

PALEONTOLOGY

The anatomy, paleobiology, and evolutionary relationships of the largest extinct side-necked turtle

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Despite being among the largest turtles that ever lived, the biology and systematics of *Stupendemys geographicus* remain largely unknown because of scant, fragmentary finds. We describe exceptional specimens and new localities of *S. geographicus* from the Miocene of Venezuela and Colombia. We document the largest shell reported for any extant or extinct turtle, with a carapace length of 2.40 m and estimated mass of 1.145 kg, almost 100 times the size of its closest living relative, the Amazon river turtle *Peltocephalus dumerilianus*, and twice that of the largest extant turtle, the marine leatherback *Dermochelys coriacea*. The new specimens greatly increase knowledge of the biology and evolution of this iconic species. Our findings suggest the existence of a single giant turtle species across the northern Neotropics, but with two shell morphotypes, suggestive of sexual dimorphism. Bite marks and punctured bones indicate interactions with large caimans that also inhabited the northern Neotropics.

INTRODUCTION

Since the extinction of non-avian dinosaurs, the northern Neotropics have harbored now-extinct vertebrates that have been at the extreme of large size within their respective clades (1). Among them are the largest snake (2), caimanine crocodile (3), gharial (4), and some of the largest rodents (5). One of the most iconic of these species is the gigantic turtle *Stupendemys geographicus*, as it is the largest nonmarine turtle ever known from a complete shell (until now rivaled only by the extinct marine turtle *Archelon ischyros* from the Late Cretaceous). It was first described in 1976 from the Urumaco Formation in northwestern Venezuela (6), but our knowledge of this animal has been based on partial specimens that have resulted in a problematic taxonomy, especially due to a lack of specimens with associated skull and shell elements. The species diversity of the giant turtles inhabiting northern South America during the Miocene is thus unclear (7, 8), with several forms having been proposed: the postcrania-based *S. geographicus* from the late Miocene, Urumaco region (6, 9–12); the skull-based *Caninemys tridentata* from the late Miocene, Acre region, Brazil (8); the controversial postcrania-based “*S. souzai*,” also from the late Miocene of Acre, Brazil (8, 13), currently attributed as *Podocnemididae incertae sedis* (14); and the skull-based *Podocnemis bassleri* from the late Miocene, Acre region (Loretto), Peru (15). The fossil record of large-sized littoral-freshwater *Podocnemididae* turtles of South America also includes the skull-based *Carbonemys cofrinii*, and the shell-based *Pelomedusoides* indet., from the middle to late Paleocene of Colombia (12).

We here describe several new shells and the first lower jaw specimens from discoveries made during regular fieldwork in the Urumaco region since 1994 (10, 16) and recent finds from La Tatacoa

Desert in Colombia. Together, these fossils shed new light on the biology, past distribution, and phylogenetic position of giant neotropical turtles. First, we report a new size record for the largest known complete turtle shell. Second, our findings support the existence of a sole giant erymnochelyin taxon, *S. geographicus*, with an extensive geographical distribution in what were the Pebas and Acre systems (pan-Amazonia during the middle Miocene to late Miocene in northern South America). Third, we hypothesize that *S. geographicus* exhibited sexual dimorphism in shell morphology, with horns in males and hornless females.

RESULTS

Systematic paleontology

Testudines Batsch, 1788.

Pleurodira Cope, 1864 sensu Joyce et al., 2004.

Podocnemididae Cope, 1868.

Eymnochelyinae sensu Ferreira et al., 2018.

Stupendemys geographicus Wood, 1976.

Synonymy

Caninemys tridentata (8)

Stupendemys souzai (7, 13)

Stupendemys sp. (17)

Podocnemididae indet. (17)

Holotype

MCNC-244, medial portion of the carapace with associated left femur, fragments of scapulocoracoid and a cervical 8? (6).

Hypodigms

Specimens described in Wood (6): MCZ(P)-4376, much of the carapace, fragments of plastron, cervical 7?, both scapula-coracoids and a caudal vertebra; MCNC-245, a plastron lacking the epiplastra and entoplastron, two nearly complete costals, several peripherals, and one neural; MCZ(P)-4378, a right humerus. Specimen described as *C. tridentata* (8): DNPM-MCT-1496-R, nearly complete skull (Fig. 4, A to D). Specimens referred to as *S. souzai* (13): UFAC-1764, incomplete right humerus; UFAC-1163, cervical vertebra; UFAC-1294, left peripheral 1; UFAC-1544, left costal 2; UFAC-1547, right xiphiplastron; UFAC-1553, cervical vertebra; UFAC-1554, cervical

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vertebra; UFAC-4370, pelvic girdle; UFAC-5275, cervical vertebra; UFAC-5508, anterior margin of the carapace and left hypoplastron, and LACM-131946, nuchal bone, originally attributed to *Stupendemys* sp. (17). Specimens referred to as Podocnemididae ind. (17): LACM-141498, left lower jaw ramus, and *Stupendemys* sp. (17): LACM-138028, right scapula. New specimens described here: CIAAP-2002-01 (allotype), nearly complete carapace (Fig. 1, A to E); AMU-CURS-85, nearly complete carapace, left humerus, and right scapula-coracoid (Figs. 2, B and C, and 3, A to D); AMU-CURS-1098, plastron and anterior portion of carapace (Fig. 2, D and E); MPV-0001, nearly complete carapace and complete plastron (Fig. 2, F to M); OL-1820, left humerus (Fig. 3, E to H); AMU-CURS-233, fragment of femur (Fig. 3, I to P); AMU-CURS-706, lower jaw (see fig. S6); VPPLT-979, lower jaw (Fig. 4, E to L).

Range and distribution

Middle to late Miocene, Tatacoa Desert, Villavieja, Departamento del Huila, Colombia; late Miocene, Urumaco, Falcón State, Venezuela; late Miocene, Acre region, Brazil; Loretto region, Peru (Fig. 5).

Diagnosis

S. geographicus is recognized as a pleurodire based on (i) sutural articulation of pelvis with shell, (ii) loss of medial contact of mesoplastra,

(iii) well-developed anal notch, (iv) fusion of gulars, (v) formed central articulations of cervical vertebrae, (vi) a well-developed processus trochlearis pterygoidei, and (vii) quadrate-basioccipital contact. It is a podocnemidid based on (i) a fully developed, medially extensive cavum pterygoidei with a completely developed pterygoid flange; (ii) an incisura columellae auris enclosing stapes and eustachian tube; (iii) an exoccipital-quadrate contact absent; and (iv) a cervical centra with saddle-shaped posterior condyles. It shares with *Peltocephalus dumerilianus* and *Erymnochelys madagascariensis* (i) a long parietal-quadrate contact; (iii) large postorbital bones; (iii) cheek emargination potentially reduced or absent; (iv) potentially advanced posterior roofing of the skull (reduced temporal emargination); (v) an articular with a processus retroarticularis posteroventromedially projected, differing from the ventrally projected *Podocnemis* spp. (Fig. 4, M to T, and fig. S6) acute tip of dentary at symphysis; and (vii) foramen chorda tympani enclosed in processus retroarticularis.

Further description and dimensions

Detailed anatomical descriptions, comparisons, and measurements of the fossilized bones and body mass estimation for *S. geographicus* and other fossil and extant giant turtles are presented in Fig. 3 (Q to V)

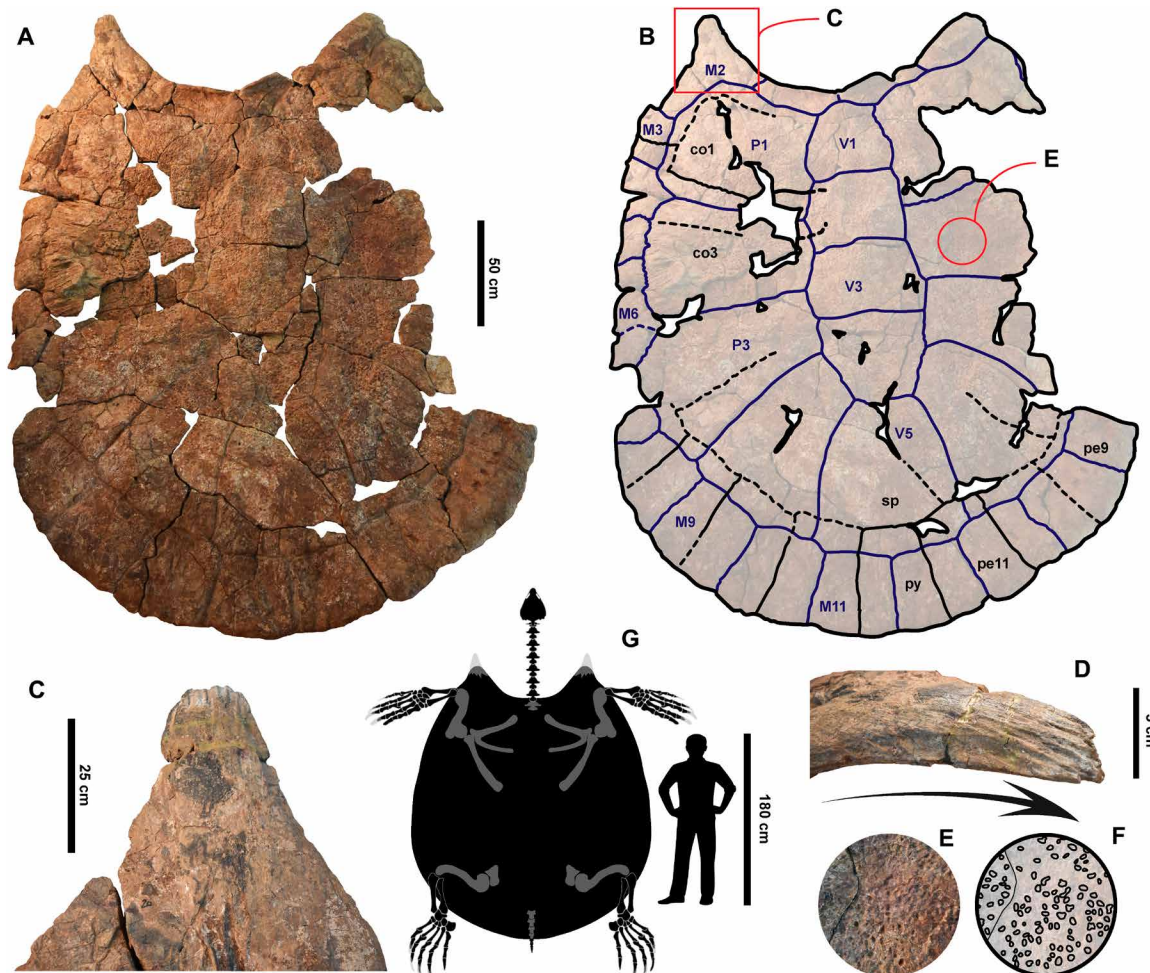


Fig. 1. New specimen and reconstruction of *S. geographicus* from Venezuela. (A and B) CIAAP-2002-01 carapace in dorsal view. (C) Close-up of the left horn in CIAAP-2002-01 [see red square in (B)]. (D) Medial-right view of the left horn showing its ventral projection. (E and F) Close-up of one of bone surface of the carapace showing the pitted sculpture [see red circle in (B)]. (G) General reconstruction of CIAAP-2002-01 including the horns covered with keratinous sheath (light gray). co, costal bone; M, marginal scute; P, pleural scute; pe, peripheral bone; py, pygal bone; sp, suprapygal; V, vertebral scute. Blue lines indicate sulci. Photo credit: Edwin-Alberto Cadena, Universidad del Rosario.

