

A new fossil turtle ends the controversy on the occurrence of the extant genus *Podocnemis* Wagler, 1830 at the Miocene fauna of La Venta, Colombia

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A new fossil turtle ends the controversy on the occurrence of the extant genus *Podocnemis* Wagler, 1830 at the Miocene fauna of La Venta, Colombia

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ABSTRACT

The estimate divergence time for extant taxa based on molecules usually exceed the age of their oldest fossil evidence; a situation that turtles do not escape. An extant genus with this situation, and thus having a controversial oldest record is *Podocnemis* Wagler, 1830. Here we present a new fossil turtle that constitutes a new species for this genus and represents its oldest so far known record, from the Miocene (Serravallian) of La Tatacoa Desert, Colombia. The new taxon named *Podocnemis tatacoensis* n. sp. shares with all extant members of *Podocnemis* a nuchal bone wider than long; lateral musk foramina at the hyoplastron-peripherals (except *P. sextuberculata* Cornalia, 1849), pectoral scales do not contact mesoplastra, but do contact entoplastron and epiplastra. We explored the phylogenetic position of *P. tatacoensis* n. sp. finding support for its inclusion as part of *Podocnemis* clade, particularly in a clade composed by the extant *P. unifilis* Troschel, 1848, suggesting a potential closer relationship of the new fossil taxon with this taxon.

RÉSUMÉ

Une nouvelle tortue fossile met fin à la controverse sur l'occurrence du genre *Podocnemis* Wagler, 1830 existant dans la faune miocène de La Venta, en Colombie.

L'âge de divergence estimé pour les taxons, fondé sur l'étude moléculaire des taxons actuels, dépasse généralement celui de l'occurrence des plus anciens taxons fossiles connus; une situation qui n'échappent pas aux tortues. *Podocnemis* Wagler, 1830 est un genre actuel présentant ce type de situation et l'âge de sa plus ancienne occurrence est controversé. Nous présentons ici une nouvelle tortue fossile qui constitue une nouvelle espèce pour ce genre et représente son plus ancien enregistrement connu à ce jour, du Miocène (Serravallian) du désert de La Tatacoa, en Colombie. Le nouveau taxon, nommé *Podocnemis tatacoensis* n. sp., partage avec tous les membres de *Podocnemis* un os nuchal plus large que long; forams musqués latéraux au niveau des périphériques de l'hyoplastron (sauf *P. sextuberculata* Cornalia, 1849), les écailles pectorales n'entrent pas en contact avec le mésoplastré, mais entrent en contact avec l'entoplastron et l'épiplastré. Nous avons exploré la position phylogénétique de *P. tatacoensis* n. sp. et trouvé une hypothèse supportant sa position dans le clade de *Podocnemis*, en particulier dans un clade composé de l'espèce actuelle *P. unifilis* Troschel, 1848, ce qui suggère une relation de parent plus étroite ente les deux taxons.

KEY WORDS

Podocnemididae,
Podocnemis,
Colombia,
Neogene,
Turtles,
new species.

MOTS CLÉS

Podocnemididae,
Podocnemis,
Colombie,
Néogène,
Tortues,
espèce nouvelle.

RESUMEN

Una nueva tortuga fósil pone fin a la controversia sobre la presencia del género actual Podocnemis Wagler, 1830 en la fauna miocena de La Venta, Colombia.

El tiempo de divergencia estimado para especies actuales basado en datos moléculares generalmente excede la edad de su evidencia fósil más antigua; una situación de la que las tortugas no escapan. Un género existente con esta situación y, por lo tanto, con un registro más antiguo controvertido es *Podocnemis* Wagler, 1830. Aquí presentamos un nuevo fósil de tortuga que constituye una nueva especie para este género, y que representa su registro más antiguo hasta ahora conocido, del Mioceno (Serravalliense) del desierto de La Tatacoa, Colombia. El nuevo taxón llamado *Podocnemis tatacoensis* n. sp. comparte con todos los miembros existentes de *Podocnemis* un hueso nuchal más ancho que largo; forámenes laterales de almizcle en el hioplastrón-periféricos (excepto *P. sextuberculata* Cornalia, 1849), los escudos pectorales no hacen contacto con el mesoplastrón, pero sí con el entoplastrón y el epiplastrón. Exploramos la posición filogenética de *P. tatacoensis* n. sp. encontrando apoyo para su inclusión como parte del clado *Podocnemis*, particularmente en un clado compuesto por el actual *P. unifilis* Troschel, 1848, lo que sugiere una posible relación más cercana del nuevo taxón fósil con este.

PALABRAS CLAVE

Podocnemididae,
Podocnemis,
Colombia,
Neógeno,
Tortugas,
nuevas especies.

INTRODUCTION

The lifespan of extant lower taxonomic groups (genera and species) in geological time (millions of years) is relevant for understanding the dynamics of evolution, origin of current biodiversity, and strengthening conservation plans of threatened species (Joyce *et al.* 2013). An example of an extant genus for which the lifespan is still controversial and requires a better understanding of its evolutionary history is the turtle genus *Podocnemis* Wagler, 1830 (Wagler 1830). Currently this genus is represented by six species (*P. erythrocephala* Spix, 1824, *P. expansa* (Schweigger, 1812), *P. lewyana* Duméril, 1852, *P. sextuberculata* Cornalia, 1849, *P. unifilis* Troschel, 1848, and *P. vogli* Müller, 1935) restricted to northern South America (Turtle Taxonomy Working Group 2021), one of them (*P. lewyana*) is critically endangered (Páez *et al.* 2016).

Molecular clocks suggest that *Podocnemis* originated during the late Eocene (c. 36.86 Ma) (Vargas-Ramírez *et al.* 2008, Pereira *et al.* 2017). Although several fossils have been attributed to this genus over the course of the last century, most of these attributions have lacked undisputable diagnostic features or are considered invalid (dubious or *taxa nomina dubia*) following Gaffney *et al.* (2011). At present, the oldest undisputable record of *Podocnemis* is represented by only a skull attributed to *P. bassleri* from the Late Miocene, Río Aguaytia region of Peru, which is nearly indistinguishable from *P. expansa* (Williams 1956; Gaffney *et al.* 2011). In the most recent diagnosis given for *Podocnemis* (Gaffney *et al.* 2011: 28), includes the following diagnostic shell features: “nuchal bone width greater than length; seven neurals extending to costal eight; axillary musk duct absent from buttress (except in *P. erythrocephala*), axillary buttress reaching second peripheral (except in *P. vogli*), pectoral scales do not contact mesoplastra, but do contact entoplastron and epiplastra”. Some of these characteristics are revised in this work, based on the examination of a large population of extant specimens.

