

# Exceptionally well preserved late Quaternary plant and vertebrate fossils from a blue hole on Abaco, The Bahamas

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We report Quaternary vertebrate and plant fossils from Sawmill Sink, a “blue hole” (a water-filled sinkhole) on Great Abaco Island, The Bahamas. The fossils are well preserved because of deposition in anoxic salt water. Vertebrate fossils from peat on the talus cone are radiocarbon-dated from  $\approx$ 4,200 to 1,000 cal BP (Late Holocene). The peat produced skeletons of two extinct species (tortoise *Chelonoidis* undescribed sp. and *Caracara Caracara creightoni*) and two extant species no longer in The Bahamas (Cuban crocodile, *Crocodylus rhombifer*; and Cooper’s or Gundlach’s Hawk, *Accipiter cooperii* or *Accipiter gundlachi*). A different, inorganic bone deposit on a limestone ledge in Sawmill Sink is a Late Pleistocene owl roost that features lizards (one species), snakes (three species), birds (25 species), and bats (four species). The owl roost fauna includes *Rallus* undescribed sp. (extinct; the first Bahamian flightless rail) and four other locally extinct species of birds (Cooper’s/Gundlach’s Hawk, *A. cooperii/gundlachi*; flicker *Colaptes sp.*; Cave Swallow, *Petrochelidon fulva*; and Eastern Meadowlark, *Sturnella magna*) and mammals (Bahamian hutia, *Geocapromys ingrahami*; and a bat, *Myotis* sp.). The exquisitely preserved fossils from Sawmill Sink suggest a grassy pineland as the dominant plant community on Abaco in the Late Pleistocene, with a heavier component of coppice (tropical dry evergreen forest) in the Late Holocene. Important in its own right, this information also will help biologists and government planners to develop conservation programs in The Bahamas that consider long-term ecological and cultural processes.

birds | extinction | islands | tortoises | crocodiles

In 2004 Brian Kakuk discovered an entire associated skeleton of a tortoise in a blue hole called Sawmill Sink in the pinelands of south-central Great Abaco Island (hereafter “Abaco”), northern Bahamas (Fig. 1). Subsequent underwater investigations in Sawmill Sink have disclosed abundant fossils of the indigenous reptiles, birds, and mammals that once lived on Abaco. The value of these fossils is enhanced by being deposited in sediment rich in plant macrofossils (leaves, twigs, flowers, fruits, and seeds) and microfossils (pollen and spores), thus giving us evidence of both the flora and fauna that existed on Abaco just before and during the prehistoric arrival of people.

## Sawmill Sink

**Description.** Sawmill Sink is an inland “blue hole,” a subsurface void in carbonate bedrock that is open to the Earth’s surface. Inland blue holes contain tidally influenced water of fresh, marine, and mixed chemistry, extend below sea level for most of their depth, and commonly provide access to submerged cave passages (1). The nearly circular opening of Sawmill Sink has a diameter up to 15.5 m and a circumference of 50 m. Dissolution undercutting and subsequent collapse of the carbonate rock has created a bell-shaped profile dominated by a well developed

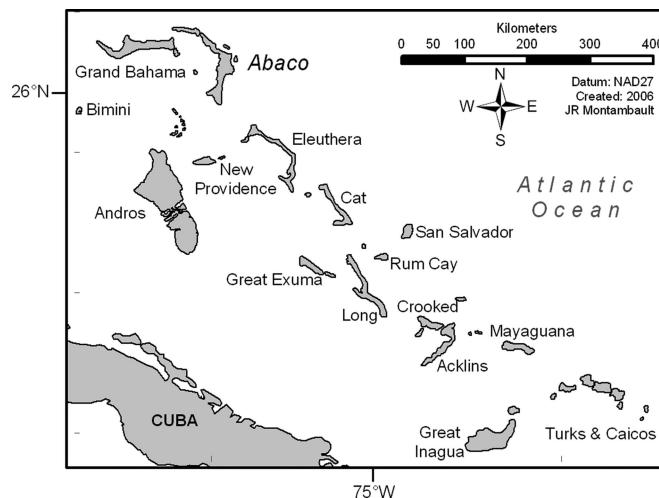


Fig. 1. The Bahamian Archipelago (The Bahamas and Turks and Caicos Islands).

talus cone from a depth of 9 to 34 m (Fig. 2). Much of this talus is covered with peat that is a rich source of plant micro- and macrofossils as well as spectacular vertebrate fossils (Fig. 3). An associated underwater cave system extends southward  $>$ 600 m to depths of 54 m. The top of the talus cone is littered with remnants of a former sawmill operation, an industry that dominated Abaco in the early 1900s and from which Sawmill Sink derives its name.

