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Original Article

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The onset of large size in Cretaceous marine turtles (Protostegidae) evidenced by new fossil remains from the Valanginian of Colombia

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ABSTRACT

The evolution of large size in vertebrates is a fascinating research topic, relevant, for example, for the Cretaceous turtles of the Protostegidae clade, which includes some of the largest turtles to have ever inhabited the Earth. However, there is still limited understanding regarding when and under what conditions large size emerged in this group. Here we describe several limb bones and fossil shell remains from the upper Valanginian, Rosa Blanca Formation of Colombia that, together, shed light on the onset conditions and characteristics of large-size evolution in protostegids. The material, although fragmentary, preserves enough features, such as the sigmoidal curvature of the shaft of the humeri in anterior view and their strong waist, to be attributed to Protostegidae. The fossil turtles described here constitute the largest ever known for the Early Cretaceous worldwide and the oldest record for their group. The ecological and climatic conditions of northern South America during the Late Valanginian are discussed as potential triggers of the emergence of large body size in protostegid turtles.

Key words: Testudines; South America; Early Cretaceous; Body size; Rosa Blanca Formation

INTRODUCTION

The time frame between the Late Jurassic to the Late Cretaceous (163.5 to 66.0 Mya) was marked by extreme gigantism in several groups of vertebrates, including dinosaurs (sauropods, ornithischians, theropods, ceratopsians, and hadrosaurs), marine sauropterygians, crocodilians, and turtles (Benson *et al.* 2014, Vermeij 2016, Foffa *et al.* 2018, Stockdale and Benton 2021). In the case of turtles, Mesozoic gigantism was exhibited principally by some members of the cryptodiran (hidden-necked) Protostegidae clade, which constitute the first clade of fully marine-adapted turtles (Hirayama 1994, Hooks 1998, Cadena and Parham 2015, Joyce *et al.* 2021a). In particular, the Late Cretaceous taxa *Archelon ischyros* (Wieland 1896) with a maximum carapace length of 220 cm (Cadena *et al.* 2020a) and *Protostega gigas* (Cope 1872) with a maximum carapace length of 310 cm (Danilov *et al.* 2022); both taxa with an estimated total body length of 4 m, representing some of the largest turtles that ever inhabited the world. Late Cretaceous protostegids were not all giants. Mid- to small-size taxa (<1.5 m) also occupied different marine ecosystems of the world, including members of *Desmatochelys* (Williston 1894), *Bouliachelys* (Kear and Lee 2006), *Rhinochelys* (Seeley 1869), *Calcarichelys* (Zangerl 1953), among others (Zangerl and Sloan 1960, Hooks 1998, Kear and Lee 2006, Tong *et al.* 2006, Raselli 2018, Evers *et al.* 2019).

It is currently not known if protostegid gigantism evolved in a progressive trend of increasing size (Cope's rule; Stanley 1973), or with a burst of size increase at the base of the clade. A recent global study of body-size evolution suggests that turtles do not follow Cope's rule (Farina *et al.* 2022); one alternative hypothesis is that protostegids started to exhibit large size right at the beginning of its origin, as in many of the groups of dinosaurs (O'Gorman and Hone 2012). A first piece of evidence supporting the early onset of size in protostegids was provided by the discovery of *Desmatochelys padillai* (Cadena and Parham 2015) from

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the upper barremian–lower Aptian of Colombia. A turtle with a carapace of at least 2 m length and a total body length estimated of 3 m, indicates the development of large size in early protostegids. However, whether *D. padillai* (the oldest record of Protostegidae known so far) was part of a general trend in increasing body size exhibited by marine vertebrates, including turtles, during the Late Jurassic–early Cretaceous (O'Gorman and Hone 2012), and how the climate, particularly the cooling conditions of the Tithonian–early Barremian Cool Interval (TEBCI)(Scotese *et al.* 2021) could have played a key role in controlling the size of lower latitude vertebrates, particularly of protostegids, are questions that have not yet been resolved.

Another unresolved and problematic issue about protostegid turtles is the lack of consensus in terms of their phylogenetic relationships with the other clades that involved different evolutionary radiations of turtles adapted to marine or costal–littoral lifestyles. There are at least three possible phylogenetic places for protostegids: (i) the earliest and most recurrent hypothesis suggests that they are a stem-group of the lineage represented by the extant *Dermochelys coriacea* (Hirayama 1994, 1998, Lehman and Tomlinson 2004, Brinkman *et al.* 2006, Kear and Lee 2006, Bardet *et al.* 2013, Cadena 2015, Cadena and Parham 2015, Evers and Benson 2019); (ii) outside of Chelonioidea, on the stem-group of either cryptodires or turtles (Joyce 2007, Sterli 2010, Anquetin 2012); and (iii) as stem-group chelonioids (Raselli 2018, Evers *et al.* 2019, Gentry *et al.* 2019, Joyce *et al.* 2021a). Considering the discrepancies in the phylogenetic position of Protostegidae, in a recent work that defined clade names for extinct and extant turtles following PhyloCode nomenclature, the marine to costal turtles that represent different evolutionary radiations are considered as separated clades (Joyce *et al.* 2021b). The clades are: (i) Thalassochelydia Anquetin *et al.* (2017), converted name clade, including marine turtles from the Late Jurassic to Early Cretaceous of Europe and South America; (ii) Sandownidae Tong and Meylan (2013), converted name clade, including four taxa of Cretaceous to Palaeocene coastal–marine turtles with a circum-Atlantic distribution; and (iii) Protostegidae Cope (1872), converted clade name, including Early to Late Cretaceous fully adapted marine turtles with a worldwide distribution. These clade compositions were utilized in this manuscript.

Besides the La Paja Formation, from where *Desmatochelys padillai* and other iconic marine vertebrates of northern South America come (Noé and Gómez-Pérez 2020), another formation that is also relevant for lower latitude vertebrates of South America, with the possibility of shedding light on the questions above-mentioned, is the lower Valanginian to lower Hauterivian (137 to 131 Mya) Rosa Blanca Formation (Etayo-Serna and Guzmán-Ospitia 2019). Fossil vertebrates of the Rosa Blanca Formation include pleurodiran turtles (Cadena and Gaffney 2005, Cadena *et al.* 2013, Cadena 2020), potential eucryptodiran turtles (Cadena 2011), sharks (Carrillo-Briceño *et al.* 2015, Carrillo-Briceño and Cadena 2022), pterosaurs (Cadena *et al.* 2020b), fishes and ichthyosaur remains (Etayo-Serna and Guzmán-Ospitia 2019), plesiosauroids (Benavides-Cabra and Páramo-Fonseca 2021), and thalattosuchian crocodyliforms (Larson *et al.* 2011). Here, we describe the fossil remains of large-size turtles attributable to the marine Protostegidae and discuss their implications in terms of body-size evolution and palaeoecology.

Institutional abbreviations

CIP, Centro de Investigaciones Paleontológicas, Villa de Leyva, Colombia; UR-CP, palaeontological collection, Faculty of Natural Sciences, Universidad del Rosario, Bogotá, Colombia.