The well-known Miocene fossiliferous region of La Tatacoa Desert (La Venta Fauna) in south central Colombia (Kay *et al.* 1997), has yielded an abundant record of fossil turtles, including both pleurodires (side-necked) and cryptodires (hidden-necked)

turtles. The pleurodires of La Venta are represented by the chelids *Chelus colombianus* (Wood 1976; Ferreira *et al.* 2016), and the recently described *Mesoclemmys vanegasorum* (Cadena *et al.* 2020a); the podocnemidids include *Stupendemys geographica* (Cadena *et al.* 2020b; Cadena *et al.* 2021) and *Podocnemis pritchardi* Wood, 1997. Another taxon attributed to *Podocnemis* by Wood (1997) is *P. medemi* Wood, 1997, from Carmen de Apicalá, a town located c. 150 km north of the La Tatacoa Desert (Wood 1997). *Podocnemis pritchardi* and *Podocnemis medemi* were both determined to be dubious taxa only referable to Podocnemididae incertae sedis by Gaffney *et al.* (2011) due to the absence of undisputable diagnostic shell characters that can separate the extant genus *Podocnemis* from other podocnemidids, suggesting to consider them as “*Podocnemis*” *pritchardi* and “*Podocnemis*” *medemi*. A third podocnemidid specimen from La Venta, represented by a single partial skull, was also attributed by Wood (1997) to *Podocnemis*, as *Podocnemis* cf. *P. expansa* (specimen IGM-182911). However, since its publication, this specimen has gone missing from the collections of the Museo Geológico Nacional José Royo y Gómez (IGM, Bogotá, Colombia), or the University of California Museum of Paleontology (UCMP, Berkeley, United States) where most of the La Venta fossil turtles collected by the Duke University expedition are housed. The photos of the specimen presented in Wood (1997) indicate that the regions of the skull that document diagnostic characters are missing, in particular the size of a small postorbital that allows a jugal-parietal contact, an unusually large jugal, and the presence of an interorbital groove (Gaffney *et al.* 2011). The occurrence of *Podocnemis* in the Miocene of northern South America is, therefore, still controversial and open for discussion.

Here we describe a recently discovered fossil turtle shell that exhibits strong evidence for the occurrence of the *Podocnemis* genus in the La Venta fauna during the Middle Miocene. We compare it to extant and some relevant fossil podocnemidids and discuss the importance of this fossil for a better understanding of *Podocnemis* evolution. Furthermore, we discuss the validity of previously considered dubious taxa from the Neogene of South America as representatives of *Podocnemis* genus. As the new shell shows a number of apomorphic characteristics, we refer it to a new species of fossil turtles, *Podocnemis tatacoensis* n. sp.

MATERIAL AND METHODS

The fossil that we describe herein belongs to the palaeontological collection of the Museo de Historia Natural La Tatacoa (VPPLT), located at the small village of La Victoria, Villavieja town, Huila Department, Colombia. Almost all shell bones (carapace and plastron) were found disarticulated and carefully assembled in the lab. Some of the missing parts of the carapace and plastron were reconstructed using epoxy resin and artificially painted to match the colours of their surrounded original bones. We photographed, described and compared the articulated shell (VPPLT-1727) with as many specimens as possible for each of the three extant genera of podocnemidids, including *Podocnemis* spp., *Peltocephalus dumerilianus* and *Erymnochelys madagascariensis* based on EAC personal observations at different collections and museums around the world. Also, we compared VPPLT-1727 specimen with select fossil taxa, including “*Podocnemis*” *pritchardi* (here reattributed to the genus) based on high-resolution photos of the specimen and “*Podocnemis*” *medemi* (here reattributed to the genus) based on the photos provided in Wood (1997).

To explore the phylogenetic relationships of the fossil, we added and coded it into the matrix of Cadena *et al.* (2021), as well as *Podocnemis pritchardi*, *Podocnemis medemi*, and *Podocnemis negrii*. We added one character (Character 269; PLA, hyoplastra, number of lateral musk ducts in each hyoplastron-peripherals contact: 0 = none; 1 = 1; 2 = 2; 3 = 3; 4 = 4 or more). The new character-taxon matrix is composed of 108 taxa and 269 characters (Supplementary Data S1, Appendix 1). We performed the phylogenetic analyses in TNT 1.5 (Goloboff & Catalano 2016) to establish the position of *P. tatacoensis* n. sp. inside Pan-Pleurodira, using *Proganochelys quenstedtii* as the outgroup taxon. For the first analysis we included all taxa and characters. In the second analysis we excluded all the fossils of *Podocnemis* (except *P. tatacoensis* n. sp.) to explore its close proximity among extant taxa., and for the third analysis with combine morphological plus molecular data taken from Thomson *et al.* (2021) (Supplementary Data S2, Appendix 2), for a total of 13938 characters. We used the following settings for the analyses: traditional search, 20 trees to save per replication, and other parameters by default; memory tree increased to max. trees 10 000; collapse of zero-length branches according to rule 1; light implied weighting *k* value of 12; and 1000 replicates of random addition sequences. All characters were equally weighted and some were treated as ordered (characters 1, 10, 14, 18, 19, 51, 52, 56, 57, 75, 78, 81, 82, 86, 88, 95, 96, 99, 101, 103, 112, 114, 115, 119, 128, 130, 171, 172, 174, 175, 182, 183, 193, 195, 202, 220, 224, 225, 231 and 242, from Joyce *et al.* [2021a], and Cadena *et al.* [2021]); and characters 221, 222, and 269 from this study, because they represent morphoclines and are informative for resolving interrelationships within *Podocnemis*. A strict consensus tree was generated for each of the three analyses and statistics obtained included Consistency (CI) and Retention (RI) indexes and Bremer support, calculated using implemented scripts in TNT.

INSTITUTIONAL ABBREVIATIONS

AMNH	American Museum of Natural History, New York;
CRI	Chelonian Research Institute, Ojai, California (previously located in Oviedo, Florida);
ICN	Instituto de Ciencias Naturales, Universidad Nacional de Colombia, Bogotá;
MNHN	Muséum national d'Histoire naturelle, Paris;
NHMW	Naturhistorisches Museum Wien, Vienna;
USNM	herpetological collection, Smithsonian Natural History Museum, Maryland;
UF	University of Florida, Herpetological Collection, Gainesville, Florida;
VPPLT	Museo de Historia Natural La Tatacoa, La Victoria, Huila Department, Colombia.

SYSTEMATIC PALAEONTOLOGY

TESTUDINES Batsch, 1788
(Joyce *et al.* 2020b)

PLEURODIRA Cope, 1865
(Joyce *et al.* 2020a)

PODOCNEMIDIDAE Cope, 1868
(Joyce *et al.* 2021b)

PODOCNEMIDINAE Zangerl, 1947
(Joyce *et al.* 2021b)

Podocnemis Wagler, 1830

Podocnemis tatacoensis n. sp.
(Figs 1; 3)

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HOLOTYPE. — Specimen VPPLT-1727, nearly complete shell missing: left peripheral 1; the most anteromedial portion of nuchal; left costal 4; portions of left costals 2, 3, and 5; right costal 2, portions of right costal 5, peripherals 8, 9, and 10; portions of peripherals 9-11; portion of the left epiplastron, and the most anteromedial region of hyoplastron.