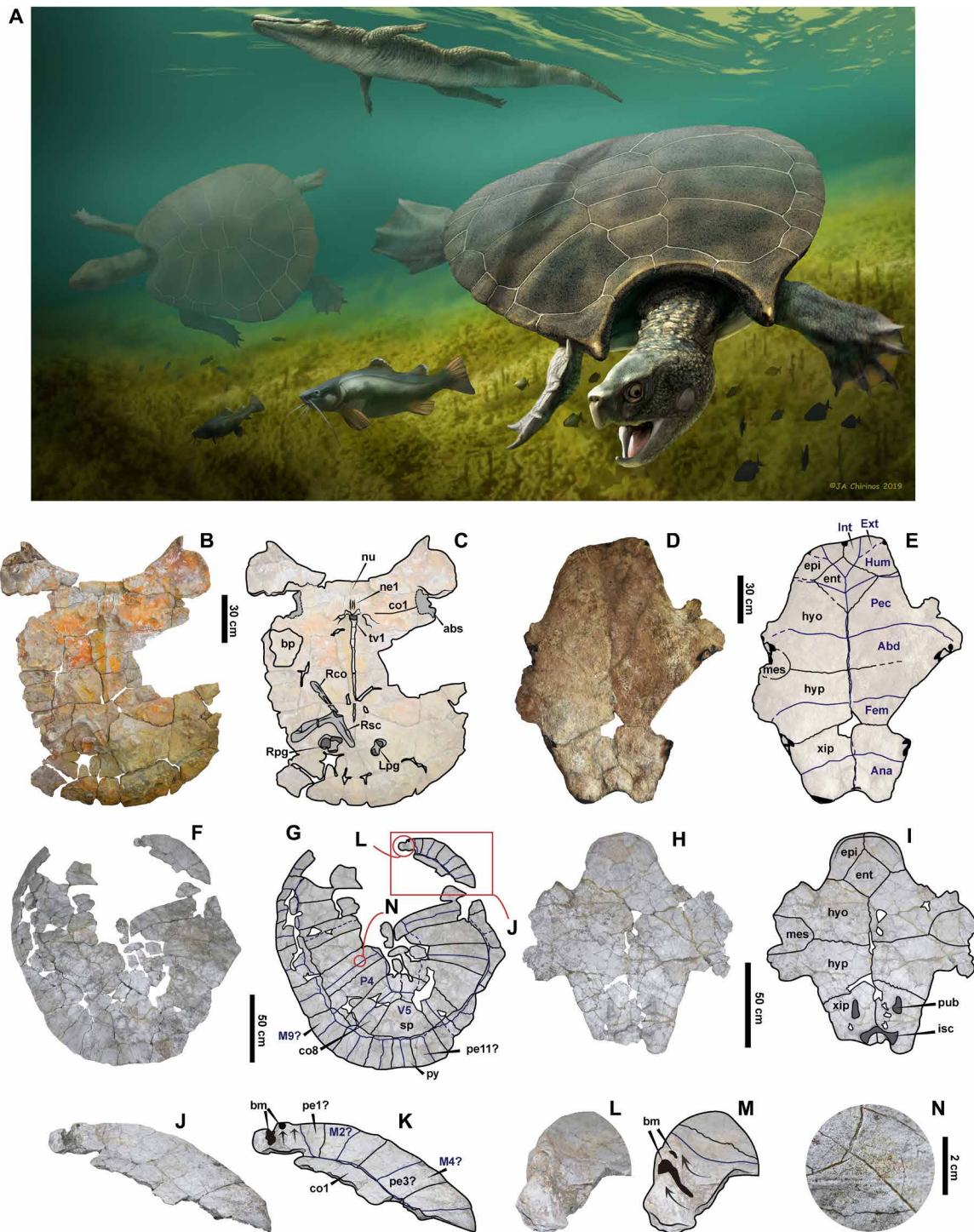


Fig. 2. Male and female shell anatomy of *S. geographicus*. (A) Reconstruction of *S. geographicus* male (front) and female (middle-left), together with the giant caimanine *Purussaurus mirandai* and the large catfish *Phractocephalus nassi*. (B and C) AMU-CURS-85 nearly complete carapace in ventral view. (D and E) AMU-CURS-1098 nearly complete plastron in ventral view. (F to N) Female shell anatomy of *S. geographicus* MPV-0001 from Colombia. (F and G) Carapace in dorsal view. (H and I) Plastron in ventral view. (J and K) Close-up of the right anterior portion of the carapace in dorsoposterior view, showing bite marks and punctured bone [(J) and rectangle in (G)]. (L and M) Nuchal-anterior peripheral in dorsomedial view, showing thickened and moderately to strongly upturned (arrows) [(L) and circle in (G)]. (N) Close-up of the bone surface of one of the costal bones [(N) and circle in (G)], exhibiting microvermiculation sculpturing pattern. Abd, abdominal scute; Ana, anal scute; bm, bite mark; bp, bridge peripheral; co, costal bone; ent, entoplastron; epi, epiplastron; Ext, extragular scute; Fem, femoral scute; Hum, humeral scute; hyo, hyoplastron; hyp, hypoplastron; Int, intergular scute; isc, ischium scar; M, marginal scute; mes, mesoplastron; ne, neural bone; nu, nuchal bone; pe, peripheral bone; Pec, pectoral scute; pub, pubis bone; py, pygal bone; Rco, right coracoid; Rpg, right pelvic girdle; Rsc, right scapula; sp., suprapygial; V, vertebral scute; xip, xiphiplastron. Blue lines indicate sulci. Art: Jaime Chirinos. Photo credit: Edwin-Alberto Cadena, Universidad del Rosario.

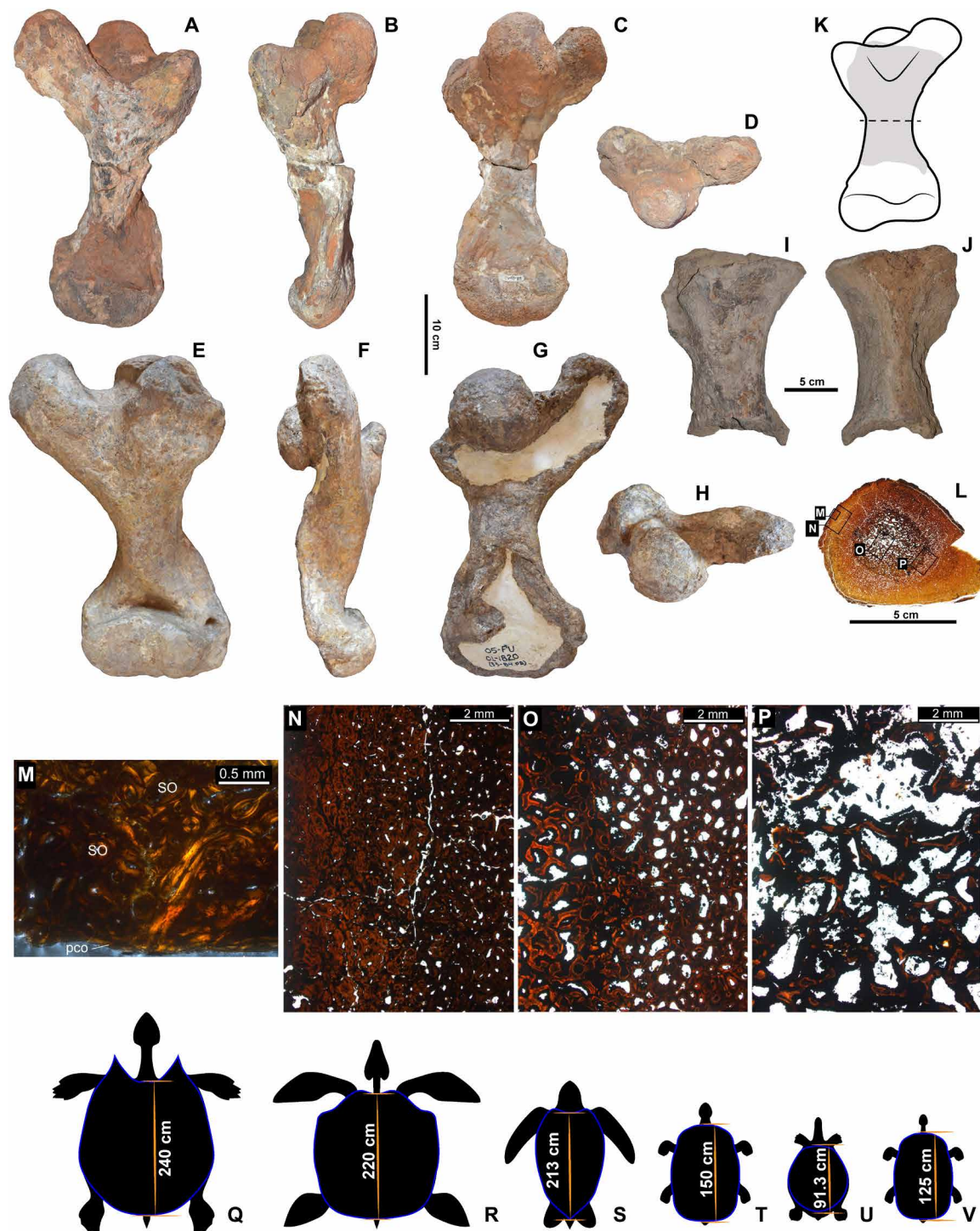


Fig. 3. New humeri and bone histology of a partial femur of *S. geographicus*. (A to D) AMU-CURS-85 left humerus in ventral (A), medial (B), dorsal (C), and proximal (D) views. (E to H) OL-1820 left humerus in ventral (E), lateral (F), dorsal (G), and proximal (H) views. (I and J) AMU-CURS-233 partial femur in ventral (I) and dorsal (J) views. (K) Outline of the femur indicating the region where the thin section was elaborated. (L) Thin section of the partial femur, indicating the close-up presented in (M) to (P). (M) Close-up of the cortical region of the bone. (N) Close-up of the deeper part of the cortex. (O) Close-up of the central region of the bone. (P) Close-up of the transitional region of the bone. Outlines of the largest extant and extinct turtles ever, indicating their maximum carapace length (see table S2): (Q) *S. geographicus*. (R) *A. ischyros*. (S) *D. coriacea* (extant). (T) *M. cf. sivalensis*. (U) *R. swinhoei* (extant). (V) *C. niger* (extant). pco, primary cortex; SO, secondary osteon. Photo credit (A to H): Edwin-Alberto Cadena, Universidad del Rosario; (I to P): Torsten Scheyer, University of Zurich.

