

## POTENTIAL EARLIEST RECORD OF PODOCNEMIDOID TURTLES, FROM THE EARLY CRETACEOUS (VALANGINIAN) OF COLOMBIA

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**ABSTRACT**—A costal and a peripheral bone from the Early Cretaceous (Valanginian, ca. 135 Ma) Rosablanca Formation, Zapatoca town, Colombia are described. These specimens represent the earliest record of podocnemidoid turtles. Evolutionary and paleogeographical implications are also discussed.

### INTRODUCTION

PODOCNEMIDOID TURTLES are formed, according to Gaffney et al., (2006), by the two most diverse groups of pleurodiires or side-necked turtles: the extinct Bothremyidae and the extant and fossil members of Podocnemididae plus *Brasilemys josai* Lapparent de Broin, (2000), and *Hamadachelys escullellae* Tong and Buffetaut, (1996). The superfamily (Podocnemidoidea) is equal in composition to Panpodocnemididae clade defined by Cadena et al., (2010) under (PhyloCode 2010; Joyce et al. 2004). Previous to this report, the oldest podocnemidoid corresponds to a specimen represented by skull and lower jaw fragments, plus carapace and some limb elements from the Morro do Chaves Formation, Early Cretaceous (Barremian) of Estado de Alagoas, Brazil, (Gallo et al., 2009). Recently, it has been proposed that Pelomedusoides (Podocnemidoidea, Pelomedusidae, Euraxemydidae, and Araripemydidae) would have derived from a northern South America ancestor (Riff et al., 2010). However, this hypothesis lacks of any Cretaceous record that support the occurrence of pelomedusoides turtles in northern South America.

Here a costal and a peripheral bone from the Early Cretaceous (Valanginian, ca. 135 Ma) Rosablanca Formation, Zapatoca town, Colombia is described, which represents potentially the earliest record of podocnemidoid turtles. Furthermore, their evolutionary and paleogeographical implications are discussed. The new podocnemidoid also represents an additional faunal component for the Rosablanca Formation, which thus far is known to include the platychelyid turtle *Notoemys zapatocaensis* (Cadena and Gaffney, 2005), as well as undescribed plesiosaurs, ichthyosaurs, crocodylomorphs, fish remains, and a diverse fauna of marine invertebrates.

**Abbreviations.**—AMNH, American Museum of Natural History, New York, U.S.A.; CRI, Chelonian Research Institute, Oviedo, Florida, U.S.A.; IPN-EAC, Museo Geológico José Royo y Gómez-Instituto Colombiano de Geología y Minería-Ingeominas, Bogotá, Colombia.

### SYSTEMATIC PALEONTOLOGY

TESTUDINES Linnaeus, 1758

PLEURODIRA Cope, 1864

PODOCNEMIDOIDEA Cope, 1868

Incertae Sedis

Figure 1.1–1.9

**Referred specimens.**—IPN 16 EAC-14012003-1A (IPN 1A), left partial costal 5 (Fig. 1.1–1.6); IPN 16 EAC-14012003-1B (IPN 1B), posterior peripheral bone (Fig. 1.7–1.9).

**Diagnosis.**—The specimens are referred to Podocnemidoidea by the presence of an inguinal buttress very extended medially on the ventral surface of costal 5.

**Occurrence.**—Upper segment of the shallow marine Rosablanca Formation (Guzman, 1985), correlated to the base of the Late Valanginian (approximately 135 Ma) based on the occurrence of the ammonite *Saynoceras verrucosum*, according to the biochronostratigraphic framework of Ogg et al. (2008).

**Type locality.**—Pico de La Vieja road, (N 6°51'39", W 73°13'31") northeast of Zapatoca town, Department of Santander, Colombia.

**Description.**—The left costal bone (IPN 1A) is complete along most of its lateral portion (9.5 cm long, 6 cm width as preserved). On the dorsal surface, it lacks a sulcus between pleural scales and on the ventral surface the inguinal buttress scar is massive, extending medially onto it, as well as ventrally projected (Character 150, Gaffney et al., 2006). The combination of these two characteristics indicates that this is the costal 5, as in other podocnemidoids. Except in the bothremyids *Foxemys mechinorum* (fig. 259 in Gaffney et al., 2006) and *Polysternon provinciale* (fig. 260 in Gaffney et al., 2006), which have an inguinal buttress medially reduced onto costal 5.