MATERIALS AND METHODS

Study material

The fossil material includes three different limb bone fragments (UR-CP-0126, UR-CP-0128, and UR-CP-0146), and some shell remains, including a nearly complete right xiphiplastron, a fragment of the left hypoplastron?, a left epiplastron, a costal bone fragment, and several peripheral bones (UR-CP-0127, UR-CP-0145, UR-CP-0147). All specimens are housed at the palaeontological collection of the Universidad del Rosario, Bogotá, Colombia.

Preparation and examination

Part of the rock matrix was easily removed from some of the specimens using dental picks, and for the case of UR-CP-0126, was prepared with air scribe and sulphamic acid (H_3NSO_3) at the CIP. The fossils were measured using a calliper, photographed, and examined with a Nikon Eclipse SMZ1270 stereomicroscope at the laboratory of the Traditional and Molecular Neotropical Paleontology Group (PaleoNeo) at the Universidad del Rosario.

Size analysis

To explore the implications of the fossils described here in terms of understanding size evolution among marine Cretaceous turtles, we compiled information on humerus and carapace length from previous studies (Supporting Information, Table S1), for 14 extant and fossil taxa. It is important to notice that some of these carapace lengths were estimations [i.e. *Protostega* specimens listed in Danilov *et al.* (2022)]. We used PAST 4.10 (Hammer *et al.* 2001) to plot humerus against carapace length, finding their correlation equation using ordinary least squares' regression that allowed us to estimate the carapace size for some of the fossils described here. The potential effect of phylogenetic autocorrelation on the slopes and intercepts (Felsenstein 1985) was not calculated due to the aforementioned uncertainty that *protostegidae* and other marine turtles have in terms of their phylogeny. We also plotted humerus sizes on to a diagram that shows the chronostratigraphic ranges of taxa, based on the estimation or measurements of the fossil bones figured in previous works using ImageJ 1.52a (Rasband 2018).

GEOLOGICAL SETTING

The fossils come from four different localities situated north-east of the Zapatoca town, Santander Department, Colombia (Fig. 1A). All of them, belonging to the Carrizal Member, Rosa Blanca Formation (Fig. 1B) of different stratigraphic horizons following the stratigraphic nomenclature for Rosa Blanca Formation of Etayo-Serna and Guzmán-Ospitia (2019). UR-CP-0126 was found at La Virgen locality (6°52′12.46′′N, 73°14′03.42′′W), between the horizons P′–P′′ (Fig. 1C), inside of calcareous concretion. UR-CP-0127 and UR-CP-0147 come from the Pico de la Vieja South locality (6°51′20.20′′N, 73°14′3,05′′W), between

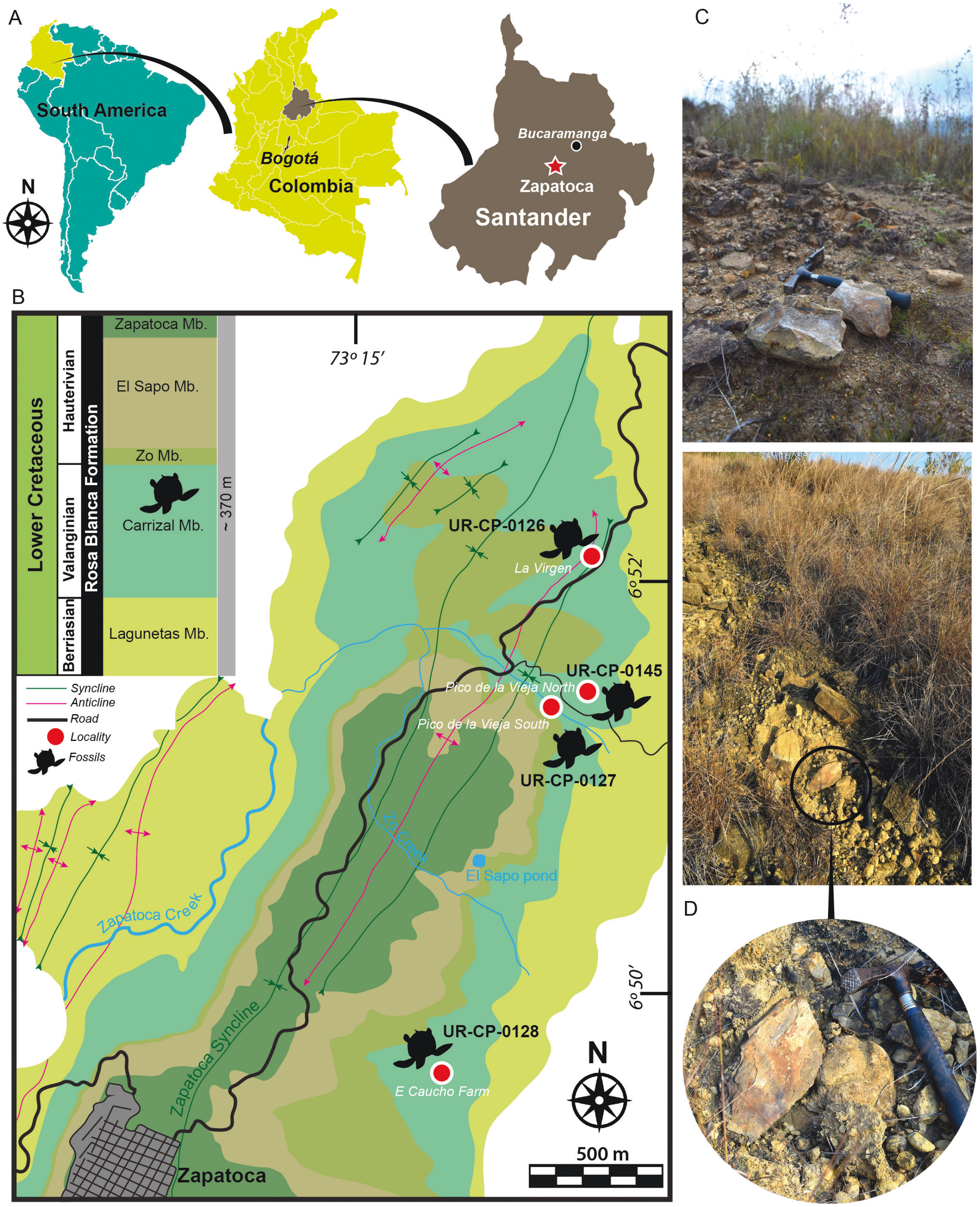

Figure 1. Geographical and geological settings of the fossils described. A, location of Zapatoca town inside Santander Department, Colombia, and South America. B, geologic map and stratigraphic context indicating the four localities where the fossils described here were found, based on Etayo-Serna and Guzmán-Ospitia (2019), figure modified from Carrillo-Briceño and Cadena (2022). C, photo of the outcrop at the moment that the left humerus UR-CP-0126 was found inside a calcareous concretion. D, photo of the outcrop at the moment the right xiphiplastron part of UR-CP-0127 was found.

