

Fossil Land Tortoises (Testudines: Testudinidae) from the Dominican Republic, West Indies, with a Description of a New Species

NANCY A. ALBURY,¹ RICHARD FRANZ,² RENATO RIMOLI,³ PHILLIP LEHMAN,⁴
AND ALFRED L. ROSENBERGER⁵

ABSTRACT

A new fossil tortoise, *Chelonoidis dominicensis*, is described from a flooded cave in La Altigracia Province in the southeastern Dominican Republic on the island of Hispaniola. The holotype, and only known specimen, includes a nearly complete shell, skull, and appendicular skeleton. The new Dominican species, *Chelonoidis dominicensis*, shares morphological features with the Bahamian tortoise, *Chelonoidis alburyorum*, and the Cuban tortoise, *Chelonoidis cubensis*. *Chelonoidis dominicensis* can be distinguished from *C. alburyorum* by its weak prognathous-shaped rostrum, stronger and sharper vomerine septum, more angular posterior skull margins, distinctive caudal hump as seen in shell profile, the centrum of first dorsal vertebra narrow without a strong ventral keel, massive sacral buttresses, weak presacral and sacral ribs, more tapered anterior plastral lobe with prominent gulars, elevated gular shelf. An interclavicular sculpture (bird face) occurs on the internal surface of the entoplastron, composed of a massive brow-line and an elongated, narrow keel (beak). *Chelonoidis dominicensis* is distinguished from *C. cubensis* (based on incomplete specimens), by its more narrow anterior plas-

¹ National Museum of the Bahamas/Antiquities, Monuments and Museum Corporation, Marsh Harbour, Abaco, the Bahamas.

² Florida Museum of Natural History, University of Florida, Gainesville, Florida.

³ Department of Biology, Universidad Autónoma de Santo Domingo, Ciudad Universitaria, Santo Domingo, Dominican Republic, and Museo del Hombre Dominicano, Santo Domingo, Dominican Republic.

⁴ Dominican Republic Speleological Society, Santo Domingo, Dominican Republic.

⁵ Department of Anthropology and Archaeology, Brooklyn College, Brooklyn, New York.

tral lobe and gulars, oval entoplastron, a strong wedge-shaped xiphiplastral notch, and a slight indentation at the junction of the cervical sulcus. The West Indian tortoises are allied with Galapagos tortoises, *Chelonoidis nigra* species complex, and possibly Chaco tortoises, *Chelonoidis chilensis*, based on morphology. These relationships are further supported by DNA evidence.

A second tortoise, *Chelonoidis marcanoi*, was recently named from dry caves in Pedernales Province, in the southwestern part of the country. The designated holotype for *C. marcanoi* is a right humerus, but this element is inadequate to differentiate taxa in the West Indian genus *Chelonoidis*; thus, we consider *C. marcanoi* a nomen dubium. The concept of multiple populations of tortoises on Hispaniola has merit and is discussed in terms of biotic patterns associated with south and north paleo-islands, which are separated from each other by the Hispaniolan Rift Valley.

KEYWORDS: Fossil tortoises, *Chelonoidis dominicensis*, *Chelonoidis alburyorum*, *Chelonoidis cubensis*, *Chelonoidis marcanoi*, Testudinidae, Oleg's Bat Cave (flooded cave), Dominican Republic.

INTRODUCTION

Tortoises are extinct in the Bahamian and West Indian archipelagos. They were once widespread in the West Indies area, as shown by fossil records in the Bahamas (multiple islands), Turks and Caicos Islands, Cuba, Dominican Republic on the island of Hispaniola, Navassa Island, Mona Island, Sombrero Island, Anguilla, and Barbados (fig. 1). Five of these island tortoises are named species: *Chelonoidis alburyorum* Franz and Franz, 2009 (Abaco, the Bahamas), *Testudo cubensis* Leidy, 1868 (Cuba), *Chelonoidis marcanoi* Turvey et al., 2017 (southern Hispaniola), *Testudo (Monochelys) monensis* Williams, 1952 (Mona Island), and *Emys sombrerensis* Leidy, 1868 (Sombrero Island). All of them are currently placed in the Neotropical genus *Chelonoidis* (Franz and Franz, 2009).

The occurrence of endemic tortoises in the Dominican Republic was documented earlier by Franz and Woods (1983), who reported fossilized shell fragments and limb elements of a large tortoise that were collected from a cave near Bayaguana in San Cristobal Province, in the Los Haitises region (specific location unknown). This sample was collected by Eugenio de Jesus Marcano F., Ricardo Ramirez, and Jose Eugenio Marcano M. in 1964 and donated to Charles Woods, at the Florida Museum of Natural History, where the specimens currently reside. This collection includes the following bones: a nearly complete left humerus (UF 26095), a complete 11th left peripheral (UF 26096), a proximal end of third or fifth costal bone (UF 26097), a broken left peripheral (probably tenth) (UF 26098), a distal section of bridge peripheral from right side (UF26099), and a fragment of a plastral element (possibly part of hypoplastron) (UF 26100) (see Franz and Woods, 1983: figs. 1, 2), apparently all from the same individual. This tortoise from the Bayaguana site was estimated to be about 600 mm carapace length, based on bone comparisons with other Neotropical species. This material was considered too incomplete to assign a name (Franz and Woods, 1983).

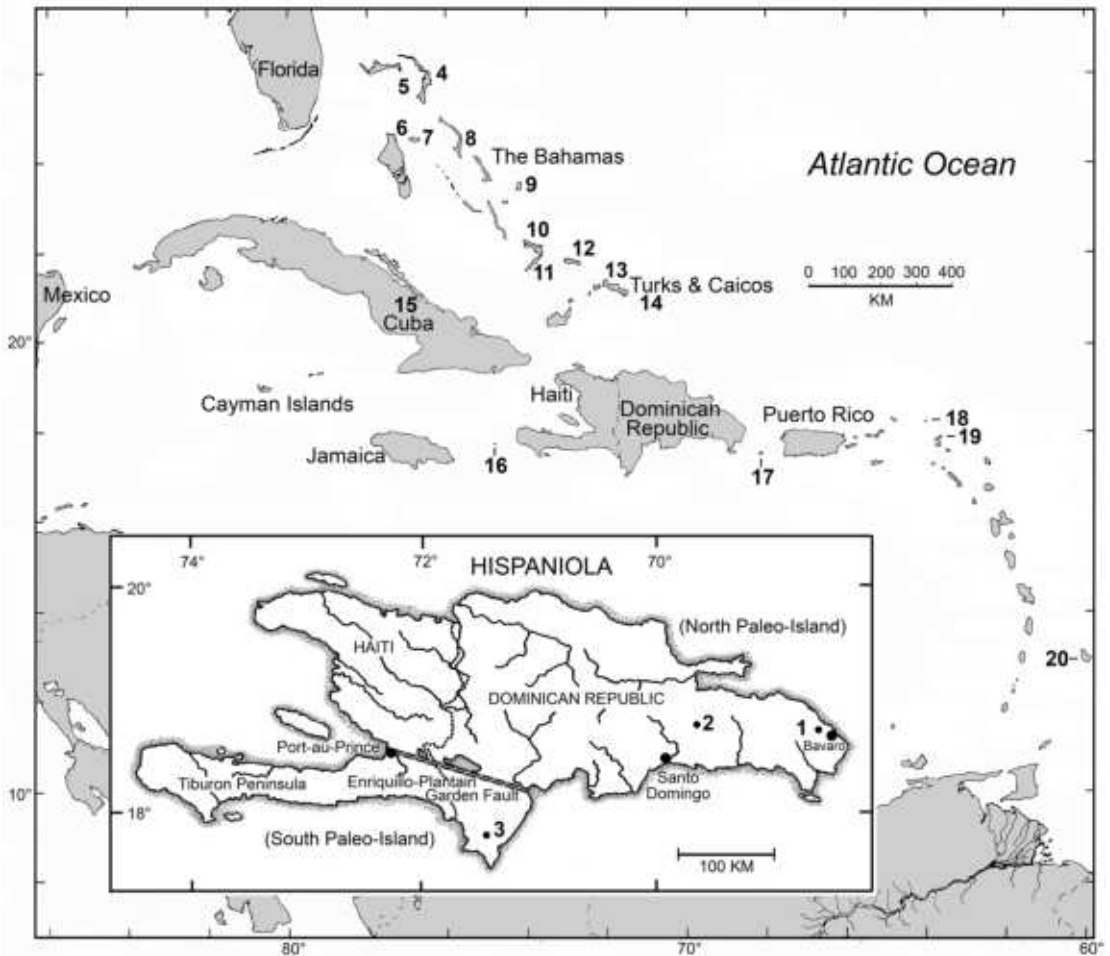


FIGURE 1. Map of the West Indies region and Hispaniola (modified from Velazco et al., 2013). Localities of Hispaniolan caves with tortoise fossils (inset) are: 1. Oleg's Bat Cave; 2. Bayaguana (Franz and Woods, 1983); 3. Barahona area (Turvey et al., 2017). Dotted line delineates the border between Haiti and the Dominican Republic; the heavy dashed line indicates the Enriquillo-Plantain Garden Fault. Other tortoise records, summarized in Franz and Franz (2009) and Steadman et al. (2017), are shown on the larger map. The Bahamas: 4. Abaco; 5. Moore's Island; 6. Andros; 7. New Providence; 8. Eleuthera; 9. San Salvador; 10. Crooked Island; 11. Acklins Island; 12. Mayaguana. Turks and Caicos Islands, British West Indies: 13. Middle Caicos; 14. Grand Turk. Greater Antilles: 15. Cuba; 16. Navassa Island; 17. Mona Island. Lesser Antilles: 18. Sombbrero Island; 19. Anguilla; 20. Barbados.

