

Unusual shell anatomy and osteohistology in a new Late Cretaceous panchelid turtle from northwestern Patagonia, Argentina

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Rionegrochelys caldieiroi de la Fuente, Maniel, and Jannello gen. et sp. nov. is a Late Cretaceous turtle from Rio Negro Province, Argentina. The holotype and the referred specimens of this new species show an unusual shell morphology and microanatomy. The proportion between the carapace and plastron and the peculiar morphology of the shell such as the heart shaped carapace, a very deep nuchal notch, peripheral bones 2–11 with strongly gutter, the first vertebral scute twice as wide as long and subrectangular in shape, the posterior margin of vertebral scute 5 is three lobe shaped, and the unexpected osteohistology characterized by a massive structure, with higher compactness (80.6%) than other chelids, suggests beyond doubt that this turtle may be considered a new taxon. A semi-aquatic habitat with tendency towards terrestrial environments is inferred for *Rionegrochelys caldieiroi* similar to that of the extant pelomedusid *Pelomedusa subrufa* among the extant pleurodires. *Rionegrochelys caldieiroi* is recovered as a stem chelid. This new species seems to be closely related to *Bonapartemys bajobarrealis* and the clade formed by *Lomalatachelys neuquina* plus *Mendozachelys wichmanni*.

Key words: Testudines, Pleurodira, post-cranial morphology, paleohistology, Cretaceous, Argentina, Río Negro.

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Introduction

“El Anfiteatro” is an area located in northwestern Patagonia with expansive outcrops of five different Cretaceous hori-

zons of the Neuquén Group (i.e., Huincul, Cerro Lisandro, Portezuelo, Plottier, and Bajo de la Carpa formations). Its significant abundance of vertebrate remains has only been explored in recent years (Canudo et al. 2004; Salgado et al.

2009). At the beginning of the 21st century, a state institution of the Province of Río Negro (Argentina) (Endemas, “Ente para el Desarrollo de la Margen Sur”), the National University of the Comahue (Argentina), and the University of Zaragoza (Spain) organized a series of field trips headed by one of us (LS) to the area of the “El Anfiteatro” in search of fossil vertebrates. The remains recovered from these five different lithostratigraphic units were described by Salgado et al. (2009). The Plottier Formation in particular has yielded remains of panchelid turtles, crocodyliforms, titanosaur sauropods, theropods (cf. Carcharodontosauridae, Coelurosauria indet., cf. Unenlagiinae), and ornithopods. Among them, the most complete specimen is the shell of a pleurodire turtle (Panchelidae) referred by Salgado et al. (2009) to Chelidae gen. et sp. indet. The term Panchelidae is herein used to refer to the total group that includes the crown chelids and the stem (Joyce et al. 2004). Panchelidae is the sister group of Panpelomedusoides within Pleurodira but has an opposing geographic distribution and evolutionary history (see Maniel and de la Fuente 2016, and references therein, for most recent summary of the fossil record of the group).

The main goals of this paper are to describe the macro and microanatomy of this new taxon, to point out its morphological and paleohistological peculiarities, and to explore its paleoecology and the relationships of this new chelonian species within the panchelid clade.

Institutional abbreviations.—AMNH, American Museum of Natural History, New York, USA; MACN, Museo Argentino de Ciencias Naturales “Bernardino Rivadavia”, Buenos Aires, Argentina; MHNSR, Museo de Historia Natural de San Rafael, Argentina; MPA, Museo Municipal de Ciencias Naturales “Carlos Darwin” de Punta Alta, Argentina; MPCA, Museo Provincial “Carlos Ameghino”, Cipolletti, Argentina; MZUSP, Museu de Zoologia da Universidade de São Paulo, Brazil; NHMUK, Natural History Museum, London, UK; QM, Queensland Museum, Brisbane, Australia; SMF, Senckenberg Museum Frankfurt, Germany; USNM, National Museum of Natural History, Smithsonian Institution, Washington DC, USA.

Other abbreviations.—MPT, most parsimonious tree; SE, standard error.

Material and methods

Cladistic analysis.—A cladistic analysis was performed to evaluate the phylogenetic relationships of the new species of turtle presented here. A dataset of 23 taxa and 62 morphological characters (see SOM 1, Supplementary Online Material available at http://app.pan.pl/SOM/app62-Fuente_etal_SOM.pdf) based on de la Fuente et al. (2017) was enlarged for the present analysis by adding five new taxa (extant species *Chelydra serpentina* and *Pelomedusa sub-*

rufa, and extinct Upper Cretaceous species *Bonapartemys bajobarrealis*, *Lomalatachelys neuquina*, and *Prochelidella portezuelae*) and one character (character 3, contact frontals-nasals). However, one species was also removed (*Notemys laticentralis*) due to its scarce availability of characters. Four taxa (*Chelydra serpentina*, *Araipemys barretoii*, *Pelomedusa subrufa*, and *Podocnemis sextuberculata*) form the outgroup and 19 taxa of extinct and extant turtles the ingroup. *Chelydra serpentina* was the taxon selected to root the analysis. All characters were weighted equally and twelve characters were ordered (characters 4, 5, 28, 30, 36, 41, 43, 45, 54, 55, 58, 61, and 62). In order to evaluate the phylogenetic relationships of turtles and find the most parsimonious tree (MPT), two cycles of heuristic search were performed as implemented in the phylogenetic program TNT (Goloboff et al. 2008a, b). If more than one MPT was found, a strict consensus tree was calculated. Furthermore, if the strict consensus tree had polytomies in the region of interest, the IterPcR script, written by Pol and Escapa (2009) was run. The script presented by these authors looks for the least stable taxa within the trees, prunes them from the strict consensus, and shows the source of instability (due to contradicted characters or missing data). Clade support was calculated using Bremer support as well as jackknife and bootstrap analyses. In the figure for the cladistic analysis we only show the jackknife and bootstrap values that exceed 50%.

Paleohistology.—We performed five thin sections on five elements, in particular three costal and two peripheral plates of the referred specimen (MPCA-AT 26). The planes of sectioning varied among the different shell bone elements: the costal elements were cut parallel to the anteroposterior axis (perpendicular to the incorporated ribs) and the peripheral elements were cut perpendicular and parallel to the anteroposterior axis of the turtle shell. All thin sections were prepared in accordance with the methodology outlined in Chinsamy and Raath (1992). The bone microstructure of the thin sections was documented using a petrographic polarizing microscope (Nikon ECLIPSE E200). Nomenclature and definitions of structures follow Francillon-Vieillot et al. (1990). The terms “external” and “internal” are used throughout the text instead of “dorsal” and “ventral” to prevent confusion between the dorsal carapacial and ventral plastral bones of the turtle shell (i.e., the “dorsal” surface of a neural plate corresponds to the external surface of the bone, whereas the “dorsal” surface of a plastral plate corresponds to the visceral surface of the bone). The terms “inner/outer” refer to the relative position within the cortical bone, toward the core or toward the surface of the plate, respectively (Scheyer and Sánchez-Villagra 2007). To infer the lifestyle of *Rionegrochelys caldieiroi* de la Fuente, Maniel, and Jannello gen. et sp. nov. on the basis of its shell bone histology, compactness parameters were calculated using the Windows version 4.5.5 of BONE PROFILER Software (Girondot and Laurin 2003; Laurin et al. 2004). Since several of the sampled plates are incomplete or crushed,

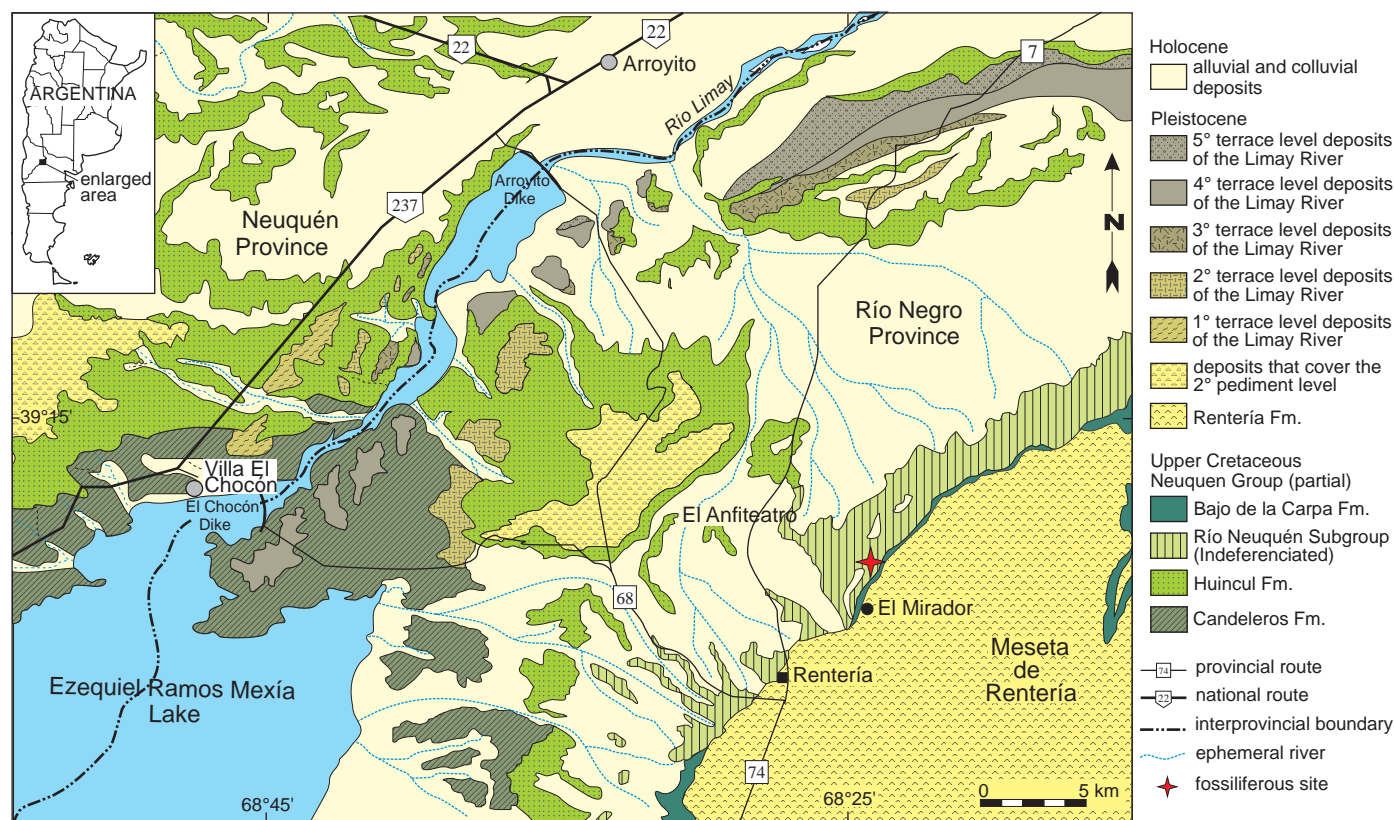


Fig. 1. Geologic map of the “El Anfiteatro” area. Modified from Salgado et al. (2009).

we performed the compactness analysis only on two costal elements. For image analysis, the picture of the sectioned bone was transferred into black and white (black for bone and white for vascular spaces).

Geological setting

The landscape in the area of “El Anfiteatro” comprises a natural depression at the foot of the northern escarpment of the Meseta de Rentería (Fig. 1), which displays an completeness sequence of continental sediments of the Upper Cretaceous assigned to the Neuquén Group (Cazau and Uliana 1973; Hugo and Leanza 2001; Leanza et al. 2008). This sequence includes a set of predominantly fluvial deposits and scarce aeolian and lacustrine deposits. The sequence was deposited between the Cenomanian and the lower Campanian, during the beginning of the foreland basin stage of the Neuquén Basin (Legarreta and Gulisano 1989; Franzese et al. 2003). According to Salgado et al. (2009), in the area of El Anfiteatro, vertebrate-bearing fossiliferous levels have been found in deposits of the Cerro Lisandro (lower Turonian), Portezuelo (upper Turonian–lower Coniacian?), and Plottier (upper Coniacian–lower Santonian), formations included recently by Garrido (2010) as part of the redefined Río Neuquén Subgroup (Figs. 1, 2).

In general, the deposits of the Río Neuquén Subgroup exhibit extensive outcrops along the topographic fronts of

the plateau relief that characterizes the extra-Andean area of the Neuquén Basin. Stratigraphically and sedimentologically this subgroup is characterized by the alternation of meandering fluvial deposits with different sediment-carrying capacities, yielding interstratified intervals of sand-bed and fine-grained meandering streams that define each lithostratigraphic unit (the formations) mainly regulated by climate control (Garrido 2010, 2011). In this context, fluctuating paleoclimatic regimes have been established for the deposits of the Neuquén Group, ranging from humid and subhumid to semiarid conditions, with marked seasonal dry periods (Garrido 2000).