DIAGNOSIS. — *Podocnemis tatacoensis* n. sp., differs from all other extant species of *Podocnemis* by having eight neurals, of which neural 8 interrupts the medial contact between costals 7 and the most anteromedial portion of costals 8. It shares with *P. unifilis*, *P. vogli* and *P. erythrocephala* three lateral musk ducts in each hyoplastron-peripherals contact. It shares with *P. unifilis*, *P. sex-tuberculata* and *P. negrii* keeled neurals. It shares with all extant *Podocnemis* spp. a nuchal bone being much wider than long. It shares with all extant and many fossil pelomedusoids (except *P. pritchardi*) a nearly rounded mesoplatra. It shares with all extant podocnemidids (*Podocnemis* spp., *Erymnochelys madagascariensis* and *Peltocephalus dumerilianus*) at least one musk foramen located at the most anterior tip of the sutural contact between hyoplastron and peripherals (axillary buttress region).

TYPE LOCALITY. — La Repartidora locality (3°19'40.98"N, 75°5'58.63"W), La Tatacoa Desert, Huila Department, Colombia.

ETYMOLOGY. — ‘*tatacoensis*’, from the Tatacoa Desert.

STRATIGRAPHY, OCCURRENCE AND AGE. — Southeast from the Centro Poblado La Victoria, La Repartidora locality (3°19'40.98"N, 75°5'58.63"W), La Tatacoa Desert, Huila Department, Colombia. Lower segment of La Victoria Formation (Guerrero 1997), Middle Miocene (Serravallian) 13.778 ± 0.081 Ma (Flynn *et al.* 1997). San Alfonso Beds (Montes *et al.* 2021) (Fig. 2A).

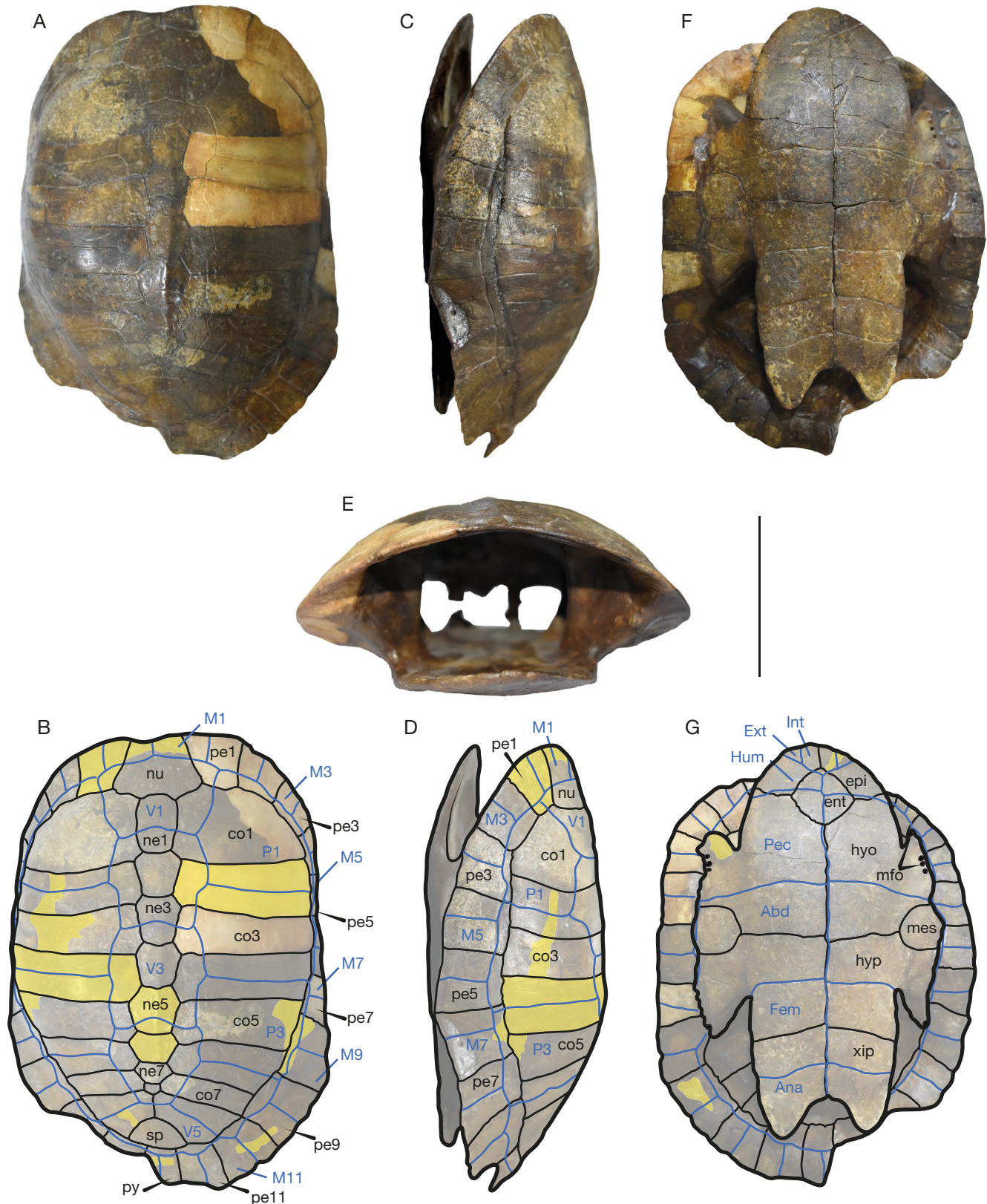


FIG. 1. — *Podocnemis tatacoensis* n. sp. from the Middle Miocene (Serravalian), La Tatacoa Desert, Colombia: **A**, **B**, carapace in dorsal view; **C**, **D**, shell in left lateral view; **D**, shell in anterior view; **F**, **G**, plastron in ventral view. Abbreviations: **Abd**, abdominal scute; **Ana**, anal scute; **co**, costal; **ent**, entoplastron; **epi**, epiplastron; **Ext**, extragular scute; **Fem**, femoral scute; **Hum**, humeral scute; **hyo**, hyoplastron; **hyp**, hypoplastron; **Int**, intergular scute; **M**, marginal scute; **mes**, mesoplastron; **mfo**, musk foramina; **ne**, neural; **nu**, nuchal; **P**, pleural scute; **pe**, peripheral; **Pec**, pectoral scute; **sp**, suprapygal; **py**, pygal; **V**, vertebral scute; **xip**, xiphiplastron. Reconstructed bones showed in yellow shading. Scale bar: 10 cm.