A second collection of tortoise fossils is now available from five dry caves on the Barahona Peninsula, Pedernales Province, in the southwestern Dominican Republic, consisting of limb bones and shell fragments; this collection was described as *Chelonoidis marcano* by Turvey et al., (2017). The material is housed in the Museo Nacional de Historia Natural "Prof. Eugenio de Jesús Marcano" (MNHNSD), Santo Domingo, Dominican Republic, and the Natural History Museum (NHMUK), London. Their description also included the material reported by Franz and Woods (1983).

We consider all the Dominican Republic tortoise specimens to represent members of the Neotropical genus *Chelonoidis*. Morphological data suggest that *Chelonoidis cubensis*, *C. alburyorum*, the new Dominican tortoise from Oleg's Bat Cave, and by inference, *C. marcano*, are closely related. The exquisite preservation of the *Chelonoidis* fossils from Oleg's Bat Cave provides opportunities to make morphological comparisons with new fossil finds in the West Indies as they become available. Ancient DNA (aDNA) evidence supports the close relationship of *C. alburyorum* with the Galapagos tortoise and other South American *Chelonoidis*, and by illation, other West Indian *Chelonoidis*. It also suggests relationships to African tortoises, rather than North American *Hesperotestudo* and *Gopherus* (Kehlmaier et al., 2017). No aDNA data are available yet from any Dominican tortoises.

In a previous paper on a Bahamian fossil tortoise, Franz and Franz (2009) presented a limited morphological assessment of Neotropical *Chelonoidis*, and we refer you to that commentary. Further morphological studies are necessary to address the variability among and between members of *Chelonoidis*, and their African relatives.

MATERIALS AND METHODS

Due to the extraordinary preservation of the complete shell and skull of the tortoise from Oleg's Bat Cave and the Bahamian tortoise *Chelonoidis alburyorum*, we were able to make direct morphological comparisons between these two species. See tables 1 and 2 for lists of shell and skull measurements. We also examined and compared the tortoise shell fragments and postcranial bones from the Marcano collection reported by Franz and Woods (1983), the Turks and Caicos Islands specimens (Franz et al., 2000) and compared them with the description and images of *C. marcano* (Turvey et al., 2017), *C. cubensis* (Leidy, 1868) (see images in Williams, 1950), *C. sombreroensis* (Leidy, 1886), and *C. monensis* (Williams, 1952). General morphological assessments for South American relatives are available in Franz and Franz (2009).

ABBREVIATIONS AND TERMINOLOGY: Museum acronyms: **AMNH**, American Museum of Natural History, New York; **MHD**, Museo del Hombre Dominicano, Santo Domingo, Dominican Republic; **MNHNSD**, Museo Nacional de Historia Natural, Professor Eugenio Jesus Marcano, Santo Domingo, Dominican Republic; **NHMUK**, Natural History Museum, London; **NMB**, National Museum of the Bahamas/Antiquities, Monuments and Museums Corporation, Abaco, the Bahamas; **UF**, Florida Museum of Natural History, University of Florida, Gainesville.

We follow the terminology used in Bramble (1971) and Franz and Franz (2009), for shell measurements and the names for carapacial and plastral bones, sutures, scutes, and sulci. The abbreviations for shell nomenclature presented in figure 3, follow those in Franz and Franz (2009). The terminology for cranial features follows Bramble (1971) and Joyce and Bell (2004); for limb bones follows Hulbert (2001).

TABLE 1. Shell measurements in mm for *Chelonoidis alburyorum* (UF 22540), Sawmill Sink, Abaco, the Bahamas), and *C. dominicensis* (MHD 1000, Oleg's Bat Cave, La Altagracia Province, Eastern Dominican Republic).

GENERAL CHARACTERS	<i>C. alburyorum</i> UF 225400	<i>C. dominicensis</i> MHD 1000
Sex	Male	Male
Standard carapace length	453	421
Over-the-shell carapace length	595	546
Entoplastron plus hyoplastron length (greatest length)	151.2	148
Width of shell at midsection	273	295
Greatest height of shell	224	215
Minimum bridge length	181	163
Midline length of plastron	345	344
Greatest length of plastron	354	366
Anterior plastral lobe length	88	102
Posterior plastral lobe length	85	103
Combined lobe lengths	173	205
CARAPACE BONES		
Nuchal plate length at midline	75.2	73
Nuchal plate width at shell margin	72.6	71
Greatest width of nuchal plate	108.2	100
Length of suture between nuchal plate & neural I	39.3	27
Midline length of neural I	57.5	59
Width of neural I at transverse sulcus	49.1	42
Number of sides on neural I	4	4
Midline length of neural II	53.4	48
1st width on neural II	64.7	56
2nd width on neural II	74.7	63
Number of sides of neural II	8	8
Midline length of neural III	52.5	50
Width on neural III at transverse sulcus	57.9	51
Number of sides on neural III	4	4
Midline length of neural IV	53.4	Damaged
Greatest width on neural IV	82.2	65
Number of sides of neural IV	8	8
Midline length neural V	46.2	Damaged
Width of neural V at transverse sulcus	61.7	52
Number of sides on Neural V	4	4
Midline length of neural VI	37.1	32
Greatest width of neural VI	73.4	59

TABLE 1 *Continued*

GENERAL CHARACTERS	<i>C. alburyorum</i> UF 225400	<i>C. dominicensis</i> MHD 1000
Number of sides on neural VI	8	6
Number of sides of neural VII	6	6
Number of sides on neural VIII	4	4
Length of sulcus between suprapygal II & pygal	79.7	72
Width of pygal at shell margin	45.7	50
PLASTRAL BONES		
Epiplastron length at midline	34.6	44
Entoplastron length at midline	45.1	50
Entoplastron greatest width	70.8	66
Hyoplastron length at midline	106.1	90
Hypoplastron length at midline	115.0	100
Xiphiplastron length at midline	55.3	60
Distance between the entoplastron & humeral/pectoral sulcus	27.7	16.8
CARAPACE SCUTES		
Midline length of vertebral scute I	89.7	94
Midline length of vertebral scute II	106.0	95
Midline length of vertebral scute III	95.3	95
Midline length of vertebral scute IV	111.7	100
Midline length of vertebral scute V	118.6	103
Greatest width of vertebral scute I	112.5	110
Greatest width of vertebral scute II	130.3	130
Greatest width of vertebral scute III	154.0	155
Greatest width of vertebral scute IV	134.4	116
Greatest width of vertebral scute V	123.8	107
PLASTRAL SCUTES		
Midline length of gular scute	31.3	37
Midline length of humeral scute	72.8	99
Midline length of pectoral scute	22.8	21
Midline length of abdominal scute	129.0	126
Midline length of femoral scute	77.0	64
Midline length of anal scute	20	14
Depth of anal notch	8	18

TABLE 2. Skull measurements (mm) of *Chelonoidis alburyorum* (the Bahamas) and *C. dominicensis* (Dominican Republic).

MEASUREMENTS	<i>C. alburyorum</i> UF 225400	<i>C. dominicensis</i> MHD 1000
Skull length from anterior end of premaxilla to occipital condyle	67.4	61.5
Greatest skull width (across quadratojugals)	58.9	50.8
Skull width/length ratio	1:1.12	1:1.13
Skull length from anterior margin of prefrontals to terminus of the supraoccipital crest	82.2	67.4
Skull width between posteroventral projection of maxilla	43.7	38.6
Width between quadratojugals condyles	37.3	33.3
Width between the outside margins of the quadratojugals condyles	55.6	47.1
Width between orbits at prefrontal-frontal sutures	23.5	19.5
Width of palate between posterior palatine foramen	21.3	16.3
Length of maxillary portion of the triturating surface along median ridge	23.6	22.6
Length of median ridge	23.6	22.6
Length of maxilla along labial ridge	32.2	26.1
Orbit greatest diameter (anteroposterior)	21	18.5
Breadth of occipital condyle	6.8	4.9
Height of foramen magnum	11.3	ND
Breadth across external nares	17.1	13.5
Height of skull anterior to orbits	25.9	22.6
Length of ear opening	14	10.4
Height of ear opening	14.5	13

SYSTEMATIC PALEONTOLOGY

Order TESTUDINES

Family TESTUDINIDAE

Genus *CHELONOIDIS* Fitzinger 1835

Chelonoidis dominicensis, n. sp.

Figures 2–8, tables 1–2

HOLOTYPE: MHD 1000, adult male, with complete carapace and plastron (separated at the bridge), skull, cervical vertebrae, scapula (L/R), coracoid (L/R), humerus (L/R), radius (L/R), ulna (L/R), pelvic girdle (L/R), femur (L), tibia (L), fibula (L). All material appears to represent a single individual. The holotype is on loan to the FLMNH.

TYPE LOCALITY: Oleg's Bat Cave (= Oleg's Bat House), 7 km west and inland of Bavaro in the La Altagracia Province, located on the southeastern coast of the Dominican Republic. The approximate coordinates in WGS84 Datum are N 18°42', W 68°32' (fig. 1). The elevation



FIGURE 2. Photos of Oleg's Bat Cave. **A.** Main cavern. **B.** Cave diver examining the MHD 1000 tortoise shell; **C.** tortoise shell in place before it was collected.

of the cave entrance is 22 m above sea level. Property owners are Frank and Jack Guerrero Herrera. The specimen was discovered by Oleg Shevchuk and collected by Cristian Pittaro and Phillip Lehman.

AGE: We suspect that the tortoise from Oleg's Bat Cave is probably Late Quaternary. Radio-carbon dates have not been obtained from this tortoise.

