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Domination by Reptiles in a Terrestrial Food Web of the Bahamas Prior to Human Occupation

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ABSTRACT.—Human activities in the Bahamas and other oceanic islands have damaged terrestrial ecosystems irreparably through the extinction of indigenous species. Tortoise and crocodile bones from Abaco Island in the Bahamas sampled for ¹⁴C-dating revealed a small overlap between the last occurrence of these large reptiles and early human settlement in the Bahamas. Before their extermination approximately 1,000 years ago, the dominant herbivore and carnivore on Abaco Island were the endemic Albury's Tortoise (*Chelonoidis alburyorum*) and the formerly widespread Cuban Crocodile (*Crocodylus rhombifer*). Stable isotope data from carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$) in bone collagen from Late Holocene fossils suggest that these large reptiles were part of a terrestrial rather than marine or estuarine food web. Our proposal that Cuban Crocodiles were once the apex terrestrial predator in the Bahamas is supported by comparisons with published $\delta^{13}\text{C}$ values for modern marine/estuarine crocodylians as compared to those of nonmarine reptilian and mammalian carnivores. For reptiles to occupy terrestrial trophic roles distinguishes Bahamian Islands from nearby Greater Antillean Islands (Cuba, Jamaica, Hispaniola, Puerto Rico) where endemic mammals represent the largest herbivores and carnivores in prehuman times. This distinction is even greater when compared with Late Quaternary mammals of prehuman vertebrate communities in neighboring North America.

During the past two decades, it has become apparent that few, if any, terrestrial plant or animal communities on tropical oceanic islands have been spared human impact (Woods and Sergile, 2001). Conspicuous among these impacts are the losses of indigenous, if not endemic, species and populations. For vertebrates, such extinctions (species-level losses) and extirpations (population-level losses) have depleted communities to a point where ecosystem function has been altered (Steadman, 2006). Learning how insular animal communities functioned before human arrival is critical for setting conservation goals for indigenous species. Well-preserved fossils are the primary source of information about the past biota of oceanic islands.

In 2004, scuba diver Brian Kakuk discovered the complete skeleton of an extinct tortoise in Sawmill Sink, an inland blue hole on Abaco in the northern Bahamas. "Blue hole" is a term applied to the entrances of water-filled voids in carbonate bedrock that extend below sea-level and often lead to flooded cave passages (Mylroie et al., 1995). Further diving in Sawmill Sink and other blue holes has disclosed abundant, superbly preserved vertebrate fossils (Steadman et al., 2007; Franz and Franz, 2009; Morgan and Albury, 2013). Here, we present new information from stable isotope ratios in bone collagen about the ecology of the largest herbivore (tortoise) and carnivore (crocodile) that occupied these islands in prehuman times. These mega-reptiles were part of a rare terrestrial vertebrate biota that lacks a modern analog (Williams and Jackson, 2007).

The Bahamas consist of 23 major islands and many smaller ones lying on shallow carbonate banks separated by deep water (Fig. 1). Our study focuses on Abaco, the second largest Bahamian island (1,681 km²; Sealey and Burrows, 1992). Sawmill Sink is an inland blue hole on Abaco with a nearly circular opening 15.5 m in diameter (Fig. 2). Its bell-shaped underwater profile is dominated by a talus cone (depth 9–34 m) of limestone rubble and Holocene peat rich in plant and

vertebrate fossils, including those of tortoises, crocodiles, and humans (Steadman et al., 2007; Franz and Franz, 2009). Lost Reel Cave is another blue hole on Abaco and fossils from tortoises and crocodiles found at this location are included in our analyses. To put the Abaco data in perspective with human presence in the archipelago, we also report isotopic and chronologic data from prehistoric human bones recovered from two blue holes (Sanctuary Cave, Stargate Cave) on Andros, the largest Bahamian island (5,959 km²; Sealey and Burrows, 1992). The prehistoric inhabitants of the Bahamas were Arawakan (Taino) peoples known as Lucayans (Keegan, 2007). Radiocarbon-dated evidence for the first arrival of Lucayans across the Bahamian Archipelago ranges from approximately 1,200 years ago in the south to approximately 1,000 years ago on northern islands (Carlson and Keegan, 2004; Keegan, 2007; Steadman et al., 2007). The first Lucayans in the Bahamas likely came from the large islands to the south, such as Cuba and Hispaniola, that were inhabited several millennia earlier. The early archaeological sites in the Bahamas have yielded abundant bones from species of reptiles, birds, and mammals that no longer occur in the islands (Steadman et al., 2007).

Modern Bahamian vertebrate communities feature substantial species- and subspecies-level endemism, although no endemic genera are known; most taxa are part of West Indian radiations with nearest relatives in the Greater Antilles, especially Cuba (Olson and Pregill, 1982; Steadman et al., 2007). Late Quaternary fossils document richer vertebrate communities before human arrival. For example, the fossil vertebrates from the Holocene peat at Sawmill Sink represent 13 species (2 reptiles, 10 birds, 1 mammal), among which both reptiles, two birds, and the mammal (rodent) no longer occur on Abaco (updated from Steadman et al., 2007). The fossils include at least 14 individuals of the extinct Albury's Tortoise (*Chelonoidis alburyorum*) (Franz and Franz, 2009), featuring the first intact shells of West Indian tortoise fossils ever found (Fig. 3). Known only from Abaco so far, we presume that *C. alburyorum* was endemic to islands on the Little Bahama Bank (Fig. 1). Endemic species of tortoises, all now extinct, once were widespread on Bahamian islands and