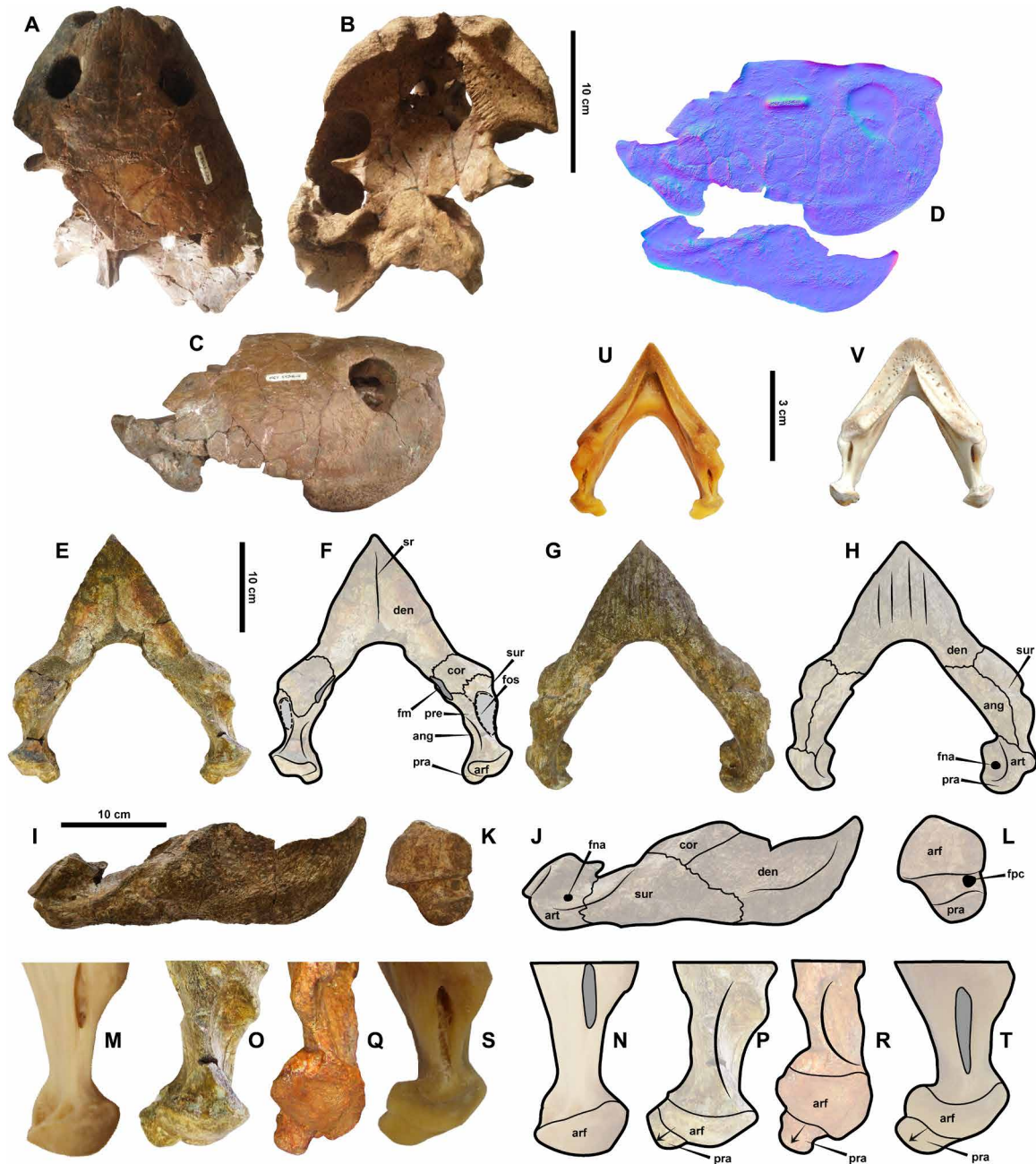


Fig. 4. Skull DNP-MCT-1496-R and new lower jaws of *S. geographicus*. (A to D) DNP-MCT-1496 skull described by Meylan *et al.* (8), from Acre, Brazil in dorsal (A), ventral (B), and right lateral (C) views. (D) Composite skull and lower jaw (not a scale) of *S. geographicus* using relief images of DNP-MCT-1496 skull and VPPLT-979 lower jaw. (E to L) VPPLT-979 lower jaw from La Tatacoa Desert, Colombia in dorsal (E and F), ventral (G and H), and right-lateral (I and J) views. (K and L) VPPLT-979 articular bone and facet in posterior view, exhibiting the foramen posterius chorda tympani. (M to T) Right articular region of the lower jaw, *Podocnemis expansa* NHMW-137 (M and N), *S. geographicus* VPPLT-979 (O and P), *S. geographicus* AMU-CURS-706 (Q and R), *P. dumerilianus* AMNH-1886 (S and T). (U) Lower jaw of *P. dumerilianus* AMNH-1886 in dorsal view. (V) *P. expansa* NHMW-137 lower jaw in dorsal view. ang, angular; arf, articular facet; art, articular; cor, coronoid; den, dentary; fm, fossa Meckelii; fna, foramen nervi auriculotemporalis; fos, fossa articularis mandibularis; fpc, foramen posterius chorda tympani; pra, processus retroarticularis; pre, prearticular; sr, symphysis ridge; sur, surangular. Photo credit (A to C): Orangel Aguilera-Socorro, Universidade Federal Fluminense; (E to V): Edwin-Alberto Cadena, Universidad del Rosario.

and in the Supplementary Materials (text, figs. S1 to S6, tables S1 and S2, and data files S1 and S2).

Remarks

Skull: Unique among podocnemidids (and all other pleurodires, the side-necked turtles) in having greatly inflated maxillae, each with a ventral, tooth-like process, which, together with a single process

formed on the midline of the premaxillae, form a tridentate condition in the upper triturating surfaces. Lower jaw: Triturating surface deep, forming an oval concavity, deeper than in any known living or extinct podocnemidid, labial ridge curved anteriorly ending in acute tip; lingual ridge is a blunt margin forming an accessory ridge that increases in height and width anteriorly and runs as a narrow

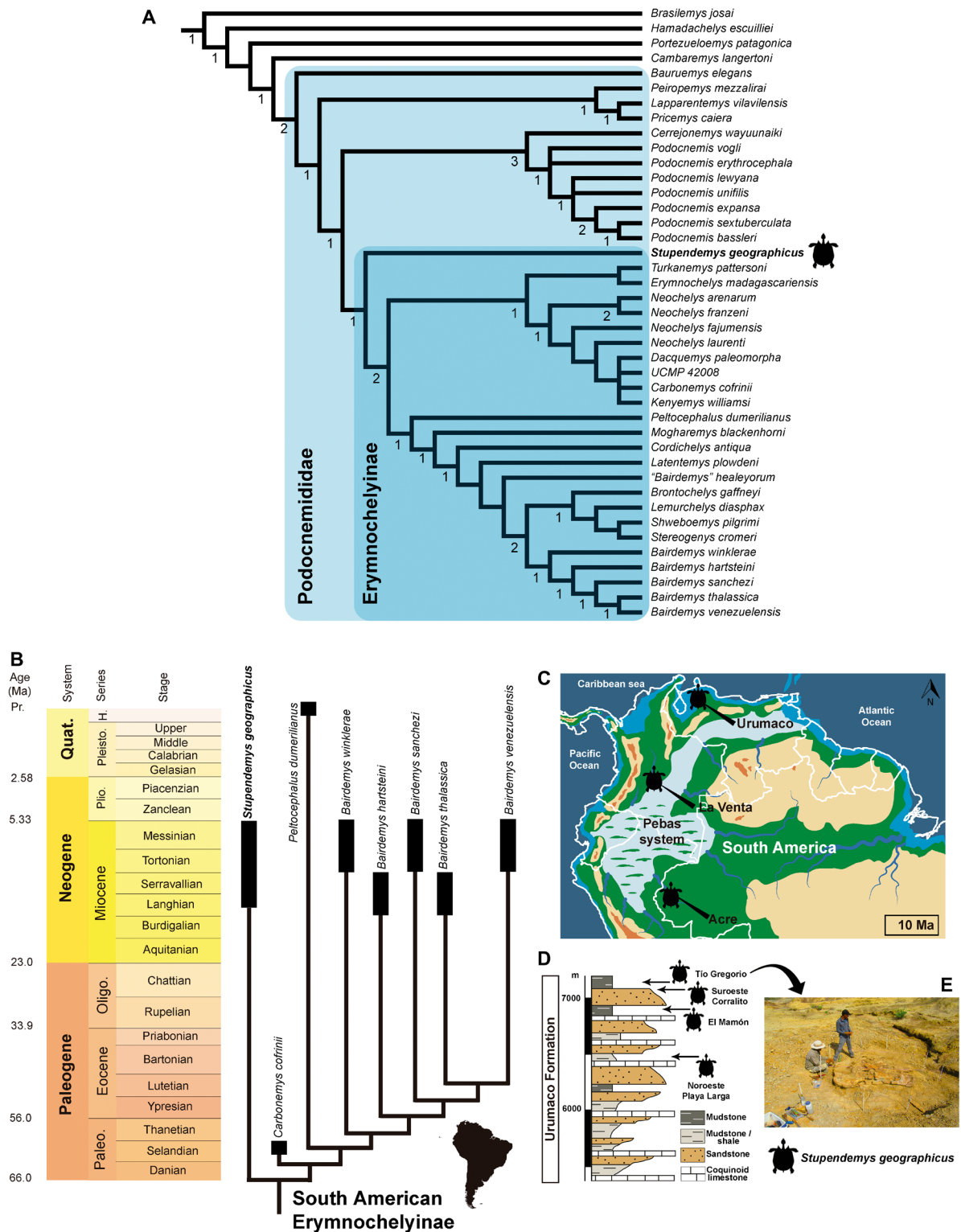


Fig. 5. Phylogenetic relationships and geographic-temporal occurrences of *S. geographicus*. (A) The phylogeny is based on the single MPT, resulting from the analysis of 245 characters [L = 1180, consistency index (CI) = 0.319, and retention index (RI) = 0.748]. Bremer support indices are indicated next to the internodes. (B) A time-calibrated cladogram of South American Erymnochelyinae; the bars indicate the stratigraphic occurrence of taxa; internode length is hypothetical. (C) Paleogeographic reconstruction of northern South America during the late Miocene (10 Ma), including the localities with fossil record of *S. geographicus* and extension of the Pebas system, modified from Hoorn (44). (D) General stratigraphic column of Urumaco Formation, including the four localities where the new fossils of *S. geographicus* described here were found. (E) Excavation of AMU-CURS-85 carapace from Tio Gregorio locality. H, Holocene; L, tree length; Oligo, Oligocene; Paleo, Paleocene; Pleisto, Pleistocene; Plio, Pliocene. Pr, present.

ridge at the medial symphysis; high coronoid process; large dorsal opening of fossa Meckelii; the fossa Meckelii fills the posterior end of the jaw to such an extent that the area articularis mandibularis forms part of the posterior margin, and the fossa opens posterolaterally next to the jaw articulation. Shell: Carapace ≥ 2 m straight midline length, carapace low-arched, with irregular nodular contours on external surface and deep median notch at front; anterior border of nuchal-peripheral bones thickened and moderately to strongly upturned; carapace with massive anterolateral horns slightly projected ventrally in forms attributed as male; carapace dorsal bone surface smooth to striated or slightly pitted; posterior peripheral bones moderately scalloped along margins; thickness of carapace relatively thin at the costals. Shell (plastron): Pectoral-abdominal sulcus very anterior to mesoplastra, reaching almost the hyoplastra lateral notch level. Neck: Cervical vertebrae (probably 7 and 8) with neural arches relatively high in relation to anteroposterior lengths of centra, and articular facets of postzygapophyses forming acute angle of less than 90°; cervical 8? neural arch with large horizontal plane, prezygapophyses directed perpendicularly, thin bladellike spine on anterior face of neural arch and no ventral keel on centrum. Humerus: Humerus squat, massive; deep bicipital fossa between lateral and medial articular facets on ventral surface; prominent ridge traversing ventral surface of shaft from medial process to distal end, terminating just above lateral condyle; medial condyle broadest at anterior end; medial and lateral condyles facing very ventrally; straight to slightly slender shaft and triangular in cross section than circular. Femur: Femur squat, massive, greatly flattened dorsoventrally; breadth of tibial condyle approximately one-third total length of bone. Scapula: A dorsal strongly bowed scapular process with a flattened flange projecting laterally from the main axis.