In the area of El Anfiteatro (Fig. 3A), the dominant fine-grained intervals, such as the Cerro Lisandro Formation, form a characteristic relief of badlands (called “huayquerías” in Argentina). By contrast, the sandy-dominated units form high-stepped walls exhibiting their best outcrops in the ravines that cross the region occupying the topographic projections that form the erosive front of the Meseta de Rentería (to the east of El Anfiteatro viewpoint, El Mirador, on Provincial Road 7) (Hugo and Leanza 2001; Leanza et al. 2008).

Several fossils have been reported for these units. In the Cerro Lisandro Formation, bivalves with both valves preserved, teeth and cranial fragments of fishes, and turtles (poorly preserved plates) have been found. In the Plottier Formation (Fig. 3B–D), well-preserved and highly abundant remains of turtles and crocodiles (osteoderms and cranial remains) have been recovered. Dinosaurs are known in

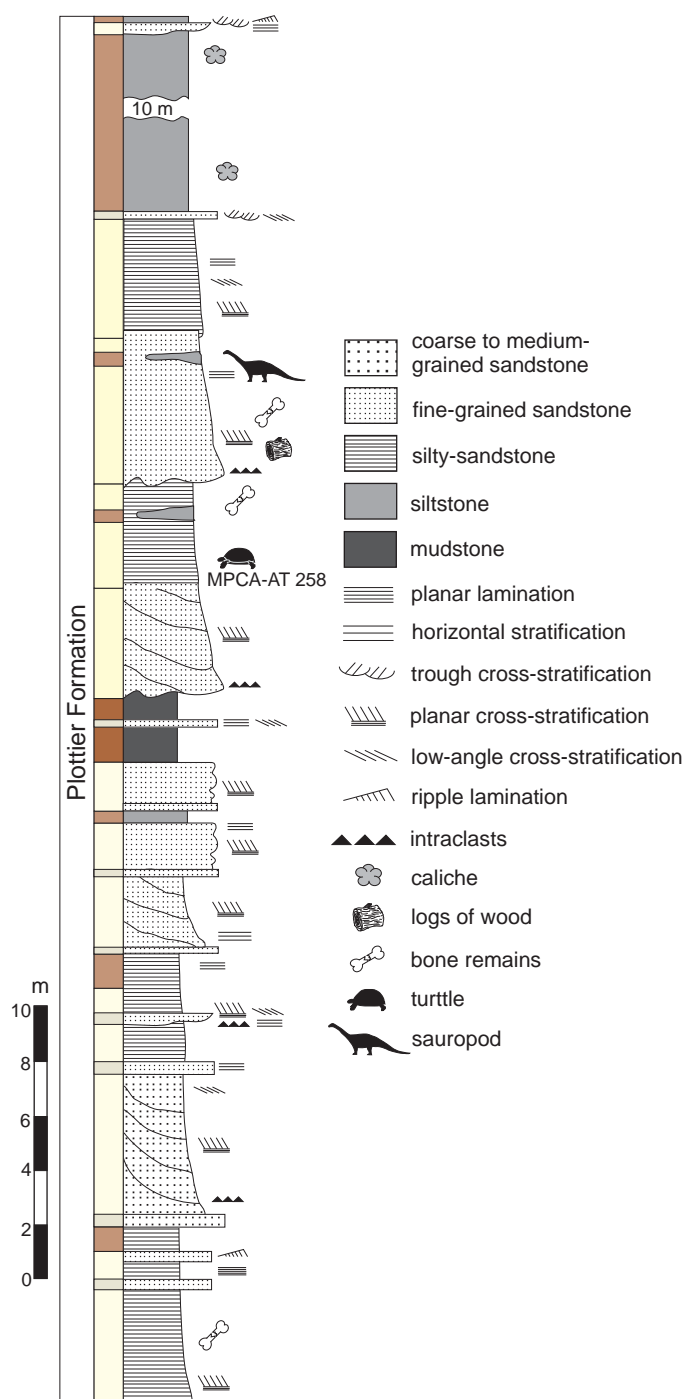


Fig. 2. Stratigraphic profile of the Plottier Formation outcrop, showing the levels where *Rionegrochelys caldieiroi* de la Fuente, Maniel, and Jannello gen. et sp. nov. was recovered. Colours of deposits are indicated accord to Rock-Color Chart Committee (1991). Modified from Salgado et al. (2009).

all these formations, while abundant petrified trunks are known in the Portezuelo and Plottier formations (Salgado et al. 2009). In general terms, the fish and bivalve remains were found in deposits originating in abandoned channels of an ox-bow type, whereas numerous isolated teeth and other small bony remains are mainly associated with sheet flood deposits formed on the flood plain. The channel-filling de-

posits usually contain sizeable remains of silicified wood, as well as large isolated bones of sauropod dinosaurs, most of which are poorly preserved and show evidence of transport. In contrast, the best-preserved and/or most associated bone remains, have been recovered from crevasse deposits. Among them the holotype of *Rionegrochelys caldieiroi* was found in a yellowish mudstone level where no other specimens were retrieved (Fig. 3B–D).

Systematic palaeontology

Testudines Batsch, 1788

Pleurodira Cope, 1865

Panchelidae Joyce, Parham, and Gauthier, 2004

Genus *Rionegrochelys* de la Fuente, Maniel, and Jannello nov.

Type species: Rionegrochelys caldieiroi sp.nov.; see below.

Etymology: From Río Negro Province (Argentina) and from Greek *chelys*, aquatic turtle.

Diagnosis.—As for the type species by monotypy.

Rionegrochelys caldieiroi de la Fuente, Maniel, and Jannello sp. nov.

Figs. 4–6.

Etymology: In honour of the late Ing. Victorino Caldiero (1945–1999), for his contribution to the project of developing the southern margin of Cipolletti, Río Negro Province, Argentina.

Holotype: MPCA-AT 258; carapace and plastron of an adult specimen.

Type locality: Northern flank of the Parrita site (39°18'13" S; 68°24'35" W), El Anfiteatro, Río Negro Province, Argentina.

Type horizon: Upper Cretaceous, Plottier Formation, according to Musacchio (2006) and Musacchio and Vallati (2007), this horizon is Coniacian–Santonian in age, but Garrido (2010, 2011) more recently referred this horizon to the upper Coniacian–lower Santonian.

Material.—MPCA-AT 30, right lateral edge of carapace with plastral bridge suture; MPCA-AT 29, right hypoplastral bone; MPCA-AT 26, isolated plates of a carapace. All from type locality and horizon.

Diagnosis.—*Rionegrochelys caldieiroi* can be diagnosed as a panchelid pleurodire by the suturing of the pelvic girdle to the shell, the presence of a cervical scute, only one suprapygial bone, and vertebral scutes that are narrower than the pleural scutes. It shares with South American panchelids and *Chelodina*: vertebral 1 wider than vertebral 2 and axillary buttresses parallel or adjacent to costal rib 1. It differs from other panchelids by the following unique combination of characters: the first vertebral scute is twice as wide as long and subrectangular in shape, a prominent and discontinuous mid-carapace crest, a strong nuchal notch, peripheral bones 2–11 with strongly gutter ends, posterior margin of the vertebral 5 in the carapace is three lobe shaped, the plastron longer than the carapace, an anteriorly wide thoracic vertebra 1 that is tapered posteriorly in ventral view, in

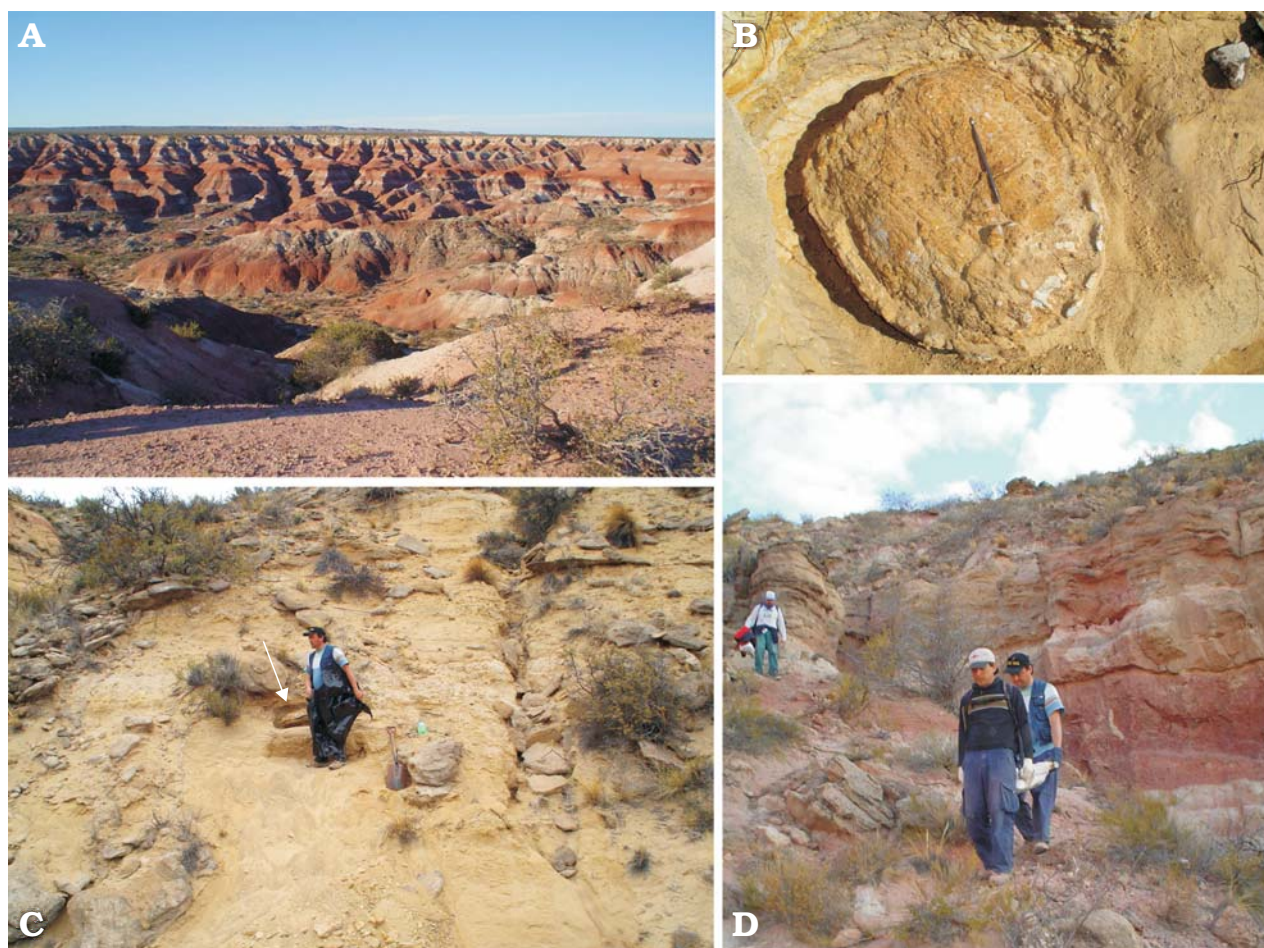


Fig. 3. **A.** General view of the Upper Cretaceous outcrops of the “El Anfiteatro” area, northern Patagonia, Argentina, where the holotype of *Rionegrochelys caldieroi* gen. et sp. nov. was found. **B.** In situ photograph of the holotype of *Rionegrochelys caldieroi* gen. et sp. nov. **C.** Levels of the Plottier Formation (arrow indicates the location of specimen). **D.** Transportation of the holotype.

its heart-shaped carapace, and in its wide and short cuneiform mesoplastra crossed by a humeropectoral sulcus.

Description.—**Carapace:** The carapace of the holotype of *Rionegrochelys caldieroi* is low and wide (length/width ratio 1.03) with a strong nuchal notch (reaching peripheral 1), moderately large in size (carapace length 430 mm), and equivalent in size to *Lomalatachelys neuquina* (Lapparent de Broin and de la Fuente 2001). Contrary to other Cretaceous panchelid species (e.g., *Bonapartemys bajobarrealis*, *Yaminuechelys gasparinii*) and extant South American and Australasian chelids (e.g., *Phrynops hilarii*, MHNSR H-1550, NHMUK 86-3-10-1; *Emydura macquarii*, QMJ 61586, QMJ 78979), where the maximum width is at the margin of the seventh and eighth peripheral bones, in *Rionegrochelys caldieroi* the greatest width is at the margin of the fourth peripheral bones (MPCA-AT 258 carapace maximum width 410 mm). The nuchal notch, the carapace width/length ratio of 1.03, and the curved lateral margins of the posterior peripherals produce a heart-shaped carapacial outline. Although this carapace shape is a characteristic of this species, intraspecific variation in carapace outline is recognized in some chelid species (e.g., *Chelus fimbriatus*, Pritchard and Trebbau 1984;

Sánchez Villagra et al. 1995). These authors point out that the carapace outline of this extant species can be oval, subquad-rangular with straight lateral sides, or with expanded anterior or posterior margins. However, the heart-shaped outline of the *Rionegrochelys caldieroi* carapace is an unusual shape for both extant and extinct panchelid turtles (Maniel and de la Fuente 2016).

