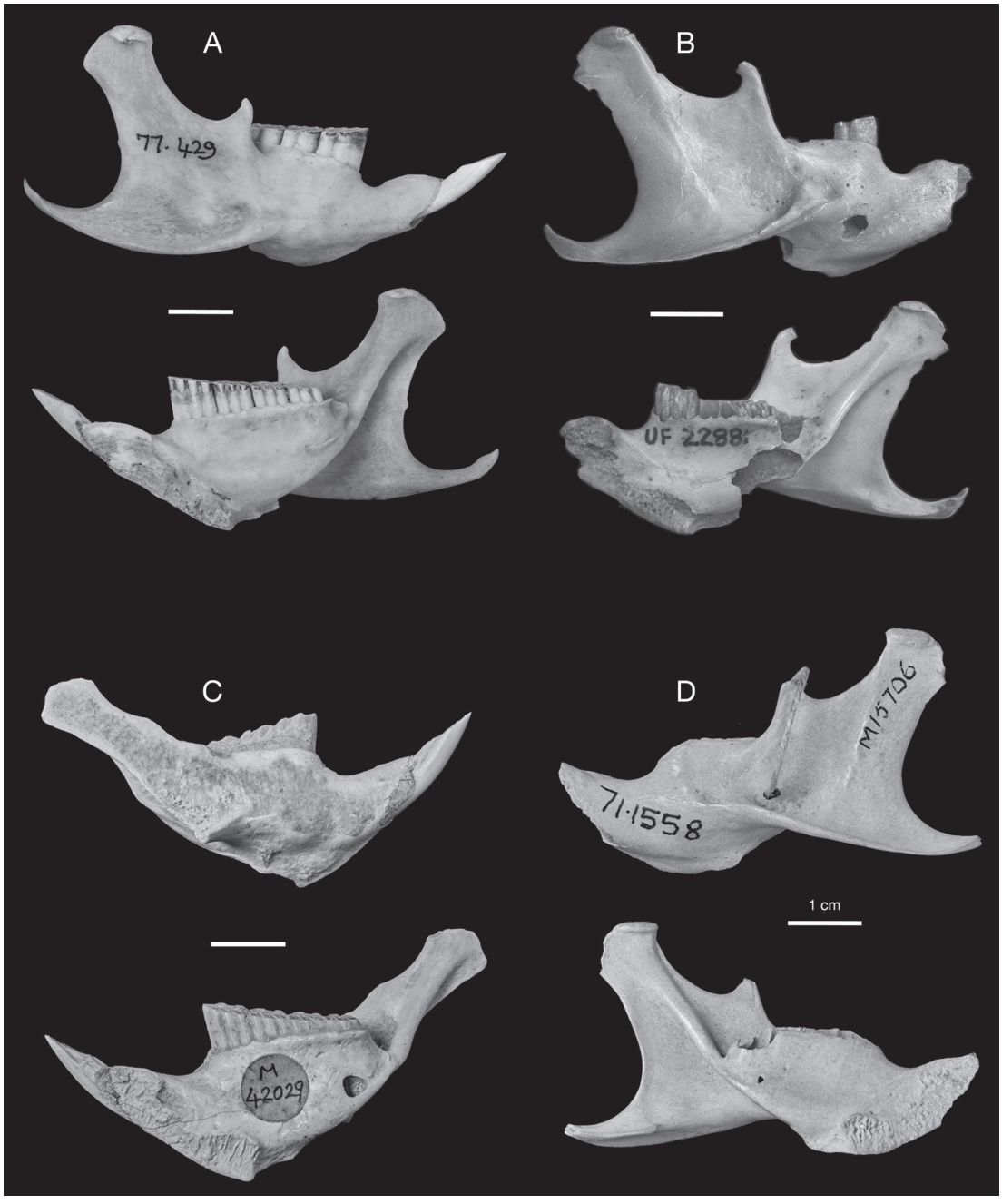


FIG. 14. *Capromys pilorides* hemimandibles in labial and lingual view. **A,** *Capromys pilorides pilorides* NHM (Mammalogy) 77.429 (Cuba); **B,** *Capromys pilorides lewisi* UF 22881 (Old Man Cave, Grand Cayman); **C,** *Capromys pilorides lewisi* NHM (Palaeontology) M42029 (Stake Bay Cave, Cayman Brac); **D,** *Capromys pilorides lewisi* NHM (Mammalogy) 71.1558/M15706 (Stake Bay Cave, Cayman Brac).

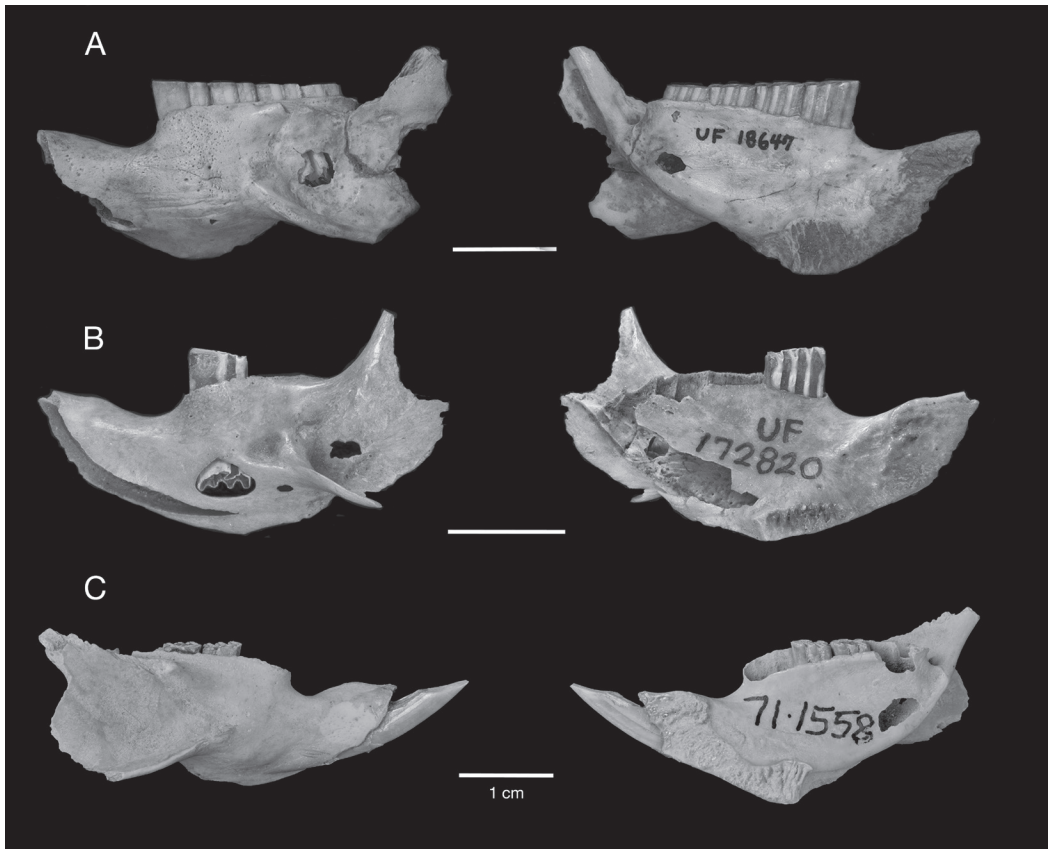


FIG. 15. *Capromys pilorides lewisi* hemimandibles in labial and lingual view. **A,** UF 18647 (Patton's Fissure, Cayman Brac); **B,** UF 172820 (Chisholm Cow Well, Grand Cayman) (image reversed); **C,** NHM (Mammalogy) 71.1558/unnumbered (Stake Bay Cave, Cayman Brac).

root of the zygomatic. The root capsules of all four cheekteeth are visible as external swellings on the maxilla.

The ascending or dorsal process of the maxilla is relatively thin and oriented noticeably anteriorly. The dorsoventral height of the infraorbital foramen is almost twice that of the orbit. The small size of the orbit compared to other *Capromys* is a result of both the deep zygomatic arch ventral to the orbit and the inflated frontals dorsal to the orbit. The zygomatic arch, composed primarily of the jugal and also the dorsal maxillary process anteriorly, is vertically deep. The jugal fossa is rather large and oriented at approximately 45° to the ventral margin of the zygomatic arch. A well-developed jugal spine projects posteroventrally from the jugal. The frontals are noticeably inflated, from the anterior edge of the orbits posteriorly to the frontoparietal suture (fig. 12). This inflation is also evident on the portion of the frontals that comprises the internal wall of the orbits, and is especially prominent ventral to the postorbital processes. Only the anterior third of the frontals is not inflated, between the anterior edge of the orbits and the nasofrontal suture. In lateral view, the frontal inflation is emphasized by noticeable depressions both anteriorly dorsal to the anterior edge of the orbits and posteriorly along the frontoparietal suture. Because of this inflation, the width of the frontals posterior to the postorbital processes is greater than their width anterior to these pro-

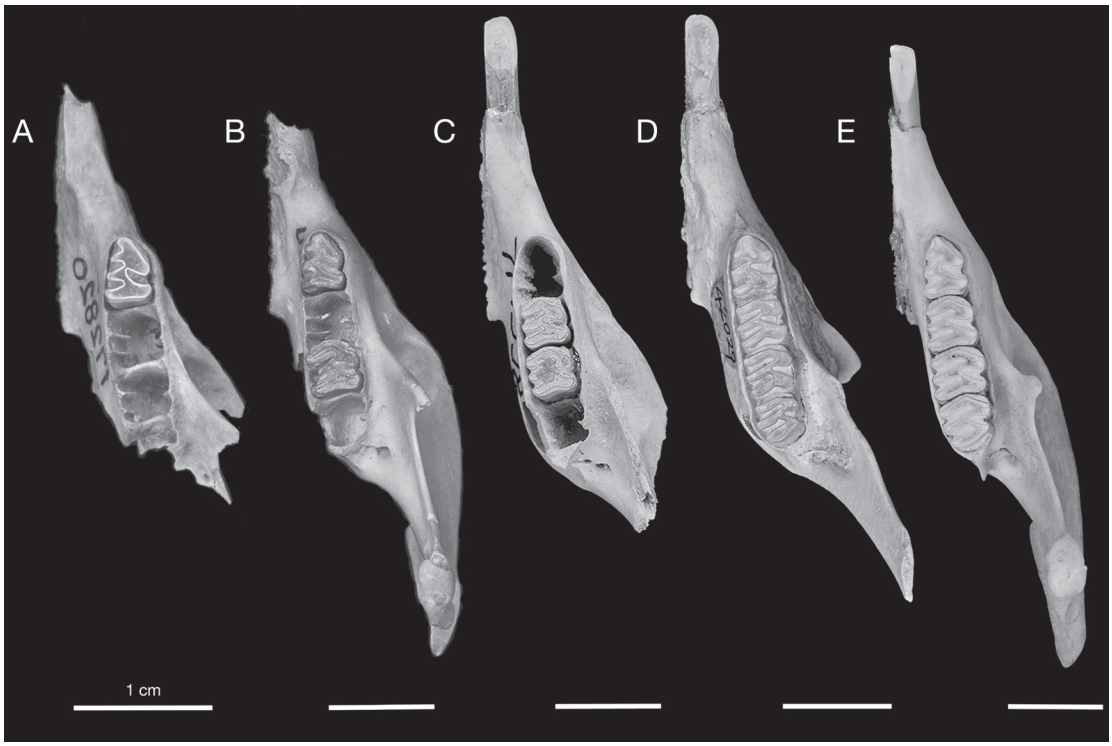


FIG. 16. *Capromys pilorides* hemimandibles in occlusal view. **A,** *Capromys pilorides lewisi* UF 172820 (Chisholm Cow Well, Grand Cayman) (image reversed); **B,** *Capromys pilorides lewisi* UF 22881 (Old Man Cave, Grand Cayman); **C,** *Capromys pilorides lewisi* NHM (Mammalogy) 71.1558/unnumbered (Stake Bay Cave, Cayman Brac); **D,** *Capromys pilorides lewisi* NHM (Palaeontology) M42029 (Stake Bay Cave, Cayman Brac); **E,** *Capromys pilorides pilorides* NHM (Mammalogy) 77.429 (Cuba).

cesses (table 3). The temporal crests are well defined and nearly meet posteriorly along the midline of the skull, although they do not form a sagittal crest. The auditory bullae are comparatively short anteroposteriorly, giving them a somewhat circular to elliptical outline. The bullae are not inflated.

The posterior margin of the m3 alveolus in the mandible is oriented at a slight angle to the long axis of the toothrow. The mandibular symphysis is quite broad and well developed, but is truncated posteriorly with a reduced posterior margin. A thin ridge of bone extends posteriorly along the ventral margin of the mandible from the symphysis to approximately the level of m1 or m2. In side view, this thin elongate ridge gives the mandible the appearance of being deeper vertically. The mandible is relatively deep below the cheekteeth, indicating that the cheekteeth are quite hypsodont. The condyloid process is wide at its base, and the area for insertion of the masseter on the labial portion of the ramus ventral to the condyloid process is expanded in area, especially vertically.

The upper incisors are relatively broad and highly arched. As with most other capromyids, the cheekteeth are rootless and ever growing, but are relatively small compared to other *Capromys*. The p4 is longer and narrower than the other cheekteeth, and has a rounded anterior margin. The nature of the enamel band along the anterior lingual margin is quite variable: some specimens have no trace of a third reentrant in the anterior position, while other specimens have a notice-

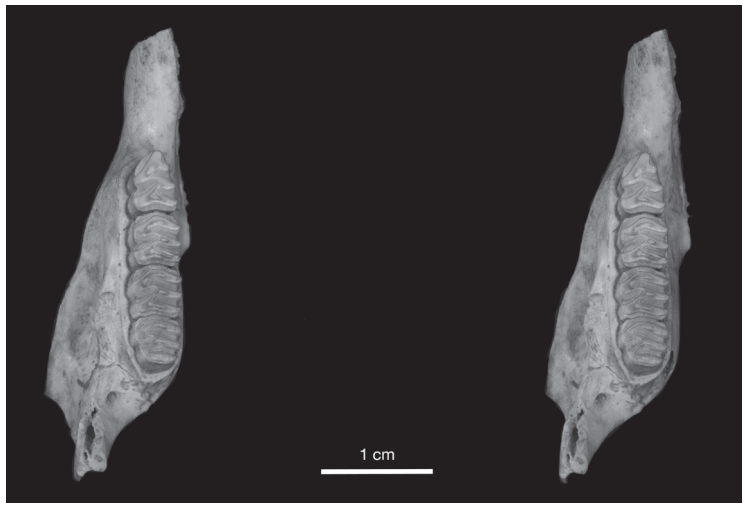


FIG. 17. *Capromys pilorides lewisi* UF 18647 (Patton's Fissure, Cayman Brac), left hemimandible in occlusal view (stereopair).

able infolding of the enamel band along the anterior margin of p4, and the average condition is a slight, medially directed infolding of the enamel band along the anterior lingual margin of p4. If this anterior infolding of the enamel band is not considered a true reentrant, then there are only two lingual reentrants on p4. The anterior lingual reentrant is the best developed of the two lingual reentrants. This anterior reentrant extends medially well beyond the median long axis of the tooth, and is anterior in position with respect to the single labial reentrant. The posterior reentrant is less well developed than the anterior reentrant, and does not extend medially past the median long axis of p4. The m3 is oriented at a slight angle to the other cheekteeth in the mandible, such that in an edentulous mandible the posterior margin of the m3 alveolus is also oriented at a slight angle to the long axis of the toothrow as opposed to the other three cheekteeth, which are perpendicular to this axis. The occlusal surfaces of the upper and lower dentition are flat and horizontal.

Morphometrics: The new subspecies displays some overlap in the observed range of most cranial measurements seen in a sample of 14 modern skulls of Cuban *Capromys pilorides pilorides* (tables 3, 4). The Cuban sample has a total skull length ranging from 85–106 mm (mean = 95 mm), whereas six complete or semicomplete skulls of *C. pilorides lewisi* range from 88–96 mm in total length (mean = 92 mm). However, there is no overlap in the alveolar length of the upper toothrows between these two samples (*C. pilorides pilorides*: 21–24 mm, mean = 22 mm; *C. pilorides lewisi*: 18–20 mm, mean = 19 mm).

The largest available measurement series for the Cayman *Capromys* sample is mandibular alveolar toothrow length (Grand Cayman, n = 29; Cayman Brac, n = 13; Little Cayman, n = 2). Too few specimens are available from Little Cayman to permit statistical morphometric comparison with the other islands, but comparison between the Grand Cayman and Cayman Brac measurement series shows no statistically detectable size difference between samples from these two islands (Welch two-sample t-test not assuming equal variance: Grand Cayman, mean = 19.81 mm; Cayman Brac, mean = 19.33 mm; p = 0.240). The entire available Cayman *Capromys* sample (mean = 19.70 mm) can therefore be pooled for analysis with Cuban *Capromys* samples.

TABLE 3
Comparative measurements (in mm) of the skull and upper dentition of *Capromys pilorides lewisi* from the Cayman Islands (combined data for Grand Cayman and Cayman Brac), and *Capromys pilorides pilorides* from mainland Cuba. Abbreviations: **M,** mean; **R,** range; and ***N,*** sample size.

Subspecies		Upper toothrow length (alveolar)	Upper incisor length	Upper incisor width	Palate width (anterior to P4)	Palate width (betw. P4 and M1)	Palate width (betw. M1 and M2)	Palate width (betw. M2 and M3)	Skull length	Upper diastema length	Width of frontals (ant. to supraorbital process)	Width of frontals (post. to supraorbital process)
lewisi	M	19.0	3.8	3.1	3.3	3.3	4.2	5.8	92.3	23.5	27.7	28.9
	R	18.0–20.2	3.5–4.3	2.8–3.5	2.8–3.8	2.6–3.9	3.5–4.8	5.5–6.0	88.3–95.7	23.4–23.6	26.6–28.8	28.2–29.6
	N	6	33	33	7	7	6	5	6	2	2	2
pilorides	M	21.9	3.7	3.4	3.9	4.3	5.2	6.6	95.2	25.7	26.5	25.4
	R	20.4–23.7	3.3–4.1	2.9–3.8	3.1–4.6	3.5–4.8	4.4–5.9	5.8–7.8	84.8–105.8	23.0–29.3	23.8–29.8	22.9–28.8
	N	13	11	13	13	13	13	13	13	13	13	13

The pooled Cayman *Capromys* sample has a significantly smaller mandibular alveolar toothrow length compared to a sample of *C. pilorides pilorides* from mainland Cuba measured from museum collections (n = 39; mean = 21.56 mm; p <0.001; appendix 2), to measurement data for the type series of *C. pilorides doceleguas* reported in Varona (1980) (n = 7; mean = 23.23 mm; p <0.001), and to measurement data for mandibular toothrow length (likely to be very close to alveolar toothrow length) for the type series of *C. pilorides gundlachianus* reported in Varona (1983) (n = 6; mean = 21.80 mm; p = 0.001). These represent the only unpooled measurement series available for direct statistical comparison with our Cayman *Capromys* sample. Borroto Páez et al. (1992) provided pooled measurement series and summary statistics for mandibular alveolar toothrow length for the other two described subspecies of *C. pilorides*, *C. pilorides relictus* (n = 18; mean = 22.30 mm) and *C. pilorides ciprianoi* (n = 19; mean = 22.63 mm), and reported that neither subspecies showed a statistically significant difference in this measurement from their sample of *C. pilorides pilorides*. We therefore interpret our Cayman *Capromys* sample as almost certainly also having a significantly smaller mandibular alveolar toothrow length than these two subspecies. The smaller toothrow lengths in Cayman *Capromys* appear to be a result of the more compressed molariform teeth (premolars and molars) with reduced cement on the anterior and posterior margins of the individual teeth.

Among the larger species of extinct Cuban capromyids in the general size range of *C. pilorides*, Silva Taboada et al. (2007) recognized two species in the genus *Macrocapromys*, *M. acevedo* and *M. latus*, both of which have since been placed in *Capromys* (Borroto-Páez et al., 2012). Neither of these large species of *Capromys* is known from a complete skull, but measurements of the upper toothrow of *C. acevedo* and *C. latus* (range = 21–24 mm) are larger than the upper toothrow length of *C. p. lewisi* (range = 18–20 mm) (Silva Taboada et al., 2007).

Morphological Comparison with Cuban *Capromys*: In addition to size, *Capromys pilorides lewisi* differs from Cuban subspecies of *C. pilorides* in several cranial and dental characters. Cuban *C. pilorides* are characterized by having the infraorbital foramen considerably greater in height than the orbit compared to species of *Mesocapromys* and *Mysateles*, in which the infra-

TABLE 4
Comparative measurements (in mm) of the mandible and lower dentition of *Capromys pilorides lewisi* from the Cayman Islands (combined data for Grand Cayman and Cayman Brac), and *Capromys pilorides pilorides* from mainland Cuba. Abbreviations: **M,** mean; **R,** range; and ***N*,** sample size.

Subspecies		Lower toothrow length (alveolar)	Lower incisor length	Lower incisor width	p4 length	p4 width	Lower diastema length	Mandibular symphysis length
lewisi	M	19.7	4.0	2.9	5.5	4.1	13.1	22.9
	R	16.5–22.2	3.6–4.5	2.7–3.2	5.1–6.0	3.8–4.5	9.2–15.9	18.8–25.9
	N	44	21	23	10	10	22	22
pilorides	M	21.6	3.9	3.1	6.0	4.5	16.0	27.8
	R	16.7–24.8	3.5–4.4	2.6–3.6	5.4–6.6	4.1–5.2	14.3–18.0	25.0–30.4
	N	39	12	13	13	13	13	13

orbital foramen and orbit are similar in height. This character is even more extreme in the Cayman *Capromys*, in which the orbit is even smaller than in Cuban *C. pilorides* owing to the deeper zygomatic arch ventral to the orbit and the dorsal inflation of the frontals (figs. 12, 13).