PROVENIENCE: The tortoise was found in the flooded La Tortuga section of Oleg's Bat Cave, totally buried in silt (fig. 2), approximately 147 m from the nearest entrance. The discovery occurred when a fortuitous fin kick by a cave diver removed silt that was covering the dorsal portion of the carapace. Recovery required several dives to acquire the entire specimen. The only damage to the shell was a single crack in the carapace. The skull and postcranial bones were found in association with the shell. Photos and a video (8:11 min) by Pittaro and Lehman show the retrieval of the specimen. These images are archived on Vimeo (<https://vimeo.com/197976404>). Phillip Lehman brought the specimen to the attention of A.L.R., who alerted N.A.A. and R.F. of its discovery. It was brought to the AMNH for final reconstruction and study with permissions from R.R. and MHD. This specimen was thoroughly studied by N.A.A. and R.F., on 18–21 January 2016, while it was in residence at the AMNH.

RECONSTRUCTION NOTES: The shell of MHD 1000 was separated along natural sutures after recovery. It was transported in pieces from the MHD and to the United States for reconstruction and study. Ana Balcarcel, AMNH Department of Vertebrate Paleontology, completed the preparation process by hardening the material, and molding and casting the carapace. Balcarcel's notes accompanied the prepared specimen: "Carapace was in-filled with Whitman Fibrous Cellulose powder and Paraloid B-72 in acetone. It was consolidated with Butvar B-76 throughout (several applications). Fills are white and serve to stabilize the carapace, reducing the risk of fracturing. If desired, fills could be removed with acetone solvent, which softens the fill and allows for it to be extracted manually. Two casts were made with polyester resin for the Dominican Republic and Rosenberger."

ETYMOLOGY: We take pleasure in naming this new fossil tortoise from the La Altagracia, Dominican Republic, *Chelonoidis dominicensis* in honor of the people of the Dominican Republic.

DESCRIPTION

SHELL FEATURES: The standard carapace length of the single adult male is 421 mm; over-shell length, 546 mm; greatest shell height, 215 mm; shell width at midsection, 295 mm. See table 1 for a complete list of shell measurements. The bridge length is considerably shorter than that of *Chelonoidis alburyorum*. *Chelonoidis dominicensis* has a caudal bump that begins at suprapygal I and curves downward to meet the pygal (fig. 3). The anterior and posterior plastral lobes are nearly equal in length (102 mm and 103 mm respectively) and are longer than in *C. alburyorum* (fig. 3E, F). Shell thickness is 4.7 mm at the bridge and 2.6 mm and 3.1 mm along midline of the hyoplastron and hypoplastron. The shell is moderately elongate with greatest shell width 70% of carapace length. Shell bones are tan in color and very thin. The exterior surfaces of the shell bones are minutely roughened to the feel with no signs of growth annuli

on the carapace or plastron. Bones along the margins of the plastral lobes are thickened, and their surfaces appear porous or often fibrous. Some sutures are tightly fused, often obscuring the normal zigzag appearance of these unions. This condition is most prevalent on the posterior surface of the carapace, making sutures difficult to trace. In contrast, scutes are well outlined with prominent sulcal channels embedded on elevated bony ridges and easily traced (fig. 4). An obvious lateral keel is developed along base of the bridge peripherals.

Cervical scute is absent; the first marginals meet to form a short, longitudinal cervical sulcus (15 mm, or 20.5% of nuchal length, compared with the *Chelonoidis alburyorum* series, 27%–37%). The length of the nuchal is shorter than its greatest width. The nuchal width at the shell margin is narrower than either its midline length or its greatest width. Five vertebral scutes, four plural scutes, 11 marginal scutes, and one supracaudal scute overlay the bones of the carapace (fig. 4A, C).

The anterior portion of the neural series formula is 4-8-4-8-4-6; neural VII and neural VIII are distorted. An extra ninth neurallike bone lies between the neural VIII and suprapygal I (figs. 3A, 4A). This bone may be the anterior portion of suprapygal I and separated by a suture from its parent bone. Transverse vertebral scute sulci cross neural I, III, V, and VIII. The pygal complex includes the pygal and bifurcated suprapygal I. The arms of suprapygal I enclose a smaller suprapygal II. The arms of suprapygal I come in contact with peripherals XI on both sides. The suprapygal II is broadly oval, much wider than long.

Eleven peripherals occur on each side of the carapace. The bridge peripherals form a vertical wall connecting the plastron with the costals of the carapace. The anterior and posterior peripherals located on either side of the bridge show little or no flaring. The tip of the pygal, in lateral view, is slightly hooked under (figs. 3C, 4C).

The anterior lobe of the epiplastron forms a distinct gular projection (figs. 3E, 4B). This extension expands forward from the branching gular/humeral sulcus. The entoplastron lies posterior to, and widely separated from the gular scutes, a condition different from *Chelonoidis alburyorum* where the entoplastron is adpressed to the gular sulcus (fig. 3F). The distance between the gular and entoplastron is 25 mm in *C. dominicensis*; its distance between the entoplastron and the humeral-pectoral sulcus is 16 mm. These distances are 0 and 27.7 mm, respectively, in the holotype (UF 225400) of *C. alburyorum*.

The external face of the entoplastron is roughly oval, wider than long (1:1.32) (figs. 3E, 4B). It possesses a single, unbranched sulcus that passes through the midline axis of the bone. The humeral scute is elongated along the midline (99 mm), while the femoral scute is much reduced (64 mm) (fig. 3E). A similar condition was used by Williams (1960) to distinguish *Chelonoidis denticulata* from *C. carbonaria*. This relationship in *C. alburyorum*, however, is different with the scutes nearly equal in length (UF 225400), 72.8 mm and 77.0 mm, respectively (fig. 3F). The pectoral scutes in both taxa are about equal in midline length. The abdominal scutes are longer than the humeral and femoral scutes taken together. The anal scutes for *C. dominicensis* are very short at the midline (14 mm), compared to those in *C. alburyorum* (20 mm); the combined width of the anal scutes in *C. dominicensis* is wider, the apices more divergent, and the anal notch, wedge shaped and deeper.

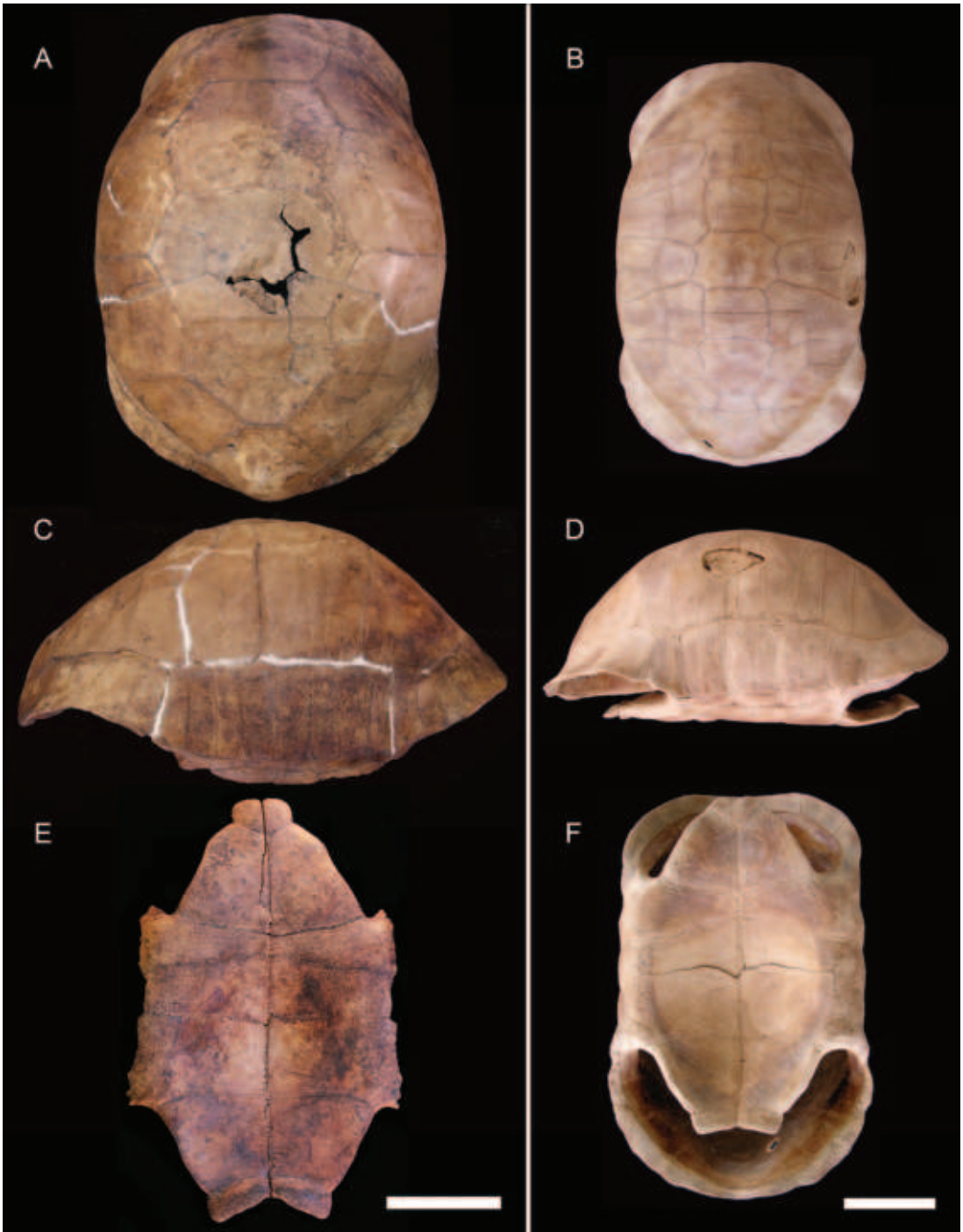


FIGURE 3. Comparative views of the shells of *Chelonoidis dominicensis* (left column) in A. dorsal view; C. lateral view; E. ventral (plastral) view; and *C. alburyorum* (right column) B. dorsal view; D. lateral view; F. ventral (plastral) view. Separate scale bars represent 10 cm for each specimen. Scale bars = 10 mm.

