Valanginian occurrence of Pelomedusoides turtles in northern South America: Revision of this hypothesis based on a new fossil remain (#49823)

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Valanginian occurrence of Pelomedusoides turtles in northern South America: Revision of this hypothesis based on a new fossil remain

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Pelomedusoides constitutes the most diverse group of Mesozoic and Cenozoic side-necked turtles. However, when it originated is still being poorly known and controversial. Fossil remains from the Early Cretaceous (Valanginian) Rosablanca Formation of Colombia were described almost a decade ago as potentially belonging to Podocnemidoidea (a large subclade inside Pelomedusoides) and representing one of the earliest records of this group of turtles. Here, I revise this hypothesis based on a new fragmentary specimen from the Rosablanca Formation, represented by a right portion of the shell bridge, including the mesoplastron and most of peripherals 5 to 7. The equidimensional shape of the mesoplatron allows me to support its attribution as belonging to Pelomedusoides, group to which the previously podocnemidoid material is also attributed here. Although, the Valanginian pelomesudoid material from Colombia is still too fragmentary as to be considered the earliest undisputable record of the Pelomedusoides clade, their occurrence is at least in agreement with current molecular phylogenetic hypotheses that suggest they split from Chelidae during the Jurassic and should occur in the Late Jurassic and Early Cretaceous fossil record

Valanginian occurrence of Pelomedusoides turtles in northern South America; revision of this hypothesis based on a new fossil remain.

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Abstract

Pelomedusoides constitutes the most diverse group of Mesozoic and Cenozoic side-necked turtles. However, when it originated is still being poorly known and controversial. Fossil remains from the Early Cretaceous (Valanginian) Rosablanca Formation of Colombia were described almost a decade ago as potentially belonging to Podocnemidoidea (a large subclade inside Pelomedusoides) and representing one of the earliest records of this group of turtles. Here, I revise this hypothesis based on a new fragmentary specimen from the Rosablanca Formation, represented by a right portion of the shell bridge, including the mesoplastron and most of peripherals 5 to 7. The equidimensional shape of the mesoplatron allows me to support its attribution as belonging to Pelomedusoides, a group to which the previously podocnemidoid material is also attributed here. Although the Valanginian pelomesudoid material from Colombia is still too fragmentary as to be considered the earliest indisputable record of the Pelomedusoides clade, their occurrence is at least in agreement with current molecular phylogenetic hypotheses that suggest they split from Chelidae during the Jurassic and should occur in the Late Jurassic and Early Cretaceous fossil record.

Introduction

One of the most diverse clades of Mesozoic and Cenozoic turtles is Pelomedusoides, with fossils worldwide distributed and extant representatives restricted to southern hemisphere (Ferreira et al. 2018; Gaffney et al. 2011; Gaffney et al. 2006; Hermanson et al. 2020; Vlachos et al. 2018). Recent molecular phylogenetic hypotheses suggest that they split from Chelidae during the Late Jurassic at 161.7 Ma (149.3–168.9 Ma) (Pereira et al. 2017), and total-evidence tip-dating (TE

TD) suggest even older date for this splitting during the Early Jurassic at 172.6 Ma (Holley et al. 2019). However, at present, the earliest indisputable fossil record of Pelomedusoides is the bothremydid *Atolchelys lepida* (Romano et al. 2014), from the upper Barremian of Brazil; meaning approximately 36 Ma of ghost-lineage.

Almost a decade ago, I described some fragmentary material from the Early Cretaceous (Valanginian) Rosablanca Formation of Colombia, which I attributed as potentially belonging to Podocnemidoidea (one of the subclades inside Pelomedusoides) (Cadena 2011). This occurrence has been questioned and considered dubious by Romano et al (2014), arguing that the presence of an inguinal buttress that medially extends onto the ventral surface of costal 5 is highly variable within Pelomedusoides, even within all of Testudines. Here, I present new material from a locality nearby to the one from where the material described in 2011 came from; from the same segment of the Rosablanca Formation. This new fossil material allows me to revise the hypothesis proposed back in 2011, and present new evidence and comparisons that support the occurrence of Pelomedusoides during the Valanginian in northern South America.