One of the most diagnostic features of *Capromys pilorides lewisi*, and one in which this subspecies differs from Cuban *C. pilorides*, is the strong anterior convergence of the upper toothrows. The maxillary toothrows in *C. pilorides lewisi* are highly convergent anteriorly, and are essentially parallel between the P4s and M1s (figs. 10A, B, 11A, B). In contrast, the upper toothrows of Cuban *C. pilorides* are not as convergent anteriorly, diverging gradually from anterior to posterior (fig. 10C). Another characteristic feature of *C. pilorides lewisi* related to the convergence of the upper toothrows is the strongly constricted internal narial opening, which is smaller in both the vertical and transverse dimensions than in Cuban *C. pilorides*.

The frontals are noticeably inflated in *Capromys pilorides lewisi* from the anterior edge of the orbits posteriorly to the frontoparietal suture, and are particularly inflated dorsal to the orbits (fig. 12). In lateral view, this frontal inflation is delineated anteriorly by a depression dorsal to the anterior margin of the orbits and posteriorly by a depression along the frontoparietal suture. In contrast, the frontals of Cuban *C. pilorides* typically show no dorsal inflation and are essentially flat, with a smooth transition between the frontals and parietals and no depression along the frontoparietal suture. Because of this inflation, the width of the frontals is somewhat greater in *C. pilorides lewisi* than in Cuban *C. pilorides*, even though Cuban samples are larger in most other cranial measurements (tables 3, 4). However, some variation is observed in dorsal inflation of the frontals between Cuban *Capromys* individuals (fig. 13). The width of the frontals posterior to the postorbital processes is greater in *C. pilorides lewisi* than their width anterior to these processes, the opposite of the condition in Cuban *C. pilorides* in which the frontals are broader anterior to the postorbital processes. The auditory bullae also differ between Cayman and Cuban *Capromys*; the auditory bullae in *C. pilorides lewisi* are rather small, anteroposteriorly short, with a rounded shape, and show no evidence of inflation, compared to Cuban *C. pilorides* in which the bullae are larger, longer, somewhat compressed laterally, and moderately inflated.

Genetics: Extraction and amplification of UF 18588 from Patton's Fissure on Cayman Brac successfully yielded the entire mitogenome (15,908 base pairs). Maximum likelihood and Bayesian analyses of hutia mitogenome data generated congruent phylogenetic trees, showing UF

TABLE 5
Average pairwise estimates of mitogenome sequence divergence (main value) and cytochrome *b* sequence divergence (value in parentheses) between a specimen of *Capromys* from Cayman Brac (UF 18588) and GenBank data for extant hutia species.

	1	2	3	4	5	6
1. Cayman Brac *Capromys*						
2. *Capromys pilorides*	0.5 (0.6)					
3. *Mesocapromys melanurus*	7.5 (9.1)	7.4 (9.0)				
4. *Mysateles prehensilis*	7.4 (9.1)	7.4 (9.1)	6.4 (8.0)			
5. *Geocapromys brownii*	10.2 (12.3)	10.3 (12.5)	10.8 (12.0)	10.9 (13.1)		
6. *Geocapromys ingrahami*	9.8 (13.2)	9.8 (13.5)	10.2 (12.5)	10.0 (13.1)	4.7 (5.5)	
7. *Plagiodontia aedium*	12.6 (12.1)	12.7 (12.0)	13.4 (13.8)	13.0 (14.7)	14.2 (16.2)	13.6 (15.8)

18588 as the sister taxon to the *Capromys pilorides* mitogenome sample available on GenBank (fig. 18). The monophyly of the Cayman + Cuban *Capromys* clade is supported by extremely strong Bayesian approximated posterior probability values (1) and bootstrap values for maximum-likelihood analysis (1).

Sequence divergence between UF 18588 and *C. pilorides* is low (table 5). Estimated divergence from the mainland Cuban *C. pilorides* sequence used in our analyses is only 0.5% across the entire mitogenome, and only 0.6% across the entire 1140 base pair cytochrome *b* (cyt *b*) gene (table 5).

Remarks: The larger of the two hutia taxa present in the Quaternary record of the Cayman Islands is clearly referable to the genus *Capromys* on the basis of the considerably greater dorsoventral diameter of the infraorbital foramen relative to that of the orbit, the relatively thin and anteriorly oriented dorsal process of the maxilla, the presence of a small medial enamel infolding (anteroflexid) along the anterior lingual margin of p4, and its overall large size (Kratochvil et al., 1978; Díaz-Franco, 2001; Silva Taboada et al., 2007; Borroto-Páez and Mancina, 2011). Our genetic analysis also confirms genus-level assignment of the extinct Cayman population to *Capromys*.

Capromys is the most abundant and widespread fossil mammal in Quaternary deposits on the Cayman Islands, and the specimens of *Capromys* reported from Little Cayman are the only fossil vertebrates recorded from that island (Morgan, 1994a). It was the first fossil vertebrate reported from the Cayman Islands (Moyne, 1938; Westermann, 1953), and the former occurrence of *Capromys* on the Cayman Islands has been widely recognized by previous authors who have reviewed fossil material from the islands without providing a formal description of the taxon (Varona, 1974; Morgan, 1977, 1994a; Steadman and Morgan, 1985; Morgan and Woods, 1986; Harvey et al., 2016). The only exception to this is Patton (1966), who mentioned only *Geocapromys* as occurring on Cayman Brac, but investigation of material that he collected reveals that this sample also contains *Capromys*.

Except for its presence in the Quaternary record of the Cayman Islands, *Capromys* is restricted to Cuba and its satellite islands (Isla de la Juventud and offshore archipelagos), where only one extant described species, *C. pilorides*, is currently assigned to the genus. *Capromys garridoi*, a second named species that was described by Varona (1970) from a single individual collected from Cayo Majá, Archipiélago de los Canarreos, has been reinterpreted as a misidentified specimen of *C. pilorides* (Silva Taboada et al., 2007; Borroto-Páez and Mancina, 2011). Based on information provided by C.B. Lewis, Westermann (1953) and Varona (1974) interpreted *Capromys* fossils from Cayman Brac as conspecific with *C. pilorides*; other authors have conversely left the Cayman *Capromys* in open

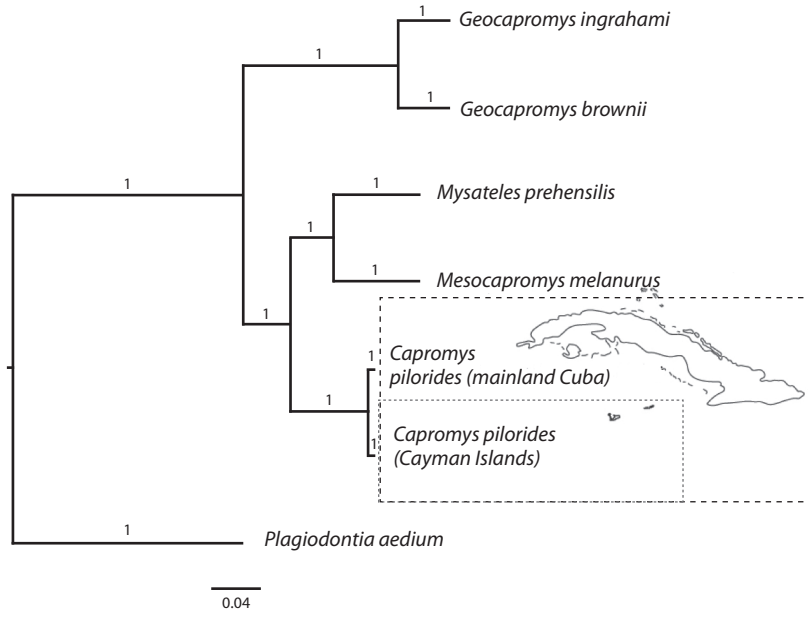


FIG. 18. Mitogenomic phylogenetic tree for selected capromyids, showing high support for monophyly of *Cayman pilorides* populations from Cuba and Cayman Brac. Posterior probabilities and bootstrap values, indicated on tree branches, are identical (1). See text for details.

nomenclature, or have considered it to represent a distinct but undescribed species. Cayman *Capromys* specimens can be differentiated from Cuban *Capromys* according to both qualitative morphological characters and statistical morphometric size differences. Several of these differences may represent evolutionary adaptations to the distinct ecological conditions of the Cayman Islands. The reduction in body size may be explicable on biogeographic grounds, consistent with vertebrate body size decreasing with land area on other oceanic islands (Burness et al., 2001). Compared to Cuban *Capromys*, the Cayman *Capromys* has cheekteeth that are vertically shorter (even though both taxa have rootless teeth) and with a reduced occlusal surface area, and has a reduced mandibular symphysis possibly indicative of altered biomechanical bite forces, all of which might be associated with differences in dietary ecology caused by differing vegetation structure and diversity between the Cayman Islands and Cuba (Brunt, 1994; Proctor, 1994). Comparable differences in crown height and area of cheekteeth are also shown between other Quaternary hutia taxa (*Plagiodontia*, *Hyperplagiodontia*) that likely differed in their trophic ecology (Hansford et al., 2012).

Considerable morphological variation has been documented between different mainland and insular Cuban *Capromys* populations, but the relationship between this morphological variation and genetic differentiation between populations is complicated and very poorly understood, leading to confusion over the taxonomic status and relationships between allopatric *Capromys* populations. Five Cuban subspecies of *C. pilorides* have been proposed, all of which have been diagnosed morphologically on the basis of craniodental and soft tissue characters: *C. pilorides pilorides* (Cuban mainland), *C. pilorides relictus* (northern Isla de la Juventud), *C. pilorides ciprianoi* (southern Isla de la Juventud), *C. pilorides doceleguas* (Archipiélago de las Doce Leguas), and *C. pilorides gundlachianus* (Archipiélago de Sabana) (Varona, 1980, 1983; Borroto Páez et al., 1992; Silva Taboada et al.,

2007; Borroto-Páez and Mancina, 2011). Based on analysis of the first 415 base pairs of cyt *b* for four of these five subspecies, however, the two putative subspecies from Isla de la Juventud (*C. pilorides ciprianoi* and *C. pilorides relictus*) show a low level of divergence (0.4%) similar to that observed within other subspecies of *C. pilorides* (0.0–0.5%) (Woods et al., 2001; Borroto-Páez et al., 2005); *C. pilorides ciprianoi* has therefore been interpreted as a junior synonym of *C. pilorides relictus* by some authorities (e.g., Woods et al., 2001), but is retained as a valid taxon by others (e.g., Silva Taboada et al., 2007).

Cyt *b* divergence data have also been used to propose the existence of an undescribed subspecies from Cayo Campo, Archipiélago de los Canarreos (Woods et al., 2001), and a further three offshore Cuban populations have been proposed to also represent distinct but unnamed subspecies (Borroto-Páez et al., 2012). A *Capromys* specimen studied by Borroto-Páez et al. (2005) from Cayo Ballenato del Medio, Archipiélago de Sabana-Camagüey, which was reportedly morphologically similar to individuals of *C. pilorides*, showed a markedly higher level of sequence divergence within the first 415 base pairs of cyt *b* (5.5%–6.4%) compared with levels of divergence seen between samples from the five named *C. pilorides* subspecies (0.4%–1.9%). This specimen has been variously interpreted as representing a previously unrecognized cryptic *Capromys* species (Borroto-Páez et al., 2005), or as representing the existing subspecies *C. pilorides gundlachianus* (Kilpatrick et al., 2012), potentially elevated to species level as *C. gundlachianus* (Woods and Kilpatrick, 2005); however, it remains undescribed because the skull of the only available specimen is damaged. Most recently, analysis of three mitochondrial genes (cyt *b*, COI, 12s rRNA) by Upham and Borroto-Páez (2017) demonstrated a primary cyt *b* divergence of 5.2% between populations all previously considered to represent *C. pilorides pilorides* from eastern and western mainland Cuba, which is probably consistent with species-level divergence. These authors also demonstrated a further divergence of 2.0% within the western clade between populations from mainland Cuba and from Isla de la Juventud and nearby Cayo Cantiles. However, these patterns of genetic divergence have not yet been related to named taxonomic units within *Capromys*.

Although the morphological differentiation shown by the Cayman *Capromys* population led Morgan (1994a) to consider that it had likely diverged from the Cuban *Capromys* source population early in the Pleistocene, sequence divergence demonstrated in our ancient DNA analysis between UF 18588 and a *C. pilorides* sample from central mainland Cuba is surprisingly low in comparison to divergences between other hutia taxa (table 5). Insight into the taxonomic status of the extinct Cayman *Capromys* population is provided by consideration of sequence divergence within the cyt *b* region, for which previously published data are available across a wider sample of extant hutia taxa. Whereas estimated sequence divergence across the entire cyt *b* gene is only 0.6% between UF 18588 and the mainland Cuban *C. pilorides* sequence used in our analysis, cyt *b* sequence divergence between the two recognized extant *Geocapromys* species (*G. brownii* and *G. ingrahami*), which constitute the other congeneric hutia taxon pair included in our analysis, is almost an order of magnitude greater at 5.5%. Conversely, levels of estimated divergence for the first 415 base pairs of cyt *b* reported by Borroto-Páez et al. (2005) between the named allopatric subspecies of *C. pilorides* vary between 0.4%–1.9%, and are therefore much more comparable to the estimated divergence between UF 18588 and mainland Cuban *C. pilorides* in our analyses. Indeed, the values reported by Borroto-Páez et al. (2005) may represent underestimates of sequence divergence across the entire cyt *b* region, as the first half of cyt *b* evolves at a slower rate than the second half (Irwin et al., 1991; Spotorno et al., 2004). Levels of divergence across the entire cyt *b* region between the three subspecies of *Plagiodontia aedium* (1.0%–2.9%) are also greater than seen between UF

18588 and mainland Cuban *C. pilorides* (Brace et al., 2012).

Available sequence divergence data therefore do not support recognition of the Cayman *Capromys* population as a distinct species, as although it is genetically distinct from mainland Cuban *C. pilorides*, it shows much lower divergence from this population compared with any interspecific divergence values between well-defined species seen across the Capromyinae, with genetic variation instead consistent with evolutionarily recent subspecies-level differentiation. As this extinct population is demonstrably morphologically distinct from all described Cuban subspecies of *C. pilorides*, we recognize it as a new subspecies, *C. pilorides lewisi*. Given the confusion over the taxonomic status of different allopatric *Capromys* populations, however, it is currently impossible to reconstruct the precise evolutionary affinities of *C. pilorides lewisi* either to other named subspecies of *C. pilorides* or to the various putative unnamed but apparently distinct taxa within the genus that have been identified by different authors, and this must await further sampling of the genus across its Quaternary distribution.

Geocapromys Chapman, 1901

***Geocapromys caymanensis*,** new species

Figures 19–24

Holotype: UF 21388, nearly complete skull with right M3, lacking the left premaxilla, both nasals, and portions of the left and right zygomatic arches (figs. 19C, 20C).

Type Locality: Patton's Fissure, near Spot Bay, northern coast of Cayman Brac, Cayman Islands. The holotype was recovered from layer 7 (120–140 cm below the surface), which has been radiocarbon dated at 13,230 ± 135 yr BP.

Etymology: The name *caymanensis* refers to the Cayman Islands.

Age: Late Pleistocene–Holocene (see Radiocarbon Dating).

Distribution: Known only from Cayman Brac and Grand Cayman.

Referred Specimens: **Cayman Brac:** Fig Tree Cave: UF 172761, edentulous mandible. Hutia Cave: UF 172756, nearly complete edentulous skull, lacking nasals, left jugal, and left auditory bulla. Patton's Fissure: UF 18835, partial skull with left M3, lacking nasals, anterior portion of frontals, left zygomatic arch, and braincase; UF 18836, partial skull, lacking rostrum, teeth, and zygomatic arches; UF 18768, 21358, partial skulls with associated mandibles; UF 21365, partial skull lacking teeth, nasals, zygomatic arches, and braincase; UF 21389, braincase; UF 21398, rostrum with left M2–M3 and right M1–M3; UF 61098, partial skull with left and right M3 and anterior portion of frontals, lacking nasals, zygomatic arches, and braincase; UF 61084, 61086–61089, rostra with edentulous palates; UF 61083, 61090, rostrums; UF 17025, 18553, 18768, 18833, 18836, 21390, 21392, 61099, 61100, partial skulls; UF 61093, palate with right M1–M3; UF 61094, maxilla with M1–M3; UF 61095, palates with left and right M2–M3; UF 21403, associated edentulous maxilla and mandible; UF 61058, 61059, 61078, 61079, mandibles with p4–m3; UF 18821, mandible with p4–m3; UF 61052, mandible with p4–m1; UF 61053, 61060–61062, mandibles with m1–m3; UF 61054, 61063, 61064, mandibles with m1–m2; UF 61049, 61050, 61055, 61065, 61066, mandibles with m2–m3; UF 21403, 61048, 61051, 61057, 61080, 61082, edentulous mandibles; UF 18651, 18652, 18670–18678, mandibles. Peter Cave: UF 22856, partial skull lacking teeth, nasals, zygomatic arches, and braincase; UF 23707, partial skull. Pollard Bay Cave: UF 17025, 18553, partial skulls; UF 18542, mandible; UF 17048, mandible with i1. Spot Bay Cave: UF 61272, partial skull with left M1–M2 and right P4–M3; UF 61273, partial skull with right M1; UF 21674, palate with left M1–M3 and right M1; UF 172780, partial skull with left otic region; UF 172768, edentulous palate; UF 61256, mandible with i1, p4–m3; UF 61257, 172769, mandibles with p4–m2; UF 172775, mandible with m1–m3;

UF 172770, mandible with i1, m1–m2; UF 172776, mandible with i1, m2–m3; UF 61260, 61261, 61269–61271, 172772–172774, 172777–172779, edentulous mandibles. **Grand Cayman:** Agouti Cave: UF 172883, mandible with i1, m1; UF 172884–172886, edentulous mandibles. Barn Owl Cave: UF 23742, mandible with p4–m2; UF 23741, mandible with m2–m3; UF 23738, 23739, 23745, edentulous mandibles. Bodden Cave: UF 23749, partial maxilla with P4; UF 23747, 23748, edentulous palates. Chisholm Cow Well: UF 172831, 172832, humeri; UF 172833, 172834, ulnae; UF172835, tibia. Crab Cave: UF 23729, partial maxilla with P4; UF 23722, mandible with p4–m1; UF 23712–23721, 23723–23727, edentulous mandibles. Dolphin Cave: UF 172941, palate with left P4–M2 and right M1–M2; UF 172858, palate with left M1; UF 172913, 172930, 172931, edentulous palates; UF 172859, 172914, 172916, 172932, mandibles with p4–m3; UF 172850, 172852, mandibles with p4–m2; UF 172851, 172936, 172937, mandibles with m1–m3; UF 172933, mandible with m1–m2; UF 172917, mandible with m1; UF 172853–172857, 172915, 172918, 172919, 172922, 172923, 172925, 172935, 172938, 172942, 172943, 411278, 411279, edentulous mandibles. Furtherland Farms Cow Well: UF 172544, nearly complete edentulous skull, lacking nasals, left premaxilla, and jugals; UF 172808, partial skull; UF 172805, mandible with i1, p4–m3; UF 172806, mandible with i1, p4–m2; UF 172807, mandible with i1, p4–m1; UF 172545, associated mandibles with left i1, p4 and right i1; UF 172546, edentulous mandible. Miller's Cave: UF 172903, edentulous mandible; UF 172904, 17290, humeri. Old Man Cave: UF 23743, partial edentulous skull with maxillae and frontals (juv.); UF 23745, 23746, 172903, edentulous mandibles. Queen Elizabeth II Botanic Park: UF 172949, palate with left and right P4. Tadarida Cave: UF 172839, edentulous mandible.

Diagnosis: *Geocapromys caymanensis* is a small species of *Geocapromys*, slightly larger than *G. ingrahami*, similar in size to *G. thoracatus*, and smaller than *G. brownii* and *G. columbianus*. The most distinctive feature of *G. caymanensis* is the strong anterior convergence of the upper toothrows, with left and right P4 separated by less than 2 mm anteriorly and medially. This anterior convergence gives the upper toothrows of *G. caymanensis* a gentle but noticeable curvature from anterior to posterior. The dorsal surface of the frontals is comparatively narrow and essentially parallel sided from the nasofrontal suture posteriorly to the frontoparietal suture. The anterior portion of the frontals shows an incipient inflation from the orbit anterior to the nasofrontal suture, particularly on the lateral surface. The postorbital processes are weak and bluntly triangular. The dorsal process of the maxilla is vertical and broad anteroposteriorly. The lateral jugal fossa on the zygomatic arch is comparatively small and narrow. The posteroventral edge of the jugal lacks a spine. The zygomatic arch in not rotated ventrally. In lateral view, the ventral surface of the zygomatic arch is level with the alveolar margin of the toothrow. The auditory bullae are rounded and short anteroposteriorly, but show moderate inflation.

Description: The description of *Geocapromys caymanensis* is based primarily on one nearly complete skull (the holotype, UF 21388) and three partial skulls (UF 18835, 18836, 21365) from Patton's Fissure on Cayman Brac, and a nearly complete but edentulous skull (UF 172544) from the Furtherland Farms Cow Well on Grand Cayman (figs. 19, 20). Three of the skulls preserve M3 but are otherwise edentulous. *Geocapromys* has unrooted, ever-growing, high-crowned (hypseledont) teeth that are not firmly rooted in the skull, which results in most of the teeth falling out of the skulls and jaws upon death. Large samples of isolated teeth are often found in fossil sites that contain *Geocapromys*. The descriptions and illustrations of the teeth are based on other specimens listed above.

