THE CUBAN CROCODILE (*CROCODYLUS RHOMBIFER*) FROM LATE QUATERNARY FOSSIL DEPOSITS IN THE BAHAMAS AND CAYMAN ISLANDS

Gary S. Morgan and Nancy A. Albury

JOHN BJORN THORBJARNARSON
(1957–2010)

We dedicate this paper to the memory of our good friend and colleague Dr. John Thorbjarnarson, one of the world's leading experts on crocodile biology and conservation. John made many contributions to our studies of West Indian fossil crocodiles before his untimely death in 2010. Through the Wildlife Conservation Society, John obtained the funding to pay for several radiocarbon dates on crocodile fossils from Sawmill Sink in Abaco and for our travel expenses to attend a conference on Cuban crocodiles that he organized in Cuba in June 2009. Our presentation at that conference on fossil Cuban crocodiles from The Bahamas forms the basis for this paper. John's enthusiasm for crocodile biology, advice on all things crocodylian, and above all, his friendship, will be greatly missed.

Top left: John at the crocodile farm, Zapata Swamp, Cuba, holding a young Cuban crocodile (photograph by Nancy Albury). Bottom left: John in Cuba (photograph courtesy of Avecita Chicchón). Right: John when a young boy with a spectacled caiman on his head (photograph courtesy of the Thorbjarnarson family).

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Gary S. Morgan[1] and Nancy A. Albury[2]

ABSTRACT

Late Quaternary fossil deposits from The Bahamas, Cayman Islands, and Cuba contain fossils of the Cuban crocodile *Crocodylus rhombifer*. This species survives today only in Cuba and Isla de la Juventud (formerly Isla de Pinos); the populations in The Bahamas and Cayman Islands are locally extinct. Large fossil samples, including skulls, are known from underwater caves (blue holes) on Abaco in the northern Bahamas and organic peat deposits on Grand Cayman. Diagnostic cranial characters shared by the fossil crocodile skulls from Abaco and Grand Cayman and recent skulls of *C. rhombifer* from Cuba are: short, broad, and deep rostrum; prominent orbit; concave interorbital region and cranial roof; strong ridge on internal margin of the orbit and lateral margin of the cranial table; large, rounded protuberance on the posterolateral corner of the squamosal; premaxillary-maxillary suture on the palate transverse at the level of the first maxillary tooth; and 13 teeth in the maxilla. Using a ratio derived from living crocodylians of head length (premaxilla to parietal) to total length of about 1:7.2, approximate total lengths for fossil specimens of *C. rhombifer* from Abaco range from 1.3–2.3 m (mean 1.9 m) and Grand Cayman from 1.6–2.0 m (mean 1.7 m). Quaternary crocodylian remains are known from many other islands in The Bahamas, including Acklins, Crooked Island, Eleuthera, Grand Bahama, Mayaguana, New Providence, and San Salvador; however, most of these fossils are not complete enough for a species identification. Shells of an extinct species of the land tortoise *Chelonoidis* from Abaco and Mayaguana with crocodylian bite marks, jaws and teeth of capromyid rodents from Grand Cayman that appear to have been digested by a crocodylian, and data from carbon ($^{13}C/^{12}C$) isotopes derived from crocodile bones, as well as the lack of large freshwater vertebrates, suggest that *C. rhombifer* in The Bahamas and Cayman Island had a diet primarily consisting of terrestrial vertebrates. Evidence from stomach contents and behavioral ecology of extant Cuban crocodiles from Cuba further supports the terrestrial feeding habits of *C. rhombifer*. Radiocarbon (^{14}C) dates on crocodile postcranial bones from Sawmill Sink and Dan's Cave on Abaco range from 2,780–3,680 years Before Present (BP). Radiocarbon dates on peat associated with fossils of *C. rhombifer* from the Crocodile Canal site on Grand Cayman range from 375–860 years BP. These dates confirm that Cuban crocodiles survived into the late Holocene on Abaco and into the historic period on Grand Cayman. Evidence from a variety of sources, including radiocarbon dates, fossil and archaeological sites, and historical records confirms that the local extinction of crocodiles in The Bahamas and Cayman Islands occurred within the past 500 years, probably resulting from overhunting by humans. Fossils of *C. rhombifer* on Grand Cayman and Abaco, and probably throughout The Bahamas, verify that the Cuban crocodile was considerably more widespread in the West Indies during the Late Quaternary.

Key words: Cuban crocodile; *Crocodylus rhombifer*; Quaternary; blue holes; The Bahamas; Grand Cayman; taxonomy; paleoecology; extinction.

[1]New Mexico Museum of Natural History, 1801 Mountain Rd., NW, Albuquerque, New Mexico, USA 87104; <gary.morgan1@state.nm.us>
[2]National Museum of The Bahamas / Antiquities, Monuments and Museums Corporation, P.O. Box AB20755, Marsh Harbour, Abaco, The Bahamas; <nancyalbury@gmail.com>

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INTRODUCTION

Crocodiles are known from Late Quaternary (late Pleistocene and Holocene) fossil deposits on all four of the Greater Antilles (Cuba, Hispaniola-Dominican Republic, Jamaica, and Puerto Rico), as well as Mona Island between Puerto Rico and Hispaniola. With the exception of fossils from several sites in Cuba and the Dominican Republic, the other crocodile specimens from the Greater Antilles are not complete enough to permit identification beyond the generic level (*Crocodylus*). Surprisingly, two small islands where crocodiles no longer occur, Abaco in the northern Bahamas and Grand Cayman in the Cayman Islands, have yielded the largest fossil samples of crocodiles so far known from the West Indies (Morgan et al. 1993; Morgan 1994; Franz et al. 1995; Steadman et al. 2007). Sawmill Sink, a water-filled cave or inland blue hole on Abaco, has produced a diverse and well-preserved sample of Late Quaternary vertebrates, invertebrates, and plants. Sawmill Sink contains more than 50 individuals of the Cuban crocodile *Crocodylus rhombifer*, many of which consist of associated skulls and mandibles, some with partial postcranial

skeletons (Steadman et al. 2007). Crocodile skulls and/or skeletons are also known from four other inland blue holes on Abaco, Dan's Cave, Lost Reel Cave, Nancy's Cave, and Ralph's Cave. Crocodile fossils referable to *C. rhombifer*, including five partial to nearly complete skulls, are also known from sites on Grand Cayman (Morgan et al. 1993; Morgan 1994).

Despite the fact that the American crocodile *Crocodylus acutus* is widespread in the Greater Antilles, and occurs as far north as the Florida Keys and southern peninsular Florida, the samples of fossil crocodiles from Abaco and Grand Cayman are referable to the Cuban crocodile *Crocodylus rhombifer*, which is now restricted to the Ciénaga de Zapata (Zapata Swamp) in southern Cuba and the Ciénaga de Lanier (Lanier Swamp) on the Isla de la Juventud (formerly known as Isla de Pinos). We provide descriptions, comparisons, and measurements of the fossil crocodile samples from The Bahamas and Cayman Islands, as well as a discussion of their paleoecology, taphonomy, biogeography, and extinction, and a brief review of Quaternary crocodile records from elsewhere in the West Indies.

METHODS AND MATERIALS

The primary focus of our paper is on fossils of Late Quaternary crocodiles from The Bahamas and Cayman Islands. We have studied all of the crocodile fossils from Abaco and Grand Cayman, as well as specimens from Acklins, Eleuthera, Grand Bahama, and Mayaguana in The Bahamas. We also examined crocodile specimens from archaeological sites on Crooked Island and Acklins in The Bahamas (Keegan 1992). Other records of Quaternary crocodiles from the West Indies are mostly reviewed from the literature, including New Providence (Pregill 1982) and San Salvador (Olson et al. 1990) in The Bahamas, Jamaica (Anthony 1920; Morgan 1993), Puerto Rico (Vélez-Juarbe & Miller 2007), and Mona Island (Frank & Benson 1998). Varona (1984) reviewed the Quaternary record of crocodiles from Cuba. Fossil crocodiles from Cuba also have been mentioned in several other papers (Leidy 1868; Brown 1913; Varona 1966; Iturralde-Vinent et al. 2000).

See Figure 1 for photographs of dorsal, ventral, lateral, and posterior views of a skull and Figure 2 for dorsal, ventral, lateral, and medial views of a mandible of *Crocodylus rhombifer* from Sawmill Sink, Abaco, with the individual bones identified. Photographs of dorsal and ventral views of a skull and dorsal and lateral views of a mandible of *C. rhombifer* from Sawmill Sink, with measurements indicated, are presented in Figure 3.

Crocodylus rhombifer: cranial and mandibular measurements (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 called "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. Dorsal length of premaxilla (measured on dorsal surface of skull)
E. Ventral length of premaxilla (measured ventrally on palate)
F. Length of maxillary toothrow (measured ventrally on palate)
G. Breadth of premaxilla
H. Breadth of snout at fifth maxillary tooth
I. Breadth of snout at anterior edge of orbits
J. Minimum interorbital breadth
K. Breadth at anterior edge of cranial roof (at postorbitals)
L. Breadth at posterior edge of cranial roof (at squamosal protuberances)
M. Maximum breadth of skull at quadratojugals
N. Breadth of skull at quadrates
O. Posterior width of quadrate
P. Width of occipital condyle
Q. Total length of mandible (from anterior tip of dentary to posterior tip of articular)
R. Maximum length of dentary
S. Length of mandibular toothrow
T. Length of articular
U. Width of articular

For each skull, we also recorded several additional morphological characters including: structure of the cranial table (consisting of the frontals, parietals, postorbitals, and squamosals); 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 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 largest three teeth.

Guidelines for collecting fossils from blue hole environments and processing in the laboratory were developed by Brian Kakuk and Nancy A. Albury (NAA). Upon the discovery of a new fossil, a field number is written on a non-directional identification marker and placed next to the fossil where it is photographed in place. Selected specimens and associated sediments are carefully collected in appropriately sized zipper locking bags and plastic boxes that are secured with lids and straps. This arrangement limits movement and damage to the fossils, retains the original water chemistry, and reduces oxygen exposure to the bones until processing in the laboratory. At
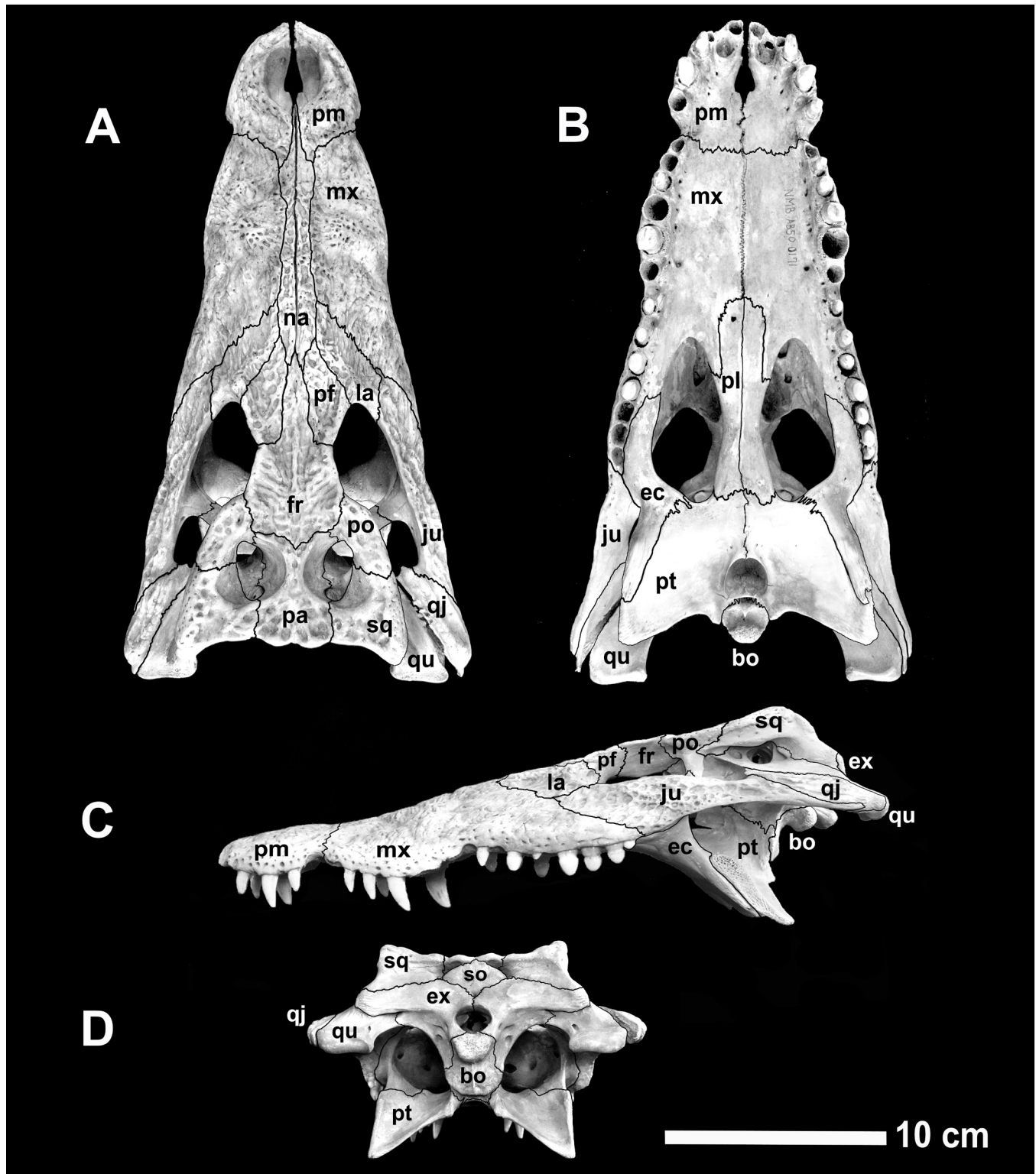
Figure 1. Skull of a Cuban crocodile (*Crocodylus rhombifer*) from Sawmill Sink (NMB.AB50.171; C52), Abaco, The Bahamas, in dorsal (A), ventral (B), lateral (C), and posterior (D), views. The individual bones in the skull are identified using the following abbreviations: **bo** (basioccipital = occipital condyle), **ec** (ectopterygoid), **ex** (exoccipital), **fr** (frontal), **ju** (jugal,), **la** (lacrimal), 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*) from Sawmill Sink (NMB.AB50.171; C52), Abaco, The Bahamas, in dorsal (A), ventral (B), lateral (C), and medial (D) 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..
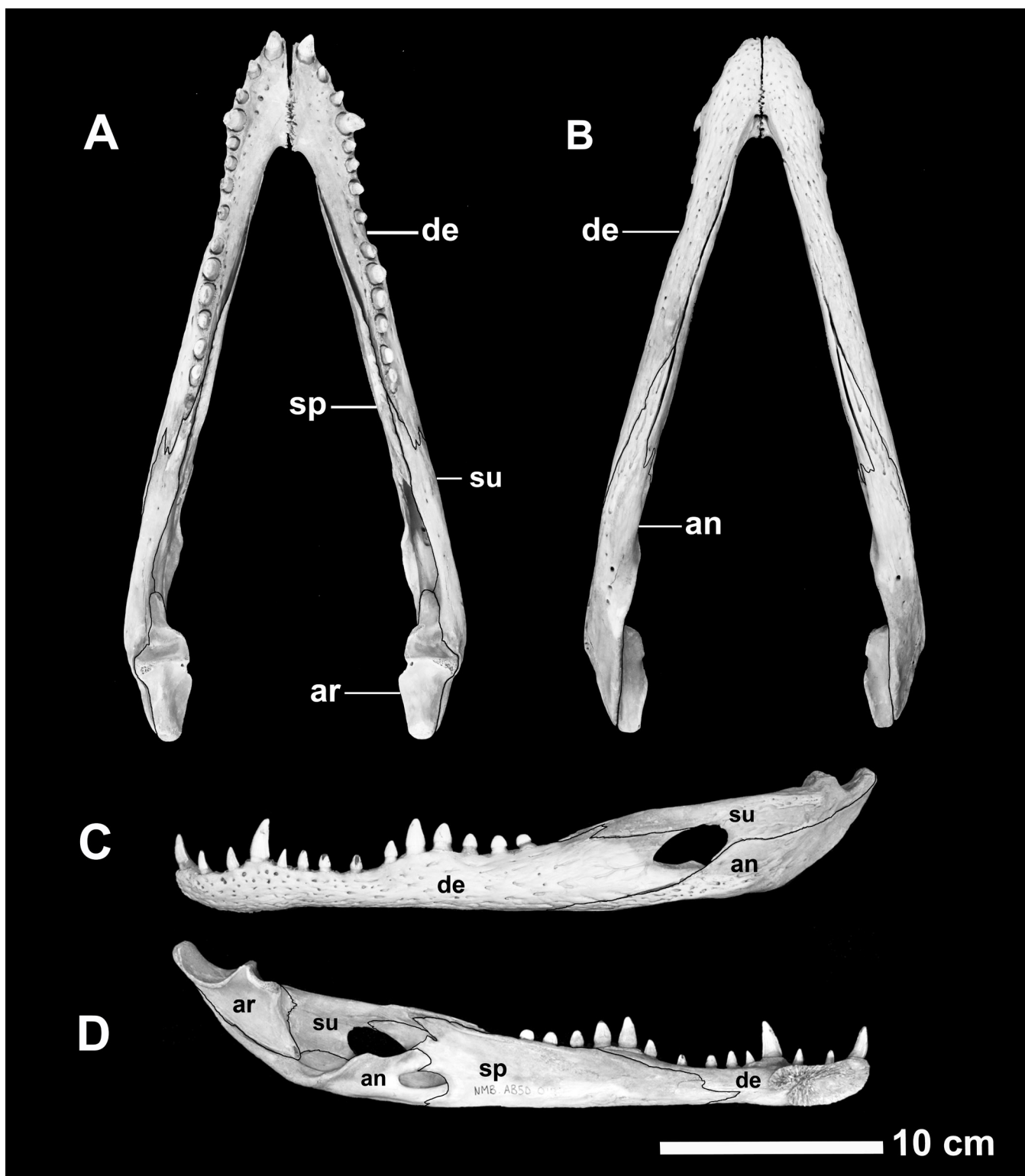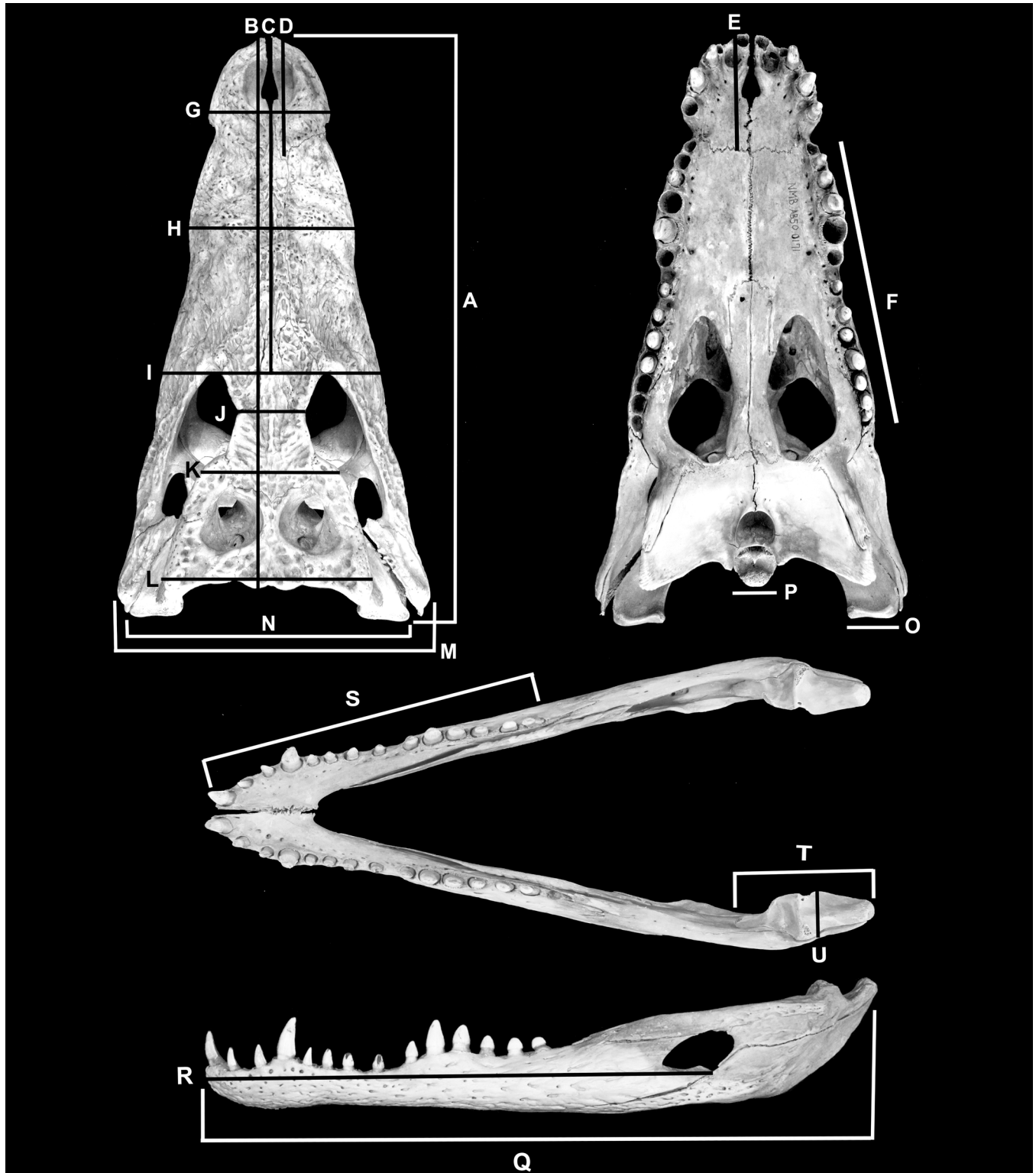
Figure 3. Skull and mandible of a Cuban crocodile (*Crocodylus rhombifer*) from Sawmill Sink (NMB. AB50.171; C52), Abaco, The Bahamas, showing the measurements taken on crocodile specimens from Abaco, Grand Cayman, and Cuba (AMNH). The measurements (letters A–U) are explained in the Methods section of the text.

the surface the fossils are secured for transport to the lab with cloth towels fitted snugly around the specimens. In the lab, after a series of lengthy freshwater baths to remove the salts and sediments, the bones are slowly air-dried and stabilized when necessary with the consolidant Polyvinyl Butyral (PVB) Butvar 76®. Franz and Franz (2009) also provided a detailed discussion of the sampling protocol for collecting vertebrate fossils from blue holes in The Bahamas.

We use an informal system to identify individual crocodile specimens from Sawmill Sink, including fossils that have not yet been (and may never be) collected. Only 12 individuals of *Crocodylus rhombifer*, represented by skulls and mandibles, or in the case of one specimen, several skull fragments and associated postcranial elements, have been collected from Sawmill Sink, yet 54 separate individuals have been identified in the fossil site. The Sawmill Sink crocodile specimens are designated C1–C54, consecutively numbered in the chronological order in which they were discovered and mapped on a site survey. Only fossils that have been collected and prepared are assigned catalogue numbers (e.g., NMB.AB50.020 for C15).

Radiocarbon (¹⁴C) dates are cited in radiocarbon years Before Present (yr BP). All radiocarbon dates from Abaco were obtained on bone collagen using the Accelerator Mass Spectrometry (AMS) method and were analyzed by Beta Analytic, Inc. in Miami, Florida. A radiocarbon date using the traditional method was obtained on bone collagen derived from a large sample of capromyid rodent (*Geocapromys*) bones from the Banana Hole site on New Providence. Two radiocarbon dates from the Crocodile Canal site on Grand Cayman were obtained from peat containing crocodile bones. 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 dated and thus we are uncertain if the sites are Holocene or Pleistocene in age. If radiocarbon dates are available, such as the series of dates on crocodile bones from

Sawmill Sink on Abaco, then we refer to dated sites as either Holocene (less than 10,000 years) or Pleistocene (older than 10,000 years). The ages for several Pleistocene sites, especially sites older than 100,000 years (100 ka) dated by the uranium-series method, are expressed in ka (kilo-anna, or thousands of years).

All measurements are in mm. We calculated the Minimum Number of Individuals (MNI) of crocodiles present in several sites. The MNI is determined by counting the largest number of a particular bone from either the right or left side of the skeleton. For instance, 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. In several instances, we determined the MNI from different sizes of individuals, which gave a slightly higher MNI. For example, we identified three crocodile maxillae (two right, one left) from the Queen Elizabeth II Botanic Garden site on Grand Cayman for an MNI of two. However, the three maxillae were from very different-sized individuals, a tiny hatchling, a small adult, and a very large adult, which yields an MNI of three.

For the names of the islands in The Bahamas, we follow the map of the Commonwealth of The Bahamas, published in 1988 by the Department of Lands and Surveys, government of The Bahamas. As used on this map, certain islands in The Bahamas have the word "island" or "cay" (pronounced key) in their name and others do not (e.g., Crooked Island, Green Turtle Cay, Abaco). The official name for the country is "The Bahamas" (both words capitalized). With a few exceptions, the names we use for blue holes, dry caves, or other Quaternary fossil sites on Abaco, other islands in The Bahamas, and Grand Cayman do not appear on topographic maps. The site names generally have been assigned by the paleontologists who first described the sites, with the names referring to local villages or other topographic features, the landowner, or in the case of several blue holes in The Bahamas, the person who discovered the site.

The crocodile fossils from The Bahamas and Cayman Islands are housed in seven museums or

other institutions (with acronyms or abbreviations): Cayman Islands National Museum (**CINM**), George Town, Grand Cayman; Florida Museum of Natural History (**FLMNH**), University of Florida, Gainesville (**UF**, acronym for catalogued fossil specimens); Mosquito Research and Control Unit and Natural Resources Study (**MRCU/NRS**), Cayman Islands Department of the Environment, George Town, Grand Cayman; Museum of Comparative Zoology (**MCZ**), Harvard University, Cambridge, Massachusetts; National Museum of The Bahamas / Antiquities, Monuments and Museums Corporation (**NMB**), Nassau and Marsh Harbour, The Bahamas; National Trust for the Cayman Islands (**NTCI**), George Town, Grand Cayman; and U. S. National Museum of Nat-ural History (**USNM**), Smithsonian Institution, Washington, DC.

QUATERNARY CROCODILE SITES IN THE WEST INDIES

Abaco, The Bahamas

Six Late Quaternary sites from Abaco in the northern Bahamas (Fig. 4) contain fossils of crocodiles, Sawmill Sink, Dan's Cave, Ralph's Cave, Nancy's Cave, and Lost Reel Cave are inland blue holes, whereas Gilpin Point is a peat deposit. Blue holes are water-filled caves that are found throughout The Bahamas. Their flooded cave passages extend below sea-level for most of their depth and contain water that may be fresh, salt, or mixed chemistry (Mylroie et al. 1995; Mylroie & Mylroie 2007). Blue holes are classified relative to their location and the position of current sea level stands, thus "ocean" blue holes are caves that are completely flooded by salt water with entrances that open into the current marine environment, whereas "inland" blue holes open onto dry land or into an isolated pond or lake. Because of their surface isolation from marine conditions, inland blue holes reflect an island's subsurface water chemistry. On islands with sufficient rainfall, freshwater floats on the underlying marine salt water that permeates the porous carbonate platforms of The Bahamas and provides a source of freshwater for living plant and animal communities. A detailed listing of the crocodile fossils from sites on Abaco is provided

in Appendix 1. All six of these sites contain either complete or partial skulls that can be confidently identified as the Cuban crocodile *Crocodylus rhombifer*.

Sawmill Sink.—The largest sample of Quaternary crocodiles so far known in the West Indies is from Sawmill Sink, located in the pinelands of south-central Abaco (26°13'N, 77°12'W; Fig. 4, site 1). Fossil crocodiles were first discovered in Sawmill Sink in 2004 by cave divers Brian Kakuk and Jim Pickar, and were first mentioned in an article by Kakuk and Curt Bowen in *Advanced Diver Magazine* (2005). Sawmill Sink is an inland blue hole with a nearly circular opening 15.5 m in diameter that connects to an underwater cave system reaching depths of 54 m and a length of >600 m (Steadman et al. 2007). Nancy Albury (in prep.) will provide a detailed discussion of all aspects of Sawmill Sink elsewhere; only a brief summary is presented here. The Cuban crocodile *Crocodylus rhombifer* is the most abundant large vertebrate in Sawmill Sink, with 54 individuals currently documented. This site also contains a significant sample of a recently described species of large extinct land tortoise, *Chelonoidis alburyorum* (Franz & Franz 2009), as well as more than 25 species of birds and smaller samples of fish, lizards, snakes, bats, and the Bahamian hutia (a large capromyid rodent) *Geocapromys ingrahami* (Steadman et al. 2007). The majority of the crocodile fossils are derived from a Holocene peat deposit that comprises a talus cone extending from a depth of 9 to 34 m. A few crocodile fossils have been found at greater depths peripheral to the talus cone, including isolated elements from a single individual (NMB.AB.50.026; C21; Fig. 25) that are larger and more heavily mineralized than the crocodile bones from the peat deposit. An attempt to radiocarbon date this large crocodile was unsuccessful because of the lack of datable collagen, suggesting it is considerably older than the crocodiles from the peat deposit, possibly late Pleistocene in age. The general preservation quality of the crocodile fossils from the peat deposit is excellent. Many of the specimens collected consist of nearly 100% intact skulls and still-attached
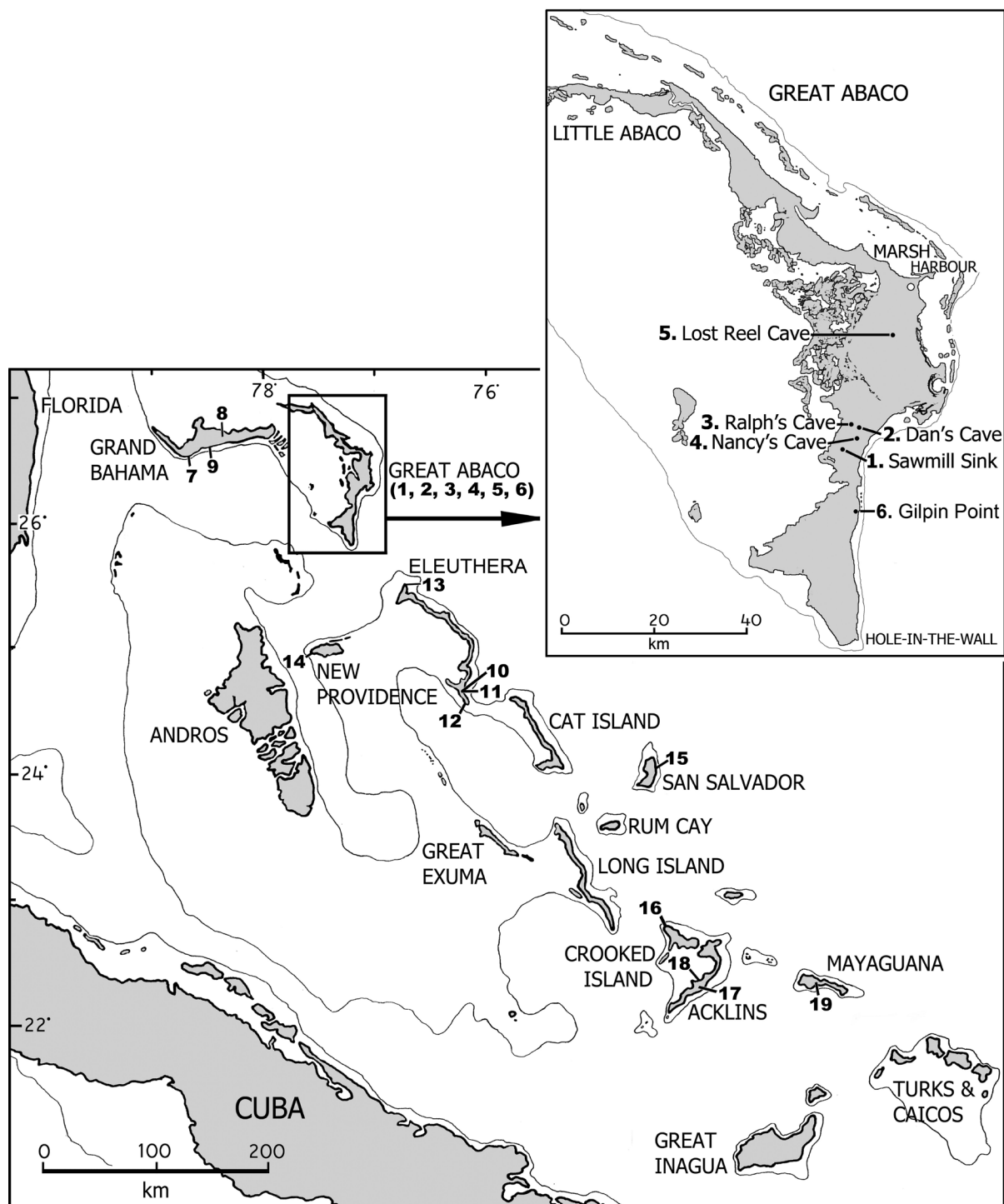
Figure 4. Map of The Bahamas, with an enlarged map of Abaco, showing the location of inland blue holes, dry caves, and Amerindian archaeological sites containing Quaternary crocodiles. Site numbers on the map are as follows (numbers assigned in the order the sites are discussed in the text): **Abaco**: 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. **Crooked Island**: 16. Pitts Town. **Acklins**: 17. Rupert's Pond; 18. Delectable Bay. **Mayaguana**: 19. The Fountain.

mandibles retaining most of the teeth, and a few individuals have partial associated postcranial skeletons. Eleven complete skulls and associated mandibles of crocodiles have been removed from the Holocene peat deposit in Sawmill Sink, eight of which appear to be of adult size.