Phylogenetic analysis

The first analysis (all taxa separated) produced 156,070 most parsimonious trees [MPTs; length = 1154, consistency index (CI) = 0.326, and retention index (RI) = 0.749]. The strict consensus tree (fig. S7) shows the lower jaws from Acre, Urumaco, and La Tatacoa in polytomy at the base of the Stereogenyini clade, sensu Ferreira *et al.* (18), with the same position for *C. tridentata* and *S. geographicus* as presented in Ferreira *et al.* (18). The second analysis [*C. tridentata* + Acre jaw and *S. geographicus* + (Urumaco, La Tatacoa jaws)] produced 1157 MPT (length = 1157, CI = 0.325, and RI = 0.748). Here, the strict consensus tree (fig. S7) shows *C. tridentata* and *S. geographicus* forming a monophyletic clade inside the Erymnochelyinae clade sensu Ferreira *et al.* (18), suggesting them to be closely related or potentially the same taxon. We favor the latter monospecific scenario based on the following considerations: (i) the three lower jaws from Urumaco, La Tatacoa, and Acre resemble each other in all morphological aspects, varying only in size and in preservation; (ii) the lower jaws from Urumaco, La Tatacoa, and Acre were found in localities and/or formations where shell material of *S. geographicus* was also found; and (iii) as Meylan *et al.* (8) stated, “there is a higher probability that the lower jaw, LACM-141498, does belong to *Caninemys*, and they are sufficiently complementary to suggest that they are from closely related taxa.” This scenario receives additional support from the third phylogenetic analysis, which produced 36 MPTs (length = 1180, CI = 0.319, and RI = 0.748). The strict consensus tree (Fig. 5A) and the time-calibrated cladogram pruned to the South American Erymnochelyinae clade (Fig. 5B) show *S. geographicus* at the base, as sister taxon to all remaining erymnochelyin turtles. This position

is in agreement with the hypothesis presented by Meylan *et al.* (8) for *C. tridentata* (now *S. geographicus*), based on a relatively different character-taxon matrix. Jointly considering all these lines of evidence, we hypothesize that the skull of *C. tridentata* and the lower jaws described here together correspond to the skull of *S. geographicus*. It is thus both telling and fitting that turtle expert Eugene Gaffney, when supervising the exhibit of the reconstructed skeleton of *S. geographicus* at the American Museum of Natural History in New York, provided the skull of *Caninemys* for that model.

Body size and body mass estimation

The measurements of the new specimens are given in fig. S2 and table S2. Of particular interest is the new *S. geographicus* specimen CIAAP-2002-01 that we describe here. With its 286 cm parasagittal straight carapace length, it is not only the largest known specimen for this taxon but also the largest turtle shell found to date, considering that the hitherto largest known specimen is the so-called Vienna specimen of the turtle *A. ischyros* (NHMW-1977/1902/0001) with a shell length of 220 cm (19). Among Asian trionychids, giant forms have been reported from the Eocene of Pakistan, some reaching up to 2 m in shell length (20). Badam (21) reported on giant tortoises from the Pliocene of India that, based on reconstructed shell fragments, may have been larger than 3 m in carapace length.

We estimated the body mass using the straight carapace length method (see data file S1) (22). For the largest specimen, CIAAP-2002-01, we obtained an estimate of 871 kg [compared to the 744 kg obtained by Iverson (22) for MCZ(P)-4376, previously the largest and most complete specimen]. However, in the case of *S. geographicus*, to compensate for the effect of the large nuchal embayment, calculating the body mass estimate as the average between estimations based on the carapace midline and parasagittal lengths likely yields a more precise body mass estimate. Doing this results in a body mass estimate of 1145 kg for the CIAAP-2002-01 specimen.

Bone histology

The thin section of AMU-CURS-233 (Fig. 3, L to P) reveals an overall dense microanatomy with a central medullary region completely filled by cancellous bone, surrounded by a transitional zone with regular formed smaller spaces, which leads into a compact, external cortex. Because of erosion of the femur surface, the external-most layers of the bone are visible only in a few places.

The cortical tissue is increasingly dense toward the outer bone surface (Fig. 3M). The deeper parts of the cortex show a dense Haversian bone (Fig. 3N), consisting mostly of longitudinally arranged or slightly angled secondary osteons. In the more surficial parts of the cortex, remodeling into dense Haversian bone is prominent, but remnants of primary parallel-fibered bone matrix with numerous longitudinally arranged primary osteons are still present. In these remnants, cell lacunae are more irregular or of a roundish shape. The cortex also does not reveal growth marks that could be counted, with the exception of a single spot in the external-most cortical fragment that splits off from the main section due to delamination processes and gypsum growth. In this outermost-cortical layer, a few closely spaced lines (five lines?), interpreted as lines of arrested growth (LAGs), form an outer circumferential layer.

The cancellous bone in the center of the section (Fig. 3O) consists of short bone trabeculae and few irregular larger intertrabecular spaces. The trabeculae are secondarily remodeled and consist of lamellar bone.

The transitional bone (Fig. 3P) does not have distinct margins but is a zone of decreasing size of individual extravascular spaces and increasing bone compactness. Vascularization of the tissue is found in the form of longitudinally arranged osteons and only few circumferentially oriented ones. Remodeling by secondary osteons is extensive so that only interstitial pockets of primary parallel-fibered bone tissue are discernible. The overall bone compactness is 0.873, with modeled values at the center of 0.543 and at the periphery of 0.97 (see data file S2).

DISCUSSION

A pleurodiran turtle with a horned shell

In vertebrates, different body parts have independently evolved into protruding structures that are associated with a wide variety of purposes, e.g., defense or attack, mating, display, communication, or thermoregulation. Some of the most remarkable of these structures include horns, antlers, spikes, spurs, plates, tail clubs, and tusks (23–25). In turtles, a notable example is the posterolateral horns of the skull of the extinct meiolaniids (26, 27). Most examples, though, are connected to their shell, covering a diversity of types. Knobby ridges can be found on the carapaces of the extant matamata *Chelus fimbriatus* (28) and the alligator snapping turtle *Macrochelys temminckii* (29) and the extinct stem turtle *Proganochelys quenstedti* possessed serrations along the posterior shell margin (30). Among other examples, the extant spiny turtle *Heosemys spinosa* has peripherals with marginal spines (31) that disappear ontogenetically, and many groups of testudinid tortoises have highly lobulated and protruded anterior and posterior peripherals or anterior plastron edges (32). Horn-like structures at the anterolateral margin of the carapace, such as those we report here for *S. geographicus*, have previously only been documented in the Cretaceous nanhsiungchelyid *Anomalochelys angulata* (see fig. S8) (33). For this medium-sized (~65-cm straight parasagittal carapace length) extinct terrestrial turtle, one interpretation of the horns' purpose was proposed as the protection of a large skull.

This hypothesis may also apply for *S. geographicus*, considering that we here interpret the massive skull DNPM-MCT-1496-R as its head. This specimen was previously described as *C. tridentata*, and it had lower jaws, which in several morphological aspects resemble the lower jaw of the extant South American big-headed turtle *P. dumerilianus* (Fig. 5 and the Supplementary Materials), including an acute symphyseal tip. Another feature that supports the robustness of the head of *S. geographicus* is the posterolateral opening of the fossa Meckelii in the newly recovered lower jaws described here (AMU-CURS-706 and VPPLT-979), implying a large main adductor tendon and associated musculature (17).

The occurrence of deep grooves in the massive horns of all three new specimens of *S. geographicus* from Urumaco described here (Fig. 1, C and D, and the Supplementary Materials) indicates that they were true horns with a bony core covered by a keratinous sheath that was strongly attached via the grooves, similar to horns of extant artiodactyl bovid mammals (34), and has been argued for meiolanid horns (26).

Sexual dimorphism

If the horns were for protection, then why do several *S. geographicus* specimens lack horns? The anteroventrally facing orientation of the horns is a distinct feature, suggesting that potentially they were exclusively used not only for protection but also for combat. We therefore hypothesize that the horned shells from Venezuela described

here represent males of *S. geographicus* and that the horns served the main purpose of weapons in male-male combat behaviors. This hypothesis is consistent with the occurrence of similar structures in males of other groups of vertebrates, for example, in artiodactyl mammals (23, 34). In addition, in snapping turtles (Chelydridae), some of the largest extant freshwater turtles, males that occupy overlapping areas often establish dominance through fights (35). The elongated and deep scar in the left horn of CIAAP-2002-01 (see the Supplementary Materials) could be interpreted as a mark resulting from combat between males. Many extant tortoises use their protruding epiplastral horns for combat, often with the goal of flipping the opponent (36–38).

The putative *S. geographicus* males would also have been larger than females (see table S1), a pattern similar to that documented in the closely related extant taxon *P. dumerilianus*, which exhibits a male-biased sexual size dimorphism (39). Other sexually dimorphic traits of the turtle shell, such as a xiphiplastral concavity in males, or a deeper anal notch in males than in females (40, 41), are not distinct in *S. geographicus*, at least from a comparison between the specimens AMU-CURS-1098 (attributed to a male) and MPV-0001 (attributed to a female).

Paleoecology

The climate and the productivity of the environment, habitat size, and predation-competition interactions are some of the factors usually considered as triggers or in favor of gigantism (42, 43). We hypothesize that in the case of *S. geographicus*, a combination of several factors favored the evolution of its large size.

Habitat size, both in terms of individuals (home ranges large enough to sustain giant body sizes) and in terms of populations (species distribution ranges that can sustain long-term viable populations), was surely a major determinant. During the Paleogene and until the late Miocene [~66 to 5 million years (Ma)], after the retreat of the dominant marine conditions of the Cretaceous, northern South America harbored the most extensive freshwater and littoral ecosystems in its geological history. The coverage reached a particular peak during the Miocene, with the development of a large wetland and lake system known as the Pebas system (44), which offered not only increased connectivity between habitats but also the opportunity for the diversification and migration of faunas, including turtles. It seems that the size of these wetland habitats in northern South America during the Miocene facilitated the occurrence of gigantism not only in turtles (this study) but also in several vertebrate lineages such as crocodylians (Fig. 6 and table S3) and rodents (3–5).