The extent of the inguinal buttress scar is a diagnostic character for turtles. The inguinal buttress scar does not extend to costal 5 but is completely restricted to the peripherals in stem testudines, most cryptodires (for instance *Caretta caretta* Fig. 1.15–1.18; *Chelydra serpentina* Fig. 1.21–1.24), and in some chelids (*Hydromedusa tectifera* Fig. 1.31–1.34). In some cryptodires and pelomedusoides the inguinal buttress extends slightly on costal 5, as is the case in *Trachemys scripta* (Fig. 1.11–1.14), *Pelomedusa subrufa* (Fig. 1.35–1.38), and in platychelyids. In most chelids the inguinal buttress scar is located between costal 5 and 6 as seen in *Platemys platycephala* (Fig. 1.27–1.30). Restriction of the inguinal buttress scar to costal 4 is exclusive to *Chelus* spp. (Cadena et al., 2008). As mentioned above most podocnemidoids are characterized by a narrow inguinal buttress scar that extends medially onto costal 5, as depicted for *Podocnemis vogli* (Fig. 1.19, 1.20) and *Podocnemis unifilis* (Fig. 1.25, 1.26).

The nearly complete peripheral bone (IPN 1B: 7 cm long, 4.2 cm width as preserved) is probably left peripheral 9. The dorsal surface is smooth, with visible sulcus between the marginals, as well as the sulcus between the marginals and the pleural on the most medial portion of the bone. In anterotransversal view (Fig. 1.9), the peripheral has a low angle dorsal projection, indicating a low dome carapace, at least posteriorly, which is the most typical condition in podocnemidoids and other freshwater and marine turtles.