Dan's Cave.—Franz et al. (1995) reported a partial skull and partial postcranial skeleton of *Crocodylus rhombifer* collected in 1993 by Nancy Albury and George Irvine from a blue hole near Bahama Palm Shores in south-central Abaco. This blue hole, since named Dan's Cave (26°14'N, 77°11'W; Fig. 4, site 2), is about 2 km northeast of Sawmill Sink. From only one known entrance, more than 25,000 feet (7,600 m) of flooded cave passages have now been explored in Dan's Cave. The crocodile skeleton was found in very fine-grained, silty sediments on a rock at a depth of 16 m and about 20 m from the entrance. Although the skull was mostly intact when discovered, it fell apart when collected. Franz et al. (1995) described and illustrated this specimen, which as now preserved includes the dorsal portion of the skull from the nasals to the cranial table, several associated but isolated cranial elements, the posterior portion of both mandibles, numerous isolated teeth, partial limb bones, vertebrae, and osteoderms (see Appendix 1). A second crocodile skull and skeleton was also observed in Dan's Cave in 1993 just a few meters away but was not collected. Based on recent observations, it is no longer present in the cave. According to Nancy Albury and Brian Kakuk, the crocodile fossils from Dan's Cave are extremely fragile and although they appear well preserved when still in place, upon being touched may disintegrate. Figure 5 shows a third, disarticulated skull, nearly complete mandible, and associated vertebrae and limb elements of *C. rhombifer* from Dan's Cave that was photographed in 2008 at a depth of 20 m. This is not the same specimen as the second skull from Dan's Cave found in 1993, and likewise has not been collected. A fourth crocodile specimen from Dan's Cave, consisting of a metapodial, two vertebrae, and two osteoderms (NMB.AB53.003), was collected from a micrite deposit (fine-grained calcium carbonate mud) at a depth of 28 m, approximately 275 m from the cave entrance. Figure 6 illustrates a crocodile vertebra encased in the micrite deposit in Dan's Cave.

Ralph's Cave.—Ralph's Cave is located in south-central Abaco less than 1 km from Dan's Cave (26°15'N, 77°11'W; Fig. 4, site 3), and is

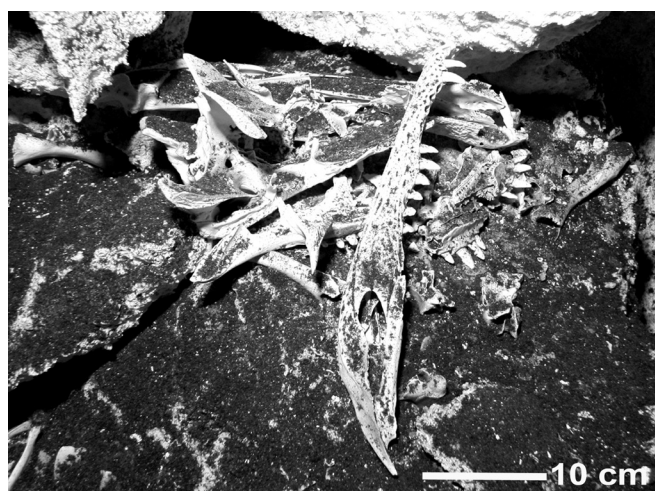**Figure 5.** Underwater photo of disarticulated skull, lower jaws, and partial skeleton of Cuban crocodile (*Crocodylus rhombifer*), Dan's Cave, Abaco. Specimens not collected, still in place (photograph by Brian Kakuk).
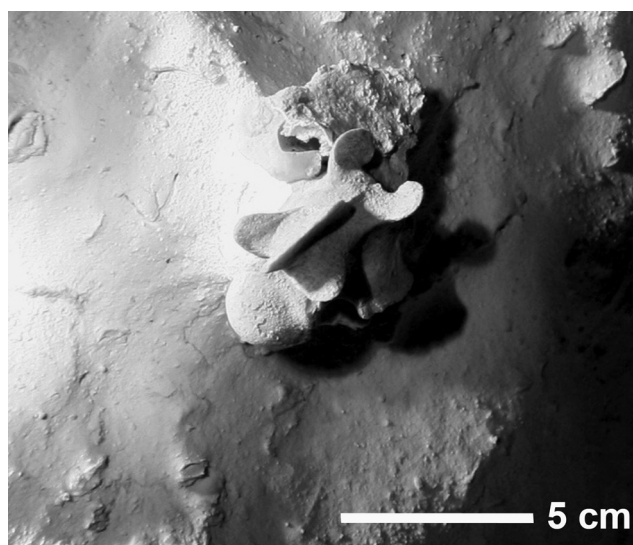

Figure 6. Underwater photo of crocodile (*Crocodylus* sp.) vertebra preserved in micrite deposit, Dan's Cave, Abaco. Specimen not collected, still in place (photograph by Brian Kakuk).

probably part of the same larger underwater cave system. The small surface opening is the collapsed ceiling of a shallow dissolutional void where bats occasionally roost. Near the entrance, the remains of bats, tortoise, and crocodile were found within the black organic sediments of the debris cone. Further into the cave system, several bats are entombed in clear calcite flowstone at a depth of 15 m, approximately 300 m from the nearest entrance. A nearly complete *Crocodylus rhombifer* skull and partial associated skeleton (NMB.AB51.002) have been recovered from Ralph's Cave.

Nancy's Cave.—Nancy's Cave is located in south-central Abaco (26°14'N, 77°11'W; Fig. 4, site 4), in the same general vicinity as Dan's Cave and Ralph's Cave. The cave entrance is within a small pool of water at the edge of a 40-m-wide sinkhole that is almost completely filled with littoral vegetation growing from wet, spongy peat. Organic sediments flow through a small entrance

and down a steep debris slope to a depth of 29 m. From the base of the slope a cave passage continues for more than 300 m. Fossils of crocodile, tortoise, iguana, and hutia, as well as pre-European human remains, are found in the both organic sediments and deeper cave passages. In February 2010, Brian Kakuk collected a skull, mandibles, and partial associated skeleton of a large *Crocodylus rhombifer* from Nancy's Cave (NMB.AB57.003), and an associated front and hind limb of a second crocodile.

Lost Reel Cave.—Lost Reel Cave is located in central Abaco south of Marsh Harbour (26°25'N, 77°05'W; Fig. 4, site 5). Part of a larger sinkhole feature, the cave's steep talus slope is composed of dark, organic sediments that flow through a narrow cave entrance. At the bottom of the slope, cave passages continue to the west to depths of 40 m. Fossils occur in two main deposits, an organic peat deposit on the talus slope and second and

Figure 7. Underwater photo of Cuban crocodile (*Crocodylus rhombifer*) skull, lower jaws, and semi-articulated skeleton, Lost Reel Cave, Abaco. A femur from this skeleton (NMB.AB52.009) was collected. The remainder of the skeleton has not been collected, and is still in place (photograph by Brian Kakuk).

presumably older deposit embedded in calcite flowstone in the deeper areas beyond the base of the talus slope. Most of the vertebrate fossils have been collected at depths of 28–34 m. A nearly complete, partially articulated skeleton of a large individual of *Crocodylus rhombifer* was discovered in Lost Reel Cave in 2009 and has been photographed underwater (Fig. 7). Only a femur of this individual has been collected (NMB.AB52.009), which represents one of the largest individuals of *C. rhombifer* from Abaco. The only other crocodile fossils from this cave consist of a large sample of coprolites or fossilized dung (Fig. 26). Other vertebrates from Lost Reel Cave include several partial shells of the large land tortoise *Chelonoidis*, birds, and a skull of the rodent *Geocapromys ingrahami*.

Gilpin Point.—Gilpin Point is located about 10 km south of Sawmill Sink and 1.5 km south of Crossing Rocks, along the east coast of Abaco (26°06'N, 77°11'W; Fig. 4, site 6). The Gilpin Point site consists of dark organic peaty sediments containing abundant wood, preserved within a sandy beach deposit along the coast. The site is almost always underwater, even during low tide. The uppermost layers of peat are exposed only during extremely low spring tides and are usually covered with a thick layer of beach sand. The Gilpin Point site is located on land belonging to Pericles (Perry) Maillis, who collected most of the fossils between 2009 and 2013 and donated them to the NMB collection in Marsh Harbor. Vertebrate remains found at Gilpin Point include *Crocodylus rhombifer* (Fig. 10F–I), *Chelonoidis*, sea turtles, birds, and several teeth of the hutia *Geocapromys*. Gilpin Point is similar to peat deposits on Grand Cayman that have produced large samples of fossil crocodiles, as well as the Bell Channel site on Grand Bahama (see site descriptions below).

OTHER ISLANDS IN THE BAHAMAS

Crocodiles have been recovered from Quaternary fossil deposits on six other islands in The Bahamas: Acklins, Eleuthera, Grand Bahama, Mayaguana, New Providence, and San Salvador. Crocodile remains are also known from Amerindian archaeological sites on Acklins, Crooked Island, and Eleuthera. With the exception of Grand Bahama, all other Bahamian crocodile records outside of Abaco currently consist of non-diagnostic elements (isolated teeth, postcranial bones, coprolites) that cannot be identified to the species level. We discuss both new discoveries of crocodiles and several records from the published literature. The sites are listed in geographic order from north to south within The Bahamas.

Grand Bahama.—The second crocodile fossil discovered in The Bahamas was actually one of the last records recognized. In May of 1965, Dora Weyer discovered a nearly complete left dentary with at least five teeth of a small crocodile on Grand Bahama. This specimen has been housed in the herpetology collection of the Museum of Comparative Zoology (MCZ 85546) at Harvard University for more than 40 years, but was only recently "discovered" in the collection by John Thorbjarnarson who alerted us to its presence. We have not yet had the opportunity to study this specimen, but have examined a photograph taken by Thorbjarnarson (here reproduced as Fig. 8). Locality information on the specimen label with this fossil states that it was collected from "black swamp muck at Bell Channel Site, Lucaya." This fossil was almost certainly uncovered during the extensive excavation and dredging for Port Lucaya in Freeport (26°31'N, 78°38'W; Fig. 4, site 7). The preservation of the jaw in "black swamp muck" is similar to the occurrence of the majority of crocodile fossils from Grand Cayman, as well as fossils from Gilpin Point on Abaco, all of which were preserved in organic peat deposits. The jaw from the Bell Channel site on Grand Bahama differs in its occurrence from most other Bahamian fossil crocodile sites, which are primarily from inland blue holes.

Cristina Zenato and Arkadiusz Pers discovered crocodile fossils in two blue holes in the vicinity of Lucayan Caverns on Grand Bahama, Mermaid's Lair and Anaconda Pond (26°36'N, 78°24'W; Fig. 4, sites 8 & 9). Crocodile fossils were first found and photographed underwater in Mermaid's Lair in May 2009 and a sample of these fossils was collected in December 2011. Crocodile fossils were found in Anaconda Pond in May 2010.
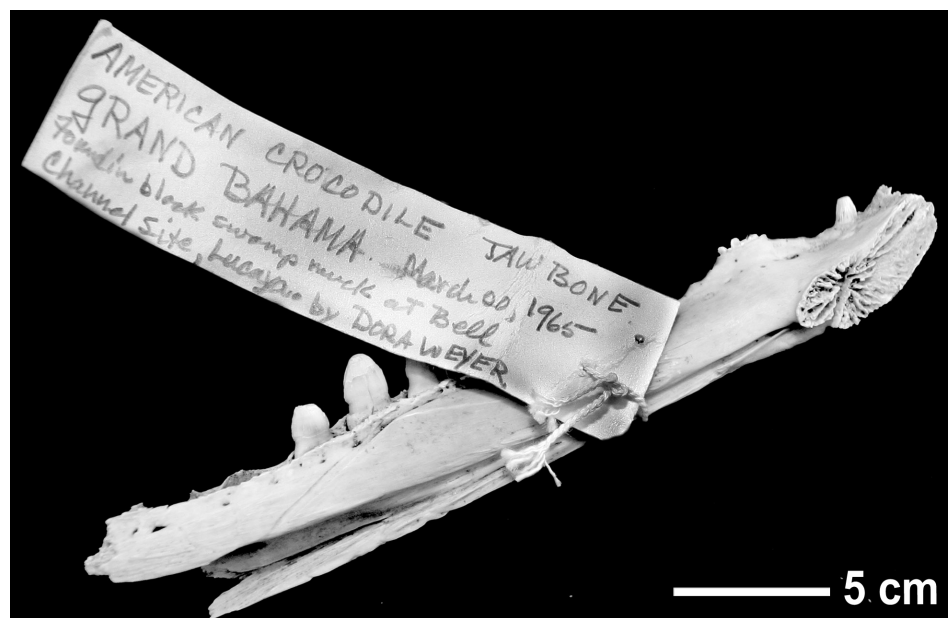
Figure 8. Medial view of left dentary of crocodile (*Crocodylus* sp.; MCZ 85546) from Bell Channel site, Grand Bahama (photograph courtesy of John Thorbjarnarson).

Both of these sites are inland blue holes with fresh surface water. The occurrence of crocodile bones in Anaconda Pond was described by Cristina Zenato (pers. comm.) as follows: "In about 90 ft. of water, one half of the bottom jaw of a crocodile was intact with all the teeth still in place and fragments of the skull right below it, all of which are black in color. The cave is situated in the middle of a flooded swampy area over rocky terrain. The walls of the cave are covered in stalactites, tannic acid is thick, and visibility limited at about 4 ft. for the first 60 ft. in depth. The halocline is very deep at 70 ft. and the sulfur presence is enormous. Visibility is crystal clear below the halocline and water temperature is constant at 74° F."

The crocodile fossils from Mermaid's Lair were photographed underwater, several of which were later collected, including a frontal, partial jugal, articular, angular, surangular, and ilium (NMB.GB016.001). Some of the crocodile fossils from Mermaid's Lair that remain underwater are shown in Figure 9, while Figures 10A–E illustrate fossils that were collected. All of these elements are diagnostically crocodylian and almost certainly represent *Crocodylus*. A frontal is clearly referable to *C. rhombifer* based on characters described in

more detail below, in particular, the concave dorsal surface and strong ridges along the internal margins of the orbits.

Eleuthera.—In August 2007, Brian Kakuk and Gregg Stanton collected the remains of tortoise and a fragment of a left dentary (NMB. EL185.001), a tooth (NMB.EL185.002), and a complete humerus (NMB.EL185.003) of a large crocodile from a depth of 46 m in White Lake Cave (24°44'N, 76°13'W; Fig. 4, site 10), an inland blue hole located along the perimeter of White Lake in southern Eleuthera. The fossils are well mineralized, heavy, and an orangish-brown color, and were collected from coarse-grained sand and rubble sediments. The specimens represent a large crocodile and are probably from the same individual, although they have been assigned different catalogue numbers (Fig. 11).

In 2011, a partial dentary of a crocodile (NMB.EL.180.001) was found in Kelly's Blue Hole (also known as "Bung Hole"), an inland blue hole located near White Lake Cave in southern Eleuthera (24°44'N, 76°13'W; Fig. 4, site 11). The cave begins in the center of the pond and descends through a small conduit with black, organic bottom sediments. Near the bottom of a steep
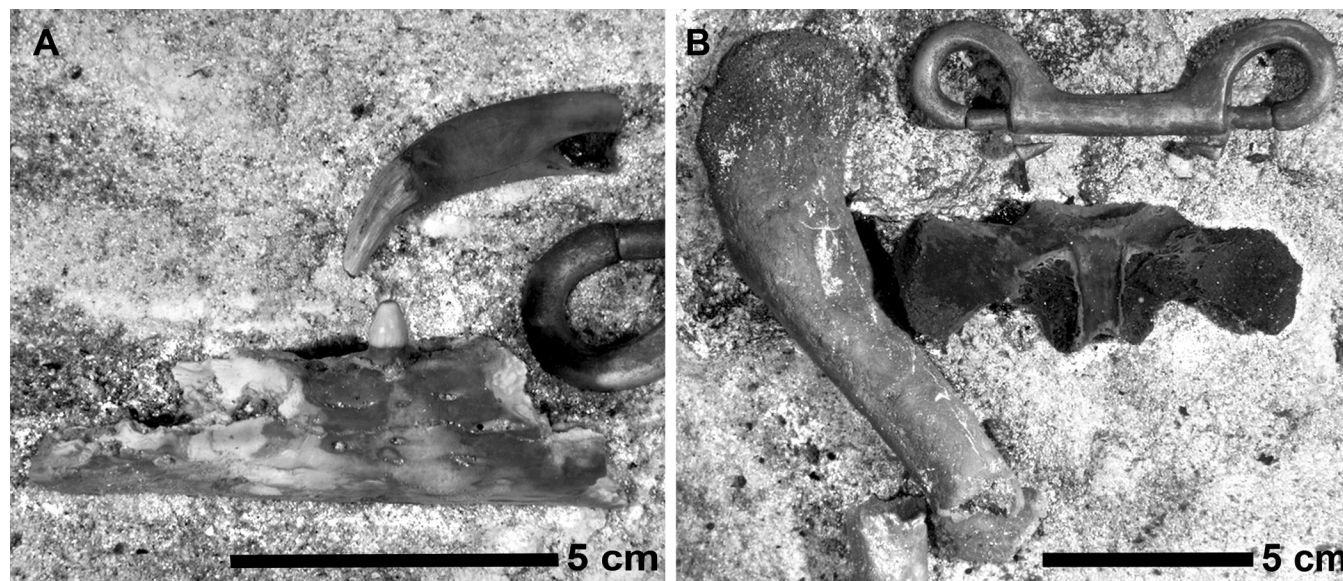
Figure 9. Underwater photos of Cuban crocodile (*Crocodylus rhombifer*) specimens in Mermaid's Lair, Grand Bahama. A. Dentary fragment with tooth (bottom) and isolated tooth (top). B. Partial femur (left) and sacral vertebra (right). Specimens not collected, still in place. Photographs courtesy of Arkadiusz Pers.

talus slope, fragments of disarticulated crocodile and tortoise fossils were scattered through deep flocculent sediments. A small crocodile femur (NMB.EL.183.001) was found in 2011 in another inland blue hole in southern Eleuthera known as Mermaid's Pool (24°39'N, 76°10'W; Fig. 4, site 12), situated within a dense coppice near the abandoned settlement of Bannerman Town.

Carr et al. (2006) reported and illustrated two crocodile teeth from an archaeological site in Preacher's Cave in northern Eleuthera (Fig. 4, site 13). The teeth were recovered from two different excavation units. One tooth (FS 175) was found in spoil adjacent to a Lucayan burial. The second tooth (FS 115) was associated with 17th century artifacts. These records indicate that both crocodile teeth are probably younger than 1,000 years.

New Providence.—Pregill (1982) identified a partial vertebra of a juvenile crocodile from the Banana Hole site, a sinkhole/cave deposit near Clifton on the western end of New Providence (Fig. 4, site 14). This vertebra (UF 2994), the first crocodile fossil reported from the Bahamas, was collected in 1958 by Walter Auffenberg and J. C. Dickinson of the Florida State Museum (now FLMNH). Limb bones of the rodent *Geocapromys ingrahami* from Banana Hole, recovered from the same strata that produced the crocodile fossil, yielded a radiocarbon date of 7,980 ± 230 yrBP derived from bone collagen (Morgan 1989).

San Salvador.—Olson et al. (1990) reported a partial jugal and an osteoderm of a crocodile from a site called Hanna's Bananas, a sinkhole deposit on the east coast of San Salvador (Fig. 4, site 15). They noted that the jugal was heavily mineralized, but no other information is available on the age of vertebrate fossils from San Salvador.

Crooked Island.—Keegan (1992) mentioned a crocodile femur from the Pitts Town archaeological site (CR-14), found near a freshwater pond at the northwestern end of Crooked Island (22°50'N, 74°20'W; Fig. 4, site 16).

Acklins.—In November 2008, Brian Kakuk and Nancy Albury recovered an osteoderm of a crocodile (NMB.AC20.001) from a depth of 21 m in an inland blue hole known as Rupert's Pond (22°21'N, 74°03'W; Fig. 4, site 17). Beginning near the center of Rupert's Pond, a steeply sloping cave passage leads to a maximum depth of 29 m. The crocodile osteoderm was found in the bottom

sediments, together with a tortoise scapula.

A crocodylian tooth was identified from an archaeological site near Delectable Bay (AC-14) on Acklins (Keegan 1988; Franz et al. 1995; FLMNH Zooarchaeology Collection; Fig. 4, site 18). Delectable Bay is only about 5 km from Rupert's Pond. Based on the discoveries of crocodile remains in archaeological sites on Crooked Island and
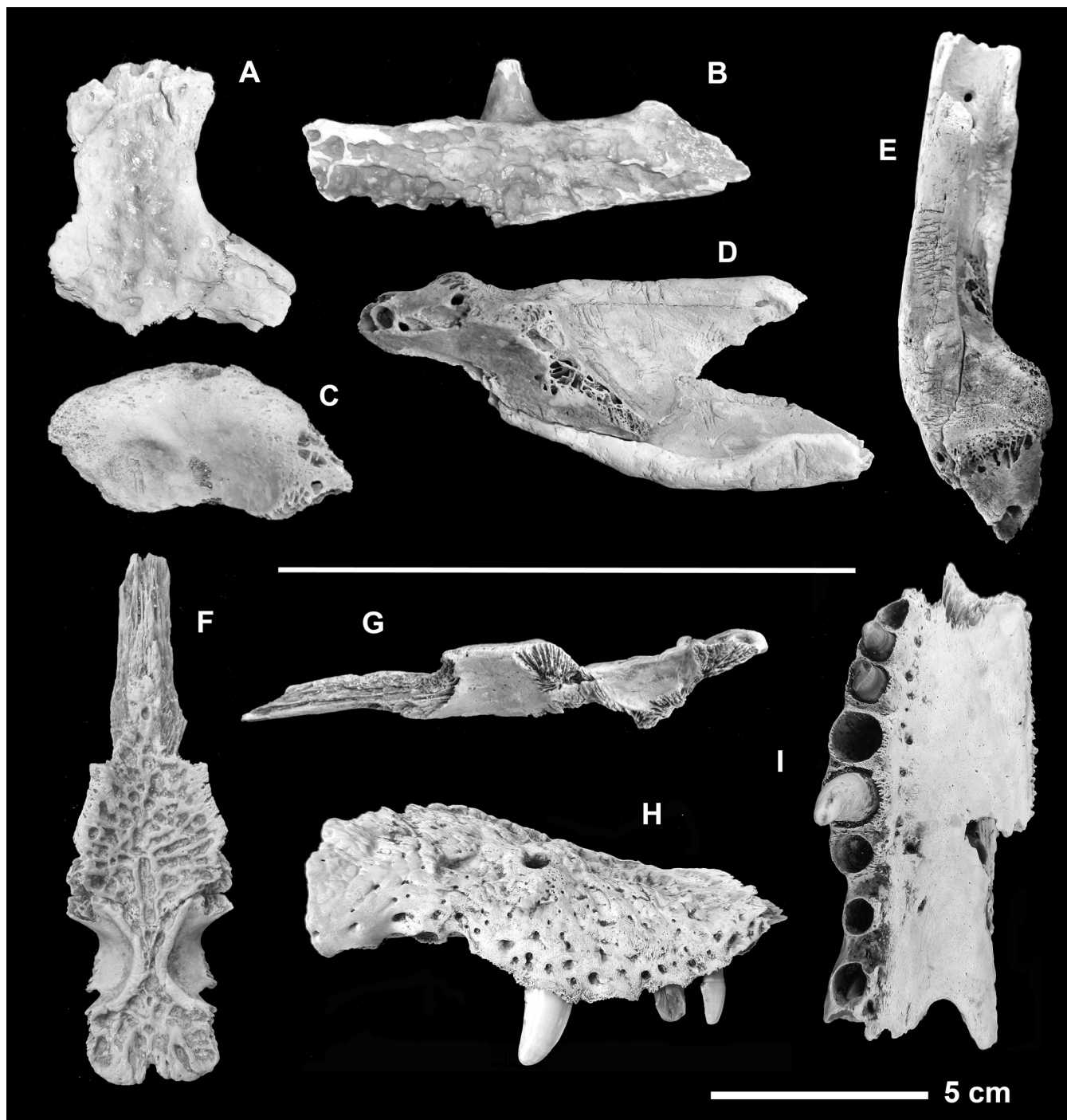
Figure 10. Fossils of Cuban crocodile (*Crocodylus rhombifer*) from Mermaid's Lair, Grand Bahama (A-E) and Gilpin Point, Abaco (F–I). A. frontal in dorsal view; B. left jugal in dorsal view; C. left partial ilium; D. medial view and E. dorsal view of articulated left angular and surangular. F. dorsal view and G. lateral view of partial cranial table, consisting of frontals and parietals; H. lateral view and I. ventral view of right maxilla.
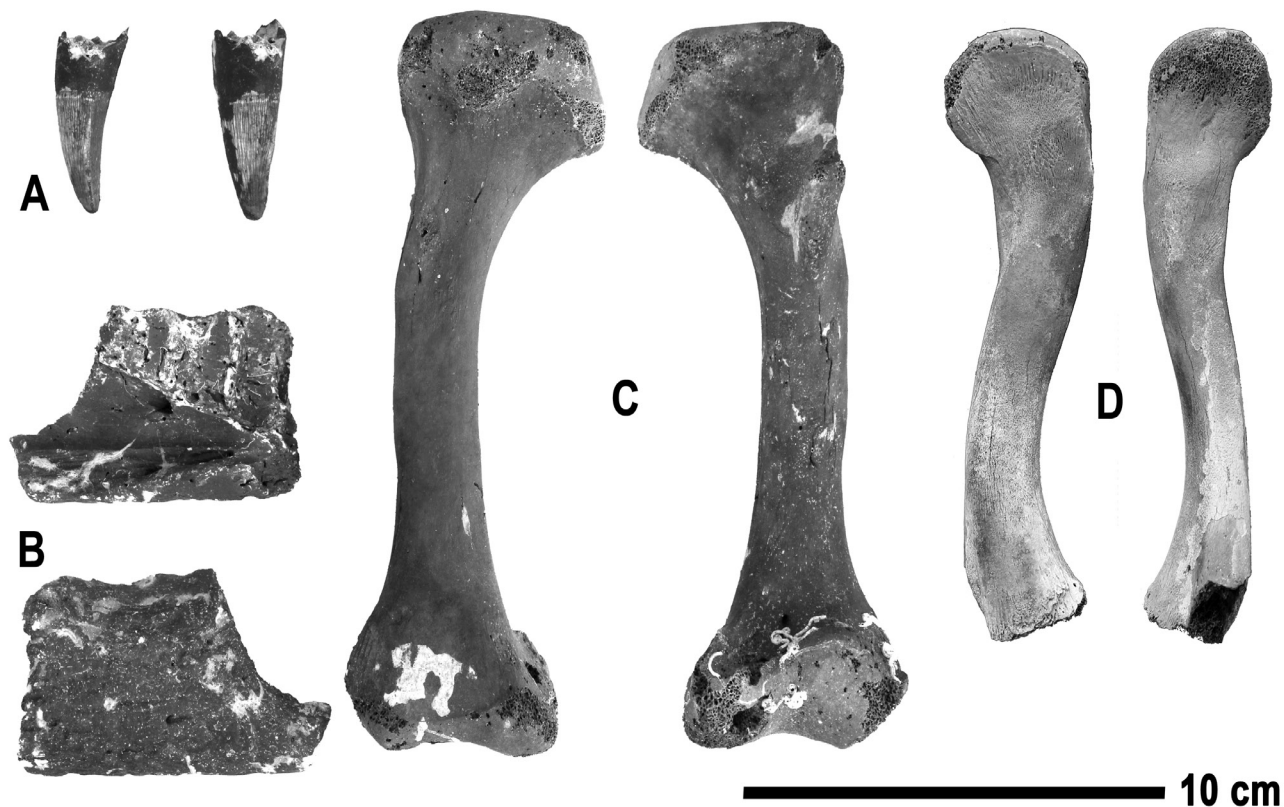
Figure 11. Crocodile fossils (*Crocodylus* sp.) from blue holes on Eleuthera. A. tooth (NMB.EL185.002), B. dentary fragment (NMB.EL185.001), and C. humerus (NMB.EL185.003) from White Lake. D. proximal two-thirds of femur (NMB.EL183.001) from Mermaid's Pool.

Acklins, Keegan (1988:31) made the following observations, "A crocodile population was living on [nearby] Crooked Island in the vicinity of Pitts Town. Furthermore, the crocodiles of Crooked Island either inhabited the entire Bight of Acklins, or the crocodile tooth from Acklins Island site AC-14 arrived there through trade. The latter is possible because the tooth's root has an indentation along its edge that may have been made by a drill. It is not, however, clear whether this "hole" is part of the natural break or the preserved crescent of a perforation."

Mayaguana.—In April 2008, Brian Kakuk collected a crocodylian coprolite and a partial tortoise carapace with crocodile bite marks from a depth of 13 m in The Fountain (22°23'N, 77°00'W; Fig. 4, site 19), an inland blue hole located adjacent to the airport runway in Mayaguana in the southeastern Bahamas. The coprolite is similar in size and shape to the coprolites from Lost Reel Cave and Nancy's Cave in Abaco.