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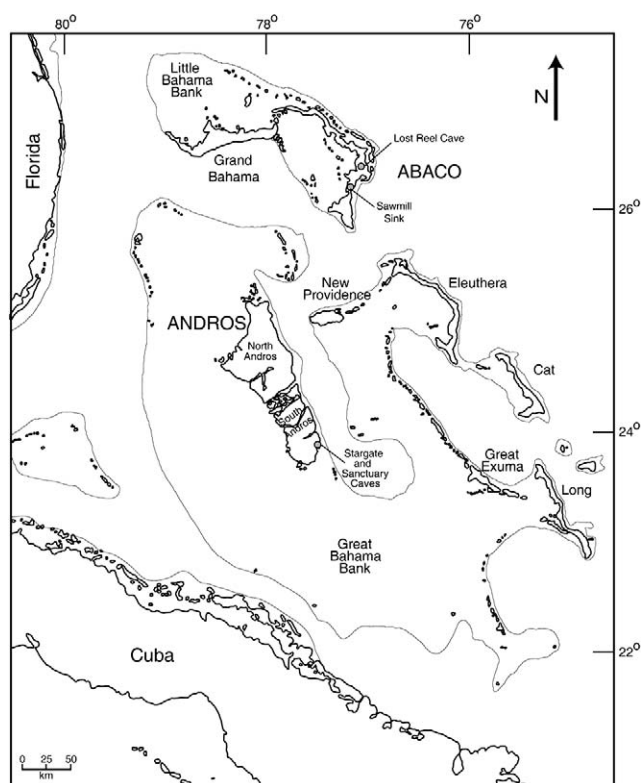


FIG. 1. Western portion of the Bahamian Archipelago, with fossil sites noted. Thin gray line represents the 200-m isobath.

the Greater Antilles (Carlson and Keegan, 2004; Franz and Franz, 2009).

The Cuban Crocodile (*Crocodylus rhombifer*) is the most common vertebrate at Sawmill Sink, with most of the 54 individuals including skulls and lower jaws (Fig. 3) as well as associated partial to nearly complete postcranial skeletons. The Cuban Crocodile is restricted now to freshwater habitats in Zapata Swamp on Cuba and Lanier Swamp on Isle of Pines (Ross, 1998). *Crocodylus rhombifer* is convergent on the terrestrial mekosuchine crocodiles of the southwest Pacific (Mead et al., 2002) in having a distinctively broad, high, and short rostrum and a highly differentiated tooth row (very crooked bite margins, highly variable tooth size; De Sola, 1930; Varona, 1984; Morgan et al., 1993). A post-cranial terrestrial adaptation of *C. rhombifer* is that its body is elevated and its head is held erect when standing (De Sola, 1930). Also it has been known to traverse long distances on land, for a crocodylian, and prey on terrestrial mammals (Soberón et al., 2001).

Although it is now well established that prehistoric human arrival on oceanic islands led to the extinction of many species of vertebrates (e.g. Steadman, 2006; Borroto-Páez et al., 2012), we are only beginning to understand the roles played by extinct species in prehistoric ecosystems. Because stable isotope values from bone reflect diet (Peterson and Fry, 1987; Lee-Thorp, 2008), the study of stable isotopes from bone collagen (a protein biomolecule) can give important clues as to how an extinct species functioned in ancient food webs.

Carbon is ubiquitous in plant and animal tissues, and most carbon is derived from atmospheric CO_2 . There are three principle isotopes of carbon, one radioactive (^{14}C) and two stable isotopes, ^{13}C and ^{12}C , the latter considerably more abundant in natural systems (Bowling et al., 2008). Stable isotope ratios of carbon ($^{13}\text{C}/^{12}\text{C}$) vary in plants, the primary

producers, depending on their mode of photosynthesis or how plants incorporate carbon into their tissues (Bowling et al., 2008). Terrestrial plants derive carbon from atmospheric CO_2 (avg. $\delta^{13}\text{C} = -7.8\text{‰}$), and most woody plants follow the C_3 (Calvin) photosynthetic pathway with $\delta^{13}\text{C}$ values averaging -28.5‰ (typical range -20 to -37‰ ; O'Leary, 1981, 1988; Kohn, 2010). Certain arid-adapted plants, especially grasses, follow instead the C_4 (Hatch-Slack) photosynthetic pathway, with $\delta^{13}\text{C}$ values averaging -12‰ (typical range -10 to -16‰). Significantly, C_3 and C_4 plants do not overlap in $\delta^{13}\text{C}$ value and this isotopic distinction is maintained in the tissues of consumers that eat the plants, although intermediate $\delta^{13}\text{C}$ values can result in the consumer tissue of animals with a mixed C_3 – C_4 diet (van der Merwe and Vogel, 1978; Schoeninger and DeNiro, 1984; Hobbie and Werner, 2004). A third group of plants (e.g., succulents and bromeliads) use a third form of photosynthesis referred to as Crassulacean Acid Metabolism (CAM), and these plants have intermediate $\delta^{13}\text{C}$ values between C_3 and C_4 plants.

In contrast to terrestrial systems, carbon in the ocean occurs as dissolved bicarbonate (HCO_3^-) with a $\delta^{13}\text{C}$ value of 0‰ , thereby enriched in ^{13}C by approximately 7 – 8‰ compared to that of atmospheric CO_2 (Hoefs, 2009). Therefore, marine consumers are enriched in ^{13}C and as a result exhibit less negative $\delta^{13}\text{C}$ values compared to terrestrial consumers. The use of bone collagen offers isotopic data for long-term protein consumption of approximately $10+$ years (Ambrose, 1990), and a slight trophic effect in $\delta^{13}\text{C}$ values (approximately $+1\text{‰}$) can distinguish between primary consumers, secondary consumers, etc. (Schoeninger and DeNiro, 1984; Abrantes et al., 2013). Where C_4 and CAM plants are not a factor in the diet, $\delta^{13}\text{C}$ values in consumer tissue can distinguish between animals with terrestrial diets versus those with marine diets (Chisholm et al., 1982; Richards and Hedges, 2003; Milman et al., 2010).

Nitrogen stable isotopes derive principally from atmospheric N_2 that may be variably incorporated into plant tissue (e.g., leguminous vs. nonleguminous plants). In consumer tissue, nitrogen is derived principally from dietary protein. Nitrogen stable isotope ratios ($^{15}\text{N}/^{14}\text{N}$) demonstrate stepwise enrichment of approximately $+3\text{‰}$ per trophic level in bone collagen (Schoeninger et al., 1983). When coupled with $\delta^{13}\text{C}$, the $\delta^{15}\text{N}$ values of consumer tissue can help to clarify the isotopic complexity of a mixed C_3/C_4 diet, as well as suggest a consumer's relative trophic position (Schoeninger and DeNiro, 1984; Milman et al., 2010; Abrantes et al., 2013). Guided by these



FIG. 2. Exterior of Sawmill Sink, Abaco, Bahamas. Diver Brian Kakuk stands on the dive platform.

