

A SMALL PODOCNEMIDOID (PLEURODIRA, PELOMEDUSOIDES) FROM THE LATE CRETACEOUS OF BRAZIL, AND THE INNERVATION AND CAROTID CIRCULATION OF SIDE-NECKED TURTLES

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Abstract: Pleurodires are less diverse than cryptodires, together forming the two major lineages of crown turtles. Their fossil record, however, is rich. A particularly large number of fossil pleurodires, many belonging to the Podocnemididae, has been recovered from the Upper Cretaceous Bauru Group outcrops of south-central Brazil. Herein we describe an additional pleurodire from this region, *Amabilis uchoensis* gen. et sp. nov., based on a partially preserved skull. *A. uchoensis* is recognized as belonging to the Podocnemididae by the small entrance to the antrum postoticum and completely developed cavum pterygoidei, being unique among other non-podocnemidid podocnemidoids for its medially open fenestra postotica and absent basioccipital–opisthotic contact. Our cladistic analysis places *A. uchoensis* as a sister taxon to

Hamadachelys + other podocnemidoids. We further explore the neuroanatomy of side-necked turtles with the aid of micro-computed tomography of specimens of the main pleurodiran lineages. Our data shed light on the different carotid circulation patterns in pleurodires, and we propose new phylogenetic characters to describe the neuroanatomical variation of the group. Optimization of these characters shows two independent acquisitions of a foramen for the palatal branch of the carotid in chelids and podocnemidoids, and a unique loss of the vidian nerve canal in chelids, in turtles in general.

Key words: Pleurodira, micro-computed tomography, Podocnemididae, Bauru Group, neuroanatomy, carotid circulation.

LIVING pleurodires, 93 species of which are currently recognized, account for nearly one-quarter of extant turtle diversity (TTWG 2017), with all remaining extant turtles being cryptodires. Extant pleurodires are restricted to freshwater environments of southern landmasses, namely South America, Africa, Madagascar and Australasia (de la Fuente *et al.* 2014). Today, three pleurodire clades are recognized: Chelidae, Pelomedusidae and Podocnemidae. However, the fossil record of the group indicates that pleurodire diversity (both in terms of lineages and ecological adaptations) was higher in the past. For instance, by the end of the Early Cretaceous there were at least four established lineages (Romano *et al.* 2014; Vlachos *et al.* 2018) and the group included at least two independent

invasions of littoral/marine environments (Rabi *et al.* 2012; Ferreira *et al.* 2015, 2018a; Joyce *et al.* 2016). Additionally, a much broader distribution, reaching all continents except Antarctica and central and northern Asia, can be inferred from the fossil record (Gaffney *et al.* 2011; Ferreira *et al.* 2018a).

Among extant side-necked turtles, Podocnemididae is less diverse (only eight species) compared with pelomedusids and chelids (27 and 58 spp., respectively; TTWG 2017). However, the fossil record of Podocnemididae (as defined in França & Langer 2006) is represented by more than 40 described taxa (Ferreira *et al.* 2018a), 31 of which belong to its crown lineage (Podocnemididae), more than any other pleurodiran group (e.g. Gaffney *et al.* 2006;

Maniel & de la Fuente 2016). Although some stem-group podocnemidids (i.e. non-podocnemidid Podocnemididae) have been found elsewhere (e.g. Lapparent de Broin 2000; Tong & Buffetaut 1996; de la Fuente 2003; Gaffney *et al.* 2011), the large majority of such turtles have been found in the Upper Cretaceous Bauru Group deposits (França & Langer 2006; Hermanson *et al.* 2017). These include six valid taxa: *Roxochelys wanderleyi* Price, 1953; *Bauruemys elegans* (Suárez, 1969); *Cambaremys langertoni* França & Langer, 2005; *Pricemys caiera* Gaffney *et al.*, 2011; *Peirouemys mezzalirai* Gaffney *et al.*, 2011; and *Yuraramirim montealtensis* Ferreira *et al.*, 2018b, as well as some dubious forms such as 'Podocnemis' *harrisii* Pacheco, 1913, and 'Pod.' *brasiliensis* Staesche, 1937, and several fragmentary remains (e.g. Gaffney *et al.* 2011; Rogério *et al.* 2013; Menegazzo *et al.* 2015; Hermanson *et al.* 2017; Ferreira *et al.* 2018b).

Although the fossil record of pleurodire cranial remains is relatively rich (e.g. Gaffney *et al.* 2006, 2011; Ferreira *et al.* 2018b), little attention has been given to their carotid and innervation patterns compared with other turtle groups (e.g. Jamniczky *et al.* 2006; Jamniczky & Russell 2007; Rabi *et al.* 2013; Joyce *et al.* 2018; Rollot *et al.* 2018; Raselli & Anquetin 2019). The carotid system in pleurodires is a matter of high systematic interest, given that a notable variation in position for the related foramina has been recognized, especially among fossils (Gaffney *et al.* 2006; Miyashita 2013), and also because the patterns of arterial circulation appear to be conservative at the family level in turtles (e.g. McDowell 1961; Albrecht 1967, 1976; Jamniczky & Russell 2007; Jamniczky 2008). Whereas the position of the foramina related to the entrance of the carotids in the braincase is more commonly taken into account (e.g. Gaffney *et al.* 2006; Sterli & de la Fuente 2010; Sterli *et al.* 2010), very little information is known regarding their size, trajectory and development inside the pleurodire skull. These are commonly extrapolated from a small sample of taxa (e.g. Albrecht 1976; Gaffney 1979; Sterli & de la Fuente 2010; Miyashita 2013; Werneburg & Maier 2019), hindering more thorough interpretation, if the topography of canals and foramina is actually not conserved across the pleurodiran lineage. Recent efforts using non-invasive techniques such as micro-computed tomography (μ CT) have shed light on these patterns for turtles in general (e.g. Paulina-Carabajal *et al.* 2013, 2017; Evers & Benson 2019; Raselli & Anquetin 2019; Evers *et al.* 2019a), but to date these have not been applied to a comprehensive sample of pleurodires.

Here, we present a new podocnemidoid turtle from the Late Cretaceous Bauru Group, represented by a single

skull from the São José do Rio Preto Formation. We describe its osteology and neuroanatomy, and include the taxon in a phylogenetic analysis with additional characters based on new μ CT data. Further, we investigate the morphological variation related to the carotid arterial circulation and cranial nerves in Pleurodira, which traditionally have been considered to follow a consistent pattern across most representatives (e.g. Sterli & de la Fuente 2010; Sterli *et al.* 2010). We conclude that they are not as conservative as previously thought, having substantive phylogenetic value.

GEOLOGICAL SETTING

The Bauru Basin consists of a large (c. 370 000 km²) depression developed during the Late Cretaceous in the south-eastern portion of the South American Plate. Filled between the Coniacian and Maastrichtian (Fernandes & Coimbra 1996, 2000), the basin has one of the most detailed Cretaceous fossil records of Brazil (see Menegazzo *et al.* 2016). Within the basin, the São José do Rio Preto Formation crops out in topographic highs of the homonymous region. This unit corresponds essentially to immature sand deposits, often conglomerates, accumulated in bars and fluvial plains of intertwined, wide and shallow river systems. Bone fragments and other bioclasts are common in the conglomeratic beds (Fernandes 2004), including isolated coprolites, scales, bones, teeth and carapace fragments, pertaining to lepisosteiform fishes, anurans, testudines, crocodyliforms and dinosaurs (Iori *et al.* 2017). Menegazzo *et al.* (2016) suggest a Santonian age (c. 86.3 Ma) for the São José do Rio Preto Formation based on the stratigraphy and faunal associations.

The Uchoa region harbours countless outcrops of the São José do Rio Preto Formation. The new taxon comes from the 'Zero Um' palaeontological site (Fig. 1), the same locality in which peirosaurid crocodyliform dentaries and the holotype of the theropod *Thanos simonattoi*, among other significant fossils, were found (Marinho & Iori 2011; Iori *et al.* 2011; Méndez *et al.* 2014; Delcourt & Iori 2018). The site consists of several conglomeratic outcrops in a cattle pasture area owned by Milton Roberto Palharini (Ibirá County, São Paulo State, Brazil). Fossils in this locality are found in the bedrock or in isolated, weathered blocks on the ground. In particular, MPPC 01-0040 was found in an isolated block, the origin of which was probably the 'Escadaria' site (21°01'01.6" S, 49°13'06.9" W), an exposure of conglomeratic strata subject to constant erosion, frequently revealing new fossils.