Historical records of crocodiles from The Bahamas.—Crocodiles no longer occur in the Bahamas (Neill 1971), but there are several credible historical records. In his diary (*diario*), Christopher Columbus reported the capture of a 5.7 foot crocodile in a freshwater lagoon on Crooked Island in October 1492, and Martín Alonso Pinzón, captain of the *Pinta*, killed a second crocodile of similar size on Crooked Island the next day (Dunn & Kelley 1989). These crocodiles were skinned and their skins brought back to Spain. The crocodiles were described in the *diario* as serpents (*sierpe*), but their identification had long been considered a mystery because crocodiles were unknown from The Bahamas. The discovery of a crocodile femur from a Lucayan archaeological site near Pitts Town on Crooked Island (site CR-14), very near where Columbus landed, and a crocodile tooth from another Lucayan site at Delectable

Bay on nearby Acklins (site AC-14), confirms that crocodiles were indeed present in The Bahamas when Columbus "discovered" the islands (Keegan 1988, 1992). Catesby (1771) described "alligators" in the swamps of Andros. Campbell (1978) reviewed the Catesby account, as well as reports of "alligators" from the Bahamas in travelogues by Peter Henry Bruce in 1782 and Daniel McKinnen in 1804. McKinnen (1804) specifically mentioned "alligators" from Acklins in the southern Bahamas. Gardiner (1886) reported an 8-foot "alligator" from Great Inagua, also in the southern Bahamas.

Columbus called the crocodylian from Crooked Island a serpent (*sierpe* in Spanish) and the remainder of the records were reported as "alligators." However, it is most likely that these records represent crocodiles, not alligators. Except for fossils, no other museum specimens exist of crocodiles from The Bahamas to confirm which species might have inhabited the islands in the recent past. The early descriptions of these crocodiles are not detailed enough to provide an accurate identification. Considering the abundant fossils of *Crocodylus rhombifer* from Abaco, it is possible that these early historical records from The Bahamas pertain to Cuban crocodiles.

GRAND CAYMAN, CAYMAN ISLANDS

Crocodile fossils are known from seven Late Quaternary fossil sites on Grand Cayman in the Cayman Islands (Morgan & Patton 1979; Morgan et al. 1993; Morgan 1994), located in the northwestern Caribbean Sea south of Cuba (Fig. 12). Until the recent discovery of fossil crocodiles from blue holes on Abaco in the northern Bahamas, Grand Cayman had the richest known samples of Quaternary crocodiles from the West Indies. Although the majority of fossil sites in the Cayman Islands occur in caves (Morgan 1994), only one of the seven crocodile sites is from a cave, whereas the six remaining sites occur in mangrove swamps or in organic peat deposits in small limestone depressions or sinkholes. Local farmers excavate the peat from these small depressions creating wells that fill with fresh rainwater for their cows, hence the Caymanian term "cow well" for these features. During the removal of the peat from the limestone depressions or cow wells, crocodile bones are occasionally discovered. Submerged caves containing freshwater, known as inland blue holes in The Bahamas, appear to be absent in the Cayman Islands. Unlike The Bahamas, the Cayman Islands are not located on extensive, shallow carbonate banks, but instead each of the three islands (Grand Cayman, Little Cayman, Cayman Brac) is the tip of a large submarine pinnacle with Cenozoic carbonate rocks at the surface underlain by a core of granodiorite capped with basalt (Jones 1994). Detailed descriptions of the crocodile sites from Grand Cayman have been published elsewhere (Morgan et al. 1993; Morgan 1994), except for the Queen Elizabeth II Botanic Garden site that was discovered after these two papers were written. The following are brief summaries. Crocodile fossils from Grand Cayman are listed in Appendix 1. The most complete skulls of *Crocodylus rhombifer* from Grand Cayman have been illustrated previously (Morgan et al. 1993; Morgan 1994). The crocodile sites on Grand Cayman are discussed in geographic order from west to east (Fig. 12).

Crocodile Canal.—The Crocodile Canal site is located in a mangrove swamp about 3 km north of George Town on the western end of Grand Cayman (19°19'N, 81°23'W; Fig. 12, site 20). The fossils from this site were recovered after the excavation of a mosquito control canal through a mangrove swamp located barely a meter above sea level, and were preserved in a dark, organic peat deposit. The Crocodile Canal site was discovered in 1979 by Edward Materne and Robert Materne, who found fossils in piles of organic sediment that had been dumped alongside the canal by heavy machinery. Gary Morgan, Margaret Langworthy, and Jacqueline Belwood visited this site in 1980, and found additional fossils still encased in peat in the sides and bottom of the canal. They obtained many fossils by soaking the peat and washing the sediments through a window screen. The great majority of fossils from this site represent juveniles or subadults of the Cuban crocodile *Crocodylus rhombifer*, consisting of a minimum of six individuals. Associated vertebrates include the rock iguana *Cyclura*, the water snake *Tretanorhinus*,
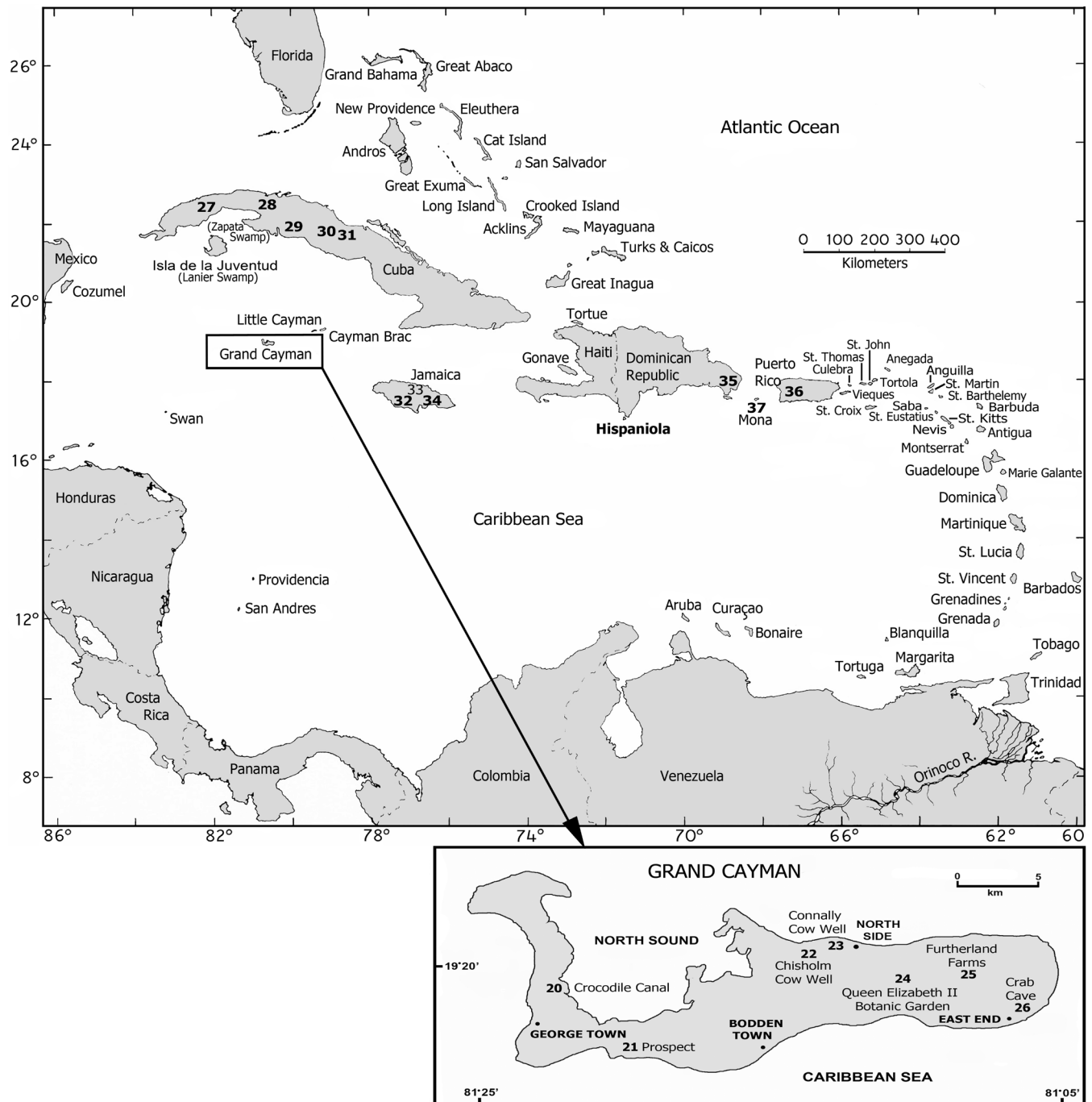
Figure 12. Map of the West Indies, with an enlarged map of Grand Cayman, showing the location of Quaternary sites containing crocodiles. Only published sites are shown. Many additional undescribed sites from Cuba are currently being studied by Osvaldo Jimenez. Site numbers are as follows (numbers assigned in the order the sites are discussed in the text): **Grand Cayman**: 20. Crocodile Canal; 21. Prospect; 22. Chisholm Cow Well; 23. Connally Cow Well; 24. Queen Elizabeth II Botanic Garden; 25. Furtherland Farms Cow Well; 26. Crab Cave. **Cuba**: 27. Cueva Lamas; 28. Las Breas de San Felipe; 29. Ciego Montero; 30. Casimbas de las Llanadas; 31. Caves of Cueiba. **Jamaica**: 32. Wallingford Roadside Cave; 33. Dairy Cave; 34. Belleview. **Hispaniola: Dominican Republic**: 35. Oleg's Bat Cave. **Puerto Rico**: 36. Cueva Salida. **Mona Island**: 37. Cueva de los Losetas.

the rail *Rallus*, and the large capromyid rodent *Capromys*. The fossils from the Crocodile Canal site are housed in the vertebrate paleontology collection at the Florida Museum of Natural History, University of Florida (UF; list in Appendix 1) and in the herpetology and vertebrate paleontology collections at the U. S. National Museum of Natural History, Smithsonian Institution (USNM).

Prospect.—A skull and partial skeleton of a crocodile were found in a mangrove swamp north of Prospect, a few kilometers inland from the south coast of Grand Cayman (19°16'N, 81°20'W; Fig. 12, site 21). Few details on this locality are available; however, the skeleton was apparently found on the surface. The fossil was collected in about 1980 by a Mrs. Pierce who gave it to Lear Grimmer. The age of the skeleton appears to be very recent, certainly no more than a few hundred years old, as the bones are white and unmineralized. The Prospect crocodile skeleton is housed in the UF vertebrate paleontology collection (Appendix 1).

Chisholm Cow Well.—The Chisholm Cow Well is located about 0.3 km inland from the Caribbean Sea, south of Grape Tree Point on the north coast of Grand Cayman (19°21'N, 81°13'W; Fig. 12, site 22). The site is only a few meters above sea level and consists of a small depression or sinkhole in the limestone about 5 m long, 3 m wide, and 1–2 m deep. The fossils are preserved in dark, organic sediments at the bottom of the sinkhole. Fossils were first discovered in the Chisholm Cow Well in the late 1970s, after the sediments had been removed from the sinkhole during the dry season. The original fossil discovery was made by Rolin Chisholm, the landowner after whom the site is named, and Ira Thompson. Chisholm, Richard Franz, and Gary Morgan conducted further excavations at this site in February 1986. Crocodiles are the most numerous fossils in the Chisholm Cow Well, including several complete skulls and lower jaws and numerous postcranial bones. There are also smaller samples of several terrestrial vertebrates, including the capromyid rodents *Capromys* and *Geocapromys*, *Cyclura*, and snakes. The UF vertebrate paleontology collection has a representative sample of fossils from Chisholm Cow Well (Appendix 1). Ira Thompson donated many fossils from this site to the Cayman Islands National Museum (CINM) and Rolin Chisholm also retained a sizeable collection.

Connally Cow Well.—A nearly complete skull of a crocodile was collected from the Connally Cow Well, located 0.5 km southwest of Hutland (19°21'N, 81°13'W; Fig. 12, site 23) in the same general vicinity as the Chisholm Cow Well. This site is just inland from the north coast of Grand Cayman and only a few meters above sea level. No other fossils are known from the Connally Cow Well. Based on the limited information provided by the collector, this is a typical cow well containing organic sediments. The skull was found by a private individual and obtained by the MRCU/NRS in George Town, Grand Cayman. The UF vertebrate paleontology collection has a cast of this skull (Appendix 1).

Queen Elizabeth II Botanic Park.—The national botanic gardens of the Cayman Islands, called the Queen Elizabeth II Botanic Park, are located in east-central Grand Cayman, 1.5 km east of the Frank Sound Road or cross-island road (19°20'N, 81°10'W; Fig. 12, site 24). When the gardens were being developed in the early 1990s, a sediment-filled depression in the limestone about 2 m diameter and 3 m deep was excavated to create a pond as a habitat for the local freshwater turtle or higatee. Dark organic sediments were removed from the sinkhole/cow well with a backhoe and dumped in a pile alongside the road through the gardens. Crocodile bones were discovered in these organic sediments in 1993 by Fred Burton of the National Trust for the Cayman Islands. He and Teddy Ebanks, a member of the work crew that excavated the sinkhole, collected a sample of the fossils. In April 1993, Gary Morgan and a FLMNH field crew, including Bill Keegan, Anne Stokes, Barbara Toomey, Reed Toomey, and Rob Roberston, met Burton, Ebanks and a volunteer crew at the site and collected many more fossils. The Queen Elizabeth II Botanic Park site produced a large sample of crocodile bones (see list of UF specimens in Appendix 1), including several partial skulls, numerous isolated cranial elements, 10

mandibles/dentaries (seven left, three right for an MNI of seven individuals), abundant isolated teeth, and a large number of isolated postcranial elements (vertebrae, limbs, osteoderms, etc.). Other species of vertebrates from this site include *Cyclura*, smaller lizards, snakes, several species of large wading birds, and *Capromys* and *Geocapromys*. A maxilla of *Geocapromys* and mandible of *Capromys* from the Botanic Park site have corroded teeth that appear to have been digested, possibly by a crocodile. We discuss these specimens in the section on Taphonomy and Paleoecology. Fossils from the Queen Elizabeth II Botanic Park site are housed in the UF collection and National Trust for the Cayman Islands (NTCI), which operates the Botanic Park.

Furtherland Farms Cow Well.—Furtherland Farms Cow Well is in the east-central portion of the island, 3 km north of Half Moon Bay and about 10 m above sea level (19°19'N, 81°08'W; Fig. 12, site 25). This site is a small water-filled sinkhole or cave about 5 m in diameter and 3-4 m deep. It was found on a banana plantation when sediments were removed from a sinkhole so it could function as a well, filling with rainwater that was then pumped out to irrigate the banana trees. Most of the fossils were found by digging and screening several large piles of sediment removed from the sinkhole, but some fossils were also removed from in-place sediments collected about 1 m underwater. The crocodile fossils were found in dark, organic peaty sediments, whereas fossils representing a substantial terrestrial fauna occurred in reddish cave sediments. Apparently, terrestrial sediments accumulated when the cave/sinkhole was dry, and then the site flooded and became filled with dark organic sediments. Fossils were discovered in the Furtherland Farms Cow Well site in the mid 1980s by a Cayman Islands High School student named Blair Smith. His science teacher Reginald Koster brought a sample of bones to the MRCU/NRS for identification. Gary Morgan, Richard Franz, and Jack Andresen collected a sample of fossils from Furtherland Farms in 1986, Shelley Franz and Richard Franz screened additional fossils from the site in 1987, and Morgan, Barbara Toomey, Reed Toomey, and Rob Robertson collected another sample in 1993. Besides crocodiles, the organic sediments contained many bones of a wading bird, the white ibis *Eudocimus*. The diverse terrestrial fauna from the cave sediments includes the shrew-like lipotyphlan (= insectivore) *Nesophontes*, *Capromys* and *Geocapromys*, *Cyclura*, the small iguanid lizard *Anolis*, and a rich avifauna including two extralimital species no longer found on Grand Cayman, the lizard cuckoo *Saurothera merlini* and the Cuban crow *Corvus nasicus*. Although no radiocarbon dates are available from Furtherland Farms, the presence of the introduced Old World rat *Rattus rattus* indicates that at least a portion of the deposit is post-Columbian in age (<500 yr BP). Fossils are housed in the UF vertebrate paleontology collection (list of specimens in Appendix 1).

Crab Cave.—Crab Cave is located in the village of East End near the southeastern point of Grand Cayman (19°18'N, 81°06'W; Fig. 12, site 26), about 200 m inland from the coast and a few meters above sea level. The cave has a small entrance at the base of a 7 m high limestone ridge and a single linear passage about 50 m in length. In 1976, a Florida State Museum (now Florida Museum of Natural History) field team consisting of Gary Morgan, Greg McDonald, and Nina Thanz recovered a tooth of a crocodile from a thin layer (about 0.5 m thick) of dry, calcareous sediment beneath a ledge about 4 m inside the cave entrance. This tooth was the first fossil record of a crocodile reported from Grand Cayman (Morgan & Patton 1979), and is also the only crocodile fossil from that island found in a terrestrial cave deposit. Morgan and Patton tentatively identified the Crab Cave tooth as *Crocodylus* because this is the only genus of crocodile in the West Indies; however, isolated crocodylian teeth are generally non-diagnostic at the species or genus level. This tooth was discovered and reported shortly before several large samples of crocodile fossils were found elsewhere on Grand Cayman, including Crocodile Canal and Chisholm Cow Well. The remainder of the vertebrate fauna from Crab Cave is entirely terrestrial, including *Cyclura*, several species of smaller lizards, snakes, birds, bats, *Capromys*, and *Geocapromys* (Morgan

1994). There are no radiocarbon dates from Crab Cave. A Late Quaternary age is indicated by the heavy mineralization of the fossils, as well as the presence of an extralimital species of bat (*Pteronotus parnellii*) normally found in large cave systems that no longer occur on Grand Cayman. The crocodile tooth from Crab Cave is housed in the UF vertebrate paleontology collection (Appendix 1).

Historical records of crocodiles in the Cayman Islands.—The historical occurrence of crocodiles in the Cayman Islands has been of great interest to herpetologists, paleontologists, and historians alike, as the name of the island group suggests the former presence of crocodiles despite their current absence there. The Spanish word *caimán* (from the Carib *cayman*) is one of several terms applied to tropical American crocodylians. The Spanish name for the island group is *Islas Caimán* or roughly translated as "Crocodile Islands."

The earliest historical documentation of crocodiles in the Cayman Islands was in 1586 on one of Sir Francis Drake's West Indian voyages. The following historical quotes are presented exactly as they appear in Drake's original journals (abstracted from Keeler 1981), including any misspellings or archaic English usage. We have added comments in [brackets]. A quote from Drake's journal (from Keeler 1981:68; called the "Map Text") is as follows: "The 20 of Aprill [1586] ve fell with two Ilands called Caimanes, vhere we refreshed our selues with many Allagartas [alligators] and greate Turtoises [sea turtles], being very vgly and fearefull beasts to behold, but were made good meate to eate…" This same quote with slightly different word usage has also been attributed to Walter Bigges (1589). Another account of Drake's same 1586 visit to the Cayman Islands stated the following (in Keeler 1981:113; called "A Newsletter") "The 20 of Apryll [1586] we Landed our men at Cuny Grand [Grand Cayman] and tooke plenty of turtles, Alygathaes [alligators], Coneys, etc." [coneys or hutias are large rodents in the family Capromyidae, now extinct in the Cayman Islands; see Morgan 1994]. A third account of Drake's same 1586 visit to the Cayman Islands stated the following (in Keeler 1981:203–204; called the "*Primrose* Journal") "…

the xxij [actually the 20th] of Aprill [1586] we fell with an Ile that had no people in hit. There wee fownde strawnge kindes of beastes & killed more than xx [20] *Alligatos* [alligators]. Those bee suche serpentes as have bin in London to be seene. There weare *Crocadiles* which did Incounter & fighte with vs, they live bothe in the sea & on lande. Wee tooke divers & made verie good meate of them; some of the same weare ten foote in lenghte." "Allagartas," "Alygathaes," and "Alligatos" are archaic English spellings of alligator but almost certainly refer to a crocodile. Although it is not obvious from these quotes to which of the three Cayman Islands Drake was referring, it is clear from both the "Map Text" and the "Newsletter" (two separate sections of Drake's journals; Keeler 1981), that the quotes refer to Grand Cayman. This is consistent with the abundance of fossil crocodiles on Grand Cayman and their absence from fossil deposits on Cayman Brac and Little Cayman.

The next reference to crocodiles in the Cayman Islands was in 1642 or 1643 by a Captain William Jackson (from Grant 1940:3) who stated, "…ye island of Chimanos [Grand Cayman] … this place is low land and all rockye, and there bee other two islands of ye same name and Quallitie [Cayman Brac and Little Cayman], being by ye Spanyards called Chimanos, from ye multitude of Alligators here found which are Serpents, if not reseembling ye Crocodiles of Egypt." In a trip to the West Indies and Mexico in 1675–1676, William Dampier (1705:75) commented that "At the Isle Gran Caymanes there are crocodiles but no alligators. At Pines by Cuba there are an abundance of crocodiles but I cannot say there are no alligators tho I never saw any there. Both kinds are called Caymanes by the Spaniards, therefore probably they may reckon them for the same." In his history of Jamaica, Edward Long (1774) noted that crocodiles were living on Grand Cayman.

These historical records document that crocodiles inhabited Grand Cayman until at least the late 18th century, after which they apparently were eliminated by European colonists. A radiocarbon date of 375 yr BP associated with a crocodile tooth and osteoderm from the Crocodile Canal site and jaws of the introduced *Rattus* associated

with crocodile fossils from the Furtherland Farms Cow Well, both corroborate the historical records documenting the survival of crocodiles on Grand Cayman well into the historic period (i.e., post 1492). Moreover, the widespread occurrence of fossils of *Crocodylus rhombifer* on Grand Cayman discovered since 1979 confirms the historical accounts that documented the abundance of crocodiles on the island when European explorers first arrived in the 16th century. The absence of archaeological sites on Grand Cayman indicates that this island was uninhabited when Columbus discovered the Caymans in 1503 (Stokes & Keegan 1996).

It is highly unlikely that the historical accounts from the Cayman Islands actually refer to alligators, which occur in Florida but nowhere in the West Indies, and instead almost certainly pertain to crocodiles. Although these historical accounts do not provide enough descriptive detail to accurately identify which of the two species of West Indian crocodiles (*Crocodylus acutus* or *C. rhombifer*) occurred on Grand Cayman, the abundance of fossil specimens of *C. rhombifer* reported from that island, together with the absence of fossil evidence of *C. acutus*, strongly suggests they were Cuban crocodiles (Morgan et al. 1993; Morgan 1994). It is of interest that one of these accounts mentioned the crocodiles lived both in the sea and on land. As discussed in more detail below, the Cuban crocodile (*C. rhombifer*) is one of the most terrestrial of all living crocodylians.

The earliest herpetological collection from the Cayman Islands was made by W. B. Richardson on Grand Cayman in the 1880s and reported by Samuel Garman (1887). The only reference to crocodiles by Garman (1887:277) was the statement "Mr. Richardson states that the natives reported a crocodile in the swamps. This might be expected from the presence of two species on Cuba, one of which appears also on Jamaica and San Domingo [Hispaniola]." In his review of the herpetology of the Cayman Islands, Grant (1940) mentioned a small individual of the American crocodile *Crocodylus acutus* captured in Charles Bay along the southern coast of Little Cayman in 1939. In 2007 and 2009, two individuals of *C. acutus* were

found on Grand Cayman. An eight foot American crocodile was captured in 2007 near Old Man Bay on the north coast of Grand Cayman and placed in captivity at the Cayman Turtle Farm. Another American crocodile was observed swimming along Seven Mile Beach on the western shore of Grand Cayman. With the exception of a few stray individuals of *C. acutus* that periodically appear in the Cayman Islands, crocodiles have been absent from their namesake island group for the past several hundred years.

GREATER ANTILLES

Cuba.—Fossils of the Cuban crocodile *Crocodylus rhombifer* have been reported from several Quaternary localities in Cuba (Fig. 12). These sites are listed in geographic order from west to east within Cuba. Only published sites are included in this discussion. Additional Quaternary records of crocodiles from Cuba are currently under study by Osvaldo Jiménez.

Varona (1966) described an extinct Quaternary species of crocodile, *Crocodylus antillensis*, from Cueva Lamas west of Havana, Cuba (Fig. 12, site 27). The fragmentary type specimen of *C. antillensis* from Cueva Lamas consists of a basioccipital and partial basisphenoid, premaxilla, maxilla, and jugal. Whether *C. antillensis* can be distinguished from *C. rhombifer* on the basis of the type material is unclear at present. Bones identified as *Crocodylus* sp., including osteoderms, were recovered from an asphalt seep at Las Breas de San Felipe near Martí in Matanzas Province on the north coast (Fig. 12, site 28; Iturralde-Vinent et al. 2000).

The first Quaternary crocodile described from the West Indies was collected in the 1860s by the Cuban naturalist Felipe Poey from the Ciego Montero spring deposit, about 50 km northwest of Cienfuegos in Cienfuegos Province, south-central Cuba (Fig. 12, site 29). Leidy (1868) named the extinct crocodile species *Crocodilus* (= *Crocodylus*) *pristinus* based on the centrum of a vertebra from Ciego Montero. Although a partial vertebra is almost certainly nondiagnostic, Leidy did suggest that *C. pristinus* was larger than the living *Crocodylus rhombifer* from Cuba. Varona

(1984) formally synonymized *C. pristinus* with *C. rhombifer*. It is probably more accurate to consider *C. pristinus* a nomen dubium, as it was based on an insufficient type specimen. In 1911, Barnum Brown from the AMNH and Cuban naturalist Carlos de la Torre revisited the hot springs at Ciego Montero. According to Brown (1913) there are actually three thermal springs at Ciego Montero, one of which named Chapapote has produced a majority of the vertebrate fossils, including those described by Leidy (1868). In the center of the Chapapote spring at a depth of about 2 m, Brown's field party removed a large sample of vertebrate fossils from a black organic mud. Brown (1913) specifically mentioned that the first fossil he identified from the spring was a crocodile vertebra. Brown (1913:225–226) noted that "Bones stuck out of the black mud in great profusion, jaws and bones of sloths, skulls of crocodiles and alligators, and parts of turtle shells." Brown also mentioned (1913:227–228) that "Many bones…showed the tooth marks of alligators…" Brown's references to "alligators" from Ciego Montero are almost certainly inaccurate, as only crocodile fossils are known from these deposits. Matthew (1919) and Mook (1921) briefly mentioned the crocodile sample from Ciego Montero collected by Brown and de la Torre. According to Matthew (1919), a study of the fossil crocodile skulls from Ciego Montero was undertaken by Charles Mook, but apparently never published. It was not until more than 70 years later that a skull of a crocodile from Ciego Montero was finally described and illustrated (Varona 1984). The Ciego Montero crocodile sample in the AMNH still has not been adequately studied or compared with modern skulls of *C. rhombifer*. Brief comments on several skulls and mandibles of crocodiles from Ciego Montero in the AMNH collection are included in the section below on "Size differences and morphological variation." Measurements of these specimens are presented in Table 7, together with several photos of the most complete fossil skull of *C. rhombifer* from Ciego Montero (Fig. 13).

Unidentified Quaternary crocodylian fossils have been reported from a fissure deposit at Casimbas de las Llanadas in the Sierra de Jatibonico and in the caves of Cueiba in Sancti Spiritus Province, central Cuba (de la Torre 1910; Brown 1913; Varona 1984; Fig. 12, sites 30 & 31).

Jamaica.—Harold E. Anthony and Charles Falkenbach of the American Museum of Natural History excavated a large number of caves in Jamaica in 1919–1920 (Anthony 1920), including an indurated breccia deposit in Wallingford Roadside Cave located in St. Elizabeth Parish in southwestern Jamaica (Fig. 12, site 32). This cave is located near Balaclava, approximately 25 km inland from the southern coast and at an elevation of about 230 m, near the One Eye River, a tributary of the Black River (MacPhee 1984). Several authors have mentioned the presence of crocodylian fossils in Wallingford Roadside Cave (Anthony 1920; Koopman & Williams 1951; MacPhee 1984; Morgan 1993). Koopman and Williams (1951) stated that Anthony collected a crocodile vertebra from breccia deposits in this cave, but the specimen has never been described, measured, or illustrated. Besides being clearly recognizable as crocodylian, vertebrae are otherwise nondiagnostic. A series of uranium-series (U/Th) dates from Wallingford Roadside Cave indicate a maximum age of 130–180 ka for the fossils, making the crocodile vertebra from this site the oldest dated Quaternary crocodylian specimen from the West Indies (MacPhee et al. 1989; McFarlane & Lundberg 2004).

Morgan (1993) reported three crocodylian teeth from Dairy Cave, situated about midway along the northern coast of Jamaica in St Ann Parish (Fig. 12, site 33), about 1 km inland and at an elevation of 15 m. The crocodile teeth were recovered from the undated "lizard layers" in Dairy Cave (Koopman & Williams 1951), but are probably Late Quaternary in age. Wing (1977) identified *Crocodylus acutus* from the Bellevue site, an Amerindian archaeological site on the south coast of Jamaica (Fig. 12, site 34), dating to about 1,000 years ago.

Dominican Republic.—Crocodylian fossils were discovered recently in an underwater cave site of Late Quaternary age in the eastern Dominican
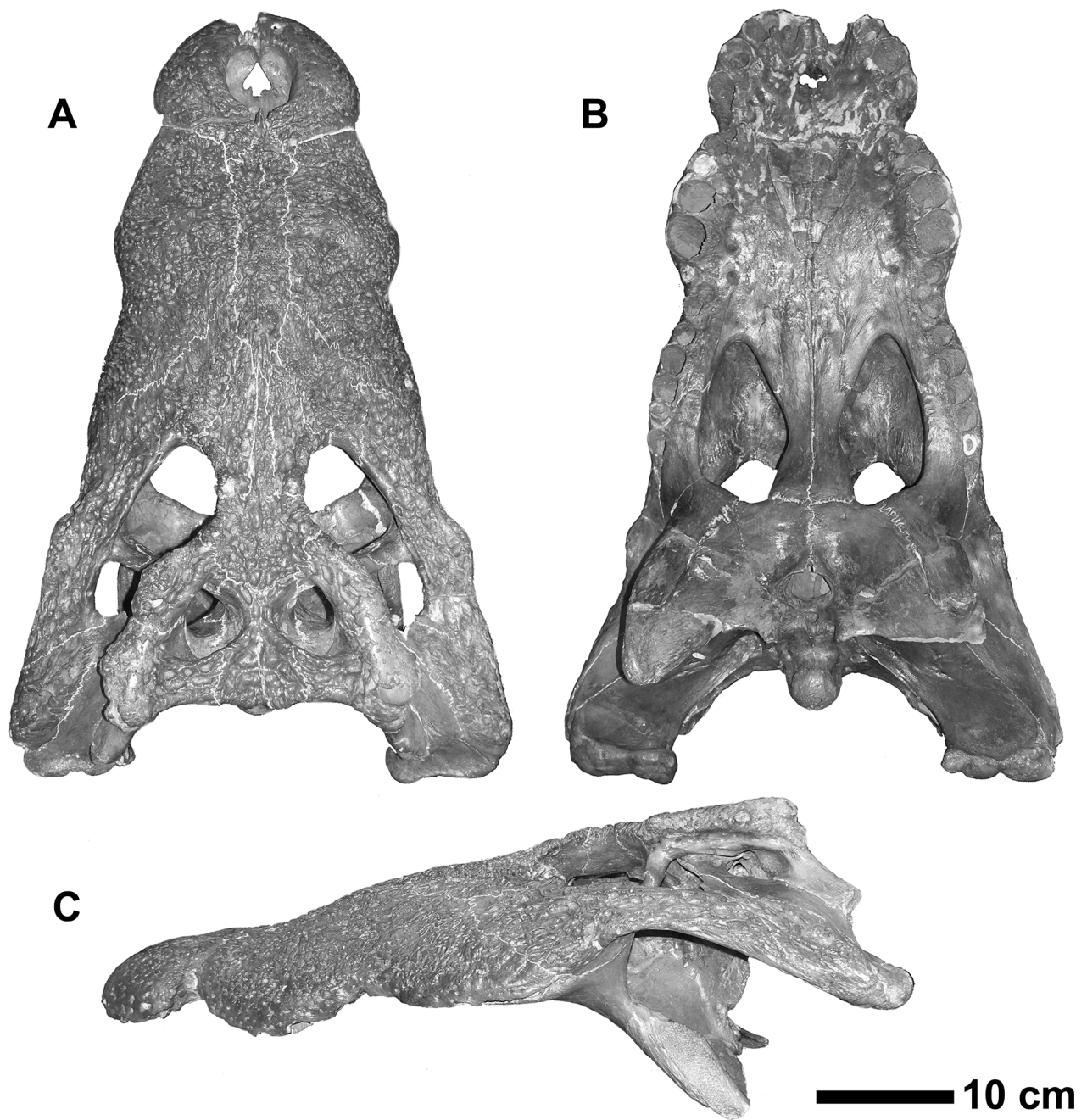
Figure 13. Dorsal (A), ventral (B), and lateral (C) views of a large skull of *Crocodylus rhombifer* (AMNH 6179) from the late Quaternary spring deposit at Ciego Montero, Cuba.

