

The Cuban Crocodile (*Crocodylus rhombifer*) from Late Quaternary Underwater Cave Deposits in the Dominican Republic

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ABSTRACT

Late Quaternary fossils representing a locally extinct population of the Cuban crocodile (*Crocodylus rhombifer*) are reported from two underwater caves in the Dominican Republic. A large fossil sample of *C. rhombifer*, from Oleg's Bat Cave near Bavaro in the southeastern Dominican Republic, consists of four nearly complete skulls, numerous isolated cranial elements and mandibles, and more than 100 postcranial bones representing most of the skeleton. These fossils were collected from a completely submerged portion of the cave at a depth of 11 m and about 100 m from the nearest entrance. A skull, mandibles, and two vertebrae of a Cuban crocodile were also found in a second cave called Ni-Rahu, northeast of Santo Domingo.

We identify the fossil crocodile skulls from the Dominican Republic as *Crocodylus rhombifer* because they share the following characters with modern skulls of *C. rhombifer* from Cuba (as well as fossil skulls from Cuba, the Bahamas, and Cayman Islands): short, broad, and deep rostrum; large orbits; convex nasals along the midline (midrostral boss); prominent swelling

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on the lacrimals anterior and medial to the orbits; low but obvious ridges extending anteriorly from the lacrimals to the nasals and posteriorly from the lacrimals to the prefrontals and frontals, outlining a distinct diamond- or rhomboid-shaped structure; strongly concave interorbital region and cranial roof; high, narrow ridges on the internal margins of the orbits, extending from the prefrontals to the frontals and posteriorly to the postorbitals; prominent ridges along the lateral margins of the cranial roof on the postorbitals and squamosals, terminating as noticeable protuberances on the posterolateral corners of the squamosals; premaxillary/maxillary suture on the palate essentially horizontal or transverse to the long axis of the skull at the level of the first maxillary tooth; 13 teeth in the maxilla.

Certain aspects of the ecology and anatomy of living *Crocodylus rhombifer* in Cuba, and carbon isotope data from fossil crocodile bones from both the Dominican Republic and the Bahamas, indicate that the Cuban crocodile is a terrestrially adapted predator. The fossil deposits in Oleg's Bat Cave and other underwater caves in the Dominican Republic lack freshwater vertebrates, such as fish and turtles, but contain abundant samples of hystricognath rodents, small ground sloths, and other terrestrial vertebrates, including large land tortoises, that apparently were the primary prey of the crocodiles. Bats are abundant in the fossil deposits in Oleg's Bat Cave, and may have been an additional food source. Bone collagen from a tibia of *C. rhombifer* from Oleg's Bat Cave yielded an AMS radiocarbon date of 6460 ± 30 ryrBP (equivalent to 7320 to 7430 cal yrBP). The chronology for the local extinction of *C. rhombifer* in Hispaniola is currently unknown, except to document the presence of this species in the eastern Dominican Republic in the early Holocene. Radiocarbon dates and historical records confirm that Cuban crocodiles survived into the period of European colonization (post-1492) in the Bahamas and on Grand Cayman. The only species of crocodile currently found in Hispaniola, the American crocodile (*C. acutus*), occurs in coastal marine habitats and in two inland brackish-water lakes: Lago Enriquillo in the Dominican Republic and the nearby Etang Saumâtre in Haiti. *C. acutus* has no fossil record in Hispaniola or elsewhere in the West Indies, suggesting that this species may be a very recent (late Holocene) immigrant in the Antillean region. *Crocodylus rhombifer* has one of the most limited geographic ranges of any living crocodylian species, known only from freshwater swamps in south-central Cuba and the Isla de Juventud (Isla de Pinos) off the southwestern coast of Cuba. Locally extinct or extirpated populations of *C. rhombifer* from fossil deposits in the Dominican Republic, Grand Cayman, and the Bahamas document a considerably wider distribution for this species during the Late Quaternary.

INTRODUCTION

Within the past decade, cave divers in the Dominican Republic have discovered large samples of Late Quaternary vertebrate fossils in underwater caves, mostly in the eastern part of the country. In 2009, Walter Pickel and Curt Bowen discovered a nearly complete cranium and several postcranial elements of the extinct Hispaniolan monkey *Antillothrix bernensis* from La Jeringa Cave, an underwater cave in Padre Nuestro State Park in the eastern Dominican Republic (Pickel and Bowen, 2009; Rosenberger et al., 2011). That same year, a team from Indiana University collected a second complete skull of *Antillothrix* from the Padre Nuestro underwater cavern complex, also in Padre Nuestro State Park (Kay et al., 2011). In the next few years, cave divers from the Dominican Republic Speleological

Society (DRSS) recovered vertebrate fossils from the caves in Padre Nuestro State Park and several additional underwater caves. Large samples of Late Quaternary bats, collected by members of the DRSS, were reported from two underwater caves, Oleg's Bat Cave in La Altagracia province in the southeastern Dominican Republic and Cueva de Lily in María Trinidad Sánchez province in the northeastern region of the country (Velazco et al., 2013). An extinct species of land tortoise, *Chelonoidis dominicensis*, was recently described from Oleg's Bat Cave (Albury et al., 2018).

Only the primates, bats, and a tortoise have been described from Quaternary deposits in underwater caves in the Dominican Republic. The vertebrate faunas in most of these submerged caves are dominated by hystricognath rodents in the endemic West Indian family Capromyidae and extinct ground sloths in the family Megalonychidae (personal obs. by the authors). The relative abundance of rodents and ground sloths in the faunas from these underwater caves is similar to the faunas from Quaternary dry cave and sinkhole deposits from the Dominican Republic and neighboring Haiti (e.g., Miller, 1929a, 1929b, 1930; Woods, 1989a, 1989b; McFarlane et al., 2000; MacPhee et al., 2000). Several of these underwater caves have yielded fossils representing vertebrates that are rare or absent in Hispaniolan dry caves, including the monkeys mentioned above, as well as a tortoise and a number of crocodiles. The complete shell and skull of a giant land tortoise were recovered from Oleg's Bat Cave (Albury et al., 2018), the same underwater cave in the eastern Dominican Republic that produced a large sample of bats (Velazco et al., 2013), as well as most of the crocodile fossils described here. In addition to bats, Velazco et al. (2013) also mentioned that Oleg's Bat Cave contained ground sloths, rodents, the endemic Greater Antillean lipotyphlan insectivore *Solenodon*, and an extinct bird with Cuban affinities, as well as the Cuban crocodile *Crocodylus rhombifer*. In our study of the crocodiles from Oleg's Bat Cave, we also identified several dentaries and maxillae and numerous vertebrae of a large boid snake representing the genus *Chilabothrus* (formerly placed in the Neotropical genus *Epicrates*).

Here, we provide descriptions, measurements, and illustrations of Late Quaternary crocodile remains from two submerged caves in the Dominican Republic. Most of the fossils, representing at least five individuals, are from Oleg's Bat Cave, together with a skull, mandibles, and several associated vertebrae from a second submerged cave named Ni-Rahu (also known as Cueva de Lynn). We compare the Dominican crocodile fossils to modern specimens of *Crocodylus rhombifer* from Cuba, several fossil samples of *C. rhombifer* from elsewhere in the West Indies, including Cuba, Grand Cayman, and Abaco in the Bahamas, and modern skulls of the American crocodile *C. acutus* from Lago Enriquillo in the southwestern Dominican Republic. We also discuss the taphonomy and paleoecology of crocodiles in the Dominican Republic, and the extinction chronology and biogeography of *C. rhombifer* in the West Indies.

MATERIALS AND METHODS

Quaternary crocodiles were collected in the Dominican Republic as part of a joint project between Brooklyn College and the Museo del Hombre Dominicano (MHD), focusing on the

recovery of primates and other vertebrate fossils from underwater caves. Fossil crocodiles were recovered by cave divers from the Dominican Republic Speleological Society (DRSS), working under the auspices of the MHD. All fossil specimens of *Crocodylus rhombifer* from the Dominican Republic described here are housed in the MHD, Santo Domingo, Dominican Republic. We examined comparative specimens of fossil and modern West Indian crocodiles from the following museums, with acronyms in parentheses: American Museum of Natural History (AMNH), New York; Museo Nacional de Historia Natural República Dominicana (MNHNRD), Professor Eugenio Jesús Marcano, Santo Domingo, Dominican Republic; National Museum of the Bahamas (NMB), Marsh Harbour, Abaco, the Bahamas; Florida Museum of Natural History, University of Florida (UF), Gainesville, Florida; and the U.S. National Museum of Natural History (USNM), Smithsonian Institution, Washington, DC.

Cranial bones of *Crocodylus rhombifer* are identified in figure 1, which includes dorsal, ventral, lateral, and posterior views of a skull. Mandibular elements are identified in figure 2, which includes dorsal, ventral, lateral, and medial views of a mandible. Cranial measurements, defined below, are shown in figure 3, which illustrates dorsal and ventral views of a skull and dorsal and lateral views of a mandible of *C. rhombifer*. The skull and mandibles in figures 1–3 are late Holocene fossil specimens of *C. rhombifer* from Sawmill Sink in Abaco, Bahamas (Morgan and Albury, 2013).

The following list defines the cranial and mandibular measurements of *Crocodylus* in table 1 (letters refer to measurements illustrated in fig. 3):

- A. Total length of skull (premaxilla to quadrate)
- B. Length from premaxilla to posterior edge of parietal along midline (a similar measurement, head length, is taken on living crocodiles, which can then be used to provide a fairly accurate prediction of total length)
- C. Length of snout (premaxilla to anterior edge of orbits)
- D. Length of maxillary toothrow (measured ventrally on palate)
- E. Maximum breadth of premaxillae
- F. Breadth of snout at 5th maxillary tooth
- G. Minimum interorbital breadth
- H. Breadth at anterior edge of cranial roof (at postorbitals)
- I. Breadth at posterior edge of cranial roof (at squamosal protuberances)
- J. Breadth of skull at quadrates
- K. Maximum breadth of skull (at quadratojugals)
- L. Length of mandibular toothrow
- M. Total length of mandible (from anterior tip of dentary to posterior tip of articular)
- N. Maximum length of dentary

For each skull, we also recorded several additional morphological characters including: structure of the cranial table (consisting of the frontals, postorbitals, squamosals, and parietals); development of various ridges and/or bosses on the lacrimals and internal margin of the orbits; character of the premaxillary/maxillary suture on the palate; the presence or absence of a small hole at the anterior end of the premaxilla caused by a penetration of the first dentary tooth

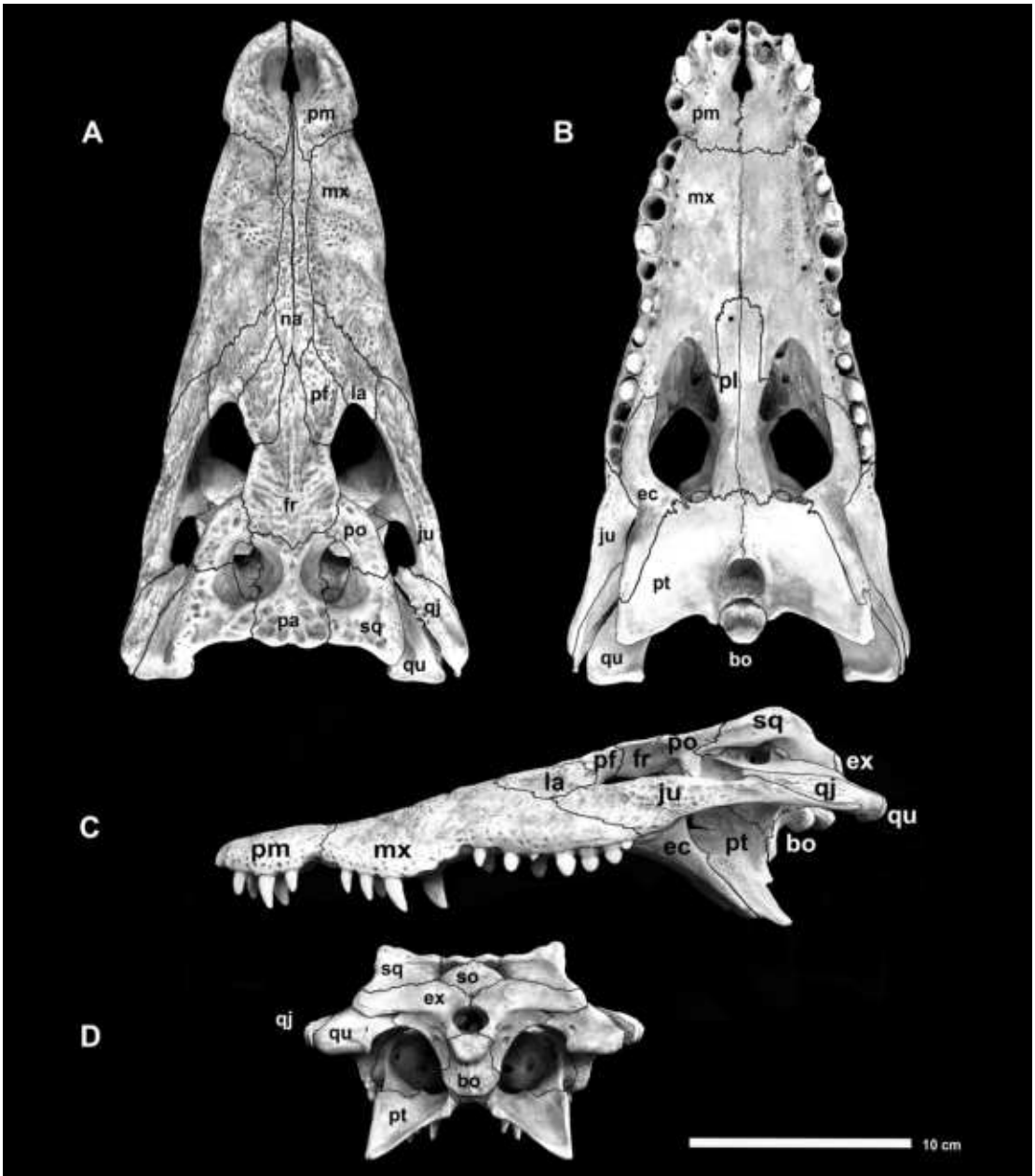


FIGURE 1. Skull of a Cuban crocodile (*Crocodylus rhombifer*) of late Holocene age from Sawmill Sink (NMB. AB50.171; C52), Abaco, Bahamas, in **A**. dorsal, **B**. ventral, **C**. left lateral, and **D**. posterior, views. The individual bones in the skull are identified using the following abbreviations: **bo** (basioccipital = occipital condyle), **ec** (ectopterygoid), **ex** (exoccipital), **fr** (frontal), **ju** (jugal), **la** (lacrima), **mx** (maxilla), **na** (nasal), **pa** (parietal), **pf** (prefrontal), **pl** (palatine), **pm** (premaxilla), **po** (postorbital), **pt** (pterygoid), **qu** (quadrate), **qj** (quadratojugal), **so** (supraoccipital), **sq** (squamosal).

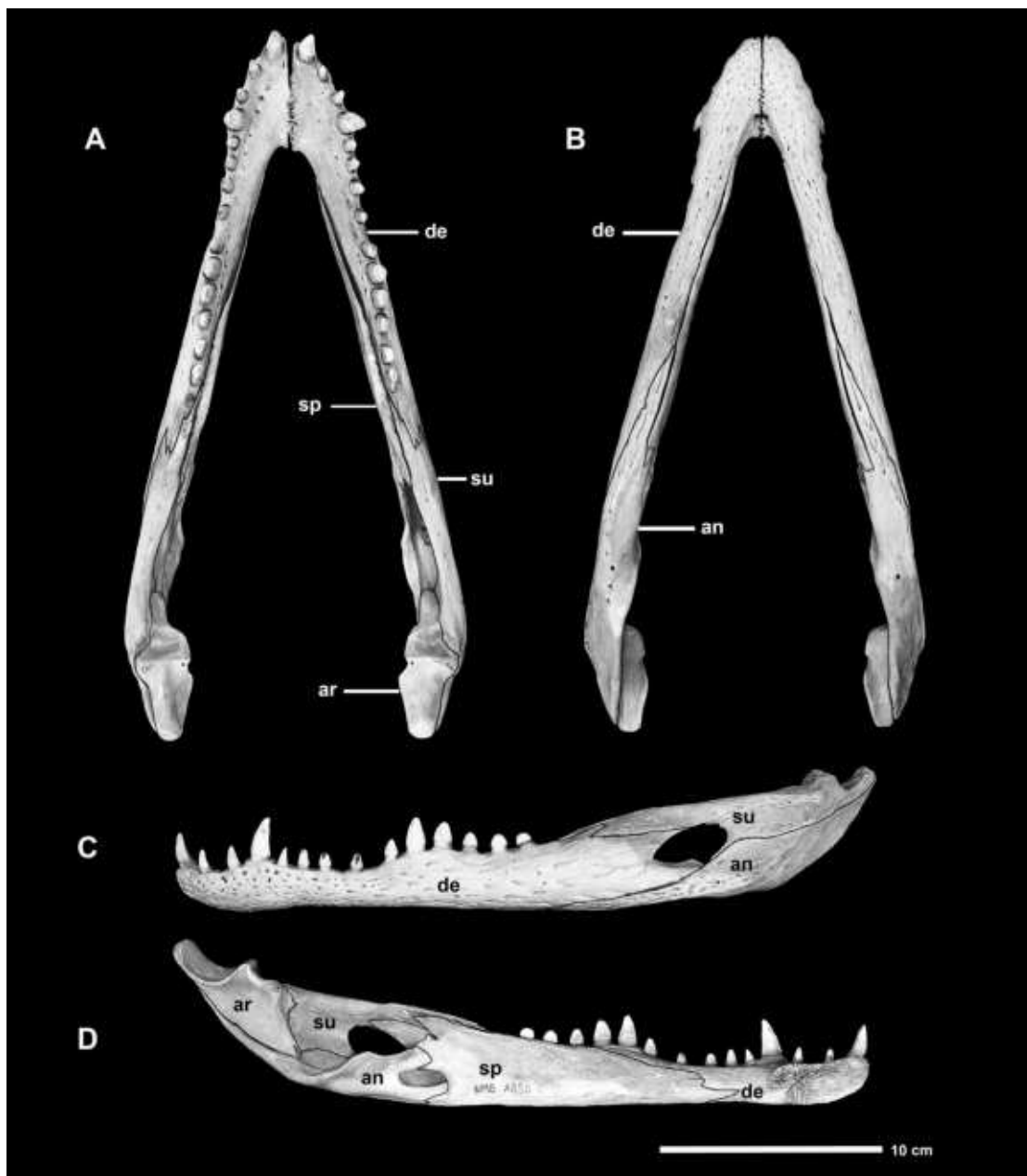


FIGURE 2. Mandible of a Cuban crocodile (*Crocodylus rhombifer*) of late Holocene age from Sawmill Sink (NMB.AB50.171; C52), Abaco, Bahamas, in **A**, dorsal, **B**, ventral, **C**, left lateral, and **D**, left medial views. The individual bones in the mandible are identified using the following abbreviations: **an** (angular), **ar** (articular), **de** (dentary), **sp** (splenial), **su** (surangular). The coronoid bone is missing from this specimen.