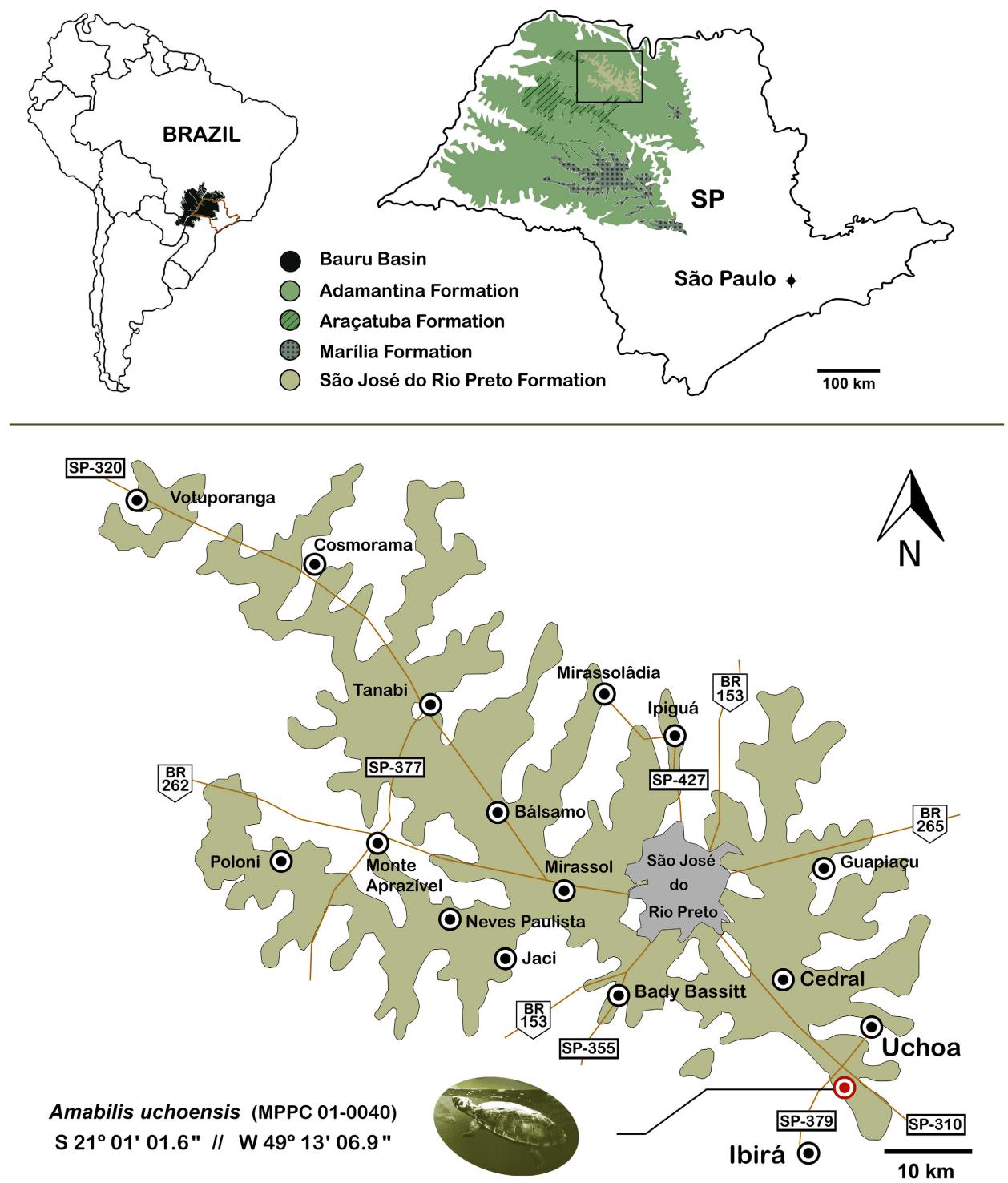


FIG. 1. Location of the Bauru Basin in South America and São Paulo state showing the distribution of the stratigraphic units of the basin (top), and map of São José do Rio Preto region (bottom) highlighting the locality where the described fossil was found. Modified from Delcourt & Iori (2018). Colour online.

MATERIAL AND METHOD

Virtual preparation of the material

Micro-CT scanning was carried out using the GE Phoenix v|tome|x S240 scanner housed at the Centro para Documentação da Biodiversidade (Departamento de Biologia, Universidade de São Paulo at Ribeirão Preto), using 1000 projections, exposure time of 0.3 s, voltage of 130 kV, and a current of 150 μ A, with a voxel size of 25.8 μ m. We used Avizo (v. 7.0.0; Visualization Sciences Group) to virtually and manually segment skull bones and to produce virtual casts of the endocranum, endosseous labyrinth, vessels, and nerves. All 3D models are compiled and available as separate supplementary files (Hermanson *et al.* 2020) along with a VAXML script that can be readily open in SPIERS (Sutton *et al.* 2012).

Phylogenetic analysis

We added *A. uchoensis* and 29 other taxa to the matrix of Ferreira *et al.* (2018c; modified from Ferreira *et al.* 2018a) to evaluate the phylogenetic position of the new taxon. Some taxa were re-scored to correct previous miscodings and to add information from μ CT of 31 taxa, as well as from reinterpretations of original descriptions (see Hermanson *et al.* 2020). Based on these data, 18 new characters were added to the data matrix, whereas 22 other characters were added from different literature sources (see Hermanson *et al.* 2020). The resulting character-taxon matrix was analysed in TNT 1.5 (Goloboff & Catalano 2016) with traditional search, using 1000 replicates, hold 20, tree bi-section and reconnection (TBR), random seed 0, and collapse of zero-length branches according to rule 1, with *Pro. quenstedti*, *Platychelys oberndorferi*, *Notemys zapatocaensis*, and *N. laticentralis* set as the out-group taxa. All characters were equally weighted and some treated as ordered (following Ferreira *et al.* 2018a). The most parsimonious trees (MPTs) retrieved in the first analysis were subjected to a second round of TBR to identify extra MPTs. Consistency (CI) and retention (RI) indexes, Bremer support, and resampling values (bootstrap and jackknife) were calculated using implemented functions in TNT and are given in Hermanson *et al.* (2020).

Institutional abbreviations. AMNH, American Museum of Natural History, New York, USA; LPRP/USP, Laboratório de Paleontologia de Ribeirão Preto (USP), Ribeirão Preto, Brazil; MPPC, Museu de Paleontologia 'Pedro Candolo', Uchoa, Brazil.

SYSTEMATIC PALAEONTOLOGY

PLEURODIRA Cope, 1864

PELOMEDUSOIDES Broin, 1988

PODOCNEMIDOIDAE Cope, 1868

Genus AMABILIS nov.

LSID. urn:lsid:zoobank.org:act:4F970E7F-2344-47AD-9956-07052F2FE12E

Derivation of name. Latin for 'lovable', for its tiny size.

Type species. *Amabilis uchoensis* sp. nov.

Diagnosis. *Amabilis* can be identified as a member of the Podocnemidoidae based on the presence of a processus trochlearis pterygoidei and a complete cavum pterygoidei. *Amabilis* differs from all other Podocnemidoidae in possessing a medially open fenestra postotica and lacking a basioccipital–opisthotic contact (also absent only in *Mogharemys blanckenhorni*). It is similar in size to *Y. montealtensis*, but smaller than all other Bauru Group turtles; the anterolateral emargination of the skull reaches the level of the orbit, similar to *Bauruemys elegans*, *Hamadachelys escuilliei*, and podocnemidids, but differing from peiropemydids; its foramen palatinum posterius is formed only by the palatine as in *Pe. mezzalirai* and *Podocnemis* spp., whereas in *Y. montealtensis*, *Ba. elegans*, *Brasilemys josai*, and most Podocnemidoidae it is formed by both the pterygoid and the palatine; the foramen jugulare posterius is confluent with the fenestra postotica as in *Br. josai*, *H. escuilliei*, and *Por. patagonica*; it lacks the anterior foramen for the palatal branch of the carotid, which is otherwise present in *H. escuilliei*, *Ba. elegans*, peiropemydids, and most podocnemidids, and lacks a horizontal occipital shelf as in *Br. josai*; there is no sign of an exoccipital–quadrate contact, similar to all Podocnemidoidae (except for *Br. josai*); the basioccipital tubera are closer to the median line of the skull, differing from podocnemidids and peiropemydids.

Amabilis uchoensis sp. nov.

Figures 2–6

LSID. urn:lsid:zoobank.org:act:09EB4626-7D37-4182-9F88-8CCA8B914778

Derivation of name. The name refers to Uchoa municipality, where the holotype is housed.

Material. Holotype MPPC 01-0040, a partial skull lacking only the prefrontals, maxillae, premaxillae and squamosals, which are not preserved. The specimen is housed at the Museu de Paleontologia Pedro Candolo, Uchoa, Brazil.

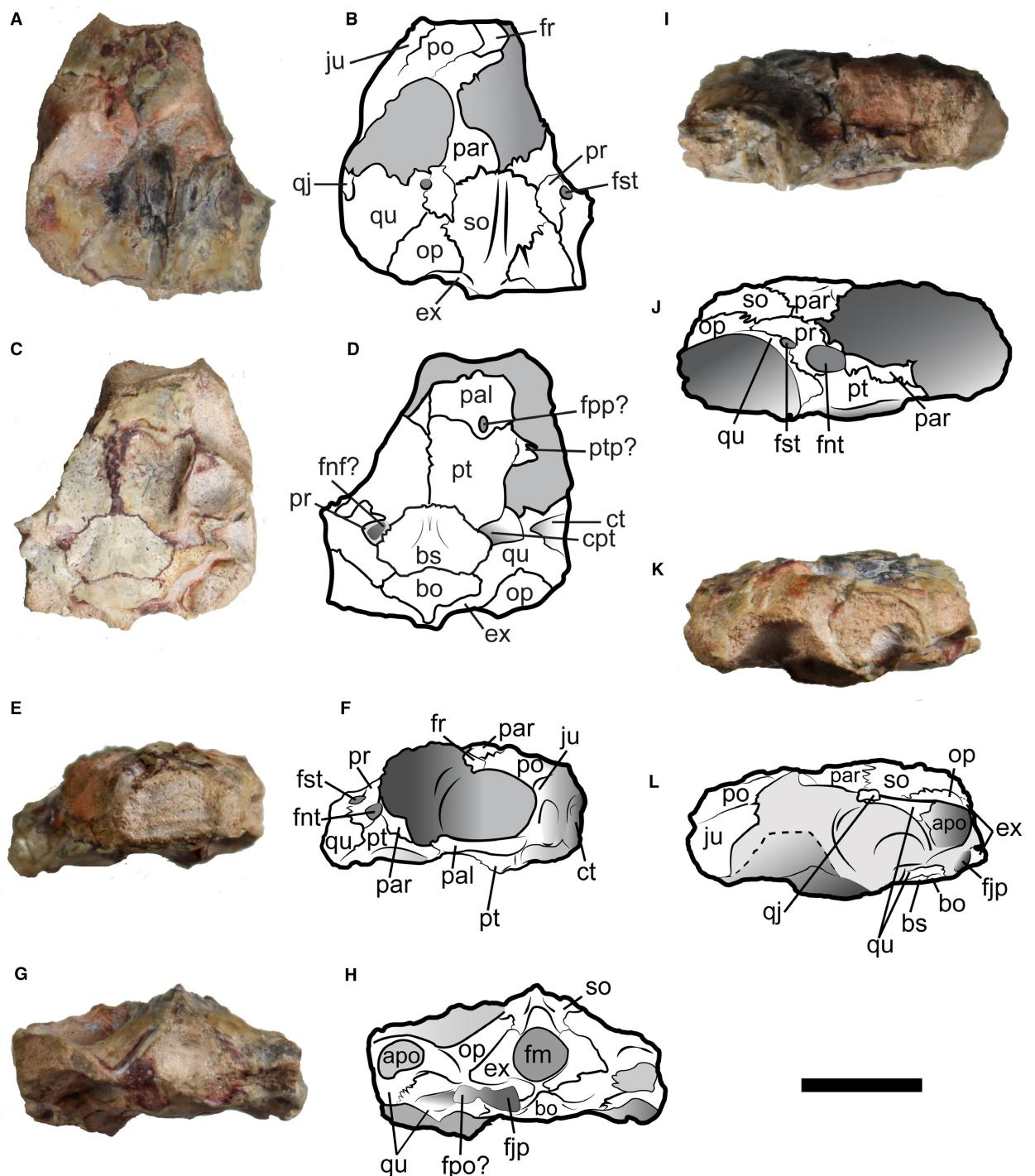


FIG. 2. *Amabilis uchoensis* gen. et sp. nov., MPPC 01-0040. Photographs and interpretative drawings in: A–B, dorsal; C–D, ventral; E–F, anterior; G–H, posterior; I–J, right lateral; K–L, left lateral view. Abbreviations: apo, antrum postoticum; bo, basioccipital; bs, basisphenoid; cpt, cavum pterygoidei; ct, cavum tympani; ex, exoccipital; fjp, foramen jugulare posterius; fm, foramen magnum; fnf, foramen nervi facialis; fnt, foramen nervi trigemini; fpo, fenestra postotica; fpp, foramen palatinum posterius; fr, frontal; fst, foramen stapedio-temporale; ju, jugal; op, opisthotic; pal, palatine; par, parietal; po, postorbital; pr, prootic; pt, pterygoid; ptp, processus trochlearis pterygoidei; qj, quadratojugal; qu, quadrate; so, supraoccipital. Scale bar represents 1 cm. Colour online.