The most distinctive feature of *Geocapromys caymanensis* is the extreme anterior convergence of the upper toothrows (figs. 19, 21). The left and right P4 nearly meet at the anterior margin of the toothrow. The width of the palate remains very narrow for the entire length of the P4s, with left and right toothrows separated by less than 2 mm

at the alveolar margin between P4 and M1. Based on measurements of palatal width (table 6), the palate is actually slightly narrower at the alveolar margin between P4 and M1 (1.7 mm, mean of five individuals) than anterior to P4 (1.9 mm, mean of five individuals). Posterior to the middle of M1, the toothrows begin to diverge laterally, with the distance between toothrows reaching a width of about 5 mm at the posterior margin of the palate. This is similar to the posterior width of the palate in the two other small species of *Geocapromys*, *G. ingrahami* and *G. thoracatus*. Because of their strong anterior convergence at the level of P4 and rather sharp divergence posterior to M1, the upper toothrows have a gentle but noticeable curvature from anterior to posterior, particularly obvious on the lateral alveolar margin.

Another diagnostic character of *Geocapromys caymanensis* is the narrow, parallel-sided frontals on the dorsal surface of the skull (fig. 19). Compared to other species of *Geocapromys*, the frontals of *G. caymanensis* are especially narrow anteriorly, from the level of the least interorbital breadth anteriorly to the nasofrontal suture, and are only slightly broader posteriorly between the postorbital processes and the frontoparietal suture. Measurements that reflect the narrow frontals are the breadth of the frontals both anterior to the supraorbital processes (interorbital breadth) and posterior to the supraorbital processes (postorbital breadth). These frontal measurements are narrower than the same measurements in all other species of *Geocapromys*, even though *G. caymanensis* is not the smallest species in the genus (tables 6, 7). Although narrow transversely, the anterior frontals in the Cayman *Geocapromys* are moderately inflated, from dorsal to the anterior edge of the orbit anteriorly to the nasofrontal suture. This anterior frontal inflation is primarily obvious laterally along the internal margin of the orbit and dorsal to the superior process of the maxilla, but not along the midline where the frontals are essentially flat. The widest portion of the frontals occurs at the level of the postorbital processes, which are small and bluntly triangular. Compared to other *Geocapromys*, the postorbital processes are weak in *G. caymanensis*. The temporal crests are low, rather weak, U-shaped, and do not meet to form a sagittal crest; they are separated by 3–4 mm on the posterior surface of the parietals, just anterior to their connection with the nuchal crest.

The dorsal process of the maxilla is preserved in only one skull of *G. caymanensis* (holotype; fig. 19C), in which this process is vertical and relatively broad anteroposteriorly. The lateral jugal fossa (a character present on the posteroventral margin of the zygomatic arch ventral to the orbit in capromyines) is preserved in only one of the *Geocapromys* skulls from Cayman Brac (UF 18835), in which this fossa is narrow and its ventral margin lacks a jugal spine. In lateral view, the zygomatic arch in this skull of *G. caymanensis* is not noticeably downturned or rotated ventrally. The ventral edge of the zygomatic arch is only slightly inclined posteroventrally and is on essentially the same level as the alveolar margin of the toothrow. In ventral aspect, the pterygoid region is constricted anteroposteriorly. This compressed pterygoid region is indicative of a rather foreshortened braincase that is also noticeably downturned ventrally. The auditory bullae are comparatively short, rounded, and somewhat inflated. In posterior view, the auditory bullae extend ventrally to the occipital condyles.

Morphometrics: As for *Capromys*, the largest available measurement series for the Cayman *Geocapromys* sample is the mandibular alveolar toothrow length (Grand Cayman, $n = 41$; Cayman Brac, $n = 30$). Although *Geocapromys* skulls from Grand Cayman and Cayman Brac are otherwise morphologically very similar, statistically detectable size differences are present between samples from these two islands (Welch two-sample t-test not assuming equal variance: Grand Cayman, mean = 15.25 mm; Cayman Brac, mean = 16.52 mm; $p < 0.001$). Sample series from each island were therefore compared separately with morphometric data for other extant and extinct *Geocapromys* populations measured from museum collections: *G. brownii* ($n = 17$, mean = 19.11

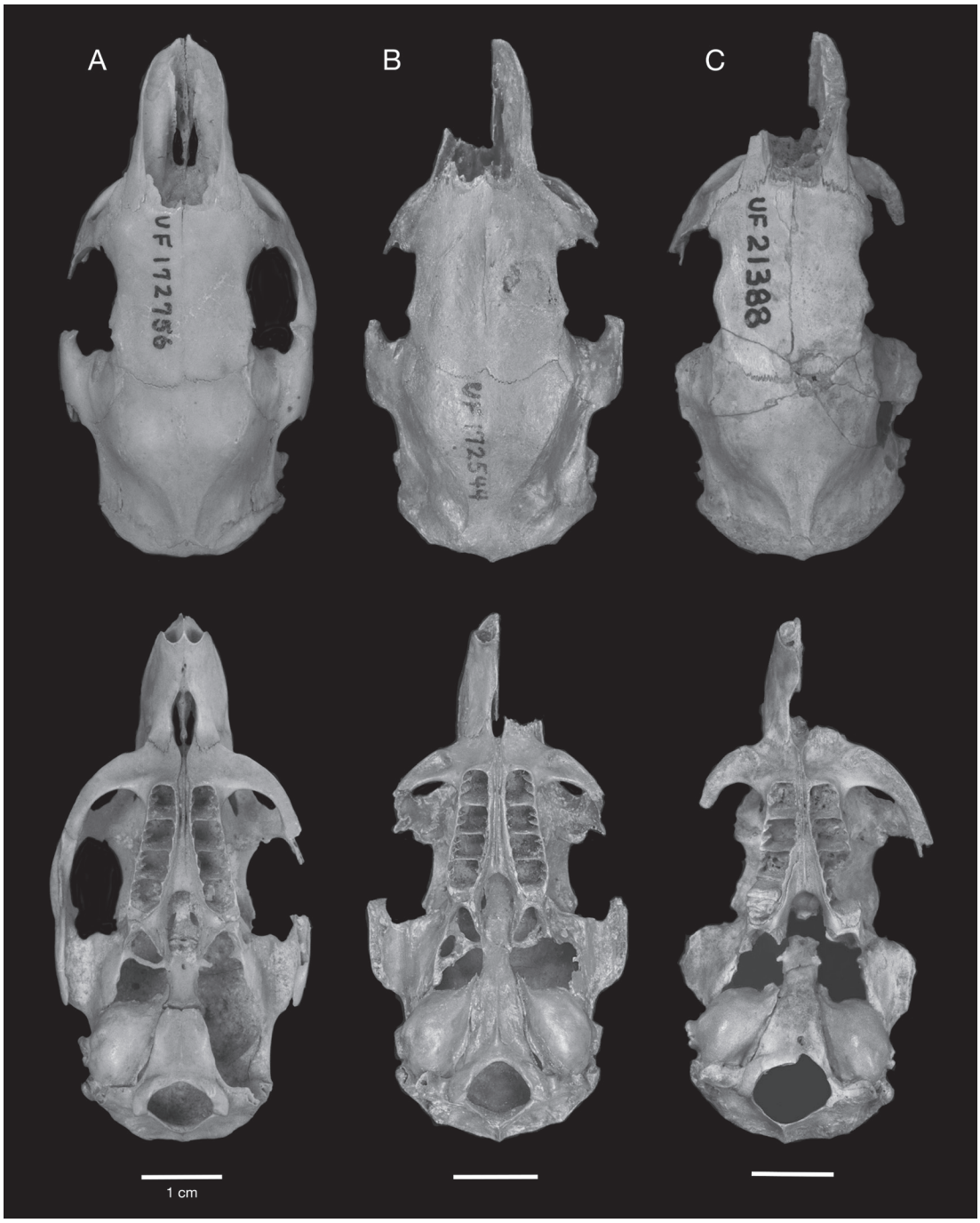


FIG. 19. *Geocapromys caymanensis*, n. sp., skulls in dorsal and ventral view. **A,** UF 172756 (Hutia Cave, Cayman Brac); **B,** UF 172544 (Furtherland Farms Cow Well, Grand Cayman); **C,** holotype, UF 21388 (Patton's Fissure, Cayman Brac).

FIG. 20. *Geocapromys caymanensis*, skulls in lateral view. **A,** UF 172756 (Hutia Cave, Cayman Brac); **B,** UF 172544 (Furtherland Farms Cow Well, Grand Cayman); **C,** holotype, UF 21388 (Patton's Fissure, Cayman Brac).

mm), *G. columbianus* (n = 40, mean = 18.76 mm), *G. ingrahami* (sample comprising both recent specimens from East Plana Cay, and Quaternary fossil specimens from Abaco, Crooked Island, and Exuma: n = 57, mean = 16.12 mm), and *G. thoracatus* (n = 12, mean = 14.72 mm) (appendix 2). Our Grand Cayman *Geocapromys* sample has a significantly smaller mandibular alveolar toothrow length compared to *G. brownii* (p <0.001), *G. columbianus* (p <0.001) and *G. ingrahami* (p <0.001), and a significantly greater mandibular alveolar toothrow length compared to *G. thoracatus* (p = 0.016). Our Cayman Brac *Geocapromys* sample has a significantly smaller mandibular alveolar toothrow length compared to *G. brownii* (p <0.001) and *G. columbianus* (p <0.001), a significantly greater mandibular alveolar toothrow length compared to *G. thoracatus* (p <0.001), and does not differ statistically in size from *G. ingrahami* (p = 0.089).

Morphological Comparison with Other Species of *Geocapromys*: *Geocapromys* is the

FIG. 21. *Geocapromys caymanensis* UF 21398 (Patton's Fissure, Cayman Brac), palate in occlusal view (stereopair).

most widespread genus in the Capromyinae, known as either a living animal or from historical museum specimens or fossils from the Cayman Islands, Bahamas, Cuba, Jamaica, and Little Swan Island. *Geocapromys caymanensis* is a rather small species of *Geocapromys*, comparable in size to the smallest of the three living species, *G. ingrahami* from the Bahamas (tables 6, 7). Among the three extant species of *Geocapromys*, *G. caymanensis* is most similar to the Bahamian hutia *G. ingrahami* and least similar to the Jamaican hutia *G. brownii*.

Geocapromys ingrahami survives today as a wild population on a single island, East Plana Cay in the southern Bahamas, with translocated populations also established on Little Wax Cay and Warderick Wells Cay (Clough, 1972; Turvey et al., 2017). Two extinct subspecies have been described based on fossils from the Bahamas: *G. ingrahami irrectus* from Crooked Island, with referred samples from Eleuthera and Long Island, and *G. ingrahami abaconis* from Abaco (Lawrence, 1934). Both subspecies were distinguished from the living *G. ingrahami* primarily on the basis of their larger size (e.g., longer alveolar toothrows). Numerous additional extinct populations of *G. ingrahami* have been reported since, mostly from islands on the Great Bahama Bank, although these samples were not referred to either of the two extinct subspecies (Morgan, 1989a). *Geocapromys caymanensis* overlaps with *G. ingrahami* in many of the most important cranial measurements indicative of size, including total length and condylobasal length of the skull, and breadth of the

TABLE 6
Comparative measurements (in mm) of the skull and upper dentition of *Geocapromys caymanensis*, and other living and extinct species of *Geocapromys* from Jamaica, Bahamas, and Little Swan Island. Abbreviations: **M,** mean; **R,** range; and ***N*,** sample size.

Species		Greatest skull length	Condylo-basal skull length	Width at auditory meatus	Width of frontals (ant. to supraorbital process)	Width of frontals (post. to supraorbital process)	Width of superior zygomatic root	Palate width (anterior to P4)	Palate width (betw. P4 and M1)	Palate width (post. margin)	Upper diastema length	Upper toothrow length (alveolar)
G. caymanensis (Cayman Brac)	M	63.9	58.4	26.4	17.3	17.5	4.6	1.9	1.7	5.0	16.5	16.9
	R	—	—	25.2–27.1	15.7–18.8	16.1–19.3	—	1.8–2.0	1.6–1.8	4.5–5.5	15.8–17.4	16.1–17.6
	N	1	1	3	4	5	1	5	5	5	5	5
G. brownii (Jamaica)	M	81.1	75.3	29.5	23.9	19.7	5.5	3.4	3.4	6.4	19.6	19.3
	R	75.1–87.0	68.9–81.6	27.2–30.9	20.5–26.1	18.0–22.6	4.0–7.6	2.6–4.2	2.4–4.6	5.5–7.0	17.9–21.6	18.0–20.3
	N	19	14	17	18	19	19	18	16	18	19	19
G. thoracatus (Little Swan Isl.)	M	68.6	63.6	25.0	17.8	19.9	4.5	2.6	2.9	5.6	17.0	15.2
	R	65.9–73.0	60.4–67.9	23.4–27.1	16.3–19.3	18.8–21.3	4.0–5.2	2.3–3.1	2.3–3.7	5.3–6.5	16.0–18.5	14.4–15.9
	N	19	18	17	21	21	20	21	19	19	20	21
G. ingrahami (East Plana Cay, Bahamas)	M	63.2	59.3	24.4	17.1	17.9	3.2	2.4	2.2	4.8	15.4	15.6
	R	61.5–65.6	57.5–61.6	23.2–26.5	15.3–18.5	17.1–19.3	1.9–4.3	1.9–2.8	1.6–2.8	3.8–5.6	14.7–16.6	19
	N	16	12	15	19	19	18	19	19	19	18	14.8–16.4

skull at the auditory meatus. The general size similarity in *Geocapromys* individuals from these two geographically separate island groups may be explained by the relatively small land area of islands in both regions compared to the much larger islands of Cuba and Jamaica; this may have resulted in common constraints on maximum body size attainable in both regions (cf. Burness et al., 2001). The Bahamian and Cayman species of *Geocapromys* differ in the degree of anterior convergence of upper toothrows, which are highly convergent in *G. caymanensis*, and convergent but less extreme in *G. ingrahami*. Measurements of the anterior palatal width show that the toothrows are more strongly convergent anteriorly in these two species than in *G. brownii* and *G. thoracatus* (table 6). The frontals of *G. ingrahami* are slightly broader than in *G. caymanensis*, which has narrower frontals compared with all other species in the genus. *G. ingrahami* shows no evidence of the anterior frontal inflation that is characteristic of *G. caymanensis*, and also has more prominent, sharply triangular postorbital processes compared to the small, blunt processes of *G. caymanensis*. The dorsal process of the maxilla is vertical in both *G. caymanensis* and *G. ingrahami* but is noticeably broader in the Cayman species. These two species share several characters of the zygomatic arch that may also indicate a close phylogenetic relationship, including the narrow jugal fossa, lack of a jugal spine, and the minimal ventral rotation of the entire zygomatic arch with the ventral edge of the arch level with the alveolar margin of the toothrow. Both *G. ingrahami* and *G. caymanensis* also have a foreshortened braincase that is downturned ventrally. The short braincase is reflected ventrally in the constricted pterygoid regions of these two species. *G. ingrahami* has

TABLE 7
Comparative measurements (in mm) of the mandible and lower dentition of *Geocapromys caymanensis*, and other living and extinct species of *Geocapromys* from Jamaica, Bahamas, and Little Swan Island.
Abbreviations: **M,** mean; **R,** range; and ***N*,** sample size.

Species		Lower toothrow length (alveolar)	Lower incisor length	Lower incisor width	p4 length	p4 width	Lower diastema length	Mandibular symphysis length
G. caymanensis (Cayman Brac)	M	16.5	2.4	1.7	4.4	3.2	11.2	18.9
	R	13.4–18.4	1.7–3.0	1.1–2.0	3.4–4.8	2.5–3.4	8.6–13.8	14.4–21.2
	N	30	8	8	7	7	20	20
G. brownii (Jamaica)	M	19.1	3.0	2.5	4.8	3.8	13.7	21.6
	R	17.8–20.8	2.4–3.7	2.0–3.0	4.2–5.6	3.2–4.5	12.6–16.0	18.0–24.9
	N	17	11	12	12	12	19	12
G. thoracatus (Little Swan Isl.)	M	14.7	2.4	2.0	3.9	3.1	12.8	19.7
	R	13.9–15.4	2.2–2.6	1.9–2.1	3.7–4.0	2.9–3.2	11.5–14.3	19.3–20.1
	N	12	2	2	2	2	20	2
G. ingrahami (East Plana Cay, Bahamas)	M	15.1	2.4	1.9	3.9	2.8	10.1	18.1
	R	13.9–16.3	2.1–2.5	1.6–2.1	3.7–4.1	2.5–3.3	9.2–11.3	17.4–19.2
	N	18	14	14	14	14	18	13

comparatively larger auditory bullae that are more inflated than in the Cayman species.

Geocapromys caymanensis differs in size and most diagnostic cranial characters from the largest living species in the genus, *G. brownii* from Jamaica. Measurements in tables 6 and 7 reveal no overlap in cranial measurements between the smaller *G. caymanensis* and the larger *G. brownii*. The strong anterior convergence of the upper toothrows in *G. caymanensis* is not observed in *G. brownii*. The characters of the dorsal surface of the frontals also differ considerably between these two species. In *G. brownii*, the frontals are very broad and strongly inflated anterior to the postorbital processes, especially laterally, whereas the frontals are quite narrow and constricted posterior to the postorbital processes. Overall, the frontals in *G. brownii* are much broader anterior to the postorbital processes than posterior to these processes (table 6). In *G. caymanensis*, the frontals are comparatively narrow and almost parallel sided, exhibit only a minor degree of anterior inflation, and are slightly broader posterior to the postorbital processes. *G. brownii* has rather weak V-shaped temporal crests that meet to form a prominent sagittal crest on the parietals about midway between the frontal and occipital sutures. The temporal crests are also weak in *G. caymanensis*, but tend to be more U-shaped, converge (but do not meet) much farther posteriorly on the parietals, and do not form a sagittal crest. *G. caymanensis* has a foreshortened and ventrally downturned braincase compared to *G. brownii*, in which the braincase is more elongated. The comparative length of the braincase is especially obvious in the pterygoid region, in which the distance between the posterior edge of the toothrow and the anterior edge of the auditory bulla is much shorter in *G. caymanensis* than in *G. brownii*. The dorsal process of the maxilla is vertical in *G. caymanensis*, whereas this process is more posteriorly oriented in *G. brownii*. The posterior orientation of the dorsal process of the maxilla in *G. brownii* is related to the overall ventral rotation of the zygomatic arch, with the ventral edge of the arch located markedly ventral to the alveolar margin and occlusal surface of the upper teeth. The zygomatic arch is not rotated ventrally in *G. cay-*

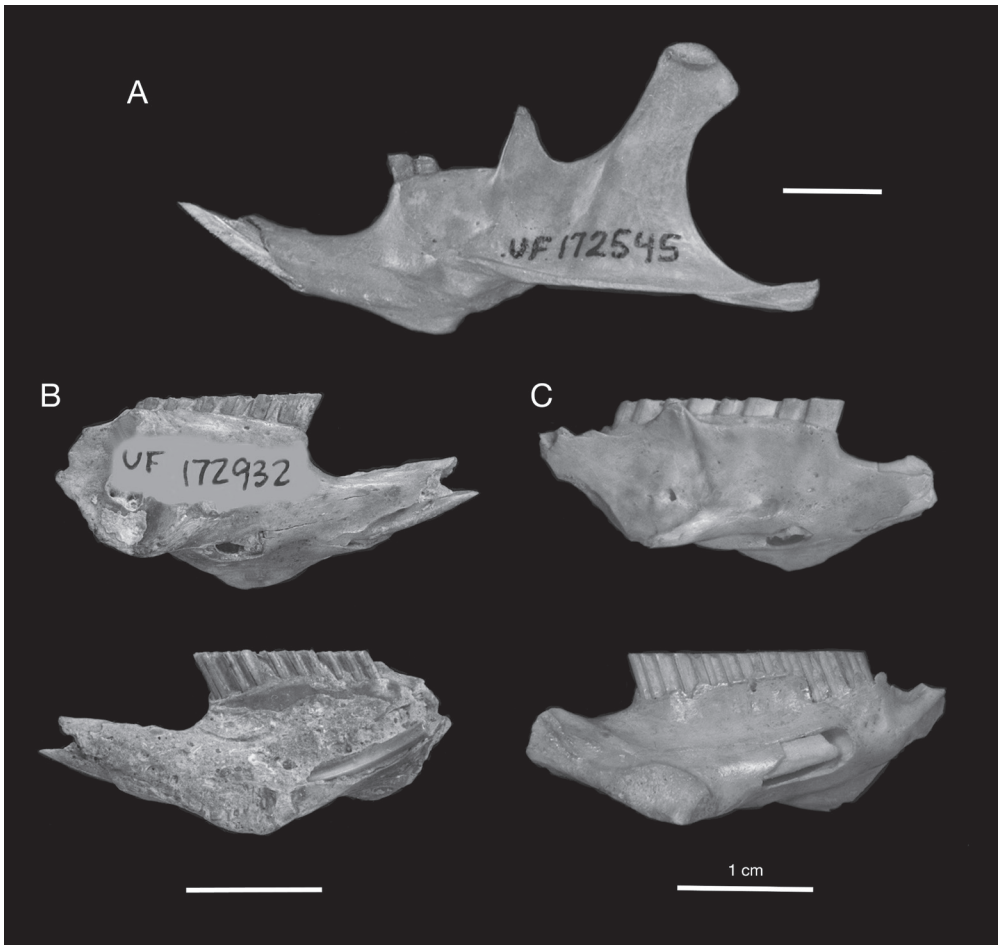


FIG. 22. *Geocapromys caymanensis* hemimandibles in labial and lingual view. **A,** UF 172545 (Furtherland Farms Cow Well, Grand Cayman), labial view only; **B,** UF 172932 (Dolphin Cave, Grand Cayman); **C,** UF 61079 (Patton's Fissure, Cayman Brac).

manensis; the ventral edge of the arch is instead located approximately level with the alveolar margin of the toothrow. *G. brownii* has a large, broad jugal fossa with a prominent jugal spine located on the posteroventral margin of the jugal; a jugal spine is absent in *G. caymanensis*, and the jugal fossa is narrow. The auditory bullae are larger and more elongated in *G. brownii,* versus shorter and rounded in *G. caymanensis*.