Material & Methods

Fossil material. I found the fragmentary material described here in 2016. Recently I added it to the emerging Paleontological Collection of the Facultad de Ciencias Naturales from Universidad del Rosario, in Bogotá, Colombia. Its collection identification number is UR-CP-0025. I obtained permit from the Ethics committee of the Universidad del Rosario to execute this study via the DVO005 672-Cv1066 communication.

Institutional abbreviations. CRI, Chelonian Research Institute, Oviedo, Florida, USA; ICN, herpetological collection, Instituto de Ciencias Naturales, Universidad Nacional de Colombia, Bogotá, Colombia; IPN, Museo Geológico Nacional José Royo y Goméz, Bogotá, Colombia; MNHN, Muséum National d'Histoire Naturelle, Paris, France; UR-CP, paleontological collection, Facultad de Ciencias Naturales, Universidad del Rosario, Bogotá, Colombia; USNM, herpetological collection, Smithsonian Natural History Museum, Maryland, USA.

Carapace length estimation. In order to establish an estimation of the total length of the carapace to which the fossil fragment belongs, I measured two of the largest specimens of the extant *Podocnemis expansa* that I have examined in recent years, specimens ICN-6319 and USNM-29476. Using the software Image J2 (Rueden et al. 2017), I set the scale to the one provided in the photos of the specimens and measured the maximum length of both mesoplastra, peripherals 6, 7, and the total length of the carapace. I established the simple linear regression and its equation using Microsoft-Excel (Data. S1), and used it to estimate the maximum length of the carapace of UR-CP-0025.

Comparisons. For comparisons with other pan-pleurodires including several Pelomedusoides, I created a comparative figure redrawing only the right bridge region from figures or photographs of previous literature or from direct examination of specimens as follow: *Platychelys oberndorferi*, *Notoemys laticentralis*, and *Notoemys zapatocaensis* from Cadena & Joyce (2015); *Notoemys oxfordiensis* from de la Fuente & Iturralde-Vinent (2001); *Francemys gadoufaouaensis* from Pérez-García (2019); *Bonapartemys bajobarrealis* from Lapparent de Broin & de la Fuente (2001); *Mendozachelys wichmanni* from de la Fuente et al (2017); *Prochelidella cerrobarcinae* from de la Fuente et al (2011); *Euraxemys essweini* and *Cearachelys placidoi* from Gaffney et al (2006); *Araripemys barretoi* from Meylan (1996); *Dortoka vasconica* from Lapparent de Broin & Murelaga (1996); *Pelomedusa subrufa* CRI-5200, *Podocnemis expansa* USNM-29476 and *Chelus fimbriata* MNHN-2581A from personal reference photo gallery; and UR-CP-0025 from this study.

Results

Systematic Paleontology

PLEURODIRA Cope, 1864
PELOMEDUSOIDES Cope, 1868
Incertae Sedis
Fig. 1

Referred material.—UR-CP-0025, a portion of the right shell bridge including the mesoplastron, peripheral 6, portions of peripherals 5 and 7, as well as the lateral most portions of right hyoplastron and hypoplastron. From Cadena (2011): IPN 16 EAC-14012003-1A, left partial costal 5; IPN 16 EAC-14012003-1B, posterior peripheral bone.

Locality and Age.—I collected UR-CP-0025 from a locality nearby the Laguna del Sapo (6º50'34"N, -73º14'17.3"W), approximately 1.5 km southwest of the Pico de la Vieja road locality where I found the material reported in Cadena (2011) (Fig. 2A–B). The Laguna del Sapo locality is northeast of Zapatoca, Santander Department, Colombia; and it is part of the upper segment of the shallow marine Rosablanca Formation (Guzman 1985), correlated to the base of the late Valanginian (~135 Ma) based on the occurrence of the ammonite *Saynoceras verrucosum*, according to the biochronostratigraphic framework of Ogg et al (2016). I found UR-CP-0025 at the base of a calcareous yellow siltstone layer (Fig. 2C).

Remarks.—UR-CP-0025 is attributed as belonging to Pelomedusoides based on having an equidimensional mesoplastron (Fig. 3).