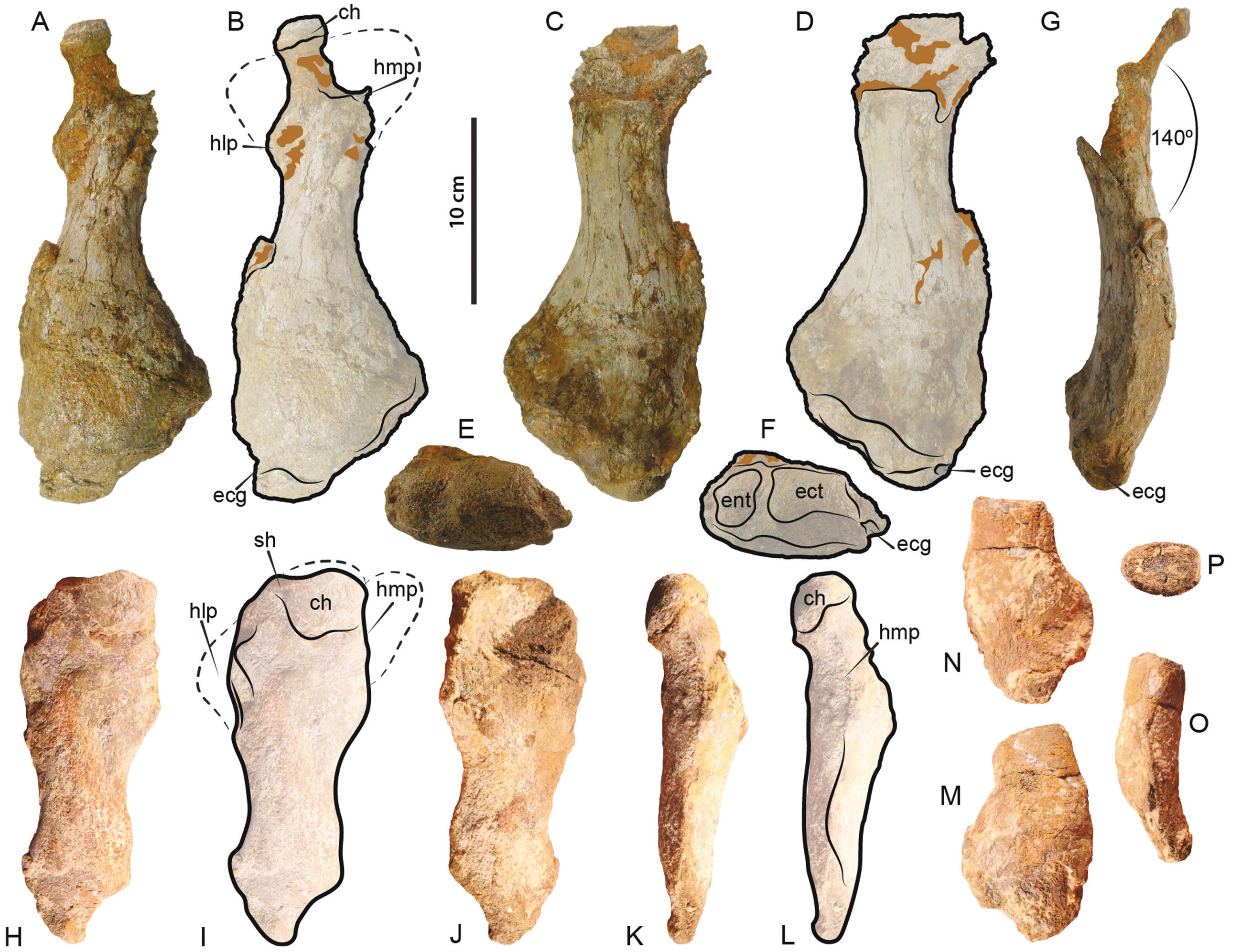

Figure 2. Fossil humeri of *Protostegidae* incertae sedis from the Carrizal Member, Rosa Blanca Formation. A–G, UR-CP-0126 left humerus in dorsal view (A, B), ventral view (C, D), distal view (E, F), and anterior view (G). H–L, UR-CP-0128 right humerus shaft to proximal regions in dorsal view (H, I), ventral view (J, K), and posterior view (K, L). M–P, UR-CP-0146 distal portion of a right humerus in dorsal view (M), ventral view (N), anterior view (O), and cross-section at the shaft region (P). Abbreviations: ch, caput humeri; ecg, ectepicondylar groove; ect, ectepicondyle; ent, entepicondyle; hlp, humerus lateral process; hmp, humerus medial process; sh, shoulder. Brow shadowed regions indicate rock matrix.

the Q”–Q’ horizons, found on the surface of the Q” limestone layer (Fig. 1D). UR-CP-0128 and UR-CP-0145 come from El Caucho Farm locality (6°49′20.38′′N, 73°15′0.32′′W), between T–T’ horizons, from a calcareous mudstone layer. UR-CP-0146 was found in Pico de la Vieja North locality (6°51′18.35′′N, 73°13′50.85′′W), in a layer of brown calcareous mudstone between the R–R’ horizons.

The age for the Carrizal Member, intervals between the Q and P horizons of the Rosa Blanca Formation has been established as late Valanginian, based on ammonoids particularly by the occurrence of *Saynoceras verrucosum* (d´Orbigny 1841), in correlation with what has been established for the Western Mediterranean province (Reboulet *et al.* 2014, Etayo-Serna and Guzmán-Ospitia 2019). Palaeoenviromental reconstruction for the Carrizal Member suggests the alternation between hardgrounds and claystones formed in a barrier beach that separated a 10-m depth lagoon from the shallow sea (Etayo-Serna and Guzmán-Ospitia 2019). Favouring the accumulation and preservation of the diverse marine fauna that inhabited this region, due to shallow waters and probably warm temperatures.

SYSTEMATIC PALAEONTOLOGY

Testudines

Cryptodira

Americhelydia

Pan-Chelonioidea

Protostegidae

Incertae sedis

Figs 2–4

Referred material: UR-CP-0126 nearly complete left humerus. UR-CP-0127, a nearly complete right xiphiplastron, left hypoplastron? fragment, a bridge region peripheral, and a costal bone fragment (single individual). UR-CP-0128, proximal to the shaft regions of a right humerus. UR-CP-0145, at least 10 peripheral bones from the anterior and bridge regions of the shell