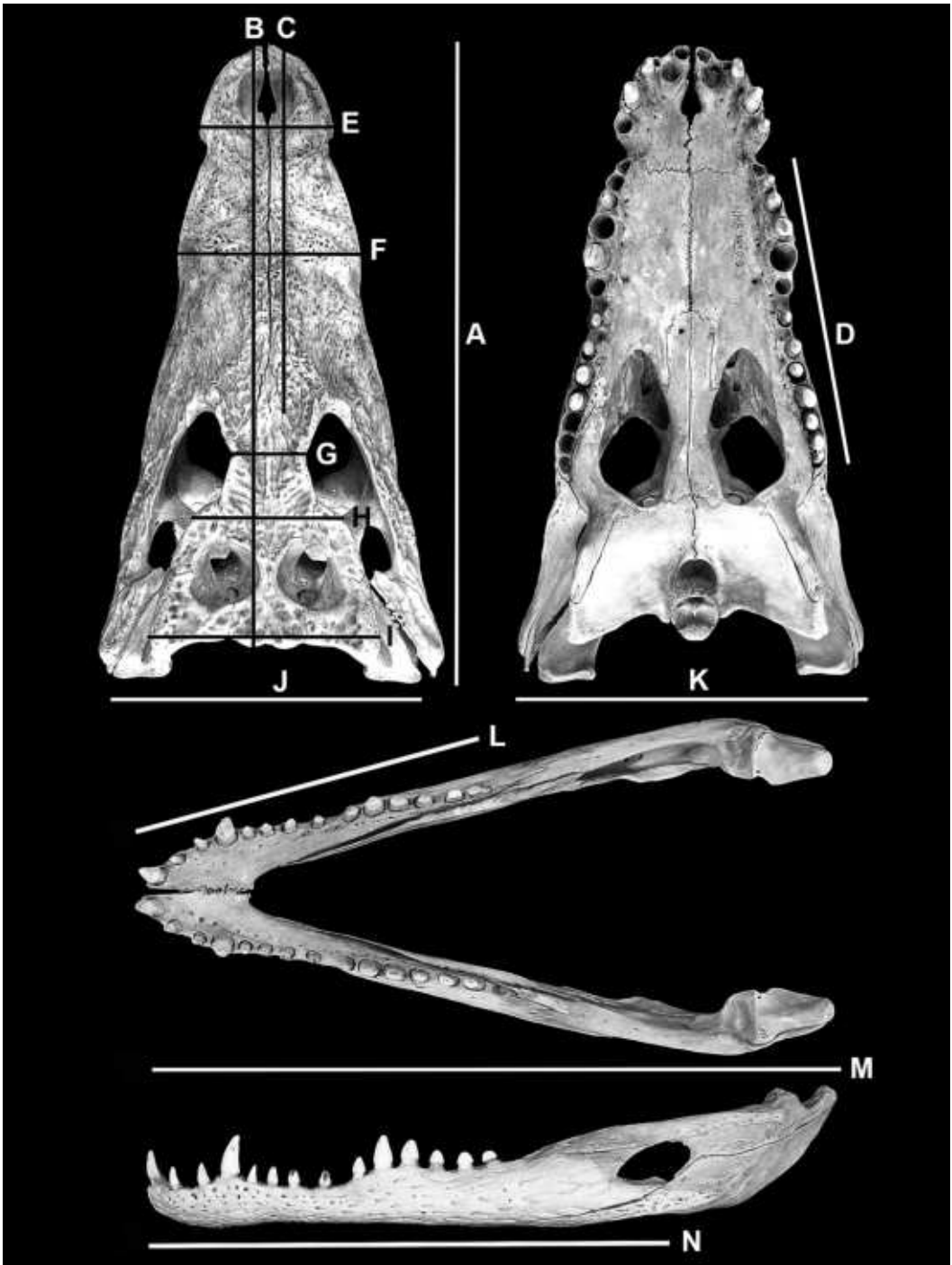


FIGURE 3. Skull and mandible of a Cuban crocodile (*Crocodylus rhombifer*) from Sawmill Sink (NMB.AB50.171; C52), Abaco, Bahamas, showing the measurements taken on crocodile specimens from the Dominican Republic, Abaco, Grand Cayman, and Cuba. The measurements (letters A–N) are explained in Materials and Methods.

through the premaxilla; and the number of teeth in the maxilla. On the mandibles, we recorded the number of teeth in the dentary and the tooth position of the three largest teeth.

We compare the fossil crocodiles from the Dominican Republic to skulls and skeletons of *Crocodylus rhombifer* from elsewhere in the West Indies, including fossil and modern specimens from Cuba and fossils from Abaco in the Bahamas and Grand Cayman in the Cayman Islands. In their preliminary study of the fossil crocodile sample from the Dominican Republic in the MHD collection in November 2014, G.S.M. and N.A.A. had a specimen of *C. rhombifer* available for direct comparisons, a nearly complete fossil skeleton from Sawmill Sink on Abaco (NMB.AB50.020, C22), including a skull, mandibles, and most of the major limb and girdle elements. Cranial comparisons of the Dominican fossil crocodiles are also made with two other living species of crocodiles from the West Indian region, the American crocodile *C. acutus*, including specimens from Lago Enriquillo in the Dominican Republic and the Florida Keys, and Morelet's crocodile *C. moreletii* from the Caribbean coast of Mexico. The appendix provides a complete list of fossils of *C. rhombifer* from the Dominican Republic and modern and fossil comparative specimens.

When discussing the general age of crocodile fossils from the West Indies, we often use the term Late Quaternary, which refers to sites of Holocene and late Pleistocene age. Most Quaternary sites with crocodiles in the West Indies have not been radiocarbon (^{14}C) dated, and thus we do not know for certain whether these sites are Holocene or Pleistocene in age. When radiocarbon dates are available, we refer to dated sites as either Holocene (less than 10,000 years) or Pleistocene (older than 10,000 years). We obtained an accelerator mass spectrometry (AMS) radiocarbon date on a tibia of *Crocodylus rhombifer* from Oleg's Bat Cave. The date was determined by the Beta Analytic, Inc., radiocarbon dating lab in Miami, Florida.

We calculated the minimum number of individuals (MNI) of crocodiles present in Oleg's Bat Cave. The MNI of a sample is determined by counting the largest number of a particular bone from either the right or left side of the skeleton. For example, if a sample contains seven right femora and four left femora and no other element is as numerous, then we would assume that the crocodile sample from that site contained a minimum of seven individuals. The MNI of Cuban crocodiles from Oleg's Bat Cave was determined on the basis of the number of brain-cases. All measurements are in mm.

LATE QUATERNARY CROCODILE SITES IN THE DOMINICAN REPUBLIC

OLEG'S BAT CAVE

Oleg's Bat Cave, also known as Oleg's Bat House, was discovered by cave diver Oleg Shevchuk in 2009. Oleg's Bat Cave was named for the large number of bats roosting in the cave, as well as the remarkable sample of fossil bats collected and described from underwater deposits on the cave floor (Velazco et al., 2013). A pelvis of a small sloth of the genus *Neocnus* and a mandible of *Solenodon paradoxus* also were recovered from the same region of the cave as the crocodiles. The cave is about 7 km inland from (west of) Bávaro, which is located on the southeastern coast of the Dominican Republic in La Altagracia province (fig. 4: site 1). The approxi-

mate coordinates of the cave are 18°42' N, 68°32' W. The cave is currently being modified by the landowners who are planning to open Oleg's Bat Cave as a commercial venture under the name "Fossil Cave of Punta Cana-Macao." Punta Cana and Macao are two other towns on the east coast of the Dominican Republic, near Bávaro. The cave's owners have installed an extensive stairway system that extends from the entrance down to a large, water-filled chamber.

The main entrance to Oleg's Bat Cave is at an elevation of 22 m, and from here the cave descends about 20 m to water, indicating that the water level in the cave is near current sea level. From this entrance, the dry portion of the cave ends in a fairly sizeable room containing water up to several meters deep with a large air-filled chamber above. Several passageways originate in this large room and lead in different directions, but these passageways rather quickly become submerged. The explored portion of Oleg's Bat Cave is about 900 m long, mostly consisting of flooded passages with a maximum depth of 11 m and an average depth of about 6 m. The water in Oleg's Bat Cave is freshwater. There is no halocline with a denser layer of saltwater underlying the freshwater, as is often present in submerged caves, called "blue holes" in the Bahamas (Steadman et al., 2007). The limestone walls of the cave are decorated. Many of the cave formations show dark, tannic-acid staining. The floor of the cave is covered with a layer of soft, fine-grained sediment. The original entrance to Oleg's Bat Cave is located about 150 m from the main cave entrance. This second entrance is barely 2 m in diameter, with about a 13 m vertical drop to water, and opens into a large room filled with bat guano from the thousands of bats that live in the cavities in the ceiling.

Crocodile fossils were collected from Oleg's Bat Cave on three different dive trips by members of the DRSS, in August 2011, August 2012, and May 2013. The fossils were recovered from the underwater portions of the cave approximately 100 m from each cave entrance at a depth of 11 m. No fossil material was recovered from the dry portions of the cave. The crocodile fossils were partially buried, with some elements of the skeleton protruding from the sediments on the cave floor and visible to the divers (see fig. 5).

NI-RAHU

A second cave called Ni-Rahu, also known as Cueva de Lynn, has produced a skull and jaws and several associated vertebrae of a crocodile. This cave yielded more species of nonvolant mammals (nonbats) than Oleg's Bat Cave (personal obs. by the authors). The nonvolant mammals recovered thus far include: the small insectivoran, or "island shrew," *Nesophontes paramicrus*; a large-bodied sloth likely of the genus *Parocnus* but currently unidentifiable to species because of a thick speleothem crust; and two rodent species, the extinct *Isolobodon portoricensis* and the extant *Plagiodontia aedium*. Postcranial specimens of squamate reptiles and several birds were also recovered. Skeletal material from three domestic animals (dog, pig, and goat) were found in the cave as well.

Ni-Rahu is located about 50 km northeast of Santo Domingo in Guerra province, Santo Domingo Este (fig. 4: site 2). It is part of a large dry cave system that contains 1500 m of known passages, although to date the cave has not been mapped completely. The flooded portion of the

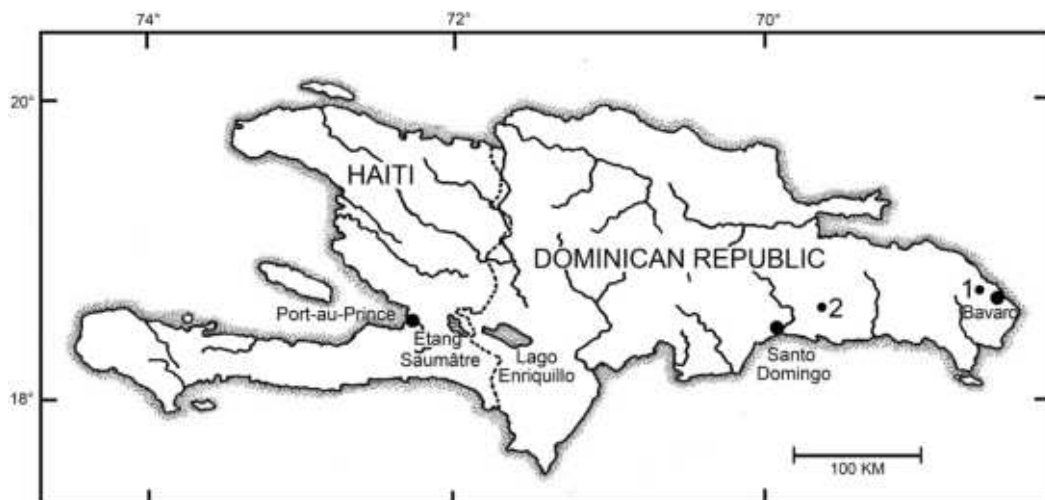


FIGURE 4. Map of Hispaniola (Dominican Republic and Haiti), showing Late Quaternary fossil localities of the Cuban crocodile (*Crocodylus rhombifer*), as well as several cities and topographic features mentioned in the text. 1. Oleg's Bat Cave, Altagracia province; 2. Ni-Rahu (= Cueva de Lynn), Guerra province (map modified from Velazco et al., 2013).

cave is located 80 m from the entrance and has a maximum depth of 10 m. It is accessed by rappelling 15 m from the dry cave down to the water surface. Fossils were found in the flooded cave near the entry to the pool at a depth of 7 m. The floor of the flooded portion of the cave is covered with 8–15 cm of silt above solid rock. Fossils were not recovered in the deeper regions of the flooded portion or in the dry cave. No excavations have been conducted in the dry cave. Phillip Lehman and Cristian Pittaro of the DRSS collected fossils from Ni-Rahu on August 10, 2013.

Many of the specimens recovered from Ni-Rahu were covered in a thick crust of flowstone, including not only the crocodile remains but also portions of the skeletal material of the domestic animals recovered. While dogs were introduced into Hispaniola with Amerindian populations (Lawrence, 1977; Stahl, 2013), the first record of goats and pigs on the island was by Europeans in the early 16th century (Street, 1962; Long, 2003). This suggests speleothem-forming processes may have occurred relatively rapidly in this cave—over hundreds rather than thousands of years. While most speleothems form in dry caves, calcite can be deposited underwater in pools of supersaturated water. Thus the presence of speleothem-covered specimens does not necessarily imply that the skeletal remains were deposited when the cave was dry. Nevertheless, the speleothem layer on the indigenous animal remains is far thicker than that on the nonnative species.

OTHER UNDERWATER CAVE SITES IN THE DOMINICAN REPUBLIC WITH CROCODILE FOSSILS

Phillip Lehman and divers from the DRSS have discovered fossils of crocodiles in two additional underwater caves near Oleg's Bat Cave, west of Bávaro in the southeastern Dominican Republic. The crocodile fossils from these two caves have not been collected. Figure 5F

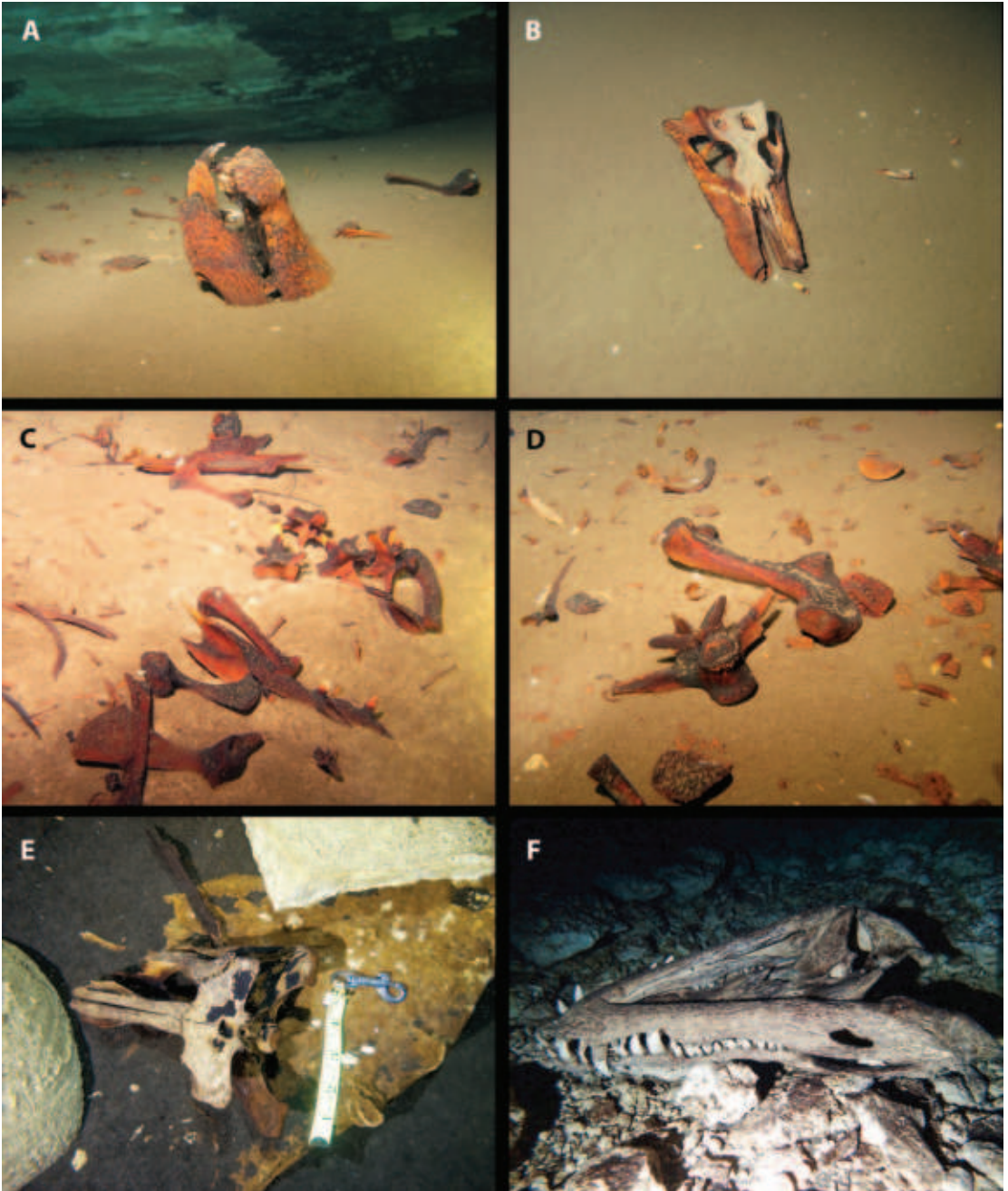


FIGURE 5. Underwater photographs of Late Quaternary fossils of the Cuban crocodile (*Crocodylus rhombifer*) from the Dominican Republic. A–E, Oleg’s Bat Cave: A. Skull and articulated mandible. B. Skull of second individual. C. Dentary and postcranial elements. Note very small slender bones of bats. D. Humerus and vertebra in center of photo, surrounded by osteoderms. E. Partial crocodile skull (scale in inches). F. Complete skull and articulated mandibles, from unnamed cave near Oleg’s Bat Cave. Specimen is “upside down” with mandibles on top. The skull and jaws in panel F were not collected.

illustrates a complete skull and articulated mandibles, with a nearly complete set of teeth, from an unnamed cave near Oleg's Bat Cave. Numerous crocodile fossils have also been found in Cueva de Macho, which is only about 150 m north of Oleg's Bat Cave. To reach the water in Cueva de Macho requires a 30 m vertical rappel.