The Little Swan Island hutia, *G. thoracatus*, is somewhat larger than *G. caymanensis* in most cranial measurements (table 6), and shares many morphological features with the larger Jamaican *G. brownii*, to which *G. thoracatus* appears to be closely related (Morgan, 1985). This species is now extinct but survived on Little Swan Island until the 1950s, and is represented by skins, skulls, and skeletons in several museum collections (Morgan, 1989b; Tonge, 2014). Unlike *G. caymanensis*, *G. thoracatus* does not exhibit a strong anterior convergence of the upper toothrows. This species has a small spinous process that projects 1–2 mm beyond the posterior palatal margin along the midline; this process is not observed in any other species of the genus, including *G. caymanensis*. One of the most char-

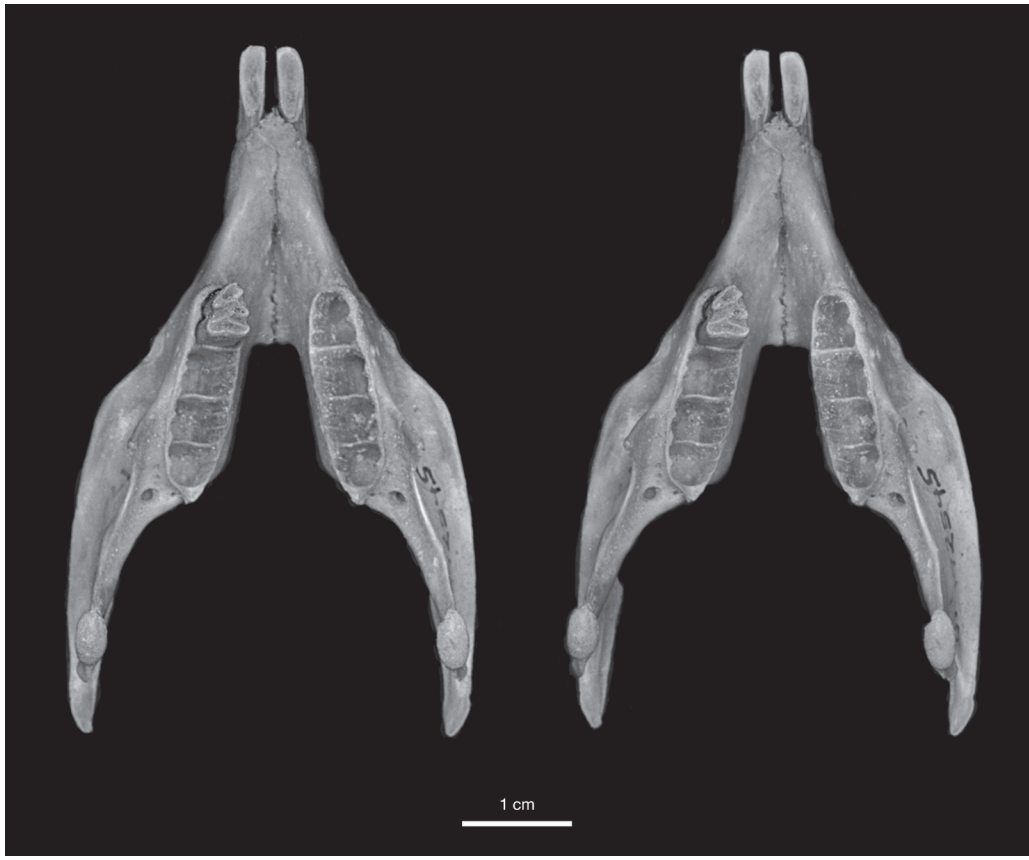


FIG. 23. *Geocapromys caymanensis* UF 172545 (Furtherland Farms Cow Well, Grand Cayman), mandible in occlusal view (stereopair).

acteristic features of *G. thoracatus* compared to its congeners is its comparatively small teeth. The frontals are broad in *G. thoracatus*, especially posterior to the postorbital processes, and there is no evidence of anterior inflation of the frontals, compared with *G. caymanensis*, which has narrow, parallel-sided frontals with a minor degree of inflation anteriorly. Features of the dorsal process of the maxilla and zygomatic arch of *G. thoracatus* are similar to those of *G. brownii*, although less pronounced. *G. thoracatus* has a broad, posteriorly oriented dorsal process of the maxilla, a broad jugal fossa with a well-developed jugal spine, and a ventrally rotated zygomatic arch, all of which are quite distinct from *G. caymanensis*; the Cayman species instead has a vertical dorsal process of the maxilla, a narrow jugal fossa lacking a jugal spine, and an absence of ventral rotation of the zygomatic arch. *G. thoracatus* has longer and narrower auditory bullae than *G. caymanensis*, which has shorter, rounded, and more inflated bullae.

Four extinct species of *Geocapromys* have been named from Cuban fossil deposits, but only *G. columbianus* is now considered valid (Silva Taboada et al., 2007). *G. columbianus* is not well described or illustrated, with little cranial material having been figured in the literature (Silva Taboada et al., 2007; Díaz-Franco and Jiménez Vázquez, 2008). In his original description of *G. columbianus*, Chapman (1892) characterized this species as having strongly convergent upper toothrows, with a measurement of "0.04 in" (= 1.0 mm) between the anterior margins of

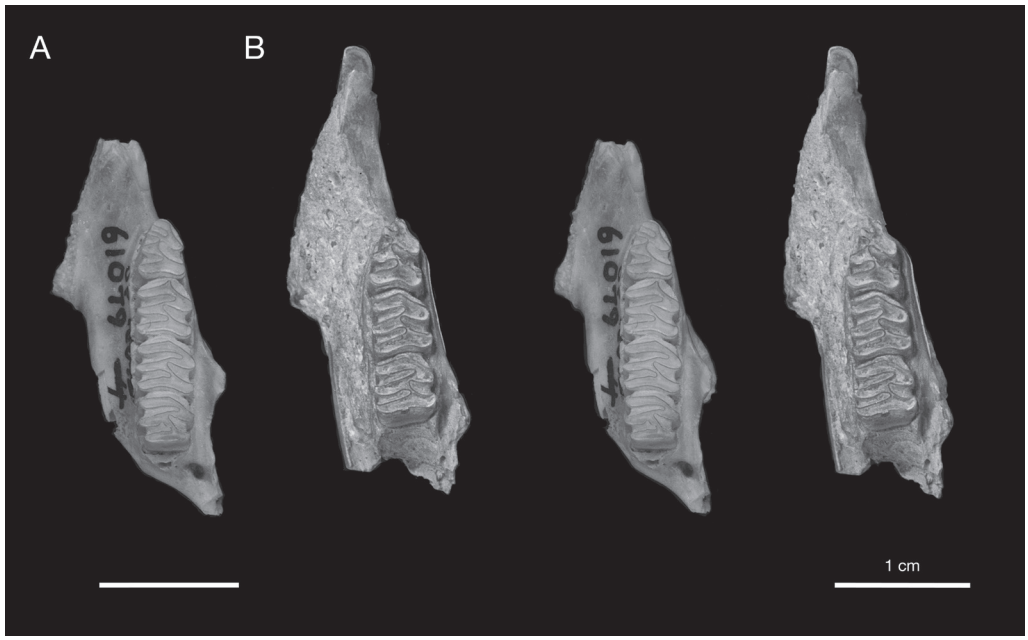


FIG. 24. *Geocapromys caymanensis*, right hemimandibles in occlusal view (stereopairs). **A,** UF 61079 (Patton's Fissure, Cayman Brac); **B,** UF 172932 (Dolphin Cave, Grand Cayman).

the P4s. He also noted that the left and right alveoli essentially meet between the upper premolars. Allen (1917) obtained additional fossil specimens of *G. columbianus* from Cuba and confirmed several of the morphological features of this species reported by Chapman (1892), in particular the strong anterior convergence of the upper toothrows. The Cayman species also has strongly convergent upper toothrows, with the anterior margins of the P4s separated by 1.9 mm (mean of five individuals; table 6), but this convergence is apparently not quite as extreme as in the Cuban species. The toothrows in *G. caymanensis* are also highly convergent between P4 and M1, separated by only 1.7 mm (mean of five individuals; table 6); however, the left and right toothrows do not nearly meet between the P4s as in *G. columbianus* (Chapman, 1892: 314–315, fig. 3). The strong anterior convergence of the upper toothrows may indicate a close phylogenetic relationship between *G. caymanensis* and *G. columbianus*. The Bahamian hutia *G. ingrahami* also demonstrates an anterior convergence of the upper toothrows, although to a lesser degree than the Cayman and Cuban species of *Geocapromys*. Although not specifically mentioned in the description, the illustration of the holotype of *G. columbianus* shows a rather strong curvature of the upper toothrows, especially along the lateral margin (Chapman, 1892: fig. 3), a feature also characteristic of *G. caymanensis* but not quite as pronounced. Chapman (1892) did not provide a measurement of the alveolar length of the toothrow in the holotype of *G. columbianus* because the palate is broken off posterior to M2.

Silva Taboada et al. (2007) presented selected measurements of *Geocapromys columbianus*, including several cranial measurements of a single skull. The condylobasal length of this skull (65.9 mm) is about 12% larger than the only skull of *G. caymanensis* on which this measurement could be taken, the holotype (58.4 mm). The breadth at the auditory meatus in the single skull of *G. columbianus* is 28.1 mm, versus a mean of 26.4 mm (range of 25.2–27.1 mm) for three specimens of *G. caymanensis*, about 10% smaller than the Cuban species. Silva Taboada et al. (2007) listed a mean of 16.5 mm (range of

14.4–18.2 mm; 48 specimens) for the alveolar length of the upper toothrow of *G. columbianus*. Although the mean for the alveolar length of the upper toothrow in five specimens of *G. caymanensis* is slightly larger at 16.9 mm, the upper limit for the observed range is 17.6 mm, somewhat less than in *G. columbianus*. Based on the wide range of values, we suspect Silva Taboada et al. (2007) included some juveniles in their sample, whereas we excluded juveniles, thus increasing the mean length of the alveolar toothrow compared with the Cuban sample. Overall, the available measurements suggest that *G. columbianus* is about 10% larger than the Cayman species. Other cranial characters of *G. columbianus* that differ from *G. caymanensis* are: the posterior orientation of the dorsal process of the maxilla, a slight ventral rotation of the zygomatic arch, the presence of a small jugal spine, and the near convergence of the temporal crests on the parietals to form a short low sagittal crest. In contrast, *G. caymanensis* has a vertical dorsal process of the maxilla, no ventral rotation of the zygomatic arch, no jugal spine, and the temporal crests do not meet.

Remarks: The species of *Geocapromys* form a monophyletic group that is distinguished from *Capromys* by a number of external and cranial characters (Morgan, 1985; 1989b). External characters that distinguish *Geocapromys* from *Capromys* include: shorter tail, reduced first digit on the front foot, and shorter finer fur. Dental and cranial features that characterize *Geocapromys* are: more procumbent incisors, origin of the upper incisor root capsule high on maxilla above P4, broad vertically or posteriorly oriented dorsal process of the maxilla, 30° inclination of all cheekteeth, and presence of an anteroflexid on p4. Among the three living or recently extinct species of *Geocapromys*, *G. ingrahami* is distinguished from *G. brownii* and *G. thoracatus* by the following characters that are considered derived for *G. ingrahami*: more convergent upper toothrows, constricted pterygoid region, shortened and more inflated braincase, and inflated auditory bullae. The extinct taxa of *Geocapromys* from Cuba and the Cayman Islands possess most of the derived characters present in *G. ingrahami,* although the expression of these characters varies significantly between species. The shared possession of these derived characters suggests that *G. caymanensis* and *G. columbianus* are probably more closely related to *G. ingrahami* than they are to *G. brownii* or *G. thoracatus*, and these species were previously associated as the *ingrahami* species group within *Geocapromys* (Morgan, 1985).

From a biogeographic standpoint, the extinct *G. columbianus* from Cuba represents a plausible source population for *G. caymanensis*. Only *G. columbianus* and *G. caymanensis* exhibit extreme anterior convergence of the upper toothrows, which is almost certainly a derived feature indicating a close relationship between these species. Considering Cuba's central location between the Bahamas to the north and the Cayman Islands to the south, as well as the long history and evolutionary diversity of capromyine rodents in Cuba, it seems most likely that *G. columbianus* or a precursor probably gave rise to both *G. caymanensis* and *G. ingrahami* sometime prior to the Late Pleistocene.

Geocapromys occurs in almost every cave deposit excavated in both Cayman Brac and Grand Cayman (see list of Referred Specimens). No fossils of *Geocapromys* are known from Little Cayman, although only limited fossil exploration has been conducted on that island. As in his initial assessment of the status of the then-undescribed *Nesophontes* populations from Grand Cayman and Cayman Brac, Morgan (1994a) proposed that *Geocapromys* populations from these two islands varied in size, and should therefore be interpreted as representing two distinct species. We support Morgan's (1994a) observation by revealing statistically detectable size differences between *Geocapromys* samples from Grand Cayman and Cayman Brac, but, as with the allopatric Cayman *Nesophontes* populations, these samples are otherwise morphologically indistinguishable and lack any island-specific unique morphological synapomorphies. We are therefore reluctant to taxonomically

differentiate the two allopatric Cayman *Geocapromys* populations in the absence of further information about their phylogenetic relationships, and we encourage future investigation of the evolutionary history of these populations using ancient DNA techniques.

RADIOCARBON DATING AND EXTINCTION CHRONOLOGIES

Reconstructing the chronology of Caribbean mammal extinctions, and identifying the likely drivers of these extinctions, requires the establishment of a robust radiometric framework within which the timing of species losses can be assessed against the timing of relevant historical events such as first regional human arrival (e.g., MacPhee et al., 1999, 2007; Steadman et al., 2005; Turvey et al., 2007; Cooke et al., 2017a, b). Unfortunately, the radiometric date record for the Caribbean mammal fauna remains sparse, and only 60 of 180 regional mammal extirpation/extinction events, comprising 40 extinct and seven locally extirpated species, have even one direct or indirectly associated date (Cooke et al., 2017a). Although the extinct Cayman mammal fauna has up to now been undescribed, a relatively large series of radiometric dates are available to infer extinction timing and causation for this fauna, and in particular for the extinct *Capromys* population on Cayman Brac (table 8). Steadman and Morgan (1985), Morgan et al. (1993) and Morgan (1994a) reported five indirect non-AMS ^{14}C dates associated with extinct vertebrate remains, providing a late Pleistocene age for fossiliferous deposits from Patton's Fissure on Cayman Brac, and a late Holocene age for two samples of peat from the Crocodile Canal Site on Grand Cayman that contain skeletal material of *Capromys* and the now-extirpated Cuban crocodile *Crocodylus rhombifer*. Dates for Patton's Fissure were run on samples of inorganic carbonate from shells of an arboreal snail (*Hemitrochus caymanensis*) that rarely feeds on the ground and thus presumably ingests very little old limestone in comparison with terrestrial snail taxa (Steadman and Morgan, 1985), to minimize the possibility of anomalously old dates that can occur as a result of the ingestion of "old" or "dead" carbon that can become incorporated into the shell, the so-called limestone effect (Goodfriend and Stipp, 1983). McFarlane et al. (2002) used an error factor of 320 years to compensate for the limestone effect when evaluating their radiocarbon dates from the land snail *Pleurodonte* from a cave in southern Jamaica. Although the maximum age anomaly for radiocarbon dates obtained from land snail shell carbonate is approximately 3000 years (Goodfriend and Stipp, 1983), the error factor associated with the dates from Patton's Fissure should be minimal because they were obtained from the shells of arboreal snails. More recently, Harvey et al. (2016) provided a series of eight direct AMS dates on *Capromys* bone samples from three cave sites (Bedding Plane II, Green Cave, Pebble Cave) on Cayman Brac. Two additional new direct AMS dates on *Capromys* bone samples from Patton's Fissure on Cayman Brac were also generated for this study.

The radiometric dates available from Cayman Brac establish the presence of *Capromys*, *Geocapromys*, and *Nesophontes* on that island by the late Pleistocene. Consideration of these radiometric dates at face value also shows that the Cayman Brac and Grand Cayman populations of *Capromys*, the best-sampled extinct Cayman mammal, have closely similar last-appearance dates (LADs) of 1440–1624 CE and 1439–1643 CE, respectively. Unlike other Caribbean islands, the Cayman Islands were apparently never reached by Amerindians in the prehistoric period, and remained ecologically intact until the arrival of Columbus in 1503 (Stokes and Keegan, 1996; Scudder and Quitmyer, 1998). The Cayman Brac and Grand Cayman *Capromys* populations therefore both definitely survived at least to within a century of first European arrival, and may have survived for a century or more thereafter based on the 2σ ranges of the LADs.

Due to the incompleteness of the fossil record, a species' LAD is almost certain to predate its

TABLE 8
Direct and indirect ^{14}C dates (AMS and non-AMS) for extinct Cayman Island vertebrates. Dates reported in descending chronological order for each island. All dates have been calibrated using the IntCal13 curve in OxCal 4.2 (Bronk Ramsey, 2009). Lab acronyms: OxA, Oxford Radiocarbon Accelerator Unit; SI, Smithsonian Institution Radiocarbon Laboratory.

Island	Site	Date (yr BP)	Lab number	AMS	Calibrated age (BC/CE)	Material	Associated taxa
Cayman Brac	Pebble Cave	393 ± 25	Unreported (OxA)	Y	1440–1624 CE	*Capromys* femur	unreported
Cayman Brac	Green Cave	609 ± 26	Unreported (OxA)	Y	1296–1404 CE	*Capromys* mandible	unreported
Cayman Brac	Bedding Plane II	897 ± 23	Unreported (OxA)	Y	1042–1210 CE	*Capromys* tibia	unreported
Cayman Brac	Green Cave	928 ± 26	Unreported (OxA)	Y	1031–1162 CE	*Capromys* mandible	unreported
Cayman Brac	Bedding Plane II	930 ± 25	Unreported (OxA)	Y	1031–1160 CE	*Capromys* femur	unreported
Cayman Brac	Green Cave	1134 ± 34	Unreported (OxA)	Y	777–987 CE	*Capromys* vertebra	unreported
Cayman Brac	Green Cave	1166 ± 34	Unreported (OxA)	Y	771–969 CE	*Capromys* long bone	unreported
Cayman Brac	Patton's Fissure	1266 ± 27	OxA-17415	Y	666–857 CE	*Capromys* mandible (UF 18597)	*Capromys, Geocapromys, Nesophontes*
Cayman Brac	Green Cave	1588 ± 26	Unreported (OxA)	Y	411–540 CE	*Capromys* humerus	unreported
Cayman Brac	Patton's Fissure	1716 ± 27	OxA-17414	Y	252–392 CE	*Capromys* humerus (UF 225368)	*Capromys, Geocapromys, Nesophontes*
Cayman Brac	Patton's Fissure, Layer 5	11,180 ± 105	SI-6518	N	11,308–10,847 BCE	arboreal snail (*Hemitrochus caymanensis*)	*Capromys, Geocapromys, Nesophontes*
Cayman Brac	Patton's Fissure, Layer 7	13,230 ± 135	SI-6519	N	14,329–13,483 BCE	arboreal snail (*Hemitrochus caymanensis*)	*Capromys, Geocapromys, Nesophontes*
Cayman Brac	Patton's Fissure, Layer 9	13,850 ± 135	SI-6520	N	15,240–14,372 BCE	arboreal snail (*Hemitrochus caymanensis*)	*Capromys, Geocapromys, Nesophontes*
Grand Cayman	Crocodile Canal	375 ± 60	SI-5069	N	1439–1643 CE	Peat	*Capromys* (femur)
Grand Cayman	Crocodile Canal	860 ± 50	SI-5068	N	1040–1263 CE	Peat	*Crocodylus rhombifer* (tooth, osteoderm)

true extinction date, especially for relatively poorly sampled taxa and geographic regions; this phenomenon is known as the Signor-Lipps effect (Signor and Lipps, 1982). To attempt to correct for the acknowledged temporal mismatch between LAD and true extinction date, a range of probabilistic methods have now been developed to estimate species' extinction dates based on the quantity and temporal spacing of available records (Collen and Turvey, 2009; Saltré et al., 2015). Comparative assessment of a range of these approaches suggests that the most robust method for estimating extinction date using radiometric data is the Gaussian-resampled inverse-weighted McInerny (GRIWM) method, which incorporates Gaussian resampling to account for date uncertainty, and inversely weights older dates according to their temporal distance from the LAD to account for declining population sizes and thus decreasing detection probability (Bradshaw et al., 2012; Saltré et al., 2015). The GRIWM method is increasingly being used to estimate true extinction dates for Quaternary taxa (e.g., Johnson et al., 2013; Barnosky et al., 2016), and for the Caribbean region, it has recently been used to reconstruct the extinction chronology of the Jamaican monkey *Xenothrix mcgregori* (Cooke et al., 2017b).

The GRIWM method requires a minimum of five dates to infer extinction timing (Bradshaw et al., 2012; Saltré et al., 2015), so the only extinct Cayman mammal population for which an extinction chronology can be reconstructed using this method is the Cayman Brac *Capromys* population. Based on the series of 10 direct late Holocene AMS dates reported by Harvey et al. (2016) and generated for this study (table 8), and using the R code for GRIWM given in Saltré et al. (2015), we calculate a median estimated extinction date for the Cayman Brac *Capromys* population of 1700 CE, with a 95% confidence interval of 1632–1774 CE. Following Cooke et al. (2017b), we also assessed the sensitivity of the GRIWM method for estimating an extinction date for the Cayman Brac *Capromys* population, by calculating further estimates for five data subsets that each contained a sample size of five dates randomly selected from the available AMS dataset. Median estimated extinction dates for these data subsets range from 1717 CE to 1791 CE (mean = 1760 CE), as estimates based on these reduced data series have wider confidence intervals that extend closer to the present (upper confidence intervals range from 1807 CE to 14 years into the future).