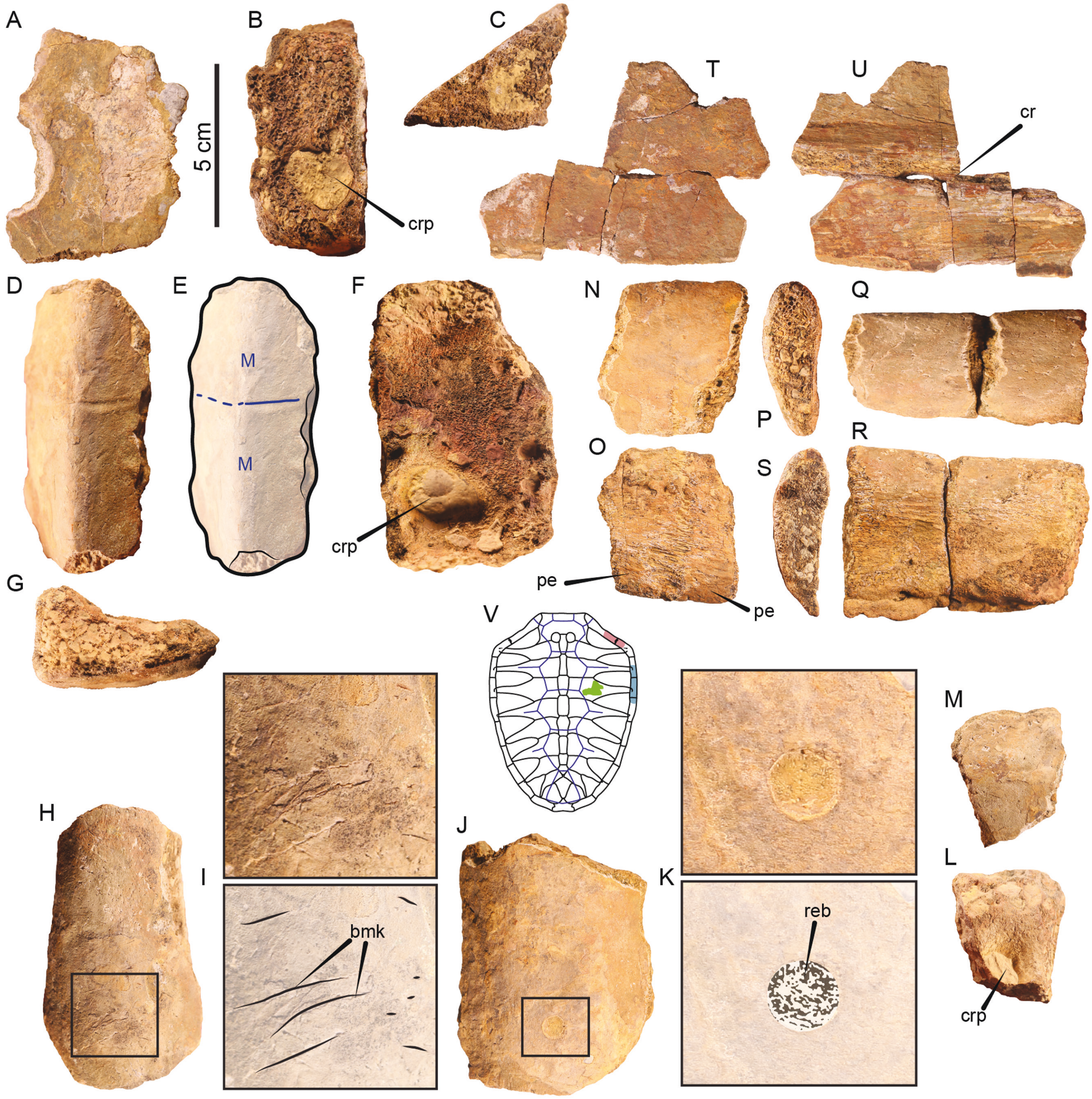

Figure 3. Fossil carapacial fragments of Protostegidae incertae sedis from the Carrizal Member, Rosa Blanca Formation. A–C, UR-CP-0127 bridge peripheral in dorsal view (A), medial view (B), posterior view (C). D–G, UR-CP-0145 bridge peripheral in lateral view (D, E), medial view (F), and posterior view (G). H–I, UR-CP-0145 bridge peripheral lateral view (H), and close-up of the bone surface showing bite marks (I). J–K, UR-CP-0145 bridge peripheral in lateral view (J), and close-up of the bone surface showing a circular boring, similar to the ichnogenus *Karethraichnus*, exhibiting bone remodelling (K). L–M, UR-CP-0145 bridge peripheral in medial view (L) and dorsal view (M). N–P, UR-CP-0145 anterior carapace peripheral in dorsal view (N), ventral view (O), and medial view (P). Q–S, UR-CP-0145 anterior carapace peripheral in dorsolateral view (Q), ventral view (R), and medial view (S). T–U, UR-CP-0127 costal bone fragment in dorsal view (T) and ventral view (U). V, carapace outline of *Desmatochelys lowi* redraw from Zangerl and Sloan (1960) to indicate the bridge peripherals (light blue), anterior carapace peripheral (pink) and costal bone fragment (green). Abbreviations: bmk, bite marks; cr, costal rib; crp, pit for costal rib insertion; M, marginal scute; pe, peripheral; reb, remolded boring pit.

(single individual). UR-CP-0146, distal portion of a humerus. UR-CP-0147, nearly complete right epiplastron.

Although UC-CP-0128 and UR-CP-0146 were found in the same stratigraphic layer, a couple meters away from each other, we avoided considering them as belonging to a single individual, due to the impossibility of assembling them as a part of a single bone. However, this could be an artefact of the taphonomic events that both bones have suffered.

Remarks: The fossil material described herein can be attributed as belonging to Cryptodira by: the humerus having a smaller lateral process (Gaffney 1990), as indicated in UR-CP-0126 (Fig.