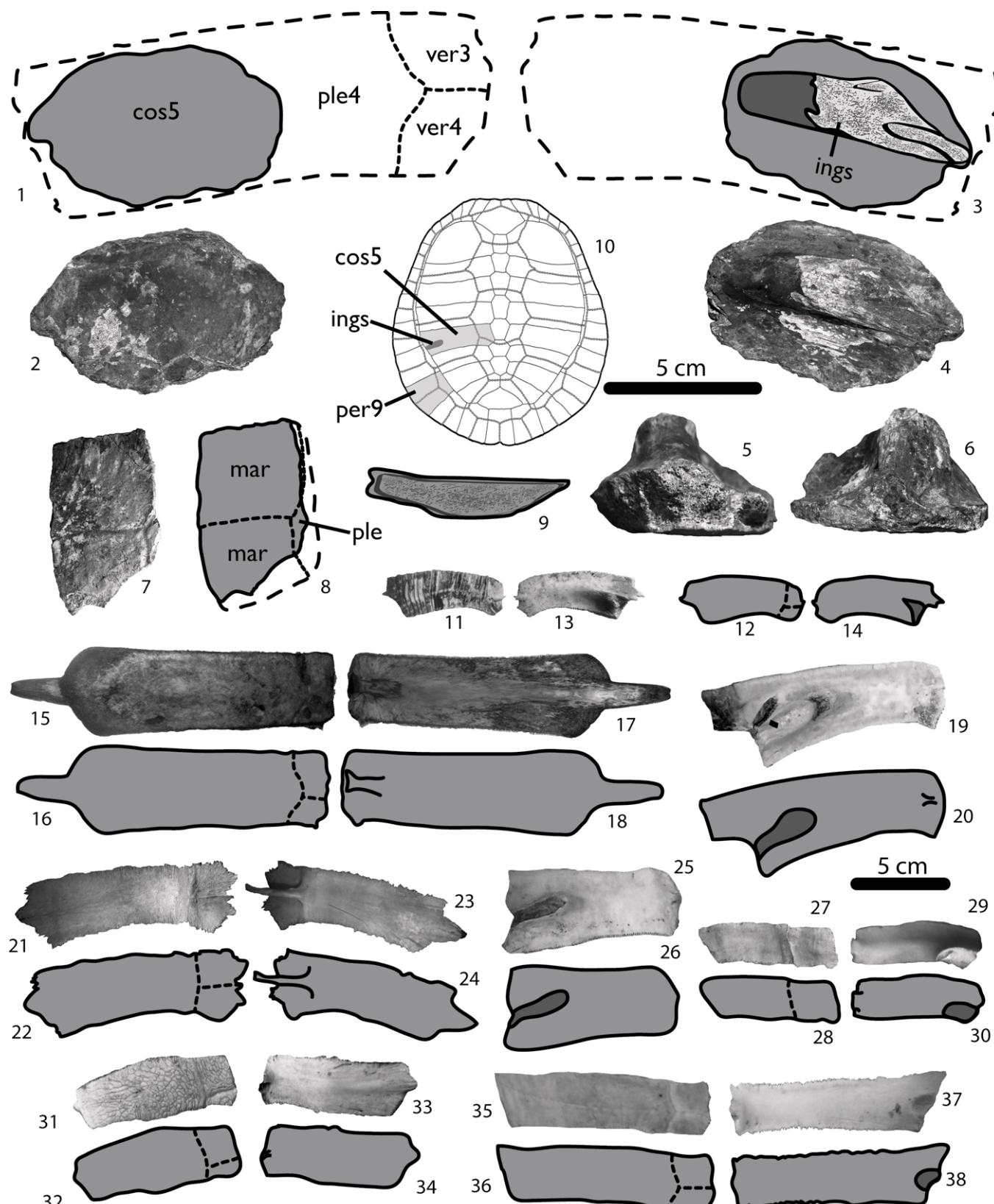


FIGURE 1—Left costal 5 and left peripheral 29 of the new podocnemidoid from the Valanginian of Colombia described here, with the same elements in different species of turtles for comparison. IPN 16 EAC-14012003-1A, left costal 5: 1, 2, dorsal view; 3, 4, ventral view; 5, medial view; 6, lateral view; IPN 16 EAC-14012003-1B, left peripheral 29: 7, 8, dorsal view; 9, anterotransversal view; 10, *Podocnemis sextuberculata* carapace outline in dorsal view, modified from Joyce (2007, fig. 8f); the correspondence with the costal 5 and peripheral 29 from Zapotoca is shown in light gray, and the inguinal scar in dark gray; left (otherwise indicated) costal 5 of different species of extant turtles; *Trachemys scripta*: 11, 12, dorsal view; 13, 14, ventral view; *Caretta caretta*: 15, 16, dorsal view; 17, 18, ventral view; *Podocnemis unifilis*: 19, 20, right costal 5, ventral view; *Chelydra serpentine*: 21, 22, dorsal view; 23, 24, ventral view; *Podocnemis vogli*: 25, 26, right costal 5, ventral view; *Platemydas platycephala*: 27, 28, dorsal view; 29, 30, ventral view; *Hydromedusa testicifera*: 31, 32, dorsal view; 33, 34, ventral view; *Pelomedusa subrufa*: 35, 36, dorsal view; 37, 38, ventral view. Upper scale bar applies for figures 1–9, and the lower for figures 11–38. Abbreviations: cos=costal; ings=inguinal buttress scar; mar=marginal scale; per=peripheral; ple=pleural scale.