These results therefore demonstrate the survival of the Cayman Brac *Capromys* population, the best-sampled extinct Cayman mammal population, for well over a century following first European arrival in the Cayman Islands and possibly for over half the time between European arrival and the present day, and support the likely identity of the animals observed by Sir Francis Drake in 1586 as being capromyids (Keeler, 1981). While we cannot provide similar support for historical-era survival of other, more poorly sampled extinct Cayman mammal taxa, we therefore consider that Cayman populations of both *Geocapromys* and *Nesophontes* may also have persisted beyond the timing of first European arrival on these islands, as further suggested by the stratigraphic association of both *Geocapromys* and *Nesophontes* with invasive *Rattus rattus* in Patton's Fissure, Pollard Bay Cave, Bodden Cave, Furtherland Farms Cow Well, and Old Man Cave (Morgan, 1994a).

European arrival in the insular Caribbean was associated with extensive ecological disruption caused by human activities including direct hunting of native vertebrate species, clearance of native vegetation, and introduction of a wide range of invasive plants and animals (including black rats, house mice, feral cats and dogs, and ungulates such as pigs, horses, cattle, and goats shortly after European arrival, and brown rats in the 18th century) (Watts, 1987). All these factors likely had rapid and major effects on native biotas. For example, invasive carnivores and murid rodents are known to pose severe risks to insular mammal faunas through predation, competition, and disease transfer, especially on islands lacking native mammalian predators (Courchamp et al.,

2003; Wyatt et al., 2008), and establishment of feral ungulate populations would have altered plant communities and ecosystem structure (Watts, 1987). *Capromys*, *Geocapromys*, and *Nesophontes* populations elsewhere in the Caribbean have been impacted by several direct and indirect human activities. Populations of *Capromys pilorides* across mainland Cuba and its offshore archipelagos have been extirpated through direct overharvesting, habitat loss, predation of adults by feral dogs, and predation of young by feral cats (Berovides Álvarez et al., 2009; Borroto-Páez, 2009; Borroto-Páez and Mancina, 2011; Turvey et al., 2017). *Geocapromys brownii* has declined and become locally extirpated across Jamaica primarily due to overhunting and habitat loss (Clough, 1976; Wilkins, 2001; Turvey et al., 2017), *G. ingrahami* has become extinct across most of the Bahamas due to a combination of hunting, predation by dogs, and competition with other invasive mammals (Clough, 1972; Morgan, 1989a; Steadman et al., 2017), and *G. thoracatus* became extinct on Little Swan Island in the 1950s probably as a result of the introduction of feral cats (Clough, 1976). Black rats have been implicated in the loss of *Nesophontes* species across the Greater Antilles (MacPhee et al., 1999).

The vulnerability of these Caribbean mammal taxa to multiple anthropogenic threats, combined with the limited written record available on the early European history of the Cayman Islands before naturalists began to record the region's fauna in the late 19th century (Morgan, 1994a), prevents easy identification of specific human activities that may have been primarily responsible for the disappearance of endemic *Capromys*, *Geocapromys*, and *Nesophontes* populations. Different potential anthropogenic threats impacted the ecosystems of the Cayman Islands at different times following first European arrival. Shortly after their discovery, the islands were visited frequently by European sailing vessels, as they provided a useful source of water and sea turtle meat (Davies and Brunt, 1994). Populations of black rats therefore almost certainly became established in the Cayman Islands during the early decades of the 16th century, and sailors may also have targeted the large hutias for meat during this period. The islands were not colonized for over 150 years after their discovery, however, with the first settlements established in 1661 (Little Cayman, Cayman Brac) and 1685 (Grand Cayman). Our estimated extinction date of 1632–1774 CE for the Cayman Brac *Capromys* population indicates that this well-sampled population is likely to have survived into the settlement period. Although the islands remained underpopulated and with relatively little farming or associated habitat clearance for much of the post-Columbian historical period (Giglioli, 1994), in contrast to other parts of the insular Caribbean (Watts, 1987), permanent settlement on the Cayman Islands would likely have been associated with increased and continuous hunting pressure on native mammal populations, together with likely establishment of feral cat, dog, and ungulate populations, and subsequent establishment of invasive brown rats. It is therefore probable that some combination of these pressures during the historical settlement period led to the extinction of *Capromys* on Cayman Brac. The factors responsible for the disappearance of other endemic Cayman terrestrial mammal populations are less apparent due to poorer temporal sampling of these taxa, and it is possible that different endemic taxa became extinct at different times following first European arrival (e.g., *Nesophontes* may have disappeared earlier if it was more vulnerable to the presence of invasive black rats; MacPhee et al., 1999). We encourage further radiometric analysis of Cayman mammal samples to provide a more robust radiometric framework for understanding mammalian extinction dynamics and patterns of ecological vulnerability and resilience in this island system.

In the context of the extinction of *Capromys* and *Geocapromys* in the Cayman Islands within the past 300–400 years, it is instructive to make comparisons with another hystricognath rodent of similar size, the Central American agouti *Dasyprocta punctata*, which was introduced into Grand Cayman from Honduras in the early 1900s.

According to agricultural records (reviewed in Morgan, 1994b), agoutis became so abundant on Grand Cayman in the mid 20th century they were considered a nuisance. Agoutis have coexisted with ever-increasing populations of humans and their introduced predators on Grand Cayman for the past century; conversations with farmers, hunters, and agricultural officials on Grand Cayman in the 1980s confirmed that agoutis were common there in forested areas (Morgan, 1994b), and 30 years later agoutis are still relatively abundant in the less populated and more forested northern and eastern portions of the island (F. Burton and J. Haakonsson, personal commun., June 2017). Differences in diet, reproductive strategy, or predator avoidance may have contributed to the divergent fates of these two different groups of hystricognath rodents in the Cayman Islands, and it may be important that the introduced agouti population evolved in a continental ecosystem containing numerous native mammalian predators and competitors, whereas the Cayman nonvolant mammal fauna otherwise contained only a single species of *Nesophontes* before human arrival. Competition between these two groups of rodents was not a factor, as hutias became extinct on Grand Cayman at least a hundred years before agoutis were introduced.

DISCUSSION

Taxonomy

Our formal description of the extinct Quaternary land mammal fauna of the Cayman Islands represents the first published taxonomic treatment of this fauna since mammal fossils were first recovered on this island group 80 years ago. We recognize two previously undescribed extinct species, *Nesophontes hemicingulus* and *Geocapromys caymanensis*, and one new extinct subspecies referable to the extant *Capromys pilorides*, of which other subspecies still survive on mainland Cuba and its associated near-shore islands. All three of these extinct taxa are morphologically diagnosable and distinct on the basis of both qualitative and quantitative morphological characteristics. We were also able to use genetic sequence data derived from ancient DNA analysis to further assess the evolutionary affinities of one of the extinct Cayman mammals, the Cayman *Capromys*. This additional independent data source revealed surprisingly high genetic similarity to extant Cuban *Capromys*, which led to our evaluation of this population as distinct only as a subspecies rather than as an extinct species.

In the absence of information from ancient DNA, some previous authors have considered that the cranial and dental features exhibited by the Cayman *Capromys* were sufficiently divergent from other *Capromys* taxa to represent a distinct (albeit previously undescribed) species, which was similar to, but distinct from *C. pilorides* (e.g., Morgan, 1994a). We note, however, that other previous authors have considered the extinct Cayman *Capromys* to represent a subspecies of *Capromys pilorides* on the basis of cranial characters alone, even without the additional insights provided by ancient DNA (e.g., Westermann, 1953; Varona, 1974). Unfortunately, we still lack comparable ancient DNA data for the Cayman *Nesophontes* and *Geocapromys*, and also for geographically adjacent extinct Cuban populations of both genera, and so we are unable to evaluate the taxonomic status of either of these other Cayman mammals using anything other than classic cranial and dental characters. However, both of these taxa exhibit substantial morphological differences from other described representatives of their genera, and we feel confident in interpreting them as extinct species based on comparable patterns of morphological variation exhibited between other members of each genus.

We also note that subspecies-level differences are observed between populations of many extant terrestrial vertebrates found across different islands within the Cayman group (Seidel and Franz, 1994), and our *Geocapromys* sample displays a statistically significant difference in mandibular toothrow length between individuals from Grand Cayman and Cayman Brac. Indeed, the most comprehensive previous assessment of the Quaternary Cayman

mammal fauna considered that populations of both *Geocapromys* and *Nesophontes* found on Grand Cayman and Cayman Brac were likely to represent distinct allopatric island-endemic species (Morgan, 1994a). Although we reject this taxonomic hypothesis due to the lack of any consistent morphological differentiation between these populations beyond minor size variation, it is possible that future research using ancient DNA or other methods may reveal further taxonomic differentiation between allopatric Cayman mammal populations. We encourage further investigation of the evolutionary history and affinities of the extinct Quaternary Cayman mammal fauna using both quantitative morphometric and ancient biomolecule methods.

Paleobiogeography

Considering the geographic position of the Cayman Islands, lying halfway between Cuba and Jamaica, it is unsurprising that the Cayman land vertebrate fauna, both living and fossil, show close affinities with species from one or the other of these larger islands. However, the biogeographic origins of the three new taxa described here seem to be uniquely Cuban, rather than Jamaican or from further afield. Several parameters favor Cuba over Jamaica as a source area for the land mammal fauna of the Cayman Islands, including its larger area, longer coastline, closer proximity during Pleistocene glacial intervals, direction of prevailing currents, and more diverse mammalian fauna.

A Cuban connection for *Capromys pilorides lewisi* seems incontrovertible, as all previously described species of *Capromys* sensu stricto are restricted to Cuba and its satellite islands (Varona, 1974; Kratochvil et al., 1978; Silva Taboada et al., 2007; Borroto-Páez and Mancina, 2011). *Geocapromys* has a wider geographic distribution, but *G. caymanensis* appears to be morphologically closer to the Cuban species *G. columbianus* than to the Jamaican hutia *G. brownii*. Likewise, although nesophontids are also known from Hispaniola, Puerto Rico, and the Virgin Islands (but not Jamaica), *Nesophontes hemicingulus* bears a strong resemblance to the Cuban species *N. micrus* in terms of dental characteristics. It is also relevant to mention that there is no evidence that any other vertebrate populations from the Cayman Islands were derived from source populations on the more distant islands of Hispaniola and Puerto Rico.

Recent molecular investigations of the evolutionary history of living capromyids provide temporal constraints on the earliest possible time for colonization of the Cayman Islands by this group. The crown radiation of capromyine genera (including *Capromys* and *Geocapromys*) is estimated to have probably occurred during the Pliocene or end-Miocene, with recent estimates ranging from: 5.8 Ma (minimum-maximum estimate range = 4.7–6.9 Ma) by Fabre et al. (2014); either 3.5 Ma (range = 2.7–4.3 Ma) or 4.5 Ma (range = 3.2–6.3 Ma) by Fabre et al. (2017), based on either nucleotide or amino acid data in the concatenated mitochondrial + nuclear dataset of these authors; or 5.4 Ma (range = 4.3–6.4 Ma) by Upham and Borroto-Páez (2017). Diversification of sampled extant allopatric populations within both *Capromys* and *Geocapromys* is much more recent and occurred during the Pleistocene, with the crown radiation within *Geocapromys* dated to 1.4 Ma (range = 0.9–1.8 Ma), and within *Capromys* dated to 1.1 Ma (range = 0.7–1.5 Ma) (Upham and Borroto-Páez, 2017). The arrival of capromyids in the Cayman Islands is therefore constrained by genetic data to have almost certainly taken place during the Pleistocene.

The geology of the Cayman Islands also imposes several broad constraints on the time and place of origin of the Cayman terrestrial vertebrate fauna, and provides insights into the possible earliest arrival of *Nesophontes*, for which molecular data are not yet available to constrain the possible timing of colonization. The Cayman Islands are classic oceanic islands. They are surrounded by deep water and probably have never been connected to other land areas. As noted previously (see Geographic and Geologic Setting), depths greater than 1000 m separate the Cayman Islands from all other land areas, elimi-

nating the possibility of dry land connections during the Pleistocene, Pliocene, or most of the Miocene. Judging from projected subsidence rates and current water depths, it is possible that the Cayman Islands were connected to one another and perhaps even to Cuba along the Cayman Ridge in the early to middle Miocene, but not thereafter. The Cayman Islands have probably existed as either small isolated oceanic islands or shallow carbonate banks for at least the last 20 million years.

The length of time that the Cayman Islands have been continuously above sea level is perhaps the single most important factor in attempting to determine the antiquity of their known land vertebrate fauna. All three of these islands have topographic highs that attain elevations of at least ~10 m, but their tectonic history and therefore age is poorly constrained. Certainly, sea levels have been high enough several times since the late Oligocene to have completely inundated the Cayman Islands at their current elevations. Eustatic sea-level curves (Miller et al., 2005) indicate that sea level was at least 25 m higher than present several times during the interval between the late Oligocene and the middle Miocene (25–11 Ma), corresponding to the deposition of the marine Brac and Cayman Fms, and again in the Pliocene (between 3 and 5 Ma), corresponding to the deposition of the marine Pedro Castle Fm. By contrast, at least some land in the Cayman Islands has probably been above water continuously since the late Pliocene, based on data suggesting that sea level was at most 10–15 m higher than present during the last 3 million years (Miller et al., 2005). Woodroffe et al. (1983) demonstrated that raised coral reef terraces up to 2 m above present sea level dating from the last interglacial (Marine Isotope Stage [MIS] 5e; uranium-series dates average approximately 125,000 yr BP) are horizontal on all three of the Cayman Islands, suggesting that the islands were tectonically stable during the late Pleistocene. This tectonic stability, coupled with data indicating that sea level has not been higher than present since the last interglacial (Spratt and Lisiecki, 2016), clearly establishes that the Cayman Islands have been continuously above water for at least the past 125,000 years. This date is consistent with molecular data constraining the likely earliest possible arrival of both *Capromys* and *Geocapromys* (Upham and Borroto-Páez, 2017). The absence of endemic genera and the low percentage of endemic species in the Recent and Quaternary terrestrial vertebrate faunas also strongly argue against a much older origin for most taxa (Morgan, 1994a).

Although there is no fossil evidence to corroborate this inference, it may be plausible to assume that dispersal of mammalian colonists from Cuba to the Cayman Islands would have been easiest during glacial maxima, when sea levels were low. Lowstand estimates are reasonably well constrained for the last ~800 kyr, with maxima of 100+ m modelled for MIS 2 (18–25 kyr BP), 6 (135–141 kyr BP), 10 (342–353 kyr BP), 12 (427–458 kyr BP), and 16 (625–636 kyr BP) (Spratt and Lisiecki, 2016). With the exception of MIS 2, which is probably too young to be pertinent here, any of these maximum lowstands would have witnessed the emergence of shallow carbonate banks along Cuba's southern coast, reducing the overwater distance to the Cayman Islands to ~100 km.

The role of overwater dispersal in the origin of the West Indian flora and fauna has been in dispute for more than a century (e.g., Matthew, 1918; Darlington, 1938; Hedges 1996; but see MacPhee and Iturralde-Vinent, 2005). Given the lack of evidence for land connections to other West Indian islands or to Middle America, overwater dispersal would seem to be the primary, if not the only, method by which land vertebrates reached the Cayman Islands. The predominant dispersal mode by which terrestrial (i.e., nonvolant) vertebrates reached the Cayman Islands was presumably on rafts of floating vegetation. Large natural rafts are rare, but have occasionally been documented in the Caribbean. King (1962) observed large numbers of floating rafts composed of water hyacinths and grasses off the mouth of the Rio Tortuguero on the Caribbean

coast of Costa Rica, and noted that fisherman had seen these floating islands as far as 75 km from land. A large natural raft 15 m in diameter, and carrying 10–15 trees up to 15 m in height, was observed in July 1969 about 100 km south of the Guantanamo Bay Naval Base in southeastern Cuba (Anonymous, 1970; Morgan, 1994a). According to observers the trees were mostly palms missing their tops, and the whole island was held together by a "mangrove-type matting." The U.S. Navy tracked the island for more than a week, during which time it drifted southwest at a speed of 4.5 kilometers per hour. Conceivably, at this rate such a floating island might have reached the Cayman Islands in about a week, depending on factors such as wind direction and currents. Unfortunately, the island sank before its flora and fauna could be documented. There is even direct evidence of successful overwater transportation of vertebrates between islands in the West Indies by such rafts: several green iguanas (*Iguana iguana*) were rapidly transported from Guadeloupe to Anguilla (a distance of 175 km) aboard floating mats of uprooted trees during the hurricane season of 1995 (Censky et al., 1998).

Paleoecology and Taphonomy

Vertebrate fossils have been recovered from two general types of deposits in the Cayman Islands: (1) caves and fissures; (2) accumulations of organic sediment in limestone depressions ("cow wells") or mangrove swamps. Among the 31 vertebrate fossil deposits known from the Cayman Islands in the early 1990s (Morgan, 1994a), 25 were from caves or fissures and six occurred in organic deposits, all of the latter on Grand Cayman. Since then, five more cave deposits were reported from Cayman Brac (Harvey et al., 2016) and one additional site containing organic sediments was found on Grand Cayman (Morgan and Albury, 2013). The vertebrate faunas of these two types of fossil deposits are quite distinct since they formed under very different paleoenvironmental conditions. The organic deposits are dominated by the Cuban crocodile (*Crocodylus rhombifer*) and also contain other aquatic vertebrates including several species of wading birds. Terrestrial vertebrates are rare in these contexts, but each site discussed in this paper usually produced a small sample of capromyine rodents, iguanas and snakes, as well as other smaller species. These sites probably originated as shallow aquatic depositional environments, such as mangrove swamps, brackish lagoons, or freshwater ponds.

The majority of vertebrate fossil deposits in the Cayman Islands and elsewhere in the West Indies occur in caves. Cave deposits often yield hundreds or even thousands of bones of small vertebrates, including frogs, lizards, snakes, birds, bats, insectivores, and rodents. Bone accumulations of very similar composition are currently forming on the floors of many West Indian caves underneath owl roosts, in particular roosts of the barn owl (*Tyto alba*), a species that occurs throughout the West Indies, including all three of the Cayman Islands (Bradley, 1994). Although *T. alba* is the only species of owl now found on these islands, the burrowing owl (*Athene cunicularia*) is also represented in several fossil deposits on Grand Cayman and Cayman Brac (Morgan, 1994a). However, since burrowing owls do not roost in caves and are primarily insectivorous, it is unlikely that any bone accumulations in the Cayman Islands are related to their feeding activity.

Many of the vertebrates represented in cave fossil deposits on Grand Cayman and Cayman Brac are of small body size, and thus are within the size range of prey items normally consumed by *Tyto alba* (Andrews, 1990). The abundance of well-preserved bones of small vertebrates, including many species not known to inhabit caves, indicates that the feeding activity of barn owls is likely to have been responsible for some portion of highly fossiliferous cave deposits (Morgan, 1994a). However, in only a few cases do barn owls appear to have been the dominant factor in producing fossil accumulations in the Cayman Islands. Examples include Patton's Fissure and Pollard Bay Cave on Cayman Brac, and Crab Cave

and the entrance chamber of Dolphin Cave on Grand Cayman. In other sites the accumulations are more likely to be composed of individuals representing species that naturally inhabit caves (e.g., many bats) or cave mouths (e.g., iguanas, snakes, and possibly capromyine rodents).

Morgan (1994a) analyzed large bone accumulations under Recent barn owl roosts in Barn Owl Cave on Grand Cayman and Bluff Cave on Cayman Brac in an effort to explain how the fossil deposits containing the endemic mammals were formed. Two Recent owl roost sites contained the introduced rodents *Rattus rattus* and *Mus musculus*, whereas the fossil deposits contained the shrew-sized *Nesophontes* and the two large endemic capromyid rodents. *Nesophontes* was the most abundant mammal at Patton's Fissure, constituting 14% of the total faunal remains (158 individuals), a similar percentage to that of *Rattus* and *Mus* in the modern roost sites. Braincases were consistently missing from the *Nesophontes* skulls, indicating that all individuals died in the same manner. In a study of the feeding behavior of captive *Tyto alba*, Dodson and Wexlar (1979) noted that, after consumption and regurgitation, the skulls of its prey (mice) always lacked the braincase region, and Anthony (1919) also observed that Cuban barn owls broke open the skulls of their small mammalian prey prior to swallowing the animals whole (see also Andrews, 1990).

Presumably, the extinction of *N. hemicingulus* quickly followed, and was a consequence of, the human-mediated introduction of *Rattus rattus* and *Mus musculus* to the Cayman Islands (Morgan and Woods, 1986; Morgan, 1994a). Introduced murid rodents thereafter replaced *Nesophontes* as the favored mammalian prey item in barn owl diet in the Cayman Islands. However, the presence of extinct capromyids in more ancient bone accumulations requires a different explanation. Recent individuals of *Capromys pilorides* from Cuba range between ~2–7 kg in body mass (Borroto-Páez and Mancina, 2011), and extant species of *Geocapromys* range between 0.7–1.5 kg (Clough, 1972; Anderson et al., 1983). By contrast, individuals of *Tyto alba* generally weigh less than 500 g, making it unlikely that they would have preyed upon rodents the size of *Capromys* or *Geocapromys* (Andrews, 1990). It is thus of interest that two other large predatory birds have also been identified from fossil deposits on Grand Cayman: an extinct caracara, *Caracara creightoni*, and a giant extinct hawk, *Titanohierax gloveralleni* (Morgan, 1994a). Both of these birds were easily large enough to have preyed upon the Caymanian capromyines.