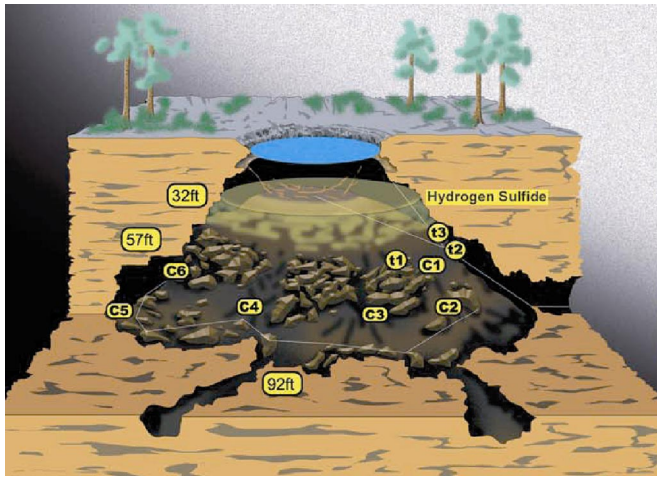
**Hydrology and Water Chemistry.** The water profile for Sawmill Sink is similar to that of other inland blue holes in Abaco. Geographically separated from surface marine water, the stratified water chemistry varies seasonally with rainfall and temperature. Fresh water extends from the surface to a depth of 9.5 m. A halocline and mixed water chemistry extends from 9.5 to 27 m, a zone in which hydrogen sulfide and sulfur-reducing bacteria block all penetrating light. Below 27 m, tidally influenced, anoxic marine

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Conflict of interest statement: D.W.S. coauthored a paper about faunal remains in Tobago with reviewer Sharyn Jones in 2006. Jones now works primarily in the tropical Pacific, whereas D.W.S. works mainly in the Caribbean region. They have no joint research taking place now. There is no reason to suspect that the review by Jones is anything other than objective.

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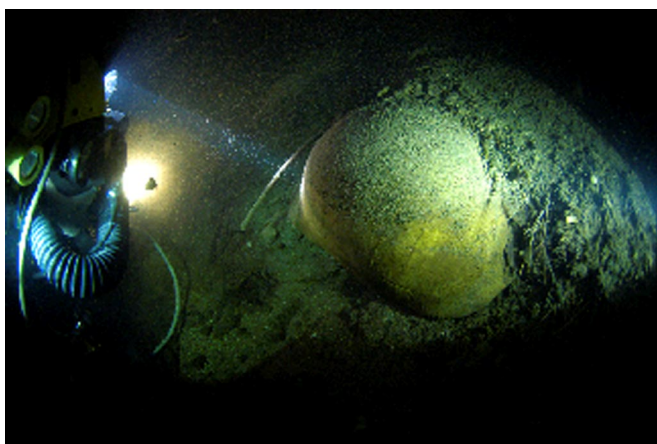


**Fig. 2.** Preliminary vertical profile of Sawmill Sink and its talus cone. C, crocodile; t, tortoise. Note water depths (in feet). [Reproduced with permission from Curt Bowen (Copyright 2005, *Master Diver Magazine*, Bradenton, FL).]

water flows throughout the system, lagging behind the coastal tides by an hour or more.

**Underwater Techniques.** Underwater operations at the Sawmill Sink site are conducted by using industry-standard cave-diving techniques and scientific diving protocols. For two reasons, dive team members use modern closed-circuit, mixed-gas rebreathers. First, standard open-circuit diving operations on a large scale would be detrimental to the site's anoxic environment. The closed-circuit apparatus recirculates the diver's air and allows little if any oxygen to be released in the cave via exhaled bubbles, thereby maintaining relatively undisturbed water chemistry. Second, the unique bacterial colonies that exist in Sawmill Sink cover almost every surface of the cave, making work at the site difficult; visibility often is reduced to zero as excavations begin. Because no bubbles are produced by the rebreathers, bacterial mats on the ceiling of the cave are undisturbed and visibility at the work site is increased.

As fossil material is identified, photographed, and determined to be significant, it is marked with weighted identification tags, then surveyed and mapped in relation to circumference lines that encircle the talus cone at depths of 20 m and 30 m. Latitudinal and longitudinal reference lines intersect the center of the



**Fig. 3.** Diver Brian Kakuk in Sawmill Sink with an undisturbed tortoise (*Chelonoidis*) shell in peat. [Reproduced with permission from Curt Bowen (Copyright 2005, *Master Diver Magazine*, Bradenton, FL).]

surface opening and traverse the entire talus cone. The three-dimensional data associated with each fossil collection are entered into a digital mapping program. For excavation and collection, a 2 × 3-m grid is placed over a site and secured with permanent PVC posts. Fossils are collected in zipper lock bags and plastic boxes, which secure the material from movement and retain the original water chemistry until preparation in the laboratory.

### Radiocarbon Chronology

Following the methods and concepts in ref. 2, the chronology of the fossil deposits in Sawmill Sink is based on six accelerator-mass spectrometer (AMS) radiocarbon ( $^{14}\text{C}$ ) dates from individual bones from the peat deposit identified to species (Table 1). Each date is within the Late Holocene. The youngest date ( $\approx 1,000$  cal BP) is from a human tibia. Two bones of an extinct tortoise (*Chelonoidis* undescribed sp.) range in age from  $\approx 2,700$  to 2,500 cal BP, whereas the three bones of the Cuban crocodile (*Crocodylus rhombifer*) are slightly older at  $\approx 3,900$  to 2,900 cal BP.

From the owl roost, tibiotarsi of an extinct flightless rail (*Rallus* undescribed sp.) and a meadowlark (*Sturnella magna*) were sent to Beta Analytic for AMS  $^{14}\text{C}$  dating but, as with two of the crocodile bones from the peat deposit, yielded no datable collagen. This finding adds some support to the idea that the owl roost fauna is older than that of the peat deposit and in fact probably dates to the last glacial interval ( $>12,000$  cal BP), when sea level would have been as much as 130 m below modern (3, 4), allowing the owl roost deposit to have formed subaerially.