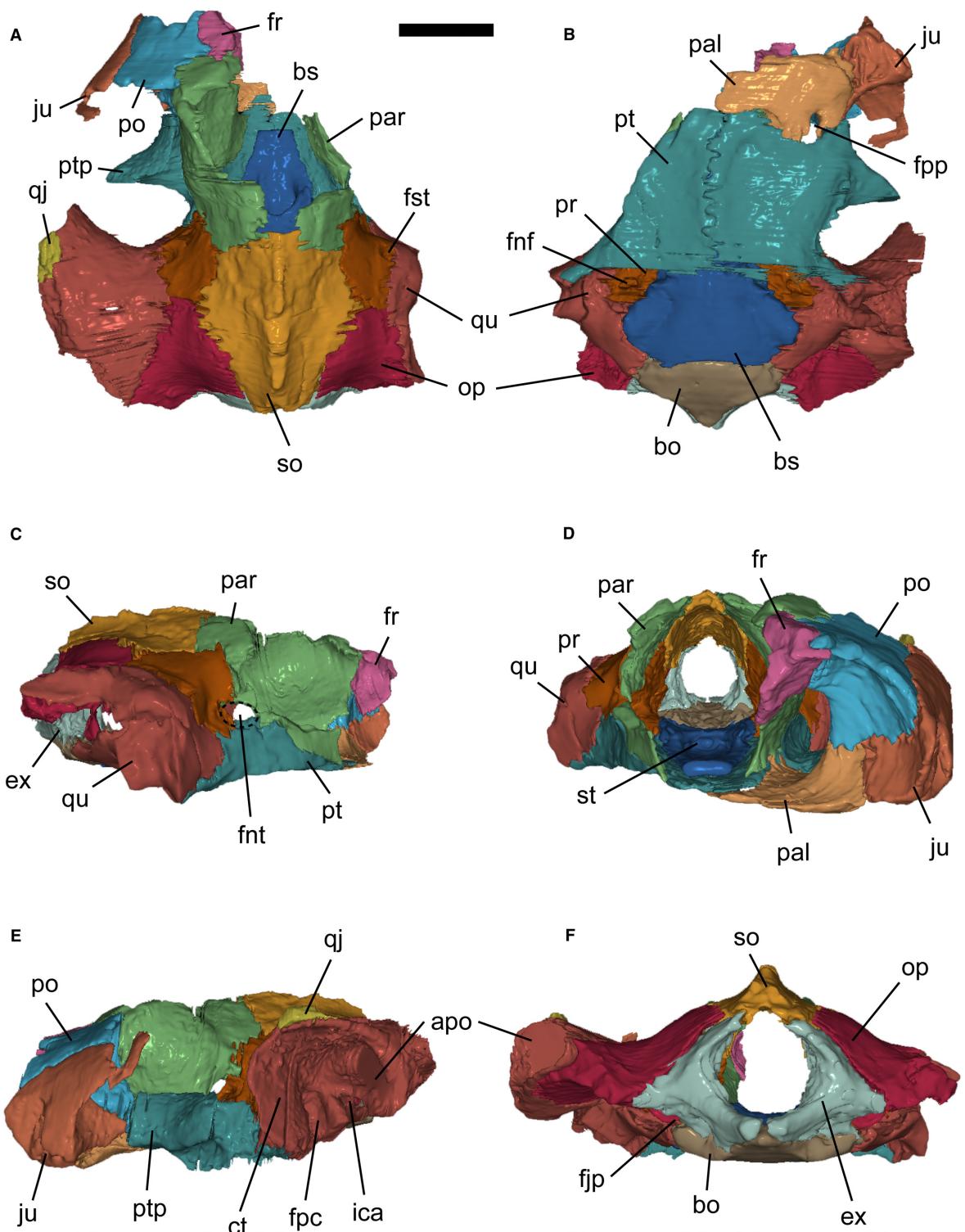


FIG. 3. *Amabilis uchoensis* gen. et sp. nov., MPPC 01-0040. Digital reconstruction of skull bones in: A, dorsal; B, ventral; C, right lateral; D, anterior; E, left lateral; F, posterior view. Abbreviations: apo, antrum postoticum; bo, basioccipital; bs, basisphenoid; ct, cavum tympani; ex, exoccipital; fjp, foramen jugulare posterius; fnf, foramen nervi facialis; fnt, foramen nervi trigemini; fpc, fossa precolumellaris; fpp, foramen palatinum posterius; fr, frontal; fst, foramen stapedio-temporale; ica, incisura columellae auris; ju, jugal; op, opisthotic; pal, palatine; par, parietal; po, postorbital; pr, prootic; pt, pterygoid; ptp, processus trochlearis pterygoidei; qj, quadratojugal; qu, quadrate; so, supraoccipital; st, sella turcica. Scale bar represents 0.5 cm. Colour online.

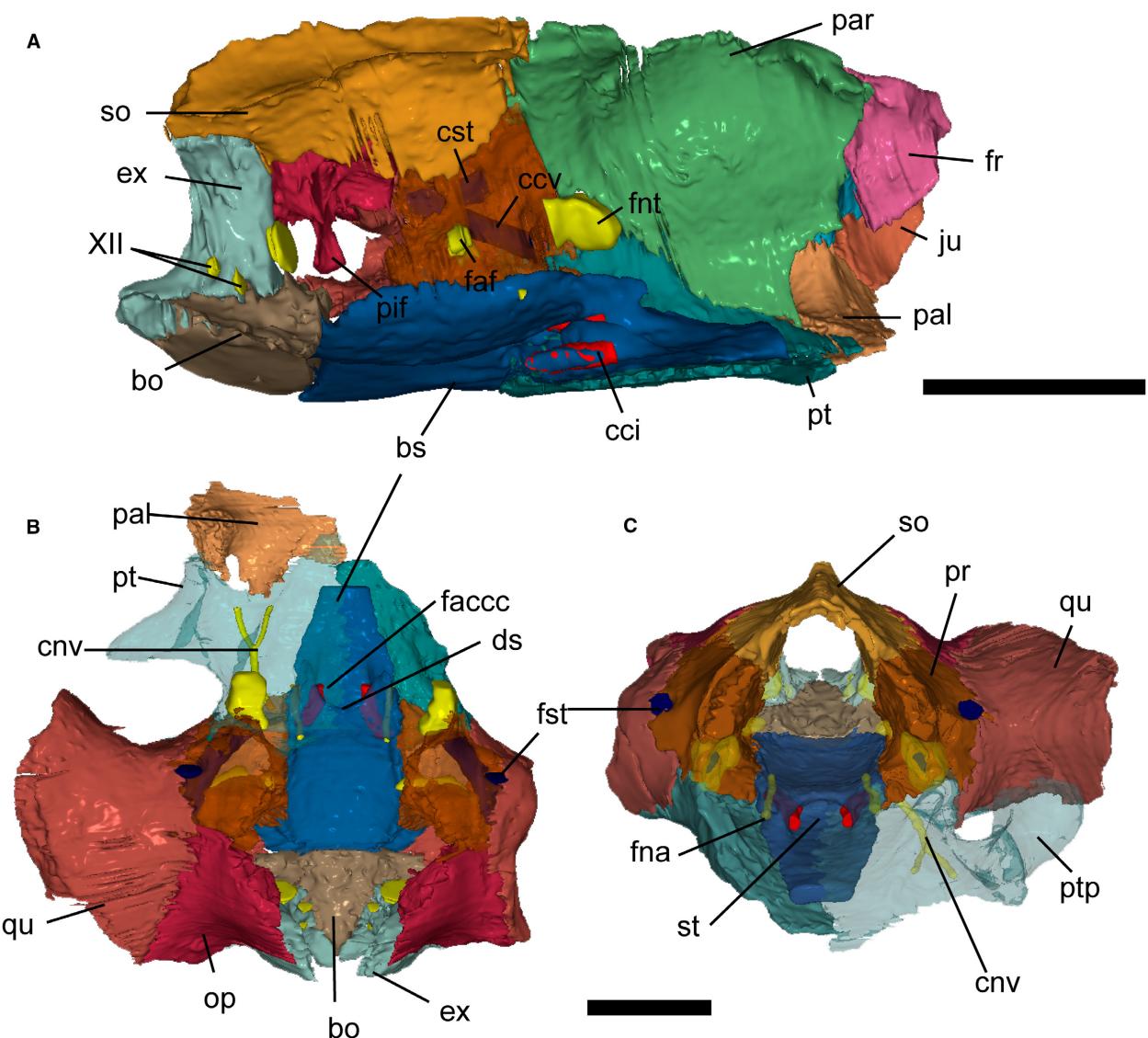


FIG. 4. *Amabilis uchoensis* gen. et sp. nov., MPPC 01-0040. Segmented skull in: A, medial; B, dorsal; C, anterior view. Abbreviations: bo, basioccipital; bs, basisphenoid; cci, canalis caroticus internus; ccv, canalis cavernosus; cnv, canalis nervi vidiani; cst, canalis stapedio-temporalis; ds, dorsum sellae; ex, exoccipital; faccc, foramen anterius canalis carotici cerebralis; fnt, foramen nervi trigemini; fr, frontal; fst, foramen stapedio-temporale; ju, jugal; op, opisthotic; pal, palatine; par, parietal; pif, processus interfenestralis; pt, pterygoid; ptp, processus trochlearis pterygoidei; so, supraoccipital; XII, cranial nerve XII. Scale bar represents 0.5 cm. Colour online.