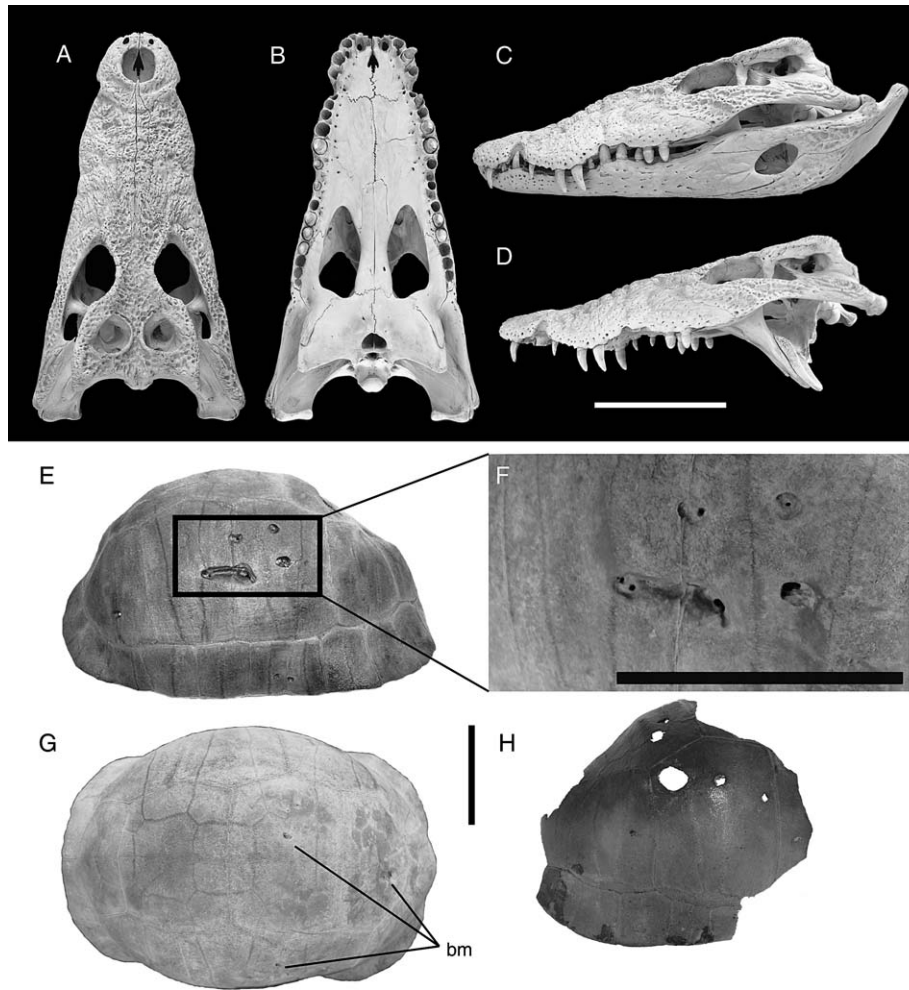


FIG. 3. Fossils of the Cuban Crocodile, *Crocodylus rhombifer*, and extinct tortoise, *Chelonoidis alburyorum*, from Abaco, Bahamas. (A–D) NMB.AB50.021, adult skull of *C. rhombifer* in dorsal view (A), ventral view (B), lateral view with mandible (C), and lateral view without mandible (D). (E–G) NMB.AB50.0007, adult complete shell of *C. alburyorum* (with healed bite marks from the Cuban Crocodile) in lateral view (E, F) and dorsal view (G). (H) NMB.MY11.0001, adult partial carapace of *C. alburyorum*, with fully penetrating bite marks from the Cuban Crocodile. Scale bars = 10 cm.

and related concepts of bone isotope biogeochemistry, we investigated the trophic roles of the large herbivores and carnivores that existed in the Bahamas until only a millennium ago.

MATERIALS AND METHODS

Underwater paleontological operations in blue holes involve industry-standard cave-diving techniques and scientific diving protocols (Steadman et al., 2007; Franz and Franz, 2009). All fossils are sealed in Ziploc® bags and plastic boxes to secure them during transport as well as retain the original water chemistry (typically anoxic salt water). Preparation in the lab consists of a series of increasingly fresh water washes (to remove salts), followed by gradual air drying. No chemicals are applied to the fossils, which are cataloged in the collections of the National Museum of the Bahamas (NMB), with representative specimens housed in the Florida Museum of Natural History, at the University of Florida (UF).

Our chronological data are based on accelerator-mass spectrometer (AMS) radiocarbon (^{14}C) dates from ultrapurified collagen in individual cortical bones identified to species (tortoise, crocodile, and human). Sample pretreatment and

analysis were conducted by Beta Analytic, Inc. (see Appendix 1 for sampling details).

Fossils of tortoises, crocodiles, and humans (Fig. 4) were sampled for stable isotopes by the authors at the Bone Chemistry Laboratory (Department of Anthropology), University of Florida in Gainesville, Florida. Bone collagen stable isotope ratios of carbon ($^{13}\text{C}/^{12}\text{C}$) and nitrogen ($^{15}\text{N}/^{14}\text{N}$) are reported in delta notation ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) in parts per thousand, or per mil (‰) against their respective standards (VPDB and AIR). For isotopic sampling methods and conventions, see Appendix 1. Humans were included in the study to provide comparative information as to their influence on the ancient food web of the Bahamas.

RESULTS

We report 13 AMS ^{14}C dates on purified collagen from single bones of different individual tortoises ($N = 5$), crocodiles ($N = 5$), and humans ($N = 3$) from talus surfaces in the blue holes (Table 1). There is no stratigraphic reason to expect one specimen to be older than any other. Each ^{14}C date is within the Late Holocene, a time interval with minimal change in climate and sea level in the West Indies (Steadman et al., 2005). At 2σ (95.4% confidence), the five ^{14}C dates on tortoise bone



FIG. 4. Subset of representative bones from Sawmill Sink, Abaco, Bahamas, sampled for stable isotope collagen analysis. (A) *Homo sapiens*, NMB.AB50.0691, tibia. (B) *Crocodylus rhombifer*, NMB.AB50.0048, ulna. (C) *Crocodylus rhombifer*, NMB.AB50.0698, humerus. (D) *Chelonoidis alburyorum*, NMB.AB50.0008, humerus. (E) *Crocodylus rhombifer*, NMB.AB50.0029, radius. Scale bar = 10 cm.