### Plant Fossils

The two major upland plant communities in The Bahamas today are a tropical dry evergreen forest known as "coppice" and a tropical pine-dominated woodland called "pineland" or "pineyard" (5–8). No quantitative descriptions of the coppice on Abaco exist, although it has been analyzed in some detail on Andros, with variably dominant woody species (shrubs, small trees) in the genera *Metopium*, *Coccoloba*, *Exothea*, *Bursera*, *Swietenia*, *Acacia*, *Bumelia*, *Eugenia*, *Ficus*, and *Alvaradora* (8). The signature woody plant of the Bahamian pinelands is *Pinus caribaea* var. *bahamensis*, often with a shrubby understory of *Metopium toxiferum* and ferns (9).

**Macrofossils.** In January 2006 three sediment cores were taken from the Sawmill Sink peat using 6-foot lengths of polycarbonate pipes (1.75-inch outside diameter). Each pipe was inserted horizontally 2.4 m into the side of the talus cone at water depths of 14.3 m (Core 1), 22.9 m (Core 2), and 27–30 m (Core 3). The uppermost core was 3.1 m below the hydrogen sulfide layer. Each core was brought to the surface in a horizontal position. After draining, the sediment was extruded in 2-cm increments, with 14 such increments for Core 1, 33 for Core 2, and 21 for Core 3. Two grab samples also were collected near Core 2 (C-10, Peat Cave). For comparative material, leaf samples from living plants were collected near Sawmill Sink and prepared as herbarium specimens. The peat preserves invertebrates as well, although they have not yet been studied.

Of 65 plant morphotypes based on diagnostic characters (especially of the leaves), 10 are most conspicuous or common (Table 2). Fern allies and gymnosperms are represented by Eaton's spikemoss *Selaginella eatonii* and Caribbean pine *P. caribaea*. Pine is found throughout Core 1 and as fragments in C10 grab sample but is absent in Cores 2 and 3 and the Peat Cave grab sample. Among angiosperms, monocots include possible grass stems (Poaceae) in Core 2 and possible palm wood (Arecaceae) in Core 3. The dicots feature leaves of lignum vitae *Guaiacum sanctum*, stickpea *Calliandra haematomma*, stopper cf. *Eugenia*, and possible Malvales (Table 2). A general trend is

Table 1. AMS radiocarbon (<sup>14</sup>C) dates on purified bone collagen from Sawmill Sink, Abaco, The Bahamas

Laboratory no.	Provenience	Species and skeletal element	Measured <sup>14</sup> C age, yr BP	<sup>13</sup> C/ <sup>12</sup> C ratio	Conventional <sup>14</sup> C age, yr BP	Calibrated age, 2σ
Beta-228852	Peat	Human: tibia	870 ± 30	-14.7	1,040 ± 40	Cal BP 1,050–1,030, 1,000–920
Beta-225509	Peat	Tortoise T3: scapula	2,520 ± 50	-21.1	2,580 ± 50	Cal BP 2,770–2,690, 2,640–2,610, 2,590–2,500
Beta-225508	Peat	Tortoise T1: thoracic vertebra	2,660 ± 40	-21.2	2,720 ± 40	Cal BP 2,880–2,750
Beta-230221	Peat	Crocodile CA: humerus	2,900 ± 50	-19.3	2,990 ± 50	Cal BP 3,340–3,000
Beta-230223	Peat	Crocodile C6: lumbar vertebra	3,680 ± 50	-19.0	3,780 ± 50	Cal BP 4,340–4,340, 4,290–4,060, 4,050–3,990
Beta-230222	Peat	Crocodile CB1: femur	3,680 ± 50	-16.4	3,820 ± 50	Cal BP 4,410–4,080
Beta-230224	Peat (RF-B-0356)	Crocodile C21: thoracic vertebra	Not datable; no collagen	—	—	—
Beta-230225	Peat (RF-B-0354)	Crocodile C24: humerus	Not datable; no collagen	—	—	—
Beta-229507	Owl roost	Rail: tibiotarsus	Not datable; no collagen	—	—	—
Beta-229508	Owl roost	Meadowlark: tibiotarsus	Not datable; no collagen	—	—	—

Measured and conventional <sup>14</sup>C ages are reported in radiocarbon years before present (yr BP). Calibrated ages are reported in calendar years before present (Cal BP). Human, *Homo sapiens*; tortoise, *Chelonoidis* undescribed sp.; crocodile, *Crocodylus rhombifer*; rail, *Rallus* undescribed sp.; meadowlark, *Sturnella magna*.