Diagnosis. As for genus.

Type stratum and locality. Late Cretaceous (possibly Santonian), São José do Rio Preto Formation, Zero Um palaeontological site (21°01'01.6" S, 49°13'06.9" W), Ibirá-SP, Brazil.

Description

The skull of MPPC 01-0040 is smaller than that of all other Bauru Group turtles, being 2.25 cm long, 2.06 cm wide and 0.95 cm high as preserved. It is similar in size to those of

Br. josai, *Y. montealtensis* and some extant *Podocnemis* spp. (Lapparent de Broin 2000; Bonin *et al.* 2006; Hermanson *et al.* 2017). The anterior region of the cavum cranii as well as the cavum tympani on the left side are filled with rock matrix. Dorsally, on the left side, the broken lateral margins of the parietal and the posterior portion of the postorbital expose the adductor fossa (Fig. 2).

Frontals. The medial margins of the left frontal (the only preserved element) is incomplete, but the bone contacts are similar to those of other podocnemidoids such as *Ba. elegans*,

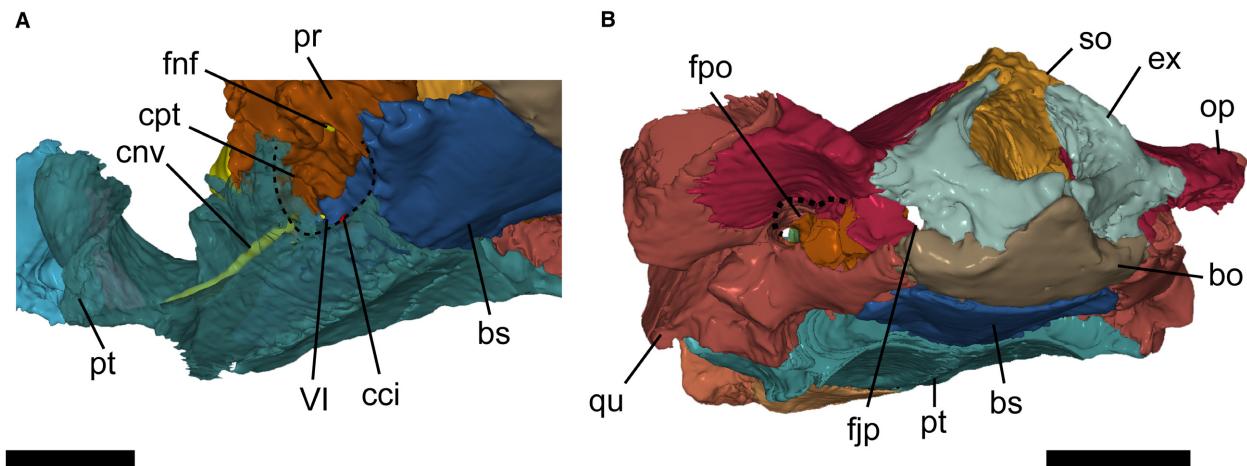


FIG. 5. *Amabilis uchoensis* gen. et sp. nov., MPPC 01-0040. Segmented skull in: A, left ventrolateral; B, posterior view. Abbreviations: bo, basioccipital; bs, basisphenoid; cci, canalis caroticus internus; cnv, canalis nervi vidiani; cpt, cavum pterygoidei; ex, exoccipital; fjp, foramen jugulare posterius; fnf, foramen nervi facialis; fpo, fenestra postotica; op, opisthotic; pr, prootic; pt, pterygoid; qu, quadrate; so, supraoccipital; VI, cranial nerve VI. Scale bars represent 0.5 cm. Colour online.

peiroemydids and *Podocnemis* spp., in which it contacts the parietal posteriorly and the postorbital laterally (Gaffney *et al.* 2011; Ferreira *et al.*, 2018b). Laterally, the frontal extends to form the dorsal margin of the orbit.

Parietals. The horizontal plate of the parietal, which usually forms a large portion of the skull roof, is not preserved so that the temporal (posteroventral) emargination of the skull cannot be observed (Fig. 3A). The parietal contacts the frontal anteriorly and the postorbital anterolaterally, the prootic posterolaterally, the supraoccipital posteriorly, and the pterygoid anteroventrally. The parietal only marginally contributes to the medial wall of the septum orbitotemporale, but does not contact the pterygoid laterally, given the presence of a posterior extension of the postorbital, similar to what is seen in other Podocnemididae (Meylan *et al.* 2009; Gaffney *et al.* 2011; Ferreira *et al.* 2015). As in other pleurodires (and turtles in general), the parietal contributes dorsally to the margin of the foramen nervi trigemini (Figs 3C, 4A), along with the prootic posteriorly and the pterygoid ventrally (Gaffney 1979; Gaffney *et al.* 2011).

Jugal. The jugal is preserved only on the left side and the only visible contacts are dorsomedially with the postorbital, ventrally with the palatine, and posteroventrally with the pterygoid (Figs 2L, 3). The jugal forms the lateroventral margin of the orbit as in other Podocnemididae (Gaffney *et al.* 2011). Yet, the rock matrix seems to have preserved a natural cast of the bone, allowing inference of the development of the cheek (anterolateral) emargination of *A. uchoensis*. The emargination surpasses the ventral level of the orbit and reaches about half the level of the cavum tympani (Fig. 2L), differing from the shallower emargination of *H. escuilliei* and *Ba. elegans*, and the more extensive emargination of peiroemydids (Gaffney *et al.* 2011; Ferreira *et al.* 2018b), being more similar to that of *Pod. unifilis* and *Pod. vogli* (Gaffney *et al.* 2011).

Quadratojugal. Only a slender remnant of what appears to be the quadratojugal is preserved on the left side (Fig. 3A), which forms the posteroventral contact with the quadrate, dorsal to the cavum tympani, its only visible contact.

Postorbital. The left postorbital is nearly complete and contacts the frontal anteromedially, the parietal posteromedially, the jugal laterally, and forms the posteroventral margin of the orbit (Fig. 3D), as in other podocnemidoids. It is not reduced as in *Podocnemis* spp., in some species of which it is not even exposed in the skull roof (Gaffney 1979; Gaffney *et al.* 2011). The postorbital of *A. uchoensis*, as in all pleurodires, possesses a ventral projection that contributes to the formation of the septum orbitotemporale, where it contacts the jugal laterally and the pterygoid ventrally, at the base of the processus trochlearis pterygoidei. Anteriorly, the postorbital also contacts the palatine ventrally and the frontal medially, with which it forms the anterior surface of the septum orbitotemporale. As in other pelomedusoids, the postorbital forms the dorsolateral part of the roof of the sulcus palatino-pterygoideus (Fig. 3D; Gaffney *et al.* 2011).

Palatines. The anterior parts are not preserved, but all the posterior contacts can be identified. Apart from contacting its counterpart medially, it possesses a narrow posteromedial contact with the parietal at the base of the sulcus palatino-pterygoideus (Fig. 3D), a posterior contact with the pterygoid, a dorsal contact with the postorbital, and an anterolateral contact with the jugal (Fig. 3B, D). The posterior margin of the foramen palatinum posterius is slightly incomplete, but it is clear that this foramen is restricted to the palatine (Fig. 3B), as in some specimens of *Ba. elegans* (e.g. LPRP/USP 0200; G.S. Ferreira, unpub. data), and in *Pe. mezzalirai*, and *Podocnemis* spp., differing, for instance, from the peiroemydids *Lapparentemys vilavilensis* and *Y. montealtensis* (Gaffney *et al.* 2011; Ferreira *et al.* 2018b), in

which the foramen is instead located along the sutural contact between the palatine and the pterygoid.

Quadrat. The ventralmost portion of both quadrates is incomplete, but the cavum tympani is entirely formed by the bone, as in other pleuropodires (Gaffney 1979; Gaffney *et al.* 2006, 2011). The quadrate contacts the prootic anteriorly and the opisthotic posteromedially with its medial surface (Figs 2B, 3A), as in most other pleuropodires, except for bothremydids, namely *cearachelyines* and *bothremydines*. In these two groups the quadrate extends medially, reaches the supraoccipital and prevents the contact between prootic and opisthotic on the surface of the otic capsule (Gaffney *et al.* 2006). A small contact with the putative quadratojugal can be seen dorsal to the cavum tympani in MPPC 01-0040 (Fig. 3E). The fossa precolumellaris is large, as is also the case in *Pe. mezzalirai* and *Y. montealtensis*. It is larger than in *Ba. elegans* and other non-podocnemidid podocnemidoids (e.g. Tong & Buffetaut 1996; Lapparent de Broin 2000;

Gaffney *et al.* 2011). The antrum postoticum is well-developed, but not as much as in *Y. montealtensis* (Ferreira *et al.* 2018b), resembling more the condition seen in *Podocnemis* spp. Despite being ventrally broken, it is possible to infer that the Eustachian tube and the stapes were enclosed by bone within the *incisura columellae auris*, as in most pleuropodires (Gaffney *et al.* 2006, 2011).