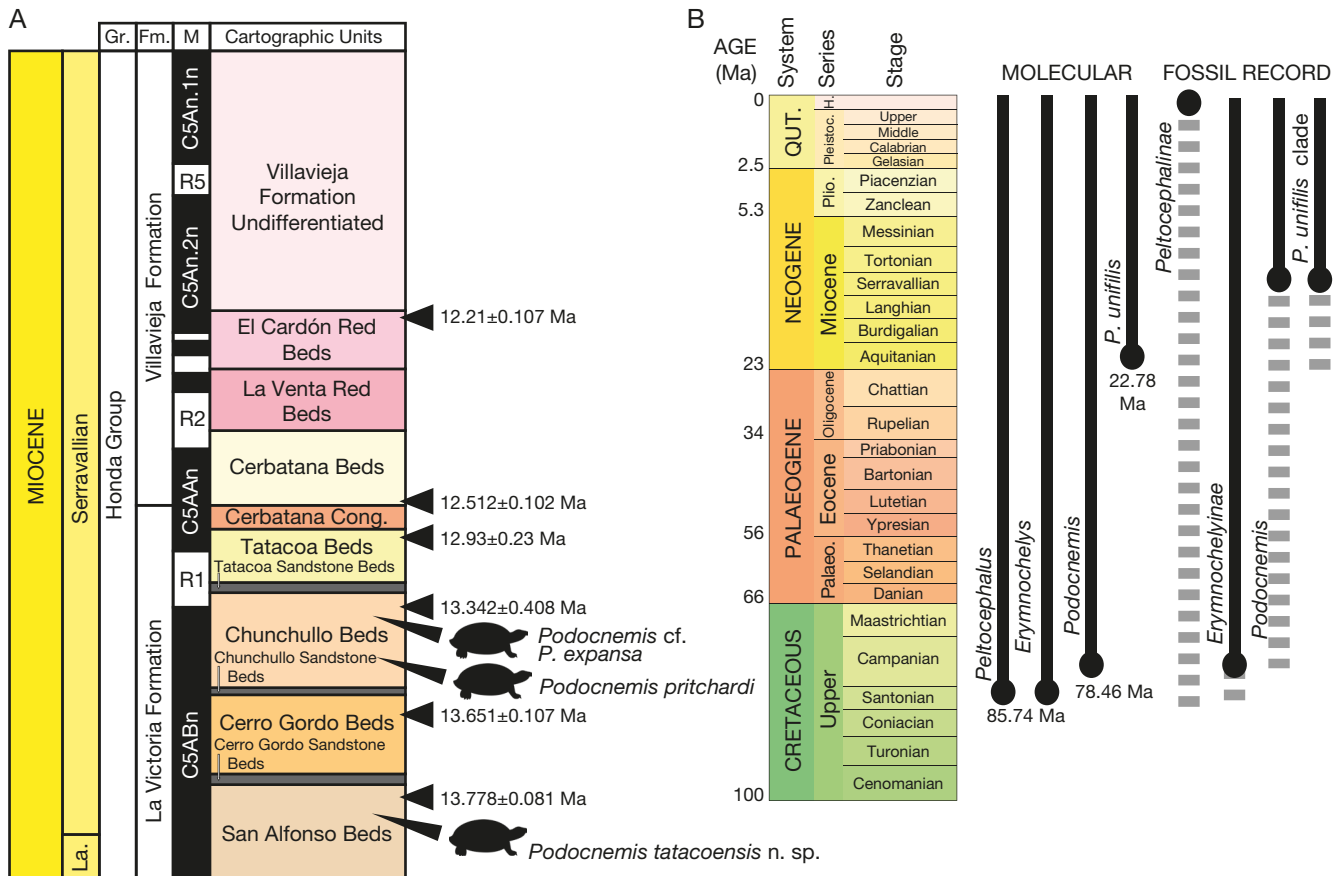


FIG. 2. — Stratigraphic context and temporal frame for *Podocnemididae*: **A**, chronostratigraphic context for the Honda Group (La Victoria and Villavieja formations), including the magnetostratigraphy, cartographic units, horizons and radiometric ages, as well as where the fossil podocnemidids occur including *Podocnemis tatacoensis* n. sp. Redrawn and modified from Montes *et al.* (2021); **B**, time of origination for the genera and some species of *Podocnemididae* based on the molecular hypothesis of Vargas-Ramírez *et al.* (2008) and fossil record (this study) for the clades that they represent. Abbreviations: **Fm**, formation; **Gr**, group; **H**, Holocene; **L**, Langhian; **M**, magnetostratigraphic chrons; **Ma**, million of years; **Pleistoc.**, Pleistocene; **Quat.**, Quaternary. Dotted lines indicate ghost lineage duration.

DESCRIPTION AND COMPARISONS

Carapace

The carapace of *Podocnemis tatacoensis* n. sp. (Fig. 1A, B) is elongated (23.2 cm maximum length) with anterior (16.5 cm) and posterior (17.5 cm) regions exhibiting almost similar width. This aspect shows wide variation among podocnemidids, but it is very common that the carapace of *P. expansa*, *P. lewyana* and *P. sextuberculata* are wider in the posterior region, a condition maintained during their ontogeny. A similar shape is exhibited by the fossil *Podocnemis pritchardi* (here reattributed to the genus), but is unknown for *P. medemi* (here reattributed to the genus) and *P. negrii* (Carvalho *et al.* 2002, here reattributed to the genus) due to preservation. The bone surface of *P. tatacoensis* n. sp. is smooth as in almost all other extant and fossil podocnemidids. The carapace exhibits a low domed shape in lateral and anterior views (Fig. 1C-E).

The nuchal bone of *P. tatacoensis* n. sp. is trapezoidal in shape, being much wider than long. This was considered to be a diagnostic feature of *Podocnemis* by Gaffney *et al.* (2011). The neural series is composed of eight bones. This contrasts all extant *Podocnemis* and the fossil *P. negrii*, which exhibit seven neurals. Some specimens of

P. sextuberculata and *P. lewyana* exhibit six neurals, similar to the fossil *P. pritchardi*, as well as the extant podocnemidid *Erymnochelys madagascariensis*. The neural series number is unknown for *P. medemi* due to preservation. In the extant podocnemidid *Peltocephalus dumerilianus* the number of neurals can be either eight or seven. Neural 8 of *P. tatacoensis* n. sp. hinder a medial contact between costals 7 and the most anteromedial portion of costals 8, but does not reach the suprapygal, as can be the case of other turtles with eight neurals as for example the bothremydid *Cearachelys placidoi* (Gaffney *et al.* 2006). Neurals 2-4 are moderately keeled dorsally (Fig. 3A, B) as in *P. sextuberculata*, *P. negrii* and some *P. unifilis*. *Podocnemis tatacoensis* n. sp. has eight pairs of costals, eleven pairs of peripherals, a suprapygal and a pygal bone, as in all other extant and fossil podocnemidids specifically and most pelomedusoids in general. Costal 1 exhibits a strong axillary scar on the ventral surface that occupies most of the central portion of the bone and projects onto peripherals 2 and 3 (Fig. 3C, D). The left posterior margin of the carapace of *P. tatacoensis* n. sp. shows a pathology affecting peripherals 10, 11 and pygal (Fig. 3E), potentially caused by a predator attack. There is evidence that the individual

recovered from this injury via bone remodeling, expressed as a major thickening and smooth surface of bone in this region (Fig. 3F).

The sulci left by the scutes are well preserved in *P. tatacoensis* n. sp., lacking cervical scute as in all other pelomedusoids. There were five vertebral scutes, vertebral 1 reaching peripherals 1 anterolaterally as in all other podocnemidids and many other pelomedusoids. Vertebrae 2-4 had almost similar width, and vertebral 5 reached peripherals 10. Despite minor variations in the shape, all these vertebrae exhibit the same contacts between each other and pleurals, as well as covered the same bones (neurals, costals, peripherals, suprapygals, and pygals) as in all other extant and fossil podocnemidids. *Podocnemis tatacoensis* n. sp. had four pleural and twelve marginal scutes, as is common for podocnemidids.