Table 2. Very preliminary list of common or conspicuous plant macrofossils and pollen identified from Cores 1–3 and grab samples (C-10, Peat Cave), Sawmill Sink, Abaco, The Bahamas

Characteristic habitat	Taxon
Pinelands	PTER: bracken fern, <i>Pteris</i> sp. <sup>‡</sup> GYMNO: Caribbean pine, <i>Pinus</i> cf. <i>P. caribaea</i> <sup>†</sup> DICOT: gumbo-limbo, <i>Bursera</i> cf. <i>B. simaruba</i> <sup>†</sup> ; red powderpuff (stickpea), <i>Calliandra</i> cf. <i>C. haematomma</i> <sup>*</sup> ; holly, <i>Ilex</i> sp. <sup>‡</sup> ; wax myrtle, <i>Myrica</i> cf. <i>M. cerifera</i> <sup>†</sup> ; grape, cf. <i>Vitis</i> sp. <sup>*</sup>
Scrublands	DICOT: <i>Calliandra</i> cf. <i>C. haematomma</i> <sup>*</sup> ; stopper, <i>Eugenia</i> sp. <sup>*</sup> ; hibiscus, <i>Hibiscus</i> sp. <sup>‡</sup> ; <i>Ilex</i> sp. <sup>‡</sup>
Coppice	PTER: swordfern, <i>Nephrolepis</i> sp. <sup>‡</sup> ; goldback fern, cf. <i>Pityrogramma</i> sp. <sup>‡</sup> DICOT: mallow, cf. <i>Abutilon</i> sp. <sup>‡</sup> ; <i>Bursera</i> cf. <i>B. simaruba</i> <sup>†</sup> ; <i>Calliandra</i> cf. <i>C. haematomma</i> <sup>*</sup> ; lignum vitae, <i>Guaiacum</i> cf. <i>G. sanctum</i> <sup>*</sup> ; <i>Eugenia</i> sp. <sup>*</sup> ; <i>Hibiscus</i> sp. <sup>‡</sup> ; <i>Ilex</i> sp. <sup>‡</sup> ; <i>Myrica</i> cf. <i>M. cerifera</i> <sup>†</sup> ; pouteria, <i>Pouteria</i> sp. <sup>‡</sup> ; cf. <i>Vitis</i> sp. <sup>*</sup>
Wetlands/ponds	FELA: Eaton's spikemoss, <i>Selaginella</i> cf. <i>S. eatonii</i> <sup>*</sup> PTER: leatherfern, <i>Acrostichum</i> sp. <sup>‡</sup> MONO: pickerelweed, cf. <i>Pontederia</i> <sup>‡</sup> ; bulltongue arrowweed, <i>Sagittaria</i> cf. <i>S. lancifolia</i> <sup>†</sup> DICOT: pond apple-type, <i>Annona</i> type <sup>‡</sup> ; waterhyssop, cf. <i>Bacopa</i> sp. <sup>‡</sup> ; <i>Hibiscus</i> sp. <sup>‡</sup> ; <i>Ilex</i> sp. <sup>‡</sup>
Disturbed lands	DICOT: cf. <i>Abutilon</i> sp. <sup>‡</sup> ; peppertree, <i>Schinus</i> sp. <sup>‡</sup>
General/unknown	FUNG: <i>Dictyosporites</i> sp. <sup>‡</sup> ; <i>Fusiformisporites</i> sp. <sup>‡</sup> ; <i>Meliolinites</i> sp. <sup>‡</sup> ; <i>Microthyricites</i> spp. <sup>‡</sup> ; <i>Palaeomycites</i> sp. <sup>‡</sup> ; <i>Quilonia</i> sp. <sup>‡</sup> PTER: antlerfern, <i>Ceratopteris</i> sp. <sup>‡</sup> ; polypody, Polypodiaceae <sup>‡</sup> GYMNO: cycads, Cycadaceae sp. <sup>‡</sup> MONO: grasses, Poaceae <sup>†</sup> ; palms, Arecaceae <sup>†</sup> DICOT: cashews, Anacardiaceae <sup>†</sup> ; composites, Asteraceae <sup>†</sup> ; goosefoot/amaranths, Chenopodiaceae/Amaranthaceae <sup>†</sup> ; legumes, Fabaceae <sup>†</sup> ; mallows, cf. Malvales <sup>†</sup> ; myrtles/Stoppers, Myrtaceae <sup>†</sup> ; soapberries, Sapindaceae <sup>†</sup>

Identification based on palynomorphs only (‡), macrofossils only (\*), or both macrofossils and palynomorphs (†). Common names are given at first mention. General/unknown, habitat unidentified and indeterminate until more resolved identifications are available. Plants are in habitat lists divided into Fungi (FUNG), Pteridophyta (PTER), Fern-Like Allies (FELA), Gymnospermae (GYMNO), Monocotyledoneae (MONO), and Dicotyledoneae (DICOT).

the dominance of pine in Core 1, whereas coppice taxa dominate Cores 2 and 3. Although both upland habitats are well represented, the macrofossil flora contains a larger number of taxa found exclusively in coppice rather than pineland, suggesting Late Holocene habitats in the immediate vicinity of Sawmill Sink of mixed coppice and pinelands. A few fresh and brackish water taxa also are present.

**Pollen.** A sample of Late Holocene peat associated with a tortoise fossil (T1) was processed for palynomorphs using standard techniques (ref. 10 and the guide to the operations and procedures adopted in the palynology laboratory of the Florida Museum of Natural History/University of Florida). A scan of all 10 slides resulted in the identification of 32 palynomorphs, including fungal and fern spores and gymnosperm and angio-



sperm pollen (Table 2). The fungal assemblage includes several morphotypes within the Fungi Imperfecti (11, 12). Gymnosperm pollen is common. Airborne pollen of pine (*Pinus*) is easily carried great distances from its source to be deposited in wetlands. To identify the pine pollen to species will require scanning electron microscopy, although the fossil pine pollen has several features in common with that of *P. caribaea*.