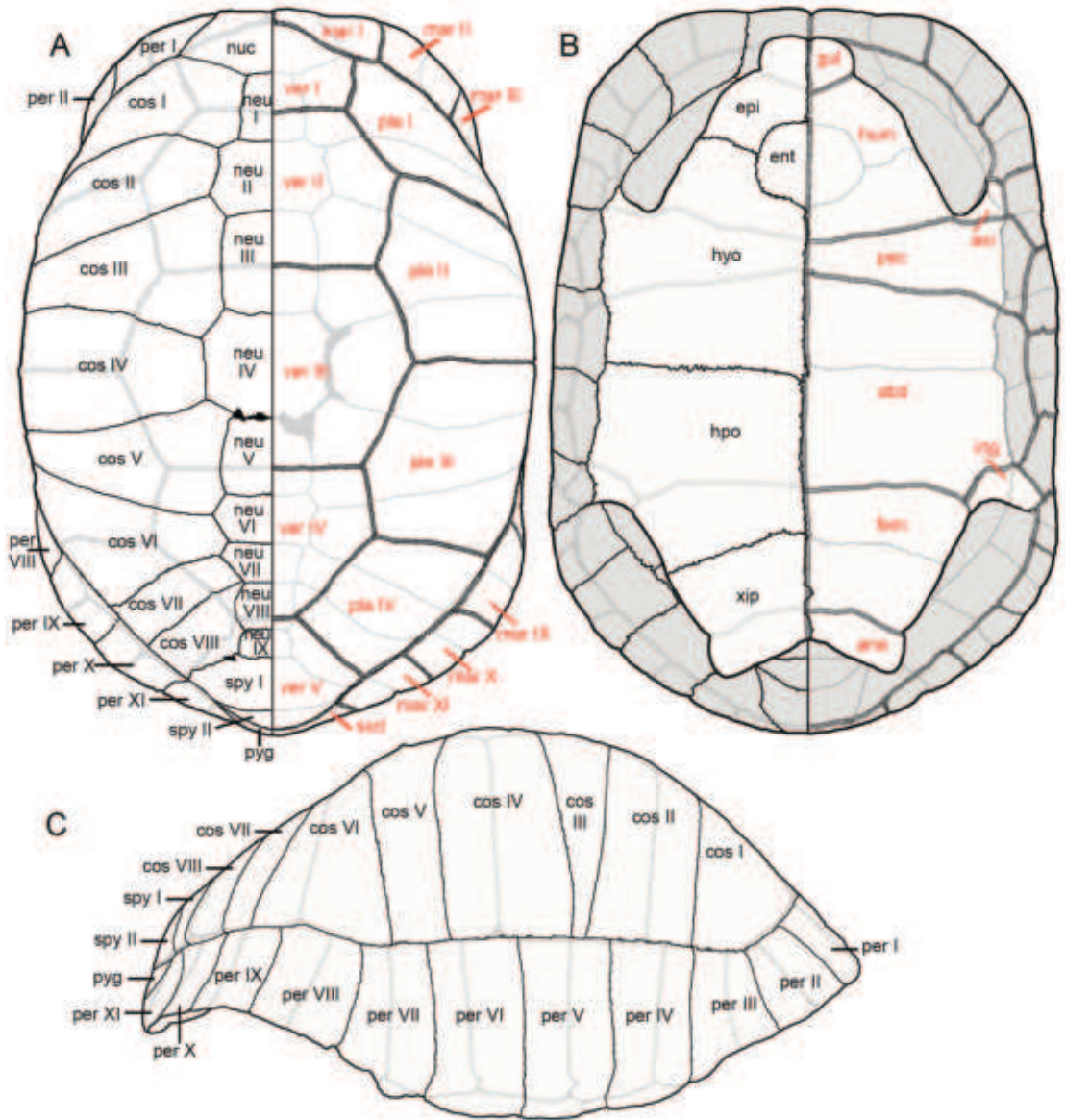


FIGURE 4. Outline showing scutes as a solid line; sulci as a double line on *Chelonoidis dominicensis*: **A**. carapace, dorsal; **B**. plastron, ventral; **C**. carapace, right lateral. Abbreviations followed by roman numerals indicate bone order in a series. Bones = black; scutes = red. Carapace bones: **cos**, costal; **neu**, neural; **nuc**, nuchal plate; **per**, peripheral; **pyg**, pygal; **spy I**, suprapygal I; **spy II**, suprapygal II. Plastron bones: **epi**, epiplastron; **ent**, entoplastron; **hyo**, hyoplastron; **hpo**, hypoplastron; **xip**, xiphoplastron. Carapace scutes: **mar**, marginal; **ple**, pleural; **sca**, supracaudal; **ver**, vertebral. Plastron scutes: **abd**, abdominal; **ana**, anal; **axi**, axillary; **fem**, femoral; **gul**, gular; **hum**, humeral; **ing**, inguinal; **pec**, pectoral.

A raised shelf forms the posterior edge of the gular, which delineates it from a prominent anterior lobe excavation (fig. 5A, B). The interclavicular bird-face structure, located on the interior surface of the entoplastron in *Chelonoidis dominicensis*, consists of a prominent two-part brow that is separated by a V-shaped depression that crosses the upper part of the entoplastron. The brow lines converge to form a very narrow, keeled beak that extends onto the hyoplastron. A pair of prominent fossae, lateral to the interclavicular keel, represent the paired eyes of the bird face.

VERTEBRAE, RIBS AND GIRDLES: Vertebrae of the holotype consist of six cervicals, including the atlas. They are loose, separated from the shell, and stored in a separate container. The shell vertebrae are suspended from a thin wall of bone (modified neural spines), and hence not in direct contact with the inner shell surface (fig. 6A). Complete ribs are not present in the sample, but based on remnants from the inner surfaces of the costals, the ribs are thin, very fragile, and project dorsally toward the neural spine wall. The ribs all originate from mounded bone masses on the upper portions of individual costal bones; these attachment mounds occur below and lateral to the costal-neural sutures.

FIRST DORSAL VERTEBRA: The first dorsal vertebra is suspended from the interior surface of neural I (fig. 6A). The centrum (length 20.2 mm, width 10 mm) is moderately constricted at its waist (near midpoint of the centrum); the ventral longitudinal keel present on *Chelonoidis alburyorum* is absent in *C. dominicensis* (fig. 6B, E). The zygapophyses are elongated and divergent. The first rib on this vertebra articulates at the base of these zygapophyses and with the anterolateral aspect of the centrum. This rib is laterally compressed with a beveled keel that merges with and continues onto the centrum. This rib is directed posterolaterally, beginning as a straight bone for 26 mm, then making an abrupt angle and becoming more laterally directed; the rib extension joins a sheer bony web that connects it to costal I. The second pair of ribs articulates with the posterior part of the centrum, near its junction with the second dorsal vertebra. This pair of ribs is more laterally directed, straight, shorter, and more delicate than the first pair; they lie dorsal to the first pair; both pairs merge onto a thin curtain of bone that attaches to the first costal.

PECTORAL GIRDLE AND FRONT LIMBS: Scapulae in the sample are separated from the coracoids. The straight acromion process makes an angle 120° to the blade. This angle is greater than the 111° and 85° reported by Franz and Franz (2009) and Meylan and Sterrer (2000), respectively, for other species of *Chelonoidis*. Coracoids are short, 41 mm in length and fan shaped; the distal margin of the fan is 34.7 mm wide.

The humerus is strongly recurved, with a total length of 100.3 mm. The trochanteric tuberosities are moderately divergent, separated by a short, deep intertrochanteric fossa. The greater trochanter extends about 30 mm above the shorter lesser trochanter. An obvious muscle scar, 10×12 mm, for the attachment of *M. latissimus dorsi*, occurs on the outside surface of the greater trochanter; the scar's interior surface is roughened. A second weakly developed muscle scar is found on the lower part of the lesser trochanter. The midshaft of the humerus is rounded, 11×12 mm, with a ratio of nearly 1:1. The shaft becomes broader and more flattened distally, incorporating two riblike reinforcements that merge with the distal articulating surface; low facets on