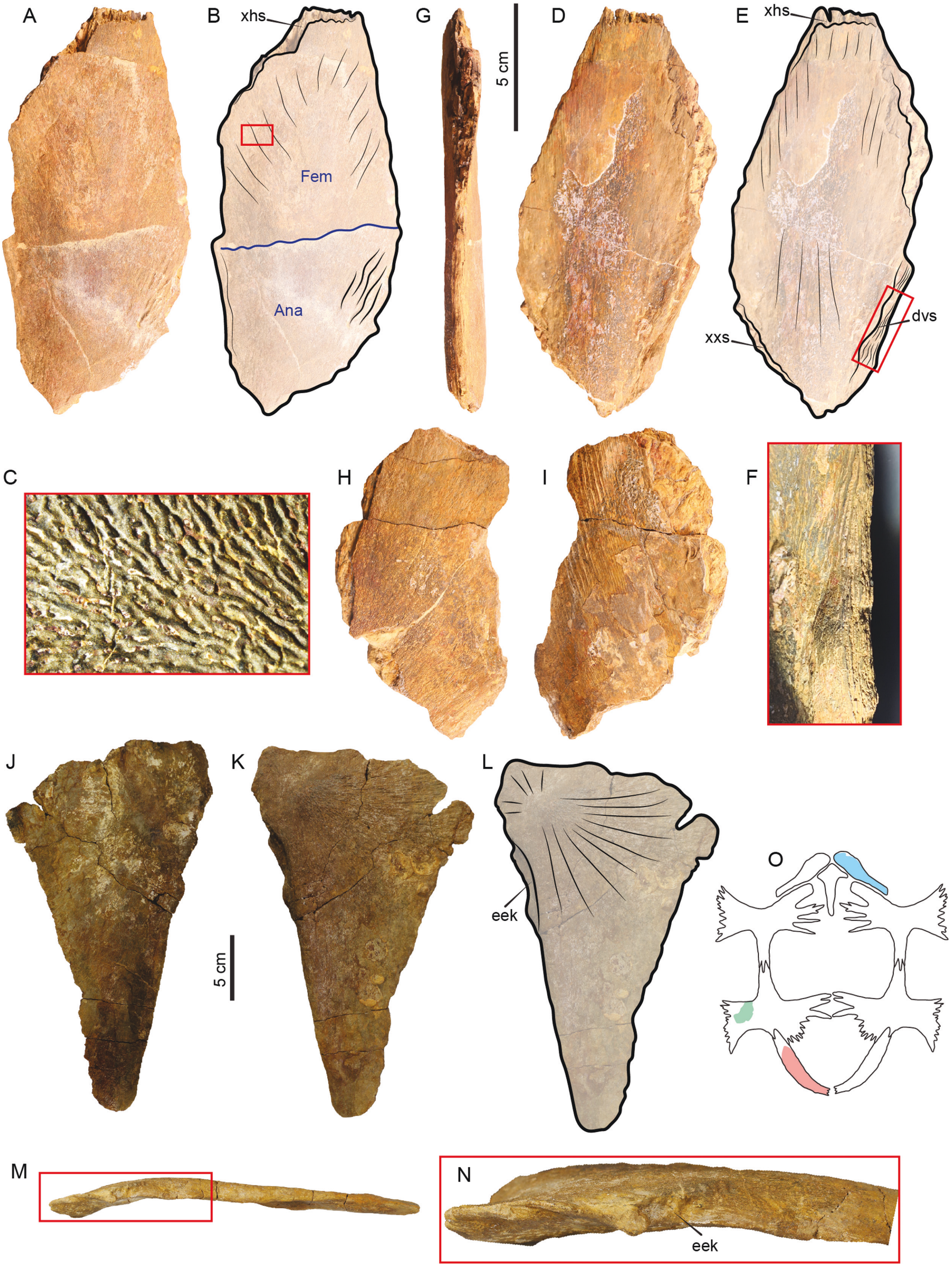

Figure 4. Fossil plastral fragments of Protostegidae *incertae sedis* from the Carrizal Member, Rosa Blanca Formation. A–G, UR-CP-0127 right xiphiplastron in ventral view (A, B), bone surface vermiculated decoration (C) from the red rectangle region shown in (B), dorsal view (D, E), close-up of the posterolateral edge, red rectangle showed in (E), and lateral view (G). H–I, UR-CP-0127 fragment of the left hypoplastron? in ventral view (H) and dorsal view (I). J–N, UR-CP-0147 left epiplastron in ventral view (J), dorsal view (K, L), lateral view (M), close-up of the most anterolateral edge at the contact with the entoplastron (N), red rectangle showed in M. O, plastron outline of *Desmatochelys lowi* redrawn from Zangerl and Sloan (1960) to indicate the epiplastron UR-CP-0147 (light blue), the right xiphiplastron UR-CP-0127 (pink) and the left hypoplastron? fragment (green). Abbreviations: Ana, anal scute; dvs, dorsal-visceral surfaces contact; eek, epiplastron–entoplastron kinesis contact; Fem, femoral scute; xhs, xiphiplastron–hypoplastron suture; xxs, xiphiplastron (rigth)–xiphiplastron (left) suture.

2); a humerus exhibiting an anterior shoulder at the proximal articular surface (caput humeri) (Gaffney 1990, Cadena and Parham 2015), seen in UR-CP-0128 (Fig. 2); and lack of sutural articulation of the pubis and ischium to the xiphiplastron (Joyce 2007, Cadena 2015, references therein), as in UR-CP-0127 and UR-CP-0147 (Fig. 4). The humeri described here also shared with chelonioids the relatively low position of the lateral process along the humerus shaft (Zangerl 1953, Gaffney and Meylan 1988, Hirayama 1994, Evers *et al.* 2019). The material is attributed to Protostegidae by: (i) having a lateral process of the humerus enlarged within the anterior portion of shaft, not easily visible from ventral view (Hirayama 1992, 1998), as exhibited by UR-CP-0126 (Fig. 2E) and UR-CP-0128 (Fig. 2K, L); (ii) a sigmoidal curvature of the shaft in anterior view and strong waist of the humerus, considered primitive for Cretaceous marine turtles (Lehman and Tomlinson 2004); (iii) distal humerus trochlea absent, instead having a rounded epiphyseal surface without clearly defined articulation facets (Evers *et al.* 2019), UR-CP-0126 shows a very incipient trochlea, indicating its reduction; (iv) also the flattening of the humeri indicates a forelimb of flipper-type, characteristic of chelonioid marine turtles, including protostegids (Evers *et al.* 2019, Joyce *et al.* 2021b); and (v) ectepicondylar foramen in a groove (seen in UR-CP-0126), similar as in most chelonioids, including protostegids (Hirayama 1994).

Descriptions

Measurements of the all fossils described herein are presented in Table 1 and Supporting Information, Fig. S1.

Humeri: UR-CP-0126 is a left humerus, missing most of its lateral and medial processes, as well as most of its proximal region (Fig. 2A–E). In dorsal view (Fig. 2A, B), a small portion of the caput humeri is preserved. The bone surface is smooth to slightly striate, and from the shaft region the bone starts increasing its width towards the most distal portion of it, exhibiting a slightly eroded bone surface. In ventral and distal views (Fig. 2C–F), the distal region exhibits well-defined entepicondylar and ectepicondylar surfaces separated by a moderately deep depression, and the ectepicondylar groove is particularly visible in both views. The trochlea, although existent, is very incipient. In anterior view (Fig. 2G), the humerus exhibits a sigmoidal curve from the proximal to the distal ends, and a general flat volume along its entire length. The preserved portion of the caput humeri is projected dorsally approximately 140º from the midline axis of the bone.

UR-CP-0128 is a right humerus, preserved from its shaft to the proximal region (Fig. 2H–L). In dorsal view (Fig. 2H, I), the bone surface is moderately eroded and the most remarkable feature preserved is the slightly rounded caput humeri with a narrow lateral shoulder. In ventral view (Fig. 2J), the proximoventral portion of the bone is completely eroded. In posterior view (Fig. 2K, L), the bone exhibits an incipient sigmoidal shape, showing the prominent caput humeri and the base of the humerus medial process completely eroded.

UR-CP-0146 is a distal portion of a right humerus (Fig. 2M–P), with most of its entire bone surface eroded and the ectepicondylar groove filled with a hard layer of haematite. In cross-section (Fig. 2P) the bone exhibits a nearly oval shape, with thin cortical bone, and is densely filled to the centre with cancellous bone.