(which range from 2880–2750 to 920–780 Cal BP) include two that overlap with the oldest ^{14}C date on sampled human bones, demonstrating that humans and this extinct species existed contemporaneously. The adult human tibia from the peat deposit at Sawmill Sink dates to 1050–920 Cal BP (Table 1), which is the oldest direct ^{14}C date on a human bone in the Bahamas. The five ^{14}C -dated bones of the Cuban Crocodile range from 4410–4080 Cal BP to 2890–2770 Cal BP. The youngest

crocodile ^{14}C date overlaps with the two oldest tortoise dates. Nevertheless, we know that the Cuban Crocodile survived on Abaco into the time of human occupation because of crocodile bite marks on the carapace of tortoise NMB.AB50.0008, which is ^{14}C dated at 970–920 Cal BP.

The human isotope values show a narrow range of both $\delta^{15}\text{N}$ (9.6–10.7‰) and $\delta^{13}\text{C}$ values (–14.8 to –16.0‰; Table 2; Fig. 5) relative to those of tortoise or crocodile. The Cuban Crocodile samples also exhibit a narrow range of $\delta^{15}\text{N}$ (5.7–7.4‰) but exhibit more variable $\delta^{13}\text{C}$ values (–16.4 to –20.9‰). The $\delta^{13}\text{C}$ values for Albury's Tortoise are consistent (–21.1 to –22.9‰), but one sample (NMB.AB50.0008) had an anomalously high $\delta^{15}\text{N}$ value (+8.8‰) compared to that of the two other specimens (+2.5, +4.4‰). Beta Analytic, Inc. also tested this sample and reported a $\delta^{15}\text{N}$ value of +9.4‰, suggesting that this individual sample did indeed have a high $\delta^{15}\text{N}$ value.

DISCUSSION

Tortoise Herbivory.—The tortoise $\delta^{13}\text{C}$ values all being less than –20‰ confirm an herbivorous terrestrial C_3 diet, matching well with low-trophic feeders (vertebrates that do not regularly eat other vertebrates) from nonmarine habitats (Shoener and DeNiro, 1984; Figs. 6–7). Of the three tortoise collagen samples, two have $\delta^{15}\text{N}$ values that are also within a predictable terrestrial herbivore value (Fig. 7). These two tortoises lived prior to known human occupation of the island. The Bahamas have C_3 -plant-dominant terrestrial ecosystems, surrounded completely by marine ecosystems. Two other fossil tortoise shells from Sawmill Sink contained abundant pericarps and seeds of two sapotaceous C_3 trees (mastic *Mastichodendron foetidissimum* and satinleaf *Chrysophyllym oliviforme*; Franz and Franz, 2009).

The one tortoise that lived when humans were present on Abaco, had a high $\delta^{15}\text{N}$ value (+8.8‰; NMB.AB50.0008), which may be explained by an unusually large amount of carrion in its diet. Living congeneric species of Neotropical tortoises (*Chelonoidis denticulata* and *Chelonoidis carbonaria*) are known to consume carrion (Pritchard and Trebbau, 1984). Considering this is a single data point, no strong explanations can be determined for the reason for this apparent shift in tortoise diet at the onset of human occupation. Perhaps carrion was easier to obtain after humans occupied the island, and this tortoise may have scavenged food scraps.

These extinct Albury's Tortoises were the largest terrestrial herbivores in Bahamian prehistory (max. carapace length 466 cm; max. body mass approximately 25 kg; Franz and Franz, 2009). The next largest herbivore from the Bahamas was also a reptile, the Rock Iguana *Cyclura carinata* that is now extirpated from most islands, including Abaco (max. adult body mass approximately 2.6 kg, ♀; Pregill, 1982; Iverson et al., 2004). The only isotope data for the rock iguana are from an individual from the Turks and Caicos Islands with a reported $\delta^{13}\text{C}$ value of –19.5‰ and a $\delta^{15}\text{N}$ value of +6.0‰ (Keegan and DeNiro, 1988), similar to the tortoise values. The only native mammalian herbivore is the Bahamian Hutia, *Geocapromys ingrahami*, now extirpated from most islands, including Abaco (max. adult body mass 0.95 kg; Clough, 1972; Olson and Pregill, 1982). The single published Bahamian Hutia value ($\delta^{15}\text{N}$ 4.1‰) is comparable to the $\delta^{15}\text{N}$ of two of the three tortoises sampled (Keegan and DeNiro, 1988).

Crocodile Carnivory.—The collagen isotopic data for the Cuban Crocodile samples suggest they fed within a terrestrial

TABLE 1. Radiocarbon (^{14}C) data for specimens of Cuban Crocodile (*Crocodylus rhombifer*), Albury's Tortoise (*Chelonoidis alburyorum*), and human (*Homo sapiens*) from the Bahamas. NMB, National Museum of the Bahamas.

| Island | Site | Species | Skeletal element | Specimen | Sampling number | Measured ^{14}C age (yr BP) | $\delta^{13}\text{C}$ | ^{14}C age (Cal BP, 2σ) |
|--------|----------------|-----------|------------------|---------------|-----------------|--------------------------------------|-----------------------|--|
| Abaco | Sawmill Sink | Crocodile | radius | NMB.AB50.0029 | Beta-298217 | 2620 \pm 30 | -17.0 | 2920–2900, 2890–2770 |
| Abaco | Sawmill Sink | Crocodile | humerus | NMB.AB50.0696 | Beta-230221 | 2900 \pm 50 | -19.3 | 3340–3000 |
| Abaco | Sawmill Sink | Crocodile | radius | NMB.AB50.0030 | Beta-298218 | 3440 \pm 30 | -16.5 | 3970–3830 |
| Abaco | Sawmill Sink | Crocodile | dorsal vertebra | NMB.AB50.0019 | Beta-230223 | 3680 \pm 50 | -19.0 | 4340, 4290–4060, 4050–3990 |
| Abaco | Sawmill Sink | Crocodile | femur | NMB.AB50.0364 | Beta-230222 | 3680 \pm 50 | -16.4 | 4410–4080 |
| Abaco | Lost Reel Cave | Tortoise | carapace | NMB.AB52.0039 | Beta-298220 | 880 \pm 30 | -22.1 | 920–780 |
| Abaco | Sawmill Sink | Tortoise | humerus | NMB.AB50.0008 | Beta-298219 | 940 \pm 30 | -20.3 | 970–920 |
| Abaco | Lost Reel Cave | Tortoise | humerus | NMB.AB52.0040 | Beta-298221 | 1130 \pm 30 | -20.9 | 1230–1210, 1180–1060 |
| Abaco | Sawmill Sink | Tortoise | scapula | NMB.AB50.0003 | Beta-225509 | 2520 \pm 50 | -21.1 | 2770–2690, 2640–2610, 2590–2500 |
| Abaco | Sawmill Sink | Tortoise | dorsal vertebra | NMB.AB50.0001 | Beta-225508 | 2660 \pm 40 | -21.2 | 2880–2,750 |
| Andros | Sanctuary Cave | Human | humerus | NMB.AN12.0003 | Beta-268510 | 520 \pm 40 | -14.8 | 690–630, 600–560 |
| Andros | Stargate Cave | Human | radius | NMB.AN13.0001 | Beta-268511 | 620 \pm 40 | -16.0 | 740–660 |
| Abaco | Sawmill Sink | Human | tibia | NMB.AB50.0691 | Beta-228852 | 870 \pm 30 | -14.7 | 1050–1030, 1000–920 |