Plastron

The plastron of the holotype of *P. tatacoensis* n. sp. is nearly complete (21 cm maximum length) (Fig. 1F, G), missing only a small portion of the left epiplastron and the most anterolateral edge of the right hyoplastron, exhibiting smooth bone surface. The anterior lobe (7.6 cm long) reaches the level of the anterior margin of the carapace, having a convex margin. The posterior lobe (7.3 cm long) terminates anterior to the posterior margin of the carapace with a deep U-shaped anal notch. An almost similar anterior and posterior length of the plastral lobes is the most frequent condition in podocnemidids, in contrast, for example, to shorter anterior lobe of bothremydids (de Araújo-Carvalho *et al.* 2016: fig. 5). The pelvic bones are strongly sutured to the plastron and carapace (Fig. 3G-H), as in all other pan-pleurodires.

The entoplastron of *P. tatacoensis* n. sp. is diamond in shape, with slightly curved margins, located anterior to the axillary bridge level, similar as in all other podocnemidids. The mesoplastra are nearly circular in shape and restricted laterally as in all other pelomedusoids, except *P. pritchardi*, which has mesoplastra almost rectangular in shape (Wood 1997). The epiplastron, hyoplastron, hypoplastron, and xiphiplastron exhibit similar contacts, shape and proportions as in all other extant and fossil podocnemidids. The hyoplastron of *P. tatacoensis* n. sp. have an anterior-most dusky foramen near the axillary buttress-peripherals 3 contact, as in all other extant podocnemidids (Figs 1F, G; 4). The presence and location of musk duct foramina is rarely reported for fossil podocnemidids specifically and fossil pleurodires in general. *Podocnemis tatacoensis* n. sp. has three additional lateral musk ducts in each hyoplastron-peripherals contact (Figs 1F, G; 3I, J; 4A, B), as in *P. vogli* (Fig. 4C, D), *P. unifilis* (Fig. 4E-H), and *P. erythrocephala* (Fig. 3I-L). There is only one lateral musk duct in *P. expansa* (Fig. 4M-P), and they are completely absent in *P. sextuberculata* (Fig. 4Q-T), *Erymnochelys madagascariensis* (Fig. 4A'-D'), and *Peltocephalus dumerilianus* (Fig. 4E'-H'). In *P. lewyana* there are more than four, usually six (Fig. 4U-X).

Similar to the carapace, the plastron of *P. tatacoensis* n. sp. has a well defined sulci left by the scutes. There was a single gular scute (commonly called the intergular, but not homologous with the intergular of chelydroids) restricted to the medial portions of epiplastron and reaching only a small corner of the entoplastron. The two extragulars were restricted to the epiplastron and were triangular in shape. The humeral scutes met each other medially over the entoplastron. All of these contacts and shapes resembling the scutes of extant and fossil podocnemidids. The pectoral scutes covered most of the entoplastron, the most posterior margins of epiplastron, and did not reach the mesoplastra. This is the most frequent condition in extant and fossil podocnemidids, with some exceptions observed in specimens of *Peltocephalus dumerilianus* and *Podocnemis erythrocephala* where the most posterolateral corners of the pectorals covered the mesoplastra. The abdominal scutes were the longest of the plastron, slightly longer medially than the pectorals and femorals, similar as in all other extant and fossil podocnemidids, differing from the most variable condition of medial length exhibited by these three pairs of scutes of bothremydids (Cadena *et al.* 2012; de Araújo-Carvalho *et al.* 2016; Pérez-García 2016; Pérez-García *et al.* 2020). The anal scutes of *P. tatacoensis* n. sp. met medially and covered most of the posterior plastral tips.

RESULTS

PHYLOGENETIC ANALYSES

The first analysis (all taxa, all morphological characters) produced 192 most parsimonious trees (MPTs), with a tree length (TL) of 1318, a consistency index (CI) of 0.275 and a retention index (RI) of 0.741. The strict consensus of all these trees is shown in Fig. 5A, B and Supplementary Data S3 (all taxa included, Appendix 3). *Podocnemis tatacoensis* n. sp. is recovered inside *Podocnemis* clade, forming a polytomy with *P. negrii* and *P. unifilis*, supported by character 222 (the axillary musk duct location) and character 269 (number of lateral musk ducts in each hyoplastron-peripherals contact). The second analysis (excluding all fossil *Podocnemis* except *P. tatacoensis* n. sp.) produced 48 MPTs (TL = 1310, CI = 0.277, RI = 0.744). The strict consensus is shown in Fig. 5C (only *Podocnemis* taxa) and Supplementary Data S4 (full tree, Appendix 4). *Podocnemis tatacoensis* n. sp. is found as the sister taxon of the extant *P. unifilis*, supported by the following common synapomorphies, characters: 179, keeled neurals; 269, number of lateral musk foramina. The third analysis (morphology plus molecular data) produced a single MPT (TL = 4225, CI = 0.699, RI = 0.794), also supporting *Podocnemis tatacoensis* n. sp. as member of *Podocnemis* and forming a clade with the extant *P. unifilis* and the fossil *P. negrii* (Fig. 5D, only *Podocnemis* taxa and Supplementary Data S5, full tree, Appendix 5).