Carapace: Bridge to posterior region peripherals is preserved for two different individuals: UR-CP-0127 (Fig. 3A–C) and UR-CP-0145 (Fig. 3D–M). The peripherals are large in size (see Table 1), all of them exhibiting a smooth to slightly vermiculated bone surface in dorsal and ventral views (Fig. 3A, D, E, H, J, M). On their medial surface, all of them exhibit a circular and deep pit for the insertion of the most lateral ending tip of the costal rib (Fig. 3B, F, L). In anterior or posterior views, they are triangular in shape with a V-shaped medial embayment (Fig. 3C, G). Some of them preserve evidence of the sulcus, indicating the contact between marginal scutes (Fig. 3A, D, E). Two of the peripherals of UR-CP-0145 show evidence of attacks and possible bioerosional activity on the bone. The first corresponds to bite

Table 1. Measurements for the fossil specimens described herein as preserved. Abbreviations: ML, maximum length, MW, maximum width. See Supporting Information Figure S1 for graphical indication of the measurements

Specimen	ML, mm	MW, mm
UR-CP-0126, left humerus (Fig. 3A–F)	248	98
UR-CP-0127, right xiphiplastron (Fig. 4A–G)	210	151
UR-CP-0127, left hypoplastron? fragment (Fig. 4H–I)	108	97
UR-CP-0127, costal fragment (Fig. 3T–U)	62	84
UR-CP-0127, peripheral (Fig. 3A–C)	79	65
UR-CP-0128, right humerus fragment (Fig. 2H–L)	187	72
UR-CP-0146, right humerus fragment (Fig. 3M–P)	113	67
UR-CP-0146, bridge peripheral (Fig. 3D–F)	112	59
UR-CP-0146, bridge peripheral (Fig. 3H)	105	57
UR-CP-0146, bridge peripheral (Fig. 3J)	74	50
UR-CP-0146, bridge peripheral (Fig. 3M)	39	47
UR-CP-0146, anterior peripheral (Fig. 3N–P)	45	56
UR-CP-0146, anterior peripheral (Fig. 3Q–S)	82	61
UR-CP-0147, left epiplastron (Fig. 4J–N)	287	155

marks characterized by deep and almost parallel cuts (Fig. 3H, I), and the second is a circular pit exhibiting bone remodelling (Fig. 3R, S).

Some peripherals from the anterior margin of the carapace of UR-CP-0145 are longer than wide, and lack of pit for the costal rib end. They exhibit smooth bone surface in ventral view (Fig. 3J, M). In ventral view, the suture between peripherals is well defined (Fig. 3K, N), and in medial view the peripherals are oval in shape with the posterior edge being much narrower than the anterior (Fig. 3L, O). A fragment of a large costal bone is preserved for UR-CP-0127 (Fig. 3D, E), possibly a right costal 3 or 5. In ventral view (Fig. 3E), the costal rib is well defined. The preserved carapacial bones are indicated in an outline of the carapace of *Desmatochelys lowi* (Zangerl and Sloan 1960) redrawn from that study (Fig. 3V).

Plastron: Plastral bones from two different individuals UR-CP-0127 and UR-CP-0147 represent two large turtles. The first of these bones corresponds to a nearly complete right xiphiplastron, UR-CP-0127 (Fig. 4A–G), rectangular in shape. In ventral view (Fig. 4A, B), the sutural edge with the hypoplastron is preserved at its most medial region. The bone surface exhibits a vermiculate decoration and some striations, particularly at the sutural region that contacted with the left xiphiplastron (Fig. 3C). Also, in this view, the sulcus between the anal and femoral scutes is well defined. In dorsal view (Fig. 4D, E), the xiphiplastron lacks any scars for attachment with the pelvic girdle bones, and the indented sutural edge that contacted with the left xiphiplastron is visible. At its most posterolateral margin, the contact between the visceral and the dorsal surfaces is indicated by parallel striations of the bone surface. Other plastral bones of UR-CP-0127 are very fragmentary (Fig. 4H, I) and seems to be part of the left hypoplastron.

UR-CP-0147 corresponds to a large left epiplastron (Fig. 4J–L), having a blade-shape. In dorsal view (Fig. 4K, L), the bone exhibits a striate surface and the contact with the entoplastron is indicated by a concavity suggesting plastral kinesis between these two bones (Fig. 4M, N). The preserved plastral bones are indicated in an outline of the plastron of *Desmatochelys lowi* redrawn from Zangerl and Sloan (1960) (Fig. 4O).

DISCUSSION

Taxonomic considerations

Although the fossils that we describe here are fragmentary and correspond to at least four different individuals, we discuss some taxonomic considerations. For example, the humeri UR-CP-0126 and UR-CP-0146 resemble in several of their features those exhibited by some of the Cretaceous marine turtles included in the still controversial clade Pan-Chelonioidea following Joyce *et al.* (2021a). Shared features particularly with members of Protostegidae include: a relatively flat shape in its shaft and distal regions, a broad distal end, and an anterodistally positioned ectepicondylar groove (Fig. 2), as in, for example, *Desmatochelys lowi* Zangerl and Sloan (1960: fig. 16) and *Desmatochelys padillai* Cadena and Parham (2015: fig. 5). This differs from the Upper Cretaceous protostegids, which exhibit broader shaft regions (Hirayama 1994, Danilov *et al.* 2022).

Shell features of the described material also resemble the shells of protostegids and, in general, of pan-chelonioids marine turtles. For example, the medial pits of peripherals for the insertion of the tips of the costal ribs, exhibited by UR-CP-0127 and UR-CP-0145 individuals, and the rib-free peripherals of UR-CP-0145 (Fig. 3), characters discussed in Cadena and Parham (2015: chs 132, 133). The oval-elongated shape of the left xiphiplastron UR-CP-0127 (Fig. 4) is very similar to the one exhibited by other protostegids, particularly of *Calcarichelys gemma* (Hooks 1998: fig. 8). The blade-shape of the left epiplastron UR-CP-0147 is similar to the shape exhibited by *Desmatochelys lowi* (Zangerl and Sloan 1960: fig. 11) and also others figured in Hirayama (1994: figs 8, 9). The left epiplastron UR-CP-0147 shares also with *Desmatochelys lowi* (Zangerl and Sloan 1960: fig. 11) a medial margin smooth and free of sutural texture for most of its length, only with sutural contact with the entoplastron, at its anterior region.

It is possible that all the material described here corresponds to a protostegid closer to the genus *Desmatochelys*, based on the aforementioned similarities with some of its members, including a younger taxon occurring in the same geographical and geological basin, *D. padillai* from the Barremian–Aptian of Colombia (Cadena and Parham 2015). Considering the Late Valanginian age for the Carrizal Member of Rosa Blanca Formation, these fossils represent the earliest so far known record for large, fully adapted, marine turtles and, potentially, for the entire Protostegidae clade.

The onset of large size in Protostegidae

Another remarkable implication of the fossil material described here is the combination of its age (late Valanginian) and the large size of limb and shell bones. Our estimate, based on the equation ($y = 0.2273x - 12.1833$) obtained for the correlation between humerus and carapace length (Fig. 5; Supporting Information, Table S1), indicates that the UR-CP-0126 humerus belonged to a turtle with a carapace of approximately 1145 mm and potentially a body length of 2 m. Another example of the large size of the marine turtles of Zapatoca is indicated by the epiplastron UR-CP-0147 (Fig. 4; Table 1), with its 287 mm length, it could have corresponded to a turtle with a plastron of approximately 957 mm length (Supporting Information, Fig. S2) and total body length of around 2.5 m, making it the largest turtle of the Early Cretaceous and the first giant turtle that ever existed.