Three late Quaternary specimens of capromyid rodents from Grand Cayman have an unusual preservation that appears to represent digestion by crocodiles. The fossils are from two different sites: a mandible of *Capromys* (UF 172947) and a palate of *Geocapromys* (UF 172949) from the Queen Elizabeth II Botanic Park; and a mandible of *Capromys* (UF 172820) from the Chisholm Cow Well (fig. 15B, 16A). In all three of these fossils, enamel, dentine, and cement are missing from around the perimeter of the teeth, specifically that portion of the teeth that would have been exposed above the gum line. The portion of the teeth still contained within the mandible, comprising about two-thirds the length of each tooth, was unaffected. Both Cayman capromyids have hypsodont, rootless, ever-growing teeth, with more than half the length of each tooth contained within the mandible below the gum line. The missing enamel, dentine, and cement on the teeth of these rodents appear to have been dissolved, not removed by typical tooth wear. Also, the preserved bone is unusually thin in the two *Capromys* mandibles, and is completely missing, represented by an elliptical hole, on the lateral surface ventral to the base of the p4s (fig. 15B). A similar type of dissolution of enamel, dentine, cement, and bone has been observed in several horse mandibles with teeth from the Miocene of Florida, also attributed to predation and digestion by a crocodylian (R. Hulbert, personal commun.). In a laboratory experiment in which alligators were fed mice and other small mammals (Fisher, 1981), the teeth often survived the digestive pro-

cess and were defecated, although exposed enamel was usually decalcified, whereas the portions of the teeth included within the mandible/skull or in contact with other teeth suffered minimal or no decalcification of enamel, dentine or cement, just as we observe in the capromyid jaws from Grand Cayman. Conversely, raptorial birds generally regurgitate pellets containing bones and teeth that show little or no damage from digestion. The Cuban crocodile is one of the most terrestrially adapted of all crocodylian species and is known to regularly hunt *Capromys pilorides* in Cuba (De Sola, 1930; Varona, 1984); indeed, Soberón et al. (2001) determined that hutias were the most important prey by mass in the Cuban crocodile specimens they examined, accounting for over 90% of recovered stomach contents. Predation of capromyids by Cuban crocodiles on Grand Cayman is supported by the abundant fossils of *Crocodylus rhombifer* recovered from the two sites from which we identified digested hutia jaws, Chisholm Cow Well and Queen Elizabeth II Botanic Park (Morgan et al., 1993; Morgan, 1994a).

The cause(s) of the extensive vertebrate extinctions that occurred throughout the West Indies since the late Pleistocene have been discussed extensively in the literature (e.g., Pregill and Olson, 1981; Morgan and Woods, 1986; Morgan, 2001; MacPhee, 2009; Cooke et al., 2017a). Some extinctions, particularly those that affected bats and birds, may have resulted from climatic changes and rising sea levels in the late Pleistocene and early Holocene (Pregill and Olson, 1981; Morgan, 1989a). However, most losses appear to have been connected in one way or another with the regional arrival of different waves of human colonists from the mid-Holocene onward (Cooke et al., 2017a). The former presence of birds such as burrowing owl and caracara in the Cayman Islands are consistent with more open, grassland habitats such as prairies or savannas during periods of the late Quaternary, but overall climatic conditions in the Cayman Islands during the late Pleistocene and Holocene were probably not very different from those at present, considering that more than half of the species known from fossil deposits still occur on these islands (Morgan, 1994a). Our analysis of native mammal LADs indicates that European-era anthropogenic activities were responsible for the disappearance of the Cayman native land mammal fauna, and perhaps at least a few of the other 20 species of vertebrates now extinct on the Cayman Islands might have survived up to the present had the islands not suffered through the last 500 years of human depredation, habitat alteration, and exotic introductions.

ACKNOWLEDGMENTS

G.S.M. is grateful to the many people who have participated in the Florida State Museum/Florida Museum of Natural History paleontological surveys of the Cayman Islands between 1965 and 1993, including Jacqueline Belwood, Richard Franz, Shelley Franz, William Greenhood, Margaret Langworthy, Gregory McDonald, Thomas Patton, Nina Thanz-Borremans, Barbara Toomey, and Reed Toomey. Thanks are due to Tom Patton who discovered several large samples of fossil vertebrates on Cayman Brac and encouraged G.M. to undertake a study of these fossils for his master's thesis at the University of Florida. Additional field assistance was provided by Jack Andresen, Rolin Chisholm, and Edward Materne. The late Garrett Clough donated several fossil skulls and skeletons of *Capromys* from Cayman Brac to the FLMNH, and Rolin Chisholm generously contributed a collection of fossils from a cow well on Grand Cayman to the FLMNH. Laurie Beech, Carol Bordegaray, Sybil Burger, Janet Crosby, Rachael Montenegro, and Barbara Toomey helped sort fossiliferous matrix from Grand Cayman and Cayman Brac. G.S.M. is indebted to the staff of the Mosquito Research and Control Unit and Natural Resources Study (MRCU; now the Terrestrial Resources Unit of the Environment Department) of the Cayman Islands for their help. J.E. Davies and M.E.C.

Giglioli (deceased), both past directors of the MRCU, deserve special thanks, as does Floyd Banks of the Cayman Brac MRCU unit. Fred Burton of the Cayman Islands National Trust and Anita Ebanks of the Cayman Islands National Museum assisted G.S.M. in many ways with his paleontological studies in the Cayman Islands. The following museum curators and staff kindly allowed the authors to examine specimens of Recent and fossil vertebrates from the West Indies: Karl F. Koopman (deceased), Malcolm C. McKenna (deceased), and Guy G. Musser of the American Museum of Natural History, New York; Pip Brewer, J.E. Hill (deceased), Jeremy Hooker, and Roberto Portela Miguez of the Natural History Museum, London; Farish A. Jenkins, Jr. (deceased), and Maria E. Rutzmoser of the Museum of Comparative Zoology, Cambridge, Massachusetts; and Michael D. Carleton, Charles O. Handley, Jr. (deceased), and Clayton E. Ray of the U.S. National Museum of Natural History, Smithsonian Institution, Washington, D.C. Destructive sampling of *Capromys* material from the FLMNH for ancient DNA analysis was kindly permitted by Richard Hulbert. We are greatly indebted to Lorraine Meeker (AMNH) for undertaking most of the photography and all of the plate organization for this paper. G.M. received financial support from the government of the Cayman Islands through the MRCU, Florida Museum of Natural History, Society of Sigma Xi, and Smithsonian Institution. S.T.T. was supported by a Royal Society University Research Fellowship (UF130573). We also thank Ian Barnes and Selina Brace for assistance with ancient DNA analysis, and James Hansford for assistance with statistical analysis.

This is Contribution 17 to the series "Origin of the Antillean Land Mammal Fauna."

REFERENCES

Adler, C.J., W. Haak, D. Donlon, and A. Cooper. 2011. Survival and recovery of DNA from ancient teeth and bones. Journal of Archaeological Science 38: 956–964.

Allen, G.M. 1917. New fossil mammals from Cuba. Bulletin of the Museum of Comparative Zoology 61: 1–12.

Altschul, S.F., W. Gish, W. Miller, E.W. Myers, and D.J. Lipman. 1990. Basic Local Alignment Search Tool. Journal of Molecular Biology 215: 403–410.

Anderson, S., C.A. Woods, G.S. Morgan, and W.L.R. Oliver. 1983. *Geocapromys brownii*. Mammalian Species 201: 1–5.

Andrews, P. 1990. Owls, caves, and fossils. Chicago: University of Chicago Press.

Anonymous. 1970. Windward passage floating island (event 86-69). Smithsonian Institution Center for Short-lived Phenomena, Annual Report 1969: 50–52.

Anthony, H.E. 1916. Preliminary diagnosis of an apparently new family of insectivores. Bulletin of the American Museum of Natural History 35 (41): 725–728.

Anthony, H.E. 1918. The indigenous land mammals of Porto Rico, living and extinct. Memoirs of the American Museum of Natural History 2 (2): 331–435.

Anthony, H.E. 1919. Mammals collected in eastern Cuba in 1917, with descriptions of two new species. Bulletin of the American Museum of Natural History 41 (20): 625–643.

Arredondo, O. 1970. Dos nuevas especies subfosiles de mamiferos (Insectivora: Nesophontidae) del Holoceno precolombino de Cuba. Memoria de la Sociedad Ciencias Naturales La Salle 30 (86): 122–152.

Asher, R.J., and M.R. Sánchez-Villagra. 2005. Locking yourself out: diversity among dentally zalambdodont therian mammals. Journal of Mammalian Evolution 12: 265–282.

Barnosky, A., et al. 2017. Merging paleobiology with conservation biology to guide the future of terrestrial ecosystems. Science 355. [DOI: 10.1126/science.aah4787]

Barnosky, A.D., et al. 2016. Variable impact of late-Quaternary megafaunal extinction in causing ecological state shifts in North and South America. Proceedings of the National Academy of Sciences of the United States of America 113: 856–861.

Beard, J.S. 1955. The classification of tropical American vegetation types. Ecology 36: 89–100.

Benson, D.A., I. Karsch-Mizrachi, D.J. Lipman, J. Ostell, and D.L. Wheeler. 2005. GenBank. Nucleic Acids Research 33: 34–38.

Berovides Álvarez, V., O. Pimentel Pimentel, M. Cañizares Morera, J. Castillo Pérez, and M. Morales Díaz. 2009. Estudios de la jutía conga (*Capromys pilorides*) como recurso natural. Alicante: Universidad de Alicante.

Borroto-Páez, R. 2009. Invasive mammals in Cuba: an overview. Biological Invasions 11: 2279–2290.

Borroto-Páez, R., and C.A. Mancina. 2011. Mamíferos en Cuba. Vaasa, Finland: UPC Print.

Borroto Páez, R., A. Camacho Pérez, and I. Ramos García. 1992. Variation in three populations of *Capromys pilorides* (Rodentia: Capromyidae), and the description of a new subspecies form the south of the Isle of Youth (Cuba). Miscellanea Zoologica Hungarica 7: 87–99.

Borroto-Páez, R., C.A. Woods, and C.W. Kilpatrick. 2005. Sistemática de las hutias de las Antillas (Rodentia, Capromyidae). Monografies de la Societat d'Història Natural de les Balears 12: 33–50.

Borroto-Páez, R., C.A. Mancina, C.A. Woods, and C.W. Kilpatrick. 2012. Updated checklist of endemic terrestrial mammals of the West Indies. *In* R. Borroto-Páez, C.A. Woods, and F.E. Sergile (editors), Terrestrial mammals of the West Indies: contributions: 389–415. Gainesville: Florida Museum of Natural History.

Brace, S., et al. 2012. Population history of the Hispaniolan hutia *Plagiodontia aedium* (Rodentia: Capromyidae): testing the model of ancient differentiation on a geotectonically complex Caribbean island. Molecular Ecology 21: 2239–2253.

Brace, S., S.T. Turvey, M. Weksler, M.L.P. Hoogland, and I. Barnes. 2015. Unexpected evolutionary diversity in a recently extinct Caribbean mammal radiation. Proceedings of the Royal Society B, Biological Sciences 282: 20142371.

Brace, S., et al. 2016. Evolutionary history of the Nesophontidae, the last unplaced Recent mammal family. Molecular Biology and Evolution 33: 3095–3103.

Bradley, P.E. 1994. The avifauna of the Cayman Islands: an overview. *In* M.A. Brunt and J.E. Davies (editors), The Cayman Islands: natural history and biogeography: 377–406. Dordrecht: Kluwer Academic.

Bradshaw, C.J.A., A. Cooper, C.S.M. Turney, and B.W. Brook. 2012. Robust estimates of extinction time in the geological record. Quaternary Science Reviews 33: 14–19.

Bronk Ramsey, C. 2009. Bayesian analysis of radiocarbon dates. Radiocarbon 51: 337–360.

Brunt, M.A. 1994. Vegetation of the Cayman Islands. *In* M.A. Brunt and J.E. Davies (editors), The Cayman Islands: natural history and biogeography: 245–282. Dordrecht: Kluwer Academic.

Brunt, M.A., and J.E. Davies (editors). The Cayman Islands: natural history and biogeography. Dordrecht: Kluwer Academic.

Burness, G.P., J. Diamond, and T. Flannery. 2001. Dinosaurs, dragons, and dwarfs: the evolution of maximal body size. Proceedings of the National Academy of Sciences of the United States of America 98: 14518–14523.

Censky, E.J., K. Hodge, and J. Dudley. 1998. Over-water dispersal of lizards due to hurricanes. Nature 395: 556.

Chapman, F.M. 1892. Notes on birds and mammals observed near Trinidad, Cuba, with remarks on the origin of West Indian bird-life. Bulletin of the American Museum of Natural History 4 (16): 279–330.

Choate, J.R., and E.C. Birney. 1968. Sub-recent Insectivora and Chiroptera from Puerto Rico, with the description of a new bat of the genus *Stenoderma*. Journal of Mammalogy 49: 400–412.

Clough, G.C. 1972. Biology of the Bahamian hutia, *Geocapromys ingrahami*. Journal of Mammalogy 53: 807–823.

Clough, G.C. 1976. Current status of two endangered Caribbean rodents. Biological Conservation 10: 43–47.

Collen, B., and S.T. Turvey. 2009. Probabilistic methods for determining extinction chronologies. *In* S.T. Turvey (editor), Holocene extinctions: 181–191. Oxford: Oxford University Press.

Condis Fernández, M.M., O. Jiménez Vázquez, and C. Arredondo. 2005. Revision taxonómica de genero *Nesophontes* (Insectivora: Nesophontidae) en Cuba, análisis de los caracteres diagnósticos. Monografies de la Societat d'Història Natural de les Balears 12: 95–100.

Cooke, S.B., L.M. Dávalos, A.M. Mychajliw, S.T. Turvey, and N.S. Upham. 2017a. Anthropogenic extinction dominates Holocene declines of West Indian mammals. Annual Review of Ecology, Evolution, and Systematics 48: 301–327.

Cooke, S.B., A.M. Mychajliw, J. Southon, and R.D.E. MacPhee. 2017b. The extinction of *Xenothrix mcgregori*, Jamaica's last monkey. Journal of Mammalogy 98: 937–949.

Courchamp F., J.-L. Chapuis, and M. Pascal. 2003. Mammal invaders on islands: impact, control and control impact. Biological Reviews 78: 347–383.

Dabney, J., et al. 2013. Complete mitochondrial genome sequence of a Middle Pleistocene cave bear recon-

structed from ultrashort DNA fragments. Proceedings of the National Academy of Sciences of the United States of America 110: 15758–15763.

Darlington, P.J. 1938. The origin of the fauna of the Greater Antilles, with discussion of dispersal of animals over water and through the air. Quarterly Review of Biology 13: 274–300.

Dávalos, L.M., and S.T. Turvey. 2012. West Indian mammals: the old, the new, and the recently extinct. *In* B.D. Patterson and L.P. Costa (editors), Bones, clones, and biomes: the history and geography of Recent Neotropical mammals: 157–202. Chicago: University of Chicago Press.

Davies, J.E., and M.A. Brunt. 1994. Scientific studies in the Cayman Islands. *In* M.A. Brunt and J.E. Davies (editors), The Cayman Islands: natural history and biogeography: 1–12. Dordrecht: Kluwer Academic.

Dengo, G., and J.E. Case (eds.) 1990. The geology of North America, vol. H, The Caribbean region. Boulder, CO: Geological Society of America.

De Sola, C.R. 1930. The Cuban crocodile: an account of the species *Crocodilus rhombifer* Cuvier, with notes on its life history. Copeia 1930: 81–83.

Díaz-Franco, S. 2001. Situación taxonómica de *Geocapromys megas* (Rodentia: Capromyidae). Caribbean Journal of Science 37: 72–80.

Díaz-Franco, S., and O. Jiménez Vázquez. 2008. *Geocapromys brownii* (Rodentia: Capromyidae: Capromyinae) en Cuba. Solenodon 7: 41–47.

Dodson, P., and D. Wexlar. 1979. Taphonomic investigations of owl pellets. Paleobiology 5: 275–284.

Domning, D.P., R.J. Emry, R.W. Portell, S.K. Donovan, and K.S. Schindler. 1997. Oldest West Indian land mammal: rhinocerotoid ungulate from the Eocene of Jamaica. Journal of Vertebrate Paleontology 17: 638–641.

Fabre, P.H., et al. 2014. Rodents of the Caribbean: origin and diversification of hutias unravelled by next-generation museomics. Biology Letters 10: 20140266.

Fabre, P.H., et al. 2017. Mitogenomic phylogeny, diversification, and biogeography of South American spiny rats. Molecular Biology and Evolution 34: 613–633.

Fisher, D.C. 1981. Crocodilian scatology, micro-vertebrate concentrations, and enamel-less teeth. Paleobiology 7: 262–275.

Giglioli, M.E.C. 1994. The boom years in Grand Cayman; environmental deterioration and conservation. *In* M.A. Brunt and J.E. Davies (editors), The Cayman Islands: natural history and biogeography: 509–526. Dordrecht: Kluwer Academic.

Goodfriend, G.A., and J.J. Stipp. 1983. Limestone and the problem of radiocarbon dating of land-snail shell carbonate. Geology 11: 575–577.

Hansford, J., J.M. Nuñez-Miño, R.P. Young, S. Brace, J.L. Brocca, and S.T. Turvey. 2012. Taxonomy-testing and the 'Goldilocks Hypothesis': morphometric analysis of species diversity in living and extinct Hispaniolan hutias. Systematics and Biodiversity 10: 491–507.

Haq, B.U., J. Hardenbol, and P.R. Vail 1987. Chronology of fluctuating sea levels since the Triassic. Science 235: 1156–1167.

Harvey, V.L., V.M. Egerton, A.T. Chamberlain, P.L. Manning, and M. Buckley. 2016. Collagen fingerprinting: a new screening technique for radiocarbon dating ancient bone. PLoS ONE 11: e0150650.

Hedges, S.B. 1996. Historical biogeography of West Indian vertebrates. Annual Review of Ecology and Systematics 27: 163–196.

Hibbard, C.W. 1949. Techniques of collecting microvertebrates. Contributions from the Museum of Paleontology, University of Michigan 8 (2): 7–19.

Holdridge, L.R. 1967. Life zone ecology. San Jose, Costa Rica: Tropical Science Center.

Irwin, D.M., T.D. Kocher, and A.C. Wilson. 1991. Evolution of the cytochrome *b* gene in mammals. Journal of Molecular Evolution 32: 128–144.

Iturralde-Vinent, M.A. 2006. Meso-Cenozoic Caribbean paleogeography: implications for the historical biogeography of the region. International Geology Review 48: 791–827.

Iturralde-Vinent, M.A., and R.D.E. MacPhee. 1999. Paleogeography of the Caribbean region: implications for Cenozoic biogeography. Bulletin of the American Museum of Natural History 238: 1–95.

Johnson, C.N., C.J.A. Bradshaw, A. Cooper, R. Gillespie, and B.W. Brook. 2013. Rapid megafaunal extinction following human arrival throughout the New World. Quaternary International 308–309: 273–277.

Jones, B. 1994. Geology of the Cayman Islands. *In* M.A. Brunt and J.E. Davies (editors), The Cayman Islands: natural history and biogeography: 13–49. Dordrecht: Kluwer Academic.

Kearse, M., et al. 2012. Geneious Basic: an integrated and extendable desktop software platform for the organization and analysis of sequence data. Bioinformatics 28: 1647–1649.

Keeler, M.F. (editor). 1981. Sir Francis Drake's West Indian voyage, 1585–1586. London: Hakluyt Society.

Kehlmaier, C., et al. 2017. Tropical ancient DNA reveals relationships of the extinct Bahamian giant tortoise *Chelonoidis alburyorum*. Proceedings of the Royal Society B, Biological Sciences 284: 20162235.

Kilpatrick, C.W., R. Borroto-Páez, and C.A. Woods. 2012. Phylogenetic relationships of recent capromyid rodents: a review and analyses of karyological, biochemical, and molecular data. *In* R. Borroto-Páez, C.A. Woods, and F.E. Sergile (editors), Terrestrial mammals of the West Indies: contributions: 51–69. Gainesville: Florida Museum of Natural History.

King, W. 1962. The occurrence of rafts for dispersal of land animals into the West Indies. Quarterly Journal of the Florida Academy of Sciences 25: 45–51.

Kratochvil, J., L. Rodrigues, and V. Barus. 1978. Capromyidae (Rodentia) of Cuba 1. Acta Scientiarum Naturalium Brno 12 (11): 1–60.

Lanfear, R., B. Calcott, S.Y. Ho, and S. Guindon. 2012. PartitionFinder: combined selection of partitioning schemes and substitution models for phylogenetic analyses. Molecular Biology and Evolution 29: 1695–1701.

Larkin, M.A., et al. 2007. Clustal W and Clustal X. Bioinformatics 23: 2947–2948.

Leite, Y.L.R., and J.L. Patton. 2002. Evolution of South American spiny rats (Rodentia, Echimyidae): The star-phylogeny hypothesis revisited. Molecular Phylogenetics and Evolution 25: 455–464.

Lillegraven, J.A., M.C. McKenna, and L. Krishtalka. 1981. Evolutionary relationships of middle Eocene and younger species of *Centetodon* (Mammalia, Insectivora, Geolabididae) with a description of the dentition of *Ankylodon* (Adapisoricidae). University of Wyoming Publications 45: 1–115.

MacFadden, B.J. 1980. Rafting mammals or drifting islands? Biogeography of the Greater Antillean insectivores *Nesophontes* and *Solenodon*. Journal of Biogeography 7: 11–22.

MacPhee, R.D.E. 2009. *Insulae infortunatae*: establishing a chronology for Late Quaternary mammal extinctions in the West Indies. *In* G. Haynes (editor), American megafaunal extinctions at the end of the Pleistocene: 169–193. Dordrecht: Springer.

MacPhee, R.D.E. 2011. Basicranial morphology and relationships of Antillean Heptaxodontidae (Rodentia, Ctenohystrica, Caviomorpha). Bulletin of the American Museum of Natural History 363: 1–70.

MacPhee, R.D.E., and C. Flemming. 1999. Requiem æternam: the last five hundred years of mammalian species extinctions. *In* R.D.E. MacPhee (editor), Extinctions in near time: causes, contexts, and consequences: 333–371. New York: Kluwer Academic.

MacPhee, R.D.E., and M.A. Iturralde-Vinent. 1995. Origin of the Greater Antillean land mammal fauna, 1: new Tertiary fossils from Cuba and Puerto Rico. American Museum Novitates 3141: 1–30.

MacPhee, R.D.E., and M.A. Iturralde-Vinent. 2005. The interpretation of Caribbean Cenozoic paleogeography: a reply to Hedges. Monografies de la Societat d'Història Natural de les Balears 12: 175–184.

