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A new species of extinct Late Quaternary giant tortoise from Hispaniola

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Abstract

Insular giant tortoise diversity has been depleted by Late Quaternary extinctions, but the taxonomic status of many extinct populations remains poorly understood due to limited available fossil or subfossil material, hindering our ability to reconstruct Quaternary island biotas and environments. Giant tortoises are absent from current-day insular Caribbean ecosystems, but tortoise remains from Quaternary deposits indicate the former widespread occurrence of these animals across the northern Caribbean. We report new Quaternary giant tortoise material from several cave sites in Pedernales Province, southern Dominican Republic, Hispaniola, representing at least seven individuals, which we describe as ***Chelonoidis marcanoi* sp. nov.** Although giant tortoise material was first reported from the Quaternary record of Hispaniola almost 35 years ago, tortoises are absent from most Quaternary deposits on the island, which has been studied extensively over the past century. The surprising abundance of giant tortoise remains in both vertical and horizontal caves in Hispaniola's semi-arid ecoregion may indicate that this species was adapted to open dry habitats and became restricted to a habitat refugium in southeastern Hispaniola following climatic-driven environmental change at the Pleistocene-Holocene boundary. Hispaniola's dry forest ecosystem may therefore have been shaped by giant tortoises for much of its evolutionary history.

Key words: Caribbean, *Chelonoidis*, Dominican Republic, megafauna, Quaternary extinction, Testudinidae

Introduction

Giant chelonians are a characteristic component of "depauperate" vertebrate faunas on oceanic-type islands around the world, often constituting the largest endemic vertebrates on these island systems and providing important roles as "ecosystem engineers" in maintaining habitat structure and native plant regeneration (Burness *et al.* 2001; Hansen & Galetti 2009; Griffiths *et al.* 2011; Froyd *et al.* 2014; Gibbs *et al.* 2014). Endemic island vertebrates have experienced high levels of extinction following the spread of humans across the world's island systems throughout the prehistoric Late Pleistocene-Holocene and more recent historical era (MacPhee 1999; Steadman 2006; Turvey 2009), and giant chelonians (including giant tortoises of the family Testudinidae and giant horned terrestrial turtles of the family Meiolaniidae) were particularly severely affected by Late Quaternary extinctions. At least 28 insular taxa in these two families are known to have disappeared from the Late Pleistocene onwards, with evidence for overexploitation for food by human settlers (chelonophagy) available to explain many of these extinctions (Carlson 1999; Cheke & Hume 2008; White *et al.* 2010; Gerlach 2014; Rhodin *et al.* 2015). However, the taxonomic status, morphology, landscape-level distribution, ecology and extinction chronology of many of these extinct giant chelonian populations remain poorly known, often due to very limited fossil or subfossil material available for many taxa (Rhodin *et al.* 2015), hindering our ability to reconstruct Quaternary island biotas and environments, and understand the potential ecosystem-level impacts and implications of insular chelonian extinctions.

The insular Caribbean has experienced substantial levels of vertebrate biodiversity loss during the Late Quaternary. In particular, the endemic Caribbean land mammal fauna has lost well over 100 species or distinct island populations during this interval, nearly all of which represent anthropogenically-mediated postglacial extinction events probably driven by direct human persecution or the effects of invasive mammals (MacPhee 1999, 2009; Woods & Sergile 2001; Turvey 2009). Late Quaternary extinctions of other vertebrates in the Caribbean region are more poorly understood and appear to have been less severe, but regional losses have also been documented for birds (e.g. Olson & Steadman 1977; Steadman & Takano 2013; Steadman & Franklin 2015) and reptiles (e.g. Pregill 1981; Vélez-Juarbe & Miller 2007; Kemp & Hadly 2015).

Giant tortoises are absent from current-day insular Caribbean ecosystems, but their former regional occurrence in the northern Caribbean region—referring to the oceanic-type islands of the Bahamian Archipelago, Greater Antilles, and adjacent islands north of the main Lesser Antillean chain—has been recognised since the earliest scientific studies of Caribbean Quaternary faunas. Giant tortoise bones were first reported from Cuba and Sombrero Island by Leidy (1868), and described as *Testudo cubensis* and *Emys sombrerensis* respectively; the Cuban taxon was subsequently further described from additional material by Williams (1950), and further material of the Sombrero taxon was reported by Julien (1978) and Auffenberg (1967). Other giant tortoise remains were also discovered in the twentieth century on Mona Island (described as *Testudo (Monachelys) monensis* by Williams 1952), the Bahamas (Auffenberg 1967; Olson *et al.* 1982; Pregill 1982), Navassa Island (Auffenberg 1967), and Hispaniola (Franz & Woods 1983), indicating the former widespread occurrence of these animals across the northern Caribbean.

All of these tortoises are known only from limited and fragmentary material, and other than the Cuban, Sombrero and Mona taxa, they have been left in open nomenclature. Caribbean giant tortoises were typically assigned to "*Geochelone* sp." by later twentieth century authors, but *Geochelone* as previously understood (e.g. Loveridge & Williams 1957; Auffenberg 1974) has been shown to be polyphyletic. Extant Neotropical continental and insular tortoises are instead now referred to *Chelonoidis* (Le *et al.* 2006).

More recently, giant tortoise specimens have been recovered from "blue holes", caves, and archaeological sites from 10 islands on seven island banks in the Bahamian Archipelago, including both the Bahamas and the Turks and Caicos Islands (Carlson 1999; Franz *et al.* 2001; Steadman *et al.* 2007; Franz & Franz 2009; Rhodin *et al.* 2015). Most of this material has not yet been published, but extremely well-preserved and nearly complete late Holocene specimens from the Sawmill Sink blue hole on Great Abaco Island, Little Bahama Bank, have been described as *Chelonoidis alburyorum* by Franz & Franz (2009), providing the first detailed morphological understanding of Caribbean giant tortoises against which material from other islands can now be compared. Recent ancient DNA analysis has confirmed that *C. alburyorum* is phylogenetically nested within the extant *Chelonoidis* radiation (Kehlmaier *et al.* 2017), indicating that morphologically similar extinct tortoises from other Caribbean islands are also very likely to be referable to this genus. However, the limited material currently available for other Caribbean tortoises means that their morphology and wider relationships remain unclear; although they all apparently display the derived characteristic of having an extremely thin shell, it is also possible that some of these taxa are not closely related (e.g. *Chelonoidis cubensis* may not be closely related to the Bahamian tortoise clade; Franz & Franz 2009). Genus-level assignment of Caribbean giant tortoises is further complicated by the fact that the North American testudinid *Hesperotestudo* is known to have dispersed overwater to Bermuda (Meylan & Sterrer 2000; Olson & Meylan 2009), suggesting that genera other than *Chelonoidis* may also have been able to colonise the insular Caribbean. It is therefore important that new tortoise material is described from other Caribbean islands in order to understand their evolutionary and ecological history.