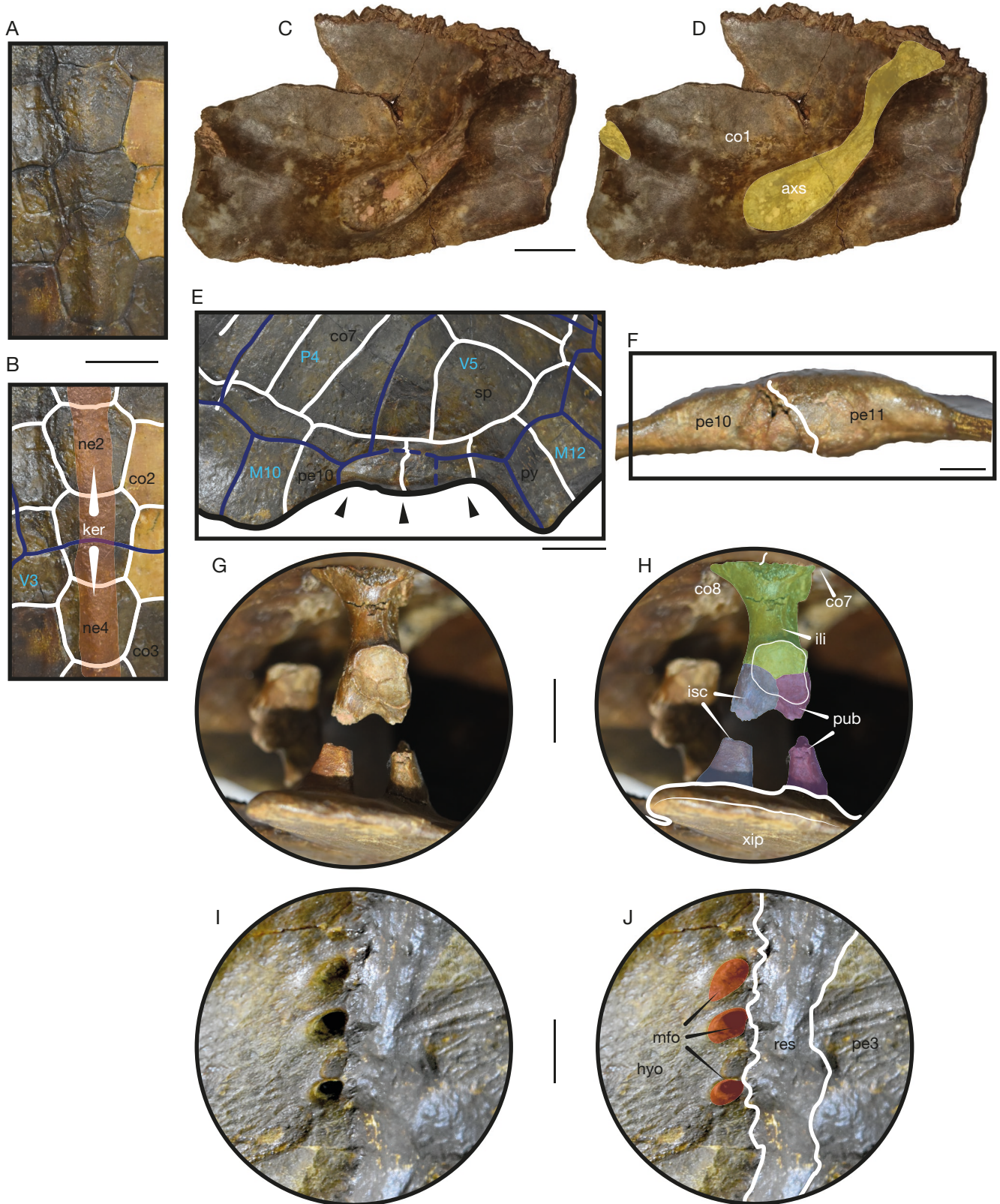


FIG. 3. — *Podocnemis tatacoensis* n. sp. details of its anatomy: **A, B**, close-up of the keeled neurals 2-4; **C, D**, left costal 1 in ventral view, showing the shape of the axillary scar; **E**, left posterior margin of the carapace showing the bone predation trauma occurred to the peripherals; **F**, left peripherals 10-11 where the bone healed from the injury increasing the thickness and smoothing the surface; **G, H**, view of the right pelvic girdle; **I, J**, close-up of the three lateral musk foramina of the left hyoplastron-peripherals region. Abbreviations: **axs**, axillary scar; **co**, costal; **hyo**, hyoplastron; **ili**, ilium; **isc**, ischium; **ker**, keel ridge; **M**, marginal scute; **mfo**, musk foramina; **ne**, neural; **sp**, suprapygal; **P**, pleural scute; **pe**, peripheral; **pub**, pubis; **py**, pygal; **res**, resin; **V**, vertebral scute; **xip**, xiphiplastron. Scale bars: A, B, E, G, H, 2 cm; C, D, 1 cm; F, I, J, 5 mm.