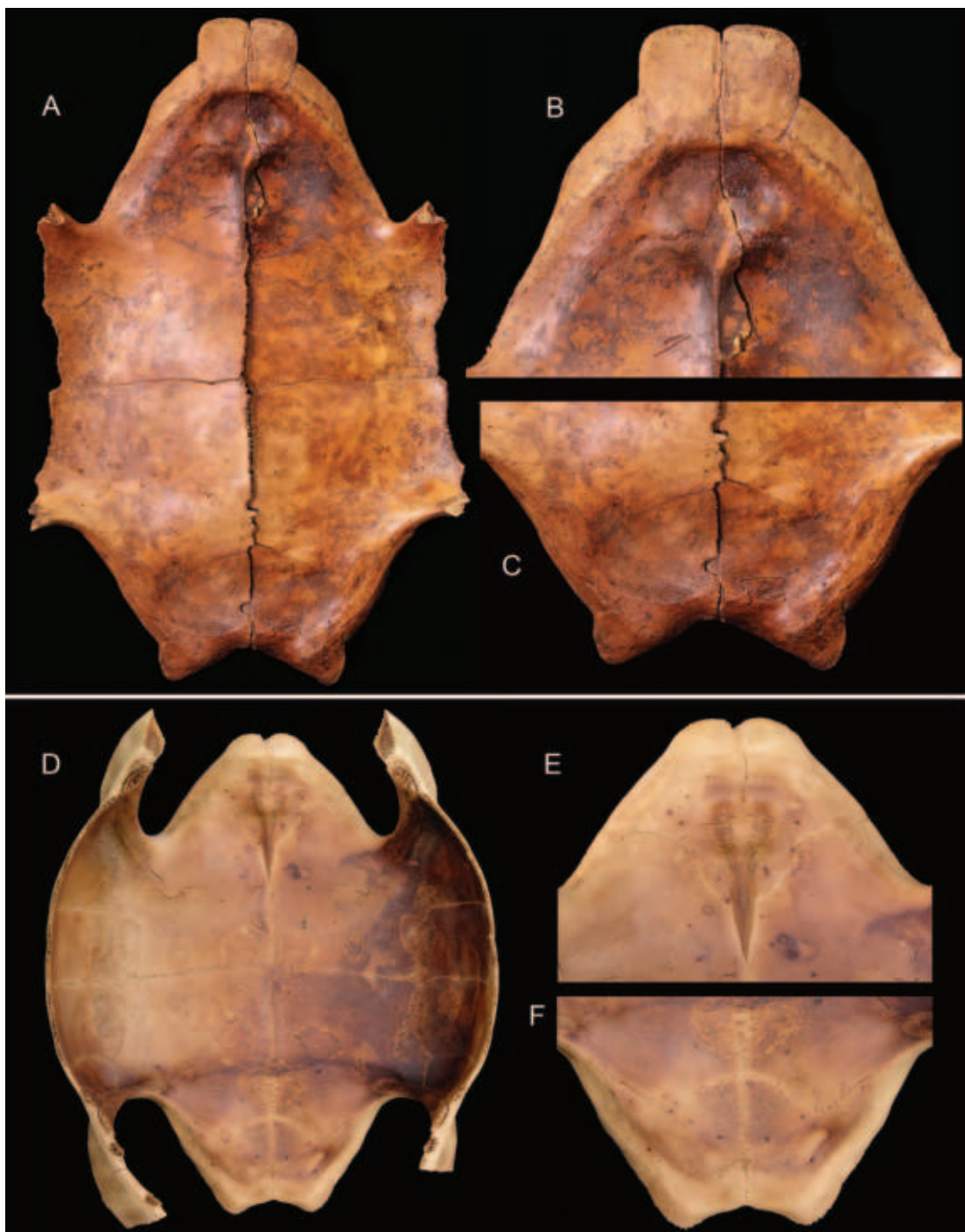


FIGURE 5. Internal views of the plastron of *Chelonoidis dominicensis* (upper panels) showing: A. complete plastron; B. close-up of anterior plastral lobe; C. posterior plastral lobe. Comparative views of *C. alburyorum* (lower panels; specimen T4) showing D. complete plastron; E. close-up of anterior plastral lobe; F. posterior plastral lobe.

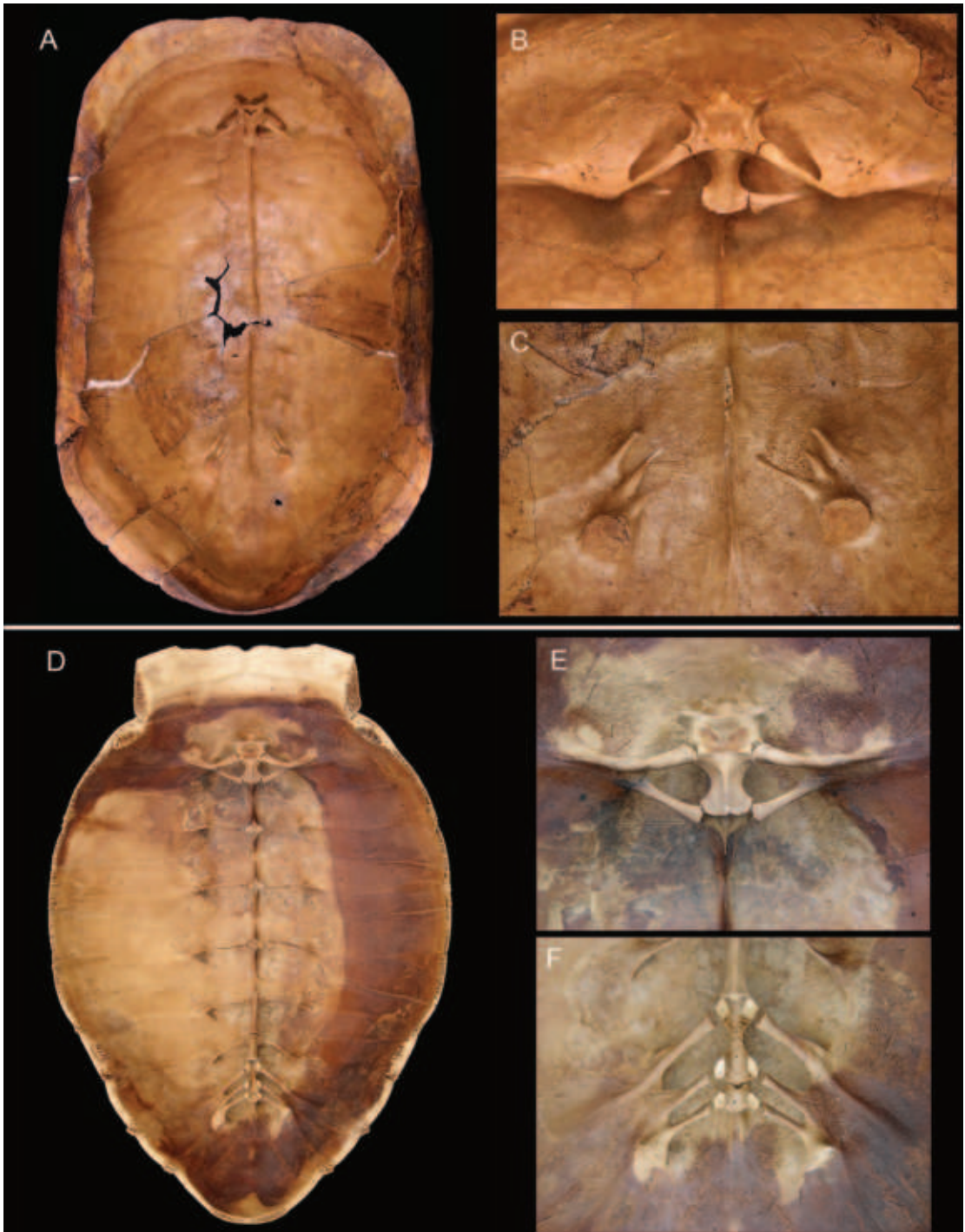


FIGURE 6. Internal views of carapace of *Chelonoidis dominicensis* (upper panels) showing the A. vertebral column; B. first dorsal vertebra; C. sacral rib complex. Comparative views of *C. alburyorum* (lower panels) showing the D. vertebral column; E. first dorsal vertebra; F. sacral rib complex.

this surface correspond to the sites for the ulnar and radial juncture. The greatest width across the distal articulating surface is 34.6 mm, or about 34.5% of the total length of the humerus.

PELVIS AND HIND LIMBS: The pelvic girdle in this specimen is articulated but separated from the shell. The ilia are flared outward and then arc inward at the distal end, forming an elongate interior space between the two pelvic halves. The pectineal process on the pubis is lobelike and elongated. The posteroventral process on the ischium is broad and slopes gently toward the midline suture. The ischiopubic fenestrae are nearly circular. The acetabulum is moderately deep, generally triangular in shape, with the ilium providing the greatest contribution.

The interior carapacial wall of *Chelonoidis dominicensis* has remnants of one presacral and two sacral ribs, the first attached to costal VII and the last two to costal VIII (fig. 6D, C). They arise from thickened areas of bone formed from the costal interior walls. The closely spaced ribs are obliquely directed toward the anterior. They are thin, laterally flattened and delicate. The sacral ribs are attached to a sacral buttress; the buttress articulates with the ilium; this articulating structure is robust, flattened in a horizontal plane with respect to the shell. In contrast, the sacral rib complex in *C. alburyorum* is more robust; the sacral buttresses are smaller and in oblique positions relative to the wall of the carapace (fig. 6D, F).

The femur is 80.1 mm in length and represents 80% of the total length of the humerus. The trochanters are united behind the head to form a trochanteric crest, which encloses a deep medial trochanteric fossa on the proximal surface. The greater trochanter is more robust and slightly taller than the lesser trochanter. The femoral shaft is short, angular, and supports small muscle scars. The tibial and fibular condyles are weakly developed with a slight notch between them.

SKULL: The single skull of *Chelonoidis dominicensis* was found associated with the shell and internal bones. The skull is brachycephalic, with a width/length ratio of 1:1.13 (similar to the 1:1.12 ratio for the skull of *C. alburyorum*) (figs. 7–8). The external surface of the rostrum has a granulated texture. The prefrontals and frontals border the anterior portion of the orbits. In lateral profile, the premaxillae become weakly prognathous, sloping from the frontals, toward the anterior ventral tip of the snout. In dorsal view, the combined prefrontals and frontals appear squarish anteriorly forming the dorsal surface of the rostrum. The lateral margins of the maxillae are straight (not bowed as in *C. alburyorum*) with a more acute tapering toward the anterior apex of the narrower snout. The posterior part of the maxillae end as weak blunted processes. The jugal-quadratojugal portion of the skull is broken; we are thus unable to comment on it. The external narial opening on the snout is larger than that in *C. alburyorum*; the narial floor is also essentially flat without obvious premaxillary ridges.