VERTEBRATE PALEONTOLOGY

CROCODYLIA Owen, 1842

CROCODYLIDAE Cuvier, 1807

CROCODYLUS Laurenti, 1768

Crocodylus rhombifer Cuvier, 1807

Cuban Crocodile

Figures 6–10

REFERRED SPECIMENS: The sample of Quaternary crocodile fossils from the Dominican Republic consists of about 100 specimens, five of which consist of partial to complete skulls with partial associated postcranial skeletons. The following list of specimens includes only the most complete fossil skulls and mandibles of *Crocodylus rhombifer* from Oleg's Bat Cave and Ni-Rahu used in the cranial descriptions and comparisons. The appendix provides a more complete list of the fossil sample of *C. rhombifer* from the Dominican Republic, including postcranial material associated with several of the skulls listed here. Isolated postcranial elements from Oleg's Bat Cave are listed as *C. rhombifer* in the appendix. Although most postcranial elements of crocodiles cannot be confidently identified to the species level, it seems reasonable to tentatively refer these specimens to *C. rhombifer* considering that all diagnostic cranial material from this same site represents this species.

NI-RAHU: MHD 414. Complete skull and articulated mandibles, and two associated vertebrae. Collected by Phillip Lehman and Cristian Pittaro of the DRSS on August 10, 2013. The skull and mandibles from Ni-Rahu are illustrated in figure 6. The left half of the skull from the premaxilla to the quadrate is covered with a thick layer of calcite flowstone. No observations could be made on the palate of this specimen because of the flowstone coating. The mandibles are also covered with flowstone, with only the teeth on the right side visible. Several cranial measurements either could not be taken or are estimates (table 1). The mandibles are firmly attached to the skull, and are so completely covered in flowstone that little of their anatomy is evident, except for the teeth in the right mandible.

OLEG'S BAT CAVE: MHD 572. A nearly complete skull lacking only the left premaxilla, right nasal, and the ectopterygoids and palatines (fig. 7). This specimen also includes associated postcranial elements (see appendix). Collected "under mud" on the floor of Oleg's Bat Cave by members of the DRSS on August 12, 2012. A handwritten note in the MHD collection identifies this specimen as "crocodile 1."

MHD 573. A partial skull consisting of the right and left maxillae, right lacrimal, frontals, squamosals, quadrates, and occipital region. This specimen also includes associated postcranial elements (see appendix). Collected from the surface deposits on the floor of Oleg's Bat Cave by members of the DRSS on August 12, 2012. A handwritten note in the MHD collection identifies this specimen as "crocodile 2." This is the smallest individual among the four complete or nearly complete skulls in the fossil crocodile sample from the Dominican Republic.

MHD 574. Complete skull and right and left mandibles. This specimen also includes associated postcranial elements (see appendix). Collected by members of the DRSS in August 2012. A handwritten note in the MHD collection identifies this specimen as "crocodile 3." This is the largest individual crocodile in the fossil sample from the Dominican Republic, and is also the most complete (fig. 8). Figure 5A shows this skull in the field, protruding from the sediment underwater on the floor of Oleg's Bat Cave. A tibia associated with MHD 574 was sampled for radiocarbon dating (see below).

MHD 575. Right and left dentaries. This specimen also includes associated postcranial elements (see appendix). Collected by members of the DRSS in August 2012. A handwritten note in the MHD collection identifies this specimen as "crocodile 4."

MHD 576. Right and left premaxillae and right and left mandibles of a small individual. This specimen also includes a partial associated postcranial skeleton (see appendix). Collected by members of the DRSS in August 2012. A handwritten note in the MHD collection identifies this specimen as "crocodile 5."

MHD 577. Left maxilla and left surangular. This specimen also includes several associated postcranial elements (see appendix). Collected by Cristian Pittaro and Dave Pratt of the DRSS in August 2011.

MHD 579, 580. Both specimens consist of partial braincases collected by Phillip Lehman and Cristian Pittaro of the DRSS on May 11, 2013.

The minimum number of individuals (MNI) of *Crocodylus rhombifer* represented in the sample from Oleg's Bat Cave is five based on the braincase region, which is preserved in the three partial to nearly complete skulls (MHD 572–574), as well as two isolated partial braincases (MHD 579, 580). Several limb bones of *C. rhombifer* from Oleg's Bat Cave, including the humerus, femur, tibia, and fibula, are each represented by an MNI of four.

SKULLS AND MANDIBLES

The following description is based primarily on the three most complete skulls of *Crocodylus rhombifer* from the Dominican Republic, MHD 414, 572, 574 (see measurements of these three skulls in table 1). MHD 574 from Oleg's Bat Cave is the largest and most complete of these skulls (fig. 8). MHD 572 from Oleg's Bat Cave is somewhat smaller and not quite as complete (fig. 7). MHD 414 from Ni-Rahu, a complete skull with articulated mandibles, is intermediate in size between the other two skulls, but much of the specimen is covered with a thick layer of calcite flowstone (fig. 6). Most dorsal cranial features of MHD 414 can be observed, but all palatal and basicranial features are obscured. Comparisons among these three



FIGURE 6. Skull and articulated right and left mandibles of a Cuban crocodile (*Crocodylus rhombifer*) of Late Quaternary age from Ni-Rahu (= Cueva de Lynn), Dominican Republic (MHD 414). The skull and mandibles of this specimen are partially covered with a thick layer of calcite flowstone, obscuring many morphological features. A. Dorsal, B. ventral, C. left lateral, D. right lateral, and E. posterior views.



FIGURE 7. Skull of a Cuban crocodile (*Crocodylus rhombifer*) of Late Quaternary age from Oleg's Bat Cave, Dominican Republic (MHD 572) in A. dorsal, B. ventral, C. left lateral, and D. posterior views.



FIGURE 8. Skull and left mandible of a Cuban crocodile (*Crocodylus rhombifer*) of Late Quaternary age from Oleg's Bat Cave, Dominican Republic (MHD 574). Skull in **A.** dorsal, **B.** ventral, **C.** left lateral, and **D.** posterior views. Left mandible in **E.** medial and **F.** lateral views.

skulls, description of additional fragmentary cranial specimens, and assessment of minor morphological differences and individual variation are discussed in the following section.

The snout or rostrum of the fossil crocodile skulls from the Dominican Republic is comparatively short and broad. In lateral view, the snout anterior to the orbits is very deep, especially from the orbits anterior to a point dorsal to the 5th maxillary tooth. The convex nasals along the midline contribute to the appearance of a deeper snout. The combination of the deep snout and elevated ridges on the internal margins of the orbits contributes to a comparatively large and prominent orbit, especially evident in lateral view.

The interorbital region and cranial roof or cranial table are noticeably concave, in particular the frontals medial to the orbits and anterior to the supratemporal fenestrae or dorsal temporal openings and the parietals along the midline. There are high, narrow ridges on the internal margins of the orbits, on the prefrontals and frontals, continuing posteriorly to the postorbitals at the posterointernal margins of the orbits. Prominent ridges continue posteriorly on the postorbitals and squamosals, along the lateral margins of the cranial roof. The anterior margin of the cranial roof meets the ridge on the internal margin of the orbit at nearly a 90° angle. The lateral margins of the cranial roof are not quite parallel, forming a very gentle angle trending posterolaterally, such that the anterior breadth of the cranial table at the postorbitals is somewhat less than the posterior breadth of the cranial table at the squamosals (table 1). Beginning at the postorbitals, the lateral margins of the cranial roof consist of prominent raised ridges that are thick and rounded throughout most of their length. The ridges on the cranial roof terminate posteriorly as swollen protuberances or processes on the posterolateral extremities of the squamosals. In posterior view, the squamosal protuberances are particularly prominent. The lateral ridges on the cranial table are thicker and more rounded dorsally than the thin, sharp interorbital ridges. Immediately ventral to the lateral ridge on the cranial table is a horizontal depression that is anteroposteriorly oriented on both the postorbitals and squamosals. This deep groove is parallel to and accentuates the cranial ridge dorsal to the groove. There are also distinct, narrow ridges along the internal margins of the supratemporal fenestrae, although these ridges are lower and less prominent than the lateral ridges on the cranial roof.

Medial to the ridges on the internal margins of the orbit and lateral margins of the cranial roof, the dorsal surface of the skull from the orbits to the posterior edge of the skull is noticeably concave. The interorbital region is strongly concave on the frontals, especially the posterior portion of the frontals where they meet the parietals, and on the anteromedial extension of the postorbitals. The posteriormost portion of the cranial table, consisting of the parietals and posteromedial portion of the squamosals, is also notably concave. The narrow anterior extension of the parietals, along the midline between the supratemporal fenestrae, is also concave.

Anterior and medial to the orbits, there is a prominent swelling or boss on the lacrimals. This boss is best developed on the posteromedial portion of the lacrimals at the anteromedial margin of the orbits. There is also a ridge on the lacrimals that extends transversely along the anterior edge of the orbits. The ridges on the internal margins of the orbits begin anteriorly at this boss at the anteriormost extension of the orbits. The ridges extend anteromedially along the medial

edge of the lacrimals from the lacrimal boss to the suture between the lacrimals and nasals. The lacrimal ridges, extending posteriorly from the lacrimal boss to the anterointernal margin of the orbits, are lower and less prominent than the interorbital ridges. From the anterior edge of the orbits, the interorbital ridges continue posteriorly along the internal margin of the orbits, on the posterolateral margins of the prefrontals and the lateral margin of the frontals. In dorsal view, these ridges extend anteriorly from the lacrimals to the nasals and posteriorly from the lacrimals to the prefrontals and frontals, forming a distinct diamond or rhomboid shape. This diamond-shaped structure is somewhat narrower at its anteriormost extension at the nasal-lacrimal suture than at its posteriormost extension at the prefrontal-frontal suture, reaching its maximum breadth just anterior to the orbits. The anterior portion of the diamond-shaped structure forms a convex swelling or boss on the lacrimals anterior to the orbits, whereas the posterior portion of the rhomboid is concave on the prefrontals medial to the orbits.

In lateral view, the skull has a midrostral boss anterior to the orbits, consisting of a broad, low convexity located primarily on the nasals. This midrostral boss is more prominent than the smaller, paired lacrimal bosses. The nasals are noticeably convex along the midline, from the lacrimal suture anteriorly to a point dorsal to the 5th maxillary tooth. There is also a swelling or convexity on the lateral margins of the maxillae dorsal to the 4th and 5th maxillary teeth, the two largest teeth in the maxilla. Anterior to the 4th tooth and extending almost to the premaxillary/maxillary suture, the maxillae are concave, especially medially where they contact the nasals, consisting of an elongated depression oriented anteroposteriorly. There is also a depression or concavity on the posterior edge of the premaxillae posterior to the nasal aperture. Along the premaxillary/maxillary suture is a broad, low ridge, while there are concavities both anterior to this suture on the posterior portion of the premaxillae and posterior to the suture on the anterior portion of the maxillae. The premaxillae have a small triangular posterior extension between the nasals and maxillae, extending posteriorly to the level of the 2nd maxillary tooth.

In ventral view, the premaxillary/maxillary suture on the palate is essentially horizontal or transverse to the long axis of the skull, at the level of the 1st maxillary tooth. The suture begins laterally at the level of the anterior edge of the alveolus for the 1st maxillary tooth and extends transversely across the palate, meeting the midline at about the same level (i.e., at the level of the anterior edge of the 1st maxillary tooth). As discussed in the next section, there are minor variations in the location of the premaxillary/maxillary suture, with several skulls having the lateral extremity of this suture located slightly more posteriorly, and in several skulls the suture takes a slight anterior or posterior excursion about a third of the distance across the palate. With one exception, all maxillaries from the Dominican Republic have 13 teeth. One skull (MHD 574) has 14 teeth in both the right and left maxillae. The largest tooth in the maxilla is the 5th tooth followed in size by the 4th tooth and then the 10th. The teeth from 1 to 9 are rounded in cross section, whereas teeth from 10 to 13 are somewhat laterally flattened.

The mandibles in the Dominican Republic fossil crocodile sample are fairly typical of the genus *Crocodylus* (fig. 8E, F; also see fig. 2). In all mandibles in the sample, the dentary has

15 teeth. The three largest teeth, in order from the largest, are the 4th followed by the 1st and then the 10th.

CRANIAL VARIATION: MHD 574 from Oleg's Bat Cave is the largest fossil skull of *Crocodylus rhombifer* from the Dominican Republic, while the skull from Ni-Rahu (MHD 414) is the second largest (table 1). Even though somewhat smaller than MHD 574, the cranial ridges of MHD 414 from Ni-Rahu are more prominent, including the ridges on the internal margins of the orbits and on the lateral edges of the cranial table. Both the cranial table and interorbital region of the Ni-Rahu skull are noticeably more concave, especially on the posterior portion of the prefrontals and the entire frontal region. MHD 414 is very similar to, and only slightly larger than, a skull of *Crocodylus rhombifer* from Sawmill Sink on Abaco, Bahamas (NMB. AB50.20).

An unusual feature of the largest fossil skull in the Dominican sample, MHD 574 from Oleg's Bat Cave, is the presence of several round holes or perforations in the dorsal surface (see fig. 8A). Two of the perforations are on the right frontal, with the more medially placed hole the deeper of the two. A third perforation in the parietals, along the midline medial to the posterior edges of the supratemporal fenestrae, appears to perforate the cranial roof into the underlying braincase. There is another smaller hole in the parietals along the midline just anterior to the posterior edge of the skull. A fifth hole is located on the left squamosal just medial to the posterolateral margin of the skull. These holes or perforations are atypical for this species, and probably represent either a pathology or, more likely, bite marks inflicted by another crocodile.

The location of the premaxillary/maxillary suture on the palate is variable in skulls of *Crocodylus rhombifer* from the Dominican Republic. In most skulls, this suture is horizontal, beginning laterally at the level of the anterior edge of the alveolus for the 1st maxillary tooth and extending transversely across the palate, meeting the midline at about the same level. In several skulls, the premaxillary/maxillary suture takes a slight excursion, either anteriorly or posteriorly, at a point about a third of the distance between the toothrow and the midline, closer to the toothrow. In one skull (MHD 574), the premaxillary/maxillary suture has a slight anterior excursion, meeting the midline at a point slightly anterior to the 1st maxillary tooth, whereas in a second skull (MHD 572) this suture has a slight posterior excursion, meeting the midline at a point corresponding to the midpoint of the alveolus for the 1st maxillary tooth. Laterally, the suture is located at the anterior edge of the alveolus of the 1st maxillary tooth in several specimens, whereas in several other skulls this suture begins laterally at the level of the middle of the alveolus for the 1st maxillary tooth.

With one exception, all skulls or isolated maxillae of *Crocodylus rhombifer* from the Dominican Republic have 13 teeth in the maxilla. One skull (MHD 574) has 14 teeth in both the right and left maxillae. The last or 14th tooth in MHD 574 is tiny and round in cross section. The presence of this tooth is unusual for *C. rhombifer*, as most skulls of this species have only 13 teeth in the maxilla. Skulls of *C. acutus* typically have 14 teeth in the maxilla.

Cranial measurements are provided for the three most complete skulls of *Crocodylus rhombifer* from the Dominican Republic (table 1). This table also presents measurements of skulls of comparative specimens of *Crocodylus* from elsewhere in the West Indies, including fossil

TABLE 1. Cranial measurements of Late Quaternary and modern crocodiles (*Crocodylus*) from the West Indies. The letters following the measurements (A, B, etc.) correspond with letters for these measurements in Methods and in figure 3. Measurements of *C. rhombifer* from Abaco and Grand Cayman are from Morgan and Albury (2013), and include only mean, observed range, and sample size, not measurements of individual specimens. Missing measurements are indicated by “-”. All measurements are in mm. L = length; W = width; ant. = anterior; post. = posterior.

Species	Island and site	Catalog number and sample statistics	Skull L (A)	Premaxilla-parietal L (B)	Snout L (C)	Maxillary tooththrow L (D)	Premaxilla W (E)	Snout W at 5th maxillary tooth (F)	Interorbital W (G)	Cranial roof W-ant. (H)	Cranial roof W-post. (I)	Skull W (K)	Skull W at quadrates (J)
<i>Crocodylus rhombifer</i>													
Dominican Republic (fossil)													
Oleg's Bat Cave													
		MHD 572	271	247	159	133	-	82	24	60	79	143	132
		MHD 574	349	304	198	178	81	110	34	78	107	185	173
Ni-Rahu (= Cueva de Lynn)													
		MHD 414	286	256	164	142	66	88	25	64	83	149	-
		Mean	302	269	174	151	74	93	28	67	90	159	153
		Observed range	271-349	247-304	159-198	133-178	66-81	82-110	24-34	60-78	79-107	143-185	132-173
		Sample size	3	3	3	3	2	3	3	3	3	3	2
Cuba (modern)													
Cienega de Zapata													
		6214 (Havana) Uncat.	349	330	218	-	76	106	-	91	-	196	172
		(Crocodile Farm)	475	398	265	218	109	154	-	109	166	274	245
Captive													
		UF 45189	346	303	199	160	78	110	-	77	111	203	190
		Mean	390	344	227	189	88	123	-	95	139	224	202
		Observed range	346-475	303-398	199-265	160-218	76-109	106-154	-	77-109	111-166	196-274	172-245
		Sample size	3	3	3	2	3	3	-	3	2	3	3
Cuba (fossil)													
Ciego Montero													
		AMNH 6179	653	550	355	292	191	254	-	136	236	400	384
		AMNH 6180	-	-	355	247	173	234	-	-	-	-	-

Species and site	Catalog number and sample statistics	Skull L (A)	Premaxilla-parietal L (B)	Snout L (C)	Maxillary tooththrow L (D)	Premaxilla W (E)	5th maxillary tooth (F)	Interorbital W (G)	Cranial roof W-ant. (H)	Cranial roof W-post. (I)	Skull W (K)	Skull W at quadrates (J)
AMNH 6181		504	436	292	236	146	200	-	120	175	320	306
AMNH 6185		382	335	224	185	79	115	-	86	112	214	202
Mean		513	440	307	240	147	201	-	114	174	311	297
Observed range		382-653	335-550	224-355	185-292	79-191	115-254	-	86-136	112-236	214-400	202-384
Sample size		3	3	4	4	4	4	-	3	3	3	3
Abaco, Bahamas (fossil) ¹												
Mean		286	260	161	139	66	94	28	67	92	155	143
Observed range		233-361	212-321	132-206	117-153	49-89	68-136	21-34	53-83	71-119	125-181	116-169
Sample size		12	12	12	11	12	12	13	13	13	11	11
Grand Cayman												
Cayman Islands (fossil) ²												
Mean		289	241	151	132	53	79	25	62	83	-	133
Observed range		247-385	223-276	139-175	108-174	53	71-100	22-31	56-76	75-104	-	117-163
Sample size		5	4	4	9	2	4	4	4	4	-	3
<i>Crocodylus acutus</i>												
Dominican Republic (modern) ³												
MNHNRD 1		532	470	335	259	93	139	53	112	126	238	220
MNHNRD 2		530	478	342	262	102	149	53	115	123	-	-
MNHNRD 3		522	469	344	264	94	145	53	109	127	-	-
MNHNRD 4		470	412	290	228	80	114	43	94	106	-	191
Mean		514	457	328	253	92	137	51	108	121	238	206
Observed range		470-532	412-478	290-344	228-264	80-102	114-149	43-53	94-115	106-127	238	191-220
Sample size		4	4	4	4	4	4	4	4	4	1	2

¹The fossil sample from Abaco includes 10 skulls from Sawmill Sink, and 1 skull each from Nancy's Cave and Ralph's Cave.