Description. UR-CP-0025 constitutes a portion of the right shell bridge, preserving the mesoplastron, the most posterolateral corner of the right hyoplastron, the most anterolateral portion of the right hypoplastron, peripheral 6, and portions of peripherals 5 and 7. In ventral view (Fig. 1A–B), the mesoplastron exhibits an almost equidimensional circular-shape, and it is in lateral and posterolateral contact with peripherals 5 and 6 respectively. Medially and posteromedially is in contact with the right hyoplastron and right hypoplastron respectively. The most lateral portion of peripherals 5 to 7 is missing (natural breaking). Also in this view, there is evidence of some of the sulci, particularly between marginals and of these with the abdominal scute. There is not indication that the pectoroabdominal sulcus reached the anterolateral corner of mesoplastron. In dorsal and lateral views (Fig. 1C–F), the peripheral 6 is the most complete of the three preserved, showing a rectangular shape with its most medial margin (contact with costals) missing. The sulci between marginals are poorly preserved, however there is enough evidence that they were restricted to the peripherals, without reaching the costoperipheral sutural margin. The sutural contact between peripherals shows a medial indentation (Fig. 1E–F), however this seems to be due to that the bone is naturally cut and cancellous tissue exposed. In anterior view (Fig. 1G–H), the peripheral 5 and mesoplastron contact is well defined, and the bridge angle formed between the peripherals and the plastron indicates that the shell was probably low to moderate dome-shaped. Also in this view is evident the considerable thickness of these bones. A close-up of the margin of peripheral 5 (Fig. I–J) shows a very thin external bone cortex and abundance of large pores at the cancellous bone. A large (88.17 cm, carapace length) of the extant *Podocnemis expansa* USNM-29476 is shown in Fig. 1K for comparison and anatomical location of UR-CP-0025 in a turtle shell.

Discussion

Mesoplastra of Pan-Pleurodira. The mesoplastra bones have exhibited important modifications along turtle evolution. In basal Pan-Testudines as for example *Odontochelys semitestacea* they were two separate bony plates meeting medially (Li et al. 2008). In basal Testudines as for example *Kayentachelys aprix* there was a reduction in the number of mesoplastra, being only one pair extended medially reaching the central fontanelle (Joyce 2007, fig. 11). Another transformation of mesoplastra occurred in the both major groups of turtles, with their complete lost in Cryptodires and being one pair but they do not contact one another medially in Pan-Pleurodira (Cadena & Joyce 2015; Joyce 2007). Inside Pan-Pleurodira the mesoplastra have exhibited additional transformations from the primitive condition exhibited by Platychelyidae and Cretaceous members of Pan-Chelidae (Fig. 3A–C, G–I) of being almost triangular in shape, much wider than long to the condition exhibited by almost all Pelomedusoides of having almost equidimensional mesoplastra (Fig. 3E–F, J–L, P). An equidimensional mesoplastron was considered by Gaffney et al (2006) as characteristic of a Nanorder that they defined as Eupleurodira (Cheloides = Pan-Chelidae plus Pelomedusoides). As I show in Fig. 3, the condition in pan-chelids who have mesoplastra is similar to the one exhibited by platychelids, which allow me to suggest that instead this is a characteristic of Pelomedusoides, shared by UR-CP-0025 described herein (Fig. 3E). Another transformation of mesoplastra inside Pan-

Pleurodira is their complete lost in Dortokidae, Araripemydidae, crown-Chelidae, and *Pelusios* spp. (Gaffney et al. 2006) (Fig. 3M–O).

Carapace size estimation of UR-CP-0025. Using the simple linear regression equation (y = 7.1767x - 4.266, x corresponding to maximum mesoplastron length, and y maximum carapace length) obtained from specimens of the extant *Podocnemis expansa* (Data. S1). I estimated that the length of the carapace of UR-CP-0025 was of ~34.27 cm, indicating a much larger size in contrast to the exhibited by Jurassic and Early Cretaceous platychelids, which fluctuated between 20 to 27 cm (Cadena et al. 2013, table 8.1). This suggests that the increase in shell size was a characteristic exhibited by early representatives of Pelomedusoides; a trend that continued during the Late Cretaceous (Hermanson et al. 2016) and the Cenozoic, with the giant pelomedusoids from the Paleocene of Colombia (Cadena et al. 2012a; Cadena et al. 2012b), and the Miocene *Stupendemys geographicus* from northern South America (Cadena et al. 2020).