MacPhee. R.D.E., D.C. Ford, and D.A. McFarlane. 1989. Pre-Wisconsinan mammals from Jamaica and models of late Quaternary extinctions in the Greater Antilles. Quaternary Research 31: 94–106.

MacPhee, R.D.E., C. Flemming, and D.P. Lunde. 1999. "Last occurrence" of the Antillean insectivoran *Nesophontes*: new radiometric dates and their interpretation. American Museum Novitates 3261: 1–19.

MacPhee, R.D.E., M.A. Iturralde-Vinent, and O.J. Vazquez. 2007. Prehistoric sloth extinctions in Cuba: implications of a new "last" appearance date. Caribbean Journal of Science 43: 94–98.

Matley, C.A. 1926. The geology of the Cayman Islands (British West Indies) and their relation to the Bartlett Trough. Journal of the Geological Society of London 82: 352–387.

Matthew, W.D. 1918. Affinities and origins of the Antillean mammals. Bulletin of the Geological Society of America 29: 657–666.

McDowell, S.B., Jr. 1958. The Greater Antillean insectivores. Bulletin of the American Museum of Natural History 115 (3): 113–214.

McFarlane, D.A. 1999. A note on dimorphism in *Nesophontes edithae* (Mammalia: Insectivora), an extinct island-shrew from Puerto Rico. Caribbean Journal of Science 35: 142–143.

McFarlane, D.A., J. Lundberg, and A.G. Fincham. 2002. A late Quaternary paleoecological record from caves of southern Jamaica, West Indies. Journal of Cave and Karst Studies 64: 117–125.

McKenna, M.C. 1962. Collecting small fossils by washing and screening. Curator 5: 221–235.

Meyer, M., and M. Kircher. 2010. Illumina sequencing library preparation for highly multiplexed target capture and sequencing. Cold Spring Harbor Protocols 5 (6). [doi:10.1101/pdb.prot5448]

Miller, G.S., Jr. 1929. A second collection of mammals from caves near St. Michel, Haiti. Smithsonian Miscellaneous Collections 81 (9): 1–30.

Miller, K.G., et al. 2005. The Phanerozoic record of global sea-level change. Science 310: 1293–1298.

Miller, M.A., W. Pfeiffer, and T. Schwartz. 2010. Creating the CIPRES Science Gateway for inference of large phylogenetic trees. Gateway Computing Enviroments Workshop (GCE) 2010: 1–8.

Morgan, G.S. 1977. Late Pleistocene fossil vertebrates from the Cayman Islands, British West Indies. M.S. thesis, University of Florida, Gainesville.

Morgan, G.S. 1985. Taxonomic status and relationships of the Swan Island hutia, *Geocapromys thoracatus* (Mammalia: Rodentia: Capromyidae), and the zoogeography of the Swan Islands vertebrate fauna. Proceedings of the Biological Society of Washington 98: 29–46.

Morgan, G.S. 1989a. Fossil Chiroptera and Rodentia from the Bahamas, and the historical biogeography of the Bahamian mammal fauna. *In* C.A. Woods (editor), Biogeography of the West Indies: past, present, and future: 685–740. Gainesville: Sandhill Crane Press.

Morgan, G.S. 1989b. *Geocapromys thoracatus*. Mammalian Species 341: 1–5.

Morgan, G.S. 1994a. Late Quaternary fossil vertebrates from the Cayman Islands. *In* M.A. Brunt and J.E. Davies (editors), The Cayman Islands: natural history and biogeography: 465–508. Dordrecht: Kluwer Academic.

Morgan, G.S. 1994b. Mammals of the Cayman Islands. *In* M.A. Brunt and J.E. Davies (editors), The Cayman Islands: natural history and biogeography: 435–463. Dordrecht: Kluwer Academic.

Morgan, G.S. 2001. Patterns of extinction in West Indian bats. *In* C.A. Woods and F.E. Sergile (editors), Biogeography of the West Indies: patterns and perspectives: 369–407. Boca Raton: CRC Press.

Morgan, G.S., and N.A. Albury. 2013. The Cuban crocodile (*Crocodylus rhombifer*) from late Quaternary fossil deposits in the Bahamas and Cayman Islands. Bulletin of the Florida Museum of Natural History 52: 161–236.

Morgan, G.S., and J.A. Ottenwalder, 1993. A new extinct species of *Solenodon* (Mammalia: Insectivora: Solenodontidae) from the Late Quaternary of Cuba. Annals of the Carnegie Museum 62: 151–164.

Morgan, G.S., and T.H. Patton. 1979. On the occurrence of *Crocodylus* (Reptilia, Crocodilidae) in the Cayman Islands, British West Indies. Journal of Herpetology 13: 289–292.

Morgan, G.S., and C.A. Woods. 1986. Extinction and the zoogeography of West Indian land mammals. Biological Journal of the Linnean Society 28: 167–203.

Morgan, G.S., C.E. Ray, and O. Arredondo. 1980. A giant extinct insectivore from Cuba (Mammalia: Insectivora: Solenodontidae). Proceedings of the Biological Society of Washington 93: 597–608.

Morgan, G.S., R. Franz, and R.I. Crombie. 1993. The Cuban crocodile, *Crocodylus rhombifer*, from Late Quaternary fossil deposits on Grand Cayman. Caribbean Journal of Science 29: 153–164.

Moyne, Lord. 1938. Atlantic circle. London: Blackie and Son Ltd.

Patterson, B., and A.E. Wood. 1982. Rodents from the Deseadan Oligocene of Bolivia and relationships of the Caviomorpha. Bulletin of the Museum of Comparative Zoology 149: 371–543.

Patton, T.H. 1966. Occurrence of fossil vertebrates on Cayman Brac, B.W.I. Caribbean Journal of Science 6: 181.

Perfit, M.R., and B.C. Heezen. 1978. The geology and evolution of the Cayman Trench. Bulletin of the Geological Society of America 89: 1155–1174.

Pregill, G.K., and S.L. Olson. 1981. Zoogeography of West Indian vertebrates in relation to Pleistocene climatic cycles. Annual Review of Ecology and Systematics 12: 75–98.

Proctor, G.R. 1994. Phytogeography of the Cayman Islands. *In* M.A. Brunt and J.E. Davies (editors), The Cayman Islands: natural history and biogeography: 237–244. Dordrecht: Kluwer Academic.

Quitmyer, I.R. 2003. Zooarchaeology of Cinnamon Bay, St. John, U.S. Virgin Islands: pre-Columbian overexploitation of animal resources. Bulletin of the Florida Museum of Natural History 44: 131–158.

Ronquist, F., and J.P. Huelsenbeck. 2003. MRBAYES 3: Bayesian phylogenetic inference under mixed models. Bioinformatics 19: 1572–1574.

Saban, R. 1954. Phylogenie des insectivores. Bulletin du Muséum National d'histoire naturelle 26: 419–432.

Saltré, F., et al. 2015. Uncertainties in dating constrain model choice for inferring extinction time from fossil records. Quaternary Science Reviews 112: 128–137.

Scudder, S.J., and I.R. Quitmyer. 1998. Evaluation of evidence for pre-Columbian human occupation at Great Cave, Cayman Brac, Cayman Islands. Caribbean Journal of Science 34: 41–49.

Seidel, M.E., and R. Franz. 1994. Amphibians and reptiles (exclusive of marine turtles) of the Cayman Islands. *In* M.A. Brunt and J.E. Davies (editors), The Cayman Islands: natural history and biogeography: 407–433. Dordrecht: Kluwer Academic.

Signor, P.W., and J.H. Lipps. 1982. Sampling bias, gradual extinction patterns, and catastrophes in the fossil record. *In* L.T. Silver and P.H. Schultz (editors), Geological implications of impacts of large asteroids

and comets on the Earth: 291–296. Geological Society of America Special Publication 190.

Silva Taboada, G., W. Suárez Duque, and S. Díaz Franco. 2007. Compendio de lo mamíferos terrestres autóctonos de Cuba vivientes y extinguidos. Havana: Museo Nacional de Historia Natural.

Simpson, G.G. 1956. Zoogeography of West Indian land mammals. American Museum Novitates 1759: 1–28.

Soberón, R.R., R. Ramos, and B. Barr. 2001. Cuba: population survey and stomach content analysis. Crocodile Specialist Group Newsletter 20 (1): 13.

Spotorno, A.E., J.P. Valladares, J.C. Marin, R.E. Palma, and R.C. Zuleta. 2004. Molecular divergence and phylogenetic relationships of chinchillids (Rodentia: Chinchillidae). Journal of Mammalogy 85: 384–388.

Spratt, R.M., and L.E. Lisiecki. 2016. A late Pleistocene sea level stack. Climate of the Past 12: 1079–1092.

Stamatakis, A., P. Hoover, and J. Rougemont. 2008. A rapid bootstrap algorithm for the RAxML web servers. Systematic Biology 57: 758–771.

Steadman, D.W., and G.S. Morgan. 1985. A new species of bullfinch (Aves: Emberizinae) from a Late Quaternary cave deposit on Cayman Brac, West Indies. Proceedings of the Biological Society of Washington 98: 544–553.

Steadman, D.W., et al. 2005. Asynchronous extinction of late Quaternary sloths on continents and islands. Proceedings of the National Academy of Sciences of the United States of America 102: 11763–11768.

Steadman, D.W., et al. 2017. Late Holocene historical ecology: the timing of vertebrate extirpation on Crooked Island, Commonwealth of the Bahamas. Journal of Island and Coastal Archaeology 12: 572–584.

Stokes, A.V., and W.F. Keegan. 1996. A reconnaissance for prehistoric archaeological sites on Grand Cayman. Caribbean Journal of Science 32: 425–430.

Szalay, F.S. 1969. Mixodectidae, Microsyopidae, and the insectivore-primate transition. Bulletin of the American Museum of Natural History 140 (4): 195–330.

Tamura, K., J. Dudley, M. Nei, and S. Kumar. 2007. Molecular revolutionary genetic analysis (MEGA) software version 4.0. Molecular Biology and Evolution 24: 1597–1599.

Tonge, S. 2014. Additions to the hypodigm of the extinct Swan Island hutia (*Geocapromys thoracatus*, Capromyidae; Rodentia). Caribbean Journal of Science 48: 63–65.

Turvey, S.T. 2009. Holocene extinctions. Oxford: Oxford University Press.

Turvey, S.T., J.R. Oliver, Y. Narganes Storde, and P. Rye. 2007. Late Holocene extinction of Puerto Rican native land mammals. Biology Letters 3: 193–196.

Turvey, S.T., et al. 2016. Holocene range collapse of giant muntjacs and pseudo-endemism in the Annamite large mammal fauna. Journal of Biogeography 43: 2250–2260.

Turvey, S.T., R.J. Kennerley, J.M. Nuñez-Miño, and R.P. Young. 2017. The last survivors: current status and conservation of the non-volant land mammals of the insular Caribbean. Journal of Mammalogy 98: 918–936.

Ungar, P.S. 2010. Mammal teeth: origin, evolution, and diversity. Baltimore: Johns Hopkins Press.

Upham, N.S., and R. Borroto-Páez. 2017. Molecular phylogeography of endangered Cuban hutias within the Caribbean radiation of capromyid rodents. Journal of Mammalogy 98: 950–963.

Van Valen, L.M. 1967. New Paleocene insectivores and insectivore classification. Bulletin of the American Museum of Natural History 135: 1–284.

Varona, L.S. 1970. Descripción de una nueva especie de *Capromys* del sur de Cuba (Rodentia: Caviomorpha). Poeyana 74: 1–16.

Varona, L.S. 1974. Catalogo de los mamiferos vivientes y extinguidos de las Antillas. Havana: Academia de Ciencias de Cuba.

Varona, L.S. 1980. Una nueva subespecie de *Capromys pilorides* (Rodentia, Capromyidae). Memoria Sociedad Ciencias Naturales La Salle 40: 141–150.

Varona, L.S. 1983. Nueva subespecie de jutia conga, *Capromys pilorides* (Rodentia: Capromyidae). Caribbean Journal of Science 19: 77–79.

Varona, L.S. 1984. Los cocodrilos fosiles de Cuba (Reptilia: Crocodylidae). Caribbean Journal of Science 20: 13–18.

Varona, L.S., and O. Arredondo. 1979. Nuevos táxones fósiles de Capromyidae (Rodentia: Caviomorpha). Poeyana 195: 1–51.

Watts, D. 1987. The West Indies: patterns of development, culture and environmental change since 1492. Cambridge: Cambridge University Press.

Welker, F., et al. 2015. Ancient proteins resolve the evolutionary history of Darwin's South American ungulates. Nature 522: 81–84.

Westermann, J.H. 1953. Nature preservation in the Caribbean. Monograph 9: 1–106. Utrecht: Founda-

tion for Scientific Research in Surinam and the Netherlands Antilles.

Whidden, H.P., and R.J. Asher. 2001. The origin of the Greater Antillean insectivorans. *In* C.A. Woods and F.E. Sergile (editors), Biogeography of the West Indies: patterns and perspectives: 237–252. Boca Raton, FL: CRC Press.

Wilkins, L. 2001. Impact of hunting on Jamaican hutia (*Geocapromys brownii*) populations: evidence from zooarchaeology and hunter surveys. *In* C.A. Woods and F.E. Sergile (editors), Biogeography of the West Indies: patterns and perspectives: 529–545. Boca Raton, FL: CRC Press.

Woodroffe, C.D., D.R. Stoddart, R.S. Harmon, and T. Spencer. 1983. Coastal morphology and Late Quaternary history, Cayman Islands, West Indies. Quaternary Research 19: 64–84.

Woods, C.A., and C.W. Kilpatrick. 2005. Infraorder Hystricognathi Brandt, 1855. *In* D.E. Wilson and D.M. Reeder (editors), Mammal species of the world: a taxonomic and geographic reference, 3rd ed.: 1538–1600. Baltimore: Johns Hopkins University Press.

Woods, C.A., R. Borroto Paez, and C.W. Kilpatrick. 2001. Insular patterns and radiations of West Indian rodents. *In* C.A. Woods and F.E. Sergile (editors), Biogeography of the West Indies: patterns and perspectives: 331–351. Boca Raton, FL: CRC Press.

Wyatt, K.B., et al. 2008. Historical mammal extinction on Christmas Island (Indian Ocean) correlates with introduced infectious disease. PLoS ONE 3: e3602.

Zachos, J., M. Pagani, L. Sloan, E. Thomas, and K. Billups. 2001. Trends, rhythms, and aberrations in global climate 65 Ma to present. Science 292: 686–693.

APPENDIX 1

Description of Fossil Deposits

Brief descriptions and coordinates are provided for the major late Pleistocene and Holocene fossil deposits on Grand Cayman, Little Cayman, and Cayman Brac (figs. 1, 2). More detailed locality data and field notes for these sites are available in the vertebrate paleontology database of the FLMNH.

As with most other islands in the West Indies, the great majority of fossil deposits in the Cayman Islands are found in caves. The combination of carbonate bedrock and abundant rainfall has led to the formation of a large number of caves in this island group. The majority of these caves consist of small openings leading into low chambers with passageways much less than 100 m in length. There are several fairly extensive cave systems in the Cayman Islands with passageways in excess of 100 m in length, including Barn Owl Cave and Miller's Cave on Grand Cayman, and Peter Cave and Pollard Bay Cave on Cayman Brac. Most vertebrate fossils collected in caves on Grand Cayman occur on or very near the surface. Controlled excavation of deeper sediment layers has produced abundant bones in only two caves on Grand Cayman, Crab Cave and Dolphin Cave. Patton's Fissure and Pollard Bay Cave on Cayman Brac have produced fossils from the surface to more than 1 m in depth.

Caves containing vertebrate fossils are abundant on Grand Cayman and Cayman Brac, but are much less common on Little Cayman. Most of the fossiliferous caves on Grand Cayman occur in the eastern half of the island (fig. 2). The largest cluster of fossiliferous caves on Grand Cayman is located in a limestone forest about 0.5 km south of Old Man Bay, including Agouti Cave, Barn Owl Cave, Big Ear Cave, Old Man Cave, and Tadarida Cave. All are located within several hundred meters of one another and are 5–7 m above sea level. Miller's Cave and Dolphin Cave occur in a limestone ridge about 7–10 m in elevation that parallels the north coast to the east of Old Man Bay. Miller's Cave probably is the most extensive cave system yet explored on Grand Cayman. Most caves on Cayman Brac are located in the eastern half of the island and are formed in the side of the Bluff that outlines the high central plateau of the island (fig. 1).

Very few of the caves in the Cayman Islands had names before the inception of the FSM/FLMNH field program in 1965. Miller's Cave and Pirate's Cave on Grand Cayman and Peter Cave on Cayman Brac are the only caves that had local names, and Pirate's Cave was not named until 1980, which is the reason that the original name for this cave, Bodden Cave, is used here. Most of the cave names used herein were coined by members of the various FSM/FLMNH field

crews, and would not be familiar to local Caymanian residents.

Four general sediment types are encountered in caves in the Cayman Islands. The most common and widespread sediments are reddish-orange lateritic soils typical of caves throughout the Greater Antilles and Bahamas. Several caves, most notably Crab Cave on Grand Cayman and Pollard Bay Cave on Cayman Brac, contain a chalky, whitish sediment composed of fined-grained carbonate matrix and rounded pebbles and cobbles of flowstone. A third type of sediment, known only from the deepest chamber in Dolphin Cave on Grand Cayman, consists of dark-colored, fine-grained sediments that appear to represent decomposed bat guano. The large numbers of fossil bat bones in these sediments attest to the former abundance of bats, although bats no longer occur in this cave. The fourth type of sediment is composed of a significant fraction of organic constituents, including dark brown soil, undecomposed plant material, and a minor component of bat guano. This organic sediment appears to have been derived in part from external sources, more so than the lateritic, carbonate, or guano sediments.

A second type of vertebrate fossil deposit in the Cayman Islands is restricted to Grand Cayman. In these sites, fossils are preserved in dark brown to black, highly organic peaty sediments. The predominant fossil preserved in these organic sediments is the Cuban crocodile (*Crocodylus rhombifer*), a species now extinct in the Cayman Islands (Morgan et al., 1993). In three of these sites—Chisholm Cow Well just west of North Side, and Furtherland Farms Cow Well and the Queen Elizabeth II Botanic Park, both located in the eastern interior—the fossiliferous organic sediments were deposited in small depressions or sinkholes in the limestone. These depressions are called "cow wells" by island residents because they are used to water cattle, especially after the organic sediments have been removed to deepen the holes so that they can fill with rain water. It is during the process of removing the organic sediments from these limestone depressions that fossils have been discovered. The fourth major locality of this type, the Crocodile Canal Site, is different because it was not formed in a limestone depression. This site consists of a mangrove peat deposit that was uncovered during the excavation of a mosquito-control canal north of George Town. Although the cow-well deposits and the mangrove peat formed under somewhat different depositional conditions, they are similar in having dark organic sediments and abundant bones of *Crocodylus rhombifer*. The organic peat deposits also contain bones of other species, including several aquatic taxa such as an ibis, a rail, and a water snake, that are unknown from other fossil deposits on Grand Cayman, as well as small samples of the terrestrial mammals *Nesophontes*, *Capromys*, and *Geocapromys*.

Grand Cayman

Agouti Cave (19°20′N, 81°11′W): Small cave located about 0.8 km south of Old Man Bay. It is part of the Old Man Bay cave system that is developed in an east-west oriented limestone ridge about 5–7 m above sea level. A small opening leads into a large chamber about 10 m across and 1 m in height. Several smaller passageways lead from this chamber. Bones of capromyine rodents were collected from the floor of this cave, along with a skeleton of the introduced agouti, *Dasyprocta punctata*. A single test pit was excavated in the reddish-orange lateritic sediments to a depth of about 1 m. Bones were very sparse in this pit, but mandibles of *Capromys* were found at about 40 cm and 80 cm below the surface. Excavated by G.S.M., M.K. Langworthy, and J.J. Belwood in April 1980.

Barn Owl Cave (19°20′N, 81°11′W): One of the two largest cave systems explored on Grand Cayman. It is part of the Old Man Bay cave system and is located about 0.6 km south of Old Man Bay. Barn Owl Cave has a large opening in the ceiling about 5 m in diameter and 8 m above the cave floor. The opening leads into a

large chamber 15 m across that is floored with reddish-orange lateritic sediments. Passageways lead in all directions from this chamber, only a few of which were thoroughly explored. The majority of fossils in this cave were found on the surface and were covered with a thick layer of flowstone. Two small test pits were excavated to a depth of 25 cm in side passageways off the main chamber. A large sample of bones was collected from a modern barn owl (*Tyto alba*) roost located at the base of a large stalagmite in the main chamber. The bones from this deposit were identified and compared to several Cayman fossil deposits that were thought to have been formed by barn owls (Morgan, 1994a). Barn Owl Cave was excavated by G.S.M., H.G. McDonald, and N.R. Thanz in March 1976.

Bodden Cave (also called Pirate's Cave) (19°17′N, 81°15′W): This cave is located behind the Presbyterian Congregational Church on the eastern edge of Bodden Town about 200 m inland from the southern coast. The cave formed in a narrow limestone ridge about 5–7 m in elevation. Bodden Cave consists primarily of an open linear fissure about 5 m wide and several hundred meters in length. There are several small, enclosed chambers and passageways leading to both the north and south from this east-west oriented fissure. Three test pits were excavated in three different enclosed chambers in Bodden Cave, two to a depth of about 1 m and one 0.5 m deep. The richest fossil accumulation was found in a tiny chamber barely 3 m across and 1 m in height. The chamber was connected to the main fissure above by a narrow solution pipe more than 3 m in length. The sediments in this deposit were composed of dark brown organic-rich soil, angular limestone fragments, and undecomposed plant material. Bones of capromyine rodents are uncommon in Bodden Cave, whereas small vertebrates are abundant and well preserved, particularly frogs, lizards, snakes, and bats. Bodden Cave was excavated by G.S.M., H.G. McDonald, and N.R. Thanz in March 1976 and by G.S.M. and M.K. Langworthy in April 1980.