Angiosperms account for most taxa in the pollen assemblage, with four monocots and 14 dicots recognized. By far the most common pollen is of *Myrica cerifera* (wax myrtle), an insect-pollinated plant that grows at the edges of sinkholes. Other common pollen types include small, syncolpate (colpi meeting at polar area) forms as in several taxa of Myrtaceae, tricolporate forms of Anacardiaceae, *Bursera simaruba*, *Ilex*, and many Asteraceae. Additional forms not yet confirmed include *Pouteria*, *Annona*, and at least 15 forms of unidentified, tricolporate pollen.

Nothing determined thus far in the diverse, well preserved pollen flora from Sawmill Sink seems to be foreign to the plant communities near the site today (pineland and coppice). The pollen and spores from living wetland plants of the Florida Everglades (13) show many similarities with the Late Holocene fossil flora from Abaco.

### Human Remains

The prehistoric Lucayan people of The Bahamas (A.D. ≈600–1500) appear to have buried their dead in limestone caves, including blue holes (14). A human tibia and sacrum were found between 25 and 28 m below the surface at Sawmill Sink. These materials were analyzed by using the methods in ref. 15. Age at death (10–13 years) was estimated from epiphyseal closure at the proximal and distal ends of the tibia (16). The AMS <sup>14</sup>C date for this individual (≈1,050 to 920 cal BP) (Table 1) is the earliest for human occupation in the northern Bahamas and the oldest <sup>14</sup>C date directly on human bone in the entire Bahamian Archipelago (The Bahamas and Turks and Caicos Islands). No cultural materials were found with skeletal remains in the sink.

### Vertebrate Fossils

The 38 non-fish vertebrate taxa identified thus far from Sawmill Sink (peat and owl roost contexts combined) represent at least six species of reptiles, 27 birds, and five mammals (Table 3). Although it seems likely that our efforts to date have recovered the most common species of large vertebrates that are interred at Sawmill Sink, we are confident that further research will increase the prehistoric taxonomic diversity of the site.

**Reptiles.** The 150-plus identifiable squamate reptile bones from the owl roost fauna include three genera of snakes (a colubrid, *Alsophis*; a boa, *Epicrates striatus*; and the blind snake *Typhlops*) and the lizard *Anolis sagrei*. The boa *E. striatus* accounts for >99% of the snake vertebrae; fossils of *E. striatus* were common as well at Banana Hole, New Providence (17). Several limb bones from a moderate-sized lizard possibly represent the diurnal *Leiocephalus carinatus*, but this identification is tentative without dentaries or maxillae.

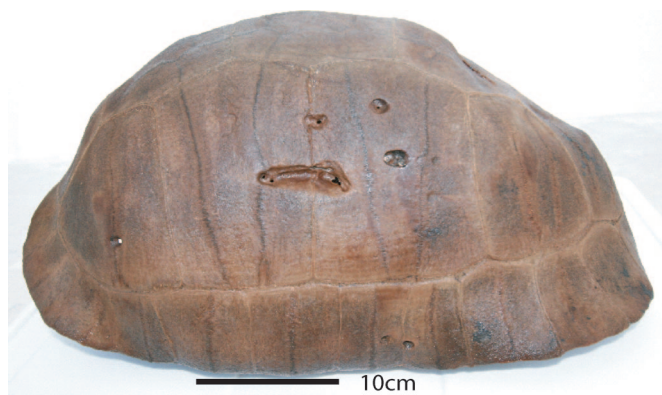
The peat produced five complete or nearly complete shells, a partial shell, a perfectly preserved skull, and most of an appendicular skeleton of a new species of moderate-sized tortoise (46-cm carapace length) in the genus *Chelonoidis* (Figs. 3 and 4). These specimens represent the most complete tortoise material ever recovered in the West Indies, where tortoise fossils typically are rare and fragmentary (17, 18). The tortoise fossils from Sawmill Sink will be integral in studying the evolution of West Indian tortoises. This new species shares many primitive and derived features with the Galápagos tortoises (*Chelonoidis nigra* and related forms) but also differs from them in several characters of skull, carapace, and plastron.