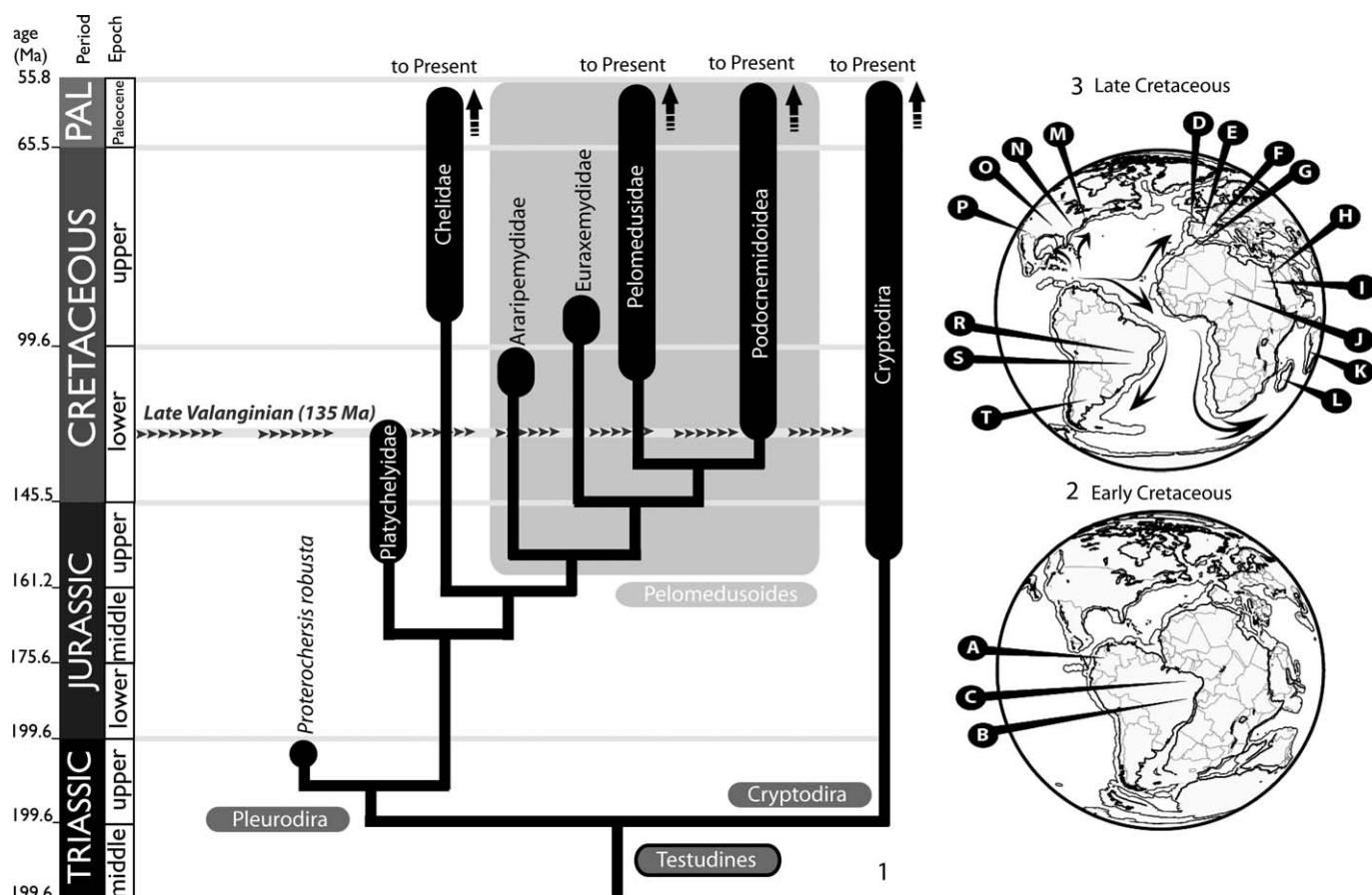


FIGURE 2—1. Splitting events through time for the major clades of Testudines, based on Gaffney and Jenkins (2010) considering *Proterochersis robusta* as the most basal representative of Pleurodira; 2–3, dispersal pathways and paleobiogeographical distribution of podocnemidoids plotted on paleoreconstruction templates downloaded from the Paleobiology Database on 19 June, 2010: 2, Early Cretaceous: A, Podocnemidoid incertae sedis, Valanginian, Colombia (this study); B, Podocnemidoid, Barremian, Brazil (Gallo et al., 2009); C, *Brasilemys josai* Lapparent de Broin (2000) Albian, Brazil, *Cearachelys placidoi* Gaffney et al. (2001a) Albian, Brazil; 3, Late Cretaceous: D, *Rosasia soutoi* Carrington da Costa (1940) Late Campanian-Maastrichtian, Portugal; E, cf. *Elochelys* Perez et al. (2009) Late Campanian-Early Maastrichtian, Spain; F, *Foxemys mechinorum* Tong et al. (1998) Late Campanian-Early Maastrichtian, France, *Polysternon provinciale* Matheron (1869) Campanian, France, *Elochelys convenarum* Laurent et al. (2002) Late Maastrichtian, France; G, *Galianemys emringeri* and *G. whitei* Gaffney et al. (2002) Cenomanian, Morocco; H, *Bothremys arabicus* Gaffney et al. (2006) Santonian, Jordan; I, *Zolhafah bella* Lapparent de Broin and Werner (1998) Maastrichtian, Egypt, *Arenila krebsi* Lapparent de Broin and Werner (1998) Maastrichtian, Egypt; J, *Nigeremys gigantean* Bergounioux and Crouzel (1968) Maastrichtian, Niger; K, *Kurmademys kallamedensis* Gaffney et al. (2001b), Maastrichtian, India; *Sankuchemys sethnae* Gaffney et al. (2003) Maastrichtian, India; Podocnemididae indet and Bothremydidae indet. Lapparent de Broin et al. (2009) Maastrichtian, India, *Shweboemys pisidurensis* Jain (1986), Maastrichtian, India; L, cf. *Erymnochelys* Gaffney and Forster (2003) Maastrichtian, Madagascar, Bothremydidae gen. et sp. indet, Gaffney and Forster (2003) Maastrichtian, Madagascar, *Kinkonychelys rogersi* Gaffney et al. (2009b) Maastrichtian, Madagascar; M, *Bothremys cooki* Leidy (1856) Maastrichtian, New Jersey, U.S.A.; N, Bothremydina indeterminate Gaffney et al. (2009) Campanian, North Carolina, U.S.A., *Bothremys* sp. Gaffney et al. (2009) Campanian, North Carolina, U.S.A., *Chedighaii* sp. Gaffney et al. (2009) Campanian, North Carolina, U.S.A.; O, *Chedighaii barbari* Schmidt (1940) Campanian, Arkansas, U.S.A.; P, *Chedighaii hutchisoni* Gaffney et al. (2006) Late Campanian, New Mexico, U.S.A.; R, *Cambaremys langertoni* França and Langer (2005) Maastrichtian, Brazil; S, *Bauremys elegans* Suarez (1969), *Bauruemys brasiliensis* Staesche (1937), *Roxochelys harrisi* Pacheco (1913) Turonian-Maastrichtian, Brazil; T, *Portezueloemys patagonica* De La Fuente (2003) Late Turonian-Early Coniacian, Argentina. Light gray represents continental platform, black arrows potential pathways for dispersal.