Implications of UR-CP-0025 for Pelomedusoides history understanding. With the description of UR-CP-0025 and its attribution as belonging to Pelomedusoides (see above), I show that they inhabited northern South America during the Early Cretaceous. A hypothesis that is in agreement with recent molecular phylogenetic hypotheses that suggest they split from Chelidae during the Jurassic (Holley et al. 2019; Pereira et al. 2017), therefore their fossil record should be expected to occur in Late Jurassic and Early Cretaceous sequences (Fig. 3Q). However, it is important to point out that UR-CP-0025 and the material previously described also from Rosablanca Formation (Cadena 2011) are still too fragmentary to be recognized as the earliest indisputable record of the group, which it is not intention of this study. With this study, I once again showed that the Rosablanca Formation is still being a very productive and promising rock sequence in northern South America for future paleontological studies and the understanding of the Early Cretaceous faunas, including the evolution of Pelomedusoides turtles.

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Figure 1

UR-CP-0025 Pelomedusoides shell bridge fragment.

Figure 1. UR-CP-0025 Pelomedusoides shell bridge fragment.(**A-B**) ventral view. (**C-D**) dorsal view. (**E-F**) lateral view. (**G-H**) anterior view. (**I-J**) close-up of the margin of peripheral 5, showing the external cortex and cancellous bone. (**K**) A complete shell in ventral view of *Podoncemis expansa* USNM-29476 specimen, grey region indicates the anatomical corresponding part preserved in UR-CP-0025. Abbreviations: Ab, abdominal scute; An, anal scute; ent, entoplastron; EC, external cortex; epi, epiplastron; Ex, extragular scute; Fe, femoral scute; Gu, gular scute; Hu, humeral scute; hyo, hyoplastron; hyp, hypoplastron; M, marginal scute; mes, mesoplastron; pe, peripheral; py, pygal; xip, xiphiplastron. 10 cm scale bar applies only for K. Red lines indicate sulci, black sutures and dotted lines possible shape and location. Light gray regions represent naturally bone cuts and dark gray, rock matrix.