Predation interactions could have also been involved in the evolution of large body size in *S. geographicus*, as it shared its habitat with gigantic crocodylians, including *Purussaurus* spp. and *Gryposuchus* spp., which could reach up to 10 m or more in body length. There is direct evidence of interactions between *S. geographicus* and large South American crocodylians, in the form of bite marks in Colombian and Venezuelan specimens, and an isolated tooth attached on the ventral surface of the carapace in the CIAAP-2002-01 specimen (see fig. S3).

Climate, particularly warmer temperatures, could have been a potential factor favoring the evolution of large body size in Miocene South American reptiles. For example, this causal link has been inferred for the Paleocene fauna of Cerrejón, Colombia, which includes the largest snake ever, *Titanoboa cerrejonensis* (2), and the

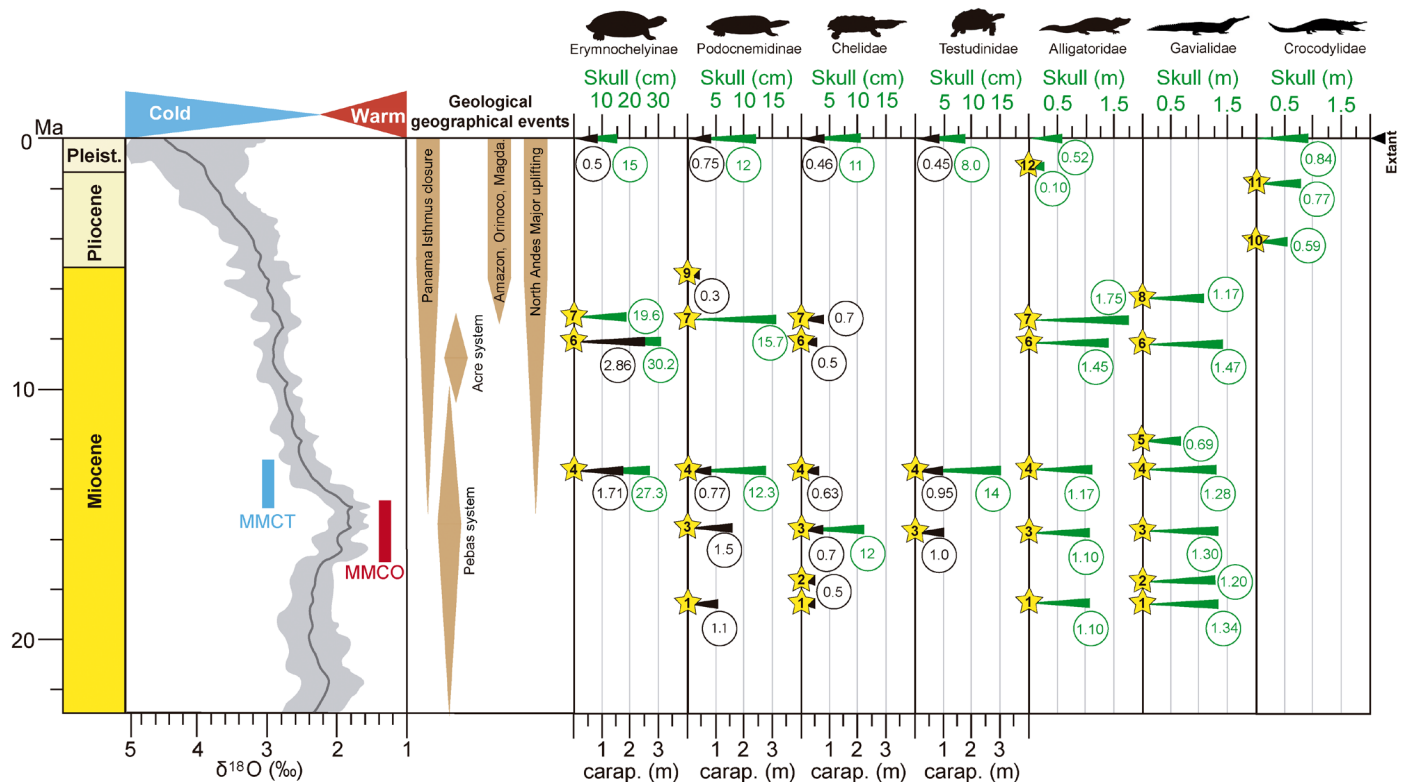


Fig. 6. Climate and geological events versus size of Neogene to present tropical South American turtles and crocodylians. Deep-sea benthic foraminifer oxygen isotope curve for 0 to 23 Ma, redraw from Zachos *et al.* (46), showing major global climatic events (left). Major geological and geographical events for northern South America (light brown bars). Maximum skull or lower jaw (green values) and carapace (black values) for turtles and crocodylians from northern South American fossil sites. Formations are represented by yellow stars: 1, Barzalosa Fm., early Miocene, Colombia; 2, Castillo Fm., early Miocene, Venezuela; 3, Castilletes Fm., early-middle Miocene, Colombia; 4, La Victoria and Villavieja Fms., middle-late Miocene, Colombia; 5, Pebas Fm., middle Miocene, Peru; 6, Urumaco Fm., late Miocene, Venezuela; 7, Madre de Dios and Ipururo Fms., late Miocene, Brazil; 8, Pisco Fm., late Miocene, Peru; 9, Solimões Fm., late Miocene-Pliocene, Brazil; 10, San Gregorio Fm., early Pliocene, Venezuela; 11, Ware Fm., Pliocene-Pleistocene, Colombia; 12, Mesa Fm., Pleistocene, Venezuela. Carap., carapace; MMCO, middle Miocene climatic optimum; MMCT, middle Miocene climatic transition; Magda, Magdalena; Pleist., Pleistocene. Detailed information on localities, specimens, and sources are in table S3.

largest Paleogene pelomedusoid turtles and crocodylians (12, 45). Although less warm than the Paleocene and the Eocene, the Miocene was also an epoch with notable climatic events that could have affected the body size of neotropical animal species, for example, the warm middle Miocene climatic optimum (MMCO) (46, 47), the global cooling between ~15 and 13 Ma known as middle Miocene climatic transition (MMCT), and continuous decreasing of global temperature during the late Miocene (48). The time range so far known for *S. geographicus* (middle Miocene to late Miocene) (this study) indicates that this taxon overcame the MMCT event. It exhibited a gigantic (and potentially its maximum) size during global cooling times (late Miocene) (Fig. 6). The latter rules out a direct and rather unlikely simple effect of climate on gigantism in neotropical Miocene reptiles. Thermally imposed upper limits to body mass are more likely than a simple tracking of changing temperature in body size evolution (49). Unfortunately, the climatic conditions of terrestrial ecosystems during the Miocene in tropical South America are still poorly known, and better reconstructions of climatic conditions await information from geochemical analyses of paleosols and carbonate isotopes. In addition, for neotropical faunas in general and reptiles in particular, the considerable gap in the South American Eocene and Oligocene fossil record is a major obstacle to a clear understanding of the effect of these climatic

events on body size trends through time. It is therefore currently impossible to track the evolutionary path of evolution of body size that started during the Paleocene in detail or to establish whether body sizes of late Eocene and Oligocene neotropical reptiles remained large or decreased due, in part, to other cooling events such as the late Eocene-Oligocene transition from “greenhouse” to “icehouse.” To test the existence of a passive or driven trend in body size evolution (50), better sampling of the neotropical fossil record is needed. Both internal or external factors could be associated with such trends (51), and discoveries such as that reported here provide the primary evidence with which to start to understand the range of possibilities in morphospace occupation.

Turtles are a particularly challenging group when it comes to the identification of potential causal correlates in body size evolution, given the “atypical patterns” in relation to latitude they show in body size and in geographic range (52), as opposed to major tendencies identified for other vertebrate groups.

Last, the phylogenetic framework is likely an additional important factor, given the association of biological attributes such as body size and physiology to clades. Teasing out the relative importance of physiological boundaries related to clades is currently equally limited by the Eocene and Oligocene gap in neotropical faunas. For example, the large body size of *S. geographicus* could be an inherited ancestral

trait, rooted in the Paleocene forms from Cerrejón, Colombia [*Carbonemys cofrinii* and its potential shell, *Pelomedusoides* indet. (12)]. Our phylogenetic analysis (Fig. 5) supports the view that *S. geographicus* and *Ca. cofrinii* both belong to the Erymnochelyinae clade but not as closely related taxa. What is clear is that at least two separate clades inside Podocnemididae exhibited large body size during the Miocene: one including *S. geographicus* and another with *P. bassleri* (15) (15.7-cm skull length, potentially 2 m carapace length) in the line of *Podocnemis* group. In other turtle clades of the neotropics, this trend is represented by *Chelonoidis* sp. (1 m carapace length estimate) inside the terrestrial Testudinidae and *Chelus colombianus* (70 cm carapace length estimate) within the freshwater-inhabitant Chelidae (Fig. 6).

Paleogeography

Adding to the previously known records of *S. geographicus* from Urumaco and Acre (6–8, 13, 17), we here report the first occurrence of this taxon in the well-known fauna of La Venta, Tatacoa Desert. This notably expands the known distribution of *S. geographicus*, highlighting that it likely was a common taxon throughout the entire Pebas system, well adapted to both fluvial conditions (La Venta and Acre) and fluvial-littoral conditions (Urumaco) (Fig. 5C). It is likely that the changes in the configuration of the Pebas and the posterior Acre systems due to the uplifting of the Andes starting in the middle Miocene (ca. 12.5 Ma) (53) (Fig. 6) had a deep impact on the populations of *S. geographicus*, considerably reducing their habitat size and leading to its final extinction, probably during the early Pliocene.

Paleodiet

Taking into account the morphology of the massive skull elements (skull and lower jaws, Fig. 4D) of *S. geographicus*, Meylan *et al.* (8) interpreted this turtle as a pleurodiran snapping turtle, involving a vacuum feeding system and capable of capturing and holding prey of very large size, including fish, small caimanines, and snakes. In this questionable interpretation, it was a carnivore much like the extant cryptodires *Macrochelys*, *Claudius*, and *Staurotypus*, which also exhibit a depression in the upper triturating surface and have lower jaws with a well-developed symphyseal hook (8). The very acute symphyseal end and wider anteromedial triturating surface of the well-preserved jaw (VPPLT 979 specimen) from La Tatacoa described here indicate that *S. geographicus* may have had a diet much broader than one consisting of the abovementioned vertebrate preys. It could have had a more diverse diet. For example, it could have had a generally durophagous diet, crushing hard-shelled prey such as mollusks with the help of its large triturating surface and facilitated by its large main adductor tendon and associated musculature. Increasing the diet niche breadth would have favored maintaining a very large body size in this turtle, resulting in a body size–environment productivity correspondence (42).

Another previously underestimated aspect of paleodiet is the potential of large extinct turtles having acted as seed dispersers for many plant species. A recent review of frugivory and seed dispersal in extant turtles (54) highlighted that many species consume fruits, and thus potentially disperse the seeds, even if fruits are not considered part of their standard diet. Seasonally, high-energy fruits from, e.g., palms (Araceae) can even form the major part of Amazonian turtles' diets. This is the case for the closest extant relative of *S. geographicus*, the big-headed Amazon river turtle, *P. dumerilianus*, where (55) found that fruits and seeds formed the most diverse component of its stomach contents and that palm seeds were the most common item (55).