The only giant tortoise material previously reported from Hispaniola, the second largest Caribbean island, consists of a nearly complete left humerus, some carapace fragments and a single plastron element, recovered from an undated cave deposit near Bayaguana in the Los Haitises region of Monte Plata Province, northeastern Dominican Republic (formerly San Cristóbal Province, as reported by Franz & Woods 1983) (Figure 1). Franz & Woods (1983) provided a description of this material and made some morphological comparisons with other Quaternary Caribbean tortoises, but left the Hispaniolan taxon in open nomenclature as "*Geochelone* sp.". Subsequent authors (e.g. Franz & Franz 2009; Rhodin *et al.* 2015) have considered the unnamed Hispaniolan giant tortoise only briefly, in contrast to the better-known giant tortoise from the neighbouring island of Cuba. Here, we describe considerable further material of the Hispaniolan giant tortoise that we have recovered from new palaeontological excavations in several cave sites in southern Dominican Republic. These finds improve our

understanding of its morphological differentiation from other Caribbean giant tortoises, permit the formal naming of this currently undescribed species, and provide important new insights into the ecology, biogeography and extinction dynamics of the Late Quaternary Caribbean vertebrate fauna.

Materials and methods

Palaeontological fieldwork was conducted in 2007, 2011, 2012 and 2013 in Pedernales Province, southern Dominican Republic, during which Late Quaternary giant tortoise material was collected from five cave deposits (Figure 1). Sampling involved dry-screening with 2 mm screens and subsequent residue sorting.

(1) Cueva del Papayo (17.85444 N, 71.49972 W, 14 m asl). A down-sloping gallery cave close to the shore of Laguna Oviedo; full site description given in Trias *et al.* (1997), who reported a Late Quaternary mammal assemblage containing *Brotomys voratus*, cf. *Hyperplagiodontia araeum*, *Isolobodon* cf. *montanus*, *I. portoricensis*, ?*Neocnus comes* and *Plagiodontia aedium* (nomenclature of Trias *et al.* 1997 updated to reflect current Hispaniolan mammal taxonomy, following MacPhee *et al.* 2000 and Hansford *et al.* 2012). Our excavation in May 2007 collected further Late Quaternary fossils including giant tortoise material together with a caniniform lower incisor of the lipotyphlan mammal *Solenodon paradoxus*, further material of *Isolobodon portoricensis*, non-diagnostic capromyid rodent postcrania assignable to multiple species on the basis of size variation, and non-diagnostic megalonychid sloth vertebrae, ribs and teeth.

(2) Cueva No. 12 (17.91388 N, 71.46861 W, 57 m asl). A previously unreported fossil site; a cave with a vertical entrance and a depth of 6.5 m, descending to a 5 m × 1.8 m chamber. Fieldwork in November 2011, May 2012 and August 2012 excavated sediments to a depth of 27 cm, and recovered giant tortoise material at a depth of 9-16 cm together with fossils of the mammal taxa *Acratocnus* sp., *Hexolobodon* sp., *Hyperplagiodontia araeum*, *Isolobodon montanus*, *I. portoricensis*, *Neocnus* sp., *Nesophontes hypomicrus*, *N. zamicrus* and *Plagiodontia aedium*, and the reptile taxa *Anolis* sp., *Celestus* sp. and *Leiocephalus* sp.

(3) Cueva de las Tortugas (17.79786 N, 71.44858 W, 63 m asl). A previously unreported fossil site; a cave with a narrow vertical entrance and a depth of 3 m, descending to a chamber 4.50 m² in area. Fieldwork in September 2013 recovered giant tortoise material in sediment partly bound by organic material, from the sediment surface to a depth of 23 cm, together with fossils of the mammal taxa *Acratocnus* sp., *Hyperplagiodontia araeum, Isolobodon* sp., *Nesophontes hypomicrus* and *Plagiodontia aedium,* the reptile taxa *Anolis* sp., *Celestus* sp.*, Leiocephalus* sp. and unidentified snake remains, and a fragmentary human jaw and molars.

(4) Cueva del Muerto (17.80312 N, 71.44418 W, 51 m asl). A previously unreported fossil site; a cave with a vertical entrance and a depth of 4 m, containing three chambers excavated in January 2013. The smallest chamber, with an area of 2.72 m², yielded giant tortoise material at a depth of 37 cm. The largest chamber, with an area of 6.21 m², yielded abundant material of the extinct sloth *Acratocnus* sp., and the third chamber, with an area of 4.50 m², contained a complete human skeleton identified as pre-Columbian in age by Professor Renato Rímoli (Museo Nacional del Hombre Dominicano, Santo Domingo), together with lithic tools. The site also contained fossils of the mammal taxa *Hyperplagiodontia araeum, Isolobodon portoricensis*, *Nesophontes hypomicrus, N. zamicrus* and *Plagiodontia aedium,* the reptile taxa *Anolis* sp., *Celestus* sp.*, Leiocephalus* sp., and unidentified snake remains.

(5) Cueva de las Caritas (17.79738 N, 71.44304 W). A previously unreported fossil site; a large cave with a vertical entrance with easy access, a depth of 3 m and an area of 104 m², and which contains two pre-Columbian petroglyphs of human faces. Giant tortoise material was recovered at a depth of 47 cm in September 2013, together with fossils of the mammal taxa *Isobolobon portoricensis* and an unidentified megalonychid sloth, the reptile taxa *Anolis* sp. and *Celestus* sp., and human bone fragments.

Repositories of described or cited specimens are: MNHNSD, Museo Nacional de Historia Natural "Prof. Eugenio de Jesús Marcano", Santo Domingo, Dominican Republic; NHMUK, The Natural History Museum, London, UK (Palaeontology Collections); UF, Florida Museum of Natural History. Specimens were cleaned using air abrasion with a DirectFlo DF1400, using aluminium oxide as an added abrasive. Measurements were made with dial calipers, accurate to the nearest 0.1 mm. Bone samples from a tortoise plastron fragment from Cueva de las Tortugas (MNHNSD FOS 23.1060) and a tortoise humerus from Cueva de las Caritas (MNHNSD FOS 23.1064) (selected for dating based on minimal calcite encrustation compared to other specimens) were submitted for accelerator mass spectrometer (AMS) ^{14}C dating at the [14]CHRONO Centre, Queen's University, Belfast (UK).
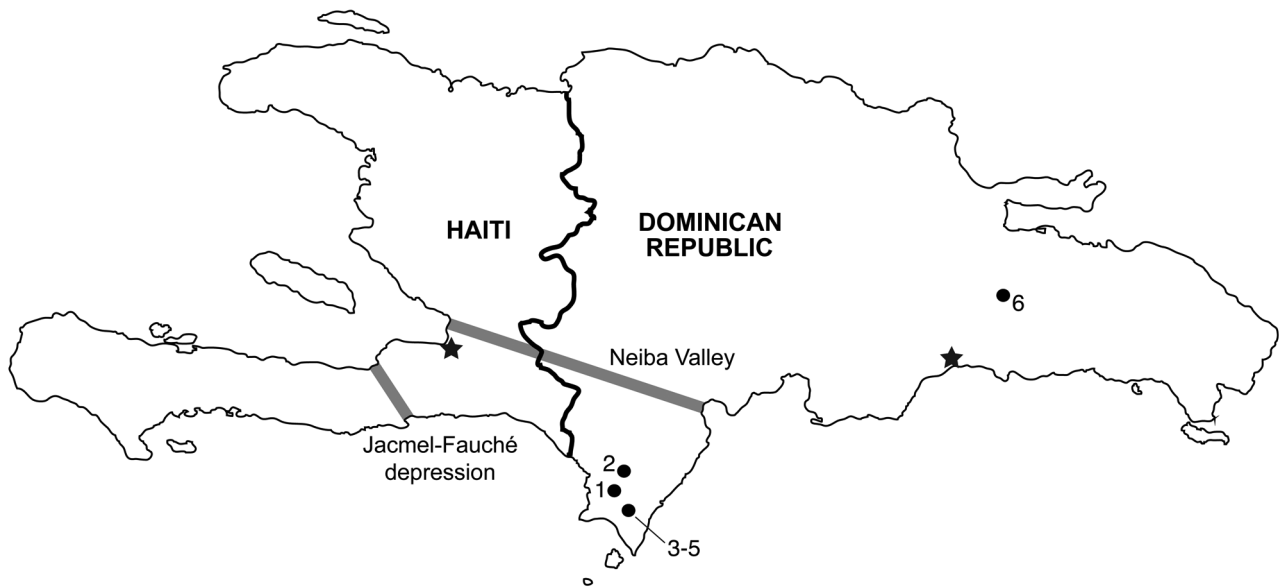
FIGURE 1. Map of Hispaniola, showing geotectonic boundaries and locations of cave sites from which giant tortoise fossils have been reported. Capital cities indicated with filled stars. Key: 1, Cueva del Papayo; 2, Cueva No. 12; 3, Cueva de las Tortugas; 4, Cueva del Muerto; 5, Cueva de las Caritas; 6, Bayaguana.