**Table 3. Vertebrates recorded from Sawmill Sink, Abaco, The Bahamas**

Taxon	Peat	Owl roost
Reptiles		
<i>Chelonoidis</i> undescribed sp., Abaco tortoise*	++	+
<i>Crocodylus rhombifer</i> , Cuban crocodile†	++	+
<i>Anolis sagrei</i> , anole	—	+
<i>Typhlops</i> sp., blind snake	—	+
<i>Epicrates striatus</i> , boa	—	++
<i>Alsophis</i> sp., colubrid snake	—	+
Birds		
<i>Puffinus lherminieri</i> , Audubon's Shearwater	—	+
<i>Nyctanassa violacea</i> , Yellow-crowned Night-heron	++	+
<i>Eudocimus albus</i> , White Ibis	++	+
<i>Pandion haliaetus</i> , Osprey	+	+
<i>Accipiter cooperii/gundlachi</i> , Cooper's/Gundlach's Hawk†	+	+
<i>Falco sparverius</i> , American Kestrel	—	+
<i>Caracara creightoni</i> , Bahamas Caracara*	++	—
<i>Rallus</i> undescribed sp., Abaco flightless rail*	—	++
<i>Gallinago</i> sp., snipe	—	+
<i>Columba leucocephala</i> , White-crowned Pigeon	+	+
<i>Zenaida aurita</i> , Zenaida Dove	+	+
<i>Geotrygon chrysis</i> , Bridled Quail-dove	+	—
<i>Amazona leucocephala</i> , Rose-throated (Bahamas) Parrot	—	+
<i>Tyto</i> sp., Barn Owl	+	+
<i>Athene cunicularia</i> , Burrowing Owl	—	++
<i>Colaptes</i> sp., flicker†	—	+
<i>Contopus caribaeus</i> , Cuban Pewee	—	+
<i>Petrochelidon fulva</i> , Cave Swallow†	—	+
<i>Margarops fuscatus</i> , Pearly-eyed Thrasher	—	+
<i>Geothlypis rostrata</i> , Bahamas Yellowthroat	—	+
<i>Spizella passerina</i> , Chipping Sparrow	—	+
<i>Tiaris bicolor</i> , Black-faced Grassquit	—	+
<i>Sturnella magna</i> , Eastern Meadowlark†	—	++
Passeriformes spp., unidentified songbirds (4+ spp.)	+	++
Mammals		
<i>Macrotus waterhousii</i> , Waterhouse's Leaf-nosed Bat	—	+
<i>Eptesicus fuscus</i> , Big Brown Bat	—	+
<i>Myotis</i> sp., unidentified myotis†	—	+
<i>Tadarida brasiliensis</i> , Mexican Free-tailed Bat	—	+
<i>Geocapromys ingrahami</i> , Bahamian Hutia†	+	—
Species totals (all species vs. †/* species)		
Reptiles	2/2	6/2
Birds	10/2	25+/5
Mammals	1/1	4/1
All species	14/6	35+/8

++, common fossil; +, uncommon fossil; —, not recorded from this provenience; †, extant species, no longer occurs on Abaco, i.e., extirpated; \*, extinct species. Marine species (sea turtles) were excluded.

Crocodyles are the most abundant large (>1-kg body mass) vertebrate in Sawmill Sink, with 42 individuals currently documented. Most of the specimens include skulls, lower jaws (Fig. 5), and partial to nearly complete postcranial skeletons. The crocodyles are primarily from the peat deposit, but a few have been found at greater depths peripheral to the talus cone. Among seven complete and several partial crocodyle skulls, six appear to be of adult size (total lengths from 253 to 310 mm; mean 283 mm). The Abaco skulls possess these diagnostic cranial characters of the Cuban crocodile *Crocodylus rhombifer*: short, broad, deep rostrum; concave cranial roof and interorbital region; rounded protuberance on the posterolateral corner of the squamosal; 13 maxillary teeth; and a suture on the palate

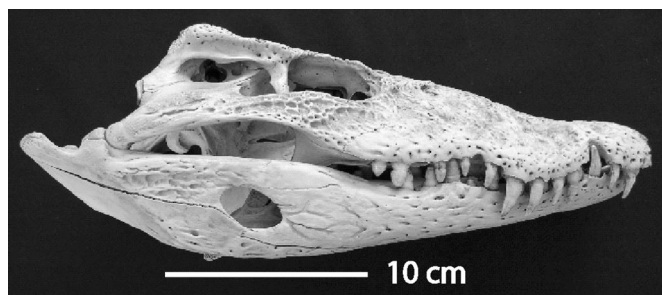


**Fig. 4.** The extinct tortoise, *Chelonoidis* undescribed sp., Sawmill Sink, Abaco, The Bahamas. This adult individual (T7) shows three sets of healed bite marks from the Cuban crocodile, *Crocodylus rhombifer*. Note the highly domed carapace, the alternating proximal and distal widths of costal bones in advanced tortoises to stabilize the domed shell, little or no flaring of the anterior and posterior peripherals, and the nearly vertical peripherals that make up the bridge connecting the carapace to the plastron.

between the premaxilla and maxilla that is transverse at the level of the first maxillary tooth. The most widespread crocodile in the West Indies today is the American crocodile, *Crocodylus acutus*, which has a longer and narrower rostrum, a flat cranial roof, no squamosal protuberances, 14 maxillary teeth, and a W-shaped premaxillary/maxillary suture that extends posteriorly to the third maxillary tooth.

The crocodile skulls from Sawmill Sink are similar in size and morphology to a partial skull, lower jaw, and associated skeleton referred to *C. rhombifer* from Dan's Cave, a blue hole  $\approx 3.6$  km northeast of Sawmill Sink (19). An AMS  $^{14}\text{C}$  date of  $2,780 \pm 60$  years BP (Beta-71576) on the Dan's Cave specimen overlaps with the dates on tortoises from Sawmill Sink (Table 1). Fossils of *C. rhombifer* also were reported from Late Holocene peat deposits on Grand Cayman in the Cayman Islands, where these crocodiles lived until being extirpated by European colonists only  $\approx 400$  years ago (20). The Cuban crocodile is currently restricted to freshwater habitats in the Zapata Swamp of Cuba and the Lanier Swamp on Isla de Pinos (21).

The remains of two sea turtles (Cheloniidae) were found in Sawmill Sink. One specimen is a large, well mineralized humerus of the green turtle *Chelonia mydas*. The other is a nearly complete, unmineralized skeleton of a hawksbill, *Eretmochelys imbricata*. We suspect that the carcass of the hawksbill was discarded by humans in the sink in modern times, possibly by the sawmill workers. The marine turtles do not pertain to the terrestrial vertebrate community, so they are not listed in Table 3.