Because of its huge gape size, *S. geographicus* could have swallowed even the largest South American fruits and thus qualify as a mega-faunal frugivore and seed disperser [sensu (56)]. In general, larger turtles also include more fruits in their diet than do smaller ones; for example, in the extant Asian big-headed turtle, *Platysternon megacephalum*, there is a positive relationship between body size and amount of fruit in their diet (57). Overall, *S. geographicus* could thus have been a highly efficient seed disperser [sensu (58)].

Paleohistology and life history considerations

As with the previously analyzed shell bones of *S. geographicus* (from CIAAP-2002-01) (59), our histological analysis of the femur did not reveal anything unusual about *Stupendemys* growth, only that it is overall comparable to the microanatomical build and the histology of smaller turtles. The high amount of Haversian bone in the femur fragment might be related to the giant size as pointed out by Foote (60) or by advanced age of a skeletally mature specimen, as is tentatively indicated by the tightly spaced LAGs in the outer circumferential layer. The estimated compactness values of AMU-CURS-233 are comparable to those of other aquatic, nonmarine turtles (61).

We see the almost universal conserved arrangement of scutes of turtles in the gigantic specimen described here, emphasizing how the developmental program of turtles (62) results in early differentiation in which prolonged growth does not result in changes in epidermal structures. *S. geographicus* probably lived for at least 110 years to be able to reach the largest recorded size we report here, assuming a growth rate similar to that of extant, large turtles (59).

MATERIALS AND METHODS

Institutional repositories

The fossils referred here are in the collections of American Museum of Natural History, New York, USA; Alcaldía Bolivariana de Urumaco, Urumaco, Falcón State, Venezuela (AMU-CURS); Centro de Investigaciones Antropológicas, Arqueológicas y Paleontológicas (CIAAP) of the Universidad Nacional Experimental Francisco de Miranda, Coro, Falcón State, Venezuela; Departamento Nacional de Produção Mineral, Divisão de Geologia e Mineralogia, Ciências da Terra, Rio de Janeiro, Brazil (DNPM-MCT); The Geological Museum, Geology Survey Institute, Bandung, Indonesia (K); Natural History Museum of Los Angeles, Los Angeles, USA (LACM); Museo de Ciencias Naturales de Caracas, Caracas, Venezuela (MCNC); Museum of Comparative Zoology-Harvard University, Cambridge, USA [MCZ(P)]; Museo Paleontológico de Villavieja, Villavieja, Huila Department, Colombia (MPV); Naturhistorisches Museum Wien, Vienna, Austria (NHMW); Universidad Simón Bolívar, Caracas, Venezuela (OL; specimens housed in the Museo Paleontológico de Urumaco); and Museo de Historia Natural La Tatacoa, La Victoria, Huila Department, Colombia (VPPLT).

Phylogenetic analyses

To explore the phylogenetic position of *S. geographicus*, three separate maximum parsimony analyses were run using PAUP 4.0 (63) and using the character-taxon matrix of Ferreira *et al.* (18) as the original template with some modifications (see the Supplementary Materials). For all the analyses, *Pr. quenstedti*, *Notoemys laticentralis*, and *Platycheilus oberndorferi* comprised the outgroup taxa; all the 245 characters were considered equally weighted, and multistate states were treated as polymorphic. Heuristic search, random search for 10,000 replicates, and tree-bisection reconnection option were performed, seed 1000,

holding one tree per replicate and collapse branches if minimum length is zero. Strict consensus trees and their decay index (Bremer support) were also obtained. For the first analysis, we considered each of the three giant lower jaws from Acre (17), Urumaco, and La Venta (described here) as separate taxa, as well as *C. tridentata* (8) and *S. geographicus*, with the addition of information from previous and the new specimens described here. A second analysis considering the lower jaw LACM-141498 from Acre as belonging to *C. tridentata* as considered originally by Meylan *et al.* (8) and the lower jaws AMU-CURS-706 from Urumaco and VPPLT-979 from La Tatacoa as belonging to *S. geographicus* was performed. For the third analysis, we considered a single taxon, *S. geographicus*, formed by the new and previously described *S. geographicus* shells and postcrania; the three lower jaws from Acre, Urumaco, and La Tatacoa; and the skull of *C. tridentata* (see fig. S7). Twelve morphocline characters were treated as ordered characters (14, 18, 19, 71, 95, 96, 99, 101, 119, 129, 174, and 175) following Ferreira *et al.* (18). Results are also presented in a time-calibrated cladogram of South American Erymnochelyinae turtles (Fig. 5B) based on this and previous studies (12, 64).

Body mass estimation

Body mass estimation of *S. geographicus* and some other taxa mentioned in table S1 was obtained using the correspondence between carapace length and body mass reported by Iverson (22) in extant representative of all lineages of turtles. Specifically, we used the general allometric equation $y = ax^b$, where y is the body mass (in grams), x is the carapace length (in centimeters), and a and b are the correlation coefficients established for each of the taxa (see the Supplementary Materials) (22). Considering that none of the taxa included in this study were part of Iverson's study, we used the coefficients of the closest phylogenetic and/or similar lifestyle representative, for example, in the case of *S. geographicus* as it was also used by Iverson (22), we used the coefficients established for *Podocnemis unifilis*; for *A. ischyros* and *D. coriacea* (both marine turtles), we used the coefficients of *Chelonia mydas*; for *Megalochelys sivalensis* and *Chelonoidis niger* (both tortoises), we used the coefficients of *Geochelone elegans*; and for *Rafetus swinhoi* (freshwater soft-shelled turtle), we used the coefficients of *Apalone (Trionyx) spinifera*.

Bone histology

We sectioned a shaft fragment of a femur of *S. geographicus* (AMU-CURS-233) recovered from a site next to the gas pipeline at El Mamón locality, Urumaco, Falcón state, Venezuela (11°13'1.46"N; 70°16'51.2"W). The shaft section was roughly oval shaped, with the longest axis of 8 cm and a perpendicular shorter axis of 6.2 cm. The bone was cut with an iron hand saw and processed afterward, following standard petrographic thin-sectioning procedures (65). The thin section was studied and analyzed using a compound microscope (DM 2500M, Leica) with a digital camera (DFC 420C, Leica). Comparative material of *S. geographicus* included already published shell bone sections (59), and overall bone compactness was calculated using Bone Profiler software (66).

Maximum size versus climate and geological events

We plotted the largest as-preserved or estimated length of skull, lower jaw, and/or carapace of turtles and crocodylians from each of the neotropical Neogene to Quaternary fossil sites, putting them in context with the global climatic curve of Zachos *et al.* (46) and the major geological and geographical events of northern South America.

We included the following lineages of turtles: Erymnochelyinae, Podocnemidinae, Chelidae, and Testudinidae, and for the crocodylians: Alligatoridae, Gavialidae, and Crocodylidae (Fig. 6, fig. S9, and table S3), adding also the largest reported extant representatives. We excluded from this plot very recently immigrant lineages of turtles: Geoemydidae, Kinosternidae, Emydidae, and Chelydridae, and turtles that occasionally reached South America, for example, Trionychidae, as well as sea turtles and the extant Galápagos tortoises (gigantism due to phylogenetic history and island isolation). The extremely fragmentary *Charactosuchus* spp. were also excluded considering that they are still controversial if they are truly members of Crocodylidae (67).

SUPPLEMENTARY MATERIALS

Supplementary material for this article is available at <http://advances.sciencemag.org/cgi/content/full/6/7/eaay4593/DC1>

Supplementary Text

Fig. S1. *S. geographicus* CIAAP-2002-01 details.

Fig. S2. Outlines and indication of the measurements of the new specimens described here and reported in tables S1 and S2.

Fig. S3. *S. geographicus* CIAAP-2002-01 carapace.

Fig. S4. AMU-CURS-85 carapace of *S. geographicus* from Venezuela.

Fig. S5. Details of *S. geographicus* AMU-CURS-1098 from Venezuela.

Fig. S6. Lower jaws of *S. geographicus* from Venezuela, Colombia, and extant podocnemids.

Fig. S7. Additional strict consensus trees.

Fig. S8. *A. angulata* from the Cretaceous of Japan.

Fig. S9. Phylogeny versus skull–lower jaw length for Miocene neotropical crocodylians.

Table S1. Measurements and body mass estimation for *S. geographicus* and other extant and extinct giant turtles as preserved in centimeters and kilograms.

Table S2. Specific measurements and thickness (see fig. S2) of new specimens of *S. geographicus*.

Table S3. Data on size for the Neogene to extant neotropical turtles and crocodylians.

Data file S1. Body mass estimation calculations.

Data file S2. Bone compactness calculations using Bone Profiler.

Data file S3. Character–taxon matrix Nexus file raw data.

Data file S4. Character–taxon matrix Nexus file final version.

Movie S1. Video of CIAAP-2002-01 specimen.

Movie S2. Video of the excavation of AMU-CURS-85 specimen.

References (68–93)

[View/request a protocol for this paper from Bio-protocol.](#)

REFERENCES AND NOTES

1. D. R. Prothero, *Giants of the Lost World* (Smithsonian Books, 2016).
2. J. J. Head, J. I. Bloch, A. K. Hastings, J. R. Bourque, E. A. Cadena, F. A. Herrera, P. D. Polly, C. A. Jaramillo, Giant boid snake from the Palaeocene neotropics reveals hotter past equatorial temperatures. *Nature* **457**, 715–717 (2009).
3. B. Barbosa-Rodrigues, Les reptiles fossils de la Vallée de L'Amazone. *Vellozia* **2**, 41–56 (1892).
4. D. Riff, O. A. Aguilera, The world's largest gharials *Gryposuchus*: Description of *G. croizati* n. sp (Crocodylia, Gavialidae) from the Upper Miocene Urumaco Formation, Venezuela. *PalZ* **82**, 178–195 (2008).
5. M. R. Sánchez-Villagra, O. Aguilera, I. Horovitz, The anatomy of the world's largest extinct rodent. *Science* **301**, 1708–1710 (2003).
6. R. C. Wood, *Stupendemys geographicus*, the world's largest turtle. *Breviora* **436**, 1–31 (1976).
7. F. Lapparent de Broin, J. Bocquentin, F. R. Negri, Gigantic turtles (Pleurodira, Podocnemididae) from the late Miocene–early Pliocene of south western Amazon. *Bull. Inst. Fr. Etudes Andin.* **22**, 657–670 (1993).
8. P. A. Meylan, E. S. Gaffney, D. de Almeida Campos, *Caninemys*, a new side-necked turtle (Pelomedusoides: Podocnemididae) from the Miocene of Brazil. *Am. Mus. Novit.* **3639**, 1–26 (2009).
9. O. A. Aguilera, *Tesoros Paleontológicos de Venezuela: Urumaco, Patrimonio Natural de la Humanidad* (Arte, 2004), pp. 87.
10. M. R. Sánchez-Villagra, T. M. Scheyer, in *Urumaco and Venezuelan Paleontology*, M. R. Sánchez-Villagra, O. A. Aguilera, A. A. Carlini, Eds. (Indiana University, 2010), pp. 173–191.