ecosystem. Like these crocodiles, terrestrial tetrapod carnivores from nonpolar regions have bone collagen $\delta^{13}\text{C}$ values less than -15.5‰ (Shoeninger and DeNiro, 1984; Figs. 6–7). Coupled with the high $\delta^{15}\text{N}$ values, this suggests a principally nonmarine diet for the crocodile. The only surface fresh water in the Bahamas is in the upper water layer of certain blue holes; this fresh water lens sustains no fish, meaning that the inland Cuban Crocodiles in the Bahamas must have depended on nonaquatic terrestrial foods.

Healed and unhealed bite marks on several Albury's Tortoise shells suggest predation by crocodiles (Fig. 3; Table 3). Furthermore, data from Late Quaternary fossils on Grand Cayman suggest *C. rhombifer* consumed hutias (Morgan and Albury, 2013). The Cuban Crocodile samples are more enriched in ^{13}C (-16.4‰ to -20.9‰) than the tortoise samples which is typical for predator–prey relationships. Because the crocodiles were unlikely to have eaten plants, their $\delta^{13}\text{C}$ values represent enrichment from the more negative $\delta^{13}\text{C}$ values of their herbivorous prey (tortoises, iguanas, and hutias; Figs. 3, 7). Similar levels of enrichment are seen in the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of terrestrial carnivores versus herbivores in Late Pleistocene fossils from Rancho La Brea, California (Coltrain et al., 2004), as well as in modern and Late Pleistocene terrestrial mammals from Europe (Bocherens and Drucker, 2003). Modern *C. rhombifer* are known to regularly consume the large Cuban

Hutia, *Capromys pilorides* (De Sola, 1930; Targarona et al., 2010). Furthermore, the terrestrial life style of *C. rhombifer* relative to other living crocodylian species has been noted based on observations of the living population, including long-distance travel by land and a jumping-based hunting strategy for obtaining hutias (Soberón et al., 2001; Morgan and Albury, 2013).

Wheatley et al. (2012) presented bone collagen $\delta^{13}\text{C}$ values for coastal *Crocodylus acutus* (-2.5 to -14.5‰ , mean -9.6‰ , $N = 9$), coastal *Alligator mississippiensis* (-7 to -15.1‰ , mean -10.3‰ , $N = 16$), and inland *A. mississippiensis* (-13 to -17.6‰ , mean -15.7‰ , $N = 12$). Our $\delta^{13}\text{C}$ values for *C. rhombifer* (-16.4 to -20.9‰ , $N = 8$) lie outside the range for coastal *C. acutus* and coastal *A. mississippiensis* but instead are more depleted, as those of inland *A. mississippiensis*. Rosenblatt and Heithaus (2011, 2013) also reported more negative $\delta^{13}\text{C}$ values for *A. mississippiensis* that fed only in freshwater compared to those feeding in estuarine habitats.

Based on skull length data presented in Morgan and Albury (2013) and size regressions based on *Crocodylus porosus* (Seren et al., 2001), we estimated total body length of Quaternary *C. rhombifer* from Abaco, Grand Cayman, and Cuba. For the island of Abaco they ranged from 1.22–2.27 m (4–7.46 ft). The fossil *C. rhombifer* from Grand Cayman was of a similar size, 1.59–1.93 m (5.21–6.32 ft). The fossils reported from Cuba were much larger,

TABLE 2. Stable isotope ($\delta^{15}\text{N}$, $\delta^{13}\text{C}$) data for specimens of Cuban Crocodile (*Crocodylus rhombifer*), Albury's Tortoise (*Chelonoidis alburyorum*), and human (*Homo sapiens*) from the Bahamas.

| Island | Site | Species | Skeletal element | Specimen | Isotope Sample Number | $\delta^{15}\text{N}$ | $\delta^{13}\text{C}$ |
|--------|----------------|-----------|------------------|----------------------------|-----------------------|-----------------------|-----------------------|
| Abaco | Sawmill Sink | Crocodile | radius | NMB.AB50.0030 ^a | C-9-1623 | 7.4 | -18.1 |
| Abaco | Sawmill Sink | Crocodile | radius | NMB.AB50.0029 ^a | C-9-1624 | 6.0 | -17.7 |
| Abaco | Sawmill Sink | Crocodile | humerus | NMB.AB50.0049 | C-9-1631 | 6.19 | -17.5 |
| Abaco | Sawmill Sink | Crocodile | ulna | NMB.AB50.0699 | C-9-1628 | 6.60 | -16.4 |
| Abaco | Sawmill Sink | Crocodile | humerus | NMB.AB50.0698 | C-9-1627 | 5.70 | -17.4 |
| Abaco | Sawmill Sink | Crocodile | humerus | NMB.AB50.0050 | C-9-1632 | 6.67 | -20.9 |
| Abaco | Sawmill Sink | Crocodile | tibia | NMB.AB50.0047 | C-9-1629 | 6.82 | -20.5 |
| Abaco | Sawmill Sink | Crocodile | hyoid | NMB.AB50.0700 | C-9-1658 | 6.75 | -18.9 |
| Abaco | Sawmill Sink | Tortoise | humerus | NMB.AB50.0008 ^a | C-9-1630 | 8.85 | -21.1 |
| Abaco | Lost Reel Cave | Tortoise | humerus | NMB.AB52.0040 ^a | C-9-1666 | 2.48 | -22.9 |
| Abaco | Lost Reel Cave | Tortoise | carapace | NMB.AB52.0039 ^a | C-9-1667 | 4.36 | -22.8 |
| Abaco | Sawmill Sink | Human | tibia | NMB.AB50.0691 ^a | C-9-1668 | 9.60 | -15.8 |
| Andros | Sanctuary Cave | Human | humerus | NMB.AN12.0003 ^a | Beta-268510 | 10.7 | -14.8 |
| Andros | Stargate Cave | Human | radius | NMB.AN13.0001 ^a | Beta - 268511 | 10.1 | -16.0 |