The quadrate forms a posteromedial process that extends from the base of the articular process for the mandible along the ventral surface of the cranium and reaches the braincase, forming a triple contact with the basioccipital and the basisphenoid (Fig. 3B), as is characteristic of Podocnemidoidea (Gaffney *et al.* 2006, 2011). Besides that, as a synapomorphy for Podocnemididae, the quadrate of *A. uchoensis* laterally contributes to the formation of the cavum pterygoidei (Figs 2D, 3B). The cavum pterygoidei is otherwise enclosed by the basisphenoid posteromedially, the prootic anterodorsomedially, and the pterygoid anterolaterally (Gaffney *et al.* 2011). The mandibular condyle is

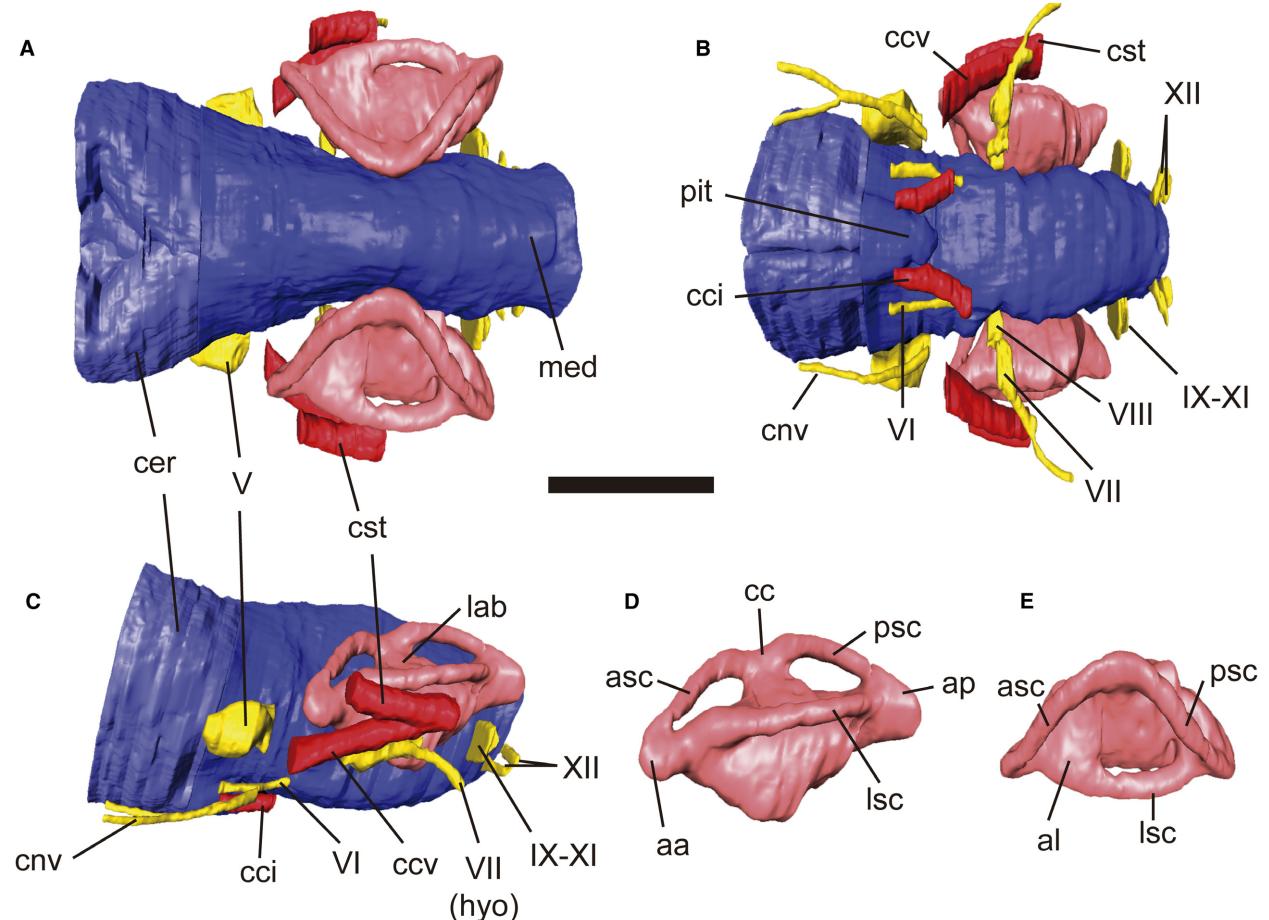


FIG. 6. *Amabilis uchoensis* gen. et sp. nov., MPPC 01-0040. Endocranial cast with associated structures virtually reconstructed in: A, dorsal; B, ventral; C, left lateral view; D–E, left labyrinth in: D, left lateral; E, dorsal view. Abbreviations: aa, anterior ampulla; al, lateral ampulla; ap, posterior ampulla; asc, anterior semicircular canal; cc, crus communis; cci, canalis caroticus internus; ccv, canalis cavernosus; cer, cerebral hemispheres; cnv, canalis nervi vidiani; cst, canalis stapedio-temporalis; lab, labyrinth; lsc, lateral semicircular canal; med, medulla oblongata; pit, pituitary cast; psc, posterior semicircular canal; V–XII, cranial nerves V–XII; VII (hyo), hyomandibular branch of the cranial nerve VII. Scale bar represents 0.5 cm. Colour online.

not preserved in MPPC 01-0040, but it is possible to infer its position anterior to the basioccipital/basisphenoid suture, as in most of the Podocnemididae (Gaffney *et al.* 2011; Ferreira *et al.* 2018b). The posteriormost portion of the quadrate is not preserved. However, it is possible to identify the fenestra postotica, an opening that allows the passage of some cranial nerves and blood vessels, such as the stapedial artery (Gaffney 1979). The posterior opening for the jugular vein, the foramen jugulare posterius, has merged with the fenestra postotica, resulting in a mediolaterally wide opening. This morphology is identical with that of other podocnemidoids such as *Br. josai* and *Por. patagonica*, but distinct from the slit-like fenestra postotica of carachelyine bothremydids (Gaffney *et al.* 2006, 2011).

Pterygoid. The pterygoid contacts its counterpart medially, the parietal dorsally, the prootic posterodorsally, the palatine anteriorly, the basisphenoid posteromedially, and the quadrate posterolaterally, as in other podocnemidoids (Gaffney *et al.* 2011; Ferreira *et al.* 2018b; Fig. 2D). As typical in the Podocnemididae lineage, the pterygoid of *A. uchoensis* has a well-developed flange on its ventral surface, which approximately parallels its lateral margin (França & Langer 2006), broadly forms the floor of the fossa pterygoidea, and forms a complete cavum pterygoidei. As in other pleurodires, the pterygoid also forms the processus trochlearis pterygoidei laterally (Gaffney 1979). The angle between the body of the process and the skull midline is almost 90° (Fig. 3A), similar to that of *Y. montealtensis*, *Podocnemis* spp., *Por. patagonica*, and *Pe. mezzalirai* (de la Fuente 2003; Gaffney *et al.* 2011; Ferreira *et al.* 2018b), but differing from the condition of *H. escuilliei*, *Ba. elegans*, and *L. vilavilensis*, in which that angle is slightly narrower (Tong & Buffetaut 1996; Gaffney *et al.* 2011).

Unlike *H. escuilliei*, *Ba. elegans*, peiropemydids, and some podocnemidids (Albrecht 1976; Gaffney *et al.* 2011; Ferreira *et al.* 2018b), *A. uchoensis* lacks a foramen anterius canalis caroticum palatinum or a palatine canal along the dorsal surface between the pterygoid and basisphenoid (Fig. 4C), through which the palatine artery usually exits the basicranium into the cavum cranii (Gaffney 1979; Gaffney *et al.* 2011; Rabi *et al.* 2013). The absence of such structures hints at the possibility of the complete loss of this artery, as previously suggested for pleurodires by Albrecht (1976). However, all the other foramina described by Gaffney *et al.* (2011) as present in the cavum pterygoidei, that is, the foramen nervi abducentis, foramen posterius canalis carotici interni, foramen nervi facialis, and foramen nervi vidiani, could be identified in MPPC 01-0040 (Fig. 5A).

The foramen nervi abducentis is positioned posteromedially along the basisphenoid contact, and the foramen posterius canalis carotici interni opens at the anterior edge of the cavum pterygoidei (Fig. 5A). The cavum pterygoidei is roofed by the prootic, differing from that of erymnochelyines, in which the cavity is continuous with the canalis cavernosus, as seen in *Peltocephalus dumerilianus* and *Erymnochelys madagascariensis* (Gaffney *et al.* 2011). The palatal (vidian) branch of the facial nerve extends to the anterior region of the crista pterygoidea (Fig. 4), opening into a small foramen (foramen anterius canalis nervi vidiani of Rollot *et al.* 2018) and in another posterior foramen located laterally to the suture between pterygoid and

basisphenoid. The sulcus cavernosus extends parallel to the basisphenoid contact on the dorsal surface of the pterygoid.

Supraoccipital. Parts of the dorsal and posterior regions of the supraoccipital are broken in MPPC 01-0040, preventing assessment of the degree of exposure on the skull roof. Yet, most of its contacts could be identified, including those with the parietals anterodorsally, the prootics anterolaterally, and the opisthotics posterolaterally on the dorsal surface of the otic chamber (Fig. 3A). The supraoccipital also forms the dorsal margin of the foramen magnum, where it contacts the exoccipitals posteroventrally.

Exoccipital. Each exoccipital contacts the supraoccipital anterodorsally, the opisthotic anterolaterally, and the basioccipital ventrally (Fig. 3F). As in all Podocnemididae, it possesses no contact with the quadrate, differing from the narrow contact of *Br. josai* and the characteristic wide contact of bothremydids (Gaffney *et al.* 2006, 2011). The exoccipital forms the lateral margin of the foramen magnum and bears two foramina for the hypoglossal nerve (XII), as in most turtles (Gaffney 1979). As in *Br. josai*, *H. escuilliei*, and *Por. patagonica*, the foramen jugulare posterius of *A. uchoensis* is laterally confluent with the fenestra postotica, not forming a separate opening (Fig. 3F) as in *Ba. elegans*, peiropemydids, and podocnemidids (Tong & Buffetaut 1996; Lapparent de Broin 2000; de la Fuente 2003; Gaffney *et al.* 2011).

Basioccipital. The basioccipital contacts the basisphenoid anteriorly, the quadrates anterolaterally, and the exoccipitals dorsally (Fig. 3). It contributes to the ventral third of the occipital condyle, differing from *Pe. mezzalirai*, Pelomedusidae and bothremydids, in which this structure is formed solely by the exoccipitals. In occipital view, the tubera basioccipitale are closer to the skull midline (Fig. 3F), as in *H. escuilliei* and *Ba. elegans* (Gaffney *et al.* 2011; Ferreira *et al.* 2018b).

Prootic. The dorsal part of the prootic contacts the parietal anteromedially, the supraoccipital posteromedially, the opisthotic posteriorly, and the quadrate laterally (Fig. 3). Ventrally, the prootic has an extended contact with the basisphenoid medially and the pterygoid laterally, so that it is almost completely covered in ventral view (Fig. 3B), as also seen in other Podocnemididae (França & Langer 2006; Gaffney *et al.* 2011; Ferreira *et al.* 2018b). The prootic is partially exposed within the cavum pterygoidei. The foramen nervi facialis is positioned centrally within the prootic and on the dorsal surface of the cavum pterygoidei. As in other pleurodires, the prootic forms the posterior margin of the foramen nervi trigemini (Gaffney 1979).