The carapace of *Rionegrochelys caldieroi* is decorated with relatively sharp longitudinal crests on the costal bones, as in some Australasian chelids (e.g., *Elseya novaeguineae*, USNM 313654). Along the midline, a discontinuous keel is recognized from the first neural bone to the suprapygial bone. Although the carapace decoration partially obscured sutures between bones in several sectors, the shell seems to be formed, as in crown pleurodires, by one nuchal, eight neurals, 16 costals, 22 peripherals, one suprapygial, and one pygal bone (Maniel and de la Fuente 2016).

The strong nuchal emargination is formed by the first peripheral and the nuchal bone. This emargination is deeper than the condition recognized in *Yaminuechelys gasparinii* and *Y. maior* (de la Fuente et al. 2001; Bona and de la Fuente 2005). Although the nuchal notch of *Rionegrochelys caldieroi* is strongly developed, it is not reaching the first

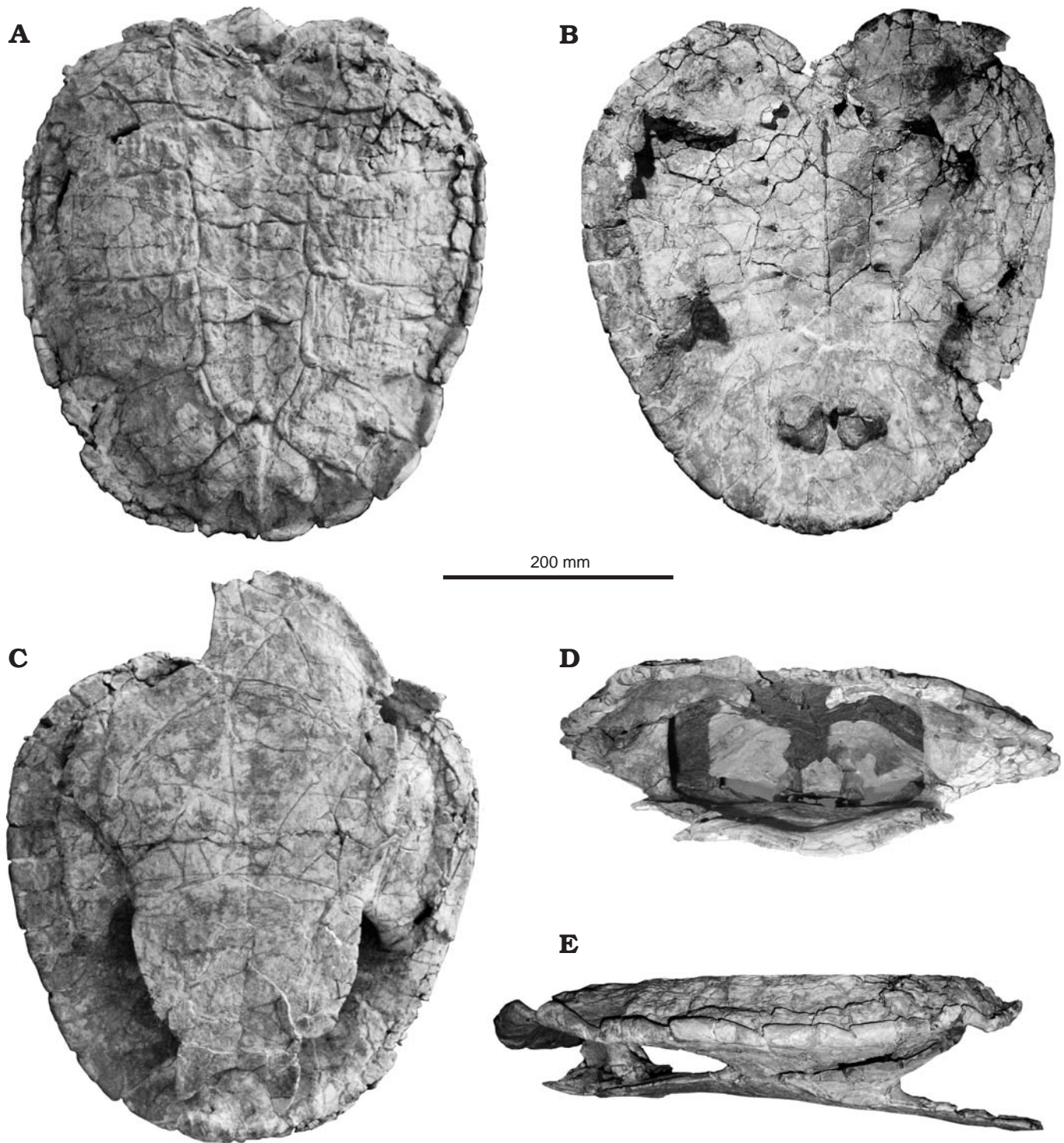


Fig. 4. Photographs of the holotype of the panchelid turtle *Rionegrochelys caldiei* gen. et sp. nov. (MPCA-AT 258) from Parrita site, Upper Cretaceous. Carapace in dorsal (A) and visceral (B) views. Plastron in ventral view (C). Carapace and plastron in anterior (D) and lateral (E) views. Note suturally attached pelvic girdle.

costal as in *Araripemys barretoi* (Meylan 1996). The anterior peripherals, the bridge peripherals, and the posterior peripherals show a strong gutter. Each gutter end is coincident with a marginal scute that extends over half of two consecutive peripheral bones. The posterior free margin of the peripheral bones is slightly indentation in coincidence

with the marginal scutes. A more extreme condition can be recognized in the panpleurodire *Platychelys oberndorferi* (Bräm 1965) and in the chelid *Chelus fimbriatus* (Sánchez-Villagra et al. 1995) which is formed by a strong indentation of the posterior peripheral bones.

The nuchal bone is twice as wide as long, with a wide

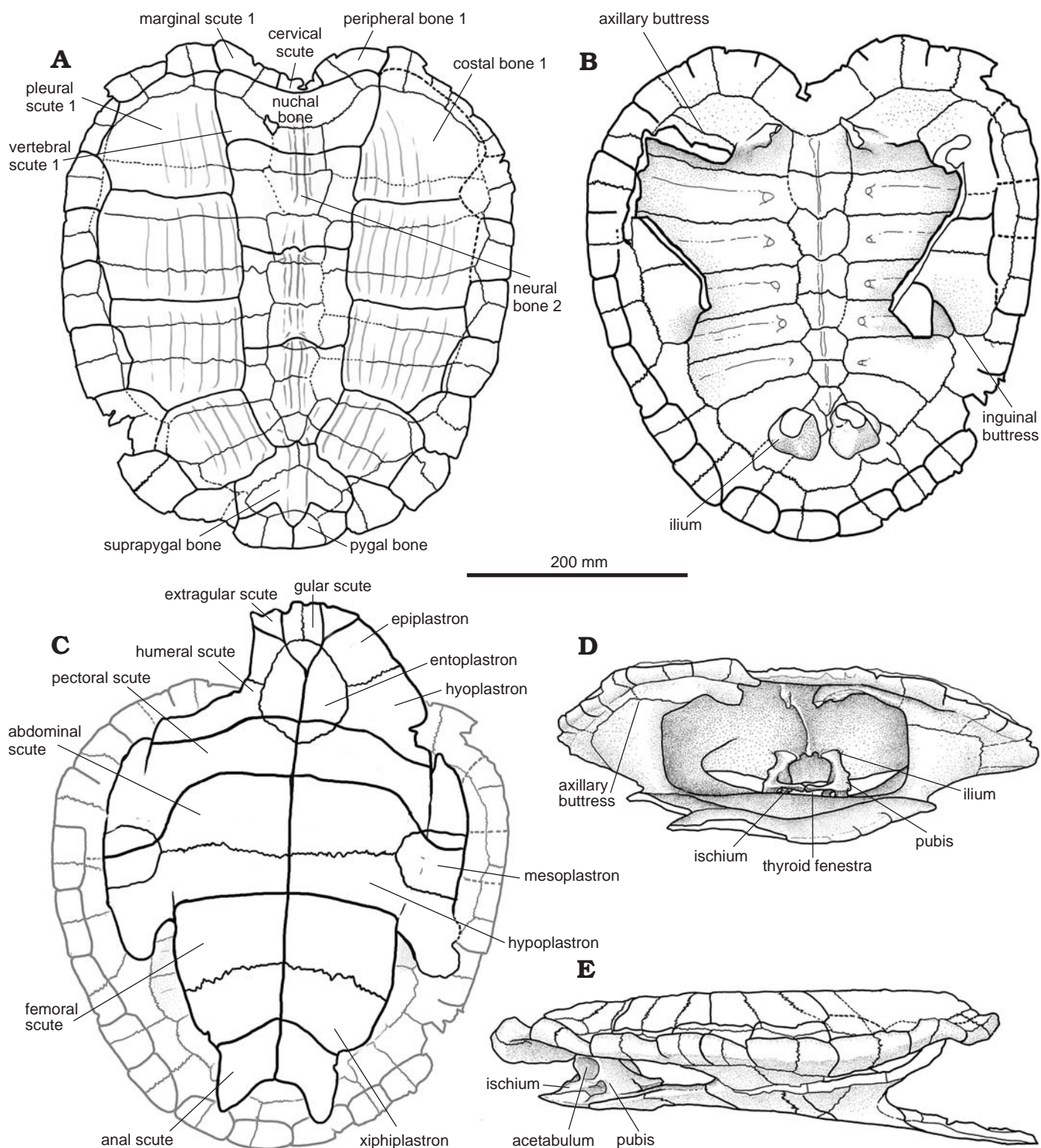


Fig. 5. Explanatory drawings of the holotype of the panchelid turtle *Rionegrochelys caldieroi* gen. et sp. nov. (MPCA-AT 258) from Parrita site, Upper Cretaceous. Carapace in dorsal (A) and visceral (B) views. Plastron in ventral view (C). Carapace and plastron in anterior (D) and lateral (E) views. Note suturally attached pelvic girdle.

cervical scute. Although the costal-neural sutures of the first and second neural bones are not apparent on the left side in dorsal view, they are recognized in visceral view, these neural bone are subquadrangular in shape. The third

to fifth neurals are also sub quadrangular, while the sixth and seventh neural bones are hexagonal. The anterior neural bones are relatively wide as in the extant *Chelus fimbriatus*. This neural pattern with predominant sub quadrangular

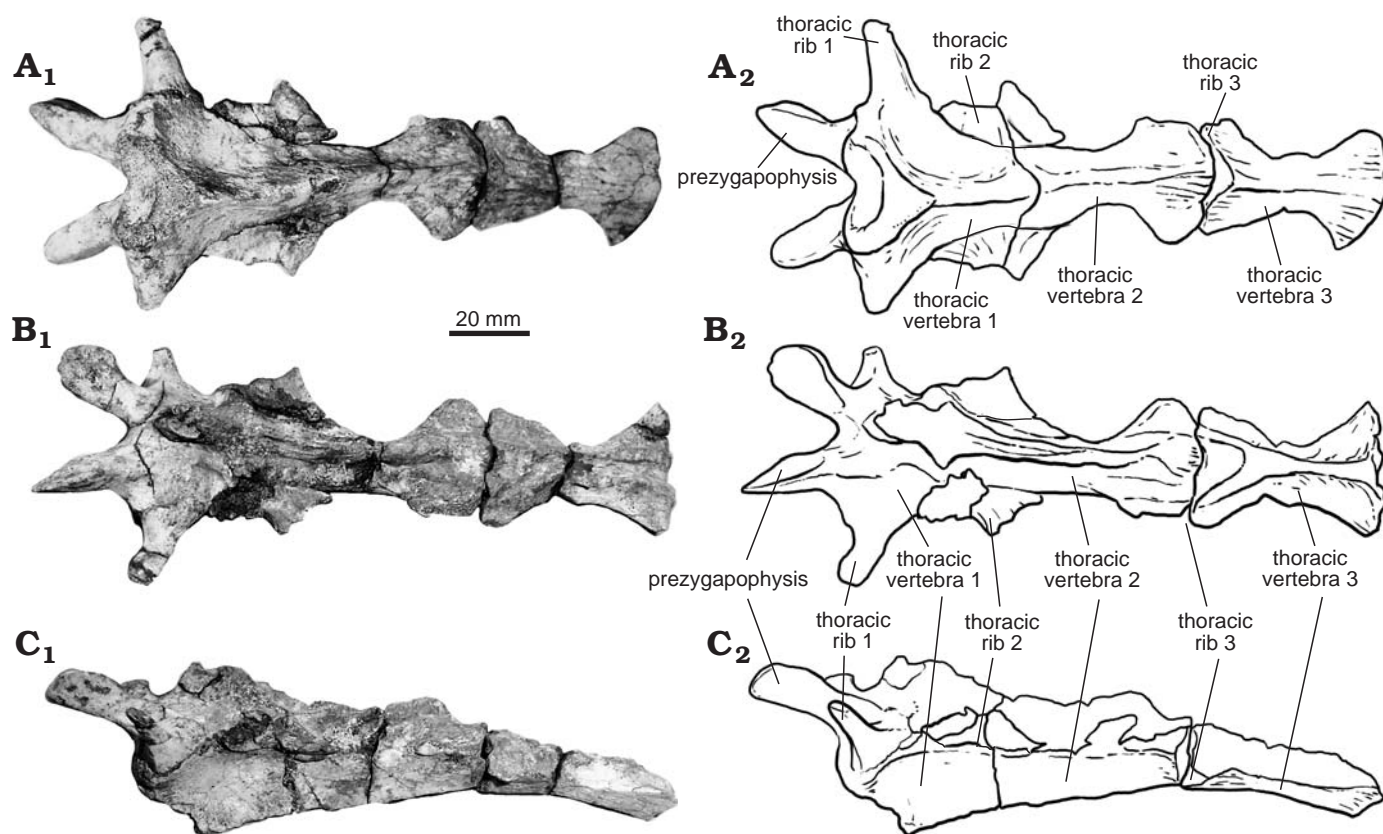


Fig. 6. The holotype of the panchelid turtle *Rionegrochelys caldieroi* gen. et sp. nov. (MPCA-AT 258) from Parrita site, Upper Cretaceous. Thoracic vertebrae 1–3 in dorsal (A), ventral (B), and lateral (C) views. Photographs (A₁–C₁) and explanatory drawings (A₂–C₂).

neural bones deviates from the more frequent chelid condition characterized by narrow quadrangular or hexagonal neural bones (Pritchard 1988). The suprapygal bone is quite large and subpentagonal in shape, while the pygal is nearly trapezoidal. The eighth pair of costal bones contacts one another along the carapace midline. The first to fourth costals have parallel lateral sides, while the lateral end of the fifth and seventh costal bones is much narrower than the lateral end of the adjacent elements.