Results

We recovered 13 giant tortoise skeletal elements, comprising six humeri (NHMUK PV R 36954; MNHNSD FOS 23.1054, 23.1057-23.1059, 23.1064; Figure 2), two femora (MNHNSD FOS 23.1055, 23.1063; Figure 3), and two plastron fragments, one carapace fragment, and two carapace-plastron fragments (NHMUK PV R 36955; MNHNSD FOS 23.1056, 23.1060-23.1062; Figures 4–6), in total representing at least seven individuals. One of the humeri (MNHNSD FOS 23.1054) shows post-mortem gnawing marks made by rodent incisors on its lateral shaft surface, which match the size of the incisors of the living Hispaniolan hutia *Plagiodontia aedium*.

Unfortunately, prescreening revealed that the samples from both MNHNSD FOS 23.1060 and MNHNSD FOS 23.1064 contained insufficient collagen to allow AMS dating. This almost certainly reflects geologically recent sample degradation under subtropical conditions, as has also been widely reported for other Late Quaternary (including Holocene) vertebrate fossils from the Caribbean region (e.g. Steadman *et al.* 2005; Turvey *et al.* 2007), rather than antiquity of fossil material or a locally specific taphonomic process.

Systematic taxonomy

Reptilia Laurenti 1768

Testudines Linnaeus 1758

Cryptodira Cope 1868

Testudinidae Batsch 1788

***Chelonoidis* Fitzinger 1835**

***Chelonoidis marcanoi* sp. nov.**

Holotype. Right humerus (NHMUK PV R 36954), collected on 12 May 2007 (Figure 2a–b).
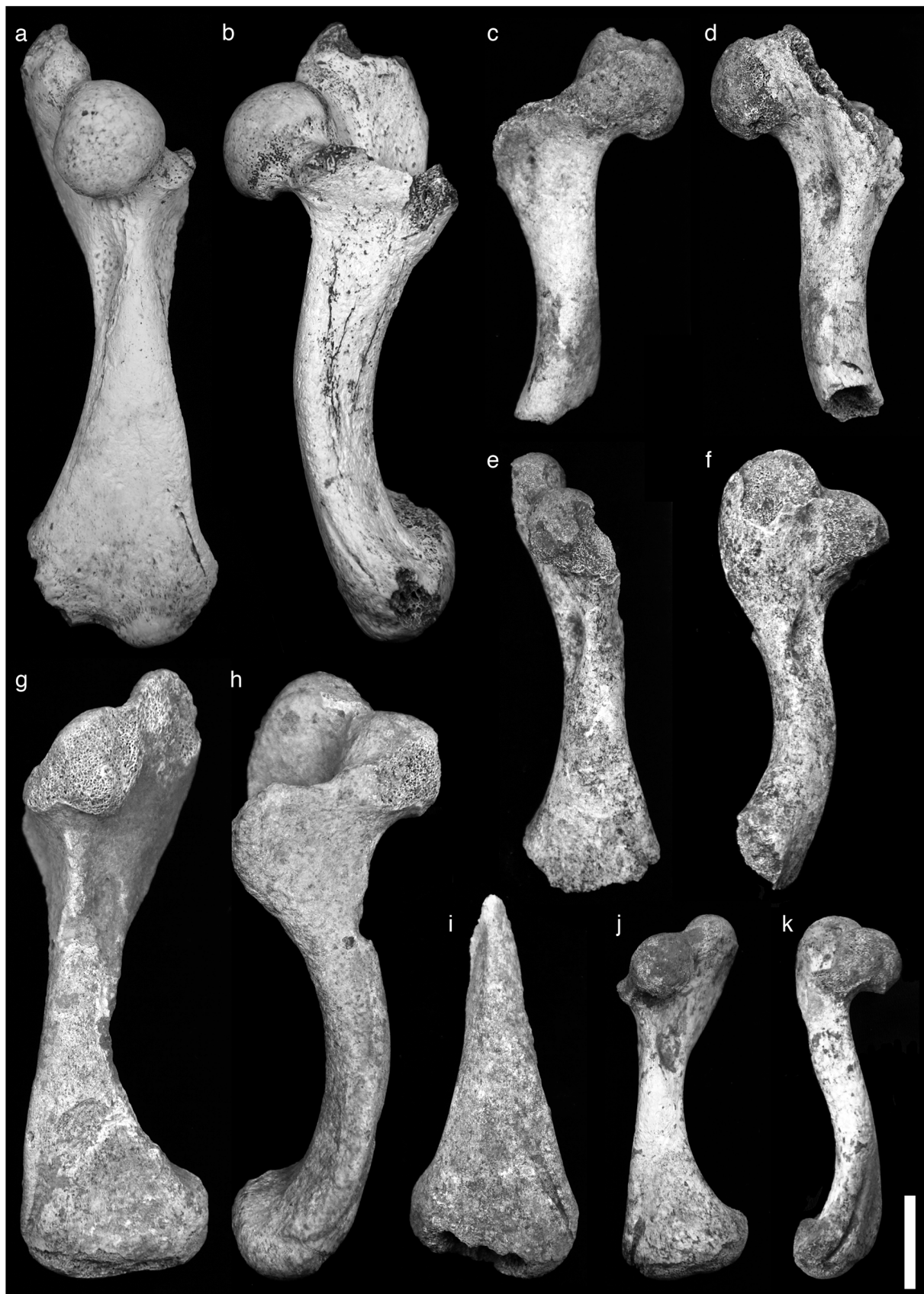
FIGURE 2. Humeri of *Chelonoidis marcanoi* **sp. nov.** from Pedernales Province, Dominican Republic: a–b, NHMUK PV R 36954 (holotype), right humerus, anterior and medial views; c–d, MNHNSD FOS 23.1064, left proximal humerus, medial and lateral views; e–f, MNHNSD FOS 23.1058, right humerus, anterior and lateral views; g–h, MNHNSD FOS 23.1054, left humerus, anterior and medial views; i, MNHNSD FOS 23.1059, right distal humerus, anterior view; j–k, MNHNSD FOS 23.1057, left humerus (young individual), anterior and medial views. Scale bar=2 cm.