Chisholm Cow Well (19°21′N, 81°13′W): This site is located about 0.3 km south of Grape Tree Point and 1.8 km southwest of North Side. It is only a few meters above sea level and consists of a small depression or sinkhole in the limestone about 5 m long, 3 m wide, and 1–2 m deep. The bones are preserved in a dark, organic sediment deposited in the bottom of the sinkhole. The bones from the Chisholm Cow Well are predominantly of *Crocodylus rhombifer*, but also include small samples of *Nesophontes*, *Capromys*, *Geocapromys*, *Cyclura lewisi*, and the snake *Cubophis* (formerly *Alsophis*). Bones were originally discovered at this site in the 1940s or 1950s when sediments were being removed from the cow well during the dry season. The largest sample of bones from the Chisholm Cow Well was obtained by Rolin Chisholm and the late Ira Thompson in the late 1970s. G.S.M., R. Chisholm, and R. Franz conducted further excavations at this site in February 1986.

Crab Cave (19°18′N, 81°06′W): This small cave is located in East End on the north side of the main island road. The small opening to the cave is situated at the base of a 7–8 m high ridge of the Cayman Fm that is parallel to and about 200 m inland from the south shore of the island. It is a small linear cave barely 50 m in length and with no side passageways. The sediments in Crab Cave are whitish to buff in color and are primarily composed of calcium carbonate. All fossils recovered from this deposit were covered by a thin layer of whitish calcium carbonate precipitate. The most productive sediment accumulation was located underneath a ledge about 4 m inside the cave opening. A large test pit, 2 m long, 1 m wide, and 0.5 m deep, was excavated under this ledge. Crab Cave produced rich samples of both species of capromyine rodents, *Cyclura*, *Anolis*, two species of snakes, and several species of bats. Crab Cave was excavated by G.S.M., H.G. McDonald, and N.R. Thanz in March 1976 and by G.S.M. and M.K. Langworthy in April 1980.

Crocodile Canal (19°19′N, 81°23′W): This site is located in a mosquito control canal about 3 km north of George Town. The canal was dug through a mangrove swamp and is only several meters above sea level. The bones were derived from a dark, organic peat deposit exposed in the canal. Most of the bones were collected from spoil piles of organic sediment dug from the in-place mangrove peat deposit by heavy equipment and piled on the canal bank. The majority of bones from this site were from small individuals of *Crocodylus rhombifer*. Other taxa recovered include *Capromys*, the snakes *Cubophis* and *Tretanorhinus*, *Cyclura lewisi*, and clapper rail (*Rallus longirostris*). The Crocodile Canal site was originally discovered by E. and R. Materne in 1979. G.S.M., J.J. Belwood, and M.K. Langworthy conducted further excavations there in April 1980.

Dolphin Cave (19°21′N, 81°08′W): A small cave located about 200 m inland from Great Bluff on the south side of the Queen's Highway. The cave formed in a limestone ridge about 5–7 m in elevation. A 1 m^2 test pit was excavated to a depth of 0.7 m just inside the cave mouth. The bones occur in an orangish-brown sediment. Many of the bones found on or near the surface were covered with a thick layer of flowstone. The entrance excavation in Dolphin Cave produced large samples of *Capromys* and *Geocapromys*, along with smaller samples of *Nesophontes*, bats, and birds. Two smaller test pits were dug about 10–20 m farther back in the cave in moist, dark, organic-rich sediments that appear to represent decomposed bat guano. These excavations deeper in the cave produced large samples of bats, as well as some capromyine bones. Dolphin Cave was discovered and excavated by G.S.M. and R. Franz in February 1986. Further excavations were conducted by R. and S. Franz in August 1987 and by G.S.M., B. Toomey, and R. Toomey in March and April 1993.

Furtherland Farms Cow Well (19°19′N, 81°08′W): This site is located on an old banana plantation in the interior at the eastern end of the island about 3 km north of Half Moon Bay and about 7–8 m above sea level. The site consists of a small cave about 10 m across and 3–4 m deep, containing water in the bottom about 1–2 m in depth. The sediments in the bottom of the cave were partially removed by the owners of the plantation so that the cave would function as a cistern, filling with rainwater that was then pumped out to irrigate banana plants. Spoil piles on the surface near the mouth of the cave consisted of both dark organic sediments containing predominantly crocodile bones, and of orangish cave sediments containing smaller bones and land snails. The Furtherland Farms site consists of samples of both aquatic vertebrates and small terrestrial vertebrates, suggesting that the fossil fauna sampled two distinct depositional environments, a freshwater pond or swamp and a dry cave. Cuban crocodiles are abundant in this site, but they do not totally dominate the fauna as they do in the Botanic Park, Chisholm Cow Well, and Crocodile Canal sites. Because of the terrestrial and aquatic components, Furtherland Farms has a more diverse vertebrate fauna than other fossil sites from Grand Cayman, with 17 species of vertebrates having been identified. The Furtherland Farms fauna includes four species of reptiles (crocodile, iguana, the anole *Anolis conspersus*, and the snake *Cubophis*); eight species of birds; and four native mammals (the bat *Macrotus waterhousii* as well as *Nesophontes*, *Capromys*, and *Geocapromys*). The most abundant bird in the deposit, represented by several dozen bones, is the white ibis (*Eudocimus albus*), a wading bird indicative of aquatic habitats. The remaining seven species are land birds, including: the great lizard cuckoo (*Saurothera merlini*); two species of doves, the Caribbean dove (*Leptoptila jamaicensis*) and the Zenaida dove (*Zenaida aurita*); the Cuban crow (*Corvus nasicus*); and three unidentified species of small passerines. The presence of the introduced Old World murid rodent *Rattus rattus* establishes that at least a portion of the deposit is post-Columbian in age. A small sample of bones from this site was originally brought to the MRCU by Reginald Koster, a science teacher at a local school, who had

obtained them from a student named Blair Smith. G.S.M., J. Andresen, and R. Franz rediscovered the site and removed a sizeable sample of bones in February 1986. R. Franz and S. Franz screened more bones from the Furtherland Farms sediments in August 1987, and G.S.M., R. Robertson, B. Toomey, and R. Toomey worked the site again in April 1993.

Miller's Cave (19°21′N, 81°10′W): This cave is located 1 km east of Old Man Bay and 0.5 km south of the Queens Highway. The cave is formed in an east-west oriented limestone ridge at 5–7 m above sea level. Miller's Cave is the most extensive cave system yet explored on Grand Cayman. Through a rather small entrance the cave opens into a long winding passageway with numerous smaller side passageways and chambers. Bones were collected from the surface of the cave and from several small depressions up to 20 cm deep. The richest bone concentrations were over 100 m from the main cave entrance near a vertical chimney opening to the surface. The most numerous taxa identified from these deposits are *Capromys*, *Geocapromys*, and several species of bats. The bones are preserved in a whitish, chalky matrix and many of the fossils are covered with a thick layer of calcium carbonate precipitate. Miller's Cave was excavated by G.S.M., J.J. Belwood, and M.K. Langworthy in April 1980.

Old Man Cave (19°20′N, 81°11′W): This cave is located 0.5 km south of Old Man Bay alongside a trail through dense limestone forest. Most of the ceiling of this cave has collapsed forming a narrow linear fissure about 2–5 m wide and about 5 m deep. The main passageway is sinuous, with numerous side passageways and small, enclosed chambers leading from it. Almost the entire floor of Old Man Cave is covered by a thick layer of bright reddish-orange cave sediment. The majority of larger bones recovered from this cave were found on the surface and were covered with flowstone. Numerous test pits were excavated throughout Old Man Cave, but most were barren of bone below the surface layer. The most productive test pit was dug in a small circular chamber about 4 m across and less than 2 m in height. A pit 1 m^2 and 0.5 m deep was excavated and screened for microvertebrates. This cave yielded mostly bones of capromyine rodents, along with scattered remains of *Nesophontes*, lizards, and snakes. Old Man Cave was discovered and excavated by G.S.M., H.G. McDonald, and N.R. Thanz in April 1976.

Queen Elizabeth II Botanic Park (19°20′N, 81°10W): This site is located on the grounds of the Queen Elizabeth II Botanic Park, 1.5 km east of the cross-island road in the eastern interior. The site consists of a small sinkhole or depression in the limestone 2 m in diameter and 3 m deep, containing dark, organic sediments. Fossil bones were discovered when the organic sediments were excavated from the sinkhole to create a small pond for exhibiting specimens of the native turtle, or higatee (*Trachemys decussata*). Bones of *Crocodylus rhombifer* dominate the fossil sample, including at least 10 individuals ranging in size from hatchling to large adult (Morgan and Albury, 2013). The sample also includes several mandibles and limb bones of *Capromys* and *Geocapromys*, as well as bones of the great blue heron (*Ardea herodias*), *Cyclura lewisi*, a smaller lizard, and a snake. This site was excavated by G.S.M., F. Burton, and T. Ebanks in March and April 1993.

Little Cayman

Agave Cave (19°42′N, 79°59′W): This cave is located at the eastern end of the island in a low (5 m) limestone ridge immediately north of the main highway about 100 m inland from the south coast and 2 km west of Sandy Point. Agave Cave consists of a small hole in the limestone with a slight overhang containing a shallow accumulation of loose cave sediments. Virtually all the sediments in Agave Cave were screened in an attempt to establish the presence of fossil vertebrates on Little Cayman. A few bones of *Capromys* were the only fossils recovered. Agave Cave was excavated by G.S.M. in February 1986.

Franz's Shelter (19°41′N, 80°04′W): This site is located in the Mahogany Forest Estates at an elevation of less than 5 m, about 0.2 km north of the main highway and 2.5 km northeast of South Town. Franz's Shelter consists of a small limestone overhang about 3 m wide and 1–2 m high. One test pit was excavated to a depth of 40 cm. The light orangish-brown sediments contained a small sample of jaws and limb bones of *Capromys*. Franz's Shelter was found by R. Franz and excavated by G.S.M. in February 1986.

Weary Hill Cave: This cave is located on the eastern end of Little Cayman near Weary Hill, the highest point on the island at an elevation of about 14 m. Sediments from the cave contained a small sample of *Capromys*. Weary Hill Cave was excavated by archaeologists from the Environmental Archaeology Program at FLMNH, although there is no evidence for pre-European settlement in the Cayman Islands (Stokes and Keegan 1996; Scudder and Quitmyer, 1998).

Cayman Brac

Fig Tree Cave (19°43′N, 79°47′W): Fig Tree Cave is located on the top of the Bluff, 10 m north of Lighthouse Road and 1.1 km east of its intersection with Bluff Road. The small entrance is less than 1 m square and opens at the base of a large fig tree. The cave consists of a single chamber about 6 m long by 3–4 m wide and less than 2 m high. The majority of the bones were collected from the surface of the cave. Several test pits were excavated to a maximum depth of 50 cm, but in most areas of the cave the sediments were only 10–20 cm thick. Most of the bones found were from *Capromys* and *Geocapromys*. Fig Tree Cave was discovered by G.S.M. and R. Franz in February 1986.

Hutia Cave (19°43′N, 79°48′W): Hutia Cave is also on the top of the Bluff, immediately north of the Lighthouse Road, only 0.1 km east of its intersection with Bluff Road. This cave has a narrow opening barely 1 m across that descends 3–4 m into a small chamber. Hutia Cave consists of three small chambers trending in an easterly direction from the entrance. Most of the fossils were collected from the surface of the deepest chamber 50 m from the entrance. This chamber is about 10 m in diameter, but barely 1 m in height. Sediments in this innermost chamber consisted of rounded flowstone cobbles and angular fragments of limestone. Fossils found in this chamber included several very well preserved and essentially unmineralized skulls and mandibles of *Capromys* and *Geocapromys*. Hutia Cave was discovered and collected by G.S.M. and R. Franz in February 1986.

Patton's Fissure (originally called Cave 2 by T.H. Patton) (19°45′N, 79°45′W): This site is located in the village of Spot Bay, 3 km west of North East Point. The fissure is in the side of the Bluff about 15 m above sea level and 250 m inland from the northern coast. Patton's Fissure is a narrow linear fissure about 50 m long and a maximum of 4 m wide at the base, trending east to west parallel to the cliff face. A layer of unconsolidated sediments 1–2 m deep covers the floor of the fissure. These sediments consist of buff to reddish-colored silts and clays, angular limestone fragments, land snail shells, and bones. Three test pits were excavated in Patton's Fissure, only one of which (Test Pit 1) produced a significant amount of bone. Test Pit 1 (Hole 1 of Patton) was approximately 2 m square by 1.6 m deep. The stratigraphy of Patton's Fissure is as follows: layer 1 (0–20 cm) contains abundant bones including both extinct mammals and *Rattus*, indicating a post-Columbian age; layers 2–4 (20–80 cm) are sparsely fossiliferous, but contain no remains of introduced species; layers 5–7 (80–140 cm) are extremely rich in both land snail shells and bones, including both species of capromyine rodents, *Nesophontes*, and a diverse assemblage of small vertebrates; layers 8–9 (140–160 cm) have few bones, and most are either covered with a calcareous precipitate or are contained in an indurated breccia. Solid limestone was encountered below layer 9. Radiocarbon dates have been obtained from three samples of shells of land snails from Patton's Fissure (see discussion under Radiocarbon

Dating). The fossil vertebrate fauna from Patton's Fissure contains more species than any other single fossil deposit in the Cayman Islands and is especially rich in remains of *Nesophontes*, *Geocapromys*, bats, land birds, lizards, and snakes. The site was discovered and excavated by T.H. Patton and field crew during the summer of 1965.

Peter Cave (19°45′N, 79°44′30″W): Peter Cave is located in the village of Spot Bay about 2 km west of North East Point and 400 m inland from the northern coast. It is situated in the side of the Bluff about 25 m above sea level, not far below the top of the Bluff. Through a small entrance about 2 m square, Peter Cave opens into a complex system of linear passageways, most of which trend north to south angling downward toward the center of the island. This cave was not thoroughly explored, but there are probably several hundred meters of passageways. A number of fossils of extinct vertebrates were collected from reddish-orange lateritic sediments on the surface, only several meters inside the entrance. Several skulls of *Capromys* and *Geocapromys* and a partial skeleton of the now-extirpated Audubon's shearwater (*Puffinus lherminieri*) were collected from these loose surficial sediments. Most of the bones were covered by a thick layer of flowstone. The sediments near the cave entrance are reddish in color, while sediments in several deeper chambers are whitish and carbonate rich. A test pit excavated in a small chamber about 100 m inside and 10 m below the entrance contained capromyine rodents, bats, lizards, and *P. lherminieri*. Material from the cave was first collected by G.S.M., H.G. McDonald, and N.R. Thanz in April 1976. G.S.M. excavated several small test pits in February 1986.

Pollard Bay Cave (originally called Cave 1 by T.H. Patton) (19°44′N, 79°44′W): Pollard Bay Cave is located at the eastern end of the south coast highway, about 2.5 km southeast of North East Point and only 100 m inland from the southern shore of the island. The entrance is about 10 m above sea level and is 5 m across and 2 m high. From the large entrance, the main passage descends 3 m into a very large chamber 15–20 m in diameter and 4–5 m in height that is floored with a thick layer of whitish carbonate sediments. Patton dug two test pits in this large chamber, each about 1.0 m by 1.5 m and 1.0 m deep. A third smaller test pit was located about 20 m deeper the cave in a narrow passageway. Numerous bones, particularly those of *Puffinus lherminieri*, were found on the surface. All bones from Pollard Bay Cave are highly mineralized, pinkish orange in color, and covered with flowstone. The most common taxa in this cave are *Capromys*, *Geocapromys*, several species of bats, and *Puffinus*. Pollard Bay Cave was originally located and excavated by T.H. Patton in the summer of 1965. G.S.M. made additional surface collections and dug a test pit in February 1986.

Shearwater Caves 1 and 2: The two Shearwater caves are located next to one another in the side of the Bluff approximately 2 km west of North East Point near Pollard Bay Cave. These two caves are 6–7 m above sea level and 100 m inland from the coast. They consist of several broad, low interconnected chambers that extend as much as 20 m into the Bluff. Bones were recovered from the surface to about 30 cm deep in fluffy reddish cave sediments deposited less than 10 m from the entrance. *Puffinus lherminieri* was by far the most abundant species represented in these two contiguous caves. Other taxa present include *Nesophontes*, *Geocapromys*, and *Anolis*, along with several species of land birds. Barn owls probably inhabited these nearly inaccessible caves as well. The Shearwater caves were dug by G.S.M. in February 1986.

Spot Bay Cave (19°45′N, 79°44′30″W): Spot Bay Cave is a small cave system located in the village of Spot Bay about 2 km west of North East Point. It is situated in the side of the Bluff, about 25 m above sea level and 400 m inland from the north coast. Spot Bay Cave is less than 100 m west of Peter Cave. It consists of a high narrow entrance that opens into a single linear passageway oriented east to west parallel to the Bluff. Bones were

recovered primarily from loose surficial sediments at the eastern and western ends of the cave. Bones were abundant on the surface of the cave and included *Capromys*, *Geocapromys*, *Cyclura*, *Puffinus*, bats, lizards, and several species of land birds. Spot Bay Cave was collected by G.S.M. in July 1979 and February 1986.

Stake Bay Cave: Lord Moyne (1938: 83) mentioned "Bones found in caves on Cayman Brac show that capromys of at least one other species, now extinct, formerly existed on the Cayman Islands." Although Moyne did not mention the location of these caves, specimen labels associated with several *Capromys* skulls and long bones in the Vertebrate Palaeontology collection of the NHM indicate that he collected these fossils from a cave near Stake Bay, Cayman Brac in 1937. During the Oxford University Cayman Islands Biological Expedition in 1938, C. Bernard Lewis collected several additional skulls and mandibles of *Capromys*, including the holotype skull of *C. pilorides lewisi*, from a cave located about a quarter mile west of Stake Bay on the north coast of Cayman Brac (C.B. Lewis, in litt., January 20, 1975). This locality is confirmed by specimen labels associated with the *Capromys* fossils in the Mammalogy Collection of the NHM, which record the locality as "¼ mile W. of Stakes Bay, Cayman Is." The spelling of the locality as it appears on the NHM specimen labels is clearly a clerical error, as the largest community on the north coast of Cayman Brac is Stake (not Stakes) Bay. In 1979, G.S.M. made an unsuccessful attempt to relocate this site.

Cayman Brac caves sampled by Harvey et al. (2016): Additional fossils of *Capromys* have recently been reported from five caves located on the southern coast of Cayman Brac (Harvey et al., 2016), with the following reported names and coordinates: Green Cave (19°43′9.12″N, 79°46′4.02″W); Pebble Cave (19°43′7.13″N, 79°46′12.69″W); Shelby's Bolt Hole (19°44′01.36″N, 79°46′45.76″W); Bedding Plane Cave I (19°44′7.73″N, 79°44′15.64″W); and Bedding Plane Cave II (19°44′6.82″N, 79°44′16.71″W). Harvey et al. (2016) did not provide any further information about the size of the caves, nature of the sediments, or the associated vertebrate faunas. Since most of the caves in the Cayman Islands do not have formal names, there is some possibility that one or more of these caves were discovered previously by FSM/FLMNH field crews on Cayman Brac between 1965 and 1980, but were given different names. In particular, the latitude and longitude of Bedding Plane Caves I and II indicate that these two caves are in the same general vicinity as our Pollard Bay Cave and Shearwater Caves 1 and 2. Harvey et al. (2016) illustrated a partial skull of *Capromys* from Bedding Plane Cave II, which was covered with a thick layer of calcium carbonate precipitate typical of many cave fossils in the Cayman Islands.

APPENDIX 2

Specimens Examined

Capromyid specimens for which comparative data on mandibular alveolar toothrow length were used for analysis in this study are as follows:

1. *Capromys pilorides pilorides*. AMNH: 4923/3809, 4924/3810, 4925/3811, 7981, 7983, 7984, 15912, 16726, 18049, 22806, 22821, 35246, 35768, 41051, 41052, 41053, 41054, 99659, 99660. USNM: 35226, 49979, 103884, 103885, 103886, 114033, 142096 (two specimens), 181232, 253232, 260783, 260784, 260785, 260787, 260788, 260790, 260830, 269281, 300626, 522971.

2. *Geocapromys brownii.* AMNH: 15976, 19147, 41558, 45151, 45152, 45153, 45154, 45155, 45156. MCZ: 11040, 25842, 25843, 29425, 29426, 46430. USNM: 141908, 143851.

3. *Geocapromys columbianus.* AMNH: 128 (two specimens), 474 (20 specimens). MCZ: 9505 (18 specimens).

4. *Geocapromys ingrahami.* AMNH: 3969/3033, 3972/3036, 3974/3038, 3976/3040, 3978/3042, 3979/3043, 3980/3044, 3981/3045. MCZ: 2107, 2108, 2116D, 2116E, 2116F, 2116H, 2712, 2712A, 14377, 29427, 29428, 29429, 29430, 29431, unnumbered (32 specimens). USNM: 35680, 395696, 396327.

5. *Geocapromys thoracatus.* AMNH: 34546, 34547. MCZ: 12816, 12817, 12818, 12819, 12821, 13177, 14535, 27882, 34846. USNM: 22692.

Scientific Publications of the American Museum of Natural History

American Museum Novitates
Bulletin of the American Museum of Natural History
Anthropological Papers of the American Museum of Natural History

Submission procedures can be found at http://research.amnh.org/scipubs

All issues of *Novitates* and *Bulletin* are available on the web (http://digitallibrary.amnh.org/dspace). Order printed copies on the web from:
http://shop.amnh.org/a701/shop-by-category/books/scientific-publications.html

or via standard mail from:
American Museum of Natural History—Scientific Publications
Central Park West at 79th Street
New York, NY 10024

♾ This paper meets the requirements of ANSI/NISO Z39.48-1992 (permanence of paper).

On the cover: Holotype of *Capromys pilorides lewisi* (Natural History Museum, London [Mammalogy] 71.155/M15705), one of three newly described extinct late Quaternary mammals from Cayman Islands, West Indies.