Some internal structures of the prootic could be identified. On its medial wall, posterior to the foramen nervi trigemini, there is an opening shared by the facial (VII) and acoustic (VIII) nerves, the fossa acustico-facialis (Fig. 4A). Also, both the canalis cavernosus and the canalis stapedio-temporale could be digitally reconstructed. The canalis cavernosus is bordered laterally by the quadrate and medially by the prootic, extending from the foramen cavernosum, its anterior opening into the cavum cranii, posteriorly towards the fenestra postotica. The canalis stapedio-

temporale branches off the canalis cavernosus at a position approximately halfway along the latter (Fig. 4A) and is also bordered laterally by the quadrate and medially by the prootic. This canal transmits the stapedial artery from the fenestra postotica to the adductor chamber, exiting through the foramen stapedio-temporale, surrounded by the prootic and the quadrate bones too. This foramen opens anterodorsally in *A. uchoensis* (Figs 3, 4), unlike most podocnemidoids in which it is located more dorsally (Gaffney *et al.* 2006, 2011; Ferreira *et al.* 2018c).

Opisthotic. As in other podocnemidoids (e.g. *Br. josai*, *H. escuilliei*, *Ba. elegans* and peiropemydids), the opisthotic of *A. uchoensis* contacts the quadrate laterally, the supraoccipital medially, the exoccipital posteriorly, and the prootic anteriorly (Tong & Buffetaut 1996; Lapparent de Broin 2000; Gaffney *et al.* 2011; Fig. 3A). The processus interfenestralis of the opisthotic is ventrally covered by bone, as in euraxemydids and Podocnemidoidea (Gaffney *et al.* 2006, 2011). However, it does not contact the floor of the basicranium and instead projects as a free process into the cavum acustico-jugulare (Fig. 4A).

Basisphenoid. The ventrally exposed surface of the basisphenoid is pentagonal in shape (Figs 3, 4), as in most Podocnemidoidea (Gaffney *et al.* 2011), and lacks a ventrally exposed anterior process that separates the pterygoids, as in chelids and some pan-pelomedusoids (Gaffney 1977; Gaffney *et al.* 2006; Ferreira *et al.* 2018b). The basisphenoid contacts the pterygoids anteriorly, the quadrates posterolaterally, the basioccipital posteriorly, and the prootics anterolaterally, the latter at the dorsal region of the cavum pterygoidei. On the dorsal surface of the basisphenoid, the rostrum basisphenoidale extends anteriorly over the pterygoids (Fig. 4), similar to that of other podocnemidoids (Gaffney *et al.* 2011).

Posteriorly, the sella turcica is deeply excavated, and the low dorsum sellae forms a well-defined margin to the sella. Each posterolateral margin of the sella turcica is pierced by a foramen anterius canalis carotici cerebralis (Rabi *et al.* 2013; foramen anterius canalis carotici interni of Gaffney 1979; Fig. 4C). Right and left foramina are widely separated from the skull midline. Similar to *H. escuilliei*, *Ba. elegans* and peiropemydids, the canalis caroticus internus of *A. uchoensis* is a distinct canal that extends posterolaterally within the basisphenoid, differing from the condition of *Podocnemis* spp., in which the foramen anterius canalis carotici cerebralis is extremely short, almost reducing the course of the artery to a planar opening (Gaffney *et al.* 2011). The foramen nervi abducentis opens at the base of the small, anteriorly projecting processus clinoideus, and pierces the basisphenoid in a straight trajectory (Fig. 4). This foramen is small, in contrast to the large opening seen in *Podocnemis* spp. and *Pr. caiera*, and also opens laterally to the basisphenoid, within the cavum pterygoidei (Gaffney *et al.* 2011).

Cranial endocast. The chelonian cranial endocast has a tubular shape and can be subdivided into anterior, middle, and posterior regions (Wyneken 2001; Paulina-Carabajal *et al.* 2013, 2017). Because of the incomplete preservation of the dorsal part of the parietal of MPPC 01-0040, as well as of the medial portion of the frontals, and the lack of the anterior part of the skull, the

anterior region of the endocast of *A. uchoensis* could not be digitally reconstructed, precluding the visualization of its nasal cavity and olfactory nerve canal. In contrast, part of the left cerebral hemisphere was reconstructed and mirrored to generate a bilateral model (Fig. 6A–C).

The cerebral hemispheres resemble those of some fossil podocnemidoids (e.g. *Stereogenys cromeri* and *Y. montealtensis*; Gaffney *et al.* 2011; Ferreira *et al.* 2018b) and extant turtles (e.g. *Pod. unifilis*, *Gopherus berlandieri* and *Rhinoclemmys funerea*; Paulina-Carabajal *et al.* 2017; Lautenschlager *et al.* 2018), being slightly expanded laterally. They differ from the condition seen in some bothremydid natural endocasts, in which the cerebral hemispheres appear to be very laterally expanded (e.g. Gaffney & Zangerl 1968; Gaffney *et al.* 2006). As in all turtles (except maybe *Proganochelys quenstedti*; Bhullar & Bever 2009), the unossified anteroventral and anterolateral walls of the braincase prevent the reconstruction of the paths of cranial nerves II–IV, which can be seen in the preserved laterosphenoid of *Pro. quenstedti* (Bhullar & Bever 2009; Lautenschlager *et al.* 2018). In turn, the midbrain region is usually poorly defined in the endocast of turtles (Paulina-Carabajal *et al.* 2017).

The posterior region of the *A. uchoensis* endocast contains structures such as the cartilaginous rider, the medulla oblongata and cranial nerves V–XII (Gaffney & Zangerl 1968; Paulina-Carabajal *et al.* 2013, 2017). Projecting posteriorly from the ventral part of the endocast is the pituitary cast (Fig. 6B). Dorsally there is no sign of a cartilaginous rider, apparently due to the preservation of the fossil. This structure would correspond to the position of the pineal gland, but the correspondence between both structures is well established only for the sea turtles *Dermochelys coriacea* and *Eretmochelys imbricata* (Wyneken 2001; Paulina-Carabajal *et al.* 2013). According to some authors (e.g. Zangerl 1960; Paulina-Carabajal *et al.* 2017; Lautenschlager *et al.* 2018; Evers *et al.* 2019a), the cartilaginous rider represents the unossified anterior portion of the supraoccipital, which would be filled in life only by cartilaginous rather than encephalic tissue.

Laterodorsally to the pituitary, the path for the trigeminal nerve (V) projects laterally from the cranial endocast, as in all other turtles for which there are digital reconstructions or natural endocasts (e.g. Gaffney & Zangerl 1968; Paulina-Carabajal *et al.* 2013, 2017; Mautner *et al.* 2017; Ferreira *et al.* 2018b; Lautenschlager *et al.* 2018). The hyomandibular branch of the facial nerve (VII) pierces the prootic in an almost straight line (Fig. 6B), perpendicular to the cerebral endocast, to the point in which it divides into two short canals (chorda tympani), next to the incisura columellae auris in the quadrate. The palatal (or vidian) branch of the facial nerve (Fig. 6) exits the pterygoid anteriorly and opens posteriorly within the cavum pterygoidei in the prootic, while the acoustic nerve (VIII) projects laterally from the same opening as the facial nerve, the fossa acustico-facialis (Fig. 4A).

The glossopharyngeal (IX), vagus (X), and accessory (XI) nerves were reconstructed as a single digital structure (Fig. 6), given that they share the same cranial path in most turtles (Gaffney 1979). As for the canals for the hypoglossal nerve (XII), two branches exit the cavum cranii and pierce the exoccipitals posterovertrally as in most turtles (Gaffney 1979), but not in *Pro. quenstedti*, some bothremydids, and stereogenyines, in

which the two branches share a single foramen (Gaffney *et al.* 2006; Ferreira *et al.* 2015; Lautenschlager *et al.* 2018).

Last, only the cerebral branch of the carotid artery is present in *A. uchoensis*, as in the pleurodires *Chelus fimbriatus*, pelomedusids, araripemydids, euraxemydids and bothremydids, in which the canal for the palatal branch is absent (Gaffney *et al.* 2006). The cerebral canal pierces the basisphenoid anterolaterally at a slightly acute angle and enters the braincase at the foramen posterius canalis carotici interni, within the cavum pterygoidei, as in other Podocnemididae (Gaffney *et al.* 2011; Ferreira *et al.* 2018b).

Inner ear. The virtually reconstructed inner ear of *A. uchoensis* is very similar to those of other turtles, with a short lagena and dorsoventrally low semicircular canals that have subequal lengths and an elliptical inner cross-section (Wever 1978; Paulina-Carabajal *et al.* 2013; Ferreira *et al.* 2018b; Fig. 6). It is 0.7 cm long, 0.56 cm high and 0.38 cm wide. The vertical canals (anterior and posterior) are more elongated than in sea turtles and tortoises (e.g. Georgi 2008; Neenan *et al.* 2017; Lautenschlager *et al.* 2018; Evers *et al.* 2019a) and also thinner, but not as slender as those of chelid turtles (Georgi 2008; Georgi & Sipla 2008; Evers *et al.* 2019a).

The anterior semicircular canal (ASC) is somewhat arched as in other pelomedusoids (Ferreira *et al.* 2018b; Lautenschlager *et al.* 2018), differing from that of chelids, in which it is straighter (Georgi 2008; Lautenschlager *et al.* 2018). The ASC is slightly longer than the posterior semicircular canal (PSC; 0.48 cm vs 0.35 cm, respectively). Differently from those of *Pod. unifilis* and *Y. montealtensis*, the ASC and PSC of *A. uchoensis* are located at the same height (Ferreira *et al.* 2018b; Lautenschlager *et al.* 2018; Fig. 6D). The crus communis is not as anteroposteriorly wide as in sea turtles and some tortoises (Neenan *et al.* 2017; Paulina-Carabajal *et al.* 2017; Lautenschlager *et al.* 2018; Evers *et al.* 2019a), possessing a shallow dorsoventral notch, as in *Pod. unifilis* and *Y. montealtensis* (Ferreira *et al.* 2018b; Lautenschlager *et al.* 2018), and the angle between the ASC and PSC is 82°.