Republic on the island of Hispaniola (Fig. 12, site 35). These fossils are currently under study and will be described elsewhere (Rimoli, Rosenberger, Morgan, & Cooke in prep.).

Puerto Rico.—Vélez-Juarbe and Miller (2007) described and illustrated a Quaternary crocodylian tooth from Cueva Salida in the county of Utuado in northern Puerto Rico (Fig. 12, site 36). Cueva Salida (or Exit Cave) is located near the Rio Tanamá at an elevation of about 320 m, about 15 km inland from the northern coast of the island. The isolated tooth has a conical crown, striated surface, and a pair of carinae. It is clearly crocodylian based on the description and photograph (Vélez-Juarbe & Miller 2007) and is quite large, nearly 40 mm in length. No radiocarbon dates are associated with the crocodile tooth from Cueva Salida, although its association with a typical fauna of extinct Puerto Rican mammals, including the ground sloth *Acratocnus*, a large species of the lipotyphlan (= insectivore) *Nesophontes*, and the caviomorph rodents *Elasmodontomys* and *Heteropsomys*, indicates a late Quaternary age (Vélez-Juarbe & Miller 2007).

Mona Island.—Excavations in caves on Mona Island or Isla de Mona, located in the Mona Passage about halfway between Puerto Rico and the Dominican Republic, have yielded a small sample of vertebrate fossils (Williams 1952; Frank & Benson 1998). In 1995, Edward Frank and Richard Benson collected a small crocodile vertebra from Cueva de los Losetas, located on the east side of Mona Island (Fig. 12, site 37). The cave is located on top of a cliff 45 m above the sea. The closest current sea level access is many kilometers distant (Frank & Benson 1998). The fossil was described as a typical procoelous vertebra less than 1 cm in length, but the authors did not attempt to identify it beyond crocodylian nor was the specimen illustrated (Frank & Benson 1998). The very small size of this vertebra, even for a hatchling crocodile, suggests the possibility that the specimen may represent the rock iguana *Cyclura*, which is a common inhabitant of Mona Island. We attempted to borrow this vertebra from the Bell Museum of Natural History at the University of Minnesota, where the Mona

Island fossils collected by Frank and Benson are curated, to confirm its identification. However, the curatorial staff at the Bell Museum was not able to locate the supposed crocodile vertebra. There are no radiocarbon dates associated with the crocodile vertebra from Cueva de los Losetas, but the lack of extinct species of vertebrates from the deposit suggests a Late Quaternary age.

DESCRIPTIONS AND COMPARISONS OF QUATERNARY CROCODILES FROM ABACO AND GRAND CAYMAN

SKULLS AND MANDIBLES

The following descriptions and comparisons are based primarily on a sample of 14 complete or nearly complete skulls of *Crocodylus rhombifer* from Abaco in the northern Bahamas, 11 from Sawmill Sink and one each from Dan's Cave, Ralph's Cave and Nancy's Cave. Figures 14 and 15 illustrate three of the most complete skulls of *C. rhombifer* from Sawmill Sink, including one of the smallest skulls in the sample (Figs. 14A, 15A), an average-sized skull (Figs. 14B, 15B), and one of the largest skulls (Figs. 14C, 15C). Mandibles associated with these same three skulls are illustrated in Figures 15 and 16. There are also partial to nearly complete Cuban crocodile skulls from five sites on Grand Cayman in the Cayman Islands, one skull each from Chisholm Cow Well, Connally Cow Well, Crocodile Canal, Prospect, and the Queen Elizabeth II Botanic Park. Most of the Grand Cayman skulls of *C. rhombifer* have been described and illustrated previously (Morgan et al. 1993; Morgan 1994), and are less complete than the skulls from Sawmill Sink. Measurements of the skulls and mandibles are presented in Tables 1–3.

Comparisons between the fossil samples of *Crocodylus rhombifer* from Abaco and Grand Cayman reveal no significant differences in overall morphology, although the Abaco sample does average somewhat larger. We discuss the size ranges, size differences, and variation in the two populations. Following the morphological descriptions, the fossils from Abaco and Grand Cayman are compared to modern skulls of the

Figure 14. Three skulls of Cuban crocodiles (*Crocodylus rhombifer*) from Sawmill Sink in dorsal, ventral, lateral, and posterior views. These skulls are from A. small (NMB.AB50.025; C20), B. medium **(**NMB. AB50.022; C17**),** and C. large **(**NMB.AB50.0030; C30**)** crocodiles. See Table 1 for measurements of these three skulls.

Figure 15. Lateral views of three skulls and articulated mandibles of the Cuban crocodile (*Crocodylus rhombifer*) from Sawmill Sink. These are the same three skulls in the same order as in Fig. 14.
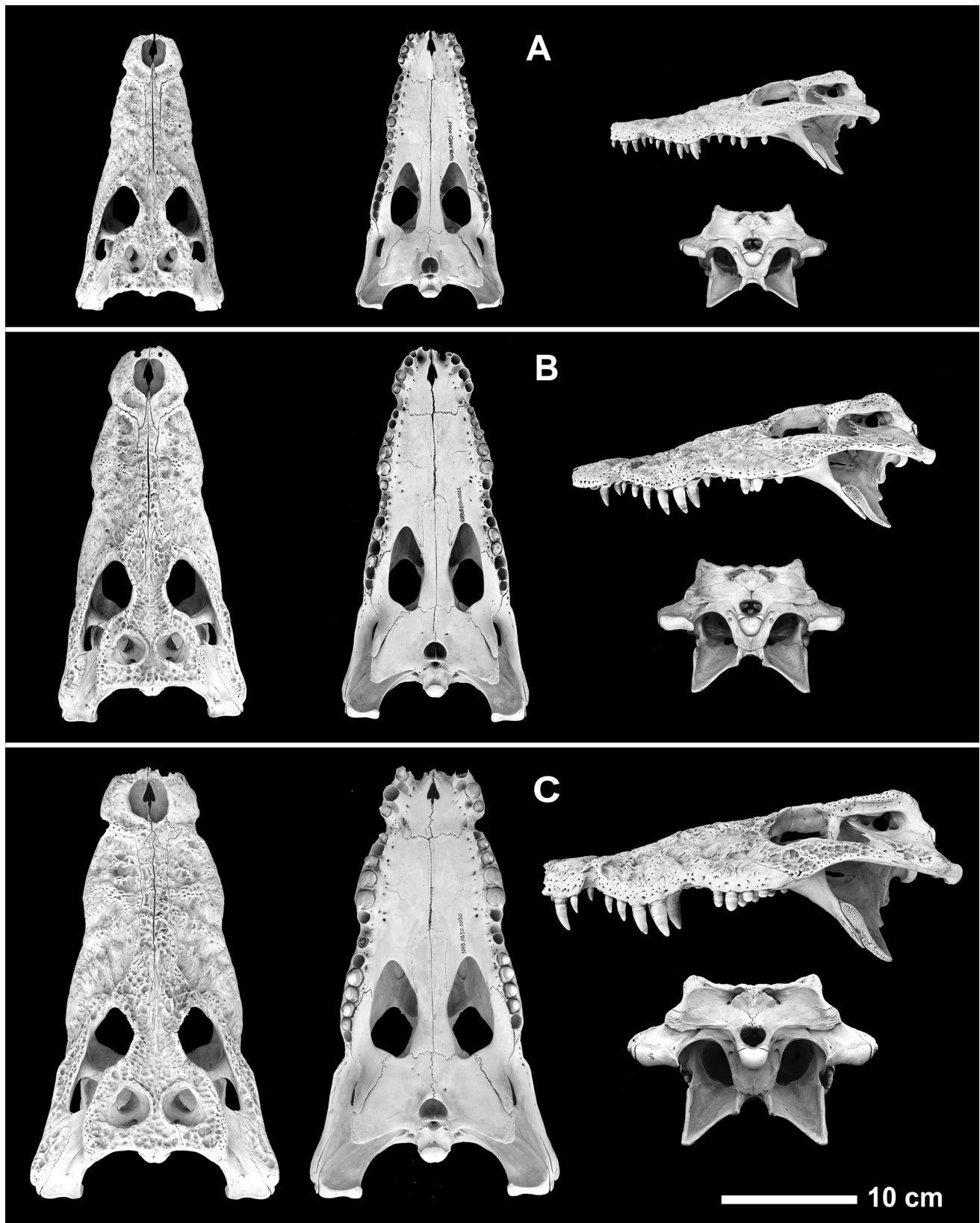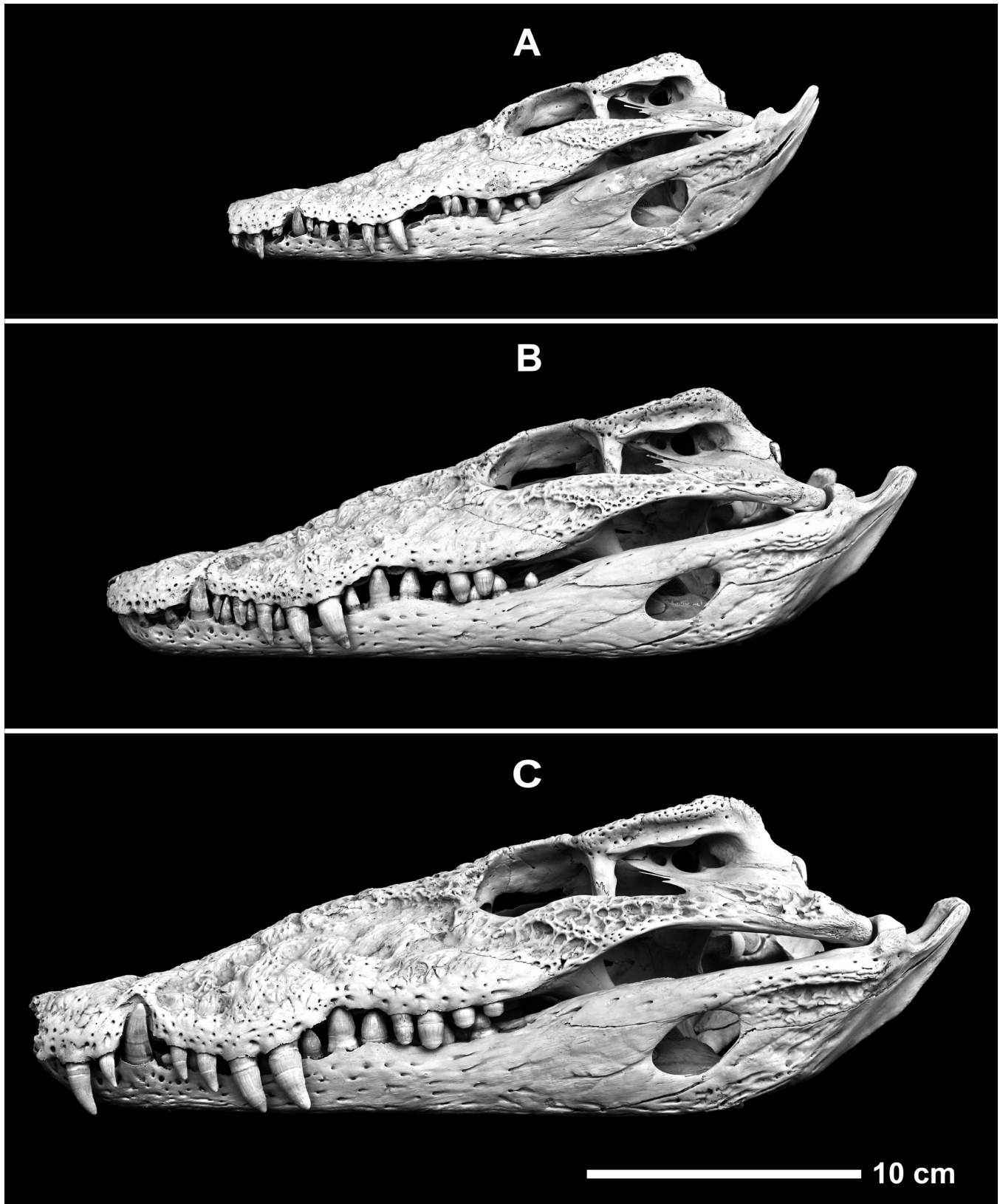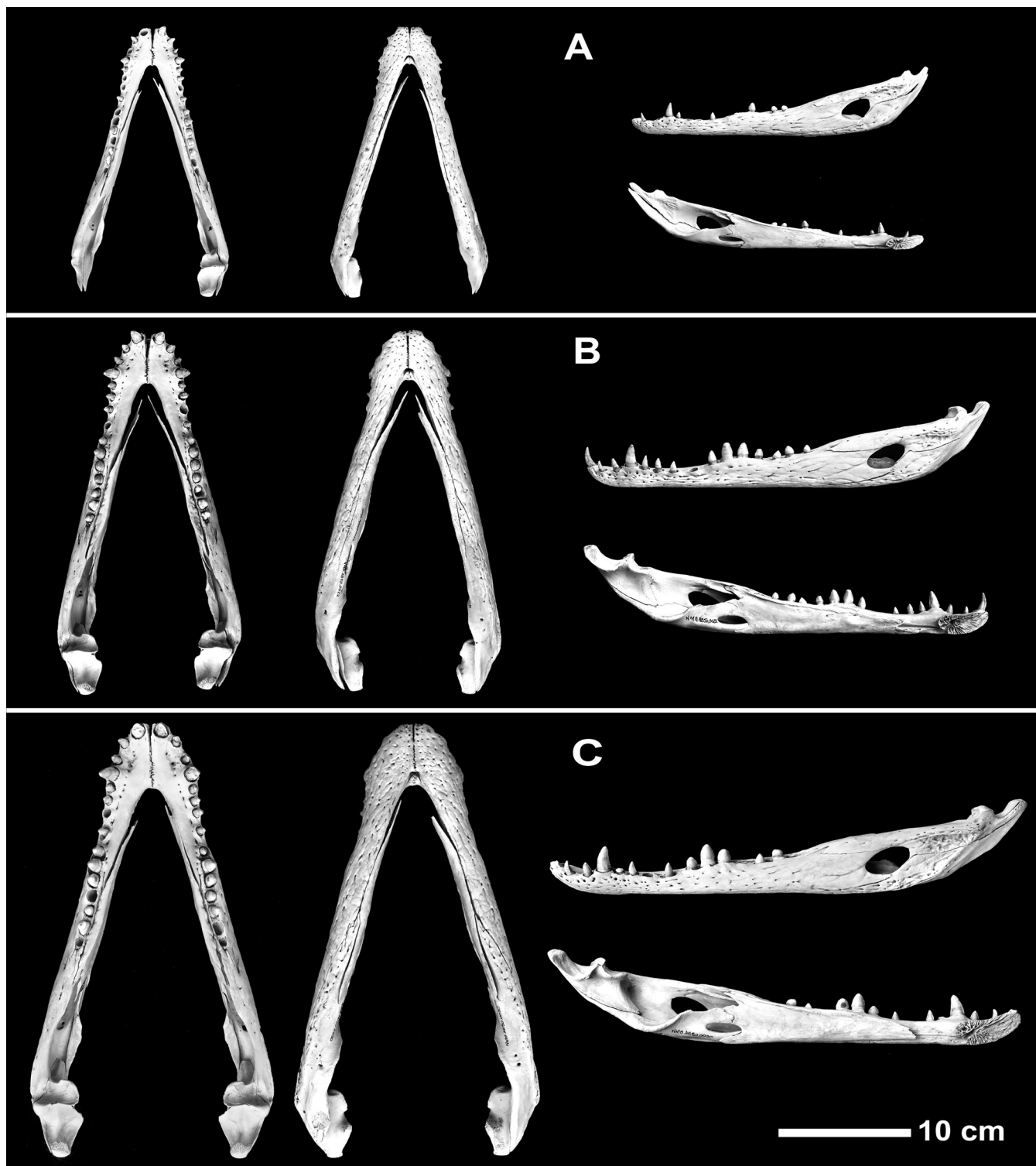
Figure 16. Three mandibles of Cuban crocodiles (*Crocodylus rhombifer*) from Sawmill Sink in dorsal, ventral, lateral, and medial views. These are the same three mandibles in the same order as in Fig. 15.

Table 1. Cranial measurements of Late Quaternary Cuban crocodiles (*Crocodylus rhombifer*) from Abaco, Bahamas. Measurements are described in the Methods section and illustrated in Fig. 3. All measurements in mm; missing measurements indicated by "—".

Site and catalog number	total length of skull	length premaxilla-parietal[1]	length of snout	length of maxillary toothrow	breadth of pre-maxilla
Sawmill Sink					
UF 225401 (C6)	253	238	139	126	56
NMB.AB50.020 (C15)	312	283	174	153	74
NMB.AB50.021 (C16)	297	270	165	148	68
NMB.AB50.022 (C17)	267	245	148	133	61
NMB.AB50.023 (C18)	292	265	164	150	67
NMB.AB50.024 (C19)	243	224	137	124	55
NMB.AB50.025 (C20)	200	184	114	103	46
NMB.AB50.027 (C24)	305	278	171	148	71
NMB.AB50.695 (C29)	233	212	132	117	49
NMB.AB50.030 (C30)	311	277	173	153	73
NMB.AB50.171 (C52)	281	256	165	139	64
Dan's Cave					
UF 137893	—	—	—	—	—
Ralph's Cave					
NMB.AB51.002	271	246	153	136	62
Nancy's Cave					
NMB.AB57.003	361	321	206	—	89
Sample statistics					
N (sample size)	13	13	13	12	13
X (mean)[2]	286	260	161	139	66
Observed range	200–361	184–321	114–206	103–153	46–89

[1]The length from the premaxilla to the parietal along the mid line is similar to the measurement called "head length" in living crocodylians.
[2]Mean excludes the smallest skull in the sample (NMB.AB50.025; C20), which is from a very young, juvenile individual.

three species of crocodiles found in the Caribbean area: *Crocodylus acutus*, *Crocodylus moreletii*, and *Crocodylus rhombifer* (Fig. 17).

The Abaco and Grand Cayman skulls possess diagnostic cranial characters of the Cuban crocodile *Crocodylus rhombifer*, including: short, broad, and deep rostrum; concave interorbital region and cranial roof; and strong ridges on the internal margins of the orbits and lateral margins of the cranial table, ending in a large, rounded protuberance on the posterolateral corner of the squamosal. The strongly concave cranial table

and prominent ridges on the lateral margins of the cranial table ending in large, rounded swellings or protuberances on the posterolateral corners of the squamosals are perhaps the most characteristic cranial features of the Abaco and Grand Cayman crocodile skulls. The ridges on the internal margins of the orbits begin as a conspicuous swelling or boss on the posteromedial portion of the lacrimals at the anterior edge of the orbits. This swelling is rounded in some specimens, more sharply triangular in others. The ridge continues posteriorly from the lacrimal boss as a thin, sharp, high ridge

Table 1. Extended.

breadth of snout at 5th tooth	inter-orbital breadth	breadth of cranial roof (ant.)	breadth of cranial roof (post.)	maximum breadth of skull	breadth at quadrates
78	23	58	74	138	128
106	33	76	100	181	169
94	28	69	93	164	149
86	25	63	82	142	134
94	27	68	92	158	149
79	24	57	76	128	116
62	18	47	58	109	101
104	32	67	100	179	166
68	21	53	71	125	117
105	31	74	102	180	167
87	29	60	89	153	138
—	36	81	115	—	—
88	24	61	82	154	145
136	34	83	119	—	—
13	14	14	14	12	12
94	28	67	92	155	143
62–136	18–36	47–83	58–119	109–181	101–169

on the internal margin of the orbits, extending entirely across the posterolateral margins of the prefrontals and lateral margins of the frontals. A continuation of this ridge begins at the suture between the frontals and postorbitals and extends posteriorly along the lateral margins of the cranial table on the postorbital and squamosal bones. The prominent ridge on the lateral margin of the cranial table is high, broad and rounded, and terminates in a very well-developed, rounded protuberance or swelling on the squamosals at the posterolateral corner of the cranial table. This ridge is especially thick on the lateral margins of the squamosals. The protuberance on the squamosals is most evident in lateral and posterior views of the skull (Figs. 14–15).

A low ridge extends anteromedially along the internal margin of the lacrimals, from the lacrimal boss at the anterior edge of the orbits anteriorly to the point where the lacrimals meet the nasals. In dorsal view, the ridges that extend anteriorly from the lacrimals to the nasals and posteriorly from the lacrimals across the prefrontals to the frontals form a distinct diamond or rhomboid shape. The narrow points of the diamond terminate anteriorly at the lacrimal-nasal suture and posteriorly at the prefrontal-frontal suture or the interorbital constriction, and the diamond is widest at the

Table 2. Cranial measurements of Late Quaternary Cuban crocodiles (*Crocodylus rhombifer*) from Grand Cayman, Cayman Islands. Format as in Table 1.

Site and catalog number	total length of skull	length premaxilla-parietal[1]	length of snout	length of maxillary toothrow	breadth of pre-maxilla
Crocodile Canal					
USNM 216197	251	233[3]	139	129	—
UF 61103	—	—	—	112	—
Prospect					
UF 65800	305	276	175	148	—
Chisholm Cow Well					
UF 80000	255	232	147	133	53
UF 128085	—	—	—	125	—
Connally Cow Well					
UF 128064	247	223	144	128	53
Queen Elizabeth II Botanic Park					
UF 143687	385[4]	—	—	174	—
UF 244484	—	—	—	133	—
UF 244499	—	—	—	25[5]	—
Furtherland Farms Cow Well					
UF 128134	—	—	—	108	—
Sample statistics					
N (sample size)	5	4	4	10	2
X (mean)	289	241	151	132	53
Observed range	247–385	223–276	139–175	25–174	53

[1]The length from the premaxilla to the parietal along the mid line is similar to the measurement called "head length" in living crocodylians.

[2]The maximum breadth of the skull is taken at the posteriormost extension of the quadratojugals (See Fig. 3). The quadratojugal is missing from one or both sides in every skull from Grand Cayman; thus we were not able to take this measurement on any specimen in the sample.

[3]This measurement is actually the length from the anterior edge of the premaxilla to the posteriormost extension of the squamosal. The measurement to the posterior end of the parietals along the midline would be slightly less.

lacrimal boss at the anterior edge of the orbits. The nasals are convex or swollen along the midline from the lacrimal suture anteriorly to a point dorsal to the largest (fifth) tooth in the maxilla. In lateral view, the nasals sit distinctly higher than the more lateral maxillae.

Medial to the ridges on the internal margins of the orbits, the interorbital region is highly concave, comprising the posterior half of the prefrontals and the frontals. The cranial table is also concave medially, composed of the posteriormost portion of the frontals and the parietals, which stands in stark contrast to the upraised, convex lateral margins of the cranial table composed of the postorbitals and squamosals. The anterior portion of the parietals is very narrow and forms a thin, raised, ridge on the internal margins of the rounded, dorsal temporal openings.

The snout or rostrum in the Abaco and Grand Cayman crocodiles is comparatively short and broad. In lateral view, the snout anterior to the orbits is rather deep, from the orbits anteriorly to the level of the fifth maxillary tooth. The convex or swollen nasals contribute to the appearance of

Table 2. Extended.

breadth of snout at 5th tooth	inter-orbital breadth	breadth of cranial roof (ant.)	breadth of cranial roof (post.)	maximum breadth of skull^2	breadth at quadrates
72	22	57	75	—	117
—	—	—	—	—	—
100	31	76	104	—	163
71	22	59	79	—	119
—	—	—	—	—	—
73	23	56	75	—	—
—	—	—	—	—	—
—	—	—	—	—	—
—	—	—	—	—	—
—	—	—	—	—	—
4	4	4	4	—	3
79	25	62	83	—	133
71–100	22–31	56–76	75–104	—	117–163

[4]This measurement is not actually the maximum length of the skull, but is the length from the anterior end of the premaxilla to the posterior end of the quadratojugal, which is slightly less than the measurement to the posterior end of the quadrate, which is absent in this specimen.

[5]This specimen is from a very small hatchling crocodile. The mean for the length of the maxillary toothrow excludes this specimen.

a deeper snout. The combination of the deep snout and elevated ridges on the dorsal margins of the orbit gives the fossil skulls a large and prominent orbit.

In ventral view, several diagnostic characters are evident in the skulls of *Crocodylus rhombifer* from Abaco and Grand Cayman. The premaxillary-maxillary suture on the palate is essentially horizontal or transverse at the level of the first maxillary tooth. At its lateral extremity, the premaxillary-maxillary suture is anterior to the first maxillary tooth. About one-third the distance across the palate between the lateral edge of the maxilla and the midline (closer to the toothrow than the midline), this suture takes a slight posterior excursion to the level of the middle of the first maxillary tooth in some skulls or to the posterior edge of the alveolus of the first maxillary tooth in other specimens. From that point, the remainder of the premaxillary-maxillary suture is horizontal until it reaches the midline of the palate. Another characteristic feature is the number of teeth in the maxilla. The majority of skulls from Abaco and Grand Cayman have 13 teeth in the maxilla; four skulls and five isolated maxillae from Grand Cayman have 13 teeth, whereas 10 of 12 skulls from Abaco have 13 teeth, one skull has 12

Table 3. Mandibular measurements of Late Quaternary fossils of Cuban crocodiles (*Crocodylus rhombifer*) from Abaco, Bahamas and Grand Cayman, Cayman Islands. Measurements are described in the Methods section and illustrated in Fig. 3. All measurements in mm; missing measurements indicated by "—

Island, site, and catalog number	total length of mandible	length of dentary	length of mandibular toothrow	number of mandibular teeth
Abaco				
Sawmill Sink				
UF 225401 (C6)	281	208	153	14
NMB.AB50.020 (C15)	362	257	195	15
NMB.AB50.021 (C16)	339	245	184	15
NMB.AB50.022 (C17)	305	221	162	15
NMB.AB50.023 (C18)	330	241	177	15
NMB.AB50.024 (C19)	268	194	148	15
NMB.AB50.025 (C20)	229	170	120	14
NMB.AB50.027 (C24)	—	239	182	15
NMB.AB50.030 (C30)	359	256	190	15
NMB.AB50.171 (C52)	316	229	172	14 (R), 15 (L)
Grand Cayman				
Crocodile Canal				
UF 61112 (dentary)	—	199	151	15
UF 61113 (dentary)	—	203	153	15
Prospect				
UF 65800	338	243	176	15
Chisholm Cow Well				
UF 128065 (dentary)	—	199	149	15
Queen Elizabeth II Botanic Garden				
UF 244488 (dentary)	—	224	167	15
UF 244489 (dentary)	—	177	133	15
Furtherland Farms Cow Well				
UF 128139 (dentary)	—	174	129	15

teeth, and another has 14 teeth. Several characters in the mandibles of the Abaco and Grand Cayman crocodiles appear to have taxonomic significance. The mandibular toothrow is composed of either 14 or 15 teeth, 15 in the majority of specimens. The three largest teeth in the dentary are in order of size, fourth, first, and tenth.

      Comparisons with extant *Crocodylus*.—Three extant species of crocodiles are known from the West Indies and Caribbean region. The American crocodile *Crocodylus acutus* is the most widespread of these three species, occurring in southern peninsular Florida and the Florida Keys, Cuba, Jamaica, Hispaniola, and the Caribbean

and Pacific coasts of Mexico, Central America, and northern South America (Thorbjarnarson 2010). Morelet's crocodile, *Crocodylus moreletii*, is restricted to the Gulf and Caribbean drainages of Middle America from central Tamaulipas in Mexico south to Guatemala, including the Yucatan peninsula of Mexico and Belize (Platt et al. 2010). The Cuban crocodile, *Crocodylus rhombifer*, has the most restricted range of any living crocodylian, found today only in the Ciénaga de Zapata in southern Cuba and the Ciénaga de Lanier on the Isla de la Juventud off the southwestern coast of Cuba (Ramos et al. 2010).

      In virtually all of the morphological features

described above, the crocodile skulls from Abaco and Grand Cayman are similar to, if not identical with, modern skulls of *Crocodylus rhombifer* from Cuba and differ from those of *C. acutus* and *C. moreletii* (Fig. 17). All characters discussed here for modern Cuban skulls of *C. rhombifer* also pertain to the Abaco and Grand Cayman crocodile skulls. In the following discussion, the most diagnostic morphological characters of *C. rhombifer*, including modern specimens from Cuba and fossils from Abaco and Grand Cayman, are compared and contrasted with the same characters in *C. acutus* and *C. moreletii*. Several previous authors have discussed cranial characters that distinguish the extant species of Neotropical crocodiles, including *C. acutus*, *C. moreletii*, and *C. rhombifer* (e.g., Mook 1921; Schmidt 1924).

Skulls of *Crocodylus rhombifer* have a comparatively shorter, broader, and deeper snout or rostrum than *C. acutus* which has a longer, narrower, and more flattened rostrum. The rostrum of *C. rhombifer* is particularly deep just anterior to the orbits. The rostrum of *C. moreletii* is somewhat intermediate in length between *C. acutus* and *C. rhombifer*, 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 second maxillary tooth. The premaxilla of *C. acutus* has a narrow, elongated process that extends posteriorly on either side of the midline to the level of third or fourth maxillary tooth. In *C. rhombifer*, the cranial roof is markedly concave along the midline both anterior and posterior to the dorsal temporal openings, on the frontals and parietals, respectively, although there are ridges on the internal margins of the dorsal temporal openings. Conversely, the lateral edges of the cranial roof, composed of the postorbitals anteriorly and squamosals posteriorly, have prominent, thick, raised ridges that terminate posteriorly in a strong rounded protuberance on the posterolateral corner of the squamosals. *C. acutus* and *C. moreletii* have a very different structure of the cranial roof, which is essentially flat and lacks the raised lateral ridges, squamosal protuberances,

medial concavity, and ridges medial to the dorsal temporal openings. The interorbital region in *C. rhombifer* is deeply concave on the frontals and prefrontals, a feature that is accentuated by the strong ridges on the dorsal or internal margins of the orbits. In *C. acutus* and *C. moreletii* the interorbital region is only slightly concave and the ridges on the inner margin of the orbits are weakly developed. The combination of a deeper snout and upraised ridges on the dorsal margin of the orbits, gives *C. rhombifer* the appearance of having a noticeably larger orbit in lateral view than *C. acutus* or *C. moreletii*. *Crocodylus rhombifer* also has prominent ridges on the lacrimals anterior to the orbits which, together with the ridges on the prefrontals and frontals, produce a distinct rhomboid or diamond-shaped convexity in dorsal view, extending from the lacrimal-nasal suture posteriorly to the interorbital constriction. This rhomboid shape is visible on the head just in front of the eyes in the living Cuban crocodile. Ridges on the lacrimals and prefrontals are weak to absent in *C. acutus* and *C. moreletii*. A midrostral boss is diagnostic of Neotropical species of *Crocodylus*, but is more prominent in *C. acutus* and *C. moreletii* than in *C. rhombifer*.