²The fossil sample from Grand Cayman includes skulls or partial skulls from six different sites, including (number of skulls in parentheses): Chisholm Cow Well (2), Connally Cow Well (1), Crocodile Canal (2), Furtherland Farms Cow Well (1), Prospect (1), and Queen Elizabeth II Botanic Park (3).

³The modern sample of *Crocodylus acutus* from the Dominican Republic consists of 4 skulls from Lago Enriquillo in the Museo Nacional de Historia Natural, República Dominicana (MNHNRD), Santo Domingo, Dominican Republic.

samples of *C. rhombifer* from Abaco, Grand Cayman, and Cuba, a modern sample of *C. rhombifer* from Cuba, and a modern sample of *C. acutus* from the Dominican Republic.

POSTCRANIAL SKELETON

Measurements are presented in table 2 for the primary limb elements in forelimb (humerus, radius, ulna) and hind limb (femur, tibia, fibula) of fossil *Crocodylus rhombifer* from the Dominican Republic. This table also provides measurements of limb bones for comparative fossil specimens of *C. rhombifer* from Abaco and Grand Cayman. The humerus, radius, ulna, femur, tibia, and fibula of an associated individual (MHD 576) of *C. rhombifer* from Oleg's Bat Cave are illustrated in figure 9 (all limb bones are from the left side). The right and left ilia from another individual of *C. rhombifer* from Oleg's Bat Cave are illustrated in figure 10 (MHD 575). Several of the fossil skulls of *C. rhombifer* from Oleg's Bat Cave (MHD 572, 574–576) have associated partial postcranial skeletons, including most of the major limb and girdle elements. Since all of the skulls from Oleg's Bat Cave represent *C. rhombifer*, it seems reasonable to assume that limb bones and other unassociated postcranials from the same cave also represent *C. rhombifer*. These isolated postcranial elements, in particular the limb bones, are not only identical to the same elements from the associated skeletons from Oleg's Bat Cave, they are also very similar to postcranial elements of Late Quaternary *C. rhombifer* from Abaco and Grand Cayman. In addition to the limb bones measured in table 2 and listed in the appendix, there are also samples from Oleg's Bat Cave representing the remainder of the postcranial skeleton, including the pectoral and pelvic girdles, vertebrae, ribs, metapodials, carpals, tarsals, phalanges, and osteoderms. Although most of these postcranial elements are not described in this paper (see discussion of vertebrae below), they may prove useful for future studies of the postcranial anatomy, functional morphology, and ontogenetic and individual variation of *Crocodylus rhombifer*.

ESTIMATED TOTAL LENGTH

We provide estimates for the total length of the Late Quaternary specimens of *Crocodylus rhombifer* from the Dominican Republic, based on cranial measurements of the fossil sample. Crocodile biologists use a standard ratio to calculate the approximate total length of a crocodile based on its head length. According to Kent Vliet (personal commun.), the "head length" in living crocodiles, measured from the tip of the snout to the back of the head or cranial table along the midline, multiplied by 7.2, is roughly equal to the total length of the animal (from tip of snout to tip of tail), although this ratio varies somewhat ontogenetically and by species. In other words, the total length of a crocodile is a little more than seven times the head length. The head length in a living crocodile rather closely approximates the skull measurement in table 1 called "premaxilla to parietal length" (fig. 3; measurement B), which is the length from the anterior tip of the premaxilla to the posterior margin of the parietals along the midline. Since skulls lack the skin and underlying connective tissue found in living animals, the total length prediction based on a skull probably slightly underestimates the total length. Using this ratio, we calculated the approximate total length of the crocodiles represented by the three fossil skulls of *C. rhombifer* from the Dominican Republic on which we could measure the "head length" (= premaxilla to parietal length). The largest fossil crocodile skull from

TABLE 2. Postcranial measurements of Late Quaternary Cuban crocodiles (*Crocodylus rhombifer*) from the West Indies. Measurements of *C. rhombifer* from Abaco and Grand Cayman are from Morgan and Albury (2013), and include only mean, observed range, and sample size, not measurements of individual specimens. All measurements are in mm. L = length; W = width.

Island	Site	Element	Catalog number	Sample statistics	L	Proximal W	Shaft W	Distal W	
Dominican Republic	Oleg's Bat Cave	Humerus	MHD 574		148	51	20	50	
			MHD 575		114	37	14	36	
			MHD 576		93	29	12	28	
			MHD 587		153	53	21	54	
			Mean		127	43	17	42	
			Observed range		93–153	29–53	12–21	28–54	
			Sample size		4	4	4	4	
			Radius	MHD 575		78	18	7	22
				MHD 576		64	14	6	15
				MHD 593		100	25	11	26
				Mean		81	19	8	21
				Observed range		64–100	14–25	6–11	15–26
				Sample size		3	3	3	3
			Ulna	MHD 572		90	28	11	19
		MHD 576			73	22	9	14	
		MHD 594			114	37	12	27	
		Mean			92	29	11	20	
		Observed range			73–114	22–37	9–12	14–27	
		Sample size			3	3	3	3	
		Femur	MHD 572		147	36	15	36	
			MHD 574		190	49	21	50	
			MHD 576		123	29	12	29	
			MHD 583		158	39	15	41	
			Mean		155	38	16	39	
			Observed range		123–190	29–49	12–21	29–50	
			Sample size		4	4	4	4	

Island	Site	Element	Catalog number	Sample statistics	L	Proximal W	Shaft W	Distal W
		Tibia						
			MHD 572		108	33	12	29
			MHD 574		133	40	17	37
			MHD 576		91	24	10	24
			MHD 584		113	33	12	28
				Mean	111	33	13	30
				Observed range	91-133	24-40	10-17	24-37
				Sample size	4	4	4	4
		Fibula						
			MHD 572		105	18	7	18
			MHD 576		88	14	6	15
			MHD 582		134	25	10	24
			MHD 586		112	17	8	20
				Mean	110	19	8	19
				Observed range	88-134	14-25	6-10	15-24
				Sample size	4	4	4	4
Bahamas								
	Abaco ¹							
		Humerus						
				Mean	107	35	14	35
				Observed range	83-144	25-51	10-23	24-50
				Sample size	7	7	7	7
		Radius						
				Mean	80	21	9	21
				Observed range	57-111	13-32	5-16	13-30
				Sample size	7	7	7	7
		Ulna						
				Mean	93	29	11	21
				Observed range	66-134	17-46	6-17	12-35
				Sample size	8	8	7	8
		Femur						
				Mean	153	39	16	38
				Observed range	109-193	26-51	11-22	26-51
				Sample size	8	8	8	8
		Tibia						
				Mean	105	33	13	29

Island	Site	Element	Catalog number	Sample statistics	L	Proximal W	Shaft W	Distal W
				Observed range	79–129	23–42	8–18	21–37
				Sample size	4	4	4	4
		Fibula		Mean	94	16	7	16
				Observed range	76–103	12–20	5–8	12–19
				Sample size	4	4	4	4
Cayman Islands	Grand Cayman ²	Humerus		Mean	107	32	13	32
				Observed range	90–130	26–40	10–17	26–40
				Sample size	7	7	7	7
		Radius		Mean	75	17	7	17
				Observed range	61–88	13–20	5–8	13–21
				Sample size	4	4	4	4
		Femur		Mean	140	33	13	32
				Observed range	103–166	23–40	9–17	23–40
				Sample size	6	6	6	6
		Tibia		Mean	95	26	10	25
				Observed range	76–108	19–32	7–12	18–29
				Sample size	6	6	6	6
		Fibula		Mean	93	15	6	16
				Observed range	82–104	11–16	5–7	15–17
				Sample size	4	4	4	3

¹ The postcranial sample of *Crocodylus rhombifer* from Abaco includes specimens from four localities: Sawmill Sink, Nancy's Cave, Ralph's Cave, and Lost Reel Cave. See Morgan and Albury (2013) for a complete list of postcranial specimens of *C. rhombifer* from fossil sites on Abaco.

² The postcranial sample of *Crocodylus rhombifer* from Grand Cayman includes specimens from five localities: Chisholm Cow Well, Crocodile Canal, Furtherland Farms Cow Well, Prospect, and Queen Elizabeth II Botanic Park. See Morgan and Albury (2013) for a complete list of postcranial specimens of *C. rhombifer* from fossil sites on Grand Cayman.



FIGURE 9. Limb bones of the Cuban crocodile (*Crocodylus rhombifer*) of Late Quaternary age from Oleg's Bat Cave, Dominican Republic. All limb bones are from the left side and are from the same associated individual (MHD 576). A. Humerus, B. radius, C. ulna, D. femur, E. tibia, F. fibula. In each pair of photographs, the anterior view is on the left and posterior view on the right.

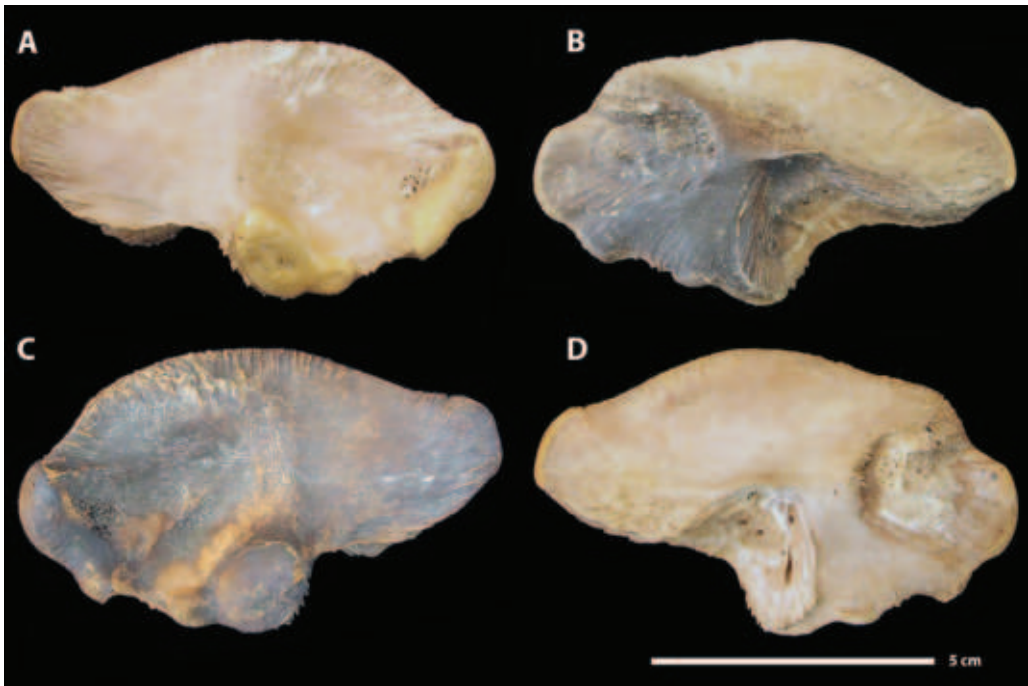


FIGURE 10. Ili of the Cuban crocodile (*Crocodylus rhombifer*) of Late Quaternary age from Oleg's Bat Cave, Dominican Republic (MHD 575). A. External and B. internal views of the right ilium; C. external and D. internal views of the left ilium.

the Dominican Republic, from Oleg's Bat Cave (MHD 574), had an approximate total length of 2.19 m (0.304 m head length $\times 7.2$), whereas the smallest skull, also from Oleg's Bat Cave (MHD 572), had an approximate total length of 1.78 m (0.247 m head length $\times 7.2$).

Platt et al. (2009) presented several regression equations to predict the total length of living or recently deceased individuals of Morelet's crocodile, *Crocodylus moreleti*, based on various measurements of the head. Three head measurements in Platt et al. (2009) are comparable to our measurements on crocodile skulls (table 1), including (our skull measurements in parentheses): dorsal cranial length = head length (= premaxilla to parietal length), snout length (= length of snout), and cranial width (= maximum breadth of skull). As noted in the previous paragraph, because of the presence of skin and underlying connective tissue, the head measurements on the living animals will be somewhat greater than the similar measurements on the skull, and thus the length predictions from the fossil skulls are probably underestimates.

The regression equation from Platt et al. (2009) to predict the total length (TL) of a crocodile from the dorsal cranial length (DCL) is: $TL = 7.09DCL - 2.69$, with measurements of the TL and DCL in cm. Using the measurement of 30.4 cm for the premaxilla to parietal length (= DCL) in the largest fossil skull of *Crocodylus rhombifer* from Oleg's Bat Cave (MHD 574), the formula $TL = 7.09(30.4) - 2.69 = 213$ yields an estimated total length for this specimen of 2.13 m (= 213 cm, from the regression equation). This is very similar (6 cm less, within 3%) to the estimated total length of 2.19 m for this same fossil skull using the ratio of premaxilla to pari-

etal length $\times 7.2$. Using this same regression equation for the smallest fossil skull of *C. rhombifer* from Oleg's Bat Cave (MHD 572), with a measurement of 24.7 cm for the premaxilla to parietal length, the formula $TL = 7.09 (24.7) - 2.69 = 172$ yields an estimated total length for this specimen of 1.72 m (= 172 cm, from the regression equation). Once again, this is very similar (6 cm less; within 4%) to the estimated total length of 1.78 m for this same fossil skull using the ratio of premaxilla to parietal length $\times 7.2$.

A second regression equation from Platt et al. (2009) estimates the TL of a crocodile using the snout length (SL): $TL = 10.48SL + 6.20$. Using the measurement of 19.8 cm for the snout length (length from premaxilla to anterior edge of orbits) in the largest skull of *Crocodylus rhombifer* from Oleg's Bat Cave (MHD 574), the formula $TL = 10.48 (19.8) + 6.20 = 214$ yields an estimated total length for this specimen of 2.14 m (= 214 cm, from the regression equation). This is almost exactly the same length predicted by the regression equation based on the premaxilla to parietal length of the same skull (2.13 m), and only 5 cm less than the TL of 2.19 m using the ratio of premaxilla to parietal length $\times 7.2$. A third regression from Platt et al. (2009) estimates the TL using the cranial width (CW): $TL = 12.31CW + 5.83$. Using the measurement of 18.5 cm for the maximum breadth of the skull (= cranial width) in the same fossil crocodile skull from Oleg's Bat Cave (MHD 574), the formula $TL = 12.31 (18.5) + 5.83 = 234$ yields an estimated total length for this specimen of 2.34 m (= 234 cm, from the regression equation). The total length predicted by the maximum breadth of the skull (= cranial width) is somewhat greater (about 20 cm longer, 9%) than the estimates based on the two length measurements.

It is not surprising that different head or cranial measurements would yield somewhat conflicting results with regard to regression equations for estimating the total length of crocodiles. Our data suggest that the two length measurements of the skull, premaxilla to parietal length and length of snout, are more accurate for predicting total length. The total length estimates from the regression equations of Platt et al. (2009) from these two measurements of the largest fossil skull of *Crocodylus rhombifer* from the Dominican Republic (MHD 574) are very similar (TL of 2.13 m based on the premaxilla to parietal length; 2.14 m based on the length of snout), and are also similar to the length estimate (2.19 m) from the ratio of premaxilla to parietal length (= head length = dorsal cranial length) $\times 7.2$ of this same skull.

ONTOGENETIC AGE

There is a substantial range of sizes of crocodiles represented in the large fossil sample of skulls, mandibles, limb bones, and other postcranial elements from Oleg's Bat Cave in the Dominican Republic (tables 1, 2). Presumably, these size differences reflect differences in the ontogenetic ages represented by the fossils, although Brochu (1996) cautioned against using size alone as an indicator of maturity in crocodylians. According to Brochu, one of the best indicators of ontogenetic age in crocodylians is the degree of fusion of the neurocentral suture between the neural arch and centrum of the vertebrae. Except for the caudal vertebrae, the neural arches are not fused to the centra in vertebrae of immature crocodylians. Based on the vertebrae of several crocodylian species, including Late Quaternary fossils of *Crocodylus rhombifer* from Grand Cayman, Brochu (1996) observed a sequence in neurocentral suture closure progressing anteriorly from the caudal

to the cervical vertebrae, with the sutures on the caudal vertebrae fusing at a very young age and dorsal and cervical vertebrae fusing later in ontogeny. The closure of the neurocentral sutures on the cervical vertebrae indicates the attainment of physical or morphological maturity of an individual crocodylian, regardless of the overall size of the vertebrae.

The fossil crocodile sample from Oleg's Bat Cave includes numerous isolated vertebrae (>50), representing all segments of the vertebral column (caudals, sacrals, dorsals, and cervicals). We assume all the vertebrae in the crocodile sample from this site belong to the same species as the skulls, *Crocodylus rhombifer*, even though the vertebrae are probably not diagnostic at the species level. Under Referred Material and in the appendix, we list a number of postcranial elements, in particular limb bones, that were associated in the field with certain skulls (e.g., "crocodile 1," "crocodile 2") and were cataloged with the same numbers as the skull. Even though many of the crocodile vertebrae were found in close proximity to several of the skulls on the cave floor, there were no articulated skeletons and thus we cannot be certain that specimens found together actually belonged to the same individual. Consequently, our analysis of these vertebrae is based on individual specimens that cannot be directly associated with other crocodile fossils from this same deposit, including skulls, mandibles, and limb bones. All caudal vertebrae in the crocodile sample have a fused neurocentral suture. About 10 vertebrae, all of which are either dorsals or cervicals, have an unfused neurocentral suture and are represented by either a separate centrum or neural arch. These are invariably the smallest vertebrae in the sample, not including caudals, and their unfused sutures indicate they are from juvenile individuals. The majority of the sample (>75%) consists of medium-sized vertebrae, primarily dorsals and cervicals, in which the neurocentral suture is fused, indicating physically mature individuals. We examined two cervical vertebrae in which the neurocentral suture was partially fused but the line of fusion between the centrum and neural arch was still visible, indicating these specimens were not quite fully mature. Most of the crocodile vertebrae from Oleg's Bat Cave meet the criteria of Brochu (1996) for mature individuals. The sample of vertebrae agrees reasonably well with the crania, in which only one of the five skulls is from a very small individual, presumably a juvenile, and the remaining four medium-sized skulls are from adult crocodiles.