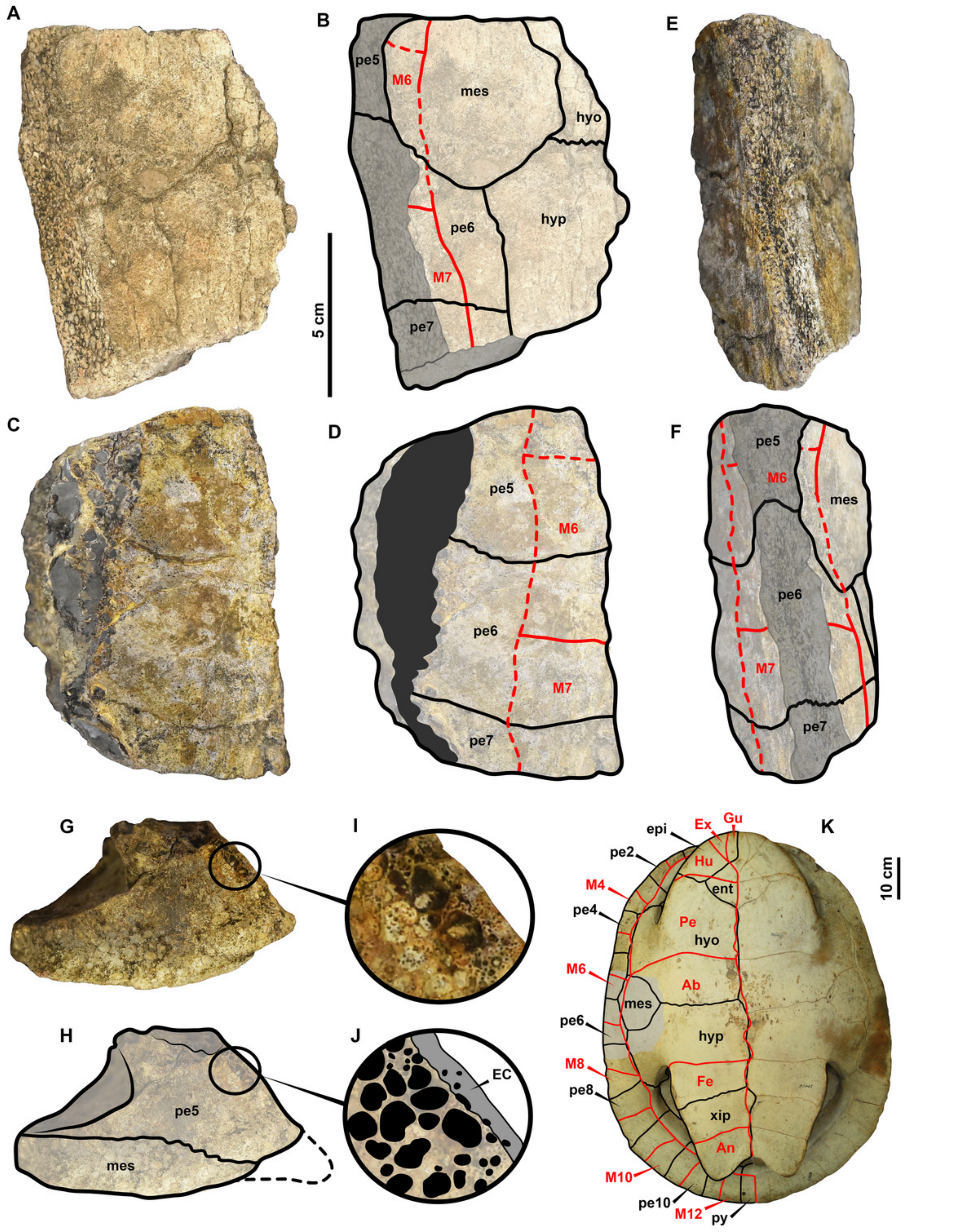
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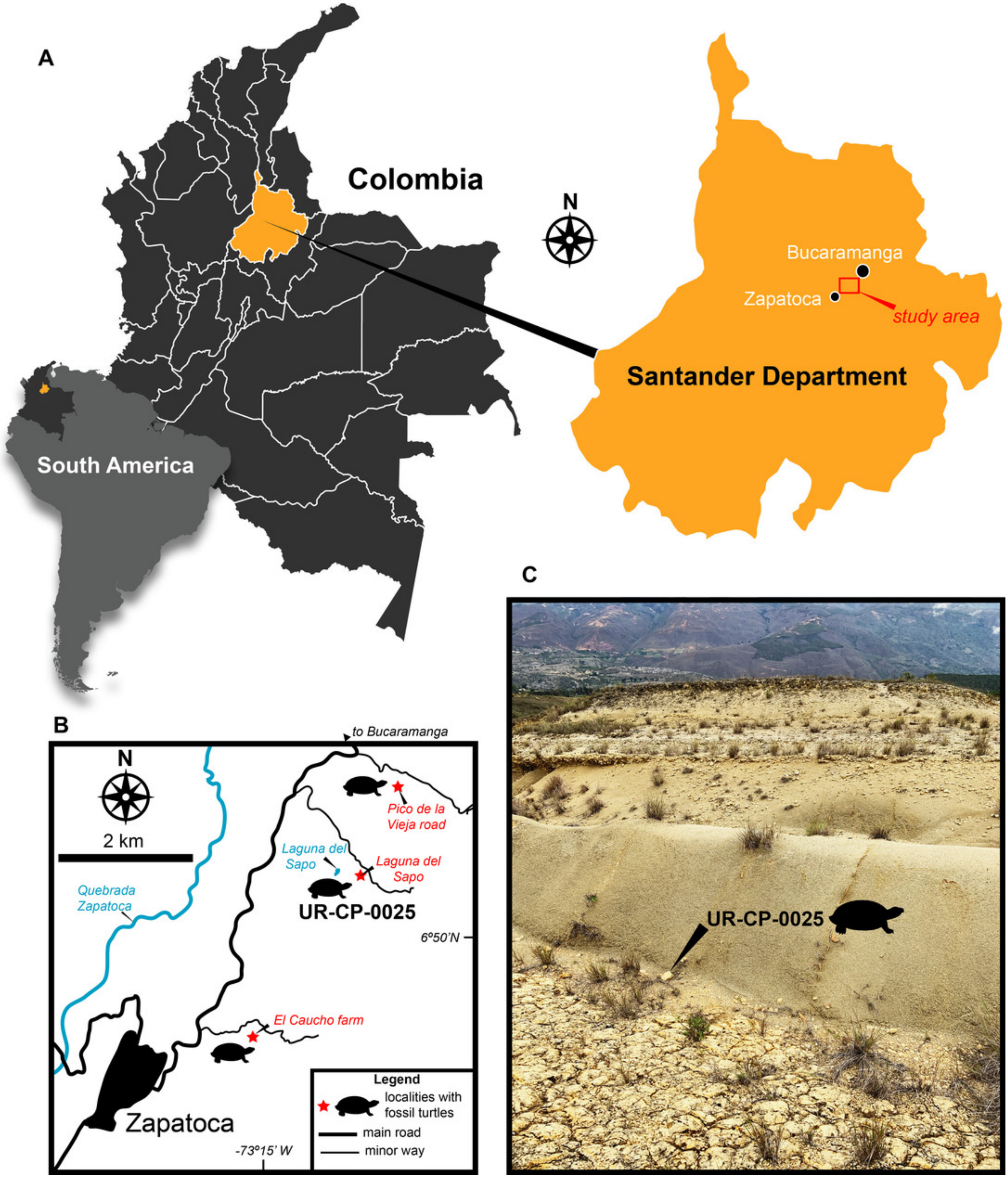
Figure 2