Crocodylus acutus, *C. moreletii*, and *C. rhombifer* differ in the shape of the premaxillary-maxillary suture on the palate. The suture is essentially transverse or horizontal at the level of the first maxillary tooth in *C. rhombifer* and *C. moreletii*. In most skulls of these two species, the premaxillary-maxillary suture has a short, rounded posterior extension to the level of the middle or posterior edge of the first maxillary tooth, about one third the distance between the lateral edge of the maxilla and the midline, and then from that point to the midline the suture is transverse. The premaxillary-maxillary suture extends much farther posteriorly in *C. acutus*, to the level of the second or third maxillary tooth, giving this suture a distinct V-shaped or W-shaped outline. Most of the modern skulls of *C. rhombifer* from Cuba and the fossils from Abaco and Grand Cayman have 13 teeth in the maxilla. All specimens examined of *C. acutus* and *C. moreletii* have 14 maxillary teeth. In *C. rhombifer*, the third largest tooth in the
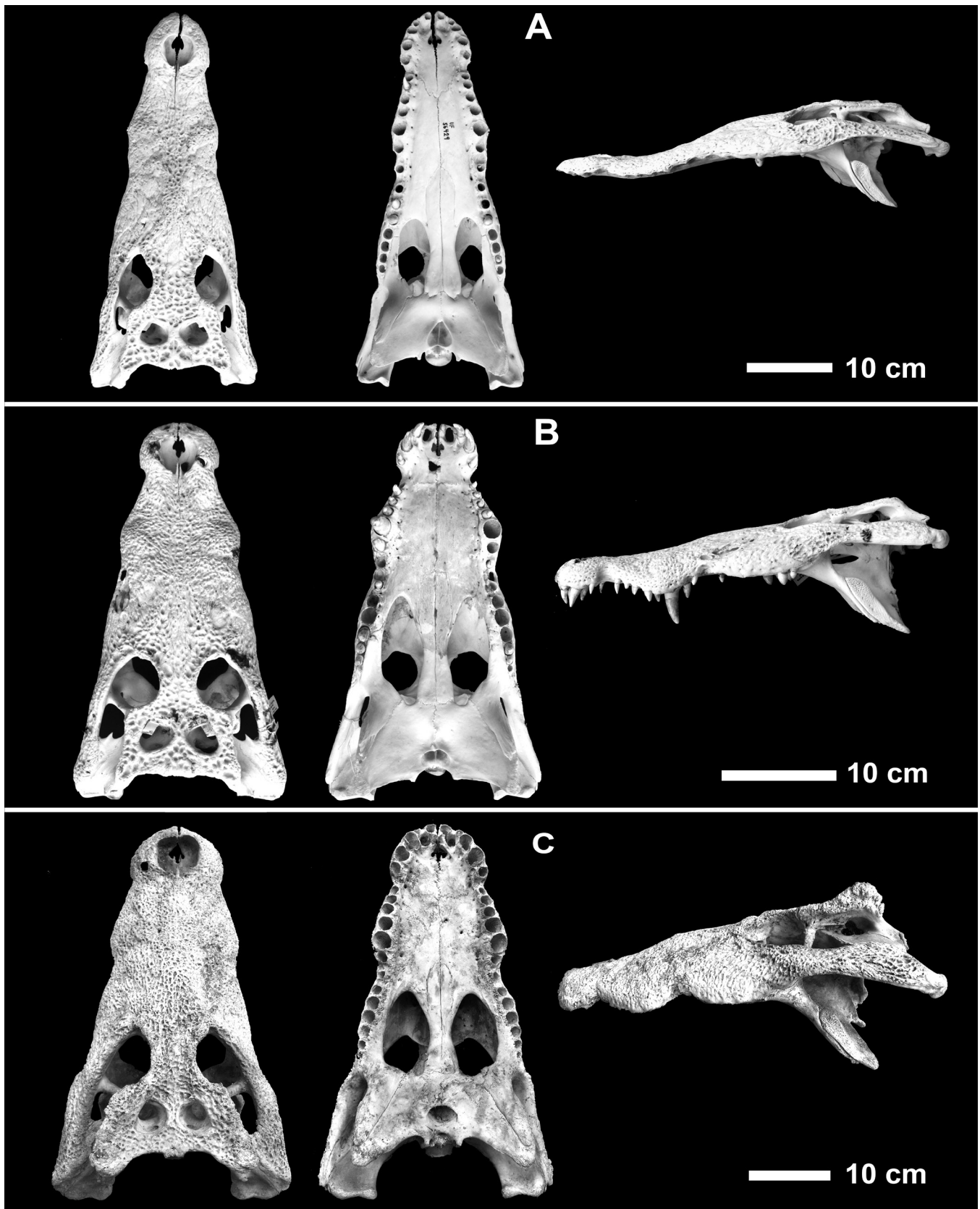
Figure 17. Comparison of modern skulls of three species of *Crocodylus* from the West Indian region in dorsal, ventral, and lateral views. A. *Crocodylus acutus* from Florida; B. *C. moreletii* from the Yucatan Peninsula, Mexico; and C. *C. rhombifer* from Cuba.

dentary (after the fourth and first) is the tenth tooth, but the eleventh is the third largest dentary tooth in *C. acutus* and *C. moreletii*. In summary, the cranial, mandibular, and dental characters of the fossils from Abaco and Grand Cayman cannot be distinguished from modern Cuban specimens of *C. rhombifer* of similar size, and differ significantly from those of *C. acutus* and *C. moreletii*.

POSTCRANIAL SKELETON

Tables 4 and 5 present series of measurements of postcranial elements of Quaternary crocodiles from Abaco and Grand Cayman, respectively. These measurements are of the primary elements in the forelimb (humerus, radius, ulna) and hindlimb (femur, tibia, fibula), as well as the ilium from the pelvic girdle. Figures 18-24 illustrate postcranial elements (humerus, radius, ulna, femur, tibia, fibula, ilium, respectively) of Late Quaternary *Crocodylus rhombifer* from Sawmill Sink on Abaco. For most of the major limb elements listed above, we provide photographs of the anterior and posterior views of the smallest, average-sized, and largest individuals in the sample. There are also large samples of the remainder of the postcranial skeleton of fossil crocodiles from Abaco and Grand Cayman, including the pectoral and pelvic girdles, vertebrae, ribs, carpals, tarsals, metapodials, phalanges, and osteoderms. Although these postcranial elements are not covered in detail in this paper, they should prove useful for future studies of the postcranial anatomy, functional morphology, and ontogenetic and individual variation of *Crocodylus rhombifer*.

Three of the specimens from Abaco (Sawmill Sink, NMB.AB50.030; Nancy's Cave, NMB. AB57.003; Ralph's Cave, NMB.AB51.002) and one specimen from Grand Cayman (Prospect, UF 65800) have partial postcranial skeletons directly associated with skulls identified as *Crocodylus rhombifer*. Thus, we can accurately associate postcranial elements and skulls belonging to this species. Since all of the skulls from both Abaco and Grand Cayman are *C. rhombifer*, we assume that the unassociated postcranials from the same sites on these islands also represent *C. rhombifer*. The isolated crocodile fossils from other islands in The Bahamas that are not associated with skulls

are only identifiable as crocodylian, presumably *Crocodylus*. We use the measurements to provide size ranges of individual postcranial elements from the various sites, and in some cases, particularly on Grand Cayman, to provide an estimate of the number of individual crocodiles present in a site based on minimum number of individuals (MNI).

Limbs, girdles, vertebrae, and other postcranial elements of crocodylians are fairly conservative, and thus within genera rarely demonstrate diagnostic differences. 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" (Brochu, 2000, fig. 3B). *Crocodylus rhombifer* lacks this "wasp-waisted" condition, having a modest indentation along the dorsal edge of the ilium near the posterior tip (Fig. 24), and as such resembles the ilium of most other crocodylians such as *Alligator*. There are large samples of isolated ilia from fossil sites on both Abaco and Grand Cayman, as well as several ilia associated with associated crocodile skeletons from Sawmill Sink and Ralph's Cave on Abaco. All of these ilia closely resemble the ilium of *C. rhombifer* and do not possess the "wasp-waisted" condition of the ilium seen in *C. acutus* and *C. moreletii*. We were unable to find other characters in the postcranial skeleton that would distinguish *C. rhombifer* from *C. acutus* and *C. moreletii*.

MORPHOLOGICAL AND SIZE VARIATION

No consistent morphological characters reliably separate the Abaco and Grand Cayman samples from each other or from modern examples of the Cuban crocodile *Crocodylus rhombifer*. Nevertheless, the large sample of skulls, mandibles, and postcranial elements of *C. rhombifer* from Abaco and Grand Cayman (Tables 1-5, Appendix 1) provides a wealth of information on variation in size and in several morphological characters.

The strong ridges on the internal margins of the orbits and on the lateral edges of the cranial table and the prominent tuberosity on the posterolateral corners of the squamosals, which are characteristic of modern *Crocodylus rhombifer* skulls, are present in all skulls from Abaco and Grand Cayman.

Table 4. Postcranial measurements of Late Quaternary fossils of Cuban crocodiles (*Crocodylus rhombifer*) from The Bahamas. For the ilium, only the total length and maximum width (recorded under "proximal width") are provided. R and L following the bone identifications (femur, tibia, ilium, etc.) indicate right or left side, respectively. All measurements in mm.

Island, site, element, and catalog number	length	proximal width	proximal depth	shaft width	distal width	distal depth
Abaco						
Sawmill Sink						
humerus						
NMB.AB50.030(R)	114	37	16	14	38	20
NMB.AB50.062(L)	83	25	11	10	24	14
NMB.AB50.085(R)[1]	85	26	11	10	25	14
NMB.AB50.087(L)[1]	85	26	11	10	25	14
NMB.AB50.084(R)	99	32	14	12	31	17
NMB.AB50.083(R)[1]	122	41	18	17	42	24
NMB.AB50.086(L)[1]	121	41	19	17	42	24
radius						
NMB.AB50.026(L)	111	32	18	16	30	18
NMB.AB50.067(R)	77	20	12	8	20	11
NMB.AB50.068(R)[1]	70	17	9	6	17	9
NMB.AB50.066(L)[1]	70	18	9	6	17	8
NMB.AB50.092(L)	57	13	8	5	13	8
NMB.AB50.091(L)[1]	80	22	13	9	22	12
NMB.AB50.093(R)[1]	80	22	13	9	21	12
ulna						
NMB.AB50.026(L)	134	46	37	28[2]	35	15
NMB.AB50.030(R)	87	25	22	11	18	9
NMB.AB50.064(L)	91	28	24	12	21	10
NMB.AB50.065(L)[1]	80	23	19	8	16	8
NMB.AB50.063(R)[1]	80	23	19	8	16	7
NMB.AB50.090(L)	66	17	15	6	12	6
NMB.AB50.089(L)[1]	94	31	26	12	23	10
NMB.AB50.088(R)[1]	94	30	26	12	23	11
femur						
NMB.AB50.030(R)[1]	152	38	19	15	39	28
NMB.AB50.030(L)[1]	152	39	19	15	40	28
NMB.AB50.070(R)	140	34	18	14	34	25
NMB.AB50.112(R)[1]	131	32	16	14	33	24
NMB.AB50.114(L)[1]	131	32	17	13	32	23
NMB.AB50.113(R)[1]	108	26	13	11	26	20
NMB.AB50.116(L)[1]	109	26	13	10	26	19
NMB.AB50.111(R)[1]	157	41	22	17	40	31
NMB.AB50.115(L)[1]	157	41	22	17	40	31

Table 4. Continued.

Island, site, element, and catalog number	length	proximal width	proximal depth	shaft width	distal width	distal depth
Abaco						
Sawmill Sink (cont.)						
tibia						
NMB.AB50.117(R)	79	23	19	8	21	11
NMB.AB50.118(R)[1]	106	35	30	13	31	19
NMB.AB50.119(L)[1]	106	38	28	13	31	19
fibula						
NMB.AB50.071(L)	95	16	11	6	16	6
NMB.AB50.123(L)	76	12	8	5	12	5
NMB.AB50.122(L)[1]	102	20	13	8	19	7
NMB.AB50.121(R)[1]	103	19	13	8	19	8
ilium						
NMB.AB50.026(R)	126	81				
NMB.AB50.030(L)	87	49				
NMB.AB50.069(R)	81	45				
NMB.AB50.094(R)	92	55				
NMB.AB50.097(L)	60	34				
NMB.AB50.095(R)[1]	73	43				
NMB.AB50.098(L)[1]	73	43				
Ralph's Cave (associated skeleton, all elements are from right side; NMB.AB51.002)						
humerus	112	31	11	15	34	18
radius	77	17	9	7	18	9
ulna	83	25	17	10	16	7
femur	150	35	14	14	35	25
tibia	106	30	26	13	27	14
fibula	103	15	9	7	17	7
ilium	77	48				
Nancy's Cave (associated skeleton; NMB.AB57.003)						
humerus	144	51	23	23	50	30
radius	91	28	17	11	26	16
ulna	110	35	30	17	24	12
femur	190	51	27	22	51	30
tibia	129	42	37	18	37	22
Lost Reel Cave						
femur						
NMB.AB52.009(L)	193	50	22	20	46	36

Table 4. Continued.

Island, site, element, and catalog number	length	proximal width	proximal depth	shaft width	distal width	distal depth
Eleuthera						
White Lake Cave						
humerus (L)						
NMB.EL185.003	140	50	23	20	51	31
Mermaid's Pool						
femur (L)						
NMB.EL183.001	—	27	13	12	—	—

[1] Indicates that the right and left limb/girdle elements with very similar measurements are probably from the same individual crocodile; however, they were not collected in direct association so were assigned different catalog numbers. A large sample of crocodile postcranial elements was recovered from Grid A in Sawmill Sink and probably represents three or four individuals.

[2] Shaft width is unusually broad due to pathology in which the shaft appears to have been broken and healed in life.

These ridges tend to be better developed in larger specimens. Likewise, the ridges on the lacrimals and the ridges on the snout anterior to the orbit (that outline the rhomboid shape typical of *C. rhombifer*) are well developed in all skulls from Abaco and Grand Cayman, but tend to be more prominent in larger skulls. The frontals are deeply concave medial to the strongly raised ridges on the internal margins of the orbits and on the anterior portion of the cranial table, but certain skulls having more strongly concave frontals than others.

The penetration of the anterior portion of the premaxilla by the first dentary tooth has been mentioned as a character that is typical of *Crocodylus acutus* but lacking in *C. rhombifer* (Toby Ramos, Roberto Soberón, pers. comm.). However, penetration of the premaxilla by the first dentary tooth is widespread in the Crocodylia and is of little taxonomic significance (C. Brochu, pers. comm.). This character also is highly variable in the skulls and isolated premaxillae from Abaco and Grand Cayman. Approximately half of the premaxillae in our sample have a small rounded hole anterior to the narial opening caused by the tip of the first tooth in the dentary, and half of the specimens lack this perforation. There are even a few skulls in which the perforation is present on one side of the premaxilla but not the other side. We interpret the variation in this character to be of little or no taxonomic importance. There is some variation in the expression of the premaxillary-maxillary suture on the palate that does not appear to be size-related. This suture is horizontal at the level of the first maxillary tooth in most specimens. In a few skulls, the suture has a slight posterior excursion about one-third of the distance between the lateral surface of the maxilla and the midline of the palate that extends back to the level of the posterior alveolus of the first maxillary tooth. This posterior extension of the premaxillary-maxillary suture in several specimens of *C. rhombifer* from Abaco and Grand Cayman is minor compared to the strong posterior excursion of this suture to the level of the second or third maxillary tooth observed in skulls of *C. acutus*. There is some variation in the number of teeth present in the maxilla. Most modern skulls of *C. rhombifer* from Cuba and the fossils from Abaco and Grand Cayman have 13 teeth in the maxilla. A few of the fossil specimens have 12 teeth in the maxilla and a skull from Abaco has 14 teeth, although the last tooth is tiny.

The primary difference between the crocodile samples from Abaco and Grand Cayman is the overall size of individuals (skulls and mandibles,

Figure 18. Humerus of Cuban crocodiles (*Crocodylus rhombifer*) from Sawmill Sink in anterior (top) and posterior (bottom) views. Two left humeri on left, three right humeri on right.

Table 5. Postcranial measurements of Late Quaternary fossils of Cuban crocodiles (*Crocodylus rhombifer*) from Grand Cayman, Cayman Islands. Format as in Table 4.

Site, element, and catalog number	length	proximal width	proximal depth	shaft width	distal width	distal depth
Crocodile Canal						
humerus						
UF 61127 (R)	90	27	11	10	28	14
UF 61128 (L)	90	28	12	10	25	15
femur						
UF 61129 (R)	103	23	11	9	23	17
UF 61130 (R)	—	30	16	—	—	—
tibia						
UF 61131 (R)	76	19	17	7	18	11
UF 61132 (L)	95	25	23	10	25	15
fibula						
UF 61133 (L)	90	16	10	7	15	5
ilium						
UF 61137 (L)	70	42				
Prospect						
humerus						
UF 65800 (L)	130	40	18	17	40	24
radius						
UF 65800 (L)	88	20	12	8	21	13
femur						
UF 65800 (R)	166	40	21	17	40	29
Chisholm Cow Well						
humerus						
UF 128078 (L)	108	30	13	13	31	17
femur						
UF 128079 (R)	138	32	17	13	32	22
UF 128080 (L)	152	35	18	14	34	24
tibia						
UF 128081 (R)	101	26	22	11	25	15
fibula						
UF 128082 (L)	104	16	10	6	17	6
ilium						
UF 128095 (R)	86	51				
UF 128073 (L)	73	41				

Table 5. Continued.

Site, element, and catalog number	length	proximal width	proximal depth	shaft width	distal width	distal depth
Queen Elizabeth II Botanic Park						
humerus						
UF 244496 (R)	103	31	15	13	32	17
UF 244497 (L)	122	36	16	14	37	20
femur						
UF 244493 (R)[1]	147	35	19	15	35	26
UF 219978 (L)[1]	148	35	18	15	34	26
UF 244494 (L)	134	30	16	12	30	21
tibia						
UF 244495 (R)	108	32	28	12	29	17
ilium						
UF 244482 (R)	129	82				
Furtherland Farms Cow Well						
humerus						
UF 128148 (R)	107	31	13	12	32	17
UF 128113 (L)	92	26	12	10	26	14
radius						
UF 128149 (R)	61	13	8	5	13	7
UF 128115 (L)	69	16	10	6	16	9
UF 128150 (L)	81	19	11	7	18	10
tibia						
UF 128116 (R)	95	27	24	10	25	16
UF 128157 (R)	96	27	23	10	25	15
fibula						
UF 128117 (R)	94	15	10	6	16	6
UF 128118 (L)	82	11	9	5	—	5
ilium						
UF 128131 (R)	58	34				
UF 128144 (R)	87	49				
UF 128106 (L)	72	41				
UF 128107 (L)	63	37				

[1]UF 219978 and 244493 are probably the right and left femora of the same individual crocodile; however, they were not found in association so were assigned different catalog numbers.

Figure 19. Radius of Cuban crocodiles (*Crocodylus rhombifer*) from Sawmill Sink in anterior (top) and posterior (bottom) views. All bones are from the left side.
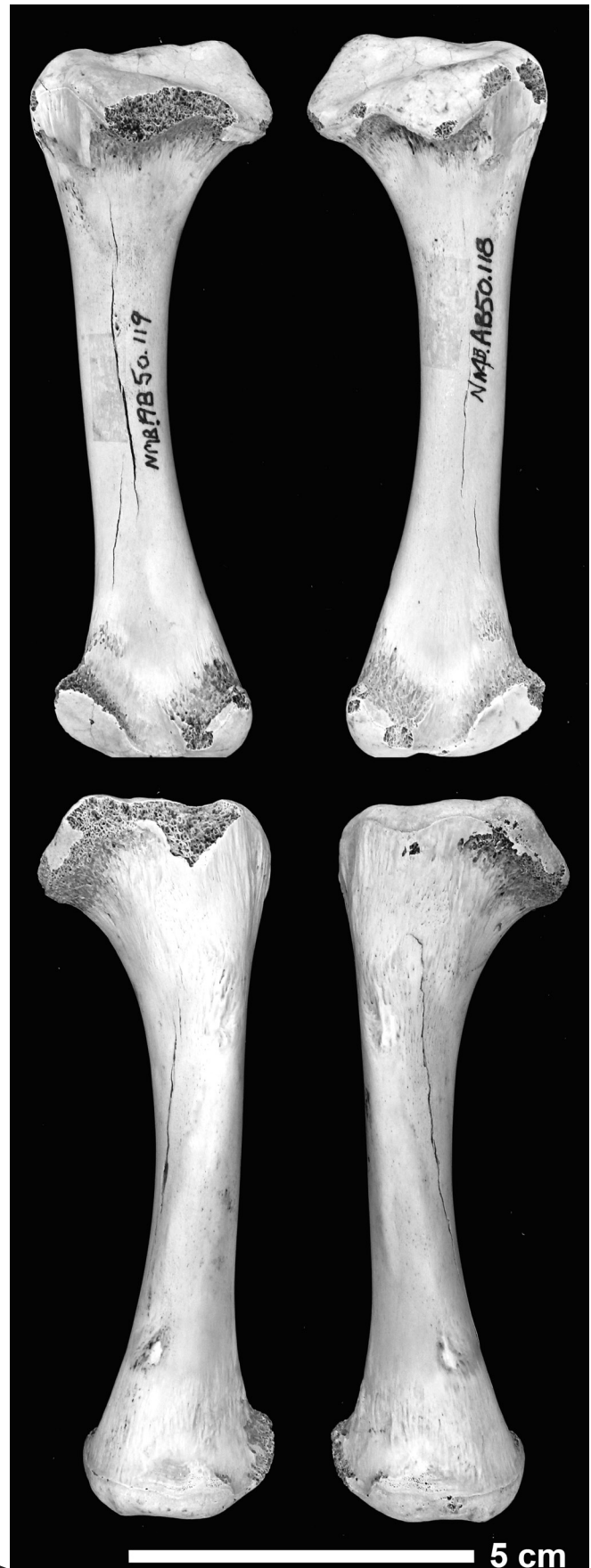
Figure 20. Ulna of Cuban crocodiles (*Crocodylus rhombifer*) from Sawmill Sink in anterior (top) and posterior (bottom) views. All bones are from the left side.

Figure 21 Left femora of Cuban crocodiles (*Crocodylus rhombifer*) from Sawmill Sink in anterior (top) and posterior (bottom) views.

Figure 22 Tibia of Cuban crocodiles (*Crocodylus rhombifer*) from Sawmill Sink in anterior (top) and posterior (bottom) views. Left tibia on left, right tibia on right.

Figure 23. Fibula of Cuban crocodiles (*Crocodylus rhombifer*) from Sawmill Sink in anterior (top) and posterior (bottom) views. All from the left side.

Tables 1-3; postcranials, Tables 4, 5). It should be noted that the following are general statements about size trends in the populations of *Crocodylus rhombifer* from these two islands that could be tested with larger samples and more sophisticated statistical analyses. The Grand Cayman crocodiles are somewhat smaller, with a mean total skull length of 265 mm (observed range, 247–305 mm; 4 individuals). The average skull of *C. rhombifer* from Abaco is about 10% larger at 286 mm (observed range, 243–361 mm; 12 individuals, excluding one very small juvenile skull). The largest skull from Abaco (Nancy's Cave, 361 mm) is about 15% larger than the largest complete skull from Grand Cayman (Prospect, 305 mm). Several fragmentary skulls from both Grand Cayman and Abaco indicate that even larger individuals were present in both populations. A partial skull from the Queen Elizabeth II (QEII) Botanic Park site on Grand Cayman (UF 143687) measures 385 mm in length from the tip of the premaxilla to the posterior extension of the quadratojugal. The maximum total length of this skull from the premaxilla to the posterior edge of the quadrate, which is lacking in this specimen, would be somewhat larger. Thus, the QEII skull is actually somewhat larger (almost 10%) than the largest complete skull of *C. rhombifer* from Abaco. A highly fragmented skull from Sawmill Sink (NMB. AB50.0026; C21) is similar in size to the QEII skull based on comparisons of isolated cranial elements (jugal, quadratojugal, occipital condyle; Table 6).

Similar trends are observed in the postcranials. Measurements for the two proximal limb bones of *C. rhombifer* from Grand Cayman are: humerus, mean length, 107 mm (observed range 90–130; 7 individuals); femur, mean length 140 mm (observed range, 103–166; 6 individuals). For the Abaco population of *C. rhombifer*, the same measurements are: humerus, mean length, 108 mm (observed range 83–144; 7 individuals); femur, mean length, 153 mm (observed range, 109–193; 8 individuals). The Abaco postcranials average larger, by about 10%, and the observed ranges are greater. Because of the limited sample sizes, the observed ranges and means of the limb bones
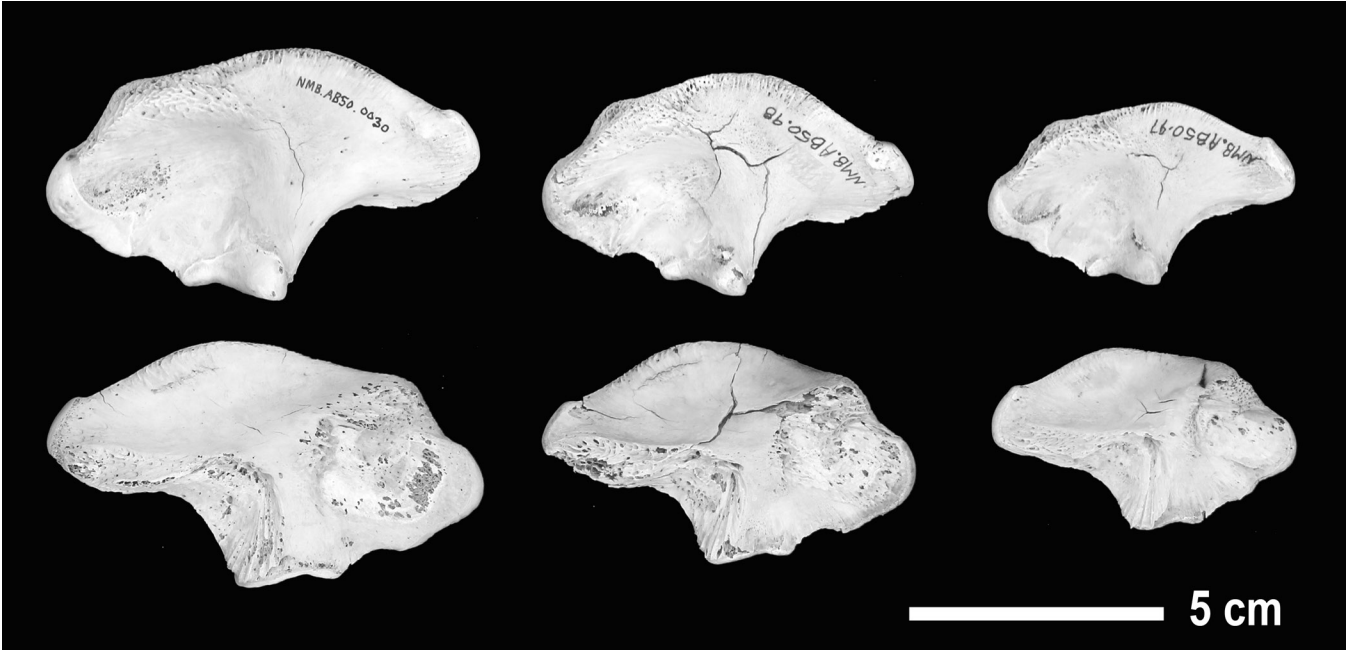
Figure 24. Ilium of Cuban crocodiles (*Crocodylus rhombifer*) from Sawmill Sink in anterior (top) and posterior (bottom) views. All bones are from the left side.

Table 6. Selected cranial and mandibular measurements of the four largest specimens of Late Quaternary fossils of Cuban crocodiles (*Crocodylus rhombifer*) from Sawmill Sink, Abaco, The Bahamas. Measurements are described in the Methods section and were designed to provide information on the largest crocodile specimen from Sawmill Sink (NMB.AB50.026; C21) that consists of broken/disassociated elements. All measurements in mm; missing measurements indicated by "—". See Figure 25A–C.

catalog number	posterior width of quadrate	width of occipital condyle	length of articular	width of articular
NMB.AB50.026 (C21)	52	29	109	47
NMB.AB50.020 (C15)	34	23	87	36
NMB.AB50.027 (C24)	31	21	—	—
NMB.AB50.030 (C30)	34	23	86	36

are strongly affected by single specimens of either large or small size. For instance, the mean length of the humeri from Abaco is only slightly greater than that of humeri from Grand Cayman primarily because the Sawmill Sink sample includes two very small juveniles.

We provide general estimates of the possible total lengths of the Quaternary specimens of *Crocodylus rhombifer* from Abaco and Grand Cayman. The approximate total length of the smallest, largest, and average-sized crocodiles

from these two islands are calculated based on the standard ratio used by crocodile biologists on living crocodiles of head length to total length. According to Kent Vliet (pers. comm.), the "head length" in living crocodiles, from the tip of the snout to the back of the head or cranial table measured along the midline, multiplied by 7.1 or 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 between species. In other words, the total length of a crocodile is a little more

than seven times the head length. The head length rather closely approximates the skull measurement in Tables 1 and 2 called "length from premaxilla to parietal" (Fig. 3; measurement "B"), which is the length from the anterior tip of the premaxilla to the posterior tip of the parietal along the midline. Since the skulls lack the skin and underlying connective tissues found in the living animals, the total length predictions based on skulls probably underestimate the total length. We use the ratio of 1:7.2 since *C. rhombifer* is rather short-snouted compared to most other species of *Crocodylus*. The smallest crocodile skull from Abaco (Sawmill Sink; NMB.AB50.025; C20) has a head length (= length from premaxilla to parietal) of 184 mm which predicts a total length of 1.32 meters (m) for this animal. The largest skull from Abaco (Nancy's Cave; NMB.AB57.003) has a head length of 321 mm which predicts a total length of 2.31 m. The mean head length for the 12 adult *C. rhombifer* skulls from Abaco is 260 mm, indicating an average length of 1.87 m for this population. The smallest crocodile skull from Grand Cayman (Connally Cow Well, UF 128064) has a head length of 223 mm which predicts a total length of 1.61 m. There are much smaller individuals of crocodiles in the Grand Cayman population, including an apparent hatchling, but they consist of fragmentary specimens in which the head length cannot be measured. The largest complete skull from Grand Cayman (Prospect, UF 65800) has a head length of 276 mm, with a predicted total length of 1.99 m. The mean head length for four adult *C. rhombifer* skulls from Grand Cayman is 241 mm, indicating an average length for this population of 1.74 m. The largest individual from Grand Cayman, a partial skull from Queen Elizabeth II Botanic Park, is too fragmentary to yield a head length measurement. However, this specimen is more than 20% larger than any other skull of *C. rhombifer* from Grand Cayman, suggesting a total length in excess of 2 m.

Perhaps some factor or factors relating to the taphonomy or paleoecology of the sites from Grand Cayman with abundant crocodile samples led to the preservation of mostly juvenile to small adult animals. We know based on the presence of a very large partial skull from the Queen Elizabeth II Botanic Park site that large individuals of *C. rhombifer* did occur on Grand Cayman during the Late Quaternary and were occasionally preserved. The same is true of the Abaco crocodile sample. We cannot be certain that the size of the crocodile fossils preserved in the Abaco blue holes accurately reflects the overall size range of the individuals in the population. Once again, taphonomic or paleoecological factors could be involved. As a hypothetical example, perhaps large crocodiles did not regularly inhabit blue holes and their skeletons are preserved elsewhere on the island or not at all. There is a single individual representing a very large crocodile from Sawmill Sink that is considerably larger than any another other crocodile measured from Abaco (Fig. 25; NMB.AB50.026, C21; estimated total length over 3 m). Moreover, the bones from this crocodile are from a deep area of Sawmill Sink, are mineralized, and lack collagen. This individual appears to be considerably older, possibly dating to the late Pleistocene, than the unmineralized skulls from the shallower peat deposit in Sawmill of late Holocene age.