The crocodile vertebrae in the sample from Oleg's Bat Cave represent a range of sizes, from small to medium-sized individuals, but none appear to be from really large crocodiles. The vertebrae reflect the overall fossil crocodile sample from this site, which is represented primarily by medium-sized but physically mature specimens. The overall size range of the Quaternary skulls and limb bones of *Crocodylus rhombifer* from the Dominican Republic is similar to the size of comparable fossils from Abaco and Grand Cayman (comparative measurements in tables 1, 2). The fossil sample of *Crocodylus rhombifer* from Ciego Montero in Cuba includes skulls that are considerably larger than any fossil skulls from the Dominican Republic (see discussion in next section). We have not examined or measured the fossil postcranials of *C. rhombifer* from Ciego Montero, but we presume this sample also contains larger specimens of limb bones and vertebrae than are present in the fossil crocodile samples from the Dominican Republic, Abaco, and Grand Cayman.

COMPARISONS WITH OTHER WEST INDIAN CROCODILES

CROCODYLUS RHOMBIFER

We compared the sample of four fossil skulls of *Crocodylus rhombifer* from Oleg's Bat Cave and Ni-Rahu in the Dominican Republic to modern and fossil skulls of *C. rhombifer* from Cuba and fossil skulls referred to this species from Abaco and Grand Cayman (see list of fossil and modern comparative cranial material of *C. rhombifer* in the appendix). All the cranial features described above for the fossil crocodile skulls from the Dominican Republic also characterize other West Indian samples of fossil and recent skulls of *C. rhombifer*. As expected, there is variation in certain cranial features, observed both within the small sample of fossil skulls from the Dominican Republic (as discussed above) and between the Dominican sample and skulls from Cuba, Abaco, and Grand Cayman. Cranial characters that show minor variation among the West Indian samples of *C. rhombifer* include: degree of development of the prominent ridges on the lateral edges of the cranial table on the postorbitals and squamosals (always prominent, but these ridges are better developed in some specimens than others); degree of development of the pronounced squamosal protuberances at the posterolateral corners of the cranial table (always pronounced, but these protuberances are larger in some specimens than others); location of the lateral border of the premaxillary/maxillary suture (lateral border of this suture is located anterior to the 1st maxillary tooth in some specimens, near the middle of this tooth in other specimens, and as far posterior as the posterior edge of the 1st maxillary tooth in other specimens); orientation of the premaxillary/maxillary suture (at a point about a third of the distance between the tooththrow and the midline, closer to the tooththrow, the premaxillary/maxillary suture takes a slight excursion either anteriorly to a point slightly anterior to the alveolus of the 1st maxillary tooth or posteriorly to a point corresponding to the middle of the 1st maxillary tooth); and the number of maxillary teeth (13 teeth in the majority of specimens, but 14 teeth are present in one skull from Oleg's Bat Cave and a skull from Abaco, while another skull from Abaco has only 12 teeth).

The primary difference among the fossil samples of *Crocodylus rhombifer* from the Dominican Republic, Cuba, Abaco, and Grand Cayman is the overall size of individuals (measurements of skulls in table 1; of limb bones in table 2). The largest skulls of *C. rhombifer* are from Cuba, with two fossil skulls from the Ciego Montero spring deposit representing the largest known individuals of this species, living or fossil. The total length of the skull in modern specimens of *C. rhombifer* from Cuba averages 390 mm (observed range, 346–475 mm; 3 individuals, 2 from the Zapata Swamp, 1 captive). The total length of the skull in Late Quaternary specimens of *C. rhombifer* from Ciego Montero in Cuba averages 513 mm (observed range, 382–653 mm; 3 individuals). The skulls of *C. rhombifer* from the three other islands are considerably smaller than the skulls from Cuba. The fossil crocodile skulls from the Dominican Republic (Hispaniola) have a mean total skull length of 302 mm (observed range, 271–349 mm; 3 individuals). The fossil skulls of *C. rhombifer* from Abaco are somewhat smaller on average, with a mean total skull length of 286 mm (observed range, 243–361 mm; 12 adult individuals), although the largest skull from Abaco (361 mm) is slightly larger than the largest skull from

the Dominican Republic (349 mm). The Cuban crocodile skulls from Grand Cayman are the smallest on average, with a mean total skull length of 265 mm (observed range, 247–305 mm; 4 individuals), although a partial skull from Grand Cayman has an estimated total length of more than 385 mm, which is larger than any of the skulls from the Dominican Republic or Abaco (Morgan and Albury, 2013).

The skulls of modern specimens of *Crocodylus rhombifer* from Cuba average more than 20% larger than the fossil skulls of this species from the Dominican Republic, and the fossil skulls from Ciego Montero in Cuba average 40% larger than the Dominican skulls. Admittedly, the sample sizes are small, but the considerably larger size of the Cuban individuals of *C. rhombifer* is puzzling. In a previous study of fossil *C. rhombifer* from Abaco and Grand Cayman, Morgan and Albury (2013) suggested that the smaller size of the crocodiles on those two islands was related to limited food resources, which was primarily a result of their smaller land area and reduced ecological diversity compared to Cuba. However, this hypothesis does not provide an adequate explanation for the smaller size of crocodiles from the Dominican Republic, as the island of Hispaniola is similar in ecological diversity to Cuba and nearly as large. We suspect that larger crocodiles were present in Hispaniola during the Late Quaternary, but have not yet been sampled.

We also compared the approximate total lengths predicted by the Late Quaternary skulls of *Crocodylus rhombifer* from the Dominican Republic to the predicted lengths of the Cuban crocodile from Cuba, Abaco, and Grand Cayman, using the same ratio discussed above (total length = head length $\times 7.2$). As discussed in more detail above, the length of the skull from the premaxilla to the parietal along the midline (see table 1) is a fairly accurate proxy of “head length” in modern crocodiles. The Late Quaternary skulls of *C. rhombifer* from Ciego Montero in Cuba are much larger than fossil skulls of this species from the Dominican Republic. Accordingly, the predicted total length of the crocodiles from Cuba is also much larger, with the observed range from 2.41 m–3.96 m (0.335 m–0.550 m, premaxilla to parietal length $\times 7.2$; 3 individuals), compared to the predicted size range of the Dominican crocodiles of 1.78 m–2.19 m. As predicted by this same ratio, the approximate total length of the fossil Cuban crocodiles from Abaco of 1.52 m–2.31 m (0.212 m–0.321 m, premaxilla to parietal length $\times 7.2$; 12 individuals) and Grand Cayman of 1.61 m–1.99 m (0.223 m–0.276 m, premaxilla to parietal length $\times 7.2$; 4 individuals) are within the same general size range as the fossil crocodiles from the Dominican Republic.

We also estimated the total length (TL) of fossil specimens of *Crocodylus rhombifer* from Cuba, Abaco, and Grand Cayman using the regression equation of Platt et al. (2009), developed from a large modern sample of Morelett’s crocodile *C. moreletii* from Belize. As above, we used our cranial measurement of premaxilla to parietal length on the fossil skulls as a close equivalent of dorsal cranial length (DCL; from Platt et al., 2009) in modern crocodiles. Using the equation of $TL = 7.09DCL - 2.69$ (measurements of the TL and DCL in cm), yielded the following estimated total length ranges for the fossil samples of *C. rhombifer* from Cuba (TL = 2.35 – 3.87 m); Abaco (TL = 1.48 – 2.25 m); and Grand Cayman (1.55 – 1.93 m). In all of these specimens, the estimated total lengths from the regression equation of Platt et al. (2009) are slightly smaller (~3%) than the length estimates from the formula of head length $\times 7.2$.

C. ACUTUS FROM LAGO ENRIQUILLO

We examined, measured, and photographed five modern skulls of the American crocodile *Crocodylus acutus* from Lago Enriquillo in the southwestern Dominican Republic, housed in the MNHNRD in Santo Domingo. The most complete of these skulls of *C. acutus* (MNHNRD1) is illustrated in fig. 11. All five of the skulls are adults, four are from large individuals, and one is somewhat smaller, in the same size range as the largest fossil skull of *C. rhombifer* from Oleg's Bat Cave (see table 1 for measurements of the skulls of *C. acutus* from Lago Enriquillo). All five of these skulls of *C. acutus* lack associated lower jaws and postcranial skeletons. The following comparisons are limited to the samples of modern skulls of *C. acutus* from Lago Enriquillo and fossil skulls of *C. rhombifer* from Oleg's Bat Cave and Ni-Rahu in the Dominican Republic (specimens examined listed in the appendix). The following section provides comparisons of the fossil skulls of Dominican *C. rhombifer* with modern skulls of *C. acutus* from localities outside of Hispaniola, as well as skulls of Morelet's crocodile, *C. moreletii*, from the Gulf of Mexico and Caribbean coasts of Mesoamerica.

The rostrum of the modern skulls of *Crocodylus acutus* from Lago Enriquillo is much longer and narrower than in *C. rhombifer*. The Lago Enriquillo skulls of *C. acutus* have a prominent convexity, the midrostral boss, located along the midline anterior to the orbit. The midrostral boss is primarily situated on the posterior third of the nasals, but also incorporates small portions of the posteromedial portion of the maxilla, and the anterior portion of the lacrimals and prefrontals. *C. rhombifer* also has a midrostral boss on the nasals, but it is lower and less prominent. In lateral view, *C. acutus* has a steep angle in the dorsal margin of the rostrum anterior to the midrostral boss, at about the level of the 7th maxillary tooth. The anterior portion of the rostrum, including both the maxilla and premaxilla, is much shallower in this species compared to *C. rhombifer*, in which the rostrum is much deeper anteriorly. The orbit is not as prominent in lateral view in *C. acutus*, owing to a narrower maxilla and weak interorbital ridges. The orbit in *C. rhombifer* appears larger because of the deep maxilla and anterior process of the jugal below the orbit and strongly upraised ridges on the internal margin of the orbit.

Crocodylus acutus lacks a lacrimal boss and a low transverse ridge on the lacrimals anterior to the orbits, both of which occur in the skulls from Oleg's Bat Cave. The large midrostral boss is located farther anteriorly along the midline in *C. acutus*. The American crocodile also lacks the rhomboid- or diamond-shaped structure anterior to the orbits characteristic of *C. rhombifer*, which is defined by prominent ridges that extend anteriorly from the lacrimals to the nasals and posteriorly from the lacrimals to the prefrontals. *C. acutus* has low, weak ridges on the medial edge of the lacrimals and also has ridges on the internal margin of the orbits, but these ridges are not nearly as high or prominent as in *C. rhombifer*. The interorbital region, especially the frontals, is considerably broader and only weakly concave in *C. acutus*, compared to the narrower and strongly concave interorbital region of *C. rhombifer*. The low interorbital ridge continues posteriorly to the posteromedial margin of the orbits on the postorbital in *C. acutus*, where the ridge terminates. Unlike *C. rhombifer*, there are essentially no ridges on the lateral edges of the cranial table in *C. acutus*, and no protu-

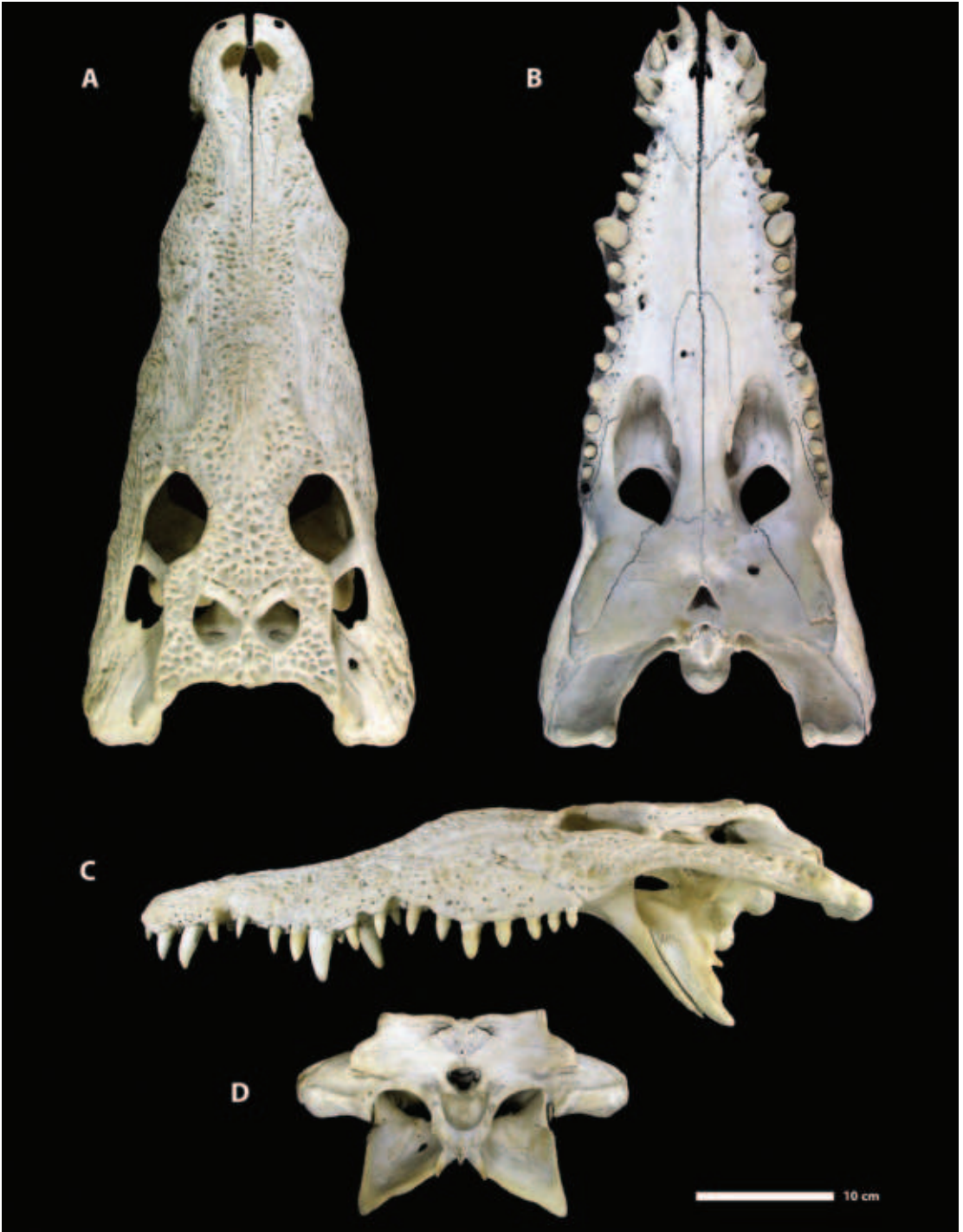


FIGURE 11. Modern skull of an American crocodile (*Crocodylus acutus*) from Lago Enriquillo, Dominican Republic (MHNHRD1) in A. dorsal, B. ventral, C. left lateral, and D. posterior views.

berances on the squamosals at the posterolateral margin of the cranial table. In *C. acutus*, the cranial table is almost perfectly flat, especially the frontals and squamosals, with only the anterior portion of the parietals slightly concave. The medial portion of the cranial table is highly concave in *C. rhombifer*, and its lateral margins are characterized by prominent ridges. In posterior view, the posterior margin of the cranial table is flat in *C. acutus*, with no evidence of a midline concavity in the parietals or the curved and upraised lateral protuberances on the squamosals that are characteristic of *C. rhombifer*.

The premaxillae of the skulls of *Crocodylus acutus* from Lago Enriqueillo have round perforations anteriorly on both the right and left sides that correspond to the 1st teeth in the dentary and also have narrow, triangular processes that extend posteriorly between the nasals and maxillae to the level of the 4th maxillary tooth. The premaxilla is shorter and broader in *C. rhombifer* and the fossil skulls, the posterior processes of the premaxillae are much shorter, extending posteriorly to the level of the 2nd maxillary tooth, and no perforations are present anteriorly. The posterior portion of the premaxilla is flattened in *C. acutus*, but has a strong concavity or groove in *C. rhombifer* just anterior to the premaxillary/maxillary suture. There is a slight ridge at the premaxillary/maxillary suture in *C. acutus*, but a much more prominent ridge along this suture in *C. rhombifer*. Immediately posterior to the premaxillary/maxillary suture, the anterior portion of the maxilla on the dorsal surface of the skull is slightly concave in *C. acutus*, and deeply concave in *C. rhombifer*.

On the ventral surface of the skull in *Crocodylus acutus*, the premaxillary-maxillary suture is strongly W-shaped or V-shaped, with a triangular-shaped process that extends posteriorly along the midline. The premaxillary-maxillary suture begins laterally anterior to the 1st maxillary tooth and then angles posteromedially toward the midline, meeting the midline suture at the level of the 2nd or 3rd maxillary tooth. Just before reaching the midline, this suture has a slight anterior excursion in some individuals, giving the suture a W shape. In specimens of *C. acutus* that lack this anterior excursion near the midline, the suture is V-shaped. The premaxillary/maxillary suture in *C. rhombifer* is transverse at the level of the 1st maxillary tooth, not V- or W-shaped, showing only minimal posterior excursion in some skulls. All five skulls of *C. acutus* from Lago Enriqueillo have 14 teeth in the maxilla, the typical number for this species. Most skulls of *C. rhombifer* have only 13 teeth, although one of the skulls from Oleg's Bat Cave (MHD 574) has a tiny 14th tooth on both the right and left sides. In both *C. acutus* and *C. rhombifer* the 5th tooth is the largest tooth in the maxilla, but this tooth is relatively larger in *C. acutus*.

CROCODYLUS RHOMBIFER, *C. ACUTUS*, AND *C. MORELETII*

All characters discussed here for *Crocodylus rhombifer* pertain to the Late Quaternary crocodile fossils from the Dominican Republic, as well as modern and fossil specimens of *C. rhombifer* from Cuba and fossil specimens from Abaco, Bahamas, and Grand Cayman in the Cayman Islands. In the following discussion, the most diagnostic cranial characters and several postcranial characters of *C. rhombifer* are compared and contrasted with the characters in two other species of *Crocodylus* known from the Caribbean region, *C. acutus* and *C. moreletii*. In addition to the sample of five skulls of *C. acutus* from Lago Enriqueillo, we also examined a skull

of *C. acutus* from the Florida Keys and a skull of *C. moreletii* from the Yucatan Peninsula of Mexico. (See the appendix for a list of the modern and fossil comparative material of *Crocodylus* examined.) Mook (1921), Schmidt (1924), and Brochu (2000) discussed cranial characters that distinguish among the extant species of Neotropical crocodiles, including *C. acutus*, *C. moreletii*, and *C. rhombifer*.