Costals 1–8 are preserved on both sides of the holotype. As is typical in turtles, costal 1 is the largest costal bone. It is also wider than long. This bone contacts anteromedially the nuchal, anterolaterally peripherals 1–3, laterally peripheral 4, medially neural 1 and 2, and posteriorly costal 2. Costal 2 contacts anteriorly costal 1 and laterally peripherals 4 and 5. Both costals 2 contact posteriorly costals 3. Both costals 3 contact laterally peripherals 5 and 6, medially neurals 3 and 4, and posteriorly costal 4. Costals 4 contact laterally peripherals 6 and 7, medially neurals 4 and 5, and anteriorly and posteriorly costals 3 and 5, respectively. Costals 5 contact anteriorly and posteriorly costals 4 and 6, respectively, laterally peripherals 6 and 7, and medially neurals 5 and 6. Costals 6 contact laterally peripherals 8 and 9, medially neurals 6 and 7, anteriorly costal 5, and posteriorly costal 7. Costals 7 contact laterally peripherals 9 and 10, and medially neurals 7 and 8. Costals 8 contact each other in the midline of the carapace and anteriorly contact neural 8

and costal 7, laterally peripherals 10 and 11, and posteriorly the suprapygal. The suprapygal is pentagonal and contacts anterolaterally costal 8 and posterolaterally peripheral 11. The pygal is trapezoidal in shape and contacts anteriorly the suprapygal and laterally both peripherals 11.

The peripheral bones are relatively narrow in the anterior free margin and slightly wider in the posterior one. Peripheral 1 is the largest and, like the other peripherals of the anterior margin, is trapezoidal in outline. This bone contacts the nuchal medially, peripheral 2 laterally, and costal 1 posteriorly, as is usual in turtles. Peripheral 2 contacts peripheral 1 medially, peripheral 3 laterally and costal 1 posteriorly. The third to seventh peripheral bones contribute to the bridge. As well as the second peripheral, the bridge peripherals, and the eighth to eleventh peripheral bones are characterized by strongly dorsally curved, gutter-like margins. The axillary buttress fits between the third peripheral and the first costal, while the inguinal buttress is attached between the seventh peripheral and the lateral extreme of the fifth costal. As is typical in pleurodires, the ilia in *Rionegrochelys caldieroi* are sutured to the carapace (Gaffney and Meylan 1988). The iliac suture extends over the posterior area of the seventh costal, the eighth costal, and the anterolateral edge of the suprapygal. A different condition is seen in *Yaminuechelys gasparinii* and *Y. maior* where this suture extends over the eighth costal and the anterolateral edge of the suprapygal.

The cervical scute is wider than long. The vertebral scutes are strongly marked on the carapace. The first and fifth vertebral scutes are the widest. The first vertebral scute is twice as wide as long and subrectangular in shape. This scute covers most of the nuchal bone, the caudal-medial portions of both peripherals 1, the medial part of both costals 1, and probably half of neural 1. A slightly sinuous intervertebral sulcus between vertebral scutes 1 and 2 crosses the caudal portion of neural 1. The second and third vertebral scutes are slightly wider than long and subquadrangular in outline. Vertebral scute 2 covers the caudal portion of neural 1, neural 2, and most of neural 3, a small mediocaudal portion of costal 1, the medial part of both costals 2, and a portion of the anteromedial part of costal 3. The intervertebral sulcus between vertebrals 2 and 3 crosses at least neural 3 and both costals 3 in their medial part. Vertebral scute 3 covers the caudal medial portion of both costals 3, the medial part of both costals 4, neural 4, and most of the medial portion of both costals 5. The intervertebral sulcus between vertebrals 3 and 4 with an anteriorly marked inflection crosses both costals 5 in their medial portion, and the posterior part of neural 5. By contrast, vertebral 4 is slightly longer than wide and pentagonal in shape. This vertebral scute covers neurals 6–8, the caudal medial part of costals 5, the medial part of costals 6 and 7, and the cranial medial part of costals 8. The intervertebral sulcus between vertebrals 4 and 5 crosses both costals 8. The fifth vertebral scute is slightly wider than long and characterized by a three lobed posterior margin. This vertebral scute covers part of the caudal portion of both costals 8, most of the suprapygal, and small portion of the proximal margins of the pygal and peripheral bones 11. Four pairs of pleural scutes are recognized in *Rionegrochelys caldieroi* as is usual in turtles. Pleural 1 is slightly longer than wide and covers the posterolateral portion of peripheral 1, the medial part of peripherals 2–4, the central and lateral part of costal 1, and the cranial centrolateral portion of costal 2. Pleural 2 is wider than long and covers costals 2–4. Pleural 3 is also wider than long and covers costals 4–6. Pleural 4 is as wide as long and covers costals 6–8. The interpleural sulci between pleural scutes cross costals 2, 4, and 6 as usual in turtles. The sulcus between pleural 4 and vertebral 5 crosses costals 8.

On the anterior margin of the carapace, marginal scutes 1–4 are recognized. Marginal scutes 4–8 are also identified on the right and left peripheral bridge. Although the intermarginal sulcus between marginal 1 and 2 is scarcely discernible, marginal scute 1 is subrectangular in shape, as does marginal scute 2. Marginal scute 1 covers the proximolateral sector of the nuchal and only the cranial medial part of peripheral 1. Marginal scutes 2–4 also cover two peripheral bones each without extending onto costal bone 1. From marginal scutes 5–11 (with the exception of marginal 10), the scutes cover the costal bone and show an alternating pentagonal and rectangular outline. Marginal 12, pentagonal in shape, covers the pygal, peripheral 11, and the suprapygal.

Plastron: The plastron of the holotype of *Rionegrochelys caldieroi* is preserved in good condition. It is medium sized (450 mm length along the midline) and slightly longer than the carapace (430 mm length along the midline). The anterior and posterior lobes are nearly equal in length. The bridge (= axillo-inguinal distance) is about 70% of the anteroposterior length of the posterior plastral lobe. The relative length of the bridge of *Rionegrochelys caldieroi* is greater than in long necked chelids such as *Yaminuechelys* and *Hydromedusa* or short necked chelids such as *Prochelidella portezuelae* (de la Fuente 2003) and *Phrynops Geoffroanus* (AMNH 79048, USNM 306646), but it is shorter than the bridge of other extinct species (e.g., *Bonapartemys bajobarrealis*; see Lapparent de Broin and de la Fuente 2001).

The broad anterior plastral lobe (width/length ratio 1.71) in *Rionegrochelys caldieroi* is U-shaped. As in the panpleurodire *Platycheilus oberndorferi* (Bräm 1965) and the chelid *Chelus fimbriatus* (AMNH 70638, USNM 64154), the anterior lobe extends beyond the anterior margin of the carapace. The posterior plastral lobe of *Rionegrochelys caldieroi* is as long as wide. The lateral margins of the posterior lobe are curved and have a strong femoral-anal notch, as is usual in species of the *Phrynops Geoffroanus* complex (see Rhodin and Mittermeier 1983). The anal notch in *Rionegrochelys caldieroi* is U-shaped as in *Bonapartemys bajobarrealis* and *Lomalatachelys neuquina*, and unlike the V-shaped condition of *Yaminuechelys gasparinii* among extinct chelids. However, intraspecific variation of this feature has been pointed out in some fossil and extant pleurodires (Wood and Díaz de Gamero 1971; Cadena et al. 2008; Ferreira et al. 2016).

The epiplastra in *Rionegrochelys caldieroi* are long and broad with a relatively short medial contact. These bones are partially separated by a large, rounded entoplastron. Between the large hyo and hypoplastra, the mesoplastra are located. They are cuneiform and they are relatively long in comparison to those of *Yaminuechelys* spp. The xiphiplastron show slight interdigitating sutures with the hypoplastra. They are broad, but deeply notched at the limit imposed of the femoral-anal sulcus. On their visceral surface, the pubis and ischium are attached by a suture to the xiphiplastron. The pubic scar is lateral in position and obliquely oriented at an obtuse angle with respect to the plastral midline, whereas the ischial scar is L-shaped with the short branch of the L extended on the xiphiplastral tips and the longer one oriented slightly obliquely towards the shorter. The xiphiplastral tips end in nearly blunted margins.

As in other pleurodires, *Rionegrochelys caldieroi* has six pairs of plastral scutes (extragular, humeral, pectoral, abdominal, femoral, and anal) and one odd scute (gular). The plastron has a simple extragular-gular scheme with small extragular scutes on the epiplastra and a small, subtriangular gular scute over the anterior margin of the entoplastron. The large entoplastron is crossed posteriorly by the humero-pectoral sulcus, which is unusual among South American panchelids. An entoplastron crossed by this sulcus can otherwise be seen in some Australasian species, such as *Elseya*