FIGURE 3. Femora of *Chelonoidis marcanoi* **sp. nov.** from Pedernales Province, Dominican Republic: a–c, MNHNSD FOS 23.1063, left femur (young individual), lateral, anterior and medial views; d–e, MNHNSD FOS 23.1055, right distal femur, anterior and lateral views. Scale bar=2 cm.

Paratypes. NHMUK PV R 36955; MNHNSD FOS 23.1054-23.1064; UF 26095-26100.

Type locality. Cueva del Papayo, Pedernales Province, Dominican Republic (NHMUK PV R 36954-36955).

Other known localities. Unnamed cave near Bayaguana, Monte Plata Province, Dominican Republic (UF 26095-26100); Cueva No. 12 (MNHNSD FOS 23.1054-23.1056), Cueva de Las Tortugas (MNHNSD FOS 23.1057-23.1062), Cueva del Muerto (MNHNSD FOS 23.1063) and Cueva de las Caritas (MNHNSD FOS 23.1064), Pedernales Province, Dominican Republic. Only known from Hispaniola.

Etymology. After Professor Eugenio de Jesús Marcano, who collected the first giant tortoise fossils discovered on Hispaniola that were described by Franz & Woods (1983).

Diagnosis. Thin-shelled, large-bodied testudinid tortoise with adult humerus much larger than in *C. alburyorum* but probably smaller than in *C. sombrerensis*; humerus more slender than in *C. alburyorum* or *C. cubensis*; *M. latissimus dorsi* muscle scar on lateral surface better defined than in *C. monensis* but not as prominent as in *C. cubensis*; humeral shaft rounded/oval or slightly triangular and approximately as long as wide in middle shaft cross-section, unlike the narrower, deeper shaft of *C. cubensis*. Femur with maximum distal width markedly greater than maximum proximal width in single available young specimen, versus the equal proximal and distal widths shown by *C. alburyorum*. External carapace surface showing sulci with edges raised as distinct low ridges, unlike the indistinct and scarcely apparent sulci of *C. monensis*, *C. sombrerensis*, and the undescribed giant tortoises from Navassa and New Providence; gular scutes much shorter than in *C. cubensis*, with sulci defining their posterior border curving posteriorly rather than anteriorly as in *C. alburyorum*.

Description. Humerus: Shaft straight along proximal half, recurved ventrally along distal half; relatively long and slender. Proximal width across trochanters and distal width across articulating surface approximately equal. Head subspherical, slightly laterally compressed, oriented anteriorly at almost 90°. Trochanteric tuberosities straight, diverging proximally at about 40°; posterior edges raised up as narrow laterally flattened ridges at their base, becoming more rounded towards proximal surfaces. Intertrochanteric fossa short, deep, with roughened surface at distal end. Lesser trochanter short; proximal surface flattened, almost level with midline of humeral head in well-preserved specimens. Greater trochanter much longer, extending considerably beyond upper surface of humeral head; proximal surface rounded. Prominent, relatively deep and oval *M. latissimus dorsi* muscle scar well-defined on lateral surface of humerus in front of base of greater trochanter; with roughened inner surface. Second much shallower circular muscle scar also present on medial surface of humerus, more anteriorly situated than *M. latissimus dorsi* muscle scar. Sides of shaft flattened immediately distal to humeral head, with anterior surface raised as narrow ridge between medial and lateral muscle scars; anterior surface becoming broader distally to form smooth, posteriorly curved and mediolaterally flattened surface across distal half of humerus. Medial surface approximately straight; lateral surface curving outwards distally, giving flared outline to humerus in anterior

profile. Shaft midlength rounded/oval or slightly triangular in cross-section, approximately as long as wide. Distal anterior surface with prominent long, straight, deep and narrow incised entepicondylar groove close to medial margin, running mediodistally up to or into the medial corner of the articular surface. Posterior distal surface with two short, low raised ridges, which diverge towards distal articulating surface. Distal articulating surface of holotype developed into two low, swollen facets that correspond to the ulnar and radial articulating surfaces; facets less developed in other specimens. Humeral measurements given in Table 1.
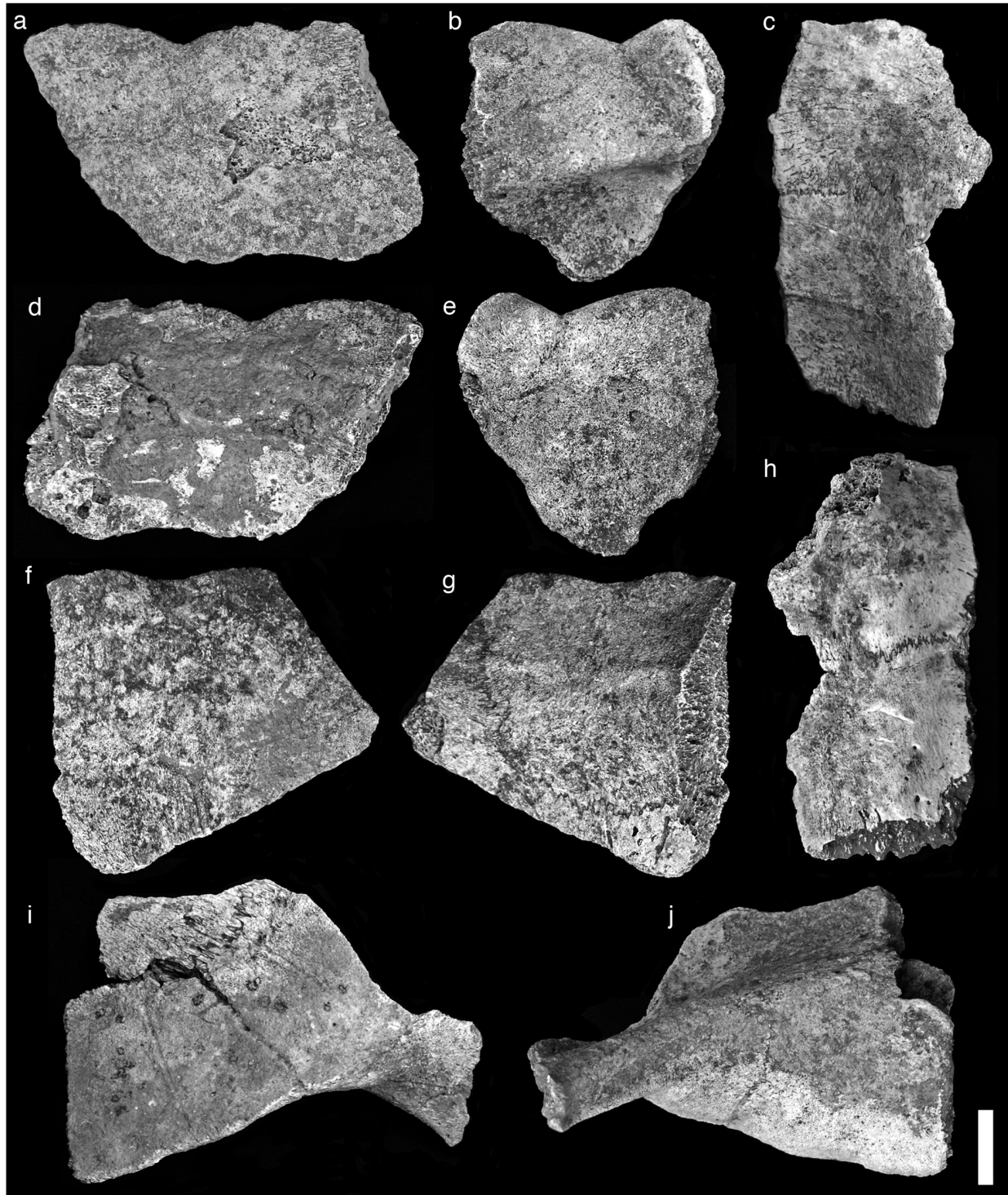