The marine turtle remains from Zapatoca provide evidence that protostegid turtles rapidly evolved large body size at the beginning of its evolution, as indicated by the shell and limb bones described here. A trend that reached a maximum during the Late Cretaceous, a period when the largest protostegids, such as *Archelon* Wieland 1896, *Protostega* (Cope 1872), and *Atlantochelys* (Agassiz 1849), existed. However, the increase in size among protostegids was not a gradual process. Small forms also existed during the Albian to Cenomanian, indicating that size variation in protostegids was not strictly correlated with geological time (Fig. 6A, B; Supporting Information, Table S2). A similar pattern of early onset of large body size in evolution, as suggested here for protostegids, appears to have occurred also in the Thalassochelydia clade as well. This is demostrated by *Thalassemys bruntrutana* (Joyce *et al.* 2021b) (Fig. 6A, B), and also in ichthyosaurs (Sander *et al.* 2021), another remarkable

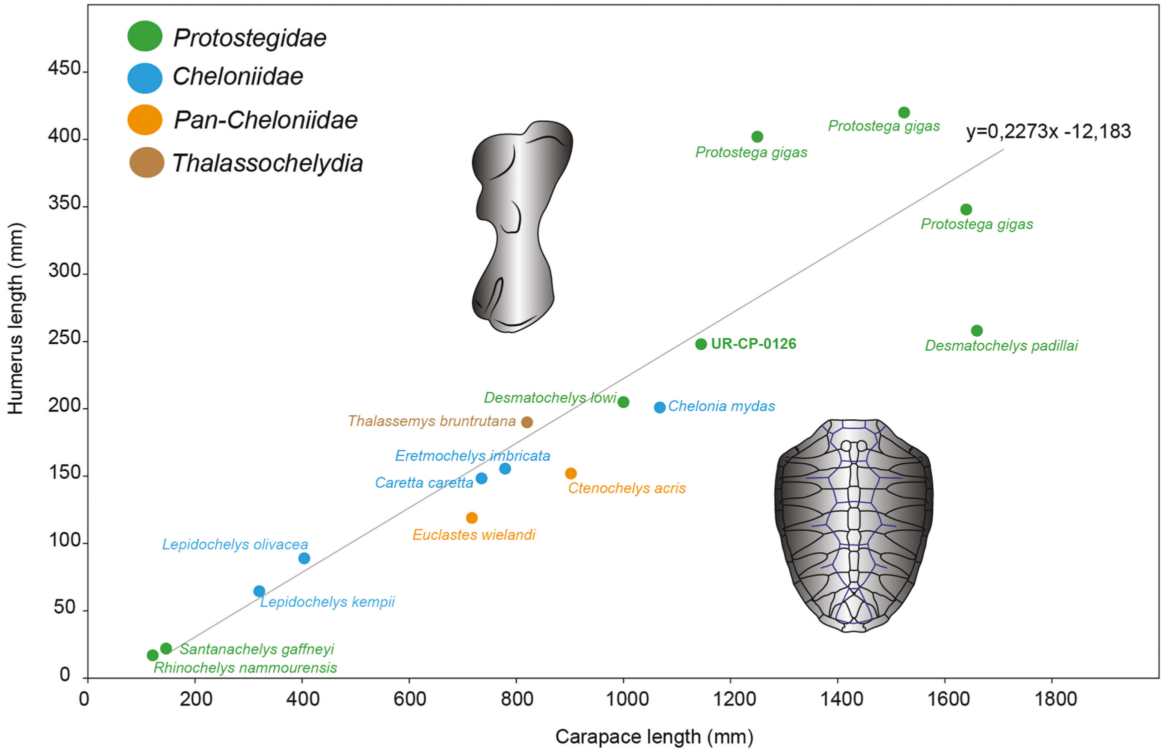

Figure 5. Correlation between humerus length (Y-axis) and carapace length (X-axis) for several marine and coastal–littoral turtles of the groups Protostegidae, Cheloniidae, Pan-Cheloniidae and Thalassochelydia, showing the correlation equation used to estimate the carapace length of UR-CP-0126, which is one of the largest turtles from the Early Cretaceous taking this relationship into account, only surpassed by *Desmatochelys lowi* and *Protostega gigas*, both from the Late Cretaceous. For raw data and sources see Supporting Information, Table S1.

group of marine Mesozoic reptiles. The development of large size in marine turtles inhabiting the tropical latitudes of South America during the Early Cretaceous could have been the product of different causes, including, for example, the increase in primary productivity of ecosystems during most of the Valanginian (Erba and Tremolada 2004), something evidenced in the abundant record of microfossils, invertebrates, and other vertebrates found associated with these turtles in the Carrizal Member of the Rosa Blanca Formation. Climate, indeed, could also have played a key role on the onset of large size of these turtles, because the oceans were well oxygenated, preventing them from being anoxic, and the particular conditions for lower latitudes were dry and warm (Scotese *et al.* 2021). Precise evidence and testing of these hypotheses await further research, by analysing, for example, isotopes in the teeth of some of the vertebrates preserved in this region, or by integrating the entire fossil record (nano, micro, and macro) from the Carrizal Member in a robust palaeoecological study, which is currently in progress.

Palaeoecological implications

The new record of marine protostegids from Zapatoca adds a new group to the turtle fauna already known from the Carrizal Member of the Rosa Blanca Formation, which includes, the pleurodire *Notoemys zapatocaensis* (Cadena and Gaffney 2005), and some remains of *Pelomedusoides* indet. (Cadena 2020). All together they indicate a well-structured and diversified ecosystem that was able to provide good conditions for the development of large, fully adapted, marine and coastal–littoral turtles from different lineages, cryptodires and pleurodires.

The large body size reached early by Early Cretaceous protostegids could also have been an ecological advantage by reducing the risk of predation, similar to what occurs in extant marine turtles (Heppel *et al.* 2003). Potential predators of large turtles in this past ecosystem included thalattosuchian crocodyliforms (Larson *et al.* 2011), and other marine reptiles such as elasmosaurid and ichthyosaurs (Etayo-Serna and Guzmán-Ospitia 2019, Benavides-Cabra and Páramo-Fonseca 2021). Other potential predators are the sharks, and although at this time only durophagus hybodontiform sharks are known for the Carrizal Member (Carrillo-Briceño *et al.* 2015, Carrillo-Briceño and Cadena 2022), there is circumstantial evidence that other sharks with triangular sharp teeth could have existed in this ecosystem, as shown by the bite marks in the peripheral UR-CP-0127 (Fig. 3P, Q). Sharks are one of the predators of juvenile and adult extant marine turtles (Heithaus 2013).

One of the peripherals of UR-CP-0127 shows other particular evidence of palaeoecological interactions between the protostegid turtles from Zapatoca and other organisms: a circular boring completely healed (Fig. 3R, S), matching the morphology of the ichnogenus *Karethraichnus* (Zonneveld *et al.* 2016) of circular to subcircular and oval pits and holes bored into bony substrates. This ichnogenus is interpreted as created by parasites while the host animal was alive (Zonneveld *et al.* 2022), something that UR-CP-0127 was able to recover from, as evidenced by the bone remodelling of the circular pit.