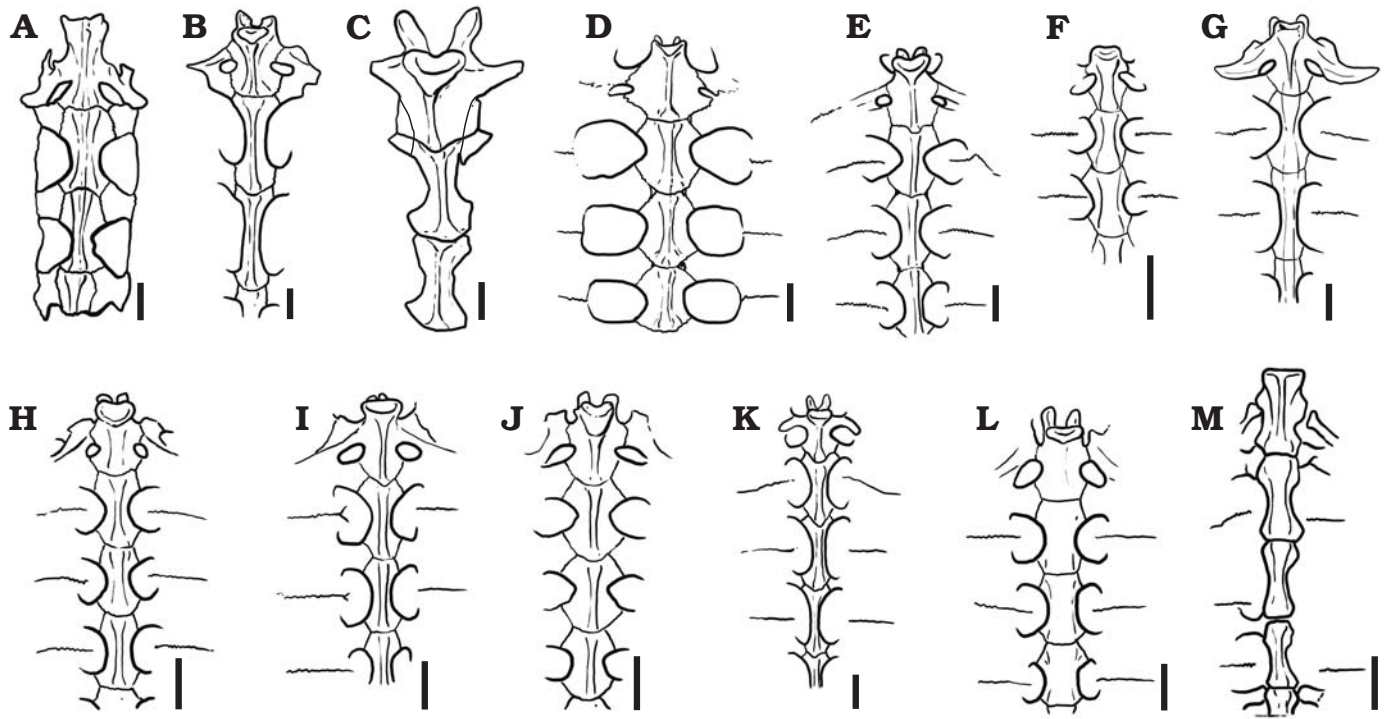


Fig. 7. Comparison of thoracic vertebrae 1–3 in some extinct and extant pleurodiran turtles. **A.** *Chelodina colliei* Gray, 1856 (NHMUK 64-12-22-66). **B.** *Elseya dentata* (Gray, 1863) (NHMUK 76-5-19-27). **C.** *Rionegrochelys caldieiroi* gen. et sp. nov. (MPCA-AT 258). **D.** *Chelus fimbriatus* (Schneider, 1783) (MZUSP 2619). **E.** *Phrynops hilarii* (Duméril and Bibron, 1835) (MHNSR H-1550). **F.** *Platemys platycephala* (Schneider, 1792) (MHNSR H-1554). **G.** *Rheodytes leukops* Legler and Cann, 1980 (QM J 7693). **H.** *Acanthochelys macrocephala* (Rhodin, Mittermeier, and McMorris, 1984) (MACN H-8288). **I.** *Hydromedusa tectifera* Cope, 1870 (MHNSR-H 1615). **J.** *Mesoclemmys nasuta* (Schweigger, 1812) (MACN H-11967). **K.** *Podocnemis sextuberculata* Cornalia, 1849 (MZUSP 2501). **L.** *Pelomedusa subrufa* (Bonnaterre, 1789) (SMF 7953). **M.** *Yaminuechelys gasparinii* de la Fuente, Lapparent de Broin, and Manera de Bianco, 2001 (MPA 86-86-IC). Scale bars 20 mm.

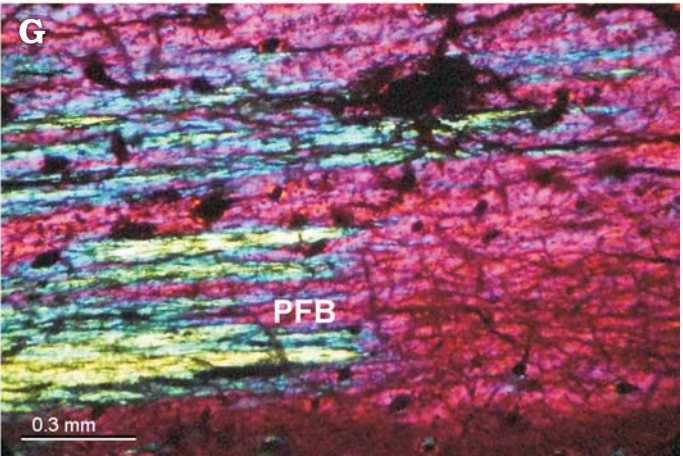
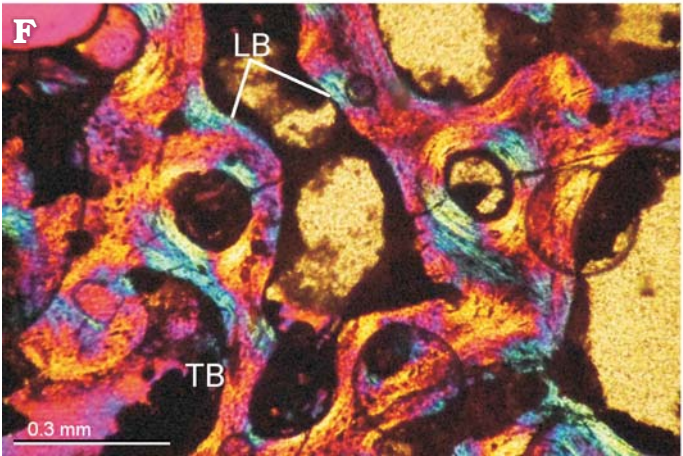
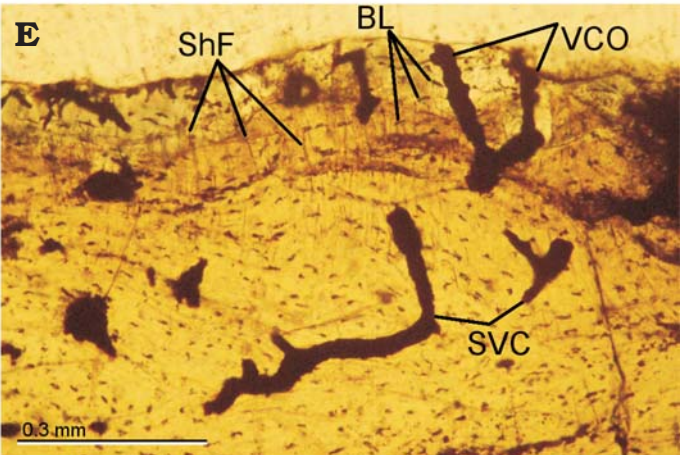
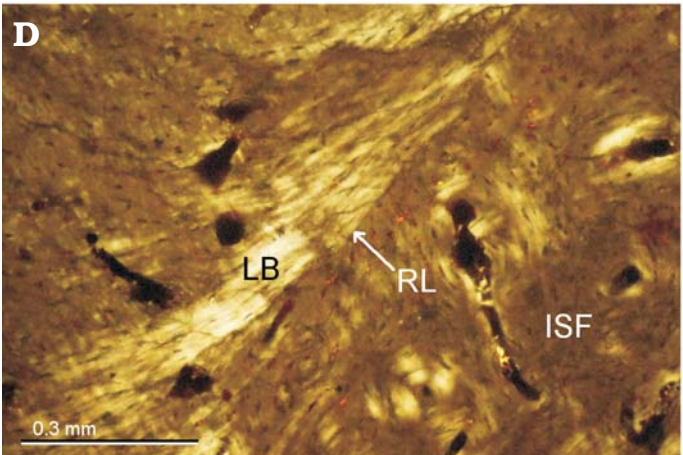
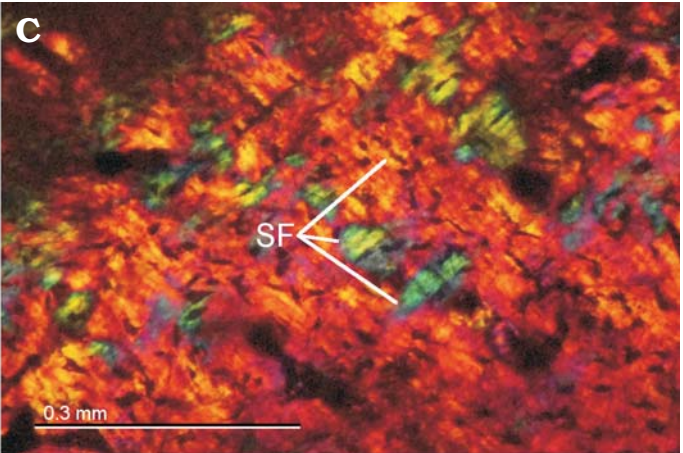
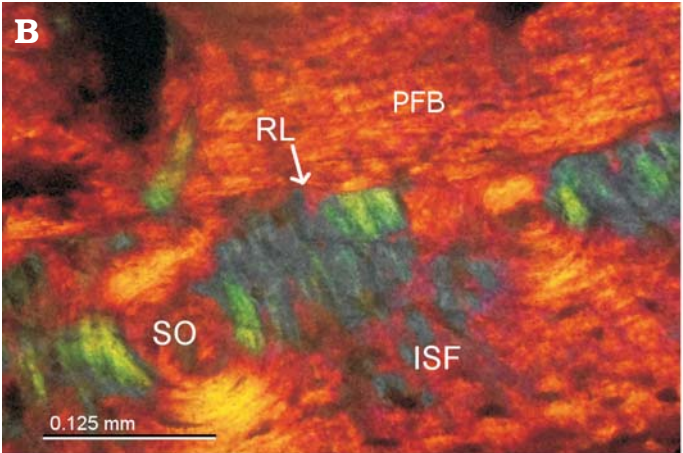
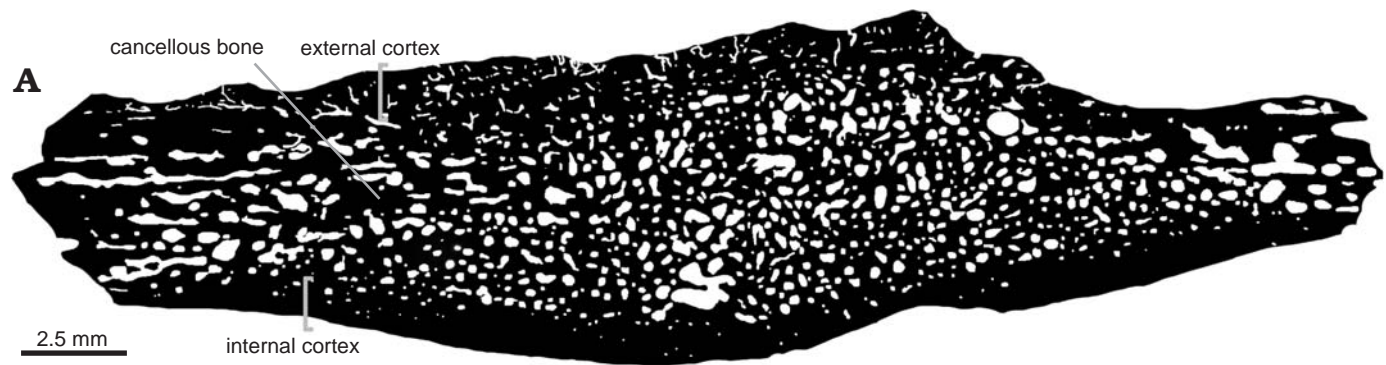
novaeguineae (USNM 313654), *E. schultzei* and *E. rhodini* (Thompson et al. 2015), *E. flaviventralis* (Thompson and Georges 2016), *Emydura macquarii* (NHMUK 86-8-26-5), and *Rheodytes leukops* (QM J 85198). The interfemoral sulcus is longer than any of the other median sulci of the plastron. The interanal sulcus and gular scutes are the shortest, whereas the interpectoral sulcus is longer than the interhumeral or interabdominal sulci. This peculiar plastral formula is recognized in some specimens of extant *Chelus fimbriatus* (e.g., USNM 64154). Although many authors have used these midline contact lengths of plastral scutes to characterize species of turtles, Lovich and Ernst (1989) and Sánchez-Villagra et al. (1995) reported a great amount of intraspecific variation in extant turtles such as *Mauremys reevesii*, *Graptemys pulchra*, *Platemys platycephala*, and *Chelus fimbriatus*. The lateral cuneiform mesoplastra are crossed by the pectoro-abdominal sulcus. A similar condition can be seen in other extinct Patagonian species of panchelid turtles (e.g., *Bonapartemys bajobarrealis*, *Linderochelys rinconensis*, *Lomalatachelys neuquina*, *Prochelidella portezuelae*,

Yaminuechelys gasparinii, *Y. maior*) and platychelyid panpleurodire such as *Notoemys oxfordiensis*, *Notoemys lat-centralis*, and *Platychelys oberndorferi* (see Bräm 1965; de la Fuente and Iturralde-Vinent 2001; de la Fuente et al. 2001, 2007; Lapparent de Broin and de la Fuente 2001; de la Fuente 2003; Bona and de la Fuente 2005; Lapparent de Broin et al. 2007; Cadena and Joyce 2015).

Pelvic girdle: The pelvic girdle is represented by both right and left halves in the holotype (Figs. 4, 5). Each one is tri-radiate in lateral view. As is typical in pleurodires, the pubis and ischium of each half are attached by suture to the xiphiplastron. The iliac blade of the ilium expands dorsally to be attached by suture to the carapace. The pubis is sutured only by the lateral process, whereas the ischium is suturally attached by a broad surface extending from its symphysis to a lateral process. As is typical in pleurodires, the pubis and ischium are separated from each other by a large and confluent thyroid fenestra.