11. D. Riff, P. S. R. Romano, G. R. Oliveira, A. O. Aguilera, in *Amazonia Landscape and Species Evolution: A Look into the Past*, C. Hoorn, F. P. Wesselingh, Eds. (Wiley-Blackwell, 2010), chap. 16, pp. 259–280.
12. E. A. Cadena, D. T. Ksepka, C. A. Jaramillo, J. I. Bloch, New pelomedusoid turtles from the late Palaeocene Cerrejón Formation of Colombia and their implications for phylogeny and body size evolution. *J. Syst. Palaeontol.* **10**, 313–331 (2012).
13. J. Bocquentin, J. Melo, *Stupendemys souzai* Sp. Nov. (Pleurodira, Podocnemididae) from the Miocene-Pliocene of the Solimões Formation, Brazil. *Rev. Bras. Paleontol.* **9**, 187–192 (2006).
14. E. S. Gaffney, P. A. Meylan, R. C. Wood, E. L. Simons, D. de Almeida Campos, *Evolution of the Side-Necked Turtles: The Family Podocnemididae* (Bulletin American Museum of Natural History, 2011), no. 350, pp. 1–237.
15. E. E. Williams, *Podocnemis basleri*, A New Species of Pelomedusid Turtle from the Late Tertiary of Peru (American Museum Novitates, 1956), no. 1782, pp. 1–10.
16. J. D. Carrillo, E. Amson, C. Jaramillo, R. Sánchez, L. Quiroz, C. Cuartas, A. F. Rincón, M. R. Sánchez-Villagra, in *The Neogene Record of Northern South American Native Ungulates* (Smithsonian Institution Scholarly Press, 2018).
17. E. S. Gaffney, E. C. Kenneth, R. C. Wood, *Pelomedusoid Side-Necked Turtles from Late Miocene Sediments in Southwestern Amazonia* (American Museum Novitates, 1998), no. 3245, pp. 1–12.
18. G. S. Ferreira, M. Bronzati, M. C. Langer, J. Sterli, Phylogeny, biogeography and diversification patterns of side-necked turtles (Testudines: Pleurodira). *R. Soc. Open Sci.* **5**, 171773 (2018).
19. K. Derstler, A. Leitch, P. L. Larson, C. Finsley, L. Hill, in *Journal of Vertebrate Paleontology, SVP Program and Abstracts Book* (Society of Vertebrate Paleontology, 1993), vol. 13, pp. 33A.
20. J. J. Head, S. M. Raza, P. D. Gingerich, *Drazinderetes tethyensis*, a new large trionychid (Reptilia: Testudines) from the marine Eocene Drazinda Formation of the Sulaiman Range, Punjab (Pakistan), in *Contributions from the Museum of Paleontology, University of Michigan* (University of Michigan Press, 1999), vol. 30, pp. 199–214.
21. G. L. Badam, *Colosochelys atlas*, a giant tortoise from the Upper Siwaliks of North India. *Bull. Deccan College Res. Inst.* **40**, 149–153 (1981).
22. J. B. Iverson, Proportional skeletal mass in turtles. *Fla. Sci.* **47**, 1–11 (1984).
23. R. A. Kiltie, Evolution and function of horns and hornlike organs in female ungulates. *Biol. J. Linn. Soc.* **24**, 299–320 (1985).
24. B. W. Li, H. P. Zhao, X. Q. Feng, W. W. Guo, S. C. Shan, Experimental study on the mechanical properties of the horn sheaths from cattle. *J. Exp. Biol.* **213**, 479–486 (2010).
25. K. Padian, J. R. Horner, The evolution of ‘bizarre structures’ in dinosaurs: Biomechanics, sexual selection, social selection or species recognition? *J. Zool.* **283**, 3–17 (2011).
26. E. S. Gaffney, *The Cranial Morphology of the Extinct Horned Turtle, Meiolania platyceps, from the Pleistocene of Lord Howe Island, Australia* (American Museum of Natural History, 1983), vol. 175, pp. 1–124.
27. J. Sterli, M. S. de la Fuente, New evidence from the Palaeocene of Patagonia (Argentina) on the evolution and palaeo-biogeography of Meiolaniformes (Testudinata, new taxon name). *J. Syst. Palaeontol.* **11**, 835–852 (2013).
28. J. D. Schneider, *Allgemeine Naturgeschichte der Schildkröten, Nebst Einem Systematischen Verzeichnisse der Einzelnen Arten und Zwey Kupfern* (Leipzig, 1783).
29. G. Troost, in *Medical and Physical Researches; or Original Memoirs in Medicine, Surgery, Physiology, Geology, Zoology, and Comparative Anatomy*, R. Harlan, Ed. (Bailey, 1835), pp. 157–158.
30. E. S. Gaffney, *The Comparative Osteology of the Triassic Turtle Proganochelys* (American Museum of Natural History, 1990), vol. 194, pp. 1–268.
31. J. E. Gray, *Illustrations of Indian Zoology, Chiefly Selected from the Collection of Major-General Hardwicke*, J. A. Richter, Ed. (London, 1830), vol. 1.
32. E. E. Williams, Two species of tortoises in northern South America. *Breviora* **120**, 1–13 (1960).
33. R. Hirayama, K. Sakurai, T. Chitoku, G. Kawakami, N. Kito, *Anomalochelys angulata*, an unusual land turtle of family Nanhsiungchelyidae (Superfamily Trionchoidea; Order Testudines) from the Upper Cretaceous of Hokkaido, North Japan. *Russ. J. Herpetol.* **8**, 127–138 (2001).
34. B. Lundrigan, Morphology of horns and fighting behavior in the family Bovidae. *J. Mammal.* **77**, 462–475 (1996).
35. D. E. Pearce, J. C. Avise, Turtle mating systems: Behavior, sperm storage, and genetic paternity. *J. Hered.* **92**, 206–211 (2001).
36. I. R. Swingland, M. W. Klemens, *The Conservation Biology of Tortoises* (IUCN, 1989).
37. T. Keswick, B. T. Henen, M. D. Hofmeyr, Sexual disparity in activity patterns and time budgets of angulate tortoises (*Chersina angulata*) on Dassen Island, South Africa. *Afr. Zool.* **41**, 224–233 (2006).
38. D. M. Stojadinovic, D. D. Milošević, K. S. Sretić, M. P. Cvetković, T. R. Jovanović, B. L. Jovanović, J. M. Crnobrajca-Isailović, Activity patterns and habitat preference of eastern Hermann’s tortoise (*Testudo hermanni boettgeri*) in Serbia. *Turk. J. Zool.* **41**, 1036–1044 (2017).
39. C. P. Ceballos, D. C. Adams, J. B. Iverson, N. Valenzuela, Phylogenetic patterns of sexual size dimorphism in turtles and their implications for Rensch’s rule. *Evol. Biol.* **40**, 194–208 (2013).
40. P. C. H. Pritchard, in *Biology of Turtles*, J. Wyneken, M. H. Godfrey, V. Bels, Eds. (CRC Press, 2008), pp. 45–84.
41. E. A. Cadena, C. A. Jaramillo, J. I. Bloch, in *Morphology and Evolution of Turtles*, D. B. Brinkman, P. A. Holroyd, J. D. Gardner, Eds. (Springer, 2013), pp. 105–120.
42. G. J. Vermeij, Gigantism and its implications for the history of life. *PLOS ONE* **11**, e0146092 (2016).
43. H. G. Ferrón, C. Martínez-Pérez, H. Botella, The evolution of gigantism in active marine predators. *Hist. Biol.* **30**, 712–716 (2017).
44. C. Hoorn, F. P. Wesselingh, H. ter Steege, M. A. Bermudez, A. Mora, J. Sevink, I. Sanmartín, A. Sanchez-Meseguer, C. L. Anderson, J. P. Figueiredo, C. Jaramillo, D. Riff, F. R. Negri, H. Hooghiemstra, J. Lundberg, T. Stadler, T. Särkinen, A. Antonelli, Amazonia through time: Andean uplift, climate change, landscape evolution, and biodiversity. *Science* **330**, 927–931 (2010).
45. A. K. Hastings, J. I. Bloch, C. Jaramillo, A new longirostrine dyrosaurid (Crocodylomorpha, Mesoeucrocodylia) from the Paleocene of north-eastern Colombia: Biogeographic and behavioural implications for New-World Dyrosauridae. *Palaeontology* **54**, 1095–1116 (2011).
46. J. C. Zachos, G. R. Dickens, R. E. Zeebe, An early Cenozoic perspective on greenhouse warming and carbon-cycle dynamics. *Nature* **451**, 279–283 (2008).
47. A. Goldner, N. Herold, M. Huber, The challenge of simulating the warmth of the mid-Miocene climatic optimum in CESM1. *Clim. Past* **10**, 523–536 (2014).
48. A. Frigola, M. Prange, M. Schulz, Boundary conditions for the Middle Miocene Climate Transition (MMCT v1.0). *Geosci. Model Dev.* **11**, 1607–1626 (2018).
49. J. J. Saarinen, A. G. Boyer, J. H. Brown, D. P. Costa, S. K. M. Ernest, A. R. Evans, M. Fortelius, J. L. Gittleman, M. J. Hamilton, L. E. Harding, K. Lintulaakso, S. K. Lyons, J. G. Okie, R. M. Sibly, P. R. Stephens, J. Theodor, M. D. Uhen, F. A. Smith, Patterns of maximum body size evolution in Cenozoic land mammals: Eco-evolutionary processes and abiotic forcing. *Philos. Trans. R. Soc. Lond., B, Biol. Sci.* **281**, 20132049 (2014).
50. J. Alroy, Understanding the dynamics of trends within evolving lineages. *Paleobiology* **26**, 319–329 (2000).
51. D. W. McShea, Mechanisms of large-scale evolutionary trends. *Evolution* **48**, 1747–1763 (1994).
52. K. D. Angielczyk, R. W. Burroughs, C. R. Feldman, Do turtles follow the rules? Latitudinal gradients in species richness, body size, and geographic range area of the world’s turtles. *J. Exp. Zool. B Mol. Dev. Evol.* **324**, 270–294 (2015).
53. V. J. Anderson, B. K. Horton, J. E. Saylor, A. Mora, E. Tesón, D. O. Breecker, R. A. Ketcham, Andean topographic growth and basement uplift in southern Colombia: Implications for the evolution of the Magdalena, Orinoco, and Amazon river systems. *Geosphere* **12**, 1235–1256 (2016).
54. W. Falcón, D. Moll, D. Hansen, Frugivory and seed dispersal by chelonians: A review and synthesis. *bioRxiv* 379933. [Preprint]. 30 July 2018. <https://doi.org/10.1101/379933>.
55. J. L. Pérez-Emán, A. Paoililo, Diet of the pelomedusid turtle *Peltecephalus dumerilianus* in the Venezuelan Amazon. *J. Herpetol.* **31**, 173–179 (1997).
56. P. R. Guimarães Jr., M. Galetti, P. Jordano, Seed dispersal anachronisms: Rethinking the fruits extinct megafauna ate. *PLOS ONE* **3**, e1745 (2008).
57. Y.-H. Sung, B. C. H. Hau, N. E. Karraker, Diet of the endangered big-headed turtle *Platysternon megacephalum*. *PeerJ* **4**, e2784 (2016).
58. E. W. Schupp, P. Jordano, J. M. Gómez, Seed dispersal effectiveness revisited: A conceptual review. *New Phytol.* **188**, 333–353 (2010).
59. T. M. Scheyer, M. R. Sánchez-Villagra, Carapace bone histology in the giant pleurodiran turtle *Stupendemys geographicus*: Phylogeny and function. *Acta Palaeontol. Pol.* **52**, 137–154 (2007).
60. J. S. Foote, *A Contribution to the Comparative Histology of the Femur*, A. Hrdlicka, Ed. (Smithsonian Institution, 1916), vol. 35, pp. 242.
61. Y. Nakajima, R. Hirayama, H. Endo, Turtle humeral microanatomy and its relationship to lifestyle. *Biol. J. Linn. Soc.*, 719–734 (2014).
62. J. E. Moustakas-Verho, R. Zimm, J. Cebara-Thomas, N. K. Lempiäinen, A. Kallonen, K. L. Mitchell, K. Hämäläinen, I. Salazar-Ciudad, J. Jernvall, S. F. Gilbert, The origin and loss of periodic patterning in the turtle shell. *Development* **141**, 3033–3039 (2014).
63. D. L. Swofford, PAUP*. Phylogenetic analysis using parsimony and other methods. version 4 (Sinauer Associates, Sunderland, Massachusetts, 2003).
64. G. S. Ferreira, S. Bandyopadhyay, W. G. Joyce, A taxonomic reassessment of *Piramys auffenbergi*, a neglected turtle from the late Miocene of Piram Island, Gujarat, India. *PeerJ* **6**, e5938 (2018).
65. A. Chinsamy, A. Raath, Preparation of fossil bone for histological examination. *Palaeontol. Afr.* **29**, 39–44 (1992).
66. M. Girondot, M. Laurin, Bone Profiler: A tool to quantify, model and statistically compare bone-extinction compactness profiles. *J. Vertebr. Paleontol.* **23**, 458–461 (2003).