**Discussion.**—Despite the fact that both shell elements described here might not correspond to a single individual since they were found horizontally separated by at least 100 m, both share a large size indicating that they represent elements of shell(s) between 40–60 cm midline length based on comparisons with the relative size of extant shells of podocnemidids (*Podocnemis expansa* AMNH 62947, *Erymnochelys madagascariensis* AMNH 2518, *Peltocephalus dumeriliana* CRI 7524). The thickness of both elements (1.4 cm average) also indicates a very ossified shell, in contrast to the thin shell of *Notoemys* spp. Thick shells are a very common characteristic of adult podocnemidoids particularly in Late Cretaceous (Gaffney et al., 2009a) and Paleocene (Cadena et al., 2010).

The new podocnemidoid from the Valanginian of Colombia is potentially the earliest record for the superfamily, indicating

that the divergence event between Pelomedusidae and Podocnemidoidea (Fig. 2.1) occurred at least 25 million years earlier than previous molecular clocks had hypothesized (Vargas-Ramirez et al., 2008, fig. 4). Furthermore, the occurrence of *Notoemys zapatoensis* and podocnemidoids (IPN 1A, IPN 1B) at the upper segment of the shallow-marine Rosalblanca Formation indicates that both clades shared similar environments. A preference for marine-brackish environments is also expressed in the similar body plans, such as the low dome shells characteristic of capable swimmers. The specimens described here further imply that late Early Cretaceous to Paleogene dispersal events in podocnemidoid turtles would have proceeded from the tropical Proto-Caribbean sea outwards towards the north, east, and southeast, simultaneous with the opening of the Atlantic

Ocean and the subsequent separation between South America and Africa, as well as the opening of the Caribbean sea between North America and South America (Fig. 2.2–2.4); thus supporting the hypothesis proposed by Riff et al. (2010) and Romano et al. (in press) that pelomedusoids, including podocnemidoids, had a northern South American ancestor.

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