FIGURE 4. Plastron and carapace fragments of *Chelonoidis marcanoi* **sp. nov.** from Pedernales Province, Dominican Republic: a, d, epiplastron fragment (MNHNSD FOS 23.1056), external and internal views; b, e, epiplastron fragment (MNHNSD FOS 23.1060), external and internal views; c, h, costal fragment (NHMUK PV R 36955), internal and external views; f–g, peripheral fragment (MNHNSD FOS 23.1061), external and internal views; i–j, fragment from border of carapacial rim, including two peripherals and part of costal plate (MNHNSD FOS 23.1062), external and internal views. Scale bar=2 cm.
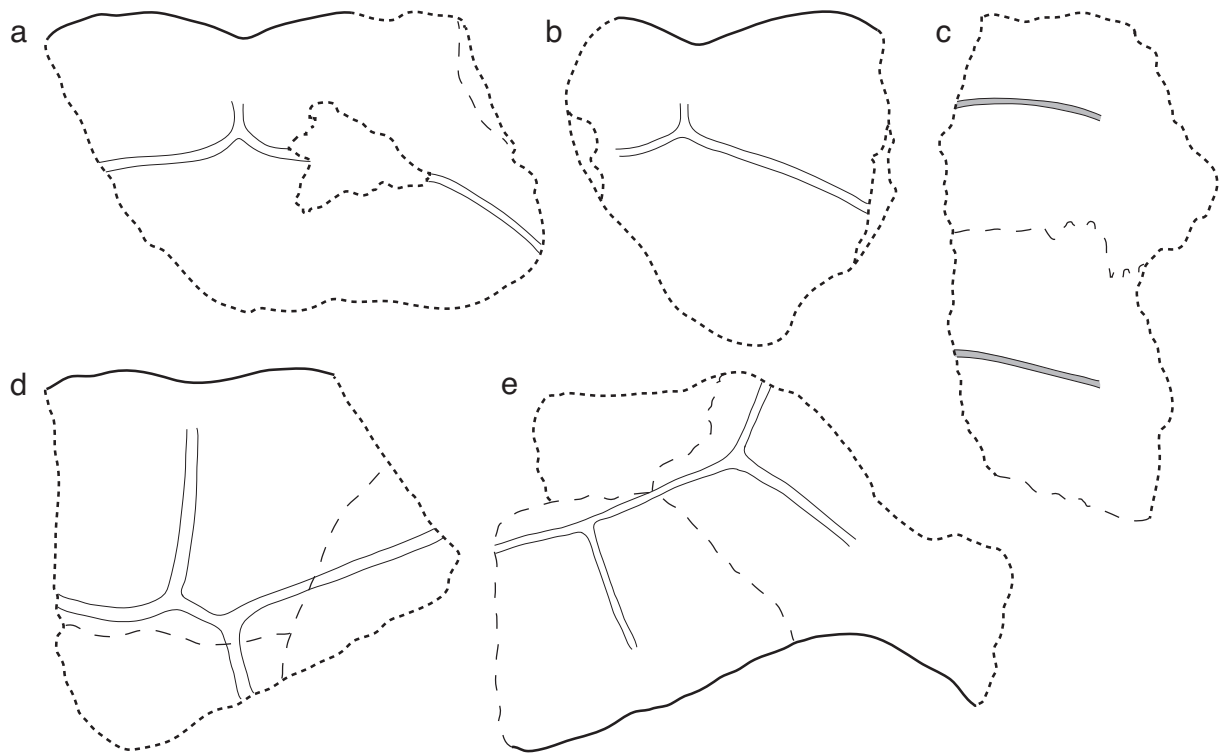
FIGURE 5. Schematic interpretation of surface features of plastron and carapace fragments of *Chelonois marcanoi* **sp. nov.** from Pedernales Province, Dominican Republic, showing natural borders (thick solid lines), broken borders (dotted lines), sutures (dashed lines), external sulci (thin solid lines), and internal ridges associated with costal ribs (grey filled lines). a, external surface of epiplastron fragment (MNHNSD FOS 23.1056); b, external surface of epiplastron fragment (MNHNSD FOS 23.1060); c, internal surface of costal fragment (NHMUK PV R 36955); d, external surface of peripheral fragment (MNHNSD FOS 23.1061); e, external surface of fragment from border of carapacial rim, including two peripherals and part of costal plate (MNHNSD FOS 23.1062). All specimens drawn to scale.
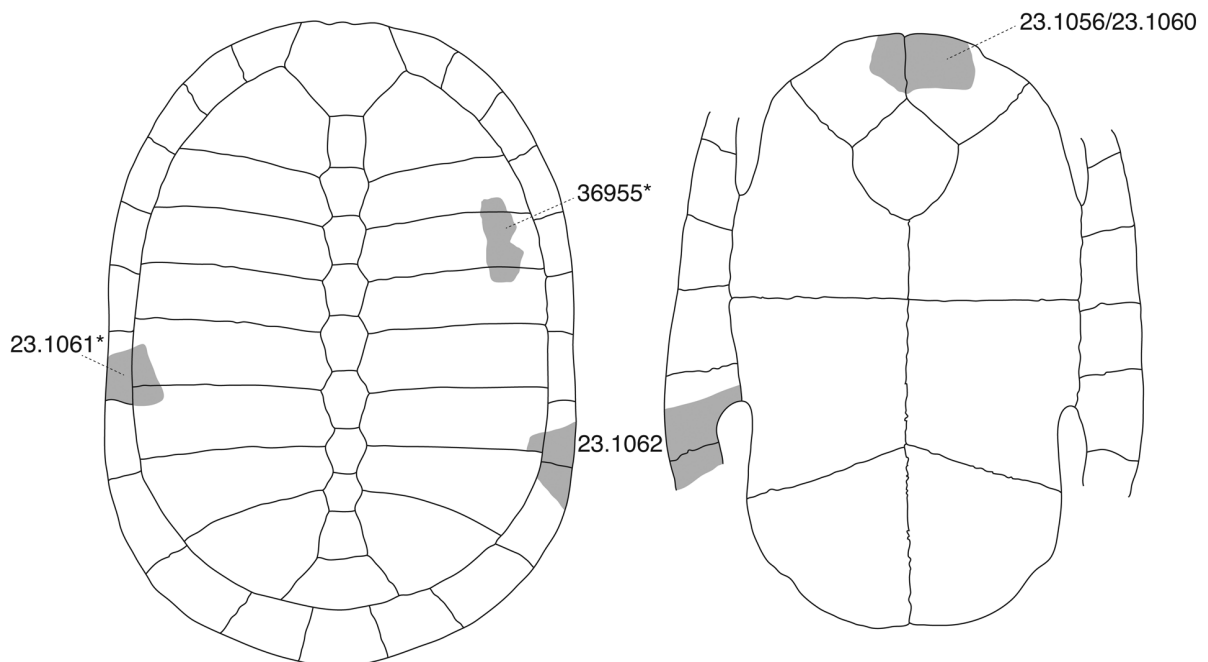