67. T. M. Scheyer, O. A. Aguilera, M. Delfino, D. C. Fortier, A. A. Carlini, R. Sánchez, J. D. Carrillo-Briceño, L. Quiroz, M. R. Sánchez-Villagra, Crocodylian diversity peak and extinction in the late Cenozoic of the northern Neotropics. *Nat. Commun.* **4**, 1907 (2013).
68. L. Quiroz, C. Jaramillo, in *Urumaco and Venezuelan Paleontology*, M. R. Sánchez-Villagra, A. O. Aguilera, F. Carlini, Eds. (Indiana Univ. Press, 2010), pp. 153–172.
69. P. Dentzien-Dias, J. D. Carrillo-Briceño, H. Francischini, R. Sánchez, Paleoeological and taphonomical aspects of the Late Miocene vertebrate coprolites (Urumaco Formation) of Venezuela. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* **490**, 590–603 (2018).
70. J. Guerrero, in *Vertebrate Paleontology in the Neotropics, The Miocene Fauna of La Venta, Colombia*, R. F. Kay, R. H. Madden, R. L. Cifelli, J. J. Flynn, Eds. (Smithsonian Institution Press, 1997), pp. 13–43.
71. C. R. McClain, M. A. Balk, M. C. Benfield, T. A. Branch, C. Chen, J. Cosgrove, A. D. M. Dove, L. C. Gaskins, R. R. Helm, F. G. Hochberg, F. B. Lee, A. Marshall, S. E. McMurray, C. Schanche, S. N. Stone, A. D. Thaler, Sizing ocean giants: Patterns of intraspecific size variation in marine megafauna. *PeerJ* **3**, e715 (2015).
72. E. Setiyabudi, An early Pleistocene giant tortoise (Reptilia; Testudines; Testudinidae) from the Bumiayu area, Central Java, Indonesia. *J. Fossil Res.* **42**, 1–11 (2009).
73. P. A. Meylan, R. G. Webb, *Rafetus swinhoei* (Gray) 1873, a valid species of living soft-shelled turtles (Family Trionychidae) from China. *J. Herpetol.* **22**, 118–119 (1988).
74. E. A. Cadena, C. Jaramillo, M. E. Parámo-Fonseca, New material of *Chelus colombiana* (Testudines; Pleurodira) from the lower Miocene of Colombia. *J. Vertebr. Paleontol.* **28**, 1206–1212 (2008).
75. G. S. Ferreira, A. F. Rincón, A. Solórzano, M. C. Langer, Review of the fossil matamata turtles: Earliest well-dated record and hypothesis on the origin of their present geographical distribution. *Sci. Nat.* **103**, 28 (2016).
76. C. A. Brochu, A. D. Rincón, A gavialoid crocodylian from the lower Miocene of Venezuela. *Spec. Pap. Paleontol.* **71**, 61–79 (2004).
77. E. A. Cadena, C. Jaramillo, Early to middle Miocene turtles from the northernmost tip of South America: Giant testudinids, chelids, and podocnemidids from the Castilletes Formation, Colombia. *Ameghiniana* **52**, 188–203 (2015).
78. E. A. Cadena, C. A. Jaramillo, The first fossil skull of *Chelus* (Pleurodira: Chelidae, matamata turtle) from the early Miocene of Colombia. *Palaeontol. Electron.* **18.2.32A**, 1–10 (2015).
79. J. W. Moreno-Bernal, J. Head, C. A. Jaramillo, Fossil crocodylians from the high Guajira Peninsula of Colombia: Neogene fauna change in northernmost South America. *J. Vertebr. Paleontol.* **36**, e1110586 (2016).
80. R. C. Wood, in *Vertebrate Paleontology in the Neotropics: The Miocene Fauna of La Venta, Colombia*, R. F. Kay, R. H. Madden, R. L. Cifelli, J. J. Flynn, Eds. (Smithsonian Institution Press, 1997), pp. 155–170.
81. R. C. Wood, Two species of *Chelus* (Testudines: Pleurodira) from the late Tertiary of northern South America. *Breviora* **435**, 1–26 (1976).
82. J. W. Langston, Fossil crocodylians from Colombia and the Cenozoic history of the Crocodylia in South America. *Univ. Calif. Publ. Geol. Sci.* **52**, 1–169 (1965).
83. W. Langston Jr., *Mourasuchus* Price, *Nettosuchus* Langston, and the Family Nettosuchidae (Reptilia: Crocodylia). *Copeia* **1966**, 882–885 (1966).
84. J. W. Langston, Z. Gasparini, in *Vertebrate Paleontology in the Neotropics: The Miocene Fauna of La Venta, Colombia*, R. F. Kay, R. H. Madden, R. L. Cifelli, J. J. Flynn, Eds. (Smithsonian Institution, 1997), pp. 113–154.
85. R. Salas-Gismondi, J. J. Flynn, P. Baby, J. V. Tejada-Lara, J. Claude, P.-O. Antoine, A new 13 Million year old gavialoid crocodylian from proto-Amazonian mega-wetlands reveals parallel evolutionary trends in skull shape linked to longirostry. *PLOS ONE* **11**, e0152453 (2016).
86. O. A. Aguilera, D. Riff, J. Bocquentin-Villanueva, A new giant *Purussaurus* (Crocodyliformes, Alligatoridae) from the Upper Miocene Urumaco Formation, Venezuela. *J. Syst. Paleontol.* **4**, 221–232 (2006).
84. J. Bocquentin Villanueva, On the turtle *Chelus lewisi* (Testudinata, Pleurodira). *J. Vertebr. Paleontol.* **22**, 343–344 (1988).
88. R. Kraus, The cranium of *Piscogavialis jugaliperforatus* n.gen., n.sp. (Gavialidae, Crocodylia) from the Miocene of Peru. *PalZ* **72**, 389–406 (1998).
89. P. Carvalho, J. Bocquentin, F. Lapparent de Broin, Une nouvelle espèce de *Podocnemis* (Pleurodira, Podocnemididae) provenant du Néogène de la formation Solimões, Acre, Brésil. *Geobios* **35**, 677–686 (2002).
90. D. C. Fortier, A. D. Rincon, Pleistocene crocodylians from Venezuela, and the description of a new species of *Caiman*. *Quat. Int.* **305**, 141–148 (2013).
91. M. R. Sánchez-Villagra, P. C. H. Pritchard, A. Paolillo, O. J. Linares, Geographic variation in the Matamata turtle, *Chelus fimbriatus*, with observations on its shell morphology and morphometry. *Chelonian Conserv. Biol.* **1**, 293–300 (1995).
92. C. Forth, P. Bona, J. B. Deaso, Intraspecific variation in the skull morphology of the black caiman *Melanosuchus niger* (Alligatoridae, Caimaninae). *Acta Zool.* **96**, 1–13 (2015).
93. R. Whitaker, N. Whitaker, Who's got the biggest? *Specialist Group Newslett.* **27**, 26–30 (2008).

Acknowledgments: We are indebted to D. Gutiérrez and F. Parra for helping with the preparation of fossil specimens and collaboration in fieldwork. We thank R. Hirayama for color photos of *Anomalochelys*; M. Claus for discussion on the early stages of this work; and editors J. Jackson and D. Erwin, reviewer W. Joyce, and an anonymous reviewer for input to improve this paper. We thank the curators and museum staff of the following institutions for permits and access to collections and specimens: American Museum of Natural History; Alcadía Bolivariana de Urumaco; Chelonian Research Institute; Instituto de Ciencias Naturales Universidad Nacional de Colombia; Instituto del Patrimonio Cultural de Venezuela; Museo Paleontológico de Urumaco; Centro de Investigaciones Antropológicas, Arqueológicas y Paleontológicas de la Universidad Experimental Francisco de Miranda; Museo de Ciencias Naturales de Caracas; Museum of Comparative Zoology-Harvard University; Museo Paleontológico de Villavieja; Museo de Historia Natural La Tatacoa; Naturhistorisches Museum Wien; Servicio Geológico Colombiano; Divisão de Geologia e Mineralogia Museu de Ciências da Terra do Rio de Janeiro; Smithsonian Natural History Museum Collections; and University of Florida Herpetology Collection. We thank H. Moreno, C. Morón, G. Ojeda, A. Blanco, A. Reyes-Céspedes, J. Hernández, and the communities of Urumaco and La Victoria for their valuable assistance. We thank the Brazilian Council of Science and Technological Development (productivity researches 305269/2017-8). We thank J. Moreno for information on some fossil crocodylians. **Funding:** This research was funded by grant 40215 from the National Geographic Society-Waitt Foundation Grants Program and the Vicerrectoría Universidad del Rosario. **Author contributions:** R.S., O.A.A.-S., M.P., A.V., M.R.S.-V., J.D.C.-B., and E.-A.C. collected the fossils. E.-A.C. and T.M.S. designed the study. E.-A.C., T.M.S., M.R.S.-V., and J.D.C.-B., collected data, made comparisons, and wrote the paper. All authors gave final approval for publication. **Competing interests:** The authors declare that they have no competing interests. **Data and materials availability:** All data needed to evaluate the conclusions in the paper are present in the paper and/or the Supplementary Materials. Additional data related to this paper may be requested from the authors.

Submitted 20 June 2019

Accepted 22 November 2019

Published 12 February 2020

10.1126/sciadv.aay4593

Citation: E.-A. Cadena, T. M. Scheyer, J. D. Carrillo-Briceño, R. Sánchez, O. A. Aguilera-Socorro, A. Vanegas, M. Pardo, D. M. Hansen, M. R. Sánchez-Villagra, The anatomy, paleobiology, and evolutionary relationships of the largest extinct side-necked turtle. *Sci. Adv.* **6**, eaay4593 (2020).