^aSpecimen also radiocarbon dated (see Table 1).

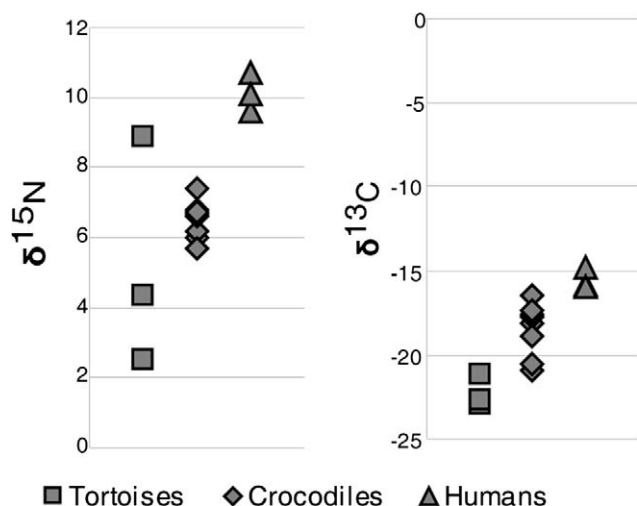


FIG. 5. $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ isotopic values derived from collagen of 14 bone samples (*Crocodylus rhombifer*, *Chelonoidis alburyorum*, and *Homo sapiens*) from blue holes on Abaco and Andros, Bahamas (see data in Table 2).

ranging from 2.38–4.04 m (7.82–13.26 ft). These values are similar to those reported in Morgan and Albury (2013), which were based on a skull to body-length ratio. Morgan and Albury (2013) suggested that Cuban Crocodiles were larger than those on the Bahamian islands because of the availability of large mammals (e.g. sloths, monkeys, large rodents) as prey. The larger landmass of Cuba likely contributed to the greater presence of terrestrial mammals compared to other smaller islands.

Human Omnivory.—Humans were included in this study primarily to provide indications of their impact on the ancient terrestrial food web of the Bahamas. Only one human bone was recovered from the island of Abaco, but two more were recovered from the nearby island of Andros and were included to provide a greater context than a single individual (Table 2). The $\delta^{13}\text{C}$ values (−14.8 to −16.0‰; Fig. 6, Table 2) found in human bone suggest a diet without C_4 plants (maize and certain native grasses) or isotopically intermediate CAM plants such as cactus. Both C_4 and CAM plants are rare on Abaco and Andros but are more common in the arid southern part of the Bahamas. Terrestrial fruit consumption is unlikely to have played a large part in their diet, because this would yield lower $\delta^{15}\text{N}$ values (Hobbie and Werner, 2004). Two widespread, indigenous trees with highly edible fruit in the Bahamas are the mastic (*Mastichodendron foetidissimum*) and dilly (*Manilkara bahamensis*), but both only bear fruit seasonally.

The human $\delta^{15}\text{N}$ values (9.6–10.7‰) suggest that their diet included meat, with all three samples having values greater than those of the crocodiles (Fig. 5). Given the overlap of ^{14}C dates for tortoises and humans, it is likely that early human settlers ate some terrestrial game such as tortoises, iguanas, hutias, and crocodiles while these species still existed on the island. Nevertheless, the high $\delta^{15}\text{N}$ values suggest that the early human settlers took much of their diet from marine sources, primarily fish and mollusks that have more elevated concentrations of $\delta^{15}\text{N}$ (Keegan and DeNiro, 1988; Milman et al., 2010).

Human values from Puerto Rico show very similar levels of $\delta^{15}\text{N}$ but more commonly have lower $\delta^{13}\text{C}$ values (Fig. 7; Stokes, 2005). This suggests the early Bahamians fed on roughly similar proportions of marine and terrestrial diet but likely consumed less C_4 plants (such as maize) than the early inhabitants of

Puerto Rico. After the loss of tortoises, iguanas, hutias, and crocodiles in the Bahamas, the human diet probably became more marine oriented. Further study of more recent Bahamian humans could test this.

Human Impact on Ancient Bahamian Terrestrial Food Web.—The Bahamas once sustained a terrestrial food web where the largest carnivore (Cuban Crocodile) and the two largest herbivores (Albury's Tortoise, Rock Iguana) were reptiles. The population densities of these animals before human arrival may have been large, but this cannot be determined directly from fossil evidence. The second largest carnivores in the prehistoric Bahamas were a Barn Owl, *Tyto pollens*, and an eagle, *Titanohierax gloveralleni*, both known from islands on the Great Bahama Bank but not yet from Abaco or other islands on the Little Bahama Bank (Olson and Pregill, 1982; Steadman et al., 2007). These avian predators were much smaller than the crocodile but would have been capable of preying on juvenile tortoises. Having reptiles in apex trophic roles distinguishes Bahamian islands from the nearby Greater Antillean islands (Cuba, Jamaica, Hispaniola, Puerto Rico) where a variety of endemic mammals (sloths, monkeys, insectivores, large rodents) lived in prehuman times (Morgan and Woods, 1986; Silva Taboada et al., 2007; Borroto-Páez et al., 2012). The Cuban Crocodile was indeed more widespread in the Quaternary, including known fossil locations on Grand Bahama, mainland Cuba, and Grand Cayman (Varona, 1984; Morgan et al., 1993; Morgan and Albury, 2013). Also, an indeterminate crocodylian tooth was recovered from an inland cave on Puerto Rico (Vélez-Juarbe and Miller, 2007). The Cuban Crocodile was likely present on the Great Bahama Bank as well, although fossils recovered thus far from these islands are not diagnostic enough to determine that they do not belong instead to the more marine-adapted *C. acutus* (Morgan and Albury, 2013). Fossil tortoises are known from Hispaniola and Cuba (Auffenberg, 1967; Franz and Woods, 1983). On each of these islands, however, tortoises shared the role of largest herbivores with ground sloths (Borroto-Páez et al., 2012).