RESULTS AND DISCUSSION

Phylogenetic analysis

The phylogenetic analysis (see Fig. 7 for a simplified version of the strict consensus tree; the complete version can be found in the supplementary material provided in Hermanson *et al.* 2020) resulted in 90 MPTs with 1480 steps each (CI = 0.251, RI = 0.732; best score hit 100 times). The present results differ from those of Ferreira *et al.* (2018a, b) in finding araripemydids and euraxemydids nested within Pelomedusoides, and not as pan-pelomedusoids outside Pelomedusoides; the same phylogenetic position was previously retrieved by other analyses (e.g. Meylan 1996; Gaffney *et al.* 2006, 2011; Romano *et al.* 2014). In all MPTs, *Amabilis uchoensis* is positioned as a non-podocnemidid member of Podocnemididae. Podocnemididae is characterized by the small entrance of the

antrum postoticum, a complete cavum pterygoidei, parallel craniolateral margins of vertebral scale 1 (char. 207), a short path for the cerebral carotid canal that enters the braincase anteriorly to the foramen stapedio-temporale (char. 257), and foramina nervi hypoglossi ventrally covered by an extension of the basioccipital and exoccipital (char. 265).

Some of the new characters based on the available µCT data were retrieved as synapomorphic for different pleurodiran clades in the analysis. For example, an angle between the vertical (i.e. anterior and posterior) semicircular canals of the labyrinth less than 90° (char. 248) was identified as characteristic of Pelomedusoides. According to Paulina-Carabajal *et al.* (2017), this feature is commonly observed in turtles with a more aquatic lifestyle. However, little research has so far been done to quantitatively determine whether aspects of the labyrinth shape of turtles can be explained by ecological preferences (but see Evers *et al.* 2019a).

The presence of a canal for the palatal (vidian) branch of the facial nerve (char. 262) was also recovered as synapomorphic for Pelomedusoides. The clade formed by Taphrosphyini + Bothremydini (Bothremydodda of Gaffney *et al.* 2006) has a small opening between the lateral semicircular canal and the vestibule (char. 250), and a ratio between the lengths of the ASC and PSC of less than 1.1 (char. 252). Yet, a groove on the posterior surface of the condylus mandibularis (char. 264) was found synapomorphic for Bothremydini and for some Taphrosphyini (see Hermanson *et al.* 2020). Additionally, members of the clade Peiropemydidae + Podocnemididae (Podocnemidinae of Gaffney *et al.* 2011) have ASCs that extend dorsoventrally higher than the PSCs (char. 251). Also, a more laterally positioned path for the carotid canal (char. 258) was found only in the analysed taphrosphyines, with the angle between the foramen anterius canalis carotici cerebralis and the foramen posterius canalis carotici interni being greater than 140°.

Although not recovered as synapomorphic for any clade in the phylogenetic analysis, some other characters also deserve attention. A medulla oblongata positioned completely below the level of the cerebral hemispheres (char. 255) and a <1.1 ratio between the ASC and PSC lengths (char. 252) were found to be homoplastic, given that they are optimized as appearing independently in bothremydids and stereogenyines (which are considered littoral or marine taxa; Gaffney *et al.* 2006; Ferreira *et al.* 2015). This last feature can also be seen in some extant and extinct marine turtles (Paulina-Carabajal *et al.* 2013; Neenan *et al.* 2017). Finally, in both *Phosphatochelys telfordi* and *Ummulisani rutgersensis*, part of the internal carotid canal is dorsally open, forming a groove between the basisphenoid and prootic (char. 260), a condition somewhat similar to that found in modern chelonioids

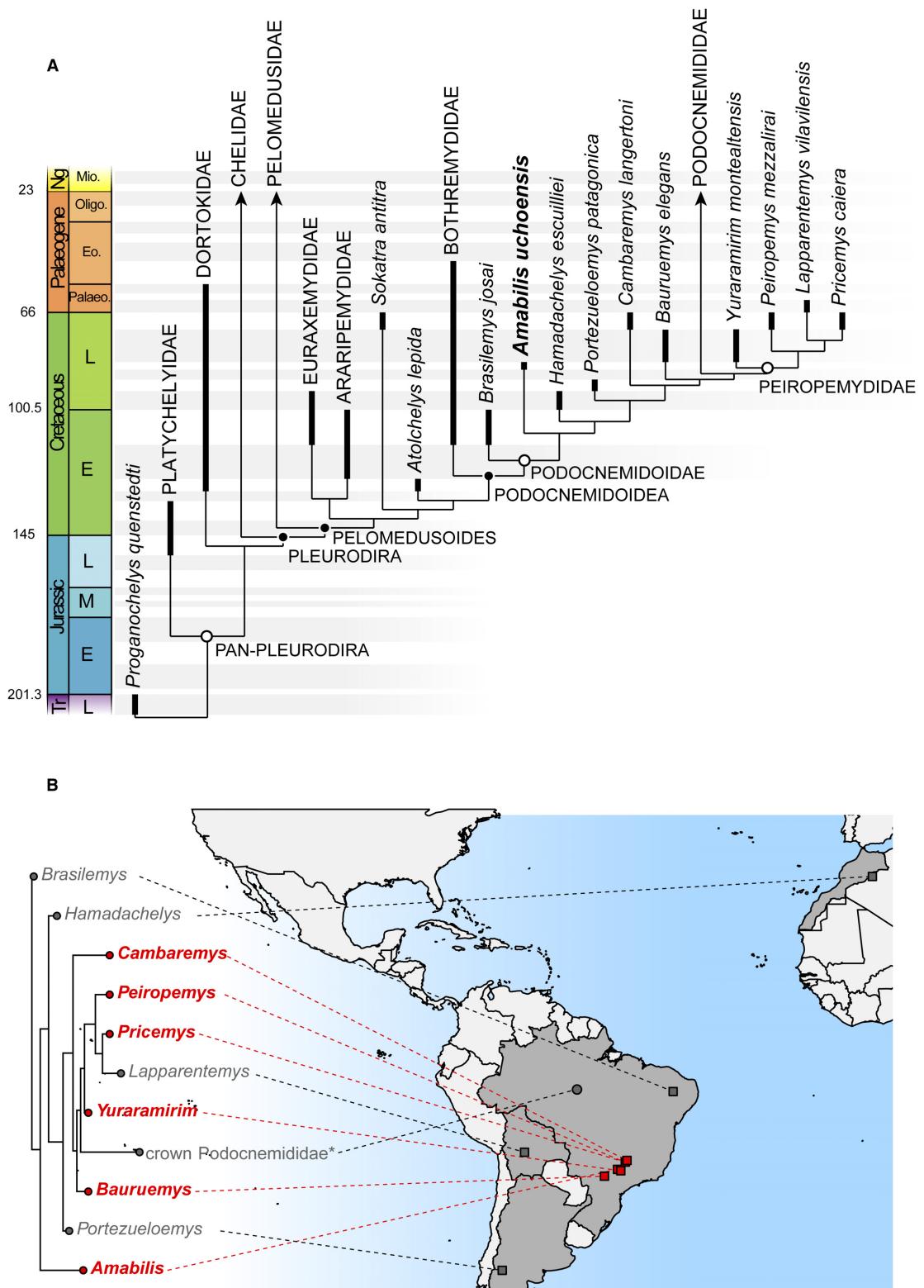


FIG. 7. A, simplified strict consensus tree of the phylogenetic analysis; black-filled circles represent node-based clades and white-filled circles represent stem-based clades. B, part of the strict consensus tree, showing the relationships between non-podocnemidid Podocnemididae (squares) plotted against their geographical occurrences, highlighting the Bauru Group taxa. *Crown Podocnemididae indicated as South American based on ancestral area reconstruction in Ferreira *et al.* (2018a). Figure constructed using *phytools* (Revell 2012) function *phylo.to.map()* in R (R Core Team 2019). Colour online.

(Albrecht 1976; Evers & Benson 2019; Matzke & Maisch 2019). Given that this is one of the pioneer studies using CT in a cladistic analysis of turtles (e.g. Evers & Benson 2019; Evers *et al.* 2019b), and given the small sample of taxa for which there is available data of this kind (c. 24%), further studies should be conducted to confirm the above character optimizations.

Innervation and carotid circulation in pleurodires

In all pleurodires, the internal carotid artery enters the basicranium through the foramen posterius canalis carotici interni (Rabi *et al.* 2013), commonly located within the basisphenoid or prootic (e.g. Gaffney *et al.* 2006; Sterli & de la Fuente 2010; Evers & Benson 2019). The entire course of the carotid artery, as well as its split into the cerebral and palatal branches, is floored by bone (Sterli & de la Fuente 2010). The split of the internal carotid into two subordinate branches, however, may be absent in some pleurodires (see also Gaffney *et al.* 2006): only chelids and some podocnemidoids possess a foramen anterius canalis carotici palatinum, that is, the anterior opening through which the palatine artery exits the basicranium (Rabi *et al.* 2013), and therefore unambiguous osteological evidence for the presence of a palatine artery. It is possible, however, that the split between the two branches takes place anteriorly to the sella turcica, as suggested by Joyce *et al.* (2018) for carettochelyids. Also, whereas in chelids the palatine and cerebral canals possess approximately the same diameter, podocnemidoids evolved a much larger foramen and canal for the palatine branch (Fig. 8), possibly related to the development of the cavum pterygoidei.

In pleurodires that lack osteological evidence for a palatine artery, the canal of the internal carotid takes an anteromedial path that is identical to that of the cerebral artery of pleurodires with both arterial branches, i.e. it traverses the basisphenoid and exits into the sella turcica. We also found that *Araripemys barretoi*, previously interpreted as having the foramen for the palatine artery (e.g. Meylan 1996; Gaffney *et al.* 2006), also lacks that aperture. In fact, the structure identified by Meylan (1996) and Gaffney *et al.* (2006) as the foramen caroticum laterale is actually the opening for the abducens nerve (VI) that pierces the basisphenoid. Thus, we propose that probably the plesiomorphic condition for pelomedusoids is the absence of the foramen, which is regained in Podocnemididae, and lost again in the coastal/marine stereogenyines (Fig. 8).