Thoracic vertebrae. At least six dorsal vertebrae are preserved in the holotype of *Rionegrochelys caldieiroi*. Among

Fig. 8. Shell bone histological section of the panchelid turtle *Rionegrochelys caldieiroi* gen. et sp. nov. (MPCA-AT 26) from Parrita site, Upper Cretaceous. → **A.** Black and white processed image from costal element. **B.** Close view of external cortex in costal element showing a resorption line. External cortex of peripheral element showing structural fibers (**C.**), a resorption line and lamellar bone (**D.**). **E.** Vascularization in external cortex of costal element. **F.** General view of cancellous bone of peripheral element. **G.** Transition in the orientation of PFB (parallel-fibered bone) in the internal cortex of costal element. Abbreviations: BL, bone lacunae; ISF, interwoven structural collagenous fibre bundles; LB, lamellar bone; PFB, parallel-fibered bone; RL, resorption line; SF, structural fiber; ShF, Sharpey's fibres; SO, secondary osteon; SVC, simple vascular canal; TB, bone trabeculae; VCO, vascular canal opening to the external surface.



them, the first, second, and third are in articulation and in good condition, allowing detailed description (Fig. 6). All contacts of the preserved thoracic vertebrae are platycoelous synchondroses. Thoracic vertebra 1 is well preserved and is as long as wide. The anterior articular end is concave facing anteriorly and slightly ventrally. It is also as wide as long. In ventral view, thoracic vertebra 1 is wide anteriorly and tapered posteriorly. A different condition is seen in other extant and extinct crown chelids (Fig. 7), where an hourglass shape is the most common pattern recognized in the ventral view of the first thoracic vertebra. The well-developed prezygapophyses face medio-dorsally and are laterally strongly divergent. Thoracic rib 1 is articulated with the anterior end of thoracic vertebra 1, whereas thoracic rib 2 is articulated between the posterior end of thoracic vertebra 1 and the anterior end of thoracic vertebra 2. Thoracic vertebra 2 is longer than the first one, and longer than wide. Its anterolateral end contacts thoracic rib 2, whereas its posterolateral end contacts thoracic rib 3. Thoracic vertebra 3 is also slightly longer than wide like the second one. The anterolateral margin of this thoracic vertebra contacts thoracic rib 3, whereas the posterolateral margin contacts thoracic rib 4.

Paleohistology.—The microanatomy shows a compact diploe structure with the external and internal cortex framing in the interior area of cancellous bone (Fig. 8A). The external cortex is thicker, double in size compared with the internal cortex. The cancellous bone is well developed, occupying 70% of the cross-sectional area in peripheral elements and less than 50% in costal elements. The osteohistology of all the shell elements is described together. Variation among samples is mentioned if applicable.

External cortex: The external cortex is mostly composed of primary bone. In the peripheral plates, primary bone consists of interwoven bundles of structural collagenous fibers. On the other hand, costal plates are formed by mineralized collagenous fibers arranged parallel/sub-parallel to the external surface. These fibers exhibit two main orientation, which are parallel and transversal to the progression of the element (Fig. 8B, C). Sharpey's fibers are present in the costal plates. They are short and oriented mostly perpendicularly or oblique to the outer surface. Resorption lines associated with successive episodes of bone resorption and deposition are clearly observed in the outer (ornamented) portion of the cortex of one peripheral and one costal plate (Fig. 8B, D). Vascularization is mostly formed by simple vascular canals that run in parallel or perpendicular to the anteroposterior axis. Simple vascular canal openings to the external surface can be clearly made out (Fig. 8E). Some primary osteons are also observed and these commonly anastomose. Secondary osteons are more commonly distributed in the inner (i.e., perimedullary) portion of the cortex. These osteons are more abundant in some costal plates, in which they even reach the outer cortex (Fig. 8B). Secondary osteons have bone composed of alternating lamellae (Fig. 8B). Bone cell lacunae are commonly arranged following the orientation of the structural fibers in which they are embedded.

Short canaliculi are preserved. Growth marks are present, mostly discontinuous, and not easily discerned.

Cancellous bone: The cancellous bone is quite massive and strongly remodeled. Short trabeculae appear in the costal elements and long ones in the peripheral elements. The trabeculae themselves are composed of centripetally deposited secondary lamellar bone formed over different growth generation with variation in the orientation of each lamella. Intertrabecular spaces are generally small and circular or sub-circular in section. Interstitial areas within the trabecular bone are composed by primary and secondary bone, as seen in the external cortex. Flattened bone cell lacunae follow the centripetally deposited lamellar bone linings (Fig. 8F).

Internal cortex: The internal cortex is composed mainly of parallel-fibered bone matrix that can locally form lamellar bone. In one costal element, the fibers are parallel to the latero-medial axis in the central area (which corresponds to the rib), and gradually change their arrangement toward the suture margins, where they become parallel to the antero-posterior axis (Fig. 8G). This is made visible by the monorefringent properties of the bone in the center and the birefringent properties toward the margins, as well as by the change in the shape of the bone cell lacunae, which are circular/sub-circular in section in the center and strongly elongated and flattened toward the suture margins. Vascularization is typically poor (mainly avascular in several cases). Some simple vascular canals and primary osteons appear to be longitudinally oriented. At least five lines of arrested growth are visible (Fig. 8G).

Sutures: The structure of sutures could be studied in the three costal elements. The microanatomical structure is typically "peg and socket". The matrix principally consists of woven bone. Dense Sharpey's fibers are oriented parallel to the protrusions in all samples. In some samples, Sharpey's fibers continue into the cancellous bone.

The results of the compactness parameters calculated for a costal element of *Rionegrochelys caldieiroi* using BONE PROFILER Software were: modeled compactness 80.6%, lowest compactness at the center 11.1% (SE 0%), modeled compactness at the center 70.5%, compactness at the maximum periphery 87% (SE 0%), modeled compactness at the periphery 87.2%, compactness at the transition between cancellous bone and compact bone (point P) 36% (SE 0.6%), and the slope of compactness change at point P 1.15 (SE 0.008%).

Stratigraphic and geographic range.—El Anfiteatro, Río Negro Province, Argentina. Plottier Formation (upper Coniacian–lower Santonian), Río Neuquén Subgroup, Neuquén Basin.

Phylogenetic analyses

Results.—Four MPTs of 209 steps (CI: 0.421; RI: 0.598) were found after the two cycles of the two cycles of heuristic search in TNT (Goloboff et al. 2008a, b) and a strict

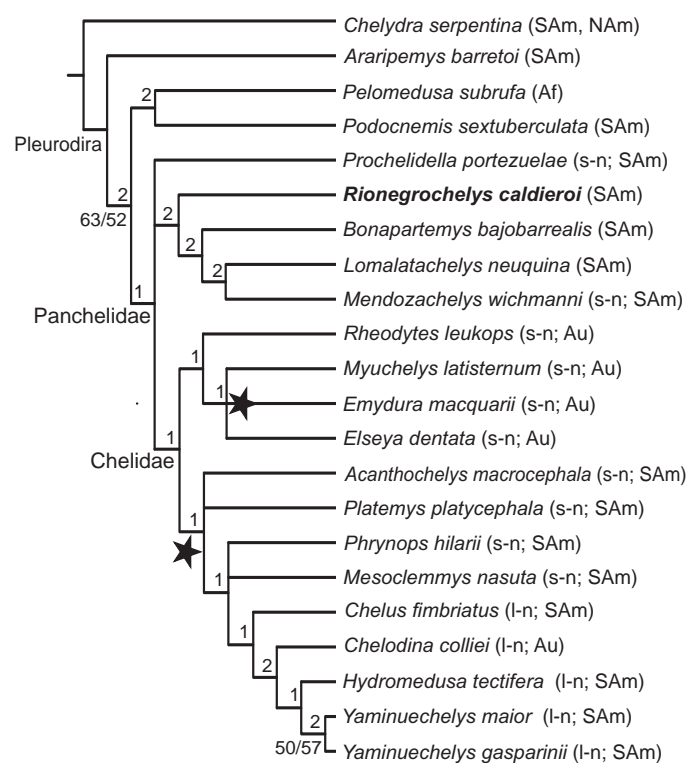


Fig. 9. Strict consensus tree from the four MPT's obtained from the morphological cladistic analysis of *Rionegrochelys caldiero* gen. et sp. nov. The stars show the alternative positions of *Pseudemysdura umbrina*. The numbers in the left of the lines are Bremer support values, whereas the numbers in the right of the lines are Jackknife and Bootstrap support values, respectively, that exceed 50%. Abbreviations: Af, Africa, SAm, South America, NAm, North America, Au, Australia; l-n, long-necked pancchelids, s-n, short-necked pancchelids.

and *Podocnemis sextuberculata*). By contrast, *Mesoclemmys nasuta* and *Chelodina colliei* present a discontinuous series of neural bones lacking the first one and also not reaching the suprapygal. The cervical scute that is longer than wide is a condition present in some Australasian chelids (such as *Emydura macquarii*, *Rheodytes leukops*, and *Myuchelys latisternum*) and South American chelids (such as *Platemys platycephala*, *Mesoclemmys nasuta*, and *Phrynops hilarii*), the rest of the extant chelids presenting a cervical scute that is wider than long. In *Hydromedusa tectifera* the cervical scute does not even reach the anterior margin. Two characters (characters 34 and 61) were recovered as autapomorphies of *Rionegrochelys caldieroii*: the development of an enlarged costal-vertebral tunnel along the entire thoracic vertebrae series (character 34, state 0), and the presence of a pectoral scute on the middle of the entoplastron (character 61, state 1). The first one is shared with *Chelydra serpentina* and *Chelus fimbriatus*. This condition was probably present in the *Yaminuechelys* clade, but it has not been recognized yet. The pectoral scute extending over the middle of the entoplastron is also present in *Podocnemis sextuberculata*, *Elseya dentata*, *Emydura macquarii*, *Chelus fimbriatus*, and *Chelodina colliei*. The Taxon list is shown in SOM 3.

Discussion

Taxonomic and phylogenetic remarks.—The carapace, plastron, and pelvic girdle of *Rionegrochelys caldieiroi* fit well with those of panchelid pleurodiran turtles. The elements of the pelvic girdle (pubis, ischium and ilium) are suturally attached to the shell, a synapomorphy recognized for Pleurodira (see Gaffney and Meylan 1988, and references therein). Although the skeletal elements that yield panchelid synapomorphies, such as the skull or the cervical vertebrae are not preserved in the holotype of the new species, the type of pelvic-shell connection, in conjunction with an assemblage of shell characters, such as the presence of a cervical scute, short and wide mesoplastra crossed by a pectoro-abdominal sulcus, the presence of a single suprapygial bone, vertebral scutes narrower than the pleural ones, and inguinal buttress extending over peripherals 7 and 8, allow *Rionegrochelys caldieiroi* to be assigned to the clade Panchelidae. The unusual proportion between carapace and plastron (plastron longer than carapace) and the peculiar morphology of the shell such as the heart-shaped carapace, a very deep nuchal notch, peripheral bones 2–11 with strongly dorsally curved margins, the first vertebral scute being twice as wide as long and subrectangular in shape, the trilobate posterior margin of vertebral scute 5, the development of a wide costal-vertebral tunnel along the entire thoracic vertebral series, and a pectoral scute extending over the middle of the entoplastron together with the results of the phylogenetic analysis shows that this taxon is a new species.

Some Cretaceous panchelid species such as *Prochelidella portezuelae*, *Lomalatachelys neuquina*, and *Bonapartemys bajobarrealis*, that are only known from postcranial remains, mainly the shell, were added to this phylogenetic analysis. When the analysis was performed, some of the cranial characters recovered previously as synapomorphies of Chelidae (Gaffney 1977; Bona and de la Fuente 2005; de la Fuente et al. 2017), such as the absence of the quadratojugal, the lateral cheek emargination or the presence of nasals, were neither recovered as Panchelidae nor as Chelidae, due to the low percentage of characters scored in the matrix by these taxa. Indeed, *Mendozachelys wichmanni* is the only fossil taxon with cranial and post-cranial remains with over 50% of characters scored in the matrix, whereas other extinct Patagonian species known mainly by shells do not reach this percentage (*Bonapartemys bajobarrealis* 43%, *Lomalatachelys neuquina* 37%, *Prochelidella portezuelae* 42%, and *Rionegrochelys caldieiroi* 46%).

It is noteworthy that *Mendozachelys wichmanni* and *Lomalatachelys neuquina* were recovered as stem chelid in contrast with previous morphological analyses (Cadena et al. 2008; de la Fuente et al. 2015b, 2017) in which they appear within the chelid crown clade. The absence of skulls in most of the extinct South American species including in this analysis, and the amount of the plesiomorphic condition present on their post-cranial remains not allow us clarified the position of these taxa. De la Fuente et al. (2017) real-

ized a constrained analyses following a molecular topology leading to two topologies showing a different position of *Mendozachelys wichmanni*. This taxon was recovered in one of the two topologies as a sister taxa of the crown Chelidae (de la Fuente et al. 2017: fig. 11B), a position more closely related to the topology recovered here.