FIGURE 6. Schematic drawing of dermal bones of chelonian carapace (left) and plastron (right), indicating approximate estimated position of described shell fragments of *Chelonois marcanoi* **sp. nov.** from Pedernales Province, Dominican Republic. Original position on either the left or right side of the carapace is uncertain for the two specimens indicated with asterisks.

TABLE 1. Humeral measurements (in mm) for six specimens of *Chelonoidis marcanoi* **sp. nov.** from Pedernales Province, Dominican Republic. Asterisks indicate approximate measurement due to damaged specimen.

Measurement	NHMUK PV R 36954 (holotype)	MNHNSD FOS 23.1054	MNHNSD FOS 23.1057	MNHNSD FOS 23.1058	MNHNSD FOS 23.1059	MNHNSD FOS 23.1064
Total length	127.6	125.7	86.9	100.6*	—	—
Head length	24.9	22.0*	16.3	19.6*	—	27.8
Head width	22.4	—	15.2	—	—	22.2
Width across trochanters	38.1	40.4	28.2	—	—	—
Lesser trochanter length	—	29.3	22.1	—	—	—
Greater trochanter length	51.8	52.3	34.0	43.5	—	—
Greater trochanter distance above head	13.5	12.1	9.9	12.7	—	—
M. latissimus dorsi length × width	14.5 × 6.5	16.5 × 6.0	10.0 × 6.7	12.8 × 5.8	—	15.5 × 6.8
Shaft midpoint height × width	16.4 × 14.8	12.9 × 14.8	9.8 × 10.5	13.9 × 14.0	14.7 × 15.2	15.5 × 15.4
Distal articulating surface width	—	38.6	30.9	—	40.2	—

Femur: Proximal morphology only available for single small specimen of young individual with spongy, incompletely formed articular surfaces (MNHNSD FOS 23.1063); adult distal femoral morphology displayed by second, incomplete specimen (MNHNSD FOS 23.1055). Femoral head damaged; probably originally spherical. Trochanters low, not extending above level of femoral head; greater trochanter slightly higher than lesser trochanter, with more rounded proximal surface. Trochanters enclose deep, rounded medial trochanteric fossa on proximal surface. Shaft flat in medial/lateral profile, with distal articulating surface curving posteriorly along distal quarter of shaft. Prominent ovoid muscle scar present on lateral shaft surface below femoral head, about one-third length along shaft. Shaft midpoint robust and approximately square in cross-section. In dorsal profile, shaft narrows slightly below head then flares laterally and expands in width across distal half of shaft, so that maximum distal width is markedly greater than maximum proximal width, and anterior surface of distal shaft is broad and flattened. No prominent grooves on distal anterior surface. Distal articulating surface shows very weak development of facets on adult specimen, defined by faint notch and corresponding to tibial and fibial articulating surfaces. Femoral measurements given in Table 2.

TABLE 2. Femoral measurements (in mm) for six specimens of *Chelonoidis marcanoi* **sp. nov.** from Pedernales Province, Dominican Republic. Asterisks indicate approximate measurement due to damaged specimen.

Measurement	MNHNSD FOS 23.1055	MNHNSD FOS 23.1063
Total length	—	65.4*
Head length	—	4.5*
Head width	—	6.2*
Width across trochanters	—	18.5
Shaft midpoint height × width	—	9.1 × 7.5
Distal articulating surface width	36.6	25.1

Plastron and carapace: Epiplastron represented by two fragments (MNHNSD FOS 23.1056, 23.1060) that are identifiable from their deeply scalloped natural border, thin non-triangular cross-section, and lack of insertion of costal plates or ribs. These fragments represent two individuals from different sites. External surface of epiplastron slightly rounded. Gular apices consist of two gently anteriorly rounded lobes, separated at midline by shallow

notch. Sulci defining gular scutes on external surface expressed as simple shallow unraised grooves. Gular scutes short, separated at midline by sulcus measuring 17.9 mm in length in MNHNSD FOS 23.1056, and 18.6 mm in length in MNHNSD FOS 23.1060. Sulci defining posterior border of gular scutes first curve gently outwards posterolaterally from midline, then curve more posteriorly as they expand. Inner surface inflated towards skin line; surface behind skin line slopes sharply from epiplastral shelf. Shell very thin; skin line thickness measures 15.5 mm in MNHNSD FOS 23.1056, and 16.0 mm in MNHNSD FOS 23.1060; behind skin line, shell thickness narrows to c.3 mm at inner margin of MNHNSD FOS 23.1056, and 4.2 mm at inner margin of MNHNSD FOS 23.1060. No external or internal ornamentation (e.g. "bird face" of Franz & Franz 2009) seen on either available epiplastron fragment. Peripheral fragment (MNHNSD FOS 23.1061) thicker and distinctly triangular in cross-section in comparison to epiplastral fragments, and with very gently lobed margin; skin line thickness measures 20.5 mm, narrowing to 3.8 mm at inner margin. Fragment comprising two successive costal plates (NHMUK PV R 36955) with curved external and internal surfaces; maximum thickness of 11.0 mm, minimum thickness of 4.5 mm. No external ornamentation; internal surface with two low raised parallel ridges associated with development of costal ribs. Fragment from border of carapacial rim (MNHNSD FOS 23.1062) consists of axillary buttress supporting right anterior corner of carapace-plastron bridge at a position immediately behind the buttress, and includes two peripherals and part of a costal plate; maximum buttress thickness 21.7 mm; lateral margin very gently scalloped; carapace with a minimum thickness of 2.9 mm, and with external surface showing sulci with edges raised as low ridges. Additional description of carapace fragments previously given by Franz & Woods (1983).