Geographic location of the fossil finding

Figure 2. Geographic location of the fossil finding. (**A**) Map of South America, Colombia, and Santander Department, including the study area. (**B**) Northeast region of Zapatoca showing the three localities from which fossil turtles have been collected: El Caucho Farm, type locality for *Notoemys zapatocaensis* (Cadena et al. 2013); Pico de la Vieja road, from where IPN 16 EAC-14012003-1A and IPN 16 EAC-14012003-1B (Cadena 2011) refered here to Pelomedusoides came from; and Laguna del Sapo locality from where UR-CP-0025 Pelomedusoides described here came from. (**C**) Laguna del Sapo locality outcrop showing the discovery of UR-CP-0025 at the base of a calcareous yellow siltstone layer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Laguna del Sapo
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UR-CP-0025
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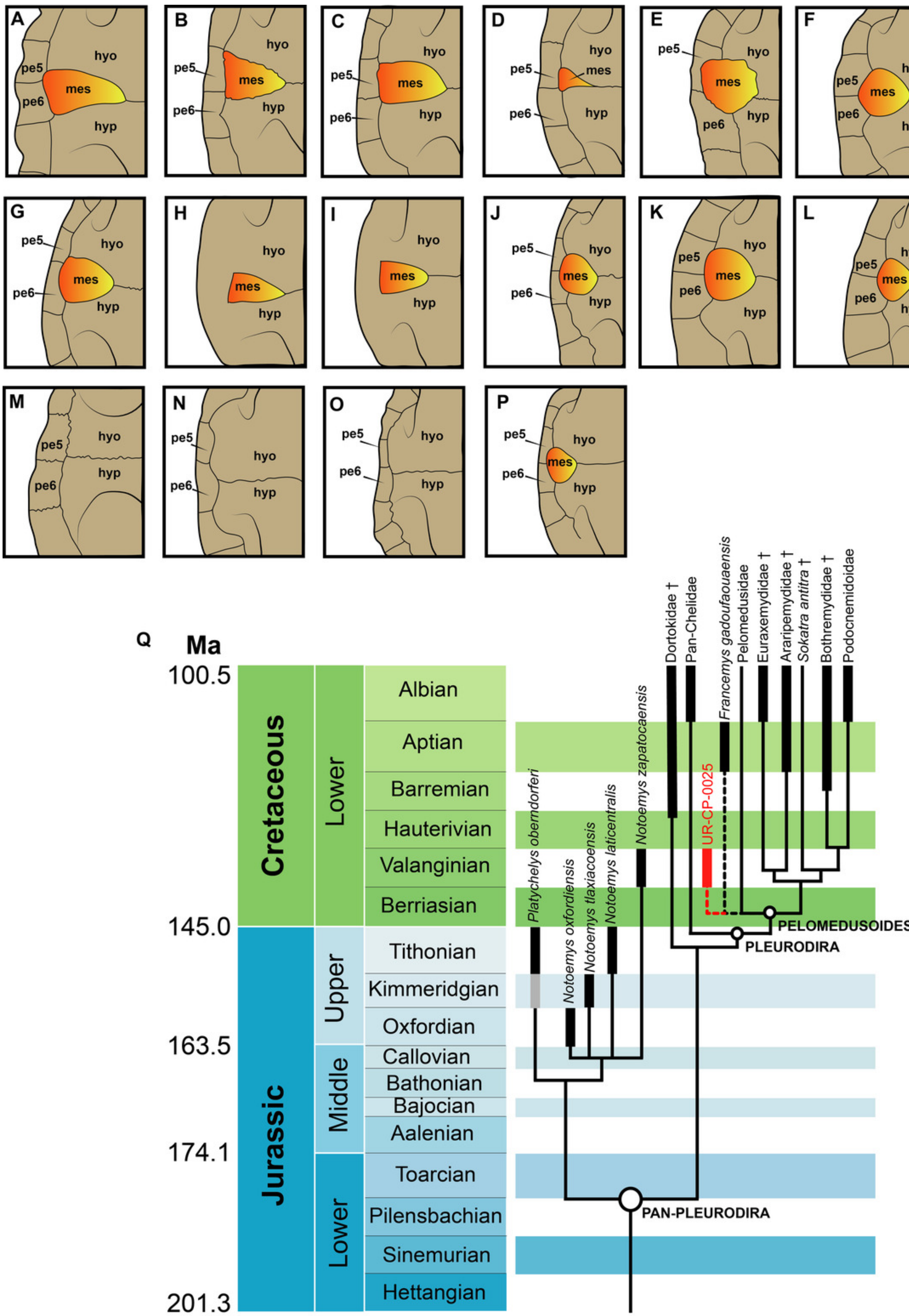
Zapatoca
-73°15' W
Legend
localities with fossil turtles
main road
minor way
C
UR-CP-0025