The orbits of *Chelonoidis dominicensis* are rotated slightly forward, which in life probably enhanced binocular acuity. This condition has also been documented for closely related, fruit-eating *C. alburyorum* (Franz and Franz, 2009), and is thought to improve their search capabilities for finding fallen ripe fruits on the forest floor. The prominent trochlear processes on the quadrates are bilobed and project anteriorly into the orbits (figs. 7, 8). The stapedio-temporal foramen lies embedded in the prootic-quadrates suture in *C. dominicensis*. This foramen is significantly larger, than in *C. alburyorum*. The squamosals form acute angles near their posterolateral intersections with the quadrate and opisthotic on each side of the skull. These exten-

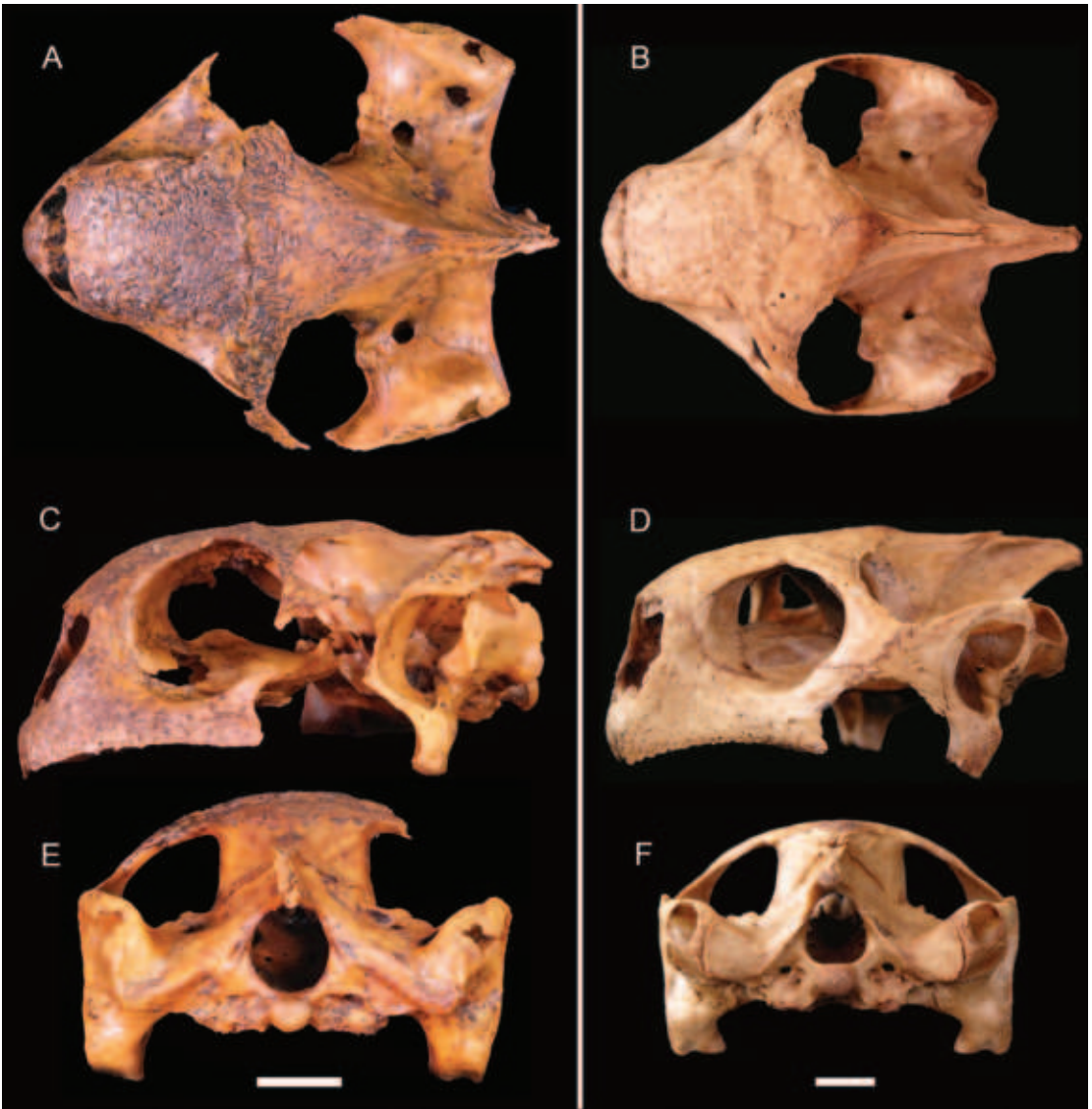


FIGURE 7. Comparative views of the skulls of *Chelonoidis dominicensis* (left column) in A. dorsal view; C. lateral view; E. posterior view; and *C. alburyorum* (right column) B. dorsal view; D. lateral view; F. ventral posterior view. Separate scale bars represent 10 mm for each specimen.

sions tend to be slightly curvilinear in profile extending medially from the corner of the squamosals, unlike the more rounded corners and extensions in *C. alburyorum*.

Tomial ridges of the maxillae form sharp cutting edges along the upper jaw, presumably for cutting plant material (fig. 8). The maxillae possess weakly developed serrated cutting edges. The axial juncture of the left and right premaxillae form a very weak cup in the front of the mouth, compared to a deeper cup in *Chelonoidis alburyorum*. There is little or no transverse ridge to separate the cup from the adjoining triturating ridges of the mouth, as there is in *C.*



alburyorum. Triturating ridges do not intrude onto the cup. The tomial edge, the middle triturating ridge, and the lingual margin are less developed than those in *C. alburyorum*; they are generally straight edged and divergent along an expanding palate.

The vomer in *Chelonoidis dominicensis* begins as a straplike bone at the anterior part of the mouth roof, as in *C. alburyorum* (fig. 8). A triad of small openings occurs on this strap, with two foramen praepalatia represented as pinholes, and below them a centrally located, closed slitlike vomerine foramen. The vomer widens and ascends into the roof of the mouth, forming a weakly vaulted cavity. The lateral margins of the vomer are thickened forming an abrupt sutural ridge. A prominent septum is seated in a shallow, panlike longitudinal depression, formed by the vomer. The midline septum is sharper edged in *C. dominicensis* than the blunted septum in *C. alburyorum*. The secondary ridges along margins of the vomer separate the vomer from the palatines. The palatines form secondary channels parallel to the vomerine ridges. The shieldlike basiosphenoid bone is strongly triangular with an acutely pointed end facing toward the pterygoids. There is a strong waistlike constriction where the palatines and the pterygoids meet, which is absent in *C. alburyorum*.

The sagittal crest in *Chelonoidis dominicensis* begins at a dip in the skull associated with the supraoccipital at about the level of the tympanic cavity and extends posteriorly to the back of the skull (fig. 7). The crest is anomalous, slightly twisted, off-center, and not aligned with the projecting occipital condyle and ending at the level of the terminus of the occipital condyle. The foramen magnum is round in *C. dominicensis*, and pear shaped in *C. alburyorum* (fig. 7). The head of the occipital condyle is much smaller (4.9 mm) in *C. dominicensis*.

The ear openings are large (fig. 7). They penetrate into the initial precolumellar chamber that extends laterally into the postotic atrium. The otic chamber terminates at the thin-walled quadrate and squamosal bones. The stapes are not apparent in *Chelonoidis dominicensis*, but are visible in the ear openings of the *C. alburyorum* specimen. The peculiar secondary holes found in the skull of *C. alburyorum*, which penetrate each of the squamosals into the postotic chamber, are weakly developed in the *C. dominicensis* skull. Unlike *C. alburyorum*, the holes are smaller and more irregular, which may represent degenerative bone disease or postmortem damage.

SHELL WOUNDS: The carapace of *Chelonoidis dominicensis* possesses three types of woundlike scars in the exterior surface of the carapace (fig. 3A). The largest is a massive, oval-shaped break of unknown origin that penetrates into the body cavity. A similar gash was also reported in the

FIGURE 8. Comparative ventral views of the holotype skulls of *Chelonoidis dominicensis* (top) from the Dominican Republic and *C. alburyorum* (bottom) from the Bahamas. Scale bars = 10 mm. Figure 1. Map of the West Indies region and Hispaniola (modified from Velazco et al., 2013). Localities of Hispaniolan caves with tortoise fossils (inset) are: **1.** Oleg's Bat Cave; **2.** Bayaguana (Franz and Woods, 1983); **3.** Barahona area (Turvey et al., 2017). Dotted line delineates the border between Haiti and the Dominican Republic; the heavy dashed line indicates the Enriquillo-Plantain Garden Fault. Other tortoise records, summarized in Franz and Franz (2009) and Steadman et al. (2017), are shown on the larger map. The Bahamas: **4.** Abaco; **5.** Moore's Island; **6.** Andros; **7.** New Providence; **8.** Eleuthera; **9.** San Salvador; **10.** Crooked Island; **11.** Acklins Island; **12.** Mayaguana. Turks and Caicos Islands, British West Indies: **13.** Middle Caicos; **14.** Grand Turk. Greater Antilles: **15.** Cuba; **16.** Navassa Island; **17.** Mona Island. Lesser Antilles: **18.** Sombrero Island; **19.** Anguilla; **20.** Barbados.

holotype of *C. alburyorum* (Franz and Franz, 2009). We do not believe these wounds were inflicted by predators. So then, what are the sources of these massive wounds? Did they have a common origin, such as falling rocks or tortoises falling onto rocky, sinkhole terrain? In either case, these wounds may have not been fatal, as evidenced by regrowth of new bone in both shells.

A second type is a single hole that penetrates the left side of suprapygal I near its suture with costal VIII. The hole occurs at a point where the underlying ischium of the pelvis comes in contact with the carapace. Similar holes, located in the same exact position, are found in the type series of *Chelonoidis alburyorum* and in other thin-shelled, land-dwelling turtles. It has been suggested that these holes occur as a result of wear by the pelvic girdle and hind limbs as a consequence of terrestrial locomotion or limb retraction (Franz and Franz, 2009).