The Bahamian mega-herbivore and mega-carnivore fauna were even more different from that of nearby Florida, where 23 families of large (>10 kg) mammalian herbivores (edentates, perissodactyls, artiodactyls, proboscideans) and carnivorans (felids, ursids, canids) lived until human arrival in the Late Pleistocene (Hulbert, 2001).

The loss of tortoises and crocodiles in the Bahamas correlates chronologically with human settlement and mirrors a pattern of loss associated with human occurrence in the Greater Antilles

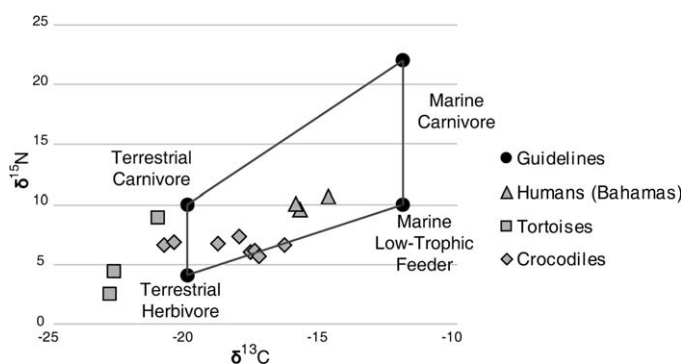


FIG. 6. Bahamian bone collagen isotopic values plotted against established guidelines for terrestrial- versus marine-derived food sources (Richards and Hedges, 2003).

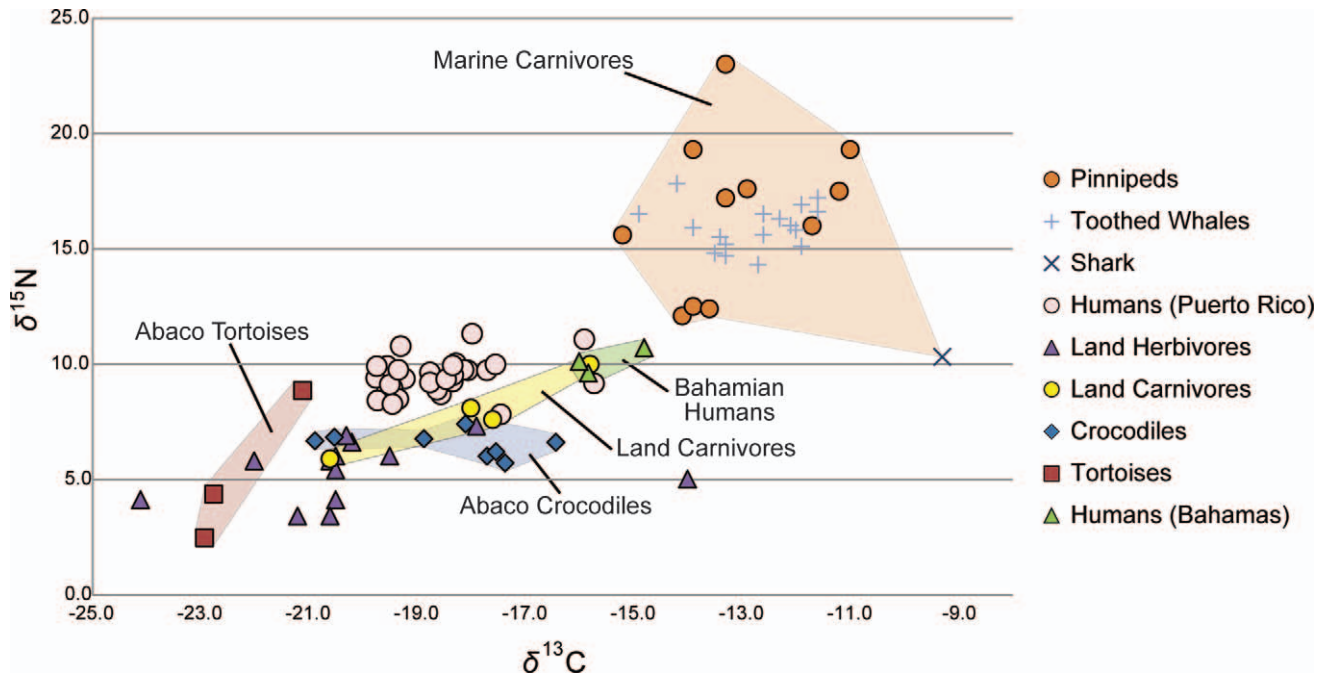


FIG. 7. $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ -isotopic values derived from bone collagen plotted against known bone collagen isotopic values for terrestrial and marine organisms, including early human data from Puerto Rico. Isotopic data were compiled from three literature sources (Schoeninger and DeNiro, 1984; Keegan and DeNiro, 1988; Stokes, 2005). Values for crocodiles, tortoises, and Bahamian humans are all from this study.

(ground sloths, e.g., *Neocnus*, *Parocnus*; Steadman et al., 2005) and numerous other species of mammals, birds, and reptiles across the Caribbean region (Morgan and Woods, 1986; Pregill et al., 1994; Newsom and Wing, 2004). Given the presence of *C. rhombifer* on other islands in the Caribbean (Varona, 1984; Morgan et al., 1993; Morgan and Albury, 2013), as well as large tortoises, the scenario of extinction and extirpation in Abaco may have played out many times on other islands of the circum-Caribbean. No major island in the Bahamas (or elsewhere in the West Indies) has been spared human influence (especially the loss of indigenous species and introduction of nonnative species), and today there are no insular vertebrate communities functioning as they would have under prehuman conditions. The food web of Abaco was restructured after people arrived with the loss of all three large reptile species (*C. alburyorum*, *C. rhombifer*, and *C. carinata*).