The skull of *Crocodylus acutus* has a longer, narrower, and more flattened rostrum than *C. rhombifer*, whereas the rostrum of *C. moreletii* is somewhat intermediate in length between those two species but the depth of the snout is more similar to that of *C. acutus*. The premaxilla of *C. rhombifer* and *C. moreletii* is shorter than that of *C. acutus*, and on the dorsal surface along the midline the former two species have a short, blunt process that extends posteriorly no farther than the 2nd maxillary tooth. The longer and narrower premaxilla of *C. acutus* has a thin, elongated process that extends posteriorly to the level of the 3rd or 4th maxillary tooth. *C. acutus* and *C. moreletii* have an essentially flat cranial roof, lacking the raised lateral ridges on the postorbitals and squamosals, squamosal protuberances, medial concavity, and ridges medial to the supratemporal fenestrae that are characteristic of *C. rhombifer*. In *C. acutus* and *C. moreletii*, the interorbital region, composed of the frontals and prefrontals, is only slightly concave and there are weakly developed ridges on the inner margin of the orbits, while in *C. rhombifer* the interorbital region is deeply concave and there are strong ridges on the internal orbital margins. In lateral view, *C. acutus* and *C. moreletii* have smaller orbits because of the combination of a shallow snout and weak ridges on the dorsal margin of the orbits, while a deeper snout and upraised orbital ridges give *C. rhombifer* the appearance of having a larger orbit. A midrostral, or median, boss is diagnostic of Neotropical species of *Crocodylus* (Brochu, 2000), but is more prominent in *C. acutus* and *C. moreletii* than in *C. rhombifer*. Ridges on the lacrimals and prefrontals are weak to absent in *C. acutus* and *C. moreletii*. The lacrimal and prefrontal ridges are more prominent in *C. rhombifer*, producing a distinct rhomboid- or diamond-shaped convexity in dorsal view that is absent in the two other Caribbean crocodiles.

The premaxillary-maxillary suture on the palate is transverse at the level of the first maxillary tooth in *C. rhombifer* and *C. moreletii*. This suture extends much farther posteriorly in *C. acutus*, to the level of the 2nd or 3rd maxillary tooth, giving this suture a distinct V-shaped outline on the palate. Some specimens of *C. acutus* have a distinct anterior excursion of the premaxillary-maxillary suture near the midline, giving this suture a W-shaped outline. All specimens examined of *C. acutus* and *C. moreletii* have 14 maxillary teeth. Most modern and fossil skulls of *C. rhombifer* from Cuba and fossil skulls from the Dominican Republic, Abaco, and Grand Cayman have 13 teeth in the maxilla. Exceptions among the fossil sample of *C. rhombifer* include two skulls from Abaco, one with only 12 teeth in the maxilla and a second skull with 14 teeth, and a skull from Oleg's Bat Cave in the Dominican Republic with 14 teeth. In *C. acutus* and *C. moreletii*, the third largest tooth in the dentary (after the 4th and 1st) is the 11th tooth, whereas the 10th is the third largest dentary tooth in *C. rhombifer*. In summary, the cranial, mandibular, and dental characters of the crocodile fossils from the Dominican Republic, Abaco, and Grand Cayman are very similar to modern Cuban specimens of *C. rhombifer* of similar size, and differ significantly from those of *C. acutus* and *C. moreletii*.

Postcranial elements of crocodylians are fairly conservative, and rarely demonstrate diagnostic differences within genera. However, Brochu (2000) pointed out that all living species of *Crocodylus*, except *C. rhombifer*, have a deep constriction in the posterior blade of the ilium that he described as “wasp-waisted.” *C. rhombifer* lacks this wasp-waisted condition, having a very slight indentation along the dorsal edge of the ilium near the posterior tip, resembling the ilium of most other crocodylians such as *Alligator*. A partial skeleton of a small crocodile from Oleg’s Bat Cave (MHD 575) has an associated right and left ilium that are very similar to *C. rhombifer* in having a slight indentation along their dorsal margins (fig. 10). Ilium from associated skeletons of *C. rhombifer* from Quaternary sites on Abaco, as well as isolated ilia from fossil sites on Grand Cayman, are similar to the ilia from Oleg’s Bat Cave. All of these fossil ilia closely resemble the ilium of *C. rhombifer* in lacking the wasp-waisted condition observed in other species of *Crocodylus*, including *C. acutus* and *C. moreletii* (Brochu, 2000).

In their examination of crocodile fossils from Crooked Island in the southern Bahamas, Steadman et al. (2017) discussed several characters of the humerus and femur that distinguish *Crocodylus rhombifer* and *C. acutus*. Their comparisons revealed that the humerus of *C. rhombifer* has the delto-pectoral crest located more distally and the shaft is more robust compared to *C. acutus*, and that the femur of *C. rhombifer* is more strongly curved and also has a more robust shaft.

DISCUSSION

TAPHONOMY

Late Quaternary vertebrates have been known from Hispaniola for over a century (Miller, 1916, 1922, 1929a, 1929b, 1930; Wetmore, 1922), but only within the past decade have fossils of crocodiles been found there. This clearly represents a bias in the fossil record resulting from the types of fossil deposits collected. Prior to the past 30 years, the vast majority of Late Quaternary vertebrate fossils from the West Indies were recovered from dry caves and other karst features such as sinkholes (Morgan and Woods, 1986). Nowhere in the West Indies was this collecting bias more prevalent than in Hispaniola, where before 2009 virtually all Late Quaternary vertebrate fossils were from dry caves or sinkholes. During the 1980s, Charles Woods, Dan Cordier, and field teams from the Florida Museum of Natural History (FLMNH) conducted an extensive paleontological survey of Hispaniola, collecting large samples of vertebrate fossils in Haiti and to a lesser extent the Dominican Republic. The FLMNH field teams discovered dozens of new sites and collected many thousands of Late Quaternary vertebrates, virtually all of which were derived from caves or from deep sinkholes, called “trouings” in Haitian creole. Several of these sinkholes or trouings on the Tiburon Peninsula of southwestern Haiti (e.g., Trouing Jérémie #5, Trouing Jean Paul) produced remarkable samples of mammals, including capromyid rodents, small ground sloths, lipotyphlan “insectivores,” and rarer taxa such as primates (Woods, 1989a, 1989b; Woods et al., 2001; MacPhee et al., 2000; Cooke et al., 2011). Despite a monumental effort by many paleontologists over

nearly a decade, not a single fossil crocodile was found during this comprehensive Hispaniolan paleontological survey.

Crocodile fossils are seldom preserved in dry cave or sinkhole deposits in the West Indies, and then usually as isolated elements such as teeth, limb bones, vertebrae, or osteoderms. An exception is a partial crocodylian skull from Cueva Lamas in western Cuba, the type specimen of the extinct Quaternary species *Crocodylus antillensis* (Varona, 1966). Other examples of Late Quaternary crocodile fossils from dry caves or sinkhole deposits in the West Indies include: a cranial fragment and osteoderm from San Salvador in the Bahamas (Olson et al., 1990); a humerus from a cave on Crooked Island in the Bahamas (Steadman et al., 2017); isolated teeth from Grand Cayman, Jamaica, and Puerto Rico (Morgan and Patton, 1979; Morgan, 1993; Vélez-Juarbe and Miller, 2007); and isolated vertebrae from Jamaica, New Providence in the Bahamas, and Mona Island (Koopman and Williams, 1951; Pregill, 1982; Frank and Benson, 1998). N.A.A. recently collected crocodylian fossils from dry caves on two islands in the Bahamas where crocodiles were previously unknown, a tooth from Isaac Bay Cave on Great Exuma (fig. 12: site 16) and a humerus from Bobby's Cave on Rum Cay (fig. 12: site 17). N.A.A. also collected several cranial elements of *C. rhombifer* from 1702 Cave on the north end of Crooked Island (fig. 12: site 19), representing the first diagnostic cranial material of the Cuban crocodile from that island. Previously, only postcranial elements of crocodiles were known from Crooked Island (Morgan and Albury, 2013; Steadman et al., 2017). Two partial maxillae and a frontal from Crooked Island are certainly *C. rhombifer*, but as with most other fragmentary crocodile fossils from caves in the West Indies, the specimens from Great Exuma and Rum Cay can be identified only as crocodylian, although they probably represent *C. rhombifer* as well.

As a result of this dry cave bias, crocodiles were rare in the West Indian fossil record before paleontologists began expanding their search parameters for vertebrate fossils over the past 30 years. Quaternary fossil deposits from the West Indies now include: wet sites, such as underwater caves in the Dominican Republic and throughout the Bahamas (Franz et al., 1995; Steadman et al., 2007; Rosenberger et al., 2011; Morgan and Albury, 2013; Velazco et al., 2013; Albury et al., 2018); several types of open sites (i.e., noncaves), such as peat deposits on Grand Cayman, Abaco, and Grand Bahama (Morgan et al., 1993; Morgan, 1994; Morgan and Albury, 2013; Steadman et al., 2014); and a natural asphalt or tar pit deposit in Cuba (Iturralde-Vinent et al., 2000). An additional source of crocodile remains is from Amerindian archaeological sites, especially in the Bahamas (Wing, 1977; Keegan, 1988, 1992, 1997; Carr et al., 2006; Steadman et al., 2014, 2017). As in cave deposits, crocodile remains from archaeological sites mostly consist of isolated nondiagnostic elements.

Noncave sites containing Late Quaternary fossils were occasionally found in the West Indies before the 1980s, including a significant sample of crocodiles, ground sloths, land tortoises, turtles, and other vertebrates collected from the geothermal springs at Ciego Montero in Cuba, first in the mid-1800s and again in the early 1900s (Leidy, 1868; Brown, 1913; Matthew, 1919; Williams, 1950; Matthew and de Paula Couto, 1959; Varona, 1984). In the 1980s and 1990s, a number of Late Quaternary fossil deposits were discovered in open sites on Grand Cayman in the Cayman Islands, most of which were formed through the deposition of organic

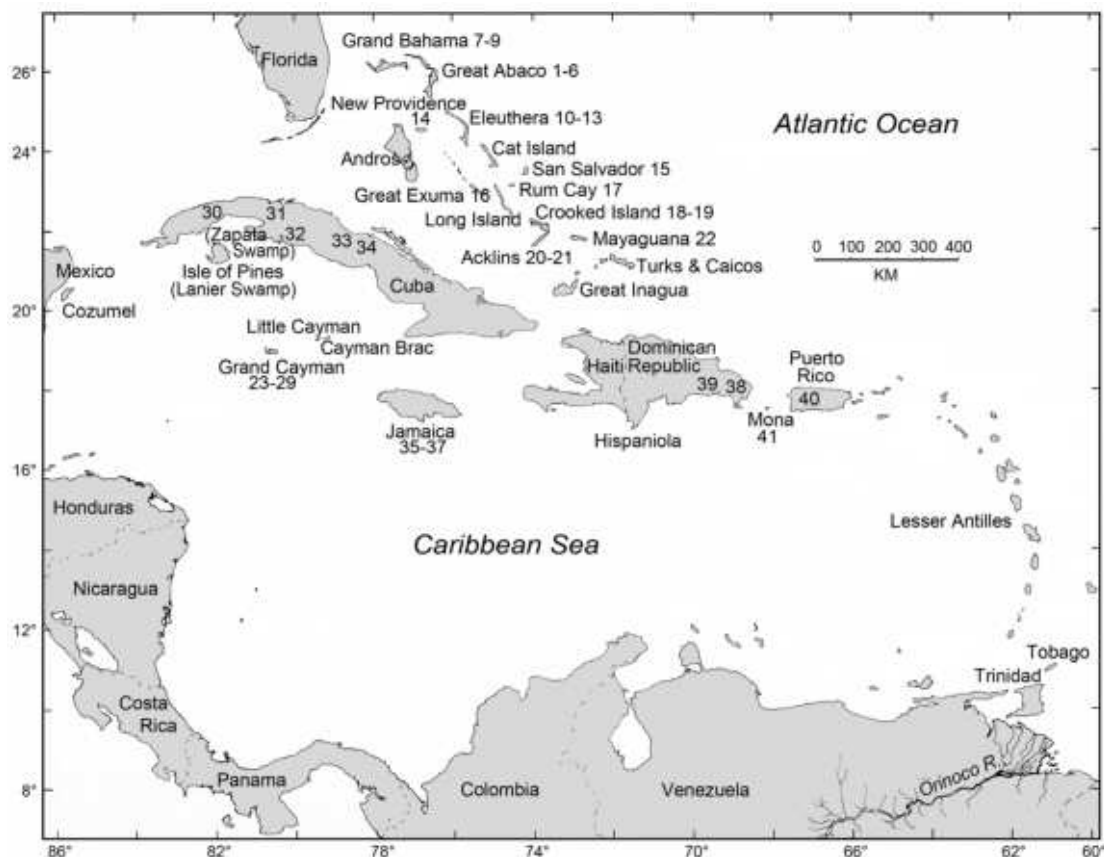


FIGURE 12. Map of the West Indies showing the location of Late Quaternary sites containing crocodiles. Fossil samples from Abaco and Grand Bahama in the Bahamas, Cuba, Dominican Republic, and Grand Cayman include skulls or partial skulls that can be confidently identified as the Cuban crocodile (*Crocodylus rhombifer*). All other records consist of fragmentary or isolated specimens identified as either *Crocodylus* sp. or *Crocodylia* indeterminate. Site numbers are as follows (sites 1–22 are from various islands in the Bahamas): **Abaco** (see Morgan and Albury, 2013, for an enlarged map of Abaco showing the location of these fossil sites): 1. Sawmill Sink; 2. Dan’s Cave; 3. Ralph’s Cave; 4. Nancy’s Cave; 5. Lost Reel Cave. 6. Gilpin Point. **Grand Bahama**: 7. Bell Channel; 8. Anaconda Pond; 9. Mermaid’s Lair. **Eleuthera**: 10. White Lake Cave; 11. Kelly’s Blue Hole (= Bung Hole); 12. Mermaid’s Pool; 13. Preacher’s Cave. **New Providence**: 14. Banana Hole. **San Salvador**: 15. Hanna’s Bananas. **Great Exuma**: 16. Isaac Bay Cave. **Rum Cay**: 17. Bobby’s Cave. **Crooked Island**: 18. Pittstown Landing; 19. 1702 Cave. **Acklins**: 20. Rupert’s Pond; 21. Delectable Bay. **Mayaguana**: 22. The Fountain. **Grand Cayman** (see Morgan and Albury, 2013, for an enlarged map of Grand Cayman showing the location of these fossil sites): 23. Crocodile Canal; 24. Prospect; 25. Chisholm Cow Well; 26. Connally Cow Well; 27. Queen Elizabeth II Botanic Park; 28. Furtherland Farms Cow Well; 29. Crab Cave. **Cuba**: 30. Cueva Lamas; 31. Las Breas de San Felipe; 32. Ciego Montero; 33. Casimbas de las Llanadas; 34. Caves of Cueiba. **Jamaica**: 35. Wallingford Roadside Cave; 36. Dairy Cave; 37. Bellevue. **Hispaniola (Dominican Republic)**: 38. Oleg’s Bat Cave; 39. Ni-Rahu (= Cueva de Lynn). **Puerto Rico**: 40. Cueva Salida. **Mona Island**: 41. Cueva de los Losetas.

sediments (peat) in freshwater or brackish water environments (Morgan et al., 1993; Morgan, 1994). One of these open sites was a mangrove peat deposit discovered during the construction of a canal, whereas several other sites occurred in peat deposits that accumulated in small, water-filled depressions in the limestone bedrock called “cow wells” by local Caymanian farmers. The Cuban crocodile *Crocodylus rhombifer* was the most common species in all of these open sites containing organic sediments on Grand Cayman (Morgan et al., 1993; Morgan, 1994). A crocodile skull was recently found in an underwater cave at the eastern end of Grand Cayman (William Verhoeven, personal commun.), the first record of a Late Quaternary fossil from a submerged cave in the Cayman Islands. Prior to the 1980s, the only fossil record of a crocodile from the Cayman Islands was a single isolated tooth from a dry cave on Grand Cayman (Morgan and Patton, 1979).

Beginning in the mid-1990s and continuing to the present, cave divers in the Bahamas have made remarkable discoveries of Late Quaternary vertebrate fossils in so-called blue holes, especially on Abaco in the northern Bahamas (Franz et al., 1995; Kakuk and Bowen, 2005; Steadman et al., 2007, 2015). Blue holes are underwater caves with a surface entrance, generally flooded, many of which have well-developed horizontal passageways containing extensive development of cave formations or speleothems (stalactites, stalagmites, flowstone, etc.) that form only in subaerial conditions, presumably during Pleistocene low sea level stands when the caves were dry. Based on the available radiocarbon chronology (Hastings et al., 2014), it appears that crocodiles inhabited these Bahamian blue holes primarily during the Holocene when the caves became flooded as sea levels rose. Sawmill Sink, a blue hole on Abaco, has produced numerous well-preserved fossil skeletons of *Crocodylus rhombifer* (Morgan and Albury, 2013), as well as complete shells of a large extinct land tortoise, *Chelonoidis alburyorum* (Franz and Franz, 2009).

One of the cave divers who made some of the early finds of fossils from blue holes on Abaco, Curt Bowen (Kakuk and Bowen, 2005), was also one of the first divers to discover vertebrate fossils in underwater caves in the Dominican Republic (Pickel and Bowen, 2009), including a skull of the monkey *Antillothrix* (Rosenberger et al., 2011). One of us (P.L.), Victoria Alexandrova, Cristian Pittaro, Dave Pratt, and other cave divers from the DRSS have since recovered many additional fossils in underwater caves in the Dominican Republic (e.g., Velazco et al., 2013), including the crocodiles from Oleg’s Bat Cave described here.

The dominant taphonomic factor that characterizes the fossil sites where large samples of crocodiles have been recovered on Abaco, Grand Cayman, Cuba, and the Dominican Republic is that these deposits represent freshwater or brackish-water depositional environments, not dry caves. Considering that crocodiles generally inhabit freshwater, brackish water, or coastal marine environments, their occurrence in fossil sites representing these types of environments is not surprising. Nonetheless, questions still remain regarding the process of fossilization or taphonomy of the crocodile remains in these aquatic sites.

On Grand Cayman, most of the fossils of *Crocodylus rhombifer* were found in open sites containing peat deposits and, although well preserved, consist of isolated elements, not articulated or associated skeletons (Morgan and Albury, 2013). At present, substantial areas in the

western half of Grand Cayman consist of brackish-water mangrove swamps (Brunt and Burton, 1994). Most of the fossil sites containing large samples of Cuban crocodiles were found in this area of extensive mangrove swamps, which would have provided suitable habitat and aquatic prey for *C. rhombifer*.