Remarks. We interpret our new collection of giant tortoise fossils as all representing a single species, as the multiple humeri in this collection exhibit no morphological differences other than ontogenetic variation, and the fossils were all preserved in comparable depositional conditions with similar co-occurring vertebrate faunas, suggestive of similarity in geological age. The humeri in our new collection are also indistinguishable from the single chelonian humerus from Bayaguana previously described and illustrated by Franz & Woods (1983), and our new carapace and plastron fragments show identical morphological characteristics to the Bayaguana material, so we refer all of the known giant tortoise specimens from Hispaniola to the same new species.

Although carapace and neural characteristics that can be used to differentiate *Chelonoidis* from other New World testudinid genera (cf. Franz & Franz 2009) cannot be determined from available material of the new species, several characters of the humerus (the best-preserved and most commonly represented element in our collection) support genus-level assignment of the new species to *Chelonoidis* rather than to North American xerobatin testudinids (*Gopherus*, *Hesperotestudo*), the other candidate genera to which the extinct Caribbean tortoises might be referable (Williams 1952; Auffenberg 1974; Meylan & Sterrer 2000). Unlike the Hispaniolan giant tortoise, mainland Neotropical *Chelonoidis* species or *C. alburyorum*, the humeri of *Gopherus* and of mainland and insular *Hesperotestudo* species lack either an obvious insertion site for *M. latissimus dorsi*, or an entepicondylar groove or foramen; the greater trochanter also does not extend beyond the head of the humerus in *Hesperotestudo*, in contrast to the marked extension of the greater trochanter in the Hispaniolan giant tortoise and other *Chelonoidis* species, and this character is interpreted as a derived condition in *Chelonoidis* (Auffenberg 1963; Meylan & Sterrer 2000; Franz & Franz 2009). The shell of the insular *Hesperotestudo bermudae* is also not markedly thinner than in mainland American xerobatin testudinids (Meylan & Sterrer 2000), in contrast to the very thin-walled shell seen in the Hispaniolan giant tortoise and other described *Chelonoidis* species (Franz & Franz 2009). Whilst variation in shell thickness may represent an ecological response to insular environmental conditions (e.g. absence of predatory mammals) rather than a phylogenetic signal, the shell state in the Hispaniolan tortoise is consistent with that described for species of *Chelonoidis*.

We therefore consider that even in the absence of information on skull morphology or detailed shell morphology, the Hispaniolan tortoise can be confidently referred to *Chelonoidis* on the basis of comparative postcranial characteristics. This taxonomic hypothesis is consistent with other available data on Quaternary testudinid biogeography for the insular Caribbean, as *Chelonoidis* definitely occurred on the nearby Bahamian Archipelago (Kehlmaier *et al.* 2017). The only potentially unusual characteristic shown by the Hispaniolan tortoise compared to well-described *Chelonoidis* species is the apparent absence of diagnostic interior sculpture on entoplastral elements in the new collection, but this may simply reflect the limited preservation of available incomplete entoplastral specimens from the new species.

The Hispaniolan species differs from *C. alburyorum*, the best-described Caribbean giant tortoise, in being

considerably larger in body size. Although the total shell length is unknown for the Hispaniolan species, Franz & Woods (1983) estimated an approximate total carapace length of c.600 mm through comparison with modern giant tortoise specimens of known size, and available adult tortoise humeri from Hispaniola have a total length of c.125– 135 mm (Table 1; Franz & Woods 1983); in contrast, *C. alburyorum* has a total carapace length of 345–466 mm, and a humerus length of 96.1 mm (Franz & Franz 2009). The humerus of the Hispaniolan species is also more slender and gracile than in *C. alburyorum*; despite being markedly longer, the maximum width across the distal articulating surface in well-preserved adult Hispaniolan humeri is only 38.6–40.2 mm (30.7% of total humerus length in MNHNSD FOS 23.1054), compared to 37.4 mm in *C. alburyorum* (38.9% of total humerus length) (Franz & Franz 2009). Femoral comparisons between the two taxa are based on more limited available material, but the single complete femur of the Hispaniolan species has a maximum distal width that is markedly greater than its maximum proximal width, in contrast to the similar proximal and distal widths seen in femora of *C. alburyorum*. The available Hispaniolan femur is from a young individual, however, so it is possible that this difference may at least partly reflect ontogenetic variation. The Hispaniolan species also apparently lacks the diagnostic interior "bird face" sculpture seen on the entoplastron of *C. alburyorum*, and has shorter gular scutes defined on the external surface by sulci which curve outwards and gently backwards rather than running outwards and forwards from the plastron midline as in *C. alburyorum*.

Detailed comparison with other Caribbean giant tortoises is more difficult due to the limited material available from other islands, but diagnostic differences can also be identified between the Hispaniolan species and other previously described Caribbean tortoise taxa. Humeral measurements have not been reported for *C. cubensis* or *C. monensis*, but *C. cubensis* differs from the Hispaniolan species in having a shorter, more robust humerus with a shaft depth c.1.5 times the shaft width and that shows a much more strongly developed, extremely large and deep *M. latissimus dorsi* muscle scar, and also in having an extremely elongate gular scute and a prominent "bird face" sculpture on the entoplastron (Williams 1950; Franz & Franz 2009); and *C. monensis* conversely differs from the Hispaniolan species in reportedly having a reduced *M. latissimus dorsi* muscle scar that merely consists of a roughened area rather than a pit (Williams 1952). *Chelonoidis sombrerensis* is much more poorly known; one described humerus is similar in length to that of the Hispaniolan species (estimated at approximately 130 mm), but this specimen lacks both ends and so may not be fully grown; another reported humerus for this species is markedly larger (approximately 300 mm), and with a considerably greater shaft depth than in the Hispaniolan species (1.3 times the shaft width) (Julien 1878; Williams 1952). The Hispaniolan species also differs from *C. monensis*, *C. sombrerensis*, and the undescribed "moderate-sized" tortoises from Navassa and New Providence in having carapace sulci with raised ridges rather than having sulci that are indistinct and scarcely apparent (Auffenberg 1967); carapace sulci defined by raised edges along their margins are otherwise only shown by *C. alburyorum* and *C. cubensis* in the Caribbean region (Williams 1950; Franz & Franz 2009).

Discussion

Although our newly collected giant tortoise fossil material from Hispaniola is not as complete as the exceptionally preserved blue hole tortoise specimens reported from the Bahamas by Franz & Franz (2009), it is still sufficient to diagnose the unique morphological characteristics of the Hispaniolan taxon and formally recognise it as a distinct species, almost 35 years since tortoise remains were first reported from the Quaternary record of this large Caribbean island. It is not surprising that Hispaniola's tortoise represents a different species to the taxa described from other islands in the Caribbean, as extant or historically extinct allopatric giant tortoise populations from different islands in both the Galápagos and Indian Ocean archipelagos, which constitute independent evolutionary units often previously interpreted as representing only subspecies-level differentiation, are now generally all interpreted as different species (Bour 1980; van Dijk *et al.* 2014; Rhodin *et al.* 2015); multiple allopatric giant tortoise species are further recognised within larger Galápagos islands (Russello *et al.* 2005; Poulakakis *et al.* 2015).