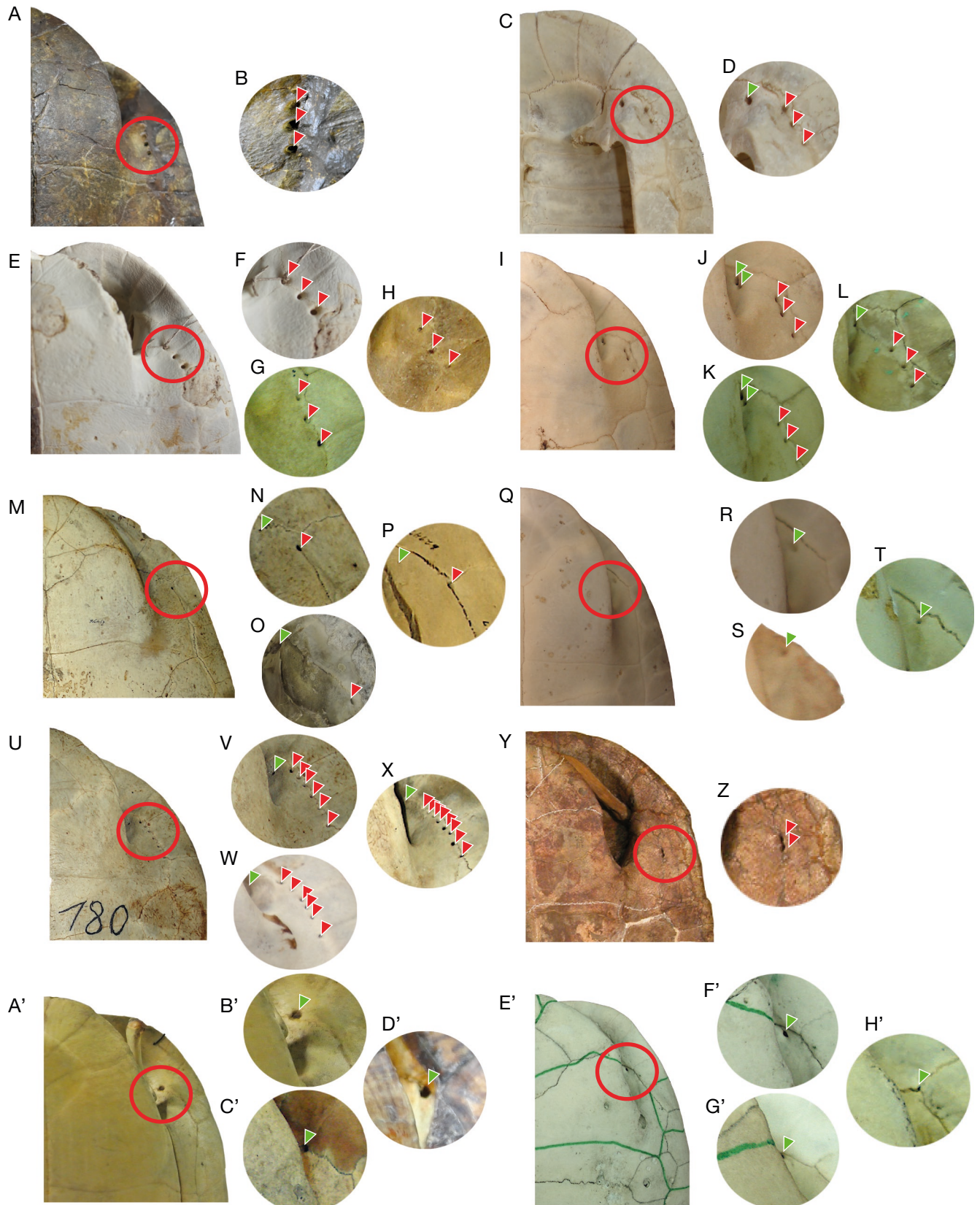


FIG. 4. — Left hyoplastron-peripherals region in extant and some fossil podocnemidids: **A, B**, *Podocnemis tatacoensis* n. sp., specimen VPPLT-1727; **C, D**, *P. vogli* UF-39060; **E, F**, *P. unifilis* MTKD-45847; **G**, *P. unifilis* CRI-2778; **H**, *P. unifilis* ICN-6455; **I, J**, *P. erythrocephala* CRI-6023; **K**, *P. erythrocephala* CRI-8207; **L**, *P. erythrocephala* CRI-1194; **M, N**, *P. expansa* USNM-29476; **O**, *P. expansa* NMW-35550; **P**, *P. expansa* AMNH-62947; **Q, R**, *P. sextuberculata* CRI-6543; **S**, *P. sextuberculata* CRI-2830; **T**, *P. sextuberculata* CRI-5500; **U, V**, *P. lewyana* ICN-7653; **W**, *P. lewyana* MNHN-286; **X**, *P. lewyana* ICN-1699; **Y, Z**, *P. pritchardi* UCMP-63782; **A', B'**, *Erymnochelys madagascariensis* NMW-1811; **C'**, *E. madagascariensis* MNHM-1534; **D'**, *E. madagascariensis* NMW-139; **E', F'**, *Peltocephalus dumerilianus* CRI-1344; **G'**, *Pe. dumerilianus* CRI-3295; **H'**, *Pe. dumerilianus* CRI-7524. Red circle indicates the close-up region showed in the right images. Green arrows indicate the axillary musk foramen of the hyoplastron (character 222), and red arrows indicate the lateral musk foramen or foramina at the hyoplastron-peripherals contact (character 269). Specimens not to scale.

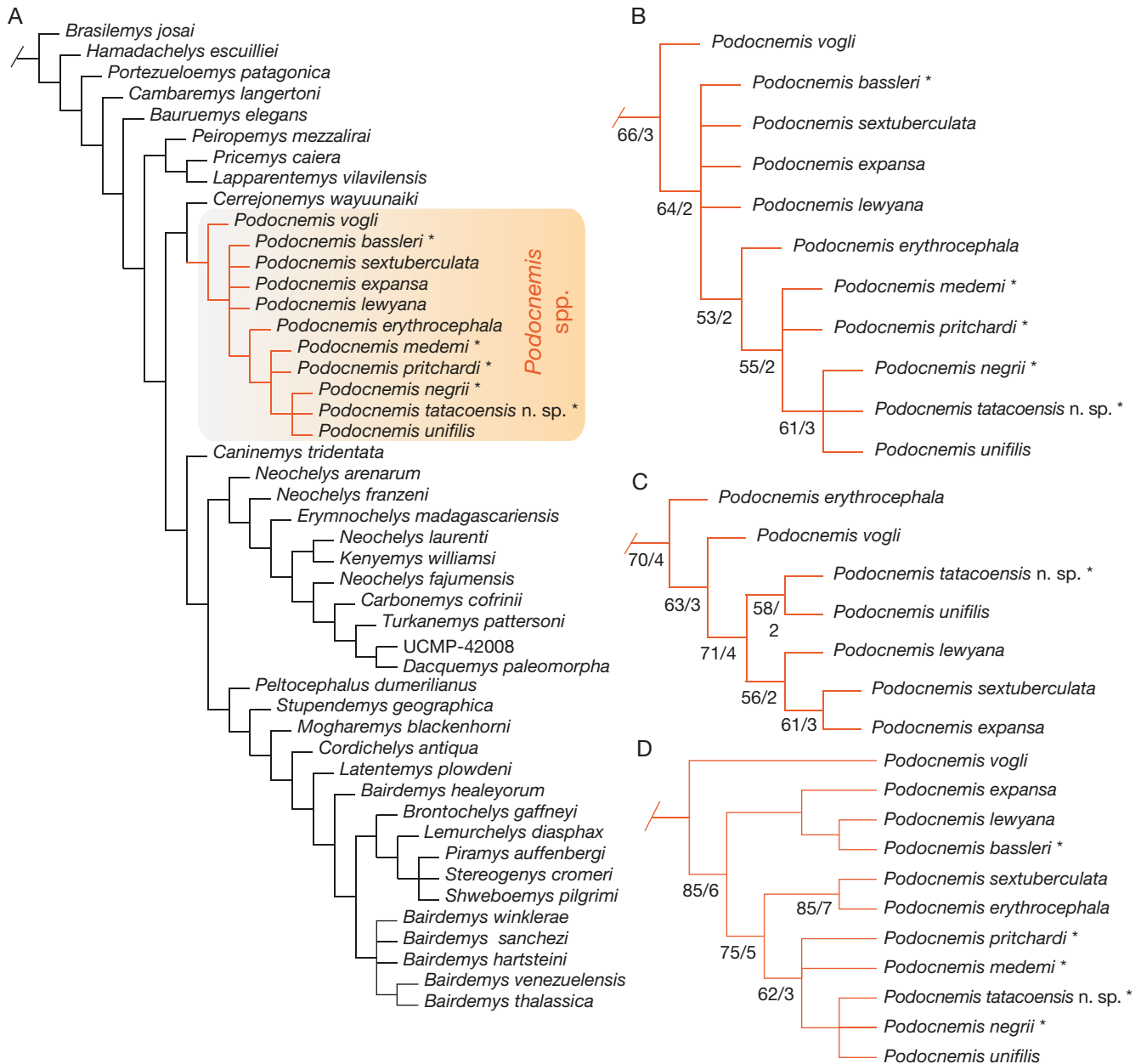


FIG. 5. — Phylogenetic hypotheses including *Podocnemis tatacoensis* n. sp.: **A**, strict consensus of 192 most parsimonious trees (MPTs), obtained from the first analysis (all taxa, all morphological characters), tree length (TL) = 1318, consistency index (CI) = 0.275, retention index (RI) = 0.741, see the full tree in Supplementary Data S3 (Appendix 3); **B**, close up of the *Podocnemis* clade shown in (A). **C**, close up of the *Podocnemis* clade obtained in the strict consensus from the second analysis excluding all fossil *Podocnemis* except *P. tatacoensis* n. sp., see the full tree in Supplementary Data S4 (Appendix 4), MPTs = 48, TL = 1310, CI = 0.277, and RI = 0.744. Bootstrap (upper) and Bremer support (lower) indices are shown for some clades in (B) and (C); **D**, close up of the *Podocnemis* clade obtained from the total evidence analysis that produced a single MPT, TL = 4225, CI = 0.699, and RI = 0.794, as in the morphology only analyses, *P. tatacoensis* n. sp. is found to be part of *Podocnemis* and closer to the extant *P. unifilis* and the fossil *P. negrii*. Symbol: *, fossil taxa.