In Abaco in the northern Bahamas, the majority of fossils of *Crocodylus rhombifer* have been found in underwater caves or blue holes (Morgan and Albury, 2013). Unlike Grand Cayman, many of the fossil specimens of *C. rhombifer* from Abaco consist of articulated or associated skeletons, particularly from Sawmill Sink, the richest of these deposits. Most of the crocodile fossils from Sawmill Sink were derived from a peat deposit located at a depth of from 9 to 34 m beneath the cave opening. The present habitat in the vicinity of Sawmill Sink is a pine forest, not a mangrove swamp or other type of freshwater or brackish-water environment. The surface openings to some of the blue holes on Abaco do provide a limited area of freshwater habitat, but these tend to be rather small ponds, about 15 m in diameter in the case of Sawmill Sink. It seems unlikely that a small pond or lake only a few hectares in area, representing the surface opening of a blue hole, could support a population of crocodiles. Perhaps the crocodiles lived elsewhere, but died and became fossilized in the blue holes. The blue holes in Abaco contain few fish or other aquatic vertebrates (e.g., turtles) that would provide a food source for crocodiles. Blue holes on nine other islands in the Bahamas have also produced fossil remains of crocodiles, most of which consist of isolated postcranial elements that presumably represent *C. rhombifer* (Morgan and Albury, 2013; see map in fig. 12).

Oleg's Bat Cave in the Dominican Republic is partly dry and partly underwater, but, unlike most of the blue holes in Abaco, the water in this cave does not reach the land surface. The two entrances to Oleg's Bat Cave are rather small (less than 5 m in diameter), and the water is from 13 to 20 m below the ground surface. At least five individuals of *Crocodylus rhombifer* are preserved in the underwater portion of Oleg's Bat Cave, at a water depth of 11 m (30 m below the surface) and a distance of about 100 m from the closest cave entrance. There are no articulated skeletons of crocodiles from Oleg's Bat Cave, but several of the specimens do appear to represent associated partial individuals. The crocodile fossils from this cave do not occur in organic sediments or peat, but are preserved in more typical cave sediments that were probably deposited when the cave was dry. Most of the explored portion of Oleg's Bat Cave, nearly 1 km in length, consists of flooded passages that could not currently support air-breathing crocodiles. The majority of the crocodile fossils were found in these flooded passages, together with a large sample of bat fossils (Velazco et al., 2013). Scattered cranial and postcranial remains of bats can be seen in the photographs in figure 5C and D, interspersed on the cave floor with crocodile fossils. Presumably, when the crocodiles and bats inhabited this now-flooded portion of the cave, these rooms were connected to the surface entrance by continuous air-filled passageways.

About 20 m below the largest of the two entrances to Oleg's Bat Cave is a fairly large room containing water with an air-filled chamber above. The bats now found in this cave roost in these chambers near the entrance, the only places in the cave where crocodiles could survive today. As with the blue holes in Abaco, Oleg's Bat Cave contains few aquatic vertebrates (e.g., fish, turtles) that would provide a food source for crocodiles. Another difference from the Abaco blue holes

is that Oleg's Bat Cave supports a large population of bats, both now and in the Late Quaternary (Velazco et al., 2013). Although it seems highly improbable that crocodiles lived in the totally dark environment of Oleg's Bat Cave and fed on bats, a similar scenario has been observed in the Abanda caves in Gabon, West Africa. In the Abanda caves, dwarf crocodiles (*Osteolaemus tetraspis*) were found living 7 m underground in a dry cave in total darkness, and preyed primarily on bats and insects (Testa, 2011). The prey base of Cuban crocodiles in the Dominican Republic during the Late Quaternary will be investigated further in Paleoecology below.

PALEOECOLOGY

The Cuban crocodile *Crocodylus rhombifer* was one of the largest vertebrates in the Dominican Republic during the Late Quaternary. Although the American crocodile *Crocodylus acutus* is similar in size and inhabits the Dominican Republic today, there is currently no Late Quaternary record of *C. acutus* from Hispaniola (see discussion of Antillean crocodile biogeography below). Extant populations of *C. rhombifer* in Cuba inhabit freshwater swamps, whereas *C. acutus* favors coastal and brackish-water habitats. The American crocodile is found today in two large, inland, brackish lakes in Hispaniola, Lago Enriquillo in the southwestern Dominican Republic and the nearby Etang Saumâtre in southeastern Haiti, both of which are located near or below sea level (Thorbjarnarson, 1988; see fig. 4). The diet of American crocodiles in Etang Saumâtre consists mostly of fish, although domestic animals, including dogs and goats, are occasionally captured along the shores of the lake (Thorbjarnarson, 1988). Besides fish, several species of freshwater turtles provide an additional aquatic food source for crocodiles in Hispaniola, both now and in the Late Quaternary.

Field and behavioral observations in Cuba indicate that *Crocodylus rhombifer* is more terrestrial than other species of crocodylians and will often capture nonaquatic prey, in particular a large hystricognath rodent, the Cuban hutia *Capromys pilorides* (De Sola, 1930; Varona, 1984; Soberón et al., 2001). The Cuban hutia is arboreal, but also spends quite a bit of time on the ground. Field observations suggest Cuban crocodiles will jump from the water or the ground and capture hutias from low branches in trees (John Thorbjarnarson, personal comm.). De Sola (1930) identified remains of the Cuban hutia and the Cuban gar *Atractosteus tristoechus* in the intestinal tract of several Cuban crocodiles, indicating that *C. rhombifer* feeds in both terrestrial and freshwater environments. 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. Varona (1984) commented on the Cuban crocodile's surprising abilities of terrestrial locomotion, including walking, running, and jumping. Soberón et al. (2000) elaborated further on the terrestrial capabilities of Cuban crocodiles, noting that this species has more terrestrial habits than other crocodiles, and is capable of walking long distances across dry and rocky terrain. They also stated that Cuban crocodiles have the ability to prey on terrestrial mammals, such as the primarily arboreal hutias, using a hunting technique based on jumping. According to Soberón et al. (2000), *C. rhombifer* possesses numerous adaptive traits characteristic of a more terrestrial lifestyle, including: powerful dermal armor, robust limbs, reduction of the interdigital membrane in the feet and total

absence in the hands, robust skull and mandibles with strong masticatory muscles, and a reduced and specialized dentition.

Mammalian predators (Order Carnivora) are absent from both the modern and Quaternary faunas of the West Indies (Morgan and Woods, 1986; Dávalos and Turvey, 2012), unlike the continental portions of North or South America, where large mammalian carnivores in the families Canidae, Felidae, and Ursidae fill the predatory niches in both recent and Pleistocene faunas. In the West Indies, by contrast, most carnivorous niches are filled by either large reptiles (crocodiles and boid snakes) or large birds (eagles, hawks, and owls). The terrestrial habits of the living Cuban crocodile in Cuba suggest this species was one of the primary predators of medium- and large-sized land mammals in the Late Quaternary faunas of Cuba, and presumably Hispaniola as well. West Indian boid snakes in the genus *Chilabothrus* (formerly included in the mainland boa genus *Epicrates*; see Reynolds et al., 2013) are among the few large terrestrial, carnivorous vertebrates in the extant fauna of Hispaniola and elsewhere in the Greater Antilles, with the exception of *Crocodylus rhombifer* in Cuba. Although the largest of these boas may reach lengths of 3 m, they generally prey on vertebrates of 1 kg body mass or smaller. The boas probably consumed various species of hystricognath rodents that inhabited Hispaniola in the Late Quaternary, but not the larger ground sloths or land tortoises. These same rodents would have been prey for extinct or extirpated predatory birds in Hispaniola, including the extinct barn owl *Tyto noeli* and several species of eagles and hawks (Olson, 1978).

Many of the medium- to large-sized terrestrial vertebrates that would have comprised the prey base for *Crocodylus rhombifer* in Hispaniola during the Late Quaternary are now extinct, especially among terrestrial or nonvolant mammals (i.e., nonbats). The current terrestrial mammal fauna from Hispaniola is extremely depauperate, consisting of only two species, an arboreal rodent, the Hispaniolan hutia *Plagiodontia aedium*, and a large lipotyphlan “insectivore,” the Hispaniolan solenodon *Solenodon paradoxus*. *Plagiodontia* is an arboreal folivore similar in habits and diet to the Cuban hutia *Capromys pilorides*. *Solenodon* has an insectivorous/carnivorous diet, feeding on arthropods, land snails, worms, and small reptiles, but is too small (<1 kg) to prey on hutias or other larger vertebrates. The Late Quaternary mammalian fauna of Hispaniola was considerably more diverse than the modern fauna, both in terms of body size and the number of taxa, consisting of at least 24 species, but had an unbalanced distribution of feeding types. There were several small- to medium-sized insectivorous species and a wide variety of herbivores ranging from small- to large-bodied species, but like the modern fauna lacked mammalian carnivores. In addition to the living *Solenodon paradoxus*, there were four extinct species of Late Quaternary insectivores, a second species of *Solenodon* and three small species in the extinct “island shrew” genus *Nesophontes*. The mammalian herbivore fauna in Hispaniola during the Late Quaternary consisted of a minimum of 19 species, the extant *Plagiodontia aedium* and at least 18 extinct species including: three extinct genera and six additional species of capromyid rodents; an extinct genus and two species of small rodents in the family Echimyidae; a large species in the extinct rodent family Heptaxodontidae; two genera and species of platyrrhine primates; and four extinct genera and seven extinct species in the ground sloth family Megalonychidae (Morgan and Woods, 1986; MacPhee et al., 2000;

Woods et al., 2001; Cooke et al., 2011; Rosenberger et al., 2011; Dávalos and Turvey, 2012; White, 2012). The sloths were the largest herbivores from Hispaniola, ranging from arboreal forms similar in size to the extant tree sloths of Central and South America to bear-sized, terrestrial species (MacPhee et al., 2000; White, 2012).

Another large terrestrial vertebrate from Hispaniola that probably was an important prey item for Cuban crocodiles during the Late Quaternary was a now extinct giant land tortoise. A complete shell of this large land tortoise was collected from Oleg's Bat Cave, and was recently described as a new species *Chelonoidis dominicensis* (Albury et al., 2018). Morgan and Albury (2013) discussed and illustrated several examples of predation by *Crocodylus rhombifer* on another extinct species of tortoise, *Chelonoidis alburyorum*, from Abaco in the Bahamas (Franz and Franz, 2009), based on crocodile tooth marks on tortoise shells. Hastings et al. (2014) further documented crocodile predation of tortoises on Abaco using isotopic analyses of both crocodile and tortoise bones (see below). In summary, the Late Quaternary land vertebrate fauna of Hispaniola provided a diverse prey base for the terrestrially adapted Cuban crocodile, including a wide variety of rodents and small ground sloths, as well as land tortoises. An additional intriguing possibility is that some Late Quaternary populations of *C. rhombifer*, including the crocodiles from Oleg's Bat Cave, may have been adapted for living in caves and feeding, at least in part, on bats. As noted above, crocodile researchers in Gabon in West Africa documented a population of the dwarf crocodile (*Osteolaemus tetraspis*) that lives in caves and preys on bats (Testa, 2011).

Hastings et al. (2014) discussed the Late Quaternary vertebrate food web in the Bahamas, in which both the largest predator, *Crocodylus rhombifer*, and the largest herbivore, the extinct giant land tortoise *Chelonoidis alburyorum*, were reptiles. These two large reptiles are no longer found in Bahamas. Only two herbivorous vertebrates with a body mass larger than about 0.5 kg occur in the modern fauna of the Bahamas, the Bahamian hutia, *Geocapromys ingrahami*, a rodent in the family Capromyidae, and several species of rock iguanas in the genus *Cyclura*. Both *Geocapromys* and *Cyclura* have very restricted distributions in the Bahamas at present, but were considerably more widespread during the Late Quaternary (Pregill, 1982; Morgan, 1989). The fossil data suggest that the Late Quaternary food web in the Bahamas was a reptile-dominated system in which terrestrially adapted Cuban crocodiles fed on two other large reptiles, the land tortoise *Chelonoidis alburyorum* and rock iguana *Cyclura*, as well as the rodent *Geocapromys ingrahami* (Hastings et al., 2014). The fossil record documents three other large predators in the Bahamas during the Late Quaternary, two extinct raptorial birds, the eagle *Titanohierax gloveralleni* and the giant barn owl *Tyto pollens* (Olson and Hilgartner, 1982), and several species of the large boa *Chilabothrus*. The two birds and the snake were certainly large enough to prey on hutias, and possibly iguanas, but not land tortoises.

Hastings et al. (2014) documented the feeding habits of *Crocodylus rhombifer* from Sawmill Sink on Abaco in the Bahamas using stable isotopes derived from bone collagen. They reported stable isotope ratios of carbon ($^{13}\text{C}/^{12}\text{C}$) in delta notation ($\delta^{13}\text{C}$) in parts per thousand, or per mil (‰). Collagen from bones of eight individuals of *C. rhombifer* from Abaco had $\delta^{13}\text{C}$ values ranging from -16.4‰ to -20.9‰ (Hastings et al., 2014). These are similar to the $\delta^{13}\text{C}$ values

(less than -15.5%) of terrestrial carnivores (Schoeninger and DeNiro, 1984), indicating that the Bahamas crocodiles fed primarily in a terrestrial ecosystem. Crocodile bite marks on fossil tortoise shells from Abaco (Morgan and Albury, 2013) support the carbon isotopic data suggesting Cuban crocodiles in the Bahamas were terrestrial predators.

Bone collagen from a crocodile tibia (MHD 574) from Oleg's Bat Cave was analyzed by Beta Analytic (Beta - 457181) for stable isotopes of carbon and nitrogen, as well as an AMS radiocarbon date (see below). A $\delta^{13}\text{C}$ value of -19.3% for the tibia of *Crocodylus rhombifer* from Oleg's Bat Cave is also within the range of $\delta^{13}\text{C}$ values for the sample of crocodiles from Abaco (Hastings et al., 2014), supporting our hypothesis that Cuban crocodiles from the Dominican Republic were also primarily terrestrial carnivores.

QUATERNARY FOSSIL RECORD OF CROCODILES IN THE WEST INDIES

Prior to the discoveries of fossils of the Cuban crocodile *Crocodylus rhombifer* from two caves in the Dominican Republic reported here, Oleg's Bat Cave and Ni-Rahu, Late Quaternary fossils of this species have been found on many other islands in the West Indies where this species no longer occurs (fig. 12), including Grand Cayman in the Cayman Islands and 10 islands in the Bahamas (Morgan et al., 1993; Franz et al., 1995; Morgan and Albury, 2013). From the early 1980s through the early 1990s, several large fossil samples of *C. rhombifer* were found in Grand Cayman, including six partial to nearly complete skulls (Morgan et al., 1993; Morgan, 1994; Morgan and Albury, 2013). Seven sites on Grand Cayman have produced Late Quaternary specimens of *C. rhombifer* (see fig. 12): Chisholm Cow Well, Connally Cow Well, Crab Cave, Crocodile Canal, Furtherland Farms Cow Well, Prospect, and Queen Elizabeth II Botanic Park.

Beginning in the mid-1990s and continuing to the present, Late Quaternary crocodile fossils have been found in underwater caves or blue holes on islands throughout the Bahamas, as well as in several peat deposits and dry caves (fig. 12). Crocodile fossils are particularly common in blue holes on Abaco in the northern Bahamas (Franz et al., 1995; Steadman et al., 2007; Morgan and Albury, 2013; Hastings et al., 2014). Identifiable cranial material of *Crocodylus rhombifer* on Abaco is known from five blue holes (Dan's Cave, Lost Reel Cave, Nancy's Cave, Ralph's Cave, Sawmill Sink) and a peat deposit (Gilpin Point) that appears to have a cultural component (Steadman et al., 2014). *C. rhombifer* has also been identified from two sites on Grand Bahama in the northern Bahamas (Morgan and Albury, 2013), a blue hole (Mermaid's Lair) and a peat deposit (Bell Channel), and two sites on Crooked Island in the southern Bahamas (Steadman et al., 2017), a cave (1702 Cave) and an archaeological site (Pittstown Landing). Other fossil specimens of crocodiles, mostly consisting of isolated postcranial elements that probably represent *C. rhombifer*, are known from seven other islands in the Bahamas (fig. 12; Morgan and Albury, 2013): Acklins, Eleuthera, Great Exuma, Mayaguana, New Providence, Rum Cay, and San Salvador. In addition to the Bahamian sites listed above, fragmentary remains of crocodiles are also known from archaeological sites on Acklins and Eleuthera (Morgan and Albury, 2013).

The only other island in the West Indies that has produced fossil remains of Quaternary crocodiles that can be identified to species is Cuba, where *Crocodylus rhombifer* has been

reported from about a half dozen fossil sites, including a freshwater spring, a tar pit deposit, and several caves (fig. 12). The most significant of these fossil sites is the geothermal spring deposits at Ciego Montero in south-central Cuba that have produced complete skulls and mandibles of *C. rhombifer*, including several extremely large individuals (Leidy, 1868; Brown, 1913; Varona, 1984; Morgan and Albury, 2013). Cuba is the only island where the Cuban crocodile still survives, found in freshwater swamps in south-central Cuba and on the Isla de la Juventud (formerly known as Isla de Pinos, or Isle of Pines) off the southwestern coast of Cuba. Several cranial fragments from a Late Quaternary cave deposit in Cueva Lamas in western Cuba (fig. 12) were described as an extinct species of *Crocodylus*, *C. antillensis* (Varona, 1966). Brochu (2000) suggested that *C. antillensis* might be a synonym of *C. rhombifer*, but the fossil material is probably too fragmentary for a definite identification.

There are Quaternary records of crocodiles from dry cave deposits on three other islands in the West Indies (fig. 12), consisting of fragmentary fossils that cannot be identified to genus or species, including: several teeth and vertebrae from two caves in Jamaica (Koopman and Williams, 1951; Morgan, 1993); a tooth from a cave in Puerto Rico (Vélez-Juarbe and Miller, 2007), and a vertebra from a cave on Mona Island, located in the Mona Passage between Puerto Rico and the Dominican Republic (Frank and Benson, 1998).