A third set of small penetrations in *Chelonoidis dominicensis* is irregularly dispersed over its carapace. They are small, round, and shallow; they also appear to taper to a point. These wounds occur in the nuchal, neural I, left costal I (2 piercings), left costal III, right costal V, right costal VIII, left peripheral I, left peripheral III, left peripheral V; some of these wounds lie in close proximity to sulci. Similar piercings are reported in *C. alburyorum* specimens (Franz and Franz, 2009) and may have the same origins, i.e., tooth marks from crocodile bites (Morgan and Albury, 2013).

SUMMARY: *Chelonoidis dominicensis* is a moderate-sized tortoise, with a domed, thin-walled shell, showing a prominent caudal shell hump (when seen in profile). The carapace lacks a cervical scute. The neural series formula is 4-8-4-8-4-6. The centrum of the first dorsal vertebra is short, narrow waisted, with enlarged, divergent zygapophyses; centrum lacks a ventral keel. The sacral and presacral ribs are equally spaced, thin and delicate; the sacral buttresses are robust and horizontally flattened with respect to the shell. The minimum bridge lengths are considerably shorter than the combined lengths of the anterior and posterior plastral lobes in *C. dominicensis*. The pronounced gular projection extends out from a raised gular shelf. *Chelonoidis dominicensis* has a unique interclavicular “bird face” sculpture on the interior surface of the entoplastron. The anterior plastral lobe is long and tapers toward the narrow gular scutes. The posterior plastral lobe is wider and its terminal anal scutes are roughly rectangular in shape; their apices are weakly developed and separated by a broad, V-shaped anal notch. The skull is brachycephalic. The snout is weakly prognathous. The roof of the mouth is vaulted, with a moderately keeled septum. Raised ridges separate the vomer and palatines. A strong waistlike constriction occurs where the palatines and pterygoids meet. The orbits are oriented slightly forward. The squamosals at the posterior corners of the skull form acute angles near their intersections with the quadrates and opisthotics. From these angled corners, the posterior margins of the skull tend to be slightly curvilinear in profile. The foramen magnum is round. The head of the occipital condyle is small.

TAXONOMIC COMPARISONS

CHELONOIDIS CUBENSIS SAMPLES: The Cuban tortoise (*Chelonoidis cubensis*) was originally described by Leidy (1868) based on a single, partial, water-worn pleural plate from Chapepote

thermal spring in a bend of the Analla River at the Baños de Ciego Montero, Santa Clara Province, 30 miles northwest of Cienfuegos, Cuba. Subsequent samples include Casimba (fissure) in the Sierra de Jatibonico (eastern Santa Clara Province) and a tar pit near Hato Nuevo (Matanzas Province). These fossils were described and illustrated in Williams (1950: 9–16, pls. 1–5). We follow Williams' paper, particularly his photographs, to make the following comparisons with *C. dominicensis*.

The shell of *Chelonoidis dominicensis* is very similar to that of *C. cubensis*. Unfortunately, little of the carapace of *C. cubensis* is available except for a nuchal and a few costals, and thus most of the following distinctions are garnered from the plastral bones, which are better represented in the samples. The anterior plastral lobes of both species have margins that taper toward the narrow gulars; they exhibit a strong epiplastral shelf that separates the gulars from the internal floor of the lobe; gular scutes do not encroach onto the entoplastron; entoplastral areas possess similar-appearing internal interclavicular sculptured bird faces. The few available carapacial features include the nuchal without a cervical scute, a short midline cervical sulcus that replaces the cervical scute, neural and costal sulci poised on raised ridges, other sulci embedded in simple channels. The costal, neural, and midplastron bones are extremely thin.

Chelonoidis dominicensis differs from *C. cubensis* by having an oval entoplastron, rather than the pentagonal-shaped one in *C. cubensis*; a strong wedge-shaped xiphoplastral notch, minimal or absent in *C. cubensis*; free margin of the nuchal with only a slight suggestion of a cervical dent, in contrast to the prominent indentation found in *C. cubensis*; and humerus with a shallow scar for the attachment of the *M. latissimus dorsi*, instead of the deep, pitlike one in *C. cubensis*.

CHELONOIDIS (MONACHELYS) MONENSIS SAMPLES: The Mona Island tortoise was described by Ernest Williams in 1952, based on two first dorsal vertebrae, holotype AMNH 1969 and paratype AMNH 1935; the following fossils were listed as referred materials: partial skull and fragments of limb bones, pectoral and pelvic girdles, cervical vertebrae, and miscellaneous shell bones. We used Williams' (1952: 541–560, figs. 1–4, pls. 44–47) as the source for information about this species. All specimens were collected in Liro Cave and two other nearby sites on the east side of Mona Island, which is a small limestone island in the Mona Passage, between Hispaniola and Puerto Rico. The unique first dorsal vertebrae, with their very elongate centra, prompted Williams to erect the new subgenus *Monachelys* for this tortoise. This character distinguishes *Chelonoidis monensis* from both *C. alburyorum* and *C. dominicensis*, which have much shorter compact centra; this particular vertebra is not represented in samples with other named tortoise species from the West Indies.

CHELONOIDIS MARCANOI SAMPLE: A recent description of a giant tortoise, *Chelonoidis marcanoii*, from the Dominican Republic, by Turvey et al. (2017), was based on fragmentary limb bones (6 humeri, 2 femora) and 4 shell fragments (3 epiplastra with evidence of gular scutes, 1 partial hyoplastron or hypoplastron). Their sample represented at least seven individuals from five caves in Pedernales Province, in the southwestern part of the country. The type series also included specimens reported by Franz and Woods (1983), from Bayaguana, in San Cristobal Province.

The designated holotype for *Chelonoidis marcanoii* was a right humerus (MHMUK PV R 36954) from Cueva del Papayo, collected 12 May 2007; they included the rest of the Pedernales samples (NHMUK PV R 36955, MNHNSD FOS 23.1054–23.1064), and those reported (UF

26095–26100) by Franz and Woods (1983), as paratypes. Since the description of the Pedernales tortoise is based primarily on limb elements, we prepared table 3, which compares the humeri and femora in the type series of *Chelonoidis marcanoii* with the limb bones from the Bayaguana tortoise, *C. dominicensis*, and *C. alburyorum*. The information in this table was extracted from the diagnosis and descriptions presented by Turvey et al. (2017), Franz and Franz (2009), and our direct observations of *C. alburyorum*, *C. dominicensis*, and the Bayaguana tortoise. The obvious conclusion is that all of these limb elements are very similar, except for slight differences in the total length, shape and depth of the muscle scars, and degree of openness of the shaft groove of the humeri, widths of the distal and proximal articulations, and shape and size of muscle scars of the femora. We also noted variability in the muscle scars and the openness of the shaft grooves between individuals, as well as left and right humeri and femora in the same individuals in the *C. alburyorum* series (NMB.AB50.001, NMB.AB50.003, NMB.AB51.001, and NMB.AB52.004).

The limb bones in West Indian tortoises (and *Chelonoidis carbonaria*, *C. denticulata*, and *C. nigra*) are morphologically similar and not very useful to distinguish among species, especially when complete shells and skulls are available for *C. dominicensis* and *C. alburyorum*. We consider the bone samples listed in Turvey et al. (2017) inadequate for differentiating *C. marcanoii* from other *Chelonoidis*. It is also not feasible to assign the Bayaguana specimens to either *C. marcanoii* or *C. dominicensis*, based on its lone humerus and its meager shell sample. Thus, we consider *C. marcanoii* to be a nomen dubium and of uncertain affinities.

DISCUSSION

BIOGEOGRAPHY: Biogeographical evidence could support the possibility that more than one species of tortoise may have occurred on Hispaniola in the past. The Bayaguana tortoise and the type specimen of *Chelonoidis dominicensis* were recovered from sites on the north paleo-island, which lie north of the Hispaniolan Rift Valley. The fossil sample described by Turvey et al. (2017) as *C. marcanoii* originated from caves south of the Hispaniolan Rift Valley (named Hoya de Enriquillo in the Dominican Republic and Cul-de-Sac Depression in Haiti), an area referred to as the south paleo-island. This south island includes the Barahona (Dominican Republic) and Tiburon (Haiti) peninsulas, which border the Caribbean Sea (fig. 1). These two prehistoric “islands” are separated by the Enriquillo-Plantain Garden Fault and other intersecting faults (Calais et al., 2010) that pass through the Hispaniolan Rift Valley between the Neiba and Port-au-Prince bays (fig. 1). Portions of this valley lie below sea level and include dry, desertlike vegetative communities, and are watered by several springs and hypersaline lakes. The valley has flooded periodically in the geologic past creating an open seaway. Each paleo-island supports a distinctive modern biota, including terrestrial plants (Judd and Beaman, 1988; Judd, 2007), terrestrial snails (Thompson, 1986), freshwater fishes (Burgess and Franz, 1989), amphibians and reptiles (Schwartz, 1980; Parham et al., 2013), and birds (Pregill and Olson, 1981; Graves and Olson, 1986). The distinctive nature of each biota implies the possibility that Hispaniola could support more than one species of tortoise.

TABLE 3. Comparison of characters between *Chelonoidis marcanoii*, the Bayaguana tortoise, *C. dominicensis*, and *C. alburyorum*. Abbreviations: **DR**, Dominican Republic; **HUM**, humerus; **FEM**, femur, **ND**, no data.