**Fig. 5.** Skull of the crocodile *Crocodylus rhombifer* (specimen C15), Sawmill Sink, Abaco, The Bahamas. Note the short, deep rostrum, the rounded protuberance on the posterolateral corner of the squamosal, and the 13 maxillary teeth (nos. 1 and 11 missing).



**Fig. 6.** Skull and mandible of the extinct Bahamas Caracara, *Caracara creightoni*, Sawmill Sink, Abaco, The Bahamas. Features that distinguish *C. creightoni* from the living *C. cheriway* include the larger, stouter mandible and rostrum as well as the larger nares.

**Birds.** Whereas only 10 species of birds have been identified so far from the peat deposit at Sawmill Sink, 25 species already have been recognized from the owl roost (Table 3). The peat features an associated skull, mandible (Fig. 6), and postcranial elements of the extinct Bahamas Caracara *Caracara creightoni*, originally described from fragmentary fossils from New Providence (22, 23). Based on much better material, *C. creightoni* has been discovered as well on Cuba (24). The peat also has yielded a humerus from an *Accipiter*, probably Cooper's Hawk, *A. cooperii* (North American), or Gundlach's Hawk, *A. gundlachii* (considered to be endemic to Cuba). The most abundant birds from the owl roost are an extinct rail *Rallus* undescribed sp. (the first flightless rail discovered in The Bahamas); the Burrowing Owl, *Athene cunicularia* (rare today on Abaco); and the Eastern Meadowlark, *Sturnella magna* (a grassland indicator, extirpated in The Bahamas but still inhabiting North America and Cuba).

Other extirpated birds from the owl roost are the Cooper's/Gundlach's Hawk, *Accipiter cooperii/gundlachii* (another single humerus); a flicker, *Colaptes* sp. (scapula); and Cave Swallow, *Petrochelidon fulva* (two humeri). The nearest relatives of these three species are North American, Cuban, or generally Greater Antillean.

**Mammals.** Except for a radius of the Bahamian hutia *Geocapromys ingrahami* from the peat, all mammal fossils from Sawmill Sink are bats from the owl roost and a small deposit peripheral to the talus cone termed the "bell hole." The hutia represents a large extinct subspecies, *G. ingrahami abaconis*, described from Hole in the Wall Cave (25) and also known from other cave deposits on Abaco. The Bahamian hutia is extirpated on Abaco and on eight other islands in The Bahamas, surviving only on tiny East Plana Cay in the southeastern Bahamas (26). Three of the four species of bats identified from the owl roost still occur on Abaco. The exception (*Myotis* sp.) represents the only record of the genus *Myotis* in the Greater Antilles or The Bahamas; it also has been found as a fossil from Hole in the Wall Cave, Abaco (27).

### Summary, Conclusions, and Future Research

We are still in the early phases of exploration and discovery at Sawmill Sink and other blue holes on Abaco. As we wrote this article, for example, recent diving in blue holes called Ralph's Chimney Cave, Dan's Cave, and Lost Reel Cave disclosed new vertebrate fossil assemblages.



Because many of the bones from Sawmill Sink retain collagen for  $^{14}\text{C}$  dating, these fossil and cultural materials have great promise for continuing to improve the chronology of vertebrate extinction and prehistoric human presence in the region. The  $^{14}\text{C}$ -dated human tibia represents the oldest solid evidence of people on the Little Bahama Bank, comparable to that from Grand Turk (14, 28, 29) and North Eleuthera (30). A sediment sequence from a blue hole on Andros (Great Bahama Bank) had evidence (increased charcoal influx) for prehistoric human impact on native vegetation at  $\approx 900$  cal BP (31), a time comparable to that for the dated human bone on Abaco. A period of  $\approx 1,500$  years separates our date for the human tibia from the youngest dates for Abaco's extinct fauna (Table 1). We expect this gap to be reduced with additional  $^{14}\text{C}$  dating.

From an evolutionary and biogeographic standpoint, the fossils of extinct and extirpated species discovered thus far on Abaco reinforce the strong affinities between the vertebrates of Cuba and The Bahamas (23, 24). The Bahamian prehistoric terrestrial vertebrate community had ectotherms as dominant species, with browsing tortoises as the largest herbivores and crocodiles as the largest predators. The  $^{13}\text{C}/^{12}\text{C}$  ratios of the dated Cuban crocodile bones suggest that, on Abaco, it probably preyed mainly on terrestrial species such as tortoises, birds, and hutias.

Based on their modern habitat preferences, two of the most common birds (Burrowing Owl and Eastern Meadowlark) from Sawmill Sink argue for a grassland or grassy woodland (open canopy; probably dominated by pine) when the presumably Late Pleistocene owl roost fauna accumulated. On the other hand, species that require some trees, although not necessarily closed-canopy forest, occur in the Late Holocene peat and the earlier owl roost fauna, such as Cooper's/Gundlach's Hawk, White-crowned Pigeon, Zenaida Dove, Bridled Quail-Dove, Rose-throated Parrot, Cuban Pewee, Pearly-eyed Thrasher, and Bahamas Yellowthroat. Thus, a coppice component probably was present in both the Late Pleistocene and Late Holocene, although more strongly expressed in the latter period.