Larger crocodiles may have inhabited Abaco when sea levels were much lower during the late Pleistocene and the Little Bahama Bank islands (Abaco, Grand Bahama, and smaller cays) were merged into a single island larger than modern-day Jamaica or Puerto Rico. If the size of crocodiles in The Bahamas is related to island size, with larger crocodiles on larger islands, then we might expect even larger fossil specimens in blue holes on islands located on the Great Bahama Bank (Andros, Cat Island, Eleuthera, Great Exuma, Long Island, New Providence, and innumerable smaller cays), which would have been part of a huge island about the size of modern-day Hispaniola during the low sea level stand of the late Pleistocene glacial maximum. The only evidence currently available pertaining to the size of crocodiles on the Great Bahama Bank consists of small samples from blue holes on Eleuthera, including a possibly associated dentary fragment, isolated tooth, and humerus of a large crocodile from White Lake Cave (Fig. 11, Table 4). The humerus of this individual is similar in size (total length, 140 mm) to the humerus (total
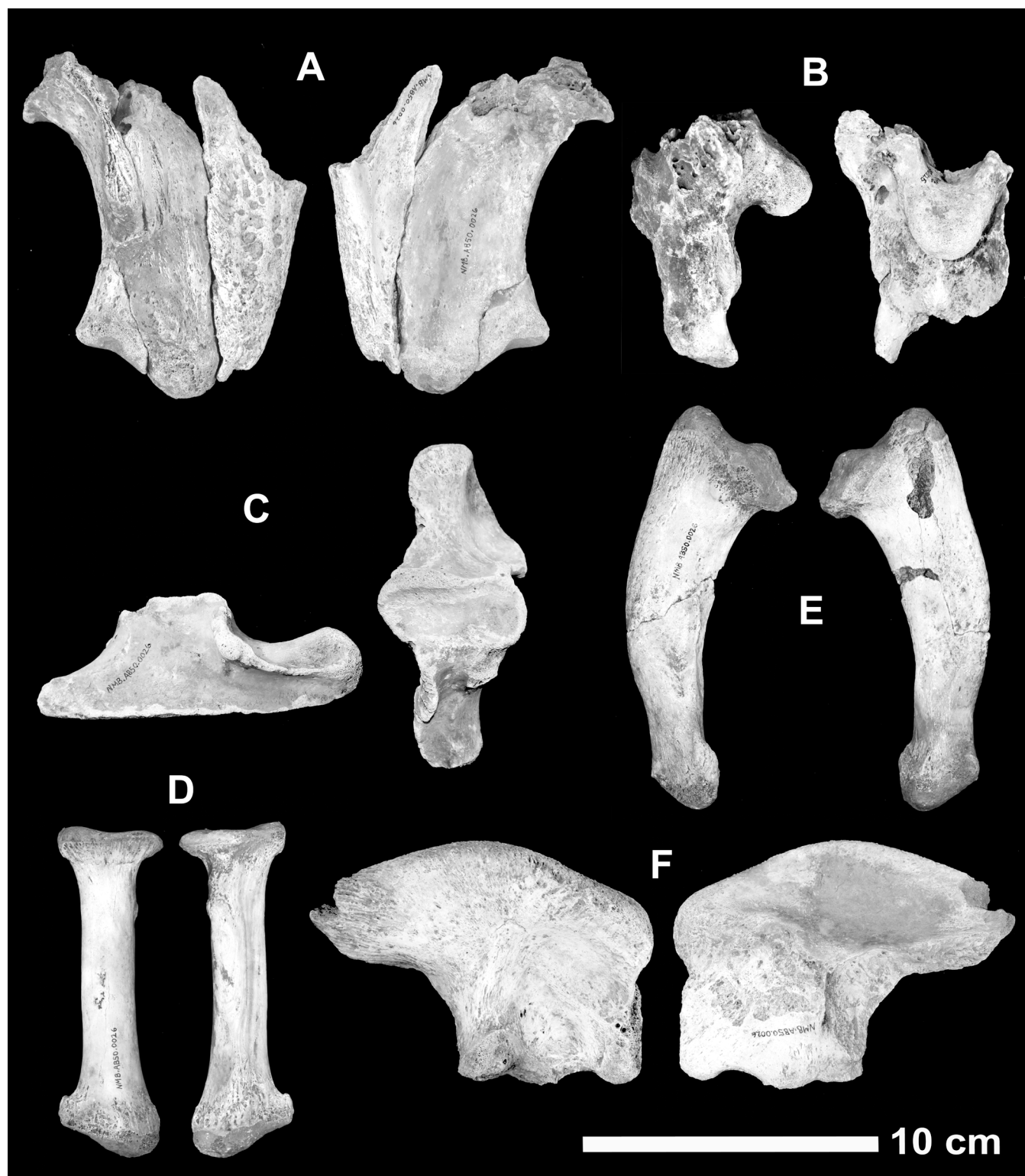
Figure 25. Isolated cranial and postcranial elements of the largest specimen of *Crocodylus rhombifer* known from Sawmill Sink (NMB.AB50.026; C21). A. quadrate, B. occipital condyle, C. articular, D. radius, E. ulna, F. ilium**.** See Tables 4 and 6 for measurements.

length, 144 mm) of a large crocodile from Nancy's Cave, Abaco. We need much larger samples of Quaternary crocodiles from islands on the Great Bahama Bank, preferably with radiocarbon dates, before we can make any further predictions about the correlation between crocodile body size and island size in The Bahamas. Grand Cayman did not increase greatly in size during Pleistocene glacial intervals because it is surrounded by deep water on all sides. Therefore, if island size is an important factor related to body size in crocodiles, then we would not expect late Pleistocene animals from Grand Cayman to be significantly larger than the fossil crocodiles currently known from that island, all of which appear to be late Holocene in age.

In both size and morphological characters, the Quaternary crocodiles from Abaco and Grand Cayman are similar. The available data do not support a separate taxonomic designation (species or subspecies) for these two populations. We found no morphological features that distinguish these fossils from the living Cuban animals based on the cranial characters of *Crocodylus rhombifer* summarized by Varona (1966, 1984). The only obvious difference between the Abaco and Grand Cayman populations of *C. rhombifer* and those from Cuba is size — the Cuban animals appear to average considerably larger. Although large individuals of *C. rhombifer* are now rare in Cuba, historical evidence and the fossil record demonstrate that this species formerly reached a very large size. Gundlach (1880) mentioned a specimen of *C. rhombifer* 16.5 feet (5 m) in length, whereas adults of this species are now generally less than 3.5 m (Varona 1966). The maximum length of modern *C. rhombifer* from Cuba (3.5–5 m) is much larger than predicted maximum lengths of Quaternary crocodiles from Abaco (2.3 m) and Grand Cayman (2.0 m).

We measured three modern skulls of *Crocodylus rhombifer* from Cuba, as well as four skulls of this species from the Quaternary spring deposits at Ciego Montero, Cuba in the AMNH collection, several of which came from very large individuals (Table 7). AMNH 6179, a fossil skull from Ciego Montero (Fig. 13), is nearly twice

as long (653 mm) as the largest Late Quaternary crocodile skulls known from Abaco (361 mm) and Grand Cayman (385 mm). A mandible from Ciego Montero is well over two times the total length (818 mm) of the largest mandibles from Abaco (362 mm) and Grand Cayman (338 mm). The head length of the largest skull from Ciego Montero (AMNH 6179) is 550 mm, which would predict a total length for this animal of about 4 m. Barbour and Ramsden (1919:209) noted that the skull associated with the 5 m long individual of *C. rhombifer* described by Gundlach (1880) was displayed in a locked case in the Museo Gundlach in Havana and could not be measured, but appeared to be "…fully two feet long" (about 600 mm, similar in size to the largest skulls of *C. rhombifer* from Ciego Montero). It should be noted that the sample sizes of modern *C. rhombifer* skulls and skeletons in museum herpetology collections are very limited, and many of those specimens are captive individuals, not wild caught animals from Cuba.

ICHNOFOSSILS

Ichnofossils or trace fossils differ from body fossils because they do not represent the hard anatomy of a fossil species (teeth or bone), but instead are formed through the biological activity of the living animal. Footprints are perhaps the best known vertebrate ichnofossils; however, no fossil footprints or tracks of vertebrates are known from The Bahamas. Coprolites or fossilized feces/dung of crocodiles are the most common ichnofossils from blue holes in The Bahamas. Most of the underwater blue hole sites on Abaco contain at least a few crocodile coprolites, and Lost Reel Cave contains a large sample of coprolites, three of which are illustrated in Figure 26. A single coprolite is the only fossil of a crocodile known from The Fountain blue hole on Mayaguana in the southeastern Bahamas. Small samples of crocodylian coprolites are also known from the Chisholm Cow Well and Queen Elizabeth II Botanic Park sites on Grand Cayman. The coprolites from Abaco and Grand Cayman, particularly the large sample of well-preserved coprolites from Lost Reel Cave, are similar in size and morphology to modern alligator feces and to

Table 7. Cranial measurements of modern and late Quaternary Cuban crocodiles (*Crocodylus rhombifer*) from Cuba. Measurements are described in the Methods section and illustrated in Fig. 3. All measurements in mm; missing measurements indicated by "—".

Locality and catalog number	total length of skull	length premaxilla-parietal	length of snout	length of maxillary toothrow	breadth of premaxilla
Modern					
Zapata Swamp					
6214 (Havana)[1]	349	330	218	—	76
Uncat.[2]	475	398	265	218	109
Captive					
UF 45189	346	303[3]	199	160	78
Quaternary					
Ciego Montero					
AMNH 6179	653	550	355	292	191
AMNH 6180	—	—	355	247	173
AMNH 6181	504	436	292	236	146
AMNH 6185	382	335	224	185	79

	breadth of snout at 5th tooth	breadth of cranial roof (ant.)	breadth of cranial roof (post.)	maximum breadth of skull	breadth at quadrates
Modern					
Zapata Swamp					
6214 (Havana)[1]	106	91	—	196	172
Uncat.[2]	154	109	166	274	245
Captive					
UF 45189	110	77	111	203	190
Quaternary					
Ciego Montero					
AMNH 6179	254	136	236	400[4]	384[4]
AMNH 6180	234	—	—	—	—
AMNH 6181	200	120	175	320	306
AMNH 6185	115	86[4]	112[4]	214[4]	202[4]

[1] This skull is housed in the Gabinete de Arquelogía, Oficina del Historiador, Havana, Cuba

[2] This skull, from the Zapata Croc Farm, is housed in the Criadero de Cocodrilos, Zapata Swamp, Cuba

[3] This measurement is actually the length from the anterior edge of the premaxilla to the posteriormost extension of the squamosal. The measurement to the posterior end of the parietals along the midline would be slightly less.

[4] This specimen is damaged and the measurements indicated with superscript "4" could not be taken on a complete skull. However, measurements were taken from the complete structure on one side of the skull to the midline and then doubled, giving a reasonable approximation of the measurement.
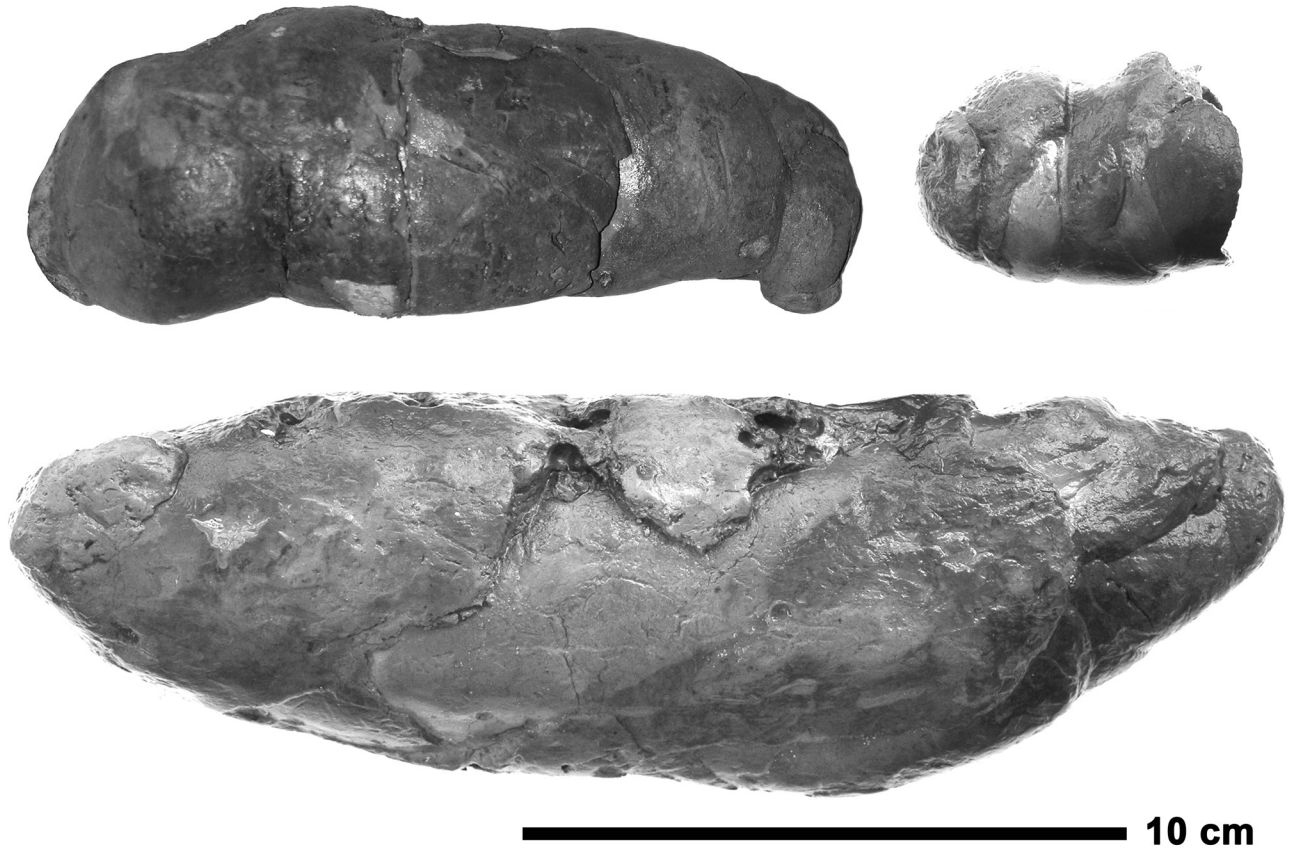
Figure 26. Sample of crocodylian coprolites from Lost Reel Cave, Abaco.

coprolites attributed to alligators from Pleistocene underwater sites in Florida, particularly the Ichetucknee River (e.g., a large sample in the UF vertebrate paleontology collection). A characteristic feature of the coprolites from Lost Reel Cave is their smooth texture and fine-grained groundmass. No bones, teeth, or fish scales are visible in any of the coprolites. Although the smooth texture and lack of bones is also characteristic of Pleistocene alligator coprolites from Florida, the latter will on rare occasion contain identifiable vertebrate remains, in particular the ganoid scales of the garfish *Lepisosteus*. We strongly suspect that the fossil coprolites from Abaco and Grand Cayman belong to *Crocodylus rhombifer*, considering that this is the only fossil crocodylian known from these two islands.

Several shells of the large extinct land tortoise *Chelonoidis alburyorum* from Sawmill Sink on Abaco possess round depressions that correspond very closely in size and shape to the conical teeth of a large crocodile. Figure 27 is a lateral view of a large shell of *C. alburyorum* (NMB.AB50.007; Tortoise T7) from Sawmill Sink that bears four rounded bite marks on two successive costal bones. This shell has a carapace length of 424 mm and a maximum shell height of 218 mm (Franz & Franz 2009), indicating that it must have been a fairly large crocodile that produced the bite marks. One of the bite marks consists of an elongated furrow that extends for a distance of 45 mm over two successive costals, giving the appearance that the tooth slid as the crocodile was attempting to bite down, possibly because the tortoise was struggling to escape. Several of these bite marks penetrated the shell and all of the bites appear to show some regrowth or healing, suggesting that the tortoise escaped and was not killed by the crocodile that inflicted the bites. The same shell has several smaller bite marks, one of which on an anterior
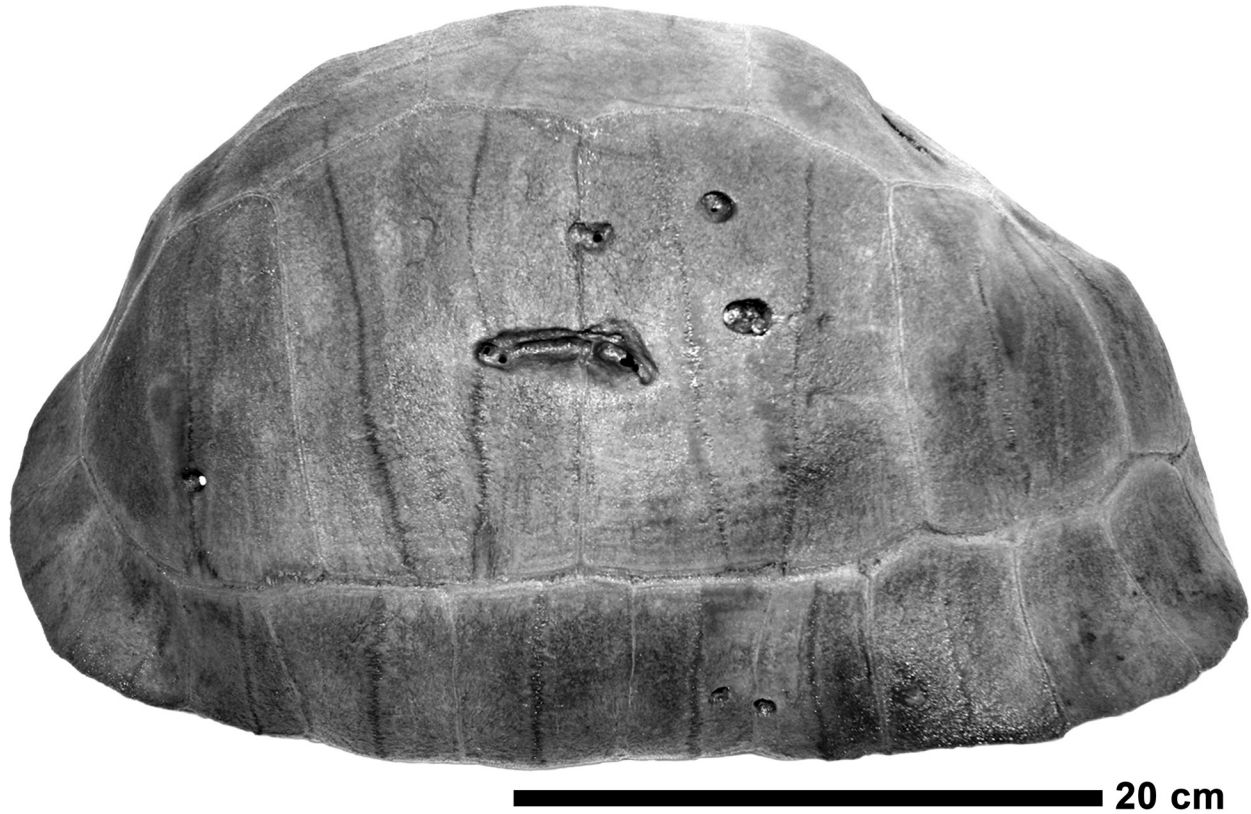
20 cm

Figure 27. Shell of extinct land tortoise *Chelonoidis alburyorum* (T7) from Sawmill Sink, Abaco, with crocodylian bite marks.

costal also penetrates the shell. There is also a smaller bite mark on a bridge peripheral ventral to the costals with the larger bite marks.

A sizeable fragment of a tortoise carapace from The Fountain blue hole on Mayaguana also shows evidence of crocodile bite marks (Fig. 28A). The carapace fragment is very thin shelled, as are all specimens of extinct Bahamian tortoises in the genus *Chelonoidis*, and consists of four peripherals and parts of six costals and four neurals. The shell has eight rounded bite marks that appear to have been caused by the conical teeth of a crocodile. Seven of the bite marks consist of holes that penetrate the shell and one is a depression where the bone of the shell is compressed. One bite completely penetrates a neural on the dorsal surface of the carapace, six holes penetrate costals, one with inward splintering, and one bite mark consists of a deep depression in a peripheral. The holes are different sizes, including a very large bite mark on

an anterior costal that is 30 mm in diameter. The size and shape of the bite marks, distance between them, and their overall orientation all appear to correspond to the dental arcade of a crocodile. Moreover, there does not appear to be any bone regrowth around the bite marks, suggesting that the Mayaguana tortoise did not survive the attack.

Tortoise shells from six Bahamian blue holes have possible evidence of crocodile bite marks, including the two sites discussed above, Sawmill Sink on Abaco and The Fountain on Mayaguana, as well as Dan's Cave, Nancy's Cave, and Ralph's Cave on Abaco and Kelly's Blue Hole on Eleuthera. Nine specimens from a total sample of 27 individuals (33%) exhibited evidence of crocodile bite marks. Thus, approximately one third of the fossil tortoise shells from blue holes in The Bahamas show predation or attempted predation by crocodiles.
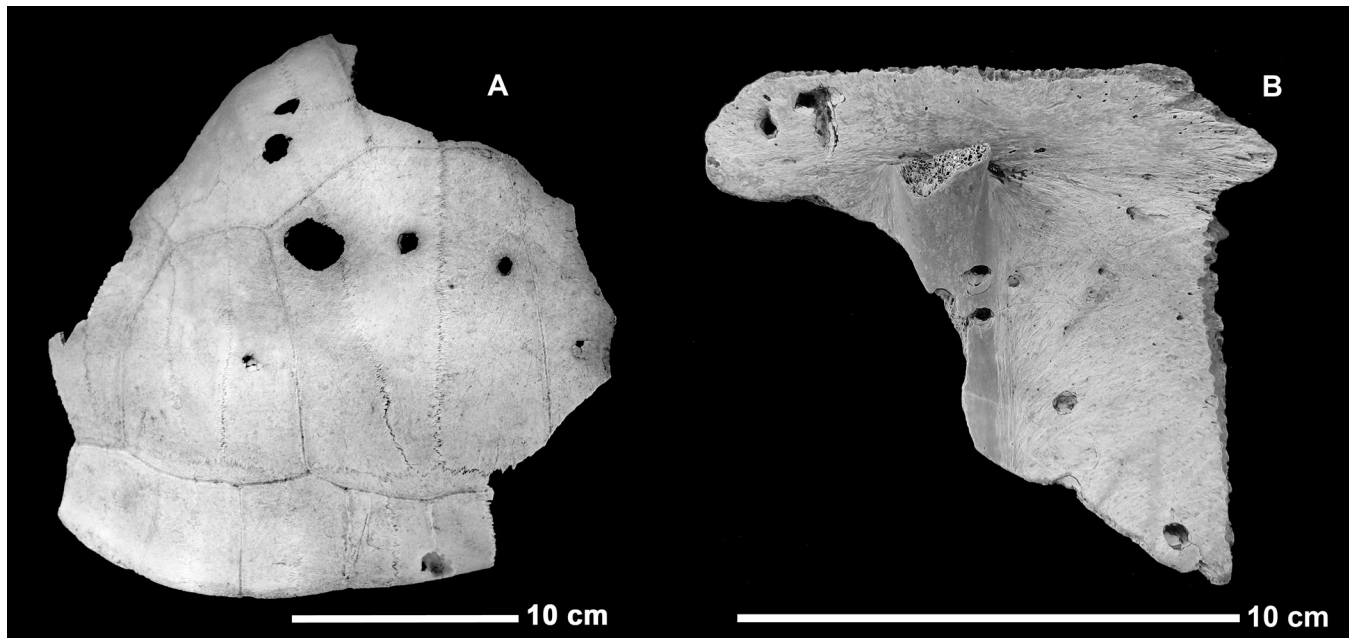
Several shell elements of the tortoise

Figure 28. A. Partial carapace of extinct land tortoise *Chelonoidis* from The Fountain blue hole on Mayaguana, with crocodylian bite marks. B. Partial costal of a sea turtle (internal view) from Gilpin Point, Abaco with crocodylian bite marks.

Chelonoidis and a partial costal bone of a sea turtle (Cheloniidae) from the Gilpin Point site on Abaco have crocodylian bite marks. Unlike the complete tortoise shells with bite marks from blue hole sites on Abaco, both the tortoise and sea turtle bones with bite marks from Gilpin Point consist of single or partial elements. A partial costal of a sea turtle illustrated in Fig. 28B has at least 10 rounded bite marks on the internal surface. On most of the bite marks, the surface of the bone has been pressed several millimeters into the concavity caused by the conical tip of the crocodile's tooth. The largest of the bite marks consists of a conical portion and a deep furrow where the crocodile's tooth appears to have dragged across the bone. There are corresponding bite marks on the external surface of this same costal, but they are not as prominent. Perhaps at the time the bite was inflicted the carapace still retained the keratinous scutes on its external surface, and these bore the brunt of the force of the crocodile's bites. The features of the bite marks and the fragmentary nature of the bone suggest the crocodile may have scavenged a dead sea turtle, rather than capturing it alive. Moreover, a freshwater crocodile with notable terrestrial habits (see discussion below) would only rarely encounter a live sea turtle, probably when a female was on land laying her eggs. Gilpin Point represents the only occurrence of crocodylian bite marks on a sea turtle bone from the Bahamas.

Several papers have discussed rounded punctures or "bite marks" on fossil bones that have been attributed to crocodylians (e.g., Njau & Blumenschine 2006; Noto et al. 2012). The supposed crocodylian bite marks occurred on bones from faunas with several types of large predators that could have inflicted the bites, including crocodylians. Late Quaternary faunas from The Bahamas contain no mammalian carnivores, the only large predators were crocodiles. We feel confident that crocodiles caused the bite marks on the shells of tortoises from Abaco and Mayaguana, as well as the costal bone of a sea turtle from Gilpin Point on Abaco, based on the size, shape, and arrangement of the tooth impressions or holes in the bones, as well as the absence of other large predators in The Bahamas.

Two specimens of capromyid rodents from

the Queen Elizabeth II Botanic Garden site on Grand Cayman have a peculiar preservation that appears to represent digestion by a crocodylian (Fig. 29). The specimens are a right mandible with four teeth of the large capromyid rodent *Capromys* (UF 172947) and a palate with two premolars of the small capromyid *Geocapromys* (UF 172949). In both specimens, much of the enamel, dentine, and cement around the perimeter of the teeth is missing, specifically that portion of the teeth that would have been exposed above the gum line, whereas the teeth below the crown, comprising about two-thirds the length of each tooth, were unaffected. *Capromys* and *Geocapromys* both have high-crowned or
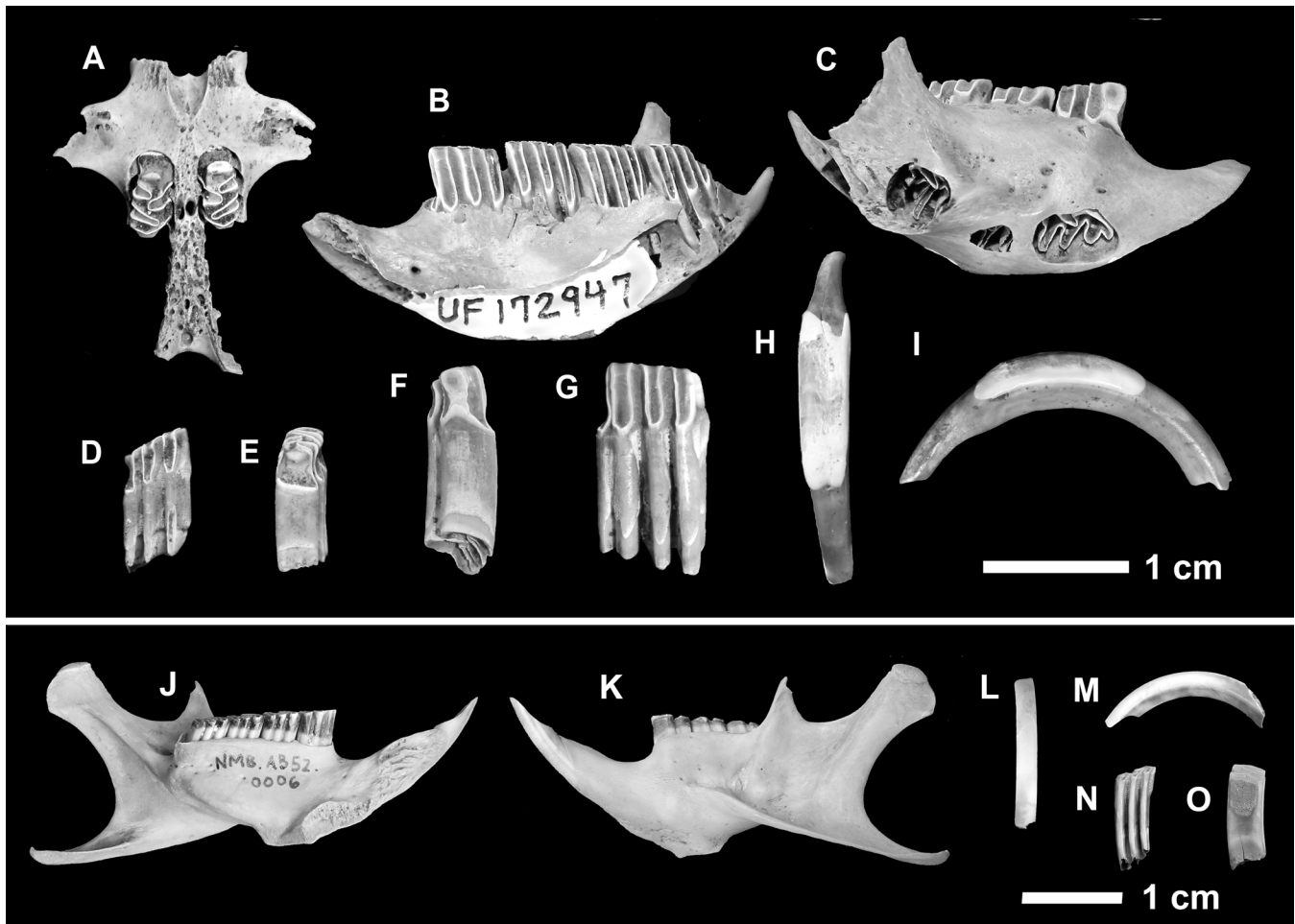
Figure 29. A–I, are from Queen Elizabeth II Botanic Park site on Grand Cayman. A, D, E, H, I are a maxilla with right and left P4 and associated I1 of the small capromyid rodent *Geocapromys* (UF 172949): A. maxilla with right and left P4 in occlusal view; right P4 in lateral (D) and anterior (E) views, and upper incisor in anterior (H) and lateral (I) views. B, C, F, G, right mandible with p4–m3 of the large capromyid *Capromys* (UF 172947): Right mandible in medial (B) and lateral (C) views and right p4 in anterior (F) and medial (G) views. Both of these specimens display a dissolution of enamel and dentine in the teeth, as well as loss of bone in the maxilla and lower jaw, that we interpret to result from digestion by a crocodylian. J, K are a left mandible with i1, p4–m3, in medial (J) and lateral views (K), of the capromyid *Geocapromys ingrahami* (NMB AB52.006) from Lost Reel Cave, Abaco. L–P are isolated teeth of *Geocapromys ingrahami* from Arieto Cave, Andros. Upper incisor in lateral (L) and anterior (M) views (NMB.AN03.001). Left m2 in medial (N) and anterior (O) views (NMB.AN03.002). The fossils of *Geocapromys* from Lost Reel Cave and Arieto Cave are typical specimens lacking any evidence of digestion.

hypsodont, ever-growing, rootless teeth, with more than half the length of each tooth contained in soft tissue below the gum line. The missing enamel, dentine, and cement on the teeth of these rodents appear to have been dissolved away, not removed by typical tooth wear. Also, the bone is unusually thin in the *Capromys* mandible and is completely missing ventral to all four teeth (Fig. 29C). A similar type of dissolution of enamel, dentine, cement, and bone has been observed in several horse mandibles with teeth from the Miocene of Florida, also attributed to predation and digestion by a crocodylian (R. Hulbert, pers. comm.). The tooth and bone dissolution in both the rodents from Grand Cayman and horses from Florida appears to have been caused by the extremely caustic digestive fluids of crocodylians. In a laboratory experiment in which alligators were fed mice and other small mammals, the teeth often survived the digestive process and were defecated, although the enamel of the teeth was usually decalcified (Fisher 1981). Moreover, portions of the teeth that were included within the jaw or skull or were in contact with other teeth suffered minimal or no decalcification of the enamel and other tooth materials (dentine, cement), just as we observed in the two jaws of hutias from the Queen Elizabeth II Botanic Garden site.