DISCUSSION

KEY SHELL CHARACTERS

Two morphological shell characters with potential relevance to support the attribution of fossil taxa to the extant *Podocnemis* genus were mentioned by Gaffney *et al.* (2011), but they were considered to be unknown for all fossils and were scored only for the living podocnemidids. Since then, these characters have been included by other more recent studies (Cadena 2015; Ferreira *et al.* 2018; Cadena *et al.* 2020b, Cadena *et al.* 2021). These

two characters are: the axillary musk duct location (character 222: 1, this study) and number of lateral musk ducts in each hyoplastron-peripherals contact (character 269: 2–4, this study). In this study we explored in detail these characters, based on a considerable population of extant specimens for each of the extant taxa of *Podocnemididae*, and the two fossil taxa from La Venta Fauna that preserved the traits, *P. pritchardi* and *P. tatacoensis* n. sp. (Fig. 4). This allowed us to suggest that at least character 269 is a key character to support the attribution of fossil shell taxa as belonging to *Podocnemis*, because in five of the six species

TABLE 1. — Musk foramina among extant and fossil podocnemidids included in this study.

Taxon	Anterior musk foramina	Number of lateral musk foramina
<i>Podocnemis sextuberculata</i> Cornalia, 1849	present (one)	absent
<i>Podocnemis expansa</i> (Schweigger, 1812)	present (one)	one
<i>Podocnemis erythrocephala</i> Spix, 1824	present (one or two)	three
<i>Podocnemis unifilis</i> Troschel, 1848	present (one)	three
<i>Podocnemis vogli</i> Müller, 1935	present (one)	three
<i>Podocnemis lewyana</i> Duméril, 1852	present (one)	six or more
<i>Podocnemis pritchardi</i> Wood, 1997	present (one)	two
<i>Podocnemis tatacoensis</i> Podocnemis Wagler, 1830	present (one)	three
<i>Peltocephalus dumerilianus</i> (Schweigger, 1812)	present (one)	absent
<i>Erymnochelys madagascariensis</i> (Grandidier, 1867)	present (one)	absent

(except *P. sextuberculata*), the lateral musk foramen or foramina are present (Table 1). The foramina are absent in the other extant genera of *Podocnemididae*, *Peltocephalus* and *Erymnochelys*, and for example in the exceptionally preserved podocnemidid fossil *Neochelys franzenii* (Cadena 2015).

The presence of three lateral musk foramina and keeled neurals in *Podocnemis tatacoensis* n. sp., supports its close relationship with other *Podocnemis* taxa, particularly with *P. unifilis* as suggested by the phylogenetic results, when it is included only with the extant taxa (Fig. 5C; Table 1). The first phylogenetic analysis presented here also suggests that the three controversial taxa *P. pritchardi*, *P. medemi* and *P. negrii* are part of the *Podocnemis* clade (Fig. 5A, B) supporting their exclusion from the “dubious taxa” list of Gaffney *et al.* (2011) and to be considered as valid representatives of *Podocnemis*. From this analysis, *Podocnemis tatacoensis* n. sp., is also found closer to *P. unifilis* and *P. negrii*, all three of which share keeled neurals, a feature that is also present in *P. erythrocephala* but with some other characters that make it to be outside of this triple taxa configuration. A stronger support for the phylogenetic hypotheses presented, in addition to the total evidence analysis presented here (Fig. 5D) may be found in the future by expanding observations of musk foramina to a bigger population of extant and fossil podocnemidids, and with the potential discovery of specimens with associated skull and shell in Miocene sequences of northern South America. All three controversial taxa (*P. pritchardi*, *P. medemi*, and *P. negrii*) and the *P. tatacoensis* n. sp. described herein, exhibit the shell characters listed in the diagnosis of *Podocnemis* given by Gaffney *et al.* (2011) and are resolved inside *Podocnemis* clade based on the phylogenetic analyses presented here.

OLDEST RECORD OF *PODOCNEMIS*

The occurrence of *Podocnemis tatacoensis* n. sp. from the San Alfonso Beds, lowermost part of La Victoria Formation (Fig. 2A) (a sequence with a well-defined stratigraphic and geochronologic frame), makes it the earliest record for *Podocnemis* genus so far known, with an age of 13.778 ± 0.081 Ma (Flynn *et al.* 1997), Middle Miocene (Serravallian). Divergence times based on molecular data suggest that the separation of *Erymnochelys* and *Podocnemis* should have occurred during the Late Cretaceous around 78.46 Ma (Vargas-Ramírez *et al.* 2008, Pereira *et al.* 2017). Based on the age for *P. tatacoensis* n. sp., the ghost lineage time for crown *Podocnemis* is still being of approximately 64.682 Ma

(Fig. 2B), and of approximately 85.74 Ma for the other extant South American podocnemidid genus *Peltocephalus*, which lacks of any undisputable fossil record. Considering the phylogenetic results obtained here (Fig. 5), which supports a closer relationship between *P. tatacoensis* n. sp. and the extant *P. unifilis*, a taxon that split from *P. sextuberculata* during the Early Miocene (22.78 Ma based on molecular clock estimates) (Vargas-Ramírez *et al.* 2008), the ghost lineage time for the *P. unifilis* clade (*P. unifilis* + *P. tatacoensis* n. sp.) is of only 9.002 Ma (Fig. 2B) (time of the *P. sextuberculata* and *P. unifilis* split minus the age of *P. tatacoensis* n. sp.).

PALAEOECOLOGY

The carapace of *Podocnemis tatacoensis* n. sp., shows an injury at its left posterior region, potentially caused by a predator (Fig. 3E). Evidence of potential predators of freshwater turtles from La Venta is found in different horizons of the Repartidora locality, where, it is very common to find crocodilian remains, particularly isolated teeth. We suggest this injury was caused by a crocodile bite. Fortunately for this turtle, the attack occurred in a peripheral floating region, beyond the visceral chamber where important organs are encapsulated, which facilitated a healing process of the bone from this trauma possibly via bone remodeling (Hadjidakis & Androulakis 2006), as it has been also interpreted for other fossil injured turtles including *Heckerochelys romani* (Scheyer *et al.* 2014). As a result of this healing process the bone increased in thickness and the surface smoothed (Fig. 3F). Considering the maximum length of the carapace of *P. tatacoensis* n. sp. (23.2 cm), the total length of this individual was of approximately 30 cm, indicating that preys of this size were in the diet spectrum of crocodilians sharing the environment.

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Data archiving statement

DOIs were attributed to Supplementary Data S1-S5 online files (Appendices 1-5) and are available in the Dryad Digital Repository: <https://datadryad.org/stash/share/>.

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SUPPLEMENTARY DATA (APPENDICES)

APPENDIX 1. — Supplementary Data S1. Nexus file used in the phylogenetic analysis (all characters and all taxa):
https://doi.org/10.5852/geodiversitas2023v45a3_s1

APPENDIX 2. — Supplementary Data S2. Nexus file used in the phylogenetic analysis (total evidence: morphology plus molecular):
https://doi.org/10.5852/geodiversitas2023v45a3_s2

APPENDIX 3. — Supplementary Data S3. Full strict consensus tree obtained from the first phylogenetic analysis:
https://doi.org/10.5852/geodiversitas2023v45a3_s3

APPENDIX 4. — Supplementary Data S4. Full strict consensus tree obtained from the second phylogenetic analysis:
https://doi.org/10.5852/geodiversitas2023v45a3_s4

APPENDIX 5. — Supplementary Data S5. Full strict consensus tree obtained from the third phylogenetic analysis, total evidence:
https://doi.org/10.5852/geodiversitas2023v45a3_s5