There is no modern terrestrial ecosystem like that of Abaco before human occupation, with reptiles being both the largest herbivore and the largest carnivore. Even modern island examples such as Komodo and Flores of Indonesia with the

large varanid predator, the Komodo Dragon, *Varanus komodoensis* (Ciofi et al., 2011) lack a large reptilian herbivore. In turn, the Galapagos have large herbivorous tortoises but lack a large reptilian carnivore (Blake et al., 2012). The closest similarity for Abaco appears to be the Pacific island of Vanuatu, which possessed mekosuchine crocodyliforms thought to have been herbivorous (Mead et al., 2002) and meiolaniid turtles thought to have been herbivorous (White et al., 2010), both present right up until shortly after human occupation of the island. However, isotopic studies have not been conducted to determine trophic position, terrestriality, and diet of these animals. Realizing a need for herbivorous function on islands, Hansen et al. (2010) have called for introducing tortoises of various species to islands where they have been extirpated; perhaps, selectively, the same could be done with Cuban Crocodiles (as well as tortoises) in the Bahamas. Conservation efforts enacted on Round Island in the Pacific to preserve rare reptile species by removing invasive rabbits and goats experienced some success in increased reptile populations (Bullock et al., 2002).

TABLE 3. Crocodylian bite marks on fossil tortoise shells (*Chelonoidis alburyorum*) from the Bahamas. Bite marks are divided into readily recognized, definite marks and less clear possible marks. The possible bite marks do not represent full penetration of the carapace/plastron. All specimens are housed in the National Museum of the Bahamas (NMB).

| Site | Island | Number of individuals | Number of individuals with definite marks | Number of individuals with possible marks |
|-------------------------|-----------|-----------------------|---|---|
| Sawmill Sink | Abaco | 10 | 2 (NMB.AB50.0007, NMB.AB50.0008) | 1 (NMB.AB50.0682) |
| Dan's Cave | Abaco | 2 | 0 | 1 (NMB.AB53.006) |
| Ralph's Cave | Abaco | 2 | 2 (NMB.AB51.001, NMB.AB51.007) | 0 |
| Nancy's Cave | Abaco | 2 | 1 (NMB.AB57.006) | 0 |
| Cherokee Road Extension | Abaco | 1 | 0 | 0 |
| Lost Reel Cave | Abaco | ~8 | 0 | 0 |
| Prophet's Cave | Abaco | 1 | 0 | 0 |
| Bung Hole | Eleuthera | 1 | 1 (EL180.012) | 0 |
| The Fountain | Mayaguana | 1 | 1 (MY11.001) | 0 |
| Total (Abaco) | | ~26 | 5 | 2 |
| Total (all islands) | | ~28 | 7 | 2 |

Stable isotope data are a potentially rich source of new information about the function of prehuman island ecosystems. Because human activities have depleted native vertebrate communities on virtually all tropical islands (Steadman, 2006), carbon and nitrogen stable isotope ratios ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) are important to discern the structure of food webs in prehuman times. This may be particularly relevant for the Cuban Crocodile, which is a little studied, endangered species today (Ross, 1998). With so few individuals alive in nature, a better understanding of its natural role in ecosystems might improve this crocodile's prospects for survival.

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APPENDIX 1

Sampling Method for ^{14}C Dating.—Our chronological data are based on accelerator-mass spectrometer (AMS) radiocarbon (^{14}C) dates from purified collagen in individual bones identified to species. Pretreatment of each sample (at Beta Analytic, Inc.) consisted of physical cleaning, followed by scraping the external surface, crushing the bone, and then a series of acid/alkali/acid washes to purify the collagen, limit absorption of atmospheric CO_2 , and remove potential contaminants (humic acids, fulvic acids, secondary carbonates). The pretreated samples were oxidized to CO_2 , cryogenically purified, converted to graphite, and then placed into the AMS for counting. The results are reported using standard ^{14}C conventions (Heaton et al., 2009; Reimer et al., 2009).

Sampling Method for Carbon ($^{13}\text{C}/^{12}\text{C}$) and Nitrogen ($^{15}\text{N}/^{14}\text{N}$) Isotopic Ratios.—We used a modified Longin method (Longin, 1971; Ambrose, 1990) to acquire and purify bone collagen samples for isotopic analysis. The bones (Fig. 4) were sampled using a Dremel MultiPro, Model 395 with a 1/4-inch cutting disc. Bone samples with good cortical integrity were selected and soaked in deionized, distilled water, sonicated for 30 min, completely air dried, ground using a mortar and pestle, and sieved through a 500 μ screen. Approximately 200 mg of the 250–500- μ fraction was transferred to pre-weighed 15 ml centrifuge tubes. The samples were demineralized for 10–16 h by adding 12 mL of 0.2 M HCl, centrifuged ($\sim 3,500$ rpm), drained, and refreshed with new 0.2 M HCl. This process was repeated until the bone collagen had equalized with the HCl. Samples were rinsed to normal pH (3 times). Then ~ 12 mL of 0.125 M NaOH was added for 16–20 h to remove humic acids (Ambrose, 1990). Samples were rinsed again to normal pH, acidified with 12 mL of 10^{-3} M HCl, transferred to 20 mL scintillation vials, and placed in an oven at 95°C for 4–5 h to break the collagen helix and allow them to go into solution. Samples then were centrifuged, and the liquid solution was placed into the DI-rinsed scintillation vials with loosened caps in a different oven at 60 – 65°C . Once collagen was reduced to approximately 2 mL in the vials, samples were capped and frozen. Purified bone collagen was lyophilized (freeze-dried), and then 0.8–1.0 mg of sample was loaded into tin capsules for elemental analysis (C:N) using a Carlo Erba elemental analyzer. The $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ analyses were done using a Finnigan DeltaPlus isotope ratio mass spectrometer. Samples were measured against USGS40 (RM 8573) standard with certified values for $\delta^{13}\text{C}_{\text{VPDB}}$ ($-26.39 \pm 0.09\text{‰}$) and $\delta^{15}\text{N}_{\text{AIR}}$ ($-4.52 \pm 0.12\text{‰}$). Precision of the analytical runs ($N = 7$) for $\delta^{13}\text{C}_{\text{VPDB}}$ was 0.071‰ and for $\delta^{15}\text{N}_{\text{AIR}}$ was 0.128‰.