There is no fossil record of the American crocodile *Crocodylus acutus* in Hispaniola during the Late Quaternary. In fact, there is no fossil record of *C. acutus* anywhere in the West Indies or in southern peninsular Florida, which has a rich late Pleistocene fossil record (Morgan, 2002). Alligator (*Alligator mississippiensis*) fossils are known from several southern Florida Pleistocene sites, indicating that, together with other taphonomic and paleoecologic evidence, these sites sampled freshwater depositional environments. For the most part, alligators inhabit freshwater rivers, swamps, and lakes in the inland portion of peninsular Florida, whereas American crocodiles in southern Florida and the Florida Keys prefer coastal brackish water habitats such as mangroves. This ecological separation is reminiscent of Cuba where two crocodylian species occur in the same general geographic area, with *C. acutus* in coastal marine habitats and the Cuban crocodile *C. rhombifer* found primarily in freshwater swamps (Thorbjarnarson, 2010). *C. acutus* was reported from the Bellevue archaeological site on the southern coast of Jamaica (Wing, 1977; Wing and Reitz, 1982). Although we have not examined the crocodile material from the Bellevue site, we are skeptical of this identification because *C. acutus* is not known from any other Late Quaternary paleontological or archaeological sites in the West Indies. We tentatively consider the Bellevue crocodylian to be *Crocodylus* sp., pending further comparisons with the original archaeological material.

In summary, the Late Quaternary fossil record establishes the presence of a single species of crocodylian in the West Indies, the Cuban crocodile *Crocodylus rhombifer*. The American crocodile *C. acutus* has no Antillean fossil record, even though this species is currently the most common and widespread crocodylian in the region. Late Quaternary fossils document a wider distribution of *C. rhombifer* in Cuba, as well as locally extinct or extirpated populations of the Cuban crocodile on many other islands in the West Indies, including ten islands in the Bahamas, Grand Cayman, and the recently discovered fossil sample from the Dominican Republic described here (fig. 12).

RADIOCARBON DATES AND EXTINCTION CHRONOLOGY

Radiocarbon dates derived directly from Late Quaternary fossils of the Cuban crocodile are known from only three islands in the West Indies: a date reported here from Oleg's Bat Cave in the Dominican Republic; seven dates from three sites on Abaco in the northern Bahamas (Franz et al., 1995; Steadman et al., 2007, 2014; Hastings et al., 2014); and two dates from two sites on Crooked Island in the southern Bahamas (Steadman et al., 2017). A 5 g sample of bone removed from the shaft of a tibia of *Crocodylus rhombifer* from Oleg's Bat Cave (MHD 574; associated with a skull, mandible, humerus, and femur) was submitted to Beta Analytic, Inc., in Miami, Florida for an AMS radiocarbon (^{14}C) date on bone collagen (Beta-457181). The conventional radiocarbon age for the crocodile tibia from Oleg's Bat Cave is 6460 ± 30 radiocarbon years before present (ryrBP). The calibrated age (with 2σ calibration) is 7320 to 7430 cal yrBP. This is the oldest radiocarbon date on a fossil of *C. rhombifer* from the West Indies.

Bone collagen from a combined sample of several postcranial bones that were part of an associated skeleton of *Crocodylus rhombifer* from Dan's Cave on Abaco in the Bahamas, yielded an AMS ^{14}C date of 2780 ryrBP (Franz et al., 1995). Five postcranial bones (humerus, two radii, femur, vertebra) of the Cuban crocodile from Sawmill Sink on Abaco have been radiocarbon dated, with measured ^{14}C ages ranging from 2620 to 3680 ryrBP and calibrated ^{14}C ages ranging from 2770 to 4410 cal yrBP (Steadman et al., 2007; Hastings et al., 2014). A ^{14}C date on a postorbital bone of *C. rhombifer* from Gilpin Point on Abaco is much younger, with a measured age of 1020 ryrBP and a calibrated age of 920 to 970 cal yrBP (Steadman et al., 2014). The Gilpin Point site was thought to be cultural in origin (Steadman et al., 2014). The radiocarbon date on the crocodile from Gilpin Point overlaps with the early human occupation of the Bahamas by Amerindian people, the Lucayans (Keegan, 1992, 1997). The seven published radiocarbon dates on *C. rhombifer* from Abaco are all late Holocene in age, ranging from 920 to 4410 cal yrBP (Hastings et al., 2014; Steadman et al., 2014).

Steadman et al. (2017) obtained two AMS radiocarbon dates on crocodile bones from Crooked Island in the Bahamas: a femur from the Pittstown Landing archaeological site (measured ^{14}C age of 860 ± 30 ryrBP; calibrated age of 700 to 900 cal yrBP) and a humerus from 1702 Cave (measured ^{14}C age of 460 ± 30 ryrBP; calibrated age of 535 to 655 cal yrBP). The Crooked Island dates are younger than the youngest crocodile date from Abaco. The radiocarbon dates from Crooked Island confirm that crocodiles coexisted with Amerindian people on that island, and the date from 1702 Cave overlaps with early European colonization (Keegan, 1992, 1997; Steadman et al., 2017). There are also written records confirming that crocodiles survived in the Bahamas well into the historic period, including two crocodiles killed on Crooked Island by the crew of Christopher Columbus on his first voyage in 1492 (Dunn and Kelley, 1981) and sight records from the 18th and 19th centuries on Acklins, Andros, and Great Inagua (Catesby, 1743; McKinnen, 1804; Gardiner, 1886).

Although no fossil crocodile bones from Grand Cayman have been directly radiocarbon dated, an in-place peat containing a crocodile tooth and an osteoderm from the mangrove peat deposit in the Crocodile Canal site on Grand Cayman yielded a conventional radiocarbon date of 860 ryrBP. A second in-place peat sample from the same site containing a limb bone of the

rodent *Capromys*, now locally extinct in the Cayman Islands, was ^{14}C dated at 375 ryrBP (Morgan et al., 1993; Morgan, 1994; Morgan and Albury, 2013). The younger of these two dates supports historical records of crocodiles from Grand Cayman reported by members of Sir Francis Drake's crew in 1586 (Keeler, 1981) and by William Jackson in 1642 (Grant, 1940).

Radiocarbon dates establish that the Cuban crocodile *Crocodylus rhombifer* inhabited the Dominican Republic, Abaco and Crooked Island in the Bahamas, and Grand Cayman in the Holocene. Fossils of crocodiles from other islands in the Bahamas are probably Holocene as well, although radiocarbon dates are lacking (Morgan and Albury, 2013). The oldest radiocarbon date for *C. rhombifer* in the West Indies is the early Holocene age of 6460 ryrBP (7320 to 7430 cal yrBP), reported here from Oleg's Bat Cave in the Dominican Republic. There are no other radiocarbon dates for Cuban crocodiles from the Dominican Republic, and no records of this species from Amerindian archaeological sites in Hispaniola. Lacking more complete data, we cannot establish a chronology for the local extinction of *C. rhombifer* in Hispaniola, except to state that the species was present until at least 6000 years ago. Radiocarbon dating of additional specimens of *C. rhombifer* from the Dominican Republic will likely establish that this crocodile persisted in Hispaniola into the late Holocene, and probably coexisted with Amerindians and possibly survived until the arrival of Europeans. Radiocarbon dates and/or historical records confirm that Cuban crocodiles survived in the Bahamas and Grand Cayman into the historic period, becoming locally extinct only within the last 400 years or less.

A major extinction event affecting most groups of vertebrates (reptiles, birds, and mammals), including numerous local populations of *Crocodylus rhombifer*, occurred in the West Indies in the late Holocene (Olson, 1978; Morgan and Woods, 1986; MacPhee, 2009; Dávalos and Turvey, 2012; Morgan and Albury, 2013), during a period when the climate was fairly stable and similar to modern conditions (Pregill and Olson, 1981). West Indian extinctions appear to coincide with the arrival of Amerindian people in that island group, beginning about 5500 years ago (Rouse, 1989; Fitzpatrick, 2006; MacPhee, 2009; Cooke et al., 2017). This evidence has led most West Indian paleontologists to implicate humans in those extinctions (Morgan and Woods, 1986; Steadman et al., 2005, 2017; MacPhee, 2009; Cooke et al., 2017). *Crocodylus* has been identified from several Amerindian archaeological sites in the Bahamas, including sites on Abaco, Acklins, Crooked Island, and Eleuthera, as well as the Bellevue site on the southern coast of Jamaica, confirming that the first human inhabitants of the West Indies hunted crocodiles (Wing, 1977; Wing and Reitz, 1982; Keegan, 1988, 1992; Carr et al., 2006; Steadman et al., 2014, 2017).

Although the precise chronology for the extinction of most of the vertebrate species in the West Indies remains to be determined (MacPhee, 2009), the cause and effect of the arrival of people on an island and the subsequent extinction of vertebrate species seems too obvious to be coincidental. Species began disappearing rapidly from the West Indies in the late Holocene about 5000 years ago, and these extinctions continued throughout the remainder of the Amerindian period and into the era of European colonization. The specific reasons for the extinction of vertebrates in the West Indies caused by Amerindian and European peoples are varied, including direct predation, habitat alteration and destruction, and the introduction of exotic species. The local extinction of Cuban crocodiles in the Bahamas and Grand Cayman, and

probably Hispaniola as well, almost certainly resulted from overhunting. *C. rhombifer* managed to survive in a small area of southern Cuba and on Isla de Juventud.

BIOGEOGRAPHY

Beginning in the early 1980s and continuing to the present, discoveries of Late Quaternary fossils of *Crocodylus* in the Cayman Islands, Bahamas, and Dominican Republic have led to a significant improvement in our understanding of the historical biogeography of crocodiles in the West Indies. Prior to that time, the biogeography of West Indian crocodiles was based primarily on their modern distribution and, to a much lesser extent, fossil remains from a few scattered Late Quaternary deposits, primarily in Cuba. At the present time, the American crocodile, *Crocodylus acutus*, is the most widespread crocodile species in the West Indies, occurring in Cuba, Jamaica, and Hispaniola, as well as southern peninsular Florida and the Florida Keys and the Caribbean and Pacific coasts of Mexico, Central America, and northern South America (Thorbjarnarson, 2010). The only other Antillean crocodile, the Cuban crocodile, *C. rhombifer*, has a very restricted geographic range, found at present only in the Ciénaga de Zapata (Zapata Swamp) in southern Cuba and the Ciénaga de Lanier (Lanier Swamp) on the Isla de Juventud, an island off the southwestern coast of Cuba (Ramos Targarona et al., 2010).

Two other species of crocodiles, Morelet's crocodile *Crocodylus moreletii* and the Orinoco crocodile *C. intermedius*, occur in the greater Caribbean region but not in the Greater Antilles, Bahamas, or Cayman Islands. *C. moreletii* is found in freshwater drainages flowing into the southwestern Gulf of Mexico and the northwestern Caribbean Sea in southern Mexico and northern Central America, from central Tamaulipas in Mexico south to Guatemala, including the Yucatan peninsula of Mexico and Belize (Platt et al., 2010). *C. intermedius* occurs primarily in the freshwater drainages of the Orinoco River and its tributaries in Venezuela and Colombia in northern South America, but is also known from the southeastern Caribbean coast of Venezuela and Trinidad (Crocodile Specialist Group, 1996).

Previously reported fossils of *Crocodylus rhombifer* from Grand Cayman in the Cayman Islands and 10 islands in the Bahamas (Morgan et al., 1993; Franz et al., 1995; Morgan and Albury, 2013) document the existence of locally extinct or extirpated populations of Cuban crocodiles on small West Indian islands beyond the current range of this species. The fossils from Oleg's Bat Cave and Ni-Rahu in the Dominican Republic provide evidence of yet another locally extinct population of *C. rhombifer*, and also confirm the presence of the Cuban crocodile on one of the large Greater Antillean islands outside Cuba. The Late Quaternary fossil record establishes a much wider distribution of *C. rhombifer* in the West Indies during the Late Quaternary than is indicated by the very restricted modern range of this species in southern Cuba and the Isla de Juventud (Morgan and Albury, 2013). Prior reports of Late Quaternary crocodiles from Jamaica (Morgan, 1993) and Puerto Rico (Vélez-Juarbe and Miller, 2007) were based on isolated fossils (teeth and vertebrae) that are not identifiable to species. Based on the current fossil record of Late Quaternary crocodiles in the West Indies, which confirms that virtually all identifiable fossils belong to *C. rhombifer*, we strongly suspect that future discoveries of Quaternary crocodiles from other Antillean islands, in particular Jamaica and Puerto Rico, will also prove to be *C. rhombifer*.

The fossil record establishes that *Crocodylus rhombifer* was nearly as widespread in the West Indies during the Late Quaternary as *C. acutus* is at present. Moreover, many of the extinct populations of Cuban crocodiles are late Holocene in age based on radiocarbon dates. The early Holocene record of *C. rhombifer* from the Dominican Republic and late Holocene records of this species from Abaco, Crooked Island, and Grand Cayman, together with the absence of a fossil record for *C. acutus* in the West Indies, suggest that the current distribution of the American crocodile in the West Indies may be a very recent phenomenon. The American crocodile may have become established in the West Indies only within the past several thousand years or fewer, within the time period of Amerindian colonization of this region (Rouse, 1989; Fitzpatrick, 2006). This leads to the speculation that humans were involved in the widespread local extinctions and subsequent range contraction of the Cuban crocodile, and may also have inadvertently contributed to the range expansion of the American crocodile.

Although we are not advocating for a change in the common name of the Cuban crocodile, the more extensive geographic range of this species during the Late Quaternary suggests that “West Indian crocodile” would probably be a more appropriate name for *Crocodylus rhombifer*. The distinctive cranial anatomy of *C. rhombifer*, compared with other species of *Crocodylus* in the Caribbean area, suggests a long period of independent evolution of this species, presumably in the West Indies. With the reports of several different taxa of Oligocene and Miocene crocodylians from Puerto Rico and Cuba (Brochu et al., 2007; Brochu and Jiménez-Vázquez, 2014), we anticipate that pre-late Pleistocene fossils of *C. rhombifer*, or its precursor, may eventually be found somewhere in the Antillean area.

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APPENDIX

COMPARATIVE SPECIMENS OF FOSSIL AND MODERN CROCODILES FROM THE WEST INDIES EXAMINED FOR THIS STUDY

The specimens of fossil and modern crocodiles examined during this study are listed here. Complete samples of cranial and postcranial fossils are listed from the Dominican Republic. Only the most complete skulls and mandibles of *Crocodylus rhombifer* from Late Quaternary sites in Cuba, Abaco in the Bahamas and Grand Cayman in the Cayman Islands are listed here (from Morgan and Albury, 2013).

***Crocodylus rhombifer* (fossil)**

DOMINICAN REPUBLIC

Oleg's Bat Cave: MHD 572, nearly complete skull, lacking left premaxilla, right nasal, and both ectopterygoids and palatines, with associated right and left ulna, left femur, left tibia, and right and left fibula; MHD 573, partial skull with right and left maxillae, frontals, squamosals, quadrates, occipital region, and braincase; MHD 574, complete skull with right and left mandibles and associated left humerus, right femur, right tibia, and 12 vertebrae; MHD 575, right and left dentaries, with associated right and left humerus, right and left radius, right and left ilium, right ischium, right femur,

and right calcaneum; MHD 576, small individual consisting of right and left premaxillae and right and left dentaries, with associated left humerus, left radius, right ulna, left and right coracoid, left femur, left tibia, left fibula, left ilium, left and right ischium, left and right pubis; MHD 577, left maxilla, left surangular, and two vertebrae; MHD 578, left articular, right coracoid, left ulna, right ilium, three phalanges, one unguis phalanx, and numerous vertebrae; MHD 579, partial braincase; MHD 580, partial braincase; MHD 581, left dentary; MHD 589, 598, left coracoid; MHD 599, left scapula, 590, right scapula; MHD 587, 591, 592, right humerus; MHD 593, left radius; MHD 594, left ulna; MHD 583, left femur; MHD 595, 596, right femur; MHD 584, left tibia; MHD 585, 588, 597, right tibia; MHD 586, left fibula; MHD 582, right fibula. Minimum number of individuals (MNI) is at least five, based on the presence of braincases from five different crocodiles.

Ni-Rahu (= Cueva de Lynn): MHD 414, nearly complete skull and articulated mandibles with two associated vertebrae. The skull and mandibles and both vertebrae are mostly covered with a layer of calcite flowstone.

ABACO, BAHAMAS

Dan's Cave: UF 137893, partial cranial roof.

Gilpin Point: NMB.AB62.011, frontal and parietal; NMB.AB62.012, right maxilla.

Nancy's Cave: NMB.AB57.003, complete skull and associated mandibles.

Ralph's Cave: NMB.AB51.002, complete skull.

Sawmill Sink: UF 225401, skull and associated mandibles; NMB.AB50.020–NMB.AB50.025, NMB.AB50.027, NMB.AB50.030, NMB.AB50.171, skulls and associated mandibles.

COMMENTS: The Abaco sample of *Crocodylus rhombifer* includes 12 complete skulls, most with associated mandibles: 10 skulls from Sawmill Sink and one skull each from Nancy's Cave and Ralph's Cave, as well as partial skulls from Dan's Cave and Gilpin Point. There is also extensive postcranial material of crocodiles from Sawmill Sink and several of the other blue holes on Abaco. For a complete listing of crocodile fossils from the Bahamas see Morgan and Albury (2013).

GRAND CAYMAN, CAYMAN ISLANDS

Chisholm Cow Well: UF 80000, complete skull; UF 128065, left mandible.

Connally Cow Well: UF 128064, complete skull.

Crocodile Canal: USNM 216197, complete skull; UF 61112–61114, 3 dentaries.

Furtherland Farms Cow Well: UF 128128, cranial table; UF 128139, dentary.

Prospect: UF 65800, complete skull and associated mandibles.

Queen Elizabeth II Botanic Park: UF 143687, partial skull; UF 244488, 244489, 2 dentaries.

COMMENTS: The Grand Cayman sample of *Crocodylus rhombifer* includes four complete skulls, one with associated mandibles, and several additional partial skulls and dentaries. There is also postcranial material of crocodiles from most of the Grand Cayman

sites. For a complete listing of crocodile fossils from Grand Cayman, see Morgan and Albury (2013).

CUBA

Ciego Montero: AMNH 6179, nearly complete skull of a very large individual; AMNH 6180, partial skull; AMNH 6181, complete skull; AMNH 6185, nearly complete skull.

COMMENTS: This is only a partial list of cranial material of fossil *Crocodylus rhombifer* from Ciego Montero. Additional cranial and postcranial fossils of crocodiles from Ciego Montero are housed in the AMNH vertebrate paleontology collection.

***Crocodylus rhombifer* (modern)**

CUBA: Zapata Swamp: Number 6214, Gabinete de Arqueología, Oficina del Historiador, Havana, Cuba, skull; Uncataloged specimen, Criadero de Cocodrilos, Zapata Swamp, Cuba, skull. Captive: UF 45189, captive individual, skull and mandibles.

***Crocodylus acutus* (modern)**

DOMINICAN REPUBLIC: Lago Enriquillo: five skulls lacking mandibles in the Museo Nacional de Historia Natural, Republica Dominicana, (MNHNRD) Santo Domingo, Dominican Republic.

FLORIDA: Florida Keys, Key Largo, UF 56429, skull.

***Crocodylus moreletii* (modern)**

MEXICO: Yucatan Peninsula, UF 29160, skull.

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