CHARACTERS	<i>C. marcanoii</i> Turvey et al., 2017 (DR)	Bayaguana Franz & Woods 1983 (DR)	<i>C. dominicensis</i> Albury <i>et al.</i> , this paper (DR)	<i>C. alburyorum</i> Franz & Franz 2009 (Bahamas)
HUM length (mm)	125	135	100.3	96.1
HUM shape	Long, slender, recurved distally	Robust, recurved distally	Strongly recurved	Strongly recurved
HUM proximal & distal articulations	Equal in width	Nearly equal in width (eroded)	Nearly equal in width	Nearly equal in width
HUM lesser trochanter	Level with midline of humeral head	(broken)	Level with midline of humeral head	Level with midline of humeral head
HUM greater trochanter	Extends above upper humeral head	(broken)	Extends above the upper humeral head	Extends above upper humeral head
HUM <i>M.latissimus dorsi</i> scar	<i>Well defined</i>	Faint depression, roughened surface	Oval, roughened surface	Well-defined, roughened surface
HUM medial scar	Shallow, circular	Shallow, oval	Shallow, oval	Shallow, oval
HUM shaft dimensions	Rounded, oval or slightly triangular	More or less rounded	Rounded	Rounded
HUM head	Subspherical	Subspherical	Subspherical	Subspherical, bent anteriorly 90°
HUM shaft groove	Groove to medial corner of distal articulation	Prominent groove, partially open	Partially open groove	Groove weakly developed
FEM length (mm)	65.4 (damaged)	ND	80.1	83.7
FEM shaft shape	Flat in medial/lateral profile, with distal quarter curving posteriorly	ND	Robust, recurved at distal end	Robust, strongly recurved at distal end
FEM shaft diameter at midpoint	Robust, square in cross section	ND	Angular in cross section	Triangular in cross section
FEM proximal & distal articulations	Distal width greater than proximal width	ND	Widths about equal	Widths about equal
FEM greater & lesser trochanter	Proximal ends of trochanters meet to enclose deep, rounded medial fossa	ND	Trochanteric crest with medial fossa	Proximal end of trochanter united to form crest and medial fossa
Trochanter heights	Low, greater trochanter slightly higher than lesser one	ND	Low, greater trochanter slightly higher than lesser one	About equal in height, positioned slightly below head
FEM scar	Prominent ovoid scar on lateral shaft below head	ND	Scattered small muscle scars	Two roughened muscle scars
FEM head	Damaged, probably spherical	ND	Spherical	Spherical
FEM tibial & fibial facets	Weak facets separated by faint notch	ND	Weakly defined	Weakly defined

Multiple taxa of tortoises have been documented in island populations in the Mascarene Islands (Austin et al., 2003; Bour et al., 2014) and the Galapagos Islands (Poulakakis et al., 2015). These inraisland populations are morphologically and genetically distinct. Two and five unique taxa of *Chelonoidis* cohabitate simultaneously on the islands of Santa Cruz and Isabela, respectively, with hyperarid lowlands separating populations on Isabela (Poulakakis et al., 2015). These conditions may have once prevailed on Hispaniola as well as other islands in the West Indies.

Chelonoidis dominicensis and the Bayaguana tortoise samples are more likely to be aligned with each other and less so with the tortoise sample from the Barahona Peninsula on the south paleo-island based exclusively on their close geographic proximity (fig. 1). The potential radiation of tortoises between the paleo-islands may have been further limited by the intervening Cordillera Central mountain range, which lies north of the Hispaniolan Rift Valley. This taxonomic and biogeographic quandary will be difficult to resolve without more complete specimens. All three samples are certain to belong to the genus *Chelonoidis* and are probably closely related. Resolution of the taxonomic status of the Bayaguana and Barahona sample must await further discoveries of critical specimens that, it is hoped, will include skulls and much more complete shell material.

TAPHONOMIC AND ECOLOGIC IMPLICATIONS: Oleg's Bat Cave and other flooded caves in the Dominican Republic and the Bahamas provide some of the best-preserved and richest deposits for vertebrate fossils in the West Indies. The majority of earlier fossil collections came from dry caves, tar pits, peat deposits, and archaeological sites. In the past 20 years, cave divers have found fossil vertebrates in context with fossil-rich sediments that include plant macrofossils, pollen, and insects (Steadman et al., 2007, 2015). Within these flooded caves, the skeletal remains were buried in the submerged bottom sediments in total darkness, which helped to preserve them. In Oleg's Bat Cave, the fossils are found on a nearly level bottom that has provided a platform to stabilize the remains from disarticulation; otherwise, skeletal remains deposited on an undulating floor or a steeply dipping talus slope would be mechanically abraded or disarticulated. Perhaps most importantly, the skeletal remains were completely immersed in quiescent water, thus providing an environmentally stable repository.

Oleg's Bat Cave is accessible through at least two vertical cave entrances (fig. 2A); *Chelonoidis dominicensis* may have fallen into the cave entrance that resulted in a fractured (or refractured) carapace (fig. 2B). Other vertebrates from Oleg's Bat Cave include the skeletal remains of extinct rodents in the Capromyidae family, ground sloths, numerous bats, a solenodon, an extinct Cuban bird, and extirpated Cuban crocodiles, *Crocodylus rhombifer* (Velazco et al., 2013; Morgan et al., in review). Like many Bahamian tortoises, the shell of *C. dominicensis* shows signs of crocodile bite marks, as well as other wounds, including a major gash on the dorsal surface of the carapace that showed some new bone growth (fig. 2C). Preservation of the specimen was excellent, which presents the possibility for radiocarbon dating and ancient DNA analysis in the future when permission has been granted.

Likewise, the Bayaguana tortoise fossils were collected from a wet cave environment, although an advanced degree of mineralization may preclude future organic chemical analyses.

The specimens have a shiny, blackened patina and are heavily mineralized suggesting that they may be older than the Holocene. The remains of the Bayaguana tortoise were found in a pool of water just inside the entrance of an unidentified cave near the town of Bayaguana in the San Cristobal Province, Dominican Republic, in 1964 (Franz and Woods, 1983). Four species of ground sloths were found in association with this tortoise (MacPhee et al., 2000). As is evident on other fossil tortoise in the Bahamas and on *Chelonoidis cubensis*, the Bayaguana tortoise show crocodile bite marks on the few carapacial fragments that are available.

During the 19th and early 20th centuries, mariners circumnavigating the globe hunted tortoises for their meat and oil, recording their presence in surveys. They also noted crocodiles in association with tortoises on oceanic islands (Cheke and Bour, 2014). Early reports mentioned crocodiles on Mahé in the Seychelles where they were found to be actively preying upon very large tortoises in mountainous terrain. Large tortoises have an affinity to soak in rivers and ponds to disperse heat, where they were more likely to become prey for crocodiles. On Abaco, a relatively small island in the Bahamas, fossils of *Chelonoidis alburyorum* are commonly found in blue holes (= flooded caves) in association with the skeletal remains of the Cuban crocodile, *Crocodylus rhombifer*. This crocodile was probably widespread in the West Indies before European contact. Today, *C. alburyorum* is extinct and the crocodile, *C. rhombifer*, is extirpated from the Bahamas and most of the West Indies, but continues to survive in very limited numbers in freshwater swamps on the southern coast of Cuba. All tortoise populations in the West Indies are currently extinct and the crocodiles and tortoises, once part of the island megafauna, played significant roles in the ecology of the West Indies (Hastings et al., 2014). Cuban crocodiles (*C. rhombifer*) are reported as fossils, from Oleg's Bat Cave, the same crocodylian species found as fossils in blue holes in the Bahamas (Morgan and Albury, 2013; Morgan et al., in review).

DISPERSAL MECHANISMS: Tortoises are known to have the ability to readily colonize oceanic islands by means of overwater dispersal from continental populations or other island groups (Hansen et al., 2016). Meylan and Sterrer (2000) reported a fossil tortoise (*Hesperotestudo bermudae*) from the island of Bermuda. This oceanic island lies more than 1000 km east of Cape Hatteras, North Carolina, in the Atlantic Ocean. The proposed launching point for the ancestors of *H. bermudae* was the Florida east coast, which added 600 km to this distance, accounting for the Gulf Stream. The tortoise was believed to have been resident on Bermuda about 300,000 years ago, based on the age of the confining geologic formation. This early date places the dispersal well before humans, at a time when the Gulf Stream circulation was much like today's pattern (Meylan and Sterrer, 2000).

Large land tortoises are well adapted to float and are buoyant due to their large-capacity lung-to-body mass ratio associated with their high-domed shells (Patterson, 1973). Gerlach et al. (2006) reported the occurrence of a female Aldabra tortoise, *Dipsochelys dussumieri* (= *Aldabrachelys gigantea*), found coming ashore at Kimbiji, Tanzania, on the east coast of Africa, some 750 km from its probable point of origin, the Aldabra Atoll. Judging from its emaciated condition and the size of the goose barnacles that covered its plastron, bridge, and lower legs, this Aldabra tortoise had been at sea for six to seven weeks. Interestingly, the only areas not

encrusted with goose barnacles on this tortoise were its head and upper carapacial surfaces, dorsal to the bridge, implying that tortoises are able to maintain their body position with their heads out of the water.

Several modern taxa of freshwater turtles, *Trachemys*, are thought to be native to the Greater Antilles and the Bahamas. However, fossils of *Trachemys* are rare and recent evidence suggests human-mediated dispersals in the region (Parham et al., 2013). There is currently no evidence to suggest that populations of West Indian tortoises were translocated through anthropogenic events. Although there are no radiocarbon dates for *Chelonoidis dominicensis*, tortoises from the Bahamas predate the arrival of humans (Steadman et al., 2007; Steadman et al., 2015; Kehlmaier et al., 2017).

Galapagos tortoises are assumed to have initially populated the Galapagos Islands through overwater dispersal events from South America. Recent ancient DNA studies further support overwater dispersal for the Galapagos, as well as the West Indian tortoises (Kehlmaier et al., 2017). Specifically, *Chelonoidis alburyorum* in the extreme northern Bahamas was found to have its origins in the South American clade. This relationship extends to other *Chelonoidis* in the West Indies. The Galapagos tortoise paradigm appears to hold true for the West Indies. In the absence of radiocarbon dates, we presume *C. dominicensis* was present on Hispaniola during the Late Quaternary and humans were not part of their dispersal.

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