Crocodiles were the only large predators in Quaternary faunas in the Cayman Islands. Furthermore, large mammalian carnivores generally chew up the bones of their prey and the bones and teeth in their coprolites do not appear to be strongly etched or dissolved by stomach acids. We propose that the capromyid rodents on Grand Cayman were captured on land and consumed by crocodiles, presumably *Crocodylus rhombifer*, and that the partially digested palate and mandible were contained in feces/coprolites that disintegrated. We present a more detailed discussion below on the possible predation of capromyid rodents and other terrestrial vertebrates by Cuban crocodiles on Abaco, Grand Cayman, and Cuba.

DISCUSSION

Taphonomy and Paleoecology

The abundance of well-preserved crocodile fossils on Abaco and Grand Cayman provides important data on the taphonomy and paleoecology of the Cuban crocodile *Crocodylus rhombifer* on those islands. In simple terms, taphonomy is the study of the processes a living organism undergoes between its death and eventual preservation as a fossil. Taphonomy involves studying the interaction between the biota (i.e., fossils), sediments, and features such as location (e.g., terrestrial vs. aquatic) that lead to the eventual formation of a fossil site or assemblage. When we analyze the nature of the Late Quaternary fossil deposits on Abaco and Grand Cayman where *C. rhombifer* has been found in large numbers, one dominant taphonomic factor becomes immediately obvious– none of these sites occur in dry caves. Even though the vast majority of fossil deposits throughout the West Indies occur in dry or terrestrial caves (Morgan & Woods 1986), almost all of the crocodile fossils from Abaco and Grand Cayman have been found in sediments typical of freshwater or brackish-water depositional environments, including blue holes, mangrove swamps, and cow wells. The two richest deposits in Cuba for crocodile fossils are also non-cave sites, the Ciego Montero hot spring (Brown 1913) and the asphalt seep at Las Breas de San Felipe (Iturralde-Vinent et al. 2000). Crocodiles do not inhabit dry caves and their fossilized remains are only rarely preserved in this type of deposit, and then usually as isolated nondiagnostic elements such as teeth, vertebrae, and osteoderms. The type cranial material of *Crocodylus antillensis* from Cueva Lamas in western Cuba is a notable exception (Varona 1966). The vast majority of Quaternary vertebrates from the West Indies discovered prior to 1980 were derived from caves. As a result of this cave bias, crocodiles were rare in the West Indian fossil record before paleontologists began expanding their search parameters over the past 30 years to include underwater or wet sites and asphalt deposits, among other non-traditional (i.e., non-cave) sites. The large sample of crocodile fossils recovered from the Ciego Montero spring deposit in the early 1900s was an obvious exception. A minor, but significant, additional source of crocodile remains is from Amerindian

archaeological sites, especially in The Bahamas (Wing 1977; Keegan 1992; Carr et al. 2006).

The Late Quaternary crocodile sites on Abaco have been discovered in the past 20 years, and all but one, Dan's Cave, were found after 2004. With the exception of Gilpin Point, discovered in 2009, the crocodile-producing sites on Abaco consist of inland blue holes in which the fossils have been preserved underwater. In Sawmill Sink, the richest of these crocodile samples, the most productive sediments for fossils are dark organic peats that formed (and still occur) in a quiet-water depositional environment. The peat deposits and crocodile fossils in Sawmill Sink occur below both a halocline (i.e., denser saltwater below a layer of freshwater) and a hydrogen sulfide layer formed by the decomposition of the peat. These two factors have created anoxic conditions that resulted in the exceptional preservation of the peat, containing leaves with chlorophyll, seeds, and other unaltered macroplant fossils and insect remains, as well as a diverse sample of vertebrates (Steadman et al. 2007; Albury in prep.). Skeletons of crocodiles, land tortoises, and several birds from Sawmill Sink are so remarkably well preserved that the bone appears almost modern except for a light brown to dark brown staining from the dark brown to black organic material in the peat.

Most of the crocodile specimens from Sawmill Sink consist of complete skulls and still-attached mandibles, several of which have partial to nearly complete postcranial skeletons. Their incredible preservation suggests that after death the crocodile carcasses came to rest on the sediment cone of peat and were not disturbed by scavengers. The soft tissue decomposed and the skeletons were buried in the peat and preserved in place with little or no movement in the quiet water. The occlusion of the skull and lower jaws in most of the crocodile specimens has led to the preservation of the majority of the teeth. In life, the teeth are held in their sockets or alveoli by soft tissue; however, once the animal dies and begins to decompose, the teeth generally fall out unless they are held in place by the opposing skull or lower jaw. Surprisingly, the crocodile skulls from Sawmill Sink are better preserved than some modern skulls of crocodylians in herpetology collections, which in many cases lost their teeth before collection or in the preparation process (e.g., maceration).

Four other inland blue holes on Abaco, Dan's Cave, Lost Reel Cave, Nancy's Cave, and Ralph's Cave, have at least one partial to nearly complete associated or articulated skeleton, which also suggests quiet water conditions and lack of scavengers. The bones from these sites are not as well preserved as those from Sawmill Sink. Three skeletons of crocodiles from Dan's Cave were deposited in fine-grained silts not peat, and the bones are rather poorly preserved. The bones are very light in density compared to modern bone or crocodile bones from the peat deposit in Sawmill Sink, suggesting that removal of the mineral and/or organic content of the bones has occurred. Several crocodile fossils found much deeper in Dan's Cave in a micrite or fine-grained carbonate mud consist of much better-preserved, dense, mineralized bone than the previously collected specimens from this cave. We are uncertain why these crocodile bones occurred so far from the entrance to Dan's Cave (275 m from entrance), although it is possible that a closer entrance was present in the late Pleistocene but has since become blocked with rocks or sediment.

The fossil crocodile bones from Ralph's Cave, Lost Reel Cave, and Nancy's Cave were soft when collected, and became even softer when placed in a water bath after collection. After these fossils were fully prepared and dried, the bones became harder and could be handled without damage, but like most of the specimens from Dan's Cave, the bones are less dense than modern bone or crocodile bones from the peat deposit in Sawmill Sink. The fossils from Dan's Cave, Lost Reel Cave, Nancy's Cave, and Ralph's Cave are preserved in saltwater beneath a halocline, but unlike Sawmill Sink these four blue holes do not have a prominent hydrogen sulfide layer. Most of these sites have a talus cone of organic matter or peat that is much smaller than in Sawmill Sink, and the crocodile fossils are generally found in fine-grained sediments peripheral to the peat.

Outside of Abaco, Quaternary crocodile fossils are known from at least six other inland

blue holes in The Bahamas: Anaconda Pond and Mermaid's Lair on Grand Bahama, Kelly's Blue Hole, Mermaids Pool, and White Lake Cave on Eleuthera, and Rupert's Pond on Acklins. The crocodile fossils from White Lake Cave are heavily mineralized and a humerus has attached calcium carbonate shells of tube worms and bryozoans, both typical of marine conditions (Fig. 11C), although the marine invertebrates may have become attached to the bone at a later date. Other fossils from White Lake Cave belong to terrestrial species, including tortoise and hutia.

In addition to blue holes, several other types of Late Quaternary deposits in The Bahamas have produced crocodile fossils. A crocodile dentary from the Bell Channel site on Grand Bahama and a cranial roof and several other crocodile bones from the Gilpin Point site on Abaco were derived from organic peat deposits, probably in a mangrove swamp. These specimens are well preserved and unmineralized. The depositional environment of the Bell Channel and Gilpin Point sites was probably very similar to that of fossil crocodile samples from Grand Cayman (Morgan et al. 1993; Morgan 1994). Crocodylian bones have been reported from two dry caves in The Bahamas. A single partial vertebra of a juvenile crocodile was found in the Banana Hole on New Providence (Pregill 1982), which is a dry cave/sinkhole deposit with inorganic, orangish, lateritic sediments containing thousands of bones of terrestrial amphibians, reptiles, birds, and mammals (Olson 1982; Morgan 1989). A sinkhole on San Salvador called Hanna's Bananas contained a partial jugal and an osteoderm of a crocodile (Olson et al. 1990). Hanna's Bananas contained both black organic sediments and orangish inorganic sediments, although the authors did not specify in which of these two sediment types the crocodile fossils were found. Crocodiles are also known from archaeological sites on Crooked Island, Acklins, and Eleuthera (Keegan 1988, 1992; Franz et al. 1995; Carr et al. 2006). Presumably, crocodiles were captured and consumed by the Amerindian inhabitants of The Bahamas (Keegan 1992), and their remains (several teeth and a femur) were discarded in kitchen middens where they were excavated by archaeologists.

With the exception of a single tooth from Crab Cave, the remainder of the Quaternary crocodile sites on Grand Cayman, Chisholm Cow Well, Connally Cow Well, Crocodile Canal, Furtherland Farms Cow Well, Prospect, and Queen Elizabeth II Botanic Park site, occur in peat deposits. The paleobotany of these crocodile-bearing organic peat deposits has not been analyzed, but they probably formed through the deposition of organic matter in brackish-water habitats such as mangrove and associated swamp communities, which cover more than 50% of the area of Grand Cayman (Brunt and Burton 1994). Most of these sites are small sinkholes or depressions in limestone ("cow wells") or mangrove swamps located at very low elevation (less than 5 m above sea level), and are either totally submerged or are wet most of the year. The Chisholm Cow Well, Furtherland Farms, and Queen Elizabeth II Botanic Park sites consist of small water-filled sinkholes that are now mostly surrounded by dry land, but probably were more extensive swampland in the recent past before much of the land was drained for agriculture. The sinkholes are depressions or low areas that served as small depositional basins, trapping and preserving bones of crocodiles that inhabited the swamps. The crocodile fossils from the cow well and mangrove swamp sites are in excellent condition and unmineralized, like modern bone but stained a brown color from the dark organic sediments in which they were preserved.

Unlike the crocodiles from blue holes on Abaco, there appears to be little if any articulation or association of the crocodile bones in the Grand Cayman sites. However, the manner in which most of the sites were discovered and collected may have contributed to a loss of data pertaining to the original nature of the bone accumulations. Most of these sites were not carefully excavated by paleontologists, but instead the sediments containing the fossils were removed with hand tools by local farmers (e.g., Chisholm Cow Well, Furtherland Farms) or excavated by heavy equipment (Crocodile Canal, Queen Elizabeth

II Botanic Park). Paleontologists were alerted to the presence of bones only after the sites already had been excavated, and thus the bones were collected from spoil piles. Bones of crocodiles overwhelmingly dominate the faunas from the cow well (Chisholm Cow Well, Furtherland Farms, and Queen Elizabeth II Botanic Park) and mangrove (Crocodile Canal) sites on Grand Cayman. Other species of vertebrates in these sites of sufficient size to have been potential prey items for crocodiles include snakes, wading birds (heron, ibis, rail), and several terrestrial species, including a rock iguana and two species of capromyid rodents.

Although Cuban crocodiles today are limited to freshwater habitats in the Zapata Swamp in south-central Cuba and in the Lanier Swamp on Isla de la Juventud, historical records and Late Quaternary fossil deposits indicate that *Crocodylus rhombifer* was more widespread in Cuba before the arrival of humans. Presumably, they inhabited freshwater rivers, ponds, lakes, and swamps throughout much of the island. The large sample of crocodile fossils from Ciego Montero in southern Cuba was found in dark organic sediments deposited in a freshwater spring (Brown 1913). Fossils of small ground sloths, capromyid rodents, birds, freshwater turtles, and land tortoises, all potential prey items of *C. rhombifer*, were also found in the organic sediments at Ciego Montero (Brown 1913). The discovery of the fossils several meters underwater suggests that the bones have probably been submerged since their deposition, which contributed to their excellent preservation. Las Breas de San Felipe, an asphalt seep on the northern coast of Cuba, samples a diverse vertebrate fauna representing several different environments, including freshwater species such as crocodiles and turtles and terrestrial species such as ground sloths, capromyid rodents, and land birds (Iturralde-Vinent et al. 2000).

Fossil tortoise shells from Sawmill Sink, Dan's Cave, Nancy's Cave, and Ralph's Cave on Abaco, Kelly's Blue Hole on Eleuthera, and The Fountain blue hole on Mayaguana bear tooth-like scars that are thought to have been produced by bites from crocodiles (see discussion above, under "Ichnofossils"). The presence of bite wounds on about a third of tortoise specimens from The Bahamas indicates that crocodiles preyed upon living tortoises and/or scavenged dead tortoises with some regularity. The capromyid rodent *Geocapromys ingrahami* has been found in three of blue hole sites on Abaco, Lost Reel Cave, Nancy's Cave, and Sawmill Sink, although none of these specimens show evidence of predation. Evidence from Cuba and Grand Cayman (see below) strongly suggests that capromyid rodents are/were an important part of the diet of *Crocodylus rhombifer* on those islands. Since land tortoises and capromyid rodents rarely enter freshwater, we presume that the crocodiles who preyed upon them encountered these species in terrestrial habitats.

Several species of large birds, including both wading birds such as the white ibis (*Eudocimus albus*) and yellow-crowned night heron (*Nyctanassa violacea*) and land birds such as an extinct caracara (*Caracara creightoni*), were identified from fossils in the peat deposits in Sawmill Sink (Steadman et al. 2007), and may have been prey for *C. rhombifer*. Besides wading birds and crocodiles, other freshwater vertebrates are conspicuously absent in Quaternary blue hole sites on Abaco. Freshwater turtles and garfish are not found on Abaco now or in the fossil deposits, and other large fish are uncommon in inland blue holes. Additional evidence for the terrestrial feeding habits of *C. rhombifer* on Abaco comes from carbon isotopes (^{13}C/^{12}C) of the dated crocodile bones from Sawmill Sink. ^{13}C/^{12}C ratios in the range of -16 to -20 suggest that Cuban crocodiles preyed primarily on terrestrial vertebrates, such as tortoises and hutias (Steadman et al. 2007).

The prey base for Cuban crocodiles on Grand Cayman during the Quaternary was somewhat more limited because land tortoises are unknown from the Cayman Islands. Two large capromyid rodents (*Capromys* and *Geocapromys*) were present in the same fossil deposits with *Crocodylus rhombifer*. As described above under "Ichnofossils," two capromyid rodent jaws from the Queen Elizabeth II Botanic Garden site on Grand Cayman, one each of *Capromys* and *Geocapromys*, show clear evidence of having been digested by a crocodile, presumably

C. rhombifer. The presence of an extinct species of *Capromys* on Grand Cayman is particularly significant because a closely related living species, *C. pilorides*, has been shown to constitute an important component of the diet of modern Cuban crocodiles in Cuba (see below). The other large land vertebrate found in most of the Grand Cayman crocodile sites is the rock iguana *Cyclura*. Exclusive of crocodiles, freshwater and brackish-water species are uncommon in the Quaternary cow well and mangrove sites on Grand Cayman, consisting of wading birds (rail, ibis, and heron) and a water snake. Turtles and fish are unknown from these deposits.

Field and behavioral observations in Cuba indicate that *Crocodylus rhombifer* is more terrestrial than most other species of crocodylians and will often capture terrestrial prey, in particular the large hutia *Capromys pilorides*. Although this species of hutia does occasionally come to the ground, it is primarily arboreal, and field observations suggest that Cuban crocodiles will jump from the water or the ground and catch hutias sitting on low branches in trees (John Thorbjarnarson pers. comm.). Varona (1986) commented on the Cuban crocodile's exceptional abilities of terrestrial locomotion, including walking, running, and jumping. The following are field observations on the terrestrial behavior of the Cuban crocodile from Roberto Soberón (pers. comm.). "I remember several occasions when I witnessed Cuban crocodiles walking away from the water through very rough terrain. In 1990, I was visiting Cayo Potrero Crocodile Farm, which is located in the middle of the Lanier Swamp on Isla de la Juventud. A truck driver brought a roadkill Cuban crocodile to the farm; it was an adult female of about 2 m of total length. She had escaped from the farm, as evidenced by the mark on her tail (a numeral pattern of cut tail scutes). He killed the animal when it was crossing the road, close to the meteorological radar and field station at Punta del Este, more than 18 km in a straight line from the farm, across dry, rocky ("dogtooth limestone") and densely vegetated shrub land. In October 1996, Perran Ross, Bill McMahan, and I witnessed an adult female Cuban

crocodile in the Lanier Swamp that followed us for more than 2 kilometers, across the same rough terrain." The following is a quotation from Soberón et al. (2000) regarding the terrestrial habits and feeding behavior of *Crocodylus rhombifer*. "This is a species with comparatively more terrestrial habits than other crocodiles, capable of walking long distances across dry and stony terrain, getting advantage of trophic and thermoregulatory niches such as isolated water holes ("casimbas and cenotes"), characteristic of the Zapata and Lanier Swamps. The crocodiles have the ability to secure their food from terrestrial and arboreal mammals such as the primarily arboreal hutias (*Capromys* sp.), using a hunting technique based on jumping. Adaptive traits characteristic of this life style are the powerful dermal armor, robust extremities, notable reduction of the interdigital membrane in the feet and its total absence in the hands, the massive shape of skull and mandible, with strong masticatory muscles, and a considerably reduced and specialized dentition."

In a paper on the natural history of *Crocodylus rhombifer*, De Sola (1930) mentioned that in dissecting the intestinal tract of several Cuban crocodiles he identified incisor teeth and claws of *Capromys pilorides*, as well as jaws of the Cuban gar or manjuari *Atractosteus tristoechus*. These observations suggest that Cuban crocodiles hunt for prey in both freshwater environments where gar occur and terrestrial habitats where hutias live. In a study of stomach contents of Cuban crocodiles, Soberón et al. (2001:13) determined that "Hutias were clearly the most important prey by mass, accounting for over 90% of the total recovered stomach contents. Hutias were the only mammals seen in the swamp and seem to play an important role in the diet of the crocodiles." Barbour and Ramsden (1919:210) noted that ground sloth bones from the Quaternary spring deposit at Ciego Montero "…were often pitted with crocodile tooth marks."

The lack of mammalian carnivores from modern and Quaternary faunas in Cuba and throughout the West Indies (Morgan & Woods 1986) may have been a factor in the development

of terrestrial behavior of Cuban crocodiles. Large terrestrial predators now found in Cuba include the Cuban crocodile and the large boa *Epicrates striatus*. Cuban Quaternary faunas document the presence of the extinct meter-tall, flightless barn owl *Ornimegalonyx* and several species of extinct eagle-sized raptors. The modern nonvolant (i.e., not including bats) mammalian fauna of Cuba consists of about four species of capromyid rodents and the large primitive lipotyphlan ("insectivore") *Solenodon cubanus*. During the late Pleistocene, Cuba supported a much more diverse fauna of mammals that would have provided a larger prey base for Cuban crocodiles, including five species of small ground sloths (family Megalonychidae), a monkey (*Paralouatta*), several additional capromyid rodents, echimyid rodents, and a large extinct species of solenodon (*Solendon arredondoi*), as well as the large extinct land tortoise *Chelonoidis cubensis*.

BIOGEOGRAPHY

The presence of the Cuban crocodile *Crocodylus rhombifer* in fossil deposits on Abaco and Grand Cayman, two islands where crocodiles no longer occur, has been perhaps the single most intriguing factor relating to our study of these fossils. When GSM first examined a large series of crocodylian bones discovered by Edward Materne and Robert Materne in 1979 in a mangrove swamp at the western end of Grand Cayman, uncovered during the excavation of a mosquito-control canal, he assumed the fossils belonged to the American crocodile *Crocodylus acutus*, the most widespread and common crocodile in the West Indies at the present time. Surprisingly, a skull from the Crocodile Canal site and all identifiable crocodylian fossils found subsequently on both Grand Cayman and Abaco pertain instead to the Cuban crocodile, *C. rhombifer*, a much rarer species restricted to freshwater swamps in Cuba. Although *C. rhombifer* was more widespread in Cuba during the Pleistocene (Varona 1966, 1984), there was no evidence prior to the Grand Cayman discovery that Cuban crocodiles ever occurred outside of Cuba. The fossil record confirms that *C. rhombifer* was considerably more widespread in the West

Indies during the late Pleistocene and Holocene, with identifiable cranial material from Abaco and Grand Bahama in the northern Bahamas and Grand Cayman, as well as crocodile fossils from six other islands in The Bahamas that probably pertain to this species.

The fossil and archaeological record suggests that crocodiles were essentially ubiquitous throughout The Bahamas before the arrival of Amerindians about 1,200 years ago. Crocodiles have been identified from most of the larger banks and several smaller banks/islands in The Bahamas, including the Little Bahama Bank (Abaco and Grand Bahama), Great Bahama Bank (Eleuthera and New Providence), Crooked-Acklins Bank (Crooked Island and Acklins), San Salvador, and Mayaguana. These records encompass almost the entire geographic extent of The Bahamas, including the northernmost islands (Abaco and Grand Bahama, 27° North latitude) and several of the southern islands (Crooked Island, Acklins, Mayaguana, all between 22 and 23° N), and from the westernmost island (Grand Bahama, 79° West longitude) to the easternmost island (Mayaguana, 73° W). The current lack of a fossil record of crocodiles from the remainder of the larger islands in The Bahamas (e.g., Andros, Great Exuma, Cat Island, Long Island, Great Inagua), as well as the Turks and Caicos Islands at the southeastern end of the Bahamas archipelago, almost certainly represents a collecting bias. Ironically, several of the best-documented historical records of crocodiles in The Bahamas are from Andros and Great Inagua (Catesby 1771; Gardiner 1886; Campbell 1978). Among the islands in The Bahamas where fossil crocodiles are currently unknown, only on Andros have cave divers explored inland blue holes for fossils. Three blue holes on Andros have been surveyed for fossils, including Arieto Cave which contains abundant remains of *Geocapromys ingrahami* that appear to have accumulated under terrestrial conditions when sea levels were much lower in the late Pleistocene. The discovery of crocodile fossils over the past decade in inland blue holes on Abaco, Grand Bahama, Eleuthera, Acklins, and Mayaguana strongly suggests that crocodiles

will eventually be discovered in this same type of fossil deposit elsewhere in The Bahamas.

The former occurrence of the Cuban crocodile in the Cayman Islands appears to be limited to Grand Cayman. No crocodile fossils are yet known from Cayman Brac or Little Cayman. The fossil record appears to reflect the historical record in which crocodiles were reported only from Grand Cayman (Keeler 1981). Compared to Grand Cayman, mangrove swamp habitats are more limited in extent on Little Cayman and especially on Cayman Brac (Brunt & Burton 1994). Descriptions of crocodiles from Grand Cayman in the early historical chronicles are not detailed enough to permit a positive identification, although we presume from the fossil record that they were *Crocodylus rhombifer*. It is worth noting that crocodiles encountered in the Cayman Islands over the past 70 years have been identified as the American crocodile *C. acutus*, including a specimen collected on Little Cayman in 1939 (Grant 1940) and two specimens captured on Grand Cayman in 2007 and 2009.

The following discussion presumes that Cuban crocodiles originated in Cuba and later dispersed overwater to The Bahamas and Cayman Islands. As noted above, crocodile fossils are widespread throughout The Bahamas, occurring over a distance of about 700 km from Abaco and Grand Bahama at the northwestern end of the Bahamas archipelago to Mayaguana in the southeastern Bahamas. Only fossil samples from blue holes on Abaco and Grand Bahama can be positively identified as *Crocodylus rhombifer*, although we strongly suspect that most, if not all, other crocodile records from The Bahamas pertain to this species. Abaco is located slightly more than 400 km north of the Cuban mainland, the closest place where *C. rhombifer* occurs today. Cuban crocodiles probably dispersed from Cuba to The Bahamas during a Quaternary glacial interval when sea levels were much lower and the overwater distances were greatly reduced. During the last glacial maximum between 15 and 20 ka, when sea levels were as much as 120 m lower than present, many of the smaller islands in The Bahamas were joined together into two very

large islands, one conforming to the Little Bahama Bank and incorporating the islands of Abaco and Grand Bahama, as well as many smaller islands and cays, and a second island conforming to the Great Bahama Bank and incorporating Andros, Cat Island, Eleuthera, Great Exuma, Long Island, New Providence, and numerous smaller islands and cays (Morgan 1989). At this time, the northern coast of Cuba and the southern edge of the Great Bahama Bank were separated by as little as 20 km across the Old Bahama Channel, which is from 200 to 1,000 m deep. Although *C. rhombifer* is currently restricted to freshwater habitats in Cuba, the presence of Cuban crocodiles in The Bahamas indicates that this species must have been able to tolerate saltwater long enough to cross the Old Bahama Channel, a trip that would have taken only a few days. The Great Bahama Bank is now mostly submerged, but probably was a vast area of low elevation supporting extensive swamp habitats during glacial intervals, especially south and west of Andros. Crocodiles dispersing through freshwater swamps and rivers on the exposed Great Bahama Bank could have gotten within 50 km of Abaco in what is now the Berry Islands north of Andros, and at the north end of Eleuthera. The Great Bahama Bank and Little Bahama Bank are separated by the narrow (about 50 km wide) but deep (over 1,000 m) Providence Channel. The rest of the banks (Crooked-Acklins Bank, Caicos Bank) and larger islands (San Salvador, Rum Cay, Mayaguana, Great Inagua) in the Bahamas archipelago are currently separated by fairly deep (over 200 m and thus submerged during glacial intervals) but narrow (mostly less than 50 km) water gaps that apparently did not prevent the dispersal of crocodiles through most of the island archipelago.

For *Crocodylus rhombifer* to reach Grand Cayman involved an open ocean journey of some 250 to 300 km. At the present time, Isla de la Juventud off the southwestern coast of Cuba, located 275 km northwest of Grand Cayman, is the closest island that supports a population of *C. rhombifer*. The least distance between Grand Cayman and the Cuban mainland occurred in the late Pleistocene during the last glacial maximum,

when the shallow Gulf of Batobanó south of the Zapata Peninsula and Zapata Swamp would have been exposed as dry land to the edge of the Cuban "continental" shelf, 250 km due north of Grand Cayman. The overwater distance between Cuba and Grand Cayman was never less than 250 km, as profound depths of over 4,000 m in the Yucatan basin in the northwestern Caribbean Sea have separated these two islands throughout the Late Cenozoic (Jones 1994). Cuban crocodiles must be able to tolerate long exposure to saltwater and open marine conditions based on their dispersal from Cuba across the Caribbean Sea to Grand Cayman. Studies of living estuarine crocodiles (*Crocodylus porosus*) suggest they can swim 20–25 km/day under ideal circumstances (Campbell et al. 2010). Even under the most favorable conditions of weather and currents, it would take a crocodile, possibly a gravid female, ten days to two weeks to make the 250 km crossing. We know that individuals of *C. acutus* have made the oceanic journey to Grand Cayman and Little Cayman several times over the past century, including twice during the past ten years. The origin of these animals is unknown since this species is widespread in the West Indies and Central America. Cuba supports a population of *C. acutus* but this species also occurs in Jamaica, located 225 km southeast of Little Cayman and 325 km southeast of Grand Cayman, and on the Caribbean coast of Central America about 500 km southwest of Grand Cayman.

Unlike the islands in the Bahamas archipelago, the Cayman Islands are not located on extensive shallow carbonate banks, but are the peaks of steep-sided submarine mountains surrounded by deep water. Thus, their land area would not have increased greatly during Ice Age glacial periods (Morgan 1994). Furthermore, during the low sea level stand of the last glacial maximum, most of Grand Cayman would have been 50–100 m above sea level thereby limiting the extent of mangrove and other swamp habitats that crocodiles prefer. This suggests that the dispersal of *Crocodylus rhombifer* from Cuba to Grand Cayman may have occurred during the higher (= modern) sea levels of the Holocene (i.e., the last 7,000 years). All dated

fossils of Cuban crocodiles from Grand Cayman are late Holocene in age (see below and Table 8), supporting their possible late arrival on that island.

During the Quaternary, *Crocodylus rhombifer* may have occurred in freshwater habitats on other islands in the West Indies besides Cuba, The Bahamas, and Grand Cayman. Quaternary crocodile fossils from Jamaica and Puerto Rico are not diagnostic enough to allow identification to the species level. Crocodile fossils, including several skulls, have recently been discovered by divers in underwater caves in the Dominican Republic (Pickel & Bowen 2009; Velazco et al. 2013; Rimoli et al. in prep.). Distances between the major islands in the Greater Antilles are less than 150 km (Cuba to Hispaniola–80 km; Cuba to Jamaica–140 km; Hispaniola to Puerto Rico–110 km), considerably less than the distance between Cuba and Grand Cayman (250 km) which is known to have been traversed by *C. rhombifer* at some point in the Quaternary. Thus, the fossil occurrence of *C. rhombifer* in freshwater depositional environments on other islands in the West Indies is certainly a possibility. Several fossil skulls and skeletons of crocodiles, probably Morelet's crocodile (*Crocodylus moreletii*), have been discovered recently by cave divers in cenotes (similar to Bahamian blue holes) in the Yucatan peninsula of Mexico (T. Iliffe pers. comm., with photographic documentation). The discovery over the past decade of *Crocodylus* fossils in submerged caves (blue holes and cenotes) in The Bahamas and Mexico strongly suggests that underwater caves elsewhere in the West Indies and Caribbean area will eventually produce additional crocodile fossils.

Based on current paleontological data, the most likely scenario for the Quaternary history of crocodiles in the West Indies places the origin of *Crocodylus rhombifer* in Cuba with later dispersal to The Bahamas, Grand Cayman, and possibly elsewhere in the Greater Antilles. Future fossil discoveries may alter this hypothesis. Our fossil evidence from Abaco and Grand Cayman clearly demonstrates that *C. rhombifer* was more widespread in the West Indies during the late

Pleistocene and Holocene. The argument could be made that this species might be more accurately called the West Indian crocodile, particularly if fossils of *C. rhombifer* are found on other islands in the Greater Antilles outside of Cuba. The lack of a fossil record of *C. acutus* from the West Indies and Florida suggests that this species may have evolved in the southern Caribbean along the coasts of Central America and northern South America, and only recently invaded the Antilles and southern Florida, possibly in the late Pleistocene or Holocene.