Figure 3

Comparisons of the right shell bridge for several pan-pleurodires and their simplified phylogeny

Figure 3. Comparisons of the right shell bridge for several pan-pleurodires and their simplified phylogeny. (**A**) *Platychelys oberndorferi*. (**B**) *Notoemys oxfordiensis*. (**C**) *Notoemys laticentralis*. (**D**) *Notoemys zapatocaensis*. (**E**) UR-CP-0025 Pelomedusoides. (**F**) *Francemys gadoufaouaensis.* (**G**) *Bonapartemys bajobarrealis*. (**H**) *Mendozachelys wichmanni*. (**I**) *Prochelidella cerrobarcinae*. (**J**) *Pelomedusa subrufa* CRI-5200. (**K**) *Euraxemys essweini*. (**L**) *Cearachelys placidoi.* (**M**) *Araripemys barretoi*. (**N**) *Dortoka vasconica*. (**O**) *Chelus fimbriata* MNHN-2581A (**P**) *Podocnemis expansa* USNM-29476. (**Q**) Simplified phylogeny of Pan-Pleurodira based on Lopéz-Conde et al (2016) and Hermanson et al (2020), with the potential position of UR-CP-0025 and *Francemys gadoufaouaensis* (Pérez-García 2019); *Atolchelys lepida* (Romano et al. 2014) included inside Bothremydidae. Abbreviations: Ma, million years; mes, mesoplastron; hyo, hyoplastron; hyp, hypoplastron; pe, peripheral. See methods for full references of the taxa illustrated here. Grayline in taxa represents referred material. Right mesoplastron highlighted in orange-yellow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Upper
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Albian
Aptian
Barremian
Hauterivian
Valanginian
Berriasian
Tithonian
Kimmeridgian
Oxfordian
Callovian
Bathonian
Bajocian
Aalenian
Toarcian
Pilensbachian
Sinemurian
Hettangian
Platychelys oberndorferi
Notoemys oxfordiensis
Notoemys tlaxiacoensis
Notoemys laticentralis
Notoemys zapatocaensis
Dortokidae †
Pan-Chelidae
UR-CP-0025
Francemys gadoufaouaensis
Pelomedusidae
Euraxemydidae †
Araripemydidae †
Sokatra antitra †
Bothremydidae †
Podocnemidoidae
PELOMEDUSOIDES
PLEURODIRA
PAN-PLEURODIRA