Paleohistological remarks.—The general histology of *Rionegrochelys caldieiroi* shows plesiomorphic characters for turtles, including the diploe structure of the shell with external and internal compact bone framing interior cancellous bone, the metaplastic incorporation of dermal interwoven structural fiber bundles, the presence of Sharpey's fibers in the external cortex, and parallel-fibered bone in the internal cortex (e.g., Scheyer et al. 2007; Cerda et al. 2016). Within chelids, the presence of canal openings as small foramina on the surface of the external cortex has only been reported for *Phrynops Geoffroyanus* and *Yaminuechelys* spp. (Scheyer 2007; Jannello et al. 2016)

The characteristic resorption from the outside in the external cortex has been reported in some lineages of turtles in recent years (de la Fuente et al. 2015a; Buffrénil et al. 2016; Jannello et al. 2016). Buffrénil et al. (2016) reported a superficial ornamented layer separated from the subjacent bone strata by a reversion line, with discordant bone deposits above and under this line in members of Trionychidae (*Amyda cartilaginea*, *Trionyx triunguis*, *Aspideretoides* cf. *riavinini*, and *Cyclanorbis senegalensis*) and in Araripemydidae (*Araripemys barretoii*). Specimens of other taxa with resorption lines in the external cortices, such as *Condorchelys antiqua*, *Bothremys barberi*, and *Podocnemis erythrocephala*, have been interpreted as pathological conditions (e.g., Cerda et al. 2016). Within Chelidae, *Yaminuechelys* spp. are the only taxa for which resorption processes have been reported to date (Jannello et al. 2016). Buffrénil et al. (2016) proposed two distinct modalities for the formation and maintenance of ornamentation in turtles: (i) local bone surface flattened by resorption, sculpturing relief resulting from slight differences in bone accretion rates between the top of the ridges and the floor of the pits, and (ii) the surface of the bone not entirely flattened by resorption, with the subsequent accretion of bone enhancing the preexisting reliefs. The second modality, previously reported for *Yaminuechelys* spp. (Jannello et al. 2016), seems to correspond with that observed in *Rionegrochelys caldieiroi*.

Paleoecology.—Several authors (e.g., Scheyer and Sander 2007; Scheyer et al. 2014) have studied the correlation between the shell microstructure and the lifestyle of extant and extinct turtles and concluded that it is a valuable tool for inferring different ecological habits in the group. In this respect, those bones with a low degree of compactness and homogenization of the compact cortical and cancellous shell areas are correlated with aquatic specializations. The bone shell microanatomy of *Rionegrochelys caldieiroi* has a massive structure, with higher compactness (80.6%) than other chelids such as *Yaminuechelys* spp. (68%). The high

compactness of the shell bones of *Rionegrochelys caldieiroi* is comparable with that reported in terrestrial turtles (e.g., Solemydidae; Scheyer et al. 2014). These results are rather unexpected, since chelids are characterized by living in freshwater aquatic to semiaquatic environments (de la Fuente et al. 2014). Taphonomic data also contradict fully terrestrial habits for *Rionegrochelys caldieiroi*. The relationship between the stylopodium, zeugopodium, and autopodium of the forelimb is a good indicator of habitat as well (Joyce and Gauthier 2004), but this parameter could not be applied to *Rionegrochelys caldieiroi* because the limbs were not preserved. Although the terrestrial interpretation needs to be tested with further histological sections, we provisionally suggest semi-aquatic habits with a tendency to terrestrial ones, similar to the extant pelomedusid *Pelomedusa subrufa* (Pritchard 1979; Ernst and Barbour 1989; Boycott and Bourquin 2008) and the extant chelid *Platemys platycephala*, a poor swimmer that frequently roams the forest floor (Ernst and Barbour 1989). The presence of an enlarged costo-vertebral tunnel in *Rionegrochelys caldieiroi* are recognized within suction feeders turtles as *Chelydra serpentina*, *Macrochelys temminckii*, and *Chelus fimbriatus* could be suggest this kind of alimentation patterns to *Rionegrochelys caldieiroi*. Indeed, these last species (*Chelydra serpentina*, *Macrochelys temminckii*, and *Chelus fimbriatus*), are bottom walkers (Joyce and Gauthier 2004) and sometimes could be found outside the freshwater (Ernst and Barbour 1989).

Conclusions

Rionegrochelys caldieiroi de la Fuente, Maniel, and Jannello gen. et sp. nov. is assigned to Panchelidae on the basis of a combination of characters such as the pelvis shell attached by suture, the presence of a cervical scute, the first vertebral scute wider than the second one, short and wide mesoplastral bones crossed by a pectoro-abdominal sulcus, the presence of a single suprapygial bone, and vertebral scutes narrower than pleural ones. In a preliminary analysis, *Rionegrochelys caldieiroi* is recovered as a stem chelid and as a sister taxon of *Bonapartemys bajobarrealis* and the clade formed by *Lomalatachelys neuquina* and *Mendozachelys wichmanni*. The unusual proportion between carapace and plastron and the peculiar morphology of the shell (such as the heart-shaped carapace, the very deep nuchal notch, peripheral bones 2–11 with strongly dorsally curved margins, vertebral scute 1 subrectangular in shape and twice as wide as long, and the posterior margin of vertebral scute 5 three lobe shaped) suggest that this specimen represents a new taxon.

The bone shell microanatomy of *Rionegrochelys caldieiroi* has a massive structure, with higher compactness (80.6%) than other chelids, comparable to that reported for terrestrial turtles. These results are rather unexpected, since chelids are characterized by living in freshwater aquatic to semiaquatic environments. Taking into account that the

taphonomic data and the geological context suggest fluvial deposits, semi-aquatic habits with terrestrial tendencies, similar to the extant pelomedusid *Pelomedusa subrufa*, are proposed for *Rionegrochelys caldieiroi*.

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http://app.pan.pl/SOM/app62-Fuente_etal_SOM.pdf

SUPPLEMENTARY ONLINE MATERIAL FOR

Unusual shell anatomy and osteohistology in a new Late Cretaceous panchelic turtle from northwestern Patagonia, Argentina

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Supplementary Online Material

SOM 1. A dataset of 23 taxa and 62 morphological characters.

http://app.pan.pl/SOM/app62-Fuente_etal_SOM/Matrix_R_caldieroi.nex

http://app.pan.pl/SOM/app62-Fuente_etal_SOM/R_caldieroi.tnt

http://app.pan.pl/SOM/app62-Fuente_etal_SOM/results.txt

SOM 2. The list of synapomorphies common to the MPTs.

SOM 3. Taxon list.

SOM 2. Synapomorphies common to 4 trees

(Node numbers refer to nodes in consensus)

Chelydra serpentina:

All trees:

No autapomorphies:

Araripemys barretoii:

All trees:

Orbits position (4): Lateral → Dorsal

Medial process of the Basisphenoid in ventral view (19): Not extending beyond the processus trochlearis pterygoidei or processus pterygoideus externus → Extending until processus trochlearis pterygoidei or processus pterygoideus externus

Lower jaw (22): Fused in midline → Separated by symphyseal suture

Hook development of the lower jaw (23): Present → Absent

Midline fusion on cervical postzygapophyses (26): Absent → Present

Podocnemis sextuberculata:

All trees:

Dorsal portion of parietals (9): Not covering dorsal area of abductor fossa → Covering dorsal area of abductor fossa

Suprapygial posterior contact (38): Pygal and eleventh peripheral bones → Only pygal

Axillar buttresses shape (42): Anterior and posterior edges diverge towards lateral end, without medial constriction → Anterior and posterior edges are suparallel medially suddenly narrowing laterally ending in a ridge

Plastron (52): Axillar-inguinal distance shorter than each plastral lobes → Axillar-inguinal distance longer than each plastral lobes

Pectoral scute extending over epiplastra (59): Absent → Present

Pectoral scute extending over entoplastron (60): Absent → Present over entoplastron half

Pectoral scute extending over mesoplastra (61): Present → Absent

Some trees:

Orbits position (4): Lateral → Dorso-lateral

Foramen stapediale temporalis (10): Seen in dorsal view → Not seen in dorsal view

Pelomedusa subrufa:

All trees:

Medial process of the Basisphenoid in ventral view (19): Not extending beyond the processus trochlearis pterygoidei or processus pterygoideus externus → Extending until processus trochlearis pterygoidei or processus pterygoideus externus

Peripheral bones (39): Peripheral bones anterior to bridge shorter than posterior one → Peripheral bones anterior to bridge longer than posterior one

Axillar buttresses extension (40): Extend to second to third peripheral, or Extend to third peripheral → Extend to third and fourth peripheral

Some trees:

Axillar buttresses contact with first costal rib (41): Axillar buttresses angled between 15 and 50 degrees respect to the rib → Axillar buttresses parallel or adjacent to the costal rib

Mendozachelys wichmanni:

All trees:

No autapomorphies:

Pseudemydura umbrina:

All trees:

Anterior process of frontals relative to nasal (3): Anterior process short, partially separating the nasals → Anterior process absent

Dorsal portion of parietals (9): Not covering dorsal area of abductor fossa → Covering dorsal area of abductor fossa

Supraoccipital-Squamosal contact (12): Absent → Present, through the temporal bar

Incisura columelae auris (20): Closed → Open

Inguinal buttresses (45): Extending onto costal bones → Not extending onto costal bones

Shape of cervical scute (49): 2 → Longer than wide

Gular extending over entoplastron (57): Yes, over anterior half → Yes, over posterior half

Pectoral scute extending over epiplastra (59): Absent → Present

Pectoral scute extending over entoplastron (60): Absent, or Present over entoplastron half → Present over most of the entoplastron

Some trees:

Hook development of the lower jaw (23): Present → Absent

Suprapygal posterior contact (38): Pygal and eleventh peripheral bones → Pygal, eleventh peripheral and tenth peripheral bones

Ischial scar position (56): Extending onto the xiphiplastral tips → Not extending onto the xiphiplastral tips

Elseya dentata:

All trees:

No autapomorphies:

Emydura macquarii:

All trees:

Nuchal bone (34): Wider than long → Longer than wide

Some trees:

Medial contact of palatines (16): Present → Absent

Length of epiplastral suture (53): More than half entoplastral length → Half entoplastral length

Rheodytes leukops:

All trees:

Splenial (21): Present → Absent

Inguinal Buttresses extends over peripherals (44): Peripheral 7, or Peripheral 7 and 8 → Peripheral 6 and 7

Pubic scar position (55): In the medial part of the xiphiplastron → Lateral, located in the margin of the xiphiplastron

Some trees:

Expansion of the paraoccipital process of the opisthotic (8): Expanded → Not expanded

Christa supraoccipital (13): Developed behind the occipital condyle → Not developed behind the occipital condyle

Myuchelys latisternum:

All trees:

Anterior process of frontals relative to nasal (3): Anterior process short, partially separating the nasals → Anterior process well-developed, completely separating the nasals

Incisura columelae auris (20): Closed → Open

Inguinal buttresses (45): Extending onto costal bones → Not extending onto costal bones

Some trees:

Christa supraoccipital (13): Developed behind the occipital condyle → Not developed behind the occipital condyle

Axillar buttresses shape (42): Anterior and posterior edges are subparallel, without medial constriction, or Anterior and posterior edges are superparallel, but with a medial constriction → Anterior and posterior edges diverge towards lateral end, without medial constriction

Platemys platycephala:

All trees:

Postzygapophyses orientation on the atlas (31): Ventro-lateral → Lateral

Iliadic suture restricted to costal bones (46): No → Yes

Some trees:

Expansion of the paraoccipital process of the opisthotic (8): Expanded → Not expanded

Foramen stapediale temporalis (10): Seen in dorsal view → Not seen in dorsal view

Suprapygial posterior contact (38): Pygal and eleventh peripheral bones → Pygal, eleventh peripheral and tenth peripheral bones

Inguinal Buttresses extends over peripherals (44): Peripheral 7 → Peripheral 7 and 8

Length of epiplastral suture (53): Half entoplastral length → More than half entoplastral length

Acanthochelys macrocephala:

All trees:

Orientation of postzygapophyses on cervical vertebra 8 (30): Ventro-lateral → Lateral

Some trees:

Length of epiplastral suture (53): Half entoplastral length, or More than half entoplastral length → Half entoplastral length

Mesoclemmys nasuta:

All trees:

Supraoccipital-Squamosal contact (12): Absent → Present, through the temporal bar

Some trees:

When the iliadic suture reaches the suprapygial (47): Reaches only costal 8 → Reaches also costals 7 and 8

Phrynosoma marmoratus:

All trees:

Inguinal Buttresses extends over peripherals (44): Peripheral 7 → Peripheral 7 and 8

Some trees:

Inguinal buttresses extends over costals (43): Costal 5 → Costal 5 and 6

Chelonoidis mydas:

All trees:

Anterior process of frontals relative to nasal (3): Anterior process short, partially separating the nasals → Anterior process well-developed, completely separating the nasals

Medial contact of palatines (16): Absent → Present

Suprapygial posterior contact (38): Pygal and eleventh peripheral bones → Pygal, eleventh peripheral and tenth peripheral bones

Inguinal buttresses (45): Extending onto costal bones → Not extending onto costal bones

Gular extending over entoplastron (57): Yes, over anterior half → Yes, over posterior half

Extragulars (58): Present and not contacting in midline → Present and contacting in midline

Pectoral scute extending over epiplastra (59): Absent → Present

Some trees:

Neural series (35): Neural bones forming a continuous series not reaching the suprapygial bones → Neural bones forming a discontinuous series without nuchal bone contact

Chelonoidis fimbriatus:

All trees:

Nasals (1): Present → Absent

Orientation of postzygapophyses on cervical vertebra 8 (30): Ventro-lateral → Lateral

Postzygapophyses orientation on the atlas (31): Ventro-lateral → Dorso-lateral

Costo-vertebral tunnel (33): Slightly developed → Developed through dorsal vertebrae series

Axillar buttresses contact with first costal rib (41): Axillar buttresses parallel or adjacent to the costal rib → Axillar buttresses angled between 15 and 50 degrees respect to the rib

Pubic scar position (55): In the medial part of the xiphiplastron → Lateral, located in the margin of the xiphiplastron

Ischial scar position (56): Not extending onto the xiphiplastral tips → Extending onto the xiphiplastral tips

Some trees:

Quadrato-Basisphenoid contact (7): Present → Absent

When the illiadial suture reaches the suprapygial (47): Reaches only costal 8 → Reaches also costals 7 and 8

Hydromedusa tectifera:

All trees:

Orientation of postzygapophyses on cervical vertebra 8 (30): Ventro-lateral → Ventral

Axillary buttresses extension (40): Extend to third and fourth peripheral → Extend to fourth peripheral

Vertebral B (51): Vertebral 1 wider than vertebral 2 → Vertebral 1 equal or narrower than vertebral 2

Some trees:

When the illiadial suture reaches the suprapygial (47): Reaches only costal 8 → Reaches also costals 7 and 8

Yaminuechelys gasparinii:

All trees:

No autapomorphies:

Yaminuechelys maior:

All trees:

No autapomorphies:

Rionegrochelys caldieroi:

All trees:

Costo-vertebral tunnel (33): Slightly developed → Developed through dorsal vertebrae series

Pectoral scute extending over entoplastron (60): Absent → Present over entoplastron half

Bonapartemys bajobarrealis:

All trees:

Axillar buttresses shape (42): Anterior and posterior edges are subparallel, without medial constriction → Anterior and posterior edges are subparallel medially suddenly narrowing laterally ending in a ridge

Plastron (52): Axillar-inguinal distance shorter than each plastral lobes → Axillar-inguinal distance longer than each plastral lobes

Gular extending over entoplastron (57): Yes, over anterior half → Yes, over posterior half

Lomalatachelys neuquina:

All trees:

Suprapygial posterior contact (38): Pygal and eleventh peripheral bones → Pygal, eleventh peripheral and tenth peripheral bones

Iliadic suture restricted to costal bones (46): No → Yes

Prochelidella portezuelae:

Some trees:

Axillar buttresses contact with first costal rib (41): Axillar buttresses angled between 15 and 50 degrees respect to the rib → Axillar buttresses parallel or adjacent to the costal rib

Node 24 :

All trees:

No synapomorphies

Node 25 :

All trees:

Quadrato-basisphenoid contact (7): Absent → Present

Orientation of dorsal process of neural arch in cervical vertebrae 3-7 (29): Between 30 degrees and 40 degrees respect to vertebral body → More than 40 degrees with respect to vertebral body

Nuchal bone (34): Wider than long → Longer than wide

Iliadic suture restricted to costal bones (46): No → Yes

Node 26 :

All trees:

Incisura columelae auris (20): Open → Closed

Relative length of neural arch on 3-7 cervical vertebrae (25): Longer than wide of vertebral body → Shorter than wide of vertebral body

Orientation of dorsal process of neural arch in cervical vertebrae 3-7 (29): Less than 30 degrees with respect to vertebral body → Between 30 degrees and 40 degrees respect to vertebral body

Orientation of postzygapophyses on cervical vertebra 8 (30): Ventral → Ventro-lateral

Neural series (35): Neural bones forming a continuous serie reaching the suprapygal bonee → Neural bones forming a continuous series not reaching the suprapygal bones

Neural bones shape (36): Irregular → Regular

Vertebral A (50): Vertebral scute wider than pleural scute → Vertebrall scute narrow than pleural scute

Some trees:

Mesoplastron (54): Absent → Longer than wide or squarish

Node 27 :

All trees:

Nuchal bone (34): Wider than long → Longer than wide

Peripheral bones (39): Peripheral bones anterior to bridge shorter than posterior one → Peripheral bones anterior to bridge longer than posterior one

Node 28 :

All trees:

Axillar buttresses shape (42): Anterior and posterior edges diverg towards lateral end, whitout medial constriction → Anterior and posterior edges are subparallel, whitout medial constriction

Inguinal buttresses extends over costals (43): Costal 5 → Costal 5 and 6

Node 29 : Clade with the extinct forms

All trees:

Pubic scar position (55): In the medial part of the xiphiplastron → Lateral, located in the margin of the xiphiplastron

Ischial scar position (56): Not extending onto the xiphiplastral tips → Extending onto the xiphiplastral tips

Some trees:

Inguinal Buttresses extends over peripherals (44): Peripheral 7 → Peripheral 7 and 8

Mesoplastron (54): Longer than wide or squarish → Wider than long

Node 30 : Pan-Chelidae

All trees:

Splenial (21): Absent → Present

Cervical centrum (24): 3-8 procoelous → Only 6 procoelus

Some trees:

Medial ventral crest on 8 cervical vertebrae (27): Absent → Slightly development without covering all vertebral body length

Inguinal Buttresses extends over peripherals (44): Peripheral 7 → Peripheral 7, or Peripheral 7 and 8

Vertebral B (51): Vertebral 1 equal or narrower than vertebral 2 → Vertebral 1 wider than vertebral 2

Node 31 : Crown-group Chelidae

All trees:

Neural series (35): Neural bones forming a continuous series not reaching the suprapygal bones → Absent

Shape of cervical scute (49): Squarish or wider than long → 2

Some trees:

Expansion of the paraoccipital process of the opisthotic (8): Expanded → Not expanded

Peripheral bones (39): Peripheral bones anterior to bridge shorter than posterior one → Peripheral bones anterior to bridge longer than posterior one

Mesoplastron (54): Longer than wide or squarish → Absent

Node 32 :

All trees:

Dorsal process of the exoccipital (14): Whitout contact in midline over the foramen magnum → Contact in midline over the foramen magnum

Medial process of the Basisphenoid in ventral view (19): Not extending beyond the processus trochlearis pterygoidei or processus pterygoideus externus → Extending beyond the processus trochlearis pterygoidei or processus pterygoideus externus

Lower jaw (22): Fused in midline → Separated by symphyseal suture

Nuchal bone (34): Wider than long → Longer than wide

Axillar buttresses extension (40): Extend to second to third peripheral, or Extend to third peripheral → Extend to third and fourth peripheral

Some trees:

Orbits position (4): Lateral → Dorso-lateral

Christa supraoccipital (13): Developed behind the occipital condyle → Not developed behind the occipital condyle

Medial contact of palatines (16): Present → Absent

Hook development of the lower jaw (23): Present → Absent

Axillar buttresses contact with first costal rib (41): Axillar buttresses angled between 15 and 50 degrees respect to the rib → Axillar buttresses parallel or adjacent to the costal rib

Vertebral B (51): Vertebral 1 equal or narrower than vertebral 2 → Vertebral 1 wider than vertebral 2

Node 33 :

All trees:

Neural series (35): Absent → Neural bones forming a continuous series not reaching the suprapygal bones, or Neural bones forming a discontinuous series without nuchal bone contact

Some trees:

Quadrato-Basisphenoid contact (7): Absent → Present

Node 34 :

All trees:

Lateral edges of the dorsal portion of parietals (11): Reduced at medial portion → Tapering posteriorly

Incisura columelae auris (20): Closed → Open

Relative length of neural arch on 3-7 cervical vertebrae (25): Shorter than wide of vertebral body → Longer than wide of vertebral body

Midline fusion on cervical postzygapophyses (26): Absent → Present

Orientation of dorsal process of neural arch in cervical vertebrae 3-7 (29): Between 30 degrees and 40 degrees respect to vertebral body → Less than 30 degrees with respect to vertebral body

Neural arch elements of the atlas (32): Dorsally sutured → Dorsally fused

Node 35 :

All trees:

Orbits position (4): Dorso-lateral → Dorsal

Palatines separated in midline (17): Separated by vomer → Separated by pterygoideus

Medial process of the Basisphenoid in ventral view (19): Extending beyond the processus trochlearis pterygoidei or processus pterygoideus externus → Extending until processus trochlearis pterygoidei or processus pterygoideus externus

Inguinal Buttresses extends over peripherals (44): Peripheral 7 → Peripheral 6 and 7

Shape of cervical scute (49): 2 → Longer than wide

Some trees:

Length of epiplastral suture (53): More than half entoplastral length → Half entoplastral length

Node 36 :

All trees:

Supraoccipital-Squamosal contact (12): Absent → Present, through the temporal bar

Relatively large bony apertura narium interna (18): Absent → Present

Postzygapophyses orientation on the atlas (31): Ventro-lateral → Ventral

Shape of cervical scute (49): Longer than wide → Squarish or wider than long

Node 37 :

All trees:

Quadrates (6): Not forming part of the temporal arch → Laterally expanded, forming part of temporal arch

Costo-vertebral tunnel (33): Slightly developed → Developed narrowing toward posterior edge

Peripheral bones (39): Peripheral bones anterior to bridge longer than posterior one → Peripheral bones anterior to bridge shorter than posterior one

Axillar buttresses extension (40): Extend to third and fourth peripheral → Extend to third peripheral

Inguinal Buttresses extends over peripherals (44): Peripheral 6 and 7 → Peripheral 7

Mesoplastron (54): Absent → Wider than long

SOM 3. Taxon list.

Chelydra serpentina (photographs: MNHNP-AC 1870-465)

Araripemys barretoii (drawings from Meylan 1996)

Pelomedusa subrufa (photographs: AMNH 131262, NHMUK 87.3.11.10, specimen handled: SMF 7953)

Podocnemis sextuberculata (photographs: NHMUK 1947.3.5.83, NHMUK 16075, specimens handled: SMF 65274, MHNSR H-2501)

Rionegrochelys caldieroi (specimens handled: MPCA-AT 258, MPCA-AT 26, MPCA-AT 29, MPCA-AT 30)

Bonapartemys bajobarrealis (specimen handled: MACN-CH-1469)

Lomalatachelys neuquina (photographs and drawings from Lapparent de Broin and de la Fuente 2001 from MOZ 5117P)

Mendozachelys wichmanni (specimen handled: MACN-M-02)

Prochelidella portezuelae (specimen handled: MCF-PVPH-161)

Yaminuechelys gasparinii (photographs and drawings: MPA 86-86-IC)

Yaminuechelys maior (specimens handled: MPEF PV 1273, MPEF PV 1274, MPEF PV 1930, MPEF PV 1932, MPEF PV 1939, MPEF PV 599, MPEF PV 627)

Pseudemydura umbrina (specimen handled: NMW 1296, photographs: WAM R29338, WAM R 29348)

Rheodytes leukops (photographs and drawings from Legler and Cann 1980: UU 17114; photographs: QM J 76293, QM J 85198, QM J 85199)

Emydura macquarii (specimens handled: NBM C 1774, NBM C 2138, photographs: QM J 61586, NHMUK 26.8.26.5, NHMUK 86.8.26.5)

Elseya dentata (photographs: QM J 59279, QM J 59280, NHMUK 76.5.19.27)

Myuchelys latisternum (photographs: NHMUK 71.9.25.8, CRI 6572, CRI 6573, specimens handled: NMW 17224, NBM C 1453)

Chelodina oblonga (photographs: NHMUK 64.12.22.6, CRI 4632, CRI 5067)

Platemys platycephala (photographs: FMNH 45659, MNHN 1979-8304, specimens handled: MHNSR H-1554, MZUSP 2786)

Acanthochelys macrocephala (specimen handled: MZUSP 3069)

Mesoclemmys nasuta (specimens handled: MACN-H-11967, ZSM 1-1925; photographs: NHMUK 1936.7.5.1)

Phrynops hilarii (specimens handled: SMF 33058, SMF 33670, NMW 30564, MNHNP-AC-A-5183, MHNSR H-1550; photographs: NHMUK 86-3-10-1)

Chelus fimbriatus (specimens handled: MZUSP 2619, MHNSR H-2133, SMF 37146, NMW 39830, NMW 39245, NMW 1859, NBM C 1682, MNHNP-AC 1930-365; photographs: USNM 64154, FMNH 22113, AMNH 70638)

Hydromedusa tectifera (specimens handled: NMW 1826, NMW 1827, NMW 34629, NBM C 2024, MNHNP-AC-1870-9, MNHN-AC-1874-394, SMF 7992, SMF 7996, SMF 50238, MHNSR H-1614, uncatalogued specimens from MMHNSR; photographs: AMNH 64519, AMNH 133629).

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- Meylan, P.A. 1996. Skeletal morphology and relationships of the Early Cretaceous side necked turtle, *Araripemys barretoii* (Testudines: Pelomedusoides: Araripemydidae), from the Santana Formation of Brazil. *Journal of Vertebrate Paleontology* 16: 20–33.