Molecular data from *Crocodylus rhombifer* in Cuba and from *C. acutus* populations in Cuba, elsewhere in the West Indies, and Central America provide very interesting results (Milián-García et al. 2011). The molecular data indicate that *C. acutus* populations from Cuba and Central America are very distinct, and that Cuban *C. acutus* is more similar genetically to *C. rhombifer*, even though the mainland and Cuban *C. acutus* populations are very similar morphologically and are considered the same biological species. Milián-García et al. (2011) proposed that the ancestor of *C. rhombifer* arrived in Cuba during the early Pleistocene (about 2.5 Ma) through marine dispersal from Central America. The exceptional preservation of *C. rhombifer* fossils from the peat deposit in Sawmill Sink on Abaco suggests that these specimens might be suitable for ancient DNA analysis, thereby providing complementary molecular data for comparison with the genetics of living *Crocodylus* from Cuba and the Caribbean area.

Chronology and Extinction

Four AMS radiocarbon (^{14}C) dates were obtained directly from bones of *Crocodylus rhombifer*, from Dan's Cave (Franz et al. 1995) and Sawmill Sink (Steadman et al. 2007) on Abaco. These dates are presented in Table 8, together with conventional radiocarbon dates associated with crocodile fossils from New Providence and Grand Cayman. The three ^{14}C dates from Sawmill Sink range from 2,900–3,680 years BP (measured ^{14}C age). They are AMS dates obtained from bone collagen derived from *C. rhombifer* postcranial elements (humerus, radius, femur, vertebra) collected from the peat deposit (Steadman et al.

2007). Bone collagen from a *C. rhombifer* skeleton discovered in Dan's Cave yielded a ^{14}C date of 2,780 yr BP (Franz et al. 1995). An attempt to date two additional crocodile bones from Sawmill Sink was unsuccessful owing to the lack of datable collagen (Steadman et al. 2007). The inability to date one of these specimens (NMB.AB50.026; C21) is significant because it was recovered from considerably deeper in the cave than the dated crocodiles from the peat deposit and consists of denser bone that appears to be mineralized. The lack of collagen in this specimen is probably a result of its greater age, likely dating to the late Pleistocene. The oldest crocodile fossil from The Bahamas with an associated radiocarbon date is a vertebra from the Banana Hole site on New Providence. The crocodile vertebra was found in association with a large sample of fossils of *Geocapromys ingrahami*. Bone collagen from limb bones of *Geocapromys* from Banana Hole yielded a conventional radiocarbon date of 7,980 yr BP (Morgan 1989). The fossil deposit in Banana Hole yielded bones with a consistent preservation from a rather restricted layer (about 20 cm thick), suggesting a similar early Holocene age for the crocodile fossil. Although we currently have no pre-Holocene dates on crocodiles in The Bahamas, highly mineralized crocodile bones from at least three Bahamian blue holes, Sawmill Sink and Dan's Cave on Abaco and White Lake Cave on Eleuthera, are strongly indicative of a late Pleistocene age.

The youngest radiocarbon-dated bone of *Crocodylus rhombifer* from The Bahamas (2,780 yr BP), from Dan's Cave on Abaco, is about 2,000 years older than a human tibia from Sawmill Sink with an AMS radiocarbon date of 870 yr BP (Steadman et al. 2007). The occurrence of crocodylian remains in undated archaeological sites on Crooked Island, Acklins, and Eleuthera establishes the survival of crocodiles in The Bahamas until between about 1,200 and 500 years ago, based on the time period of Lucayan occupation of the Bahamas archipelago (Keegan 1988, 1992; Carr et al. 2006). Neither archaeological specimens nor historical records of crocodiles in The Bahamas between the late 1400s (Dunn and Kelley 1989) and the late 1800s

Table 8. Radiocarbon (^{14}C) dates associated with crocodiles (*Crocodylus rhombifer*) from The Bahamas and Cayman Islands. The dates from Abaco were obtained using the AMS (Accelerator Mass Spectrometry) method and were taken directly on bones of crocodiles. The dates from Banana Hole on New Providence and Crocodile Canal on Grand Cayman used the conventional radiometric method and were taken on associated organic materials, not directly on crocodile bones. Radiocarbon (^{14}C) ages are reported as Measured Ages in years before present (yr BP) and in Calendar Years BP, with two standard deviations. Beta stands for the Beta Analytic, Inc. radiocarbon dating laboratory in Miami, Florida; SI stands for the Smithsonian Institution radiocarbon dating laboratory in Washington, DC, which is no longer in existence.

Island and Site	Lab number	Material dated & method	Specimen, element, & catalogue #	Sediment type	Measured ^{14}C age (yr BP)	^{14}C age (Cal BP, 2σ)	^{13}C/^{12}C ratio	Reference
Abaco								
Dan's Cave	Beta 71576	bone collagen AMS	crocodile vertebra NMB.AB53	silt	2,780 ± 60	—	—	Franz et al. (1995)
Sawmill Sink	Beta 230221	bone collagen AMS	crocodile humerus NMB.AB50.696	peat	2,900 ± 50	3,340-3,000	-19.3	Steadman et al. (2007)
	Beta 230222	bone collagen AMS	crocodile femur NMB.AB50.364	peat	3,680 ± 50	4,410–4,080	-16.4	Steadman et al. (2007)
	Beta 230223	bone collagen AMS	crocodile vertebra NMB.AB50.019	peat	3,680 ± 50	4,340 4,290–4,060 4,050–3,990	-19.0	Steadman et al. (2007)
New Providence								
Banana Hole	Beta 24481	bone collagen Conventional	*Geocapromys* limb bones	terrestrial cave sediment	7,980 ± 230	—	—	Morgan (1989)
Grand Cayman								
Crocodile Canal	SI 5068	peat Conventional	contained crocodile tooth & osteoderm	peat	860 ± 50	—	—	Morgan et al. (1993)
Crocodile Canal	SI 5069	peat Conventional	associated w/ numerous crocodile bones	peat	375 ± 60	—	—	Morgan et al. (1993)

(Gardiner 1886) include material that can be identified as either *C. rhombifer* or *C. acutus*.

No fossil crocodiles from Grand Cayman have been directly radiocarbon dated. An in-place chunk of peat containing a crocodile tooth and an osteoderm from the mangrove peat deposit in the Crocodile Canal site was radiocarbon dated at 860 yr BP and a second in-place peat sample containing a bone of an extinct hutia was ^{14}C dated at 375 yr BP (Table 8; Morgan et al. 1993). Organic sediments from the Furtherland Farms Cow Well that produced abundant *C. rhombifer* fossils also contained several jaws of the introduced Old World rat *Rattus rattus*, indicating a post-Columbian age (i.e., younger than 1503, the earliest date of European contact in the Cayman Islands). The only crocodile specimen from Grand Cayman that appears to be mineralized, and thus presumably of somewhat greater age than the crocodile fossils from the cow well and mangrove peat deposits, is a tooth from Crab Cave (Morgan & Patton 1979). Crab Cave also contains well-mineralized fossils of extinct species of the rodents *Capromys* and *Geocapromys*, both of which also occur in association with crocodiles in the cow well and mangrove swamp sites. Based on an historic period radiocarbon date (375 yr BP or about 1600 AD) from a site on Grand Cayman containing crocodiles and the association of crocodiles with an introduced European rat in a second site on Grand Cayman, we can be fairly certain that *C. rhombifer* survived there until at least 400 years ago. Historical records confirm the presence of crocodiles on Grand Cayman between 1586, during a visit there by Sir Francis Drake (Keeler 1981), and the late 18th century (Long 1774).

Widespread extinctions of large mammals and other large vertebrates in the late Pleistocene and Holocene have long been a subject of great interest to Quaternary vertebrate paleontologists. Although the extinctions of numerous large mammals, the so-called megafauna, at the end of the Pleistocene in continental North America and South America are better known (Koch & Barnosky 2006), extensive Late Quaternary extinctions of mammals and birds in the West Indies are also well documented (Morgan & Woods 1986; Steadman et

al. 2005; MacPhee 2009). The major differences between Late Quaternary extinctions in the West Indies and those on the mainland include the timing and the taxonomic composition and average body size of the species that went extinct. On the mainland, the extinctions took place very rapidly at the end of the Pleistocene (between 13,000 and 11,000 yr BP) and mostly involved large mammals. The West Indian extinctions occurred over a longer period of time, primarily in the late Holocene between about 5,000 years BP and the colonial or post-Columbian era beginning about 500 years ago, and affected a wider range of vertebrate groups, including small to medium-sized mammals, birds, and larger reptiles, especially land tortoises, rock iguanas, and crocodiles. The difference in the timing of extinctions between the West Indies and the mainland of North America and South America is almost certainly related to the cause(s) of those extinctions. The latest Pleistocene was a time of extreme climate change from cooler glacial conditions to warmer interglacial environments in the early Holocene. The megafaunal extinctions in North America and South America occurred during the period of major climatic change in the latest Pleistocene, which also corresponds with the first arrival of Paleoindians in the New World across the Bering landbridge from Eurasia. The coincidence of climate change and the arrival of humans has led to the major debate focusing on which one of these two events caused the extinction of the megafauna (Koch & Barnosky 2006).

The major extinction event in the West Indies did not coincide with a period of significant climate change, but instead occurred in the late Holocene when the climate was fairly stable and similar to modern conditions (Pregill & Olson 1981). The West Indian extinctions do appear to coincide with the arrival of Amerindian people in that island group, beginning about 5,000 years ago (Rouse 1989; MacPhee 2009). This evidence has led most West Indian paleontologists to single out humans as the cause for those extinctions (e.g., Morgan & Woods 1986; Steadman et al. 2005; MacPhee 2009). The human colonization of the West Indies occurred over a rather extended period of time, with various islands in the West

Indian archipelago being colonized by Amerindian peoples (Carib, Gaunahatabey, Lucaya, Taino) over a period of some 4,000 years in the late Holocene (Rouse 1989; Keegan 1992). The Gaunahatabeys may have arrived in western Cuba from Central America as early as 5,000 years ago, whereas the Lucayans did not reach the Bahamas until 1,200 years ago. Likewise, the vertebrate extinctions on various islands in the West Indies appear to have occurred on a rather protracted time scale of several thousand years or more, probably corresponding to the timing of the first arrival of Amerindians on a particular island. 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 Amerindian 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, after 5,000 yr BP, and continued to go extinct throughout the remainder of the Amerindian period and well into the era of European colonization (after 1492). 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 Bahamas and Cayman Islands provide intriguing test cases for the timing and possible causes of West Indian extinctions because of their differing patterns of human colonization. Both of these island groups were colonized by humans later in the Holocene than the four major islands of the Greater Antilles, and much later than the continental mainland of North America and South America. The Amerindian people who inhabited The Bahamas when Columbus first landed there in 1492 were the Lucayans, who arrived in The Bahamas about 1,200 years ago (about A.D. 800), from either Cuba or Hispaniola or both, and disappeared barely 700 years later in the early 1500s (Keegan 1992). With the exception of a crocodile from an archaeological site on the south coast of Jamaica (Wing 1977), The Bahamas are the only other islands in the West Indies where crocodiles have been found in

Amerindian archaeological sites (Wing & Reitz 1982). Although the three archaeological sites in The Bahamas containing crocodile remains have not been radiocarbon dated, these sites establish the presence of crocodiles on Crooked Island, Acklins, and Eleuthera sometime between 1,200 and 500 years BP (Keegan 1988, 1992; Carr et al. 2006). After the disappearance of the Lucayans in the early 1500s, crocodiles survived in The Bahamas for another 400 years. There are several records of crocodiles (almost certainly either *Crocodylus acutus* or *C. rhombifer*) from historical chronicles dating between 1492 and 1886 (Catesby 1771; McKinnen 1804; Gardiner 1886; Dunn & Kelley 1989; Campbell 1986). Crocodiles went extinct in The Bahamas in the late 19th century, almost certainly as a result of human hunting, first by the Lucayans and later by Europeans.

There is no archaeological evidence that Amerindians inhabited the Cayman Islands (Stokes & Keegan 1996). The first European visitor to the Cayman Islands was Columbus in 1503. The earliest mention of crocodiles was later in the 16th century during Sir Francis Drake's visit to Grand Cayman in 1586. There are at least three places in Drake's journals recounting his visit to Grand Cayman where it is stated that the crew members killed and/or ate crocodiles (Keeler 1981). Between the time of the first permanent settlements on Grand Cayman in the mid 17th century (Williams 1970) and the late 19th century when the first herpetological expeditions to the Cayman Islands were undertaken (Garman 1887), crocodiles disappeared from Grand Cayman. The local extinction of Cuban crocodiles on Grand Cayman almost certainly resulted from overhunting.

CONCLUSIONS

Late Quaternary deposits from five underwater caves or inland blue holes on Abaco in the northern Bahamas (Sawmill Sink, Dan's Cave, Nancy's Cave, Ralph's Cave, and Lost Reel Cave) contain skulls, mandibles, and skeletons of the Cuban crocodile *Crocodylus rhombifer*. Sawmill Sink has the richest Quaternary fauna among the Abaco blue holes, including at least 54 individuals of *C. rhombifer*. Eleven complete skulls of Cuban

crocodiles have been collected from this site, most with associated mandibles and several with postcranial skeletons. Sawmill Sink also contains well-preserved fossils of the extinct land tortoise *Chelonoidis alburyorum*, several birds, insects, and leaves from a late Holocene peat deposit and hundreds of bird bones and other small vertebrates from a late Pleistocene owl roost deposit. Crocodiles are known from Late Quaternary sites on seven other islands in The Bahamas, including a peat deposit and two blue holes on Grand Bahama, three blue holes and an archaeological site on Eleuthera, dry caves/sinkholes on New Providence and San Salvador, an archaeological site on Crooked Island, a blue hole and an archaeological site on Acklins, and a blue hole on Mayaguana. Skulls from the five blue holes on Abaco and cranial fragments from Gilpin Point on Abaco and Mermaid's Lair on Grand Bahama are complete enough to confirm their identification as *C. rhombifer*. None of the other Bahamian crocodile fossils can to be identified beyond the genus level (*Crocodylus*). Partial to nearly complete crocodile skulls of *C. rhombifer* are also known from six Late Quaternary fossil sites on Grand Cayman, including two mangrove peat deposits (Crocodile Canal and Prospect) and four peat deposits in limestone depressions or "cow wells" (Chisholm Cow Well, Connally Cow Well, Furtherland Farms Cow Well, Queen Elizabeth II Botanic Garden).

There are no significant morphological differences between samples of Late Quaternary crocodiles from Abaco and Grand Cayman. Crocodile skulls and mandibles from these two islands share the following diagnostic cranial and mandibular characters with modern skulls and jaws of *Crocodylus rhombifer* from Cuba: short, broad, and deep rostrum; prominent orbit; concave interorbital region and cranial roof; strong ridges on the internal margin of the orbit and lateral margin of the cranial table; large, rounded protuberance on the posterolateral corner of the squamosal; premaxillary-maxillary suture on the palate transverse at the level of the first maxillary tooth; 13 teeth in the maxilla; and three largest teeth in the dentary are in order of size, fourth, first, and tenth. Most of these cranial characters differ

significantly from those of the two other extant species of West Indian crocodiles, *C. acutus* and *C. moreletii*. The ilium of *C. rhombifer* from Cuba and fossil ilia from Abaco and Grand Cayman have a weak indentation along the dorsal edge near the posterior tip. Other species of *Crocodylus* have a deep constriction in the posterior blade of the ilium. Crocodylian ichnofossils are common in the blue holes on Abaco, including abundant coprolites, especially from Lost Reel Cave, and several land tortoise shells with crocodile bite marks from the peat deposit in Sawmill Sink. Intraspecific variation in the Late Quaternary populations of *C. rhombifer* from Abaco and Grand Cayman is mostly limited to size differences. Skulls of *C. rhombifer* from Abaco range from 243–361 mm in length (mean of 286 mm; 12 individuals); the Grand Cayman skulls are slightly smaller on average, ranging from 247–305 mm in length (mean of 265 mm; 4 individuals). Incomplete skulls from both Abaco and Grand Cayman confirm that even larger individuals of Cuban crocodiles were present in those populations. Both modern and Late Quaternary skulls of *C. rhombifer* from Cuba are considerably larger. The largest modern skull from Cuba is 475 mm in length; fossil skulls with lengths of 653 and 503 mm are known from the Ciego Montero spring deposit. Based on a ratio derived from living crocodylians of head length (premaxilla to parietal) to total length of about 1:7.2, predicted total lengths of Late Quaternary individuals of Cuban crocodiles from Abaco range from 1.3–2.3 m (mean 1.9 m) and Grand Cayman from 1.6–2.0 m (mean 1.7 m). The largest fossil skull of *C. rhombifer* from Ciego Montero yields a predicted total length for this individual of nearly 4 m. The smaller size of crocodiles from Abaco and Grand Cayman compared to the Cuban animals may be related to smaller island size.

All Late Quaternary sites on Abaco and Grand Cayman with abundant fossils of Cuban crocodiles represent freshwater or brackish-water depositional environments, including blue holes, mangrove swamps, and peat-filled limestone depressions. The exceptional preservation of crocodiles and other fossils from a late Holocene peat deposit in the Sawmill Sink blue hole on

Abaco can be attributed to deposition under anoxic conditions below both a halocline and a hydrogen sulfide layer derived from the decomposition of the peat. Large freshwater vertebrates (large fish, turtles, etc.) are rare to absent in Abaco and Grand Cayman suggesting that, despite an aquatic depositional environment, Cuban crocodiles on those islands had a diet consisting primarily of terrestrial vertebrates, including land tortoises (absent on Grand Cayman) and capromyid rodents. Predation on terrestrial animals by Cuban crocodiles is supported by several land tortoise (*Chelonoidis*) shells from Abaco and one from Mayaguana that have crocodylian bite marks, jaws of capromyid rodents from Grand Cayman apparently digested by a crocodylian, and *Crocodylus rhombifer* bones from Sawmill Sink with carbon isotope ratios ($^{13}C/^{12}C$) indicative of a terrestrial diet.

Crocodylus rhombifer was considerably more widespread during the Late Quaternary, including a number of sites in western and central Cuba outside the current range of the Cuban crocodile on that island, as well as records from Abaco, Grand Bahama, and Grand Cayman. Crocodile fossils from six other islands in The Bahamas probably also pertain to this species. Holocene AMS radiocarbon dates, ranging from 2,780 to 3,680 yr BP, were obtained from *C. rhombifer* bones from Sawmill Sink and Dan's Cave on Abaco. A mineralized bone from a large specimen *C. rhombifer* from a deeper portion of Sawmill Sink could not be dated, but suggests a possible late Pleistocene age. Highly mineralized crocodile bones also occur in White Lake Cave on Eleuthera. The youngest records of crocodiles from The Bahamas are specimens from Lucayan archaeological sites on Eleuthera, Crooked Island, and Acklins dating to between AD 800 and the early1500s, and historical records on Andros and Great Inagua from the 18th and 19th centuries. Crocodiles survived into post-Columbian time (after 1492) on Grand Cayman based on a radiocarbon date of 375 yr BP on a peat sample containing bones of *C. rhombifer* from the Crocodile Canal site, jaws of the introduced Old World rat *Rattus rattus* associated with Cuban crocodile fossils from the Furtherland Farms site, and historical records from the 16th through the 18th centuries. Data from fossil and archaeological sites and historical chronicles document the disappearance of crocodiles from The Bahamas and on Grand Cayman over the past two hundred years, almost certainly resulting from overhunting by humans.

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Appendix 1. Late Quaternary Specimens of Crocodiles from The Bahamas and Cayman Islands.

Samples that contain diagnostic cranial material are identified as the Cuban crocodile (*Crocodylus rhombifer*). Sites consisting of a mixture of skulls, mandibles, and postcranial material are identified as *C. rhombifer* if the samples include a partial to nearly complete skull that is diagnostic of this species. Several sites contain specimens of dentaries or cranial fragments that are identifiable as *Crocodylus*, but the material is not complete enough for a species-level identification. Other samples that consist of non-diagnostic material (isolated teeth, postcranial elements, etc.) are identified as Crocodylia, even though these specimens are almost certainly referable to the genus *Crocodylus* and probably to *C. rhombifer*. The large samples of crocodile fossils from Sawmill Sink on Abaco and several sites on Grand Cayman (Chisholm Cow Well, Crocodile Canal, Furtherland Farms Cow Well, Queen Elizabeth II Botanic Park) are not listed in their entirety here. We list only the most diagnostic fossils included in the descriptions and tables (e.g., we do not include the hundreds of isolated vertebrae, ribs, and osteoderms from Sawmill Sink). Museum acronyms are explained in the text under Methods. For specimens from Sawmill Sink on Abaco, informal numbers used to designate individual crocodile specimens are listed after the catalogue numbers (e.g., C15, C52, etc.). For specimens we did not personally examine (e.g., fossils from New Providence and San Salvador and archaeological specimens from Eleuthera), we include references where those specimens were cited and described. For several blue hole sites on Abaco and Grand Bahama, we list fossils identified through photographic documentation but not yet collected or catalogued. Some of these specimens almost certainly will not be collected (e.g., skull, jaws, and partial skeleton from Dan's Cave), whereas other fossils currently underwater may eventually be collected and curated (e.g., skeleton from Lost Reel Cave and material from Mermaid's Lair on Grand Bahama). Photographs of these underwater specimens are archived in the NMB museum collection facility in Marsh Harbour, Abaco (available through N. Albury), and several are illustrated in this paper.

BAHAMAS: ABACO

Sawmill Sink. *Crocodylus rhombifer*: UF 225401 (C6), complete skull and associated mandibles. NMB. AB50.020 (C15), complete skull and associated mandibles. NMB.AB50.021 (C16), complete skull and associated mandibles. NMB.AB50.022 (C17), complete skull and associated mandibles. NMB. AB50.023 (C18), complete skull and associated mandibles. NMB.AB50.024 (C19), complete skull and associated mandibles.NMB.AB50.025 (C20), complete skull and associated mandibles. NMB. AB50.026 (C21), associated cranial and postcranial elements of a large individual, including: right quadrate, quadratojugal, and posterior process of jugal; left quadrate with partial quadratojugal; occipital condyle and foramen magnum, including basioccipital and exoccipitals; right and left articulars, 12 vertebrae, including 2 sacrals; left radius and ulna; right ilium; 5 osteoderms. NMB.AB50.027 (C24), nearly complete skull and associated mandibles. Skull complete except for anterior tip of premaxilla and palate. Articulars of mandibles incomplete. NMB.AB50.030 (C30), complete skull and associated mandibles and partial postcranial skeleton, including right scapula, humerus, and ulna, right and left ischium and pubis, left ilium, and right and left femur. NMB.AB50.171 (C52), complete skull and associated mandibles. NMB.AB50.062, NMB.AB50.083–087, humerus (6); NMB.AB50.066–068, NMB.AB50.091–093, radius (6); NMB.AB50.063–065, NMB.AB50.088–090, ulna (6); NMB.AB50.070, NMB.AB50.111–116, femur (7); NMB.AB50.117–119, tibia (3); NMB.AB50.071, NMB.AB50.121–123, fibula (4); NMB.AB50.069, NMB.AB50.094, NMB.AB50.095, NMB.AB50.097, NMB.AB50.098, ilium (5).

Dan's Cave. *Crocodylus rhombifer*: UF 137893 (cast; original specimen curated in NMB in Nassau), dorsal portion of skull including cranial table, posterior portions of right and left mandibles; 42 teeth, several partial limb bones, vertebrae, and osteoderms. NMB. AB53.003, associated vertebrae (2), osteoderms (2), and metapodial. Nearly complete but partially disarticulated skull and associated mandibles, photographed at a depth of 65 feet (20 m). Photo documentation only, specimens not collected (see Fig. 5).

Ralph's Cave. *Crocodylus rhombifer*: NMB. AB51.002, nearly complete skull, angular, and associated partial postcranial skeleton, including 12 vertebrae (1 sacral), right scapula, humerus, radius, and ulna, right ilium, ischium, pubis, femur, tibia, and left fibula, astragalus, and calcaneum.

Nancy's Cave. *Crocodylus rhombifer*: NMB. AB57.003, nearly complete skull, associated mandibles, and partial postcranial skeleton. NMB. AB57.002, complete dorsal vertebra of large individual.

Lost Reel Cave. *Crocodylus rhombifer*: NMB. AB52.009, nearly complete skull, mandibles and partial articulated/associated postcranial skeleton. The only specimen collected from this skeleton is a complete femur. The remainder of the skeleton is still underwater and was identified by photographic documentation (Fig. 7). Crocodylia: NMB.AB52.041, large sample of coprolites.

Gilpin Point. *Crocodylus rhombifer*: Partial cranial roof with frontals and parietals. Partial right maxilla. Partial costal of sea turtle with crocodylian bit marks.

BAHAMAS: Grand Bahama

Bell Channel. *Crocodylus* sp.: MCZ 85546, left dentary with at least 5 teeth (Fig. 8).

Mermaid's Lair. *Crocodylus rhombifer*: NMB. GB016.001, frontal, partial left jugal, partial left articular, left angular, left surangular, and partial right ilium (Fig. 10). Fossils identified from underwater photographs but not collected include a dentary fragment with one tooth, numerous isolated teeth, sacral vertebra, and partial femur (Fig. 9).

BAHAMAS: Eleuthera

White Lake Cave. Crocodylia: NMB.EL185.001, edentulous fragment of left dentary; NMB. EL185.002, isolated tooth, NMB.EL185.003, left humerus (Fig. 11A–C).

Kelly's Blue Hole (=Bung Hole). Crocodylia: NMB. EL180.001, partial dentary.

Mermaid's Pool. Crocodylia: NMB.EL183.001, proximal end of left femur (Fig. 11D).

Preacher's Cave (archaeological site). Crocodylia: NMB.186.001 (FS 175), tooth, (FS 115), tooth (Carr et al. 2006).

BAHAMAS: New Providence

Banana Hole. Crocodylia: UF 2994, partial juvenile vertebra (Pregill 1982).

BAHAMAS: San Salvador

Hanna's Bananas. Crocodylia: USNM uncatalogued, partial left jugal; USNM uncatalogued, osteoderm (Olson et al. 1990).

BAHAMAS: Crooked Island

Pitts Town (archaeological site, CR–14). Crocodylia: FLMNH Zooarchaeology Collection, femur (Keegan 1992).

BAHAMAS: Acklins

Rupert's Pond. Crocodylia: NMB.AC20.001, osteoderm.

Delectable Bay (archaeological site, AC–14). Crocodylia: FLMNH Zooarchaeology Collection, tooth (Franz et al. 1995).

BAHAMAS: Mayaguana

The Fountain. Crocodylia: NMB.MY11.002, large coprolite. NMB.MY11.001, partial tortoise carapace with eight crocodylian bite marks (Fig. 28).

CAYMAN ISLANDS: Grand Cayman

Crocodile Canal. *Crocodylus rhombifer*: USNM 216197, nearly complete skull missing only the right and left nasals, left quadratojugal, and left ectopterygoid. UF 61101, 61102, premaxilla (2); UF 61103, 61104, maxilla (2); UF 61162, frontal; UF 61105, associated jugal and lacrimal; UF 61106, associated jugal and quadratojugal; UF 61107, 61108, pterygoid (2); UF 61109–61111, ectopterygoid (3); UF 61112–61114, dentary (3); UF 61115, 61116, angular (2); UF 61117–61119, 61163, surangular (4); UF 61120–61126, articular (7); UF 61127, 61128, humerus (2); UF 61129, 61130, femur (2); UF 61131, 61132, tibia (2); UF 61133, fibula; UF 61137, ilium. Sample also contains 69 isolated teeth (UF 61142, 61164, 61165) and many other assorted

postcranial elements, including girdle elements, vertebrae, ribs, osteoderms, metapodials, phalanges, etc. (UF 61134–61145, 61166–61171). The FLMNH/UF sample contains an MNI of 6 individuals based on right articulars. Besides the skull listed above, a representative sample of isolated cranial and postcranial elements is also housed in the USNM collection.

Prospect. *Crocodylus rhombifer*: UF 65800, nearly complete skull, right and left mandibles, humerus, radius, femur, and about 10 vertebrae, all from a single individual. The skull lacks the right premaxilla, much of the palate from the left side (palatine, pterygoid, and ectopterygoid), and the left quadrate. The skull and left mandible are illustrated in Morgan et al. (1993, fig. 2) and Morgan (1994, fig. 22.4).

Chisholm Cow Well. *Crocodylus rhombifer*: UF 80000, nearly complete skull lacking only the left and right nasals, left lacrimal, prefrontal, jugal, quadratojugal, pterygoid, and ectopterygoid, and left and right palatines. The skull is illustrated in Morgan et al. (1993, fig. 1). UF 126085, left premaxilla and maxilla; UF 128065, UF 128086, associated right and left frontals; UF 128070, prefrontal; UF 128069, 128087, ectopterygoid (2); UF 128065, left mandible with all bones except articular; UF 128066, 128067, 128088, angular and surangular (3); UF 128068, articular; UF 128078, humerus; UF 128079, 128080, femur (2); UF 128081, tibia; UF 128082, fibula; UF 128073, 128095, ilium (2). The sample also contains 35 isolated teeth (UF 128089) and many other assorted postcranial elements, including girdle elements, vertebrae, ribs, osteoderms, metapodials, phalanges, etc. (UF 128071–128084, 128090–128098). The FLMNH/UF sample contains an MNI of 4 based on the presence of 3 left surangulars and a right surangular from a much larger individual. Many more individuals of crocodiles are present in the Chisholm Cow Well sample based on the collections made by Rolin Chisholm (fossils in his possession) and Ira Thompson (fossils in CINM).

Connally Cow Well. *Crocodylus rhombifer*: UF 128064 (cast, original in MRCU/NRS), nearly complete skull lacking only the right nasal, left jugal and quadratojugal, right quadratojugal, and left palatine. The skull is illustrated in Morgan et al.

(1993, fig. 3) and Morgan (1994, fig. 22.3).

Queen Elizabeth II Botanic Park. *Crocodylus rhombifer*: UF 143687, partial skull of a large individual consisting of the premaxilla, maxilla, jugal, and quadratojugal, all from the right side, as well as a fragment of the left maxilla with the four anteriormost teeth, the left quadrate and ectopterygoid, right and left partial pterygoids, and the left articular. UF 244484, premaxilla and maxilla; UF 244499, tiny maxilla of a hatchling; UF 244488, 244489, left dentary (2); UF 244496, 244497, humerus (2); UF 219978, 244493, 244494, femur (3); UF 244495, tibia; UF 244482, ilium. The FLMNH/UF sample contains an MNI of 3 based on the presence of three different sizes of maxilla, from a tiny hatchling, a young adult, and a very large adult. The FLMNH has only a small representative sample of the crocodile fossils from this site. A much larger collection was retained by the National Trust for the Cayman Islands (NTCI). GSM's field notes indicate that the original sample collected in 1993 contained at least 10 dentaries (7 left, 3 right), yielding an MNI of 7.

Furtherland Farms Cow Well. *Crocodylus rhombifer*: UF 128128, cranial table consisting of frontals, postorbitals, squamosals, and parietals; UF 128134, 128135, maxilla (2); UF 128101, 128136, 128137, lacrimal (3); UF 128138, squamosal; UF 128139, left dentary; UF 128140, articular; UF 128102, 128129, splenial (2); UF 128113, 128148, humerus (2); UF 128115, 128149, 128150, radius (3); UF 128116, 128157, tibia (2); UF 128117, 128118, fibula (2); UF 128106, 128107, 128131, 128144, ilium (4). The sample also contains 12 isolated teeth (UF 128111, 128141) and many other assorted postcranial elements, including gir-dle elements, vertebrae, ribs, osteoderms, meta-podials, phalanges, etc. (UF 128102–128127, 128130–128133, 128142–128159).The FLMNH/UF sample contains an MNI of 3 based on the presence of 3 left calcanea, as well as 3 different sizes of ilia and radii.

Crab Cave. Crocodylia: UF 22739, isolated tooth (Morgan & Patton, 1979).

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