Both the plant and animal fossils from Sawmill Sink are beautifully preserved, greatly facilitating our upcoming morphological and systematic descriptions. These specimens also provide unparalleled opportunities to reconstruct ancient environments in the Bahamian Archipelago. Eventually we hope to be able to estimate long-term changes in such phenomena as fire regimes, plant communities, vertebrate turnover rates, body sizes of reptiles, terrestrial food webs including predator-prey relationships, and human impact on biotic communities. Such information is only beginning to be well documented in The Bahamas or on most other West Indian islands (2, 17, 23, 31–33).

The Bahamian government has gone to great lengths to protect its coastal natural resources, including a plan for one of the world's most ambitious marine protected area networks. Among marine habitats, blue holes have received relatively little attention. Some of these cave systems are under immediate threat from tourist development. Furthermore, many of the inland blue holes are linked hydrologically to the marine blue holes and thus play an important role in the integrity of offshore ecosystems. As our studies proceed, a primary goal is to generate correlated sets of paleoenvironmental information that will aid government planners and conservation biologists in reassessing priorities for integrated marine and land management in The Bahamas.

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1. Myroie JE, Crew JL, Moore AI (1995) *Carbonate Evaporites* 10:225–235.
2. Steadman DW, Martin PS, MacPhee RDE, Jull AJT, McDonald HG, Woods CA, Iturralde-Vinent M, Hodgins GWL (2005) *Proc Natl Acad Sci USA* 102:11763–11768.
3. Clark PU, Mix AC (2000) *Nature* 406:689–690.
4. Clark PU, Mix AC (2002) *Q Sci Rev* 21:1–7.
5. Correll DS (1979) *Taxon* 28:35–40.
6. Byrne R (1980) *Atoll Res Bull* 240:1–200.
7. Correll DS, Correll HB (1982) *Flora of the Bahama Archipelago* (Cramer, Vaduz, Liechtenstein).
8. Smith IK, Vankat JL (1992) *Bull Torrey Bot Club* 119:181–191.
9. Henry PWT (1974) *The Pine Forests of The Bahamas: Land Resource Study 16* (Overseas Dev Assoc, Surrey, UK).
10. Traverse A (1988) *Paleopalynology* (Unwin Hyman, London).
11. Pirozynski KA, Jarzen DM, Carter A, Day RG (1988) *Grana* 27:123–139.
12. Kalgutkar RM, Jansonius J (2000) *Synopsis of Fossil Fungal Spores, Mycelia, and fructifications* (Am Assoc Stratigraphic Palynologists Foundation, Nottingham, UK).
13. Willard DA, Bernhardt CE, Wiemer L, Cooper SR, Gamez D, Jensen J (2004) *Palynology* 28:175–227.
14. Keegan WF (1997) *Bahamian Archaeology: Life in The Bahamas and Turks and Caicos Before Columbus* (Media Publishing, Nassau, The Bahamas).
15. Buikstra J, Ubelaker D (1994) *Standards for Data Collection from Human Skeletal Remains* (Arkansas Archaeological Survey, Fayetteville, AR).
16. Anderson M, Messner MB, Green WT (1964) *J Bone Joint Surg* 46:1197–1202.
17. Pregill GK (1982) *Smithsonian Contrib Paleobiol* 48:8–21.
18. Auffenberg W (1967) *Herpetologica* 23:34–44.
19. Franz R, Morgan GS, Albury N, Buckner SD (1995) *Caribb J Sci* 31:149–152.
20. Morgan GS, Franz R, Crombie RI (1993) *Caribb J Sci* 29:153–164.
21. Ross JP, ed (1998) *Crocodiles: Status Survey and Conservation Action Plan* (World Conservation Union/Species Survival Commission Crocodile Specialist Group, Gainesville, FL).
22. Brodkorb P (1959) *Bull Florida State Museum Biol Sci* 4:349–371.
23. Olson SL, Hilgartner WG (1982) *Smithsonian Contrib Paleobiol* 48:22–56.
24. Suárez W, Olson SL (2001) *Proc Biol Soc Wash* 114:501–508.
25. Lawrence B (1934) *Boston Soc Nat Hist* 8:189–196.
26. Morgan GS (1989) in *Biogeography of the West Indies: Past, Present, and Future*, ed Woods CA (Sandhill Crane, Gainesville, FL), pp 685–740.
27. Morgan GS (2001) in *Biogeography of the West Indies: Patterns and Perspectives*, eds Woods CA, Sergile, FE (CRC Press, Boca Raton, FL), pp 369–406.
28. Carlson LA, Keegan WF (2004) in *Voyages of Discovery*, ed Fitzpatrick S (Westwood, Darien, CT), pp 85–107.
29. Keegan WF (2007) *Taino Indian Myth and Practice: The Arrival of the Stranger King* (Univ Press of Florida, Gainesville, FL).
30. Carr RS, Day J, Ransom J, Shaffer WC, Berialt J (2006) *Technical Report 4* (Archaeological and Historical Conservancy, Miami, FL).
31. Kjellmark E (1996) *J Paleolimnol* 15:133–145.
32. Pregill GK, Steadman DW, Watters DR (1994) *Bull Carnegie Museum Nat Hist* 30:1–51.
33. Newsom LA, Wing ES (2004) *On Land and Sea: Native American Uses of Biological Resources in the West Indies* (Univ of Alabama Press, Birmingham, AL).