Large-size Early Cretaceous protostegids probably functioned also as predators of small vertebrates, such as fishes, invertebrates, and regulators of the ecosystem, as consumers of seagrasses,

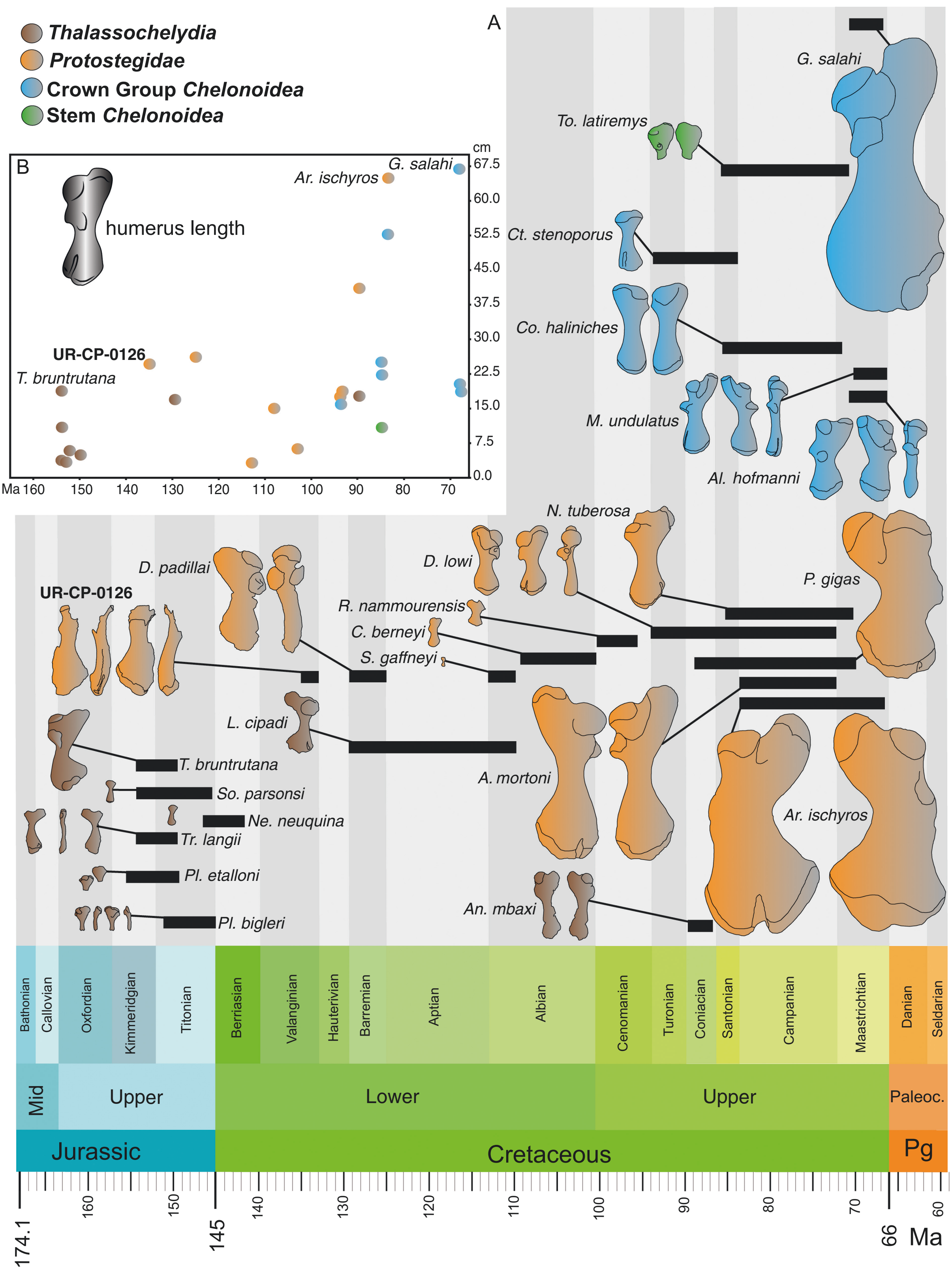

Figure 6. Graphical illustration of the humeri for some members of Thalassochelydia, Protostegidae and Pan-Chelonioidea along geologic time and their relative size. A, outline of the humeri for taxa previously known and the new record UR-CP-0126 described herein, indicating their chronostratigraphic range. B, plot of humeri length in centimetres (Y-axis) versus geologic time in millions of years (My) (X-axis) for the taxa shown in (A), the taxa with the largest values for each of the clades is labelled, as well as the UR-CP-0126 specimen described herein. Abbreviations: A., *Atlantochelys*; Al., *Allopleuron*; An., *Angolachelys*; Ar, *Archelon*; C, *Cratochelone*; Co, *Corsochelys*; Ct, *Ctenochelys*; D, *Desmatochelys*; G, *Gigantatypus*; L, *Leyvachelys*; M, *Mesodermochelys*; N, *Neptunochelys*; Ne, *Neusticemys*; P, *Protostega*; Paleoc, Paleocene; Pg, Paleogene; Pl, *Plesiochelys*; R, *Rhinoclemys*; S, *Santanachelys*; So, *Solnhofia*; T, *Thalassemys*; To, *Toxochelys*; Tr, *Tropidemys*. For raw data and sources see Supporting Information, Table S2.

macroalgae, and plankton, ecosystem engineers, and possibly also as nutrient transporters, as the extant marine turtles do (Parham and Pyenson 2010, Heithaus 2013). Future fieldwork and new potential findings of better or more complete fossils could validate these ecological hypotheses for lower latitude Early Cretaceous turtles.

SUPPLEMENTARY DATA

Supplementary data is available at *Zoological Journal of the Linnean Society* online.

Figure S1. Outlines of the fossil material figured here, indicating their maximum length (ML) and width (MW). A, UR-CP-0126 left humerus (Fig. 2A). B, UR-CP-0127 right xiphiplastron (Fig. 4A). C, UR-CP-0127 fragment of left hypoplastron? (Fig. 4H). D, UR-CP-0127, costal bone fragment (Fig. 3T). E, UR-CP-0127, bridge peripheral (Fig. 3A). F, UR-CP-0128, fragmentary right humerus (Fig. 2H). G, UR-CP-0145 bridge peripheral (Fig. 3D). H, UR-CP-0145 bridge peripheral (Fig. 3H). I, UR-CP-0145 bridge peripheral (Fig. 3J). J, UR-CP-0145 bridge peripheral (Fig. 3L). K, UR-CP-0145 anterior peripheral (Fig. 3N). L, UR-CP-0145 anterior peripheral (Fig. 3R). M, UR-CP-0146 distal right humerus (Fig. 2M). N, UR-CP-0147 left epiplastron (Fig. 4K).

Figure S2. Comparison between the plastron size of an extant marine turtle, *Desmatochelys lowi* and UR-CP-0147. A, *Eretmochelys imbricata* MTKD-D-8295 plastron in ventral view (Senckenberg Museum of Natural History, Dresden collections, Germany) measuring 277 m. B, *Desmatochelys lowi* CNHM-PR385 epiplastra and entoplastron outline redraw from Zangerl and Sloan (1960). C, UR-CP-0147 right epiplastron in ventral view. D, reconstructed plastron size for UR-CP-0147 being almost three times larger than the size of *E. imbricata* MTKD-D-8295.

Table S1. Raw data on humerus and carapace length from previous studies for several marine Cretaceous turtles (Fig. 5)

Table S2. Raw data on humerus length and geologic occurrence for several marine Mesozoic and Cenozoic turtles used to create Figure 6.

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DATA AVAILABILITY

All available data available is given in the supporting information of this paper.

CONFLICT OF INTEREST

The authors declare that they have no conflicts of interest.

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