Although formal comparative assessment of inter-island relationships and biogeographic patterns shown by Caribbean tortoises (e.g. through cladistic analysis) must await collection of more extensive fossil material from other islands, our new tortoise fossil collection still provides an important new perspective for interpreting intra-island biogeographic and ecological patterns across Hispaniola, a large Caribbean island with a complex

geotectonic history that has shaped local patterns of endemic biodiversity. Hispaniola consists of independent northern and southern palaeo-islands that docked tectonically during the middle-late Miocene (Mann *et al.* 1991; Graham 2003) but remained separated by the Neiba Valley, a prominent depression periodically or continually inundated by a narrow seaway until the Late Pleistocene (Maurrasse *et al.* 1980). The southern palaeo-island is further subdivided into distinct southeastern and southwestern physiographic provinces separated by the Jacmel-Fauché depression in southeastern Haiti, which bisects the peninsula and was also inundated during some or all of the Plio-Pleistocene (Maurrasse *et al.*, 1980) (Figure 1). All three regions are biogeographically distinct, and characterized by substantial local endemism and congruent phylogenetic patterns in many extant and extinct terrestrial vertebrate taxa (Williams 1961; Schwartz 1980; Woods 1989; Hedges 1999; Cooke *et al.* 2011; Brace *et al.* 2012; Turvey *et al.* 2015, 2016). In particular, *Cyclura* iguanas, which constitute some of Hispaniola's few surviving large-bodied terrestrial reptiles, show species-level biogeographic differentiation associated with the island's distinct physiographic provinces, with rhinoceros iguana (*C. cornuta*) occurring only in Hispaniola's northern biogeographic region and Ricord's iguana (*C. ricordi*) restricted to the southeastern region (Lemm and Alberts 2012). We note however that the tortoise material described by Franz & Woods (1983) was collected in Hispaniola's northern biogeographic region, so that our discovery of new tortoise fossils in Pedernales Province, southeastern Hispaniola, indicates that giant tortoises formerly occurred widely across the island on both sides of the Neiba Valley (Figure 1).

Given the incomplete and fragmentary nature of available tortoise fossil material from Hispaniola, it is impossible to assess whether giant tortoises displayed any biogeographic differentiation across the island at the subspecific or population level, as recently demonstrated for some Hispaniolan mammals (Brace *et al.* 2012; Turvey *et al.* 2015, 2016). Even if intra-island biogeographic differentiation can be detected in the future, though, the newly demonstrated wide past distribution of tortoises across Hispaniola raises important questions. Hispaniola's Quaternary fossil record has been studied extensively over the past century, and many extinct vertebrates are well-represented in collections from the island (e.g. Miller 1916, 1929a, 1929b, 1930; Rímoli 1976; Woods 1989; Woods & Ottenwalder 1992; MacPhee *et al.* 2000; Cooke *et al.* 2011; Hansford *et al.* 2012). Despite this collection effort, however, tortoise fossils were known from a single locality on Hispaniola prior to our discovery of fossils in Pedernales, and their absence from most Quaternary deposits on the island has previously been remarked upon (Williams 1952; Franz & Woods 1983). The newly recognized wide distribution of tortoises across the island, and their relative abundance in caves in southeastern Hispaniola, therefore makes their general absence from other Quaternary fossil deposits even more surprising.

Williams (1952) and Franz & Woods (1983) suggested that the general absence of tortoises from Hispaniola's fossil record may reflect either a taphonomic bias, or an older, Pleistocene extinction. The Bayaguana tortoise material is darkly stained and highly mineralized; although it has not been directly dated, it was considered by Franz & Woods (1983) to be probably Pleistocene in age on the basis of this preservation. Williams (1952) and Franz & Woods (1983) considered that most Hispaniolan cave deposits are probably Holocene in age, suggesting that tortoises may therefore have already been extinct before the island's fossiliferous cave sediments were deposited. A climatic-driven shift at the Pleistocene-Holocene boundary in dominant Caribbean terrestrial environments, from glacial xeric open habitats to interglacial mesic forest habitats, was proposed as a potential driver of regional Quaternary vertebrate extinctions by Pregill & Olson (1981), and Franz & Woods (1983) considered that this environmental change was a likely driver of giant tortoise extinction on Hispaniola.

There is, however, increasing evidence that other extinct large vertebrates (e.g. megalonychid sloths) persisted into the Holocene on Hispaniola, with their extinction instead likely to have been mediated by interaction with prehistoric human settlers who reached Hispaniola by c.5500 yr BP (Steadman *et al.* 2005; Turvey & Fritz 2011). Semi-arid climates also still occur in southeastern Hispaniola, in the rain shadow to the south of the island's major east-west mountain ranges, with dry forest and open xeric vegetation rather than moist forest representing the dominant low-elevation habitat types (Peel *et al.* 2007). Other than the preliminary investigations reported by Trias *et al.* (1997), extremely little palaeontological research has previously been conducted in this distinct ecoregion compared to other parts of Hispaniola. The relative abundance of tortoise fossils in both vertical and horizontal caves in southeastern Hispaniola, compared to their near-absence from the rest of the island, may therefore be explained by the hypothesis that the Hispaniolan tortoise was adapted to open dry habitats, similar to the ecology of extant insular giant tortoises (Kricher 2006; Gerlach 2014), and experienced range contraction following climatic-driven change in Hispaniolan terrestrial environments at the Pleistocene-Holocene boundary but survived in a

geographically restricted habitat refugium in southeastern Hispaniola. We therefore consider it likely that giant tortoises persisted into the Holocene on Hispaniola, and that extinction of a geographically restricted Holocene tortoise population was probably caused by prehistoric human settlers. A similar model of prehistoric human overexploitation of megafaunal taxa that were periodically restricted to intrinsically vulnerable small populations in environmental refugia during glacial-interglacial climatic cycles is also proposed to explain many continental Late Quaternary extinctions (Stuart 1999; Stuart *et al.* 2004). Unfortunately the age of all of the Hispaniolan tortoise fossil deposits remains unknown, and our hypothesized extinction model must be tested by further radiometric investigation of Hispaniolan fossil deposits.

Morphological assessment of available giant tortoise material from Hispaniola does not permit detailed understanding of its potential ecological impacts on vegetation or habitat structure. For example, more complete material is necessary to determine carapace shape and likely feeding behavior (e.g. high versus low browsing). Although no predictive regression equations based on limb bone measurements are available to provide meaningful estimates of giant tortoise body masses, however, the Hispaniolan tortoise was one of the largest terrestrial vertebrates in Hispaniolan Quaternary ecosystems, with only megalonychid sloths in the genera *Megalocnus* and *Parocnus* likely to have been substantially larger (MacPhee *et al.* 2000; Turvey & Fritz 2011), and it is likely to have been an important "ecosystem engineer" in the island's open dry habitats. We encourage further investigation of the former ecological function of now-extinct Caribbean giant tortoises, for example through the use of stable isotope analysis to determine diet and niche partitioning between co-occurring large-bodied reptilian and mammalian herbivores in Late Quaternary Caribbean landscapes (cf. Hastings *et al.* 2014). Environmental management of Hispaniola's remaining dry forests may also require increased awareness that this ecosystem was potentially shaped by giant tortoises for much of its evolutionary history.

Acknowledgements

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