In the majority of the analysed pleurodires, the internal carotid artery enters the braincase at a slightly acute angle (Fig. 8), almost parallel to the skull midline axis, as in other non-pleurodire turtles such as *Pro. quenstedti*,

baenids (*Eubaena cephalica* and *Arundemys dardeni*), thalassochelydians (*Plesiochelys* spp.) and carettochelyids (e.g. Joyce *et al.* 2018; Lautenschlager *et al.* 2018; Rollot *et al.* 2018; Evers & Benson 2019; Evers *et al.* 2019a; Raselli & Anquetin 2019), or even at more acute angles, as in the case of podocnemidoids and *Galianemys* spp. However, taphrosphyine bothremydids (*Labrostochelys galkini* AMNH 30043, *Taphrosphys ippolitoi* AMNH 30500, *Phosphatochelys tedfordi* AMNH 30008 and *Ummulisani rutgersensis* AMNH 30569) evolved a different condition exhibiting a very lateralized path for the carotid artery, in which the angle between the anterior and posterior foramina for the canal is greater than 140° (Fig. 8).

Last, the facial nerve (VII) path is also variable in pleurodires. None of the analysed specimens possesses a foramen pro ramo nervi vidiani, which is typical of cryptodires (Gaffney 1979; Evers & Benson 2019) and baenids (at least for *Eu. cephalica*; Rollot *et al.* 2018). Chelids lack an exclusive canal for the palatal (vidian) branch of the facial nerve, which is seen in all other pleurodires (Fig. 8). A closer examination of the inner skull anatomy of pan-pleurodires such as *Pl. oberndorferi* and *N. laticentralis* (Lapparent de Broin *et al.* 2007) may clarify whether this canal was lost in the chelid lineage or if its absence represents the plesiomorphic condition for the group. The canal for the vidian branch was observed in all other side-necked turtles, extending from the geniculate ganglion (where the hyomandibular branch also originates; Evers & Benson 2019) to the anterior portion of the pterygoid, close to the crista pterygoidea, opening into the foramen anterius canalis nervi vidiani, as in *Eu. cephalica* (Rollot *et al.* 2018). The hyomandibular branch, in contrast, is found in all pleurodires, but in two different conditions. It may extend laterally and then bend posteriorly (Fig. 8), as seen in chelids and non-Podocnemidoidea pelomedusoids, as well as in most groups outside Pleurodira (e.g. testudinids and carettochelyids) and Testudines (e.g. baenids, plesiochelyids, and *Pro. quenstedti*; Paulina-Carabajal *et al.* 2013; Joyce *et al.* 2018; Lautenschlager *et al.* 2018; Rollot *et al.* 2018; and Evers & Benson 2019). In contrast, podocnemidoideans (Bothremydidae and Podocnemididae) have a canal for the hyomandibular branch that extends through the prootic almost entirely perpendicular to the midline axis (Figs 6, 8).

The analysis of the nerve and carotid circulation patterns of pleurodires revealed an unappreciated variation. For example, although the posterior foramen for the entrance of the carotid artery is positioned in the pterygoid–quadrate region (Gaffney *et al.* 2006) in the analysed Bothremydinae, that is, Bothremydini plus Taphrosphyini, a more lateralized path is found only in the latter group (Fig. 8), having evolved a single time in pleurodires.

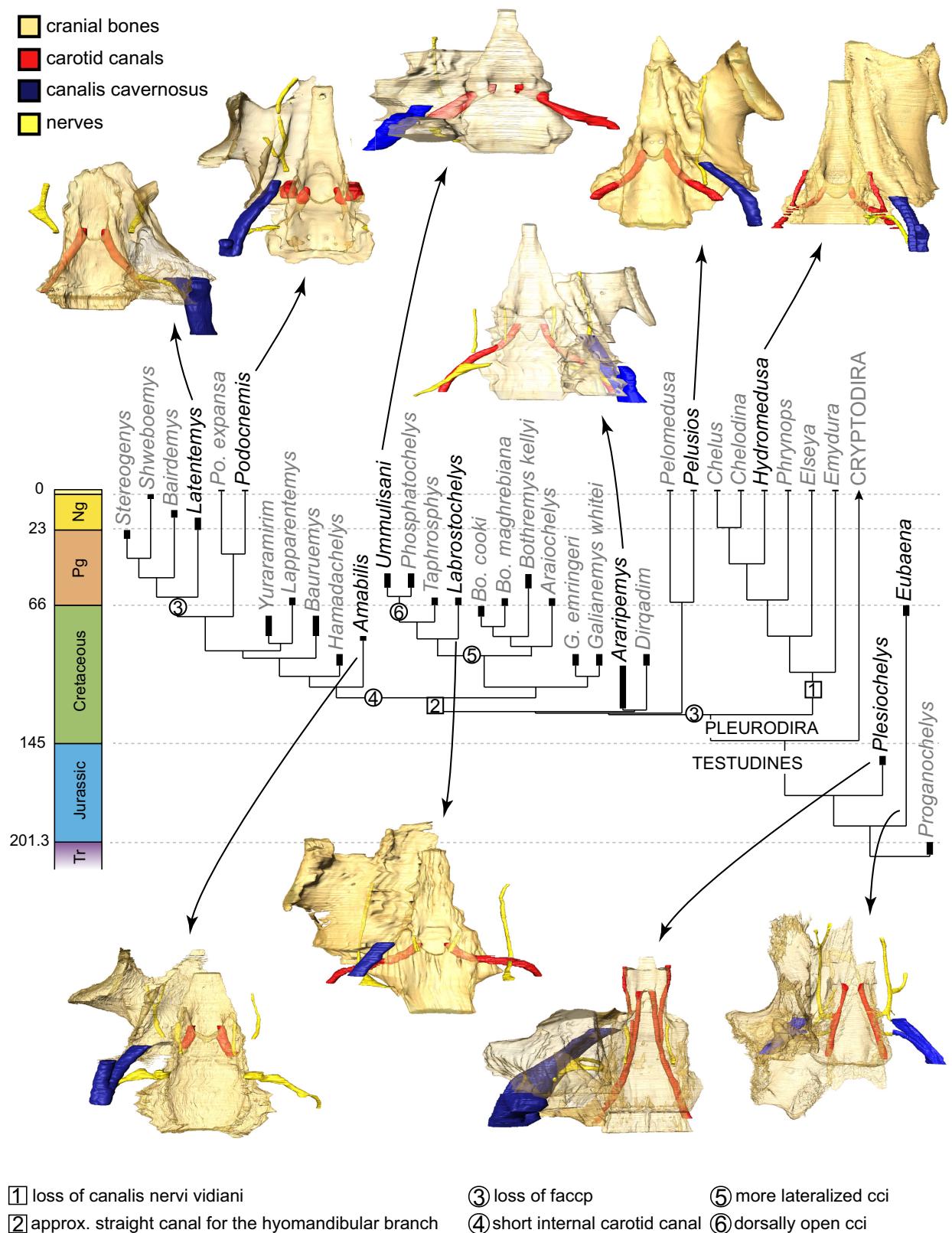


FIG. 8. Evolution of carotid circulation and innervation features in the main lineages of pleurodires, represented in the tree by the taxa for which CT data were investigated. Abbreviations: cci, canalis caroticus internus; faccp, foramen anterius canalis carotici palatinum. Colour online.

Instead, the foramen can be located in the pterygoid–basisphenoid region, within the cavum pterygoidei, both in some bothremydids (e.g. cearachelyines) and in Podocnemididae. Of these, however, the entry for the internal carotid is situated anteriorly to the foramen stapedio-temporale only in the Podocnemididae lineage, being relatively shorter than in the remaining pleurodiran turtles. This highlights the importance of the inner anatomy for establishing relationships in groups for which the external morphology is not variable.

According to Miyashita (2013), although the bones (basisphenoid, prootic, pterygoid and quadrate) enclosing the foramen posterius canalis carotici interni in pleurodirans vary considerably (Gaffney *et al.* 2006), its position in relation to other cranial landmarks is ‘stable within the clade’ (Miyashita 2013, p. 88). Yet, our analysis of innervation and carotid circulation in pleurodirans using μ CT data shows that there is a previously unappreciated variation of paths and internal foramina for the cranial nerves and arteries. The variation in both the internal structures and the bones enclosing the foramen posterius canalis carotici interni might be related to the later timing of palatoquadrate fixation to the braincase in pleurodirans, which is accomplished only when dermal and endochondral ossifications are already well-developed (Werneburg & Maier 2019). The resulting variation is of interest for systematics, as shown by the present phylogenetic analysis, and should be further explored in future works.

CONCLUSION

The new podocnemidoid turtle from the Late Cretaceous São José do Rio Preto Formation increases the diversity of taxa on the stem-lineage to Podocnemididae, highlighting the importance of the Bauru Group fossils in the understanding of the origins of the group (Fig. 7B). Based on an exclusive set of characters, *A. uchoensis* can be attributed to the Podocnemididae lineage. Also, based on μ CT data, new characters were proposed, previous scorings were re-interpreted, and these were included in a new phylogenetic analysis. The recovering of some of these novel characters as synapomorphic for main pleurodiran clades (e.g. Pelomedusoides, Bothremydidae) indicate that, as with other vertebrates (e.g. Coates 1999; Mennecart *et al.* 2017; Pierce *et al.* 2017), neuroanatomy reflects important phylogenetic signals also for pleurodirans.

Our investigation has revealed a previously unknown variety of carotid circulation patterns in pleurodirans. Among Testudines, we find a single loss of the canal for the palatal (vidian) branch of the facial nerve (VII) in chelids, as suggested by Albrecht (1976). We also mapped two independent origins of a specific foramen for the

palatal branch of the carotid artery, in chelids and in the Podocnemididae lineage, although the origin of this foramen appears to be homoplastic across turtle lineages (Fig. 8), given that the presence of the canal varies outside crown Testudines (e.g. present in plesiochelyids and absent in baenids; Rollot *et al.* 2018; Evers & Benson 2019; Raselli & Anquetin 2019). Furthermore, taphrosphyne bothremydids evolved one of the most lateralized paths for the internal carotid among pleurodirans, in which the canal extends virtually perpendicular to the midline axis of the skull, whereas in the majority of pleurodirans (and turtles in general) the carotid enters the braincase at a much more acute angle. We hope that this contribution will serve as a basis for future surveys exploring the inner skull anatomy of a larger sample of pleurodirans, broadening our understanding of the evolution of the cranial innervation and carotid systems in the group.

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DATA ARCHIVING STATEMENT

Data for this study are available in the Dryad Digital Repository: <https://doi.org/10.5061/dryad.sm61m9s>. This published work and the nomenclatural acts it contains, have been registered in ZooBank: <http://zoobank.org/References/9DEEDDFB-0188-4CF4-B46C-5E3E9CED0D4F>.

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